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High level of male-biased Scandinavian admixture in Greenlandic Inuit shown by Y-chromosomal analysis

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Abstract We have used binary markers and microsatellites on the Y chromosome to analyse diversity in a sample of Greenlandic Inuit males. This sample contains Y chromosomes typical of those found in European populations. Because the Y chromosome has a unique and robust phylogeny of a time depth that precedes the split between European and Native American populations, it is possible to assign chromosomes in an admixed population to either continental source. On this basis, $58\pm 6\%$ of these Y chromosomes have been assigned to a European origin. The high proportion of European Y chromosomes contrasts with a complete absence of European mitochondrial DNA and indicates strongly male-biased European admixture into Inuit. Comparison of the European component of Inuit Y chromosomes with European population data suggests that they have their origins in Scandinavia. There

are two potential source populations: Norse settlers from Iceland, who may have been assimilated 500 years ago, and the Danish-Norwegian colonists of the eighteenth century. Insufficient differentiation between modern Icelandic and Danish Y chromosomes means that a choice between these cannot be made on the basis of diversity analysis. However, the extreme sex bias in the admixture makes the later event more likely as the source.

Introduction

In about AD 985, ships set out from Iceland to settle southwest Greenland, which at that time was unpopulated. These ships carried Icelandic Norse, who had settled Iceland itself beginning in AD 870 and could trace their origins to Scandinavia and coastal regions of the northwestern British Isles. Over the next few years, Norse people established two settlements (Fig. 1), one around present-day Nuuk (Western settlement) and one north of present-day Nanortalik (Eastern settlement; Kleivan 1984). From archaeological evidence, these settlements were inhabited for the next 500 years by an average of 1400 people (Lynnerup 1998), leaving the remains of 17 churches and over 300 farms. The last reliable records of contact between Icelanders and the Norse Greenlanders date to the year 1414 (Kleivan 1984).

The native people of northern Alaska, northern Canada and Greenland are known as the Inuit (previously, Eskimos). The first settlement of Greenland was in the north about 4500 years ago and archaeological evidence exists of several distinct Palaeo-Eskimo cultures until the end of the late Dorset culture about 1100 years ago (Fitzhugh 1984). The Neo-Eskimo Thule culture, which had its origins in north Alaska and covered a wide geographical range from Siberia to Greenland, arrived in northwestern Greenland around 1050–1100 AD (Jordan 1984) and spread southwards. The first records of contacts between the Norse and Inuit date from the end of the twelfth century. A Papal brief of 1448 states that, in 1418, the Norse had been attacked by “hostile barbarians” (Kleivan 1984),

Electronic database information: URLs for the data in this article are as follows:

European Y-STR Haplotype Reference Database,
http://ystr.charite.de/index_gr.html
Asian Y-STR Haplotype Reference Database, <http://ystr.org/asia>
Network 3.0, <http://www.fluxus-engineering.com/>
Y Chromosome Consortium Nomenclature, <http://ycc.biosci.arizona.edu/>

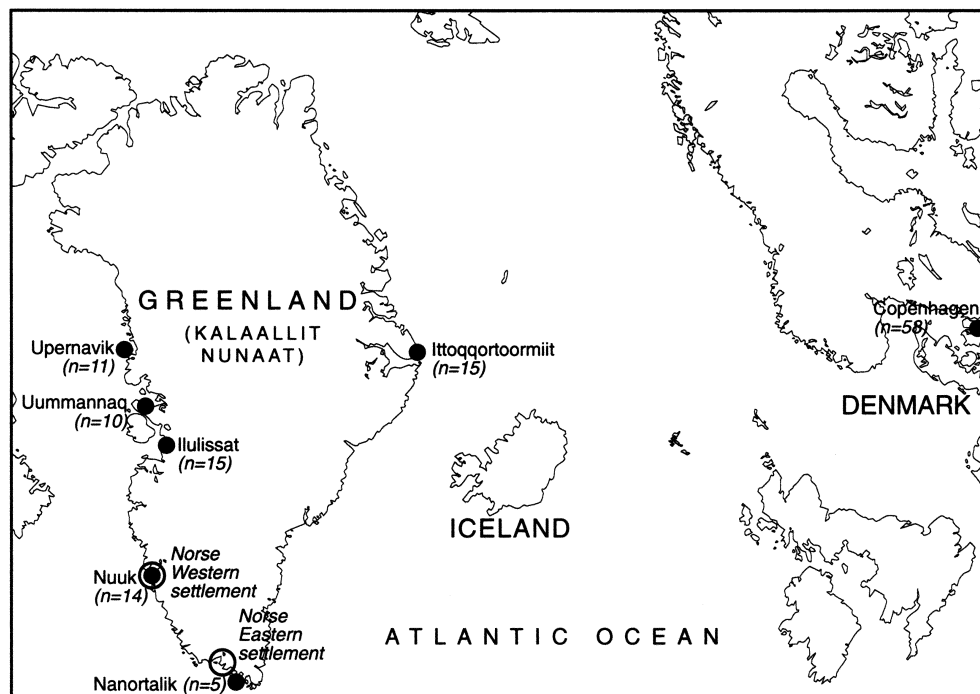
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Fig. 1. Population sample sites. Sample sizes of populations are given in parentheses (un-filled circles locations of the two medieval Norse settlements in southern Greenland)



churches were destroyed, and people were captured as slaves. Occasional European visitors in the sixteenth century encountered only Inuit people. The lingering hope that Norse Greenlanders might remain was one of the motivations for the Danish-Norwegian colonization, beginning in 1721, which aimed to convert any surviving Norse to Lutheranism (Gad 1984). The Norse, however, had disappeared and much debate has been devoted to the question of what happened to them. It is thought that they either died out, emigrated or became integrated into the Inuit population, perhaps as a consequence of ecological changes during one of the region's periodic cold phases (Dansgaard et al. 1975; Pringle 1997). Several lines of evidence have been pursued in attempts to show that there was substantial contact between the Inuit and Norse (Kleivan 1984), including characteristics of artefacts and houses, shared mythologies, word borrowings and behavioural practices. Serological evidence has also been claimed for interbreeding between Norse and Inuit in the Eastern Settlement area (Persson 1969). However, alternative explanations exist for most of these phenomena, including, in the case of the linguistic evidence, contacts post-dating the colonizations of the eighteenth century. Physical anthropological analyses of skeletal remains, both Norse and Inuit, have failed to demonstrate commingling (Lynnerup 1998; Scott and Alexandersen 1991).

Analysis of genetic diversity offers a powerful means to investigate the ancestry of a population and, in particular, to detect admixture of populations originating from different continents, since many DNA markers display geographical specificity. Previous mitochondrial (mt) DNA typing of a sample of 82 Greenlandic Inuit (Saillard et al. 2000) has shown the complete absence of any European mtDNA types, but a spectrum of lineages consistent with descent from Alaskan Inuit.

Here, we analyse the diversity of Y chromosomes in males forming a subset of the 82 Greenlandic Inuit studied previously. As cases from Polynesia (Hurles et al. 1998) and the Americas (Alves-Silva et al. 2000; Carvajal-Carmona et al. 2000; Carvalho-Silva et al. 2001) have shown, admixture is often sex-biased, and whereas maternal lineage analysis may not detect European admixture, paternal lineage analysis may present a different picture. The robust phylogeography of the sequence of the non-recombining region of the Y chromosome now available permits the convenient distinction of European from non-European lineages, since the emergence of the Y chromosome variation precedes the historical migrations that may have resulted in gene flow. The question of sex-specific gene flow can thus be addressed in detail.

Materials and methods

Subjects

Sixty-nine DNA samples from Greenlandic Inuit males were collected from six different locations (Fig. 1): Nanortalik, Nuuk, Ilulissat, Uummannaq and Upernavik on the west coast, and Ittoqqortoormiit on the east coast. Numbers for each sample site are given in Table 1 and Fig. 1. These samples are a subset of those previously analysed for mtDNA variation (Saillard et al. 2000). Fifty-eight DNA samples from Danish males, which include the 56 described previously (Rosser et al. 2000), were from Copenhagen. All samples were collected with appropriate ethical approval and informed consent.

Binary markers

Binary markers (YAP, *SRY*-1532, *SRY*-2627, 92R7, *DYS*257, M9, sY81, Tat, *SRY*-8299, 12f2 and LLY22g) analysed in a previous study of European diversity (Rosser et al. 2000) were typed as described. In addition, five other binary markers were typed by using

Table 1 Haplogroup frequencies in Inuit and Danes. Chromosomes belonging to HGs 1a, 2a, 4, 7, 8, 12, 16, 22 and 26 are absent from all samples

Population	Number	No. (%) of individuals with HG							
		1c	2b	3	9	21	1b	10	18
All Inuit	69	12 (17)	20 (29)	6 (9)	1 (1)	1 (1)	21 (30)	2 (3)	6 (9)
Upernavik	11	1 (9)	4 (36)	2 (18)	0	1 (9)	3 (27)	0	0
Uummannaq	10	2 (20)	3 (30)	1 (10)	0	0	2 (20)	0	2 (20)
Ilulissat	15	5 (33)	7 (47)	1 (7)	0	0	1 (7)	0	1 (7)
Nuuk	14	3 (21)	4 (29)	1 (7)	1 (7)	0	3 (21)	0	2 (14)
Nanortalik	5	0	1 (20)	0	0	0	4 (80)	0	0
Ittoqqortoormiit	14	1 (7)	1 (7)	1 (7)	0	0	8 (57)	2 (14)	1 (7)
Danish	58	32 (55)	21 (36)	3 (5)	2 (4)	0	0	0	0

denaturing high-performance liquid chromatography (DHPLC) on a Transgenomic WAVE: *DYS199* (Underhill et al. 1996), *RPS4Y* (Bergen et al. 1999), M89, M173 (Underhill et al. 2000), and a new marker, MEH2 (Y Chromosome Consortium 2002), involving a G to T transversion lying in the fourth intron of the gene *PCDH1Y* (Blanco et al. 2000). MEH2 primers were e4f2 (5'-CTG TTG ATC CTG ACG TAG GC-3') and e4r (5'-TAC CAT GAA AAT TCA TAA TCC ACA-3'). The polymorphic base lies at nucleotide 190 of the 247-bp polymerase chain reaction (PCR) product. PCR conditions for all markers typed by DHPLC were as follows: 95°C for 10 min; 14 cycles of 94°C for 20 s, 63°C for 60 s, decreasing by 0.5°C each cycle, and 72°C for 60 s; 20 cycles of 94°C for 20 s, 56°C for 45 s and 72°C for 60 s; 72°C for 5 min.

Phylogenetic relationships of the haplogroups are known (Y Chromosome Consortium 2002) and are shown in Fig. 2. To-

gether, the 16 markers define 17 haplogroups. Two previously named haplogroups (Jobling and Tyler-Smith 2000), HG1 and HG2, are subdivided here. The new sub-haplogroups are not assigned new numbers but are indicated by the previous haplogroup number and a suffix letter in order to emphasize their relationships to previously described haplogroups. Figure 2 also includes the formal nomenclature of these haplogroups according to the Y Chromosome Consortium (YCC) (Y Chromosome Consortium 2002).

Microsatellite haplotyping

Typing of seven Y-specific microsatellites (*DYS19*, *DYS389I*, *DYS389II*, *DYS390*, *DYS391*, *DYS392*, *DYS393*) was carried out

Fig. 2 Haplogroups found in Inuit and Danes. The binary markers typed and haplogroups assayed are indicated on a rooted maximum parsimony tree based on that published by the YCC (Y Chromosome Consortium 2002). *Right* Schematic representation of haplogroup frequencies in Inuit and Danish Y chromosomes typed here: areas of *filled circles* are proportional to haplogroup frequency (*small unfilled circles* unobserved haplogroups). Haplogroup nomenclature used here is indicated, as is the formal YCC nomenclature (Y Chromosome Consortium 2002)

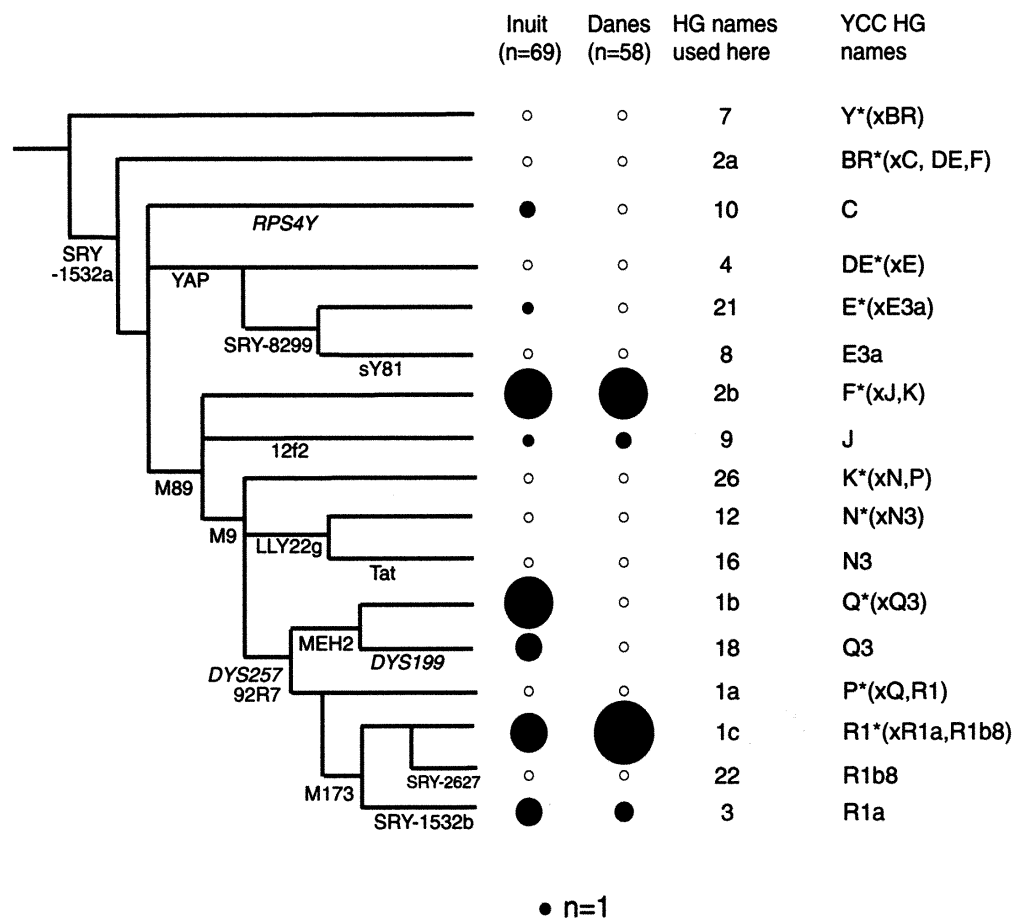


Table 2 Seven-locus Y-specific microsatellite haplotypes found in Inuit and Danes and matches found in 181 Icelandic, 300 Norwegian (Dupuy et al. 2001) and 8592 chromosomes from other European populations compiled in the European Y-STR Haplotype Reference Database (YSTRDB-12/13/2001 update; Roewer et al. 2001). Haplotype 15, which has “null” alleles at DYS389I and DYS389II, is not found in the Icelandic or Norwegian data but cannot be sought in the YSTRDB (UP Upernavik, UU Uummannaq, // Ilulissat, Nu Nuuk, Na Nanortalik, It Ittoqqortoormiit, ht haplotype)

HG	DYS19	DYS389I	DYS389II	DYS390	DYS391	DYS392	DYS393	ht	Up	Uu	U	II	Nu	Na	It	All Inuit	Den-mark	Ice-land	Nor-way	YSTRDB-Norway
3	15	13	29	24	11	11	14	1	-	-	-	-	-	-	-	-	1	0	0	1
-	15	13	29	25	11	11	13	2	-	1	-	-	-	-	-	1	-	0	4	12
-	15	13	30	25	10	11	13	3	-	-	-	-	-	-	-	-	0	5	39	
-	15	13	31	25	10	11	13	4	1	-	-	-	-	-	-	1	-	0	2	13
-	16	13	29	25	11	10	13	5	-	-	-	-	-	1	-	-	-	0	0	0
-	16	13	31	25	11	11	13	6	1	-	-	-	-	-	-	1	-	0	0	22
-	17	13	30	25	10	11	13	7	-	-	1	-	-	-	-	1	-	0	0	86
-	17	13	30	25	11	11	13	8	-	-	-	-	-	-	-	-	1	0	0	24
-	17	13	31	26	10	11	13	9	-	-	-	1	-	-	-	1	-	0	0	0
9	15	13	27	23	10	11	12	10	-	-	-	1	-	-	-	1	-	0	0	0
-	15	13	30	22	10	11	13	11	-	-	-	-	-	-	-	-	1	0	0	7
-	16	13	32	24	10	12	14	12	-	-	-	-	-	-	-	-	1	0	0	0
21	13	14	31	25	10	11	13	13	1	-	-	-	-	1	-	-	0	0	0	2
10	16	13	29	24	9	11	14	14	-	-	-	-	-	2	2	-	0	0	0	0
18	13	-	-	24	10	14	13	15	-	1	-	-	-	-	-	1	-	0	0	n/a
-	13	14	31	23	10	14	13	16	-	-	1	-	-	-	-	1	-	0	0	0
-	13	14	31	24	10	14	13	17	-	-	-	1	-	-	-	1	-	0	0	0
-	13	14	31	24	10	14	14	18	-	1	-	-	1	-	3	-	0	0	0	0
1b	13	14	30	23	10	15	14	19	-	-	-	-	1	-	1	-	0	0	0	0
-	13	14	30	24	10	14	14	20	-	-	-	-	-	1	1	-	0	0	0	0
-	13	14	30	24	10	15	14	21	-	1	-	1	3	2	7	-	0	0	0	0
-	13	14	30	24	10	16	14	22	-	-	1	-	-	-	1	-	0	0	0	0
-	13	14	30	24	11	15	14	23	-	-	-	1	-	-	1	-	0	0	0	0
-	13	14	30	25	10	15	14	24	-	-	-	-	-	4	4	-	0	0	0	0
-	13	14	31	25	10	15	14	25	-	-	-	-	-	1	1	-	0	0	0	0
-	13	14	32	24	10	15	14	26	3	1	-	-	-	-	4	-	0	0	0	0
-	13	15	31	24	10	15	14	27	-	-	-	1	-	-	1	-	0	0	0	0
1c	14	12	28	23	11	13	13	28	-	-	-	-	-	-	-	-	2	0	0	13
-	14	13	28	23	11	13	13	29	-	-	-	-	-	-	-	-	1	0	2	30
-	14	13	28	23	12	13	13	30	-	-	-	-	-	-	-	-	0	0	0	6
-	14	13	28	24	10	13	13	31	-	-	-	-	-	-	-	-	1	0	0	24
-	14	13	29	23	10	13	13	32	-	-	-	-	-	-	-	-	0	3	102	
-	14	13	29	23	11	13	13	33	-	1	1	-	-	-	-	3	6	5	5	214
-	14	13	29	24	10	13	13	34	-	-	-	-	-	-	-	-	2	6	6	217
-	14	13	29	24	10	13	14	35	-	-	-	-	-	-	-	-	0	0	0	17
-	14	13	29	24	10	14	13	36	-	-	-	-	-	1	1	-	0	0	0	15
-	14	13	29	24	11	13	13	37	1	-	-	-	-	-	1	4	15	12	492	
-	14	13	29	24	12	13	13	38	-	-	-	-	-	-	-	1	0	0	0	20
-	14	13	29	25	11	13	13	39	-	-	-	-	-	-	-	-	7	2	2	80

-	14	13	30	23	10	13	13	40	-	-	-	-	-	-	-	-	-	-	2	-	1	0	17
-	14	13	30	25	11	13	13	41	-	-	-	-	-	-	-	-	-	-	1	-	0	0	15
-	14	14	29	23	11	13	13	42	-	-	-	-	-	-	-	-	-	-	1	-	0	0	3
-	14	14	30	24	10	13	13	43	-	-	-	-	-	-	-	-	-	-	1	-	0	0	45
-	14	14	30	24	11	13	13	44	-	-	-	-	-	-	-	-	-	-	3	-	4	0	112
-	15	13	28	25	10	13	13	45	-	-	-	-	-	-	-	-	-	-	1	-	0	0	1
-	15	13	29	24	10	13	13	46	-	-	-	-	-	-	-	-	-	-	1	-	0	0	11
-	15	13	29	24	11	13	13	47	-	-	-	-	-	-	-	-	-	-	1	-	0	3	59
-	15	13	30	24	10	13	13	48	-	-	-	-	-	-	-	-	-	-	5	-	0	0	9
-	15	14	28	23	10	13	13	49	-	-	-	-	-	-	-	-	-	-	1	-	0	0	0
-	15	12	29	23	10	13	13	50	-	-	-	-	-	-	-	-	-	-	1	-	0	0	2
2b	13	12	29	23	10	11	13	51	-	-	-	-	-	-	-	-	-	-	1	-	0	0	0
-	14	12	26	23	10	11	13	52	-	-	-	-	-	-	-	-	-	-	1	-	0	0	0
-	14	12	28	22	10	11	13	53	-	-	-	-	-	-	-	-	-	-	3	4	0	8	174
-	14	12	28	22	10	11	14	54	-	-	-	-	-	-	-	-	-	-	1	-	0	3	21
-	14	12	28	22	11	11	13	55	-	-	-	-	-	-	-	-	-	-	2	-	0	3	12
-	14	12	28	22	11	11	15	56	-	-	-	-	-	-	-	-	-	-	1	-	0	0	0
-	14	12	28	23	10	11	13	57	-	-	-	-	-	-	-	-	-	-	5	1	0	26	122
-	14	12	28	23	10	11	14	58	-	-	-	-	-	-	-	-	-	-	2	-	1	0	7
-	14	12	29	22	10	11	13	59	-	-	-	-	-	-	-	-	-	-	1	-	0	3	27
-	14	13	29	22	10	11	13	60	-	-	-	-	-	-	-	-	-	-	1	-	0	1	26
-	14	14	30	23	10	11	13	61	-	-	-	-	-	-	-	-	-	-	1	-	0	0	4
-	15	11	27	22	10	12	12	62	-	-	-	-	-	-	-	-	-	-	1	-	0	0	0
-	15	12	28	22	10	11	13	63	-	-	-	-	-	-	-	-	-	-	2	-	0	9	35
-	15	12	28	22	11	11	13	64	-	-	-	-	-	-	-	-	-	-	1	-	0	0	2
-	15	12	28	23	10	11	13	65	-	-	-	-	-	-	-	-	-	-	1	-	1	1	20
-	15	13	29	22	10	11	13	66	-	-	-	-	-	-	-	-	-	-	1	-	0	1	6
-	15	13	29	23	10	12	15	67	-	-	-	-	-	-	-	-	-	-	1	-	0	0	6
-	15	13	29	24	11	11	13	68	-	-	-	-	-	-	-	-	-	-	1	-	0	0	2
-	15	13	31	23	10	12	14	69	-	-	-	-	-	-	-	-	-	-	1	-	0	0	7
-	15	14	32	23	10	12	13	70	-	-	-	-	-	-	-	-	-	-	1	-	0	0	2
-	15	14	32	23	10	12	14	71	-	-	-	-	-	-	-	-	-	-	1	-	0	2	17
-	15	14	33	23	10	12	15	72	-	-	-	-	-	-	-	-	-	-	1	-	0	0	0
-	16	12	28	21	10	11	13	73	-	-	-	-	-	-	-	-	-	-	1	-	0	0	0
-	17	14	29	23	10	11	13	74	-	-	-	-	-	-	-	-	-	-	1	-	0	0	2
-	15	12	29	22	11	11	13	75	-	-	-	-	-	-	-	-	-	-	1	-	0	0	5

within two multiplexes on an ABI377 sequencer as described (Bosch et al. 2002). Allele nomenclature was the same as that used by the European Y-STR Haplotype Reference Database (Roewer et al. 2001).

Comparative data

Searches for matching microsatellite haplotypes were made in the European Y-STR Haplotype Reference Database (Roewer et al. 2001) as a whole and in the Norwegian component of this database (Dupuy et al. 2001; Roewer et al. 2001). Searches for any particular matching microsatellite haplotypes were also made in the Asian Y-STR Haplotype Reference Database (<http://www.ystr.org/asia/>).

Binary marker data were available for an independent set of 52 Norwegian samples (Rosser et al. 2000) and could therefore be included in population pairwise F_{ST} comparisons, together with the following populations (Rosser et al. 2000): Icelandic ($n=28$), Saami (48), N. Swedish (48), Gotlander (64), Danish (56), Finnish (57), Estonian (207), Latvian (32), Lithuanian (38), Russian (122), Belarusian (41), Ukrainian (27), Mari (48), Chuvash (17), Georgian (64), Ossetian (47), Armenian (89), Turkish (167), Cypriot (45), Greek (36), Bulgarian (24), Czech (53), Slovakian (70), Romanian (45), Yugoslavian (100), Slovenian (70), Hungarian (36), Polish (112), Italian (99), Sardinian (10), Bavarian (80), German (30), Dutch (84), French (40), Belgian (92), W. Scottish (120), Scottish (43), Cornish (51), E. Anglian (172), Irish (257), Basque (26), Spanish (126), S. Portuguese (57), N. Portuguese (329), Algerian (27), N. African (129).

Statistical methods and network construction

Standard diversity indices and ϕ_{ST} values were computed within Arlequin (Schneider et al. 2000). Median joining networks (Bandelt et al. 1999) containing chromosomes belonging to haplogroups 1c or 2b were constructed by using the program Network 3.0. Weighting of microsatellites was based on intra-haplogroup variance, normalized on a scale of 1–10 (Hurles et al. 2002).

Results

Binary marker data suggest European admixture in Inuit

Y chromosomes from 69 Greenlandic Inuit males were analysed by using a set of 16 binary markers and assigned to eight of a possible 17 haplogroups (Table 1, Fig. 2). This sample contains eight chromosomes (~12%) belonging to two lineages, HG10 and HG18, known to be present at high frequencies in Native American populations (Bergen et al. 1999; Karafet et al. 1999; Underhill et al. 1996), and absent from Europeans (Hammer et al. 2001). However, it also contains eight chromosomes (~12%) belonging to HGs 3, 9 and 21, lineages that are almost absent from Native American samples (0, 0.3%, and 0.3%, respectively, in a sample of 273 chromosomes; Hammer et al. 2001). These lineages are common in Europeans (14%, 8% and 9%, respectively of a sample of 3616 chromosomes; Rosser et al. 2000) however and, thus, this indicates some admixture from Europe.

No such clear-cut origins can be ascertained for the Inuit chromosomes belonging to the remaining haplogroups, namely HG1b, HG1c and HG2b. To determine the extent of European admixture in the Inuit, we needed to ask which of those chromosomes were of European ori-

gin by analysing the Y chromosomes of a sample of European males with the same set of binary markers. We chose to use Danish samples because they represented a candidate population for contribution of Y chromosomes to Inuit.

The Danish sample of 58 chromosomes contains only four of the eight haplogroups found in the Inuit sample and therefore has significantly lower diversity (Nei's estimator of diversity, $D=0.5705\pm 0.0410$ compared with 0.7882 ± 0.0246). The relatively high diversity of the Inuit is likely to be a reflection of their admixed composition. The Danes contain no HG10 or HG18 chromosomes. The previously defined HG1 exists in Eurasia and the Americas (Santos and Tyler-Smith 1996) but here is divided into three sublineages, HG1a, HG1b and HG1c: HG1a is found in neither Inuit nor Danes and published information (Underhill et al. 2000) indicates that chromosomes belonging to this lineage are overwhelmingly Asian and Oceanian; HG1b is found only in Inuit and is thus identified as another indigenous Inuit lineage, together with HGs 10 and 18. Although little comparative data are available for HG1b, since MEH2 has not yet been widely typed, our finding is consistent with the Native American origins of the four chromosomes in the YCC collection (Y Chromosome Consortium 2002) that belong to this haplogroup. However, from this analysis, the remaining sublineage, HG1c, cannot be clearly ascribed either to indigenous or to European origin. HG2b also has poorly defined origins. It is rare in Native Americans (1.5%; Hammer et al. 2001) and much more frequent in Europeans (~20%; Rosser et al. 2000). This suggests that it is present in Native Americans (and Inuit) through admixture, although the poor phylogenetic definition of this haplogroup may preclude a firm conclusion and further study may be needed.

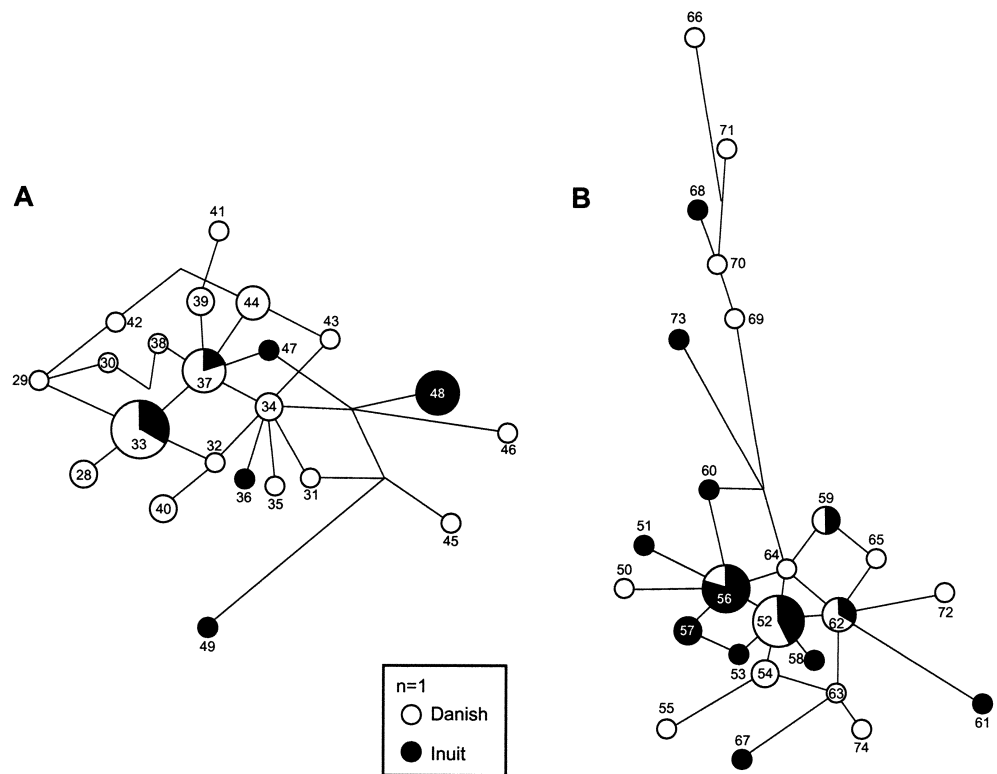
This latter haplogroup together with HG1c constitutes a major proportion of chromosomes in both populations. In order to understand the origins of these two groups of chromosomes, namely HG2b and HG1c, the internal diversities of both Danish and Inuit samples were analysed by using Y-specific microsatellites.

Origins of Inuit chromosomes inferred from microsatellite analysis

The Inuit and Danish samples were analysed by using seven Y-specific microsatellites (*DYS19*, *DYS389I*, *DYS389II*, *DYS390*, *DYS391*, *DYS392*, *DYS393*; Table 2). The 127 chromosomes carry 74 different haplotypes. One Inuit chromosome belonging to HG18 has "null" alleles for *DYS389I* and *DYS389II* (ht 15), which could be explained by a Yq deletion. This haplotype is omitted from the diversity analyses below.

There is no historical evidence suggesting substantial gene flow from Inuit to Europeans and this is supported by the absence of HG1b, HG10 and HG18 chromosomes from Danes. In the following analysis, we therefore assume that admixture has been unidirectional (from Euro-

Fig. 3A, B Within-haplogroup median joining networks in Inuit and Danes (*circles* haplotypes with the area being proportional to the number of individuals, *filled circles or sectors* Inuit, *unfilled circles or sectors* Danes). Microsatellites are weighted according to intra-haplogroup variance. *Numbers* within or adjacent to *circles* are haplotype names as given in Table 2. **A** Network constructed by using seven-locus microsatellite haplotypes within HG1c. **B** Network within HG2b



peans to Inuit) and regard shared haplotypes between Inuit and Europeans as evidence of European introgression. This is expected given the high mutation rate of microsatellites and the time-depth of an alternative scenario, i.e. that European-related Y chromosomes may have been ancestrally introduced into the Inuit through Siberia and Beringia. The separation time between European and Native Americans can be estimated conservatively at 15,000 years or 750 generations. Thus, Y-chromosome microsatellites in the Europeans and Inuit are likely to have been accumulating mutations independently for 1500 generations, at a rate of 2.1×10^{-3} mutations per locus per generation (Heyer et al. 1997; Jobling et al. 1999). For a seven-locus haplotype, this would imply an average square distance (Thomas et al. 1998) of 22.05, with a 95% confidence interval of 12.85–31.25. Thus, Inuit and European microsatellite haplotypes presenting an average square distance <12.85 to each other (and, in particular, shared identical haplotypes) are likely to have been introduced into the Inuit at a more recent date.

Five haplotypes are shared between Inuit and Danes and all belong to haplogroups 1c and 2b, suggesting that Inuit chromosomes carrying these five haplotypes at least are of European origin. To assess the origins of the remaining Inuit-specific haplotypes within these two haplogroups, we first asked whether there were matches in two reference sets of European haplotypes: a set of haplotypes of 181 Icelandic Y chromosomes (Helgason et al. 2000) and a set of 8592 haplotypes constituting the European Y-STR Haplotype Reference Database (YSTRDB–12/13/2001 update; Roewer et al. 2001). Within the

YSTRDB, we also recorded matches to a subset of haplotypes of 300 Norwegian Y chromosomes (Dupuy et al. 2001). The numbers of matching haplotypes are given in Table 2.

In addition to seeking perfect matches for haplotypes, we constructed median joining networks of Inuit and Danish chromosomes within HGs 1c and 2b in order to assess how closely related the chromosomes within these two populations were (Fig. 3).

There are twelve Inuit chromosomes belonging to HG1c and carrying six different microsatellite haplotypes. All but one of the HG1c microsatellite haplotypes in the Inuit were found in the European YSTRDB. In particular, two of these haplotypes (ht33 and ht37) are shared with Danes, Icelanders, Norwegians and non-Norwegian chromosomes in the YSTRDB and one (ht47) is found in Norwegians. In the network of Inuit and Danish HG1c haplotypes (Fig. 3A), all except one of the Inuit-specific haplotypes (ht49) are no more than two mutational steps away from Danish haplotypes. Ht49 is found neither in the European nor in the Asian YSTRDB (19/9/02 update). However, the average square distance of ht49 to the closest Danish haplotype is 3; thus, as discussed above, it is very unlikely to be an ancestral Inuit haplotype. Given that all microsatellite haplotypes in HG1c in our Inuit sample are closer to Danish haplotypes than is expected if they were ancestral Inuit haplotypes, it is reasonable to deduce that all of HG1c was absent in the ancestral Inuit population and was introduced through recent gene flow.

In HG2b there are 20 Inuit chromosomes, belonging to 13 haplotypes. These haplotypes also show a high degree

of sharing with haplotypes in Danes, Icelanders, Norwegians and the YSTRDB (Table 2). Only two of them (ht51 and ht61) are unrepresented in these datasets. It is worth noting that some Danish haplotypes are also not found in the YSTRDB and so the lack of a match is not an unusual occurrence, despite the size of the database. HG2b is less well-defined by binary markers than HG1c; it is therefore unsurprising that the HG2b network (Fig. 3B) is less compact than the HG1c network. However, only three of the Inuit-specific haplotypes (hts61, 67, 73) lie more than two steps away from Danish haplotypes. The respective square distances to the closest Danish haplotypes are 4, 6 and 9; thus, they are smaller than expected if these haplotypes were ancestral to the Inuit. Again, this suggests a European origin for the HG2b chromosomes within the Inuit sample.

The complete absence of microsatellite haplotypes from HGs 1b, 10 and 18 within the European datasets (Table 2) confirms that these chromosomes are of Inuit origin. In summary, we infer that HGs 1b, 10 and 18 are ancestral to the Inuit, whereas HGs 1c, 2b, 3, 9, and 21 are present in the Inuit through European admixture.

Admixture analysis

Quantifying the relative contributions of different populations to an admixed population is far from trivial (Chikhi et al. 2001) and commonly requires the specification of appropriate parental populations. However, the phylogeographical structure of the Y chromosome in this particular case greatly facilitates the calculation of admixture proportions. Indeed, we have identified, in the admixed population (the Inuit), a set of lineages that are ancestral to the Inuit and absent from Europeans and also a set of complementary lineages common in Europeans but rare in Native Americans, suggesting that they are not ancestral to the latter. Therefore, calculation of the proportion of European lineages in the Inuit gives a direct measure of the European contribution to the Inuit Y-chromosomal pool. Thus, the joint frequency of HGs 1c, 2b, 3, 9, and 21 in the Inuit, namely $58 \pm 6\%$ (binomial standard error), can be taken as the European Y-chromosomal contribution to the Inuit.

Independent production of an admixture figure by traditional methods of analysis is problematic, since no suitable Inuit parental population (such as the Siberian Inuit; Lell et al. 2002) has yet been typed for MEH2 and M173, which would allow us to discriminate between HGs 1a, 1b, and 1c; as described above, the latter two haplogroups have clearly distinct origins. Moreover, non-Inuit Native American populations may not be suitable as putative parental populations for a number of reasons, such as the possible different origins of Inuit and Amerindians and the pervasive European admixture known to exist in modern Native North American populations (Chakraborty 1986). Additional sampling and analysis of Canadian Inuit is desirable.

Comparison with another Inuit sample

We can ask whether this high proportion of chromosomes of European origin is typical of Inuit, by examining a separate Greenland Inuit sample (Karafet et al. 1999) comprising 62 chromosomes from a single location (Nanortalik) typed for 12 binary polymorphisms. From this set of markers, it is possible to identify HGs 2, 3 and 26 (presumably of European origin), 18 (ancestral Inuit) and 1, encompassing 1a, b, and c. The same sample has been typed for the seven Y-chromosome microsatellites (Kayser et al. 2001), although, unfortunately, cross-referencing information is unavailable. Since we found seven-locus haplotype matches in this Nanortalik sample to chromosomes in our Inuit sample bearing HGs 1b and 1c, it is likely that both HGs are present in the additional Nanortalik sample. However, determination of the frequencies of HGs 1b and 1c is necessary to estimate the European contribution. We can assess the possible range of this contribution by assuming that either all HG1 chromosomes are HG1b or all are HG1c. Then, the European contribution to the Nanortalik sample is between 15% and 56%, i.e. possibly smaller than that observed in the overall Greenland Inuit sample presented here, but nonetheless substantial.

Origins of the European component of Inuit chromosomes

Given the high degree of geographical structure of the Y chromosome in Europe (Rosser et al. 2000), we can attempt to narrow down the possible origins of the European component of the Inuit Y chromosomes by comparing haplogroup frequencies, and, at a finer level, by using microsatellite haplotypes. We can compare the haplogroup frequencies of the European component of the Inuit with published data on 46 European populations (Rosser et al. 2000) and with the sample of Danes studied here. In population pairwise F_{ST} comparisons, the Inuit are not statistically significantly different ($P \geq 0.05$) from ten other populations: Swedish (48), Gotlander (64), Bulgarian (24), Norwegian (52), Icelandic (28), Dutch (84), Yugoslavian (100), Hungarian (36), Georgian (64) and Ukrainian (27).

The study of Helgason et al. (2000) also provides relevant comparative data (on Icelanders, Norwegians, Swedes, Danes, Irish, Scots, British, Germans, Greeks, Italians and Russians) but does not distinguish between HGs 2b and 9; we therefore pooled data for these two haplogroups in the Inuit. In these comparisons, the Inuit were not distinguished ($P \geq 0.05$) from the Norwegian (112), Danish (12), Swedish (110), Italian (332), German (32) and Icelandic (181) samples.

Icelandic, Swedish and Norwegian populations feature in both of these independent sets of samples, as do a number of other populations that cannot be considered as plausible populations of origin for the Inuit European component.

In addition to using the gross information in haplogroup frequencies, we can use the more fine-grained information in microsatellite haplotypes to compare the

Table 3 Φ_{ST} between populations, based on microsatellite haplotypes

Population comparison	All HGs	HG1c	HG2b/9	HG3
Danish vs Icelandic	0.050	0.011	0.129	-0.065
Inuit vs Danish	0.034	0.097	0.023	-0.102
Inuit vs Icelandic	0.019	0.121	-0.001	0.128

Inuit Europeans with Danes and Icelanders. The haplotype diversity of the European component of the Inuit samples (0.965 ± 0.016) is not significantly different from that of the Danish sample (0.977 ± 0.009) and is significantly greater than that of the Icelandic sample (0.954 ± 0.010). This piece of information alone suggests that, if a simple choice is to be made between an Icelandic/Norse and a Danish source for the European Y chromosomes within Inuit, then the Danish is more likely. Table 3 shows the Φ_{ST} values between the three populations; the use of Φ_{ST} corrected for intrapopulation variance (not shown) leads to the same conclusions. Φ_{ST} between Icelandic and Danes is small but significantly different from zero, which may allow us to discriminate between these two potential parental sources. When the samples are not subdivided by haplogroup, differences in all three comparisons are small. Since Y chromosome variation is partitioned more by haplogroup than by population (Bosch et al. 1999), it makes sense to repeat the comparisons by haplogroup, within population. In comparisons for HG1c and HG3, the differences between Icelanders and Danes are small. For the only haplogroup where this difference is significant, HG2b/9, the Inuit Europeans are more similar to the Icelanders than they are to the Danes. The general conclusion of these comparisons is to confirm the origin of this component among Scandinavian populations, although no clear distinction between Icelandic and Danish populations as potential sources emerges.

The preferential distribution of European Y chromosomes around the Inuit sample sites close to the Eastern and Western settlements might suggest a Norse contribution but it is difficult to make a meaningful comparison between the different sites, because the individual sample sizes are small. However, proportions of European chromosomes in the six places do vary significantly: the three localities with the largest sample sizes have proportions of $21 \pm 11\%$ (Ittoqqortoormiit, $n=14$), $64 \pm 13\%$ (Nuuk, $n=14$) and $87 \pm 9\%$ (Ilulissat, $n=15$). There is no convincing evidence here for a concentration around the old settlements and differences in the proportions of European chromosomes could reflect drift or different numbers of founding European males in different places.

Discussion

Y-chromosomal variation exhibits high intercontinental F_{ST} (Seielstad et al. 1998), which makes it a sensitive marker for detecting admixture between populations from

different continents. Here, we have used Y-chromosomal binary polymorphisms and microsatellites to show that $58 \pm 6\%$ of the Y chromosomes of a sample of 69 Greenlandic Inuit males are of European origin. This contrasts starkly with the complete absence of European mtDNAs in the same sample (Saillard et al. 2000) and represents a novel case of highly sex-biased admixture into a non-European population. Analysis of published data on an independent sample of 62 Inuit Y chromosomes (Kayser et al. 2001) also suggests a high (though imprecisely determined) degree of European admixture and indicates that our sample is not greatly atypical of Inuit.

Historical records suggest two major potential source populations for the European chromosomes among Inuit; the early possible source is the Norse settlers from Iceland who had vanished by the sixteenth century and may have been assimilated by the Inuit and the later source is the Danish-Norwegian colonizers arriving after 1721. We have attempted to choose between these two simple options by comparing the European component of the Inuit with samples of chromosomes from a number of European populations. This approach has a number of potential pitfalls. First, the Inuit European chromosomes could include examples from both the early and the later contacts with Europeans. Second, the Danish-Norwegian colonization included more than just Danish males and is documented as including five Icelanders (Persson 1969). Third, some European chromosomes among Inuit could owe their origin to sailors travelling to Greenland from further afield. Fourth, our comparative datasets necessarily comprise the haplotype distributions of modern populations, rather than those of populations contemporary with the potential introgression events.

Nonetheless, comparisons of the pooled European components of the two Inuit samples with data from European populations show clearly that they are most closely allied to Scandinavians. However, evidence allowing us to choose between Danes and Icelanders (Norse) as source populations is contradictory. A simple consideration of diversity suggests that the Danes are the more likely source, whereas consideration of Φ_{ST} within haplogroups is consistent with a closer relationship with the Icelanders. In principle, it might be possible to distinguish between the options by estimating dates for notional population fissions between Inuit Europeans and Danes and between Inuit Europeans and Icelanders. However, the events that we wish to distinguish are so close in time, and the errors in dating methods so large, that this does not seem worthwhile.

The high degree of sex bias in the admixture seems to favour the later events as the source of European chromosomes among Inuit, since historical evidence suggests that the majority of the Danish-Norwegian immigrants were men (Persson 1969). An earlier assimilation of the Norse is likely to have involved both women and men and thus would have introduced European mtDNA lineages and Y chromosomes into the Inuit, although it is possible that these remain unsampled or have been lost through drift. The European Y chromosomes are distributed widely in Greenland and not concentrated around the regions of the

Norse settlements. This may be taken as further support of the case that the later colonization was responsible for the European introgression. Wider sampling, additional typing of Y-chromosomal, mitochondrial and autosomal markers and further study of the historical records of colonization are likely to throw more light on the origins of European admixture in the Greenlandic Inuit. Its recognition has important implications for research projects related to health (<http://www.cam.ac.uk/engelsk/inussuk/2health/>) and, in particular, genetic epidemiology in the 59,000 people who today make up this geographically isolated population.

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