Journal of Archaeological Science: Reports 26 (2019) 101860

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

From mountains to towns: DNA from ancient reindeer antlers as proxy for domestic procurement networks in medieval Norway

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ARTICLE INFO

Keywords:
Ancient DNA
Comb production
Domestic procurement networks
Mitochondrial DNA
Raw material provenance
Outland resources

ABSTRACT

In medieval archaeology there are long traditions for studying foreign, exotic material culture as *proxy* for procurement networks of international reach. A paradox is that domestic networks, which brought products to consumers at home, has attracted little attention. During the Middle Ages (1030–1537), antler from reindeer was a north Scandinavian outland resource that found its way from remote mountains to settlements at home and abroad for use in hair combs. In the current pilot study, molecular genetic methods were employed to test whether antler debris from comb production workshops in the four medieval Norwegian towns Bergen, Trondheim, Skien and Oslo can be assigned to its original reindeer population. The study shows that ancient DNA (aDNA) can be used to provenance antler material to its origin with varying degrees of certainty: When samples from the four towns are considered as *collective units*, there is a high level of certainty in the discovered provenance pattern, whereas there is more uncertainty attached to provenancing *individual* antler fragments. Some immediate culture historical insights from the project's results are that urban comb makers used antler from the closest mountain areas, while analysis of individual-reindeer-based relationships on resource procurement adds some possible nuances to this picture. Furthermore, assigning dated antler debris to its population of origin adds new dates for commercial exploitation of reindeer resources in the specific mountain areas and adds new and high-definition empirical substance to the picture of long traditions for far-reaching procurement networks for Norwegian outland resources.

1. Introduction

In Norway, domestic raw materials from the sea and outlands have been of the utmost importance for the subsistence and economy of people on local, national and, at times, international scales. In the Viking and Middle Ages the latter is witnessed by exotic Norwegian reindeer antler combs, schist hones, soapstone vessels, furs, iron and timber identified in northern European consumer contexts or mentioned in documentary sources (e.g. Ashby et al., 2015; Baug, 2017; Hansen, 2017; Helle, 1982; Mikkelsen, 1994; Resi, 1979; von Holstein et al., 2014). Medieval archaeology has long traditions for studying exotic material culture as *proxy* for different kinds of long-distance relations across borders. A paradox is that domestic networks, which brought materials to home consumer sites, has attracted little attention. Many domestic household products are often rather plain and hard to sufficiently provenance by traditional archaeological tools such as artefact typology. With recent development in cross-disciplinary methods, the movement of objects and raw materials, and their associated cultural and economic networks, can now be studied on a much higher resolution than previously seen (e.g. Ashby et al., 2015; Hansen, 2017; Hansen et al., 2017; Star et al., 2018; von Holstein et al., 2014). In this pilot study, ancient DNA (aDNA) analyses are employed on antler materials from reindeer (*Rangifer tarandus*) to test whether antler debris from comb production workshops in the four medieval Norwegian towns Bergen, Trondheim, Skien and Oslo can be assigned to its population of origin. If successful, new and high-definition archaeological data for the study of links between hunters in remote alpine mountain areas, urban artisans as well as domestic and international consumers of antler products, will become available.

Reindeer antler was an outland resource that found its way from remote north Scandinavian mountain areas to settlements, domestic as well as foreign, during the Middle Ages (e.g. Ashby et al., 2015; Hansen, 2017). In Norway, reindeer antler was used for hair combs and is frequently found in urban comb production workshops and consumer

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https://doi.org/10.1016/j.jasrep.2019.05.025
Received 7 December 2018; Received in revised form 16 April 2019; Accepted 22 May 2019

contexts. Trapping systems for catching reindeer are found in most mountain areas of Norway. Archaeological investigations of these systems, and related refuse heaps at butchering sites, give evidence of large-scale reindeer exploitation during Viking and Middle Ages (Barth, 1996; Hufthammer et al., 2011; Indrelid and Hufthammer, 2011; Jordhøy et al., 2005; Mikkelsen, 1994). Investigations of such refuse heaps show that antlers are often strongly underrepresented compared with other bone elements in medieval assemblages (Hufthammer et al., 2011). Antler has thus not been regarded as butchering waste, but rather as valuable raw materials that were transported from the outlands and entered resource procurement networks (Indrelid and Hufthammer, 2011; Hufthammer et al., 2011).

Comb-making was a key craft during the Middle Ages, as testified by production debris at urban sites across northern Europe (e.g. Ashby et al., 2015; Hansen, 2017; Linaa, 2015; Luik, 2015; Smirnova, 2005). In early and high medieval Norway (c. 11th–13th centuries), combs made of reindeer antler were a common personal accessory and comb-making is one of the first, and most frequently encountered, crafts in the six Norwegian towns where major archaeological excavations have been carried out. In the early Middle Ages, comb makers in Norway were itinerant craftspeople who paid short visits to the towns where they produced affordable hair combs (Hansen, 2017). Later in the Middle Ages, urban comb-making workshops seem to be established on a more permanent basis in Norway (Flodin, 1989; Rytter, 1997). Little detail, however, is known about the raw material procurement networks that supplied the comb makers with antler.

A common assumption has been that medieval towns were primarily supplied with resources from their hinterland; alpine raw materials, like antler, would thus end up in the nearest towns (e.g. discussions by Indrelid and Hufthammer, 2011; Mikkelsen, 1994, 176; Rytter, 2007; Schia, 1989). Recent studies of Norwegian outland products have benefitted from theoretical approaches, involving a higher resolution on actors along the chain of operations associated with the procurement and use of raw materials, as well as from new archaeological data sets obtained through natural scientific methods (e.g. Ashby et al., 2015; Baug, 2015; Baug, 2017; Hansen, 2017 with references; Hansen and Storemyr, 2017 with references; Loftsgarden, 2017; Stene and Wangen, 2017). An important new observation is that there are many producers on the scene. Quernstones of mica schist, frequently found in foreign consumer contexts, are now shown to be quarried in several places in Norway; with geochemical methods, it is now possible to distinguish between the quarry sites (Baug, 2015). Soapstone vessels and iron were produced on a large scale in several places during both the Viking Age and the Middle Ages (e.g. chapters in Hansen and Storemyr, 2017; Loftsgarden, 2017 with references). It is furthermore recognized that there is a great variety in the geographical reach of different raw material- and product procurement networks. For instance, during the Viking Age and the Middle Ages, schist hones of the Eidsborg type and the Caledonian type from southern and western Norway were distributed via networks spanning from local to international (Baug et al., 2019; Resi, 1990). Also, soapstone vessels entered networks spanning all levels from local to international during the Viking Age (Baug, 2017; Resi, 1979), whereas medieval soapstone vessels had a more limited local and regional reach (Hansen, 2017). The complexity of domestic networks regarding the hierarchies of hubs where produce changed hands is also being unveiled. For example, it has been suggested that surplus production from mountainous areas may have reached the coastal communities – towns – via smaller inland marketplaces (Loftsgarden, 2017). Actors from many levels of the social hierarchy would be involved in procurement, and it is likely that competing networks operated within different geographical zones and social orbits and that such networks were apt to change over time (Baug, 2017; Hansen, 2017). It is, thus, interesting to study medieval reindeer procurement networks on a higher resolution than what has been possible so far. For this purpose, detailed information on the provenance of antler is a central piece in the puzzle.

Molecular methods are increasingly being used to assign organic archaeological artefacts (Ashby et al., 2015; Brandt et al., 2011; Hartnup et al., 2011; Olivieri et al., 2014). In previous research, aDNA in tandem with collagen peptide mass fingerprinting analysis, also called Zooarchaeology by Mass Spectronomy (ZooMS) has been applied on prehistoric combs from Scotland to identify local and non-local species of deer used as raw materials. Reindeer was identified and subsequently linked to Scandinavian presence (von Holstein et al., 2014). Using ZooMS, reindeer has also been identified as exotic materials in Danish Viking Age settlements (Ashby et al., 2015). These successful species identifications among finds in the North Sea region show the general area of provenance for the raw materials/combs; i.e. the Scandinavian peninsula. In the current pilot study, we go into further detail and address provenance on the reindeer population level, within the Scandinavian peninsula. Present day Scandinavian reindeer show a significant genetic structuring among populations in different mountain areas (Røed et al., 2008), but a profound history of foreign introduction, translocations and population changes have caused large temporal genetic changes in many populations (Bjørnstad et al., 2012; Røed et al., 2011, 2014, 2018). Thus, to be able to successfully provenance archaeological antler material it is important to compare contemporary contexts of both the antler material and the candidate source areas. Ancient reindeer DNA have previously been analysed extensively from several different archaeological hunting sites in Norway. This offers a unique possibility to try to provenance the antler material in urban medieval sites on a relatively finer scale. If successful, this will provide valuable new data sets for high-resolution studies of movement, and subsequently domestic and international procurement networks involved in the exploitation and use of reindeer antler. The successful assignment of well-dated urban antler debris to its population of origin may also provide new dating evidence for the commercial exploitation of reindeer resources in these mountain areas.

2. Materials and methods

Reindeer antler debris from comb-making was sampled from medieval Bergen, Trondheim, Skien and Oslo in south and central Norway (Fig. 1). In these towns, extensive archaeological sites with favourable conditions for preserving organic materials have yielded antler debris from comb production workshops and combs made of reindeer antler (Flodin, 1989; Hansen, 2005; Hansen, 2017; Myrvoll, 1992; Wikstrøm, 2006). To investigate whether an aDNA approach could be used to identify the origins of reindeer antler, we compared the mitochondrial control region (CR) variation in the samples of workshop debris to the reported genetic structure of medieval wild reindeer populations from three mountain areas in south-central Norway: Dovrefjell, Reinheimen and Hardangervidda (Røed et al., 2014). These represent the three main wild reindeer regions of south-central Norway. Given that the four towns in case were involved in domestic trade networks with a very wide reach (Hansen, 2017), we also included samples of medieval reindeer from Finnmark in northern Norway (Fig. 1).

2.1. Contexts and dates for the comb production workshops (CPWs)

To ensure that data derived from different reindeer/individuals, waste from burrs and/or from different workshop areas were preferred for sampling. Archaeological information on the CPW samples with sufficient DNA are found in Table 1.

Bergen is located on the west coast in southern Norway. During the Middle Ages, the town, which was large by Norwegian standards, became the most important international trading center in Norway (Hansen, 2017; Helle et al., 2006). The aerial distances between Bergen and the mountain areas in Finnmark, Dovrefjell, Reinheimen and Hardangervidda are about 1400 km, 300 km, 260 km and 130 km, respectively. CPW samples were taken from three sites located in different parts of the medieval town area. From the Bryggen site, ten samples

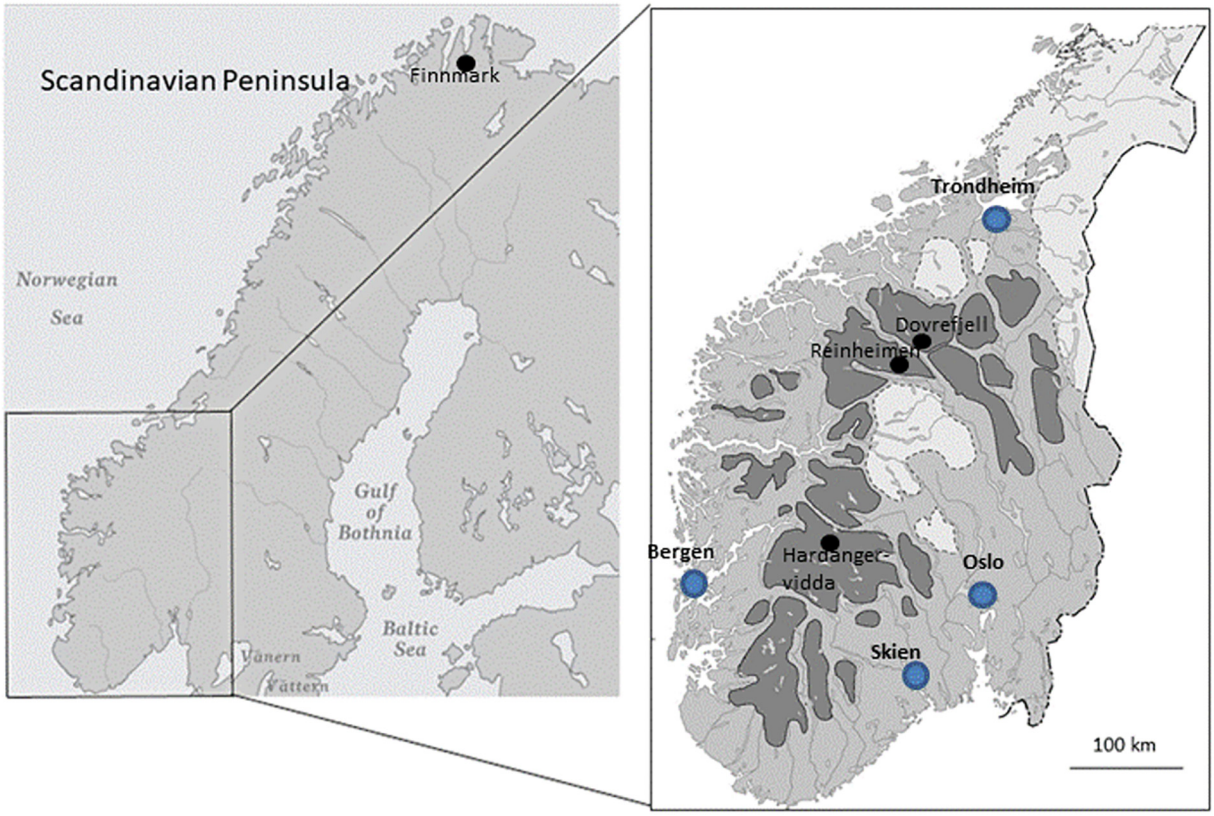

Fig. 1. Location of towns (blue dots) where debris of reindeer antler from comb production was obtained and the alpine archaeological sites (black dots) used for establishing the reference sequences in the mountain regions in south-central Norway. The Finnmark material is a collection of several archaeological sites in eastern Finnmark. The dark (wild) and light (domestic) shaded areas show the present-day distribution of reindeer in southern Norway. Both light and dark shaded areas were inhabited by wild reindeer in historic times. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

derived from different workshop areas dating to 1120–1170 and 1170 − 1198, respectively. The Rosenkrantzgate 4 site delivered four samples from a workshop area dating to 1200 − 1248 and the Domkirkegaten 6 site delivered four samples from one workshop area dating to 1160/70 − 1230/40 and 1230/40 − c. 1280, respectively (Hansen, 2005,159 − 162, 180 − 186; Hansen, 2015). University Museum of Bergen (UM/UIB) provided the 18 sampled objects, of which 12 gave sufficient DNA.

Trondheim is located on the estuary of the river Nidelva in south-central Norway. The town may be characterized as large in a medieval Norwegian context and an important ecclesiastic centre during the Middle Ages (Hansen, 2017; Helle et al., 2006). Trondheim is located about 130 km from Dovrefjell, about 170 km from Reinheimen and about 390 km from Hardangervidda. The distance between Finnmark and Trondheim is about 980 km. CPW samples were collected from the Folkebibliotekstomten site centrally located in the medieval town area. The site comprises several individual properties/plots (Christophersen and Nordeide, 1994) and revealed antler debris from numerous comb maker workshops (Flodin, 1989). The analysed debris was collected on plot 6B from phases dating to respectively c. 1150–1175 and c. 1175–1225 (plot number and dates according to Christophersen and Nordeide, 1994, 35, Fig. 23). The Norwegian University of Science and Technology (NTNU) University Museum in Trondheim (UM/NTNU) provided the 20 sampled artefacts, of which 13 gave sufficient DNA.

Skien is located in south-east Norway on the western side of the Oslofjord. The town was of medium size in a medieval Norwegian context and was well placed for traffic between inland areas and the sea (Hansen, 2017; Helle et al., 2006). Aerial distances from Skien to Finnmark, Dovrefjell, Reinheimen and Hardangervidda mountain areas are about 1400 km, 360 km, 330 km and 170 km, respectively. CPW samples were obtained from the Handelstorget site, located centrally in the medieval town area (Myrvoll, 1992). The samples stem from phases dating to 950–1000, 1100–1170 and 1170–1230, respectively. The Museum of Cultural History, University of Oslo (KM/UIO) provided the 15 artefacts, of which eight samples gave sufficient DNA.

Oslo is located in south-eastern Norway at the end of the Oslofjord. The town was large by Norwegian standards and well placed for traffic between inland areas and the sea (Hansen, 2017; Helle et al., 2006). The distance between Oslo and Finnmark, Dovrefjell, Reinheimen and Hardangervidda mountain areas is about 1300 km, 280 km, 260 km and 180 km, respectively. CPW samples were obtained from the Nordre felt II site, located centrally in the medieval town area. The samples were taken from phases dating to 1200–1230, 1230–1250 and the 1300s, respectively (UNIMUS; Molaug, Pers.com.). KM/UIO provided the three sampled objects, of which only one gave sufficient DNA.

The 34 CPW samples with reliable DNA sequences were assigned to four time horizons: horizon 1: 950 − 1000, horizon 2: 1100 − 1175, horizon 3: 1175 − 1230/40 and horizon 4: 1230/40 − 1280 (see Table 1 and Table 4). Observe that no samples date to the period between 1000 and 1100.

2.2. Contexts and dates for the reference populations (REFs)

The material used as references for provenancing the CPW material were medieval reindeer from hunting sites at the Dovrefjell, Reinheimen and Hardangervidda mountain areas as well as medieval reindeer from Finnmark (Fig. 1). The reference material comprises 210 sequences. In addition, nucleotide BLAST searches (https://blast.ncbi.nlm.nih.gov) were performed on the sequences to look for identical haplotypes elsewhere.

Table 1
Antler from comb production workshops (CPWs), archaeological data. References for context and date information: (A) UNIMUS; Komber et al., 1994; Hansen, 2005, 2015), (B) Flodin, 1989; Christophersen and Nordeide, 1994), Pers. com. Ian Reed), (C) Pers. com. Petter Molaug, (D) Myrvoll, 1992. Horizon 1: 950 − 1000, horizon 2: 1100 − 1175, horizon 3: 1175 − 1230/40 and horizon 4: 1230/40 − 1280.

Lab code	Collection	Museum no.	Town/Site[References (A − D)]	Date [(Horizon 1–4)]	Genbank no.
B-1773	UM/UIB	BRM76/21471	Bergen/Rosenkrantzgate 4[A]	1200–1248 [(4)]	MK614260
B-1774	UM/UIB	BRM0/55912	Bergen/Bryggen[A]	1170–1198 [(3)]	MK614261
B-1776	UM/UIB	BRM76/21550	Bergen/Rosenkrantzgate 4[A]	1200–1248 [(4)]	MK614262
B-1777	UM/UIB	BRM245/2460	Bergen/Domkirkegaten 6[A]	1160/70–1230/40 [(3)]	MK614263
B-1779	UM/UIB	BRM245/2468	Bergen/Domkirkegaten 6[A]	1230/40–1280 [(4)]	MK614264
B-1780	UM/UIB	BRM245/4005	Bergen/Domkirkegaten 6[A]	1230/40–1280 [(4)]	MK614265
B-1781	UM/UIB	BRM0/44816	Bergen/Bryggen[A]	1170–1198 [(3)]	MK614266
B-1783	UM/UIB	BRM0/44010	Bergen/Bryggen[A]	1170–1198 [(3)]	MK614267
B-577 A	UM/UIB	BRM0/81304 J.S.-540	Bergen/Bryggen[A]	1170–1198 [(3)]	MK614268
B-579 B	UM/UIB	BRM0/80868/01 J.S.-540	Bergen/Bryggen[A]	1120s − 1170 [(2)]	MK614269
B-582 D	UM/UIB	BRM0/80846/01 J.S.-540	Bergen/Bryggen[A]	1120s − 1170 [(2)]	MK614270
B-584 A	UM/UIB	BRM0/80860/01 J.S.-540	Bergen/Bryggen[A]	1120s − 1198 [(3)]	MK614271
T-2333	NTNU/UM	N78211	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614272
T-2336	NTNU/UM	N78211	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614273
T-2337	NTNU/UM	N77790	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614274
T-2338	NTNU/UM	N78042	Trondheim/Folkebibliotekstomten[B]	1150–1175 [(2)]	MK614275
T-2339	NTNU/UM	N77598	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614276
T-2340	NTNU/UM	N77598	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614277
T-2341	NTNU/UM	N77598	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614278
T-2342	NTNU/UM	N77598	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614279
T-2343	NTNU/UM	N77598	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614280
T-2344	NTNU/UM	N77598	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614281
T-2346	NTNU/UM	N77599	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614282
T-2387	NTNU/UM	N77599	Trondheim/Folkebibliotekstomten[B]	1175–1225 [(3)]	MK614283
T-2390	NTNU/UM	N78041	Trondheim/Folkebibliotekstomten[B]	1150–1175 [(2)]	MK614284
S-2459	UM/UIO	C35300 S2/3868/1	Skien/Handelstorget[D]	950–1000 [(1)]	MK614286
S-2461	UM/UIO	C35300 S2/3306/1	Skien/Handelstorget[D]	1170–1230 [(3)]	MK614287
S-2462	UM/UIO	C35300 S2/3293/1	Skien/Handelstorget[D]	1170–1230 [(3)]	MK614288
S-2463	UM/UIO	C35300 S2/3214/2	Skien/Handelstorget[D]	1100–1170 [(2)]	MK614292
S-2464	UM/UIO	C35300 S2/3209/2	Skien/Handelstorget[D]	1100–1170 [(2)]	MK614289
S-2465	UM/UIO	C35300 S2/3209/1	Skien/Handelstorget[D]	1100–1170 [(2)]	MK614291
S-2468	UM/UIO	C35300 S2/3159/1	Skien/Handelstorget[D]	1170–1230 [(3)]	MK614293
S-2470	UM/UIO	C35300 S2/2977/1	Skien/Handelstorget[D]	1100–1170 [(2)]	MK614290
O-2458	UM/UIO	C35990 G42403	Oslo/Nordre felt II[C]	1200–1230 [(3)]	MK614285

Dovrefjell is a mountain region located > 100 km north-east of the Hardangervidda plateau and covers an area of about 7500 km^2. Numerous reindeer pitfall hunting systems used from the Stone Age and up into historic times suggest the presence of important reindeer migration routes within and between mountain habitats that are now isolated due to infrastructure development (Jordhøy et al., 2005; Skogland and Mølmen, 1980). The genetic profiles representing the ancient populations are 24 sequences derived from the Vesle Hjerkinn site at Dovrefjell (Fig. 1) obtained from Røed et al. (2014). Vesle Hjerkinn is characterized as a mountain lodge and hunting site, with refuse heaps containing large amounts of reindeer bones (Mikkelsen, 1994; Weber, 2007). Radiocarbon dating of three samples revealed use of this site sometime between 1045 − 1195 CE (Røed et al., 2014).

Reinheimen is a mountain area covering approximately 5000 km^2, adjacent to Dovrefjell (Fig. 1), but well separated from this area by vigorous rivers and deep, forested valleys. The 29 sequences representing the medieval Reinheimen reference reindeer were obtained from Røed et al. (2014) from the hunting site Verket in Slådalen in Reinheimen (Fig. 1), where a large reindeer funnel-trapping system was recently discovered, and where a test excavation revealed midden deposits covered by a thin sod under which reindeer bones were found (Einbu, 2005). Three samples were radiocarbon-dated to between 1015 and 1285 CE (Røed et al., 2014).

Hardangervidda is a mountain plateau, which is part of the Langfjella mountain region covering approximately 17,000 km^2. The mitochondrial DNA (mtDNA) profiles of 51 samples representing the medieval Hardangervidda populations were obtained from Røed et al. (2011). This material derives from a prehistoric and medieval hunting station at Sumtangen at Hardangervidda (Fig. 1), with large refuse heaps containing reindeer bones, suggesting ancient mass-trapping of reindeer (Hufthammer et al., 2011). Previous radiocarbon dating of fifteen reindeer samples from this site revealed that all were from a relatively short time span between 1240–1290 CE (Indrelid and Hufthammer, 2011).

The Finnmark reference material was obtained from Røed et al. (2018) and consists of 106 sequences from six medieval sites in the eastern part of Finnmark. The sites Brodtkorbneset, Steintjørna and Kjerringneset are situated in the interior boreal forest zone in the Pasvik river valley. The first two are dated to between 1050 and 1300 CE, while Kjerringneset is slightly younger (between 1300 and 1500 CE). The archaeological material from these three sites indicate an economy based on hunting and fishing, possibly in combination with small-scale reindeer and sheep husbandry (Halinen et al., 2013; Hedman et al., 2015). The site Gollevárri (dated between 1200 and 1600 CE) is interpreted as a hunting site located on the isthmus ridge between the Tana River and Varanger Fjord, with a nearby large trapping system for wild reindeer (Hansen and Olsen, 2014; Munch and Munch, 1998). While all the previous sites represent seasonal Sámi settlements, the samples from the sites Kongshavn and Skonsvika (both dated between 1200–1450 CE) on the northern coast, originate from more ethnically heterogeneous and sedentary sites involving the presence of representatives of distant Norse and Russian powers as well as native middlemen (Olsen et al., 2011).

2.3. Laboratory protocols

DNA from powdered antler, bones, or teeth were isolated using DNeasy Blood & Tissue kit (Qiagen) following Bjørnstad and Røed (2010). To ensure authenticity and minimize the risk of contamination, standard precautions for working with ancient samples were

undertaken (see Hofreiter et al., 2001; Wandeler et al., 2007). All equipment and working surfaces were cleaned using sodium hypochlorite, ethanol or UV-light. Drilling of antler/tooth/bone powder, DNA isolation and polymerase chain reaction (PCR) set-up was carried out in spatially separate lab facilities. Lab coats and breathing masks were used, and gloves and drill bits were changed for each sample. Samples were mechanically cleaned and the outer surface was removed before drilling out the powder. To test for contamination, blank extraction and PCR controls were used in each PCR reaction, and only DNA sequences that could be replicated from at least two independent amplifications of each primer pair were accepted. Some samples were extracted twice for authentication.

From the ancient material a 266 base pair (bp) fragment of the mitochondrial CR was amplified using either the primer pair 259F/524R (5′–TGCCCCATGCTTATAAGCAAG–3′/5′–GTGAGATGGCCCTGAAGAAA–′3), or by amplifying two overlapping amplicons of respectively 140 bp with primers 259F and 398R (5′-CCTTTCTTGTCAACATGCGTA – 3′) and 178 bp with primers 347 F (5′–TGCCCCATGCTTATAAGCAAG–3′) and 524R. PCR amplification and sequencing were performed as in Bjørnstad and Røed (2010).

All sequences reported in this study have been deposited in GenBank (Table 1).

2.4. Data analyses

After removing primer sequences, sequence lengths were trimmed and adjusted to 190 bp according to previously published reference sequences in Røed et al. (2011, 2014, 2018). To determine the potential of aDNA for provenancing reindeer antler, genetic variability within the CPW samples as collective units on a town level, and the REF population were analysed. Estimates of number of haplotypes (Nh), haplotype diversity (*Hd*) and nucleotide diversity (π) were all calculated in DnaSP v5 (Librado and Rozas, 2009). Estimates of pairwise genetic differences (F_{ST}) between reference populations and pooled town samples were estimated in Arlequin v3.5 (Excoffier and Lischer, 2010), taking haplotype frequencies as well as nucleotide variation among haplotypes into account. Statistical significance was assessed using 1000 permutations. Phylogenetic structure among reference haplotypes at the population level, including CPW haplotypes not shared with any REF haplotypes, was analysed using a median-joining haplotype network implemented in Network v4.6 (fluxus-engineering.com), depicting the shortest and alternative connections between haplotypes. Samples from the different reference populations were colour-coded. After this, the individual CWP inferences were assessed while adding the temporal dimension.

3. Results from the ancient DNA analyses

3.1. Genetic variability and relationships on a town level

Among 55 CPW samples altogether analysed, reproducible CR sequences were obtained from 34 samples. Nucleotide substitutions defined 14 mtDNA haplotypes, of which seven were singletons, three were detected twice and four were detected more than twice. Table 2 shows that among the REF material the amount of variation, as defined by the number of haplotypes and haplotype diversity, appears to be highest in Finnmark and Dovrefjell and lower in Hardangervidda and Reinheimen. The CPW material from Bergen and Trondheim appears to have a relatively high amount of haplotype diversity (Table 2).

At the population level, there were significant genetic differences among all the four reference populations (Table 3). Population pairwise F_{ST} differences were particularly strong when both the Hardangervidda and the Finnmark samples were compared with the others, while reduced differentiation was the trend between the Dovrefjell and Reinheimen samples. The generally strong differentiation indicates that the analysed mtDNA fragment is highly informative for establishing the provenance of medieval reindeer remains.

Table 2
Levels of genetic variability in 190 bp fragment of the mitochochondrial CR in reindeer antler debris from comb production workshops (CPWs) in medieval Bergen, Trondheim, Skien and Oslo compared with variability in the medieval reference populations (REFs) Dovrefjell, Reinheimen and Hardangervidda in south-central Norway and Finnmark in northern Norway. N = number of individuals, Nh = number of haplotypes, Hd = haplotype diversity, π = nucleotide diversity, SD = ± standard deviation.

Location	N	Nh	Hd (SD)	π (SD)
CPW Bergen	12	6	0.848 (0.074)	0.013 (0.008)
CPW Trondheim	13	8	0.923 (0.050)	0.018 (0.011)
CPW Skien	8	3	0.607 (0.164)	0.004 (0.004)
CPW Oslo	1	1		
REF Dovrefjell[a]	24	10	0.837 (0.051)	0.020 (0.012)
REF Reinheimen[a]	29	6	0.756 (0.053)	0.021 (0.012)
REF Hardangervidda[b]	51	8	0.708 (0.059)	0.009 (0.006)
REF Finnmark[c]	106	32	0.939 (0.011)	0.026 (0.014)

[a] From Røed et al., 2014.
[b] From Røed et al., 2011.
[c] From Røed et al., 2018.

When seen as collective units, the CPW material from both Bergen and Skien are genetically similar to the Hardangervidda reference material and significantly different from the three other reference sites. Similarly, the CPW material obtained in Trondheim assigned clearly to the Dovrefjell reference population and was genetically different from the others.

Thus, these results show that the antler material can be well provenanced based on DNA, when samples from within the different towns/CPW sites are considered as collective units. As such, the genetic results presented strongly indicate that generally the raw material sampled here and used by medieval comb makers in Norwegian towns were harvested from the nearest mountain areas.

3.2. Individual-based relationships on resource procurement during horizons 1 – 4

While collectively, the CPW antler fragments show strong trends, there is more uncertainty attached to provenancing individual antler fragments, because several of the different CR haplotypes are not strictly confined to single mountain areas. The network diagram (Fig. 2) reflects this uncertainty, showing several possible relationships between haplotypes and geography. Individual-based inferences, however, do have the potential to reveal more complex relationships in the distribution networks between outland hunters and town craftspeople. Different frequencies among the wild reindeer populations of these shared haplotypes could indicate a likelihood for the origin of a CPW sample. With these uncertainties in mind, we have thus attempted to infer a *best match* between individual CPW samples and the various mountain areas by comparing the CPW sample's haplotype to its relative occurrence in our available REF populations (i.e. Fig. 2). The chronological distribution of CPW samples varies between the sites (Table 4), but we have nonetheless attempted to look for indications of temporal patterns in the data set.

Chronologically the Bergen samples span horizons 2–4 (Tables 1 and 4). The haplotype sharing of the individual CPW samples to the minimum spanning three (Fig. 2) reveals that also at the individual level most of the samples obtained from Bergen have a best match with the Hardangervidda reference population. Ten of the 12 Bergen samples (B-579B, B-582D, B-1773, B-1774, B-1776, B-1777, B-1779, B-1780, B-1781, B-1783) had haplotypes most commonly seen at Hardangervidda. The remaining samples, both from horizon 3, had a haplotype not detected in Hardangervidda REF. One of these samples (B-577A) had a haplotype that gave a best match to the Reinheimen REF, but which is also known in the Dovrefjell REF. This might indicate that antler from

Table 3
Pairwise genetic differences (F_{ST}) in mitochochondrial CR between samples of antler debris from comb production workshops (CPW) in medieval Bergen, Trondheim and Skien and medieval reference wild reindeer populations (REF) in Dovrefjell, Reinheimen, Hardangervidda and Finnmark.

	CPW Bergen	CPW Trondheim	CPW Skien	REF Dovrefjell	REF Reinheimen	REF Hardangervidda
CPW Bergen						
CPW Trondheim	0.150*					
CPW Skien	0.061^{ns}	0.366***				
REF Dovrefjell	0.180*	0.001 ^{ns}	0.346***			
REF Reinheimen	0.167**	0.104**	0.271***	0.075*		
REF Hardangervidda	0.003^{ns}	0.329***	0.000^{ns}	0.346***	0.297***	
REF Finnmark	0.198***	0.147***	0.256***	0.163***	0.140***	0.270***

*** = $P < 0.001$, ** = $0.001 < P < 0.01$, * = $0.01 < P < 0.05$ and ns = non-significant.

Reinheimen or possibly Dovrefjell found its way to Bergen. The other sample (B-584A) had a new haplotype not present among any reference material (BLAST analyses in GenBank gave no match of this haplotype) and with no clear relationships to any geographic clusters. All in all, the assessment of the individual CPW samples shows that comb makers in Bergen used materials from Hardangervidda, between ca. 1100 and 1280 (horizons 2–4). Between 1175 and 1230/40 (horizon 3), there may also have been input from other populations − Reinheimen or possibly Dovrefjell − as well as from an unidentified source.

The support for assigning the individual 13 CPW samples from Trondheim to discrete mountain areas was variable (Fig. 2). Two samples from Trondheim date to horizon 2, the remaining date to horizon 3 (Tables 1 and 4). Three of the 13 samples point clearly to Dovrefjell, producing haplotypes that are only identified in medieval reindeer from this mountain area (T-2333, T-2337, T-2341). Two had haplotypes that are found equally often in Dovrefjell and Finnmark (T-2339, T-2390) and no best fit can be determined. Three samples had haplotypes that were most common among the medieval reindeer of Hardangervidda; one of which was also present in Reinheimen (T-

Table 4
The number of CPW samples (n = 34) with amplified DNA by horizon in each town.

Town	Horizon 1 950 – 1000	Horizon 2 1100 – 1175	Horizon 3 1175 – 1230/40	Horizon 4 1230/40 – 1280
Bergen		2	6	4
Trondheim		2	11	
Skien	1	4	3	
Oslo			1	

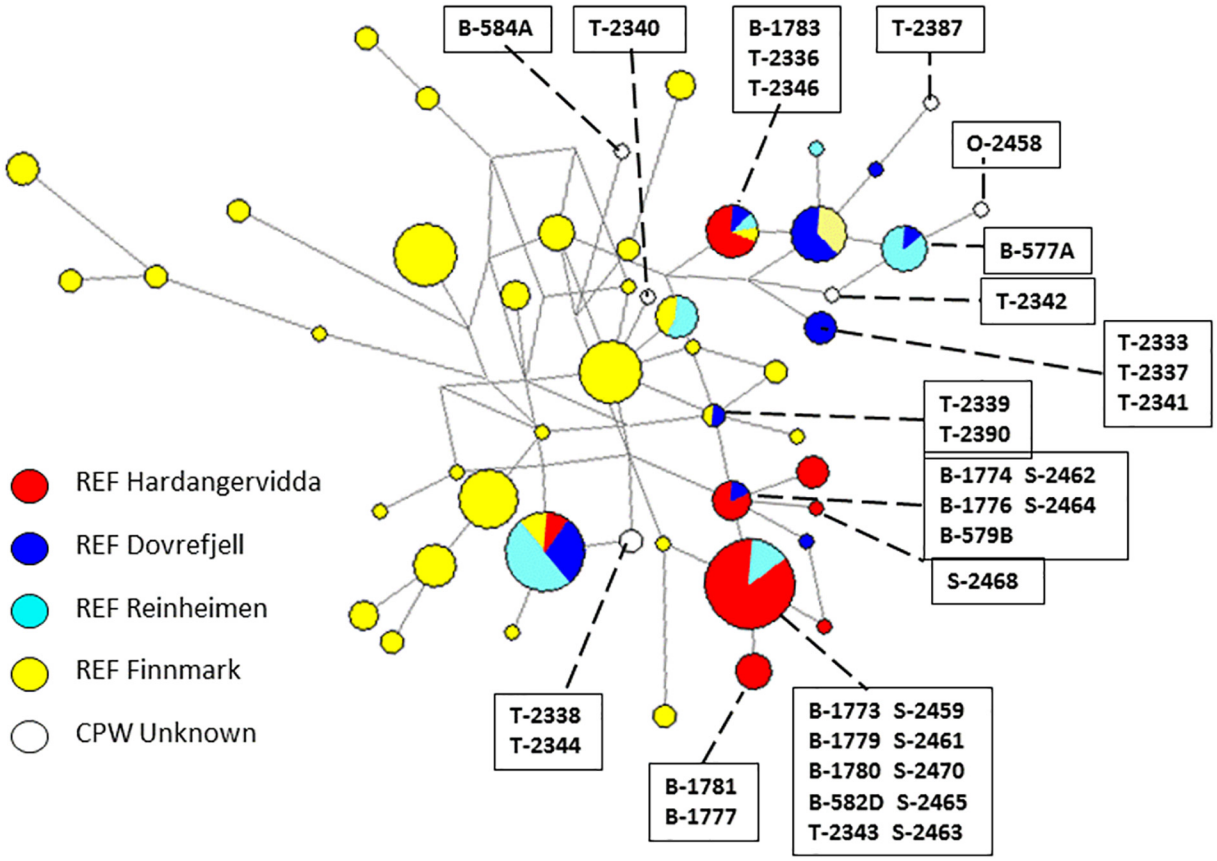

Fig. 2. Median-joining network that shows the potential genetic relationships (solid lines) between mitochondrial CR haplotypes (colour-coded circles) obtained from the medieval reference populations. Circle sizes reflect the number of REF samples with the respective haplotypes. Branch lengths of the solid lines reflect the genetic distance in the relationships. Text boxes show the 14 different haplotypes that were found among the individual CPW samples (B = Bergen, T = Trondheim, S = Skien, O = Oslo, see Table 1) and where they fit in this relationship. CPW haplotypes that were not found among the reference material are shown by white circles.

2343), and two in both Reinheimen, Dovrefjell and Finnmark (T-2336, T-2346), making separation between these source populations more uncertain. Nevertheless, following a best match principle, the three samples open up the way for the possibility of deliveries from Hardangervidda to Trondheim. Five of the samples display haplotypes not present among the REF material. Two of these (T-2342, T-2387) are, in the network (Fig. 2), located close to central haplotypes characteristic of the Dovrefjell and Reinheimen areas (haplotype cluster III, Røed et al., 2008, 2014). Support for such an origin is given by BLAST analyses that revealed identical haplotypes in older reindeer samples, which had emerged from melting alpine ice patches within the Dovrefjell mountain region (radiocarbon dated to 651–772 CE; Røed et al., 2014). Two of the samples with unrecognized haplotypes (T-2338, T-2344) are located in an undefined region of the network and were not found in GenBank. Thus, their origins are too ambiguous for conclusions in the individual-based analysis. The last sample (T-2340), also without any haplotype sharing and not present in GenBank, appears to have a different origin from the other CPW samples from Trondheim. This sample is closely related to samples from the Finnmark REF (Fig. 2). Apart from Finnmark, the ancient reindeer populations from the areas north of Trondheim are hitherto largely unsampled. The close relation of T-2340 to Finnmark samples may suggest deliverances from potentially unsampled populations of a more northern origin. To sum up, the two samples dating to between 1100 and 1175 (horizon 2) (T-2338 and T-2390) have unidentified or ambiguous origins. The assignment of the 11 individual CPW samples dating to 1175–1230/40 (horizon 3) imply that comb makers in Trondheim used antler from Dovrefjell, with potential input from unsampled populations north of Trondheim, and from Hardangervidda and/or Reinheimen.

Among the samples from Skien, dating to horizons 1–3, all eight (S-2459, S-2461, S-2462, S-2463, S-2464, S-2465, S-2468, S-2470) had haplotypes that had best match with medieval reindeer at Hardangervidda (Fig. 2), and which, to a lesser degree, are represented among the Dovrefjell or Reinheimen populations, respectively. Following the best match, comb makers in Skien seem to have had access to raw materials from the Hardangervidda population between 950 and 1000 and between 1100 and 1230/40 (horizons 1–3).

Uncertain origin characterizes the single CPW sample from Oslo (O-2458) from horizon 3, since the haplotype from this sample was also absent from both reference samples and GenBank. However, as for T-2342 and T-2387, the location of O-2458 in the network diagram (Fig. 2) may indicate this haplotype to be part of the genetic lineage characteristic of ancient reindeer in the Dovrefjell and Reinheimen regions. This may indicate that comb makers in Oslo accessed antler from either of these areas during horizon 3, or perhaps that they used antler material from some unsampled population south-east of Dovrefjell and Reinheimen, but more material is needed to substantiate this.

4. Culture – historical implications and future avenues

Most important, the pilot study shows that aDNA can be used to provenance reindeer antler material to its origin when the contemporary source populations are well analysed. When CPW samples from within our four towns are considered as collective units, there is a high level of certainty that the discerned trends are trustworthy, whereas there is more uncertainty attached to assigning the origin of individual antler fragments. The number of CPW samples that gave reliable DNA sequences in this study is not large enough to warrant representativity for what was used in the towns, especially when considering temporal trends. However, the results are altogether encouraging for future research. Even at this stage, the pilot project's provenancing results offer some immediate culture – historical insights if we accept the provenanced CPW samples as a *proxy* for connections between mountain areas and urban sites in the period between c. 950 CE and c. 1280 CE.

The results indicate that artisans in the towns used antler from the closest mountain areas. From another perspective, one may point out that mountain areas delivered antlers to their closest towns. The analysis of the individual-based relationships on resource procurement adds some possible nuances; during horizon 3, comb makers in Bergen may have accessed raw material from Reinheimen, or possibly Dovrefjell, in addition to the nearest mountain area Hardangervidda. Similarly, artisans in Trondheim may have used raw materials harvested north of Trondheim, and possibly from Hardangervidda and Reinheimen, in addition to the nearest mountain area Dovrefjell. The connections between mountain sites and towns are illustrated in Fig. 3.

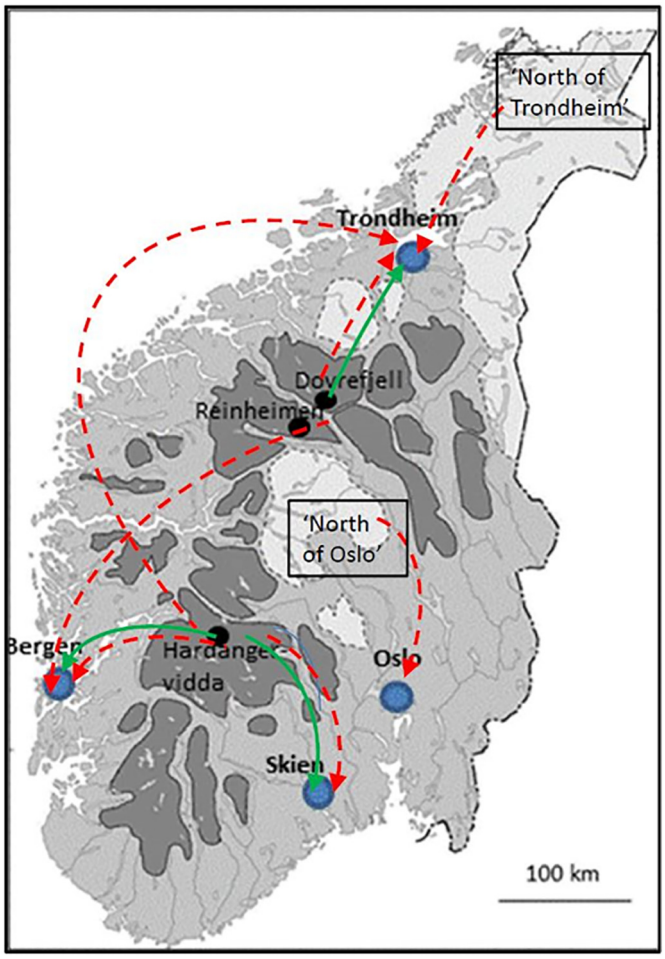

Fig. 3. Links between mountain areas and towns as indicated by the provenancing results. Solid lines represent relationships identified on the collective CPW materials from the towns. Stippled lines show possible relationships based on individual CPW sample assignments.

From a mountain perspective, assigning independently dated urban antler debris to its population of origin adds new dates for what one may characterize as commercial exploitation of reindeer resources in the specific mountain areas. According to the dating of Bergen and Skien CPW, antlers must have been collected in the Hardangervidda mountains as early as the late Viking Age and from the twelfth century throughout the mid-thirteenth century. This is an earlier date for commercial exploitation of antler at Hardangervidda than previously documented (e.g. Hufthammer et al., 2011). The dates of the Trondheim CPW, with assignment to Dovrefjell, show that antlers were retrieved here during the late twelfth and early thirteenth centuries. This is in accordance with previously published dates from this mountain area (e.g. Mikkelsen, 1994). The time depth of the deliverances between for example, Hardangervidda and Skien, indicate long traditions of contact and network connections. The movement of raw materials over vast distances fits well with the otherwise known picture of far-

reaching domestic procurement networks where the towns became increasingly important hubs from the early Middle Ages and through the high Middle Ages (Hansen, 2017; Helle et al., 2006).

It is interesting that our new data sets add empirical substance to the assumptions that antler found in urban contexts derive from the nearest mountain areas, but also that there may be some nuances. The nuances are thought provoking because they tie in well with the fact that none of the mountain areas studied here can be said to lie in the immediate hinterland of our four towns. The distances between the mountains and towns are by all standards great. Antler must have been carried out of the mountain areas on foot and perhaps packhorse (cf. Indrelid and Hufthammer, 2011). A fair assumption is that the materials would be transferred to sea-going boat traffic as soon as possible. Skien, connected by waterways to the Oslofjord/Skagerrak traffic artery, was a central node in medieval procurement networks involving schist hones from the Eidsborg quarries (Myrvoll, 1992). Similar to quarry-products, reindeer antlers were moved through networks with a wide domestic and international reach, and Hardangervidda-antler may well have been distributed along with hones through Skien into networks of wide domestic and international reach. The late fourteenth-century Darss cog found on the Baltic coast by Mecklenburg-Vorpommern contained hones of Norwegian type as well as some reindeer antlers and shows that stone products and reindeer antler did indeed circulate in the same networks during the late Middle Ages (Förster, 2003). Both Trondheim and Bergen were located along the main traffic arteries along the Norwegian west coast. Here, busy north- and south-going boat traffic is documented, not least in connection with the transport of stockfish from northern Norway through to Bergen and further on to European markets (e.g. Helle, 1982, 162). A scenario could be that when antler was transferred to boat traffic, it could be shipped either north or south. The connections between mountain areas and towns, indicated by the nuances in our aDNA provenancing, would fit into such a scenario, but remain to be further substantiated through more comprehensive provenancing efforts.

Stating the obvious, the five centuries of the Middle Ages saw many changes and should be studied with this in mind. It has been suggested that prehistoric reindeer hunters were also comb makers (Christensen, 1986), and an association between antler crafts and hunting grounds is recognized in case studies dealing with different parts of the medieval period (Indrelid and Hufthammer, 2011; Mikkelsen, 1994; Rytter, 2007). As mentioned, the organization of the urban comb-making craft in Norway seems to have gone through changes from the early to the later part of the medieval period; from itinerant to more permanent workshops. One may address to what degree the organization of collecting antler changed through the Middle Ages. As part of such a discussion one must also consider if and how the character of antler as a product changed over the centuries throughout the Middle Ages. When did reindeer antler become a bulk good traded on an anonymous market, as indicated, for example, by the Darss cog (cf. Förster, 2003)? In future research, larger assemblages of CPW materials should be thus provenanced. Through such analyses, a higher resolution of the procurement, production and consumption networks associated with reindeer antler and combs can be obtained, on spatial, temporal, and eventually social and cultural dimensions.

No source category can stand alone and provide a complex picture of medieval domestic procurement networks. This pilot study has shown that studies of aDNA can produce new and high-definition archaeological data for provenancing reindeer antler. Such data has the potential to open to way for a new level of insight into the details of the movement of antler between mountains and workshop sites. In the pursuit of the social dimensions of the reindeer produce networks, the new data sets should be studied on a broad canvas.

Acknowledgements

We thank Ian Reed NIKU Trondheim, Petter Molaug NIKU Oslo, and Anne Karin Hufthammer UIB, for helping out on identifying and dating suitable materials for sampling of workshop debris from Trondheim, Oslo and Bergen. Liv Midthjell at NMBU Oslo is acknowledged for her skillful laboratory analyses. We are grateful to two anonymous reviewers for their valuable comments on an early draft of the manuscript. This work was supported by the Norwegian Environment Agency, the Meltzer foundation (UIB) and *ReiGN* 'Reindeer Husbandry in a Globalizing North – Resilience, Adaptations and Pathways for Actions' (NordForsk-funded 'Nordic Centre of Excellence', project number 76915).

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