

# Taphonomy of phytoliths and macroplants in different soils from Olduvai Gorge (Tanzania) and the application to Plio-Pleistocene palaeoanthropological samples

Rosa Maria Albert<sup>a,\*</sup>, Marion K Bamford<sup>b</sup>, Dan Cabanes<sup>c</sup>

<sup>a</sup>*Catalan Institution for Research and Advanced Studies (ICREA)/Research Group for Paleoeological and Geological Studies, Department of Prehistory, Ancient History and Archaeology, University of Barcelona, c/Baldiri Reixac, s/n, 08028 Barcelona, Spain*

<sup>b</sup>*Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, P Bag 3, WITS 2050, South Africa*  
<sup>c</sup>*Àrea de Prehistòria, Department of Geography, History and History of Art, University Rovira i Virgili, Pl. Imperial Tàrraco, 1, 43005 Tarragona, Spain*

Available online 24 January 2006

## Abstract

The abundance and types of phytoliths in the fossil record are taphonomically biased and do not correspond with the macroplant record. To better understand the bias and improve the interpretation of samples from Olduvai Gorge, Tanzania, we analysed the phytoliths from three sample sets: modern grasses, sedges, palm and dicots in the area; modern soils in the area; and the fossil soils from the eastern palaeolake margin in lowermost bed II. Fourier transform infrared spectrometry analyses were performed in parallel to compare the mineral composition of both modern soils and fossil soils. We found that the abundance of phytoliths is greatly reduced in soil samples compared with modern plant material, but the morphotypes can be reliably interpreted. Dicotyledonous wood/bark phytoliths appear to be over represented in the soil types. Grass phytoliths, and sedges to a lesser degree, are preserved in the soils but in lower abundances resulting in these groups being under-represented. The macroplant fossils are fragments of grass and sedge aerial culms, and dicotyledonous stems that are preserved in fluvial and lacustrine deposits. It is suggested that phytoliths represent the continuous flora whereas macroplant fossils represent the more robust tissues of selected plants preserved under more catastrophic conditions. A post-depositional model is proposed and the palaeovegetation is reinterpreted as being richer and more complex than indicated by other fossil data.

© 2005 Elsevier Ltd and INQUA. All rights reserved.

## 1. Introduction

A variety of methods have been employed to interpret the palaeoenvironments of early hominin sites since it is generally accepted that the vegetation and climate affect the distribution and behaviour of the hominins and other faunas. The sedimentological record provides broad palaeoecological signatures such as fluvial, lacustrine, volcanic or dune settings. Isotope analyses of carbonates can provide a temperature and moisture regime. Faunal composition and comparison with modern faunas is another common method employed. A refinement of this method is that of functional ecomorphology where

physical adaptations of modern animal limbs to certain conditions (running, climbing, burrowing) are extrapolated to the fossils. These methods can provide an indication of the general type of vegetation: open woodland, closed woodland, bushy grassland, etc, but the fossil plants themselves should be considered when a more detailed reconstruction of the vegetation is required.

At Olduvai Gorge in northern Tanzania, there already is a good geographic and stratigraphic framework for the occupation by hominins of the basin and palaeolake margins (Hay, 1976, 1996) and this is being further refined by the multidisciplinary efforts of the Olduvai Landscape and Palaeoanthropological Project (OLAPP) team members.

Palynological samples from uppermost bed I (UMBI) and lowermost bed II (LMBII) separated by the marker tuff, IF (dated at ca. 1.785 myr, Blumenshine et al., 2003), have been processed by Bonnefille (1984). She interpreted

\*Corresponding author. Tel.: +3493 3333466x3198;  
fax: +3493 4498510.

E-mail address: [rosamaria.albert@icrea.es](mailto:rosamaria.albert@icrea.es) (R.M. Albert).

the vegetation as changing from wetter conditions (montane pollen such as *Olea*) to drier conditions just below tuff IF, with an increase in Sudano-Zambezi taxa. Not all the other strata, however, contain pollen. Silicified wood has been identified from one locality and, based on comparisons with the distribution of the modern analogue, it indicates a medium-sized shade tree growing on well drained soils (*Guibourtia coleosperma*; HWK-East locality, probably LMBII; Bamford, 2005). Silicified wood, however, is not common and fossil leaves have not been recovered to date.

Fossil macroplants and phytoliths (Hay, 1976; Peters and Blumenschine, 1995) have been widely recognised in the fossil record and were interpreted as representing a general marshland type of vegetation along the eastern palaeolake margin, an area of 10–20 km long by 1–10 km wide. On closer inspection, however, the macroplants have a more precise distribution within this large area and time.

Phytoliths have been widely used for palaeoecological reconstruction (Bamford et al., this volume, and references therein). When applied to archaeological contexts, phytoliths have been used to identify plants used by prehistoric populations as well as to distinguish between those used by people, and those that are natural accumulations and that indicate the past vegetation (Rosen and Weiner, 1994; Runge, 1999; Albert et al., 1999, 2000, 2003; Mercader et al., 2000; Madella et al., 2002; Berlin et al., 2003; Pearsall et al., 2004; Albert and Henry, 2005). To date, there have been different approaches to reconstruct the palaeoenvironment. Some have focused on the comparison between phytoliths and fossil plants, for example Zucol et al. (2005), or have compared phytoliths from modern plants and modern soils (Blinnikov, 2005). The comparison of modern and fossil soils has also been done (Fredlund and Tieszen, 1997). For the first time, however, we attempt to correlate phytoliths from modern plants and modern soils, following a quantitative and morphological approach, and apply these data to the early hominin-bearing sediments at Olduvai Gorge, within a well-constrained stratigraphical framework.

The macroplants (fragments of stems and culms) and phytoliths have been used to reconstruct the vegetation and how it has changed during the relatively short period of time represented by LMBII and confined to the eastern palaeolake margin (Bamford et al., this volume). The interpretation of the results showed that the vegetation during this time was composed of a variety of grasses, sedges and dicotyledonous plants in different proportions and in different areas and in one specific place showed the presence of palm trees (Bamford et al., this volume). The caveats are that there are taphonomic biases in the preservation of certain phytolith morphologies and the abundance of phytoliths varied between sites and between similar facies for no apparent ecological reason. Furthermore, the vegetation signature from the macroplants and from the phytoliths did not always correlate. With the very narrow time stratigraphic and spatial constraints at play

within the Olduvai Basin localities we would expect the macro and micro fossil plant data to be comparable. Since this is not always the case, we attempt here to determine the taphonomic biases and then correlate the plant data. Then the phytoliths and macroplants can be used for other areas within Olduvai, and other time frames.

Several modern soil types have been sampled to reflect as closely as possible those in the fossil record, Fourier transform infrared spectrometry (FTIR) analyses were done as well as noting the plants growing in the modern soil samples. By comparing the phytoliths from the living plants with those found in the modern soils we are able to get an indication of which plants and plant parts are represented in the soils, whether or not they relate to the extant vegetation, and finally some of the ways in which the types of soil affect the preservation and diversity of the phytoliths, macroplants and pollen. Using this database, we can better interpret the fossil soil phytoliths for palaeoenvironmental reconstructions.

Several basic assumptions are made: firstly, that most plants produce a variety of phytoliths, some of which are diagnostic for that species/genus/group. This we have shown (Bamford et al., this volume) and others before us (Piperno, 1988; Rosen and Weiner, 1994; Runge, 1999; Albert and Weiner, 2001 and references therein). Secondly, the abundance of phytoliths produced by various plants and plant parts is an important factor and diagnostic for the taxon (Albert et al., 1999, 2000, 2003). Thirdly, the phytoliths from the dead plants are deposited in the soil where the plant grew. Transportation of plant litter is minimal but can be recognised by fluvial or eolian signatures. Dune formation is minimal in the Olduvai sediments and these deposits were not sampled. Thus, we can analyse a variety of soils from various types of vegetation and the phytoliths should reflect the local vegetation. The longevity and durability of the phytoliths is unknown but we assume that it will depend upon the mineralogical conditions of soils and diagenetic processes suffered after their deposition in the soil. The frequent pyroclastic fallout effectively capped and sealed the successive layers of clays through beds I and II.

We present here the comparison of the results of modern plants, modern soils and fossil samples, both from phytoliths and silicified plant fragments, from LMBII, to obtain more reliable information on the changing vegetation of the area after the catastrophic event of the deposition tuff IF and its relation to the recolonisation of the area by hominins.

## 2. Materials and methods

### 2.1. Sample selection

Although phytoliths are produced by the aerial parts of plants, they are preserved in soils after the decay and disappearance of the organic matter. Since the mineralogical composition of the soils, as well as the pH, fluctuating

ground water, reworking and chemical and physical post-depositional processes appear to affect the preservation of phytoliths, different soils have been sampled. Selection of modern soil samples (from different localities) has been correlated with fossil soil types present at Olduvai Gorge, namely earthy clays, waxy clays, tuffs, surge, reworked tuff, lacustrine and fluviually associated clays (Hay, 1976; Peters and Blumenschine, 1995; Blumenschine and Peters, 1998). From analogous regions close by we have collected soils from lake margins, river bed and banks, the edge of the Serengeti plains, and with different vegetation types such as open grassland, open woodland and riverine woodland. The phytoliths have been extracted from these samples and compared to the modern plant reference collection analysed from the same area, thus enabling identification of the soil phytoliths. From these results a model to explain the taphonomy of phytolith preservation in a silica-rich environment, such as the one present at Olduvai Gorge (Hay, 1976) is proposed and compared with macroplant and pollen preservation.

Olduvai Gorge sampling, thus far, has concentrated on the UMBI, tuff IF and LMBII levels in the eastern palaeolake margin localities of HWK-East, MCK, FLK-North and VEK (locality notation of Leakey, 1967). From each of these sites, soil samples have been taken at various levels for phytolith analyses. The sediments have been excavated within 1–2 m wide archaeological–geological trenches, and sieved to recover all the contained stone artefacts, bone and silicified plants.

## 2.2. Preparation of modern soil samples for phytoliths

The phytolith extraction method followed was described in detail by Albert et al. (1999) for the Tabun cave study. A weighed aliquot of about 1 g of air-dried sediment was treated with 10 ml of an equivolume solution of 3 N HCl and 3 N HNO<sub>3</sub> for 30 min and then centrifuged to eliminate the carbonates and phosphates present in the soils. After washing the pellet with water the organic material was oxidised with 30% hydrogen peroxide at 70 °C. The sample was dried and the remaining sediment was weighed. This is referred to as the inorganic acid insoluble fraction (AIF).

Mineral components of the AIF were separated according to their densities in order to concentrate the phytoliths by adding 5 ml of sodium polytungstate solution [Na<sub>6</sub>(H<sub>2</sub>W<sub>12</sub>O<sub>40</sub>).H<sub>2</sub>O] of 2.4 g/ml density. The suspension was centrifuged and the supernatant was transferred to another centrifuge tube, 1.0 ml of deionised water was added and the tube was vortexed and again centrifuged as above. This cycle was repeated until no visible mineral particles remained in the supernatant. The heavy liquid was then diluted by filling the centrifuge tube with deionised water, to ensure that even the lightest minerals are recovered. After each centrifuge step, the sediment deposited at the bottom of the tube (pellet) was transferred to a 1.5 ml microcentrifuge tube. Note that this method has the advantages of creating separation conditions that

concentrate the relatively light opaline phytoliths, which have a density between 1.5 and 2.3 g/ml (Jones and Beavers, 1963), in the last two cycles.

Slides of the pellets were prepared for the three lightest fractions by weighing approximately 1 mg of sample, with an accuracy of 0.1 mg, onto a microscope slide. The samples were mixed with Entellan New (Merck), and a cover slip was placed over the suspension. The aerial coverage of the sample on the slide was estimated by counting the total number of fields containing sample grains. Slides were studied using an Olympus BX41 optical microscope and digital images were taken and stored with a digital camera Olympus Camedia C-5060 and Olympus DP soft 5.0 software.

Since phytoliths are produced by many living plants, and many phytolith morphologies are common to a variety of different plants, only some morphologies, or suites of morphologies, are useful for the identification of particular plants. According to previous results (Albert and Weiner, 2001), the counting of only 50 phytoliths with diagnostic morphologies gives an error margin of 40% and is considered too unreliable for interpretation, whereas the counting of 200 diagnostic phytoliths gives an error margin of around 20%. Thus, whenever possible, a minimum number of 200 diagnostic morphologies were counted in order to obtain the maximum reliability in the identification and interpretation of the phytolith record. Siliceous fragments were not counted.

## 2.3. Description and identification of phytoliths

To estimate the phytolith abundance in the different samples we followed standard methods described in Albert (2000); Albert et al. (1999) and Albert and Weiner (2001). The morphological identification of phytoliths was based on the results obtained from the study of the modern plant reference collection carried out in the same area and, when possible, on the same plants growing where the soil samples were collected (Bamford et al., *this volume*). Comparison of morphologies with other modern plant reference collections was also performed (Twiss et al., 1969; Brown, 1984; Ollendorf et al., 1987; Piperno, 1988; Bozarth, 1992; Mulholland and Rapp, 1992; Ollendorf, 1992; Runge, 1999; Mercader et al., 2000). The terms used to describe the phytoliths followed the anatomical terminology of the cell in which they were formed and, when this was not possible, we followed geometrical definitions (Albert, 2000; Albert and Weiner, 2001). The new phytolith code of terminology has also been checked to homogenise some of the terminologies used (Madella et al., 2005).

## 2.4. FTIR analysis of soils

Infrared spectra of modern soils were obtained using KBr pellets (about 0.1 mg or less of sample in about 50 mg of KBr) and a Fourier transform infrared spectrometer (FTIR) (Jasco 680 plus with Spectra Manager software).

Samples were dried under a hot lamp for 12 h. About 1 mg of initial sample, previous to acid treatment, was added to KBr to make pellets. The spectrometer was calibrated twice and blank samples of known composition were checked. The spectra were collected at  $4\text{ cm}^{-1}$  resolution. The FTIR analysis provides information on the nature of the siliceous minerals that constitute the bulk of the sample, namely quartz, volcanic siliceous minerals, clay and phytoliths (Weiner and Goldberg, 1990). This complements the identification of the minerals using a petrographic optical microscope, which provides information on mineral grain morphology and colour.

Macroplant fragments were identified on the external morphology, for example triangular culms of sedges, and also on the internal anatomy (vascular bundle arrangement).

### 3. Results

Modern soil samples and the localities from where they were collected, the type of vegetation and type of soil, FTIR results, percentage of AIF, estimated amount of phytolith numbers per gram of AIF, and the percentage of weathered ones are listed in Table 1. Phytoliths were divided morphologically into different groups depending on the origin of the plant or plant part where they were formed: monocotyledonous plants (when it is not possible to differentiate between grasses, sedges or palms, i.e. elongate morphologies with smooth or rugose margins), grasses, sedges, palms, dicotyledonous-leaf phytoliths, dicotyledonous wood-bark phytoliths and others not determined.

#### 3.1. Mineralogy of the soil samples

The mineralogical composition of the modern soils is dominated by clay in most of the samples. In Lake Manyara and Msasa River samples the type of clay has been identified as kaolinite. Water bending at  $1630\text{ cm}^{-4}$  is noted to a higher or lesser degree in all the samples and probably corresponds to the water contained in some of these clays. Calcite is also clearly present in some samples and seems to be related to the open grassland and/or areas with no vegetation. The third mineral of importance is opal, although most of the times it appears as a shoulder of clay. The opal usually corresponds to the presence of phytoliths, and therefore when opal is noted in FTIR this relates to the phytolith presence. Quartz also appears as a shoulder of clay and its presence is not associated with high phytolith content. Finally, only in the black organic sample from Lake Manyara (Table 1) has the presence of alkali feldspar been detected.

The main differences noted between the two black organic sediments from Lake Manyara and Lake Masek are related to the major presence of clay (kaolinite) in the former and the calcite in the latter. Lake Masek sediments are distinguished because of clear calcite peaks not

observed in other samples and also reflected in the percentage of AIF.

Within each soil type the difference in percentage of AIF is fairly consistent, varying from 7% to 15%. Between soil types it varies more with the sandy-clay soils having an average AIF percentage of 88% compared to the 45% for the saline-alkaline soil, a difference of 43%. The percentage of weathered morphologies is variable with the volcanic lava soils showing the least degree of weathering and the saline-alkaline soils the most.

#### 3.2. Phytoliths from the modern soil samples

##### 3.2.1. Pyroclastic clays

The pyroclastic clay soil samples from the Leakey camp in the Olduvai Basin (Table 1, samples 1–4) were collected from two open grassland sites on shallow soils above calcrete hardpan and from the *Commiphora* open woodland under the trees which tend to grow where there is better drainage along cracks or faults in the hardpan. Samples collected from the open grassland (samples 3 and 4) showed twice the number of phytoliths than samples collected from the *Commiphora* woodland (samples 1 and 2), related, however to almost double the percentage of dissolution (weathering). The increasing dissolution rate might be related to the higher presence of calcite observed in the FTIR results (Table 1). The morphological results (Fig. 1) indicate that, contrary to expectation, monocotyledonous plants, most probably grasses, are more abundant in *Commiphora* woodland than in open grassland, although it needs to be pointed out that the grasslands also have many herbaceous dicots whereas in the *Commiphora* woodland, the dicotyledonous plants correspond mostly to the trees. At this stage of the research, it is not possible to distinguish between herbaceous and woody dicots.

The non-determined phytolith group includes big cylindroid morphologies with one of the margins echinate. This morphology has not been identified in the modern plant reference collection analysed to date. Grasses are represented mainly by bulliform cells (Fig. 2a, k) and trichomes (Fig. 2b) from the leaves, and short cells (Fig. 2c–e) that can also be found, apart from the leaves, in the inflorescences and the stems of the same plants. Long cells with echinate margins produced in the inflorescences were also noted although in low quantities (less than 2%). The morphological characteristics of the grass short cells indicated that the C3 group (Fig. 2c) was present both in the *Commiphora* woodland and in the open grassland. C4 grass phytoliths (Fig. 2d, e), however, are more common in the *Commiphora* woodland and are practically absent in the open grassland, especially those belonging to the chloridoid group (Fig. 2d). From our own collections during the dry season (June–August) modern grasses growing in the *Commiphora* woodland are *Setaria* sp. (Panicoidae, C4) and in the open grassland are *Aristida* sp. (Arundinoideae, C4), *Dactyloctenium aegyptiacum*, *Eragrostis* spp. and *Sporobolus spicatus* (Chloridoideae, C4). Overgrazing and

Table 1

Modern soil samples; from different localities and vegetation types with the soil type, FTIR analysis, percentage acid insoluble fraction (AIF), number of phytoliths per gram of AIF, percentage of weathered forms

| Sample number | Localities                            | Vegetation type   | Type of soil                            | FTIR <sup>a</sup>                 | % AIF | No. Phytoliths/1 g AIF | % weathered material |
|---------------|---------------------------------------|---|---|-----------------------------------|-------|------------------------|----------------------|
| 1             | Olduvai Gorge, west of Leakey camp    | <i>Commiphora</i> woodland  | Pyroclastic clay                        | Cl, C                             | 61.3  | 700 000                | 14.9                 |
| 2             | Olduvai Gorge, west of Leakey camp    | <i>Commiphora</i> woodland, <i>Acacia mellifera</i> , <i>Sanseveria</i>   | Pyroclastic clay                        | Cl, C                             | 65.0  | 600 000                | 11                   |
| 3             | Olduvai Gorge, west of Leakey camp    | Open grassland with herbaceous dicotyledonous plants (100 m away from sample 2)   | Pyroclastic clay                        | Cl, C+                            | 60.1  | 1 600 000              | 24.5                 |
| 4             | Olduvai Gorge, west of Leakey camp    | Open grassland closer to trees with more grasses than sample 3, 78 m away from sample 1 and 360 m away from Leakey camp           | Pyroclastic clay                        | Cl,C++                            | 58.0  | 1 100 000              | 20                   |
| 5             | Lake Manyara                          | Open woodland, the lower and middle fan zone. <i>Phoenix reclinata</i>  | Volcanic lava                           | Cl, C, O                          | 61.8  | 15 700 000             | 7.1                  |
| 6             | Lake Manyara                          | Open woodland, the lower and middle fan zone. Below <i>Hyphaene petersiana</i>  | Volcanic lava                           | Cl, C+, O                         | 61.4  | 18 000 000             | 6.2                  |
| 7             | Lake Manyara                          | Open woodland, ground water forest in lower and middle fan zone. <i>Acacia xanthophloea</i> , <i>Senna</i> and <i>Achyranthes</i> | Volcanic lava                           | Cl, C, O                          | 60.9  | 6 900 000              | 9.9                  |
| 8             | Lake Manyara                          | Open woodland, lower and middle fan zone. <i>Acacia albida</i> , grasses, <i>Achyranthes</i> and Malvaceae                        | Volcanic lava                           | Cl (kaol), C                      | 75.5  | 4 800 000              | 5.3                  |
| 9             | Lake Manyara, Msasa River             | Bottom of the river bed with few grasses. Seasonal water  | Sandy-clay                              | Cl (kaol), Q                      | 91.6  | 400 000                | 8                    |
| 10            | Lake Manyara, Msasa River             | Bank side with herbaceous plants  | Sandy-clay                              | Cl (kaol), Q                      | 86.3  | 400 000                | 11.6                 |
| 11            | Lake Manyara, Msasa River             | Top of bank side with herbaceous plants and a few trees   | Sandy-clay                              | Cl (kaol), Q                      | 85.7  | 500 000                | 12.5                 |
| 12            | Lake Manyara                          | Open grassland next to lake (flooded in 1997)   | Waxy-clay                               | Cl (kaol), Q                      | 84.6  | 300 000                | 12.8                 |
| 13            | Lake Manyara                          | Open area (seasonally no vegetation) next to lake   | Black organic sediment                  | Cl (kaol), C, O, alkali feldspars | 65.0  | 1 100 000              | 12.2                 |
| 14            | Lake Masek                            | Open area (no vegetation). First line next to the lake. Bird footprints. Roots below  | Black organic sediment, saline-alkaline | Cl, C+++ , Q                      | 63.9  | —                      | —                    |
| 15            | Lake Masek                            | Open area (seasonally no vegetation). Second line next to the lake  | Saline-alkaline                         | C, Cl                             | 45.7  | 1 200 000              | 25                   |
| 16            | Lake Masek                            | Fringing grassland ( <i>Sporobolus consimilis</i> )   | Sand, saline-alkaline                   | C, Cl                             | 55.3  | 1 600 000              | 31.8                 |
| 17            | South of Lake Jipe, below Kilimanjaro | <i>Cyperus papyrus</i> and <i>Cyperus immensus</i> marsh  | Sandy-clay                              | Cl, O                             | 88.0  | 3 700 000              | 8.6                  |

Samples 1–17 are used in the text and graph.

<sup>a</sup>For the FTIR results: Cl = clay; C = calcite; O = opal; Q = quartz; kaol = kaolinite.

the lack of inflorescences means that the diversity of grasses is most probably under estimated in the extant vegetation and is also poorly represented in the soil phytoliths. The accumulation of dung, weeds of disturbance and grazing

and browsing are strong evidence of animal activity concentrated under the trees.

Phytoliths characteristic of sedges (hat shape) have only been noted in sample 4. This is consistent with the ground



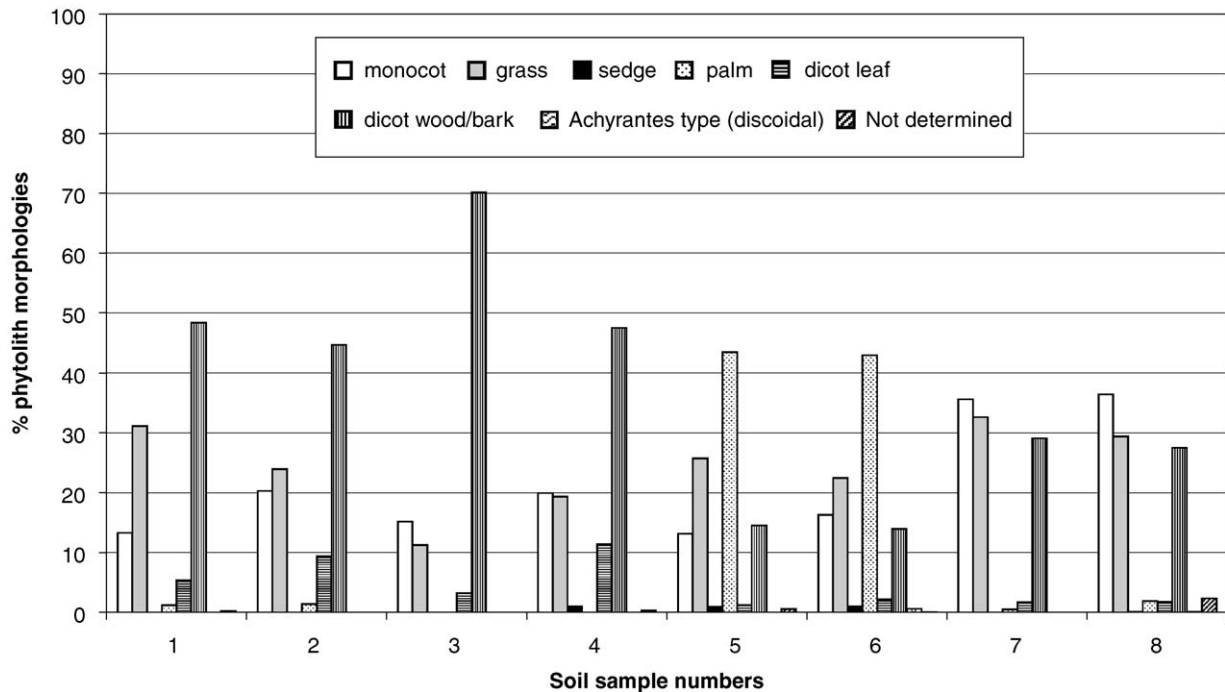


Fig. 1. Histogram showing percentages of different phytolith morphologies in modern soil samples listed in Table 1. Samples 1–4 from pyroclastic clays near the Leakey camp, Olduvai Gorge; 1–2 in *Commiphora* woodland; 3–4 in open grassland. Samples 5–8 from volcanic lava soils of Lake Manyara open woodland; 5—*Phoenix reclinata*, 6—*Hyphaene petersiana*, 7—*Acacia xanthophloea*, 8—*Acacia albida*.

vegetation where the small dryland sedge, *Kyllinga* sp. was observed. Nevertheless, it is important to note, that in the analysis of the living plant *Kyllinga* sp. from the same open grassland area (Bamford et al., this volume), the percentage presence of hat-shaped phytoliths was about 77%, whereas in soil samples 3 and 4, this morphological type was only noted in sample 4 and at less than 1%. Other monocot phytoliths identified were cylindroid morphologies with smooth and rugose margins (Fig. 2f, g). The relatively few multicellular structures found (only in the *Commiphora* samples) indicate that silicification was not intense enough for the individual cells to remain adherent. Note, however, that multicellular structures were not abundant either in the modern plant reference collection or in the modern soils (Bamford et al., this volume).

Dicotyledonous wood/bark phytoliths are mostly represented by parallelepiped forms, common in bark (Fig. 2h) and a few spheroid and irregular morphologies more characteristic of wood. The wood/bark phytoliths were common in the open grassland (70% and 48%) and presented a similar proportion in the *Commiphora* woodland samples (Fig. 1). The identification of dicotyledonous wood/bark phytoliths is also based on the results from the Middle East modern plant reference collection (Albert

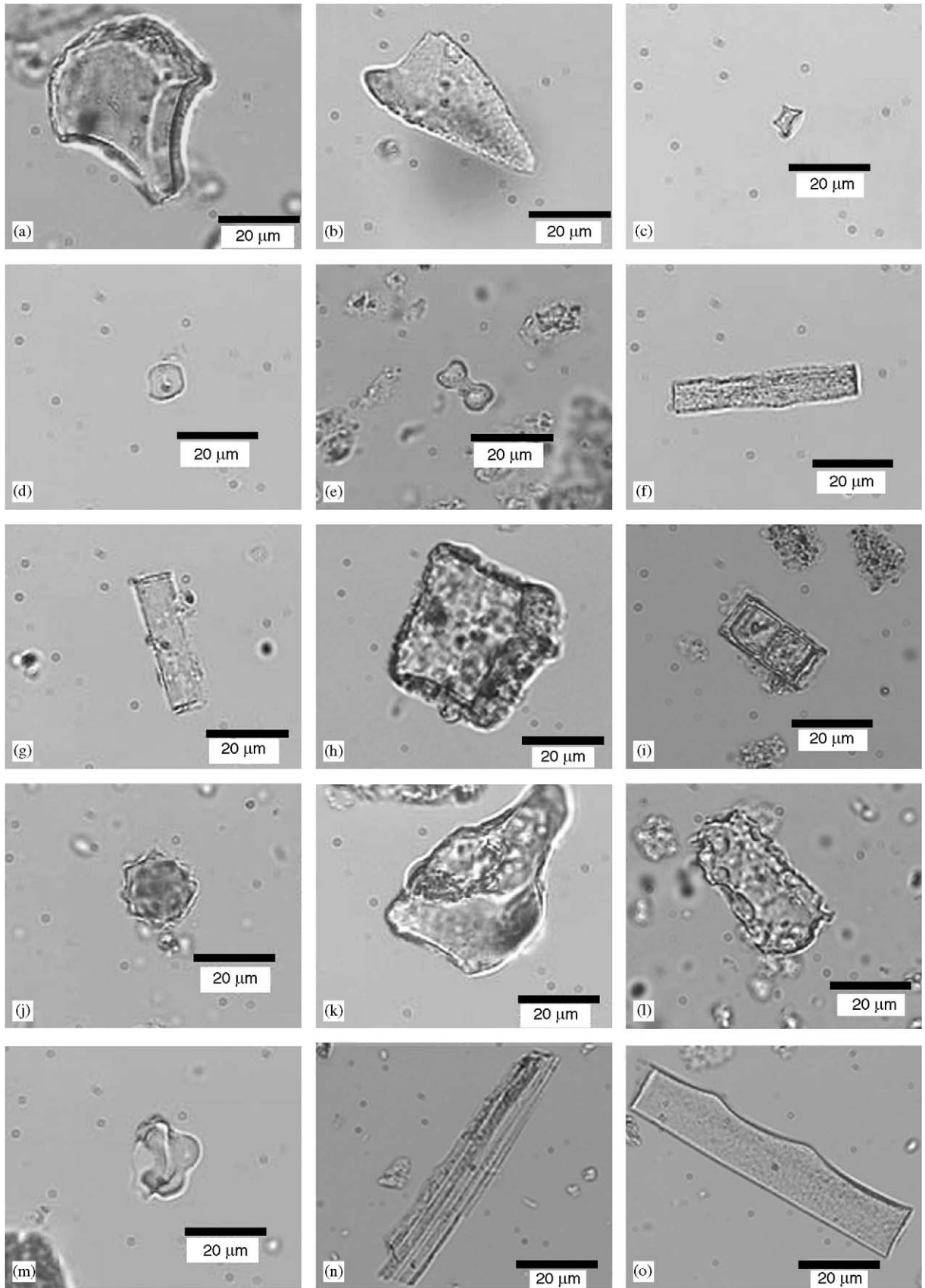
et al., 1999, 2000, 2003; Albert and Weiner, 2001). Due to the difficulty of differentiating between phytoliths from wood and bark and until there is a complete modern plant reference collection from the greater Olduvai area, we have decided to group together the phytoliths characteristic of wood and bark.

Dicotyledonous leaf phytoliths occur in all the soil samples and comprise 3–11% of the total phytolith record. They are characterised mainly by hairs, platelets and brachiforms, whereas multicellular structures with polyhedral morphologies (typical of modern leaf samples) have not been identified. One important observation was the identification of diatoms (Fig. 2i) in the *Commiphora* woodland samples indicating some degree of moisture in these soils, probably derived from the rainy season.

### 3.2.2. Volcanic lava soils

In contrast to the pyroclastic soils and despite the similar AIF percentage obtained from both areas, phytoliths are more abundant and better preserved in the volcanic lava soils from the open woodland of Lake Manyara (Table 1, samples 5–8). They are especially numerous in those samples collected from below palm trees (*Phoenix reclinata* and *Hyphaene petersiana*) (Fig. 2j). The dissolution

Fig. 2. Photomicrographs of phytoliths from modern soil samples. Pictures taken at 400 × : (a) bulliform cell from the leaves of grasses, (b) trichome from the leaves of grasses, (c) short cell from grasses C3 type, (d) short cell from grasses (saddle) from the C4 group grasses, (e) short cell bilobate from the C4 group, (f) and (g) cylindroid morphologies with smooth and rugose margin from monocotyledonous plants, (h) parallelepiped blocky morphology from dicotyledonous plants, (i) diatom, (j) spheroid echinate from palms, (k) bulliform cell from the leaves of grasses with signs of chemical alteration, (l) parallelepiped morphologies with strong signs of chemical alteration, (m) hat shape with rounded tip probably from sedges, (n) multicellular structure with long cells smooth margin from monocotyledonous plants (sedges?) and (o) parallelepiped elongate with facetated margins from monocotyledonous plants (sedges?).



percentages in these Lake Manyara samples range from 5% to 10%, which is low. Note that mineralogically these soils differ from the pyroclastic clays in showing less calcite, similar to the *Commiphora* woodland. The presence of opal, derived from phytoliths, is visible microscopically and detected in the FTIR analysis. Furthermore, the open woodland samples from below the dicot trees yielded a higher total number of phytoliths than the open grassland samples from the pyroclastic soil samples at the Olduvai Gorge Leakey camp, despite the higher production of phytoliths by modern grasses (Bamford et al., this volume).

Considering the phytolith morphological results (Fig. 1, samples 5–8), monocots (probably grasses) and phytoliths characteristic of grasses are more abundant below the dicot trees. Sedges are rare in all four samples and were not noted as a part of the living vegetation. Palm phytoliths are ubiquitous under the palm trees and rare under the dicot trees. Dicot wood/bark phytoliths, as expected, exhibit higher percentages under the dicot trees. Dicot leaf phytoliths are low in all four samples. One phytolith type (circular double ring) characteristic from *Achyranthes spicata*, a shrub which is an indicator of shady conditions, was noted in samples 6–8 (below *Hyphaene* and dicot trees). These phytoliths were present, however, in low numbers, which is consistent with the modern reference collection (Bamford et al., this volume). *A. spicata* was present in the extant vegetation in samples 7 and 8.

Looking in more detail at the suites of phytoliths that characterise the different plants, within the palms the percentage of spheroid echinate morphologies is considerably lower (15.8% in the soil sample below *P. reclinata* and 8.5% in the sample below *H. petersiana*) than that observed in the living plants (in *Phoenix* it is 27% for the leaves and above 90% for the flowers, rachis and roots, whereas in *Hyphaene* it is always above 34% with the exception of the fruits where smooth spheroid morphologies dominated the phytolith record) (Bamford et al., this volume). Grasses are represented by all their parts: phytoliths from the inflorescences represent 4–9% of the total record, (which is higher than the percentage observed in pyroclastic soil samples. C3 and C4 phytoliths from grasses (Fig. 2c–e) are present in the volcanic lava soil samples.

### 3.2.3. Sandy-clay soils

Samples collected from the Msasa River that flows into Lake Manyara, defined as sandy-clay soils, show an elevated AIF percentage (85–92%, Table 1, samples 9–11). The FTIR results indicate that this high AIF percentage is due to the major presence of the clay kaolinite, and is accompanied by quartz. These samples contain a lower number of phytoliths than both previous soil types. The dissolution percentage of phytoliths is slightly higher than the former set of samples with the exception of the one collected from the bottom of the river, which is also the sample with highest AIF percentage. The apparently lower number of phytoliths may be due to the masking effect of the kaolinite.

The sample from the river bottom (sample 9) contained a higher percentage of grass and other monocot phytoliths (Fig. 3). Sedges and palms were not seen in the vicinity of the sample sites but they are represented by very low percentages in the soil samples. Dicot wood/bark phytoliths are present in fairly low numbers in the river bottom sample and more abundant on the bank side and top whereas the dicot leaf phytolith morphologies are present in similar amounts in all three samples. Although no vegetation grows on the river bottom soils, most probably are washed in and deposited there. This accumulation would reflect the vegetation of a wider area. A variety of trees, shrubs and grasses grow in the immediate vicinity of the river.

### 3.2.4. Lake Manyara sandy/waxy clay

The last two samples from Lake Manyara (samples 12 and 13) were collected from an open area next to the lake (Table 1, Fig. 3). Sample 12 was from a grassy area and 13 from a seasonally denuded area close to the lake shore on black organic sediment. Mineralogically the waxy clay sediment (sample 12) is identical to the samples collected next to the Msasa River, in bulk mineralogical composition (major presence of the clay kaolinite), percentage of AIF and phytolith abundance (Table 1). The black organic sediment (sample 13), on the contrary, contained calcite and alkali feldspar minerals not noted in the Lake Manyara open grassland. It is interesting to note that sample 13, with some organic matter but no above ground vegetation in the dry season, showed almost three times more phytoliths than the waxy-clay (sample 12), which was below grasses and dicotyledonous plants. The presence of opal was observed in the FTIR analysis. In spite of the current difference in vegetation cover, no morphological differences were noted between these two samples (Fig. 3); both have grass and other monocot phytoliths as a major component, some dicotyledonous wood/bark phytoliths and a significant number of non-determined phytoliths including parallelepiped blocky elongate morphologies that have also not been identified in the reference collection. The presence of phytoliths in a seasonally non-vegetated area should be noted.

### 3.2.5. Saline-alkaline soils

Three samples were collected from the shores of Lake Masek (Table 1, samples 14–16) where there was little or no vegetation along the margin between low and high water lake levels. None of these samples showed an abundance of phytoliths. The AIF percentages are lower in two of these samples than any other soil type analysed here (45–55%) and they are related to a major presence of calcite noted in the FTIR results (Table 1). Sample 14 yielded no phytoliths. The dissolution percentage of phytoliths in the other two samples is high (25–32%) (Fig. 2k, l), and is associated with the calcite and water that would have increased the pH above 9 and dissolved the phytoliths. The AIF percentage, presence of calcite and



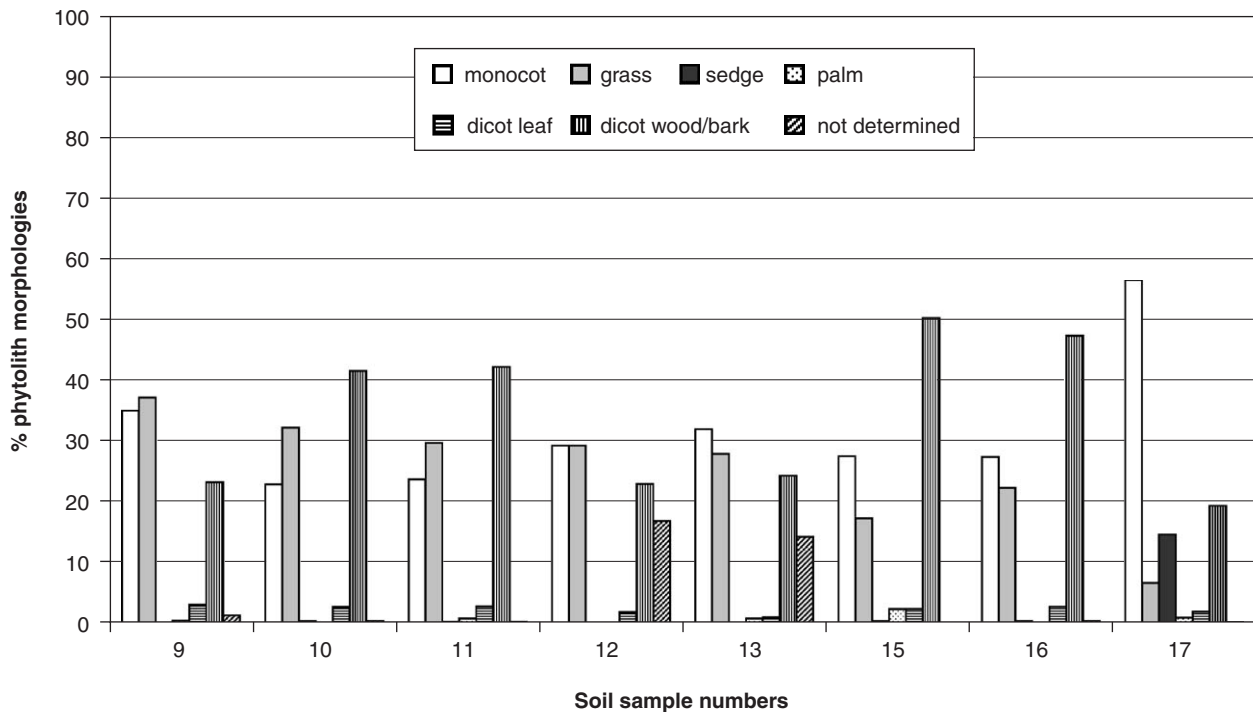


Fig. 3. Histogram showing percentages of different phytolith morphologies in modern soils listed in Table 1. Samples 9–11 from the sandy-clay soils of the Msasa River, Lake Manyara: 9—river bottom, 10—side of bank, 11—top of bank; Samples 12–13 from the shore of Lake Manyara: 12—open grassland on waxy clay, 13—black organic sediment in open area, no vegetation; Samples 15–16 from the saline-alkaline shore of Lake Masek; 15—un-vegetated, 16—fringing grassland. Sample 17—Lake Jipe sedge marsh on sandy clay.

degree of dissolution differs notably from the equivalent samples collected from Lake Manyara which, however, is more densely vegetated and presumably has fresher water than Lake Masek.

The phytolith composition is similar for samples 15 and 16 (Fig. 3) with some minor differences, such as the presence of palm phytoliths, in low amounts, in the open area but absent from the fringing grassland. In the two samples, monocotyledonous and characteristic grass phytoliths occur in similar numbers, whereas dicotyledonous wood/bark phytoliths predominate. Grass phytoliths are represented mostly by short cells and trichomes. No silica skeletons were noted. Surprisingly, sample 16 does not completely correspond to the morphological types of the leaves of *Sporobolus consimilis* (Chloridoideae, C4) which were isolated from the modern plant reference collection and is dominated (72%) by short cells of the festucoid type (C3 grasses). In this sample, collected next to this grass, short cells are represented by C3 grasses and also from C4 grasses (both panicoid and chloridoid) in similar quantities but altogether in much lower percentages (5%). A similar situation was observed, however, when analysing the modern plant reference collection for the grass *Cynodon dactylon*, (Chloridoideae, C4), where both types of short cells (C3 and C4, chloridoid) were noted (Bamford et al., this volume).

Assuming that the present vegetation has not changed significantly in the recent past, the high number of dicot

wood/bark phytoliths is surprising given the present vegetation in the area; the low number of dicot leaf phytoliths would seem to be more representative as there are no trees within several hundred metres of the sample sites. Many trees were killed by the El Niño high water stand in 1997–1998, and along some old channels dead trees can still be observed. This phenomenon has been observed in other shallow lake systems in east and southern Africa (Lake Eyasi, Lake Ngami). The vegetation has shifted several hundreds of metres over a few decades.

### 3.2.6. Sedge marsh on sandy-clay

In the sandy-clay sample from Jipe Lake (Table 1, 17; Fig. 3), collected from a marsh where *Cyperus papyrus* and *Cyperus immensus* were growing, phytoliths are numerous and relatively well preserved. The AIF percentage is high (88%) due to the major presence of clay and opal derived from phytoliths (FTIR). Percentage of dissolution is relatively low and it is similar to the other sandy-clay samples from the Msasa River.

Morphologically, grass phytoliths were present in low numbers (6%). Monocotyledonous forms probably corresponding to sedges (Fig. 2m–o) dominated the phytolith record. It is interesting to note the very low occurrence of hat-shaped phytoliths (characteristic of sedges) as individual cells, although they occur as components of multicellular structures. Cylindroid bulbous morphologies, common in some of the plant parts of the living samples

of both *C. immensus* and *C. papyrus*, have not been identified either in the soil sample. These results indicate that although hat-shaped and cylindroid bulbous morphologies are widely distributed among sedges the single components are easily dissolved, thus forming a bias in the morphological interpretation which can be only resolved by including the identification of associated morphologies. The dicot leaf and wood/bark phytolith morphologies are in low numbers in this sample (Fig. 3), which appears consistent with the modern vegetation at the site.

### 3.3. Summary

Phytolith morphologies in soils commonly represent the modern vegetation but their abundance is greatly decreased, to different degrees, depending on the mineralogical conditions of soils. Volcanic soils and lake margins with more acidic conditions are good for the preservation of phytoliths whereas pyroclastic and saline-alkaline soils are worse.

- (a) Specific phytolith types can disappear almost completely from the soil record, independent of the mineralogical conditions of soils. This is the case of hat-shaped and cylindroid bulbous morphologies from sedges. Other morphological types such as short cells from grasses and spheroid echinates from palms remain in the soil but in lesser amounts.
- (b) Wood/bark phytoliths are resistant and preserve well and reduce the apparent abundance of the less resistant types such as those of sedges and grasses.
- (c) FTIR analysis helps in understanding the soil chemistry and its effect on the phytolith preservation. For example, the presence of calcite in combination with hydrological activity considerably reduces the preservation of phytoliths.
- (d) Drainage, both palaeo and extant, is also a factor to take into account when studying the conditions for phytolith preservation. The slope and aspect of any setting should be noted so that any possible input of phytoliths from wind or water borne soils can be considered. (LMBII is flat where we sampled but some other sites are gently dipping.)

## 4. Comparison of modern plant, modern soil, and fossil phytoliths

We have selected those plants that have been identified as part of the vegetation of the modern soils studied. Table 2 shows the most characteristic morphologies identified in the modern plant reference collection, the plants and plant parts that produce them and their relative abundance, expressed as a percentage, in the living plants, modern and fossil soils. Regarding the fossil samples studied, the mineralogical analyses (FTIR) show that there

was little variation, the main minerals being alkaline feldspar or zeolite group or probably both. No evidence of clay is shown by the FTIR but XRD showed a small amount and only two samples have a significant content of calcite. Most of the phytoliths showed strong signs of chemical dissolution but some were preserved well enough for a reliable morphological interpretation (Bamford et al., this volume).

As a first observation, most of the morphologies decrease in abundance from living plant to modern soils to fossil soil. Therefore, there is a dissolution process that affects the phytolith preservation through time. Some of the morphologies present in the modern soils are absent in the fossil record. The absence of these morphotypes may be related to two different factors:

- (a) the plants that produce this type were not there and
- (b) the phytoliths have been dissolved/removed by some post-depositional processes.

Most of the morphologies that have “disappeared” from the fossil record were either absent or not present in high numbers in the modern soil samples (always below 1%), yet we know that some of these morphologies are produced in large numbers in the living plants (Table 2). The differential preservation of phytoliths is outlined below, but this analysis is limited by the fact that some of those found in the modern and fossil soil samples have not been identified in the reference collection.

Verrucate morphologies (elongates and parallelepipeds) were only noted in the leaves of *P. reclinata* (Table 2). These morphologies are absent from the modern soils even though they were heavily silicified and the fact that other elongate and parallelepiped morphologies are well preserved in soils. These results suggest that in this specific situation, the leaves of *P. reclinata* palms are not represented in modern soils and have not been recognised, to date, in the fossil record.

The comparison of phytoliths from all three sample sets showed the following:

- (a) Preservation of phytoliths depends, first of all, on the degree of silicification in the plant, which at the same time is reflected in the different morphological types.
- (b) Some morphologies, although they are produced in huge numbers in the plants, are much less abundant in the modern and fossil soil records (for example, short cells from the epidermal tissue of grasses).
- (c) Some morphologies are produced in high numbers in plants, but they do not preserve well in the modern soils and disappear from the fossil record: cylindroid bulbous from sedges.
- (d) Some morphologies are produced in relatively low numbers in modern plants but once they have been silicified and deposited in the soils they remain more or less stable for long periods of time (more than one

Table 2

Percentages of different morphological types in the modern plant reference collection from Olduvai Gorge (Bamford et al., 2006) and represented in the modern and fossil soils

| Phytolith type   | Species                      | Plant part             | % Presence | % Average presence in modern soils | % Average presence in LMBII fossil samples |
|--|------------------------------|------------------------|------------|------------------------------------|--|
| Bulliform (fan and pillow shape)   | <i>Sporobolus consimilis</i> | Leaves                 | 2          | 1                                  | 1  |
| Circular double ring   | <i>Achyranthes spicata</i>   | Leaves                 | 10         | 0.5                                | Absent                                     |
| Cylindroid bulbous (single or in group)  | <i>Cyperus immensus</i>      | Stem                   | 10         | 0.3                                | Absent                                     |
|  | <i>Cyperus papyrus</i>       | Culm                   | 28         |                                    |  |
| Ellipsoid smooth/rugose surface  | <i>Cyperus immensus</i>      | Stem                   | 16         | 1                                  | 3  |
|  | <i>Cyperus immensus</i>      | Leaves                 | 19         |                                    |  |
| Elongate forms granulated surface  | <i>Phoenix reclinata</i>     | Leaves                 | 52         | Absent                             | Absent                                     |
| Elongate forms smooth/rugose margin (single or in group)                               | <i>Cyperus immensus</i>      | Stem                   | 30         | 6                                  | 27   |
|  | <i>Cyperus immensus</i>      | Leaves                 | 34         |                                    |  |
|  | <i>Cyperus papyrus</i>       | Flowers                | 21         |                                    |  |
|  | <i>Kyllinga</i> sp.          | Whole plant            | 8          |                                    |  |
|  | <i>Sporobolus consimilis</i> | Leaves                 | 12         |                                    |  |
| Hair   | <i>Acacia xanthophloea</i>   | Leaves                 | 4          | 1                                  | 1  |
|  | <i>Cyperus papyrus</i>       | Flowers                | 17         |                                    |  |
| Hat-shaped morphologies (single or in group)   | <i>Cyperus immensus</i>      | Leaves                 | 15         | 0.4                                | 1  |
|  | <i>Cyperus immensus</i>      | Stem                   | 19         |                                    |  |
|  | <i>Kyllinga</i> sp.          | Whole plant            | 77         |                                    |  |
| Multicellular silicified tissue with hairs, parallelepiped thin and cylindroid bulbous | <i>Cyperus papyrus</i>       | Culm                   | 20         | Absent                             | Absent                                     |
| Multicellular silicified tissue with polyhedral morphologies                           | <i>Acacia xanthophloea</i>   | Leaves                 | 50         | 0.2                                | 1  |
| Parallelepiped granulated margin   | <i>Phoenix reclinata</i>     | Leaves                 | 19         | Absent                             | Absent                                     |
| Parallelepiped thin rugose (single or in group)  | <i>Acacia xanthophloea</i>   | Leaves                 | 20         | 9                                  | 23   |
|  | <i>Cyperus immensus</i>      | Leaves                 | 19         |                                    |  |
|  | <i>Cyperus immensus</i>      | Stem                   | 14         |                                    |  |
|  | <i>Kyllinga</i> sp.          | Whole plant            | 3          |                                    |  |
| Parallelepiped smooth (single or in group)   | <i>Hyphaene petersiana</i>   | Leaves                 | 15         | 1                                  | Absent                                     |
| Parallelepiped smooth & stomata cells (in group)                                       | <i>Hyphaene petersiana</i>   | Leaves                 | 7          | Absent                             | Absent                                     |
| Parallelepiped elongates with hat shape in groups                                      | <i>Cyperus papyrus</i>       | Flowers                | 14         | Absent                             | Absent                                     |
|  | <i>Cyperus immensus</i>      | Leaves                 | 7          |                                    |  |
| Trichome   | <i>Sporobolus consimilis</i> | Leaves                 | 1          | 5                                  | 2  |
| Short cell   | <i>Sporobolus consimilis</i> | Leaves                 | 72         | 6                                  | 4  |
| Silica Skeleton long cells smooth  | <i>Sporobolus consimilis</i> | Leaves                 | 1          | 0.4                                | 6  |
| Spheroid echinates (single or in group)  | <i>Phoenix reclinata</i>     | Leaves                 | 27         | 15                                 | 31   |
|  | <i>Phoenix reclinata</i>     | Flower, rachis, roots  | >90        |                                    |  |
|  | <i>Hyphaene petersiana</i>   | Leaves, flower, rachis | 35–43      |                                    |  |
| Spheroid smooth/rugose (single or in group)  | <i>Hyphaene petersiana</i>   | Rachis, flowers        | 31–52      | 6                                  | 3  |
|  | <i>Hyphaene petersiana</i>   | Fruits                 | 95         |                                    |  |
| Stomata cells (single or in groups)  | <i>Cyperus papyrus</i>       | Culm                   | 31         | 0.3                                | 0.01                                       |
|  | <i>Sporobolus consimilis</i> | Leaves                 | 9          |                                    |  |
| Tracheary  | <i>Hyphaene petersiana</i>   | Flowers                | 3          | 0.3                                | 1  |
|  | <i>Phoenix reclinata</i>     | Flower                 | 4          |                                    |  |

The % average presence in modern and fossil soils was calculated and divided by the total number of appearances in the different samples.

- million years). They are indicative of plant parts and specific families (e.g. bulliform cells from grass leaves).
- (e) Elongate morphologies with smooth surfaces tend to become rugose as a result of post-depositional processes. This fact has been already observed in a modern plant reference collection from Israel (Albert and Weiner, 2001).

The macroplants have been identified using a 40 × hand lens to determine their internal anatomy but there is a large proportion of them that are unidentifiable without the preparation of thin sections or scanning electron microscopy. The external morphology was only found to be reliable in identifying the triangular sedge culms; cylindrical or irregularly shaped forms were found to be grasses, sedges, dicots or monocots (when it was not possible to distinguish between grasses and sedges). No palm forms were noted.

### 5. Development of taphonomic model

The taphonomy of angiosperm leaves has been studied extensively (Ferguson, 1985; Burnham, 1989; Gastaldo et al., 1989; Martín-Closas and Gomez, 2004) and the relative durability of plant tissues is known (Cleal, 1991) but less is known about the taphonomy of phytoliths. Phytoliths dissolve in basic conditions with pH above 9 (Benayas, 1963; Piperno, 1988), especially when combined with constant hydric conditions that keeps the pH elevated for long periods of time (Albert et al., 1997, 2000, 2003), but little is known about other mineralogical or taphonomic conditions that can affect the durability of phytoliths. Here, we develop a model based on the observations above for the phytoliths and also outline a comparative model, based on a variety of other works as well as field observations, for the macroplants. The term “preservation” is used here to mean long-lasting survival, without alteration, and the term “petrification” to include chemical alteration resulting in long-lasting survival. Silicification is one form of petrification.

In the natural environment where plants are growing in the soils, rain falls seasonally, resident and migrating animals graze or browse on the plants, plants die and new ones grow, we can assume that there are two cycles in progress, one is the phytolith silica cycle and the other is the macroplant silicification process.

#### 5.1. Phytolith silica cycle

1. Living plants take up monosilicic acid from the moist soil and deposit silica in various cells.
2. Either as a factor of age, increase in humid conditions that favour the heavier silicification of plant cells, or physical attributes of the plant, some phytoliths are robust and some are fragile.
3. Plants are eaten by browsers or grazers and removed from the immediate environment or re-deposited in dung.

4. Some plant parts are present year-round (wood, bark, some leaves) whereas others only appear seasonally (flowers, seeds).
5. The plant dies and disintegrates, leaving the robust and fragile phytoliths in the soil.
6. Phytoliths from the wood and bark of trees will be deposited after the death of the tree or branch. Herbaceous plants, with a shorter life cycle, on the contrary, will be deposited in the soil more frequently. Herbaceous dicots occur in grassland, shrubland and woodland, i.e. are widespread. Trees are confined to woodlands. Their phytoliths should reflect their distribution.
7. It can be assumed then, that herbaceous (monocot and dicot) phytoliths are more abundant than woody dicots in soils.
8. External environmental processes remove or deposit some soil and phytoliths (wind, water erosion) or increase the silica content of the soil e.g. volcanic ash fallout. Since phytoliths become part of the soil, only where soils accumulate will there be an accumulation of phytoliths from other areas.
9. Soil processes (alkalinity, ground water movement, recycling by new roots) can destroy some of the phytoliths, partially dissolve or do not affect the phytoliths.
10. New plants continuously inhabit an undisturbed habitat or eventually recolonise a disturbed habitat, resulting in a net accumulation of phytoliths.
11. The cycle repeats.

There can be a net input of silica, a net loss or equilibrium. In a silica-rich environment such as the Olduvai Basin we do not think that silica would ever be a limiting factor for the formation of phytoliths. The number of phytoliths in the soil will be less than that produced by one generation of vegetation but they would accumulate over hundreds or thousands of years in a stable environment.

#### 5.2. Macroplant silicification process

1. Plants die and disintegrate into leaves, stems, seeds, trunks and roots, most organic parts being recycled by fungi, bacteria and arthropods in a sub-aerial environment.
2. The more robust parts of plants (wood fragments, stems or seeds) are sometimes transported and buried in a saturated anoxic environment, such as a pond or river bank, thus greatly reducing the rate of decomposition.
3. In a monosilicic acid saturated environment where the buried organic material is beginning to decompose so is negatively charged, it attracts the  $\text{Si}^{2+}$  ions and is slowly replaced by silica. (Duration of process unknown but could be quick in certain conditions).
4. New plants inhabit the same environment or the recently deposited sediments.
5. The cycle repeats.

The petrified proportion of the total original vegetation is probably very small, but in such a silica-rich environment such as the Olduvai Basin, we would expect that all the plant fragments that are buried would have a good chance of being petrified. The cycles of burial are probably not seasonal but more likely to be catastrophic events such as mud slides, so called “hundred year” floods or El Niño events.

Assuming that the sediments have not been reworked and based on these two models we would expect the following:

1. Phytoliths are inorganic, internally silicified cells, and do not need to undergo any petrification process. Macroplants are organic and time and suitable conditions are required for the replacement of organic material by mineral silica—petrification.
2. Phytoliths represent a continuous record of vegetation whereas macroplant fossils represent burial (flood) events only.
3. Despite some external factors (wind, water erosion, etc.), phytoliths represent, in general, the immediate vegetation (autochthonous) and macroplant fragments represent transported vegetation (allochthonous or parautochthonous).
4. Phytoliths represent the soft tissues of all herbaceous and woody vegetation (i.e. a greater diversity of plants) whereas the macrofossils represent only the more robust plant parts (low diversity).
5. Post depositional conditions such as ground water movement or change in pH, or root acids, will dissolve or destroy some of the phytoliths but do not affect the already silicified plant fragments.
6. Phytoliths and macroplants are not always expected to be correlated but the presence of each can be complementary and interpreted as such.

As far as we can tell, the main filters (removal of plant material from the preservation cycle) that would introduce biases for phytolith preservation occur at two stages in the cycle. The first stage is between death of the plant and incorporation of phytoliths into the soil. Leaves of trees and grasses are the parts eaten by animals, so depending on the grazing/browsing pressure, these parts of the plants may be under-represented in the record. Some of the leaf material may be returned to the soil in the form of dung but this is usually recognised either by micromorphology or by the identification of faecal spherulites produced by herbivore ruminants when the soil conditions are adequate (Brochier et al., 1992; Canti, 1997, 1998, 1999; Korstanje, 2002; Shahack-Gross et al., 2002; Albert and Henry, 2005). Edible pods and seeds would suffer the same fate as the leaves but thorns should be well represented, as should the bark and wood. Nevertheless, as already pointed out, the bark and the wood of trees will only be represented in the soil after the death of the tree, which does not occur with the same frequency. No work has been done on

phytoliths from roots. Ground vegetation cover, although it will be eaten by certain grazers, is unlikely to disappear completely from the soil phytolith record.

The second filter is post depositional and includes the affects of the soils and soil processes on the phytoliths. Different soils are formed from different parent materials and under different conditions and factors such as fluctuating ground water, pH, chemical composition and bioturbation can dissolve phytoliths partially or completely but may have less of an effect on larger (with respect to the phytoliths) silicified plants.

## 6. Conclusion

### 6.1. Re-interpretation of fossil samples from Olduvai Gorge

As a test case, we consider the phytolith and macroplant samples from LMBII from the eastern palaeolake and at different localities (FLKN, HWKE, HWKEE, VEK and MCK). The phytolith morphological results from each fossil sample (Fig. 4) are compared to the macroplant results (Table 3) and the modern soil samples and interpreted using the taphonomic information above, where the sedge phytoliths are most likely to be under-represented, the palm phytoliths are likely to be a reasonably accurate representation and the dicot phytoliths are likely to be over-represented. Thus, taking both phytoliths and macroplants into account for these well-constrained deposits, the overall interpretation of the palaeovegetation is re-assessed

### 6.2. FLKN

This locality is the most westerly one within the eastern palaeolake margin where most of the research to date has been concentrated. From FLKN (trench 116), the only sample with a minimum amount of phytoliths for a reliable interpretation showed the presence of monocotyledonous plants (grasses) and dicotyledonous plants. Phytoliths from these samples showed strong signs of chemical dissolution. Macroplants are represented by roots and biogenic tubules and can only be interpreted as there having been a vegetated surface and, if the biogenic tubules were formed by invertebrates such as termites, then the ecosystem was well established and complex. Comparing the phytolith presence with the modern soils samples (Fig. 4), the closest in vegetation type would be the open woodland from Lake Manyara (sample 7) where monocots and grasses dominate the phytolith record. Trees would not have been abundant and the vegetation would then have been dominated by monocotyledonous plants and fewer herbaceous dicots during LMBII times (ca. 1.785 myr).

### 6.3. HWKE and HWKEE

Samples from HWKE, trench 115, the palaeolake margin, showed a relatively significant number of phytoliths



where dicotyledonous plants dominate the phytolith record followed by grasses. No macroplant fossils were found. The phytolith assemblage is similar to that from open grassland sample from Olduvai Leakey camp (sample 3), that was dominated by herbaceous vegetation and some *Commiphora* trees (Fig. 4). We interpret the palaeovegetation to be open woodland with dicotyledonous trees and a mixture of grasses and herbs. Sedges may have been present but would be few in number and have not been preserved. The amount of palms is too low but it suggests that these plants would be present in the vicinity of trench 115.

If the macroplant record from HWKEE, trench 107, in the earthy and siliceous earthy claystone layer from 52–92 cm above tuff IF (plant level 3b) is considered first, it shows a rich diversity of plants from a wetland with at least three species of sedge, two grasses, unknown

Table 3

Percentages of macroplant specimens belonging to the different plant groups from fossil soils in Olduvai gorge, lowermost bed II, eastern palaeolake margin

| Localities                | HWKEE Tr-107    | MCK Tr-108     |
|---------------------------|-----------------|----------------|
| Plant groups (%)          | Level 3b plants | Level 7 plants |
| Sedge                     | 5.9             | 18.6           |
| Grass                     | 4.1             |                |
| Monocot                   | 20.0            | 6.6            |
| Palm                      |                 |                |
| Dicot wood/bark           | 1.8             |                |
| Dicot leaves              |                 |                |
| Other                     | 62.3            | 74.6           |
| Total number <sup>a</sup> | 170             | 75             |

<sup>a</sup>The total number of specimens recovered from that level within the 2 m trench.

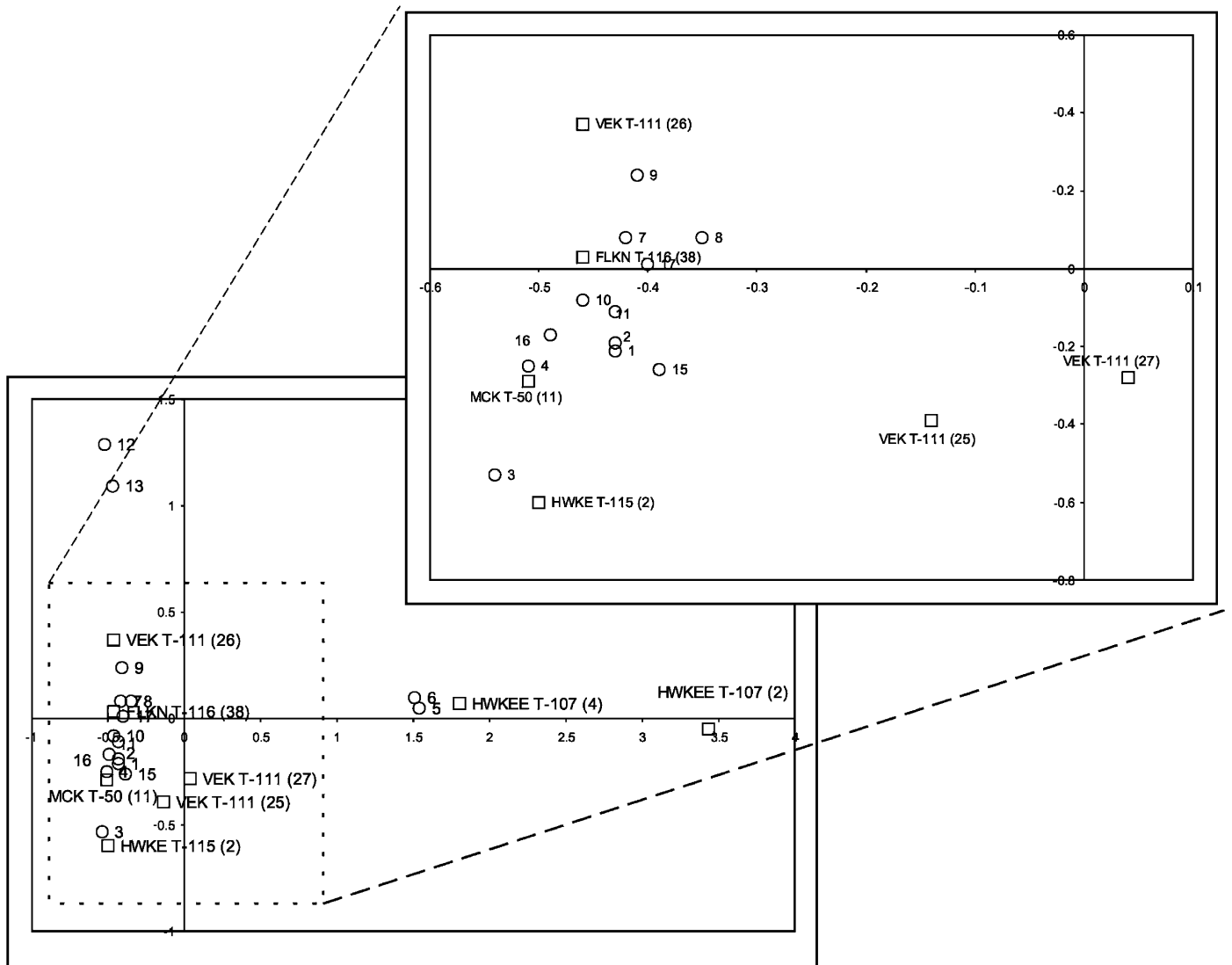


Fig. 4. Results from the correspondence analysis in x-y graphic. Modern soil samples are plotted as circles and palaeoanthropological samples as squares. Soil samples: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17; palaeoanthropological samples: FLKN T-116 (38), HWKE T-115 (2), HWKEE T-107 (2), HWKEE T-107 (4), VEK T-111 (25), VEK T-111 (26), VEK T-111 (27), MCK T-50 (11).

monocots and several dicots (Table 3). Amongst the large number of unidentified plant fragments, there could well be some more dicot and monocot species represented. From our own field observations, we know that the diversity of sedges likely to be preserved in the mud of a typical African wetland is only a fraction of the true diversity (1 of 20 sedge species, 1 of 12 grasses and 1 of 6 dicots; Bamford and Peters, in preparation).

Considering the phytoliths from the same level (HWKEE, trench 107, sample 4, above the calcareous nodular horizon) sedges are absent, and in descending order of abundance are palms, monocots, grasses and dicots. This phytolith assemblage is most similar to the modern soil samples 5 and 6 which are from grassland with clumps of palms spread throughout (Fig. 4). Beneath the clumps are several shrubs and there were signs of animals having rested amongst the vegetation. When the macroplant record is added it shows that sedges were present too and implies that the palaeovegetation was probably denser and richer than the modern analogue.

The sample below 4, sample 2, from this trench shows an overwhelming dominance of palm phytoliths followed by low numbers of monocots, dicots and grasses with no comparison among the modern soil samples (Fig. 4). No macroplants were recovered from this level. (The level below this which is below the calcareous nodular layer and 5 cm above tuff IF, contained no macroplants and too few phytoliths to interpret.) Dicotyledonous leaf phytoliths were also noted and sedges were uncommon. The reinterpretation of this sequence of vegetation is that the palms were more common and their numbers and density reduced over time as the climate dried out and canopy cover was reduced to more open grassland.

#### 6.4. VEK

Below the calcareous nodular layer in VEK (trench 111) phytoliths occurred in low numbers, whereas above this layer, they were relatively abundant and well preserved (sample 27), which is the same pattern as in the HWKEE samples. The VEK samples were dominated by monocots and dicots in different amounts. Spheroid echinate morphologies from palms were less numerous than in both the HWKEE and modern reference samples. Only roots and biogenic tubules (unidentifiable silicified tubes sensu; Bamford et al., *this volume*) occur above tuff IF at this locality. Pollen samples from just above tuff IF indicated predominantly grasses, few sedges, few Sudano-Zambeian elements and Afromontane taxa (Bonnieffille, 1984). The phytolith record of sample 25 is closer to that of the modern sample 15 from the Lake Masek margin with saline tolerant grasses. The fossil site is interpreted as having had a variety of trees or shrubs in a mixed grass and sedgeland but was subject to lake inundation and tree dieback. This locality had more palms and sedges than HWKE trench 115 (2) sample which might be explained by the fact that it was farther from the palaeolake.

Sample 26 is higher up and younger and has a reduction in the wood/bark phytoliths with a corresponding increase in monocots and grasses. This implies no palms, fewer trees, shrubs or herbs and a more open grass-(sedge). Sample 27 shows a shift back to more dicots, but still has lots of monocots, grasses, sedges and palms in the vicinity. The shifts could be a result of climatic shifts such as moister to drier to moister which occur with lake level fluctuations of low, high, low. If that is the case, then the lake levels are out of synchrony with the rainfall.

#### 6.5. MCK

Finally, in phytolith samples from MCK (trench 50, sample 11), in the waxy brown claystone sample, dicotyledonous plants were dominant, followed to a lesser degree by monocots and grasses. The other samples from MCK contained too few phytoliths for a reliable interpretation of the plants represented. Macroplants were recovered from another trench in MCK, trench 108, in level 7, (just above tuff IF and equivalent to this phytolith sample). Most of the macroplants were unidentified but sedges and monocots are present (Table 3). The interpretation of the paleovegetation for this sample would be comparable to that of the open grassland (sample 4) from Olduvai Leaky camp, with monocots, sedges and herbs and few trees in the surroundings but much more species rich.

The palaeovegetation reconstruction of the eastern palaeolake margin of Olduvai Gorge during LMBII times, when phytolith and macrofossil taphonomy are taken into consideration shows that the vegetation varied over small distances (100–200 m) and over relatively short periods of time. The palaeovegetation was also much more diverse and species rich than has been interpreted from other data such as faunal and isotopic analyses. It is possible to reconstruct the vegetation on a small spatial and temporal scale and apply the data to the facet-level models developed by Blumenschine and Peters (1998) for predicting hominin land use. The fine scale sampling of fossil plants and phytoliths can now be applied to other stratigraphic levels and localities, using and expanding the modern plant and soil reference collections, to reconstruct more of the palaeovegetation.

#### Acknowledgements

We thank COSTEC for permission to carry out research at Olduvai Gorge, the excavators and members of OLAPP for assistance in the field, Marta Portillo of the University of Barcelona for preparing the phytolith samples, and Rob Blumenschine for useful discussions. The Ministerio de Ciencia y Tecnología (Spain) is acknowledged for financial support to RMA for the acquisition of the material necessary to perform the digital image data base catalogue and to process the modern soil samples (Ref. BSO2002-12596-E). Financial support was gratefully received from the NSF (SBR-0109027) to OLAPP, and from

Palaeoanthropological Scientific Trust (PAST), South Africa to MKB for actualistic studies in East Africa and South Africa.

## References

- Albert, R.M., 2000. Study of ash layers through phytolith analyses from the Middle Palaeolithic levels of Kebara and Tabun caves. Ph.D. Thesis, Universitat de Barcelona, Barcelona.
- Albert, R.M., Weiner, S., 2001. Study of phytoliths in prehistoric ash layers using a quantitative approach. In: Meunier, J.D., Coline, F. (Eds.), *Phytoliths: Applications in Earth Sciences and Human History*. A.A. Balkema Publishers, Lisse, pp. 251–266.
- Albert, R.M., Henry, D., 2005. Herding and agricultural activities at the early Neolithic site of Ayn Abū Nukhayla (Wadi Rum, Jordan). The results of phytolith and spherulite analyses. *Paléorient* 30/2, 81–92.
- Albert, R.M., Mangado, X., Martín, A., 1997. Study about phytolith preservation in calcareous sediments. Analysis of a stratigraphic column from Cova del Frare (Matadepera, Barcelona). *Estudio actual de los estudios de fitolitos en suelos y plantas*. Monografías 4. Consejo Superior de Investigaciones Científicas, Madrid, Spain, pp. 187–196.
- Albert, R.M., Tsatskin, A., Ronen, A., Lavi, O., Estroff, L., Lev-Yadum, S., Weiner, S., 1999. Mode of occupation of Tabun cave, Mt Carmel, Israel during the Mousterian period: a study of the sediments and phytoliths. *Journal of Archaeological Science* 26, 1249–1260.
- Albert, R.M., Weiner, S., Bar-Yosef, O., Meignen, L., 2000. Phytoliths in the Middle Palaeolithic deposits of Kebara Cave, Mt Carmel, Israel: study of the plant materials used for fuel and other purposes. *Journal of Archaeological Science* 27, 931–947.
- Albert, R.M., Bar-Yosef, O., Meignen, L., Weiner, S., 2003. Phytolith and mineralogical study of hearths from the Middle Palaeolithic levels of Hayonim cave (Galilee, Israel). *Journal of Archaeological Science* 30, 461–480.
- Bamford, M.K., 2005. Early Pleistocene fossil wood from Olduvai Gorge, Tanzania. *Quaternary International* 129, 15–22.
- Bamford, M.K., Albert, R.M., Cabanes, D., 2006. Plio-Pleistocene macroplant fossil remains and phytoliths from Lowermost Bed II in the eastern palaeolake of Olduvai Gorge, Tanzania. *Quaternary International*, this volume, doi:10.1016/j.quaint.2005.11.027.
- Benayas, J., 1963. Disolución parcial de sílice orgánica en suelos. *Anales de Edafología y Agrobiología* tomo XXII (11–12), 623–626.
- Berlin, A.M., Ball, T., Thompson, R., Herbert, S.C., 2003. Ptolemaic agriculture. “Syrian Wheat” and *Triticum aestivum*. *Journal of Archaeological Science* 30, 115–121.
- Blinnikov, M.S., 2005. Phytoliths in plants and soils of the interior Pacific Northwest, USA. *Review of Paleobotany and Palynology* 135, 71–98.
- Blumenschine, R.J., Peters, C.R., 1998. Archaeological predictions for hominid land use in the Palaeo-Olduvai Basin, Tanzania, during lowermost bed II times. *Journal of Human Evolution* 34, 565–607.
- Blumenschine, R.J., Peters, C.R., Masao, F.T., Clarke, R.J., Deino, A.L., Hay, R.L., Swisher, C.C., Stanistreet, I.G., Ashley, G.M., McHenry, L.J., Sikes, N.E., van der Merwe, N.J., Tactikos, J.C., Cushing, A.E., Deocampo, D.M., Njau, J.K., Ebert, J.I., 2003. Late Pliocene Homo and hominid land use from western Olduvai Gorge, Tanzania. *Science* 299, 1217–1221.
- Bonnefille, R., 1984. Palynological research at Olduvai Gorge. *National Geographic Society Research Reports* 17, 227–243.
- Bozarth, S.R., 1992. Classification of opal phytoliths formed in selected dicotyledons native to the Great Plains. In: Rapp, Jr., G., Mulholland, S.C. (Eds.), *Phytolith Systematics. Emerging Issues, Advances in Archaeological and Museum Science*. Plenum Press, New York, pp. 193–214.
- Brochier, J., Villa, P., Giacommarra, M., 1992. Shepherds and sediments: geo-ethnoarchaeology of pastoral sites. *Journal of Anthropological Archaeology* 11, 47–102.
- Brown, D.A., 1984. Prospects and limits of a phytolith key for grasses in the central United States. *Journal of Archaeological Science* 11, 345–368.
- Burnham, R.J., 1989. Relationships between standing vegetation and leaf litter in a pantropical forest: implications for palaeobotany. *Review of Palaeobotany and Palynology* 58, 5–32.
- Canti, M., 1997. An investigation of microscopic calcareous spherulites from herbivore dung. *Journal of Archaeological Science* 24, 219–231.
- Canti, M., 1998. The micromorphological identification of faecal spherulites from archaeological and modern materials. *Journal of Archaeological Science* 25, 434–444.
- Canti, M., 1999. The production and preservation of faecal spherulites: animals, environment, and taphonomy. *Journal of Archaeological Science* 26, 251–258.
- Cleal, C.J., 1991. Plant fossils in geological investigation. *The Palaeozoic. Ellis Horwood Series in Applied Geology* 233pp.
- Ferguson, D.K., 1985. The origin of leaf assemblages—new light on an old problem. *Review of Palaeobotany and Palynology* 46, 117–144.
- Fredlund, G.G., Tieszen, L.L., 1997. Calibrating grass phytolith assemblages in climatic terms: application to late Pleistocene assemblages from Kansas and Nebraska. *Paleogeography, Paleoclimatology, Paleoecology* 136, 199–211.
- Gastaldo, R.A., Bearce, S.C., Deges, C., Hunt, R.J., Peebles, M.W., Violette, D.L., 1989. Biostratigraphy of a Holocene oxbow lake: a backswamp to mid-channel transect. *Review of Palaeobotany and Palynology* 58, 47–59.
- Hay, R.L., 1976. *Geology of Olduvai Gorge*. University of California Press, Berkeley.
- Hay, R.L., 1996. Stratigraphy and lake-margin palaeoenvironments of lowermost bed II in Olduvai Gorge. *Kaupia (Darmstadter Beiträge zur Naturgeschichte)* 6, 223–230.
- Jones, L.H., Beavers, A.H., 1963. Some mineralogical and chemical properties of plant opal. *Soil Science* 96, 375–379.
- Korstanje, A., 2002. Microfossils in camelid dung: taphonomic considerations for the archaeological study of agriculture and pastoralism. In: O’Connor, T.T. (Ed.), *Biosphere to Lithosphere*. Ninth ICAZ Conference, Durham, pp. 69–77.
- Leakey, L.S.B., 1967. *Olduvai Gorge 1951–1961 Volume I. A Preliminary Report on the Geology and Fauna*. Cambridge University Press, Cambridge.
- Madella, M., Jones, M.K., Goldberg, P., Goren, Y., Hovers, E., 2002. The exploitation of plant resources by Neanderthals in Amud cave (Israel): the evidence from phytolith studies. *Journal of Archaeological Science* 29, 703–719.
- Madella, M., Alexandre, A., Ball, T., 2005. International code for phytolith nomenclature 1.0. *Annals of Botany* 96, 253–260.
- Martín-Closas, C., Gomez, G., 2004. Taphonomie des plantes et interprétations paléocologiques. Une synthèse. *Geobios* 37, 65–88.
- Mercader, J., Runge, F., Vrydaghs, L., Doutrelepon, H., Corneile, E., Juan-Treserras, J., 2000. Phytoliths from archaeological sites in the tropical forest of Ituri, Democratic Republic of Congo. *Quaternary Research* 54, 102–112.
- Mulholland, S.C., Rapp Jr., G., 1992. A morphological classification of grass silica-bodies. In: Rapp Jr., G., Mulholland, S.C. (Eds.), *Phytolith Systematics. Emerging Issues, Advances in Archaeological and Museum Science*. Plenum Press, New York, pp. 65–89.
- Ollendorf, A.L., 1992. Toward a classification scheme of sedge (Cyperaceae) phytoliths. In: Rapp Jr., G., Mulholland, S.C. (Eds.), *Phytolith Systematics. Emerging Issues, Advances in Archaeological and Museum Science*. Plenum Press, New York, pp. 91–111.
- Ollendorf, A.L., Mulholland, S.C., Rapp Jr., G., 1987. Phytoliths from some Israeli sedges. *Israel Journal of Botany* 36, 125–132.
- Pearsall, D.M., Chandler-Ezell, K., Zeidler, J.A., 2004. Maize in ancient Ecuador: results of residue analysis of stone tools from the Real Alto site. *Journal of Archaeological Science* 31, 423–442.

- Peters, C.R., Blumenschine, R.J., 1995. Landscape perspectives on possible land use patterns for Early Pleistocene hominids in the Olduvai Basin, Tanzania. *Journal of Human Evolution* 29, 321–362.
- Piperno, D.R., 1988. *Phytolith Analysis: An Archaeological and Geological Perspective*. Academic Press, San Diego.
- Rosen, A.M., Weiner, S., 1994. Identifying ancient irrigation: a new method using opaline phytoliths from emmer wheat. *Journal of Archaeological Science* 21, 125–132.
- Runge, F., 1999. The opal phytolith inventory of soils in central Africa—quantities, shapes, classification, and spectra. *Review of Palaeobotany and Palynology* 107, 23–53.
- Shahack-Gross, R., Marshall, F., Weiner, S., 2002. Geo-ethnoarchaeology of pastoral sites: the identification of livestock enclosures in abandoned Maasai settlements. *Journal of Archaeological Science* 30, 439–459.
- Twiss, P.C., Suess, E., Smith, R.M., 1969. Morphological classification of grass phytoliths. *Soil Science Society of America* 33, 109–115.
- Weiner, S., Goldberg, P., 1990. On-site Fourier transform-infrared spectrometry at an archaeological excavation. *Spectroscopy* 5, 46–50.
- Zucol, A.F., Brea, M., Scopel, A., 2005. First record of fossil wood and phytolith assemblages of the Late Pleistocene in El Palmar National Park (Argentina). *Journal of South American Earth Sciences* 20, 33–43.