CHAPTER 7

Reconstructing vegetation history of the Olorgesailie Basin during the Middle to Late Pleistocene using phytolith data

Rahab N. Kinyanjui[1]

Department of Earth Sciences, National Museums of Kenya, Nairobi, Kenya

Michael Meadows[2]

Department of Environmental and Geographical Science, University of Cape Town, Rondebosch, South Africa

Lindsey Gillson

Plant Conservation Unit, Botany Department, University of Cape Town, Rondebosch, South Africa

Marion. K. Bamford

The Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

Anna K. Behrensmeyer

Department of Paleobiology, Smithsonian Institution, Washington, DC USA

Richard Potts

Human Origins Program, Smithsonian Institution, Washington, DC USA

ABSTRACT: The Olorgesailie basin, located in the East African Rift System (EARS), southern Kenya (1.5–1.6°S, 36.4–36.5°E, 940–1040 m asl), is an important site for palaeoanthropological, palaeontological and geological research, with sediments dating back more than 1 Ma. Little is known about the palaeovegetation and palaeoenvironmental context of this important site and how this varied through space and time. Here we use phytolith data to reconstruct the vegetation history through the Middle and Late Pleistocene (*c*. 670 ka to *c*. 64 ka). The analysis of 24 samples from

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[1]Other affiliation: *Department of Environmental & Geographical Science, University of Cape Town, South Africa; School of Geographical Sciences, East China Normal University, Shanghai, China; and College of Geography and Environmental Sciences, Zhejiang Normal University, Jinhua, China*
[2]Other affiliation: *School of Geographic Sciences, East China Normal University, Shanghai, China; and College of Geography and Environmental Sciences, Zhejiang Normal University, China*

palaeosols within the Olorgesailie and Oltulelei Formations uses diagnostic phytoliths to plot relative phytolith abundance diagrams documenting temporal and spatial vegetation variations. We use three phytolith indices (climate index, aridity index and tree density index) to estimate temperature, precipitation, and vegetation structure from sediments that are well-constrained chronologically by $^{40}Ar/^{39}Ar$ dating. Spatial vegetation variation is captured through examining phytoliths from three distinct localities (Loc. OLT, Loc. B and Loc. G) over a distance of about 5 km. Results suggest that local vegetation changes approximately correspond with stratigraphic units. Phytolith indices reflect warm and moist conditions *c*. 670 ka, with cool and dry conditions from *c*. 650 ka during which time riparian and a variety of other habitats were present. An unconformity, which extends over *c*. 180,000 years (500 to 320 ka), is interpreted as largely caused by tectonic processes coupled with precipitation variability. A shift from woody vegetation to C_4 grasslands is evident following the unconformity, and riparian habitats were again present. Considerable climate variability is apparent thereafter, with inconsistent precipitation conditions until *c*. 220 ka when more stable and moist conditions set in until *c*. 64 ka. The study documents vegetation dynamics directly associated with the Middle to Late Pleistocene palaeontological and archaeological record of Olorgesailie.

7.1 INTRODUCTION

East Africa is well known for its archive of human evolutionary history and the long-term history of ecological interactions between faunal and floral species and their environments (Bobe and Behrensmeyer 2002; Potts 1998). Tectonic processes created the episodic fossilization and preservation of records of ancient life in the East Africa Rift system (EARS) (Brown and Feibel 1991; Feibel 1999; Campsiano and Feibel 2008). Extensively collected and documented EARS fossils have addressed a variety of research questions including human and faunal evolutionary history, extinction and speciation events, species-environment interactions and the impact of climate change on past ecosystems (Bobe and Behrensmeyer 2004; deMenocal 2004; Feakins *et al.* 2007; Lepre *et al.* 2007; Potts and Faith 2015; Trauth *et al.* 2007).

Previous studies suggest that African climate and vegetation cover have been highly variable since the early Pliocene, oscillating from warm and humid to cool and dry episodes that can be correlated with orbital oscillations (Cerling *et al.* 2011; deMenocal 1995; Feakins *et al.* 2007; Lepre *et al.* 2007; Potts 2013; Trauth *et al.* 2007). These oscillations resulted in habitats that varied between woodland, wooded grassland and open grassland. Such vegetation dynamics influenced hominin diets and ecomorphology in the region, such as in the Awash and Olduvai basins (Albert *et al.* 2009; Ashley *et al.* 2010a; Bamford *et al.* 2006; Basell 2007; Cerling *et al.* 2010; White *et al.* 2010; WoldeGabriel *et al.* 2009).

In the Olorgesailie basin, vegetation cover has previously been reconstructed in only a single palaeosol dated *c*. 1 Ma, based on carbon isotope data and faunal remains (Sikes *et al.* 1999). The rich palaeontological, archaeological and geological data published from the basin have otherwise lacked a parallel body of evidence on vegetation cover and how its structure changed over time and across the landscape. Initial steps geared to reconstructing the vegetation cover and structure were hindered by poor preservation of fossil pollen and other organic plant remains due to high salinity in the basin (Livingstone and Mworia 1999). A subsequent feasibility study showed the potential for using fossil phytoliths to reconstruct vegetation cover and structure during the Middle to Late Pleistocene of the basin (Kinyanjui 2012).

Phytoliths are plant silica bodies that form when silica is deposited within and around plants cells during evapotranspiration, resulting in cell casts/replicas that are morphologically distinct. The silica cells are preserved in the soils after the decomposition of the parent plants (Mulholland and Rapp 1992; Piperno 1988; 2006). They are inorganic in nature, preserve well in a variety of depositional regimes, and are particularly useful because of good preservation in

regions where organic plant remains are susceptible to oxidation and thus less likely to accumulate (Piperno 2006). Phytolith research in East Africa has gained popularity as a reliable proxy for reconstructing past vegetation cover (Alexandre *et al.* 1997; Bremond *et al.* 2005a, b; 2008; Fredlund and Tieszen 1994) geared toward understanding past environments (Albert *et al.* 2012; 2015; Bamford *et al.* 2006; Barboni *et al.* 2009; 2010; Estaban *et al.* 2020; Kinyanjui 2013). In addition, phytolith indices can be used to determine changes in precipitation, vegetation structure dynamics, and provide coarse estimates of variations in temperature through time (Aleman *et al.*, 2008; Alexandre *et al.* 1997; Bremond *et al.* 2008; Fredlund and Tieszen 1997).

This paper presents phytolith data from the upper Olorgesailie Formation dated between *c*. 670 ka and 500 ka (Deino *et al.* 2018; Isaac 1978) and the Oltulelei Formation dated between *c*. 320 ka to *c*. 36 ka (Behrensmeyer *et al.* 2018; Deino *et al.* 2018). The stratigraphic sequence covers a significant period when hominins acquired new adaptive strategies associated with changing environments, which also coincided with replacement of mega-herbivore species by smaller herbivore taxa in the basin (Potts 1998; Potts and Faith 2015; Potts *et al.* 2018) associated with climate and local tectonic processes (Behrensmeyer *et al.* 2018; Potts *et al.* 2020).

7.2 STUDY SITE: OLORGESAILIE BASIN

The Olorgesailie basin is located in the southern part of the Kenyan Rift Valley (1°3′S and 36°2′E; 940–1040 m asl) (Figure 1). It is renowned for its high concentration of Acheulean hand axes dated *c*. 1.2 Ma to 500 ka (Deino and Potts 1990; Isaac 1977; 1978; Potts 1989; Potts *et al.* 1999). The basin lies near the southern end of the Eastern Arc of the East African Rift System (EARS). To the south it is bounded by lavas associated with Mt. Olorgesailie, an extinct Pliocene-Early Pleistocene age volcano, while to the north, east and west the basin is delimited by faulted ridges of trachytes, phonolites, and basalts extruded during the Plio-Pleistocene (Baker and Mitchell 1976; Isaac 1978; Shackleton 1978). The basin's present drainage system flows from north to south following the slope of the rift floor (Baker 1958), and from east to west along the northern foothills of Mt. Olorgesailie, although tectonic movements and volcanism altered these drainage patterns in the past (Behrensmeyer *et al.* 2002; 2018). The main outcrops of the basin north of Mt. Olorgesailie cover an area of *c*. 65 km^2.

7.2.1 Present-day climate and vegetation

Climate in the Olorgesailie region is largely controlled by the annual north-south oscillation of the Intertropical Convergence Zone (ITCZ) (Hills 1978; Kenworthy 1966; Nicholson 1996) resulting in two distinct rainy seasons: (i) long rains from March to June, and (ii) short rains from October to December (Asani and Kinuthia 1979; Griffiths 1958; 1972; Nicholson 1996; Sansom 1954). There are, however, anomalies in the rainfall pattern influenced by local topography. In this regard, the southern Kenya Rift Valley receives variable mean annual rainfall, for example 1000–1500 mm in the rift-margin highlands and 250–500 mm in the rift-axis lowlands (Griffiths 1972; Mutai and Ward 2000). The mean annual rainfall around the Olorgesailie basin is less than 500 mm which, combined with an evapo-transpiration rate exceeding 2400 mm/year, results in the negative hydrological balance responsible for the semi-arid condition of the basin (Damnati and Taieb 1995).

Vegetation in the Olorgesailie basin today is classified as a semi-arid variant of *Commiphora-Acacia* bushland (White 1983) or as a Northern *Acacia-Commiphora* bushland (WWF Eco-regions) (Figure 1). The dominant woody species include *Acacia tortilis* (Forssk.) Hayne, *A. senegal* (L.) Willd., *A. mellifera (Vahl)Benth,* (Figure 2B), *Commiphora africana* (A. Rich) Engl., *C. campestris* Engl., *C. samharensis* Schweinf., *C. schimperi* (O. Berg) Engl. *Terminalia* sp., *Balanites* spp., *Grewia bicolor* Juss., *G. villosa* Willd., *Boscia coriacea* Pax, (Figure 2B)
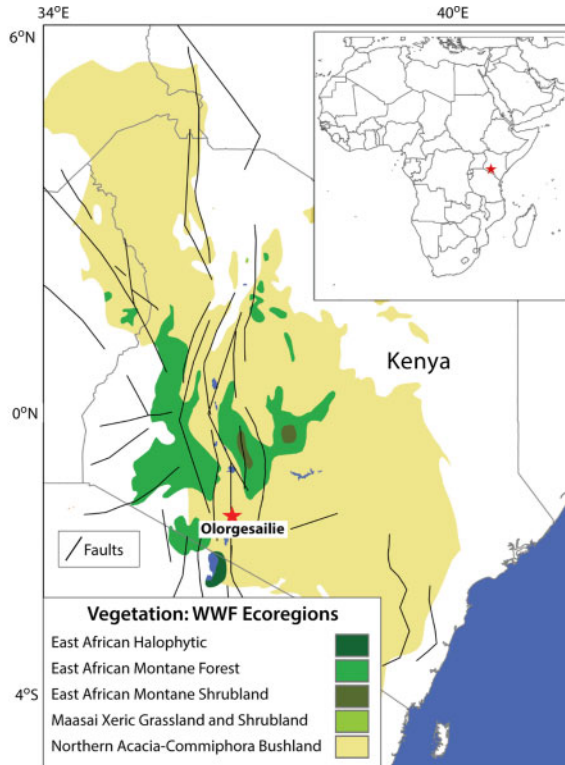
Figure 1. Map showing the location of the Olorgesailie basin and WWF vegetation designated ecoregions (White 1983).

and *Salvadora persica* L. The shrub component comprises *Sericocomopsis hildebrandtii* Schinz, *Barleria* sp., *Aerva* sp. and *Indigofera* sp. Most of the trees are deciduous and are in leaf during and after rains (Livingstone and Mworia-Maitima 1999; Mworia *et al.* 1988). Grasslands are C_4-dominated, mostly Chloridoideae family such as *Chloris roxburghiana* Schult., *Dactyloctenium bogdanii* S.M Phillips, *Eragrostis cilianesis* (All.) F.T. Hubb., *Tetrapogon cenchriformis* (A. Rich.) W.D Clayton, *Sporobolus jacquemontii* Kunth. and *Brachyachne* spp. (Livingstone and Mworia-Maitima 1999; Mworia *et al.* 1988). Elements of riverine gallery forest are also present along the seasonal river channels (lagas); they include *Syzygium cordatum* Krauss, *S. guineense* (Willd.) DC., *Delonix elata* (L.) Gamble and *Terminalia* spp., while *Kyllinga alba* Nees and *K. welwitschii* are C_4 sedges common in the floodplains (Livingstone and Mworia-Maitima 1999; Mworia *et al.* 1988).

7.2.2 Geoarchaeology

Current lithostratigraphic description distinguishes two units: the Olorgesailie and Oltulelei Formations (Behrensmeyer *et al.* 2002; 2018; Isaac 1978; Shackleton 1978), dated primarily by the single-crystal $^{40}Ar/^{39}Ar$ method (Behrensmeyer *et al.* 2018; Deino and Potts 1990; 1992; Deino *et al.* 2018; Potts *et al.* 2018).
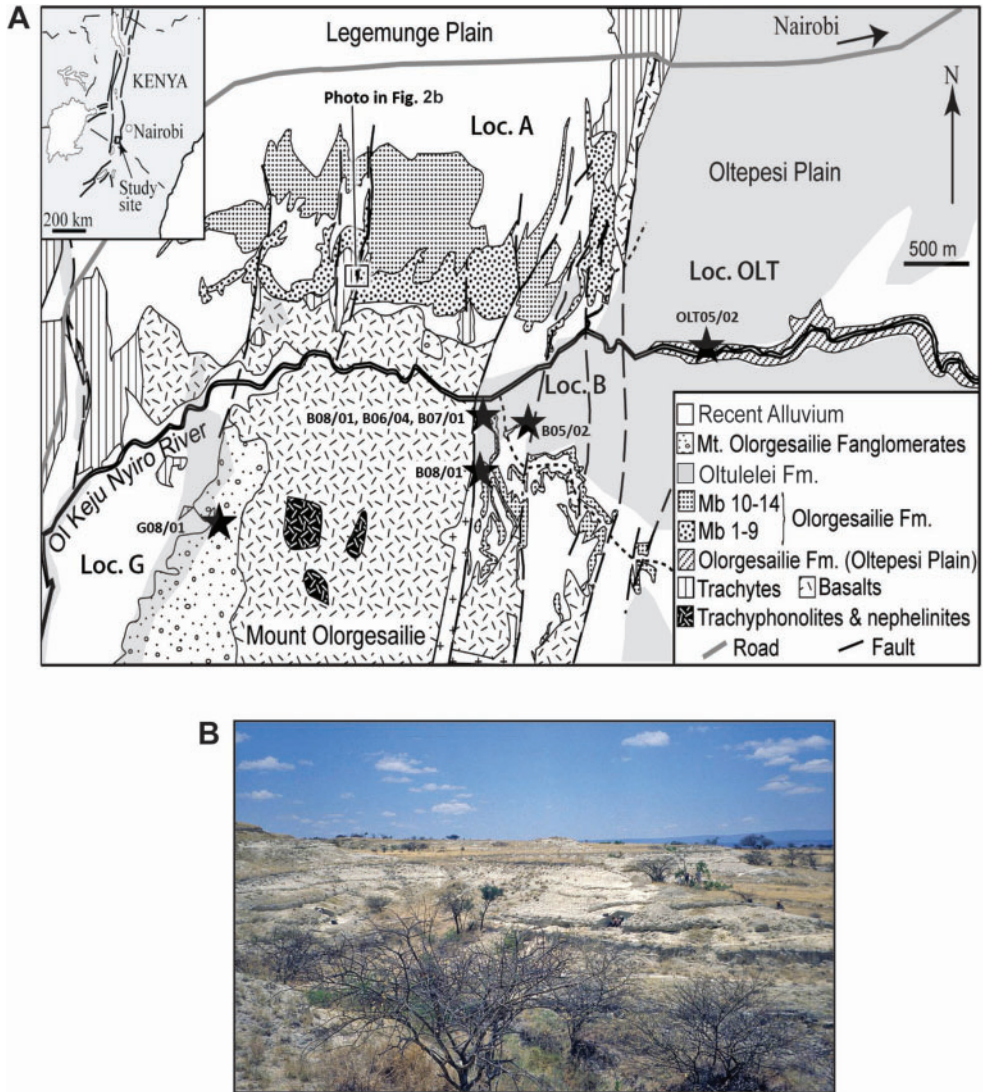
Figure 2. (A) Map showing Olorgesailie basin, localities, geo-trenches (marked with star) and the basin's geology. (B) *Acacia melliferae* and *Boscia coriaceae* visible in the photograph are among the dominant woody species in the basin.

7.2.2.1 Olorgesailie formation

These are deposits comprising lacustrine, wetland/swampy, fluvial and colluvial sediments forming a composite thickness of *c*. 80 m (Behrensmeyer *et al.* 2002). There are fourteen members (Isaac 1978; Shackleton 1978) with the base of the oldest member (Member 1) dated *c*. 1.2 Ma and the youngest Member (Member 14) *c*. 499 ka (Behrensmeyer *et al.* 2002; Deino and Potts 1990, 1992; Deino *et al.* 2018). Erosion and excavations have exposed a rich archaeological record including Acheulean stone artifacts associated with extinct mammals, butchery sites and
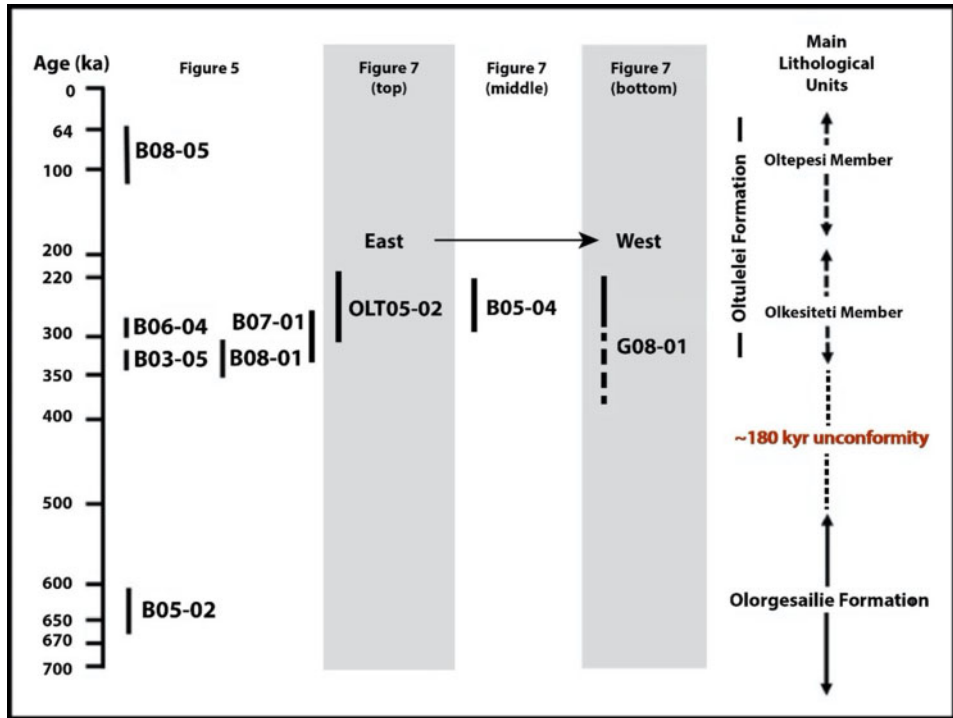
Figure 3. Schematic diagram showing lithostratigraphic/age relationship between sections.

hominin remains of *Homo erectus* (Potts 1994; Potts *et al.* 1999; 2004). Stable isotope data suggest vegetation structure around 1 Ma was predominantly C_4 grasslands (Sikes *et al.* 1999).

7.2.2.2 Oltulelei formation

These are younger deposits that overlie the Olorgesailie Formation, dated between *c*. 320 ka and *c*. 36 ka (Figure 3). The sediments rest on a major erosional unconformity, representing a hiatus of *c*. 180,000 years (Behrensmeyer *et al.* 2002; 2018; Deino *et al.* 2018) and consist of colluvial, alluvial, freshwater and saline lake deposits preserved in a series of erosional and channel filling regimes (Behrensmeyer *et al.* 2002; 2007; 2018). There are three successive members; Olkesiteti (*c*. 320–190 ka), Oltepesi (*c*. 190–50 ka) and Tinga (*c*. 50–36 ka) (Behrensmeyer *et al.* 2018; Deino *et al.* 2018). Exposures of these sediments have yielded stone tools of Middle Stone Age (MSA) technology and vertebrate fossils (Brooks *et al.* 2018; Potts *et al.* 2018).

7.3 METHODS

7.3.1 Laboratory methods, microscopy and identification

Phytolith extraction followed Albert's (1999) protocol with additional Acid Insoluble Fraction (AIF) steps (Mercader *et al.* 2010). All samples reached the minimum of 250 phytoliths counted for inclusion in the analysis, of these all but three samples yielded >500 phytoliths. Phytoliths
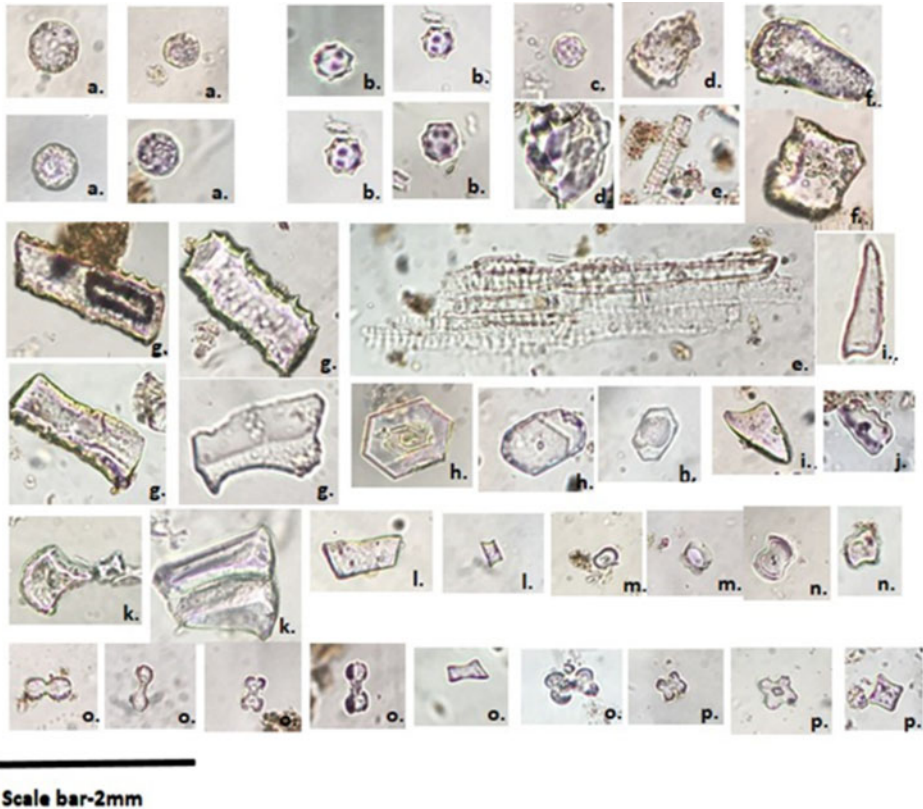
Scale bar-2mm

Figure 4. Micro-photographs of key fossil phytolith morphotypes identified. (a) Globular granulate, (b) globular echinate (Palm phytoliths), (c) Globular echinate (d) Globular verrucate, (e) Tracheid types, (f) Blocky types, (g) Sclereid bodies, (h) Achene (sedge phytoliths), (i) Scutiform/trichome types, (j) Crenate type, (k) Bulliform types, (l) Trapeziforms, (m) rondels, (n) saddles, (o) bilobates, (p) crosses.

were identified at $400\times$ magnification using an Olympus BX52 light microscope. Microphotographs were taken and viewed using image processing software; Image-Pros plus 5.1 and Infinity Capture 2. Images were stored as TIFF/JPEG files.

Morphological description and classification were based on phytolith shape and size based on the International Codes for Phytolith Nomenclature (ICPN) (Madella *et al.* 2005), while additional literature was consulted for specific taxa. Grass short cell phytoliths (GSCPs) assignments were based largely on the following studies (Barboni and Bremond 2009; Bremond *et al.* 2008; Esteban *et al.* 2016; Mercader *et al.* 2010; Neumann *et al.* 2009; 2017; Novello *et al.* 2012; Piperno 2006; Rossouw 2009; Strömberg 2004; Twiss 1992; Twiss *et al.* 1969), Woody (tree and shrub) (Albert and Weiner 2001; Mercader *et al.* 2009; Neumann *et al.* 2009; Piperno 2006; Runge 1999; Strömberg 2004) and Palm phytoliths (Figures 4b) (Albert *et al.* 2009; Ashley *et al.* 2010b; Neumann *et al.* 2009), Cyperaceae morphotypes (Honaine *et al.* 2006; Ollendorf 1992; Piperno 2006; Strömberg 2004), while the non-diagnostic types (trichomes, bulliforms, elongates) followed (Albert and Weiner 2001; Mercader *et al.* 2009; Neumann *et al.* 2009; Piperno 2006; Runge 1999; Strömberg 2004) (see Table 1).

Table 1. Summary of the diagnostic morphotypes used to identify various taxa presented herein.

Major Taxa	Diagnostic morphotype (s)	Morphotype description	Comparable references
Aristidoideae	• Bilobate convex outer margin long shaft.	• Bilobate with rounded lobes and long shaft ($>10\,\mu$m).	Piperno and Pearsall 1998; Piperno 2006; Neumann *et al.*, 2009.
Panicoideae	• Bilobates panicoid type. • Bilobates concave outer margin long/short shaft. • Bilobates convex outer margin outer margin short shaft. • Quadra-lobates/ crosses.	• Bilobate that is symmetrical, with rounded lobes. Shaft $<10\,\mu$m). • Bilobates with lobes curving inwards with either long shaft ($>10\,\mu$m) or short shaft ($<10\,\mu$m). • Bilobate with rounded lobes and short shaft ($<10\,\mu$m). • Equidimensional bodies with four lobes	Fredlund and Tieszen 1994; Pieperno 2006; Fahmy 2008; Rossouw 2009; Neumann *et al.* 2009; Mercader *et al.* 2010; Novello *et al.*, 2012.
Chloridoideae	• Saddle (Figure 4n). • Saddle squat.	• Saddle bodies with two opposite convex edges and two opposite concave edges in top view. • Saddle with side notches and a much longer axis than its tangential line.	Piperno 2006; Rossouw 2009; Neumann *et al.* 2009; Novello *et al.* 2012; Mercader *et al.*, 2010.
Undifferentiated grasses	• Bulliforms (Figure 4k).	• Parallelepipedal bulliform cells.	Madella *et al.* 2005; Neumann *et al.* 2009; Novello *et al.*, 2012.
Palm trees	• Globular echinate (palm type) (Figure 4c).	• Globular echinate, with defined spines.	Albert *et al.* 2006; 2009; Piperno 2006; Barboni *et al.*, 2007; 2009.
Woody taxa (Dicot)	• Globular granulate (Figure 4a). • Globular verrucate (Figure 4d). • Tracheids (Figure 4g). • Sclereids (Figure 4e).	• Spheroid/ spherical with fine knobs or knots, grainy. • Spheroid/spherical with irregularly shaped wart-like processes. • Tracheids. • Silicified elongate to slightly curved treachery tissue.	Strömberg 2004; Madella *et al.* 2005; Albert *et al.* 2005; Piperno 2006; Neumann *et al.* 2009.
Herbaceous taxa	• Globular psilate, elongate spiny.	• Spheroid/spherical with smooth to sub-smooth surface.	Madella *et al.* 2005; Piperno 2006; Neumann *et al.*, 2009.
Cyperaceae	• Achene types, hat shapes (Figure 4h).	• Pentagonal or hexagonal shape, with psilate surface and a central rounded cone.	Ollendorf 1992; Piperno 2006; Neumann *et al.*, 2009.

7.3.2 Data analyses

Morphotypes with >2% occurrence were plotted against sampling depths and age estimates using TILIA software (Grimm 2007).The zonation is determined statistically by constrained incremental sum-of-squares analysis (CONISS), a component of the TILIA and TILIA GRAPH software (Grimm 2007), based on sequential samples that coincide with the geological age bracket from which they were sampled.

We calculated three phytolith indices: (i) tree cover density (D/P) to distinguish grassland versus wooded vegetation, whereby a high D/P ratio indicates woody vegetation, and a low D/P ratio indicates open grassland, (ii) climate index ((I_C) to estimate the temperature gradient, whereby high I_C indicates cool climates, and low I_C indicates warmer climates, and (iii) aridity index (Iph) to estimate aridity-humidity gradient across time (Alexandre *et al.* 1997; Diester-Haas *et al.* 1973), whereby a high Iph indicates arid while low Iph indicates moist-conditions (Alexandre and Bremond 2009; Bremond *et al.* 2005a, Bremond *et al.* 2005b; 2008; Neumann *et al.*, 2009).

The D/P index is calculated as the ratio of diagnostic woody dicotyledons morphotypes (globular granulate/ornate) versus diagnostic grass short cell phytoliths (GSCPs) (saddles+bilobates+crosses+polylobates+trapeziform rondels) (Alexandre *et al.* 1997; Bremond *et al.* 2005b; Bremond *et al.* 2008; Neumann *et al.* 2009). The Iph index is calculated as the ratio of Chloridoideae (saddle) versus the sum of Chloridoideae (saddle) and Panicoideae (cross + bilobates + polylobates) (Bremond *et al.* 2005b; Neumann *et al.* 2009). The I_C index is the ratio of Pooideae C_3 grasses (trapeziform and keeled rondels) versus C_4 Panicoideae and Chloridoideae grasses (saddles + bilobates + crosses + polylobates+trapeziform) (Bremond *et al.* 2008).

7.4 RESULTS

7.4.1 Temporal changes

Temporal variation in phytolith assemblages are presented in summary diagrams which shows changes in the proportion of the various morphotypes (Figure 5). Five main taxonomic categories are identified and classified into: (i) C_3 grasses (Pooideae), (ii) C_4 grasses (Panicoideae, Chloridoideae and Aristidoideae), (iii) other grasses (undifferentiated grasses), (iv) tree-shrub-herbs (woody and other taxa), and (v) aquatic taxa (palms and sedges).

A total of 18,679 phytoliths were assigned to 41 different morphotypes . Concentrations of phytoliths averaged 747 per sample, of which around 61% were grasses, 12% trees and shrubs, while palms and sedges morphotypes accounted for 2% each. Non-diagnostic morphotypes accounted for 0.01% only. Of the 11,400 grass phytoliths 91% are diagnostic. Grass phytoliths were the most prominent component in all samples except for three from the Olorgesailie Fm. (R9, R16 and R17) which were dominated by trees/shrubs morphotypes. Variations in the phytolith assemblage where clustered into zones using CONNISS; these vegetation based divisions were found to correspond closely with the chronostratigraphic units (Figure 5).

7.4.1.1 Upper Olorgesailie formation zone (c. 670 ka to 500 ka)
The phytolith assemblages in the Upper Olorgesailie Fm. zone show greater abundance of trees/shrubs morphotypes relative to the grass morphotypes (Figure 5). C_4 Aristidoideae morphotypes are consistently low in this unit. Palm and sedge phytoliths are present in moderate abundance in nearly all of the six samples from this zone. Phytolith indices, I_C, Iph and D/P in the Olorgesailie Fm zone are as follows:- mean and max. respectively I_C (0.3, 0.6), Iph (0.5, 0.7) and D/P (0.4, 1.0). The I_C maximum is recorded in the sample prior to 650 ka while Iph and D/P maxima are recorded around 650 ka (Figure 6).
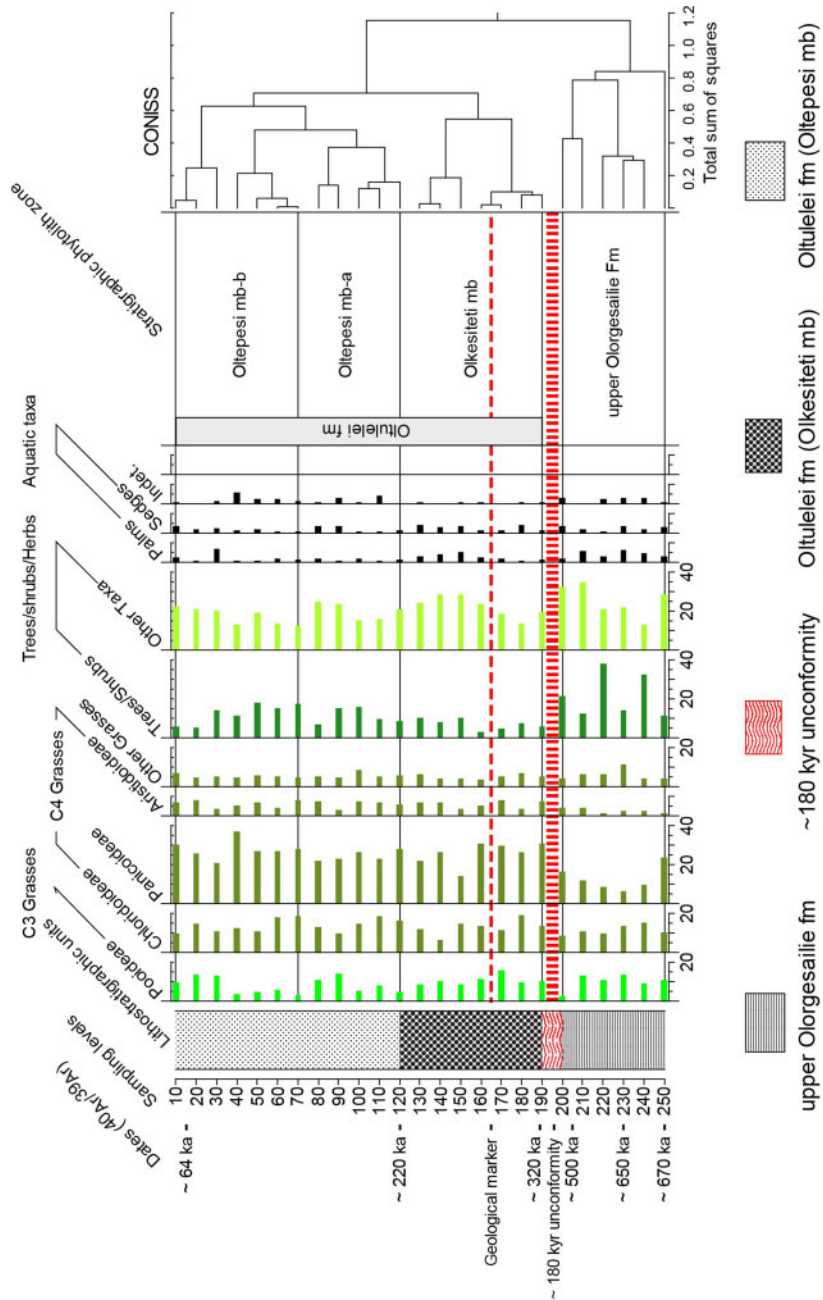
Figure 5. Phytolith relative abundance plotted against sample levels 10 – 250, representing the combined stratigraphic sequence through the Oltulelei and upper Olorgesailie formations. Note that actual sample intervals are variable in thickness but are equalized for this diagram.. See text for explanation of phytolith zones. CONISS = constrained incremental sum-of-squares analysis, a component of the TILIA and TILIA GRAPH software (Grimm 2007).
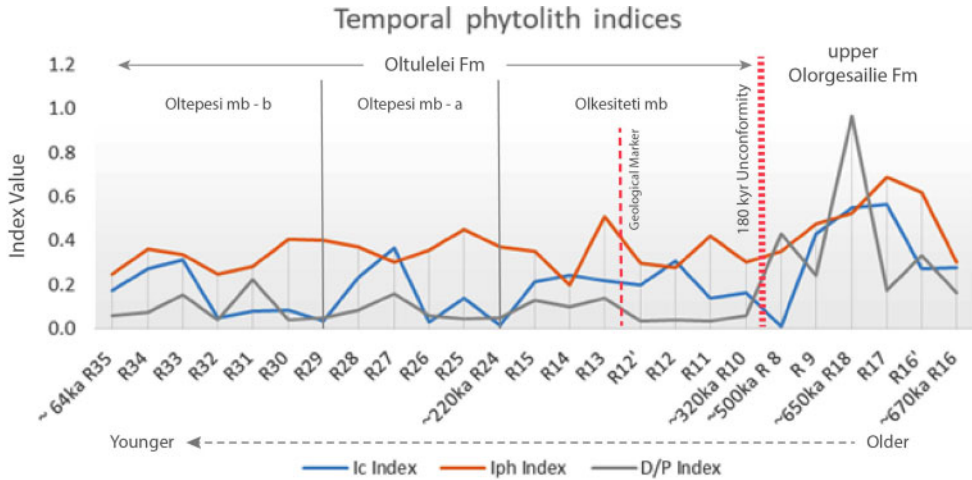
Figure 6. Phytolith indices plotted against samples. Climate index (I_C) increases with cool conditions, Aridity index (Iph) increases with low precipitation and Tree cover density (D/P) increases with more wooded vegetation structure. Graph plotted with older to younger going from right to left. Geological markers indicate with dotted red lines.

7.4.1.2 Olkesiteti mb zone (c. 320 ka to 220 ka)
This zone is separated from the underlying Olorgesailie Fm. zone by the *c*. 180,000 year unconformity (Behrensmeyer *et al.* 2002; 2018). Phytolith assemblages are mostly dominated by grasses, especially C_4 Panicoideae. The Olkesiteti mb zone represents phytolith data for samples R10 to R24 and marks the beginning of reduced frequencies of trees/shrubs phytoliths with increased GSCPs dominated by C_4Panicoideae morphotypes (Figure 5). Through the zone there is a significant increase in palm phytoliths, which had virtually disappeared following the unconformity. Interestingly, this variation, along with increased GSCPs and reduction of trees/shrubs morphotypes, appears to correspond with the geological marker in the unit. Phytolith preservation is good, as indicated by the low count in the indeterminate category. Phytolith indices, I_C, Iph and D/P in the zone are as follows:- mean and max. respectively I_C (0.2, 0.3), Iph (0.3, 0.5) and D/P (0.1, 0.1) (Figure 6).

7.4.1.3 Oltepesi mb zone (c. 220 ka to 64 ka)
The Oltepesi mb zone is marked by increased GSCPs, especially C_4 Panicoideae morphotypes, similar to the Olkesiteti mb zone. However, in this zone a slight increase in trees/shrubs morphotypes is evident, exceeding 15% in most of the samples. The zone is further sub-divided into two sub-zones, *viz*. Oltepesi mb zone-a and -b following the CONNISS clustering.

a) Sub-zone Oltepesi mb-a exhibits a continuation of C_4 Panicoideae and C_4 Chloridoideae grass dominance. Palm phytoliths are rare but an increase in tree/shrub phytoliths >15% occurs, especially in samples R26 (100) and R27 (90) (Figure 5).
b) Sub-zone Oltepesi mb-b is characterized by trees/shrubs and C_4 Panicoideae grasses with the exception of sample R33 (30), which has a high occurrence of C_3 Pooideae grasses, while both C_4 Panicoideae and Chloridoideae grasses are relatively low in this sub-zone. Phytolith indices, I_C, Iph and D/P in the entire zone are as follows:- mean and max. respectively I_C (0.1, 0.4), Iph (0.3, 0.4) and D/P (0.1, 0.2) (Figure 6).

7.4.2 Spatial variation

We documented variations in phytolith assemblages across the three localities sampled from three geological sections, OLT05-02, B05-04 and G08-01 (Figure 2). The distance between Localities OLT and B is *c*. 2.2 km and between B and G *c*. 2.5 km, in the east-west direction (Behrensmeyer *et al.* 2018). Summary phytolith diagrams (Figure 7) show percentage occurrence of selected morphotypes identified and classified by taxonomic affiliation, which are then grouped into five major categories: (i) C_3 grasses, (ii) C_4 grasses, (iii) woody and herbaceous taxa, (iv) Other taxa, and (v) riparian/aquatic taxa. The percentages are plotted for each sample for the period between *c*. 320 ka and *c*. 220 ka (Figure 7).

OLT05-02 samples, which is farthest east, show two major clusters (Figure 7). The lower three samples are characterized by low occurrence of C_4 Chloridoideae grasses (<10%) and relatively higher occurrence of trees/shrubs and dicots phytoliths at >20%. The upper cluster is dominated by grass morphotypes, derived especially from C_4 Panicoideae and Chloridoideae. Chloridoideae morphotypes increase to more than 10% in this cluster. C_3 Pooideae morphotypes are more or less consistent across all six samples. Palm and sedge phytoliths are rare in all samples. Phytolith indices, mean and max. respectively for the OLT05-02 samples are as follows: I_C (0.7, max. 1.6), Iph (0.3, 0.4) and D/P (0.1, 2.1) (Figure 8).

B05-04 samples are similar except for sample number R19 (*c*. 320 ka), which is dominated by tree/shrub morphotypes with a high occurrence of 60% dropping sharply to 20% or less in the subsequent samples towards *c*. 220 ka. Also present in low frequencies in this sample (R-19) are palm phytoliths, which are absent in the other samples in this section. Sedges are present in low percentages only across all five samples. Phytolith indices, mean and max. respectively for the B05-04 samples are as follows: I_C (0.5, max. 0.6), Iph (0.5, 0.6) and D/P (0.5, 0.6) (Figure 8).

G08-01 samples from the site situated farthest to the west, are divided into two major clusters that correspond with the red soil zone , which is geologically significant as the oldest unit of the Oltulelei Fm. in this locality (Behrensmeyer, *et al.* 2018) (Figure 7); the top of the red soil forms the 'geological marker' indicated in Figure 5. The lower cluster consists of samples R35, R36 and R37. Sample R37 differs from the rest in that it has the highest occurrence grass morphotypes coupled with lowest occurrence of tree/shrub morphotypes (10%). The upper cluster (R39, R41, and R42) is characterized by the presence of phytolith morphotypes from all categories. Palm phytoliths are present in significant frequencies except for R38 (*c*. 320 ka), which is notable for its high proportion of dicots, trees and shrubs.

We calculated phytolith indices for only five samples because it was not possible to do so for sample R38; C_4 grass morphotypes in this sample were absent, and extremely low C_3 Pooideae and tree/shrub morphotypes did not permit calculation of indices. Phytolith indices, mean and max. respectively for the B05-04 samples are as follows: I_C (0.6, max. 0.8), Iph (0.3, 0.5) and D/P (2.3, 7.5) (Figure 8).

7.5 DISCUSSION

7.5.1 Temporal vegetation change in the Olorgesailie basin (*c*. 670 ka to 64 ka)

Temporal changes in the vegetation cover and structure correspond to a relatively stable tectonic intervals in the basin around 670 ka to 500 ka, when vegetation structure was characterized by wooded grasslands as indicated by a higher D/P index (>0.5). The landscapes during this time window were characterized by riparian habitats and fresh water resources indicated by palms and sedges (Albert *et al.* 2009; Ashley *et al.* 2010 a, b; Bamford *et al.* 2006). Iph index suggests moderately moist conditions in the upper Olorgesailie Formation. After the *c*. 180,000 years unconformity, vegetation cover transitioned to C_4 Panicoideae dominated grasslands, that
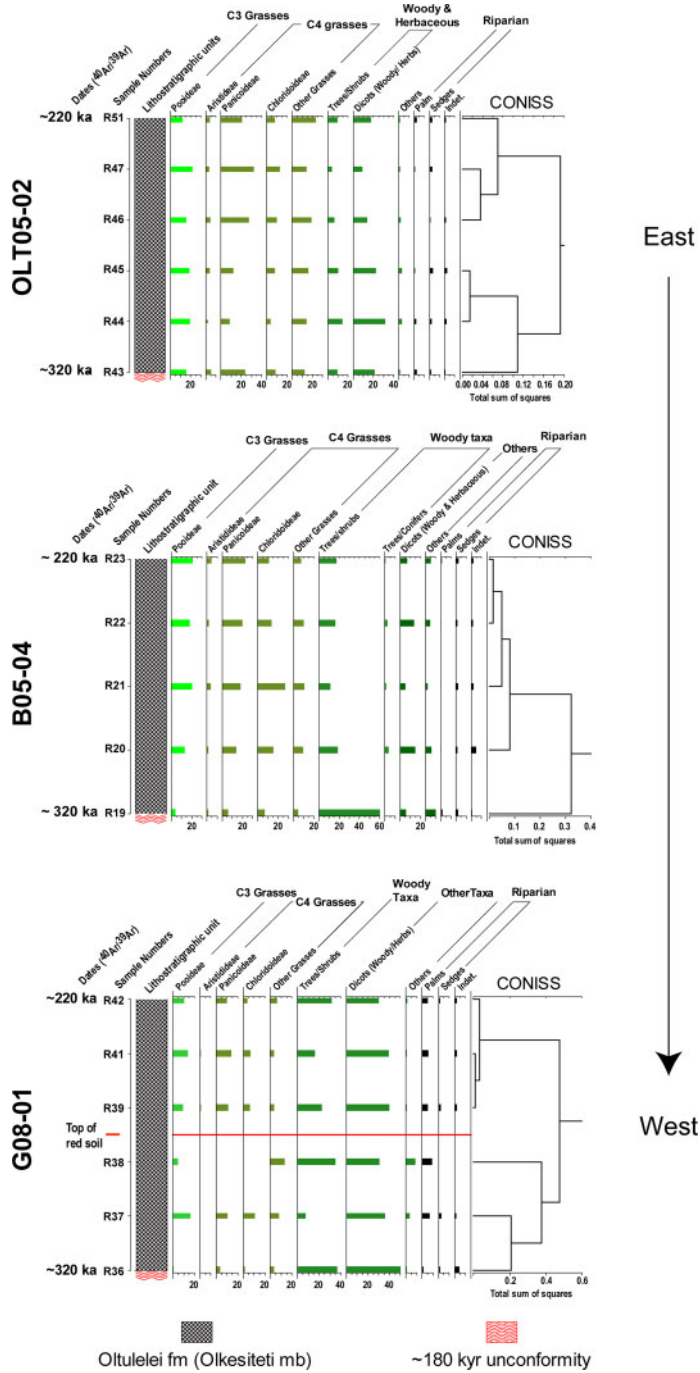
Figure 7. Phytolith relative abundance plotted against samples from the same 100 ka time interval for Localities OLT, B and G, which shows kilometre-scale landscape variability in local vegetation across the Olorgesailie basin. In G08-01, 'Top of red soil' = 'Geological Marker' in Figures 5 and 6. See text and caption to Figure 5 for further information.
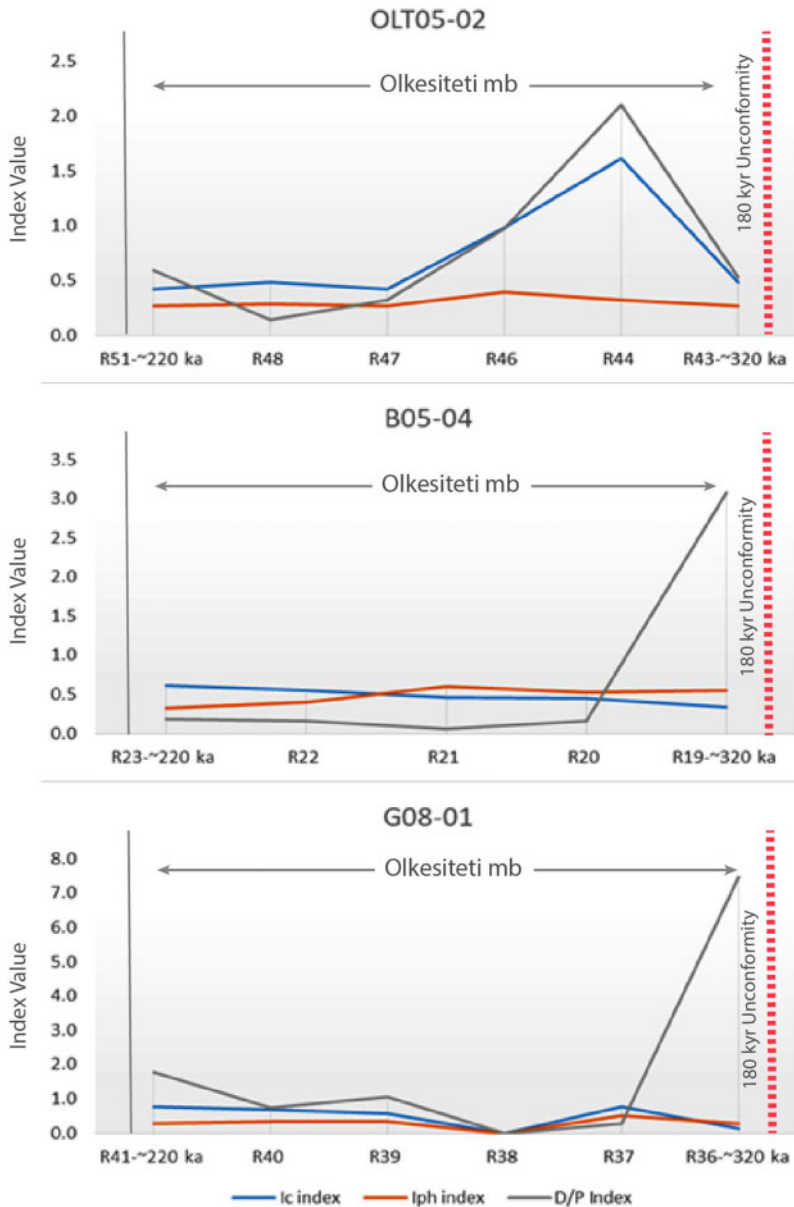
Figure 8. Olorgesailie phytolith indices plotted against samples for localities OLT, B and G. Graphs plotted with older to younger going from right to left. Climate index (I_C) increases with cool conditions, Aridity index (Iph) increases with low precipitation and Tree cover density (D/P) increases with more wooded vegetation structure. Geographically, OLT05-02 is farthest east, B05-04 in the middle, and G08-01 is farthest west (Figure 2).

fluctuates subtly through to *c*. 64 ka. I_C and Iph indices suggest warm and moist conditions. Vegetation cover between *c*. 220 ka and 64 ka, was stable and dominated by C4 Panicoideae grasslands with low proportions of woody elements. Wetlands were present through to *c*. 220 ka. As mentioned earlier, variation corresponds to lithostratigraphic units.

7.5.2 Vegetation heterogeneity across the Olorgesailie basin (*c*. 320 ka to 220 ka)

Vegetation heterogeneity existed across the landscapes of the Olorgesailie basin between *c*. 320 ka and *c*. 220 ka. Within locality OLT, toward the eastern part of the rift basin (Figure 2), vegetation cover was initially dominated by woody elements that shifted towards C_4 Panicoideae grasslands. Palms and sedges were rarely present. Locality B, near the northern shoulder of Mt. Olorgesailie, was also dominated by C_4 Panicoideae grasslands except around *c*. 320 ka, which was marked by high dominance in woody vegetation. Sedges were rarely present and palms completely absent. Locality G on the western side of Mt. Olorgesailie was consistently dominated by woody and dicot vegetation, with abundant palms. C_3 Pooideae grasses across the three localities follows an east-west declining trend and are more prominent across the eastern and central localities (B and OLT) than at Locality G. This suggests that topographic complexity in the basin also influenced vegetation variation across the palaeolandscapes at least 5 km distance. Mt. Olorgesailie, which is today characterized by C_3 vegetation, likely also was a source of the C_3 Pooideae phytoliths input into the basin during the Oltulelei Fm. The evidence overall indicates considerable spatial variation in vegetation structure across the basin during the period of sedimentation.

7.5.3 Palaeoanthropological significance of vegetation data

The phytolith data presented here represent temporal resolution of 10^{4-5} years over a total interval of *c*. 600,000 years and are currently the only comprehensive outcrop-based data in East Africa for inferring vegetation during the Middle to Late Pleistocene transition in early hominin technology from Acheulean to Middle Stone Age (MSA) tools, by *c*. 350 ka to 320 ka (Brooks *et al.* 2018; Potts *et al.* 2018). Before the *c*. 180,000-year erosional phase, the vegetation structure associated with the late Acheulean technology at Olorgesailie was more wooded, and included wetlands/riparian resources, contrasting with the vegetation structure associated with MSA technology, which was dominated by warm and moist-adapted C_4 Panicoideae grasslands. This corresponds with a marked change in the geology and lithology of the basin between *c*. 500 and 320 ka, which exhibited a shift to a landscape with fluvial channels, flood plains and spring deposits (Behrensmeyer *et al.* 2018; Potts *et al.* 2018). The vegetation change was accompanied by large mammal turnover, evidenced by the paleontological evidence in the southern Kenyan rift (Potts *et al.* 2018). Herbivores may have played a significant role in engineering the vegetation structure as it shifted from more wooded to open grasslands in the basin (Potts *et al.* 2020). These dynamics could have influenced human adaptive strategies that led to new technological innovations (Brooks *et al.* 2018; Potts *et al.* 2020).

Vegetation heterogeneity, specifically the occurrence of a mosaic of riparian, grasslands and woodland patches in the time interval between 320 ka and 220 ka, suggests a variety of habitats that availed key resources for hominins and offered attractive spots for food resources. Such mixed habitats have been inferred at other prehistoric sites such as Olduvai and Awash and proved to be of palaeoanthropological significance (Albert *et al.* 2009; Ashley *et al.* 2010; Bamford *et al.* 2006; Barboni *et al.* 1999).

7.6 CONCLUSIONS

Phytolith data show that vegetation structure and cover in the Olorgesailie basin was more wooded prior (*c*. 670 ka to 500 ka) to the *c*. 180,000 year unconformity. Riparian habitats were present with subtle variation between palaeolandscapes. Trees and shrubs fluctuated between landscapes while grasslands remained stable. From 320 ka to 64 ka vegetation cover shifted to grasslands dominated by C_4 Panicoideae with some riparian habitats. Between *c*. 320 ka and 220 ka, our evidence shows that relatively adjacent habitats in the basin included a diversity of open grasslands, woodland, and riparian elements.

Phytolith data from this study assist in developing an understanding of local palaeoenvironments with which early hominins interacted during the Pleistocene (*c*. 670 ka to 64 ka). The data suggest that late Acheulean technology in the southern Kenya rift was associated with more woody vegetation structure than early MSA technology, which appears to have coincided with grassy landscapes in the Olorgesailie basin. This technological transition at Olorgesailie represents the oldest example currently known of the replacement of the Acheulean by the MSA (Brooks *et al.* 2018; Deino *et al.* 2018). We propose that this important transition may have occurred in response to changing vegetation and food resources available to the fauna, and may help to explain the replacement of large-bodied by smaller-bodied herbivores that were increasingly reliant on mixed vegetation diets (Potts *et al.* 2020). The varied habitats present in the basin offered critical resources such as fresh water and forage that would have sustained hominins and other animals.

In conclusion, vegetation dynamics in Olorgesailie during the Pleistocene reflected responses to both precipitation variability and tectonic processes. The vegetation data presented here are significant in that they are directly extracted from and related to fossil- and artifact-bearing outcrops and shed new light on the evidence for interactions between hominins and other faunal and floral communities in the basin. We postulate that such interactions likely played a critical role in shaping hominin behavior and technological innovations.

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