

The hidden sources

Combining aDNA, stone tools, and computer modeling in the study of human colonization of Norway

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Abstract

A two-way colonization pattern has been observed for most terrestrial pioneer and boreal forest species in Norway after the last glacial period: One route from the south, and another from the east through northernmost Fennoscandia. It is generally accepted that these routes represent plant and animal populations spreading from separate glacial refugia, a pattern manifested by genetic differences. The traditional model of pioneer colonization of the Scandinavian peninsula, however, suggests only a southern route for the early human dispersal and only recently has this view started to change. Here we present the foundations for the Pioneers of North-Western Europe project (Museum of Cultural History, University of Oslo, Norway) that aims at clarifying the colonization patterns of the early post-glacial humans in north-western Europe by challenging and testing the views of unidirectional human dispersal. This is achieved by tracing the spread of distinct knowledge-intensive operational chains of stone tool technology and by comparing the results with independent ancient human DNA data.

Keywords: aDNA, mtDNA, lithic technology, bone technology, colonization, modeling

Introduction: Objectives of the project

The timing and tempo of ice sheet retreat in north-western Europe at the end of the last glacial cycle caused the main part of Fennoscandia to remain unsettled until the end of the cold Younger Dryas period ca. 9700 BC. During the

following Preboreal, rapid climate changes signified improvements for settlement and facilitated human expansion into Scandinavia (Wygal & Heidenreich 2014; Bjerck 2008; Brinch Petersen 2009; Riede 2014). To determine where these pioneer colonizers of north-western Europe, and more specifically Norway, came

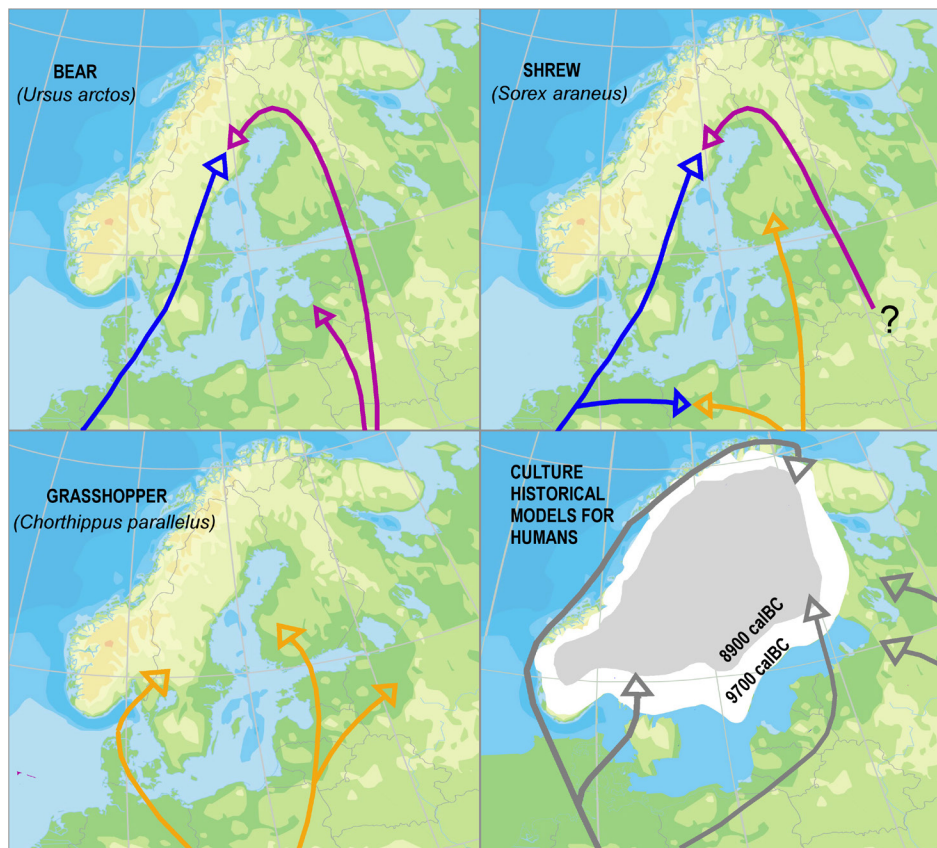


Figure 1. Examples of post-glacial colonization patterns of animal species into Scandinavia (modified from Hewitt 2001) and a schematic map indicating the extent of the Scandinavian Ice Sheet at 9700 BC and 8900 BC as well as different culture-historical models for human dispersal into Fennoscandia during ice sheet retreat. Coloured arrows in the colonization maps indicate genetic markers ascribed to different glacial refugia.

from, we will produce new data and evaluate the plausibility of different models of late- and post-glacial human dispersal in Europe.

It is well known that many animal species spread into Fennoscandia along two routes, a southern and an eastern (Figure 1), and from different Ice Age refugia in Eurasia (e.g., Hewitt 1999; 2001). Combined with new evidence of the spreading of knowledge and know-how into early post-glacial Norway from the east in form of technological concepts (Sørensen et al. 2013; Bergsvik & David 2015; Damlien 2016), this brings to the fore the question whether and to what extent a similar pattern can be detected for post-glacial human dispersal (Knutsson & Knutsson 2012; Kleppe 2014; Riede & Tallavaara 2014).

In the past few years, the methodology of ancient DNA (aDNA) research has gone forward in great leaps with the advent of next generation

sequencing, while valuable insight into demographic processes have been gained from an increasing number of ancient individuals having their full genome sequenced (Slatkin & Racimo 2016). We aim to add more individuals from the region to this list and use the combined power of full genome and mitochondrial DNA (mtDNA) analysis.

Computer simulation will be used to evaluate different models of post-glacial pioneer settlement in north-western Europe. The outcome of the simulations will be compared with archaeological and genetic data. The genetic data consists of aDNA results achieved in our project as well as other relevant genetic information. The archaeological source material consists of lithic and bone artefacts and the results of technological analyses conducted using these artefacts. In this paper we present the background for the study and an overview of the research in progress.

Background for the study of late- and post-glacial colonization of north-western Europe

Archaeology

From the location of the ecologically most favourable areas in Europe during the Late Glacial Maximum, it has for long been assumed that analogously to that of other species, also human presence was restricted to two major refugia in Europe during the Late Glacial Maximum (LGM) (e.g., Indreko 1948; Dolukhanov 1979; 1998; Zvelebil 2001). According to the most favoured view today, the Franco-Cantabrian “Mediterranean province”, connected to less-well-defined regions along the Mediterranean, provided a refugium for the human population of Atlantic Europe, while the “Periglacial province”, located on the East-European Plain, is argued to have provided favourable circumstances for Upper Palaeolithic communities in central and eastern Europe. From these refugia hunter-gatherer groups are then assumed to have colonized the north-west European lowland and the Russian Plain when these areas gradually became habitable (e.g., Jochim 1987; Soffer 1987; Straus 1991; Gamble et al. 2005; 2006; Brewster et al. 2014).

At the end of the last glacial period, humans started to colonize those areas that were gradually exposed during the retreat of the Scandinavian ice sheet. In north-western Europe this expansion is usually seen as connected to reindeer hunting. It is believed that reindeer hunters changed their foraging ranges accordingly as the ice sheet became smaller and the favourable environment for reindeer moved north. Typological reasoning and radiocarbon dating are used to link earlier south-west and central European Paleolithic cultures to the terminal Paleolithic Ahrensburg

culture, suggesting that the earliest immigrants in north-western Europe had their roots in the Upper Paleolithic population of south-western Europe (Price 2015: 32–56, and references within) and later possibly Doggerland, i.e., the now submerged North Sea continent (Ballin & Bjerck 2015; Bjerck 1995). In this case the dispersal of these groups towards north would have started ca. 14,000 BC, the first settlement of southern Scandinavia ca. 12,500 BC, and while interrupted by the Younger Dryas, the pioneer colonization would finally have reached Norway ca. 9500 BC. For the final phases of the process, many researchers today argue that the Ahrensburg culture underwent a transformation from reindeer hunting to hunting of sea mammals in West-Sweden (e.g., Schmitt 2015 and references within). This formed a new type of “coastal epi-Ahrensburgian” that expanded further north along the Norwegian coast.

Researchers in Norway have for long acknowledged that the earliest known sites in the area of present day Norway to a large extent are located along former sea shores. It was therefore considered likely that people came in boats rather than over land bridges. However, at the same time it was also noted that there was a possibility for pioneer colonizers to have arrived from the east into the northernmost part of the country (Bøe & Nummedal 1936; Gjessing 1945; Odner 1966; Hagen 1977).

The alternatives presented for the origin and ways of arrival of the first postglacial inhabitants of Norway can be summarized as: 1) directly by boat from Doggerland or southern Scandinavia, 2) moving along the coast from Doggerland, 3) from Eastern Europe via Lapland, 4) following reindeer from south-western Europe

through land bridges, and 5) reindeer hunters transforming into maritime hunters in West-Sweden and continuing northward by boat. All of these alternatives have shown to be hard to prove due to taphonomic reasons. In Norway the preservation of bone assemblages is poor at the earliest sites, and therefore practically nothing is known about the animal species targeted by the Early Mesolithic groups, nor is there knowledge on possible boats, fishing, or sea mammal hunting in Doggerland during Late Paleolithic time, due to a ca. 100 meters rise of sea level since the end of the Ice Age (Fairbanks 1989).

East of Norway, in Finland, the roots of pioneer population were earlier often traced to central Europe, or both east and southwest of the country, on the basis of culture-historical reasoning, typology, and an assumed connection to central European Late Paleolithic cultures, such as the Swiderian and Federmesser (e.g., Luho 1956; Siiräinen 1984; Nuñez 1987; Matiskainen 1996; Schulz 1998). However, many culture-historical assumptions have been later shown not to hold. For example, the view that the Early Mesolithic quartz industry in Finland had types from the central European Federmesser, as well as other Paleolithic technocomplexes, was shown to result from a misclassification of quartz fragments (Siiräinen 1981) and the idea that so-called post-Swiderian points descended from Swiderian points has also been rejected, while the post-Swiderian is nowadays considered unrelated to the Swiderian (see, e.g., Zhilin 2005). Since the mid-1980's the "post-Swiderian" finds in Finland are associated with Early Mesolithic cultures in Estonia and Russia, namely Kunda and Butovo (see, e.g., Zhilin 2003; Hertell & Manninen 2006; Rankama & Kankaanpää 2011; Hertell & Tallavaara 2011 and references therein).

In recent years the study of technological trajectories and the transmission of technology have begun to replace typological studies. Stone tool and related bone tool technologies at the Paleolithic/Mesolithic transition seem to divide northern Europe, broadly speaking, into two Early Mesolithic traditions: an eastern tradition characterized by so-called post-Swiderian eastern technologies found, for example, in north-western Russia and Fennoscandia, and a western tradition, in Norway characterized by the Ahrensburgian and epi-Ahrensburgian (Hensbacka/Fosna/Komsa) technology (Figure 2).

aDNA

Tracing kinship back to past generations seems an ideal way to detect the origin of people. If, for example, the origin of the Mesolithic groups in Fennoscandia could be traced, it would be possible to detect correlations between genetic and cultural evolution. However, before the end of the 20th century, methods for reconstructing human ancestry did not exist. Craniology and then mainly measurement of skull proportions (Coon 1939, and references therein), and later also blood-groups (Mourant 1983) were investigated, but the results never become widely accepted. When research on mtDNA was launched in the mid-1980's, a more reliable method became available (Cann et al. 1984). In Europe, mtDNA studies have focused on Ice Age refugia as the main explaining factor for the distribution of mtDNA types, or haplogroups, among present-day Europeans. A classic example can be found in Bryan Sykes' book *Seven daughters of Eve* (2001) in which the origins of most mitochondrial groups among present day Europeans are pinpointed to different refugia in southern Europe. However, a series of alternative scenarios have been presented. For example, in 2012 Maria Pala and co-workers wrote that:

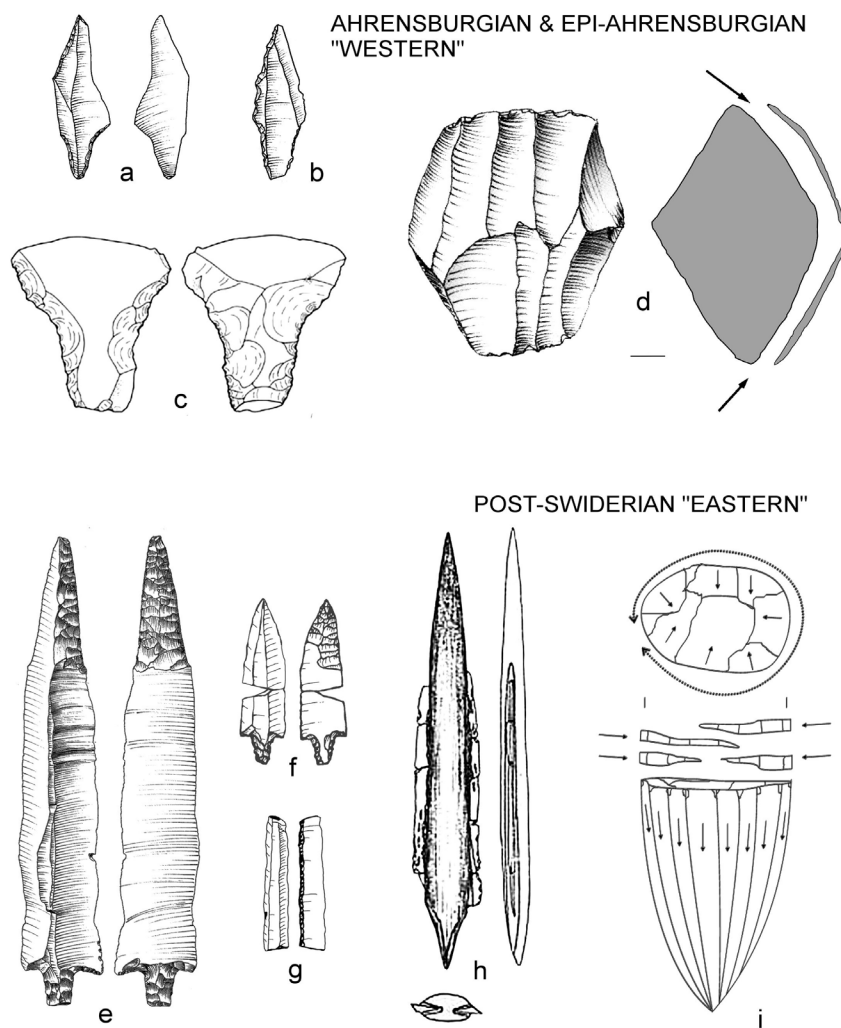


Figure 2. Examples of typical “western” Ahrensburgian and epi-Ahrensburgian tools and blade core reduction practices and “eastern” post-Swiderian counterparts: a) Ahrensburgian point (after Taute 1968 in Ballin & Saville 2003: Fig. 5); b) single-edged tanged point (after Ballin & Bjerck 2015: Fig. 6); c) early Hensbacka flake axe (after Schmitt & Svedhage 2015: Fig. 3); d) opposed platform soft hammer blade core (after Andersson & Knarrström 1999 in Fuglestad 2012: Fig. 4); e) post-Swiderian Pulli point (after Manninen & Hertell 2011); f) post-Swiderian arrowhead (after Takala 2004); g) flint insert for slotted bone tool (after Jussila et al. 2012); h) slotted point with flint inserts (after Skakun et al. 2011); “eastern” conical blade core with faceted platform (after Sørensen et al. 2013: Fig. 1). Not to scale. Redrawn from original drawings.

“Human populations, along with those of many other species, are thought to have contracted into a number of refuge areas at the height of the last Ice Age. European populations are believed to be, to a large extent, the descendants of the inhabitants of these refugia, and some extant mtDNA lineages can be traced to refugia in Franco-Cantabria (haplogroups H1, H3, V, and U5b1), the Italian Peninsula (U5b3), and the East European Plain (U4 and U5a).”
(Pala et al. 2012:1).

These studies draw conclusions about past events in population history from the genes of present-day Europeans. The genetic data that are utilized in the studies include the distribution of mtDNA haplogroups, the amount of genetic

variation within each of these groups, and the difference within their area of distribution. Dating is carried out by the “molecular clock”, assuming a constant rate of mutations. These studies were also tried for uncovering the origin of the pioneer colonizers of Fennoscandia (Riede et al. 2013). The problem is, however, that there has not been an independent way to verify the achieved results. Today, studies of ancient DNA (aDNA) can yield the needed independent test and are therefore a major step forward.

The first attempts to extract DNA from old remains and use them for genetic study were carried out in the 1980’s. The first breakthrough in aDNA studies was the application of PCR technology (polymerase chain reaction) on ancient remains

(Pääbo & Wilson 1988). The interest in ancient DNA increased rapidly after the first study of DNA in old bones (Hagelberg et al. 1989). The “amplification” of old DNA with PCR seemed like the perfect method for studying all kinds of archaeological problems related to genetics (Ross 1992). A multitude of aDNA projects were launched. Among these were studies on the introduction of agriculture in Europe, which addressed the question of population continuity over the introduction of agriculture, and therefore included DNA from Mesolithic individuals.

Ancient DNA seemed ideal for solving the old dispute about the role of immigrant farmers in the spread of agriculture, but results turned out to be much harder to obtain than initially hoped. This was because of contamination by recent human DNA which turned out to be a major problem. A breakthrough came in 2009 when Barbara Bramanti and co-workers published a study of twenty individuals representing the pre-Neolithic European population (Bramanti et al. 2009). The study showed strong dominance of the U5 and U4 groups of mtDNA in the Mesolithic samples while these haplogroups were absent in the early farmer population investigated in the same study. The agriculturalists represented groups H, HV, K, T, W, and N1a, which did not appear among the studied hunter-gatherers.

The two populations, Mesolithic and Early Neolithic, showed very little overlap in their mtDNA group composition (Figure 3), which strongly indicates that the Early Neolithic population in Central Europe did not descend from the local Mesolithic population. Although methods for verifying the authenticity of the aDNA results were not available at the time, it is highly unlikely that contamination should lead to two

populations showing such distinct grouping as Bramanti and co-workers found. That all Mesolithic samples were contaminated by present day individuals from the same haplogroups, while the Early Neolithic samples were not, or vice versa, is not probable. The mitochondrial group N1a also carries some importance in this respect, as it is rare among Europeans today. Therefore, it is not very likely that its high proportion among the studied Neolithic individuals in the Bramanti et al. (2009) study was the result of contamination.

At the moment, there are more than 140 Mesolithic individuals from Europe with their mtDNA type determined and the number is rapidly raising. Some of them are from old investigations and the authenticity of each and every result is not 100% secure. Despite this, there is a clear dominance of haplogroups U5, U4 and U2, which together constitute over 80% of the individuals (Figure 4). Because of their proportion and distribution among individuals living today, already before the aDNA studies, these three mitochondrial haplogroups were considered to have their origin in Europe (Soares et al. 2010). Considering the aDNA results, the strong presence of these haplogroups among Mesolithic Europeans can now be said to be confirmed.

A second breakthrough in aDNA research took place around 2010 when new sequencing methods came into use. These methods were first developed by a group led by Svante Pääbo working with the sequencing of the Neanderthal genome (Green et al. 2010). However, the group was surpassed by a new team led by Eske Willerslev in Copenhagen, starting later but using newer technology which helped to finish earlier and to be the first team to present a “total” ancient genome, in this case from a 4000 years old Greenlander (Rasmussen et al. 2010).

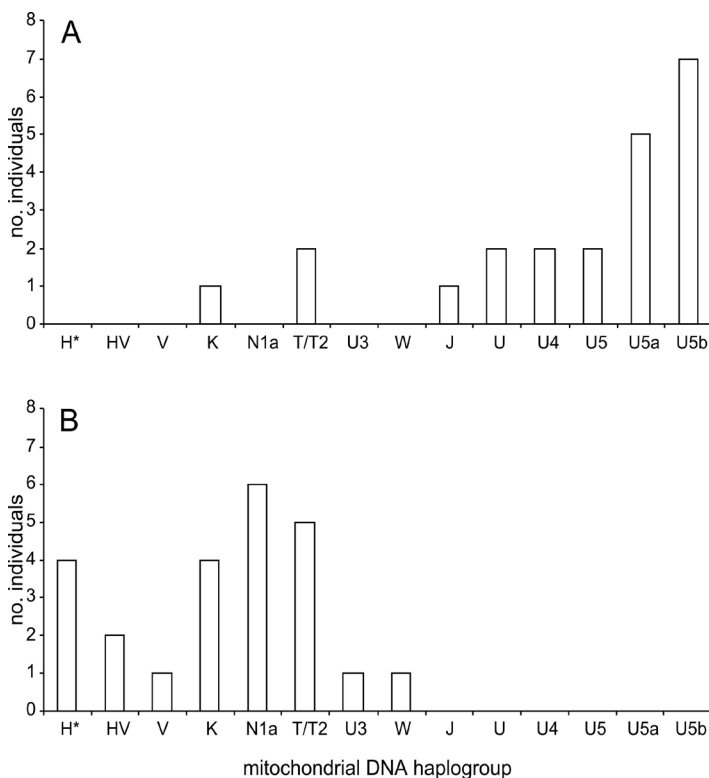


Figure 3. The number of individuals per mitochondrial DNA haplogroup in the Bramanti et al. (2009) study, the first successful aDNA study on Mesolithic samples. All studied individuals derive from European Stone Age contexts and are divided into two groups according to subsistence strategy: A) Hunter-Gatherers and B) Neolithic farmers. The farmer group consists of individuals from the Linearbandkeramik culture (the earliest Neolithic culture in central Europe) while the hunter-gatherers group is more heterogeneous and contains Mesolithic individuals together with individuals from “sub-Neolithic” cultures. Data from Bramanti et al. 2009: table 1.

The new methods enabled to greatly increase the number of DNA sequences from ancient samples and made it possible to investigate, not only the mitochondrial DNA sequences, but also the rest of the six billion base pairs that make up the human genome. For the first time it was also possible to confirm the authenticity of aDNA sequences, since characteristic damage typical for ancient DNA molecules can be used to distinguish them from modern contamination. As a result of these methodological improvements, we nowadays have access to genomic information from more than 80 Mesolithic individuals in Europe (Mathieson et al. 2017: Supplementary Table 1 lists 82 Mesolithic individuals). The best preserved of these Mesolithic individuals has more than 50 times coverage of its total DNA sequence, which for the time being can be considered a very good result, although the average coverage for all Mesolithic individuals is much lower. The low coverage means that the Mesolithic individuals cannot be directly compared with each other gene by gene. Instead they are compared with living humans.

The results of such comparison can be presented in different ways. Of these, the PCA plot is considered the most illustrative. A number of such plots have been published in recent years, while the highest numbers of Mesolithic European individuals; 79, are presented in papers by Iain Mathieson et al. (2017: Fig. 1). A few details in this plot (Figure 5) are worth emphasizing here: 1) All Mesolithic individuals plot outside the genetic variation of present populations; 2) There seems to be structure in the distribution of the Mesolithic individuals in that three Russian individuals make up a group of their own in one end of the distribution while 11 individuals from southern and central Europe constitute an other group at the other end. Mesolithic individuals from Sweden, Ukraine, Latvia and the Iron Gates of the Danube River all fall in groups of their own, all placed in the plot between the first mentioned two; 3) Taken as a whole, the total genetic variation within the Mesolithic sample population is large. It is in the same range as the variation in the European population today.

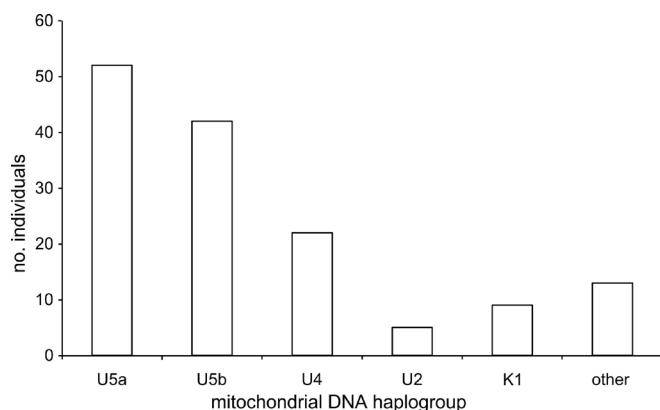


Figure 4. European Mesolithic individuals with information on mtDNA haplogroup (n=143) in June 2017.

Pioneers of Norway – the way forward

Archaeology

Although the spread of archaeologically detectable material culture traits and technology cannot be directly linked with population movement, it can be argued that changes in cultural traditions

should usually be slow and that history explains a significant fraction of human behaviour (e.g., Boyd & Richerson 1985: 56–60; see also Pagel & Mace 2004; Shennan 2009), while rapid change is more probably a consequence of outside pressure, such as environmental crisis or demic diffusion. People acquire most of their skills by imitation and social interaction, and therefore language differences and hinders for movement, such as the Scandinavian Ice Sheet in the case of Pleistocene and early Holocene north-western Europe, and to smaller degree also the Baltic Sea basin and the Caledonian mountain range, consequently prompt cultural divergence that is self-reinforcing (Boyd & Richerson 2005: 379–396; Pagel & Mace 2004). The basis of the *chaîne opératoire* approach used in the study of pre-industrial technology can be tracked down to this same general notion. In this approach the *chaîne opératoire*, that is, an

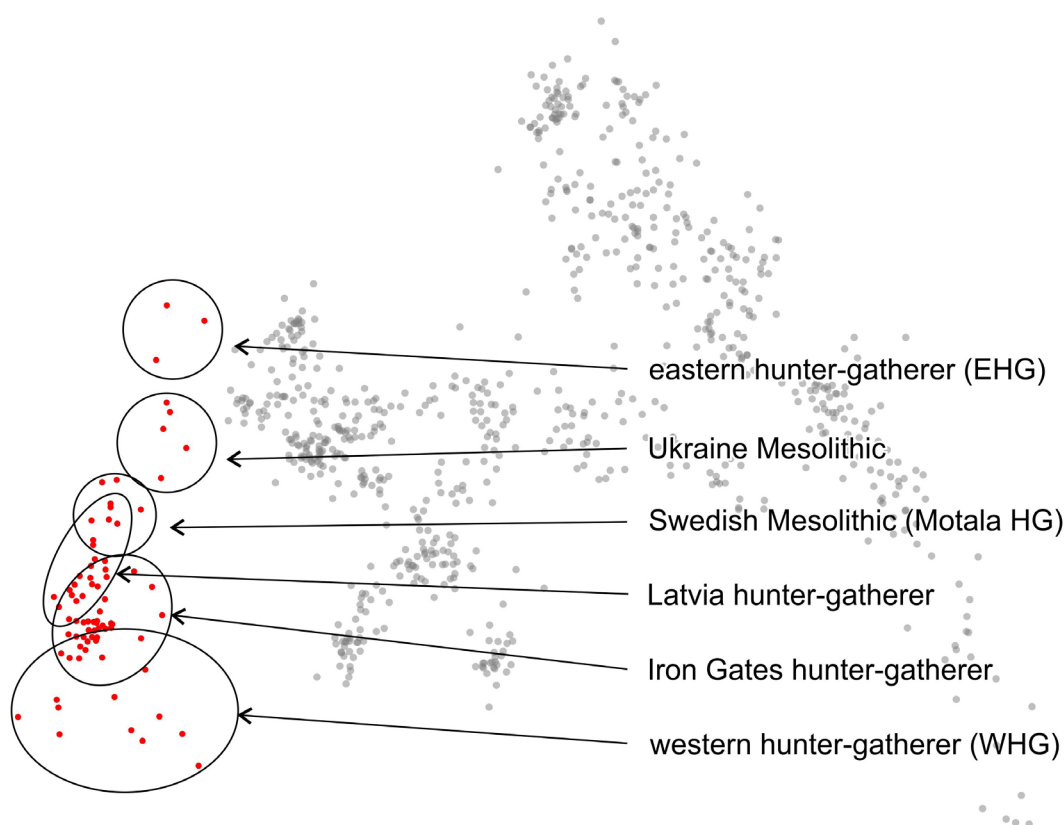


Figure 5. PCA plot redrawn from Mathieson et al. 2017: Extended Data Figure 1.

ordered set of gestures and actions that lead to the transformation of raw material to a finished product, is regarded as a socially transmitted system the use of which is indicative of group affiliation (e.g., Karlin & Julien 1994; Lemonnier 1990).

Gradual change in the *chaînes opératoires*, on the other hand, is best explained by cultural evolution and especially by the ways it structures the transmission of socially acquired information (Mesoudi & O'Brien 2008; Riede 2006), while the speed of change is potentially enhanced by constraints set by the physical environment, such as raw material or prey availability. This means that although history explains a considerable part of the way things are done, in the long run socially transmitted operational sequences are not static but instead subject to evolution (Manninen 2014).

With these premises in mind, technological studies in the *Pioneers of North-Western Europe* -project aim at detecting patterns that indicate migration of people and/or transmission of information and skills from the two major late-glacial cultural areas located at the gates of the (then) largely ice-covered Scandinavian peninsula, namely the Terminal Paleolithic/Early Mesolithic cultures of the northern parts of the East European plain, i.e., the “post-Swiderian” groups, and the North-European late-glacial groups known best from the areas of present-day Denmark and northern Germany, that is, the Ahrensburgian and related groups.

The stone tool technology of the early inhabitants of Norway was to a large degree based on lithic blade production. Experimental studies have shown that blade production by differing operational chains leave tell-tale signs in the resulting end-

products and waste, which in some cases are very distinct (e.g., Inizan et al. 1999; Pelegrin 2012). These traces, or *stigmata*, can be used to detect and separate differing technological traditions. Recently, the recognition of the use of a pressure technique to produce regular blades from conical to semi-conical cores in the early post-glacial assemblages from Finland and Norway (Inizan 2012; Jussila et al. 2012; Kankaanpää & Rankama 2012; Knutsson & Knutsson 2012; Manninen & Hertell 2011; Rankama & Kankaanpää 2011; Sørensen et al. 2013; Damlien 2016), has brought new evidence to support a north-eastern route for the migration of people and knowledge to northernmost Norway in the early Holocene.

At the moment, the eastern or “post-Swiderian” technology can be distinguished by the use of pressure blade technology and related core preparation methods (see Sørensen et al. 2013; Damlien 2016 for detailed technological descriptions). A probably related technology (see Knutsson et al. 2016; Manninen et al. 2018), that is, slotted point manufacture using the so called Z-method (Zamostje) is also distinguished in the east, while blade production by direct percussion and opposite platform cores as well as bone tool production using the so-called D-method (Danish) is characteristic for the “western” epi-Ahrensburgian and Maglemosian assemblages (Figure 6; David 2009; Sørensen et al. 2013; Bergsvik & David 2015).

The presence of this technology in southern Norway and south-eastern Sweden by ca. 8000 BC is suggested to indicate spreading of the technology from north to south in Norway and the speed at which this happened according to radiocarbon dating, to indicate probable population migration (Sørensen et al. 2013; Damlien 2016).



Figure 6. The border zone (dotted line) between the North European (Maglemosian) bone technology (D-method) and the North-East European bone technology (Z-method) at ca. 7500-6000 BC (after Bergsvik & David 2015) and pre 7000 BC finds of slotted bone points in northern Europe (black dots). Dates indicate median values calculated using OxCal 4.2 (IntCal 13) on the earliest cluster of dates per site that the *r_combine* function of the program combines without error warning (approximately 200 year bins). When available, bone dates have been preferred over charcoal dates). Slotted bone point data from Edgren 1997; Carpelan 2008; Hartz et al. 2010; Skakun et al. 2011; Persson 2014; Kjällqvist et al. 2016; Knutsson et al. 2016; Jussila, T., Kriiska, A. & Rostedt, T. pers. comm. 2016.

However, the relatively early occurrence of the technology in south-eastern Sweden and southern Norway could also be a consequence of a southern route directly from the eastern Baltic across or around the Baltic Sea basin (Figure 7) – possibly using dog sleds on sea ice. However, it is unclear how the speed of technology spreading through horizontal transmission of knowledge and know-how in a low population density situation would differ from that of population migration. It should be noted, that technological concepts that can be related to an early post-glacial eastern influence in Scandinavia, at present are confined to the eastern Early Mesolithic blade core treatment process and

slotted bone points with straight blade insets, while blade arrowheads of the “post-Swiderian” types are not known from Norway and Sweden (Sørensen et al. 2013) but are present at many pioneer stage sites in the eastern Baltic and Finland (e.g., Zhilin 2006; Manninen & Hertell 2011).

Ancient DNA

Southern Sweden seems to have been the receiver of substantial immigration associated with the introduction of agriculture ca. 4000 BC. In Sweden there are known Early Neolithic agricultural sites close to the coast up to the area around Stockholm (Sørensen 2015). In Norway



Figure 7. Early post-glacial sites and suggested colonization routes to Norway from Ahrensburgian (red) and post-Swiderian (black) cultural spheres (modified from Sørensen et al. 2013). Red dots indicate a selection of radiocarbon dated early sites with reported Ahrensburgian or epi-Ahrensburgian technology. Black dots indicate a selection of early sites with reported post-Swiderian technology. Dates indicate median values calculated using OxCal 4.2 (IntCal 13) on the earliest cluster of dates per site that the *r_combine* function of the program combines without error warning (approximately 200 year bins). When available, bone dates have been preferred over charcoal dates). Data from Meling 2008, Brinch Petersen 2009, Oshibkina 2008, Hartz et al. 2010, Hertell & Tallavaara 2011, Jussila et al. 2012, Gjerde & Hole 2013, Pesonen et al. 2014; Damlien 2016.

those first agriculturalists had a limited spread restricted to the area around the south-eastern part of Oslofjord next to Sweden. For the rest of Norway the hunter-gatherer way of living continued for most of the Neolithic. It is first in the Late Neolithic, around 2000 BC, that agriculture spread on a larger scale in Norway, most probably by new immigrants (Lazaridis et al. 2014; Haak et al. 2015). The same is the case for northern Sweden and Finland. Parts of the Mesolithic genome is still present in today's Norwegian population. In fact, together with Finland and Sweden, Norway has a greater proportion of

Mesolithic traits in the human genome than any other country in Europe. Since remains of very few Mesolithic individuals are found in Norway, and nearly none from Finland and northern Sweden, it is tempting to use individuals from later periods to reconstruct the Early Mesolithic genetics. This is, however, complicated, as gene flow between European Mesolithic and Neolithic groups happened already before the Neolithic groups arrived to Fennoscandia. It has for instance been proposed that the Early Neolithic Funnel Beaker Culture people already had a West European Mesolithic element when

arriving into Scandinavia (Chyleński et al. 2017, and references within).

The first condition for the use of genetics in tracing the origin of the Mesolithic population in Norway is therefore that Mesolithic individuals from the area need to be included in the study. A second condition is that there were considerable genetic differences between the potential areas of origin for the pioneer colonizers of north-western Europe at ca. 10,000 BC. Small and isolated refugia during the LGM are a potential source for such genetic divergence through the genetic bottleneck effect. However, recently it has been discussed whether settlement in fact was restricted into geographically isolated refugia during the LGM, or not (Banks et al. 2008; 2011; Tallavaara et al. 2015).

William E. Banks and co-workers applied “eco-cultural niche modeling” in two papers (Banks et al. 2008; 2011). In the study they begin with archaeological site locations and map areas that have similar environmental conditions as the surroundings of the known sites. From this they produced a model of LGM settlement in Europe. The result suggests that settlement was very restricted, with a population of only a few thousands during the LGM (Banks et al. 2011: 370). If such small populations are isolated for a longer time, they will get genetic characteristics, and it will be possible to distinguish their descendants when population expansion occurs alongside better climatic conditions. Miikka Tallavaara and co-workers (2015), on the other hand, used niche modeling as well as ethnographic and archaeological data to study LGM population density with climate envelope modeling tools. Their results indicate continuous human population through the LGM in large

areas in Europe, thus undermining the idea of isolated refugia with small populations. Their results suggest a continuous population with a minimum size of 130,000 individuals at 21,000 BC. The bottleneck effect would, if this is correct, not give rise to any drastic genetic differences in a population of this size. The genetic differences would instead be gradual over the distribution area and depend on the degree of mobility.

From the aDNA results achieved so far, it seems likely that there were at least some isolated enclaves during the LGM. Most obvious is the difference between the eastern Mediterranean and Western Europe. The groups that came into Europe at the start of the Neolithic had their origins somewhere in the Middle East. The genetic difference between the Mesolithic and the incoming Early Neolithic population in central Europe around 5500 BC may therefore derive from populations descending from groups isolated in two separate LGM refugia. The more precise place of origin for the Early Neolithic population has been subject to some speculation. It is logical to think that they came from Anatolia to Europe, but the fact that the Early Neolithic people happened to have genetic similarities with present day Sardinians has caused some confusion (Sikora et al. 2014). However, recently results from Neolithic Turkey (Mathieson et al. 2015) as well as Neolithic and Mesolithic Greece (Hofmanová et al. 2016) confirm that the Neolithic farmers originated in eastern Mediterranean. In addition, the study by Zuzana Hofmanová and co-workers (2016), which includes two Mesolithic samples from Greece, shows that these two individuals belong to the K1c mitochondrial haplogroup, a group typical for the Early Neolithic in Europe and Anatolia while unknown among Mesolithic

individuals from other parts of Europe. The most likely explanation for this is that the ancestors of the two Mesolithic individuals from Greece on one hand, and the Mesolithic individuals from the rest of Europe, on the other, were located in different refugia during the LGM.

The parts of the world from which human aDNA results are available, are still quite restricted, but an area of interest in this connection is Lake Baikal where several individuals have been sampled (Vahdati Nasab 2011). Stone Age burials in the area have yielded samples with considerably different mtDNA haplogroup composition when compared to both Mesolithic Europeans and Early Neolithic Anatolians (Figure 8). Lake Baikal is far from Europe, ca. 5000 km east of Moscow, so it may not be a surprise that the mtDNA composition there is quite different from both Mesolithic and Early Neolithic Europe. However, Lake Baikal is relatively close to the presumed eastern LGM refugium, and if the model presented by Tallavaara and co-workers (2015) is correct, there was nothing to hinder east-west contact over southern Siberia. Despite this, there is only minor overlap with Mesolithic Europe and Anatolian Neolithic.

The ways mtDNA groups have been ascribed to different refugia in Europe are not uniform between researchers. As most of the Mesolithic individuals studied belong to U5, U4 or U2, the discussion on the origin of the Mesolithic population in Europe can be restricted to these groups. Most researchers seem to agree that U5a and U5b originated in separate refugia. U5b in a western refugium, while U5a together with U4 and U2, both are considered eastern (Pala et al. 2012). Mapping of the distribution of these mtDNA types in the studied Mesolithic individuals shows

that there is a tendency for U5b to have a more limited distribution centering in south-western Europe. It can be noted that so far a Mesolithic individual belonging to the U5b haplogroup has not been found in Scandinavia or north of Latvia in the north-east (Figure 9). If this reflects a real absence of U5b in northern Europe, it may suggest that all of the Mesolithic population in Scandinavia derived from eastern female ancestral lines.

While the mtDNA is inherited strictly from mother to child, the effect of mixing on the genomic DNA is that a child will locate genetically between the two parents. The 82 Mesolithic European individuals with genomic information investigated by Mathieson et al. (2017) fall in a continuum with one endpoint in individuals from SW Europe and the other in individuals from Russia. (Figure 5). The Swedish individuals appear to be a group of their own in this respect, placed about midways between the two endpoints. This could either be interpreted as an indication of at least three different LGM refugia and that the Swedish Mesolithic individuals are representatives of one of these and thus forming a separate group, or alternatively, the results could indicate that there were two populations representing separate LGM refugia, one south of Scandinavia and one to the east, which expanded when the ice withdrew, and met and got mixed in Scandinavia. The latter explanation fits with the archaeological evidence suggesting that Scandinavia first got Early Mesolithic pioneers from the south and slightly later a second wave of human dispersal from the northeast.

All skeletal remains found on the Scandinavian Peninsula so far are dated after 8000 BC, i.e., after the change in stone technology assumed to indicate immigration from east. Therefore is it not possible to directly investigate if the change

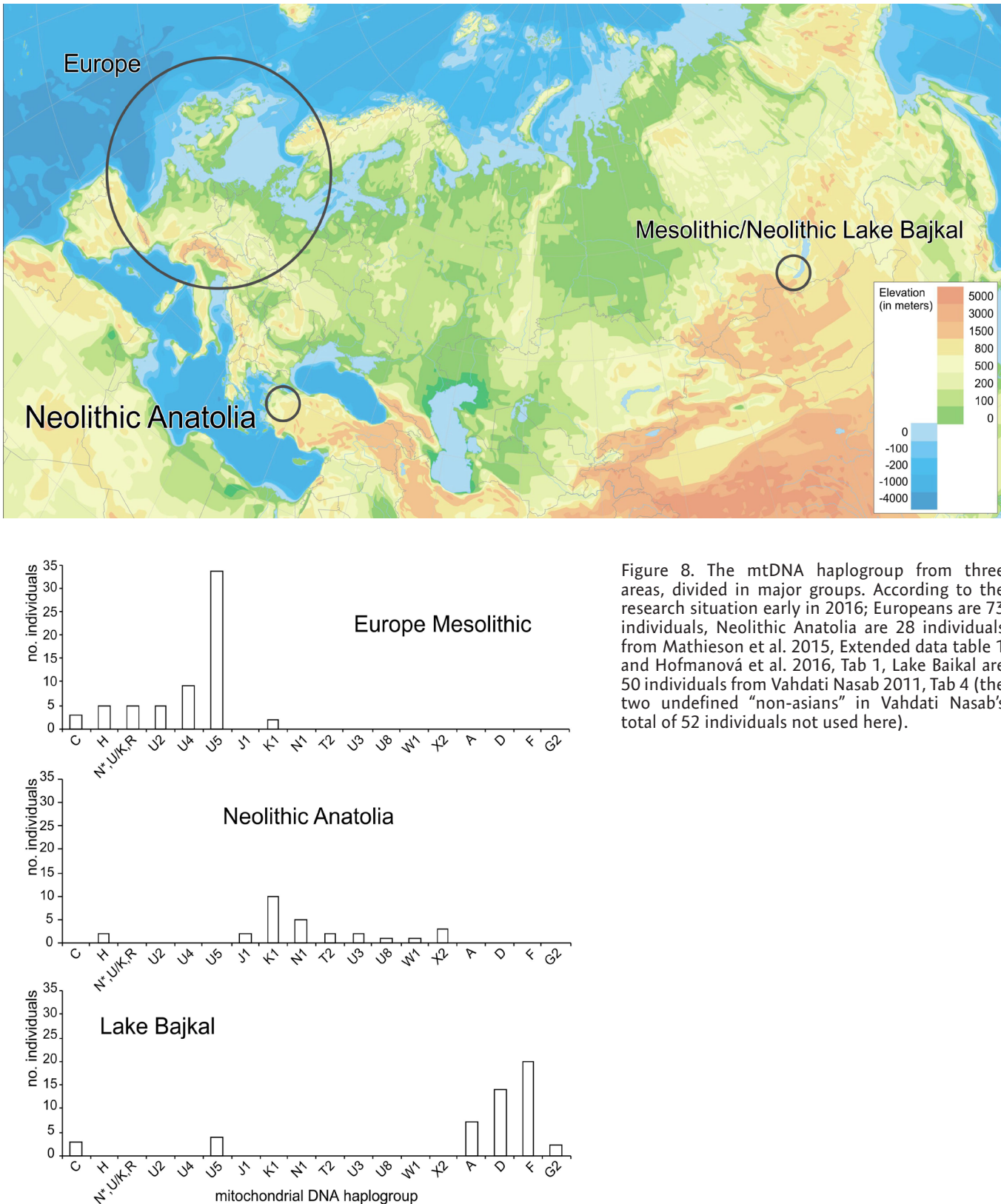


Figure 8. The mtDNA haplogroup from three areas, divided in major groups. According to the research situation early in 2016; Europeans are 73 individuals, Neolithic Anatolia are 28 individuals from Mathieson et al. 2015, Extended data table 1 and Hofmanová et al. 2016, Tab 1, Lake Baikal are 50 individuals from Vahdati Nasab 2011, Tab 4 (the two undefined “non-asians” in Vahdati Nasab’s total of 52 individuals not used here).

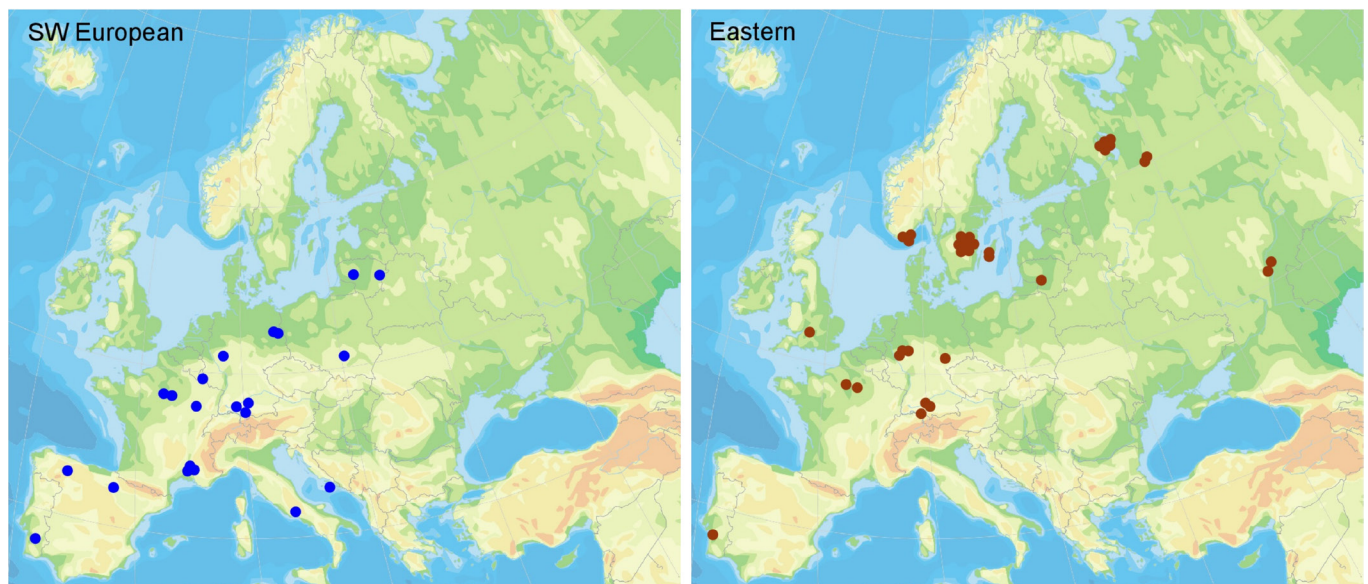


Figure 9. The mtDNA haplogroups ascribed to a south-western refugium (U5b) and an eastern refugium (U2, U4 and U5a). Sources: Chandler et al. (2005), Haak 2006, Bramanti et al. 2009, Delsate et al. 2009, Der Sarkissian 2011, Hervella et al. 2012, Bollongino et al. 2013, Brandt et al. 2013, Skoglund 2013, Lazaridis et al. 2014, Olalde et al. 2014, Skoglund et al. 2014, Haak et al. 2015, Mathieson et al. 2015, Fu et al. 2016, Szécsény-Nagy 2015, Posth et al. 2016.

in stone technology is connected with a genetical change. However, if Mesolithic Scandinavians were mostly a mix of people deriving from two refugia, an analysis of their DNA sequences will make it possible to estimate the probabilities for this mixing happening before or after these groups arrived into Norway.

Modeling the past

The re-colonization of north-western Europe was part of a larger process in Europe that started with the end of the Last Glacial Maximum, ca. 18,000 BC. For humans, the development from LGM to Holocene in Europe meant changes in environmental conditions, social organization, technological knowledge, and equipment, with accelerating speed. However, there is no way to grasp the effects of these changes for the population growth and dispersal in simple mathematical formulas. The logistic population growth model, for instance, presupposes one population in one delimited geographical area with a stable environment. In order to get a realistic view of the development, the model

should be dynamic both in time and space. In our project we will use computer simulations in which all the individuals in the model will be entities represented with individual sex, age, and other characteristics. The procedure therefore differs from models in which the entire population is represented by a single value, the sexes represented by a fraction of the population, etc. In our simulation the modelled individuals will also acquire a place on the map and can move around in the geography (it will, in that respect, be an “agent based model”, cf. Romanowska 2015). The model will be dynamic as it is run in one year time steps while the individuals grow older every year until they eventually die. Changes in the environment, such as the retreat of the ice sheet, changes between land and sea, and so forth, will be modelled on a coarser time scale, but updated continuously in accordance with what is known of the environmental changes. A similar approach has recently been applied by Tarja Sundell and co-workers to periods post-dating the pioneer colonization phase in Finland (Sundell et al. 2010; 2014).

This model will make it possible to simulate different scenarios for the pioneer settlement of north-western Europe and consequently allows comparison of the modeled scenarios with what is known from archaeological and genetic research. For instance, it will be possible to compare the outcome of simulations with and without isolated refugia in southern Europe during LGM. Different scenarios in this respect can result in quite different genetic and cultural patterns 10,000 years later.

As discussed earlier in this paper, ancient DNA indicates that there were considerable changes in European population since the end of the last glacial period, especially with the immigrations in the Neolithic (Haak et al. 2015, Mathieson et al. 2015) and that therefore it is not possible to reconstruct the course of events using only the genes of people living in Europe today. Ancient DNA from a few Mesolithic and Neolithic individuals, however, improves the situation considerably. If we accept that mtDNA haplogroups U5a and U5b were established before the end of LGM, we can simulate the fate of these groups through time. It might, for instance, be possible to decide whether individuals with U5a or U5b mtDNA haplogroups dated to Neolithic, descend from the local Mesolithic people or represent new Late Neolithic immigrants as proposed by Guido Brandt (2015; Brandt et al. 2015). Moreover, if local Mesolithic origin is the most likely scenario, these individuals can be used as representatives of the Mesolithic population despite their late date and yield a valuable addition to the few Mesolithic individuals available, while providing information on the line of events during the Mesolithic.

Simulations of geographical trends with an ecological model are similar to phylogeography carried out for many species in regard to their

refugial history and dispersal after the LGM. These studies infer population dynamics mainly from genetic signatures that are still detectable today. For warmth-demanding species, with refugia in southern Europe, a decreasing gradient of diversity is expected from south towards the north, with maximum levels of variation in putative glacial refugia. This is the case with wild boar (Vilaça et al. 2014), as well as red and roe deer (Sommer et al. 2008; Sommer et al. 2009).

Concluding remarks

The history of research into the early colonization of northern Europe shows a tight connection between Late Paleolithic archaeology and ecology, as it was deglaciation that provided new land for the expanding population at the end of the last glacial cycle. Connections also exist between linguistics and archaeology especially in early treatments of the subject, as archaeological cultures have been seen as representing precursors for later historical language groups. Purely archaeological studies of the subject have relied mostly on tool types. Since the late 20th century, references to genetics and technological trajectories have increased in number, initially quite slowly, but recently in rapidly increasing numbers. The genetic data available today seems to be in favour of separate glacial refugia for humans, as well as other species, during the LGM, while archaeological data strongly points towards early post-glacial human dispersal to Norway from two directions. The challenge for our project is to combine the available knowledge with a focus on Early Mesolithic Norway and contribute with new data on aDNA and movement of technological knowledge and know-how in early post-glacial Europe.

This article was written in 2017. Since then new contributions on the genetics of the Mesolithic populations on the Scandinavian Peninsula have been published (Kashuba et. al. 2019, Günther et al. 2018).

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