



Bed II Phytolith Palaeolandscapes (1.5-1.1 Ma) at Oldupai Gorge, Tanzania

Makarius Peter Itambu

Department of Archaeology and Heritage Studies, College of Humanities, University of Dar es Salaam, P.O. Box 35050, Dar es Salaam, Tanzania.

E-mail: mcpeter7@gmail.com ORCID: <https://orcid.org/0000-0001-5517-5500>

Received 4 Jun 2022, Revised 13 Sep 2022, Accepted 21 Sep 2022, Published Sep 2022

DOI: <https://dx.doi.org/10.4314/tjs.v48i3.12>

Abstract

The primary approach for reconstructing ancient plant landscapes is normally through the analysis of environmental proxy data and ultimately the application of the data from plant micro-remains to infer the vegetation patterns, distribution, and nature of past environments. Phytolith analyses serve as an important tool for identifying different micro-ecological niches in which human activities occurred. They are indicative of certain plant types and vegetation patterns, and the way in which plant landscapes respond to regional climate changes. Hence, in order to understand the ancient plant landscape of the Pleistocene Bed II sites of Oldupai Gorge 1.5 to 1.1 million years ago (Ma), a location inhabited by our early ancestors, the phytoliths research was conducted in order to reconstruct the ancient plant environments of Oldupai's Bed II sites, namely Sam Howard Korongo (SHK), Thiongo Korongo (TK), and Bell's Korongo (BK) because there is no enough phytolith data from these upper sections of Bed II. The preliminary results from this study indicate that TK and BK sites' plant landscape was dominated by arboreal plants.

Keywords: Phytolith, hominin, palaeoecology, palaeoenvironments, palaeolandscape.

Introduction

Phytoliths are plant biosilica microminerals (silica minerals) that form within and between cells of different plant structures and are used as diagnostic markers of plant families or ecosystem functional groups (Strömberg 2004). Phytoliths are produced when soluble silica (monosilicic acid) is absorbed along with ground water during plant growth. This soluble silica is eventually deposited as solid silica within and between plant cell walls (Mercader et al. 2011, Itambu 2020). When silica enters plants through their roots, and when the plants take up water from the soil, silica minerals are always distributed throughout plants and into different parts, such as the stem, bark, or leaves. Eventually, silica forms into specific shapes that are representative of

the plants that produced it. When a plant dies and decays, most of its phytoliths are released directly into the soil, creating a highly localised in situ assemblage (Strömberg 2004). Similarly, when the plants die and decompose, the hard phytoliths are released into the soil and can be preserved for millions of years (Pearsall and Trimble 1983, Piperno 1988, Pearsall and Piperno 1993, Strömberg 2004). In other words, phytoliths are plant biosilica microfossils that form within and between cells of different plant structures (i.e., stems, leaves, fruits, and bark) and are used as diagnostic markers of plant families or ecosystem functional groups.

Phytoliths are morphologically distinct, consistent, and resistant to decomposition in most sedimentary environments. The shapes of phytoliths in many plants are highly

distinctive and, in rare cases, are identifiable to species level (Mercader et al. 2011, Itambu 2020). Phytoliths are also useful in the genetic classification of the soil. In many cases, phytolith assemblages are either directly or predictably representative of original vegetation types and abundances, and have been used worldwide, mostly in North and South America, to reconstruct past ecosystems (Strömberg 2004) such as forested or grass-dominated habitats. When we find these phytoliths along with archaeological remains, we interpret their distinct shapes to infer ancient plant landscapes in which human activities happened in the past (Itambu 2020).

Due to their exceptional preservation in palaeosols, phytoliths are incorporated as components of archaeological research across the globe such as in the Americas, Europe, and Asia. Phytoliths have been used in archaeological and environmental studies to reconstruct palaeolandscapes (Itambu 2017, 2020, Mercader et al. 2021), subsistence strategies (Piperno and Pearsall 1993), and prehistoric plant use (Madella et al. 2005) for several decades. In North America, phytolith analysis has been a powerful tool for reconstructing palaeoenvironments (Fredlund and Larry 1994), while in Europe, phytolith research has been used as a proxy to reconstruct early-to-late Miocene vegetation structure (grassland vs. forest) localities in Greece and in reconstructing grass-dominated habitats in Turkey during the Cenozoic (Itambu 2020). In addition, phytolith research has generated data on vegetation history that has acted as a proxy for environmental and climatic information from Quaternary sediments and has been applied to study natural components of vegetation, seasonality, and climatic fluctuations during the Quaternary-Pleistocene times.

Phytoliths and palaeoenvironmental reconstruction in Africa

Although phytolith studies have been carried out on modern soils from Central Africa, West Africa and East Africa, quantitative work on silica bodies from living African plants is scarce, and only focuses on

grasses from two phytochoria north of the equator (Mercader et al. 2009): the Somalia-Masai and the Sudano-Sahelian (White 1983, Mercader et al. 2011) vegetation zones. In addition, an extremely small amount of qualitative information is known about the phytoliths produced by some African trees and bushes from the Guineo-Congolian region (Mercader et al. 2011). Similar studies were conducted by Barboni et al. (2010) in the Afar region, Ethiopia, and on the Zambezi vegetation zone by Mercader et al. (2011), which focused on phytolith analysis from modern sediments, plants, and palaeosol sediments that provided the first quantitative taxonomy of phytoliths for the largest phytochorion of sub-Saharan Africa (Zambezi ecotone). These are now available and valuable assets for palaeoecological reconstruction in the region.

Several compendia have shown the importance of understanding phytolith production, reference collections, and the information that phytoliths from modern surfaces reveal about the vegetation growing on these surfaces today in the Sudano-Zambezi and Somalia-Masai vegetation zones (Mercader et al. 2011, 2019). The comparisons of modern phytoliths from plants and terrestrial sediments are the only way to normalize the taphonomic biases that we encounter in the fossil record. These modern types are analogues for interpreting ancient phytoliths. Because of that, I utilized modern referentials already published and the extracted phytoliths from selected plant taxa known to represent local ecosystems in Ngorongoro region by Mercader et al. (2019). These samples were made accessible through a collaboration research with the Arusha Herbarium (Tanzania).

In the Oldupai Gorge region and the adjacent areas, phytoliths have been a useful tool for palaeoecological reconstruction (Bamford 2012, Barboni 2012, Mercader et al. 2019, 2021, Itambu 2020). When applied to archaeological contexts, phytoliths have helped identify plants used by prehistoric populations, but also to aid in distinguishing between those used by people, and those that are natural accumulations and represent past

vegetation (Mercader et al. 2019). The preservation of phytoliths in the African fossil record makes them one of the most valuable tools for studying hominin plant communities. Furthermore, the palaeoethnobotanical interpretation of phytoliths relies on the comparison of ancient types with morphotypes extracted from living reference collections (Mercader et al. 2019, Itambu 2020).

Multiple types of proxies have been utilized recently to reconstruct the overall environmental context of human evolution in Africa, including pollen, stable isotopes, and phytoliths (Hay 1976, Leakey 1976, Bunn 1996, Copeland 2007, Itambu 2020). There is also macrobotanical data composed of silicified macro-remains of wood, leaves, roots, and silicified fruits (Bamford 2012). Previous research conducted in this region using stable carbon isotopes ($\delta^{12}\text{C}$ and $\delta^{13}\text{C}$) measured from palaeosol carbonated nodules, bulk organic matter, and lipid biomarkers evaluated the relative abundance of C_3 (mainly woody plants but also mesophytic and aquatic herbaceous) versus C_4 plants (mostly tropical grasses, but also some sedges, and xerophytic dicots) (Ashley et al. 2010a, Barboni 2012, Patalano 2019). Overall, these studies detail a diverse landscape composed of complex vegetation patterns linked to oscillating precipitation, varying lake levels, and the presence of geological faults with reconstructed paleo-precipitations at 250-700 mm/y. C_4 grasslands, closed woodlands, wetlands, and palm-groves seemed to occur on short spatial scales near saline Lake Oldupai (Barboni 2012, Itambu 2020).

At Oldupai Gorge (Figure 1), available palaeoecological and palaeoenvironmental evidence from previous research suggests a vegetation record composed of silicified macro-remains such as pieces of wood, leaves, roots, and silicified fruits (Bamford 2012), organic microremains such as pollen grains, and phytoliths (Patalano 2019). Although an extensive bibliography exists on phytolith-based environmental reconstruction for Bed I (Barboni 2012), very little information exists for Bed II or the rest of the

Oldupai Gorge's upper sequences and it is this avenue that this research wanted to underscore.

Bed II at Oldupai Gorge (1.7-1.1 Ma) (Hay 1976, Leakey 1976, Dominguez-Rodrigo et al. 2007, Egeland 2014) is of special geoarchaeological interest because of its lithofacies and environmental palaeo-lake deposits, and aeolian and alluvial sediments (see Figure 1). This bed is important because its archaeological layers contain numerous records that represent the earliest stone tools (Palaeolithic industries) and the transition from the Oldowan, to the Acheulian industries. Bed II layers also yield one of the most continuous records of human bio-cultural evolution for the last two million years (Hay 1976, Leakey 1976, Dominguez-Rodrigo et al. 2007, Benito-Calvo and De la Torre 2011, Egeland 2014). These archaeological records, however, have had very few palaeobotanical analyses that are crucial for palaeoenvironmental reconstruction during the transition period despite a substantial number of taphonomical, archaeological, and anthropological studies that have been conducted in upper Bed II sites. The stratigraphic sequences that I worked are found in the upper sections of Bed II (Sam Howard Korongo, 1.5-1.34 Ma), famously known as the site of SHK (Leakey 1976, Diez-Martín et al. 2014), the Bell's Korongo (BK site, 1.3 Ma), and the Thiongo Korongo (TK site, 1.3-1.1 Ma). The lithofacies represented in these Bed II sites are varied but include both lacustrine and fluvial deposits (Hay 1976, Leakey 1976, Dominguez-Rodrigo et al. 2007, Benito-Calvo and De la Torre 2011).

In the case of SHK (1.5-1.3 Ma), the archaeological levels are found in both the filling and the margins of various channels that were an integral part of a wider lacustrine system. SHK is located in the mouth of a lateral gully, the outlet of which is positioned on the right bank of the Side Gorge, two km from the confluence with the Main Gorge (Leakey 1976, Hay 1976, Diez-Martín et al. 2014). Archaeologically, SHK is one of the most important localities for Bed II; the site was discovered by S. Howard in

the framework of the 1935 expedition to Oldupai Gorge (Leakey 1976, Diez-Martín et al. 2014). SHK preserves a rich accumulation of lithic artifacts and fossil bones (Leakey 1976), along with a 0.75 m tuff in the annex laterally related to 2.4 m of tuffs and clayed tuffs overlying the channel in the main site (Hay 1976, Diez-Martín et al. 2014). Its geological context is characterized by broad, flat muddy plains, which are clayish and show signs of subaerial exposure (Hay 1976). Fluvial and aeolian facies are represented by layers with variable thickness (up to 1 m) of tuffaceous muds, massive in aspect. At the contact between both lithofacies, small fluvial channels with coarse bed loads display many archaeological materials deposited within these channels (Hay 1976, Leakey 1976).

In the same vein, the TK site (1.3-1.1 Ma) stratigraphically represents a palaeolandscape context for the Oldowan–Acheulean transition. Its stratigraphic sequences have produced data that links human activities and stone tools manipulation to process food, also; preserves the highest concentration of lithic artifacts of any site in Bed II (Domínguez-Rodrigo et al. 2007, Santonja et al. 2014). It is believed to have been occupied

by early humans on a flat palaeosurface of clay stone and calcrete (Yravedra and Cobo-Sánchez 2015). It was also in the vicinity of a quartzite ridge and most probably in the proximity to water collection points. The TK site is characterized by volcanic and sedimentary outcrops, clasts of conglomerates, lacustrine, clays, stones, and fluvial deposits that are geologically common in most Bed II localities (Hay 1976).

The BK site is also situated in Bed II of Oldupai Gorge, above tuff IID (1.3 Ma). Stratigraphically, the site's archeological deposits are located just above Tuff IID, which was previously dated to 1.2 Ma (Leakey 1976, Hay 1976) and, more recently, to 1.35 Ma (Domínguez-Rodrigo et al. 2013). This locality, BK, is made up of the alluvial and fluvial deposits of a medial to distal fan zone and floodplain facies association. The sediments accumulation originated in the eroding slopes of Lemagrut, a volcano located at the south of the Oldupai Basin (Hay 1976). The sedimentary record of the study area contains a rich faunal and cultural record of our earliest ancestors that is important to human evolutionary studies (Ashley et al. 2010b).

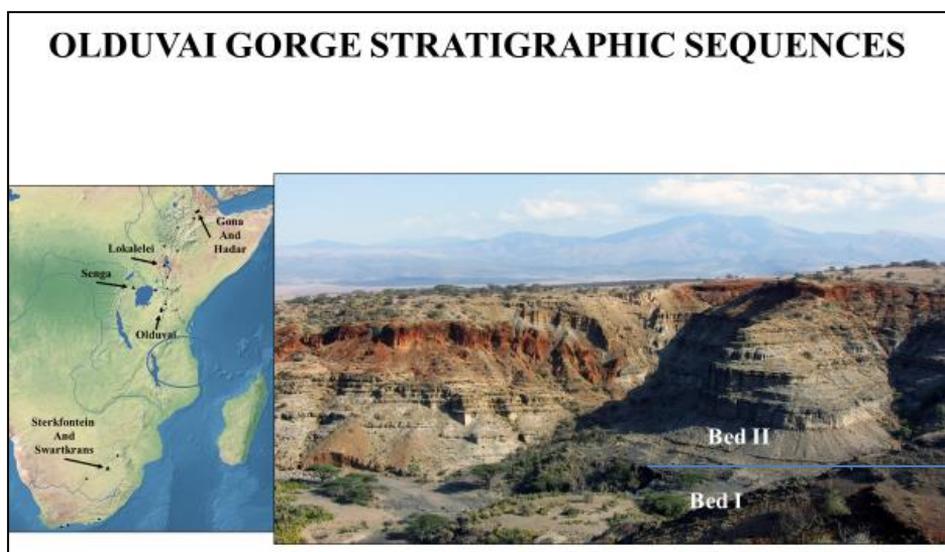


Figure 1: Location of the study area: The Oldupai Gorge sites (Photo credits: Courtesy of Patalano 2015).

Materials and Methods

The study builds upon existing microbotanical research methods used to reconstruct palaeolandscapes in sites with a diverse sedimentary context/setting like Oldupai Bed II (Mora and de la Torre 2005, Diez-Martín et al. 2014). For instance, it has been argued (Hay 1976, Leakey 1976, Yravedra and Cobo-Sánchez 2015) that most of the Bed II sites (such as Thiongo Korongo) are located along ancient complex sedimentary environments such as rivers, streams, and fluvial channels.

A hypothesis about variability of the ecological setting, bones, and stone tools density could allow the identification of hominin behavioural variability along the unearthed, well-preserved portion of the local palaeo-landscape present at these sites. This is especially true of the sedimentary units that consist of a fluvial channel and part of its adjacent overbank, both of which are covered by Tuff 2C (Santonja et al. 2014, Diez-Martín et al. 2014). The remarkably abundant accumulations of fossil bones and lithic artifacts that occur on both features could be representative or be contemporaneous features of the same palaeolandscape. In the same vein, it is theorized that sites comprising a diversity of sedimentary environments, i.e., Sam Howard Korongo (SHK) and Frida Leakey Korongo North (FLK N), reflect a variety of positions in the greater horizon that may prove optimal to address the questions above. These sites had high-energy depositional river channels that could have impacted the plants' landscape during early Pleistocene times. This study concentrated on the Oldupai Gorge Bed II sites SHK (1.5-1.3 Ma), TK (1.3-1.1 Ma), and BK (1.3-1.1 Ma). For example, Diez-Martín et al. (2015) argued that Bed II sites are attributable to the Acheulean and *Homo erectus*. Therefore, these sites are crucial for

understanding Bed II plant landscapes, early humans environmental niches, and the context in which the transition from the Oldowan to the Acheulean occurred.

The sediment samples that were collected for phytolith analysis at SHK are bracketed by marker Tuffs IIA and IIC. Three archaeological horizons have been identified at SHK—A, B, and C (Diez-Martín et al. 2014). The lowermost horizon (A) has the highest energy consisting of sandy silt with pebbles and cobbles. The other two horizons (B and C) represent a low energy environment with clay decantation from lacustrine (shoreline) environments. The entire sediment package of SHK is presumed to have taken place within 200,000 years (1.53 and 1.34 Ma), but the archaeological horizons A, B, and C are interpreted as being deposited within several thousand years according to taphonomic analysis of bone materials (Dominguez-Rodrigo et al. 2007).

Sampling procedures

Sampling of sediments was done both horizontally and vertically for landscape scale (offsite-spatial sampling), regional scale over the landscape, and local scale (site-temporal sampling at SHK) to reconstruct paleovegetation at the sampling spot (Figure 2). Sampling was performed by age, strata, levels, and associated units. The geological samples were taken from outcrops exposed on the palaeosols in the gully over an area of about 50-100 km² at three localities in Bed II of Oldupai Gorge. In addition, the sediment samples were collected in excavated stratigraphic sections at SHK, BK, and TK whereby controlled excavations by layers, unit, age, and size on both trenches and exposed paleosols were carried out, and samples were collected spatially and temporally across the dug trenches.

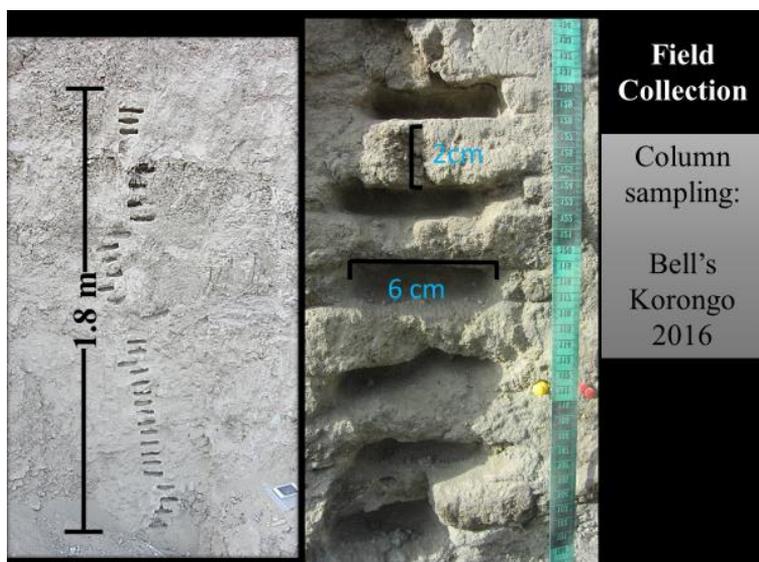


Figure 2: High resolution sediments collection and sampling strategies at BK site.

Laboratory methods

In the laboratory, sediment samples passed through grinding, sieving, sonic cleaning, and acid treatment (following Madella et al. 2005 and the modifications made by Mercader 2016 protocol). After phytolith extraction, phytoliths were counted and quantified. The percentage of each morphotype identified per species was calculated, and their types were described according to the descriptors from the International Code for Phytolith Nomenclature. Phytoliths were identified at magnifications of 400x (Olympus standard light microscope).

Counting: The issue of counting phytolith morphotypes to obtain valid ecological interpretations has been very controversial in African palaeoethnobotany, and significant debate has ensued (Strömberg 2004, Albert et al. 2006, Mercader et al. 2009). Some authors count a minimum of 200 consistent types (Albert et al. 2006), while others count up to 200 Poaceae short cell types regardless of how many phytoliths of other categories may be present (Strömberg 2004), thus resulting in much higher overall counts that are often in excess of 500 total phytoliths. I followed the latter system, for it seems to yield more reliable and reproducible reconstructions.

Classification system: The International Code for Phytolith Nomenclature was followed. To make environmental inferences, the same morphotypes that previous work in tropical Africa has shown to provide the strongest basis for palaeovegetation structure reconstruction were used.

Modern referentials: After the laboratory analysis, along with the counting and the identification of phytoliths, phytoliths from living plants and modern sediments were compared with those found in palaeosols at Bed II sites. This was done in order to provide an indication of which plants and plant parts are represented in the ancient soils, whether or not they relate to the extant vegetation, and some of the ways in which the types of soil affect the preservation, translocation, and diversity of the phytoliths. For referential baseline, published dataset from this region were used, the phytolith datasets were applied in order to better interpret palaeoenvironments and reconstruct ancient vegetation patterns across the palaeolandscapes.

Results and Discussion

The palaeoenvironmental reconstructions of the BK, TK, and SHK sites through phytolith analysis reported in this study infer arboreal plant landscapes, which were

composed of more xeric grassland landscapes utilized by early hominins, as well as the distribution of ancient vegetation patterns across the Oldupai palaeolandscape. The key phytolith morphotypes to infer palaeovegetation from the ancient sediments, as per the reference datasets as well as other pertinent supporting bibliography, include globular granulates from dicot trees and shrubs (Mercader et al. 2019, Itambu 2020) (Figures 3 and 7). Other arboreal indicators are the blocky type and tabular elongate types (Figure 5), globular psilates and cylindroids (Figures 5 and 6), tabular sinuates with heavily decorated surfaces, and globular echinates and short saddles from xeric chloridoid grasses (Figures 3, 4, and 6).

The dominance of phytolith percentages that represent wood types would suggest that

hominins at TK and BK were probably occupying a wooded landscape during the period of 1.3-1.1 Ma, even after the disappearance of the Oldupai palaeolake, while at SHK preservation is not clear, so it is so difficult to ascertain or affirm the nature and patterns of the plant landscape during the time in question. The ecological niches would therefore be reconstructed as to include forests, dense and open woodlands, and grasslands at TK and BK. It is significant that altogether, phytolith assemblages suggest that the arboreal cover is overrepresented by phytolith types from both sites during Upper Bed II time. The saddle phytoliths from short cell grasses from TK site (Figure 6) would suggest an increase in drying trends towards upper sections of TK site.

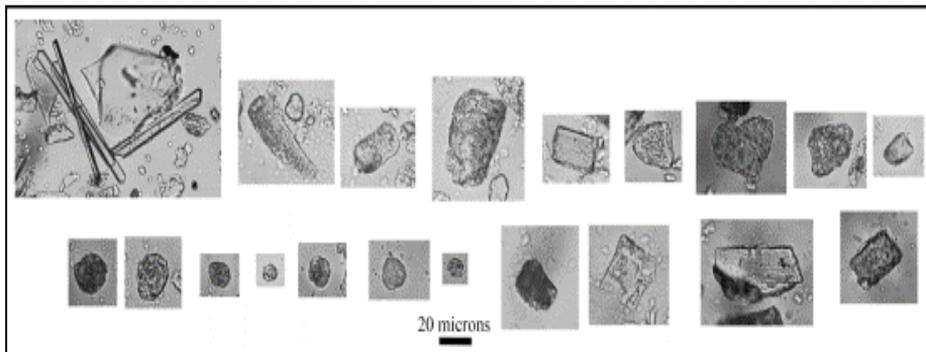


Figure 3: Arboreal phytoliths extracted from TK site (cork/bark).

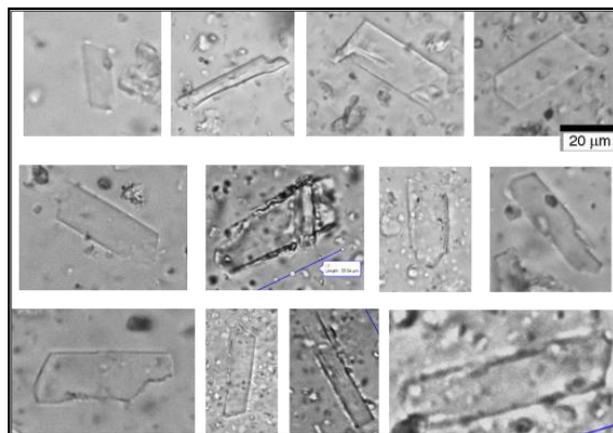


Figure 4: Tabular elongate morphotypes from BK site.

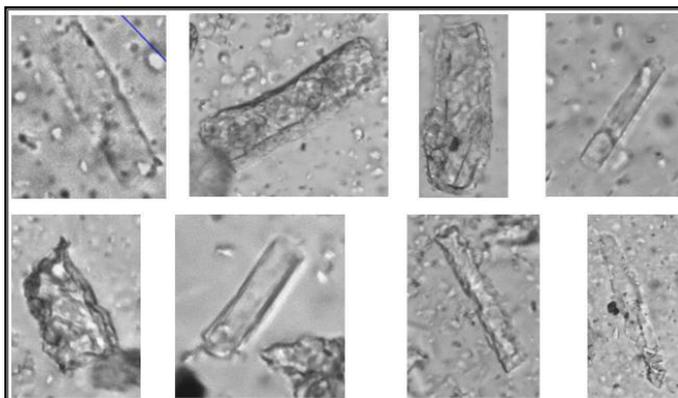


Figure 5: Tabular thick and blocky morphotypes from BK site.

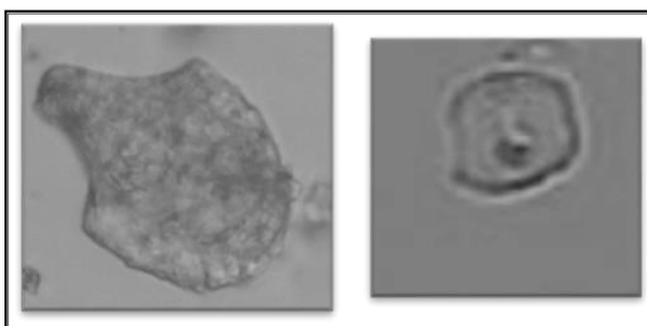
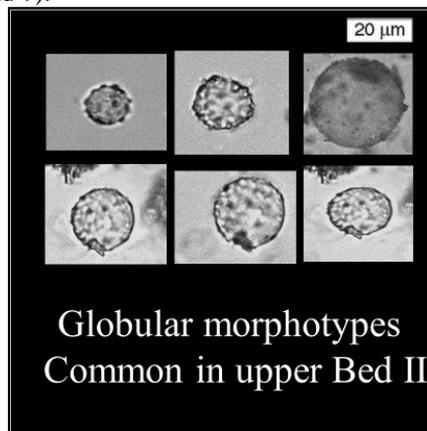


Figure 6: Bulliform and short cell (saddle) phytoliths from BK site.

Globular morphotypes are common in upper Bed II at both TK and BK sites

Overall, key phytolith morphotypes, especially the globular granulates, globular psilates, and globular crenates, revealed the abundance of phytoliths from wood taxa, which represented more than 40% of the total counts. Other arboreal/woody taxa at both BK and TK sites (Figures 5–7) are represented by blocky, cylindroids, tabular thick, cylindrical, and elongate phytoliths, which characterize more than 30% of the total morphotypes analyzed. In all the samples that were counted, there was a good number of globular granulates and globular psilates (Figure 7); these are the key morphotypes that dominate the entire analyzed assemblages in this study. Some grasses were represented in a lower percentage, together with very few other undiagnostic morphotypes that could be probably common in both woody and grassy taxa. The common morphotypes identified representing grasses are saddles, rondels, and

a very low number of bulliforms (Figures 6 and 7).



**Globular morphotypes
Common in upper Bed II**

Figure 7: Globular granulate and globular crenate phytoliths.

However, very few phytoliths preserved at SHK site would require a better refined phytoliths extraction protocol and methodology in the laboratory, although it has confirmed that phytoliths are present and

preserved at the SHK ancient soils and sediments. At the SHK site, although the preserved phytoliths assemblage was not inasmuch as at the TK and BK, the woody dicot types were common with no grass short cells counted. Very few elongate and globular shapes were extracted from the SHK site. The relatively low counts at the SHK site could suggest the presence of complex ancient sedimentary environments such as winnowing or high energy sedimentary environments that are not highly conducive for phytolith preservation. Again, this will require another study at the SHK site which will be extensive and will entail large landscape-oriented sampling approaches (Itambu 2020).

In these three sites, phytolith analysis was accomplished in order to identify vegetation changes and to reconstruct paleoenvironments of the sites that are characterized by ancient fluvial channels, springs, and high energy deposition of sediments like SHK site. Here, phytoliths are used as an important tool for diagnostic markers in plant systematics because they are proxy indicators, especially when one is trying to make some inferences about drying climatic trends of the early Pleistocene for paleoenvironmental reconstruction. Additionally, phytoliths in this research are potential sources of information for reconstructing structural changes in grasslands/woodlands throughout Bed II time. This is especially true because previous studies have indicated that generic woody plant phytoliths are representative of the landscape openness of the vegetation in tropical Africa (Albert et al. 2006, Bamford 2012, Mercader et al. 2019, Itambu 2020).

Conclusions and Way forward

Phytolith characterization by this research has inferred the habitat patterns of early humans and the nature of plants' landscape, which are corroborative and concordant with other archaeological and correlative data of the palaeoecology from the same region, as evinced by the changing tool technologies and their micro-plant data. In order to understand the ancient plant landscape of the

Pleistocene for Oldupai Gorge 1.5 to 1.1 Ma, a location inhabited by our early ancestors, this research studied phytoliths to reconstruct the environments of the Oldupai Bed II sites Thiongo Korongo (TK) and Bell's Korongo (BK). The results presented herein will expand the research on phytolith analysis and its usefulness as an archaeological and environmental proxy at Oldupai's Bed II and other upper sequences such as Beds III-V. Further phytolith analysis of the upper beds and other younger sequences will help to establish the relationship between human ecology and changing climatic conditions at the Oldupai Gorge region entirely.

It is therefore commendable for this research to result in a sustainable practice in palaeoanthropology in which research is led by Africans themselves, because it will inspire others to follow the footsteps of this author. Currently, there are very few African nationals who are trained in phytolith analyses and who are working in this area of expertise. It is high time that our governments include the training and capacity building of young scholars in archaeometry, specifically in emergent new lab techniques and protocols will help mobilize knowledge and create sustainable practice for future research endeavours of this nature of Tanzania. Phytolith analysis, a research method that has been employed for decades, has never been enticing to the interests of African archaeologists. However, this type of lab analysis only requires modest capital investment and small functioning labs which can be established easily at African universities.

Acknowledgements

I wish to express my sincere gratitude to Prof. Julio Mercader and his Tropical Archaeology Laboratory (TAL-University of Calgary) for the assistance in the lab and offering me the equipment and facilities. I am also so thankful to the project members of Stone Tools, Diet, and Sociality (SDS) for their help in various capacities in the field and lab, as well as the University of Calgary undergraduate and graduate students who helped me run the samples for phytolith

analysis in the lab. Lastly, I am grateful to have worked with the local Maasai from the Oldupai region in a myriad of avenues during data collection.

Declaration: The author declares that no competing interests exist.

References

- Albert RM, Bamford MK and Cabanes D 2006 Taphonomy of phytoliths and macroplants in different soils from Oldupai Gorge (Tanzania) and the application to Plio-Pleistocene palaeoanthropological samples. *Quat. Int.* 148: 78-94.
- Ashley GM, Barboni D, Dominguez-Rodrigo M, Bunn HT, Mabulla AZP, Diez-Martín F, Barba R and Baquedano E 2010a Palaeoenvironmental and palaeoecological reconstruction of freshwater oasis in savannah grassland at FLK North, Oldupai Gorge, Tanzania. *Quat. Res.* 74: 333-343.
- Ashley G, Dominguez-Rodrigo M, Bunn HT, Mabulla AZP and Baquedano E 2010b Sedimentary geology and human origins: A fresh look at Oldupai Gorge, Tanzania. *J. Sed. Res.* 80: 703-709.
- Bamford MK 2012 Fossil sedges, macroplants and roots from Oldupai Gorge, Tanzania. *J. Hum. Evol.* 63: 351-363.
- Barboni D, Ashley GM, Dominguez-Rodrigo M, Bunn HT, Mabulla AZ and Baquedano E 2010 Phytoliths infer locally dense and heterogeneous paleovegetation at FLK North and surrounding localities during upper Bed I time, Olduvai Gorge, Tanzania. *Quat. Res.* 74(3): 344-354.
- Barboni D 2012 Phytolith signal of aquatic plants and soils in Chad, Central Africa. In: *Review of Palaeobot. Palynol.* 178: 43-58.
- Benito-Calvo A and de la Torre I 2011 Analysis of orientation patterns in Oldupai Bed assemblages using GIS techniques: Implications for site formation processes. *J. Hum. Evol.* 61: 50-60.
- Bunn HT 1996 Reply to Rose and Marshall. *Curr. Anthropol.* 37: 321-323.
- Copeland SR 2007 Vegetation and plant food reconstruction of lowermost Bed II, Oldupai Gorge, using modern analogs. *J. Hum. Evol.* 53: 146-175.
- Diez-Martín F, Sánchez-Yustos P, Uribelarrea D, Domínguez-Rodrigo M, Fraile-Márquez C, Obregón RA, Díaz-Muñoz I, Mabulla A, Baquedano E, Pérez-González A and Bunn HT 2014 New archaeological and geological research at SHK main site (Bed II, Oldupai Gorge, Tanzania). *Quat. Int.* 322-323: 107-128.
- Diez-Martín F, Sánchez Yustos P, Uribelarrea D, Baquedano E, Mark DF, Mabulla A, Fraile C, Duque J, Díaz I, Pérez-González A and Yravedra J 2015 The Origin of the Acheulean: The 1.7-million-year-old site of FLK West, Oldupai Gorge (Tanzania). *Sci. Rep.* 5: 17839.
- Dominguez-Rodrigo M, Barba R and Egeland CP 2007 Deconstructing Olduvai: A taphonomic study of the Bed I sites, Vertebrate *Paleobio. Palaeoanth. Ser.* Springer Science & Business Media.
- Domínguez-Rodrigo M, Pickering TR, Baquedano E, Mabulla A, Mark DF, Musiba C, Bunn HT, Uribelarrea D, Smith V, Diez-Martin F and Perez-Gonzalez A 2013 First partial skeleton of a 1.34-million-year-old *Paranthropus boisei* from Bed II, Olduvai Gorge, Tanzania. *PLoS One* 8(12): e80347.
- Egeland CP 2014 Taphonomic estimates of competition and the role of carnivore avoidance in hominin site use within the Early Pleistocene Oldupai Basin. *Quart. Int.* 322-323: 95-106.
- Fredlund G and Larry TT 1994 Modern phytolith assemblages from the North American Great plains. *J. Biogeo.* 21(3): 321-335.
- Hay RI 1976 Geology of Oldupai Gorge. University of California Press, Berkeley.
- Itambu MP 2017 Bed II Phytolith palaeolandscapes at Oldupai Gorge (Tanzania), a paper presented at the

- EAAPP Conference, Addis Ababa-August 2017.
- Itambu MP 2020 *Diversity of plant niches available for hominin settlement during upper Bed I-Lower Bed II: A phytolith perspective, Oldupai Gorge (Tanzania)*. PhD dissertation, Calgary-Alberta.
- Leakey L 1976 Oldupai Gorge. A report on the evolution of the hand-axe culture in Beds I-IV. Cambridge University Press.
- Madella M, Alexandre A and Ball T 2005 International code for phytolith nomenclature 1.0. *Ann. Bot.* 96: 253-260.
- Mercader J, Bennet T, Esselmont C, Simpson S and Walde D 2011 Soil phytoliths from miombo woodlands in Mozambique. *Quart. Res.* 75(1): 138-150.
- Mercader J, Clarke S, Bundala M, Favreau J, Inwood J, Itambu M, Larter F, Lee P, Lewiski-McQuaid G, Mollel N and Mwambwiga A, Patalano R, Soto M, Tucker L and Walde D 2019 Soil and plant phytoliths from the Acacia-commiphora Mosaics at Olduvai Gorge (Tanzania). *Peer J.* 7: e8211.
- Mercader J, Clarke S, Itambu M, Mohamed A, Mwitondi MS, Siljedal G, Soto M, Bushozi PM 2021 Phytolith paleoenvironments at Mumba rock shelter. *Front. Ecol. Evol.* 423.
- Mora R and De la Torre I 2005 Percussion tools in Oldupai Beds I and II (Tanzania): implications for early human activities. *J. Anthropol. Archaeol.* 24: 179-192.
- Patalano RV 2019 *The Environmental Context of the Earliest Acheulean at Olduvai Gorge, Tanzania*. PhD dissertation, University of Calgary (Canada).
- Pearsall DR and Piperno DM 1993 Current research in phytolith analysis: *Applications in archaeology and paleoecology, MASCA Research Papers in Science and Archaeology* Vol. 10. Philadelphia: The University Museum of Archaeology and Anthropology.
- Pearsall DM and Trimble MK 1983 Phytolith analysis of soil samples: report 18. In: Clark JT and Kirch PV (Eds), *Archaeological investigations of the Mudlane-Waimea-Kawaihae Road Corridor, Island of Hawaii: An interdisciplinary study of an environmental transect, Bernice P. Bishop Museum Departmental Report Series 83-1* (pp. 472-497).
- Piperno DR 1988 *Phytolith analysis: An archaeological and geological perspective* (280 pp.). San Diego: Academic Press.
- Santonja M, Panera J, Rubio-Jara S, Pérez-González A, Uribelarrea D, Domínguez-Rodrigo M, Mabulla AZ, Bunn HT and Baquedano E 2014 Technological strategies and the economy of raw materials in the TK (Thiongo Korongo) lower occupation, Bed II, Oldupai Gorge, Tanzania. *Quart. Int.* 322-323: 181-208.
- Strömberg C 2004 Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207: 239-275.
- White F 1983 *The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa*. Natural Resources Research. UNESCO, Paris, p. 336.
- Yravedra J and Cobo-Sánchez L 2015 Neanderthal exploitation of ibex and chamois in southwestern Europe. *J. Human Evol.* 78: 12-32.