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Abrupt climate change and its influences on hominin evolution during the early Pleistocene in the Turkana Basin, Kenya

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ABSTRACT

Rapid climate variability has been hypothesized to play an important role in hominin evolution, yet our knowledge of Plio-Pleistocene climate change on short timescales is poor. Here, we developed centennial-scale reconstructions of precipitation from leaf wax biomarker hydrogen isotope ratios (δD_{wax}) using lacustrine sediment from West Turkana, Kenya. We analyzed two time intervals (~1.72 and ~1.60 Ma) with different orbital configurations (0.043 and 0.025 eccentricity, respectively) to examine the influence of seasonal insolation forcing on high-frequency climate variability and the rates of climate transitions. Our data indicate that under low summer insolation, which should induce high latitude glaciation and tropical African aridity, millennial-scale climate variability was stronger. This suggests that hominins may have been forced to contend with increased climate variability during already extreme environmental conditions. Additionally, we observe a rapid shift from arid to humid conditions occurring in less than 200 years under high-amplitude precessional-scale insolation change. The rate of this transition is similar to that observed in some proxy records of the onset of the African Humid Period, indicating high sensitivity to gradual insolation forcing in the Turkana Basin. Such abrupt climate changes could induce evolutionary selection for generalist behavioral traits in hominins.

1. Introduction

Hominins evolved through the accumulation of behavioral and morphological adaptations that allowed them to exploit a wide range of habitats and resources. There are various hypotheses about the nature of the environmental change that acted on and selected for these adaptations. The savannah hypothesis (Dart, 1925) was built on evidence that Africa gradually became drier through the Plio-Pleistocene, selecting for bipedality, encephalization, and other traits under drier, more open conditions. As evidence arose that many African climate changes were abrupt rather than gradual, the turnover pulse hypothesis emerged and emphasized the role of abrupt, unidirectional (i.e. non-oscillatory) changes in the environment as a selective agent acting on hominins and other large mammalian species (Vrba, 1985, 1993). This hypothesis is supported by numerous, well-dated fossil assemblages from the Turkana Basin that have demonstrated large faunal turnovers occurring in relatively short amounts of time (Behrensmeyer et al., 1997). These hypotheses dominated discussions of human evolution for years, but more recent hypotheses focus on the role of climate variability in hominin evolution. The variability selection hypothesis (Potts, 1996; Potts and Faith, 2015) posits that environmental variability, rather than directional change, selects for generalist traits, such as enhanced mobility and encephalization (Roberts and Stewart, 2018). There is increasing evidence that many key transitions in hominin evolution occurred in the context of extreme environmental variations; for instance, first and last appearance dates (FADs and LADs), new technological manipulations of the environment, and human dispersal events often occur

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during intervals of high climate variability (Grove, 2012; Potts, 2013). New paleoanthropological and paleoclimatological evidence has led to more specific evolutionary hypotheses such as the pulsed-climate variability hypothesis, which specifically invokes eccentricity-paced packets of high-amplitude environmental variability as the driver of evolutionary transitions (Maslin and Trauth, 2009). Testing these hypotheses requires long records that capture a range of timescales (orbital to interannual) of environmental variations during the Plio-Pleistocene in eastern Africa. Understanding the relationship between humans and their environment is of particular importance in this sensitive, water-stressed region.

Tests of the hypotheses based on variability selection have focused on precession-driven climate variability, the amplitude of which is a function of orbital eccentricity and seasonal changes in insolation (Kutzbach, 1981; Pokras and Mix, 1987). Indeed, paleoclimate reconstructions that capture the amplitude of orbitally driven environmental change, such as isotope records from marine sediment cores (Rose et al., 2016; Tierney et al., 2008), lake sediment cores (Lupien et al., 2018), and outcrops (Joordens et al., 2011), as well as terrestrial dust accumulation in the ocean (deMenocal, 1995), all document large changes in the variability of eastern African hydroclimate correlated to varying amplitude of precessional insolation forcing. Many of these records also suggest large changes in precessional-scale climate variability during critical times of hominin evolutionary change. For instance, Lupien et al. (2018) documented high-amplitude hydrological variability in the Turkana Basin during an interval of large oscillations in seasonal insolation at ~1.75 Ma, roughly coincident with the appearance of *Homo erectus*, Out of Africa I, and Acheulean stone tool technology (Potts and Faith, 2015).

Despite such results, it is unclear how environmental changes on orbital timescales (tens of thousands of years) would effect evolutionary changes in populations of hominins given the relatively short timescales of human generations (~25 years). In particular, for orbitally driven climate change to select for generalist traits requires that hominins retain adaptations for dry, or wet, environments during long (10^4 years) time intervals with contrasting environmental conditions. However, orbitally driven insolation changes may also trigger higher-frequency climate variations. Orbital precession strengthens and weakens the seasonal insolation cycle, and to some extent, hypotheses linking precession to human evolution assume (explicitly or implicitly) that the orbital-scale environmental changes are associated with variations in seasonal dynamics (e.g. Potts and Faith, 2015). Moreover, changes in seasonal insolation could influence eastern African climate in many ways. For instance, deMenocal et al. (2000) suggest an ‘insolation threshold’ to explain the abrupt onset and termination of the African Humid Period (AHP)—the most recent example of extreme, insolation-driven environmental change in Africa from ~15 to 5 ka, which had strong impacts on eastern African populations (Garcin et al., 2012a; Kuper and Kröpelin, 2006). Although the rate of the onset and termination of the AHP remains widely debated (Shanahan et al., 2015), centennial- to millennial-scale climate variability is also known to vary in relation to high-latitude ice sheet dynamics (e.g. Stager et al., 2011), which vary in response to high-latitude orbitally driven insolation changes. Thus, diverse types of abrupt and/or short-term climate variability may arise from changes in seasonal insolation. To expand our understanding of high-frequency eastern African climate variations under different orbital configurations, and building on records of orbital-scale climate oscillations from the Turkana Basin from our previous work (Lupien et al., 2018), we present a high-resolution analysis of the paleohydrology in the Turkana Basin during the early Pleistocene.

2. Evolutionary and climatic history of the Turkana Basin, Kenya

The Turkana Basin is a north-south oriented structure situated in the eastern branch of the East African Rift System in northern Kenya and southern Ethiopia (Fig. 1). It contains modern Lake Turkana, which spans 2.5–4.5°N and is the largest desert lake in the world (Feibel, 2011). Paleolake Lorenyang sediment from the Nachukui Formation in West Turkana was drilled in 2013 (HSPDP-WTK13 drill core hereafter WTK13) as part of the Hominin Sites and Paleolakes Drilling Project (HSPDP) to recover an archive of early Pleistocene climate and environmental change (Cohen et al., 2016). The basin hosts numerous fossil and archaeological sites (Wood and Leakey, 2011) and contains evidence for *Homo erectus*, including the KNM-WT15000 or Nariokotome Boy skeleton located only a few kilometers from the WTK13 drill site (~1.6 Ma; Walker and Leakey, 1993) and the emergence of Acheulean stone tool technology (~1.76 Ma; Lepre et al., 2011). *H. erectus* is thought to be the first hominin species to disperse widely, aided by permanent bipedality and encephalization (Holliday, 2012), leading to the first hominin dispersal out of Africa around 2 Ma (Zhu et al., 2018). WTK13 spans the interval from ~1.9 to 1.4 Ma (Lupien et al., 2018; Sier et al., 2017), also covering the LADs of *H. habilis* (~1.65 Ma) and *H. rudolfensis* (1.8 Ma), dates of which are part of a large turnover event in the early Pleistocene (Fig. 2b; Vrba, 1995).

Early Pleistocene climate in the Turkana Basin is thought to have experienced large, precession-driven fluctuations in rainfall, inferred from numerous proxies including the hydrogen isotopic composition of terrestrial leaf waxes (δD_{wax}; Lupien et al., 2018) and strontium isotopes (Joordens et al., 2011). Indicators of

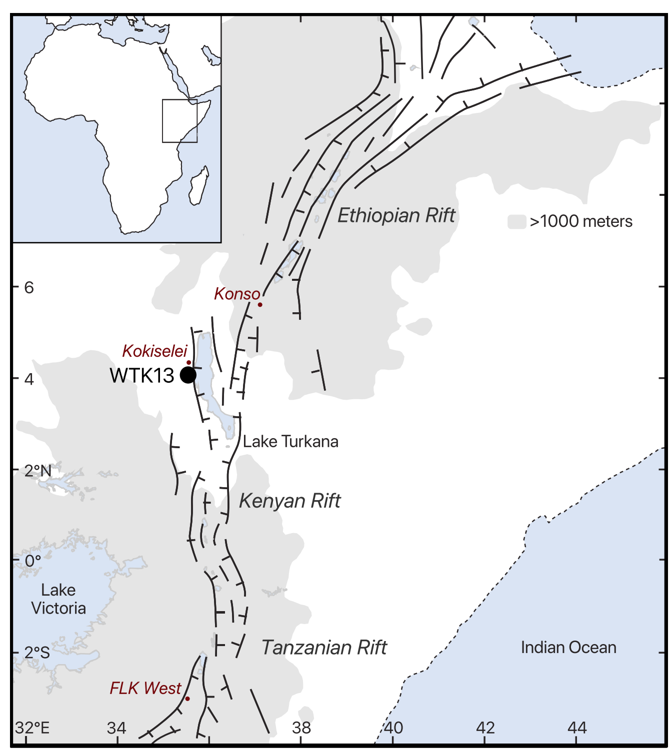

Fig. 1. Site map of eastern Africa with WTK13 drill core location in West Turkana indicated by black circle. Acheulean handaxe site locations discussed in text noted in red. Adapted from Trauth et al. (2005), grey shading of topography over 1000 meters above sea level from the 2 arc-minute ETOPO2 dataset. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

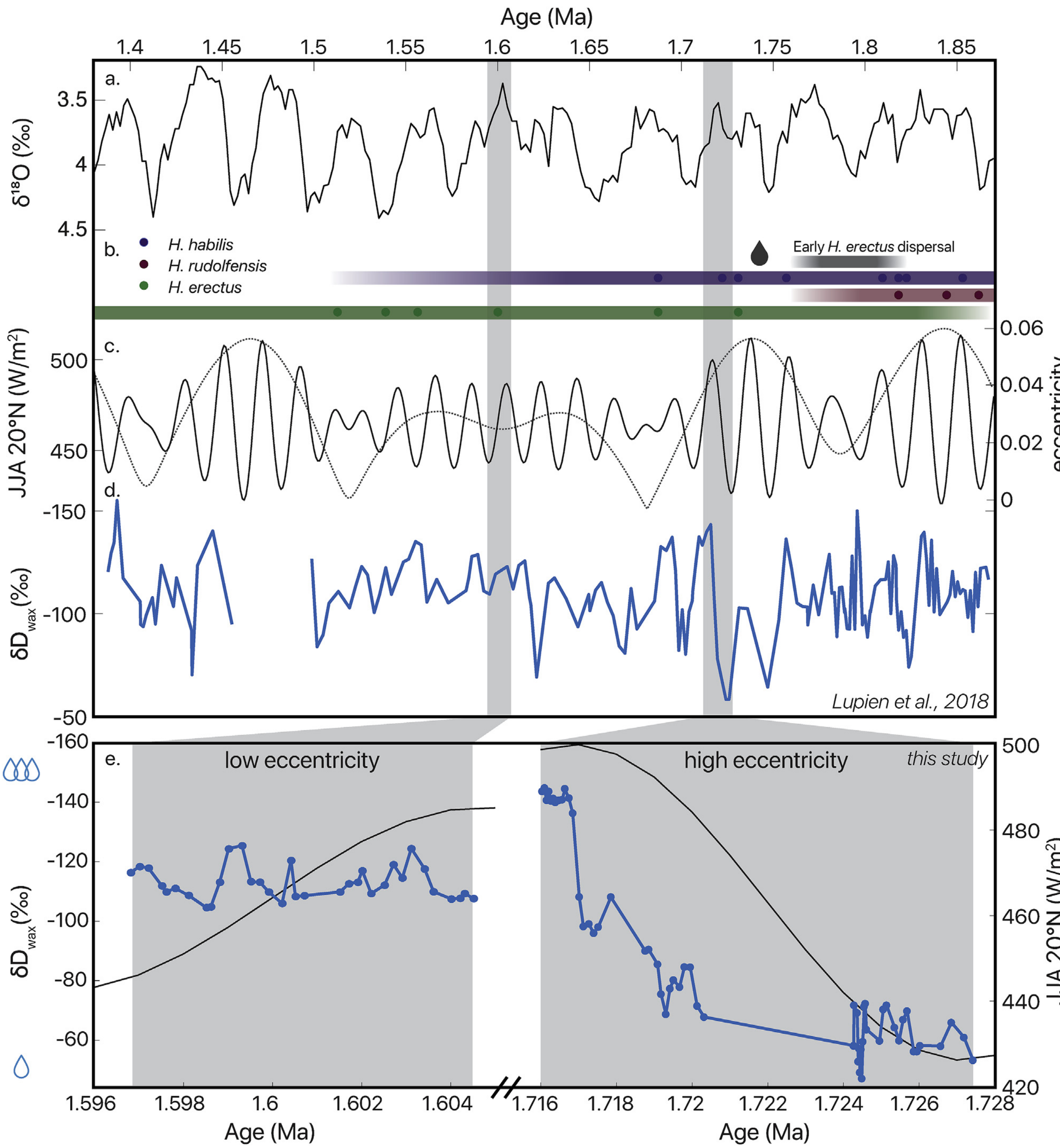

Fig. 2. Evolutionary and climate background of early Pleistocene Turkana Basin. (a) Global stack of oxygen isotope records from benthic foraminifera (Lisiecki and Raymo, 2005). (b) Hominin species (denoted by dots as individual dated fossils with FADs, and LADs; Wood and Leakey, 2011), early dispersal (Zhu et al., 2018), and first Acheulean stone tools (denoted by teardrop symbol; Lepre et al., 2011) contextualize this paleoclimate study. (c) JJA mean insolation at 20°N (left, solid), eccentricity (right, dashed; Laskar et al., 2004), and (d) orbitally resolved WTK13 *n*-C_{28} δD_{wax} (Lupien et al., 2018) show clear relationships during the early Pleistocene. (e) *n*-C_{28} δD_{wax} (three raindrops at top of y-axis to signify wetter conditions than one raindrop at bottom of y-axis) from a low eccentricity and a high eccentricity interval with centennial resolution from WTK13 (left, blue; this study) paired with JJA mean insolation at 20°N (right, black; Laskar et al., 2004). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

terrestrial environmental conditions from the WTK13 drill core, such as $\delta^{13}C_{wax}$ (Lupien et al., 2018), demonstrate that the landscape also fluctuated dramatically between C_3- and C_4-dominated biomes on orbital timescales. Fossil (e.g. Leakey et al., 2012) and archaeological (e.g. Lepre et al., 2011) evidence suggests that there were more evolutionary transitions in the Turkana Basin (i.e. turnovers, technological advances, dispersals) during an interval of high-amplitude precipitation and vegetation variation (~1.8–1.7 Ma) than later intervals of low eccentricity and dampened precessional variability (Fig. 2; Lupien et al., 2018), lending support to the variability selection and pulsed-climate variability hypotheses.

The record of tropical African climate is replete with evidence of local and regional abrupt climate changes—i.e. climate changes that occur at a faster rate than the forcing itself (e.g. Tierney and deMenocal, 2013; Trauth et al., 2018). Indeed, within the Turkana Basin, reconstructions of climate since the Last Glacial Maximum (LGM) indicate abrupt transitions between environmental states. Low lake levels and arid conditions during the LGM rapidly gave way to wet conditions just prior to the Holocene (Beck et al., 2019; Butzer et al., 1972; Morrissey and Scholz, 2014). Lake levels were high during the AHP, then rapidly fell to levels similar to present day in the middle Holocene (Garcin et al., 2012a). There is considerable debate about the synchroneity of rapid hydroclimate transitions at the end the AHP across Africa (e.g. Shanahan et al., 2015), suggesting that abrupt transitions may result from local climate changes rather than continental-scale changes in precipitation. However, the patterns observed at Turkana are similar to shifts observed in records of precipitation change, such as δD_{wax}, in much of eastern Africa (Costa et al., 2014 and references therein; Morrissey, 2014). In addition to the locally abrupt onset and termination of the AHP, eastern African precipitation is affected by abrupt, centennial- to millennial-scale oscillations originating from glacial processes in the northern high latitudes; during the last glacial termination, much of eastern Africa experienced strong aridity during the Younger Dryas (YD) and Heinrich Event 1 (H1; c.f. Otto-Bliesner et al., 2014; Stager et al., 2011). These events, triggered by weakening of the Atlantic Meridional Overturning Circulation resulting from ice and meltwater discharge to the North Atlantic (McManus et al., 2004), are characterized by rapid cooling in the northern high latitudes, which in turn affects the strength and position of the tropical rainbelt (Schneider et al., 2014).

The links between millennial-scale variability in ice-age climates of the northern high latitudes and late Pleistocene tropical eastern African hydroclimate are well-established (e.g. Stager et al., 2011), as is evidence for locally abrupt hydroclimatic transitions in response to precessional insolation forcing during the AHP (deMenocal et al., 2000). Despite the potential significance of such abrupt and high-frequency climate variability to eastern African environments and hominin populations, little is known about the rates of orbitally forced climate transitions and the dynamics of high-frequency climate variability in eastern Africa during the Pliocene and early to middle Pleistocene. Here we present new, centennial-scale records of early Pleistocene δD_{wax} from the Turkana Basin to investigate these timescales of variability and their potential importance to hominin evolutionary processes. We compare climate variability under contrasting intervals with low and high eccentricity forcing, evaluate the abrupt and oscillatory nature of high-frequency hydroclimate fluctuations under these states, and discuss the potential effects that such climate variability has on hominin evolution, behavior, and technological innovation.

3. Methods

We analyzed sediments from the WTK13 core, which has been dated using paleomagnetic (Sier et al., 2017), tephrostratigraphic, and $^{40}Ar/^{39}Ar$ ages (Lupien et al., 2018). To study millennial-scale changes in precipitation in the Turkana Basin, we analyzed the hydrogen isotopic composition of terrestrial leaf wax biomarkers from sediment samples from WTK13. Plants produce waxy cuticles to shield leaf surfaces from evaporation (Eglinton and Hamilton, 1967). Leaf waxes may be ablated and transported by eolian and fluvial processes to a lake, where they are preserved in sediment over geological time. Leaf waxes include long-chain *n*-alkanoic acids, the hydrogen isotopes of which we used to reconstruct past changes in rainfall. Lipid extraction, purification, and isotopic analytical procedures were identical to those of Lupien et al. (2018) and were performed at Brown University. Lipids were extracted from freeze-dried and homogenized sediment using a DIONEX Accelerated Solvent Extractor 350 with dichloromethane:methanol (9:1). The total lipid extract was separated into neutral and acid fractions via aminopropylsilyl gel column with dichloromethane:isopropanol (2:1) and ethyl ether:acetic acid (24:1). The acids were then methylated using acidified methanol, and the resulting fatty acid methyl esters (FAME) were purified over a silica gel column. Concentrations of the FAME chain lengths were quantified with an internal *cis*-eicosenoic acid standard using an Agilent 6890 gas chromatograph (GC) equipped with a HP1-MS column (30 m × 0.25 mm × 0.25 mm) and flame ionization detector. Hydrogen isotopes were measured on an Agilent 6890 GC, equipped with HP1-MS column (30 m × 0.32 mm × 0.25 mm), coupled to a Thermo Delta Plus XL isotope ratio mass spectrometer (IRMS) with a reactor temperature of 1445 °C. We report δD_{wax} relative to Vienna standard mean ocean water (VSMOW) in per mil (‰) notation. H_2 gas was used as the internal standard, and D/H ratios were measured in triplicate and samples had an average standard deviation of 1.4‰. An internal FAME standard was run every seventh injection and was used to correct the isotopic composition of samples for instrument drift. All measurements were corrected for the isotopic composition of an added methyl group with a δD of −123.7‰ (Tierney et al., 2011). Isotopic analyses of the FAME standard had a standard deviation of 2.1‰, and the H_3^+ factor, determined between 1 and 9 V, was 2.6 ppm/nA.

Previous studies have shown that δD_{wax} is strongly correlated with the mean annual δD of precipitation (e.g. Garcin et al., 2012b). In the tropics, the 'amount effect' is the dominant influence on δD_{precip} variation (Dansgaard, 1964) and describes the distillation of isotopically enriched vapor during condensation and other related processes. Factors such as moisture source, transport distance, temperature, and an array of cloud-scale processes may also influence δD_{precip} (Dansgaard, 1964; Vuille et al., 2005), but are generally associated with precipitation amount changes. These secondary effects are difficult to constrain, and a variety of observational (Rozanski et al., 1993; Vuille et al., 2005) and paleoclimate (Rose et al., 2016; Tierney and deMenocal, 2013; Tierney et al., 2017a; Tierney et al., 2011) studies have revealed δD_{precip} to be a robust indictor of eastern African paleohydrology, which we assume to hold for our study. We interpret more depleted δD_{wax} values as increased mean annual rainfall amounts. We do not correct for additional biosynthetic fractionation effects on δD_{wax} by C_3 and C_4 plants as previous studies show this effect is small relative to the amplitude of δD_{wax} variations in the WTK13 core (Lupien et al., 2018). We also do not correct for ice volume effects on ocean water isotopes due to the uncertainties in age constraints in our δD_{wax} record. However, the methodology used to correct for ice volume effects on ocean water isotope compositions would result in a maximum adjustment of δD_{wax} of ~3.5‰ in this early Pleistocene study interval (Fig. 2a; Lisiecki and Raymo, 2005). This is much lower than both the orbital- and centennial-scale changes in our record, and is near the analytical uncertainty for δD_{wax}, so we consider this effect to be negligible.

A previous record from WTK13 (Lupien et al., 2018) was analyzed at an ~3-kyr resolution. To investigate high-frequency and rapid climate changes, and their relationship to precessional orbital forcing, we analyzed two intervals chosen to represent different orbital configurations. These consist of 54 new samples selected from 139.1 to 133.3 m below surface (mbs), an interval with large, precessional-scale variations in δD_{wax}, when orbital eccentricity was high, and 38 new samples from a low variability/low eccentricity interval (94.2–91.6 mbs). This comparison allows us to evaluate whether sub-orbital climate variability differed in these intervals. Seven samples did not yield enough lipids for isotopic analysis, and we observed one outlier in δD_{wax} (92.089 mbs). By combining our new results with five previous measurements

(Lupien et al., 2018) our new record has 89 δD_{wax} datapoints.

The sediments we analyzed are composed of massive to laminated green, brown, and grey clays, with sporadic carbonate nodules and shell fragments (Fig. 3). A more detailed lithostratigraphic description can be found in Cohen et al. (2016), and further discussion of the relationship between lithology and δD_{wax} in Lupien et al. (2018). Our previous work (Lupien et al., 2018) demonstrated a strong correlation between δD_{precip} and mean summer insolation at 20°N, so for the present study we use published ages (Lupien et al., 2018; Sier et al., 2017), described above, and a two-point tune of δD_{wax} maximum and minimum to JJA insolation maximum and minimum during the high eccentricity interval at ~1.72 Ma. The sediment samples integrate up to 2 cm (~60 years) and have a mean time resolution (after tuning and excluding gaps) of 204 years. Weak pedogenic overprinting of lacustrine sediments occurs in parts of these two intervals, but the potential time gap resulting from these processes in the high eccentricity interval is minimal. There are three coring gaps in our record, the longest of which is estimated to last ~4 kyr (Fig. 3a). Within the interval of untuned low-amplitude insolation forcing, there is more significant pedogenesis, which we assume represent minimal missing time. We have not quantitatively evaluated climatic transitions over this interval of potential aerial exposure. Gaps in the high eccentricity core interval resulted from drilling rather than subaerial exposure, and we take these into account during quantitative change analyses.

We performed statistical analyses on the high-resolution WTK13 δD_{wax} record to investigate the rate and amplitude of short-term climate changes. To analyze millennial-scale variability, we removed the long-term trend in the data. We split the data from the high eccentricity interval into four segments (Fig. 3b) that were separated by gaps between δD_{wax} measurements due to low lipid yield or other constraints. We then removed the long-term trend from each segment using linear regressions. Data from the low-amplitude segment was linearly resampled to the same step in order to perform direct variance comparisons. To compare variance between high and low insolation segments within the high eccentricity interval, they were resampled to the same time step as the lowest-resolution section. To test the presence/absence of an abrupt change in the high and low eccentricity intervals, and in the latest Pleistocene, we performed a changepoint analysis using the findchangepts tool from the Signal Processing Toolbox in MATLAB to determine statistically robust changes in slope and mean in δD_{wax}. This function creates a step-wise model with a cost penalty for each additional change point to reduce the residual mean squared error to find the optimal timing, in this case with a required minimum improvement in the error set to 1000.

4. Results

The hydrogen isotopic composition of long-chain leaf waxes (n-C_{26}, n-C_{28}, and n-C_{30} alkanoic acids) are strongly correlated in our data (C_{26} and C_{28} $r = +0.97$, $n = 26$, $p < 0.01$; C_{30} and C_{28} $r = +0.97$, $n = 38$, $p < 0.01$), demonstrating that these compounds were derived from a common source and record similar climate processes. The Average Chain Length (ACL) of the n-alkanoic acids

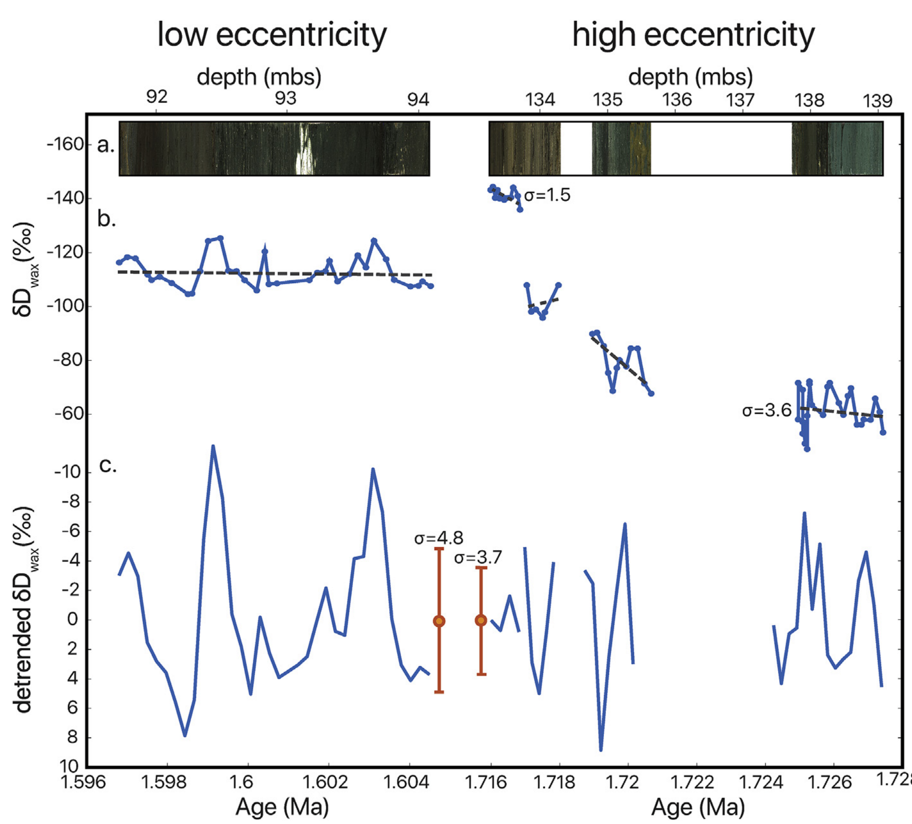

Fig. 3. Two study intervals, termed 'low eccentricity' (left) and 'high eccentricity' (right), of n-C_{28} δD_{wax} from different insolation regimes. Core images from WTK13 from each interval are shown with core gaps in white (a). δD_{wax} data are plotted against depth with the detrending lines for the low eccentricity interval and the four segments of the high eccentricity interval marked by dashed lines and standard deviations (1σ) for high and low insolation segments of the high eccentricity interval (b). Resampled and detrended data (c) are plotted against age (bottom axis) and show that variability between the two intervals (orange; 1σ) is not significantly different. However, variability in the low and high insolation segments of the high eccentricity interval are significantly different. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(C_{24}–C_{32}) of measured samples is 28.2. The Carbon Preference Index (CPI), measured as the ratio of even chain length abundance to odd chain length abundance (Bray and Evans, 1961) was used to assess the degradation state of the organic compounds in the sediment. A high even:odd chain length signifies good preservation of alkanoic acids, and a ratio of 1 or less signifies strong degradation. The WTK13 samples have a mean C_{24}–C_{32} CPI of 5.5 with a minimum value of 2.5, signifying generally good preservation. δD_{wax} and CPI are not significantly correlated ($r = +0.16$, $n = 87$, $p > 0.05$), indicating degradation has had minimal impact on the δD_{wax}. As n-C_{28} is the most abundant long chain n-acid in WTK13, resulting in lower analytical error, and in light of the CPI values that indicate minimal degradation, we used the hydrogen isotopic ratio of C_{28} n-acid for all further analyses of climate variability in the Turkana Basin.

The high- and low-amplitude time intervals yield different δD_{wax} ranges and variability (Fig. 3b). In the high eccentricity interval, δD_{wax} ranges from −144.4 to −47.5‰, nearly a 100‰ difference, whereas in the low eccentricity interval, δD_{wax} ranges from −125.4 to −104.6‰, a ~20‰ difference. Changepoint analysis demonstrates mean and slope changes in the high eccentricity interval at 1.720 Ma and 1.717 Ma (Fig. 4). The low eccentricity interval does not have a changepoint that fits the statistical qualifications. δD_{wax} variability in the high and low eccentricity intervals ($1\sigma = 3.7$ and 4.8, respectively) does not differ significantly ($p > 0.05$; Fig. 3c). However, we do find significantly more variability ($p < 0.05$) in the low insolation segment ($1\sigma = 3.6$; 1.728–1.725 Ma) than in the high insolation segment ($1\sigma = 1.5$; 1.717–1.716 Ma) of the high eccentricity interval.

5. Discussion

5.1. Sub-orbital climate variability in tropical eastern africa

Numerous records link high-amplitude hydroclimate variations in tropical eastern Africa with critical hominin evolutionary transitions. Diatomite and paleosol sequences from the Baringo Basin in central Kenya suggest swings between deep lake and dry basin conditions 2.7–2.55 Ma (Deino et al., 2006; Kingston et al., 2007) associated with important events within early *Homo* and the record of lithic technology. In the Turkana Basin, high-amplitude orbital-scale δD_{wax} variation corresponds with evolutionary transitions in the hominin fossil record (Lupien et al., 2018), including the first Out of Africa dispersal and the introduction of Acheulean stone tools (Fig. 2b, c, and d). In the Olorgesailie Basin, Middle Stone Age technology appears during a time of heightened environmental instability (499–320 ka; Potts et al., 2018). However, it remains unclear how these gradual climate shifts occurring over orbital timescales would influence human evolutionary processes over relatively shorter timescales.

Late Pleistocene records indicate high-amplitude, centennial-scale climate oscillations occurred in tropical Africa during time intervals with increased ice volume. Records spanning the last deglaciation indicate that Heinrich Events, and H1 in particular, are prominent features in many climate records from Africa, as is the YD (e.g. Stager et al., 2011; Tierney et al., 2008). Geochemical signals from Chew Bahir (Foerster et al., 2014; Trauth et al., 2018) and Lake Malawi (Brown et al., 2007) provide evidence of potential centennial-scale fluctuations during D-O events, though other high-resolution records suggest little variation in hydroclimate associated with D-O variability (e.g. Tierney et al., 2008). There is now widespread evidence that Heinrich Events and the YD were triggered by glacial meltwater routing to the North Atlantic (e.g. Dahl et al., 2005; McManus et al., 2004). The resulting changes in oceanic and atmospheric heat transport altered the position of the tropical rain belt, causing negative precipitation anomalies in northern and equatorial Africa (Otto-Bliesner et al., 2014). Although the mechanisms of D-O variability remain uncertain, their expression in Marine Isotope Stage 3 (MIS3) suggests that they could be linked to fluctuations in the Laurentide Ice Sheet margin during

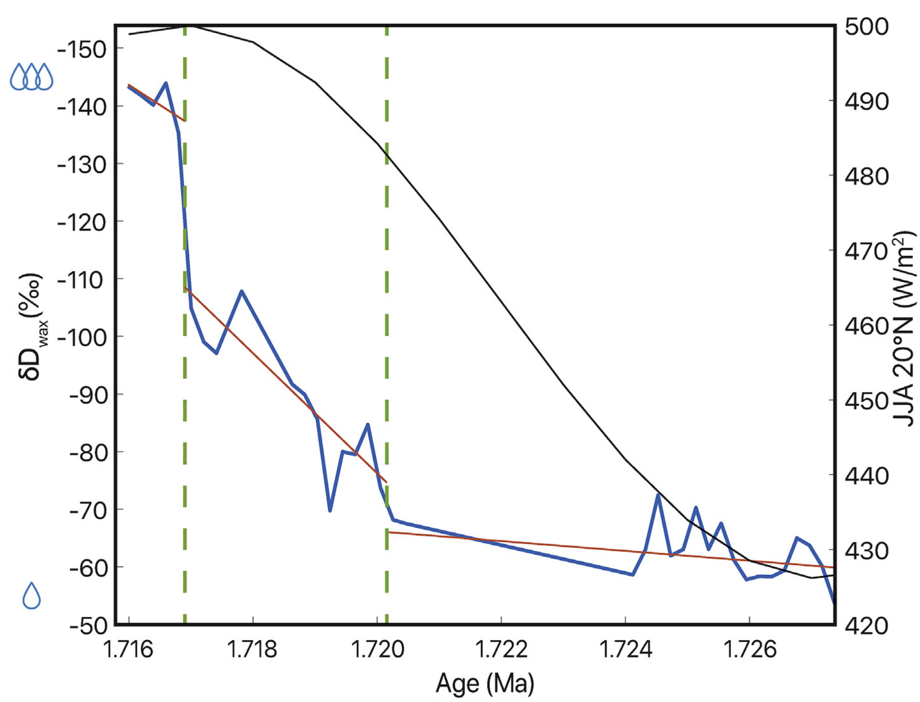

Fig. 4. The high eccentricity interval of n-C_{28} δD_{wax} (left, blue) with corresponding JJA 20°N insolation (right, black; Laskar et al., 2004). Changepoint analysis (orange) determines that two mean and slope changes (green dashed) occur during the rapid onset of a humid interval in the early Pleistocene, with the most dramatic change in δD_{wax} (~30‰) at ~1.717 Ma. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

glacial climates (Clark et al., 1999). Speleothem isotope records from Asia suggest the largest rapid oscillations occur during glacial climates, and in particular during glacial terminations and periods of intermediate ice volume such at MIS3 (e.g. Wang et al., 2008). However, there is virtually no research on the potential for centennial- to millennial-scale variability in eastern African climate during the early Pleistocene.

It is unclear whether one should expect high-frequency, high-amplitude variations in northern high-latitude forcing of rapid variability in eastern African hydroclimate during the early Pleistocene given the different climate boundary conditions and smaller ice sheets present at that time, nor whether such events could have affected tropical African climate. Bartoli et al. (2006) evaluated high-frequency climate variability through the onset of Northern Hemisphere Glaciation (NHG) in the North Atlantic and found that these events did occur in the early Pleistocene, after the onset of northern hemisphere glaciation, and only during glacial periods. Despite the potential for high-frequency events in the North Atlantic during the time interval we analyzed in WTK, we observe no significant difference in δD_{wax} variability between the high and low eccentricity intervals (Fig. 3c); in fact, the amplitude of high-frequency variability is lower, although insignificantly so, during the period of high eccentricity. Although it is difficult to know the exact temporal relationship between our record and the marine $\delta^{18}O$ record of global ice volume, $\delta^{18}O$ values indicate generally similar ice volume fluctuations during the two intervals. Although we do not find a difference in the variance in δD_{wax} between high and low eccentricity intervals, we do observe a significant ($p < 0.05$) difference in δD_{wax} variance between intervals of low and high mean JJA insolation (W/m^2) at 20°N within the high eccentricity interval. The increased variability during the low insolation segment supports previous work linking millennial-scale variability in the tropics to ice-atmosphere-ocean interactions (Brown et al., 2007; Foerster et al., 2014; Otto-Bliesner et al., 2014; Stager et al., 2011; Tierney et al., 2008; Trauth et al., 2018, 2019). Although the age uncertainty in our record limits our ability to make definitive links between the enhanced high-frequency variability and global ice volume, it is clear that this low insolation segment coincides with extreme aridity (enrichment in δD_{wax}; Fig. 3). Based on these data, we suggest that drier climates were also more variable, which could have impacted hominin evolutionary processes (see Section 5.3).

5.2. Unidirectional abrupt climate change

Tropical African precipitation is highly sensitive to insolation forcing (Kutzbach and Street-Perrott, 1985; Otto-Bliesner et al., 2014; Shanahan et al., 2015). Dust accumulation in marine cores off West Africa, a measure of Saharan climate, exhibits abrupt responses to insolation forcing, marking the onset and termination of the AHP (deMenocal et al., 2000). Similarly, various records indicate that the Turkana Basin experienced abrupt changes in hydroclimate during increasing summer insolation at the start of the AHP (Beck et al., 2019; Morrissey, 2014). Climate modeling and geochemical studies have explored the mechanisms that could lead to this threshold-like response, suggesting that changes in latent and sensible heating from variably vegetated land surfaces and soil moisture change may serve as strong positive feedbacks to insolation-driven precipitation changes in the Saharan region (deMenocal et al., 2000). Changes in western Indian Ocean SST could also drive feedbacks that are influenced by the temperature threshold for deep convection and result in a similarly abrupt climate response to a change in forcing in eastern Africa (Tierney and deMenocal, 2013). It remains unclear whether these shifts represent locally abrupt transitions in response to gradual migration of the tropical rainbelt (Shanahan et al., 2015) or large-scale abrupt responses of African precipitation to land surface and oceanic feedbacks. Moreover, leaf-wax isotopic records from offshore west Africa indicate more gradual transitions than the dust records (Tierney et al., 2017b), suggesting proxy system effects influence the rates of observed transitions. Thus, abrupt changes can arise from diverse mechanisms. For instance, abrupt increases in tropical African precipitation at the termination of the YD to early Holocene levels may have been caused by suppression of precipitation during the YD (Otto-Bliesner et al., 2014) rather than threshold responses to insolation (deMenocal et al., 2000). Whatever their origins, the rapid changes during the onset and termination of the AHP have been associated with impacts on human populations (Kuper and Kröpelin, 2006), such as the transition to pastoralism in the Turkana Basin (e.g. Garcin et al., 2012a; Ndiema et al., 2011). High-resolution hydroclimate records from other time intervals can help elucidate forcings of abrupt changes as well as the relationships between mean climate and millennial-scale variability.

During the high eccentricity study interval in the early Pleistocene, there is an abrupt, very large (30‰ depletion in δD_{wax}) transition to wetter conditions that could have occurred in less than 200 years (less than 300 years pre-tuning; Fig. 4). This change is significant, as indicated by a changepoint analysis, and accounts for nearly 40% of the isotopic shift occurring between low and high summer insolation within this precession half-cycle. Despite the presence of pedogenic overprinting in the high eccentricity interval, no significant sedimentological gaps are observed in the vicinity of the abrupt δD_{wax} change.

In contrast, the low eccentricity interval lacks any such change. This difference in responses between the high- and low-amplitude variability sections suggests that the early Pleistocene abrupt increase in rainfall reflects a nonlinear response to gradual insolation forcing (Fig. 3). The abrupt transition at ~1.717 Ma appears similar to the onset of the AHP, yet occurred under different global climate boundary conditions. Importantly, the insolation change that occurred at the onset of the AHP was less than either of our study intervals during the early Pleistocene, and yet the AHP was still associated with abrupt transitions, at least in the Turkana Basin (Morrissey, 2014). The magnitude of δD_{wax} change in the early Pleistocene is much larger than most records that capture the onset of the AHP, yet is difficult to compare to other locations as the AHP manifests differently in different regions within eastern Africa (Costa et al., 2014 and references therein). The larger climate shift we observe in WTK13 likely records a larger shift in climate driven by a larger insolation change, but could also be caused by changes in other climate boundary conditions. Although our age model is poorly constrained, we estimate that the rate of change is roughly equivalent between the two time periods, implying similar amplifying feedbacks operating across the Pleistocene and Holocene (deMenocal et al., 2000; Shanahan et al., 2015). Previous work suggests that abrupt changes marking the onset of the AHP were caused by the timing and effects of the high latitude events such as H1 and the YD (Otto-Bliesner et al., 2014), rather than a nonlinear response to gradual insolation forcing (deMenocal et al., 2000). High-latitude cooling during H1 and the YD suppressed eastern African precipitation during a time of rising summer insolation and greenhouse gas forcing, such that when these events ended, precipitation rose abruptly. Although it is difficult to directly compare hydroclimate response to insolation forcing in the early and late Pleistocene, the weak millennial-scale variability present in the latter half of the early Pleistocene precessional cycle suggests that the abrupt transition we observe is unlikely to have been related to millennial-scale events and was more likely an abrupt response to high-amplitude insolation forcing. More high-resolution data from deglaciations are needed to test this hypothesis.

The early Pleistocene response likely had drastic effects on the environment, changing the lake basin dramatically in less than a few centuries, similar to the onset of the AHP. For instance, the Turkana pollen assemblage established an expanded forest and increase in dense vegetation during the AHP (Owen et al., 1982), associated with the increase in lake level and humidity (Beck et al., 2019; Butzer et al., 1972; Morrissey and Scholz, 2014). Although high-resolution vegetation records from WTK have yet to be published, the low-resolution (precession-scale) $\delta^{13}C_{wax}$ (Lupien et al., 2018) record demonstrates significantly higher amplitude variability during the high eccentricity interval with dramatic shifts of up to 10‰ in one cycle. These findings suggest that the Turkana Basin is particularly sensitive to precipitation changes, which would have had important impacts on hominins living in this area.

5.3. Impacts of abrupt change on hominins

We observe evidence for an abrupt, unidirectional change in δD_{wax} marking a large transition in climate and environment in a period (~200 years) of only eight hominin generations (~25 years). Given the resolution of most early Pleistocene records, abrupt sub-orbital climate transitions could not previously be detected and analyzed in the Turkana Basin. Although our δD_{wax} record reported here only characterizes one transition from a dry to wet climate, if our data reflect the general patterns of eastern African climate responses to insolation forcing, these dramatic, abrupt environmental shifts could have exerted selection pressures on early Pleistocene hominins. Concurrent high-resolution $\delta^{18}O$ from a South African cave flowstone demonstrates high-amplitude fluctuation during our earlier study interval ~1.73−1.71 Ma, though Hopley et al. (2007) attribute any hominin response to the orbital-scale expansion of grasslands, which was not found in the orbital-scale record of $\delta^{13}C_{wax}$ from WTK13 (Lupien et al., 2018), perhaps pointing to regional differences in vegetation change. A more recent abrupt state change in African climate, the AHP, affected anatomically modern humans in northern and eastern Africa, including large-scale migration and changes in food gathering and agricultural practices, such as transitions to pastoralism (Foerster et al., 2015; Garcin et al., 2012a; Kuper and Kröpelin, 2006; Ndiema et al., 2011). In a general sense, these transitions are similar to the dispersals (Out of Africa) and technological changes (Acheulean tool-making) that occurred during the early Pleistocene.

Indeed, abrupt, extreme changes in the environment could have a large effect on mammalian species, as posited by the turnover pulse hypothesis (Vrba, 1985, 1993). Population modeling of environmental tolerance and plasticity suggests that the amplitude, rate, and frequency of environmental perturbations are significant in shaping evolutionary responses (Grove, 2014). The findings of these models indicate that rapid, directional environmental changes require increased tolerance of a broader range of environments and can mimic results produced by increasing variability over short timescales (Grove, 2011, 2014). More generally, abrupt, extreme events are known to exert strong selection pressure on organisms, as seen in both the geological record and in the present day, as they often trigger large changes in community composition and therefore species and resource interactions (Grant et al., 2017). If, as suggested by previous records (Lupien et al., 2018; Trauth et al., 2005) and theory (Potts and Faith, 2015), more evolutionary transitions occur during the times of high-amplitude precession-scale climate variability (i.e. high eccentricity), our findings suggest that rapid ‘state-changes’ in African climate would also have exerted a strong influence on physical and cultural evolution.

Although our data span only one half-precession cycle, in light of our evidence and widespread records documenting abrupt changes during the AHP it is plausible that repeated abrupt rainfall transitions occurred in eastern Africa during times of high-amplitude insolation change, particularly if our hypothesis that this represents a non-linear response to insolation forcing is correct. The high-resolution record reported here for the earlier period (1.727−1.716 Ma) demonstrates a change in δD_{wax} of 28‰ at around 1.717 Ma, indicative of a dramatic, abrupt increase in precipitation associated with a peak in insolation (Fig. 4). Changes of this magnitude are likely to have had substantial environmental effects, impinging upon the adaptations of both hominins and other animals. A hominin such as *Homo erectus*, which is assumed to operate at a high trophic level (e.g. Antón et al., 2014), would have been affected not only directly by the influence of an abrupt environmental change, but also indirectly by the effects of that change on the flora and fauna that formed its subsistence base.

The rapidity of such changes rules out the possibility of a genetic response, particularly for relatively long-lived hominin species living in what were likely to have been relatively small, fragmentary populations (Grove, 2017; Scerri et al., 2018). In such populations, responses to rapid environmental changes are likely to be behavioral, and to depend on innovation, social transmission and ultimately cultural change. Both theoretical (Boyd and Richerson, 1985) and empirical (Perreault, 2012) analyses suggest that cultural responses enable more rapid accommodation to novel environments, and that slowly reproducing animals become increasingly dependent upon learning as rates of environmental change increase (Grove, 2019).

The rapid environmental changes indicated by this study is within the longer interval of high-amplitude climate variability investigated by Lupien et al. (2018), which coincides with one of the most significant cultural changes seen in hominin evolution: the origins of the Acheulean. The earliest Acheulean is currently dated to ~1.76 Ma at Kokiselei (KS4) in West Turkana, Kenya (Lepre et al., 2011) and to ~1.74 at Konso (KGA6-A1 Locus C) in southwest Ethiopia (Beyene et al., 2013), with a slightly later occurrence at ~1.7 Ma at the FLK West site in Olduvai Gorge, Tanzania (Diez-Martín et al., 2015) (Fig. 1). Not only do the innovations comprising the Acheulean accord with the need for a cultural response to rapidly changing environments, but the central component of the Acheulean, the handaxe, is particularly well suited to dealing with unpredictable environmental change. Handaxes are regarded as multi-purpose tools, used for wood and plant processing (Domínguez-Rodrigo et al., 2001), digging (Brumm and Rainey, 2015), and butchery, including the splitting of long bones for access to marrow (Yravedra et al., 2017). General purpose tools are an ideal response to an unpredictable environment, and handaxes have an additional benefit in that they could also have served as cores for the production of flakes when required. Indeed, some early handaxes directly resemble Oldowan (or Developed Oldowan) cores, whereas ‘proto-bifaces’ (Leakey, 1971) are best interpreted as choppers or cores that have assumed their handaxe-like form through the intensive removal of flakes from both dorsal and ventral surfaces rather than by deliberate shaping (Semaw et al., 2009). Some (e.g. Clark and Riel-Salvatore, 2006; Davidson, 2002) have argued that handaxes might be cores as well as (or even rather than) tools, and this seems particularly likely for some of the earliest specimens. Whether or not this is the case, the fact that they could have acted both as robust tools and as sources of flakes in effect makes them highly flexible toolkits rather than just tools, which would have been of considerable advantage in periods of rapid environmental change.

It has often been suggested that the production of handaxes is more cognitively demanding than is the production of Oldowan tools (e.g. Gowlett et al., 2006; Stout, 2011; Wynn, 1989), and the Acheulean has frequently been associated with *H. erectus* rather than the less encephalized *H. habilis* or *Paranthropus boisei* (Antón, 2003). This association, however, remains unclear and rests primarily on theoretical arguments rather than direct archaeological or paleoanthropological data. Following the recent re-dating of the KNM-ER 3733 cranium to ~1.63 Ma (Lepre and Kent, 2015), the KNM-ER 2598 occipital at ~1.87 Ma is the sole pre-Acheulean *H. erectus* specimen from the Turkana region. No remains are associated with the Acheulean artefacts at Konso or Kokiselei, and the earliest *H. erectus* fossils in eastern Africa are found at Koobi Fora during a chronological window in which no handaxes are present in East Turkana (de la Torre, 2016). Therefore, the cognitive sophistication involved in handaxe production is perhaps the strongest argument for the association of *H. erectus* with the Acheulean (Gowlett et al., 2006; Wynn, 1989). Modern ethnographic studies have also shown that the production of large bifaces is indeed technologically challenging (Stout et al., 2002). For instance, Semaw et al. (2018) argue that the transition to the Acheulean would have created increased learning challenges for knappers, whereas Morgan et al. (2015) suggest that it may even have required active teaching or some kind of ‘proto-language’.

Direct tests of the hypothesis that rapid and/or frequent climate shifts favored various adaptations for flexibility in the hominin lineage, including encephalization (Potts, 1998, 2013) have been supportive (e.g. Ash and Gallup, 2007; Grove, 2012), and broader analyses have demonstrated that larger-brained mammals are better at dealing with environmental novelty, resulting primarily from their ability to innovate (Sol et al., 2008). The substantial excursions seen in early Pleistocene δD_{wax} show precisely the kind of signal that would have required rapid, behavioral responses facilitated by encephalization and the associated innovative and social learning capabilities. Chronologically, these data fall towards the end of one of the eight high-variability stages over the last five million years identified by Potts and Faith (2015; their interval is 1.888−1.695 Ma) and give a higher-resolution picture of environmental change during this period. Hydroclimate derived from δD_{wax} also shows that environments changed even more quickly than the insolation analyses carried out by these authors suggest, and that the environmental response to orbital forcing was likely nonlinear.

The δD_{wax} results presented here, while not exactly coincident with a specific technological adaptation, are thus in broad accordance with the contention of Potts and Faith (2015) that the Acheulean first appeared during a period of environmental instability, as a behavioral response to the need for greater flexibility in subsistence practices. Although hominins may have experienced selective effects associated with aridity as well as stronger environmental and climatic variability during the low insolation segment of the high eccentricity interval (Fig. 3), the data presented here suggest that rapid, directional changes may have been as important as general increases in environmental variability. The variability selection hypothesis, which points to orbital-scale climate fluctuations as a control on human evolution, should therefore consider the role of precession-driven abrupt changes linked to intervals of high eccentricity (Potts, 1996; Potts and Faith, 2015).

6. Conclusions

Evolutionary hypotheses pertaining to climate instability assume that orbital-scale climate variation influences hominin evolution by way of high-amplitude climate variations. However, late Pleistocene records indicate that eastern African climate can have a wide range of sub-orbital responses to insolation forcing and high-latitude climate variations in the late Quaternary. Our new, millennially resolved records of δD_{wax} from two different orbital configurations in the early Pleistocene allow us to study high-frequency precipitation changes and their relevance to hominin evolutionary processes. We find that a highly variable climate at orbital timescales is not necessarily associated with significantly more variability at centennial to millennial timescales. However, we observe a large, abrupt climate change, similar to the hydroclimate response at the onset of the African Humid Period, which occurred during a time with high-amplitude insolation change. In light of the impacts of the AHP on modern humans, we suggest that such changes could have impacted our hominin ancestors as well. Rapid environmental changes would have necessitated greater behavioral flexibility in hominin responses, and the origins of the Acheulean at ~1.76 Ma, including the production of multi-functional handaxes, may have been a result of this necessity. Repeated abrupt onsets and, potentially, terminations of humid periods during intervals with high-amplitude insolation change (i.e. high eccentricity) could have had a strong impact on eastern African environments, and thus provide a link between orbital-scale climate forcing and generation-scale environmental change. It is clear that climate and environment in eastern Africa is highly sensitive to both high- and low-latitude forcings. Understanding the timing and relative contributions of these responses is of utmost importance in this water-stressed region.

Author Statement

R.L.L. and J.M.R. conceptualized the project. R.L.L. performed biomarker and statistical analyses, interpreted data, and wrote most of the manuscript with substantial contributions from J.M.R. J.M.R. supervised and interpreted the biomarker analyses conducted by R.L.L. M.G. wrote the human evolution section (5.3) of the manuscript and contributed significant discussion. C.C.B. and C.S.F. were the WTK site leaders and contributed significant discussion on core sedimentology. A.S.C. was the Principal Investigator on the Hominin Sites and Paleolakes Drilling Project. All authors reviewed the paper prior to submission.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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