## **Genetics and southern African prehistory: an archaeological view**

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**Summary -** Southern African populations speaking languages that are often - but inaccurately - grouped together under the label 'Khoisan' are an important focus of molecular genetic research, not least in tracking the early stages of human genetic diversification. This paper reviews these studies from an archaeological standpoint, concentrating on modern human origins, the introduction of pastoralism to southern Africa and admixture between the region's indigenous foragers and incoming Bantu-speaking farmers. To minimise confusion and facilitate correlation with anthropological, linguistic and archaeological data it emphasises the need to use ethnolinguistic labels accurately and with due regard for the particular histories of individual groups. It also stresses the geographically and culturally biased nature of the genetic studies undertaken to date, which employ data from only a few 'Khoisan' groups. Specific topics for which the combined deployment of genetic and archaeological methods would be particularly useful include the early history of  $Ju \neq Hoan-$ and Tuu-speaking hunter-gatherers, the expansion of Khoe-speaking populations, the chronology of genetic exchange between hunter-gatherers and farmers, and the origins of the Sotho/Tswana- and Nguni-speaking populations that dominate much of southern Africa today.

**Keywords –** Southern Africa, Genetics, 'Khoisan', Archaeology, Hunter-gatherers, Pastoralism, Sotho/ *Tswana*, Nguni.

## Introduction

One of the most exciting developments in anthropology over the last twenty years has been the growth of molecular genetics. From the initially startling, but now generally accepted, claim that humankind has a geologically recent ancestry south of the Sahara to a myriad of applications tracking the movements and relationships of populations, analyses of the human genome have made increasingly frequent contributions to understanding the past. Contemporary southern African populations speaking what are often described as 'Khoisan' languages hold an important position in these developments as numerous studies evidence their retention of mitochondrial (mtDNA) and Y chromosome DNA lineages from the earliest stages of modern humans' genetic diversification. Other research has focused on their relationships with East African populations who also speak languages containing click sounds, one conclusion being the possibility that a relatively recent movement of people from East Africa contributed to the genesis of southern Africa's Khoe-speaking pastoralists. Admixture between 'Khoisan' hunter-gatherers and herders and more recently arrived Bantuspeaking populations has also received attention. Recent publication of the complete genomes of four San individuals from Namibia (Schuster et al., 2010) will undoubtedly encourage research across all these fronts.

In reading – and now writing about – the issues I have just mentioned I am conscious of my own inadequacies on the biological front and make no pretence of being able to evaluate the specific protocols or methodologies employed by geneticists. Summaries of some of the studies considered here are provided from a genetic standpoint by Tishkoff et al. (2007, 2009), Soodyall et al. (2008), and Güldemann & Stoneking (2008). No such survey has, however, yet emerged from an archaeological background. It therefore seems worthwhile to summarise for fellow archaeologists the key findings of recent genetic studies, while simultaneously identifying for workers in genetic history some of the difficulties that their research raises for prehistorians. Such difficulties include lack of clarity as to the source of some of the DNA samples analysed, question marks over how far such samples are representative of all 'Khoisan' populations, the complete omission of archaeological data from some studies (e.g. Wood et al., 2005) and the inappropriate citation by others of non-archaeological sources as authorities on archaeological evidence (e.g. Nurse et al., 1985 in Semino et al., 2002, p.265; Cavalli-Sforza et al., 1994 in Campbell & Tishkoff, 2008, p.407). Recognising that closer collaboration between molecular genetics and archaeology should benefit both disciplines, I also identify several questions of archaeological concern for which molecular genetics may be able to offer help and guidance. Those seeking more detail on the southern African archaeological sequence should consult Mitchell (2002) and the more recent surveys of Huffman (2007; Iron Age farming communities), Barham & Mitchell (2008; hunter-gatherer and earlier hominin research), Lombard et al. (2008; the Middle Stone Age) and Sadr & Fauvelle-Aymar (2008; early herders).

## What's in a name? The diversity of the 'Khoisan'

Thus far I have been careful to place the word 'Khoisan' in quotation marks and there is good reason for this. Invented by Schulze (1926)

as a biological (physical anthropological) label covering all southern Africa's hunter-gatherer and herder communities, it soon came to be employed as a collective term that also reflected shared features of both language and culture (Schapera, 1930). Today, it retains popularity as a general term for groups better differentiated as Bushmen (or San; used here to refer to huntergatherer populations) or Khoe (earlier Khoi and - pejoratively - 'Hottentots') (Barnard, 1992; Mitchell, 2002, pp.7-8). Despite a complete lack of corroborating physical anthropological evidence (Schepartz, 1998; Morris, 2003) or anything other than the most superficial parallels in stone tool industries (Barham & Mitchell, 2008), the term was also extended to East Africa where some populations (the Hadzabe and Sandawe of Tanzania) do indeed speak languages that use click sounds, just like the aboriginal herders and foragers of southern Africa. Assuming that this coincidence reflects a more profound linguistic association and shared ancestry, Greenberg (1963) and Ehret (1998) argued that Hadzane (the language spoken by the Hadzabe), Sandawe and the many 'Khoisan' languages spoken now or in the recent past in South Africa, Lesotho, Namibia, Botswana, Zimbabwe and Angola constitute a single linguistic macro-family comparable to the Kordofanian, Nilo-Saharan and Afroasiatic groupings that are also indigenous to Africa (Blench, 2006). This interpretation continues to be reflected in some recent syntheses in which language serves as a proxy for ethnic affiliation and constitutes a framework against which genetic data are analysed (e.g. Cavalli-Sforza, 2001; Wood et al., 2005; Tishkoff et al., 2009).

There are two problems with this approach. First, as MacEachern (2000) has emphasised in a much more wide-ranging analysis, no one-to-one fixed relationships are likely to exist, or to have existed, between language and ethnicity in Africa or elsewhere. The assumption that they do may be a useful first step, but it needs to be treated with appropriate caution and, wherever possible, questioned and tested against other data for, as Smith (2006) reminds us, many contemporary 'identities' have demonstrably recent origins. Second, and more specifically, 'Khoisan's' own validity as an analytical unit is extremely weak, in part because all but a tiny minority of linguists conclude that Hadzane has *no* demonstrable connection to any other language (Sands, 1998; Güldemann & Vossen, 2000; Blench, 2006; Güldemann & Stoneking, 2008; König, 2008; cf. Ehret, 1998; Honken, 1998).

Within southern Africa the shared presence of clicks may reflect inheritance from some common language(s), but any such derivation lies so far in the past as to be beyond the reach of current linguistic analysis. Instead, three completely isolated families are discernible and no genealogical relationship is demonstrable between them (Güldemann & Stoneking, 2008; König, 2008). These families go by various names. Güldemann & Stoneking (2008) call them Tuu, Ju and Khoe, the usage followed here. Other authors, such as Blench (2006), term them Southern, Northern and Central Khoisan (or Khoesan), while Crawhall (2006a) employs !Ui-Taa, Ju and Khoe, all derived from the word for 'person' in languages of each family. Figure 1 shows the approximate locations of those groups known from the ethnographic and historic records, while Table 1 enumerates the languages belonging to each group. Ju and Tuu speakers are described ethnographically as hunter-gatherers and include the Ju/'hoasi of the Dobe and Nyae-Nyae areas of the northwestern Kalahari Desert immortalised, often under the appellation '!Kung', by Marshall (1976, 1999) and Lee (1979). Khoe-speakers, on the other hand, encompass both herders and hunter-gatherers, the latter including such well-known groups as the G/ wi and G//ana of the central Kalahari (Tanaka, 1980; Silberbauer, 1981), the Nharo, who live further west near Ghanzi (Bleek, 1928; Guenther, 1979) and several now extinct Nama-speaking groups in southern and central Namibia (Barnard, 1992, pp. 218-219). Khoe-speaking pastoralists include the Nama of modern Namibia and South Africa's Namaqualand region, as well as the Cape Khoekhoen encountered by European explorers and settlers after 1488 (Barnard, 1992).

The position within this framework of ≠Hoã (spoken by a small hunter-gatherer population

in eastern Botswana) and Kwadi (extinct and known only from limited field notes but once spoken in southern Angola) has been uncertain (Crawhall, 2006a, p.114). However, Güldemann (2008) presents a strong case for linking Kwadi with Khoe, while ≠Hoã affiliates with Ju into what may more properly be called the Ju-≠Hoã or Ju-≠Hoan family (Güldemann, 2003, 2008). Other languages certainly once existed, among them those spoken by the foraging 'Sonqua' encountered by seventeenth century Dutch explorers in the mountains north of Cape Town and those belonging to the hunter-gatherers who inhabited the eastern third of southern Africa before their assimilation/displacement by Bantuspeaking farmers in the first and second millennia AD. We cannot exclude the possibility that some of these languages differed so much from those surviving today as to have warranted the recognition of yet more language families than the Tuu, Ju and Khoe groupings already identified (Güldemann, 2008, p.100).

A further complication is that some populations who speak, or spoke, languages of the Khoe-Kwadi family differ significantly in their phenotype from other speakers of these languages, as well as from Ju-≠Hoan and Tuu speakers. Typically taller and darker skinned, they comprise at least three groups: the Damara (Dama) of central Namibia, who speak a dialect of Nama; the Kwadi of Angola; and a variety of communities living in southeastern Angola, Namibia's Caprivi region and northern and eastern Botswana. Described under the umbrella terms Kxoe and Tshwa by Vossen (1997) and as Northern and Eastern Khoe Bushmen by Barnard (1992), many of these last communities, like the Kwadi, combine cultivation with herding, hunting and gathering (Barnard, 1992, pp.116-133).

To sum up, the term 'Khoisan' falsely homogenises an enormous degree of linguistic diversity. Nor does it neatly correspond with patterns of phenotypic variation. Moreover, while some Khoe-speakers are recorded ethnographically as pastoralists, in subsistence, cosmology and social organisation others affiliate more closely with Tuu- and Ju-≠Hoan-speaking hunter-gatherers



Fig. 1 - Southern Africa locating populations speaking languages of the Ju-≠Hoan, Khoe-Kwadi and Tuu families. Ju-≠Hoan languages are in bold, Khoe-Kwadi in capitals and Tuu in italics.

(Barnard, 1992). Finally, while one East African click-containing language (Sandawe) may have a genuine genealogical connection to Khoe-Kwadi, the other (Hadzane) does not, and neither physical anthropology nor archaeology countenance grouping East African foragers, past or present, within the same 'Khoisan' entity as Khoe, Ju-≠Hoan or Tuu speakers in southern Africa.

# Further issues of nomenclature: whose genes have been sampled?

One reason for going into these issues in such detail is that considerable confusion has entered the genetic literature because of imprecision about the ethnolinguistic affiliation of the individuals who have provided samples for analysis. This is confounded further by the multiple names by which some groups are known (cf. Barnard, 1992, p.16) and made still worse when authors make only vague references to 'Khoisan', 'Khoi', 'San' or fail to acknowledge the particular historical circumstances of certain communities (for a recent instance, see Shi *et al.*, 2010).

A prime example concerns the people living at Schmidtsdrift, Northern Cape Province, South Africa. Two populations, now intermarrying to some degree, are represented here, the Ju-speaking !Xũ (!Xun) and the Khoe-speaking Khwe. Having fought in the then South African Defence Force (partly from a base at Camp Omega in northern

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/'Auni, /Haasi	
g, `Seroa',	
na-Dama	
ise	
ig hoe)	

Tab. 1 - Classification of southern African click-languages (after Barnard, 1992; Trail, 1996; Güldemann, 2008). Extinct languages are denoted in italics, spellings after Barnard (1992), Traill (1996) and Mitchell (2002).

Namibia), they moved to Schmidtsdrift in 1990 at the close of South Africa's military involvement in that country (Sharp & Douglas, 1996). Far from being "South African Kung and Khwe" as described by Chen et al. (2000), implied by Salas et al. (2002), erroneously mapped by Richards et al. (2004, Fig. 6.2) and Barkhan & Soodyall (2006, Figs. 1 cf. 2), and popularised in a major recent synthesis of anthropological genetics (Crawford, 2007, p.362), the origin of both communities is actually Angolan! Regrettably, these are not the only errors of this kind. Coelho et al. (2009), for example, repeat the mistake in their Additional File 4 where '!Kung' and '!Xun/Khwe' mtDNA samples are given a South African origin. True of their current residence, this makes no more sense than to state the same of the thousands of Nigerians, Congolese and Zimbabweans now living in South Africa. Presumably the 'Kwe' of Coelho *et al.*'s (2009) Additional File 5, which presents the Y chromosome samples they use, are the same as the 'Khwe' of their mtDNA analysis, although this is unclear. However, differentiating Namibian 'Omega San' (an entirely artificial name) from South African 'Sekele San', when both must refer to !Xun speakers of Angolan origin (cf. Soodyall & Jenkins, 1992) surely borders on the absurd.

Confusion over the geographical origins of the Schmidtsdrift communities is perhaps the most egregious error to have crept into the literature, but it is not alone. Pilkington *et al.* (2007), for example, employ the DNA of 25 'Khoisan' from Namibia, described as hunter-gatherers, but located on their map in an area where no huntergatherers have been present for centuries. One wonders if these are the same 25 individuals whom Garrigan et al. (2007) simply term "San", while noting that Underhill et al.'s (2000) 'Khoisan' sample mixes !Xũ (i.e. Angolan) with Ju/'hoã (i.e. Namibian) individuals (Knight et al., 2003, p.469). Wood et al. (2005), inappropriately lumping together Ju and Khoe speakers as 'Khoisan', work with individuals they describe as Tsumkwe San (presumably Ju/'hoasi; Marshall, 1976) and !Kung/Sekele (i.e. !Xũ), the latter located by them in the far northwest of Namibia, a surprising datum as the !Xũ come from southeastern Angola and lived in the northeast of Namibia before relocating to South Africa (Soodyall & Jenkins, 1992, p.316). Supplementary online data provided by Behar et al. (2008) also astonish: their 'San' sample consists of two individuals without geographical affiliation, two more from Namibia, 15 reported to come from 'South Africa' (does this mean Schmidtsdrift?) and three more whose state of origin is given as 'South African', a subtle (and perplexing) distinction. The same authors also list four Dama and ten Khoi as being from "South Africa", another surprising designation since the Dama live in north-central Namibia and most other references to "Khoi" in the literature seem to relate to Nama-speaking individuals, again from Namibia (e.g. Soodyall & Jenkins, 1992, p.316). What unites these individuals, or justifies grouping them all under the umbrella term 'Khoisan', must, in the light of these classifications and previous discussion, be doubted.

Though not exhaustive, these examples illustrate the lack of ethnographic and geographical clarity in many genetic studies of southern African click-speaking populations (for a partial exception, see Knight *et al.*, 2003, p.469). Such murkiness may be of less concern if the question posed is a high order one, such as the relationship of these communities to other African (and/or non-African) groups, but becomes more acute if we wish to relate genetic analyses to the history of specific populations within southern Africa itself. Terminology needs to be used more carefully, not least "because the term Khoisan is vacuous in terms of language classification and social organization [and] its generalized use in and outside science can only lead to misunderstanding" (Güldemann & Stoneking, 2008, p.106). Historical inferences drawn from studies that persist in classifying populations as 'Khoisan' or 'Khoisan-speaking' must be treated with due caution, whether they follow the minority position of Ehret (1998) and Honken (1998) in extending the terms to include the Hadzabe (e.g. Semino *et al.*, 2000) or accept the majority view and restrict them to southern Africa (e.g. Tishkoff *et al.*, 2007, 2009).

### The contributions of genetics: an archaeological appraisal

With these points clarified, I turn to the genetic analyses themselves. A principal concern of research has been their relevance to understanding the antiquity and early history of Homo sapiens as a whole. As with most genetic studies, attention has focused on mutations in mitochondrial DNA (mtDNA) and the non-recombining region of the Y chromosome (NRY). Transmitted through only one parent (from the mother to all offspring and from father to son respectively) without undergoing recombination at reproduction, both are particularly well suited to tracing phylogenetic lineages over long periods of time from people alive today to their most recent common female and male ancestors. Such lineages can also be clustered in groups sharing a common ancestor which are usually refereed to as haplogroups. Their high-resolution analysis now provides more refined understandings of genetic diversity than earlier low-resolution mtDNA studies and studies of blood groups, enzymes and proteins (summarised in Soodyall & Jenkins, 1992), but is likely to be increasingly complemented by whole genome studies over the coming years of the kind recently pioneered by Schuster et al. (2010).

#### Origins

In a recent assessment of African genetic structure and history Tishkoff *et al.* (2009) reaffirm

earlier findings (e.g. Chen et al., 2000) that southern African click-speaking populations have the most diverged genetic lineages, not only from a mtDNA and Y chromosome standpoint but also in their autosomal chromosome diversity. L0, for example, is one of four main haplogroups indigenous to Africa found at the base of the human mtDNA tree. Its oldest branches (L0d and L0k (previously described as L1d and L1k, e.g. Salas et al., 2002)) occur at high frequencies only among what Atkinson et al. (2009: 367-368) inaccurately describe as "Khoisan hunter-gatherers of South Africa," although L0d is also found at lower frequency among the Sandawe of Tanzania (Gonder et al., 2006). Varieties of the exclusively African Y chromosome haplogroup A (A-M51 and A-M23) are also almost entirely present within 'Khoisan' populations in southern Africa (Scozzari et al., 1999; Underhill et al., 2000; Cruciani et al., 2002; Semino et al., 2002; Soodyall et al., 2008). Haplogroup B, on the other hand, has a wider sub-Saharan distribution, with B-M112 lineages mostly occurring in hunter-gatherers, including tropical forest foragers ('Pygmies') and the Hadzabe. Together, the two haplogroups account for 59-88% of Y chromosome variation among sampled 'San' groups, though this is diluted to only 35% in those termed 'Khoe' (Soodyall et al., 2008, p.45).

Comparative studies of the mtDNA and Y chromosome diversity of southern African 'Khoisan'-speakers, Sandawe, Hadzabe and 'Pygmies' suggest that their divergence predates 35 kya (Underhill et al., 2000), with the Hadzabe splitting off from southern African 'Khoisan' at least 55 kya, but diverging from, or engaging in high levels of gene flow with, ancestral Sandawe much more recently around 15-20 kya (Knight et al., 2003; Tishkoff et al., 2007, 2009). These results also fit with Hadzane's isolated linguistic status and more recent comparisons of African mtDNA and global Y-chromosome sequences suggesting that today's 'Khoisan' speakers in southern Africa diverged from the ancestry of other modern humans at least 90,000 years ago (Behar et al., 2008; Shi et al., 2010). Complete genome analysis of four San individuals from

Namibia (three of them Ju-speaking and the fourth Tuu- (presumably !Xo-) speaking) adds further support to the antiquity of southern African hunter-gatherer lineages by indicating that they display greater variation from each other in terms of nucleotide substitution than do a European and an Asian individual (Schuster et al., 2010, p.944). Archaeological observations indicate that the trajectories leading to the replacement of Mode 3 (Middle Stone Age) stone tool technologies by microlithic ones followed quite different paths in East Africa than south of the Zambezi, perhaps implying little, if any, contact between the two regions; Zambia, both then and subsequent to the appearance of the microlithic Nachikufan complex c. 18 kya, aligns more closely with East Africa than with areas to its south (Barham & Mitchell, 2008, pp.280-286). Though few and in need of better radiometric dating these data are at least consistent with the results of genetic studies.

Where within sub-Saharan Africa modern humans first evolved remains uncertain, the fossil record itself being far too fragmentary unequivocally to support any particular regional claim about either this (pace Gonder et al., 2007, p.759) or the origins of complex behaviours such as the symbolic use of material objects (Barham & Mitchell, 2008; Campbell & Tishkoff, 2008, p.404). Caution is also appropriate when drawing inferences from the current distribution of genetic diversity in today's populations as we cannot assume that this has remained unaltered over time. Investigating the correlation between genetic diversity and geographic position, Tishkoff et al. (2009) nevertheless identify the Namibe/Kaokoland area of southwestern Angola/northwestern Namibia (17.5°S, 12.5°E) immediately inland of the Atlantic Ocean as the likely point of origin for the migratory expansion of modern humans through sub-Saharan Africa. The correspondence between this location and "the current San homeland" (Tishkoff et al., 2009, p.1041) is, however, looser than their sentence structure implies (cf. Fig. 1), and other analyses indicate that "the poverty of information that can be retrieved, as the TMRCA [time

to the most recent common ancestor] is approached, also makes it rather difficult to establish a geographical center of gravity for the origin of modern humans" (Salas et al., 2002, p.1106; cf. Behar et al., 2008). An origin in East Africa with an early southern African offshoot thus remains possible. Subsequent expansion of other mtDNA haplogroups (L2/L3) within Africa does not, however, appear to have affected some southern African 'Khoisan', supporting the case for their extended genetic isolation from other populations (Watson et al., 1997). Reconciling any of these observations with the archaeological and palaeoenvironmental records remains a considerable challenge, but may become easier as their chronology improves, especially in East Africa (Jacobs & Roberts, 2009); for the moment relevant archaeological observations from the Namibe/Kaokoland area simply do not exist (Mitchell, 2002).

#### Diversity: whence came the Khoe?

The origin of southern Africa's historically/ ethnographically recorded Khoe-speaking herders has recently engaged much academic attention (Sadr & Fauvelle-Aymar, 2008), with one focus the precise date, route(s) and social processes by which sheep-keeping, cattle-keeping and pottery (with which herding has traditionally been linked) entered and spread through southern Africa. A related debate centres on whether Khoe-speakers ancestral to the Cape Khoekhoen who were met with by European explorers and settlers were the vehicle for these introductions a little more than 2 kya, or whether they arrived in southwestern South Africa more recently, perhaps around 1200 years ago (Sadr, 2008; cf. Smith, 2008).

At a general level, several genetic studies (summarised by Güldemann & Stoneking, 2008) confirm that the Nama (a Khoe-speaking pastoralist group) are more closely related to Ju-≠Hoan-speaking foragers than to other African populations, providing molecular support to Schultze's (1928) biological designation of both as 'Khoisan' and implying a similar origin. However, matters are complicated by the fact that other Khoe-speaking groups (the Dama and

Khwe) do group genetically with other Africans and may thus have different origins (Güldemann & Stoneking, 2008). Further light is shed on this situation by recent Y chromosome evidence for a late Holocene movement of people from East Africa into southern Africa (Henn et al., 2008). Analysis of the E3b1f haplogroup and microsatellite data for 13 East and southern African populations reveals that the M293 mutation is much more common among the Schmidtsdrift Khoe (the 'Kxoe' of Henn et al., 2008) than their !Xũ (the '!Kung' of Henn et al., 2008) counterparts or Bantu-speakers in South Africa. The mutation itself most likely evolved in East Africa and direct haplotype sharing between Khoe and Sandawe and between !Xũ, Hadza and Datoga individuals indicates a movement of people from Tanzania into southern Angola/northern Namibia (or possibly from some third area into both regions). The maximum age of this movement is estimated as  $2700 \pm 1100$  years ago, although the numbers of people involved may have been small, something supported by the lack of evidence for recent contact between East and southern African A clade and B2b-M112 haplotypes (Henn et al., 2008, p.10696). Both the likely date and the genetic data themselves indicate that this migration was independent of, and probably earlier than, the arrival in southern Africa of Bantu-speaking populations in the first centuries of the Christian era.

As Henn et al. (2008, p.10696) note, "the inferred date and geographic route of this migration is particularly relevant in the context of archaeological evidence for the spread of pastoralism to southern Africa". Unfortunately, however, the evidence that they then cite is tenuous at best: radiocarbon dates of as early as 2300 BP associated with Iron Age ceramics in Zambia are equivocal (Mitchell & Whitelaw, 2005, p.216), Bambata pottery is not known from either northern Namibia or Zambia, and its associations with pastoralism are debatable (Huffman, 2005). Bambata's similarities with Pastoral Neolithic (Elmenteitan) pottery in East Africa may also be merely superficial as Huffman (2005) is certain that it is an Iron Age ware. The quite different - and diverse - ceramic traditions found in other parts of southern Africa from a little before 2 kya cannot be securely linked stylistically to anything further north, leaving open the possibility, however coincidental, of independent innovation south of the Zambezi (Sadr & Sampson, 2006).

We are on slightly firmer ground when considering the date of the earliest livestock in southern Africa as bones and teeth can, in principle, be directly dated using radiocarbon accelerator mass spectrometry. Results indicate that sheep were present at Spoegrivier, northwestern South Africa, by 2105 ± 65 BP (OxA-4862; Sealy & Yates, 1994), while both sheep and cattle are only a little younger at Toteng, northern Botswana (2020 ± 40 and 2070 ± 40 BP respectively; Beta-186669 and -1904888; Robbins et al., 2005). Dates and locations are both consistent with a pre-Iron Age movement of livestock - and thus perhaps of people - into south-central Africa as Henn et al.'s (2008) analysis implies. However fast livestock and people might have moved south from the Zambezi Valley and however propitious climatic conditions may have been for that movement during the late Holocene Neoglacial c. 3000-2000 BP, it thus seems probable that both sheep and cattle were present on the northern margins of southern Africa not long after the middle of the first millennium BC. The coincidence with the admittedly broad date provided by Henn et al. (2008) for the arrival of the M293 Y chromosome mutation is striking.

Recently published linguistic work on the Khoe-Kwadi language family is also relevant as Güldemann (2008) presents convincing evidence for it a) having links to East Africa, where Sandawe is a likely relative; b) being intrusive into southern Africa (in the form of Proto-Khoe-Kwadi); and c) developing through at least two stages of profound interaction with first Ju-≠Hoan (separation of Kwadi from Proto-Khoe) and later on Tuu speakers (diversification of Proto-Khoe). Lexical reconstructions allow for even Proto-Khoe-Kwadi speakers having been familiar with both sheep and cattle, while the family as a whole, and especially its Khoe branch, is "relatively young" (Güldemann, 2008, pp.107,110).

Further research is undoubtedly required, not least sustained archaeological fieldwork in Angola and Zambia, but for the moment genetic studies (Güldemann & Stoneking, 2008; Henn et al., 2008) and linguistics (Güldemann, 2008) can most parsimoniously be understood as suggesting that a (small?) East African-derived migrant population entered the northern margins of southern Africa in the mid-first millennium BC, bringing with them both cattle and sheep. A complicated mix of demic expansion, intermarriage with indigenous hunter-gatherers (some of whom themselves acquired domestic animals; Sadr, 2008) and abandonment of herding by pastoralists when/where conditions were ecologically too marginal to sustain herding then saw livestock and Khoe languages spread south as far as the Cape. Increasing levels of admixture with aboriginal foragers speaking Ju-≠Hoan and Tuu languages can thus account for both the evolution of the Khoe languages (Güldemann, 2008) and the greater biological and genetic similarity between them and Nama-speakers relative to more northerly Kwadi, Dama and Khwe populations (Nurse et al., 1985; Soodyall & Jenkins, 1992, 1993; Güldemann & Stoneking, 2008, Fig. 5). The genetically founded inability of sampled Ju- and Tuu-speaking individuals to digest lactose as adults (Schuster et al., 2010) is consistent with this pattern .

#### Admixture

Linguistics, history and physical anthropology have long indicated that the Bantu-speaking majority living in southern Africa today has, in at least some cases, experienced considerable interaction with Ju- $\neq$ Hoan-, Khoe- and Tuu-speaking hunter-gatherer and herder populations. This presents an obvious arena for genetic research and several studies are now available. Pereira *et al.* (2001), for example, used the frequency of the LOd (previously L1d) mtDNA haplogroup to estimate an assimilation rate of 'Khoisan' of around 5% among Bantu-speakers in southeastern Africa, a conclusion confirmed by Salas *et al.* (2002), who noted its compatibility with both recurrent gene flow and a more time-specific event-like genetic exchange, perhaps most likely some time after initial arrival. In both studies the data employed came only from Mozambique, but a decade earlier Soodyall (1993) demonstrated much higher frequencies of L0d in South African populations, concluding that among Xhosa speakers some 25% and among Zulu speakers approximately 50% of all mtDNA lineages derive from a 'Khoisan' source. Consistent with historical traditions and arguments that specific elements of Nguni (i.e. Xhosa and Zulu) divination practices derive from the incorporation of hunter-gatherer women into agropastoralist societies (Hammond-Tooke, 1998), these data also indicate that intermarriage was biased toward the female side; whether this bias was affected/strengthened by very recent incorporation of hunter-gatherers into Ngunispeaking groups as a result of the population displacements associated with the early nineteenth century Mfecane/Difagane (Hamilton, 1995) remains to be investigated. Interestingly, the reverse situation, i.e. limited assimilation of Negroid women into hunter-gatherer populations, is indicated by mtDNA and NRY data from !Xũ ('Sekele') Bushmen originating in southeastern Angola (Soodyall & Jenkins, 1992; Knight et al., 2003). However, this seems to have been far from universal as very little admixture on either maternal or paternal lines is evident among Namibian Ju/'hoãsi (Underhill et al., 2000, 2001; Knight et al., 2003). Studies of the ancestry of South Africa's 'Coloured' population are fewer and merely corroborate historical records of European marriage and miscegenation with indigenous herders and hunter-gatherers (Patterson et al., 2010).

On the western side of the continent, archaeological evidence (principally the spatial organisation of settlements and ceramic typology) indicates that while cattle were most likely introduced into Angola from the east, the principal source of its Iron Age population lay to the north, in Congo (Denbow, 1990; Huffman, 2007). This is consistent with the linguistic fact that, unlike elsewhere in southern Africa, Bantu-speaking populations in Angola and northern Namibia do not speak Eastern Bantu languages, but rather languages affiliated to those found in the Congo Basin and

Cameroon (Vansina, 1990). Excavations at Benfica near Luanda (Dos Santos & Ervedosa, 1970) also suggest that agropastoralist settlement here predated farmer expansion into the eastern half of southern Africa. Different patterns of interaction between agropastoralist arrivals and indigenous hunter-gatherers (and/or herders) may therefore be anticipated. MtDNA data reported by Plaza et al. (2004) suggest that the expansion of Bantuspeaking farmers here involved a more wholesale degree of population replacement than was the case in southeastern southern Africa. However, their sample came from essentially just one group, the Ovimbundu of south-central Angola. A more extensive study focused on the genes of southwestern Angolan populations identified a more significant contribution from 'Khoe-San' speakers, particularly among the Herero-speaking Kuvale (Coelho et al., 2009). Comparison with Namibian Herero shows that the Kuvale have greatly enhanced 'Khoe-San' contributions to both their Y chromosome (12% v. 0%) and mitochondrial (22% v. 8%) DNA. Estimates of the time of divergence between the haplotypes concerned (L0d and NRY B2b) and sequences available from 'Khoisan'-speaking populations are very uncertain, but consistently predate the beginning of the Iron Age, leading Coelho et al. (2009) to speculate that they are picking up a genetic legacy from now extinct Kwadi speakers who once lived in this area of Angola. Finally, let us note a rare instance of genetic research specifically aimed at investigating the histories of different Bantu-speaking peoples within southern Africa, the mtDNA polymorphism study of Soodyall & Jenkins (1993), which suggests quite distinct origins for the Owambo and Herero populations of northern Namibia, both of whom speak Western Bantu languages. Additional work to take this pioneering observation further would be welcome.

#### **Discussion and conclusions**

This brief archaeological contextualisation of recent genetic research pertaining to the history of 'Khoisan'-speaking populations confirms the

relevance of such work for providing additional perspectives on the past of southern African foragers and pastoralists. In particular, archaeological and linguistic data independently lend support to the conclusions reached by Henn et al. (2008) on the likelihood of a (small?) movement of people (with livestock?) from East Africa into the northern part of southern Africa before 2 kya. Together with cultural anthropology, the same two disciplines also reinforce the genetic case for admixture between (mostly female) aboriginal hunter-gatherers and newly arriving Bantu-speaking farmers in southeastern southern Africa, though the picture is more complex elsewhere. Archaeologically plausible correlations with research indicating that southern African 'Khoisan' populations are close to the baseline of modern human genetic diversity are more difficult to identify or sustain.

One of the most striking observations about the studies reviewed is that all emphasise just a few of the known Khoe-, Ju-≠Hoan- and Tuu-speaking populations of southern Africa. While their correct nomenclature has, as I have shown, been a matter of some confusion, the genetic samples analysed and published to date themselves derive almost entirely from very few sources: the !Xũ and Khwe of Schmidtsdrift, Ju/'hoasi from both northwestern Botswana and northeastern Namibia, and Nama and Dama from Namibia. Not only is this a highly selective subset of all extant 'Khoisan' populations, it is also biased toward the north and northwest of southern Africa (Tab. 2). Samples from elsewhere in the Kalahari or from areas to its south are unrepresented, while conclusions are typically reached using just two sets of genetic data, mtDNA and the Y chromosome. These problems have not gone unremarked (Jobling et al., 2004, p.328; Crawhall, 2006a, p.114; Güldemann & Stoneking, 2008, p.104), but a great deal remains to be done to address them.

An obvious strategy is to develop genomewide studies of genetic variation, something scarcely begun for African populations (Campbell & Tishkoff, 2008, p.422), though now pioneered for San groups by Schuster *et al.*  (2010), who included one Tuu-speaker from the Gobabis area of eastern Namibia in their complete genome analysis of four San individuals; the others - and the wider sample from which these four were selected - were all Ju-speaking. A second, and more fundamental, necessity is thus to expand the range of populations sampled (Reed & Tishkoff, 2006, p.602). (Whether any of the existing samples need to be increased, or whether they are, in all cases, already sufficiently large for reliable results is a question that an archaeologist cannot answer, but one that should also be considered). Logistical and political factors (the need for appropriate research permits and consent) can clearly not be dismissed, but neither are they overwhelming. In the Kalahari sampling of G/wi, G//ana, Nharo, Kxoe, Tshwa and ≠Hoa communities among others would significantly increase the range of Khoe- and Ju-+Hoan-speaking populations for whom genetic data exist, but what of more southerly foragers?

Here a real problem exists, as the !Xo of western Botswana/easternmost Namibia and the ≠Khomani of South Africa's Gordonia District (Northern Cape Province) are the only extant Bushman populations still speaking languages of the Tuu family (and the ≠Khomani language, N/u, has virtually disappeared; Crawhall, 2006b). However, all is not necessarily lost as ≠Xegwi was spoken as late as the 1980s by a very few individuals in South Africa's Mpumalanga province and /Xam into the early twentieth century in the Northern Cape (Traill, 1996). Bushmen speaking essentially unrecorded, but nevertheless clearly Tuu, languages also survived in sustainable communities in highland Lesotho into the 1870s and 1880s, and as individuals for several decades beyond this, before assimilating into surrounding Bantu-speaking populations (Jolly, 1994; Vinnicombe, 2009). But while languages died out, cultures were displaced and individuals intermarried, genes will have survived. In each of the cases mentioned it may thus be possible to sample extant populations of Bushman descent, and relevant research to do this (and simultaneously gauge the degree of admixture from recently arrived Sotho-speaking farmers) is currently

MTDNA	Y CHROMOSOME	GENETIC POLYMORPHISM
Merriwether <i>et al.</i> (1991) Vigilant <i>et al.</i> (1991)	Knight <i>et al.</i> (2003)	Nurse <i>et al.</i> (1985)
Merriwether et al. (1991)	Wood et al. (2005)	-
-	-	Nurse <i>et al.</i> (1985)
Merriwether <i>et al.</i> (1991) Chen <i>et al.</i> (2000)	Knight <i>et al.</i> (2003) Wood <i>et al.</i> (2005)	-
Merriwether et al. (1991)	Wood et al. (2005)	Nurse <i>et al.</i> (1985)
Chen et al. (2000)	Knight <i>et al.</i> (2003)	-
Merriwether et al. (1991)	Wood <i>et al.</i> (2005)	Nurse <i>et al.</i> (1985)
	MTDNA Merriwether <i>et al.</i> (1991) Vigilant <i>et al.</i> (1991) Merriwether <i>et al.</i> (1991) - Merriwether <i>et al.</i> (1991) Chen <i>et al.</i> (2000) Merriwether <i>et al.</i> (1991) Merriwether <i>et al.</i> (1991)	MTDNA Y CHROMOSOME   Merriwether et al. (1991) Knight et al. (2003)   Merriwether et al. (1991) Wood et al. (2005)   Merriwether et al. (1991) Wood et al. (2005)   - -   Merriwether et al. (1991) Knight et al. (2003)   Merriwether et al. (1991) Knight et al. (2003)   Merriwether et al. (1991) Wood et al. (2005)   Merriwether et al. (1991) Wood et al. (2005)   Merriwether et al. (1991) Wood et al. (2005)   Merriwether et al. (1991) Wood et al. (2005)

Tab. 2 - Principal genetic studies of southern African 'Khoisan' populations.

underway in Lesotho (Cristian Capelli, pers. comm.). Similar initiatives ought to be developed for //Xegwi descendants in Mpumalanga and among the (at least partly /Xam-descended) 'Coloured' rural population and nomadic Karretjiemense (de Jongh, 2002) of the Northern Cape.

Whether scope exists for investigating the ancient DNA of human skeletal material is less clear. Preservation may be an issue in tropical areas (Caramelli & Lago, 2006), but perhaps less so for the many hundreds of burials known from the Mediterranean-like biomes of South Africa's Western and Eastern Cape Provinces, which in rare instances include individuals whose remains are extraordinarily intact (Stevn et al., 2007). Contamination after decades of handling in museums may, however, create challenges of its own and access may also be difficult: several recently excavated precolonial burials have been reburied in deference to concerns raised by communities who claim Khoekhoe or Bushman descent (e.g. Sealy et al., 2000) and some institutions may be reluctant to permit analysis of human remains in their collections. Such potential difficulties with recovering ancient human DNA only reinforce the need to sample extant populations more widely. However, this needs to be guided by clear research questions, of which compensating for the restrictively northern Kalahari/ Namibian/Angolan bias in the current dataset to see if more broadly based observations alter any of the conclusions already reached is merely one. Genes, like languages, have poor chronological resolution compared to the archaeological record (Forster, 2004, pp.256-257) and it thus behooves archaeologists to engage effectively with genetic researchers (and *vice versa*) to identify problems of common concern. Such problems include the following:

#### The history of southern African forager populations

The history of specific southern African hunter-gatherer communities, rather than the general question of their antiquity in relation to the diversification of the human genome as a whole, has thus far received little attention. Nevertheless, the fact that the Ju-≠Hoan and Tuu language families have no demonstrable genealogical connection (Güldemann & Stoneking, 2008) implies that their ancestral forms have an extremely long history of separation and invites a search for correlations between genetic and linguistic boundaries (Crawhall, 2006a, p.123). Recalling that their current distributions have undoubtedly been influenced by the recent expansion of Khoe-Kwadi (Güldemann & Stoneking, 2008), Ju-≠Hoan's concentration in the northwest of southern Africa and that of Tuu in South Africa and southwestern Botswana suggests that we should perhaps be seeking some event(s) that could separate people into northern and southern refugia (Crawhall, 2006a, pp.123-124). The most obvious such context is the earlier

part of Marine Isotope Stage 2 (25-16 kya) when most of southern Africa experienced conditions significantly drier than those of today and population probably concentrated in those areas with the most abundant, predictable resources. The archaeological record is clearest for the period at and immediately after the Last Glacial Maximum (c. 18 kya) when microlithic bladelet-rich stone tool assemblages known as Robberg are found at sites in South Africa's winter rainfall zone and eastward within, or toward the Indian Ocean side of, the Great Escarpment. A preference for higher, more reliable rainfall and topographically (and thus ecologically) more diverse terrain may explain this distribution, which, until around 13 kya, apparently left South Africa's central interior unoccupied (Mitchell, 1990). By contrast, the archaeological signatures of contemporary populations in southern Namibia, southwestern Zimbabwe and northwestern Botswana cannot be subsumed under the Robberg label. The temptation to connect the latter's confinement south of the Limpopo and Orange Rivers with the origin of Tuu is clear (Mitchell, 2002, p.125). If, on the other hand, this is too recent for the differentiation of Tuu and Ju-≠Hoan, then the next most likely palaeoenvironmental scenario is the preceding glacial maximum during Marine Isotope Stage 4 (75-60 kya) as Isotope Stage 3 repeatedly saw climatic conditions as wet as or wetter than today across much of southern Africa, including the Kalahari (Mitchell, 2008). Bandelt & Foster's (1997, p.982) observation that the differentiation of the '!Kung' (i.e. Botswanan Ju/'hoãsi) "from other Khoisan populations may have occurred quite recently relative to the !Kung coalescence time" could, in the present state of our ignorance, fit either possibility. Widespread sampling of a much greater diversity of 'Khoisan' populations is needed to move forward with this issue.

The separation of the Ju-≠Hoan and Tuu families may be the biggest, but is far from the only, question about southern African forager prehistory onto which genetics might shed some light. Although it may have persisted a little longer in southeastern southern Africa (Mitchell, 2002, p.120), elsewhere the Robberg was followed

around 12 kya by a very different complex of stone tool assemblages, the Oakhurst. Moreover, Oakhurst assemblages also occur in southern Namibia and southern Zimbabwe, as well as the now recolonised South African interior, though not northern Botswana (Barham & Mitchell, 2008, p.316): do genetic traces survive of population growth and expansion as climate ameliorated across the Pleistocene/Holocene boundary? And what of more recent population expansions, such as the split between speakers of N/u (i.e. ≠Khomani) and !Xõ (!Xóõ), both Tuu languages, that glottochronology suggests took place >2.5 kya with expansion north from somewhere in the Free State or southern Cape (Crawhall, 2006b, p.126)? Should access to ancient DNA from the latter region become possible then a further question to consider is whether it will support the case for increasingly endogamous, territorially restricted populations now emerging from material culture studies, physical anthropology and stable isotope analysis of past diet (Hall, 2000; Sealy & Pfeiffer, 2000; Sealy, 2006).

### The origins and expansion of Khoe-Kwadispeaking populations

For now, the origin and subsequent history of Khoe-Kwadi-speaking populations offers the best opportunity for usefully triangulating between archaeological, genetic and linguistic data. One way to extend this triangulation is to pursue the genetic history of the various breeds of cattle, sheep (and, indeed, goats) kept by southern African herders and farmers before European arrival. A second topic to which molecular genetics can certainly contribute is the history of the many Khoe-speaking huntergatherer groups known from the Kalahari: what patterns of genetic variation exist among them, or between them and other (Khoe-Kwadi- and Ju-≠Hoan- and Tuu-speaking) populations, in the light of Güldemann's (2008) recent hypotheses about their origin and the possibility that many may be 'devolved' herders (Walker, 1995)? Was admixture between aboriginal hunter-gatherer groups and incoming pastoralists greater in some areas than others and how does that map

on to patterns of linguistic and cultural variation? Finally, there is the yet broader question arising from Smith & Ouzman's (2004) identification of a distinctively Khoekhoe (but still poorly dated) style of geometric rock art and the suggestion that this originated in the geometric rock art of south-central and East Africa, where it was supposedly produced by populations physically and culturally related to modern tropical forest foragers ('Pygmies') (Smith, 1997, 2006). As Smith (2006, p.89) himself points out, not only is the latter claim eminently amenable to genetic testing (by seeking similarities between 'Pygmies' and recent Zambian/Malawian BaTwa groups), but so too is the rock art-based argument itself as it predicts "that some Khoekhoen groups will retain remnant southern Pygmy genetic markers" alongside evidence of admixture with southern San and Bantu-speaking farmers (B. Smith, 2006, p.94). Although there is an obvious need to differentiate such recent derivations from much older evidence of a common origin for southern African 'Khoisan' and central African 'Pygmies' (Underhill et al., 2000), the clarity of the claim makes it an appealing research target. Recent genetic sampling of individuals in Zambia should also help (Barham, 2006), though initial results have focused on hunter-gatherer/farmer interactions, identifying little or no gene flow between Bisa/Kunda ancestors and pre-existing forager populations despite many centuries of coexistence (de Filippo et al., 2009).

#### Hunter-gatherer/farmer genetic exchanges

Studying admixture between farmers and hunter-gatherers has, as we have seen, also been a focus of genetic research in southern Africa, but studies like that of de Filippo *et al.* (2009), which combine mtDNA with a variety of Y chromosome traits, let alone autosomal markers, are few. Apart from the pioneering work of Soodyall (1993; Soodyall & Jenkins, 1992), investigations have been confined to the northeastern (Pereira *et al.*, 2001; Salas *et al.*, 2002) and northwestern (Coelho *et al.*, 2009) peripheries of agropastoralist settlement, leaving largely unanswered the questions of how such patterns of admixture varied (by date and by gender) across the wider region. Might genetic analyses of samples from Zimbabwe confirm, for example, the archaeological suspicion that hunter-gatherers disappeared quite rapidly (presumably via assimilation) from most of the country (Mitchell, 2002, p.297)? And could they also support Mazel's (1989) argument, again based on material culture studies, that in the Thukela Basin of KwaZulu-Natal relations between hunter-gatherers and farmers were more equally structured during the first millennium AD (thus less intermarriage and assimilation?) than thereafter?

## The origin of second millennium AD farmers in southernmost Africa

This suggestion in turn raises one last issue, the origin of the Sotho/Tswana- and Nguni-speaking populations who today constitute the majority of the inhabitants of Botswana, Lesotho, South Africa and Swaziland. Archaeological data are clear that the pottery associated with these groups cannot be derived from the ceramics of the farming communities who settled southernmost Africa during the first millennium AD and disjunctions in settlement pattern and other aspects of material culture are also evident (Huffman, 2007). Blackburn (i.e. Nguni) and Moloko (i.e. Sotho/Tswana) tradition pottery is instead most readily matched with ceramics in eastern Zambia and southern Tanzania, suggesting that it was from this area that populations speaking ancestral forms of these languages moved into southernmost Africa (Huffman, 1989). Linguistics supports this claim as Nguni and Sotho/Tswana share with KiSwahili and some other East African Eastern Bantu languages the use of suffixes for denoting the locative and diminutive, a marked contrast to the practice of Shona (spoken in Zimbabwe) or the much more distant Bantu languages of northern Namibia (Huffman & Herbert, 1994/95; Finlayson, 2006; Huffman, 2006). Similarities in kinship terminology and the use of particular forms of respectful language in speech point more specifically to connections with East Africa's Interlacustrine area (Hammond-Tooke, 2004). An input into these issues from genetics would be perhaps the clearest sign of the

application of molecular genetic research to better understanding the *recent* history of southern Africa's present inhabitants.

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