

Excavating Past Population Structures by Surname-Based Sampling: The Genetic Legacy of the Vikings in Northwest England

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The genetic structures of past human populations are obscured by recent migrations and expansions and have been observed only indirectly by inference from modern samples. However, the unique link between a heritable cultural marker, the patrilineal surname, and a genetic marker, the Y chromosome, provides a means to target sets of modern individuals that might resemble populations at the time of surname establishment. As a test case, we studied samples from the Wirral Peninsula and West Lancashire, in northwest England. Place-names and archaeology show clear evidence of a past Viking presence, but heavy immigration and population growth since the industrial revolution are likely to have weakened the genetic signal of a 1,000-year-old Scandinavian contribution. Samples ascertained on the basis of 2 generations of residence were compared with independent samples based on known ancestry in the region plus the possession of a surname known from historical records to have been present there in medieval times. The Y-chromosomal haplotypes of these 2 sets of samples are significantly different, and in admixture analyses, the surname-ascertained samples show markedly greater Scandinavian ancestry proportions, supporting the idea that northwest England was once heavily populated by Scandinavian settlers. The method of historical surname-based ascertainment promises to allow investigation of the influence of migration and drift over the last few centuries in changing the population structure of Britain and will have general utility in other regions where surnames are patrilineal and suitable historical records survive.

Introduction

Studies of the human past draw on lines of evidence from many fields, including paleoclimatology, archaeology, paleontology, linguistics, and history (Jobling et al. 2004), and recent years have seen an increasing influence of genetics. Unlike most other sources of evidence, genetic studies generally rely upon the collection of data from contemporary sources—modern, living populations—and use various statistical methods of inference to make deductions about events many generations ago. However, modern populations have been influenced by recent migration and expansion, associated with events such as the industrial revolution, and may provide a blurred and misleading picture of the past. Ancient DNA methods have promised direct access to the genetic diversity of past populations, but unfortunately the practical difficulties of retrieving verifiable and contamination-free DNA data mean that sample sizes are inconveniently small for population genetic analysis (Topf et al. 2006), except in rare cases of exceptional preservation (Keyser-Tracqui et al. 2003).

A possible alternative approach is suggested by the link between a heritable cultural marker, the patrilineal surname, and an informative genetic marker, the non-recombining region of the Y chromosome, demonstrated

through studies of men sharing surnames (Sykes and Irven 2000; King et al. 2006; McEvoy and Bradley 2006). Although the link between surname and Y-chromosomal haplotype is imperfect, due to multiple founders for names and historical nonpaternities and adoptions (Jobling 2001), unrelated men sharing surnames are significantly more likely to share haplotypes than are men carrying different names. This demonstrates that surnames have been associated with specific haplotypes for many generations and suggests that access to the Y-chromosomal diversity of past populations might be possible through the selection of modern samples based on surnames known to exist in a particular region during the medieval period. A similar approach has been proposed independently (Manni et al. 2005), based on a spatial analysis of ~200-year-old Netherlands surnames.

A useful test case to evaluate the potential of surname-based ascertainment is provided by the 1,000-year-old Viking settlement of the British Isles. The Viking age of raiding, exploration, trading, and colonization began in the late eighth century, with a series of attacks on the coasts of Britain, Ireland, and France. In England, a shift from raiding to permanent settlement began after AD 865. The modern consensus has moved from the earlier view of a mass migration of Viking settlers to a more geographically variable and gradual process, with much assimilation of local culture, under the administration of a Scandinavian elite (Richards 2004). Even though Viking rule in England came to an end nearly 1,000 years ago and the settlers were soon integrated linguistically and culturally, abundant evidence of Scandinavian influence remains today. Important archaeological findings exist, but the most striking evidence is linguistic and onomastic—many words in Standard English and in local dialects, and many place-names, are

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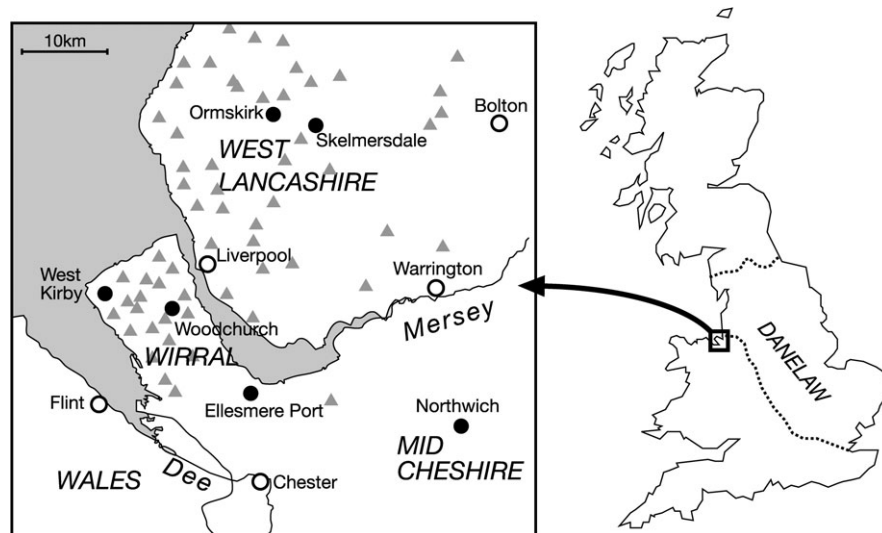


FIG. 1.—Location of the Wirral Peninsula and West Lancashire. Sampling locations for the modern samples are shown by filled circles, and unfilled circles show major towns for orientation. Gray triangles show the locations of Scandinavian major place-names (Harding 2002).

of Scandinavian origin. In some areas of English counties that formed part of the Danelaw (fig. 1), the region under the administrative control of the Vikings from the late ninth century, up to 70% of major place-names are in this category, with endings such as “-by” and “-thorp(e).”

Attempts to identify a corresponding genetic legacy of Viking settlement in modern populations of the British Isles have focused on North Atlantic Islands with archaeologically and culturally defined histories of Viking contact (Helgason, Sigurdardóttir, Gulcher, et al. 2000; Helgason, Sigurdardóttir, Nicholson, et al. 2000; Helgason et al. 2001; Wilson et al. 2001; Capelli et al. 2003; Goodacre et al. 2005). These studies have exploited the phylogeographic resolution of the paternally inherited Y chromosome and the maternally inherited mitochondrial DNA to reveal strong signals of Scandinavian admixture. For example, the proportion of Scandinavian patrilineal ancestry in Iceland has recently been estimated at 75%, and this proportion has been described as declining through Shetland (44.5%), Orkney (31%), and the Western Isles and Skye (22.5%) to the coastal regions of northern and western Scotland (15%) (Goodacre et al. 2005).

In mainland Britain, abundant evidence exists for a past Viking presence in the Wirral Peninsula and West Lancashire, in the northwest of England. Scandinavian major place-names are common (Cavill et al. 2000; Harding 2002) (fig. 1), and these 2 regions possess the only definite examples of the place-name “Thingwall” (from Old Norse “þingvöllr” meaning “Assembly Field”) in England, indicating settlements of sufficient density and autonomy to warrant their own parliaments. Moreover, in the case of Wirral, the intensity and distribution of minor place-name elements attest to the persistence of a Scandinavian-influenced dialect through the centuries that may reflect the intensity of the original settlement (Wainwright 1943; Cavill et al. 2000). This onomastic evidence is supported by archaeological discoveries such as jewelry, weaponry, or treasure hoards at Meols, Crosby, and Cuerdale

(Graham-Campbell 1992; Harding 2002) or Hiberno-Norse ring-headed crosses (Bu’Lock 1958) and hogback tombstones (Collingwood 1928; Bailey et al. 2006), which reflect Scandinavian presence.

In one version of events, Vikings of Norwegian origin, under their leader Ingimund, arrived in the region in AD 902 after having been expelled from Dublin. Æthelflæd, Lady of the Mercians, granted them land in north Wirral, where they settled (Wainwright 1942, 1948, 1975). More complex models have also been proposed, based on place-names analysis, including elements of migration from the Isle of Man as well as Dublin (Fellows-Jensen 1992). Specific historical evidence for the migration of Vikings into West Lancashire is lacking, although place-names and archaeological evidence clearly demonstrate that this occurred.

Widespread migration and population expansion in recent centuries present a particular problem in genetic analyses of mainland regions of Britain. The Wirral experienced a major influx of people since the medieval period, its population growing over 70-fold between 1545 and 1921 (Roberts 2002)—almost 10 times the national average increase. In conventional sampling strategies, where 2 generations of residence in an area are sufficient to qualify a DNA donor for participation in a study, the signal of Viking influence is likely to be weakened by the noise of more recent population movement.

Here, we exploit the relationship between patrilineally inherited surnames and Y-chromosomal haplotype using surname-based ascertainment to ask if targeted subsampling of modern populations can retrieve samples that more accurately represent the structures of populations in the past. Historical documents can provide lists of relevant surnames, and in our study, we have used such sources to provide a set of names present in the Wirral and West Lancashire prior to 1572. We show that samples taken under these criteria are significantly different from samples taken on the 2 generations of residence criterion. They preserve a markedly stronger signal of Scandinavian

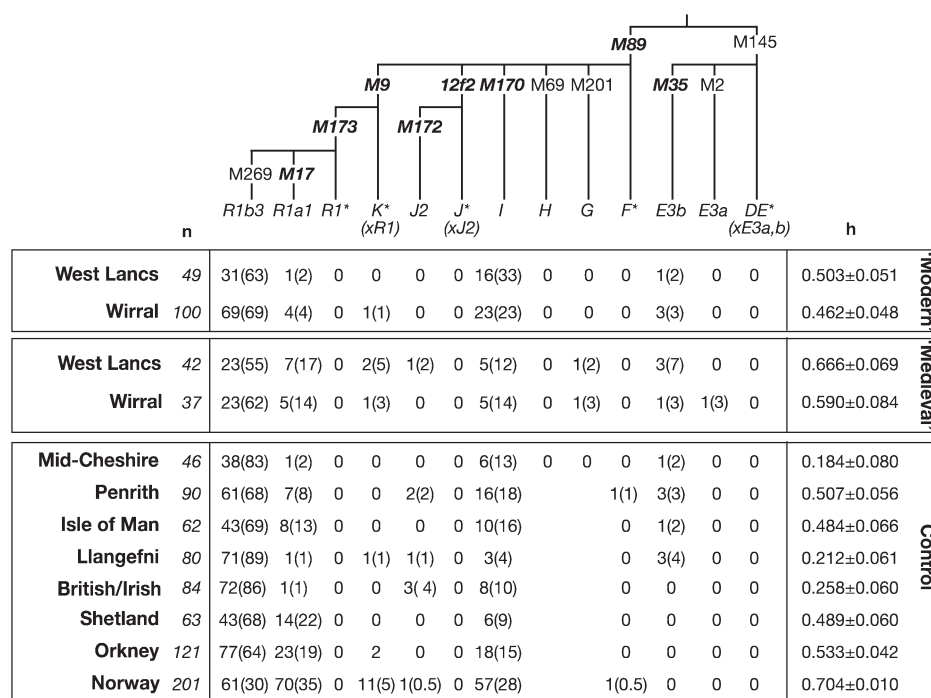


FIG. 2.—Y-chromosomal haplogroups in Wirral and West Lancashire samples and controls. Binary marker phylogeny of the Y chromosome, showing mutations on the branches of the tree, and shorthand haplogroup names (Jobling and Tyler-Smith 2003) beneath. Mutations in bold italic type were also typed in the study of Capelli et al. (2003). Below the phylogeny are given the number of chromosomes carrying the haplogroup, with percentages in parentheses. *n*, sample size; *h*, Nei's unbiased estimator of gene diversity. With the exception of Mid-Cheshire, data on the control populations are from Capelli et al. (2003), and in these samples, haplogroups *G* and *H* are subsumed under *F** because the markers M69 and M201 were not typed. Lancs: Lancashire.

admixture than their modern counterparts, support the idea that the northwest England was once heavily populated by Scandinavian settlers, and validate the surname-ascertainment approach.

Materials and Methods

DNA Samples

Buccal samples were taken with informed consent, and DNA was extracted as described (King et al. 2006).

Samples were collected from Mid-Cheshire, Wirral, and West Lancashire under the 2 generations of residence criterion.

Independent samples were also collected from the Wirral and West Lancashire based upon a patrilineal residence criterion and possession of a surname known from historical documentary sources to have been present in the region prior to 1572. For the Wirral, we compiled a list of 236 surnames from the 1545 subsidy rolls (Irvine and Sanders 1894) listing all households in the Wirral recorded during the reign of Henry VIII, supplemented with 2 surnames from records of court proceedings dating from 1353 (Booth 1983), 1 from alehouse licensing records from 1572 (Bennett and Dewhurst 1940) and 3 based on specific old local place-names. For West Lancashire, we used a list of 232 surnames based on a list of inhabitants of Ormskirk, Scarisbrick with Hurlton, Bickerstaffe, Burscough with Marton, Westhead with Lathom, and Skelmersdale who promised to contribute to the stipend of the priest of the altar

of Our Lady at Ormskirk in 1366 (Peet 1991); this was supplemented with 37 surnames based on specific old local place-names (Ekwall 1922; McKinley 1981) and allowing additional surnames containing particular old place-name elements of Scandinavian origin. Some surnames were converted into their current equivalents to allow matching to modern donors' names. Within each sample, duplicate surnames (including known spelling variants) were avoided, though some surnames are found in both Wirral and West Lancashire samples, carried by different and, to our knowledge, unrelated individuals.

Comparative data were also taken from the literature (Capelli et al. 2003).

Y-Chromosomal Haplotyping

Binary markers (Y Chromosome Consortium 2002) shown in figure 2 were typed hierarchically using the SNaP-shot minisequencing procedure (Applied Biosystems, Foster City, CA) and an ABI3100 Genetic Analyzer (Applied Biosystems). Initially, all chromosomes were typed with Multiplex I of Bosch et al. (2006) containing markers M9, M69, M89, M145, M170, M172, M201, and 12f2. Chromosomes belonging to haplogroup DE were further typed with Multiplex III (Bosch et al. 2006) containing markers M33, M35, M75, M78, M81, M96, M123, and P2, whereas chromosomes in haplogroup K*(xR) were typed with the markers M17 and M173 (Bosch et al. 2006) and M269 (Adams et al. 2006).

For the purposes of comparison with published data, haplogroups were combined in some cases; in particular, chromosomes defined by us as hgG were placed into the superhaplogroup F*(xIJK). The haplogroup we defined as R1b3 was taken to be equivalent to R1(xR1a1) (Capelli et al. 2003).

Six Y-specific microsatellites (DYS19, DYS388, DYS390, DYS391, DYS392, and DYS393), chosen to be compatible with published control data (Capelli et al. 2003), were typed in a single multiplex as described (Thomas, et al. 1999).

Analysis

Population differentiation tests and the generation of F_{ST} and R_{ST} matrices were carried out using Arlequin (Schneider et al. 2000). Multidimensional scaling was done using PROXSCAL within SPSS 14.0.

Admixture analysis was carried out using the mp estimator (Helgason et al. 2001). The probability that a particular haplotype from the admixed population originated from the Norwegian parental population is determined by its relative frequency in Norwegian and British/Irish samples. If the haplotype is not present in the parental populations, this probability is derived from the relative frequency of the most closely related haplotypes in terms of mutational differences. The average proportion of haplotypes assigned a Norwegian origin, plus standard deviation, was derived from 5,000 runs of a Monte Carlo simulation. Note that the assumptions underlying the admixture estimation do not permit significance testing of differences between proportions. Binary markers and microsatellites were used together, with the former given a relative weight of 100 to reflect their lower mutation rates. The Norwegian parental sample ($n = 201$) was from a published data set (Capelli et al. 2003), and the British/Irish parental sample was assembled from the same source. We followed precedent (Goodacre et al. 2005) by pooling central Scottish and central Irish haplotypes (Pitlochry and Castlereas samples [Capelli et al. 2003] combined, $n = 84$). To reduce bias, we equalized the sizes of the parental population samples by random subsampling of 84 chromosomes from the larger Norwegian set prior to analysis. Comparison of 10 random subsets (Fisher's exact test) showed no significant differences.

Results

Two independent samples of unrelated males representing the Wirral and 2 representing West Lancashire were collected using different criteria. The first type of sample (which we refer to here as modern) is based simply on 2 generations of residence and ignores surname. Subjects for the second sample (medieval) were also required to have at least 2 generations of residence and to have their earliest recorded patrilineal ancestor born in the relevant area. However, in addition they were required to carry surnames (supplementary information, Supplementary Material online) that were present in the relevant region prior to 1572 as judged by documentary sources (see Materials and Methods). Note that hereditary surnames were not established

until long after the end of Viking rule, so our ascertainment does not require names themselves to be of Scandinavian origin; the fact that many of them do contain Scandinavian elements reflects the use of local place-names in the locative surnames. The approach of surname-based ascertainment yielded samples of 37 and 40 males, respectively, for Wirral and West Lancashire.

The Y chromosomes of the "modern" and "medieval" Wirral and West Lancashire samples were analyzed using 6 microsatellites (supplementary table, Supplementary Material online) and a total of 13 binary markers defining 13 haplogroups (fig. 2), of which 8 were observed. These haplogroups are typical of western European Y chromosomes, with one exception: a single example of hgE3a in the Wirral medieval sample. This haplogroup is typical of sub-Saharan African populations, comprising 48% of a continent-wide sample of 1,122 African chromosomes (Wood et al. 2005), and is not reported in a composite sample of 2,193 British Isles males (Capelli et al. 2003; King et al. 2007). It probably represents an African migrant but not a recent one because the individual carrying the chromosome reports at least 4 generations of residence in the Wirral. It may, like an hgA1 chromosome found previously in a man with ancestry in Yorkshire (King et al. 2007), represent African presence (Fryer 1984) via the Roman occupation or the Atlantic slave trade, and the proximity of the Wirral to the port of Liverpool might suggest the latter.

To ask if our 2 sampling methods led to a significant difference in haplogroup profiles, the modern and medieval samples were compared in population differentiation tests. Both Wirral and West Lancashire showed significant modern–medieval differences with P values of 0.032 and 0.006, respectively. In both cases, the medieval samples contain a greater number of haplogroups than do the modern samples. Gene diversity in both medieval samples is increased compared with their modern counterparts (fig. 2), suggesting that some degree of recent homogenization has occurred possibly through immigration from relatively low-diversity populations.

To illuminate the basis for this modern–medieval difference, we compared all 4 samples with a modern sample from Mid-Cheshire (a nearby region lacking Scandinavian place-names) collected and analyzed as part of this study and with other modern data from the literature (Capelli et al. 2003). From Britain, we chose nearby western British populations (the Isle of Man, Llangefni in Anglesey, and Penrith) and a sample (British/Irish) representing the putative population of the western British Isles prior to the Viking incursions made by pooling central Scottish and central Irish samples (see Materials and Methods). Samples from Orkney and Shetland were included because these are known to show substantial Scandinavian admixture (Goodacre et al. 2005), and a sample from Norway was used to represent a possible Viking source population (fig. 3).

HgR1a1 is a relatively frequent lineage in Norway, Shetland, Orkney, and the Isle of Man but rare in most mainland English and Welsh samples (Capelli et al. 2003) (fig. 3). The medieval sample from West Lancashire shows a significant increase in the proportion of hgR1a1 with respect to its modern counterpart ($P = 0.044$, Fisher's

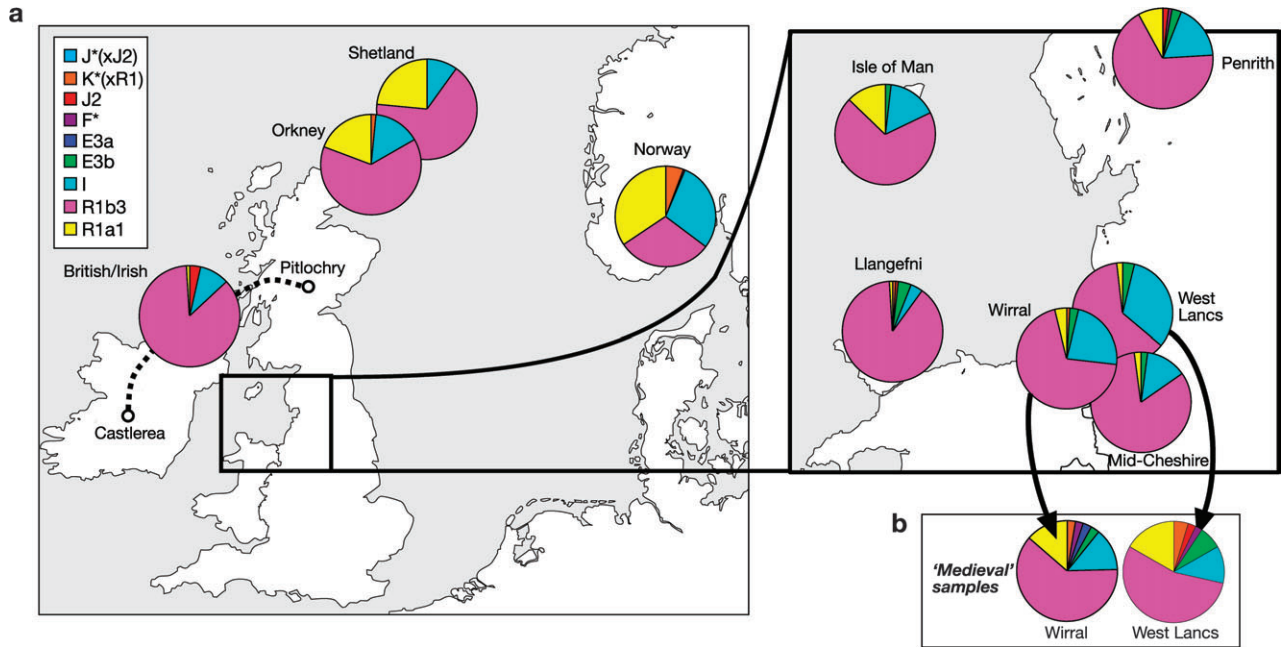


FIG. 3.—Haplogroup distributions in Wirral, West Lancashire, and control populations. (a) Haplogroup profiles of modern samples from the Wirral and West Lancashire and from control populations. Sectors in pie charts are colored according to haplogroup, and sector areas are proportional to haplogroup frequency. Lancs: Lancashire. (b) Haplogroup profiles of medieval samples from the Wirral and West Lancashire ascertained by surname.

exact test), and for the Wirral samples, the increase is close to significance ($P = 0.051$). These observations seem compatible with a higher proportion of Viking lineages in the medieval than in the modern Wirral and West Lancashire samples. Comparison of the microsatellite haplotypes of these modern and medieval examples of hgR1a1 chromosomes (supplementary table, Supplementary Material online) shows that they form a coherent haplotype cluster, suggesting that the use of the surnames-based sampling is not altering the nature of the hgR1a1 haplotypes sampled but simply increases their proportions. However, this conclusion might change if the resolution of microsatellite typing were higher.

Figure 4a shows the result of a multidimensional scaling analysis based on population pairwise F_{ST} values calculated from haplogroup frequencies. The medieval Wirral and West Lancashire samples are differentiated from their modern counterparts primarily in dimension 2 of the plot and lie closer to samples from the Isle of Man and Orkney, known to have experienced significant Scandinavian input (Capelli et al. 2003; Goodacre et al. 2005). In a parallel analysis based on population pairwise R_{ST} values calculated from microsatellite data, the trend is similar (fig. 4b).

Admixture analysis, in which individual samples are treated as hybrid populations made up of contributions from 2 parental populations, provides a means of assessing statistically the relative degree of putative Viking genetic input into the modern and medieval samples. Following published precedent (Goodacre et al. 2005), we assessed admixture between the Norwegian and the “British/Irish” samples in the 2 Wirral and 2 West Lancashire samples. As controls, we also considered admixture within the samples from Llangefni in Anglesey (Wales), Mid-Cheshire,

Penrith, the Isle of Man, and Shetland and Orkney. We employed the mp estimator of Helgason et al. (2001), analyzing admixture using a combination of binary and microsatellite marker data (table 1).

Where comparisons can be made, the proportions of Scandinavian admixture that we estimate differ somewhat from those seen in a previous study (Goodacre et al. 2005): for Shetland, we observe 41% Scandinavian ancestry compared with the previously published figure of 44% and the corresponding figures for Orkney are 50% compared with 31%. Such differences may reflect sampling variance or differences in the compositions of the parental and hybrid samples and in the marker resolution—we used greater numbers of both binary markers and microsatellites. Note that direct comparisons with the study from which we draw our comparative data (Capelli et al. 2003) are problematic because it used a different admixture method and considered admixture between a Norwegian sample and a sample chosen to represent Anglo-Saxons. The lowest proportions of Scandinavian admixture among our samples are seen in Llangefni and Mid-Cheshire, at 10% and 21%, respectively. In agreement with previous results (Capelli et al. 2003), a higher proportion (39%) is seen in the Isle of Man, where there is a known history of Viking presence, and Penrith (37%), which shows Scandinavian dialect influence (Reaney 1927). The modern samples from Wirral and West Lancashire both show 38% Scandinavian admixture, markedly higher than the nearby sample from Mid-Cheshire (21%). This is consistent with the historical and place-name evidence for greater Viking presence in Wirral and West Lancashire than in Mid-Cheshire.

The medieval sample from West Lancashire shows an increased proportion ($51 \pm 4\%$) of Scandinavian ancestry

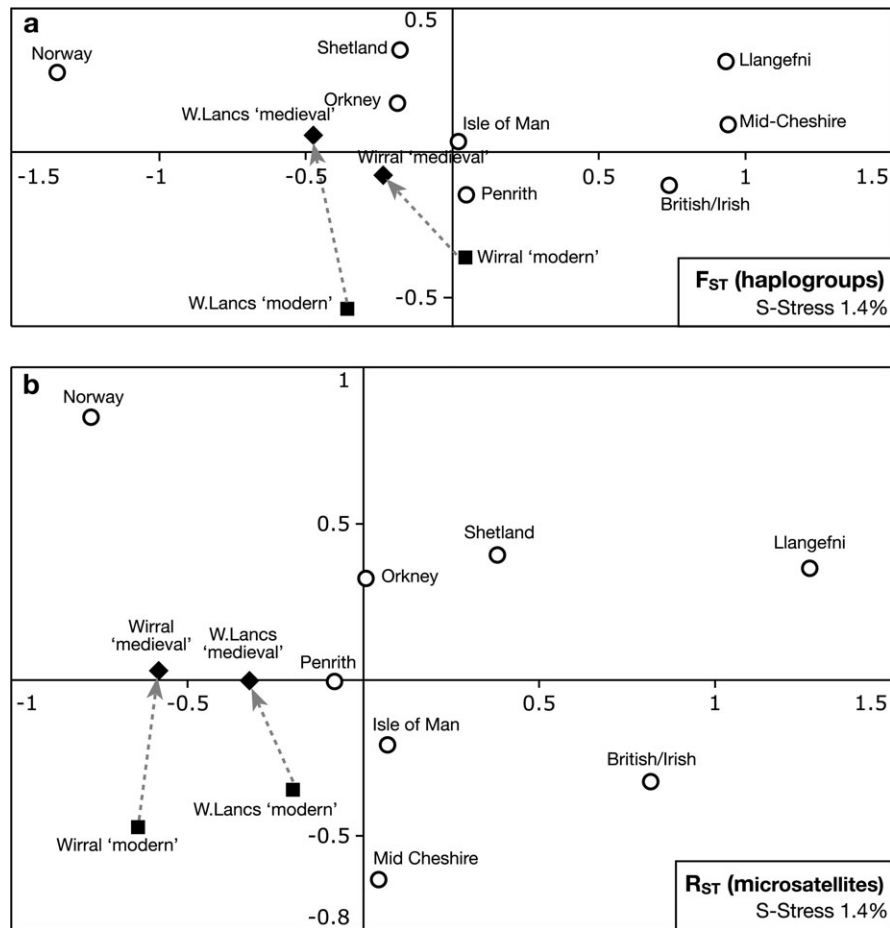


FIG. 4.—Multidimensional scaling (MDS) plots illustrating the relationships between Wirral, West Lancashire, and control populations. (a) MDS based on population pairwise F_{ST} values from haplogroup data. Dotted arrows highlight the differences between modern and medieval Wirral and West Lancashire samples. Lancs: Lancashire. (b) MDS based on population pairwise R_{ST} values from microsatellite data.

compared with its modern counterpart ($38 \pm 4\%$); the equivalent values for Wirral are $47 \pm 5\%$ and $38 \pm 3\%$. These differences, revealed by our different sampling strategies, are likely to reflect a change in haplotype frequencies due to postmedieval immigration and are supported by genetic distances (F_{ST}) between the Norwegian sample and the Wirral

and West Lancashire samples. F_{ST} between Norwegians and the West Lancashire modern sample is 0.130, whereas the value for the medieval sample is only 0.069; corresponding values for the Wirral samples are 0.162 and 0.096.

The surnames that we used to ascertain the medieval samples belong to a wide range of frequencies—from

Table 1
Admixture Proportions in British Isles Populations

Admixed Population	n^a	Proportion Scandinavian Ancestry \pm Standard Deviation	Proportion British Ancestry \pm Standard Deviation
Llangefni	80	0.10 ± 0.02	0.90 ± 0.02
Mid-Cheshire	46	0.21 ± 0.03	0.79 ± 0.03
Isle of Man	62	0.39 ± 0.04	0.61 ± 0.04
Penrith	90	0.37 ± 0.03	0.63 ± 0.03
Orkney	121	0.50 ± 0.03	0.50 ± 0.03
Shetland	63	0.41 ± 0.04	0.59 ± 0.04
Wirral modern	100	0.38 ± 0.03	0.62 ± 0.03
Wirral medieval	37	0.47 ± 0.05	0.53 ± 0.05
Wirral medieval rarer surnames	26	0.51 ± 0.06	0.49 ± 0.06
West Lancs ^b modern	49	0.38 ± 0.04	0.62 ± 0.04
West Lancs ^b medieval	40	0.51 ± 0.04	0.49 ± 0.04
West Lancs ^b medieval rarer surnames	30	0.53 ± 0.05	0.47 ± 0.05

^a Sample size.

^b Lancashire.

“Otty,” with only 146 bearers in 1998 (www.spatial-literacy.org/UCLnames/) to “Brown,” with 242,765 (supplementary table, Supplementary Material online). The more frequent names are likely to have had multiple founders and are relatively widespread in Britain and so may provide less reliable links to medieval presence in the specific regions under study. To address this, we subsampled from the 2 medieval samples by removing surnames with frequencies of greater than 20,000 (supplementary table, Supplementary Material online), resulting in reduced sample sizes of 26 and 30 for Wirral and West Lancashire, respectively. We then repeated the admixture analysis. In both cases, the proportions of Scandinavian admixture in the subsampled medieval populations increased further compared with the original medieval samples: admixture proportions in the modern and medieval subsampled Wirral populations are now $38 \pm 3\%$ compared with $51 \pm 6\%$ and the corresponding values for West Lancashire are $38 \pm 4\%$ compared with $53 \pm 5\%$.

Discussion

Since the discovery of the first genetic polymorphisms over a century ago, genetics has contributed much to our understanding of the human past. However, despite advances in ancient DNA technologies, genetic studies remain limited by the requirement to study extant populations, drawing conclusions about the compositions of past populations using various methods of inference. The tempo and mode of change in populations through time are difficult to discern, though we know that migration, drift, and alterations in social structure through changes in lifestyle can all influence population structure markedly and, in some cases, can cause dramatic change in only a few generations (Thomas et al. 2006; Chaix et al. 2007).

The association of Y chromosomes with patrilineal surnames, which were established in England some 700 years ago (McKinley 1990), provides a potential tool to investigate changes in population structure over the last few centuries (Manni et al. 2005)—an era in which population growth and migration have been considerable. Here, we have focused on a region in which historical and place-names evidence suggests a past presence of Viking incomers and demonstrated that samples ascertained using surnames present in medieval times show a markedly greater proportion of Scandinavian ancestry. Our genetic analysis appears to confirm a belief, based on archaeological and place-names evidence, that the northwest of England was once heavily settled by Scandinavians, many of whom were refugees expelled from Ireland in AD 902 (Wainwright 1942, 1945, 1948, 1975).

Nearby Mid-Cheshire, with its absence of Viking place-names, shows a much weaker signal of Viking presence than West Lancashire or the Wirral (table 1). Prior to arriving in Wirral, Ingimund’s Scandinavian refugees expelled from Ireland are reported to have made an attempt to settle in Anglesey (Wainwright 1942, 1975; Cavill et al. 2000; Harding 2002); recent archaeological evidence (Redknap 2000) for some Scandinavian activity supports this, but we observe a low level of Scandinavian admixture

there. In contrast, significant and lasting settlements appear to have been made in the northwest of England and the Isle of Man, and there is genetic evidence (Capelli et al. 2003) (table 1) for a substantial contribution in Cumbria (Penrith). The detailed relationship of the settlements described in this paper to other Viking activities in the Irish Sea region still remains to be unravelled, but the combination of linguistic, archaeological, historical, literary, and, where possible, genetic evidence will continue to provide valuable clues.

Our findings suggest that the approach of surname-based ascertainment is promising and may provide a means to address the issue of population change through time, as well as some specific questions in the histories of regions having patrilineal surnames. The robustness of conclusions will be improved by the inclusion of both modern and medieval samples from places not thought to have experienced particular population incursions, such as Mid-Cheshire in our study (surname-based sampling from this region will form part of a future project). The approach relies on the existence of appropriate historical surname lists, which are plentiful, and, as we have shown, can also be supplemented by lists based on place-names. However, regions in which the time depth of patrilineal surnames is shallow, such as Wales, where patronymic systems persisted to some extent until the 19th century (McKinley 1990), will be more difficult to study in this way.

To maximize the benefits of surname-based ascertainment, care needs to be taken in sampling. The effects on the Scandinavian admixture proportions of subsampling from our medieval samples suggest that common surnames should be avoided where possible. In this study, we sampled 1 male per surname for each of the 2 regions studied. However, previous studies of the relationships between surnames and Y haplotypes have shown the effects of nonpaternities in breaking the link between the 2 (Sykes and Irven 2000; King et al. 2006; McEvoy and Bradley 2006), and a recent nonpaternity could introduce the Y haplotype of an outsider into a surname which has medieval roots in a study area. To obviate this problem, it may be desirable to sample more than one male per surname and to treat the majority haplotype as a founder. In fact, the chance of sampling recently introgressed Y chromosomes increases as sample size per surname increases but the power to distinguish such chromosomes from the earlier founding types also increases because a consensus Y chromosome type can more readily be derived.

Genetic drift is a powerful force patterning the diversity of Y haplotypes, and computer simulations (Sturges and Haggert 1987), as well as the experience of genealogists (McKinley 1990), show that the effect of drift upon the survival of surnames and on the number of their bearers is correspondingly strong. The degree of drift since the period of surname adoption may have a large impact on the diversity of haplotypes and surnames, and the value of using our approach to compare different populations may be compromised if these populations have experienced different magnitudes of drift. In comparing populations, it will be important to take into account historical information on their demographic histories. Furthermore, drift during the 300–400 years between the Viking age and the era in which surname adoption took place may mean that estimates

based on surnames may not be an accurate reflection of haplotype frequencies at the earlier time of the introduction of Viking Y chromosomes.

The admixture approach we have employed has been useful in providing evidence that surname-based ascertainment reveals some aspects of the past compositions of populations. However, it is clearly not ideal to use modern parental populations to assess admixture in medieval hybrids, and the results are likely to be more reliable if the parental samples themselves could be ascertained in a similar way to the hybrids. A further shortcoming of our admixture analysis is that we have assumed that the non-Celtic contributions are all due to Scandinavians. A more sophisticated approach would also consider an Anglo-Saxon contribution, though distinguishing this from a Danish Viking contribution to more easterly British populations would be difficult because modern proxies for these 2 different source populations are so similar in their Y-chromosomal haplotype compositions (Capelli et al. 2003).

The use of patrilineal surnames in ascertainment provides both the power of our approach and its major limitation because any analysis of the structure or history of populations based on a single genetic locus, the Y chromosome, has inherently low power and population statistics calculated from Y data have high variance (Wilson et al. 2001). Furthermore, we can learn nothing about changes in the maternal genetic landscape, which is unfortunate, because the role of women in the Viking colonizations was as important as that of men (Jesch 1991). Nonetheless, in the absence of a time machine, the link between a haplotype and a cultural marker, the surname, may provide the only practical means to access the genetic composition of populations in the past. As well as allowing us to investigate the influence of migration and drift over the last few centuries in changing the population structure of Britain, the method should be applicable to other regions where surnames are patrilineal and suitable historical records survive.

Supplementary Material

Supplementary table and information are available at *Molecular Biology and Evolution* online (<http://www.mbe.oxfordjournals.org/>).

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