Y Chromosome Evidence for Anglo-Saxon Mass Migration

Michael E. Weale,[*1] *Deborah A. Weiss,*[†1] *Rolf F. Jager,*[*‡] *Neil Bradman,** *and Mark G. Thomas**

*The Centre for Genetic Anthropology, Departments of Biology and Anthropology, University College London, University of London; †Department of Anthropology, University of California, Davis; and ‡Faculteit Biologie, Vrije Universiteit, Amsterdam, The Netherlands

British history contains several periods of major cultural change. It remains controversial as to how much these periods coincided with substantial immigration from continental Europe, even for those that occurred most recently. In this study, we examine genetic data for evidence of male immigration at particular times into Central England and North Wales. To do this, we used 12 biallelic polymorphisms and six microsatellite markers to define high-resolution Y chromosome haplotypes in a sample of 313 males from seven towns located along an east-west transect from East Anglia to North Wales. The Central English towns were genetically very similar, whereas the two North Welsh towns differed significantly both from each other and from the Central English towns. When we compared our data with an additional 177 samples collected in Friesland and Norway, we found that the Central English and Frisian samples were statistically indistinguishable. Using novel population genetic models that incorporate both mass migration and continuous gene flow, we conclude that these striking patterns are best explained by a substantial migration of Anglo-Saxon Y chromosomes into Central England (contributing 50%–100% to the gene pool at that time) but not into North Wales.

Introduction

Following depopulation during the last glacial maximum and subsequent resettlement by hunter-gatherers ca. 7000 B.C., the history of Britain has been marked by a series of cultural transitions. These include the appearance of sedentary agricultural communities (the Neolithic transition) (ca. 4000 B.C.), the arrival and spread of Late Bronze-Iron Age and Celtic material culture (ca. 1000–100 B.C.), Roman occupation and influence (A.D. 43–410), the rise of Anglo-Saxon language and culture (ca. A.

Mol. Biol. Evol. 19(7):1008–1021. 2002

of continental culture in England (Esmonde-Cleary 1993) and suggested a contemporaneous desertion of continental Germanic settlements. More recently, however, authors have questioned the evidence for large-scale immigration (Crawford 1997; Hamerow 1997) and continental emigration (Näsman 1988; Petersen 1991) and emphasized the continuity of the Romano-British population in England. The sudden change to an Anglo-Saxon culture has been attributed instead to rapid acculturation and indigenous developments, with only a small number of Germanic immigrants (perhaps a male military elite) settling in Britain (Arnold 1984; Hodges 1989; Higham 1992). The contribution of Anglo-Saxon immigration to the modern English gene pool thus remains uncertain.

Genetic data comprise an obvious source of information to help resolve these issues. Previous studies examining biological variation in Britain have identified various patterns of genetic variation. These include studies on blood groups (Bodmer 1993; Mascie-Taylor and Lasker 1996), serum proteins and isoenzymes (Cartwright, Hargreaves, and Sunderland 1977; Mastana et al. 1993), HLA genes (Papiha, Duggan Keen, and Rodger 1985; Bodmer 1993), and multiple classical genetic markers (Falsetti and Sokol 1993; Cavalli-Sforza, Menozzi, and Piazza 1994; Mastana and Sokol 1998), as well as on patterns of disease incidence, such as phenylketonuria (Tyfield, Osborn, and Holton 1997), multiple sclerosis (Poser 1994), skin cancer (Long, Darke, and Marks 1998), and haemochromatosis (Merryweather-Clarke et al. 1997). These data have been interpreted as reflecting historical migrations and settlement patterns, but formal testing of alternative migratory models has not been attempted.

The non–recombining portion of the Y chromosome and the mitochondrial genome are useful sources of data because they provide exceptionally detailed high-resolution haplotypes, allowing fine definition of the underlying gene genealogies. The Y chromosome, which is much larger, is particularly useful because it has many slowly mutating biallelic markers to help resolve genealogical clades as well as rapidly mutating microsatellite markers to aid in the dating of very recent events (Thomas et al. 1998; Kayser et al. 2001). The extra information provided by these high-resolution haplotypes facilitates the fitting of population genetic models. Although the resulting demographic inferences are based on only a single locus, increasing the effects of evolutionary variance derived from chance differences in the genealogy, such systems are still useful because they are the only ones that allow sex-specific demographic inferences to be made.

Previous studies of mtDNA and Y chromosome variation across Europe have reported evidence of Paleolithic and Neolithic expansions reflected in large-scale clines (Torroni et al. 1998; Casalotti et al. 1999; Hill, Jobling, and Bradley 2000; Malaspina et al. 2000; Richards et al. 2000; Rosser et al. 2000; Semino et al. 2000; Simoni et al. 2000), but these studies did not consider the effects of historical migrations on more local patterns of genetic variation. Helgason et al. (2000) examined Y chromosome and mtDNA variation in the modern Icelandic population to assess the relative proportions of Scandinavian and Celtic ancestry stemming from historical migrations, whereas Wilson et al. (2001) compared Y chromosome, X chromosome, and mtDNA variation in eight population samples (including the Llangefni, Norway, and Friesland samples reported here) to investigate genetic changes associated with cultural transitions in North Wales and Orkney, two areas at the fringes of the British Isles. Through a comparison of signature haplotypes, Wilson et al. (2001) found evidence for Celtic male ancestry in the North Welsh and/or both Celtic and Scandinavian (Viking) male ancestry in the modern Orcadian population. Further comparisons of these British samples with Basque data suggested that the male Celtic genetic component was Paleolithic in origin, and therefore, that subsequent cultural transitions in North Wales were not associated with substantial incoming male gene flow. However, the study of Wilson et al. did not directly address the effects of cultural transitions in other areas of Britain.

This study is the first to analyze data from an east-west transect across Central England and North Wales to evaluate evidence of male population migration under a wide range of flexible population genetic models. Samples were collected in seven towns along this transect, and a combination of slowly evolving biallelic markers (so-called Unique Event Polymorphisms or UEPs) and rapidly evolving microsatellites on the Y chromosome were typed to look for evidence of local or small-scale genetic transitions. We compared the data with samples from Friesland and Norway to look for evidence of male immigration from the continent. In addition to comparing signature haplotypes among population samples, we applied novel model-based methods to make inferences about both the possible timing and extent of male continental migration into Central England.

Materials and Methods

Population Samples and Genotyping

Buccal swabs were collected from 313 males in the British towns of North Walsham, Fakenham, Bourne, Southwell, Ashbourne, Abergele, and Llangefni (fig. 1). These towns were selected because they lie approximately 50 km apart along an east-west transect of Britain and are long established market towns (mentioned in the Domesday Book of A.D. 1086 with current populations of 5,000–10,000) that are less likely to be influenced by recent migration than large cities (Pooley and Turnbull 1998). We apply the labels ''East Anglia'' to the North Walsham and Fakenham samples, ''Midlands'' to the Bourne, Southwell, and Ashbourne samples, ''North Wales'' to the Abergele and Llangefni samples, and ''Central England'' to the combined Midlands and East Anglia samples, although these labels are for convenience and only designate the general geographical area of these samples. Samples were acquired if both the donor and the donor's paternal grandfather were born within 30 km of one of these market towns. For

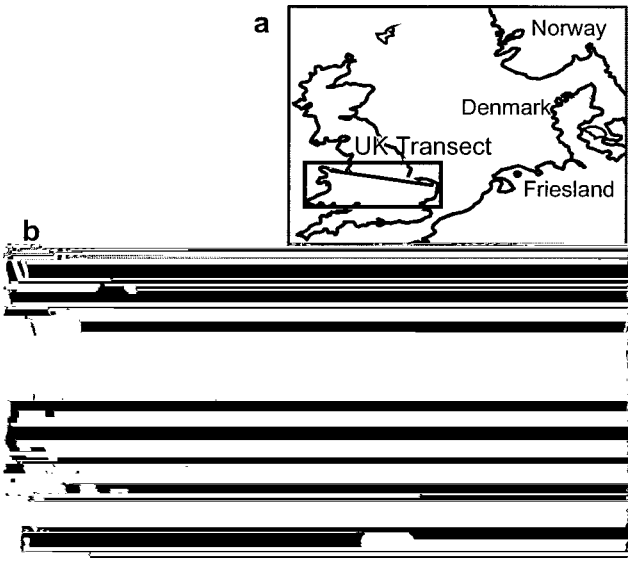

FIG. 1.—(*a*) Map of Britain and neighboring area. (*b*) Enlargement showing towns within Britain along east-west transect.

comparison, we also collected DNA samples from 94 males in Friesland (northern Netherlands) and 83 males in Norway, two nearby locations with different roles in Britain's immigration history. Friesland is thought to be one of the source locations for Anglo-Saxon immigration both because of its geographical location and because Frisian is considered to be the closest extant language to Old English (Nielsen 1985). Norway represents one source of the Viking invaders. Samples were collected anonymously, and informed consent was obtained from all individuals before samples were taken.

Standard phenol-chloroform DNA extractions were performed. Six microsatellites (DYS19, DYS388, DYS390, DYS391, DYS392, DYS393) and 11 of the biallelic UEP markers (92R7, M9, M13, M17, M20, SRY1465, SRY4064, SRY10831, sY81, Tat, YAP) were typed and analyzed, as described by Thomas, Bradman, and Flinn (1999). One additional UEP marker, 12f2, was typed, as described by Rosser et al. (2000). Microsatellite repeat sizes were assigned according to the nomenclature of Kayser et al. (1997). Haplogroups were defined by the 12 UEP markers according to a nomenclature modified from Rosser et al. (2000) and Weale et al. (2001) and are presented in figure 2. The correspondence between this nomenclature and that proposed by the Y Chromosome Consortium (2002) is as follows: hg1 5 P*(xR1a), hg2 5 BR*(xDE,JR), hg3 5 R1a1, hg4 5 DE*(xE), hg7 5 A3b2, hg8 5 E3a, hg9 5 J, hg16 5 N3, hg20 5 O2b, hg21 5 E*(xE3a), hg26 5

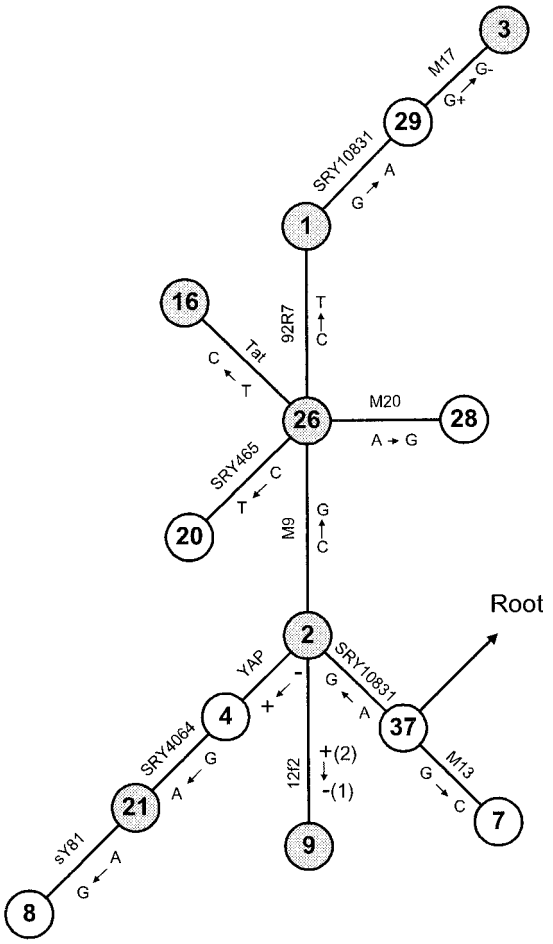

FIG. 2.—Y chromosome haplogroup network defined by the 11 UEP markers used in this study following a nomenclature modified from Rosser et al. (2000) and Weale et al. (2001). The root has been deduced by comparison with other great ape species (Underhill et al. [2000]; P. Underhill, personal communication for position of SRY10831). Shading indicates haplogroups observed in this study.

(URL: http://www.maths.abdn.ac.uk/ ; ijw), extended from the Markov chain Monte Carlo (MCMC) algorithm presented by Wilson and Balding (1998). Microsatellite mutation likelihoods were calculated using an unbounded symmetric stepwise mutation model. The priors chosen for major BATWING parameters are summarized in table 1. Locus-specific priors for the mutation rate per generation were based on observed mutations for these loci, as reported in Heyer et al. (1997), Bianchi et al. (1998), and Kayser et al. (2000), combined with a standard exponential pre-prior. As a precautionary measure, DYS388 was excluded from BATWING analysis (and also from the Monte Carlo likelihood method described later) because no published data on observed meioses are available for this locus, and therefore, no direct verification exists of stepwise mutation behavior. Unique-event mutations inferred from binary marker data were

Table 1
Prior Distributions of Major BATWING Parameters and Posterior Values Based on a Splitting Model Between Central England and Friesland.

		Prior Quantiles			Posterior Quantiles		
Parameter	Prior	2.50%	50%	97.50%	2.50%	50%	97.50%
DYS19 mutation rate	Gamma(3,1459)	0.00042	0.0018	0.0050	0.0013	0.0025	0.0043
DYS390 mutation rate	Gamma(5,929)	0.0017	0.0050	0.011	0.0017	0.0033	0.0056
DYS391 mutation rate	Gamma(3,878)	0.00070	0.0030	0.0082	0.00066	0.0014	0.0026
DYS392 mutation rate	Gamma(2,878)	0.00028	0.0019	0.0063	0.00058	0.0012	0.0022
DYS393 mutation rate	Gamma(1,878)	0.000029	0.00079	0.0042	0.00067	0.0013	0.0025
Initial effective population size	Gamma(1.1,0.0001)	371	7,903	38,960	125	356	987
Growth rate	Gamma(1.01,1)	0.026	0.703	3.71	0.029	0.08	2.02
Time growth starts (in generations)	Uniform(0,TMRCA[a])	—	—	—	47	91	192

[a] TMRCA: time to most recent common ancestor.

Table 2
Haplogroup Frequencies and Genetic Diversities in Seven British Towns, Friesland and Norway

	North Wales		Midlands			East Anglia			
Haplogroup	Llangefni (n = 80)	Abergele (n = 18)	Ashbourne (n = 54)	Southwell (n = 70)	Bourne (n = 12)	Fakenham (n = 53)	N. Walsham (n = 26)	Friesland (n = 94)	Norway (n = 83)
hg1	0.888	0.556	0.648	0.643	0.667	0.566	0.577	0.553	0.265
hg2	0.038	0.056	0.222	0.186	0.333	0.415	0.308	0.340	0.446
hg3	0.013	—	0.037	0.057	—	—	0.038	0.074	0.217
hg9	0.013	—	0.037	0.057	—	—	0.038	0.011	0.024
hg16	—	—	—	—	—	—	—	—	0.036
hg21	0.038	0.389	0.056	0.057	—	0.019	0.038	0.021	0.012
hg26	0.013	—	—	—	—	—	—	—	—
Genetic diversity, h	0.212 (±0.0607)	0.569 (±0.0707)	0.535 (±0.0660)	0.550 (±0.0606)	0.485 (±0.1059)	0.517 (±0.0301)	0.591 (±0.0767)	0.578 (±0.0339)	0.690 (±0.0290)

Note.—Dash indicates haplogroup was not observed. Genetic diversities (based on haplogroup frequencies) are given ± standard error.

large gene flow event. A program was written (available from M.E.W.) to simulate the coalescent under growth from an initially constant effective population size, allowing a single split T_S generations ago of the parent population into two descendent populations, A and B, and subsequent background migration at a rate m, where a proportion m migrates from population A to B and simultaneously from B to A in each generation. A further extension to the program allowed for a single unidirectional migration event from B to A at a time T_F generations ago, such that lineages in A immediately after this event had a probability F of having just migrated from B. Final sample sizes in each population were set to match those obtained in our study, and microsatellite repeat sizes in these samples were simulated using the unbounded symmetric stepwise mutation model. Parameters for population growth and mutation rates were set as fixed constants based on BATWING posterior modal values and were validated firstly by checking that the simulated within-population microsatellite variances were similar to observed values and secondly through comparison with BATWING results under scenarios involving no background migration. These parameters were fixed as follows: initial effective population size = 300; start of growth = 80 generations before present (BP); growth rate = 0.06; ratio of effective sizes of population A to population B = 1:1; mutation rates—DYS19 = 0.0023, DYS390 = 0.0030, DYS391 = 0.0012, DYS392 =

Table 3
UEP 1 Microsatellite Haplotype Frequencies and Genetic Diversities in Seven British Towns, Friesland, and Norway

Ht #	Microsatellite Haplotype[a]	Llan. (n 5 80)	Aber. (n 5 18)	Ash. (n 5 54)	South. (n 5 70)	Bour. (n 5 12)	Fak. (n 5 53)	N.Wal. (n 5 26)	Fries. (n 5 94)	Nor. (n 5 83)	Total Counts
Haplogroup 1											
1	14-12-24-11-13-13	0.275	0.056	0.130	0.186	—	0.113	0.231	0.128	0.060	72
2	14-12-23-11-13-13	0.063	—	0.111	0.086	0.083	0.094	0.077	0.170	0.024	43
3	14-12-24-10-13-13	0.025	—	0.130	0.129	—	0.075	—	0.021	0.036	27
4	14-12-25-11-13-13	0.113	0.111	0.037	0.014	0.083	0.038	—	—	0.012	18
5	14-12-23-10-13-13	0.025	—	0.037	0.014	0.167	0.019	0.077	0.021	—	12
6	14-12-24-11-13-14	0.088	0.056	—	—	—	—	—	0.011	0.012	10
7	15-12-24-11-13-13	0.063	0.056	0.037	—	—	—	—	—	0.012	9
8	15-12-24-10-13-13	—	—	0.019	—	—	—	0.038	0.032	0.012	6
9	14-12-24-12-13-13	0.025	—	—	—	0.167	—	—	—	0.012	5
10	15-12-23-11-13-13	—	0.056	—	0.029	—	0.019	—	—	—	4
11	14-12-25-11-13-12	—	—	0.056	0.014	—	—	—	—	—	4
12	14-12-25-10-13-13	0.013	—	—	—	—	0.057	—	—	—	4
13	14-12-24-11-12-13	—	0.056	—	0.014	—	0.038	—	—	—	4
14	14-12-24-11-11-13	0.025	0.056	—	—	—	—	—	—	0.012	4
15	15-12-25-11-13-13	0.038	—	—	—	—	—	—	—	—	3
16	14-13-23-11-13-13	0.025	—	0.019	—	—	—	—	—	—	3
17	14-12-25-11-14-13	0.013	—	—	—	—	0.038	—	—	—	3
18	14-12-24-11-13-12	0.013	—	—	0.014	—	—	—	0.011	—	3
19	14-12-23-11-13-14	—	—	—	0.014	—	0.019	—	—	0.012	3
20	14-12-24-10-13-12	—	—	—	0.014	—	—	—	0.021	—	3
21	14-11-23-11-13-13	—	—	—	—	—	—	0.077	—	—	2
22	15-12-23-10-13-13	—	—	—	0.014	0.083	—	—	—	—	2
23	14-13-24-11-13-13	—	—	—	—	—	—	—	0.021	—	2
24	14-12-26-11-14-14	0.025	—	—	—	—	—	—	—	—	2
25	14-12-24-10-13-14	—	—	0.019	—	—	—	—	0.011	—	2
26	14-12-26-11-14-13	—	0.056	—	—	—	—	0.038	—	—	2
27	14-12-25-12-13-13	0.025	—	—	—	—	—	—	—	—	2
28	12-12-23-11-13-13	—	—	—	0.014	0.083	—	—	—	—	2
29	14-12-22-11-13-13	—	—	—	0.014	—	0.019	—	—	—	2
30	16-12-25-11-13-13	—	—	—	—	—	—	—	—	0.012	1
31	11-12-24-11-13-13	0.013	—	—	—	—	—	—	—	—	1
32	13-12-24-10-13-14	—	—	—	0.014	—	—	—	—	—	1
33	14-12-24-11-14-12	—	—	—	—	—	—	—	0.011	—	1
34	14-12-24-11-14-13	0.013	—	—	—	—	—	—	—	—	1
35	14-12-24-11-14-14	—	0.056	—	—	—	—	—	—	—	1
36	14-12-21-11-13-13	—	—	—	—	—	—	—	0.011	—	1
37	14-12-24-12-13-14	—	—	—	—	—	—	—	0.011	—	1
38	14-12-22-12-13-13	—	—	—	—	—	—	—	—	0.012	1
39	14-12-23-11-14-13	—	—	—	—	—	—	0.038	—	—	1
40	12-12-24-11-13-13	—	—	—	0.014	—	—	—	—	—	1
41	14-12-25-11-13-14	0.013	—	—	—	—	—	—	—	—	1
42	13-12-23-10-13-13	—	—	—	0.014	—	—	—	—	—	1
43	14-12-23-10-14-13	—	—	—	—	—	0.019	—	—	—	1
44	14-12-26-10-13-13	—	—	—	—	—	—	—	0.011	—	1
45	14-12-24-10-14-13	—	—	0.019	—	—	—	—	—	—	1
46	14-12-24-10-13-15	—	—	—	—	—	—	—	0.011	—	1
47	14-12-23-11-13-12	—	—	—	—	—	—	—	—	0.012	1

Table 3
Continued.

Ht #	Microsatellite Haplotype[a]	Llan. (n 5 80)	Aber. (n 5 18)	Ash. (n 5 54)	South. (n 5 70)	Bour. (n 5 12)	Fak. (n 5 53)	N.Wal. (n 5 26)	Fries. (n 5 94)	Nor. (n 5 83)	Total Counts
48	14-13-24-10-12-13	—	—	0.019	—	—	—	—	—	—	1
49	12-12-24-10-13-13	—	—	—	0.014	—	—	—	—	—	1
50	14-14-24-10-13-12	—	—	—	—	—	—	—	0.011	—	1
51	14-14-25-10-13-13	—	—	—	—	—	—	—	—	0.012	1
52	14-12-23-12-13-13	—	—	—	—	—	—	—	0.011	—	1
53	14-12-22-11-13-12	—	—	—	—	—	—	—	—	0.012	1
54	15-12-23-12-13-13	—	—	—	—	—	0.019	—	—	—	1
55	14-12-24-10-12-13	—	—	—	—	—	—	—	0.011	—	1
56	13-12-24-10-14-13	—	—	—	—	—	—	—	0.011	—	1
57	15-12-24-11-13-14	—	—	0.019	—	—	—	—	—	—	1
58	15-12-24-11-15-13	—	—	—	0.014	—	—	—	—	—	1
59	14-12-23-11-11-13	—	—	—	—	—	—	—	0.011	—	1
Haplogroup 2											
60	14-14-22-10-11-13	—	—	0.093	0.029	0.083	0.094	0.077	0.053	0.084	27
61	14-14-23-10-11-13	—	—	0.019	0.014	0.083	0.113	—	0.032	0.133	23
62	15-14-23-10-11-13	—	—	—	—	—	0.019	—	0.021	0.072	9
63	15-14-22-10-11-13	—	—	—	—	0.083	—	—	0.011	0.048	6
64	15-13-23-10-12-14	—	—	—	0.014	—	—	0.077	0.011	0.024	6
65	15-13-23-10-12-15	—	—	—	0.029	—	0.019	—	0.021	—	5
66	15-15-23-10-11-13	—	—	—	—	—	0.019	0.077	0.011	—	4
67	16-14-22-10-11-13	—	—	0.019	0.014	—	—	—	—	0.012	3
68	14-14-22-10-11-14	—	—	—	—	—	0.019	—	0.011	0.012	3
69	17-13-25-11-11-13	0.025	—	—	—	—	—	—	—	—	2
70	16-13-24-10-11-13	—	—	—	—	—	0.038	—	—	—	2
71	16-13-23-10-12-15	—	—	—	—	—	—	—	0.021	—	2
72	14-14-23-11-11-13	—	—	—	—	—	—	—	0.011	0.012	2
73	16-13-23-10-12-13	—	—	—	0.014	—	—	—	0.011	—	2
74	14-14-22-11-11-12	—	—	0.019	—	—	0.019	—	—	—	2
75	15-14-22-11-11-13	—	—	0.019	—	—	0.019	—	—	—	2
76	15-13-24-10-12-15	0.013	—	—	—	0.083	—	—	—	—	2
77	14-14-22-11-11-13	—	—	—	—	—	—	—	—	0.012	1
78	15-12-22-10-10-13	—	—	—	—	—	0.019	—	—	—	1
79	15-12-22-11-11-14	—	—	—	0.014	—	—	—	—	—	1
80	15-13-22-10-11-13	—	—	—	—	—	—	—	0.011	—	1
81	15-13-22-10-11-14	—	—	—	—	—	—	0.038	—	—	1
82	15-13-23-09-12-14	—	—	—	—	—	—	0.038	—	—	1
83	15-13-23-10-12-13	—	—	—	—	—	—	—	0.011	—	1
84	14-14-22-09-11-13	—	—	—	—	—	—	—	0.011	—	1
85	13-14-22-10-11-13	—	0.056	—	—	—	—	—	—	—	1
86	15-13-23-11-11-13	—	—	—	—	—	—	—	0.011	—	1
87	15-13-23-11-12-14	—	—	0.019	—	—	—	—	—	—	1
88	15-12-21-10-11-14	—	—	—	0.014	—	—	—	—	—	1
89	15-14-22-09-11-13	—	—	—	—	—	0.019	—	—	—	1
90	14-13-22-10-11-15	—	—	—	—	—	—	—	0.011	—	1
91	14-16-22-10-11-14	—	—	—	—	—	—	—	0.011	—	1
92	14-12-22-10-11-13	—	—	0.019	—	—	—	—	—	—	1

Table 3
Continued.

Ht #	Microsatellite Haplotype[a]	Llan. (n = 80)	Aber. (n

Table 3
Continued.

Ht #	Microsatellite Haplotype[a]	Llan. (n = 80)	Aber. (n = 18)	Ash. (n = 54)	South. (n = 70)	Bour. (n = 12)	Fak. (n = 53)	N.Wal. (n = 26)	Fries. (n = 94)	Nor. (n = 83)	Total Counts
Haplogroup 16											
137	15-12-23-11-14-14	—	—	—	—	—	—	—	—	0.012	1
138	14-12-23-11-14-14	—	—	—	—	—	—	—	—	0.012	1
139	14-12-24-11-14-14	—	—	—	—	—	—	—	—	0.012	1
Haplogroup 21											
140	13-12-24-11-11-13	0.025	0.222	—	—	—	—	—	—	0.012	7
141	13-12-24-10-11-13	—	0.056	0.019	0.029	—	—	—	0.021	—	6
142	13-12-25-10-11-13	—	—	—	0.014	—	0.019	—	—	—	2
143	14-12-24-10-11-13	—	—	—	0.014	—	—	—	—	—	1
144	13-12-23-10-11-13	—	—	0.019	—	—	—	—	—	—	1
145	13-12-24-10-11-14	—	0.056	—	—	—	—	—	—	—	1
146	13-12-22-10-11-13	—	—	0.019	—	—	—	—	—	—	1
147	13-12-24-12-11-13	0.013	—	—	—	—	—	—	—	—	1
148	13-12-23-10-12-13	—	—	—	—	—	—	0.038	—	—	1
149	14-12-23-10-11-13	—	0.056	—	—	—	—	—	—	—	1
Haplogroup 26											
150	13-12-23-10-12-13	0.013	—	—	—	—	—	—	—	—	1
	Genetic diversity, h	0.899 ± 0.0239	0.954 ± 0.0394	0.949 ± 0.0145	0.945 ± 0.0169	0.970 ± 0.0443	0.954 ± 0.0123	0.935 ± 0.0327	0.952 ± 0.0134	0.964 ± 0.0096	

NOTE.—Microsatellite haplotypes within haplogroups are arranged in decreasing order of total frequency. Dash indicates haplotype was not observed. Genetic diversities (based on haplotype frequencies) are given ± standard error.

[a] Microsatellite haplotypes are defined by a string of six numbers giving the repeat size at loci DYS19, DYS388, DYS390, DYS391, DYS392, and DYS393, respectively.

Table 4
Genetic Distances and *P*-values

	Llangefni	Abergele	Ashbourne	Southwell	Bourne	Fakenham	N. Walsham	Friesland	Norway
Llangefni		0.008*	,						
Abergele.	0.123								
Ashbourne . . .	0.168	0.081							
Southwell	0.126	0.063							
Bourne	0.202	0.082							
Fakenham. . . .	0.234	0.112							
N. Walsham . .	0.174	0.082							
Friesland.	0.184	0.097							
Norway.	0.310	0.175							

plained by a substantial contribution originating in Friesland only.

Population Genetic Models

We explored various population genetic models (see *Materials and Methods*) to evaluate whether or not a large Anglo-Saxon migration event is needed to explain the extremely high Central English-Frisian affinity. We started with a simple model of population fission with no background migration. We found a 95% credible interval for the split date using BATWING of 0–88 generations (0–2,200 years BP, assuming 25 years per generation), which corresponded well with the 95% confidence interval from the Monte Carlo likelihood method with no background migration (0–91 generations or 0–2,275 years BP assuming 25 years per generation).

Next, we looked at the levels of background migration, operating continuously from generation to generation, needed to maintain the Central English-Frisian genetic similarity under two other scenarios not involving Anglo-Saxon mass migration. Under an Island Model scenario (constant background migration between two populations that split at $T_S = \infty$) the 95% confidence interval for m, estimated from the Monte Carlo likelihood method, is 0.3%–50% (where 50% indicates complete panmixia and is a maximum value for m). The same result (to the significant digit given) is found under a Neolithic mass migration scenario (population split 240 generations BP). We note that a figure of $m = 0.3\%$ is three times higher than the figure we estimated as representing an implausibly high value for m, well in excess of realistic values, based on migration statistics to and from the European Economic Area as a whole over the past 25 years. If we set m at the implausibly high value of 0.1%, the 95% confidence interval for a Central English-Frisian split date is 0–97 generations (0–2,425 years BP, assuming 25 years per generation). The figure of 97 generations BP represents an extreme upper limit for the migration event in this case both because it is based on such an implausibly high value for background migration and because it requires the most severe mass migration event imaginable, namely a 100% replacement of the English Y chromosome pool.

Next, we assumed that an Anglo-Saxon migration event did take place 60 generations ago (i.e., 1,500 years BP assuming 25 years per generation) and asked how big an event would be needed to explain the Central English-Frisian genetic similarity. If the Central English and Frisian populations were very different at the time of the event, a larger mass migration would be needed. We therefore started by assuming complete genetic identity of the two populations at the time of the Neolithic (i.e., a Central English-Frisian population split 240 generations BP). Assuming no background migration, the 95% confidence interval of the proportion F of the Central English population derived from an Anglo-Saxon mass migration event is 65%–100%. If a background migration rate since the Neolithic of $m = 0.1\%$ is allowed, the 95% confidence interval for F widens to 50%–100%. This result is unchanged if a 30-year generation time is assumed (i.e., an Anglo-Saxon migration event 50 rather than 60 generations ago).

Discussion

Our results indicate the presence of a strong genetic barrier between Central England and North Wales and the virtual absence of a barrier between Central England and Friesland. Any attempt to explain these results in terms of demographic history and migration needs to encompass both these findings satisfactorily. The Central English-North Welsh barrier cannot be explained purely as a simple isolation-by-distance phenomenon because it contrasts strongly with the lack of evidence for a cline among the five widely separated English towns. Our findings are particularly striking, given the high resolution and rapid mutation rate of the Y chromosome haplotypes on which they are based. These allow genetic barriers, if they exist, to be clearly defined.

The best explanation for our findings is that the Anglo-Saxon cultural transition in Central England coincided with a mass immigration from the continent. Such an event would simultaneously explain both the high Central English-Frisian affinity and the low Central English-North Welsh affinity. If we use a rate of 0.1%, as observed over the past 25 years, to represent an extremely high value for continuous background migration between Central England and continental Europe, then we estimate that an Anglo-Saxon immigration event affecting 50%–100% of the Central English male gene pool at that time is required. We note, however, that our data do not allow us to distinguish an event that simply added to the indigenous Central English male gene pool from one where indigenous males were displaced elsewhere or one where indigenous males were reduced in number. Furthermore, although our models assume a

glish-Frisian split extends as far back as 425 B.C. (if one allows a background migration rate of 0.1% and a generation time of 25 years). Archaeology and the testimony of Caesar combine to suggest an immigration of the Belgae, a Celtic tribe from northern Gaul, into central southern England (Hampshire and West Sussex) between 100 and 80 B.C. (Hawkes 1968; Cunliffe 1988, pp. 147–149; Cunliffe 1991, pp. 108–110). Furthermore, although Friesland lay outside the maximum extent of the Roman Empire, small numbers of Frisian mercenaries were recruited by the Romans and stationed as far north as Hadrian's Wall (Breeze and Dobson 1978, pp. 139–140; Collingwood, Wright, and Tomlin 1995, p. 501). However, most historians would see these movements, if they would acknowledge them at all, as preludes to post-Roman Anglo-Saxon migration, and it would be odd indeed to deny the latter while at the same time assigning an extremely large mass migration status to the former.

Finally, we accept that our inferences are based on population genetic analyses that assume a particular model of microsatellite evolution under selective neutrality and growth and that departures from these assumptions may influence our results. However, we note that the accuracy of the mutation model is diminished in importance by the small number of generations that would allow new mutations to accumulate since Anglo-Saxon times and also that any selective sweeps would also have to have been very recent in order to have influenced our conclusions greatly, especially because the effects of such sweeps would partly be accommodated by our model of exponential population growth. In addition, the estimates provided by BATWING for

BIANCHI, N. O., C. I. CATANESI, G. BAILLIET, V. L. MARTINEZ-MARIGNAC, C. M. BRAVI, L. B. VIDAL-RIOJA, R. HERRERA, and J. S. LOPEZ-CAMELO. 1998. Characterization of ancestral and derived Y-chromosomal haplotypes of New World populations. Am. J. Hum. Genet. **63**:1862–1871.

BODMER, W. F. 1993. The genetics of Celtic populations. Proc. Br. Acad. **82**:37–57.

BREEZE, D. J., and B. DOBSON. 1978. Hadrian's Wall, Revised edition. Pelican, Harmondsworth.

BURMEISTER, S. 2000. Archaeology and migration: approaches to an archaeological proof of migration. Curr. Anthropol. **41**:539–567.

CARTWRIGHT, R. A., H. J. HARGREAVES, and E. SUNDERLAND. 1977. Serum protein and isoenzyme polymorphisms from Nottingham, England. Hum. Biol. **49**:629–640.

CASALOTTI, R., L. SIMONI, M. BELLEDI, and G. BARBUJANI. 1999. Y-chromosome polymorphisms and the origins of the European gene pool. Proc. R. Soc. Lond. B **266**:1959–1965.

CAVALLI-SFORZA, L. L., P. MENOZZI, and A. PIAZZA. 1994. The history and geography of human genes. Princeton University Press, Princeton, NJ.

CHAPMAN, J. 1997. The impact of modern invasions and migrations on archaeological explanation. Pp. 11–20 *in* J. CHAPMAN and H. HAMEROW, eds. Migrations and invasions in archaeological explanation. BAR International Series 664, Oxford, UK.

CHAPMAN, J., and H. HAMEROW, eds. 1997. Migrations and invasions in archaeological explanation. BAR International Series 664, Oxford, UK.

CLARK, G. 1966. The invasion hypothesis in British archaeology. Antiquity **40**:172–189.

COLLINGWOOD, R. G., R. P. WRIGHT, and R. S. O. TOMLIN. 1995. The Roman inscriptions of Britain, Vol. 1, 2nd edition. Sutton, Stroud.

CRAWFORD, S. 1997. Britons, Anglo-Saxons and the Germanic burial ritual. Pp. 45–72 *in* J. CHAPMAN and H. HAMEROW, eds. Migrations and invasions in archaeological explanation. BAR International Series 664, Oxford, UK.

CUNLIFFE, B. 1988. Greeks, Romans and Barbarians: spheres of interaction. Batsford, London.

———. 1991. Iron Age communities in Britain. 3rd edition (Archaeology of Britain series). Routledge, London.

DAVIES, J. 1993. A History of Wales. Penguin Press, London.

DAVIES, N. 1999. The Isles: a history. Macmillan, London.

ESMONDE-CLEARY, A. S. 1993. Approaches to the differences between Late Romano-British and Early Anglo-Saxon archaeology. Anglo-Saxon Stud. Archaeol. Hist. **6**:57–63.

FALSETTI, A. B., and R. R. SOKOL. 1993. Genetic structure of human populations in the British Isles. Ann. Hum. Biol. **20**: 215–229.

GOLDSTEIN, D. B., A. RUIZ LINARES, L. L. CAVALLI-SFORZA, and M. W. FELDMAN. 1995. Genetic absolute dating based on microsatellites and the origin of modern humans. Proc. Natl. Acad. Sci. USA **92**:6723–6727.

HAMEROW, H. 1997. Migration theory and the Anglo-Saxon ''identity crisis.'' Pp. 33–44 *in* J. CHAPMAN and H. HAMEROW, eds. Migrations and invasions in archaeological explanation. BAR International Series 664, Oxford, UK.

HÄRKE, H. 1998. Anthropologists and migrations: a problem of attitude? Curr. Anthropol. **39**:19–45.

NÄSMAN and J. LUND, eds. Folkevandringstiden i Norden: En krisetid mellem ældre og yngre jernalder. Aarhus Universitetsforlag, Aarhus.
NEI, M. 1987. Molecular evolutionary genetics. Columbia Uni-