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Revisiting the Kalahari debate in the highlands: ancient DNA provides new faunal identifications at Sehonghong, Lesotho

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ABSTRACT

Large numbers of domestic stock have been reported among the faunal remains recovered from archaeological sites with predominantly forager-associated material culture in the highlands of Lesotho. These remains, in conjunction with the presence of artefacts of apparent agropastoralist origin, have led to the suggestion that either a process of neolithisation saw the adoption of livestock-keeping by traditionally foraging peoples, or that extensive contact and trade occurred between foraging groups in the mountains and distant agropastoralist communities. We present here ancient DNA evidence that the frequency of domestic stock in the faunal assemblages has been significantly overestimated and that, as a consequence, the nature of the relationships between highland foragers and agropastoralists has been misconstrued.

ABSTRAIT

De fortes proportions de bétail domestique ont été signalées dans les restes fauniques de sites archéologiques dans les hautes terres du Lesotho dont la culture matérielle indique plutôt des associations avec des groupes de chasseurs-cueilleurs. Ces restes, et la présence d'artefacts provenant apparemment de groupes d'agro-pasteurs, ont conduit à la proposition qu'un processus de néolithisation vit des groupes traditionnellement chasseurs-cueilleurs adopter l'élevage de bétail, ou alors que des contacts et échanges substantiels existaient entre les groupes chasseurs-cueilleurs dans les montagnes et les communautés d'agropasteurs éloignées. Ici, nous présentons des résultats d'ADN ancien qui montrent que la fréquence du bétail domestique dans les assemblages fauniques a été considérablement surestimée et que, par conséquent, le caractère des liens entre chasseurs-cueilleurs des hautes terres et agropasteurs a été mal interprété.

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Introduction

Southern Africa has been pivotal in anthropological attempts to understand prehistoric and historic relationships between foraging and food producing peoples. Debate has

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centred around two major issues: the processes by which animal husbandry was adopted by formerly foraging peoples and the nature of the interactions between food-producing and foraging groups occupying the same landscape. Labelled the Kalahari debate because its early incarnation centred specifically on the Bushmen of the Kalahari Desert and their relationships with neighbouring herding and agropastoralist groups (Marshall 1976; Lee 1979; Wilmsen 1989a; Wilmsen and Denbow 1990; Barnard 1992; Lee and Guenther 1993; Sadr 1997), the conversation soon expanded south to the Western Cape Province of South Africa (Schrire 1992a, 1992b; Whitelaw *et al.* 1992; Yates and Smith 1993) and east to the Maloti-Drakensberg mountains (Hobart 2004; Mitchell *et al.* 2008). It has been argued, particularly in the Kalahari (Yellen and Brooks 1989, 1990) and Western Cape (Sadr 1997) contexts, that there is very little concrete archaeological evidence for extensive contacts between foraging and food producing peoples (but see Denbow and Wilmsen 1986; Wilmsen 1989b).

The degree of interaction between foragers and agropastoralists is especially important because modern foragers are used as analogies for ancient foragers. For example, in the highlands of Lesotho it has been argued that foraging groups successfully adopted live-stock management in the eighth or ninth centuries AD (Hobart 2004; Mitchell *et al.* 2008; Mitchell 2009) and this direct historical approach suggests that foragers in the region are poor models for ancient foraging. In this case, an intimate economic relationship between foragers and agropastoralists is inferred based on the abundance of domestic stock remains at forager sites, particularly at Pitsaneng (Hobart 2004), but also at Likoaeng (Plug *et al.* 2003) and Sehonghong (Mitchell 1996; Plug and Mitchell 2008; Figure 1). It has further been argued that the identified domestic stock remains include those of adult teeth, which suggests that the animals probably arrived at the site alive (Mitchell *et al.* 2008). The alternative requires us to imagine that foragers carried a traded, scavenged or stolen head of a domestic animal a considerable distance, which is not impossible, but seems improbable. We undertook a genetic study of faunal specimens excavated from Sehonghong rock shelter in an attempt to use domestic stock genetics to better understand the degree and geographic patterns of interactions between farmers and foragers.

Methods and materials

Sehonghong is a rock-shelter in the Thaba Tseka District of the highlands of Lesotho with evidence of sporadic occupation over more than 30,000 years (Carter *et al.* 1988). The archaeological bones analysed here were excavated from the Dung Crust (DC) layer which has, until now, been undated but which overlies the Grey White Ash (GWA) and the Grey Ash with Pottery (GAP) strata that date to the mid- and late-Holocene respectively (Carter *et al.* 1988; Mitchell and Vogel 1994; Plug and Mitchell 2008; Figure 2).

We attempted to recover DNA from 19 faunal specimens, all from the DC layer and identified by morphological analysis as *Bos taurus* (N = 9), *Ovis aries* (N = 5) or *Ovis/Capra* (N = 5). The identifications of the bones submitted for DNA testing were based on keys published in the literature and on the skeletons of cattle (*Bos taurus*), eland (*Tragelaphus oryx*), hartebeest (*Alcelaphus buselaphus*), wildebeest (*Connochaetes taurinus* and *C. gnou*), sheep (*Ovis aries*), goat (*Capra hircus*), springbok (*Antidorcas marsupialis*), grey rhebok (*Pelea capreolus*) and the two reedbuck (*Redunca fulvorufula* and *R. arundinum*).

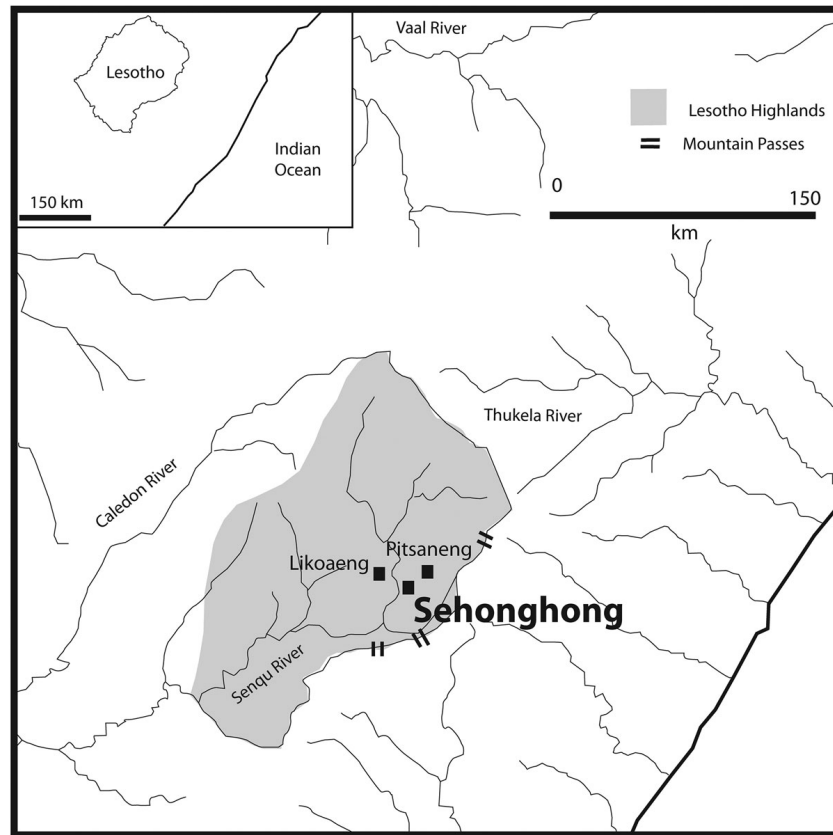


Figure 1. Map of the Maloti-Drakensberg region of southern Africa showing the location of Sehonghong rock shelter, as well as the sites of Likoaeng and Pitsaneng.

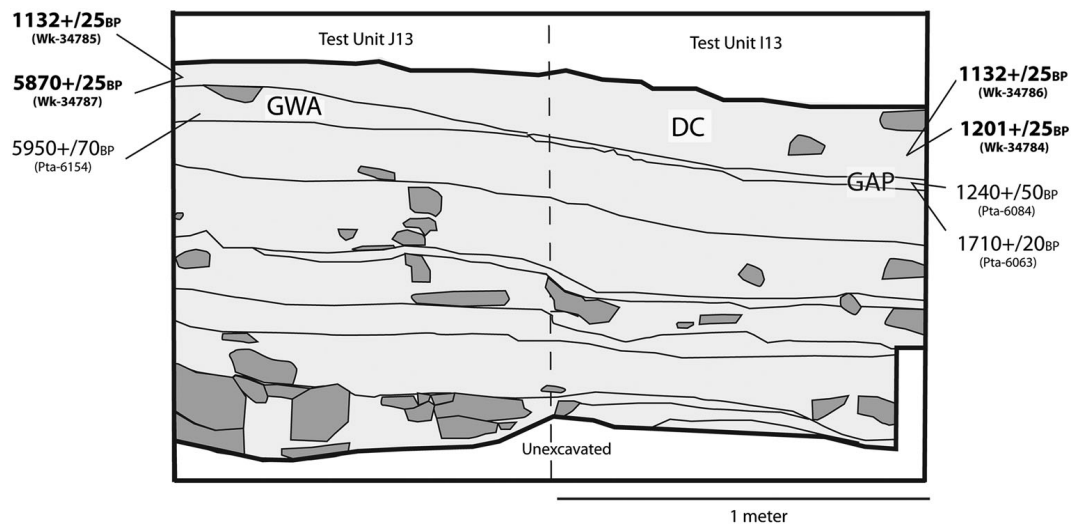


Figure 2. Stratigraphic section of the relevant portion of Sehonghong rock shelter (after Mitchell 1996). Accelerator Mass Spectrometry (AMS) radiocarbon determinations shown on the figure in boldface are those we are newly reporting here, while those in regular type are previously published determinations (Mitchell 1996).

The morphological characteristics of the bones fitted best with those displayed in cattle and sheep/goat' (Ina Plug, pers. comm. July 2015).

DNA extraction, Illumina library preparation and in-solution mitochondrial DNA capture were undertaken in the University of Otago's ancient DNA laboratory as described in Horsburgh and Moreno-Mayar (2015). In brief, DNA was extracted from between 0.38 and 1.67 g of bone or tooth using a silica and guanidium thiocyanate protocol. A negative control was processed alongside every group of no more than five specimens. Barcoded Illumina sequencing libraries were constructed directly from the ancient DNA extracts and the negative controls using custom Illumina shotgun adapters as described by Meyer and Kircher (2010). Nine of the sequencing libraries did not contain enough DNA to allow for immortalisation and were therefore not processed further. Libraries were enriched for the mitochondrial genome following Maricic *et al.* (2010) with the modifications described in Horsburgh and Moreno-Mayar (2015).

Specimens morphologically identified as *Ovis aries* or *Ovis/Capra* were captured using bait manufactured from DNA extracted from a supermarket-bought lamb chop. Likewise, specimens morphologically identified as *Bos taurus* were captured using bait constructed from DNA extracted from supermarket-bought beef. Enriched libraries were pooled in equimolar ratios and sequenced on the Illumina MiSeq platform with 2×75 base paired-end reads. Negative controls were likewise pooled and sequenced on the MiSeq.

We were able to recover enough DNA to diagnose species in ten of the nineteen specimens with confidence. Sequences were processed and species identified employing the same strategies as described in Horsburgh and Moreno-Mayar (2015), with one difference. The organic preservation of the analysed specimens was poor, so none yielded complete coverage of the mitochondrial genome. We therefore extracted each contiguous fragment larger than 150 bp. We approached these contiguous sequence fragments in two ways. First, we compared each fragment with the reference genome of the morphologically identified species and with that of the species to which we assigned the specimen on the basis of the genetic data. Part One of the Supplementary Materials presents these data. Tables S1a-j provide information on each fragment, including the number of mutational differences between the recovered ancient DNA and (i) the morphologically assigned species and (ii) the genetically assigned species. Position numbers refer to those in either the sheep (NC_001941) or cattle (V00654), depending on the species to which the specimen was morphologically assigned. To allow better visualisation of the patterns of genetic diversity among the Sehonghong specimens and the candidate wild and domestic species we calculated phylogenetic trees. To maximise the available phylogenetic signal we concatenated all recovered fragments from each specimen. Phylogenetic trees were calculated using a Jukes-Cantor model of molecular evolution and a neighbour-joining distance algorithm, executed in *Geneious 6.1.8* (Drummond *et al.* 2006). A phylogenetic tree displaying each specimen is presented following the data tables in Part One of the Supplementary Materials (Figures S1a-1j). Mapping statistics are provided in Part Two of the Supplementary Materials. Coverage is generally low, but, as Rasmussen *et al.* (2015) have recently shown, low coverage does not significantly compromise the phylogenetic signal detected. Finally, we compared the cattle specimen with those of modern southern African Nguni cattle (Horsburgh *et al.* 2013).

Results

We were able to recover DNA from ten specimens, including ones morphologically identified as *Ovis aries* (N = 3), *Ovis/Capra* (N = 1) and *Bos taurus* (N = 6). Part Three of the Supplementary Materials provides details of the recovered DNA sequences. In only one specimen (SHH_7358) did the morphological and genetic studies agree on taxon, *Bos taurus*, and we return to this specimen below. DNA sequences from the remaining nine specimens show that none belong to domestic stock species. The five specimens morphologically identified as *Bos taurus* are all eland (*Tragelaphus oryx*), the three specimens identified as *Ovis aries* are grey rhebok (*Pelea capreolus*), mountain reedbuck (*Redunca fulvorufula*) and eland (*Tragelaphus oryx*) and the one specimen from which we could recover DNA that had been morphologically identified as *Ovis/Capra* is from grey rhebok (*Pelea capreolus*). Furthermore, an additional specimen morphologically identified as *Ovis aries*, and from which we were unable to recover DNA (SHH_7459), produced a direct Accelerator Mass Spectrometry (AMS) radiocarbon determination of 4790–4590 cal. BC [Wk-34787, 2013 southern hemisphere calibration curve (Hogg *et al.* 2013)] which is several thousand years before we expect to see domesticated fauna in southern Africa. While we are unable to assign this particular specimen to species as a consequence of its poor organic preservation, we can nonetheless be confident that it is not domestic in origin. Table 1 lists each specimen, its original morphological identification, element, relevant stratigraphic information, its molecular identification and, when available, a direct AMS date.

The single cattle specimen we sequenced was a fragment of a distal metapodial and only 1.8 g in mass. It was completely consumed by the ancient DNA analysis. We were, however, able to obtain an AMS determination of 810–980 cal. AD (Wk-34784) from SHH_7356, a specimen we have identified as eland and which was excavated from the same unit as the cattle specimen (I12–011). Sealy and Yates (1994) have shown that small teeth and bones, or bone fragments, can migrate through sediments, so we must at this stage remain cautious in our interpretation of this associated date.

Next, we looked at how the single example of cattle was related to other known African cattle. The vast majority of African cattle belong to the mitochondrial haplogroup T1 (Cymbron *et al.* 1999; Troy *et al.* 2001; Dadi *et al.* 2009; Horsburgh *et al.* 2013), which is subdivided into six sub-haplogroups defined by mutations across the mitochondrial genome relative to the Bovine Reference Sequence (BRS) GenBank Accession number V00654 (Bonfiglio *et al.* 2012). Membership in the haplogroup T1, and its sub-haplogroups, is defined by mutations at positions 16,050, 16,113 and 16,255. The DNA sequence we recovered from SHH_7358 does not have coverage of positions 16,050 or 16,113. It does, however, have 16,255 and shows the T to C mutation expected of T1 cattle. There is coverage of the mutations defining membership in the sub-haplogroups T1a (2055 +C), T1b (7542), T1c (16,122), T1d (6235), but SHH_7358 shows none of those mutations. Coverage for one of the mutations that defines T1f (16,113) is lacking, but there is coverage of the other (12,492) and this does not show that mutation. The specimen SHH_7358 is therefore not a member of any of the T1 sub-haplogroups a, b, c, d or f. There is no coverage of either of the mutations defining sub-haplogroup T1e (8 and 16,055) so we are unable to determine whether it is a member of T1e or is a basal T1 lineage without downstream mutations.

Table 1. Sehonghong: specimen information including morphological and genetic species identifications and direct AMS radiocarbon determinations and dates calibrated with the 2013 southern hemisphere calibration curve (Hogg *et al.* 2013). Radiocarbon laboratory identifications are as follows: SHH_7355 (Wk-34786), SHH7459 (Wk-34787), SHH_7356 (Wk-34784) and SHH_7449 (Wk-34785).

Specimen	Morphological Species Diagnosis	Molecular Species Diagnosis	Morphological Element	Provenience	AMS Determinations
SHH_7355	<i>Ovis aries</i>	<i>Redunca fulvorufula</i>	Distal metapodial fragment	J12-011	1130 ± 30 bp; cal. AD 940-1017
SHH_7435	<i>Ovis aries</i>	<i>Pelea capreolus</i>	Right lower molar	J13-011	
SHH_7459	<i>Ovis aries</i>	No DNA recovered	Right proximal lateral radial fragment	J12-011	5870 ± 30 bp; cal. BC 4786-4587
SHH_7806	<i>Ovis aries</i>	No DNA recovered	Proximal metacarpal fragment	M13-005	
SHH_7807	<i>Ovis aries</i>	<i>Tragelaphus oryx</i>	Proximal metacarpal fragment	M13-005	
SHH_7246	<i>Ovis/Capra</i>	No DNA recovered	Pelvis ischium/acetabulum fragment	I13-DC	
SHH_7315	<i>Ovis/Capra</i>	No DNA recovered	Pelvis spine fragment	I13-011	
SHH_7319	<i>Ovis/Capra</i>	No DNA recovered	Left mandible diastema	I13-011	
SHH_7785	<i>Ovis/Capra</i>	No DNA recovered	Metacarpal fragment	I12-011	
SHH_7416	<i>Ovis/Capra</i>	<i>Pelea capreolus</i>	Left 2 nd and 3 rd carpals	J12-003	
SHH_7135	<i>Bos taurus</i>	No DNA recovered	Distal 1 st phalanx fragment	H12-DC	
SHH_7227	<i>Bos taurus</i>	No DNA recovered	Proximal 2 nd phalanx fragment	I12-DC	
SHH_7297	<i>Bos taurus</i>	<i>Tragelaphus oryx</i>	Left upper P3	I13-011	
SHH_7230	<i>Bos taurus</i>	<i>Tragelaphus oryx</i>	Distal tibia fragment	I12-DC	
SHH_7356	<i>Bos taurus</i>	<i>Tragelaphus oryx</i>	Distal 1 st phalanx fragment	I12-011	1200 ± 30 bp; cal. AD 814-976
SHH_7357	<i>Bos taurus</i>	<i>Tragelaphus oryx</i>	Complete proximal sesamoid	I12-011	
SHH_7358	<i>Bos taurus</i>	<i>Bos taurus</i>	Distal metapodial fragment	I12-011	
SHH_7449**	<i>Bos taurus</i>	<i>Tragelaphus oryx</i>	Os centroquartale fragment	J12-011	1130 ± 30 bp; cal. AD 940-1017
SHH_7450	<i>Bos taurus</i>	No DNA recovered	Complete proximal sesamoid	J12-011	

There are limited interpretive options given that we have results from a single cattle specimen, but pending results from other cattle from the Maloti-Drakensberg region we can say that SHH_7358 does not closely resemble the currently sampled southern African cattle. African cattle in general (Bonfiglio *et al.* 2012), and southern African cattle in particular, are poorly sampled for mitochondrial DNA variation, however the vast majority of southern Africa cattle for which mitochondrial DNA sequences have been reported are members of sub-haplogroup T1b (Horsburgh *et al.* 2013), a group to which the single specimen we report here does not belong. A single basal T1 individual has been reported from modern specimens in southern Africa (Horsburgh *et al.* 2013) and no T1e individuals have been reported from anywhere in Africa (Bonfiglio *et al.* 2012; Horsburgh *et al.* 2013).

Based on the final sequence alignments to the assigned species we employed *bam-damage* (Malaspinas *et al.* 2014) to investigate if our sequences bear misincorporation patterns characteristic of ancient DNA. We observed an excess of C to T substitutions towards the 5' ends of the reads, which supports the authenticity of the extracted ancient DNA (Briggs *et al.* 2007; Krause *et al.* 2010; Skoglund *et al.* 2014). Damage pattern plots are presented in Part Four of the Supplementary Materials. Note that in some cases the

expected complementary G to A substitutions towards the 3' ends are increased to a lesser extent. This is probably the consequence of reads being shorter than the actual DNA fragments that were built into sequencing libraries. The heavy tail present in read length distributions further supports this scenario. We also observed an overall increased substitution rate, which could be attributed to specificity limitations of our species assignment, which is ultimately determined by the species representation in the nucleotide database.

We also produced sequencing data from seven negative extraction controls, which we analysed with the above mapping pipeline. As expected, these experiments yielded zero mapped reads to any of the three reference mitochondrial genomes. This result, together with the observed misincorporation patterns towards the reads' termini, supports the authenticity of the genetic data produced in this study.

Discussion

Zooarchaeological analyses of remains excavated from archaeological sites in the Maloti-Drakensberg region of southern Africa (Sehonghong, Likoaeng and, in particular, Pitsaneng) have been used to argue for an early and moderately extensive adoption of domestic fauna by foragers in the Lesotho Highlands (Plug *et al.* 2003; Hobart 2004; Mitchell *et al.* 2008; Plug and Mitchell 2008; Mitchell 2009). Including both the specimens we were able to identify by species using their preserved ancient DNA, and the single specimen morphologically identified to *Ovis aries*, but now dated to the fifth millennium BC, we are able to confirm the accurate morphological identification of only 9% (1 out of 11) specimens. Original morphological analyses of the Sehonghong faunal assemblage reported a NISP of 37 cattle, 17 sheep and 40 sheep/goat. We lack further ancient DNA to assess the accuracy of the remaining species assignments, but if the pattern we have detected so far pertains to the rest of the faunal assemblage, we can expect the total NISP for domestic fauna to drop from 94 to approximately eight.

In previous work (Mitchell *et al.* 2008) it has been argued that the element composition in the domesticate assemblage implies that domestic stock reached the Likoaeng site alive. This follows especially from the presence of domesticate teeth since foragers would have had little reason to transport the head of a domestic animal there over a long distance. We are unable, with the data we have, to confirm the presence of cranial elements from domestic stock. The single cattle specimen we have identified from Sehonghong is a fragment of a distal metapodial, which could have been brought to that site while the animal was alive, but equally within a leg or foot transported there after butchery.

The same methods of morphological faunal identification were applied at the forager sites of Likoaeng (Mitchell *et al.* 2008) and Pitsaneng, where a large number of sheep (NISP = 253) and cattle (NISP = 69) were reported (Hobart 2004). If, as seems likely, our results at Sehonghong apply to Pitsaneng we would expect the faunal remains to include no more than a couple of dozen examples of domesticates. We must thus consider the possibility that many fewer domestic animals were present in the Maloti-Drakensberg during the first and second millennia AD than previously thought. We have analysed only specimens that were morphologically identified as deriving from domestic stock. Among these we have found a pattern of systematic

misidentification. While wild specimens are perhaps especially likely to be misidentified as domestic stock, the reverse is also possible and the abundant indigenous faunal remains from Sehonghong could actually include the bones of domestic animals. In the absence of a systematic genetic study of a substantial sample across all morphologically identified taxa we can do no more than speculate.

It is worth noting that this is not the first time that the accuracy of morphological identifications of domestic stock in the southern African archaeological record has been questioned, or has been critical in the evaluation of the nature of interactions between foraging and farming peoples. Throughout the 1970s and 1980s Wilmsen (1978, 1989b) argued that the presence of a maxilla of cattle origin associated with a radiocarbon date of 1150 ± 60 BP (772–1030 cal. AD, Beta-3971) indicated that the residents of /Xai /Xai in northwestern Botswana had engaged in pastoralism before the end of the first millennium AD. Yellen and Brooks (1989, 1990) disputed both the association between the maxilla and the radiocarbon date and the certainty with which it could be assigned to *Bos taurus* in preference to *Syncerus caffer*, the African (or Cape) buffalo. It is in precisely these kinds of disputes that molecular identification of species can prove valuable.

The case for interactions between foraging and agropastoralist peoples in the Maloti-Drakensberg highlands towards the end of the first millennium AD has not rested entirely on the abundance of identified domestic stock. Iron Age ceramics, glass beads and pieces of iron have all been found in archaeological contexts in the mountains. Unlike the previously reported domesticates, however, none of these artefacts are present in large numbers. The majority of the ceramics excavated in the Maloti-Drakensberg seem to indicate forager manufacture, although there are a small number of sherds at Mhlwazini (Mazel 1990), Likoaeng (Mitchell *et al.* 2008), Pitsaneng (Hobart 2004) and Lithakong (Kaplan and Mitchell 2012) of apparent agropastoralist origin. The oldest of these comes from a layer at Likoaeng dating to cal. AD 681–884 (Mitchell 2009) and resembles ceramics found in KwaZulu-Natal of the Msuluzi (cal. AD 650–750) or Ndondonwane (cal. AD 750–950) traditions (Huffman 2007). These sherds are few and it remains unclear whether the ceramics of agropastoralist origin reached the mountains intact or as already broken ceramic fragments (Mitchell 2009).

Glass beads and small fragments of iron are particularly likely to suffer from the same vertical displacement documented among small animal bones (Sealy and Yates 1994). There are, however, two pieces of corroded iron that were recovered from the same layer at Likoaeng that yielded the Msuluzi/Ndondonwane pottery fragment, one of which was directly dated to cal. AD 682–879 cal. AD (1290 ± 30 BP, GrA-26831; Mitchell *et al.* 2008).

The volume of the artefactual evidence is, however, limited and we can now confirm the presence of only one *Bos taurus* individual at Sehonghong. It has been argued elsewhere (Huffman 1998) that the identification of a single specimen of *Bos taurus* in the archaeological record is evidence for the presence of a breeding population of at least 100 head. This seems a reasonable argument when we can be confident that the residents of a site were engaged in the management and breeding of domestic stock. Extrapolation of the argument to sites in the Maloti-Drakensberg at which evidence for contact with food producers is limited and that for kraaling is non-existent does not seem reasonable. If the pattern of systematic over-identification of domesticates at Sehonghong holds for

other sites in the region, then we suggest that foragers in the Maloti-Drakensberg were engaged in unsystematic and sporadic trade with food producing peoples, or occasional stock-theft, rather than in a process of neolithisation as has been described for other regions of southern Africa (Sadr 2003).

Conclusion

The development of accurate and explanatory models for the movement and adoption of domestic stock in prehistory has been greatly improved by technical advances, such as direct AMS determinations on the remains of the stock themselves (Sealy and Yates 1994, 1996). To understand better the relationships between the domestic fauna of the highlands of Lesotho and other prehistoric populations of domestic stock in southern Africa (Horsburgh and Rhines 2010; Horsburgh *et al.* 2013; Orton *et al.* 2013; Horsburgh and Moreno-Mayar 2015) we undertook a genetic study of domestic stock recovered from Sehonghong. We discovered that of the specimens originally identified as sheep, sheep/goat or cattle, the majority (*c.* 90%) did not come from domesticates, but from wild species the fragmentary bones of which had been mistaken for those of domestic stock. Results of ancient DNA analyses here and elsewhere (Orton *et al.* 2013; Horsburgh and Moreno-Mayar 2015) show clearly that the morphological identification of archaeological taxa is challenging and that genetic data can be valuable in resolving ambiguities. These results require that we revisit the importance of domestic fauna in forager sites in the Lesotho highlands and indicate a much lower frequency of domestic stock there than previously thought.

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