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Review

Ancient DNA unravels the truth behind the controversial GUS Greenlandic Norse fur samples: the bison was a horse, and the muskox and bears were goats

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ABSTRACT

The Norse Greenlandic archaeological site known as 'the Farm Beneath the Sand' (GUS) has sourced many well-preserved and unique archaeological artefacts. Some of the most controversial finds are tufts of hair, which previous morphological-based examination concluded derive from bison, black bear, brown bear and muskox, all species whose natural presence in South Greenland is unlikely. If true, the consequences are potentially significant, as they could imply Viking trading with, or hunting within, North America. To validate these previous findings, we genetically profiled the samples, through mitochondrial 16S DNA analysis. The results revealed that the putative bison was, in fact horse, while the bears and muskox were goat. The results demonstrate the importance of using genetic analyses to validate results derived from morphological analyses on hair, in particular where such studies lead to sensational claims.

1. Introduction

The Scandinavian Norse (Viking) culture established settlements in Iceland from ca. 900 CE (Ogilvie et al., 2000), and southern Greenland from the late tenth century to the last decades of the fifteenth century (Arneborg, 2008). Evidence that the Norse ventured further west than this is represented by the North American east coast site of L'Anse aux Meadows, Newfoundland (Wallace, 2000). The extent of Norse interaction and settlement in North America has been heavily debated (Wallace, 2000), as physical evidence relating to the topic is scarce. In this regard, the archaeological excavations of the Norse Greenlandic 'Farm Beneath the Sand' (also known as GUS, from its Danish name, "Gården Under Sandet") have played a role, with regards to the provenance of fur remains at the site that suggested a link between the Norsemen with Native Americans (Location of GUS at Fig. 1). Specifically, based on morphology, it has been argued that the hair remains derived from species that were not native to South Greenland, such as the bison *Bison* ssp., brown bear *Ursus arctos* ssp. and/or black bear *Ursus americanus* ssp. (Rogers, 1998; Arneborg, 2003; Østergård, 2004), and given that no evidence of these species is found in Greenlandic Inuit settlement, Norse-Inuit trade seems unlikely to be the source.

If the original identifications are accurate, given that the pre-Columbian distribution of black bear *U. americanus* ssp. (Garshelis et al., 2008), brown bear (Grizzly) *Ursus arctos horribilis* (McLellan et al., 2008) and bison *Bison bison* ssp. (Gates and Aune, 2008) in the Americas are well documented, and that the genetic distribution of these species is known, thus enabling distinction between American and non-American brown bear and bison [Polziehn et al. (1996), Wilson and Strobeck (1999), Shapiro et al. (2004) and Cronin et al. (2013) for bison; Byun et al. (1997), Van Den Bussche et al. (2009) and Miller et al. (2012) for black bear; Paetkau et al.,

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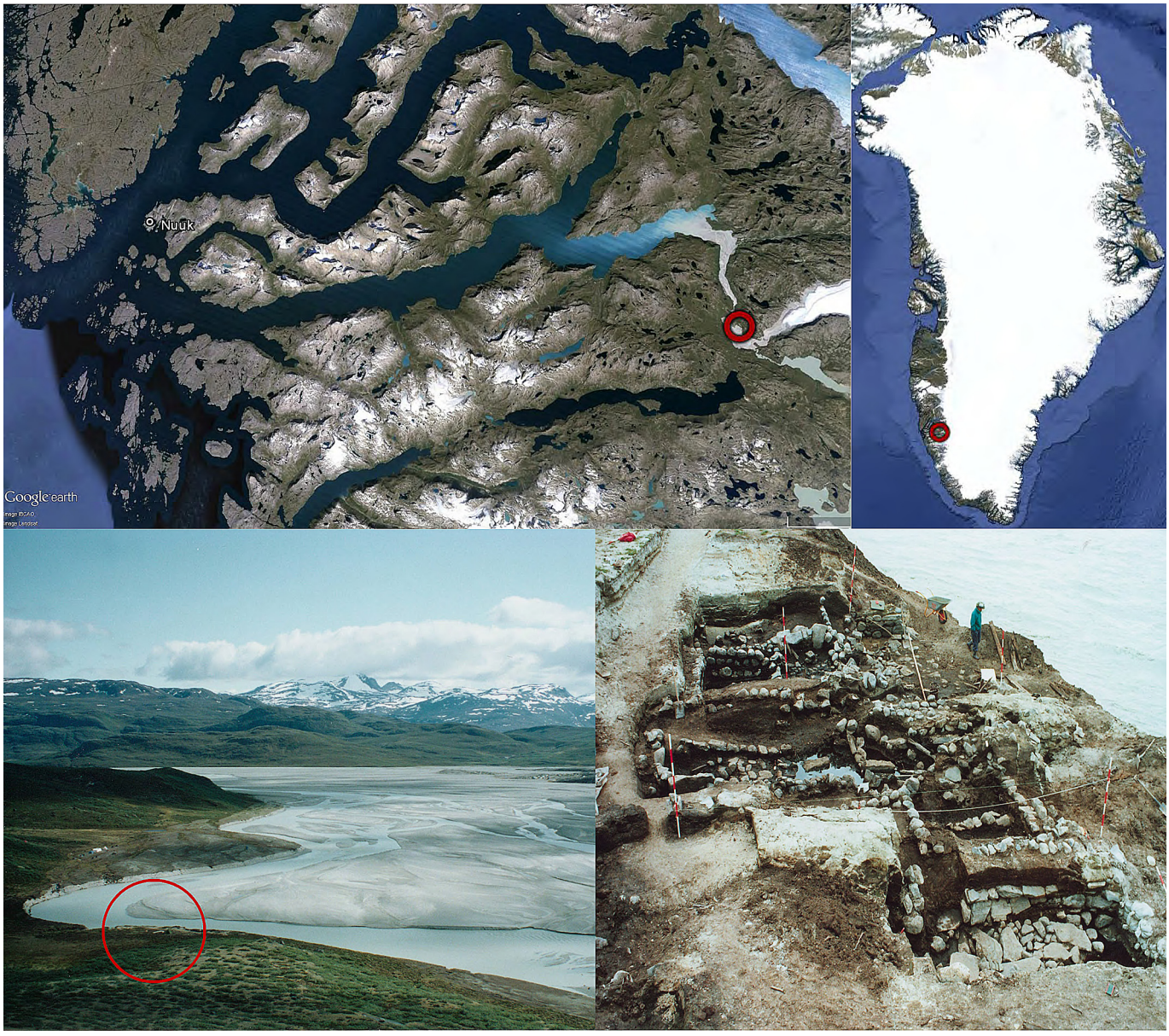

Fig. 1. Location of GUS in Southwest Greenland. The upper charts were sourced from Google Earth. The bottom photos are from Greenland National Museum & Archives.

(1998), Waits et al. (1998) and Miller et al. (2012) for brown bear], then in theory genetic profiling of the fur samples could not only confirm the original species attribution, but also confirm whether or not they represent samples derived from the Americas – if yes, with potentially exciting revelations of Viking trade with, or hunting within, the Americas. Further samples from GUS have been identified as muskox *Ovibos moschatus* (Rogers, 1998; Østergård, 2004), which if true would indicate Norse trading or hunting either north of Melville Bay in Greenland, or in arctic Canada behind Baffin Island, corresponding to the muskox distribution at the time (Gunn and Forchhammer, 2008). As with the other species, sufficient genetic information exists for muskox that the samples should be assignable to either Canada or Northern Greenland (Groves, 1997; Campos et al., 2010). To further explore the provenance of the hair, we therefore genetically profiled them to (a) confirm species assignation, and (b) should the assignations prove to be correct, confirm geographic provenance.

2. Materials and methods

Hair is a keratinous tissue structurally similar to feather, nail and baleen. These tissues have been reported as a potential source of historical or ancient DNA (Ellegren, 1991; Bonnichsen et al., 2001; Gilbert et al., 2004, 2007a; Sinding et al., 2012), with the distinct benefit that the keratin structure appears to protect the endogenous DNA against contamination from exogenous DNA and microorganisms (Gilbert et al., 2006, 2007b). The GUS material is held by the Greenland National Museum & Archives, ID numbers and archaeological details are given in Table 1, photographs in Fig. 2. Given the archaeological value of the samples and the sparse amount of material expendable from them, varying amounts of hair were selected for extraction from each of the objects. Due to the possibility that hairs in one object could represent more than one individual or species, each object [with the exception of KNK 1950x1925 ("brown bear") that had very few hairs remaining] was

Table 1
List of artefacts used in this study, museum accession number, previously published species origin based on morphology, the finding context in GUS, number of DNA extractions made from each artefact, and the amount of hair material used in each extract.

Sample ID.	Putative species	Context	Artefact	Extract	Material	
KNK 1950x633	Bison	a	Braided string	I	1 hair	7 cm
KNK 1950x633	Bison	a	Braided string	II	3 hair	2–5 cm
KNK 1950x633	Bison	a	Braided string	III	10 hair	1 cm
KNK 1950x1925	Brown bear	a	Fur tuft	I	4 hair	3–5 cm
KNK 1950x2519	Brown/black bear	b	Fur tuft	I	7 hair	3–5 cm
KNK 1950x2519	Brown/black bear	b	Fur tuft	II	5 hair	3–5 cm
KNK 1950x479	Muskox	c	Twisted string	I	20–30hair	2–3 mm
KNK 1950x479	Muskox	c	Twisted string	II	10–15hair	2–3 mm

[a] KNK 1950x633 and KNK 1950x1925 were found in room I, also called the weaving workshop because of the finds of several parts of looms and other tools for making textiles. The weaving workshop is dated to between ca. CE 1280 and the latter half of the 1300s.
[b] KNK 1950x2519 was found in room III, believed to be a combined stable for sheep and goats and a byre for cattle dating to between ca. CE 1250 and the latter half of the 1300s.
[c] KNK 1950x479 was found below the last floor in room VI, and is dated to before ca. CE 1150.

sampled to enable more than one DNA extraction (see Table 1). Sampling was performed so as to have minimal impact on the objects, thus as far as possible, hairs that had naturally fallen from the object or were hanging loose were selected. Loose hairs were closely examined by eye to ensure they we the same type and structure as the entangled ones, checking they are from the specific artefact.

2.1. DNA extraction and purification

All laboratory work prior to PCR amplification of DNA was carried out in a designated clean laboratory, set up specifically for ancient DNA analyses. Negative DNA extraction and PCR controls were incorporated to monitor for contamination. All post-PCR laboratory work on amplified DNA was conducted in a separate laboratory facility. Prior to DNA extraction, the hair was washed in a 10% dilution of commercial bleach solution (final NaClO concentration ca. 0.5%) and then rinsed in molecular grade water. Hairs over 2 cm were then cut in to 1 cm fragments and all samples were then placed in a sterile 1.5 ml tube. The samples were then immersed in 1.0 ml of a buffer containing 10 mM Tris, 10 mM NaCl, 5 mM $CaCl_2$, 2.5 mM EDTA, 2% SDS, 1 mM DTT and 100 μg proteinase K. For every three samples, we included one blank extraction containing molecular biology grade ddH_2O to monitor for contamination. This was then incubated with agitation for 24 h at 55 °C. The samples were then centrifuged for 5 min at maximum speed to pellet any remaining solid and the supernatant was transferred into a 15 ml Centricon micro-concentrator (30kD filter). Once the solution had concentrated down to approximately 100 μl above the filter, this was pipetted into a Qiagen (Valencia, CA) 'Qiaquick' spin column, 500 μl of Qiagen PN buffer was added and mixed before being spun at

Fig. 2. The artefacts sampled in this study, with a 1 cm scale: (**a**) a braided string tied to a piece of reindeer antler KNK 1950x633, (**b**) a fur tuft KNK 1950x1925, (**c**) a fur tuft KNK 1950x2519, (**d**) a twisted string KNK 1950x479.

6000 g for 1 min. The column was subsequently washed with Qiagen PE buffer, and the purified genomic DNA was eluted in 50 μl of Qiagen EB buffer.

2.2. PCR

To check the DNA quality within extractions, and to verify the species origin of the samples, we initially attempted to PCR amplify a short region of the mammalian mitochondrial 16S region (16S) using previously published primers (16Smam3: 5-TGGGGTGACCTCGGAGAAY-3; 16Smam4: 5- TCAACGGAMC AAGTTACCCTA-3; Haile et al., 2009), that resulting in a ca. 120 base pair (bp) amplicon that has species diagnostic capabilities for mammals. Museum material can be extremely exposed to contamination (Cooper, 1994; Morin et al., 2005), and given that these objects have been handled with human hands, they were especially sensitive to human contamination. In this regard, primer sets 16Smam3 and 16Smam4 are beneficial, having been designed to exclude amplification of primate DNA (Haile et al., 2009). Given they were initially designed to PCR amplify mammoth, we successfully verified their ability to bind to other mammalian species, using an alignment that contained bison *B. bison* ssp. and *Bison bonasus* ssp., bear *U. arctos* ssp., *U. americanus* ssp. and *Ursus maritimus*, muskox *O. moschatus*, moos *Alces alces* ssp., reindeer *Rangifer tarandus* ssp., cow *Bos primigenius taurus*, horse *Equus ferus caballus*, sheep *Ovis aries aries*, goat *Capra aegagrus hircus*, dog *Canis lupus familiaris* and cat *Felis catus* DNA-sequences. Each 25 μl PCR contained 1 μl of DNA extract, 1x PCR buffer, 2.5 mM $MgCl_2$, 1 μM of each primer, 0.2 mM mixed dNTPs and 0.2 μl AmpliTaq Gold polymerase (Applied Biosystems, Foster City, CA). PCR amplifications were performed using an MJ Thermocycler with a 1.5 min activation step at 97 °C, followed by 50 cycles of 94 °C for 45s, 57 °C for 45s, 68 °C for 1.5 min, followed by a final extension period of 68 °C for 10 min. For every three samples, we included one blank PCR using molecular biology grade ddH_2O to monitor for contamination. Following visualization on agarose gels, any amplified PCR products were purified using MinElute PCR purification kits (Qiagen). To detect possible amplification of more than one species, these 16S PCR-products were subsequently cloned using the Topo TA system (Invitrogen, Carlsbad, CA), and insert containing colonies (8–10 per amplicon) were PCR amplified following the manufacturers' guidance using vector primers M13F and M13R, then sequenced in one direction using the vector primer M13R and ABI sequencing chemistry by the Macrogen commercial sequencing service (Macrogen, Europe, Amsterdam). DNA sequences were subsequently edited and aligned by eye and checked against reference DNA sequences in NCBI GenBank using the BLAST algorithm implemented in MEGA 5 (Tamura et al., 2011) or Geneious Pro 5.5.7.

Following the initial sequencing results, a further analysis was undertaken of the goat HVI fragment of the mitochondrial control region. A hypervariable region in the Goat HVI, was identified by eye using MEGA 5 (Tamura et al., 2011) from an alignment of 946 GenBank sequences from Naderi et al. (2007), accession numbers gi156970873-gi156971818. To amplify this HVI region we used the previously published primers (CAP_FII: 5- GATCTTCCYCATGCATA-TAAGCA -3; Fernandez et al., 2006; CAP_CR_R_1long: 5- GTGATG-TAGTGGRCGGGATA -3; Schlumbaum et al., 2010), resulting in a 133 base pair (bp) amplicon. Amplification and data treatment were performed as described above with the exceptions of 5 μl of DNA extract and 0.5 μM of each primer in each reaction, under the conditions 4 min activation step at 94 °C, followed by 55 cycles of 94 °C for 30s, 55 °C for 30s, 72 °C for 30s, followed by a final extension period of 72 °C for 10 min.

3. Results

We successfully amplified the ca. 120 bp (species dependant) amplicon of 16S-DNA from each extract (Table 1), although one extraction blank also amplified and was therefore cloned together with the additional amplifications. Following Sanger sequencing of 8–10 clone colonies per extract, 100% species and sequence match were obtained within all cloned sequences, from all extracts, from each individual GUS object. A consensus alignment for each sample is presented in Fig. 3, together with a sequence of species they were previously published as and a GenBank sequence, that BLAST search affiliate the consensus sequences with 100%. The 16S sequences clearly revealed sample KNK 1950x633 (previously bison) to be horse *E. ferus caballus* and KNK 1950x1925 (previously brown bear), KNK 1950x2519 (previously brown/black bear) and KNK 1950x479 (previously muskox) as goat *C. aegagrus hircus*. 75% of the cloned sequences from the amplified extraction blank were pig *Sus scrofa* ssp., with the remaining 25% indeterminate. The goat HVI mitochondrial control region fragment was successfully amplified from KNK 1950x1925, KNK 1950x2519 and KNK 1950x479, with the resulting sequences exhibiting 100% agreement between forward and reverse reads, and between PCR replicates. No DNA was amplified from the negative controls, indicating that there was no contamination during PCR set up. Fig. 4 contains an alignment of the consensus of the HVI sequences against a reference position 15965–16054 of the goat mitochondrial genome (Hassanin et al., 2010). KNK 1950x1925, KNK 1950x2519 and KNK 1950x479 feature different genetic variation in the sequences indicating three different individual as sources of the hair in the three objects. The sequences generated in this study are available in Appendix 1 as supplementary material.

4. Discussion

Although the cold and dry Arctic environment is optimal for long-term preservation of the DNA in keratinous tissue (Gilbert et al., 2004, 2007a), given the small amounts of hair that were available for study, and the fact that DNA in hair is generally degraded due to the hair biogenesis process (Linch et al., 2001; Bengtsson et al., 2012) we *a priori* assumed that it would be challenging to recover authentic DNA from the fur objects studied. However, consistency of the sequences obtained between multiple extractions, PCRs and clones per sample, provides compelling evidence that we have identified the correct species of origin for the materials. The finding of horse and goat indicate a farmer existence in the period at GUS and the species are well represented in the sites bone assembly (Enghoff, 2003). The amplification of pig DNA in an extraction blank was unfortunate, contamination is a common risk of aDNA, and in that regard pig is one of the most common contaminants observed in aDNA studies (Leonard et al., 2007; Haile et al., 2009). The pig 16S sequence carries no variation that could give any clues to the pig type or breed sourcing the contamination. Given the importance of the artefacts studied, it is worth considering a few additional points that we believe support the authenticity of the results. Firstly, all laboratory work on putative bison sample KNK 1950x633 (revealed as horse) was performed three months before the remaining samples, in the absence of any observed contaminated blanks. The HVI sequences of the putatively bear and muskox samples KNK 1950x1925, KNK 1950x2519 and KNK 1950x479 (revealed as goats) each exhibit sample specific genetic variation, thus underscore their authenticity, since the chance of contamination from three different goats during a single analysis seems unrealistic. In this regard, even though only sparsely informative, the 90 bp HVI sequences from KNK 1950x1925, KNK 1950x2519 and KNK 1950x479, enable approximate placement of

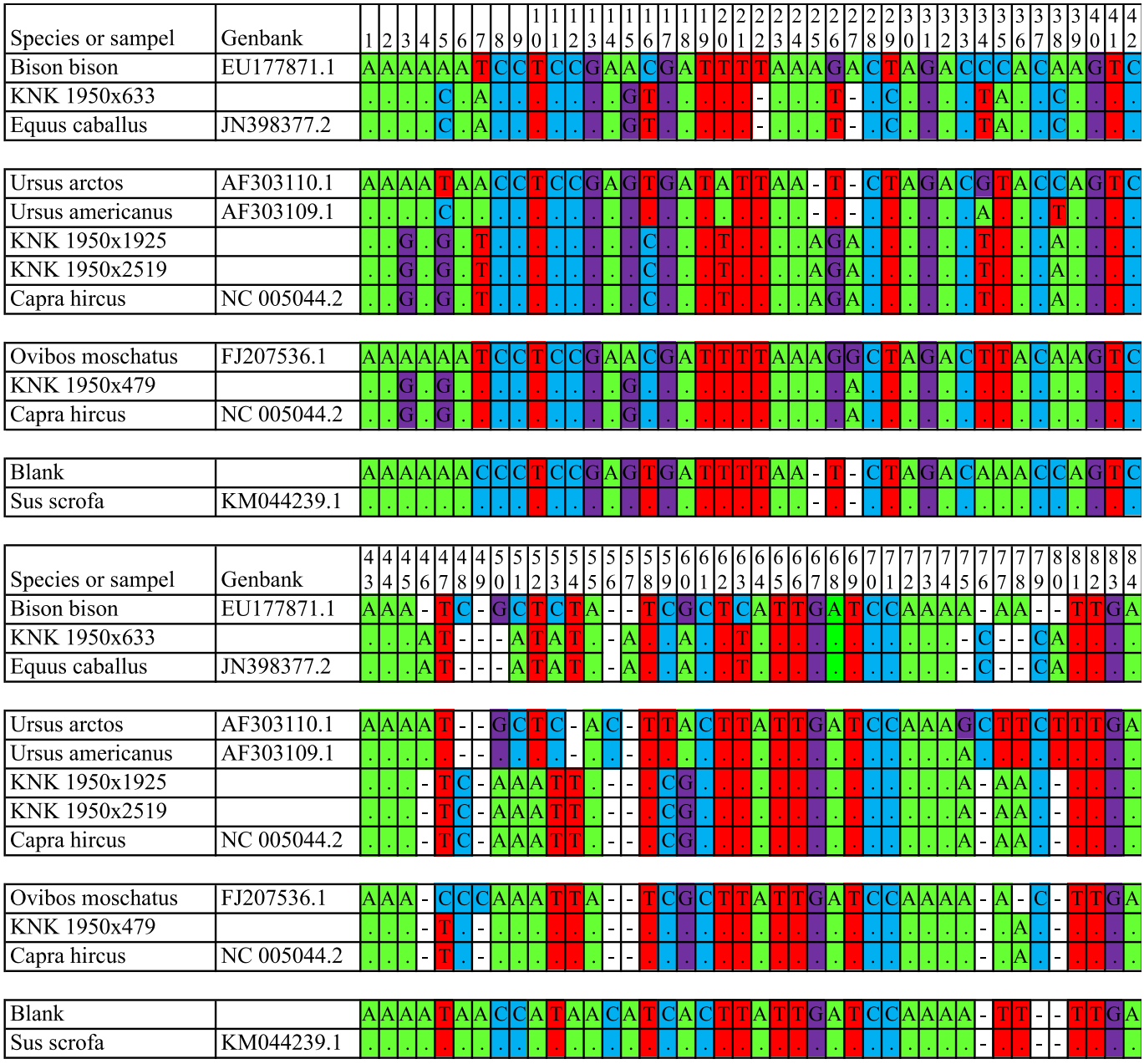

Fig. 3. An alignment of the 16S amplicon from samples against, GenBank sequences of previously believed source species and the sequences of top blast hits authenticating the true species.

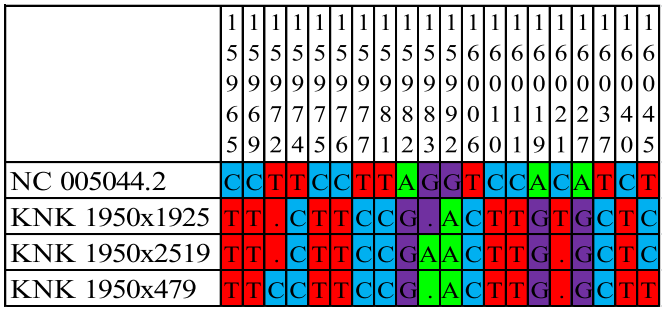

Fig. 4. An alignment of the goat HVI amplicons found in this study against a GenBank sequences.

the sequences into the context of mitochondrial haplogroups in modern goat breeds. Specifically, BLAST analysis against GenBank indicates the sequences map with 100% identity with haplotypes in the haplogroup generally referred to as A (see Naderi et al., 2007 for a haplogroup overview).

Comparing the success rate of DNA amplification between samples of different extracts showed little evidence of an effect due to the amounts of hair of the sample in the extracts investigated, thereby illustrating the potential of genetics in bioarchaeology, as well as the potential of obtaining informative genetic information from minimal and non-destructive sampling of high value archaeological objects (most of the extracted material was taken from hairs already shed from the artefacts). Another obvious point

is the improved power of genetics over morphological analyses in accurate species identification of hair samples. Unfortunately, the specific criteria that were originally used in the morphological analysis of the samples are unknown, as the original analyst is deceased.

5. Conclusions

Although the initial intention of this study was an attempt to obtain a phylogeographic based connection between the putatively exotic and controversial animal-derived materials found in the Norse Greenlandic GUS, this intention became irrelevant once preliminary screening results identified that sample KNK 1950x633 (previously bison) was horse, and samples KNK 1950x1925 (previously brown bear), KNK 1950x2519 (previously brown/black bear) and KNK 1950x479 (previously muskox) were derived from three distinct goats. We advocate the importance for future studies to use genetic analyses to validate results derived from hair morphological analyses, in particular when the conclusions drawn are controversial or high profile. A future study of interest might be to genetically test the remaining hair samples excavated at GUS, currently labelled as less sensational animals – it may be that the bison, the bear and the muskox remain hidden as goat and horse.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jas.2014.10.028.

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