Language replacement in Scandinavia

Sir — While the majority of Europeans speak Indo-European languages, about 24 million Europeans speak Finno-Ugric languages1, such as Hungarian, Finnish and Saami. The latter two languages are closely related2 and spoken by Finns and Saami, who live in Fennoscandia. Based originally on the linguistic relationship of Finnish and Saami with languages spoken in Russia and Siberia, it has traditionally been thought that the Finns migrated to their current location from a common origin of Finno-Ugric-speaking populations in the east, either in the Altai, Uralic, or Volga regions3. Although studies of gene frequencies4,5 have shown that the majority of the Finnish gene pool is “European”, the view of this as a recent admixture overlaying an older “eastern” component is favored by many investigators5,7.

To reassess the genetic relationship of Finns and Saami, we have analysed gene frequency data that have been collected in European populations8, and new data on mitochondrial sequence variation9 and mini- and microsatellite variation (A.S. et al., unpublished). We constructed trees relating Saami, Finns and representative European populations that speak Indo-European languages with the neighbour-joining10 and UPGMA11 algorithms. In all cases (Fig. 1), the Saami are clearly outliers among the group studied, whereas the Finns are more closely related to other groups, including Italians, English and Germans, than to the Saami. In fact, in some trees the Finns fall within clusters containing Indo-European speakers, whereas other trees show the Finns to be closely related to the Indo-European speaking populations, albeit falling as an outgroup among them. This can be attributed to a low level of admixture between the Finns and the Saami which has been detected both in studies of nuclear markers5,12 and mitochondrial DNA sequences9. Thus, data from the mitochondrial and nuclear genomes show that, in contrast to their close linguistic affiliation, the Finns and the Saami do not share a recent biological ancestry.

These genetic relationships do not support the traditional notion of a “Finno-Ugric homeland” in the east from which the Finns and the Saami would have come to north-western Europe, but is more compatible with language replacement(s). A formal possibility is that all European populations in the past spoke Finno-Ugric languages and that the majority has changed subsequently to Indo-European languages. However, since language replacements are rare events in human history13, this is unlikely. Another possibility is that the Saami, having a different genetic history than the Finns, would have taken their language from the Finns. However, this does not explain why the Finns, having a genetic history similar to Indo-European speakers, speak a Finno-Ugric language. Finally, if the Finns originally spoke an Indo-

Fig. 1 Linguistic and genetic trees of Indo-European and Finno-Ugric speaking populations in Europe. Genetic distances among Saami, Finns, Italians, English and Germans for 29 polymorphic protein, blood group and human leucocyte antigen loci were obtained from ref. 8. Loci used are ABO, Di, FY, JK, K, MNS, P, RH, SE, ACP1, ADA, AK1, ESD, GLO1, GLO2, GPT, NPA, PGD, PGM1, PGM2, GC, HP, PI, TF, HBB, GM, KM, HLA-A, HLA-B and PTC (for gene frequencies and symbols, see ref. 20). The genetic distances for the mini- and microsatellite loci D1S80, apob, D17S530, VWA and TH01 in Saami, Finns, Swiss, French, Spanish and European Americans stem from unpublished data by Sajantila et al. The mitochondrial DNA sequences from Saami, Finns and Indo-European speaking populations were from ref. 9. For nuclear loci, neighbour-joining16 (NJ) and unweighted pair-group method using arithmetic averages11 (UPGMA) trees were constructed from modified Cavalli-Sforza's distances $D_{ij}$ using the DISPAN program kindly provided by M. Nei (Penn State University, University Park, Pennsylvania, USA) and the PHYLPackage22. From the mtDNA sequences, pairwise differences within and between the population samples were calculated using an unpublished program by A. von Haessler (Ludwig Maximilians University, Munich). Genetic distances $D_{SQ}$ were calculated as follows: $D_{SQ} = D_{SP} + D_{SQ} - D_{SQ}^{d}$, where $D_{SP}$ means mean pairwise difference between population 1 and 2, $D_{SQ}^{d}$ means mean pairwise difference within population 1, and $D_{SQ}^{d} = D_{SQ}^{d}$ mean pairwise difference within population 2. Negative $D_{SQ}$ values were converted to zero. $D_{SQ}$ values were used to construct NJ and UPGMA trees. The NJ trees were rooted with the midpoint method.
European language, but in prehistoric times changed to a proto-Saami language, the genetic as well as the linguistic data can be explained by a single case of language replacement.

At first glance, such a language replacement is surprising as it does not seem to fit any of three main categories into which known cases of language replacements fall. These involve a population that is either demographically expanding, culturally or technologically dominant, or outwitting another population in the context of a collapse of a large political system. In the process, the former population forces the latter population to change its language. One such example involving Finno-Ugric speaking population is known from historic records. When the Magyars arrived in Hungary in the late 9th century A.D., the local population came to replace their Indo-European language by the proto-Hungarian spoken by the Magyars.

In contrast to other cases of language replacements, the relationship of the Finns to the Saami seems to be a classical case of agriculturalists colonising an area inhabited by non-agriculturalists, depriving the latter of the land and thus of the basis for their subsistence. From this point of view, the Saami, rather than the Finns, might be expected to have changed their language. However, the relationship between the Saami and the Finns may not always have been the one that we know from historical records. A hint of this comes from the occurrence of a number of autosomal recessive diseases in Finland, which suggest that the Finns have gone through a substantial bottleneck in population size. If this occurred during their prehistoric colonisation of eastern Fennoscandia, then that may represent a period when the Finns were scarce and lived for a long time among a majority of Finno-Ugric speakers. Consequently, they may have changed their language from an Indo-European one to a Finno-Ugric one.

The archaeological record is compatible with this scenario. After the Ice Age, Finland as well as Northern Scandinavia was peopled by hunter-gatherers. At about 2,900–2,400 BC (calibrated years) animal husbandry and agriculture arrived in the area, represented by the corded ware/battle-axe culture, which had its centre in Central Europe. Thus, we suggest that instead of representing a migration from a putative “Finno-Ugric homeland” in the east, the Finns are the descendants of the agriculturalists that shaped much of the genetic landscape of Europe and which may also have spread Indo-European languages over the continent. The Finns are, however, exceptional in that they have been profoundly affected not only genetically but also linguistically by their small population size and close interaction with indigenous non-agriculturalists during their prehistoric colonisation of eastern Fennoscandia. Further studies of genetic lineages will shed additional light on how Finns and Saami are related. Similar studies in other Finno-Ugric-speaking populations which live in geographic proximity but differ in being and not being agriculturalists will address the question if language replacements may have been a common phenomenon at the fringe of the agriculturalist expansion.

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Microsatellite ‘evolution’: directionality or bias?

Sir—In the July 1995 issue of Nature Genetics, Rubinsteins et al. claim to have found evidence for directionality in the evolution of microsatellites and for a difference in microsatellite mutation rate between humans and other primates—human repeats tending to be longer than primate repeats. We argue that this conclusion has been reached because of an ascertainment bias in the selection of loci analysed: microsatellites chosen on the basis of being highly polymorphic in one species will generally tend to harbour shorter repeats in a related species. In support of our view, we present such data for a number of avian microsatellites. The abundance of human (CA)_n loci decreases with increasing mean repeat length; for instance, loci with n > 20 constitute only 5–10% of all loci with n ≥ 6 (ref. 2). There is a