Progressive aridification in East Africa over the last half million years and implications for human evolution

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Edited by Donald E. Canfield, Institute of Biology and Nordic Center for Earth Evolution (NordCEE), University of Southern Denmark, Odense M., Denmark, and approved September 11, 2018 (received for review January 25, 2018)

Evidence for Quaternary climate change in East Africa has been derived from outcrops on land and lake cores and from marine dust, leaf wax, and pollen records. These data have previously been used to evaluate the impact of climate change on hominin evolution, but correlations have proved to be difficult, given poor data continuity and the great distances between marine cores and terrestrial basins where fossil evidence is located. Here, we present continental coring evidence for progressive aridification since about 575 thousand years before present (ka), based on Lake Magadi (Kenya) sediments. This long-term drying trend was interrupted by many wet–dry cycles, with the greatest variability developing during times of high eccentricity-modulated precession. Intense aridification apparent in the Magadi record took place between 525 and 400 ka, with relatively persistent arid conditions after 350 ka and through to the present. Arid conditions in the Magadi Basin coincide with the Mid-Brunhes Event and overlap with mammalian extinctions in the South Kenya Rift between 500 and 400 ka. The 525 to 400 ka arid phase developed in the South Kenya Rift between the period when the last Acheulean tools are reported (at about 500 ka) and before the appearance of Middle Stone Age artifacts (by about 320 ka). Our data suggest that increasing Middle- to Late-Pleistocene aridification and environmental variability may have been drivers in the physical and cultural evolution of *Homo sapiens* in East Africa.

Quaternary | paleoclimate | paleolimnology | hominins | Lake Magadi

Several hypotheses have attempted to explain human evolution and its possible relationship with environmental change (1, 2). The savanna hypothesis suggested that bipedalism resulted from hominins moving from forests to grassy savannas (3). Other theories emphasized climate as an evolution driver, including the aridity, turnover pulse, variability selection, and accumulated plasticity hypotheses (4–7). Evaluation of these ideas has been hindered by a lack of basin-scale records that can provide a high-resolution environmental context. The Hominin Sites and Paleolakes Drilling Project (HSPDP) has attempted to fill this gap by providing continental sedimentary records that can be linked to nearby hominin fossils and artifacts in Ethiopia and Kenya (8).

Here, we present evidence from the southernmost HSPDP site, at Lake Magadi (Fig. 1), that is relevant to debates about the climatic context of human evolution, from an area close to some of the most important records of hominin prehistory. The Lake Magadi record spans the past one million years (Fig. 2; see *SI Appendix*, *Supplementary Information Text*, Figs. S1–S3, and Tables S1–S7 for details of dating methods) and can be compared with a sequence that is 1.2 million years (Ma) old at Olorgesailie, 25 km to the northeast (9–11). The Olorgesailie deposits and archeological record document a transition from Acheulean to Middle Stone Age (MSA) toolkits (12–14), with the Magadi core, as well as cores from the neighboring Koora Basin drilled by the Olorgesailie Drilling Project (8, 15), covering the period when *Homo sapiens* emerged in Africa (16). The Magadi and Olorgesailie records also span a turnover in large mammals before 320 thousand years (ka) ago (14), which has also been documented at Lainyamok between 500 and 400 ka, 15 km west of Magadi (17). Thus, Lake Magadi is located in a region containing archeological and paleontological Middle Pleistocene sites that provide critical information about the relationships between climate dynamics and human prehistory.

Lake Magadi is a seasonally flooded saline, alkaline pan about 606 m above sea level in the South Kenya Rift (Fig. 1*A*) surrounded by poorly correlated cherts, silts, and evaporites (18, 19). Core HSPDP-MAG14-2A (hereafter MAG14-2A, Fig. 1*B*)

Significance

Previous research hypotheses have related hominin evolution to climate change. However, most theories lack basin-scale evidence for a link between environment and hominin evolution. This study documents continental, core-based evidence for a progressive increase in aridity since about 575 ka in the Magadi Basin, with a significant change from the Mid-Brunhes Event (~430 ka). Intense aridification in the Magadi Basin corresponds with faunal extinctions and changes in toolkits in the nearby Olorgesailie Basin. Our data are consistent with climate variability as an important driver in hominin evolution, but also suggest that intensifying aridity may have had a significant influence on the origins of modern *Homo sapiens* and the onset of the Middle Stone Age.

Author contributions: R.B.O., V.M.M., T.K.L., R.W.R., S.L., A.L.D., M.J.S., G.D.-N., and A.C. designed research; R.B.O., V.M.M., T.K.L., R.W.R., N.R., S.L., A.L.D., M.J.S., G.D.-N., E.P.M., K.L., A.C., C.C., D.D., C.-C.S., A.B., and A.M. performed research; R.B.O., V.M.M., T.K.L., R.W.R., N.R., S.L., A.L.D., M.J.S., G.D.-N., E.P.M., K.L., A.C., C.C., D.D., C.-C.S., and A.B. analyzed data; and R.B.O. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1801357115/-/DCSupplemental.

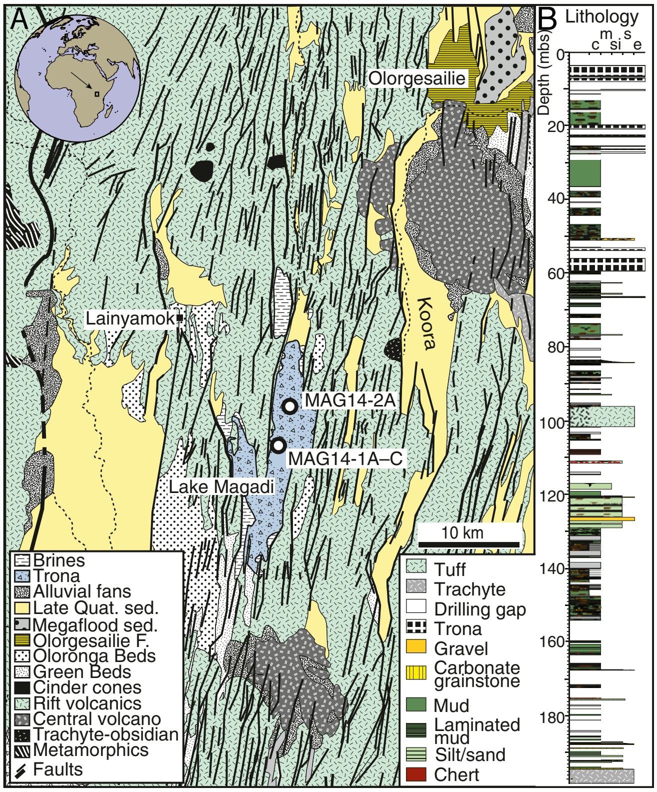

Fig. 1. Core location and lithology. (*A*) Location of MAG14-2A and MAG14-1A–C and geology. (*B*) Sediment log for MAG14-2A. c, clay; e, evaporites; m, mud; s, sand; si, silt.

includes trona, zeolitic mud, chert, tuff, and carbonate grainstone deposited in a regional tectonic sump that has been occupied by a lake since eruption of the underlying lavas (1.08 Ma). This study combines geochemical, mineralogical, diatom, and pollen analyses that indicate a trend toward a more saline, alkaline lake and a more arid climate from about 575 ka to the present. This progressive change was interrupted by wetter episodes but was directional in overall character toward increasing aridity.

Results

Progressive Changes in Geochemistry and Mineralogy. Loss on ignition (LOI) at 1,000 °C (Fig. 2*A* and *SI Appendix*, Table S7) indicates combustible carbonates (calcite and trona) and organic matter. High LOI values before 950 ka, or 187 m below surface (mbs), reflect shallow-water carbonate grainstones. LOI at 550 °C is low (<3%) between 950 and 800 ka (187 to 178 mbs), with higher values (5 to 20%) in younger sediments suggesting greater lake floor anoxia. Major increases in LOI in sediments after 111 ka (65 mbs) reflect increases in organics and trona, which accumulated in highly saline, alkaline, anoxic waters. Na/Ca ratios increased with time (Fig. 2*A*) as a result of a shift from calcium-rich (calcite and Mg-calcite) to Na- and K-rich (erionite and trona) chemical sediments. The upward decline in Ca probably reflects both early precipitation of $CaCO_3$ near shorelines where streams entered an alkaline paleolake and relative increases in groundwater contributions as drier conditions developed, which would have favored lower Ca through subsurface precipitation.

Mineralogical data also document progressive changes (Fig. 2*A*). Authigenic minerals are dominated by calcite and Mg-calcite in sediments before 385 ka (103 mbs), indicating fresh to mildly saline groundwater. Analcime occurs throughout the core with other zeolites accumulating since 375 ka, indicating a shift toward more saline, alkaline conditions. The zeolites were formed from Na-Al-Si alkaline spring gels washed into the basin or by alteration of aluminosilicate minerals or volcanic glass (20). Trona was deposited after 111 ka (65 mbs) in highly saline, alkaline water.

Diatom and Pollen Stratigraphy. Diatoms are absent in MAG14-2A sediments before 545 ka (132 mbs), but are present in basal limestones in a second core, MAG14-1A (Fig. 1*A*), in which benthic and epiphytic taxa indicate freshwater swamps. A few cherts contain *Anomoeoneis sphaerophora*, a moderate- to high-salinity taxon present in shallow springs today (21). The occurrence of diatoms only in well-cemented chert and limestone suggests that they may have dissolved from unlithified deposits. The dominant taxa in the diatomaceous interval (about 545 to 16 ka; 132 to 38 mbs) include mixed planktonic freshwater species (*Aulacoseira granulata* and *Aulacoseira agassizi*) and saline species (*Cyclotella meneghiniana* and *Thalassiosira faurii*; details in *SI Appendix*, Fig. S4 and Dataset S1), suggesting a deep meromictic lake with permanent saline waters that were periodically overtopped by fresh fluvial inputs. The evidence for flooding is supported by intermittent freshwater benthic taxa (22) such as *Cocconeis placentula*, *Encyonema muelleri*, and *Epithemia* spp.

Mean transfer functions for all diatoms indicate a pH of about 7.4 to 11.4 and conductivities of 300 to 40,000 μS cm^{-1} (Fig. 3). However, given the evidence for episodic meromixis, there is a need to recalculate the data separately for surface freshwater and deeper saline-water taxa (Fig. 3), which suggests that the pH of freshwater inputs ranged between 7.3 and 8.5, with conductivities of 200 to 2,000 μS cm^{-1}. The saline floras

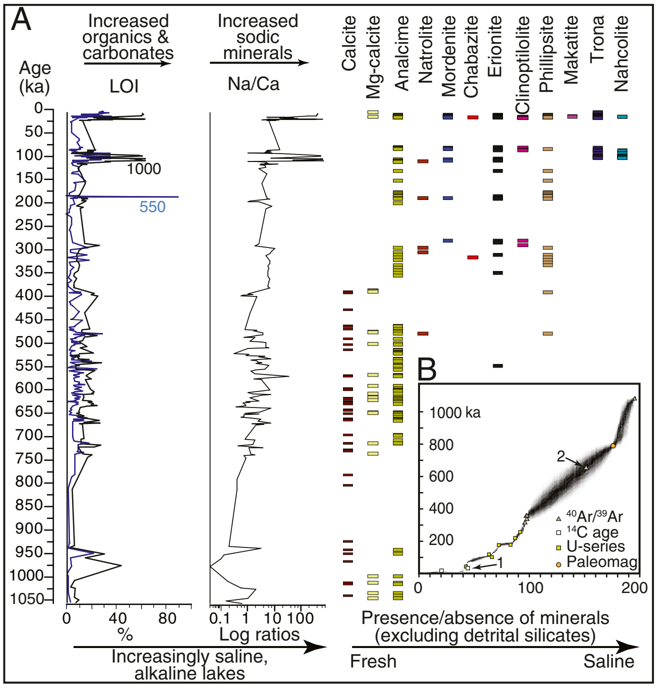

Fig. 2. Core chronology, geochemistry, and mineralogy. (*A*) Geochemistry and mineralogy. LOI at 550 °C/1000 °C; profile of Na/Ca ratios; and major authigenic minerals (excluding clays, quartz, and feldspar) determined by X-ray diffraction (minerals are ordered from left to right to reflect generally higher salinities). (*B*) Bayesian chronological model. 1, Excluded ^{14}C date that fails to follow a monotonic ordering; 2, excluded $^{40}Ar/^{39}Ar$ date from a single crystal. Two chert dates from samples later found to contain secondary chalcedony were also excluded from the model. See *SI Appendix* for details.

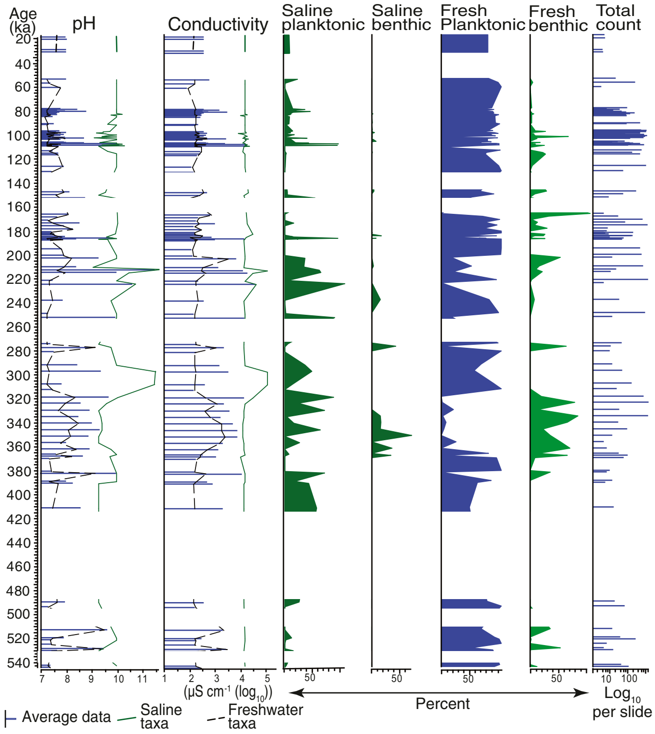

Fig. 3. Diatom-based environmental data. Diatoms accumulated in a meromictic lake, so separate conductivity and pH transfer functions are shown for saline water, freshwater, and mixed taxa. Habitats indicated separately for saline-water and freshwater taxa.

document increased pH after about 385 ka (103 mbs), from pH 9.2 to 10 to pH 9.4 to 11.5. An absence of diatoms after about 16 ka suggests that pH and conductivity exceeded tolerance limits or resulted in dissolution.

Grasses (Poaceae) dominated, with a smaller sedge (Cyperaceae) component, before about 900 ka (184 mbs), with pollen not preserved between 900 and 735 ka (184 to 168 mbs) (Fig. 4; detailed floras in *SI Appendix*, Figs. S9 and S10 and Dataset S2), possibly due to oxygenated conditions. Cyperaceae increased relative to Poaceae between about 735 and 520 ka (168 to 127 mbs) and dominated between 605 and 568 ka (143 to 136 mbs), with other minor aquatics (*Typha* and *Potamogeton*), suggesting shallow fresh waters (21). There were also significant increases in *Podocarpus* (735 to 520 ka) and *Olea* (698 to 635 ka; 160 to 147 mbs), with *Juniperus* appearing after 735 ka. *Podocarpus* is common in modern upland forests in Kenya and, where abundant, has been used to infer expansion of Afromontane forests or changes in fluvially transported regional pollen (23, 24). The parallel trends for *Podocarpus*, Cyperaceae, and the other aquatic indicators imply a climatic control. Although broadly classified as the wettest interval in the last million years, climate varied, with a drier episode at about 662 to 625 ka (153 to 146 mbs) marked by increased Amaranthaceae, and with the wettest conditions at 575 ka (137 mbs) (Fig. 4).

Cyperaceae and *Podocarpus* declined between about 520 and 400 ka (127 to 105 mbs), suggesting greater aridity at a time when diatoms indicate a meromictic lake and/or alternating saline-water and freshwater lakes. A recovery in *Podocarpus* and Cyperaceae between 400 and 275 ka (105 to 94 mbs) suggests a wetter interval that was followed by a decline in these taxa. During the last 275 ka (94 mbs), a variety of taxa expanded and contracted, reflecting wetter and drier settings but with an overall trend toward greater aridity. *Olea*, for example, is derived from wet and dry upland evergreen forests and varies in abundance from about 275 to 5 ka (94 to 7 mbs), when it disappears. *Commiphora* and *Acacia* increase after 205 ka (87 mbs), suggesting dry semideciduous dense bushland, with drought-related Amaranthaceae and *Juniperus* associated with drier upland forests (25) also common. Increases in Cyperaceae along with herbaceous pollen such as *Hydrocotyle* between about 12 and 8 ka (17 to 12 mbs) suggest fresher waters. Afromontane and woodland species were replaced by herbaceous pollen and Poaceae through the last 8 ka, with Poaceae forming nearly 100% of the flora after 4 ka (6 mbs).

Na/Ca ratios, principal components analysis (PCA) data for all pollen, and grass/aquatic pollen ratios indicate an overall progressive change during the last half million years (Fig. 5). Before 575 ka, the basin had trended toward wetter conditions, but then there was an overarching shift toward greater aridity superimposed on multiple wet–dry cycles. Independent terrestrial and aquatic datasets that vary in unison indicate that this change was not simply due to lake hydrology and local tectonics but was driven by a directional climate shift. Intermittent positive spikes in diatom PCA data between 350 and 70 ka reflect increases in shallow freshwater diatoms. The strong contrast in habitat preferences between the dominant mixed saline-water (*Thalassiosira* spp.) and deep freshwater planktonic taxa (*A. granulata* and *Aulacoseira granulata* var. *valida*) and the episodic shallow freshwater lake/wetland (*A. agassizi* and *A. granulata* var. *angustissima*) and benthic floras (Fig. 3) suggests that the latter may have been transported intermittently by floods from nearby swampy and/or fluvial settings to the core site (22). Many of the younger spikes also match pollen evidence for wetter periods (195, 170, 125, 95, and 80 ka) and interglacial episodes. The amplitude of the spikes decreases with time, as does their temporal spacing. A lack of diatoms after about 16 ka reflects the formation of an ephemeral hypersaline playa.

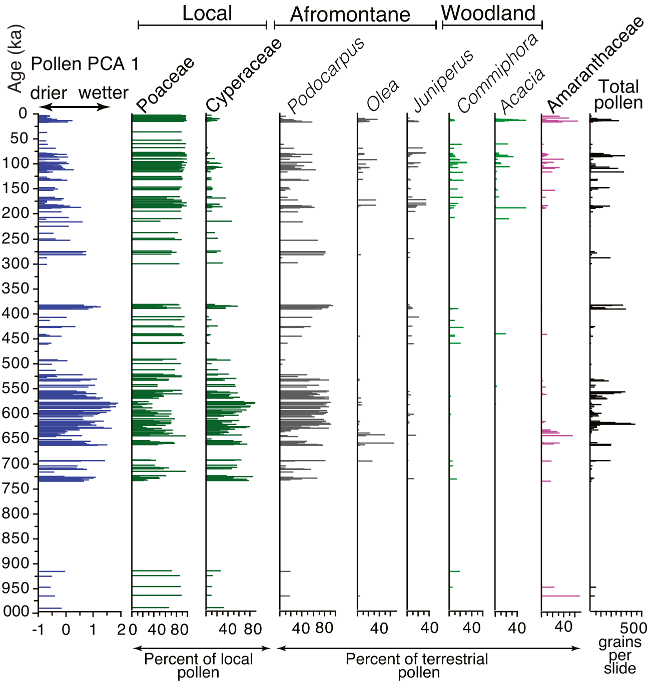

Fig. 4. Pollen stratigraphy. Selected taxa are shown. Pollen PCA 1 summarizes all pollen data and shows a long-term reduction in PCA values from ~575 ka that reflects increased aridity. Poaceae increases upward, with Cyperaceae and *Podocarpus* declining. Other taxa suggest increasing aridity during the last half million years.

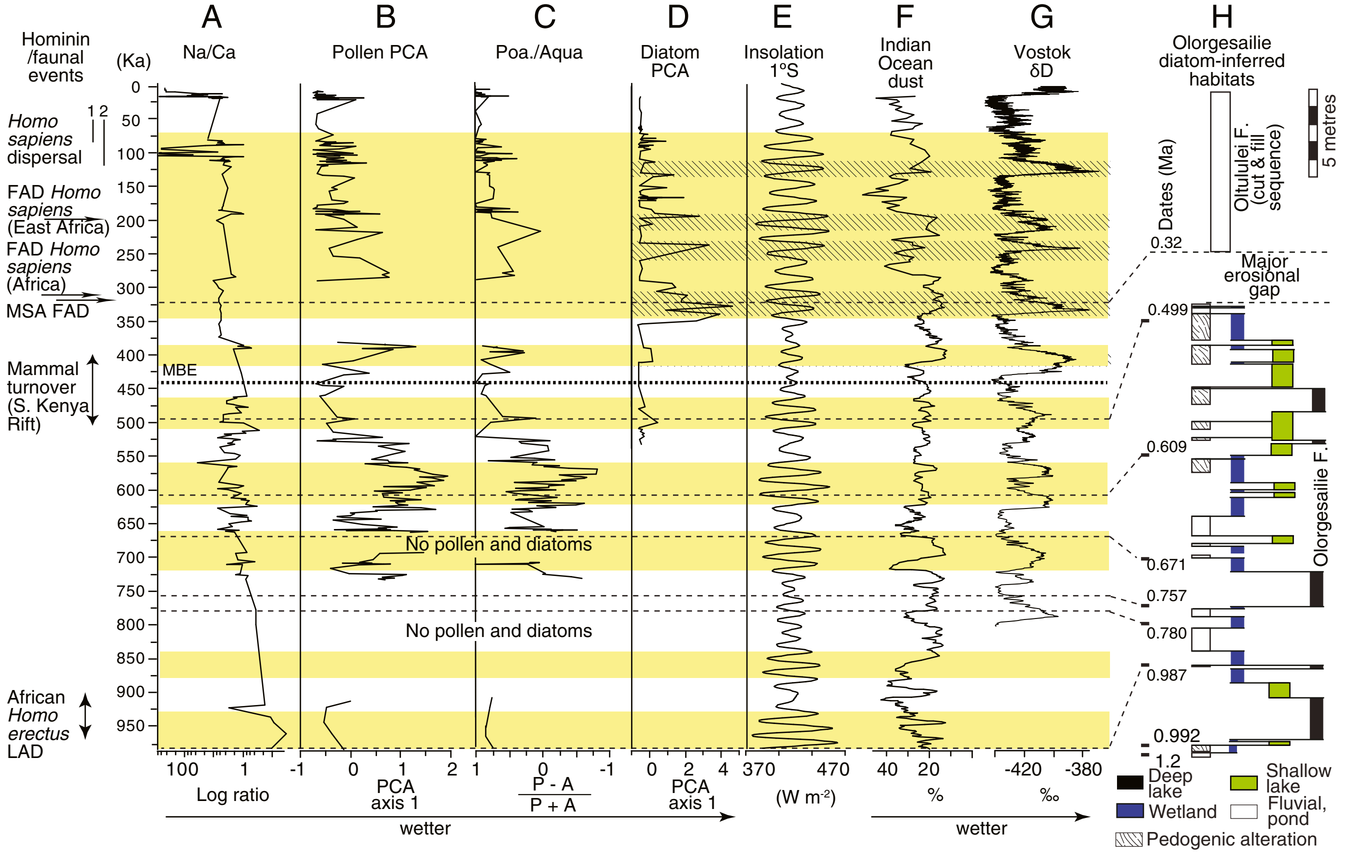

Fig. 5. Temporal environmental change in the Magadi Basin and regional comparisons. Thick dashed line shows the MBE. (*Left*) Major hominin/faunal events in eastern Africa (except where noted) (8). First appearance of *H. sapiens* in Africa from Morocco data (16). *H. sapiens* dispersal: 1, genetic data (41); 2, fossil data (39, 40). FAD, first appearance datum; LAD, last appearance datum. (*A*) Na/Ca ratios. Decline reflects change from freshwater to saline, alkaline lake. (*B*) Pollen PCA 1. Low values reflect increased aridity. (*C*) Poaceae (Poa, P)/aquatic (Aqua, A) pollen ratios (P − A/P + A). High values indicate wetter episodes. (*D*) Diatom PCA. High values reflect benthic taxa introduced to a meromictic lake by flooding. Note that many of these flood events broadly correlate (diagonal shading) with interglacial episodes in *G*. (*E*) Insolation (1°S) from AnalySeries 2.0. High-variability periods are shaded. (*F*) Northwest Indian Ocean dust record (26). Note long-term increasing aridity through the last 400 ka. (*G*) Change in deuterium in Vostok ice core, East Antarctica (27). Note increased variability in glacial–interglacial cycles after the MBE. (*H*) Diatom-inferred environmental change, Olorgesailie Basin (47).

Discussion

Climate Change. On a global scale, a major inflection point in Pleistocene climate—the Mid-Brunhes Event (MBE), close to the boundary between marine oxygen isotope stages 12 and 11—took place about 430 ka. Subsequently, there was increased climate variability with the development of colder glacial periods and warmer interglacial episodes (26, 27), although it has been suggested that the MBE is regionally inconsistent. Terrestrial data from the United Kingdom (28), for example, have been used to infer no significant change across the MBE, whereas continental evidence from Spain (29) supports a climate transition.

The continental pollen record from equatorial Lake Magadi provides strong support for a climate transition at the MBE (Fig. 5), suggesting a potential link to global CO_2/glacial cyclicity, with a major change from wetter conditions to greater aridity after about 430 ka. The overall trend toward dryer conditions was initiated about 575 ka, with particularly intense aridity developing between 525 and 400 ka, which partially overlaps with marine oxygen isotope stage 11 (424 to 374 ka), the warmest interglacial episode of the last 500 ka (30). Subsequently, many wetter and drier cycles were superimposed on progressive aridification, with diatomaceous parts of the core documenting a tendency toward increased flood inputs of benthic taxa (increased PCA values) during interglacial episodes (Fig. 5).

This directional increase in aridity since ∼575 ka has not previously been documented in continuous continental cores from East Africa, although there is support from pedogenic carbonate carbon isotopes in outcrops (31) and eolian dust records from the northwest Indian Ocean (7, 26) (Fig. 5), which suggest a similar pattern of increasing aridity and intermittently wetter intervals through the last half million years. Limited pedogenic carbonate carbon isotope data from Olorgesailie indicate an overall increase in C4 grasslands during the last 800 ka (14). Oxygen and carbon isotopes from several sites within a 990 ka Olorgesailie Formation paleosol, for example, suggest an abundance of wooded grassland in a cooler and moister environment at that time compared with the modern grassy semiarid basin (32).

There are also clear correlations for specific intervals in the Magadi record with other African regions. For example, the deposition of trona and intermittent severe reductions in aquatic pollen between about 110 and 80 ka indicate a series of very dry phases that alternated with wetter intervals. The termination of this drought period lies close to a transition from megadroughts to wetter conditions at Lake Malawi and more widely across tropical Africa (33, 34). However, in contrast, the overall drying trend at Magadi is inconsistent with an inferred shift toward wetter conditions noted at Lake Malawi (35), indicating regional African contrasts in vegetation and climate patterns. However, pollen data (36) show some similarities, with high percentages of

Podocarpus between 455 and 325 ka at Malawi coinciding with increased *Podocarpus* at Magadi after 455 ka.

Climate and Hominin Evolution. The nearby Olorgesailie Basin provides detailed information on hominin evolution for the last million years, with evidence for a major transition in stone technologies (Fig. 5). The Olorgesailie Formation (∼1,200 to 500 ka) includes Acheulean tools (14), whereas MSA artifacts (12) are present in the Oltululei Formation (∼320 to 36 ka) (11), with the transition between these toolkits taking place during a period of erosion at Olorgesailie that has been related to faulting and base-level change (10). Our environmental data from Magadi show increasing aridity during the period of hiatus at Olorgesailie, with intense desiccation between 525 and 400 ka. This suggests that erosion at Olorgesailie might partly reflect climatic conditions, with aridity lowering lake and base levels and changing/reducing the vegetation cover, which would, in turn, tend to enhance erosion of more exposed land surfaces (37). Magadi pollen data (*SI Appendix*, Fig. S5), for example, indicate an expansion of grasslands and a reduction in aquatic pollen after about 525 ka. The arid interval also closely overlaps with a major overturn in mammal faunas, with local extinction of large-bodied specialized grazing mammals reported from both Olorgesailie (14) and Lainyamok (17).

The 525 to 400 ka dry phase and environmental variability would likely have had a significant impact on contemporary hominin populations regionally. It has been hypothesized (14), for example, that environmental pressures and variability can lead to an uneven distribution of resources that could drive hominins to travel more widely and to interact increasingly with other groups for both raw materials and information. In turn, this would help to drive technological change and its dissemination, resulting in increased foraging success rates and ability to survive.

The Magadi terrestrial pollen record suggests that the interval with greatest climate variability took place between about 650 and 350 ka, with moister periods tending to be linked to high-amplitude insolation variability and drier episodes developing at times of low-amplitude insolation (e.g., 655 to 620, 560 to 510, 455 to 410, and <75 ka; Fig. 5). Similarly, changes in toolkits overlap with the 650 to 350 ka period, with modest reductions in Olorgesailie Acheulean stone tool sizes reported between 615 and 499 ka (14) and with the smaller toolkits of the MSA developing by about 320 ka (12–14). This increased environmental variability and the intense period of aridity also overlap with a major turnover in mammal faunas, with several large-bodied specialized grazing mammals becoming locally extinct and being replaced by related species with smaller body sizes (14, 17). As the earlier fauna was already arid-adapted, the progressive increase in aridity was unlikely to have led to any turnover. However, a change in variability, which very specialized grazers could not adapt to, may have led to the turnover. It is also possible that increased aridity, or more-variable environmental conditions in the context of increasing aridity, may have impacted hominin populations during this transitional period by selecting for cognitive abilities to, for example, transport increasingly diversified toolkits over greater distances, as is evidenced in the nearby Olorgesailie archeological record (12).

Major steps in Quaternary hominin evolution have also been linked to eccentricity-modulated high-amplitude insolation cycles specifically associated with extreme climate variability during moist intervals, rather than low-amplitude periods when monsoons are weakened and climate becomes drier (38). However, the possible overlap between intense aridity, major changes in toolkits, and mammal extinctions in the Magadi–Olorgesailie region argue against this version of a climate–evolution linkage.

The period between 350 and 50 ka represents the longest episode of eccentricity-modulated high-amplitude insolation variability in the Middle to Late Pleistocene (Fig. 5). This coincides with significant environmental change when MSA tools emerged, symbolic cultures developed, *H. sapiens* appeared, and the Late Stone Age commenced (2). Early anatomically modern human fossils from Asia indicate that they dispersed from Africa between 120 and 50 ka (39, 40), with genetic data suggesting that ancestral modern non-African populations originated from Africans that dispersed between 75 and 50 ka (41). Gulf of Aden leaf wax isotopes, close to a possible southern migration route, indicate multiple wet–dry cycles set against an overall drying trend (42). Our continental record indicates arid climates that were punctuated by moist episodes, which may have supported a greener Sahara, opening the possibility of northern routes.

Recent hominin studies have noted that *H. sapiens* and the cultural materials that they produced may have a polycentric African origin, with reproductively semiisolated populations adapting to local environments alongside genetic drift (43). In the South Kenya Rift, the 300 ka period of high-amplitude insolation variability was characterized by major environmental and hominin changes, providing support for hypotheses such as variability selection, which advocates adaptive evolutionary change during periods of increased environmental variability (4, 38, 44–46). However, it is important to note that this variability was superimposed on a strongly directional long-term trend toward increased aridity, especially during the critical 525 to 400 ka interval of drying documented here, which coincides with major technological and evolutionary events in the regional human prehistory. The Magadi record thus suggests that the species and technological changes in the South Kenya Rift were occurring against a backdrop of both increased aridity and enhanced variability, both of which could have acted as strong selective agents during the transition from the Early Stone Age to the MSA and in the evolution of anatomically modern humans.

Methods

Details of the drilling (June 2014) are presented in *SI Appendix, Supplementary Information Text*. Three holes were drilled at Site 1, with one core (MAG14-2A) recovered from Site 2 (Fig. 1*A*). Core recovery for MAG14-2A was 65%, with drilling terminated in trachyte at ∼194 mbs.

The chronology model (Fig. 2*B*) made use of one radiocarbon date from humate fractions of bulk organic matter in the upper core, nine replicate ^{40}Ar/^{39}Ar dates from midcore tephra, one ^{40}Ar/^{39}Ar date on a basal trachyte lava, and seven U-series dates from chert. An ^{40}Ar/^{39}Ar date for a single feldspar grain from ash at 151 mbs was treated as supplementary and not included in the model but plots within the 95% probability range for this depth (see *SI Appendix, Supplementary Information Text* for dating techniques). One ^{14}C date did not follow a monotonic sequence and was excluded from the model but is shown in Fig. 2*B*. In addition, the model includes the Brunhes-Matuyama boundary in the lower core.

Samples for geochemical (n = 343) and LOI (n = 332) analyses were collected at about 32-cm intervals and where distinctive lithologies were present (see *SI Appendix, Supplementary Information Text* for techniques). Diatom samples (n = 355) were collected every 32 cm, with additional sampling at 10- to 15-cm intervals for diatomaceous sections, yielding 113 samples and 62 diatom taxa between 38 and 132 mbs (16 to 545 ka in *SI Appendix*, Fig. S4 and Datasets S1 and S2). A minimum of 400 diatoms were counted per slide, except where diatoms were rare, in which case all diatoms were included. Environmental reconstructions are based on the "Combined Salinity Dataset" in the European Diatom Database (EDDI) (craticula.ncl.ac.uk/Eddi/jsp/index.jsp), with taxa matched to the EDDI classification system. Pollen taxa (n = 105) were identified in 354 samples, with common pollen shown in *SI Appendix*, Figs. S5 and S6 and Datasets S3 and S4. Pollen and spores were mounted on slides and counted at 400× magnification. Pollen identification was made to the lowest possible taxonomic level, although some pollen types could only be identified to family level. The total count per sample generally ranged between 250 and 500 grains, except in a few samples in which preservation was poor.

ACKNOWLEDGMENTS. We thank Julia Richter for LOI analyses, the National Museums of Kenya for support, and the National Council for Science and Technology and the National Environmental Management Authority of

Kenya for permits. Drilling, Observation and Sampling of the Earth's Continental Crust Exploration Services (DOSECC) provided drilling supervision, and the Operational Support Group of International Continental Drilling Program (ICDP) provided downhole logging services. Support was also provided by LacCore, the National Oil Corporation of Kenya, Tata Chemicals, and the County Government of Kajiado. Funding was provided by the Hong Kong Research Grants Council (Grant HKBU201912), the ICDP, the US National Science Foundation (Grant EAR-1338553), and the Ministry of Science and Technology of Taiwan Republic of China (Grants 107L901001 and MOST107-2119-M-002-051). This is Publication 15 of the Hominin Sites and Paleolakes Drilling Project.

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