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Elucidating recent history by tracing genetic affinity of three 16th century miners from

Sweden.

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ABSTRACT

Objectives: Sala silver mine in central Sweden was an important manufacturer of silver from at least the 16th till the early 20th century, with production peaking in the 16th , mid 17th and 19th centuries. The job opportunities offered by the mine drew people to the area resulting in the development of a small township with associated cemetery in the vicinity of the mining center. The cemetery served people affiliated to the mine for around 150 years. Written sources reveal that common convicts and war prisoners from the numerous wars fought by Sweden during the time were exploited in the mine, and some of them were likely buried on the cemetery. The cemetery has been excavated on several occasions and the recovered human remains were divided into two different groups based on burial custom, demography and biochemical results. One group was believed to contain war prisoners and the aim of this study was to produce and interpret genomic data from these individuals to test the hypothesis regarding their origins. **Materials**: Dental material from seven different individuals was sampled. **Results:** Three of the analyzed teeth contained sufficient amounts of indigenous human DNA allowing for generation of genomic sequence data with genome coverages of 0.04, 0.19 and 0.83. **Discussion**: The results show that despite this apparent heterogeneity the three individuals fell within genetic variation of modern and contemporary Swedes yielding little support to their hypothetical foreign origin. However, due to the lack of contemporary or modern Danish genomic data we cannot exclude the Danish origin of these individuals.

INTRODUCTION

Silver mining constituted an important contribution to the Swedish economy during several centuries. The most important mine was located in Sala in east central Sweden (Figure 1). The earliest records mentioning an operational mine date to the beginning of the 16th century and

51   before abandonment of the mine in 1908, approximately 450 tons of silver were extracted from it

52   (Jansson and Geovetenskaper, 2007; Norberg, 1978). A village, Salberget, including a small

53   church was located in close vicinity of the mine. The cemetery of the church was used for only

54   150 years between the end of the 15th century to mid-17th century (Bäckström and Price, 2016;

55   Price et al., 2017). The site was excavated in 2004, 2008, 2009 and 2011, revealing in total 102

56   skeletons in 93 graves (Bäckström et al., 2009; Bäckström and Ingvarsson-Sundström, 2014,

57   2010; Onsten-Molander et al., 2005). The cemetery is believed to have been used for all social

58   groups in the village and mine, including local families, miners and other workers, foreign

59   specialists, but also forced labor in the form of prisoners of war and individuals convicted of

60   various crimes. Landless manual workers came from Sweden and present day Finland; the

61   specialists arrived from Germany, the Netherlands and Austria, and the prisoners, according to

62   the historical records, originated in Denmark, Russia and Poland (Boëthius, 1951; Eriksson et al.,

63   2003; Frankius, 2008; Norberg, 1978). During the excavations, two different types of burials

64   were discovered which are believed to mirror the social hierarchy. The first type consisted of 84

65   coffin-burials with 80 skeletons in which men, women and children were buried in shrouds. A

66   majority of the coffins contained single burials. Only three cist graves contained more than one

67   individual; one cist held two children and two cists contained an adult male and a child). The

68   second type containing only men (22 individuals, primarily younger men), were nine earthen

69   burials located primarily in the southern part of the cemetery. Most of the graves in the latter

70   category were multiple inhumations containing between two to eight individuals interred in their

71   everyday clothes (Bäckström and Ingvarsson-Sundström, 2010). The men in latter group show a

72   high frequency of perimortem fractures and one individual was buried with an iron shackle

73   around the neck (Bäckström and Ingvarsson-Sundström, 2010; Bäckström and Price, 2016). Two

74   isotope studies, using strontium (Sr), oxygen (O) and lead (Pb), have demonstrated significant

75   differences in values between the individuals associated with the two burial types (Bäckström

76   and Price, 2016; Price et al., 2017). The sampled skeletons from coffins exhibit values consistent

77   with being local, perhaps families, from the Sala area, while the isotope values from men in the

78   earthen burials are consistent with non-local origin. Due to the simple burial type, the many

79   perimortem fractures, finding of the man with the iron collar and the isotopic values, it has been

80   suggested that the men in the earthen burials could be identified as the prisoners of war forced to

81   work in the mine (Boëthius, 1951; Eriksson et al., 2003; Norberg, 1978; Price et al., 2017). Here

82   genome-wide sequence data was generated for three individuals in earthen burials in order to

83   explore their genetic relationship to modern-day European populations. Seven skeletons were

84   selected for the analyses. The sampling strategy focused primarily on investigating mobility in

85   the mining community by investigating correlation between Sr-analysis results and genetic

86   affinities of individuals. Lower Sr values around 0.712 earthen graves were linked to the

87   southern Baltic region and higher Sr values of around 0.721 (coffin graves) were interpreted as

88   more 'local'. Therefore, the individuals picked out for DNA analyses consisted of four skeletons

89   from graves without coffins with lower Sr values (Sk6854, Sk6866, Sk6990, Sk6994),and three

90   skeletons from coffin graves with higher Sr-values (Sk5498, Sk7031 and Sk7980). Only three

91   skeletons with lower Sr-values contained preserved DNA, rendering this comparison impossible.

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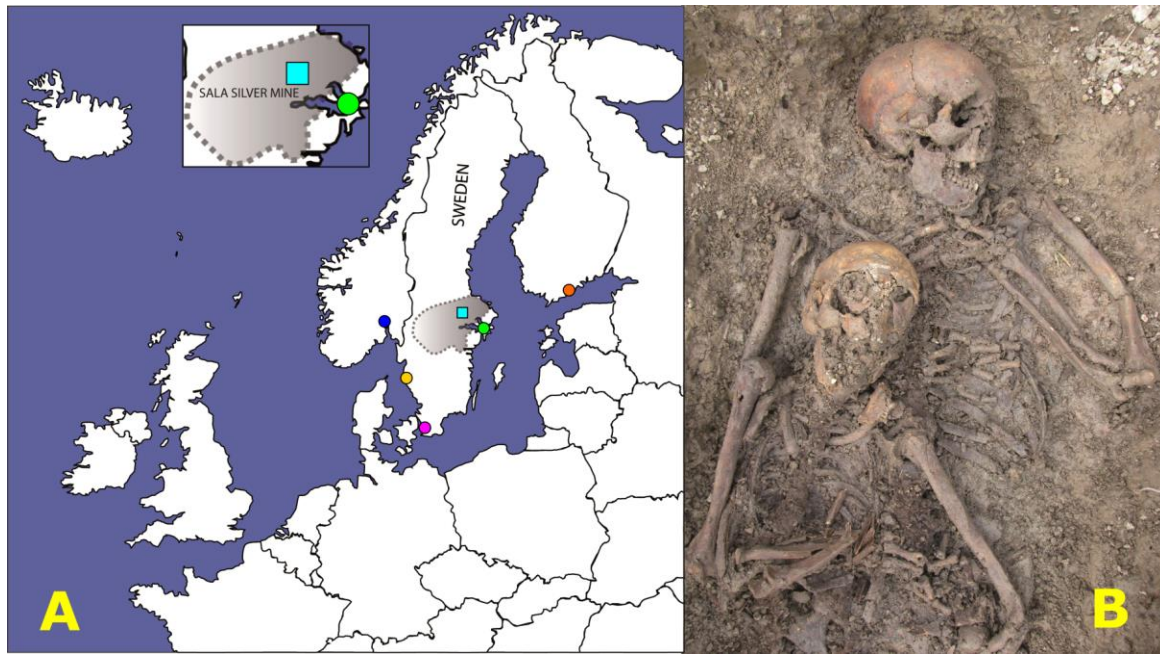
Figure 1. A) Map of Northern Europe with the location of Sala silver mine marked with blue square and major cities marked with dots: navy blue - Oslo, yellow – Gothenburg, green – Stockholm, orange - Helsinki. B) Skeletons no 6990 and 6994 in double grave 6975. Photograph by: Lena Persson.

MATERIALS AND METHODS

The anthropological analysis of the skeletons from Salberget involved international standard techniques (Bäckström and Price, 2016). Samples for the genomic analysis were taken from teeth in the mandible of seven men from the earthen burials. Three individuals generated enough DNA for a continuing productive analysis (Table 1). One of the men (Sk6866) was buried together with seven other individuals (Grave 6826) (Bäckström and Ingvarsson-Sundström, 2010). The other two men were found together in a double grave (Grave 6975), where one of the individuals (Sk6990) was buried on top (in the arms) of the other (Sk6994) (Figure 2). All three were buried according to the Christian tradition; on their backs with their heads to the west.

Extraction of DNA and preparation of libraries

111   All sample preparations were performed in dedicated clean-room facilities in the ancient DNA

112   laboratory at the Archaeological Research Laboratory, Stockholm University. Teeth were wiped

113   (decontaminated) with 1% sodium hypochlorite solution, ddH_2O and 70% EtOH, and UV-

114   irradiated (254nm wave length) at approximately 1 J/cm^2 per side. Dentine powder was extracted

115   in a dead-air cabinet using a Dremel drill at the lowest possible rpm (5000rpm).

116

117   DNA was extracted following previously published protocols (Svensson et al., 2007; Yang et al.,

118   1998). In brief, dentine powder was mixed with lysis buffer containing 0.45M EDTA (pH 8), 1M

119   Urea, and 100μg proteinase K, and incubated with constant agitation for at least 18 hours at 37°C

120   until fully dissolved. DNA was concentrated on Amicon Ultra-4 columns (Merck Millipore) and

121   purified on MinElute silica columns (Qiagen) following manufacturer recommendations but with

122   the addition of a second wash step. Purified DNA was eluted in 100μL EB buffer (Qiagen). We

123   included two negative (blank) DNA extractions for every eighth bone sample.

124

125   Double stranded DNA sequencing libraries were prepared from 20μL DNA following Meyer &

126   Kircher (2010). Libraries were PCR amplified, pooled at equimolar concentrations, and purified

127   as described in Günther et al. (2015). Library pools were shotgun-sequenced on the Illumina

128   HiSeq-2500 platform at the SciLife DNA sequencing facility, Stockholm.

129

130   *Sequence analyses*

131   Sequence data was analyzed following previously published procedures (Günther et al., 2015;

132   Omrak et al., 2016). In summary, reads were de-multiplexed based on their respective index

133   sequences (Meyer and Kircher, 2010). Pair-end reads were merged, trimmed and mapped to the

134   human reference genomes, build 36 and 37, with BWA v. 0.7.13 (Li and Durbin, 2010) while the

135   PCR duplicates were removed with FilterUniqueSAMCons.py (Kircher, 2012). The presence of

136   3' and 5' cytosine deamination patterns characteristic of ancient DNA (Briggs et al., 2007;

137   Hansen et al., 2001; Hofreiter et al., 2001; Orlando et al., 2011; Sawyer et al., 2012) was

138   estimated using PMDtools (Skoglund et al., 2014). Additionally, levels of contamination were

139   estimated based on the analyses of polymorphic site distribution in mitochondrial sequences

140   (Green et al., 2008). Individuals' molecular sex was estimated using the method by Skoglund and

141   colleagues (2013). The consensus sequences for the mitochondrial genomes were called using

142   mpileup and vcfutils.pl (vcf2fq) from the *samtools* package (Li et al., 2009). Only reads with a

143   minimum mapping score of 30 and a minimum base quality of 30 were used to call confident

144   bases for the final consensus sequences. We identified the haplogroups using HAPLOFIND

145   (Vianello et al., 2013) and PhyloTree Build 17 (18th February 2016)(van Oven and Kayser,

146   2009). The Y chromosome sequences were filtered out using mpileup from the *samtools* package

147   (Li et al., 2009). The pileup file was then merged with both the PyloTree Y haplogroup

148   definitions (van Oven et al., 2014) as well as the ISOGG database v. 04/2016

149   (http://isogg.org/tree)(International Society of Genetic Genealogy, 2017). For population based

150   analyses the genetic data from the investigated individuals was merged with the reference

151   population panel of 21 population samples from the Human Origins (HO) dataset (Lazaridis et

152   al., 2014; Patterson et al., 2012), and 13 populations from Estonian Biocentre Human Genome

153   Diversity Panel (EGDP) (Pagani et al 2016). The Human Origins dataset was additionally

154   merged with ancient Swedish reference consisting seven 17th century unpublished genomes from

155   southern Sweden (in prep.). The reference ancient genomes were all males sequenced between

156   0.38x – 1.1 x genome coverage. Only positions with minimum base and mapping qualities of 30

157   were used in the analyses. In order to visualize the relationship between the ancient individuals

158   and modern reference populations we performed principal component analyses (PCA) using

159   EIGENSOFT v.6.0.1 (Patterson et al., 2006). Furthermore, to obtain information on genetic

160   affinities between the three individuals and the modern populations, we performed f_3-outgroup

161 statistics using qp3Pop v. 204 (Patterson et al., 2012; Raghavan et al., 2014) and *D*-statistics

162 which were calculated using qpDstat of ADMIXTOOLS (Durand et al., 2011; Patterson et al.,

163 2012). All analyses were performed with exclusion of transition sites and using pseudo-haploid

164 genomes. The computations were performed on resources provided by SNIC through Uppsala

165 Multidisciplinary Center for Advanced Computational Science (UPPMAX)(Lampa et al., 2013)

166 under the following projects: b2013240, b2015307 and b2016056.

167

168 **RESULTS**

169 We generated genomic sequence data from three individuals from Sala silvergruva (Sk6866,

170 Sk6990, Sk6994) to 0.04, 0.19 and 0.82-fold genome coverage. Basic sequence statistics are

171 listed in Table 1. All individuals were males and all show cytosine deamination patterns typical

172 of ancient DNA, ranging from 8-12% increase in C>T transitions at 5' ends of sequenced DNA

173 fragments, while contamination levels were estimated to range between 1.29% – 2.08%.

174

175 The numbers of SNPs supporting each called mitochondrial haplotype are 51 for individual

176 Sk6866, 53 for individual Sk6994, 56 for individual Sk6990. The calls were recorded as

177 deviations from the Reconstructed Sapiens Reference Sequence (RSRS) and the obtained

178 haplotypes are listed in Table 1 (Behar et al., 2012). The mitochondrial lineage U5b2a1a1 found

179 in individual Sk6866 is characteristic of central and eastern European populations (Malyarchuk

180 et al., 2010). Haplogroup I1a1b, found in individual Sk6994, and T2b21b, found in individual

181 Sk6990, are common in north Europe (Behar et al., 2012). Only one Y chromosome haplogroup

182 assignment was possible using haplogroup definitions from PhyloTree: individual Sk6990 was

183 assigned to subclade R1b1b (R-P297) which is a common haplogroup in Western Europe (Myres

184 et al., 2011). The other individuals were assigned their respective Y haplogroups using ISOGG

185 haplogroup definitions. Individual Sk6866 belonged to Y chromosome lineage R1b1a, while SK

186   6994 was a carrier of I2a2a. The subclade R1b1a is the most frequent haplogroup in Eurasia

187   (Balaresque et al., 2010) while I2a2a (formerly I1c) is widespread throughout Europe with

188   highest frequencies in Germany and the Netherlands (Rootsi et al., 2004).

189

	Sk6866	Sk6990	Sk6994
Age	15-19 years	Middle Adult	Young Adult
Osteological sex	Male	Male	Male
Molecular sex	Male	Male	Male
Sampled material	second premolar	second incisor	second incisor
Genome coverage	0.04	0.19	0.83
mtDNA genome	260.8	366.6	379.8
SNPs overlapping HO db	16,550	83,210	242,251
SNPs overlapping EGDP db	1,476,314	6,907,830	20,272,957
mtDNA haplogroup	U5b2a	T2b21b	I1a1b
Y chr haplogroup (ISOOG)	R1b1a	R1b1	I2a2a
Contamination estimate	1.6% (0.85%-2.36%)	2.08% (1.54%-2-62%)	1.29% (0.81%-1.78%)

190   Table 1. Summary statistics of the genomic and anthropological data from the three analyzed

191   individuals.

192

193   The f_3-outgroup statistics were performed with two modern population reference panels: Human

194   Origins (Lazaridis et al., 2014; Patterson et al., 2012) merged with seven 17th century Swedish

195   genomes and Estonian Biocentre Human Genome Diversity Panel (EGDP) (Pagani et al., 2016)

196   using Yoruban population as an outgroup and 51 populations from the Human Origin reference

197   panel and Congo Pygmy population as an outgroup with 125 populations from EGDP. The

198   number of SNPs used in the f_3-outgroup statistics was 68250 and in individual Sk6994, 23229

199   and 6907830 in individual Sk6990 and 4768 and 1476314 in individual Sk6866 for HO+ancient

200   and EGDP reference panels respectively. The standard errors were obtained by performing a

201   block jackknife with the number of blocks ranging from 557 to 699. According to the f_3-outgroup

202   test with HO+ancient, individual Sk6866 shared most genetic drift with the Baltic and central

203   European populations (i.e. Belarusian, Lithuanian, Estonian, Norwegian and ancient Swedish).

9

204   Individual Sk6990 shared most genetic drift with the Baltic and western European populations

205   (including Lithuanian, English, Basque, Czech, French and ancient Swedish). And individual

206   Sk6994 shared most genetic drift with the western and northern European populations (including

207   Lithuanians, English, Orcadians and Norwegians) (Figure 2). When compared to the f_3-outgroup

208   test with EGDP Sk6866 shared most genetic drift with Swedes, Western Russians and Poles;

209   Sk6990 shared most genetic drift with Swedes and Belarussians, then Finnish, while Sk6994

210   shared the most genetic drift with present-day Lithuanians, Swedish, and Latvians (Figure 3).

211

212   The D-statistics were performed to test whether investigated individuals shared excess drift with

213   present day Scandinavians, here represented by Norwegians/Swedish/ancient Swedish, or

214   individuals from other European geographical regions with either Yoruban or Congo Pygmies

215   population as an outgroup depending on the reference panel used. A selection of D-statistic

216   results is presented in Table 2. As expected most D-statistic results had low values, oscillating

217   around 0, but a number of significant Z score values (Z>2) suggest that individual Sk6866 shared

218   more genetic drift with Norwegians and Swedish than southern and western European

219   populations, such as the French, the Italians and the Germans. Individual Sk6990 had broad

220   European affiliations sharing most affinities with the Swedish, Lithuanians and Norwegians.

221   Finally, individual Sk6994, shared most genetic drift with the Swedish and Norwegians (Table

222   2).

223

Reference population (DB)	Individual 6866		Individual 6990		Individual 6994	
	D-statistic	Z score	D-statistic	Z score	D-statistic	Z score
Belarusian (HO)	0.0077	0.666	-0.003	-0.565	-0.0164	-2.489*
Czech (HO)	-0.0083	-0.741	0.0058	1. 031	-0.0076	-2.264*
Estonian (HO)	0.0012	0.108	-0.0035	-0.662	-0.0054	-1.511
Lihuanian (HO)	0.0046	0.398	0.0092	1.754	0.0024	0.683
FinnishFIN (HO)	-0.0055	-0.428	0.0013	0.222	-0.0097	-2.605*
French (HO)	-0.0185	-2.027*	-0.0014	-0.326	-0.0076	-2.768*
GreekComas (HO)	-0.0144	-1.371	-0.0093	-1.841	-0.018	-5.493*

ItalianTuscan (HO)	-0.0389	-3.116*	0.0018	0.303	-0.0159	-4.465*
Ancient Swedish (HO)	-0.0039	-0.218	0.0021	0.258	-0.0074	-1.476
Belarusians (EGDP)	-0.0032	-0.615	-0.0014	-0.382	-0.0041	-1.110
Poles (EGDP)	-0.0015	-0.268	-0.0044	-0.382	-0.0071	-2.019*
Germans (EGDP)	-0.0133	-2.361*	-0.008	-2.187*	-0.0071	-1.849
Estonians (EGDP)	-0.0044	-0.893	-0.014	-1.171	-0.0043	-1.241
Lithuanian (EGDP)	-0.009	-1.607	-0.0024	-0.614	0.0003	0.075
Karelians (EGDP)	-0.0081	-1.405	-0.0166	-4.051*	-0.0109	-2.863*
Finnish (EGDP)	-0.0105	-1.869	-0.0016	-0.392	-0.0054	-1.421
UkrainiansWest (EGDP)	-0.016	-2.805*	-0.009	-2.171*	-0.0094	-2.441*
Western Russian (EGDP)	0	-0.007	-0.0023	-0.517	-0.005	-1.172

224 Table 2. Selection of the *D*-statistic test results. Depending on the reference panel used (either

225 HO or EGDP) the population tree topology tested was: (Yoruba/Congo Pygmies, sample:

226 Norwegian/Swedish, reference population), where either 'Yoruba' or 'Congo Pygmies' are the

227 outgroup, 'sample' is any of the ancient individuals and 'reference population' is comparative

228 population from the Human Origins dataset merged with ancient Swedish individuals.

229 Significant values are highlighted in red and marked by *.

230

231 **DISCUSSION**

232 The samples in the present study are approximately 400 years old. Out of the original seven

233 sampled individuals, four yielded DNA, and in three of those the proportion of human DNA was

234 >1%, (which is a cut-off value we employ to decide whether further, non-enriched, shotgun

235 sequencing is feasible). The three individuals were thus sequenced further to obtain suitable

236 amount of genomic data for downstream analyses. The proportion of human DNA in a sample is

237 generally a good indicator of endogenous DNA preservation, as long as presence of major

238 contaminants can be excluded. Here, mitochondrial DNA based testing indicated that the three

239 samples were relatively free from contamination, and the damage patterns suggest that much of

240 the DNA in these samples is of ancient origin.

241

242 On PCA plots Sk6866 clusters between Ukrainians and Scandinavians (Figure 2A, 3A). At the

243 same time the f_3-outgroup statistics provides a somewhat stronger support for shared drift with

244 Swedes and populations on the eastern side of the Baltic Sea (Western Russians). The *D*-statistics

245 suggests that this individual shared most genetic with populations from the north, especially

246 Swedish. The mitochondrial haplogroup is one that is common among modern Finns, Saami,

247 Estonians, and Ukrainians (Malyarchuk et al., 2010). Thus, this individual is likely from Sweden

248 or the eastern region of the Baltic Sea (Figure 2B, 3B).

249

250 Sk6990 clusters with central and northern European populations on the PCA plot, and this is also

251 where the *D*-statistics indicate he has his affinities, since shared drift with some southern

252 European populations can be excluded and most genetic drift is shared with the Swedish. The

253 mitochondrial haplogroup is one that is widespread in Europe (Pala et al., 2017), as is the Y

254 haplogroup (Myres et al., 2011). However, the f_3-outgroup statistics points to the north and

255 shared genetic drift with the Swedish, Finnish and Baltic populations including Western Russian
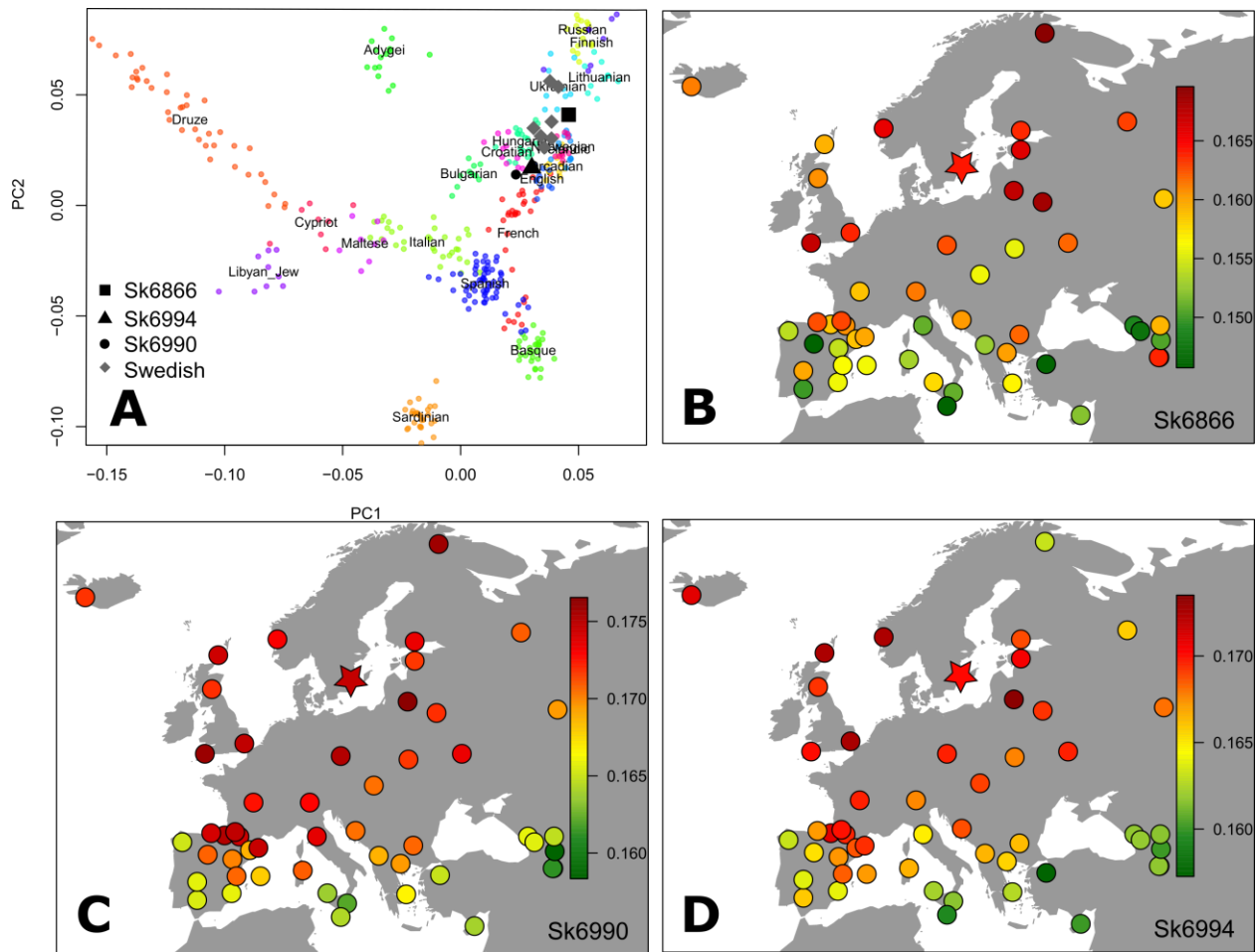
256 (Figure 2C, 3D).

257

Figure 2. A) Principle Component Analyses visualizing the relation between the three

investigated individuals from Sala silver mine and seven ancient Swedish individuals compared

to a panel of reference of 51 modern populations form Human Origins dataset. B-D) Outgroup f_3-

statistics calculated between each of the ancient individuals and modern populations from

Human Origins reference panel (Patterson et al., 2012; Lazaridis et al., 2014). The comparative
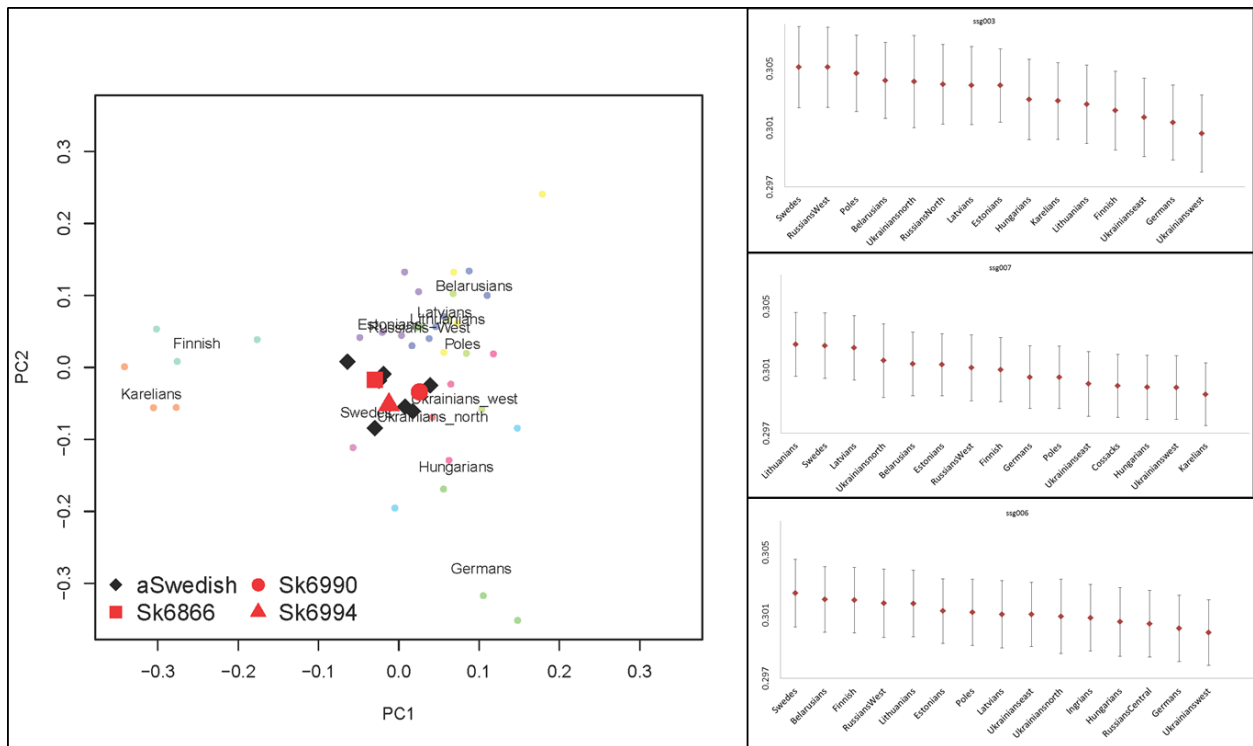
ancient population is marked by a star.

264

Figure 3. A) Principle Component Analyses visualizing the relation between the three investigated individuals from Sala silver mine and seven ancient Swedish individuals compared to a panel of reference of 13 modern populations from Estonian Biocentre Human Genome Diversity Panel (EGDP) (Pagani et al 2016). B-D) The 15 highest f_3-statistics values calculated between each of the ancient individuals and 125 modern populations Estonian Biocentre Human Genome Diversity Panel (EGDP) (Pagani et al 2016). (NB! The Figure is still undergoing editing to make it more aesthetically pleasing)

Sk6994 also clusters with central and northern European populations on the PCA plot, similarly to Sk6990. The f_3-outgroup statistics shows affinities for the same area as do individuals with a historic background in northern Europe (Rootsi et al., 2004) albeit with most shared genetic drift with the present-day Swedish, Lithuanians and Latvians. This is also supported by the D-statistics suggesting shared drift with a modern population from these areas, more specifically with Scandinavia, Norway and Sweden. The mitochondrial haplogroup is one that is common in Denmark and southern and central Scandinavia, but also in many other parts of Europe (Figure

14

281   2D, 3B).

282

283   **CONCLUSIONS**

284   The three individuals reported in this study genetically represent a group of north Europeans with

285   close affinities to contemporary and modern Swedish. Both PCA plot and *D*-statistic analyses

286   suggest that these individuals are not German, Polish nor Russian. The two latter being countries

287   at war with Sweden at that time so a potential source of war prisoners. These results narrowed

288   down the probable origin of the individuals analyzed. However, due to the absence of modern

289   and contemporary Danish genomic data we could not refute hypothesis that these individual

290   were war prisoners from Denmark. This study highlights the difficulties of fine scale

291   differentiation in historical times between European neighboring countries with a recent common

292   ancestry and an intermittent shared history. On the other hand close affinities to present-day

293   Swedish and the fact that tested individuals fall within genetic variation of contemporary

294   Swedish combined with strontium results suggest that these individuals likely were from

295   southern Sweden. It is noteworthy that the double burial from which two individuals (Sk6990

296   and Sk6994) (Figure 1b) were sampled expressed little homogeneity. Different strontium values

297   suggested that the two men grew up in different areas (Bäckström and Price, 2016). Moreover,

298   the men did not share neither mitochondrial nor Y chromosome lineage thus they were not

299   members of a nuclear family unit. The finding is in line with expectation that the burial ground

300   was populated by aliens who may have been foreign soldiers or Swedish convicts since such

301   individuals are not expected to be close relatives. That is in sharp contrast to what is known

302   about silver mining in Sala, where free workers are believed to have worked in pairs consisting

303   of related males (Tallqvist, 2007). However, taken together the genetic and isotopic results are

304   consistent with the three individuals originating in southern Sweden.

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317

318

319

320

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