

Ancient DNA illuminates how humans travelled and interacted in Stone Age Africa

Archaeologists have various hypotheses for how populations changed in Africa about 50,000 years ago, during the Later Stone Age transition. Now, the earliest available ancient-DNA sequences from sub-Saharan Africa reveal a complex Late Pleistocene population structure, pointing to large shifts in human movement and in patterns of social interaction.

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The problem

By around 50 thousand years ago (ka) – during the Late Pleistocene age – new technologies and symbolic behaviours (for example, bead wearing) were becoming so widespread in sub-Saharan Africa that archaeologists refer to this period as the transition from the Middle to Later Stone Age¹. What prompted this shift, at least 200,000 years after our species evolved, is a long-standing mystery. It's possible that people began living in larger, more-connected groups and started interacting over longer distances, bringing together previously isolated populations. Although ancient-DNA research holds promise for testing such hypotheses, it has been limited by a lack of Pleistocene-epoch sequences from sub-Saharan Africa. Most ancient-DNA samples are from the past 5,000 years, when other processes – such as a shift from foraging to herding and farming – led to dramatic demographic changes^{2–4}. This makes it difficult to reconstruct deeper population structures using DNA from present-day African people alone.

The discovery

We sampled individuals associated with the Later Stone Age at Late Pleistocene and early Holocene sites across eastern and south-central Africa. We generated genome-wide data for 6 individuals from 5 sites in Tanzania, Zambia and Malawi dated to around 18–5 ka – three of these ancient-DNA sequences are the oldest from sub-Saharan Africa obtained so far (Fig. 1a). We analysed these sequences alongside new and published data from 28 individuals associated with foraging contexts in eastern, central and southern Africa dated to between 9,000 and 400 years ago. Using new statistical methods and comparative sequences from present-day groups, we identified patterns that existed before the sweeping changes of the past 5,000 years.

We found that all individuals, despite being separated by thousands of kilometres and years, could be modelled as a variable mix of central African ancestry (represented by present-day Mbuti foragers), eastern African ancestry (represented by an ancient forager from Mota, Ethiopia) and southern African ancestry (represented by ancient and present-day southern African foragers) (Fig. 1b). Geographical proximity was the strongest predictor of genetic similarity, indicating that this population structure had formed and remained stable for thousands of years before the sampled individuals lived – that is, well before around 20 ka. It must have developed after the emergence

of the Mota-related lineage about 80–60 ka and the split between central African Mbuti and Aka lineages around 50 ka. Within this overall pattern, we observed different regional trajectories: some movement and gene flow persisted over time in Kenya and Tanzania, whereas interactions in Malawi and Zambia became highly localized.

The implications

Our results can be explained by Late Pleistocene changes in human mobility and gene flow. Around 50 ka, people began travelling farther and encountering reproductive partners from different groups, spreading Mota-related ancestry as far south as Zambia, and southern-African-related ancestry as far north as Kenya. However, the high degree of homogeneity in each region indicates that, by about 20 ka, people had returned to choosing partners locally. This was especially true in Malawi and Zambia, where high relatedness was found only between individuals from the same site.

Our genetic data add to archaeological, skeletal and linguistic evidence that the Later Stone Age involved elaborate exchange networks and interregional connections between certain groups, resulting in widespread, shared cultural traditions^{1,5}. Archaeological findings suggest that materials such as obsidian and ostrich eggshells were moved across long distances in the Pleistocene. Our findings suggest that, at least initially, people travelled widely, too. By the end of the Pleistocene, people were once again remaining local, perhaps explaining trends towards 'regionalization' or the appearance of regionally distinct artefact traditions. However, our study was limited by the few individuals with well-preserved ancient DNA and direct dates from sub-Saharan Africa. Studying individuals from more sites could clarify the differences in gene flow that we noted across both space and time.

Future research should focus on evaluating these broad demographic trends against local ecological and archaeological records to understand why people might have changed their behaviour⁵. These findings also highlight the need for archaeological research that is focused on central Africa, a crucial yet understudied reservoir of human diversity and interaction.

Elizabeth Sawchuk is at the University of Alberta, Edmonton, Canada, and **Mary Prendergast** is at Rice University, Houston, Texas, USA.

EXPERT OPINION

The results are an exciting contribution that should be of interest to a wide range of researchers in human-population genetics and evolution. The study demonstrates well that, although the conditions of ancient-DNA preservation in Africa are not optimal, there

are at least some sites and remains that can be made to work well enough.” (CC BY 4.0)

Diyendo Massilani is at the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

FIGURE

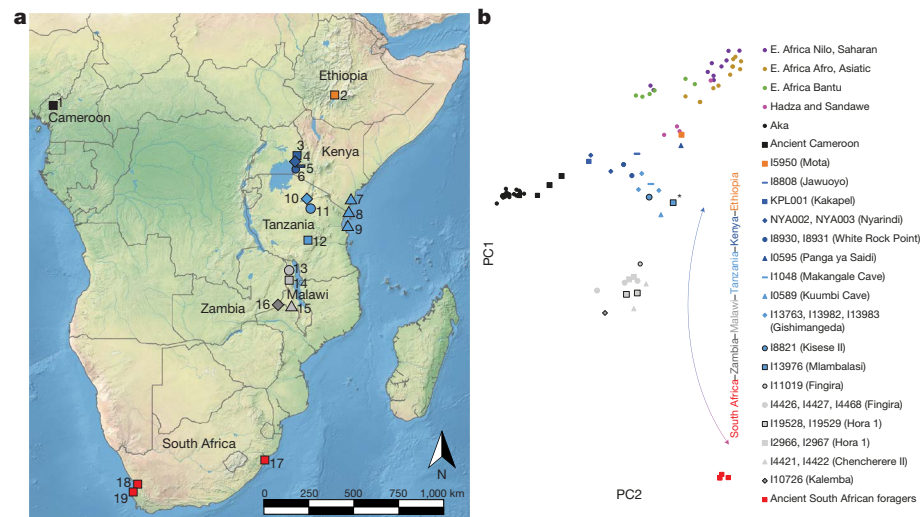


Figure 1 | Ancient-DNA-sampling locations and results. a, Archaeological site locations for the individuals analysed in this study. 1, Shum Laka; 2, Mota Cave; 3, Kakapel Rockshelter (RS); 4, Nyarindi RS; 5, Jawuoyo RS; 6, White Rock Point; 7, Panga ya Saidi; 8, Makangale Cave; 9, Kuumbi Cave; 10, Gishimangeda Cave; 11, Kisese II RS; 12, Mlambalasi RS; 13, Fingira; 14, Hora I; 15, Chencherere II; 16, Kalemba RS; 17, Ballito Bay; 18, Faraoskop RS; 19, St Helena. The base map is from Natural Earth (<https://www.naturalearthdata.com>). **b**, Results of a principal-component (PC) analysis showing the individuals' genetic relatedness, for which the axes were computed using present-day groups: Jul'hoansi foragers (San) from southern Africa, Mbuti foragers from central Africa and Dinka pastoralists from northeastern Africa. Small circles represent present-day individuals; other symbols represent ancient individuals matching the markers in **a**. The strong correlation between the data shown in **a** and **b** indicates that geographical proximity is the greatest predictor of relatedness. E, east. Lipson, M. *et al. Nature* (CC BY 4.0).

BEHIND THE PAPER

Ancient DNA from Africa has enormous potential to illuminate our species' origins and early history, but it is difficult to recover. This study relied on recent sampling methods and technology to extract and sequence Pleistocene-epoch ancient DNA — but it was possible only because of decades of archaeological research and a 5-year collaboration between more than 40 archaeologists, bioarchaeologists, curators and geneticists. Although some of the individuals we sequenced were recovered in the past decade, others were excavated more than half a century ago, highlighting

the crucial role of African museums and their curators in preserving our shared human history. We have only scratched the surface of human genetic diversity in Africa, past and present. Future research on understudied regions and time periods will succeed only through strong international collaborations and an interdisciplinary approach.

E.S. and M.P.

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FROM THE EDITOR

Retrieving DNA of sufficient quality for genomic analysis from ancient bones from Africa is difficult because of the increased degradation of DNA in hot climates. The genome-wide data sets from the Late Pleistocene and Holocene epochs from sites in eastern and south-central Africa reported in this study (including the analysis of six previously unreported individuals) are precious and allow insights into the genetic make-up and interactions of past human populations who lived in sub-Saharan Africa.

Michelle Trenkmann, Senior Editor, *Nature*