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UNIVERSITY OF CALGARY

Diversity of plant niches available for Hominin settlement during Upper Bed I-Lower Bed II: A phytolith perspective, Oldupai Gorge (Tanzania)

by

Makarius Peter Itambu

A THESIS

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ABSTRACT

This research focused on reconstructing the diversity of plant landscapes that framed hominin evolution in Oldupai Gorge. The study had two main overarching goals with interrelated objectives. The first goal was to assess the synergetic links between hominin habitats and ecological preferences during the Pleistocene at Oldupai Gorge, and the second was the reconstruction of vegetation patterns characteristic during Upper Most Bed I to Lower Most Bed II. It also aimed at the reconstruction of plant landscape and the diversity of ecological niches for hominin interactions in a variety of sedimentary environments during the 1.83-1.60 million years ago.

In an attempt to understand the spatial-temporal distribution of plant landscape in specific sites and across the landscape, we employed high resolution and horizon level sampling approaches to examine differences in phytoliths representation between the sites and the exposed palaeosols. Sediments were systematically collected from trenches at Frida Leakey Korongo-North, Frida Korongo-West, Castle sites; and from the exposed palaeosols at the Lower Augitic Sanstone and at the Bird Print Tuff. Sediments were collected according to stratigraphic layering and features. In the laboratory, sediment samples were sieved, dispersed, and treated with acids for removal of inorganic and organic matter prior to heavy liquid separation. After phytolith extraction, microscopy, counting, classification, the phytolith morphotypes were analysed and interpreted in order to provide ecological inferences and thus explain the vegetation distribution between the sites. Phytolith assemblages applied in this research were used to identify the palaeosurface and ecosystems that characterised UMBI and LMBII sites to be able to infer whether the landscape wooded, forested, or grassland dominated environments. This is especially true

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because phytolith data are the key tool for palaeoecological interpretations that is used to inform about ancient landscapes that were inhabited by our ancestors, and the ability to characterise similarity of the vegetation cover existed during key period under study.

The results from this study showed that the hominins during UMBI-LMBII occupied a landscape that was ranging from woodlands to mosaics of open to patchy forested landscapes. The phytolith morphotype distribution, their representatives and abundances together show a wooded landscape during UMBI-LMBII times. The statistical analyses that were performed show that the plant landscape was not significantly different between UMBI and LMBII in terms of vegetation structure. Thus, hominins could have occupied wooded, humid, and wet landscape as indicated by phytolith assemblage, which is characterised by the vegetation patterns indicative of woody taxa and herbaceous dicots. These types spatially and temporally dominate the landscape over grassy taxa during UMBI- LMBII. The abundance of palm phytoliths, and the presence of sedges and ferns could possibly suggest wet-humid or wetland environments with seasonal and permanent streams that would have attracted the hominin settlements.

Arboreal phytolith morphotypes such as blocky, globular granulate, and tabular are abundantly represented chronologically and well preserved in the sediments, unlike the grassy indicators such as rondel, bilobates and, saddle morphotypes of various shapes. The documented phytoliths indicative of sedges (papillae) and ferns (tabular, and blocky bodies with striations) are suggestive of wetland habitats that would have provided hominin with variety of food resources such as drinkable water, plant foods, while palm trees would have served as area for stone tool manufacture under the shade, nuts processing, bone marrow exploitation or human sociality in different activities such as hunting and scavenging of meat resources. It is recommended that future research should expand upon the data from this study and use it in conjunction with modern iii referential baseline from the region to further explore and examine the vegetating dynamics towards the upper sections of Bed II-V and the younger sequences of Oldupai Gorge.

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TO MY WIFE, IRENE MUSA

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LIST OF ABBREVIATIONS

A.I.F = Acid Insoluble Fraction **BPT**= Bird Print Tuff EARS = East African Rift System EDTA = Ethylenediaminetetraacetic acid ESA = Early Stone Age Fig.= Figure FLK-N=Frida Leakey Korongo North FLK-W=Frida Leakey Korongo West g = gramHCl = Hydrochloric acid $HNO_3 = Nitric acid$ $H_2O_2 = Hydrogen peroxide$ ICPN = International Code for Phytolith Nomenclature Ka = Kilo-annum kg = kilogram km = kilometre LAS = Lower Augitic Sandstone LMBI = Lower Most Bed I LMBII = Lower Most Bed II LSA = Later Stone Age m = metreMa = Mega-annumMag = magnetitem.a.s.l. = metres above sea level ml = millilitremm = millimetreMSA = Middle Stone Age $(NaPO_3)_6 = Sodium hexametaphospate$ NCAA = Ngorongoro Conservation Area Authority NTDZ = North Tanzania Divergence Zone NVH = Ngorongoro Volcanic Highlands OGAP = Oldupai Geochronology and Archaeology Project OLAPP = Oldupai Landscape Palaeoanthropology Project RPM = Revolution per Minute SDS = Stone Tools, Diet, and Sociality s.g. = specific gravity SPT = Sodium polytungstate TOPPP = The Oldupai Palaeoanthropology and Palaeoecology Project $\mu m = Micrometre$ UMBI = Upper Most Bed I UMBII = Upper Most Bed II

CHAPTER 1: INTRODUCTION TO THE RESEARCH PROBLEM

Palaeoenvironmental studies facilitate the understanding of the relationship between human ecology and changing climatic conditions in the past and explores the connections between hominin habitats and ecological change over time and space. Multi-proxy climatic reconstructions have produced distinctive information specific to different components of the environment; for example, pollen and phytolith data for the analysis of vegetation, charcoal data for the analysis of past environments, foraminifera to investigate sea level change and diatoms to assess water regimes in the past (Seppä and Bennett, 2003). A major development in Quaternary studies over the past 25 years has been the study of pollen in conjunction with oxygen $({}^{18}O/{}^{16}O)$ and carbon isotopes $({}^{13}C/{}^{12}C)$ in terrestrial and sediment carbonates a proxy as for palaeoenvironmental conditions (Leng, 2004, Patalano, 2019). These new techniques have been widely applied to pedogenic carbonates (Cerling et al., 1989; Cerling and Quade, 1993; Andrews et al., 1998), tuffs and palaeosols (Andrews, 2006), and lacustrine carbonates (Patalano, 2019). The advantage of these approaches is that the oxygen and carbon composition of carbonates is strongly controlled by prevailing environmental factors such as temperature and vegetation cover.

Across East Africa, the palaeoecological evidence we have at hand clearly show periods of extreme environmental variability during the Plio-Pleistocene (Trauth et al., 2005, 2007, 2010; Deino et al., 2006; Kingston et al., 2007; Maslin and Trauth, 2009; Magill et al., 2013; Potts, 2013; Ashley et al., 2014; Maslin et al., 2005, 2014). These periods of extreme climate variability would have had a profound effect on the climate and vegetation of East Africa and, by extension, hominin evolution. Hominin evolution in East Africa has distinct speciation events, some of which are

linked to increasing brain size. The hominin encephalisation is a combination of processes with an underlying gradual trend towards larger brains, punctuated by several large step increases at least from around 1.9 Ma -200 Ka (Shultz and Maslin, 2013; Maslin et al., 2005, 2014).

1.1 IDENTIFICATION OF THE PROBLEM

Shultz et al., (2013) and Maslin et al., (2013) have had suggested that large steps in brain expansion in East Africa region may have been driven by climate variability while the smaller steps were due to regional aridity conditions (Trauth et al., 2009; Shultz and Maslin, 2013). What is more fundamental to the understanding of the evolutionary mechanisms, which could be applied to the studies of hominin evolution in East Africa, is to critically assess the speed and form of the transitions between lakes appearing and disappearing from the landscape as it is was proposed by Maslin et al., (2005, 2014). At first it may seem that orbitally forced climatic oscillations may be too long-term to have noteworthy effects on biota of the region. However, Maslin et al., (2005, 2014) and Shultz and Maslin (2013), believe that this does not take account of the sinusoidal nature of orbital forcing or the threshold nature of the African lake systems (Shultz and Maslin, 2013; Maslin et al., 2014). All orbital parameters are sinusoidal, which means that there are periods of little or no change followed by periods of large change (Potts, 2013; Shultz et al., 2013; Shultz and Maslin, 2013; Maslin et al., 2005, 2014). For example, the sinusoidal precessional forcing at the equator consists of periods of less than 2000 years during which 60% of total variation in daily insolation and seasonality occurs (Shultz and Maslin, 2013). These are followed by about 8000 years when relatively little change in daily insolation occurs (Maslin et al., 2005, 2014; Shultz et al., 2013; Shultz and Maslin, 2013). Hence, precession does not result in smooth forcing, but rather

produces rapid, strong forcing periods that are combined with long periods of comparatively weak forcing (Shultz and Maslin, 2013).

Similarly, using records of continental dust derived from marine drilling projects in the Arabian Sea and Gulf of Aden, deMenocal (1995, 2004) has suggested three step-like increases in aridity, as evinced by an increase in dust, in East African landscapes over the last few million years. Dust production increased between 3.0–2.6 Ma, 1.8–1.6 68 Ma, and 1.2–0.8 Ma, all three of which are broadly consistent with periods of turnover in African faunas previously proposed by Vrba (1995). This hypothesis is supported elsewhere in East Africa by the more recent study by Yost et al. (2018), whereas phytolith and charcoal record from Lake Malawi sediments are likely reflecting a weighted average of the watershed vegetation mosaic closest to each collected core location. This is again suggesting an existence of volcanic winter conditions in East Africa after the Toba super-eruption, which was detectable through the phytolith record and charcoal analyses (Yost et al., 2018).

Oldupai Gorge also provides artifacts, in the form of stone tool assemblages, that traces cultural changes since 2 Ma. These artifacts show the evolution of tool technology from the most basic Oldowan to the elaborate Acheulean (Díez-Martín et al., 2015; Domínguez- Rodrigo, 2001). However, cultural mechanisms, ecological factors, biological and behavioural adaptations that led to the disappearance of a culture that had lasted for a million years (the Oldowan), and sparked the emergence of a new one (the Acheulean), are extremely important for human evolution, yet remain very poorly understood; there is a need for further examination of the beginnings and ends of these cultures. This will help to understand whether environmental-climate change mediated or not (see de la Torre et al., 2012). We know that major vegetation changes affected this region, and that the East African Rift System played a major role in triggering these changes, both at the regional scale 21

by controlling precipitation and Afromontane forests distribution, and at the local scale by creating a unique hydrological context that allowed the formation of "oases" (Ashley et al., 2009). If volcanoes strongly transformed the landscape and modified the regional climate, the faulting triggered by the opening of the East African Rift is another geological factor that affected both fauna and flora. Faulting linked to the development of the East African Rift led to the slow tilting of the Oldupai basin towards the East, which led to the displacement of Palaeolake Oldupai to the East and, eventually, to its disappearance (about 1.2 Ma) and to the erosion of Oldupai Gorge (since 500,000 yrs) (Hay, 1976; Foster et al., 1997; Hay and Kyser, 2001). Faulting modified the nature of the stream drainage within the Oldupai Basin, not only by displacing the drainage sump to the east (Hay, 1976), but also by creating aquifer outcrops or barriers that forced groundwater to the surface, therefore leading to the development of freshwater wetlands (Deocampo and Ashley, 1999b; Deocampo, 2002).

1.2 EXPLORATION OF THE PROBLEM

Phytolith analysis serve as an important tool for identification of different micro-ecological niches. Determining early human-environmental interactions is challenging, therefore it is important to continue developing methodological approaches to assess the interpretive potential of sediment proxies in palaeoenvironment reconstruction. Presently, phytoliths and pollen grains are the only fossils that provide insights into the floristic aspect of Plio-Pleistocene palaeovegetation because they allow taxonomical identification sometimes up to the species-levels (see Barboni et al., 2010; 2014; Magill et al., 2013; Mercader et al., 2000; Madella et al., 2002). It helped plant landscape reconstruction especially enabling to affirm whether grassland or woodland

environments characterised the Upper Bed I and Lower Bed II palaeolandcape during the time that is believed to expand into a more open landscape.

Phytolith research has helped in the identification of prehistoric landscapes in terms of their vegetation communities and dynamic effects of human and natural disturbance (Boyd et al., 1998). Phytolith data were used throughout this dissertation to determine and reconstruct palaeoenvironments, with particular emphasis on changing grassland versus woodland assemblages on Upper Bed I and Lower Bed II sites. Consequently, the episodic drying environments experienced during the early Pleistocene sedimentary depositional record are reconstructed through phytoliths. To meet the research objectives, the analysis of phytoliths from the excavated units/palaeosols and from the exposed palaeosurfaces were conducted to determine significant intra and inter similarities or differences that could be used as an analogue between the sites, and in a more landscape-oriented approach as well (Mercader pers. comm., 2016, 2018). This provides a basis for later comparisons of ancient plants of Oldupai's Bed Upper Bed I and Lower Bed II landscapes, when phytoliths from old sediments are compared with the modern reference collections from the same area, to offer an identification at different levels of taxonomic hierarchy. In order to meet the second objective, that is to determine the ancient plant ecosystems, phytoliths from this study were used to infer the differences in vegetation cover during the transition period from Oldowan to Acheulean stone tool industrial techno-complexes.

1.3 CHAPTER OUTLINES

One of the key goals of this dissertation was to address the palaeo-ecological issues pertinent to early human adaptation to changing environments and increasing aridity from 1.83 to 1.60 million years ago (Ma) during the Pleistocene, as reflected in palaeoenvironmental proxies from Oldupai Gorge (Tanzania) Lower Bed I (LBI) and Upper Bed II (UBII) sites. This timeframe is important because it spans the Oldowan to Acheulian transition (Hay, 1976; Santonja et al., 2014; Domínguez-Rodrigo et al., 2007; Díez-Martín et al., 2014; Yravedra et al., 2015) that also included a significant opening of the East African plant landscapes as evinced by the available dataset from the region's palaeoreconstructions. This is an important endeavor because the 1.78-1.3 Ma period experienced climatic stresses and environmental changes, but also archeologically visible stone tools of two major traditions i.e. Oldowan and Acheulean (Mora, & de la Torre, 2005; Barboni et al., 2010; Magill et al., 2012, 2013; Beyene et al., 2013; Díez-Martín et al., 2014, 2015). Phytoliths were extracted from sediments collected at excavation trenches, exposed palaeosols and corresponding surrounding landscapes. The phytolith indicators were then compared analytically to reconstruct the spatial distribution of vegetation types in response to increasingly aridity from 1.83-1.1.60 Ma. The study focused on the reconstruction of plant landscape, diversity of niches, and human-environmental interactions in a variety of complex depositional sedimentary environments of Oldupai Gorge Upper Bed I and Lower Bed I respectively (spanning the transition from Oldowan to Acheulean stone tool industrial techno-complexes). The following objectives guided this study:

Identify and characterise the differences in phytoliths representation between the active excavation sites and exposed palaeosols (palaeosurfaces).

Determine the differences in plant ecosystems that characterise Bed I and Bed II sites; i.e. inferring grassland versus forested environments through phytoliths analysis.

Reconstruct the Oldupai palaeolandscape, palaeoenvironments, and palaeogeography of Bed I and Bed II for an approximately 230,000-year time period. To achieve these goals, focus was on answering these key research questions:

- How can phytolith analysis be used to distinguish palaeo-habitats that existed in the Upper Bed I, and those along the shores of palaeo-lake Oldupai during the initial deposition of Bed II?
- 2. Was there any change(s) in vegetation cover that influenced phytoliths distribution, and therefore, characterised Oldupai's Bed I and II landscapes between 1.83-1.60 Ma?
- How does the proportion of various plant (niches) change spatially and temporally in upper Bed I, and the Bed II localities for over 230,000-year period?

Although Oldupai Bed I and II (2.1-1.1 Ma) have credible archaeological localities, there are not enough palaeoecological phytolith data to examine vegetation changes and environmental fluctuations during the transition from Oldowan to Acheulean stone tool industrial technocomplexes. This study addresses this problem by providing phytolith data from this crucial period that can be used to explore possible ecological factors that led to early human's technological adaptations and manipulation of those plant landscapes.

To tackle the first research question phytolith morphotypes were used to distinguish the plant landscape during UMBI times, key phytolith types indicate the vegetation structure might have consisted of good proportion of wooded plants and with more elaborated stable patterns while towards upper sections of LMBII the vegetation variability is recorded by phytolith assemblages, which appear to be controlled mostly by changing climates of the eastern Africa region during that time. The vegetation reconstructed during UMBI was mainly dense woodland with possibility open forests as indicated by palms trees and sedges. Such vegetation structure was likely a valuable resource for hominin hunting and tool making activities. To address the second research question phytoliths from different sites were compared statistically in order to detect morphotype distribution per sample and sites, and intra site comparison as made as well. For instance, phytolith assemblages from samples collected at the eastern palaeolake margin, clays immediately in contact below Tuff IF, At FLK-N many phytoliths are well preserved and shows diversity of plants such as monocots – sedge phytoliths, palms and few grassy morphotypes. However, there is good representation of palm phytoliths in FLK-N and FLK-W respectively.

The characterisation of phytoliths both in high resolution and horizon level in this work show that at FLK-W (Bed II), the phytolith morphotypes indicate a shift in dominance from dicots to monocots to a mixture of the two and including palms, and grassy cover to more open landscape. The open landscape is more pronounced towards upper sections of Bed II. The low phytolith counts at LAS and Castle sites as well as the sparse presence of GSSC phytoliths, may be the result of taphonomical processes. Taphonomy must be considered because it can affect the representativeness of phytolith assemblages. Taphonomic conditions affects phytolith preservation in assemblages and is one of the causes that leads to unidentifiable phytolith types. Other factors such as basic (high pH) environments concentration affect phytoliths by increasing their solubility, but it affects more the surface decoration/details than the three-dimensional shape of phytoliths (Cabanes et al., 2011). There is an over-representation of several morphotypes, such as dicotyledonous from wood/bark (blocky, tabular, and globular types, and mesophyll cells), with an under representation of grasses and sedges across all sites.

This study provides a general picture to understand the temporal and spatial resolution and precision of phytolith analysis in detecting different ecological niches and plant diversity existed 26

during UMBI-LMBII. The hypothesis that there were no significant differences in terms of plant vegetations during this time period in question is validated by the phytolith data from this research. Statistically, there are no significant differences between UMBI-LMBII vegetation types as indicated by phytolith assemblages. However, the ability to identify vegetation change through phytolith analysis from ancient sediment is not without limitations, it depends on the sediment type, phytolith spatial-temporal distribution, degree of preservation, and well-established baselines as modern analogs. This dissertation compared phytolith data with the published modern reference collection dataset from the same ecoregion to infer specific vegetation types (Mercader et al., 2019). This study suggests that the phytoliths from UMBI show a wooded arboreal cover like those ones from LMBII, but also suggest a mixed woodland with more open plant landscape towards upper sections of LMBII times.

CHAPTER 2: PALAEOENVIRONMENTAL ANALYSIS

Over the past several decades, considerable effort has been made in Palaeoanthropology to quantitatively reconstruct quaternary hominins' palaeoecology and the palaeoenvironmental conditions that governed hominin bio-cultural adaptation, evolution, speciation, and stone tool technology. Palaeoenvironmental interpretations of hominin habitats have become increasingly more sophisticated over time; where early palaeoanthropologists previously inferred habitats based on one or two species, it is now more common to use fossil groups or lineages (see Vrba, 1995), the entire faunal assemblage (Bobe and Eck, 2001; Reed, 1997), or combined evidences such as biomarkers and plant micro-remains, as the basis of inferring ancient habitats across the landscape. The newly emerging analytical approaches in Palaeoanthropology have globally facilitated our understanding of how early human evolutionary processes might have been affected by climate and/or habitat change.

In the field of Palaeoanthropology, the incorporation of diverse methodologies for archaeobiological, palaeoenvironmental, and palaeoecological reconstructions, such as plant macro- and micro-remains, residue analysis, plant markers (Patalano, 2019), provisioning of lithic raw materials (Favreau, 2019), socioeconomic analysis, and the technological study of stone tool use, has provided a significant contribution to the science of human-environmental interactions. Shifting vegetation in response to changes in evapotranspiration, rainfall, soil composition, and topographic relief applied selective pressures to hominins in regard to habitat modification (Cohen et al., 2007). In order to adjust to the new environment, hominins adopted new strategies to conform to the changing landscape, which eventually led to adaptation, speciation, or extinction (Cohen et al., 2007; Scholz et al., 2007). The adaptations seen in faunal assemblages provide

valuable lines of evidence that can be used to reconstruct palaeoenvironments and track environmental and landscape change over time and space (Cohen et al., 2007; Scholz et al., 2007). Within the field of Palaeoanthropology, researchers have created advanced field methods and have incorporated stringently controlled analytical techniques, allowing for a more collaborative and multidisciplinary manner of palaeoreconstruction. These analytical techniques are the cutting-edge research avenues in our field, and many scholars have devoted their work solely to integrating and combining emerging methods to sedimentary analyses for this purpose. These include sedimentological examination of outcrops and sub-surface cores, such as phytolith and starch analysis, stable isotope ratios derived from fossils and carbonates, and analyses of chemical biomarkers of animals and plants (see also Patalano et al., 2016, 2019; Mercader et al., 2019).

2.1 HISTORICAL OVERVIEW OF PALAEOENVIRONMENTAL RECONSTRUCTIONS

The reconstruction of environmental contexts has been a research focus since the 1970s, but it was not until the 1980s that many researchers began trying to reconstruct the Quaternary environments and climates. From the 1990s onward, most of this research has been conducted to study the environmental contexts of human origins (Seppä and Bennett, 2003). Palaeoanthropologists use data from fossils and other lines of evidence to examine early humans and how their environments change throughout time. Palaeoenvironmental studies, especially when plant microremains are considered, facilitate the understanding of the relationship between human ecology and changing climatic conditions in the past, and explore the connections between hominin habitats and ecological change. In order to produce high resolution reconstructions and understandings of past environments, studies with combined data from sediments, floras, and faunas, are required.

Climatic and environmental reconstructions using multiple indicators and analytical methods have produced distinctive information specific to different components of the environment. Such indicators include biogenic silica (phytoliths), charcoal, macro plant remains (seeds), micro plant remains (pollen), and stable isotopes (Fig. 2-1). Because of their botanical and ecological importance, the microfossil-based approach to archaeology are vital tools that produce data to interpret terrestrial and aquatic vegetation changes (Seppä and Bennett, 2003), as well as palaeoclimatic trends. The following section will discuss key botanical indicators used in the reconstruction of ancient ecosystems.



Figure 2-1: Materials and proxies used in palaeoenvironmental reconstructions. SDS images, and images with Creative Common Licence (Stockvault.net, FreeImages and pixabay.com).

2.2 PALAEOBOTANY

Three micro-botanical remains likely to be preserved in the archaeological record are diatoms, phytoliths, and pollen. Diatoms are microscopic aquatic and sub-aquatic algae common in a range of aquatic environments, including streams, ponds, lakes and estuaries (see Werner, 1977) and like phytoliths, their preserved remains are composed of silica. Many types of pollen and phytolith can be identified as belonging to particular families, genera or species.

2.2.1 DIATOMS

Diatoms are unicellular algae, and each cell (or 'frustule') consists of two valves which are made of hydrated silica (SiO₂) (Bathurst et al., 2010), which is a robust material that is mostly resistant to diagenic deterioration and favours preservation in the archaeological record. They can exist in colonies on wet or submerged surfaces (benthic) or as solitary cells in open water (planktonic), however most are photosynthetic and require light exposure to thrive, limiting them to shallow depths (Bathurst et al., 2010). Some live on moist terrestrial surfaces such as soil, plants or rocks. Frustules exhibit a broad diversity of morphologically distinct shapes and patterns that allow for taxonomic differentiation, oftentimes to species or sub-species level (Battarbee, 1988).

The richest sources of diatom fossils are deposits of their skeletons, known as diatomite or diatomaceous earth. This mineral is formed as ancient diatoms dies and settle to the bottom of lakes or oceans (Smol, 1992). Today, they form large deposits of white chalky material, which is mined for use in cleansers, paints, filtering agents, and abrasives. Many toothpastes contain bits of fossil diatoms. In seasonal lakes, rivers, and streams, diatom deposits may even occur in layers which correspond to annual cycles (Smol, 1992). In these deposits, it is possible to observe changes

over many years, and palaeoenvironmentalists uses diatom in conjunction with pollens and phytoliths for palaeoreconstructions.

Given their durability and distinctiveness, diatoms are valuable forms of evidence for reconstructing past environments. They are good indicators of a range of water quality variables, namely water availability, pH, salinity, and seasonality (Cumming and Smol, 1993) and can provide historical evaluations of long-term water chemistry in aquatic ecosystems; a significant indicator when palaeclimatic data are scarce. Palaeolimnologists can inference past ecological changes through the analysis of shifts in diatom frequencies and species composition.

Diatom research has been used in archaeological science for over 50 years, however despite their high rate of archaeological recovery, it is an under-used technique. This is mainly due to difficulties in taxonomic identification, few specialised researchers, and a lack of understanding taphonomic processes. Despite these challenges, there are several case studies on diatom analyses performed from different parts of Africa, Asia, and Europe, demonstrating effectiveness of diatoms in locating prehistoric settlement sites along former shorelines, in reconstructing salinity and tidal regimes in estuaries, and in locating clay sources for pot manufacture (Battarbee, 1988; Gasse and Fourtanier, 1991). They have also been used in studies to infer anthropogenic eutrophication (Birks, 2000) resulting from sewage inputs and land-use activities, such as agriculture, road construction, and cottage and municipal land development (Engstrom et al., 1985). Diatoms as bioindicators have been used in locating turf structures in different time horizons in archaeological sites. For example, diatoms have been analysed from archaeological sites in order to determine ecological conditions of turf (peat-bog) at the time of site deposition in European historical sites (Bathurst et al., 2010). Although diatoms by themselves cannot give us enough palaeoenvironmental data, but when combined with analyses of other proxies in archaeological 32

investigations it yields useful clues pertinent to the presence, absence, level, pollution, productivity, acidity, and salinity of a waterbody on or near to an excavation (Battarbee, 1988; Gasse and Fourtanier, 1991).

2.2.2 Phytoliths

Phytoliths are plant biosilica microminerals (silica minerals) that form within and between cells of different plant structures (i.e. stems, leaves, fruits, and bark) and are used as a diagnostic marker of plant family or ecosystem functional group (Pearsall and Trimble, 1983; Piperno, 1988; Pearsall and Piperno, 1993; Strömberg, 2007; Pearsall, 2000). 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. When a plant dies and decays, most of its phytoliths are released directly into the soil, creating a highly localised in situ assemblage (Stromberg, 2009; Mercader et al., 2000, 2009, 2010, 2011, 2013, 2019). When we find these phytoliths alongside archaeological remains, we interpret their distinct shapes to infer ancient plant landscapes in which human activities occurred.

The origin of phytolith research was in the field of biology and geological science before being brought to archaeology and Palaeoanthropology (Piperno 1988, 2006; Piperno et al., 2003). The first observation of mineral particles from plants goes back to the late 17th century when Loeuwenhoek reported calcium phytoliths (Mulholland and Rapp, 1992; Cummings and Magennis, 1997, Piperno, 1998), but the term "phytolith" was not used until the mid-19th century by Ruprecht (Baker, 1959). The "German School" of phytolith analysis began in the second half of the 19th century, continuing to the later 20th century, with the works of Struve, Hohner, and Grob (Powers, 1992). They produced a series of papers investigating silica bodies in cereals and other species of grass. Their works formed the foundation of understanding phytolith anatomy and morphology, which were fundamental later studies on phytoliths. During the late 1950s to early 1970s, phytolith research gained momentum and it was used in archaeology with Helbaek (1961) working on ashes and ceramics from the Near East, and Watanabe (1955, 1970) who identified rice phytoliths in prehistoric deposits from Japan. However, it was studies published between the late 1990s to 2010s that allowed for phytolith analysis become routinely used in archaeological reconstructions of palaeoenvironment and palaeoclimate (Piperno, 2006).

Phytoliths, like pollen, were known as plant fossils by the European scientists as an important constituent in plants, sediments, and aerosols since mid 19th century, and since then phytolith analysis has been an avenue for palaeoreconstruction because of its own unique history as an indicator of the environment and plant physiognomy (Piperno, 1998, 2006). Until the American archaeobotanists began to apply phytoliths as markers of plant use and domestication during the late 1970s and early 1980s, many fundamental issues related to phytoliths production, taxonomy and identification, and preservation were not explored. Hence, their ecological applications were limited largely to broad depictions of aspects such as forest versus grassland of past vegetation obtained from modern soils underneath standing plant formations (Piperno, 2006; Barboni and Bremond et al., 2008; Stromberg 2009; Mercader et al., 2000, 2009, 2010, 2011; Albert et al., 2015).

In the discipline of archaeology, phytolith research was applied first by researchers such as Piperno (1998) who aimed at providing evidence that phytoliths at low taxonomic levels are spread are reliable indicators of past plant life and climate in a variety of ancient sedimentary contexts from archaeological sites. Since then applications of phytolith analysis have greatly expanded, mirroring the multidisciplinary scope of most fields of science such as botany, biology, 34

palaeoecology, and archaeology, and were mainly used to trace the domestication of food crops, the origin and dispersal of domesticated plants, and the development of agricultural systems (Piperno, 2006). Additionally, phytoliths have been used to diagnose the availability and the economic usage of wild plants, reconstructing the chronology of plant use and domestication, function of pottery and stone tools and the general aspects related to prehistoric plant subsistence, and agricultural technology using phytolith analyses.

2.2.3 POLLEN

Pollen was recognised as an environmental indicator in 1916 when palynologist Von Post first presented his pollen analysis of a Swedish peat bog. He noted that pollen and spores are produced in great abundance by plants, however, only a very small fraction fulfils their natural function of fertilisation, and the remaining majority are deposited onto the ground. He recognised that this atmospheric pollen (pollen rain) is well-mixed, and that pollen will decay unless processes of biological decay are inhibited (e.g. in places poor in oxygen, such as lake bottoms, oceans, bogs). Since the 1960s, palynological research has been combined with modern comparativeanalog studies and subsequently, pollen research has been widely used in palaeoanthropological research. Despite its origins at the start of the 20th century, palynology has been referred to as a "young science" by Erdtman (2013), an opinion based on Van Zinderen Bakker's (1995) statement that the significant technological and methodological developments made during the latter half of the century increasingly improved the discipline. Today, the analyses of pollen data provide information that contributes to the understanding of the current environment and its prospective changes, consequently adding value to efforts towards recognising and key issues on climate change in the past and human evolution.
The widespread use of pollen in palaeoenvironmental reconstruction is attributed to how this pollen rain can be identified on multiple taxonomic levels and quantified, providing an index of vegetation specific to that location and time period. There is a direct relationship between the pollen percentage of key taxa and the proportional occurrence of these taxa on the landscape (Bunting, 2008) which ca be applied to palaeoenvironmental reconstruction. This argument is in agreement with Birks and Birks (2000), who echoed that the basic principle of pollen analysis is based on the notion that pollen abundance and pollen type are directly associated with the occurrence of the parent taxon in the surrounding landscape. Several palynological studies have been conducted on production, dispersal, taphonomy, and sampling methodology (Jackson and Williams 2004). Anaerobic sites such as lakes, wetlands, peat deposits are said to highly favour the preservation of pollen, such sites are preferred for palynological research and construction of ancient pollen assemblages (Bennett and Willis, 2002). There have been significant efforts to model the spatial representation of pollen records in lake sediments, which is important for more precise interpretation of the pollen records in terms of past vegetation patterns (Jackson and Williams, 2004).

Pollen assemblages from fossil record provides a snapshot of historical vegetation patterns representing a time period (Bennet and Willis, 2002). This is useful for understanding long-term ecosystem processes, how modern vegetation has been formed from past vegetation shifts as a response to environmental change, overall vulnerability or disturbance of an ecosystem to past climatic-ecological fragmentation and species fluctuation (Bennet and Willis, 2002), and biological responses to environmental change and land degradation. Core drilling in dams, glaciers, lakes, and seas yield samples containing pollen records of past vegetation and provide information on large-scale environmental change that includes multiple vegetation zones across 36

large regions. Pollen research helps to trace variation in plant community biodiversity and sometimes these records are locally analysed to confirms model simulations of palaeoclimate and biome distribution in a certain time period (Lézine et al., 2019). Long-term fire history can be interpreted from charred particles extracted from sediment cores and information on vegetation dynamics is conveyed by the pollen record (Conedera et al., 2009). Pollen data can also be used to inform our understanding of rainfall and moisture conditions. Sedge pollen (Cyperaceae) is thought to be indicative of hydrological change and water availability, specifically fluctuations in moisture conditions; a decline in Cyperaceae is believed to reflect the frequency of wetland occurrences, vegetation containing rare species or poor soils (Bunting, 2008).

CHAPTER 3: THE EAST AFRICAN EARLY STONE AGE IN ECOLOGICAL PERSPECTIVE

The palaeoecological context of hominin occupation in East Africa during the Pleistocene has been long debated (e.g Potts 1998; Kingston 2007). This chapter begins by outlining the numerous research works on aspects such as ancient climate regimes and environments that have shaped the origin of humanity in the past, specifically focusing on the Eastern Africa Rift System (EARS). Next, the various ecological primers relevant to palaeo-reconstruction in sub-Saharan Africa and in the Eastern Africa region, and the significance in understanding the palaeolandscapes that were used by early hominins during the early Pleistocene (starting at 2.5 Ma), will be discussed. Finally, this chapter presents a broad overview of various palaeoecological proxies that are currently employed to reconstruct hominin-utilised landscapes in the past.

3.1 THE EAST AFRICAN RIFT VALLEY SYSTEM

The geological record of the African continent is one of the oldest on Earth and spans three quarters of its history (Schlüter, 1997). It contains records of events which occurred in the Archaean when the Congo, Kaapvaal, Tanzanian, West African, and Zimbabwe, cratons formed. The EARS started to form 25-30 Ma when the Somalian and Nubian Plates pulled away from the Arabian Plate (Dawson, 1992; Ring, 2014), revealing a progression of magmatism and rifting from South to North. It is a valley with two broadly parallel rifts and extends for 4000 km from Mozambique to the Red Sea. It is an active intra-continental extension zone, meaning the African plate is still in the process of splitting into two separate plates along the Arabian plate. It has three

main branches: the Albertine, Ethiopian, and Gregory rifts (Ebinger et, al., 1999, 2017; Scoon, 2018).

Rift-related volcanism commenced in the Eocene and a major phase of flood basalt volcanism occurred in Ethiopia by 31-30 Ma. Rift development in the Eastern Branch has a distinct northward progression with a juvenile rifting stage in northern Tanzania, well advanced rifting in Kenya and the transition of continental rifting to incipient sea-floor spreading in Ethiopia and Afar. The Western Branch in general has not yet progressed to an advanced rifting stage and rift basin architecture retains an original geometry (Ring, 2014). The most juvenile rift sector (i.e. Tanzanian sector), marks the southern termination of the Eastern Branch. The rift termination is structurally and morphologically expressed by a pronounced splay, the Tanzanian Divergence Zone (Dawson, 1992; Ebinger et al., 2017). The splaying of the Eastern Branch resembles the termination of ductile and brittle-ductile shear zones. In contrast to the narrow (about 50 km wide), and welldefined Kenyan rift sector, the Tanzanian Divergence Zone is at least 300 to 400 km wide and consists of three separate grabens, which from West to East, are the Eyasi Rift, the Manyara Rift and the Pangani Rift. There are also normal faults in between those three grabens showing how diffuse extension is accommodated in the Tanzanian Divergence Zone. It appears that the strong Archaean Tanzania Craton largely restricted fault slip and this resistance caused splaying of the major rift faults of the southward propagating Eastern Rift Branch (Ebinger et al., 1999, 2017; Roberts et al., 2012).

The EARS is a classic example of continental rift, evidenced by the active faulting and magmatism which still occurs slowly across a large part of the African continent between the Horn of Africa southwest of the Okavango region of Botswana and in a second diffuse arm that continues from southwestern Ethiopia to southeastern Mozambique, including offshore regions of the Indian 39 Ocean, such as the Davie Ridge. The southern Red Sea, Main Ethiopian, and Eastern, Western, and Southwestern rift systems have developed atop broad topographic plateaus, whereas the Malawi rift and its southeastward continuation transect low elevation regions in Mozambique. Continental rift zones are typically made up by a series of asymmetric grabens and are truly 3-dimensional features. From their inception, rift zones show regular along-axis structural segmentation into basins bounded on one or both sides by large offset border faults (Ebinger et al., 1984; Rosendahl, 1987). The border faults are flanked by broad uplifts that can rise 3 km above the surrounding regional elevations, such as the Rwenzori Mountains in Uganda, which are more than 4 km high (Ring, 2008; Bauer et al., 2010). Initially, discrete border-fault segments interact and are mechanically connected through transfer faults and relay ramps oriented oblique to the strikes of border faults (Morley et al., 1990). In general, border fault lengths, rift flank uplift, and basin dimensions increase with increasing strength of the lithosphere (Ebinger et al., 1999). This is why young rift segments in strong, cratonic lithospheres are characterised by long, narrow grabens with deep rift lakes bounded by escarpments (Ring, 2014).

The Eastern Branch is known as the Gregory Rift and splays into a diffuse network of three separate segments to form a tectonic depression known as the North Tanzanian Divergence Zone (NTDZ) (Baker et al., 1972; Dawson 1992; Ebinger et, al., 2017). From east to west, it comprises of the Pangani graben, the Natron-Manyara-Balangida half-graben, and the Eyasi-Wembere half-graben (Foster et al., 1997). In northern Tanzania, the EARS (Fig. 3-1) is characterised by substantial volcanic activity, including lavas erupted from fissures along the rift in the region, such as the Ngorongoro Volcanic Highlands in Tanzania (Fig. 3-1). There are individual volcanoes elsewhere along the rift. Some of these are very large, including Mount Kilimanjaro and Oldonyo Lengai in Tanzania and Mount Kenya in central Kenya (Ring, 2014).

The Western Branch extends more than 2000 km from Lake Albert in the north to Lake Malawi in the south. Regional doming/uplift is much less pronounced than in the Eastern Branch, though parts of the Western Branch show the greatest absolute subsidence on earth as expressed by deep rift lakes (i.e. Lake Tanganyika) whose bottom is at or below sea level. Furthermore, the rift flank uplift is, at least in part, pronounced. The Rwenzori mountains are the highest rift mountain ranges on the world that are found with the rift system as are indicated by individual rift basins, which are as long as 100-150 km and narrow as 50-70 km; and are said to be in the process of linking up (Ring, 2014). The Rwenzori Mountains, the most striking example, are a promontory of the eastern rift shoulder in Uganda, which rise to more than 5 km above sea level (Ring, 2008; Bauer et al., 2010, 2013).



Figure 3-1: Map of the East African Rift System (EARS). (Source: Geospatial data from Fritz et al. (2013) and Macgregor (2015; and minor modifications by Favreau, 2019)

Recent reviews on various rift segments of the EARS show that increasing maturity of the rift sectors corresponds with thinning of the lithosphere, and the amount of decompression increases and melts, which in turn creates a weaker lithosphere. In the EARS these features should be best expressed in the Main Ethiopian Rift, which represents the northernmost rift sector of the East African Rift system and links into the Afar Depression with the spreading centers of the Red Sea and Gulf of Aden (Ring, 2014).

Apart from its unique geology and history of continental drift, volcanism, faulting and rifting, the EARS is important in understanding the climatic-environmental variability and context of human evolution. Most of the key sites for human evolution and speciation are located within the EARS. Although the EARS was instrumental in driving the climate and biosphere of that region, which in turn might have influenced habitats and the pattern of migration of human species in East Africa, and possibly even conditioned hominin evolution, we do not yet definitively know what biological effects it had on primate behaviours, hominids and hominin evolution, extinction, speciation, and radiation.

3.1.1 HOMININ ECOLOGY

The development of hominin adaptations over time was a fluid process in which environmental challenges affected reproductive fitness and survivorship. Because the measure of fitness used when calculating selection is relative to other members of the population (Lande and Arnold, 1983), the changes in population density and distribution that accompanied each environmental perturbation doubtlessly led to shifting in the outcomes of natural selection over time and space. Thus, habitat specific approaches to human evolution are less tenable than originally thought. Evidence of environmental variability instead focuses attention on how the adaptability of human ancestors expanded over time and enhanced their capacity to respond to unexpected climatic change and resource uncertainty (Potts, 2012).

Early hominin-environmental-climatic interactions and the relationship with evolutionary change is of a paramount focus among the archaeologists, biologists, geoscientists, palaeoanthropologists, and palaecologists in human evolution research (e.g. Vrba, 1995; Klein, 2009; Potts, 2013). Objectives have concentrated on how evolutionary events correspond in time and space with types of environmental stress and episodes, such as shifts in climate that result in shifts in habitats. Intrinsic (Klein, 2009, Potts, 2013) and extrinsic factors (Vrba, 1995; Potts, 1998; Trauth et al., 2007; Potts 2012) have been put forward to explain the appearance of morphologies favouring bipedal locomotion after c. 4.2 Ma. Bipedalism occurred early in human evolution and should probably be seen as a complex pattern affected by vegetation changes (Potts, 2012).

Hominin dispersal events in East Africa during the Pleistocene coincided with periods of high climatic variability. It has been suggested that both lake presence and absence could also be associated with these dispersal events (Trauth et al., 2010; Shultz and Maslin, 2013). For example, when the lake basins are dry, they become 'hyper-arid' and are unsuitable as habitats for hominins; thus, hominin populations would have been forced to migrate to the north and south (Trauth et al., 2010; Du et al., 2018). However, harsh conditions and diminishing resources would imply that there was only a small and possibly shrinking population that could migrate. The absence of lakes may have facilitated allopatric speciation in some key refugia such as Turkana, which may have remained wet in the early to late Pleistocene (Trauth et al., 2010; Du et al., 2018).

Hominin dispersal is therefore most likely to have occurred when the basins were filled with water, as there would have been limited space for the hominin populations on the tree covered 43

Rift shoulders and river flood plains (Foerster et al., 2012; Shultz and Maslin, 2013). The wetter conditions could have been more conducive to dispersal because hominin populations could expand due to the availability of water and variety of food resources and hominins could follow the Nile tributaries northward and through a green Levant region (Foerster et al., 2012; Larrasoaña et al., 2013; Du, et al., 2018). Thus, the occurrence of deep freshwater lakes would have forced expanding hominin populations both northwards and southwards, pushing them out of the East African savannah landscape towards the Ethiopian highlands and the Sinai Peninsula or into Southern Africa with each successive precessional cycle (Foerster et al., 2012; Shultz and Maslin, 2013; Du et al., 2018). Two competing theories connecting environmental change to early human evolution are in place in East African human origins research to account for aridity trends, opening of the plant landscapes, episodic droughts accompanied by the climatic backdrop, environmental change, of which both ultimately triggered human evolution in sub-Saharan Africa (Maslin et al., 2005).

The *turnover pulse hypothesis* was brought into anthropology to explain specific patterns in ungulate speciation and suggests that acute climate shifts drove adaptation and speciation (see Maslin et al., 2015; Vrba, 1995, 2000) and argues that environmentally induced extinctions hurt specialist species more than generalist species. According to this hypothesis, when there is an environmental disruption, the generalists will tend to thrive by using new environmental opportunities and by moving elsewhere to take advantage of other areas that have lost specialist species and become more spread out across the landscape (Vrba, 1995, 2000). Oppositely, the specialists will experience more extinctions, and therefore an increased speciation rate within their group, leading to more rapid evolution in isolated islands or patches (e.g. allopatric/geographic speciation). Vrba's turnover-pulse hypothesis stressed that the increases in aridity during critical 44

time intervals across equatorial Africa occurred in response to global climate cooling, which itself was a response to variations in Earth's orbit (Milankovitch cycles) relative to the position of the sun along with feedbacks between the atmosphere, oceans, and landmasses (Vrba, 1995). Each major drying period led to a significant rise in species turnover; that is, the origination and extinction of lineages in tune with the direction of habitat change (cooling and drying). Moist woodland-dependent mammals tended to become extinct, whereas arid savanna-dependent species became dominant in the region (Vrba, 1988, 1995). The dry-adapted fauna of Africa thus arose in a series of steps from 5 Ma to 1 Ma, with the most critical turnover pulse occurring between 2.8 and 2.4 Ma, during which *Homo* and *Paranthropus* arose and lithic technology first became prominent (Vrba, 1995, 2000).

On the other hand, the *variability selection hypothesis* suggests that environmental unpredictability has a large role in selecting for behavioural or ecological flexibility (Potts, 1998, 2013). In this hypothesis, the variability refers to the general history of environmental instability experienced by a population of organism (Bobe and Behrensmeyer, 2004; Bonnefille et al., 2004; Trauth et al., 2005, 2007; Owen et al., 2008; Maslin et al., 2015). This theory is an extension of the original turnover pulse hypothesis, but instead splits species into their varying ability to adapt and evolve to a more variable and unpredictable environment. The variability selection hypothesis emphasises the long-term trends toward a drier and more variable climate would result in some species adaptation to these xeric environments (Potts, 2013). These theories provide crucial trajectory and an essential link between the mechanisms driving evolution and the biological response to different climatic and environmental stress. The pulsed climate variability hypothesis should be seen as a framework, which describes the palaeoclimatic contexts within which early human evolution occurred. However, this theory does not provide a thorough 45

mechanism in which the evolutionary process occurred and geographic separation, environmental stress, accelerated evolution, and extinction of generalist versus specialists, variability selection, and inter-species competition could all have played a role (Maslin et al., 2015). It should also be noted that climate may not have always been the underlying cause; intrinsic social factors may have played a significant role especially with increase in brain size among early humans which enabled them to design and manufacture more improved tools thus providing better mechanisms to subsist in different biomes and obtain a variety of dietary nutrients (Maslin et al., 2015). This hypothesis is based on the observation that the global climate moved steadily toward a cooler, drier planet over the past several million years was also accompanied by large climate fluctuations.

These two hypotheses, the turnover-pulse hypothesis and the variability selection hypothesis, have provided testable predictions about how key events in human evolution occurred and about the environmental conditions that stimulated evolutionary change and more importantly hominin adaptability to those critical climatic and environmental pressures. The variability selection hypothesis predicts that new adaptations originated, or spread from one area to others, during eras of sensitive environmental variability, whether due to climate or to other factors. On other hand, the turnover-pulse hypothesis predicts that species turnover and the rise of new adaptations were concentrated in times of growing aridity and the expansion of open habitats (Trauth et al., 2005, 2007). However, both assumptions focus on the overall correlation between environmental and evolutionary change, but they also identify processes of evolution that represent different understandings about the origin of new behaviours and the pattern of survival and extinction of different lineages (Trauth et al., 2005). These hypotheses are therefore trying to bring about the possible links between environment and the evolution of different species, in different climatic stress or conditions. The evolution of humans alongside other organisms and the

environmental change potentially are related in many ways. The key evolutionary events in the past might have been concentrated in periods of directional environmental change, however, the turnover-pulse hypothesis suggest that the cooling and drying of climates were the key trends pertinent to hominin evolution, and some increases in aridity or moisture or cooling or warming could have warranted the evolution of new species which are adaptive to those new changes, so the connection between environment and evolution is paramount.

Going forward, this chapter briefly outlines and reviews a variety of palaeoecological methods that are currently used to advance reconstructions of the past habitat, climate, and behaviours of early hominins. The culmination and development of these and other methods of environmental interpretation have progressed impressively over the past several decades, and now are key tools for palaeoreconstruction across East Africa. Palaeoreconstructive research normally explores and cross-examines interplay between climate, ecology, and macroevolution, and the interests of many researchers in this discipline have led to the advent of microscopic analyses of sedimentary proxies for palaeoclimate during the African Plio-Pleistocene. While fauna analyses have been traditionally used (Vrba, 1995; Ungar et al., 2010; Rowan and Reed, 2015), new methods have come to the forefront of palaeoecological studies, such including records of dust in marine drilling cores (Rowan and Reed, 2015), stable isotope analyses of palaeosols (Cerling et al., 2011a), tooth enamel (Tucker, 2018), and leaf waxes (Patalano, 2019).

3.2 THE AFRICAN EARLY STONE AGE

3.2.1 (PRE) OLDOWAN TECHNO-COMPLEX

Recent work in West Turkana, Kenya, has reported pre-Oldowan technology at Lomekwi, a 3.3 Ma old archaeological site where artefacts occur in spatial-temporal association with faunal Pliocene fossils in a wooded palaeoenvironment (Harmand et al., 2015). Although the Lomekwi industries might represent a pre-Oldowan horizon, its stratigraphic position has been questioned by several authors (eg. Domínguez-Rodrigo et al., 2015). Although the idea of an industry older than the Oldowan is not new (Panger et al., 2002) further evidence is required before extrapolating the Lomekwi horizon to pancontinental phenomenon.

There is currently a large body of literature on the Early Stone Age (ESA) through intensive fieldwork and labwork in Ethiopia, Kenya, and Tanzania, with a multitude of sites along the EARS being surveyed and excavated almost continually (Asfaw et al., 1992). The trend has been to direct research to localities alongside sedimentary basins that have been known to be productive (Harmand, et al., 2015). The world's oldest and first undisputable evidence of stone tool manufacture by hominins comes from Gona (Ethiopia) and dates to between 2.6 and 2.5 Ma. However, currently we have a newly discovered Oldowan tool kit dated at least 2.6-2.58 Ma at Mieso valley that is slightly younger than the Gona industry (Braun et al., 2019), with toolkits characterised by hammerstones, cores, flakes, debris, and unmodified stone. Hadar (2.36 Ma), Omo (2.34 Ma), and Lokalalei (2.34 Ma) in Kenya provide us with insight into complex lithic reduction, planning depth, manual dexterity, and raw material selectivity (Lepre et al., 2011) (Fig. 3-2). The Oldowan, however, is not restricted to East Africa, and is also found in Northern and



Figure 3-2: Oldowan Map. 1-2 Gona and Hadar; 3. Mieso; 4. Omo; 5.Lokalalei; 6. Lomekwi; 7. Senga; 8. Oldupai; 9-10. Sterkfontein and Swartkrans. Map Source Data. Airbus, USGSm NGA, NASA, CGIAR NRobinson, NCEAS, NLS, OS, NMA.

Southern Africa (Kuman 1998; Sahnouni et al., 2002; Semaw et al., 2003; Quade et al., 2004; Stout et al., 2005; Kuman and Field 2009).

At the continental level, the Oldowan is known to co-occur with nine hominin species from three different genera (e.g. Plummer et al., 1999; Blumenschine et al., 2012; Braun et al., 2008): *Australopithecus africanus*, *A. garhi*, *Paranthropus aethiopicus*, *P. boisei*, *P. robustus*, *H. habilis*, *H. rudolfensis*, and *H. ergaster* (Toth and Schick 2018). This industrial complex is characterised by battered artefacts and simple core/flakes showing conchoidal fracture, reduced by hard percussion and are fundamentally dissimilar from those found amongst non-human primates (Ambrose, 2001). Hammerstones and cores generate flakes with sharp edges, choppers, and polyhedrons (Schick and Toth, 2006). It is said that the Oldowan reflects ape-like cognitive abilities, primarily involving the coordination of visual attention and motor control. The thinking abilities of *H. habilis* might have required the integration of higher-order motor planning, working memory and auditory feedback ability to manipulate a variety of crude tools (Putt et al., 2017).

3.2.2 ACHEULEAN

Its emergence from the Oldowan constitutes one of the major transitions in human history (Díez-Martín et al., 2015; de la Torre, 2016; Sánchez-Yustos et al., 2017) across Africa, Asia, and Europe during the Lower and Middle Pleistocene, from 1.75 - 0.125 Ma. The Acheulean associates with archaic *Homo* and Middle Pleistocene *Homo*, and is characterised by the presence, irrespective of frequency, of amygdaloidal, hand-held artefacts (de la Torre, 2016). The number of Acheulean sites in Africa increases notably between 1.6 and 1.3 Ma (de la Torre, 2016). The earliest appearance of the Acheulean industry has been reported in East Africa at 1.76 Ma, and it

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is characterised by Large Cutting Tools (LCTs) such as handaxes, cleavers, choppers, core scrapers, and picks (Beyene et al., 2013; Díez-Martín et al., 2015; de la Torre, 2016). The earliest Acheulean known today comes from Kokiselei and Konso Gardula (Asfaw et al., 1992), and FLK-W at Oldupai Gorge (Díez Martín et al., 2015). The origin of the Acheulean is thought to have coincided with changes in the human brain, allowing for further technological developments. Nonetheless, the emergence of the Acheulean remains unclear because of the limited number of well-dated sites >1.4 Ma and at this stage, behavioural diversity may be as important as biology to explain the patchy and environmentally-patterned occurrence of early Acheulean stone tool industries (Díez-Martín et al., 2015, de la Torre et al., 2016). All in all, one can argue that the Acheulean complex from East Africa is a response to changing ecological conditions, increasing aridity in the context of climate pulses which were endured by a newly emerged species *H. erectus* (de la Torre, 2016).

Shortly after 1.5 Ma, Acheulean technology disperses across Africa (Chazan et al., 2008; Gibbon et al., 2009; Kuman and Clarke, 2000), the Near East (Bar-Yosef and GorenInbar, 1993), India (Pappu et al., 2011), and China (Zhu et al., 2004). The Acheulean industry spread to Europe and Asia as early as 1.4 Ma according to the evidence in the Middle East (Bar Yosef and Goren Inbar, 1993) and India (Petraglia et al., 1999). In Tanzania, Acheulean stone tools are documented at key localities outside Oldupai Gorge. For instance, at Peninj, in the Magadi-Natron basin. Here, Howell reported rich finds in 1963, including Acheulean LCTs and prepared cores (Isaac, 1965, 1967; Díez-Martín et al., 2009), with layers deposited during the early Pleistocene containing *Paranthropus robustus* in association with stone tools dated to 1.4 Ma (Díez-Martín et al., 2009).

Apart from Peninj there are other prominent Acheulean sites in south western Tanzania such as Isimila. This complex lies along an erosional system five kilometres long with dense



Figure 3-3: Acheulean site Map. 1. Buia; 2. Gona; 3. Bouri; 4. Bodo; 5.Melka Kunture; 6. Gadeb; 7. Konso-Gardula; 8. Kokiselei; 9. Koobi Fora; 10.Kathpurin; 11. Kilombe; 12.Kariandusi; 13. Isenya; 14. Olorgesailie; 15. Peninj; 16. Oldupai; 17. Isimila; 18. Broken Hill; 19. Broken Hill; 20.

Maunganidze; 21. Namib IV; 22. Olieboomspoort; 23. Makapansgat; 24. Sterkfontein, Kromdraai and Swartkrans; 25. Kathu Pan; 26. Wonderwerk; 27. Cornelia; 28. Reitptus Formation; 29. Rooidam; 30. Power's Site; 31. Elandsfontein; 32. Montagu; 33. Amanzi; 34. Duinefontein. Map Source Data. Airbus, USGSm NGA, NASA, OS, NMA.

surface scatters of handaxes and cleavers from 300,000-250,000 years ago (Howell et al., 1972; Bergstrom et al., 2019). The site has been compared to Olorgesailie (Isaac 1977) in Kenya, as well as to Kalambo Falls in Zambia (Clark, 1962), providing a temporal and geographic window into the late Acheulean at the Acheulean–MSA transition in East Africa (Fig. 3-3).

As discussed previously, the Acheulean is distinguished from the Oldowan mainly by the addition of handaxes, cleavers, and other large bifacial tools. It represents the emergence of a complex behaviour, expressed in the recurrent manufacture of large-sized tools, with standardised forms, implying more advance forethought and planning by hominins than those required for the Oldowan. However, like most Oldowan sites, Acheulean hominins used local outcrops where quartzite was available. Bearing in mind that quartzitic rocks in the Oldupai region preserve their cutting edges better than igneous rock types (Jones, 1994), this implies that hominins may not have felt the need to obtain alternative material from potentially more distant sources. Several trends for the Acheulean suggest that unworked, partially worked, and finished pieces were procured <10 km away (Leakey and Roe, 1994; Santonja et al., 2014). The artifacts were said to be recovered from laterally diverse loci within Lowermost Bed II. For instance, the landscape classification system implemented by Peters and Blumenschine in 1995 and 1996 respectively has been referred to as a discrete geomorphologic grouping, or 'palaeogeographic locales' identified by modern geological outcrops in the eastern Oldupai sub-basin. The systematic technological analysis revealed variation in artifact assemblage characteristics such as raw material and artifact type, composition, and density between various palaeogeographic locales (Tactikos, 2005). The 53

observed variations in the characteristics of a specific artifact assemblage were hypothesised as resulting from different technological strategies, or tool-using behaviours linked to specific ecological factors. While raw material transport cost and predation risk were shown to be factors in the early hominin expedient and optimisation tool-using strategies, the predominant strategy was found to be somehow opportunistic, in which the determining factor is the availability of raw materials in a proximal landscape (Tactikos, 2005).

3.3 PLANT LANDSCAPES THROUGH ISOTOPES AND POLLEN

3.3.1 ISOTOPES

The palaeoclimate and palaeodietary reconstructions of East African environments using stable isotopes are well established. Cerling and Hay (1986) were the pioneers of isotopic research in East Africa. The δ^{13} C and δ^{18} O data vary considerably with time, but overall, there is a trend toward warmer and drier conditions starting at 1.67 Ma (Cerling and Hay, 1986). Cerling (1984) developed a model that described the isotopic composition of soil carbonate δ^{13} C values in terms of the proportion of biomass using the C₄ photosynthetic pathway and predicts δ^{13} C values for carbonates produced under pure C₄ flora to be about +2.0‰ and for pure C3 flora to be about - 12.0‰. The isotopic signature of environmental carbon (δ^{13} C) incorporated during plant biosynthesis represent changes in relative temperatures, precipitation/aridity, evapotranspiration of leaf and soil moisture, and the relative abundance of C₃ and C₄ plants that are useful in determination of ancient climate and dominating plant cover.

Recent advances in Palaeoanthropology have measured stable oxygen isotopes (δ^{18} O) on sea bottom-dwelling microorganisms, called foraminifera, which are indicators of past ocean temperature and worldwide glacial-ice fluctuations (Potts, 2013; Shultz and Maslin, 2013; Maslin et al., 2014; Rowan and Reed, 2015). The airborne continental dust that accumulated on the ocean bottom provides a record of aridity fluctuations and the deep-sea drill cores provide the evidence for these types of records (Rowan and Reed, 2015). In terrestrial settings, stable carbon isotopes $(\delta^{13}C)$ are measured from pedogenic carbonates: carbonate nodules or organic material that formed in palaeosols. These have successfully provided some key indications of past vegetation, including the proportion of grass versus woody plants or the percentage of shade cover in low-latitude habitats (Rowan and Reed, 2015). By assembling all available palaeoclimate data, such as the global benthic foraminifera δ^{18} O record, regional aeolian dust flux data and the East African lake record, found that hominin speciation events and changes in brain size seem to be statistically related to the appearance of ephemeral deep-water lakes (Shultz and Maslin, 2013; Maslin et al., 2005, 2014). An example is the appearance of *Homo erectus*, which is said to be associated with the period of maximal ephemeral lake coverage at least 2.0 Ma (Maslin et al., 2013, 2014). The expansion in cranial capacity occurred during one of only two periods when there is evidence for at least 5 of the 7 major intra-rift lake basins being active (Trauth et al., 2009). Afterward, the underlying trend towards increasing brain size in Homo is most strongly correlated with both decreases in lake presence and high levels of dust deposition in the Mediterranean record (Shultz and Maslin, 2013), indicating drier conditions in East African region (Trauth et al., 2009; Shultz and Maslin, 2013).

If this is combined with the notion that many of the East African lakes are amplifier lakes that respond very quickly to a small increase or decrease in the precipitation-evaporation balance, then it is relatively easy to envisage threshold responses of the landscape to precessional forcing (Olaka et al., 2010; Trauth et al., 2010; Borchardt and Trauth, 2012; Junginger and Trauth, 2013; 55 Shultz and Maslin, 2013). In addition, deMenocal (2004) also has already noticed the similar patterns thus described the potential effects of millennial-scale climate fluctuations which originate in the North Atlantic but have had a profound effect on East African climate in the late Pleistocene (Potts, 1998, 2013; Shultz and Maslin, 2013) and may have had an influence in the Pliocene and early Pleistocene (Foerster et al., 2012; Shultz and Maslin, 2013). Accordingly, the isotopic values of environmental carbon (δ^{13} C) incorporated into plants and soils during plant biosynthesis represents changes in relative temperatures, precipitation/aridity, evapotranspiration of leaf and soil moisture, and the relative abundance of C₃ and C₄ plants that are useful in determination of ancient climate, and the grassland versus arboreal plant cover dominated.

Some of the earliest stable isotope studies was conducted by Vrba (1995; 2000), who explored the interplay between palaeoclimate and macroevolution using the fossil record of African mammals (Rowan and Reed, 2015). Using δ^{13} C and δ^{18} O from fauna as palaeoenvironmental and palaeoecological indicators, she argued that the radiation of cool and arid-adapted mammals over warm and moist adapted mammals suggested that Africa became increasingly cooler and more arid over the past 5 million years. Marine isotopic stages evidence (MIS) (Zachos et al., 2001) also suggests cooling in Africa during this time, along with an intensification of glaciation in the Northern Hemispheres.

Analyses of soil carbonate nodules near hominin fossil localities (Wynn, 2004) indicate that East African savannah grasslands expanded at these times. Increased numbers of grazing bovid species parallel the grassland expansion. The ecological niche occupied by early Acheulean toolmakers and the food procurement strategies on which they based their subsistence are also practically unknown. Palaeobiological studies of human fossils suggest that *Homo erectus* occupied more open and arid environments than early Homo, and that their ecological niche was 56 substantially larger and more diverse than that of their Oldowan ancestors. However, archaeological evidence supporting these inferences is almost non-existent, and more empirical data are needed to reconstruct the palaeoecological background of the early Acheulean (see Patalano, 2019: 362-443).

Stable carbon isotope analysis can be done on palaeosols if there are carbonate nodules (Cerling, and Hay, 1986; Wynn, 2000). These nodules usually form under drying conditions and can be used to estimate of the percentages of grasses and dicots (bushes and shrubs) that were present when the soil formed. In addition, the soil carbon and carbonates can be used to estimate carbon dioxide in the atmosphere, which allows for a better understanding of the palaeoclimate (Cerling, 1992; Rowan and Reed, 2015). Similarly, Cerling et al., (2011) developed a method using soil carbon isotopes to evaluate the percentage of woody cover that was present on the landscape when the palaeosols were formed. The percentage of woody cover is based on the number of shrubs, bushes, and trees that used the C₃ photosynthetic pathway in the palaeosol.

The term C_3 photosynthesis is based on the observation that the first product of photosynthesis is a 3-carbon molecule, and the C_3 photosynthesis is the ancestral pathway for carbon fixation and occurs in all taxonomic plants. In C_4 photosynthesis, the initial photosynthetic product is a 4-carbon molecule. C_4 photosynthesis occurs in the more advanced plant taxa and is especially common among monocots, such as grasses and sedges, but not very common among dicots (most trees and shrubs). The C_3 and C_4 plants are isotopically distinct and can be used in studies on palaeoenvironmental change. These two photosynthetic pathways respond quite differently to changes in atmospheric carbon dioxide (CO_2) concentration and to changes in temperature (Cerling et al., 2011). C_3 photosynthesis is a multi-step process in which the carbon from CO_2 is fixed into stable organic products; it occurs in virtually all leaf mesophyll cells in the 57

first step at the ribulose bisphosphate (RuBP) or (Rubisco) that combines RuBP (a 5C molecule) with CO₂ to form two molecules of phosphoglycerate (3C molecule). The C₄ photosynthesis represents a biochemical and morphological modification of C₃ photosynthesis to reduce Rubisco oxygenase activity and thereby increase photosynthetic rate in low CO₂ environments (Ehleringer and Cerling, 2002). The result is that C₃ plants tend to have more-negative isotopic values (reported in per mille notation ‰, or parts per thousand) relative to a standard (modern C₃ mean δ^{13} C: -27.4 ± 1.6‰), whereas C₄ plants tend to have a more-positive isotopic value relative to a standard (modern C₄ mean δ^{13} C: -12.7±1.1‰). The δ 13C of soil carbonate indicates the proportion of C₃ and C₄ plant biomass contributing to soil CO₂ that diffuses downward to form carbonates. Consequently, the carbon isotope composition of pedogenic carbonate in palaeosols is used to infer the relative proportions of C₃ versus C₄ plants during pedogenesis (Patalano, 2019). The soil carbonate oxygen isotope compositions are moderated by the isotopic configuration of soil water which derives from localised meteoric water.

In C₄ plants, the C₃ cycle of the photosynthetic pathway is restricted to interior cells within the leaf (usually the bundle sheath cells). Surrounding the bundle sheath cells are mesophyll cells in which a much more active enzyme, phosphoenolpyruvate (PEP) carboxylase, fixes CO₂ (but as HCO₃) into oxaloacetate, which is a C₄ acid. The C₄ acid diffuses to the bundle sheath cell, where it is decarboxylated and refixed in the normal C₃ pathway (Cerling et al., 2011). As a result of the higher activity of PEP carboxylase, CO₂ is effectively concentrated in the regions where Rubisco is located, and this results in a high CO₂/O₂ ratio and limited photorespiratory activity. The additional cost of C₄ photosynthesis is the adenosine triphosphate (ATP) requirement associated with the regeneration of PEP from pyruvate (Ehleringer and Cerling, 2002).

C₄ photosynthesis is advantageous under low atmospheric CO₂ and/or high temperatures, therefore it is the kind of photosynthesis which occur in lower CO₂ environments and/or high temperature environments, where photorespiration rates are relatively high in C₃ plants. Under these conditions, the efficiency of C_4 photosynthesis is greater than that of C_3 photosynthesis. However, under elevated CO₂ environments or at cool temperatures, the efficiency of photosynthesis is greater in C₃ photosynthesis because photorespiration is reduced and the additional ATP cost of C₄ photosynthesis makes it less efficient (Ehleringer and Cerling, 2002; Cerling et al., 2011). Thus, Ehleringer and Celing (2002) noted that C₄ plants are not expected in environments where atmospheric CO_2 is greater than at least 600 parts per million (ppm). As atmospheric CO₂ decreases, C₄ plants should become most common first in the warmest environments, then in progressively cooler environments as CO₂ levels then will continue to decrease (Ehleringer and Cerling, 2002; Rowan and Reed, 2015). This method is especially important in reconstructing environments for ancient African landscapes, as most hominin fossil localities in eastern and southern Africa are believed to have been deposited under "savanna environments" (Cerling et al., 2011a; Rowan and Reed, 2015), with C₄ grasses as the ground cover. Reconstructions of past habitats and hominin sites using multiproxies to examine hominin ecology allows for better understanding of the taxa and their relationship with their environments that they have been occupying.

Strontium isotopes (⁸⁷Sr/⁸⁶Sr) are used to investigate movement of hominin species on the landscape. Various stable and non-stable isotope values of flora and fauna which are dependent upon the composition of underlying bedrock, plants, so locals and non-locals, and all have been identified based on similarities and differences between tissues of individuals and the local geology. These have been widely used in past landscapes, water regimes, and ecological 59

reconstruction (Copeland et al., 2011, Tucker, 2018). Interestingly, Copeland et al., (2011) used these data in South Africa to examine ranging patterns in early hominins and showed that the smaller hominins recovered in the Malmani dolomite region of South Africa had evidence of ingesting strontium outside of the range seen in that area. They hypothesised that this might reveal why male Australopithecines had relatively small home range compared to their female counterparts, who had a much wider range. Therefore, various combined isotopic analyses permit inferences of social and reproductive behaviour in the hominin fossil records.

Pedogenic carbonate forms in soils that become supersaturated with calcite when CO₂ decreases in the soil, when carbonate precipitates in soils due to weathering processes at the land surface, or when there is a net water loss due to evapotranspiration and evaporation (Cerling and Quade et al., 2004; Koch et al., 2003). Carbonate supersaturation due to evapotranspiration is regarded as the primary mechanism for CaCO₃ precipitation, particularly in well-drained soils in the unsaturated zone above the influence of the groundwater table (Koch et al., 2003; Sikes and Ashley, 2007). Because pedogenic carbonates form in soils with a net water deficit, they occur globally in soils today where annual rainfall is less than 1000 mm per year (Retallack, 1990). Climate regimes with rainfall less than 1000 mm per year include most of East Africa today at elevations below ~1000 meters, explaining pedogenic carbonates under much of the modern and ancient East African landscape (Quade and Levin, 2013).

The pedogenic carbonates preserved in palaeosols are important for palaeoenvironmental reconstructions, but they have relatively restricted distributions as they only form in arid to semiarid environments (Lee-Thorp and Sponheimer, 2007). Nevertheless, true pedogenic carbonates form well below the active soil horizon, where there is no mixing with atmospheric CO₂ and diffusion enrichment is complete (Cerling and Quade, 1993). Moreover, carbonates that 60

precipitate at depths greater than 50 cm in soils with moderate to high evaporation rates, reflect the isotopic composition of plant-derived CO_2 with no direct contribution from the atmosphere (Cerling, 1992).

Most of the pedogenic carbonate δ^{18} O values are largely controlled by climate, which ultimately determines local water-balance through precipitation and evaporation, and soil temperature, which is related to ambient temperatures and solar radiation. The δ^{18} O of modern, deeply formed soil carbonate is correlated with the δ^{18} O of meteoric water, though typically offset by 2‰ - 10‰ because of evaporation (Quade and Levin, 2013; Koch et al., 2003; Patalano, 2019), particularly in arid environments, but also because of the distanced traveled from the source of moisture, elevation, and extent of rainout from local cloud masses. The oxygen isotope composition of pedogenic carbonate in palaeosols is used as a proxy to infer relative palaeoprecipitation and temperatures (Fig. 3-4).

In certain environmental circumstances, especially under arid to semi-humid climatic conditions, dissolution of primary carbonate and recrystallisation with carbon from soil CO₂ leads to accumulation of significant amounts of pedogenic (secondary) carbonate (Quinn et al., 2007; Wynn, 2004; Cerling et al., 2013). Most soils of arid and semiarid regions contain a carbonate accumulation horizon, the depth of which is related to climatic conditions and properties of parent material. Most current research directions on pedogenic carbonate (PC) have been focused on trying to understand the anthropogenic effects of fertilisation. PC is an important part of soil

a) Equilibrium Fractionation



Figure 3-4: Oxygen isotope fractionation

inorganic carbon (C) that does reflect the time periods and formation processes in soils. In other aspects, the mechanistic understanding of PC formation is a prerequisite to predicting terrestrial C stocks and changes in the global C cycle, and to link the long-term geological and sedimentological records with short-term biological C cycles (Quinn et al., 2007; Wynn, 2004; Cerling et al., 2013).

The palaeosol isotope record from the Koobi Fora Formation in Kenya was the first of its own kind, especially on the eastern Africa palaeoenvironmental reconstructions. The Koobi Fora Formation is located east of modern Lake Turkana and dated to between ~4.4-0.6 Ma. Pedogenic carbonates sampled within the Koobi Fora Formation yielded δ^{13} C values that range from -10.6 to -2.0% and average -6.7‰. δ^{18} O values range from -7.6 to +1.6‰ and average -3.1‰. Like both the Shungura and Nachukui formation, the δ^{13} C values from Koobi Fora increase throughout the stratigraphic section suggesting a change toward more arid conditions. Additionally, more positive δ^{13} C values at Koobi Fora at 1.88 Ma (-2.0%), coincide with the transition to C₄ environments at 1.8 Ma that was recognised by Cerling et al. (1988) and Quinn et al., (2007). The isotopic results from the basin-wide sampling demonstrate that the soils in the Omo-Turkana Basin supported a mosaic vegetation community and diverse hydrologic regimes, contrasting in water availability, slope, and drainage across short distances. The δ^{13} C values from the Shungura Formation are lower than δ^{13} C values from contemporary palaeosols in the Nachukui and Koobi For aformations, whereas the δ^{18} O values in the Nachukui Formation are higher than δ^{18} O values from concurrent palaeosols upstream in the Shungura Formation (Zacho et al., 2001; Quinn et al., 2007).

Following the deposition of the KBS Tuff at East Turkana 1.89 Ma, C₄ grasses became well established as a result of increased aridity and temperature. Unlike at Oldupai Gorge, there are few calcrete deposits in the Koobi Fora Formation, likely due to the less reactive parent material and 63 higher sedimentation rates in the Turkana Basin, but pedogenic carbonates (nodules) exist. The δ^{13} C values for modern soil carbonate from the Koobi Fora region are about -4.0 to -2.0‰, and according to Cerling's (1984) model, this would correspond to a biomass made up of about 60-80% C₄ flora. Finally, differences in the isotopic composition of palaeosol carbonates from the Koobi Fora Formation are due to changes in the isotopic composition of meteoric and soil waters over the past 3.5 Ma (Cerling et al., 1988)

Before 2.1 Ma, δ^{13} C values in the formation are said to range from -10.0 to -6.0‰, corresponding to a percentage of C₄ plants of only 20-40% (Joordens et al., 2013) A change is first recognised in the upper Burgi Member (2.15-1.9 Ma) (Patterson et al., 2017) in which δ^{13} C pedogenic carbonate values range from -10 to -3.0% and δ^{18} O values from -3.0 to -6.0% (lower stratigraphic units) and -3.0 to +1.5‰ (upper stratigraphic units). These values likely coincide with changes in the isotopic composition of lake water resulting from changes in the lake's water budget or changes in the isotopic composition of inflowing water or the amount of water precipitations during that time) (Patterson et al., 2017). Major changes are evident beginning in the KBS member (1.89 Ma) and continue through the Chari Member (0.7 Ma). Average δ^{13} C values in sediments below the KBS Tuff are from -9.0 to -6.0%, whereas those above the tuff are -4.0 to -3.0%. The oxygen isotopes infer an increasingly xeric environment. This likely represents a change in the proportion of C₄ flora from about 25% below the KBS Tuff to about 65% above. This would also indicate significant drying in the basin, or increased temperatures, or both. This trend is more apparent in the δ^{18} O record. The average δ^{18} O value for palaeosol carbonates at the KBS Tuff was 0.7‰, increasing to 0.9‰ in the Okote unit dated between 1.64 and ~1.39 Ma, and finally to 1.2‰ in the Chari Member between <1.39 and 0.74 Ma (Cerling et al., 1984; Wright et al., 2017). This trend toward more positive carbon and oxygen isotope values suggests that prior to 1.9 Ma, 64

palaeosols were developed on the Omo River floodplain, but the later soils formed in more arid climatic conditions (Joordens et al., 2013).

Wynn (2004) also identified a change in C₄ biomass through time in both the eastern and western parts of the Turkana Basin. Three episodes of aridification in the basin were marked by spatial and temporal changes in open and closed habitats from 3.58-3.35 (Kanapoi Formation), another between 2.52-2.0 (Lokalalei Member at West Turkana), and lastly from 1.81-1.58 Ma (KBS Member at East Turkana). Prior to 2.52 Ma, δ^{13} C values from east and west Turkana were depleted and less variable with a mean of -8.0‰. Between 2.52 and 1.82 Ma, δ^{13} C became enriched and ranged between -7.5 and -4.9‰ with a mean value of -6.2‰. At 1.81 Ma, carbon isotope values became further enriched whereby the mean δ^{13} C value of palaeosol carbonate approached modern soil carbonate value of -3.8‰ but ranged from -5.8 to -1.8‰. Following 1.58 Ma, δ^{13} C values would return to around -4.38‰, but would never become as depleted as they were prior 1.81 Ma. The basin-wide ¹³C enrichment represents an increase of C₄ biomass through time, with major punctuations at 2.52 and 1.81 Ma, but at no point in the record is there evidence for pure C₄ habitats (Zacho et al., 2001; Quinn et al., 2007)

The stable carbon isotope values are more characteristic of mixed tree-grass savanna habitats such as grassy woodlands and low tree-shrub savannas, which would have been slightly more open than the contemporary Oldupai environment. Quinn et al. (2007) present a follow-up study in which they detail a δ^{13} C record for the Koobi Fora Formation between 2.0 and 1.5 Ma by showing a pronounced increase in δ^{13} C values after 1.8 Ma. This change, however, is not uniform throughout the Turkana Basin as it is only represented in some regions (Koobi Fora Ridge) but not in others (Karari Ridge). δ^{13} C values of pedogenic carbonates from the Koobi Fora Formation have a mean value of -5.5‰ but range from as low as -10.43‰ to as high as 0.43‰. This would indicate 65

that over time, the environmental setting fluctuated from a nearly closed C₃ forest (-10.43‰) to an open C₄ savanna grassland (0.43‰), but likely resembled a mosaic composition of grassy woodland or wooded grassland (-5.5‰) for most of this period (Cerling, 1984; Cerling et al., 1988). Interestingly, the δ^{13} C values from the Koobi Fora Ridge subregion corroborates the previous interpretation of C₄ expansion after 1.8 Ma (Wynn, 2004), but this trend is not shown in the data from the Karari Ridge which is about 20-30 km northeast of the Koobi Fora Ridge today. This is likely due to the palaeogeographic history of the Karari Ridge and that it may have had a different water-availability regime that was supplying a consistent supply of water to C₃ floral communities.

Another study was undertaken at the Nachukui Formation in Kenya Quinn et al., 2007), located west of modern Lake Turkana and dated to between ~4.2-0.5 Ma. Though this is a nearly four-million-year exposure, few palaeosols were sampled between 2.03 and 1.5 Ma or in the Nariokotome Member younger than 1.2 Ma due to an absence of calcareous palaeosols in the region. When data from the entire formation are compiled, the carbon isotopic composition of nodules from the palaeosol ranged from -9.1 to -0.4‰ with an average value of -6.1‰. δ^{18} O values from all palaeosols sampled from the Nachukui Formation range from -6.9 to 4.5‰ and average - 2.6‰. Both δ^{13} C and δ^{18} O values increase from the early Pliocene to the top of the section at 0.7 Ma, again indicating an increase in C₄ biomass and a shift toward warmer temperatures (Quinn et al., 2007).

The isotopic data from Omo Group (Ethiopia) palaeosol carbonates document systematic environmental variability within the Omo–Turkana Basin from three formations, the Shungura, Nachukui, and Koobi Fora, for the past 4 million years (Levin et al., 2011). The Shungura Formation (~3.9-1.0 Ma) is located north of Lake Turkana along the modern Omo River. When 66 jointed together, the carbon isotopic values of the Shungura formation are averaged, represented by the composition of nodules from the palaeosol ranged from -10.2 to -4.2‰ with an average value of -8.1‰. δ^{18} O. Thus, values from all palaeosols sampled from the Shungura Formation range from -8.3 to -0.3‰ and average -4.0‰. over the nearly three-million-year period. The Shungura Formation is divided into two distinct strata based on δ^{13} C values; those older than ~1.9 Ma that yield an average δ^{13} C value of -8.9‰, and those younger than ~1.9 Ma that yield an average δ^{13} C value of -6.3‰. The positive shift after 1.9 Ma signifies a major restructuring of vegetation along the ancestral Omo River from a C₃ dominated ecosystem (~20% C₄ biomass) to a more mixed grassy woodland ~40% C₄ biomass (Quinn et al., 2007, Cerling et al., 2013).

3.3.2 POLLEN

Palynological research have been undertaken in East Africa for over 50 years with the first publication by Dubois and Dubois, appearing in 1939 (Van Zinderen and Coetzee, 1988) followed in 1948 by Hedberg and his "Swedish East Africa Expedition", which collected samples from Lake Victoria, Lake Tanganyika, Mount Kenya and the Ruwenzori Mountains (Van Zinderen and Coetze, 1988). Those early palynological work in eastern Africa described Pleistocene to Holocene-aged lacustrine and peat sediment sequences, largely collected from mesic and wet regions in montane western Uganda (Morrison, 1968) and the Kenyan highlands-Mount Kenya, (Van Zinderen, 1962; 1995). The early studies focused on Afromontane taxa timing and response to climatic variability during the Late Pleistocene glacial retreat and subsequent broad-scale at the Late Pleistocene-Early Holocene transition (Livingstone, 1967; Morrison, 1968; Githumbi et al., 2018). This was followed by other research works that used pollen data to map anthropogenic deforestation of Afromontane forests in order to explain vegetation changes spatial-temporally (see Hamilton et al., 1986). Pollen results from longer sequences found that these forests had previously expanded, as Afromontane glaciers coverage increased leading into the global Last Glacial Maximum (Bonnefille and Riollet, 1988). Montane vegetation patterns were described as altitudinal bands (Coetzee, 1967), however more examination of pollen records and forest biogeographies showed a high degree of complexity in montane forests from the lower montane to forest-ericaceous zone transitions and non-linearity in vegetation responses to climatic variability (Platts et al., 2013). Van Zinderen and Coetzee (1988) summarised the last 32,000 BP of East Africa as warm and humid (32,000–20,000 BP), cool and dry from 20,000 to 14,000 BP, warm and dry until 12,000 BP, warm and humid from 12,000 BP- 4,000 BP and then regionally arid from 4,000 BP (Van Zinderen and Coetzee, 1988).

Pollen analytical studies have been carried out in East Africa savannah and tropical Africa, and these have identified the pollen signature of vegetation associations along latitudinal or altitudinal gradients (Bonnefille et al., 1994; Watrin et al., 2007). They have also been used to characterise specific ecosystems: Somalia-Masai drylands (Bonnefille et al., 1987); Sudanian dry forest of West Africa, savannas-forest transitional ecosystems, rain forest (Elenga, 1992; Elenga et al., 2000); and montane forest. These studies are based on a precise knowledge of the local vegetation, plant inventories (Elenga et al., 2000b) and an investigation of pollen-transport patterns (Watrin et al., 2007). The overall goal has been to produce a more precise tool for vegetation and climate reconstructions in East Africa, as it identifies taxa that have a high correspondence between pollen and plant distribution patterns. Pollen analyses in this region has been a useful tool to reassess biome reconstructions in Africa and to characterise accurately the vegetation and climate conditions at a regional scale especially when it is utilised (Bonnefille et al., 1993) in conjunction with stable isotopic data.

Pollen has been recovered from many fossil localities (i.e. Hadar, Ethiopia), but only from particular strata, such as the Sidi Hakoma Tuff and in the base of the Denen Dora Member, and it has been noted that no pollen was preserved from the upper Kada Hadar Member. The conclusion is that reeds and grasses from the palaeolake dominated Hadar, and through the section there were both increasing and decreasing proportions of tree and shrub species (Henry et al., 2012). Again, these data can be compared with the faunal data and isotopic data, where available, to arrive at a better understanding of the habitat of *Australopithecus afarensis*.

Coetzee (2007), performed a palynological study in order to document pollen analysis and its interpretation, together underscoring ecological situation and appropriate site descriptions, for five sites – three in Kenya (Cherangani and two lakes on Mount Kenya), and one each in Tanzania (Kilimanjaro) and South Africa (Aliwal North) in order to examine the effects of changing climate on altitudinal vegetation near the equator. The pollen sequence was shown to illustrate very significant shifts in vegetation zonation around the site, the most remarkable result being the finding that, for several thousand years towards the end of the last glacial and specifically around the time of the Last Glacial Maximum, montane forest was distributed well below the elevation of the lake and that very cold (and drier) climates prevailed at this time (see also Githumbi et al., 2018), and a mean annual temperature depression of between 5.1 and 8.8°C relative to the present day is proposed during a period referred to by Coetzee (1967) as the Mount Kenya hypothermal. Based on this evidence, which was also supported by sediment cores from Lake Rutundu with a projected basal age of around 21, 000 BP, and Cherangani with a projected maximum age of around 300,000 BP, variations in temperature were the primary factors responsible for ecological changes on Mount Kenya and Kilimanjaro over the time in question (Githumbi et al., 2016, 2018).

At Amboseli and Lake Chala, Githumbi et al., 2016, 2018), performed a study in to understand the environmental change and emerging socio-ecological interactions across the Amboseli region of southwestern Kenya. The focus was on late Holocene (<5,000 BP) changes and continuities reconstructed from sedimentary, archeological, historical records and socioecological models. The multi-disciplinary approaches were employed to understand environmental-ecosystem-social interactions across the Holocene epoch (Githumbi et al., 2016, 2018). Pollen suggest that the environmental conditions were dry between ~5,000 and 2,000 BP, followed by two wet periods at $\sim 2,100-1,500$ and 1,400-800 BP with short dry periods; the most recent centuries were characterised by variable climate with alternative dry and wet phases with high spatial heterogeneity (Githumbi et al., 2016, 2018). Also, pollen data indicate an ecosystem change in the lowlands surrounding Mount Kilimanjaro, including Lake Challa and Namelok wetland (Githumbi et al., 2016), these palaeoenvironmental data from montane region provide evidence of late Holocene environmental change at a decadal to centennial scale and are being complemented by sedimentological (Githumbi et al., 2016, 2018) and multidisciplinary historical ecology studies Githumbi et al. (2018). Several spatially isolated, perennial and ephemeral wetlands persist across Amboseli today and these wetlands are topographically divided at 1,250m asl causing groundwater and channelised flowing westward to Lake Amboseli or eastward toward the Chyulu Hills (Githumbi et al., 2016, 2018). Most evident in palaeo and historical records is the changing woody to grassy cover ratio, driven by changes in climate and fire regimes entwined with fluctuating elephant, cattle and wild ungulate populations moderated by human activity, including elephant ivory trade intensification. The pollen data provide insight into how large-scale and long-term interactions of climate, people, livestock, wildlife and external connections have shaped the ecosystems across the Amboseli landscape (Githumbi et al., 2016, 2018).

CHAPTER 4: PHYTOLITH ANALYSIS

Phytoliths form when dissolved silica enters plants through their roots during water uptake (Rovner, 1971). Silica, together with other liquid nutrients, are then distributed throughout the plant and into different parts, such as the bark, stem, or leaves (Parry and Smithson, 1964; Twiss et al., 1966). Eventually, the silica forms into specific shapes that are representative of the plants that produced it (Rovner, 1971; Piperno, 1988). When plants die and decompose, the hard phytoliths are released into the soil and can preserve for millions of years (Stromberg et al., 2016) (Fig. 4-1). When we find these phytoliths along with archaeological remains, we get palaeobotanical signatures which are represented by different phytolith morphotypes (Piperno 2016), whereby in turn we interpret their distinct shapes to infer ancient plant landscapes on which human activities occurred (Prychid et al., 2003).

Due to their exceptional preservation in palaeosols, phytoliths are incorporated as a component of archaeological and palaeoanthropological research in Africa, the Americas, Asia, and Europe to study the palaeovegetations and palaeoecologies of human origin. Phytoliths have been used in archaeological and environmental studies to reconstruct palaeolandscapes, (Zhao and Piperno, 2000; Stromberg, 2004), subsistence strategies (Pearsall and Piperno 1993; Piperno and Pearsall, 1993; Cyr et al., 2011), and prehistoric plant use (Madella et al., 2002). Phytolith assemblages are useful indicators in arid environments and are a key tool for establishing modern referential baselines for ancient sediment phytolith analyses (Mercader et al., 2019). In order to interpret such data on past ecosystems, documentation of modern plant-derived minerals is important, especially in arid regimes like the savannah woodlands of Eastern Africa and other tropical regions.


Figure 4-1: Phytoliths in soils

Phytoliths can supply additional information on past environments and landscapes (Albert et al., 2006; 2009) where other disciplines might be silent or ambiguous, e.g., distinguishing C_3/C_4 grasses, short versus tall grasslands, arboreal versus herbaceous vegetation (Iriarte et al., 2003).

This has been fundamental in archaeological research and it has opened new avenues of investigation on the past use of plants in hunter–gatherer and agriculturalist societies, the development of early agriculture and domestication, agricultural practices, and the use of space. Morphological studies of phytoliths have helped in clarifying crop processing of staple cereals while new approaches in isotopes and molecular composition of the silica bodies can aide in understanding agricultural, environmental (Madella et al., 2002; Gracia-Granero et al., 2015; Vrydaghs et al., 2016; Zurro et al., 2016; Mercader et al., 2019), and possibly evolutionary trajectories. A further application of phytolith analysis is gaining momentum for identifying domestic activities in foragers (Zurro et al., 2016) and agriculturalist societies using a qualitative and quantitative stance (Cabanes et al., 2017; Zurro et al., 2016). Significantly, all these applications need the fundamental support of phytolith botanical studies that highlight morphological variability of opal and patterns of silicification in plants (Hodson, 2016) as well as advances in methodological approaches (Stromberg, 2004; 2007; 2016).

4.1 PHYTOLITHS IN SOILS

Phytoliths usually stay where they were produced or deposited, since they are not easily transported through the air like pollen, so they indicate their activity area or their actual sedimentary depositional context (McNamee, 2013). They indicate where the certain plant taxa grew and the microenvironment in which they thrived in relation to their landscape and vegetation pattern, which thereby informs researchers whether a certain plant is local or exotic to particular landscape/site under study. At the regional scale, plant composition is closely associated with temperature and moisture gradients (Fredlund and Tieszen, 1997). Calibration of grass phytolith

assemblages in climatic terms has opened a way to the direct palaeoclimatic reconstructions from phytoliths by developing a combined use of it with isotopic and pollen analyses. Using phytolith analysis to measure the balance of woodland and grassland is possible but requires additional modern soil analysis and closer scrutiny of the potentially biasing effects of differential preservation (Fredlund and Tieszen, 1997). Phytolith data could supplement palaeoclimatic reconstructions provided by pollen (Williams et al., 2001). More extensive sampling of different vegetation and climate zones would be required before quantitative palaeoclimatic reconstructions could be made with phytolith inferences alone (Williams et al., 2001).

Soil assemblages may or may not reflect plant community structure and composition with fidelity (Bremond et al., 2008; Mercader et al., 2019). The analysis of soil phytolith assemblages are sometimes are biased due to differential production (Mercader et al., 2009, 2010, 2019), accumulation (Gao et al., 2018; Hodson et al., 2005), and preservation biases (Cabanes et al., 2011, 2015). Pre- and post-depositional taphonomic processes may affect phytolith deposition and preservation in soils (Piperno, 1988, 2006). Pre-depositional processes are the factors that may influence the plant accumulation in soils and their subsequent release of phytoliths after organic material decay. External factors like the degree of vegetation cover, differential phytolith production in different plants, and life cycles of specific plants have all been shown to influence the pre-deposition of phytoliths in modern soils (Piperno, 1988, 2006; Henriet et al., 2006; Hodson et al., 2005). Aeolian vectors impact may also influence phytolith deposition in soils increasing mobility on a micro and macro scale in specific site (de Menocal et al., 1993; Street-Perrott and Barker 2008).

Preservation relates to sedimentary conditions (McNamee, 2011). Phytoliths are therefore a useful tool for understanding the impact of post-depositional processes on a landscape and for 74 examining sediment minerals contexts. Understanding the preservation state of the phytoliths is also important for obtaining high-resolution data regarding the ancient landscape. Understanding the influence of sedimentary records on palaeoecology and sedimentology assists in palaeolandscape interpretation, as we depend on knowledge of the depositional environments of the sites where we are conducting research. Phytoliths were commonly thought to reflect subtle shifts in vegetation composition at the local scale, because they are primarily deposited *in situ* (Piperno, 1988; Fredlund and Tieszen, 1994). However, Fredlund and Tieszen (1994) argued that phytoliths are displaced from the original deposition site both vertically and horizontally as a result of fire, flood, grazing, burrowing, or other disturbances. Such mixing may blur the vegetation signal offered by phytolith assemblages in modern soils. Indeed, Fredlund and Tieszen (1994) found that phytoliths from a given geographic location appeared to reflect vegetation of a larger area than previously thought.

Additional research of production and preservation is required, because some phytoliths may prove to be systematically underrepresented in the palaeo-assemblages based on either their low production or low preservation rate in soils (Blinnikov, 2005; Honaine et al., 2009). The combined phytolith studies of modern plants and modern soils have been useful in understanding the depositional processes of phytoliths and post-depositional effects that may affect their preservation under different mineralogical and climatic conditions (Albert et al., 2006). Fossil and genetic records indicate that difference in silica content among different plant groups is due to local soil and climate conditions that regulate the concentration of plant-available silica (Barboni and Bremond, 2009; Mercader et al., 2011, 2019).

Phytoliths from modern soils under known vegetation and environmental conditions act as control samples that test the accuracy of conventional interpretive assumptions for reconstructing 75

ancient plant landscapes (Alexandre et al., 1997; Barboni et al., 2007; Bremond et al., 2008). Moreover, the actualistic insights obtained from soils are the foundation of phytolith taphonomy, which aides in understanding how geological, edaphic, and biological processes preserve, mix, bias, and delete the phytolith record (Strömberg, 2004; Mercader et al., 2010; 2011, 2019). Therefore, tackling these questions about soil phytoliths requires a concurrent study of phytoliths from local plants to assist in taxonomic identification and taphonomic normalisation (Barboni and Bremond et. al., 2005; Bremond et al., 2008; Gao et al., 2018; Mercader et al., 2009, 2019). Recent studies have suggested that any palaeoenvironmental reconstructions using phytoliths must begin with analyzing modern phytolith distribution in plants and soils in the given region (Gao et al., 2018; Mercader et al., 2019).

In regard to the Oldupai palaeolandscape, the potential of phytolith transportation by wind at Oldupai Gorge to the sampled localities could be also a possible scenario worth for a discussion, however further discussion is provided in the discussion chapter in this study. This is because it has been noticed that aeolian forces can impact phytolith deposition and movements in the soils (see Prokras and Mix, 1985; Piperno, 2006) for more details. Phytoliths have been shown to be subjected to movement by wind forces across the landscapes, and the movement by wind transport could deposit phytoliths to the lakes, which are usually a good context for sampling.

Phytoliths have preservation in the soils are said to be impacted by the movements from topsoil to underground soil profiles and could be redeposited to various soils horizons across the landscape. The soil profiles would contain phytoliths which resulted from mobility of them through wind, water action, soil redeposition by animal or human disturbances. The distribution pattern of phytoliths in various soil horizons can be generated under strong mass movement of water and soils, the phytolith mobility events in soils affects phytolith size and shape on their 76

transport behaviour especially in sandy and loamy soils (see Madella, et al., 2005): Phytolith size can significantly affect transport behaviour which ca lead to translocation of small-sized phytoliths

The already suggested potential drivers of phytoliths mobility in soils are most probably water flow and soil biota (see Alexandre et al., 1997; Alexandre et al., 1999; Hart and Humphreys, 2003; Madella et al., 2005. Beyond the mechanisms directly initiating phytolith mobility in soils, several soil processes and soil characteristics affect the phytolith distribution in a soil profile. These include the availability of macropore channels, the intensity of phytolith aggregation with clay particles, organic substances and oxides, and phytolith dissolution (Fishkis et al., 2010).

4.2 PHYTOLITHS IN PLANTS

Modern plant phytolith assemblages are important tools that can be used to differentiate vegetation types in a region under study in order to distinguish vegetation on the basis of their phytolith record in modern soils (Strömberg, 2007; Mercader et al., 2019), and for deciphering the relationship between modern phytolith assemblages in soils and the climate of a particular region (Strömberg, 2005, 2007). Their morphological characteristics often allow for the identification of the original taxa (Piperno, 1998, 2016) and, in certain cases, the part of the plant in which they were formed. Examining and understanding modern plants and soil phytolith assemblage is vital in inferring the nature and distribution of the past vegetation landscapes that were occupied by our early ancestors.

Previous studies have indicated that the plants most subject to significant variation in phytolith content are primarily those that would be heavy accumulators of silica in any environmental conditions. Studies of modern plants have always aimed at identifying diagnostic morphotypes, which can later be used for the identification of botanical remains in fossil records (Runge, 1999; Runge and Runge, 1997; Albert and Weiner, 2001; Bamford et al., 2006; Fahmy, 2008; Albert et al., 2009; Mercader et al., 2009, 2010, 2019; Rossouw, 2009). Phytoliths from modern plants have been able to complement studies of modern soils, as modern soils phytoliths by themselves have some limitations for reconstructing past vegetation and climatic conditions (Bremond et al., 2005, 2008; Albert et al., 2015; Barboni et al., 2007; Barboni and Bremond, 2009; Mercader et al., 2011, 2018; Novello et al., 2012).

Production in plants sometimes follows specific evolutionary groupings (Hodson et al., 2005; Strombert 2018). Some plants, particularly grasses, produce many more phytoliths than arboreal taxa, as it strengthens their tissues. Some other plants do not produce phytoliths. However, grasses of the Poaceae family are main phytolith producers and produce diagnostic phytoliths; more taxonomically specific than seeds or pollen (e.g. Stromberg, et al., 2007). This is important because grasses have different growing environments and different geographic origins, understanding the production of phytoliths in both grasses and other plants is useful for reconstruction of past vegetation.

Although phytolith production in plants has been known since the mid-19th century (Neumann, et al, 2017), studies on the production, taxonomy, and preservation of phytoliths did not become common until the 1970s (Piperno 2006). This is due to the diversity of forms within and among species thus requiring the establishment of regional comparative collections. Over the past 30 years, research on taphonomic impacts and modern phytolith analogues has increased (Blinnikov et al., 2013; Mercader et al., 2009), but many geographic and depositional settings are yet to be studied.

The modern study of phytoliths in plants and soils so far has provided a modern analog dataset required for any palaeoenvironmental reconstruction of the Plio-Pleistocene, Pleistocene, and Holocene vegetation in different parts of the world. Importantly, the datasets from modern samples are useful in ethnobotanical and palaeoecological studies when identifying the overall diversity in the main phytolith-producing plants in different ecosystems. Modern samples are used to answer questions such as which taxa can be identified based on their phytoliths and at what level; e.g., species, genus, or family (Blinnikov et al., 2002, 2005). As analogues that can be used to interpret ancient phytolith assemblages, the comparison of modern phytoliths from plants and terrestrial sediments are the only way to normalise the taphonomic bias that we encounter in the fossil record (Albert and Bamford, 2007; Mercader et al., 2009, 2010, 2018). Published modern referential baselines have been used to protocols to extract phytoliths from selected plant taxa known to represent local ecosystems (Mercader et al., 2009; 2011; Andrews et al., 2012). Because the palaeo-ethnobotanical interpretation of phytoliths relies on the comparison of ancient types with morphotypes extracted from living reference collections (Mercader et al., 2009; Mercader et al., 2011, 2018), it helps to provide high-resolution data regarding the ancient landscape and the exploitation and use of vegetal resources by our ancestors (Cabanes 2009; 2011; Mercader et al., 2009; 2011; 2013, 2018).

4.3 PHYTOLITH ANALYSIS OUTSIDE AFRICA

The most traditional use of phytolith analysis in the deep-time record is the reconstruction of vegetation type, as plant silica assemblages can provide unique information about plant communities and/or habitats for fauna, such as in the Miocene and Pleistocene of Europe, and other parts of the Old and New World (Retallack et al., 1990). Recently, the use of phytoliths has permitted palaeobotanists to address broader questions about vegetation change in response to temporal or spatial changes in abiotic or biotic environments, aspects like climate, uplift, mass extinction or the influence of habitat alteration on animal evolution (Strömberg 2006). For example, comparison between phytolith assemblages in Turkey and Spain revealed a sharp earlymiddle Miocene vegetation gradient across the Mediterranean, with forests in the west and grassdominated plant communities in the east (Strömberg et al., 2007, Strömberg, 2011). Other application of European research have included the late history of the Mediterranean (Tsartsidou et al., 2007) and northern European environments (Carneli et al., 2004). In archaeological sites occupied by Neanderthals, for example, phytolith have been extracted from terrestrial and lacustrine sediments; and were well preserved in European Palaeolithic sites where macroremains are not preserved (Henry et al., 2011). This shows the potential of phytoliths in food consumption in the middle Pleistocene (Henry et al., 2011, 2012).

In Australia, opal-phytoliths occur in sediments from the Tertiary and Quaternary periods in Victoria (Baker 1959a) proving that they can survive transportation and become preserved in the fossil state for varying periods of time ranging back to the Palaeocene (Hart & Wallis, 2003). Baker (1959b), subsequently examined phytoliths from a variety of sedimentary contexts and plants collected across the Australian continent. His identification of phytoliths preserved in soil beneath a basalt flow dated to 4.35 million years ago was especially important in demonstrating to the international community their capacity for resisting weathering processes over extended periods of time (Hart & Wallis, 2003). Hart (1997 cited in Hart, 2016) studied phytolith taphonomy, exploring discrepancies between the amounts of silica produced by Australian plants and those recovered from adjacent terrestrial sediments. She concludes that fire and rain can have 80 major detrimental effects on the quantities of phytoliths available for incorporation into sediment profiles. Hart (1997) also considered issues of phytolith mobility through the study of soils. Hart and Wallis (2013) investigated silica in the epidermis of the grasses. Bowdery's research (1998, 1999) was significant for a number of reasons: Firstly, it demonstrated that phytolith analysis could be successfully applied in the Australian arid zone context to provide information relating to climatic-vegetation change; secondly, it provided the beginning to the onerous task of assembling a comparative, modern phytolith collection for the unique Australian flora, and; finally, the identification scheme developed by Bowdery serves as a modern baseline for further studies in the region. Kondo et al., (1994) studied phytoliths from New Zealand and built the first reference baseline for the region. They studied and analysed modern samples from soils throughout the country then examined the records of ancient tephras and palaeosols from road cuts and reconstructed the degree and patterns of forest cover versus grassland.

One of the most notable palaeobotanical studies was performed by Kondo et al., (1994) in New Zealand, which built the first ever systematic modern reference baseline for of phytoliths from the region and established a system of nomenclature that went on to be used in European research (see also Piperno, 2003). This work aimed to provide a platform for studying phytoliths from old sediments in archaeological sites. They studied and analysed modern samples from soils throughout the country then examined the records of ancient tephras and palaeosols from road cuts and reconstructed the degree and patterns of forest cover versus grassland which existed between 50 to 20 ka (Piperno, 2003). They described the shapes of the phytoliths according to terminology and classes previously used in studies in Europe and Japan. They presented electron micrographs of a range of phytoliths and used phytolith analysis to determine the major types of vegetation contributing to the accumulation of some modem and buried soils. Kondo et al. (1994) separated 81 a wide range of phytoliths from living New Zealand native grasses, trees, and soils, hence the work that has been useful in studying vegetation types of Europe and the Oceania.

Phytolith research in New World and Neo tropics has supplied additional information on past environments and landscapes where other disciplines might be silent or ambiguous e.g. distinguishing C3/C4 grasses, short versus tall grasslands, arboreal versus herbaceous vegetation (Iriarte et al., 2004, Albert et al., 2015). This has been fundamental in archaeological research and it has opened new avenues of investigation on the past use of plants in hunter-gatherer and agriculturalist societies, the development of early agriculture and domestication, agricultural practices and the use of space. Morphological studies of phytoliths have helped in clarifying crop processing of staple cereals while new approaches in isotopes and molecular composition of the silica bodies can aide in understanding agricultural/environmental (Madella et al., 2002; Gracia-Granero et al., 2015; Vrydaghs et al., 2016; Zurro et al., 2016) and possibly evolutionary trajectories. A further application of phytolith analysis is gaining momentum for identifying domestic activities in foragers (Zurro et al., 2016) and agriculturalist societies using a qualitative and quantitative stance (Cabanes, 2011; Zurro et al., 2016). Significantly, all these applications need the fundamental support of phytolith botanical studies that highlight morphological variability of opal and patterns of silicification in plants (Hodson 2016) as well as advances in methodological approaches (Stromberg 2005; 2007; 2016).

A major implication for palaeoenvironmental reconstructions in Palaeoanthropology, especially in younger sites like Holocene localities in the New World, is the dating of the sites. Hart (2016) has proposed the use of radiocarbon dating and isotope analyses in contemporary archaeological and palaeoecological research (Hudson 2016; Piperno 2016), although this dating not yet proven, and has created some controversies among phytolith researchers. Piperno (2016) 82 similarly, insists on the combined use of new techniques in phytolith analysis such as ¹⁴C and isotopes in phytoliths, the development of digital technologies for refining and sharing phytolith identifications, renewed efforts for standardisation of phytolith nomenclature, and laboratory protocol. The incorporation of these innovations will culminate in the development of the field of applied phytolith research world-wide (Hart 2016; Hodson 2016; Piperno 2016).

Nevertheless, it is currently believed that the analysis of multiple archaeobotanical proxies from the same archaeological contexts improves and enriches our understanding of ancient plant use by humans such as to trace the beginning of domestication of food crops. The combined multiproxy analytical approaches, in which several botanical indicators and a broad-spectrum sampling strategy have been used together, is possibly the best way to explore diet and plant use strategies in past societies (García-Granero et al., 2015). Macrobotanical evidence helps, regardless of its paucity, in identifying some of the staple grains that were exploited by the first farmers. The microbotanical remains broaden the information available on the plant spectrum used for food such as sedges and tubers. In some sites these microbotanical remains are found connected with processing devices such as with the grinding stones (García-Granero et al., 2015; Pearsall 2016). Beyond tracing the food types and diet of our ancestors, when combined with other multiproxy data, phytolith research provides a critically important long-term perspective on past environmental variability and the evolution of vegetation patterns and ecological systems (García-Granero et al., 2015, Pearsall 2016).

However, like any other scientific disciplines, phytolith research presently face problems worldwide such as a lack of synthesis in terminological consistency, taphonomy that is not well understood, and problems of multiplicity and redundancy. Pearson and Piperno (1993) argued that scientists have to show others how techniques in their disciplines can benefit others or their discoveries are doomed to obscurity and funds for research will disappear.

As an attempt to solve the problems of redundancy and multiplicity Vrydaghs et al., (2016; 2017) have recently proposed the combined use of sediment micromophology and phytolith analysis. They noted that the integration of sediment thin sections with phytolith analysis can be used to address issues related to depositional history, arguing that this would provide more accurate vegetation history reconstructions (Vrydaghs et al.2016). They also stated that, when following this technique, special attention should be given to the phytoliths observed in the soil matrix rather than those known to be intrusive such as those found in coprolithic or ceramic material (Vrydaghs et al., 2016).

In East Asia, phytolith research from China and Japan has been conducted in conjunction with other plant proxies and stable carbon isotopes from ancient sediments and from modern soils to give important clues on past climates and environments. Inoue and Sase (1996) and Sase and Hosono (2001) studied a series of deep-sea volcanic sediments and soils and found a continuous phytoliths record spanning about 130, 000 years establishing changes in vegetation and climate by using opal phytolith distribution in tephra and aeolian deposits and associated palaeosols. Currently, phytolith research in this region has established the potential of rice phytoliths to investigate the origins of rice agriculture. Large reference studies of rice and related wild grasses from southern China have been undertaken and phytolith identification criteria established (Pearsall, 2000). For example, Fuller et al. (2010) were able to identify morphotypes from double peaked hair cells (from husks), and further characteristics have been suggested to differ between wild and domestic species, although these remain controversial (Fuller et al., 2010; Ryan, 2014). Other cell types identifiable to the rice genus are keystone bulliforms with flared edges (Fuller et al.

al., 2010) These show differences between indica and japonica subspecies of rice, although this variation is also found in wild populations, making application of this useful in regions like Japan without wild rice (Ryan, 2014). In their study on rice and millet farming in Neolithic and Bronze Age central China, Weisskopf et al., (2014) presented an alternative to the long-lasting discussion on phytoliths as indicators of early rice and millet domestication in the region. This research has opened a window for understanding the beginning of farming in Neolithic China, which probably had a longer pre-domestication cultivation phase than was previously thought, thus enabling reconstruction of several ecological variations of the rice cultivation regimes in China and probably India e.g. inferring differences in past agricultural practices, identifying wet cultivation systems, dry millet-dominated agriculture and rainfed/dry rice during the Neolithic.

In India, multiproxy research by García-Granero et al., (2016) who employed the classical models for cereal processing by introducing phytoliths as additional evidence, thus exploiting the differing preservation potential of the two proxies. The macrobotanical remains allowed them to conduct a species level analysis, while the early stages of processing cereals was documented by the less highly resolved but better preserved phytolith remains (Lancelotti and García-Granero, 2013; García-Granero et al., 2016). Different patterns for the macro- and micro-remains of winter and summer crops indicated that wheat and barley were less commonly used and less regularly processed than small hulled millets which are cultivated in summer. The authors conclude that seasonality of cropping drove decisions relating to labour organisation at these settlements, which is contrary to many of the models of crop processing that have been developed for the Indus civilisation (García-Granero et al., 2016). These studies show the potential of phytoliths for reconstructing plant use at sites where macro-remains are absent or poorly preserved.

In their study of phytoliths and starch remains on grinding stones from archaeological sites in northern India, García-Granero et al., (2016) showed that North Gujarat (India) was a primary center of plant domestication during the mid- Holocene. The results showed the progressive weakening of the Indian summer monsoon ca. 7,000 years ago, thus compelling human populations to adopt seminomadic pastoralism and plant cultivation, which resulted in the domestication of several small millet species, pulses, and sesame (Lancelotti and García-Granero, 2013 cited in García-Granero et al., 2016).

In the Middle East, phytoliths have been used to study pre-agrarian shifts towards wild grass exploitation at late Natufian Levantine settlements (Rosen, 2005), early agriculture and plant use at Neolithic sites such as Çatalhöyük (Rosen, 2005), and urban centers such as Bronze Age Tel Dor (Albert et al., 2008). Studies from cave sites including from Middle Palaeolithic through to Natufian levels have revealed information about plants used for fuel (Albert and Weiner, 2001) as well as about possible Neanderthal wild grass husk exploitation (Madella et al., 2005). In Syria, Portillo et al., (2016) at the Tell Seker al-Aheimar, located in the Upper Khabur, northeastern Syria to study the ancient settlement patterns and agricultural activities, identifying domestic activities and their spatial distributions in the site through integrated studies of phytoliths and dung spherulites using an ethnoarchaeological approaches (Shahack-Gross et al., 2009 cited in Portillo et al, 2011). Dung assemblages have been studied through microfossils in varied contexts, including animal enclosures (Portillo et al., 2011) and midden deposits, but also in combustion structures such as hearths and ovens in many Near Eastern sites.

Despite its above-mentioned pitfalls, phytoliths are very significant indicators of vegetation dominated by grasses and non-grasses. Phytolith research is a very potential palaeoecological and archeological reconstruction tool, especially when its application is combined with pollen analyses 86 in palaeoenvironmental studies. The complementarity of phytolith and pollen data has had been successful in tracking changes in ancient vegetation composition and climatic conditions of the quaternary environments (see Pearsall and Piperno 1993). Because pollen grains are poorly preserved in most of the fossil sediments, and because grass pollen is indistinguishable at the generic level, phytolith assemblage analysis have been seen as a new and complementary palaeoecological indicator.

4.4 PHYTOLITH CLASSIFICATION

Presently, the number of studies in all fields of phytolith analyses has grown dramatically, mainly due to a diversification of research topics (Hart, 2016; Neumann et al., 2017, 2019; Strömberg et al., 2018). Significant strides have been made in the application of phytolith analysis for answering key archaeological, palaeoenvironmental, evolutionary, taxonomic and climatological questions, often within the framework of interdisciplinary research (Neumann et al., 2017, 2019). One of the most persistent needs in the discipline of phytolith analysis is a universally accepted nomenclature and classification system. Over the decades, numerous synonyms (different names for the same morphotype), and homonyms (identical names for different morphotypes) have hampered the communication between researchers and comparison of their data without big controversies (Neumann et al., 2019).

Traditionally, there have been several efforts to standardise the naming of opal phytoliths, oftentimes connected with the establishment of different classification systems (Pearsall, 2016; Neumann et al., 2017, 2019). However, most of these suggestions refer to either geographically restricted areas or single taxonomic groups, and none of them has become universally accepted

(Neumann et al., 2019). Persistent-consistent and universally accepted names of scientific items are essential for successful communication in any scientific research. Since Linnaeus' Species plantarum of 1753, each plant (or animal) species has had a unique binomial name (Neumann et al., 2017, 2019). The species and higher-ranked taxonomic names of algae, fungi and plants for instance, are governed by the International Code of Nomenclature (ICN) for algae, fungi and plants. Within binomial names, principles are defined for a formal, 'valid' publication of a correct name. One of these principles is that the name has to be associated with a precise and detailed description (diagnosis) of the item, which is 'a statement of that which in the opinion of its author distinguishes the taxon from other taxa' (Neumann et al., 2019), the name must be a unique identifier (i.e. one item, one name), and naming must follow transparent, precise, and consistent rules, which include its publication in a peer-reviewed journal or similar international article (Neumann et al., 2019). The isolated plant parts in ancient sediments, such as pollen, wood or other microbotanical remains or seeds, can bear the name of the species or taxonomic group from which they come from (Neumann et al., 2019). However, there is disagreement about whether taxonomic names are justified for isolated plant organs, which cannot be unambiguously attributed to a species or higher-ranked taxonomic group (Neumann et al., 2017, 2019).

It has noted by ICPN 2.0 that some phytoliths, especially those from reproductive structures, can be specific for certain taxonomic groups and may be named after them (e.g. fruit and seed phytoliths from Burseraceae, Marantaceae or Commelinaceae, but the majority of phytoliths show such a degree of redundancy (same shapes produced in multiple taxa) that they typically cannot be attributed to a single taxon (Neumann et al., 2019). Moreover, very often the anatomical origin of a phytolith morphotype is uncertain or unknown, and consequently the name of the morphotype must be given according to morphological characters, such as shape, size and 88

texture; hence the term 'morphotype' (Mercader et al., 2012; Neumann et al., 2019). A morphotype can be defined as a group of individual specimens that have the same, unique shape; the term 'shape' should be understood in a broad sense and includes different morphological traits (Neumann et al., 2019). However, using morphological features as part of the name can lead to extremely long and complicated names and constitutes a mixing of naming and describing, reminiscent of the common practice for plant species in pre-Linnaean times. Formalising and harmonising the naming of phytolith morphotypes is therefore a major challenge for the international phytolith research community. In 2000, the primary governing body for the discipline of phytolith analysis, now the International Phytolith Society (IPS), recognised the need for standardisation of nomenclature and terminology in the discipline and subsequently commissioned a committee to draft an *International Code for Phytolith Nomenclature* known as ICPN 1.0, was published in the Annals of Botany (Madella et al., 2005), and has become a widely cited in phytoliths research. As anticipated by this first committee, a decade of use of the code revealed the need to revise, update, expand and improve the ICPN 1.0.

In 2019, the *International Committee for Phytolith Taxonomy* (ICPT) (see Neumann et al., 2019) published an updated version *International Code for Phytolith Nomenclature* (ICPN 2.0), with revised names and new descriptions and diagnoses/definitions of the morphotypes that were modified and included in the previous ICPN 1.0, plus three others commonly encountered in phytolith assemblages from modern and fossil soils, sediments and archaeological deposits; whereby they provided illustrations for different morphotype types, illustrated glossary of common terms for description on Stearn's Botanical Latin (Neumann et al., 2019). This updated nomenclature is a steppingstone towards creation of commonly agreeable and more standardised phytolith classification system.

CHAPTER 5: PHYTOLITH ANALYSIS IN AFRICA

5.1 NORTH AFRICA

Fahmy and El-Bakry (2011) provided evidence for the origin and spread of grassland ecosystems in North Africa with their botanical and phytolith research conducted at Wadi Wateer (Egypt) and the Aqaba Gulf. The aim was to provide a plant reference collection that would be able to provide a baseline for microbotanical analysis from ancient archaeological sites. The botanical survey of Wadi Wateer, located in the southeastern Sinai, revealed the presence of a plant that provided an important new addition to the flora record of Egypt: Cocculus hirsutus (L.) Theob. This plant had not been recorded previously as existing in its wild form in Egypt. The plant cover in Wadi Wateer is dominated by plant taxa belonging to the Saharo-Sindian phytogeographical element. However, many plants in the Wadi had been attributed to the Sudanian chorotype. The presence of Sudanian chorotype plant taxa, including the newly recorded *Cocculus* hirsutus, reported in this study functioned as migratory tracks for African plants, assisting their penetration into the Saharo-Sindian, Mediterranean and Irano-Turanian phytogeographical regions in the Sinai and Asia (Fahmy and El-Bakry, 2011). This study suggested that Wadi Wateer should be declared a protected area for its habitat and climatic diversity, as well as for its phytogeographical botanical significance for past vegetation inferences; doing this would aide in establishing an extensive modern reference collection baseline for the entire region (Fahmy and El-Bakry, 2011). To understand the role of environmental change and shifting human adaptations in the North African region in the past, Ship et al., (2013) examined changing subsistence practices among of early-to mid-Holocene foragers in northwest Africa (Capsian groups) using phytolith analysis. These foragers were located in eastern Algeria and southern Tunisia from approximately 10,000 to 6000 cal. BP and were among the last North African foragers (Rahmani, 2004 cited in Ship et al., 2010). Phytoliths analysed from this region provide evidence for the presence and use of plants at archaeological sites, making them a valuable tool for investigations in palaeoecology and human adaptations in Capsian region (Ship et al., 2013). Phytolith data from archaeological sites were indicative of diet, climate and environment, use of space, farming techniques, seasonality, and use of fuel (Ship et al., 2013). The abundance of short cell phytoliths were the indicators of grassland types. The phytolith data from this region are also consistent with other lines of proxy evidence for North Africa in the early to mid-Holocene, which indicated that conditions were significantly wetter than the later Holocene and the present (Ship et al., 2013). The environmental setting might have provided a favourable and productive habitat for Capsian foraging activities at around 10, 000 BP.

5.2 SOUTH AFRICA

Phyolith analysis has been carried out in this region around and underneath caves and rock shelters that contain well preserved evidence of human activity, cultural material complexity and at those that contain evidence of early modern humans, fossils dating from the Middle Stone Age to modern times. The palaeoanthropological research in this region has been performed to reconstruct past climates and environments pertinent to the understanding of the survival strategies of hominins and hunter-gatherers. Several studies of modern assemblages from extant habitats have been carried out in order to develop analogies for the past and improve our research methods for palaeoenvironmental reconstructions (Cabanes et al., 2017).

In South African hominin sites, the capacity to detect remnants of fire usage in archaeological sites was inferred through phytolith research by Albert and Marean (2012). Alongside the understanding of its use by prehistoric populations, this phytolith research has shed light on hominin cognition, social organisation, and technology. Pinnacle Point 13B (PP13B) is one of several South African Middle Stone Age (MSA) sites that exhibited an abundance of lenses of burnt material and intact hearths. Phytolith analyses at PP13B were used to identify the types of plants used as fuel in the hearths around the site. The phytoliths overall showed high levels of alteration, and varying alteration (Albert and Marean, 2012). Phytolith conditions were assessed in order to identify areas with higher alkaline conditions related to dripping water. In some areas of the site, good preservation of multicellular structures from the epidermal leaves of dicotyledonous plants was noted, implying in situ structures with practically no chemical or postdepositional alteration. One of the interesting notable patterns is the abundance of dicotyledonous leaves from the rear of the cave, which might be indicative of specific leaf-fuels for the fires, shortterm fire activities, or other actions such as cooking or defence against wild animals (Albert and Marean, 2012). The application of phytolith studies to understand fire and its use during Palaeolithic times might become widely applicable if plants contain phytoliths that are identifiable to different taxonomic levels are encountered in archaeological records.

Cabanes et al., (2017) did a phytolith study of modern surface soil samples from different vegetation types of the south coast of South Africa. Their results show that phytolith concentration relates mostly to vegetation types and the dominant vegetation rather than to the type of soils. More abundant phytoliths from Restionaceae and woody/shrubby vegetation are also noted from fynbos (fine-leaved shrubs) and grass phytoliths are a recurrent component in all the vegetation types despite being a minor component in the modern vegetation (Cabanes et al., 2017). The grass 92

silica short cells from these plants, however, suggested a mix between C₃ and C₄ grasses in most of the vegetation types with a major presence of the rondels ascribed to C₃ grasses (Rossouw, 2009; Cabanes et al., 2017). Another similar study was undertaken in the Klasies River to provide information about human behaviours and uses of plants, and also to reconstruct the environment in which people were taking their resources whereby fossil samples were assisted by modern phytolith reference materials to infer early human manipulation of the landscape across the Klasies River (Novello, et al., 2018). Novello et al. (2018) demonstrated that most of the eudicot species studied produce large amounts of silicified tabular ovate/orbicular and polygonal unit/mass cells in their leaf tissues, but that these phytoliths were not represented in modern soils. Also, the abundant eudicot component present in the Klasies vegetation is largely underestimated by phytoliths in its underneath soils, suggesting that they would not be necessarily recorded in archaeological deposits. Hence, they called for more phytolith research from modern plant samples that would help to interpret data from ancient sediments.

5.3 TROPICAL AFRICA

The discussion in this topic has several foci, mainly on the analyses of phytoliths in palaeoanthropological sites and modern reference collections in order to underscore aspects pertinent to phytoliths and human origins, and clearly show its usefulness in understanding the past human landscapes and ecologies and why it has been widely used in sub-Saharan African key sites that have yielded scientific data for human evolution.

Ancient phytoliths have been a useful tool for palaeoecological reconstruction of the palaeopanthropological sites that yield some of the oldest Pliocene and Pleistocene hominid remains known in the world; especially in sub-Saharan Africa (Albert and Bamford, 2012, Barboni, 2010, 2014). Although research on modern plants and soil phytolith referentials in archaeological contexts is still in its infancy, phytoliths have helped identify plants used by prehistoric populations, and aided in distinguishing between those used by people, and those that are natural accumulations and represent past vegetation (Mercader et al., 2009, 2019). The preservation of phytoliths in the African fossil record makes them one of the most valuable tools for studying hominin plant communities (Mercader et al., 2009; 2012, 2019). Nevertheless, the palaeo-ethnobotanical interpretation of phytoliths relies on the comparison of ancient types with morphotypes extracted from living reference collections (Mercader et al., 2009; Mercader et al., 2012, 2019). As a result, the modern referential dataset for phytoliths produced by arboreal plants and grasses of this region is a prerequisite in Palaeoanthropology. Similar studies were conducted by Albert and Bamford (2007) in the Afar region of Ethiopia, and on the Zambezian vegetation zone by Mercader et al., (2009, 2010, 2012) which focused on phytoliths analysis from modern sediments, plants and palaeosols that provided the first quantitative taxonomy of phytoliths for the largest phytochorion of sub-Saharan Africa (Zambezian ecotone). These are now valuable assets for palaeoecological reconstruction in the region.

Except for Albert and Bamford, (2007) and Mercader et al. (2009, 2010, 2019), no other research in this region has studied large samples of modern reference collections of plants that are thriving on the Zambezian-Somalia-Masai ecotones although these few studies have shown the importance of understanding phytolith production, the value of reference collections, and the correlation between phytoliths from modern surfaces and what they say about the vegetation growing on these surfaces today in the Sudano-Zambezian and Somalia-Maasai (Albert and Bamford, 2007; Mercader et al., 2009, 2010, 2019). Also, very few studies of this nature, with the 94

exception of one by Murungi et al., (2017) have explored or documented the mountainous plant's phytolith record, at the high elevation in east Africa. This research has provided insights into past grassland composition in the grass-dominated Alpine belt of Mount Muhavura. This study tested if phytoliths occur in sufficient amounts in the alpine lake sediments, and extracted phytoliths from the modern soils and plants so as to explore their distribution in the sediment profile and attribute them to specific plant taxa found at the modern mountainous landscape, specifically those plants found in selected alpine plants. In this study, sediment samples from an alpine lake and ten alpine plant species were analyzed for their phytolith content to study the phytoliths characteristic of alpine grassland and document their potential to reconstruct the vegetation history of this mountain (Murungi et al.2017). Their results suggested that alpine-mountain vegetation was more open and grass dominated, and they were able to discern the potential of phytoliths to reconstruct grassland history in the Alpine belt and infer associated environmental conditions. Overall, however, data from savannah woodlands (*Acacia commiphora* woodlands) or from typical most arid areas of eastern African region are still scarce (Mercader et al., 2019).

At Oldupai and the sites in proximity to Oldupai Gorge and the adjacent areas, (i.e. along the Eastern Africa Rift Valley System) phytoliths have recently been useful tools for palaeoecological reconstruction (Albert and Bamford, 2012; Barboni 2010, 2014). Phytolith studies in this region detailed a diverse landscape composed of complex vegetation patterns linked to oscillating precipitation, varying lake levels, and the presence of geological faults, with reconstructed palaeo-precipitations at 250-700 mm per year. C₄ grasslands, closed woodlands, wetlands, and palm-groves seemed to occur on short spatial scales near saline Lake Oldupai (Barboni et al., 2014). This previous research suggests a notable preserved record of past vegetation that is composed of silicified macro-remains such as pieces of wood, leaves, roots and 95 silicified fruits (Barboni, 2014), organic microremains such as pollen grains (Bonnefille and Riollet, 1987; 1988; Bonnefille et al., 1987; Bonnefille, 1984; Domínguez-Rodrigo et al., 2007), and phytoliths (Domínguez-Rodrigo et al., 2001b; Albert et al., 2006; 2009; Bamford et al., 2006; Barboni et al., 2010; Ashley et al., 2010a, 2010b; Rossouw and Scott, 2011). In East African palaeoenvironmental and Palaeoanthropology particularly, phytoliths have been used to understand phytolith production, to reconstruct past ecosystems, and understand the composition of current vegetation. The most significant aspect of phytolith analysis includes the archaeological and environmental reconstruction of palaeolandscapes used by hominin populations (Albert et al., 2006, 2009; Bamford et al., 2006; Barboni et al., 2010) in Lower Most and Upper Most Bed I, whereas phytoliths have helped to identify plants used by prehistoric populations, while providing a vegetation record representing the various taxa as reflected by the recovered silicified macroremains (Bamford et al., 2006; Barboni et al., 2010).

These ancient environmental proxies have both temporal and spatial components of climates and vegetation which help demonstrate evolutionary trends within hominin lineages, faunal and artifact assemblages, follow these changes across plant landscapes and in time and space, and correlate these trends with palaeoenvironmental contexts of early humans. This thesis work therefore advances our current understanding of phytoliths preservation in a more diverse and complex sedimentary environments (Linking Upper Bed I and Lower Bed II sites) and providing a bigger picture of phytolith plant landscapes are represented in archaeological contexts.

Regarding Oldupai Gorge phytolith research, although an extensive bibliography exists on phytolith-based environmental reconstruction for the lower most Bed I (see Barboni et al., 2009; 2010; 2014) very little information exists for the upper parts of Bed I and lower-most Bed II or the rest of the Oldupai sequence. This study addresses this gap, providing useful palaeobotanical 96 information on vegetation structure, patterns of palaeohabitat change and the general trend from wetlands to more xeric and open palaeohabitats between 1.83-1.1.60 Ma through phytolith analysis. More details about the palaeoenvironmental reconstructions of Upper Bed I and Lower Bed II are presented and discussed in chapter eight and nine as well. Specifically, phytolith data extracted from Frida Korongo Leakey Korongo North site (FLK-N), Frida Leakey Korongo West site (FLK-W), Castle Clays, Lower Augitic Sandstone (LAS), and the Bird Print Tuff (BPT); both (LAS and BPT) are time intervals of Oldupai sedimentary sequence which are represented across the landscape. Though phytoliths analysis from this study has inferred the plant landscapes used by early hominins, it has also inferred the distribution of ancient vegetation patterns across the Oldupai palaeo-landscape as it shown by this thesis in the sections of data presentation, analyses, and the discussion. Phytoliths have offered the possibility to further investigate and comprehend the structure of past vegetation both spatially and temporally within the Gorge (see chapter eight, nine, and appendices respectively).

Palaeoanthropogical data from Oldupai's fossil sediments and from excavation sites are plenty but there is a lack of data from the landscapes surrounding the Gorge, and not enough data from the reference collections and from modern phytoliths, except the recent one by Mercader et al. (2019). This doctoral research fills the existing research gap, by putting more emphasis on the need and significance of combining data from modern reference collections and from fossil sediments to reconstruct the palaeoenvironments of early hominins, and thus calls for more phytolith studies in East Africa and Oldupai in particular. This should go hand in hand with extensively employed modern plant and soil reference collections, even beyond the *Acacia commiphora* region. Extensive sampling to the areas distant from Oldupai Gorge such as the Usambara, Kilimanjaro, Meru mountains, or the western sides adjacent to Lake Victoria and Tanganyika are inevitably required.

Several studies have shown the importance of understanding phytolith production, reference collections, and the correlation between phytoliths from modern surfaces and what they say about the vegetation growing on these surfaces today in the Sudano-Zambezian and Somalia-Maasai (Albert and Bamford, 2007; Mercader et al., 2009, 2010, 2012). The comparison of modern phytoliths from plants and the terrestial sediments are the only way to normalise the taphonomic bias that we encounter in the fossil record (Albert and Bamford, 2007; Mercader et al., 2010).

However, on the origin of domestication of food crops in Africa, there have been comparatively few phytolith studies of African crops on archaeological settlements. For instance, Radomski and Neumann, (2011) performed a study which examined inflorescence phytoliths from wild and domesticated West African grasses and applied this to the analysis of phytoliths from archaeological grinding stones in the Eastern Sahara and Western Sahel savannah (Radomski and Neumann 2011; Ryan, 2014). Findings included that certain lobate phytoliths could be used to group some grasses within the Paniceae tribe, and that Digitaria (which includes the crop fonio) was distinguishable due to papillae density and was different from distinctive bilobes and dendritic long cells phytolith of sorghum husks. However, Radomski and Neumann, (2011) noted that many Panicoideae grass genera are known, such as Panicum and Sorghum, to potentially produce husk silica skeletons and further identifications of African millet grasses may be possible with multicell identification methods analogous to those applied to common and foxtail millet However, the applicability of this method will depend on the presence of silica skeletons in archaeological samples as opposed to predominantly single cells, which may vary in likelihood among genera and

be influenced by plant growing conditions such as water availability in very dry environments as well as post taphonomic factors (Radomski and Neumann 2011; Madella et al., 2013).

Again, phytoliths of bananas (Musa sp.) have been shown to differ from those of indigenous African Ensete (Vrydaghs et al., 2003; Ryan, 2014). Archaeological applications of phytolith analysis in Africa span vastly contrasting landscapes, time frames, and settlement types, including early modern human plant exploitation from cave sites (Albert and Marean, 2012), equatorial forest sites during the Late Stone Age (Mercader et al., 2009, 2000) to Late Holocene settlements such as a Numidian site in Tunisia (Portillo and Albert, 2011), and the New Kingdom colonial town of Amara West in northern Sudan (see Ryan, 2014).

Although phytolith studies have been carried out in modern soils from Central Africa (Runge 1999; Mercader et al., 2009), West Africa (Bremond et al., 2005) and East Africa (Shahack-Gross et al., 2003, 2004; Albert et al., 2006; Bremond et al., 2008; Mercader, 2009) (Table 5-1), quantitative work on silica bodies from living African plants is scarce. Those previous studies focused on grasses from two phytochoria north of the equator (Mercader et al., 2000, 2009): the Somalia-Masai (Palmer and Tucker, 1983) and the Sudano-Sahelian (White, 1983; Fahmy, 2008; Mercader et al., 2009) vegetation zones. An extremely small amount of qualitative information is known about the phytoliths produced by some African trees and bushes from the Guineo-Congolian region and the Somalia-Masai (Runge and Runge, 1997, cited in Mercader et al., 2009).

Lead	Year	Locality	Country	Nationality	Lab location
Albert RM et	2006, 210,	Olduvai	Tanzania	Spaniard	Barcelona
al.	2012	Gorge			
	2009, 2012		South Africa		
Alexandre A	1999	Lake Guiers	Senegal	French	Marseille
Ashley GM	2005, 2010,	Olduvai	Tanzania	American	Marseille
	2014	Gorge			
Bariboni	2010, 2012,	Olduvai	Tanzania	French	Marseille
	2014	Gorge			
	1999	Middle	Ethiopia		
		Awash			
Bamford M	2006, 2009	Olduvai	Tanzania	South	Johannesburg
et al.		Gorge		African	
	2005, 2008	Klasies	South Africa		
		river,			
		Malapa			
Bremond L	2005, 2008	West Africa	Senegal, Mali	French	Marseille
	2008	West Africa	Mauritania		
Eichhorn et al.	2010	Ounjougou	Mali	German	Frankfurt
Estaban I et	2017	Cape Coast	South Africa	South	Barcelona
al.		•		African	
Fahm	2008	Sahel region	Egypt	Egyptian	Frankfurt
Jacobs WL	2000, 2016	Cunene	Namibia	Australian	Utrecht
Mercader J et	2009,2011,	Niassa	Mozambique,	Canadian	Calgary
al.	2012, 2018,	Ngalue	Congo,		
	2019	Ituri	Tanzania		
		Olduvai			
		Gorge			
	2010	Ituri Forest	DRC		
Murungi ML	2017	Virunga	Uganda	Ugandan	Johannesburg
		volcanoes			
Neumann K	2015	West Africa	Sahara/Guinea	German	Frankfurt
Roussouw J	2005	Laetoli	Tanzania	South	Bloemfontein
and Scott L				African	
Roussou et	2005, 2012,	Malapa,	South Africa		
al.	2017	Cape north			
Runge J	1999	Kivu, Ituri	DRC	German	Paderbon
z S et al.	2017, 2018	Klasies	South Africa	South	Johannesburg
		river, Cape		African	
1	•	•	•		

CHAPTER 6: MATERIALS AND METHODS

This chapter provides a description of the study area, along with stratigraphical and sedimentological information of each site/horizon of a certain geological time interval from which we sampled sediments for phytolith analyses. It also presents the research design employed during sample collection in the field, and outlines the sample preparations in the laboratory, including the phytolith sediment-extraction protocol, microscopy, phytolith counting and classification, and analytical procedures.

Fundamentally, this research built upon existing plant micro-remain methods used to reconstruct palaeo-landscapes in sites with a diverse sedimentary context like Oldupai's Bed I and II (Mora & de la Torre, 2005; Ashley et al., 2010; Magill et al., 2013; Beyene et al., 2013; Díez-Martín et al., 2014, 2015). One of the best methods to reconstruct the palaeohabitats and ecosystems in which hominins lived has been to analyse the fossil sediments and fossil flora (micro-palaeobotanical data) associated with hominin sites, such as silica, starch, chemical biomarkers, pollens, stable isotopes, leaf fossils, and other plant parts (Mercader et al., 2018, 2019; Patalano, 2019). Although, direct evidence of palaeovegetation is typically better preserved only at younger palaeoanthropological sites, opal phytoliths have been found well preserved even to older Miocene African palaeoanthropological localities, solving the problem of archaeological data preservation in older sites (Mercader et al., 2010, 2012). These recent advances have dramatically improved the ability to assess the timing, rates, and magnitudes of past environmental fluctuations along with biotic responses to such disturbances, this research is trying to further explain these and discuss in detail how phytolith research can be applied in Palaeoanthropology to

establish and reconstruct the palaeolandscapes, palaeoenviroments, and the palaeogeographies of sites that were once inhabited by our ancestors.

Most of the Oldupai Gorge's Upper Bed I sites, such as FLK- N, are located along ancient complex sedimentary environments such as lakes, streams and fluvial channels (Hay, 1976; Leakey, 1976; Ashley et al., 2010; Yravedra, et al., 2015). 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 portions of the local palaeolandscape present at these sites. This is especially true of the sedimentary units that consist of a fluviatile river channels like the Frida Leakey Korongo North (FLK-N) site, the entire FLK-N horizon, and the rest of the Lower Bed II sites which reflect a variety of environmental palaeo-horizons that has proved to be optimal in addressing the key issues about site formation processes and human-habitat variability during Upper Bed I to Bed II period. The sites in these diverse and complex stratigraphic sequences consist of a fluviatile, and sometimes at certain intervals, high-energy depositional river channels (FLK-West: is a channel that represents a high-energy depositional environment), which are useful in providing insights on the factors that could have impacted the plants' landscape during early Pleistocene times.

This research focused and concentrated on the upper sections of Oldupai Gorge Bed I, and the lower-mid parts of Bed II i.e. (1.83-1.60 Ma). Previous research has attested that this time period combines two ESA stone tool industries (Oldowan and Acheulean) and more significantly, it is when Acheulean stone tool industrial techno-complexes appeared hand in hand with the emergence of *H. erectus* (Beyene et al., (2013), de la Torre and Mora (2014), and Díez-Martín (2014). These sites are therefore crucial for understanding upper Bed I and lower Bed II plant landscapes, environmental parameters, and the context in which the transition from the Oldowan 102 to the Acheulean occurred, as well as characterising the early hominin manipulation and adaptability to these ancient habitats.

6.1 STUDY AREA

6.1.1 LOCATION

The Oldupai Gorge is in northeastern Tanzania. It is a valley incised into the Serengeti Plain exposing about 70-centimetre-thick pile of basic, silica-poor volcaniclastics, lavas and fluvio-lacustrine strata of the Plio-Pleistocene (Hay, 1976, 1979; Hay and Kyser, 2001). Since its discovery, the Gorge has proven to be a credible palaeoanthropological site, important worldwide, especially for studying and furthering our understanding of early hominins' bio-cultural evolution. While it is mainly renowned for its content of early human artifacts and hominin remains, for decades, Oldupai Gorge has also been a focus of numerous scientific research projects varying from geology to human evolution. Similarly, a substantial number of other related research disciplines such as stratigraphy, sedimentology, geochemistry, palaeontology, taphonomy, lithic and fauna analyses, palaeoecology, palaeoenvironment analyses, human evolution/origins, and climate change has been actively and conspicuously taken place for over five decades.

More importantly, these scientific investigations have provided a wealth of scientific information concerning the nature and palaeoenvironmental history of the Oldupai Gorge in relation to the contexts of human evolution. The Gorge has yielded an abundance of stone tool assemblages and fauna that has attracted many researchers from different parts of the world and has triggered a significant body of multi-disciplinary research works. This the world's most renowned site for human origins in the Arusha region within the Ngorongoro Conservation Area (Fig. 6-1). The Oldupai Gorge is located within the East African Rift region, and it is one of the

most important palaeoanthropological locations in the world, and therefore identified as a UNESCO World Heritage site.



Figure 6-1: Map showing the location of Oldupai Gorge (Tanzania) and the Ngorongoro Volcanic Highlands (Source: Esri, DigitalGlobe, GeoEye, modified after Tucker et.al., 2019).

There is no single site in the world that is more important for human evolution than Oldupai Gorge (Mercader pers. Comm., 2018) (Fig.6-2). The Oldowan stone tools recovered here represent the emergence of typically human features, such as the use of stone tools technology to manipulate the various more diverse and difficult environment, a selective management of lithic material to



Figure 6-2: Sampling locations at FLK-N, FLK-W, Geolocality 44a, LAS, and BPT (Source: modified from Patalano, 2019)

manufacture stone tools, and the development of complex dietary behaviours. The Oldupai Gorge is home to some of the greatest archaeological findings of all time and has been the subject of human origin studies for decades, beginning with *Paranthropus boisie* discovered in 1959 by the Leakey family. With its beautiful and unique archeological localities, the site is popularly referred to as the "Cradle of Humankind," because it has and continues to yield and preserve much of the oldest fossil evidence of P. boisie (Zinjanthropous), Homo habilis, Homo erectus, and Homo sapiens in the world. The very important early geoarchaeological research work in the area was undertaken by Dr. Louis Leakey and his wife Mary Leakey in 1931. Leakey organised an expedition to the Gorge together with Hans Reck, whereby they found stone tools within a few hours of arriving at the Gorge. In further excavations, Leakey and his wife Mary found and described many stone tools and fossil animals but found no significant hominid ("human-like") fossils until 1959, when Mary Leakey discovered the first skull of "Zinjanthropus boisie". The fossil skull that later was renamed as an *Australopithecus boisei*, was a creature that had a massive skull with huge teeth that date about 1.8 Ma. Ongoing research from the 1950s to the present day has unearthed hundreds of early humans' remains, and tonnes of lithics ranging from the earliest stone tools: Oldowan, Acheulean, Middle Stone Age, and Later Stone Age.

Since its discovery in 1910's, the Oldupai Gorge has become the "Fossil-Treasure Trove" of studying the origin of humanity. The unearthed animals and early human fossil remains from Oldupai Gorge have been a valuable key in teasing out the mystery of dawn of humanity. Intriguingly, the wonderful palaeoanthropological data from this Gorge have now become important fossil evidence in relation to the emergence of anatomical modern humans (Mercader pers.comm., 2018, 2019). Several sites in Bed I, II, III and IV have yielded unprecedented as well as very remarkable records of our earliest ancestor's food procurement technologies, which has 106

helped a lot in shedding light to the dawn of humanity. The archaeological expeditions in the Gorge were preceded by geological investigations in the vicinity of Gorge which begun in 1913 when a German Professor Hans Reck led an expedition to the lower 9 kilometres of the Gorge whereby he collected and eventually studied the fossils and geological samples. Significantly, it was this time when the geology Oldupai was studied for the first time (Hay, 1976).

More comprehensive, intensive, and extensive geological work was carried out in Oldupai Gorge by Professor Richard Hay in 1970s whereby he produced a very definitive geological framework for the Gorge's stratigraphic interpretation. He explained the significance of sedimentary environmental records of Oldupai Gorge by deciphering the mineralogic, geologic composition of its strata (Beds), and establishing the palaeoclimatic record of arid environments of the Oldupai palaeobasin.

According to Richard Hay (Hay, 1970, 1976, 1979), the Oldupai Basin is a depocenter that was formed by the split-off/splay fault valley at the southwestern toe of the Gregory Rift, the southern extension of the eastern branch of the Cenozoic East African Rift System (EARS) (Hay, 1976; Dawson, 1992; Morley et al., 1990). The widespread volcanism is said to have accompanied the formation of this rift system. The Gorge falls within the Northern Tanzania Divergence Zone (NTDZ) along the EARS (Foster et al., 1997). It represents the boundary between central Tanzania's Archaean craton and the north-south trending Mozambique belt, a product of the neo-Proterozoic Pan-African orogeny (Cahen et al., 1984; Dawson, 1992; Holmes, 1951).

The Oldupai Gorge is located on the western flank of the Gregory Rift in the Ngorongoro Conservation Area (2° 59 ' 46.87 " S, 35° 21' 7.50" E) between the volcanic highlands to the south and east, the metamorphic complexes to the north, and the Serengeti Plains to the west (Cahen et al., 1984; Mercader et. al., 2018). Palaeolake Oldupai was part of an endorheic basin formed 107
around 2 Ma because of tectonic subsidence and concomitant uplift in the Ngorongoro Volcanic Highlands (Hay, 1976), where numerous volcanoes existed (Mollel and Swisher, 2012). Oldupai Gorge boasts well-dated archaeological and fossil records (Deino, 2012; Hay, 1976; Leakey et al., 1972). Its sedimentary beds span the Pleistocene to Later Stone Age (Beds I – IV, Masek, Ndutu, and Naisiusiu) and situates two million years of evolutionary history, from the Oldowan to the Later Stone Age period (Leakey, 1971; Hay 1976).

6.1.2 GEOGRAPHY

In terms of topographic and climatic setting, the Oldupai Gorge is a cut 45 to 90 metres into Pleistocene deposits from a small basin to the west of the major faults and volcanoes of the Eastern Rift Valley in Tanzania (Hay, 1976). The climate around Oldupai Gorge and nearby localities is hot and dry. Generally, the climate of the region is arid; tropical with seasonal rain that falls in a bimodal pattern. The long rains occur from January to March and the short rains fall in the months of November to December. Similarly, annual rainfall ranges from 380 mm to 803 millimetre (mm) per year, but at the Gorge itself can fluctuates from 331 mm- 531 mm (Herlocker and Dirschl, 1972). The dry months in Oldupai Gorge extend from June to October, with the wettest phase lasting from December to April. Rainfall patterns and localised soil conditions influence the vegetation communities observed in the Serengeti (Anderson and Talbot, 1965; Mercader et al., 2019). This is one of the driest ecoregions in Tanzania. Oldupai's climate was probably not greatly different during most of the Pleistocene (Hay, 1976, 1979).

The rainfall patterns and its weather are mainly influenced by its geographical, altitudinal, setting and its location adjacent to the modern Ngorongoro Volcanic Highlands (NVH) to the east of the Gorge. The NVH is over 3000 metres high, which traps moisture-laden easterly winds

blowing from the Arabian Sea and creates a rain shadow to its west. The modern rainfall on Ngorongoro highlands is 1150 mm per year (Deocampo, 2004) and could have been twice that during Milankovitch wet periods. Some rainfall runs off in ephemeral surface streams, but most infiltrates into the relatively porous volcaniclastic deposits of the Highlands and moves westward in the subsurface into the Oldupai basin (Anderson 1965; Deocampo and Tactikos, 2005; Reck, 1951; Mercader et al., 2019).

The Oldupai topography is characterised by volcanic uplands of Lemagrut at the southwest, and another part is bordered by volcanic highlands to the east and the margin of the Eastern Rift Valley-Serengeti Plain to the north and west. Upland from the Gorge there are gentle slopes from east to west in a series of steps. The present-day Oldupai Basin has undergone considerable geomorphologic change from the palaeo-Oldupai Basin, largely due to geologic faulting. The drainage sump, the lowest part of the basin, for instance, lies much further east today than in the Pleistocene. Faulting occurred during the deposition of the Oldupai Beds and continued through to the Holocene. The majority of the main faulting episodes were downward displacements on the eastern side of the faults, creating a west-to-east step-like topography in the basin (Hay, 1976, 1979). Displacements range from a few centimeters up to 40 metres in the west, and further east, at the western margin of the Olbalbal Depression, the displacement may be up to 100 metres (see Hay, 1976, 1979; Mollel and Swisher, 2012). The principal branch of Oldupai Gorge, the Main Gorge, originates in Lemagrut, through Lakes Masek and Ndutu and extends at least 46 kilometers eastward to Olbalbal. The rivers forming the Main and Side Gorges meet before emptying in to the Olbalbal Depression. The Side Gorge stems from the volcanic uplands of Lemagrut (one of the volcanoes in what is collectively known as the volcanic highlands) to the south and joins the Main Gorge about 9 km west of the Olbalbal depression (Mollel and Swisher, 2012). The western margin 109

of the Oldupai Basin is described by a succession of rapids and falls known as Granite Falls. The western head of the Gorge is broad and shallow while the eastern half is relatively narrow and deep. The steep-sided eastern part of the Main Gorge can be up to 90 metres deep and between 0.5 and 1.5 kilometres wide. The modern Oldupai basin is a remnant of the palaeo-basin, which was formed by the growth of the volcanic highlands on the metamorphic basement rock and has been filled in by Pleistocene sedimentary deposits known as the Oldupai Beds (Hay, 1976; Mollel and Swisher, 2012; Mercader et al., 2019).

Presently, the groundwater exits at the base of the slope contributing to the lake/swamp called Obalbal. The Obalbal is a sump collecting groundwater flowing from the Highlands to the east and seasonal run-off from the modern Oldupai River flowing from the west. The hydrogeologic setting was possibly similar in the past (Deocampo and Tactikos, 2010; Ashley et al., 2010; Mollel and Swisher, 2012). It is now known that groundwater discharge into the basin was important to animals and hominins in the past. High-resolution palaeoclimate and palaeoenvironmental reconstruction have revealed several springs and wetlands associated with archaeological sites in the Oldupai Basin, Middle Bed I, Upper Bed I, and Lowermost Bed II (Liutkus and Ashley, 2003; Ashley et al., 2009, 2010; Deocampo and Tactikos, 2010).

The Oldupai Gorge can be divided into three major physiographic parts: The Western, the Southwest, and from Lake Ndutu to the Ngorongoro-Seronera road. The Western part from the mouth of the Gorge where it crosses with the Ngorongoro-Seronera road, is the lower Gorge. It is deep with steep with eroded walls, a narrow floor, and a steep stream gradient with rapid runoff. Southwest from the road crossing to Lake Ndutu, the Gorge is shallower with more gradually sloping sides (Herlocker, 1967; Mercader et al., 2019). The stream gradient is gentler, and water remains longer in or beneath the stream bed. The south fork of the Gorge is much narrower and 110 shallower than the main Gorge and has a steep gradient in its upper reaches. The soils here are laterites and dark loams which are the typical soils of dry tropical and arid regions of northern Tanzania ecoregion (Mercader et al., 2019).

The current day topography is characterised by elongate basins filled with volcanic sediments, as well as fresh and saline lakes due to large scale extensional fracturing of the African Plate. In its eastern branch, rifting was associated with or preceded by voluminous eruptions of basalts, trachytes and phonolites since the Oligocene epoch (Hay, 1976; Morley et al., 1992). The earliest volcanic eruptions along the Gregory Rift occurred at the beginning of the Pliocene and were mainly of alkali basalt/trachyte-phonolite association (Hay 1976). This period of activity included Elanairobi, Olmoti, Ngorongoro, Lemagurut, Satiman, and other volcanic edifices (Hay, 1976; Dawson, 1992; Foster et al., 1997; Hay and Kyser, 2001). A second phase of volcanic activity occurred after a 1.2 Ma old faulting episode, and encompassed the Oldoinyo Lengai, Meru, Monduli, and Kerimasi (Manega, 1993). These later magmas were ultra-basic to ultra-alkaline in composition thus producing mainly nephelinites, phonolites and feldspathoidal syenites, as well as carbonatites (Manega, 1993; Dawson et al., 1994, Bell and Simonetti, 1996; Foster et al., 1997).

6.1.3 STRATIGRAPHY

To understand the later discussion of the different palaeoreconstructions that took place in this area over several decades, it is imperative to understand the stratigraphic sequences and their chronologies of the Oldupai Gorge, with more on Beds I and II, the stratigraphic sequences where this research was conducted. This section will provide a full historical overview of all the seven geological units (Beds) of the Gorge including aspects such as past ecological and climatic conditions i.e. modern and past topography, geography, and climatic conditions. Additionally, this section will assess the role of the climate shifts in the east African landscape during the Pleistocene period, to infer a clear connection between climate change and the evolutionary history of early humans, especially how the climatic shifts in the past altered hominin environments in east Africa and particularly in the Oldupai Gorge basin. It is also important to understand the Oldupai past and present plant physiognomical nature in relation to its environment in order to reconstruct the palaeohabitas in which our ancestors resided, and to highlight the history of research on human origins in this area.

The sedimentary strata of Bed I sequences were formed around 2.1 Ma adjacent to the East African (Gregory) Rift in response to extensional tectonics and the growth of a large volcanic complex (Ngorongoro Volcanic Highland) within a prominent divergence in the rift valley (Hay, 1976; Ashley et al., 2014). The Oldupai basin was gradually infilled with volcanic flows and ash falls from Ngorongoro to the east and sediments transported by rivers draining the basin margin (Reck, 1951; Hay, 1976; Ashley et al., 2014). Deposition filled in around a highly irregular quartzose-feldspathic metamorphic basement and left exposed several resistant outcrops (inselbergs) of quartzite (Naibor Soit and Naisiusiu) and granite gneiss (Kelogi and Naisiusiu) and phonolite (Engelosin) (Reck, 1951; Hay, 1976). Metamorphic rock highlands border the Gorge 20 kilometres to the north and other basaltic basement outcrops may have been covered with sediments in post Bed II time. It is the100-metre-deep Gorge that was formed during mid-to-late Pleistocene time when the Oldupai river, in response to rift tectonics, incised through the thick stack of volcaniclastic sediments thus exposing rich palaeontological and archaeological records (Leakey, 1971; Hay, 1976; Ashley et al., 2014).

The overall sedimentary environments of the entire region are characterised by the past fragments and particles of volcano tephra erupted from the NVH. The tephra deposits are 112

interbedded with fluvial, wetland, and lacustrine hominin-bearing deposits of Oldupai Gorge. The stratigraphic sequences of the region are composed of tephritic beds which provide a means of studying hominin habitats spatially-temporally in a recognised stratigraphic units of Oldupai Gorge palaeo-deposits (McHenry et al., 2008). Currently, these tephra deposits are useful in reconstructing the development and evolution of past landscapes that were occupied by our ancestors (Australopithecus boisei, Homo habilis, Homo erectus, and Homo sapiens) in the Oldupai Basin. On top of that, the tephra provides records of explosive volcanic activity for the nearby NVH, a record that would be difficult to reconstruct using only the eroded and vegetated volcanoes remaining today (McHenry et al., 2008). Also, by correlating these tephra deposits directly to their volcanic sources make it possible to reconstruct the eruptive history of the NVH and provides insight into the magmatic evolution of NVH volcanic centres (McHenry et al., 2008). The Oldupai Gorge exposes a 20 kilometres long section of Pliocene to Holocene strata up to 100m thick that contains hominin fossils, stone artifacts, and palaeoecological indicators critical for the study of hominin evolution (Hay, 1976). Tephra layers interspersed in these fossiliferous deposits Olmoti, Ngorongoro, and Lemagurut are the three younger volcanoes closest to Oldupai Gorge and they are the most probable source for the Oldupai Bed I pyroclastic deposits. Many of the Bed I geolocalities and archaeological sites mentioned in the Hay's book (1976) "The Geology of Oldupai Gorge" contain pyroclastic deposits that are marked along the First Fault, at Olmoti, and Ngorongoro landscapes. Ashley and Hay (2002) used these pyroclastic deposits to establish a local stratigraphic and temporal framework of Bed I (Hay, 1976; Ashley and Hay, 2002 cited in McHenry, 2004, 2005). Pyroclastic deposits within the Bed I sequence include airfall tephra, ignimbrites, and pyroclastic surges and flows likely produced by the nearby NVH to the east and south of the Oldupai Basin (McHenry, 2004, 2009).

Epoch	Stratigraphy	Subdivisons	Markers	Dates	Sites
Holocene			Namorod Ash	1,250 BP	
	Naisiusiu				
	Beds				
	Ndutu Beds	Upper Unit		400 32 ka	
		Lower Unit		400-52 Ka	
	Masek Beds	Norkilili			
		Member		600-400 ka	
		Lower Unit			
	Bed IV		Tuff IVB	800, 600 1	
			Tuff IVA	000-000 Ka	
			Tuff 4		
	Bed III		Tuff 3	1.22 + 0.06 Ma	IK WK
	Det III		Tuff 2	1.55 ± 0.00 Ma	
			Tuff 1		
			Tuff IID	1.48 ± 0.05 Ma and	
			Tuff IIC	1.338 ± 0.024 Ma	
	Bed II	Upper Bed	Upper Augitic Sandstone		
		Π	Bird Print Tuff		BK, JK, PLK, TK
		Middle Bed	Middle Augitic Sandstone		CK, EFHR, SHK
		П	Tuff IIB		MNK
		Lower Bed	Upper Lemuta		FLK West, HWK-EE
Pleistocene		П	Tuff FLK W B	$1.664 \pm 0.019 \; Ma$	
			Lower Augure Sandstone	$1.698\pm0.015~Ma$	
			Lower Lemuta Twiglet Tuff	$1.74\pm0.03~Ma$	
			Tuff IF	1.803 + 0.002 Ma	
			Tuffs between tuffs IE and IF	1.828 ± 0.005 Ma	
	Bed I		Tuffs between tuffs IE and IF	1.836 ± 0.015 Ma	
			Tuffs between tuffs IE and IF	1.833 ± 0.005 Ma 1.831 ± 0.006 Ma	
			Tuffs between tuffs IE and IF	$1.818\pm0.006~Ma$	
			Kidogo Tuff (?)	$1.831\pm0.004~Ma$	
			Ng'eju Tuff Tuff IE	$1.837\pm0.006~\mathrm{Ma}$	
			Tuff IE Vitric	$1.854 \pm 0.011*$ Ma	HWK
		Upper Bed I	Tuff ID (Plagioclase)	1.832 ± 0.003 Ma and	FLK North
		Lower Bed I	Tuff IC	$1.848 \pm 0.008*$ Ma	FLK Level 22, PTK, DS
			Chapati Tuff (?)	1.848 ± 0.003 Ma	DK Levels 1-3, FLK NN
			Bed I Lavas	1.911 ± 0.016 Ma	
			Tuff above IA	and 1.891 ± 0.010 Ma	
			Mafic Tuff	2.060 ± 0.018 * Ma	
			Tuff IA	$1.88 \pm 0.05 \text{ Ma}$	
			Coarse Feldspar Crystal Tuff	2.015 ± 0.006 Ma	
			Tuff between NI and CFCT	2.005 ± 0.007 Ma 2.038 ± 0.005 Ma	
			Naabi Ignimbrite	2.050 ± 0.005 IMa	

Dates from Deino, 2012; Diez-Martín et al., 2015; Hay, 1976; Leakey et al., 1972; modified from Favreau, 2019 & Patalano, 2019). ¹¹⁴

The stratigraphic record is divided into a series of geological layers, named Bed I–IV, Masek, Ndutu, and Naisiusiu Beds from the oldest to youngest (Hay, 1970, 1976) (Table 6-1). This section is solely describing only two stratigraphic units namely: Bed I and II because the sediment data for phytolith analyses were collected from here. The other upper Beds (Bed III-VII) are also described but not inasmuch as Bed I and II. The Oldupai Bed I, which has an age range of 2.1-1.79 Ma (Hay, 1976; Walter et al., 1992; Hay and Kyser, 2001) is a conformable sequence of lava flows with varied sedimentary deposits that extend upward from a welded tuff overlying the Precambrian basement to the top of a widespread marker bed. This dissertation followed Hay's (1963, 1976) geological nomenclature to describe Bed I and II stratigraphic units, their chronologies, and their palaeoenvironmental settings. To begin with the oldest geological strata in the Gorge, such as the lower part of Bed I, Hay (1976) detailed that the bed is exposed mainly in the western-part of the Oldupai Basin (palaeolake shores, and contains predominantly quartzbearing rhyolitic/trachytic tephra layers (Hay 1976; Ashley et al., 2009) whereby the green rhyolitic Naabi Ignimbrite directly underlies lower Bed I as per Hay (1976), but he described this as the lowermost tephra layer within Bed I based on its compositional similarity to the overlying coarse feldspar crystal tuff (CFCT) and Tuff IA and it is superimposed by the CFCT and Tuff IA (Hay, 1976, cited in Ashley et al., 2009). The upper Bed I contain six major tephra of trachytic or trachyandesitic composition: Tuffs IB through IE, the Ng'eju Tuff, and Tuff IF (McHenry, 2005).

The stratigraphy of Bed I tephra has been used to establish time horizons between widely separated sites within the Oldupai Basin (Hay, 1976). A revised stratigraphic framework based on tephra composition (primarily major and minor elements in phenocrysts) by Blumenschine et al., (2003) helped to link sites in the eastern and western parts of the Gorge, between which physical 115

correlation was difficult or impossible before (Blumenschine et al., 2003; McHenry, 2004, 2005). The basaltic lavas of Bed I mark the transition between lower and upper Bed I in the eastern part of the Gorge (Hay, 1963, 1976), whereas Tuff IA marks this transition in the west (Hay, 1976). The terms lower and upper Bed I have different meanings in the archaeological literatures such as in Leakey (1971).

Bed I of the Oldupai Gorge, exposes one of the most famous Plio-Pleistocene records of hominin behaviour and evolution (Leakey, 1971). These fossils, artifacts, and palaeoecological indicators which are preserved in these sediments representing a wide variety of depositional environments, including fluvial, freshwater wetlands, saline-alkaline lake and lake margins, and alluvial and volcaniclastic fans that contains channel deposits (Hay, 1976; Ashley and Hay, 2012). The nearby NVH contributed volcanic material in the form of airfall tephra, ignimbrites, ash flows, surges, and lava flows to the sedimentary deposits, providing material for radiometric dating and tephrostratigraphic correlation between sites (Hay, 1976). Despite the presence of these volcanic layers, the Oldupai Basin is not a simple stratigraphic "layer cake" as many would presume; and this is mainly because the post-depositional faulting, erosion, and differentials in preservation condition, as well as complex depositional environment the sedimentary record contains that Oldupai Gorge contains, making physical correlation throughout the basin very difficult to almost impossible to imagine (McHenry, 2012).

The following geological layers are the Oldupai Bed II, dated about 1.8-1.5 Ma, and is located directly above Tuff IF. It contains tephra composition that has changed to silicaundersaturated compositions, such as nephelinite and foidite that are reflecting probably a transition to a different volcanic source in the past (McHenry, 2012). Bed II contain sequences of lacustrine clays and laterally equivalent fluvial, eolian, and pyroclastic deposits. The sedimentary 116 deposits of the Oldupai lake basin of Bed I and lower Bed II are divided into three lithofacies from which are inferred the Central Basin, Lake margin zone, and the Alluvial Fan. They are demarcated based on lithology, biogenic and archaeological evidence, and mineral composition (Hay, 1976; Tactikos, 2005).

The palaeoenvironmental reconstructions based on lithofacies characterisation classify the Pleistocene deposits in the westernmost area of the modem day Main Gorge, referred to as lake margin deposits. that consist primarily of clays and claystones, (Hay, 1976; Tactikos, 2005) whereas fluvial lacustrine deposits include sandstones (Hay, 1976; Tactikos, 2005). Also, the Bed II sequence is stratigraphically subdivided into five major sequences 1 -5, all floored by major disconformities that incise deeply into the underlying succession. Tactikos (2005) argued that it is not possible to identify the "layer cake" stratigraphy on Bed II sequences. Previous establishment of the Lemuta Member has invalidated the use of Tuff IIA as the boundary between Lower and Middle Bed II, now redefined at the disconformity between sequences 2 and 3 (Tactikos, 2005) a lithostratigraphic contact that is underlying the succession containing the Lower, Middle, and Upper Augitic Sandstones. For example, the outcrop of Henrietta Wilfrida Korongo East East (HWK EE) site records Oldowan technology in the Lower Augitic Sandstone at the base of sequence 3, within Middle Bed II (Hay, 1976; Tactikos, 2005); while Tactikos (2005), placed a boundary between the Oldowan and Acheulean technologies at Oldupai in the Tuff IIB zone or earliest Middle Augitic Sandstone. A major disconformity between sequences 3 and 4 at and nearby the Acheulean site known as Evelyn Fuchs and Hans Reck (EF-HR) cuts through the level of Tuff IIC, placing the main Acheulean EF-HR assemblages at the base of sequence 4, within Upper rather than Middle Bed II (Hay, 1976; Tactikos, 2005, Ashley et al., 2009).

According to Tactikos (2005), some of the Bed II sites such as FLK are made up of a diverse sequence of fluvial, eolian, and pyroclastic deposits which are about 50-90 feet thick. The clays, sandstones, and conglomerates of fluvial origin form most of the eastern sequences of Bed II but some of the clays and sandstones appear to have been deposited by the lake when it spread eastward beyond its usual limits (Hay, 1976; Tactikos, 2005). Detritus of the sandstones and conglomerates is largely trachytic, and stream-channel trends suggest that most of it may have been supplied by the Ngorongoro tephra. Trachyte, nephelinite, and olivine basalt cobbles in conglomerates near sites like Henrietta Wilfrida (HWK) and at locality 85- Vivian Evelyn Korongo (VEK) were derived from the direction of Lemagrut (Hay, 1976; Tactikos, 2005). Trachyte tuffs of ash-fall origin and pyroxene-rich tuffs redeposited by wind constitute about a fifth of the eastern sequence. The eolian tuffs consist of mineral grains and rock fragments that were rounded and polished by wind action, and the thickness and extent of these eolian tuffs suggest a climate like that of the present time at Oldupai Gorge (Ashley et al., 2009). At about the time these eolian tuffs were deposited, the lake to the west temporarily shrank (Ashley et al., 2009). Some of the known lacustrine chert nodules were likely eroded at its margin, and mud cracks formed over much of its floor.

The available archaeological evidences revealed that some stone artifacts and wellpreserved fossils are relatively abundant in beds deposited along the eastern and southern margin of the lake to the Upper Bed II sites; for example, in sites like: FLK, Sam Howard Korogo (SHK), and Bell's Korongo (BK) (Ashley et al., 2009). In the lower part of Bed II there are tools made from chert obtained from the margin of the lake during its brief period of desiccation (Tactikos, 2005). Bed II covers a most interesting interval at Oldupai Gorge, this is the Bed that contained relevant information about the disappearance of the Oldowan and appearance of the Acheulean 118 lithic technologies, and the disappearance of *Homo habilis* and emergence of *Homo erectus* (Leakey, 1971; de la Torre and Mora, 2014). The stratigraphic framework for Bed II has been very crucial in establishing the relative timing and palaeoenvironmental context for these major transitions.

Bed III strata are made up of alluvial deposits and a laterally equivalent assemblage of fluvial, lacustrine, and eolian beds (Hay, 1976). To the west, Bed III consists of yellowish-gray sandstones and smaller amounts of conglomerate, clay, and dolomite. Within Bed III to the southeast of site Hopwood's Korongo (HK); for instance, these beds intergrade with the reddishbrown alluvial deposits which are dominantly from the volcanic detritus, but many of them also contain a small to moderate proportion of gneissic debris and calcite oolites. Ages for Bed III and Bed IV have been determined using magnetostratigraphy and sedimentation rates (Hay, 1976). Bed III was deposited between 1.15 and 0.8 Ma and Bed IV between 0.8 and 0.6 Ma (Brock et al., 1972; Hay, 1976). Bed III contains four tuffs, but only the lowermost has been used for correlating as the rest have only been recognised in a few localities. Similarly, Bed IV contains two marker tuffs, but only the lower one is widespread enough to be useful for correlation (Hay, 1976). Most of the known and documented tuffs in Bed III and Bed IV have been altered by different geological and geomorphological factors and are therefore unsuitable to date using radiometric techniques (Brock et al., 1972).

Bed IV comprises a widespread of lower unit clays, sandstones, and conglomerates in lower units and an equally widespread upper unit of eolian tuffs. On the proximity to the mouth of the Gorge the eolian tuffs are overlain by conglomerates, sandstones, and clays. The lower member of Bed IV, as much as 80 feet thick, consists almost exclusively of Precambrian debris which coarsens westward along the Gorge (Hay, 1976; Tactikos, 2005; Ashley at. al., 2009). The Earth's 119 crust here may have been slightly warped before Bed IV was deposited, for the direction of stream flow near Oldupai Gorge seems to have been reversed between Beds III and IV (Hay, 1976). Bed III received most of its debris from a volcanic source to the south and possibly southeast, whereas most debris at the base of Bed IV, nearly as far east as the Third Fault, was derived from exposures of welded tuff and Precambrian basement to the west and north (Hay, 1976). Crustal warping also accounts for the channeling of Bed III by the base of Bed IV and the abrupt disappearance or displacement of the lake which had existed in approximately the same place for much of the time that Beds I, II, and III were deposited at the Gorge (Hay, 1976; Tactikos, 2005; Ashley at.al., 2009).

The sediments from Bed IV are covered by receding slopes and gray volcaniclastic channelised fluvial sandstones and conglomerates and the columns represent fluvial-dominated systems (Hay, 1976). Research investigations especially those ones focused on the depositional processes of Bed III and Bed IV localities have enabled palaeoenvironmental reconstructions, which have important implications for the evolution of *Homo erectus*. Bed III and Bed IV contains archaeologically significant localities that are exposed on the upper beds of the Gorge, which are ideal for large-scale palaeoenvironmental reconstructions, specifically with great importance for the palaeoreconstruction of *Homo erectus* habitats.

One of the most important sites found in these beds is Juma's Korongo (JK) site which is located on the northern edge of the main Gorge (Leakey, 1971). One of the earliest notable expeditions to the JK site involved Dr. Maxine Kleindienst in 1964. She was responsible for the only detailed report on the geology of this site, and all stratigraphic interpretations of this site have depended on her publication (Tactikos, 2005). Again, Hay (1976) reported on the general stratigraphy of these upper beds at several other sites. Since then, a considerable amount of 120 palaeoenvironmental research has been done to expand upon Hay's work in Bed I and Bed II (Lower Beds), but not so much recent geological works for Bed III, Bed IV, the Masek Beds, Ndutu Beds, and Naisiusiu Beds (upper beds) since then; the initial investigation works by pioneers like Louis and Mary Leakey in 1969, 1971, and more greater efforts by Richard Hay's 1976 momentous work that has been used mainly as the referential bibliography for Oldupai.

The superimposing Beds after Bed IV are the Masek Beds of which are made up of two units, a lower section composed mainly of eolian tuffs and an upper Norkilili Member. It is within the lower Norkilili Member that mandibular fragment namely O.H.23 was recovered in situ at FLK by Mary Leakey in 1968 (Leakey, 1969). Dating of the Masek Beds were established by dating the tuffs that were probably derived from Kerimasi (Tactikos, 2005); Kerimasi, is a volcano to the east of the Gorge which supplied large amounts of ash to the Oldupai region in the later part of the Pleistocene. The age of Kerimasi is known from K-Ar determinations to exceed 0.4 million years (Ashley et al., 2009; Tactikos, 2005). An estimate of 0.6 million years for the top of Bed IV then suggests that the Masek deposits, which are normal in magnetic polarity, are between 0.6 and 0.4 million years in age (Hay, 1976; Tactikos, 2005). Tactikos' 2005 assumption fits well with Hay's 1976 whom both proposed the figure of 200,000 years as the length of time needed for Masek sediments deposition (Tactikos, 2005).

The Ndutu Beds (400-32 Ka old) are preserved perhaps over five percent of the Gorge and form a relatively continuous layer over the plain adjacent to the Gorge (Hay, 1976, Tactikos, 2005). Over the plain they are generally 0-3 to 4-5 metres thick, and within the Gorge their thickness generally ranges from 3-5 metres with a maximum of 27 metres near the Fifth Fault. The thickest sections are of stream-laid sediment in the axial part of the Gorge. The Ndutu Beds within the Gorge comprise two units separated in most places by an unconformity (Hay, 1976). The lower 121 unit is largely conglomerates and sandstones, and it composed of five to one per cent of tuffs. Only a few patches remain to the west of the second fault, but eastward, 8-14 metres of beds are widely preserved (Hay, 1976). The conglomerates are coarse and contain lava boulders as much as 0-6 metres and tuff blocks as much as more than ten metres long together with algal limestone which are at least 2-3 centimeters thick, coats clasts in many conglomerates, are ubiquitous and are found in no other beds of Oldupai Gorge (Hay, 1976).

The upper unit of the Ndutu Beds is much more widespread than the lower unit and it contains basal conglomerates, the lowermost of which lie 12 - 27 metres above the present riverbed in the eastern six kilometres of the Gorge. The riverbed deposits which had been eroded to about two-thirds of its present depth when the gravels were deposited (Hay, 1976; Tactikos, 2005). The tuffs in the axial part of the Gorge are commonly laminated and water-worked; those on the sides of the Gorge commonly have steep, large-scale eolian cross-bedding (Hay, 1976; Ashley, et al., 2009, 2010; Tactikos, 2005). The surface of the Ndutu Beds is generally compacted and calcareous, and on the plains, is usually overlain by 1-2 centimetres of laminated calcrete. These calcareous tuffs and laminated calcretes resemble those of both the Naisiusiu Beds and the Masek Beds, which underlie the Ndutu Beds in many places along the rim of the Gorge (Hay, 1976; Ashley, et al., 2009, 2008; Tactikos, 2005).

The youngest geological layers in the Oldupai Gorge are known as Naisiusiu Beds. These Beds were deposited after faulting had ceased and the Gorge had been eroded to nearly its present depth (Hay 1976). The Naisiusiu Beds are uppermost late Pleistocene layers that have been C14 dated to about 10,400- 600 years B.P., the C14 date was obtained from the collagen of bone collected from eolian tuffs at the fifth fault (Leakey et al., 1972). Tactikos, 2005). The Naisiusiu Beds are largely eroded within the Gorge and cover no more than a tenth of its surface area (Hay 122 1976; Ashley, et al., 2009, 2010; Tactikos, 2005), and these Beds form an extensive but discontinuous layer over the surface of the Serengeti Plain adjacent to the Gorge.

The Naisiusiu Beds are usually ranging between 0-3 and 3 metres in thickness. The Beds consist of huge and massive eolian tuffs that form at least 90 percent of the formation and its general surface is about 15 -30 centimetres. These eolian tuffs are generally calcareous and hard, and laminated calcretes that ranges between 1-3 centimetres thick, and are commonly overlying the tuffs on the Serengeti Plain. There are some stream-laid conglomerates and sandstones which form the basal part of the Naisiusiu Beds in the axial part of the Gorge, and clay-sand-stones deposited by sheet wash which are noticeable near the bottom of the Gorge (Leakey, et al., 1972). A pale yellow phonolitic vitric tuff generally 15-30 centimetres thick is wide- spread and useful in correlating within the Naisiusiu Beds around the Oldupai Gorge's vicinity (Leakey and Leakey, 1964; Leakey et al., 1972).

6.1.4 VEGETATION

In this dissertation, special attention was paid to the Serengeti ecosystem that lies entirely within the Somalia-Masai Regional Centre of Endemism because within the Serengeti National Park, whereby human activity has been minimal and the modern landscape more less disturbed by antropogenic activities. This differs from outside the park where the intensity of human influence varies greatly from place to place. The Serengeti ecosystem comprises 35,000 km² of grassland and wooded grassland in northern Tanzania extending into southern Kenya. More than one hundred species of grass occur in the region but are mainly restricted to areas in which soils are derived from volcanic ash, which favour grasses rather than woody vegetation. The *Acacia-Commiphora* bushland and thicket is very poorly represented inside the Serengeti National Park,

but *Acacia-Commiphora* wooded grassland is the most extensive woody vegetation type in the Serengeti National Park and represents 88% of all woody vegetation.

The present-day plant landscape found around the vicinity of the Oldupai Gorge landscape itself is characterised by dry Acacia commiphora woodland (the Acacia mosaics type of northern Tanzania). The woodland overstory is composed mainly by the *Commiphora madagascariensis*, and Acacia meliffera and lesser amount of A. tortilis and C. meskeri (Herlocker, 1967; Mercader et al., 2019). Associated lower vegetation includes: Sansevieria ehrenbergiana, Salvadora perisca, Lyciucm spp., Cissus quadrungularis, C. cactiformis, Euphorbia schimperi, and E. tirucalli, Grewia spp., Cordia spp., Pluchea ovalis, Justicia bentonica which grow along the streams (Herlocker 1967). Southern Acacia-Commiphora is part of a continuum of woodland-grassland mosaics, that runs through Serengeti National Park and the Ngorongoro Conservation Area, to some parts of South Western Kenya. It is composed of open grasslands, bushland, and thicket, which are ubiquitous in Northern Tanzania especially to the entire Serengeti-Maasai Mara ecoregion (Mercader et al., 2019), commonly referred to as the Greater Serengeti. The Great Serengeti area falls within the Somalia-Masai floristic region in which Acacia Commiphora deciduous bushland and thicket are the dominant vegetation types (Mercader et al., 2019). This ecoregion is transitional to the miombo woodlands to the south and the Zanzibar Inhambane coastal forest mosaic to the east. Covering regionally 10 - 40 % of the terrain (White, 1983), the most common physiognomy is low woodland (Andrews and Bamford, 2008; Herlocker and Dirschl, 1972, Mercader et al., 2019). Grasses are inconspicuous at Oldupai Gorge the average perennial cover today is at least 22 % which is comparable to that observed in the 1960s (Anderson and Talbot, 1965; Kindt et al., 2011; Niboye, 2010; Mercader et al., 2019), with bare terrain exposing only 45 % of the area (Mercader et al., 2019).

The nature and distribution of modern vegetations in the Oldupai Gorge ecoregion are useful clues to the prevailing influences and to the modifying effects of past and present human use, and thus provide an index to the productivity of the various landscape units (Herlocker, 1967). The geology, climate, and soil-vegetation relationships (Herlocker 1967) indicate the presence of three major soil types: juvenile soils on volcanic ash, calcimorphic soils with hard pans, and vertisols of lithomorphic origin. The northern part of Oldupai Gorge region is composed of an extensive area of stabilised dunes composed of fine sand overlying calcareous tuff (Herlocker, 1967; Mercader et al., 2019). Soil types are calcimorphic, yellowish brown, with low humic values less than 1 % organic carbon, and a hard pan (Anderson and Talbot, 1965; Mercader et al., 2019).

From Lake Ndutu roughly to the crossing of Ngorongoro-Seronera road, the vegetation is characterised by low woodland of *Commiphora madagascariensis, Acacia meliffera*, and *A. tortilis*. Although *A. tortilis* is the least common of the three, it grows taller with a wider crown and thus predominates (Herlocker, 1967). Towards the eastern margin to the proximities of the eastern Serengeti Plains, the region is comprised of natural topography that varies between 1350 metres to 1550 metres above sea level with a central plateau around Oldupai Gorge towards Endulen highlands which experiences wide temperature oscillations and high winds (Anderson and Talbot, 1965; White, 1983; Mercader et al., 2019).

The layer of bush species ranges in density from low to moderate and consist typically of *Sansivieria ehrenbergiana, Cissus quadrulangularis* and *C. cactiformis*. The grass layer is mostly *Digitaria macroblephara* and *Sporobolus marginatus*, and short grass such as *Aristida adscensionis*, all of which are very common in the area. It is significant to understand modern plant distribution in relation to soil where plants grow and rainfall in the area is a vital tool for comparisons between modern vegetation versus fossil plant proxy data. The comparisons between 125

plant micro-remains data from the past to the present offer some important clues about changes in vegetation structure that might have taken place to the landscape over time and space.

The modern vegetation and plant physiognomy of the eastern Africa (likewise Oldupai Gorge) region is referred to as the "Somalia-Masai Regional Center of Endemism", an expansive region occupying a large part of East Africa between 16°N and 9°S and 34°E and 51°E (White, 1974). It incorporates an area of 1,873,000 km2 and includes eastern and southern Ethiopia (except the mountains), most of Somalia and Kenya, Djibouti, eastern Eritrea, northcentral Tanzania, southeastern South Sudan, northeastern Uganda, and transversely the Red Sea into southern Arabia. This centre of endemism situated between 0 and 900 m.a.s.l, has an arid to semi-arid climate whereby rainfall is often less than 500 mm per year and can be as low as 20 mm, and the mean monthly temperatures are between 25° and 30°C (White, 1974). The biogeography of the Somalia-Masai region is dominated by deciduous bushland and thicket that grade into and are replaced by evergreen and semi-evergreen bushland and thicket on the lower slopes of mountains.

The Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket is a dense, 3-5 m tall impenetrable bushland that forms thickets of plants often armed with spines that greatly hinder movement. Trees rarely exceed 8 m in height, although emergent 9-10 m tall trees are scattered throughout the bushland, particularly on rocky hills. There are about 2,500 species of flora, and possibly 50% of these are endemic. There is one endemic family, Dirachmaceae (Dirachma socotrand), which is found on the island of Socotra (Yemen) and in Somalia, and about 50 endemic genera occurring on both the African mainland and in Arabia and Socotra. While most plant species are deciduous, evergreens contribute 2.5-10% of the biomass (White, 1974). Smaller areas of scrub forest, riparian forest, secondary grassland and wooded grassland, seasonally waterlogged grassland, semi-desert grassland and shrubland, and desert are also found throughout this centre 126

of endemism. Modern human activities, especially in areas where domestic animals are abundant, are responsible for the conversion of bushland into grassland over hundreds of square kilometers where grasses were once inconspicuous. Acacia-Commiphora deciduous bushland and thicket is still widespread in the Ngorongoro Conservation Area, near Lake Eyasi, and in Oldupai Gorge. East African evergreen and semi-evergreen bushland and thicket occurs on the drier slopes of mountains and upland areas from central Tanzania to Eritrea and beyond, forming an ecotone between montane forest and the Acacia-Commiphora bushland and thicket

The semi-desertic grassland and shrubland dominate the Somalia-Masai RCE wherever rainfall is between 100 and 200 mm per year. Edaphic grassland covers large areas in Tanzania but is less well-developed further north, and the near absence of trees on the Serengeti Plains is partly due to unfavourable edaphic conditions. In the ecotone between forest and grassland in Nairobi National Park, a combination of grazing, browsing, and fire has created grassland in areas capable of supporting evergreen bushland or forest. As for forests, Somalia-Masai scrub forest develops at relatively low altitudes where rainfall is higher (>500 mm) than that of deciduous bushland and thicket but too low to support true forest. Scrub forest vegetation usually reaches between 7-10 m tall. Riparian forest occurs only on the banks of the larger rivers, such as the Tana River (Kenya), and often includes many species that are widespread throughout Africa.

6.2 MATERIALS

This research focused on Oldupai Gorge's Upper Bed I and Lower Bed II, at the archaeological sites of Frida Leakey Korongo North and West, and at geological exposures at the

Bird Print Tuff, Oldupai's Castle, and Lower Augitic Sandstone (Fig. 6-2). These five sites were sampled and sediments for phytolith analysis were collected; this section provides a general



Figure 6-2: Sampling locations at FLK-N, FLK-W, Geolocality 44a, LAS, and BPT (Source:Modified from Patalano, 2019).

overview of the archaeologically investigated sites on aspects similar to those described previously such as geology, sedimentology, palaeoecology, palaeogeographies, and the palaeoenvironmental significance of these sites in regard to human evolution. The choice of sampling methods and its rationale (site level versus aerial/horizon level sampling) is explained in greater detail below.

We designed sampling approaches by combining both temporal (site level approach) and spatial (horizon level approach) strategies to identify variations in phytolith assemblage preservation within and between specific sites versus horizon level. These strategies were employed to test the two hypotheses from this study: i) that environmentally speaking, there are no significant differences between the UMBI-LMBII plant landscapes, or even within, Upper Bed II, and; ii, the hominins were occupying fundamentally different ecological niches between Upper Bed I- Lower Bed II time frame. To address the first hypothesis, twice in the sampling there was high-resolution sampling (site specific approach), and where horizon-oriented sampling was used to test the second. The site high-resolution sampling, in combination with horizon level sampling across the landscape through phytolith analyses would provide a better understanding of changes in habitats and palaeoenvirnoments that were occupied by early humans in a broader scale (Barboni et al., 2007; Bremond et al., 2008). The reason behind the choice of these strategies is to determine if the high-resolution phytolith assemblages correlate or do not correlate directly with the analyzed horizon palaeosol assemblages, or vice versa. Phytolith analysis from the total assemblage (high resolution site level versus horizon level) both provide a wider spectrum on intra and inter-site phytolith assemblage similarity and dissimilarity and ability to see how both assemblages compare.

6.2.1 FRIDA LEAKEY KORONGO NORTH (1.83 MA)

Since its discovery in 1959, multiple archaeological excavations at the site have been carried out, with many others currently in progress, yielding hundreds of stone tools, large mammal skeletons, carnivore-ravaged bones, and some copious micro-mammal remains (Ashley et al, 2004). The artifact analysis by Leakey (1971) and re-analyses of her published data or specimens by others (eg. Potts, 1988; Egeland, 2008; Ashley, et al., 2014) continued to fuel the controversy regarding the origin of the site. Early on, Leakey (1971) had arbitrarily subdivided Levels 1-3, as this unit was relatively uniform and unchanging in composition and consists of at least 80 cm of a grey-brown silty/waxy clay. She did combine Levels 1 and 2 but excluded Level 3 on the grounds that it was archaeologically poor in artifact and faunal remains. This came to be criticised by other scholars later on because they did not see any tangible fact for distinguishing between Levels 1 and 2, and 3 (Domínguez-Rodrigo, et al., 2007).

The FLK-N horizon (2° 59' 21.08"S, 35° 20' 53.4"E) is a 3.0 m, 15,000-year sequence in Upper Bed that I subdivided into nine archaeological units dated between 1.803 ± 0.002 Ma (Tuff IF) and 1.818 ± 0.006 Ma (Ng'eju Tuff) (Ashley et al., 2014). It occurs stratigraphically in Upper Bed I and Lower Most Bed II. It hosts the famous FLK-N archaeological site which was discovered over 50 years ago, it is situated on a low relief ridge, the uplifted (hanging wall) side of the Zinj Fault (Ashley et al., 2010a). This is one of the first sites to be discovered in the Gorge by Leakey in 1959 (Leakey, 1971; Ashley et al., 2004, Ashley et al., 2014). The geological record of the FLK-N indicate that the site is composed primarily of magnesium-rich smectitic clays, called "waxy-clays" as suggested by Hay (1976). After the original documentation by Leakey in 1971, a detailed geological mapping in the environments of the site was done by Ashley et al., (2014) which

revealed the occurrence of rich sedimentological and palaeoecological records and a thin, but persistent tuff known as "Kidogo Tuff" that is about 1.5 m below Tuff IF (Ashley et al., 2014).

The geological study by Ashley et al., (2014) discovered that Middle Bed II sediments at FLK-N are superimposed by sections containing clayey layers, which are unconformably overlain with younger sediments of Masek Beds. Also, it was noticed that the Bed III and IV sediments were eroded from this site during incision of the Gorge in the Late Pleistocene. Ashley et al., (2014), argued that the FLK-N site was slightly higher than the surrounding terrain on the broad lake margin, but low enough to be periodically flooded and covered by lake water, and the sediments. Lake expansion occurred frequently during Milankovitch wet periods (Ashley et al., 2014), and even during drier times monsoon-driven seasonal lake flooding could occur (Ashley et al., 2007; Liutkus et al., 2005). According to Ashley et al., (2014), the clay deposits are the possible amalgamation of hundreds to thousands of short and long-term lake expansions episodic events; and each expansion depositing a thin veneer of sediment. Sedimentation rate of non-tuff sediments in Bed I and Lower Most Bed II has been calculated to be around 0.1 mm/y (Hay, 1976; Ashley, 2007; Magill et al., 2012a; Ashley et al., 2014). This estimate suggests that the time period between Ng'eju Tuff and Tuff IF could be 22,000 years long (within the error of the 40Ar–39Ar tuff dates). The time between Kidogo Tuff and Tuff IF (levels 1–5) could be as much as 15,000 years (Ashley, et al., 2014).

Level 4 is a dark chocolate-brown silty/waxy clay varying in thickness from 8 to 45 cm. The lack of association among faunal remains and hominin butchering activities in FLK-N Levels 1-4 suggests carnivores accumulated bone assemblages, most likely by felids such as leopards (Domínguez-Rodrigo et al., 2007b). Level 5 is a greenish-yellow clay that includes a hominin toe bone (OH 10) and is situated atop the 10 cm fine-grained pyroclastic Kidogo Tuff (Ashley et al., 131 2014), which separates Levels 1-5 from 6-9. Levels 1-5 were interpreted as hominin "living floors" by Leakey (1971). Level 6 is a dark greyish-brown silty/waxy clay 20-50 cm thick, which Mary Leakey described as an elephant (*Elephas recki*) butchery site (Potts, 1988), that also consisted of a 75 mm proto-biface made on basalt as noted by Mary Leakey in 1971. The Levels between 7-9 have not yet been extensively excavated, but were detailed by Domínguez-Rodrigo et al., (2010) as a 1520 cm light-grey clay (Level 7), a 13-18 cm light-grey to yellowish clay (Level 8), and a 16 to 31 cm dark waxy clay (Level 9). The FLK-N archaeological record ended when Level 1 was covered with 0.4 m of Tuff IF in a violent volcanic eruption of nearby Mount Olmoti (Ashley et al., 2014) its interpretation has been somewhat controversial since then (Ashley et al., 2014).

The violent volcanic eruptions from Mount Olmoti have caused a controversy on inferring or interpreting the site's taphonomy, stone tools accumulations, and on interpreting other aspects pertinent to site formation processes. Because of these mentioned forceful volcanic eruptions, there are emerging differing dense bone and stone tool accumulation range from a site on a featureless lake margin that is dominantly anthropogenic in origin to a site near a freshwater wetland that is dominated by carnivore activity i.e. felids and hyenas. The analysis of recovered fossil bones and artifacts by (Ashley et al., 2014) has shown that the bones of large animals are largely the product of felid hunting and feeding behavior, followed by hyena gnawing and breakage of some bones (Hay, 1976; Ashley et al., 2009, 2014). This raises a question about whether the site formation is dominantly anthropogenic involving the butchering of animals obtained through scavenging and/or hunting, or was the site produced by carnivore predation and feeding activity, or a combination of both and whether there were there tool-carrying hominins and carnivores at the site at the same or different times. Ashley et al. (2014) found that the overlying Bed II sediments contain scattered archaeological material and a freshwater carbonate deposit that is similar to those found associated with other Bed II archaeological sites, e.g. VEK, HWK and HWKE.

In addition, microbotanical proxy data from phytolith and pollen recovered from FLK-N site indicate that the low ridge supported a woodland with palm trees (Barboni, et al., 2010), with the exact location of the site caused by geologic factors related to the Zinj Fault. The "Zinj Fault" was identified in Ashley et al. (2010a, 2014), and is an extension of an unnamed normal fault mapped in the Side Gorge near locality 88a (Hay, 1976). Therefore, Ashley et al., (2014) concluded that the Zinj Fault runs northeast-southwest parallel to the FLK Fault, but lies at least 150 m to the east, the geologically-controlled setting warranted the longevity of the landscape thus allowed the repeated use of the area by carnivores and hominins likely leading to its palimpsest character (Hay, 1976; Bunn et al., 2010; Domínguez-Rodrigo et al., 2010; Ashley et al., 2009; Magill et al., 2012; Ashley et al., 2014).

Several samples were collected from the FLK-N Clays in contact below Tuff IF (1.803 \pm 0.002 Ma) (Fig. 6-3), the marker tuff dividing Bed I from Bed II that is exposed for more than two kilometers throughout the main confluence of the Gorge. In this area, we collected (n=30) sediment samples across the landscape for phytolith analyses (Table 6-2). Also, we collected 12 samples (column sampling) from the geological trench and sampled (n=10) from the archaeological trench thus make a sum of 52 samples from the FLK-N site (Table 6-3 and Table 6-4). Sediment samples for phytolith extractions were collected in 5 cm intervals from below Tuff IF to a depth of 40 cm in Levels 1 and 2 of FLK-N Geological Trench 7. It is within these levels that a high-density concentration of faunal remains was recovered in association with Oldowan stone tools (Leakey, 1971; Bunn et al., 2010; Díez-Martín et al., 2010; Domínguez-Rodrigo et al., 2010). Levels 1 and 2 have been described as a living floor (Leakey, 1971), a central foraging place (Bunn, 1986), a 133

spot for intensive percussion behaviour, particularly on long bone shafts (de la Torre and Mora, 2005; Díez-Martín et al., 2010), a palimpsest of non-related animal and hominin activity (Bunn et al., 2010), a felid-responsible bone accumulation site (Díez-Martín et al., 2010), and a hammerand-anvil locality that was special for plant resource processing (Domínguez-Rodrigo et al., 2007).



Figure 6-3: FLK-N site stratigraphy and sample locations (Source: McHenry and Stanstreet, 2018; modified after Patalano, 2019).

Sample	Amount (g)	Latitude	Longitude
01	3	-2.9878	35.34755
02	3	-2.9885	35.34722
03	3	-2.9891	35.34814
04	3	-2.9899	35.34848
05	3	-2.9907	35.34947
06	3	-2.9910	35.34974
07	3	-2.9920	35.35027
08	3	-2.9940	35.35079
09	3	-2.9939	35.35149
10	3	-2.9941	35.35194
11	3	-2.9945	35.35202
12	3	-2.9941	35.35379
13	3	-2.9949	35.35362
14	3	-2.9941	35.35426
15	3	-2.9946	35.35495
16	3	-2.9933	35.35459
17	3	-2.9926	35.35647
18	3	-2.9925	35.34998
19	3	-2.9928	35.34934
20	3	-2.9928	35.34855
21	3	-2.9943	35.34463
22	3	-2.9956	35.34095
23	3	-2.9945	35.34927
24	3	-2.9944	35.34994
25	3	-2.9942	35.36521
26	3	-2.9945	35.36449
27	3	-2.9965	35.36398
28	3	-2.9954	35.36224
29	3	-2.9948	35.36195
30	3	-2.9891	35.35952

Table 6-2: FLK-N horizon clays below Tuff 1F sampling locations

Table 6-3: FLK-N ho	orizon site	samples
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Sample	Unit	Location Description	Height (cm)	Weight (g)
1	7B	West profile; column under occupation floor	0 - 5	3.0
2	7B	West profile; column under occupation floor	5 -10	3.1
3	7B	West profile; column under occupation floor	10 -15	3.0
4	7B	West profile; column under occupation floor	15-20	3.0
5	7B	West profile; column under occupation floor	20 - 25	3.0
6	7B	West profile; column under occupation floor	25 -30	3.1
7	7C	Western face of zone 2	0 - 5	3.0
8	7C	Western face of zone 3	5 -10	3.0
9	7C	Western face of zone 4	10 -15	3.0
10	7C	Western face of zone 5	15-20	3.0
11	7C	Western face of zone 6	20-25	3.0
12	7C	Western face of zone 7	25-30	3.0

Sample	Height below Tuff IF (cm)	Amount (g)	
10	N/A	3.0	
9	N/A	3.0	
8	0-5	3.0	
7	5-10	3.0	
6	10-15	3.1	
5	15-20	3.1	
4	20-25	3.0	
3	25-30	3.0	
2	30-35	3.0	
1	35-40	3.0	

Table 6-4: FLK-N site samples

There are clays below Tuff IF that are famously known as "Waxy Clays" which divides Bed I from Bed II, and the tuff is the most widespread of the Bed I tuffs (Hay, 1976). Sediment samples were collected in the clays right in contact below the tuff for more than 2 kilometers throughout the main confluence of the Gorge to track spatial-temporal changes in vegetation cover before the transition from Bed I- II. The clays are waxy, and greenish brown to dark brown in colour, and were probably deposited through fluviatile-lacustrine processes on the alluvial fans andfloodplains surrounding palaeolake Oldupai.

6.2.2 GEOLOCALITY 44A, "CASTLE" (1.74 MA)

The archaeological excavations in Lower Bed II took place in 1959-60, to the north-eastern side of the Castle Clays (Geolocality 44b) by Mary Leakey. Also, there is HWK East site, that likely formed the same time as the Castle Clays. HWK East is a gully beginning at the saddle and running mainly eastwards for at least 0.4 kilometers, then northwards to drain into the Main Gorge (Hay, 1976); the excavations in Lower Bed II and the lower part of Middle Bed II were carried out in 1962-63. In the whole of the HWK area the Upper of Bed I is represented only by the upper series of deposits that we do not have enough geological and sedimentary environmental data since the 'Castle' is made of red sediments belonging to Bed III, and the underlying basalt rises in irregular hummocks to within 20 feet (6 0 metre) of Tuff IF (Hay, 1976). Nearby the HWK Sites, there are HWK gullies that lie to the south of the confluence of the Main and Side Gorges. Some archaeological sites here were first located in 1931. They originate from a saddle connecting two pinnacles capped with Beds III and IV, which are known as the 'Castle' and the 'Tower''. HWK Main or ''Castle'' is a long, narrow gully running northwards from the saddle down to the floor of the Gorge; and are comprised mostly of Bed II sedimentary environments.

The "Castle" is the most famous tourist attraction and probably the most beautiful natural feature in the Gorge, seen just about 100 metres from the Oldupai Museum.From this locality, a sum of (n=14) were collected systematically (site specific sampling), from two packages separated by a at least 10 cm carbonate horizon in the tuffaceous clays above Tuff IIA; four samples came from above the carbonate horizon, nine from below the horizon, and one sample from underneath Tuff IIA (Table 6-5). The Tuff IIA is about 30 cm thick at the Castle, and sample 14 was collected 2.0 cm below Tuff IIA, or roughly 32 cm below the top of Tuff IIA) (Fig. 6-4). Sample dimensions

Sample	Depth (cm)	Amount (g)	Package	
		below LAS		
14	0-5	38.3		
13	10-13	40.7	Upper	Carbonate Horizon
12	17-21	40.1		
11	25-28	39.6		
10	40-46	42.5	Lower	Tuff IIA
09	55-61	44.4		
08	75-79	30.4		
07	93-96	37.4		
06	104-110	40.0		
05	124-133	40.0		
04	147-149	41.1		
03	163-167	22.1		
02	181-186	32.4		
01	226-235	34.0	Below IIA	

Table 6-5: Geolocality 44a, "Castle" Clays, height above Tuff II

were uneven, averaged width of 7.9 cm (max: 12; min: 4) and height of 4.8 cm (max: 9; min: 2). We processed 14 samples for phytolith analyses.



Figure 6-4: FLK-W site stratigraphy and sampling locations at Geolocality 44a "Castle" Clays (Source: Modified from Patalano, 2019).

6.2.3 FRIDA LEAKEY KORONGO WEST (1.69 MA)

The FLK-W site is found in lowermost Bed II at Oldupai Gorge and it is located in a fluvial palaeochannel embedded in the clay unit that forms the base of Bed II (Díez-Martín et al., 2015; Yravedra et al., 2017); and it is comprised of an ancient river channel and it is approximately 40 metres in width, with 1.2 metres of maximum depth and it is infilled with a sequence of six stratigraphic levels; and each one corresponds with a flood event, which resulted in a fluvial deposit (Díez-Martín et al., 2015; Uribelarrea, et al., 2017; Yravedra et al., 2017). This palaeochannel flowed North-South, from the Lemagrut mountain slopes to the central part of the Oldupai palaeo-lake. With a lensed and symmetric shape, the deepest part of the channel is about 20m wide and her both margins are shallow. Its complete sedimentary sequence is fining upwards, according with the typical infilling of a fluvial channel the lowermost level (Díez-Martín et al., 2015), which is level 6, is a 20-centimetre-thick matrix-supported conglomerate, composed of blocks, cobbles and gravels (150 millimetre of maximum diameter), and a matrix of coarser sands (Díez-Martín et al., 2015). Most of the cobbles are basaltic in nature. Although it is a bedload unit, no flow structures, such as cross-bedding or imbricated cobbles that have been found (Díez-Martín et al., 2015; Uribelarrea et al., 2017; Yravedra et al., 2017).

According to Díez-Martín et al., (2015), the lowermost levels of FLK-W such as Level 5 and Level 6 are denser and are archaeologically important in terms of their abundance of stone tools (Díez-Martín et al., 2015; Yravedra et al., 2017). The more detailed stratigraphic analysis by Uribelarrea, et al., (2017) shows that FLK-W and HWK sites were part of the same palaeolandscape, found along the same fluvial system, which changes pattern in the last 1.5 kilometre of its course. The Upper levels at the nearby contemporaneous site of HWK suggests that these sites would have been deposited in sandy and conglomeratic braided shallow channels, whereas downstream, at FLK-W, they would have converged into at least one sinuous channel, deeper and narrower over a clayey and silty floodplain (Uribelarrea, et al., 2017). A geomorphological reconstruction by Uribelarrea, et al., (2017) has shown that the HWK sites and FLK-W both were deposited in sedimentary environments with significant ecological differences. FLK-W would have better access to hydric ecologies and would probably offer a denser vegetation cover and other resources (Uribelarrea, et al., 2017). Moreover, the FLK-W site contains lakemargin clay. This is ~6m thick and its surrounding area and marker Tuff IF is in the middle of this clay unit. This tuff underlies the FLK-W site and it has been dated to 1.698± 0.015 Ma. The waxy clay that contains it is partially eroded by the FLK-W channel that is overlying the channel there is a 30-centimetre laminated tuff (FLK-Wb). This tuff has a greater lateral outcropping than FLK-W and has been dated to $1,664 \pm 0.019$ Ma (Yravedra et al., 2017). These chronological constraints situate FLK-W right above Tuff IIA, which was previously dated to c. 1.70 Ma (Uribelarrea, et al., 2017). However, among these sites, FLK-W constitutes the chronologically best-braked site, as the dates obtained (1.69 and 1.66 Ma) from tuffaceous sediments underlying and overlying the site are close in time, and the Acheulean materials are stratigraphically situated much closer to the lower tuff (Sanchez-Yustos 2017). The FLK-W site at Oldupai Gorge has recently provided evidence for the association of early Acheulean tools with carcass exploitation (Díez-Martín et al., 2015; Yravedra et al., 2017).

Recently, this site has demonstrated the existence of open landscapes during lower Bed II times at Oldupai Gorge. The open palaeohabitats have also been observed in the upper levels of Bed I at sites like the FLK-N and could have probably spread entirely area during Bed II times 142

(Vravedra et al., 2017). FLK-W, an excavation site dated between 1.698 ± 0.015 Ma and 1.664 ± 0.019 Ma, consisting of fluviatile conglomerates and sands (Díez-Martín et al., 2015) that contains



Figure 6-5: FLK-W site stratigraphy and sampling locations (Source: Modified from Patalano, 2019).
Table 6-6: FLK-W samples collected

Sample	Description	Height (cm)	Set
00001	Level 6: Conglomerate/Mafic Sands	0-2	Column
00002	Level 5: Base of Mafic Sands	4-6	Column
00003	Level 5c: Mafic Sands	10-12	Column
00004	Level 5: Mafic Sands	14-16	Column
00005	Level 5	20-22	Column
00006	Level 5: Mafic Sands	26-28	Column
00007	Level 5: Mafic Sands	32-34	Column
00008	Level 5: Mafic Sands	38-40	Column
00009	Level 5: Top - Contact w/ Level 4	44-46	Column
00010	Level 4: Bottom	50-52	Column
00011	Level 4: Contact w/ Dark 4	56-58	Column
00012	Level 4: Dark Sands	62-64	Column
00013	Level 4: Dark Sands	68-70	Column
00014	Level 3/4: Contact	74-76	Column
00015	Level 3: Silt	80-82	Column
00016	Level 3: Silt	86-88	Column
00017	Level 3: Silt/Level 2: Coarse Sand	92-94	Column
00018	Level 2: Coarse Sand	98-100	Column
00019	Level 2: Coarse Sand	104-106	Column
00020	Level 1/2: Base of Tuffaceous Sand	110-112	Column

00021	Level 1: Tuff Sand	116-118	Column
00022	Level 1: Tuff Sand	122-124	Column
00023	Level 1: Tuff Sand	128-130	Column
00024	Clays Above 1F	6-8 (-22-24)	Clays below Layer 6
00025	Clays Above 1F	12-14(-16-18)	Clays below Layer 6
00026	Clays Above 1F	18-20 (-10-12)	Clays below Layer 6
00027	Clays in Contact w/ FLK-W Lvl 6	(0-2)	Clays below Layer 6

Oldupai's earliest known Acheulean assemblage. More detailed archaeological work was done by Díez-Martín et al., (2015) who thoroughly described the six stratigraphic levels rich in archaeological occurrences as follows: Level 1 (L1), a homogeneous fine-grained sand and silt, overlaid by Tuff FLK-Wb; Level 2 (L2), an erosive unit of cut-and-fill up to 50 cm wide and 20 cm deep, which corresponds to small braided channels that reworked the previous fluvial deposit; Level 3 (L3), a 30 cm layer of massive clayish silt without flow structures; Level 4 (L4), a mediumgrained mafic (upper) and felsic (lower) sand and tuffaceous sand unit, increasing in thickness from 15 to 30 cm; Level 5 (L5), composed of three layers of coarse sand 20-30 cm thick, with cross bedding and horizontal lamination in the lower and western parts of sequence; and lastly Level 6 (L6) a 20 cm thick conglomerate composed of blocks, cobbles, and gravels within a matrix of coarser-sands (Fig. 6-5). The most significant Acheulean artifacts are contained in L5 and L6, where 26 large cutting tools (LCT), including classic bifacial handaxes, were uncovered. Both simple LCTs and the symmetrical and bifacially flaked handaxes co- exist in the lower level assemblage. A total of 28 samples were collected from the FLK- W for phytolith analyses (Table 6-6).

6.2.4 LOWER AUGITIC SANDSTONE (1.66 MA)

Leakey (1971) conducted a study at LAS that was the first one to reveal the presence of several archaeological levels, which contain Oldowan artifacts, in a level called "Sandy Conglomerate", present in levels 3, 4 and 5 in HWK and HWK-E sites. A few years later, Hay (1976) renamed this geological exposure "Sandy Conglomerate" as the LAS unit, and describes archaeological level 4 at HWK-E (Geolocality 43) as 1.20 metre of conglomeratic sandstone, part of the Lower Augitic Sandstone unit, and clearly in the same stratigraphic position as other archaeological levels found at geolocalities HWK-EE and HWK (Uriberralea et al., 2017). The Lower Augitic Sandstone (LAS) was deposited along the eastern fluvial lacustrine deposits (eastern lake-margin), all part of the same fluvial system, flowing towards the central lake towards the northwest, overlying plains progressively more clayey towards the inner part of the basin. All the channel is controlled by the base level in the graben between the FLK Fault and the Fifth Fault (Uribelarrea et al., 2017). The LAS is a sedimentary unit (Fig. 6-6) and is one of the highly unconsolidated geological exposure, a time interval that is made up of fluviatile system similar to FLK-W. Its sediments are mafic and augitic composed of at least 50-75% volcanic rock fragments of pyroclasryic nature (Uribelarrea et al., 2017). As it was mentioned earlier on, the LAS unit was deposited along the eastern margin of the palaeolake Oldupai as a braided stream channel flowing northwest towards the centre of the lake, and therefore converging into a single channel at the FLK West site (see Uribelarrea et al., 2017). Dated between 1.70-1.66 Ma in Bed II, the LAS palaeolandscape reconstructions by Uribelarrea et al., (2017, 2019) is represented by alluvial fans, possibly coalescent, with a bedload clearly trans

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ported from the volcanoes to the southeast and its



Figure 6-6: LAS sampling locations (Source: McHenry and Stanistreet, 2018; Modified from Patalano, 2019).

caused the reactivation and progradation of drainage networks to the Oldupai Basin which changed the nature of the sedimentation from lacustrine to fluvial. It is well understood that the faults in the rift system are associated with deep-seated springs, characterised by the temperature and salinity of the water, thus by the time of LAS deposition, volcanism was very active and was characterised by the deposition of rich phenelinites-foidite tuffs and volcanic ashes whose pyrolysis products can be identified in the LAS sediments to date. Oldowan artifacts are very abundant in every conglomerate channel, as well as flakes of brown chert (Hay, 1976; Uriberralea et al., 2019). Uribelarrea and colleagues' (2017) reconstructions of the LAS landscape show that the Oldowan occurrences at HWK sites are part of a proximal shallow braided stream system, whereas FLK-W occupies a more distal location towards the lake floodplain, in which the braided streams had coalesced into a wider channel system.

Sample	Geolocality	Amount	Latitude	Longitude
		(g)		
01	Lava Tongue Korongo	3.0	-2.9948	35.3520
02	Lava Tongue Korongo	3.0	-2.9944	35.3516
03	Playground	3.0	-2.9942	35.3511
04	Leakey's Road	3.0	-2.9919	35.3501

Table 6-7: Lower Augitic Sandstone samples

05	Maiko Gully	3.0	-2.9913	35.3499
06	Maiko Gully	3.0	-2.9912	35.3495
07	Maiko Gully	3.0	-2.9905	35.3496
08	FLK-NW	3.0	-2.9884	35.3471
09	HWK-E	3.0	-2.9943	35.3550
10	HWK-EE	3.0	-2.9950	35.3552
11a	Long Korongo	3.0	-2.9943	35.3653
11b	Long Korongo	3.0	-2.9943	35.3653
12	Long Korongo	3.0	-2.9966	35.3639
13	Long Korongo	3.0	-2.9952	35.3619
14	Side Gorge	3.0	-2.9937	35.3404
15	Side Gorge	3.0	-2.9937	35.3404

We sampled along the unconsolidated sedimentary unit between LAS palaeosuraface, which is exposed for roughly three kilometers in the main confluence of the Gorge and is stratigraphically related to the lower units of FLK-W. Sum of (n=15) sediment samples were collected in the unconsolidated sandstones that comprise the LAS for about 3 km from east-to western side and about 1.2 km north-west to south-east in the main confluence of the Gorge (Table 6-7). The aim of doing this is to track spatial-temporal changes across the fluviatile system and to compare with FLK-W L6 & L5 samples. The sandstone is either roughly consolidated or unconsolidated; most samples were collected as loose sands (1-4, 9-12), while the others were consolidated into singular units (5-8, 13-15). The unconsolidated samples were collected in a 6 cm

high, by 6 cm wide, and 4 cm deep arrangement (Maximum 12x9x8; and Min: 2x4x3), while consolidated samples were collected as sandstone blocks.

6.2.5 BIRD PRINT TUFF (1.60 MA)

The Bird Print Tuff (BPT) is one of the marker tuffs in the main Gorge which is located between localities 35 and 85 of Oldupai Gorge's Bed II, and it is found between Tuffs IIB and IIC (McHenry et al., 2005, 2008). It is locally preserved in the Junction, Side Gorge, and Lake Center. The dates for Bed II tuffs are less well established, varying, with the most recent published dates for Tuff IIA ranging from 1.60-1.74 Ma; McHenry and Stanistreet, 2018). The Bird Print Tuff and Tuff IID are the most widespread and easily identifiable Tuffs in Bed II of Oldupai Gorge, in upper Bed II, they have been dated using the 40Ar/39Ar Single Crystal Laser Fusion (SCLF) method by Manega (1993) to (1.48 \pm 0.05 Ma) and by Domínguez-Rodrigo et al., (2013; McHenry and Stanistreet, 2018), suggesting the age of 1.338 \pm 0.024 Ma), and inferred based on sedimentation rates at 1.35–1.4 Ma by McHenry et al. (2008); and again by McHenry and Stanistreet, (2018). Significantly, this tuff is currently being used in making the correlations between the eastern and western parts of the main Gorge (Hay, 1976; McHenry et al., 2008; 2016, McHenry and Stanistreet, 2018).

Recent geochemical research by McHenry and Stanistreet, (2018), noted that the middle sections of the BPT layers are compositionally more variable than previously reported but is still valuable as a stratigraphic marker over short distances. The geochemical type characterises the BPT upper part is a typical basaltic- glass and a narrow compositional range of high-Ca plagioclase (McHenry et al., 2016; McHenry and Stanistreet, 2018) which is also contains trachytic- textural sediments (Hay, 1976). However, unlike the Bird Print Tuff, Tuff IID is easily distinguished from Lower and Middle Bed II tuffs based on the presence of abundant hornblende, though distinguishing it from overlying hornblende-bearing tuffs relies on subtler compositional differences i.e. Titanium dioxide (TiO₂) concentrations in augite and hornblende minerals (McHenry and Stanistreet, 2018).

Research investigations on the he Middle Bed II has established a fingerprint for the Bird Print Tuff (BPT), which appears to be unique within the Oldupai sequence (McHenry and Stanistreet, 2018) because it is one of the most distinctive marker units that nowadays help in making correlation to western Oldupai Gorge's locality 80 (McHenry et al., 2016; McHenry and Stanistreet, 2018). Despite its distinctive appearance (thin, fine grained, weathering yellow, often resistant to weathering and occasionally exhibiting bird track imprints on its top surface), it is compositionally variable and distinctive, with a high-Ca plagioclase composition that helped to fingerprint the BPT between HWK W sites such as (Locality 44) and the FLK (Locality 45) (McHenry et al., 2016).

McHenry and Stanistreet, (2018), commented that the BPT tuff in the Western shores of the palaeolake area can be physically traced in the outcrop between HWK-W site at locality 45 and VEK at locality 85 where it retains its fine-grained, thin, yellow appearance. To the east of HWK-W locality 44 at HWK Castle, also the BPT can still be traced physically, whereas the sediments there yield a mixture of distinctively high-Ca plagioclase and other feldspars (McHenry and Stanistreet, 2018). Moving eastward, the high-Ca plagioclase component is lost entirely, while the tuff still maintains its distinctive appearance and again can be traced physically (McHenry and Stanistreet, 2018). Even at HWK-W site, the geochemical "type" section for this tuff designated in McHenry et al. (2016), as a high Ca plagioclase is restricted to the upper, fine, yellow portion of the tuff while the thicker, coarser, gray found in to the lower portion (McHenry and Stanistreet, 151 2018) which also contain feldspar more consistently with the rest of Lower and Middle Bed II. It has a more varied composition, including high-K anorthoclase and intermediate plagioclase while slightly to the west at VEK site (Locality 85), where there is a more varied feldspar composition which dominates the entire tuff, and the Ca-plagioclase is absent here, something which contrast it with the Locality 44 (McHenry and Stanistreet, 2018).

Samples for phytoliths analysis were collected in the waxy, silty clays that underline the BPT; (n=10) and major of the samples came from a 780-metre, north-west to south-east transect in the main confluence of the Gorge (Table 6-8). Only one sample came from the clays above Tuff FLK-Wb at FLK-W. Ordinarily, samples were collected in a 3.5 cm high, by 12 cm wide, and 6.45 cm deep arrangement (maximum: 5x21x11; minimum:2x7x3) and came from clays directly in contact with the BPT, or slightly below. The clays below the Bird Print Tuff were likely deposited within the lake-margin zone that connected the alluvial fans and streams draining the Crater highlands from the southeast with Oldupai palaeolake

Sample	Code	Geolocality	Amount (g)	Latitude & l	Longitude
01	BPT1	FLK-W	51.5	-2.9900	35.3484
02	BPT2	Maiko Gully	46.7	-2.9906	35.3493
03	BPT3	Maiko Gully	45.3	-2.9903	35.3492
04	BPT4	Maiko Gully	47.6	-2.9911	35.3495
05	BPT5	Maiko Gully	53.4	-2.9911	35.3500
06	BPT6	Maiko Gully	43.4	-2.9916	35.3497

Table 6-8: Bird Print Tuff samples

07	BPT7	Leakey's	40.0	-2.9920	35.3499
		Road			
08	BPT8	OGAP Mine	46.0	-2.9920	35.3513
09	BPT9	Lava Tongue	56.1	-2.9942	35.3521
		Korongo			
10	BPT10	Castle	51.8	-2.9948	35.3530
11	BPT11	HWK	47.8	-2.9951	35.3533

6.3 FIELD METHODS

Sampling for phytoliths was systematically conducted using both a site level (Fig. 6-7) and horizon approach. We sampled both horizontally (spatial) and vertically (temporal) in order to reconstruct the palaeovegetation at each of the six archeo-localities. Across the landscape, the sediment samples for phytoliths extraction were collected systematically at least 1-5 meters apart, and along the exposed palaeosols. We walked over 100 metres horizontally collecting sediment samples from the exposed palaeo-horizons. Before taking any samples, we cleaned the earth and cleared the litters by scrapping the whole area.

All the digging equipment were caustic soda cleaned, sterilised, and cleaned with alcohol after each single dig to avoid intra-samples contamination. Samples were placed for storage in clean sample bags. Sediments were also collected from trenches according to stratigraphic layering and features.



Figure 6-7: Column sampling strategy at FLK-W site

6.4 Laboratory Methods

From a methodological perspective, the research methods applied in this study were significant in answering key research questions pertinent to phytolith extractions from volcanic, lacustrine, clay, sandstone, and fluviatile ancient sediments. Sample processing took place at the Tropical Archaeology Laboratory (Earth Science 811, Department of Anthropology and Archaeology, University of Calgary. Mercader's (2018) sediment-extraction protocol was followed: samples were sieved and weighed, and 10ml of sodium hexametaphosphate (NaPO₃)₆ solution (0.1%) was added to each sample to promote clay dispersion, followed by the addition of 10ml of each 3N hydrochloric acid (HCl) and 3N nitric acid (HNO₃) for removal of inorganics, 10ml hydrogen peroxide (H₂O₂, 30%) for removal of organics, finally using 2.4 s.g. sodium polytungstate (SPT) for heavy liquid separation.

Processing was followed by microscopy: samples were mounted on slides using *Entellan New*[®] and counted under 40x magnification using a Motic BA310E microscope. Counts were completed within 24 hours after mounting the slide to ensure that phytoliths could be rotated to confirm 3D shape. Photographs were taken using a Moticam 5+ (Motic Images Plus 3.0) for every phytolith encountered in both 2- and 3D; more than 50,000 images were obtained. Naming and grouping phytoliths was done according to their classes, following descriptors from ICPN 1.0 (Madella, 2002; 2003) with minor modifications according to Mercader et al. (2009, 2010, 2019). For cases of those phytoliths with undiagnostic shapes, multiple photos were taken, along with hand illustrations, which were used for comparisons with other morphotypes published elsewhere (Madella et al., 2005), or to be compared with other types that are known to be occurring at the nearby localities or similar ecoregions (Mercader et al., 2019).

The methodological issues surrounding counting to obtain valid ecological interpretations has been controversial at times in African palaeoethnobotany (Albert et al., 2006; Barboni et al., 2010; Stromberg, 2008; Mercader et al., 2009, 2012, 2019). Some authors count a minimum of 200 consistent types (e.g. Albert et al., 2006, 2009), while others count up to 200 Poaceae short cell types regardless of how many phytoliths of other categories may be present (e.g. Stromberg, 2008) resulting in much higher overall counts often times in excess of 500 total phytoliths. The 155 latter system was followed in this study due to the varied nature of sediments, environmental composition, varied nature of deposition, chronology, and age of sediments. Additionally, higher overall counts were considered beneficial for these assemblages in order to obtain reliable, reproducible results for ancient plant reconstruction, and in order to attain representativeness between sites. A minimum of 300 phytoliths were counted whenever the sample was not very rich in phytoliths content. Previous results (e.g. Albert and Weiner, 2001) indicate that the counting of only 50 phytoliths with diagnostic morphologies gives an error margin of 40%, whereas the counting of 200 diagnostic phytoliths gives an error margin of around 20%. Siliceous fragments were not counted, but any presence of diatoms, spores, zeolite and raphide crystals was recorded. Phytolith taxonomic identification, which is not straightforward, was tentatively carried out by comparison with published photographs and descriptions (Runge, 1999; Ball et al., 2002, 2016; Strömberg, 2003, 2004; Piperno, 2006; Albert et al., 2006, 2015, Barboni et al., 2010; Collura and Neumann, 2017; Neumann, et al., 2018; Novello et al., 2018; Mercader et al., 2009, 2018), crosschecking with the already established referential baselines, and some personal experience with modern soil phytolith data from the region, and again with the comparison with the modern plant datasets from Arusha ecoregion prepared by Dr. Mercader and his "Stone Tools, Diet, and Sociality" project from 2015-2019 (Mercader et al., 2019).

6.4.1 NOMENCLATURE

The ICPN 1.0, (Madella et al., 2004, Piperno, 2006; Mercader et al., 2019) was followed to standardise nomenclature. To make more specific environmental inferences, comparisons to previous research in tropical Africa that had shown to provide the strongest basis for palaeovegetation structure reconstruction were made (Albert et al., 2005; Barboni et al., 2007; Mercader et al., 2011) and minor modifications by Mercader et al. (2011, 2019) to name and describe phytoliths. In most cases, this dissertation adhered to the geographically pertinent reference collections prepared by Mercader et al. (2010, 2019) for the ancient sediment versus modern soil and pant phytolith assemblages, while cross-checking other ones (i.e. Fahmy 2008; Eichorn et al., 2010; Albert et al., 2006, 2015; Bamford et al., 2006; Barboni and Bremond, 2009; Collura and Neumann, 2017; Neumann et al., 2017; Mercader et al., 2009, 2010, 2019).

Phytolith assemblages were classified into four large groups: Woody, Grass Short Cells, Undetermined/Irregular, and Rare/Unique, with 66 classes encompassing 63 discrete phytolith types. The woody group comprised of blocky (Collura and Neumann, 2017; Mercader et al., 2009; Novello et al., 2012), globular (Mercader et al., 2009; Runge 1999), tabular (Collura and Neumann, 2017; Mercader et al., 2009,2010, 2019), cylindrical (Mercader et al., 2009, 2019), clavate (Mercader et al., 2009, 2019), and sclereid (Collura and Neumann, 2017) classes. Phytoliths from short cells were subdivided in three classes: bilobate (Fahmy 2008; Neumann et al., 2017), rondels (Mercader et al., 2010, 2019; Neumann et al., 2017; Novello et al., 2012), and saddles (Mercader et al., 2010, 2019; Twiss et al., 1969). Several additional classes comprised undetermined/irregular, and the rare/unique morphotypes.

6.5 STATISTICAL ANALYSIS

For the distribution between the commonly known arboreal taxa, and ability to see how they compare with short cell grass phytolith proportions, descriptive statistics were used to examine whether redundant forms could be categorised into specific subfamilies. Although Madella et al.'s (2005) International Code for Phytolith Nomenclature was used whenever necessary, other commonly used descriptive terminologies such as (blocky, globular types, and tabular types) were found to simplify the classification schema that facilitated statistical analyses. The classification nomenclature was also broken down further depending on the 2D or 3D visualisation of phytolith shapes.

The effects of site-specific variability on the phytolith record was further examined using multivariate statistical analyses such as Normality Tests, Kruskal-Wallis Test, Correspondence Analysis (CA), and Cluster Analysis. The CA helped to infer phytolith distribution patterns and representation across the landscape and intra site variability and relatedness in order to answer key research questions. For the normality tests, Shapiro-Wilk test was employed to compare the scores in the sample to a normally distributed set of scores with the same mean and standard deviation; the null hypothesis is that "sample distribution is normal." For small sample sizes, normality tests have little power to reject the null hypothesis, and therefore, small samples most often pass normality tests (Thode, 2002). For large sample sizes, significant results would be derived even in the case of a small deviation from normality, although this small deviation will not affect the results of a parametric test. Some researchers recommend the Shapiro-Wilk test as the best choice for testing the normality of data (see Thode, 2002, Steinskog, 2007). The Shapiro–Wilk test is more appropriate method for small sample sizes (<50 samples) although it can also be handling on larger sample (Steinskog, 2007).

The Kruskal-Wallis Test was employed in this study, this is a nonparametric (distribution free) test, and is used when the assumptions of one-way ANOVA are not met. The Kruskal-Wallis test assess for significant differences on a continuous dependent variable by a categorical independent variable (with two or more groups). However, when using the Kruskal-Wallis Test, no assumptions should be made. Also, the Kruskal-Wallis test used for both continuous and 158

ordinal-level dependent variables. However, like most non-parametric tests, the Kruskal-Wallis Test is not as powerful as the ANOVA.

Correspondence analysis (CA) is yet another ordination method, somewhat like Principal Component Analysis (PCA) but for counted data (see Legendre and Legendre 1998). For comparing associations (columns) containing counts of taxa, or counted taxa (rows) across associations, CA is the more appropriate algorithm. Also, CA is more suitable if species are expected to have unimodal responses to the underlying parameters, that is they favour a certain range of the parameter, becoming rare for lower and higher values (this contrasts with PCA, which assumes a linear response). The CA routine finds the eigenvalues and eigenvectors of a matrix containing the Chi-squared distances between all rows (or columns, if that is more efficient – the result is the same). The algorithm follows Greenacre (2010), with SVD. The eigenvalue, giving a measure of the similarity accounted for by the corresponding eigenvector, is given for each eigenvector. The percentages of similarity accounted for by these components are also given. The scatter plot allows a reader to see all the data points (rows) plotted in the coordinate system given by the CA. If the rows are grouped, the different groups can be shown using separate convex hulls and concentration ellipses. In addition, the variables (columns, associations) can be plotted in the same coordinate system (Q mode), optionally including the column labels. If the data are well behaving, taxa typical for an association should plot in the vicinity of that association (see Legendre and Legendre 1998).

CA was run on the full data set to determine the consistency and robustness of the phytolith morphotype signal between sites, through site by site according to age in order to test and explore important diachronic patterns in ecological change. Also, Cluster Analysis was conducted in order to see the diachronic evolution of plant landscape through phytolith analysis, by comparing 159 results from each site studied. Cluster Analysis is a multivariate method which aims to classify a sample of subjects (or objects) based on a set of measured variables into a number of different groups such that similar subjects are placed in the same group (see Rencher, 2002). The hierarchical clustering routine produces a 'dendrogram' showing how data points (rows) can be clustered (see Rencher, 2002). CA was run using Ward's method as one of the agglomerative clustering methods that is based on a classical sum-of-squares criterion, producing groups that minimise within-group dispersion at each binary fusion. In addition, Ward's method was applied in order to look for clusters in multivariate Euclidean space. This is a minimum variance method which is related to the centroid methods in that it also leads to a geometric representation in which cluster centroids play an important role. To form clusters, the method minimises an objective function which is, in this case, the same "squared error" criterion as that used in multivariate analysis of variance (Rencher, 2002).

CHAPTER 7: ENVIRONMENTAL RECONSTRUCTION AT OLDUPAI GORGE 1.83-1.60 Ma, A Phytolith Perspective

The descriptive statistical analysis illustrates the phytolith results from Oldupai's samples for each studied site whereby a total of 17,624 phytoliths were counted (Table 7.1). The phytolith assemblages are also presented as bar graphs, which show occurrence frequency and percentage of the identified morphotypes among samples. In this chapter, the phytolith assemblage results are presented following sites age (from older to younger), site by site to detect the site-specific variability in phytolith types, distribution, and abundance.

Phytolith taxonomy: code, name, descriptors, and their respective figures in the assemblage			
Number	Morphotype	Source	Descriptors
1	Bilobate-concave- short (outer margin)	Fahmy, 2005: 15	Bilobate with caved lobes connected with short shank <20µm.
2	Bilobate-convex- short (outer margin)	Runge, 1999; Mercader et. al., 2009:94, 2019	Bilobate with rounded lobes connected with a short shank. <20µm.
3	Blocky	Mercader et. al.2009, 2019; Novello et. al., 2012, 2017; Collura & Neumann, 2017	Block with lacunose/slightly scrobiculate texture

Table 7-1: Phytolith morphotypes used in this study

4	Blocky cavate	Runge, 1999; Mercader et. al., 2010, 2019	Block with granular texture and centric depression
5	Blocky dendriform	Collura and Neumann, 2017:230	Block with dendrite processes
6	Blocky facetate	Albert, 1999; Madella et al., 2005; Albert et.al., 2009	Faceted, psilate block
7	Blocky lacunate	Neuman et. al., 2009; Mercader et. al., 2019	Block with scrobiculate/lacunose texture
8	Blocky hairy	Mercader et. al., 2009:94	Polygonal or irregular block with irregular/scrobiculate texture; long pointed projections
9	Blocky ridged	Mercader et. al., 2019	Block with surface covered by ridges
10	Blocky pilate	Neumann et. el., 2009, 2019	Polygonal or irregular block with scrobiculate texture and projections that have straight or slightly curved ends
11	Blocky polygonal	Novello et.al., 2012; 2018	Polygonal/irregular block with a psilate/scrobiculate texture

12	Blocky radiating	Mercader et. al.,	Block with a surface covered by
		2009:94	concentric layers
13	Blocky sulcate	Mercader et. al., 2019	Block decorated body marked with
			parallel grooves
14	Blocky tuberculate	Mercader et. al.,	Irregular block with
		2009:94	lacunose/scrobiculate/tuberculate
			texture
15	Bulliform	Madella et.	Fan- shaped cells
		al.,2005:259; Piperno,	
		2006: 74	
16	Clavate	Mercader et.al., 2019	Club-shaped body with granular
			texture
17	Cylindroid	Mercader et. al,	Cylindroid mostly with a psilate
		2009:94	texture
18	Cylindroid granulate	Mercader et. al,	Cylindroid mostly with a granular
		2009:94	texture
19	Cylindroid crenate	Mercader et. al,	Cylindroid with scalloped edges
		2009:94	
20	Cylindroid	Mercader et. al,	Large cylindroid with scrobiculate
	scrobiculate	2009:94	texture
21	Elongate orthogonal	Mercader et. al,	Elongate, irregular shape
		2010:1956;	

22	Epidermal cell tissue	Mercader et. al., 2010,	Epidermal polygonal cells. Variable
		2019	textures
23	Large globular	Mercader et. al., 2019,	Large spheroid with granular
		This study	texture
24	Globular crenate	Bhat et al., 2018:17	Spiky-irregular prjections around
			the edge 6-10µm.
25	Globular echinate	Albert et al., 2009;	Spheroid, pricks, spiky star,
		Bremond et al., 2008;	spheroid/globular echinate
		Barboni & Bremond,	
		2009; Novello et al.,	
		2017.	
26	Globular granulate	Mercader et.al., 2010,	Globular, with granular surface
		2019; Albert, 1999;	
		Madella et. al., 2005	
27	Globular psilate	Barboni et. al., 1999;	Globular, smooth/sub-smooth
		2007; Bamford et. al.,	surface.
		2006	
28	Globular tuberculate	Barboni et. al., 1999;	Globular with irregular projections
		2007; Bamford et. al.,	
		2006; Ashley et. al.,	
		2010	
29	Globulose	Mercader et. al., 2019	Ovate with granular texture

30	Guttiform	Mercader et. al., 2019	See cited source
31	Hair base	Mercader et.al., 2010,	Silicified mesophyll cells with
		2019	radial outline, stomatal complex,
			hairs and hair bases
32	Hair articulated	Mercader et.al., 2019	Silicified elongated outgrowths
			from mesophyll
33	Hemisphere	Mercader et.al.,	See cited source
		2010	
34	Irregular	This study	Irregular body with rugose texture
	indeterminate		
35	Irregular ridged	This study	Orthogonal, irregular
			undifferentiated body
36	Irregular striated	This study	Blocky or tabular body with parallel
			striations
37	Mesophyll cells	Mercader et. al., 2019	See cited source
38	Oblong	Mercader et. al., 2019	See cited source
39	Oblong granulate	Madella et. al.,	Longer than broad and with nearly
		2005:259; Mercader	parallel side
		et. al., 2009, 2019	
40	Orthogonal	Mercader et. al., 2000;	See cited source
		Eichhorn et.al., 2010	

41	Ovate granulate	Mercader et. al., 2010; 2019	Sub-tabular, orbicular to ovate
42	Perforated plate	Mercader et. al., 2019	See cited source
43	Rondel	Stromberg 2003;	See cited source
		Barboni and Bremond,	
		2009; Mercader et al.,	
		2010	
44	Rondel horned	Stromberg, 2003;	Conical, tall body in which the apex
		Rossouw, 2009;	ends in one
		Mercader et. al., 2010;	
		Kinyanjui, 2013	
45	Rondel tower	Stromberg, 2003;	Conical, tall body with tapering/flat
		Rossouw, 2009;	apex
		Mercader et. al., 2010;	
		Kinyanjui, 2017:36	
46	Rondel wide	Collura and Neumann,	Conical, tall body with tapering/flat
		2017:230	apex; its base
47	Saddle	Twiss et. al., 1969;	Grass short silica cell with two
		Mercader et. al., 2010	opposite convex edges and two
			straight or concave edges
48	Saddle long	Mercader et. al.,	Saddles with long convex edges.
		2010:1956, 2019.	

49	Saddle short	Barboni et. al., 2010, Mercader et. al., 2019.	See cited source
50	Saddle squat	Collura and Neumann, 2017:230	Saddle with side notches and a much longer
51	Sclereid	Collura and Neumann, 2017:230	Tracheary elements and other related silicified cells (Stromberg, 2003)
52	Scutiform	Madella et. al., 2005:259; Mercader et. al., 2010	See cited source
53	Tabular cavate	Mercader et. al., 2019	See cited source
54	Tabular crenate	Mercader et. al., 2019	Tabular body with granular texture and scalloped edges
55	Tabular dendriform	Mercader et. al., 2010; 2011	Large elongate parallelepiped with psilate
56	Tabular elongate	Mercader et. al., 2011: 144; Neumann et. al., 2009, Novello et. al., 2018	Elongate
57	Tabular oblong radiating	Collura and Neumann, 2017:230	Large tabular body with orbicular, ovate or oblong outline and granular texture

58	Tabular pilate	Albert, 1999; Madella	Polygonal or irregular body
		et. al., 2005; Albert et.	with scrobiculate texture and
		al., 2009	projections that have straight or
			slightly curved ends
59	Tabular	Neumann et. al., 2009,	Variably wide parallelepiped with an
	scrocubiculate	Novello et. al., 2018	elongate outline and scrobiculate
			texture
60	Tabular sinuate	Neumann et. al., 2009,	Body with one or two sides are
		Mercader et. al.,	sinuate
		2009:95; Novello et.	
		al., 2019	
61	Tabular sulcate	Mercader et. al., 2019	See cited source
62	Tabular thick	Mercader et. al., 2010	Thick parallelepiped with a
			contorted profile and irregular to
			laminate texture
63	Vessel	Mercader et. al., 2011,	Tabular, sub-
		2019	polygonal body covered with layers

7.1 FLK-N HORIZON

From the 30 samples analysed, a total of 3,621 phytoliths were counted, representing 35 distinct morphotypes (Table 7-2) (Figs. 7-1 and 7-2). Almost all of the phytolith presence

documented in the sediment samples for FLK-N horizon are accounted for by a subset of nine morphotypes (n = 2781, approx. 88.8%) (Table 7-3).

Phytolith morphotype	Count	%
1. Blocky sulcate	824	22.57
2. Mesophyll cells	487	13.34
3. Irregular indeterminate	461	12.63
4. Hair base	445	12.19
5. Blocky hairy	230	6.30
6. Globular granulate	225	6.16
7. Hair articulated	213	5.83
8. Tabular srobiculate	184	5.04
9. Blocky ridged	173	4.74
10. Cylindroid crenate	80	2.19
11. Globular echinate	44	1.21
12. Elongate orthogonal	43	1.18
13. Rondel	43	1.18
14. Tabular elongate	30	0.82
15. Cylindroid	26	0.71
16. Tabular elongate	14	0.38
17. Blocky facetate	13	0.36

Table 7-2: Phytolith morphotypes at FLK-N horizon

18. Blocky lacunate	13	0.36
19. Ovate granulate	13	0.36
20. Bulliform	12	0.33
21. Blocky	9	0.25
22. Globulose	9	0.25
23. Globular tuberculate	8	0.22
24. Tabular sinuate	8	0.22
25. Cylindroid scrobiculate	6	0.16
26. Oblong granulate	6	0.16
27. Clavate	5	0.14
28. Globular psilate	5	0.14
29. Oblong	5	0.14
30. Saddle	4	0.11
31. Sclereid	4	0.11
32. Scutiform	3	0.08
33. Bilobate concave	2	0.05
34. Bilobate convex	2	0.05
35. Guttiform	2	0.05
Total:	3651	100



Figure 7-1: FLK-N horizon selected key phytolith morphotype



Figure 7-2: FLK-N horizon phytolith counts and morphotypes encountered per sample

Table 7-3: FLK-N horizor	n descriptive	statistics
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Attribute	Total	%
N	35	35
Min	2	0.05
Max	824	22.57
Sum	3651	100.01
Mean	104.3143	2.857429
Std. error	31.40232	0.860149
Variance	34513.69	25.89498
Stand. dev	185.7786	5.088711
Median	13	0.36
25 percentile	5	0.14
75 percentile	173	4.74
Skewness	2.430382	2.430418
Kurtosis	6.200773	6.200587
Geom. mean	23.03804	0.627162
Coeff. var	178.0951	178.0871

7.1.1 Common Morphotypes

The 88.8% variability at the FLK- N horizon documented here is accounted for by a subset of phytoliths comprising nine morphotypes. In order of frequency these are as follows: Blocky sulcate (n=824, 22.57%); Mesophyll cells (n=487, 13.34%); Irregular indeterminate (n=461, 12.63%); Hair base (n=445, 12.19%); Blocky hairy (n=230, 6.30%); Globular granulate (n=225, 6.16%); Hair articulated (n=213, 5.83%); Tabular scrobiculate (n=184, 5.04%), and; Blocky ridged (n=173, 4.74%).

7.1.2 INFREQUENT AND RARE MORPHOTYPES

The remaining 21.2% of the assemblage contributed below the average, and occasionally less significantly to the total FLK-N horizon assemblage. These are less common and rare morphotypes which include: Cylindroid crenate (n=80, 2.19%), while below average, this morphotype was relatively well represented across all 30 samples; Globular echinate (n= 44, 1.21%); Elongate orthogonal (n=43, 1.18%); Rondel (n=43, 1.18%), was relatively well distributed among the short cells morphotype; Tabular cavate (n=3 0, 0.82%); Cylindroid (n26, 0.71%); Tabular elongate, with striated body (n=14, 0.38%); Blocky facetate (n=13, 0.36%); Blocky lacunate (n=13, 0.36); Ovate granulate (n=13, 0.36%); Bulliform (n=12, 0.33).; Blocky (n=9, 0.25%); Globular tuberculate (n=8, 0.22%); Tabular sinuate (n=8, 0.22%); Cylindroid scrobiculate (n=6, 0.16%); Oblong granulate (n=6, 0.16%); Clavate (n=5, 0.14%); Globular psilate (n=5, 0.14%); Oblong (n=5, 0.14%); Saddle (n=4, 0.11%,); Sclereid (n=4, 0.11%); Scutiform (n=2, 0.05%).

7.1.3 DIACHRONIC PATTERNS

The key morphotypes to infer ecological context of palaeovegetation patterns at FLK-N horizon as per the reference datasets and supporting bibliography from region include: Globular granulates from dicot trees and shrubs (Runge, 1999; Neumann et al., 2009; Mercader et al., 2009, 2010, 2019). Other arboreal indicators are the blocky type (Mercader et al., 2019) globular psilate 174

(Mercader et al., 2010), tabular sinuate with heavily decorated surfaces (Mercader et al., 2009), sclereids, clavate granulates, globular echinates from palms (Albert et al., 2009; Barboni et al., 2010; Collura and Neumann, 2017; Mercader et al., 2019), bilobates (Bremond et al., 2005, 2008; Barboni and Bremond, 2009; Mercader et al., 2010; Novello et al., 2012), long saddles from wet-adapted bambusoids (Piperno and Pearsall, 1998), rondel wide and tower, as well as short saddles (Fig. 7-3). All (n =30) samples from 0-2 km distance suggest that phytolith data are abundant, representing woody plants such as trees and/or shrubs, and palms with little to no grasses but probably some sedges, in the landscape across FLK-N upper Bed I time (~1.83 Ma). Age zone level 0-400, the FLK-N sample #06 (level 400-800 m) and sample #30 (level 1600-2000 m), yield 10-15% of globular echinate phytoliths which are indicators of palm tree environments (Fig. 7-4).



Figure 7-3: FLK-N horizon wetland adapted taxon indicators



Figure 7-4: FLK-N horizon morphotype percentages per sample

Age zone level 0-400: Samples #02 and #03 are poor phytolith producers, however, the majority of the samples counted yielded a relatively large quantity of morphotypes which indicate an increase in arboreal trends, similar to patterns in age level 800-1200 m across the landscape

(blocky, tabular, globular granulate, globular tuberculate, globular psilate, sclereid, and clavate granulate) morphotypes together form approximately 80% or more at certain intervals.

Age zone level 1200-1600: there is a slight decline in arboreal cover, but it peaks again at 2000 m. The highest arboreal representation comes from samples collected between 1600-2000 m, whereas grass short cells recorded low at these horizons. Within the GSSCs category, rondels both wide and tower, records higher while bilobates and saddles both has relatively lower abundances $\leq 25\%$ and almost the pattern is similar in all samples from levels 400-800 m, the rondels types dominate the GSSCs (n =43) thus make $\geq 70\%$ of the grassy types.

AERIAL SAMPLING AT FLK-N 1.83 MA		ZONE (LEVEL 0-2 KM)				
КЕҮ ТҮРЕ	Plant Category	0-400	400-800	800-1200	1200-1600	1600-2000
BILOBATE CONVEX/CONCAVE	Grassy	1	0	2	1	0
CLAVATE GRANULATE	Woody dicot	1	1	2	2	0
GLOBULAR	Woody dicot	430	254	292	113	432
GRANULATE/PSILATE/TUBERCULATE,						
BLOCKY, TABULAR						
GLOBULAR ECHINATE	Palms	0	27	0	0	17
RONDEL WIDE/TOWER/HORNED	Grassy	4	5	34	0	0
SADDLE SHORT/LONG/SQUAT	Grassy	1	1	3	0	0
SCLEREID	Woody	0	3	3	0	0

Table 7-4: Phytolith types used for classification at FLK-N horizon

7.2 FLK-N SITE

From the 23 samples collected, a sum of 2,762 phytoliths were counted, representing 36 morphotypes from the FLK-N site (Table 7.5) (Figs. 7-5 and 7-6). More than half of the variability documented from the FLK-N site samples is accounted for by a subset of seven morphotypes that, in a typical assemblage, may occur at levels twice the average or higher (Table 7-6). The key variability is represented by seven morphotypes (n =2047, approx. 74%) of the total phytoliths assemblage at this site, which are also the prominent contributors.

Phytolith		Count	%
morphotype			
1. Tabular	491		17.77
scrobiculate			
2. Blocky	429		15.53
sulcate			
3. Blocky	364		13.17
ridged			
4. Globular	218		7.89
granulate			
5. Blocky	199		7.20
hairy			

Table 7-5: Phytolith morphotypes at FLK-N site

6. Tabular	186	6.73
elongate		
7. Tabular	160	5.79
sulcate		
8. Irregular	108	3.91
indeterminate		
9. Oblong	82	2.96
granulate		
10. Blocky	76	2.75
11. Globular	59	2.13
tuberculate		
12. Globulose	52	1.88
13. Elongate	48	1.73
orthogonal		
14. Blocky	41	1.48
facetate		
15. Blocky	36	1.30
tuberculated		
16. Globular	32	1.15
psilate		
	I	
17. Sclereid	28	1.01
---------------	----	------
18. Tabular	26	0.94
sinuate		
19. Hair base	22	0.79
20. Tabular	22	0.79
cavate		
21. Ovate	14	0.50
granulate		
22.	12	0.43
Orthogonal		
23. Large	10	0.36
globular		
24. Clavate	10	0.36
25. Mesophyll	7	0.25
cells		
26. Blocky	6	0.21
cavate		
27. Bulliform	4	0.14
28. Globular	4	0.14
echinate		

29. Epidermal	3	0.10
cell tissues		
30. Scutiform	3	0.10
31. Blocky	2	0.07
polygonal		
32. Tabular	2	0.07
dendriform		
33.	2	0.07
Cylindroid		
34. Blocky	2	0.07
dendriform		
35. Blocky	1	0.03
radiating		
36. Saddle	1	0.03
short		
Total:	2762	100



Figure 7-5: FLK-N site selected key phytolith morphotypes



Figure 7-6: FLK-N site phytolith counts and morphotypes encountered per sample

Table 7-6: FLK-N site descriptive statistics

Attribute	Total	%
N	24	24
Min	1	0.07
Max	434	28.78
Sum	1508	99.99
Mean	62.83333	4.16625
Std. error	20.60407	1.366387
Variance	10188.67	44.80835
Stand. dev	100.9389	6.693904
Median	19	1.26
25 percentile	5.5	0.3625
75 percentile	69	4.575
Skewness	2.552931	2.55288
Kurtosis	7.404453	7.40354
Geom. mean	19.03198	1.265181
Coeff. var	160.6455	160.6698

7.2.1 Common Morphotypes

The key contributors of the 74% variability of the total FLK-N site assemblage, from higher to lower rank, are: Tabular scrobiculate (n=491, 17.70%); Blocky sulcate (n=429, 15.50%);

Blocky ridged (n=364, 13.10%); Globular granulate (n=218, 7.90%); Blocky hairy (n=199, 7.20%); Tabular elongate (n=186, 6.70%), and; Tabular sulcate (n=160, 6.50%).

7.2.2 INFREQUENT AND RARE MORPHOTYPES

The morphotypes that yielded less phytolith below average were grouped as infrequent and rare morphotypes and contributed < 24% of the total phytolith assemblage (see Table 11a and b, Fig. 12-13). These are: Irregular indeterminate (n=108, 3.9%); Oblong granulate (n = 82, 2.9%); Blocky (n=76, 2.7%); Globular tuberculate (n=59, 2.1%); Globulose (n= 52, 1.8%); Elongate orthogonal (n=48, 1.7%); Blocky facetate (n=41, 1.4%); Blocky tuberculated (n=36,1.3%); Globular psilate (n=32, 1.1%); Sclereid (n=28, 1%); Tabular sinuate(n=26, 0.9%); Hair base (n=22, 0.73%); Tabular cavate (n=22, 0.73%); Ovate granulate (n=14, 0.5); Orthogonal (n=12, 0.4%); Large globular (n=10, 0.3%); Clavate (n=10, 0.3%); Mesophyll cells (n=7, 0.2%); Blocky cavate (n=6, 0.2%); Bulliform (4=0.14%); Globular echinate (n=4, 0.14%); Epidermal cell tissues (3 0.1%); Scutiform (n=3, 0.1%); Blocky dendriform (n=2, 0.07%); Tabular dendriform (n=2, 0.07%); Cylindroid (n=2, 0.07%); Blocky dendriform (n=2, 0.07%); Blocky radiating (n=1, 0.03%), and; Saddle short (n=1, 0.03%).

7.2.3 DIACHRONIC PATTERNS

Figure 7-7 shows the diachronic patterns for FLK-N site. Eight samples are from levels 1-3 (0-40 cm) below Tuff IF, of which four samples 9-12 come from at the sediment between and underneath Tuff IF: from bottom to top, the arboreal component decreases from 54 to 46%, while the globular echinate increase to 5-15%. Rondels decrease 50% while sclereid peak in 20-30 (Table 7-7). Age zone level 0-10 also indicate Palms peaks but the short cell grasses are scarce. The highest arboreal representation comes from sample –level 0-10 and 10-20 (85%), where grass short cells are at a record low phytoliths average 10-15% in all levels.

Levels 10-20 and 20-30 show that woody phytoliths decrease to 45%, while globular echinate peaks again. The two upper zone level samples reflect the lowest arboreal component of all samples (40%). Sample level 30-40 arboreal cover returns to previous normal arboreal trends.



Figure 7-7: FLK-N site morphotype percentages per sample

COLUMN SAMPLING THROUGH LEVELS 1-3, 1.8		ZONE (LEVEL N=)			
МА					
KEY TYPE	Plant Category	0-10	10-	20-	30-40
			20	30	(cm)
GLOBULAR ECHINATE	Palms	3	6	8	8
GLOBULAR	Woody dicot	202	183	123	133
GRANULATE/PSILATE/TUBERCULATE,					
BLOCKY, TABULAR					
RONDEL WIDE/TOWER/HORNED	Grassy	4	10	28	6
SCLEREID	Woody	6	1	0	2

Table 7-7: Phytolith types used for classification at FLK-N site

7.3 THE CASTLE SITE

A total of 14 samples were analysed from the Castle site, resulting in a total of 243 phytoliths counted (Table 7-8) (Figs. 7-8 and 7-9). Phytolith preservation show a great homogeneity and less variability, with only two key contributors accounting for the variably (Table 7-9).

Table 7-8: Phytolith morphotypes at Geolocality 44a, Castle Clays

Phytolith morphotype	Count	%
1. Mesophyll cells	140	57.61
2. Blocky ridged	33	13.58

Phytolith morphotype	Count	%
3. Blocky tuberculate	20	8.23
4. Blocky sulcate	17	7.00
5. Tabular scrobuculate	12	4.94
6. Globular granulate	7	2.88
7. Irregular indeterminate	7	2.88
8. Tabular sinuate	4	1.65
9. Oblong granulate	2	0.82
10. Globulose	1	0.41
Total:	243	100



Figure 7-9: Geolocality 44a phytolith counts and morphotypes encountered per sample



Figure 7-8: Geolocality 44a selected key phytolith morphotypes

 Table 7-9: Castle descriptive statistics

Attribute	Total	%
Ν	10	10
Min	1	0.41
Max	140	57.61
Sum	243	100
Mean	24.3	10
Std. error	13.22292	5.441218
Variance	1748.456	296.0685
Stand. dev	41.81454	17.20664
Median	9.5	3.91
25 percentile	3.5	1.4425
75 percentile	23.25	9.5675
Skewness	2.858456	2.858351

Kurtosis	8.520007	8.519566
Geom. mean	9.701945	3.990698
Coeff. var	172.0763	172.0664

7.3.1 Common Morphotypes

There are only two morphotypes interpreted as prominent contributors. These are: Mesophyll cells (n=140, 57.61%), and Blocky ridged (n=33, 13.58%)

7.3.2 INFREQUENT AND RARE MORPHOTYPES

The majority of the morphotypes at the Geolocality 44a palaeosol site level samples are dominated by rare and infrequent types which include: Blocky tuberculate (n=20, 8.23%); Blocky sulcate (n=17, 7.00%); Tabular scrobiculate (n=12, 4.94%); Globular granulate (n=7, 2.88%); Irregular indeterminate (n=7, 2.88%); Tabular sinuate (n=4, 1.65%); Oblong granulate (n=2, 0.82%); and Globulose (n=1, 0.41%). No grass short cell phytoliths was tallied from Geolocality 44a site.

7.3.3 DIACHRONIC PATTERNS

Figure 7-10 shows patterns of diachronic change for the Castle site. Age zone level 25-28 cm, sample # 011 account for 95% of arboreal indicators such as the blocky type (also see Mercader et al., 2019) and globular granulate (Mercader et al., 2010), and tabular scrobiculate both with heavily decorated surfaces.

It was noticed that in samples # 08 zone level (75-79 cm) and # 09 (55-61 cm), the phytolith assemblage is dominated by mesophyll cells \leq 80%. From bottom to the top, woody phytoliths average 70% at the site. Mesophyll cells are abundant and grassy taxa are scarce. Globulose reach 0.04 % in sample 09 (50-100 cm) (Table 7-10).

Age zone level 100-150 to 150-200 cm, apart from mesophyll cells, other silica bodies such as the tabular elongate phytoliths, the medium-size (20–60 μ m) and blocky-type phytoliths (40-80 μ m) were found abundant in most samples. Oblong granulate (n=2) were counted at the Geololacilty 44b, but their taxonomic origin is still unclear, therefore it is not easy to explain their significance for palaeolandscape evolution.



Figure 7-10: Geolocality 44a morphotype percentages per sample

Table 7-10: Phytolith types used for classification at Castle

Column sampling levels above Tuff IIA, 1.74 Ma			,	Zone (level	n=)
Key type	Plant Category	0-50	50-100	100-150	150-200 (cm)
Globular granulate, blocky,	Woody dicot	18	41	19	12
tabular					
Globulose	Grassy	0	1	0	0

7.4 THE FLK-W SITE

The 27 samples analysed produced 8,711 phytoliths from FLK-W (Table 7-11) (Figs. 7-11 and 7-12), of which eight types are prominent contributors with frequencies above the average sub-totalling 90% (n=7,647). Type variability slightly similar throughout the FLK-W column

Phytolith	Count	%
morphotype		
1. Blocky sulcate	3799	43.61
2. Tabular	1238	14.21
scrobiculate		

Table 7-11: Phytolith morphotypes at FLK-W

3. Tabular	950	10.91
elongate		
4. Tabular cavate	550	6.31
5. Blocky ridged	518	5.95
6. Globular	329	3.78
granulate		
7. Globular	284	3.26
echinate		
8. Blocky	263	3.02
9. Tabular sinuate	195	2.24
10. Globular	104	1.19
sinuate		
11. Cylindroid	94	1.08
scrobiculate		
12. Sclereid	65	0.75
13. Oblong	43	0.49
14. Cylindroid	37	0.42
15. Hemisphere	28	0.32
16. Globular	25	0.29
tuberculate		
17. Saddle short	24	0.28
18. Tabular thick	21	0.24

19. Tabular	18	0.21
crenate		
20. Tabular pilate	17	0.20
21. Vessel	15	0.17
22. Globular	13	0.15
crenate		
23. Bulliform	12	0.14
24. Clavate	12	0.14
25. Scutiform	12	0.14
26. Rondel tower	10	0.11
27. Tabular	9	0.10
dendriform		
28. Rondel wide	5	0.06
29. Blocky	4	0.05
facetate		
30. Blocky hairy	4	0.05
31. Rondel wide	3	0.03
32. Blocky pilate	3	0.03
33. Perforated	3	0.03
plate		
34. Cylindroid	2	0.02
granulate		

35. Tabular	2	0.02
oblong radiating		
36. Papillae	2	0.02
37. Rondel horned	1	0.01
38. Saddle long	1	0.01
39. Saddle squat	1	0.01
Total:	8711	100

samples. The relative higher representation of phytolith types in lower levels (10-10cm and 10-27cm), the mid-upper layers does not show marked differences. Mean value per sample is 2.7% (Table 7-12). The sum of morphotypes from FLK-W column samples is 39, and a total of eight morphotypes are above-average contributors (at least twice more than average).

.4.1 COMMON MORPHOTYPES

The eight most common morphotypes, accounting for 90% of the variability include: Blocky sulcate (n=3,799, 43.61%); Tabular scrobiculate (n=1,238, 14.21%); Tabular elongate (n=950, 10.91%); Tabular cavate (n=550, 6.31%); Blocky ridged (n=518, 5.95%); Globular granulate (n=329, 3.87%); Globular echinate (n=284, 3.26%), and Blocky (n=263, 3.02%).

About 5% of the total phytolith assemblage at FLK-W is made up of few types that account slightly below average rates, one on one, still are relatively common: just \leq 1.4% of the mean value per sample. In order of higher frequency, these four types are: Tabular sinuate (n = 195, 2.24%); Globular psilate (n = 104, 1.19%); Cylindroid scrobiculate (n=94, 1.08%), and; sclereid (n=65, 1.75%).







Figure 7-12: FLK-W phytolith counts and morphotypes encountered per sample

Table 7-12: FLK-W descriptive statistics

Attribute	Total	%
Ν	37	37
Min	1	0.01
Max	3799	43.61
Sum	8711	100
Mean	235.4324	2.702703
Std. error	108.6183	1.246888
Variance	436523.2	57.52496
Stand. dev	660.699	7.584521
Median	18	0.21
25 percentile	4.5	0.055
75 percentile	149.5	1.715
Skewness	4.723619	4.723345
Kurtosis	24.74093	24.7387
Geom. mean	26.67277	0.300119
Coeff. var	280.6321	280.6273

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7.4.2 INFREQUENT AND RARE MORPHOTYPES

At the bottom, the lowest ranked phytolith contributors form at least 5% of the total morphotypes at FLK- W. The total count per type under these low contributors comprised of (25 morphotypes); in order of higher frequency, these are: Oblong (n=43, 0.49%); Cylindroid (n= 37, 0.42%); Hemisphere (n= 28, 0.32%); Globular tuberculate (n=25, 0.29%); Saddle short (n= 24,

(0.28%); Tabular thick (n= 21, 0.24%); Tabular crenate (n= 18, 0.21\%); Tabular pilate (n=17, 0.20\%); Vessel (n=15, 0.17\%); Globular crenate (n=13, 0.15\%); Bulliform (n=12, 0.14\%); Clavate (n=12, 0.14\%); Scutiform (n=12, 0.14\%); Rondel tower (n=10, 0.11\%); Tabular dendriform (n=9, 0.10\%); Rondel wide (n= 5, 0.06\%); Blocky facetate (n= 4, 0.05\%); Blocky hairy (n=4, 0.05\%); Blocky pilate (n= 3, 0.03\%); Perforated plate (n=3, 0.03\%); Cylindroid granulate (n=2, 0.02\%); Papillae (n=2, 0.02\%); Tabular oblong radiating (n=2, 0.02\%); Rondel horned (n=1, 0.01\%); Saddle long (n= 1, 0.01\%); and Saddle squat (n= 1, 0.01\%).

Of these twenty-five morphotypes, only six are short cells (short saddle, long saddle, saddle squat, and rondel tower, rondel horned, and rondel wide). It was noted that tabular crenates represent 0.21% of the assemblage; although are less in percentage, they are documented throughout the column even though are relatively low contributors. This was also seen with bulliform and scutiform morphotypes, which each amounted to 0.14% of the assemblage.

7.4.3 DIACHRONIC PATTERNS

The key phytolith counts per level as appears in Figure 7-13. Age zone level 0-25: Ten samples from the lower levels above Tuff A FLK-W, samples collected from the "Waxy Clay", indicate that the arboreal phytolith group dominate the assemblage (e.g. blocky, tabular, globular granulate, and sclereid), and together accounts for 80% of the assemblage. Globular echinate alone representing palm trees are abundant and are distributed throughout level 0-25 and accounts for approximately 20%. Papillae phytoliths representing sedge environments (n=2), ranked the lowest. Silica short cell grasses are 18-20% of the total sum, of which half are Saddle short and squat. Inversely, arid adapted types such as Rondel wide, short and tower are not many as much as short

cells Saddle, however Rondels and tower are proportionally well distributed throughout level 0-25 cm (Table 7-13).

Age zone level 25-50: Samples collected from the coarse sand and conglomerate, and towards the cross-bedded sands above it. The most noticeable phytolith group is arboreal again at \geq 75%. The arboreal cover is decreasing significantly but the globular crenate peaks. The two lower samples reflect the highest arboreal component of all samples (55%).

Age zone level 50-75. Samples collected from clayish silt, arboreal taxa are common, interestingly the Palm (globular echinate) phytoliths are declining below average here, this is contrary to the other zones. The short cell phytoliths range from 5 to 10% (average for saddles, rondels, and tower decline by 55%).

Age zone level 75-100. Sediments collected from the fine-grained sand and silt layer; all 5 samples retain the previous arboreal trends. Woody taxa dominate at \geq 90%, and globular echinate peaks again.

Age zone level 100-130. Only two samples were collected above the Tuff FLK-Wb at the waxy clays. The samples show general trends towards decreasing of phytolith types, both grassy and arboreal indicators. Globular echinate phytolith peaks reach 15% per sample.



Figure 7-13: FLK-W morphotype percentages per sample

Column sampling at FLK-W 1.69 Ma		Zone (level, n=)				
Key type	Plant	0-25	25-50	50-75	75-100	100-130
	Category					cm
Globular crenate	Woody	6	7	0	1	0
Globular echinate	Palms	114	76	19	30	27
Globular	Woody dicot	2021	1097	958	246	125
granulate/psilate/tuberculate,						
blocky, tabular						
Clavate granulate	Woody dicot	1	2	2	2	5
Papillae	Sedges	2	0	0	0	0
Short cells rondel wide/horned	Grassy	1	5	1	0	0
Short cells saddle short/long/squat	Grassy	16	1	0	1	0
Sclereid	Woody	29	13	3	17	0
Scutiform	Grassy	0	3	1	0	8
Tower	Grassy	9	1	0	0	0

7.5 THE LAS HORIZON

A total of 469 phytoliths, from 16 samples, were counted from the LAS horizon (Table 7-14) (Figs. 7-14 and 7-15). In this assemblage, there were three prominent contributors with frequencies above the average sub-totaling 79 % (n = 369). One sample (#12) contains the highest

representation of phytoliths, with the rest of the samples containing very few to none at all. The mean value per sample is 5.8% (Table 7-15).

Table 7-14: Phytolith morphotypes at LAS

Phytolith morphotype	Count	%
1. Mesophyll cells	291	62.05
2. Hair base	49	10.45
3. Blocky	29	6.18
4. Tabular scrobiculate	16	3.41
5. Blocky ridged	15	3.20
6. Blocky sulcate	14	2.99
7. Irregular striated	11	2.35
8. Hemisphere	7	1.49
9. Globular tuberculate	7	1.49
10. Guttiform	6	1.28
11. Globular granulate	6	1.28
12. Irregular indeterminate	6	1.28
13. Cylindroid	2	0.43
14. Globulose	2	0.43
15. Oblong granulate	2	0.43
16. Rondel	2	0.43

17. Saddle	2	0.43
18 Bulliform	1	0.21
19. Globular psilate	1	0.21
20. Ovate granulate	1	0.21
Total:	469	100



Figure 7-14: LAS selected key phytolith morphotypes



Figure 7-15: LAS phytolith counts and morphotypes encountered per sample

Table 7-15: LAS descriptive statistics

Attribute	Total	%
Ν	17	17
Min	1	0.21
Max	291	62.05
Sum	469	100.01
Mean	27.58824	5.882941

Attribute	Total	%
Std. error	16.72288	3.565806
Variance	4754.132	216.1545
Stand. dev	68.95022	14.70219
Median	7	1.49
25 percentile	2	0.43
75 percentile	15.5	3.305
Skewness	3.920993	3.920996
Kurtosis	15.75616	15.75616
Geom. mean	7.979739	1.700892
Coeff. var	249.9262	249.9123

7.5.1 Common Morphotypes

At LAS palaeosols, the type variability is less diverse and not pronounced due to homogeneity. There are three morphotypes that represent the top 79% of the assemblage, with one key contributor (mesophyll cells). This morphotype alone its frequency is above the average sub-totaling 62% of all counts. The top contributors are: Mesophyll cells (n=291, 62.05%); Hair base (n=49, 10.45%), and; Blocky (n=29, 6.18%).

7.5.2 INFREQUENT AND RARE MORPHOTYPES

Low ranked phytolith contributors, in order of their frequency include: Tabular scrobiculate (n=16, 3.41%); Blocky ridged (n=15, 3.20%); Blocky sulcate (n=14, 2.99%); Irregular striated (n=11, 2.35%); Globular tuberculate (n=7, 1.49%); Guttiform (n=7, 1.49%); Globular granulate (n=6, 1.28%); Hemisphere (n =6, 1.28%); Irregular indeterminate (n =6, 1.28%); Cylindroid (n=2,

(0.43%); Globulose (n=2, 0.43\%); Oblong granulate (n=2, 0.43\%); Bulliform (n=1, 0. 21\%); Saddle short (n=1, 021\%); Saddle long (n=1, 021\%) Rondel tower (n=1, 021\%); Rondel wide (n=1, 021\%); Globular psilate (n=1, 0.21\%); and Ovate granulate (n=1, 0.21\%).

7.5.3 DIACHRONIC PATTERNS

Age zone level 0-50 and 50-100 m, woody phytoliths average 35%, but grass short cells are extremely low, approximately 0.21% per zone. Xeric grasses are absent from samples # 01-06 but present in sample # 09 and 11 and represent 1% of the assemblage (Table 7-16).

Age zone level 100-150, and 150-200 m, arboreal cover increases from 40% to 60%. From the bottom to the top, woody phytoliths increased.

For all but one sample, i.e. sample # 12 (age zone level 0-50 m) the counts of mesophyll cells are very high 62% of the total LAS assemblage. For both samples at LAS, a statistically valid count of 220 GSSCs could not be reached , very few rondel and saddle types were counted. The assemblage is characterized by small diversity and five samples were negative and did not yield any phytoliths (Fig. 7-16).

7.6 THE BPT HORIZON

A total of 1,788 phytoliths were counted at the BPT horizon, from analysis of 10 samples (Table 7-17). There were 29 distinct morphotypes encountered, with nine accounting for 88% of the variability within the assemblage (Figs. 7-17 and 7-18) (Table 7-18).

7.6.1 Common Morphotypes

Approximately 88% of the variability of this assemblage is from nine morphotypes (Table 16 ab and b, fig. 24-25) that are as follows: Hair articulated (n=362, 20.25%); Globular granulate (n=213, 11.91%); Globular tuberculate (n=213, 11.91%); Irregular indeterminate (n=197, 11.02%); Hair base (n=164, 9.17%); Mesophyll cells (n=134, 7.49%); Blocky hairy (n=127, 7.10%); Blocky sulcate (n=86, 4.81%); Tabular scrobiculate (n=77, 4.31%).

Aerial sampling at LAS 1.66 Ma			Zone	e (Level,	n=)
Key type	Plant	0-50	50-100	100-	150-200
	Category			150	m
Globular	Woody dicot	13	14	23	40
granulate/psilate/tuberculate,					
blocky, tabular					
Short cells -rondel wide, tower	Grassy	1	5	1	0
Short cells-saddle short, long	Grassy	0	1	0	1

Table 7-16: Phytolith types used for classification at LAS



Figure 7-16: LAS morphotype percentages per sample

Phytolith	Count	%
1. Hair articulated	362	20.25
2. Globular granulate	213	11.91
3. Globular tuberculate	213	11.91
4. Irregular indeterminate	197	11.02
5. Hair base	164	9.17
6. Mesophyll cells	134	7.49

Table 7-17: Phytolith morphotypes at BPT

7. Blocky hairy	127	7.10
8. Blocky sulcate	86	4.81
9. Tabular scrobiculate	77	4.31
10. Irregular striated	43	2.40
11. Tabular elongate	43	2.40
12. Globulose	25	1.45
13. Blocky ridged	20	1.12
14. Irregular ridged	17	0.95
15. Elongate orthogonal	15	0.84
16. Oblong granulate	15	0.84
17. Cylindroid	10	0.56
18. Globular psilate	8	0.45
19. Tabular cavate	5	0.28
20. Tabular sinuate	5	0.28
21. Oblong	3	0.17
22. Rondel	2	0.12
23. Saddle	2	0.12
24. Blocky facetate	1	0.06
25. Bulliform	1	0.06
26. Blocky polygonal	1	0.06
27. Epidermal cell tissues	1	0.06
28. Sclereid	1	0.06

29. Tabular dendriform	1	0.06
Total:	1788	100



Figure 7-17: BPT selected key phytolith morphotypes encountered per sample



Figure 7-18: BPT phytolith counts and morphotypes encountered per sample

Table 7-18: BPT descriptive statistics

Attribute	Total	%
Ν	26	26
Min	1	0.06
Max	362	20.25
Sum	1788	100.01
Mean	68.76923	3.846538

Attribute	Total	%	
Std. error	18.3	1.023364	
Variance	8707.145	27.22914	
Stand. dev	93.31208	5.218154	
Median	18.5	1.035	
25 prentil	4.5	0.2525	
75 prentil	128.75	7.1975	
Skewness	1.664142	1.665431	
Kurtosis	2.54656	2.552518	
Geom. mean	18.78717	1.065782	
Coeff. var	135.6887	135.6584	

7.6.2 INFREQUENT AND RARE MORPHOTYPES

Further variability is documented by low ranked phytolith contributors, which include: Irregular striated (n= 43, 2.40%); Tabular elongate (n=43, 2.40%); Globulose (n=26, 1.45%); Blocky ridged (n= 20, 1.12%); Irregular ridged (n=17, 0.95%); Elongate orthogonal (n=15, 0.84%); Oblong granulate (n=15, 0.84%); Cylindroid (n=10, 0.56%); Globular psilate (n=8, 0.45%); Tabular cavate (n=5, 0.28%); Tabular sinuate (n=5, 0.28%); Oblong (n=3, 0.17%); Blocky facetate (n=1, 0.06%); Blocky polygonal (n=1, 0.06%); Epidermal cell tissues (n=1, 0.06%); Bulliform (n=1, 0.06%); Rondel wide (n=1, 0.06%); Rondel tower (n=1, 0.06%); Saddle short (n=1, 0.06%); Saddle squat (n=1, 0.06%); Sclereid (n=1, 0.06%); and Tabular dendriform (n=1, 0.0 0.06%). Out of all the sites analysed, the BPT contained the lowest number of grassy short cell phytoliths.

7.6.3 DIACHRONIC PATTERNS

The BPT phytolith record is characterised by abundant woody dicot taxa which account for 50% to 90% of the total phytoliths count and make the signal of arboreal taxa dominance at each zone documented (Fig. 7-19) (Table 7-19).



Figure 7-19: BPT morphotype percentages per sample

Age level 0-200 cm: The woody phytolith diversity is high with the presence of various blocky types, globular oblong, globular granulate and tabular morphotypes.

Age zone level 200-400 cm: There is a peak in arboreal cover which is represented by blocky, tabular, and granulate morphotypes. This locality strongly suggests the presence of rare grasses as they account for 1% only.

Age zone level 400-600 cm: The arboreal trend decreases slightly, however the presence oblong granulates bodies (10-30 μ m), elongate orthogonal together with tabular and blocky, globular granulate, tuberculate morphotypes which can be attributed to woody types still indication an arboreal plant cover.

Levels 600-800 cm show a peak in forest indicators because of the morphotypes that resemble types produced by miombo tree species (blocky, globular granulate, and blocky morphotypes (also see Mercader et al., 2009, 2013) (Table 7-19). Grassy indicators are extremely low at BPT and ranks.

Aerial sampling at BPT 1.60 Ma		Zone (Level, n=)			
Key type	Plant Category	0-200	200-400	400-600	600-800 m
Globular granulate/psilate/tuberculate,	Woody dicot	126	200	188	274
blocky, tabular					
Short cells -rondel wide, tower	Grassy	0	1	0	1
Short cells-saddle short, long	Grassy	0	1	1	0

Table 7-19: Phytolith types used for classification at LAS
CHAPTER 8: DISCUSSION

This chapter interprets the phytolith assemblage results and discusses available vegetation niches for hominin exploitation as reconstructed through phytolith analysis during UMBI-LMBII at Oldupai Gorge. It discusses the diversity of plant landscapes that were inhabited by early humans at Oldupai Gorge Upper Bed I and Lower Bed II, at the archaeological sites of Frida Leakey Korongo North and West, and at geological exposures at Oldupai's Castle, the Lower Augitic Sanstone, and the Bird Print Tuff. The phytolith assemblages provide an ecological understanding of human environments during time in question and identify the signal of vegetation dynamics that influenced human behaviour in the greater Oldupai region.

Various environmental hypotheses of human evolution are built on the link between environmental change and past climate change. The intersection between these two fields has provided the ways in which climate may have influenced human origins and the ways in which humans come to influence environmental change and adaptations to various and diverse environmental settings (Potts, 1998, 2012, 2013; Vrba, 1995, 2000). The important implications for human evolution can be constructed by looking at the relationship between climatic shifts in the past and changes that accompanied the environments that surrounded hominins (Potts, 2012). The emergence of hominin habitual bipedality, stone transport, diversification of artifact contexts, encephalization, and enhanced cognitive and social functioning all may reflect adaptations to environmental novelty and highly varying selective contexts (Potts, 1998: 93–136; Vrba, 1995).

Phytoliths from this study contain environmental data suggestive of a range of habitats and the availability of various niches throughout Bed I to Bed II times, all of which are associated with a particular hominin species and stone tools industrial technologies. *Paranthropus boisie* and *Homo habilis* might have exploited different niches from what was occupied by *Homo erectus* and during the same time, the two hominin species that coexisted (toolmakers) during the same time considerably altered their landscape interactions. This is also supported by other archaeological evidence and records from East Africa that show the growing diversity of palaeoenvironments in which stone tools were discarded. The phytolith data from this study span the period in which the transition from Oldowan to Acheulean occurred and these two early industrial technologies are said to be associated with environmental change which happened in the East African landscape during the Pleistocene (see Potts, 1998; deMenocal, 2004; Ashley et al., 2010, 2014; Dominguez-Rodrigo et al., 2010, 2015). Climate and environment were major driving forces in early human evolution and change in stone tool technologies, as well as adaptations to new environments in the entire East Africa region.

At Oldupai Gorge, the sediments of Bed I and lower Bed II are considered to span perhaps 50–100 Kya, bracketed between dates of 1.9 and 1.7 Ma (Hay, 1976). A small alkaline lake (7–25 km wide) persisted throughout this time, and thus, hydrological change was active but less dramatic as in the case of other early hominin sites of the east Africa region (Hay, 1976). Previous sedimentary, isotopic, faunal, and pollen studies, however, pointed to impressive shifts in climate and vegetation cover during this time (Hay, 1976; Cerling, 1992; Potts, 1988; Bonnefille, 1995; Vrba, 2000). Stone tool sites contain higher concentrations and scatters of artifacts which occur throughout the Bed I sequence. This suggests that Oldowan toolmakers had the means to adjust to both the climatic and environmental changes they encountered.

During a period of landscape instability approximately 1.9 to 1.5 Ma, toolmakers became less tethered to local rock sources and particular habitats. They carried stones further and made clusters of tools in more diverse areas of the landscape. The favoured areas included both old and

new habitats near the axial channels and on fluvial floodplains (Leakey, 1976). The evidence thus points to an expansion in landscape use rather than a directional shift. The toolmakers of Bed I Oldupai tended to use stone sources within the confines of the lake floodplain. Transport distances rarely exceeded 3 km (Leakey, 1971, 1976). After a series of environmental fluctuations, the toolmakers of Bed II expanded their range to depositional environments both within and beyond the immediate lake margin area. Stone sources outside the lake margin were also newly exploited. These developments at Oldupai, then, parallel those in the Oldupai basin (Leakey, 1971, 1976). At both localities, toolmakers were active through substantial shifts in environment and were present in arid, moist, warm, cool, more wooded, more open, lake-dominated, and fluvialdominated phases (Leakey, 1971). This suggests that Oldowan toolmakers could accommodate to periodic shifts in climate, basin hydrology, and vegetation (Ashley et al., 2010). The persistence of hominin toolmakers and their eventual expansion into a greater range of habitats is consistent with the variability selection hypothesis. In this light, the transport of resources over longer distances, occupation of a wider habitat range, and intensification of animal food exploitation may represent means of dealing with large changes in the distribution of habitats, water, food, and other life necessities for hominins (Vrba, 2000; Maslin et al., 2014, 2015).

Evidently, two major important developments that span this time were the origin of early African *H. erectus* around 1.8 Ma and the expansion of the ranging patterns of the toolmakers. One explanation is that the adaptive shift in body form was decoupled from speciation, which is also evident in the climatic adaptation of modern humans (Maslin et al., 2014). Further discoveries of postcranial bones indicate that body form changed in this species before 1.8 Ma, and the adaptive shift preceded the most notable grassland expansion discovered so far in the East African Plio-Pleistocene records (Ashley et al., 2010, 2014; Dominguez-Rodrigo et al., 2010, 2015; Maslin

et al., 2014, 2015). The second key development in the period is reflected by archeologically visible behaviours related to habitat use and stone transport (Vrba, 2000; Dominguez-Rodrigo et al., 2015). The early hominin environments and their bio-cultural changes derive mostly from stone tool technology, and the transition from the Oldowan to the Acheulean that took place during this interval is certainly a key aspect in hominin technological development which happened about 1.7 Ma (de la Torre and Mora, 2013).

The technological change and transition from Oldowan to Acheulean tools is said to be associated with an emergence of a new hominin species, which with its new stone tools such as large cutting bifacial tools (i.e. handaxes and cleavers) could have modified the environment and landscape ecosystems, including the fauna. The transition from the Oldowan to the Acheulean was also likely associated with more advanced tool technology and behavioural traits, which allowed the hominins to increase their impact on the surrounding environments. Hominin and faunal evolution in general were likely driven by a complex interplay between climatic change and biotic interactions at various spatial and temporal scales, and not simply by climatically driven biome changes alone (see Vrba, 2000). Potts (1998) pointed out that environmental change has affected the course of human evolution and the development of human adaptations to new environments and eventual novel technological innovations. Over the past two decades, understandings of the relationship between past climate change and human evolution have flourished and the consideration of environmental change in the study of early human evolution has been inevitable.

8.1 MULTIVARIATE ANALYSIS

Normality tests were applied in this study to analyse distribution of phytolith types and detect possible outliers. When analyzing all the samples, they were not normally distributed: Shapiro-Wilk Test = 0.3647; p (normal) = 0. When analyzing samples individually, they tend to not present normal distributions according to phytolith morphotypes p (normal) < 0.05. Nine samples present normal distributions (Tables 8-1 – 8-6).

As the data in this study are not normal, non-parametric tests were performed using Kruskal-Wallis to analyze possible correlations between samples. The Kruskal-Wallis test is a non-parametric ANOVA, which used in comparing the medians of several univariate groups. In all samples, there is a significant difference between sample medians (Chi–square = 576.4, p

Table 8-1: Normality table for FLK-N horizon

	FLK	FLKN	FLKN	FLKN	FLKN	FLKN								
	N-L 1	N-L 2	N-L 3	N-L 4	N-L 5	N-L 6	N-L 7	N-L 8	N-L 9	-L 10	-L 12	-L 13	-L 14	-L 15
Ν	13	10	11	7	5	10	9	13	7	9	6	7	3	5
SHAPIRO-	0.59	0.62	0.60	0.70	0.64	0.72	0.83	0.80	0.76	0.45	0.78	0.79	0.96	0.80
WILK W														
P(NORMAL)	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.01	0.02	0.00	0.04	0.04	0.64	0.08
ANDERSON-	2.14	1.70	1.78	1.05	0.94	1.12	0.73	0.94	0.78	2.38	0.64	0.69	0.23	0.53
DARLING A														
P(NORMAL)	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.01	0.02	0.00	0.05	0.04	0.49	0.09
P(MONTE	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.02	0.00	0.05	0.04	0.63	0.09
CARLO)														
JARQUE-	26.18	8.29	17.93	1.76	1.74	8.64	1.08	5.19	1.88	15.18	2.03	1.18	0.35	0.77
BERA JB														
P(NORMAL)	0.00	0.02	0.00	0.41	0.42	0.01	0.58	0.07	0.39	0.00	0.36	0.56	0.84	0.68
P(MONTE	0.00	0.00	0.00	0.05	0.00	0.00	0.19	0.02	0.05	0.00	0.02	0.11	0.64	0.16
CARLO)														

	FLK	FLKN-													
	N-L	L 17	L 18	L 19	L 20	L 21	L 22	L 23	L 24	L 25	L 26	L 27	L 28	L 29	L 30
	16														
Ν	7	7	4	5		7	6	9	6	6	7	9	7	8	8
SHAPIRO-	0.82	0.78	0.77	0.64		0.84	0.88	0.78	0.54	0.55	0.87	0.63	0.94	0.89	0.72
WILK W															
P(NORMAL)	0.06	0.03	0.06	0.00		0.10	0.26	0.01	0.00	0.00	0.20	0.00	0.65	0.22	0.00
ANDERSON-	0.57	0.72	0.54	0.97		0.65	0.39	0.93	1.43	1.40	0.42	1.49	0.24	0.52	0.97
DARLING A															
P(NORMAL)	0.09	0.03	0.06	0.00		0.05	0.26	0.01	0.00	0.00	0.22	0.00	0.66	0.13	0.01
P(MONTE	0.09	0.03	0.06	0.00		0.05	0.29	0.01	0.00	0.00	0.23	0.00	0.71	0.13	0.01
CARLO)															

Table 8-2: Normality table for FLK-N site

	FLKN GEO7							
	OCR 1	OCR 2	OCR 3	OCR 4	OCR 5	OCR 6	OCR 7	OCR 8
N	15	11	4	9	11	8	7	4
SHAPIRO-WILK W	0.86	0.87	0.73	0.94	0.92	0.91	0.81	0.90
P(NORMAL)	0.02	0.08	0.02	0.55	0.29	0.36	0.06	0.41
ANDERSON-DARLING A	0.80	0.52	0.58	0.26	0.37	0.37	0.67	0.30
P(NORMAL)	0.03	0.14	0.05	0.62	0.37	0.33	0.04	0.36
P(MONTE CARLO)	0.03	0.14	0.04	0.67	0.37	0.35	0.05	0.46
JARQUE-BERA JB	1.71	2.44	0.67	0.91	0.91	0.84	1.23	0.55
P(NORMAL)	0.43	0.29	0.72	0.63	0.64	0.66	0.54	0.76
P(MONTE CARLO)	0.14	0.06	0.15	0.29	0.35	0.30	0.10	0.32

	FLKN GEO7 OCR 10	FLKN GEO7 OCR 11	FLKN GEO7 OCR 12	FLKN GEO7 OCR 13
N	3	19	14	2
SHAPIRO-WILK W	1.00	0.45	0.68	1.00
P(NORMAL)	1.00	0.00	0.00	1.00
ANDERSON-DARLING A	0.19	3.97	1.73	0.25
P(NORMAL)	0.63	0.00	0.00	0.23
P(MONTE CARLO)	1.00	0.00	0.00	1.00
JARQUE-BERA JB	0.28	139.00	18.47	0.33

P(NORMAL)	0.87	0.00	0.00	0.85
P(MONTE CARLO)	1.00	0.00	0.00	0.88

FLK GEO 7 CR 8 FLK GEO 7 CR 9 FLK GEO 7 CR 10

	7 CR 1	7 CR 2	7 CR 3	7 CR 4	7 CR 5	7 CR 6	7 CR 7			
N	20	18	6	9	11	12	12	11	6	15
SHAPIRO-WILK	0.87	0.72	0.67	0.66	0.95	0.66	0.80	0.52	0.75	0.66
W										
P(NORMAL)	0.01	0.00	0.00	0.00	0.69	0.00	0.01	0.00	0.02	0.00
ANDERSON-	1.01	2.04	0.99	1.35	0.25	1.52	1.02	2.34	0.76	2.22
DARLING A										
P(NORMAL)	0.01	0.00	0.00	0.00	0.66	0.00	0.01	0.00	0.02	0.00
P(MONTE	0.01	0.00	0.00	0.00	0.70	0.00	0.01	0.00	0.02	0.00
CARLO)										
JARQUE-BERA JB	2.02	7.55	2.07	6.65	0.58	19.39	3.66	19.85	1.10	8.44
P(NORMAL)	0.37	0.02	0.36	0.04	0.75	0.00	0.16	0.00	0.58	0.01
P(MONTE	0.13	0.02	0.02	0.01	0.61	0.00	0.03	0.00	0.10	0.01
CARLO)										

Table 8-3: Normality table for Castle

	CASTLE CLAYS 4	CASTLE CLAYS 7	CASTLE CLAYS 8	CASTLE CLAYS 9	CASTLE CLAYS 11	CASTLE CLAYS 13	CASTLE CLAYS 14
Ν	4		6	4	5	3	3
SHAPIRO-WILK W	0.63		0.83	0.69	0.65	0.75	0.75
P(NORMAL)	0.00		0.10	0.01	0.00	0.00	0.00
ANDERSON-	0.83		0.53	0.69	0.92	0.49	0.49
DARLING A							
P(NORMAL)	0.01		0.10	0.02	0.01	0.06	0.06
P(MONTE CARLO)	0.00		0.11	0.01	0.00	0.00	0.00
JARQUE-BERA JB	0.96		1.25	0.94	1.76	0.53	0.53
P(NORMAL)	0.62		0.54	0.63	0.41	0.77	0.77
P(MONTE CARLO)	0.00		0.07	0.01	0.00	0.00	0.00

Table 8-4: Normality table for FLK-W

	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-
	W 1	W 2	W 3	W 4	W 5	W 6	W 7	W 8	W 9	W 10	W 11	W 12	W 13	W 14
N	24	20	21	18	14	13	13	16	14	14	15	17	14	18
SHAPIRO-WILK W	0.64	0.66	0.52	0.55	0.57	0.60	0.61	0.49	0.52	0.64	0.55	0.42	0.49	0.49
P(NORMAL)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ANDERSON- DARLING A	3.11	3.08	4.72	3.70	2.41	2.02	1.92	3.17	2.63	1.93	2.60	3.92	2.93	3.35
P(NORMAL)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P(MONTE CARLO)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
JARQUE-BERA JB	60.48	9.62	18.67	24.53	34.15	26.70	26.35	78.23	52.94	25.62	46.49	119.50	52.10	109.90
P(NORMAL)	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P(MONTE CARLO)	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-	FLK-
	W 15	W 16	W 17	W 18	W 19	W 20	W 21	W 22	W 23	W 24	W 25	W 26	W 27
Ν	14	18	15	8	11	11	15	8	9	16	14	14	6
SHAPIRO-	0.46	0.43	0.44	0.59	0.56	0.54	0.47	0.52	0.61	0.67	0.65	0.76	0.86
WILK W													
P(NORMAL)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
ANDERSON-	3.09	4.11	3.49	1.51	1.96	2.17	3.14	1.85	1.53	2.39	2.27	1.40	0.45
DARLING A													
P(NORMAL)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17
P(MONTE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18
CARLO)													
JARQUE-BERA	60.74	123.90	77.23	8.56	23.17	22.67	71.45	9.44	11.37	5.46	5.80	4.96	1.21
JB													
P(NORMAL)	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.07	0.06	0.08	0.55
P(MONTE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.02	0.09
CARLO)													

Table 8-5: Normality table for LAS

	LAS 2	LAS 6	LAS 8	LAS 9	LAS 12	LAS 15	LAS 16
N	5	3	4	5	4	5	5
SHAPIRO-WILK W	0.90	0.96	0.63	0.63	0.81	0.92	0.68
P(NORMAL)	0.38	0.64	0.00	0.00	0.13	0.50	0.01
ANDERSON-DARLING A	0.31	0.23	0.83	0.97	0.45	0.28	0.80
P(NORMAL)	0.40	0.49	0.01	0.00	0.12	0.47	0.01
P(MONTE CARLO)	0.45	0.64	0.00	0.00	0.13	0.54	0.01
JARQUE-BERA JB	0.49	0.35	0.96	1.81	0.68	0.58	0.84
P(NORMAL)	0.78	0.84	0.62	0.40	0.71	0.75	0.66
P(MONTE CARLO)	0.56	0.64	0.00	0.00	0.14	0.41	0.13

Table 8-6: Normality table for BPT

	BPT 1	BPT 2	BPT 3	BPT 4	BPT 5	BPT 6	BPT 7	BPT 8	BPT 9	BPT 10
N	10	4	2	5	6	8	11	13	16	7
SHAPIRO-WILK W	0.84	0.74	1.00	0.75	0.74	0.58	0.61	0.44	0.63	0.69
P(NORMAL)	0.04	0.03	1.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00
ANDERSON-DARLING A	0.71	0.61	0.25	0.65	0.76	1.59	2.02	3.12	2.50	1.10
P(NORMAL)	0.04	0.04	0.23	0.04	0.02	0.00	0.00	0.00	0.00	0.00
P(MONTE CARLO)	0.04	0.03	1.00	0.03	0.02	0.00	0.00	0.00	0.00	0.00
JARQUE-BERA JB	1.24	0.90	0.33	1.37	2.21	8.87	5.16	51.43	13.95	1.44
P(NORMAL)	0.54	0.64	0.85	0.50	0.33	0.01	0.08	0.00	0.00	0.49
P(MONTE CARLO)	0.15	0.03	0.88	0.03	0.02	0.00	0.02	0.00	0.00	0.07

<0.001). From the null hypothesis that there are no significant differences between sample medians, however it was noted that there is no significant difference between sample medians in four sites namely FLK-W (Chi–square = 18.09, p=0.15), The Castle (Chi–square = 0.41, p 0.61), the LAS (Chi–square = 0.64, p=0.8266), and at the FLK-N horizon (Chi–square = 7.96, p=0.54). Meanwhile, in two sites there is significant difference between sample medians as follows: FLK-N site (Chi–square = 7.59, p=0.02), and the BPT (Chi–square = 7.24, p=0.01) (Table 8-7).

Variance analysis (Kruskal-Wallis test) on all samples grouped by morphotypes allowed us to determine the morphotypes variability among samples. When comparing all samples, the Kruskal-Wallis test results in a p (same) = <0.001. Samples from FLK-W site [p (same) =0.15], the Castle [p (same) =0.61], LAS [p (same)= 0.82], and FLK-N Horizon [p (same) = <0.54], samples from these localities are the most homogeneous among the analyzed samples. Also, samples from FLK-N site [p (same) = <0.04], and BPT [p (same) = <0.01], show variable intrasite phytolith assemblages.

All samples	H (chi2)	576.4
	P (same)	<0.001
FLK-W	H (chi2)	18.09
	P (same)	0.1523
FLK-Geo 7-CR	H (chi2)	7.954
	P (same)	0.0476
BPT	H (chi2)	7.244
	P (same)	0.01311

Table 8-7: Kruskall-Wallis values for sample sites

FLK-Geo 7-OCR	H (chi2)	7.244
	P (same)	<0.001
Castle Clays	H (chi2)	0.4169
	P (same)	0.6164
LAS	H (chi2)	0.6492
	P (same)	0.8266
FLK N - L	H (chi2)	7.969
	P (same)	0.5449

8.1.2 Correspondence Analysis

Table 8-8: Correspondence Analysis Morphotype Identifiers

Morphotype	Correspondence Analysis (CA) Identifiers
Bilobate concave	1
Bilobate convex	2
Blocky	3
Blocky cavate	4
Blocky dendriform	5
Blocky facetate	6
Blocky lacunate	7
Blocky hairy	8
Blocky pilate	9

	Blocky polygonal	10
	Blocky ridged	11
	Blocky sulcate	12
	Blocky tuberculated	13
_	Blocky radiating	14
	Bulliform	15
	Clavate	16
	Cylindroid	17
	Cylindroid granulate	18
	Cylindroid crenate	19
	Cylindroid scrobiculate	20
	Elongate orthogonal	21
_	Epidermal cell tissues	22
	Large globular	23
	Globular crenate	24
	Globular echinate	25
	Globular granulate	26
	Globular psilate	27
	Globular tuberculate	28
	Globulose	29
	Guttiform	30
	Hair base	31

Hair articulated	32
Hemisphere	33
Irregular indeterminated	34
Irregular ridged	35
Irregular striated	36
Mesophyll cells	37
Oblong	38
Oblong granulate	39
Orthogonal	40
Ovate granulate	41
Perforated plate	42
Rondel	43
Rondel horned	44
Rondel tower	45
Rondel wide	46
Saddle	47
Saddle long	48
Saddle short	49
Saddle squat	50
Sclereid	51
Scutiform	52
Tabular cavate	53

Tabular crenate	54
Tabular dendriform	55
Tabular elongate	56
Tabular oblong radiating	57
Tabular pilate	58
Tabular scrobiculate	59
Tabular sinuate	60
Tabular sulcate	61
Tabular thick	62
Vessel	63

8.1.2.1 FLK-N HORIZON

Correspondence analysis (CA) results from FLK-N show that first five axis in the CA for FLK- N Horizon explains the 63.4% of the cumulative variance (Table 8.9); Axis 1- 2 explains 34.6%, and shows that most of the FLK-N samples are in the positive sector (exceptions are samples 01, 05, 18,19, 20, 24, and 25) for both axes. Blocky and hair types are variables that separating the samples from the rest, probably because these morphotypes are more abundant while the later are less in content. Axis 3 show less variance among the samples but in the similar pattern, while sample # 20 is still showing huge differences from the rest of the samples because of its content in blocky morphotypes (*approx*. $\leq 100\%$) blocky morphotype. The representation of Axis 4 indicates most of the FLK- N horizon samples are in the positive sector (except for sample # 05, 09, 10, 12, 13, 21, 25, and 26), and is represented by morphotypes such as globular granulate,

cylindroid, tabular elongate, guttiform, sclereid, irregular indeterdeminate, and ovate granulate. Sample # 20 is separated from the rest like previously because of dominance in blocky morphotype. Axis1- 5 is only explaining the 7% of the variance that separates the samples in the positive and negative sector, mostly due to different content in blocky, cylindroids, scutiform, globular granulate, and tabular types because of positive axis 1. Sample # 20 is still showing a striking difference probably due to the prominent contribution of blocky morphotype (Figs. 8-1 to 8-4).

8.1.2.2 FLK-NORTH SITE

The first four axis in the CA for FLK-N site explain 77.05% of the cumulative variance (Table 8-10). Axis 1-2 explains the 54.6 %; according to it, most of the FLK-N site samples are in the positive sector of both axes (expect for for the samples # 01, 04, 07,10, 11, and 12). Sample #11 is showing the overrepresentation of blocky sulcate morphotype. Morphotypes such as tabular scrobiculate, tabular elongate, blocky hairy, mesophyll cells, blocky radiatong, and short saddle are also separated to the negative sector. Blocky sulcate tabular scrobiculate, and tabular elongate morphotypes are separated to the negative sector, while also forming the majority in the assemblage. Meanwhilte, the oblong granulate, and globulose are rare in the total assemblage, therefore they are separated to the more positive sector from the rest of the analysed samples.

Axis1- 3, is explaining the 68.6% variance, samples show less variance but in a similar pattern, the presence of tabular scrobiculate justifies the similarities among the samples because they are distributed fairly to each sample analysed. Blocky, globulose and oblong granulate morphoypes are more positively grouped and are very diverse, fairly distributed to each sample and they are grouped in the negative axis. Axis 1-4, only explaining the 8.4 % of the variance,



Figure 8-1: Correspondence analysis variables determining the 1-2 axis at FLK-N horizon



Figure 8-2: Correspondence analysis variables determining the 1-3 axis at FLK-N horizon



Figure 8-3: Correspondence analysis variables determining the 1-4 axis at FLK-N horizon



Figure 8-4: Correspondence analysis variables determining the 1-2 axis at FLK-N horizon

Axis	Eigenvalue	% of total	Cumulative
1	1	19.696	19.696
2	0.757416	14.918	34.614
3	0.638954	12.585	47.199
4	0.457246	9.0059	56.205
5	0.3685	7.258	63.463

Table 8-9: Eigenvalues and variance percentages of the CA axis for FLK-N horizon

Table 8-10: Eigenvalues and variance percentages of the CA axis for FLK-N site

Axis	Eigenvalue	% of total	Cumulative
1	0.04602	32.793	32.793
2	0.03061	21.812	54.605
3	0.01965	14.002	68.607
4	0.011855	8.4473	77.054

separates the samples in the positive and negative sector, mostly due to a different content in blocky, cylindroids, scutiform, globular granulate, and tabular types. Tabular scrobiculate morphotype is still in the higher negative sector. The representation of axis 4 indicates most of the FLK-N site samples are grouped in the positive sector, except for only six samples which are represented to the negative sector. These include morhotypes such as tabular sulcate, tabular scrobiculate, blocky, blocky hairy, hair base, elongate orthogonal, saddle short, large gobular



Figure 8-5: Correspondence analysis variables determining the 1-2 axis at FLK-N site



Figure 8-6: Correspondence analysis variables determining the 1-3 axis at FLK-N site



Figure 8-7: Correspondence analysis variables determining the 1-4 axis at FLK-N site

granulate, and mesophyll cells, which implies that they are well represented throughout the landscape. The rest types are on the positive sector while globular psilate, sclereid, globular tuberculate, and ovate granulate separate the samples towards the positive axis (Figs. 8-5 to 8-7).

8.1.2.3 GEOLOCALITY 44B, THE CASTLE

The first three axis in the CA for Geolocality 44a site are explaining the 85.94 % of the cumulative variance (Table 8-11). The samples at the Castle are similar; Axis 1-2 explains 74.07% and according to them, most of the site samples are located in the positive sector of axis except for only one sample # 08 which is located in the negative sector; this is the only sample that is more diverse than the rest of the samples in the Castle horizon assemblage. Axis 3 is only explaining the 11.8 % of the variance, when combined with Axis 1 samples are separated in the positive and negative sectors. The samples here show a big variance but in the similar fashion like axis 2, while the majority are in the positive sector, three morphytypes (blocky tuberculate, oblong granulate, and globulose), justifies the representation of the rest of the samples in the Castle site yields although in a minimum quantitites (Figs. 8-8 to 8-9).

Axis	Eigenvalue	% of total	Cumulative
1	0.745887	50.031	50.031
2	0.358436	24.043	74.074
3	0.176949	11.869	85.943

Table 8-11: Eigenvalues and variance percentages of the CA axis for Geolocality 44a



Figure 8-8: Correspondence analysis variables determining the 1-2 axis at Castle



Figure 8-9: Correspondence analysis variables determining the 1-3 axis at Castle

8.1.2.4 FLK-WEST SITE

The first three Axis in the CA for FLK-W site explains the 66.75% of the cumulative variance (Table 8-11). The samples at FLK-W are diverse; Axis 1-2 explains the 57.85%, and most of the samples are grouped in the positive sector of axis 1, due to the fair content of globular granulate, rondel, tabular and blocky morphotypes. The samples that are grouped in the negative axis are separated because of the content of the less or minimum number of morphotypes (tabular crenate, tabular pilate, vessel, globular crenate saddle short, long, cylindroid, hemisphere, globular tuberculate blocky hairy, rondel tower and rondel wide, tabular dendriform, and the perforated plate morphotypes). Axis 3 explains 8.9% of the variance, indicating most of the samples from FLK-W are grouped according globular granulate, globular pilate, globular echinate, tabular, blocky ridged, and blocky sulcate morphotypes, which are relatively prominent contributors. The samples # 02 and 03 yield 51% of the total phytolith count what justify their being in the negative sector of the CA. Blocky morphotype is separated in this graph due to the lower percentage representation (Figs. 8-10 to 8-11).

Axis	Eigenvalue	% of total	Cumulative
1	0.356624	39.883	39.883
2	0.160621	17.963	57.846
3	0.079616	8.9038	66.75

Table 8-12: Eigenvalues and variance percentages of the CA axis for FLK-W site



Figure 8-10: Correspondence analysis variables determining the 1-2 axis at FLK-W



Figure 8-11: Correspondence analysis variables determining the 1-3 axis at FLK-W

8.1.2.5 THE LAS HORIZON

The first four axis in the CA for LAS horizon explaining the 81.8 % of the cumulative variance (Table 8-13). Axis 1- 2 explains 53.65 %, according to them most of the LAS samples are in the positive sector of both axis (except for for the samples # 09 and 12), which yeilded a fair amount of phytoliths; the rest samples are poor producers. The majority of the samples are grouped in the positive sector of both axes. Axis 1-3, explaining 69.1% the samples, show less variance but in the similar fashion like Axis 2, while the majority are in the positive sector except three samples that had no phytoliths documented. The majority of phytolith types are grouped along the positive sector except three morphotypes (tabular scrobiculate, mesophyll cells, and ovate granulate). Axis 1-4 only explains the 12.78% of the variance, separating the samples in the positive and negative sector, mostly due to a different content in phytolith representation (Figs. 8-12 to 8-14). The positive sector includes the morphotypes such as hair base, blocky, blocky ridged, blocky sulcate, irregular striated, hemisphere, globular tuberculate, guttiform, globular granulate, irregular indeterminate, cylindroid, globulose, oblong granulate, and globular psilate.

Axis	Eigenvalue	% of total	Cumulative
1	0.863549	29.296	29.296
2	0.718014	24.359	53.655
3	0.455335	15.448	69.103
4	0.376828	12.784	81.887

Table 8-13: Eigenvalues and variance percentages of the CA axis for LAS horizon

8.1.3.6 THE BIRD PRINT TUFF HORIZON

The first four axis in the CA for BPT horizon explains the 84.03% of the cumulative variance (Table 8-14).

The samples at BPT samples are grouped in the positive sector of the two axes and are well represented by the content of globular granulate, tabular, and blocky types. Axis 1- 2 explaining the 46.03 %, according to them most of the BPT horizons samples are in the positive sector of both axes (except only four samples # 04, 07, 09, and 10). This samples are overrepresented by only single morphotype (hair base). Here, morphotypes such as gobular tuberculate, hair atriculated, sclereid, tabular sinuate, tabular elongate, and scutiform morphotypes are on negative sector. Axis 1-3 explaining 64% the samples, show less variance but in the similar pattern like the previous one; only samples # 03, 07, and 10 are on the negative sector.

Axis 1-4, explaining the 9.1% of the variance, separates the samples in the positive and negative sector, mostly due to a different content of morphotypes such as blocky globular granulate, hair articulated, globular tuberculate, irregular indeterminate, blocky hairy, hair base, mesophyll cells, blocky sulcate, tabular scrobiculate, and irregular striated, which are almost equally distributed on the both positive and negative axes (Figs. 8-15 to 8-17).


Figure 8-12: Correspondence analysis variables determining the 1-2 axis at LAS



Figure 8-13: Correspondence analysis variables determining the 1-3 axis at LAS



Figure 8-14: Correspondence analysis variables determining the 1-4 axis at LAS



Figure 8-15: Correspondence analysis variables determining the 1-2 axis at BPT



Figure 8-16: Correspondence analysis variables determining the 1-3 axis at BPT



Figure 8-17: Correspondence analysis variables determining the 1-4 axis at BPT

Axis	Eigenvalue	% of total	Cumulative
1	0.789143	25.974	25.974
2	0.609329	20.056	46.03
3	0.546175	17.977	64.006
4	0.329507	10.845	74.852
5	0.278849	9.1781	84.03

Table 8-14: Eigenvalues and variance percentages of the CA axis for BPT horizon

8.1.3 CLUSTER ANALYSIS

A dendogram (Fig. 8-18) was employed to test if the related phytolith morphotypes could be identified and grouped based on their respective sites and frequency of types. When the full dataset is employed the ensuing cluster analysis shows several behaviours such as intermixing of samples from UMBI to LMBII or vice versa, and some of the samples observed jumping to different clusters, such as phytolith samples from the Castle site. The FLK-W and FLK- N horizon samples are more clustered together, not jumping to the other clusters like the FLK-N site, LAS and BPT samples. Cluster analysis shows that samples from all sites are not diverse in regard to phytolith morphotypes and cannot be explained by chronology and time to differentiate between UMBI-LMBII plant landscape. The hypothesis being that, no significant differences that could be detected by phytoliths types between the studied sites. The similarity of the cluster analysis results imply that the samples are not diverse and there is more similarity in morphotypes distribution per site than the dissimilarities. Therefore, no differences can be detected by clusters from sites' chronology when using the phytolith morphotypes occurring between the UMBI and LMBII samples.

In the dendrogram shown in Figure 8-18 (Wards' method, Euclidean distance, normalised data), samples are classified into six main clusters based on phytolith preservation and abundance per sample in the full dataset. The first cluster groups represented by samples mainly from the FLK-W site followed by FLK-N site, and FLK-N Horizon, respectively. Samples FLK-N site # 8, FLKN horizon # 30, and FLK-W samples # 4, 5, 6, 9, 12, 13, 14, 15, 18, 19, 20, 21, 22, and 23 are closer than the rest, thus indicating that they are rich in phytoliths, documenting \geq 300 phytolith count per sample and have good preservation too, therefore are separated from the other clusters. There is an intermixing between UMBI and LMBII phytolith samples as it is indicated by those samples grouped under this cluster. The second cluster groups are FLK-N horizon sample # 5, 19, 23, 24, 25, LAS sample # 9, Castle sample # 9, and BPT sample # 5. They merge together because the phytolith preservation in these samples is relatively good. The samples in this cluster tallied between (n= 100-180) phytoliths. No sample from FLK-W and FLK-N site is grouped in this cluster.

The third cluster groups belong to two sites only: FLK-N and FLK- W, and are represented by FLK-W sample # 2, 3, and 25, as well as FLK-N sample # 11 and 12 and all of them belong to this cluster because of their phytoliths abundance which ranges from (n = 340-400) phytolith counts per sample. The preservation of phytoliths in this cluster is excellent with relatively good distribution of different phytolith types throughout. The fourth cluster comprises samples from three sites only, the FLK-N site, BPT, and FLK-N horizon, as indicated by BPT sample # 1, 2, 5, 6, and 10, FLK-N site #1, and 2, as well as FLK-N horizon # 1, 2, 3, 4, 6, 7, 9. 10, 12, and 27. These are the samples that yielded \leq 200 phytoliths. The fifth cluster group is made up by samples from FLK-N site, BPT, Castle, FLK-N horizon; these samples are documented relatively poor in terms of phytoliths preservation. The sum of phytolith tallied from each sample in this cluster is ≥ 80 counts. The six cluster groups samples from different sites and were assigned to the same cluster, mainly since the phytolith samples from these different sites which are intermixing between the cluster and comprised mostly samples from the LAS and Castle. In these samples, either phytoliths were recorded at a very low amount or non-observable at all. In these samples, during the phytoliths counting, the microscopic slides were mounted more than three times, but their counts were below (n=50) phytoliths per sample.

The last cluster comprises mostly phytolith samples from all studied sites that yielded ≥ 100 counts per sample. They assigned to the same cluster because of few to moderate phytolith abundances. They consist of a big intermixing of samples from UMBI and LMBII. In summary, statistical analyses of phytolith morphotypes and frequencies show no significant differences in site clustering and correlation in many samples that could be easily used to detect the shift in arboreal versus grassy vegetation cover during time in question.



Figure 8-18: Cluster analysis dendrogram

8.2 LANDSCAPE DIVERSITY IN UPPER BED I/LOWER BED II

8.2.1 UPPER MOST BED I (UMBI)

The UMBI phytolith data shows variability in both assemblage's composition and diversity, which can be attributed to, or be driven mainly by, Pleistocene climate scenarios that are considered to influence hominin subsistence behaviours in east African region. The climatic shifts in the past influenced human behaviours and their eventual adaptations to various and different ecological niches as indicated by the phytolith data below. The phytolith data infer a wooded, an arboreal vegetation structure which provided hominins a variety of habitats ranging from forests to woodlands during 1.83-1.80 Ma.

8.2.1.1 FLK-North

Most of the phytolith assemblages at the FLK-N horizon represents dicotyledonous wood/bark types about \geq 80 dominated by these types. Palms are also abundant at FLK- N as indicated by globular echinate phytoliths, and the globular-spiky with tuberculate indicating marantaceous monocot plants. Aerial sampling at FLK-N horizon towards eastern side between the distance of 0.8-2 km towards the confluence of the main Gorge, yields globular echinate morphotypes suggesting that palms were distributed throughout. At these levels, globular echinates and other arboreal taxa characteris e the horizon by more than 88%. Additionally, the presence of wet adapted phytoliths, diatoms, and spores might be an evidence of wet environments at the FLK-N horizon during 1.83 Ma (see Appendix Table 1-3), as inferred by long saddle phytoliths, which are attributed to wet adapted, dense forest. Other morphotypes, such as tower phytoliths for cool adapted grasses, bilobate, short shaft, convex ends, which typically infer seasonal, partly wet-adapted grasses, and bilobate short shaft with concave ends, were used to infer seasonal, partly 262

wet-adapted grasses. The presence of bilobate with long shaft and globular granulate-ridged can imply that the vegetation during this time composed of a gallery forest that is characteris ed by herbaceous plants at the FLK-horizon. Similarly, diatom, spore, sponge, and non-pollen palynomorph which acts as indictors of wetland environments were documented scattered throughout FLK-N landscape .

The FLK-N phytolith assemblages from lower levels (1.83 Ma) consist mainly of arboreal types, palms, and GSSC phytoliths, with arboreal phytoliths outnumbering both palms and grassy taxa, average $\geq 70\%$ compared to $\leq 5\%$ of the latter. In all samples collected at the clays below Tuff IF (1.80 Ma), they indicate that the vegetation is diverse with globular spiky with tuberculate (marantaceous monocots) being well represented. During the UMBI times it is believed that this site was vegetated after lake regressions as suggested by Albert and Bamford (2012), who believe that the whole landscape have been very unstable with flushes of plant growth being frequently totally or partially destroyed by the various pyroclastic events. The scenario of small groups of hominins making brief visits to the eastern palaeolake margin during UMBI times as put forward by previous researchers is probable. However, their study generally did not yield direct evidence of hominins visiting during Tuff IF times (1.80 Ma), but food was likely available at various intervals. Previous palaeoenvironmental studies in the Oldupai Gorge show the landscape was wooded during 1.83-1.75 Ma, that climate and tectonic activity probably controlled the fluctuating lake levels, but locally the palaeorelief and drainage were probably the controlling factors for the vegetation changes during UMBI-UMBII.

Multiproxy data from stable isotopes, plant biomarkers, and plant micro-remains (Ashley et al., 2010, 2014; Albert et al., 2010; Patalano, 2019) provide scenarios that would imply that

small groups of hominins used to make brief visits to the palaeolake during upper most Bed I times, followed by a more desirable vegetative environment during lowermost Bed II times. Hence, based on phytolith abundance, prior to the eruption of the Mount Olmoti volcano, the lake margin where the sedimented samples were collected was probably lightly vegetated by grassland associated with woody dicot plants (Albert et al., 2010). A recent isotope study by Patalano (2019) suggest that, based on the carbon and hydrogen isotope data, the vegetation community of FLK-N was unlike anything found at Olduvai Gorge today. Current annual rainfall at Olduvai averages 550-570 mm (Hay, 1976; Deocampo, 2004; Patalano, 2019; Mercader et al., 2019), a substantial decrease from that of Bed I times which was estimated to be slightly less than 850 mm (Cerling, 1984; Cerling and Hay, 1986, Patalano, 2019).

Moreover, if Oldupai was generally wetter during the Early Pleistocene than the Crater Highlands, which receives nearly twice as much rainfall as Oldupai, it likely received precipitation in excess of the 1,037 mm documented in Ngorongoro today (Deocampo, 2004, Mercader et al., 2019). Because the Crater Highlands act as a recharge zone for aquifers in the Oldupai region (Ashley et al., 2009), groundwater originating in the highlands likely discharged along faults or impervious beds in and around the FLK area. On top of that, fluviatile systems fed by rainfall in the highlands could have provided fresh surface water through incised channels on the palaeo-alluvial fan (Stanistreet, 2012). Again, it is possible that a constant supply of freshwater resulted in the dense vegetation structure at the FLK-N landscape as documented by leaf wax lipid biomarkers (see Patalano, 2019).

The dominance of arboreal vegetation suggests that the FLK-N may have been like the dense evergreen forest on the northwestern shore of Lake Manyara or the Lerai Forest of Ngorongoro Crater (Copeland, 2007). While substantial progress has been achieved in teasing out the environmental context of early human evolution and available plant niches, our understanding of the interface between the earliest stone tool technology (Oldowan and Acheulean tools kit), plant use, habitat choice, and dietary ecology remains impoverished during this time period. The micro-botanical, isotopic, and taphonomical studies of faunal remains converge on the same concluded that the area surrounding FLK- N site which attracted both carnivores and hominins in the early Pleistocene, was densely wooded and wet during uppermost Bed I time. The phytolith-based palaeoenvironmental reconstruction of a palaeo-groundwater forest close to the spring heads by (Ashley et al., 2009, 2010; Barboni et al, 2010, Albert and Bamford, 2012) suggest FLK -N was formed on bushlands to wooded grasslands. This sounds plausible as the assemblages from this study interpreted FLK- N site as reflecting the large proportion of trees, achene -sedges, ferns, palms, and shrubs versus few grasses both on site and across the landscape.

8.2.2 LOWER MOST BED II (LMBII)

The phytolith data during LMBII show a wooded to open grasslands which might have provided a variety of resources that attracted and sustained hominins on these landscapes. These types of plants niches were probably located at the more open landscape, which provide favorable settlements to subsist, interact, manufacture stone tools, and the ability to spot and avoid predators. Hominins would have interacted for different activities and for exploitation of variety of resources there adjusting into various changing environmental conditions during Bed II time. These are the habitats that favoured the settlements for Acheulean tool makers during 1.7 Ma. Therefore, there is a significant difference between plant landscape occupied by hominins as indicated by phytolith data from Castle, LAS, and BPT localities. However, no significant differences could be detected by phytolith data from FLK-W with the Bed I phytolith records. The more marked differences in plant vegetation are the clearly indicated by phytolith assemblages from LAS, Castle, and BPT which altogether show an open landscape with extremely low woodland indicators.

8.2.2.1 CASTLE SITE

The phytolith assemblages from all levels at the Castle site have characteristics suggesting the influence of long-term vegetation trends and soil mixing. Arboreal phytoliths dominate the assemblage, but it is dominated by only one type of blocky phytoliths while GSSC phytoliths have no contribution because were not documented. The presence of silicified mesophyll cells and the complete absence of grass silica short cells in all samples from Castle strongly suggest the presence of either high energy water-environment, winnowing, or other chemical factors relating to site pre and post-deposition. One type alone, mesophyll cells dominated 57% the total sum of the sites assemblage; this may be due to the nature of the site or methodological issues in the lab.

In the laboratory, the first extractions were negative. We changed our protocol for clay dispersals shifting from EDTA solution to sodium hexametaphosphate. The second time of phytolith extractions, there were no phytolith from the Castle clays again. After using 0.1 ml of (NaPO₃)₆ to disperse the clays for the third time, we were able to see phytolith from the Castle sediments. The preservation of phytolith assemblages at the Castle site is relatively poor and the reasons behind this might be lab extraction procedures or site taphonomical issues that needs to be further explored. The recent stable carbon isotope study from this site by Patalano (2019), suggest that the Castle was an open grassland with a small woodland or bushland and thicket component whereby C4 grasses never comprised less than 60% of the total plant biomass and at times, may have accounted for 99-100% of the vegetation. Phytolith from this study diachronically indicate

that the Castle site is composed of arboreal cover as represented globular granulate, blocky, and tabular phytolith morphotypes.

8.2.2.2 FLK-WEST

The FLK-W phytolith data suggest abundant woody plants (highest of all the documented sites $\geq 50\%$). The vegetation including trees and/or shrubs, palms, and Marantaceae monocots (globular spiky with tuberculate and globular crenate), which are well distributed at FLK-W site, whereas there are very few grasses. Few morphotypes indicator of wetlands or sedges (papillae) were documented in the lower most Bed II time (~1. 69 Ma). At the level 1-3 of the column, the relative abundance of grasses attests for a more open vegetation such as wooded grassland whereas trees and/or shrubs and palms were scattered throughout.

All samples documented are productive and high amount of globular granulate phytolith types which are attributed to woody dicotyledons, which indicates the presence of trees and/or shrubs in the palaeovegetation. Other arboreal indicators such as globular crenate, psilate, and globular echinate forms 10% in the assemblage. Another category of arboreal indicators such as blocky, cylindroid, and tabular types forms over 65% of the total assemblage. Forest indicator phytoliths, which are made up by globular granulate and blocky with decorated bodies plus the striated/pitted-like bodies as well as sclereids are found most abundant at FLK W site upper units. The GSSC were found rare to moderate in many samples at this site comprised of (Rondel: tower, wide, horned, and Saddle long, short, as well as Bilobate: long and short) which together forms less than 10%.

Interestingly, at FLK-W phytoliths are well preserved and well distributed as well as diverse than at any site, and they resulted to many counts than all studied sites. Palm phytoliths

(globular echinate) were abundant in samples found in association with phytoliths that are globular crenate, globular-spiky, and globular echinate with small (micro) spines arranged in a fuzzy pattern, which could be probably assigned to the tall understory monocots Marantaceae/Costaceae (see Sikes and Ashley, 2007; Mercader et al., 2010, 2019). Palms and Marantaceae/Costaceae plants possibly were, therefore, have been locally abundant in the palaeolandscape dwelled by hominins. These results are correlative to Barboni et al., (2010) who argued that the FLK- W during that time period as wetter and somehow wooded. Again, this could be attributed to more wetter conditions which are often colonis ed by palms, palm forest most coming from species producing globular echinate morphotypes.

Archaeological research at the FLK-W has shown that faunal assemblage is dominated by open-habitat taxa, and at least 20 individuals from Bovidae, Suidae, and Equidae were identified in Levels 6 and 5 (Díez-Martín et al., 2015; Uribelarrea et al., 2017)), while the minimum number of individuals in L1, L2, L3, and L4 was 13, three, two, and twelve, respectively (Yravedra et al., 2017; Uribelarrea et al., 2017). Several bones from the recovered assemblage show signs that they had been affected by exposure to water before burial, and Uribelarrea et al. (2017) suggest that the FLK-W was located along a sinuous stream that converged into a single channel at the site. Therefore, if water was abundant at FLK-W, specifically during the period when L6 and L5 were deposited, then the hominin-used landscape can be constructed as both wetland and woodland types as evidenced by the presence of papillae phytoliths, diatoms, and spores (see Appendix Table 1-3 and Fig. 7-3) as well as grasses as indicated by the long saddle, for wetland adapted grasses.

8.2.2.3 LAS

Phytoliths were identified in only six samples at the LAS, and there are no sufficient numbers of identifiable morphologies to infer with confidence the specific type of vegetation. The problems might be methodological issues in the lab again as the case of the Castle site, and significantly the sites' taphonomical biases are issues that need to be taken into consideration. The few abundances of phytolith types, and the situation whereby 75 % of the total counts is dominated by only two types (mesophyll cells and hair articulated), might have been caused by taphonomical factors. The pattern is almost similar in all samples may suggests somewhat drought stress environment (less than 1%) for the grasses across the LAS horizon. At the LAS, a statistically valid count of \geq 300 phytoliths could not reached out. The phytolith morphotypes representing mostly by arboreal types, the LAS horizon arboreal assemblage is characteris ed by blocky and tabular phytoliths of various morphotypes (54%), globular granulate (15%) and saddle and Rondel (1%), Oblong granulates (0.43%), and cylindroids (0.43%).

Geologically, the LAS is interpreting the area downstream connecting to the site of FLK-W, which was a well-watered locale during lowermost Bed II time. In terms of archaeological record, the accumulation of stone tools in the LAS unit palaeosurface could have taken place either when the river was dry or during low flow stages. FLK-W was formed in the first scenario (Díez-Martín et al., 2015), which would mean that most channels found upstream would also be found dry. In this same interval, it is also possible that the neighbor HWK sites were formed. During medium or low flow stages, a braided river only occupies some of the channels, leaving several islands (Uribelarrea et al., 2017). In this situation, with no bank-full, it is very probable that flooded and

dry braided channels coexisted, whereas downstream, the convergent channel would always carry the same amount of water.

During these periods, hominins would have been able to accumulate tools in these abandoned riverbeds around the HWK sites, whereas this could not be possible in the FLK-W channel. In any case, the only Acheulean industry accumulation is found at FLK-W, in a single downstream channel, which could be explained by ecological or landscape related limitation environments is especially noteworthy in Bed II, where 90% of all faunal remains are found associated with fluvial systems (Hay, 1976; Uribelarrea et al., 2017). The progressive aridification of Bed II could explain this faunal concentration near fluvial environments where water is more accessible, hominin could have settled nearby or adjacently to the fluviatile wetlands. Phytolith assemblages indicate that at the time of deposition, the LAS would have been an open woodland- grassland with small input of arid-plants, and the open woodlands with few shrubs and other aridity adapted plants would have accommodated the hominins. The true grass input to the phytolith assemblages averaged less than 1%, and this situation is an unjustifiable, we were expecting to encounter the same pattern as the FLK-W, which is predictable since palm forests are also a type of open forest that were commonly abundant at the nearby site.

8.2.2.4 BPT

Phytolith assemblages at BPT indicate high variability in vegetation structure throughout sampled horizons, thus showing a general trend of woody dicots (over 70%) continuously and therefore dominating most of the plant landscape during 1.60 Ma. The globular granulate/tuberculate phytoliths comprise ≥ 26 % of the total sum at BPT, arboreal indicators are forming the second majority after the hair articulated types, which are the majority. Most of the phytoliths at the BPT horizon are heavily decorated and dissolute, with granular-pitted bodies ranging from globular to globulose, and oblong granulate shapes that are well distributed in all ten samples.

However, the high amount of hair base and hair articulated ≥ 30 % phytolith morphotypes may raise some preservation questions. Taphonomically speaking, the BPT, like the samples from the LAS, may suggests additional taphonomic processes at work as noted by the current study of multiproxy (plant lipid biomarkers) study undertaken by Patalano (2019), who noted that the depositional and sedimentary environments at the BPT horizon might include translocation or diagenetic processes related to within-sediment chemical imbalances, changes in interstitial water composition, or changes in temperature that altered hydrocarbons after deposition and burial, or the role soil chemistry and soil temperature has in compounding the effects of microbial activity either shortly after lipid deposition or after burial. These sedimentary and chemicals could have impacted phytoliths preservation in many ways.

Despite these varied depositional histories, the plant landscape which evolved during the 1.60 Ma might have altered the available niches for hominin exploitation, and thus have concentrated towards more open landscapes, most likely the BPT being the ideal place. The vegetation cover during this period would have been possibly open arid grasslands with less or no tree cover (see Uriberralea et, 2017). Phytolith assemblages at BPT reflect both local and regional vegetation cover with dominance of arboreal taxa with very few grassy taxa. From previous vegetation studies at Oldupai have shown that the palaeovegetation evolution and hominin landscapes during UMBI-LMBII was wood/bark phytoliths are robust and tend to be overrepresented in the fossil record whereas sedge and grassy phytoliths are fragile and under-

represented in the fossil record (Albert et al., 2006; Albert and Bamford, 2012; this study). The interpretation of the vegetation, however, is not straightforward because of the taphonomic biases in sites with complex deposition histories like the Oldupai's Bed I- II.

8.3 DIVERSITY OF PLANT NICHES

The phytolith results from this study show that there is a dominance of woody/arboreal phytoliths during Bed UMBI (1.83 Ma). However, this could be interpreted not as a closed woodland but rather as woody vegetation (trees or shrubs or woody herbs) with a herbaceous monocot component as well. The presence of papillae phytolith from sedges at FLK- W (1.69 Ma), suggest the area was still wet, characterised with sedges and a mixture of grass and woodland as a main component that was probably favoured the hominin settlements. Towards LMBII times, the dataset at FLK-W, at the Castle, LAS, and BPT does not support a dense wooded environment and instead suggests a more open plant landscape during this time. The dominance of mesophyll cells and irregular indeterminate types that looks like leaf anatomy at Castle site and LAS horizon may be suggestive to water action conditions or may suggest that the landscape preserved these morphotypes is not the growing surface. Most of the samples from the LAS (e.g. sample # 8) are affected by dissolution, a condition that may suggest a high alkalinity, which is also observed at the Castle site as well. Unfortunately, the soil geology of the Castle and FLK-N sites are unknown at the time of this dissertation, as geologists were not involved during sample collection. And at the FLK-N horizon for example, sample #16 is very rich and diverse of several morphotypes as well as sample # 30, collected nearby the confluence of the main Gorge, and at the FLK-W upper levels (samples from clays above IF) produced over 10% globular echinate which is an arboreal

indicator of palms environment. The hypothesis which can be deduced is that an oasis could have been located around the same landscape. The phytolith data show ancient landscape that is dominated by arboreal types. The arboreal plant cover can be interpreted as dense throughout in FLK-N horizon and closely resembles that of the FLK-Site from the UMBI and the lower units at FLK-W site. Phytolith assemblages from palaeosols deposited between 1.83 Ma to 1.60 Ma be suggestive of a general trend in vegetation cover which dominated woodlands to lesser extent mixed grasslands.

The relative representation of phytolith types documented in lower levels and higher levels does not show marked differences at FLK-N and FLK-W sites, the only notable differences are observed at the LAS where preservation was very poor in all samples. At the Castle site, phytolith preservation-diversity is not well established, the phytoliths homogeneity is very high unlike other sites. At LAS for example, one type alone (Mesophyll cells) accounts for over 62% of the assemblage. However, at all of the other sites three phytolith types present dichotomised distributions, i.e. globular granulate, blocky, and tabular types, these are arboreal indicators. The higher contributor among short cells class is represented by rondel types which are indicators grasses. These forms most of the GSSC at FLK-N horizon and FLK-W site respectively. Almost the 1/4 of the variability in grassy indicators documented in this study is accounted by a subset of GSSC phytoliths that, in a typical assemblage, encountered to majority of the samples at the FLK-N site, FLK-N horizon and FLK-W site, these are: Rondels (horned, tower and horned), Saddle (long and Short), Bilobate (concavity and convex). Other types are long cells from bulliform and scutiform however these ranked the lowest.

The landscape evolution can be constructed by general vegetation patterns, which shows that woody and herbaceous dicots were more prominent than grasslands during UMBI, and lesser at the most of the LMBII sites. Data from the BPT, LAS, and Castle would suggest that vegetation structure was not quite stable; there would be specific periods when landscape expanded to xeric environments. Phytolith assemblage suggest that the vegetation structure changed in response to changing environmental settings that was mainly influenced by climatic factors especially changes in water regimes.

Both intra and inter site differences in eigenvalue scores between phytolith samples implies that hominins occupied a diverse landscape that consisted of various niches across the horizons, which means that hominins inhabited variable environmental settings during the Bed I-II times. The correspondence analysis data, based on sample eigenvalues and variance percentage components, presents a high degree of correlation among Bed I sites and no correlation in most of the Bed II assemblages. There is not so much significant correlation between the Bed I plant landscape, i.e. the FLK-North horizon and the FLK-North site level, of which both have eigenvalue loadings that range from 19-35%. Similar trends occur towards Bed II but they are limited to only one site in Bed II (FLK-West, eigenvalue loadings are approximately 39%), while the Castle Clay (Geolocality 44B) has eigenvalue loadings average around 50%. This geolocality has more differentiated scores and isolated eigenvalues loadings in comparison to other Bed II localities. This would suggest the presence of a variety of niches that were favourable for hominin settlements during time in question. Interestingly, a very similar pattern is observed in the LAS and BPT geolocalities, as both are characterized by eigenvalue loadings which range from 25-29% (see Tables 8-9 to 8-14). The differences in eigenvalues and variance percentages in both Bed I and

Bed II sites implies the occurrence of very diverse environmental niches that probably offered hominins variable settlements and food exploitation patterns.

Hominins would have occupied a wide range of environments, variable ecological settings, and a variety of microhabitats, ranging from forested to open wooded vegetation cover, or even a mixture of woodlands and forested environments. It is probable that rivers, streams, and channels would have sustained hominins and provide them with drinkable water and were probably also occupied as home bases for stone tool manufacture across Bed I-II landscapes. The landscape could have been a water-fed and wooded arboreal landscape, which was suitable for hominin settlements. The phytolith data suggests that Beds I and II were characterized by a plant landscape composed of vegetation mosaics. Hominins would have acquired various foods, accessed water resources, engaged in hunting activities, and sought shade for tool making, breaking nuts, food sharing, and carcass processing home bases. However, it should be noted that the statistical data based on phytolith morphotypes distribution between Bed I and Bed II sites as indicated by the descriptive statistical analyses show some differences in niche distribution throughout Bed I-II time. On other hand, the multivariate statistical analyses show no significant differences in vegetation distribution as indicated by phytolith types from Bed I and II, however, these are two different spheres of statistical analyses with different resolutions.

Differential production of phytolith assemblages in plants and preservation in soils are key issues that need a thorough understanding in this field. Phytolith taphonomy research has noted several pitfalls inherent in phytolith analysis, that is essentially phytolith analysis has some potential problems ranging from post-depositional displacement (Rovner, 1983) to dissolution (Cabanes et al. 2011), redundancy, and multiplicity (Rovner 1971, 1983, Mercader et al., 2009,

2019) and phytolith translocation in soils. The post-depositional displacement refers to the movement of phytoliths as a result of redeposition or pedogenesis. Phytolith particles are silt sized and can be moved through aeolian, alluvial, or hydrologic processes. Luckily, morphological characteristics of phytoliths, such as the presence of abrasion or fragmentation, can be used to assess the extent of transport (Piperno, 1988, Fredlund and Tieszen, 1997; McNamee, 2013). Fragmentation, which is easier to identify than abrasion, is particularly useful when most of the assemblage has been impacted. Also, the consideration of post-depositional processes is particularly important in archaeological sediments with complex nature and varied depositional environments like Oldupai Gorge's UMBI-LMBII.

About the problem of redundancy and multiplicity of phytolith types, researchers analysing only extracted phytoliths from these samples might create a prejudiced reconstruction of the vegetation of these sites based on the assumption that all the phytoliths in the samples shared the same depositional history and pathway (Vrydaghs et al., 2009, 2016). These inherent problems i.e. multiplicity and redundancy: multiplicity is when different phytolith morphotypes are produced within a taxon, and redundancy is when the same phytolith morphotypes are produced by different taxa, both have been very persistent challenges in phytolith analysis research (see Rovner, 1971; Mercader et al., 2009, 2019). Importantly, the phytolith assemblages from terrestrial sediments are generally considered to represent decay-in-place or in situ deposition (Piperno, 1988; Mercader et al., 2010; 2013), but they are susceptible to the said issues of inheritance (accumulation over time) (Fredlund and Tieszen, 1994), bioturbation (Runge, 1999; Madella and Lancelotti, 2012), or dispersal through colluvial, alluvial, or aeolian means or both (Twiss et al., 1969; Fredlund and Tieszen, 1994; Alexandre et al., 1997; Strömberg, 2004).

Bioturbation and inheritance might have slightly impacted phytolith assemblages documented by this study, however, phytoliths were probably affected by both alluvial and colluvial transport like at the LAS samples. Also, aeolian transport might have had some impacts at the LAS and BPT samples because environmentally speaking, these horizons are characterised by a more open environment and aridification conditions towards 1.66-1.60 Ma period as indicated by Uribelarrea et al. (2017) and Patalano (2019). Phytoliths inheritance and dispersal could help to explain some of the differences observed in the phytolith assemblages from the documented sites. On top of that, after being released, phytoliths can be transported, either before or after burial, by water (Vrydaghs, 2003, Mercader et al., 2010, 2013; 2019), soil fauna or wind (Twiss et al., 1969; Fredlund and Tieszen, 1994). This transport might be at the origin of altered distribution patterns as well as physical degradation of the phytoliths (Vrydaghs, 2003). For instance, Vrydaghs et al. (2016) believe that phytolith clusters are a clear signature of a certain degree of disturbance, and the articulated phytoliths are those that appear to maintain the relative distribution they had within the plant tissues in which they were accumulated. Also, it has been shown that phytolith analysis using soil thin sections can yield valuable information about taphonomy and local to regional changes in vegetation in some cases, however, again the type representation is heavily affected by differential production, preservation, and age (Albert and Marean, 2012; Vrydaghs, 2016). The micromorphological analysis of the thin sections of sediment will help to explain whether the collected sediment samples in the field are intrusive or originating in outside settings (Vrydaghs et al., 2007, 2016). For better reconstructions of accurate local vegetation histories for a site using phytoliths, micromorphological analysis of thin sections to establish depositional histories is a useful and perhaps critical step (Vrydaghs et al., 2016). An archaeological deposit or soil and as such can help researchers answer questions concerning redundancy, multiplicity and depositional history because phytolith assemblages are susceptible to issues of over- and under-representation (Vrydaghs et al., 2009, 2016).

The integration of phytolith analysis with micromorphological analysis of a series of thin sections should be inevitable in phytolith research. Thin sections preserve the distribution patterns of phytoliths within, thus will solve the problem of phytoliths "not recorded" rather than "absent" when phytoliths are not observed (Vrydaghs et al., 2016). In addition, a true absence of phytoliths, the quality of the thin sections, preservation conditions, the presence of coatings and the nature of the groundmass can also account for a lack of recorded phytoliths (Albert and Marean, 2012). The occurrence of other types of biogenic silica, particularly diatom remains, chrysophycean cysts and sponge spicules, could at least indicate that poor preservation is not an issue (Albert and Marean, 2012). In addition, the occurrence of plant tissue or organ residues points to the presence of plant remains, which may have released phytoliths into the soil, here the basic paradigm of phytolith taphonomy is that phytoliths are released into the environment through the decay of plant remains, before or after the burial of those remains (Madella and Lanceoletti, 2012). Besides natural decay of organic matter, human-induced processes, such as fire and plant processing can also be at the origin of phytolith release (Powers-Jones, 1994; Madella, 2003).

As it was mentioned earlier on, phytolith analysis, however, as with all palaeoenvironmental proxies, its taphonomy is not without limitations. For example, the internal cavities which may also appear as opaque spots due to the occurrence of trapped air, independent of the presence of organic compounds was a centre of debate during the previous decade. Based on the assumption that phytC originated from the photosynthesis of atmospheric CO_2 in the host

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plant, several studies used phytC δ^{14} C and δ^{13} C signatures respectively as a dating tool (Piperno and Stother, 2003) and a palaeoenvironmental proxy (Alexandre, et al., 2015). However, very recently, ¹⁴C-AMS measurements of phytC samples from modern grasses yielded ages of several thousand years, which suggested that phytoliths may incorporate a substantial amount of old carbon, potentially from the soil (Alexandre et al., 2015). Amino acids from soils have been shown to be taken up by plants, and transported in small proportions to roots, stems and shoots (Gao et al., 2018). Thus, it is not inconsistent to assume that C and N derived from these soil amino acids have been trapped in phytoliths.

Although the hypothesis still needs to be verified, it raises the question of the molecular nature of phytC. Several techniques such as high-performance liquid chromatography (HPLC), gas chromatography mass spectrometry (GC–MS), protein staining, micro-Raman analysis and X-ray photoelectron spectroscopy (XPS) have been used to characterise phytC and led to contradictory results, especially regarding the presence or not of amino acids (Elbaum et al., 2009; Watling et al., 2016). The problem is that these methods were applied on phytolith concentrates that were not proven to be completely devoid of extraneous organic remains. Chemical extractions leading to high-purity phytolith concentrates are indeed difficult to implement (Elbaum et al., 2009). Although the absence of organic particles can be checked by scanning electron microscopy (SEM) coupled with EDX, the presence of extraneous organic remains on the phytolith surface cannot be accurately detected. Differences in the efficiency of phytolith extraction protocols may also explain the inconsistencies in phytC quantification. Accurately quantifying the phytC is important for the assessment of its significance in the terrestrial C cycle (Elbaum et al., 2009; Watling et al., 2016).

Multiple studies have recently claimed that phytC may play a role in atmospheric CO₂ sequestration and climate change mitigation (Zuo et al., 2014), although the fluxes of phytC from vegetation to soils and the residence time of phytC in soils are still largely unknown. The assumption that phytC may be located at different sites in the silica structure, with different accessibility to oxidation, has been put forward (Parr and Sullivan, 2014 cited in Alexendre et al., 2015). This assumption supplemented a previous one, widely found in the literature, that micrometric opaque areas observed by natural light (NL) microscopy on some phytoliths were holes containing the phytC (Prychid et al., 2003; Piperno, 1988; 2006). No measurements were however performed to support any of these hypotheses.

Finally, the debates on content, location, nature, origin and palaeoenvironmental meaning of phytC have been fed by the scarcity of in situ characterisations of phytC in phytoliths, thus culminated the study by Alexandre et al. (2015) who we reconstructed, at high spatial resolution, the 3-D structure of grass phytoliths using 3-D X-ray microscopy. Simultaneously, Alexandre et al. (2015) characterised the location of phytC using nanoscale secondary ion mass spectrometry (NanoSIMS), noted that phytoliths occlude small amounts of organic compounds, first evidenced by the production of carbon (C) and nitrogen (N) during dry ashing (Alexandre et al., 2015). This condition has been assessed by the scanning transmission electron microscopy (STEM) and energy dispersive X-ray (EDX) analyses of phytoliths in the plant tissues of which both confirmed that the occluded organic compounds contained C, N, and phosphorus (P) (Alexandre et al., 2015). These occluded compounds are called phytC, the PhytC, which is assumed to be protected from natural oxidation by the siliceous structure, has been the subject of increasing attention and debate in phytolith research. The silica structure contains micrometric internal cavities, these cavities

were sometimes observed isolated from the outside as noted by Alexandre et al. (2015), and their opening may be an original feature or may result from a beginning of dissolution of silica during the chemical extraction procedure, mimicking the progressive dissolution process that can happen in natural environments. The phytC that may originally occupy the cavities is thus susceptible to rapid oxidation. Alexandre et al. (2015) findings constitute a basis to further characterise the origin, occlusion process, nature and accessibility of phytC, as a prerequisite for assessing its significance in the global C cycle rather than to phytoliths in archaeological record (Alexandre et al., 2015).

However, the issues of inheritance and dispersal, previously discussed, as well as differential preservation and solubility of phytolith types, should be considered in any phytolith research. The baseline analogues from modern soils and plants from the region under study is a prerequisite endeavour, the referential baselines will serve as modern analogues to interpret phytoliths from archaeological and palaeoecological records. For instance, in modern plants some phytolith types have large surface areas or are not as heavily silicified as more robust morphotypes and are therefore more susceptible to fragmentation and/or dissolution (Piperno, 2006). For this reason, some types of phytoliths may be under-represented in older sediments (Alexandre et al., 1997; Piperno, 2006; Barboni et al., 2010).

For example, several studies have noted that conical phytoliths typical of Cyperaceae tend to be poorly preserved in soils (Alexandre et al., 1997; Albert et al., 2006; Novello et al., 2012), while some experiments have been conducted on phytolith robustness and preservation (Cabanes et al., 2011); therefore, these issues warrants more attention in phytolith analysis. Several researchers have noted that phytolith abundance often decreases towards the bottom of soil profiles (see Runge and Runge, 1997) although this is not always the case (see Piperno, 2006) and may relate to saturation levels of biogenic silica within tropical soils (Alexandre et al., 1997). However, it is important for any phytolith research to consider analysis of modern samples from different parts of plant versus grass leaves, shoots, and other plant parts in order to see the comparative developmental patterns of phytoliths in plants and grasses in order to identify and clarify the evolution and development of silica cells (Rudall et al., 2014).

The homologous studies from this area have indicated that pre-and post-depositional processes may affect phytolith deposition and preservation in soils (Albert et al., 2010, 2012; Barboni et al., 1999, 2010; Mercader et al., 2019). Pre-depositional processes are the factors that may influence the plant accumulation in soils and their subsequent release of phytoliths after organic material decay. External factors like the degree of vegetation cover, the differential phytolith production in different plants, and the life cycles of specific plants have all been shown to influence the pre-deposition of phytoliths in modern soils (Piperno, 1988, 2006; Mercader et al., 2019). Other external factors may relate to dissolution, which can also impact phytolith preservation (as the case of Castle, LAS and BPT phytolith assemblages). The understanding of taphonomy of phytolith dissolution is related to knowing the history of the available moisture in the study area and soil pH, whereby the increases in dissolution are associated with alkaline conditions, and the nature and type of dissolution may vary among phytolith types based on chemical composition form, time, and age (see Cabanes et al., 2009, 2011).

Nevertheless, the inherent problems of redundancy and multiplicity in phytolith production in plants has been studied and understood through the study of specific diagnostic morphotypes which are not the confuser types in their identifications. Current studies, such as those by Vrydaghs et al. (2016), have demonstrated that the micromorphological and phytolith analyses of soil thin sections, whenever integrated with phytolith analyses, have been able to thoroughly address the issues of redundancy and multiplicity, as well as depositional histories of archaeological soils and sediments. The critical analysis of phytoliths within soil thin sections is becoming a more frequently applied alternative to analysing phytoliths extracted from buried ancient soils and sediments (Vrydaghs et al., 2016). Soil and sediment thin sections normally preserve the distribution patterns of phytoliths within an archaeological deposit or soil and can thereby help researchers answer questions concerning redundancy and multiplicity. An incorporation of phytolith and micromorphologic analysis allows researchers to discriminate among phytoliths sharing different depositional histories, such as those associated with coprolithic or burned material and those that enter the soil matrix as part of buried plant tissue (Vrydaghs et al., 2016).

Importantly, in contrast to the study of phytoliths extracted from bulk soils and deposits, analysis of thin sections allows researchers to better examine the distribution patterns of phytoliths in a specific sample in detail. For example, it is now understood that articulated phytoliths are found to be more widely preserved in thin sections than in extracted samples (Vrydaghs et al., 2016). The distribution patterns of articulated phytoliths in thin sections can help researchers identify those phytoliths that entered the sample as the result of in situ decomposition of plant fragments and those that share a common botanical origin, thus helping resolve some of the taxa identification challenges that are related to multiplicity and redundancy. Researchers conducting morphometric analysis of phytoliths in thin sections have attained the ability to identify those assemblages that are produced by a single taxon or vice versa (Vrydaghs et al., 2007; Vrydaghs et al., 2016), while other researchers deal with the problems of multiplicity and redundancy by taking an assemblage approach that examines the proportion of different forms in broad vegetation zones,

such as studying the proportions between C4 vs. C3 dominated grasslands, forested vs. grasslands, and wetland vs. dryland dominated plants (see McNamee, 2013).

These recent investigations into phytolith production in the modern plant kingdom have helped phytolith researchers to overcome the pitfalls of multiplicity and redundancy when reconstructing source vegetation from a very dispersed assemblage in archeological sites (Wallis, 2003; McNamee, 2013). The distinctive phytolith types are presently being identified at the family, genus, and, increasingly, species level (Pearsall, 2000). These diagnostic phytoliths are produced by some plant taxa and various plant species, thus enabling a more precise identification of many plants to the family and species level, as well (also see McNamee, 2013; Mercader et al., 2009). However, in order to carefully underscore the problems of redundancy and multiplicity, one requires an understanding of the assemblages produced within and between modern living plants. Most recent studies (see Mercader et al., 2019) have insisted on the importance of having an established and extensive regional comparative collection from modern plants and soils which could be used later to aid in the interpretation of phytolith morphotypes extracted from ancient soils and sediments.

In addition, the identifications made on phytoliths that are known to have the same depositional history, which has been confirmed by micromorphological analysis of thin sections, are nowadays considered to be more reliable than those based on phytoliths extracted from the soil of which the depositional history is partially known or completely unknown. Traditionally, early research made phytolith morphotype classifications by following three general approaches: taxonomic, typological, and taxonomic-typological (Powers, 1992; Piperno, 2006) analyses. All of these morphotype classifications were based on the morphological appearance of silica particles

under microscopic slides. The taxonomic approach emphasizes morphology in relation to the structure of the original plant tissues and considers phytoliths as one of the anatomical characteristics of the specific plant. For example, phytolith morphotypes with a taxonomic meaning are trichomes, stomata, and bulliforms, to mention a few. Each of these categories has a defined anatomical origin, and a shape that is repetitive, representative, consistent, well determined, and easily identifiable (Powers, 1992). The approach allows for distinction among taxonomical groups and/or anatomical plant parts or cells (Powers, 1992; Piperno, 2006). Recently, some of the redundancy-reducing methods include the use of phytolith size measurements, frequency, three-dimensional shape characteristics, and additional morphometric characteristics derived from stereology, all of which have offered some additional ways to reduce phytolith morphotype redundancy. Additionally, phytolith reference collections of contemporary vegetation have helped in the identification and interpretation of soil phytolith assemblages (Mercader et al., 2019).

Modern reference collections from plants (also see Mercader et al., 2019) is now a prerequisite endeavour in eliminating the problem of phytolith multiplicity and redundancy in the discipline of phytolith analysis. Frequency of phytolith assemblages and measurements of phytoliths are found to be consistent within a species and have been useful for developing key morphotype identifications (Piperno, 1998). Even though phytolith multiplicity and redundancy occur mostly in grassy taxa, frequency assemblages reveal that a certain morphotype always dominates over the others in a given species under study, and thus, Fredlund and Tiezen (1994) suggest that phytolith descriptions at species level should include all morphotypes and their relative frequency, which together characterize specific phytolith assemblages. Therefore, all of

these approaches have dramatically improved the differentiation between arboreal vs. grassy dominated plant landscapes, especially when they are applied in conjunction with a threedimensional examination of phytolith shapes, which is crucial in minimizing the problems associated with multiplicity and redundancy of phytolith forms (Powers, 1992; Fredlund and Tiezen, 1994; Piperno, 1998).

CHAPTER 9: CONCLUSIONS

This chapter provides the concluding remarks on the diversity of environmental niches for hominin settlements at Oldupai Gorge from during Upper Most Bed I to Lower Most Bed II time. It identifies various plant landscapes existed along the Frida Leakey Korongo North, which is situated at the Bed I and the Bed II sites such as the Castle, Frida Leakey Korongo - West, Lower Augitic Sandstone and Bird Print Tuff horizons. It sheds light on various available plant resources for early human exploitation and other affordances being offered by these localities during the dawn of *Paranthropus boisei* and *Homo habilis* to the emergence of *Homo erectus* at the Oldupai Gorge basin. Additionally, this study give contribution to palaeoanthropological theory and debate by advancing the current knowledge of human-ecological interactions through the characterisation of phytoliths.

Phytolith assemblages from this study show the vegetation structure that varied through time, e.g. during Upper Most Bed I (UMBI), indicating a wooded and forested environment as indicated by wetland and humid adapted woody and grassy taxa (long saddle, tower, achene (sedges), and various striated body morphotypes, which are fern-indicator phytoliths), and thereafter some vegetation changes in structure pattern towards a more open, dynamic vegetation cover with either is characterised by patchy woodlands, grasslands or mixture of both. The changes in vegetation structure during Bed II (UMBII) are probably caused by the availability of moisture or hydrological changes across the Oldupai landscape through time. The similar pattern of environmental conditions was also suggested by the previous palaeoenvironmental and palaeobotanic studies that were conducted at Oldupai Gorge basin at different localities and stratigraphic levels since the 1950s. These past research ranged from the pollen spectra, carbon
isotopes, and dependent fauna, to a more recently plant biomarkers of which both have revealed a shift in vegetation from more wooded cover during Mid-Upper Bed I time to more open vegetation by Uppermost Bed II, to woodland mosaics in Lower Bed II (Bonnefille, 1984; Sikes, 1994; Kappelman et al., 1997).

The palaeovegetation studies on Beds I and lower Bed II, especially those ones based mostly on phytoliths and plant macroplant fossil remains (Albert et al., 2006; Albert et al., 2009; Albert et al., 2015; Bamford et al., 2006; Bamford et al., 2008; Ashley et al., 2010; Barboni et al., 2010; Albert and Bamford, 2012; Bamford, 2012; Barboni, et al., 2014; Mercader et al., 2019,) have shown that other proxies such as diatoms are preserved under the palaeosols. Similarly, this study noted that the palaeosol sediments at the studied sites are particularly rich in diatoms and small amounts of other indicators such as spores, non-pollen palynomorphs and sponge spicules are also well preserved (see Appendix Fig.1-3).

At the lower levels (1-4) at FLK- North vegetation shifts through these sequences show more palms and sedges, and in the upper levels indicate some grassy phytoliths such as rondels, short saddle, and bilobates that can be and associated with C₄ grasses. At the Castle site, analysis of the abundance of diatom and spore assemblages points to a potentially complex freshwater wetland characterised by variable soil pH, ranging from neutral to medium alkaline environments. The diatoms and sponge spicules found mainly in the FLK-West samples, indicate availability of abundant streams or water channels across the site including small isolated vegetated ecosystem. The high amount of diatom assemblages at the FLK-West site can be related to a river-fed palaeowetlands, while at the Castle site might be a vegetated fluvial channel that is affected by the river dynamic and suffering periodic droughts. These periodic episodic trends could have possibly impacted various niches and affordances available for hominin exploitation in the landscape during Bed II times.

Prior palaeoenvironmental reconstructions across Upper Bed II sites have suggested the landscape was ranging from grassland to (Bamford et al., 2008) or a range of habitats from open to closed. At the Castle and FLK- West site diatoms and spore are ubiquitous, for example at the FLK-West alone over 700 diatoms were counted, of which the morphology of over 100 of them indicate wetland environments. Elsewhere around the world it was noted that diatom species found in wetlands vary systematically with the water chemistry and are biological indicators of permanently wet ground (Owen et al., 1982). The permanent freshwater sources would likely have affected food-procurement strategies and may have influenced the likelihood of scavenging versus hunting behavior, or vice versa (Potts, 1982; Blumenschine, 1987; Potts 1988; Domínguez-Rodrigo et al., 2007).

Generally, the fossil diatom, spore, and phytolith data provide evidence that the vegetation varied over both short and long distances and over relatively brief periods of time. The study insists for the importance of understanding the nature of the variations of hominin local habitats/landscape and diversity of environmental niches pertinent to hominin affordances across horizon level and any interpretation should be not restricted to the traditional site level approach (see also Albert et al., 2006, Albert et al., 2015). The seasonal streams at Bed II sites would have afforded hominins with fresh water, plant resources such as palm fruits, tubers, and starch-rich rhizomes of *Typha spp*. and sedges, as well as any other scavengeable meat resources in the vicinity. The abundance of palm trees at FLK-West would have provided fleshy seeds for food among hominins again

would have provided a relatively shade for hominins to interact, and this palm forest could have been useful as a refuge for hominin to avoid predators.

Hence, phytolith assemblages during Bed II time in relation to plant landscape, would suggest the likely proximity of trees to these sites, and these trees would have afforded easy access to food resources and a place for refuge against predators (Albert et al., 2006, Albert et al., 2015). Hominins who possibly used this heterogeneous environment would leave behind a diverse assemblage of artifacts and butchery-marked bones, as was predicted by Blumenschine and Peters (1998). Additionally, it has been suggested that Acheulean technologies at Olduvai Gorge first appeared somewhere after the deposition of the Lower Augitic Sandstone towards Middle Bed II, i.e. whereby the scavengeable carcasses may have been concentrated along the edge of the marshland near the center of the valley in the lake margin (Peters and Blumenschine, 1995). During the deposition of Lower Augitic Sandstone affordances were probably the plant foods, portable water, and refuge trees, which together may have been concentrated along the riverine woodland expected for the streams on the distal alluvial fan, and may also have provided a relatively safe travel corridor for hominins along Lower to Mid Lower Augitic Sandstone (see Peters and Blumenschine, 1995). However, the integrative data from multiproxy research are required before making any valid interpretation on landscape evolution in relation to hominin resources acquisition and adaptation to various climatic changes. All multiproxy research should be conducted jointly at the same time to provide an ability to see how these data speak concurrently.

Nevertheless, as noted earlier on, the relatively poor understanding of phytolith production and preservation patterns hampers application of the phytolith analysis in direct palaeoclimatic reconstructions (also see Fredlund and Tieszen, 1997). This is because phytoliths are said to commonly reflect subtle shifts in vegetation composition at the local scale, because they are primarily deposited in situ (Piperno, 1988; Williams et al., 2001). However, phytoliths are displaced from the original deposition site both vertically and horizontally as a result of different depositional activities, or other disturbances caused by animals and other biological factors. Such mixing may blur the vegetation signal offered by phytolith assemblages in terrestrial sediments. However, in most cases phytolith assemblages from archaeological sites are likely to reflect regional climate (see Blinnikov, 2005). For example, at the regional scale, grassland composition is closely associated with temperature and moisture regimes. The calibration of grass phytolith assemblages in climatic terms has now opened a way to the direct palaeoclimatic reconstructions from phytoliths by developing response surfaces and transfer functions (Fredlund and Tieszen, 1997). Presently, the phytolith data could thus supplement palaeoclimatic reconstructions provided by other proxies such as pollen and diatoms (Alexandre et al., 1997; Bremond et al., 2005; Blinnikov, 2005).

During the UMBI towards LMBII times, phytolith data are characterised by wet adapted environment phytolith types e.g. indicators of plants such as sedges and palms and mostly are found in Bed I sites however, by phytolith morphotypes there is a different in vegetation types between Bed I and II sites but when you apply multivariate statistics, results from both correspondence analysis and cluster analysis indicate there is no differences in vegetation types between the UMBI-LMBII. Statistically, the correspondence analyses for Bed I and II phytolith morphotypes suggest an absence of differences in vegetation patterns that is detected, and the data values for Bed I and II phytolith morphotypes are similar in many ways. The correspondence analysis data show an intermixing of phytolith types from different sites and cannot truly applied to differentiate the vegetation types but show some patterns that could possibly suggest similarity in vegetation types but do not show the actual differences. Statistically, no marked differences are indicated by phytolith types during UMBI-LMBII.

Future studies should incorporate multiproxy research for palaeoreconstructions i.e. sampling, collection, and analysis of samples from phytolith, starch grains, pollen, and other plant micro-remains from the same ecoregion in order to complement each other for high resolution environmental reconstruction. Modern referential baselines for ancient starches and phytolith from a wider and broader regional- scale should be a perquisite and sampling for modern plants thriving today at the higher elevations such as Mount Kilimanjaro, Mount Meru, Usambara mountain ranges, and plant samples from around Lake Victoria region should sampled and studied in order to be used as modern analogue for the entire region. For example, by complementing starch, lakebased pollen analyses with phytolith analyses of surrounding ecoregion will provide a much more detailed understanding of spatial-temporal changes in ecosystem dynamics during the Pleistocene time. For instance, Piperno (1988, 2006) has noted, the strength of phytolith analysis in palaeoecological studies lies not in providing specific information of taxonomic diversity and composition, but in using an assemblage approach to investigate and distinguish vegetation communities, particularly when coupled with pollen analysis, stable carbon isotope analysis, and other proxies.

An integrative and innovative complementary approach, which combines phytolith analyses with starch, pollen and stable carbon isotope analyses will provide the greatest potential for accurate and comprehensive botanical, palaeovegetation, and palaeoenvironmental reconstructions in region. Their combined use of these proxies will result into a finer resolution in distinguishing vegetation communities within various East African ecosystems. A more extensive sampling research and even sampling of different vegetation and climate zones would be required before quantitative palaeoclimatic reconstructions could be made with phytolith analyses. This study advocates for an extensive sampling even more sampling of sites outside the Acacia *Commiphora* woodlands. Therefore, future studies should consider sampling a larger geographical area or ecotone to obtain samples from other proxies such as regional pollen from (e.g. Lake Eyasi) which would better illustrate current phytolith-pollen climate relationships. These in the future will provide a basis for the interpretation of fossil pollen and phytolith assemblages recovered from the Pleistocene palaeosols of East Africa, the region is famed by fossil evidences of early human evolution. The research on direct phytolith-environmental relationships has proven that certain morphotypes occur preferentially in certain climates and at certain higher elevations (Bremond et al., 2005; Watling et al., 2016). For instance, long cells as a group and short wavy morphotype tend to occur in higher proportion in drier and warmer habitats at lower elevations, while spiked and other conifer morphotypes occur under moist and cool conditions at higher elevations. Other phytolith types such as rondels tend to be more abundant in samples from moderately dry to moderately moist habitats. Bilobates have a distinct bimodal distribution, occurring in either the dry and warm climate of the lowlands, or in the cool climate of the higher altitudes (see Bremond et al., 2005; Murungi et al., 2017). Blocky types are mostly restricted to dry and warm habitats in lowland areas but are also found in high mountainous forest environments. The regional-wise plant proxy data ranging from starch grains, pollen, phytolith, etc., and their relationships, could further improve our understanding of the potential of phytolith to infer climate relationships when is examined in integration along with these proxies.

For future research therefore, it is needed to explore the possibilities of taking plant samples from Mount Meru, Kilimanjaro, around Lake Victoria and pollen samples from lakes cores, mostly likely the best candidate would be Lake Eyasi basin which will offer opportunity to obtain a higher resolution botanical data from which continuous vegetation reconstruction can be interpreted.

Additional research on modern plants and soils, specifically on production and preservation of phytolith from the higher altitudes of Northern Tanzania is required. Unlike the Miombo woodlands phytochorion of Mozambique that have provide extensive dataset for phytolith production and preservation in modern plants and soils, the Northern Tanzania ecotone has limited reference data from a wider region except the recent one by Mercader et al. (2019). The suggested modern reference dataset should include pollen, spore, diatom, and starch grain data of the ecoregion. This is because some phytoliths may prove to be systematically underrepresented in the palaeoassemblages based on either their low production today or low preservation rate in soils, therebefore would need to be complemented by other proxies from pollen, diatom, spore, and starch granules for better ecological interpretation.

On other hand, one of the most significant findings of this study is the confirmation that even the key proxies which are past indicators of water availability, quality, and seasonality i.e. diatoms are so well preserved in archeological sediments of both Bed I and Bed II sites. For example, over 100 diatoms at FLK- North site were counted, and almost the same number of spores while at the FLK-West site a sum 760 diatoms were counted. Other proxies extracted from sediments are spores, the (mostly from the Castle, FLK-North, and FLK- West sites) sponge spicules, and non-pollen-palynomorphs (see Appendix Fig. 1-3)

Thus, investigations of various proxies of plants will widen are understanding on East African palaeogeographic patterns than influenced hominin settlements in the past. It will further help in the identification of ancient plant physiognomy, endemism, and understanding the physical and biological geographies of the plants in different ecosystems of East Africa during the Pleistocene times. These will precisely interpret the plant environments that served and provided a variety of affordances to our ancestors and adjustment to different climatic stress in the past. Although, the integrating multi-proxy data in archaeological research is very crucial, but it requires several disciplines working together, hence a need of undertaking the cross-disciplinary approach that can provide necessary means and results to reconstruct palaeoenvironments, subsistence strategies, and human-environmental interactions in a variety of complex sedimentary environments. The contribution brought by this phytolith research in the Oldupai Gorge is that future researchers especially from the same region would be able to follow similar methodologies, use results from this research to expand their research avenues, there an ability to refine palaeoecological contexts of human evolution, evolution of plant landscapes, and use of various plant resources by hominins.

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APPENDICES



Appendix Figure 1: Non-phytolith botanical remains observed from FLK-North



Appendix Figure 2: Non-phytolith botanical remains observed from Castle site



Appendix Figure 3: Non-phytolith botanical remains observed from FLK- West

Axis	Eigenvalue	% of total	Cumulative
1	1	19.696	19.696
2	0.757416	14.918	34.614
3	0.638954	12.585	47.199
4	0.457246	9.0059	56.205
5	0.3685	7.258	63.463
6	0.323167	6.3651	69.828
7	0.304662	6.0006	75.829
8	0.21076	4.1511	79.98
9	0.201189	3.9626	83.942
10	0.154565	3.0443	86.987
11	0.1194	2.3517	89.338
12	0.106744	2.1024	91.441
13	0.087861	1.7305	93.171
14	0.074106	1.4596	94.631
15	0.06762	1.3318	95.963
16	0.05435	1.0705	97.033
17	0.046196	0.90987	97.943
18	0.036339	0.71574	98.659
19	0.021293	0.41939	99.078
20	0.014802	0.29154	99.37
21	0.011727	0.23097	99.601
22	0.006753	0.13301	99.734
23	0.005382	0.106	99.84
24	0.004766	0.093874	99.934
25	0.001986	0.039107	99.973
26	0.001058	0.020846	99.993
27	0.000251	0.004934	99.998
28	8.05E-05	0.001586	100

Appendix Table 1: FLK-N horizon CA eigenvalues, scores

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11	Axis 12	Axis 13	Axis 14
FLKN-L 1	0.05	-0.15	0.58	0.43	0.51	0.05	-0.10	-0.57	0.23	0.10	-1.08	-1.32	0.27	-0.16
FLKN-L 2	0.05	0.56	0.23	1.02	0.65	0.34	0.35	-1.04	0.93	0.56	0.72	-0.20	-1.59	-0.09
FLKN-L 3	0.05	0.69	0.22	0.83	0.57	0.36	0.15	-0.73	0.40	0.00	0.61	-0.75	-0.53	0.15
FLKN-L 4	0.05	0.53	0.07	1.01	0.76	-0.02	0.17	-0.18	0.44	1.84	-1.29	1.31	-0.04	0.23
FLKN-L 5	0.05	-1.93	1.44	-0.31	-0.10	-0.38	1.28	0.07	-0.18	-0.19	0.31	0.14	-0.02	0.71
FLKN-L 6	0.05	0.55	-0.04	0.71	0.52	0.48	0.14	-0.27	0.09	0.24	0.21	0.25	-0.06	0.38
FLKN-L 7	0.05	0.82	0.27	0.30	0.05	1.36	0.21	3.20	0.05	-1.35	0.50	0.56	-0.37	-0.26
FLKN-L 8	0.05	1.07	0.42	1.05	-4.94	-1.68	-0.11	0.64	-1.13	2.01	0.03	0.25	-0.46	0.20
FLKN-L 9	0.05	0.90	0.18	-2.15	-0.33	0.28	-0.15	0.14	-1.11	-0.48	-0.56	0.17	-1.13	-0.50
FLKN-L 10	0.05	0.82	0.06	-2.57	0.29	-0.66	-0.27	-1.04	0.79	0.38	1.60	0.55	0.64	-0.44
FLKN-L 12	0.05	0.70	0.10	-1.72	0.38	0.45	0.13	0.42	1.36	1.97	0.49	0.62	1.00	0.20
FLKN-L 13	0.05	0.88	0.26	-2.05	-0.42	0.44	-0.10	1.54	0.64	1.21	-2.55	-5.44	1.16	2.52
FLKN-L 14	0.05	0.72	0.21	1.09	0.57	0.54	0.00	-0.37	-0.37	-1.01	1.30	-0.69	0.73	0.32
FLKN-L 15	0.05	0.74	0.02	0.53	2.26	-5.38	-1.21	1.78	-0.08	-0.78	-0.26	0.06	-0.16	0.11
FLKN-L 16	0.05	0.83	0.24	0.27	0.22	0.23	-0.03	-1.50	-2.47	-1.44	-0.51	0.44	1.08	0.20
FLKN-L 17	0.05	0.62	0.19	0.54	0.85	0.50	0.19	-0.22	0.55	1.51	-2.07	1.65	0.62	0.73
FLKN-L 18	0.05	-1.68	1.00	0.25	-0.31	1.19	-5.96	0.01	0.05	-0.10	1.62	0.31	0.29	2.58
FLKN-L 19	0.05	-0.70	-2.31	0.28	-0.12	0.03	0.28	0.10	-0.14	-0.23	0.09	-0.03	0.24	0.61
FLKN-L 20	-20.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FLKN-L 21	0.05	0.63	0.31	-0.04	-0.81	0.94	-0.13	0.87	3.90	-4.03	-4.41	-2.90	3.91	-0.91
FLKN-L 22	0.05	0.64	0.16	0.76	0.36	1.15	0.18	1.18	0.13	0.64	-2.90	3.92	2.70	2.38
FLKN-L 23	0.05	-1.35	-0.09	0.05	-0.13	0.21	-1.01	0.02	0.08	0.30	-1.09	0.06	-0.37	-2.48
FLKN-L 24	0.05	-0.85	-2.51	0.02	-0.28	-0.06	0.33	0.10	-0.06	-0.32	0.41	-0.30	-0.25	0.53
FLKN-L 25	0.05	-0.84	-2.43	-0.12	-0.21	-0.13	0.33	0.02	-0.14	-0.18	0.12	-0.10	0.09	0.53
FLKN-L 26	0.05	0.04	-1.03	-0.59	0.23	0.03	0.17	-0.58	0.32	0.87	0.20	0.67	0.21	0.21
FLKN-L 27	0.05	0.74	0.27	1.51	-0.28	-0.05	0.09	-0.08	-0.70	0.63	2.16	-1.78	3.21	-1.74
FLKN-L 28	0.05	0.92	0.35	0.39	-2.95	-0.94	-0.01	-1.98	4.71	-4.03	-0.70	1.16	0.52	0.11

Appendix Table 2: FLK-N horizon axis values per sample

FLKN-L 29	0.05	-0.32	0.29	0.44	0.25	0.59	1.04	1.70	0.70	0.40	2.42	0.73	3.09	-2.20
FLKN-L 30	0.05	0.69	0.24	0.73	0.26	0.39	0.18	-0.24	0.14	-0.06	0.59	-0.58	-1.49	0.17

	Axis 15	Axis 16	Axis 17	Axis 18	Axis 19	Axis 20	Axis 21	Axis 22	Axis 23	Axis 24	Axis 25	Axis 26	Axis 27	Axis 28
FLKN-L 1	0.28	-1.40	0.78	1.14	0.19	-1.83	-0.47	-0.58	-1.50	-0.78	-1.01	0.03	-0.99	-0.15
FLKN-L 2	-1.24	1.67	-0.80	0.54	1.20	-0.66	2.55	-0.80	1.24	-0.36	-0.89	-0.82	-0.85	-0.83
FLKN-L 3	0.43	0.38	0.78	1.18	0.05	1.50	1.07	0.59	-2.72	3.39	0.62	0.27	1.01	0.66
FLKN-L 4	-0.56	-1.16	-1.53	-0.75	-2.56	-1.24	0.31	1.93	0.56	1.04	0.23	0.41	-0.11	-0.22
FLKN-L 5	0.12	0.09	-0.14	-0.08	-0.19	0.23	0.17	0.11	0.07	-0.06	0.02	0.09	0.08	0.01
FLKN-L 6	0.74	0.18	0.34	-1.55	-1.63	0.52	-0.41	-3.11	0.30	0.03	0.30	-0.72	-0.97	2.64
FLKN-L 7	-0.06	-0.77	1.03	0.41	-0.36	-0.46	1.09	0.18	0.33	-0.30	0.08	0.32	0.11	0.00
FLKN-L 8	-0.05	0.56	0.80	1.05	-0.30	-0.30	-0.14	-0.44	-0.09	0.11	0.04	-0.25	-0.16	-0.03
FLKN-L 9	0.48	-0.14	-2.10	-0.22	0.09	0.37	0.05	-0.27	-1.00	0.08	-0.45	-0.27	-0.49	-0.20
FLKN-L 10	1.57	0.09	1.47	0.69	-0.41	-1.24	0.08	0.38	1.52	0.71	-0.16	0.16	0.04	0.07
FLKN-L 12	-3.14	0.49	1.32	-0.47	-0.24	2.07	-0.71	0.61	-1.59	-1.57	-1.42	0.11	-0.34	0.20
FLKN-L 13	-0.99	-0.35	0.18	-2.05	1.32	-0.03	0.72	-0.24	2.45	1.79	1.60	-0.31	0.67	-0.17
FLKN-L 14	2.02	0.27	2.48	-1.73	-2.77	2.63	-1.43	1.44	-1.04	-0.25	4.04	-7.38	-5.23	-8.01
FLKN-L 15	-0.35	0.39	-0.15	-0.15	0.37	0.43	-0.05	-0.26	-0.19	-0.13	0.06	-0.07	0.03	0.02
FLKN-L 16	-1.54	0.12	0.75	0.13	0.03	0.01	0.06	0.22	0.72	0.02	0.25	0.23	0.28	0.10
FLKN-L 17	1.83	-2.29	-0.61	3.57	1.86	3.76	-0.24	-0.67	2.23	-1.03	0.83	-0.14	0.13	-0.11
FLKN-L 18	-0.24	-0.11	-1.06	0.47	-0.19	-0.08	-0.01	0.03	-0.05	-0.07	-0.04	0.01	0.00	0.00
FLKN-L 19	0.22	-0.25	0.10	-0.29	-0.96	0.59	-0.40	-1.89	0.35	0.99	-2.31	1.19	1.24	-2.62
FLKN-L 20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FLKN-L 21	1.25	9.72	-3.01	6.23	-6.84	0.52	-1.51	0.83	0.52	-2.41	0.08	0.54	0.95	0.59
FLKN-L 22	3.16	3.90	0.79	-2.76	4.24	-1.98	-0.29	0.72	-1.68	1.00	-1.46	-0.34	-0.43	-0.33
FLKN-L 23	-0.05	0.33	0.75	-0.63	0.29	0.38	0.06	0.07	0.40	0.29	0.28	-0.05	0.22	0.03
FLKN-L 24	-0.12	0.39	-0.14	0.35	0.62	0.22	-0.30	0.99	0.15	0.20	1.07	2.19	-3.30	0.68
FLKN-L 25	0.00	-0.39	-0.21	0.42	0.15	-0.45	0.36	1.05	-0.23	-0.62	-0.31	-2.65	1.20	1.34
FLKN-L 26	-0.03	0.28	-0.24	-0.27	0.07	-1.28	1.12	-1.69	-1.84	-2.29	4.24	1.44	2.12	-1.28

Appendix Table 2b: FLK-N horizon axis values per sample

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FLKN-L 27	1.80	-0.52	-1.74	-1.46	0.37	1.04	1.50	1.03	-0.21	-1.45	-0.91	0.84	0.11	0.18
FLKN-L 28	-0.79	-2.17	-0.61	-1.83	0.84	0.50	0.24	0.10	-0.12	0.13	0.17	0.08	0.02	0.01
FLKN-L 29	-2.81	-0.18	-3.16	1.74	2.09	-1.98	-3.85	-2.12	0.30	3.22	1.53	-1.60	-0.18	-0.34
FLKN-L 30	0.39	0.38	0.01	-0.46	0.46	-0.03	-2.07	0.80	0.42	-0.65	0.03	0.36	0.91	-0.02

	A. 1	A. 2	A. 3	A. 4	A. 5	A. 6	A. 7	A. 8	A. 9	A. 10	A. 11	A. 12	A. 13	A. 14
Bilobate concave	0.05	0.83	0.24	0.27	0.22	0.23	-0.03	-1.50	-2.47	-1.44	-0.51	0.44	1.08	0.20
Bilobate convex	0.05	-0.07	-1.18	0.50	0.20	0.26	0.21	-0.09	-0.02	0.01	0.15	0.11	0.09	0.49
Blocky	-20.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blocky facetate	0.05	-0.01	0.09	-0.98	-0.33	0.35	-0.48	0.21	0.12	-0.73	-1.36	-0.35	-0.06	-1.32
Blocky lacunate	0.05	-1.68	1.00	0.25	-0.31	1.19	-5.96	0.01	0.05	-0.10	1.62	0.31	0.29	2.58
Blocky hairy	0.05	0.58	0.10	0.54	-0.03	0.42	-0.06	0.21	-0.12	-0.40	0.39	-0.01	0.21	0.08
Blocky ridged	0.05	0.41	0.10	0.22	0.07	0.16	0.20	-0.34	0.53	0.30	0.42	-0.07	-0.52	-0.04
Blocky sulcate	0.05	0.52	0.17	0.66	0.40	0.03	0.05	-0.26	-0.06	-0.01	-0.01	-0.13	-0.04	-0.01
Bulliform	0.05	0.63	0.14	0.44	-0.13	0.29	0.04	-0.39	-1.04	-0.17	-0.99	1.15	1.12	0.73
Clavate	0.05	0.45	-0.34	-0.71	0.12	0.01	0.05	-0.68	-0.40	-0.23	0.27	0.17	-0.18	-0.06
Cylindroid	0.05	0.77	0.32	0.11	-1.81	-0.57	-0.03	-1.32	3.17	-2.46	-0.56	0.37	0.54	-0.06
Cylindroid crenate	0.05	0.88	0.24	-0.43	-0.54	0.03	-0.07	-0.72	-1.88	-0.74	-0.47	0.33	0.19	-0.03
Cylindroid scrobiculate	0.05	1.02	0.40	1.12	-4.16	-1.41	-0.08	0.52	-1.06	1.78	0.39	-0.09	0.15	-0.12
Elongate orthogonal	0.05	0.63	0.24	-0.07	0.12	1.08	0.31	2.42	0.47	-0.55	0.66	0.51	0.47	-0.46
Globular echinate	0.05	0.98	0.38	0.87	-3.67	-1.20	-0.04	-0.09	0.38	0.33	-0.01	0.29	-0.29	0.13
Globular granulate	0.05	0.76	0.22	-0.35	-0.35	0.45	0.04	0.89	-0.19	-0.19	-0.28	-0.10	-0.54	0.06
Globular psilate	0.05	0.90	0.33	0.61	-2.17	-0.61	-0.03	0.54	-0.60	1.30	0.37	-1.70	1.33	-0.11
Globular tuberculate	0.05	0.35	0.34	0.57	0.65	0.30	0.07	-0.48	0.39	0.61	-1.03	-0.07	0.20	0.25
Globulose	0.05	0.70	0.22	0.47	0.23	1.06	0.16	1.51	0.61	-0.35	-1.75	1.54	1.35	0.77
Guttiform	0.05	0.72	0.12	-1.01	0.57	-0.08	-0.04	-0.63	0.67	0.95	-0.23	1.10	0.63	0.14
Hair base	0.05	-1.60	1.04	-0.15	-0.05	-0.19	0.67	0.04	-0.07	-0.08	0.08	0.01	0.02	0.15
Hair articulated	0.05	-1.39	0.52	0.05	-0.08	0.25	-1.33	-0.04	0.04	0.09	-0.28	-0.04	-0.09	-0.56
Irregular indeterminate	0.05	0.65	0.04	-1.46	0.08	-0.10	-0.07	-0.25	0.07	0.14	0.18	0.05	0.07	-0.04
Mesophyll cells	0.05	-0.78	-1.88	0.02	-0.12	-0.04	0.10	0.04	-0.04	-0.06	0.01	-0.03	0.00	0.04
Oblong	0.05	0.49	-0.07	0.73	0.35	0.23	0.22	-0.60	0.31	0.57	0.80	-0.25	0.04	-0.27

Appendix Table 3: FLK-N horizon axis values per phytolith morphotype

Oblong granulate	0.05	0.69	0.24	0.71	0.42	0.69	0.24	0.47	0.46	-0.26	0.61	-0.13	-0.83	-0.07
Ovate granulate	0.05	0.65	0.24	-1.55	0.04	0.37	-0.01	0.68	0.72	1.20	-1.00	-2.04	0.79	0.98
Appendix Table 3: Contin	ued													
	A. 1	A. 2	A. 3	A. 4	A. 5	A. 6	A. 7	A. 8	A. 9	A. 10	A. 11	A. 12	A. 13	A. 14
Rondel	0.05	0.71	0.04	0.20	1.89	-4.33	-0.98	1.26	0.06	-0.44	-0.13	0.17	-0.05	0.05
Saddle	0.05	0.58	0.19	-1.82	0.34	-0.48	-0.23	-0.93	0.65	0.31	0.93	0.08	0.55	-0.37
Sclereid	0.05	0.78	0.18	-1.30	0.09	0.67	0.10	1.40	0.85	0.95	-0.26	-0.91	0.70	0.67
Scutiform	0.05	0.15	0.20	0.87	-1.78	-0.51	-0.34	0.19	-0.58	0.98	0.37	-0.49	0.79	-1.34
Tabular cavate	0.05	0.88	0.29	0.97	-2.19	-1.37	-0.13	0.49	-0.62	1.34	0.19	-0.26	0.41	-0.12
Tabular elongate	0.05	0.39	0.40	-0.50	-0.01	0.34	-0.09	0.38	0.91	-0.10	-1.96	-2.98	1.05	0.71
Tabular scrobiculate	0.05	0.19	-0.02	0.33	0.39	0.30	0.12	0.05	0.40	0.84	-0.51	0.71	0.19	0.07
Tabular sinuate	0.05	0.34	0.28	1.11	-0.08	0.19	0.44	0.59	-0.17	0.54	2.26	-0.84	3.16	-1.91

Axis	Eigenvalue	% of total	Cumulative
1	0.04602	32.793	32.793
2	0.03061	21.812	54.605
3	0.01965	14.002	68.607
4	0.011855	8.4473	77.054
5	0.00799	5.6937	82.748
6	0.005314	3.7867	86.535
7	0.00395	2.8145	89.349
8	0.003698	2.635	91.984
9	0.002274	1.6204	93.605
10	0.0019	1.354	94.959
11	0.001648	1.1747	96.133
12	0.001319	0.9402	97.074
13	0.001086	0.77389	97.847
14	0.000961	0.68507	98.532
15	0.000771	0.54931	99.082
16	0.000489	0.34824	99.43
17	0.000394	0.28062	99.711
18	0.000247	0.17616	99.887
19	0.00011	0.078052	99.965
20	2.64E-05	0.018815	99.984
21	1.82E-05	0.012998	99.997
22	4.67E-06	0.00333	100

Appendix Table 4: FLK-N site CA eigenvalues, scores

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11
FLK GEO 7 CR 1	-0.30	-0.62	-1.60	-2.61	0.27	1.22	-0.50	0.21	-0.51	0.87	2.19
FLK GEO 7 CR 2	-0.54	-0.92	-0.33	-0.04	-3.40	-0.78	-0.29	2.65	-1.64	0.19	-1.20
FLK GEO 7 CR 3	0.60	-0.08	0.29	0.07	0.28	-1.10	-1.01	0.07	-0.52	-0.63	1.47
FLK GEO 7 CR 4	0.41	0.54	-0.01	0.99	0.36	1.97	1.99	2.54	-0.55	1.21	2.72
FLK GEO 7 CR 5	0.16	0.03	0.29	0.03	-1.57	-0.51	-0.04	0.25	0.49	-0.58	-1.00
FLK GEO 7 CR 6	0.12	-0.20	0.94	-0.64	-2.42	1.82	1.01	-3.09	0.66	0.67	0.67
FLK GEO 7 CR 7	0.10	-0.15	-0.46	-0.14	0.84	1.80	-0.11	-1.77	-3.59	0.73	-2.85
FLK GEO 7 CR 8	0.57	1.91	-2.07	1.22	-0.45	-0.10	-0.31	-0.38	0.21	0.00	0.15
FLK GEO 7 CR 9	0.64	0.19	0.39	0.75	1.69	0.77	1.47	0.40	1.22	-1.94	-1.09
FLK GEO 7 CR 10	-0.08	-2.37	-1.14	1.02	0.46	-0.41	0.46	-0.39	0.29	0.13	0.03
FLKN GEO7 OCR 1	-0.38	0.22	-0.81	-1.93	0.91	0.55	-1.40	0.87	1.34	0.78	-1.13
FLKN GEO7 OCR 2	0.28	0.46	0.00	-1.37	0.02	0.16	2.65	0.79	-0.30	-1.26	-0.50
FLKN GEO7 OCR 3	0.95	-0.01	0.62	0.28	0.47	-0.71	-0.89	-0.21	-0.89	-0.66	1.05
FLKN GEO7 OCR 4	0.28	-0.29	0.30	-0.59	-0.31	-1.20	-1.14	-0.34	-0.86	-2.04	1.68
FLKN GEO7 OCR 5	0.19	0.18	-0.39	-1.28	0.47	-0.63	-0.55	-1.00	-0.21	-1.82	-0.84
FLKN GEO7 OCR 6	0.45	0.22	0.98	0.62	-0.94	0.23	-0.36	0.37	0.76	0.62	-1.00
FLKN GEO7 OCR 7	0.91	-0.10	0.73	-0.60	-0.62	-1.26	0.18	-0.18	2.34	0.57	0.08
FLKN GEO7 OCR 8	1.18	-0.01	0.93	0.09	0.63	-0.41	-0.30	0.20	-0.28	1.25	-0.19
FLKN GEO7 OCR 9	1.06	0.21	1.23	0.49	0.92	-0.57	-0.46	-0.09	-0.88	0.10	0.75
FLKN GEO7 OCR 10	0.83	-0.02	1.19	0.59	1.06	-0.44	-0.23	0.01	-0.60	0.08	1.21
FLKN GEO7 OCR 11	-2.63	0.79	0.45	0.14	0.49	-1.24	0.64	-0.42	-0.14	0.74	0.14
FLKN GEO7 OCR 12	-1.12	-0.15	0.94	0.96	0.04	1.78	-1.26	0.50	0.48	-1.01	0.11
FLKN GEO7 OCR 13	0.87	0.61	1.35	0.31	0.62	-0.48	-0.32	-0.24	-1.46	-0.01	0.66

Appendix Table 5a: FLK-N site axis values per sample

	Axis 12	Axis 13	Axis 14	Axis 15	Axis 16	Axis 17	Axis 18	Axis 19	Axis 20	Axis 21	Axis 22
FLK GEO 7 CR 1	-0.95	-0.25	-1.03	-2.27	1.78	0.04	0.83	-0.19	-0.11	-0.17	0.04
FLK GEO 7 CR 2	-2.28	-0.25	0.59	0.35	-0.10	0.13	-0.33	0.01	-0.12	-0.04	0.02
FLK GEO 7 CR 3	-0.41	1.63	-0.90	0.50	-2.17	0.19	0.25	-11.23	0.70	3.82	1.26
FLK GEO 7 CR 4	1.17	-2.23	-1.19	1.97	-1.24	0.74	-1.45	0.20	0.81	0.08	0.05
FLK GEO 7 CR 5	2.55	1.04	-2.86	0.54	3.07	0.31	-1.26	-0.40	0.37	-0.29	-0.16
FLK GEO 7 CR 6	-0.86	0.89	0.31	1.03	-0.56	0.75	-0.41	0.08	0.03	-0.02	0.00
FLK GEO 7 CR 7	0.80	-2.22	-0.43	1.17	0.47	-1.41	1.27	-0.63	-0.22	0.19	-0.05
FLK GEO 7 CR 8	-0.07	0.21	0.43	-0.16	0.11	-0.14	0.11	0.07	-0.09	0.04	0.03
FLK GEO 7 CR 9	-3.24	-0.16	-1.46	0.90	1.24	1.10	1.25	-0.06	0.35	-0.07	0.01
FLK GEO 7 CR 10	0.26	0.38	0.01	-0.09	-0.37	-0.20	-0.18	0.18	0.07	0.00	0.01
FLKN GEO7 OCR 1	0.10	1.14	-0.21	1.81	-1.19	-0.26	-0.21	0.34	-0.09	-0.03	-0.10
FLKN GEO7 OCR 2	1.13	0.99	1.30	-0.76	-0.35	-0.66	0.36	-0.15	-0.44	-0.02	-0.05
FLKN GEO7 OCR 3	-0.15	0.02	-0.22	0.38	-1.23	0.60	-0.02	-2.59	-2.53	-7.71	-5.66
FLKN GEO7 OCR 4	0.71	-0.26	0.17	1.56	-0.19	0.44	1.79	0.96	0.23	0.43	0.26
FLKN GEO7 OCR 5	-0.18	-1.93	-0.09	-1.28	-1.13	1.68	-3.04	0.17	0.49	0.18	0.24
FLKN GEO7 OCR 6	0.91	-0.39	-2.20	-2.33	-2.51	1.02	2.27	0.54	-0.69	0.29	0.17
FLKN GEO7 OCR 7	-0.18	-2.60	0.44	0.12	0.51	-2.45	0.24	-0.45	0.05	-0.04	-0.10
FLKN GEO7 OCR 8	0.13	0.31	1.10	-0.20	0.71	1.12	0.02	0.07	0.35	0.11	0.06
FLKN GEO7 OCR 9	-0.48	0.72	-0.80	0.86	-0.34	-1.23	-1.23	-1.08	-5.49	-9.97	17.59
FLKN GEO7 OCR 10	-0.91	0.17	-0.91	0.80	1.00	-0.37	-2.47	1.12	-10.51	4.60	-1.26
FLKN GEO7 OCR 11	-0.14	-0.12	-0.13	0.05	0.11	0.29	0.16	-0.03	0.02	-0.07	-0.02
FLKN GEO7 OCR 12	0.35	-0.04	1.03	-0.63	0.39	-0.52	-0.23	-0.17	0.03	-0.01	0.01
FLKN GEO7 OCR 13	-1.18	1.66	-1.45	-0.68	-0.86	-2.67	-1.20	0.98	1.27	0.15	-0.26

Appendix Table 5b: FLK-N site axis values per sample

	A. 1	A. 2	A. 3	A. 4	A. 5	A. 6	A. 7	A. 8	A. 9	A.10	A. 11
Placky	-	-	0.25	-	-	0.10	0.05	-	0.06	0.02	0.00
ыоску	0.04	0.18	0.25	0.17	0.04	0.10	0.03	0.27	0.00	0.02	0.00
Blocky cavate	0.22	0.11	0.04	0.04	- 0.06	0.06	- 0.26	- 0.07	0.04	0.03	- 0.05
Blocky		-	-	-	-		-			-	-
dendriform	0.23	0.07	0.04	0.01	0.04	0.11	0.06	0.04	0.01	0.06	0.01
		-			-				-	-	
Blocky facetate	0.21	0.33	0.30	0.10	0.25	0.01	0.08	0.24	0.02	0.08	0.03
Blocky											
lacunate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	-		-		-		-	-	-	-	
Blocky hairy	0.29	0.00	0.04	0.14	0.06	0.06	0.05	0.07	0.06	0.16	0.10
Blocky pilate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blocky								-		-	
polygonal	0.02	0.03	0.01	0.00	0.10	0.02	0.01	0.07	0.05	0.01	0.03
		-	-		-	-		-			-
Blocky ridged	0.24	0.09	0.18	0.02	0.01	0.14	0.05	0.05	0.03	0.11	0.11
			-		-					-	-
Blocky sulcate	0.30	0.68	0.41	0.18	0.02	0.13	0.11	0.05	0.10	0.02	0.01
Blocky								-		-	
tuberculated	0.01	0.02	0.02	0.02	0.06	0.01	0.01	0.06	0.04	0.01	0.00
Blocky								-		-	
radiating	0.02	0.03	0.01	0.00	0.10	0.02	0.01	0.08	0.05	0.01	0.04
					-	-		-	-	-	-
Bulliform	0.03	0.01	0.09	0.18	0.06	0.07	0.09	0.05	0.05	0.07	0.01
				-		-					
Clavate	0.09	0.31	0.03	0.17	0.02	0.23	0.01	0.19	0.00	0.02	0.04
		-		-			-		-	-	-
Cylindroid	0.20	0.27	0.16	0.14	0.00	0.13	0.03	0.08	0.01	0.07	0.03
Cylindroid	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix Table 6: FLK-N horizon axis values per phytolith morphotype

granulate											
Cylindroid											
crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cylindroid											
scrobiculate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elongate		-	-	-		-	-	-		-	
orthogonal	0.37	0.04	0.19	0.13	0.22	0.22	0.02	0.01	0.09	0.07	0.03
Epidermal	-			-	-		-		-		
cell tissues	0.01	0.24	0.11	0.13	0.10	0.02	0.10	0.03	0.07	0.05	0.03
						-				-	-
Large globular	0.00	0.01	0.02	0.03	0.00	0.01	0.01	0.00	0.01	0.01	0.03
Globular											
crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Globular		-	-	-	-	-			-		-
echinate	0.35	0.06	0.13	0.10	0.05	0.04	0.05	0.00	0.03	0.02	0.02
Globular			-	-			-		-		-
granulate	0.11	0.09	0.10	0.02	0.20	0.14	0.04	0.05	0.18	0.04	0.11
Globular		-					-		-		-
psilate	0.26	0.05	0.01	0.55	0.18	0.16	0.11	0.02	0.10	0.05	0.02
Globular			-	-				-	-	-	
tuberculate	0.41	0.25	0.03	0.26	0.09	0.06	0.05	0.10	0.08	0.02	0.15
				-	-						-
Globulose	0.45	0.08	0.53	0.05	0.01	0.15	0.27	0.05	0.11	0.09	0.04
Guttiform	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	-			-	-	-	-				
Hair base	0.01	0.15	0.07	0.08	0.10	0.04	0.07	0.06	0.04	0.03	0.10
Hair articulated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemisphere	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irregular		-	-	-					-		
indeterminated	0.30	0.03	0.25	0.10	0.26	0.01	0.07	0.00	0.13	0.03	0.07

Appendix Table 6 continued

	A. 12	A. 13	A.14	A. 15	A. 16	A. 17	A. 18	A. 19	A. 20	A. 21	A. 22
Blocky	-0.05	0.08	0.02	0.02	-0.04	0.04	0.01	0.00	-0.01	0.00	0.00
Blocky cavate	-0.08	0.01	-0.03	-0.01	0.04	-0.01	0.00	0.01	0.00	0.01	0.00
Blocky											
dendriform	0.01	0.01	0.01	0.00	-0.01	-0.03	-0.01	0.00	0.00	0.01	0.00
Blocky facetate	-0.06	0.07	0.05	0.02	0.02	-0.03	0.04	-0.01	0.00	0.00	-0.01
Blocky lacunate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blocky hairy	-0.04	-0.04	-0.12	0.00	-0.01	-0.03	-0.01	0.00	-0.01	-0.01	0.00
Blocky pilate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blocky polygonal	0.06	0.01	-0.02	-0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Blocky ridged	-0.06	-0.07	-0.05	-0.02	-0.01	-0.06	-0.03	-0.02	0.00	0.00	-0.01
Blocky sulcate	0.00	0.00	0.01	0.03	-0.04	0.00	0.01	-0.01	0.00	0.00	0.00
Blocky											
tuberculated	0.08	0.01	-0.02	0.01	0.02	0.00	-0.01	0.02	0.00	-0.01	0.00
Blocky radiating	0.07	0.01	-0.02	-0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Bulliform	0.02	-0.05	0.04	-0.02	0.00	0.01	-0.02	-0.01	0.01	0.01	0.00
Clavate	-0.05	-0.02	-0.09	-0.02	0.02	0.07	0.02	0.01	-0.01	0.00	0.00
Cylindroid	0.02	-0.01	-0.03	0.01	-0.02	-0.01	-0.03	-0.01	0.01	0.00	0.00
Cylindroid											
granulate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cylindroid											
crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cylindroid											
scrobiculate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elongate											
orthogonal	-0.04	0.07	0.06	-0.03	0.02	-0.07	0.01	0.01	-0.01	0.00	0.00
Epidermal cell											
tissues	0.08	-0.04	0.05	-0.02	0.00	-0.01	-0.02	-0.02	-0.02	0.00	0.00

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Large globular	0.01	0.00	0.01	0.03	-0.02	0.00	-0.01	0.00	0.00	0.00	0.00
Globular crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Globular											
echinate	-0.02	0.01	-0.08	0.05	-0.04	0.02	0.00	0.02	0.00	0.01	0.00
Globular											
granulate	0.00	0.03	0.03	0.05	0.03	-0.01	0.00	0.04	-0.01	0.00	0.00
Globular psilate	0.02	0.07	-0.03	-0.09	0.01	0.04	0.01	-0.03	0.00	0.00	-0.01
Globular											
tuberculate	-0.07	-0.06	0.04	0.06	0.08	0.00	0.00	-0.03	0.01	0.00	0.00
Globulose	0.07	0.05	-0.09	-0.05	0.09	-0.03	-0.01	0.00	-0.01	0.00	0.01
Guttiform	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hair base	0.05	0.03	0.05	-0.05	-0.02	0.02	-0.05	0.01	-0.01	0.00	0.00
Hair articulated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemisphere	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Appendix Table 6 continued

	A. 1	A. 2	A. 3	A. 4	A. 5	A. 6	A. 7	A. 8	A. 9	A.10	A. 11
Irregular ridged	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irregular striated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mesophyll cells	-0.05	-0.16	0.17	-0.10	0.30	-0.02	0.00	0.06	-0.01	-0.01	0.03
Oblong	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oblong											
granulate	0.13	0.19	0.45	0.15	0.02	0.17	-0.07	0.00	0.08	0.14	0.05
Orthogonal	-0.05	-0.18	0.19	-0.11	0.04	0.01	0.03	0.03	-0.02	0.00	-0.01
Ovate granulate	0.37	0.20	-0.02	-0.30	-0.20	-0.06	-0.13	-0.04	-0.10	0.04	-0.08
Perforated plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel horned	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel tower	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel wide	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saddle	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saddle long	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saddle short	-0.05	-0.18	0.19	-0.11	0.04	0.01	0.03	0.04	-0.02	0.00	-0.01
Saddle squat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sclereid	0.36	-0.11	0.02	0.31	-0.25	-0.15	-0.09	-0.06	-0.05	0.16	0.15
Scutiform	0.03	0.01	0.10	0.19	-0.06	-0.07	0.10	-0.05	-0.05	-0.07	-0.02
Tabular cavate	0.08	0.00	0.05	0.13	-0.07	-0.20	0.12	-0.14	-0.07	-0.05	-0.08
Tabular crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular											
dendriform	0.02	0.28	0.18	-0.02	-0.06	0.00	-0.03	0.03	-0.01	-0.05	-0.08
Tabular elongate	-0.01	-0.68	-0.16	0.15	0.17	-0.04	-0.02	0.05	0.08	0.04	0.00
Tabular											
oblong radiating	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Tabular pilate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular											
scrobiculate	-0.90	0.36	0.22	0.10	0.12	-0.08	0.02	0.01	-0.03	0.05	-0.01
Tabular sinuate	0.01	0.31	0.19	0.05	0.10	-0.15	-0.22	0.01	0.14	-0.08	-0.05
Tabular sulcate	-0.02	-0.24	-0.11	0.09	-0.05	-0.08	0.04	0.06	0.03	0.00	0.02
Tabular thick	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vessel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix Table 6 continued

	A. 12	A. 13	A.14	A. 15	A. 16	A. 17	A. 18	A. 19	A. 20	A. 21	A. 22
Irregular											
indeterminated	-0.05	0.07	0.01	-0.02	-0.02	0.04	-0.03	0.00	0.00	0.00	0.00
Irregular ridged	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irregular striated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mesophyll cells	0.04	-0.08	0.01	-0.05	-0.08	-0.03	0.05	0.00	0.00	0.01	0.00
Oblong	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oblong											
granulate	-0.17	-0.12	0.06	-0.04	-0.02	0.01	0.01	0.02	0.00	-0.01	0.00
Orthogonal	0.01	-0.02	-0.04	0.01	-0.01	0.01	-0.01	-0.01	0.01	0.00	0.00
Ovate granulate	0.05	0.04	0.02	-0.04	-0.02	-0.02	0.03	-0.01	0.01	-0.02	0.01
Perforated plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Rondel horned	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rondel tower	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel wide	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saddle	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
saddle long	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
saddle short	0.01	-0.02	-0.04	0.01	-0.01	0.01	-0.01	-0.01	0.01	0.00	0.00
Saddle squat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sclereid	0.07	0.01	-0.03	0.07	-0.01	-0.02	0.03	0.02	0.01	0.01	0.00
Scutiform	0.03	-0.06	0.05	-0.02	0.01	0.01	-0.02	0.04	0.01	-0.01	0.00
Tabular cavate	-0.02	-0.01	0.02	-0.04	0.02	0.02	0.03	-0.01	-0.01	0.01	0.00
Tabular crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular											
dendriform	0.01	-0.03	0.04	0.09	-0.02	0.02	-0.01	-0.01	0.00	0.01	0.00
Tabular elongate	0.05	-0.04	0.04	0.09	0.03	0.02	0.00	-0.02	-0.01	-0.01	0.01
Tabular oblong											
radiating	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular pilate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular											
scrobiculate	-0.03	0.06	-0.01	0.04	0.00	-0.04	-0.01	-0.01	0.00	0.00	0.00
Tabular sinuate	0.02	0.01	0.00	0.01	0.03	0.04	0.00	0.00	0.00	0.00	0.00
Tabular sulcate	-0.06	0.06	0.01	-0.02	-0.04	0.01	-0.03	0.00	0.01	0.00	0.00
Tabular thick	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vessel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix	Table 7	: Castle CA	eigenvalues,	scores
rpponuix	I doite /	. Custie Ch	ergenvarues,	500105

Axis	Eigenvalue	% of total	Cumulative
1	0.745887	50.031	50.031
2	0.358436	24.043	74.074
3	0.176949	11.869	85.943
4	0.139835	9.3796	95.323
5	0.069722	4.6767	99.999
6	8.08E-06	0.000542	100
7	1.47E-33	9.83E-32	100

Appendix Table 8: Castle axis values per sample

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
CASTLE CLAYS 4	0.18	3.28	-2.30	-3.69	0.09	4.23	0.68
CASTLE CLAYS 7	0.62	1.73	5.15	-0.89	-1.67	0.46	-3.05
CASTLE CLAYS 8	-2.39	0.03	0.12	0.11	0.04	0.00	0.68
CASTLE CLAYS 9	0.42	-0.59	0.00	0.20	0.12	0.37	0.68
CASTLE CLAYS 10	0.62	1.73	5.15	-0.89	-1.67	0.46	5.66
CASTLE CLAYS 11	0.34	0.45	-0.63	-0.85	-0.76	-1.67	0.68
CASTLE CLAYS 13	0.61	3.53	-1.03	4.35	-0.93	0.26	0.68
CASTLE CLAYS 14	0.60	2.14	1.12	-0.36	6.18	-1.76	0.68

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
Blocky ridged	0.46	0.62	0.91	-0.12	-0.12	0.00	0.00
Blocky sulcate	-2.39	0.03	0.12	0.11	0.04	0.00	0.00
Blocky tuberculated	-0.87	0.09	-0.19	-0.24	-0.09	-0.01	0.00
Globular granulate	0.33	1.50	-0.86	-1.59	0.48	0.00	0.00
Globulose	-2.39	0.03	0.12	0.11	0.04	0.00	0.00
Irregular indeterminated	0.43	2.17	-1.04	0.97	-0.71	0.00	0.00
Mesophyll cells	0.35	-0.40	-0.11	0.01	-0.04	0.00	0.00
Oblong granulate	-2.39	0.03	0.12	0.11	0.04	0.00	0.00
Tabular elongate	-2.39	0.03	0.12	0.11	0.04	0.00	0.00
Tabular scrobiculate	0.48	0.55	0.01	0.80	0.96	0.00	0.00

Appendix Table 9: Castle axis values per phytolith morphotype

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11
FLK GEO 7 CR 1	-0.30	-0.62	-1.60	-2.61	0.27	1.22	-0.50	0.21	-0.51	0.87	2.19
FLK GEO 7 CR 2	-0.54	-0.92	-0.33	-0.04	-3.40	-0.78	-0.29	2.65	-1.64	0.19	-1.20
FLK GEO 7 CR 3	0.60	-0.08	0.29	0.07	0.28	-1.10	-1.01	0.07	-0.52	-0.63	1.47
FLK GEO 7 CR 4	0.41	0.54	-0.01	0.99	0.36	1.97	1.99	2.54	-0.55	1.21	2.72
FLK GEO 7 CR 5	0.16	0.03	0.29	0.03	-1.57	-0.51	-0.04	0.25	0.49	-0.58	-1.00
FLK GEO 7 CR 6	0.12	-0.20	0.94	-0.64	-2.42	1.82	1.01	-3.09	0.66	0.67	0.67
FLK GEO 7 CR 7	0.10	-0.15	-0.46	-0.14	0.84	1.80	-0.11	-1.77	-3.59	0.73	-2.85
FLK GEO 7 CR 8	0.57	1.91	-2.07	1.22	-0.45	-0.10	-0.31	-0.38	0.21	0.00	0.15
FLK GEO 7 CR 9	0.64	0.19	0.39	0.75	1.69	0.77	1.47	0.40	1.22	-1.94	-1.09
FLK GEO 7 CR 10	-0.08	-2.37	-1.14	1.02	0.46	-0.41	0.46	-0.39	0.29	0.13	0.03
FLKN GEO7 OCR 1	-0.38	0.22	-0.81	-1.93	0.91	0.55	-1.40	0.87	1.34	0.78	-1.13
FLKN GEO7 OCR 2	0.28	0.46	0.00	-1.37	0.02	0.16	2.65	0.79	-0.30	-1.26	-0.50
FLKN GEO7 OCR 3	0.95	-0.01	0.62	0.28	0.47	-0.71	-0.89	-0.21	-0.89	-0.66	1.05
FLKN GEO7 OCR 4	0.28	-0.29	0.30	-0.59	-0.31	-1.20	-1.14	-0.34	-0.86	-2.04	1.68
FLKN GEO7 OCR 5	0.19	0.18	-0.39	-1.28	0.47	-0.63	-0.55	-1.00	-0.21	-1.82	-0.84
FLKN GEO7 OCR 6	0.45	0.22	0.98	0.62	-0.94	0.23	-0.36	0.37	0.76	0.62	-1.00
FLKN GEO7 OCR 7	0.91	-0.10	0.73	-0.60	-0.62	-1.26	0.18	-0.18	2.34	0.57	0.08
FLKN GEO7 OCR 8	1.18	-0.01	0.93	0.09	0.63	-0.41	-0.30	0.20	-0.28	1.25	-0.19
FLKN GEO7 OCR 9	1.06	0.21	1.23	0.49	0.92	-0.57	-0.46	-0.09	-0.88	0.10	0.75
FLKN GEO7 OCR 10	0.83	-0.02	1.19	0.59	1.06	-0.44	-0.23	0.01	-0.60	0.08	1.21
FLKN GEO7 OCR 11	-2.63	0.79	0.45	0.14	0.49	-1.24	0.64	-0.42	-0.14	0.74	0.14
FLKN GEO7 OCR 12	-1.12	-0.15	0.94	0.96	0.04	1.78	-1.26	0.50	0.48	-1.01	0.11
FLKN GEO7 OCR 13	0.87	0.61	1.35	0.31	0.62	-0.48	-0.32	-0.24	-1.46	-0.01	0.66

Appendix Table 10: FLK-W CA eigenvalues, scores

	Axis 12	Axis 13	Axis 14	Axis 15	Axis 16	Axis 17	Axis 18	Axis 19	Axis 20	Axis 21	Axis 22
FLK GEO 7 CR 1	-0.95	-0.25	-1.03	-2.27	1.78	0.04	0.83	-0.19	-0.11	-0.17	0.04
FLK GEO 7 CR 2	-2.28	-0.25	0.59	0.35	-0.10	0.13	-0.33	0.01	-0.12	-0.04	0.02
FLK GEO 7 CR 3	-0.41	1.63	-0.90	0.50	-2.17	0.19	0.25	-11.23	0.70	3.82	1.26
FLK GEO 7 CR 4	1.17	-2.23	-1.19	1.97	-1.24	0.74	-1.45	0.20	0.81	0.08	0.05
FLK GEO 7 CR 5	2.55	1.04	-2.86	0.54	3.07	0.31	-1.26	-0.40	0.37	-0.29	-0.16
FLK GEO 7 CR 6	-0.86	0.89	0.31	1.03	-0.56	0.75	-0.41	0.08	0.03	-0.02	0.00
FLK GEO 7 CR 7	0.80	-2.22	-0.43	1.17	0.47	-1.41	1.27	-0.63	-0.22	0.19	-0.05
FLK GEO 7 CR 8	-0.07	0.21	0.43	-0.16	0.11	-0.14	0.11	0.07	-0.09	0.04	0.03
FLK GEO 7 CR 9	-3.24	-0.16	-1.46	0.90	1.24	1.10	1.25	-0.06	0.35	-0.07	0.01
FLK GEO 7 CR 10	0.26	0.38	0.01	-0.09	-0.37	-0.20	-0.18	0.18	0.07	0.00	0.01
FLKN GEO7 OCR 1	0.10	1.14	-0.21	1.81	-1.19	-0.26	-0.21	0.34	-0.09	-0.03	-0.10
FLKN GEO7 OCR 2	1.13	0.99	1.30	-0.76	-0.35	-0.66	0.36	-0.15	-0.44	-0.02	-0.05
FLKN GEO7 OCR 3	-0.15	0.02	-0.22	0.38	-1.23	0.60	-0.02	-2.59	-2.53	-7.71	-5.66
FLKN GEO7 OCR 4	0.71	-0.26	0.17	1.56	-0.19	0.44	1.79	0.96	0.23	0.43	0.26
FLKN GEO7 OCR 5	-0.18	-1.93	-0.09	-1.28	-1.13	1.68	-3.04	0.17	0.49	0.18	0.24
FLKN GEO7 OCR 6	0.91	-0.39	-2.20	-2.33	-2.51	1.02	2.27	0.54	-0.69	0.29	0.17
FLKN GEO7 OCR 7	-0.18	-2.60	0.44	0.12	0.51	-2.45	0.24	-0.45	0.05	-0.04	-0.10
FLKN GEO7 OCR 8	0.13	0.31	1.10	-0.20	0.71	1.12	0.02	0.07	0.35	0.11	0.06
FLKN GEO7 OCR 9	-0.48	0.72	-0.80	0.86	-0.34	-1.23	-1.23	-1.08	-5.49	-9.97	17.59
FLKN GEO7 OCR 10	-0.91	0.17	-0.91	0.80	1.00	-0.37	-2.47	1.12	-10.51	4.60	-1.26
FLKN GEO7 OCR 11	-0.14	-0.12	-0.13	0.05	0.11	0.29	0.16	-0.03	0.02	-0.07	-0.02
FLKN GEO7 OCR 12	0.35	-0.04	1.03	-0.63	0.39	-0.52	-0.23	-0.17	0.03	-0.01	0.01
FLKN GEO7 OCR 13	-1.18	1.66	-1.45	-0.68	-0.86	-2.67	-1.20	0.98	1.27	0.15	-0.26

Appendix Table 11: FLK-W axis values per sample

	A. 1	A. 2	A. 3	A. 4	A. 5	A. 6	A. 7	A. 8	A. 9	A.10	A. 11
Blocky	-0.04	-0.18	0.25	-0.17	-0.04	0.10	0.05	-0.27	0.06	0.02	0.00
Blocky cavate	0.22	-0.11	-0.04	0.04	-0.06	0.06	-0.26	-0.07	0.04	-0.03	-0.05
Blocky											
dendriform	0.23	-0.07	-0.04	-0.01	-0.04	0.11	-0.06	0.04	0.01	-0.06	-0.01
Blocky facetate	0.21	-0.33	0.30	0.10	-0.25	0.01	0.08	0.24	-0.02	-0.08	0.03
Blocky lacunate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blocky hairy	-0.29	0.00	-0.04	0.14	-0.06	0.06	-0.05	-0.07	-0.06	-0.16	0.10
Blocky pilate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blocky polygonal	0.02	0.03	0.01	0.00	0.10	0.02	0.01	-0.07	0.05	-0.01	0.03
Blocky ridged	0.24	-0.09	-0.18	0.02	-0.01	-0.14	0.05	-0.05	0.03	0.11	-0.11
Blocky sulcate	0.30	0.68	-0.41	0.18	-0.02	0.13	0.11	0.05	0.10	-0.02	-0.01
Blocky											
tuberculated	0.01	0.02	0.02	0.02	0.06	0.01	0.01	-0.06	0.04	-0.01	0.00
Blocky radiating	0.02	0.03	0.01	0.00	0.10	0.02	0.01	-0.08	0.05	-0.01	0.04
Bulliform	0.03	0.01	0.09	0.18	-0.06	-0.07	0.09	-0.05	-0.05	-0.07	-0.01
Clavate	0.09	0.31	0.03	-0.17	0.02	-0.23	0.01	0.19	0.00	0.02	0.04
Cylindroid	0.20	-0.27	0.16	-0.14	0.00	0.13	-0.03	0.08	-0.01	-0.07	-0.03
Cylindroid											
granulate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cylindroid											
crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cylindroid	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Flongate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
orthogonal	0.37	-0.04	-0 19	-0.13	0.22	-0.22	-0.02	-0.01	0.09	-0.07	0.03
Epidermal	0.37	0.01	0.15	0.15	0.22	0.22	0.02	0.01	0.05	0.07	0.00
cell tissues	-0.01	0.24	0.11	-0.13	-0.10	0.02	-0.10	0.03	-0.07	0.05	0.03
Large globular	0.00	0.01	0.02	0.03	0.00	-0.01	0.01	0.00	0.01	-0.01	-0.03
Globular crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix Table 12: FLK-W axis values per phytolith morphotype

Globular											
echinate	0.35	-0.06	-0.13	-0.10	-0.05	-0.04	0.05	0.00	-0.03	0.02	-0.02
Globular											
granulate	0.11	0.09	-0.10	-0.02	0.20	0.14	-0.04	0.05	-0.18	0.04	-0.11
Globular psilate	0.26	-0.05	0.01	0.55	0.18	0.16	-0.11	0.02	-0.10	0.05	-0.02
Globular											
tuberculate	0.41	0.25	-0.03	-0.26	0.09	0.06	0.05	-0.10	-0.08	-0.02	0.15
Globulose	0.45	0.08	0.53	-0.05	-0.01	0.15	0.27	0.05	0.11	0.09	-0.04
Guttiform	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hair base	-0.01	0.15	0.07	-0.08	-0.10	-0.04	-0.07	0.06	0.04	0.03	0.10
Hair articulated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemisphere	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irregular											
indeterminate	0.30	-0.03	-0.25	-0.10	0.26	0.01	0.07	0.00	-0.13	0.03	0.07

Appendix Table 12: continued

	A. 12	A. 13	A.14	A. 15	A. 16	A. 17	A. 18	A. 19	A. 20	A. 21	A. 22
Blocky	-0.05	0.08	0.02	0.02	-0.04	0.04	0.01	0.00	-0.01	0.00	0.00
Blocky cavate	-0.08	0.01	-0.03	-0.01	0.04	-0.01	0.00	0.01	0.00	0.01	0.00
Blocky											
dendriform	0.01	0.01	0.01	0.00	-0.01	-0.03	-0.01	0.00	0.00	0.01	0.00
Blocky facetate	-0.06	0.07	0.05	0.02	0.02	-0.03	0.04	-0.01	0.00	0.00	-0.01
Blocky lacunate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blocky hairy	-0.04	-0.04	-0.12	0.00	-0.01	-0.03	-0.01	0.00	-0.01	-0.01	0.00
Blocky pilate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blocky polygonal	0.06	0.01	-0.02	-0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Blocky ridged	-0.06	-0.07	-0.05	-0.02	-0.01	-0.06	-0.03	-0.02	0.00	0.00	-0.01
Blocky sulcate	0.00	0.00	0.01	0.03	-0.04	0.00	0.01	-0.01	0.00	0.00	0.00
Blocky											
tuberculate	0.08	0.01	-0.02	0.01	0.02	0.00	-0.01	0.02	0.00	-0.01	0.00

Blocky radiating	0.07	0.01	-0.02	-0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Bulliform	0.02	-0.05	0.04	-0.02	0.00	0.01	-0.02	-0.01	0.01	0.01	0.00
Clavate	-0.05	-0.02	-0.09	-0.02	0.02	0.07	0.02	0.01	-0.01	0.00	0.00
Cylindroid	0.02	-0.01	-0.03	0.01	-0.02	-0.01	-0.03	-0.01	0.01	0.00	0.00
Cylindroid											
granulate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cylindroid											
crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cylindroid											
scrobiculate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elongate											
orthogonal	-0.04	0.07	0.06	-0.03	0.02	-0.07	0.01	0.01	-0.01	0.00	0.00
Epidermal cell											
tissues	0.08	-0.04	0.05	-0.02	0.00	-0.01	-0.02	-0.02	-0.02	0.00	0.00
Large globular	0.01	0.00	0.01	0.03	-0.02	0.00	-0.01	0.00	0.00	0.00	0.00
Globular crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Globular											
echinate	-0.02	0.01	-0.08	0.05	-0.04	0.02	0.00	0.02	0.00	0.01	0.00
Globular											
granulate	0.00	0.03	0.03	0.05	0.03	-0.01	0.00	0.04	-0.01	0.00	0.00
Globular psilate	0.02	0.07	-0.03	-0.09	0.01	0.04	0.01	-0.03	0.00	0.00	-0.01
Globular											
tuberculate	-0.07	-0.06	0.04	0.06	0.08	0.00	0.00	-0.03	0.01	0.00	0.00
Globulose	0.07	0.05	-0.09	-0.05	0.09	-0.03	-0.01	0.00	-0.01	0.00	0.01
Guttiform	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hair base	0.05	0.03	0.05	-0.05	-0.02	0.02	-0.05	0.01	-0.01	0.00	0.00
Hair articulated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemisphere	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix Table 12: continued

	A. 1	A. 2	A. 3	A. 4	A. 5	A. 6	A. 7	A. 8	A. 9	A.10	A. 11
Irregular ridged	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irregular striated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mesophyll cells	-0.05	-0.16	0.17	-0.10	0.30	-0.02	0.00	0.06	-0.01	-0.01	0.03
Oblong	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oblong											
granulate	0.13	0.19	0.45	0.15	0.02	0.17	-0.07	0.00	0.08	0.14	0.05
Orthogonal	-0.05	-0.18	0.19	-0.11	0.04	0.01	0.03	0.03	-0.02	0.00	-0.01
Ovate granulate	0.37	0.20	-0.02	-0.30	-0.20	-0.06	-0.13	-0.04	-0.10	0.04	-0.08
Perforated plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel horned	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel tower	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel wide	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saddle	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saddle long	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saddle short	-0.05	-0.18	0.19	-0.11	0.04	0.01	0.03	0.04	-0.02	0.00	-0.01
Saddle squat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sclereid	0.36	-0.11	0.02	0.31	-0.25	-0.15	-0.09	-0.06	-0.05	0.16	0.15
Scutiform	0.03	0.01	0.10	0.19	-0.06	-0.07	0.10	-0.05	-0.05	-0.07	-0.02
Tabular cavate	0.08	0.00	0.05	0.13	-0.07	-0.20	0.12	-0.14	-0.07	-0.05	-0.08
Tabular crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular											
dendriform	0.02	0.28	0.18	-0.02	-0.06	0.00	-0.03	0.03	-0.01	-0.05	-0.08
Tabular elongate	-0.01	-0.68	-0.16	0.15	0.17	-0.04	-0.02	0.05	0.08	0.04	0.00
Tabular											
oblong radiating	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Tabular pilate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular											
scrobiculate	-0.90	0.36	0.22	0.10	0.12	-0.08	0.02	0.01	-0.03	0.05	-0.01
Tabular sinuate	0.01	0.31	0.19	0.05	0.10	-0.15	-0.22	0.01	0.14	-0.08	-0.05
Tabular sulcate	-0.02	-0.24	-0.11	0.09	-0.05	-0.08	0.04	0.06	0.03	0.00	0.02
Tabular thick	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vessel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix Table 12: continued

	A. 12	A. 13	A.14	A. 15	A. 16	A. 17	A. 18	A. 19	A. 20	A. 21	A. 22
Irregular											
indeterminate	-0.05	0.07	0.01	-0.02	-0.02	0.04	-0.03	0.00	0.00	0.00	0.00
Irregular ridged	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irregular striated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mesophyll cells	0.04	-0.08	0.01	-0.05	-0.08	-0.03	0.05	0.00	0.00	0.01	0.00
Oblong	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oblong											
granulate	-0.17	-0.12	0.06	-0.04	-0.02	0.01	0.01	0.02	0.00	-0.01	0.00
Orthogonal	0.01	-0.02	-0.04	0.01	-0.01	0.01	-0.01	-0.01	0.01	0.00	0.00
Ovate granulate	0.05	0.04	0.02	-0.04	-0.02	-0.02	0.03	-0.01	0.01	-0.02	0.01
Perforated plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel horned	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rondel tower	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rondel wide	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saddle	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
saddle long	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
saddle short	0.01	-0.02	-0.04	0.01	-0.01	0.01	-0.01	-0.01	0.01	0.00	0.00
Saddle squat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

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Sclereid	0.07	0.01	-0.03	0.07	-0.01	-0.02	0.03	0.02	0.01	0.01	0.00
Scutiform	0.03	-0.06	0.05	-0.02	0.01	0.01	-0.02	0.04	0.01	-0.01	0.00
Tabular cavate	-0.02	-0.01	0.02	-0.04	0.02	0.02	0.03	-0.01	-0.01	0.01	0.00
Tabular crenate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular											
dendriform	0.01	-0.03	0.04	0.09	-0.02	0.02	-0.01	-0.01	0.00	0.01	0.00
Tabular elongate	0.05	-0.04	0.04	0.09	0.03	0.02	0.00	-0.02	-0.01	-0.01	0.01
Tabular oblong											
radiating	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular pilate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabular											
scrobiculate	-0.03	0.06	-0.01	0.04	0.00	-0.04	-0.01	-0.01	0.00	0.00	0.00
Tabular sinuate	0.02	0.01	0.00	0.01	0.03	0.04	0.00	0.00	0.00	0.00	0.00
Tabular sulcate	-0.06	0.06	0.01	-0.02	-0.04	0.01	-0.03	0.00	0.01	0.00	0.00
Tabular thick	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vessel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix Table 13: LAS CA eigenvalues, scores

Axis	Eigenvalue	% of total	Cumulative
1	0.863549	29.296	29.296
2	0.718014	24.359	53.655
3	0.455335	15.448	69.103
4	0.376828	12.784	81.887
5	0.310635	10.538	92.426
6	0.136405	4.6276	97.053
7	0.086862	2.9469	100

Appendix Table 14: LAS axis values per sample

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
LAS 2	1.83	-3.31	1.50	1.05	-0.79	-0.06	0.47
LAS 6	2.34	0.11	1.63	-5.37	3.69	-0.88	2.49
LAS 7	1.78	-2.28	0.79	-3.67	3.02	2.51	-13.99
LAS 8	1.45	-1.09	-4.59	-0.32	0.26	0.57	0.41
LAS 9	-0.40	0.05	-0.11	0.24	0.23	-1.33	-0.24
LAS 12	-0.57	0.04	0.14	-0.26	-0.27	0.79	0.15
LAS 15	2.28	2.07	0.33	0.45	-1.06	0.07	-0.29
LAS 16	0.49	0.87	0.51	4.34	5.67	2.25	0.51

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
Blocky	1.13	-0.54	-1.67	0.16	-0.12	-0.13	0.12
Blocky ridged	1.69	1.64	0.30	0.94	0.01	0.17	-0.18
Blocky sulcate	1.54	-1.63	0.36	-1.38	0.94	0.34	-1.21
Cylindroid	0.49	0.87	0.51	4.34	5.67	2.25	0.51
Globular granulate	0.12	-0.38	0.26	1.06	0.96	-0.52	0.00
Globular psilate	2.34	0.11	1.63	-5.37	3.69	-0.88	2.49
Globular tuberculate	1.83	-3.31	1.50	1.05	-0.79	-0.06	0.47
Globulose	1.45	-1.09	-4.59	-0.32	0.26	0.57	0.41
Guttiform	1.83	-3.31	1.50	1.05	-0.79	-0.06	0.47
Hair base	-0.57	0.04	0.14	-0.26	-0.27	0.79	0.15
Hemisphere	2.28	2.07	0.33	0.45	-1.06	0.07	-0.29
Irregular							
indeterminated	2.28	2.07	0.33	0.45	-1.06	0.07	-0.29
Irregular striated	2.30	1.36	0.80	-1.67	0.67	-0.28	0.72
Mesophyll cells	-0.49	0.04	0.04	-0.03	-0.04	-0.10	-0.01
Oblong granulate	1.45	-1.09	-4.59	-0.32	0.26	0.57	0.41
Ovate granulate	-0.57	0.04	0.14	-0.26	-0.27	0.79	0.15
Tabular scrobiculate	-0.29	0.15	-0.03	0.75	0.91	-0.88	-0.15

Appendix Table 15: LAS axis values per phytolith morphotype

Axis	Eigenvalue	% of total	Cumulative
1	0.789143	25.974	25.974
2	0.609329	20.056	46.03
3	0.546175	17.977	64.006
4	0.329507	10.845	74.852
5	0.278849	9.1781	84.03
6	0.20341	6.6951	90.725
7	0.159884	5.2625	95.988
8	0.072873	2.3986	98.386
9	0.049033	1.6139	100

Appendix Table 17: BPT axis values per sample

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9
BPT 1	1.14	-0.65	0.47	-1.49	2.24	0.48	0.43	-0.08	-0.08
BPT 2	2.26	1.06	-0.08	0.50	-0.41	0.00	-2.73	-0.10	-0.17
BPT 3	-0.05	-1.58	0.77	2.11	0.67	-1.00	0.16	14.84	-11.29
BPT 4	2.29	1.41	-0.36	0.90	-1.08	-0.15	3.11	0.19	0.27
BPT 5	0.14	-1.02	0.48	-2.85	-2.67	-0.65	-0.03	0.06	-0.29
BPT 6	0.17	-2.04	0.28	1.35	-0.34	0.29	0.00	-0.22	0.31
BPT 7	-0.56	0.19	-0.63	0.32	0.35	-1.36	0.21	-1.88	-2.24
BPT 8	-0.53	0.27	0.35	0.17	0.61	-2.56	-0.16	0.83	1.47
BPT 9	-0.60	0.17	-1.65	-0.21	0.03	0.63	-0.10	0.37	0.35
BPT 10	-0.83	0.82	1.24	0.16	-0.11	0.76	0.02	-0.04	-0.04

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9
Blocky facetate	-0.53	0.27	0.35	0.17	0.61	-2.56	-0.16	0.83	1.47
Blocky hairy	0.06	-0.77	0.34	-1.32	-1.08	-0.07	0.03	0.02	-0.06
Blocky polygonal	1.14	-0.65	0.47	-1.49	2.24	0.48	0.43	-0.08	-0.08
Blocky ridged	1.69	0.89	-0.19	0.40	-0.27	-0.19	-2.21	0.04	0.04
Blocky sulcate	0.54	-0.46	0.41	-0.63	0.54	0.00	-0.09	-0.07	0.00
Cylindroid	0.29	-1.54	0.23	0.68	0.24	0.17	0.11	-0.36	-0.03
Elongate orthogonal	-0.60	0.17	-1.65	-0.21	0.03	0.63	-0.10	0.37	0.35
Epidermal cell tissues	-0.60	0.17	-1.65	-0.21	0.03	0.63	-0.10	0.37	0.35
Globular granulate	0.18	-1.40	0.05	0.71	0.02	0.16	0.00	-0.12	0.10
Globular psilate	-0.60	0.17	-1.53	-0.14	0.07	0.38	-0.06	0.09	0.02
Globular tuberculate	-0.81	0.78	1.06	0.14	-0.10	0.75	0.01	-0.02	-0.02
Globulose	0.12	-1.87	0.21	1.27	-0.29	0.17	0.02	-0.35	0.11
Hair base	-0.46	0.23	-1.21	0.02	0.10	-0.14	0.13	-0.32	-0.42
Hair articulated	-0.67	0.47	0.26	0.14	0.18	-0.54	-0.02	-0.06	0.05
Irregular indeterminated	1.98	0.79	-0.06	0.17	-0.15	0.03	-0.17	-0.01	-0.02
Irregular ridged	2.29	1.41	-0.36	0.90	-1.08	-0.15	3.11	0.19	0.27
Irregular striated	1.14	-0.65	0.47	-1.49	2.24	0.48	0.43	-0.08	-0.08
Mesophyll cells	-0.59	0.16	-1.59	-0.21	0.02	0.53	-0.09	0.30	0.27
Oblong	0.21	1.02	0.71	0.40	-0.43	0.45	1.05	0.04	0.06
Oblong granulate	0.10	0.09	0.20	-0.25	0.89	-1.38	0.22	0.52	0.90
Sclereid	-0.60	0.17	-1.65	-0.21	0.03	0.63	-0.10	0.37	0.35
Tabular cavate	0.47	-0.28	0.42	-0.83	1.59	-0.74	0.20	0.29	0.54
Tabular dendriform	-0.53	0.27	0.35	0.17	0.61	-2.56	-0.16	0.83	1.47
Tabular elongate	-0.09	-0.86	0.51	0.69	0.23	-0.29	0.03	1.38	-0.72
Tabular scrobiculate	-0.28	-0.43	0.12	-0.44	-0.63	-0.51	-0.03	0.00	0.09
Tabular sinuate	-0.45	-0.27	-1.27	0.10	-0.05	0.56	-0.08	0.25	0.34

Appendix Table 18: BPT axis values per phytolith morphotype