

Title: Ancient Ethiopian genome reveals extensive Eurasian admixture throughout the African continent

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Abstract: Characterizing genetic diversity in Africa is a crucial step for most analyses reconstructing the evolutionary history of anatomically modern humans. However, historic migrations from Eurasia into Africa have affected many contemporary populations, confounding inferences. Here, we present a 12.5x coverage ancient genome of an Ethiopian male ('Mota') who lived approximately 4,500 years ago. We use this genome to demonstrate that the Eurasian backflow into Africa came from a population closely related to Early Neolithic farmers, who had colonized Europe 4,000 years earlier. The extent of this backflow was much greater than previously reported, reaching all the way to Central, West and Southern Africa, affecting even populations such as Yoruba and Mbuti, previously thought to be relatively unadmixed, who harbor 6-7% Eurasian ancestry.

One Sentence Summary: An ancient genome from Ethiopia reveals widespread Eurasian admixture into modern African populations.

Main Text: The ability to sequence ancient genomes has revolutionized our understanding of human evolution. However, genetic analyses of ancient material have focused on individuals from temperate and arctic regions, where ancient DNA is preserved over longer time frames (1). Africa has so far failed to yield skeletal remains with much aDNA, with the exception of a few poorly preserved specimens from which only mitochondrial DNA could be extracted (2). This is particularly unfortunate, as African genetic diversity is crucial to most analyses reconstructing the evolutionary history of anatomically modern humans, by providing the baseline against which other events are defined. In the absence of ancient DNA, geneticists rely on contemporary African populations, but a number of historic events, in particular a genetic backflow from West Eurasia into Eastern Africa (3, 4), act as confounding factors.

Here, we present an ancient human genome from Africa, and use it to disentangle the effects of recent population movement into Africa. By sampling the petrous bone (5), we sequenced the genome of a male from Mota Cave (herein referred to as 'Mota') in the southern Ethiopian highlands, with a mean coverage of 12.5x (6). Contamination was estimated to be between 0.29 and 1.26% (6). Mota's remains were dated to ~4,500 years ago (direct calibrated radiocarbon date (6)), and thus predate both the Bantu expansion (7), and, more importantly, the 3ky-old West Eurasian backflow which has left strong genetic signatures in the whole of Eastern and, to a lesser extent, Southern Africa (3, 4).

We compared Mota to contemporary human populations (6). Both Principal Component Analysis (Fig. 1A) and outgroup f_3 analysis using Ju|'hoansi (Khoisan) from Southern Africa as the outgroup (Fig. 1B,C) place this ancient individual close to contemporary Ethiopian populations, and more specifically to the Ari, a group of Omotic speakers from southern Ethiopia, to the West of the highland region where Mota lived. Our ancient genome confirms the view that the divergence of this language family results from the relative isolation of its speakers (8), and indicates population continuity over the last ~4,500 years in this region of Eastern Africa.

The age of Mota means that he should predate the West Eurasian backflow, which has been dated to ~3,000 years ago (3, 4). We formally tested this by using an f_4 ratio estimating the West Eurasian component (6), following the approach adopted by Pickrell et al (3). As expected, we failed to find any West Eurasian component in Mota (Table S5), thus providing support for previous dating of that event (3, 4).

Given that Mota predates the backflow, we searched for its most likely source by modelling the Ari, the contemporary population closest to our ancient genome, as a mixture of Mota and another West Eurasian population (6). We investigated both contemporary sources (3) as well as other Eurasian ancient genomes (5, 9). In this analysis, contemporary Sardinians and the early Neolithic LBK (Stuttgart) genome stand out (Fig. 2A). Previous analyses have shown Sardinians to be the closest modern representatives of early Neolithic farmers (10, 11), implying that the backflow came from the same genetic source that fuelled the Neolithic expansion into Europe from the Near East/Anatolia, before recent historic events changed the genetic makeup of populations living in that region. An analysis with haplotype sharing also identified a connection between contemporary Ethiopians and Anatolia (4, 12). Interestingly, archaeological evidence dates the arrival of Near Eastern domesticates (such as wheat, barley and lentils) to the same time period (circa 3,000 years ago) (13, 14), suggesting that the direct descendants of the farmers that earlier brought agriculture into Europe may have also played a role in the development of new forms of food production in the Horn of Africa.

Using Mota as an unadmixed African reference and the early farmer LBK as the source of the West Eurasian component, it is possible to reassess the magnitude and geographic extent of historical migrations, avoiding the complications of using admixed contemporary populations (6). We estimated a substantially higher Eurasian backflow admixture than previously detected (3), with an additional 4-7% of the genome of most African populations tracing back to a Eurasian source, and, more importantly, we detected a much broader geographical impact of the backflow, going all the way to West and Southern Africa (Fig. 2B). Even though the West Eurasian component in these regions is smaller than in Eastern Africa, it is still sizeable, with Yoruba and Mbuti, who are often used

as African references (15, 16), showing 7% and 6%, respectively, of their genomes to be of Eurasian origin (Table S5).

Since Mota predates recent demographic events, his genome can act as an ideal African reference to understand episodes during the out-of-Africa expansion. We used him as the African reference to quantify Neanderthal introgression in a number of contemporary genomes (6). Both Yoruba and Mbuti, which are routinely used as African references for this type of analysis (15, 16), show a marginally closer affinity with Neanderthal than Mota based on D statistics, and an f_4 ratio analysis detected a small Neanderthal component in these genomes at around 0.2-0.7%; greater than previously suggested (16), and consistent with our estimates of the magnitude of their Western Eurasian ancestry (6). Whilst the magnitude of Neanderthal ancestry in these contemporary African populations is not enough to change conclusions qualitatively (estimates of Neanderthal ancestry in French and Han only increased marginally when tested with Mota as a reference), it should be accounted for when looking for specific introgressed haplotypes (17) or searching for unknown ancient hominins who might have hybridized with African populations (18).

We also investigated the Mota genome for a number of phenotypes of interest (6). As expected, Mota lacked any of the derived alleles found in Eurasian populations for eye and skin colour, suggesting that he had brown eyes and dark skin. Mota lacked any of the currently known alleles that give lactose tolerance, which may have implications concerning when pastoralism appeared in southwestern Ethiopia. In addition, Mota did possess all three selected alleles that have been recently shown to play a role in the adaptation to altitude in contemporary highland Ethiopian populations (19). The presence of these mutations supports our conclusion that Mota is the descendant of highland dwellers, who have lived in this environment long enough to accumulate adaptations to the altitude (20, 21).

Until now, it has been necessary to use contemporary African populations as the baseline against which events during the worldwide expansion of Anatomically Modern Humans are defined (16, 22–24). By obtaining an ancient whole genome from this continent, we have shown that having an unadmixed reference that predates the large number of recent historical migrations can greatly improve our inference. This result stresses the importance of obtaining unadmixed baseline data to reconstruct demographic events, and the limitations of analyses that are solely based on contemporary populations. Even older African genomes will thus be needed to investigate key demographic events that predate Mota, such as earlier instances of back-flows into Africa (25).

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Figure legends

Fig. 1. Mota shows a very high degree of similarity with the highland Ethiopian Ari populations. (A), PCA showing Mota projected onto components loaded on contemporary African and Eurasian populations. The inset magnifies the PCA space occupied by Ethiopian and Eastern African populations. (B), outgroup f_3 quantifying the shared drift between Mota and contemporary African populations, using Ju|'hoansi (Khoisan) as an outgroup; bars represent standard error; (C), map showing the distribution of outgroup f_3 values across the African continent. In (A) and (B), populations speaking Nilo-Saharan languages are marked with blue shades, Omotic speakers with red, Cushitic with orange, Semitic with yellow, and Bantu with green. Mota is denoted by a black symbol.

Fig. 2. Quantifying the geographic extent and origin of the West Eurasian component in Africa. (A), admixture f_3 identifying likely sources of the West Eurasian component (lowest f_3 values). Contemporary populations in blue, ancient genomes in red; bars represent standard error. (B), map showing the proportion of West Eurasian component, $\lambda_{\text{Mota,LBK}}$, across the African continent.

Supplementary Materials:

SOM Text

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Figures S1-S8

Tables S1-S14