

The linguistic and genetic landscape of southern Africa

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Summary - *The present-day diversity of southern African populations was shaped by the confluence of three major pre-historic settlement layers associated with distinct linguistic strata: i) an early occupation by foragers speaking languages of the Kx'a and Tuu families; ii) a Late Stone Age migration of pre-Bantu pastoralists from eastern Africa associated with Khoe-Kwadi languages; iii) the Iron Age expansion of Bantu-speaking farmers from West-Central Africa who reached southern Africa from the western and eastern part of the continent. Uniting data and methodologies from linguistics and genetics, we review evidence for the origins, migration routes and internal diversification patterns of all three layers. By examining the impact of admixture and sex-biased forms of interaction, we show that southern Africa can be characterized as a zone of high contact between foraging and food-producing communities, involving both egalitarian interactions and socially stratified relationships. A special focus on modern groups speaking languages of the Khoe-Kwadi family further reveals how contact and admixture led to the generation of new ethnic identities whose diverse subsistence patterns and cultural practices have long puzzled scholars from various disciplines.*

Keywords - Southern Africa, “Khoisan”, Bantu, Pastoralism, Migrations, Admixture.

Introduction

In 1917, Joachim Helmuth Wilhelm embarked on a hunting expedition to southeastern Angola, right into the heart of the confluence zone between the Cuito, Luyana, Cuando and Okavango rivers. Wilhelm was of German origin and had arrived to Namibia, then a German colony, in 1912, at the age of 20. After several years of managing a frontier farm, he had decided to pursue his own interests and make a living out of trade and professional hunting while devoting part of his time to develop his ethnographic passion and study the peoples of southwestern Africa (Heintze 2007).

During his forays into Angola, Wilhelm encountered the “Hukwe”, a dark-skinned

foraging people speaking a click language, who immediately caught his interest (Wilhelm 1921/2, 1954). Hukwe (or *Xuu-khoe*) translates to ‘people left behind’ and is still in use among various foraging groups of the Okavango River Basin, commonly serving as their term of self-reference (Fehn 2016). The people encountered by Wilhelm would nowadays be referred to as Khwe (or Kxoe), an ethnographic unit numbering 7,000 to 8,000 individuals with a geographic distribution spanning across Angola, Zambia, Namibia, Botswana and South Africa (Brenzinger 2013).

In the beginning of the 20th century, Wilhelm’s observation of foragers bearing physical resemblance to their food-producing neighbors was somewhat of a curiosity. Back

then, the predominant view of the population landscape of southern Africa assumed a clear-cut division between pristine “Khoisan” foragers – light-skinned and of small stature – and Bantu-speaking farmers (Cashdan 1986). In this dichotomy, the Bantu were seen as dominant, especially in the light of contemporary observations which suggested that relations between foragers and food-producers were generally characterized by violence, oppression and servitude (Dornan 1917; Wilhelm 1954). In this context, the existence of a foraging group like the Khwe who spoke a click-language while sharing many cultural and phenotypical features with their Bantu-speaking Mbukushu and Barotse neighbors certainly required explanation (Wilhelm 1921/2, 1954).

Being also familiar with the !Xun who constitute one of the more “classical” southern African forager groups, Wilhelm solved this dilemma by considering the Khwe as the result of contact and admixture between indigenous foragers and Bantu-speaking food-producers. This view was shared by other scholars from the first half of the 20th century who observed the Khwe and a whole range of similar peoples living along the northern Kalahari Basin fringe (Cashdan 1986). These groups are united by their dark skin color and past or present use of non-Bantu click languages, and include the Khwe, Shua and Tshwa foragers, as well as the Damara from Namibia, and the formerly Kwadi-speaking Kwepe small-stock herders from southwestern Angola (Fig. 1).

While contact seems to be the more obvious explanation for the occurrence of different combinations of cultural and physical characteristics, some scholars have deviated from Wilhelm in interpreting the Khwe and related peoples as unadmixed remnants of enigmatic pre-Bantu populations (Blench 2006; Cashdan 1986; Vedder 1923). This view may be rooted in a more general difficulty to accept the idea that the linguistic, cultural and genetic heritage of distinct populations can be derived from more than one parental group. Especially foraging communities like the Khwe bear the implicit connotation of ancient origins, which often

implies cultural and genetic continuity over millennia. In this context, the genesis of new combinations of languages, genes and subsistence models through contact-related processes like intermarriage, multilingualism and exchange of knowledge are disregarded in favor of purely cladistic models valorizing vertical over horizontal transfer mechanisms (Moore 1994).

In spite of multiple hypotheses interpreting the dark-skinned click-speakers of the northern Kalahari Basin fringe as last representatives of an ancient foraging layer (Cashdan 1986) or remnants of an early pastoral migration (Güldemann 2008a), recent research has shown that Wilhelm was indeed right in considering the Khwe and related peoples to be the result of contact and admixture. Rather than displaying overall continuity from a remote common ancestor, they carry the genetic and cultural legacy of at least three prehistoric settlement layers which came to shape the population landscape of southern Africa: these include an ancient layer associated with resident forager populations, remnant traces of a pre-Bantu migration introducing Late Stone Age pastoralism from eastern Africa, and the heritage of Bantu-speaking farmers from West Central Africa.

In this review, we present an overview of the evidence provided by genetic, linguistic and ethnographic data revealing the migratory movements and patterns of contact which lead to the superimposition of these distinct population layers. We trace their origins and relationships with other peoples on the continent, thereby locating the settlement history of southern Africa within the wider history of Africa.

The linguistic landscape of pre-historical southern Africa

While southern Africa is now widely considered a hotspot of linguistic and cultural diversity, the traditional view merely assumed two major linguistic strata: the “Khoisan” languages, best known for their use of phonemic click sounds, which are primarily spoken by foragers



Fig. 1 - Speakers of non-Bantu click-languages from the northern Kalahari Basin fringe (delimited in the map). Photographs taken by JR and AMF with permission.

thought to be indigenous to the area, and the “Bantu” languages spoken by food producers who reached the Cape in the course of a major migratory wave from West-Central Africa. In the following sections, we review the evidence casting doubts on this dichotomy and provide an introduction to linguistic methodologies highlighting different aspects of the history of languages and their speakers. In this framework, “Khoisan” appears as a genealogically diverse group of languages, joined together by processes of horizontal transfer, while Bantu maintains its status as a robust genealogical unit with a tree-like structure capable of reflecting the speakers’ migratory pathways.

“Khoisan”

The term “Khoisan” dates back to the early 20th century and was originally coined by physical anthropologist Leonhard Schultze-Jena to refer to shared physical traits of herders (Khoekhoe) and hunters (San) in the Cape area of South Africa, all of whom spoke click-languages (Schultze-Jena 1928). Later on, linguist Joseph Greenberg extended its use to designate a family of click-languages which grouped languages from the Cape and other parts of southern Africa with Hadza and Sandawe from Tanzania (Greenberg 1963).

While phonemic click sounds are indeed largely restricted to southern and eastern Africa, they are not exclusive to Greenberg’s “Khoisan” unit but also appear in some southern African Bantu languages like Xhosa and Zulu, as well as in the Cushitic language Dahalo from Tanzania. However, as neither Bantu nor Cushitic display clicks outside of areas where “Khoisan” languages are spoken, it can be safely assumed that the feature entered the languages in question through contact. Hence, “Khoisan” languages remain the sole African languages which are thought to have received clicks from their remote ancestors, rather than through borrowing. Since “Khoisan” languages are overwhelmingly associated with a foraging subsistence strategy – frequently considered a “primitive” way of life – clicks tend to be seen as markers of antiquity (Güldemann and Stoneking 2008) and feature prominently in the ongoing debate on the origins of human language (Sands and Güldemann 2009).

While Greenberg (1963) attempted to justify his “Khoisan” family with shared lexical and morphological material, his grasp on the little data available at the time was limited and most of his comparative series are now considered erroneous by specialists (Güldemann 2008b; Sands 1998). Notwithstanding these criticisms, “Khoisan” is still widely used to label

a presumed language family, especially among non-linguists who may feel that the shared feature of phonemic clicks is sufficient proof for a however deeply rooted common ancestry. Still, seen from the perspective of historical comparative linguistics, the mere presence or absence of any particular type of sound – click or not – does not provide conclusive information about the historical relationship between languages. This becomes apparent when the words for ‘bone’ in multiple eastern and southern African “Khoisan” languages (Supplementary Fig.1) are considered. While the great majority of them contains one of the four most widely distributed click sounds (ǀ - dental, ǃ - palatal, ǁ - alveolar, ǂ - lateral), they trace back to nine distinct roots, rather than to a single common ancestor.

Although clicks are not actually useful in determining genealogical relationships between languages, they still constitute a rare typological feature which may be revealing of areal tendencies, i.e. horizontal transfer through contact. It has been shown that unrelated languages spoken in close geographical proximity tend to become more similar over time, resulting in a convergence zone commonly referred to as “linguistic area” (Aikhenvald 2011). In this context, many linguists agree that the phonological, lexical and even structural similarities between “Khoisan” languages spoken in southern Africa today are not merely owed to chance, but are the outcome of intense contact relations within a linguistic area encompassing the Kalahari Basin and adjacent regions (Güldemann 1998; Güldemann and Fehn 2017). In the more remote past, this contact zone may have extended into eastern Africa, with Hadza and Sandawe, the two sole click languages now spoken in Tanzania, constituting remnants of a possibly much wider geographical area in which phonemic clicks were once common (Güldemann and Stoneking 2008).

While many similarities between “Khoisan” languages of southern and eastern Africa can be explained by contact, the available linguistic methodology still allows for the establishment of genealogical relations between subsets of individual languages. By applying the comparative

method (Supplementary Text 1) to the languages included in Greenberg’s “Khoisan” unit, linguists have established three unrelated families spoken in southern Africa (Kx’a, Tuu and Khoe-Kwadi) (Fig. 2A-C), and two isolates (Hadza and Sandawe) spoken in eastern Africa (Güldemann 2014). Within southern Africa, Kx’a and Tuu are spoken exclusively by populations with the prototypical profile of southern African foragers; Khoe-Kwadi-speaking populations are culturally and phenotypically diverse, encompassing the Khwe and other dark-skinned foragers from the northern Kalahari Basin fringe, as well as the Kwadi small-stock herders from Angola, and the Khoekhoe who form one of the most important herding traditions of southern Africa (Fig. 2C).

Apart from their exclusive association with foraging, the Kx’a and Tuu families also share more typological affinities – such as word order patterns (Supplementary Fig. 2) – with one another than either does with Khoe-Kwadi, indicating that they have spent more time in close geographical proximity, with Khoe-Kwadi possibly constituting a later arrival to the region (Güldemann 2008a; Güldemann and Fehn 2017). While linguistic data alone cannot resolve the family’s origin, typological evidence as well as similarities with the Tanzanian language Sandawe suggest a link between Khoe-Kwadi and eastern Africa (Güldemann 2008a; Güldemann and Elderkin 2010).

Bantu

Unlike the “Khoisan” languages, all Bantu languages of southern Africa form part of the same genealogical unit: Bantu is a relatively recent language family which makes part of the Niger-Congo macro-phylum, one of the world’s biggest linguistic entities (Dimmendaal and Storch 2014). The original proposal for Niger-Congo encompasses 1,500 languages spoken across sub-Saharan Africa, over one third of which belong to the Bantu subfamily (Bostoen 2018). At present, Bantu languages are spoken in no less than 23 African countries as the result of a major expansion which occurred between 5 and 1.5 kya (Bostoen 2018). This expansion most

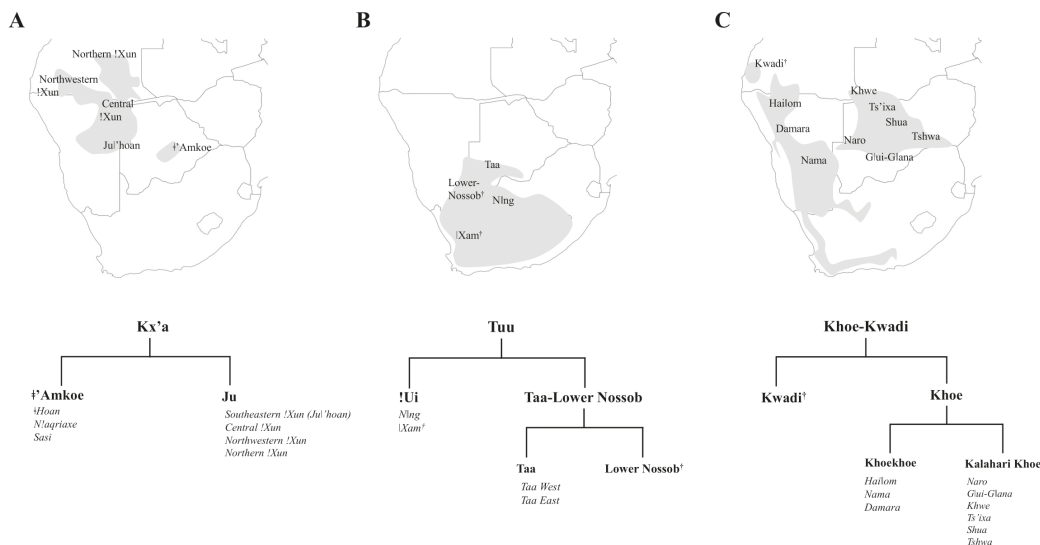


Fig. 2 - Geographical distribution and internal classification of the three southern African language families previously included in Greenberg's "Khoisan": Kx'a (A), Tuu (B) and Khoe-Kwadi (C). Sources: Güldemann (2004, 2014); Heine and Honken (2010); Vossen (1997).

likely originated in the borderlands between south-eastern Nigeria and western Cameroon where the closely related Bantoid or Wide Bantu languages are still spoken today (Fig. 3A) (Bostoen 2018; Grollemund et al. 2015).

Although it was initially suggested that Bantu languages may have spread through cultural diffusion, it is now widely accepted that the Bantu expansion involved a demic movement in the course of which languages, peoples and technological innovations spread across sub-Saharan Africa (Bostoen 2018; Rocha and Fehn 2016).

The shallow time-depth of the Bantu migration resulted in a relative homogeneity of the language family, with all present-day Bantu languages displaying great lexical and structural similarities, including a particular type of grammatical gender commonly referred to as noun-class system (Bostoen 2018; Dimmendaal and Storch 2014). This unmistakable similarity of all living Bantu languages is also encapsulated by the name of the language family, first coined by Wilhelm Bleek (1862), which derives from the widespread Bantu root *ntu meaning 'person', combined with the noun class prefix *ba-* which

usually precedes terms for human beings in the plural (Supplementary Fig. 3).

Despite their overall homogeneity, Bantu languages are usually divided into two broad geographic clusters: West and East Bantu (Fig. 3A). When applied to modern Bantu languages, Bayesian phylogenetic methods (Supplementary Text 2) provide valuable insights into the major routes of migration followed by Bantu-speaking peoples (Bostoen et al. 2015). Considered in a phylogeographic framework, the linguistic data suggests a single passage through the rainforest, followed by a late split of East Bantu from West Bantu, before Bantu-speakers reached southern Africa around 1,5 kya (Fig. 3B) (Currie et al. 2013; Grollemund et al. 2015; Koile et al. 2022).

On reaching the southern tip of the continent, eastern Bantu speakers became dominant in present-day Zambia, Zimbabwe, Mozambique, Botswana and South Africa, while western Bantu speakers are the majority in Angola and Namibia (Fig. 3A). During their advance, Bantu farmers making use of Iron Age technologies replaced or assimilated most of the forager populations that once inhabited vast parts of sub-Saharan Africa,

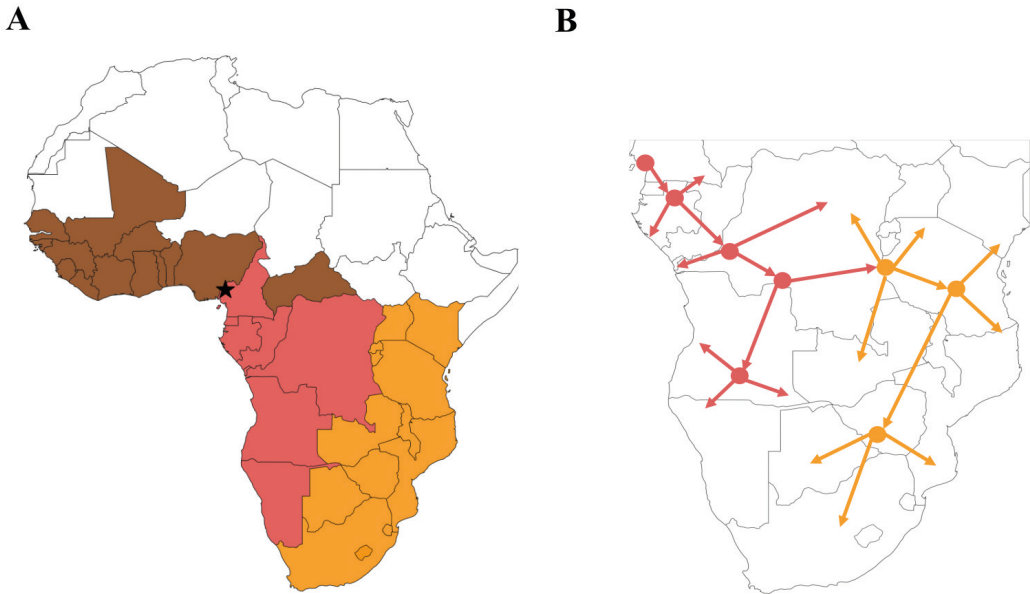


Fig. 3 - (A) Geographical distribution of the Niger-Congo macro-phylum (non-Bantu Niger Congo – brown; West Bantu – red; East Bantu – orange). Language groups were assigned according to the affiliation of the most widely distributed languages in the respective countries. The star indicates the approximate origin of the Bantu expansion. Modified from [Rocha and Fehn \(2016\)](#). **(B)** Schematic representation of the Bantu migration routes, based on linguistic data analyzed in a phylogeographic framework: after an initial migration through the rainforest, Bantu speakers split into a western and an eastern migratory stream and reached southern Africa from both sides of the continent. Modified from [Currie et al. \(2013\)](#) and [Grollemund \(2015\)](#).

most likely including the majority of southern African hunter-gatherers. Vivid evidence for pre-historic contact relations between resident populations and incoming migrants can still be found in Bantu languages like Xhosa, Zulu or Yeyi which incorporated click consonants otherwise only attested in languages of the Kx'a, Tuu and Khoe-Kwadi families ([Pakendorf et al. 2017](#)).

Combining linguistic and genetic evidence

The Principal Component (PC) plot in Figure 4 captures four main characteristics of the genetic diversity of southern Africa: 1) a strong separation between speakers of Kx'a and Tuu on one side, and Bantu speakers on the other (PC1); 2) a genetic differentiation between Kx'a and

Tuu-speaking groups (PC2); 3) a genetic homogeneity of Bantu-speaking populations; and 4) the lack of a distinct genetic profile uniting all Khoe-Kwadi-speaking populations.

In the following sections, we focus on the historical processes that underly these patterns.

Genetic diversity of Kx'a and Tuu speakers

Several studies have shown that Kx'a and Tuu-speaking foragers not only display some of the most ancient (deep-rooting) Y-chromosome and mtDNA lineages, but are also associated with one of the two deep splitting branches separating their ancestors from the ancestors of all other human populations ([Gronau et al. 2011](#); [Schlebusch et al. 2012, 2017](#); [Tishkoff et al. 2007a](#); [Veeramah et al. 2012](#)). Depending on sample choice, methodological approaches and assumed mutation rates, this split has

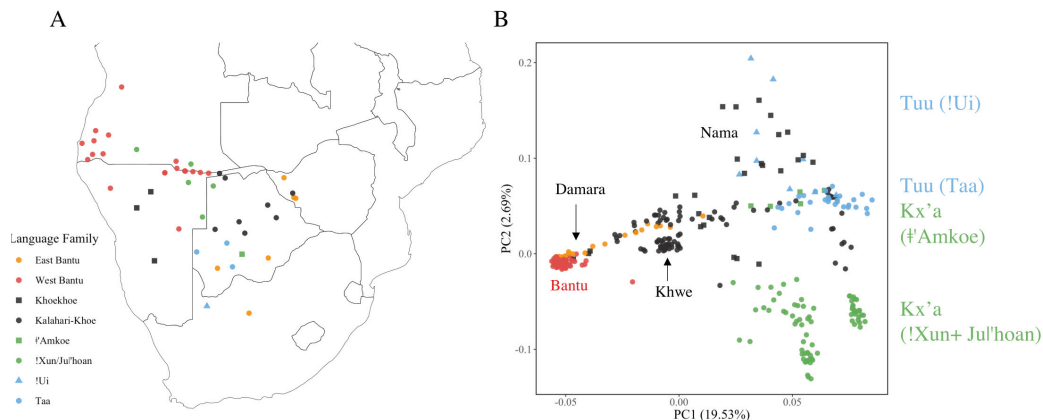


Fig. 4 - (A) Sampling locations of populations affiliated to the four major language families spoken in pre-colonial southern Africa. (B) Plot of the first two axes of genetic variation of a PC analysis based on ~500,000 autosomal SNPs, illustrating the genetic structure of southern African populations. The positions of the Khoe-Kwadi-speaking Nama, Damara and Khwe are indicated in the plot. Note the similarity with Figure 1 from Pickrell et al. (2012). Sources: Lazaridis et al. (2014); Patterson et al. (2012); Pickrell et al. (2012); own data.

been estimated to have occurred between ~150 (Gronau et al. 2011; Schlebusch et al. 2012; Veeramah et al. 2012) and 300 kya (Schlebusch et al. 2017), implying that present-day Kx'a and Tuu-speakers accumulated genetic differences distinguishing them from all other humans for at least 300 ky (2 x 150 ky). This figure contrasts with the ~1.5 ky that have elapsed since the arrival of Bantu-speakers to southern Africa (see above) and accounts for much of the high levels of genetic differentiation between Kx'a + Tuu and Bantu-speaking peoples.

The location where the ancestors of Kx'a and Tuu-speaking foragers branched off from the ancestors of all other human populations remains unknown. Kx'a and Tuu-related genomic ancestries have been detected in the Hadza and Sandawe from Tanzania (Pickrell et al. 2012), and Kx'a and Tuu-related mtDNA lineages were found in present day Bantu-speakers from Zambia (Barbieri et al. 2013). Moreover, Kx'a and Tuu-related ancestries were also identified in ancient human remains from Malawi (8.1-2.5 ky), Tanzania (1.4 kya) and Kenya (3.5 ky) (Skoglund et al. 2017; Wang et al. 2020). Together, these findings suggest that multiple forager populations genetically related to Kx'a

and Tuu-speakers might have lived in a macro-area linking eastern and southern Africa before being absorbed or extinguished by incoming food producers (Schlebusch and Jakobsson 2018; Skoglund et al. 2017). An ancient link between eastern and southern Africa is also supported by the finding of shared stylistic features of ostrich-eggshell beads produced in the two regions between 55 kya and 33 kya, before their separation by the flooding of the Zambezi Basin (Miller and Wang 2022). Additional evidence for a widespread contact between eastern and southern African foraging groups is provided by the sharing of belief systems that can be inferred from rock art themes found in southern Africa and Tanzania (Lewis-Williams 1986). These signals of genetic and cultural long-distance connections further suggest that phonemic click sounds in languages from eastern and southern Africa had a common origin and were subsequently spread by population contact, rather than representing independent innovations (see above).

Within southern Africa, the ancestors of Kx'a and Tuu-speakers may have separated as early as ~30 to 190 kya (Fan et al. 2019; Pickrell et al. 2012; Schlebusch et al. 2020). With the notable exception of the !Xun+ Jul'hoan, all modern Kx'a speakers live

in the northwestern Kalahari (Fig. 2A) while Tuu-speaking populations occupy the central Kalahari and South Africa (Fig. 2B), indicating that their genetic and linguistic differentiation is related with geography. A further split dividing Tuu speakers from the central Kalahari and South Africa into two distinct genetic groups (Fig. 4) aligns with their linguistic separation into two sub-branches labeled Taa and !Ui (Fig. 2B) (Montinaro et al. 2017; Uren et al. 2016). It is likely that the tripartite structure between populations residing in the northwestern Kalahari, central Kalahari and South Africa was strongly influenced by ecological and climatic factors shaping the southern African landscape during the last 100 ky. As the ongoing dry period of the Kalahari Basin only started at around ~10 kya, Barbieri et al. (2014) have suggested that the ancient lake Makgadikgadi in Botswana acted as an important barrier to gene flow between populations from the northwest and southeast. During about 120 ky before the onset of the current climate, the Makgadikgadi mega-lakes might indeed have been a formidable obstacle, occasionally covering an area as wide as 66,000 square kilometers which encompassed present-day lake Ngami, the Mababe Depression, lake Liambezi and the Makgadikgadi pans (Mendelsohn et al. 2010). Uren et al. (2016) additionally proposed that the rim of the Kalahari Desert could have represented an ecological boundary restricting gene flow between Tuu-speaking populations from the central Kalahari (Taa) and South Africa (!Ui).

In spite of these barriers, it is clear that most Kx'a and Tuu-speaking groups have exchanged genes with one another and with other populations migrating into southern Africa (Barbieri et al. 2014; Vicente et al. 2019) (see below). It is also likely that Kx'a and Tuu groups once had wider, overlapping geographic distributions that occasionally favored interactions between populations with different genetic and linguistic heritages. For example, the ʘAmkoe from the central Kalahari speak a language of the Kx'a family (Fig. 2A), but genetically resemble their neighbors speaking languages from the Taa-branch of Tuu (Fig. 2B and Fig. 4). While it is not clear whether this pattern was caused

by language replacement (from Tuu to Kx'a) or genetic modification through gene flow (from Kx'a-related to Tuu-related), it does suggest that Kx'a-speaking groups once penetrated into areas of the central Kalahari presently dominated by groups with Tuu (Taa)-related ancestries.

Another open question concerns the roles played by past fragmentation and admixture in establishing the high levels of genetic diversity which have consistently been found within Kx'a and Tuu-speaking populations (Henn et al. 2011; Schuster et al. 2010). While some studies suggest that these groups have larger long-term effective population sizes (N_e) than other human groups (Kim et al. 2014), Schlebusch et al. (2017, 2020) found that admixture with migrants arriving to southern Africa during the last 2 ky inflated most inferences about the ancestral size of Kx'a and Tuu-speaking populations.

Genetic diversity of Bantu-speaking peoples

The overall genetic homogeneity of Bantu-speaking groups sharply contrasts with the divergence observed between Kx'a and Tuu-speaking populations, even taking into account signals of admixture with resident populations (Fig. 4). The sharing of a distinctive genetic composition by Bantu-speaking peoples residing across subequatorial Africa proves that Bantu languages were spread through a relatively recent demic expansion, rather than by cultural diffusion involving language shift by resident populations (Diamond and Bellwood 2003; Pakendorf, et al. 2011; Rocha and Fehn 2016).

Recent studies combining the use of thousands of single nucleotide polymorphisms (SNPs) with increased sampling coverage and new analytical approaches have provided important insights into the geographic routes of the Bantu migrations. By using a dense coverage of populations residing around the Bantu homeland in the Nigeria/Cameroon border, Patin et al. (2017) have shown that Bantu-speakers from the southern part of the rainforest are more related to eastern and southern African Bantu peoples than to Bantu-speaking populations that remained in the north. In line with these observations, Semo

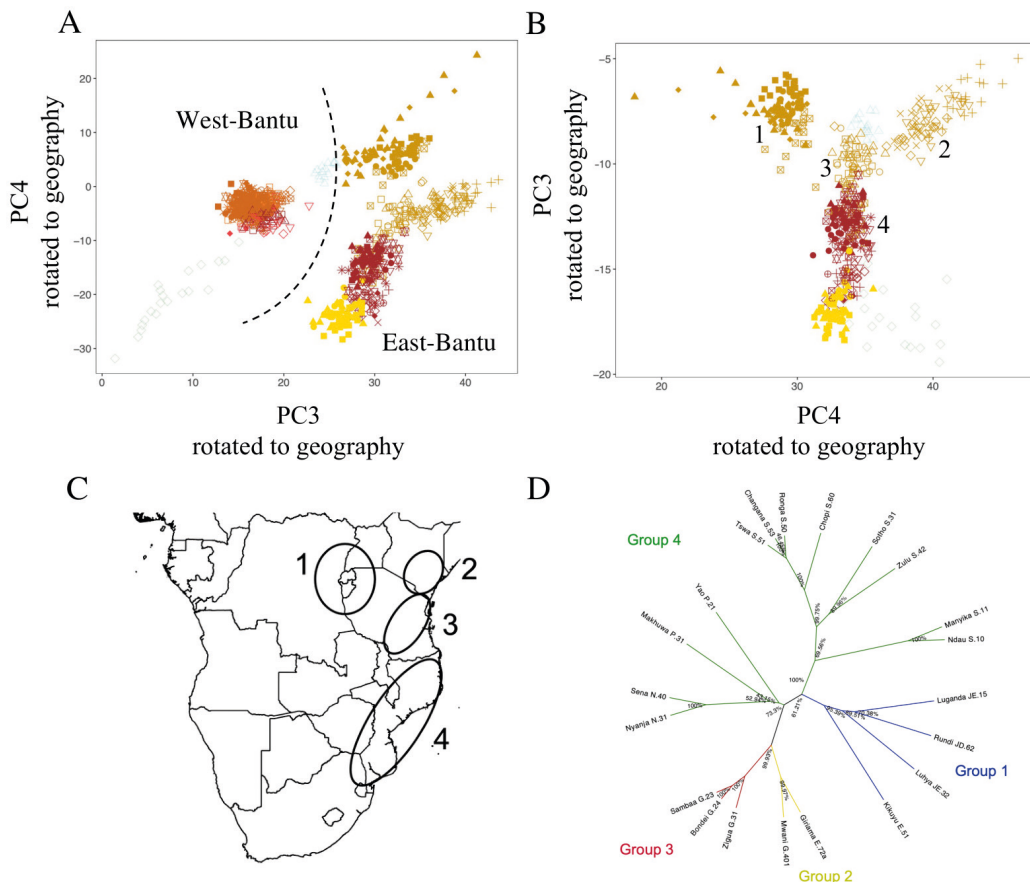


Fig. 5 - (A,B) PC plots rotated to geography displaying genetic structure of Bantu-speaking populations. (A) West and East Bantu-speaking populations. (B) Only East Bantu speaking populations. (C) Geographic locations of four East Bantu-speaking regions corresponding to the genetic clusters displayed in (B) (D) Radial Bayesian tree of Eastern Bantu languages corresponding to genetic clusters and geographic regions displayed in (B) and (C). Modified from Semo et al. (2020) under license CC BY-NC 4.0.

et al. (2020) have demonstrated that Bantu populations from Southeast Africa share more haplotypes with Bantu groups from Southwest Africa than they do with populations closer to the Bantu homeland. Taken together, these results are in line with migration routes proposed on the basis of linguistic data, which suggest that the initial spread of Bantu-speaking groups involved a southward movement across the rain forest, followed by a later split separating the ancestors of present-day southwestern and southeastern populations (cf. Fig. 3B).

Other aspects of the genetic data confirming and complementing the linguistic reconstruction of the Bantu expansion include (Fig. 3B vs Fig. 5): a) a noticeable separation between West and East Bantu-speakers (Fig. 5A); b) genetic substructure of East Bantu-speaking groups around the Great Lakes, consistent with the proposal that the initial divergence of East-Bantu languages occurred in this region (Fig. 5 B-D) (Currie et al. 2013); c) a gradient of genetic relationship along the Indian Ocean Coast with a southward decrease in genetic diversity (Semo et al. 2020), suggestive

of a sequential latitudinal dispersal out of East Africa linked to further linguistic differentiation (Currie et al. 2013).

Southern Africa comprises several contact zones marked by the encounter between West and East Bantu-speaking peoples whose ancestors and languages might have separated further north more than 3 kya (Koile et al. 2022): in the Namibian Caprivi Strip, Kavango-speakers from the West Bantu branch are in close neighborhood with the East Bantu-speaking Fwe, Lozi and Subiya; in Botswana's Okavango Delta, West Bantu-speaking groups like the Mbukushu and Gciriku are interspersed with East Bantu speakers of the Sotho-Tswana branch; further east, in Zambia, a major overlap between multiple East and West Bantu groups can be observed. All these zones constitute foci of intense exchange between diverse Bantu cultural traditions and genetic ancestries.

While Bantu speakers from different ethnolinguistic groups are known to interact with one another, their migratory movements also involved admixture with resident populations. In some East Bantu groups speaking languages of the Sotho-Tswana (Tswana, Sotho and Kgalagadi) or Nguni (Zulu and Xhosa) clusters, introgression of local forager genes can amount to more than 20% (Supplementary Fig. 4A). Interestingly, the languages of some admixed groups like Zulu and Xhosa are well known for their high load of click consonants, while others (like Tswana) do not display major traces of substrate influence (Pakendorf et al. 2017).

Admixture between Bantu incomers and resident communities was clearly sex-biased, as the proportion of Kx'a and Tuu-related ancestry found in most Bantu-speaking groups is higher for mtDNA than for the Y-chromosome (Supplementary Fig. 4B). This pattern indicates that the majority of mixed marriages in Bantu-speaking communities involved resident women and not resident men. Conversely, Bantu-related genetic material found in Kx'a and Tuu-speaking groups is mostly male-mediated, suggesting that Bantu women did not move into these forager communities, while Bantu men had non-marital

sexual relationships with Kx'a and Tuu-speaking women, who raised their offspring in their own groups. This type of sex-biased interaction is also observed between rainforest hunter-gathers and Bantu-speakers from Central Africa (Verdu et al. 2013), and can be explained by the social inequality characterizing relationships between dominant Bantu-speakers and neighboring foraging groups.

The levels and patterns of admixture are far from being spatially homogeneous. In southern Mozambique, groups like the Chopi, Tswa and Changana display lower amounts of introgression than their Sotho-Tswana and Nguni-speaking relatives from South Africa and Botswana (5% vs. 25%; Supplementary Fig. 4A). Forager-related ancestry is even more scarce in Bantu groups from regions further north, including Malawi where Kx'a and Tuu-related ancestry was found in ancient human remains pre-dating the Bantu expansion (Skoglund et al. 2017). In southwestern Bantu populations from Angola, Namibia and Botswana, low to intermediate levels of forager gene flow have been observed (Supplementary Fig. 4A). Marks et al. (2015) noted that the highest levels of forager introgression into Bantu populations are found to the south of a boundary running southeastwards from the Angola/Namibia border across northern Botswana up to the Mozambique/South Africa border. Since this line represents the edge of summer-rainfall, it might have retarded the advance of Bantu-speakers relying on summer-rainfall crops, favoring their interactions with local populations (Marks et al. 2015). Other factors may have additionally contributed to this pattern, including a surfer-like effect commonly observed in range expansions, whereby most signs of introgression with resident populations occur far from the source of the expansion (Currat et al. 2008).

The intensity of sex-biased gene flow is also variable across southern Africa (Bajić et al. 2018; Choudhury et al. 2021; Sengupta et al. 2021). Bajić et al. (2018) showed that the observed variation is geographically structured, with sex-biased admixture increasing from north to south, possibly due to changing patterns of social asymmetry

at different stages of the Bantu migrations. In this context, future research may reveal more about how local social practices and livelihoods influence the way in which different Bantu-speaking communities interact with their foraging neighbors.

Notwithstanding localized contact profiles and persisting study gaps in the geographical coverage of modern-day Bantu speakers, the available data indicates that their internal differentiation was not primarily driven by admixture with resident populations, but conforms to a relatively straightforward relationship between geography, languages and genes (but see [González-Santos 2022](#) for possible complications). Despite of recent archeological findings ([Seidensticker et al. 2021](#)), which seem to contradict some conclusions drawn on the basis of genetic and linguistic reconstruction, the observed regularities provide a general framework for understanding the current distribution of Bantu peoples and languages against which other migratory models can be compared.

Genetic diversity of Khoe-Kwadi-speaking peoples

Links to eastern Africa

Unlike Kx'a, Tuu and Bantu-speaking groups, Khoe-Kwadi-speakers cannot be associated with a distinct genetic profile but display different ancestral combinations involving the entire spectrum of genetic components present in modern-day southern Africa (Fig. 4).

However, despite their lack of homogeneity, Khoe-Kwadi groups share variable amounts of their genetic ancestry with pastoral populations from eastern Africa. Traces of eastern African ancestry were first discovered in the Khwe, who were shown to have elevated frequencies of the Y-chromosome haplogroup E1b1, common in pastoral populations from Kenya and Tanzania ([Henn et al. 2008](#)). While many Khoe-Kwadi speakers display higher average frequencies of E1b1b than other southern African groups, the haplogroup is also attested among Kx'a, Tuu and Bantu speakers (Supplementary Fig. 5A) ([Bajić et al. 2018](#)). The relatively widespread occurrence of this Y-chromosome haplogroup contrasts

with the almost total absence of eastern African mtDNA lineages in Khoe-Kwadi populations ([Barbieri et al. 2014](#); [Oliveira et al. 2018](#)), suggesting a sex-bias in the introduction of eastern African ancestry to southern Africa.

The lactase persistence mutation -14010C is another significant marker associated with eastern African pastoralists ([Tishkoff et al. 2007b](#)). In southern Africa it was first identified in the Angolan Namib Desert where the Kwadi branch of Khoe-Kwadi was once spoken ([Coelho et al. 2009](#); [Rocha 2010](#)). While it was later shown that the formerly Kwadi-speaking Kwepe only display relatively low frequencies of the mutation (-4%) ([Pinto et al. 2016](#)), other Khoe-Kwadi speakers were found to have significantly higher average frequencies than other populations from southern Africa ([Breton et al. 2014](#); [Macholdt et al. 2014](#)) (Supplementary Fig. 5B).

Once genome-wide SNP data from a diverse range of southern African populations had become available ([Pickrell et al. 2012](#); [Schlebusch et al. 2012](#)), it was further revealed that variable, yet significant fractions of an autosomal eastern African genetic ancestry are present in several Khoe-Kwadi-speaking groups ([Pickrell et al. 2014](#); [Schlebusch et al. 2012](#)) (Supplementary Fig. 5C). Additional support for a prehistoric link between southern African peoples and eastern African pastoral populations was recently provided by ancient DNA studies, which found that a 1,2 ky old fossil from the coast of modern South Africa displayed ancestry related to 3,1 ky old human remains uncovered at the pastoralist site of Luxmanda, Tanzania ([Skoglund et al. 2017](#)).

How can these signs of eastern African-related ancestry be explained? In 1980 the linguist Ernst Westphal, recognizing that Khoe had little in common with Kx'a and Tuu, proposed that proto-Khoe-speaking pastoral peoples penetrated into southern Africa from the east ([Barnard 1992](#); [Westphal 1980](#)). In this model, Westphal further assumed that the original language of the immigrants was clickless and acquired clicks only in southern Africa by contact with Kx'a or Tuu-speaking groups. [Güldemann \(2008a\)](#), later extended this hypothesis to the entire Khoe-Kwadi

family and proposed that proto-Khoe-Kwadi was a click-language displaying typological and lexical similarities with Sandawe from East Africa. Both models assumed that the Khoe(-Kwadi) languages and their speakers diversified on entering southern Africa, resulting in the diverse languages and subsistence patterns that can be observed today.

Linguistic evidence for a pastoral origin of the Khoe-Kwadi is mostly restricted to the proto-Khoe-Kwadi root **guu* ‘sheep’, which has been borrowed into a wide range of Kx’a, Tuu and Bantu languages nowadays spoken across southern Africa (Güldemann 2008a) (Supplementary Fig. 6). While the term **goe* ‘cow’ is shared between Kwadi and Kalahari Khoe and is therefore sometimes presented as a possible Khoe-Kwadi root, it most likely derives from the Bantu root **gombe* via deletion of the prenasalized plosive /mb/ which would have been a foreign sound to Khoe-Kwadi speakers. A similar process – reduction of /mb/ – led to the forms *gumi* and *gube*, both of which are widespread in Khoe-Kwadi, Kx’a and Tuu. In general, the available linguistic data suggests that the ancestors of the Khoe-Kwadi were primarily sheep herders and only encountered cattle when the first Bantu-speakers arrived in southern Africa.

This is also supported by the archaeological record which shows evidence for the appearance of sheep-based pastoralism in southern Africa around 2,3 kya, several centuries before the Bantu migrations introduced crop-farming and cattle-herding (Lander and Russell 2018; Smith 2022). The oldest sheep remains are attested from the western coast of southern Africa and are frequently associated with pottery (Lander and Russell 2018, 2020; Smith 2009, 2017). Genetic studies of present-day African sheep populations have further shown that fat-tailed sheep breeds from southern Africa – often depicted in rock art – are most closely related to fat-tailed sheep from East Africa (Muigai and Hanotte 2013). In line with these results, our own unpublished genetic data indicate that fat-tailed sheep raised by the formerly Kwadi-speaking Kwepe and other pastoralist groups from the Angolan Namib are related with fat-tailed sheep populations from Somalia and Ethiopia.

Evidence for a demic migration

Taken together, the genetic, linguistic and archeological evidence appears to provide a convincing case for a demic migration of Khoe-Kwadi speaking herders introducing pastoralism from eastern to southern Africa around 2 kya. However, some scholars have challenged the hypothesis of a major migratory event, based on a number of apparent inconsistencies. First, it has been suggested that there is little archaeological evidence for an overturn in material culture following the arrival of sheep to southern Africa (Sadr 2008), in sharp contrast with the relatively fast spread of herding in the region (Jerardino et al. 2014). Second, the ethnographic record does not necessarily support a relationship between the whole Khoe-Kwadi family and pastoralism: although the Kwadi and Khokhoe branches are presently associated with a pastoralist subsistence, other Khoe-Kwadi speakers – most notably from the Kalahari Khoe branch – are hunter-gatherers and display foraging practices similar to their Kx’a and Tuu neighbors (Barnard 1992). Third, the extreme fragmentation of the eastern African component in modern Khoe-Kwadi speakers requires explanation and may suggest that the role played by demic processes in the pre-Bantu transition to pastoralism was relatively minor (Jerardino et al. 2014; Uren et al. 2016).

Still, it would be wrong to assume that all demic migrations resemble the Bantu expansion in entailing the displacement of resident communities by immigrants carrying their own cultural, linguistic and genetic heritage. Diamond and Bellwood (2003) have summarized a set of complications obscuring overt traces of people’s movements, which can be applied to the specific conditions of the Khoe-Kwadi dispersal: 1) replacement of the migrants’ language in their original homeland; 2) admixture between resident hunter-gatherers and incoming food-producers; 3) language shift by resident populations; and 4) reversion of expanding food-producers to the hunter-gatherer lifestyle. In the following, we discuss how the interplay between these four major complications may have shaped the extreme diversity in genetic make-up and subsistence patterns observed among present-day Khoe-Kwadi speakers.

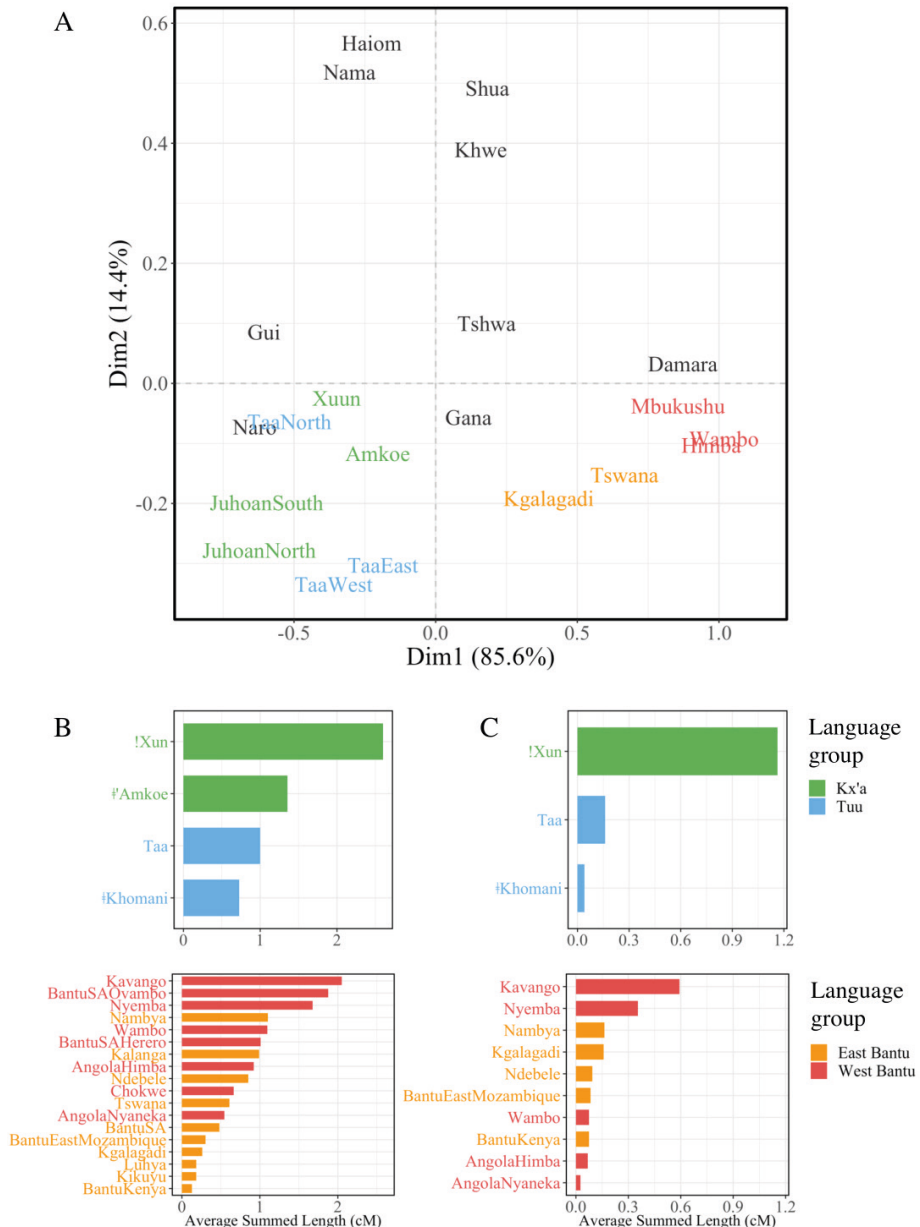


Fig. 6 - Admixture in Khoe-Kwadi speaking populations (in black). (A) Correspondence analysis plot of southern African populations based on their proportions of Tuu+Kx'a, Bantu and eastern African-related ancestries. The horizontal dimension is associated with the amounts of Tuu+Kx'a vs. Bantu ancestries, while the vertical dimension is associated with the amount of eastern African ancestry. (B) Average summed length (cM) of Identity By Descent (IBD) fragments of size 5-10 cM (~625 years) shared between the Khwe and different Kx'a, Tuu and Bantu groups from Southern Africa. (cf. Browning and Browning, 2013; Al-Asadi et al., 2019) (C) Same as in (B) for sizes over 10 cM (~225 years). Sources: Pickrell et al. (2014); Schlebusch et al. (2017); own data.

While the origin of the Bantu migrations can be traced on the basis of the Bantu family's closest relatives from the Niger-Congo macro-phylum (Greenberg 1972), Khoe-Kwadi does not have any genealogical relatives outside southern Africa (see above). Although a possible relationship between Khoe-Kwadi and Sandawe has been discussed (Güldemann 2014; Güldemann and Elderkin 2010), the number of similarities shared between the two linguistic units is small and could alternatively be explained by chance or shared contact with a third party. Thus, it seems likely that the ancestral stock of languages from which Khoe-Kwadi diverged in East Africa has disappeared.

A further complication in tracing the signals of a demic migration is the pervasive admixture that likely occurred between Khoe-Kwadi-speakers and other groups. After initial contacts involving the pastoralist incomers and resident foragers, some of the newly formed hybrid groups were further subjected to gene flow from Bantu-speaking migrants (Pickrell et al. 2014). In consequence, the present-day genetic variability of Khoe-Kwadi-speaking populations can be explained by admixture involving Kx'a and Tuu-speaking foragers, eastern African herders and Bantu-speaking agro-pastoralists (Fig. 4 and Fig. 6). The observed admixture proportions are extremely variable: the highest eastern African ancestries are nowadays detectable in the Khoekhoe-speaking Nama and Hailom who otherwise resemble their foraging neighbors; other groups display dominant Bantu (Damara) or Kx'a+Tuu ancestries (Glui-Glana, Naro), while the Khwe, Shua and Tshwa from the northern Kalahari Basin fringe have almost equal contributions from Bantu and forager populations (Fig. 6A). By analyzing the sharing of DNA fragments that are Identical By Descent (IBD), it can further be shown that the Bantu and forager-related ancestries in the Khwe are mostly derived from their Kavango+Mbukushu and !Xun-speaking neighbors (Fig. 6B) (Amorim et al. in prep). This observation is consistent with the insights of Joachim Wilhelm, who already emphasized the role played by those groups in shaping the admixed identity of the Khwe.

As the signal of eastern African ancestry detected in the Y-chromosome and autosomes is virtually absent in the mtDNA, it has been proposed that the pastoral migration into southern Africa mostly involved a movement of males (e.g. Bajić et al. 2018; Smith 2022; Vicente et al. 2021). In this scenario, it is conceivable that small numbers of male pastoralists fused with larger communities of local foragers, who would then have abandoned their own languages in favor of Khoe-Kwadi, due to the social dominance of the incomers. However, there is little evidence that the Khoe-Kwadi possessed the kind of technological or economical advantage usually associated with male-based migrations triggering large-scale language shift and cultural assimilation among resident communities (Diamond and Bellwood 2003; Goldberg et al. 2017). While the Khoekhoe-speaking herders from the Cape observed by 17th century Europeans were a powerful, strongly hierarchized people with large herds of cattle and a habit of riding oxen into battle, this image cannot be transferred to the earliest pastoralists who entered southern Africa 2 kya (Sadr 2008). In fact, the archaeological record shows that the immigrants had relatively small numbers of sheep and a Late Stone Age toolkit so similar to their foraging neighbors that some scholars have deemed their presence in southern Africa virtually “invisible” (Sadr 2008).

The frequent co-occurrence between remains of domestic and non-domestic animals at early pastoral sites in southern Africa may suggest that the ancestors of the Khoe-Kwadi followed a mixed subsistence pattern in which small-stock herding was accompanied by foraging practices similar to resident hunter-gatherer groups (Sadr 2008). In this context, dispersing Khoe-Kwadi speakers may have shifted between different livelihoods, depending on their environmental surroundings and the peoples they encountered. In the waterless deserts of the Central Kalahari and the tsetse fly-infested wetlands of the Okavango Delta, Kalahari Khoe-speakers would have abandoned pastoralism in favor of their current hunter-gatherer lifestyle (Güldemann 2008a; Westphal 1980). Along the Atlantic seaboard

and on the southern Kalahari Basin fringe, Khoekhoe speakers found better conditions to develop their pastoral practices and most likely received cattle from Bantu speakers, thus creating the powerful ethnic identity observed by the first European travelers (Sadr 2008; Smith 2022; but see Fauvelle-Aymar 2008 for a different opinion). In southwestern Angola, the formerly Kwadi-speaking Kwepe became a relatively small, marginalized group displaying a herding culture clearly rooted within the southwestern Bantu pastoral complex embodied by the Herero, Himba and Kuvale (Almeida 1965; Oliveira et al. 2018, 2019; Pinto et al. 2016).

To account for the lack of sharp socio-economic differences between incoming pastoralists and local hunter-gatherers, we suggest that the observed male-bias in the eastern African-related ancestry of Khoe-Kwadi-speaking groups may not have been caused by male-based migrations, but by accumulated female-biased gene flow from resident foragers. If in a simple deterministic model we assume, for example, that small groups of eastern African pastoralists received each generation 3% of their genes from nearby foragers, with three times more female migrants than males, the original eastern African genetic makeup in the autosomes would have been diluted to 50% in 23 generations (690 years). By this time, the Y-chromosome/mtDNA ratio for the eastern African ancestry would be around 2 (71%/35%). After 65 generations (~2 ky) the eastern African autosomal ancestry would have decreased to 14%, with a Y-chromosome/mtDNA ratio of 7.4 (37%/5%) (Supplementary Fig. 7). This incremental process is in pace with the finding that a 1,2 ky old female from a herder context in South Africa had higher amounts (40%) of eastern African-related ancestry than any modern Khoe-Kwadi-speaking group (Skoglund et al. 2017).

Since gradual, stepwise geneflow from foragers would imply that in each generation, Khoe-Kwadi-speakers constituted the majority in their own groups, the over time dilution of the original eastern African ancestry would not have been accompanied by the loss of their languages,

which still remain the most distinctive aspect of their ethnic identities. This does not mean that all modern Khoe-Kwadi speakers preserve their original languages. For example, it is likely that the presently Khoekhoe-speaking Damara and Hailom from northern Namibia abandoned their original languages in contact with Nama pastoralists. However, both cases of language shift possibly resulted from socio-economically skewed contact that occurred when dispossessed Herero (Damara) and !Xun communities (Hailom) encountered northwards migrating Khoekhoe, who had already acquired cattle and were a powerful force in the ethnographic landscape of southern Africa (Bajić et al. 2018; Barnard 1992; Oliveira et al. 2018).

While hybrid groups between eastern African Khoe-Kwadi speakers and local foragers were still in the process of being formed, the first Bantu-speaking farmers reached southern Africa. The variable amounts of Bantu-related ancestry in modern Khoe-Kwadi speakers suggest different types of interaction. Contact relations appear to have been especially dense along the northern and eastern Kalahari Basin fringe, with the Khwe, Shua, Tshwa and Glana all displaying considerable Bantu-related autosomal ancestries (Fig. 6A). The genetic profile of the Khwe from the Okavango River Basin suggests a particular type of leveled interaction in which gene-flow with southwestern Bantu peoples is symmetrically reflected in both mtDNA and Y-chromosome lineages (Bajić et al. 2018; Barbieri et al. 2014). Our own ethnographic observations in Namibia and Botswana confirm the close relationship between the Khwe and their Bantu-speaking neighbors.

Migration routes

The genetic fragmentation of modern Khoe-Kwadi speakers creates difficulties for the reconstruction of migratory pathways and splitting events. However, modern Khoe-Kwadi languages share a remote common ancestor from whom they can be shown to have descended in a tree-like fashion, similar to languages of the Bantu family. Hence, it is expected that a phylogeographic analysis of the linguistic data may lead

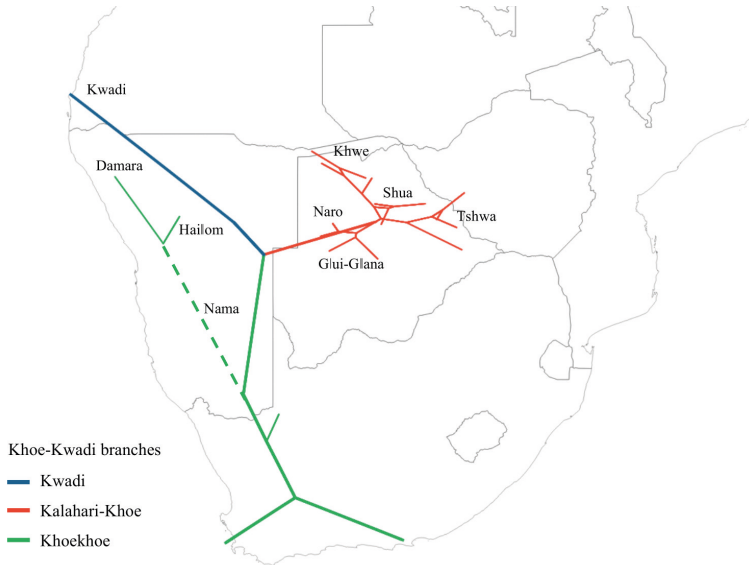


Fig. 7: Bayesian phylogeographic analysis of 23 Khoekwadi languages (Bouckaert 2016; Bouckaert et al. 2019). The analysis places the dispersion point within southern Africa in the border between Namibia and Botswana. From there, Kwadi speakers migrated northwards into Angola, while Khoekhoe-speakers went south into modern-day South Africa. The eastwards migration of the Kalahari Khoek into the Kalahari Basin is associated with a reversion to foraging. The dashed line indicates a later northwards migration of the Khoekhoe-speaking Nama associated with a language shift in the Damara and Hailom. Sources: Kwadi: Westphal (no date a); own data; Khoekhoe: Haacke and Eiseb (2002); Meinhof (1930); Nienaber (1963); Kalahari Khoek: Chebanne and Mathes (2013); Collins & Chebanne (2014); Dornan (1917); Kilian-Hatz (2003); Nakagawa (2011, 2014); Phiri (2019); Visser (2001); Vossen (1997); Westphal (no date b); own data.

to an approximate retrieval of the geographical routes taken by the ancestors of the Khoekwadi, following their arrival in southern Africa. In Figure 7, we present a Bayesian analysis of 1092 lexical roots in 23 Khoekwadi languages which were assembled and analyzed in a geographical framework (Fehn et al. in prep).

Our tree indicates that the ancestors of the Khoekwadi first migrated southwestwards, towards the border between Namibia and Botswana. Based on a different linguistic analysis, this area was previously indicated as homeland of the Khoekhoe (Heine and König 2008) and corresponds to the location of some of the oldest pastoralism-related findings in southern Africa (Lander and Russell 2018; Robbins et al. 2005). From there, one branching event involved a northward migration of Kwadi speakers towards southwestern Angola, most probably retaining a pastoralist

lifestyle. The remaining Khoek group of Khoekwadi diverged into a Khoekhoe and a Kalahari Khoek branch, who migrated south- and eastwards, respectively. The southward migration of the Khoekhoe may be linked to the rapid dispersion of herding along the Atlantic seaboard and later towards the interior of modern-day South Africa, as indicated by the archaeological record (Lander and Russell 2018; Vicente et al. 2021). More recently, Khoekhoe pastoralists moved from South Africa into modern-day Namibia where they interacted with the ancestors of the Damara and Hailom foragers (Barnard 1992). In contrast to the movement of the Khoekhoe, which targeted the fertile regions of the Cape, the eastward migration of the Kalahari Khoek towards the dry areas of the central Kalahari and the wetlands of the Okavango River Basin did not sustain a pastoral lifestyle and eventually led to the adoption of a foraging subsistence.

Irrespective of their individual migratory pathways, it seems clear that all Khoe-Kwadi groups penetrated into areas populated by foragers genetically related to Kx'a and Tuu-speaking groups: modern descendants of the Khoekhoe, including the Nama, all display significant proportions of ancestry related to speakers of the !Ui-branch of Tuu, while Kalahari Khoe-speakers share ancestry with their respective !Xun, †Amkoe and Taa-speaking neighbors (Fig. 4). Although our tree assumes that Khoe-Kwadi languages diversified mainly through processes of vertical, rather than horizontal change, there can be little doubt that genetic admixture was accompanied by the transfer of linguistic features, including lexical borrowing and structural modification. In support of this pattern, Khoekhoe can be shown to have been influenced by !Ui languages (Güldemann 2006), while Glui shares a considerable amount of lexical items and phonological features with the neighboring languages †Amkoe and Taa (Gerlach 2016; Traill and Nakagawa 2000).

Taken together, the archaeological record and contact profiles of extant Khoe-Kwadi-speaking groups are overall consistent with the phylogeographic tree, highlighting the importance of language in reconstructing the migratory movements which led to the diverse combinations of livelihoods and genetic profiles observed in present-day southern African populations. While languages cannot be equated with a given lifestyle or genetic ancestry, they are overt signals of identity and may be retained in situations which otherwise trigger contact- or environmentally-induced changes (Barth 1969). In the case of the Khoe-Kwadi, language remains the most stable common denominator shared between a heterogeneous set of peoples, in contrast with Kx'a+Tuu and Bantu speakers who are not only united by language, but also by shared cultural and genetic profiles. Like the Khwe, genetically admixed Khoe-Kwadi groups are compelling examples of ethnogenesis whose present-day ethnic identity was born from multi-layered contact. The puzzle evoked by the Khwe's unusual combination of a click-language, forager lifestyle and

dark skin color may be summarized in the words of the Angolan author Pepetela (2004), writing about an Portuguese-Angolan participant in the Angolan war of independence:

In a universe of yes and no, black and white, I represent the maybe. Maybe means no when you expect a yes, and it means yes when you expect a no.

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Author contributions

JR and AMF planned the research and wrote the paper. BA performed genetic and linguistic analyses.

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