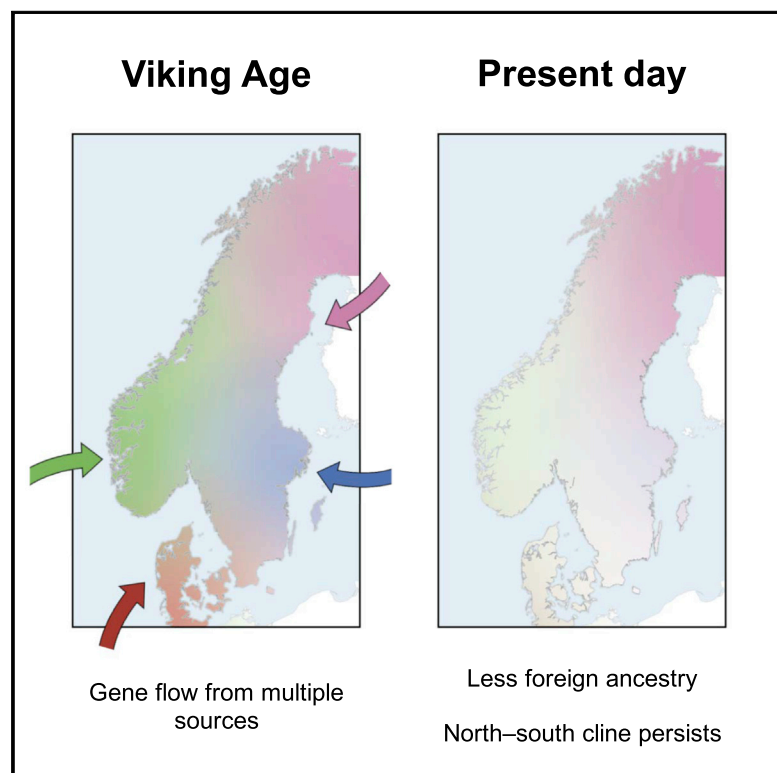# The genetic history of Scandinavia from the Roman Iron Age to the present

Graphical abstract

Authors

Ricardo Rodríguez-Varela,
Kristjan H.S. Moore,
S. Sunna Ebenesersdóttir, ...,
Kári Stefánsson, Agnar Helgason,
Anders Götherström

Correspondence

ricardo.rodriguez.varela@arklab.su.se
(R.R.-V.),
agnar.helgason@decode.is (A.H.),
anders.gotherstrom@arklab.su.se (A.G.)

In brief

The analysis of 297 ancient genomes, spanning the last 2,000 years of Scandinavian history, sampled from historically important archeological sites, resolves the complex relationship between geography, ancestry, and gene flow throughout the study period in Scandinavia, including across the Viking Age.

Highlights

- British-Irish ancestry has an impact on Scandinavia from the Viking period onward

- Eastern Baltic ancestry is more localized to Gotland and central Sweden

- Modern Scandinavians have less non-local ancestry than Viking Age samples

- The north-south genetic cline is mainly due to differential levels of Uralic ancestry

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Article

The genetic history of Scandinavia from the Roman Iron Age to the present

Ricardo Rodríguez-Varela,[1,2,34,*] Kristjan H.S. Moore,[3] S. Sunna Ebenesersdóttir,[3,4] Gulsah Merve Kilinc,[5]
Anna Kjellström,[2] Ludvig Papmehl-Dufay,[6] Clara Alfsdotter,[7] Birgitta Berglund,[8] Loey Alrawi,[2] Natalija Kashuba,[2,9,10]
Verónica Sobrado,[2] Vendela Kempe Lagerholm,[1,2] Edmund Gilbert,[11,12] Gianpiero L. Cavalleri,[11,12] Eivind Hovig,[13,14]
Ingrid Kockum,[15] Tomas Olsson,[15] Lars Alfredsson,[16] Thomas F. Hansen,[17,18] Thomas Werge,[17,19,20] Arielle R. Munters,[10]
Carolina Bernhardsson,[10] Birgitte Skar,[8] Axel Christophersen,[8] Gordon Turner-Walker,[21] Shyam Gopalakrishnan,[22]

(Author list continued on next page)

[1]Centre for Palaeogenetics, 106 91 Stockholm, Sweden
[2]Department of Archaeology and Classical Studies, Stockholm University, 10691 Stockholm, Sweden
[3]deCODE Genetics/AMGEN, Inc., 102 Reykjavik, Iceland
[4]Department of Anthropology, University of Iceland, 102 Reykjavik, Iceland
[5]Department of Bioinformatics, Graduate School of Health Sciences, Hacettepe University, 06100 Ankara, Turkey
[6]Linnaeus University, 351 95 Kalmar, Sweden
[7]Department of Archaeology, Bohusläns Museum, Museigatan 1, 451 19 Udevalla, Sweden
[8]Department of Archaeology and Cultural History, NTNU University Museum, Norwegian University of Science and Technology (NTNU), 7491 Trondheim, Norway
[9]Department of Archaeology and Ancient History, Archaeology, Uppsala University, 752 38 Uppsala, Sweden
[10]Department of Organismal Biology, Human Evolution, and SciLife Lab, Uppsala University, 75236 Uppsala, Sweden
[11]School of Pharmacy and Biomolecular Sciences, RCSI, D02 YN77 Dublin, Ireland
[12]FutureNeuro SFI Research Centre, RCSI, D02 YN77 Dublin, Ireland
[13]Department of Tumor Biology, Institute for Cancer Research, Oslo University Hospital, 0424 Oslo, Norway
[14]Centre for Bioinformatics, Department of Informatics, University of Oslo, 166 0450 Oslo, Norway
[15]Center for Molecular Medicine, Department of Clinical Neuroscience, Neuroimmunology Unit, Karolinska Institutet, 171 76 Stockholm, Sweden
[16]Institute of Environmental Medicine, Karolinska Institutet, 171 77 Stockholm, Sweden
[17]Institute of Biological Psychiatry, Copenhagen Mental Health Services, 4000 Roskilde, Denmark
[18]Danish Headache Center, Department of Neurology, Copenhagen University Hospital, 2600 Glostrup, Denmark
[19]Department of Clinical Medicine, University of Copenhagen, Copenhagen 2200, Denmark
[20]The Lundbeck Foundation Initiative for Integrative Psychiatric Research, iPSYCH, 8210 Aarhus, Denmark
[21]Department of Archaeology and Anthropology National Museum of Natural Science, 404023 Taichung City, Taiwan
[22]Center for Evolutionary Hologenomics, the GLOBE Institute, University of Copenhagen, 1353 Copenhagen, Denmark
[23]isoTROPIC Research Group, Department of Archaeology, Max Planck Institute for Geoanthropology, 07745 Jena, Germany

(Affiliations continued on next page)

SUMMARY

We investigate a 2,000-year genetic transect through Scandinavia spanning the Iron Age to the present, based on 48 new and 249 published ancient genomes and genotypes from 16,638 modern individuals. We find regional variation in the timing and magnitude of gene flow from three sources: the eastern Baltic, the British-Irish Isles, and southern Europe. British-Irish ancestry was widespread in Scandinavia from the Viking period, whereas eastern Baltic ancestry is more localized to Gotland and central Sweden. In some regions, a drop in current levels of external ancestry suggests that ancient immigrants contributed proportionately less to the modern Scandinavian gene pool than indicated by the ancestry of genomes from the Viking and Medieval periods. Finally, we show that a north-south genetic cline that characterizes modern Scandinavians is mainly due to the differential levels of Uralic ancestry and that this cline existed in the Viking Age and possibly earlier.

INTRODUCTION

The ancestry of most modern European populations can primarily be traced, in slightly variable proportions, to the following three ancient genetic sources: European Mesolithic hunter-gatherers, Anatolian Neolithic farmers, and early Bronze Age groups from the Steppe (e.g., Skoglund et al.,[1] Lazaridis et al.,[2] and Haak et al.[3]). The mixing of these sources in Scandinavia is relatively well documented.[1,4–6] However, the extent and impact of migration into Scandinavia after the Bronze Age is less clear.

Eva Daskalaki,[2] Ayça Omrak,[2] Patxi Pérez-Ramallo,[23,24] Pontus Skoglund,[25] Linus Girdland-Flink,[26,27] Fredrik Gunnarsson,[28] Charlotte Hedenstierna-Jonson,[9] M. Thomas P. Gilbert,[22,29] Kerstin Lidén,[2] Mattias Jakobsson,[10] Lars Einarsson,[30] Helena Victor,[28] Maja Krzewińska,[1,2] Torun Zachrisson,[31] Jan Storå,[2] Kári Stefánsson,[3,32] Agnar Helgason,[3,4,33,*] and Anders Götherström[1,2,33,*]

[24]Department of Medical and Surgical Specialities, Faculty of Medicine and Nursing, University of the Basque Country (EHU), Donostia-San Sebastián 20014, Spain
[25]Francis Crick Institute, London NW1 1AT, UK
[26]Department of Archaeology, School of Geosciences, University of Aberdeen, AB24 3FX Aberdeen, UK
[27]School of Biological and Environmental Sciences, Liverpool John Moores University, L3 3AF Liverpool, UK
[28]Department of Museum Archaeology, Kalmar County Museum, Box 104, Kalmar 39121, Sweden
[29]Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology (NTNU), 7491 Trondheim, Norway
[30]Kronan, Marine Archaeological Department, Kalmar County Museum, Box 104, Kalmar S-39121, Sweden
[31]Upplandsmuseet/County Museum of Uppland, Uppsala 753 10, Sweden
[32]Faculty of Medicine, University of Iceland, Reykjavik 101, Iceland
[33]These authors contributed equally
[34]Lead contact
*Correspondence: ricardo.rodriguez.varela@arklab.su.se (R.R.-V.), agnar.helgason@decode.is (A.H.), anders.gotherstrom@arklab.su.se (A.G.)
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Two studies based on ancient DNA (aDNA) indicate gene flow into Scandinavia during the Viking Age (750–1050 CE).[7,8] Other studies of modern Scandinavians have described a marked northward increase in Uralic ancestry,[9–11] which is likely linked to gene flow of Uralic ancestry to the eastern Baltic region toward the end of the Bronze Age.[12]

At the end of the Roman Iron Age (1–400 CE) and the beginning of the migration period (400–550 CE), Scandinavia saw the emergence of new hierarchies, with religious, social, and economic power concentrated among ruling elites, profiting from social networks reaching far into the Roman Empire.[13] Long-distance trading and mercenary activities provided means to acquire and accumulate wealth and status in a hierarchical and unstable political power structure.[13–17] However, the impact of migration during these periods on the Scandinavian gene pool is not well known.

The Viking Age is associated with a marked increase in the flow of goods, customs, technology, and people to and from Scandinavia relative to preceding periods.[18] One indication of migration during this period is the observation of gene flow into Scandinavia from the south, west, and east.[7,8]

Here, we make use of an extensive set of 297 ancient Scandinavian genomes spanning a 2,000-year transect from the beginning of the Roman Iron Age (1st century) to the 19th century, and genotypes from 16,638 modern individuals from Denmark and each county of Norway and Sweden to assess the impact of migration on the Scandinavian gene pool (Figure 1). We combine new whole genome sequence (WGS) data from 48 ancient individuals (Table S1A) with previously published WGS data from 249 ancient individuals[7,8,19,20] (Table S1B), including additional sequence depth for 13 previously published Viking Age individuals from the Swedish town Sigtuna.[7] The new sites include boat burials, chamber burials, and archeological sites like the migration period Sandby borg ringfort and 12 individuals from the Swedish warship Kronan that sank in 1676 CE near the island Öland off the southeast coast of Sweden. The individuals were classified into five periods: Pre-Viking (1–749 CE), Viking (750–949 CE), Late Viking (950–1099 CE), Medieval (1100–1349 CE), and Post-Medieval period (1350–1850 CE) (Figure 1). The former

periods are used here as a chronological shorthand label that is not intended to imply that all individuals from the Viking or Late Viking periods were actually "Vikings," just individuals living during these periods. By partitioning the gene pool of Scandinavia geographically and chronologically, it is possible to make inferences about the nature and magnitude of the events that shaped it from the end of the Roman Iron Age to the present. In particular, we have two main aims. First, to document the timing and geographical extent of gene flow into Scandinavia during this period. Second, to investigate when and how the currently observed north-south genetic cline was formed in Norway and Sweden and to what extent shifts in genetic ancestry played a role in this process.

RESULTS

New genomic data from 77 ancient Scandinavians

We generated WGS data from 64 new and 13 previously published individuals.[7] All the individuals exhibit typical features of aDNA,[21] including short-read length and cytosine deamination concentrated at the end of reads (Table S1). DNA contamination was estimated for both X chromosome and mitochondrial DNA (mtDNA), as described in Ebenesersdóttir et al.[22] (Table S1). We considered samples with two X chromosomes to be contaminated if they showed contamination (> 10%) for the mtDNA and samples with one X chromosome to be contaminated if they showed contamination (> 10%) for both X chromosome and mtDNA. From the new generated WGS data, we removed individuals with autosomal coverage < 0.1× (n = 10) (Table S1A) and the individual with lower coverage from each pair of genetically related individuals with a k0 value < 0.8 and pi_HAT > 0.06 (third-degree kinship) (n = 6) (Table S2; STAR Methods). The remaining 48 new individuals had an autosomal coverage ranging from 0.11 to 64.84× (median = 1.33) (Table S1A). In total, 48 new and 249 published ancient genomes were used in subsequent analyses.

The origin and fate of gene flow into Scandinavia

To explore the nature and extent of genetic differences between ancient individuals from the five different periods, we first
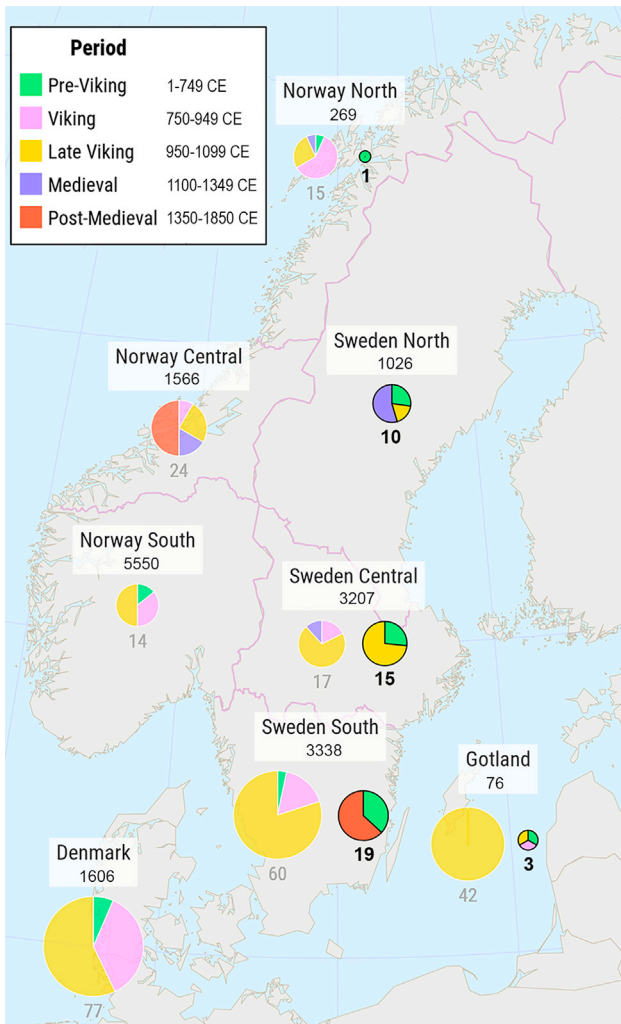
Figure 1. Map summarizing sample locations of ancient Scandinavian genomes analyzed in this study
Faded pie charts represent previously published samples, and pie charts with dark outlines represent newly presented samples. The numbers in brackets represent the number of modern Scandinavians sampled in each region. See also Table S1.

projected them onto a principal component analysis (PCA) based on microarray genotypes for 168,599 SNPs from 9,052 modern individuals from 67 west Eurasian populations (Figure 2; see Table S3 and STAR Methods). The first principal component (PC1) separates modern individuals according to a north-south geographical axis, whereas the second principal component (PC2) separates them according to an east-west axis. Modern Scandinavians, placed in the top-right of the PCA plot, are well differentiated from most western European and Baltic populations (Wilcoxon test p value < 2.2e−16, see Table S4).

Interestingly, the mean projected PC1 and PC2 coordinates of ancient Scandinavians change over time (Figures 2A and S1A–S1P). First, the Pre-Viking individuals are significantly different from modern Scandinavians for both PC1 and PC2 (Wilcoxon test p values 1.107e−11 and 0.0057, respectively; Figure 2A;

Table S4). They are consistently shifted toward the positive values for PC1 in the direction of Neolithic and Mesolithic Scandinavian hunter-gatherers, with some individuals falling outside the range of all modern Europeans (Figure S1Q). The Viking and Late Viking groups are also significantly different from modern Scandinavians on PC1, but in the opposite (negative) direction (Wilcoxon test p values are 0.0199 and 0.0084, respectively). In contrast, the more recent Medieval and Post-Medieval Scandinavians are not significantly differentiated from their modern counterparts on PC1 (Wilcoxon test p values are 0.1299 and 0.2509, respectively). However, for PC2, Post-Medieval Scandinavians are significantly different from their modern counterparts (Wilcoxon test p value 1.142e−6) (Table S4).

Our results indicate a surge of gene flow from the British-Irish Isles into Scandinavia during the Viking period, with additional gene flow from the east in the Late Viking period, consistent with results reported in a previous study.[8] We formally tested for the impact of gene flow into Scandinavia from different sources across time using f_4-statistics of the form f_4(Mbuti, ancient group; Danish, modern population). Here, the Mbuti represents an outgroup, the modern population is a proxy for a potential ancient non-Scandinavian source population and individuals from Denmark represent the southernmost Scandinavian population. To detect gene flow from the west, south, and east of Europe into the different temporal groups of Scandinavia, we selected three modern populations as proxies for different European regions: Irish for west (British-Irish), Sardinian for south (south Europe), and Lithuanian for east (Baltic). To better understand the timing and geographical extent of gene flow from east, west, and south Europe into Scandinavia, we split the ancient individuals from Norway and Sweden by sub-regions: north, central, and south, with the Swedish island of Gotland as a separate region (Figure 1).

We find that affinity to the three non-Scandinavian source populations is low in the Pre-Viking period but higher in nearly all other subsequent periods of ancient Scandinavians, consistent with gene flow from these regions into Scandinavia during the Viking period (Figures 3A–3C).

Figure 3A indicates a marked gene flow of eastern Baltic ancestry into Gotland during the Viking and Late Viking periods, a natural entry point to Sweden from the East, followed by a more gradual increase in central and south Sweden until the Post-Medieval period. Interestingly, present-day individuals from the south and central regions of Sweden are characterized by relatively low levels of eastern Baltic ancestry—similar to those from the Pre-Viking period. Figure 3A shows a lesser degree of eastern Baltic ancestry in northern Sweden and the regional groups of Norway across the different periods, consistent with their greater geographical distance from eastern Baltic source populations.

Figure 3B reveals a slightly different pattern of gene flow of British-Irish ancestry into Scandinavia, with uniformly low levels in Pre-Viking groups but with marked early increases during the Viking period in south Sweden and Denmark. In south Sweden, British-Irish ancestry then decreases to its modern level over time but remained significantly greater than in the Pre-Viking period. In all seven Scandinavian regions with Pre-Viking period individuals, we see a consistently higher level of British-Irish
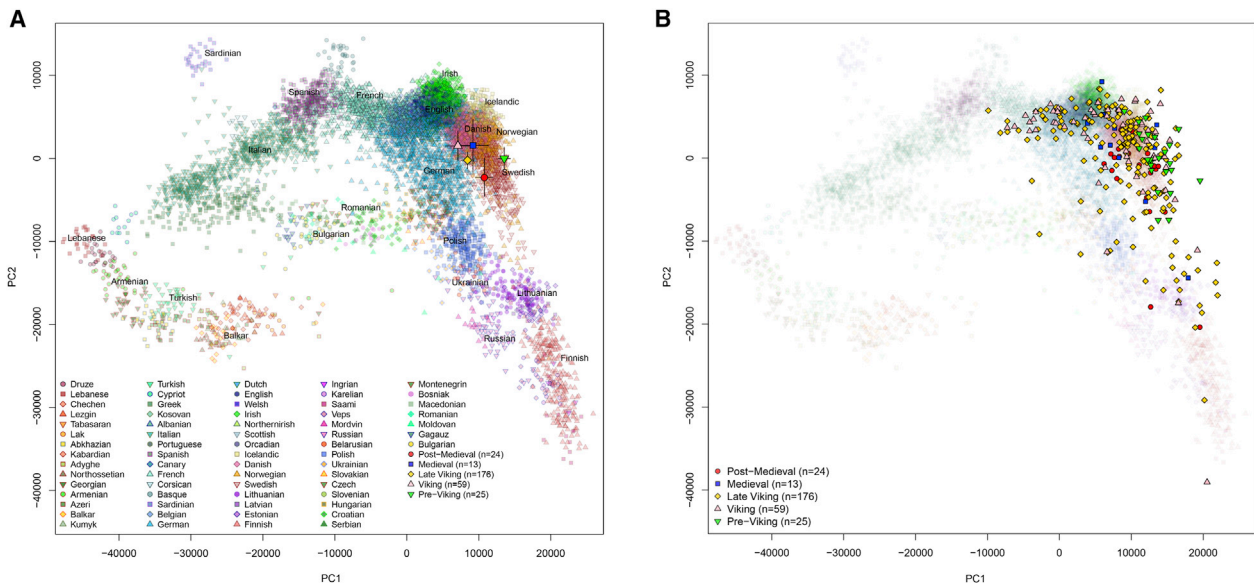
Figure 2. Genotypes from ancient Scandinavians projected onto the first two principal components of modern West Eurasians
(A) The mean and 95% confidence interval for each ancient group for PC1 and PC2.
(B) All ancient individuals from the five different periods.
See also Figure S1 and Table S3.

ancestry in modern populations than in Pre-Vikings. This points to a lasting and widespread gene flow from the British-Irish Isles into Scandinavia, most likely due to migration during the Viking period. Nonetheless, the overall magnitude of British-Irish gene flow into Scandinavia appears to have been small, as witnessed by the relatively clear distinction between modern populations from Scandinavia and the British-Irish Isles.[22]

Overall, the ancient Scandinavian groups have a greater affinity to modern Irish individuals than to modern Sardinians (Figures 3B and 3C). Nonetheless, the patterns of affinity across regions and periods are broadly similar, indicating that these two test populations partly capture the same signal of gene flow. Indeed, when the two f_4 models are calculated per ancient individual, we observe a correlation coefficient of 0.735 (p < 2.2e−16). However, both the PCA in Figure 2B and a direct comparison of the f_4 results for British-Irish and Sardinian ancestry (Figures S2A and S2B) indicate that these ancestries can be distinguished and that both individuals with British-Irish ancestry and south European ancestry were present in Scandinavia during the Viking period, as previously shown by Margaryan et al.[8] These conclusions are further supported by results based on the qpAdm method (Figures 4 and S3A for extended version).

A definitive example of British-Irish gene flow is the Late Viking period female (sal002) found in central Sweden, who appears fully British-Irish in ancestry (Figures S2A and S3B; Tables S5 and S6). Although our results indicate minimal gene flow into Scandinavia from the British-Irish Isles before the Viking period, we find one interesting exception in individual VK213, a young female excavated in Gerdrup, Denmark, and dated to the 5th century (391–527 CE).[8,23] She has the third-highest f_4 value for British-Irish ancestry among the 297 ancient individuals found

in Scandinavia, with PCA projections and qpAdm results indicating that this female is likely to have traced most of her ancestry to the British-Irish Isles (Figures S2A and S3B; Tables S5 and S6). This finding raises the possibility that VK213 ended up in Denmark as an indirect consequence of the Anglo-Saxon migration to the British Isles.

To investigate possible sex bias in the gene flow into Scandinavia, we compared previously described f_4-statistic analyses of the form f_4(Mbuti, PopX; Danish, PopC) based on autosomal loci with equivalent analyses based only on X chromosome loci. Although we note that the X chromosomal f_4-statistics have wide standard errors due to the smaller number of loci used, the results shown in Figure 5 provide at least tentative evidence that gene flow into Scandinavia of eastern Baltic ancestry and, to a lesser extent, also British-Irish ancestry was female biased. We also observe direct evidence for gene flow from the British-Irish Isles through males, in the form of two Late Vikings (VK31 and VK405) and one Medieval (wes008) individual carrying the British-Irish-characteristic[24] Y-haplogroup R1b1a1b1a1a2c (Table S1).

The north-south genetic cline in Scandinavia
Previous studies have reported a marked north-south cline of genetic variation in present-day Scandinavia.[9–11] The differentiation of northern Scandinavians has been attributed to a combination of genetic drift due to small population size and gene flow from Uralic-speaking groups.[9] To explore the geographical pattern of Uralic-associated ancestry in modern Scandinavians, we first calculated an f_4-statistic of the form f_4(Mbuti, X; Danish, Finnish) for the complete set of 16,638 modern Scandinavians, where the Danes and Finns represent the southern and northern ends of the cline, respectively, and X represents each of the 19
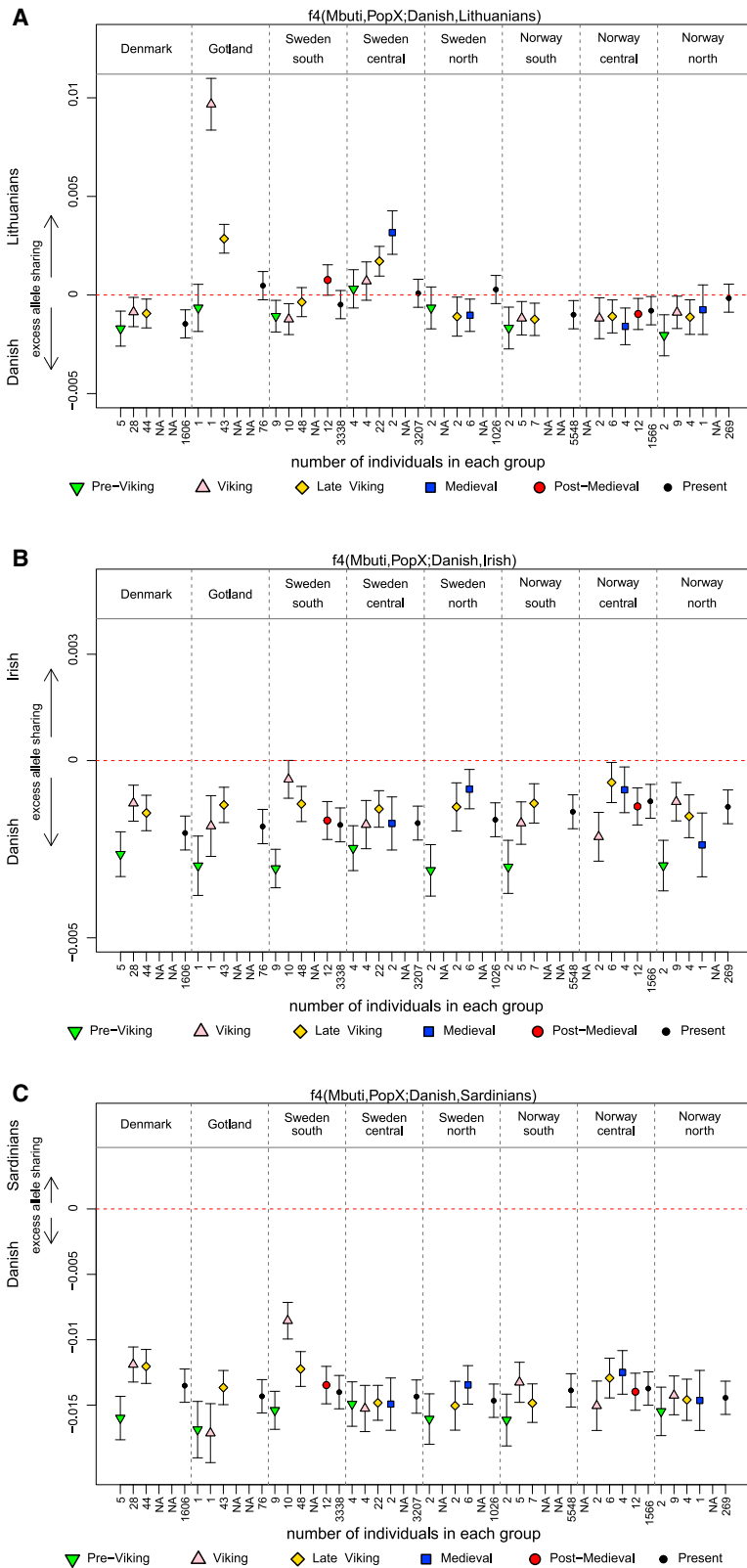
Figure 3. f_4-statistics plots

The f_4-statistics are based on the test f_4(Mbuti, PopX; Danish, modern test population), showing the contrasting allele sharing of the ancient and modern Scandinavian groups divided in period and regions between a modern test population and modern Danish populations. The sample size of each Scandinavian group is represented on the x axis. PopX represents the populations in the legend, and the bars show a 95% confidence interval.

(A) Lithuanians as the test population.

(B) Irish as the test population.

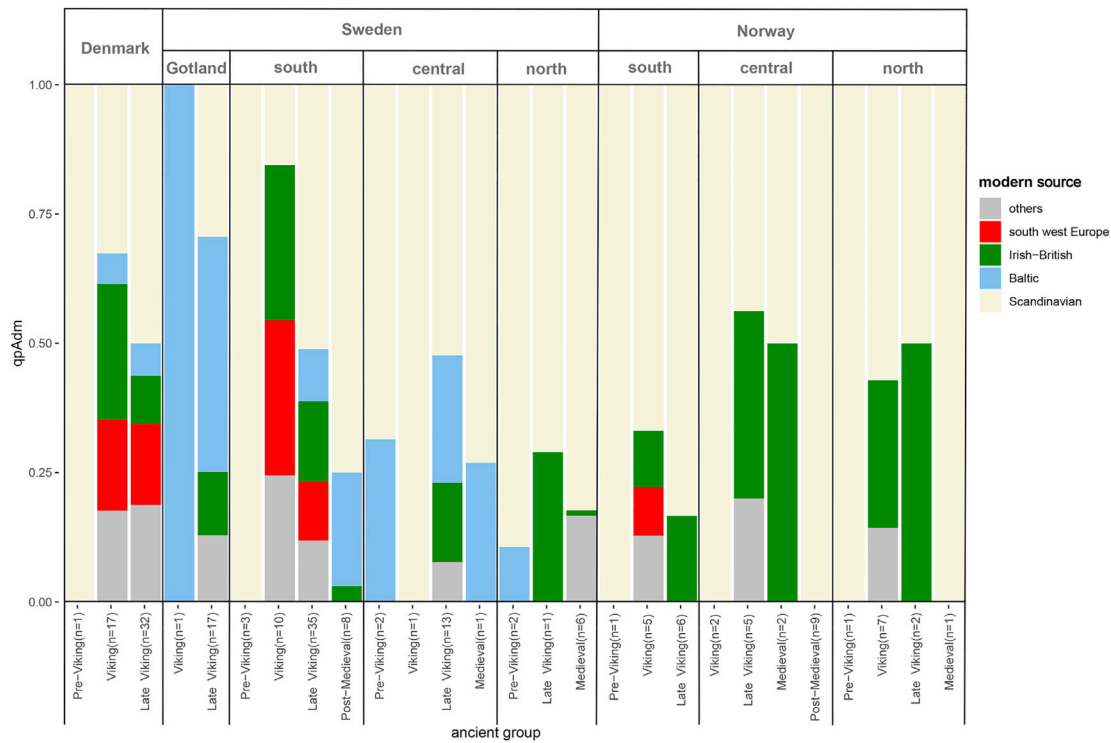(C) Sardinians as the test population.

Figure 4. Simplified qpAdm plot using modern populations as sources
Only samples with p > 0.01 and coverage >0.5× are shown.
See also Figure S3A and Table S6.

Norwegian or 21 Swedish counties. Finns represent a Uralic source population on the grounds that they are a neighboring population with relatively high levels of Uralic ancestry[25] and speak a language that belongs to the Uralic family. Figure 6A shows a clear clinal pattern of southward declining Uralic ancestry in both countries, which is more marked and linear in Sweden than in Norway. An almost identical pattern is seen for East Asian and Native American ancestry, used here as proxies of Siberian-Uralic ancestry (Figure 6B). These were estimated with a supervised run of ADMIXTURE using five training populations from the 1000 genomes dataset (Utah residents with Northern and Western European ancestry [CEU], Indian Telugu in the UK [ITU], Han Chinese in Beijing, China [CHB], Peruvian in Lima Peru [PEL], and Yoruba in Ibadan, Nigeria [YRI]) (Figure S4). To further explore the north-south differences, we used the first 10 PCs in a PCA based on the 16,638 modern Scandinavians (Figure S3C) to calculate the average Euclidean PC distance between the 1,606 modern Danes and each of the 7,385 modern Norwegian and 7,647 modern Swedish individuals. Summarizing these distances by counties in Norway and Sweden, we yet again observe a clinal pattern, with the greatest PC distances in the north (Figures 6C and 6D). We note that these PC distances do not specifically target Uralic ancestry but rather reflect any differences picked up by the PCs. Thus, the observation that f_4(Mbuti, X; Danish, Finnish), East Asian (CHB) ancestry, and Native American (PEL) ancestry account for 80% of the variation in PC distance to modern Danes in linear regression (Table S7), indicates that the clinal pattern of genetic variation between

northern and southern Scandinavia is primarily due to differential levels of Uralic ancestry.

We calculated the same statistics for the 297 ancient individuals from different regions of Scandinavia in an attempt to shed light on when and how the north-south cline appeared. Figure 7 shows one scatterplot for each period, comparing ancient individuals and modern regional groups using two of these statistics: f_4(Mbuti, X; Danish, Finnish) and the PCA distance from Danish. These results show that some version of the north-south cline existed from at least the Viking period onward. In particular, the two Viking Age samples from northern Norway with extreme values for both statistics (VK519 and VK518, the latter carrying the Saami-characteristic mitochondrial haplogroup U5b1b1a[26]) show that individuals with Uralic ancestry had settled in northern Scandinavia at that time and that ADMIXTURE was taking place with groups characterized by south Scandinavian ancestry. However, more data from ancient individuals from the central and northern regions of Scandinavia are required to determine the extent to which the latitudinal shape of the cline developed from the Viking period to the present.

In modern Scandinavians, we also see the cline reflected in the geographical distribution of the Uralic-associated[27] Y-haplogroup N1a1 (Figures S5A and S6A) and its association with the autosomal ancestry cline (p < 1.6e−14 for logit regression of N1a1 presence on CHB+PEL ancestry, f_4(Mbuti, X; Danish, Finnish) or PC1 coordinate on Figures S3C and S6B). Thus, it may be that N1a1 entered Scandinavian populations via the same Uralic gene flow that generated the north-south
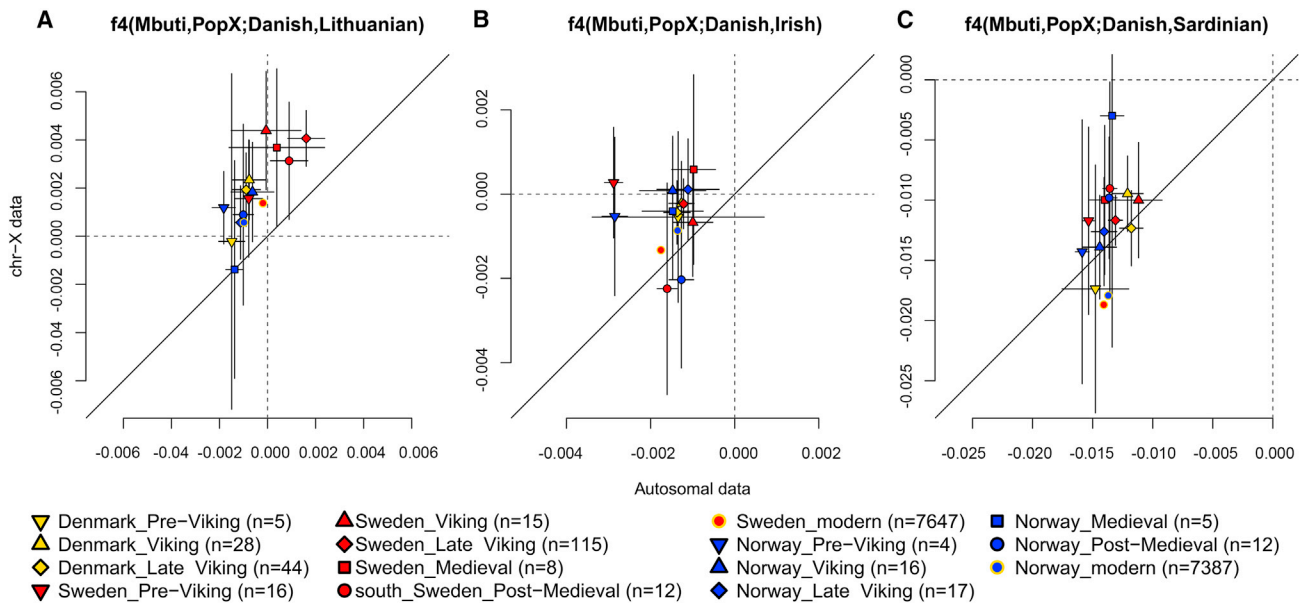
A f4(Mbuti,PopX;Danish,Lithuanian)   **B** f4(Mbuti,PopX;Danish,Irish)   **C** f4(Mbuti,PopX;Danish,Sardinian)

Figure 5. Sex bias f_4-statistic
Scatter plot of the form f_4(Mbuti, PopX; Danish, PopC) where PopX represents the ancient individuals grouped by period and country and the modern populations from Sweden and Denmark whereas PopC represents modern Lithuanians, Irish, and Sardinians. In the x axis are the results using autosomal SNPs, and in the y axis are the results of the X chromosome SNPs. Bars represent 95% confidence intervals.
(A) Lithuanian as PopC.
(B) Irish as PopC.
(C) Sardinians as PopC.

cline. Interestingly, however, the earliest Scandinavian N1a1 carriers we observe that six Pre-Vikings (200–520 CE) from four sites in eastern Sweden show less northern affinity than modern Norwegian and Swedish N1a1 carriers (t tests for CHB+PEL ancestry p = 0.040, f_4[Mbuti, X; Danish, Finnish] p = 0.087, PC1 coordinate on Figure S3C p = 0.0009; Figure S6B). Conversely, the 13 Viking to Post-Medieval N1a1 carriers are not significantly different to modern carriers (CHB+PEL ancestry p = 0.168, f_4(Mbuti, X; Danish, Finnish) p = 0.365, PC1 coordinate on Figure S3C p = 0.629). This may indicate a more ancient initial introduction of N1a1 into Scandinavia before its later dispersal along the modern cline of north-south ancestry.

It is not possible to tell from our results whether the north-south cline existed in some form before the Viking period, as none of the 25 Pre-Viking period individuals have substantial levels of Uralic ancestry. Figure 7A shows a very subtle upward curve of points that can, at best, be interpreted as suggestive evidence of some Uralic ancestry. At the end of this curve is a female (rtp003) from Rombäck in Västernorrland in northern Sweden dating to 450–500 CE, who has both the highest f_4 value among Pre-Viking period individuals and is also assigned a small proportion (1.4%) of Native American (PEL) ancestry, which may be indicative of Uralic ancestry (Table S8). However, additional individuals from the Pre-Viking period are needed to provide more definitive evidence.

From the Post-Medieval period, the only individuals showing notable levels of Uralic ancestry are four crew members of the warship Kronan (kro006, kro009, kro011, and kro014) (Figure 7E), two of whom carry Y-haplogroup N1a1. Of the 24 individuals

from this period, 12 are from the Kronan shipwreck and 12 are from central Norway. All the Kronan crew members are assigned to south Sweden in this study because that is where the wreck was found, and their remains were recovered. However, historical records indicate that infantry soldiers were recruited from the northern counties of Sweden like Västerbotten, sailors from the southeast coast of Sweden, and some officers from Finland,[28],[29] which fits well with our results (Figures S1R and S2A; Table S5).

DISCUSSION

Our analyses of the impact of gene flow on the different regions of Scandinavia across 2,000 years, from the beginning of the Roman Period to the present, indicate a major increase during the Viking period and a potential bias toward females in the introduction of eastern Baltic and, to a lesser extent, British-Irish ancestries. Gene flow from the British-Irish Isles during this period seems to have had a lasting impact on the gene pool in most parts of Scandinavia. This is perhaps not surprising, given the extent of Norse activities in the British-Irish Isles, starting in the 8th century with recurrent raids and culminating in the 11th century North Sea Empire, the personal union that united the kingdoms of Denmark, Norway, and England.[18] The circumstances and fate of people of British-Irish ancestry who arrived in Scandinavia at this time are likely to have been variable, ranging from the forced migration of slaves to the voluntary immigration of more high-ranking individuals such as Christian missionaries and monks. The female sal002 found in a boat burial in Sala in
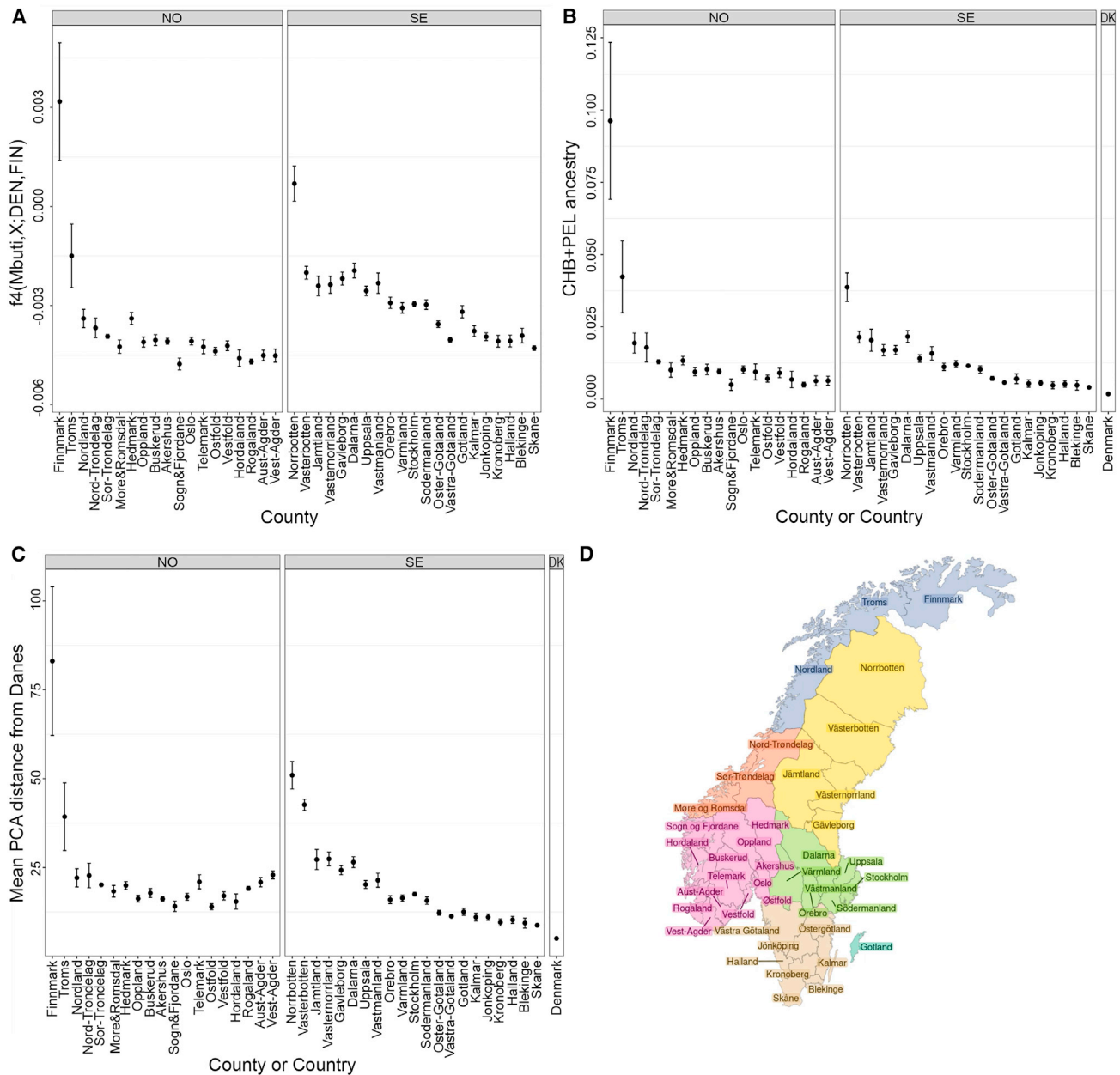
Figure 6. North-south cline of Uralic ancestry across Norwegian and Swedish counties ordered from most northern to southernmost

(A) f_4-statistics based on the test f_4(Mbuti, county; Danish; Finnish) showing the contrasting allele sharing of each modern Swedish and Norwegian county between modern Danes and Finns. Bars represent 95% confidence intervals.

(B) Percentage of CHB and PEL ancestry in the ADMIXTURE analyses (Figure S6). Bars represent 95% confidence intervals.

(C) Average Euclidean PC distance between modern Danes and modern Norwegian and Swedish individuals using the first 10 PCs from a PCA based on the 16,638 modern Scandinavians. Bars represent 95% confidence intervals.

(D) Map of the Norwegian and Swedish counties.

central Sweden from the Late Viking period represents an interesting case.[30] She appears fully British-Irish in ancestry, and the character of her burial indicates that she probably had a high social status in the community that buried her.[31] The situation may have been very different for VK213, a female from Gerdrup, Denmark, dated to the 5th century, who is also British-Irish in

ancestry but appears to have been buried without any grave goods.[23] Although this finding indicates that British-Irish gene flow into Scandinavia began at least as early as the 5th century during the Anglo-Saxon migration to the British Isles, our results suggest that most of it likely occurred during the Viking Age. Although its overall impact on the gene pool was small, we
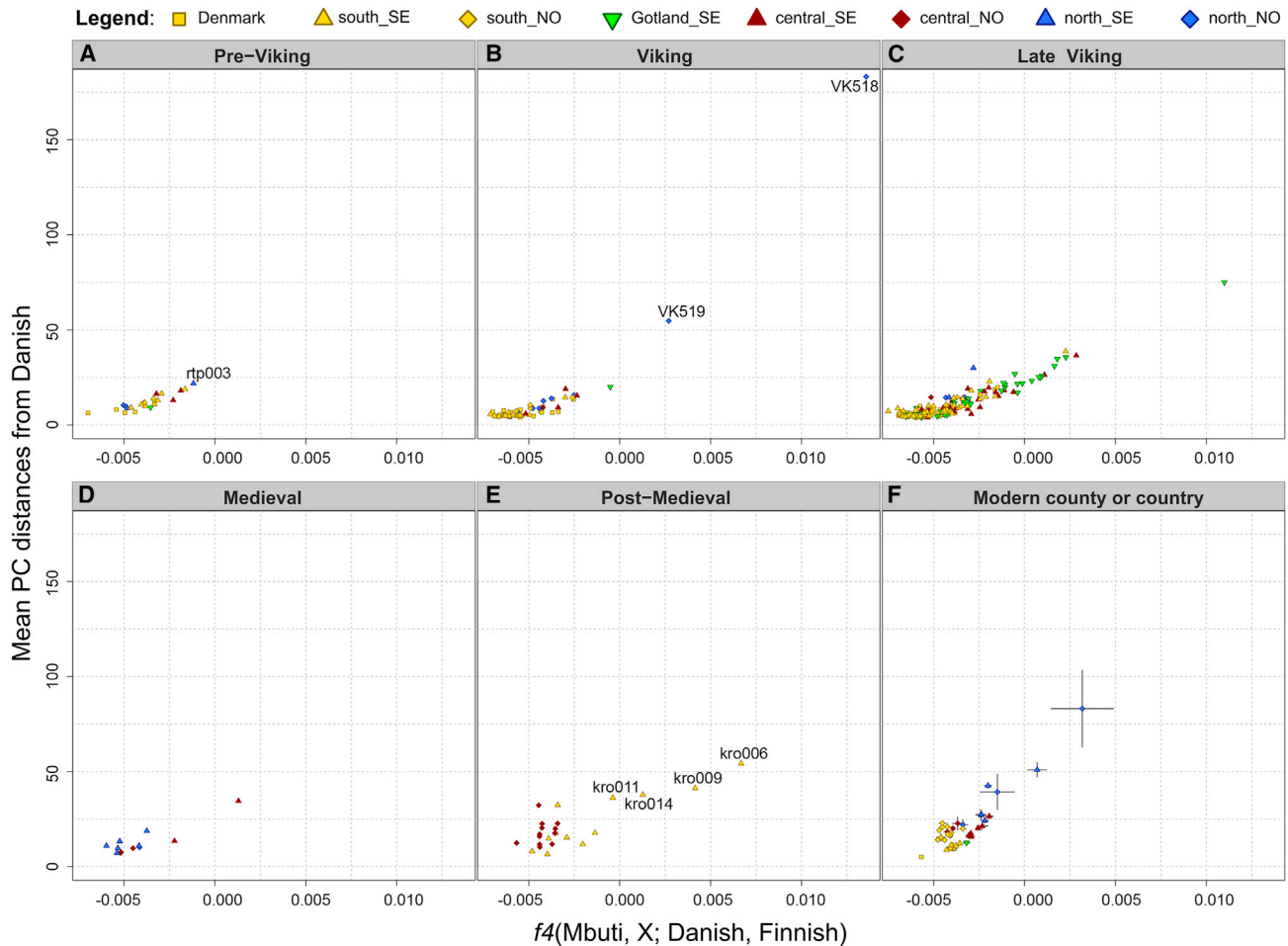
Figure 7. Scatter plots showing Uralic ancestry versus distances to Danish in the ancient individuals and the modern Scandinavian counties/countries

In the x axis, we show the Uralic affinity using f_4-statistics based on the test f_4(Mbuti, X; Danish; Finnish), and in the y axis, the average Euclidean PC distance between each individual/county or country and Danish using the first 10 PCs from a PCA based on the 16,638 modern Scandinavians. (A–E) Display ancient individuals divided into periods, and (F) show populations instead of individuals from Denmark and each county of Sweden and Norway. Bars represent 95% confidence intervals.

See also Table S8.

show that British-Irish gene flow had a lasting impact on all regions of Scandinavia, such that modern Scandinavians have more British-Irish ancestry than Pre-Viking period individuals from the same regions (Figure 3B).

Curiously, we see a tendency for the magnitude of British-Irish ancestry to be greater during the Viking and Late Viking periods than in the present, particularly in south Sweden, where we have relatively large sample sizes for the different periods. This represents a generalization of a trend recently demonstrated on a local scale for Trondheim.[19] A more striking pattern of this kind is seen for eastern Baltic ancestry in Gotland and central Sweden (Figure 3A). The increase of eastern Baltic ancestry in these regions during the Viking Age is consistent with historical sources attesting to contacts such as tributary relations, trade, conflicts, and treaties (e.g., Blomkvist[32,33] and Zachrisson[34]). However, the notable drop in eastern Baltic ancestry in modern individuals

from these regions relative to their predecessors requires further attention. There are three conceivable explanations for such a large changeover in a relatively short period of time. First, intervening gene flow from other regions with less such ancestry. Second, past restrictions on reproduction due to a social hierarchy that was stratified in some way by ancestry (similar to that postulated by Ebenesersdóttir et al.[22] in relation to Norse and Gaelic ancestry during the first generations of settlement in Iceland). Third, an overrepresentation in the archeological record of individuals with a particular ancestry relative to those alive at that time and in that place, for example, due to ancestry-related differences in funerary traditions. It is thought that cremation was the dominant funerary tradition in Scandinavia during the Iron Age until the Early Viking Age; hence, any remains from this period that yield DNA are, in an important sense, exceptional. Also, several Viking and Late Viking period samples derive

from urban environments with extensive trade networks rather than rural communities.[7,8] Thus, it is possible that the available ancient genomes from the Viking and Late Viking periods are not a random sample from all ancestors of modern Scandinavians that lived during those periods. Based on current evidence, it is hard to determine which of the three explanations listed above might account for the apparent regionally specific decline in eastern Baltic and British-Irish ancestry or whether more than one may have had an impact. Although our study is based on a relatively large number of ancient genomes, even more will be needed to answer such fine-scale questions about the evolution of gene pools in time and space.

We also shed light on the nature and origin of the currently observed north-south clinal pattern of genetic variation in Scandinavia, showing that it is mainly due to northwardly increasing Uralic ancestry that was present during the Viking period and perhaps earlier. The subset of crew members from the Kronan warship who cluster with present-day Finnish (Figures S1R and S2A; Table S5) provides a relatively late example of the kinds of migratory forces that continued the spread of Uralic ancestry within Scandinavia. With more ancient genomes from northern Scandinavia, it may be possible to both determine when groups with Uralic ancestry first entered the region and to more fully document how the distinctive modern cline emerged from subsequent bidirectional gene flow between north and south. Overall, however, our study demonstrates that like in the case of so many other human groups,[22,35–37] the long-term demographic history of Scandinavians has been characterized by gene flow from several different source populations, with an extensive impact in the case of the north-south cline of Uralic ancestry.

Limitations of the study

The lack of samples from the period 500 BCE to 1 CE, partly because cremation was the main funerary tradition during this period, resulted in this study being restricted to the last 2,000 years of Scandinavian genetic history.

STAR★METHODS

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

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AUTHOR CONTRIBUTIONS

Conceived and designed the study, A.G., A.H., R.R.-V., K.H.S.M., J.S., T.Z., M.K., S.S.E., and G.M.K.; laboratory work, R.R.-V., M.K., N.K., V.K.L., V.S., L.G.-F., and L. Alrawi; bioinformatic analysis, A.H., R.R.-V., K.H.S.M., S.S.E., and G.M.K.; modern and ancient reference datasets preparation, K.H.S.M., S.S.E., M.K., E.G., G.L.C., E.H., I.K., T.O., L. Alfredsson, T.F.H., T.W., C.B., A.R.M., K.S., M.J., P.S., P.P.-R., A.O., E.D., L. Alrawi, M.J., M.T.P.G., and S.G.; archeological support, T.Z., J.S., A.K., L.P.-D., C.A., B.B., B.S., P.P.-R., A.C., G.T.-W., F.G., C.H.-J., K.L., L.E., H.V., A.G., M.K., and R.R.-V.; writing – review & editing, A.H., A.G., R.R.-V., K.H.S.M., and S.S.E. with input from all co-authors; funding acquisition, A.G.; supervision, A.H. and A.G.

SUPPORTING CITATIONS

The following references appear in the Supplemental information: 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Ancient Human skeletal element	This study	als001, Swedish History Museum, Inventory number SHM 10035, 10289, 20061
Ancient Human skeletal element	This study	als007, Swedish History Museum, Inventory number SHM 10035, 10289, 20061
Ancient Human skeletal element	This study	als010, Swedish History Museum, Inventory number SHM 10035, 10289, 20061
Ancient Human skeletal element	This study	als015, Swedish History Museum, Inventory number SHM 10035, 10289, 20061
Ancient Human skeletal element	This study	bro100, Swedish History Museum, Inventory number SHM33379
Ancient Human skeletal element	This study	enb508, Swedish History Museum, Inventory number SHM15268
Ancient Human skeletal element	This study	frc007, Jamtli
Ancient Human skeletal element	This study	ful001, Swedish History Museum Inventory number 20724
Ancient Human skeletal element	This study	gam872, Swedish History Museum, Inventory number SHM34835
Ancient Human skeletal element	This study	gor164, Swedish History Museum, Inventory number SHM34347
Ancient Human skeletal element	This study	gor358, Swedish History Museum, Inventory number SHM34347
Ancient Human skeletal element	This study	hav001, Swedish History Museum, Inventory number SHM8064
Ancient Human skeletal element	This study	hvr009, The Directorate for Cultural Heritage: Askeladden ID 114142-1.
Ancient Human skeletal element	This study	kro001, Kalmar County Museum, Kronan 38C K16
Ancient Human skeletal element	This study	kro002, Kalmar County Museum, Kronan 25C K14
Ancient Human skeletal element	This study	kro004, Kalmar County Museum, Kronan 5C K2
Ancient Human skeletal element	This study	kro006, Kalmar County Museum, Kronan 26C K18
Ancient Human skeletal element	This study	kro008, Kalmar County Museum, Kronan 6C K9
Ancient Human skeletal element	This study	kro009, Kalmar County Museum, Kronan 31C K1
Ancient Human skeletal element	This study	kro010, Kalmar County Museum, Kronan 42C K17
Ancient Human skeletal element	This study	kro011, Kalmar County Museum, Kronan 50C K13
Ancient Human skeletal element	This study	kro012, Kalmar County Museum, Kronan 8C K8
Ancient Human skeletal element	This study	kro013, Kalmar County Museum, Kronan 3C K11
Ancient Human skeletal element	This study	kro014, Kalmar County Museum, Kronan 27C K6
Ancient Human skeletal element	This study	kro015, Kalmar County Museum, Kronan 43C K4
Ancient Human skeletal element	This study	kvi001, Swedish History Museum, Inventory number SHM19888
Ancient Human skeletal element	This study	lau001, Gotland's museum
Ancient Human skeletal element	This study	lov001, Swedish History Museum, Inventory number SHM29401
Ancient Human skeletal element	This study	rtp001, Swedish History Museum, Inventory number SHM20438
Ancient Human skeletal element	This study	rtp003, Swedish History Museum, Inventory number SHM20438

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Ancient Human skeletal element	This study	sal002, Swedish History Museum, Inventory number SHM11357
Ancient Human skeletal element	This study	snb010, Kalmar County Museum
Ancient Human skeletal element	This study	snb012, Kalmar County Museum
Ancient Human skeletal element	This study	snb013, Kalmar County Museum
Ancient Human skeletal element	This study	snb014, Kalmar County Museum
Ancient Human skeletal element	This study	snb017, Kalmar County Museum
Ancient Human skeletal element	This study	snb018, Kalmar County Museum
Ancient Human skeletal element	This study	snb019, Kalmar County Museum
Ancient Human skeletal element	This study	stg018, Sigtuna Museum
Ancient Human skeletal element	This study	ven001, Swedish History Museum, Inventory number SHM9785
Ancient Human skeletal element	This study	vls696, Swedish History Museum, Inventory number SHM34069
Ancient Human skeletal element	This study	wes001, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes003, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes004, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes005, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes007, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes008, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes056, Swedish History Museum, Inventory number SHM32079
Chemicals, peptides, and recombinant proteins		
Proteinase K	VWR Sweden	Cat#1.24568.0100
EDTA buffer solution pH 8.0 (0.5 mol/l) for biotechnology, sterile	VWR Sweden	Car#E522-100ML
Sodium acetate	Sigma Aldrich Sweden	Cat#S2889
Guanidine hydrochloride	Sigma Aldrich Sweden	Cat#50933
Isopropanol	Sigma-Aldrich Sweden	Cat#67-63-0
Tween-20	Sigma-Aldrich Sweden	Cat#9005-64-5
Sodium phosphate PH 6.0	VWR Sweden	Cat#101447-426
ATP	Fermentas/Thermo Scientific	Cat#R0441
T4 Polynucleotide Kinase	Thermo Scientific	Cat#EK0032
T4 DNA Polymerase	Fermentas/Thermo Scientific	Cat#EP0062
Bst polymerase (supplied with 10X ThermoPol reaction buffer)	NEB/BioNordika	Cat#M0275S
AmplitTaq Gold	Invitrogen/life technologies	Cat#4311816
ATP	Fermentas/Thermo Scientific	Cat#R0441
10X Tango Buffer	Fermentas/Thermo Scientific	Cat#BY5
High Pure Viral Nucleic Acid Large Volume Kit	Roche	Cat#5114403001
T4 DNA Ligase	Fermentas/Thermo Scientific	Cat#EL0011
Min Elute PCR Purification Kit	QIAGEN	Cat#28006
PEG-4000	Sigma	Cat#1546569
Agencourt AMPure XP beads (60ml)	Beckman Coulter	Cat#A63881

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Continued		
REAGENT or RESOURCE	SOURCE	IDENTIFIER
Critical commercial assays		
High Sensitivity DNA (chips + reagents) (Bioanalyzer 2100)	Agilent Technologies	Cat#5067-4626
Deposited data		
European Nucleotide Archive	PRJEB57364	(ERS13672864: ERS13672799)
Oligonucleotides		
IS1_adapter.P5:5^0-A*C*A*C*TCTTTCC CTAC ACGACGCTCTTCCG*A*T*C*T-3^0 (* indicates a PTO bond)	Meyer and Kircher[38]	Biomers
IS2_adapter.P7:5^0-G*T*G*A*CTGGAGTT CAG ACGTGTGCTCTTCCG*A*T*C*T-3^0 (* indicates a PTO bond)	Meyer and Kircher[38]	Biomers
IS3_adapter.P5+P7: 50-A*G*A*T*CGGAA*G*A* G*C-30(* indicates a PTO bond)	Meyer and Kircher[38]	Biomers
IS4:(5^0-AATGATACGGCGACCACCGAGATCTA CACTCTTTCCCTACACGACGCTCTT 3^0)	Meyer and Kircher[38]	Biomers
P7 indexing: (5^0-CAAGCAGAAGACGGCATAC GAGATxxxxxxxGTGACTGGAGTT CAGACG TGT 3^0) where x is one of 228 different 7 bp indexes provided in Meyer and Kircher[38]	Meyer and Kircher[38]	Biomers
Software and algorithms		
R	R Core Team[39]	https://www.R-project.org/
AdapterRemoval (v. 2.3.1)	Schubert et al.[40]	https://github.com/MikkelSchubert/adapterremoval
BWA aln/samse (v. 0.7.10)	Li and Durbin[41]	http://bio-bwa.sourceforge.net/
FilterUniqueSAMCons.py	Kircher[42]	https://bioinf.eva.mpg.de/fastqProcessing/
PMDtools (v.v 0.60)	Skoglund et al.[43]	https://github.com/pontussk/PMDtools
samtools (v. 1.9)	Li et al.[44]	https://github.com/samtools/samtools
MapDamage 2.0	Jónsson et al.[45]	https://ginolhac.github.io/mapDamage/
PicardTools v.1.21.3,	N/A	(http://broadinstitute.github.io/picard/)
BEDtools-2.29.2	Quinlan et al.[46]	https://bedtools.readthedocs.io/en/latest/
KING	Manichaikul et al.[47]	https://www.kingrelatedness.com/
ANGSD (v. 0.911)	Korneliussen et al.[48]	http://popgen.dk/angsd/index.php/ANGSD
EIGENSOFT (v. 6.0.1)	Patterson et al.[49]	https://github.com/DReichLab/EIG
AdmixTools (v. 3.0)	Patterson et al.[50]	https://github.com/DReichLab/AdmixTools
ADMIXTURE (v. 1.3.0)	Alexander et al.[51]	https://dalexander.github.io/admixture/download.html
PLINK (v. 1.9)	Chang et al.[52]	(https://www.cog-genomics.org/plink/1.9/)
lcMLkin	Lipatov et al.[53]	https://github.com/COMBINE-lab/maximum-likelihood-relatedness-estimation

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, RRV (ricardo.rodriguez.varela@arklab.su.se).

Materials availability
This study did not generate new unique reagents.

Data and code availability
The new aligned to NCBI build 38 (mapped, filtered and rescaled BAM files) sequence data reported in this paper can be accessed and downloaded from the European Nucleotide Archive (ENA) under the following study accession number: PRJEB57364 (ERS13672864: ERS13672799).

Data are available in the main text or supplementary figures.

Any additional information required to reanalyze the ancient data reported in this study is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Description of archaeological sites and archaeological material

*When listing samples at the end of each section below, we use (XY) for individuals that are genetically males and (XX) to refer to individuals that are genetically females. We used bold letters when genetic sex contradicts the archaeological or osteological sex determination.

Alsike

Tuna in Alsike parish, Uppland (Sweden), situated by the water route leading towards Old Uppsala, is known for its burial ground containing inhumation burials in chambers and boats under flat ground. The site was found by a local farmer in 1893. Excavations were made in 1895 and in 1928, and a full report of all fieldwork was published in 1934.[54] The oldest of the graves is a well-furnished early Vendel period burial (c. 550 CE) in a possible chamber and a child burial from the same period. Stray objects from the Migration period (c. 440–560 CE) could belong to older settlement remains at the site, or rather older burials that were ruined when later burials were constructed. Following the early Vendel period burials, there seems to have been a lacuna of c. 200 years in the excavated graves before the site was used for burials again c. 750, continuing throughout the whole Viking Age (750–1050 CE). Ten Viking Age boat burials for both men and women have been found, as well as four Viking Age burials of uncertain type or in chambers.[54,55] The shallow depressions that are still seen on the site likely represent more burials that were not excavated.

Grave XIV found in the eastern part of the burial ground is a weapon burial with one individual (als001), identified as a male based on archaeological analyses. The burial was furnished with a sword among other things. At the man's waist were sword fittings in silver, including a belt buckle with inlays of garnet cloisonné set in gold, a unique piece for the region where the garnets are from India.[54,56] Stones framed the body, which may have been placed in a wooden coffin in a shroud, features that are linked to changes in burial traditions.[57] Some scholars have suggested that the male had spent some time abroad (e.g., Arrhenius[56]). However, strontium isotopic value from molar teeth suggests that the individual was local to the Mälar region.[58] The burial is typologically dated to the transition between the Migration and Vendel periods c. 540/550–610/620 CE.[57]

Sample als010 comes from a tooth taken from a cranium which in the museum archives has been associated with boat burial XI, featuring a boat of unknown type. However, the cranium does not match the post-cranial remains from the burial, so is likely from another individual. While the skeletal material from the cemetery at Tuna in Alsike is generally very well preserved, there is some uncertainty in the first recovery by the local farmer as well as in subsequent antiquarian handling. Thus, the identification of individuals must be done with caution. Nevertheless, the individuals are as a group connected to the site. Grave XII, situated next to grave XI, was a double burial (one of the interred individuals sampled as als007) with weapons but only a single set of objects, indicating the other individual was buried without grave goods. Two horses, two dogs, a capercaillie and a black grouse were among the grave goods. The grave is typologically dated to c. 950–1000 CE.[54]

In the western part of the burial ground was boat grave III, dated to c. 800–900 CE. The grave goods consisted of mostly female dress accessories as well as some weapons, along with two horses and a dog. The human remains were in a heap, which indicated that the grave had been opened before the excavation.[54] Grave VI is a double keelboat burial for a male and a female, dated to c. 900–950 CE, furnished with weapons and jewellery such as oval brooches and beads.[54] Grave IX, possibly a chamber burial, was dated to c. 900–1050 CE. The grave goods included several animals, but few objects compared to other graves excavated at the site.[54] The remains (als002) in Grave IX were archaeologically identified as female.

Samples: als001 (XY) = grave XIV, als002 (**XY**) = grave IX, als007 (XY) = grave XII, ind. 2, als010 (XX), als014 (XX) = grave VI, als015 (XY) = grave III

Curated at: Swedish History Museum, Inventory number SHM 10035, 10289, 20061

Alstahaug

Horvnes in Alstahaug municipality, Nordland County, Norway (66 N, 12 15′E) is situated just south of the Arctic Circle on the coast of the southern part of Nordland. The site is located on the same isthmus in the mouth of a fjord as the farm Sandnes, which is mentioned as a magnate farm in the 9th century in *Egils Saga Skalla-Grímssonar*.[59] Archaeological excavations have revealed a large dwelling site at Sandnes with activities starting around the beginning of the CE.[60] The Horvnes burial is one of few known in Sandnes where people were buried before Christianization in the 11th century.[61] The grave, a stone cist or small chamber, built of eleven big boulders, situated in a low cairn, 7,5 m in diameter, was excavated in 2008 by NTNU, University Museum in Trondheim. At least six individuals were buried in the Horvnes grave during the Iron Age, spanning a period of at least 1000 years. All the deceased individuals were inhumated, which is consistent with the burial practice at this time in Northern Norway. According to radiocarbon dating, the oldest burial took place around 100 BCE and the youngest one around 900 CE. It seems that it was after the last burial that the cist was covered by the cairn. One of the stones in the cairn had a cross, probably a Christian cross, and may have marked the end of the pagan burials in the cist.[61,62]

According to osteological investigations, the individual (hvr009) died around the age of 30.[63,64] This individual (hvr009) is directly radiocarbon dated to the Roman Iron Age, 60–215 CE 95.4% probability (1888±29BP, Ua-75069) calibrated using OxCal v4.4.4[65] and IntCal 13 atmospheric curve.[66]

Samples: hvr009 (XX) = M500AD Horvnes 2008.

Curated at: Norwegian University of Science and Technology, University Museum: Museum number T24129.

The grave cairn: The Directorate for Cultural Heritage: Askeladden ID 114142-1.

Eksta

The remains of a female skeleton were accidentally found in 1931 in a gravel pit in Kvie (kvi001), five kilometres off the coast in Eksta parish in southwestern Gotland (Sweden). The remains were revealed to be part of an inhumation burial, poorly furnished with only two eyed bone pins, and five beads: two of shell, two natural stones and one amber bead, and a piece of iron thread. Four more graves were later excavated and were typologically dated to the Viking Age (RAÄ Eksta 108:1[67]). Although belonging to the Viking Age, kvi001's inhumation does not resemble a traditionally Gotlandic female burial. This may indicate that the individual could have been of low social standing, possibly a thrall. The cranium of the individual had been artificially deformed, unclear though if caused by head flattening or binding. This is most unusual, but is known in three cases in the skeletal material dated to the Viking Age that has been recovered in present Sweden. Osteologically, the skeletal parts were determined as belonging to a female 55–60 years of age.[68]

Samples: kvi001 (XX) = Swedish History Museum Inventory number SHM 19888:1 or grave 3/1931

Curated at: Swedish History Museum, Inventory number SHM19888

Enbacken

The grave field Enbacken (RAÄ 89) is situated on the grounds of the settlement Årsta is one of five grave fields located in Uppsala parish, Uppland (Sweden). The burial ground, which seems to have been used for a relatively short period, consisted of approximately 35 graves, 23 of which were examined by archaeologists in multiple excavations from the end of the 19th century to 2004.[69,70] The majority of the graves were inhumations, but there were also cremation burials. All but one grave, were dated to the late Viking Age. The graves mainly consisted of stone settings in various forms. Most individuals were buried in a southeast-northwest orientation, in a supine position with or without a coffin. Except for nails from the coffins and some knives, only objects that could be related to the deceased's clothes were documented. The grave constructions, lack of clear grave goods and the finds of knives are interpreted as Christian features.[70] In grave A (SHM15268:2A) (enb200), which consisted of a flat mound with an irregular stone setting, the skeleton of an adult man was found who was dated to 893-1044 CE with 93.6% probability (1040±40 BP, Ua-23887).[69] Some of the graves excavated in 1913 cannot be related to the exact grave description and hence lack a grave number today. The skeleton of "SHM15268: box 5086" (enb508) belongs to this group and was, after the osteological analysis, identified as an adult woman.[69]

Samples: enb200 (XY) = SHM15268:2A, enb508 (XX) = SHM15268: box 508

Curated at: Swedish History Museum, Inventory number SHM15268; and Uppsala museum, Inventory number UM29596

Frösön

The church on Frösön (Sweden) is dated to the period late 12th and early 13th century. In the autumn of 2014, the local museum Jamtli conducted archaeological investigations on the church's northern side, next to the wall surrounding the churchyard. In total, 41 burials in different stages of preservation were recovered. No grave goods were found. A few disarticulated crania were recovered that originated from burials that had been disturbed by later burials.[71] The analysed sample comes from one of these disarticulated crania (frc007) that was recovered in association with burial 8. The cranium probably comes from an older burial that had been disturbed by burial 8. The cranium may be roughly dated to the period 950–1150 CE.

Samples: frc007 (XX)

Curated at: Jamtli (the regional open-air museum of Jämtland and Härjedalen)

Fullerö

Fullerö is situated five km north of old Uppsala (Sweden), directly north of the famous Valsgärde boat burial ground. The burial from Fullerö is a richly furnished inhumation male chamber burial radiocarbon dated to the late Roman Iron Age, 242–385 CE 95.4% probability (1732±29BP, Ua-53935). Although the grave had been opened and robbed, it was still remarkably richly furnished and unique.[57,72] The chamber burial was placed in a mound belonging to the first generation of mounds that started to be erected in the early Roman Iron age in the region north of lake Mälaren.[73] The burial chamber is the largest c. 10 m² (NNE–SSW) of all known in the lake Mälar region and northern Sweden from CE 200–700.[57] The human skeletal parts that remained were a collar and a rib bone with healed trauma belonging to a middle-aged large, muscular male,[74,75] emphasising the impression that the grave was built for a trained male warrior. The gold finger rings, one of them the largest gold finger ring ever found in Sweden, were probably military honours; the chain mail, belt and the boar-like tusks, and canines from pigs, probably for a horse fitting, may indicate that the man had been in Roman service. In the grave was a worn gold coin used as a pendant, struck for the Roman emperor Maximian Hercules 291CE.[76,77] Bones from a dog and a goshawk were found in the chamber, as well as a phalanx from a bear, suggesting that bear skin was placed with the deceased. The goshawk represents the earliest evidence of hunting with birds of prey in the region, a tradition that otherwise belongs to the 6th century.[78,79] The numerous (more than 20) domestic species in the mound filling are interpreted as animals used for the burial feast.[75,78]

Samples: ful001 (XY) = indiv1 Fullerö
Curated at: Swedish History Museum, Inventory number SHM20724

Gammelbyn

At an archaeological survey in 1975, 15 Viking Age to Early Middle Age inhumation graves were excavated. The graves belonged to the grave field Gammelbyn ID (3:1), Börstil parish, in north-eastern Uppland (Sweden).[80] The grave field (RAÄ 135) is located not far from other contemporary cemeteries, settlements and a trading post in a coastal landscape near the Baltic Sea.[81] The grave field consisted of two parts with different elevations in the terrain. In the upper part of the cemetery, there were stone settings where the graves were oriented in a north-south direction. In most cases, the deceased were placed in hollowed-out logs, but there were also wooden coffins made of planks, and one individual had been placed in a crouched position.[80,81] In the lower part of the grave field, which is believed to be somewhat younger, there were additional stone settings but also graves without a visible superstructure. The majority of the graves in this area had an east-west orientation with no artefacts documented in the graves. The coffins were made of planks and had recessed ends. The osteological analysis showed that both adult men and women and children as young as two to three years old had been buried at the grave field (Kjellström, unpublished). In one of the graves from the upper part, there was a coin found (a German-minted *pfenning*) dated to 1030 CE.[81] Other grave goods, including iron knives and nails, were also found (SHM dnr 602-1008-2007 RAÄ dnr 321-4499-2004). The grave with the most well-preserved osseous material was grave 8, which was one of three double graves at the site, where the skeletons of an adult man (gam872 in A8F25) and a woman (A8F26) were discovered.[82] Apart from possible traces of a coffin belonging to the man, there were no grave goods in the grave.

Samples: gam872 (XY)= burial A8F25
Curated at: Swedish History Museum, Inventory number SHM34835

Gannor

Gannor in Lau parish in south-eastern Gotland (Sweden) is situated in the northern part of "Lau backar", a huge burial ground with many destroyed graves, with c. 500 grave monuments still visible. A chamber burial was accidentally found when a large stone was removed by a local farmer.[83] Based on archaeological and osteological evidence, the remains (lau001) found in the burial cist were identified as a female, buried c. 600 CE. She was found in a crouched position with the remains of an infant placed on her left shoulder, her left hand placed at the infant's head and her right hand at the infant's feet. The woman was placed on a bear skin, while the infant was wrapped in a lynx skin. She was furnished with two bronze needles placed by her head, two animal brooches at her shoulders and a unique gilded crab brooch at the neck.[83,84] The well-furnished woman would likely have had a prominent position at the farm. An earlier study has shown that the mitochondrial DNA sequence of the child was incomplete, but shared sufficiently many mutations with the mtDNA of the woman that it is most likely that the two were mother and daughter; nevertheless, they could also represent other types of close maternal relationships (e.g. that of a grandmother and a grandchild[85]).

Close by was a similar grave of another individual, osteologically determined as a probable female and archaeologically gendered as such (lau003). Her burial was not as richly furnished as lau001, and she had only received one animal head brooch and 20 large beads. Like lau001, she was buried in a crouched position c. 600 CE.[83] She was determined to be c. 20 years of age (grave 2[84]).

The richly-furnished woman (lau001) belonged to a mtDNA haplogroup (U5a1b1h) that was different from that of the woman (lau003) in the less well-furnished grave (H2a1). Consequently, they cannot have had the same mother, nor can the older woman be the mother of the younger woman.[85]

Samples: lau001 (XX) = grave A1, lau003 (XX) = grave A2
Curated at: Gotland's museum

Görla

Görla in Frötuna parish, Uppland (Sweden), is situated in what was once the Viking coastline of eastern Sweden. An excavated late Viking Age burial ground (900–1100 CE) at the site yielded inhumations located in mounds and under flat ground and a single cremation burial in a mound. The burial ground was placed directly on top of a Migration period farm site, and one of the Viking burial mounds had re-used the postholes of the former house for the construction of posts for the ditches that surrounded the mound. Based on osteological analyses, the individuals found in the mounds are males. Interestingly, some mounds were constructed before the burials of the bodies took place, which is uncommon.[86,87] This was probably done to underline property rights.[88] The graves of the individuals that were osteologically determined as females or children were placed under flat ground.[86]

The individual in grave 161, osteologically assessed as a female younger than 45 years, was accompanied by grave goods in the form of a belt buckle of iron, an animal-style ornamented strap divider of bronze and a knife dated to the late Viking Age.[86] The grave was placed in the midship of the former house III.[86] In grave 358 was a well-preserved skeleton, osteologically determined as a female of 30-60 years. While grave 16 contained the skeleton of an adult man.[86]

Samples: gor161 (**XY**) = grave 161, gor164 (XY) = grave 16, gor358 (XX) = grave 358
Curated at: Swedish History Museum, Inventory number SHM34347

Havor

The Iron Age burial ground at Havor in Hablingbo on southern Gotland (Sweden) encompasses c. 400 graves covering the period Pre-Roman Iron Age to Viking Age, where 70 are Viking Age burials.[67] The grave field is known for its high quantity of re-used graves.[67] One of the Viking Age inhumation burials was a stone setting c. 5 metres in diameter (grave 192). On the upper level of the grave, a skeleton was found in disorder, placed there 'much later' according to the excavator Gabriel Gustafsson. The primary burial (placed S-N) contained an archaeologically gendered female and was furnished with double sets of animal-head brooches, beads, knives, a

comb, an armring, pendants, needles, a sewing kit and a spindle whorl.[67] The grave is typologically dated to c. 1000–1100 CE.[89] The cranium of the individual had been artificially deformed, unclear though if it was caused by head flattening or binding. Osteologically the individual is determined as a female 55–60 years of age.[68] The artificially deformed head is a most unusual feature. However, it is known in three cases in the skeletal material dated to the Viking Age that has been recovered in present Sweden.

Samples: hav001 (XX) = Swedish History Museum Inventory number 8064:192
Curated at: Swedish History Museum, Inventory number SHM8064

Kronan

The Royal man-of-war "Kronan" was, when built, the biggest, most heavily armed vessel of the Swedish navy and only outsized by two other ships in the world. Well adorned and intended to impress and inspire awe, it was destined to be the Swedish navy's new flagship.[90]

The ship sank in 1676, after only four years of service, off the coast of Öland, near Hulterstad (Sweden), on its way to engage the combined Danish and Dutch navy. Most of the crew drowned, and expensive equipment, such as cannons of varying sizes and weights, and coins, were lost in the shipwreck. The basic crew consisted of 500 seamen and 300 soldiers; on this journey, there were 50 additional infantrymen. According to the historical records, out of a crew of 850 men, only 42 are known to have survived. More than 180 men washed ashore in the days that followed the catastrophe, meaning that approximately 600 men were left in the depth of the sea. The crew of approximately 850 men (sailors and soldiers) was a complete miniature society, almost the size of a medium-sized Swedish town. As a result, the Kronan crew represents a cross-section of the contemporary male population in the country. The age varies from twelve-year-old ship boys to sixty-year-old mates. The social status of the men spanned from the lowest to the highest (i.e. officers often being from the country's nobility).[28,90,91] According to historical record, the soldiers belonged to the infantry regiment of Västerbotten in the north of Sweden, whereas the sailors were recruited from Öland, Åland and Stockholm in eastern Sweden.[28,29] Only 110 casualties are known by name and occupation.[29]

Samples: kro001 (XY) = indiv Kronan 38C K16, kro002 (XY) = indiv Kronan 25C K14, kro004 (XY) = indiv Kronan 5C K2, kro006 (XY) = indiv Kronan 26C K18, kro008 (XY) = indiv Kronan 6C K9, kro009 (XY) = indiv Kronan 31C K1, kro010 (XY) = indiv Kronan 42C K17, kro011 (XY) = indiv Kronan 50C K13, kro012 (XY) = indiv Kronan 8C K8, kro013 (XY) = indiv Kronan 3C K11, kro014 (XY) = indiv Kronan 27C K6, kro015 (XY) = indiv Kronan 43C K4
Curated at: Kalmar county Museum

Rombäck

The burials from Rombäck were located on a sandy ridge a few hundred metres east of Getterån, near the river Ljungan, in Torp parish, Medelpad (Sweden). The inhumation graves were oriented E-W, probably buried under flat ground were accidentally discovered in 1933 by road workers at Knaggsveden, on grounds belonging to the vicarage at Rombäck.[92] Some of the burials had wooden remains after coffins. Two graves were examined by a local person, while the third was examined by a man sent out by the National Board of Antiquities.[93] According to the report, three individuals, or possibly all four of them, were placed face down, i.e. in prone burials, which is unique for the Migration period in Sweden and as far as we know for all of Scandinavia. Both iron and bone material were poorly preserved because of the sandy soils. Furthermore, the bones had been sorted into categories, with long bones, for instance, collected in one parcel. Thus, the individual skeletal remains had been mixed. Grave 3, which was not possible to sex archaeologically, contained an iron ring with remains of bronze and textile, and parts of a wooden object. Graves 2 and 4 were archaeologically determined as male, based on the strike-a-light stones and a weapon. Grave 2 contained a strike-a-light stone and a knife, while grave 4 contained a 50 cm long spearhead that was found by the body, as well as an oval strike-a-light stone, an iron object, and two sets of gilded clasps with remaining textile and fur skin.[94,95]

Samples: rtp001 (XY) = grave 2, rtp003 (XX) = grave 3, rtp004 (XY) = grave 4, rtp005 (XX) = grave 3
Curated at: Swedish History Museum, Inventory number SHM20438

Sala

The Sala boat burial was found by the river Sagån at Sala's old silver ore smelting furnace (Sweden). The burials dated to the Viking Age were originally placed on an island called Brytilsholmen, in the middle of the river.[55,96] The remains of four individuals were accidentally found and partly excavated. Two of them were buried in boats, and two in "chests" or sledges. Two of the individuals were more prominently interred. The archaeologically determined well-furnished female in grave 1 was placed in a logboat with a pair of oval brooches, an equal-armed brooch, four round iron jewellery pendants, a bronze chain, 58 glass beads, a knife, potsherds and a bent iron rod.[96,97] Grave 2 (sal002) also a logboat contained a woman though less well furnished, with two mismatched oval brooches and an equal-armed brooch, and a wooden box. She was buried several generations later, c. 950–1000 CE. Her genetic affinities resemble the modern genetic variation in the British-Irish Isles. The strontium isotope values of her teeth, however, show that she was probably born and raised locally. Her ancestry, together with her isotopic data, allow us to speculate that she could be a second-generation immigrant with parents with a British-Irish Isles genetic origin. The archaeologically determined female in grave 3 (sal003) was furnished with a pair of oval brooches, an equal-armed brooch, two cast pendants of tin and four glass beads. This woman was placed in a wooden chest without a bottom, and its frame was put on top of the head of the woman. Tooth wear indicated that she was middle-aged or older.[96] The brooches are contemporary with those of the woman in the first grave, and thus both were buried c. 800–850 CE.[97] The strontium isotope values of the woman's teeth indicate that she had not grown up in Sala but moved in. Grave 4 was a deviant burial, a male that had been placed prone, with his lower legs lying disorderly in the clay. Possibly the man could have been overturned, together with the stretcher, into the burial pit.[31,75]

Samples: sal002 (XX) = grave 2, sal003 (XX) = grave 3

Curated at: Swedish History Museum, Inventory number SHM11357

Sandby Borg

Sandby borg is a Migration Period (400–550 CE) ringfort on Öland, an island off the southeast coast of Sweden. The archaeological analyses suggest that a large proportion of the site's inhabitants were killed in an organised attack, after which the settlement was immediately and permanently abandoned.[98,99] The killing was dated to the late 5th century according to typological evidence.[100] To date, around ten per cent of the ringfort interior has been excavated, revealing at least thirty distinct individuals. All age groups, from infants to old adults are represented among the human remains. The locations of the bodies and patterns of perimortem trauma are more consistent with a massacre than with a battle.[98,99] The abrupt end of Sandby borg provides a rare opportunity to study human aDNA from the Scandinavian Migration Period, as the bodies were left *in situ* and not subjected to mortuary practices, which in this context typically featured cremation.[101,102]

We sampled a minimum of 15 different individuals from Sandby borg for whole genome sequencing of which nine provided sufficient depth to allow estimates of molecular sex (Table S1). Our results indicate that individual snb018 (a young adult) is so far the only female among the victims of the massacre. For seven of the nine individuals, we recovered genomes with sufficient coverage (1.04–5.42x) to perform population genomic analyses. Of these samples, the morphology shows that snb017 was a child (6–8 years old), snb014 was an elderly male, and the rest were young adults or adolescents.[98] The female individual snb018 was found in the alley next to house 4, individuals snb017, snb019 and snb014 were found together inside house 4,[103] and individuals snb010, snb012 and snb013 were found together inside house 40.[98]

Samples: snb010 (XY) = indiv 7, snb012 (XY) = indiv 6, snb013 (XY) = indiv 2, snb014 (XY) = indiv 15, snb017 (XY) = indiv12, snb018 (XX) = indiv 18, snb019 (XY)= indiv 13.

Curated at: Kalmar County Museum

Såsta, Broby bro

In close proximity to a runestone (U135) and a stone setting in Broby bro, Såsta 3:1, Täby parish, Uppland (Sweden), three previously unknown inhumation burials were found in 1995.[104] The graves were located northeast of a burial ground (RAÄ 36) with mainly cremation graves from the early Iron Age. The runestone, together with two others (U136 and U137), belonged to the Jarlabanke family, and the buried individuals have been interpreted as descendants of the same family.[104] The individuals were buried stretched out on their backs with their arms at their sides, and the graves had an east-west orientation. In grave 1 (bro100) there was a coffin with an elderly man with a piece of textile (most likely silk) that is believed to have belonged to the left sleeve still in place.[105] In grave 3 (bro300), which lacked a visible superstructure, an elderly woman was buried in a coffin made of a hollowed-out log. The woman had been buried together with a knife and a wooden box with a key, containing two silver coins, a silver ring, and three weights of iron or bronze. Based on the *terminus post quem* of the coin, the grave was arranged after 1025 CE.[104] The items in the grave of the woman are believed to reflect her high social status. Later excavations have revealed other graves with a fairly homogeneous character at the site, and all are now considered to belong to the same early Christian grave field (RAÄ 42).[106]

Samples: bro100 (XY) = burial 1, bro300 (XX) = burial 3

Curated at: Swedish History Museum, Inventory number SHM33379

Sigtuna

At the end of the 10th century (c. 970/980 CE), the town Sigtuna was founded on a peninsula in Lake Mälaren (Sweden) connected to the Baltic sea. The town quickly grew to a central hub, a judicial, administrative centre for an increasingly centralised royal power,[107–109] and for the Christian mission from both England and the Hamburg-Bremen archdiocese.[110] This is manifested not least by the fact that Sigtuna's second king, Olof Skötkonung, is depicted on the first coin minted in Sweden. The town was structured so that oblong town yards with several buildings and alleys, were organised at right angles to a wood-paved main street parallel to the shoreline.[111] The rich amount of finds and the non-local character of the artefacts indicate extensive contact with the outside world. These connections reached the whole of Europe but the networks appear to have been especially expansive towards Novgorod and the east (e.g., Krzewińska et al.,[7] Wikström,[111] and Roslund[112,113]). Some researchers have argued that Sigtuna was primarily a gathering place for the households of the local elite in the Mälaren Valley,[114] while others maintain that it was primarily a gathering place for long-distance guests and emphasised its international character, set apart from the rural countryside.[115] Possibly the answer lies in between as results from isotope and genetic analyses from sampled individuals indicate that people from both the immediate area and long distances visitors were buried in the town.[7,116] The town dwellers were, during the first burial phase (c. 970-1100) buried in a variety of contexts: in small burial grounds with superstructures such as small mounds and stone settings, or in graveyards under flat ground, without an associated church, while some at early churchyards by a wooden church; all of these burial contexts were located in a semi-circle around the settlement.[117,118] With time, starting probably as early as in the late 11th century, six Romanesque stone churches, with associated churchyards, were erected.[107,117] One of the churches (known as Biskopskyrkan or Church 1), located in the block Sankt Gertrud, has been excavated on several occasions and 167 skeletons analysed.[119] A recalibration of the individual in grave 18 (stg018) from the excavation in 1983, dated the individual to 892–1031 CE at 95.4% probability (1055 ±40 BP, Ua-22724).[65] The graves in Sigtuna follow in general a Christian expression, with no or few documented objects, and when present most are from to the clothes of the deceased.

Samples: stg018 (XX) = burial 18 (Kv St Gertrud 2980/83)

Curated at: Sigtuna Museum

Ströja

At Ströja, Kvillinge parish, Östergötland (Sweden) recent archaeological investigations revealed the remains of an elite farm with a sacrificial site, established c. 450 CE[120] Hjulström and Lindeberg forthcoming. By c. 650 CE the site grew in importance: the activities at the sacrificial site became more frequent, a marketplace was established, the hall buildings were relocated and the archaeological material became richer. The gold foil figures found at the site indicate that Ströja was linked to other elite residences in Northern Europe. At an outdoor sacrificial site bone fragments of four human skulls had been placed in, or close to, ritual deposit layers with a large amount of fire-cracked stones and animal bones. Three of the skull fragments were directly related to the ritual deposit layers and the fourth was found on top of a nearby hearth. Of the three skull fragments from the ritual deposit layer, one had been placed in a post hole and one had been placed in a red layer (unknown though what caused the colouring). In, or related to the red layer were also bones from horses (one showing signs of severe blows to the extremities), a lower jaw of a wolf and a deposition of amulets of miniature weapons (a sword, a spear, and a shield). One of the four skull fragments were analysed in this study, come from a female individual dated to the late 8th century. This individual was an adult, radiocarbon dated to 715–941 CE with 95.4 % probability (1200±30 BP, Beta-323616) (find 101, str002), and was found in the red layer 3766. The other individual radiocarbon dated to 662–775 CE with 95.4 % probability (1280±30 BP, Beta-384620), was found by a post hole in the northern part of the layer with fire-cracked stones (find 3838, str004, Hjulström and Lindeberg forthcoming).

Samples: str002 (XX) = individual 101 in layer 3766; str004 = individual 3838

Curated at: - not yet in an Inventory

Turinge

The grave field at Åby, Turinge parish, Södermanland (Sweden) was discovered during a rescue excavation in the early 1970s. The burial ground was an early Christian burial ground set in the rural landscape of the farm Åby and had been in use during the late Viking Age, c. 1000–1100 CE. It consisted of 69 graves; 23 cremation burials covered by low stone settings and 46 inhumations. Of the latter, only 12 held preserved human remains due to the acidity of the soils.[121] At the edge of the burial ground under flat ground was a Viking Age boat burial for an archaeologically determined female. It was well furnished with oval brooches; unfortunately, the human bones were too poor to be included in this study. Directly east of the boat burial was grave 8; it was dug into a heap of fire-cracked stones from the Bronze Age (tur001). It was radiocarbon dated at 95.4% probability to the late Viking Age, 1028–1159 CE (938±28 BP, Ua-63132). The grave goods consisted of a knife, iron mounting and a piece of flint which indicated a male burial. At the burial ground were also inhumations under flat ground, among them grave 71 in the eastern part of the cemetery. The grave (tur003) contained no grave goods, but the skeletal remains were dated to the late Viking Age, with a 93.9% probability of dating to 904–1115 CE (1028±28 BP, Ua-63133).

Samples: tur001 (XY) = grave 8, tur003 (XX) = grave 71

Curated at: Swedish History Museum, Inventory number SHM34902

Valsgärde

The cemetery at Valsgärde is situated three km north of Old Uppsala (Sweden), on a hill by the river Fyris in Uppland. It is famous for its richly furnished boat burials, 15 in all, marked by shallow depressions. There are also 15 other types of inhumations, of which several are chamber burials and 62 cremation burials. The burial ground was in use from the Pre-Roman Iron Age, and after a lacuna, the burials continued from the Late Roman Iron Age until the late 11th or early 12th century.[122] Boat burial 6 is one of the most spectacular boat burials, placed near the crest of the hill just below the only mound on the site. The former is typologically dated to c. 650/660–700/710 CE,[122] and contained many grave goods, including a helmet, three shields, two long swords, two weapon knives, a lance, arrows, two belts, kitchen utensils, tools such as axes, thong, hammer and iron bars of different types, animals such as horses, dogs and birds of prey.[123],[124] A few bone fragments remained of the deceased, which was an exception as boat burials normally are nearly void of human bones, while animal bones usually are much better preserved (e.g. Ljungkvist[122]). The deceased had been placed under a cover on a feather bedding. The individual had not been dressed, but metal objects like a suit of armour, helmet and weapons wrapped in textiles were found in the grave.[125]

Samples: vlg006 (XY) = boat grave 6

Curated at: Uppsala university Museum Gustavianum, Inventory number UMF 5906

Valsta

Valsta grave field (RAÄ 59) in Norrsunda parish, Uppland, (Sweden) is located between Stockholm and Uppsala, not far from Lake Mälaren, in a region rich in other contemporary sites involving graves and settlement remains. Children and adults of both sexes have been buried at Valsta since the Roman Iron Age; an archaeological survey in 1992-1993 also revealed 63 graves from the Viking Age to Early Middle Ages (750–1150 CE).[126] The grave field was clearly used by several generations of settlers at the site.[127] Among these were both cremation and inhumation graves, of which the latter consisted of burial mounds and stone settings of varied character; some graves were not visible above ground. Artefacts were found in cremations and inhumation graves, but the latter category had fewer objects, primarily related to caskets or the deceased's clothes. However, weapons, coins, urns, scissors, boxes and pear sets were also documented. Based on the radiocarbon dates of the individuals and the style of artefacts it seems that both funeral traditions (i.e. cremation and inhumations) were practised concurrently for a period. In some of the inhumation graves, traces of oak wood caskets were documented. Among the inhumation burials, a supine position of the bodies (with varied orientations) was the most common. However, there are exceptions: the woman in grave 69 (vls696) dated to 996–1192 CE (950±50 BP, Ua-6157) was buried prone, and the man in grave 75 (vls757) dated to 987–1185 CE (965±50 BP, Ua-6160) was found in a crouched position.[126]

Samples: vls696 (XX) = grave A69 F663:20, vls757 (XY) = grave A75 F755:17
Curated at: Swedish History Museum, Inventory number SHM34069

Västerhus

The large magnate's farm Västerhus was located on the island Frösön, Jämtland, in northwest Sweden. The lord and his family at Västerhus are believed to have served as representatives of the king and to have had a fiscal role in the region.[128] In association with the farm was a churchyard, which was completely excavated in 1947–1952. The churchyard has been dated from the 11th to the 14th century.[129] In the churchyard, women were buried to the north of the church and men to the south, and a hierarchical social order of the buried has been assumed to reflect contemporary Norwegian laws.[129,130] Since the publication of the first osteological analysis of the 371 skeletons in 1960, several studies have been performed focusing on the living conditions of the population at the site.[130,131] The majority of the graves had an east-western orientation, and with some exceptions, the dead were in a supine position, some in wooden caskets.[129] Few objects were identified among the buried, but coins, a bronze buckle, iron knives, a lead alloy pilgrim badge (depicting St Martin of Tours), and scallop shells were documented.[130] The scallop shells were discovered in grave 200a (wes007) radiocarbon dated to 1163–1262 (828 ± 29 BP, Ua-62712) and grave 56 (wes056) radiocarbon dated to 1016–1155 cal 95.4% (972 ± 29 BP, Ua-62567). The scallop shells are associated with the shrines at Santiago de Compostela, implying that these two individuals (male and female) may have completed the pilgrimage to Spain.[132] Three of the sampled burials (30, 56, and 67) were recovered North of the church, while the other four were found South of the church (122, 127, 138, 200a).

Samples: wes001 (XX) = grave 30, wes003 (XX) = grave 67, wes004 (XY) = grave 138, wes005 (XY) = grave 122, wes007 (XY) = grave 200a, wes008 (XY) = grave 127, wes056 (XX) = grave 56.
Curated at: Swedish History Museum, Inventory number SHM32079

Vendel

The boat-grave cemetery at Vendel in northern Uppland (Sweden) was discovered by accident in 1881. It was only visible through shallow depressions in the ground next to the church at Vendel, the former settlement site for Tuna in Vendel.[133] The burial site consists of fourteen graves: twelve boat graves and two chamber graves.[134] Most of the graves had been robbed/opened; only two graves had been undisturbed, and grave XIV (ven001), excavated in 1893, was one of them. The individual in grave XIV was archaeologically sexed as male. The deceased had probably been placed in a seated position in the stern of the eight-metre-long boat. Remains of the cheekbone were preserved inside the helmet.[134] The boat grave is dated to 560/570 – 610/620 CE.[57,122,135] It belongs to the first generation of burials at Vendel.[134] The burial is unique among the known boat graves from both Vendel and Valsgärde, as the man seems to have been buried half-seated fully dressed in a tunic - garments of fine linen tabby and woollen twill - with a belt around his waist, wearing a helmet and placed on a feather cushioned bed.[125]

Samples: ven001 (XY) = grave XIV
Curated at: Swedish History Museum, Inventory number SHM9785

Viken, Lovö

The burial site at Vikby (Viken) is situated at a former bay of the island of Lovö, Lovö parish, Uppland (Sweden) exposed towards the Baltic inlet.[136] It is renowned for three chamber burials from the Migration period, although the burial ground consisted of more than 20 graves, both cremations and inhumations from the Migration and Merovingian Periods.[136,137] The most well-furnished was chamber grave 3 (lov002), containing an individual archaeologically and osteologically determined as male, with a sword and sword belt and 50 gaming pieces among other grave goods. The grave is dated to 475–510/520 CE.[57,136,137] Contemporary to grave 3 was an adjacent burial, grave 1, osteologically also determined as male.[136] Based on osteological analysis, both individuals have been identified as older males.[136] The graves were interpreted as having been opened/robbed.[136,137] This interpretation has been questioned for grave 3,[56] as it contained a complete sword, sword belt, lance, arrows, and shield.[135] The genetically determined female XX karyotype of lov001 contradicts the male osteological assignment. A female assignment is consistent with the fact that there were no male-characteristic objects in grave 1. Instead, among the grave goods were a bead, a small gold finger ring, clasps, a spindle whorl and a scraper of elk antler (hide scraper[136]). This would indicate that the grave was erected over a woman.

Samples: lov001 (**XX**) = grave A1, lov002 (XY) = grave A3
Curated at: Swedish History Museum, Inventory number SHM29401

METHOD DETAILS

DNA extraction

The human remains were sampled in the aDNA facilities at the Archaeological Research Laboratory, Stockholm University (Sweden). All samples were decontaminated prior to analysis with a 0.5% sodium hypochlorite solution and UV irradiated (6 J/cm² at 254 nm). After removing the surface, bone was drilled to powder and the root tip of the teeth was cut with a multitool drill (Dremel) to get approximately 80 to 150 mg of bone powder/root tip.

The root tip samples were placed in an Eppendorf tube in 1 ml of pre-digestion buffer (0.45 M EDTA pH 8.0) at 37°C in a hybridization oven. After 30 minutes the supernatant was removed to reduce the microbial and exogenous DNA. Following this pre-digestion step, 1 ml extraction buffer (0.45 M EDTA pH 8.0 and 0.25 mg/ml of proteinase K) was added to all the samples and they were incubated at 37°C in the hybridization oven for 1-4 days until all powder/ root tip was dissolved. The extraction was conducted following Dabney et al.,[138] with 1 ml of digested extract being combined with 13 ml of binding buffer containing 5 M guanidine

hydrochloride, 40% (vol/vol) isopropanol, 0.05% Tween-20 and 90 mM sodium acetate (pH 5.2). 50 ml silica columns (Roche, High Pure Viral Nucleic Acid Large Volume Kit) were used for purification and the DNA was eluted in 45 μl of EB buffer (Qiagen). The remaining samples were extracted following a slightly different protocol, as described in Krzewinska et al.[7] The extraction buffer contained 1 ml of 0.5 M EDTA (pH 8.0), 1 M urea, and 10 ul of proteinase K (10 mg/ml). After digestion for 48 hours at 37°C in the hybridization oven, the 1 ml of extract was centrifuged at max speed and the supernatant was concentrated to 100 μl using Amicon Ultra centrifugal filters and purified to 110 μl of cleaned product using a MinElute kit (Qiagen).

Library preparation and sequencing

20 μl of extract was used to prepare blunt-end ligation DNA libraries coupled with P5 and P7 adapters and indexes as described in Meyer and Kircher.[38] Blank controls were used during every step of library preparation and amplification. The optimal number of PCR cycles for library amplification was determined with qPCR. The amplification reactions had a total volume of 50 μl, with 5 μl DNA library, and the following in final concentrations: 1 X AmpliTaq Gold Buffer, 2.5 mM $MgCl_2$, 250 μM of each dNTP, 2.5 U AmpliTaq Gold (Thermo Fisher Scientific, Waltham, MA), and 200 nM each of the IS4 primer and index primer.[38] PCR was done with the following conditions: an activation step at 94°C for 10 min followed by 8–20 cycles of 94°C for 30 s, 60°C for 30 s, and 72°C for 45 s, and a final elongation step of 72°C for 10 min. Four amplification reactions with the same indexing primer were made for each library to increase complexity. Finally, the amplified libraries were pooled and purified with AMPure XP beads (Agencourt; Beckman Coulter, Brea, CA), and the fragment size and concentration were checked using BioAnalyzer with the High Sensitivity Kit (Agilent Technologies, Cary, NC).

The samples with the highest proportion of endogenous human content in the conventional blunt-end libraries were also damage-repaired with a USER enzymatic treatment to remove deaminated cytosine sites[139] before further deep-sequencing.

QUANTIFICATION AND STATISTICAL ANALYSIS

Processing and alignment of sequencing reads

Purified libraries were pooled in equimolar concentration and sequenced on an Illumina HiSeq X at the SciLife Sequencing Centre in Stockholm. Sequencing reads were demultiplexed according to the index of each sample sequence. AdapterRemoval v.2.3.1[40] was used to remove adapter sequences, short reads (<25bp), and regions of consecutive low-quality bases and ambiguous bases (N's). Subsequently, reads were aligned to NCBI build 38 of the human reference genome using the Burrows-Wheeler Algorithm, as implemented by BWA v. 0.7.10,[41] with the seed disabled (-1024) to improve accuracy and the minimum base quality set to 15. Base quality scores were rescaled with MapDamage 2.0[45] to exclude likely-damaged bases. Mapped reads were filtered on a library-based level for PCR and optical duplicates using PicardTools v.1.21.3, (http://broadinstitute.github.io/picard/). Only mapped reads with Phred-scaled mapping quality (mapQ) scores ≥30 were kept. Read depth and coverage were determined using BEDtools-2.29.2[46] and an in-house python script. Ancient genomes from previously published studies (Table S1B) were processed in the same way after their read data were downloaded. As the sequencing depth for most of the ancient individuals was too low to call diploid genotypes, haploid genotypes were used for all analyses, obtained by randomly selecting a single read for each position of interest from those with base quality ≥30.

Data validation

We used several approaches to validate the dataset. Firstly, all libraries yielded short read lengths (Table S1), and patterns of cytosine deamination estimated with MapDamage2.0[45] were consistent with aDNA expectations for samples that were not USER treated (Table S1). Secondly, we estimated contamination affecting mtDNA by estimating the frequency of minor alleles at positions where the major allele was rare following Ebenesersdóttir et al.[22] (Table S1). Thirdly, we used the 'Contamination' program in ANGSD[48] v.0.911 to estimate X-chromosome contamination in males, as described in Rasmussen et al.[140] We only considered bases with quality ≥20 and reads with mapping quality ≥30. ANGSD applies two different methods to estimate the contamination rate: Method 1 considers all bases, providing greater power while assuming that errors are independent between reads and sites. However, Method 2 does not have this bias, as it randomly samples a single read at each site, but is also less precise than Method 1. Contamination estimates are shown in Table S1. Finally, sex was assigned following the method described in Skoglund et al.[141] (Table S1), with clear assignments obtained for all samples.

Kinship analysis lcMLkin

Kinship relations between the individuals analysed in this study were estimated with the program lcMLkin[53] using bam files mapped to the GRCh37 Genome. We selected a panel of 1,681,497 transversion SNPs from the Estonian Genome Diversity Project (EGDP)[142] in order to avoid post-mortem damage bias in our samples. The genotype likelihoods of the selected SNPs positions were called using 'SNPbam2vcf.py' following a maf=0.15 and using the population allele frequencies from 507 ancient individuals.

Reference population datasets
European reference panel

To help identify the ancestries of our ancient individuals, we compiled an autosomal genomic reference dataset of modern, mostly European individuals comprising 10,083 individuals (9,052 of which shown on PCA figures) containing genotypes for 168,599

variants. The sources used are described in Table S3 and consist of a variety of data sources that are either publicly available, available on request from external groups, or available only to researchers at deCODE genetics.

In order to maximise the final count of intersecting variants and to avoid some sources of batch effects, we selected only data genotyped on a set of Illumina microarrays with high overlapping marker content (600 series, Omni series). For some data sources, this involved restricting to a subset of samples that were chipped on acceptable microarrays, as identified in provided metadata or by analysing per-sample missingness (as for e.g. "urnikyte_lithuania").

All merging was performed while correcting for strand flips and discarding all ambiguous A/T and C/G SNPs. PLINK 1.9 was used at all steps.

QC, ancestry outliers, and inferred geographic/ancestry labels. For the subset of desired populations from each data source, we used PLINK to apply per-variant (–geno) and per-individual (–mind) genotype missingness filters of 3% and exclude non-autosomal variants, and then used KING –unrelated to remove one from each pair of duplicate samples and relatives closer than second degree. After merging, KING –unrelated was again run to identify and remove duplicates and relatives closer than second degree between sources. For ancestry analysis, we removed variants with MAF <1% and variants in long-range high-LD regions.[143]

We then identified and removed genetic ancestry outliers. For some data sources that we expected to have a greater proportion of individuals with recent, very divergent genetic ancestry (i.e. continental-level outliers), we first ran ADMIXTURE on LD-pruned data (plink –indep-pairwise 200 25 0.4) supervised on the 1000G populations CEU, CHB, ITU, PEL, and YRI, and then removed 190 clear outliers by inspection.

We then merged all remaining individuals and performed principal components analysis (PCA) in smartpca with "ldregress: 200" and "ldposlimit: 100000" to identify less divergent (i.e. within-continent) genetic ancestry outliers.

We aimed to use the most granular level of information when assigning population/group labels to samples. Samples have a top-level group label (e.g. "Norwegian") as well as lower-level regional and ancestry labels (e.g. "Norwegian_Troms_SaamiInferred"). In the figures in this paper that display the European reference PCA, we only show the top-level label.

In a small number of cases, we also assigned labels based on genetic ancestry. Specifically, we noticed two sets of distinctive outliers: one that included individuals labelled "French" and "Spanish" who localised with individuals labelled "Basque Spain" and "Basque France"; and another comprising individuals with labels "Norwegian", "Swedish", and "Finnish", who landed on three sparse clines lying between a shared pole and each of the three main clusters for the respective countries. After inspecting supervised ADMIXTURE assignments, the available information on sub-country region of origin, and analyses that we had performed on some of these individuals in other publications, we concluded that the set of "French" and "Spanish" outliers likely carried Basque ancestry, and the "Norwegian", "Swedish", and "Finnish" outliers likely carried Saami ancestry. These ancestries are unusually informative for identifying several kinds of modern and ancient ancestries. Furthermore, Basque were represented at low counts in our geographic/ancestry labels, and Saami not at all. For these reasons, we decided to delineate these two outlier regions using (arbitrarily chosen) PC coordinate criteria and appended "_BasqueInferred" or "_SaamiInferred" to the geographic/ancestry labels of the contained individuals.

We then used an unsupervised method which we refer to as "MVE" (minimum volume ellipsoid, in which we define Mahalanobis distance outliers of a specified quantile, such as 99.9%, from an estimated "true" multivariate distribution found using the R function MASS::cov.mve) to identify per-population outliers in the PC coordinates. We also made sure not to remove individuals as outliers if they carried a lower-level population label which we suspected could be associated with distinctive ancestry but could nonetheless rationally be placed under the top-level label (e.g. "Greek_Turkey", "Croatian_Herzegovina", "Russian_Arkhangelsk"). 433 individuals were removed as outliers at this stage, leaving 10,083 individuals.

We then performed another PCA to confirm that no obvious genetic ancestry outliers remained. However, because they were oversampled and dominated the PC space, we decided to create a subset in which we reduced the number of "Italian" individuals from 1,144 to 700 and "Finnish" from 856 to 300, leaving 9,052 individuals. The PC coordinates generated from this downsampled reference set were used in all the figures in this paper.

Scandinavian reference panel

We also created a reference panel of 16,638 individuals of Scandinavian ancestry (see Table S3). For each dataset, we removed individuals with missingness greater than 3%, the higher-missingness individual from each pair of duplicates or monozygotic twins marked by KING –duplicate, non-autosomal variants, variants with missingness greater than 3%, and variants deviating from Hardy-Weinberg equilibrium by $p < 10^{-20}$. For ancestry analysis, we also removed long-range high-LD regions[143] and variants with MAF less than 1%. Individual ancestry outliers were removed using ADMIXTURE and PCA according to a similar procedure as the one described above, making sure that individuals of putatively Finnish or Saami ancestry were not removed. For the Swedish and Norwegian datasets, we restricted to individuals for which county of residence (Swedish län or Norwegian fylke) was known.

Y-chromosome and mtDNA haplogroups

We used the method of Ebenesersdottir et al.[22] to call consensus mtDNA sequences (Table S1). Y-chromosome haplogroups were assigned to the ancient and modern Scandinavian males using the ISOGG 2019 Y-chromosome tree (Figure S5A; Tables S1).[144] The ISOGG 2019 database is based on 71,405 loci, each of which marks a mutation on the human Y-chromosome tree. For each SNP in the dataset, we determined whether our ancient sample carried the derived or ancestral allele (according to majority alleles with base quality ≥ 30), and assigned each individual to the branch in the tree most consistent with the overall configuration of derived alleles observed.

Principal components analysis

Principal components analysis was performed on modern reference data using the smartpca module in EIGENSOFT (v.6.0.1).[49] No outlier iterations were performed, and the parameters "ldregress: 200" and "ldposlimit: 100000" were used to perform LD regression. Pseudohaploid ancient data was projected onto principal components using an in-house script that accounts for missingness by multiplying coordinates by a factor relating to the sample's genome-wide missingness.[49,145]

f-statistics

Patterson's *f*-statistics were calculated using in-house scripts based on ADMIXTOOLS package v. 3.0.[50]

ADMIXTURE

ADMIXTURE v.1.3[51] was run on each ancient sample separately supervised on whole-genome sequence data from five populations from the 1000 Genomes project[146] (Utah residents with Northern and Western European ancestry (CEU); Indian Telugu in the U.K. (ITU), Han Chinese in Beijing, China (CHB); Peruvian in Lima, Peru (PEL); and Yoruba in Ibadan, Nigeria (YRI). From the training data, we filtered out variants with more than 3% missingness, non-autosomal variants, variants in long regions of high linkage disequilibrium,[143] and also filtered out individuals in second-degree or closer kinship pairs according to KING, as well as 12 individuals who were possibly ancestry outliers according to PCA and ADMIXTURE analysis. For each run of ADMIXTURE, we restricted the training data to the variants that intersected with the non-missing variants in the test individual and LD-pruned those variants using plink –indep-pairwise 200 25 0.4.

qpAdm

We used the R package admixtools (https://github.com/uqrmaie1/admixtools) to generate allele frequency products for each ancient individual with depth > 0.5x and several modern reference populations from the west Eurasian reference set (Danish, Swedish, Finnish, Lithuanian, Polish, Ukrainian, Hungarian, Romanian, Irish, English_Oxfordshire, Dutch, German, French, Spanish, Sardinian, Italian_Tuscany, Lezgin, Greek, Basque [comprising both Basque_France and Spanish_PaisVasco], Turkish, and Lebanese_Christian), using a block jackknife size of 1 Mb. Modern rather than ancient sources were used in order to avoid biases and artefactual attraction between differently processed aDNA data. We then used these allele frequency products as the input of qpadm_rotate,[147] placing all the modern reference populations in the "left-right" position. For convenience, we defined a modified version of the function which did not attempt to run models involving more than three sources. In the output, we filtered for only "plausible" models for which all ancestry proportions were in the interval [0,1] and gave p-values greater than 0.01. To create the summarised plots, we selected one model per individual by taking the filtered models with the least number of sources and choosing the one which gave the highest p-value. It is likely that some of the individual runs of qpAdm violate the assumption of no gene flow from references to sources, and ranking by *p*-value is not considered best practice;[147] however, we observed that the models selected by this procedure agreed with results from other analyses. Next, we calculated the mean proportions of each ancestry across the samples in each grouping of geographical region and time period. We then plotted the results using each individual source (Figure S3A) and merging the sources into five different groups; Irish-British (Irish and English_Oxfordshire), South-West Europe (French and Spanish), Scandinavian (Swedish and Danish), Baltic (Lithuanians, Finnish, Ukrainians and Polish), Others (Dutch, Germans, Hungarians and Romanians) (Figure 4).
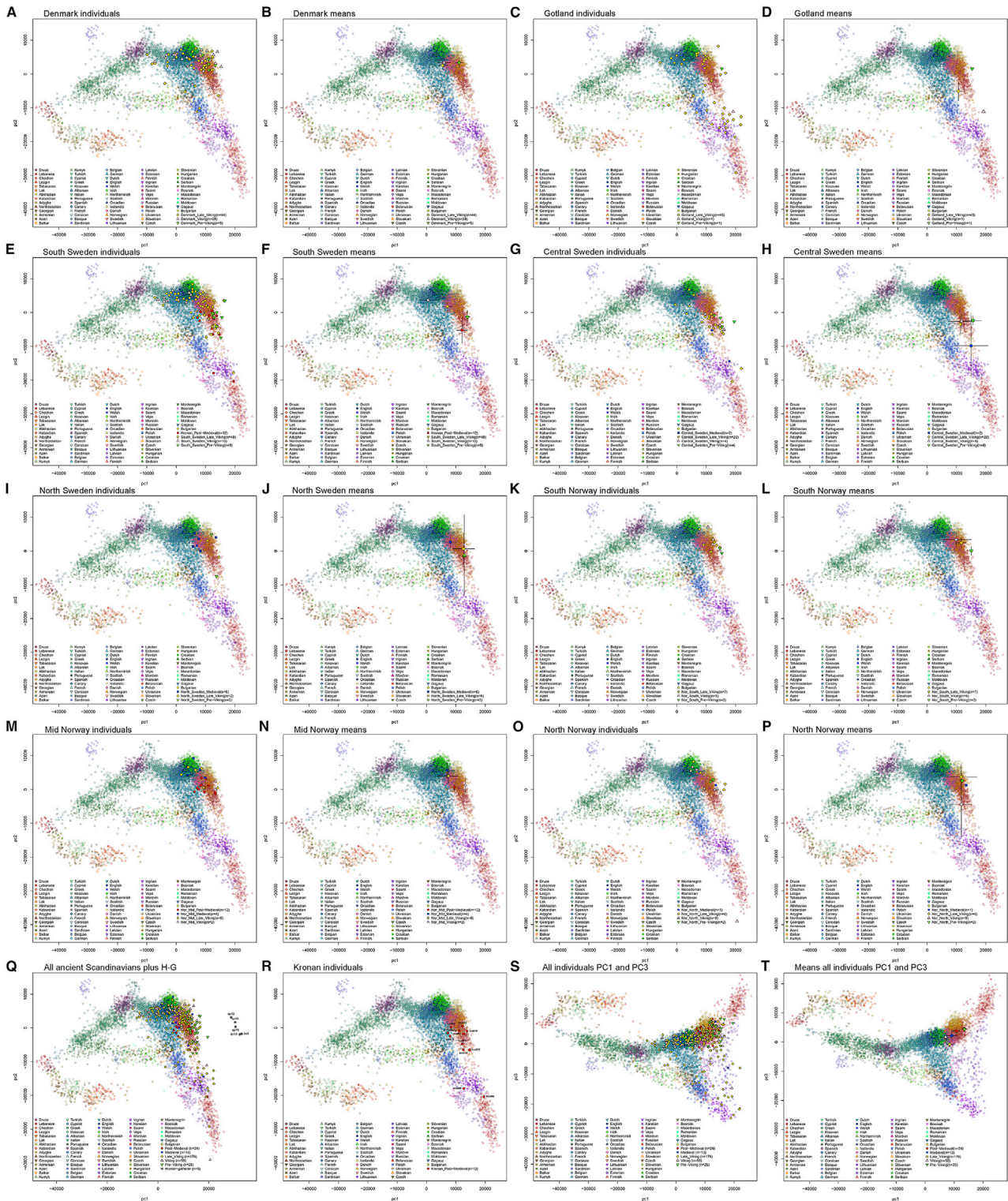
Supplemental figures

Figure S1. Ancient Scandinavians projected onto the first two or three principal components of modern West Eurasians, related to Figure 2

(A–R) Ancient Scandinavians projected onto the first two principal components.

(S and T) Ancient Scandinavians projected onto the first and the third principal components.
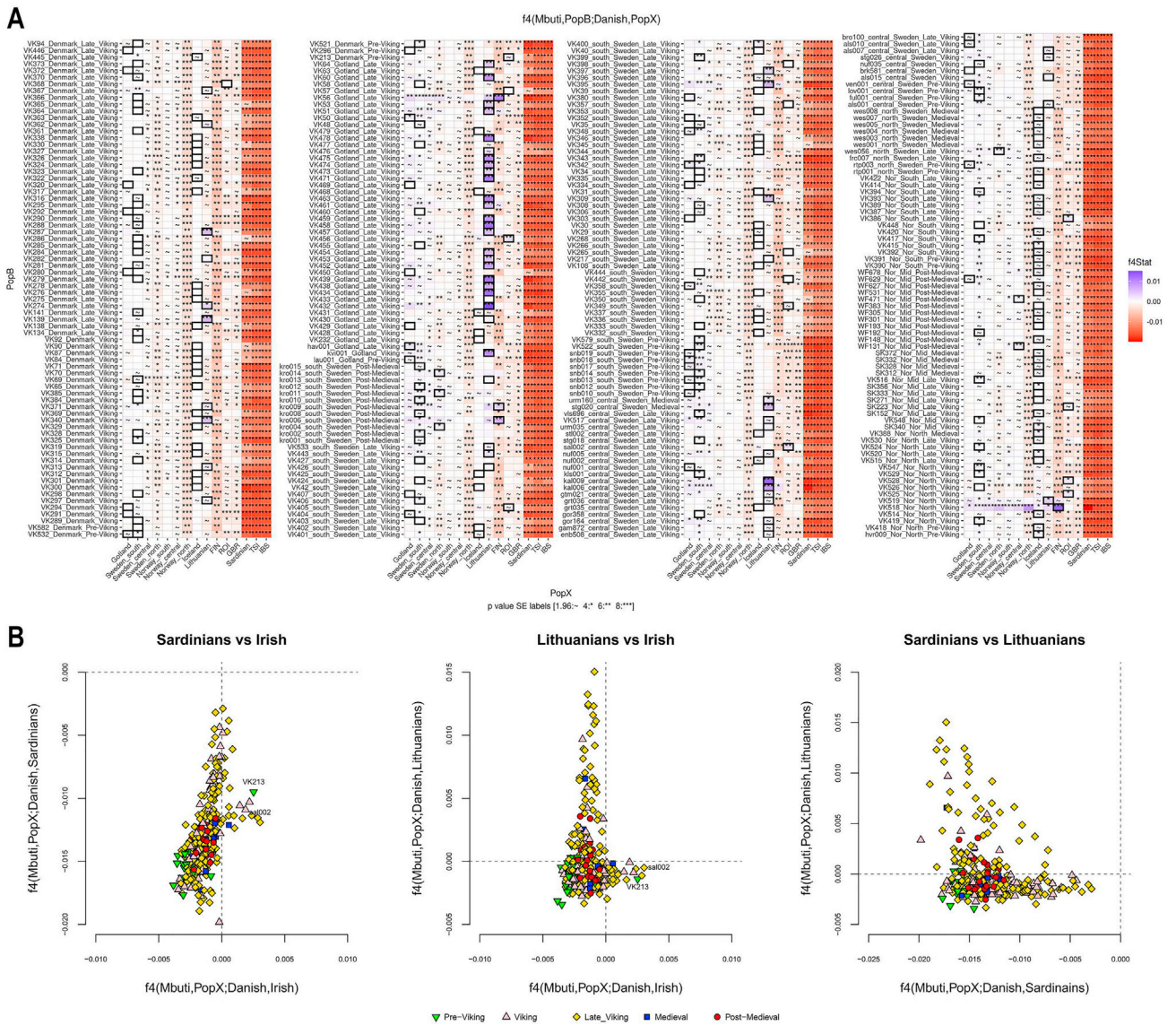
Figure S2. *f₄*-statistic analyses on ancient individuals, related to Figure 3

(A) Heatmap. *f₄*-statistic of the form *f₄*(Mbuti, Pop B; Danish, PopX). Pop X represent modern populations, and Pop B the ancient individuals. The highlighted squares in each row indicate the highest positive value.

(B) Scatterplots of the *f₄*-statistic results of the form *f₄*(Mbuti, ancient individuals; Danish, modern population) versus *f₄*(Mbuti, ancient individuals; Danish, modern population 2) reflecting the possible correlations of shared genetic drift of each Scandinavian ancient individual with different pairs of modern proxy population.
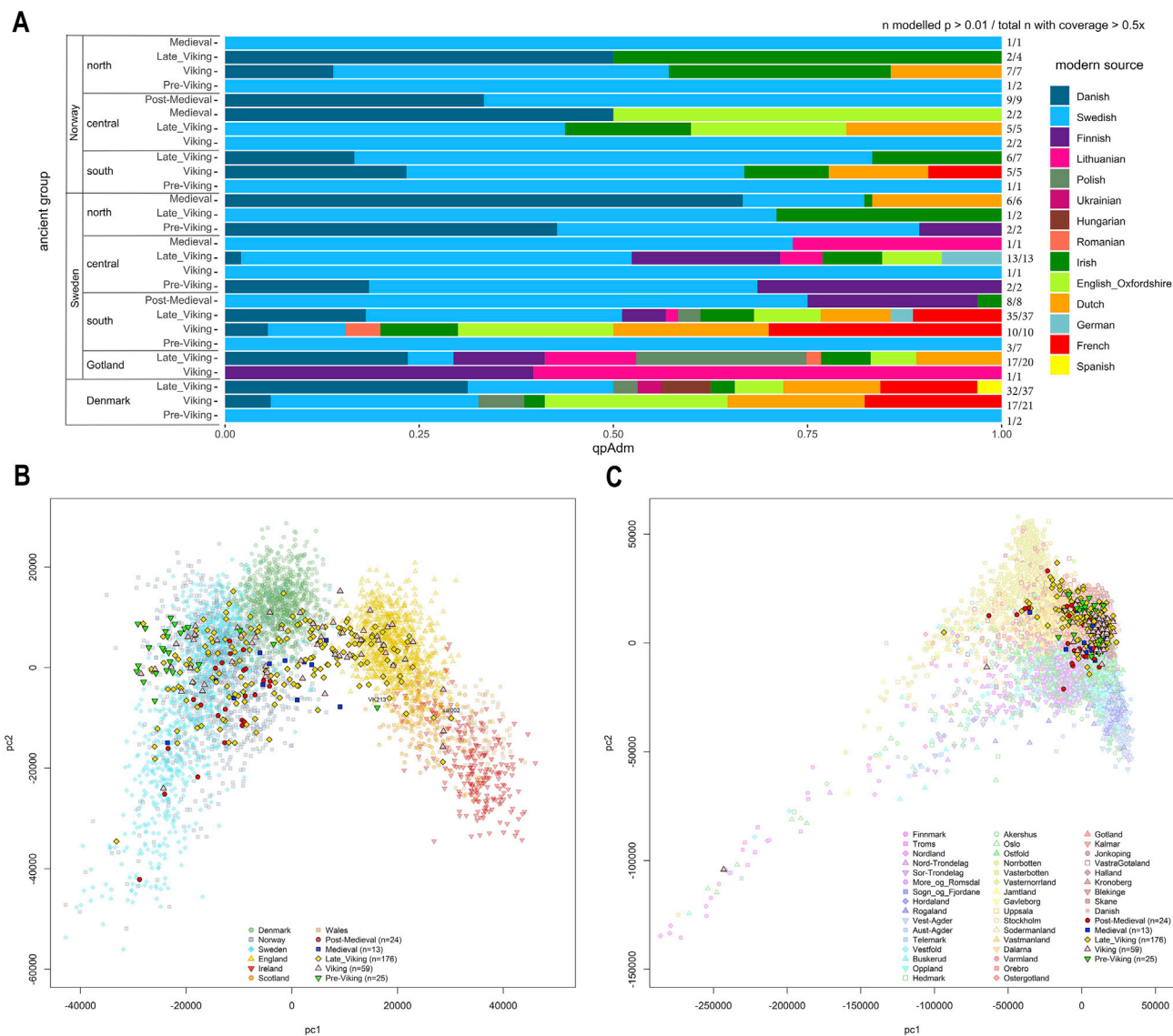
Figure S3. qpAdm and PCA projections of the ancient individuals, related to Figures 2, 4, 6, and 7

(A) qpAdm using 21 modern sources. Only samples with p > 0.01 and coverage >0.5× are plotted. Sardinians, Italian_Tuscany, Greeks, Lezgin, Basque, Turkish, and Lebanese_Christian did not appear in successful models and are not shown in the legend.

(B) Ancient Scandinavians projected onto the first two principal components of modern Scandinavians and the British-Irish Isles.

(C) Ancient Scandinavians projected onto the first two eigenvectors of a PCA from 16,638 modern Scandinavian populations.
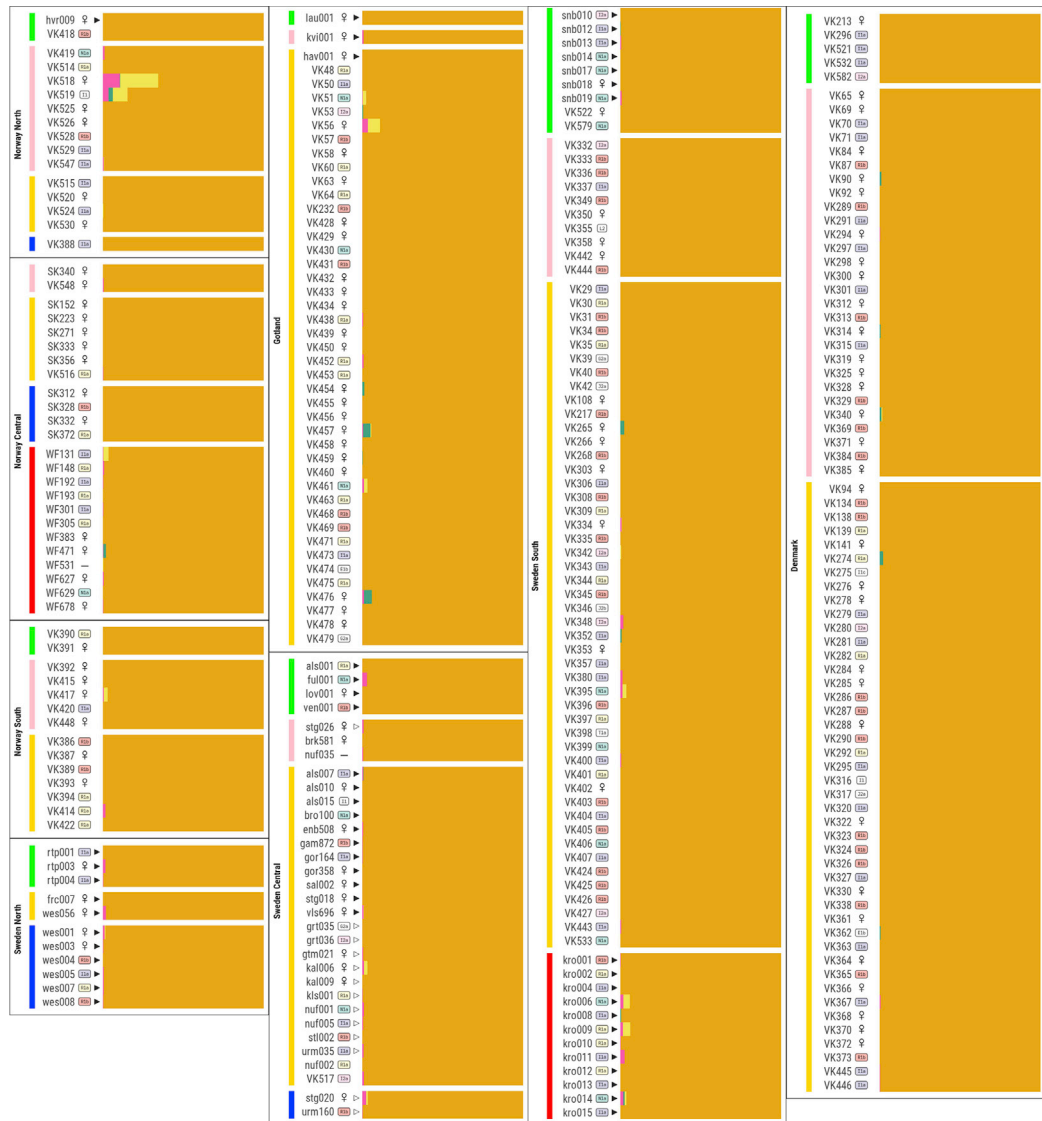
Figure S4. ADMIXTURE, related to Figures 6 and 7

Supervised run of ADMIXTURE using five training populations from the 1000 genomes (Utah residents with Northern and Western European ancestry [CEU], Indian Telugu in the UK [ITU], Han Chinese in Beijing, China [CHB], Peruvian in Lima Peru [PEL], and Yoruba in Ibadan, Nigeria [YRI]).
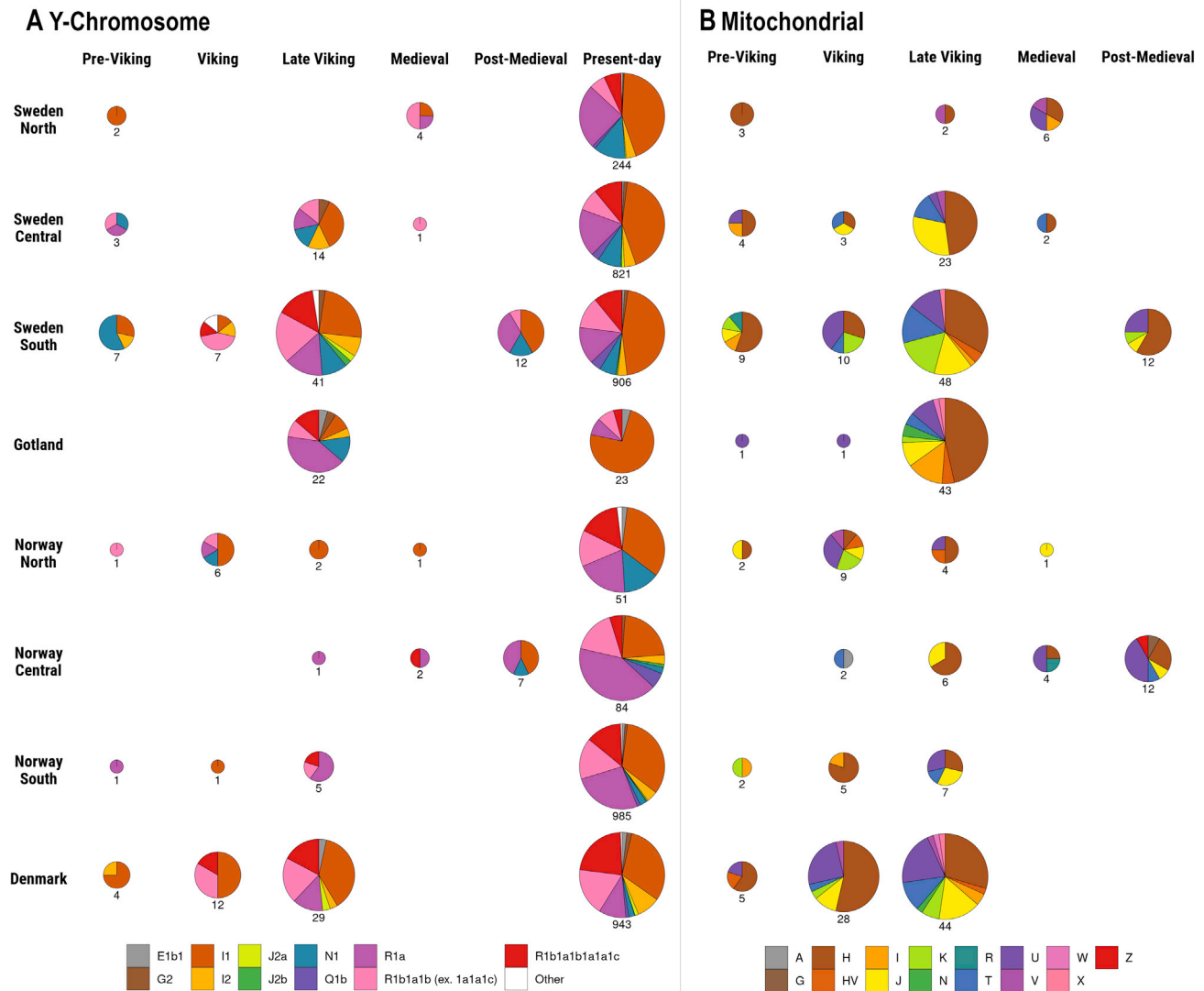
A Y-Chromosome

B Mitochondrial

Figure S5. Uniparental haplotype distribution across different periods, countries, or regions, related to STAR Methods
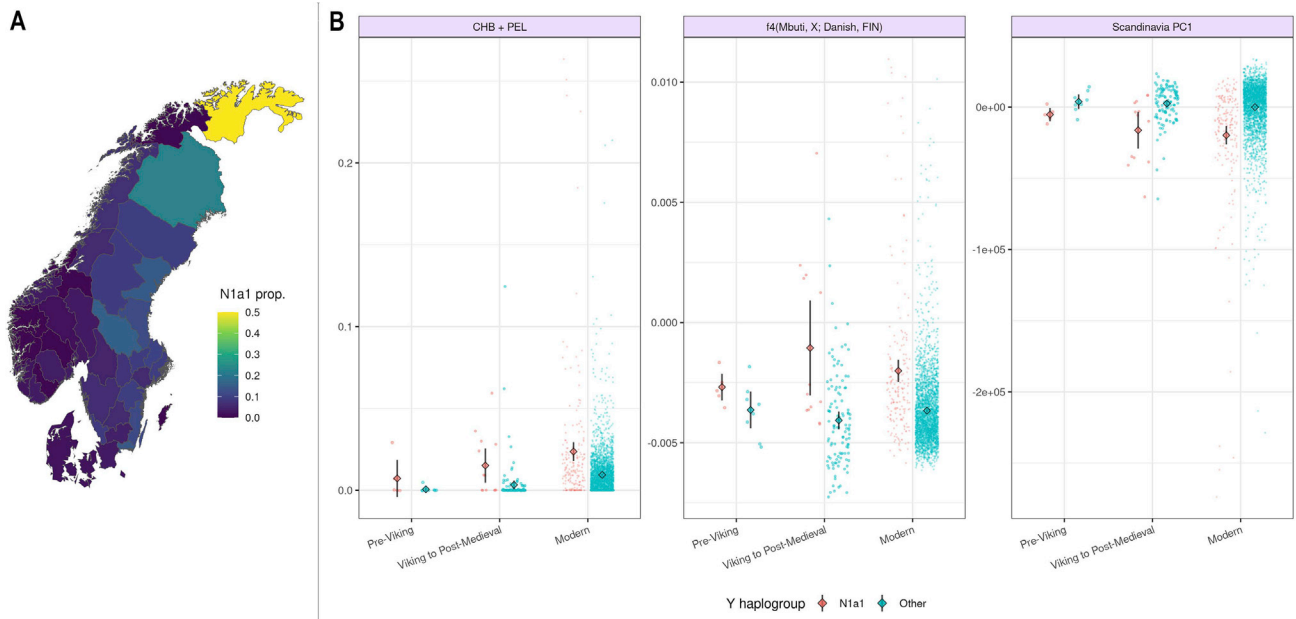(A) Y chromosome.
(B) Mitochondrial.

Figure S6. Y chromosome haplotype N1a1 distribution, related to Figures 6 and 7
(A) Modern frequency of the Y chromosome haplotype N1a1 across Scandinavia.
(B) N1a1 status in Norwegians and Swedes by time period and "northern cline" measure (bars are 2 SEs).