Phytoliths, pollen, and microcharcoal from the Baringo Basin, Kenya reveal savanna dynamics during the Plio-Pleistocene transition

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A B S T R A C T

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As part of the Hominin Sites and Paleolakes Drilling Project (HSPDP), phytoliths, pollen, and microcharcoal were examined from the 228 m (3.29 to 2.56 Ma) Baringo-Tugen Hills-Barsemoi drill core (BTB13). A total of 652 samples were collected at ~10 to 32 cm intervals, corresponding to sub-millennial to millennial scale temporal resolution. Microcharcoal was well-preserved throughout the core and often peaked in abundance ~5 kyr before and after insolation peaks. Phytolith preservation varied between excellent to total dissolution in alternating intervals throughout the core. Pollen was rarely preserved. These combined datasets indicate that prior to ~3.1 Ma, woody cover fluctuated between open savanna (<40% cover), woodland (40–80% cover), and forest (>80% cover) at typically precessional (19–23 kyr) periodicities. During the mid-Piacenzian Warm Period (MPWP; 3.26–3.01 Ma), intervals with exceptionally high microcharcoal abundance suggest that regional turnover from wooded to open habitats was driven in part by fire. After ~3.1 Ma, low-elevation woody cover likely never exceeded 40%, with oscillations between mesic tall-grass vs. xeric short-grass savanna at precessional periodicities. Mesic C₄ tall-grass (Panicoideae) peaked in abundance during insolation maxima, whereas xeric C₄ short-grass (Chloridoideae) peaked during insolation minima. The onset of Northern Hemisphere glaciation (NHG) at ~2.75 Ma coincided with the appearance of deep lake phases and increases in grass density and fire frequency. Spectral analysis and intervals with well-preserved phytoliths indicate that precession and interhemispheric insolation gradients influenced vegetation via their effects on equatorial precipitation and fire. This study fills a crucial gap in Pliocene vegetation reconstructions from the East African Rift Valley and its associated hominin localities. It also provides orbitally resolved regional vegetation data useful in paleodata-model comparisons for the onset of the MPWP (which is often used as an analog for future warming) and NHG.

1. Introduction

Late Neogene geological sections from the Baringo Basin and Tugen Hills area of the central Kenya Rift Valley have been the focus of intensive paleoenvironmental and paleoanthropological investigations for the past several decades (Pickford et al., 1983; Hill, 1985; Hill et al., 1992; Hill, 2002; Jacobs, 2002; Kingston et al., 2002; Deino et al., 2006; Kingston et al., 2007). The Hominin Sites and Paleolakes Drilling Project (HSPDP) targeted the Plio-Pleistocene fluviolacustrine deposits of the Chemeron Formation in the Tugen Hills, Kenya, as one of six East African drill sites with high potential to reveal linkages between environmental change and human evolution (Cohen et al., 2016). The Chemeron Formation contains over 100 fossil vertebrate localities, including several hominin sites, three of which are located within 3 km of the HSPDP drill site and within the time interval encompassed by the drill core (Deino and Hill, 2002; Deino et al., 2002; Campisano et al., 2017).

Various hominin-environment models such as the Savanna Hypothesis (Bender et al., 2012) and the Variability Selection Hypothesis (Potts, 1998) have been proposed to explain possible environmental drivers of hominin evolution. Variables such as precipitation, Earth orbital parameters, and tectonics (rifting and volcanism) are often invoked in these evolutionary models. However, it has been argued that regardless of the specific selection mode that was operative, ultimately
it is the availability of water (Cuthbert and Ashley, 2014; Cuthbert et al., 2017) and the structure and composition of vegetation (Barboni et al., 2019) that are critically important for hominin survival. These aspects of landscape architecture support faunal populations and set the framework for predator-prey relationships, speciesfunctional group competitionfacilitation, and dispersal into novel environments (Potts, 2004; Kingston, 2007; Wells and Stock, 2007; Bunn and Gurtov, 2014).

Almost four decades ago, Hill (1981) called for the explicit inclusion of paleoecology into discussions on the evolution of human morphological change. However, vegetation-based paleoecological data at the appropriate taxonomic resolution from the basins where hominins lived were scattered and discontinuous across the Plio-Pleistocene (Bonnefille, 2010; Jacobs et al., 2010; Barboni, 2014). Several studies have recently produced such datasets (e.g., Novello et al., 2015; Arráiz et al., 2017; Novello et al., 2017; Albert et al., 2018; Ivory et al., 2018; Owen et al., 2018), yet there remains a paucity of paleovegetation records. This is especially true for records from the Plio-Pleistocene transition that show vegetation dynamics at time scales relevant to issues of hominin adaptation to abrupt vegetation change and high-frequency variability (Campisano et al., 2017).

To specifically address this shortcoming, we use direct paleoecological evidence primarily from phytoliths and microarchaeological, complemented with pollen data where preserved, to reconstruct fire and vegetation dynamics in the Baringo Basin at millennial to sub-millennial scales from the Baringo-Tugen Hills-Barsemoi HSPDP drill core (BTB13), which spans 3.29 to 2.56 Ma. This interval captures the mid-Piacenzian Warm Period (MPWP) and the subsequent initiation of global cooling, the onset of Northern Hemisphere glaciation (NHG), the diversification of Panthorbus and Homo, and the earliest evidence for stone tools (Harmand et al., 2015). With 652 samples analyzed from a 228-m core spanning 730 kyr, this record represents one of the most extensive phytolith studies ever conducted.

2. Background

2.1. Phytoliths from lake sediments

Phytoliths are microscopic opal silica (SiO2 · nH2O: opal-A) inclusions and casts of plant cells (Piper, 2006; Strömbärg et al., 2018). When plant material decays or is burned, phytoliths persist and are incorporated into soils and sediments. Phytoliths are transported to lake sediments by sheet-wash, fluvial, and eolian processes while still embedded in fresh or burned plant fragments, or after in situ plant matter decays (Yost et al., 2013; Aleman et al., 2014). Phytolith assemblages for lakes surrounded by moderate to high relief landscapes, such as rift settings, are assumed to reflect a weighted average of the lake catchment vegetation mosaic, with individual phytoliths capable of being transported up to 10^4 m (Yost et al., 2018; Li et al., 2019).

2.2. The use of grass subfamily phytolith indicators

Grass pollen can rarely be distinguished below the family level, and stable carbon isotopic approaches cannot distinguish C3 grasses from all other C3 plants, thus the diversity and habitat specificity of grasses has not been fully exploited in paleoecology. A major strength of phytolith analysis is the ability to identify grasses, with some degree of certainty, to subfamily and sometimes lower taxonomic levels, for which there are numerous morphotypes at various taxonomic and functional type levels, and considering the fact that a small number of grass species comprise the majority of the biomass in many grass-dominated systems (Williams et al., 2016), but only 10 to 15 species are common, and often only two or three species dominate a given grass community (Belsky, 1983, 1985, 1986; Banyikwa et al., 1990).

2.3. Short-grass vs. tall-grass savanna

The short-grass/tall-grass boundary is a significant but underappreciated ecological division in paleoecology. By extension, an underutilized paleoecological tool is the Iph phytolith index, which can differentiate between short-grass and tall-grass savannas (Bremond et al., 2008; Novello et al., 2017). Short-grass savannas are dominated by Chloridoideae grasses, and their abundance is negatively correlated with precipitation (Taub, 2000). Tall-grass savannas are dominated by Panicoideae grasses, whose abundance and stature are positively correlated with precipitation (Taub, 2000; Bocksberger et al., 2016). The short-grass/tall-grass boundary occurs at ~750 mm mean annual precipitation (MAP) for the Sudanian, Sahelian, and Somali-Masai phyto-geographic zones of western, central, and eastern Africa (van Wyk, 1979; McNaughton, 1983).

Vegetation structure and ecosystem services are vastly different in short- and tall-grass savannas. Short-grass savanna grasses are typically one to several decimeters in height, highly nutritious, heavily grazed, and often form rhizomatous lawns (McNaughton, 1985; Quigley and Anderson, 2014; Hempson et al., 2015b). Short-grass savanna mammals are typified by high species diversity and very high abundances of medium-sized social mixed-diet taxa (e.g., gazelle, oryx, common eland) (Hempson et al., 2015a). Tall-grass savanna grasses can reach heights of one to two meters, are less nutritious (low in N, P, and Na), less palatable/digestible (high lignin and silica), hide predators, and promote high fire frequency and intensity (Dobson, 2009; Pats et al., 2012; Quigley and Anderson, 2014). Tall-grass savanna mammals are typified by high relative abundances of non-ruminant grazers such as equids, hippos, rhinos and suids, and water-dependent grazers such as wildebeest, hartebeest, Hippotragus sp. and Kobus sp. (Hempson et al., 2015a). Hominin behavior may have been very different within these two structurally and compositionally different savanna types. Thus, a major goal of this study is to identify periods of short- and tall-grass dominance and how these two habitat types vary over time.

2.4. Regional and local setting for the drill-core site

The Baringo-Bogoria Basin is part of the eastern branch of the East African Rift System (EARS), and contains present-day Lake Baringo and Lake Bogoria to the south. Like most of the EARS, the Baringo-Bogoria Basin is surrounded by a landscape that is topographically complex, resulting in a high level of plant diversity (Fig. 1). It is likely this complex mosaic of vegetation was in place to some degree in the central Rift Valley by the Pliocene (Jacobs, 2004; Jacobs et al., 2010). A review of the plant fossil record suggests that vegetation complexity has been increasing over the Neogene (Linder, 2017).

The modern 6569 km² Lake Baringo watershed spans an elevation range of ~1000 to ~2000 msl, and encompasses 10 vegetation types that range from open grassland to afromontane forest (van Breugel et al., 2015). The BTB13 drill site is located ~12 km west of Lake Baringo in the Tugen Hills at 1158 msl (Cohen et al., 2016). Modern vegetation at the drill site is classified as Somalia-Masai Acacia-Corn- miphora deciduous bushland and thicket with 40% or more woody cover (White, 1983; van Breugel et al., 2015). The area experiences low and erratic MAP, which varies between 500 and 750 mm, and has annual evaporation rates between 2000 and 2800 mm (Ngaira, 2005). Little is known about the extent and depth of the Chemeron Formation paleolakes, but the depocenter may have been to the east of the drill site (Deino et al., 2006).
3. Methods

3.1. Drill core extraction and core chronology

A single, vertical 227.9 m borehole was drilled at the Tugen Hills site (Lat 0°33'16.56" N, Long 35°56'15.00" E) in May–June 2013. BTB13 was drilled using truck-mounted standard wireline diamond bit drilling with standard IODP butyrate core liners. The 228 m of core was airfreighted to LacCore, the National Lacustrine Core Facility (University of Minnesota, USA) for full scanning, processing, description, and subsampling. See Cohen et al. (2016) for coring details and initial core descriptions. Core depths are reported in meters below surface (mbs). A Bayesian stratigraphic age model for the core was developed by Deino et al. (2020) using 40Ar/39Ar dating, magnetostratigraphy, and tephr stratigraphy.

3.2. Microfossil separations from sediment

With the exception of core intervals with voids, approximately 2 cm³ of sediment was initially collected for pollen and phytolith/microcharcoal separations every 32 cm along the 228 m core, resulting in 652 samples. Pollen and phytolith/microcharcoal samples were split at the University of Arizona, and ages for each sample were assigned from the age model. On average, each sample encompasses 66 years, with 1093 years between samples.

3.2.1. Phytolith, pollen, and microcharcoal separations

Phytoliths and microcharcoal particles were extracted together and counted on the same slide. All 652 samples were analyzed for phytoliths and microcharcoal using a modified version of the wet-oxidation and heavy-liquid density separation method described in Piperno (2006). In a controlled comparison of microcharcoal separation methods, density separation using a heavy liquid and chemical removal of organic matter produced a significantly higher microcharcoal yield than other common methods (Turner et al., 2008). Additionally, a direct comparison of standard sieve- versus pollen-extracted charcoal (which would agitate charcoal similarly as a phytolith extraction) found that pollen-slide concentrations were higher, but the broad-scale trends in fire between the two approaches were comparable (Carcaillet et al., 2001). Synthetic microspheres were added to each sample in order to calculate concentrations. Detailed extraction steps are provided in the Supplementary Online Material (SOM).

As an initial assessment of pollen preservation, pollen was analyzed at 96 cm intervals (every third sample collected; 108 total). Preliminary
Table 1
Phytolith morphotypes used for analysis, interpretation, and index calculations.

<table>
<thead>
<tr>
<th>Morphotype</th>
<th>Anatomical origin</th>
<th>References (morphotype names)</th>
<th>Taxonomic interpretation</th>
<th>Plant functional type</th>
<th>Interpretive index use</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rondel-angular keel</td>
<td>Leaf/Culm/infor.</td>
<td>Yost et al., 2018</td>
<td>Phalaris spp</td>
<td>C3 grass</td>
<td>Ic3, D/P</td>
</tr>
<tr>
<td>Rondel-keeled</td>
<td>Leaf/Culm/infor.</td>
<td>Barboni and Bremond, 2009</td>
<td>Pooideae</td>
<td>C3 grass</td>
<td>Ic3, D/P</td>
</tr>
<tr>
<td>Rondel-length &gt; 15 μm</td>
<td>Leaf/Culm/infor.</td>
<td>Yost et al., 2018</td>
<td>Pooideae</td>
<td>C3 grass</td>
<td>Ic3, D/P</td>
</tr>
<tr>
<td>Plateaued saddle</td>
<td>Leaf/Culm/infor.</td>
<td>Piperno and Pearssall, 1998; Yost et al., 2018</td>
<td>Phragmites spp</td>
<td>C3 grass</td>
<td>Ic3, D/P</td>
</tr>
<tr>
<td>Very tall saddle (VTS)</td>
<td>Leaf/Culm/infor.</td>
<td>Piperno and Pearssall, 1998; Yost et al., 2018</td>
<td>Bambusoideae</td>
<td>C3 grass</td>
<td>Ic3, D/P</td>
</tr>
<tr>
<td>Rondel/ Bilobate-irregular</td>
<td>Leaf/Culm/infor.</td>
<td>Yost et al., 2018</td>
<td>Bambusoideae</td>
<td>C3 grass</td>
<td>Ic3, D/P</td>
</tr>
<tr>
<td>Bilobate angulate-asym. lobes</td>
<td>Leaf/Culm/infor.</td>
<td>Esteban et al., 2017</td>
<td>Danthonioidae</td>
<td>C3 grass</td>
<td>Ic3, D/P</td>
</tr>
<tr>
<td>Bilobate-scoped ends</td>
<td>Leaf/Culm/infor.</td>
<td>Yost and Blinnikov, 2011; Neumann et al., 2017</td>
<td>Ehrhartioidae</td>
<td>C3 grass</td>
<td>Ic3, D/P</td>
</tr>
<tr>
<td>Saddle</td>
<td>Leaf/Culm/infor.</td>
<td>Madella et al., 2005</td>
<td>Chloridioideae</td>
<td>C3 xeric grass</td>
<td>Ic3, D/P, lph</td>
</tr>
<tr>
<td>Rondel-spool/horned</td>
<td>Leaf/Culm/infor.</td>
<td>Lu and Liu, 2003</td>
<td>C3 xeric grass</td>
<td>Ic3, D/P</td>
<td></td>
</tr>
<tr>
<td>Bilobate: B/VLL/VLS</td>
<td>Leaf/Culm/infor.</td>
<td>Neumann et al., 2017</td>
<td>C3 xeric grass</td>
<td>Ic3, D/P</td>
<td></td>
</tr>
<tr>
<td>Cross: Triangle</td>
<td>Leaf/Culm/infor.</td>
<td>Neumann et al., 2017</td>
<td>Panicoidae</td>
<td>C4 mesic grass</td>
<td>Ic3, D/P, lph</td>
</tr>
<tr>
<td>Cross: Q/VLL</td>
<td>Leaf/Culm/infor.</td>
<td>Neumann et al., 2017</td>
<td>Panicoidae</td>
<td>C4 mesic grass</td>
<td>Ic3, D/P, lph</td>
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<tr>
<td>Cross: Q/LL</td>
<td>Leaf/Culm/infor.</td>
<td>Neumann et al., 2017</td>
<td>Panicoidae</td>
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<td>Bilobate: B/VLL/LS</td>
<td>Leaf/Culm/infor.</td>
<td>Neumann et al., 2017</td>
<td>Panicoidae</td>
<td>C4 mesic grass</td>
<td>Ic3, D/P, lph</td>
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<td>Neumann et al., 2017</td>
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<td>Leaf/Culm/infor.</td>
<td>Neumann et al., 2017</td>
<td>Panicoidae</td>
<td>C4 mesic grass</td>
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<td>Bilobate: B/LL/LS</td>
<td>Leaf/Culm/infor.</td>
<td>Neumann et al., 2017</td>
<td>Panicoidae</td>
<td>C4 mesic grass</td>
<td>Ic3, D/P, lph</td>
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<td>Neumann et al., 2017</td>
<td>Panicoidae</td>
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<td>Neumann et al., 2017</td>
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<tr>
<td>Multicellular long cell fragment</td>
<td>Leaf/Culm/infor.</td>
<td>Rosen, 1992</td>
<td>Poaceae</td>
<td>Grass</td>
<td></td>
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<tr>
<td>Bulliform-cuneiform/rectangular</td>
<td>Leaf</td>
<td>Madella et al., 2005</td>
<td>Poaceae</td>
<td>Grass</td>
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<td>Trichome (Poaceae-type)</td>
<td>Leaf/Culm/infor.</td>
<td>Madella et al., 2005</td>
<td>Poaceae</td>
<td>Grass</td>
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<td>Substomatal/stomatal complex</td>
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<td>Yost et al., 2018</td>
<td>Poaceae</td>
<td>Grass</td>
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<td>Dentritic long cell</td>
<td>Leaf/Culm/infor.</td>
<td>Yost et al., 2018</td>
<td>Poaceae</td>
<td>Grass</td>
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<td>Elongate psulate long cell</td>
<td>Leaf/Culm/infor.</td>
<td>Madella et al., 2005</td>
<td>Poaceae &amp; Cyperaceae</td>
<td>Grass/Sedge</td>
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<td>Elongate echinate long cell</td>
<td>Leaf/Culm/infor.</td>
<td>Madella et al., 2005</td>
<td>Poaceae &amp; Cyperaceae</td>
<td>Grass/Sedge</td>
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<td>Blocky w/dark infilling</td>
<td>Leaf/Culm</td>
<td>Novello et al., 2012</td>
<td>Poaceae &amp; Cyperaceae</td>
<td>Grass/Sedge</td>
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<td>Thin sheets w/ridges (TWR)</td>
<td>Culm</td>
<td>Yost et al., 2018</td>
<td>Cyperaceae</td>
<td>Sedge</td>
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<td>Ireg. w/tubular projections</td>
<td>Root/Whizome</td>
<td>Yost et al., 2018</td>
<td>Cyperaceae</td>
<td>Sedge</td>
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<td>Cone cell–psilate/rounded</td>
<td>Leaf/Culm/infor.</td>
<td>Ollendorf, 1992; Piperno, 2006</td>
<td>Cyperaceae</td>
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<td>Cone cell–verrucate/polyhedral</td>
<td>Achene (seed)</td>
<td>Ollendorf, 1992; Piperno, 2006</td>
<td>cf. Cyperus/Kyllinga</td>
<td>Sedge</td>
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<td>Perforate decorated</td>
<td>Leaf</td>
<td>da Costa et al., 2018</td>
<td>Trisichia infaria</td>
<td>Aquatic</td>
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<td>Prismatic domed cylinder</td>
<td>Seed</td>
<td>Eichhorn et al., 2010</td>
<td>Commelina spp</td>
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<td>Conical truncated</td>
<td>Seed</td>
<td>Eichhorn et al., 2010</td>
<td>cf. Murdannia /Plascomia</td>
<td>Herbaceous</td>
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<td>Pyramidal w/ridges</td>
<td>Leaf</td>
<td>Levin, 2019</td>
<td>cf. Cyclomisia spp</td>
<td>Herbaceous</td>
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<td>Benvenuto et al., 2015; Prychid et al., 2003</td>
<td>Orchidaceae</td>
<td>Herbaceous</td>
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<td>Collura and Neumann, 2017</td>
<td>Tree/Shrub</td>
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<td>Collura and Neumann, 2017</td>
<td>Tree/Shrub</td>
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<td>Tree/Shrub</td>
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<td>Leaf/Wood</td>
<td>Wallis, 2003; Scurfield et al., 1974</td>
<td>Tree/Shrub</td>
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<td>Collura and Neumann, 2017</td>
<td>Tree/Shrub</td>
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<td>Blocky w/irreg. proj.</td>
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<td>Collura and Neumann, 2017</td>
<td>Bignoniaceae</td>
<td>Tree/Shrub</td>
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<td>Globular granulate</td>
<td>Bark/Wood</td>
<td>Collura and Neumann, 2017</td>
<td>Discussed in text</td>
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<td>Bark/Wood</td>
<td>Collura and Neumann, 2017</td>
<td>Discussed in text</td>
<td>Tree/Shrub</td>
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<td>Ellipsoidal echinate</td>
<td>Bark</td>
<td>Collura and Neumann, 2017</td>
<td>cf. Boscia</td>
<td>Tree/Shrub</td>
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<td>Nodular</td>
<td>Mostly Wood</td>
<td>Collura and Neumann, 2017</td>
<td>Discussed in text</td>
<td>Tree/Shrub</td>
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<td>Granular</td>
<td>Wood</td>
<td>Collura and Neumann, 2017</td>
<td>Discussed in text</td>
<td>Tree/Shrub</td>
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<tr>
<td>Blocky cuneiform</td>
<td>Bark</td>
<td>Collura and Neumann, 2017</td>
<td>Tree/Shrub</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Globular echinate</td>
<td>Bark, Leaf</td>
<td>Benvenuto et al., 2015; Albert et al., 2009</td>
<td>Areaceae (palms)</td>
<td>Tree/Shrub</td>
<td></td>
</tr>
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<td>Facetate blocky/globular</td>
<td>Leaf</td>
<td>Kealhofer and Piperno, 1998; Piperno, 2006</td>
<td>Annonaceae</td>
<td>Tree/Shrub</td>
<td></td>
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<td>Anticinal epimedium sheet</td>
<td>Leaf</td>
<td>Piperno, 2006</td>
<td>Piperno, 2006</td>
<td>Tree/Shrub</td>
<td></td>
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</tbody>
</table>

* Because of issues with taxonomic multiplicity and redundancy, there are few to no phytolith morphotypes unequivocally diagnostic of grass subfamilies or plant functional types (PFTs). However, the dominant association of particular morphotypes with grass subfamily membership, photosynthetic pathway, and/or ecological requirements allows for the generalized taxonomic and PFT interpretations used here.

b These morphotypes were lumped into a category called ‘drought-stressed and wetland graminoids’, based in part on Issaharou-Matchi et al. (2016).

c We attempt to separate Poaceae bulliform cells from similar Cyperaceae cells by use of the morphotype ‘Blocky w/dark infilling’.

$d$ These two morphotypes were lumped together during counting but in retrospect should have been separated.
results suggested that pollen concentrations in the BTB13 samples were very low, necessitating larger than normal sample volumes. For all 108 samples, ~10 g of sediment was processed using standard methods of Faegri and Iversen (1989) and sieved at 10 μm. Lycopodium tablets were added to each sample in order to verify pollen preservation and to calculate concentrations.

3.3. Microscopy: phytolith, pollen, and microcharcoal identifications

3.3.1. Phytoliths and microcharcoal

Entire samples or subsamples were mounted on microscope slides using Permount and sealed with fingernail polish just prior to counting. Permount requires several days to dry completely, allowing in the meantime for phytolith rotation, which is essential for many phytolith identifications. Phytolith and microcharcoal counting was conducted using an Olympus BX-43 transmitted-light microscope at 400× magnification, with a goal of 200 index-specific phytoliths counted (Strömberg, 2009).

The phytolith classification used 60 phytolith morphotypes. The primary descriptive reference(s), anatomical origin, and taxonomical interpretation for each morphotype are listed in Table 1. Morphotype names used were either derived from the International Code for Phytolith Nomenclature (ICPN 1.0; Madella et al., 2005) or from the primary references used to identify them. This classification includes the use of the bilobate and cross supertypes suggested by Neumann et al. (2017). Microcharcoal was identified (absolute counts) using the diagnostic characteristics described by Turner et al. (2008), with particular emphasis on avoiding misidentifications from pyrite and unburned plant fragments that may have darkened naturally over time.

3.3.2. Pollen

Pollen residues were mounted onto slides in glycerol and sealed with fingernail polish. Because of low pollen yields, two slides were made for each sample and completely scanned using transmitted-light microscopy at 400× magnification to verify the presence of identifiable pollen, algae, and other non-pollen palynomorphs. Samples with no pollen present were marked as “sterile”, and no further analysis was conducted. For samples with at least one identifiable pollen grain, five further slides were mounted, and pollen was identified using atlases of pollen morphology and the African Pollen Database (e.g., Maley, 1970; Bonnefille and Rioult, 1980). No samples yielded more than 12 pollen grains. Low pollen concentrations require that the data presented here be considered qualitative and not completely or robustly representative of the ancient flora, and that the absence of a pollen type does not necessarily indicate its absence on the landscape. The pollen analysis resulted in the identification of 14 pollen taxa plus fern spores and green algae. The nomenclature for these follows Vincens et al. (2007).

3.4. Phytolith abundance and index calculations

Percent relative-abundance calculations were based on the total phytolith count for each sample. Concentrations were calculated from the microsphere counts and starting volume of the sample (SOM Table S1). Influx values reported as particles per cm² per year were based on calculated concentrations and sedimentation rates determined from the age model. The relative abundance plot of C₃, C₄ mesic, and C₄ xeric grass phytoliths was based solely on grass silica short-cell (GSSC) phytoliths attributed to those plant functional types (Table 1). The tree cover (D/P°) and aridity (Iph) phytolith indices were calculated as described in Bremond et al. (2008) and Yost et al. (2018) using the specific morphotypes listed in Table 1. The 95% confidence intervals (CI) for the D/P° and Iph indices were determined by nonparametric bootstrap resampling using the ‘boot’ and ‘simpleboot’ packages in R (R Core Team, 2018). The R bootstrapping and error propagation code written to run on lists of D/P° and Iph values is provided in the SOM. The Ic₃ index used here is a variant of the Ic climatic index described in Bremond et al. (2008). We calculate the Ic₃ index by including all GSSC morphotypes ascribed as being derived from a C₃ or C₄ grass in Table 1, which then becomes (C₃ / C₃ + C₄) × 100.

3.5. Statistical and time series analyses

Detrended canonical correspondence analysis (DCCA) was conducted on the counts of specific phytolith morphotypes using CANOCO ver. 4.55 (ter Braak, 1986). Only the morphotypes ascribed to a particular taxonomic level (Table 1) were included in the analysis. Grass morphotypes that could not be identified lower than family level (Poaceae) were not included. All cross and bilobate types were summed into one category (Panicoideae), as were all woody dicot morphotypes (trees), excluding palms. DCCA applied to stratigraphic plant data with age as the only constraint (temporal gradient) yields an estimate of adjacent sample plant taxa compositional turnover in units of standard deviation (Birks, 2007).

Time series (spectral) analysis was conducted using PAST ver. 3.2 (Hammer et al., 2001). Lomb periodograms were produced using the REDITFIT procedure with a rectangular window function, and confidence intervals were determined using 1000 Monte Carlo simulations (Schulz and Mudelsee, 2002). Spectral analysis was applied to the entire microcharcoal concentration record, and to D/P° and Iph index values from three intervals with good preservation. The microcharcoal concentration data was log transformed (because of non-Gaussian high amplitude variability), detrended, and linearly interpolated to 1200 yr time steps prior to analysis. The D/P° and Iph data were detrended and linearly interpolated to 1500 and 1100 yr time steps, respectively, prior to analysis.

3.6. Compilation of relevant modern phytolith assemblages from Africa

A total of 168 samples (SOM Table S2) were selected from 10 published modern phytolith datasets compiled from eastern and western Africa (Alexandre et al., 1997; Barboni et al., 1999; Runge, 1999; Bremond et al., 2005a; Bremond et al., 2005b; Bremond et al., 2008; Garnier et al., 2012; Novello et al., 2012; Arráz et al., 2017; Barboni et al., 2019) to assess the relationship between D/P° values and tree cover, and the relative abundances of palm (Arecaceae), woody dicotyledonous (trees), and GSSC (grass; Poaceae) phytoliths (A:D:P) with vegetation formation in the form of a ternary plot. To accomplish this, each modern D/P° and A:D:P sample was assigned to a basic vegetation formation type and woody canopy cover based on White (1983) as follows: swamp (open), shrubland (open), bushland (> 40% short woody cover) grassland (0–10% tree cover), wooded grassland (10–40%) tree cover), woodland (40–80% tree cover), forest (80–100% tree cover).

4. Results

4.1. Phytolith and microcharcoal recovery

Phytolith preservation and recovery in BTB13 varied from excellent to poor, with some intervals yielding no phytoliths, ostensibly the result of total dissolution of biogenic silica (Figs. 2 and 3; Table 2). When progressing from older to younger sediments (core bottom to top), a repeated dissolution succession was observed over 19 times. As sediment pore water salinity and pH increased, as inferred by increasing fragmentation and depth and width of dissolution pits, diatoms and sedge cone cell phytoliths were the first microfossils to disappear, followed by small phytoliths (e.g., GSSCs), then, elongate, trichome, and bulliform phytoliths, followed by sponge spicules. Finally, sponge spherasters were the last microfossils observed in the dissolution successsion. Diatom, phytolith, and sponge microfossils would often reappear in the opposite order as pH apparently trended towards neutral values.
Intervals with either generally good or poor phytolith preservation delineated the five zones identified in Fig. 3. Of the 652 phytolith samples analyzed, 161 (25%) yielded no phytoliths. Additionally, 311 samples (48%) did yield few to many phytoliths, but low to no GSSC phytolith recovery precluded the calculation of D/P°, Ic3, and Iph indices, and A:D:P on those samples. However, 180 samples (27%) scattered throughout the core yielded well-preserved phytoliths with no evidence of morphotype assemblage bias. Because of significant differences in phytolith preservation and vegetation composition, the following sections often highlight pre- and post-3.04 Ma values.

A total of 50,520 phytoliths were counted from BTB13 material, with the number per sample ranging from 0 to 1866. Phytolith concentrations by volume varied between 0 and 6.728 × 10⁶ per cm³ (Fig. 3). Phytolith influx varied between 0 and 1.2 × 10⁵ per cm² yr⁻¹ (SOM Table S1). Average phytolith concentration and influx before 3.04 Ma was 93 per cm³ and 6.8 per cm² yr⁻¹, respectively. Low phytolith concentration values early in the record for the well-preserved samples were associated with coarse-grained alluvial and fluvial sediments (Scott et al., 2020). Good phytolith preservation before 3.04 Ma typically coincided with insolation minima and extended periods of dampened insolation maxima. High-amplitude peaks in phytolith concentrations and well-preserved intervals after 3.04 Ma are typically coincident with insolation maxima.

Microcharcoal was recovered in all samples. Microcharcoal concentrations varied between 30 and 1.556 × 10⁶ per cm³ (Fig. 3J) and influx varied between 1 and 7.6 × 10⁴ per cm² yr⁻¹ (SOM Table S1). Average microcharcoal concentrations before and after 3.04 Ma were 35,732 and 6487 per cm³, decreasing by a factor of 5 after 3.04 Ma. Influx values decreased 10-fold after 3.04 Ma. Phytoliths darkened from exposure to fire were rare and their occurrence was not included in the analysis.

Phytoliths from woody dicots (trees), Arecaceae (palms), Cyperaceae (sedges), C₃ Pooideae grasses, and dayflower (Commelina spp.) (Figs. 3 and 4) are most abundant from the bottom of the core at ~3.29 Ma to 3.04 Ma. Phytoliths diagnostic of riverweed (Tristicha trifaria, Podostemaceae), an aquatic plant that only grows on rocks in rapids and waterfalls at low and high elevations (Agnew, 2013; Koi et al., 2015), appears in the record only after 3.04 Ma. Peaks in riverweed abundance are coincident with insolation maxima. Phytoliths from bamboo (Bambusoideae) and orchids (Orchidaceae), which are typically montane vegetation indicators (Agnew, 2013), are most abundant after 2.59 Ma. Possible fern phytoliths (cf. Cyclosorus sp.) and Murdannia/Floscopa-type phytoliths, indicators of freshwater swamps (Lind and Morrison, 1974), are almost exclusively observed after 2.59 Ma.

When just comparing the relative abundances of C₃, C₄ mesic, and C₄ xeric GSSC phytoliths, average C₄ xeric grass values before and after 3.04 Ma are 38% and 25%. For C₃ grasses, the before and after 3.04 Ma averages are 12% (max 50%) and 8% (max 35%), respectively.
Paradoxically, arid-adapted C4 grasses and mesic/cool/shade-adapted C3 grasses were both more abundant before 3.04 Ma. This insolation-phytolith preservation relationship is discussed in detail in Section 6.1.1.

4.2. Other siliceous microfossils recovered

Diatoms, chrysophyte stomatocysts, sponge spicules, and sponge spherasters were also recovered with the phytolith extracts (Figs. 2, 3, H, and 5). Because BTB13 diatoms were studied in detail by Westover et al. (2020), only diatom presence and absence was recorded. Freshwater siliceous sponge spicules and spherasters were counted, and at times
found to be very abundant. Sponge spicule concentrations varied between 0 and $5.24 \times 10^5$ ($\approx 6.4 \times 10^5$) per cm$^3$. Very distinctive sponge asterose microscleres (Fig. 5.7), consistent with those produced by the freshwater sponge *Dosilia brownii* (Manconi and Pronzato, 2009), were observed at 131.58 mbs (3.04 Ma) and 160.77 mbs (3.12 Ma), along with *Dosilia*-like microscleres and gemmuloscleres. Concentration values for sponge spherasters, which have a striking similarity to palm (Arecaceae) phytoliths, varied between 0 and 1.13 $\times 10^5$ per cm$^3$ ($\approx 1.3 \times 10^3$).

### 4.3. Pollen recovery

Pollen recovery was poor throughout the record. Of the 108 samples processed for this study, 80 yielded no identifiable pollen and were considered sterile. The remaining 28 samples contained at least one grain of identified pollen (Fig. 3G, Table 2), however, all concentrations were extremely low (the highest concentration was < 1 grain per g dry sediment). Subaerial exposure and/or high-oxygen pore waters (oxidation) may have severely degraded the pollen record.

#### 4.4. Compilation of modern D/P° tree cover index values

Boxplots of the selected 168 modern D/P° values are presented in Fig. 6. From lowest to highest, the mean D/P° values are as follows: shrubland, 0.08 ($n = 27, \sigma = 0.10$); grassland, 0.12 ($n = 15, \sigma = 0.13$); wooded grassland, 0.21 ($n = 43, \sigma = 0.27$); swamp, 0.21 ($n = 10, \sigma = 0.21$); bushland, 0.43 ($n = 5, \sigma = 0.30$); woodland, 1.31 ($n = 29, \sigma = 0.40$); and forest, 8.51 ($n = 39, \sigma = 4.11$).

The D/P° index could not distinguish vegetation types with < 40% tree cover. However, a D/P° value of 1 separates all but three woodland samples with > 40% tree cover, one of which is nearly 2 $\sigma$ from the mean, and all of which are located near the edge of a present-day

### Table 2

List of plants identified from BTB13 sediment pollen and phytoliths.

<table>
<thead>
<tr>
<th>Plant group</th>
<th>Family</th>
<th>Subfamily/Tribe</th>
<th>Genus/Species</th>
<th>Indicator</th>
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<tbody>
<tr>
<td>Dicotyledons (Ligneous trees and shrubs):</td>
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<td>Araceae</td>
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<td>Arecaceae</td>
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<td>Commelinaceae</td>
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<td>Lamiaceae</td>
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<td>Orchidaceae</td>
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<td>Poaceae</td>
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<td>Salicaceae</td>
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<td>Urticaceae</td>
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<tr>
<td>Vochysiaceae</td>
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</table>

### Notes

* Dry lowland indicator.
* Montane indicator.
* Afromontane indicator.
woodland patch. The D/P° value of 2.2 clearly separates woodland (40–80% tree cover) from forest (> 80% cover), and is similar to the D/P° value of 2.0 used by Novello et al. (2017) to distinguish forests from more open savanna habitats. These results are discussed in the SOM.

4.5. Comparison of modern and BTB13 core sample A:D:P

A ternary plot for the percentages of palm (Arecaceae), tree (dicotyledonous/ligneous), and grass short cell (GSSC; Poaceae) phytolith indicators (A:D:P) is plotted in Fig. 7. This plot also includes 180 samples from BTB13. No samples from the core plot within forest or woodland after 3.02 Ma. Among the 17 samples that plot within woodland or forest zones, one plots within semi-evergreen forest, four plot near modern miombo woodlands, two plot near a cluster of modern riparian floodplains, and two plot near palm woodlands. Seven forest samples with 30 to 60% palm phytoliths plot between a palm (swamp) forest sample and a cluster of drier semi-evergreen forest samples. These results suggest most of the BTB13 woodland and forest samples are groundwater-supported vegetation types that may denote swamp, lake margin, or floodplain (riverine) habitats.

4.6. BTB13 core D/P°, Iph, Ic3, and plant turnover indices

4.6.1. D/P° index

The index-specific count size for D/P° ranged from 8 to 233 phytoliths (σ = 82). Calculated D/P° values range from 0 to 22, and span open (grassland, wooded grassland, woodland) to closed (forest) vegetation formations (Fig. 8A). However, because of low index-specific count sizes, the bootstrapped 95% CI range varied from 69 to 300% (σ = 163%) of the D/P° value. In many cases, except for those with high D/P° values, the large CIs did not cross a vegetation formation D/P° boundary, and a long-term trend of decreasing woody cover is evident. All but one D/P° value indicating formations of > 40% woody cover occur before 3.10 Ma, and none are observed after 3.02 Ma. Although many of the samples with high D/P° values are from intervals with low phytolith counts, these samples did not exhibit evidence of dissolution.

4.6.2. Iph (short-grass vs. tall-grass) index

The index-specific count size for Iph ranged from 4 to 233 phytoliths (σ = 82). Calculated Iph values range from 0 to 89%, spanning the short-grass/tall-grass dominance spectrum (Fig. 8B). The bootstrapped 95% CI

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Fig. 5. Selected freshwater sponge and chrysophyte cyst microremains, and non-phytolith evaporites and zeolites recovered from the Baringo-Tugen Hills-BarAIemi (BTB13) drill core (white scale bar equals 10 μm). (1–2) Sponge megascle oxeas. (3–5) Sponge megascle acanthoxeas (6) Sponge megascle strongyle. (7) Sponge asterose microscle possibly derived from Dosila. (8) sponge gemmuloscle rotule. (9–12) Sponge megascle birotules, with the birotule in 12 exhibiting minor diagenesis (dissolution). (13–15) Sponge megascle birotules exhibiting varying types of diagenesis. The birotule in 13 is exhibiting submicron pitting from silica dissolution. The birotules in 14 and 15 are exhibiting devitrification and re-precipitation of silica, with deformation of the axial filament clearly visible. (16–21) Sponge spherasters with arrows pointing to circular openings that range from indistinct to obvious. Spheraster echinate spines become blunted and the circular openings become enlarged as diagenesis progresses. Rotation (3D observation) of globular echinates is essential in separating palm (Arecaceae) phytoliths (see Fig. 4) from sponge spherasters. (22–25) Siliceous stomatocysts from chrysophycean algae. (26) Globular/hemispherical facetate zeolite (cf. analcime). (27–28) Conical zeolites disarticulated in 27 and as a rosette in 28. (29, 31) Thin hexagonal crystalline plates most likely formed as authigenic precipitates or as evaporites. (30, 32) Authigenic precipitate or evaporite resembling a bilobate phytolith morphotype.
range varied from 24 to 300% of the Iph value ($\bar{x} = 102\%$), in agreement with Iph sample size errors identified by Strömberg (2009).

4.6.3. Ic3 (C3 grass) index

The index-specific count size for Ic3 ranged from 4 to 229 ($\bar{x} = 78$). Calculated Ic3 values range from 0 to 42% (Fig. 8C). Average Ic3 values before and after 3.04 Ma are 11% and 6%, respectively. The five highest values ($\bar{x} = 34\%$) occur before 2.98 Ma; however, there is no relationship between D/P° and Ic3 values ($r^2 = 0.0008$, $n = 123$, $p = .758$), suggesting that C3 grass occurrence is neither promoted or suppressed the presence of woody plants.

4.6.4. Plant compositional turnover

The DCCA-derived measure of plant taxa compositional turnover in units of standard deviation is highest during the mid-Piacenzian Warm Period (MPWP, 3.26–3.01 Ma), with adjacent samples varying by an average of 1 $\sigma$. After 3.04 Ma the adjacent sample variability was 0.47 $\sigma$ (Fig. 8D).

4.7. Spectral analysis of Iph and D/P° indices, and microcharcoal concentrations

Results of the REDFIT spectral analyses of D/P° (grass vs. tree cover) and Iph (xeric C$_4$ short-grass vs. mesic C$_4$ tall-grass) for three time intervals are provided in Fig. 9. D/P° index variability exhibits precessional periodicity before 2.98 Ma. Iph index variability exhibits precessional periodicity only after 2.98 Ma. Half-precession and quarter-precession periodicities are detected somewhat sporadically between the different indices and time intervals. For the oldest time interval, preservation of contiguous samples spanning the transition from short-grass to tall-grass dominance were limited because phytoliths were mostly preserved only during insolation minima.

Results of the microcharcoal concentration spectral analysis are provided in Fig. 10. There is spectral power well above the 95% confidence level at periodicities of 237, 9.6, and 4.6 kyr (Fig. 10A). Power spectral density of the Lomb periodogram reveals a power dependence on frequency that resembles a 1/$f$ pink noise system (Fig. 10B). The 9.6 and 4.6 kyr periodicities correspond with half precession and quarter precession, respectively. There is no precessional (23–19 kyr) periodicity detected, but precession is likely the carrier of the half-precession signal that arises from the double-peak in charcoal concentrations often associated with peaks in insolation (Fig. 10B). Peaks in mesic C$_4$ tall-grass abundance vary at precessional periodicity (Fig. 9) and are correlated with peaks in insolation (Fig. 10C).

5. Discussion

5.1. Biogenic silica diagenesis in BTB13

5.1.1. Biogenic silica dissolution succession

To our knowledge, the biogenic silica (BSi) dissolution succession presented in Section 4.1 and illustrated in Fig. 11 has never been previously described for lake sediments. High salinity and pH in sediment pore water are the ostensible cause of poor BSi preservation. These conditions are inferred from the presence/absence of authigenic calcite and zeolites in the XRD analysis of the core (Minkara et al., 2020), many of which commonly form in saline waters at pH $\geq 8.5$ (Renaut, 1993; Renaut et al., 2002). Zeolites were sometimes in the phytolith extracts themselves, especially when BSi fossils were completely absent (Fig. 3F). Additionally, sponge spherasters, the last BSi microfossils observed in a dissolution succession, sometimes co-occurred with analcime or phillipsite, which typically form in waters with pH $\geq 9.0$ (Mariner and Surdam, 1970; Hay, 1986). This reflects the fact that phillipsite, clinoptilolite-heulandite, chabazite, and analcime, the most common zeolites detected in BTB13, have specific gravities that overlap with BSi microfossils.

This BSi dissolution/preservation sequence is not surprising given that differences in size, reactive surface area, and density between diatoms, phytoliths, and freshwater sponges lead to varying dissolution rates under conditions of increasing salinity and pH (Iler, 1979; Bartoli and Wilding, 1980; Barker et al., 1994; Van Cappellen et al., 2002; Fraysse et al., 2009). In a controlled, 6-week-long partial dissolution study, Cabanes and Shahack-Gross (2015) found that small morphotypes such as rondels and bilobates (GSSC3), and large bulliforms were
more resistant to dissolution than many other morphotypes. However, when just looking at GSSCs and bulliform phytoliths from their study, the absolute abundance of bilobates from the grass *Oryza sativa* was reduced ~55% after partial dissolution, while bulliform abundance was unchanged within the margins of error. Thus, when exposed to high pH water over a long period of time, bulliform phytoliths may still be recognizable, but severely eroded, whereas GSSC and globular arboreal phytoliths may have dissolved to unrecognizable forms because of their relatively small volume. Our observations agree with the Cabanes and Shahack-Gross (2015) conclusion that under conditions of partial dissolution, bulliforms may be overrepresented. However, Novello et al. (2012) showed that surface soil samples in a swamp dominated by reeds (*Typha*) and grasses (*Vossia, Phragmites*) produced a phytolith assemblage with <1% GSSCs, and 99% bulliform, elongates, and trichomes. Thus, the absence or rarity of GSSC phytoliths is not always an indicator of dissolution, especially if bulliforms are well preserved.

### 5.1.2. Biogenic silica replacement/re-precipitation

A type of biogenic silica replacement and/or re-precipitation has also been observed in BTB13 sediments where the opal silica matrix is partially or fully replaced and voids are infilled by crystalline material (Figs. 11 and 5.14–5.15). This replacement process is consistent with diatom frustule aluminosilicate replacement observed in near-shore marine deltaic anoxic muds (Michalopoulos et al., 2000; Michalopoulos and Aller, 2004; Derkowski et al., 2015) and saline-alkaline Bolivian lakes from the Altiplano (Badaut and Risacher, 1983). Arráziz et al. (2017) observed the growth of zeolites on phytoliths from early Pleistocene sediments at Olduvai Gorge, Tanzania. In a controlled dissolution study by Prentice and Webb (2016), evidence for re-precipitation of silica on phytolith surfaces was observed when silica saturation was above 30–40%. Sediment pore water silica saturation in combination with alkaline (high pH) conditions may play a role in the replacement/re-precipitation alteration of biogenic silica observed in BTB13, as was observed in lakes from the South American Altiplano (Badaut and Risacher, 1983).

### 5.2. Sponge spherasters and the potential for phytolith misidentifications

Sponges are notable in their ability to tolerate conditions above pH 8, as many African taxa inhabit lakes in the pH 8 to 9 range (Manconi and Pronzato, 2009). *Dosilia brouni* was collected in 1979 from Lake Baringo when it had a measured salinity of 0.5% and a pH of 8.4 (Vacelet et al., 1991), indicating its tolerance of saline and basic conditions. The possible recovery of *Dosilia brouni* in BTB13 may...
suggest a prior hydrologic connection to its type locality in the Nile River system (Vacelet et al., 1991; Stewart, 2009), or simply a wider distribution for this taxon in the past. In BTB13, sponge concentrations peaked as lakes were either transgressing from highly evaporative (high alkalinity/pH) states or regressing from higher lake level (low alkalinity/pH) states (Fig. 3H).

When pH was interpreted as increasing in the BTB13 core, sponge spherasters were often the last BSi fossils to remain. Spherasters, a type of sponge microsclere (Boury-Esnault and Rützler, 1997), are produced by some, but not all freshwater and marine sponges (e.g., Łukowiak et al., 2013; Łukowiak, 2016), and have been observed in modern lake sediments from temperate North America (Yost et al., 2013). For Africa, spherasters have been described for the tropical and equatorial taxa Corvospongilla boehmii, and C. micramphidiscoides (Manconi and Pronzato, 2009).

Spherasters are strikingly similar to globular echinate phytoliths produced by palms (Arecales); however, they have a sub-micron pore-like opening that is usually visible on the centrum or a spine (Fig. 5). As dissolution progresses, the diameter of the opening increases and the echinate projections become diminished (Fig. 11). Under conditions of silica replacement or re-precipitation, the opening can fill in. As diagenesis proceeds, the spheraster may come to resemble a globular phytolith morphotype associated with woody plants. The main implication is that globular echinates must be fully rotated to rule out the presence of a pore-like opening before being interpreted as a palm phytolith. To our knowledge, and with the exception of Yost et al. (2013, 2018), sponge spherasters have not been reported in published phytolith paleoecological studies, raising a concern that palms may have been misidentified in some of those studies.
5.3. Recognition of biased phytolith assemblages

Of the 652 phytolith samples analyzed, 48% exhibited evidence of moderate to severe dissolution and probable morphotype preservation bias. To avoid skewed and misleading results, D/P°, Iph, and Ic3 phytolith indices were not calculated from potentially biased samples (Figs. 2 and 3). For example, given the diagenetic transformation of sponge spherasters and palm globular echinate phytoliths to appear as globular granulate tree phytoliths, tree cover calculations could have been grossly overestimated in the biased samples.

5.4. Phytoliths identify ecologically diagnostic plants

5.4.1. Dayflower (Commelina spp.)

At least two species of Commelina (dayflower) were identified from the phytolith record (Table 2; Figs. 3D and 4). Commelina spp. are a common agricultural weed in Africa (Eichhorn et al., 2010), but are also an important component of undisturbed plant communities. Over 23 species are listed for the highlands of Kenya, with seven occurring in Baringo County (Agnew, 2013). Although some species in Kenya occur in dry grasslands, most are associated with wet soils in grasslands, woodlands, and forests. The highest abundances of Commelina phytoliths, and in particular C. diffusa-type phytoliths, occurred before 3.10 Ma (Fig. 3D). C. diffusa is found today at the edges of swamps, riverbanks, and wet forests (Agnew, 2013). Commelina is eaten by African primates, including lowland gorillas, monkeys, and chimpanzees (Mitani et al., 1993; Huffman et al., 1997; Isbell, 1998).

5.4.2. Riverweed (Tristicha trifaria, Podostemaceae)

Because riverweeds have an extremely narrow habitat niche, their phytoliths are an indicator of stream flow gradients and precipitation change. Riverweeds (Podostemaceae) are a family of aquatic plants restricted to flat rocks in rapids and waterfalls, especially on the rims, where they are seasonally submerged by oligotrophic waters and exposed during dry seasons (Müller et al., 2003; Koi et al., 2015). There are three Podostemaceae genera in Kenya, each with only one species. The Podostemaceae phytoliths recovered here are a good match with Tristicha trifaria (da Costa et al., 2018) (Fig. 4), which occurs today in Baringo County above 1300 m elevation (Agnew, 2013). For the other two Kenyan genera, Ledermanniella does not produce phytoliths (Ameke et al., 2003), and production in Sphaerothylax is unknown.

Riverweeds only appear in the BTB13 record after 3.04 Ma.
indicating either an increase in seasonal precipitation or a change in basin morphology and sediment sourcing. It should be noted that there is a BSI dissolution zone between ~3.10 and 3.04 Ma, so if riverweeds were on the landscape during that time, their phytoliths would not have been preserved. Prior to ~3.10 Ma, sediments may have been delivered by low gradient rivers. After ~3.10 Ma, reconfiguration of the hydrology could have resulted in sediment delivery from higher elevation source areas. Peaks in riverweed abundance are coincident with insolation peaks, indicating enhanced monsoon precipitation during insolation maxima.

(Fig. 3C), indicating either an increase in seasonal precipitation or a change in basin morphology and sediment sourcing. It should be noted that there is a BSI dissolution zone between ~3.10 and 3.04 Ma, so if riverweeds were on the landscape during that time, their phytoliths would not have been preserved. Prior to ~3.10 Ma, sediments may have been delivered by low gradient rivers. After ~3.10 Ma, reconfiguration of the hydrology could have resulted in sediment delivery from higher elevation source areas. Peaks in riverweed abundance are coincident with insolation peaks, indicating enhanced monsoon precipitation and inflow to the basin during insolation maxima (Prell and Kutzbach, 1987; Tuenter et al., 2003; Kutzbach et al., 2020).
6. Paleoenvironmental reconstructions

The combined pollen, phytolith, and microcharcoal datasets are used here to reconstruct the vegetation and fire history of the paleolake Baringo catchment from 3.29 to 2.58 Ma (Fig. 12). Discussion is organized by the phytolith preservation zones depicted in Fig. 3.

6.1. Zone 1: 3.29 to 3.10 Ma

Zone 1 represents the bottom of the core at 3.29 Ma (~228 mbs) to 3.10 Ma (~152 mbs). This interval captures the last half of the marine isotope stage (MIS) M2 global cooling event (~3.31–3.26 Ma; De Schepper et al., 2014), which caused cooler and wetter conditions in eastern Africa (Bonnefille et al., 2004; Dolan et al., 2015; Tan et al., 2017), and the first two-thirds of the MPWP (3.26–3.01 Ma), when global surface temperatures were 3° to 4 °C warmer than modern,
atmospheric pCO₂ was similar to modern values, and models and palaeodata indicate tropical savannas, woodlands, and forests expanded in Africa, at the expense of drier biomes (Salzmann et al., 2008; Haywood et al., 2016). The MPWP is often used as an analog for future global warming (Salzmann et al., 2009; Salzmann et al., 2011).

The pollen and phytolith records in the BTB13 core both indicate that woodlands and forests were more widespread compared to later in the record, particularly during the MPWP. This finding supports reconstructions based on vegetation models and palaeodata referenced above, and the BTB13 leaf wax isotopic record (Lupien et al., 2020). Pollen presence/absence data recorded the occurrence of typically high elevation afromontane trees (particularly Podocarpus), mid-elevation montane forests, and dry lowland forests in close temporal proximity. Although the presence of tree taxa that occur today in the higher elevations under cooler temperatures could be interpreted as representing the existence of montane forests near the lake during this time, recent work has shown that many montane species’ ranges are more constrained by moisture than by cooler temperatures (Ivory et al., 2016; Ivory et al., 2018). In either case, this suggests the existence of heterogeneous but largely arboreal mesic to seasonally dry vegetation during these times.

The phytolith record, which is a more localized proxy than pollen, indicates oscillations between open savanna (<40% woody cover), woodland (40–80% cover) and forest (80–100% woody cover) formations (Figs. 8 and 12). Peaks in microcharcoal concentrations are antiphased with the woodland and forest occurrences. The highest levels of plant taxa compositional turnover for BTB13 was observed in Zone 1. Arid short-grass savanna and woodlands prevailed during MIS M2, and fire frequency was at its highest levels observed for the core, particularly during the transition from MIS M2 to the MPWP, when microcharcoal concentrations were 14 × the BTB13 average. Extremely large microcharcoal peaks (truncated in Figs. 8 and 12), may point to catastrophic stand-replacing fires within the watershed. This data supports phylogenetic evidence that the late Pliocene was a peak period for the evolution of fire-adapted woody clades in Africa (Bond, 2015).

Forests with >80% woody cover appear in the phytolith record during the MPWP, but were relatively short lived (~10 kyr), and often transition to or from woodlands or savanna within 0.5 to 1 kyr. Many of the woodland and forest phytolith assemblages have a significant proportion of palm phytoliths, and comparisons to modern samples (Fig. 7) suggest these may primarily be groundwater-supported riparian settings. It is possible that the relatively rapid transitions between these vegetation types were caused by riverine corridor migration at or near the BTB13 drill site.

6.1.1. Mesic C₃–xeric C₄ hydroclimate paradox

Trees (including palms), C₃ grasses, and sedges, sometimes occurring in very high percentages and generally indicative of more mesic conditions, are most prevalent within Zone 1; yet at the same time, xeric C₄ grass dominance occurs more often than mesic C₄ grass dominance (Figs. 8 and 12). This could signal that C₃ trees and C₃ grasses were maintained by groundwater along a riverine corridor, or that the short-grass/tall-grass dynamic was decoupled from climate, as can happen when grazing laws are created under high herbivore pressure (McNaughton, 1983). However, comparison of phytolith preservation zones to the summer insolation curve shows that before ~3.10 Ma, phytoliths were best preserved at insolation minima and during periods with low amplitude insolation maxima; after ~3.10 Ma they were best preserved during insolation maxima (Fig. 3).

Based on the absence of deep lake phases and the prevalence of shallow lacustrine, floodplain, wetland (gleyed soils), and deltaic deposits before ~3.10 Ma (Scott et al., 2020; Westover et al., 2020), a conceptual phytolith preservation model is depicted in Fig. 13. Before ~3.10 Ma, enhanced precipitation during insolation maxima raises the elevation of high pH lake water above that of the drill site, resulting poor to no phytolith preservation. Because of the more proximal position of the drill site within a relatively shallow basin, reduced precipitation during insolation minima (and dampened insolation maxima) reduces the elevation of high pH lake water below that of the drill site, resulting in exposure to only relatively less saline/alkaline shallow groundwater and surface seeps, springs, and streams, and thus much better phytolith preservation. Similar scenarios of high pH lake water being drawn down during periods of low precipitation, exposing freshwater features and habitats has been documented on orbital time scales for the Bonneville Basin in Utah (Balch et al., 2005) and the Olduvai Basin in Tanzania (Ashley et al., 2009). Some of the well-preserved phytolith extracts within this zone included phillipsite crystals in the extractions that were either inherited from the substrate or transported to the drill site from adjacent areas.

For the conceptual model after ~3.10 Ma (Fig. 13), accommodation in the basin increased, allowing for deeper lakes during periods of high insolation and enhanced precipitation. The presence of riverweed (Poacetesmaceae) starting at 3.04 Ma (Fig. 3C) is evidence that steep gradient streams and rivers were established and delivering oligotrophic water into the basin. This would have diluted alkaline (high pH) lake water formerly present during periods of high insolation, allowing for good phytolith preservation. Phytoliths recovered during peak insolation after 3.10 Ma were typically well-preserved, suggesting neutral or even slightly acidic lake water pH. During periods of reduced precipitation (insolation minima and dampened insolation maxima), lake water increased in salinity and alkalinity/pH, as evidenced by the precipitation of sodic zeolites (Fig. 3F), but lake levels were not low enough to expose sediments to fresh groundwater or meteoric water, precluding phytolith preservation.

The phytolith preservation model depicted in Fig. 13 implies that prior to 3.10 Ma, phytoliths would be recording vegetation primarily during periods of decreased precipitation, and after 3.10 Ma, they would be recording vegetation primarily during periods of increased precipitation. This is in fact what we see in the grass phytolith record (Fig. 12G). However, there is a short interval centered around 3.20 Ma (204–190 mbs) when phytoliths were preserved during two probable humid periods consisting of two insolation maxima, one high- and one low-amplitude (Fig. 14). As observed elsewhere in the core, xeric C₄ grasses are dominant during insolation minima and dampened insolation maxima, and mesic C₃ grasses are dominant during prominent insolation maxima.

6.2. Zone 2: 3.10 to 3.04 Ma

Zone 2 spans from 3.10 Ma (~152 mbs) to 3.04 Ma (~132 mbs), encompassing the MIS K1 interglacial. Poor phytolith preservation, resulting in biased and sometimes no phytolith recovery, precluded vegetation reconstructions. There is a peak in phytolith concentrations coincident with a peak insolation at 3.08 Ma; however, pore water conditions were apparently still too basic for smaller phytoliths to be preserved. High microcharcoal concentrations and influx at the beginning of K1 followed by very low values for the remainder of K1 and through G21 suggests that catastrophic fires followed by drought may have drastically reduced woody vegetation on the landscape. Climate model simulations indicate that K1 was a much warmer event than KM5c in Africa (Prescott et al., 2014).

6.3. Zone 3: 3.04 to 2.91 Ma

Zone 3 spans 3.04 Ma (~132 mbs) to 2.91 Ma (~100 mbs) and occurs during the last half of a 300 kyr interval with high eccentricity. The highest 30°N to 30°S summer insolation gradient value for BTB13 (284 W/m²) occurred at 3.037 Ma (Fig. 3F; see SOM Fig. S1), which coincides with well-preserved phytolith samples and the deposition of the oldest of the thick Barsemoi outcrop diatomites, “D0”, identified by Deino et al. (2006) and recently described as Diatomite Interval 1 by Westover et al. (2020).
Another peak in the 30° N to 30° S summer insolation gradient occurs between 2.993 and 2.981 Ma (117.13–114.66 mbs), where the highest phytolith concentrations for the core were observed (mean for interval = 1.4 × 10^6 per cm^3, maximum = 6.8 × 10^6). In fact, for a few samples between ~117–116 mbs, phytoliths comprised ~30% of smear slide particles (unprocessed lake sediments smeared on microscope slides). This suggests the presence of a near-shore, emergent aquatic vegetation habitat with near-neutral pH water for a portion of this ~1 m interval, which impeded siliciclastic sediment dilution, and from which most of the original organic matter decayed, leaving a phytolith concentrate. Modern sediments with similar high phytolith abundances have been observed from the Ngoitokitok wetland, Ngorongoro Basin, Tanzania (Deocampo and Ashley, 1999).

This zone contains a third interval with good phytolith preservation and high phytolith concentrations that also coincides with a peak in the 30° N to 30° S summer insolation gradient at ~2.92 Ma. However, there is a very prominent insolation gradient peak at ~2.94 Ma that does not correspond with a zone of good phytolith preservation. This is the same region of BTB13 where Deino et al. (2020) suggest that there may be a ~40 kyr depositional hiatus. Thus, sediments associated with the insolation gradient peak at ~2.94 may not have been recovered, or the phytolith concentration peak at 2.92 Ma may actually be associated with the 2.94 Ma insolation gradient peak.

Other than the brief appearance of woodland vegetation at 3.03 Ma, vegetation during this zone had transitioned to savanna and was unlikely to have had more than 40% tree cover. Phytoliths diagnostic of woody taxa generally decrease over time across the zone. Very high percentages of bulliform grass phytoliths, as well as riparian indicators suggest the presence of a swamp at or near to the drill site (Fig. 12). No tree pollen was observed, but one sample yielded grass pollen (Fig. 3).

For the upland grass community, short-grass/tall-grass dynamics appear to be mediated by insolation, whereby mesic C4 tall-grasses become dominant during periods of high summer insolation in response to increased (presumably monsoonal) precipitation. Iph values ≤27.8% may indicate MAP in excess of 750 mm (Fig. 8). Riverweed (Tristicha trifaria, Podostemaceae) appeared for the first time in the BTB13 record in Zone 3, and its abundance also appears to peak during insolation maxima (Fig. 3C). This suggests that either basin morphology changed towards steeper gradients, allowing for more rapidly flowing oligotrophic waters over rocky substrates to enter into the basin, or there was simply more precipitation that allowed for spillover of oligotrophic waters from higher elevations.
Microcharcoal concentrations tend to peak ~5 kyr before and after peaks in insolation, similar to what is depicted in Fig. 10C, resulting in double charcoal peaks along the shoulders of an insolation peak. This ties insolation to a 10 kyr periodicity in increased fire frequency. Fire frequency in African savannas is positively correlated with annual precipitation (Lehmann et al., 2014). In eastern Africa, fire-adapted C₄ mesic tall-grasses (Simpson et al., 2016) dominate the herbaceous layer when MAP crosses an approximately ~750 mm threshold (McNaughton, 1983). It appears that fire regimes, C₄ tall-grass Pani-coideae abundance, and precipitation variability, as observed here in the BTB13 core are all influenced by eccentricity modulated peaks in insolation at precessional periodicity.

Lastly, MIS G17 interglacial (Fig. 12) appears to have been a time of significantly decreased effective moisture in the Baringo Basin, as phytolith dissolution indicates high sediment pore water pH, and very low microcharcoal concentrations suggest vegetation density was too low to carry fire. Relatively high peaks in microcharcoal at over four times the mean were observed at the onset of G17, similar to that observed for the onset of the K1 interglacial. Since woody cover was already much reduced by this time, these significant fire events could be derived from fires occurring in higher elevation forests. Humic acid content was also high during G17 indicating the presence of soils or shallow wetlands at the core site (Fig. 3).

In summary, these results suggest that precession has an influence on equatorial vegetation and fire dynamics, a unique finding that validates similar modeled results (Tuenter et al., 2003). Comparison of our results with the 30° N to 30° S insolation gradient curve also indicates that cross-equatorial advection of heat and moisture may enhance or modulate eastern African precipitation, in agreement with similar findings from southern Kenya (Verschuren et al., 2009) and Asia (Beck et al., 2018).

6.4. Zone 4: 2.91 to 2.72 Ma

Zone 4 spans from 2.91 Ma (~100 mbs) to 2.72 Ma (~75 mbs), and is characterized by no pollen, the nearly complete absence of well-preserved phytoliths, and relatively low charcoal concentrations, suggesting that plant densities were typically too low for fire transmission across the landscape (Figs. 3J and 12H). Regarding the drivers of fire in southern Africa, Archibald et al. (2009) found that fire was rare in areas with MAP < 288 mm. This zone coincides with an interval of particularly low eccentricity, when normally strong 100 kyr periodicity almost disappeared. Berger and Loutre (1991) note that this also occurred between 4.8 and 4.4 Ma and that these are unique features in the time evolution of eccentricity over the last 5 Ma. Zone 4 is subdivided into two 100 kyr intervals, 4a and 4b, which are separated by an approximately 2000 yr interval (88.47 to 88.14 mbs) with good phytolith and diatom preservation, and coeval with peak MIS G10 glacial cooling (Fig. 12). There were no zeolites or calcic minerals within this phytolith/diatom interval, but there are sodic zeolites above and below (Fig. 3F). The middle portion of Zone 4a coincides with Mineral Zones 3 and 4 from Minkara et al. (2020), which was virtually zeolite free, possibly because of unsustained inflow of solutes.

The well-preserved phytolith samples at ~88 mbs (2.81 Ma) indicate that during the MIS G10 glacial, precipitation increased significantly. Fire also returned to the landscape during this interval and for 20 kyr afterwards. There was likely an herbaceous swamp near the drill site. The lphp index indicates that tall-grass savanna was in place for part of this interval in the uplands, and this suggests that MAP may have been near or above 750 mm. However, there is no evidence that woody cover increased, suggesting the length of dry season must have remained long (> 6–7 months; Hély et al., 2006). Preserved diatoms from this same interval indicate the presence of a relatively deep, and well-mixed lake (Westover et al., 2020).

Zone 4b (~88–75 mbs) spans the MIS G9 to G7 interglacial interval and also corresponds with Mineral Zone 5 from Minkara et al. (2020), which they describe as the most sustained episode of aridity and salinity for the core. No pollen was observed, presumably from repeated wetting and drying, and phytoliths were either not present because of complete dissolution, or present as a biased assemblage, precluding index calculations. Some saddle (xeric C₄ Chloridoideae), bulliform, and larger sedge stem (TWR) phytoliths were observed. Microcharcoal concentrations were very low, suggesting low plant densities and the likely presence of a xeric short-grass savanna in the uplands.

6.5. Zone 5: 2.72 to 2.57 Ma

Zone 5 spans 2.72 Ma (~75 mbs) to 2.57 Ma (5.43 mbs) and occurred during the intensification of NHG. This zone contains the four previously described Barsemoi drainage outcrop diatomites (Deino et al., 2006; Kingston et al., 2007) and other intervals with moderate to high diatom abundance (Westover et al., 2020). There is excellent
phytolith preservation, and pollen (mostly grass) was observed in 11 samples. The first well-preserved phytolith sample occurs at 2.723 Ma (73.66 mbs) coeval with the coldest part of MIS 66 glacial, and there is an increase in microcharcoal concentrations soon after, suggesting an increase in plant density on the landscape. Short-grass/tall-grass savanna dynamics became strongly coupled with insolation at precessional periodicities, with C₃ mesic Panicoideae becoming dominant during insolation maxima and xeric C₄ Chloridoideae becoming dominant during insolation minima (Figs. 3A and 15). Iph values ≤27.8% may indicate MAP > 750 mm. This provides evidence that monsoonal precipitation was enhanced by increased insolation enough to change the composition of grasses on the landscape.

In contrast to the previously discussed zones where peaks in June/July insolation at 30° N appear to correlate with tall-grass savanna dominance, peaks in local insolation during the month that precedes the East African short rains appear to be a better match with tall-grass savanna dominance once NHG intensifies (Fig. 15). Previous studies with good chronological control have indicated that insolation maxima occurring in either March/April or September/October in East Africa may be responsible for enhancement of either the long rains or short rains, respectively (Trauth et al., 2003; Bergner and Trauth, 2004; Verschuren et al., 2009; Junginger et al., 2014). However, age model uncertainty in this part of the BTB13 core is ±17 kyr, so linking tall-grass savanna dominance to any particular individual insolation curve is difficult. It is interesting to note that the abrupt changes from either short- or tall-grass dominance suggests the existence of an insolation threshold, at which precipitation is significantly enhanced or diminished within 570 years or less. Analysis at a higher resolution than our typical 32-cm intervals may reveal even shorter transition times between humid and arid periods. This nonlinear pattern has similarities to that seen for the onset and termination of the Holocene epoch African Humid Period (Tierney et al., 2011; Armitage et al., 2015; Collins et al., 2017).

Throughout this zone, double peaks in microcharcoal concentrations, separated by ~10 kyr, are associated with peaks in insolation (Fig. 10). Phytoliths from the swamp and stream margin fern Cyclosorus, and trilete spores indicative of ferns suggest the presence of freshwater Cyclosorus–Papyrus swamps or forested streams during the uppermost part of the zone. Pollen and phytoliths from Celtis, a tree associated with a wide variety of mesic habitats, was observed in this zone. This same interval also yielded numerous indicators of afro-montane plants such as Podocarpus pollen, increased C₃ grass phytoliths, orchid and Murdannia/Floscopa (Commelinaceae)-type phytoliths, and numerous siliceous cysts from chrysophyte golden algae (Figs. 2 and 3). This suggests the possible downward migration of afro-montane vegetation from upper elevations and the expansion of swamps during early Pleistocene glacial. However, there is no evidence that woody cover increased above the 40% detection limit of the D/P phytolith index along the lake margins.

Although the diatom (Westover et al., 2020) and mineralogy (Minkara et al., 2020) datasets indicate extreme hydroclimate variability during the Zone 5 interval (Fig. 3F), it does not appear vegetation was varying to quite the same degree. In fact, there is a decreasing trend in plant compositional turnover across the extent of the BTB13 record (Fig. 8D). The previously discussed abrupt changes between short and tall-grass dominance are significant, but can be induced by a MAP change of a few hundred mm. It is possible that sometime after ~3.10 Ma, subsidence associated with rifting created a balanced-fill and/or underfilled lake-type basin (sensu Carroll and Bohacs, 1999). This new basin configuration could have then become more sensitive to changes in precipitation, a phenomena which has been referred to as an amplifier lake (Trauth et al., 2010). Junginger and Trauth (2013) have shown that relatively small changes in precipitation can result in very large changes in lake depth for paleolake Suguta. Thus, the relative changes in hydroclimate recorded by some paleolimnological and sedimentary proxies may not be proportional to that recorded or experienced by terrestrial vegetation.

7. Broader implications from this study

The results obtained here have broader implications for phytolith analysis and paleoenvironmental reconstructions from rift valley settings. Phytolith dissolution and morphotype assemblage bias must be determined to ensure robust and accurate interpretation of phytolith indices such as Iph and D/P’. Because the potential for palm phytolith misidentification resulting from the morphological similarity of sponge spherasters is very high, the results of some studies may have to be reconsidered and reinterpreted. An increase in sponge abundance at low elevation rift valley locations likely signals increasing alkalinity/pH. Phytolith studies from paleosols are likely missing precession-scale variability. Phytolith assemblages from paleosols and lake sediments formed during insolation minima (maxima) will be recording more xeric (mesic) adapted vegetation. And lastly, tree cover reconstructions based on modern calibrations of C₃/C₄ isotopic mixing models need to consider that C₃ grasses can be abundant in some low elevation mesophytic and hydropphytic habitats.

8. Conclusions

Millennial-scale phytolith and microcharcoal records from 3.29 to 2.58 Ma track short-and long-term changes in vegetation and fire during the MPWP and the onset and intensification of NHG in the Baringo Basin/Tugen Hills of Kenya. Prior to ~3.04 Ma, landscapes varied between open savanna, woodland, and forest at typically precessional (19–23 kyr) periodicities. During the MPWP, high microcharcoal abundance suggests regional turnover from wooded to open habitats was driven, at least in part, by fire. After ~3.04 Ma low elevation woody cover likely never exceeded 40%, and mesic tall-grass and xeric short-grass savanna fluctuated with precessional periodicities. Mesic C₃ tall-grass savanna dominated during insolation maxima, and xeric C₄ short-grass savanna dominated during insolation minima. This is a novel observation that likely had an influence on herbivore guild populations, predator-prey relationships, and hominin behavior and landscape use. Comparison of our results with the 30° N to 30° S insolation gradient curve suggests that cross-equatorial advection of heat and moisture may enhance or modulate eastern African precipitation.

With 652 samples analyzed from a 228 m core that spans 730 kyr, this record represents one of the most extensive phytolith studies conducted to date, and illustrates how phytoliths can complement other types of reconstruction datasets. The combined phytolith and pollen data provide the first Pliocene record of plant taxa for the Baringo Basin and Tugen Hills, helping to fill a critical gap in plant functional type data for the central Kenya Rift Valley and its associated hominin localities. This study also fills a gap in orbitally resolved regional vegetation data useful for paleodata–model comparisons for the onset of NHG and the MPWP, the latter of which is often used as an analog for future warming.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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References


Neumann, K., Fahmy, A.G., Muller-Scheessel, N., Schmidt, M., 2017. Taxonomic, ecol-
ogical and palaeoecological significance of leaf phytoliths in West African grasses.
Quat. Int. 434, 15–32.
Wandiga, S., Gichuki, N., Oyieke, H. (Eds.), Proceedings of the 11th World Lakes
signal of aquatic plants and soils in Chad. Palaeobot. Palynol. 158, 47–53.
Novello, A., Lebartad, A.-E., Mouxas, A., Barboun, D., Sylvestre, F., Bourles, D.L., Pailes,
C., Buciat, G., Deacreau, A., Duringer, P., Ghiemme, J.-F., Maley, J., Mazzur, J.-C.,
Roca, C., Schuster, M., Vignaud, P., 2015. Diatom, phytolith, and pollen records from a
108e198ka dated lacustrine succession in the Chad basin: insight on the Miocene–Pliocene
ecosystems and environmental changes in central Africa. Palaeogeogr. Palaeoclimatol.
Palaeoecol. 400, 261–280.
Mackaye, H.T., Vignaud, P., Brunet, M., 2017. Phytoliths indicate significant arable
cover at Sahelanthropus type locality TM266 in northern Chad and a decrease in later
Rapp, G.R., Mulholland, S.C. (Eds.), Phytolith Systematics: Emerging Issues. Plem-
um, New York, pp. 91–111.
Owen, R.B., Muniuir, V.M., Loverenchild, T.K., Renaud, W.R., Rabideaux, N., Loo, S., Deino,
Deocampo, D., Shen, C.C., Billingsley, A., Mbitua, A. 2018. Progressive aridification in
East Africa over the last half million years and implications for human evolution.
Detecting predators and locating competitors while foraging: an experimental study
Piperno, D.R., Pearsall, D.M., 1998. The silica bodies of tropical American grasses:
morphology, taxonomy, and implications for grass systematics and fossil phytolith
Paleoecologists. AltaMira Press, Lanham, MD.
Piper, D.R., Pearsall, D.M., 1998. The silica bodies of tropical American grasses:
morphology, taxonomy, and implications for grass systematics and fossil phytolith
Primatol. 62, 209–228.
Prill, W.L., Mullan, T., 1987. Monsoon variability over the past 150,000 years. J.
Geophys. Res. 92, 8411–8425.
silicon isotope composition of opal-A phytoliths: Implications for palaeoenviron-
Assessing orbitally-forced interglacial climate variability during the mid-Pliocene
increases with watering but not clipping: insights from a common garden study and
literature review. J. Ecol. 102, 556–568.
Renaut, R.W., Jones, B., Tiercelin, J.J., Tarits, C., 2002. Sublacustrine precipitation of
diagenetic minerals and associated calcrete formation in the Lake Bogoria Basin, Kenya.
J. Sed. Res. 72, 103–112.
Westover, K.S., Stone, J.R., Yost, C.L., Cohen, A.S., Rabideaux, N.M., Verschuren, D.,
Sinninghe Damste, J.S., Moernaut, J., Kristen, I., Blaauw, M., Fagot, M., Haug, G.H.,
members of the GeoB Bologna, Italy, and the Radiocarbon Subcommittee. In: Dumont,