



Genetic characterization of an archaeological sheep assemblage from South Africa's Western Cape

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ABSTRACT

The Neolithic Revolution, constituting a shift from food acquisition to food production, came to Africa as it did to most of the rest of the world: through processes of transmission rather than through *de novo* innovation. In contrast with other regions the pastoral management of cattle, sheep and goats was widespread in Africa thousands of years before settled agricultural communities or the use of domesticated plants were in evidence (Neumann, 2005; Marshall and Hildebrand, 2002; Gifford-Gonzalez, 2005). We report here the discovery of haplogroup B in the first genetic analysis of an African archaeological sheep assemblage.

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1. Introduction

African sheep can be described by four morphological types: thin-tailed with hair, thin-tailed with wool, fat-tailed, and fat-rumped (Blench, 1993; Epstein, 1971), of which the hairy, fat-tailed variety are reported at the Cape ethnohistorically (Raven-Hart, 1967; Robertshaw, 1978). North Africa is home to wild Barbary sheep (*Ammotragus lervia*), the remains of which have been found at frequencies of greater than 70% in the Acacus region of south-western Libya (di Lernia, 1998), at Haua Fteah on Libya's northern coast (Klein and Scott, 1986) and at similarly high frequencies at sites near the Algerian coast (Saxon et al., 1974). At Uan Afuda Cave, Libya, there are remains of Barbary sheep as well as thick deposits of sheep dung, suggestive of long-term penning (di Lernia, 1999). Among the dung was found the remains of sheep fodder as well as those of *Echium* spp., which may have been used to sedate animals. The need for a sedative implies the ritual use of non-domesticated animals, a conclusion which is echoed by the nature of the associated rock art (di Lernia, 1999). Additionally, genetic research has shown that North African Barbary sheep have not contributed to the gene pool of modern domesticated sheep (Manwell and Baker,

1975), which lends support to the contention that Barbary sheep were confined in Africa, but not domesticated prehistorically.

The first domestic caprines are found in North Africa after about 7700 years ago (Wendorf et al., 1984) at Nabta Playa (Wendorf and Schild, 1998), the Haua Fteah in Cyrenaica (Klein and Scott, 1986; Gautier, 1981; Higgs, 1967; Shaw, 1977) and the Fayum (Brewer, 1989; Hassan, 1986; Kozłowski and Ginter, 1989). Egypt saw the arrival of screw-horned sheep during the Early Dynastic Period (3100–2613 BCE), and fat-tailed sheep in the Middle Kingdom (1991–1633 BCE, Clutton-Brock, 1993; Ryder, 1983; Zeuner, 1963). Sheep, with cattle and goats, appear in the eastern African archaeological record by about 4500 years before present (b.p., Barthelme, 1985; Marshall, 1994; Phillipson, 1977), and Southern Africa saw the arrival of domesticated sheep by about 2000 b.p. (Henshilwood, 1996; Schweitzer, 1974; Schweitzer and Scott, 1973; Sealy and Yates, 1994; Webley, 2001). Rock art depictions of both fat-tailed and thin-tailed sheep have been reported from Zimbabwe (Goodall, 1946), and of fat-tailed sheep in southern Natal (Vinnicombe, 1976) and at the Cape (Robertshaw, 1978; Jerardino, 1999; Manhire et al., 1986; Manhire et al., 1984).

1.1. The arrival of food production in Southern Africa

The food producing Later Stone Age (LSA) of southwestern Africa began some 2000 years ago with the arrival of sheep

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(Henshilwood, 1996; Schweitzer, 1974; Schweitzer and Scott, 1973; Sealy and Yates, 1994; Webley, 2001; Smith, 1992, 1998a, 2005). It had been thought that sheep and ceramics were contemporary arrivals to the region (Schweitzer, 1974; Inskeep, 1978; Klein, 1986; Schweitzer and Wilson, 1982), but later direct dating of sheep remains has suggested that sheep arrived in the region after the initial appearance of ceramics (Henshilwood, 1996; Sealy and Yates, 1994) implying that sheep remains had descended through strata making them appear the contemporaries of recovered ceramics. While it is worth considering that ceramics are no less likely to migrate down through a site's stratigraphy giving erroneously early dates for their arrival, at Die Kelders 1 (DK1), the large number of ceramic sherds in a level dating to $1,960 \pm 85$ cal. BP makes the chances of vertical migration explaining all the ceramics unlikely. This probability lends credibility to the argument that ceramics did indeed arrive in the Western Cape Province before domestic stock. Of further note is that the earliest ceramics at Die Kelders 1 do not resemble those later in the sequence. They are characterized by thin-walls, and were fired, in contrast with the thick-walled ceramics fired at low temperatures found in higher strata (Schweitzer, 1979).

Interestingly, if the presence of sheep remains is discounted, there is nothing about the nature of the faunal assemblages during and following the introduction of sheep that indicates a change in subsistence. While the non-domestic fauna do not show any indication of a dramatic change in diet, analyses of stable isotopes in human remains do indicate a change in diet. After about 2000 years ago, and thus concomitant with the arrival of sheep, stable isotope data point toward a reduction in marine resources and an increasing reliance on terrestrial game (Sealy and Pfeiffer, 2000; Sealy and Van der Merwe, 1988).

1.2. Sheep domestication

Caprines, members of the subfamily Caprinae, includes both sheep and goats, which, while readily distinguishable from other bovids can be difficult to separate from each other (Gifford-Gonzalez, 2005; Clutton-Brock, 1993). The earliest archaeological evidence for the domestication of sheep comes from southwestern Asia. Eurasia is home to at least five, and perhaps as many as seven, wild species of sheep (Geist, 1990; Lydekker, 1912; Mason, 1996; Shackleton, 1997) which are geographically widely distributed representing many potential ancestral species (Legge and Rowley-Conwy, 1986; Uerpmann, 1987). Most agree that the best candidate species for the ancestor of modern domesticated sheep is the Asiatic mouflon (*Ovis orientalis*, Bruford and Townsend, 2006) in southwestern Asia (Smith, 1998b), although the urial (*Ovis vignei*) and the argali (*Ovis ammon*) which also range the highlands from southwestern to eastern Asia are also possible ancestors (Zeuner, 1963). A reduction in body size is frequently a marker of domestication, and it has been found that despite no change in body size during the preceding Paleolithic, Mesolithic or proto-Neolithic, caprine body size decreased significantly over the period of the aceramic Neolithic of southwestern Asia (Helmer, 1985; Meadow, 1984, 1993).

The first significant study of mitochondrial DNA variation in sheep is a survey of the control region sequence of flocks in New Zealand (Wood and Phua, 1996). The authors defined two major maternal lineages, haplogroups A and B. These two lineages were also reported by Hiendleder et al. (1998a) who conducted whole mitochondrial genome RFLP analyses of *Ovis aries*, *O. ammon*, *O. vignei* and *Ovis musimon*. Further analyses of the New Zealand sheep sample confirmed the presence of haplogroups A and B (Hiendleder et al., 1999). These two haplogroups have been interpreted as descendants of independent domestication events in Asia

and Europe, with their common ancestor dating to 750–375 thousand years ago (kya), and therefore long predating domestication (Hiendleder et al., 1998a, 1999). Similarly, the common ancestor of all domesticated dogs well predates any possible domestication events (Vila et al., 1997). In both cases these results are likely due to two or more independent domestications events of wild populations with deep divergence times, as back crossing of domesticated populations with contemporary wild groups. Analyses of DNA sequence from the mitochondrial genes NADH3, NADH4L, NADH4, and cytochrome *b*, among sheep from Europe, Asia and New Zealand suggested that haplogroup A derives from eastern populations of Asiatic mouflon (*O. orientalis*), and that haplogroup B originates with Asiatic mouflon populations in Turkey and western Iran (Hiendleder et al., 2002).

Haplogroups C, D and E were identified by several studies (Guo et al., 2005; Meadows et al., 2007; Pedrosa et al., 2005; Tapio et al., 2006). Lineages A, B and C all exhibit starburst phylogenies suggesting substantial geographical expansion after domestication. However, it is possible that lineages C and D may have entered the modern domestic sheep gene pool through introgression from wild sheep populations not originally involved in the domestication (Tapio et al., 2006).

2. Methods and materials

2.1. Site and specimens

Die Kelders is a two-cave complex (Die Kelders 1 and 2) located approximately 120 km southeast of Cape Town with deeply stratified deposits featuring high densities of both artifacts and fauna dating to both the Middle and Later Stone Ages (Schweitzer, 1979; Avery et al., 1997; Goldberg, 2000; Klein and Cruz-Urbe, 2000; Klein and Cruz-Urbe, 1996; Wilson, 1996). The twenty-two sheep specimens analyzed here were all excavated from Layer 2 of the Later Stone Age deposits of DK1. Four radiocarbon dates have been reported for Layer 2 giving an uncorrected age of 2720–1365 years before present, however direct radiocarbon determinations on sheep remains have never yielded a date older than 2000 years ago. Six of the specimens were taken from left half-mandibles, and the remaining sixteen were right half-mandibles. The morphology of the mandibles was examined leaving us reasonably confident that a single individual was not analyzed twice.

2.2. DNA analysis

DNA was extracted and analyzed in the dedicated ancient DNA laboratory in the Archaeology Center, Stanford University, using a guanidine thiocyanate and silica protocol modified after Matisoo-Smith et al. (1997). In this, pulverized bone or tooth specimens are digested with EDTA and Proteinase K, followed by binding the DNA to silica particles under the influence of guanidine thiocyanate. The remaining cell contents are then washed away and the DNA eluted from the silica pellet in TE or ultrapure water. Standard precautions were taken to guard against the possibility of contamination by modern DNA or by PCR products. The ancient DNA laboratory is in separate building, and strict entry protocols are maintained such that the ancient DNA laboratory is never entered after entry into the modern DNA laboratory without first showering, washing hair and changing clothes. In practice, this means that on any given day the ancient DNA laboratory is only ever entered before the modern laboratory. Furthermore, no equipment, reagents or samples are taken from the modern into the ancient DNA laboratory. Street clothes and shoes are excluded from the lab, requiring workers to change into dedicated scrubs before entry, as well as into coveralls, hairnets, lab-only shoes, facemasks, and two pairs of gloves.

Each specimen was subjected to DNA extraction at least twice, and each PCR fragment amplified at least twice a minimum of a month apart, and a negative extraction control was run in parallel with every group of five specimens.

PCR primers were designed using the complete *Ovis* mitochondrial genome published by Hiendleder et al. (1998b, AF010406). The primer sequences and their binding sites are listed in Table 1. The differing levels of DNA preservation across specimens permitted different amplicon sizes. The best preserved specimens allowed amplification of 180 bp fragments, in contrast with the less well preserved specimens with amplification restricted to less than 120 bp. Different primer pairs were used to take advantage of the level of DNA preservation in each specimen. PCR amplifications were undertaken in 25 µL volumes in a PTC-200 Peltier ThermoCycler (MJ Research) under the following conditions: 1 × PCR buffer (20 mM Tris–HCl (pH 8.4), 50 mM KCl), 8.3 µM of each primer, 2 mM MgCl₂, 0.25 mM of each dNTP (Invitrogen), and 1 unit of Platinum Taq (Invitrogen), with 4 µL of target. PCR products were visualized on 2% ethidium-bromide stained agarose mini-gels, and purified for sequencing using QIAquick PCR Purification Kits (Qiagen). Both strands of the PCR product were directly sequenced at the Stanford Protein and Nucleic Acid Biotechnology from at least two independent PCR products from each DNA extraction. DNA sequences were aligned, and a neighbor-joining tree calculated using an HKY distance model in the software package Geneious (Drummond et al., 2006).

3. Results and discussion

We recovered 506 bp of control region sequence from 15 of the 22 analyzed specimens in between two and four fragments. We recovered 148 bp of sequence from an additional five specimens (Genbank accession numbers HM236315– HM236334).

All twenty sheep belong to haplogroup B, a widely distributed haplogroup. Sheep carrying haplogroup B appear to have derived from a domestication event independent of those that let to other domesticated sheep. Hiendleder et al. (1998a, 1999) suggest that they were domesticated from the Asiatic mouflon (*O. orientalis*) in Turkey and western Iran (*O. orientalis gmelini*). It is also possible, however, that only the Asiatic mouflon in Iran is ancestral to haplogroup B sheep, and that extant Turkish Asiatic mouflon are descended from feral domesticated sheep (Bruford and Townsend, 2006). Additionally, the European mouflon (*O. musimon*) may have contributed to, or been the main ancestor of modern haplogroup B sheep (Meadows et al., 2005). Work analyzing mitochondrial diversity of African sheep is limited. Bruford et al. (2006) analyzed 40 African sheep, from eastern and southern Africa, and report only the presence of haplogroup A, while Finlay et al. (2007) report in a conference abstract that haplogroup B is “particularly frequent” among Africa sheep, but do not delineate the identities or frequencies of the other haplogroups they found. The DNA

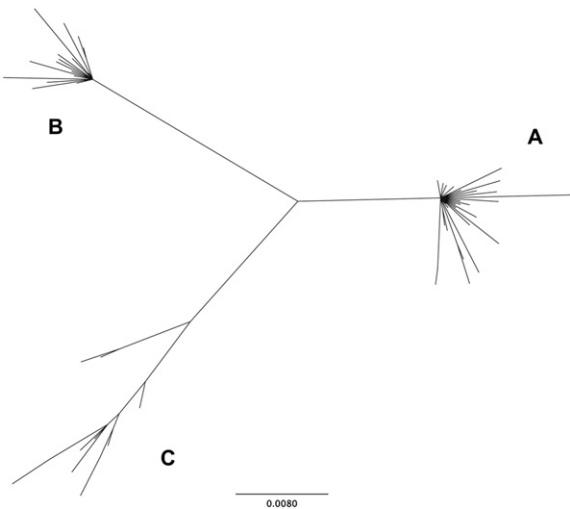


Fig. 1. A neighbor-joining network with an HKY using the sequence data generated here, and those reported by Guo et al. (2005). The sheep analyzed here form part of the starburst expansion of haplogroup B.

sequences from these studies are not yet available, so the data presented here cannot be compared directly. A neighbor-joining network was calculated with an HKY correction in Geneious (Drummond et al., 2006) using the sequence data generated here, and those reported by Guo et al. (2005), and is shown in Fig. 1. The three major haplogroups, A, B and C can be seen, and the sheep analyzed here form part of the starburst expansion of haplogroup B, indicating that they are part of the almost worldwide spread of haplogroup B sheep.

As more studies of the mitochondrial genome of African sheep are conducted we will be able to better describe the lineages of sheep brought onto the continent both as sheep were introduced into regions previously devoid of domestic caprines, and track the interbreeding between indigenous breeds and those brought by Europeans that has resulted in the diversity of modern African sheep.

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Table 1
PCR primers; five digit numbers refer to the nucleotide positions of the binding sites for each primer on the complete *Ovis aries* mitochondrial genome (NC_001941).

Caprine001F_15,522–15,541	ACAACACGGACTTCCCACTC
Caprine002R_15,708–15,689	AGGTAAATCATTTAATGTAC
Caprine003F_15,897–15,916	GACATTATATGTATAAAGTA
Caprine004R_16,129–16,110	AGTGGGCCCGGAGCGAGAAG
Caprine005F_16,070–16,090	ATGCCGCGTGAACCAACAAC
Caprine006R_16,291–16,272	CCAAATGCATGACACACACAG
Caprine007R_16,070–16,050	TGGTGAACAAGCTCGTGATC
Caprine008F_16,025–16,045	AGTCAACATGCGTATCCTGTC
Caprine009R_16,200–16,180	TTTAGATGAGATGGCCCTGA
Caprine010F_16,150–16,172	AATGAACTTTAACAGGCATCTGG

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