

Phytolith Analysis as a Palaeoecological Tool for Reconstructing Mid-to Late- Pleistocene Environments in the Olorgesailie Basin, Kenya



OLORGESAILIE BASIN

Photo by the author

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UNIVERSITY OF CAPE TOWN
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Abstract

Ologesailie Basin is an important prehistoric locus and holds a prominent place in African Quaternary research. It is located in the southern Kenya rift system (1° 35'S and 36° 27'E) and has preserved numerous archaeological findings of the Acheulean, Sangoan and Middle Stone Age occupations and most importantly, hominin cranium associated with the Acheulean hand axes. Evidence of past vegetation has hitherto been scarce, because the arid / semi-arid conditions are not conducive for preservation of organic plant microfossils. Phytolith analysis is used to reconstruct the vegetation history and understand hominin habitat preference during mid-late Pleistocene (~746-64 ka).

A localised modern phytolith analogue is used to interpret the fossil assemblage. Descriptive analysis identified fifty nine phytolith morphotypes which were categorised into three major groups; grass short-cell phytolith, epidermal silicified appendages and sedge phytoliths. The identification and classification was based on the International Code for Phytolith Nomenclature and other existing literature.

In order to determine the significance of the identified morphotypes in interpreting fossil data, two multivariate statistical analyses were performed on the database; Correspondence analysis distinguished vegetation components according to a moisture gradient while Cluster analysis identified unique morphotypes that were taxonomically affiliated to their parent plant species. However, the analyses were not able to distinguish plants along the altitudinal gradient.

Fossil phytoliths derived from sixty palaeosol samples extracted from eight geological sections in three localities of the Ologesailie Basin, were identified and tallied to determine vegetation cover and how this changed both spatially and temporarily during the mid-late Pleistocene period. Fossil phytolith frequencies were plotted on TILIA diagrams against the available $^{40}\text{Ar}/^{39}\text{Ar}$ dates.

Correspondence analysis identified three vegetation components; grasslands, woody & herbaceous and aquatic and identified moisture availability as the major underlying factor influencing the morphotype clusters on the ordination space.

An additional cluster analysis of forty morphotypes derived from grasses confirmed the known taxonomic affiliation of major grass short-cell phytoliths to four grass subfamilies (saddle ovate- C₃ Arundinoideae, bilobate concave- and convex- outer margin short shaft and quadralobate-C₄ Panicoideae, saddles-C₄ Chloridoideae and bilobates convex outer margin long shaft-C₄ Aristidoideae). From the non-grass category, achene and papillae phytolith morphotypes were identified as belonging to the Cyperaceae.

Palaeoenvironmental reconstruction based on fossil phytolith analyses suggested that vegetation cover dominated was by tall moisture indicator grasses belonging to C₃ Arundinoideae and C₄ Panicoideae sub-families during the mid-late Pleistocene period (~746-64 ka). Grass phytolith indices on the other hand suggest warm and moist climates with subtle changes to dry and warm climates, while dicotyledon *versus* Poaceae ratio suggest open-canopy vegetation structure dominated with grasslands.

Palaeolandscapes bracketed between ~340 ka and 220 ka supported a heterogeneous vegetation cover with the presence of riverine/riparian vegetation, open grasslands and wetlands (aquatics). This suggests that the landscapes consisted of a mix of ecosystems that were ideal for early hominins inhabiting the region during the mid-Pleistocene period.

This study demonstrates the potential of phytolith analysis as an important proxy in determining the cover and composition of vegetation in the absence of other organic plant fossils. Although there were limitations concerning the chronology of the available dates, the study has provided crucial information for understanding the palaeoenvironments that existed in the Olorgesailie Basin and its possible influence on the behaviour of early hominins during the Pleistocene period. This study offers a base for other studies at archaeological sites which have limited preservation of organic plant remains. The need for a clear chronology to aid in the interpretation of results is, however important.

Keywords: Olorgesailie; Phytolith; Correspondence Analysis; Cluster Analysis; Pleistocene; Palaeoenvironments.

CHAPTER ONE: INTRODUCTION

1.1 INTRODUCTION

The Olorgesailie Basin (southern Kenyan Rift, 1° 35'S and 36° 27'E) is an important prehistoric locus and holds a prominent place in African Quaternary research (Isaac, 1977; Potts, 1989; Deino and Potts, 1990; Potts, 1994; 1998; Sikes *et al.*, 1999). Hominin occupation in the area span the Pleistocene epoch, and includes the Acheulean, Sangoan, and Middle Stone Age occupations. Since the discovery of stone tools at the Olorgesailie Basin in 1942 by the Leakeys (Isaac, 1977), numerous archaeological and geological studies have been carried out, the most remarkable being the geological definition of the Olorgesailie formation (Isaac, 1977). Thereafter, from 1985 to the present, a team of scientists from the Smithsonian Institution and the National Museums of Kenya, led by Prof. Rick Potts, has been carrying out archaeological, geological and palaeoenvironmental studies on a landscape scale with the aim of understanding in-depth human evolutionary history and how humans interacted with the surrounding environment in the past (Potts *et al.*, 1999; Sikes *et al.*, 1999; Behrensmeyer *et al.*, 2002; Owen *et al.*, 2008).

Although the geology and archaeology of the basin are well understood (Isaac, 1977; Potts, 1989; 1994; Potts *et al.*, 1999) little is known of the palaeoenvironmental conditions that prevailed during early human occupation (see Sikes *et al.*, 1999; Owen *et al.*, 2008). Attempts to investigate the vegetation component of such palaeoenvironments are a step towards understanding the major drivers of changes in the past ecosystems through time and across the landscape. This enables the separation of changes due to climatic causes from those caused by anthropogenic activities, and provides an indication of the habitat preferences of hominins at the time (Sikes *et al.*, 1999). The study of plant fossils, including pollen, has proved challenging due to poor preservation of organic plant remains (Livingstone and Mworira, *unpublished report* with the National Museums of Kenya, Nairobi). In this context, phytoliths provide an opportunity to investigate directly the vegetation context that existed in the basin in the distant past.

Phytoliths are silica bodies that form as microscopic components of many vascular plants when monosilicic acid from groundwater is precipitated as opaline silica in intra- and inter-cellular space (Piperno, 1988). Deposition loci within the plant account for the variation in phytoliths morphologies that are produced by specific plants. In addition, some phytoliths have shapes which are related to the parent cell because they are deposited in the specialized silica accumulating cells of certain taxa (Metcalf, 1960; Piperno, 1988). Once the plants decompose, the silica bodies are released back to the

soils/sediments where they are preserved depending on environmental factors associated with the deposition regime (Piperno, 2006).

Phytolith assemblages reflect the composition of different plant communities and, as such, may relate to the different climatic conditions in which distinctive communities prevail (Bamford *et al.*, 2006). Climate plays a major role in determining how different vegetation types are distributed in different ecosystems (Twiss *et al.*, 1969) and varies along altitudinal gradients in relation to changes in temperature and moisture (Tieszen *et al.*, 1979; Mulholland, 1989; Mulholland and Rapp, 1992a). Critically, phytolith spectra vary from one vegetation community to another. Furthermore, grass phytoliths from grasslands growing under different climatic regimes also vary and therefore have been used in phytolith research to trace sub-families and tribes associated with different moisture and temperature regimes (Alexandre *et al.*, 1997; Strömberg, 2004; Barboni *et al.*, 2007; Barboni and Bremond, 2009). Some studies have applied phytoliths to reconstruct grassland dynamics (Alexandre *et al.*, 1997; Strömberg, 2004; Thorn, 2004), to study vegetation canopies in terms of woody plant density (Bremond *et al.*, 2005a) as well as the vegetation context of human occupation (Mercader *et al.*, 2000; Bamford *et al.*, 2006; Albert *et al.*, 2009; Barboni *et al.*, 2010).

This study applies the analyses of fossil phytolith assemblages extracted from palaeosols collected from the Olorgesailie- and Post Olorgesailie- (Olkesiteti and Oltepesi beds) formations to determine past vegetation cover and transition periods while relating the data to Hominin occupation and behaviour within the basin as indicated by archaeological findings (for example, Potts, 1994; Potts *et al.*, 1999; Brooks *et al.*, 2007).

1.2 Research objectives

The Olorgesailie Basin preserves human pre-history extending from the time immediately preceding and including the evolutionary events that led to the transition of hominins from *Homo erectus* to *Homo sapiens* in sub-Saharan Africa around 1.0 Ma-to ~0.6 Ma (Potts, 1989; Potts *et al.*, 2004). It is therefore a unique and important site in understanding human evolutionary history and, more precisely, hominin-environment interactions. To understand the latter, it is important to know the vegetation cover and associated palaeoenvironments that existed in the basin during this time period.

Although stable isotopic data from palaeosols (0.99 Ma) suggested that a mixed vegetation of woody grasslands occurred across the landscape during the early Pleistocene (Sikes *et al.*, 1999) changes in vegetation cover in the region on temporal scale have not yet been established. Paleolimnological studies, however, have indicated environmental fluctuations of wet and dry episodes on decadal-centennial scale between early-mid Pleistocene (~1.2 Ma--~0.493 Ma) within the lake basin (Owen *et*

al., 2008). Against this background, this study examines the vegetation component of the past environments of the basin, inferred directly from plant microfossils, in particular phytoliths. In addition the research investigates both temporal and spatial vegetation changes and associated climatic conditions during this important period of hominin evolution.

1.2.1 Aim and objectives

This project aims to establish the vegetation contexts of the Olorgesailie Basin and the surrounding environments during the mid-late Pleistocene occupations. Trends in vegetation changes through the said time period, as well as spatial heterogeneity, were investigated by extracting fossil phytoliths from palaeosol strata of upper Members of the Olorgesailie Fm. and from Olkesiteti and Oltepesi beds. The data were analysed to investigate the possible climatic conditions that prevailed during this period and provide insights about the cover and the composition of environments within which early hominins lived and interacted.

Fossil remains recovered from the site include mega fauna elements whose present habitats are wooded grasslands, bushlands and forests. Given that the contemporary vegetation does not support the existence of the large mammals, I therefore hypothesized that the vegetation has changed significantly through time. In order to address the main question, the following objectives were established;

- a. To derive a modern phytolith analogue model from plants growing along an altitudinal/ climatic gradient represented by the Taita Hills (~1800 m a.s.l.), Olorgesailie Basin (~990 m a.s.l.) and the Mt. Kenya region (> 2500 m a.s.l.).
- b. To perform multivariate statistical analyses of the modern phytolith analogue to identify and determine the extent to which certain morphotypes are related to particular vegetation types.
- c. To establish changes in vegetation components over time during the relevant phases of the Pleistocene period through fossil phytolith analysis thus enabling the key changes in woody cover and riverine elements to be identified.
- d. To interpret these changes in terms of changing temperatures and moisture conditions by using climatic and aridity indices computed from C₃/C₄ grass short-cell phytolith proportions.
- e. To examine the spatial variability of different vegetation types by comparing phytolith assemblages from different locations within the basin.
- f. To determine the significance of the reconstructed vegetation to hominin evolution and habitat preference in the southern Rift Valley of Kenya.

1.3 Thesis structure

This chapter has provided a brief background and has highlighted the aims and objectives of the study as well as the existing gaps in current knowledge that this research will address. Chapter 2 provides background information regarding the study site, including contemporary climate and vegetation cover characteristics and the geological and archaeological context. Chapter 3 presents a review of relevant palaeoenvironmental and paleoclimate literature of the East African region in order to understand the context of past vegetation change as derived from phytolith analyses. Chapters 4 and 5 outline the theories and methodologies applied to obtain both modern and fossil phytolith data and summarises the technical approach used in the field and laboratory. These chapters also describe the statistical analyses that were used to assess the modern phytolith reference results in Chapter 6 and to interpret fossil phytolith assemblages derived from palaeosols in chapter 7. Chapter 8 summarises and assesses the significance of the study in relation to the aims and objectives. Appendices incorporate raw data and relevant information in order to help the reader to further understand and interpret the research findings.

CHAPTER TWO: OLOGESAILIE BASIN

2.1 INTRODUCTION

This chapter describes the geographical location of the study area, including physiographic, climatic, geological and archaeological settings of the region.

2.1.1 Location and geology of the study Site

The Ologesailie Basin (36° 27'E, 1° 34'S) is 150 km² in extent. It is part of the “Gregory Rift” (Gregory, 1921), and is located 110 km south west of Nairobi city, Kenya. The basin itself lies at 940-1040 m above sea level. It was formed as a result of the tectonic upheavals in the area that characterized the Cainozoic Era (Isaac, 1977; 1978; Potts, 1989; Behrensmeyer *et al.*, 2002). Frequent palaeo-physiogeographic changes have shifted deposition regimes and exposed sediments and their fossil contents along the East Africa Rift Valley complex. The Ologesailie Basin is one of many such exposed localities (Isaac, 1977; 1978; see fig 2.1), and is one of the most important areas in Africa for studies on human evolution and associated palaeoenvironments.

2.1.2 Current vegetation

The current vegetation is characterized as a semi-arid variant of the “*Commiphora-Acacia*” bushland (White, 1983) also classified as Northern *Acacia-Commiphora* bushland (WWF Eco-regions; fig 2.1). The dominant woody components in the bushland include *Acacia tortilis* (Forssk.) Hayne, *A. Senegal* (L.) Willd., *A. mellifera*, *Balanites spp.*, *Grewia bicolor* Juss., *Grewia villosa* Willd., *Boscia coriacea* Pax, *Salvadora persica* L., *Commiphora africana* (A. Rich.) Engl., *Terminalia sp.* and *C. campestris/scheffleri* Engl. The low shrubs constitute *Sericocomopsis sp.*, *Barleria sp.*, *Aerva sp.* and *Indigofera sp.* Most of the trees are deciduous, and are only in leaf during and after the rainy season (Mworia *et al.*, 1988). The grasslands are dominated by the following species: *Chloris roxburghiana* Schult., *Dactyloctenium bogdanii* S. M. Phillips, *Eragrostis cilianensis* (All.) F. T. Hubb., *Tetrapogon cenchriiformis* (A. Rich.) W.D. Clayton and *Sporobolus jacquemontii* Kunth., all of which are C₄ grasses.

The vegetation on the alluvial plains within the basin is relatively open compared to the surrounding ridges and on Mt. Ologesailie itself, and is mainly comprised of the C₄ grasses that thrive well in hot and dry climates. Mt. Ologesailie and the surrounding ridges are characterised by bushes and small deciduous trees dominated by *Acacia mellifera*, *Commiphora campestris*, *C. africana* and *Terminalia spp.* (Mworia *et al.*, 1988).

Along the floodplains patches of sedges and tall C₄ grasses that include *Brachyachne spp.*, *Kyllinga alba* Nees and *Kyllinga welwitschii* Rindley are present. Other vegetation patches occur along the dry river channels (laggus) where riverine gallery forest, comprising *Syzygium sp.*, *Delonix elata* (L.) Gamble and *Terminalia spp.*, is present (Mworia *et al.*, 1988).

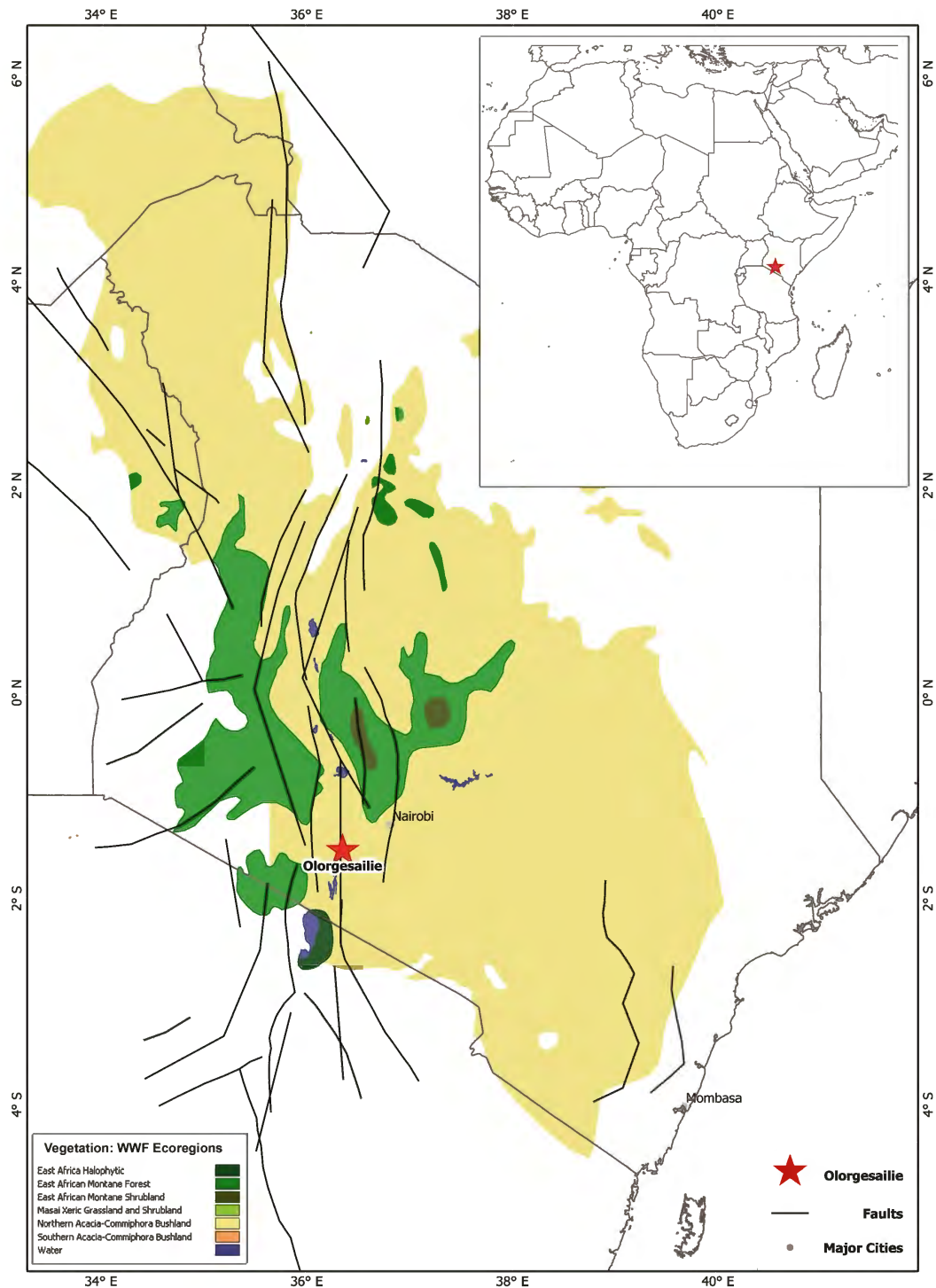


Figure 2.1 Map of Kenya showing the study site and the vegetation type as classified in WWF Ecoregions. Olorgesailie Basin lies within Northern Acacia-Commiphora Bushland.

2.1.3 Contemporary climate

East Africa lies within sub-tropical Africa, 20°-30° north and south of the equator. Its climate is controlled largely by the sub-tropical high pressure cells as the Inter-Tropical Convergence Zone (ITCZ) migrates from south to north, and vice versa following the sun's Zenith point (fig 2.2a).

The passage of the ITCZ, a low pressure belt, northwards or southwards results in high rainfall belts that correspond to the area of maximum insolation. The region influenced by the ITCZ lies between the Tropic of Cancer in the Northern Hemisphere and Tropic of Capricorn in the Southern Hemisphere, approximately 23° 26' 16" N/S (Hills, 1978). Climate variations due to latitude, distance from the coast and topography are complex (Mutai and Ward, 2000; Marchant *et al.*, 2006) and vary strongly at the local scale.

Inter-annual rainfall variability in the region is influenced by disturbances in the monsoon and trade winds, by changes in sea surface temperature (SST) and by large scale atmospheric weather patterns (Mutai and Ward, 2000). Climates within the western part of East Africa are under the influence of moist westerly winds originating from the South Atlantic through the Congo basin during the austral winter (Kenworthy, 1966; Mutai and Ward, 2000).

Regions in the eastern rift valley are characterised by two rainy seasons which follow the equinoxes. The long rains occur from March to June and short rains occur from October to December. Between the two rainy seasons, two dry seasons occur which are described as being of short (July-September) and long (December-February) duration (Sansom, 1954; Griffiths, 1958; 1972; Asani and Kinuthia, 1979). This bi-modal rainfall pattern is caused by the seasonal migration of the ITCZ (Kenworthy, 1966; Nicholson, 1996) and considerable local spatial variation results from moisture transported from the Indian Ocean and/or from westerly winds from the Congo basin (Bergner *et al.*, 2003, fig 2.2a). While the period of maximum rainfall follows the latitudinal position of the ITCZ with a time lag of around four weeks, the maximum surface temperatures coincide with periods of maximum solar radiation (Nicholson, 1996). Temporal rainfall anomalies are associated with the El Niño-Southern Oscillation (ENSO); above average rainfall is associated with warm ENSO events while below average rainfall is associated with cold ENSO events during the short rains. Mean rainfall totals are highly spatially heterogeneous due to the topographical complexity of the region, resulting in varied average annual rainfall in the highlands between 1000-1500 mm and, between 250-500 mm in the lowlands (Griffiths, 1972; Mutai and Ward, 2000).

In the central Rift valley, the pattern is altered by the rain shadow effect of the mountain ranges resulting in irregular rainfall during the long rainy season, March-May (Damnat and Taieb, 1995; Mutai and Ward, 2000). The average rainfall around the Ologresailie Basin is less than 500 mm per

annum (fig. 2.2b.) while the evapo-transpiration of the adjacent Lake Magadi is extremely high >2400 mm per annum (Damnat and Taieb 1995). This negative hydrological balance results in the formation of an evaporite known as the trona crust ($\text{NaHCO}_3 \cdot \text{Na}_2\text{CO}_3 \cdot 2\text{H}_2\text{O}$) which is mined from the lake for economic purposes (Damnat and Taieb, 1995).

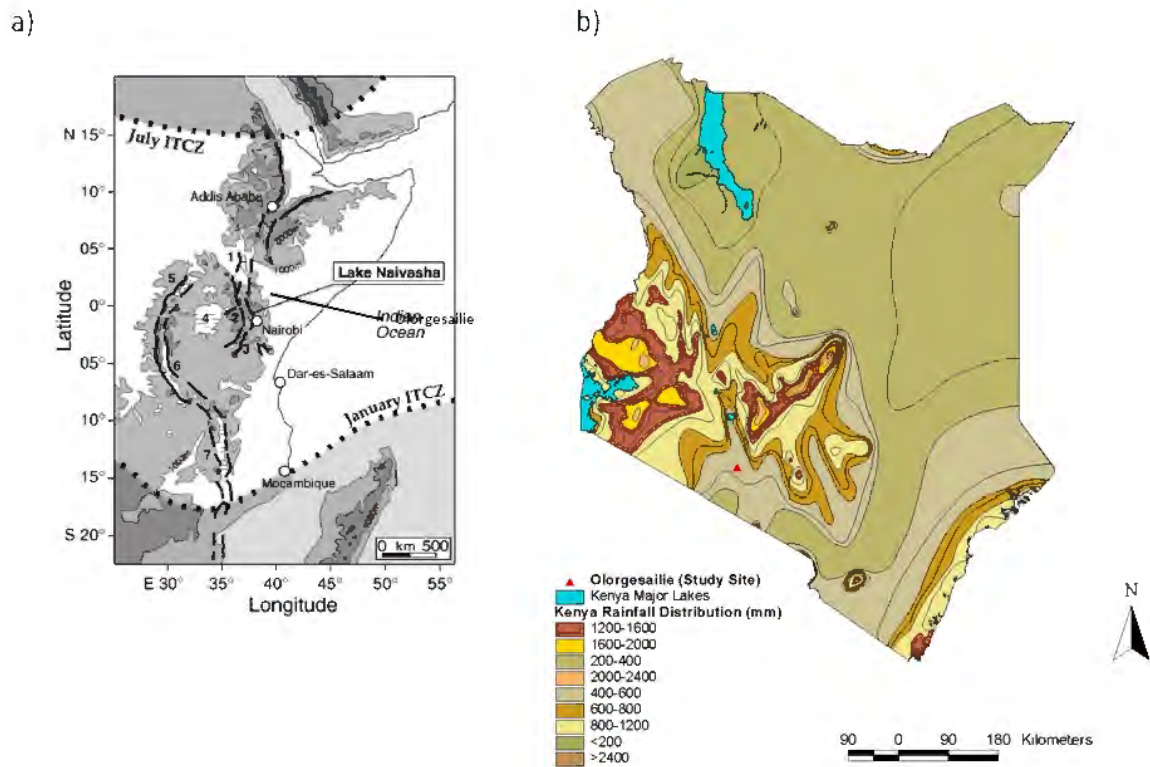


Figure 2.2 a. East African map showing the position of the July and January ITCZ, rift valley lakes and study area; L. Turkana (1), L. Magadi (2), L. Natron (3), L. Victoria (4), L. Albert (5), L. Tanganyika (6) and L. Malawi (7) (After Bergner et al., 2003). b. Map showing the distribution of annual rainfall in Kenya, Olorgesailie receives 400-600 mm.

Variability in precipitation is one of the primary reasons for differences in natural vegetation, land cover and land-use within the region (fig 2.2 b). For instance, agriculture is a prominent economic activity in the highlands due to high annual rainfall, while in the lowlands, where the climate is arid to semi-arid, the main economic activity is pastoralism.

2.1.4 Geo-archaeology

The Olorgesailie Basin is bounded by lavas associated with Mt. Olorgesailie, an extinct Pliocene volcano to the south, and to the north, east and west, by faulted ridges and outcrops of the widespread trachytes, phonolites and basalts (fig. 2.3), which were extruded during the subsiding trough of the southern Kenya rift during the Plio-Pleistocene (Baker and Mitchel, 1976). The drainage system within the basin is controlled by the gradual sloping of the rift floor from North to South over the last million years (Behrensmeyer et al., 2002).

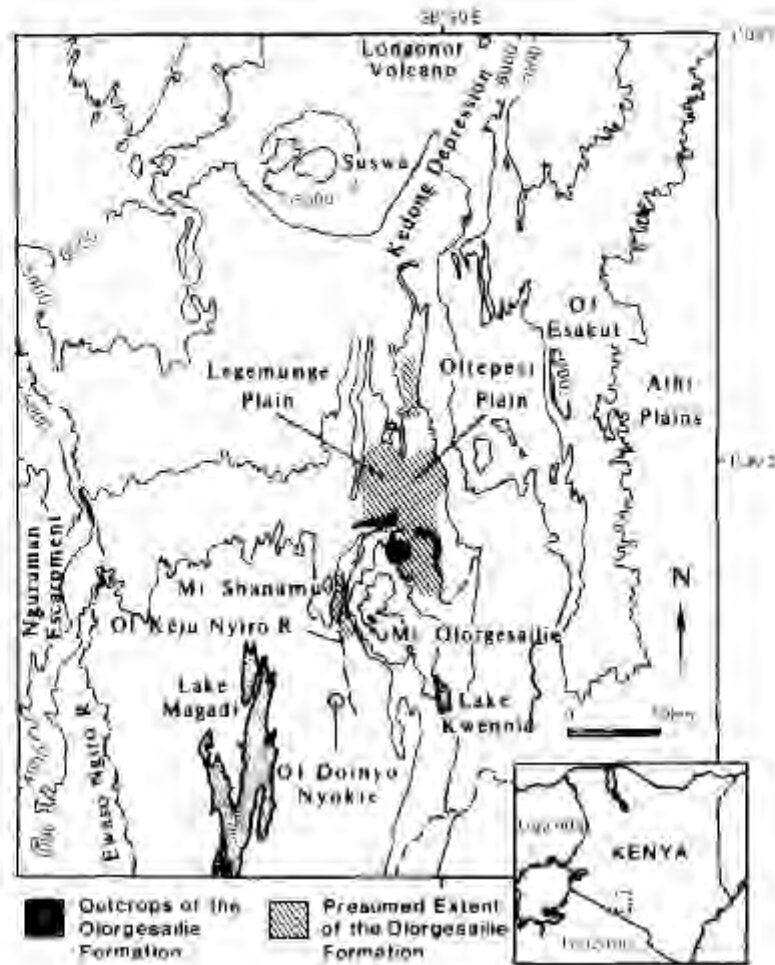


Figure 2.3 A Map showing Olorgesailie Formation in relation to other geological landforms (Deino and Potts, 1992).

Three Formations have been identified within the Olorgesailie Basin according to their lithological characteristics and stratigraphic position (Isaac, 1978); the Olorgesailie, Oltepesi and Olkesiteti Formations. The Olorgesailie formation is comprised of a wide range of lacustrine, wetland/swampy, fluvial and colluvial sedimentary facies that have an aggregate thickness of about 57-80m consisting of Member 1 (oldest 900 ka) to Member 14 (youngest; 490 ka) (Isaac, 1977; 1978; Potts, 1989; Behrensmeyer *et al.*, 2002). The Formation has been dated by single-crystal of $^{40}\text{Ar}/^{39}\text{Ar}$ from 1200 ka at the base of M-1 to 490 ka in Member 14 (Deino and Potts, 1990; 1992). The Oltepesi Formation, on the other hand, consists of a distinctive suite of relatively fine-grained, buff-brown sands and silts, re-worked tuffs and pumice gravels (Behrensmeyer *et al.*, 2002).

Following an erosional unconformity, estimated to have occurred between 490 and 340 ka, sediments that postdate the Olorgesailie Formation were deposited. These deposits mainly represent phases of channel filling that were interspersed with periods of intensive fluvial down-cutting (Behrensmeyer, 2010 *unpublished report*). Although individual strata are difficult to trace over wide areas, the

sediments of the first two or more phases of channel filling (referred to as the Olkesiteti Fm.) preserve a sequence of non-Acheulean and Middle Stone Age sites, which have been excavated in the basin in Localities B and G (Brooks *et al.*, 2007). Most of these sites, including the excavated areas sampled for phytolith analysis in this study, underlie volcanic tephra with preliminary dates of 220 ka (Deino and Potts, 1990; Potts, personal communication).

Acheulean hand axes are associated with the Legemunge beds, consisting of palaeosols and shallow river channels (Isaac, 1977; Behrensmeyer *et al.*, 2002). The highest concentration of archaeological finds is in the upper Member 1 palaeosol (UM1p) with an altitude of 980 m a. s. l. This palaeosol age has been established at 992 ± 39 / 974 ± 10 ka (Deino and Potts, 1990; 1992; see the map in fig. 2.3).

2.2 Summary

This chapter has presented the overview of the study site, the physiogeographical, geological and archaeological settings which make Olorgesailie Basin an ideal site to investigate vegetation change and spatial heterogeneity using phytolith analysis. Contemporary climates and vegetation cover is also presented here to form a basis for comparison with the investigated past climates and vegetation history. The following chapter provides a background to the literature of relevance to this study.

CHAPTER THREE: LITERATURE REVIEW

3.1 INTRODUCTION

This chapter provides a background to literature pertaining to the study in two parts; 1) review of the previous phytolith studies and their application in palaeoecological studies, particularly in Africa, and 2) review of human evolutionary studies undertaken in the East African region. Although the record for Pleistocene environments is limited, the available information inferred from various proxies and disciplines is reviewed here. Limnological and hydrological studies conducted in the Lake Naivasha basin, located to the north of the Ologesailie Basin in the central Kenyan Rift Valley is especially relevant because the chronology established in those studies overlaps the dates for this study.

3.2 Phytolith analysis as a palaeoecological tool

Phytoliths are microscopic silica bodies produced by plants via the deposition of dissolved silica; monosilicic acid $[\text{Si}(\text{OH})_4]$ within and between plants cells (Piperno, 1988, 2006; Pearsall, 1989; Rapp and Mulholland, 1992a) during evapotranspiration. The degree to which plants produce phytoliths is controlled by various factors which include: climatic conditions under which the plants grow and mature, soil chemistry, soil water, plant developmental stage and the taxonomic affinity of the plant (Piperno, 2006). Phytoliths, like pollen, are advantaged by various characters that qualify them as index fossils (Faegri and Inversen, 1975; Moore and Webb, 1978). They preserve well under oxidized conditions, hence are well preserved in dry environments where fossil pollen is absent (Piperno, 2006). In addition, phytoliths have lower specific gravity (ρ 2.4) than clastic silica, and therefore can be successfully separated through heavy liquid floatation (Twiss *et al.*, 1969; Rovner, 1971).

The history of phytolith studies has been summarised in various publications (see Mulholland and Rapp *Jr.*, 1992a; Sommer, 2003). Phytoliths were first recognised and described by Loeuwenhoek in 1675, in research relating phytoliths to plant anatomy and physiology, and they were subsequently applied in reconstructing palaeoenvironments. The application of phytoliths in palaeoecological studies proved to be possible with systematic description of phytolith morphotypes, based on their anatomical characteristics and their associations to various plant groups (Twiss *et al.*, 1969).

Although most plants are thought to produce phytoliths, dicotyledons are known to be poor silica accumulators while monocotyledons are regarded as the best accumulators; dicots in general produce

fewer phytoliths than monocots growing in the same environments (Piperno, 2006). More importantly, grasses - being prolific silica accumulators - produce numerous distinctive phytoliths that facilitate diagnosis beyond family level (Twiss, *et al.*, 1969; Piperno and Pearsall, 1998; Mulholland and Rapp, 1992b; Fahmy, 2008; Mercader *et al.*, 2010) and have even proved to be potential tools in grass systematics (e.g. Ollendorf *et al.*, 1988). Hence, phytoliths are more accurate for vegetation reconstruction than grass pollen, which can only be distinguished to the family level. They also provide gives valuable paleoclimate insights because of the association of various grass tribes with specific moisture and temperature regimes.

Phytolith researchers apply both quantitative and qualitative analyses to clearly define and interpret phytolith data for palaeocological purposes. In terms of climatic and vegetational aspects, estimates of C₃/C₄ grass composition (grass phytolith indices) can provide information on possible climatic conditions reflected in a given phytolith assemblage (Alexandre *et al.*, 1997; Bremond *et al.*, 2008), while estimates of grasses/trees and shrub composition may help determine the relative extent of closed or open habitats (Bremond *et al.*, 2005a).

Apart from grasses, which are known to produce diagnostic morphotypes, other plants such as palms and sedges which are usually associated with wetter habitats have proven useful in determining the broad habitat characteristics of the area (Ollendorf, 1992; Runge, 1999; Piperno, 2001; Albert *et al.*, 2006; Barboni *et al.*, 2010).

3.3 Environmental records in major hominin sites in East Africa

Detailed studies show that African climate and vegetation cover was highly variable from the early Pliocene to the present. Research indicates that African climates at this time oscillated from warm and humid to cool and dry episodes (deMenocal, 1995; deMenocal and Bloemendal, 1995). This resulted in habitats varying between wooded vegetation to open savannah grasslands. It has been hypothesised that this variability was an important factor driving the evolution and speciation of mammals (Environmental Forcing Hypothesis; Bobe *et al.*, 2002). Kingston *et al.* (1994) found the palaeoenvironmental setting of the Kenyan rift was best described as "...a heterogeneous environment with a mix of C₃ and C₄ plants that persisted for the last 15.5 Ma". Other hypotheses based on palaeoenvironmental changes, and associated with major fossil discoveries linked to human evolution and their interactions with environmental context, are discussed and summarised by Potts (1998; Table 3.1). Recent debate on the possible vegetation context in which *Ardipithecus ramidus* (Aramis ~4.4 Ma) interacted with the surrounding environments in Ethiopia (WoldeGabriel *et al.*, 2009; Cerling *et al.*, 2010; White *et al.*, 2010) is a perfect example that demonstrates the need for paleovegetation data from African hominin sites.

3.3.1 Plio-Pleistocene environments

Regional palaeoenvironmental data linked to human evolutionary history have been studied from two major sources; 1) Deep-sea sediment cores that contained a record of climate changes on both regional (Maslin and Christen, 2007; Trauth *et al.*, 2007) and global scales (deMenocal, 1995; 2004; Scholz *et al.*, 2007); and 2) Multi-disciplinary palaeoenvironmental analyses of major hominin sites found predominantly in the African rift valley systems (see Vrba, 1995; White, 1995; Behrensmeier *et al.*, 1997; Sikes *et al.*, 1999; Albert *et al.*, 2009; Bamford *et al.*, 2006) which showed that, major human evolution trajectories coincided with global climatic shifts (Potts, 1998). The interaction between hominins and their surrounding environments, and the role of climate change in human evolution have been discussed and summarised on millennial time-scales (Potts, 1998). Table 3.1 summarises the hypotheses relating to human evolutionary and environmental change based on different proxies (see Potts, 1998).

Table 3.1 Environmental hypotheses of hominin evolution (after Potts, 1998; Bobe and Behrensmeier, 2004)

Hypothesis	Theories (sources)
Savannah expansion	The expansion of grassland ecosystems in Africa coincides with important events of human evolution and major pulses of faunal turnover of mammalian taxa over a wide geographical scale (Vrba, 1985; Bobe <i>et al.</i> , 2002; Bobe and Behrensmeier, 2004). The idea links global climatic changes to faunal turnover and the emergence of the hominin <i>Homo</i> and <i>Paranthropus</i> (Vrba, 1985). The hypothesis was modified by linking shifts towards drier climates, and human evolution and migration on all time scales (deMenocal, 1995; Potts, 1998).
Turnover Pulse	Multiple episodes of high faunal turnover and increased number and abundance of grassland-adopted species, coincide with the appearance of <i>Paranthropus</i> , early <i>Homo</i> and <i>Homo Erectus</i> (Bobe and Behrensmeier, 2004). Adaptation of bovid species to open grasslands, led to the evolution of new species (Vrba, 1995)
Variability selection	Fluctuating climates and environments, and not a directional trend, shaped human adaptation and evolution (Potts, 1996; 1998).

Great attention has been concentrated during the period when the genera *Ardipithecus* and *Australopithecus* emerged in Africa about ~4.4 Ma and 3.6-1.2 Ma respectively as evidenced by extensive studies in east African hominin sites, including those at Hadar and Middle Awash (Ethiopia), Koobi-Fora (Kenya) and Olduvai Gorge (Tanzania) (WoldeGabriel *et al.*, 1994; Asfaw *et al.*, 1999; Sikes *et al.*, 1999; Blumenshine *et al.*, 2003; Albert *et al.*, 2006, 2009; Bamford *et al.*, 2006; White *et al.*, 2006; 2010; Sikes and Ashley, 2007). In addition, recent studies from Olduvai Basin studied phytoliths (among other proxies) to reconstruct palaeoenvironments associated with *Paranthropus boisei* (Ashley *et al.*, 2010).

A detailed chronology of human evolution with corresponding palaeoenvironments in East Africa (7.9 Ma-0.99 Ma) is presented in table 3.2 below (Albert *et al.*, 2006; 2009; Bamford *et al.*, 2006; Sikes *et al.*, 2007).

Table 3.2 Summary of the vegetation reconstructed from major hominin sites in East Africa from Plio-Pleistocene to early Pleistocene (Bonnefille, 1984; Sikes *et al.*, 1999 Albert *et al.*, 2006; 2009) see detailed references in (Potts, 1998).

Locality	Age (Ma)	Interpretation/ vegetation types	Proxies studied	Hypothesis /References
Olorgesailie	~0.99	Mixed vegetation, C ₄ grasslands and C ₃ plants	Stable isotopes from a single palaeosol	Adaptation to the mosaic (Sikes <i>et al.</i> , 1999).
Olduvai Gorge	1.795-1.71	Gallery/riparian forests	Plants microfossils & stable isotopes	Adaptation to fluctuations (Bonnefille, 1984; Sikes, 1994)
Omo-Turkana	4.0-2.5	Dramatic floral change in gallery forest. Dry to wooded savannah and, gallery forest	Plants microfossils	Forest mosaic or fluctuations Adaptation to mosaic fluctuation (Bonnefille and DeChamps, 1983)
Hadar	3.9-3.0	Forest/bush-open country-grassy/plains-forest/bush		Fluctuation (Bonnefille, 1995)
Laetoli	3.8-3.5	Open savannah with seasonal aridity Woodland savannah		Adaptation to savannah Adaptation to woodland (Bonnefille and Riollot 1987).
Kanapoi	4.2-4.0	Mixed vegetation (C ₃ & C ₄ Plants) Dry open vegetation Forest-woodland	Mammalian and isotopic data	Adaptation to mosaic Adaptation to Savannah Adaptation to forest (Winkler, 1995; Leakey <i>et al.</i> , 1995)
Aramis	4.4	Forest woodland		Adaptation to forest (WoldeGabriel <i>et al.</i> , 1994; White <i>et al.</i> , 2010)
Tugen Hills	5.0-2.5	Mixed grassy woodland	Mammalian and isotopic data	Adaptation to forest (Kingstone <i>et al.</i> , 1994)
Kanam	6.1-3.5	Closed-open-closed vegetation Mixed vegetation (C ₃ & C ₄ Plants)	Fossil vertebrate and isotopic data	Fluctuation (Potts <i>et al.</i> , 1997)
Lothagam	7.9-4.7	Mixed open woodland	Mammalian and isotopic data	Adaptation to the mosaic (Leakey <i>et al.</i> , 1996)

It is evident from table 3.2 that differences in methodological approach and hypotheses tested for each hominin site has produced a wide range of results regarding vegetation structure and composition. This can be partly attributed to the fact that most of the East African sites studied are preserved in

unstable fluvial sediments which are mainly localised resulting in differences in the proxies preserved as well as the timeline recorded (Sikes, 1994). The application of a multi-proxy approach has proven to be more accurate in reconstructing palaeoenvironments (Cerling *et al.*, 2010; White *et al.*, 2010), yielding a more robust picture of vegetation change over time, on habitat scale/site specific scale. Linking environmental findings across the landscape scale on a single sedimentary level within a site, and across sites, would enable a more reliable synthesis of palaeoenvironmental reconstructions. Synthesizing the available data from different localities within the East African region (Potts, 1998) provides a clear chronological sequence of human evolutionary history and helps to identify the remaining gaps that need to be addressed so as to fully understand hominin-environment interactions. Geological studies from the Turkana basin suggest that during the Late Pliocene period (2.3-1.7 Ma), the region underwent a series of major palaeogeographic changes which included the formation of rift valley systems, uplifting of major volcanic landforms and the formation of the Rift Valley great lakes (Feibel *et al.*, 1991; Brown and Feibel, 1991; Feibel, 1999). During this time, paleontological and archaeological evidence of patterns and spatial distribution of artefacts indicates that interactions between toolmakers and the landscapes were altered, resulting in hominin tools being discarded in different concentrations across diverse environments in the Turkana basin, as raw materials became more or less available in response to changes in the river courses (Rogers *et al.*, 1994). This is the period when African *Homo erectus* (*Homo ergaster*, 1.88Ma) first appeared, and evidence of spatial expansion of varied pattern of hominin activities were recorded (Potts, 1998). Ruff and Walker (1993) concluded that the existence of *H. ergaster* may have marked a transition in climatic adaptation of early hominins.

Records from Olduvai Gorge suggest that the basin was lake-dominated around 1.9-1.7 Ma (Walter *et al.*, 1991; Blumenshine and Masao, 1991; Bamford *et al.*, 2006). Other multidisciplinary studies suggest significant shifts of vegetation and climate over time, with wet, marshy woodland conditions followed by dry conditions with sparse vegetation cover (Albert *et al.*, 2009; Barboni *et al.*, 2010). Such climatic oscillations were also evidenced from the Turkana basin (Ruff and Walker, 1993). The latter is further evidenced by the physiological characters of the Nariokotome skeleton (1.50-1.55 Ma) whose body shape was linear, similar to modern humans living under a hot and dry climate and this matches the arid and hot climate signalled in the Turkana and the Olduvai sequence at ~1.75 Ma (Ruff and Walker, 1993).

Hominin fossils dated to the mid-Pleistocene period in Africa are rare, but one individual excavated from the Ologesailie Basin and identified as *Homo erectus* has been of great significance in connecting human evolutionary clades in Africa (1.7-0.5 Ma). This individual is comparable to Asian *Homo erectus*, which exhibits features that indicate morphological variations within *Homo erectus*

populations during this period that could probably be attributed to environmental instabilities (Potts *et al.*, 2004).

Previous studies have suggested that vegetation cover during the Pleistocene was more open and characterised by a lower density of tree and shrub cover than the periods prior to 1 Ma, and that those grasslands were persistent in the East African environments until perhaps as late as 600 ka (Potts, 1998, Bobe and Behrensmeyer, 2004). However, recent studies from the Koobi-Fora basin suggest an earlier expansion of C₄ grasslands between 2-1.75 Ma (Quinn *et al.*, 2007) which concurs with a study carried out from South African hominin sites (Lee-Thorp *et al.*, 2007).

From the available literature, it is clear that the expansion and retreat of grasslands plays a major role in defining changes in the environments in which hominins evolved (Bobe *et al.*, 2002; Bobe and Behrensmeyer, 2004). The evidence has been inferred mainly from carbon isotopic analysis, either indirectly from herbivores or directly from soil organic carbon. However, very few isotopic data are derived directly from grass remains, due to poor preservation of organic matter which is a major challenge in most hominin sites. Further, it is impossible to identify grass pollen beyond family level, making it difficult to distinguish grasses to sub families, tribes, sub-tribes or genus level which would offer crucial information of the environmental and climatic conditions relating to the expansion of grasslands (Metcalfe, 1960; Twiss *et al.*, 1969; Twiss, 1992; Alexandre *et al.*, 1997).

3.3.2 Palaeoenvironments within the Olorgesailie Basin

In the Olorgesailie Basin, initial paleovegetation studies have to date only been undertaken from the upper Member 1-palaeosol of the Olorgesailie formation, dated to ~0.992 Ma (Sikes *et al.*, 1997; 1999). Carbon isotopes ($\delta^{13}\text{C}$) indicate that the vegetation context for this palaeolandscape was heterogeneous and consisted of wooded grasslands, and open savanna grasslands. Further, Oxygen isotopes ($\delta^{18}\text{O}$) indicated local climates were cooler and wetter (Sikes *et al.*, 1999) than present semi-arid climates. In addition, research on hominin landscape use hypothesised that hominin-environment interactions varied across the landscape according to the availability of food resources, raw materials and security from predators in different vegetation elements. Such deductions are based on the distribution pattern of artefacts and stone tools across the landscape (Potts *et al.*, 1994, 1999). Paleolimnological data (Owen *et al.*, 2008) show high variability in water chemistry from fresh to saline. The UM1p, in particular was dominated by swampy diatom floras, corresponding with the 1.1 -0.9 Ma high moisture phase recorded in rift valley lakes (Trauth *et al.*, 2005).

Sedimentological studies revealed that the basin was subjected to two major geological processes; first a tectonically stable deposition of lacustrine vs. sub aerial sediments (992-974 ka) (Trauth *et al.*, 2005) and second, a tectonically active basin characterised by erosional and depositional processes

(~974-780 ka) (Potts *et al.*, 1999). The first phase was purely controlled by tectonic processes while the second phase appears to have been a result of the combination of climatic fluctuations and tectonic activity (Behrensmeier *et al.*, 2002). Table 3.3 gives a chronology of geological events recorded in the Olorgesailie formation (~992-493 ka).

Table 3.3 Chronology of geological changes as inferred from the Olorgesailie Formation (Potts, 1998).

Members	Age Estimates	Environmental context/ major events
13-14	601-493 ka	Two major environmental shifts are discussed to have caused “extensive and recurrent alteration of the hydrology and the landscape”(Potts, 1998) and expansion of grasslands was recorded (Sikes <i>et al.</i> , 1997)
10-12	662-601 ka	Disappearance-reappearance-expansion of the lake
8-9	780-662 ka	Three major shifts in deposition and hydrological regimes
6-7	974-780 ka	Fluvial environment Fluctuating lake margin Stable vegetated environment Soil formation in Upper Member 7
1-5	992-974 ka	Lake establishment in M1 Lake margin fluctuation

Extensive studies have been undertaken on the archaeology of the basin which represent different time periods (Potts, 1998; Potts *et al.*, 1999; Brooks *et al.*, 2007), but palaeoenvironmental studies are scarce and have only been carried out on selected palaeosols of the Olorgesailie Formation. There are no such studies from the post-Olorgesailie Formation (Olkesiteti and Oltepesi beds).

3.4 Climatic records in the rift valley region during the Pleistocene period

Multidisciplinary and multi proxy studies from the East African rift valley system suggest that the climate in the Plio-Pleistocene to the Pleistocene period was influenced by major internal (tectonic) and external (Orbital forcing) factors (Kingston *et al.*, 2007; Lepre *et al.*, 2007; Quinn *et al.*, 2007; Scholze *et al.*, 2007; Trauth *et al.*, 2007). The rift valley lakes show evidence of major global events at 2.7 Ma (intensification of Northern Hemisphere Glaciations), 1.9 Ma (onset of Walker Circulation) and ~1 Ma (Mid-Pleistocene Revolution) which was controlled by precessional forcing of moisture availability in the tropics (Trauth *et al.*, 2007).

Although signals and /or responses of climate change in the East African region vary greatly on a regional scale due to differences in the driving factors (e.g. tectonic processes forcing in the northern rift valley may differ from the southern forcing causing differential feedbacks), global climatic events

are well recorded across the region. Furthermore, when appropriate temporal and spatial scales are considered, long-term and short-term processes have been identified with corresponding response scale, i.e., global, regional or local responses (Maslin and Christensen, 2007). These feedbacks that are well-documented from the East African rift valley are complex, as discussed below.

Strong evidence of extreme climate variability (extreme alternating wet and dry periods) may have greatly influenced vegetation dynamics in the East African region during the Plio-Pleistocene (Lepre *et al.*, 2007; Maslin *et al.*, 2007, 2009; Trauth *et al.*, 2007), which in turn triggered the evolution of hominins through the acquisition of adaptation traits (Potts, 2002).

Lithostratigraphic and sedimentological analyses from the Hadar formation, in Ethiopia show high climate variability oscillating between warm and moist to extreme dry and cold phases ~3 Ma (Campisano and Feibel, 2007; Maslin and Christensen, 2007). Such dry episodes have been reflected by the morphological features observed on *Australopithecus afarensis* and the associated faunal remains which suggested arid open environments during the same period ~3 Ma (WoldeGabriel *et al.*, 1993; Campisano and Feibel, 2007) while in South Africa expansion of grasslands is evidenced through isotopic analyses on the proportion of C₃, mixed and C₄ vegetation feeders (Lee-Thorp *et al.*, 2007).

Between 2.7-2.55 Ma, marked lake-level changes coinciding with Milankovitch precessional forcing (23 ka- cycle), were suggested from Lake Baringo (central Kenyan rift valley) causing fragmentation of biological communities, dispersal and then speciation of diatom flora (Kingstone *et al.*, 2007).

Between 1.9-1.7 Ma, evidence from the Koobi-Fora formation suggests remarkable lake level fluctuations in the Turkana basin, Kenya (Brown and Feibel, 1991; Lepre *et al.*, 2007), while a short-term wet episode has been recorded in the Shungura and Hadar formations in Ethiopia, Olduvai Gorge in Tanzania and in the Olorgesailie Basin of Kenya, linked to the precessional orbital forcing. More evidence from Olorgesailie, Naivasha and Elementaita-Nakuru basins show the existence of large lakes between 1.1-0.9 Ma, suggesting wetter conditions (Maslin and Christensen, 2007; Sikes and Ashley, 2007; Trauth *et al.*, 2007; Owen *et al.*, 2008).

Between 900-650 ka, records based on climate model analysis/time series, applied to benthic (foraminifera) oxygen isotopes ($\delta^{18}\text{O}$) show intensification of glacial-interglacial climate cycles in response to the obliquity orbital periodicities of 41 ka cycle around 600 ka (Muldelsee and Statterger, 1997) resulting in the Mid-Pleistocene climate transition, known as the Mid-Pleistocene Revolution (MPR). This global event impacted significantly on the African climate, leading to open vegetation cover dominated by C₄ grasslands in East Africa (Schefuß *et al.*, 2003), associated with increased aridity.

Long lacustrine sediment records from Lake Malawi recorded extreme dry episodes between 135-75 ka, which were more severe than conditions in the Last Glacial Maximum (~18 ka ago) when the water level of most of African great lakes was reduced (Lake Malawi, Lake Tanganyika and Lake Bosumtwi) by at least 95% (Scholz *et al.*, 2007). The climate then shifted to more stable but humid conditions, evidenced by a rise in lake level which coincide with the reduction in precession influenced climates and diminished orbital eccentricity at around 70 ka in the African tropics (Scholz *et al.*, 2007). This corresponds to findings from Lake Naivasha sediments during the last interglacial (130-117 ka) and glacial (117-60 ka) cycles, which recorded high lake levels during 135 ka, 110 ka, 90 ka and 60 ka influenced by orbital oscillations (Trauth *et al.*, 2001; 2003). This climate variability is suggested to have played a major role in influencing human evolution in Africa (Trauth *et al.* 2001; Bobe and Behrensmeier, 2004; Scholz *et al.* 2007).

As indicated in Maslin and Christensen,(2007) ~80% (12 out of 15 specimens) of hominin species found in East Africa date between 0.5-5.0 Ma, a period when East Africa experienced extremely variable climates oscillating between wet and dry periods (Potts *et al.*, 2004; White *et al.*, 2006, Maslin and Christensen, 2007). This further strengthens the evidence of variable climates as the major driver of hominin evolution as evidenced by the emergence of *Homo erectus* in East Africa (Potts *et al.*, 2004; Lepre *et al.*, 2007) graded as premodern *Homo* and hypothesized as closely related to the modern *Homo* in the Linnaean hierarchy.

The literature and the evidence of past environmental changes suggest that drastic climate change influenced the distribution of vegetation cover in East Africa, which consequently influenced the occupants of these environments. However, the Olorgesailie Basin, a unique and important hominin site with an excellent record of hominin activities, needs palaeoenvironmental data relating to hominin specimens dating to 0.97-0.90 Ma (Potts *et al.*, 2004). This information further bridges the gap which remains in our understanding of hominin-environment-interactions in the South rift valley.

In this study phytolith analysis is undertaken for the mid-late Pleistocene palaeosols in order to reconstruct the vegetation context of hominin activities. Use of fossil phytoliths not only indicates the major vegetation components but also suggests the associated prevailing climatic conditions that might have prevailed at the time (Alexandre *et al.*, 1997; Bremond *et al.*, 2008). In order to answer the questions of this study, region-based phytolith data was collected and analysed using materials and methods as presented in the following chapter.

CHAPTER FOUR: MATERIALS AND METHODS

4.1 INTRODUCTION

The study of fossil phytolith assemblages as a proxy for reconstructing past vegetation and its likely associated climatic correlates requires both quantitative and qualitative analyses, achieved by analysing region-specific modern phytolith morphotypes (modern analogues). There are methodological limitations of phytolith analysis due to *multiplicity* (whereby a single species produces a range of phytolith morphotypes in different plant cells) and *redundancy*, (whereby different plant species produce identical or indistinguishable phytolith morphotypes (e.g. Rovner 1971; Fredlund and Tieszen, 1994), but these challenges can be minimised in order to accurately define and interpret phytolith-based palaeoecological data, by considering the following key factors: 1) a modern reference collection for the plants in the area under investigation; 2) a clear understanding of the taphonomical processes to which the soils/sediment have been subjected; and 3) phytolith composition derived from vegetation components known to thrive well under specific climatic conditions.

The Ologesailie deposits were formed under a variety of environmental conditions, including terrestrial settings associated with soil formation, fluvial situations, swamps, lake marginal wetlands and lakes of varying sizes, water depth and chemistry. It can be assumed that these different environments have each been associated with different vegetation cover types and that the extent of wetland habitats depends to some extent on regional climate as well as local hydrology and topography. Therefore, the potential of phytolith analysis as a palaeoecological proxy is governed by environmental factors and other factors outlined below:-

- Variation in phytolith production within plant species and among plant species,
- Differential preservation of plant taxa and their associated phytoliths (affecting the interpretation of phytolith assemblages),
- Taxonomic significance of phytoliths,
- Dispersal mode and the possible extent to which phytoliths are transported from the source,
- Taphonomical issues (differential phytolith preservation and resistance to destruction in soils and sediments).

This study places emphasis on the composition and frequency of phytoliths produced by grasses of various tribes, and sedges, versus those produced by woody plants. This is because different phytolith morphotypes are associated with specific grass tribes and also different grass tribes are associated with contemporary climate and altitude, as observed in the field, making it possible to accurately interpret past climatic conditions, which is a major question in this research project (Mulholland and Rapp, 1992; Ollendorf, 1992; Twiss, 1992; Alexandre *et al.*, 1997; Thorn, 2004; Barboni *et al.*, 2007; Bremond *et al.*, 2008; Mercader *et al.*, 2010; 2011) and understand how past human-environment interactions developed (Piperno *et al.*, 1990, Piperno, 1994; Kealhofer *et al.*, 1999; Mercader *et al.*, 2000; Albert *et al.*, 2005). Distribution of grasses is highly controlled by climatic conditions, specifically temperature gradient and soil moisture availability; C₃ grasses [say which tribes, so that it is consistent with the sentences below] thrive well under cool climates and in tropical Africa on high altitudes >3000 m a.s.l. while C₄ grasses thrive well in warm climates that could be either wet (e.g. Panicoideae grasses) or dry (e.g. Chloridoideae grasses) (Twiss, 1992; Tieszen *et al.*, 1979).

4.2 Materials

Materials collected and analysed in this study belonged to two major categories; modern plant specimens for the reference collection and sediment samples for the fossil assemblages.

4.2.1 Reference collection

Plants differ greatly in their ability to produce phytoliths although many angiosperms, gymnosperms and pteridophytes produce large quantities of phytoliths. Such ability is believed to be genetically controlled and related to plant metabolic factors; consequently plants can either be silica accumulators or non-accumulators (Piperno *et al.*, 2002; Piperno, 2006). More importantly, plant species belonging to the same family tend to have a similar silica accumulation pattern, hence similar phytolith production (e.g., Bozarth, 1993a; Piperno, 1998; 2006; Blinnikov *et al.*, 2002).

By creating a modern reference collection, an assessment of the potential of different plant species in phytolith production may be established. For the species studied, information on the physiogeographic distribution, ecological habitats and photosynthetic pathways (in the case of grasses) was considered (Haines and Lye, 1983; Ibrahim and Kabuye, 1987; Agnew and Agnew, 1994; Beentje, 1994). In the eastern Africa region, major Poaceae subfamilies are associated with particular environmental conditions; C₃ cool and moist (Pooideae), C₃ moisture indicator grasses (Arundinoideae), C₄ warm and humid environments (Panicoideae) and C₄ dry and hot environments (Chloridoideae, Aristidoideae) (Fredlund and Tieszen 1994; 1997; Alexandre *et al.* 1997; Bremond *et al.* 2005 a, b; 2008; Barboni and Bremond, 2009). More so, different subfamilies produce higher percentages of particular morphotypes (Twiss, *et al.*, 1969); hence the relative abundance of each category within a

sample is indicative of which sub-family dominated the vegetation cover at the time of deposition (Twiss, 1992; Alexandre *et al.*, 1997; Barboni and Bremond, 2009). The relative composition of C₃ versus C₄ grasses can therefore give estimates of the prevailing climatic conditions (Alexandre *et al.*, 1997; Bremond *et al.*, 2005a, b; 2008).

4.2.1.1 Sampling procedures

The selection of plants was based on both the contemporary vegetation in the region and the archaeological data documented from the site, which included fossil remains of terrestrial mega-fauna and fossil diatoms analysis indicative of environmental variability in the Pleistocene landscape (Potts *et al.*, 1999; Owen *et al.*, 2008). Woody plants, grasses and sedges representing both C₄ and C₃ plants species were sampled (Table 4.1). Plant identification was carried out at the Botany Department of the National Museums of Kenya (Dr. Mwachala *et. colleagues*).

Random sampling of plant species representative of varied altitudinal range between 0-3000 m a.s.l from the Taita hills, Olorgesailie Basin and Mt, Kenya was conducted. In all, 69 different plant individuals were collected from two different vegetation types; the Olorgesailie Basin (~900-1100 m a. s. l.) represented savannah vegetation types while the Taita hills (~0-1800 m a. s. l.) and Mt. Kenya (>2500 m a. s. l.) regions represented dry and moist forest respectively.

Table 4.1 Plant species analysed, from which phytoliths were extracted, elevation range and habitats in which the species are found in Kenya (Haines and Lye, 1983; Ibrahim and Kabuye, 1987; Agnew and Agnew, 1994; Beentje, 1994).

Family	Species	Plant part	Habitats/altitude range
Acanthaceae	<i>Acanthus eminence</i>	stem, flowers, roots	Moist or dry forest, also among bamboo 1500-2800 m (Mt. Kenya)
Acanthaceae	<i>Barleria taitensis</i>	Complete	Dry Acacia-Commiphora bush and Rocky bushland. 500-1050 m (Taita Hills)
Anarcadiaceae	<i>Rhus natalensis</i>	stem, leaves, fruits	Dry forest margins, (semi-)evergreen bush land, thickets and wooded grasslands. 1050-2700 m (Mt. Kenya)
Anarcadiaceae	<i>Rhus vulgaris</i>	leaves, stem	Dry forest margins, (semi-)evergreen bush land, thickets and wooded grasslands 1200-2700 m (Mt. Kenya)
Anthericaceae	<i>Anthericum sp</i>	stem, roots	1980-2450 m (Mt, Kenya)
Asteraceae	<i>Vernonia brachycalyx</i>	Leaves, Flowers	Dry forest edges ~1100 m (Olorgesailie)
Capparaceae	<i>n/a</i>	stem, leaves	~990 m (Olorgesailie)
Cyperaceae	<i>Cyperus sp</i>	Complete	930-2000 m (Olorgesailie)
Cyperaceae	<i>Cyperus papyrus</i>	Flower	650-2000 m (Olorgesailie) swampy areas
Cyperaceae	<i>Eleocharis sp</i>	Complete	950-1200 m (Olorgesailie) marshes at low altitudes
Cyperaceae	<i>Kyllinga sp</i>	stem, leaves, flowers,	1140-1500 m (Mt Kenya) Moist soils, forest edges

Cyperaceae	<i>Scleria boivinii</i>	Leaves	1140-1160 m (Mt. Kenya) swampy forest edges
Ebenaceae	<i>Euclea divinorum</i>	Leaves	Dry forest, riverine in bushland or forest semi-evergreen bushland 1400 m (Taita hills)
Iridaceae	<i>Gladiolus sp</i>	stem, leaves, fruits, flowers	~990 m (Olorgesailie) savanna grasslands
Malvaceae	<i>Abutilon sp cf. hirtum</i>	n/a	150-1000 m (Olorgesailie) dry bushlands along river banks, luggas.
Mimosoideae	<i>Acacia sp1</i>	stem, leaves, roots	200-1000 m (Olorgesailie) bushed grasslands
Moraceae	<i>Ficus natalensis</i>	Stem, leaves, fruits	Riverine and groundwater forest 900-1800 m (Taita)
Myrsinaceae	<i>Maesa lanceolata</i>	leaves, fruits	Often in secondary forest. 1300-2800 m (Mt. Kenya)
Papilionoideae	<i>Crotalaria sp</i>	stem, leaves	50-1050 m (Olorgesailie) riverine/luggas
Papilionoideae	<i>Indigofera sp</i>	Leaves, Flowers	350-1050 m (Olorgesailie), bushed grasslands
Papilionoideae	<i>n/a</i>	n/a	990 m (Olorgesailie)
Papilionoideae	<i>Rhynchosia sp</i>	Leaves, Flowers	1400 m (Taita Hills) wooded grasslands
Poaceae/ Chloridoideae	<i>Cynodon sp c4</i>	Complete	0-2000 m (Olorgesailie); mostly in disturbed places
Poaceae/Eragrostideae	<i>Eragrostis plana c4</i>	Complete	0-2000 m (Olorgesailie), dry grasslands
Poaceae/ Paniceae	<i>Pennisetum polystachion c4</i>	Complete	2000-2730 m (Mt. Kenya) open grasslands & bushlands in disturbed areas
Poaceae/Andropogoneae	<i>Andropogon sp cf. Canaliculatus c4</i>	Complete	0-2000m (Olorgesailie), moist/swampy grasslands
Poaceae/Aristidoideae	<i>Aristida junciformis c4</i>	Complete	400-2100 m (Olorgesailie); poor eroded or stony soils
Poaceae/Aristidoideae	<i>Aristida congesta c4</i>	Complete	900-2100 m (Taita hills); deciduous bushland often on eroded slopes
Poaceae/Arundinelleae	<i>Arundinella sp c4</i>	Complete	2400-3000 m (Mt. Kenya) swampy grasslands
Poaceae	<i>Bewsia biflora c4</i>	Complete	2000-2400 m (Mt Kenya)
Poaceae/Chloridoideae	<i>Brachyachne sp c4</i>	Complete	2100 m (Taita hills) shallow soils over rocky bed
Poaceae/Chloridoideae	<i>Chloris virgata c4</i>	Flower	2000 m (Mt. Kenya), Wooded grasslands, bushlands & disturbed habitats
Poaceae/Andropogoneae	<i>Coelorhachis sp cf. Lepidura c4</i>	Complete	0-300 m (Taita hills); swampy grasslands
Poaceae/Andropogoneae	<i>Cymbopogon sp c4</i>	Roots, stem, leaves	100-1300 m (Olorgesailie), deciduous bushland and semi-arid grasslands
Poaceae/Eragrostideae	<i>Dactylitenium sp c4</i>	Complete	0-2100 m (Taita Hills)open grasslands & woodlands
Poaceae/Paniceae	<i>Digitaria sp c4</i>	Complete	150-600 m (Olorgesailie); open grasslands
Poaceae/Eragrostideae	<i>Eragrostis racemosa c4</i>	Complete	300-2300 m (Olorgesailie); often on sandy/shallow stony soils
Poaceae/Eragrostideae	<i>Eragrostis superb c4</i>	Complete	0-1800 m (Olorgesailie); open thicket/ wooded grasslands, often in disturbed ground
Poaceae/Andropogoneae	<i>Hyparrhenia cymbaria c4</i>	Complete	1140-2300 m (Mt. Kenya) Bushed & wooded grasslands
Poaceae/Andropogoneae	<i>Hyparrhenia sp c4</i>	Complete	2200-2500 m (Mt. Kenya); Open bushed and wooded grassland
Poaceae/Andropogoneae	<i>Hyparrhenia hirta c4</i>	Complete	1300-2700 m (Mt. Kenya) wooded grasslands
Poaceae/Andropogoneae	<i>Ischaemum sp c4</i>	Complete	1000-2600 m (Taita hills) water logged grasslands
Poaceae/Paniceae	<i>Melinis ambigua c4</i>	Complete	1000-1720 m (Taita hills) upland grasslands

Poaceae/Paniceae	<i>Melinis sp c₄</i>	Complete	1000-1720 m (Taita hills) grasslands
Poaceae/ Paniceae	<i>Melinis repens c₄</i>	Complete	930-2520 m (Mt. Kenya) wooded grasslands
Poaceae/ Paniceae	<i>Melinis nerviglumis c₄</i>	Complete	930-2520 m (Mt. Kenya) wooded grasslands
Poaceae/ Paniceae	<i>Oplismenus sp c₄</i>	Complete	0-2300 m (Mt. Kenya) forest
Poaceae/ Paniceae	<i>Panicum sp cf.eickii c₄</i>	Complete	2800 m (Mt. Kenya) Forest edges, swamp grasslands (uplands)
Poaceae/ Paniceae	<i>Panicum maximum c₄</i>	Complete	0-2400 m (Olorgesailie) wooded grasslands, forest edges
Poaceae/ Paniceae	<i>Pennisetum purpureum c₄</i>	Complete	0-2000 m (Mt. Kenya) Forest margins & riverine
Poaceae/Arundineae	<i>Phragmites mauritianus c₃</i>	Complete	0-1500 m (Taita hills), shallow water streams, river banks & lakes, and swampy places
Poaceae/Arundineae	<i>Phragmites australis c₃</i>	Complete	600-1500 m (Taita hills) shallow water streams, river & lake banks, in swampy places.
Poaceae/Andropogoneae	<i>Rottboellia sp c₄</i>	Complete	0-1700 m (Olorgesailie) flood plains
Poaceae/Andropogoneae	<i>Schizachyrium jeffreysii c₄</i>	Complete	0-900 m (Olorgesailie) wooded grasslands on moist places
Poaceae/Andropogoneae	<i>Schizachyrium sp c₄</i>	Complete	0-900 m (Olorgesailie) along stream banks
Poaceae/Paniceae	<i>Setaria sphacelata c₄</i>	Complete	0-3300 m (Mt. Kenya) grasslands & bushlands, stony hillside to river banks
Poaceae/Paniceae	<i>Setaria sp c₄</i>	Complete	0-3300 m (Mt. Kenya) Bushed-grasslands
Poaceae/Sporoboleae	<i>Sporobulus sp c₄</i>	Complete	1300-2600 m (Mt. Kenya) Deciduous bushlands
Poaceae/Sporoboleae	<i>Sporobulus africanus c₄</i>	Complete	1300-2600 m (Mt. Kenya), disturbed grounds/alongside paths
Poaceae/Sporoboleae	<i>Sporobulus consimilis c₄</i>	Complete	390-1950 m (Mt Kenya) flood plains and lake shores
Poaceae/Andropogoneae	<i>Themeda sp c₄</i>	Complete	0-3200 m (Mt. Kenya) open grasslands
Poaceae/Andropogoneae	<i>Themeda triadra c₄</i>	Complete	0-3200 m (Mt. Kenya) Deciduous bushland/wooded grasslands.
Poaceae/Paniceae	<i>Urochloa sp cf. mosambicensis c₄</i>	Complete	0-650 m (Taita hills), Bush-grasslands on flood plains
Rubiaceae	<i>Canthium sp</i>	Stem, leaves, fruits.	1700-2350 m (Mt. Kenya) upland forest
Rubiaceae	<i>Rubus sp</i>	Leaves, Flowers	1950-2750 m (Mt. Kenya) upland forest
Rubiaceae	<i>Tarenna graveolens</i>	Stem, leaves, fruits	Bushland, drier forest margins, thickets (often riverine), bushed grassland
Salvadoraceae	<i>Salvadora persica</i>	leaves, fruits	More often along laggus, lakes or wells; also in dry (Acacia) bushland and (wooded) grassland.
Tiliaceae	<i>Grewia fallax</i>	leaves	Dry bushland or bushed grasslands, often in rocky sites near laggus or rivers.

4.2.1.2 Extracting Phytoliths from modern plants

The extraction of phytoliths from plant specimens followed a modified Albert and Weiner protocol (after Mercader *et al.*, 2009) which ensures both quantitative and qualitative data is obtained (Strömberg, 2009). Although the determination of silica accumulation among plants is beyond the scope of this research, the data base obtained can be used for future phytolith research.

Plant specimens were soaked in 5% Calgon solution overnight on an automatic shaker to loosen unwanted material adhering to the specimens. They were then washed with distilled water through a

1mm sieve after which they were sonicated for 30min using a Fisher Scientific FS 60. The specimens were then dried overnight at 100°C, weighed and ashed in the muffle furnace at 500°C for 12 hrs; some woody specimens were ashed for up to 36hrs to achieve complete combustion.

The weight of the cooled dry ash was then recorded for each specimen to determine the proportion of combustible carbon. The ash was transferred into test tubes where 10ml of equivolume solution of Hydrochloric acid (HCl) and Nitric acid (HNO₃) was added (at 3N)¹. This was then boiled until the residue formed a paste. The samples were then washed three times with distilled water each time centrifuging at 3000 rpm for 5min. 10ml of Hydrogen peroxide (H₂O₂) was added to each sample, which were then transferred into petri dishes, and placed on hot plate at 70°C until the reaction ceased. The samples were transferred back to the test tubes, washed with distilled water three times at 3000 rpm for 5min before drying in the oven at >100°C. The resulting Acid Insoluble Fraction (AIF) was weighed and stored in vials ready for slide mounting and analyses.

4.2.2 Soils and sediments

Phytolith preservation is highly dependent on taphonomical. In the Ologesailie Basin, they include a wide range of fluvial and colluvial depositional processes influenced by chemical and physical weathering; such processes may be local, extra-local or regional to the basin (Isaac, 1977; Behrensmeyer *et al.*, 2002)..

4.2.2.1 Chronology and sampling procedures

The Ologesailie Basin has been subjected to a variety of geological processes leading to four major depositional phases in an ~120 m profile of sediments spanning the past million years, calibrated by radiometric dating of volcanic ashes and pumices (Deino and Potts, 1990; 1992). The oldest of the four phases of basin filling is represented by the Ologesailie Formation which comprises sediments ~80 m in thickness dating between 992-493 ka (Deino and Potts, 1990). This formation consists of 14 Members that are well exposed across the southern part of the basin (Deino and Potts, 1990; Potts *et al.*, 1999; Behrensmeyer *et al.*, 2002). Three samples collected from different palaeosols (~662-601 ka) in this formation were processed and analysed for phytoliths (fig 4.1 Geological section # B05/04; 225 ka tuff). Overlying the Ologesailie formation are more localised deposits, ~40 m in thickness, representing at least three episodes of valley cutting and filling that occurred between ~0.5 Ma and the end of the late Pleistocene (fig 4.2). These deposits were identified as the Olkesiteti and Oltepesi beds respectively (Isaac, 1978; Behrensmeyer *et al.*, 2002).

¹ 1N means; 1g equivalent to 5 solutes per litre of solution.

OLORG 2005
 LOCALITY B
 B05/04
 07/28/05
 AKB

1/6/05

updated 2010

B05/04

GRN PUM TUFF - 225 K

7/28/05

WP 53 37M 0214891
 9525918

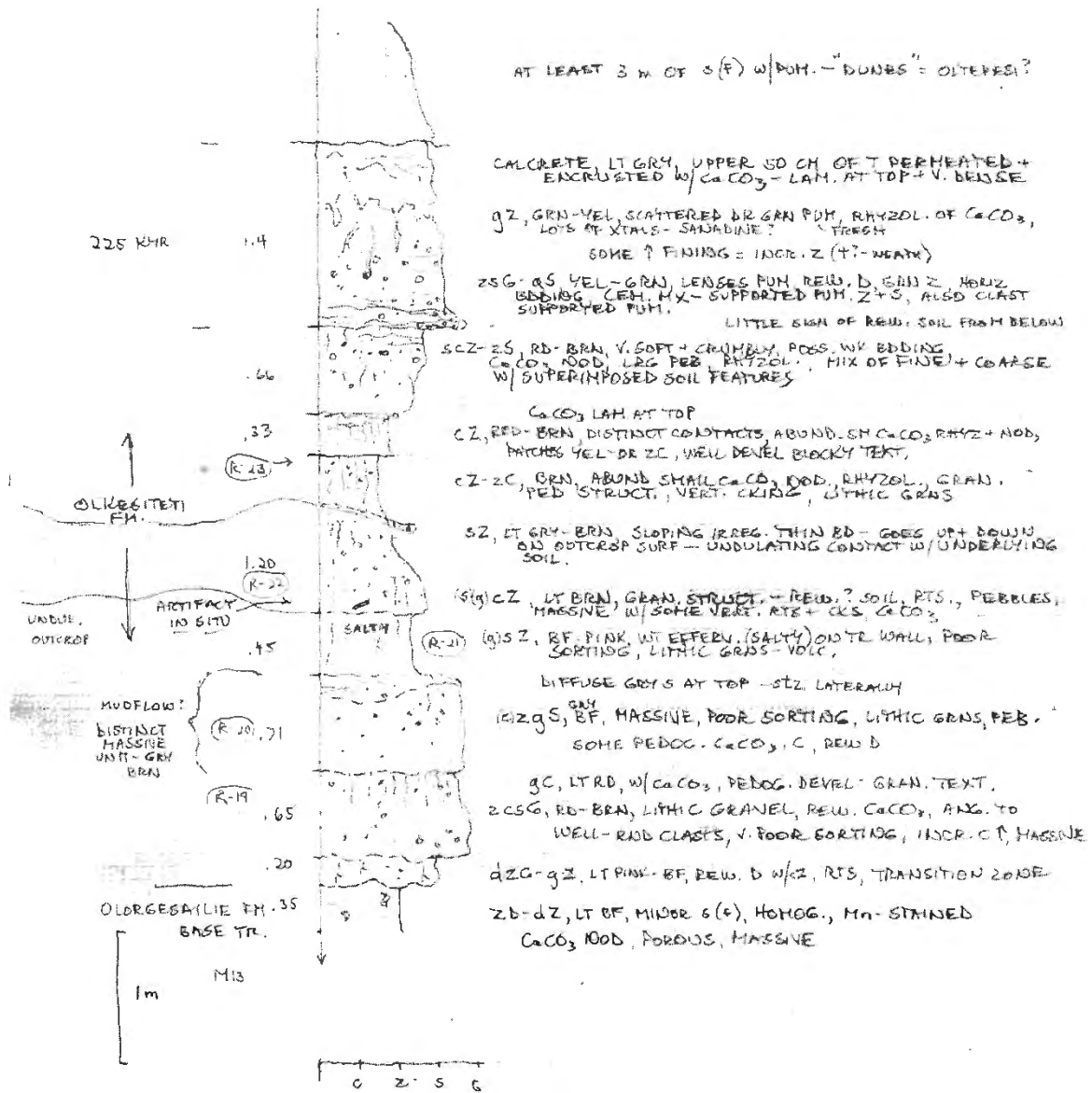


Figure 4.1 A geological trench (B05/04) showing samples taken (R19-R23) and the boundary between Olorgesailie Formation and the Olkesiteti beds and geological marker tuff (225 ka) (Behrensmeier field notes).

Unlike the Ologresailie formation, where clear lateral correlation has been successfully carried out through geological markers such as tuff, pumice (Deino and Potts, 1990) and chemical “fingerprints” of the volcanic ashes (Behrensmeyer *et al.*, 2002), the Olkesiteti and Oltepesi beds are more complicated due to the alteration of their geomorphology by faulting and volcanic flows in the Late Pleistocene (Baker and Mitchell, 1976). The Olkesiteti bed dates between ~340 -220 ka (Deino and Potts, 1992) while the later Oltepesi deposits date to ~105-64 ka. The two beds form the post-Ologresailie formation referred to ‘The New Formation’ shown in fig 4.2 which currently is being mapped (ongoing geological mapping by Behrensmeyer *et al.*, 2010).

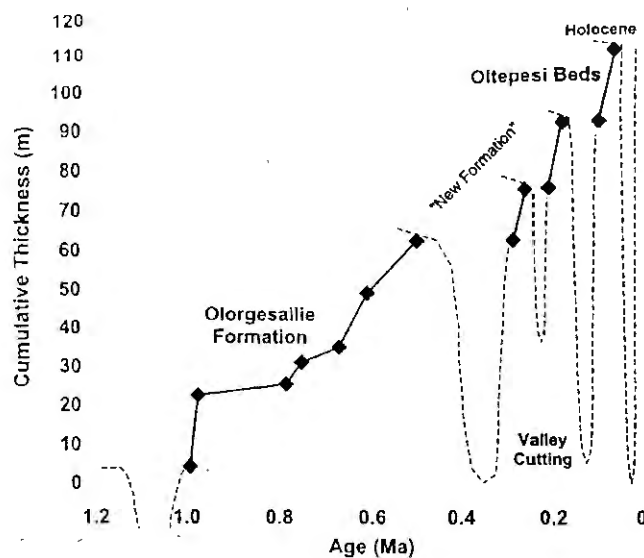


Figure 4.2 Reconstructed large-scale pattern of sediments accumulation through the past Million years at the Ologresailie Basin (after Behrensmeyer *et al.*, 2002).

4.2.2.2 Target palaeosol

All samples were collected from stratigraphic intervals identified as palaeosols. Twenty six that were vertically matched with chronological sequences from four geological sections in Locality B were processed for phytolith analysis (see map in fig 4.3), these sections are described below from the youngest deposits to the oldest,

A) Geological Section B08/05 (~3.5 m thick)

This section constitutes deposits including the dated tuff ~225 ka; of the New Formation. The base of the deposit is on Ologresailie formation M11; five samples were collected within a 2 m depth from the dated tuff while seven samples were collected above the tuff ~2.5 m. One of the samples was collected from palaeosol~ 3.5 cm from the 225 ka tuff.

B) Geological Section B06/04 (~2.5 m thick)

This section constitutes deposits of the New Formation; Olkesiteti and Oltepesi beds. All the deposits are above the dated pumice gravel ~340 ka and below the volcanic tuff ~225 ka. Six samples were collected from this section, three of which belong to the older Olkesiteti bed while the other three belong to the younger Oltepesi bed which overlays the Olkesiteti bed midway along the sequence.

C) Geological Section B08/01 (~4 m thick)

This section is comprised mostly of Olkesiteti bed deposits including the dated volcanic tuff ~340 ka; but all the three samples collected are older than this date.

D) Geological section B05/02 (~1.5 m thick)

This section constitutes sediments of the Olorgesailie Fm. Member 9 marker tuff) ~746 ka to M11' (662 ka). Three samples were collected from this section.

The map in fig. 4.3 shows all the geological trenches sampled and the three localities as described by Behrensmeyer (2001).

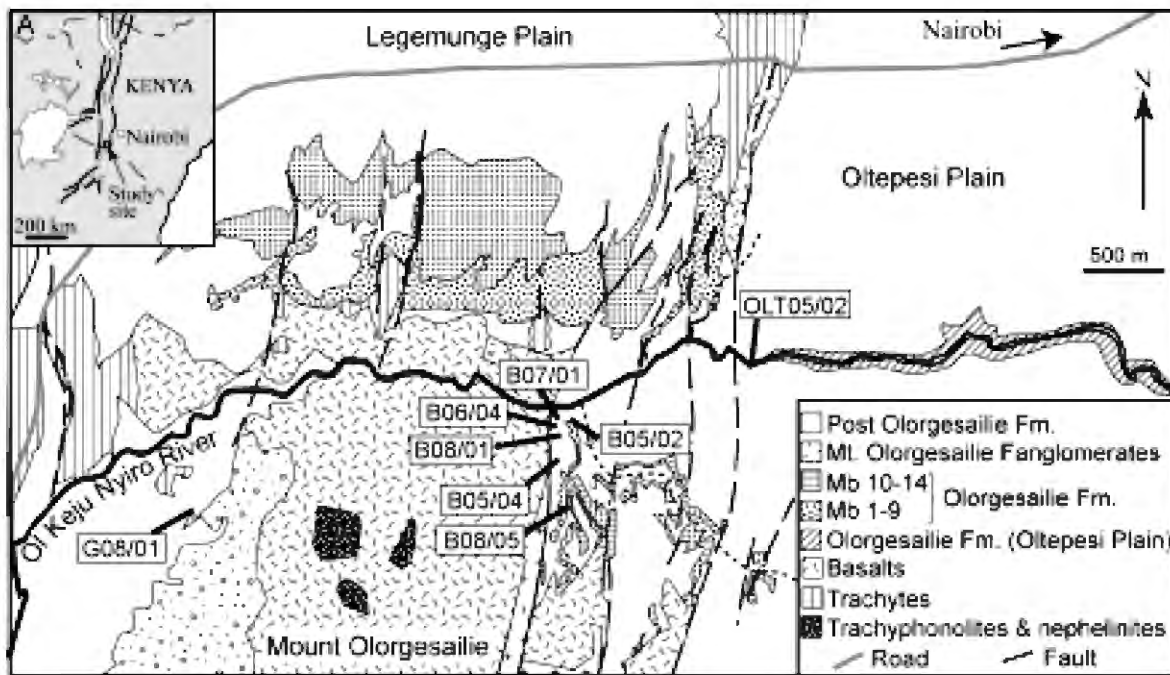


Figure 4.3 Olorgesailie Basin showing the three localities sampled for this study (Geological trenches labelled in text boxes).

A) Locality B and Oltepesi Plains

Locality B contains mid-late Pleistocene archaeological material with a series of superimposed channel fills dating from ~350-50 ka. The sequences of channel fills have been reconstructed on the

basis of a combination of lithological similarity, chemical correlations, stratigraphic superposition and the available radiometric ages (*Unpublished Behrensmeyer, 2010*).

In this locality, the three formations, *viz.* the Ologesailie formation (Members 8-14), the Olkesiteti and the Oltepesi beds have been exposed by various geological processes. The uppermost tuffaceous unit, which has been a major tracing marker of the Olkesiteti bed in the Ologesailie Basin, dates to ~340 ka. The Olkesiteti in Locality B represents the interval between 320-220 ka. The other dated markers include a green pumice tuff unit, a very distinctive deposit dated at 220 ka that correlates with pumice rich tuffs in Oltepesi plains and Locality G (Behrensmeyer, 2008; Behrensmeyer *et al.*, geological work in progress)

A total of forty two samples was obtained from Locality B, each weighing 20g, from six different sections (B08/01, B06/04, B08/04, B05/04, B05/02 OLT'05/02) and one excavation site (BOK-1) see example of a described geological trench in fig. 4.1. All of the sediment samples were collected from identified palaeosol layers of each geological section. Thirty of these samples are closely related to the Ologesailie formation and Olkesiteti bed, while twelve samples were from the Oltepesi bed (B08/05). Based on chronological representation, thirty three samples were selected and processed for the analysis of fossil phytolith assemblages.

B) Locality G

A total of sixteen sediment samples were collected. Twelve of these were sampled vertically from section G08/01 from identified palaeosols; two samples were obtained from a freshly dug excavation pit, while two were collected from surface soil beneath each of two vegetation settings; wooded grassland and open grassland as control samples.

4.2.2.3 Extracting phytoliths from sediments

Sediments were sieved through 500µm to separate larger particles. Two samples were then obtained from each sieved sample, *viz.* one, from which 1g was obtained and placed in 10ml test tubes, distilled water was added, vortexed and the pH value of each sample was measured (Basic perpHecT log R pH, Orion 310); second, from which 5g was taken and placed in 50ml test tube and processed following the protocol to attain the Acid Insoluble Fraction (AIF) and placed in 15ml centrifuge tube. For each of these sub-samples an additional step using heavy floatation (heavy liquid; Sodium Polytungstate (SPT)) which was previously prepared at a specific gravity of 2.4 was applied as follows:-

- 5ml of sodium polytungstate (SPT) was added in the 15ml centrifuge tube that contains the AIF. This was well mixed by vortexing and then centrifuged at 3000 rpm for 5minutes.

When separation was complete, the floating fraction containing lighter clay minerals was transferred to a second tube, labelled (FF1) while the pellet, heavy fraction containing the phytoliths and sand was left in the 15ml tube and labelled as fraction 1(F1) – sand fraction and heaviest phytolith types.

- 1ml of distilled water was then added to the floating fraction (FF1) using a precision pipette. This was then well vortexed, mixed and then centrifuged at 3000 rpm for 5 minutes. The floating fraction (FF2, lighter clay minerals) was then transferred to a third tube while the heavy fraction 2, containing heavier phytoliths and coarse silt was left in the 15ml tube and labelled (F2) – coarse silt fraction and heavier phytoliths types.
- 1ml of distilled water was then added to the floating fraction to FF2 using precision pipette, vortexed and centrifuged at 3000 rpm for 5 minutes. The floating fraction, containing the lightest clay minerals was then transferred to a 15ml tube and labelled FF3 while the heavy fraction, containing fine silt and light phytoliths types was labelled as (F3).
- Some samples were fractionated four times due to the abundance of clay that made separation difficult (F4). This protocol separated clay and other light mineral component from the heavier sediments (sand and silty fraction), containing phytolith component. Larger phytolith types are present in sand fraction (F2) and in the silt fraction (F3 and F4).
- Once fractions F1, F2, F3 and F4 were obtained, they were washed using distilled water, each time centrifuging at 4500 rpm for 2-3 minutes until no traces of SPT remained in the sample thereby ensuring the final weight was not affected by residual sodium polytungstate. The samples were then dried on a hot plate for two days at 70⁰C. The mass of each fraction was measured using a high precision weighing balance (Sartorius GMBH model # 7073-02).

4.2.3 Microscopic analysis

Approximately 0.001g of the AIF and final fractions (F1, F2, and F3-for the sediment samples) for each sample was mounted on a microscope slide using ‘Entellan New’ as the mounting medium. After thoroughly mixing the aliquots with this medium, a cover slip was placed carefully, so as not to trap any air bubbles and ensuring even spread of the sample. Slides containing the coarse silt and sand fraction (F1, F2), were scanned entirely and all the phytoliths encountered were counted. For the slides containing the fine silt fraction (F3) at least 250 phytoliths were counted with a few exceptions where low concentrations were encountered. However, in all cases, all slides were scanned entirely to locate rare-occurring, possibly diagnostic phytoliths (Strömberg, 2009).

Phytolith identification and counting was carried out on freshly mounted slides to ensure that the sample was not dry and could be manipulated in three dimensions to optimise identification. This was carried out on an Olympus BX52 microscope at x400 magnification. Viewing was undertaken under

polarized light, regular light microscopy and differential interference contrast (DIC) that enabled clear microphotography using image processing software; Image-Pro^s plus 5.1 and Infinity Capture software 2. Images were stored in the computer as TIFF/JPEG files from which some of the images are presented in this work (Plates 4.1 and 4.2).

4.3 Morphological classification

The morphological identification and classification of phytoliths was based on various published literature: grass short-cell phytoliths (Twiss *et al.*, 1969; Mulholland and Rapp, 1992a; Piperno and Pearsall, 1998; Thorn, 2008; ICPN, Madella *et al.*, 2005; Fahmy, 2008; Barboni and Bremond, 2009; Rossouw, 2009; Mercader *et al.*, 2010), Woody (dicots) phytoliths were identified and described based on (Runge, 1999; Albert, 1999; Albert *et al.*, 2000; Albert and Weiner, 2001; ICPN, Madella *et al.*, 2005; Piperno, 2006; Mercader *et al.*, 2009), and Cyperaceae morphotypes were identified and described based on (Ollendorf, 1992; Piperno, 1988; Madella *et al.*, 2005).

The morphotypes are named where possible, following palynological terms used for pollen classification, adopted in the International Code of Phytolith Nomenclature 1.0 (ICPN, Madella *et al.*, 2005; cf. Piperno, 2006) to categorize phytoliths (see table 4.2).

Table 4.2 Palynological terms adopted to describe phytolith morphology (Madella *et al.*, 2005)

Surface Descriptors	Definition
Psilate	Smooth surface
Scabrate	With sculptural element < μm
Verrucate	sculptural elements broad > $1\mu\text{m}$
Echinate	spiny elements
Sinuate	Wavy- a series of undulating lines/curves
Lobate	Having lobes

The grass short-cell phytoliths are described and classified according to the dimension, shape, surface outline and size into the following major categories (Table 4.3):

4.3.1 Grass short-cell phytoliths

These include silica cells derived from grass leaf epidermal cells and, include the bilobates (Twiss *et al.*, 1969; Rapp and Mulholland, 1992; Fredlund and Tieszen, 1994; Rossouw, 2009),

quadrilobates/crosses (Twiss *et al.*, 1969; Piperno, 2006), saddles (Twiss *et al.*, 1969; Bremond *et al.*, 2008; Rossouw, 2009; Barboni and Bremond, 2009), rondels (Twiss *et al.*, 1969; Fredlund and Tieszen, 1994; Bremond *et al.*, 2008), towers (Mercader *et al.*, 2010) and trapeziform polylobates (Bremond *et al.*, 2008; Rossouw, 2009). These morphotypes may vary in shape depending on the photosynthetic pathways exhibited by various species. Establishing the presence and frequencies of various short-cell morphotypes within a grass species makes it possible to distinguish between C₃ and C₄ grasses, and they are therefore especially useful as potential indicators of the climatic conditions and environments in which the parent grasses grew (Tieszen *et al.*, 1979; Twiss, 1992; Alexandre *et al.*, 1997; Rossouw, 2009). Determining the relationship between grass short-cell phytoliths and grass taxonomy (Twiss *et al.*, 1969; Twiss, 1992; Piperno and Pearsall, 1998) as well as ecological affiliation (Barboni and Bremond, 2009) has facilitated division of grasses into five major extant grass sub-families, as classified by the Grass Phylogeny working Group (GPWG) 2001 (after, Piperno 2006); Bambusoideae (C₃ tall forest grasses), Arundinoideae (C₃ tall grasses, wetlands grasses), Festucoideae or Pooideae (C₃ short grasses adapted in high elevation in the tropics, and temperate regions), Panicoideae (C₃/C₄ tall grasses adapted to tropics, wet and warm climates) and Chloridoideae (C₄ short grasses adopted in warm and dry climates) (Twiss, 1992; Alexandre *et al.*, 1997; Bremond, 2008). The ratios of grass short-cell phytoliths (rondel, trapeziform polylobate, saddle, cross/quadrilobate and bilobates) found in various grass subfamilies can provide information on the relative dominance of C₃ or C₄ grasses (Brown, 1984; Thorn, 2004; Bremond *et al.*, 2008) while the ratios of the grass short-cell phytoliths to non-grasses phytoliths can provide information regarding the relative dominance of grasslands versus woody vegetation (Alexandre *et al.*, 1997; Bremond *et al.*, 2005a).

4.3.1.1 Bilobates-

These silica cells have two distinct lobes connected by shank/shaft (Madella *et al.*, 2005). They are located between the elongated epidermal cells of grass leaves (Twiss *et al.*, 1969) and are more abundant in Panicoideae grass sub-family (Twiss *et al.*, 1969; Bremond *et al.*, 2008; Rossouw, 2009) however, they are also found in Chloridoideae and other subfamilies (Brown, 1984; Thorn, 2004; Barboni and Bremond, 2009). Bilobate variants have been described and identified according to the lobe outline and the size of the connecting shaft (bilobate convex, short and long shafts, bilobate concave short and long shaft, bilobate flared short and long shaft, bilobate panicoid type (with convex lobes, short but thick shaft appearing symmetrical on the plane) (Albert, 1999), bilobate flattened short and long shaft and bilobates flared short and long (Fredlund and Tieszen, 1994). Such detailed variation ensured that simple bilobates, i.e. those produced by Panicoideae grasses may be distinguished from the complex bilobates produced by Chloridoideae and Bambusoideae grasses

(Fahmy, 2008; Piperno and Pearsall, 1998; Mercader *et al.*, 2011) see examples in plates 4.1(a-c) and 4.2(a-d).

4.3.1.2 Saddles-

These silica cells have two opposite convex edges and two straight or concave edges (Thorn, 2004). They vary both in terms of size and in the nature of the outline (Twiss *et al.*, 1969; Fredlund and Tieszen, 1994; Bremond *et al.*, 2008; Mercader *et al.*, 2010). They have been identified and described according to their margin profile (Piperno and Pearsall, 1998; Mercader *et al.*, 2010) and include; saddle type; plate 4.2(e), saddle plateau; plate 4.3(d), saddle long; plate 4.3(e) saddle ovate; plate 4.3(a) and saddle squat; plate 4.2(f).

4.3.1.3 Towers-

These silica cells vary from circular to oval to rectangular morphotypes and are produced in large quantities in Pooideae grasses but also found in Chloridoideae grasses (Twiss *et al.*, 1969; Alexandre *et al.*, 1997; Piperno and Pearsall, 1998; Thorn, 2004; Barboni and Bremond, 2009). Towers described here were previously variants of the rondel category, but have been recently described separately by Mercader *et al.*, (2010; 2011), with the aim of distinguishing rondels derived from the Pooideae subfamily from those produced by Chloridoideae sub-family. In this study, the following tower forms have been identified; tower wide; plate 4.3(b-c) comparable to rondel-flared tall, (Thorn, 2004), tower horned; plate 4.1(f) comparable to rondel-lobed base short, (Thorn, 2004; Barboni and Bremond, 2009) and tower flat (rondel-flared short, Thorn, 2004). These forms have been described in Piperno and Pearsall, (1998). Since these types have been confirmed in Panicoideae grasses growing under humid and warm climates, they have strong palaeocological significance (Thorn, 2004; Piperno, 2006).

4.3.1.4 Crosses/ quadralobate

Silica cells with four lobes may be either symmetrical or asymmetrical (Mulholland and Rapp, 1992 Madella *et al.*, 2005). The symmetrical (with approximately equal basal minimal diameters) types have been identified mainly from Panicoideae grasses (Twiss *et al.*, 1969; Fredlund and Tieszen, 1994), while the asymmetrical types have been identified in various other grass sub-families (Alexandre *et al.*, 1997; Barboni and Bremond, 2009; Rossouw, 2009) plate 4.1(d-e).

4.3.1.5 Trapeziform polylobate

Silica bodies with more than two lobes, both symmetrical and asymmetrical, in which the maximum number of lobes in either form is three, are either cylindrical or with a trapezoidal base and a lobate

plateau (Twiss *et al.*, 1969; Thorn, 2004; Madella *et al.*, 2005), elsewhere they have been classified as crenates (Fredlund and Tieszen, 1998) plate 4.4(c).

4.3.1.6 Rondels/Trapeziforms

A grass short-cell morphotype described mainly from Pooideae grasses (Fredlund and Tieszen, 1994; Bremond *et al.*, 2008; Rossouw, 2009; Mercader *et al.*, 2010). This category presents the most challenges since they are produced in considerable amounts by other grass subfamilies (Bremond *et al.*, 2008). Notably, Fredlund and Tieszen (1994) described the rondel category into different subtypes; conical, keeled and crenate. Plate 4.4(d).

4.3.1.7 Bulliforms

These silica bodies are derived from epidermal cells specialised for water storage within plants. They are typically fan-shaped (Mulholland and Rapp, 1992; Madella *et al.*, 2005) and are found in most grasses, but are not diagnostic to any particular grass subfamily. Nevertheless, their abundance can be used to indicate the degree of moisture stress to which grass species were subjected (Albert *et al.*, 1999). Previous studies indicate that bulliforms are direct indicators of grasses growing in high humidity regimes (Piperno and Pearsall, 1998; Piperno, 2006) and therefore their abundance within an assemblage may indicate high precipitation.

4.3.2 Epidermal appendages (other silica cell phytoliths)

4.3.2.1 Hairs-

Elongated outgrowths from mesophyll cells (Madella *et al.*, 2005) with a wider base and a narrow end; they can be unicellular or multicellular, smooth or armed, with or without appendices (Albert *et al.*, 1999).

4.3.2.2 Hair base-

These are silicified epidermal cells where the hair is attached to the epidermis; these forms are commonly circular in outline with a radial structure and ornamented (Piperno, 1988; Albert *et al.*, 1999; Thorn, 2004; Piperno, 2006).

4.3.2.3 Trichomes/ scutiform-

Short forms with swollen bases and conical point (Mulholland and Rapp, 1992; Thorn, 2004) referred as 'shield shaped' also see 'lanceolate' (Madella *et al.*, 2005).

4.3.2.4 Papillae/Achene-

These are rounded cone-shaped morphotypes with a pointed apex morph-type and with satellites (achene) or without (papillae). Papillae type are produced solely by Cyperaceae family, plate 4.6(a-b); and can occur as individual cones or on platelets (Ollendorf, 1992; Piperno, 1988; 2006; Madella *et al.*, 2005) achene morphotypes; are silicified achene cells found in Cyperaceae inflorescence (Ollendorf, 1992; Piperno, 2006) plate 4.6(c).

4.3.2.5 Stomata-

Silica cells formed within intercellular guard cells and subsidiary cells which are functionally connected. In monocotyledons leaves, stomata are arranged in parallel rows while in reticulated venation they are randomly arranged (Fahn, 1990; Madella *et al.*, 2005; Piperno, 2006).

4.3.2.6 Tracheids and Schlereids-

Sclereid phytoliths form in vein-sheath parenchyma cells of leaves, occurring adjacent to xylem. They are restricted to trees and shrubs and are valuable indicators of forest and wooded vegetation (Fahn, 1990; Albert, 1999; Madella *et al.*, 2005) plate 4.7.

4.3.3 Silica skeletons

These are fossilised sections of epidermal tissue (Rosen, 1992; Albert, 1999). Different types have been identified depending on the main cell patterns as follows:-

4.3.3.1 Silica skeletons spheroids/ellipsoid/polyhedral-

The main cell patterns are spheres and ellipsoid. They are identified mostly from woody and herbaceous taxa (Rovner, 1971; Bozarth, 1992; Rosen, 1992; Albert, 1999).

4.3.3.2 Silica skeletons elongates/cylindrical-

Include silica skeletons jigsaw, silica skeletons long cell psilate, silica skeletons long cells verrucate (Albert, 1999; Mercader *et al.*, 2009), plate 4.5(e).

4.3.4 Honeycomb assemblages

These include honeycomb assemblages, honeycomb spheroids/ellipsoids and honeycomb elongates. All these types are significant in indicating the presence of woody and herbaceous non-grass taxa (Bozarth, 1992) plate 4.6(d).

4.3.5 Variable morphotypes

These are silica cells identified mostly from woody plants. Their identification and classification was based on their geometrical characteristics (Albert, 1999; Mercader *et al.*, 2009).

4.3.5.1 Cylindroids

Elongates and circular in cross-section. Depending on textural variation on the surface, the following types are identified: cylindroid psilate, cylindroid verrucate, cylindroid crenate and cylindroid scabrate (Albert *et al.*, 2000).

4.3.5.2 Parallelepiped

Four-sided geometrical figure with parallel opposite sides (Albert, 1999). Described as ‘elongates’ e.g. (Rovner, 1971) or ‘parallelepipedal’ (Madella *et al.*, 2005), plate 4.5(b).

4.3.5.3 Ellipsoids

‘A body with at least one set of parallel cross-sections resembling ellipses and the rest resembling circles’ (Albert, 1999), which are further sub-divided into various types depending on variation in their surface texture. These morphotypes have been identified in foliage, branches and twigs (Piperno, 1998; Runge, 1999) they are hence valuable indicators of woody taxa.

4.3.5.4 Spheroids

Globular shapes (Madella *et al.*, 2005); body resembling a sphere in shape (Albert *et al.*, 2000; 2009). Like ellipsoids they are further subdivided into various types and are produced within dicots fruiting organs, making them significant indicators of tree/shrubs components (Albert *et al.*, 2000; Barboni *et al.*, 2007; Mercader *et al.*, 2009). Other variants include ‘spheroid echinates’ which are derived from Palmae family (Albert *et al.*, 2009) therefore in fossil assemblages they would suggest high water table, plate 4.6(e).

4.3.6 Undifferentiated category

These are silicified bodies that cannot be geometrically defined or anatomically placed. Identification of this category was based on Albert (1999), and includes the following:-

4.3.6.1 Irregular forms

They are irregular bodies and are further subdivided into various types according to their surface textures (Albert, 1999). They are important in determining phytolith production ability by plants and also help in understanding the taphonomic characteristics of silica cells in terms of preservation resilience in sediments plate 4.5(a).

Table 4.3 Phytolith taxonomy, descriptors, corresponding figures, cited references and statistical codes.

Categories-	Morphological description/ figures in plates 4.1-4.6	References	Statistical Codes
1. Grass short-cell phytoliths (ICPN 1.0 Madella <i>et al.</i>, 2005).			
A) Bilobate	Silica bodies with two distinct lobes connected with a shaft. Formerly identified as dumbbell (Twiss <i>et al.</i> , 1969; Mulholland, 1989).	Thorn, 2004; Madella <i>et al.</i> , 2005; Mercader <i>et al.</i> , 2010.	
a) Bilobate convex outer margin short shaft/shank	Bilobate with rounded outer edges/ lobes connected with short shaft. <20µm. Plate 4.1 (a-c)	Piperno and Pearsall, 1998; Fahmy, 2008; Mercader <i>et al.</i> , 2010.	BXOMSS
b) Bilobate convex outer margin long shaft/shank	Bilobates with rounded outer edges/lobes connected with long shaft >20µm. Plate 4.2 (a-c)	Piperno, 2006; Fahmy, 2008; Mercader <i>et al.</i> , 2010.	BXOMLS
c) Bilobate concave outer margin short shaft/shank	Bilobates with semi-rounded outer edges connected with short shaft <20µm. Plate 4.2 (d)	Piperno, 2006; Fahmy, 2008; Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	BCOMSS
d) Bilobate concave outer margin long shaft/shank	Bilobate with semi-rounded outer edges connected with long shaft >20µm	Fahmy, 2008; Barboni and Bremond 2009; Mercader <i>et al.</i> , 2010.	BCOMLS
e) Bilobate flattened outer margin short shaft	Bilobate with outer margins squared, shaft<20 µm	Piperno and Pearsall, 1998; Fahmy, 2008; Mercader <i>et al.</i> , 2010.	BOMFSS
f) Bilobate flattened outer margin long shaft	Bilobates with outer margin squared with shaft >20µm	Piperno and Pearsall, 1998; Fahmy, 2008; Mercader <i>et al.</i> , 2010.	BOMFLS
g) Bilobate panicoid type	Bilobate with semi-rounded outer margin short but wider shaft. Plate 4.1 (a)	Piperno and Pearsall, 1998; Fredlund and Tieszen, 1994; Albert, 1999; Piperno, 2006.	BPT
h) Bilobate nodular	Bilobate with extra lobe on shank	Fahmy, 2008; Barboni and Bremond, 2009;	BN

		Mercader <i>et al.</i> , 2010.	
i) Bilobate outer margin flared short shaft	Bilobates with asymmetrical lobes and shaft <20µm	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	BOMFSS
j) Bilobate outer margin flared long shaft	Bilobates with asymmetrical lobes and shaft >20µm	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	BOMFLS
k) Bilobate notched, flared outer margin short shaft	Bilobate with asymmetrical lobes with nodes on the lobes, shaft <20µm	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	BNOMFSS
l) Bilobate notched, flared outer margin long shaft	Bilobate with asymmetrical lobes with nodes on the lobes, shaft >20µm	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	BNOMFLS
B) Saddles	Silica bodies have two opposite convex edges and two straight or concave edges (Twiss <i>et al.</i> , 1969; Mulholland, 1989). Plate 4.2(e)	Twiss <i>et al.</i> , 1969; Thorn, 2004; Madella <i>et al.</i> , 2005.	SAD
a) Saddle long	Saddles with long convex edges. Plate 4.3(e)	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	SADL
b) Saddle ovate	Rondels rounded /rounds (Piperno and Pearsall, 1998). Plate 4.3(a)	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	SADO
c) Saddle Plateau	Saddles with short convex edges. Plate 4.3(d)	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	SADP
d) Saddle squat	Saddle with side notches and much longer. Plate 4.2(f)	Twiss <i>et al.</i> , 1969; Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	SADS
C) Crosse/quadrilobate	Silica bodies with four lobes, symmetrical or asymmetrical. Plate 4.1(d-e)	Twiss <i>et al.</i> , 1969; Mulholland and Rapp, 1992; Madella <i>et al.</i> , 2005; Barboni and Bremond, 2009.	QCR

D) Polylobate	Silica bodies with more than two lobes	Twiss <i>et al.</i> , 1969; Thorn, 2004; Madella <i>et al.</i> , 2005.	PLY
E) Rondels/Trapeziforms	Conical, keeled and pyramidal morphotype described from Pooideae subfamily. Described as trapeziforms in Bremond <i>et al.</i> , 2008. Plate 4.4(b)	Twiss <i>et al.</i> , 1969; Fredlund and Tieszen, 1994; Madella <i>et al.</i> , 2005.	ROND
F) Towers	Variants of rondel categories	Mercader <i>et al.</i> , 2010.	
a) Tower horned	Rondels with apex ends in one or two outward apices/ top truncated (Mercader <i>et al.</i> , 2010). Plate 4.1(f)	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	TWH
b) Tower flat	Rondel with tapering/flat apex outline irregular, top flat. Plate	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	TWF
c) Tower wide	Rondel elliptical base/ tall body with tapering/flat apex; its base is at least three times wider than the apex. Plate 4.3(b-c) and plate 4.4(a-b)	Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010.	TWW
G) Trapeziforms polylobate	Elongate body with trapezoidal cross-section and wavy edges. Plate 4.4(c).	Mercader <i>et al.</i> , 2010.	TABCR
2. Epidermal Appendages (Long cells phytoliths)			
A) Epidermal appendages	Silicified mesophyll, epidermal & Parenchyma cells	Albert, 1999; Piperno, 2005.	
a) Hair base	Silicified mesophyll cells with radial outline	Albert, 1999; Mercader <i>et al.</i> , 2009.	HB
b) Hair	Silicified elongated outgrowths from mesophyll	Albert, 1999; Mercader <i>et al.</i> , 2009.	HR
c) Stomata	Intercellular guard & subsidiary	Mercader <i>et al.</i> , 2009	STMT

	cells		
d) Tracheids/Sclereids	Silicified vein-sheath cells (plate 4.7)	Fahn, 1990; Albert, 1999; Piperno, 2006.	TRCH/SCLD
B) Spheroids	Spherical or nearly so. Globular category (Mercader <i>et al.</i> , 2009)	Madella <i>et al.</i> , 2005.	
a) Spheroid psilate	Spheroid, smooth/sub-smooth surface. Plate 4.6(f)	Madella <i>et al.</i> , 2005.	SPPS
b) Spheroid echinate	Spheroid, with spikes/pricks Plate 4.6(e)	Albert <i>et al.</i> , 2009.	SPHEC
c) Spheroid scabrate/Rugose	Spheroid, with granular surface	Albert, 1999.	SPSCA
d) Spheroid verrucate	Spheroid, rough irregular surface. Plate 4.5(d)	Albert, 1999; Madella <i>et al.</i> , 2005.	SPVE
e) Spheroid colpate	Spheroid with furrow/slit	Albert, 1999.	SPCOL
C) Ellipsoids/Oblong	Longer than broad and with nearly parallel side	Albert, 1999; Madella <i>et al.</i> , 2005.	
a) Ellipsoid psilate	Ellipsoid with smooth surface	Albert, 1999; Madella <i>et al.</i> , 2005.	ELLPS
b) Ellipsoid scabrate	Ellipsoid with granular surface	Albert, 1999; Madella <i>et al.</i> , 2005.	ELLSC
c) Ellipsoid verrucate	Ellipsoid with rough irregular surface	Albert, 1999; Madella <i>et al.</i> , 2005.	ELLVE
D) Long cells (LC)	Epidermal long cells	Albert, 1999; Madella <i>et al.</i> , 2005.	
a) Long cell psilate	LC with smooth surface	Albert, 1999; Madella <i>et al.</i> , 2005.	LCPS
b) Long cell sinuate	LC with uneven concavities and convexities, plate 4.4(f)	Albert, 1999; Madella <i>et al.</i> , 2005.	LCSI
c) Long cell dendritic	LC with finely branched processes	Albert, 1999; Madella <i>et al.</i> , 2005.	LCDE
d) Long cell verrucate	LC with rough irregular surface	Albert, 1999; Madella <i>et al.</i> , 2005	LCVE

e) Long cell echinate	LC with spiked surfaces	Albert, 1999; Madella <i>et al.</i> , 2005.	LCECH
E) Parallelepiped (P)	Tabular body with opposite sides parallel to each other	Madella <i>et al.</i> , 2005.	
a) Parallelepiped thin crenate	With psilate texture and scalloped edges	Albert, 1999; Madella <i>et al.</i> , 2005; Mercader <i>et al.</i> , 2010.	PPTCR
b) Parallelepiped verrucate	With rough irregular surface	Albert, 1999; Madella <i>et al.</i> , 2005; Mercader <i>et al.</i> , 2010.	PPVE
c) Parallelepiped dendritic	With finely branched processes	Albert, 1999; Madella <i>et al.</i> , 2005; Mercader <i>et al.</i> , 2010.	PPDT
d) Parallelepiped thin psilate	With smooth surface, width<length	Albert, 1999; Madella <i>et al.</i> , 2005; Mercader <i>et al.</i> , 2010.	PPTP
e) Parallelepiped blocky psilate	With smooth surface, width >length	Albert, 1999; Madella <i>et al.</i> , 2005; Mercader <i>et al.</i> , 2010	PPBP
f) Parallelepiped blocky scabrate	With granular surface, width>length	Albert, 1999; Madella <i>et al.</i> , 2005; Mercader <i>et al.</i> , 2010.	PPBS
g) Parallelepiped facetate	With scalloped edges	Albert, 1999; Mercader <i>et al.</i> , 2010.	PPFC
F) Epidermal cells (EC)	Silicified epidermal cells in-situ	Albert, 1999; Mercader <i>et al.</i> , 2009.	
a) Epidermal crenate	EC with psilate texture and scalloped edges	Albert, 1999; Mercader <i>et al.</i> , 2009.	EPC
b) Epidermal Jig-saw	Thin epidermal cells with puzzle-like out-line	Bozarth 1992; Albert, 1999; Mercader <i>et al.</i> , 2009.	EPJG
c) Epidermal polygonal	Thin epidermal polygonal cells	Albert, 1999; Mercader <i>et al.</i> , 2009.	EPPO
G) Honeycomb Assemblages	Net-like-connected cells in situ	Bozarth 1992; Albert,	HYAS

	Plate 4.6(d)	1999; Madella <i>et al.</i> , 2005.	
a) Honeycomb elongates	Network of elongates cells	Albert, 1999; Madella <i>et al.</i> , 2005.	HYE
b) Honeycomb spheroids	Network of circular/semi-circular cells	Albert, 1999; Madella <i>et al.</i> , 2005.	HYSP
H) Silica skeletons (SC)	Silicified sections of epidermal cells	Bozarth, 1992; Rosen 1992; Albert, 1999.	
a) Silica skeleton elongate cells	SC with length>width. Plate 4.5(e)	Bozarth, 1992; Rosen 1992; Albert, 1999.	SSCEC
b) Silica skeleton spheroid cells	SC cells circular	Bozarth, 1992; Rosen 1992; Albert, 1999.	SSPEC
c) Silica skeletons cylindroids/sinuuous	SC elongate & circular cross section	Bozarth, 1992; Rosen 1992; Albert, 1999; Madella <i>et al.</i> , 2005.	SSCCS
I) Irregular forms	Silica bodies with no defined shape/don't belong to any of the above category	Albert, 1999; Madella <i>et al.</i> , 2005.	IRRF
a) Irregular verrucate	Irregular forms with rough surfaces	Albert, 1999; Madella <i>et al.</i> , 2005.	IRRVE
b) Irregular scabrate	Irregular forms with granulate surface	Albert, 1999; Madella <i>et al.</i> , 2005.	IRRSC
c) Irregular psilate	Irregular forms with smooth surface. Plate 4.5(a)	Albert, 1999; Madella <i>et al.</i> , 2005.	IRRPS
3. Cyperaceae phytoliths			
a) Papillae	Hat-shaped silica bodies in sedges. Plate 4.6(a-b)	Ollendorf, 1992; Piperno, 2006	PAPL
b) Achene	Cone shaped silica bodies in sedges. Plate 4.6(c)	Ollendorf, 1992; Piperno, 2006	ACHN

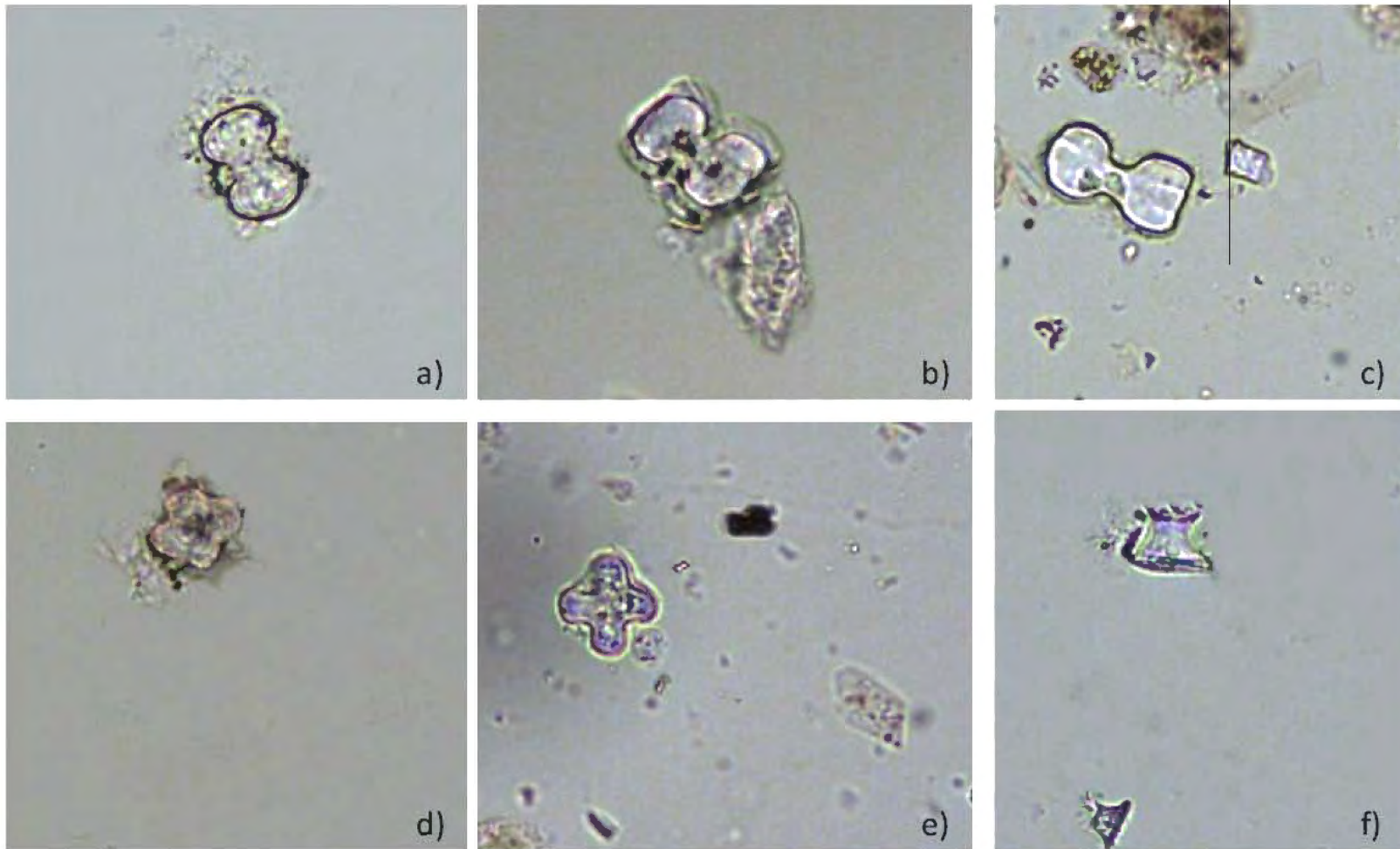


Plate 4.1- a) Bilobate panicoid type, b-c) bilobates convex outer margin short shaft, d-e) quadralobate, f) tower horned

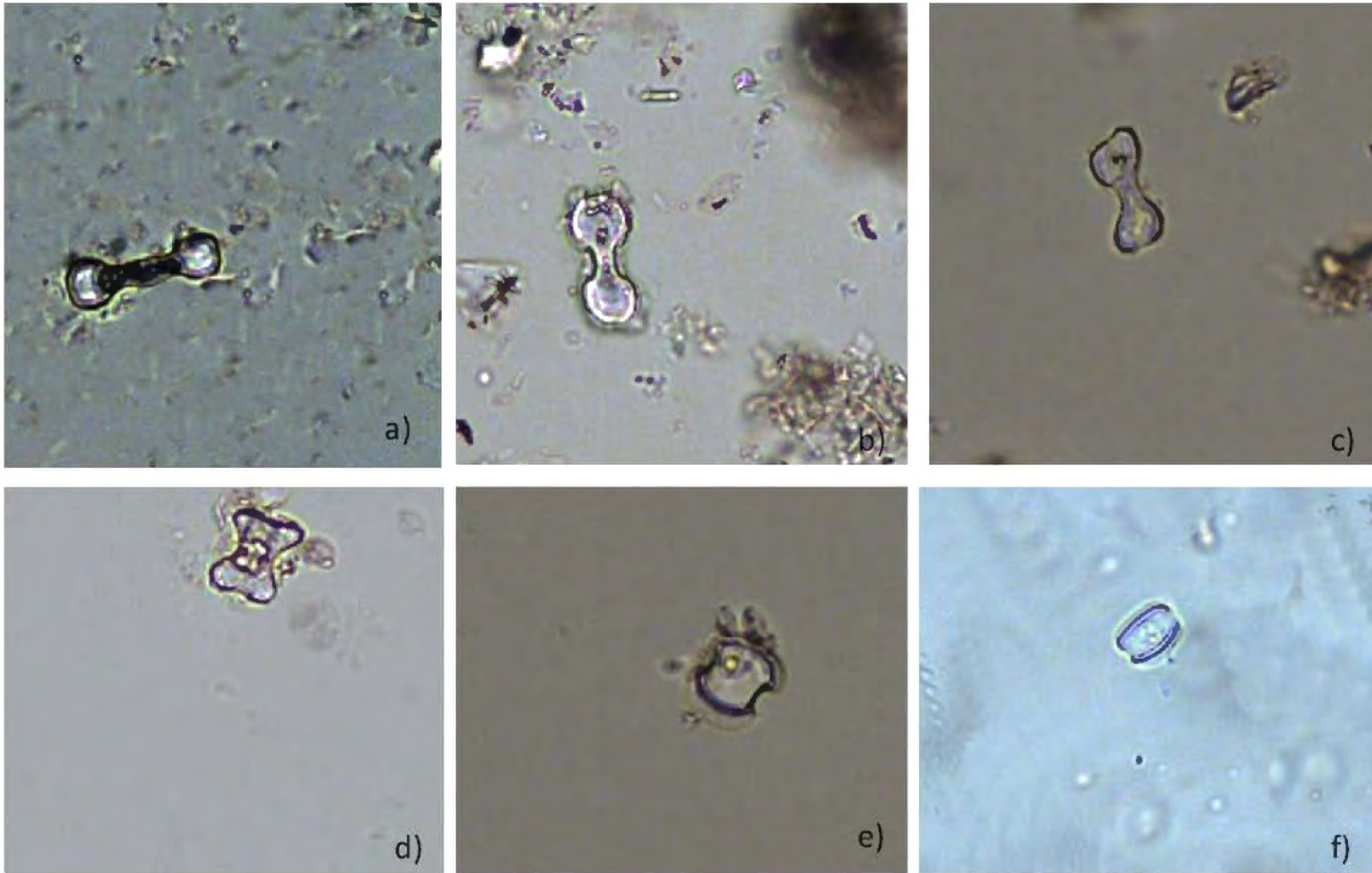


Plate 4.2-a-c) bilobate convex outer margin long shaft, d) bilobate concave outer margin short shaft, e) saddle type, f) saddle squat.

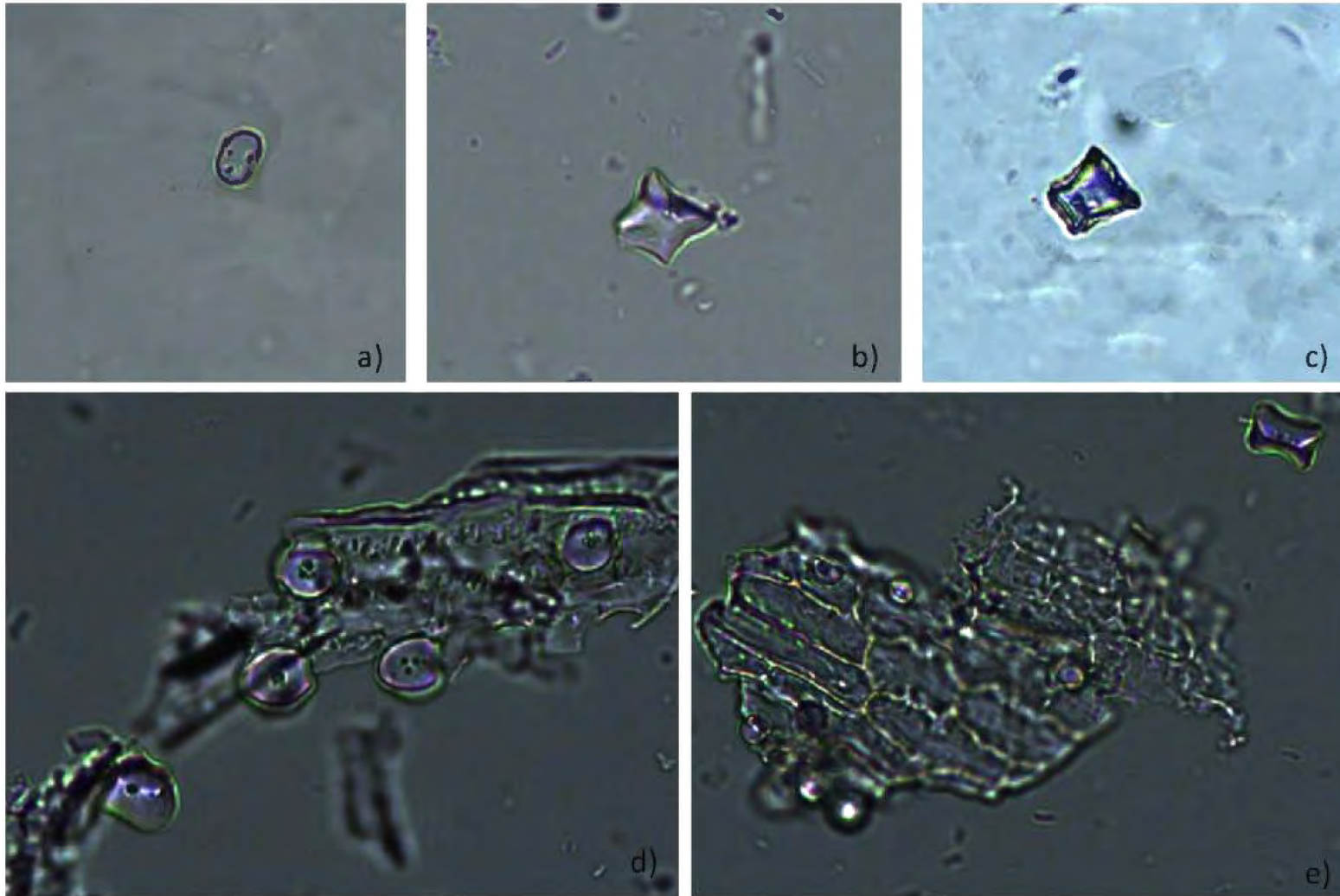


Plate 4.3-a) saddle ovate, b-c) tower wide, d) saddle plateau; e) epidermal crenate & saddle long at top-right.

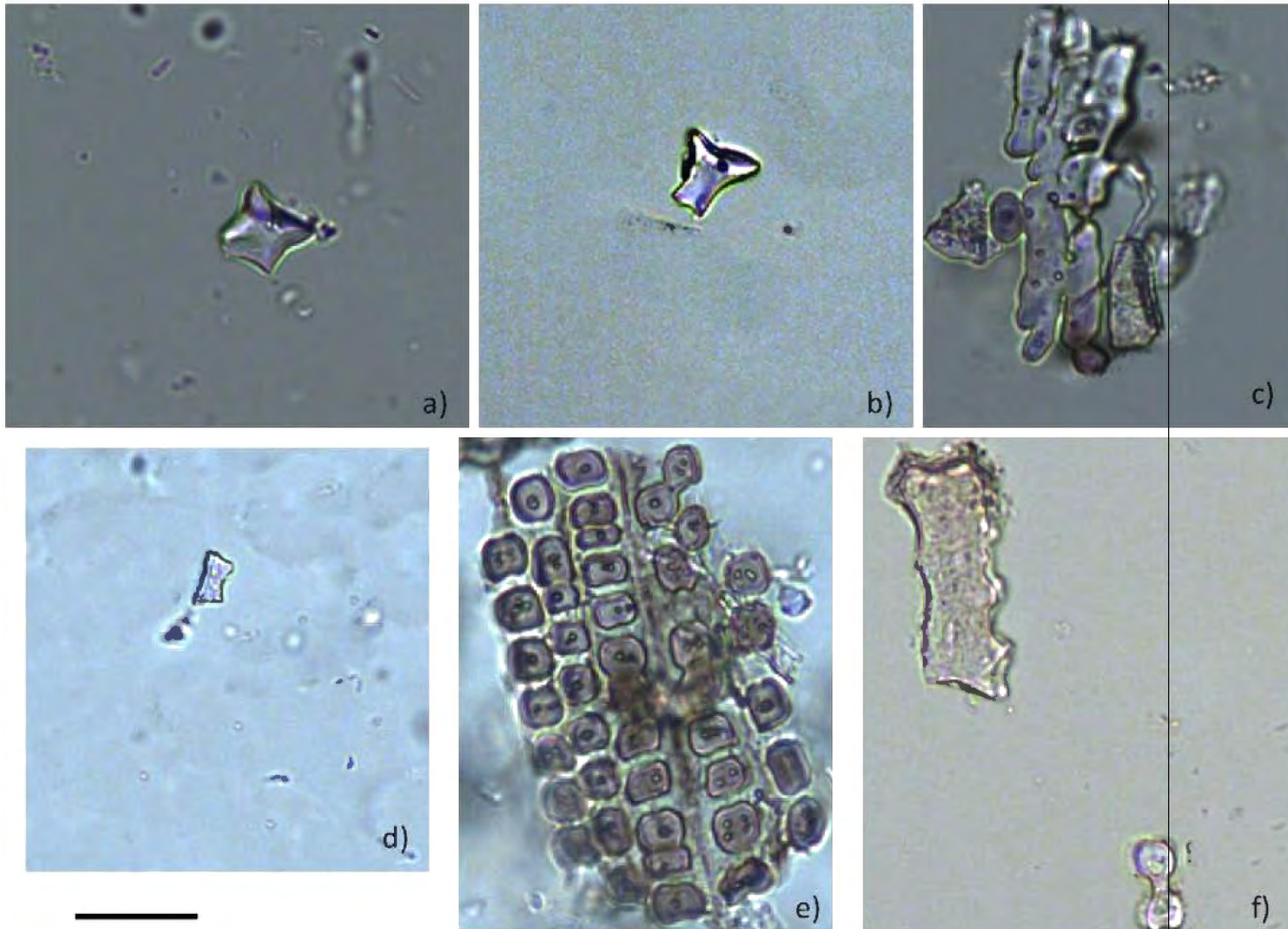


Plate 4.4- a-b) tower wide, c) trapezoid polylobates, d) trapezoid e) saddles in situ; f) long cell sinuate & bilobates convex outer margin long shaft.

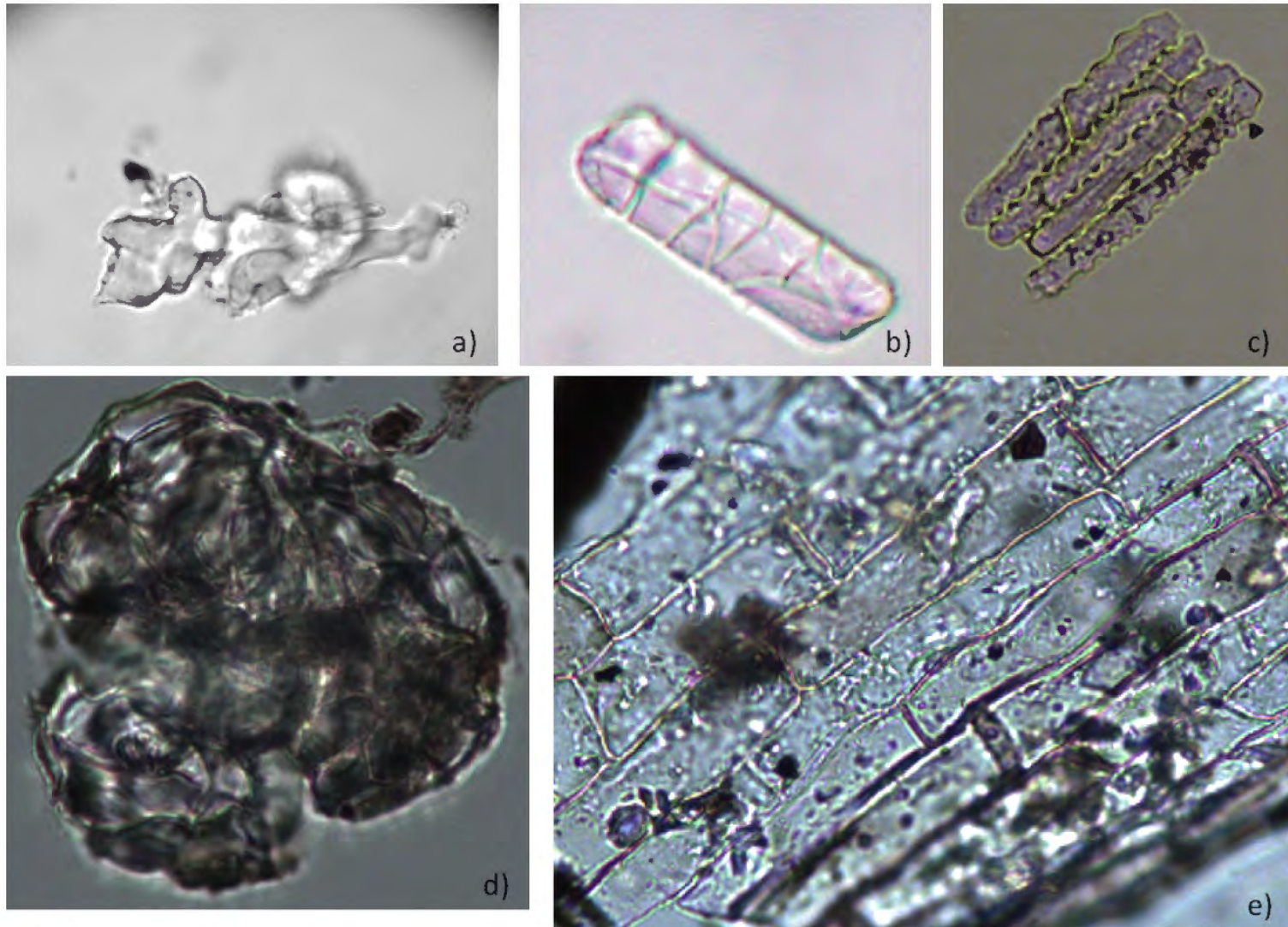


Plate 4.5-a) Irregular psilate; b) parallelepiped blocky psilate; c) long cells sinuate; d) spheroid verrucate; e) silica skeletons elongate cells.

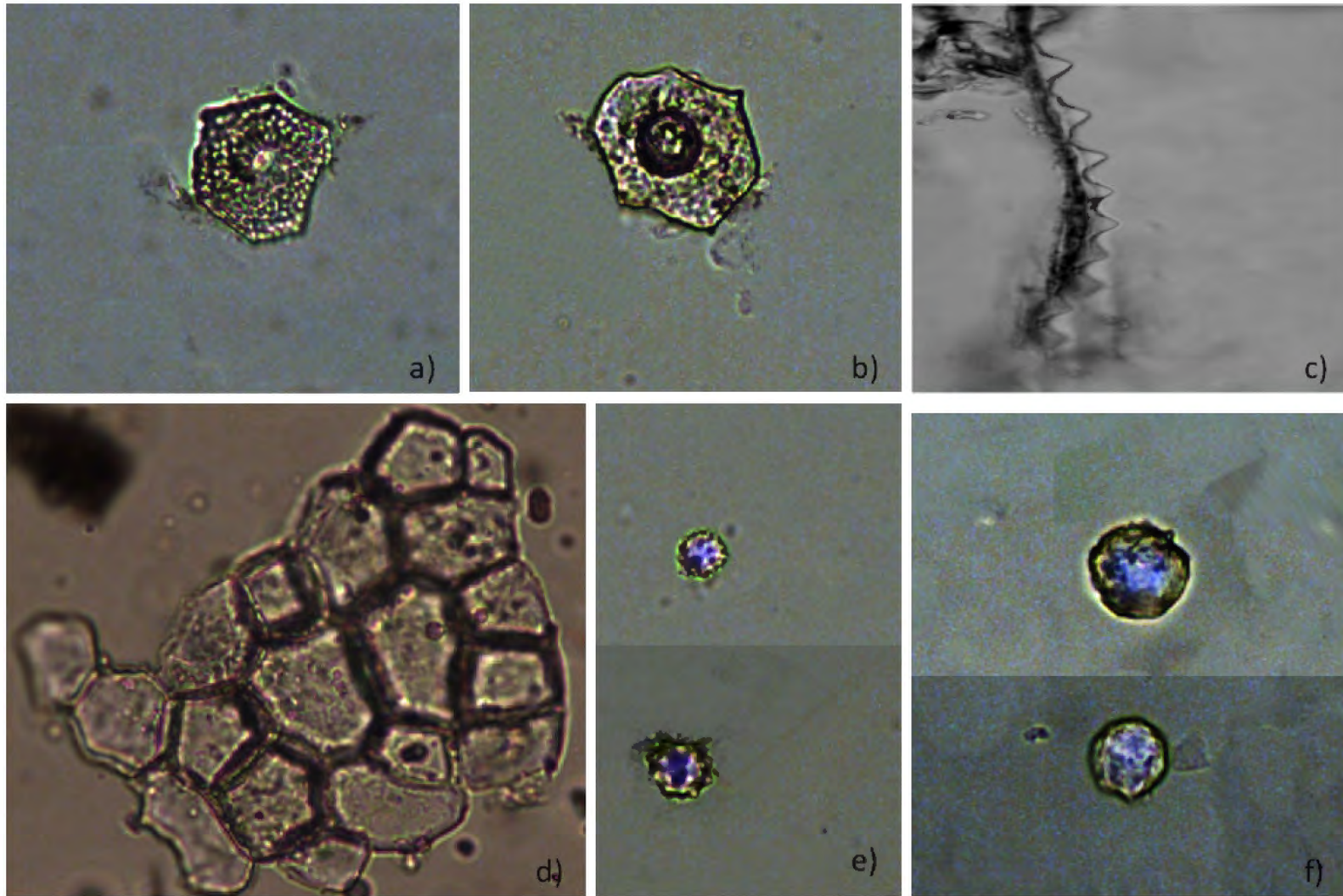


Plate 4.6- a-b) *Cyperus*-silicified papillae; c) *Cyperus*-Achene type; d) Honeycomb assemblage; e) spheroid echinate; f) spheroid psilate.



Plate 4.7 a-c) Schlereids; d-e) tracheids

4.4 Data analyses

Phytolith were grouped into 59 morphotype categories, tallied for each plant specimen and the dataset entered into an Excel spread sheet as raw data. The dataset was then normalized where all the types which were below 2% of the total morphotypes tallied for each single plant were excluded. Using PC-ORD™ software package, two forms of statistical procedures were conducted for morphotypes derived from the modern reference collection (Peck, 2009). Simple statistical analyses such as bar graphs were ran in excel to determine the general production pattern of grass short-cell phytoliths among the four major grass sub-families in this study, namely C₃ Arundinoideae, C₄ Panicoideae, C₄ Chloridoideae and C₄ Aristidoideae.

4.4.1 Correspondence analysis/Reciprocal averaging.

Correspondence analysis [CA; reciprocal averaging (Hill, 1973)] is a multivariate ordination technique used to identify similarities influencing groupings of elements/data within a specifically constructed dataset. Principal Component Analysis (PCA) identifies maximum variance between datasets (Greenacre, 1984).

In this study, correspondence analysis was carried out to evaluate the relationships between grass phytoliths and known physio-geographical distributions (in this case, altitudinal distribution; Table 4.2), ecological habitats and the photosynthetic pathways of the Poaceae sub-families (Barboni and Bremond, 2009). Additionally, to evaluate the potential of phytoliths derived from mixed vegetation types, correspondence analysis was used on a dataset consisting of morphotypes tallied from all of the plants analysed.

Different plant communities were classified on ordination space along the axes such that plants that produced similar phytoliths composition were clustered close to each other, hence the analysis distinguished phytolith morphotypes into vegetation components that require similar environmental conditions, and especially moisture content which is relevant to palaeoenvironmental reconstruction as discussed in the preceding chapters.

Further correspondence analyses helped to establish how well phytolith associations could estimate the vegetation types and, though indirectly, infer possible environmental/climatic factors influencing the distribution of morphotypes in a scatter plot. In the data matrix, plant specimens were treated as samples (rows) with morphotypes as taxa (columns) before running correspondence analysis. The statistical codes for both plants and the morphotypes categories are defined in table 4.3 of this chapter.

4.4.2 Cluster analysis

Cluster analysis is a statistical technique that groups data that are similar (but not identical) into one cluster and those that are dissimilar into a different cluster (Hill, 1973). In order to identify principal identifier-morphotypes, either singly or in associations, the raw data (modern reference) was run through cluster analysis, with grasses as a separate dataset and then for all the plant species combined.

4.4.3 Tilia diagrams

For the fossil phytolith assemblages, the identified morphotypes were counted and the data presented as A TILIA diagram composed of the assemblages from each level within the geological profile/section, plotted against depth and the available age estimates.

The diagram consists of two parts: horizontal axis with various morphotypes and their frequencies while the vertical axis shows depth and age. The change in percentages and composition of types through time is assumed to be associated with changes in vegetation composition. These changes are distinguished statistically using a constrained incremental sum-of-squares cluster analysis (CONISS) which is a graphical component of the TILIA and TILIA GRAPH software (Grimm, 2007).

4.4.4 Grass short-cell phytolith indices

In order to understand vegetation cover changes in the Olorgesailie Basin, an additional proxy was computed from the morphotype categories derived from grasses. The proportion of a grass subfamily in the fossil assemblages was analysed by computing the proportion morphotypes derived from C₃ grasses versus C₄ grasses, in order to understand the associated environmental factors controlling vegetation changes. Grass short-cell phytoliths identified from three major grass sub-families were used in the analyses; C₃ Pooideae, C₄ Panicoideae and C₄ Chloridoideae (Bremond *et al.*, 2008).

Analysing selected grass short-cell phytoliths formed in grass leaf epidermal cells can be used to distinguish C₃ and C₄ photosynthetic pathways (Twiss, 1992), therefore distinguishing major grass sub-families (Twiss *et al.*, 1969; Mulholland, 1989). C₃ grasses occur in high latitudes and high altitudes in the tropics under cool climates; trapeziform polylobate are the most typical in the subfamily. C₄ (Chloridoideae) grasses occur in arid and semi-arid regions under hot and dry climates; saddles are the most typical morphotype in this sub-family. C₄/C₃ (Panicoideae) grasses contain both photosynthetic pathways favoured by warm temperatures and moist climate; bilobates and quadralobates are the most characteristic of Panicoideae grasses (Metcalf, 1960; Twiss *et al.*, 1969; Tieszen *et al.*, 1979; Piperno and Pearsall, 1998; Rossouw, 2009).

The selected grass short-cells phytoliths used in this analyses included the following for each grass sub-family; Arundinoideae C₃ grasses (rondel, saddle ovate), Panicoideae (bilobate panicoid type,

bilobate concave outer margin short shaft, bilobate convex outer margin short shaft, polylobates, quadralobate/crosses, saddle long and tower horned); Chloridoideae (saddle, tower flat, bilobate outer margin flattened long and Short shaft) and Aristidoideae (bilobate convex outer margin long shaft). Additional grass sub-family was identified in the fossil assemblage: C₃ Pooideae grasses (trapeziform polylobates).

The key identifiers for the woody and herbaceous taxa in this study include; spheroid echinate (unique identifier of Palmae family) (Albert *et al.*, 2005; 2009), spheroid scabrate, sclereids, spheroid verrucate and other irregular forms (representing the woody and herbaceous taxa) (Albert *et al.*, 2005) and achene (unique identifier of the Cyperaceae family) (Ollendorf, 1992).

Although individual phytolith types extracted from soils/sediments are not traceable to individual grass taxa, the relative ratio of morphotypes unique to C₃ and C₄ sub-families may be traced to grass sub-family and hence serve as climatic indices for interpreting paleoclimate of a region (Twiss, 1992).

Two indices; climate index (I_C) and aridity index (I_{ph}) (Bremond *et al.*, 2008) were calculated using grass short-cell phytoliths exclusively derived from grasses, with the aim of determining the dominance of C₃ relative to C₄ grasses in the fossil assemblage in order to understand grassland dynamics in the Ologesailie Basin and the surrounding environs, as well as determine estimates of climatic changes.

4.4.4.1 Climate index (I_C)

This index refers to the total of selected grass short-cell phytoliths derived from the Pooideae grasses (trapeziform polylobates) divided by the sum of selected grass short-cell phytolith types produced by Pooideae, Chloridoideae (saddles,) and Panicoideae (Polylobates, crosses and bilobates outer margin convex short shaft) grasses (Bremond *et al.*, 2008; Barboni and Bremond, 2009).

$I_C = \text{Pooideae morphotypes} / (\text{Pooideae} + \text{Panicoideae} + \text{Chloridoideae}) \text{ morphotypes}$

High I_C (≥ 0.5) reflects grasslands dominated by Pooideae C₃ grasses while low I_C (≤ 0.4) reflects grasslands dominated by Panicoideae and Chloridoideae C₄ grasses. In Africa, I_C increases with elevation, hence decreasing temperatures (Bremond *et al.*, 2008). Low I_C indicates grasslands dominated by C₄ grasses, suggesting warm climates.

4.4.4.2 Aridity index (I_{ph})

This index refers to the ratio of total Chloridoideae (saddles) vs. the sum of C₄ grasses (both Chloridoideae and Panicoideae (bilobates concave/convex outer margin short shaft, crosses, and polylobates) grass short-cell phytoliths. This is a useful indicator of the dominance of short C₄ grasses

over tall C₄ grasses which reflects trends in aridity –humidity at low elevations (Bremond *et al.*, 2005b; 2008).

$I_{ph} = (\text{Chloridoideae Phytoliths}) / (\text{Chloridoideae} + \text{Panicoideae})$ Phytolith types

High I_{ph} indices, close to 1, indicate arid conditions while a low index close to zero indicate a humid climate (Bremond *et al.*, 2008).

4.4.5 Dicotyledon versus Poaceae index (D/P^o)

This index is the ratio of diagnostic phytolith morphologies with taxonomic significance of tropical woody plants versus grass short cell phytoliths diagnostic to grass subfamilies (Bremond *et al.*, 2008). Phytolith morphologies considered to calculate D/P^o include; all spheroid variants except for spheroid psilate for woody plants, while for Poaceae all diagnostic grass short cells phytoliths were considered.

$D/P^o = (\text{Spheroid echinate} + \text{spheroid scabrate} + \text{spheroid verrucate}) / (\text{saddle variants} + \text{rondels} + \text{bilobates variants} + \text{Quadralobates/crosses} + \text{tower variants})$.

High D/P^o indices, close to 1, indicate close-canopy vegetation dominated with woody plants/trees while low indices will indicate open-canopy vegetation dominated with grasslands (Bremond *et al.*, 2009).

4.5 Summary

This chapter presented detailed information on the materials and methods used to collect statistically viable data for both the modern phytolith analogue and the fossil assemblages analysed in this research. Field methodologies and laboratory techniques were presented. Due to the magnitude of the data, it was divided into two datasets i.e. the modern analogue and the fossil phytolith data. Results of the modern analogue dataset are presented in the following chapter.

CHAPTER FIVE: RESULTS OF THE MODERN ANALOGUE REFERENCE

5.1 INTRODUCTION

This chapter presents results of modern phytolith data obtained from sixty-nine plant species representing 17 families, which were processed and analysed in order to provide a modern phytolith analogue, for comparison with interpretation of fossil phytolith data from the Olorgesailie Basin (chapter 6 of this study). Of the seventeen families, Poaceae and Cyperaceae family yielded distinct morphotypes. The Poaceae produced short-cell phytoliths, Cyperaceae produced achene and papillae morphotypes while woody and herbaceous taxa yielded mostly variable categories which included irregular variants, spheroid variants and tracheids/schlereids types. In-situ silicified cells were observed and classified in most of the studied specimens which dominated in woody and herbaceous taxa. Appendix I shows the data sheet of the percentage occurrence of various phytolith morphotypes identified in modern plant specimens.

5.2 Differential phytolith production among grass sub-families

Results from analysing the percentage abundance of grass short phytolith among four major subfamilies shows that it is possible to identify major grass subfamilies through the analysis of the abundance of various morphotypes, as well as the presence and/or absence of certain types (Fig 5.1).

In this study, Arundinoideae grasses produced predominantly 61% of saddle ovate (SADO), 13% of both saddle long (SADL) and tower flat (TWF) while other morphotypes are rare (<3%) and saddles (SAD) are completely absent.

Panicoideae grasses produce abundant bilobates types accounting for 53% of the total phytolith count, with bilobates concave outer margin short shaft (BCOMSS) leading with 23%. Other abundant morphotypes in this group include tower horned (TWHN) with 12%, quadralobate (QCR) with 6% and polylobates (PLY) with 5%. Types that are rare to absent include saddle plateau (SADP), saddle squat (SADS) and saddle ovate (SADO).

Chloridoideae grasses produced predominantly saddles (SAD) 31%, 12% tower flat (TWF), 10% tower horned (TWHN) and 9% bilobates types except for the bilobates concave outer margin long shaft (BCOMLS), which were absent. Other saddle variants account for 8%.

Aristidoideae grasses produced predominantly bilobates convex outer margin long shaft (BCXMLS) 58%, 19% saddle plateau (SADP) and 12% tabular crenate (TBCR). Other morphotypes were rare accounting for <3%.

Chloridoideae rondels could not be distinguished from those produced by C₃ grasses because tower flat (TWF) were equally present in both subfamilies, accounting for 12% and 13% respectively.

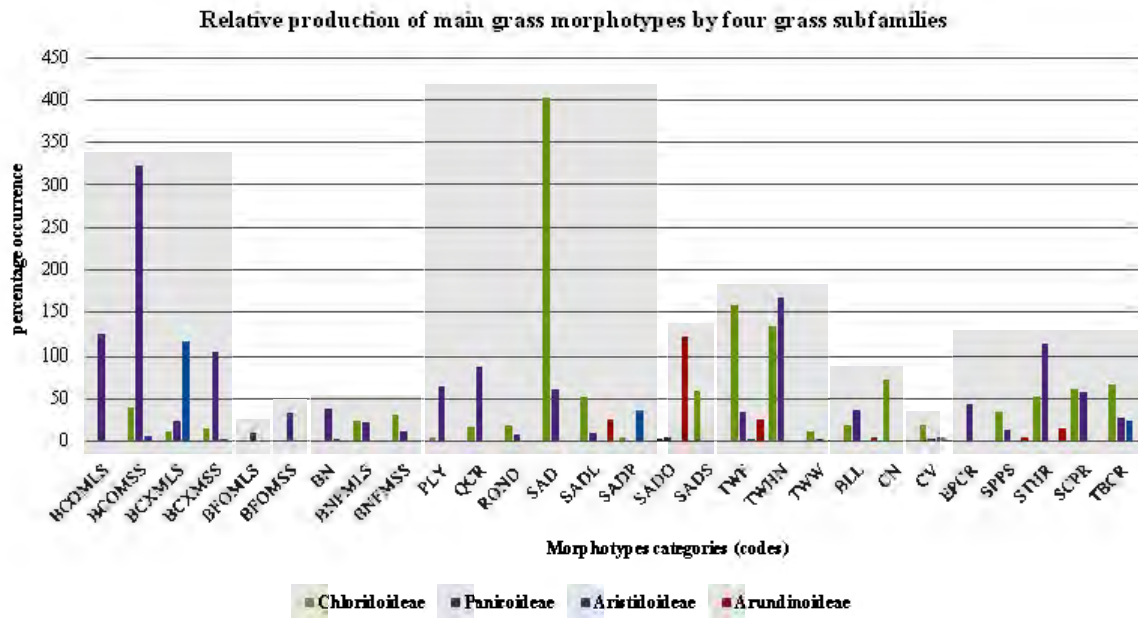


Figure 5.1 Graph showing the relative dominance of major grass morphotypes in four grass-subfamilies. See appendix II for the complete names of the morphotypes.

5.3 Relationship between phytolith morphotypes to vegetation types

Sixty-nine different plant species belonging to 17 families were processed and analysed for modern reference. Of the seventeen families, Poaceae and Cyperaceae yielded the most abundant distinct phytolith types. It was possible to identify types found in-situ with their parent cells; however, most morphotypes were disintegrated from the parent cell and were identified as described in Madella *et al.*, (2005). The herbaceous and woody taxa produced mainly the irregular forms, occasionally producing spheroids and ellipsoids. Verrucate variants were the most dominant within these two taxa. The cylindroids and parallelepiped types were also present. Analysis of non-grass morphotypes was highly significant in characterising vegetation types. Ellipsoid verrucates (ELLVE) notably occurred in abundance in *Ficus natalensis* for instance.

5.3.1 Correspondence Analysis between morphotypes and plant species

Correspondence analysis is a descriptive/exploratory statistical technique used to visualize the association between two-way tables with some measure of correspondence between rows and

columns presented graphically in ordination space (Greenacre, 1984). In this study, correspondence analysis (CA) was applied to investigate associations of various morphotype categories to the parent plant species from which they were extracted and to determine whether the distribution of various morphotypes on the scatter plot could be related to the possible underlying environmental factors. CA therefore was used to identify underlying similarities within the modern analogue morphotypes dataset by classifying plant species into different vegetation categories along the axes according to possible taxonomic, climatic and ecological significance (Tieszen *et al.*, 1979; Barboni *et al.*, 2007; Barboni and Bremond, 2009; Rossouw, 2009; Mercader *et al.*, 2010; 2011).

In this analysis, plant species were categorised as samples (rows) while morphotypes were categorised as species (columns).

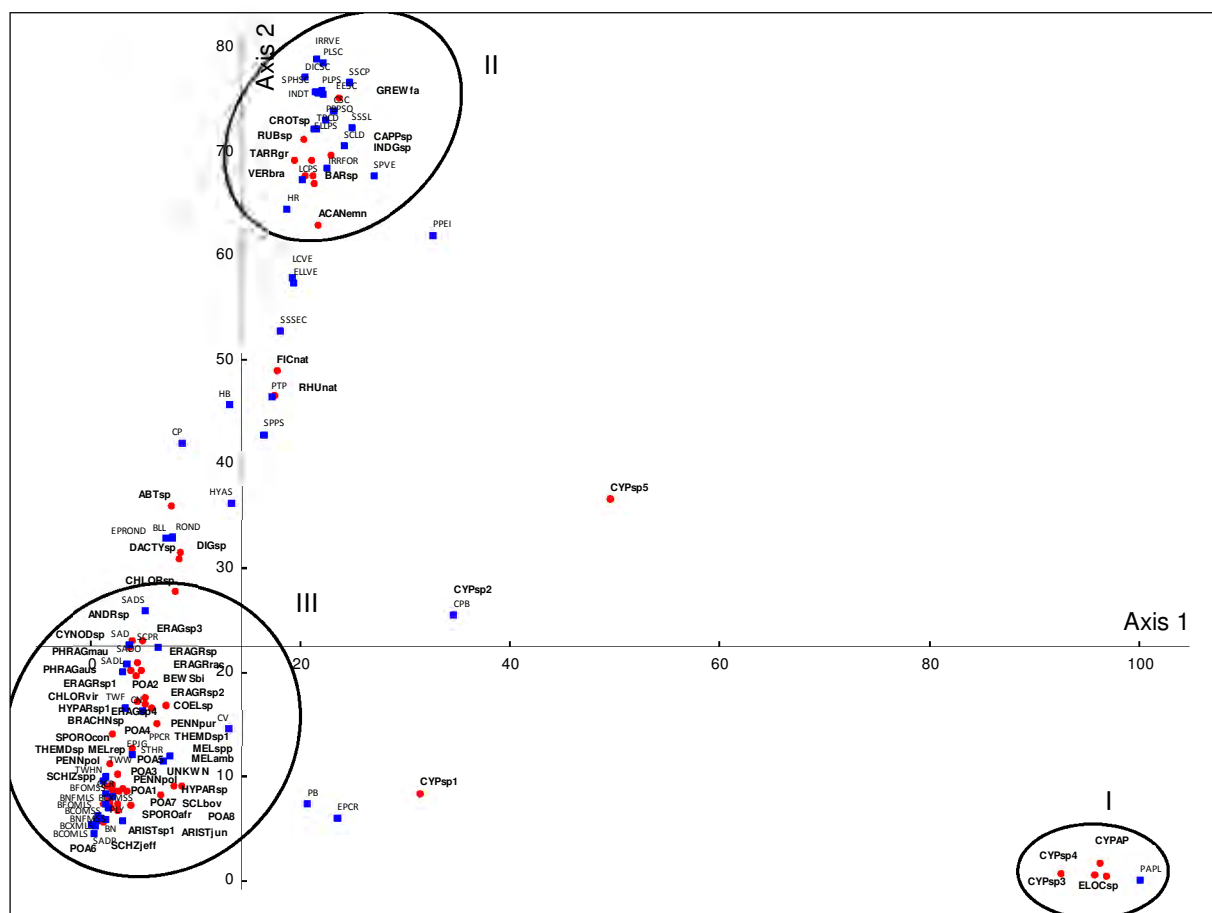


Figure 5.2 shows a scatter plot obtained from correspondence analysis of 59 different phytolith morphotypes (blue squares) identified from 69 plant species (red circles); Poaceae and non-Poaceae families.

The results of correspondence analysis show the first axis (eigenvalue 0.778) explained 27.4% of the total variance, while the second axis (eigenvalue 0.741) explained 9% of the total variance/inertia (10.25). This analysis was run using both PCORD and CANOCO software. The two major axes

explain the correlation between plant species and major morphotype categories occurring in abundance in the plant species. Furthermore, from the scatter plot indirect inference of the underlying environmental conditions can be deduced, particularly in terms of moisture conditions versus vegetation categories.

Plant species occurring under similar environmental conditions (as summarised in table 4.1) are closely distributed in the ordination space making it possible to identify three vegetation components (Fig 5.2). I) Aquatic vegetation (identified by Axis-1) comprising of Cyperaceae (*Cyperus* sp. 3, *Cyperus* sp. 4, *Cyperus papyrus* and *Eleocharis* sp.). This component is strongly distinguished by Papillae (PAPL) phytolith morphotype, identified only from these species and absent from other plant species analysed. Surprisingly, three species of the genus *Cyperus* do not seem to be strongly associated with the papillae morphotype. The axis distinguishes Cyperaceae (negatively) from other herbaceous and woody taxa (positively). II) Woody taxa (*Tarrena graveolens*, *Croton* sp. *Grewia fallax*. *Indigofera* sp. Capparaceae sp. and Rubiaceae sp. and the herbaceous component, including *Acanthaceae eminence*, *Vernonia brachiates* and *Barleria* sp. The distribution of the woody taxa is largely distinguished by the following morphotypes: schlereids (SCLD), tracheids (TRCD), spheroid verrucate (SPVE), silica skeletons *sensu lato* (SSSL) and ellipsoid psilate (ELLPS) while the herbaceous taxa are characterised by irregular forms (IRRF) and long cell psilate (LCPS). III) The Poaceae family (both C₃ and C₄ grasses) which is largely distinguished by the presence of grass short-cell phytoliths and is comprised of Chloridoideae, Panicoideae, Aristidoideae and Arundinoideae sub-families. Axis 2 distinguishes herbaceous and woody taxa negatively from grasses and sedges. This could suggest woody and non-grass herbaceous taxa are generalists in relation to moisture content and therefore do not show much correlation with the axis which is interpreted in this case to indicate increasing moisture content on the x-axis (fig 5.2).

5.3.2 Correspondence analysis between grass species and corresponding morphotypes

Correspondence analysis of 27 morphotype categories derived from 42 grass species evaluated the relationship between short grass phytoliths and grass subfamilies. This approach determined the potential of phytoliths to distinguish between C₃ and C₄ grass-sub-tribes, for the purpose of determining the relationship between grass phytoliths and the underlying environmental/ climatic factors. Grass species belonged to four main grass sub-families which are important in the area of study namely, Panicoideae C₄ (25 species), Chloridoideae C₄ (11 species), Aristidoideae C₄ (2 species), Arundinoideae C₃ (2 species) and unidentified (12 species).

Results of the correspondence analysis (fig 5.3) show that the first axis (eigenvalue 0.762) explained 18.3% of the total variance and the second axis (eigenvalue 0.662) explained 15.4% of the total variance (5.39).

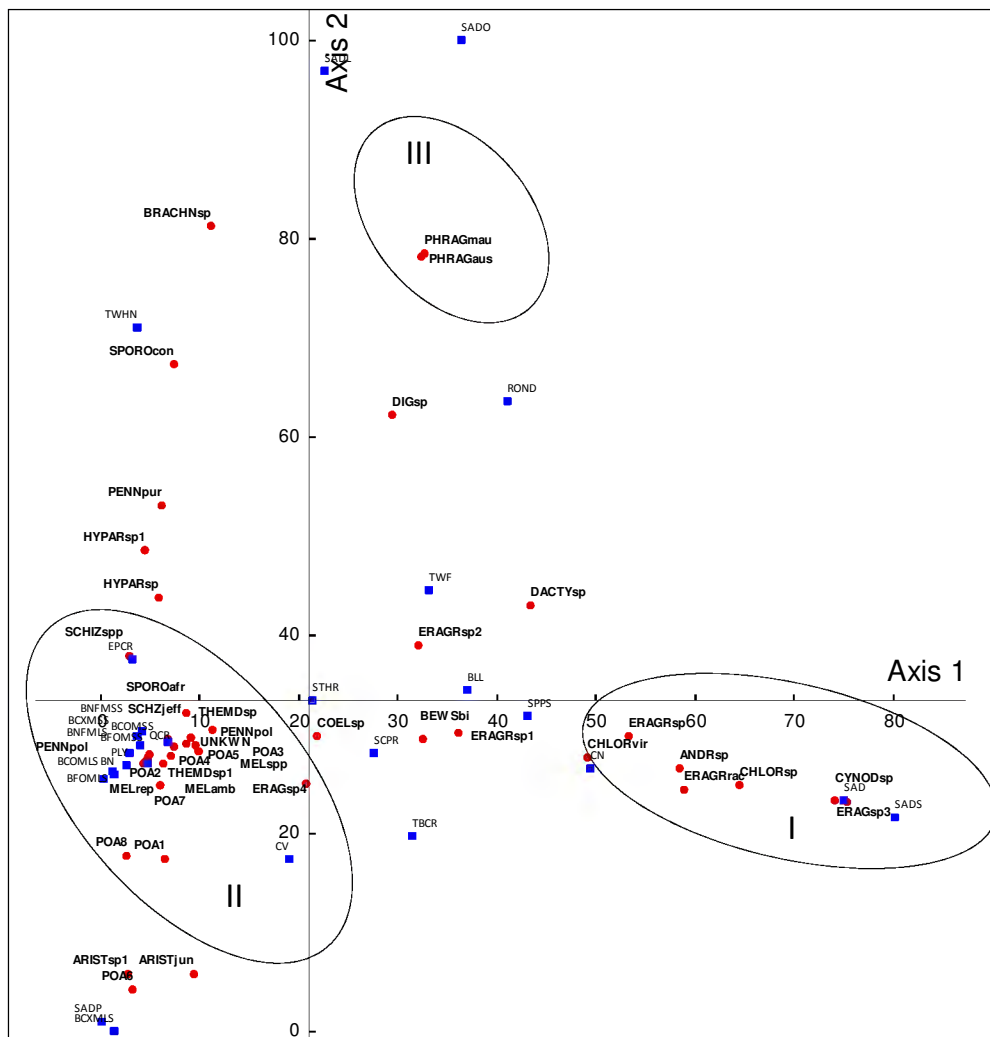


Figure 5.3 shows the scatter plot ordination obtained from correspondence analysis between grass species (red circles) and corresponding grass short-cell phytoliths (blue squares).

Three main principal groups are observed from the scatter plot (fig 5.3). I) Chloridoideae C₄ subfamily are short grasses associated with hot and dry climates and are mainly found in low altitudes in the tropics (Tieszen *et al.*, 1969; Twiss, 1992; Rossouw, 2009). They included *Cynodon* sp., *Eragrostis* sp., *Eragrostis racemosa*, *Andropogon* sp. and *Chloris virgata*. This group is largely influenced by the dominance of saddle (SAD) and saddle squat (SADS) morphotypes. II) Panicoideae C₄ sub-family are tall grasses associated with warm and moist climates and are distributed across a range of altitudes up to 3050 metres (Tieszen *et al.*, 1969; Twiss, 1992). They included *Pennisetum polystachion*, *Melinis repens*, *Melinis ambigua*, *Themeda* sp., *Schizachyrium jeffreysii* and other unidentified grasses. This group is largely influenced by the presence of quadralobate/crosses (QCR),

polylobates (PLY) and bilobates morphotypes, except for the bilobate outer margin convex long shaft types (BCXMLS); and III) Arundinoideae C₃ grasses which are associated with moist environments and are mainly distributed in both high and low altitudes in wet environments including swamps and along riverbanks. This includes *Phragmites australis* and *P. mauritanus*. It is worth noting that the Aristidoideae C₄ grasses appear to be negatively influenced by the same factors influencing the distribution of the Arundinoideae C₃ grasses on the scatter plot. They included *Aristida juncoformis* and *A. congesta* (Aristidoideae grasses). Morphotypes that correspond with the Arundinoideae grasses included saddle ovate (SADO), tower flat (TWF) and saddle long (SADL) morphotypes while Aristidoideae corresponds with saddle plateau (SADP) and bilobates outer margin convex long shaft types (BCXMLS).

Axis 1 distinguishes Arundinoideae C₃ grasses on its positive end from C₄ grasses on the negative end, indirectly reflecting increasing moisture along the x-axis while axis 2 distinguishes Panicoideae from Chloridoideae grasses. This trend shows increased aridity along the x-axis. Notably, Aristidoideae grasses appear on the same quadrant with Panicoideae grasses though on the extreme end of the scatter plot. Since their ecological habitats are mainly very dry and disturbed grounds (Ibrahim and Kabuye, 1987), their distribution on the scatter plot is not just influenced by moisture.

5.3.3 Phytolith morphotype-plant associations

Two datasets were run through cluster analysis: first, morphotypes derived from all the species analysed and second, morphotypes derived from only the Poaceae family. Morphotypes with increased distance measures showed the highest dissimilarities from other morphotypes in terms of their occurrence among the plants analysed.

These outliers are discussed as the most likely unique identifier of the associated/parent plant species (see fig. 5.4): papillae (PAPL) derived from Cyperaceae, saddle (SAD) derived from Chloridoideae C₃ grasses, tower horned (TWHN) and bilobate outer margin concave short shaft (BCOMSS), derived from Panicoideae C₄ grasses and saddle ovate (SADO) identified mostly from Arundinoideae C₃ grasses. A major cluster stands out comprising of bilobates outer margin concave long shaft (BCOMLS), bilobates outer margin convex short shaft (BCXSS), polylobates (PLY) and tower flat (TWF), all produced by the Panicoideae C₄ sub-family. Cluster analysis showed that taxonomic affiliation of phytolith morphotypes can be strongly observed for the Poaceae family but not for the woody and herbaceous taxa. Morphotypes appearing in the middle of the dendrogram are referred to as generalists.

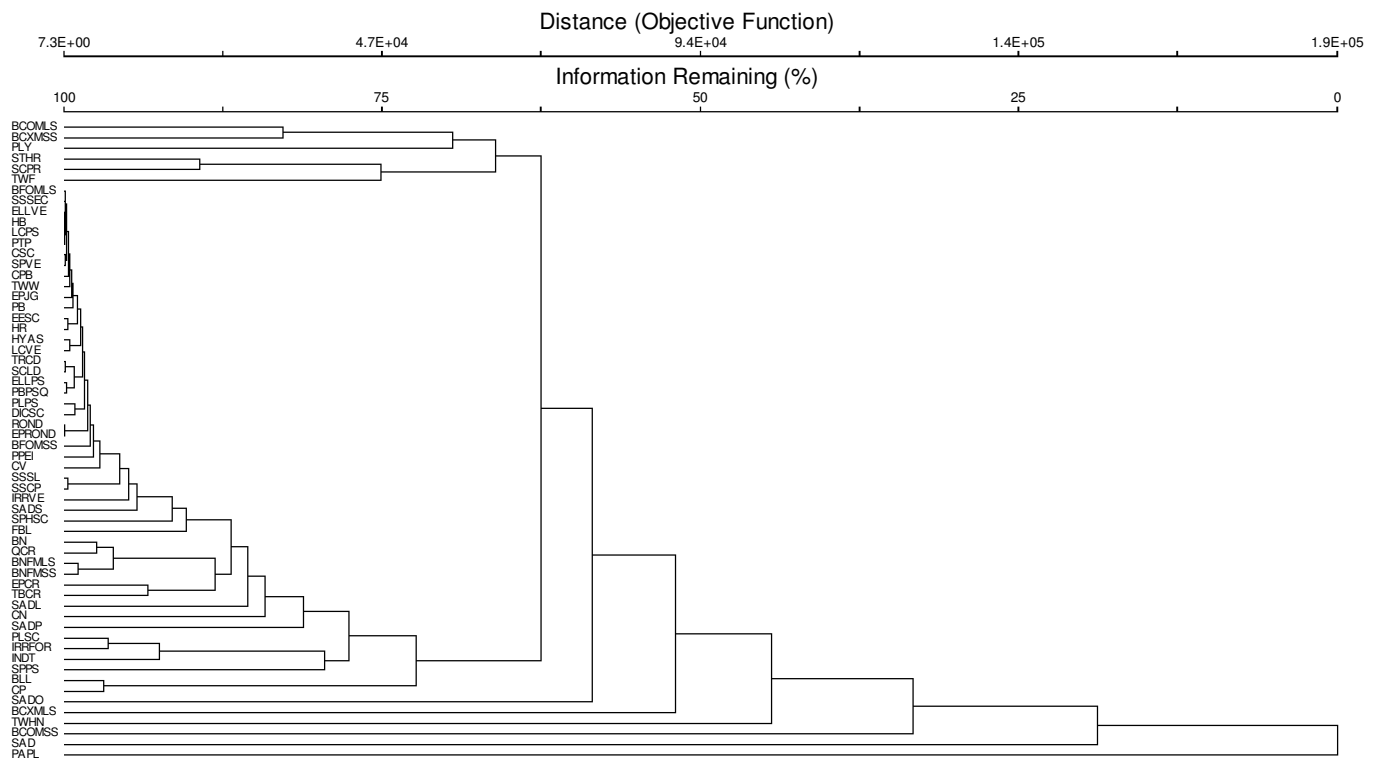


Figure 5.4 Cluster analysis dendrogram, wards linkage method and distance measure; Euclidean Pythagorean, among phytolith morphotypes from all species combined.

To further investigate the taxonomic affiliation of major grass short-cell phytoliths for grasslands classification, cluster analysis was run for 27 morphotypes derived from grasses alone (fig 5.5).

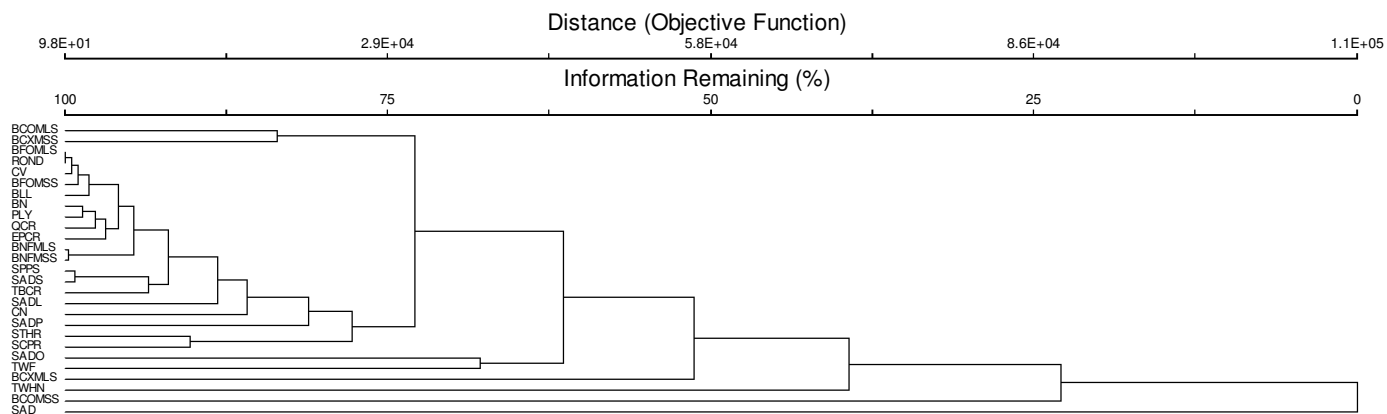


Figure 5.5 Cluster analysis dendrogram showing 27 grass morphotypes derived from 42 grass species.

The cluster analysis (fig 5.5) plots the following morphotype categories distinctively from the rest: saddle (SAD) bilobates concave outer margin short shaft (BCOMSS), tower horned (TWHN), bilobate convex outer margin long shaft (BCXMLS) and saddle ovate (SADO) which have been earlier identified as dominant in; Chloridoideae, Panicoideae, Aristidoideae and Arundinoideae grass

sub-families respectively. Other morphotypes are treated as generalist in this case and they can only suggest the presence of grasslands in a given assemblage, rather than any specific grassland type.

5.3.4 Significance of results

Correspondence analyses demonstrated the potential of using phytolith morphotypes to classify vegetation types that require similar environmental conditions, therefore indirectly suggesting the most probable environmental and/or climatic conditions associated with fossil phytolith assemblages in palaeoecological research. Vegetation types grasslands, woody and herbaceous vegetation and wetlands. Outlier morphotypes identified by cluster analysis showed the most dissimilarity, and hence are the unique-identifiers for their corresponding parent plants. They included papillae (PAPL), Saddle type (SAD), bilobates concave outer margin short shaft (BCOMSS), bilobate convex outer margin long shaft (BCXMLS) and Saddle ovate (SADO).

5.4 Summary

This chapter has presented the results of the modern phytolith data analysed from sixty-nine individual plants. The morphotypes that show a significant association (either taxonomically or ecologically) with their parent plant are used in the analyses of fossil assemblage in the following chapter.

CHAPTER SIX: RESULTS OF THE FOSSIL PHYTOLITH ASSEMBLAGES

6.1 INTRODUCTION

This chapter presents the vegetation history through 662 ka, how it changed both temporally and spatially, as well as the associated prevailing climatic conditions, as deduced from fossil phytolith assemblages from geological sections in localities B, G and Oltepesi. The sediments were obtained from the Ologresailie Formation (992-493 ka), Olkesiteti Formation (~340-166 ka) and Oltepesi Beds (~105-67 ka). The data presented here are derived from palaeosol layers in which absolute dates are not available, but relative ages are provided from various geological markers dated using $^{40}\text{Ar}/^{39}\text{Ar}$ technique unless otherwise stated (Deino and Potts, 1990). Therefore, the chronology is presented in terms of different geological phases during the early-middle-late Pleistocene (~340-64 ka) based on single crystal $^{40}\text{Ar}/^{39}\text{Ar}$ (Deino and Potts, 1990; 1992).

Phytoliths analysed from the Ologresailie sediments achieved statistically sufficient quantities required to give valuable information on the fossil plant assemblages that constituted the past vegetation cover during the Pleistocene period. Notably, several grass short-cell phytoliths were identified in the fossil assemblage which were absent in the modern analogue assemblages presented in Chapter 5. This is significant because it enabled climatic indices to be calculated (see appendix II). On one hand, some morphotypes identified in the modern analogue were rare to absent in the fossil assemblage, probably due to poor preservation caused by silica dissolution (Piperno, 2006) e.g. papillae types (PAPL). Unless otherwise stated the definition and interpretation of the fossil assemblage is based on categories discussed in Chapter 5.

Two approaches were used to achieve the palaeocological research objectives. First, changes in vegetation were reconstructed on a temporal scale spanning the mid-late Pleistocene (~760-64 ka). Second, the spatial heterogeneity in vegetation in the Ologresailie Basin was determined across the palaeolandscape during the period between ~340-220 ka. In addition, grass phytolith indices are analysed and presented in this chapter as estimates of the climatic conditions that prevailed during the mid-late Pleistocene in the Ologresailie Basin and their surrounding environments. Tree cover density is determined by calculating the ratio of dicotyledon morphotypes *versus* grass short cell phytoliths derived from the sediments.

6.2 Fossil phytolith assemblages: Temporal changes

6.2.1 Grass short cell phytolith indices

Results of phytolith indices obtained from the Olorgesailie sequence dating from ~746 to 64 ka are shown in figure 6.1. The horizontal axis presents 27 sediment samples analysed for temporal changes with the corresponding age brackets of the levels from which samples were collected. Multiple samples indicated in Roman numbers belong to a similar age bracket but different palaeosol layers.

6.2.1.1 ~746-662 ka

Four samples were analysed from this time period. The average aridity index (I_{ph}) of the period ranged between 746-662 ka is 0.65 which suggests that arid climates prevailed during this period. However, there was considerable variation in I_{ph} . For example around 746 ka the I_{ph} value is lower at 0.26 and suggests that the period was more humid, compared to around 662 ka which had an I_{ph} of 0.77. Around this time, the driest phase ($I_{ph}=0.89$) occurs in sampling level (*ii*).

The average climate index (I_C) during this period is 0.07, suggesting warm climates with highest I_C (0.14) coinciding with the driest level. Therefore the climates during this period can be considered to have been dry and hot.

6.2.1.2 ~662-340 ka

Palaeolandscapes indicated in the tuff that accumulated between ~662 ka and 340 ka have mean I_{ph} index of 0.44 suggesting wetter climates than in the preceding period. More humid episodes are suggested in some levels (~340 ka, *iii* and *vi*) with an I_{ph} value of 0.3 and one dry episode, level (*v*) with $I_{ph}=0.64$.

The average I_C index is 0.33 again suggesting warm climates. A remarkable dry and hot episode is recorded in level (*v*) with I_{ph} and I_C values of 0.64 and zero respectively, but in general this time period records moist and warm climates.

6.2.1.3 ~340-220 ka

The average I_{ph} during this age bracket is 0.43 suggesting moist climates. Two exceptions are recorded in level (*ix*), the driest episode, with an I_{ph} value of 0.71 and level (*ii*), the wettest episode, around this time with an I_{ph} value of 0.16.

The average I_C value during this time is 0.04, which is an indication of a hot climate. This period therefore records moist and warm climates, but with a higher average temperature than earlier periods and with some dry episodes.

6.2.1.4 ~220-64 ka

Six samples were analysed from this time bracket. The average Iph value for this period is 0.39, suggesting moist climates, while the average I_c value is 0.02 which is an indication of hot climates. The highest Iph value is 0.55 in level (iii), suggesting a period of mild aridity. The climates during this period are therefore generally moist and warm.

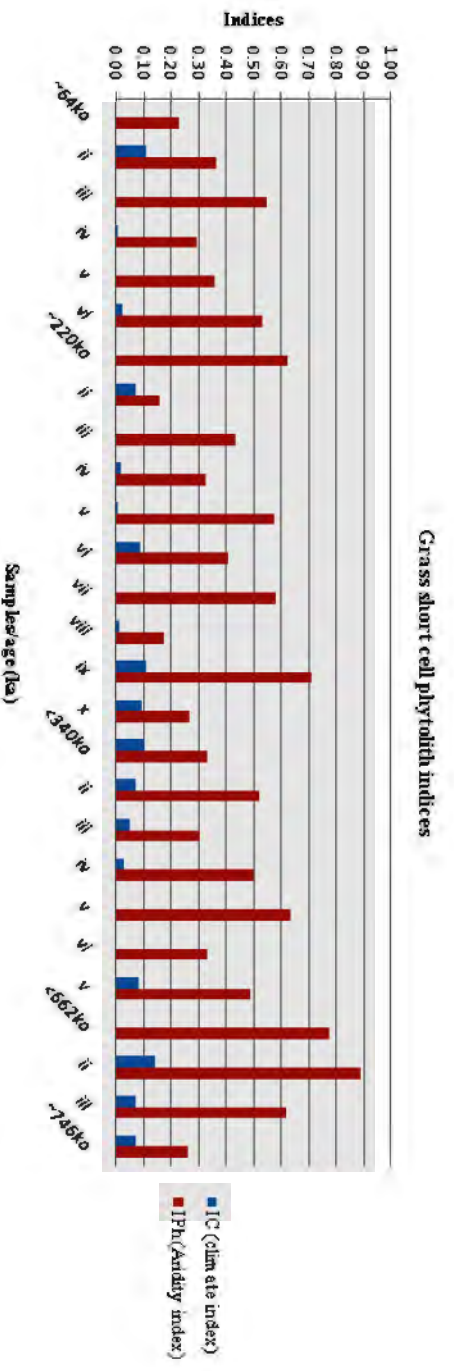


Figure 6.1 Graph showing trend of grass phytolith indices over period between ~746 to~64 ka.

6.2.2 Dicotyledon versus Poaceae morphotypes index (D/P^o)

Results obtained from calculating the ratio of phytolith morphotypes characteristic of dicotyledon plants and the Poaceae family derived from Olororgesailie sequence (~746-64 ka) are shown in fig. 6.2 below.

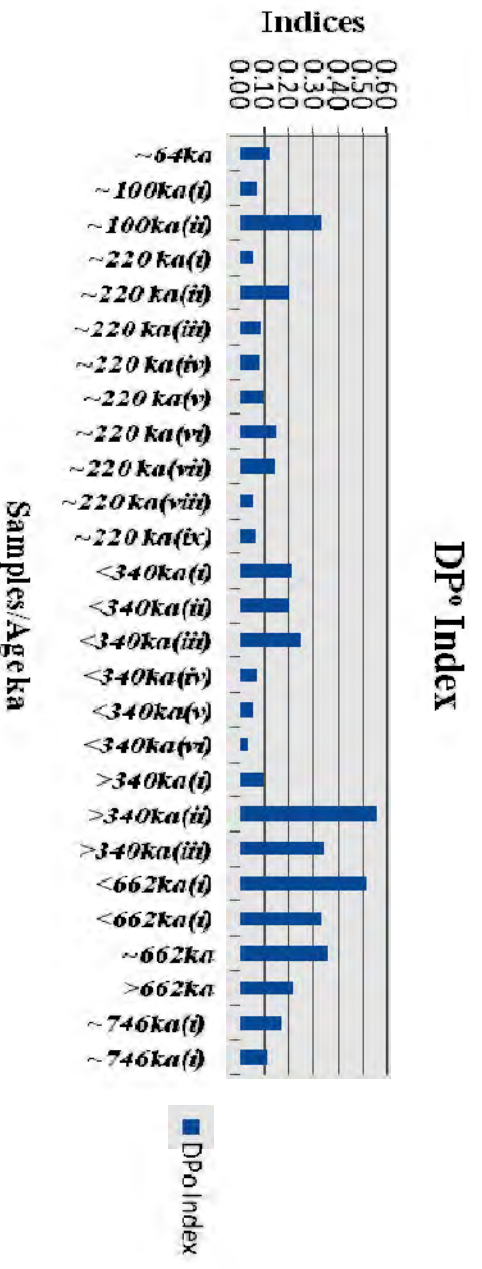


Figure 6.2 Graph showing trend of dicot/ Poaceae index over a period between~746 to ~64 ka

The figure shows that D/Po index was high during the period bracket ~662-340 ka, with the highest index of 0.55 recorded in the sample dating more than 340 ka (fig. 6.2). Low indices are recorded in

the sequence after ~340 ka, with the lowest index (0.4) occurring in the sediments younger than 340 ka.

6.3 Reconstructing vegetation history

Phytolith assemblages identified from a vertical profile matched chronologically from four geological sections and correlated to the modern phytolith analogue, give an account of the vegetation changes of the Ologesailie Basin during the Pleistocene. In addition, the data are described concurrently with climate indices computed earlier in the chapter. Data are presented as phytolith diagrams produced by the TILIA and TILIA GRAPH programs 1.01 (Grimm, 2007); zones were identified using a constrained incremental sum-of-squares cluster analysis (CONISS) which is a component integral to the TILIA software (Grimm, 2007).

6.3.1 Phytolith spectra during the Pleistocene period (~746-64 ka)

Phytolith spectra and indices produced by the Tilia program indicate that vegetation cover was dominated by grasslands during the Pleistocene period. The following is a description of the phytolith diagram (Olog) in terms of temporal changes in vegetation composition.

Three major phytolith zones were identified within the sequence and are greatly influenced by variation in Poaceae composition and distribution throughout the profile (Fig 6.3). These zones tentatively correspond to different stages of the Pleistocene period.

6.3.1.1 Olog. I (level 150-115) (~746 -662 ka)

This zone represents deposits bracketed by volcanic tuff ~746 ka in M-9 of the Ologesailie formation and M-10 tuff ~ 662 ka. The zone is characterised by the presence of phytolith morphotypes of the grass short-cell phytoliths contributed mainly by three grass sub-families (Arundinoideae, Panicoideae and Chloridoideae), and the variable phytolith categories derived from non-Poaceae taxa; hence two major taxa are represented: Poaceae, woody and herbaceous taxa including sedges (Fig 6.2). The zone comprises two sub-zones distinguished by the relative proportions of the following phytolith categories: Rondels (ROND), saddle long (SADL), bilobates convex outer margin short shaft (BCXMSS), spheroid echinate (SPHEC), spheroid psilate (SPPS), irregular verrucate (IRRVE) and irregular forms (IRRF). These combinations of morphotypes represent Arundinoideae C₃ grasses (wetlands grasses), Panicoideae C₄ grass (typical of warm and moist conditions), palm (moist conditions) and other woody & herbaceous taxa. Phytolith categories derived from Chloridoideae and Aristidoideae C₄ grasses are rare to absent in this zone accounting for <5%. The composition and proportion of the above morphotypes in this zone indicate mixed vegetation: woody grasslands dominated by moisture indicators such as Arundinoideae C₃ and Panicoideae C₄ grasses suggesting

wetter climates. C₃ Pooideae grasses remain at low percentages throughout the zone suggesting warm temperatures. There is a notable decrease of C₄ Chloridoideae and Aristidoideae grasses from sub-zone Ia to sub-zone Ib.

A) Sub-zone: Olog Ia (level 150-140)

The sub-zone marks a slight decline in rondel morphotypes from ~15% to 10%, saddle long from 5% to 2% while bilobates convex outer margin short shaft gradually increases from ~5% to 15%. The sub-zone reflects grasslands comprised of C₃ Arundinoideae and C₄ Panicoideae grasses with some herbaceous taxa present (spheroid echinate/palms, spheroid psilate and ellipsoid psilate).

B) Sub-zone: Olog Ib (level 140-115)

The sub-zone is dominated by the rondel category ~20%, saddle long ~10% and palm-type ~10%, and hence marks an expansion of C₃ Arundinoideae grasslands while C₄ grasses are rare to absent. Other phytolith categories significant in this sub-zone include irregular forms, irregular verrucate and achene (Cyperaceae), all suggesting vegetation cover consisting of grasslands with, woody and herbaceous taxa. The sub-zone suggests mixed vegetation dominated by moisture indicator grasses and with warm temperatures.

6.3.1.2 Olog. II (level 115-50) (~662-220 ka)

This zone is dominated by phytolith categories derived from C₃ grasslands and C₄ Panicoideae grasses. They include; rondel, saddle long and bilobates convex outer margin short shaft- all which are $\geq 10\%$. Also present are bilobates flattened outer margin short shaft, scutiform/prickles and spheroid psilate ~10%. Two sub-zones are influenced by relative dominance of grass short-cell phytoliths as follows:-

A) Sub-zone: Olog. IIa (levels 115-90) (~662-340 ka)

The sub-zone is dominated by grass short-cell phytoliths indicative of C₃ Arundinoideae and C₄ Panicoideae grasses. Rondel morphotype increases from <5% (level 115) to 20% (level 100) before declining to 5% (level 90). Saddle long increases from 5% (level 115) to 15% (level 105; 90). These morphotypes are strong indicators of Arundinoideae grasses suggesting an expansion of C₃ grasslands. Also on the rise are bilobates convex outer margin short shaft derived from C₄ Panicoideae grasses as well as scutiform/prickle for undifferentiated grasses. Other morphotypes prominent in this sub-zone include, bilobates convex outer margin long shaft (Aristidoideae type) (~10%) and bilobates flattened outer margin short shaft (Chloridoideae grasses) (~10%). This sub-zone suggests that vegetation was dominated by moisture indicator grasslands growing under warm climates.

B) Sub-zone: Olog. IIb (levels 90-50) (~340-220 ka)

This sub-zone is dominated by morphotypes all derived from grass sub-families; rondels (15%), bilobate convex outer margin short shaft (10%), scutiforms/prickles (15%) saddles (10%) and spheroid psilate (10%). Other significant morphotypes (~5%) include C₃ Pooideae grasses (trapezoid polylobates) palms (spheroid echinate) and Cyperaceae (achene) which influences zonation in this level. The climate seems relatively drier than sub-zone IIb.

6.3.1.3 Olog. III (levels 50-10) (~220-64 ka)

The level marks two sub-zones characterised by the abundance of phytoliths in the samples. Some samples did not yield a statistically significance phytolith count while others yielded high phytolith counts, hence the occurrence of two sub-zones. The sub-zones are distinguished (Olog IIIa &b) at level 25, where palm morphotypes peaks at ~10% and the rondel category increases from 5% to 15% while other grass morphotypes decrease, suggesting a wet episode at the boundary between the two sub-zones. In the sub-zone Olog IIIb, only one sampling level (10) records substantial phytolith counts and shows a trend in the expansion of C₄ grasses.

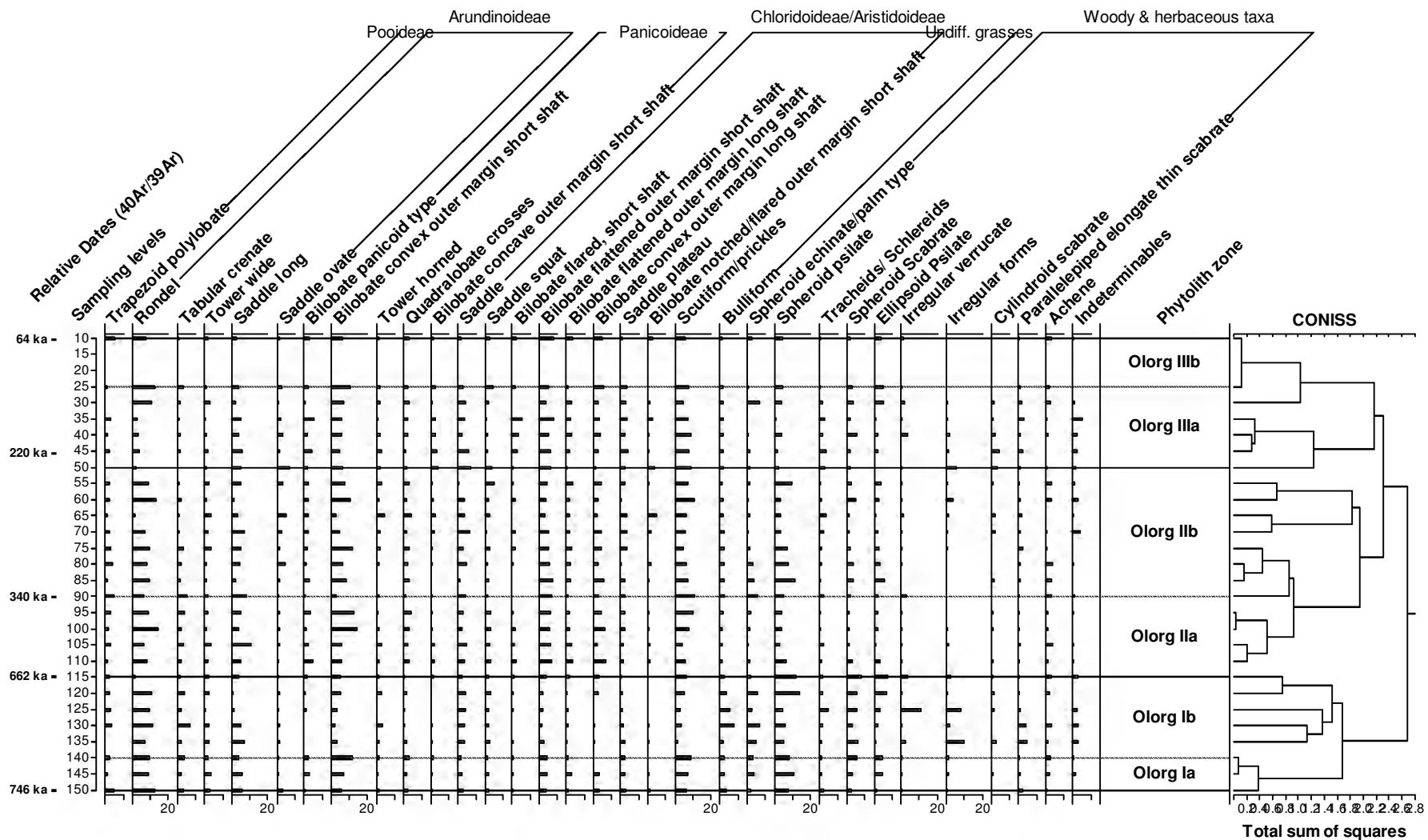


Figure 6.3 Phytolith diagram for Olorgesailie Basin. The abundance of each morphotype is expressed as a percentage of the assemblage sum.

6.4 Spatial changes during mid-Pleistocene (~220-340 ka)

As mentioned above, the Olorgesailie Basin has been subjected to a variety of geological processes resulting in a variety of palaeolandscapes. In some areas, active erosion occurs while simultaneously in other areas channel filling can take place (Behrensmeyer *et al.*, 2002). These processes may have affected the corresponding land cover, creating patches of micro-habitats across the landscape as observed in the current vegetation distribution. Such microhabitats include the occurrence of riverine vegetation along the river channels and marshy habitats on the flood plains dominated by Arundinoideae C₃ grasses, palms and sedges.

The fossil phytolith assemblages derived from three geological sections, each representing Localities B, G and Oltepesi are considered for spatial analysis. These sections are correlated with two dated geological markers: green pumice tuff at ~225 ka and 340 ka tuff. Section G08/01 is separated from section B05/04 by the Mt. Olorgesailie outcrop and whose main sources of deposits are the main Ol Keju Nyiro river channel in the east, and the Ol Keju Nyiro tributaries in the west. Further west is the flood plain of the Ol Keju Nyiro river where Oltepesi deposits form (refer to the map in chapter 4, fig. 4.3).

The three localities have been subjected to different synergies controlled by the Ol Keju Nyiro river channel systems. Localities B and G represent the high energy phase of the river systems and are separated by Mt. Olorgesailie, while the Oltepesi plain represents a lower energy phase. Depending on the exposed palaeosol layer in each locality, 5, 6 & 12 samples were analysed from G, B and Oltepesi, respectively.

Comparison of the phytolith assemblages through the sedimentation sequence of the three trenches is hereby presented.

6.4.1 Phytolith diagram for B05/04 (~340-220 ka)

The phytolith sequence from six samples is presented in the form of a TILIA diagram; phytolith morphotypes are classified into their respective vegetation components for clear discussion. Two zones are distinguished by CONISS, corresponding to variations in the major morphotypes derived from Poaceae and non-Poaceae groups selected on the basis of their dominance within the samples analysed (fig 6.4):

6.4.1.1 B05-04 I

This zone is characterised by the dominance of morphotypes derived from woody and herbaceous taxa comprising irregular verrucate (25%), ellipsoid psilate (25%), irregular forms (18%), spheroid

scabrate (10%) and spheroid echinate (palm type) (10%) while grass phytoliths were notably rare to absent except for undifferentiated grass phytoliths; scutiform/prickles category. This suggests a more densely wooded landscape. Two sub-zones are identified by CONISS:-

A) B05-04 Ia

The sub-zone is represented by palaeosol close to 340 ka tuff, where grass short-cell phytoliths are rare with <5% while three morphotypes from woody and herbaceous taxa are present with higher proportions ranging from 10% to 18%. Palm phytoliths are absent in this sub-zone. Towards the sub-zone boundary, grass short-cell phytolith morphotypes increase from 5% to 15% while those from woody and herbaceous taxa are absent. Thus the zone suggests an initially woody phase but with the landscape becoming more open and grass-dominated.

B) B05-04 Ib

Samples in this sub-zone consist of morphotypes derived from woody and herbaceous taxa, ranging between 10% and 25% which is higher than the other samples. Grass short-cell morphotypes are rare to absent in this sub-zone with rondels (5%) and saddle long (10%) mainly derived from C₃ Arundinoideae grasses.

6.4.1.2 B05-04 II.

The zone is dominated by morphotypes derived from woody and herbaceous taxa ranging between 10% and 20%. Grass short-cell phytoliths present in this zone rondel category (15%) and scutiform/prickles (15%).

Phytolith assemblages from this section indicate vegetation cover around locality B was dominated by woody & herbaceous taxa. The occurrence of palm phytoliths in all samples except for one sample (level 60, fig 6.4) indicates wetland ecosystems/marshy environments (Albert *et al.*, 2009; Barboni *et al.*, 2010). There is a notable absence of grass short-cell phytoliths derived from C₄ Chloridoideae and Aristidoideae grasses in this section which is probably an indication of moist environments and a more wooded landscape.

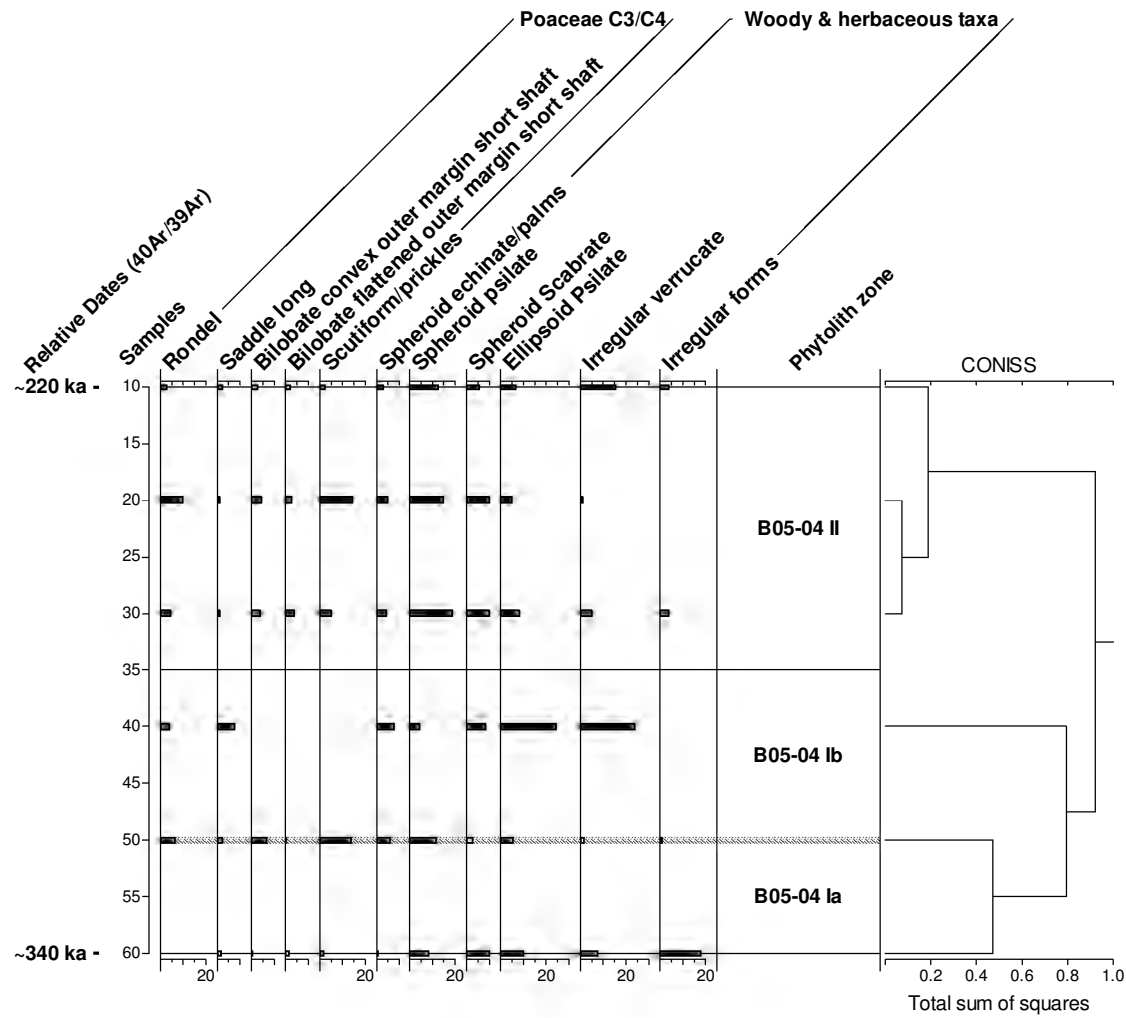


Figure 6.4 Phytolith spectra for Locality B.

6.4.2 Phytolith diagram for OLT05/02 (~340-220 ka)

The TILIA diagram (fig. 6.5) presents the results of 12 samples collected from all the palaeosols in Oltepesi locality. This sequence yielded more samples than expected since there were more palaeosol layers than in the other geological sections. From this sequence, 33 morphotypes were identified and classified into their respective vegetation components. Three major zones are distinguished as follows:

6.4.2.1 OLT05/02 I

The zone is characterised by occurrence of the morphotypes derived from both Poaceae and non-Poaceae taxa which include: rondels (10-15%), saddle long (5-10%), saddles (5-10%) and scutiform/prickles (5-15%). However, there is a slight dominance of grass short-cell phytoliths over woody and herbaceous taxa. Two sub-zones are classified through CONISS analysis as follows:

A) OLT05/02 Ia

Three samples presented in this sub-zone show a higher occurrence of grass short-cell phytoliths (fig 6.4): rondels (10%), saddle long (15%), bilobates convex outer margin short shaft (18%) as indicators of Arundinoideae C₃ grasses and Panicoideae C₄ grasses which later decline. Other significant morphotypes in this sub-zone included bilobates convex outer margin short shaft (Panicoideae), saddles and bilobates flattened outer margin short shaft (Chloridoideae) and bilobates convex outer margin long shaft (Aristidoideae) grasses.

B) OLT05/02 Ib

The sub-zone is characterised by rondel (20%), bilobates convex outer margin short shaft (20%) and scutiform/prickles (20%). Morphotypes derived from C₄ Chloridoideae & Aristidoideae are rare to absent in the sub-zone.

6.4.2.2 OLT05/02 II

The zone is characterised by an abundance of short grass cell phytoliths but with a notable decline in the rondel category (<5%); bilobate concave outer margin short shaft (15%), and C₄ saddle category slightly declining from 10% to 5%. The dominance of the following grass short-cell phytolith (bilobates panicoid type, bilobates outer margin concave short shaft and saddle long) indicate dominance in Panicoideae C₄ grasses in this zone, i.e. an open landscape lacking woody elements.

6.4.2.3 OLT05/02 III

This zone comprises phytolith assemblages from three samples. Significant morphotypes include rondels (20%), bilobates convex outer margin short shaft (10-20%), bilobates flattened outer margin short shaft (10-20%) derived from both C₃ and C₄ grass subfamilies; spheroid echinate/palm

morphotype (10%). Other morphotypes present include spheroids and ellipsoids variants derived from woody and herbaceous taxa and achene type from Cyperaceae.

The OLT05/02 sequence results suggest vegetation cover was characterised by sparsely wooded grasslands comprising both C₃ and C₄ moisture indicator grass species. The general inference is that vegetation cover between ~340-220 ka was dominated by wetland grasslands (Arundinoideae and Panicoideae grasses). The presence of spheroid echinate (palm) and achene morphotypes further indicates the occurrence of wetlands.

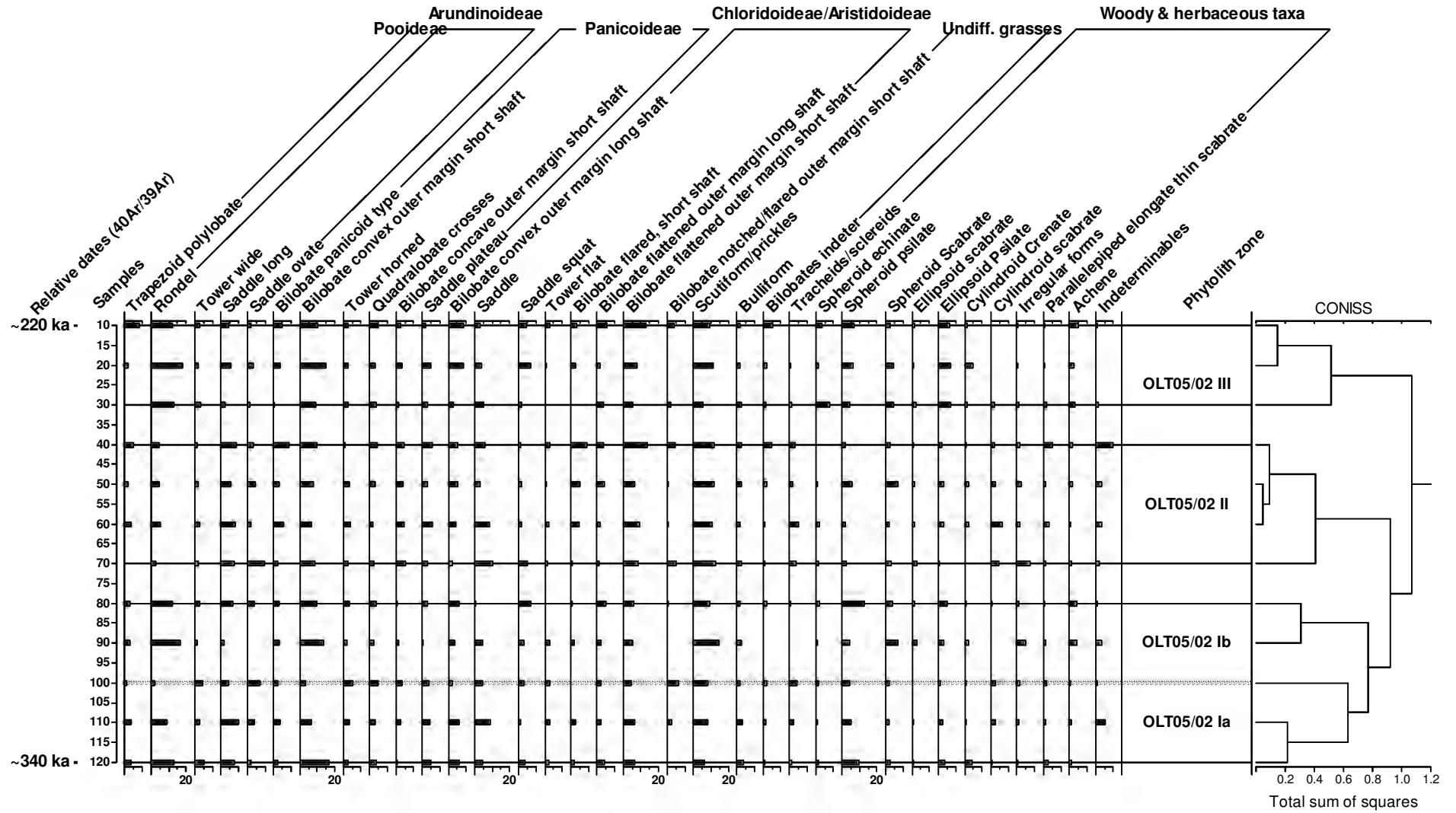


Figure 6.5 Phytolith spectra for Oltepesi plains

6.4.3 Phytolith diagram for G08/01 (~340-220 ka)

Phytolith assemblages from five samples suggest stable vegetation. Since the samples did not vary much in terms of morphotypes composition, no definite zones were classified by CONISS (fig. 6.6). Only 12 morphotypes achieved 2% of the total assemblages: grass short-cell phytoliths were the main component. The phytolith sequence did not show significant temporal variation during the period ~340-220 ka except for level 50 where woody and herbaceous taxa dominate. The rest of the sequence is dominated by grass short-cell phytoliths representing both C₃ and C₄ taxa. Although very few morphotypes were considered in this sequence, it appears that the vegetation cover indicated was open mixed grasslands with both C₃ and C₄ components.

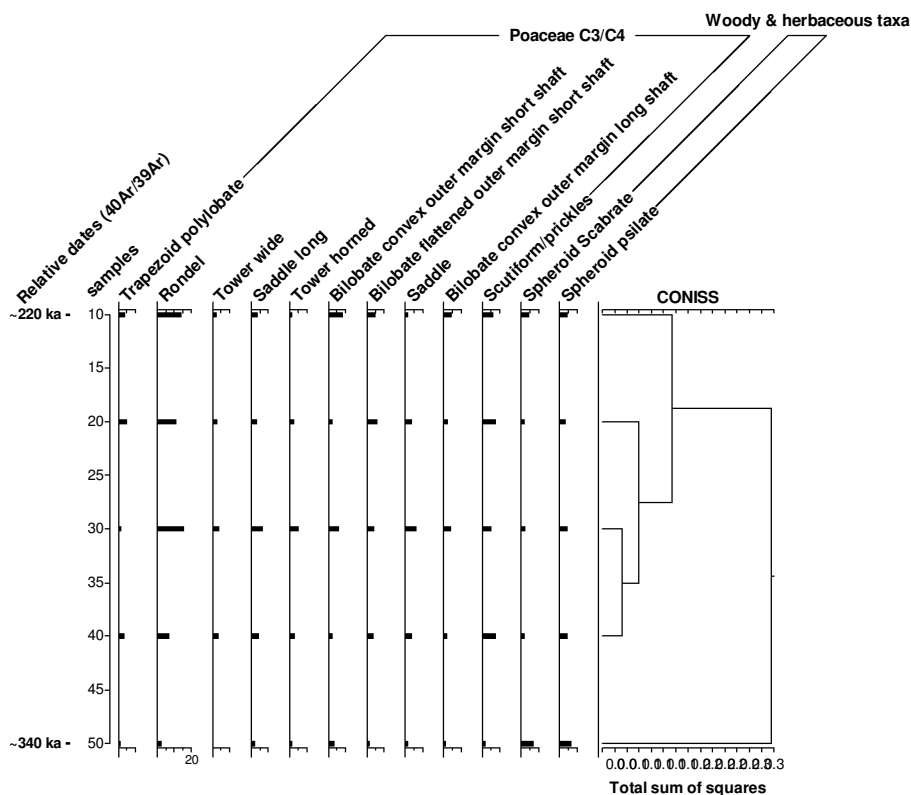


Figure 6.6 Phytolith spectra for Locality G.

6.5 Summary

This chapter has presented results of phytolith analysis of the fossil assemblages. Both temporal and spatial vegetation cover changes provide significant results that are interpreted and discussed within the context of the mid-late Pleistocene period in the following chapter. Their significance to hominin behaviour that interacted with these environments in the Ologesailie Basin is also discussed in the following chapter.

CHAPTER SEVEN: INTERPRETATION and DISCUSSION

7.1 INTRODUCTION

In this chapter, the results of phytolith data from both modern reference and fossil assemblages are interpreted and discussed within the context of the Olorgesailie Basin as an important prehistoric site. The significance of the results within the context of wider palaeocological studies is also discussed.

Phytolith analysis from three localities within the Olorgesailie Basin, in the southern part of the Rift Valley in Kenya has proved to be of importance in reconstructing past vegetation changes, and as an indirect proxy in determining the prevailing climatic conditions through the mid-late Pleistocene (~740-60 ka). This is particularly useful in view of the basin's archaeological and paleontological richness, along with the absence of other organic plant fossils (such as pollen) that could yield insights into the possible vegetation structure during the emergence and the persistence of the genus *Homo*.

The modern reference phytoliths from present-day vegetation along an altitudinal gradient played a crucial role in identifying the possible vegetation cover of the palaeo-landscapes of the Olorgesailie Basin. Multivariate analysis of the selected modern plants' phytoliths showed a correlation between phytolith morphotypes and contemporary vegetation types. Correlating the modern phytolith analogues with known temperature and rainfall gradients associated with different plant assemblages, enabled inferences to be made of the past climate-vegetation relationships as reflected by fossil phytolith assemblages (Bremond *et al.*, 2005a; 2005b).

Phytolith indices of climate (mainly temperature) and aridity, computed from selected grass short phytoliths (Bremond *et al.*, 2008) suggested the presence of warm and moist climates in the Olorgesailie Basin and the surrounding environments during the mid-late Pleistocene. Analysis of fossil phytolith assemblages through time suggest mainly open vegetation cover, dominated by moisture-indicating C₃ Arundinoideae and C₄ Panicoideae grasses during the mid-late Pleistocene (~740-64 ka). However, the presence of woody and non-Poaceae herbaceous elements suggest that sparsely wooded thickets also existed in these landscapes particularly during the mid-Pleistocene (746-662 ka) when the climate was more humid (Trauth *et al.*, 2007).

The current study provides evidence of spatial variation in the vegetation across the landscape during the period ~340-220 ka. Phytolith assemblages from different localities but particularly locality B suggest the existence of micro-habitats most commonly associated with riverine vegetation. Locality G and Oltepesi sequences on the other hand suggest vegetation dominated by grasslands.

The existence of patchy wooded habitats across the landscapes is also indicated in the fossil assemblages. This included the presence of palms which are significant indicators of wetlands or localities with a high water table (Albert *et al.*, 2009). The presence of sedges in the Ologesailie Basin further suggests marshy environments were present in these palaeolandscapes. This, however, contrasts with the current vegetation cover which is dominated by Chloridoideae (C₄) short grasses more commonly associated with semi-arid climates. Cyperaceae are still present along the water bodies but no palms are seen within the vicinity of the basin.

The interpretation of the fossil assemblage results is based on the assumption that the Palaeosols are chronologically placed and bracketed by the geological markers dated from the Ologesailie Basin by Deino and Potts, (1990) and the geological work currently in progress (unpublished ages by Deino *et al.*, 2010).

7.2 Modern phytolith analogue

Phytoliths derived from different plants were classified into different categories (Appendix I). Woody and herbaceous taxa produced the most variable categories which included spheroid variants, ellipsoid variants, tracheids, schlereids and silicified appendages. Individual woody and non-grass herbaceous plants showed insignificant association with particular morphotypes, but as a vegetation component, significant correlation with their morphotypes is generally deduced (Piperno, 2006). Morphotypes derived from grasses and sedges showed significant correlation both taxonomic and ecological, with grass short-cell phytoliths having the strongest correlation (Twiss, 1992; Barboni and Bremond, 2009; Rossouw, 2009). Thus grass short-cell phytoliths played a crucial role to achieve the main goal of this study.

Efforts made to describe various morphotypes, for instance saddle (SAD), saddle ovate (SADO), saddle squat (SADS) and saddle long (SADL), further influenced the ordination of different grass species (fig 5.3). Three grass sub-families were distinguished: Arundinoideae, Aristidoideae and Chloridoideae, depending on which saddle type dominated.

The variants described in the saddle category for this study accords with other descriptions published in the literature (Twiss *et al.*, 1969; Thorn, 2004; Barboni *et al.*, 2007; Barboni and Bremond, 2009; Rossouw, 2009; Mercader *et al.*, 2010; 2011). Saddle ovate (SADO) as “rondel with round base (Piperno and Pearsall, 1998)” and saddle long (SADL) occurred more abundantly in Arundinoideae grasses than in other taxa; saddle (SAD and saddle squat (SADS) predominated in Chloridoideae grasses while saddle plateau (SADP) was more common in Aristidoideae than in other taxa (Piperno and Pearsall, 1998; Piperno, 2006).

Results further showed that Chloridoideae grasses exhibited strong redundancy compared to other grass sub-families as they produce most of the grass phytolith categories described in this study although in varied quantities. However, the description of the tower category (Mercader *et al.*, 2010), (referred to as rondel in most publications) (Twiss *et al.*, 1969; Madella *et al.*, 2005; Barboni *et al.*, 2007; Barboni and Bremond, 2009) into three tower morphotypes was one way of dealing with the challenges of redundancy and multiplicity (Rovner, 1983) which has been critical in interpreting grass short-cell phytoliths (Piperno and Pearsall, 1998; Barboni and Bremond, 2009). For instance, tower flat (TWF) was more dominant in Chloridoideae, tower horned (TWHN) dominated in Panicoideae while tower wide (TWW) was insignificantly low in both sub-families. The tower category was rare to absent in the Arundinoideae grasses and is therefore, a type that can be considered in future to distinguish the rondels occurring in Arundinoideae, Pooideae and Chloridoideae grasses.

Description of the bilobates category to further discriminate between different grass sub-families was successful. Although a high percentage (48%) of the bilobates were recorded in Panicoideae grasses, the bilobates convex outer margin long shaft (BCXMLS) category was abundant (58%) in the Aristidoideae grasses while absent in other subfamilies, hence distinguishing the Aristidoideae grasses from other subfamilies. This bilobates category is easily separated from those in the Panicoideae grasses (Piperno, 2006; Fahmy, 2008; Rossouw, 2009). Furthermore, bilobates outer margin flattened both short and long shafts categories was common in Chloridoideae grasses, though their collective percentage occurrence was insignificantly low ~9% and therefore their potential significance requires further research.

Two Arundinoideae grasses were processed and analysed for this study. Saddle ovate (SADO) was dominant (61%) in both suggesting that this category could be used as an indicator of the presence or absence of Arundinoideae grasses in fossil phytolith assemblages.

For the mixed vegetation dataset, correspondence analysis can indirectly give estimates of the vegetation types represented by phytolith assemblages, as well as an indication of the underlying environmental and/or climatic factors, which are of great interest for palaeoecological research.

7.2.1 Phytoliths and the altitudinal distribution of plant species

Phytoliths derived from plants collected from three different ecological zones; Mount Kenya (montane forest), Taita hills (dry forest) and the Olorgesailie Basin (savanna grasslands) showed no significant trend with altitudinal change, but were instead significantly related to moisture content. Similar results from Miombo (*Brachystegia*) woodland in Mozambique (Mercader *et al.*, 2011) showed no distinction between phytoliths collected from cool highland Miombo woodland with those from Miombo woodlands from the dry lowlands. However, this seems to contradict previous studies

from Mount Kenya in East Africa (Tieszen *et al.*, 1979) and other phytolith-based climate reconstruction studies (Twiss, 1992; Fredlund and Tieszen, 1994). This contrast can be explained by the fact that such studies (Tieszen *et al.*, 1979; Twiss, 1992; Fredlund and Tieszen, 1994; Barboni and Bremond, 2009) only analysed grass short-cell phytoliths, and the distribution of grasses is strongly correlated with temperature and moisture gradients, and thus altitudinal gradient (Ibrahim and Kabuye, 1987; Livingstone and Clayton, 1979; Tieszen *et al.*, 1979; Barboni and Bremond, 2009; Rossouw, 2009). The current study shows the analyses of modern plants and all of their corresponding morphotypes indeed has potential significance in a palaeoecological context. Such a focus helps to identify vegetation structure associated with different habitats such as grasslands, woody and herbaceous and aquatic habitats, which is crucial for the reconstruction of palaeoenvironments in East Africa (Alexandre *et al.*, 1997; Barboni *et al.*, 1999; Albert *et al.*, 2006; 2009; Ashley *et al.*, 2010).

7.2.2 Multivariate analyses

Woody and herbaceous taxa produced mainly the variable phytolith morphotypes (Bozarth, 1993; Albert, 1999; Albert *et al.*, 2000; Bremond *et al.*, 2005a, Mercader *et al.*, 2009) which included spheroid variants (SPH-) ellipsoids (ELL-), irregular (IRR-), schlereids (SCLD) and tracheid (TRCH). These morphotypes are key indicators of woody and non-grass herbaceous elements in a fossil assemblage. Hence they are of great potential in palaeoecological reconstruction to distinguish past vegetation canopies and structure, specifically the presence of woody elements/patches in the landscape (Mercader *et al.*, 2000; Albert *et al.*, 2006; Barmford *et al.*, 2006; Ashley *et al.*, 2010a). The achene (ACHN) and papillae (PAPL) morphotypes identifies the Cyperaceae family (Ollendorf, 1992) and hence indicates wetland and marshy environments (Ashley *et al.*, 2010a; 2010b).

The description of grass short-cell phytoliths (Mercader *et al.*, 2010) further beyond the International Code for Phytolith Nomenclature 1.0 (ICPN, Madella *et al.*, 2005) and the regional classification scheme (Twiss *et al.*, 1969), strengthened the morphological association of various morphotypes to their respective sub-families as discussed below-

a) *Bilobates*

These morphotypes distinguished two grass subfamilies discussed in this study; Panicoideae and Aristidoideae. Panicoideae grasses contributed largely bilobates concave/convex outer margin short shaft (BCOMSS/BCXMSS) (Twiss *et al.*, 1969; Mulholland, 1989; Madella *et al.*, 2005) while Aristidoideae grasses produced bilobates convex outer margin long shaft (BCXMLS) (Piperno, 2006; Rossouw, 2009). Fossil assemblages dominated by BCOMSS/BCXMSS suggest moist grasslands under warm climates while one dominated by BCXMLS suggests short grasslands under arid climates and/or disturbed grounds (Tieszen *et al.*, 1979; Ibrahim and Kabuye, 1987; Barboni and Bremond, 2009).

b) Saddles

Two saddle categories distinguished Chloridoideae and Arundinoideae grasses. Saddle-shaped (Twiss *et al.*, 1969; Madella *et al.*, 2005; Rossouw, 2009) distinguished Chloridoideae while saddle ovate (SADO) distinguished Arundinoideae grasses. A phytolith assemblage dominated by SAD indicates arid- and semi- arid grasslands while SADO suggests wetlands/ marshy environments (Rossouw, 2009).

c) Towers

This category was initially classified as rondel category (Fredlund and Tieszen, 1994; Wallis, 2000) but was described further with the aim of reducing the multiplicity and redundancy aspect of this category (Mercader *et al.*, 2010). Tower horned (TWHN) dominated in the Panicoideae grasses, tower flat (TWF) in the Chloridoideae, and tower wide (TWW) in Arundinoideae grasses. Their variations within fossil assemblages can be discussed accordingly, hence distinguishing grassland components more accurately. This is a challenge that the rondel category has exhibited in other phytolith studies (e.g. Piperno and Pearsall 1998; Kondo *et al.*, 1994).

d) Rondels

These morphotypes refer to entirely circular and oval shaped phytoliths (Twiss *et al.*, 1969; Piperno and Pearsall, 1998; Barboni and Bremond, 2009). In this study they are predominantly produced by the Arundinoideae grasses. Hence, a high occurrence in the fossil assemblage suggests a dominance of Arundinoideae grasses associated with moist climates (see Ollendorf *et al.*, 1988).

e) Other grass morphotypes

These are grass generalist morphotypes that occurred in all the grasses analysed. They included bulliforms and scutiform/prickles which collectively identified the undifferentiated grasses. Their dominance in an assemblage allowed the differentiation between different vegetation types. For example, their abundance would indicate grass-dominated vegetation with a more open canopy compared to an assemblage dominated by variable morphotypes. Abundance of the latter in an assemblage would be associated with vegetation dominated by woody and herbaceous taxa and hence a more closed canopy, such as riverine vegetation and/or wooded savanna depending on the presence and dominance of other grass sub-families in the assemblage.

7.2.2.1 Phytolith production among grass sub-families

Phytolith production among grasses is variable. The relative abundance of short grass phytoliths (fig 5.1) showed Panicoideae grasses can be distinguished by a higher abundance of bilobates (BCOMSS/BCXMSS) and TWHN while Arundinoideae grasses are characterized by a higher abundance of SADO and TWW. Chloridoideae grasses on the other hand are associated with a higher abundance of

SAD and TWF while Aristidoideae grasses by higher abundance in BCXMLS (refer to appendix II for morphotype names). The morphotypes were thus identified as key indicators of grass sub-families in the fossil assemblages. The summary of these morphotypes is presented in appendix IV.

7.2.2.2 Correspondence analysis

Correspondence analysis (CA) grouped plant species on the basis of their phytolith compositions. Three vegetation components were identified and classified in the ordination space according to the affiliated environmental factors (fig 5.2). This indirectly identified moisture content as the major environmental factor responsible for the distribution of modern plants and their corresponding phytolith morphotypes.

The three vegetation components identified were grasslands, woody and herbaceous taxa and aquatic taxa which can be differentiated by moisture availability. This trend is further suggested by results of the correspondence analysis among grasses (fig 5.3); where Panicoideae (warm and humid) appear separate from Chloridoideae and Aristidoideae (hot and dry). This is an indication of the influence of moisture on the distribution of grasses and a result which is ecologically appropriate (Livingston and Clayton, 1979; Tieszen *et al.*, 1979; Twiss, 1992; Barboni and Bremond, 2009). This is important in assessing the climatic conditions associated with fossil phytolith data (Alexandre *et al.*, 1997; Bamford *et al.*, 2006, Piperno, 2006).

7.2.2.3 Cluster analysis

The unique phytolith morphotypes identified in this study were the major outliers in the cluster analysis (Figs 5.4 and 5.5) namely: papillae (PAPL) in Cyperaceae, saddle (SAD) in Chloridoideae, bilobate concave outer margin short shaft (BCOMSS) and tower horned (TWHN) in Panicoideae and, saddle ovate (SADO) in Arundinoideae. A similar trend is observed in fig. 5.5: where the taxonomic affiliation of grass short-cell phytoliths to the corresponding sub-family is meaningful. The results match and corroborate earlier phytolith studies in Africa (Runge, 1995; Bremond *et al.*, 2008; Barboni *et al.*, 2007; Barboni and Bremond, 2009; Rossouw, 2009; Mercader *et al.*, 2010; 2011).

The analysis of grass short-cell phytoliths indicates evidence of multiplicity and redundancy i.e. the occurrence of different morphotypes in one grass species and occurrence of certain morphotypes in more than one grass tribe (Rovner, 1983; Piperno, 2006). This is a challenge faced by other phytolith workers (e.g. Twiss *et al.*, 1969; Rovner, 1983; Mulholland, 1989; Fredlund and Tieszen, 1994; Piperno and Pearsall, 1998; Barboni and Bremond, 2009) as well as in the current study (see table 8.1). However, differential occurrences of various morphotypes in grasses contribute in identifying grasslands dominated by different sub-families and which are associated with specific moisture and

temperature regimes (Tieszen *et al.*, 1979; Fredlund and Tieszen, 1997; Barboni and Bremond, 2009; Rossouw, 2009).

This study applied a region-based modern phytolith analogue as a proxy to meaningfully reconstruct the vegetation cover of the Olorgesailie Basin both temporally and spatially, as well as in estimating the associated climatic conditions during the mid-late Pleistocene (746-64 ka).

7.3 Fossil assemblages

Previous studies demonstrated the potential of phytolith analysis, not only as a palaeocological tool to reconstruct vegetation history (Rovner, 1971; Piperno, 1988; 1989; Barboni *et al.*, 1999; Ashley *et al.*, 2010) and grasslands dynamics (Alexandre *et al.*, 1997; Rossouw, 2009), but also to determine palaeoenvironmental climatic conditions associated with these changes (Bremond *et al.*, 2005a: 2005b; Bremond *et al.*, 2008; Barboni and Bremond, 2009; Rossouw, 2009). This is a key strength evident in a range of studies which reconstruct palaeoenvironments of major prehistoric/hominin sites in the East African region (Barboni *et al.*, 1999; Albert *et al.*, 2006; 2009; Barboni *et al.*, 2010). Fossil phytolith assemblages derived from selected palaeosols (see appendix III) were classified according to vegetation types they represented in order to interpret vegetation changes and associated climates.

7.3.1 Temporal vegetation changes

The Olorgesailie phytolith sequence is characterised by an abundance of grass short-cell phytolith categories, which are indicators of both C₃ and C₄ grasses. However, there is a notable rarity of morphotypes derived from C₄ short grasses (Chloridoideae and Aristidoideae) throughout the sequence, which is a major component in the contemporary vegetation cover, suggesting that the mid-late Pleistocene climates were wetter than present.

The presence of phytolith morphotypes derived from woody and herbaceous taxa (Olog zone I; fig 6.3) is an indicator of mixed vegetation cover particularly during the mid-Pleistocene period (~746-662 ka). However, the dominant vegetation cover was grassland (both C₃ and C₄ grasses), as reflected by grass short-cell phytoliths >15% and non-Poaceae herbs while those indicating woody taxa, including palm trees, remained rare throughout the sequence suggesting an open landscape with scattered trees or patches of trees. This conclusion is based on the following selected morphotype categories: rondel, saddle long, bilobates convex outer margin short shaft, scutiforms/prickles, spheroid psilate, irregular verrucate and irregular forms (see fig 6.3).

Although achene morphotypes were not abundant, their presence in the sequence, particularly in Olog zones I&II, further indicates moist/aquatic environments during the mid Pleistocene period particularly between ~746-662 ka. Such environments are suggested by the diatom flora indicating

shallow water environments around 493 ka (Owen *et al.*, 2009) in the Olorgesailie Basin. This is further corroborated by the fact that fresh water bodies or perhaps a high water table were present in the basin, as evidenced by the occurrence of palms in the sequence (Albert *et al.*, 2009).

Interestingly, the presence of Pooideae C₃ grass phytoliths suggests cooler climates than present were experienced in the basin during the Pleistocene period. However, the signature in the phytolith record is insignificantly rare compared to other grasses, and hence cannot be relied on to interpret this as indicating the glacial period that was experienced globally during the period (Mudelsee and Stattegger, 1997).

Notable vegetation shifts from 340 ka suggest an episode of relatively wetter climate as evidenced by the expansion of Arundinoideae and Panicoideae grasses on the landscape, while Chloridoideae grasses declined significantly. These scenarios suggest that vegetation shifted from grasslands dominated by C₃ grasses to C₄ Panicoideae. Such variability has been noted previously during the Plio-Pleistocene (Sikes *et al.*, 1994; Potts, 1998). Around ~100-64 ka, the expansion of Arundinoideae C₃ grasses occurred as well as an increase in the abundance of C₄ Panicoideae grasses, suggesting warm and moist conditions as indicated by aridity index of ~0.46 and climate index of 0.48. This period coincided with a phase of high lake levels in East and West African lakes around 70 ka and provides evidence of more humid conditions (Bergner and Trauth, 2004; Scholz *et al.*, 2007; Bergner *et al.*, 2009).

Phytolith analysis therefore indicated that vegetation cover during the mid-late Pleistocene was dominated by moist-loving grasslands with a sparse cover of woody elements.

7.3.2 Phytolith indices

In order to determine the climatic/ environmental conditions and vegetation structure of the Olorgesailie Basin during the Pleistocene, results of three indices are discussed. These indices include; climate index (I_C), aridity index (I_{ph}) and dicot/Poaceae index (D/P⁰) (Bremond *et al.*, 2008).

7.3.2.1 Grass short-cell phytoliths versus climate and aridity indices.

Grass short-cell phytoliths are used to distinguish grasses beyond family level to their respective sub-families (Metcalf, 1960; Wallis, 2000), and to infer the associated climatic signals/ ecological affiliation (Twiss, 1992; Fredlund and Tieszen, 1994; Barboni and Bremond, 2009; Rossouw, 2009) in the fossil assemblages. Indices computed from selected grass short-cell phytoliths are examined from the fossil assemblages; C₃ Pooideae-trapeziform polylobate (cool climates) C₄ Panicoideae – bilobates and quadralobates (warm and moist) and C₄ Chloridoideae grasses-saddles (warm and dry)

(Bremond *et al.*, 2008) allowing estimates of paleoclimate in terms of temperature and moisture to be discussed.

The current study shows that palaeoclimates in the Ologesailie Basin were generally warm and humid during the Pleistocene period corresponding with the general wet episodes suggested by high lake levels in East Africa (Trauth *et al.*, 2001; 2003; Bergner and Trauth, 2004), especially during the late-Pleistocene (~139-133 ka). Previous studies suggest East Africa experienced regional climate changes that were independent of the global glacial and interglacial cycles during the Pleistocene (Marchant *et al.*, 2006; Trauth *et al.*, 2007). It is not surprising that the global glacial episode was not recorded in this sequence, as local topography has a strong influence on precipitation in the region.

7.3.2.2 Dicotyledon versus Poaceae index (D/P^o)

D/P^o index suggest that the vegetation structure of the Ologesailie Basin was dominated with open grasslands during the Pleistocene period. However, the period between ~662-340 ka suggest vegetation cover dominated with woody plants/trees, followed by expansion of open grasslands after ~220 ka to 64 ka (fig 6.2). This finding further explains the reason for early hominin settlement within the Basin; the availability of forest resources.

7.3.3 Spatial vegetation changes

Phytolith data from three localities within the Ologesailie Basin suggest a certain degree of heterogeneity in vegetation cover across the palaeolandscape between ~340 ka to 220 ka. This is indicated by the presence of mixed grasslands with varying tree cover although tree cover declined significantly at one point. Locality B (B05/04) records a high dominance of morphotypes derived from woody and herbaceous taxa ranging between 10%-25% while the highest occurrence of grass-derived morphotypes is 15% (rondel category) (fig 6.5). Occurrence of palm phytolith (5%-10%) in five out of six samples suggests marshy environments and/or freshwater sources (Albert *et al.*, 2009; Ashley *et al.*, 2010; Barboni *et al.*, 2010). The high occurrence of woody derived morphotypes (irregular verrucate, spheroid scabrate), indicate wooded vegetation cover in Locality B during ~340 ka to 220 ka. Although grass phytoliths are not abundant in the sequence, the occurrence of grass short-cell phytoliths indicative of Arundinoideae and Panicoideae grasses further suggest moist environments in the locality.

Oltepesi plain (OLT05/02; fig 6.5) records the highest number of morphotypes compared with B05/04 and G08/01 (fig 6.4 & 6.6). However, only 10 morphotype categories were tentatively significant for vegetation reconstruction since they recorded >10% occurrence of the total sum. Morphotypes derived from grasses are more abundant than those derived from woody and herbaceous taxa, suggesting vegetation cover dominated by grasses. However, there is little variation in the grass components, and

all the three subfamilies are represented throughout the sequence, suggesting the presence of mixed grasslands, with both C₃/C₄ grasses. Other significant non-grass morphotypes in the sequence include palm phytoliths and Cyperaceae (achene type) which suggest wet environments particularly around ~220 ka.

The Locality G sequence is dominated by grass short-cell phytoliths with the rondel category recording a higher percentage (~15%) in four out of five samples. Only two morphotypes derived from woody & herbaceous taxa are recorded in G08/01 sequence, which dominate in the oldest sample (~340 ka of age; fig. 6.6). Palm phytoliths were not recorded in this sequence. Results from G08/01 sequence are indicative of open grasslands as the main vegetation cover during this period.

There is great significance in the occurrence of different vegetation types that suggest a variety of ecosystems within the basin. The presence of palms and sedges indicate the availability of fresh water resources which justifies the occupation of hominins in the Olorgesailie Basin (Owen *et al.*, 2008) or presence of springs as suggested in Olduvai Gorge, Tanzania (Ashley *et al.*, 2009; 2010a).

In conclusion, spatial analysis of phytolith assemblages showed vegetation heterogeneity across the palaeolandscape during the time bracketed by 340-220 ka. Small scale spatial heterogeneity in vegetation cover could be explained by the presence of river channel systems and/or wetlands across the landscape that would create micro-habitats of riverine/ wetland vegetation within a grassland dominated habitat.

7.3.4 Significance to hominin evolution and habitat preference

The results show that although climate changes were subtle, they influenced the existence of variable vegetation components, specifically wooded patches and wetland environments that were heterogeneous in the Olorgesailie Basin. Specifically, the density of woody cover varied temporally and spatially and there was evidence of a habitat mosaic that included wetland ecosystems. As suggested earlier, this vegetation complexity, in turn, would provide different resources and also different challenges that may have influenced hominin occupation and behaviour during the Pleistocene period. This is evidenced by the occurrence of clusters of high stone tools concentration and barren areas where artefacts are rare to absent (Potts *et al.*, 1999; 2004; Brooks *et al.*, 2007). This pattern can be explained best by the variability selection hypothesis (Potts, 1998) which suggests that hominins deliberately exploited the landscape depending on the available resources. Consequently, this led to the evolution of hominin behaviour and more specifically their interactions with the past complex environments (Potts, 1998; Bobe *et al.*, 2002; Ashley *et al.*, 2010a; Barboni *et al.*, 2010).

Vegetation heterogeneity across the Olorgesailie palaeolandscapes would have offered crucial resources such as fresh water and raw materials as suggested by Owen *et al.*, (2008) and which the

current study confirms. Hence, the basin offered ideal hominin habitats comparable to those of the Olduvai Gorge in Tanzania (Sikes, 1994; Ashley, 2009). Further studies suggest that the vegetation cover supported mega fauna as indicated by the fossil remains of both browsers and grazers excavated from the site which included: *Elephas reckii* (extinct elephants), *Theropithecus oswaldii* (extinct primate) and *Equus oldowanyensis* (extinct zebra) whose expected habitats are wooded/riverine vegetation and tall grasslands (Bobe *et al.*, 2002; Bobe and Behrensmeyer, 2004).

These fauna may have influenced the behaviour of hominins and their interaction with a spatially heterogeneous environment, due to possible threats in terms of competition for resources and/or predation. This may mean that that the hominins only foraged for resources in the localities where there are high concentrations of stone tools and perhaps sought shelter elsewhere, within the uplands, as suggested by Potts *et al.*, (2004).

CHAPTER EIGHT: SUMMARY AND CONCLUSIONS

8.1 INTRODUCTION

The thesis examined the potential of phytolith analysis as a palaeocological tool by analysing the affiliation of modern phytolith analogues to an altitudinal gradient, through multivariate statistical analyses. This approach identified phytolith morphotypes associated with different vegetation components, as well as key phytolith morphotypes that have a strong taxonomic affinity with their parent plants. Using the modern phytolith analogue to assist interpretation, vegetation changes were reconstructed both temporally and spatially. Grassland, woody and riverine elements were identified in the fossil assemblages. Furthermore, selected grass short-cell phytoliths were used to compute climatic and aridity indices. These were then used to interpret climatic changes in the Olorgesailie Basin through the mid-late Pleistocene (~746-64 ka) as well as temporal and spatial heterogeneity of the vegetation. The results of this analysis were discussed in relation to the significance of the past environments influence on hominin behaviour and their habitat preference in the southern Rift Valley of Kenya.

8.2 Modern phytolith analogue

8.2.1 Modern phytolith analogue from plants growing along altitudinal gradient

The modern phytolith analogue did not distinguish between different plants along an altitudinal gradient. This concurs with recent research undertaken from Miombo woodland in Mozambique (Mercader *et al.*, 2011). Future research needs to reconsider the analyses of grass short-cell phytoliths derived from all grass sub-families, which show a strong relationship with ecological parameters (e.g. Rossouw, 2009). The current study lacked the representation of C₃ Pooideae grasses in the modern plants that were analysed and this could have contributed to this setback.

8.2.2 Relationship between phytolith morphotypes and vegetation types

Correspondence analysis of modern phytolith assemblages distinguished three main vegetation components: grasslands, woody and herbaceous taxa and aquatic taxa. Additionally, descriptive analysis of grass short-cell phytoliths identified different morphotypes as key indicators of specific grass sub-families (Twiss *et al.*, 1969; Piperno and Pearsall, 1998; Piperno, 2006; Bremond *et al.*, 2008; Mercader *et al.*, 2010), (see table 8.1).

Table 8.1 Summary table of main morphotype categories of significance in this study plus references to the morphotypes described and corresponding environmental significance.

Dominance of phytolith Morphotypes in an assemblage	Vegetation types/ grass components	Environmental/Climatic conditions
<i>Spheroid variants, silica skeletons, ellipsoids, schlereid, tracheids, parallelepiped and irregular forms & verrucate</i>	Woody and herbaceous vegetation	Not specified (Albert, 1999; Albert and Weiner, 2001; Mercader <i>et al.</i> , 2009; 2011)
<i>Bilobates outer margin concave short/long shaft bilobates outer margin convex short shaft, quadralobate, polylobates, tower horned</i>	Grasslands dominated by Panicoideae C ₄ grasses	Warm and moist climates (Twiss <i>et al.</i> , 1969; Piperno and Pearsall, 1998; Barboni and Bremond, 2009; Mercader <i>et al.</i> , 2010)
<i>Bilobate convex outer margin long shaft, saddle plateau</i>	Grasslands dominated by Aristidoideae C ₄ grasses.	Hot and dry climates, mainly on open eroded places. (Ibrahim and Kabuye 1987); Piperno and Pearsall, 1998; Piperno, 2006; Rossouw, 2009)
<i>Saddle, saddle squat, bilobates outer margin flattened short/long shaft</i>	Grassland dominated by Chloridoideae C ₄ grasses	Hot and dry climates. (Twiss <i>et al.</i> , 1969; Piperno and Pearsall, 1998; Barboni and Bremond, 2009; Rossouw, 2009; Mercader <i>et al.</i> , 2010)
<i>Saddle ovate, tower flat,</i>	Grasslands dominated by Arundinoideae grasses	Moist environments-Aquatic environments (Rossouw, 2009; Mercader <i>et al.</i> , 2010)
<i>Papillae, achene</i>	Vegetation dominated by Cyperaceae	Aquatic environment (Haines and Lye, 1983; Ollendorf, 1992; Albert <i>et al.</i> , 2006)

Correspondence analysis successfully grouped major phytolith categories into their respective vegetation types: grasslands and woody & herbaceous types, including sedges which are moisture-loving elements often associated with riparian or aquatic habitats. The main axis predicted moisture as the major environmental factor influencing the association and groupings of phytolith morphotypes and modern plants in ordination space. Cluster analysis identified the taxonomic affiliation of unique morphotypes to their respective taxa; Papillae (PAPL) types are strongly identified with the Cyperaceae, saddle type (SAD) with the Chloridoideae C₄ grasses, bilobate concave outer margin short shaft (BCOMSS) & Tower horned (TWHN) with Panicoideae C₄ grasses, bilobate convex outer margin long shaft (BCXMLS) with Aristidoideae C₄ grasses and saddle ovate (SADO) and tower flat (TWF) with Arundinoideae C₃ grasses (refer to figs 5.3 & 5.4).

Although it is not possible to identify plants to the genus level using phytoliths, an accurate identification of the dominant vegetation e.g. grassland or woodland may be achieved by recording the dominance of the “variable morphotypes” (e.g. spheroid variants, ellipsoid variants, tracheids, schlereids and irregular variants). This makes phytoliths a useful proxy for palaeoecological

investigations into landscape change. Using this approach one is able to distinguish closed-canopy vegetation cover from open-canopy vegetation cover. This, in turn, can provide palaeoanthropological insight into how early hominins interacted with their environment.

8.3 Fossil assemblages

8.3.1 Phytolith-based vegetation history of the Olorgesailie Basin

Using the modern phytolith analogue described above, to aid interpretation, fossil phytoliths derived from Palaeosols of the sedimentary profile of the Olorgesailie formation and the Olkesiteti and Oltepesi beds were used to investigate temporal changes in vegetation through the middle to late Pleistocene (~746~64 ka), probably in response to changes in climate. Evidence of climate oscillation between warm and moist, and dry and cold episodes has been inferred from fossil phytolith assemblages elsewhere, (see Deino and Potts, 1990; Potts *et al.*, 1999). These variable climates have been recorded elsewhere within East Africa during the Plio-Pleistocene period (Bobe and Behrensmeyer, 2004). During the mid-Pleistocene (900-600 ka) there was a dramatic expansion of open vegetation dominated by C₄ grasslands. These elements are thought to respond to increased aridity of the Mid-Pleistocene Revolution (MPR) (Scheuffß *et al.*, 2003).

Fossil phytolith assemblages showed that vegetation cover was highly dominated by moisture-loving tall grasses, belonging to the Arundinoideae C₃ and Panicoideae C₄ grass sub-families. Also present are phytoliths from woody and non-grass herbaceous taxa which indicated wooded vegetation. Vegetation cover during the mid-late-Pleistocene therefore differed from contemporary vegetation which is comprised predominantly of short grasslands belonging to the C₄ Chloridoideae and Aristidoideae grass sub-families that thrive well under hot and dry climates. The occurrence of palm and Cyperaceae morphotypes indicates the presence of wetland/marshy environments (Albert *et al.*, 2009).

However, the occurrence of woody and herbaceous morphotypes is not consistent throughout the sequence, and their absence at some points in the palaeorecord suggests some degree of variability in environmental conditions, specifically more arid and/or hot periods when aquatic taxa declined. This is consistent with the relative dominance of moisture-loving grasses versus arid grasses and, the increase/decrease of riverine elements in the sequence suggesting environmental and/or climatic variability from time to time. Similarly, limnological research from the Olorgesailie palaeolake basin suggested variation in the composition and abundance of freshwater versus saline diatom flora, as a result of variation in precipitation during the Pleistocene (Owen *et al.*, 2008).

8.3.2 Phytolith indices

The climate and aridity indices suggested that warm and moist climates predominated in the Olorgesailie Basin during the mid-late Pleistocene period (~746-64 ka). The well recorded cold (glacial period) episode may have not impacted greatly on the vegetation in the basin, although the presence of Pooideae grasses in the fossil assemblage may be indicative of cooler climates than were present within the basin and the surrounding environments during the mid-late Pleistocene.

Climate index (Ic) showed insignificant changes throughout the Pleistocene, the average values are considerably low (see fig 6.1) suggesting warm climates. This is because temperature is much less variable over time in the tropics than in higher latitudes, where changes in temperature over time in the tropics is negligible, unlike in higher latitudes, where changes in temperature throughout the Pleistocene would be more significant.. The aridity index (Iph) is more significant in the tropics since C₄ grasslands have been prominent in the region throughout the Pleistocene.

D/P^o index is a valuable proxy to determine tree cover density represented in a fossilized phytolith assemblage. This study showed closed vegetation structure existed between ~662-340 ka in the Olorgesailie Basin (see fig 6.2). Thereafter open vegetation structure dominated with grasslands has been in existence up to present.

8.3.3 Spatial vegetation heterogeneity in the Olorgesailie Basin

Fossil phytolith assemblages from ~340 to ~220 ka show subtle changes in vegetation cover over time. Phytoliths from woody and herbaceous taxa were found in different times and spaces during the mid-Pleistocene (~340-220 ka) in the Olorgesailie Basin, suggesting a heterogeneous vegetation assemblage with patchy and varying woody cover. The heterogeneity in vegetation cover across the landscape is largely controlled by topography and local hydrology in the region which is superimposed on regional climate, since evidence of different elements are found in the same time period. Our findings are best explained in terms of a vegetation mosaic, comprised of grasslands and riverine/riparian elements. This scenario still exists today.

8.3.4 Palaeoenvironments of early hominins in the Olorgesailie Basin

Phytolith data show that mixed grasslands persisted throughout the mid- Pleistocene in these environments and they were probably dominated by C₃ Arundinoideae and C₄ Panicoideae grasses, as indicated by the high and consistent occurrence of rondel, saddle ovate, bilobates and quadralobate categories in the palaeosol sequence. The mixed vegetation structure of both C₃ and C₄ components has a long history of dominance in the basin, as indicated by evidence from stable isotopes analyses (Sikes *et al.*, 1999). Furthermore, the current study shows that elements of arid short (C₄ Aristidoideae & Chloridoideae) and cool (C₃ Pooideae) grasses remained rare.

The significant presence of both C₄ and C₃ grasses during the mid- Pleistocene suggests the existence of varied habitats that were controlled by different climatic conditions and local hydrological and topographic conditions. Furthermore, the occurrence of palm and sedge phytoliths suggests that wetland environments and fresh water sources (Albert *et al.*, 2009; Barboni *et al.*, 2010) were present in the region. The presence of such heterogeneous habitats is ideal for early hominins especially in terms of the availability of crucial resources (e.g. raw materials, fresh water and nutritionally important tubers) (Ashley *et al.*, 2009). This finding is in accordance with the remains of extinct mega fauna that have been excavated in association with KNM-OL 45500, including *Theropithecus oswaldii* (wooded inhabitants), *Equus sp.* (Grazers), *Otomys sp.* (inhabit thick wet grasslands), suid and elephantid (browsers), (Potts *et al.*, 2004) which suggests that more woody elements were present in the landscape than is the case today.

Therefore, the hominins that occupied the Ologesailie Basin during the mid-late Pleistocene interacted mostly with open environments dominated by grasslands and occasional woody and herbaceous plants. These environments offered crucial resources like fresh water and food resources, and heterogeneous vegetation cover, making it possible for the hominins to exploit these resources differentially across the landscape. Such habitats may also have posed threats from other competitors and predators. While hominins might have been forced to forage within these localities, they might also have been able to seek refuge in the uplands as hypothesized² by Potts *et al.*, (2004). The dense concentration and distribution pattern of the Acheulean artefacts preserved across the landscape which is juxtaposed with relative scarcity of hominin remains (Potts, 1994; Potts *et al.*, 1997; 2004) supports this view.

8.3.5 Strengths and limitations

The analyses and interpretation of the phytolith data from the Ologesailie Basin has offered great potential in determining the vegetation cover during mid-late Pleistocene environments, both temporally and spatially. This palaeoenvironmental reconstruction, which is based directly on the evidence from plant microfossils, fills a gap that has not previously been fully addressed due to poor preservation of other organic plant fossils, particularly fossil pollen. The data interpretation was based on the published radiometric dates for geological markers directly or indirectly bracketing the palaeosols analysed.

The relative dates used, therefore, were a major limitation to accurately reconstruct the chronology of the palaeosols analysed due to the limited availability of radiometric age determinations, rendering a

² Acheulean toolmakers entered the lowland to obtain food and water and left numerous stone tools there, but died primarily in non-burial upland contexts.

more precise chronology elusive. Accordingly, the conclusions presented in this chapter are based on the available dates.

8.3.6 Directions for future research

Obtaining accurate chronology of the palaeosol layers studied in this project would be necessary to provide a clearer picture of the timing of major vegetation changes in the southern rift, which is a critical region for understanding human evolution. A more finely resolved chronology would enable closer correlation with other published palaeoclimate and palaeoecological data from East Africa, where the analysis of sediments from the east African lakes has yielded data on climate change and vegetation.

8.4 Summary

The analysis of fossil phytoliths as a sole proxy to reconstruct vegetation and palaeoenvironments remains underutilised in East Africa. The current study establishes a region-based modern phytolith analogue for the southern rift region that can be used and developed in the future, as phytolith work progresses. The modern analogue reference collection which will be based at the National Museums of Kenya is a tangible output from this study that will be a guide for future palaeoenvironmental reconstruction.

This study demonstrates the invaluable strength of phytolith analysis as a palaeoecological tool in arid and semi-arid regions, where the preservation of organic plant remains is the biggest challenge. This is of particular relevance to other prehistoric sites in East Africa (except for the Olduvai Gorge where extensive phytolith work has been undertaken). Developing a regionally-based modern analogue has increased the knowledge of the correlation between phytolith morphotypes, vegetation components and the associated ecological and climatic conditions, especially the grass short-cell phytoliths, which played a significant role in determining the palaeoclimate of the Ologesailie Basin during the mid-late Pleistocene.

Understanding the vegetation component of the past environments of the Ologesailie Basin has added value to the knowledge of early hominin behaviour and their interactions with the surrounding environments. Analyses of fossil phytoliths from palaeosols of dated lithostratigraphic layers in the Ologesailie Basin provided evidence of variable vegetation cover that was dominated by both C₃ and C₄ moisture indicator grasslands during the mid-late Pleistocene (~746-64 ka). Moist and warm environments prevailed during this period though there were periods of aridity (~746-662 ka) when woody and fresh water elements became scarce.

Vegetation cover varied both temporarily and spatially. The temporal variation was mainly due to variation in precipitation, while heterogeneity across the landscape was mainly influenced by local topography and hydrology that created microhabitats for wetland and riparian/riverine vegetation elements.

The significance of this study to hominin evolution and habitat preference is that it provides crucial information on the vegetation component of the surrounding environment, with which pre-modern humans interacted. This further explains the possibility that the basin offered a variety of resources but also threats to early hominins thus influencing their behaviour across the broader landscape; especially forest resources would have attracted the settlement of early hominins in the Basin.

References

- Agnew, A.D.Q., and Agnew, S., 1994. *Upland Kenya Wild Flowers. A Flora of the Ferns and Herbaceous Flowering plants of Upland Kenya*. Pp.374. East Africa Natural History Society, Nairobi.
- Albert, R.M., 1999. *Study of Ash Layers through Phytolith Analyses from the Middle Palaeolithic levels of Kebara and Tabun Caves*. PhD dissertation, (Faculty of Geography and History, University of Barcelona, Spain.). Pp 227.
- Albert, R.M., and Weiner, S., 2001. Study of phytoliths in prehistoric ash layers from Kebara and Tabun caves using a quantitative approach. In: Meunier, J.D., Colin, F. (Eds.), *Phytolith: Applications in Earth sciences and Human History*. A.A Balkema Published, Lisse, Pp. 251-266.
- Albert, R.M., Weiner, S., Bar-Yosef, O. and Meignen, L., 2000. Phytoliths in the Middle Palaeolithic deposits of Kebara Cave, Mt, Carmel, Israel: study of the plant materials used for fuel and other purposes. *Journal of Archaeological Science* **27**: 931-947.
- Albert, R.M., Bamford, M.K. and Cabanes, D. 2006. Taphonomy of Phytolith and macroplants in different soils from Olduvai Gorge (Tanzania) and the application to Plio-Pleistocene Palaeoanthropological samples. *Quaternary International* **148**:78-94.
- Albert, R.M., Bamford, M.K., and Cabanes, D., 2009. Palaeoecological significance of palms at Olduvai Gorge, Tanzania, based on Phytolith remains. *Quaternary International* **193**: 41-48.
- Alexandre, A., Meunier, J.-D., Lézine, A.-M., Vincens, A. and Schwartz, D. 1997. Phytoliths: indicators of grasslands dynamics during the late Holocene in intertropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **136**: 213-229.
- Alexandre, A. and Brémond, L. 2009. Comment on the Paper in Quaternary International: "Methodological concerns for Analysis of phytolith assemblages: Does count size matter?" (C.A.E. Strömberg). *Quaternary International* **193**: 141-142.
- Asani, G.C., and Kinuthia, J.H. 1979. *Diurnal variation of Precipitations in East Africa-Nairobi, Kenya*. Metrological Department Research Report, 8.

- Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S. And Suwa, G. 1999. Australopithecus garhi: A New Species of Early Homind from Ethiopia. *Science* **289**: 629-635.
- Ashley, G. M., Tactikos, J.C., Owen, R.B. 2009. Hominin use of trees and wetlands: Paleoclimate and archaeology records from Olduvai Gorge (1.79-1.74 Ma). *Palaeogeography, Palaeoclimatology, Palaeoclimatology* **272**: 1-16
- Ashley, G.M., Barboni, D., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Diez-Martin, F., Barba, R. and Baquedano, E. 2010a. A Spring and wooded habitats at FLK Zinj and their relevance to origins of Human behaviour. *Quaternary Research* **74**(3): 304-314
- Ashley, G.M., Barboni, D., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Diez-Martin, F., Barba, R. 2010b. Paleoenvironmental and Paleoecological reconstruction of a fresh water oasis in Savannah grasslands at FLK North, Olduvai Gorge Tanzania. *Quaternary Research* **74** (3): 333-343
- Bamford, M.K., Albert, R.M., and Cabanes, D. 2006. Plio-Pleistocene macroplant fossil remains and phytoliths from Lowermost Bed II in the eastern palaeolake margin of Olduvai Gorge, Tanzania. *Quaternary International* **148**:95-112
- Barboni, D., Bonnefille, R., Alexandre, A. and Meunier, J. D.1999. Phytoliths as paleoenvironmental indicators, West Side Awash Valley, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoclimatology* **152**: 87-100.
- Barboni, D., Bremond, L. and Bonnefille, R. 2007. Comparative study of modern phytolith assemblages from inter-tropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoclimatology* **246**: 454-470.
- Barboni, D. and Bremond, L. 2009. Phytoliths of East African grasses: An assessment of their environmental and taxonomic significance based on floristic data. *Review of Palaeobotany and Palynology* **158**: 29-41.
- Barboni, D., Ashley, G.M., Dominguez-Rodrigo, M. and Bunn, H.T., Mabulla, A. Z.P and Baquedano, E. 2010. Phytoliths infer locally dense and heterogeneous paleovegetation at FLK North and surrounding localities during upper Bed I time, Olduvai Gorge, Tanzania. *Quaternary Research* **74**: 344-354
- Baker, B.H. and Mitchel, J.G. 1976. Volcanic stratigraphic and geochronology of the Kedong-Olorgesailie area and evolution of the South Kenya rift valley. *Journal of Geological Society London* **132**:467-484.

- Beentjie, H.J., 1994. *Kenya Trees, Shrubs and Lianas*. National Museums of Kenya, Nairobi, Kenya. Pp. 722.
- Behrensmeyer, A.K., Todd, N.E., Potts, R. and McBrinn, G.E 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* **278**: 1589-1594
- Behrensmeyer, A.K., Potts, R., Deino, A. and Ditch field, P. 2002. *Ologesailie, Kenya: a million years in the life of a rift basin*. In Renault, R.W. and Ashley, G. (Eds.), *Sedimentation in continental rifts*. SEPM Specl. Publication, **73**:99-106.
- Behrensmeyer, A.K., Potts, R. and Deino, A. 2007. Cycles of erosion and deposition in the Pleistocene Ologesailie Basin of southern Kenya and their impact of paleoanthropological record. Abstract with programs, *Annual Meeting of the Geological society of America*, vol. **125** (2): 343.
- Behrensmeyer, A.K. 2010. *Revised Report on Locality B stratigraphy and Age relationship*. Unpublished field report Pp5.
- Bergner, A, G.N. and Trauth, M.H.2004. Comparison of the hydrologic and hydrochemical evolution of lake Naivasha (Kenya) during three highstands between 175 and 60 kyr BP. *Palaeogeography, Palaeoclimatology, Palaeoecology* **125**: 17-36.
- Bergner, A.G.N., Trauth, M.H. and Bookhagen, B. 2003. Magnitude of precipitation/evaporation changes in the Naivasha Basin (Kenya) during the last 150kyrs. *Global Planetary Change* **36**:117-135.
- Bergner, A.G.N., Loutre, M.F. and Mélice, J.L. 2006. Equatorial insolation: from precession harmonics to eccentricity frequencies. *Clim. Past* **2**:131-136.
- Bergner, A.G.N., Strecker, M.R., Trauth, M.H., Deino, A., Gasse, F., Blisniuk, P. and Dühnforth, M. 2009. Tectonic and climatic control on evolution of rift lakes in the Central Kenya Rift, East Africa. *Quaternary Science Reviews* **28**:2804-2816.
- Birks, H.J.B., and Gordon, A.D. 1985. *Numerical methods in Quaternary Pollen Analysis*. Academic Press, London.
- Blinnikov, M. Busacca, A. and Whitlock, C. 2002. Reconstruction of the Late Pleistocene Grassland of the Columbia Basin, Washington, USA, Based on Phytolith Records in Loess. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177**:77-101.

- Blumenshine, R.J., Masao, F.T. 1991. Living sites at Olduvai Gorge, Tanzania? Preliminary landscape archaeology results in the basal Bed II lake margin zone. *Journal of Human Evolution* **21**: 451-462
- Bobe, R., Behrensmeyer, A.K. and Chapman, R. 2002. Faunal Change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution*. **42**. 475-497.
- Bobe, R. and Behrensmeyer, A. K. 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeography, Palaeoclimatology, Palaeoecology* **207**: 399-420.
- Bonnefille, R. 1995. A reassessment of the Plio-Pleistocene pollen record of East Africa. In: Vrba, E.S., Denton, G.H., Partridge, T.C. and Burce, L.H. (eds.): *Paleoclimate and Evolution with Emphasis on Human Origins*. New Haven: Yale University press. Pp 299-310.
- Bonnefille, R. and DeChamps, R. 1983. *Data on fossil flora*. In J de Heinzelin (ed.): *The Omo group: Archives of the International Omo Research Expedition*. Tervuren: Musée Royal de l'Afrique Centrale, pp191-207.
- Bonnefille, R. and Riollet, G. 1987. *Palynological spectra from the upper Laetoli Beds*. In Leakey, M.D. and Harris, J.M (eds.): *Laetoli: A Pliocene site in Northern Tanzania*. Oxford: Clarendon pp 52-61.
- Bozarth, S.R. 1992. *Classification of Opal Phytoliths Formed in Selected Dicotyledons Native to the Great Plains*. In: Rapp, G. Jr. and Mulholland, S.C. 1992. *Phytolith Systematics, Emerging Issues: Advances in Archaeological and Museum Science* **1**:193-214.
- Bozarth, S.R. 1993. Biosilicate Assemblages of Boreal forests and Aspen Parklands. In: Pearsall, D.M. and Piperno, D.R. *Current Research in Phytolith Analysis: Applications in Archaeology and Paleoecology* Pp. 95-105.
- Bremond, L., Alexandre, A., Hély, C., and Guiot, J. 2005a. A Phytolith index as a proxy of tree cover density in tropical areas: calibration with Leaf Area Index along a forest-savanna transect in southeastern Cameroon. *Global and Planetary Change* **45** (4). 277-293.
- Bremond, L., Alexandre, A., Hély, C., and Guiot, J. 2005b. Grass water stress estimated from phytoliths in West Africa. *Journal of Biogeography* **32**: (2). 311-327.

- Bremond, L., Alexandre, A., Wooller, M. J., Hély, C., Williamson, D., Schäfer, P. A., Majule, A. and Guiot, J. 2008. Phytolith indices as proxies of grass subfamilies on the East African tropical mountains. *Global and Planetary Change* **61**:209-224.
- Brooks, A., Behrensmeyer, A.K., Yellen, Y., Deino, A., Sharp, W., and Potts, R., 2007. After the Acheulean: stratigraphy, dating and archaeology of two new formations in the Olorgesailie basin, southern rift. *Paleoanthropology. Internet journal of the paleoanthropology Society*, P.A5
- Brown, D. 1984. Prospects and Limits of a Phytolith Key for grasses in the Central United States. *Journal of Archaeological Science*, **11**: 221-243.
- Brown, F., and Feibel, C.S., 1991. *Stratigraphy, depositional environments, and palaeogeography of Koobi Fora Formation*. In: Harris, J.M. (Ed.), Koobi Fora Research Project, Vol. **3**. Clarendon Press, Oxford, Pp1-30.
- Campisano, C.J. and Feibel, C.S. 2007. Connecting local environmental sequences to global climate patterns: evidence from hominin-bearing Hadar Formation, Ethiopia. *Journal of Human Evolution* **53**: 515-527.
- Cerling, T.E., Levin, N.E., Quade, J., Wynn, J.G., Fix, D.L., Kingstone, J.D., Klein, R.G. and Brown, F.H. 2010. Comment on the Paleoenvironments of *Ardipithecus ramidus*. *Science* **328**: 1105d. DOI:10.1126/science.1185274.
- Damnati, B. and Taieb, M. 1995. Solar and ENSO signatures in laminated deposits from lake Magadi (Kenya) during the Pleistocene/ Holocene transition. *Journal of African Earth Sciences* **21**(3): 373-382.
- Deino, A., and Potts, R. 1990. Single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Olorgesailie Formation, southern Kenya Rift. *Journal of Geophysical Research* **95**: 8453-8470.
- Deino, A. and Potts, R. 1992. Age-probability spectra for examination of single crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating results: examples from Olorgesailie, southern Kenya rift. *Quaternary International* **13-14**:47-53.
- deMenocal, P. 1995. Plio-Pleistocene African Climate. *Science* **270**:53-59.
- deMenocal, P.B., and Bloemendal, J. 1995. *Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvironment of hominid evolution: a combined data-model approach*.

- In: Vrba, E.S., Denton, G.H., Partridge, T.C., and Burkle, L. H. Eds. 1995. Paleoclimate and Evolution. Yale University Press, New Haven, Conn. Pp262-288.
- deMenocal, P.B. 2004. African Climate Change and Faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* **220**:3-24.
- Faegeri, K., and Inversen. 1975. *Textbook of Pollen Analysis*, 3rd ed. Blackwell, Oxford. 295Pp.
- Fahmy, A. G. 2008. Diversity of lobate phytoliths in grass leaves from Sahel region, West Tropical Africa: Tribe Paniceae. *Plant Systematics and Evolution* **270**: 1-23.
- Fahn, A. 1990. *Plant Anatomy* 4th edn, Oxford: Pergamon Press.
- Feibel, C.S., Harris, J.M. and Brown, F.H. 1991. *Palaeoenvironmental context for the late Neogene of the Turkana Basin*. In: Harris, J.M. (Ed.): Koobi-Fora Research project, Oxford: Clarendon. **3**: 321-370.
- Feibel, C.S. 1999. *Basin Evolution, sedimentary dynamics, and hominid habitats in East Africa*. In: Bromage, T.G. and Schrenk, F. (Eds.), African Biogeography, Climate Change and Human Evolution. Oxford University Press, Oxford, Pp.276-281.
- Fredlund, G.G. and Tieszen, L.T. 1994. Modern Phytolith Assemblages from the North American Great Plains. *Journal of Biogeography* **21**:321-335.
- Fredlund, G.G. and Tieszen, L.T. 1997. Calibrating Grass Phytolith Assemblages in Climatic Terms: Application to Late Pleistocene Assemblage from Kansas and Nebraska. *Palaeogeography, Palaeoclimatology, Palaeoecology* **136**:199-211.
- Greenacre, M.J. 1984. *Theory and Applications of Correspondence Analysis*. Academic press, London.
- Gregory, J.W. 1921. *The Rift Valleys and Geology of East Africa*. Seeley service, London.
- Grimm, E.C. 2007. *Tilia 1.01 and Tilia Graph*. Illinois State University, Illinois.
- Griffiths, J.F. 1958. Climatic Zones of East Africa. *East African Agricultural Journal* **23**:179-185.
- Griffiths, J.F. 1972. *Climates of Africa, World survey of Climatology*. **10**:313-347.
- Haines, R.W. and Lye, K.A. 1983. *The sedges and Rushes of East Africa. A Flora of the Families Juncaceae and Cyperaceae in East Africa-with a particular Reference to Uganda*. East Africa Natural History Society, Nairobi. Pp404.

- Hart, D.M. 1988. The plant Opal content in the vegetation and sediment of swamp at Oxford Falls, New South Wales, Australia. *Australian Journal of Botany* **36**: 159-170.
- Hill, I. D. 1973. "Algorithm AS 66: The Normal Integral" *Applied Statistics*, **22**:424-427
- Hills, R.C. 1978. The structure of the Inter-Tropical Convergence Zone in Equatorial Africa and its relationship to East Africa rainfall. *Transaction of the Institute of British Geographers*, New series **4 (3)**: 329-352.
- Honaine, M. F., Zucol, A. F. And Osterrieth, M. L. 2006. Phytolith Assemblages and Systematic Associations in Grassland species of South-Eastern Pampean Plains, Argentina. *Annals of Botany* **98**: 1155-1165.
- Ibrahim, K.M. and Kabuye, C.H.S. 1987. *An Illustrated Manual of Kenya Grasses*. Food and Agriculture Organisation of the United Nations. Rome, 1987. Pp765.
- Isaac, G. L.1978. *The Olorgesailie Formation: stratigraphy, tectonics and the paleogeographic context of the middle Pleistocene archaeological sites*. In: W.W. Bishop, Ed. Geological Background to Fossil Man: Pp173-206. Edinburgh: Scottish Academic Press.
- Isaac, G. L. 1977. *Olorgesailie, Archaeological studies of Middle Pleistocene Lake Basin in Kenya*. 272pp University of Chicago press.
- Kealhofer, L., Torrence, R. and Fullagar, R. 1999. Integrating Phytoliths within Use-Wear/Residue Studies of Stone Tools. *Journal of Archaeological Science* **26**:527-546.
- Kenworthy, J.M. 1966. Temperature conditions in the tropical highland climates in East Africa. *E. Afr. Geogr. Rev.* **4**:1-11.
- Kingstone, J.D., Marino, B.D. and Hill, A. 1994. Isotopic evidence for Neogene hominid palaeoenvironments in the Kenya Rift Valley. *Science* **264**:955-959.
- Kingstone, J.D., Deino, A.L., Edgar, R.K., Hill, A. 2007. Astronomically forced climate change in the Kenyan Rift Valley 2.7-2.55 Ma: implications for the evolution of early hominin ecosystems. *Journal of Human Evolution* **53**: 487-503.
- Kondo, R., Childs, C. and Atkinson, I. 1994. *Opal Phytoliths of New Zealand*. Manaaki Press, Lincoln, New Zealand.

- Leakey, M.G., Feibel, C.S., McDougall, I. and Walker, A.C. 1995. New four-million-year-old hominid species from Kanapoi and Allis Bay, Kenya. *Nature* **376**:565-571.
- Leakey, M.G., Feibel, C.S., Bernol, R.L., Harris, J.M., Cerling, T.E., Stewart, K.M., Storrs, G.W., Walker, A., Werdelin, L. and Winkler, A.J. 1996. Lothagam: A record of faunal change in the late Miocene of East Africa. *Journal of Vertebrate Palaeontology* **6**:556-570.
- Lee-Thorp, J., Sphonheimer, M. and Luyt, J. 2007. Tracking changing environments using stable carbon isotopes in fossils tooth enamel: an example from the South African hominin sites. *Journal of Human Evolution* **53**: 595-601.
- Lepš, J. and Šmilauer, P., 2003. *Multivariate Analysis of Ecological Data of Ecological Data Using CANOCO*. United Kingdom: University Press, Cambridge. Pp.269.
- Lepre, C.J., Quinn, R.L., Joordens, J.C.A., Swisher III, C.C. and Feibel, C.S. 2007. Plio-Pleistocene facies environments from the KBS Member, Koobi Fora Formation: Implications for climate controls on the development of lake-margin hominin habitats in the northeast Turkana Basin (northern Kenya). *Journal of Human Evolution* **53**:504-524.
- Livingstone, D.A and Clayton, W.D. 1979. An Altitudinal Cline in Tropical African Grass Floras and its Paleoecological Significance. *Quaternary Research*, 13: 392-402.
- Madella, M., Alexandre, A., and Ball, T. 2005. International Code for Phytolith Nomenclature 1.0. *Annals of Botany* **96**: 253-260.
- Marchant, R.A., Mumbi, C., Behera, S., and Yamagata, T. 2006. The Indian Ocean Dipole- the unsung driver of climatic variability in East Africa. *African Journal of Ecology* **45**: 4-16
- Maslin, M. A., and Christensen, B., 2007. Tectonics, orbital forcing, global climate change, and human evolution in Africa: introduction to the African paleoclimate special volume. *Journal of Human Evolution* **53**: 443-463.
- Maslin, M.A., and Trauth, M.H., 2009. *Plio-Pleistocene east African pulsed climate variability and its influence on early human evolution, in "the first humans-origins of the genus Homo"*. In: Grine, F.E., Leakey, R.E., Fleagle, J.G. (Eds.), *Vertebrate, Paleobiology and Paleonthropology Series*. Springer Verlag, Pp. 151-158.

- Mercader, J., Runge, F., Vrydaghs, L., Doutrelepon, H., Ewango, C. E. N. and Tresseras, J. J. 2000. Phytolith from Archaeological Sites in the Tropical Forest of Ituri, Democratic Republic of Congo. *Quaternary Research* **54**: 102-112.
- Mercader, J., Bennett, T., Esselmont, C., Simpson, S. and Walde, D. 2009. Phytoliths in woody plants from the Miombo woodlands of Mozambique. *Annals of Botany* **104**(1): 91-113.
- Mercader, J., Astudillo, F., Barkworth, M., Bennett, T., Esselmont, C., Kinyanjui, R., Grossman-Laskin, D., Simpson, S. and Walde, D. 2010. Grass and Sedge phytoliths from Niassa, Mozambique. *Journal of Archaeological Science* **37** (8):1953-1967.
- Mercader, J., Bennett, T., Esselmont, C., Simpson, S., Walde, D. 2011. Soil phytoliths from miombo woodlands in Mozambique. *Quaternary Research* **75**: 138-150.
- Metcalf, C.R. 1960. *Anatomy of Monocotyledons. I. Gramineae*. Oxford, Clarendon Press: 731Pp.
- Moore, P.D. and Webb, J.A. 1978. *An Illustrated guide to pollen analysis*. Hodder and Stoughton, 133Pp.
- Mudelsee, M. and Statteger, K. 1997. Exploring the Structure of the Mid-Pleistocene revolution with advance methods of time-series analysis. *Geol. Rundsch.* **86**:499-511
- Mulholland, S.C. 1989. Phytolith shape frequencies in North Dakota grasses: A comparison to general patterns. *Journal of Archaeological Science* **16**: 489-511.
- Mulholland, S.C. and Rapp, G. Jr. 1992a. *Phytolith Systematic: An Introduction*. In: Rapp, G. Jr. and Mulholland, S.C. 1992. Phytolith Systematics, Emerging Issues: Advances in Archaeological and Museum Science **1**:1-13. Plenum Press, New York.
- Mulholland, S. C. and Rapp, G. Jr. 1992b. *A morphological classification of grass silica-bodies*. In Rapp, G. Jr. and Mulholland, S.C. 1992. Phytolith Systematic, Emerging Issues: Advances in Archaeological and Museum Science **1**:65-89. Plenum Press, New York.
- Mutai, C.C and Ward, M.N. 2000. East African rainfall and the tropical circulation/convection on interseasonal to interannual timescales. American Meteorological Society. *Journal of Climate* **13**:315-3939.
- Mworia, J., Dallmeijer, A. and Jacobs, B. 1988. Vegetation and Modern Pollen Rain at Olorgesailie, Kenya. *Utafiti* **1**(1): 1-22.

- Mworia-Maitima, J. 1997. Prehistoric fires and land-cover change in western Kenya: evidences from pollen, charcoal, grass cuticles and grass phytoliths. *The Holocene* **7-4**: 409-417.
- Mworia-Maitima, J. 1999. *Preliminary Report on Preservation status of Organic plant remains in Ologesailie basin*. Unpublished report at National Museums of Kenya.
- Nicholson, S.E. 1996. *A review of Climate Dynamics and Climate Variability in eastern Africa*. In: Johnson, T.C. and Odada, E.O. (Eds.) *The Limnology, Climatology and Paleoecology of the East Africa Lakes*. Gordon and Breach Publishers, The Netherlands.
- Ollendorf, A.L., Mulholland, S.C. and Rapp, G. Jr. 1988. Phytolith Analysis as a Means of Plant Identification: *Arundo donax* and *Phragmites communis*. *Annals of Botany* **61**:209-214.
- Ollendorf, A.L. 1992. *Toward classification Scheme of Sedge (Cyperaceae) Phytoliths*. In Rapp, G. Jr. and Mulholland, S.C. 1992. *Phytolith Systematics, Emerging Issues: Advances in Archaeological and Museum Science* **1**:91-111. Plenum Press, New York.
- Owen, R. B., Potts, R., Behrensmeyer, A. K. and Ditchfield, P. 2008. Diatomaceous sediments and environmental change in the Pleistocene Ologesailie Formation, southern Kenya rift Valley. *Palaeogeography, Palaeoclimatology, Palaeoecology* **269**: 17-37.
- Pearsall, D.M. 1989. *Paleoethnobotany: A Handbook of Procedures*. Academic Press, San Diego.
- Pearsall, D.M. and Dinan, E.H. 1992. *Developing a Phytolith Classification System*. In Rapp, G. Jr. and Mulholland, S.C. 1992. *Phytolith Systematics: Emerging Issues, Advances in Archaeological and Museums Science* **1**:37-64. Plenum Press, New York.
- Peck, J.E. 2009. *Using PC-ORDTM for Multivariate Data Analysis*.
- Piperno, D.R. 1988. *Phytolith Analysis: An Archaeological and Geological Perspective*. Academic Press, San Diego. Pp 280.
- Piperno, D.R. 1989. The Occurrence of Phytoliths in Reproductive Structures of Selected Tropical Angiosperms and their Significance in Tropical Paleoecology, Paleoethnobotany, and Systematic. *Review of Palaeobotany and Palynology* **61**:147-173.
- Piperno, D.R., 1994. Phytolith and Charcoal Evidence for Prehistoric Slash-and-Burn Agriculture in the Darien Rain Forest of Panama. *The Holocene* **4**:321-325.

- Piperno, D.R. 2001. Phytoliths. In: Smol, J.P., Birks, H.J.B. and Last, W.M. Tracking (Eds.) *Environmental Change Using Lake Sediments. Terrestrial, Algal, and Siliceous Indicators*. Vol.3: 235-251. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Piperno, D.R. 2006. *Phytoliths: A Comprehensive guide for Archaeologists and Paleoecologists*. Pp238. Altamira Press, Oxford.
- Piperno, D.R., Bush, M.B. and Colinvaux, P.A. 1990. Paleoenvironments and Human Occupation in Late-Glacial Panama. *Quaternary Research* **33**:108-116.
- Piperno, D. R. and Pearsall 1998. The Silica Bodies of Tropical American Grasses: Morphology, Taxonomy, and Implications for Grass Systematics and Fossil Phytolith Identification. *Smithsonian Contributions to Botany*. **5**. Pp 45.
- Piperno, D.R., Holst, I., Wessel-Beaver, L. and Andres, T.C. 2002. Evidence for the Control of Phytolith Formation in *Curcubita* Fruits by the Hard Rind (*Hr*) Genetic Locus: Archaeological and Ecological Implications. *Proceedings of the National Academy of Sciences USA* **99**:10923-10928.
- Potts, R.1989. Olorgesailie: new excavations and findings in Early and Middle Pleistocene contexts, southern Kenya rift Valley. *Journal of Human Evolution* **18**: 477-484.
- Potts, R. 1994. Variables versus models in early Pleistocene hominid land use. *Journal of Human Evolution*. **27**: 7-24.
- Potts, R., 1996. Evolution and climate variability. *Science* **273**: 922-923.
- Potts, R. 1998. Environmental Hypotheses of Hominin Evolution. *Yearbook of Physical Anthropology* **41**:93-136.
- Potts, R. 2002. Complexity and Adaptability in Human Evolution. In: Goodman, M. and Moffat, A.S. (Eds.) 2002. *Probing Human Origins*, pp 33-57.
- Potts, R., 2007. *Environmental context of Pliocene human evolution in Africa*. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K. (Eds.), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence*. Springer, New York, pp. 25–48.
- Potts, R., Ditchfield, P., Hicks, J. and Deino, A.1997. Paleoenvironments of late Miocene and early Pliocene strata of Kanam, western Kenya. *American Journal of Physical Anthropology* **24**:188-189.

- Potts, R., Behrensmeyer, A. K., and Ditchfield, P. 1999. Paleolandscape variation and Early Pleistocene hominid activities: Members 1 and 7, Olorgesailie Formation, Kenya. *Journal of Human evolution* **37**: 747-788.
- Potts, R., Behrensmeyer, A.K., Deino, A., Ditchfield, P., and Clark, J. 2004. Small Mid-Pleistocene Hominin Associated with East African Acheulean Technology. *Science* **305**: 75-78.
- Quinn, R.L., Lepre, C.J., Wright, J.D. and Feibel, C.S. 2007. Paleogeographic variations of pedogenic carbonate ^{13}C values from Koobi Fora, Kenya: implications for floral compositions of Plio-Pleistocene hominin environments. *Journal of Human Evolution* **53**: 560-573
- Rapp, G. Jr., and Mulholland, S.C. 1992. *Phytolith Systematics: Emerging Issues. Advances in Archaeological and Museums Science*. Plenum Press, New York. Pp 350.
- Rogers, M.J., Feibel, C.S. and Harris J.W.K. 1994. Changing Patterns of land use by Plio-Pleistocene hominids in the Lake Turkana Basin. *Journal of Human Evolution* **27**: 139-158.
- Rosen, A.M. 1992. *Preliminary Identification of Silica Skeletons from Near Eastern Archaeological Sites: An Anatomical Approach*. In: Rapp, G. Jr., and Mulholland, S.C. 1992 (Ed) *Phytolith Systematic: Emerging issues, Advances in Archaeological and Museum Science*. Plenum Press, New York 1: 129-147.
- Rossouw, L. 2009. *The application of fossil grass-phytolith analysis in the reconstruction of Cainozoic environments in the South African interior*, PhD dissertation, (Faculty of Natural and Agricultural Sciences, University of the Free State, Bloemfontein) Pp 329.
- Rovner, I. 1971. Potential of Opal Phytoliths for use in Paleoecological Reconstruction. *Quaternary Research* **1**:343-359.
- Ruff, C.B. and Walker, A., 1993. *Body size and body shape*. In: Walker, A. and Leakey, R.E. (Eds.), *The Nariokotome Homo erectus Skeleton*. Harvard University Press, Cambridge. Pp.234-265.
- Runge, F. 1995. The Opal Phytolith for Use in Paleoecological Reconstruction in the Humid Tropics of Africa. *Zeitschrift für Geomorphologie N.F. supplementbände* **99**:53-64.
- Runge, F 1999. The Opal Inventory of Soils in Central Africa-Quantities, Shapes, Classification, and Spectra. *Review of Palaeobotany and Palynology* **107**:23-53

- Sansom, H.W. 1954. The climate of East Africa based on Thornthwaite's classification. *E.Afri. Meteorol. Dept. Mem.* **3**:1-49
- Schefuß, E., Schouten, S., Jansen, J.H.F. and Sinninghe Damsté, J.S., 2003. Africa vegetation controlled by tropical sea surface temperatures in the mid-Pleistocene period. *Nature* **422**: 418-421.
- Scholz, C.A., Johnson, T.C., Cohen, A.S., King, J.W. Peck, J.A., Overpeck, J.T., Talbot, M.R., Brown, E.T., Kalindekaffe, L., Amoako, P.L.O. Lyons, R.P., Shanahan, T.M., Castañeda, I.S., Heil, C.W., Forman, S.L., McHargue, L.R., Beuning, K.R., Gomez, J. and Pierson, J. 2007. East African megadroughts between 135 and 75 thousand years ago and on early-modern human origins. *National Academy of Science of USA (PNAS)* **104** (42): 16416-16421.
- Sikes, N.E., 1994. Early hominid habitat preference in East Africa: Paleosol carbon isotopic evidence. *Journal of Human Evolution* **27**:25-45.
- Sikes, N.E., Potts, R. and Behrensmeyer, A.K., 1997. Isotopic study of Pleistocene palaeosols from the Olorogesailie Formation, southern Kenya rift. *Journal of Human Evolution* **32**: A21-A21
- Sikes, N. E., Potts, R. and Behrensmeyer, A.K., 1999. Early Pleistocene habitat in Member 1 Olorogesailie based on palaeosol stable isotopes. *Journal of Human Evolution* **37**: 721-746.
- Sikes, N. E., and Ashley, G. M., 2007. Stable Isotopes of pedogenic carbonates as indicators of paleoecology in the Plio-Pleistocene (Upper Bed I), western margin of Olduvai Basin, Tanzania. *Journal of Human Evolution* **53**: 574-594.
- Somer, B.F. 2003. *A Late Pleistocene and Holocene phytolith Record, Lower Salmon River Canyon, Idaho*. Unpublished MA thesis, (Department of Anthropology, University of Alberta, Edmonton, Alberta). Pp 186.
- Strömberg, C.A.E., 2004. Using Phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* **207**:239-275
- Strömberg, C.A.E., 2009. Methodological concerns for analysis of phytolith assemblages: Does count size matter? *Quaternary International* **193**: 124-140.

- Thorn, V.C. 2004. Phytolith evidence for C₄-dominated grassland since the early Holocene at Long Pocket, northeast Queensland, Australia. *Quaternary Research* **61**:168-180.
- Tieszen, L.L., Senyimba, M.M., Imbamba, S.K. and Troughton, J.H. 1979. The distribution of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* **37**:337-350
- Trauth, M. H., Deino, A., and Strecker, M.R., 2001. Response of the East African climate to orbital forcing during the last interglacial (130-117 ka) and the early last glacial (117-60 ka). *Geology* **29**: 499-502.
- Trauth, M.H., Deino, A., Bergner, A.G.N., and Strecker, M. R., 2003. East African climate change and orbital forcing during the last 175kyr BP. *Earth Planetary Science Letters* **206**: 297-313.
- Trauth, M. H., Maslin, M.A., Deino, A. and Strecker, M. R. 2005. Late Cenozoic Moisture History of East Africa. *Science* **309**: 2051-2053.
- Trauth, M. H., Maslin, M., Deino, A., Strecker, M.R., Bergner, A.G.N., and Duhnforth, M., 2007. High-and low-latitude forcing of Plio-Pleistocene East African climate and human evolution. *Journal of Human Evolution* **53**: 475-486.
- Twiss, P.C., Suess, E. and Smith, R.M. 1969. Morphological Classification of Grass Phytoliths. *Soil Science Society of America Proceedings* **33**:109-115.
- Twiss, P.C. 1983. Dust Deposition and Opal Phytoliths in the Great Plains. *Transactions of the Nebraska Academy of Science* **11**:73-82.
- Twiss, C. 1992. *Predicted World Distribution of C₃ and C₄ Grass Phytoliths*. In: Rapp, G. Jr. and Mulholland, S.C. 1992. Phytolith Systematics, Emerging Issues Advanced in Archaeological and Museum Science **1**:113-128. Plenum Press, New York.
- Vrba, E.S., 1985. Environmental and evolution: Alternative causes of the temporal distribution of evolutionary events. *South Africa Journal of Science* **81**: 229-236
- Vrba, E.S., 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L. H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, Pp. 385-424.

- Vrba, E.S. 2000. Major features of Neogene mammalian evolution in Africa. In Partridge, T.C. and Maud, R.R. (Eds.) *The Cenozoic of Southern Africa*. Oxford University Press, New York, Pp. 277-304.
- Wallis, L.A. 2003. An Overview of Leaf Phytolith Production Patterns in Selected Northwest Australian Flora. *Review of Palaeobotany and Palynology* 125:201-248.
- Walter, R.C., Manega, P.C., Drake, R.E. and Curtis, G.H. 1991. Laser-Fusion $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Bed I, Olduvai Gorge, Tanzania. *Nature* **354**: 145-149.
- White, F., 1983. The vegetation Map of Africa- a Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. U.N. (Eds.). *Scientific and Cultural Organization*, Paris. **20**: Pp.356.
- White, T.D., 1995. African Omnivore: global climatic change and Plio-Pleistocene hominids and suids. In: Vrba, E. S. Denton, G.H., Partridge, T.C., Burckle, L. H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, Pp. 385-424.
- White, T.D., WoldeGabriel, G., Asfaw, B., Gilbert, H., Haile-Selassie, Y., Hart, W.K., Hlusko, L.J., Howell, F.C., Kono, R.T., Lehmann, T., Louchart, A., Lovejoy, C.O., Renne, P.R., Saegusa, H., Vrba, E.S., Wesselman, H. and Suswa, G. 2006. Asa Issie, Aramis and origin of *Australopithecus*. *Nature* **440**: 883-889.
- White, T.D., Ambrose, S.H., Suwa, G. And WoldeGabriel, G. 2010. Response to Comment on Paleoenvironments of *Ardipithecus ramidus*. *Science* **328**: 1105-e. DOI: 10.1126/science. 1185466.
- Winkler, A.J. 1995. Small mammals from the early Pliocene at Kanapoi, West Turkana, northern Kenya. *Journal of Vertebrate Palaeontology* 15(3): 60A.
- WoldeGabriel, G., White, T.D., Suwa, G., Renne, P., deHeinzelin, J., Hart, W.K. and Helken G. 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* **371**:330–333.
- WoldeGabriel, G., Ambrose, S.H., Barboni, D., Bonnefille, R., Bremond, L., Currie, B., DeGusta, D., Hart, W.K., Murray, A.M., Renne, P.R. Jolly-Saad, M.C., Stewart, K.M. and White, T.D. 2009. The Geological, Isotopic, Botanical, Invertebrate and Lower Vertebrate Surroundings of *Ardipithecus ramidus*. *Science* 326: 65e5. DOI:10.1126/science.1175812.

Appendix I: Plant species processed for modern phytolith reference

The table shows all the species processed and analysed for modern phytolith analogue. It includes plants family, photosynthetic pathway, genus-species name for the fully identified plant, plant's code, the %age occurrence of each phytolith morphotype category and their codes.

Family	C4/C3 pathway Species	Species code	P8	BUL	ON	CV	SCRP	PLVE	TRCD	SCLD	PSB	HWAS	HVEL	PHSP	SPEC	SPVE	SPPS	SPASC	ELVE
Cyperaceae	<i>Cyperus papyrus</i>	CYPAP	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0
Cyperaceae	<i>Cyperus spp.</i>	CYPsp1	7.9	0.0	0.0	12.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0
Cyperaceae	<i>Cyperus spp.</i>	CYPsp2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperaceae	<i>Cyperus spp.</i>	CYPsp3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperaceae	<i>Scleria boivinii</i>	SCLbov	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperaceae	<i>Cyperus spp.</i>	CYPsp4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperaceae	<i>Eleocharis spp.</i>	ELOCsp	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperaceae	<i>Cyperus sp.1</i>	CYPsp5	0.0	0.0	0.0	2.0	0.4	0.0	0.0	2.2	0.0	1.3	0.0	1.6	0.0	3.1	4.3	0.0	0.0
Poaceae	C4 <i>Aristida junceiformis</i>	ARISTjun	0.0	0.0	0.0	4.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Aristida sp1</i>	ARISTsp1	0.0	0.0	0.0	1.1	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Eragrostis racemosa</i>	ERAGRrac	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Sporobolus africanus</i>	SPOROafri	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Sporobolus consimilis</i>	SPOROcons	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Chloris virgata</i>	CHLORvir	0.0	0.0	43.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Cynodontea</i>	CYNODsp	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Eragrostis sp</i>	ERAGRsp	0.0	9.9	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Eragrostis sp1</i>	ERAGRsp1	1.7	0.9	0.0	0.6	24.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Chloris sp</i>	CHLORsp	0.0	0.0	0.0	0.3	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.6	0.0	0.0
Poaceae	C4 <i>Eragrostideae1</i>	ERAGRsp2	0.0	0.0	0.0	0.0	7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	0.0	0.0
Poaceae	C4 <i>Eragrostideae2</i>	ERAGsp3	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Eragrostideae3</i>	ERAGsp4	0.0	0.8	0.0	0.0	15.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.1	0.0	0.0
Poaceae	C4 <i>Bewisia biflora</i>	BEWSbi	0.0	1.2	28.1	17.4	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Dactyloctenium spp.</i>	DACTYsp	0.0	2.9	0.0	0.0	1.0	0.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Poaceae	C4 <i>Hyparrhenia spp.</i>	HYPARsp	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Schizachyrium jeffreysii</i>	SCHZjeff	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0
Poaceae	C4 <i>Melinis ambigua</i>	MELamb	0.0	1.7	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
Poaceae	<i>unknown</i>	UNKWN	11.0	2.3	0.0	2.3	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Melinis spp.</i>	MELspp	0.0	1.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.4	0.0	0.0
Poaceae	C4 <i>Coelorachis</i>	COELsp	0.0	0.0	0.0	0.0	48.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0
Poaceae	C4 <i>Pennisetum purpureum</i>	PENNpur	0.0	3.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Pennisetum polystachion</i>	PENNpol	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Melinis repens</i>	MELrep	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9	0.0	0.0
Poaceae	C4 <i>Themeda spp.</i>	THEMDsp	0.0	5.2	0.0	1.4	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Pennisetum polystachion</i>	PENNpol	0.0	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Brachyachne spp.</i>	BRACHNsp	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Hyparrhenia spp.</i>	HYPARsp1	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Schizachyrium spp.</i>	SCHIZspp	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Themeda spp.</i>	THEMDsp1	0.0	0.8	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Andropogon</i>	ANDRsp	0.0	20.9	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C4 <i>Digitaria spp.</i>	DIGsp	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	<i>unknown</i>	POA1	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	<i>unknown</i>	POA2	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	<i>unknown</i>	POA3	0.0	5.1	0.0	0.0	7.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	<i>unknown</i>	POA4	0.0	3.2	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	<i>unknown</i>	POA5	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Poaceae	<i>unknown</i>	POA6	0.0	0.0	0.0	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	<i>unknown</i>	POA7	0.0	0.7	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0
Poaceae	<i>unknown</i>	POA8	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	C3 <i>Phragmites mauritianus</i>	PHRAGmau	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0
Poaceae	C3 <i>Phragmites australis</i>	PHRAGaus	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
Acanthaceae	C3 <i>Barleria sp</i>	BARsp	0.0	3.5	0.0	0.0	1.6	0.0	0.0	1.0	0.0	1.0	0.0	0.0	0.3	6.8	5.2	0.0	0.0
Acanthaceae	C3 <i>Acanthus eminence</i>	ACANemn	0.0	1.1	0.0	0.2	2.5	0.0	2.5	0.5	0.0	0.0	0.0	2.5	4.1	9.5	2.7	0.0	0.0
Anarcadiaceae	C3 <i>Rhus natalensis</i>	RHUnat	0.0	0.0	0.0	0.0	0.3	0.0	2.1	0.0	7.2	0.8	0.0	3.1	1.5	0.0	52.3	1.8	2.3
Asteraceae	C3 <i>Vernonia brachaetis</i>	VERbra	0.0	4.2	0.0	3.3	0.0	12.5	0.0	11.7	0.0	0.0	0.0	0.0	0.0	2.5	0.0	2.5	0.0
Capparaceae	C3 <i>Capparaceae</i>	CAPPsp	0.0	0.0	0.0	0.0	2.0	0.0	0.7	7.2	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0	0.7
Mimosoideae	<i>Acacia sp1</i>	ACACsp1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
Papilionoideae	C3 <i>Indigofera sp.</i>	INDGsp	0.0	0.0	0.0	0.0	0.0	0.0	4.9	3.3	0.0	0.0	0.0	1.6	0.5	0.0	7.6	44.6	0.0
Papilionoideae	C3 <i>Crotalaria sp</i>	CROTsp	0.0	0.0	0.0	0.0	6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Malvaceae	C3 <i>Abutilon sp.</i>	ABTsp	0.0	42.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Moraceae	C3 <i>Ficus natalensis</i>	FICnat	0.0	0.0	0.0	0.0	0.3	0.0	1.0	0.0	0.8	2.8	5.1	1.5	0.0	0.8	5.6	0.0	0.0
Rubiaceae	C3 <i>Tarenna graveolens</i>	TARRgr	0.0	0.7	0.0	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	2.1	4.1	6.2	0.0
Rubiaceae	C3 <i>Rubus sp.</i>	RUBsp	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tiliaceae	<i>Grewia fallax</i>	GREWfa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix II: Names of phytolith morphotypes and their codes

Morphotypes names	Morphotypes
Bilobate panicoid type	BPT
Bilobate concave outer margin long shaft	BCOMLS
Bilobate concave outer margin short shaft	BCOMSS
Bilobate convex outer margin long shaft	BXOMLS
Bilobate convex outer margin short shaft	BXOMSS
Bilobate flattened outer margin long shaft	BFOMLS
Bilobate flattened outer margin short shaft	BFOMSS
Bilobate nodular	MN
Bilobate flared, short shaft	BFSS
Bilobate flared, long shaft	BFLS
Bilobate notched/flared outer margin long	BNFMLS
Bilobate notched/flared outer margin short	BNFMSS
Trapezoids polylobates	TPLY
Polylobate	PLY
Quadralobate crosses	QCR
Rondel	ROND
Saddle	SAD
Saddle long	SADL
Saddle ovate	SADO
Saddle plateau	SADP
Saddle squat	SADS
Tower flat	TWF
Tower horned	TWH
Tower wide	TWD
Epidermal short cell (Rondels)	EPDR
Epidermal Short cell(Saddles)	EPDS
Epidermal short cell (Bilobate)	EPIDB
b) Other morphotypes	
Scutiform/prickles	SCPR
Bulliform	BLL
Carinate	CR
Tracheids	TRCH
Sclereids	SCLD
Silica skeletons sensu lato	SSSL
Silica skeleton with spheroids/ellipsoids	SSPEC
Silica skeleton jigsaw puzzle	SSJP
Silica skeleton cylindroid cells sinuous	SSCCS
Honey comb assemblage	HYAS
Honeycomb elongates	HYE
Honey comb spheroids	HYSP
Spheroid echinate	SPEC
Spheroid verrucate	SPVE
Spheroid psilate	SPPS

Spheroid Colpate	SPCOL
Spheroid Scabrate	SPSCA
Ellipsoid verrucate	ELLVE
Ellipsoid scabrate	ELLSC
Ellipsoid polylobates	ELLPO
Ellipsoid Psilate	ELLPS
Long cell wavy/polylobates	LCWV
Papillae	PAPL
Achene	ACHN
Hair bases	HB
Hair	HR
Stomata	STMT
Tabular Crenate	TABCR
Parallepiped thin crenate	PPTCR
Parallepiped elongate verrucate	PPEV
Parallepiped facetate	PPFC
Parallepiped dendtric	PPDT
Parallepiped elongate indeterminates.	PPEL
Parallepiped blocky psilate round heads	PPBPR
Parallepiped blocky scabrate	PPBS
Parallepiped thin psilate	PPTP
Parallepiped elongate thin scabrate	PPELTS
Irregular Psilate	IRRPS
Irregular scabrate	IRRSC
Irregular verrucate	IRRVE
Irregular forms	IRRF
Indeterminable	INDT

Appendix III: Occurrence of various morphotypes categories in the fossil assemblage (Raw data).

Tilia #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Sample #	R35	R34	R33	R32	R31	R30	R29	R28	R27	R26	R25	R24	R15	R14	R13	R12'	R12	R11	R10	R 8	R 9	R18	R17	R16'	R16	R7	R6
Morphotype category																											
Tower wide (TWW)	11	13	8	5	7	14	6	13	5	20	26	40	10	9	7	22	15	40	18	15	13	2	9	17	10	30	24
Trapezoids Polylobate (TPLY)	0	0	0	0	0	0	0	0	3	1	0	7	5	4	0	3	8	8	2	0	0	0	0	6	1	1	3
Pooideae C3 grasses	61	139	39	27	25	43	15	70	66	28	120	147	104	114	34	131	194	119	97	26	70	36	55	73	72	104	123
Rondel (ROND)	50	126	31	22	18	28	8	57	58	7	92	100	89	101	27	106	171	70	77	11	57	34	46	50	61	73	96
Saddle ovate (SADO)	9	25	3	17	17	9	33	19	0	29	37	14	48	17	3	14	16	18	7	7	7	2	7	12	7	5	25
Tower flat (TWF)	11	7	0	13	3	13	5	1	9	12	32	17	6	5	0	6	4	14	6	0	9	0	8	10	9	1	9
Bilobate panicoid type (BPT)	19	24	1	45	11	29	9	14	11	11	36	17	10	32	2	42	16	23	46	12	3	3	0	1	15	24	6
Bilobate convex outer margin short shaft (BXOMSS)	42	106	21	49	31	34	29	46	46	15	64	128	74	88	11	151	172	60	53	36	27	11	8	25	81	59	41
Bilobate concave outer margin long shaft (BCOMLS)	3	11	0	21	5	1	6	6	0	6	24	8	9	10	0	10	11	27	7	0	3	0	0	0	2	3	3
Polylobate (PLY)	1	0	0	3	0	1	3	0	1	4	2	2	5	1	1	7	7	4	6	0	0	0	0	2	2	4	0
Tower horned (TWH)	10	19	6	5	12	19	10	16	6	23	33	20	18	5	7	9	16	28	12	12	15	0	13	10	9	8	9
Quadralobate crosses (QCR)	20	23	9	21	12	8	9	18	9	22	28	30	26	34	4	54	35	23	30	6	9	2	2	12	20	14	17
Bilobate concave outer margin short shaft (BCOMSS)	10	26	3	23	16	24	18	4	5	13	29	7	11	0	3	10	9	25	17	12	2	0	2	5	8	7	6
Saddle plateau (SADP)	7	36	8	27	13	29	10	15	2	17	45	38	7	23	8	25	27	18	15	4	6	3	7	14	14	17	19
Bilobate notched/flared outer margin long shaft (BNFMSS)	0	2	0	6	7	12	4	2	0	15	16	2	5	0	6	16	3	14	2	1	1	0	2	1	1	5	1
Bilobate convex outer margin long shaft (BXOMLS)	34	59	7	28	21	20	7	29	12	9	64	48	29	61	11	50	78	19	65	22	13	1	3	4	1	27	24
Saddle (SAD)	12	27	12	29	13	43	35	4	16	18	90	34	52	13	17	37	29	53	32	18	21	16	15	24	13	21	22
Saddle squat (SADSQ)	17	48	5	5	7	11	18	32	10	13	10	30	15	20	5	41	36	27	29	14	16	8	7	18	8	17	15
Bilobate flared, short shaft (BFSS)	14	18	0	45	19	22	3	2	6	0	24	16	4	1	0	5	17	14	22	6	1	2	0	2	1	6	4
Bilobate flared, long shaft (BFLS)	11	3	2	6	0	8	10	2	0	0	2	7	12	0	0	0	9	12	6	5	0	0	0	0	0	0	1
Bilobate flattened outer margin short shaft (BFOMSS)	52	53	12	68	26	47	29	26	17	18	66	51	60	81	29	77	71	67	66	28	10	8	6	17	28	34	29
Bilobate flattened outer margin long shaft (BFOMSS)	22	11	9	17	17	10	3	22	8	10	23	33	23	25	5	18	21	33	35	11	1	3	3	4	5	21	8
Bilobates indeter (BI)	22	14	4	22	8	4	2	10	1	9	14	5	6	8	2	5	7	15	8	2	0	1	0	4	0	8	5
Bilobate nodular (BN)	0	2	0	0	0	2	1	5	0	0	2	1	3	1	1	3	3	0	1	1	0	0	0	1	0	0	1
Scutiform/prickles (SCPR)	38	79	13	59	47	55	42	44	49	33	80	48	69	77	45	124	92	43	54	45	29	9	14	12	58	58	47
Bulliform (BLL)	8	13	5	13	8	10	8	7	8	7	28	25	23	21	8	21	12	10	14	19	20	32	10	13	16	26	
Tracheids/ Schlereids (TRCH)	3	4	4	26	9	26	13	2	4	19	27	11	13	5	9	3	2	24	9	11	7	17	7	7	5	7	15
Mesophyll (MEPL)	0	0	0	0	2	0	0	0	0	0	0	0	3	2	0	1	15	0	0	0	2	1	1	0	5	0	0
Spheroid echinate (SPEC)	15	8	19	2	3	11	5	9	2	7	6	13	33	41	22	24	18	5	12	13	28	9	26	34	20	29	15
Spheroid verrucate (SPVE)	5	0	3	3	7	1	0	1	2	18	9	4	6	2	2	0	4	0	1	20	1	2	4	0	4	1	6
Spheroid psilate (SPPS)	28	46	11	8	21	10	9	59	16	19	51	73	89	121	22	52	46	31	62	88	72	17	24	38	56	90	60
Spheroid Scabrate (SPSCA)	11	30	10	14	29	13	10	17	23	8	18	19	45	40	7	17	13	15	27	59	30	21	13	47	35	25	18
Ellipsoid verrucate (ELLVE)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0
Irregular verrucate (IRRVE)	6	5	5	3	21	1	2	5	2	5	11	7	9	1	12	4	10	3	3	29	2	39	2	17	3	3	4
Irregular forms (IRRF)	1	1	2	7	9	7	26	5	16	8	11	4	0	0	0	0	11	12	0	17	3	30	7	74	7	11	3
Silica skeletons sensu lato (SSSL)	0	1	3	3	6	0	0	0	2	0	5	1	0	0	3	3	1	1	0	1	0	2	1	0	0	0	2
Honey comb elongate Psilate (HYEP)	0	1	0	2	0	0	0	0	0	4	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Honey comb assemblage (HYAS)	0	0	0	0	5	1	0	0	4	0	1	2	0	0	1	0	4	3	3	0	0	0	0	0	1	3	1
Honeycomb elongates (HYE)	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Honey comb spheroids (HYSP)	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	4
Long cell Psilate (LCPS)	1	0	1	0	0	3	0	4	0	1	3	1	1	0	2	0	0	0	2	3	0	2	0	4	1	0	0
long cell sinuate (LCSI)	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Long cell dendritic (LCDE)	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Long cell verrucate (LCVE)	0	0	2	0	1	1	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	1	1	0	0	0	1
Parallelepiped elongate verrucate (PPEV)	0	0	0	0	0	0	0	0	2	2	1	3	4	2	0	0	1	1	0	0	0	1	0	24	0	3	5
Parallelepiped thin psilate (PPTP)	0	0	1	0	0	2	0	3	6	11	10	3	0	0	3	1	1	0	0	4	2	3	2	11	4	1	0
Parallelepiped elongate thin scabrate (PPETS)	3	7	5	25	4	16	4	3	5	8	16	22	12	13	2	1	3	10	3	4	2	4	15	32	3	6	16
Hair (HR)	8	2	10	1	0	0	0	1	0	1	10	1	8	18	0	9	9	6	6	4	9	0	0	0	6	6	7
Papillae (PAPL)	1	0	0	0	0	1	0	2	0	0	0	6	5	0	1	0	0	3	2	1	0	0	0	0	0	3	1
Achene (ACHN)	21	18	7	7	7	1	3	20	15	1	10	6	39	33	13	13	14	39	10	24	10	1	13	11	17	14	5
Indeterminables	4	0	3	47	12	16	6	4	12	2	55	0	4	0	3	5	0	4	5	20	0	8	10	21	3	12	0

Appendix IV: Summary table showing diagnostic grass short-cell morphotypes and the supporting literature

Grass sub-family	Diagnostic Morphotypes/ Grass short-cell phytoliths	Comparable previous studies
Pooideae	<i>Trapezoid polylobates</i> <i>Tower wide</i>	Barboni and Bremond, 2009 Roussouw, 2009
Arundinoideae	<i>Rondel</i> <i>Saddle ovate</i> <i>Tower wide</i>	Piperno & Pearsall, 1998 Piperno, 2006; Fahmy, 2008 Mercader <i>et al.</i> , 2010.
Panicoideae	<i>bilobates Panicoid type,</i> <i>bilobates concave outer margin long shaft</i> <i>bilobates convex outer margin outer margin short shaft</i> <i>Quadralobate</i> <i>Tower horned</i>	Fredlund & Tieszen 1994 Albert <i>et al.</i> , 2005; Piperno, 2006 Fahmy, 2008 Mercader <i>et al.</i> , 2010; 2011.
Chloridoideae	<i>bilobate flattened outer margins short/long</i> <i>Saddle-shaped</i> <i>Saddle squat</i> <i>Tower flat</i>	Piperno & Pearsall, 1998 Fahmy, 2008 Mercader <i>et al.</i> , 2010.
Aristidoideae	<i>Bilobates convex outer margin long shaft</i> <i>Saddle plateau</i>	Piperno and Pearsall, 1998 Piperno, 2006 Mercader <i>et al.</i> , 2010
Undifferentiated grasses	<i>Bulliforms</i> <i>Prickle/scutiform</i>	Madella <i>et al.</i> , 2005 Mercader <i>et al.</i> , 2010