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## Meta Gene



# At the southeast fringe of the Bantu expansion: genetic diversity and phylogenetic relationships to other sub-Saharan tribes



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## ABSTRACT

Here, we present 12 loci paternal haplotypes (Y-STR profiles) against the backdrop of the Y-SNP marker system of Bantu males from the Maputo Province of Southeast Africa, a region believed to represent the southeastern fringe of the Bantu expansion. Our Maputo Bantu group was analyzed within the context of 27 geographically relevant reference populations in order to ascertain its genetic relationship to other Bantu and non Bantu (Pygmy, Khoisan and Nilotic) sub-equatorial tribes from West and East Africa. This study entails statistical pair wise comparisons and multidimensional scaling based on YSTR Rst distances, network analyses of Bantu (B2a-M150) and Pygmy (B2b-M112) lineages as well as an assessment of Y-SNP distribution patterns. Several notable findings include the following: 1) the Maputo Province Bantu exhibits a relatively close paternal affinity with both east and west Bantu tribes due to high proportion

*Abbreviations:* SNP, single nucleotide polymorphism; STR, short tandem repeat; mtDNA, mitochondrial DNA; MAP, Maputo Province; PCR, polymerase chain reaction; RFLP, restriction fragment length polymorphism; MJ, medial joining; MDS, multi-dimensional scaling; TMRCA, time of most recent common ancestor

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of Bantu Y chromosomal markers, 2) only traces of Khoisan (1.3%) and Pygmy (1.3%) markers persist in the Maputo Province Bantu gene pool, 3) the occurrence of R1a1a-M17/M198, a member of the Eurasian R1a-M420 branch in the population of the Maputo Province, may represent back migration events and/or recent admixture events, 4) the shared presence of E1b1b1-M35 in all Tanzanian tribes examined, including Bantu and non-Bantu groups, in conjunction with its nearly complete absence in the West African populations indicate that, in addition to a shared linguistic, cultural and genetic heritage, geography (e.g., east vs. west) may have impacted the paternal landscape of sub-Saharan Africa, 5) the admixture and assimilation processes of Bantu elements were both highly complex and region-specific.

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## Introduction

Bantu encompasses a group of related languages belonging to the Niger–Congo family (Greenberg, 1972) with wide distribution throughout sub-Saharan Africa. It is believed that the proto-Bantu language originated in West Africa in what is now North Cameroon about 5000 years ago (ya) (Greenberg, 1972; Vansina, 1995). Approximately 4000 to 3000 ya, the Bantu-speaking people of West Africa initiated a major human Diaspora and associated cultural transformation that rapidly propagated agriculture and iron work along with the Bantu language to most sub-equatorial Africa (Berniell-Lee et al., 2006; Desmond and Brandt, 1984; Diamond, 1997; Newman, 1995; Phillipson, 1993). Today, the term Bantu is associated with a culture as well. It is theorized that the Bantu demographic expansion proceeded in waves along two primary routes (Berniell-Lee et al., 2006). One path of dispersal transpired from the Bantu homeland along a southwestern course, whereas a second migration, also from North Cameroon, followed a southeastern trajectory (Berniell-Lee et al., 2006; Diamond, 1997; Newman, 1995) and reached its fringes in Southeast Africa as recent as 300 ya (Vansina, 1995). However, more recent data argues for an initial single southwestern migration from the Bantu homeland and a subsequent longitudinal dispersion eastward (Alves et al., 2011; De Filippo et al., 2012; Pakendorf et al., 2011; Russell et al., 2014). It has been proposed that limited agricultural land and overpopulation were the primary motivations for this mass migration (Oliver, 2009). During this extensive geographical and cultural diffusion, the Bantu migrants encountered and interacted with the indigenous sub-Saharan tribes practicing animal husbandry or hunting gathering (Cavalli-Sforza, 1986).

The presence of Bantu-specific markers beyond their homeland suggests that in addition to facilitating an expansive acculturation process in which the Bantu technological advances and lifestyle spread across the African continent, the expansion also included geographical dispersal of the Bantu-speaking people (De Filippo et al., 2012). The degree of Bantu-specific signals in the putative areas which were colonized seems to be population and region specific. In return, the Bantu migrants not only assimilated many elements of the indigenous cultures into the Bantu lifestyle but also expanded their gene pool by intermarriage with the native people encountered during the colonization of sub-equatorial Africa (Berniell-Lee et al., 2006; Ehret, 2001; Tishkoff et al., 2007). An interesting facet of this dispersal is the relative level of gene flow among Bantu and non-Bantu populations occurring in the different regions of contact. However, due to the limited and fragmentary nature of the genetic data from Africa in which individual studies report on different populations and marker systems, many of the demographic aspects of the Bantu expansion are highly debated and unresolved. Thus, the question concerning the relative contributions of the Bantu versus those of the indigenous people to the genetic makeup of the extant sub-Saharan African populations remains largely unanswered.

The available mtDNA data indicates that varying degrees of admixture have occurred between the Bantus and native inhabitants, depending on the indigenous tribes involved, location and the marker employed. In several sub-Saharan Bantu-speaking groups, only traces of ancient mtDNA lineages have been detected (Batini et al., 2007; Quintana-Murci et al., 2008) while in others, such as the Khoisan-speaking Southwest

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