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Paternal and maternal DNA lineages reveal a bottleneck in the founding of the Finnish population

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ABSTRACT **An analysis of Y-chromosomal haplotypes in several European populations reveals an almost monomorphic pattern in the Finns, whereas Y-chromosomal diversity is significantly higher in other populations. Furthermore, analyses of nucleotide positions in the mitochondrial control region that evolve slowly show a decrease in genetic diversity in Finns. Thus, relatively few men and women have contributed the genetic lineages that today survive in the Finnish population. This is likely to have caused the so-called "Finnish disease heritage"—i.e., the occurrence of several genetic diseases in the Finnish population that are rare elsewhere. A preliminary analysis of the mitochondrial mutations that have accumulated subsequent to the bottleneck suggests that it occurred about 4000 years ago, presumably when populations using agriculture and animal husbandry arrived in Finland.**

When genetic polymorphisms are analyzed on a world-wide scale, European populations are found to be unusually homogeneous, for example with regard to gene frequencies (1), mitochondrial lineages (2, 3), and the spectrum of genetic diseases, whereas populations in, for example, Africa show much more diversity among them (1, 2). However, Fenno-Scandinavia is an exception to this picture in at least two respects. First, the Saami, who inhabit the northern portions of the current states of Norway, Sweden, Finland, and the Kola Peninsula in Russia, are distinct when compared with other European populations with respect to nuclear (1) and mitochondrial genetic markers (3). Second, more than 30 mostly autosomal recessive diseases, which are absent or infrequent elsewhere, exist in the Finnish population, sometimes at high carrier frequencies (4, 5). Conversely, recessive autosomal diseases common in other European populations, such as cystic fibrosis, phenylketonuria, or galactosemia, are rare or absent in Finland (6). Many of the molecular changes responsible for these so-called "Finnish" genetic disorders are due to single mutations embedded in large chromosomal regions exhibiting linkage disequilibria. In contrast, outside Finland, the rare cases of these diseases are due to several different mutations (4, 5, 7, 8). Furthermore, many of the disorders occur in locally restricted areas of Finland (4–6, 9).

We have analyzed the genetic diversity of the Y chromosome and mitochondrial DNA in Finns and other European populations. The results show that Finns differ from surrounding populations in having a drastically reduced amount of Y-chromosomal and mitochondrial diversity. The results furthermore suggest that genetic founder effects have played a role in the biological history also of Estonians and the Basques.

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MATERIALS AND METHODS

Y-Chromosomal Polymorphisms. The loci YAP (10), DXYS156Y (11), and DYS19 (12) were analyzed for 54 Finnish, 28 Saami, 20 Estonian, 51 Swiss, 40 Swedish, 25 Basque, and 30 Sub-Saharan African males. The Finnish males were derived from a random sample originating from various regions of the country. Primers and PCR conditions were as described (10–12). Amplification products of the YAP insertion polymorphism were electrophoresed in a 1–3% agarose gel for 1 hr at 60 V, stained with ethidium bromide, and bands were visualized by UV illumination. When the microsatellite loci DXYS156Y and DYS19 were amplified, one of the primers was fluorescently labeled at its 5′ end and amplicons were electrophoresed through a high-resolution polyacrylamide gel and analyzed by an automated fluorescent detection system (ALF; Pharmacia). Fragment lengths were determined using FRAGMENT MANAGER software (Pharmacia).

Mitochondrial DNA Sequences. Positions 16024–16383 (see ref. 13) of a hypervariable part of the mitochondrial control region were sequenced for 32 Swedish and 20 Estonian individuals. This was added to published data on mitochondrial DNA variation in European (3) and Sub-Saharan African (14) populations.

Statistical Analysis. Gene diversity was calculated as follows: $n/(n-1) \times (1 - \Sigma p^2)$, where n = number of individuals analyzed and p = frequencies of Y-chromosomal haplotypes or mitochondrial lineages, respectively (15). For the mtDNA sequences, gene diversity was calculated by using all positions in the sequence determined as well as subsets of nucleotide positions representing classes of sites that evolve at different rates according to Hasegawa *et al.* (16). A list of these positions is given in ref. 16. To test for population substructure, the unbiased estimate of population differentiation was calculated (17) for all pairs of populations.

RESULTS

Y-Chromosomal Diversity. The Y-chromosomal loci YAP, DXYS156Y, and DYS19 were studied in 193 European males as well as in 30 Sub-Saharan Africans, and haplotypes consisting of these three loci were constructed (Table 1). Whereas 8 haplotypes were found among the Europeans, 13 were found among the Africans. Taking the difference in sample sizes into account, dramatically more Y chromosome haplotypes seem to exist among African males. Furthermore, in Europe, one haplotype [Alu−/DXYS156Y 165 bp/DYS19 190 bp] accounts for 67% of the Y chromosomes whereas the most frequent haplotype in Africa [Alu+/DXYS156Y 160 bp/DYS19 198 bp] reaches 27%. Thus, Y-chromosomal diversity in European populations seems to be similar to mitochondrial

Data deposition: The sequences reported in this paper have been deposited in the GenBank data base [accession nos. 67617–67648 (Swedish) and 67649–67668 (Estonian)].

Table 1. Y-chromosome haplotypes in the populations surveyed

		YAP negative												YAP positive						
	DXYS156	160				165						170		194					165	
Population	DYS19	190	194	198	202	178	186	190	194	198	202	190	194	186	190	194	198	202	186	198
Finns (n = 54)								0.94 (51)	0.02 (1)	0.02 (1)		0.02 (1)								
Estonians (n = 20)								0.35 (7)	0.35 (7)	0.25 (5)									0.05 (1)	
Saami (n = 28)							0.04 (1)	0.68 (19)	0.11 (3)	0.18 (5)										
Swedes (n = 40)								0.62 (25)	0.25 (10)	0.08 (3)	0.02 (1)		0.02 (1)							
Swiss (n = 51)							0.02 (1)	0.53 (27)	0.22 (11)	0.10 (5)									0.14 (7)	
Basques (n = 25)								0.72 (18)	0.16 (4)			0.04 (1)		0.08 (2)						
Sub-Saharan Africans (n = 30)		0.03 (1)	0.07 (2)	0.10 (3)	0.07 (2)	0.03 (1)	0.07 (2)	0.03 (1)						0.10 (3)	0.03 (1)	0.13 (4)	0.27 (8)	0.03 (1)		0.03 (1)

Absolute numbers are given within parentheses.

variation in being more restricted than in African populations (18) and showing little diversification among populations (2).

Among the 54 Finnish males studied, 51 (94%) carried the haplotype [Alu−/DXYS156Y 165 bp/DYS19 190 bp]. Although this haplotype occurs with frequencies from 35% to 72% in other European populations, other Y chromosome haplotypes are also relatively frequent in these populations. For example, the haplotypes [Alu−/DXYS156Y 165 bp/DYS19 194 bp] and [Alu−/DXYS156Y 165 bp/DYS19 198 bp] occur with frequencies ranging from 11% to 35% and from 8% to 25%, respectively, in the European populations whereas in the Finns, each of them were found only once among the 54 males studied (Fig. 1 and Table 1).

When genetic diversity is calculated based on the Y chromosome haplotypes, it is 0.11 in the Finns, whereas it varies between 0.47 and 0.73 in the other five European populations, and reaches 0.90 in the Africans (Table 2). Thus, in Finns, the genetic diversity of the Y chromosome is four to eight times lower than elsewhere. It is noteworthy that in populations that surround the Finns geographically—i.e., the Swedes, the Saami, and the Estonians—the genetic diversity is four to six times higher than that in the Finns. Thus, the reduction in Y chromosome diversity seems to be restricted to the Finns. When the population differentiation is tested by Fisher's exact test (17), it is found that the African population is different from all European populations studied ($P < 0.01$). Within Europe, the Basques differ from the Estonians ($P < 0.01$) but not from the Swedish, Swiss, and Saami populations. However, the Finns differ from all other populations ($P < 0.01$) studied. Thus, there is a significant difference in the frequency of Y chromosome haplotypes in Finns when compared with other European populations.

Mitochondrial Genetic Diversity. When a 360-bp segment of the mitochondrial control region is analyzed in the same populations as the Y-chromosomal haplotypes, the mean pairwise sequence difference among the sequences determined in Finns is 3.90. In other European populations the sequence differences vary between 3.24 and 5.03 (3), and in

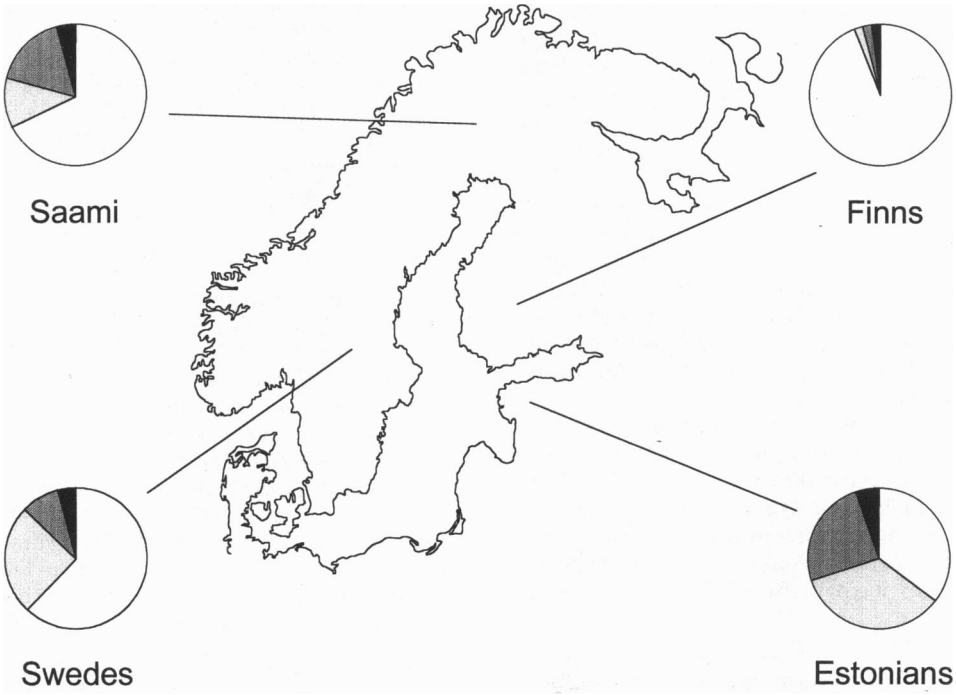

FIG. 1. Map of the Baltic Sea region indicating the frequencies of Y-chromosomal haplotypes in Finns, Saami, Estonians, and Swedes.

Table 2. Genetic diversity based on Y-chromosomal haplotypes and mitochondrial control region sequences in various populations

Population	Y chromosome	mtDNA (all)	mtDNA (1)	mtDNA (1+2)	mtDNA (3+)
Finns	0.11	0.98	0.12	0.30	0.96
Estonians	0.73	0.99	0.08	0.43	0.96
Saami	0.51	0.82	0.50	0.57	0.78
Swedes	0.56	0.99	0.31	0.65	0.96
Swiss	0.65	0.96	0.30	0.45	0.92
Basques	0.47	0.97	0.13	0.17	0.93
Sub-Saharan Africans	0.90	0.98	0.47	0.89	0.97

The mitochondrial values are based on all nucleotide positions (all), positions inferred in ref. 16 to change once (1), once and twice (1+2), and three or more times (3+).

three Sub-Saharan African populations they are 3.68–8.74 (2). Furthermore, the mitochondrial genetic diversity in Finns is 0.98 and varies between 0.82 and 0.99 in European populations, and is 0.98 in Sub-Saharan Africans (Table 2). Thus, at the first glance, the mtDNA diversity in the Finns falls into the range of variation found in other populations whereas the Y-chromosomal variation indicates a reduction in the male effective population size. This might mean that a bottleneck in population size has affected only Finnish males and not females, for example, due to a higher variation in male reproductive success in Finns than in other neighboring populations, or due to a colonization event that involved few men but many women. Alternatively, a female bottleneck may not be directly discernible by comparing mitochondrial DNA sequences in contemporary Finns. A reason for this may be that the mitochondrial diversity has been regenerated by substitutions occurring subsequent to a putative bottleneck in population size.

An Ancient Mitochondrial Bottleneck. The evolutionary rate of the mitochondrial genome is on average about 5 to 10 times faster than for noncoding nuclear sequences (19). In addition, the control region evolves on average 10 times faster than other parts of the mitochondrial genome (20). However, it has been shown that within the mitochondrial control region, nucleotide positions evolve at different rates such that at least a 15-fold difference occurs between the fastest and slowest positions (16, 21). Therefore, it should be possible to eliminate substitutions that are likely to have occurred comparatively recently by excluding from the analysis positions that evolve rapidly. This will have the effect of confining the analysis to positions that are slowly evolving and therefore likely to define lineages that have existed in the population prior to a putative bottleneck. Obviously, only such lineages are expected to show a reduction of diversity induced by a bottleneck.

The analysis was confined to 70 nucleotide positions that have changed only once in a parsimony tree relating mitochondrial control region sequences from around the world (16). Using the information from these positions, nine mitochondrial lineages were found among the 50 Sub-Saharan Africans and the genetic diversity among them was reduced to 0.47 (Table 2). Similarly, the diversity of the Saami was reduced to 0.50. The diversity of Swedes and Swiss was reduced slightly more, to 0.31 and 0.30, respectively. Among 50 Finns, four mitochondrial lineages were identified and the genetic diversity was 0.12. Similarly, in Estonians and the Basques, diversity was reduced to 0.08 and 0.13, respectively. In a test for population differentiation (17), all European populations (except the Saami) were different from the Africans and the Saami ($P < 0.05$), but not from each other. When positions that have experienced two changes (16) are added to the analysis, the genetic diversity in Finns and the Basques remains reduced (0.30 and 0.17, respectively), whereas the diversity in the Estonians raises to 0.43 and becomes similar to those of other European populations (0.45–0.65). Using these positions, the Finns and the Basques are significantly different from the Africans, the Swedes and the Saami ($P < 0.05$). In addition, the Basques are different from the Estonians ($P < 0.05$) whereas the Finns are not. Thus, the reduction in genetic diversity is seen only in the most slowly evolving positions in the Estonians whereas also slightly faster evolving positions show a reduction in Finns and Basques. In the latter case, this results in a statistically significant differentiation between these populations and some other European populations. When the 59 positions that have changed 3–19 times and thus evolve most rapidly are analyzed alone (16), the genetic diversity is close to the value of observed when all 360 positions are used (Table 2), confirming that the more rapidly evolving positions are responsible for the uniformly high diversity in all populations analyzed.

DISCUSSION

The spectrum of inherited diseases in Finns is dramatically different from that of neighboring populations in that many recessive diseases are unique to Finland whereas other diseases, common elsewhere, are rare in Finland (4–6). Within the country, some of the former diseases occur in the entire population while others are geographically restricted. This has been interpreted as the result of several founder effects, one associated with the initial colonization of Finland by the population that today speaks Finnish, and subsequent local founder effects and genetic drift in isolated local populations associated with the colonization of internal parts of the country (22). Furthermore, the amount of linkage disequilibrium that surrounds the "Finnish" disease alleles suggest a correlation with the age of the founder effects since disease mutations with a restricted geographic distribution tend to be associated with larger chromosomal regions of linkage disequilibrium than those that occur in the entire population (5). Interestingly, although the data is not extensive, the "Finnish" diseases seem to be absent from the Saami population (23). However, during the process of colonization, Finns seem to have interacted closely with the resident Saami population as judged from genetic admixture detected in the Finns (3, 24, 25) and from the putative language change in which the Finns acquired a precursory form of their present language from the Saami (26). Given this scenario, it seems paradoxical that no reduction in genetic diversity among Finns has so far been demonstrated in studies of autosomal markers (see, for example, refs. 27–29) not associated with diseases.

A Male Bottleneck in the Finns. The Y chromosome is particularly useful as a tool to detect past reductions in population size since its paternal and haploid mode of inheritance causes its effective population size to be four times lower than that of nuclear loci. Furthermore, since it lacks recombination except at pseudoautosomal regions in telomeric parts of the chromosome, haplotypes will change exclusively as a result of mutation. When haplotypes consisting of alleles at three polymorphic loci on the nonrecombining part of the Y chromosome are constructed, it is found that one haplotype is predominant in the Finnish population (Table 1 and Fig. 1). Although this haplotype is the most frequent also in other populations, these populations contain also other haplotypes at substantial frequencies. Consequently, the genetic diversity for the Y chromosome is dramatically reduced in Finns (Table 2). It is notable, that this is the case when the Finns are compared with populations in close geographical vicinity (the Saami, Estonians, and Swedes), as well as when they are compared with other European populations (the Swiss and the Basques) and to Africans. Thus, the Y chromosomes clearly indicate that the Finnish population has experienced a past

reduction in effective population size relative to other European populations.

mtDNA Diversity. Maternally inherited mtDNA is similar to the Y chromosome in having a 4-fold smaller effective population size relative to nuclear loci and in lacking recombination. Consequently, it is similarly expected to be more sensitive to bottlenecks in population size than nuclear loci. However, when mitochondrial control region sequences are analyzed, no reduction in genetic diversity of the Finnish population can be seen (2, 3). A possible reason for this is that mutations have regenerated mitochondrial genetic diversity subsequent to a bottleneck detectable in the Y chromosome gene pool. Such mutations are likely to have affected predominantly nucleotide positions that evolve rapidly. If that is the case, positions that evolve slowly would represent old mitochondrial lineages that may predate the population bottleneck. Such position could thus be used to detect, and possibly to date, the bottleneck.

Hasegawa *et al.* (16) have estimated the relative rate of evolution of nucleotide positions in the mitochondrial control region by determining the number of times that these positions have experienced evolutionary changes in a parsimony tree estimating the history of DNA sequences from the entire world. When the analysis is confined to the variable positions that evolve slowest, bottlenecks in population size that occurred between the time of the coalescence of all mitochondrial lineages to a single ancestral sequence and up to the present are expected to be detected. Interestingly, when these positions are used, the Finns, as well as the Estonians and the Basques, show a reduction in genetic diversity. Once a class of faster evolving positions is added to the analysis, the reduction in effective size is not visible in the Estonians but is still seen in the Finns and the Basques. The rapid evolution and resulting saturation of genetic diversity after a bottleneck is illustrated by confining the analysis to the 59 positions that evolve the fastest. In this case (Table 2), the Finns, as well as the other populations studied, display comparable levels of genetic diversity which are almost as high as when all nucleotide positions are analyzed. Thus, the rapidly evolving positions are responsible for most of the genetic diversity observed in populations.

Dating the Finnish Bottleneck. By studying positions of different evolutionary rates, it should in principle be possible to discern the relative age of bottlenecks in different populations. Of interest in this respect is the observation that when the positions that have changed once are studied, the Finns as well as the Estonians and the Basques show a reduction in genetic diversity. When positions that have changed twice are added to the analyses (Table 2), the Basques, and to some extent the Finns, show a reduction in diversity while the diversity of the Estonians is almost as large as that of, for example, the Swiss. This suggests that the founder effect reducing the effective population size of Estonians predates that of the Finns. The reduced diversity among the Basques may represent a small population size over time rather than a founder effect. However, more extensive sampling of both the Estonian and Basque population is needed to establish this.

By studying the amount of diversity that has accumulated in mitochondrial lineages subsequent to the bottlenecks it should be possible to arrive at an approximate date for the latter. Estimates of the evolutionary rate of the segment of the mitochondrial control region studied here vary between one substitution in 13,000 years (30) and one substitution in 5000 years (31). Using these rates, and assuming that all mitochondrial diversity in the Finnish population has been generated subsequent to the bottleneck, the mean pairwise sequence difference in Finns of 3.90 substitutions would indicate approximate dates for the bottleneck of 25,000 or 10,000 years, respectively. However, this is based on average rates across the entire nucleotide sequence whereas, as shown above, mutations subsequent to the bottleneck have been largely confined to rapidly evolving nucleotide positions. Thus, the average rate yields an over-estimate of the time since the bottle neck. A better estimate of the rate of substitution at rapidly evolving positions may come from the observation of mutations in pedigrees. A recent preliminary report (32) of observed mutations in mother-child pairs indicates that the mutation rate is approximately one substitution in 50 generations over the entire control region, roughly corresponding to one substitution in 100 generations for the segment studied here. Assuming a generation time of 20 years, this rate would result in one observed difference between individuals per 1000 years and yield a date of approximately 3900 years for the Finnish population bottleneck. This rough estimate is compatible with the archaeological record which indicates that agriculture arrived to Finland approximately 4900–4400 years ago with the corded-ware/battle axe culture (33, 34). Obviously, a more reliable estimate of the date of the bottleneck will have to await the observation of larger numbers of mutational events. Furthermore, studies of the extent of linkage disequilibrium in various Eurasian populations is expected to shed further light on the extent to which founder effects have been involved in the peopling of northern Europe.

Note Added in Proof. When a total of 94 Finns, 64 Estonians, and 81 Swedes are analyzed for Y-chromosomal haplotypes, the diversity of the Finns (0.22) remains significantly lower than in Estonians (074), Swedes (0.54), and the other populations studied.

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