Journal of Anthropological Sciences
Vol. 88 (2010), pp. 5-8

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Bantu-Khoisan interactions at the edge of the Bantu expansions: insights from southern Angola

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For a human population geneticist, an interest in Africa hardly requires an explanation. With the highest time depth of human history and over 2000 linguistic groups spreading across highly diverse geographical settings, Africa harbors a tremendous variety of genetic patterns that remain to be explained. My own interest in African populations started with São Tomé, a tiny plantation island located at the heart of the Gulf of Guinea that was peopled by slaves imported from the adjacent areas of the mainland. Presently, I am still interested in insular populations related to the slave trade, like the Cape Verde Archipelago, facing Senegal. Moreover, I became involved in the study of genetic diversity of continental areas like Angola and Mozambique, lying at the southwestern and southeastern edges of the Bantu expansions, respectively. The area of Angola, in particular, is especially interesting for understanding the push of Bantu-speaking peoples out of the rain forest into the arid steppes of southwestern Africa. In southern Angola, the cultural and geographical proximity between Bantu and Khoisan cattle herders poses intriguing questions about the development of the relatively isolated Southwest African pastoral scene and the nature of the interactions between the vanguard of the Bantu expansions and the non-Bantu peoples from the desert.

In 1955 the late Professor António de Almeida, then leading a field expedition to southwestern Angola, became particularly interested in the Kwadi people living on the banks of River Kuroca, in the Namib Desert, just a few miles from the Angolan town of Porto Alexandre (now known as Tombua). By then, the Kwadi were already a vanishing population reduced to about fifty people, which, according to de Almeida's reports and pictures, were physically very distinct from the Khoisan and resembled Herero groups from southern Angola, like the Himba and the Kuvale (de Almeida, 1994). However, in contrast to the neighboring Herero populations, the Kwadi spoke a click language. Recognizing that this language had no close relationships with the click languages typically spoken by Khoisan peoples, António de Almeida tape-recorded some examples of its vocabulary, which were subsequently studied by Westphal (1963), who confirmed the uniqueness of the Kwadi speech. More recently, Güdelmann (2004), based on Westphal's notes, showed that Kwadi lies on a separate branch of the

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Khoe family, which groups click languages spoken by pastoral Khoisan peoples, like the Nama from neighboring Namibia. Presently, Kwadi is believed to have become extinct, its last words lying in the tapes collected by de Almeida and in the notes left by Westphal.

The fact that the last living representatives of a vanished Khoisan click language were cattle herding people resembling their Bantu neighbors provides a vivid illustration of the variety of combinations between biology, language and subsistence economy that can be found in regions where the vanguard of the Bantu expansions made contact with local Khoisan populations. Recently (Coelho *et al.*, 2009), we had the opportunity to characterize the genetic variation in populations presently dwelling in the Angolan Namib desert, in and around the homonymous town of Namibe (formally Moçâmedes). The studied region, which encompasses the zone previously inhabited by the Kwadi, has been the original core area of Angolan Herero-Bantu-speaking populations, but is presently inhabited by different Bantu-speaking groups due to relatively recent migration from surrounding areas. We focused on four representative West-Savanna Bantu-speaking peoples (Ovimbundo, Ganguela, Nyaneka-Nkumbi and Kuvale) relying on different combinations of agricultural and pastoral lifeways.

Based on mitochondrial DNA (mtDNA) and Y-chromosome data, we found that, in spite of their peripheral location, the studied populations retained a clear genetic link to West-Central African populations from areas that are adjacent to the original heartland of the Bantu expansions. However, unequivocal signs of admixture with local Khoisan peoples were also observed, especially among the Herero-speaking Kuvale, where as much as 33% of their mtDNA pool was found to be of Khoisan origin. Historical and archeological evidence indicate that, before the arrival of Bantu-speaking populations, Khoisan ethnic groups with pastoral subsistence (collectively known as Khoikhoi) had a significant presence in southwestern Africa. This evidence, together with the fact that the Kuvale, like other Herero populations from southwestern Africa, are one of the most cattle-exclusive pastoral Bantu-speaking peoples, raises the interesting possibility that the sharing of a pastoral way of life played a central role in promoting gene flow between the Kuvale and the Khoikhoi; or, alternatively, that interactions with the Khoikhoi were instrumental for the pastoral specialization of the Kuvale, who needed to adapt to a new arid environment where traditional Bantu agricultural practices were no longer possible. Given the above mentioned cultural and physical resemblance between the Kuvale and their neighboring Kwadi, it is tempting to imagine that the latter were an offshoot of the former who adopted the Kwadi speech in the course of more active interactions with Khoikhoi herders originally speaking this language. Later on, the Kwadi people might have been reabsorbed by their Kuvale neighbors, raising the fascinating possibility that the genetic legacy of the vanished Kwadi is now carried, at least in part, by present-day Kuvale.

Another interesting aspect of our study, was the finding of a lactase persistence variant (-14010C) at relatively low frequency (6%) in the Kuvale people. Since the -14010C variant is a genetic marker of Nilo-Saharan and Afro-Asiatic-speaking pastoral populations from Kenya and Tanzania (Tishkoff *et al.*, 2007), our observation provides genetic evidence for a connection between the relatively isolated southwestern Africa pastoral scene and the major cattle herding centers of East Africa. Direct links between Southwest and East Africa were favorite topics of early Anthropology scholars studying southwestern Africa (Blench, 2009). Estermann (1961), for example, claimed that the Kuvale, together with other Bantu herding peoples from southern Angola, had a "Chamitic" provenance, implying that they could trace at least part of their origins to non-Bantu populations from the region of the Great

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Lakes. However, on the basis of our mtDNA and Y-chromosome data, we failed to find any consistent genetic affinity between the peoples from southwestern Angola and non-Bantu East Africans. Instead, it seems more likely that the -14010C variant was carried from East Africa into southwestern Africa by Khoikhoi herders who subsequently transferred it to adjacent Kuvale pastoralists as part of the admixture processes that are currently documented by the mtDNA data. In fact, archeological and linguistic data provide evidence that the ancestors of present-day southern Africa Khoikhoi peoples may have acquired their pastoral lifestyle from East African non-Bantu cattle herders spreading as far south as Central Zambia. In this setting, it seems reasonable to suppose that lactase persistence associated with the -14010C variant was transferred to the Khoikhoi together with domestic animals and pastoral habits. This transfer would explain early observations of moderate frequencies of lactose tolerance among the Khoikhoi (Casimir, 1990). Subsequent migrations of Khoikhoi herders across South Africa would eventually lead to a further transfer from the Khoikhoi to southern Bantu pastoral peoples in well defined contact zones like southwestern Angola. Recently (Torniainen *et al.*, 2009), the -14010C variant has been reported to occur at 13% frequency in the Xhosa population from South Africa, which is well known for extensive cultural and genetic interactions with the Gonaqua Khoikhoi, from whom it borrowed a number of click words. On the other hand, we found no lactase persistence variants in Bantu communities from southern Mozambique that are somewhat related to the Xhosa but did not interacted as extensively with the Khokhoi. Taken together, these observations add further support to our hypothesis in showing that the only Southern Bantu groups with lactase persistence are the ones that made cultural and genetic contact with the Khoikhoi. However, further investigation on the connection between lactose tolerance and pastoralism in southern Africa is clearly needed, especially on the poorly sampled Khoikhoi from whom lactase persistence data still relies on physiological tests performed more than thirty years ago.

This cover story is dedicated to the memory of Professor António de Almeida, who pioneered interdisciplinary studies on the anthropology of southern Angola and collected the last words of a vanished language.

Research work was financed by the following grants from Fundação para a Ciência e a Tecnologia (FCT): PPCDT/BIA-BDE/56654/2004 and PTDC/BIA-BDE/68999/2006.

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