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A climatic context for the out-of-Africa migration

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ABSTRACT

Around 200,000 yr ago, *Homo sapiens* emerged in Africa. By 40 ka, *Homo sapiens* had spread throughout Eurasia, and a major competing species, the Neanderthals, became extinct. The factors that drove our species "out of Africa" remain a topic of vigorous debate. Existing research invokes climate change as either providing opportunities or imposing limits on human migration. Yet the paleoclimate history of northeast Africa, the gateway to migration, is unknown. Here, we reconstruct temperature and aridity in the Horn of Africa region spanning the past 200,000 yr. Our data suggest that warm and wet conditions from 120,000 to 90,000 yr ago could have facilitated early waves of human migration toward the Levant and Arabia, as supported by fossil and lithic evidence. However, the primary out-of-Africa event, as constrained by genetic studies (ca. 65–55 ka), occurred during a cold and dry time. This complicates the climate-migration relationship, suggesting that both "push" and "pull" factors may have prompted *Homo sapiens* to colonize Eurasia.

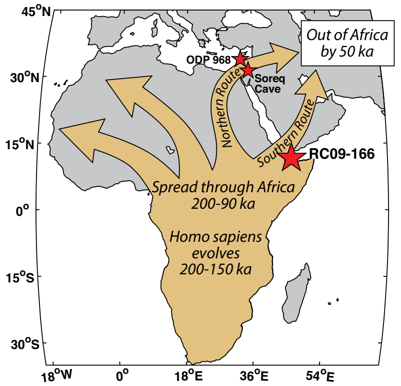

Figure 1. Site map and schematic of geographic expansion of *Homo sapiens* from 200 ka to 50 ka. Data from this study are derived from marine sediment core RC09-166. Also shown are locations of the Ocean Drilling Program (ODP) Site 968 sapropel record and Soreq Cave (Israel) $\delta^{18}O$ record.

INTRODUCTION

Homo sapiens first evolved in southern or eastern Africa ~200,000 yr ago (ca. 200 ka) and then dispersed out of Africa between 120 ka and 50 ka, based on fossil, archaeological, and genetic evidence (Groucutt et al., 2015). The exact timing of the dispersal is uncertain, with competing models arguing for an early migration during Marine Isotope Stage 5 (MIS 5; 130–80 ka) (Petraglia et al., 2010; Armitage et al., 2011), a later migration spanning MIS 4 and MIS 3 (75–50 ka) (Soares et al., 2012; Mellars et al., 2013), or a combination of these two events (Groucutt et al., 2015). The role of climate change in driving out-of-Africa migration also remains a topic of debate. Model simulations suggest that during MIS 5, a more humid climate would have created vegetated corridors for humans to disperse from North Africa (Timmermann and Friedrich, 2016). However, paleoenvironmental data across central and south Africa describe a complex mosaic of climate and environmental changes during MIS 5 that do not clearly align with orbitally driven climatic changes or patterns in human occupation (Blome et al., 2012). The Toba volcanic eruption (75 ka, in Indonesia) has been implicated as a possible cause of the out-of-Africa migration, population bottlenecks, and/or extinction of early *Homo sapiens* populations in the Levant (Ambrose, 1998). However, there is no evidence for climatic perturbation during the Toba event in southeast Africa (Lane et al., 2013; Jackson et al., 2015), and bottlenecks and migration associated with Toba are disputed (Soares et al., 2012; Mellars et al., 2013). In short, the climatic conditions under which humans first left Africa, as well as the influence of climate on human migration, remain poorly constrained.

Here, we present a new record of northeast African paleoclimate spanning the past 200 k.y. derived from Lamont-Doherty Earth Observatory (New York, USA) marine sediment core RC09-166 in the Gulf of Aden (Fig. 1). This record constrains climatic change in a region proximal to one of the hypothesized human migration routes (Fig. 1). Humans migrating out of Africa may have taken either the "northern route" across the Sinai peninsula, which would have provided overland passage (Lahr and Foley, 1994; Pagani et al., 2015), or a "southern route" across the Bab al-Mandeb strait during times of lower sea level, when island-hopping would have provided access to the Arabian peninsula (Soares et al., 2012) (Fig. 1).

METHODS

Core RC09-166 was collected in 1965 by Lamont-Doherty Earth Observatory from the R/V *Robert D. Conrad* at 12.15°N, 44.4°E, 738 m below sea level. We used radiocarbon dating and tuning to the global benthic $\delta^{18}O$ stack to provide a chronology for core RC09-166, which has an average sedimentation rate of 6 cm/ka (see the GSA Data Repository[1] for further details). To infer past changes in aridity over land, we measured the stable hydrogen isotopic composition of leaf waxes (δD_{wax}), an approach that we have used to reconstruct hydroclimate in the Horn of Africa previously (Tierney et al., 2013; see the Data Repository for analytical protocols). Leaf waxes are transported to the Gulf of Aden primarily by aeolian processes; given that aerosol transport peaks with the southwesterly summer winds, the waxes reflect climate conditions in the Horn of Africa and Afar regions (Tierney and deMenocal, 2013). δD_{wax} records the isotopic composition of precipitation (δD_P) that plants use to synthesize their lipids (Sachse et al., 2012). In the arid tropics and subtropics, the "amount effect" (Dansgaard, 1964) has a strong influence on δD_P, with low rainfall leading to higher values, and higher rainfall, lower values. δD_{wax} is thus a sensitive tracer of past aridity in these regions (Tierney and deMenocal, 2013). To investigate the evolution of regional temperatures, we reconstructed sea-surface temperature (SST) using the alkenone paleothermometer (see the Data Repository for analytical protocols). Both alkenone and leaf wax analyses were measured every 10 cm along the core, for an average time resolution of 1.6 ka.

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[1]GSA Data Repository item 2017349, supplementary materials and methods, is available online at http://www.geosociety.org/datarepository/2017/ or on request from editing@geosociety.org. Data associated with this manuscript are publicly available at the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information Paleoclimatology archive at https://www.ncdc.noaa.gov/paleo/study/22544/.

GEOLOGY, November 2017; v. 45; no. 11; p. 1023–1026 | Data Repository item 2017349 | doi:10.1130/G39457.1 | Published online 2 October 2017

RESULTS AND DISCUSSION

The δD_{wax} data reveal that changes in orbital precession have exerted a strong control on hydroclimate in northeast Africa during the past 200 ka, with humid intervals occurring regularly during maximum insolation in boreal summer (June–August) (Fig. 2A). The close relationship between insolation and Horn of Africa hydroclimate suggests that the west African monsoon, which today just barely reaches the Ethiopian highlands, expanded to the northeast during times of summer perihelion, locking the rhythm of Horn of Africa precipitation with west African precipitation over precessional time scales. The strong similarity of our shorter δD_{wax} record from the Horn of Africa (Tierney and deMenocal, 2013) to west African δD_{wax} records (Tierney et al., 2017) supports this view; all show a pronounced depletion in δD_{wax} during the early Holocene African Humid Period. However, it is important to note that during glacial periods (MIS 2–3, 4, and 6), aridity prevails in spite of changes in precession, and conversely, the stadial substages during the last interglacial period (MIS 5b and 5d) are not as dry as full glacial times (Fig. 2A). This suggests that glacial boundary conditions also influenced Horn of Africa paleoclimate, consistent with our earlier work (Tierney and deMenocal, 2013). This influence may manifest through the impact of cooler global temperatures, lower CO_2, and/or increased snow and ice in Eurasia on Afro-Asian monsoon circulation (Prell and Kutzbach, 1992).

Alkenone SST data describe how temperatures have evolved in the Horn of Africa region. Unlike δD_{wax}, alkenone SSTs do not show a clear relationship with precession or glaciation over the past 200 ka (Fig. 2B). SSTs are consistently warm from 200 ka to 80 ka, after which they cool during MIS 4–2 (Fig. 2B). Our data are similar to an alkenone record from the southwest coast of India (Fig. 2B) as well as sites in the cooler Arabian Sea upwelling zone (Rostek et al., 1997). This indicates that the temperature variations we infer are neither a local feature of the Gulf of Aden nor constrained by the thermal limits of the alkenone proxy, but rather, are characteristic of the northwestern Indian Ocean. A curious feature of these alkenone records is relatively warm conditions during the glacial period MIS 6 (Fig. 2B). It is not yet clear whether this is proxy specific, or how spatially pervasive it is beyond the northwestern Indian Ocean. Notably, these regional SST changes appear to have had little influence on Horn of Africa aridity, suggesting that orbital-scale variations in hydroclimate in northeast Africa were mediated by changes in large-scale atmospheric circulation rather than regional SSTs.

To place our data in a regional context, we compare the δD_{wax} record to other indicators of northeast African hydroclimate: the Mediterranean sapropel record from ODP Site 968 (Konijnendijk et al., 2014) and $\delta^{18}O$ from Soreq Cave, Israel (Bar-Matthews et al., 1999; Grant et al., 2012). Sapropels form during periods of enhanced freshwater input to the eastern Mediterranean, which drives water-column stratification, oxygen depletion, and burial of large amounts of organic matter. Geochemical studies indicate that fresh water largely comes from Nile River discharge and other North African sources (Rohling et al., 2015), linking sapropel formation directly to the African monsoon. Likewise, the Soreq Cave record is a "downstream" recorder of African climate. On orbital time scales, $\delta^{18}O$ of precipitation in the Levant is dominated by a "source-water effect," as the source of rainfall—the eastern Mediterranean—experiences dramatic shifts in surface-water $\delta^{18}O$ with changes in freshwater input from Africa (Grant et al., 2012). Soreq $\delta^{18}O$ therefore mainly records the impact of African monsoon circulation on regional water isotopes, although local aridity in the Levant may at times overprint the signal (Grant et al., 2012; Rohling et al., 2015).

The δD_{wax} data from the Horn of Africa share strong similarities with these other indicators of northeast African hydroclimate, principally in the dominance of high-amplitude, precessional variability (Fig. 3). Together these records provide a detailed climatic context for *Homo sapiens* expansion and migration. During MIS 5, *Homo sapiens* expanded and diversified from the basal lineages, leading to the spread of the species throughout central, western, and eastern Africa (Fig. 1) (Drake et al., 2011). Our δD_{wax} data indicate that this time of major continental-scale expansion coincided with warm and wet conditions in northeast Africa (Fig. 3). Periods corresponding to maximum insolation in the boreal summer (i.e., MIS 5a, 5c, 5e; Fig. 2A) were especially wet, and these three intervals correspond with sapropel deposition in the eastern Mediterranean and depletion in Soreq Cave $\delta^{18}O$ (Fig. 3), confirming that the north African monsoon was greatly expanded and invigorated during these times. This contrasts with paleoclimate evidence from southeast Africa (Lake Malawi), which indicate a series of precessionally paced "megadroughts" during MIS 6–5 (Johnson et al., 2016). The combination of a deteriorating climate in southeast Africa and a favorable climate in northern Africa may have facilitated expansion of *Homo sapiens* from their place of origin across Africa during MIS 5 (Figs. 1 and 3).

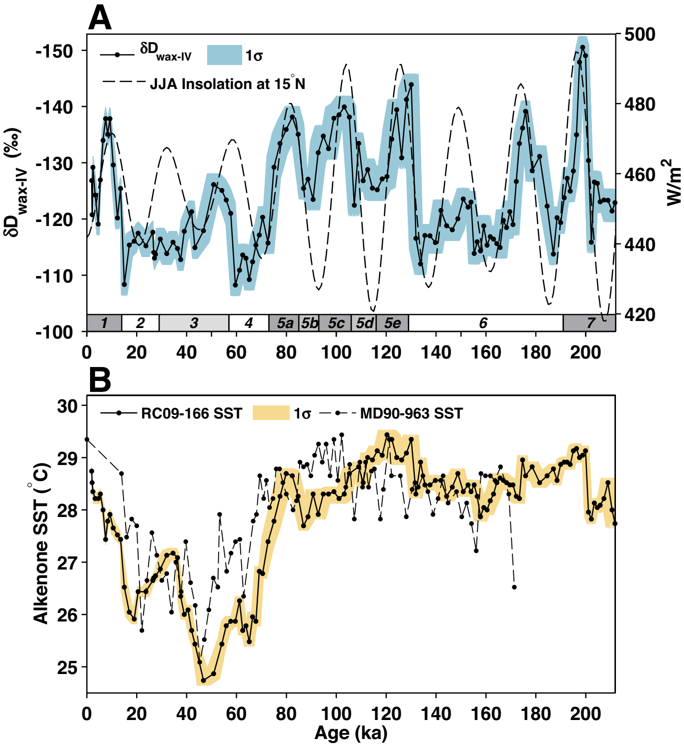

Figure 2. Paleoclimate data from the Gulf of Aden (core RC09-166). A: Stable hydrogen isotopic composition of leaf waxes, corrected for ice volume contributions ($\delta D_{wax\text{-}IV}$). Black line shows median values; blue shading indicates analytical and chronological 1σ error. Dashed line shows insolation at 15°N during June-July-August (JJA). Marine isotope stage numbers are denoted at bottom. B: Alkenone ($U^{K'}_{37}$)–based sea-surface temperatures (SSTs). Black line shows median values; yellow shading indicates analytical and chronological 1σ error. Dashed line shows alkenone SST data from core MD90-963 (Rostek et al., 1997) located southwest of India (5.04°N, 73.53°E).

Archaeological and fossil evidence indicates that *Homo sapiens* made at least limited forays into Eurasia during MIS 5. The discovery of anatomically modern human (AMH) fossils in the Qafzeh and Es Skhul caves (Israel) dating to ca. 110–80 ka (Grün et al., 2005) unequivocally demonstrates that *Homo sapiens* migrated to the Levant (Fig. 3). Lithic tools, and more recently, the presence of AMH teeth, further suggest that *Homo sapiens* may have occupied parts of Arabia and Asia (Petraglia et al., 2010; Armitage et al., 2011; Liu et al., 2015). Our paleoclimate data indicate that during this time, migration could have been facilitated by abundant rainfall during periods of maximum summer insolation, when hydroclimatic conditions were comparable to, if not more mesic than, the Holocene humid period (Fig. 3A). Given that the Holocene humid period was associated with "Green Sahara" conditions (Tierney et al., 2017), peak

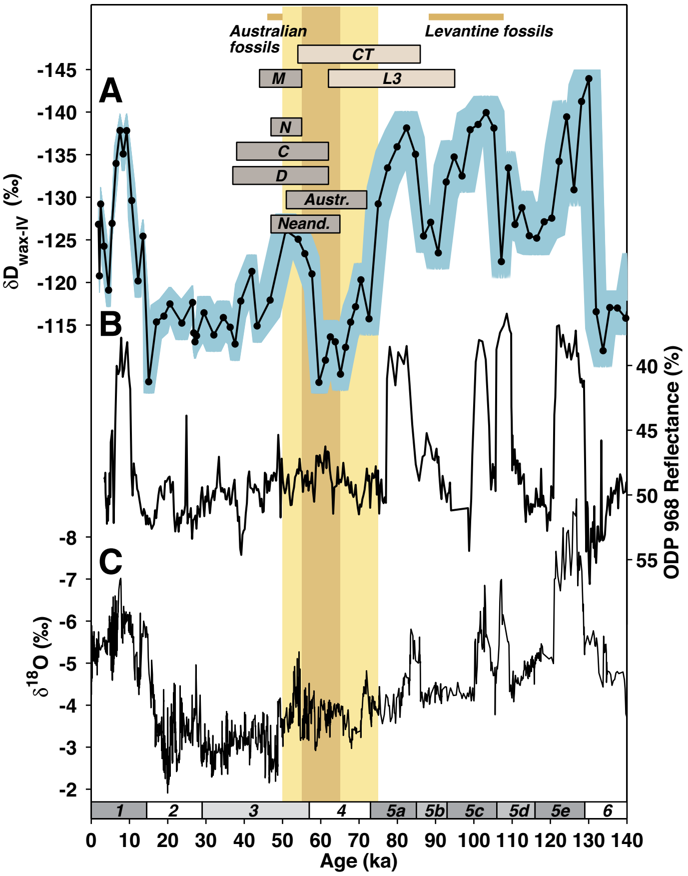

Figure 3. Hydroclimate in northeast Africa and the out-of-Africa migration. A: Stable hydrogen isotopic composition of leaf waxes corrected for ice volume contributions (δD$_{wax-IV}$) from the Gulf of Aden (this study), plotted as in Figure 2. B: Reflectance data from Ocean Drilling Program (ODP) Site 968 (Konijnendijk et al., 2014). Lower values denote sapropels. C: δ^{18}O data from Soreq Cave, Israel. For both δD$_{wax}$ and Soreq δ^{18}O, more negative values indicate a stronger northeast African monsoon. Yellow bars at top show dates of *Homo sapiens* fossils in the Levant (Grün et al., 2005) and Australia (Bowler et al., 2003). Molecular clock dates of haplogroups (denoted by letter; see Table DR2 [see footnote 1]), divergence of Aboriginal Australians (Austr.), and anatomically modern human (AMH)–Neandertal admixture (Neand.) are plotted as bars (tan = groups before the out-of-Africa [OOA] event; gray = groups and events after the OOA event). Vertical bars denote the conservative (light yellow, 50–75 ka) and most probable (dark yellow, 55–65 ka) timing of the OOA event. Marine isotope stage numbers are denoted at bottom.

wet conditions during MIS 5 likely also sustained vegetated corridors, in agreement with modeling results (Timmermann and Friedrich, 2016) and hydrological reconstructions (Drake et al., 2011). Strong sapropel formation, of the same magnitude as the Holocene signal, corroborates this interpretation (Fig. 3).

In spite of evidence for some Eurasian occupation, genetic studies preclude a dispersal event during MIS 5e–5b that made a lasting impact on the modern Eurasian genome. This is because the common matrilineal and patrilineal ancestors for all non-Africans—the mitochondrial DNA (mtDNA) haplogroup L3 and the Y chromosome DNA (YDNA) haplogroup CT—were not founded until MIS 5a or later (ca. 75 ka; Table DR2 in the Data Repository; Fig. 3). Conversely, dates constraining the founding of Eurasian haplogroups (ca. 50 ka), aboriginal Australian divergence (ca. 58 ka), gene admixture between AMHs and Neandertals (ca. 56 ka), and the presence of AMH fossils in Australia (ca. 48 ka) provide lower bounds for out-of-Africa migration (no later than 50 ka; Table DR2; Fig. 3). Thus, the wave of migration that is directly linked to the establishment of non-African populations must have taken place between 75 and 50 ka, with a most probable timing between 65 and 55 ka (Nielsen et al., 2017).

Interestingly, our paleoclimate data indicate that this prominent out-of-Africa event occurred when the climate was either transitioning into, or already within, a cold and dry state (Fig. 3). MIS 3 appears wetter than MIS 4 in our δD$_{wax}$ data (Fig. 3), but glacial boundary forcing prevented this interstadial from becoming a humid period on the order of MIS 5a, 5c, 5e, or 1 (Fig. 2A). Indeed, MIS 3 was still arid: δD$_{wax}$ values during MIS 3 are comparable to modern-day values (~ −125‰) (Tierney et al., 2015) under which the Horn of Africa receives ~200 mm of precipitation per year. Likewise, Sapropel S2, which is associated with MIS 3, is not present at ODP Site 968, which is typical for most sites in the Mediterranean (Fig. 3B; Rohling et al., 2015). δ^{18}O at Soreq decreases, but less so than during MIS 5 or the Holocene. All data from the northeast region therefore support only a modest increase in precipitation during MIS 3.

CONCLUSIONS

The commonly held assumption is that humans migrated out of Africa when conditions were humid, which would have allowed them to cross the otherwise inhospitable Sahara or Arabian Deserts (Drake et al., 2011; Timmermann and Friedrich, 2016). Yet here we show that AMHs moved out of Africa during either the MIS 5a–MIS 4 climate transition from wet to dry conditions, or during a sustained dry time (MIS 4 to early MIS 3; Fig. 3). Even if MIS 3 was slightly wetter, by analogy to present-day conditions, the climate was not sufficient to maintain ample vegetation—it was not a "Green Sahara."

Why would AMHs move during a dry time? Migration of any species is commonly subject to both "push" and "pull" forces. "Pull" forces are more commonly invoked when speaking of ancient migrations, but "push" forces are often cited as driving human movement in historical and modern times (Warner et al., 2010). The rapid deterioration of climatic conditions between MIS 5a and MIS 4 is conceivably a compelling "push," prompting *Homo sapiens* to move into Eurasia. In particular, AMH populations residing in North Africa during MIS 5 (Drake and Breeze, 2016) would have been well placed to migrate once the "Green Sahara" faded. Recent genetic work supports a "northern route" of migration (Pagani et al., 2015), lending further credence to this possibility. Alternatively, there is archaeological evidence of "southern route" migration (Armitage et al., 2011), and marine resources may have allowed populations to move through Arabia and continue on to Eurasia (Mellars et al., 2013). A thorough test of these hypotheses requires refinements in the fossil and archaeological records to more clearly demonstrate the timing and pattern of AMH movement.

More generally speaking, our paleoclimate record from the Horn of Africa enhances our understanding of long-term climatic change in northeast Africa, and provides a much-needed climatic context for interpreting an exceptionally important migration event in human history.

ACKNOWLEDGMENTS

We thank Marco Deangelis for assistance with the δ^{18}O analyses on core RC09-166. We thank Tom Johnson, Francis Brown, and an anonymous reviewer for their comments and input. Funding for this research was provided by National Science Foundation grant OCE-1203892 and the David and Lucile Packard Foundation Fellowship in Science and Engineering to Tierney. We also acknowledge support from the Columbia University Center for Climate and Life. We thank the Lamont-Doherty Earth Observatory Core Repository for assistance in selecting and sampling core RC09-166.

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Manuscript received 28 June 2017
Revised manuscript received 16 August 2017
Manuscript accepted 17 August 2017

Printed in USA