Palaeogeography, Palaeoclimatology, Palaeoecology 567 (2021) 110247

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

A million year vegetation history and palaeoenvironmental record from the Lake Magadi Basin, Kenya Rift Valley

Veronica M. Muiruri[a], R. Bernhart Owen[b,*], Tim K. Lowenstein[c], Robin W. Renaut[d], Robert Marchant[e], Stephen M. Rucina[a], Andrew Cohen[f], Alan L. Deino[g], Mark J. Sier[h,i], Shangde Luo[j], Kennie Leet[c], Christopher Campisano[k], Nathan M. Rabideaux[l], Daniel Deocampo[m], Chuan-Chou Shen[n,o], Anthony Mbuthia[p], Brant C. Davis[f], Wadha Aldossari[f], Chenyu Wang[f]

[a] Department of Earth Sciences, Palynology & Palaeobotany Section, National Museums of Kenya, P.O Box 45166 00100, Nairobi, Kenya
[b] Department of Geography, Hong Kong Baptist University, Kowloon Tong, Hong Kong
[c] Department of Geological Sciences and Environmental Studies, State University of New York, Binghamton, NY 13902-6000, USA
[d] Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2, Canada
[e] York Institute for Tropical Ecosystems, Department of Environment and Geography Wentworth Way, University of York, Heslington, York, North Yorkshire YO10 5NG, UK
[f] Department of Geosciences, University of Arizona, Tucson, AZ 85721, USA
[g] Berkeley Geochronology Center, 2455 Ridge Road, Berkeley, CA 94709, USA
[h] Department of Earth Sciences, University of Oxford, South Parks Road, OX1 3AN Oxford, UK
[i] CENIEH, Paseo Sierra de Atapuerca 3, 09002 Burgos, Spain
[j] Department of Earth Sciences, National Cheng-Kung University, 701 Tainan, Taiwan, Republic of China
[k] School of Human Evolution and Social Change, Institute of Human Origins, Arizona State University, Tempe, AZ 85287, USA
[l] Department of Chemistry, Rutgers University, Newark, NJ 07102, USA
[m] Department of Geoscience, Georgia State University, Atlanta, GA 30302, USA
[n] High-Precision Mass Spectrometry and Environment Change Laboratory, Department of Geosciences, National Taiwan University, 10617 Taipei, Taiwan, ROC
[o] Research Center for Future Earth, National Taiwan University, 10617 Taipei, Taiwan, ROC
[p] Tata Chemicals Magadi, Box 1, Magadi, Kenya

ARTICLE INFO

Keywords:
Quaternary
Pollen
Podocarpus
Palaeolakes
Climate change
Hominin evolution

ABSTRACT

This study examines a one-million-year pollen record from a 194-m-long Lake Magadi core (HSPDP-MAG14-2A) in the south Kenya Rift Valley. The pollen indicate a general trend through the last 740 kyr from wetter conditions to generally drier environments. Grassland dominated with less common *Podocarpus* and Cyperaceae in a sparse flora between 1000 and 740 ka. Poaceae, woodland and herbaceous plants are common through the remaining core and abundant between 740 and 528 ka and after 200 ka. Pollen diversity increased after 200 ka. *Podocarpus* and Cyperaceae reached a peak abundance at ~575 ka with a subsequent decline that suggests a progressive increase in aridity, interrupted by wetter intervals.

Podocarpus-dominated forests expanded and contracted many times during the Quaternary and document an anti-phased relationship with data from Lake Malawi. Similar anti-phased correlations are noted for herbaceous plants, suggesting that the two basins responded differently to the same climate or were influenced by contrasting climate regimes. Increases in macrocharcoal correlate with increasing pollen abundance and suggest wetter conditions.

Data from the Magadi, Koora and Olorgesailie basins indicate similar trends and a dominant climate control on vegetation and habitats. Large lakes characterised all three basins at 740–528 ka with climate subsequently becoming drier, but with many wetter intervals. At various times the lakes expanded, contracted and dried out, except at Lake Magadi where spring inflows maintained lacustrine conditions through the late Quaternary. Faulting also contributed to fragmentation of the landscape and formation of a mosaic of habitats.

An especially intense period of aridity at ~528–392 ka coincided with extinction of many large-bodied mammals and may have helped to drive a change from the use of Acheulean hand axes to the production of

---

* Corresponding author.
E-mail address: owen@hkbu.edu.hk (R.B. Owen).

https://doi.org/10.1016/j.palaeo.2021.110247
Received 3 October 2020; Received in revised form 19 January 2021; Accepted 20 January 2021
Available online 26 January 2021

Middle Stone Age tools by 320 ka. After 200 ka pollen diversity increased substantially with a mix of montane, riparian and dry forest associations that were present in varying amounts through to ~4.2 ka at the core top.

1. Introduction

The tectonic evolution of the East African Rift System created a series of basins within which sediments accumulated and preservation of fossils occurred, including a unique record of hominin remains. Consequently, African Plio-Pleistocene hominin fossils have been the subject of considerable interest in developing a detailed understanding of our origins, and also possible links between human cultural and/or physical evolution and environmental change (e.g., Potts, 2012a, 2012b and references therein). Over the last few decades researchers have suggested many hypotheses that explore associations between climate, environmental dynamics and hominin evolution (Potts and Faith, 2015; Maslin et al., 2015). However, many of these ideas have been based on environmental records from locations that are distant from the hominin fossil sites (deMenocal, 2004), and with relatively few records documenting interactions at the basin scale (Owen et al., 2018a). Consequently, testing these hypotheses remains a challenge, particularly as outcrops at the key fossil localities typically provide discontinuous temporal records (Potts et al., 2018).

Until recently, the most continuous Plio-Pleistocene African palaeoenvironmental records have been obtained from marine sediment cores taken from the South Atlantic and Indian Oceans (deMenocal, 1995; deMenocal et al., 2000). These provide data that are limited in their interpretative value at the local basin scale as they integrate environmental signals over large geographical regions (deMenocal, 2004). However, seismic data from Lake Tanganyika (Scholz et al., 2007; McGlue et al., 2008) and stratigraphic studies of Lake Malawi (Cohen et al., 2007; Stone et al., 2011; Beuning et al., 2011; Ivory et al., 2012; Lyons et al., 2015; Ivory et al., 2016, 2017, 2018) and Lake Challa (Moernaut et al., 2010) sediments have started to provide information for periods ranging up to 1.3 Ma from individual basins in the southern tropics. The Hominin Sites and Paleolakes Drilling Project (HSPDP) was set up in an attempt to provide similar high-resolution environmental data from sedimentary basins located close to sites with important hominin fossils (Cohen et al., 2016; Campisano et al., 2017). The HSPDP drilled in five basins in Ethiopia and Kenya, including two cores (HSPDP-MAG14-2A and HSPDP-MAG14-1A) from Lake Magadi, which contains thick sequences of lacustrine, fluvial and terrestrial sediments (Owen et al., 2019). that can be correlated with nearby sites with significant hominin fossils of differing ages. These depositional records have been supplemented by additional cores from the Koora Basin (10 km east of Magadi) collected by the Olorgesailie Drilling Project (ODP) (Potts et al., 2020).

This contribution presents a detailed environmental record for the last million years from the south Kenya Rift, based on pollen in HSPDP-MAG14-2A and charcoal recovered from both Magadi cores. Pollen were rare in HSPDP-MAG14-1A, possibly because the core site experienced greater exposure during deposition (Owen et al., 2019). The deposits provide a basis for understanding the environmental drivers that may have influenced the cultural evolution of ancestral humans in the region, documented by the nearby prehistoric site of Olorgesailie (Potts, 1989). Previous excavations at Olorgesailie have reported variations in the behaviour of our early human ancestors since ~1.2 Ma, including a major shift from the use of Acheulean hand axes to Middle Stone Age tools (Behrensmeyer et al., 2018; Brooks et al., 2018). Other important transformations during this period include the change from *Homo erectus* to *Homo sapiens* and a major regional turnover of the mammalian fauna (Potts et al., 2004; Faith et al., 2012; Potts et al., 2018).

Research on Lake Magadi core HSPDP-MAG14-2A is important because, as a depocenter site, it provides a more detailed environmental history than is available at Olorgesailie, where there are many time gaps related to episodes of pedogenesis and erosion. This is especially true for the later Quaternary when fluvial incision and non-deposition resulted in significant time gaps at ~500–320 ka and for several younger stratigraphic intervals (Behrensmeyer et al., 2002, 2018). Owen et al. (2018a, 2019) have presented detailed diatom, sediment and geochemical records for the Magadi Basin based on core HSPDP-MAG14-2A and outcrops in the region. This study presents a comprehensive pollen record from the same core and aims to: 1) develop a single-site history of long-term vegetation dynamics, 2) relate vegetation change to palaeoclimate, and 3) to explore how these changes may have contributed to hominin cultural change in the region.

2. Environmental setting

Lake Magadi lies at a height of ~605 m in the southern part of the Kenya Rift Valley and is characterised by a semi-arid climate. Rainfall, at Magadi town, averages ~500 mm/yr, with seasonal ranges between 4 (August) and 120 (April) mm per month. The rift is demarcated to the west by the Nguruman Escarpment (~1950 m) and to the east by a series of step faults that drop down from the Kajiado Escarpment (Fig. 1A). Farther north, and east of Suswa volcano, the Kikuyu Escarpment bisects an earlier volcanic massif that forms the Ngong Hills (Baker and Mitchell, 1976). North-south trending faults cut extensive flood lavas that form the Early Pleistocene Magadi Trachyte Formation (Fig. 1B). These have produced many parallel horsts and grabens that host Lake Magadi with one graben to the northwest occupied by a permanent shallow lake (Nasikie Engida) that is maintained by hot spring inflows (Fig. 1A, B) (Allen et al., 1989; Renaut et al., 2020).

The Toroka River drains the Kajiado Escarpment in the east and flows into the Kwenia depression, with the Olkeju Ngiro River feeding into the Koora Plain via the Oltepesi and Legumunge plains at Olorgesailie. Farther north the Ewaso Kedong River drains the Kikuyu Escarpment and areas east and north of Suswa. Lake Magadi (Fig. 1B–C), which is today fed by springs and ephemeral streams, has no outlet. A number of Pliocene to Late Pleistocene volcanic centres are present, notably Ol Doinyo Nyoki (~1169 m), Olorgesailie (~1760 m), Ol Esayeti (Esakut) (~1950 m) and Suswa (2356 m) (Fig. 1A).

Today, the extent of human occupation and land exploitation, together with altitude, geology, soil type and moisture variability control the vegetation in the south Kenya Rift. The main vegetation types in the Magadi and Natron catchments were mapped by Vincens (1987) and include bushland, wooded grassland, riverine vegetation, grassland and semi-desert bushland and scrub (Fig. 2). Bushland is dominated by *Vachellia tortilis* and *Salvadora persica* with a patchy understory of grass comprising *Sporobolus ioclados* and other *Sporobolus* species. The plains of Oloisinyai and Kikuro and the area surrounding the Shombole Swamp (Fig. 1A) are dominated by xerophytic trees and shrubs such as *Vachellia tortilis*, *V. mellifera, V. nubica, Balanites aegyptiaca* and *Commiphora africana* (Gichuki et al., 2002). Along the Ewaso Ngiro River are patches or riverine vegetation dominated by *Ficus sycomorus*. Grasses are common and include *Eragrotis tenifolia*, *Bothriochloa insculpta*, *Cenchrus ciliaris*, *Chloris roxburghiana*, *Pennisetum mezianum*, *Eragrotis dactylon* and *Sporobolus marginatus*. Pastoralism practiced by the Maasai community is the dominant land use in the larger part of the Magadi Basin. Cultivation is practiced on small pieces of land during the short rainy season and some agriculture is present near wetlands such as the Shombole Swamp, the Nguruman Swamp and the Ewaso Ngiro Swamp (Stevenson, 2000).

3. Methods

Core HSPDP-MAG14-2A is located at 1.8516°S and 36.2794°E and reached basement trachyte at a depth of ~194 m, with 65% core recovery. Details of coring operations and handling can be found in Cohen et al. (2016). Full details of dating techniques and chronological modelling have been given by Owen et al. (2018a) with results shown in Fig. 3B. A basal trachyte and mid-core tephra were dated using $^{40}Ar/^{39}Ar$ techniques. Radiocarbon dating was carried out on bulk organic matter, humates, charred particles and trona. Several results were problematic due to modern carbon and brine contamination, with two dates incorporated into the model. Palaeomagnetic methods identified the Brunhes-Matuyama boundary at 174.36 mbs (metres below surface) (Owen et al., 2018a). Seven U-series dates obtained from chert form a stratigraphically consistent sequence, except for one possible outlier at 107.3 m that yielded an age similar to dates at 91 m (Owen

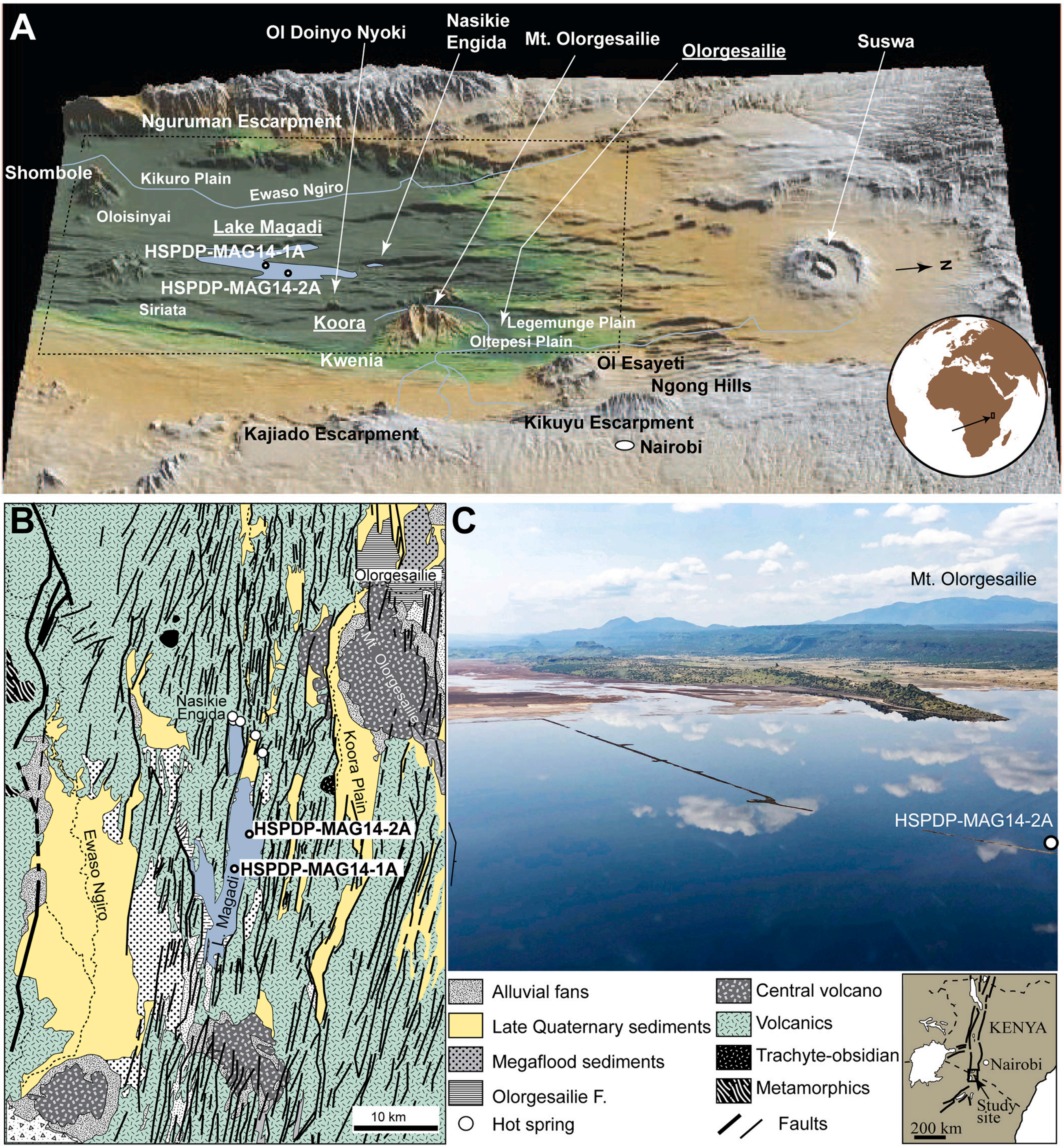


Fig. 1. Topography and geology of the south Kenya Rift. A: Topography and locations. Major basins discussed in text are underlined. Diagram constructed using GeoMapApp. B: Simplified geology of the south Kenya Rift (after Owen et al., 2019). C: Oblique photograph of Lake Magadi HSPDP-MAG14-2A coring site with Mt. Olorgesailie in the background, view towards northeast. Photographic taken in June 2019 when Lake Magadi was flooded.

et al., 2018a). Subsequent examination indicated secondary chalcedony in that sample. Bacon v.2.2 software was used to construct the chronological model (Fig. 3B; Owen et al., 2018a).

Pollen preparation followed standard procedures published in Faegri and Iversen (1989) and Moore et al. (1991). Pollen samples were collected every 30 cm from HSPDP-HSPDP-MAG14-2A and more frequently where sediments changed between these intervals, yielding 354 samples (Supplementary Table S1, see Electronic Supplementary Material). Carbonates and silicates were removed using dilute HCl (10%) and cold HF (70%), respectively. Colloidal silica was removed with warm dilute HCl. Humic acids were removed by dilution in KOH (10%) solution. Subsequently, the residue was diluted in glycerol and mounted on glass slides.

Identification was confirmed by comparison with a reference collection of over 6000 slides of modern East African pollen held at the Department of Earth Sciences (Palynology & Palaeobotany Section) at the National Museums of Kenya (NMK). Identifications also made use of a range of publications (Hamilton, 1975, 1982; Marchant et al., 1997) and digital photographs of pollen types obtained from the African Pollen Database (Vincens et al., 2007). Pollen identification was made to the lowest taxonomic level, although some pollen could only be identified to family level, with the nomenclature following that of Benninghoff and Kapp (1962). The total count per sample ranged between 250 and 500 grains, except in a few samples where preservation was poor.

The data were plotted using TILIA 1.7.16 with CONISS (Grimm, 1987) used to define the pollen assemblages (zones) and location of the boundary using stratigraphically constrained clustering procedures. Constrained zonation methods were adopted (Birks and Gordon, 1985; Birks, 1986) with relationships between non-contiguous samples and zones checked by a stratigraphically unconstrained clustering techniques using CONISS. Taxa were reduced to the 49 most common pollen, which comprised at least 2% in three or more samples, for a Principle Components Analysis (PCA) using CANOCO 4.5.

Macrocharcoal was extracted from screen washed samples (64 μm) and counted at 100× using a Leica M165 binocular microscope. Charcoal concentrations were estimated by combining counts with dry mass determinations of the original charcoal-bearing sediment samples. The resulting data are presented in Supplementary Table S2 (see Electronic Supplementary Material).

4. Results

The core is dominated by laminated or massive lacustrine mud interbedded with chert in varying proportions through most of its length, except for the upper 60 m where trona and trona-bearing mud is dominant (Fig. 3A) (Cohen et al., 2016; Owen et al., 2019). Pollen analyses document variation in the terrestrial vegetation from the regional catchment and the local palaeolake aquatic macrophytes. The core

Fig. 2. Vegetation and landscape in the south Kenya Rift. A: Typical horst and graben topography covered by wooded grassland, bushland and scrub. Nasikie Engida in middle distance; Lake Magadi in far distance. View to south with Shombole volcano on central (right) horizon. B. Riverine vegetation, Ewaso Ngiro River. Inset shows regional vegetation map, after Vincens (1987). C: Ground level photograph of wooded grasslands, northeast of Lake Magadi.

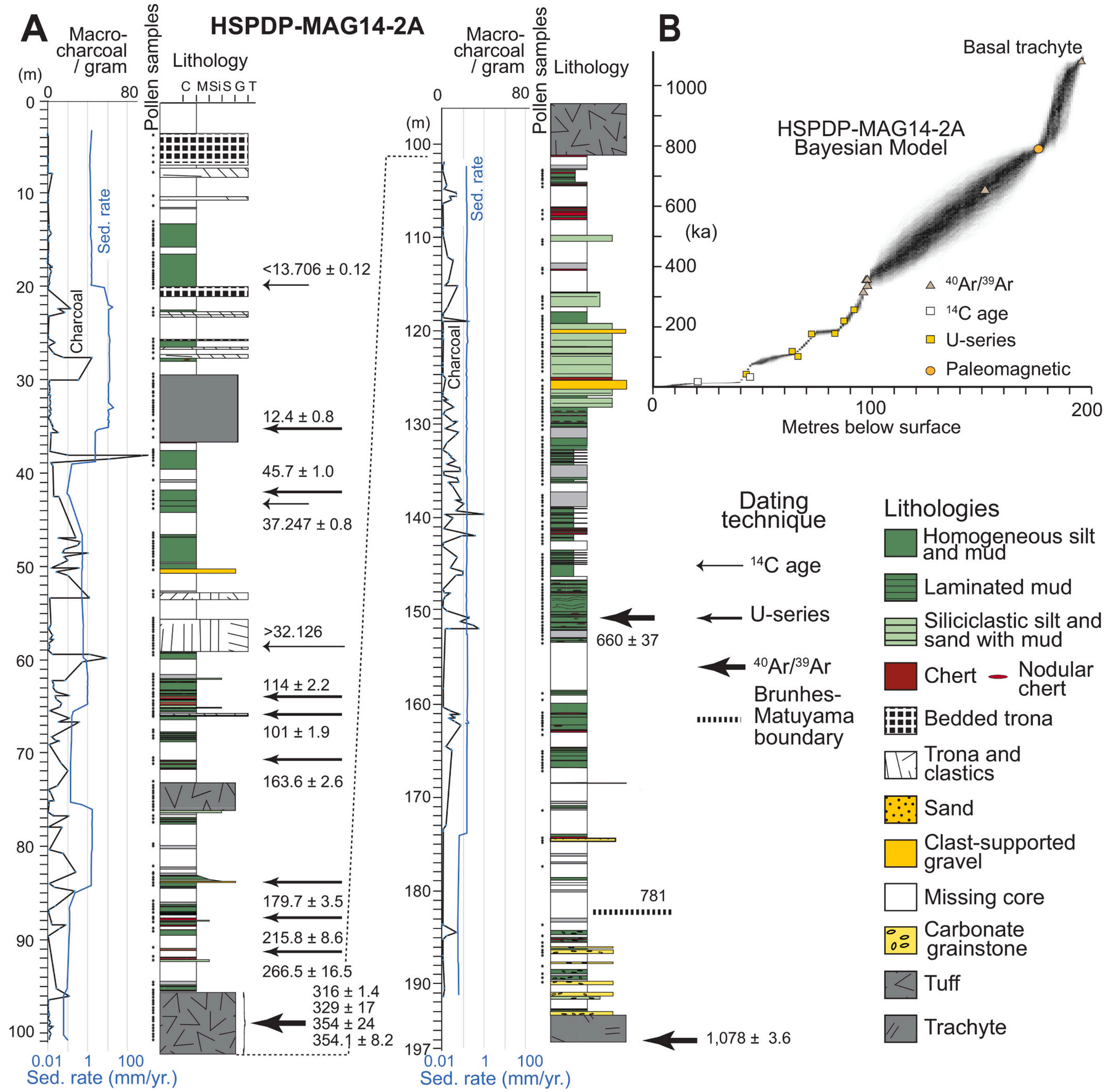


Fig. 3. Lithology and geochronology of Core HSPDP-MAG14-2A. A: Core lithologies with dates used in the geochronology marked to the right. C = Clay, M = Mud, Si = Silt, S = Sand, G = Gravel, T = Trona. Macrocharcoal and sedimentation rate data to the left of the lithological logs. B: Bayesian chronology (after Owen et al., 2018a).

contains 105 pollen taxa, with 102 belonging to trees, shrubs and herbs and three liana taxa.

A PCA analyses (Fig. 4) shows the first three axes, which account for 58.6% of the variation. Poaceae, *Podocarpus* and Cyperaceae constitute the dominant vectors. *Podocarpus* and Cyperaceae are also positively correlated on all axes, suggesting common controlling factors in their production. Wetland taxa (*Hydrocotyle* and *Typha*) lie close to zero on all axes.

PCA Axis 1, which explains 34.1% of the variance, is positively associated with *Podocarpus* and woodland taxa such as *Vachellia* with a strong negative correlation with Poaceae and weak negative correlations for most herbaceous pollen (*Acalypha*, Acanthaceae, Amaranthaceae, Apocynaceae, Asteraceae, Asclepindaceae, *Asparagus*, *Impatiens*, *Justicia*, *Legumme*, Malvacaeae, Nyctanginaceae, *Rumex*, *Sanseviera*, *Stemodia* and Urticaceae).

Axis 2 (16.8%) shows a strong positive correlation with *Podocarpus*, *Olea* and Cyperaceae with negative correlations for Afromontane *Celtis*, *Croton*, *Juniperus* and Rubiaceae. Most woodland taxa show negative values, with stronger negative values for *Vachellia*, *Cocculus* and *Commiphora* as well as the herbs *Artemesia*, *Aloe*, Chenopodeacae, *Cocculus*, *Capparis*, *Impatiens*, Labiatae and Liliacea. Weaker negative to slightly positive correlations are associated with the herbs Anonaceae, *Cleome*, Cucurbitaceae, *Indigofera*, *Stoebe* and *Valeriana*, which show considerable overlap with woodland pollen such as *Cordia*, *Euphorbia*, *Grewia* and

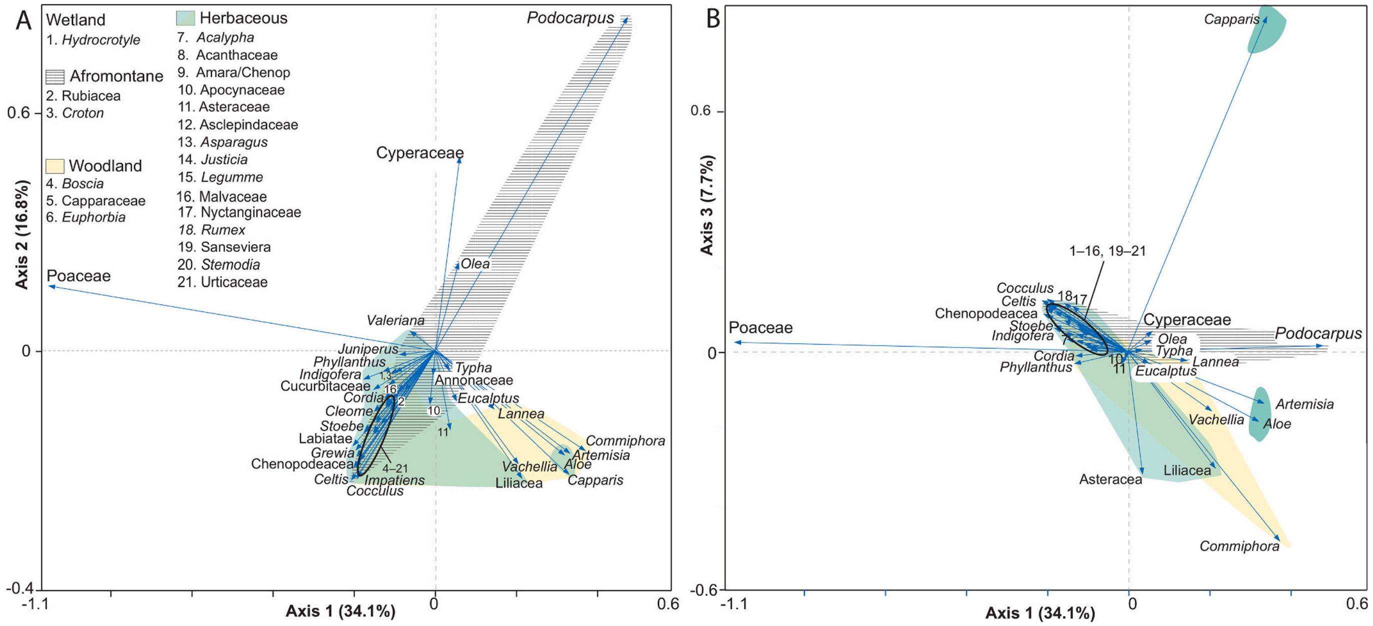


Fig. 4. PCA diagrams of axes 1–3 for common pollen. Note major vectors for *Podocarpus*, Cyperaceae and Poaceae. Fields with Afromontane, woodland and herbaceous taxa shaded.

Phyllanthus.

Axis 3 (7.7%) documents a strong positive correlation with the herbaceous taxon *Capparis* and weak positive correlations with Cyperaceae, several Afromontane taxa (*Podocarpus*, *Olea* and *Celtis*), and herbaceous pollen (*Cocculus*, Chenopodeacea, *Stoebe*, *Indigofera*). Strong negative relationships are evident for woodland *Commiphora* and *Vachellia* and herbaceous *Aloe*, *Artemisia*, Asteraceae and Liliaceae.

In general, Axis 1 contrasts grasslands (negative loadings) through herbaceous and woodland systems to predominantly Afromontane floras with dominant *Podocarpus* (positive loadings). Axis 2 contrasts woodland and herbaceous vegetation (negative loadings) with Cyperaceae, which tracks close to *Podocarpus* (positive loadings). Axis 3 shows a weaker separation of woodland and herbaceous taxa (negative loadings) from Afromontane pollen (slight positive loadings).

Two sets of fossil pollen sums were calculated; the first consisted of the total sum of Poaceae and wetland/local taxa (Cyperaceae, *Hydrocotyle*, *Potamogeton* and *Typha*). Poaceae was considered as local because of its dominance (local over-representation) among the fossil pollen flora and the numerous grasses that grow in the Magadi catchment today. Cyperaceae were considered indicative of wetter conditions because of their abundance and likely littoral growth form, with any dryland forms also requiring at least short wet periods to survive. The second fossil pollen sum included regional taxa and land pollen with unknown and undifferentiated pollen grains, but not spores.

Trees were grouped together as Afromontane taxa, with shrubs and lianas placed in a woodland group and all herbaceous taxa placed in a separate category. The three terrestrial groups (land pollen) were regarded as regional, although some of the herbs are likely to be derived from both local and regional parent taxa. In this case, they are all included in the pollen sum of the regional taxa.

Pollen variability in the core was analysed by Muiruri (2017) by using CONISS, which clusters the pollen data into 41 identifiable zones (Fig. 5), averaging ~24 ka per zone (Fig. 5). However, these divisions can be simplified into five major units. Unit 1 (193–167.5 m; ~1041–740 Ka) includes a single pollen zone and large coring gaps in sediments that rest on trachyte. Core recovery was poor in Unit 1 and no pollen samples were analysed between 167.5 and 185 m (Fig. 5). Deposits between 185 and 193 m either lack pollen or contain pollen in low abundances. The unit is distinguished by Cyperaceae and abundant Poaceae with sporadic appearances of woodland (*Commiphora*, *Euphorbia* and Ericaceae) and herbaceous taxa (*Stoebe*, *Stemodia* and *Valeriana*).

Unit 2 (167.5–129 m; 740–528 ka) includes relatively abundant and diverse floras in thirteen zones (II–XIV) that are dominated by Poaceae and Cyperaceae. The unit is also distinguished by the presence of common to abundant Afromontane pollen, primarily *Podocarpus*, with varying percentages of Ericaceae, *Juniperus*, *Olea*, Rubiaceae, and other less common Afromontane taxa (Fig. 5). The different zones reflect variations in woodland (common taxa: *Boscia*, *Commiphora, Euphorbia* and *Phyllanthus*) and herbaceous (common taxa: *Aloe*, Amaranthaceae, Asteraceae, Cucurbitaceae, *Impatiens, Indigofera*, Liliaceae, *Legumme*, Lilliaceae, Nyctanginaceae, *Stoebe* and *Valeriana*) pollen.

Unit 3 (129–104.2 m; 528–392 ka) includes three zones (XV–XVII) and is characterised by reduced pollen abundance compared with Unit 2. Pollen are absent in several parts of the unit and there are a number of core gaps (Fig. 5). Cyperaceae and *Podocarpus* are generally less common than in Unit 2, with *Olea* and Ericaceae intermittently present. Woodland taxa include varying percentages of *Vachellia*, *Commiphora*, *Grewia*, *Boscia* and *Phyllanthus*. Fewer herbaceous taxa are present than in Unit 2.

Unit 4 (104.2–86.2 m; 392–200 ka, Fig. 5) includes three zones (XVIII–XX) with pollen varying in abundance and less diverse than in Units 1–3. Intervals with pollen are intermittent due to the presence of a thick tuff and multiple coring gaps. Nevertheless, the unit is distinguished by an expansion of Poaceae with above-average percentages of grasses (mean value >70%). Cyperaceae constitute a mean of ~20%. *Podocarpus* dominate the Afromontane taxa with sporadic occurrences of *Juniperus* and *Olea*. Woodland and herbaceous taxa vary considerably between different zones.

Unit 5 extends to the core top (86.2–3.19 m; 200–1.9 ka) and includes zones XXI to XXXXI with no pollen present above 6.5 m (4.2 ka). The sediments are characterised mainly by low to common pollen counts and a diverse flora with low percentages of Cyperaceae and dominant Poaceae. Afromontane taxa are dominated by *Podocarpus*, *Juniperus* and *Olea*. Drought-related woodland (*Vachellia*, *Boscia*, *Capparis*, *Commiphora*, *Cordia*, *Grewia*, *Phyllanthus* and *Solanum*) and herbaceous taxa (*Aloe*, Amaranthaceae, *Asparagus*, *Artemisia*, *Indigofera*, Liliaceae, *Stoebe*, *Sansevieria* and *Stemondia*) are more common than in any other part of

Fig. 5

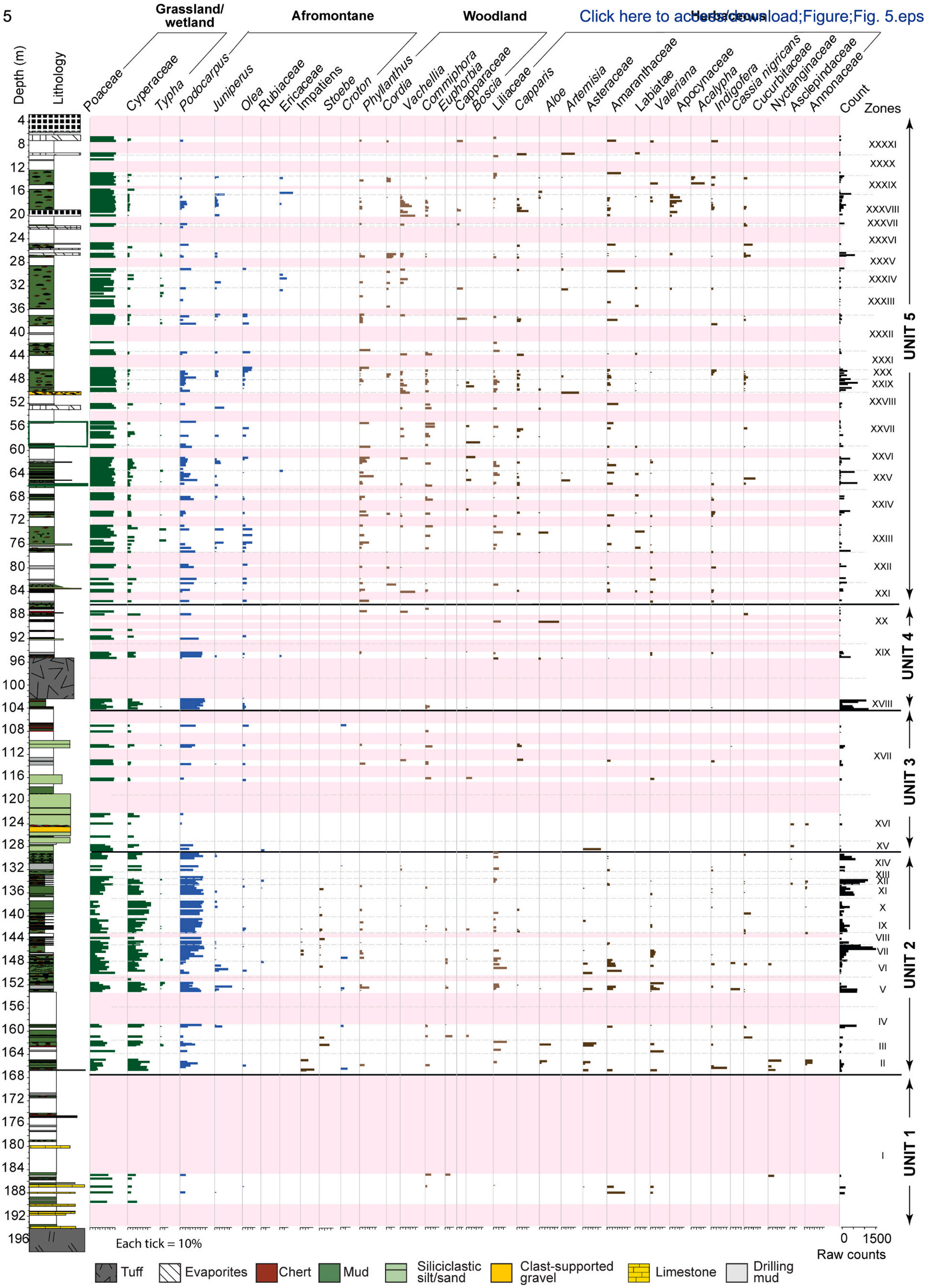


Fig. 5. Dominant pollen taxa plotted against core depth in HSPDP-MAG14-2A. Taxa forming >20% in at least two samples included. Shading marks core sediments with no pollen and coring gaps (white in the core log). Zones to the right based on CONNISS. See supplementary materials for raw data and additional taxa.

the core (Fig. 5). Pollen indicative of wetter conditions (e.g., *Commelina*, *Justicia, Rumex* and Urticaceae) are also present, varying between zones.

Macrocharcoal data also show considerable variability through both HSPDP-MAG14-2A (Fig. 3) and a second core, HSPDP-MAG14-1A (Fig. 1 for location), with charcoal counts ranging from 0 to ~100 and 0 to 570 per gram in each core, respectively (Supplementary Table S2, see Electronic Supplementary Material). Sedimentation rates are similarly variable, ranging between 0.06 and 18.57 mm per year in HSPDP-MAG14-2A with rates tending to increase upwards through the core (Fig. 3).

5. Discussion

5.1. Temporal palaeovegetation dynamics

Core MAG14-2A preserves an unusually long Middle Pleistocene to Holocene vegetation record that sheds new light on environmental and climate variability in the south Kenya Rift. Today, the Magadi Basin is one of the driest regions in East Africa, but the pollen flora shows that there were significant environmental changes through the last million years (Muiruri, 2017).

At Magadi this is partly documented by variations in Poaceae to Cyperaceae ratios, which have previously been used to infer changes in moisture (Muller et al., 2008; Githumbi et al., 2021). However, such inferences often require a knowledge of the local basin topography. For example, increases of Cyperaceae in Lake Challa sediments were used to indicate periods of drought as the lake level fell exposing littoral shelves where Cyperaceae could expand. In contrast, Ivory et al. (2018) correlated increased Poaceae with semi-arid periods in the Lake Malawi Basin. In this study, elevated ratios of Poaceae to Cyperaceae are considered to reflect decreased moisture. The basin is dominated by low-gradient north-south-oriented grabens and we see increases in Cyperaceae as reflecting expansion of swamps/wetlands near the palaeolake and lacustrine littoral zones during transgressions. To generate these types of setting would require a wetter period. This inference is also supported by increases in other shallow water taxa such as *Typha* and *Hydrocotyle*. In contrast, declines in Cyperaceae are associated with periods when lake salinity increased in response to drier conditions (mainly in younger sediments), as indicated by MAG14-2A diatom (Muiruri et al., 2021) and mineralogical evidence (Owen et al., 2019) published elsewhere. Conversely, grasses would be likely to be more common during relatively dry periods as the vegetation cover would be more open and grasses more common, as they are today.

There are many sampling gaps and pollen were not extracted from chert. Pollen preservation is poor in sediments that were analysed and dated to ~1041–740 ka (Unit 1; Fig. 6), possibly reflecting oxic bottom conditions in the palaeolake through much of this time. Owen et al. (2019), for example, noted that during this period the basin was occupied by a large, relatively shallow freshwater body. Pollen is preserved from ~1000–910 ka (~190–185 m), where Poaceae and woodland pollen dominate, with *Commiphora*, *Euphorbia* and Ericaceae being less common; together with relatively low percentages of Cyperaceae suggesting a generally drier period than those of Unit 2 times.

Cyperaceae increased relative to Poaceae between about 740 and 528 ka (Unit 2; Fig. 6) and dominated between 605 and 570 ka, when *Typha* were also present, suggesting the existence of shallow fresh water. This combination of *Typha* and Cyperaceae also supports the interpretation of increases in Cyperaceae being reflective of more mesic environmental conditions in the Magadi Basin. Unit 2 was also distinguished by a concurrent expansion of Afromontane forest (*Podocarpus* and *Juniperus*) that implies a shift to cooler and more mesic climatic conditions in the higher elevation hinterlands (Githumbi et al., 2021). This inference is supported by the absence or low abundance of woody bushes such as *Vachellia* and *Phyllanthus*, but with the presence of herbaceous taxa such as Asteraceae, Amaranthaceae and *Valeriana*. The montane forest was characterised by extensive growth of *Podocarpus*. This taxon can form a dominant element in Afromontane forests and has been used to infer cooler conditions and/or long-distance wind or fluvial transport when percentages increase in environmental reconstructions (Bonnefille, 1976a, 1976b, 2010; Elenga et al., 2000). However, Ivory et al. (2012) suggested that it may be less sensitive to average annual temperature, but more sensitive to daily temperature variability and rainfall seasonality. Today, it is also found in the upland drier forests of Kenya (Beentje, 1994). The parallel trends for *Podocarpus*, Cyperaceae and the other aquatic indicators imply a regional climatic control behind these ecosystem changes, rather than a localized tectonic control. Although the data suggest this was generally the wettest interval in the last million years, the climate appears to have been variable with, for example, a drier episode at ~662–625 ka that was marked by increased Amaranthaceae and reductions in *Podocarpus* and Cyperaceae (Fig. 6). In addition, the core interval contains gravels where alluvial fans prograded onto the lake floor with mudcracked mudstones also developing.

Pollen grains are scarce in the sediments deposited between ~528 and 392 ka (Unit 3) with the floras characterised by a major decline in Cyperaceae, implying increased aridity at a time when diatoms indicate either a meromictic lake and/or alternating saline and freshwater lakes (Owen et al., 2018a, 2019). *Podocarpus* also declined in early Unit 3 times, but started to increase after ~440 ka, implying a partial return to milder climatic conditions.

The period 392–200 ka (Unit 4) is associated with a modest increase in Cyperaceae and a reduction in pollen diversity. Pollen grains are common in sediments older than ~380 ka, but scarce subsequently. A few woodland taxa started to increase after about 300 ka, but the low diversity suggests a restricted variety of tree and herb taxa within the pollen catchment. The major contrast between Units 3 and 4 reflects a significant environmental change (Harrison and Sánchez Goñi, 2010) with a reduction of woody habitats and an increase in grass cover, perhaps driven by changes in effective precipitation or possibly enhanced seasonality. Geochemical and mineralogical data from HSPDP-MAG14-2A also indicate a major change close to the Unit 3–4 boundary with decreased Ca/Na ratios, a loss of calcite from the sediments and the appearance of zeolites. Owen et al. (2019) related these observations to a change from a fresh to mildly saline lake to a highly saline water body caused by increased evaporation and/or reduced rainfall. The comparatively dramatic changes in pollen, diatoms, geochemistry and mineralogy at this time also overlap with marine oxygen isotope stage 11 (424–374 ka), which represents the warmest interglacial of the last half million years (Owen et al., 2018a).

During the last 200 kyr (Unit 5), Cyperaceae formed a relatively small component of the flora (Fig. 6), suggesting drier conditions, although the presence of small percentages of *Typha* imply that freshwater swamps existed near the core site. Diatom data (Owen et al., 2018a) indicate a highly saline Palaeolake Magadi that would be unsuitable for riparian *Typha*, implying that freshwater wetlands with through-flowing streams may have occupied some of the north-south grabens. Unit 5 is characterised by an overall decrease in *Podocarpus* while other Afromontane taxa were increasing, as did woodland and herbaceous plants. However, individual taxa increased at different times with variations in both wetter (*Commelina*, *Justicia*, *Rumex* and Urticaceae) and drier taxa (*Vachellia, Aloe*, *Commiphora*, Ericaceae, Phyllanthus and *Valeriana*) suggesting considerable environmental change during this time interval. *Olea*, for example, is derived from wet and dry upland evergreen forests. It is also one of the more fire-resistant Afromontane taxa and charcoal data suggests a parallel increase in fires during Unit 5 times (Fig. 7), which may reflect either increased montane fire in drier uplands or mountains with longer dry seasons and fuel availability. Increases in *Commiphora* and *Vachellia* also indicate dry semideciduous dense bushland (Fig. 6), with drought related Amaranthaceae and *Juniperus* associated with drier upland forests (Beentje, 1994). *Vachellia*, for example, are commonly present only where precipitation is <1000 mm/yr (Gajewski et al., 2002). During the African Humid Period (AHP), at ~15–5 ka, there were major increases in Urticaceae, which occur along forest edges and by the shores of rivers and

Fig. 6

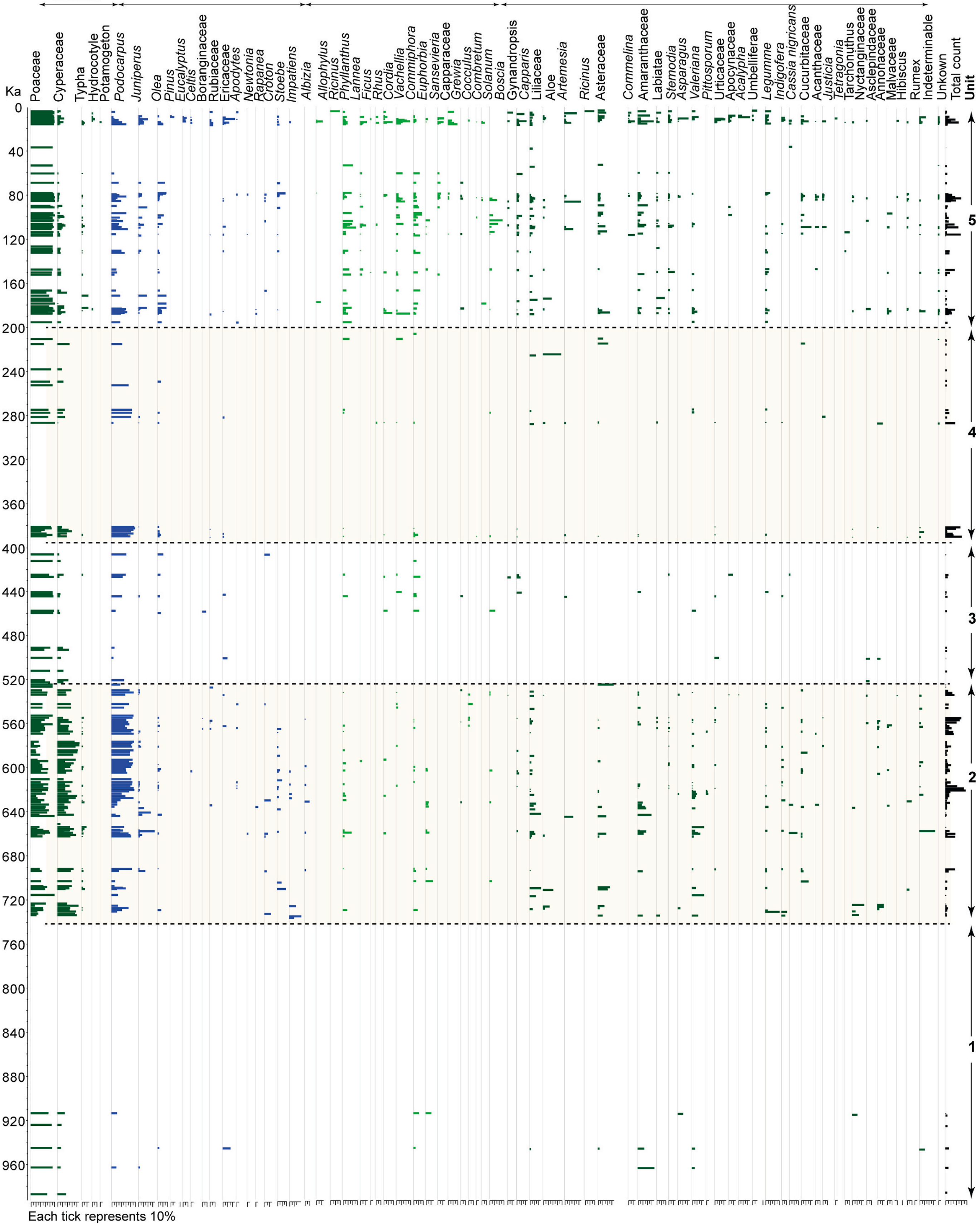
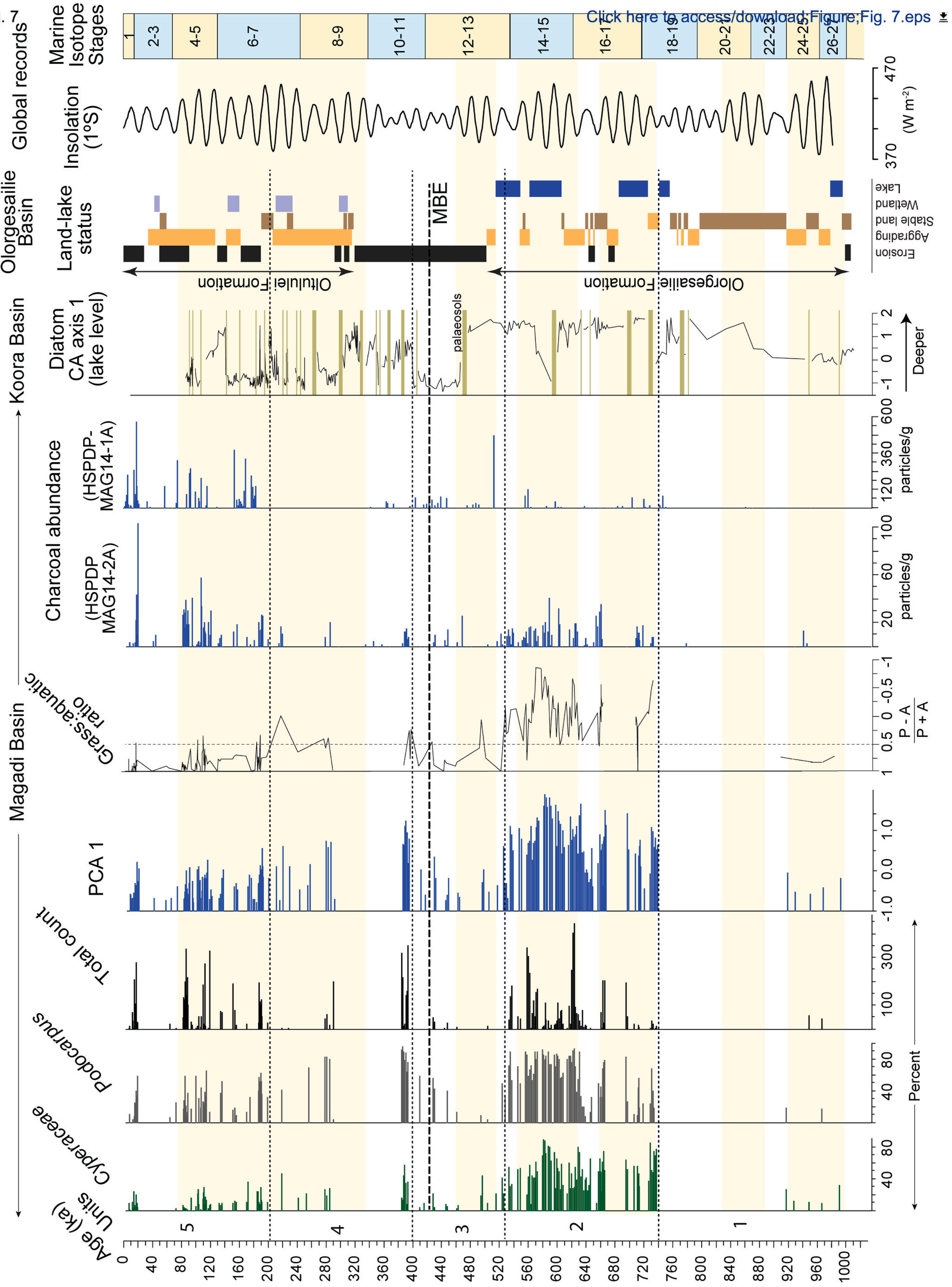


Fig. 6. Plots of pollen against time. Note upward declines in Cyperaceae and *Podocarpus*, increased diversity of herbaceous pollen, and increased abundance of woodland taxa in Units 2 and 5 where pollen are also most abundant. Alternate shading and white emphasise the major units.

Fig. 7



(caption on next page)

Fig. 7. Lake Magadi pollen, charcoal and regional correlations plotted against time. See Fig. 1 for basin locations. PCA1 summarises all pollen data and declines upwards, reflecting a trend towards generally drier conditions that was interrupted by wetter intervals. The wetness indicator shows an overall decrease upward in aquatic plants (P = Poaceae; A = aquatic plants). Charcoal data show two cores with both showing major increases in Unit 5. Note different scales. Diatom Correspondence Analysis (CA) Axis 1 reflects planktonic diatoms and implies deeper lakes to the right (after Potts et al., 2020). Land-lake status shows major environmental changes at Olorgesailie (after Potts et al., 2018). Low-amplitude insolation phases are marked by white bands. Many wet-dry cycles developed during the last million years, but overall drier episodes tend to correlate with low-amplitude insolation. MBE = Mid-Brunhes Event.

lakes, suggesting open forest habitats with more trees dispersed across the landscape.

Increases in Cyperaceae and *Hydrocotyle*, as well as a variety of herbaceous plants, at ~12–8 ka (Figs. 6), suggest wetter conditions and the presence of fresh water in the basin. This period also coincides with evidence from the High Magadi Beds and palaeoshorelines for a lake that stood ~13 m above the modern water surface (Baker, 1986; Owen et al., 2019) and coincides with the AHP, when lakes in East Africa were generally high (Blome et al., 2012; Shanahan et al., 2015). Pollen from a 9-m-long core previously recovered from the northwest arm of Lake Magadi also reflect more humid conditions at this time and imply an open vegetation (Vincens et al., 1991). Pollen records from other Kenya Rift basins support the Magadi evidence for moister conditions during this period (Kendall, 1969; Vincens, 1986; Opiyo et al., 2019; Githumbi et al., 2021).

Shanahan et al. (2015) noted that the termination of the AHP in western Africa was relatively abrupt and time transgressive between ~32°N and 9°N: termination occurred around 5500 yrs. BP in northern locations and between 2500 and 4000 yrs. BP south of 15°N. The Lake Magadi (~1°50′S) vegetation record indicates rapid floral change at the start of the AHP followed by a more gradual termination, following patterns of lake level change at Chew Bahir (4.5°N), Suguta (2°N) and Nakuru (0°20′N) in the East African Rift (Richardson and Dussinger, 1986; Garcin et al., 2009; Foerster et al., 2012; Junginger et al., 2014). Pollen are absent in HSPDP-MAG14-2A above 6.5 m depth (4.2 ka), indicating a shift to increased aridity, as confirmed by the extensive development of trona, which broadly conforms with widespread evidence for increased aridity across sub-Saharan Africa after about 4 ka (Marchant and Hooghiemstra, 2004).

5.2. *Landscape, climate and fire in the south Kenya Rift*

Positive Pollen PCA 1 values reflect greater contributions from aquatic and Afromontane pollen with negative values indicating a trend towards woodlands, herbaceous plants and grasses (Fig. 7). Negative Poaceae/aquatic pollen ratios also indicate wetter conditions. Both parameters suggest relatively wet conditions during Unit 2 times that peaked around 600–580 ka, followed by a trend towards increased aridity that was interrupted by many wetter intervals. Independent datasets for diatoms and authigenic minerals at Magadi also imply drier conditions in the Magadi Basin (Owen et al., 2018a, 2019). Potts et al. (2020) have presented a similarly well-dated multiproxy one-million-year environmental reconstruction for a 139 m long core drilled in the Koora Plain, 10 km east of Magadi (Fig. 1a, b). In contrast with Magadi, the Koora core contained only rare pollen. However, other multiproxy data suggest fluctuating conditions during deposition of the younger sediments with the Koora diatom record indicating a change from deep fresh lakes to fluctuating deep freshwater and shallow saline water bodies after about 470 ka (Fig. 7).

Palaeosols in the Koora core (Potts et al., 2020) also indicate that the former lakes in that basin periodically dried out at the drill site, especially after 470 ka. At the HSPDP-MAG14-2A site, well-developed palaeosols are absent although mudcracks are present, suggesting that desiccation events were comparatively minor, which would have facilitated pollen preservation. In contrast, the neighbouring HSPDP-MAG14-1A site (Fig. 1) contains more common alluvial fan gravels and mudcracks and generally lacks pollen, implying greater exposure there. The evidence for a more continuous lake at HSPDP-MAG14-2A may reflect both its position at a lower palaeoelevation and perhaps spring inflow in what is the hydrological sump for groundwaters in the south Kenya Rift (Allen et al., 1989; Becht et al., 2006).

At Olorgesailie, ~20 km north of the Koora Plain, a third major sedimentary basin contains well-exposed lacustrine and fluvial deposits that have been described in detailed outcrop studies (Behrensmeyer et al., 2002; Owen et al., 2008; Lee et al., 2013; Owen et al., 2014; Behrensmeyer et al., 2018; Potts et al., 2018). Sediments at Olorgesailie that correlate with Unit 1 of the Magadi core formed on stable and aggrading land surfaces with a freshwater lake developing at ~990 ka (Fig. 7). Pollen in Unit 2 at Magadi suggest wetter conditions when large lakes and stable land surfaces developed at Olorgesailie. Units 3 to 5 represent generally drier conditions interrupted by several wetter intervals. At Olorgesailie, there was a significant environmental shift with loss of large lakes at about 500 ka and the development of a major erosional hiatus that removed the sediment record for the period ~500–320 ka. This erosional episode overlaps with a period of poor pollen preservation and inferred drier conditions at Magadi. The Magadi pollen record resumes at about 290 ka in Unit 4 and continues into Unit 5, indicating alternating drier and wetter intervals. At Olorgesailie, these variable conditions coincide with fluvial, wetland and spring deposition at 320–190, 190–50 and 50–36 ka, with these intervals separated by periods of fluvial incision (Behrensmeyer et al., 2018).

All three basins therefore indicate regionally similar patterns, suggesting a dominant climate control on the palaeolakes and their associated catchment vegetation. Transitions from woodland to grassland-dominated savannah are commonly attributed to more xeric environmental conditions, disturbance by humans and/or large herbivores, and also the impact of fire (Higgins et al., 2000; Gillson, 2004; Meyer et al., 2007; Archibald et al., 2009). Colombaroli et al. (2014, 2016), for example, noted that fire can maintain grass-dominated ecosystems even when precipitation favours forests, and that the role of fire depends on its location within geographical gradients. For example, they reported that in sub-humid western Uganda the accumulation of charcoal during the late Holocene was favoured by decade-scale aridity events, which contrasted with the drier central Kenya Rift where biomass burning increased when intermediate moisture levels developed and plant biomass increased.

The climate at Magadi has been semi-arid through much of the last half million years, albeit with episodic increases in moisture (Owen et al., 2018a). Fire is reflected in charcoal accumulation rates in the core sediments, which vary considerably (0–570 particles g^{-1}; Fig. 7). Peaks in HSPDP-MAG14-2A correlate with increased pollen abundance, increased Cyperaceae percentages and higher grass/aquatic pollen ratios, which suggest wetter intervals may have boosted biomass fuel supplies. Charcoal is common in Unit 2 of HSPDP-MAG14-2A, a time when large lakes were present at Magadi, Koora and Olorgesailie. However, a second core (HSPDP-MAG14-1A; Fig. 1b) taken ~4 km away from HSPDP-MAG14-2A shows only a partial increase in charcoal at these times, perhaps because burning was highly localized at both sites, which is not uncommon in a fuel limited ecosystem. In contrast, Unit 5 is characterised by large increases in charcoal at both sites with considerable variability between different horizons. This also represents a time when woodland and herbaceous pollen increased in diversity and when diatom data at Koora suggest drier conditions that were interrupted by many wetter intervals (Muiruri, 2017; Potts et al., 2020). The AHP was the last of these wet intervals and is associated with a major increase in charcoal in both cores, suggesting that the vegetation was probably

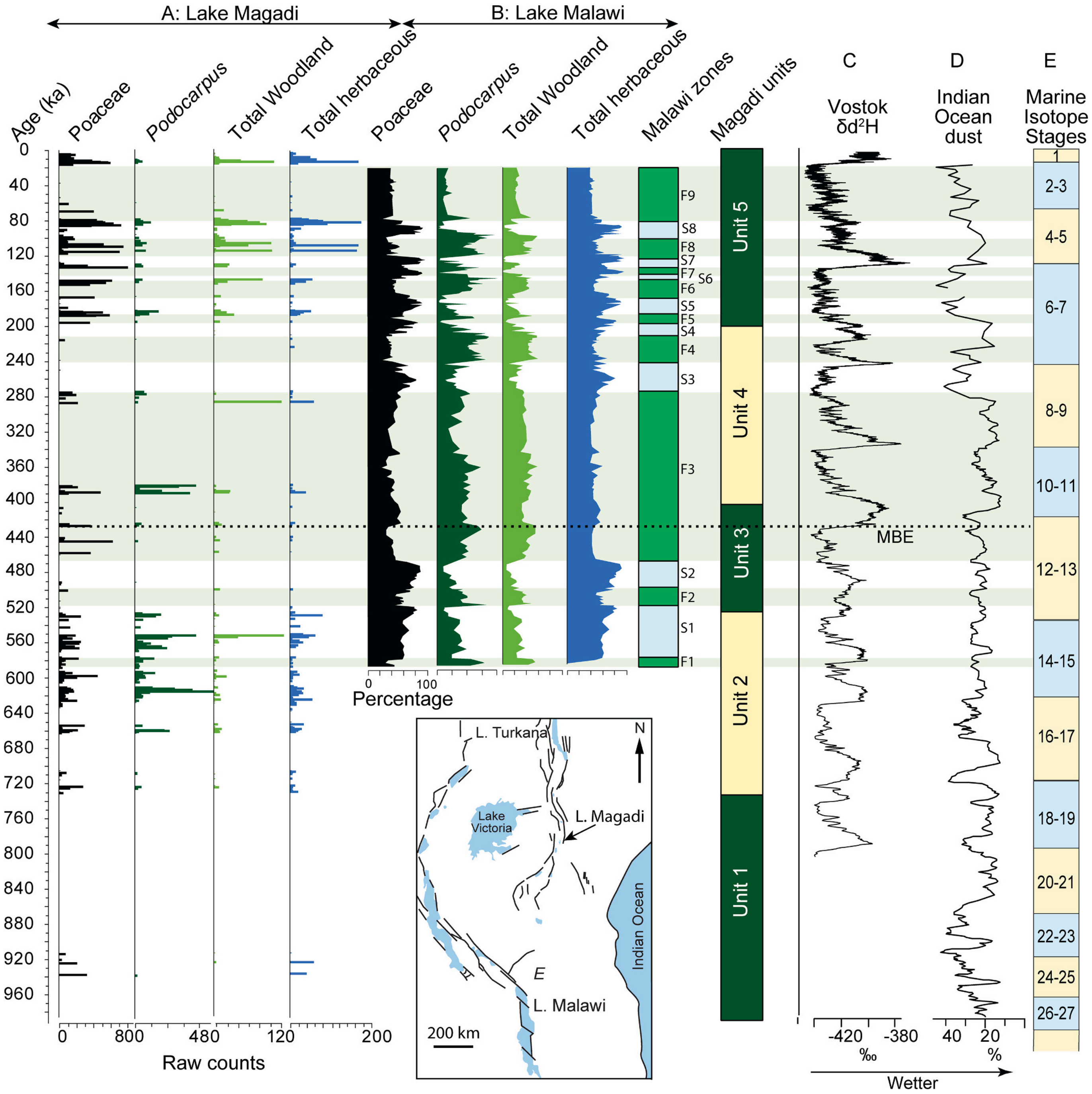


Fig. 8. Lake Magadi and Lake Malawi pollen correlations and comparisons to regional and global climate indicators. A: Lake Magadi pollen record for major plant groups. Magadi units shown to the right after Malawi data. B: Malawi pollen data for the same major pollen groups with forest (F1–F9) and semi-arid (S1–S8) phases marked to the right. Shading extends the Malawi phases across the diagram for comparison (after Ivory et al., 2018). C: Interglacial-glacial cycles shown by δD record, Vostok, Antarctica (after Jouzel et al., 2007). D: Northwest Indian Ocean dust-record showing increased aridity through the last 400 ka (after deMenocal, 2004). MBE = Mid-Brunhes Event. E: Marine Isotope Stages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

denser and more continuous, leading to larger and more widespread fires.

5.3. Global and regional correlations

Fig. 8A–B compares the Pleistocene vegetation histories of Lake Magadi and northern Lake Malawi, ~950 km to the southwest (Ivory et al., 2018). Today, these lakes lie, respectively, in the contrasting Somali-Masai and Zambezian miombo woodland phytogeographic regions, with *Podocarpus*-dominated Afromontane forests at high altitude (Beuning et al., 2011; Kindt et al., 2011; Migliore et al., 2020). The Malawi pollen record was divided by Ivory et al. (2018) into nine forest phases with abundant lowland forest, woodland and Afromontane taxa (mainly *Podocarpus*) and eight semi-arid phases dominated by grasses and non-arboreal taxa (Fig. 8B). Despite the uncertainties between different age models, the Poaceae in the Magadi record (Fig. 8A) appear to increase when Malawi Poaceae decrease, especially during the last 200 ka (Unit 5). Unit 5 herbaceous pollen at Lake Magadi also tend to show broadly opposing trends to those at Lake Malawi, but woodland taxa display a more positive relationship with most increases at Magadi coinciding with peaks in the Malawi sediments. *Podocarpus* is an important element of the Afromontane floras throughout the 600-ka Malawi core, alternating between phases of expansion and contraction, especially after 240 ka, which contrasts with the Magadi record where *Podocarpus* generally declines upwards in the cores.

Both pollen records indicate alternating cycles with drier and wetter conditions, but these are commonly anti-phased, as recorded for other regional climate signals (Blome et al., 2012). Kutzbach et al. (2020), for example, noted anti-phased wetter and drier periods and vegetation changes between the northern and southern tropics, which they attributed to contrasts in orbital forcing. Ivory et al. (2016, 2018) related changes in Lake Malawi vegetation to hydroclimatic fluctuations, noting that forest expansion occurred during periods when lake levels were high, which Lyons et al. (2015) reported were not in phase with high-latitude signals. In contrast, the Magadi record after about 575 ka shows a trend towards fluctuating conditions with many wetter-drier cycles. Conditions were particularly dry at ~528–392 ka during part of the relatively warm interglacial period of marine oxygen isotope stage 11 (424 to 374 ka) (Owen et al., 2018a). Similar variability appears to be evident in the Koora diatom record after the Mid-Brunhes Event (~430 ka; Fig. 8), when there was an intensification of global glacial and interglacial cycles (Fig. 8C).

Cohen et al. (2007) reported a series of megadroughts between 135 and 75 ka from Lake Malawi and noted that the most arid phase was associated with extremely low pollen and charcoal production (low fuel load) and cool, semidesert conditions. Although possibly reflecting insufficient time resolution, Scholz et al. (2007) and Blome et al. (2012) reported that East African records lacked this megadrought signal, which was widespread in tropical areas to the south, including Lakes Malawi, Tanganyika and Challa, and across to Lake Bosumtwi in West Africa. At Magadi, trona precipitated at times during this period (105–90 ka) with Poaceae episodically increasing to high concentrations that coincide with severe reductions in aquatic pollen between about 110 and 80 ka, suggesting very dry conditions that alternated with wetter intervals.

Despite Lake Magadi appearing to show a degree of synchronisation with the southern tropics during the megadrought period, the contrasting longer-term trends imply that the Magadi and Malawi palaeolakes responded mostly to conditions in two different climatic regions. For example, the increased aridity and variability in wet-dry cycles at Magadi resemble aeolian dust records from the northwest Indian Ocean (deMenocal, 1995, 2004) (Fig. 8D), suggesting a possible link to the East African climate region. In contrast, Ivory et al. (2018) noted that expansions in *Podocarpus* at Malawi coincided with increases in this taxon in 300-ka marine cores from offshore southwest and southeast Africa, implying a different south tropical linkage where forest growth tended to be greater during glacial periods.

The Magadi pollen record and its climatic inferences appear to show links with insolation variability, especially between ~650 and 350 ka, with relatively dry conditions developing during phases of low-amplitude insolation at about 655–635, 550–505, 460–405 and after 70 ka (Fig. 7; Owen et al., 2018a). Pollen data for a 380–360 ka phase of low insolation variability are lacking, perhaps reflecting arid conditions at that time. Kutzbach et al. (2020) note that insolation variability in the northern hemisphere summer and winter is mainly related to 21,000-yr. precession cycles that are modified by orbital eccentricity, resulting in alternating periods of high and low insolation seasonality (Fig. 7). High insolation seasonality appears to correlate with warmer summers and colder winters with low insolation seasonality generating colder summers and warmer winters. In addition, they noted that variability in insolation is at its greatest when eccentricity is large and least when eccentricity is small. Kutzbach et al. (2020) also observed that the southern hemisphere rainfall maxima are exactly out of phase with the northern hemisphere maxima, due to orbital forcing. Magadi lies close to the boundary with the south tropical climate region where Lake Malawi is positioned, but the contrasting pollen records suggest that Lake Magadi has been more influenced by the northerly East African climate regime.

5.4. Environmental implications for hominins

Habitats in the south Kenya Rift have changed dramatically through the last million years due to orbitally-controlled variations in climate (rainfall, seasonality, temperature, evapotranspiration rates) (Maslin and Christensen, 2007; Campisano, 2015; Campisano et al., 2017; Owen et al., 2018a). Environmental change has also been driven at the local scale by faulting, which fragmented the landscape, increased topographic variability, led to rainshadow effects, modified drainage, and enabled shallow meteoric and deeper hydrothermal springs to form (Owen et al., 2018b, 2019). The latter were especially important at Magadi, which lies in a tectonic sump, and springs there could potentially have provided potable water to hominin and wildlife populations during droughts (Magill et al., 2013; Cuthbert et al., 2017; Barboni et al., 2019; Sistiaga et al., 2020). The Magadi data show that these varying environments trended towards drier conditions and variability, which would have changed the resource-base (water, plant and animal foods) available to hominins and, in turn, selective pressures in the area (Kübler et al., 2015). Access to different parts of former hominin ranges would also have been influenced by the formation of physical barriers to movement including former lakes, wetlands, arid zones and steep rift escarpments (Trauth et al., 2010; Reynolds et al., 2011; Owen et al., 2018b, 2019; Potts et al., 2020).

Recent work at Olorgesailie and the Koora Graben have also illustrated the importance of changing environments in the region and their impacts on wildlife and hominins (Potts et al., 2018; Deino et al., 2019; Potts et al., 2020). The oldest deposits at Olorgesailie constitute the Olorgesailie Formation (~1200–500 Ka), which spans the time when Acheulean stone tools were being produced locally. In contrast, younger sediments in the region include the Oltululei Formation (~320–50 Ka) which contains Middle Stone Age (MSA) and Late Stone Age (LSA) artefacts (Behrensmeyer et al., 2018; Brooks et al., 2018). However, an erosional gap (~500–320 ka) between these two units means that the palaeoenvironmental record for this important transition is missing at Olorgesailie, but it is preserved in cores from Magadi and the Koora Plain (Muiruri, 2017; Owen et al., 2018a, 2018b, 2019; Deino et al., 2019; Potts et al., 2020).

The new Magadi data suggest that between ~528 and 392 ka the climate became generally drier but with wetter conditions from 440 to 380 ka, followed by a return to drier conditions. A few woodland taxa began to increase after about 300 ka but with a low floral diversity, suggesting relatively open ecosystems. The first MSA tools appear at Olorgesailie by 320 ka (Behrensmeyer et al., 2018; Deino et al., 2018; Potts et al., 2018, 2020), implying that these major changes developed during a generally dry period, albeit interrupted by wetter intervals. The major increase in aridity at 528–392 ka had a dramatic impact on the regional and local flora that also likely influenced the fauna upon which hominins may have partly depended. Climatic pressures, for example, might help to explain a major mammalian turnover (~500–400 ka) previously documented at Olorgesailie and at Lainyamok (~15 km west of Magadi) (Potts and Deino, 1995; Faith et al., 2012; 2014; Potts et al., 2018) with subsequent impacts on hominins. However, Potts et al. (2020) recently hypothesised that more complex links between the regional resource base and its response to both climate and tectonism may be needed to fully understand selective pressure on ancestral humans.

Our pollen evidence from the south Kenya Rift shows that there were large climate shifts, including a period of very dry conditions, during the development of a major erosional hiatus (~500–320 ka) at Olorgesailie. This was a time when there was a major faunal turnover and revolutionary changes in stone tools in the region. This period includes the first known appearance of *H. sapiens* on the continent of Africa at ~315 ka (Hublin et al., 2017; Richter et al., 2017). While these major changes could be coincidental, a link between environment (climate and/or tectonically controlled) and hominin cultural-physical evolution within the south Kenya Rift seems likely.

6. Conclusions

Although pollen grains are often degraded in rift valley sediments they are common and well preserved in the Lake Magadi sediments, because the bottom water of the palaeolake was often anoxic. The flora records a one-million-year history of environmental change with an overall increase in *Podocarpus* and Cyperaceae from ~1 Ma to 575 ka followed by a decrease in these taxa, reflecting an initial increase in moisture followed by greater regional aridity. Relatively drier conditions through the last half million years have been punctuated by wetter intervals, including the African humid period (AHP). Grasses, woodlands and herbaceous plants were important between about 660 and 520 ka and after 200 ka, when pollen diversity increased substantially. Charcoal accumulation increased during periods when pollen increased in abundance and comprised taxa that suggest wetter conditions, implying that increased fuel loads fed fire events during moister phases. Comparison of *Podocarpus* at Lake Magadi with similar data from Lake Malawi shows that Afromontane forest expansions in the two areas were out of phase.

Comparison of records from the Magadi, Koora and Olorgesailie basins suggests considerable palaeoenvironmental complexity and variability across the south Kenya Rift. However, the basins displayed similar trends that suggest a dominant climate control on vegetation and landscapes. All three basins experienced wetter conditions and contained large freshwater lakes between 740 and 528 ka. Subsequently, climate became drier, but with considerable variability, resulting in lakes that became more saline and which occasionally dried out. Wetter intervals led to temporary lake expansions, overflow and episodically fresh waters. Tectonism also played a role in landscape evolution as faulting fragmented the landscape into a complex mosaic of habitats. The paleoenvironmental record indicates a particularly intense arid period between ~528 and 392 ka that overlaps with a major turnover in the mammalian fauna of the south Kenya Rift. Acheulean handaxes dominated the archaeological record at Olorgesailie after 1.2 Ma, but disappeared sometime after 500 ka and were replaced by Middle Stone Age tools by 320 ka or earlier. Although the transition interval is not physically preserved in the Olorgesailie sedimentological record, the evidence suggests a possible correlation with a major desiccation episode documented at Magadi, implying that this climate transition might have contributed to changing ecological resources that, in turn, impacted hominin cultural evolution.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110247.

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.

Acknowledgements

The Hominin Sites and Paleolakes Drilling Project was funded by grants from the ICDP and US-NSF (EAR-1123942, BCS-1241859, BCS-1241790, EAR-1322017 and EAR-1338553). Pollen research was supported by the Hong Kong Research Grants Council. Permits and research support were provided by the National Museums of Kenya, the Kenyan National Council for Science and Technology, the Kenyan Ministry of Mines and the National Environmental Management Authority of Kenya. We also thank DOSECC Exploration Services for drilling support and the US National Lacustrine Core Facility (LacCore) for assistance with core curation and logging. Tata Chemicals and the Magadi County Council provided local assistance. This is publication #32 of the Hominin Sites and Paleolakes Drilling Project.

References

Allen, D.J., Darling, W.G., Burgess, W.G., 1989. Geothermics and hydrogeology of the southern part of the Kenya Rift Valley with emphasis on the Magadi-Nakuru area. Brit. Geol. Surv. Res. Rep. 1–68 (SD/89/1).

Archibald, S., Roy, D.P., van Wilgen, B.W., Scholes, R.J., 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. Glob. Chang. Biol. 15, 613–630.

Baker, B.H., 1986. Tectonics and volcanism of the southern Kenya Rift and its influence on rift sedimentation. In: Frostick, L.E., Renaut, R.W., Reid, I., Tiercelin, J.-J. (Eds.), Sedimentation in the African Rifts, Geol. Soc. Lond. Spec. Publ. 25, pp. 45–58.

Baker, B.H., Mitchell, J.G., 1976. Volcanic stratigraphy and geochronology of the Kedong-Olorgesailie area and the evolution of the south Kenya Rift Valley. J. Geol. Soc. Lond. 132, 467–484.

Barboni, D., Ashley, G.M., Bourel, B., Arráiz, H., Mazur, J.-C., 2019. Springs, palm groves, and the record of early hominins in Africa. Rev. Palaeobot. Palynol. 266, 23–41.

Becht, R., Mwango, F., Muno, F.A., 2006. Groundwater links between Kenyan Rift Valley lakes. In: Odada, E., Olago, D., Ochola, W., Ntiba, M., Wandiga, S., Gichuki, N., Oyieke, H. (Eds.), Proc. 11th World Lake Congr., Nairobi, 31 October–4th November 2005, vol. 2. Ministry of Water and Irrigation - International Lake Environment Committee (ILEC), Nairobi, pp. 7–14.

Beentje, H.J., 1994. Kenya Trees, Shrubs and Lianas. National Museums of Kenya, Nairobi.

Behrensmeyer, A.K., Potts, R., Deino, A., Ditchfield, P., 2002. Olorgesailie, Kenya: a million years in the life of a rift basin. In: Renaut, R.W., Ashley, G.M. (Eds.), Sedimentation in Continental Rifts, SEPM Spec. Publ, vol. 73, pp. 97–106.

Behrensmeyer, A.K., Potts, R., Deino, A., 2018. The Oltulelei Formation of the southern Kenyan Rift Valley: a chronicle of rapid landscape transformation over the last 500 k. y. Geol. Soc. Am. Bull. 130, 1474–1492.

Benninghoff, W.S., Kapp, R.O., 1962. Suggested notation to indicate identification status of fossil pollen. Pollen Spores 4, 332.

Beuning, K.R.M., Zimmerman, K.A., Ivory, S.J., Cohen, A.S., 2011. Vegetation response to glacial–interglacial climate variability near Lake Malawi in the southern African tropics. Palaeogeogr. Palaeoclimatol. Palaeoecol. 303, 81–92.

Birks, H.J.B., 1986. Numerical zonation, comparison and correlation of Quaternary pollen-stratigraphical data. In: Berglund, B.E., Ralska-Jasiewiczowa, M. (Eds.), Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley, Chichester, pp. 743–774 (reprinted by The Blackburn Press, 2003).

Birks, H.J.B., Gordon, A.D., 1985. Numerical Methods in Quaternary Pollen Analysis. Academic Press, London.

Blome, M.W., Cohen, A.S., Tryon, C.A., Brooks, A.S., Russell, J., 2012. The environmental context for the origins of modern human diversity: a synthesis of regional variability in African climate 150,000-30,000 years ago. J. Hum. Evol. 62, 563–592.

Bonnefille, R., 1976a. Palynological evidence for an important change in the vegetation of the Omo basin between 2.5 and 2 million years ago. In: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E.F. (Eds.), Earliest Man and Environment in the Lake Rudolf Basin. University of Chicago Press, Chicago, pp. 421–431.

Bonnefille, R., 1976b. Implications of pollen assemblage from the Koobi Fora Formation, East Rudolf, Kenya. Nature 264, 403–407.

Bonnefille, R., 2010. Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. Glob. Planet. Chang. 72, 390–411.

Brooks, A.S., Yellen, J.E., Potts, R., Behrensmeyer, A.K., Deino, A.L., Leslie, D.E., Ambrose, S.H., Ferguson, J.R., d'Errico, F., Zipkin, A.M., Whittaker, S., Post, J., Veatch, E.G., Foecke, K., Clark, J.B., 2018. Long-distance stone transport and pigment use in the earliest Middle Stone Age. Science 360, 90–94.

Campisano, C.J., 2015. Milankovitch cycles, paleoclimatic change, and hominin evolution. Nature Educ. Knowl. 4, 5.

Campisano, C.J., Cohen, A.S., Arrowsmith, J.R., Asrat, A., Behrensmeyer, A.K., Brown, E. T., Deino, A.L., Deocampo, D.M., Feibel, C.S., Kingston, J.D., Lamb, H.F., Lowenstein, T.K., Noren, A., Olago, D.O., Owen, R.B., Pelletier, J.D., Potts, R., Reed, K.E., Renaut, R.W., Russell, J.M., Russell, J.L., Schäbitz, F., Stone, J.R., Trauth, M.H., Wynn, J.G., 2017. The hominin sites and Paleolakes Drilling Project: acquiring high-resolution paleoclimate records from the east african rift system and their implications for understanding the environmental context of hominin evolution. PaleoAnthropology 2017, 1–43.

Cohen, A., Stone, J., Beuning, K., Park, L., Reinthal, P., Dettman, D., Scholz, C., Johnson, T., King, J., Talbot, M., 2007. Ecological consequences of early Late Pleistocene megadroughts in tropical Africa. Proc. Natl. Acad. Sci. U. S. A. 104, 16422–16427.

Cohen, A.S., Campisano, C., Arrowsmith, R., Behrensmeyer, A.K., Deino, A., Feibel, C., Hill, A., Johnson, R., Kingson, J., Lamb, H., Lowenstein, T., Noren, A., Olago, D., Owen, R.B., Potts, R., Reed, K., Renaut, R., Schabitz, F., Tiercelin, J.-J., Trauth, M.H., Wynn, J., Ivory, S., Brady, K., O'Grady, R., Rodysill, J., Githiri, J., Russell, J., Foerster, V., Dommain, R., Rucina, S., Deocampo, D., Russell, J., Billingsley, A., Beck, C., Dorenbeck, G., Dullo, L., Feary, D., Garello, D., Gromig, R., Johnson, T., Junginger, A., Karanja, M., Kimburi, E., Mbuthia, A., McCartney, T., McNulty, E., Muiruri, V., Nambiro, E., Negash, E.W., Njagi, D., Wilson, J.N., Rabideaux, N., Rabu, T., Sier, M.J., Smith, P., Urban, J., Warren, M., Yadeta, M., Yost, C., Zinaye, B., 2016. The Hominin Sites and Paleolakes Drilling Project: inferring the environmental context of human evolution from eastern African rift lake deposits. Sci. Drill. 21, 1–16.

Colombaroli, D., Ssemmanda, I., Gelorini, V., Verschuren, D., 2014. Contrasting long-term records of biomass burning in wet and dry savannas of equatorial East Africa. Glob. Chang. Biol. 20, 2903–2914.

Colombaroli, D., van der Plas, G., Rucina, S., Verschuren, D., 2016. Determinants of savanna-fire dynamics in the eastern Lake Victoria catchment (western Kenya) during the last 1200 years. Quat. Int. 488, 67–80.

Cuthbert, M.O., Gleeson, T., Bennett, M.R., Newton, A.C., McCormack, C.J., Ashley, G. M., Reynolds, S.C., 2017. Modelling the role of groundwater hydro-refugia in East African hominin evolution and dispersal. Nature Comm. 8, 1–11.

Deino, A.L., Behrensmeyer, A.K., Brooks, A.S., Yellen, J.E., Sharp, W.D., Potts, R., 2018. Chronology of the Acheulean to Middle Stone Age transition in eastern Africa. Science 360, 95–98.

Deino, A.L., Dommain, R., Keller, C.B., Potts, R., Behrensmeyer, A.K., Beverly, E.J., King, J., Heil, C.W., Stockhecke, M., Brown, E.T., Moerman, J., DeMenocal, P., the Olorgesailie Drilling Project Team, 2019. Chronostratigraphic model of a high-resolution drill core record of the past million years from the Koora Basin, south Kenya Rift: Overcoming the difficulties of variable sedimentation rate and hiatuses. Quat. Sci. Rev. 215, 213–231.

deMenocal, P., 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. Earth Planet. Sci. Lett. 220, 3–24.

deMenocal, P.B., 1995. Plio-Pleistocene African climate. Science 270, 53–59.

deMenocal, P.B., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L., Yarusinsky, M., 2000. Abrupt onset and rapid termination of the African Humid Period: rapid climate responses to gradual insolation forcing. Quat. Sci. Rev. 19, 347–361.

Elenga, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V., Bottema, S., Buchet, G., de Beualieu, J.-L., Hamilton, A.C., Maley, J., Marchant, R., Perez-Obiol, R., Reille, M., Riollet, G., Scott, L., Straka, H., Taylor, D., Van Campo, E., Vincens, A., Laarif, F., Jonson, H., 2000. Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr BP. J. Biogeogr. 27, 621–634.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis, 4th edn. Wiley, Chichester.

Faith, J.T., 2014. Late Pleistocene and Holocene mammal extinctions on continental Africa. Earth-Sci. Rev. 128, 105–121.

Faith, J.T., Potts, R., Plummer, T.W., Bishop, L.C., Marean, C.W., Tryon, C.A., 2012. New perspectives on middle Pleistocene change in the large mammal faunas of East Africa: *Damaliscus hypsodon* sp. nov. (Mammalia, Artiodactyla) from Lainyamok, Kenya. Palaeogeogr. Palaeoclimatol. Palaeoecol. 361–362, 84–93.

Foerster, V., Junginger, A., Langkam, O., Gebru, T., Asrat, A., Umer, M., Lamb, H.F., Wennrich, V., Rethemeyer, J., Nowaczyk, N., Trauth, M.H., Schaebitz, F., 2012. Climatic change recorded in the sediments of the Chew Bahir basin, southern Ethiopia, during the last 45,000 years. Quat. Int. 274, 25–37.

Gajewski, K., Lezine, A.M., Vincens, A., Delestan, A., Sawada, M., the African Pollen Database, 2002. Modern climate-vegetation-pollen relations in Africa and adjacent areas. Quat. Sci. Rev. 21, 1611–1631.

Garcin, Y., Junginger, A., Melnick, D., Olago, D.O., Strecker, M.R., Trauth, M.H., 2009. Late Pleistocene–Holocene rise and collapse of Lake Suguta, northern Kenya Rift. Quat. Sci. Rev. 28, 911–925.

Gichuki, N.N., Oyieke, H.A., Ndiritu, G.G., 2002. Assessment and Monitoring of Wetlands for Conservation and Development in Dry Lands: A Case Study of Kajiado District. Centre for Biodiversity, National Museums of Kenya, Nairobi, pp. 97–110.

Gillson, L., 2004. Evidence of hierarchical patch dynamics in an east African savanna? J. Landsc. Ecol. 19, 883–894.

Githumbi, E.N., Mustaphi, C.J.C., Marchant, R., 2021. Late Pleistocene and Holocene Afromontane vegetation and headwater wetland dynamics within the Eastern Mau Forest, Kenya. J. Quat. Sci. 6, 1–17.

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Elsevier 13, 13–35.

Hamilton, A.C., 1975. A quantitative analysis of altitudinal zonation in Ugandan forests. Vegetation 30, 99–106.

Hamilton, A.C., 1982. Environmental History of East Africa: a Study of the Quaternary. Academic Press, London (328 pp.).

Harrison, S.P., Sánchez Goñi, M.F., 2010. Global patterns of vegetation response to millennial-scale variability and rapid climate change during the last glacial period. Quat. Sci. Rev. 29, 2957–2980.

Higgins, S.I., Bond, W.J., Trollope, W.S., 2000. Fire resprouting and variability: a recipe for grass-tree coexistence in savannas. J. Ecol. 88, 213–229.

Hublin, J.-J., Ben-Ncer, A., Bailey, S.E., Freidline, S.E., Neubauer, S., Skinner, M.M., Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., Gunz, P., 2017. New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. Nature 546, 289–292.

Ivory, S.J., Lézine, A.-M., Vincens, A., Cohen, A.S., 2012. Effect of aridity and rainfall seasonality on vegetation in the southern tropics of East Africa during the Pleistocene/Holocene transition. Quat. Res. 77, 77–86.

Ivory, S.J., Early, R., Sax, D.F., Russell, J., 2016. Niche expansion and temperature sensitivity of tropical African montane forests. Glob. Ecol. Biogeogr. 25, 693–703.

Ivory, S.J., Mcglue, M.M., Ellis, G.S., Boehlke, A., Lézine, A.-M., Vincens, A., Cohen, A.S., 2017. East African weathering dynamics controlled by vegetation-climate feedbacks. Geology 45, 823–826.

Ivory, S.J., Lézine, A.-M., Vincens, A., Cohen, A.S., 2018. Waxing and waning of forests: late Quaternary biogeography of southeast Africa. Glob. Chang. Biol. 24, 2939–2951.

Jouzel, J., Masson-Delmotte, V., Cattani, O., Dreyfus, G., Falourd, S., Hoffmann, G., Minster, B., Nouet, J., Barnola, J.M., Chappellaz, J., Fischer, H., Gallet, J.C., Johnsen, S., Leuenberger, M., Loulergue, L., Luethi, D., Oerter, H., Parrenin, F., Raisbeck, G., Raynaud, D., Schilt, A., Schwander, J., Selmo, E., Souchez, R., Spahni, R., Stauffer, B., Steffensen, J.P., Stenni, B., Stocker, T.F., Tison, J.L., Werner, M., Wolff, E.W., 2007. Orbital and millennial Antarctic climate variability over the past 800,000 years. Science 317, 793–796.

Junginger, A., Roller, S., Olaka, L.A., Trauth, M.H., 2014. The effects of solar irradiation changes on the migration of the Congo Air Boundary and water levels of paleo-Lake Suguta, Northern Kenya Rift, during the African Humid Period (15–5 ka BP). Palaeogeogr. Palaeoecol. Palaeoclimatol. 396, 1–16.

Kendall, R., 1969. An ecological history of the Lake Victoria basin. Ecol. Monogr. 39, 121–176.

Kindt, R., van Breugel, P., Lillesø, J.-P., Bingham, M., Demissew, S., Dudley, C., Friis, I., Gachathi, F., Kalema, J., Mbago, F., Minani, V., Moshi, H.N., Mulumba, J., Namaganda, M., Ndangalasi, H.J., Ruffo, C.K., Jamnadass, R., Graudal, L.O., 2011. Potential Natural Vegetation of Eastern Africa (Ethiopia, Kenya, Malawi, Rwanda, Tanzania, Uganda and Zambia): Volume 2: Description and Tree Species Composition for Forest Potential Natural Vegetation Types. Forest & Landscape, University of Copenhagen. Forest & Landscape Working Papers, No. 62/2011.

Kübler, S., Owenga, P., Reynolds, S.C., Rucina, S.M., King, G.C.P., 2015. Animal movements in the Kenya Rift and evidence for the earliest ambush hunting by hominins. Sci. Rep. 5, 14011. https://doi.org/10.1038/srep14011.

Kutzbach, J.E., Guan, J., He, F., Cohen, A.S., Orland, I.J., Chen, G., 2020. African climate response to orbital and glacial forcing in 140,000-y simulation with implications for early modern human environments. Proc. Natl. Acad. Sci. U. S. A. 117, 2255–2264.

Lee, R.K.L., Owen, R.B., Renaut, R.W., Behrensmeyer, A.K., Potts, R., Sharp, W.D., 2013. Facies, geochemistry and diatoms of late Pleistocene Olorgesailie tufas, southern Kenya Rift. Palaeogeogr. Palaeoclimatol. Palaeoecol. 374, 197–217.

Lyons, R.P., Scholz, C.A., Cohen, A.S., King, J.W., Brown, E.T., Ivory, S.J., Johnson, T.C., Deino, A.L., Reinthal, P.N., Mcglue, M.M., Blome, M.W., 2015. Continuous 1.3-million-year record of East African hydroclimate, and implications for patterns of evolution and biodiversity. Proc. Natl. Acad. Sci. U. S. A. 112, 15568–15573.

Magill, C.R., Ashley, G.M., Freeman, K.H., 2013. Ecosystem variability and early human habitats in eastern Africa. Proc. Natl. Acad. Sci. U. S. A. 110, 1167–1174.

Marchant, R.A., Hooghiemstra, H., 2004. Rapid environmental change in tropical Africa and Latin America about 4000 years before present: a review. Earth Sci. Rev. 66, 217–260.

Marchant, R.A., Taylor, D.M., Hamilton, A.C., 1997. Late Pleistocene and Holocene history of Mubwindi Swamp, south-west Uganda. Quat. Res. 47, 316–328.

Maslin, M.A., Christensen, B., 2007. Tectonics, orbital forcing, global climate change, and human evolution in Africa: introduction to the African paleoclimate Special Volume. J. Hum. Evol. 53, 443–464.

Maslin, M.A., Shultz, S., Trauth, M.H., 2015. A synthesis of the theories and concepts of early human evolution. Phil. Trans. R. Soc. B: Biol. Sci. 370, 20140064. https://doi.org/10.1098/rstb.2014.0064.

McGlue, M.M., Lezzar, K.E., Cohen, A.S., Russell, J.M., Tiercelin, J.-J., Felton, A.A., Mbede, E., Nkotagu, H.H., 2008. Seismic records of late Pleistocene aridity in Lake Tanganyika, tropical East Africa. J. Paleolimnol. 40, 635–653.

Meyer, K.M., Wiegand, K., Ward, D., Moustakas, A., 2007. The rhythm of savanna patch dynamics. J. Ecol. 95, 1306–1315.

Migliore, J., Lézine, A.-M., Hardy, O.J., 2020. The recent colonization history of the most widespread *Podocarpus* tree species in Afromontane forests. Ann. Bot. 41, 2–11.

Moernaut, J., Verschuren, D., Charlet, F., Kristen, I., Fagot, M., De Batist, M., 2010. The seismic-stratigraphic record of lake-level fluctuations in Lake Challa: Hydrological stability and change in equatorial East Africa over the last 140 kyr. Earth Planet. Sci. Lett. 290, 214–223.

Moore, P.D., Webb, J.A., Collinson, M.E., 1991. Pollen Analysis, 2nd edn. Blackwell, Oxford.

Muiruri, V.M., 2017. Late Quaternary diatom and palynomorph stratigraphies and palaeoenvironments of the Koora Graben and Lake Magadi Basin, Kenya Rift Valley (PhD dissertation). Hong Kong Baptist University.

Muiruri, V.M., Owen, R.B., de Cort, G., McNulty, E., Rabideaux, N., Lowenstein, T., Renaut, R.W., Leet, K., Deocampo, D., Cohen, A.S., Campisano, C.J., Billingsley, A., Mbuthia, A., 2021. Middle Pleistocene to recent diatom floras and stratigraphy of the Magadi Basin, southern Kenya Rift. J. Paleolimnol. https://doi.org/10.1007/s10933-020-00173-7, 19 pages.

Muller, J., Kylander, M., Wüst, R.A.J., Weiss, D., Martinez-Cortizas, A., LeGrande, A.N., Jennerjahn, T., Behling, H., Anderson, W.T., Jacobson, G., 2008. Possible evidence for wet Heinrich phases in tropical NE Australia: the Lynch's Crater deposit. Quat. Sci. Rev. 27, 468–475.

Opiyo, B., Gebregiorgis, D., Cheruiyot, V.C., Deocampo, D.M., Kiage, L.M., 2019. Late Quaternary paleoenvironmental changes in tropical eastern Africa revealed by multiproxy records from the Cherangani Hills, Kenya. Quat. Sci. Rev. 222, 105907.

Owen, R.B., Potts, R., Behrensmeyer, A.K., Ditchfield, P., 2008. Diatomaceous sediments and environmental change in the Pleistocene Olorgesailie Formation, southern Kenya Rift Valley. Palaeogeogr. Palaeoclimatol. Palaeoecol. 269, 17–37.

Owen, R.B., Renaut, R.W., Behrensmeyer, A.K., Potts, R., 2014. Quaternary geochemical stratigraphy of the Kedong-Olorgesailie section of the southern Kenya Rift Valley. Palaeogeogr. Palaeoclimatol. Palaeoecol. 396, 194–212.

Owen, R.B., Muiruri, V.M., Lowenstein, T.K., Renaut, R.W., Rabideaux, N., Luo, S., Deino, A.L., Sier, M.J., Dupont-Nivet, G., McNulty, E.P., Leet, K., Cohen, A., Campisano, C., Deocampo, D., Shen, C.-C., Billingsley, A., Mbuthia, A., 2018a. Progressive aridification in East Africa over the last half million years and implications for human evolution. Proc. Natl. Acad. Sci. U. S. A. 115, 11174–11179.

Owen, R.B., Renaut, R.W., Lowenstein, T.K., 2018b. Spatial and temporal geochemical variability in lacustrine sedimentation in the East African Rift System: evidence from the Kenya Rift and regional analyses. Sedimentology 65, 1697–1730.

Owen, R.B., Renaut, R.W., Muiruri, V.M., Rabideaux, N.M., Lowenstein, T.K., McNulty, E.P., Leet, K., Deocampo, D., Luo, S., Deino, A.L., Cohen, A., Sier, M.J., Campisano, C., Shen, C.-C., Billingsley, A., Mbuthia, A., Stockhecke, M., 2019. Quaternary history of the Lake Magadi Basin, southern Kenya Rift: tectonic and climatic controls. Palaeogeogr. Palaeoclimatol. Palaeoecol. 518, 97–118.

Potts, R., 1989. Olorgesailie: new excavations and findings in Early and Middle Pleistocene contexts, southern Kenya rift valley. J. Hum. Evol. 18, 477–484.

Potts, R., 2012a. Evolution and environmental change in early human prehistory. Annu. Rev. Anthropol. 41, 151–167.

Potts, R., 2012b. Environmental and behavioral evidence pertaining to the evolution of early *Homo*. Curr. Anthropol. 53, S299–S317.

Potts, R., Deino, A., 1995. Mid-Pleistocene change in large mammal faunas of East Africa. Quat. Res. 43, 106–113.

Potts, R., Faith, J.T., 2015. Alternating high and low climate variability: the context of natural selection and speciation in Plio-Pleistocene hominin evolution. J. Hum. Evol. 87, 5–20.

Potts, R., Behrensmeyer, A.K., Deino, A., Ditchfield, P., Clark, J., 2004. Small mid-Pleistocene hominin associated with East African Acheulean technology. Science 305, 75–78.

Potts, R., Behrensmeyer, A.K., Faith, J.T., Tryon, C.A., Brooks, A.S., Yellen, J.E., Deino, A. L., Kinyanjui, R., Clark, J.B., Haradon, C., Levin, N.E., Meijer, H.J.M., Veatch, E.G., Owen, R.B., Renaut, R.W., 2018. Environmental dynamics during the onset of the Middle Stone Age in eastern Africa. Science 360, 86–90.

Potts, R., Dommain, R., Moerman, J.W., Behrensmeyer, A.K., Deino, A.L., Beverly, E.J., Brown, E.T., Deocampo, D., Kinyanjui, R., Lupien, R., Owen, R.B., Rabideaux, N., Riedl, S., Russell, J.M., Stockhecke, M., deMenocal, P., Tyler Faith, J., Garcin, Y., Noren, A., Scott, J.J., Western, D., Bright, J., Clark, J.B., Cohen, A.S., Heil, C.W., Keller, C.B., King, J., Levin, N.E., Shannon, K.B., Muiruri, V., Renaut, R.W., Rucina, S.M., Uno, K., 2020. Increased ecological resource variability during a critical transition in hominin evolution. Sci. Adv. 6 (43), 1–14 eabc8975.

Renaut, R.W., Owen, R.B., Lowenstein, T.K., De Cort, G., McNulty, E., Scott, J.J., Mbuthia, A., 2020. The role of hydrothermal fluids in sedimentation in saline alkaline lakes: evidence from Nasikie Engida, Kenya Rift Valley. Sedimentology. https://doi.org/10.1111/sed.12778.

Reynolds, S.C., Bailey, G.N., King, G.C.P., 2011. Landscapes and their relation to hominin habitats: case studies from Australopithecus sites in eastern and southern Africa. J. Hum. Evol. 60, 281–298.

Richardson, J.L., Dussinger, R.A., 1986. Paleolimnology of mid-elevation lakes in the Kenya Rift Valley. Hydrobiologia 143, 167–174.

Richter, D., Grün, R., Joannes-Boyau, R., Steele, T.E., Amani, F., Rué, M., Fernandes, P., Raynal, J.-P., Geraads, D., Ben-Ncer, A., Hublin, J.-J., Mcpherron, S.P., 2017. The age of the hominin fossils from Jebel Irhoud, Morocco, and the origins of the Middle Stone Age. Nature 546, 293–296.

Scholz, C.A., Johnson, T.C., Cohen, A.S., King, J.W., Peck, J.A., Overpeck, J.T., Talbot, M. R., Brown, E.T., Kalindekafe, L., Amoako, P.Y.O., 2007. East African megadroughts between 135 and 75 thousand years ago and bearing on early-modern human origins. Proc. Natl. Acad. Sci. U. S. A. 104, 16416–16421.

Shanahan, T.M., McKay, N.P., Hughen, K.A., Overpeck, J.T., Otto-Bliesner, B., Heil, C.W., King, J., Scholz, C.A., Peck, J., 2015. The time-transgressive termination of the African Humid Period. Nat. Geosci. 8, 140–144.

Sistiaga, A., Husain, F., Uribelarrea, D., Martín-Perea, D.M., Ferland, T., Freeman, K.H., Diez-Martin, F., Baquedano, E., Mabulla, A., Dominguez-Rodrigo, M., Summons, R. E., 2020. Microbial biomarkers reveal a hydrothermally active landscape at Olduvai Gorge at the dawn of the Acheulean, 1.7 Ma. Proc. Natl. Acad. Sci. 524, 202004532.

Stevenson, S., 2000. Environmental Impact Assessment of the Proposed Ash Project at Lake Magadi, Kenya. Norconsult Consultants, pp. 6–60.

Stone, J.R., Westover, K.S., Cohen, A.S., 2011. Late Pleistocene paleohydrography and diatom paleoecology of the central basin of Lake Malawi, Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 303, 51–70.

Trauth, M.H., Maslin, M.A., Deino, A.L., Junginger, A., Lesoloyia, M., Odada, E.O., Olago, D.O., Olaka, L.A., Strecker, M.R., Tiedemann, R., 2010. Human evolution in a variable environment: the amplifier lakes of Eastern Africa. Quat. Sci. Rev. 29, 2981–2988.

Vincens, A., 1986. Diagramme pollinique d'un sondage Pleistocene superieur—Holocene du Lac Bogoria (Kenya). Rev. Palaeobot. Palynol. 47, 169–192.

Vincens, A., 1987. Recent pollen sedimentation in Lake Natron, Tanzania: a model for the interpretation of fossil spectra in arid region. Sci. Géol. Bull. 40, 155–165.

Vincens, A., Bonnefille, R., Buchet, G., 1991. Étude palynologique du sondage Magadi NF1 (Kenya) implications paléoclimatiques. Geobios 24, 549–558.

Vincens, A., Lézine, A.M., Buchet, G., Lewden, D., Le Thomas, A., 2007. African pollen database inventory of tree and shrub pollen types. Rev. Palaeobot. Palynol. 145 (1–2), 135–141.