Annual Review of Earth and Planetary Sciences

Reconstructing the Environmental Context of Human Origins in Eastern Africa Through Scientific Drilling

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Annu. Rev. Earth Planet. Sci. 2022. 50:451–76

First published as a Review in Advance on February 25, 2022

The *Annual Review of Earth and Planetary Sciences* is online at earth.annualreviews.org

https://doi.org/10.1146/annurev-earth-031920-081947

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Keywords

continental scientific drilling, human evolution, East African Rift, paleoclimate

Abstract

Paleoanthropologists have long speculated about the role of environmental change in shaping human evolution in Africa. In recent years, drill cores of late Neogene lacustrine sedimentary rocks have yielded valuable high-resolution records of climatic and ecosystem change. Eastern African Rift sediments (primarily lake beds) provide an extraordinary range of data in close proximity to important fossil hominin and archaeological sites, allowing critical study of hypotheses that connect environmental history and hominin evolution. We review recent drill-core studies spanning the Plio–Pleistocene boundary (an interval of hominin diversification, including the earliest members of our genus *Homo* and the oldest stone tools), and the Mid–Upper Pleistocene (spanning the origin of *Homo sapiens* in Africa and our early technological and dispersal history). Proposed drilling of Africa's oldest lakes promises to extend such records back to the late Miocene.

- High-resolution paleoenvironmental records are critical for understanding external drivers of human evolution.
- African lake basin drill cores play a critical role in enhancing hominin paleoenvironmental records given their continuity and proximity to key paleoanthropological sites.
- The oldest African lakes have the potential to reveal a comprehensive paleoenvironmental context for the entire late Neogene history of hominin evolution.

1. INTRODUCTION

For nearly 150 years, since the time of Charles Lyell (1863) and Charles Darwin (1871), scientists have hypothesized about the role of environmental factors, specifically climate, in shaping the evolution of the hominins (humans and our close relatives). What kinds of climate, vegetation, landscape, and resources did early hominins encounter? Did environmental conditions remain stable over long periods, change directionally, or vary in time and space? How might these changes have impacted selection for characteristics that define humans and our close relatives? From the evolutionary divergence between hominins and our closest relatives, the African great apes, some 8–6 million years ago until the early Pleistocene, this history was exclusively an African chronicle. It is unsurprising, then, that since the early twentieth-century discovery of the first early hominins in South Africa (Dart 1925), extraordinary effort has gone into extracting records of African environmental history relevant to understanding evolutionary innovations, phylogeny, behavioral

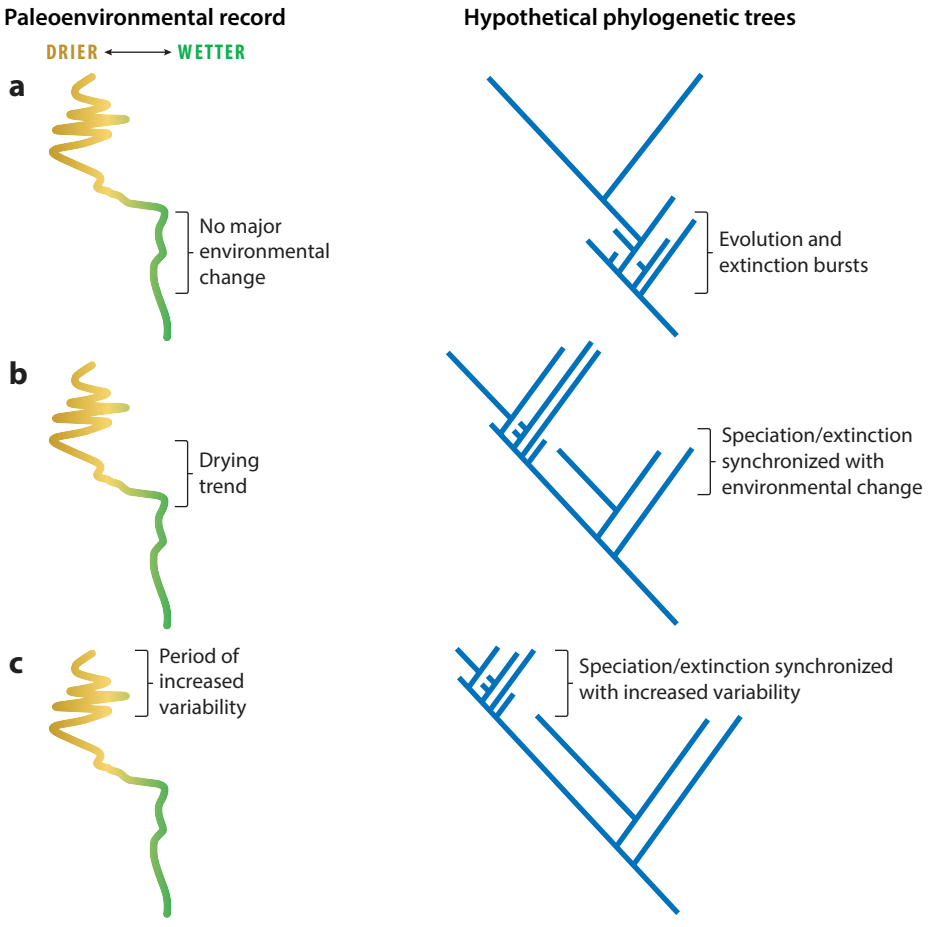

Figure 1

Conceptual model showing temporal linkages between environmental drivers and diversification/extinction events in human evolution (time advances upward in each case). (*a*) Null hypothesis: tempo of evolutionary history largely unrelated to environmental history. (*b*) Speciation/extinction/dispersal linked to strong temporal environmental gradients. (*c*) Speciation/extinction/dispersal linked to pulses of increased environmental variability. Note that whereas this diagram explicitly references correlations of cladogenetic events (or lack thereof) to environmental processes, these conceptual linkages could be extended to noncladogenetic processes such as acquisition of novel behaviors or dispersal events.

change, and dispersal within the hominin lineage. Understanding the relationship between Earth system history and human evolution remains an enduring challenge of broad scientific and public interest.

Possible linkages between hominin evolution and environmental history can be broadly placed in three categories (**Figure 1**). A null hypothesis is that environmental history has had little to do with hominin evolution and that the major drivers of selection, adaptation, diversification, and extinction in hominins were interspecific biotic interactions and intraspecific cultural interactions, rather than changes in climate and environment. If hominin evolution had been generally independent of large-scale external environmental forcing [variants of the Red Queen hypothesis (Van Valen 1973, Foley 1994)], we might expect little or no temporal correlation

between major hominin evolutionary events and environmental histories, beyond those occurring randomly (**Figure 1*a***). However, if environmental change did play a major role in shaping our evolution, we would expect significant correlations between external forcing mechanisms and evolutionary events. These might entail directional shifts in climate, for example toward more arid conditions, driving evolutionary events (Washburn 1960), or as coordinated pulses of diversification and extinction (Vrba 1988) (**Figure 1*b***). Alternatively, adaptive change might have responded to increased environmental variability (Potts 1996) (**Figure 1*c***). Correlation in time alone is insufficient to infer a causal linkage between records of environmental and phylogenetic history; a theoretical understanding of how landscapes and resources would have regulated evolutionary change must underpin the connection (Faith et al. 2021). Whereas current alternative hypotheses make predictions about the temporal linkages between environmental history and hominin evolution, data to test or support different hypotheses remain limited. These temporal correlations, however, are a necessary starting point for supporting or refuting particular hypotheses about environmental history's role in human evolution.

Over the past 25 years science has made significant advances in improving the chronology of both the environmental context of human evolution (deMenocal 1995, 2004; Behrensmeyer 2006; Kingston et al. 2007; Trauth et al. 2007; Donges et al. 2011; Blome et al. 2012; Levin 2015; Potts & Faith 2015) and African hominin phylogeny (Collard & Wood 2000, Kimbel 2015, Haile-Selassie et al. 2016, Strait & Grine 2016, Foley 2017). Our understanding of the former comes from three sources of information: (*a*) outcrop records at key fossil and archaeological sites (e.g., Bonnefille et al. 2004, Kingston et al. 2007, Cerling et al. 2011, Potts et al. 2018), (*b*) marine drill cores from offshore Africa (e.g., deMenocal 1995, Bonnefille 2010, Feakins et al. 2013, Uno et al. 2016a), and (*c*) terrestrial (primarily lacustrine) sediment drill cores from Africa and surrounding regions (e.g., Cohen et al. 2007, 2016; Campisano et al. 2017) (**Figure 2**). Each of these sources of information has strengths and weaknesses for addressing the hypotheses discussed previously. In this review, we consider the major insights in understanding the environmental context of human evolution that have been recently achieved using drill-core records derived from lacustrine sedimentary successions. These records come from a combination of extant, ancient lakes, such as those of the East African Rift System (EARS), and sediments deposited in lake basins that have long since dried up, filled in, or been destroyed through tectonic processes. Ultimately, understanding the environment/evolution nexus in hominin evolution must rely on a synthesis from all three sources, as they provide complementary information at different temporal and spatial scales, appropriate for addressing different aspects of these hypotheses.

2. INTEGRATING LAKE SEDIMENT CORES WITH OTHER RECORDS OF AFRICAN ENVIRONMENTAL HISTORY

Outcrop-based records documenting conditions at paleoanthropological sites are critical for understanding hominin evolution but present researchers with some fundamental problems in contextualizing this evolutionary history. Most eastern African fossil hominin and archaeological occurrences are in terrestrial deposits, particularly in paleosols and fluvial deposits, recording conditions near where hominins actually lived (e.g., Cerling et al. 2011, Uno et al. 2016b) (**Figure 3**). However, these deposits are highly episodic and/or time averaged over ecologically long intervals, and they typically do not provide high-resolution records of seasonality or even decadal- or centennial-scale climate events relevant to local hominin populations and their ecosystems. In regions of limited erosion, discontinuous outcrop records also limit our ability to reconstruct long climate records and precisely correlate records regionally. Nevertheless, a paleoenvironmental

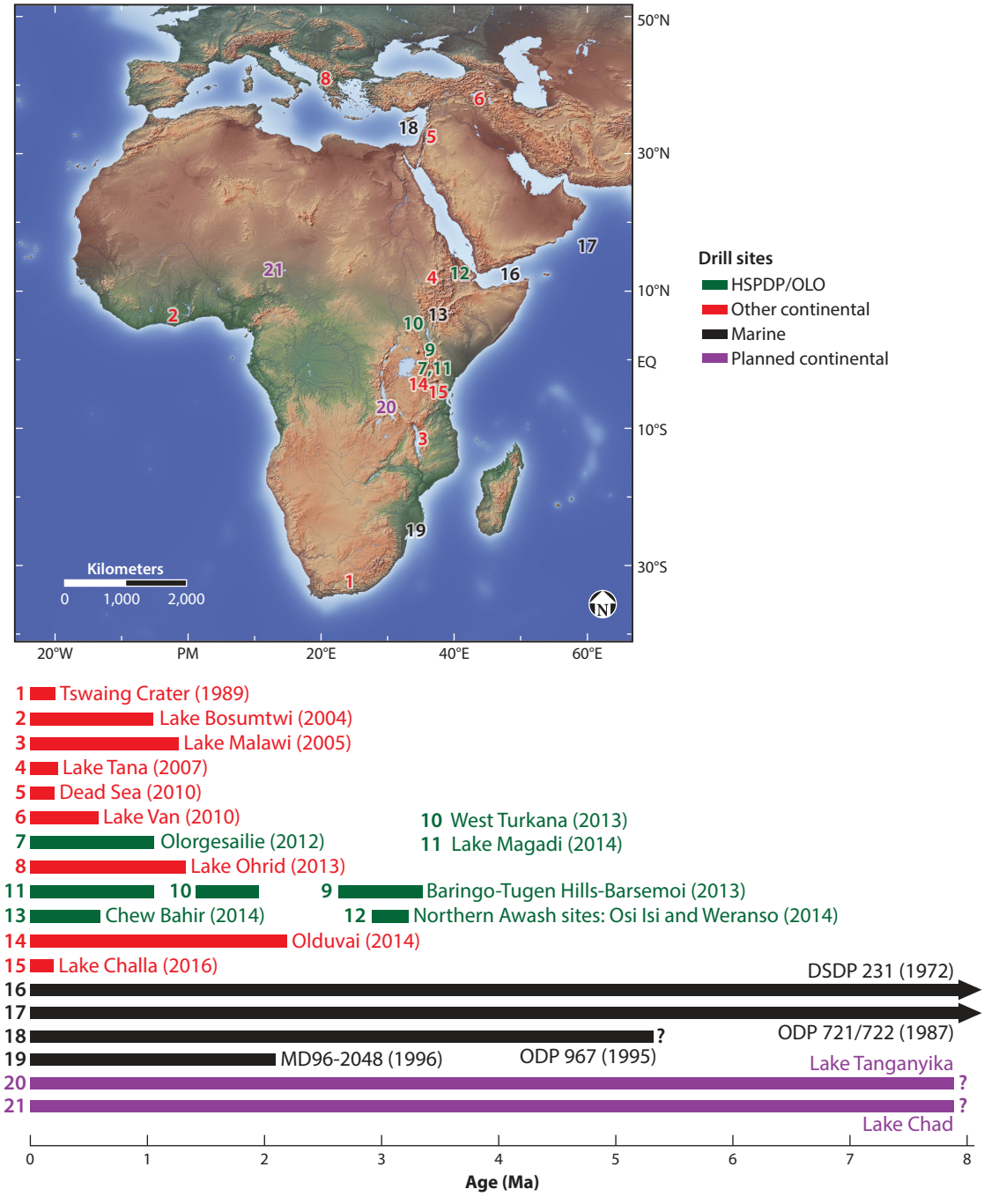

Figure 2

Key African and nearby Eurasian terrestrial drilling site locations and prior offshore records overlain on African regional topography and bathymetry. Dates indicate when drilling took place. Abbreviations: DSDP, Deep Sea Drilling Project; HSPDP, Hominin Sites and Paleolakes Drilling Project; ODP, Ocean Drilling Program; OLO, Olorgesailie Drilling Project.

Figure 3

Relative strengths (+ *blue text*) and weaknesses (– *red text*) of lake bed drill core, marine drill core, and outcrop paleoenvironmental records and how they can complement each other for contextualizing the role of environmental history in human evolution. Photo of *R/V JOIDES Resolution* courtesy of Arito Sakaguchi (photographer) and IODP/TAMU; other photos courtesy of Hominin Sites and Paleolakes Drilling Project.

record from the precise deposit in which a fossil was recovered provides highly relevant localized information about a specific paleolandscape in which early hominins lived.

Other sources of paleoenvironmental information likewise have a combination of advantages and disadvantages in terms of contextualizing human origins. Marine drill-core records from the Indian Ocean, the Mediterranean Sea, and other areas surrounding the African continent provide relatively continuous records of climate change over the entire time span of human evolution (e.g., deMenocal 2004, Liddy et al. 2017, Caley et al. 2018, Pollisar et al. 2019). However, their utility is limited by the slow sedimentation rates of the deep ocean and distance from hominin fossil and archaeological sites in the EARS, creating a filter of temporal and spatial averaging in these archives.

It was this combination of archival limitations of outcrops and marine cores that led researchers more than 40 years ago to suggest that drill cores from the large lakes of the EARS might offer an exceptional opportunity to obtain records of humanity's deep-time environmental history, particularly because much of the Plio–Pleistocene paleoanthropological record in Africa has been recovered from these deposystems (Lewin 1981). Drill cores from lacustrine sites that are close to key fossil and archaeological sites provide a wide array of paleoenvironmental records of nearby hominin habitats, typically at annual to decadal resolution (Cohen et al. 2016, Campisano et al. 2017).

Lake deposits offer important advantages for assembling information about hominin habitats. First, because of the calm and often anoxic conditions present in tropical lake floor environments, sediments typically accumulate in laminated beds, undisturbed by intensive bioturbation or current reworking, and thus register annual- or even subannual-scale environmental conditions. Second, an extraordinary range of records can be extracted from lake deposits, reflecting watershed-scale vegetation, geomorphology, internal lake hydrology and ecology, and regional-scale climate. These include paleoecological, geochemical/mineralogical, and sedimentological/facies analysis records, as well as petrophysical data obtained using multi-sensor core loggers. Associated nonlacustrine fluvial, wetland, aeolian, or paleosol deposits, commonly encountered in lake basin drill cores, can also provide information on environmental heterogeneity, although these typically lack the temporal resolution of lake beds. Unweathered drill cores frequently preserve a level of stratigraphic detail and unaltered geochemical information that is difficult or impossible to obtain from nearby outcrops (e.g., Maxbauer et al. 2016) (**Figure 4**).

This recognition of the value of lake drill-core records for paleoanthropology provided impetus for early drilling campaigns in African lakes. At the meteorite impact crater lake at Tswaing, South Africa (the Pretoria Saltpan), Partridge et al. (1993) demonstrated the role of orbital cyclicity on precipitation cycles in the region of importance to early modern humans. And at Lake Malawi, the significance of documented megadroughts for early modern human demography was an important outcome of drill-core studies (Cohen et al. 2007, Scholz et al. 2007). Efforts to obtain lacustrine drill cores specifically to address paleoanthropological questions began in the mid-2000s, involving a series of conceptual planning workshops (e.g., Cohen et al. 2006). These workshops spurred the development of the multisite Hominin Sites and Paleolakes Drilling Project (HSPDP) (sites in green in **Figure 2**) starting in the late 2000s, along with other, similar drilling projects near the paleoanthropological sites at Olorgesailie, Kenya (Potts et al. 2020), and Olduvai Gorge, Tanzania (Colcord et al. 2019, Deino et al. 2020, Rodríguez-Cintas et al. 2020, Njau et al. 2021).

Following nearly a decade of data collection, our collective experience has shown that our best hope for reconstructing the environments our earliest ancestors inhabited and how those conditions shaped the course of human evolution lies in creative synthesis of outcrop, marine, and lacustrine drill-core records.

3. IMPORTANCE OF GEOCHRONOLOGY FOR TESTING HUMAN EVOLUTION AND ENVIRONMENTAL HISTORY LINKAGES USING LAKE BED CORES

A highly resolved chronostratigraphic framework is essential for developing causal linkages between global climate change, regional environmental responses, and faunal evolution. However, these attempts have often relied on broad temporal correlations with an incomplete fossil or archaeological record. As in outcrop studies, a variety of geochronological techniques are available to study drill-core records, depending on the time span covered by those cores. But dating material derived from drill cores can be complicated compared to outcrops due to uncertainties about drill core–outcrop correlations, limited sample size, and sample artefacts and uncertainties created by the drilling process itself (e.g., core deformation, recoring, and cave-ins). These challenges have led researchers to expand and refine dating techniques to increase the geochronological toolkit available for scientific drilling, particularly addressing the geologic constraints of equatorial (e.g., for paleomagnetic studies), rift-lake settings. For example, Owen et al. (2018) successfully applied U-series dating to authigenic cherts in the HSPDP Lake Magadi drill core. U-series dating was previously applied to Lake Magadi cores, but these results provided only minimum ages for lacustrine sediments, as there was no way at the time to determine whether the dated minerals

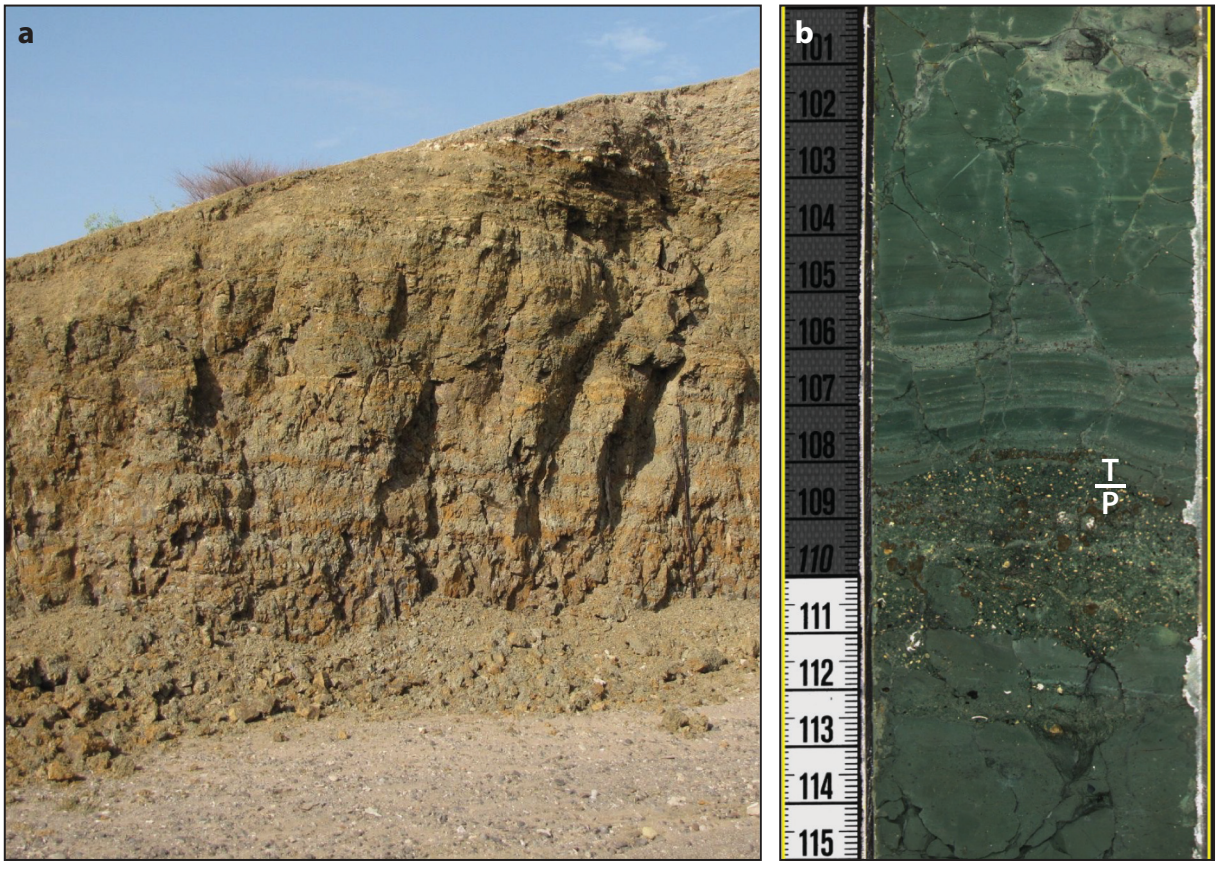

Figure 4

Outcrop (*a*) versus drill core sample (*b*) (portion of WTK-1A-35Q2; core scale bar in centimeters) from approximate correlative Nachukui Formation lacustrine deposits at West Turkana, Kenya (outcrop is less than 1 km from WTK-1 drill site and ~2.5 m high), demonstrating the much greater detail in information extractable from the unweathered core segments, even when compared with shallowly excavated (i.e., archaeologically trenched) surfaces. The core segment shows clear evidence of desiccation surfaces and incipient paleosol formation (intraclastic horizons, marked P) overlain by evidence of abrupt transgressive events marked by finer, laminated muds (T). Only vague lithologic alternations in color and degree of oxidative weathering (responsible for orange and brown outcrop coloration), lacking the millimeter-scale facies changes when observed at the same scale, were visible in the equivalent outcrop section. Photo courtesy of Craig Feibel.

were syndepositional or diagenetic (Goetz & Hillaire-Marcel 1992). Recently, the HSPDP team developed methods for determining which chert units formed syndepositionally and thereby refine the geochronology (Leet et al. 2021). Ultimately, these U-series dates were integrated with ^{14}C, $^{40}Ar/^{39}Ar$, and paleomagnetic age control points to develop a comprehensive age model for the core (Owen et al. 2018). Similarly, at Chew Bahir (CHB), multiple geochronometers (^{14}C, $^{40}Ar/^{39}Ar$, optically stimulated luminescence, and geochemical fingerprinting of known tephra) were used to develop that core's age model (Roberts et al. 2021).

Another methodological breakthrough for the HSPDP team involved the challenge of determining polarity orientation of samples from near-equatorial drill cores, where inclination is close to zero. This problem is compounded by the rotation of core segments during drilling, which can randomly redistribute declination. Sier et al. (2017, 2021) developed two independent drill-core

reorientation methods for paleomagnetic analysis of samples from the HSPDP West Turkana (WTK) and Baringo-Tugen Hills-Barsemoi (BTB) drill sites.

Tephra from cores that can be geochemically correlated to nearby outcrops and/or well-dated eruptions are extremely valuable, even if those tephra cannot be directly dated (e.g., Lowe 2011; Lane et al. 2017, and references therein). There is a long history of tephrostratigraphic research at fossil sites in eastern Africa (WoldeGabriel et al. 2005, 2013; Brown et al. 2006), and increasingly tephra correlations are being incorporated into drill-core age modeling in eastern African basins (e.g., Lane et al. 2013, 2018; McNamara et al. 2018; Deino et al. 2019, 2020; Roberts et al. 2021). Eastern African tephra have also been correlated to marine drill cores in the Gulf of Aden and the Arabian Sea, providing radiometric or orbitally tuned ages for the horizons (Brown et al. 1992, deMenocal et al. 1999). Several of the HSPDP site age models have incorporated tephra correlations to $^{40}Ar/^{39}Ar$–dated outcrop horizons. This can be advantageous as, unlike laterally extensive outcrops, drill-core sample sizes are limited by core diameter. Ages derived from thin lake-core tephra that may be poorly preserved in weathered subaerial exposures can also provide age control to outcrops. Four $^{40}Ar/^{39}Ar$ ages based on outcrop tephra correlations were incorporated into the BTB age model, compared to twelve $^{40}Ar/^{39}Ar$ ages directly from core material (Deino et al. 2019), whereas all but one of the six WTK $^{40}Ar/^{39}Ar$ ages were based on tephra correlations (Lupien et al. 2018). Core-to-outcrop tephra correlations have also been established for the Northern Awash HSPDP site (Garello 2019) as well as the Olduvai Gorge Coring Project (Deino et al. 2020, McHenry et al. 2020).

Additional geochronological tools can be deployed to determine exhumation and erosion rates in the watersheds of the lake basins. These provide a means of assessing the roles of topographic relief, tectonics, and climate drivers on sediment sources, and erosion rates over thousand- to million-year timescales during the sampled time periods. Zawacki et al. (2022) used detrital zircon U-Pb double dating of high-temperature crystallization ages and low-temperature exhumation ages on the same samples to characterize sedimentary provenance and transport. Cosmogenic ^{10}Be derived from quartz-bearing sands at the Northern Awash and WTK sites indicates millennial-scale variability in erosion rates.

Although sedimentation in large, modern lakes is often assumed to be relatively continuous, stratigraphic discontinuities are evident in most lake cores, including those of the HSPDP. Discontinuities can be associated with fluvial incisions, lava flows, erosive volcaniclastics, and subaerial exposure, often with associated pedogenesis of lacustrine sediments (Campisano et al. 2017; Lupien et al. 2018; Deino et al. 2019, 2021). These challenges led Deino et al. (2019) to develop a Bayesian age model for the Olorgesailie drill core that corrected for variable rates of deposition and accommodated different scales of discontinuities. For example, identified paleosols were classified based on a maturity index ensuring that paleosol-based indicator records (e.g., pedogenic carbonates) were not treated as coincident with the lacustrine records (e.g., diatoms) upon which the soil developed. Additionally, to account for the rapid deposition of volcanic material, sedimentary units that included a high proportion of tephra were variably temporally compressed based on sedimentary characteristics.

4. WHAT ARE DRILL-CORE RECORDS TELLING US ABOUT PAST EASTERN AFRICAN ENVIRONMENTS?

4.1. The Plio–Pleistocene Transition in Tropical Africa and Its Significance for Hominin Diversification

The intensification of Northern Hemispheric glaciation associated with the Plio–Pleistocene transition has long been posited as a driving force behind environmental change and mammalian

evolution in Africa, tethered to a shift toward more arid conditions or greater climate variability (e.g., Vrba 1988, 1995; deMenocal 1995, 2004; Potts & Faith 2015). This interval coincides with the first appearance of two hominin genera (*Homo* and *Paranthropus*) and Oldowan stone tools (Harrison 2011, Villmoare et al. 2015, Braun et al. 2019). Outcrop studies from the Baringo Basin demonstrated that equatorial Africa responded to precessional forcing between ~2.7 and 2.55 Ma (Deino et al. 2006, Kingston et al. 2007). The HSPDP BTB and Northern Awash Osi Isi (NAO) and Northern Awash Weranso (NAW) drill-core sites, selected to span the Plio–Pleistocene transition, thus provide unique opportunities to explore how tropical terrestrial communities responded across a major global climate transition and the relative roles of high-latitude boundary conditions and low-latitude insolation forcing of climate.

Rather than showing the most profound change at the Plio–Pleistocene boundary, evidence from the high-resolution BTB core (**Figure 5**) indicates significant changes in multiple records ~3.04 Ma, near the end of the mid-Piacenzian Warm Period (Dowsett et al. 2011), when a major shift in Baringo Basin hydrology occurred (Deino et al. 2021, Westover et al. 2021). Before ~3.04 Ma, environments were dominated by alluvial, fluvial, deltaic, and wetland environments with only brief intervals of deep lakes and probably overfilled depositional systems, as recorded in the high-resolution lithofacies, mineralogy, gamma density, magnetic susceptibility, elemental [X-ray fluorescence (XRF)] geochemistry, and diatom data from the BTB core (Billingsley et al. 2021, Yost et al. 2021). After ~3.04 Ma, a major environmental shift occurred, featuring dramatic swings between deep, freshwater lakes and shallow/marginal lacustrine or subaerial exposure environments, synchronous with precessional periodicity cycles during a high-eccentricity phase (Kingston et al. 2007, Billingsley et al. 2021, Westover et al. 2021). Various records indicate a dramatic change in character at ~3 Ma, from high-frequency, low-amplitude oscillations in the earlier sequence to higher-amplitude, lower-frequency oscillations that intensified over time (Westover et al. 2021).

Vegetation records from the BTB core also show a significant shift at ~3.04 Ma, demonstrating that these changes were not primarily a consequence of rift basin reconfiguration but rather reflect broad climatic changes. Change-point analysis of leaf wax carbon isotopes shows a shift from an average of over 50% C_3 vegetation (trees/shrubs) relative to C_4 grasses prior to ~3.04 Ma to ~40% afterward, suggesting increasing aridity/seasonality. The younger sequence also includes high-amplitude variability that oscillated between ~20% and 100% C_4 plants (Lupien et al. 2019). Phytoliths, which can distinguish C_3 and C_4 grasses and can further differentiate between mesophytic and xerophytic C_4 grasses, indicate a shift toward increasing C_4 grassland vegetation at ~3.04 Ma in the BTB record (Yost et al. 2021). This record is probably the most detailed, high-resolution, and long-duration vegetation reconstruction ever developed from phytoliths. In the pre-3.04 Ma sequence, phytoliths show that woody cover fluctuated at precessional periodicity between open savanna/wooded grassland and woodland/forest habitats (**Figure 5**). In contrast, the younger sequence is dominated by grasslands and wooded grasslands that include precession-scale oscillations between mesic tall-grass and xeric short-grass habitats (**Figure 5**). These oscillations were important as less nutritious tall grasses support a different herbivore community than short grasses, hide predators, and promote higher fire frequency and intensity (Dobson 2009; Pays et al. 2012; Hempson et al. 2015a,b).

The Plio–Pleistocene BTB records suggest the onset of major environmental change in eastern Africa was more likely linked to the end of the mid-Piacenzian Warm Period and subsequent cooling than the intensification of Northern Hemisphere glaciation at ~2.7 Ma. Furthermore, not only is precession-scale variability observed in these equatorial records, but also such fluctuations appear to have been much larger than the long-term secular changes and responses to high-latitude climate, an observation consistent with a recent synthesis that argues for the

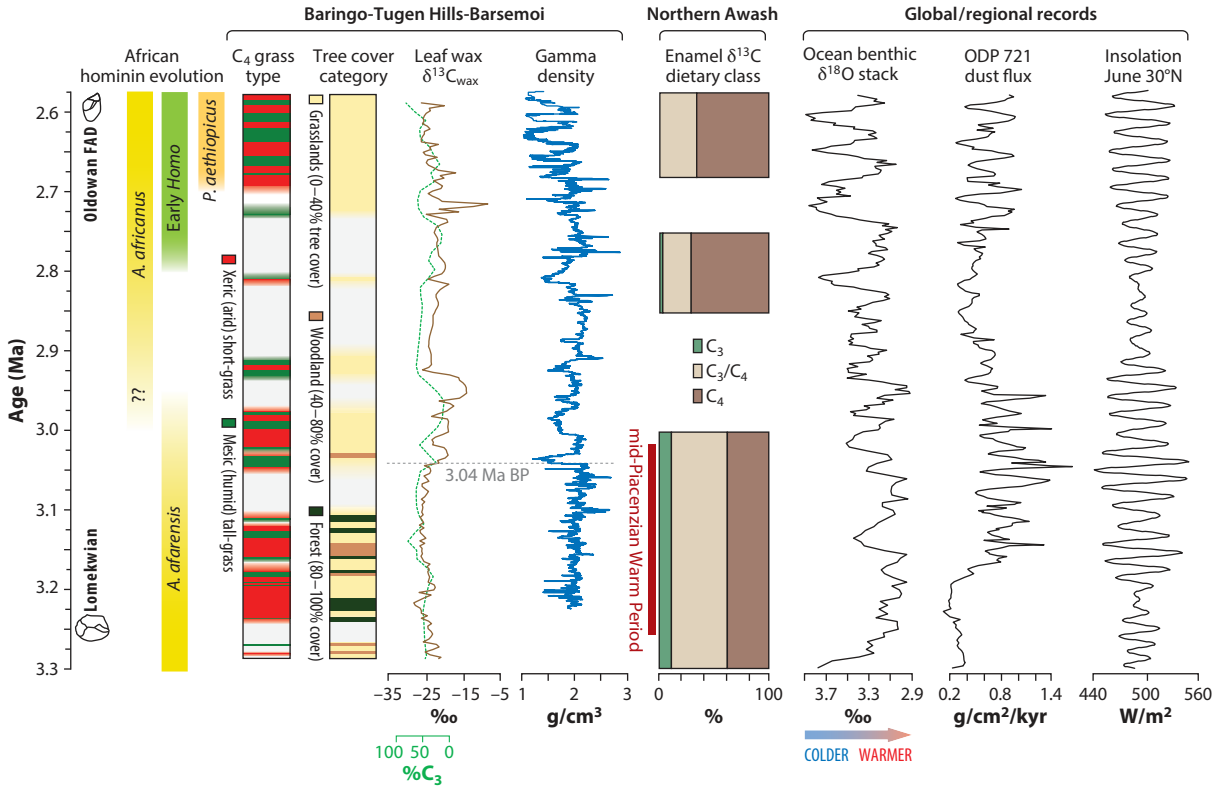

Figure 5

Comparison of the paleoanthropological record across the Plio–Pleistocene transition with stratigraphic, paleoecologic, and geochemical records from the BTB (central Kenya) drill core and Northern Awash (Ethiopia) outcrop records. BTB phytolith reconstructions are shown for C_4 grass type [phytolith index (Iph)] and percent tree cover (D/P° index; grassland category includes grasslands with 0–10% tree cover and wooded grasslands with 10–40% tree cover) (Yost et al. 2021). The BTB leaf wax biomarker ($\delta^{13}C_{wax}$, *dashed green line*) is the linearly resampled record of C_3 versus C_4 vegetation (showing a major change point at 3.04 Ma) and independently derived bulk organic matter $\delta^{13}C$ record (*brown line*) (Lupien et al. 2021). The BTB gamma density is −20 pt. running median with higher values indicative of increased terrigenous inputs and lower values indicative of deeper water and lacustrine accumulation of nonmagnetic and light components (e.g., organic matter or biogenic silica) (Billingsley et al. 2021). The dark red vertical bar is the duration of the mid-Piacenzian Warm Period. Dietary classification of Hadar and Ledi-Geraru fauna from tooth enamel $\delta^{13}C$ shows increasing C_4 consumption, reflecting more open habitats over time (Wynn et al. 2016, Robinson et al. 2017). Comparisons are made with the benthic foraminiferan ^{18}O stack (Lisiecki & Raymo 2005), calculated insolation at June 30°N, and the ODP 721 (Arabian Sea) terrigenous (dust) flux (deMenocal 1995). Abbreviations: BTB, Baringo-Tugen Hills-Barsemoi; FAD, first appearance datum; ODP, Ocean Drilling Program.

importance of low-latitude forcing of Plio–Pleistocene African climate (Trauth et al. 2021a). These extreme, short-term oscillations would have impacted terrestrial resources that mammals, including hominins, relied upon. Forthcoming results of the HSPDP cores from the Northern Awash sites (~3.3–2.9 Ma) will provide a useful comparison to test whether changes noted in the BTB core at ~3.04 Ma are local or regional (Campisano et al. 2017). The fossil record from near the Northern Awash site suggests that significant environmental changes also occurred in that area around the same time, as a distinct faunal turnover has been documented at ~3.1 Ma with an increase in more arid-adapted mammalian taxa (Reed 2008) and a further shift toward more open, drier, and seasonally variable environments by 2.8 Ma that may have played a role in the emergence of early *Homo* from *Australopithecus* (Robinson et al. 2017).

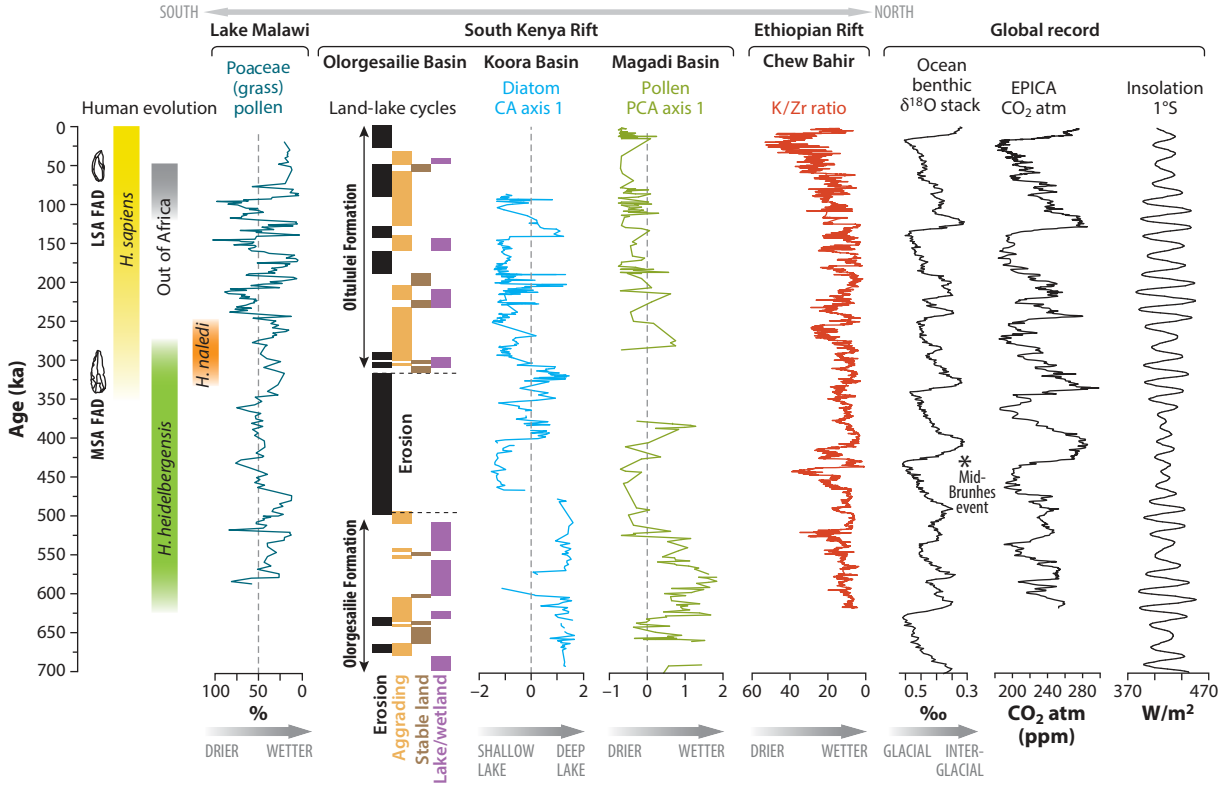

Figure 6

Comparison of Middle–Late Pleistocene eastern African drill-core and outcrop records, organized from south to north, indicative of changing paleohydrology and paleoclimate over the past 700 ka with key components of the hominin fossil and archaeological record. The Lake Malawi, Malawi (MAL05–1B/1C), Poaceae (grass) pollen record largely reflects aridity. The Olorgesailie Basin, Kenya, land-lake cycles are based on outcrop records discussed in Potts et al. (2020) and the diatom Correspondence Analysis (CA) Axis 1 record of lake depth from the hydrologically connected downstream Koora Basin ODP-OLO12-1A drill-core record (Potts et al. 2020). The Lake Magadi, Kenya (HSPDP-MAG-1A/C), pollen Principal Component Analysis (PCA) Axis 1 aridity record is shown (Owen et al. 2018). The Chew Bahir, southern Ethiopia (HSPDP-CHB14), elemental K/Zr aridity record is driven by the inverse correlation of K flux with precipitation, as illitization is controlled by evaporation (Foerster et al. 2018); data from V. Foerster et al. (unpublished paper). Comparisons are made with calculated insolation at 1°S, the European Project for Ice Coring in Antarctica (EPICA) ice core CO_2 record (Bereiter et al. 2015), and the benthic foraminiferan ^{18}O stack, including marked timing of the Mid-Brunhes event (*black asterisk*) at ~430 ka (Lisiecki & Raymo 2005). Abbreviations: FAD, first appearance datum; LSA, Late Stone Age; MSA, Middle Stone Age.

4.2. Middle–Late Pleistocene Lake Records and Their Implications for the Evolution of Modern Humans

Numerous critical transitions in African hominin evolution have been documented in the past half-million years, notably the Acheulian to Middle Stone Age (MSA) change in stone tool technology and the origin of our own species, *Homo sapiens* (Stringer 2016, Hublin et al. 2017, Richter et al. 2017, Brooks et al. 2018) (**Figure 6**). Lacustrine cores spanning this interval provide an excellent opportunity to understand how Middle to Late Pleistocene environmental change may have influenced the physical and cultural evolution of *H. sapiens* in eastern Africa. Results from these studies suggest that over the past several hundred thousand years, hominins and other fauna experienced temporal and spatial heterogeneity in ecological resources (e.g., freshwater supply,

dietary breadth, vegetation structure) coincident with critical transitions in their evolutionary history.

Lake Malawi, in the southern subtropics, was the first African rift lake to be drilled (Scholz et al. 2007). The core record from this lake provides evidence of extraordinary lake-level and climatic fluctuations (Lyons et al. 2015), some of which were in response to eccentricity-modulated precession cycles over the past 800 kyr (Ivory et al. 2016). Malawi pollen data over the past 600 kyr mirror lake-level records, with forest expansion coincident with increases in water level, demonstrating these fluctuations were climatically driven. Rapid fluctuations occurred between forested and semiarid phases, particularly during high precession variability phases (Ivory et al. 2018). In conjunction with nearby (25–150 km) MSA archaeological and geomorphic data, the Malawi pollen and charcoal records also document how early anthropogenic fire impacts, coupled with climate changes, drove landscape and ecological changes (Thompson et al. 2021). Early human use of fire appears to have altered the preagricultural anthropogenic landscape through changes in the seasonality and intensity of ignitions, which in turn influenced both vegetation composition and erosion rates.

Southern Kenyan Rift drill sites, ~900 km north of Lake Malawi, highlight the importance of spatial variation for regional ecosystem change. Olorgesailie, in southern Kenya, has a rich archaeological and paleontological record spanning the past 1.2 million years (Potts et al. 2018). Outcrops preserve evidence of the replacement of the Acheulean by MSA innovations between 500 and 320 ka, including smaller, more diverse, and complex tool types, a change in raw material type and transport distance, and the use of pigments (Brooks et al. 2018, Deino et al. 2018, Potts et al. 2018). A contemporaneous faunal turnover is recorded by the loss of large and mega-herbivores, particularly water-dependent mega-grazers, and an increase in smaller, water-independent mixed grazing or browsing herbivores (Potts & Deino 1995, Potts et al. 2018). An erosional disconformity in the Olorgesailie Basin outcrops spans 500–320 ka, coincident with these transitions, but this interval is covered by Olorgesailie Drilling Project cores in the adjacent Koora Basin, so the precise timing of these cultural and biotic transitions remains uncertain (Deino et al. 2019, Potts et al. 2020). This record shows relatively stable environmental conditions until ~450–400 ka, followed by significantly more variable and arid conditions. This includes changes in basin-scale water balance that produced substantial fluctuations in lake depth and water quality, from large, fresh, and deep to fluctuating saline and shallow. The frequency of short, dry episodes also increased, represented by evidence of subaerial exposure and soil formation. Vegetation structure also shifted, from predominantly C_4 short-grass (xeric) woodland to stronger fluctuations between woody cover and C_4 grass dominance, and then a shift to more mesic C_4 tall-grass dominance (Potts et al. 2020, Lupien et al. 2021).

The nearby Lake Magadi drill-core site (~20 km from the Koora core) was chosen because it likely experienced the same regional climatic conditions, but with a different tectonic and hydrologic history. Comparing the two core sites allows us to untangle tectonic from climatic signals. The Magadi core records a shift from early wetter conditions and a freshwater lake stage (particularly ~750–500 ka) to a stratified, saline lake reflecting a long-term trend toward a more arid climate (Owen et al. 2018, Muiruri et al. 2021a). The geochemical, diatom, and pollen data indicate a directional trend over the past 500 kyr toward more arid conditions, but with many wet/dry cycles and of increasing variability superimposed upon the longer-term drying trend. Intense aridification took place between ~525 and 400 ka, coincident with the Mid-Brunhes increase in amplitude of glacial/interglacial cycles (430 ka), with relatively persistent arid conditions from ~350 ka to present (Owen et al. 2018, 2019; Muiruri et al. 2021a,b). Drier episodes, reflected in the diatom and pollen data, mostly occurred during periods of low-amplitude insolation variability (Muiruri et al. 2021a,b). Notably, the Magadi wet/dry cycles are generally antiphased with the

Malawi record (Muiruri et al. 2021b). Such interhemispheric antiphased relationships have also been recorded and modeled for the Late Pleistocene (Blome et al. 2012, Kutzbach et al. 2020).

The timing of environmental shifts at Magadi is consistent with shifts in the Olorgesailie core record, but the Olorgesailie record does not exhibit a directional trend in aridity after 400 ka (Potts et al. 2020). The difference between these records and some of the changes in water availability and vegetation at Olorgesailie may have been the result of spatial heterogeneity related to local tectonics and increased topographic relief (Behrensmeyer et al. 2018, Potts et al. 2020). Moreover, as a regional drainage sump and terminal saline lake, Magadi may have been more sensitive to shifts in water balance. Nonetheless, the overall similarity in timing of environmental change recorded in the two basins suggests they were responding to changes in regional and global climate (**Figure 6**).

Records from the Chew Bahir basin (southern Ethiopia, ~5°N) core provide another key data point for understanding regional and latitudinal variation of environmental change with implications for hominin evolution and dispersal in eastern Africa since ~620 ka (Foerster et al. 2012; Viehberg et al. 2018; Duesing et al. 2021; Roberts et al. 2021; Schaebitz et al. 2021; Trauth et al. 2021b; V. Foerster et al., unpublished paper). A change-point analysis of the CHB K/Zr record demonstrates a three-phased history of significant changes in hydroclimate driven by orbitally forced variations in low-latitude insolation with general trends similar to those observed in the southern Kenya HSPDP site records (Schaebitz et al. 2021; V. Foerster et al., unpublished paper). The interval between ~620 and 410 ka exhibits a long-term drying trend culminating in fluctuations between hydrological extremes. A wetter phase between ~410 and 210 ka, increasingly pulsed by rapid oscillations on precessional timescales, coincides with the emergence of modern *H. sapiens* and the MSA in Africa (V. Foerster et al., unpublished paper). The most recent phase, ~210 ka to present, shows a long-term drying trend with increasing intensity since ~125 ka, superimposed on the highest variability between wet and dry pulses observed in the whole record. The humid pulses of this phase (until ~60 ka) may have opened migration corridors for *H. sapiens* out of Africa. The driest phase (~60–14 ka) during lowest eccentricity shows millennial- to centennial-scale wet/dry fluctuations, associated with Dansgaard–Oeschger and Heinrich events, which could have spurred the development of new adaptive strategies by *H. sapiens*, such as the innovation of tool technologies (Late Stone Age) or migration to the adjoining highlands (Schaebitz et al. 2021).

A pan-African synthesis of multiple high-resolution core records from both lake and marine settings spanning the past 620 kyr demonstrates an east-west alternation in precipitation regimes across Africa (Kaboth-Bahr et al. 2021). Generally wet conditions prevailed in western Africa and more arid conditions in eastern Africa between ~525 and 279 ka and ~128 and 0 ka, with a reversal of this mode during the intervening period. Kaboth-Bahr et al. argue that these alternations were driven by warming and cooling in the tropical Pacific, driving east-west positional changes in the Walker circulation on eccentricity-linked timescales. This continental-scale alternation in climate and vegetation patterns coincides with molecular phylogenetic evidence for diversification events in pan-African mammalian clades, and would have had profound effects on the resources upon which mammals including early *H. sapiens* depended, as well as their biogeography as those resources shifted.

4.3. Testing the Hypothesized Impact of the Toba Supereruption on Terrestrial Ecosystems and Anatomically Modern Human Populations in Africa Using the Lake Malawi Drill-Core Record

Our ability to resolve environmental events down to annual or even subannual timescales in laminated lake beds makes these records particularly well suited for answering questions about the

impact of extreme events on human populations, how seasonality may have influenced early hominin habitats, and the nature of the landscapes particular hominins occupied. One of the most intriguing ideas linking early modern human demography and dispersal to environmental catastrophes is the volcanic winter/weak Garden of Eden hypothesis, linking the Mt. Toba (Indonesia) supereruption to a global climate catastrophe, and subsequently to the collapse of human populations in Africa (Ambrose 1998). The youngest (~74 ka) eruption of Mt. Toba is the largest Quaternary eruption known. Its fingerprinted tephra [the Youngest Toba Tuff (YTT)] can be found across a wide swath of Africa and Eurasia in marine and continental sediments (Smith et al. 2011, 2018), and possibly in Greenland and Antarctic ice core aerosols as well (Svensson et al. 2013). The approximate concurrence of this eruption with molecular genetic evidence for a possible early modern human population bottleneck, as well as the presumed timing of the dispersal of modern humans out of Africa, prompted a lively debate on the possible connection between these events (e.g., Rampino & Ambrose 2000, Oppenheimer 2002, Robock et al. 2009, Williams 2012, Smith et al. 2018). This is difficult to test in most terrestrial occurrences, however, because the linkage between the tephra and coincident paleoenvironmental records is limited by episodic deposition.

Lane et al. (2013) recovered YTT cryptotephra from two of the Lake Malawi drill cores and argued, based on both TEX_{86} paleotemperature reconstructions and scanning XRF data, that there is no evidence supporting a major environmental perturbation or volcanic winter associated with the tephra horizon. Subsequently, Jackson et al. (2015) and Yost et al. (2018) took advantage of the wide range of paleoecological data preserved in the laminated Malawi cores at subdecadal resolution for several hundred years before and after the eruption to evaluate the volcanic winter hypothesis. They confirmed that neither lacustrine nor terrestrial ecosystems suffered the types of impacts predicted by a hypothesized volcanic winter severe enough to have catastrophic effects on human populations and generate a genetic bottleneck (Rampino & Ambrose 2000, Robock et al. 2009) (**Figure 7**). Given the degree of hypothesized cooling proposed by the volcanic winter hypothesis, Lake Malawi, a thermally stratified tropical lake, would have undergone a complete limnological overturn. Complete water column mixing would have had an immediate and long-lasting impact on a lake of this size by nutrients released into the epilimnion and oxygenation of lake floor. Jackson et al. (2015) and Yost et al. (2018) found no such major perturbations in the fossil record of dominant phytoplankton or zooplankton following the YTT, nor evidence of colonization of the normally anoxic (and thus unbioturbated) lake floor by benthic invertebrates at this time. The terrestrial records of vegetation (from phytolith fossils) and fire (from charcoal abundance) across the YTT horizon are similarly instructive. There is no evidence for the types of wholesale environmental degradation required by the volcanic winter hypothesis to cause a collapse of the ecosystems upon which contemporaneous modern humans depended, as documented by archaeological sites in this region (Thompson et al. 2018, 2021).

The two Malawi drill cores in which the YTT was encountered also allowed Yost et al. (2018) to differentiate low from high elevation impacts of the ashfall. In the central Lake Malawi core (MAL-1C), adjacent to low-elevation miombo woodland, no changes were observed immediately following the YTT in tree cover, or in either cool climate C_3 or warmth-indicating C_4 grasses that exceeded background (i.e., pre-Toba) variability. In the north basin (MAL-2A), adjacent to the Rungwe and Livingstone Mountains, there is evidence of increased charcoal and C_4 grasses immediately after the YTT, signaling some burning and aridification predicted by the volcanic winter hypothesis. However, the levels of these indicators remained well within the background levels of variability prior to the YTT, making it extremely unlikely these climatic effects were sufficiently severe to cause major human population declines across Africa.

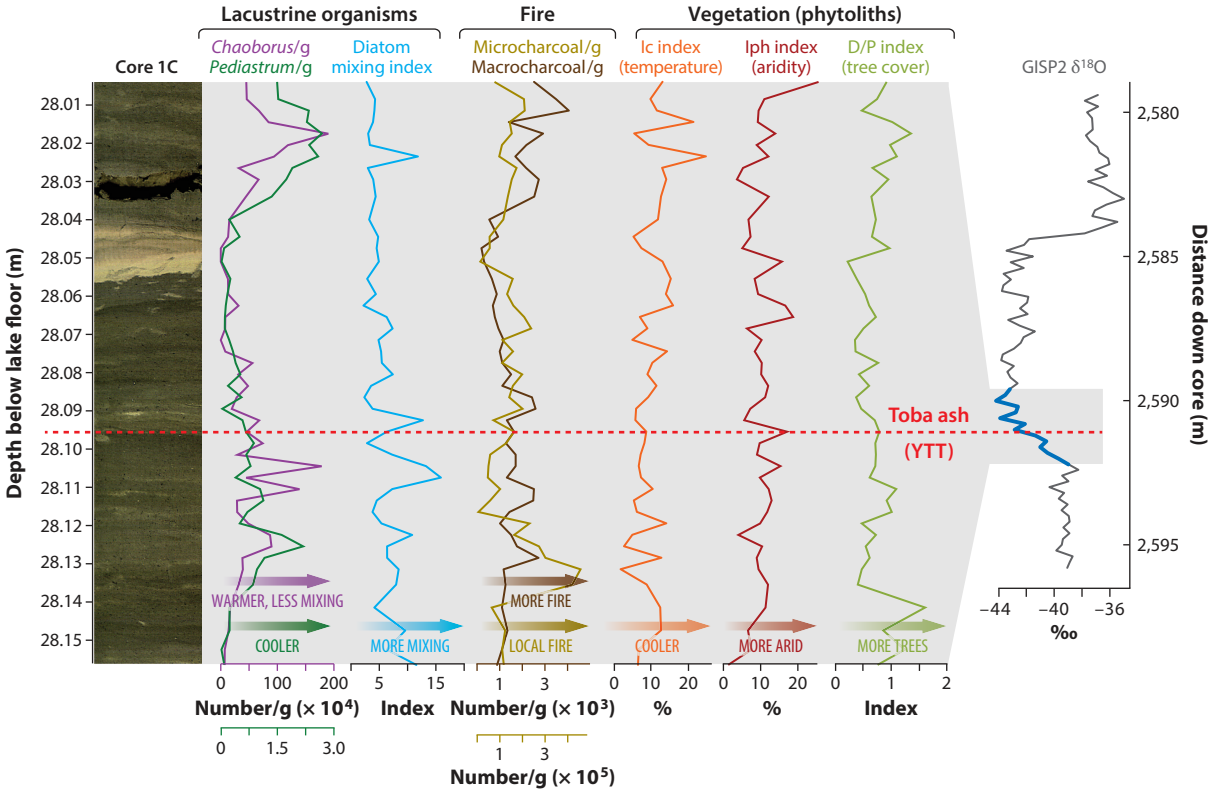

Figure 7

Indicators of lake ecology and mixing, terrestrial vegetation, and fire from the Lake Malawi drill core spanning an interval of ~100 years before and ~200 years after the Mt. Toba supereruption [Youngest Toba Tuff (YTT) horizon] recovered from the GLAD7-MAL05-1C-8H-1 core section with cryptotephra chemically matched to the YTT (Lane et al. 2013). Data are from Jackson et al. (2015) and Yost et al. (2018) and are plotted on a depth scale. Plotted data include counts per dry gram of *Pediastrum* (green algae–photic zone mixing); *Chaoborus* (phantom midge larvae, deep water mixing plus overall secondary productivity); a diatom mixing index [(*Aulacoseira* + *Stephanodiscus*)/*Cyclotella*]; and microcharcoal (<45 μm) and macrocharcoal (>45 μm) (regional and local fire activity, respectively). Phytolith-derived climate and vegetation indices are based on grass phytoliths [climate index (Ic), phytolith index (Iph), and the ratio of woody plant to grass phytoliths (D/P)]. Greenland Ice Sheet Project 2 (GISP2) $\delta^{18}O$ values are from Grootes & Stuiver (1997). All records show an absence of significant perturbations in lake or land ecology associated with the YTT beyond background variability. The red dashed line marks the position of first occurrence of YTT cryptotephra in the Lake Malawi core and links it to the position of the GISP2 H_2SO_4 spike attributed to the Toba supereruption (Zielinski et al. 1996), which shows a minor cooling event associated with this eruption against a background decline in temperatures underway long before the eruption.

5. EVALUATING THE ROLE OF ENVIRONMENTAL VARIABILITY IN HUMAN EVOLUTION WITH CORE RECORDS

Since the late 1990s there has been considerable interest among paleoanthropologists in the potential role that environmental variability may have played as a driver of evolution, technological change, and dispersal of hominins. In a series of papers, Potts (1996, 1998) argued that increased variability (as opposed to long-term directional shifts, for example toward drier conditions) resulted in adaptations that conferred greater flexibility during times of increased environmental uncertainty, potentially leading to significant species turnover. Potts termed this variability selection. As examples in the hominin lineage, Potts pointed to the expansion of arguably more adaptively flexible *Homo erectus* at the expense of dietarily specialized *Paranthropus*

(during the climatically variable early Pleistocene) or the replacement of cold climate–adapted Neanderthals by rapidly expanding and behaviorally diverse modern *H. sapiens* in Eurasia through the most extreme climate swings of the late Pleistocene. Potts (1998) recognized that testing this hypothesis required evidence that the evolution of adaptations for increased environmental flexibility be both temporally and logically (in terms of specific adaptations) associated with evidence of enhanced environmental variability. Highly resolved drill-core records are well suited for providing evidence of changes in environmental variability.

Potts & Faith (2015) evaluated the variability selection hypothesis's predictions using orbital insolation cycles to predict periods of high and low climate variability. The insolation record was then compared quantitively against Arabian Sea and Mediterranean dust records, which demonstrated that high- and low-variability orbital insolation intervals corresponded to actual increases and decreases in the two indicator records. They then showed that qualitative changes in paleoenvironmental records from a series of hominin fossil–bearing basins in eastern Africa corresponded to the timing of variability stages predicted by the orbital-control model of variability. Finally, they compared the times of high variability, as predicted by the variability selection hypothesis, with first and last appearance datums (FADs and LADs) for a variety of hominin evolutionary transitions to see if these corresponded in time. Their null model, comparable to **Figure 1*a***, predicts no statistical relationship between these events, but they found a significant relationship between the two, as would be predicted if evolutionary novelty were driven by increased climate variability (**Figure 1*c***).

More recently, Potts and colleagues (2018, 2020) have emphasized the possible role of nonclimatic aspects of environmental variability in affecting resource fluctuations and their temporal association with hominin technological change. They note that the Acheulian to MSA transition at Olorgesailie, linked to the greater technological capacity of early modern humans to procure resources over greater areas and with greater cognitive flexibility, is temporally associated in the nearby Koora drill-core record with increasing hydroclimate variability. However, the Koora record of water resource variability is itself not strongly associated with orbital cyclicity, but rather with possible tectonically and volcanically induced changes in local hydrology and spatial fragmentation of resources.

Several terrestrial core records show correspondences between important human evolutionary transitions and evidence of high hydroclimate, vegetation, or landscape variability. Lupien et al. (2018) identified a dramatic episode of high variability in δD and $\delta^{13}C$ of leaf waxes in the WTK drill-core record at 1.73 Ma, a time of high eccentricity. This timing corresponds with the last appearance of *Homo rudolfensis*, the first appearance of *H. erectus*, the dispersal of *Homo* spp. out of Africa, and the earliest evidence for Acheulian (e.g., hand axe) technology (Spoor et al. 2007, 2015; Lepre et al. 2011; Antón et al. 2014). Abrupt, high-amplitude climate variability, as registered in the Magadi (Owen et al. 2018), Koora (Potts et al. 2020), and CHB (Duesing et al. 2021; V. Foerster et al., unpublished paper) drill-core records, accompanied the technological transition from the Acheulian to the MSA. This is marked by evidence of increasing human cognition through features such as production of smaller and more complex tools, evidence for greater transport distances of raw materials, and the appearance of pigments, possibly for adornment. The significance of these temporal correspondences needs to be tempered by the fact that hominin fossil sample sizes remain small and geographically restricted; thus, uncertainties of the timing of specific hominin evolutionary transitions remain large (Faith et al. 2021).

Environmental variability is not a singular concept, and different tempos and modes of variability have been theorized to have different effects on hominin resources and populations. Trauth et al. (2021b) quantified different types of variability using recurrence quantification analysis, which allows the recognition of tipping points in hydroclimate (and thus ecosystems and hominin

resources) that may result from relatively small changes in the climate state. They analyzed the CHB potassium (aridity) and Ocean Drilling Project ODP Site 967 wet/dry index records and recognized two types of variability. One of these modes shows maximum variability at precessional frequencies and is accompanied by shorter (centennial- and millennial-scale) changes between wet and dry states. The second type of variability shows a weaker association with orbital parameters and occurs during insolation variability minima by rapid (years to decades) changes between wet and dry conditions, which increase in frequency through the entire phase of this type of variability. Trauth et al. (2021b) argued that the long-term variability associated with the first type would have corresponded to longer timescales, potentially associated with human evolutionary events and large-scale dispersal, whereas the short-term fluctuations of the second type would have more directly influenced differential mortality and fertility and population occupation of more favorable nearby habitats, as discussed by Schaebitz et al. (2021) and V. Foerster et al. (unpublished paper).

Modeling experiments are useful for understanding these potential effects of environmental variability on population growth and dispersal. Grove (2014) suggested that phenotypic plasticity (i.e., variability in phenotypes within a population allowing a broadening of habitat or dietary tolerances) could be expected to increase during periods of environmental instability. This accumulated plasticity could provide a pump for successful dispersal when a period of low climatic instability immediately follows a period of high instability. Grove et al. (2015) modeled favorable periods of dispersal for early *H. sapiens* out of Africa based on episodes of stability following extreme instability registered in the Lake Tana, Ethiopia, drill core Ca/Ti record (an indicator of relative moisture). They argued that the most favorable intervals for dispersal would have been between ~103 and 97 ka, consistent with evidence for early *H. sapiens* occupation in the Levant at the time. Lamb et al. (2018), evaluating the same Lake Tana paleoclimate record, noted three intervals favorable to dispersal (150–144, 125–93, and 82–73 ka) that also predate the latest age (~65–55 ka) from genetic evidence for the common ancestry of non-African *H. sapiens* (Nielsen et al. 2017). Some of these intervals were not marked by records of stability following extreme instability elsewhere in Africa, suggesting that if Grove's (2014) accumulated plasticity model is correct, the dispersal pump must have operated erratically around Africa.

Two important concerns can be raised about these comparisons between individual paleoclimate records of variability and the fossil/archaeological record of hominin evolution. First, it is unknown whether the individual records of variability reflect environmental conditions in the area(s) where the evolutionary transitions occurred. Second, it is well-known that FADs and LADs provide only minimal temporal bounds for the duration of any species or technology (e.g., Faith et al. 2021). This is problematic for extinct hominin species, for which the confidence intervals surrounding the FADs and LADs are very large. To address these uncertainties and further test the long-term relationships between environmental variability and hominin evolution, future studies will investigate how regionally stacked variability records from around Africa compare with the tempo of mammalian evolution and extinction during the Plio–Pleistocene, recognizing the inherent uncertainties of the fossil record.

6. FUTURE DIRECTIONS APPLYING LACUSTRINE DRILL-CORE RECORDS TO UNDERSTANDING HUMAN EVOLUTION

Research integrating paleoenvironmental reconstructions from drill-core records into our understanding of human evolution in Africa is still a work in progress. The cores described here are still under study, and as new approaches to dating these cores or reconstructing past climates and ecosystems are developed, we expect all of them to be mined more intensively for clues about the

habitats of early humans. Thus, careful preservation of these valuable materials in facilities such as the Continental Scientific Drilling Facility (**https://cse.umn.edu/csd**) is essential for maintaining their future value.

Beyond retrieving new information from existing cores, projects such as HSPDP provide a proof of concept for the transformative value of scientific drilling in ancient lake deposits for paleoanthropology. Three future directions for this science hold particular promise. First, ancient African lakes provide an extraordinary geographic range across which records can be collected and compared. It is evident even from the limited data gathered from lacustrine drill cores to date that large spatiotemporal differences exist between these records. To what extent can these be understood using existing paleoclimate models (e.g., Kutzbach et al. 2020) in terms of the relative impacts of low-latitude insolation versus high-latitude, glacial/interglacial forcing? While the evidence from lake core records makes the importance of orbital forcing for long-term climate variability in tropical Africa clear (e.g., Deino et al. 2021), strong evidence from African lake cores and climate models also exists for high-latitude forcing, particularly for abrupt/high-impact events (e.g., Tierney et al. 2008, Otto-Bliesner et al. 2014). Broad-scale syntheses are needed to evaluate the relative importance of these drivers across and adjacent to Africa (i.e., integration with core records from western Asia). From the paleoanthropological perspective, understanding the dynamics of these changes will clarify how and when various parts of the African continent, as well as corridors of dispersal out of Africa, became more or less favorable to hominins.

Second, the value of scientific drilling for addressing paleoanthropological questions is by no means restricted to studies in Africa. Many sites already drilled in Eurasia (**Figure 2**) have been incorporated into our understanding of hominin expansion out of Africa (e.g., Miebach et al. 2019). In the future we can expect similar integration of lacustrine drill-core records in deeper time, drawing on the many ancient lakes of Eurasia, to explore the habitats of Pleistocene hominins other than anatomically modern humans (AMHs), or the environmental context of the expansion of AMHs out of Africa.

Third, hopefully in the near future we can expect much longer records of African environmental history to be obtained from lake beds, spanning the entire 8–6 Ma time frame of hominin evolution. Projects in advanced stages of development from the oldest African lakes, Lakes Tanganyika (Cohen & Salzburger 2016, Russell et al. 2020) and Chad (Sylvestre et al. 2018), promise to provide records of African paleoclimate and ecosystem history since the Late Miocene from two very different regions of the continent (**Figure 2**). Along with other possible future drilling sites in other African Great Lakes, we anticipate these long records will yield tremendous advances in the emerging science of using scientific drilling to further our understanding of the deep-time environmental history of our distant ancestors. Understanding this history of environment and human evolution holds important implications for understanding our own adaptability to climate change into the future.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

AUTHOR CONTRIBUTIONS

A.S.C. and C.J.C. conceived the framework and coordinated the writing of this review and drafted the initial version of the text. Figures were produced by A.S.C., C.J.C., C.C.B., C.S.F., R.B.O., M.H.T., and C.L.Y. All authors made critical comments and substantive changes throughout the review.

ACKNOWLEDGMENTS

We thank our many colleagues of the Hominin Sites and Paleolakes Drilling Project (HSPDP) and Lake Malawi Drilling Project, whose research has contributed extensively to this review. We also thank the International Continental Drilling Program (ICDP) Operations Support Group, the National Lacustrine Core Facility (LacCore, now the Continental Scientific Drilling Facility), DOSECC Inc. and DOSECC Exploration Services for technical support with these projects, and the governments of Malawi, Kenya, and Ethiopia for authorizing this research. Financial support for this research was provided by ICDP, the National Science Foundation (EAR-0602350, EAR-1123942, BCS-1241859, EAR-1338553, BCS-1241790, and EAR-1322017), the Natural Environment Research Council (NE/K014560/1), Deutsche Forschungsgemeinschaft (DFG) priority program SPP 1006 (F.S.: SCHA 472/13 and /18; M.H.T.: TR 419/8, /10 and /16) and the Collaborative Research Center (CRC) 806, DFG Project Number 57444011 at the University of Cologne, the Hong Kong Research Grants Council (HKBU12300815; 12304018), the Peter Buck Fund for Human Origins Research (Smithsonian Institution), the William H. Donner Foundation, the Ruth and Vernon Taylor Foundation, Whitney and Betty MacMillan, the Institute of Human Origins (IHO, Arizona State University), and the Smithsonian's Human Origins Program. This is publication #45 of the HSPDP. This paper is dedicated to our deceased colleagues Andrew Hill, John Kutzbach, Charlie Lockwood, Jean-Jacques Tiercelin, and Mohammed Umer, all of whose contributions have been critical to the success of HSPDP at various stages of this project.

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Annual Review
of Earth and
Planetary Sciences

Volume 50, 2022

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