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Phylogeographic history of mitochondrial haplogroup J in Scandinavia

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Abstract

Background: Mitochondrial DNA haplogroup J is the third most frequent haplogroup in modern-day Scandinavia, although it did not originate there. To infer the genetic history of haplogroup J in Scandinavia, we examined worldwide mitogenome sequences using a maximum-likelihood phylogenetic approach.

Methods: Haplogroup J mitogenome sequences were gathered from GenBank ($n = 2245$) and aligned against the ancestral Reconstructed Sapiens Reference Sequence. We also analyzed haplogroup J Viking Age sequences from the European Nucleotide Archive ($n = 54$). Genetic distances were estimated from these data and projected onto a maximum likelihood rooted phylogenetic tree to analyze clustering and branching dates.

Results: Haplogroup J originated approximately 42.6 kya (95% CI: 30.0–64.7), with several of its earliest branches being found within the Arabian Peninsula and Northern Africa. J1b was found most frequently in the Near East and Arabian Peninsula, while J1c occurred most frequently in Europe. Based on phylogenetic dating, subhaplogroup J1c has its early roots in the Mediterranean and Western Balkans. Otherwise, the majority of the branches found in Scandinavia are younger than those seen elsewhere, indicating that haplogroup J dispersed relatively recently into Northern Europe, most plausibly with Neolithic farmers.

Conclusions: Haplogroup J appeared when Scandinavia was transitioning to agriculture over 6 kya, with J1c being the most common lineage there today. Changes in the distribution of haplogroup J mtDNAs were likely driven by the expansion of farming from West Asia into Southern Europe, followed by a later expansion into Scandinavia, with other J subhaplogroups appearing among Scandinavian groups as early as the Viking Age.

KEYWORDS
haplotype, lineage, migration, mtDNA, phylogeny

Abbreviations: calBP, calibrated years before present; kya, thousand years ago; MDS, multidimensional scaling; ML, maximum likelihood; mtDNA, mitochondrial DNA; RSRS, reconstructed sapiens reference sequence.

1 | INTRODUCTION

Early mtDNA studies revealed that European and Near Eastern populations shared a common ancestry based on the high frequency of major maternal genetic lineages present in both populations (Torroni et al., 1996, 2006). These nine major mtDNA lineages, specifically, haplogroups H, I, J, K, T, U, V, W, and X, were relatively rare among Africans and Asian populations (Torroni et al., 1996, 2006). The dispersal of these major nine lineages is thought to have begun during a warm period in Europe ~40–50 thousand years ago (kya) known as the Greenland Interstadial-12 (Hublin, 2012; Müller et al., 2011), after which they dramatically expanded into the Last Glacial Maximum (Fernandes et al., 2012; Soares et al., 2010). Over many thousand years, the proportions of the nine major lineages in populations from these regions have changed. Today, haplogroup V and some branches of U are more common in Northern Europe, while haplogroups HV and X are found at higher frequencies in the Near East (Achilli et al., 2007; Reidla et al., 2003; Simoni et al., 2000).

Of these lineages, haplogroup J has a relatively uniform distribution across Europe and the Near East, making up about 6%–22% of the mtDNAs in modern populations from these regions (Kristjansson et al., 2021; Lappalainen et al., 2009; Lembring et al., 2013; Pliss et al., 2006; Simoni et al., 2000; Vidrová et al., 2008). More specifically, haplogroup J is found at a moderate frequency among the English and Welsh (15.2%–21.7%) in Western Europe (Richards et al., 1996; Richards et al., 2000), while its frequencies among Mazandarani populations near the Caspian Sea and the Iraqi population in the East are between 15% and 18% (Al-Zahery et al., 2003; Metspalu et al., 2004; Quintana-Murci et al., 2004; Richards et al., 2000). In Scandinavia, the frequency of haplogroup J is 13% in Norway (Kristjansson et al., 2021), up to 17.6% in parts of Sweden (Lappalainen et al., 2009), and 10.1% in Denmark (Bybjerg-Grauholm et al., 2018). This pattern raises questions about the factors that shaped the distribution of haplogroup J in this part of the world.

Haplogroup J mtDNAs have been found among early human remains in Scandinavia (Bramanti et al., 2009; Malmström et al., 2015) and may be due to the arrival of Neolithic farmers, the earliest evidence of which is about six kya (Malmer, 2002). For millennia, genetically distinct Neolithic farmers and local Scandinavian hunter-gatherers co-existed (Malmström et al., 2015), differing in that farmers cultivated crops and managed husbandry year-round instead of sporadically (Fischer & Nordvik, 1987; Sørensen & Karg, 2014). Genomic admixture between hunter-gatherers and early Neolithic farmers occurred in Sweden at around five kya (Skoglund et al., 2014), suggesting that Scandinavian hunter-gatherers had been partially assimilated into agricultural communities before agriculture became the predominant subsistence strategy in Scandinavia (Skoglund et al., 2012). The Battle Ax Culture, which emerged roughly a thousand years later, had genetic ancestry that traced back to both Scandinavian hunter-gatherers and Early Neolithic farmers (Malmström et al., 2019). Based on this prehistoric evidence of migrations, it is likely that haplogroup J reached Scandinavia later than the rest of Europe.

The expansion of Viking populations in the 10th and 11th centuries may have further shaped the distribution of haplogroup J in northern Europe. Women have been cited as important agents in the Viking expansions as settlers both inside and outside Scandinavian borders (Goodacre et al., 2005; Krzewińska et al., 2015). Based on archaeological evidence, the Vikings often incorporated non-Scandinavian individuals into their populations (Krzewińska, 2014), and established several satellite communities outside of Scandinavia that persisted until the end of the Viking Age in the 11th century CE (Downham, 2012). Graves found in England, Continental Europe, and eastern areas of Viking expansions (Androshchuk, 2005; Halsall, 2000; Price, 2008) included traditional Viking burial gifts (Lund, 2005, 2008, 2017) and genetic analysis suggests that several of these foreign graves contained individuals with Norse ancestry (Margaryan et al., 2020). Within Scandinavia, genetic evidence suggests that individuals who assimilated into Viking culture were also given Viking burials, as the mtDNA haplogroups found for these individuals were uncommon among individuals with Norse ancestry (Krzewińska et al., 2015).

Furthermore, a study of mtDNA diversity in Viking Age populations from Norway (Krzewińska et al., 2015) dating between 793 and 1066 CE indicated that haplogroup J was present at a frequency of 13.9%. This frequency is quite similar to that seen in modern-day Scandinavian populations, despite statistical differences in the frequencies of other haplogroups (Krzewińska et al., 2015). Today, haplogroup J is currently the third most common maternal lineage in Norway (Kristjansson et al., 2021), and, overall, the fourth most common in Sweden (Simoni et al., 2000) and modern-day Europe (Rishishwar & Jordan, 2017; Simoni et al., 2000).

This intriguing distribution of haplogroup J coupled with the gap in knowledge regarding the dispersal of haplogroup J along migrations routes with respect to Scandinavia motivated an exploration of the pattern of genomic variation in haplogroup J and the timing of its dispersal into Scandinavia. Thus, in this study, we investigated haplogroup J diversity, considering the genetic and archaeological evidence for human settlement of Scandinavia, in an effort to gain insights into the demographic and evolutionary history of this maternal lineage within Scandinavian populations.

2 | MATERIALS AND METHODS

2.1 | Mitogenome sequences

Haplogroup J mitogenome sequences were retrieved from GenBank ($n = 2245$) (accessed on December 15, 2021) using accession numbers found in MTree (YFull, 2021). Since the geographic focus of this study was Scandinavia, we also included haplogroup J data from Viking Age graves (here called "Viking Burial Sites") available in the European Nucleotide Archive under accession number PRJEB37976 ($n = 55$). Specific information about the ethnicity or original location of the individuals was available for 2094 (91.0%) sequences in the total data set. A total of 2153 of the sequences derived from modern-day (93.7%) populations, while 147 sequences (6.4%) came from archaeological populations.

Relevant information regarding the time periods and civilization/cultures for the ancient sequences is provided in Table S1.

2.2 | Mitogenome analyses

2.2.1 | Haplogroup identification

We assigned specific haplogroups to each mitogenome sequence using the mtDNA haplogroup classification tool Haplogrep, version 2.1.21 (Weissensteiner et al., 2016). Haplogrep computes haplogroup classifications on pre-calculated phylogenetic weights that correspond to the occurrence of a polymorphism per position in Phylotree Build 17 (van Oven & Kayser, 2009), which, in turn, reflects the mutational stability of a variant. Mutations were identified relative to the Reconstructed Sapiens Reference Sequence (RSRS) (Behar et al., 2012), which enables a reference point for human mtDNA haplogroups from the perspective of an early human ancestral root.

2.2.2 | Phylogenetic analysis

All of the mitogenome sequences were aligned using MAFFT v.7 (Katoh & Standley, 2013). To make evolutionary inferences, a maximum-likelihood (ML) phylogenetic tree was constructed with the software IQ-tree v.1.6.12 using 2000 ultrafast bootstrap repetitions to assess node support with 10,000 iterations for replicates (Nguyen et al., 2015). Branch support was achieved by the approximate likelihood ratio test (aLRT) (Anisimova & Gascuel, 2006). The phylogeny was constructed under the best-fitting nucleotide substitution model inferred by jModelTest (Darriba et al., 2012; Guindon & Gascuel, 2003), which was TIM3 + F + R4 based on the Bayesian Information Criterion (BIC). The phylogenetic tree was visualized in FigTree v.1.4.4 (Rambaut, 2016).

To determine whether there was sufficient temporal structure to estimate divergence times, we used TempEst v.1.5.1 to perform a regression of root-to-tip genetic distances against year of sampling (Rambaut et al., 2016). Estimates of divergence times with 95% confidence intervals were calculated for different branches of haplogroup J using the Least Squares Dating IQ-tree plugin (To et al., 2016), which uses the maximum-likelihood tree as input.

To calibrate these estimates, we used calibrated C^{14} dates for ancient samples bearing J mtDNAs listed in Table S1. A z-score threshold of two standard deviations was used to exclude outliers. Long branches that could cause biased date estimates, such as those including the Viking Burial Site sequences, which collectively contain a high proportion of contamination in specific regions (Margaryan et al., 2020), were excluded from the dating analysis.

2.3 | Statistical analysis

An analysis of molecular variance (AMOVA) using Arlequin v.3.5.2.2 (Excoffier & Lischer, 2010) and R version 3.6.3 (RStudio Team., 2020) was carried out to evaluate the genetic differentiation of the haplogroup J sequences in the study populations. To assess pairwise differences between ethnic or linguistic groups, fixation indices (F*st*) and their respective *p*-values were estimated by permutation analysis (10,000 permutations). We assumed a Tamura-Nei (1993) model with a gamma distribution of 0.26 to account for differences in substitution rate between nucleotides and the inequality of nucleotide frequencies. The structuring of mtDNA sequence diversity by geography was assessed through the analysis of F*st* values using Multidimensional Scaling (MDS) and the PAST v.2.17b software (Hammer et al., 2001).

The Viking Burial Site sequences were substantially different from the haplogroup J sequences in the rest of the data set due to missing data in the coding region. The distinction of the Viking burials was likely due to modern mtDNA contamination described by Margaryan et al. (2020), who reported uncommon polymorphisms in regions of missing nucleotides within the coding region due to diagenetic damaging nucleotides in these sequences. Thus, to utilize these sequences as accurately as possible, we restricted the AMOVA analyses of these sequences to only the non-coding region.

Comparisons of regional differences in haplogroup distribution were conducted using the following definitions based on geography: Sub-Saharan Africa (Uganda, Tanzania), Northern Africa (Morocco, Tunisia, Algeria, and Egypt), Arabian Peninsula (Yemen, Saudi Arabia, Kuwait, United Arab Emirates), Near East (Lebanon, Syria, Iraq, Iran, Israel, Palestinian territories), Southern Caucasus (Armenia, Azerbaijan, Georgia), Central Asia (Tajikistan, Kyrgyzstan, Kazakhstan), Southern Asia (Afghanistan, Pakistan, India), Eastern Asia (Uyghurs, Mongolia, Oroqen), Siberia (Evenks, Buryat, Yakut, Khanty, Mansi), Eastern Europe (Russia west of Ural Mountains, Bulgaria, Ukraine, Belarus, Moldova), Western Balkans (Croatia, Bosnia and Herzegovina, Albania, Serbia), Central Europe (Czechia, Hungary, Romania, Slovakia, Poland, Romani), Baltic (Estonia, Latvia, Lithuania), Finland (Finland), Scandinavia (Norway, Sweden, Denmark), Mediterranean (Italy including Sardinia, France, Greece, Cyprus, Turkey), Iberian Peninsula (Spain, Portugal), Western Europe (Netherlands, Germany, Switzerland, Hutterite populations, Austria), and British Isles (United Kingdom, Ireland). Comparisons of statistical differences of haplogroup frequencies between larger regions were conducted using a Chi-squared test or Fisher's exact test, where appropriate.

3 | RESULTS

3.1 | Haplogroup J distribution

Overall, 93.6% of the 2300 haplogroup J sequences came from modern-day populations while the rest (6.4%) came from archaeological individuals dating from the Eurasian Neolithic to the Early Modern period (Table 1). The sequence from the earliest archaeological source found in this study was dated to 9.4–9.0 kya in Iran (Pereira et al., 2005). Geographically speaking, haplogroup J sequences were found in the Mediterranean region (25.2%; $n = 579$), Scandinavia (15.1%; $n = 307$), the Iberian Peninsula (7.0%; $n = 162$), the Near East

(3.4%; $n = 109$), and the British Isles (4.7%; $n = 109$), whereas very few came from Sub-Saharan Africa (0.1%). These frequencies are consistent with those reported in previously published studies, which show that Great Britain, Iran, Iraq, Italy, Norway, and Iceland have some of the highest frequencies of haplogroup J observed today (Al-Zahery et al., 2003; Côrte-Real et al., 1996; Goodacre et al., 2005; Quintana-Murci et al., 2004; Richards et al., 2000; Sajantila et al., 1996). The Baltic countries of Estonia, Latvia, and Lithuania, whose populations have ~4.2%–6.4% haplogroup J mtDNAs (Kasperavičiute et al., 2004; Pliss et al., 2006; Sajantila et al., 1995) could not be represented adequately using the data analyzed in this study.

TABLE 1 Description of haplogroup J mtDNA samples ($n = 2300$)

	n	%
Time period		
10,000–3301 BCE (Eurasian Neolithic Age)	4	0.2
3300–1301 BCE (Bronze Age)	26	1.1
1300–601 BCE (Iron Age)	12	0.5
600 BCE–476 CE (ClassicalEra)	12	0.5
477–1000 CE (Early Middle Ages)	32	1.4
1001–1250 CE (High Middle Ages)	34	1.5
1251–1450 CE (Late Middle Ages)	23	1.0
1451–1750 CE (Early Modern Era)	4	0.2
1750 CE to present (Modern Era)	2153	93.6
Geographic region		
Populations with specific labels[a]		
British Isles	109	4.7
West Europe	64	2.8
Iberian Peninsula	161	7.0
Mediterranean	579	25.2
Scandinavia	349	15.2
Finland	60	2.6
Baltic	10	0.4
Central Europe	142	6.2
Western Balkans	27	1.2
Eastern Europe	100	4.3
Siberia	15	0.7
East Asia	20	0.9
South Asia	17	0.7
Central Asia	37	1.6
South Caucasus	55	2.4
Near East	110	4.8
Arabian Peninsula	84	3.7
North Africa	37	1.6
Sub-Saharan Africa	3	0.1
Populations with unspecific or admixture label description		
Latin America (Brazil, Paraguay, self-identified Hispanic)	10	0.4
Unknown	206	9.0
United States	3	0.1
Admixed populations	16	0.7
Europe, unspecified	80	3.5
South African (Caucasian)	6	0.3
J subclades		
J	1	0.04
J1	3	0.1
J2a	306	13.3
J2b	345	15.0
J1d	92	4.0
J1b	369	16.0
J1c	1184	51.5

[a]Geographical regions are defined as follows: Sub-Saharan Africa (Uganda, Tanzania), Northern Africa (Morocco, Tunisia, Algeria, and Egypt), Arabian Peninsula (Yemen, Saudi Arabia, Kuwait, United Arab Emirates), Near East (Lebanon, Syria, Iraq, Iran, Israel, Palestinian territories), South Caucasus (Armenia, Azerbaijan, Georgia), Central Asia (Tajikistan, Kyrgyzstan, Kazakhstan), South Asia (Afghanistan, Pakistan, India), Eastern Asia (China, Mongolia, Oroqen), Siberia (Evenks, Buryat, Yakut, Khanty, Mansi), Eastern Europe (Russia west of Ural Mountains, Bulgaria, Ukraine, Belarus, Moldova), Western Balkans (Croatia, Bosnia and Herzegovina, Albania, Serbia), Central Europe (Czechia, Hungary, Romania, Slovakia, Poland), Baltic (Estonia, Latvia, Lithuania), Scandinavia (Norway, Sweden, Denmark), Mediterranean (Italy incl. Sardinia, France, Greece, Cyprus, Turkey), Iberian Peninsula (Spain, Portugal), Western Europe (Netherlands, Germany, Switzerland, Hutterite populations, Austria), British Isles (United Kingdom, Ireland).

Globally, most sequences in the data set belonged to subhaplogroup J1c (51.5%), followed by J1b (16.0%), and J2b (15.0%). The distribution of these subhaplogroups by region is shown in Table S2. Each of the major 3-digit J subhaplogroups were found within both Europe and Asia, although there were some notable regional differences (Figure 1). J1c comprised over half of the J mtDNAs found within Europe, while it comprised less than 20% of these mtDNAs in the Near East and Arabian Peninsula ($\chi^2 = 38.0$; $p < 0.001$). By contrast, subhaplogroup J1b comprised at least 30% of the J mtDNAs in continental Asia but occurred at a very low frequency in continental Europe ($\chi^2 = 278.3$; $p < 0.001$). J1d seemed to follow a similar pattern to that of J1b ($\chi^2 = 195.5$; $p < 0.001$).

There were notable differences in the distributions of subhaplogroup J2a within Asia. J2a represented nearly 30% of the J mtDNAs in the Near East and Arabian Peninsula, but less than 10% in the Near East, and was absent in South Asia and Iran ($\chi^2 = 5.3$; $p = 0.02$). J2b was also more common in South Asia compared to the rest of Asia ($\chi^2 = 14.1$; $p < 0.001$). Situated between the Near East and Central/South Asia, Iran had a J1b distribution similar to populations in the Arabian Peninsula but lacked J2a mtDNAs, which was similar to the lack of J2a found among South Asian groups.

With respect to ancient populations, the Viking Burial Sites contained a significantly higher frequency of J1b mtDNAs (21.8% to 11.4%, respectively; [$\chi^2 = 4.3$; $p = 0.04$]) and J2b (12.7% to 3.6%, respectively; [$\chi^2 = 7.0$; $p = 0.008$]) compared with modern-day Scandinavians. Notably, over 70% of the modern-day Scandinavian

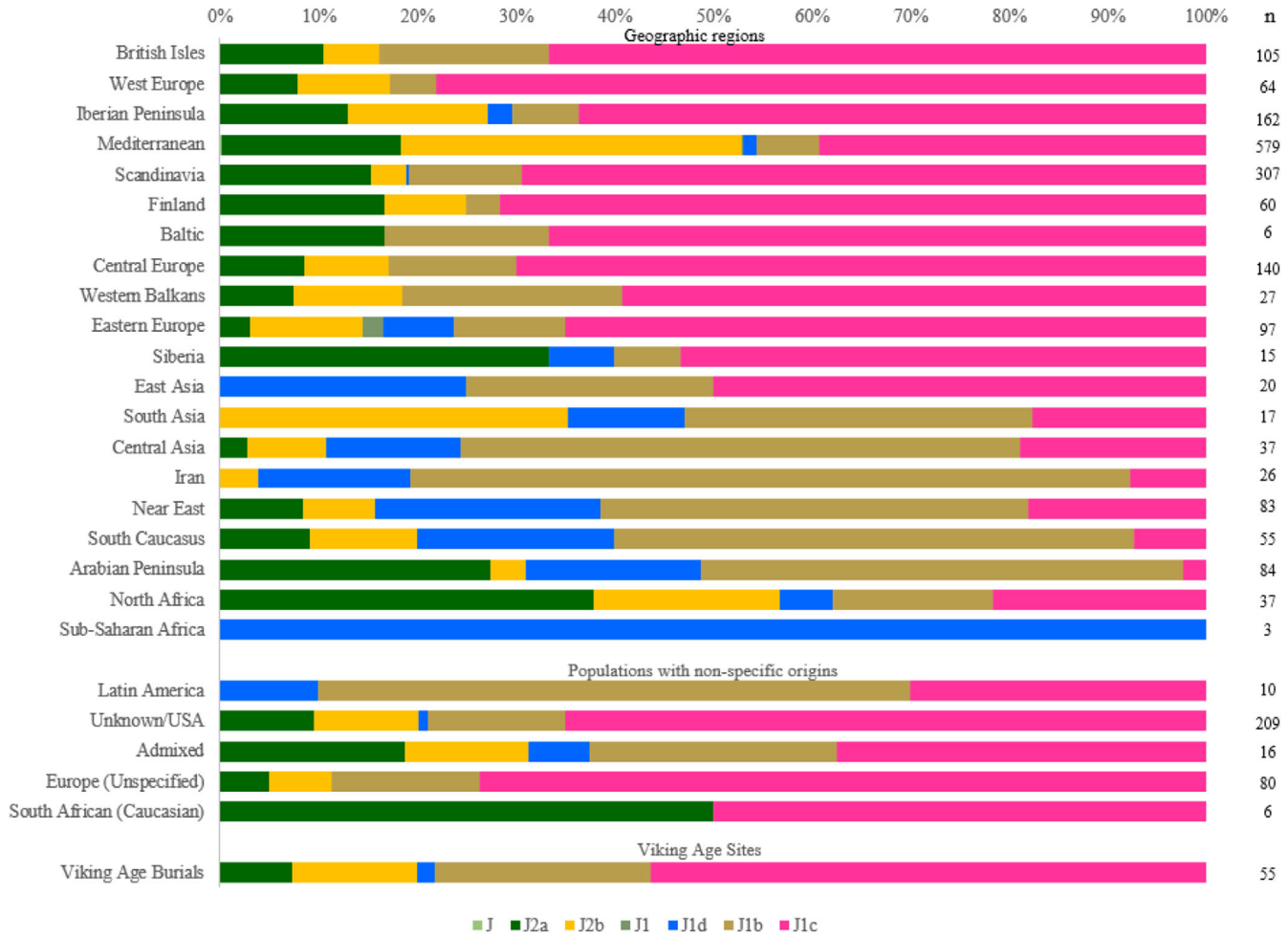

FIGURE 1 Distribution of three-digit haplogroup J subhaplogroups. The subhaplogroups were grouped into geographical region and populations with non-specific origins

population had subhaplogroup J1c mtDNA. The larger proportions of J1d, J1b, and J2b among the Viking Burial Sites suggested a greater diversity of J subhaplogroups among the Viking Age populations compared with modern-day Scandinavians.

3.2 | Interpopulation sequence diversity

The locus-by-locus analysis found differences between geographic regions. The genetic diversity over all loci ($n = 16{,}548$) was $Fst = 11.1\%$ ($p < 0.001$). The extent of genetic diversity was significantly influenced by control region loci ($n = 1122$), for which $Fst = 10.3\%$ ($p < 0.001$).

When the mitogenome data were plotted by individual countries and/or ethnic groups, the Viking haplogroup J sequences were positioned away from those of modern Scandinavian populations (Figure S1). When the analysis was restricted to the control region of the mitogenome sequence, Viking Burial Site sequences were more similar to those observed in other European populations (Figure 2). This pattern is most consistent with the genomic evidence, which indicates that Vikings were, on the whole, not matrilineally dissimilar from other historical European populations (Margaryan et al., 2020). Analysis by individual countries and/or ethnic groups are shown in Figure S2.

When comparing the Viking Burial Site control region sequences from haplogroup J to those of modern-day Scandinavians, the level of variation was low (2.3% variation; $p = 0.01$) (Table S3). This was also the case when Viking Burial Site sequences were compared to those from Norway (1.4%; $p = 0.01$) and Denmark (2.2%: $p = 0.02$) individually (Table S4). Interestingly, the Viking Burial Site sequences were more similar to those from populations in the Mediterranean region (7.3%; $p < 0.001$) and the Near East (6.2%; $p < 0.001$), whereas the converse was true for modern-day Scandinavian J sequences and populations from the Mediterranean region (9.3%; $p < 0.001$) and the Near East (10.8%; $p < 0.001$). While an MDS plot cannot reveal the temporal direction of haplogroup J dispersal, it nevertheless suggested that the haplogroup J composition of Vikings was more similar to populations from geographically southern regions than to modern-day Scandinavians.

The locations of Viking Burial Sites did not always reflect the genetic origin of the individuals interred there. While the majority of the these individuals likely had Norse ancestry, two Viking Burial Site

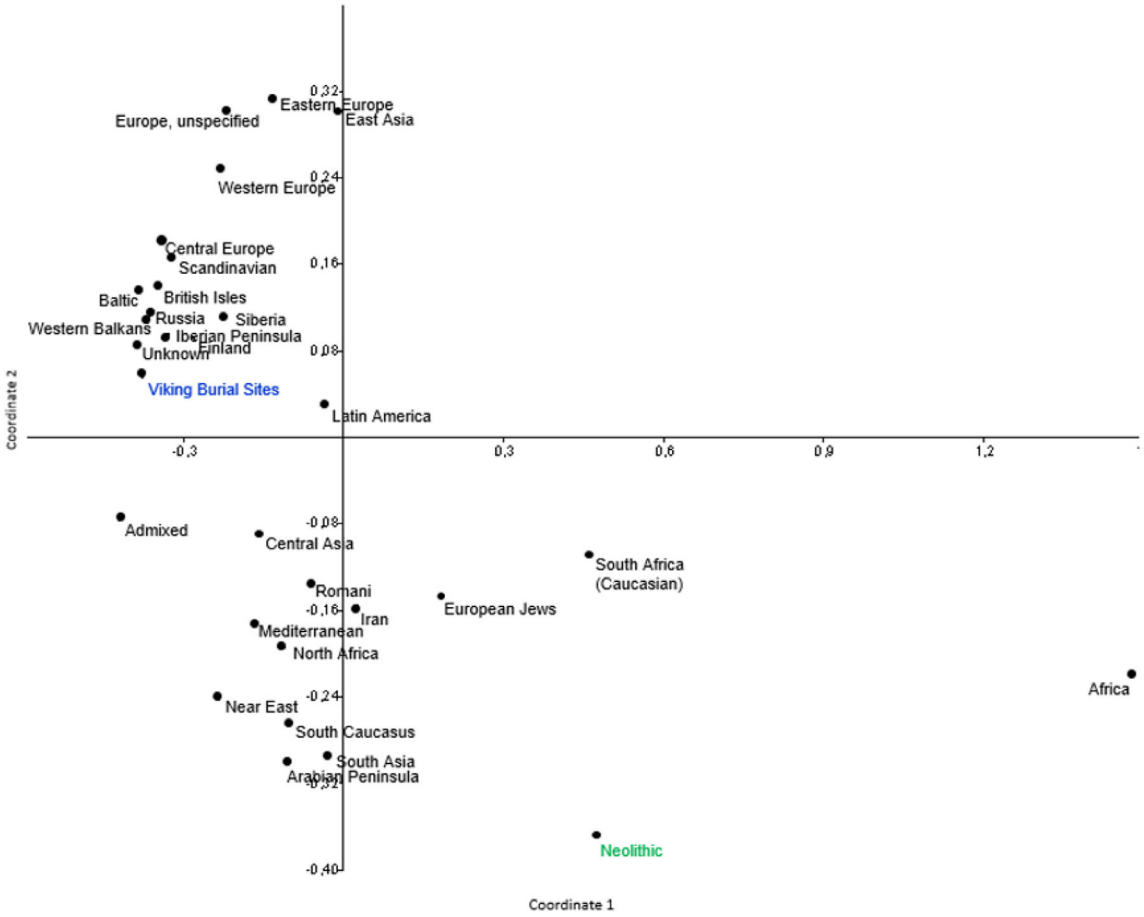

FIGURE 2 Multidimensional scaling (MDS) plot of haplogroup J to infer the level of similarity of HVS-I, II, and II by geographical regions. Viking burial site sequences are colored in blue, while Neolithic sequences are colored in green

sequences (VK397 and VK474) from Sweden had mostly Polish ancestry based on nuclear DNA analysis (Margaryan et al., 2020). Both were buried with several Viking artifacts as well as other individuals with mostly Norse ancestry (Margaryan et al., 2020). Similarly, an individual from Denmark (VK286) and another from Sweden (VK357) had >50% Mediterranean European genomic ancestry (Margaryan et al., 2020). Conversely, remains found in modern-day Poland (VK156) were of Eastern Scandinavian origin (Margaryan et al., 2020). Thus, Viking trade and colonization has played an important role in the dispersal of genetic lineages across European and Scandinavia.

3.3 | Phylogenetic analysis

To understand the evolution of haplogroup J from a temporal perspective, a phylogenetic tree was constructed from the mitogenome sequences, and the ages for its constituent branches were estimated. The specific subhaplogroups in each country and/or ethnic group and their identifying polymorphisms are listed in Table S5. Haplogroup J had an estimated age of 41.6 kya (95% confidence interval (CI): 30.0–64.7). This haplogroup subsequently split into two main subhaplogroups before the LGM, these being J1, which arose ~27.6 kya (95% CI: 22.6–40.8), and J2, which arose ~34.4 kya (95% CI) (Figure 3 and Figure 4).

Analysis of the earliest human remains indicates that Scandinavian hunter-gatherers dating from ~9.5 kya had mainly haplogroup U mtDNAs (Günther et al., 2018). Early farmers of Europe carried predominantly haplogroups H, HV, N1a, J, K, T, V, contributing to and gradually diversifying the mtDNA haplogroup profile of Europe (Bramanti et al., 2009). Evidence from genomic DNA suggests that the displacement of hunter-gatherers was higher in southern Europe, who were genetically more similar to early farmers, compared with northern Europe (Skoglund et al., 2012). The visualization of the phylogenetic trees in this study shows that the older haplogroup J lineages—predominantly J2—were found more frequently in southern Europeans, while the younger haplogroup J branches—predominantly J1—were found predominantly in Scandinavian populations.

With respect to the distribution of haplogroup J mtDNAs in Scandinavia, our analysis has provided some insights into the temporal sequence of their arrival in the region. Subhaplogroup J2a1 (9.3 kya [95% CI: 6.3–16.9]) mtDNAs have been identified in several populations of the Near East, Mediterranean, and the Iberian Peninsula, with later derived branches appearing in the British Isles, Denmark, and Sweden. A few subhaplogroups may have been brought to

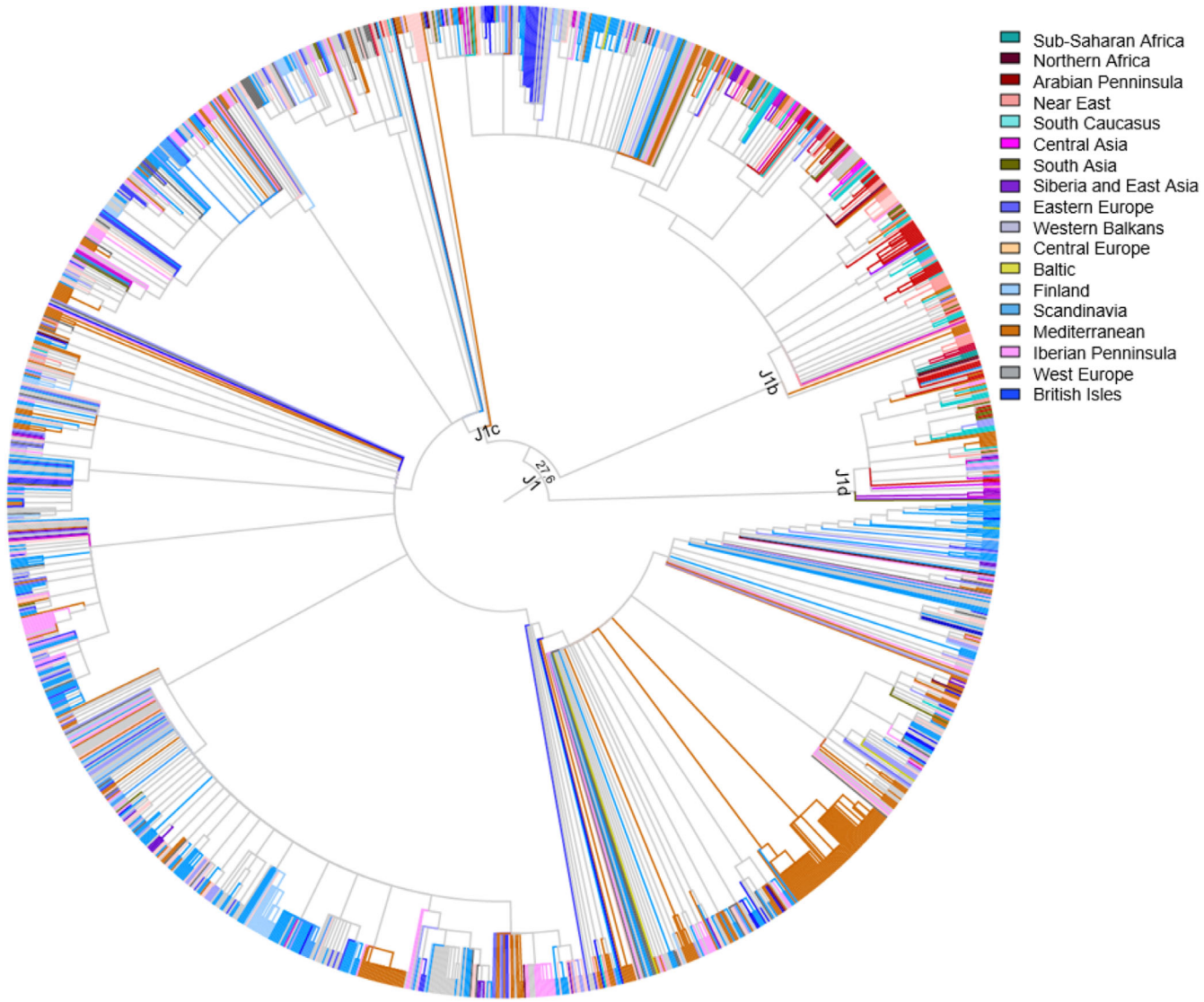

FIGURE 3 Phylogeographical tree of haplogroup J1

Scandinavia through Viking Age trades and expansions. As an example, subhaplogroup J2b1a, which has been dated to 9.1 kya (95% CI: 7.3–13.6), was found in a Viking Age burial in Sweden (Margaryan et al., 2020) and is distantly related to J2b1a sequences identified in the UK and Spain. In addition, early branching subhaplogroup J1b mtDNAs (26.8 kya [95% CI: 24.7–53.6]) have been found in Greece, Italy, and Armenia, while later evolving J1b1a1 mtDNAs (5.8 kya [95% CI: 4.4–9.6]) have been found in Denmark. Likewise, Viking burials in Norway and the Orkney and Faroe Islands (Margaryan et al., 2020) have J1b1a1a mtDNAs [3.8 kya (95% CI: 1.8–7.2)], with these derived types arising from earlier branches that appear in England and Ireland.

3.3.1 | Subhaplogroup J1

Except for a few sequences, subhaplogroup J1d (18.6 kya [95% CI: 13.6–32.9]) (Table 2) is not widely distributed in Europe. It is found across the expanse of North Africa, and some populations residing in the modern-day Russian Federation and East Asia. Meanwhile, subhaploroup J1c is found largely in West Europe, and entered Scandinavia about ten thousand years after J1d.

The earliest haplogroup J (subhaplogroup J1c5) (8.1 kya [95% CI: 5.3–12.7]) mtDNA reported in Scandinavia was found in human remains from mainland Sweden that were dated to 3090–2920 BCE (Eurasian Bronze Age/Scandinavian Neolithic Age) (Malmström et al., 2019). Archaeologically, this individual also belonged to the Funnel Beaker Culture (Malmström et al., 2019), of which the earliest settlements were likely to have occurred ~6.0–5.5 kya (Gron et al., 2016). Subhaplogroup J1c5 also derives from J1c mtDNAs found in Slovenia, Hungary, and Italy (16.4 kya [95% CI: 11.9–23.4]). Another early Scandinavian sequence belonging to haplogroup J1c2c1 was found in a fourth century CE burial in Nordland, Norway (4.1 kya [95% CI: 2.5–6.4]) (Margaryan et al., 2020). Both the J1c5 and J1c2c1 sequences can be linked to a sister branch in Scotland (subhaplogroup J1c3) (7.1 kya [95% CI: 4.7–11.4]) (Figure 3).

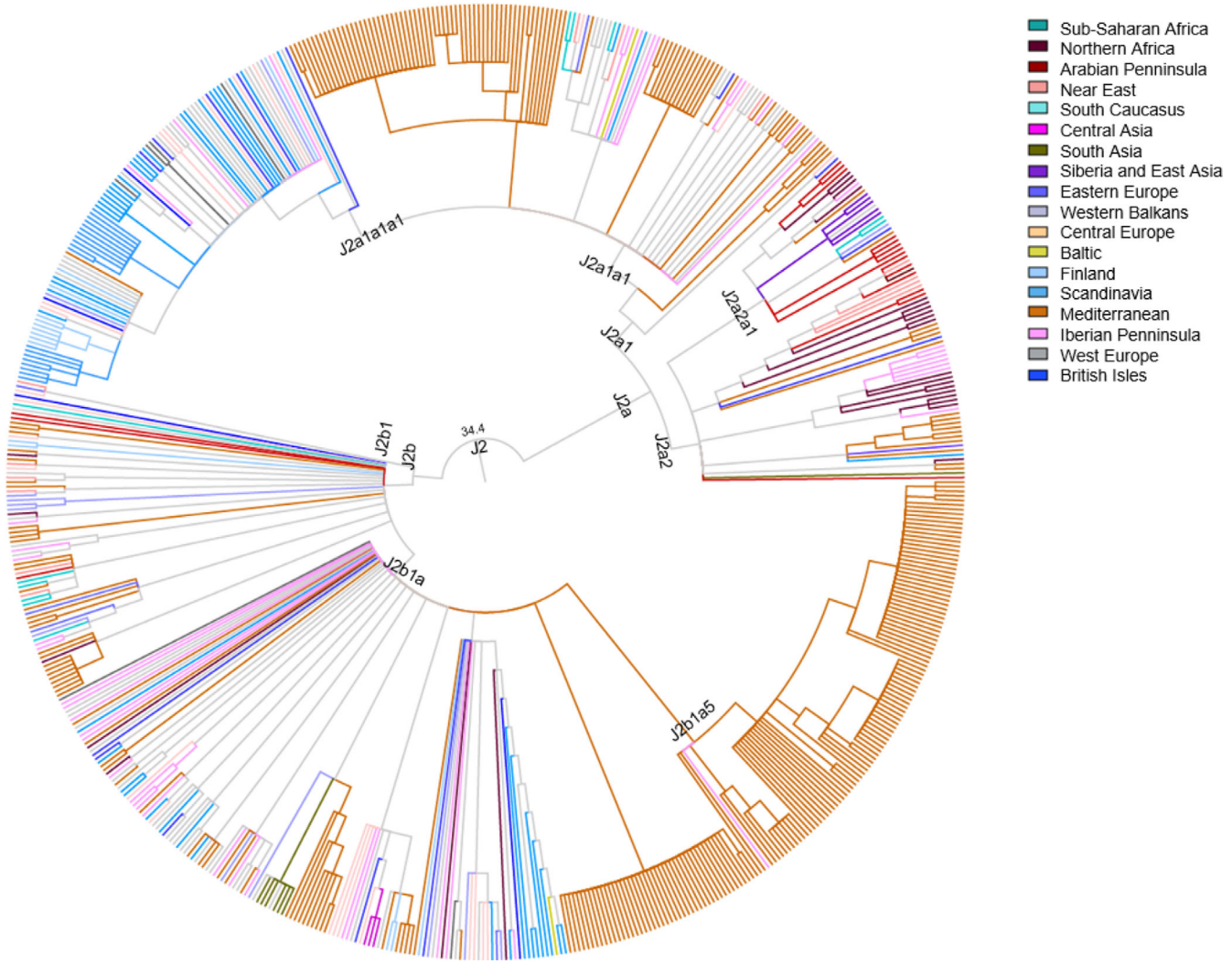

FIGURE 4 Phylogeographical tree of haplogroup J2

Subhaplogroup J1c was the most frequent maternal lineage among modern Scandinavians in our study. Several modern Scandinavian sequences such as J1c7 (8.8 kya [95% CI: 5.9–14.6]) occurred on the same subbranch with those identified in Russia, Ukraine, Spain, Italy, Greece, and the British Isles. The youngest branches of the subhaplogroup J1 phylogenetic tree are J1c3g (6.4 kya [95% CI: 4.4–9.5]) and J1c3c (4.6 kya [95% CI: 2.7–7.3]) and are shared by populations from Denmark and Germany. Subhaplogroups J1c4 (5.1 kya [95% CI: 3.5–8.3]) and J1c5 (8.1 kya [95% CI: 5.3–12.7]) are also shared between Italians and Danes. Collectively, these findings point to the Mediterranean, Germany, and British Isles as potential sources for these types of haplogroup J mtDNAs in Scandinavia.

Besides being brought into northern Europe from different places, haplogroup J sequences were disseminated from Scandinavia to other regions of Europe. In particular, subhaplogroup J1c2o (2.9 kya [95% CI: 0.3–6.6]) sequences from Denmark seem to have given rise to the ones identified in England. Poland and Denmark also share J1c2c2a (3.6 kya [95% CI: 2.2–5.8]) mtDNAs, which evolved from subhaplogroup J1c2c. This may have been due to Viking expansions and/or Norse settlements in European countries that occurred in the 9th to 11th centuries (Downham, 2012).

3.3.2 | Subhaplogroup J2

Subhaplogroup J2 separated into J2a (28.7 kya [95% CI: 21.2–43.8]) and J2b (20.4 kya [95% CI: 14.2–35.2]) before the LGM. Subhaplogroup J2a2 arose around 19.8 kya (95% CI: 15.2–31.2), most likely in the Arabian Peninsula, after which it then spread into Northern Africa and the Near East. Later dispersals went into Siberia with the migrations of nomadic pastoralists eastward, where J2 subhaplogroups are now found in Evenks and Yakuts of Siberia (Figure 4).

Within J2, subhaplogroups J2b and J2b1 (12.7 kya [95% CI: 10.2–19.4]) can be found in both the Mediterranean and Near East regions and then were dispersed into the Iberian Peninsula, North Africa, and Western Europe. While only 19% of sequences in Scandinavia belonged to J2, many of these sequences could be traced back to sequences from the Mediterranean, including Sardinia, Italy,

TABLE 2 Age estimates and 95% confidence intervals for haplogroup J

Phylotree Haplogroup	n[a.]	Age estimates in kya	95% CI (kya)	
J	**3000**	**41.6**	**30.0**	**64.7**
J1	**1648**	**27.6**	**22.6**	**40.8**
J1b	**369**	**26.8**	**24.7**	**53.6**
J1b1a1	159	5.8	4.4	9.5
J1b1a1a	17	3.8	1.8	7.2
J1b1a1b	16	5.8	4.4	9.5
J1b1a1c	2	4.8	1.5	8.6
J1b1a1d	9	1.6	1.2	3.5
J1b1a1e	9	4.7	2.9	7.6
J1b1a2a	2	8.1	2.4	15.3
J1b1a2b	3	10.2	5.9	17
J1b1a3	12	12.1	6.5	18.7
J1b1b	58	12	9.5	18.8
J1b1b1	49	12	9.5	18.8
J1b1b1a	9	6.3	3.2	11.7
J1b1b2	4	17.3	10.4	25.4
J1b1b3	4	17.2	11.3	25.9
J1b2	51	10.5	7.4	16.5
J1b2a	7	8	4.8	14.1
J1b3	24	16.5	11.8	24.3
J1b3a	11	4.3	9.5	11.9
J1b3b	9	11.1	4.8	18.5
J1b3b1	7	9.7	4.8	16
J1b4	8	10.7	3.5	23.4
J1b5	10	11.2	6.1	21.7
J1b6	11	14.9	9.5	24.2
J1b6a	5	8	2.1	15.3
J1b7a	2	8.3	2.2	19.8
J1b9	3	10.2	4.3	20.1
J1c	**1184**	**16.4**	**11.9**	**23.4**
J1c+16261T	26	8.4	5.9	14.6
J1c1	211	9	7.2	12.8
J1c1a	13	3.1	1.5	5.9
J1c1b	68	9	7.2	12.6
J1c1b1	35	9	7.2	12.6
J1c1b1a	32	6.6	2.9	10.5
J1c1b1a1	2	6.2	2.2	10.5
J1c1b2	7	4.4	1.8	10.6
J1c1c	5	6	2.4	10.6
J1c1d	14	2.1	0.5	4
J1c1g	6	2.5	0.7	5.8
J1c1g1	2	4.1	0.6	9.7
J1c2	365	8.6	5.7	14.1
J1c2a	16	5.5	2.8	8.2

TABLE 2 (Continued)

J1c2a3	6	1.3	0.5	3
J1c2b	27	5.2	0.8	7
J1c2b4	2	3.7	0.8	6.9
J1c2b5	10	2.2	0.9	4.5
J1c2c	47	6	4.7	9.4
J1c2c1	19	4.1	2.5	6.4
J1c2c2	19	3.6	2.2	5.8
J1c2c2a	12	3.6	2.2	5.8
J1c2e	52	4.1	2.9	8.2
J1c2e1	17	4.1	2.9	8.2
J1c2e2	17	2.8	1.3	5.1
J1c2h	5	6	2.2	11.2
J1c2i	5	8.8	5	14.1
J1c2k	7	2.7	1.5	5.5
J1c2m	9	6	4.7	9.4
J1c2n	13	6	4.7	9.4
J1c2o	24	2.9	0.3	6.6
J1c2p	5	2.9	0.8	6.6
J1c2q	9	4.5	2.1	7.7
J1c2q1	7	4.5	1.3	7.2
J1c2s	2	4.9	2	8.2
J1c2t	10	5	1.5	9.4
J1c3	276	7.1	4.7	11.4
J1c3+189G	4	7.1	4.7	11.4
J1c3a	22	8	4.7	14.6
J1c3a1	12	3.7	1.9	6.3
J1c3a2	8	5	2.2	9.8
J1c3b	15	2.5	0.9	4.8
J1c3b1	6	2.5	0.9	4.8
J1c3c	13	4.6	2.7	7.3
J1c3e	21	6.3	1	4
J1c3e2	10	6.3	1	4
J1c3f	22	7.6	3.4	13.4
J1c3g	18	6.4	4.4	9.5
J1c3h	42	4.3	2.1	8.2
J1c3i	3	4.8	0.9	10.7
J1c4	42	5.1	3.5	8.3
J1c4b	11	3.3	1.9	6
J1c5	114	8.1	5.3	12.7
J1c5a	42	6.6	4.3	11.7
J1c5a1	27	3.1	1.9	4.8
J1c5b	4	6.3	3.2	10
J1c5c	16	6.4	4.2	10.3
J1c5c1	14	2.4	1.1	4.5
J1c5d	4	5.5	2.2	9.7
J1c6	17	6.6	4.1	13.8

(Continues)

TABLE 2 (Continued)

J1c6+189G	6	5.9	1.6	12.8
J1c7	55	8.8	5.9	14.6
J1c7a	41	5.6	4.4	11
J1c8	41	11	7.2	18.1
J1c8a	26	4.1	3.5	8.3
J1c8a1	4	4.1	2.8	6.8
J1c8a1a	3	4.1	2.8	6.8
J1c8a2	2	2.3	0.6	4.4
J1c8b	3	8.4	1.4	18
J1c9	12	7.1	4.6	12.5
J1c10	12	12.4	7.5	20.5
J1c10a	8	10.5	5	19.8
J1c11	7	7.3	4	12.1
J1c11a	6	7.3	4	12.1
J1c12	6	5.7	3	10
J1c12a	3	3.4	0.3	7.9
J1c12b	2	4.9	1.6	9.1
J1c15	15	12.7	10.3	18.5
J1c15a	2	8.4	2.5	16.4
J1c15a1	2	7.3	2.1	16.1
J1c15b	4	3.2	1.3	9.5
J1d	**92**	**18.6**	**13.6**	**32.9**
J1d1a	25	16.4	12.5	23.9
J1d1a1	21	6.6	4.5	10.9
J1d1b	13	13.2	7	18.8
J1d1b1	9	8.6	5.3	14.1
J1d2	3	9.5	4.1	17.7
J1d2a	2	6.3	1.5	14.3
J1d3	17	14.4	10.6	21.5
J1d3a1	5	11.2	5.7	18.7
J1d3a2	8	2.8	0.6	5.8
J1d5	10	12.6	6.2	19.2
J1d5a	2	6.2	1.4	13.1
J1d6	9	5.3	2.6	9.2
J2	**651**	**34.4**	**24.7**	**53.6**
J2a	**306**	**28.7**	**21.2**	**43.8**
J2a1	**229**	**21.3**	**16.7**	**27.3**
J2a1a1	223	9.3	6.3	16.9
J2a1a1a	29	5.9	3.4	9.7
J2a1a1a1	7	3.3	1.3	5.7
J2a1a1a2	61	5.9	3.4	9.7
J2a1a1a2a	11	1.9	0.5	3.2
J2a1a1c	4	6.5	2.4	12.5
J2a1a1d	62	1.8	0.8	5.1
J2a1a1e	21	6.4	4.3	11.2
J2a1a2	4	8.6	4.4	12.9

TABLE 2 (Continued)

J2a2	**77**	**19.8**	**15.2**	**31.2**
J2a2a	21	17.6	12	27.1
J2a2a1	16	13.7	8.7	24.1
J2a2a1+16311T!	11	9.2	3.8	18.5
J2a2a1a	8	3.1	0.5	6.4
J2a2a1a1	6	3.1	0.5	6.4
J2a2a2	3	6.6	2.5	13
J2a2b	25	19.8	15.1	31.2
J2a2b1	5	16.9	10.8	25.6
J2a2b1a	4	10.6	4.7	18.4
J2a2b2	5	7.3	2.9	14.7
J2a2c	11	9.4	4.8	17.1
J2a2c1	7	4.3	0.8	11.4
J2a2d	15	4.3	1.8	8.8
J2a2e	3	10	5.4	17.2
J2b	**345**	**20.4**	**14.2**	**35.2**
J2b1	**342**	**12.7**	**10.2**	**19.4**
J2b1a	277	9.1	7.3	13.6
J2b1a+16311T!	6	7.1	4.8	11.7
J2b1a1	11	6.4	3.5	11.7
J2b1a2	35	8.3	4.5	12.3
J2b1a2a	5	5.9	2.6	10.4
J2b1a3	7	4.2	1.6	8
J2b1a4	5	5.9	3.1	11.5
J2b1a5	86	2.8	1.7	5.7
J2b1a6	9	5.6	2.8	10.5
J2b1c	10	7	4.2	12.4
J2b1c1	5	7	4.2	12.4
J2b1d	4	12.6	9.8	19
J2b1e	3	12.6	6.7	17.1
J2b1e1	2	10.2	5.5	17.1
J2b1f	10	4	1.3	7.7
J2b1g	4	4.6	0.6	10.8
J2b2	**3**	**12.2**	**6.6**	**21.6**

Note: Major haplogroups are highlighted in bold haplogroup age estimates that include confidence intervals including the present-day (0 kya) are not included.
Abbreviation: kya, kiloyears ago.
[a]Subclade ages are based on the node ages, which include daughter branches.

Greece, and France. This included J2a1a1a1 (3.3 kya [95% CI: 1.3–5.7]) found largely in Scandinavia, and the older subhaplogroup J2a1a1 (9.3 kya [95% CI: 6.3–16.9]) found largely in Mediterranean Europeans. The shared root of these sequences likely preceded the Viking Age and might be related to the interactions between southern Scandinavians and populations of the Roman empire. In addition to several Roman artifacts found within Scandinavia, the influence of the Roman Empire in Scandinavia has been observed in Viking weaponry and the construction of the written Futhark alphabet (Robertson, 2011; Strobeck, 2006).

Several early branches of J2b1a (9.1 kya [95% CI: 7.3–13.6]) in Spain and Portugal have a common root with sequences in Denmark, Sweden, and the United Kingdom, more distantly, with the Kalash and Pathan from Pakistan. The genetic affinities of the Kalash with Europeans is not entirely unexpected. The Kalash are a genetic isolate in northern Pakistan and share a substantial proportion of genetic drift with a Paleolithic Siberian hunter-gatherer ancestor that has contributed to European and West Asian ancestry (Ayub et al., 2015). The split between Europeans and South Asians likely occurred during the

Neolithic period, based on the analysis of the decay of linkage disequilibrium (Ayub et al., 2015).

Other western Eurasian haplogroups (such as H, U, and T) have been observed at low frequencies in South Asians (Palanichamy et al., 2004; Quintana-Murci et al., 2004). The eastward flow of these haplogroups were postulated to be due to gene flow from the first Paleolithic arrivals to the corridor region of eastern India from the prehistoric Middle East (Palanichamy et al., 2004; Quintana-Murci et al., 2004). This was followed later with subsequent dispersals associated with Neolithic urban civilizations, such as Mesopotamians and Elamites, who also may have brought farming practices eastwards (Quintana-Murci et al., 2004; Martin Richards et al., 2000).

4 | DISCUSSION

The earliest evidence for haplogroup J in Scandinavia is a subhaplogroup of J1c found in a Eurasian Bronze Age/Scandinavian Neolithic Age individual from Sweden, although sequences deriving from older branches of haplogroup J are also present among modern-day Scandinavian and Viking Age individuals. Based on the divergence time estimates, subhaplogroup J1c likely appeared when Scandinavia was transitioning to agriculture and animal husbandry. Given that sequences from subhaplogroups J2a, J2b, and J1b, and J1d are present in both modern-day Scandinavian populations and Viking Age individuals, the difference in subhaplogroup J distributions likely reflects the incorporation of non-Norse individuals during Viking Age expansions, who were gradually assimilated into Scandinavian populations. However, we cannot exclude other sources of these mtDNAs.

Our phylogenetic analysis provides a detailed view of haplogroup J phylogeography. It supports the origin of this major maternal lineage in Western Asia, and its dispersal into Europe and Scandinavia through the transition to agriculture over thousands of years. Ancient DNA evidence suggests that the transition from hunting-foraging to farming started in southern Scandinavia, with diverse mtDNA haplogroups gradually replacing the predominant haplogroup U mtDNAs (Melchior et al., 2010). Archaeological evidence for tools and burial sites further supports the idea that agricultural practices were brought to Scandinavia with northward migrating European farmers, and that indigenous hunter-gatherers were gradually assimilated into the farming cultures (Fischer, 2002). Radiocarbon analysis of 24 regions with known European Neolithic populations and increased population growth rates confirmed that agriculture dates for eastern and southern European regions dated to ~7500 to 7200 cal BP while in northwest Europe they were around 6000 cal BP (Downey et al., 2014). An increase in population growth rates is commonly observed in Neolithic populations due to increased access to sustenance and resources (Bocquet-Appel & Bar-Yosef, 2008), and this may have led to expanded frequencies of haplogroup J mtDNAs in them.

Although the impetus for specific haplogroup expansions is debated, the early farmers (many of whom carried haplogroup J) were likely motivated to move northwards due to a combination of factors. These factors included the growing population pressure in Middle Neolithic cultures within Europe, improved climatic conditions in northern latitudes, the discovery of arable land in the southern Scandinavian peninsula, and accessible flint resources there (Sørensen & Karg, 2014). Early Neolithic sites in southern Scandinavia show the synchronous introduction of bread wheat and naked barley cultivars within a 300 year period (4000–3700 cal BCE) across the entire region of southern Scandinavia (Sørensen & Karg, 2014; Zohary et al., 2012). Bones of domesticated cattle found throughout southern Scandinavia date to this same time period (Sørensen & Karg, 2014), consistent with the evidence of cereal cultivation. Evidence of flint tool mining characteristic of the Michelsberg Culture (4400–3500 cal BCE) in the modern-day Netherlands also appeared in Scandinavia at that time (Sørensen & Karg, 2014).

Farming arrived in Scandinavia with the Funnel Beaker culture by 4000 BCE (Iversen & Kroonen, 2017). Corded Ware/Single Grave communities later appear on the Jutland Peninsula at approximately 2850 BCE, while the late Funnel Beaker culture continued for several hundred years in the eastern parts of southern Scandinavia together with the Pitted Ware Culture (Iversen & Kroonen, 2017). Thus, several prehistoric western and central European cultures contributed to the rise of farming in Scandinavia, bringing with them maternal lineage diversity.

Many aspects of farming spread rapidly in Scandinavia, as indicated by early Neolithic agrarian habitation on the islands of Bornholm, Gotland, and large regions of the Scandinavian peninsula within a short time frame (Sørensen & Karg, 2014). The relatively rapid expansion of farming culture throughout the Scandinavian peninsula suggests that marine vessels were used by expanding farming groups (Lindqvist & Possnert, 1997). Within Norway, the frequency of haplogroup J mtDNA remains higher in Central and Western Norway, specifically Tromsø and the former Norwegian capital of Bergen (Kristjansson et al., 2021), which have historically been major regions of trade and maritime commerce. The transition to agrarian culture in Scandinavia can thus be interpreted as a complex and continuous process of migration, integration, and gradual assimilation of neighboring farmers and hunter-gatherers that extended into the Eurasian Bronze Age. By the onset of the Nordic Bronze Age (1500 BCE), the sociocultural border between the western and eastern parts of southern Scandinavia had dissipated (Sørensen & Karg, 2014).

As the third most common maternal lineage in Scandinavia, haplogroup J has been present at moderate frequencies in Scandinavia since at least the Viking Age (Krzewińska et al., 2015). While the sample size of the Viking individuals in this study was small, haplogroup J was the third most frequent haplogroup in both the Vikings and the modern-day Norwegian population. Furthermore, a study of mtDNA lineages among 264 individuals in Denmark before and after the Black Death (1347–1352 CE) found that the proportion of haplogroup J, among several other maternal lineages, did not change significantly (Klunk et al., 2019).

Although haplogroup J occurred at moderate frequency among Scandinavians over a long period of time, our study found differences in the J subhaplogroups present in the Viking Age individuals and modern-day Scandinavians. Specifically, the Viking Burial Site

individuals in our study had greater frequencies of J1b and J2b, and lower frequencies of J1c and J2a. Similarly, an analysis of Viking Age mtDNAs carried out by Krzewińska *et al*. (2015) found no J1c or J2a sequences (Krzewińska et al., 2015). Since the majority of the Viking Age individuals with J1b sequences were found in Scandinavia and had nuclear DNA genetic roots within Scandinavia (Margaryan et al., 2020), it is likely that the differences in subhaplogroup distributions may have been partly due to incorporations of J1c-carrying individuals with non-Norse ancestry following the Viking Age.

Our study found some evidence for connections between J1c sequences from Germany, the Mediterranean, and the British Isles and those in several modern-day Scandinavian popluations. This observation is supported by historical documentation of later immigration events during and following the Medieval period, particularly from Great Britain, the Netherlands, and the influx of Hanseatic League (German) settlers, who had a major influence on Scandinavian culture, religion, and economic trade (Burkhardt, 2010; Helle, 2019; Kent, 1955).

Apart from maternal lineages, Viking Age individuals differed from modern-day populations in terms of having a greater genetic predisposition for black hair color (Margaryan et al., 2020). This observation suggests that some phenotypic traits common among Viking Age individuals may have become less common over time with the emergence of modern-day Scandinavians. However, most other traits that are associated with Scandinavian populations were already present by the Bronze Age. For example, the prevalence of blue eyes were already present in Mesolithic Europe and became more frequent during the Bronze Age (Allentoft et al., 2015; Günther et al., 2018; Olalde et al., 2014). Based on this information, it is likely that blue-eyed/dark-skinned hunter-gatherers settling from Scandinavia's southwestern boarders assimilated with brown-eyed/light-skinned hunter-gatherers settling in Scandinavia from the northeast (Günther et al., 2018). The combination of light skin and blue-to-light brown eyes that became predominant among Scandinavians is likely the result of adaptation to long and dark winter months over the course of several millennia (Günther et al., 2018).

The high frequency of lactose tolerance among modern-day Scandinavians emerged following the establishment of farming culture in Scandinavia. Alleles for lactose tolerance were found among people of the Corded Ware culture (2900–2350 BCE) and individiuals from closely-related ancient cultures in Scandinavia (Allentoft et al., 2015). These alleles likely increased in frequency with expanded use of milk and dairy products by ancient farming societies in Scandinavia.

A related question is whether haplogroup J conferred an adaptive advantage that led to its significant presence in the Scandinavian population. Like those of its sister lineage, haplogroup T, haplogroup J mtDNAs share a set of polymorphisms that have been predicted to increase an individual's basal metabolic rate, possibly as a result of a survival advantage in colder climates (Mishmar et al., 2003). Certain amino acid substitutions were found to be highly conserved in the subbranches of haplogroup J, where they also represent lineages from colder Europe compared with the warmer climate origins of haplogroup J (Ruiz-Pesini et al., 2004). Several of the highly conserved haplogroup J polymorphisms were correlated with an increase of energy deficiency and longevity. More specifically, the 14798C substitution associated with subhaplogroup J1 may affect an inner CoQ-binding site that could reduce proton pumping and coupling efficiency (Di Rago & Colson, 1988; Fisher & Rich, 2000), providing more heat release in colder environments (Ruiz-Pesini et al., 2004).

Our study similarly found that the younger branches of haplogroup J, such as the several subhaplogroups of J1c, were more frequent among Scandinavians than J1b and J1d. In addition, the younger subhaplogroup of J, namely J1c, has a stronger presence in cooler European climates such as the British Isles. In the warmer climates of the Arabian Peninsula and North Africa, earlier subhaplogroups, such as J2 and J1d, tend to be more frequent. It is unclear as to whether this is a founder effect resulting from northern migrations by early European farmers or whether the sequence differences in the J subhaplogroups confer differential effects from an oxidative standpoint.

As haplogroup J has evolved to become the third most frequent haplogroup in modern-day Scandinavia, there may be certain selective advantages conferred by this haplogroup. Polymorphisms in oxidative phosphorylation (OXPHOS) genes in haplogroup J mtDNAs may contribute to increased ATP production and coupling efficiency. Notably, haplogroup J contains two missense mutations in complex I genes (Y304H in *MT-ND1* and A458T in *MT-ND5*) and an L236T variant in *MT-CYB*, a main component of respiratory chain complex III (Mishmar et al., 2003). The C150T variant is located in the non-coding region and is present in nearly all of the haplogroup J samples of this study. It may impinge on OXPHOS efficiency and reactive oxygen species (ROS) production (one-electron reduction of dioxygen (oxygen gas, O_2) to form the anionic form (O_2^-)), thus reducing oxidation stress and functional attrition that occurs with old age (Coskun et al., 2003).

A problem with this hypothesis is that the C150T mutation is present in numerous other haplogroups, including those not hypothesized to confer a benefit in colder climates. Although the C150T mutation alters the location of H-strand replication origin and might impart a replicative advantage to mtDNA, the mechanisms for how this polymorphism affects ROS production remain unclear. Systems-based studies linking haplogroup J and ATP production have yet to be conducted to elucidate whether specific mutations in haplogroup J mtDNAs are detrimental to OXPHOS.

Haplogroup J may also confer a selective advantage by protecting against several chronic diseases. Haplogroup J has been associated with a lower risk of developing osteoarthritis in patients from Spain with specific associated polymorphisms (Rego-Pérez et al., 2008; Soto-Hermida et al., 2014). In a study of Spanish individuals with ischemic cardiomyopathy ($n = 358$) and healthy controls ($n = 423$), haplogroup J mtDNAs were lower in frequency among those with ischemic cardiomyopathy (Fernández-Caggiano et al., 2012). Conversely, haplogroup J mtDNAs have also been associated with HIV-infected individuals displaying accelerated progression to AIDS and death (Hendrickson et al., 2008). While further investigation is needed to explore the mechanisms underlying the possible protective effects conferred by haplogroup J, particularly with regards to specific subhaplogroups and polymorphisms, the advantages of haplogroup J appear

to be related to chronic diseases of old age and reduced ROS production, as well as a possible adaptation to colder environments.

In conclusion, the evolution and dispersal of haplogroup J mtDNAs in Scandinavia was likely driven by the expansion of farming populations from the Near East into Europe and then into Scandinavia. Neolithic farming cultures are likely to have initially brought haplogroup J mtDNAs into Scandinavia, with later Viking expansions introducing new sequences from distant regions. Later historical processes related to the rise of European cultures over the past millennium likely reshaped the distribution of haplogroup J mtDNAs in Scandinavia. Despite this emerging picture, there remain unsolved questions about whether natural selection conferred an adaptive advantage to the haplogroup J maternal lineage that resulted in the high frequencies currently found among modern-day Scandinavians. These questions need to be answered with further mechanistic studies on the polymorphisms highlighted here and their effects on cellular respiration.

AUTHOR CONTRIBUTIONS

Dana Kristjansson: Conceptualization (lead); formal analysis (lead); investigation (lead); methodology (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Theodore G. Schurr:** Conceptualization (supporting); funding acquisition (supporting); methodology (supporting); supervision (lead); visualization (supporting); writing – review and editing (supporting). **Jon Bohlin:** Methodology (supporting); supervision (supporting); writing – review and editing (supporting). **Astanand Jugessur:** Conceptualization (equal); funding acquisition (lead); supervision (lead); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The mitogenome sequence data on which this study is based can be obtained from GenBank and the European Nucleotide Archive. Data from the European Nucleotide Archive are listed in project number PRJEB21940. The GenBank accession numbers for mitogenome sequences reported in this paper are listed in Table S5.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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