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Mitochondrial DNA variation in the Viking age population of Norway

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The medieval Norsemen or Vikings had an important biological and cultural impact on many parts of Europe through raids, colonization and trade, from about AD 793 to 1066. To help understand the genetic affinities of the ancient Norsemen, and their genetic contribution to the gene pool of other Europeans, we analysed DNA markers in Late Iron Age skeletal remains from Norway. DNA was extracted from 80 individuals, and mitochondrial DNA polymorphisms were detected by next-generation sequencing. The sequences of 45 ancient Norwegians were verified as genuine through the identification of damage patterns characteristic of ancient DNA. The ancient Norwegians were genetically similar to previously analysed ancient Icelanders, and to present-day Shetland and Orkney Islanders, Norwegians, Swedes, Scots, English, German and French. The Viking Age population had higher frequencies of K*, U*, V* and I* haplogroups than their modern counterparts, but a lower proportion of T* and H* haplogroups. Three individuals carried haplotypes that are rare in Norway today (U5b1b1, Hg A* and an uncommon variant of H*). Our combined analyses indicate that Norse women were important agents in the overseas expansion and settlement of the Vikings, and that women from the Orkneys and Western Isles contributed to the colonization of Iceland.

1. Introduction

The Viking Age, from the eighth to the mid-eleventh century of our era, was the phase between the Prehistory and Middle Ages in Scandinavia. It was characterized by the gradual economic and cultural integration of Scandinavia into Christian Europe, and human expansion in three main directions: (i) from Norway north and westwards to the North Atlantic Islands, Scotland, Ireland and even North America; (ii) from Denmark west to England, Ireland and Normandy; and (iii) from Sweden east and southwards to central Russia and the Black Sea (figure 1). There is extensive archaeological, historical and linguistic evidence of Viking activities in Russia and Byzantium, the North Atlantic, Britain, The Netherlands and France [3–6]. In recent years, genetic analyses have contributed additional information on the nature of the Viking migrations [7–9]. Population genetic studies on present-day people reveal a large excess of Norse male over female lineages in Iceland and the Faroes, suggesting that the early male Norse settlers brought with them Gaelic women [7,10–12]. By contrast, it appears that islands closer to Scandinavia, including Orkney and Shetland, were settled by an almost equal proportion of Norse men and women [8]. Archaeological and historical sources show that Viking women and children accompanied Viking armies and were important agents in the processes of migration and assimilation [13]. The Norse migrants contributed to the

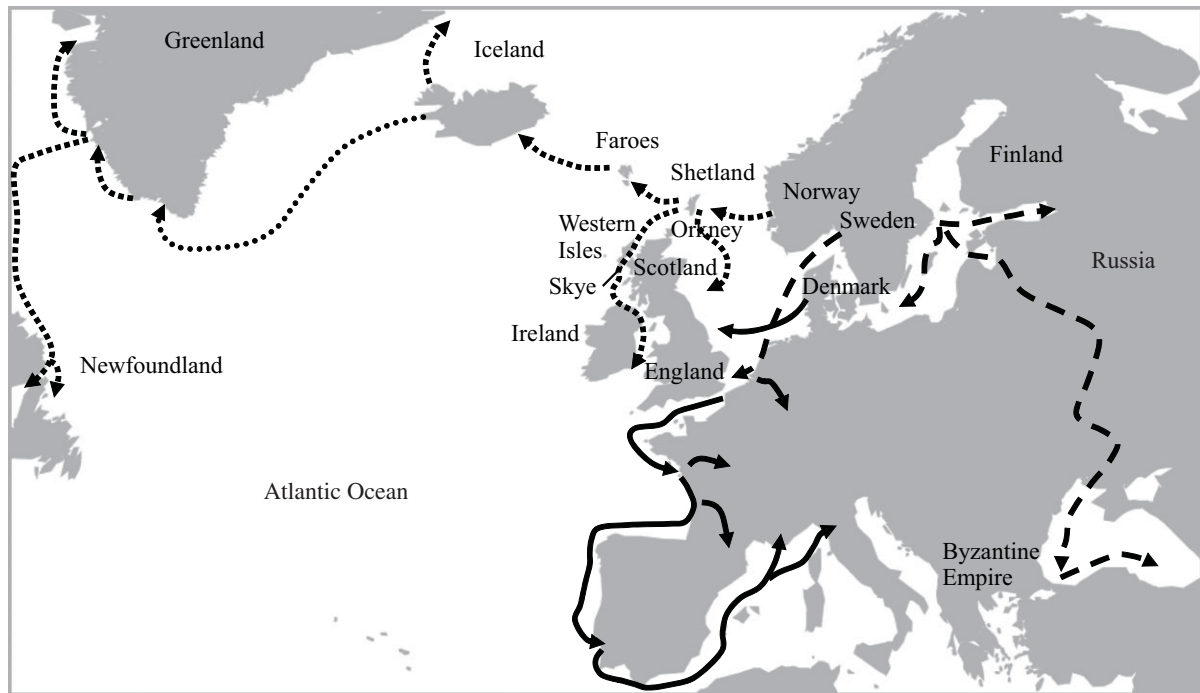


Figure 1. Map of Northern Europe showing the routes of Viking expansion [1,2].

gene pools of the inhabitants of their new homelands, and their descendants eventually carried their respective genes to other lands [9,14].

Frequencies of genes in populations change over time owing to genetic drift, migration and admixture, resulting in major shifts of genetic lineages [15]. Using maternally inherited mitochondrial DNA (mtDNA) data from archaeological bones, Helgason *et al.* [16] showed that the composition of maternal lineages changed considerably in Iceland in the past millennium, with some lineages vanishing completely. This is consistent with the demographic history of Iceland, whose small population was subjected to repeated genetic bottlenecks [16]. Norway's Iron Age population was also small, and the number of inhabitants could shift markedly over short times. In the Viking Age (late ninth century), the population was about 150 000–200 000, but it grew to approximately half a million by AD 1300, and is thought to have collapsed to half that number during the Black Death of 1349 [17–19]. By the mid-seventeenth century, Norway's population was probably just 440 000, but increased to two million in the late-nineteenth century [20]. This population growth resulted in poverty, and by the early-twentieth century, as many as 900 000 Norwegians had emigrated overseas. These demographic changes and associated random genetic drift would undoubtedly have affected gene frequencies, and cause the extinction of lineages. Such processes are ideally suited to ancient DNA techniques, which allow the genes of past populations to be investigated directly, rather than having to extrapolate information from studies on present-day populations.

The primary goal of this study was to characterize the maternal lineages of ancient Norwegians by analysis of mtDNA polymorphisms in DNA recovered from skeletal remains of the Late Iron Age population of Norway (AD 550–1050). Our data provide a picture of the genetic variation and movements of the Norse people in the North Atlantic region during the Viking era. The results reveal that the ancient inhabitants of Norway were genetically similar, but not identical to modern Norwegians, and they carried

lineages now extinct in Norway as well as lineages characteristic of distant geographical regions.

2. Material and methods

(a) Bone samples

The human skeletal remains used in this study were part of the Schreiner Collection, Department of Anatomy, University of Oslo. Eighty bone and teeth samples in different states of preservation [21] and of wide geographical distribution were chosen for DNA analysis. Most skeletons were from burial sites in northern and central Norway, where preservation is more favourable, and were excavated between 1880 and the mid-1980s [22]. The associated documentation was poor in most cases, and 15 of the individuals were from accidental finds. At least six burials contained more than one person (for additional information on the skeletal samples, see the electronic supplementary material, table S1).

Small samples of bone, or single teeth, were removed with care to avoid excessive damage. When possible, wedges of long bone (up to 3 g) were cut using a hacksaw, or a single tooth was removed manually. Sampling was carried out by one of us (M.K.), wearing a laboratory coat, face mask, hair net and disposable gloves. The study complied with the relevant guidelines for the analysis of human skeletal remains.

(b) Ancient DNA extraction and amplification

The surface of the bone samples was cleaned by sandblasting with fine alumina grit (Airbrasive 6500 System 2, S. S. White Technologies Inc., Piscataway, NJ), followed by ultraviolet exposure (254 nm) for 15–30 min on each side. Bone pieces were ground to powder using a freezer mill refrigerated with liquid nitrogen (Glen Creston Ltd., Stanmore, UK). Six teeth were prepared according to the method of Malmström *et al.* [23]. Some extractions were performed at Oslo University and some at the Evolutionary Biology Centre, Uppsala University, to increase the dataset.

In Oslo, DNA was extracted using the Qiagen Investigator Kit, following the manufacturer's instructions, with an additional 200 µl 0.5 M EDTA in the digestion step, or by the silica-based method of Rohland & Hofreiter [24]. In all extraction methods,

the bone powder (150–250 mg) was washed with 2.5% sodium hypochlorite to remove potential contaminating DNA [25], rinsed twice with dH₂O and twice with 0.5 M EDTA, pH 8.0. Thirty eight samples underwent extractions in Oslo using both methods. Forty two bone samples were extracted in Uppsala using previously described methods [26,27]. Blank extractions were carried out on average every third sample in both laboratories to screen for contamination.

The first hypervariable region of mtDNA (HVR1), from position 16 051 to 16 391 (electronic supplementary material, table S2), was amplified in five overlapping fragments as described previously [26]. Amplification primers (electronic supplementary material, table S3) were labelled using different combinations of 14 four base-pair (bp) tags [28], to aid the subsequent identification of the individual amplicons. Each sample was amplified twice using two different combinations of tagged primers, resulting in 10 amplicons per individual. The amplicons were sequenced on a 454 GS FLX platform (454 Life Sciences) with two emulsion PCRs. The overall coverage differed significantly depending on the preservation of the samples, from 0 to 1200 sequences in particularly well-preserved samples. The amplicons were sorted and aligned as described previously [29]. In brief, to avoid sequencing errors and chimaeric sequences, only reads of appropriate fragment length and both-end tag combination were selected for further analyses.

Sequence motifs were assigned to mtDNA haplogroups following the suggestions of Vincent Macaulay (University of Glasgow) (<http://www.stats.gla.ac.uk/~vincent/founder2000/motif.html>) and using the mtDNA manager at Yonsei University [30] as well as the Genographic Project [31] and GHEP-EMPOP [32] databases.

(c) Reference population data

Ancient DNA sequences were compared with a database of 5191 present-day mtDNA sequences, including 838 Norwegians: 515 individuals from the west and north (our unpublished data) and 323 from Oslo [7]. The additional 4353 mtDNA sequences were collected from published data, as listed in the electronic supplementary material, table S4. Only those present-day sequences which overlapped with the mtDNA fragment from our ancient samples (16 051–16 391) were included in the comparison. European populations are relatively poorly resolved using mtDNA HVR1 sequences, and these differences would be almost entirely erased when compared with geographically distant populations. Thus, to enhance the resolution of our analyses, we restricted our comparisons to within the North Atlantic region.

(d) Statistical analyses and population structure

The sequences were sorted and aligned using R v. 2.8.1 [33]. Ancient sequences were identified with the help of the PHYLONET v. 5 program, which was used to calculate *c*-statistics [34] from over 600 000 synthetic clones. The *c*-statistic exploits the characteristic patterns caused by cytosine deamination lesions to identify the oldest template molecules. For each sequence type in each of the amplicon sets, a *c*-statistic value ($C_{\max}$) and its significance as a *p*-value was calculated. For each set of amplicons, sequences with a *p*-value < 0.001 and highest $C_{\max}$ score were selected for further analyses [34]. Using these criteria, the HVR1 sequences were assembled from five overlapping fragments, and mutations were recorded by comparing with the revised Cambridge reference sequence (rCRS) [35,36]. Consensus sequences were assembled in BioEDIT v. 7.1.3.0 [37] and aligned using the DNA ALIGNMENT v. 1.3.1.1 package (www.fluxus-engineering.com). Haplotype frequencies and population comparisons were calculated using ARLEQUIN v. 3.1 [38]. Pairwise population differentiation values (F_{ST}) were calculated for all sample pairs assuming a Tamura–Nei model, with a gamma distribution $\alpha =$

0.26, and 10 000 iterations. The values were analysed using non-metric multi-dimensional scaling (NMDS) as implemented in the R MASS package [39]. Haplotype sharing was assessed in two ways, using a previously described haplotype-sharing permutation test (HP) [16] and as a proportion by normalizing the number of identical haplotype matches between pairs of populations with the total number of pairwise comparisons (HS). These calculations were used to compare ancient DNA sequences from Norway and Iceland, respectively, to the present-day sequences of the North Atlantic region (figure 2). In the HP, the probability of obtaining an equal or smaller number of haplotype matches is expressed as a *p*-value. The smaller the *p*-value, the less likely the tested ancient sample can be considered a random subsample of the modern reference population, meaning the two samples originate from different mtDNA pools. Permutation settings included 10 000 iterations. Because the haplotype permutation match test implements a subsampling strategy, populations smaller or similar in size to the ancient Norwegian sample, such as the Swedish Saami and the population of Skye, were collapsed with related populations (Norwegian Saami and Western Isles, respectively) for the purpose of the analyses. The results of HS were visualized using R v. 2.8.1 [33].

3. Results

We obtained mtDNA sequences from 69 of the 80 skeletons sampled. The sequences of the five short mtDNA amplicons were assembled into 341 bp fragments spanning nucleotide positions 16 051–16 391. Of the 69 individual sequences, 13 produced inconsistent amplicons, whereas a further 11 were not supported by the *c*-statistic, and were therefore excluded from further analyses (even though several had a recognizable mtDNA haplogroup, see the electronic supplementary material). The remaining 45 sequences were accepted as genuine ancient sequences based on the patterns of cytosine deamination damage, and the application of the *c*-statistic. The ‘successful’ bone samples had been excavated on average 10 years more recently than the ‘unsuccessful’ ones, indicating that length of storage is an important factor for the ability to recover useful DNA from archival bone samples.

After haplogroup (Hg) assignment, the 45 ancient Norwegians were shown to carry all major mtDNA haplogroups present in Norway today at frequencies higher than 1%, with the exception of Hg W*. A comparison of the haplogroup frequencies of the ancient and modern Norway datasets using a two-tailed *t*-test with unequal variance showed no statistically significant difference ($p = 0.99$) in the overall frequency distribution of haplogroups. However, we observed lower frequencies of Hg H* and T* in the ancient Norwegians, compared with the present-day Norwegians, as well as higher frequencies of Hg K*, Hg I*, Hg V* and Hg U* (table 1).

Haplotype-sharing analysis revealed that the ancient Norwegians shared the largest number of haplotypes with modern Norway, Shetland, Orkney, France and England (table 2 and figure 2). Conversely, the haplotype-sharing permutation test yielded statistically significant *p*-values ($p \leq 0.01$) for the matching probability between ancient Norwegians and present-day individuals from England, Scotland, Germany, France and Sweden, but not Norway, Shetland or Orkney (table 2). The haplotype match test revealed that ancient Norwegians and Icelanders were closer to each other than to their respective descendant populations.

The pairwise F_{ST} values (table 2) show that the ancient Norwegians are closest to the modern inhabitants of Norway,

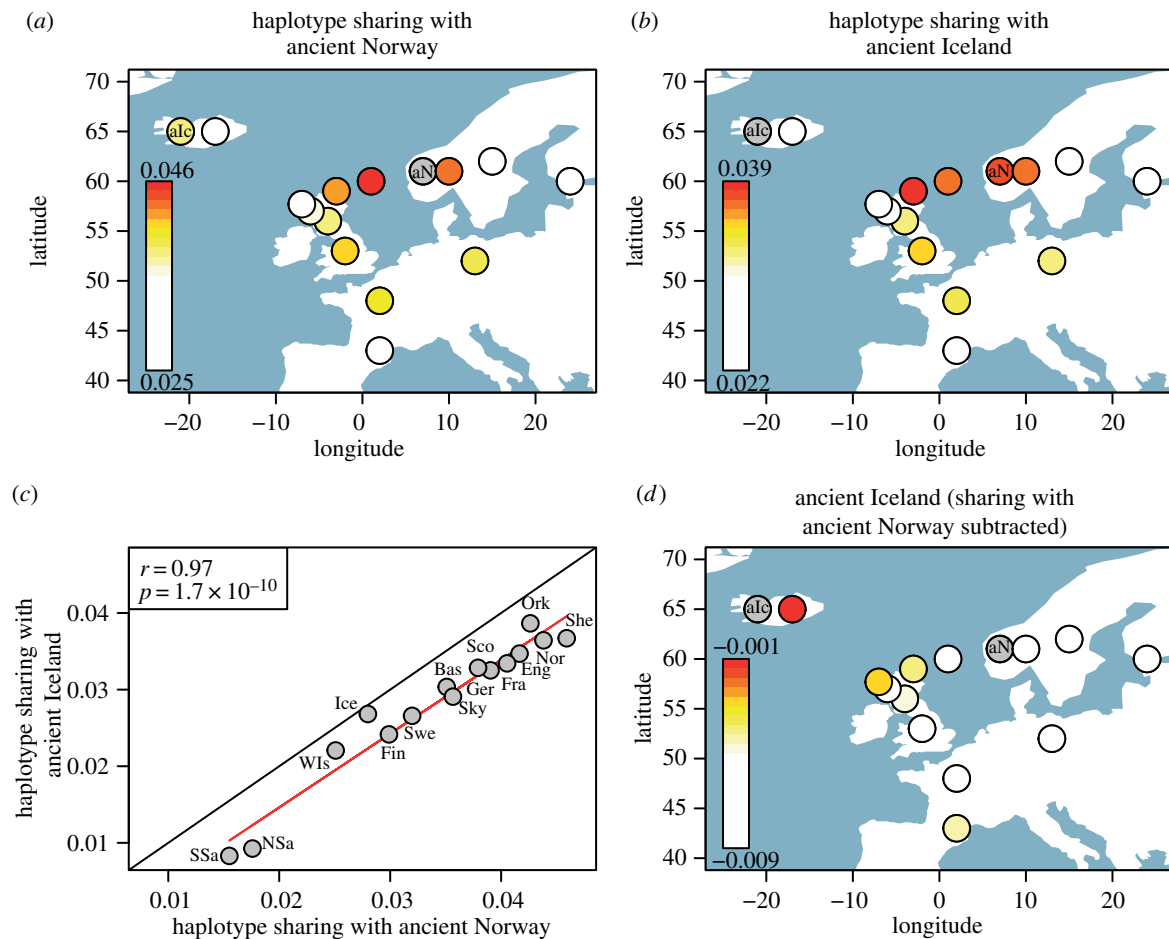


Figure 2. Haplotype sharing (HS) between ancient Norway and Iceland and 15 populations from the North Atlantic region. (a) Heat map of haplotype-sharing values for ancient Norway and the comparison dataset. (b) Heat map of haplotype sharing for ancient Iceland and the comparison dataset. (c) Scatter plot of haplotype-sharing values for ancient Iceland/ancient Norway and the comparison dataset. (d) Heat map of haplotype sharing for ancient Iceland with the value for sharing with ancient Norway subtracted for each population. The legend colours represent the observed HS value of haplotype sharing for each population.

Table 1. Mitochondrial DNA haplotype frequencies (frequency, % and number of observed instances, *N*, in *italics*) in ancient and present-day Norwegians.

sample <i>N</i>	haplogroup frequency in (% , <i>N</i>)										
	H	HV	I	J	K	N	T	U	V	W	other
Norway	37.5	3.6	1.7	15	5.5	1	8.5	17.9	0.5	1.8	7.1
838	314	30	14	126	46	8	71	150	4	15	60
aNorway	34.8	7	4.6	13.9	9.3	0	2.3	20.9	4.6	0	2.3
43	15	3	2	6	4	0	1	9	2	0	1

Germany, England, Orkney and France. The NMDS plot (stress value = 0.1438) of the F_{ST} values for 15 pairs of populations placed ancient Norway at the centre, closest to ancient Iceland, Norway, Sweden, Germany, Scotland, England and France (figure 3). The Saami were outliers in the initial NMDS analyses, and were therefore removed from the final analysis.

We identified two cases of possible maternal kinship in multiple and neighbouring burials. The first case involved two individuals (A5864A and A5864B) with the reference sequence (rCRS) buried in the same grave at Flakstad, Lofoten, Nordland. The second case involved two skeletons from Herøy, Sandnessjøen, Nordland (A5316 and A5317), carriers of Hg J*, characterized by substitutions 16 069T–16 126C–16

193T–16 278T (possibly Hg J1d or J2b). Less than 0.1% of people worldwide are known to belong to this haplotype, suggesting the two individuals were related [31]. Interestingly, isotope analyses of the two Flakstad individuals (A5864A and A5864B) suggested they were unrelated, as they consumed different diets and were probably from different social strata [47]. For the purposes of the statistical analyses, to avoid overrepresentation of lineages owing to potential family relationship, the duplicate sequences were removed. This left 43 individual sequences, representing 34 mtDNA haplotypes. Twenty-four of these were detected in our modern mtDNA database (5191 Europeans). Nine matches were identified in two larger worldwide databases [31,32]. Only one

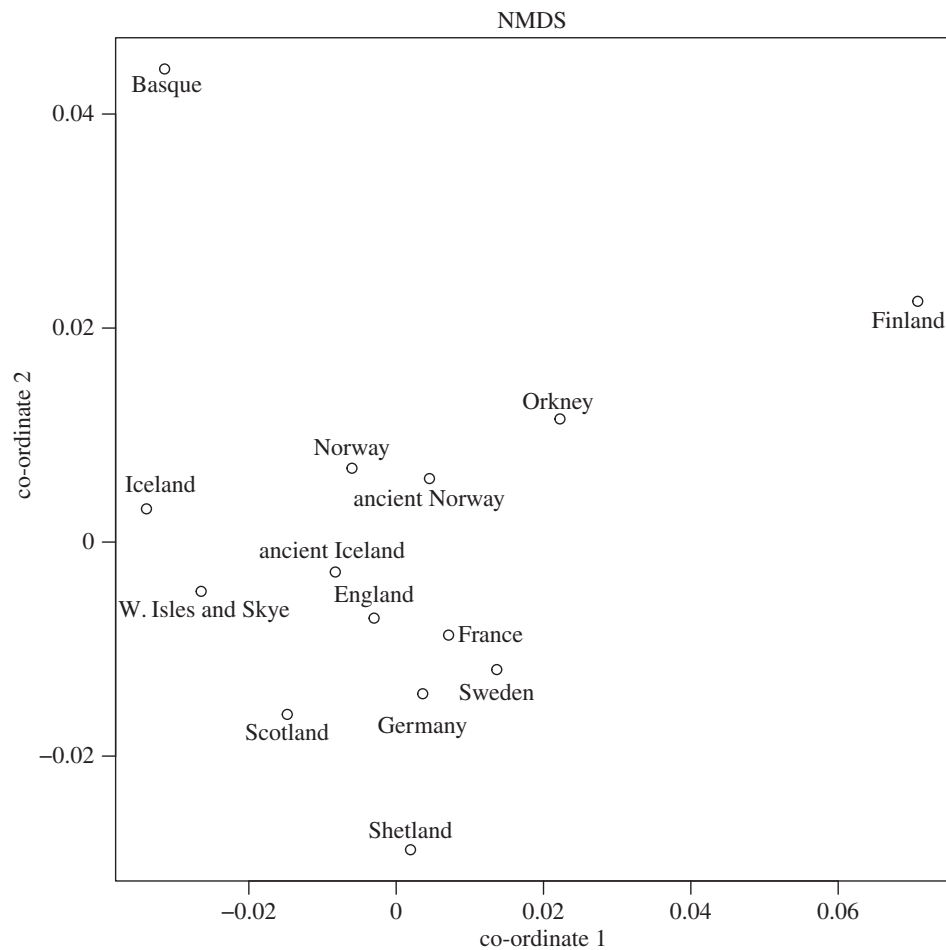


Figure 3. NMDS plot of interpopulation pairwise F_{ST} values calculated from mtDNA HVR1 control-region sequence data (stress value = 0.1438). The F_{ST} values were calculated according to the Tamura–Nei model, with a gamma distribution of 0.26. Reference data were from previously published studies [7,8,16,40–46].

Table 2. Mitochondrial DNA diversity and haplotype match probabilities in ancient Norwegians and North European populations. (N , number of individuals; k , number of haplotypes observed; HP, haplotype-sharing permutation p -value; HS, exact haplotype sharing; N_m , number of exact haplotype matches between the ancient Norwegians (aNorway) and the comparison dataset.)

sample ID	N	k	k/N	N_m	comparisons with ancient Norway (16 051–16 391)		
					HP p -value	HS	F_{ST}
Basque	110	44	0.4	4	0.0000	0.0351	0.0089
England	139	93	0.669	7	0.5485	0.0417	0.0021
Finland	403	101	0.251	11	0.0000	0.0299	0.0114
France	868	370	0.426	14	0.0498	0.0405	0.0018
Germany	109	70	0.642	8	0.1940	0.0390	–0.0004
Iceland	550	129	0.235	14	0.0000	0.0280	0.0067
aIceland	68	48	0.706	8	0.5009	0.0376	–0.0048
Norway	838	282	0.337	14	0.0031	0.0438	–0.0022
aNorway	43	34	0.791	34	—	—	—
Orkney	78	38	0.487	7	0.0067	0.0426	–0.0010
Saami	236	17	0.072	3	0.0027	0.0165	0.2180
Scotland	839	281	0.335	17	0.0267	0.0379	0.0036
Shetland	502	175	0.349	12	0.0011	0.0459	0.0022
Sweden	296	167	0.564	11	0.0136	0.0320	0.0025
W. Isles and Skye	223	97	0.435	13	0.0011	0.0304	0.0068

haplotype (individual A5863B: 16 153A–16 189C–16 304C) was not found among living individuals.

Two female skeletons, from Nordland and Nord-Trøndelag, respectively, carried rare haplotypes, namely 16 144C–16 148T–16 189C–16 270T–16 335G (Hg U5b1b1) and 16 188T–16 189C–16 223T–16 290T–16 319A–16 356C–16 362C (possibly Hg A4b). The polymorphisms detected in the former are sometimes referred to as the ‘Saami motif’, so far only described in Saami [48], whereas the latter sequence is a Central Asian lineage present in Europe at a frequency of less than 0.2% [7,49].

4. Discussion

In this study, we recovered informative DNA sequences from a relatively large number of skeletal remains of considerable antiquity (about 1000 years old), excavated several decades ago, and handled by anthropologists without precautions to avoid contamination, such as gloves or facial masks. By examining the extent of damage in the ancient sequences, we were able to discriminate between genuine ancient DNA sequences and more recent contamination. Starting with 80 skeletal samples, we recovered authentic mtDNA sequences from 45 Norwegians from the Late Iron Age, contemporary with the Viking expansion. While it is important to remember that the individuals did not necessarily live at the same time, and could have been separated by several centuries, this is the single largest ancient DNA sample-set representing the past population of Norway. For the purposes of this study, we have regarded the individuals as a single population to help understand the affinities of the ancient Norwegians to present-day peoples of the North Atlantic region.

There was little difference between our Late Iron Age Norway and the reference North Atlantic populations, and no clear variation patterns were detected. Despite this, some of our analyses, such as the haplotype-sharing permutation test and to some extent the pairwise F_{ST} values, indicated close affinities between ancient Norwegians and Icelanders, supporting the view of their common origin. Both the ancient Norwegians and Icelanders also appear less likely to share a common origin with present-day Norwegians, than with the English, Scots, Germans and French. This is possibly a consequence of the demographic changes which occurred in Norway during the last millennium, including the population collapse during the Black Death.

By contrast, both the ancient Norwegians and ancient Icelanders shared most maternal lineages with living people in Norway, Orkney and Shetland (figure 2), in agreement with historical and archaeological information on these populations. The observed discrepancies between the two estimates probably reflect the effects of genetic drift and lineage differentiation in the comparative small populations of Norway and Iceland in the intervening 1000 years [8,16,40], whereas the populations of England, Scotland, Germany and France had much larger populations during the Middle Ages (more than 500 000 in AD 1000 and one million in AD 1500) [50], and were better reservoirs of ancient lineages. The similarity of both ancient Norwegians and Icelanders to the present-day Scots may be explained by the three centuries of Viking influence in Scotland, starting with raids in the late-eighth century, and followed by colonization, cultural assimilation and incorporation of Norse mtDNA lineages

into the gene pool of the British Isles [51]. Our findings suggest that while the haplotype-sharing estimate may pick up signals of human dispersals in the North Atlantic region (e.g. the close relationships between ancient Norwegians and Icelanders, modern Shetlanders, Orkney Islanders, English, French and Norwegians), the haplotype-sharing permutation test is better suited to understand post-colonization population changes, and highlights the affinities between ancient Norwegians and Icelanders to the present-day populations of England, France and Germany [16].

Mutual affinities were illustrated by the NMDS plot of pairwise F_{ST} values, which shows that the ancient Norwegians are close to the modern Norwegians, Swedes, English, French, Scots and Germans as well as the ancient Icelanders (figure 3). However, it should be noted that the p -values for these F_{ST} estimates were rarely significant (electronic supplementary material, table S5). Previous studies have demonstrated close affinities between Norwegian and German mtDNAs [7,52], but we are the first, to the best of our knowledge, to show a close relationship between ancient Norwegian and ancient Icelandic mtDNAs. Our exact haplotype-sharing analyses revealed signals of Norse female ancestry in Iceland, whereas the haplotype-sharing permutation test indicated a high probability that the two groups shared a source population (table 2). To identify other contributions of female lineages to the ancient Icelandic gene pool, the ancient Norway haplotype-sharing values were subtracted from those of ancient Iceland (figure 2d). This revealed Orkney and the Western Isles as important outliers, with more haplotypes shared with the ancient Icelanders than expected from their sharing with ancient Norwegians, unsurprisingly perhaps, as both locations have a history of Norwegian Viking colonization and settlement.

Iceland was settled mainly from Norway and the British Isles after AD 870. While a large proportion of the settlers from Britain and Ireland were Gaelic, others were probably Scandinavians raised in Viking colonies [1]. Close affinities between ancient Norwegians and living Britons suggest that a proportion of present-day British mtDNA lineages are of Norse origin. Close affinities between ancient Icelanders and the inhabitants of Orkney and the Western Isles could potentially reflect genetic influences from Norse colonists (figure 2). A recent reanalysis of historical data suggested that Norse males often married in Scandinavia [53]. Our findings suggest Norse women may have been involved in the colonization of new territories during the Early Middle Ages, and made contributions to the genetic makeup of the populations of the North Atlantic region.

Comparisons between the ancient and present-day Norwegians revealed several genetic differences, such as changes in haplogroup frequencies (Hg: H*, I*, K*, T*, V* and U*), in agreement with previously published findings in other parts of Scandinavia. Although the sample size was smaller than several modern datasets, and the skeletal material was undoubtedly subjected to unequal taphonomic processes, the dataset is large enough to broadly reflect the situation in Late Iron Age Norway. A comparison of ancient and modern Norwegian datasets using a two-tailed t -test with unequal variance showed no statistically significant difference ($p = 0.99$) in the overall frequency distribution of haplogroups. Nevertheless, the change in the frequency of haplogroups I* and K* is noteworthy. Previous analyses of ancient Scandinavians suggested the Hg I* was an ‘ancient Scandinavian’ haplogroup

[54]. In our Iron Age Norwegians, this haplogroup has a frequency of almost 5%, lower than that observed in ancient Denmark (13%) [55], but higher than the frequency of less than 2% for Hg I* in people today. The change in frequency of Hg K* was even more marked in our dataset: we saw a reduction from 9.3% in ancient to 5.5% in modern Norwegians, compared with 4.7% in ancient Denmark [55–58]. Hg K* may be an ancient Scandinavian signature because its frequency in ancient Icelanders was 13%. Hg K* is thought to have arrived in Europe with Neolithic farmers and has been detected in Europe since at least 5500 BC [59], but it exhibits significant frequency variation throughout Europe [60] and may be difficult to explain in an historical context.

One ancient haplotype (A5863B: 16 153A–16 189C–16 304C) belonging to Hg H* was not found among modern individuals, although a number of close haplotype matches, differing at one polymorphic site, were identified in the comparison databases. A5863B may be an extinct or rare mtDNA lineage. Another individual, an adult female discovered in 1942 in Vevelstad, Helgeland, Nordland (A4448), had a sequence characteristic of Hg U5b1b1, sometimes referred to as the ‘Saami motif’ (16 144C–16 148T–16 189C–16 270T–16 335G) [48]. The skeleton was classified as Norse based on the associated archaeological findings, namely a burial mound and an axe. The skeleton could represent a secondary burial in the barrow. Mound and cairn burials with grave goods, often including weapons, were characteristic of the Norse tradition, whereas Saami burials were typically cremations or scree burials with birch-bark shrouds and faunal remains [61]. This find exemplifies some of the problems encountered when working on museum collections with poor documentation or archaeological context, which may lead to interpretation errors. In this case, the individual may have been from a secondary Saami burial in a Norse mound, a sacrificial victim or an individual of Saami origin buried according to Norse custom. The latter scenario is plausible, because Norse and Saami coexisted for centuries, and archaeological and historical evidence suggests that intermarriage was a common practice, especially among the elite [61]. This could be clarified by direct radiocarbon dating of the sample.

One individual with an exotic haplotype (A3705) was a woman found in 1927 in Nærøy municipality, Nord-Trøndelag, with an mtDNA lineage likely to belong to Hg A*. She was buried with many well-preserved objects, typical of a Norse burial. Hg A* is widespread in Asia [62] and constitutes one of four major founding mtDNA lineages of the Americas, but is rare in Europe, and observed in less than 0.2% of modern Scandinavians [7]. The haplogroup is more common in the Black Sea region, and was reported in the

Turkish population at a frequency nearing 7% [63]. It is not inconceivable that this haplogroup may reflect Viking connections to Russia and Byzantium [5,64]. A recent study has shown that Mesolithic and Early Metal Age individuals from northeast Europe carried central/east Siberian mtDNA lineages (C, D and Z), suggesting extensive gene-flow from Siberia during prehistory [65]. However, none of the reported lineages was Hg A*, suggesting the haplogroup arrived in Scandinavia at a later date.

In conclusion, the Viking Age population of Norway was diverse, cosmopolitan and genetically similar to ancient Icelanders, and to modern Scandinavians, as well as western Europeans, in particular English, French, Germans and Scots. Our results suggests that some ancient Scandinavian mtDNA lineages may have persisted in the descendants of Viking colonists in England and Scotland owing to larger population sizes and reduced effects of genetic drift. The higher proportion of mtDNA lineages shared between our ancient dataset and the Orkneys and Shetlands implies women in Late Iron Age Scandinavia were actively involved in the settlement of new lands. While undoubtedly more ancient mtDNA data are needed from the Baltic countries, North Atlantic islands and the British Isles to clarify the patterns of human mobility during the Viking Age, the presented study demonstrates how recent methods of DNA sequencing and bioinformatics analysis can be applied to the study of DNA from bones stored in museum collections. Such tools will facilitate future studies on ancient populations with larger sample sizes and greater genetic resolution.

Data accessibility. The ancient mtDNA sequences reported here were deposited in GenBank under the following accession numbers: KM656396–KM656451.

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