Int J Legal Med (2010) 124:91–98
DOI 10.1007/s00414-009-0354-7

ORIGINAL ARTICLE

Homogeneity in mitochondrial DNA control region sequences in Swedish subpopulations

Andreas O. Tillmar · Michael D. Coble · Thomas Wallerström · Gunilla Holmlund

Received: 12 December 2008 / Accepted: 12 May 2009 / Published online: 10 July 2009

Abstract In order to promote mitochondrial DNA (mtDNA) testing in Sweden we have typed 296 Swedish males, which will serve as a Swedish mtDNA frequency database. The tested males were taken from seven geographically different regions representing the contemporary Swedish population. The complete mtDNA control region was typed and the Swedish population was shown to have high haplotype diversity with a random match probability of 0.5%. Almost 47% of the tested samples belonged to haplogroup H and further haplogroup comparison with worldwide populations clustered the Swedish mtDNA data together with other European populations. AMOVA analysis of the seven Swedish subregions displayed no significant maternal substructure in Sweden (F_{ST}=0.002). Our conclusion from this study is that the typed Swedish individuals serve as good representatives for a Swedish forensic mtDNA database. Some caution should, however, be taken for individuals from the northernmost part of Sweden (provinces of Norrbotten and Lapland) due to specific demographic conditions. Furthermore, our analysis of a small sample set of a Swedish Saami population confirmed earlier findings that the Swedish Saami population is an outlier among European populations.

Keywords Mitochondrial DNA · Sweden · Saami · Control region · Demography

Introduction

Mitochondrial DNA (mtDNA) has proven to be useful in various forensic applications [1, 2]. It is often used in the context where only limited amount of nuclear DNA is present in the sample or in questions of a maternal relationship. In forensic casework applications, the DNA typing is followed by a database search to estimate the rarity of the mtDNA profile. This frequency can then be used to create a likelihood ratio [3], i.e., the evidence that the mtDNA haplotype originated from the suspect rather than from a random individual in the population. For such situations, a DNA reference database, reflecting the appropriate population that the individual(s) belong to, must be used. The reference database should be based on certain conditions [4, 5], and one crucial criterion to consider is the possibility of substructure in the population of interest. This issue is particularly important for uniparental haploid DNA markers on the Y-chromosome as well as on the mtDNA.

The aim of this study was to create a Swedish mtDNA reference database covering the complete mitochondrial control region. Individuals from geographically different Swedish subregions were typed and studied in order to examine possible hetero/homogeneity within the total Swedish population.

Electronic supplementary material The online version of this article (doi:10.1007/s00414-009-0354-7) contains supplementary material, which is available to authorized users.

A. O. Tillmar (✉) · G. Holmlund
Department of Forensic Genetics and Forensic Toxicology,
National Board of Forensic Medicine,
Artillerigatan 12,
58758 Linköping, Sweden
e-mail: andreas.tillmar@rmv.se

M. D. Coble
Armed Forces DNA Identification Laboratory,
Rockville, MD, USA

T. Wallerström
Department of Archaeology and Religious Studies, Norwegian University of Science and Technology (NTNU),
Trondheim, Norway

Included in this study were also individuals from a Swedish Saami population, nomads from Jokkmokk. In previous studies, the Saami population has shown to be a genetic outlier among European populations and it has been suggested that the Saami might originate from a limited subset of Europeans [6]. The Saami population consists of some 70,000 people in four different countries of whom maybe 20,000 persons speak one of the three different Saami languages [7]. Saami history, well described as "colonial", demonstrates a wide range of contacts with other groups resulting in differing grades of assimilation, loss of language, and cultural traditions [8–10] as well as DNA heterogeneity [6].

Northern Europe (including Sweden) was covered with ice from 22,000 to 18,000 B.P. (Before Present). The retreating ice reached the southern margin of the Scandinavian peninsular some 4,000 years later where it lingered for a further 2,000 years [11]. In Norway, however, large parts of the coast were ice-free throughout the entire late-Glacial period, at least from 13,000 B.P. and some single presumed late-Glacial artifacts are recorded indicating a still longer population history [12]. Inside northern Scandinavia, the ice melted earlier than hitherto presumed [13, 14], giving way for settlements near the Arctic Circle as early as at 8,600 B.P. in a situation of excellent ecological conditions [15, 16]. Into Scandinavia, late Paleolithic Hamburgian, Bromme, and Ahrensburg culture groups were followed by the Mesolithic Maglemose, Kongemose, and Ertebølle hunters and gatherers describing a seemingly linear, unbroken sequence for approximately 6,000 years beginning almost 12,000 years ago (9,600 B.C.) [11]. These groups originated from western Europe and is, in recent linguistic and genetic research, suggested to represent a non-Indo-European population where the Basques are the nearest surviving relatives [17]. For almost 12,000 years, immigration and population movements of various scales, descent, and directions have occurred within the present borders of Sweden. This, in combination with recorded demographic events over the last 1,000 years [18, 19], may have been the reason for the minor regional genetic differences present in the modern Swedish population, previously shown by a Y-chromosomal study [20].

Materials and methods

DNA samples and extraction

Blood samples were collected from 296 unrelated men from seven geographically different Swedish regions (Blekinge/Kristianstad, Gotland, Skaraborg, Östergötland/Jönköping, Uppsala, Värmland, and Västerbotten; see Fig. 1). The sampled areas are representative for contemporary demography and are expected to give information about possible different population histories [20].

In addition, 39 samples from a Swedish Saami population ("Jokkmokk nomads") were analyzed. For simplicity, the Saami population was not included in the term

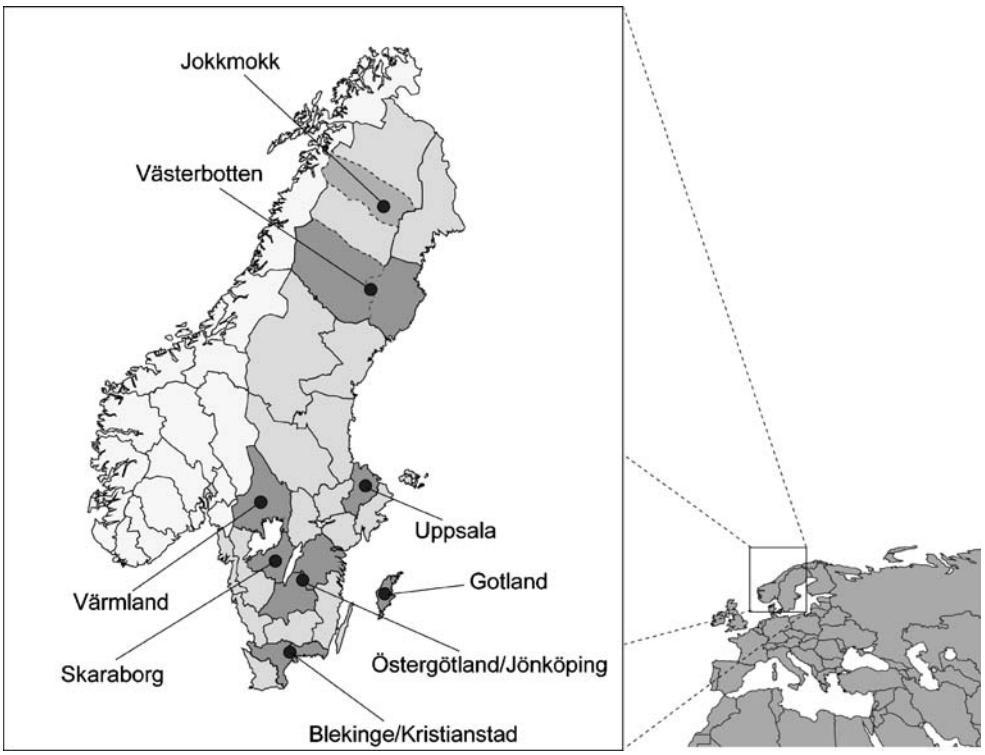

Fig. 1 Map showing the sampled regions. The Jokkmokk Saami samples were taken from the region enclosed by the *dashed line*. In the text, some discussions concern two additional Swedish regions named Lapland and Norrbotten. Lapland comprises the western part of the region Västerbotten together with the region northwest of Västerbotten. Norrbotten is located northeast of the region Västerbotten

"Swedish population" and in all statistical analyses the Swedish sample set and the Saami samples were treated separately unless otherwise stated.

DNA was extracted from the blood samples using the SDS-urea method [21].

Amplification and sequencing

PCR amplification, sequencing, and evaluation of the data were performed following the strategies outlined in Brandstätter et al. [22] and Irwin et al. [23]. Briefly, automated PCR amplification of the full control region was prepared on the Corbett Robotics CAS-1200 robotic platform (Concorde, NSW, Australia) using the primers F15971 (TTA ACT CCA CCA TTA GCA CC) and R599 (TTG AGG AGG TAA GCT ACA TA) for amplification of the control region. Each PCR reaction contained 1× AmpliTaq Gold reaction buffer (Applied Biosystems, Foster City, CA, USA), 200 μM each dNTP, 200 nM each primer, and 2.5 U AmpliTaq Gold (Applied Biosystems), in a final volume of 50 μl. Samples were amplified in an Applied Biosystems GeneAmp 9700 Thermal Cycle with ramp speeds running in the 9600 mode using the following conditions: 95°C for 10 min followed by 36 cycles of 94°C for 30 s, 56°C for 30 s, and 72°C for 1 min. Post-amplification cleanup of unincorporated primers and dNTPs was carried out by adding 1.5 μl ExoSapIt (USB, Cleveland, OH, USA) plus 18.5 μl of dilution buffer to the PCR reaction and incubating in the thermal cycler at 37°C for 20 min, followed by an inactivation of the reaction at 90°C for 20 min.

Cycle sequencing was prepared using the Big Dye Terminator version 1.1 sequencing kit (Applied Biosystems) on a Tecan Genesis Robotic Workstation (Männedorf, Switzerland) utilizing the sequencing primers described in Brandstätter et al. [22] and updated in Irwin et al. [23]. Post-sequencing cleanup of the cycle sequencing reaction was purified using the Performa V3 96-well short plate (Edge Biosystems, Gaithersburg, MD, USA) following the manufacturer's guidelines. Samples were then dried down and re-suspended in 10 μl of HiDi Formamide (Applied Biosystems) and analyzed on either an Applied Biosystems 3130 or 3730 Genetic Analyzer. Sequences were aligned according to the revised Cambridge Reference Sequence [24, 25] using Sequencher software version 4.7 (GeneCodes, Ann Arbor, MI, USA). Differences from the rCRS were transferred electronically into an in-house LIMS system and the data were verified. An additional quality control check was performed by EMPOP [26] (http://www.empop.org).

Statistical analysis

Haplogroups were assigned based on sequence data from the entire control region using mtDNAmanager (http://mtmanager.yonsei.ac.kr). For 12 individuals, the haplogroup status could not be determined due to lack of defining polymorphisms.

Haplogroup frequencies were used in order to compare the Swedish population with other worldwide populations [27–35]. Due to differences in haplogroup resolution for the reference populations, we reassigned (collapsed) the haplogroup status both for our data and for the populations to be compared making them into comparable data sets. These haplogroup frequencies were then used in a principal component analysis (PCA) to compare the Swedish and the Saami populations in a worldwide context. The PCA was carried out using MATLAB 7.1 (MathWorks, Inc.).

Forensically important values, such as haplotype diversity, number of polymorphic sites, pairwise differences, and random match probability (RMP), were considered and computed together with population statistic measurements, such as Tajima's D and mismatch distribution. Pairwise comparisons between the Swedish subregions were performed using Φ_{ST} values, which were computed with pairwise differences as the distance method. C-stretches at position 16193, 309, and 573 were ignored together with the AC length heteroplasmy at positions 523 and 524 in the statistical evaluations unless otherwise stated. Furthermore, AMOVA was performed to get an overall view of possible regional substructure in the Swedish sample set. For the AMOVA, only haplotype frequencies were considered resulting in F_{ST} values. All measurements were generated using Arlequin v3.1 [36]. Sequence data from the Swedish population were also compared with corresponding data from the geographically closely located populations in Germany [37], Finland [31], and Norway [38]. For these analyses, Φ_{ST} values were computed based on HVI and HVII data for the Swedish/German/Finnish comparison while HVI data were used for the Swedish/Norwegian comparison. P values less than 0.05 were considered to be significant.

Results and discussion

Sequence data from the complete mitochondrial control region were obtained for 296 Swedish males and 39 males belonging to the Swedish Saami population (Supplementary Table 1). Sequence data from one individual belonging to the region Värmland was excluded from the statistical analysis due to its deviating sequence (16 bases insertion at position 291), which could have had a high impact on the statistical analysis due to the limited sample size. Focusing first on the Swedish sample set, a total of 247 distinct haplotypes (224 if the polymorphic C-stretch regions were ignored) were detected corresponding to a genetic diversity of 0.998 (0.996) (Table 1). The number

Table 1 Diversity measurements for the Swedish subregions

Population statistics	Gotland	Uppsala	Östergötland/ Jönköping	Blekinge/ Kristianstad	Skaraborg	Värmland	Västerbotten	Sweden	Saami
Individuals	40	54	40	39	41	42[b]	40	296[b]	39
Diversity[a]	0.996	0.997	0.997	0.991	0.985	0.996	0.989	0.996	0.838
Random match prob.	2.6%	2.1%	2.6%	3.1%	2.8%	2.7%	3.1%	0.5%	17.7%
Polymorphic sites[a]	77	90	91	74	71	75	80	189	16
Unique haplotypes	39	51	39	36	38	39	36	247	14
Mean pairwise differences[a]	10.2	8.8	10.1	8.7	8.4	8.3	8.5	9.0	4.7

"Sweden"=all subregions combined except for the Saami population. Random match probability was calculated with sum of squares

[a] Indices were generated from the entire control region, with C insertions at 16193, 309, 573, and AC region at 523, 524 ignored

[b] Sequence data from one individual belonging to the region Värmland was excluded from the statistical analysis due to its deviating sequence

of polymorphic sites was estimated to be 189 when C-stretches were ignored and the random match probability was calculated to be in the order of 0.5%. Point heteroplasmy normally occurs for mtDNA sequences at a modest level. This was also true for our Swedish samples, which showed heteroplasmy in 8%.

The most common haplotype was "16519C 263G 315.1C", which occurred in eight individuals (2.7%) and was evenly distributed among the different subregions. The most frequent haplogroup in Sweden was H, covering 47% of the typed individuals, and 97% of the Swedish samples belonged to various western European haplogroups (H, X, T, J, U, V, I, W, K). Using PCA, the haplogroups found in the Swedish population agreed with the haplogroup distributions in other European populations (Fig. 2).

A mismatch distribution test was performed, which showed a unimodal distribution of the mtDNA sequences (Fig. 3a), which normally reflects populations that have expanded from one initial pool. A measurement of Tajima's *D* was also performed and was computed to be negative (−2.1), which strengthens the hypothesis of an expanding population.

The fact that the mtDNA follows the maternal lineages makes it, together with the paternal inherited Y-chromosome, especially informative in evolutionary studies offering knowledge about demography [39]. Comparing mtDNA sequences from the seven Swedish subregions showed no or very little signs of differences in diversity (Table 1). The Φ_{ST} values only showed one significant genetic distance, namely between Östergötland/Jönköping and Västerbotten (Φ_{ST}=0.011, P=0.04) (Table 2). This underlines our previous observation [20] that Västerbotten is unique not only by the suggested founder effect but also in the demographic history. Östergötland/Jönköping, in contrast to Västerbotten, demonstrates a recorded agrarian settlement beginning in the Neolithic [40–42]. In terms of estimated population density

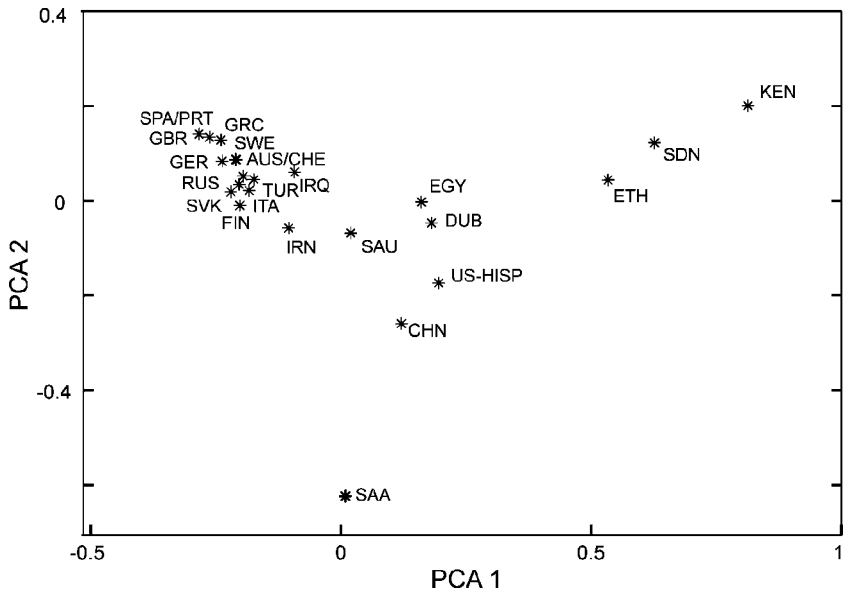

Fig. 2 Population comparison of mtDNA haplogroup frequencies using principal component analysis (*PCA*). The two principal vectors explain 79% of the total variation. The abbreviations used are as follows: *SPA/PRT* Spain/Portugal [30], *GRC* Greece [32], *GBR* England [30], *RUS* Russia [30], *GER* Germany [30], *SVK* Slovakia [33], *FIN* Finland [31], *ITA* Italy [35], *SWE* Sweden (present study), *AUS/CHE* Austria/Switzerland [30], *IRQ* Iraq [27], *IRN* Iran [27], *SAU* Saudi Arabia [27], *CHN* China [29], *EGY* Egypt [27], *DUB* Dubai [28], *US-HISP* US-Hispanic [34], *ETH* Ethiopia [27], *SDN* Sudan [27], *KEN* Kenya [27], *SAA* Saami (present study)

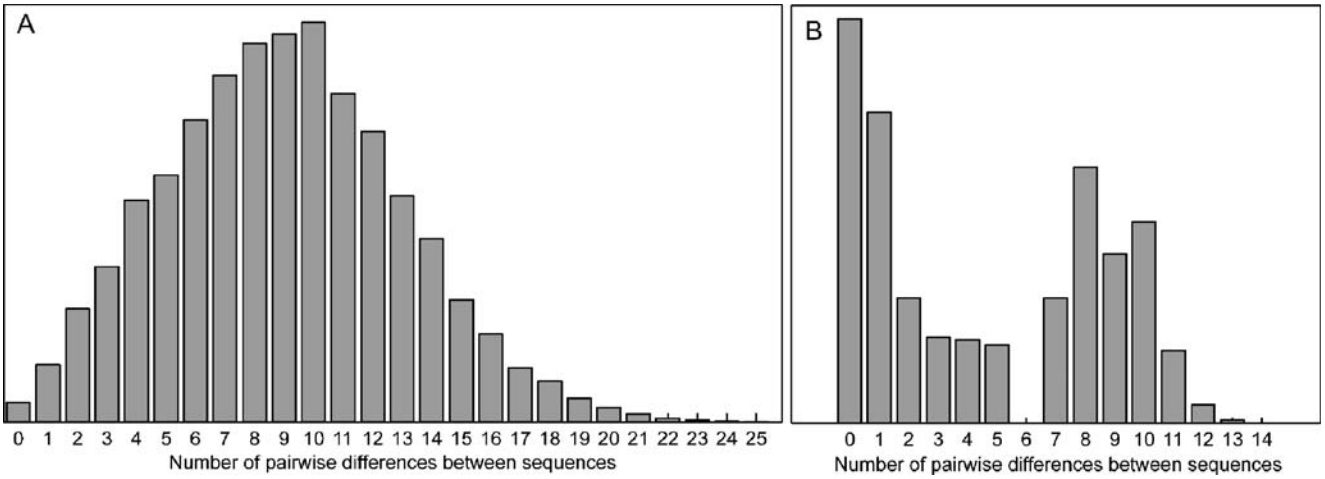

Fig. 3 Mismatch distribution for the Swedish mtDNA sequences (**a**) and the Saami mtDNA sequences (**b**)

(3.5 inhabitants/km^2 for Östergötland in the year 1571 and 11.4 in the year 1751, Jönköping 2.7 and 8.3, respectively), there is a remarkable contrast to Västerbotten with its 0.1 inhabitant/km^2 in 1571 and 0.3 in 1751 [43]. The samples from Västerbotten derived predominately from the coastal area. Furthermore, according to our previous study, Västerbotten was not capable of compensating for the wartime losses of young men in the sixteenth to eighteenth centuries thus conditioning a founder effect in Västerbotten to be associated with German and/or Dutch immigrants and/or their offspring. In contrast, the mtDNA here demonstrated suggests that some of these immigrants were women.

According to an AMOVA test on data from the seven regions, almost all the variation (>99.3%) was observed within the tested subregions rather than between them. The F_{ST} values were very low at 0.002 (complete sequence) and 0.007 (C-stretches ignored). Thus, we find no maternal substructure within Sweden, and all mtDNA sequences can be treated as one combined reference database.

In our previous Y-chromosome study [20], we showed that the northern Swedish region of Västerbotten was the region in Sweden with the significantly closest genetic distance to the Swedish Saami population. However, our present mtDNA results did not show any such evidence. All Swedish subregions showed more or less the same large significant genetic distance to the Saami population (Φ_{ST} values ranging from 0.19 to 0.22, Table 2). Comparing the Saami population with some other populations, the shortest genetic distance was shown to the Finnish population (Table 3).

Since no actual mtDNA differences were observed between the samples from the Swedish subregions, the samples were treated as one single population when distances to geographically neighboring populations were compared. Short genetic distances were observed for comparison with a Norwegian population (Φ_{ST}=0.004, $P<0.001$), a Finnish population (Φ_{ST}=0.011, $P<0.001$), and a northwestern German population (Φ_{ST}=0.001, $P>0.05$). These distances were of the same magnitude as the distances between the Swedish subregions. Thus, for the

Table 2 Φ_{ST} values from pairwise comparison of Swedish subregions

Population	Blekinge/Kristianstad	Östergötland/Jönköping	Skaraborg	Värmland	Västerbotten	Uppsala	Gotland	Saami
Bleking/Kristianstad	–							
Östergötland/Jönköping	−0.001	–						
Skaraborg	0.001	−0.003	–					
Värmland	0.007	0.002	−0.001	–				
Västerbotten	−0.005	0.011*	0.003	0.004	–			
Uppsala	−0.002	−0.001	−0.005	−0.004	0.002	–		
Gotland	−0.004	−0.003	0.008	0.006	0.006	0.005	–	
Saami	0.190**	0.209**	0.223**	0.207**	0.191**	0.194**	0.199**	–

Indices were generated from the entire control region with C insertions at 16193, 309, 573, and AC region at 523, 524 ignored

*P=0.04, **P<0.001

Table 3 Φ_{ST} values from pairwise comparison between geographically close located populations

Population	Sweden	Saami
Saami	0.107*	
Norway	0.004*	0.138*
Finland	0.011*	0.093*
Germany	0.001	0.112*

*$P<0.001$

Swedish population, a larger reference mtDNA population database (including other European populations) can be used for frequency estimations [5] in forensic casework.

Some special consideration is, however, needed in the north of Sweden due to the fact that Västerbotten and the neighboring provinces of Norrbotten and Lapland all have a very sparse population, a situation that makes founder effects and genetic drift possible. Especially the settlement history of Lapland and Norrbotten makes a striking contrast to the "normal Swedish" and even that of the neighboring Västerbotten. The prehistory of Norrbotten, Västerbotten, and Lapland is more like that of northern Norway, northern Finland, and adjacent parts of Russia, than like the rest of Sweden [44]. Furthermore, agriculture on a permanent basis emerged in Norrbotten as late as the twelfth century (at the earliest) introduced by settlers deriving from different parts of Finland and Sweden—all according to historical, linguistic, paleoecological, and archaeological data [45]. The Norrbotten province is not included in our study, but there is good reason for considering it as atypical to "Swedish standards". Like Västerbotten and Lapland, it was exposed to genetic drift and founder effects due to its sparse population (0.1 inhabitant/km^2 1571; 0.2 in 1751 [43]). Additionally, the Norrbotten gene pool can be influenced by a local Saami population living in the coastland. These people were assimilated or "just disappeared" in the Middle Ages though traced archaeologically [46].

We also included a minor sample set of individuals belonging to the Swedish Saami population of Jokkmokk, the same as in our earlier study [20]. Of the 39 sequenced control regions, only 14 unique haplotypes were found. This yielded a very low genetic diversity value and the most common haplotype among the Saami was "16298C 72C 152C 263G 315.1C" which was seen 13 times (33%) and, interestingly, was never observed in the Swedish sample set. Excluding two samples with unknown haplogroup status, only two haplogroups were present, HV0 (pre-V) (25 samples, 64%) and U5b1b (12 samples, 31%). These frequencies are in agreement with previous analyses of the Saami population shown by Tambets et al. [6].

The Saami sample showed a bimodal mismatch distribution (Fig. 3b). Together with a positive value of Tajima's D (0.75), this might indicate a constant population size originated from two or more population events or an impact from a more recent immigration. Even though we found only two haplogroups, Tambets et al. [6] found some additional low frequency haplogroups, Hg H, Z1 and D5, in their study of the Swedish Saami population. The findings of Tambets et al. can be explained by (a) contacts with settled people at the neighboring coast of Norrbotten, (b) contacts with another, "Norse" gene pool at the Tysfjord area at the Atlantic coast in the west, visited on an annual basis for reindeer grazing over the last centuries [47], and (c) a "local" gene pool, principally deriving from a Mesolithic population in Lapland.

The contacts with the local population on the Swedish side in coastal Norrbotten meant contacts with derivatives from Finland and Sweden, descendants of the colonization movements. For example, the Jokkmokk Saamis in historic time sporadically dwelled in coastal Norrbotten with their reindeer during winter [47]. Saami contacts with people of that ancestry was also possible by intermingling with settlers, in some cases Finnish speakers, inhabiting Lapland from the late seventeenth century onwards and coming from areas closer to the coast [48]. The Saami contacts with Norse people in the Tysfjorden area are a still older story, which go back to the Viking Age or earlier [10]. Here, the Jokkmokk Saami annual grazing activities in summer possibly began in the late Middle Ages [49].

Conclusions

The homogeneity of the Swedish mtDNA lineages makes the sample set analyzed a good representative reference population for use in forensic applications. No significant substructure was detected analyzing seven geographically different Swedish regions. However, the genetically different Swedish Saami population is well known to be an outlier, which was also shown here and is therefore not included in a Swedish mtDNA reference database. Samples from the northernmost part of Sweden not included in our study should however be treated with some care due to possible, but hitherto unexplored, substructures. All sequence data will be submitted to the EMPOP database (www.empop.org) upon acceptance of this publication.

Acknowledgements The authors would like to thank Anders Götherström for valuable discussions and for giving fruitful comments on the manuscript. The authors also would like to thank Jodi Irwin, Jessica Saunier, Melissa Scheible, Toni Diegoli, and Kimberly Sturk (AFDIL) for data generation and review. We also thank Dr. Walther Parson (ILM; Innsbruck, Austria) and EMPOP for the quality control review of the data and one anonymous reviewer for improving the manuscript.

References

1. Budowle B, Allard MW, Wilson MR, Chakraborty R (2003) Forensics and mitochondrial DNA: applications, debates, and foundations. Annu Rev Genomics Hum Genet 4:119–141
2. Gill P, Ivanov PL, Kimpton R et al (1994) Identification of the remains of the Romanov family by DNA analysis. Nat Genet 6:130–135
3. Buckleton J, Walsh SJ, Harbison S (2005) Nonautosomal forensic markers. In: Buckleton J, Triggs CM, Walsh SJ (eds) Forensic DNA evidence interpretation. CRC, Boca Raton
4. Parson W, Bandelt HJ (2007) Extended guidelines for mtDNA typing of population data in forensic science. Forensic Sci Int Genet 1:13–19
5. Parson W, Dür A (2007) EMPOP—a forensic mtDNA database. Forensic Sci Int Genet 1:88–92
6. Tambets K, Rootsi S, Kivisild T et al (2004) The western and eastern roots of the Saami—the story of genetic "outliers" told by mitochondrial DNA and Y chromosomes. Am J Hum Genet 74:661–682
7. Svonni M (2005) The Sami language—a historical mystery. In: Sami Parliament & Ministry of Agriculture, Food and Consumer Affairs (ed), The Sami—an indigenous people in Sweden, Kiruna, pp 50–51
8. Lundmark L (2008) Stulet land. Svensk makt på samisk mark. Ordfront, Stockholm
9. Hansen LI (1996) Interaction between Northern European subarctic societies during the Middle Ages: indigenous peoples, peasants and state builders. In: Rindal M (ed) Two studies on the Middle Ages, KULTs skriftserie 66. Research Council of Oslo, Oslo, pp 31–95
10. Hansen LI, Olsen B (2004) Samenes historie fram til 1750. Cappelen Akademisk Forlag, Oslo
11. Blankholm HP (2008) Southern Scandinavia. In: Bailey G, Spikins P (eds) Mesolithic Europe. Cambridge University Press, New York, pp 107–131
12. Bjerk HB (2008) Norwegian Mesolithic trends: a review. In: Bailey G, Spikins P (eds) Mesolithic Europe. Cambridge University Press, New York, pp 60–106
13. Hörnberg G, Bohlin E, Hellberg E et al (2005) Effects of Mesolithic hunter-gatherers on local vegetation in a non-uniform glacio-isostatic land uplift area, northern Sweden. Veg Hist Archaeobot 15:13–26
14. Lindén M (2006) Glaciodynamics, deglacial landforms and isostatic uplift during the last deglaciation of Norrbotten, LUNDAQUA Theses 54. Lund University, Sweden
15. Bergman I, Zachrisson O (2007) Early Mesolithic hunter-gatherers and landscape acquisition by the Arctic Circle. J North Stud 1–2:123–142
16. Östlund O (2005) Stenåldersboplatsen i Kangos—nästan 10 000 år i glömska. Den tidigaste kolonisationen i Norrbotten. Norrbotten, pp. 141–149
17. Zvelebil M (2008) Innovating hunter-gatherers: the Mesolithic in the Baltic. In: Bailey G, Spikins P (eds) Mesolithic Europe. Cambridge University Press, New York, pp 18–59
18. Svanberg I, Tydén M (2005) Tusen år av invandring: en svensk kulturhistoria. Dialogos, Stockholm
19. Myrdal J (2003) Digerdöden, pestvågor och ödeläggelse. Ett perspektiv på senmedeltidens Sverige. Sällskapet Runica et Mediævalia. Scripta minora 9. Stockholm
20. Karlsson AO, Wallerström T, Götherström A, Holmlund G (2006) Y-chromosome diversity in Sweden—a long-time perspective. Eur J Hum Genet 14:963–970
21. Lindblom B, Holmlund G (1988) Rapid DNA purification for restriction fragment length polymorphism analysis. Gene Anal Tech 5:97–101
22. Brandstätter A, Peterson CT, Irwin JA et al (2004) Mitochondrial DNA control region sequences from Nairobi (Kenya): inferring phylogenetic parameters for the establishment of a forensic database. Int J Leg Med 118(5):294–306
23. Irwin J, Saunier J, Strouss K et al (2007) Development and expansion of high quality control region databases to improve forensic mtDNA evidence interpretation. Forensic Sci Int Genet 1 (2):154–157
24. Anderson S, Bankier AT, Barrell BG et al (1981) Sequence and organization of the human mitochondrial genome. Nature 290:457–465
25. Andrews RM, Kubacka I, Chinnery PF et al (1999) Reanalysis and revision of the Cambridge reference sequence for human mitochondrial DNA. Nat Genet 23:147
26. Brandstätter A, Niederstätter H, Pavlic M et al (2006) Generating population data for the EMPOP database—an overview of the mtDNA sequencing and data evaluation processes considering 273 Austrian control region sequences as example. Forensic Sci Int 166(2, 3):164–175
27. Abu-Amero KK, Gonzalez AM, Larruga JM et al (2007) Eurasian and African mitochondrial DNA influences in the Saudi Arabian population. BMC Evol Biol 7:32
28. Alshamali F, Brandstätter A, Zimmermann B, Parson W (2008) Mitochondrial DNA control region variation in Dubai, United Arab Emirates. Forensic Sci Int Genet 2:e9–e10
29. Chen F, Wang SY, Zhang RZ et al (2008) Analysis of mitochondrial DNA polymorphisms in Guangdong Han Chinese. Forensic Sci Int Genet 2:150–153
30. Helgason A, Hickey E, Goodacre S et al (2001) MtDNA and the islands of the North Atlantic: estimating the proportions of Norse and Gaelic ancestry. Am J Hum Genet 68:723–737
31. Hedman M, Brandstätter A, Pimenoff V et al (2007) Finnish mitochondrial DNA HVS-I and HVS-II population data. Forensic Sci Int 172:171–178
32. Irwin J, Saunier J, Strouss K et al (2008) Mitochondrial control region sequences from northern Greece and Greek Cypriots. Int J Legal Med 122:87–89
33. Lehocký I, Baldovič M, Kádaši L, Metspalu E (2008) A database of mitochondrial DNA hypervariable regions I and II sequences of individuals from Slovakia. Forensic Sci Int Genet 2(4):53–59
34. Saunier JL, Irwin J, Just RS et al (2008) Mitochondrial control region sequences from a U.S. "Hispanic" population sample. Forensic Sci Int Genet 2:e19–e23
35. Turchi C, Buscemi L, Previdere C et al (2008) Italian mitochondrial DNA database: results of a collaborative exercise and proficiency testing. Int J Leg Med 122:199–204
36. Excoffier LLG, Schneider S (2005) Arlequin ver. 3.0: an integrated software package for population genetics data analysis. Evol Bioinform Online 1:47–50
37. Tetzlaff S, Brandstätter A, Wegener R et al (2007) Mitochondrial DNA population data of HVS-I and HVS-II sequences from a northeast German sample. Forensic Sci Int 172:218–224
38. Passarino G, Cavalleri GL, Lin AA et al (2002) Different genetic components in the Norwegian population revealed by the analysis of mtDNA and Y chromosome polymorphisms. Eur J Hum Genet 10:521–529
39. Pakendorf B, Stoneking M (2005) Mitochondrial DNA and human evolution. Annu Rev Genomics Hum Genet 6:165–183
40. Selinge KG (1996) Östergötland, Förhistoria I: Nationalencyklopedin, Höganäs, pp 480–481
41. Hörfors O (2000) Östergötland, Förhistoria I: Nationalencyklopedin Supplement III Malmö, pp 596
42. Selinge KG (1995) Småland, Förhistoria, I: Nationalencyklopedin, Höganäs, pp 7–8

43. Andersson Palm L (2000) Folkmängden i Sveriges socknar och kommuner 1571–1997. Med särskild hänsyn till perioden 1571–1751. Historiska institutionen, University of Guthenburg
44. Baudou E (1995) Norrlands forntid—ett historiskt perspektiv. Cewe-förlaget, Bjästa
45. Wallerström T (1995) Norrbotten, Sverige och medeltiden. Problem kring makt och bosättning i en europeisk periferi I. Lund Studies in Medieval Archaeology, vol 15. Almqvist & Wiksell, Stockholm, p 1
46. Broadbent N (2004) The search for a past: the prehistory of the indigenous Saami in northern coastal Sweden. In: Herva VP (ed) People, material culture and environment in the north. Proceedings of the 22nd Nordic Archaeological Conference University of Oulu, pp 13–25
47. Manker E (1953) The nomadism of the Swedish mountain lapps: the Siidas and their migratory routes in 1945. Acta Lapponica 7. Nordiska museet, Stockholm
48. Hultblad F (1968) Övergång från nomadism till agrar bosättning i Jokkmokk socken. Acta Lapponica XIV. Nordiska museet, Stockholm
49. Wallerström T (2000) The Saami between east and west in the Middle Ages. An archaeological contribution to the history of reindeer breeding. Acta Borealia 17:3–39