Late Quaternary palaeoenvironments and Middle-Late Stone Age habitat preferences in the Nakuru-Naivasha Basin, Kenya: phytolith-based evidence from the site of

Prospect Farm



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DECLARATION

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Preface and specified in the text.

It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text.

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Signed:

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ABSTRACT

The Central Rift Valley of East Africa has proven to be a key region for our understanding the emergence and diversification of our species. Genetic, fossil, archaeological, and palaeoclimatic evidence suggest that mosaic refugia may have existed here during the late Quaternary period. Such putative refugia are posited to have been centred around highland lake basins that could have buffered human populations, plant, and faunal communities from the most severe deteriorations of climate during the last glacial period. On a sub-regional scale, East Africa's heterogeneous topography and localised expressions of regional climate is hypothesised to have created a 'push-pull' system in which repeated fragmentation, isolation, and expansion of populations occurred, allowing diversity to arise. Competing Middle Stone Age (MSA) behavioural-ecological models disagree in respect to their conceptualization of the nature of past human adaptations to xeric savanna, mesic savanna, and forest/wooded habitats, as well as how MSA groups responded to various palaeodemographic pressures. Consequently, these competing models propose contrasting changes in hunter-gatherer mobility and contact/isolation between MSA groups in reaction to the same underlying palaeoenvironmetal and palaeodemographic factors. Local late Quaternary palaeoenvironmental records from archaeological sites in highland areas of East Africa are at present temporally and spatially fragmentary. As such, the relative ecological stability of the Kenyan Central Rift (KCR) and its capacity to have acted as a refugium remain poorly understood, as are the various logistic and adaptive challenges that inhabitants of different ecological zones of East Africa faced.

In order to evaluate which behavioural-ecological model(s) best explains patterns in the archaeological record in these settings, this thesis reports the results of phytolith-based vegetation reconstructions and geoarchaeological investigations from renewed excavations at the open-air site of Prospect Farm, Mt. Eburru, Nakuru-Naivasha Basin, Kenya, as part of the *In Africa* project (INAP). The Prospect Farm Formation preserves a stratified sequence covering the last glacial period and Holocene, in which four main archaeological phases covering the MSA to Late Stone Age (LSA) transition were previously identified. The site is one of the few which preserve this transition in East Africa, that is associated with major social and technological reorganisation between ~60-20 ka. Consequently, it provides a unique opportunity to establish the environmental context of the MSA-LSA transition in the KCR.

Sedimentological, stratigraphic, and elemental analysis (by ICP-OES) of the pyroclastic, colluvial and palaeosol deposits that form the Prospect Farm Formation were conducted to elucidate site formation processes alongside new archaeological investigations of the site. Phytolith analysis (samples [n = 68]) was used to determine temporal and spatial palaeovegetation changes at the site. Phytolith-based palaeovegetation reconstructions were supported by published reference material and a new modern reference collection for the Nakuru-Naivasha Basin. For this new reference set, phytoliths were extracted from little-studied non-grass plants (mainly ligneous and herbaceous dicotyledons [n = 87]) identified as indicator species of different vegetation communities within the study area. Highly diagnostic phytoliths, variation and redundancy in morphology, phytolith production rates across plant families, and

dissolution potential were recorded. Multivariate statistical analysis (unconstrained ordination) was used to compare fossil phytolith samples to modern East African soil phytolith assemblages.

Phytolith analysis from the six palaeosols studied indicates limited past spatial heterogeneity in plant communities across sampling locations. Results do however demonstrate marked changes in past vegetation composition and human habitat preferences, changing from open xeric C4 grassland to closed canopy Afromontane forest, during the two earliest phases of MSA activity at the site prior to \sim 50 ka. Environmental variability associated with MSA-LSA 'transitional' assemblages was found to be nominal. Habitat reconstructions dispute the long-held view that MSA populations exclusively tracked the ecotonal boundary between montane forest and savannah. This is taken to indicate higher levels of behavioural diversity within MSA groups in this area than had previously been imagined. A new Ar⁴⁰/Ar³⁹ based chronology and tephrostratigraphy for the site is ongoing; but the environmental variation at Prospect Farm agrees with local lacustrine records and suggests that glacial-interglacial cycles had a significant effect on the basin's vegetation history and climate. Provisional comparisons with other East African palaeoenvironmental records indicate that the Nakuru-Naivasha Basin remained relatively ecologically stable compared to adjacent lowland areas. While further archaeological analysis is necessary to more fully test competing behavioural-ecological models and the site's role as a refugium, comparisons of shifts in local ecological conditions to changes in raw material procurement strategies at Prospect Farm indicate that environments with higher arboreal cover tend to be associated with reduced mobility. However, findings also suggest that palaeoclimatic factors are most likely to have played a secondary or mediating role in techno-cultural and mobility changes that occurred during the MSA and across the MSA-LSA transition at Prospect Farm, rather than being a primary driver of these changes.

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List of Abberviations

AGPs	above ground plant foods
AI	aridity index
AIF	acid insoluble fraction
AHP	African Humid Period
АМН	anatomically modern humans
CA	correspondence analysis
CAB	Congo Air Boundary
DCA	detrended correspondence analysis
D-0	Dansgaard-Oeschger
EAM	Eastern Arc Mountains
EARH	East African Refugium Hypotheses
EARS	East African Rift System
EBT	Eburru Trachyte Formation
ENSO	El Niño-Southern Oscillation
FI-t	Forest Indicator total [phytoliths]
GSSC	grass silica short cell phytoliths
HI	hypsometric index
INAP	In Africa Project
IOD	Indian Ocean Dipole
IPC-OES	inductively coupled plasma optical emission spectroscopy
ISM	Indian Summer Monsoon
IWM	Indian Winter Monsoon
ITCZ	Intertropical Convergence Zone
KCR	Kenyan Central Rift
LGIT	Last Glacial-Interglacial Transition
LGM	Last Glacial Maximum
LSA	Later Stone Age
LVRM	Lake Victoria Regional Mosaic
MAP	mean annual precipitation
m a.s.l	meters above sea level
MAT	mean annual temperature
MIS	Marine Isotope Stage
MSA	Middle Stone Age
NAD-ME	NAD-dependent malic enzyme
NADP-ME	NADP-dependent malic enzyme

NEWH	North-easterly Winter Harmattan trade winds
NMK	National Museum of Kenya
ОН	obsidian hydration
PCA	principal components analysis
pCO ₂	atmospheric carbon dioxide
PF	Prospect Farm
PhyteG	phytoliths per gram AIF
PNV	potential natural vegetation
ppm	parts per million
RSD	relative standard deviation
SMCRE	Somali-Masaï centre of regional endemism
SRTM	Shuttle Radar Topography Mission
SST	sea surface temperature
tb-PCA	transformation bases principal components analysis
UPGMA	unweighted pair-group method using arithmetic averages
USOs	underground storage organs
VECEAE	Vegetation and climate change in Eastern Africa project
WASM	West African South-westerly summer Monsoon
X	magnetic susceptibility
XRD	X-ray Powder Diffraction

Chapter 1 Theoretical background and thesis structure

1.1 Introduction

The diversification of *H. sapiens* in Africa during late Quaternary period can be summarised as a series of complex and variable demographic changes and behavioural adaptations. The former involves variation in population size, density, distributions, and degrees of isolation and interconnectedness of regionally distinct groups; and the latter, the emergence of complex derived and innovative behaviours. Feedbacks between palaeodemographic changes and more endogenous elements of hunter-gatherer groups (i.e. changes in technological and social organisation) are believed to have set the conditions under which the evolution and diversification in our species occurred, and by extension are key in structuring the records which we are attempting to interpret (Stewart and Jones, 2016). Palaeoanthropological, genetic and archaeological evidence indicate that large-scale and regionally heterogenous fluctuation between polarising climatic conditions and associated local ecosystems responses were central in controlling regional biogeography. In turn, biogeographic change is envisaged to have had deep-seated effects on hominin population dynamics. Current evidence suggests that East Africa is central to the evolution and diversification of Homo sapiens. However, sparse fossil records, a lack of well-dated archaeological assemblages and the current uncertainty that surrounds the molecular dating of evolutionary events, means that the diversity (i.e. the range of phenotypic, genetic and behavioural variation) within the lineage of early *H. sapiens* is not well represented and is open to multiple evolutionary interpretations. Consequently, the precise timing of emergence of our species, as well as the main factors structuring and driving the diversity of early population of H. sapiens remain unclear.

The reader will notice that the appendices included in this thesis are protracted. The appendices are not intended as essential reading, but are rather, in part, included to provide more detail on the general background information and possible future research directions. They also provide greater detail of the methods employed, and report the original data generated by this thesis. Consequently, the information contained in the appendices may be of interest to readers who are curious about the wider research that acts as the basis for investigations in this thesis, or to those that may wish to conduct similar studies in the study area.

The purpose of this Chapter is not to detail patterns of behavioural and demographic changes in the East Africa records. Instead I intend to introduce evolutionary-ecological models that have been proposed to explain these changes: more specifically, evolutionary geography models (namely the *East African Refugium Hypotheses* [*EARH*]) and settlement dynamics and habitat preference models (namely the *Ecotonal Hypotheses*), are addressed. The chapter considers how this thesis will test elements of these models through set aims and objectives involving new environmental records from Prospect Farm in the Nakuru-Naivasha Basin, Kenya Central Rift (KCR), in the eastern branch of the East African Rift System (EARS) shown in Figure 1.1. The long archaeological sequence at Prospect Farm and the important position the site occupies in the highland area of East Africa with biogeographic connection

to other regions of the continent, means it has the potential to act as the key Middle Stone Age (MSA) archaeological sequence in East Africa. From a site's specific angle, this work aims to establish site formation process and a local record of palaeoenvironmental change against which changes in the archaeological record, such as the MSA to Later Stone Age (LSA) transition, at the sites can be contextualised. Through the broader lenses of changes in MSA archaeology and human evolution, it is hoped that this work will provide added regional perspective to a growing body of work on palaeoenvironmental changes and MSA population responses, by focusing on a location which has been identified as being highly sensitive to climatic change, but where relatively little is known about this relationship.



Figure 1.1 Maps of the Eastern arm of the EARS showing (A) topography and (B) tectonic settings, main faults, the location of Prospect Farm archaeological site, modern lake levels and Holocene lake highstand levels. In this thesis, East Africa is defined as the ecoregion covered by the Somali-Masaï centre of regional endemism (SMCRE) and the Lake Victoria Regional Mosaic (LVRM) (White, 1983) (see Figure 1.5). This is a biogeographic zone covering ~3.6 million km², which includes present day Eritrea, Djibouti, Somalia, Ethiopian, Kenya, Uganda and Tanzania. For information on geological development of the EARS, the reader is directed to Appendix 1.1.

1.2 Pattern of change in human evolution in East Africa

Extensive accounts of all the available evidence that relates to the emergence and spread of early populations of *H. sapiens*, has been covered elsewhere (see Mirazón Lahr, 2016; Mirazón Lahr and Foley, 2016; Stewart and Jones, 2016 for recent reviews). While the fossil record remains highly fragmentary, recent genetic and fossil evidence indicates that early members of the *H. sapiens* clade emerged in Africa as early as 350 ka, at a time when an undetermined number of other hominin species were also present across Africa (see Appendix 1.2, Figure 1.1 for a summary of the chronology and location of human fossils in Africa during the last 800 ka (thousand years ago) (Marine Isotope Stage [MIS] 21 to MIS 1).

The few early Anatomically Modern Human (AMH) fossils which have been recovered are generally associated with MSA technology (see Stringer, 2016). Indeed, for the vast majority of the time that AMH have existed the MSA has been their technology. Figure 1.2 plots key MSA localities from equatorial East Africa and eastern Tropical Africa over time. The overlap of MSA with LSA technology (which become widespread ~50 ka), combined with the high levels of morphological variability in the fossil record, suggests spatiotemporally complex evolutionary scenarios. It is likely that high levels of regional and sub-regional viability and deep population substructures existed in Africa, in which behaviourally and morphologically distinct hominin groups existed in the same regions (e.g. Hammer et al., 2011; Harvati et al., 2017; Scerri et al., 2017, 2018). How different these sub-populations were, what drove and structured this variation, and how they interacted is a central question for palaeoanthropologists and archaeologists.



Figure 1.2 Dated MSA sites from the Ethiopian Rift, the Horn of Africa equatorial and eastern Tropical Africa including associated species of Homo, site type, and approximate MIS. MSA technology (i.e. a shift away from large cores tools and the increased use of Levallois and discoid reduction techniques to produce retouched flake tools that appeared ~500 ka) becomes widespread across Africa from ~280 ka. During MIS 6 high levels of variability in the archaeological record (i.e. the contemporaneous use of late Achulean and MSA tools at different sites within the same region), is thought to indicate small isolated populations subjected to strong selection and genetic drift (Mirazón Lahr and Foley, 2016). From MIS 5 onwards, during the expansion of *H. sapiens* across Africa, habitation of rockshelters, coastal sites and hillside sites become more common, representing a change in settlement dynamics associated with the Middle to Late Pleistocene transition and the adoption of LSA elements in some MSA traditions. "Transitional" Achulean-MSA industries are present in the record as late as 154 ka. Similarly, the continued use of MSA technologies in some parts of the Africa into the terminal Pleistocene after the widespread adoption of LSA (Mode 1) technology, indicates the continuity of elements of Pleistocene population substructure, while other populations are thought to have undergone significant demographic changes (e.g. population growth and expansion, and increased mobility and regional connections). The discontinuous spatiotemporal nature of the record and the broad temporal range of dates of occupation horizons makes it difficult to establish how specific changes reflect changes in behaviour and whether continuity represents continued use of these technologies by distinct populations, or simply continuity in technological traits that were adopted by subsequent populations from different areas. This means that making inferences about timing and nature of demographic change during this period is problematic (Mirazón Lahr and Foley, 2016). Adapted and updated from Basell (2008).

<u>1.3 Patterns of change in the archaeological, fossil and genetic records of East African (MIS 6-1: ~191- 11 ka)</u>

MIS 6 (the penultimate glacial period [~191-130 ka]) records the earliest fossil evidence of H. sapiens in East Africa. However, issues with phylogeographic techniques (Nielsen and Beaumont, 2009) and excavation biases means that it is difficult to be certain if East Africa (Gonder et al., 2006; Quintana-Murci et al., 2008) or South Africa (Henn et al., 2011) is the location of a founder population and make it difficult to determine precisely when it emerged. Genetic evidence indicates the importance of MIS 5 (~130-71 ka), particularly MIS 5e (the last interglacial [130-117 ka]), in moulding the genetic diversity of modern humans (e.g. Behar et al., 2008; Tishkoff et al., 2009; Verdu et al., 2009; Gomez et al., 2014; Groucutt et al., 2018). However, the number, timing and routes of migrations and their drivers, as well as of contact and interbreeding with other hominin populations within and outside of Africa during the Pleistocene are still intensely debated (see Groucutt et al., 2015 for a recent review, and also see Mirazón Lahr and Foley, 1994; Petraglia et al., 2010; Armitage et al., 2011; Pagani et al., 2015; Tierney and Zander 2017; Molinaro and Pagani, 2018). Throughout MIS 5 the number of archaeological sites in North and South Africa increased. This is associated with an intensification of lithic production, and increased regionality, higher levels of cultural boundary formation, as well as increased frequency of complex "modern" behaviours (i.e. symbolic expression, production of microlithic bladelet technology and tanging, specialised hunting techniques, exploitation of aquatic resources, and extensive and longdistance transport of raw material). These behaviours have been equated with expanding trade networks, the expression of personal and group individuality, increased social organisation etc., and more tentatively with enhanced cognitive capabilities and the use of complex language (e.g. Clarke, 1988; Bouzouggar et al., 2007; d'Errico et al., 2012; Will et al., 2016; Mackay et al., 2018). Cultural groups with this behaviour repertoire are transient and appear to anticipate the more widespread adoption of such complex behavioural packages during the LSA period (e.g. Jacobs et al., 2008). In East Africa there are comparatively fewer MSA sequences that have been definitively assigned to MIS 5. This may represent a genuine hiatus in occupation and low population densities in the region or may be a function of the bias that exists toward the excavation of cave sites over open-air sites, which are more numerous in East Africa. This bias is also likely to be due to the lack of sites from the region that have been dated using modern techniques. The study site of Prospect Farm falls into the category of an open-air site with an imprecise chronology but with MSA occupation phases tentatively ascribed to MIS 5 (see Chapter 5.3.2).



Figure 1.3 Climatic, geological and cultural frameworks employed in this thesis. δ^{18} O curve (Lisiecki and Raymo, 2005) as a proxy of global ice volume and deep ocean temperature change plotted against the appearance of MSA and LSA technologies in Africa. Grey vertical bars delineating cold approximate MIS and white bars representing warm stages. MIS7a: ~200-185ka (penultimate interglacial) MIS 6: 191–130 ka (penultimate glacial); MIS 5e: 130-117 ka (last interglacial); MIS 5d to MIS 2 (last glacial): MIS 5d-5a: 117–71 ka; MIS 4: 71–57 ka; MIS 3: 57–29 ka; MIS 2: 29–14 ka. Geological ages (Middle and Late Pleistocene) and epoch (Holocene) correlating to MIS 6-2. Elements of LSA industries which appear in MSA assemblages ~120 ka, become more common ~80 ka and become widespread after ~50 ka. MSA technology continued to be produced as derived MSA forms up until ~25 ka (during the Last Glacial Maximum [LGM]). The MSA lithic record of East Africa at times show high levels of regional variability and sometimes short-lived appearance of cultural traditions, at times suggesting population expansion and during others contraction, set against a backdrop of a gradual reduction in point size trending towards LSA forms. Figure from Stewart and Jones (2016).

By the beginning of MIS 4 (~75-60 ka), fossil evidence suggests our species was the only remaining member of the genus *Homo* in Africa. MIS 4 and 3 (~60-25 ka) record the emergence and proliferation of the LSA industries throughout Africa, the major demographic expansion of *H. sapiens* within Africa, and a single lineage of *H. sapiens* across the globe using Mode 3 technology (also see Rabett, 2018). However, the record is so sparse for this period that populations sizes are difficult to model (Mirazón Lahr and Foley, 2016). The shift from MSA to LSA technologies is characterised by the intensification and diversification of behaviours that appear in isolation during MIS 5 and foreshadow the technological and social systems used by living and recent populations of hunter-gatherers. Changes in MSA and LSA archaeological record have been increasingly studied within behavioural-ecological frameworks which is the approach broadly adopted in this thesis (see Appendix 1.3 for an explanation of current evolutionary-ecological approaches to understanding the MSA and LSA).

1.4 The Middle to Late Stone Age transition in East Africa

1.4.1 The nature and drivers of the MSA-LSA transition

The use of LSA technology and associated extensive social/trade networks are hypothesised to be important in the creation and maintenance of complex cultural systems that could have allowed H. sapiens to expand their niche and survive and thrive in changeable and unfamiliar habitats. The use of this technology by certain H. sapiens groups has also been theorised to provide an adaptive advantage over other hominin groups, thus facilitating expansions. The emergence of LSA techonology is hypothesised to have been driven by a combination of changes in human cognition, demography and environment (Kusimba, 2005; Ambrose, 2001; Tryon and Faith, 2016), the nature and timing of which remain intensely debated (e.g. Bar-Yosef and Kuhn, 1999; Foley and Mirazón Lahr, 2003; Barham, 2013; Chase et al., 2018). Due to poor chrono-stratigraphic control and the lack of local environmental records from many sites, including Prospect Farm, few sites from East Africa provide fine-scale reliable estimates of environmental and demographic changes over the transition and their underlying causes. Figure 1.4 shows the known stratified sites in East Africa which record the MSA-LSA transition. The MSA-LSA encompassed a variety of spatial and temporally divergent changes between different environmental conditions. Consequently, if nuanced models of changes in demographic, behaviour and social change during the late Quaternary period in Africa are to be developed, individual sites must be considered as elements of extensive interconnected networks (Blome et al., 2012; Robinson et al., 2017).



Figure 1.4 Stratified sites in East Africa which record the MSA-LSA transition. Prospect Farm is one of the few sites to record the transition, but its chronology is imprecise. Enkapune ya Muto records the earliest entirely LSA assemblage in Africa at ~50 ka (Ambrose, 1998). Enkapune ya Muto, Mumba, Kisese II, and Panga ya Saidi (not shown, Shipton et al., 2018), all of which are located at the ecotone between forest and savanna environments, are the only records in East Africa to record detailed diachronic evidence from non-lithic artefacts (e.g. Ostrich eggshell beads) that have divergent evolutionary trajectories and can potentially provide greater insight into social networks and cognitive changes across the transition. Image from Van Balen et al., (2019).

1.5 Evolutionary geography models and interassemblage variability in the MSA of East Africa

Africa is vast, covering 30.3 million km², it supports a spectacular array of terrestrial environments, which can be divided broadly into Northern, Southern, Eastern, Central (Tropical) and Western regions following biogeographic gradients. Mirazón Lahr and Foley (2016) note that evolutionary patterns are heavily regulated by biogeographic processes. Thus, on a regional scale, biogeography both creates barriers to migration and contact as well as facilitating connections via migration pathways (e.g. Hewitt, 1996; Barraclough and Nee, 2001), and in theory structures regional spatio-temporal difference in the archaeological and fossil records. In turn biogeography is mediated by temporospatial environmental variability which set the biogeographic conditions for the emergence of divergent traits in isolated populations, and the environmental basis for dispersal. Generalised population responses in Africa as a whole show broad agreement with global scale climate change on orbital times scales (i.e. population expansions during MIS 5 and 3 and contractions during the Last Glacial Maximum [LGM]) (Mirazón Lahr and Foley, 2016; Blinkhorn and Grove, 2018). The growing body of palaeoenvironment evidence from Africa indicates that on millennial time scales, tropical expression of global climate changes resulted in large changes in environmental conditions, but also that different regions across Africa responded asynchronously and heterogeneously to these changes (Blome et al., 2012; Mirazón Lahr and Foley, 2016). This meant that at times regions were climatically out of phase with one another, and supported environments with no modern analogues during the last glacial period and Early Holocene before current biogeographic patterns became established (see Chapter 3). Highly asynchronous patterns of moisture availability promoted regional variability in habitat conditions and dramatic fluctuations in lake levels and vegetation distributions. In East Africa, records indicate mosaic palaeoenvironmental conditions existed, that were further emphasised on sub-regional and local geographic scales by the region's diverse topography (Blome et al., 2012; Mirazón Lahr and Foley, 2016).

Synthesis of Quaternary palaeoenvironment records from across Africa has indicated that climatic conditions fluctuated over short intervals (e.g. it is only during a short period [between 150-145 ka] that the regions of Africa shared the same pattern of aridity [Blome et al., 2012; Singarayer and Burrough, 2015; Mirazón Lahr and Foley, 2016]). It is also apparent that environmental conditions in northern and southern latitudes became more divergent after 70 ka (from MIS 4 onwards) (Tierney et al., 2008; 2010; Scholtz et al., 2007; Singarayer and Burrough, 2015) (see Chapter 3.3). Coarse grained analysis of interassemblage variability and hominin demography indicates that the preferred responses of MSA populations in East Africa to these changes was to make small shifts in their settlement locations, and that in general, the pattern of MSA variability in East Africa is more consistent with local adaptations of regional distinct groups of hominins than with regular, large scale population shift (Blome et al., 2012; Tryon and Faith, 2013).

1.6 late Quaternary climate change and East African Refugia

1.6.1 The concept of refugium

A 'refugium' can be defined as an area that supports a small population of a species during periods when the species' range is reduced due to wider adverse ecological conditions inimical to its survival (Bennett and Provan, 2008; Stewart et al., 2010; Keppel et al., 2012). Models of hominin refugium have drawn heavily from earlier biogeographic and allopatric speciation models of floral and faunal diversity during the period late Quaternary in Africa (e.g. Lönnberg, 1929; Moreau, 1933; Haffer, 1969), on which additional information is provided in Appendix 1.4.

1.6.1.1 Evaluating the refugium networks theory through the In-Africa Project

Several studies, that focus on human refugia, have highlighted East Africa as a likely core refugium and hotspot of population endemism (e.g. Basell, 2008 and Blome et al., 2012). Building on these studies and observations of high levels of climatic asynchronicity across East Africa (see Section 1.5.), Mirazón Lahr (2013) proposed that refugium in East Africa was not likely to be characterised by a single area but rather a series of interconnected enclaves. These refugia, forming a so called 'refugium network', are proposed to have been connected by a series of semi-contiguous geographic corridors that linked areas in which ecological conditions could have at times been out of phase with one another during the same climatic interval. Within such a network, an adaptation hinging on the ability to rapidly respond demographically to shifts between environmental conditions that were favourable to a group and to those that were not (i.e. behavioural flexibility) would have been selected for (Mirazón Lahr, 2013). This would have allowed hominins to move between differ biogeographic subzones in order to counteract sub-regional variability in palaeoenvironmental conditions.

Determining the changing structure and the conditions within this putative refugium network over time is of central importance to understanding human diversity in Africa. Establishing if (and if so, how) the unique ecological conditions in different refugium contributed to the emergence of derived traits and behavioural innovations in the human lineage, through niche construction processes is necessary. As is understanding how the physical and social landscapes of different refugia, and human adaptation to them, may have mediated hominin expansion within and beyond Africa. In this regard, the combination of multiple local environmental records to form a regional perspective on habitat variability and connectivity, is likely to be more important than understanding the exploitation of any one habitat type in this process (Foley and Mirazón Lahr, 2016). Understanding the biogeography of areas proposed as the geographic location of the origin of *H. sapiens* (i.e. the mosaic habitats of East Africa) is important as these factors set the demographic conditions for genetic variation (i.e. isolation, migration, drift and selection) in the evolutionary process of the emergence and phenotypic diversification of early members of our species. Even if East Africa is not the location where the first *H. sapiens* lineage emerged, it may still be central to the process of diversification, as it is connected to all other regions of Africa via the Central Rift Valley and the LVRM. Thus, it may be the base area for dispersal and a pivot, linking

different regions as proposed by Foley and Mirazón Lahr (2016), under the "hinge-zone" model of late Quaternary climate dynamics (see Chapter 3.3).

As such, generating new archaeological, palaeoanthropological and palaeoenvironmental data from parallel lake basins, that could help to test the refugium networks theory, is central to the aims of the INAP. The INAP focuses on two major centres of MSA sites where considerable environmental differences occur today: the Turkana and Nakuru-Naivasha Basins, that are connected by the KCR. In accordance with this parallel approach, sampling of MSA sites from both basins was conducted as part of my PhD research in order to establish palaeoenvironmental differences between MSA sites in these two areas during the late Quaternary period. However, unfortunately palaeoenvironmental analysis (phytoliths and pollen) of the MSA sites of Lomanimania (dated to MIS 3), Lokodongot 2 and Kalokoel 3 in Turkana, failed to produce adequate plant microfossils for palaeovegetation reconstructions. The lack of these remains was because the nature of fluvial/non-deltaic lacustrine sediments that formed deposits at these sites confounded preservation of this material due to exposure in oxidising conditions and physical degradation. Where small amounts of phytoliths were recoverable the assemblage was heavily biased by sedimentary processes (e.g. grain size sorting and destruction in higher energy fluvial environments [see Strömberg et al., 2018 and references therin]). Consequently, the focus of this thesis was shifted solely to the Nakuru-Naivasha Basin; where pilot studies indicated records were more suitable for local palaeovegetation reconstructions, but where no faunal evidence is preserved. Future comparisons between ecological conditions in the two basins will be based on ongoing local faunal assemblage analysis from these sites in Turkana as part of the INAP, as well as forthcoming basin-wide records palaeoclimate variability conducted by other studies in this area (e.g. Cohen et al., 2019). While environmental reconstructions at Prospect Farm are not intended to address all of these questions introduced here, much less solve them, it is hoped that the work in this thesis provides insight into the human ecological-evolutionary scenario in key area of East Africa during the MSA.

<u>1.6.2 Models of human occupation of xeric grassland vs mesic Mosaic forest/savanna environments</u>

Several non-mutually exclusive hypotheses exist that provide alternative explanations of the nature of refugia for hominins in Africa, and the emplacement and removal of biogeographic barriers controlling isolation, dispersal and interaction. The connectivity of populations in different regions and migration within and out of Africa are often framed in terms of unfavourable or favourable environmental conditions creating a 'push-pull' mechanism that drew populations in and out of regional refugia. Broadly speaking, under shifting regional and local climatic conditions, populations were either forced to move by tracking a habitat they were well adapted to, or were attracted to move when an adjacent area/region shared the same basic environmental conditions of their favoured habitat. Similar demographic responses are expected to have occurred when population pressure on available resources was high, forcing a sub-set of the population to relocate. Behavioural-ecological models for East Africa, that consider the role of refugia in human diversification, generally agree that during periods of hyper aridity populations would have been confined to areas around lakes or to higher altitudes where locally moist
conditions were present. Because of the adaptive flexibility of humans and the environmental heterogeneity of Africa, refugial conditions in Africa varied by region and over time. However, competing models based on the same underlying environmental evidence suggest different habitat preferences and dispersal scenarios in and between the same areas and regions, under all but the most extreme levels of aridity. These models can be roughly divided into those that: a) propose hominin groups were adapted to and expanded in mesic/mosaic biomes with higher tree cover (covered in Sections 1.7.1-1.7.2.1), and conversely: b) those that see hominin expansions as most tightly coupled to more arid open grassland biome adaptations (covered in Section 1.7.3). In theory both mesic and arid savanna could have been productive environments for hunter-gatherer groups (see Appendix 1.5 for supporting information on the ecological basis for the exploitation of East African habitats by hunter-gatherers). Assessing the evidence for and against these models of human responses to past environmental change in the KCR is the core aim of this thesis - outlined in Section 1.9.

1.7 Behavioural-ecological models of human diversification in East Africa

1.7.1 The East African Refugium Hypothesis

Basell (2008) was the first to try and establish the precise location of human refugia and whether occupation of refugia by humans was supported by the archaeological record. Basell (2008) demonstrated that clustering of MSA/LSA archaeological sites in highland zones of East Africa (e.g. Ethiopian Rift, Kenyan Central Rift [KCR], the Albertine Rift, and the Mozambican/Rukwan Rifts), as well as around Rift Lake margins (shown in Figure 1.5), occurred during periods of extreme aridity (e.g. parts of MIS 6, 4 and 2), and appears to be consistent with the population contraction into isolated highland refugia or around lakes and river margins at both high and lower elevations (e.g. Tryon et al., 2016; Wright et al., 2017). The *East African Refugium Hypothesis* (*EARH:* Basell, 2008) has adapted the earlier allopatric speciation models to propose that these areas were able to support hominin populations by providing food, water and biodiversity (see Appendix 1.6 for supporting information), but were separated by large swaths of open grassland, semi-desert and desert vegetation (Basell, 2008; Brandt et al., 2017; Vogelsang and Wendt, 2018). The Prospect Farm site is situated on both a hillside location and near to lake margins (see Figure 1.7) in the KRC, making it a potentially attractive setting for hominin groups under different climatic regimes.

The *EARH* proposes a 'push-pull' scenario in which the expansion of forest/woodland and mesic rainfall savanna habitats, as well as increased water availability during interglacials (e.g. MIS 5 and 1) and possibly interstadial (e.g. MIS 3) periods in equatorial areas of East Africa, acted as the impetus for dispersal events and increased regional interconnections between MSA and early LSA populations. The converse is proposed to be the case during stadial periods of the last glacial (Foley and Mirazón Lahr, 1998; Basell, 2008). Additionally, Basell (2008) proposes that large volcanic events such as caldera collapses may have been the stimuli for migration events, since extensive areas became uninhabitable following eruptions, and ash may remain mobile on the landscape for decades (see Jones et al., 2010 and references therein). A key pattern in the distribution of MSA sites in East Africa identified by Blome

(2008) is that, at a coarse scale, sites are located in areas where arboreal cover is present nearby today. In this respect, the *EARH* differs from models that posit xeric conditions as encouraging dispersal (see Section 1.7.3), and from the *Amplifier Lakes Hypothesis* (see Section 1.7.2.1), that is more rigid in linking increased forest/closed woodland to the expansion of hominin groups. The occupation of sites near to seasonal tropical forest and woodland habitats (i.e. dry and moist Afromontane forest that occurs in rift settings in East Africa) appears not to be contentious based on coarse site distributions and biome models (Basell, 2008; Blome et al., 2012). However, to date, the human habitation of the Afromontane zone by MSA groups under refugial or non-refugial conditions has not been proven in the KCR. Supporting information on the ethnographic basis for the exploitation of East African forest and mesic savanna environments by hunter-gatherer groups is provided in Appendix 1.7.1; on the ecological basis for the exploitation of East African forest environments and highland refugia by hunter-gatherer groups in Appendix 1.7.3; and on the Archaeological evidence in support of hunter gatherer dispersals in forest, and mesic woodland/savanna environments in Appendix 1.7.4.



Figure 1.5 MSA sites relative to White's (1983) present day vegetation map of East Africa. Vegetation distributions near Magubike Rockshelter (site No. 27) were updated to reflect that the site is currently on the border between Afromontane and Somali – Masaï vegetation zones. The study site of Prospect Farm also sits at the boundary between these two zones. The rough path of "northern route" out of Africa (through the Sahara/the Nile River Valley and across the Sinai Peninsula) and the Southern Route (across the Bab al-Mandeb straits. Site locations adapted and updated from Basell (2008) after Blinkhorn and Grove (2018).

1.7.2 Alternative 'mesic environment dispersal' hypotheses

1.7.2.1 The Amplifier Lakes Hypothesis

Like the EARH, the Amplifier Lake Hypothesis (Trauth et al., 2010) and the very similar Hydro-Refugia Hypothesis (Cuthbert et al., 2017: see Appendix 1.7.4.1) propose that lake basins acted as refugia during arid phases. Trauth et al's model draws on evidence that closed basins in rift settings "amplify" the effect of precession-paced changes in climate, causing regular shifts between high stable lakes and conditions of lake desiccation (e.g. Olaka et al., 2010; Trauth et al., 2010). High lakes are predicted to have acted as barriers to contact of populations in the same lake basin but the associated expansion of arboreal vegetation under higher precipitation regimes supported long distance migrations and increase regional interaction during periods of forest expansion. During intermediate lake levels local barriers to interaction were reduced, encouraging contact between hominin groups within the basin along lacustrine margins; while dispersal become more limited. Thus, cyclical changes in climate are proposed to have acted as a mechanism for allopatric speciation during earlier periods of human evolution in rift environments (Trauth et al., 2010; Maslin et al., 2014; 2015). Figure 1.6 shows "amplifier" and "nonamplifier" lakes in the KCR and Ethiopian Rift. The classification of Lakes Nakuru and Naivasha, proximal to the site of Prospect Farm in the study area of the Nakuru-Naivasha Basin as an "amplifier" lake means that we may expect there to have been larger swings in environmental conditions than in other lake basins in the western branch of the EARS. Archaeological evidence that both supports and contests increased mobility and dispersals under mesic conditions proposed by the EARH and the related Amplifyer Lakes Hypothesis is considered in further detail in Appendix1.7.4.



Figure 1.6 North-South topographic cross-section of lakes in the EARS corresponding to X and X' shown in Figure 1.1. (A) Aridity Index (AI) of East African Lakes is shown relative to Hypsometric index (HI) (the measurement of land elevation relative to sea level) indicated by Δ and the and \bullet symbols respectively. (B) Shows maximum increases in lake level during the Holocene and overflow pathways. Lakes at higher altitudes tend to have higher AI values. In highland closed basins rainfall is captured by valley sides creating a moisture deficit on the valley floor. When local catchment precipitation is the main source of water for the lake, changes in the local precipitation-evaporation regime can have a large effect on lake level, this affect is further "amplified" when the ratio between catchment and lake surface area is large and during transitional phases in climate (Burrough and Thomas, 2009; Street-Perrott and Harrison, 1985; Olaka et al., 2010). Adapted from Olaka et al., (2010).

1.7.3 Arid grassland expansion models

1.7.3.1 Archaeological-ecological models underpinning xeric grassland dispersal hypothesis

Contrary to the hypotheses discussed in Sections 1.7.1-1.7.2.1, an alternative view is that MSA adaptations to drier savanna environments are the central adaptation in the expansion of hominin groups. These hypotheses have their beginnings in earlier models developed by Marean (1997) which focus on the difference in the inferred/predicted subsistence behaviour and mobility of LSA groups from two broad, ecologically distinct, moist and arid types of savanna that occur in Africa (Bell, 1982; Huntley, 1982; East, 1984) (see Table 1.1).

Savanna type	Description
Moist/dystrophic savanna	Moist/dystrophic savannas have high rainfall, high woody cover of broad-leaved species
(Mesic savanna)	without thorns and abundant fruits (Sept, 1994; Copeland, 2007), low soil nutrient availability
	(e.g. miombo savannas and Sudanian savannas) and low biomass of large herbivores because
	of the unpalatable woody vegetation.
Arid/eutrophic savanna	Arid/eutrophic savannas have low rainfall, higher grass biomass which provides a high
(Xeric savanna)	nutrient food source to support greater numbers of large herbivores (East, 1984). Eutrophic
	savannas generally form on volcanic soils of the Central Rift Valley and typify the Somalia-
	Masaï phytochorion (Bell, 1982; White, 1983).

Table 1.1. Descriptions of the two main types of savanna found today in East Africa. Moist savannas tend to be located in eastern Tropical Africa and highlands areas of equatorial East Africa, while arid savannas are generally found at low elevations in equatorial East Africa.

The ethnographic record does not provide any information of hunter-gatherer adaptations to moist tropical grassland (500-1500 mm Mean Annual Precipitation [MAP]) environments (Foley, 1982). The *Generalized Grassland* models suggests that in these mesic environments, hunter-gatherer groups would follow a 'routed' hunting strategy, targeting a wide range of species. In this case residential mobility and intergroup interactions would be low (Marean et al., 1997). The *Seasonal Grassland* models predicts that in xeric environments groups used co-ordinated seasonal hunting strategies to exploit large mobile herds of ungulates, resulting in higher residential mobility and more frequent intergroup interaction (Marean et al., 1997). Consequently, the *Generalized Grassland* and the *Seasonal Grassland* models (see Appendix 1, Table 1.2) are based both on what we know about the ecology of modern moist savannas and on archaeological records of LSA hunter-gather adaptations to local palaeoenvironmental conditions in East Africa, for which more information exist than during the MSA (Ambrose and Lorenz, 1990; Marean, 1990; Tryon et al., 2010).

1.7.3.2 The Ecotonal Hypothesis

The *Ecotonal Hypothesis* (Ambrose, 2001) elaborated the earlier ideas of Isaac (1972), who proposed that land-use models of historical hunter-gatherer groups, such as the Okiek in the Nakuru-Naivasha Basin, could can be used as models for MSA and LSA settlement patterns. Ambrose does not suggest that the Okeik's specialised seasonal honey collection and non-specialised small game hunting subsistence strategy (see Appendix 1.7.1 for details) was followed rigidly by MSA and LSA groups, but that in general small bands of hunter-gatherers exploiting different eco-zones on mountains, under mesic conditions,

did not need to migrate long-distances annually (Ambrose, 2001). The Ecotonal Hypothesis suggests that during interstadial periods, in increasingly mesic environments, MSA groups focused their residential sites and activity on the boundary between forest and savanna to maximise access to multiple resources, as proposed by the Generalized Grassland Model. Under more xeric conditions during stadials, contact and movement between different areas was limited, as proposed by the Seasonal Grassland Model. The study site of Prospect Farm is a prime example of sites that fit the "ecotonal model" (i.e surface scatter lithic densities are highest at ~2150 m a.s.l. at the site [Anthony 1967; 1972; 1978; Merrick, 1975; Van Balen et al., 2019]) (see Chapter 6.1). Ambrose (2001) has linked the low proportion of more distant raw materials in the MSA assemplage of Prospect Farm to an ecotonal based model of settlement. Ambrose also inferred that higher proportions of raw material from intermediate distances (~30km) in Phase IV (~50 ka) represent increased mobility under glacial climate conditions. Archaeological evidence that supports the Ecotonal Hypothesis at Prospect Farm and at other sites in East Africa is considered in more detail in Appendix 1.7.5. While the available evidence provides broad support for the theory, Ambrose (2001) did however recognised that accurate dates for the Prospect Farm sequence and direct environmental evidence from the sites itself (which is a priority for this thesis), and from adjacent sites of comparable ages, would be key to test the model of climatically induced changes in settlement and mobility patterns proposed by the Ecotonal Hypothesis.



Figure 1.7 (A) 2D and (B) 3D maps of the Nakuru-Naivasha Basin showing the location of Prospect Farm archaeological site in the basin and landscape and geological features mentioned in the text. Maximum Holocene lake levels that approximate highstand event during the penultimate interglacial and last glacial period are shown. During lake highstand events Prospect Farm is located ~300 m from the margin of Lake Nakuru-Elementaita.

1.7.3.3 Lakeside refugium and arid grassland dispersal model

Drawing on records of MSA landscape use, faunal records, and shared traits of tools kits in the Victoria Basin and adjoining areas, Tryon et al., (2016) suggest a hybrid 'Lakeside refugium and arid grassland dispersal model' that draws on elements of both the Ecotonal Hypothesis and EARH. Tryon et al., (2016) posit that in lowland settings in East Africa, that xeric conditions encouraged mobility. As lakes expanded and regional migrations of large herds of ungulates were impeded, multi-seasonal occupations of sites around the lake shore are inferred to have been the preferred subsistence behavior of MSA groups. Tyron et al's (2016) model suggests more flexible hunter-gatherer adaptations to the complex range of resources available to them in their environment This assertion appears to be well-supported by the available archaeological and palaeoenvironmental records – at least for the lowland Victoria Basin. Details of the available archaeological evidence in support of the Lakeside refugium and arid grassland dispersal model are provided in Appendix 1.7.6.

1.8 Chapter summary

Taken together, the structure of the MSA record in East Africa indicates a scenario in which late Quaternary habitat variability and human biogeography is strongly influenced by spatially asynchronous climate and vegetation changes occurring on regional and sub-regional scales. Despite several lines of evidence pointing to the capacity of the EARS to have maintained hominin populations during climatic perturbations, it is still the case that there is very limited direct evidence of when and where refugia existed, or of how they functioned. Coarse scale mammal species richness (Appendix 1 – Figure 1.2 A) climate (Appendix 1 – Figure 1.2 B) and vegetation (Appendix 1 – Figure 1.2 C) model outputs, as well as phylogenetic studies, indicate that mosaic vegetation (grassland/shrubland/Afromontane forest) may have been present in the Nakuru-Naivasha Basin environments during the LGM; and that mosaic refugia were likely to have been present in East Africa more broadly (e.g. Lorenzen et al., 2010). However, whether the basin was able to sustain human groups during this and similar periods of climatic degradation is not clear. This ambiguity primarily arises from the lack of precise dates for archaeological records in the basin, as well as our current inability to directly link these records to specific climatic intervals and to understand how archaeological changes relate to largely undefined local palaeoenvironmental trends.

Table 1.2 lists the behavioural-ecological models presented in this Chapter. It summaries different patterns in hominin subsistence, settlement and intergroup contact, as well as the associated archaeological signature expected in the archaeological records predicted by these models in both mesic and xeric environments. At present, there is stronger evidence that diffusion of people and technology occurred during the expansion of xeric grassland ecosystems in East Africa than under mesic savanna or wooded/forested conditions (see Appendix 1.7 for supporting information). However, further testing of this and competing refugium hypotheses and dispersal models are needed to develop a more nuanced understanding of the ecological basis for both intra- and inter-regional connections, and how these changed over space and time. For example, the suggestion that mesic wooded environments in lowland

areas of East Africa in the LVRM appear to have limited dispersals in MSA groups may not be true for upland wooded savanna environments in highland areas of the KCR. The ecological outcome of increased regional rainfall and hence the productivity of these environments for human groups may have been different in these areas (see Chapter 3.6). Similarly, non-analogous savanna ecosystems may have existed during the last glacial period (due to the effects of lower rainfall and reduced levels of atmospheric CO_2 [pCO₂]) that do not conform to more detailed models of Holocene and contemporary savanna ecosystems. It is noteworthy that all the aforementioned models operate on the assumption of a simplified linear relationship between aridity and movement of forest to higher altitudes, that is recorded during arid periods of interstadial phases (e.g. in the late Holocene). However, Afromontane forest has been shown have contracted its range and shifted downslope to lower elevations by up to ~ 1000 m under low pCO_2 conditions of the last glacial period (see Chapter 3.5.1). Despite the lack of evidence for human expansions following environments with high arboreal cover, this model has still not been systematically tested by simultaneously studying indicators of local environmental conditions and hominin dispersal in highland areas of East Africa between adjacent lake basins (i.e. along connected montane forest archipelagos, both when aridity was pervasive at lower elevations [sensu Mercader et al., 2013] or when forest was more widespread [sensu Trauth et al., 2010]). The potential for exploitation by hominin groups and direct evidence of occupation of these environments, that may have no modern analogues, requires testing using local palaeovegetation information.

Current archaeological datasets show limited variation in site frequency over time in equatorial East Africa and eastern Tropical Africa from 150-30 ka relative to North and South Africa (Blome et al., 2012). This may indicate that palaeoenvironmental change was relatively muted in East Africa and that 'push and pull' forces may have exerted less pressure on populations here. It may also indicate that the environmental and topographic variability of the area meant that MSA groups were able to respond by to climatic change by opting to undertake shorter moves within a larger biome. While this seems intuitive, it may also reflect that unfamiliar habitats were still a major barrier to the movements of the MSA groups to different regions.

It may be the case that more detailed modelling of MSA population interconnection and demography reveals that the adaptive flexibility and collective knowledge of MSA groups allowed them to move between different regions of Africa in all but the most extreme climatic conditions. This would render the distinctions between adaptations to arid or mesic biomes discussed in this chapter far less meaningful. However, while this binary distinction may appear reductive, at present it has some strong archaeological and palaeoenvironmental evidence to support it. As such, it warrants further testing before alternative models can be suggested. It may also be the case that specific environmental conditions may be more of a constraint on the movement of MSA groups than in LSA groups, which show higher levels of behavioural flexibility from MIS 3 onwards. Due to the incredible ecological variability that occurs across Africa on regional and sub-regional scales, adaptations to a particular set of environmental conditions that underlie dispersal are highly likely to have varied across Africa and within East Africa (e.g. coastal adaptations in South Africa were different to those in more mosaic habitats in East Africa).

Consequently, the forcing factors that 'pushed' or 'pulled' populations may have differed between regions, or in the same regions at different times depending on local demographic pressures. This means that no adaptation of hominins to one habitat will explain evolutionary patterns in Africa. Furthermore, while the archaeological record of East Africa provides evidence of environmental mediated technological dispersals, further studies are necessary to establish whether technology itself was a significant driver of the dispersal of people in the MSA, as has been proposed by some studies for projectile technology developed during the LSA (see Chapter 7.5.4.2). Finally, changes in the MSA archaeological record are most consistent with local, regionally specific processes occurring on relatively narrow temporal time scales. Because of this, the evolutionary process underlying variability in MSA records are likely to be best explained on a regionally specific basis (Mirazón Lahr and Foley, 2016).

1.9 Aims, approaches and objectives of this thesis

<u>1.9.1 Aims</u>

In this Chapter I have argued that understanding past human environmental preferences can help to refine models of human diversification and expansions in Africa but may also help to refine the location of H. sapiens origins. With these points in mind the main aims of this thesis are to: 1) reconstruct habitat variability and human habitat preferences in the highland setting of the KCR, 2) to test competing behaviour-ecological models of human adaptation to past environmental change, and 3) to refine our understanding of the role of forest highland refugia in the supporting human populations in East Africa. Studies herein form part of the In-Africa project's research agenda (see http://in-africa.org/in-africaproject/aims/) and focus on the site of Prospect Farm. This is the only known site in KCR with an archaeological sequence spanning the last glacial, and possibly last interglacial periods, and also records the transition between MSA and LSA technological traditions. As such, the site offers an excellent opportunity to understand human evolution in this area of East Africa and has the potential to act as a key sequence from which comparisons can be made with similarly temporally expansive sequences in other regions of Africa. New palaeoenvironmental reconstructions from Prospect Farm that are reported in this thesis are important as a type site and point of comparison from this basin to similar studies in parallel lake basins. Thus, it can act as a key sequence in testing the refugium networks theory (i.e. to elucidate the possible asynchronicity and interconnectivity of individual refugial enclaves linked by geographic corridors), which is a central aim of the INAP.

1.9.2 Rationale and approach

The Prospect Farm sequence is one of the only sites in the KCR that has been identified as having a well-stratified MSA to LSA sequence. Its position in one of the most obsidian rich landscapes in the world at the base of Mt. Eburru (where numerous surface scatters and two putative occupations sites have been identified), means that it is ideally placed to test MSA habitat preferences and human recourses to past episodes of palaeoenvironmental change in highland areas of East Africa. However, no evidence currently exists from the KCR which explicitly links MSA groups to montane forests/woodland or upland savanna environments, or to dry savanna environments, which could have been present in some

highland basins during arid phases. As such, the current evidence is not complete enough to confirm these areas as stable and resource rich enough to act as refugia supporting groups, and thus not does allow testing of competing models of theoretical response of human populations to late Quaternary palaeoenvironmental change. Consequently, obtaining records of local environmental change from this site was a priority in this research, as it was anticipated it would aid in the testing of both the *EARH* and the *Ecotonal Hypothesis*, and more broadly the the refugium networks theory.

From a regional perspective, the KCR has been theorised to be a potentially key route of dispersal and as a 'pivot' linking adjacent regions of Africa. In this sense Prospect Farm has the potential to act as one of the key East African sites in contributing to our understanding the environmental conditions in the KCR during the late Quaternary period; and determining if environmental synchronisation with other regions facilitated population movement and/or cultural exchange between different areas of East Africa and Africa as a whole. At present, there are significant gaps in both the record of palaeoenvironmental change in the Nakuru-Naivasha Basin see (Chapter 3.5.4), and in our understanding of shared technological traditions with other areas of East Africa.

A summary of the competing models covered that have been introduced in this chapter, which attempt to explain variation in the MSA archaeological record of East Africa, can be found in Table 1.2. Figures 1.8 and 1.9 summarises the expected behavioural and demographic responses of human groups in Prospect Farm and the Nakuru-Naivasha Basin to past changes in vegetation under the competing behavioural-ecological models that I will attempt to test in this thesis. Also shown is Foley and Mirazón Lahr's (2011) model of cultural boundary formation, which predict the rates of inter-group contact and group-boundary formation dependant on the relationship between isolation and environmental gradients. In this model, divergent habitat conditions drive increased population isolation and drift, whereas the predictability and abundance of resources control the competitive fissioning of groups. To address these gaps in knowledge, and to test contrasting hypotheses, members of the *In-Africa* project conducted renewed excavations of Prospect Farm between 2014 and 2016 to record archaeological changes throughout the sequence, and date these through ⁴⁰Ar/³⁹Ar dating and tephrochronology. Finally, the work reported in this thesis was conducted to establish site formation process and palaeoenvironmental changes at the site, through new geoarchaeological and environmental-proxy investigations.

Behavioural- ecological model	Inferred hominin behaviour (settlement strategy, mobility, and group contact) under	Inferred hominin behaviour (settlement strategy, mobility, and group contact) under xeric conditions	Expected archaeological signatures
(A) Ecotonal Hypothesis (Ambrose, 2003)	mesic conditions Hominin activity is centred at semi-permanent sites: the ecotonal boundary between forest and mesic savanna, near water and raw material sources. There is a focus on local plant food resources and hunting of smaller game. Close vegetation conditions mean home ranges are smaller and interaction with neighbouring groups is restricted.	Hominins abandon the ecotone between forest and savanna in favour of a strategy of increased mobility to track larger herds of game. Settlement patterns are more seasonal, reflecting increased environmental seasonality. Settlement and subsistence strategy focus on the occupation of strategic points on the landscape for trapping large game, acquiring water and for plant foods (e.g. inselbergs, lake shores). Open vegetation conditions and expanded home ranges increase the rate of inter-group contact (in the form of reciprocal exchange networks) and thus reduces rates of cultural boundary formation. During periods of extreme aridity hominins may retreat into highland forested refugia.	Under mesic habitat conditions, higher concentrations of artefacts per m ⁻³ at semi-permanent sites are expected. Low levels of non-local raw material are also expected at these sites under mesic conditions. Aspect of lithic assemblages that indicate low mobility and greater economisation of raw material and reuse of tools (e.g. lower incidences of retouch [shared with B] are expected). Under xeric habitat conditions, sites should be more numerous on the landscape but should show decreased occupation intensity. Non-local raw material and retouch tools should increase (shared with B).
(B) Tryon et al's xeric grassland/lakeside model (Tryon et al., 2016)	Hominin activity is centred at semi-permanent sites near lake margins. There is a focus on local plant food resources, hunting of locally available game and aquatic resources. Closed vegetation conditions limit faunal migrations and mean that hominin home ranges are smaller, and interaction with neighbouring groups is reduced (i.e. lower level of intra-basin and inter-basin/group contact).	Hominin activity is focused on the tracking of large mobile herds of game. Settlement patterns and levels of inter-group contact are broadly the same as those propose for the <i>Ecotonal Hypothesis</i> (see above). During periods of extreme aridity hominins activity centres on lake shores.	Same as expected for A: Increased nonlocal raw material represents expanded home ranges and long-distance obsidian transport but may also indicate expanded inter-group exchange networks.
(C) Amplifier lakes hypothesis/ Hydro refugium hypothesis (Trauth et al., 2010; Cuthbert et al., 2017)	Under mesic forested conditions, hominins expand out of highland forest refugium. Expanded rift lakes act as a barrier to intra-group contact between groups in isolated lake basins but encourage expansion along the rift margins; increasing inter-basin contact (i.e. intra-basin cultural boundary formation decreases while inter- basin boundary formation increases).	The expansion of arid grassland and low lake levels limits contact between hominin groups within their home ranges, as well as limiting dispersal to other areas. Under increased aridity, hominin populations are expected to contract into forested environments on rift margins where woody vegetation and active springs exist, forming locally isolated refugium. Here increased levels of cultural boundary formation are expected through isolation.	Under mesic conditions, higher levels of non-local raw material are expected at sites, but assemblages from sites separated by large lakes may show divergent trends. Aspects of lithic assemblages are expected to indicate low mobility and greater economisation of raw material and reuse of tool (e.g. higher incidences of retouch). The reverse is expected under xeric conditions.
(D) East African Refugium hypothesis (Basel, 2008)	Under mesic condition, increasing mobility and expansion are associated with the advantages provided to hominis by some degree of arboreal cover (e.g. increase shade and protection from predators in forest, woodland or mesic savanna environments). Intra- and inter- basin contact is expected to increase along with lower rates of cultural boundary formation.	Expansion of arid grassland limits mobility and inter- and intra-basin contact, resulting in higher rates of cultural boundary formation. Under extreme arid conditions hominin groups retreat into refugium, either around lake shores or in highland forest, where woody vegetation and water resources are present (shared partly with B).	Under mesic conditions, higher proportions of non-local raw materials are expected (as in C) but increased intra-basin similarities in lithic assemblages are also expected. Under xeric conditions, non-local raw material is expected to make up a smaller proportion of the assemblage. Greater diversity in regional, sub-regional, and locally specific stone tool traditions is expected. Higher concentrations of artefacts per m ⁻³ at semi- permanent settlements sites should also occur (contra A and B).

Table 1.2 Summary of behavioural-ecological models connected to late Quaternary refugia., habitat preferences, mobility and dispersal for East Africa discussed in this thesis



Figure 1.8 Key to accompany on the visual model on the following page; which is a simplified representation of expected behavioural and demographic responses (i.e. changes in mobility, expansion/migrations, population contractions) of human groups in Prospect Farm and the Nakuru-Naivasha Basin to past changes in vegetation under the different competing models, and the traces that different behavioural strategies are expected to leave in the archaeological record. Purple coloured symbols indicate situations in which abandonment of sites in an area could have occurred if environmental conditions continued to deteriorate. Note: vegetation patterns during arid periods shown in B and C, panel 1, are not representative of periods of aridity during stadial periods (i.e. when forest is likely to have contracted but also to have move downslope nearer to the rift floor [see Chapter 3.6]).



Figure 1.8 Visualisation of expected mobility and inter-group connections of hunter-gatherer groups in the Nakuru-Naivasha Basin under different MSA behavioral-ecological models discussed in the text. 1= xeric; 2= intermediate; 3= mesic. (A) Expected intrinsic rates of cultural boundary formation after Foley and Mirazón Lahr (2011). If resource abundance was low in each of these scenarios, then cultural boundary formation would be expected to increase through competitive fissioning. The dashed line in panel A3 indicates the it is not certain if high woody cover would encourage or impede increased mobility. (B) Responses of human groups predicted under different behavioural-ecological models for arid, intermediate and humid climate conditions in the Nakuru-Naivasha Basin. (C) Predicted location of permanent settlement at Prospect Farm under different climate scenarios according to expected human habitat preferences of the *Ecotonal Hypothesis*.

1.9.3 Objectives

Habitat reconstructions at MSA sites are often achieved through the analysis of faunal remains that give an indication of both local palaeoenvironmental conditions and the species targeted by hunter-gatherer groups. However, poor preservation of bone in open-air settings, (including Prospect Farm) in the KCR, limits reconstructions following this approach. Vegetation reconstructions offer an alternative, parallel approach to faunal analysis because vegetation forms the ecological baseline for many terrestrial ecosystems. Moisture availability and spatial variability in vegetation physiognomy and floristic structure (species composition and frequencies) come together to control the distribution and abundance of resources on the landscape (i.e. the spatial availability of plant foods, predators and prey). Furthermore, vegetation distributions create corridors or barriers which influence the migration of plant and animals, including humans (Andrews and Bamford, 2008; Barboni, 2014). As pollen grains are also preserved poorly in open-air settings, such as those of the Prospect Farm Formation (see Chapter 5.4.1), a phytolith-based approach to palaeovegetation reconstructions that has proven to be successful in tropical settings has been adopted (see Chapters 4 and 5.6).

As introduced in Section 1.9.1, the aims of this thesis focus on establishing the timing and nature of palaeoenvironmental and associated archaeological changes at Prospect Farm, and using this information to test competing behavioural-ecological models of hominin habitat preference, landscape use, and the occupation of highland refugia by MSA groups in East Africa. Relatedly, this thesis also aims to establish the environmental context of the putative MSA-LSA transition at the site.

The main aims of this thesis will be addressed through the following research objectives and questions:

• 1. To identify site formation processes and to develop site formation models using sedimentological and geochemical techniques, as well as to record and interpret the lithostratigraphic changes at the sites.

Taken together, this information will be used to inform aspects of the local palaeoenvironmental setting, as well as to identify taphonomic biases affecting the phytolith and archaeological assemblages. Sub-objectives related to research Objective 1 are:

- 1.1 To carry out field-based studies of the sedimentology and stratigraphy of the Prospect Farm sequence, in-order to characterise the nature of deposits; including their spatial extent and variability, as well as the depositional and post-depositional processes controlling their formation and alteration. Note: This objective also includes the sampling of key horizons (e.g. palaeosol horizons, archaeological levels and lithostratigraphic boundaries) in the sequence for micromorphology, XRD analysis and volcanic material ⁴⁰Ar/³⁹Ar dating; that are to be completed by other members of the project.
- 1.2 To identify key archaeological and pedologic horizons in the field and to establish the relationship between these units through new excavations. The new scheme established here will be used to test, update, and revise the site stratigraphy established during previous excavations.
- 1.3 To use sediment geochemistry, including appropriate elemental weathering ratios, to constrain field-based observations of site formation processes (i.e. weathering trends, paedogenesis, diagenesis etc.) and to compliment and inform potential biases in the phytolith-based record of palaeoenvironmental change.
- 1.4 To use laser particle size analysis to refine field-based interpretations of volcanic and palaeosol deposits (e.g. to better differentiate between primary and secondary airfall and sub-aerial deposits). This technique will be combined with the phytolith record (see

Objective 2) to establish the relationship between down-profile variability in grain size and phytoliths abundance and preservation, and thus the coherency of the bio-stratigraphic record; including establishing if any possible successional vegetation changes can be inferred.

- 1.5 To combine field-based observations and laboratory studies of site sedimentology and stratigraphy with existing and newly generated archaeological data (e.g. artefact frequencies and distributions) in order to establish the relationship between eruptive and depositional episodes and hiatuses, periods of palaeosol formation, and occupation phases at the site. This includes determining how site formation processes have affected the vertical distribution of stone tools throughout the litho-profile, as well as our ability to identify archaeological horizons associated with former land surfaces. Particular attention will be paid to establishing the relationship between the final MSA and putative MSA-LSA 'transitional' phase in the sequence (i.e. whether there is continuity between these phases or if they constitute separate occupation phases at the site; associated with different depositional events and divergent palaeoenvironmental conditions).
- 2. To reconstruct the nature and timing of successive changes in local plant communities at Prospect Farm through phytolith analysis, taking into account geology, climatic controls and internal ecosystem dynamics. Sub-objectives related to research Objective 2 are:
- 2.1. To create a modern reference collection of phytoliths extracted from ecologically significant ligneous dicotyledon plants from distinct vegetation zones of the Nakuru-Naivasha Basin, so as to establish phytolith morphological-taxonomic relationships that will aid phytolith-based vegetation reconstructions in the Prospect Farm record.
- 2.2. To collate existing modern plant and soil phytolith records from East Africa: in order to adjust existing phytolith indices to East African vegetation, and to inform interpretations of the fossil phytolith bio-stratigraphy at Prospect Farm using multivariate statistical techniques.
- 2.3. To reconstruct the variables throughout the Prospect Farm sequence that are most important to understanding human ecology (e.g. vegetation openness/measures of arboreal cover, C₃/C₄ grassland ratio, xeric/mesic grassland ratio and floristic composition) through phytolith analysis.
- 2.4. To integrate the phytolith-stratigraphy with age models for the site developed by the *In-Africa* project: in order to determine diachronic changes in vegetation and facilitate comparison to local and wider palaeoenvironmental records. Note: Both objectives 2.3 and 2.4 include adopting a dual-location sampling approach (to capture spatial variation in palaeovegetation changes) at different altitudes of the two main excavation locations at Prospect Farm over time (i.e. across what is at present the savanna-forest interface).
- 2.5. Where possible, to identify and quantify the dominant controls (specific drivers and forcing factors) controlling vegetation changes through comparison to global, regional and local records (e.g. insolation changes, *p*CO₂, palaeoprecipitation estimates, fire history, volcanism etc.).
- 2.6 To extrapolate palaeovegetation distributions at the site to higher elevations on Mt. Eburru (not available for sampling) and to the wider basin, based on comparisons with modern vegetation patterns in the basin and to contemporary, comparable East African records of palaeovegetation distributions in the Afromontane zone; that occur under different climatic conditions during the last interglacial and last glacial cycle. These theoretical vegetation distribution models form one part of establishing landscape use patterns for MSA groups in the basin; as laid out in Objective 3.
- 3. To integrate newly generated records of palaeovegetation change at Prospect Farm with previously published and new archaeological datasets produced by members of the *In-Africa* project for Prospect Farm and East Africa. This will facilitate testing correlations between specific habitat conditions and archaeological

indicators of mobility and variability in intra- and inter- regional connections between hunter-gatherers at Prospect Farm and other sites in the region.

Completion of these objectives will be used to establish human habitat preference over time at the site. This will allow for testing of specific questions relating to the *Ecotonal Hypotheses* and competing/complementary theories. Sub-objectives relating to Objective 3 are:

- 3.1. To compare obsidian sourcing data (used as a proxy for mobility) and site occupation intensity over time (inferred through stratigraphic variability in lithic densities) with palaeovegetation reconstructions (that inform habitat preferences and vegetation openness). This comparison will be used to test if increased mobility and lower site occupation intensity occurs under xeric conditions (as under xeric grassland expansion models) or if the converse is true (as under mesic expansion models). For example, this will allow us to assess whether the occupation of the ecotonal zone is supported during all MSA phases of the Prospect and if so under which environmental Farm sequence, conditions this settlement/subsistence pattern was adopted. Ultimately, this will permit us to suggest which behavioural-ecological models introduced in Chapter 1, or composite models, best explains the combined pattern of archaeological and palaeoenvironmental changes explicated through new investigations of the site.
- 3.2 To establish the environmental conditions that existed during the putative shift from MSA-LSA industries in the sequence. This will allow us to better determine if local environmental factors were likely to have been a key driver of this transition in the basin or if other factors, such as demographic changes, played a more significant role.
- 3.3 To compare findings surrounding the nature of this transition at Prospect Farm, achieved through completion of Objective 3.2, to other East African sites where this transition is present. These comparisons will allow us to assess shared and divergent trends between sites across the region and facilitate better understanding of the role of environmental and demographic shifts in mediating the transition from MSA to LSA technology in this area of East Africa.
- 3.4 Where it is possible to make chronological links between vegetation and archaeological change at Prospect Farm with wider records of palaeoenvironmental change, this can be used to inform how highland areas in the KCR responded to regional palaeoenvironmental changes. This in turn informs whether the area acted as refugia for hunter-gatherer groups during the last glacial period, which can be used to help to test the EARH and alternative hypotheses. This will be achieved by comparing the local palaeoenvironmental records from the Nakuru-Naivasha Basin to contemporary, comparable records of archaeological and palaeoenvironmental change from adjacent lowland basins, such as Victoria and Turkana, as well as to sites in coastal areas. These comparisons will help to partially establish the likelihood of population movement occurring from these areas into the Nakuru-Naivasha Basin during either extremely arid periods or under more mesic conditions.

The structure of this thesis is outlined in Figure 1.9. Chapters with a dark rim indicate a focus on local events and processes in the Prospect Farm record (aims 1 and 2). Chapters highlighted in red indicate a focus on how the local information gained from studies at Prospect Farm fits within our understading broader environmental trends and related behavioural-ecological models, as well as how this information as a whole will be used in testing these models (aims 2 and 3).



Figure 1.9 Thesis structure diagram

Chapter 2 Modern climate and vegetation distributions in East Africa and the Nakuru-Naivasha Basin

2.1 Introduction

The uniformitarian principle - the idea that "the present is key to the past" (Lyell, 1842) - is central to palaeoecological investigations (Delcourt and Delcourt, 1991). Palaeoecology largely relies on observations of contemporary species-environmental associations as the basis for modelling the magnitude of reconstructed past environment change, and to contextualise the responses of species to long-term palaeoenvironmental changes observed in the fossil record (Rull, 1990; Delcourt and Delcourt, 1991). The purpose of this chapter is to introduce the body of modern environmental information that underlies the construction of detailed models of past vegetation change at Prospect Farm (PF). This information is wide-ranging: from present-day topography and controls on vegetation patterns in East Africa and the study area, to the ecophysiological mechanisms underlying adaptations of different plants and plant communities to specific niches and changing ecological conditions; as well as how feedback between biotic and abiotic factors affect the functioning of- and competition between savanna and forest ecosystems. The information here provides an overview of the current models of distributions, zonation, species composition and abundance of different plant communities in East Africa, as well as the main environmental determinates underlying the formation and moderation of distinct vegetation types. Special attention is paid to the competitive interaction of C₃ vs. C₄ grass subfamilies on East African mountains, as they are of central importance to the aims of this thesis (see Chapter 1) and are viewed as the most appropriate tool to provide insight into past vegetation dynamics in African montane settings in the absence of pollen (e.g. Parker et al., 2011; Mercader et al., 2013; Jennings et al., 2016; Breman et al., 2019). This is because: (a) The relative abundances of C_3 and C_4 grasses in more closed forested environments and more open savannah environments respectively can be used to differentiate between and within these vegetation types, as well as to indicate specific ecological conditions within these environments (b) Phytoliths are the only based palaeovegetation proxy that allow for determination of grasses to subfamily level in the fossil record (Piperno, 2006; Strömberg et al., 2018; Rashid et al., 2019; and see Chapter 4). Taken together, this material acts as a platform on which published records of late Quaternary palaeoenvironmental changes in East Africa (see Chapter 3) can be discussed, as well as forming a baseline against which to interpret the Prospect Farm palaeoenvironmental sequence. Furthermore, modern vegetation classification in the Nakuru-Naivasha Basin (specifically common and indicator species that distinguish different vegetation types) can be used to guide the selection of key modern plant taxa for phytolith extractions; which are used to create the modern phytolith reference collection for vegetation in the study region (Chapter 4).

2.2 Present-day climate of East Africa

The present-day climate of East Africa is determined by complexes of coupled atmospheric and ocean processes (Nicholson, 1996; Hastenrath, 2001; Barker and Gasse, 2003; Nicholson, 2017). Here, intraannual temperature variations are small (commonly $< 2^{\circ}C$ [Metcalfe and Nash, 2012]), meaning that seasons are largely characterised by variations in rainfall (Yang et al., 2014). Over contemporary seasonal timescales, cyclic rainfall in East Africa is controlled primarily by the migration of the tropical rainfall belt. The seasonal latitudinal movement of the rainfall belt, between 15° S (January) and 15° N (August) across the interhemispheric temperature gradient; crossing the Equator twice a year between March-May and October–November, creates a bimodal pattern of rainfall, that corresponds roughly to seasonal changes in the sun's zenith (minimal insolation). Its migration has often been simplisticly and erroneously solely linked to the movement of the Intertropical Convergence Zone (ITCZ); such that in many palaeoclimate studies the two are synonymous (see Nicholson, 2018). While low level convergence associated with the ITCZ makes a partial contribution to rainfall over the region, rainfall does not by and large track its course. In fact, it appears that other factors, such as storms originating in highland areas of the eastern rim of the Congo Basin; that move westwards and transverse the Equator (Jackson et al., 2009; Nicholson, 2018), vertically integrated moisture from the Indian Ocean tempered by topography, and static energy; all appear to have a far greater influence on the seasonal availability and distribution of rainfall across the region than the ITCZ does (Yang et al., 2015; Nicholson, 2018). In addition to seasonal variations in the distribution of solar radiation energy (insolation); which are controlled by orbital mechanisms, the intensity of the monsoon in Africa plays a major role in determining amounts of rainfall carried by the rainfall belt. Monsoon circulation and intensity is related to the land-ocean pressure gradient (created by the differential capacity of land and ocean to store heat), as well as to variability in sea surface temperatures (SSTs); which are influenced in part by insolation (Kutzbach and Street-Perrott, 1985; Chan et al., 2008; Tierney et al., 2013).

Both the West African Monsoon (WAM) and the NE and SE Indian monsoons convect moisture from the Atlantic and Indian oceans respectively, which falls as rain over East Africa. The more moisture laden WAM extends from the tropical Atlantic to the Eastern Rift where it meets Indian Ocean airmasses to form a zone of convergence named the Congo Air Boundary (CAB; Nicholson, 1996; Tierney et al., 2011b; Costa et al., 2014) (see Appendix 2.1.1 for graphical representations of seasonal changes in rainfall and SSTs associated with East African monsoon dynamics). The uplift and formation of the EARS, which is still ongoing, has increased land elevations and limited zonal wind patterns. This has caused a general trend towards increased aridity and a rain-shadow effect where moisture is reduced on the eastern side of mountains and valleys (see Figure 2.1 [A]) (Maslin and Christensen, 2007). In addition to oceanic forcing, local topographic variability created by rifting and the associated presence of large lakes, modulates rainfall across the region and accentuates intra-regional variation in climate. For example, some local drivers of rainfall variability in East Africa have been shown to be lithospheric processes (e.g. orographic lifting), vegetation and hydrological feedback loops (e.g. evaporation from lakes

andvegetation and mesoscale circulation via land water contrasts) (Hawkinel et al., 2016 and references therein). In turn these local drivers result in divergent habitat conditions over short distances (Nicholson, 1996), which is an important prerequisite for East Africa supporting refugium networks; as introduced in Chapter 1. The main drivers and mediating factors controlling hydroclimatic evolution in East Africa on multi-millennial timescales that are most relevant to this study are introduced in Chapter 3.

2.3 Present-day climate, hydrology and hydrogeology in the Nakuru-Naivasha Basin

The climate of the Nakuru-Naivasha Basin varies from semi-arid conditions on the rift floor to humid conditions on the eastern and western rift escarpments (Bergner et al., 2003). As the study area is located near the Equator, the bimodal pattern of rainfall produces peaks in precipitation in April and October. Mean Annual Temperature (MAT) in highland areas is 16°C, while on the rift floor temperatures reach 25°C (Olaka et al., 2016). An overview of climatic conditions in the basin, its regional moisture sources, as well as internal drainage pathways and sub-surface hydrological connections between the sub-basins are shown in Figure 2.1 and detailed in Appendix 2.2.

2.4 Present-day vegetation distributions in East Africa

On a sub-continental scale, contemporary natural vegetation distributions across East Africa (hereafter defined using the Somali-Masaï centre of regional endemism [White, 1983] [see Figure 2.2]) are controlled primarily by; (a) the position of an ecosystem along the rainfall gradient: this influences mean annual precipitation and length and intensity of the dry season (created by the seasonal movement of the tropical rainfall belt), (b) heterogeneous regional topography, (c) and proximity to the Indian Ocean. On regional to local scales, both geological and pedological controls can also exert as strong influence on the type of vegetation present (Bell, 1982; White, 1983; Hamilton, 1998; Lillesø et al., 2011). Figure 2.2 shows the wide range of vegetation distributions, as mapped by White (1983), that occur across the region (detailed in Appendix 2.1.2). Figure 2.3 below, shows the relative position of the Nakuru-Naivasha Basin and the site of Prospect Farm within several models of major African terrestrial Biomes and within functional models of tropical savannas. More detailed descriptions of vegetation within the Nakuru-Naivasha Basin are reported in Section 2.9.



Figure 2.1 Present-day hydro-climatic conditions in the Nakuru-Naivasha Basin. (A) Schematic hydro-climatic profile of the spatial differences of precipitation-evaporation across the Central Rift Valley from X to X' (shown in [B]) based on data compiled by Bergner et al., (2009) from 17 meteorological stations (after Bergner et al., 2003; Dühnforth et al., 2006). Adapted from Bergner et al., (2009). High elevation areas at the shoulders of the rift are humid (with high precipitation-evaporation ratios (P-E)), while the rift floor is relatively dry (with low P-E ratios). The Nakuru-Elementaita Basin has a catchment area of 2390 km² and an elevation range of 1760-3080 m a.s.l. (1320 m a.s.l.). This area receives 920 mm yr-1 and potential evaporation is around 1736 mm yr-1 (Dunforth et al., 2006). The Naivasha Basin has a larger catchment area (3400 km²) and an elevation range of 1890-3999 m a.s.l. (2109 m). Lake surface areas receive an average of 600 mm yr⁻¹ and have a potential evaportanspiration rate of 1800 mm yr⁻¹ (Clarke et al., 1990; Richardson and Richardson, 1972; Scott et al., 1980; Trauth et al., 2003). Evapotranspiration is low in areas below 2600 m a.s.l. due to sparse vegetation cover, which facilitates increased water runoff on steeper slopes. (C) Back trajectories of precipitation providing airmasses in the Kenyan Central Highlands from July 2003 to June 2004, (a year without the influence of IOD or ENSO, following Konecky et al., [2014] using the HYSPLIT; NOAA/ARL model [Draxler, 1999]) indicating that in the present-day, the region receives all of its moisture from the Indian Ocean.



Figure 2.2 Left: Relief map of East Africa and major lakes showing the annual positional maxima and minima of the Congo Air Boundary (CAB) and the Inter Tropical Convergence Zone (ITCZ), as well as the direction of the prevailing monsoonal winds which form this air boundary and the tropical rainfall belt (WASM=West African South-westerly Summer Monsoon (moist and cool), NEWH=North-easterly Winter Harmattan trade winds (dry, warm, and dusty), IWM=Indian Winter Monsoon, ISM=Indian Summer Monsoon). Vegetation zones as defined by White (1983) across the Somali-Masaï centre of regional endemism (a biogeographic zone covering ~3.6 million km², which includes present day Eritrea, Djibouti, Somalia, Ethiopian, Kenya, Uganda, Rwanda, Burundi and Tanzania): I) Guineo-Congolian Region, II) Zambezian Region, III) Sudanian Region, IV) Somalia-Masaï Region, VIII) Afromontane Region, X) Guineo-Congolian/Zambezian Region Transition zone, XI) Guineo-Congolian/Sudanian Regional Transition zone, XII) Lake Victoria Regional Mosaic. The location of the Nakuru-Naivasha Basin, Kenya, is indicated by the white box. Right: Summary climatology (monthly changes in precipitation and temperature) for lowland and highland areas of East Africa and eastern Tropical Africa, based on satellite emitted long-wave radiation for the period 1981–2010 (from IRI database: http://iri.columbia.edu); along a rough N-S transect of the course of the seasonal movement of the rainfall belt: 1) Chew Bahir Basin, Ethiopia; 2) Lake Turkana Basin, Kenya; 3) Nakuru-Naivasha Basin (study area); 4) Lowlands between Boma National Park and Lake Turkana, South Sudan; 5) Muhesi Game Reserve, Tanzania; 6) Malawi Basin, Malawi/Mozambique.



Figure 2.3 Simple abiotic models of African vegetation, modified to include the relative position of the study site (Prospect Farm) within them. (A) Johnson and Tothill's (1985) model of tropical savannas based on MAP (in mm) and the soil texture and soil-water retention properties. In this model savanna grassland occurs in clay soils (with low drainage and high water retention) with rainfall of ~600-1500 mm, as opposed to occurring in lower rainfall conditions. The ~850 mm MAP, moderately well-drained and silty soils properties of Prospect Farm lead to it being positioned close to Serengeti and Tsavo woodlands/savannas in the model. (B) Frost and colleagues' (1986) functional classification model of tropical savanna based on gradients of nutrient and water availability. (C) Whittaker's (1970) model of major terrestrial biomes along rainfall and temperature gradients, modified to include Afro-Alpine vegetation. Rectangles represent the relative position of different vegetation types across East Africa. Nakuru-Naivasha represent the relative range of all vegetation types in the Nakuru-Naivasha Basin, 'PF' indicates the position of Prospect Farm relative to Amboseli (Am) and Tsavo (Ts) National Parks and Turkana (Tur) District in Kenya; Arusha (Ar), Manyara (Ma), Ngorongoro (Ng) and Serengeti (Ser) National Parks in Tanzania; and Murchison Falls (Mu) and Kidepo (Ki) National Parks in Uganda. Note: Savannas exist under a range of different bioclimatic conditions across the continent. The placement of biomes along these gradients, are intended as a rough guide of MAP and MAT on vegetation distributions in the tropics, but in reality, there can be significant blending of vegetation where biomes overlap.

2.5 Vegetation distributions in the Afromontane Biome

The distribution of vegetation in tropical regions is more strongly influenced by annual precipitation and the seasonal distribution of rainfall than it is by temperature. While temperature does influence evapotranspiration regimes it only truly controls the altitudinal distribution of vegetation in montane zones (Hessler et al, 2010). Trapnell and Griffiths (1960) were first to systematically demonstrate the strong relationship between temperature and rainfall gradients and uniform vegetation zones on Kenyan Mountains. They proposed a climatic series of vegetation types based on differences between observed ecological zones. Since these seminal studies, additional factors; such as humidity (affected by fixed cloud condensation belts) and minimum temperatures (causing frost above 2700 m a.s.l.), have been included to explain variations in vegetation distributions (Hemp, 2005; Crawford, 2008; Platts et al., 2008; Saltré et al., 2013; Jacob et al., 2015). A simplified model of vegetation zonation on East African mountains is shown in Figure 2.4. Vegetation zones in the study area are discussed in Section 2.9. However, it is apparent from vegetation surveys on East African mountains that vegetation successions, involving unique interactions between local climate (e.g. the rain shadow effect and temperature lapse rate), topographic, and edaphic factors have resulted in distinctive Afromontane forest types; displaying both shared and divergent elements of species composition, structure, and ecological parameters. These factors often combine to create non-uniform vegetation distributions (Hamilton and Perrott, 1981; Hepper, 1983; Friis et al., 1992; Lovett, 1993; Mutangah et al., 1993; Muasya et al., 1994; Bussmann and Beck, 1995; Wass, 1995; Wilder et al., 1998; Bussmann, 2006 and references therein; Hemp, 2006a; Aerts et al., 2011) (see Appendix 2.3 for examples).



Physiognomic type	Potential natural vegetation (VECEA)	Vegetation type in literature	e	Description by White (1978, 1983) (A) Trapnell and Langdale-Brown 1972 (B) and Lind and Morrison 1974 (C)
High mountain vegetation	Alpine	Mixed afro-alpine communities		Vegetation of the highest mountains of tropical Africa ($3800-6000 \text{ m}$) that is characterised by giant <i>senecios</i> , giant <i>lobelias</i> , shrubby <i>alchemillas</i> and other plants of remarkable lifeform. There are no endemic genera and very few species do not occur in the Ericaceous and forest belt. (A)
	Mountain scrubland and moorland	Afro-montane evergreen bushland, thicket, shrubland and secondary grassland	v v	Bushland and thickets (3-13 m) occur on most of the higher mountains and on the crests and summits of the smaller mountains. On wetter mountains where the ground is not very rocky and there has been protected from fire for several years, the dominants form almost impenetrable thickets. They vary greatly in floristic composition, but some members of the <i>Erinaeee</i> are almost always present. On shallow soils, shorter shrubland occurs with stunted individuals of dominant <i>Erinaeee</i> of the bushland and thicket. (A)
	Bamboo woodland and thicket	Afro-montane bamboo		In East Africa, <i>Arundinaria alpina</i> is mostly found between 2380 – 3000 m, but it ascends to 3200 m on Mount Kenya. It grows most vigorously on deep volcanic soils on genule slopes that receive more than 1250 mm rainfall. Flowering is gregarious at intervals of at least 30 years. (A)
	and theat	Hagenia abyssinica woodland or scrub forest		This type of forest characteristally form almost pure stands in the narrow and often interrupted zones between taller types of montane forest and the thickets and shrublands of the Ericaceous belt. Some stands have the structure of woodland or scrub forest. (A)
Forest	Moist montane forest	Afro-montane rain forest		1200 – 2500 m, but the precise altitudinal limits vary according to the distance from the equator, sea and size and configuration of the massif. The mean rainfall lies between 1250 – 2500 mm. It differs from Guineo-Congolian rainforest in the occurrence of tree ferns (Cyathea), conifers (Podocarpus), a greater degree of bud protection and drip tips of leaves are less developed. (A)
	Dry montane	Undifferentiated Afromontane forest	쮎	Shorter than afro-montane rain forest and with distinctive composition. It replaces afromonantane rain forest at higher altitudes (and sometimes lower altitudes) on the wetter slopes and at comparable altitudes on the drier slopes. It usually but not always receives a lower rainfall. After fire it is sometimes replaced by almost pure stands of Juniperus procera or Hagenia abyssinica. (A)
		Juniperus procera forest		Mostly occurs on the drier slopes of mountains between $1800 - 2900$ m, but sometimes descends to 1000 m. Rainfall is $1000 - 1150$ mm. Succulents such as Dracaena and Euphorbia candelabrum are absent. Juniperus procera is a strong light demander and does not regenerate in its own shade and therefore requires fires for regeneration. (A)
	Dry intermediate forest	Dry transitional montane forest		On the drier slopes of East African mountains and uplands that rise from the Somalia-Masai plains. Only small fragments remain and there is little published informa- tion. There are some well-preserved examples near Nairobi between 1650-1800 m and rainfall around 800 mm. The main canopy is 15-18 m with emergents up to 25 m. (A)
Woodland	Acacia woodland	Somalia-Masai Acacia- Commiphora deciduous bushland and thicket		In higher rainfall areas, especially on rocky hills, the emergent trees occur closer together and are a little taller though scarcely ever more than 10 m. (A) $$
	Moist Combretum- Terminalia savanna	Wetter Combretum savanna		A small tree savanna with large-leaved species of Terminalia. Becomes woodland locally. (B)
Bushland and thicket	Evergreen and semi-evergreen bushland	East African evergreen and semi-evergreen bushland and thicket		Vegetation that occurs on the drier slopes of mountains and upland areas. It often forms an ecotone between montane forest (Juniperus) and Acacia- Commiphora bushland and thicket. (A)
Savanna	Upland Acacia savanna	Acacia-Themeda wooded grassland		The greatest development of this important vegetation type is the broad belt that encircles the Kenya highlands $1200 - 1500$ m with rainfall $500 - 750$ mm. The species composition varies from place to place depending on soil conditions and rainfall, but Acacia is always the commonest tree and Themeda triandra the dominant grass. (C)

Figure 2.4 Generalised* illustration of vegetation zones at different altitudes on East African Mountains, supplemented by a list of Potential Natural Vegetation types (after Lillesø et al., 2011), with corresponding vegetation types and associated descriptions from the studies from which they derive. The upper two zones (The Afro-Alpine and practically unvegetated Nival zones) are only found on the highest mountains (e.g. Mt. Kenya and Mt. Kilimanjaro), which stand at over 5000 m a.s.l. *Note: The uniform horizontal banding of vegetation belts depicted in this idealise model, are in fact often asymmetrical on many East African mountains. This is due to the rain shadow affect, that results in higher rainfall on the leeward side of these relief features (Olago, 1999; Bussmann, 2006; Hemp, 2006a; Street-Perrott et al., 2007) (see Figure 2.1 [A] for an example of how this phenomenon creates divergent dry (*Fb*) and moist (*Fa*) Afromontane forest types in the Nakuru-Naivasha Basin; and see Appendix 2.3 for examples of how local climatic, topographic and edaphic factors can influence non-uniform vegetation zonation and community structure on East African mountains).

<u>2.6 Contemporary environmental controls on C_3 and C_4 grass biogeography and ecology on East African mountains</u>

Under modern conditions, in the absence of large fluctuations in pCO_2 , the main environmental variables controlling C_3 vs. C_4 grass biogeography in the tropics are various combinations of temperature, moisture availability (i.e. mean annual rainfall, seasonality, and soil moisture retention), fire and light (i.e. vegetation openness relating to shade tolerance) (Livingstone and Clayton, 1980; Tieszen et al., 1979; Young and Young, 1983; Fredlund and Tieszen, 1997; Wooller et al., 2001a; Bremond et al., 2012) (see Appendix 2.4.1 for further details). Upwards of 500 species of Poaceae are native to Kenya. Surveys from East Africa (Livingstone and Clayton, 1980) including Kenya (Tieszen et al., 1979; Young and Young, 1983) of C3 vs C4 distribution and floral biomass in East Africa have shown temperature variations to be the primary factor influencing C3 vs. C4 grass dynamics. Summary findings from studies by Tieszen et al., (1979) and Livingstone and Clayton (1980) are shown in Figure 2.5. These are in agreement with studies from other tropical regions, which also indicate higher overall species diversity amongst Poaceae at lower elevations, and C4 species reaching higher altitudes in forested environments under locally drier conditions (e.g. Sage et al., 1999; Bremond et al., 2012). The relative proportions of the main C_4 Africa grass subfamilies in different lowland environmental settings are shown below in Figure 2.6. Further divisions within highland and lowland settings can be made based on the ecological preferences of different grass subfamilies and are considered in more detail in Appendix 2.4.1 The relative abundance of different grass subfamilies across soil moisture gradients is shown in Figure 2.7, and the phytogenic relationships and habitat affinities of the main grass subfamilies found in East Africa are reported in Figure 2.8. There are currently no detail vegetation surveys for Mt. Eburru that would provide a detailed picture of grass subfamily ratios at the elevations of Prospect Farm under present climate conditions. Vegetation maps of Mt. Eburru (Trapnell et al., 1976) and field observations made by the author, indicate that modern vegetation, developing on top of the Prospect Farm Formation, is evergreen and semievergreen bushland vegetation of probable forest origin (see Appendix 2.5 for details). This falls within the range of the Be PNV type which shares an ecotonal boundary with Afromontane forest [Fb]. Ecotonal conditions are modelled as being present at the site under current climate, in the absence of agricultural disturbance and degradation that effects vegetation communities at the site today (see Section 2.9).



C₄ grasses Basin (1755 - 2855 m a.s.l.). Light blue band represents range of sites at PF

Figure 2.5 The spatial distribution of C3 and C4 grasses along an altitudinal and moisture gradient in Kenya by Tieszen et al., (1979) and East Africa by Livingstone and Clayton (1980). (A) The percentage of C3 and C4 grass species along the altitudinal transect. (B) Number of grass species per square meter and per community along the transect. (C) Histogram of the number of C_3 and C_4 grass species at different altitudes in East Africa. (D) Percentage of C_3 and C_4 grass species which are in select floral lists from Kenya at altitudes above 800 m a.s.l. Collectively these surveys indicate that under recent climatic conditions, in the absence of other ecological controls, as well as anthropogenic vegetation degradation and agricultural activities; grass subfamiles at Prospect Farm would be dominated by C_4 forms (C_3 forms < 10% of the community), but are likely to be less species rich at mid to low elevation savanna sites. Competitive overlap between C_3 and C_4 species exist between 10 and 20°C. At the proposed crossover point from C4 to C3 dominance of 2500 m a.s.l., MAT on Mt. Eburru is ~15°C. Under these conditions C3 Bambusoideae growth is encouraged. If Mt. Eburru conforms to the trend recorded at other sites across Kenya, then we would expect a mix of C3 and C4 species, with higher amounts of C3 grasses present in forest settings and at higher elevations on Eburru. C4 % in box D indicates higher numbers of C4 species in the upper Afromontane forest zone in the Mau forest, associated with forest clearings. These trends suggest that above the tree line C4 grasses may be more species diverse in forest clearings, that can be often dominated by C3 forest dwelling grasses, than they are in more open woodland habitats at lower elevations on the mountain; but also that C4 grasses should have a lower biomass than C3 grasses in forest settings, as they tend to only occur in these clearings, while C3 grasses occur in both clearing and in forest understory vegetation. The subfamilies likely to be most prevalent under the inferred soil moisture regime at Prospect Farm are shown in Figure 2.7. Note that the generalised trends of this survey do not account for the limited number of C4 grasses that have been shown to grown above the tree line in the Afroalpine zone on certain mountains under high available moisture conditions (c.f. Wooller et al., 2001a). A, B, D adapted from Tieszen et al., (1979). C adapted from Livingstone and Clayton (1980).



Figure 2.6 Ternary plots of the relative proportions of species within the *Chloridoideae*, *Paniceae*, and *Andropogonae* C₄ groups from 'natural' and disturbed marshy lowland sites across Africa, compiled by Retallack (1992); following the ecological information collected by Rattray (1960) and taxonomic information from Watson and Dallwitz (1988). 'Lowland' is defined as 'vegetation occurring below 2000 m a.s.l.' by Rattray (1960). The diagrams indicate that *Chloridoideae* occur more in open grassland compared to the Panicoids *Paniceae* and *Andropogonae*, which generally prefer hot, moist climates, and occur in higher proportions in environments with woody cover. Further division between *Paniceae* and *Andropogonae* can be made based on global observations that *Paniceae* distribution are controlled primarily by rainfall, while Andropogonae requires relatively milder temperatures. *Andropogonae* are more abundant in grasslands disturbed by overgrazing and fire and so are considered to be ruderal.



Figure 2.7 Frequency of occurrence of grass species by subfamily and tribe along the moisture gradient in Kenya carried out by Tieszen et al., (1979). Soil moisture indices are those determined by Woodhead (1970) based on MAP, estimated potential evaporation and soil water storage. The solid blue bar indicates the modern available soil moisture index values in the Prospect Farm area. C₃ tribes within Pooideae (e.g. *Aveneae, Agrostideae and Festucae*) are recorded exclusively at high elevation sites under the highest available soil moisture conditions. C₄ (primarily NADP-ME) tribes *Paniceae* and *Andropogoneae* within the subfamily Panicoideae are most abundant at mid altitudes and medial soil moisture index values, and so theoretically should be the most abundant subfamily at Prospect Farm. C₄ (predominantly NAD-ME) subfamilies (e.g. Chloridoideae, and its tribes *Sporoboleae*, [containing some C₃ species] and *Eragrosteae*) and *Aristideae*, dominate at low elevations with low indices of available soil moisture > 10% of all species. They are not found at all in open grasslands. There is a sharp transition from communities of assorted C₃ and C₄ species to communities almost completely formed of C₃ taxa occurs in areas above 3000 m a.s.l.; where an abrupt drop-off in temperature (to below 10°C) occurs. This highlights the importance of physiological factors in controlling competition between grass subfamilies on East African mountains. Adapted from Tieszen et al., (1979).



Figure 2.8 Phytogenic relationships and habitat affinities of the main grass subfamilies found in East Africa. Information on grass subfamily phylogeny and photosynthetic pathways after the Grass Phylogeny Working Group II (2012), Washburn et al., (2015), and Rao and Dixon (2016). Information on habitat affinities of the main subfamilies are those complied by Barboni and Bremond (2009) following Watson and Dallwitz, (1992) onwards, Carr (1998), Aluka digital library of African plants (http://www.aluka.org), and the grass database of the FAO (http://www.fao.org/AG/AGp/agpc/doc/GBASE/Default. htm). Squares indicate the relative proportions of moisture requirements across all species (representing 79% of the grass genera listed in the flora of tropical East Africa) studied in a subfamily. This shows that individual species within subfamilies belonging to the PACMAD clade can often be assigned multiple modes of moisture requirements and are tolerant to a range of moisture conditions. The light requirements in the BOP clade broadly reflect the altitudinal distribution of C₃ grass subfamilies in East Africa i.e. the majority of Pooideae species occur in open conditions above forests in the Sub-Alpine/Afro-Alpine zone, while those located at lower altitudes occur almost exclusively in shaded habitats. Studies of the BOP and PACMAD clades indicate that winter rainfall is more important in controlling the niche preference and distributions on C₃ members of the PACMAD clade, while in C₃ BOPs and C₄ species temperature is most important (Pau et al., 2013).



Figure 2.9 Physiognomic vegetation types in Kenya after White (1983), adapted from Lillesø et al., (2011). (A) Y axis represents the minimum and maximum range of the tree heights in that vegetation type but not the proportion of different heights of trees found within that vegetation type, which is shown in (B) (i.e. tall tress (> 10m) can occur in Grassland in isolation or in riverine settings, however no trees above 2m occur in Shrubland).

2.7 Differentiating between forest and savanna

In the Afromontane vegetation zone, at the ecotone between forest/tropical woodland and upland savanna where rainfall is high, the boundary between these vegetation biomes is often distorted. Prospect Farm occupies a position in this landscape model, which in the absence of human disturbance, corresponds to the position of this ecotonal boundary under present climatic conditions (see Section 2.9). Distinguishing between the prevalence of forest or savanna ecosystems at different phases of occupation at Prospect Farm is crucial in order to test the *Ecotonal Hypothesis* and other behavioural-ecological models, as well as to establish the context of the MSA/LSA transition KCR (see Chapter 1). In general, savanna is replaced by forest when mean MAP exceeds 1500 mm and the dry season is neither too long nor too intense, thus limiting frequent fires which can destroy forest (Lenhmann et al., 2011; Murphy and Bowman, 2012). Further details on the factors that control the development these biome types are given in Appendix 2.4.2. Long-term alteration of these environmental factors during late Quaternary climatic fluctuations, in particular changes in seasonality and pCO_2 , and their effect on vegetation distributions in East Africa are discussed in Chapter 3.5.1, 3.5.2 and Appendix 3.4.1-3.4.2).

2.8 Disturbance regimes and tropical vegetation dynamics

Research over the last decade in high rainfall savannas (with MAP above ~650mm [Sankaran et al., 2005]) where the canopy cover would theoretically close up in the absence of disturbances, has identified repeated fires as playing a fundamental role in maintaining vegetation openness and thus ecosystem functioning in mesic savannas (Bond et al., 2003, Bond and Parr, 2010). In African savannas where MAP rises above ~800 mm, fires are prevented due to a shorter dry season because there is less time for grass to dry to fuel fire, and thus opportunities for ignition are reduced (Nelson et al., 2012 and references therein) (see Appendix 2.4.3 for additional supporting information related to disturbance regimes in these biomes). Other studies of historical responses of East African highland forest to abrupt climate change and other disturbances, indicate that while collapse of forest can be similarly rapid (in some cases in less than 25 years) (Eshetu and Högberg, 2000; Eshetu, 2002).

2.9 Modern vegetation of the study area

The Nakuru-Naivasha Basin falls within a single climatic zone, and variation in climate throughout the basin is controlled by altitudinal and rainfall gradients created by Rift Valley topography and local edaphic conditions. Modern vegetation distributions in the Nakuru-Naivasha Basin have been heavily impacted by agricultural activities (e.g. Hesslerová and Pokorný, 2010; Were et al., 2013), with stands of "natural" vegetation maintained within National Parks and gazetted forest reserves. Modelled Potential Natural Vegetation (PNV) distributions for the basin (Figure 2.10), based on the climatic ranges and edaphic tolerances of plant species under current climatic conditions and without anthropogenic interferences in the Nakuru-Naivasha Basin (Lillesø et al., 2011), are divided into 10 main vegetation types. At present detailed vegetation surveys of Mt. Eburru and the western Mau escapement are lacking. As such,

vegetation descriptions below are based on broad PNV types (Lillesø et al., 2011 and references therein) and those mapped by Trapnell et al., (1976). These are augmented by additional, more detailed information of plant community species composition provided by discontinuous vegetation survey observations of the main vegetation types from other areas of the basin (e.g. from the Aberdares (Schmitt, 1991) and Lake Nakuru (Mutangah, 1994; Dharani et al., 2006) National Parks; as well as guides on Kenyan vegetation (Greenway, 1973; Pratt and Gwynne, 1977; Lind and Morrison, 1974; Beentje, 1990; Beentje et al., 1994). Table 2.1 provides a summary of the common taxa found within each vegetation zone in the basin. Appendix 2.5, Figure 2.3 shows the distribution of soil types that are closely aligned with vegetation patterns across the Nakuru-Naivasha Basin. Appendices 2.6.1 and 2.6.2 provide additional details on vegetation distributions in the basin below/at and above Prospect Farm.

VECEA PNV type	Code	Location, climate elevation (m a.s.l.) and notes	Characteristic taxa	
Upland Acacia wooded grassland	We	Valley floor, between 1500 and 1890 m a.s.l. Hot and arid with very short rainy season (MAP range: 500-800 mm).	Grasses: Themeda triandra, Crynodon plectostachys, Sporobolus spicatus, Cynodon dactylon, Chloris gayana, and Cynodon nlemfluensis	
		Notes: Single Poaceae species can domiante grassland and bushed grassland of which <i>Themeda triandra</i> is the most abundant.	Shrubs/Trees: Acacia drepanolobium, Acacia bockii, Acacia seyal, Carissa edulis, Dodonaea viscosa, Euclea divinorum, Euclea racemosa, and Tarchonanthus camphoratus	
Evergreen and semi-evergreen bushland and thicke	Be	Valley floor, between 1500 and 1890 m a.s.l. Warm and arid with one long rainy season (MAP range: 500-800 mm).	Grasses: Digitaria scalarum, Themeda triandra, Crynodon plectostachys, Cynodon dactylon, Chloris gayana, and Cynodon nlemfluensis	
		Notes: On colluvial deposits at the base of hill and escarpments Tarchonanthus camph- oratus dominated bushland (<6 m tall and with canopy cover >20%) and Psiadia-As- pilia bushlands are found (included in Be vegetation type by PNV maps).	Shrubs/Trees: Acacia species (especially xanthophloea and drepanolobium), Psiadia punctulata, Digitaria scalarum, Vepris simplicifolia, Juniperus procera, Maytenus beterophylla, Aspilia mossambicensis, Dombeya burgessiae, Euclea divinorum, Euclea lanceolata, Rbus natalensis, Juniperus procera, Tarchonanthus camphoratus, Combretum splendens, Terminalia spp, Euclea lanceolata, Commiphora spp, Olea Africana, Teclea simplicifolia, Eucelea divinorum, Cordia ovalis, Euphorbia candelabrum, Psiad- ia punctulata, Aspilia mossambicense	
Edaphic wooded grassland	Wd	Low on the valley sides, between 1500 and 1890 m a.s.l. Warm and arid with one long rainy scason (MAP range: 950-1250 mm).	Grasses: Panicoideae (e.g. Andropogon spp, Cymbopogon spp, Digitaria spp, Hyparrhenia spp, Setaria spp and Pennisetum spp) as well as Themeda triandra and Chloridoideae (e.g. Cynodon spp, Eleusine spp and Eragrostis spp	
		Notes: C4 tussock grasslands growing on waterlogged ando-luvic phacozem soils are fextensive on the Kinangop Plateau.	Shrubs/Trees: Acacia species (especially Acacia drepanolo- bium, Acacia tortilis and Acacia seyal), Terminalia spp, Eupho- bia candelabrum, Tarconantbus camphoratus, Salvadora persica, Commiphora schimperi, Cordia monoica	
Freshwater swamp	Х	On the valley floor surrounding Lakes Nakuru and Naivasha, between 1500 and 1700 m a.s.l. MAP range: 500-950 mm).	Grasses and Sedges: Pennisetum macrourum, Oryza longistaminata, Phragmites australis, Cyperus papyrus, and Cyperus immensus	
			Rushes and Aquatics: Typha domingensis, Typha latifolia, Nymphaea spp	
			Shrubs/Trees: Acacia xanthophloea, Syzygium cordatum, Sesbania sesban, Syzygium cordatum	
Halophytic vegetation	Z	On the valley floor surrounding Lake Elmentatia, between 1500 and 1700 m a.s.l. MAP range: 650-950 mm).	Grasses and Sedges: Sporobolus spicatus, Cyperus laevigatus Shrubs: Pluchea indica	
		Notes: Pluchea bushlands develop on lacus- trine sediments (drainage impeded clay-loam) and diatomites.		
Riverine wooded vegetation and riverine forest	R	Valley floor, between 1500 and 1890 m a.s.l on the margins of rivers and streams. (MAP range: 500-1100 mm).	Shrubs/Trees: Syzygium guineense, Solanum incanum Maerua triphylla, Rhus natalensis, Ricinus communis, Grewie similis, Hibiscus calyphyllus Dombeya burgessiae, Diospyro mespiliformism, Trichilia emetic, Ficus spp (cspecially Ficu. sycomorus and Ficus thoningii), Ziziphus spp, Prunus africana Cordia monoica, Acacia spp	
		Notes: Riverine vegetation near Lake Nakuru (e.g. along the Nderit River) is charaterised by Acacia albida, A. xanthophloea, A. abyssinica, Albizia gummif- era, Ehretia cymosa, Ekebergia capensis, Euclea divinorum and Salix subserrata.		

VECEA PNV type	Code	Location, climate elevation (m a.s.l.) and notes	Characteristic taxa
Afromontane undifferentiated forest	Fb	Highland areas of Mt Eburru and the lower western slopes of the Aberdares ranges, between 1890-3000 m a.s.l. Climate varies between warm and arid a long rainly season in the east of the basin to Temperate and humid with a long dry season in the west of the basin. (MAP range: 950-1250 mm). Notes: In more open stands of Fbj, C3 Pooideae grasses (e.g. <i>Stipa dregeana</i> and <i>Brachypodium flexum</i>), herbs and low shrubs (e.g. <i>Berberis holstii</i>) are commonly found. In lower transitional zones where inter- mediate Fb grades into drier woodland and savanna vegetation, tree species become those that predominantly require lower available soil moisture (e.g. <i>Acacia abysinica, A. seyal, Olea stp, Nusia congesta, Calodendrum capense, Ekebergia cabensis</i>)	Trees: Juniperus procera, Podocarpus latifolius, Ochna holstii, Dombeya hurgessiae, Croton megalocarpus, Ocotea usambarensis, Chrysophyllum gorungosanum, Prunus africana, Grewia similis, Dracaena steudneri, Nuxia congesta, Bauhinia tomentosa, Syzygium guineense, Euclea divinorum, Hagenia abyssinica, Dodonaea viscosa, Zanlboxylum usamba- rense, Olea spp
			Lower canopy Trees/Shrubs: Anthocleista spp and Maytenus beterophylla
			Ferns, Herbs and Lianas: Diplazium spp, Dryoathyrium spp, Urtica massaica, Acanthaceae spp (c.g. Isoglossa gregorii, Isoglossa punctata, Justicia diclipteroides, Justicia betonica, Dicliptera laxata), Sanicula elata, Begoniaceae spp, Piperaceaespp and Ruhiaceae spp
			Forest understory Grasses: C ₃ Panicoideae (e.g. Oplismenus spp), Panicum monticola, Micrairoidcae (e.g. Isachne spp), Pooidcae (e.g. Bromus and Brachypodium) and mixed C ₃ /C ₄ tribes (e.g. Paniceae such as Setaria spp)
		(Bussmann, 2001, 2006), with an under- story that shares many species with that of moderately drier <i>Acacia</i> and <i>Olea</i> upland woodlands (e.g. Urtica massaica, <i>Rhus natalensis, Grewia similis, Hibiscus</i> calyphyllus, Senna spp etc.).	Forest clearing Grasses and Sedges: C3 sedges (typically <i>Carex monostachya</i>), with drier areas generally dominated by tufted C4 Poaceae (e.g. <i>Pennisetum Schimperi</i>), but also other C4 tribes (e.g. <i>Andropogon chrysostachyus, A. pratensis, Cymbopogon spp,</i>), C3 tribes (e.g. <i>Oplismenus</i>)) within the Panicoideae, or C3 Pooideae (e.g. <i>Agrostis spp</i>). Andropogon spp, Cymbopogon spp, Digitaria spp, Ilyparrhenia spp, and Pennisetum spp) as well as <i>Themeda triandra</i> and Chloridoideae (e.g. <i>Eleusine spp and Eragrostis spp</i>) are present above the tree line or in forest clearings on the Mua Escarpment
			Forest clearing Shrubs: Gomphacurpus fruticosus, Microglossa pyrifolia, Hypericum revolutum, Vernonia auriculifera, Thunbergia alata
Afromontane rainforest	Fa	Highland areas of castern slopes of the Aberdares ranges, between 1890-3000 m a.s.l. Temperate and humid with a long dry season (MAP range: 1250-1750 mm).	Shrubs/Trees: Cyalhea spp, Cola greenwayi, Cylicomorpha parviflora, Diospyros abyssinica, Strombosia scheffleri, Ocotea usambarensis, Ochna holstii, Syzygium guineense, Newbutonia macrocalyx, Grewia similis, Syzygy guineense, Macaranga capensis, Myrsine africana
		Notes: Where Fa replaces Fb, on locally more humid slopes of the Aberdares Range trees reaching heights of up to 50m.	Fa also containins species found in Fb (e.g. Prunus africana, Olea capensis, Juniperus procera, Podocarpus spp) (Agnew, 1985; Beentje 1990). Ocotea usambarensis has been recorded as becoming more dominant between 1550-2550 m a.sl. mainly on Mt Kenya but to a lesser extent on the eastern slopes of the Aberdares (Kigomo, 1987). The understory of this forest consists of shrubs and lianas (e.g. Drypetes gerrardii, Allophyllus cuneatus and Jaundea pinna-ta), liverworts and lichens (Agnew, 1985; Bussmann, 2006)
Afromontane bamboo	В	Highland areas of Mt Eburru and the Aberdares ranges, between 1890-3000 m	Grasses: Arundinaria alpina
·		a.s.l. Cool, and humid with one short dry season. (MAP range: 950-1750 mm).	Shrubs/Trees: Nuxia congesta, Prunus africana, Ilex mitis, Hagenia abyssinica, Podocarpus latifolius
Montane Ericaceous belt	Ε	Highland arcas of the Aberdares ranges, between 2880 - 3200 m asl. Perennially cold and humid. (MAP range: 1400-1750 mm)	Shrubs/Trees: Agauria salicifolia. Heathers: Erica arborea, Erica benguelensis, Erica trimera, Erica whyteana. Sub-Apline grasslands: C3 lawn and tussock grasses (predominantly Pooideae [e.g. Stipa spp, Poeae spp, Phalaris spp, Festuca spp, Brachypodium spp, Agrostis spp, Bromeus spp, Koeleria spp, Anthoxanthum spp]), some C3 Danthoni- oideae (e.g. Pentaschistis spp) as well as C4 Panicoideae (e.g. Pennise- tum clandestinum, Panicum subalbidum, and Andropogon lima

Table 2.1 Common/characteristic species list and associated climatic information to accompany VECEA vegetation distributions shown in Figure 2.10, and soil distributions shown in Appendix 2.5, Figure 2.3 for the Nakuru-Naivasha Basin. This information comes from Lillesø et al., 2011 (and references therin). Additional information about vegetation community composition and structure relevant to the study area is drawn from local published vegetation surveys cited in this table.



Figure 2.10 (A) Schematic hydro-climatic profile of the spatial differences of precipitation-evaporation across the Central Rift valley from X to X' (shown in [B]), based on data compiled by Bergner et al., (2009) from 17 meteorological stations. Adapted from Bergner et al., (2009). The precipitation-evaporation ratios demonstrate the rain-shadow effect; whereby the wetter western Rift flank (the Aberdares Range) supports moister Afromontane rainforest (*Fa*), while the drier eastern flank supports drier Afromontane forest (*Fb*) despite still having relatively high rainfall. (B) Potential Natural Vegetation (PNV) distributions in the Nakuru-Naivasha Basin. The PNV map was created by the Vegetation and Climate Change in Eastern Africa (VECEA) Project [Lillesø et al., 2011]). The PNV map for the study area was created using map Version 2.0 (Lillesø et al., 2011; van Breugel et al. 2011). Areas of solid colour indicate current National Park and Forest reserve boundaries. X and X' marks the cross-Rift transect shown in (A). Vegetation type codes (e.g. Fb for Afromontane undifferentiated forest) corresponds to species list in Table 2.1). The data on which PNV distributions are modelled, as well as how PVN distributions in the basin differ from modern vegetation patterns are covered Appendix 2.5. Under the PNV model, dry Afromontane undifferentiated forest (*Fb*) has its lower boundary at the Prospect Farm Formation (show in more detail in Figures 2.12 and 2.13).

Vegetation developing over the Prospect Farm Formation (Figures 2.11 and 2.12) is characterised by cultivated plots. Vegetation on uncultivated areas growing on the thin andosol developed volcanic material is patchy due to grazing and erosion; it is bushland dominated by *Tarchonanthus camphoratus*, and sparse C₄ grass cover (see Figures 2.12 and 2.13). Today, Afromontane forest on Mt. Eburru is present above ~2400 m a.s.l., within the Eburru forest reserve. Trapnell and colleagues' (1976) assertion that sporadic montane trees located at ~2000-2200 m a.s.l. originally derived from dry Afromontane forest (i.e. they constitute highly degraded *Fb*), is supported by PNV projections (Figures 2.10 and 2.13). These place the lower boundary between *Fb* and *Be* at ~2000 m a.s.l. under contemporary climate conditions (~850 mm MAP; see Figure 2.1). The lower slopes of Mt. Eburru where Prospect Farm is located, receives ~850 mm of rainfall annually. This is important as it places Prospect Farm on the border of the suggested 800 mm threshold, above which fire is thought to not have major influence on savanna and forest vegetation (Sankaran et al., 2005; see Section 2.8). This suggests that quite small shifts in MAP in the past could have resulted in switches at Prospect Farm between a vegetation system mediated by fire under lower rainfall to one in which fire played a negligible role because of higher rainfall.



Figure 2.11 (A) Image of the modern vegetation on Mt. Eburru (background) and the Prospect Farm Formation (foreground). Taken at base of the formation (marked by 'X' in Figure 2.13) at its northern limit looking south towards the north slope of Mt. Eburru. (B) Image of *Tarchonanthus camphoratus* dominated bushland that forms the principal vegetation type growing on top of the Prospect Farm Formation (Gsji7 location looking to the SW) today. (C) Aerial image of present-day Afromontane forest on Mt. Eburru (source: https://www.governorscamp.com/eburu-forest).


Figure 2.12 Near-present-day vegetation distributions on Mt. Eburru, and the surrounding area according to surveys by Trapnell et al., (1976). The location of sediment exposures of the Prospect Farm Formation and archaeological excavations studies considered in this thesis are indicated. The species composition of these vegetation types as well as how the relate to broader PNV vegetation types is disused in more detail in Appendix 2.5.



Figure 2.13 Comparison of vegetation zonation on Eburru in relation to the altitude of archaeological sites, and studies of sediment exposures identified as belonging to Prospect Farm Formation. White circles corresponded to the upper and lower limits of the Prospect Farm Formation. Blue and Red circles show the location of archaeological excavations (see Chapter 5). A) topographic profile (shown in C) of vegetation zonation based on those mapped by Trapnell et al., (1976) shown in Figure 2.12) Topographic profile VECEA PNV distributions (Lillesø et al., 2011) shown in Figure 2.10. C) Google earth satellite image of present day (2017) extent of Afromontane vegetation (diamond shape delimits the MT Eburru forest reserve fence at ~2300 m a.s.l.) and path of topographic transect on the north facing slope of Mt. Eburru shown in (A) and (B). Trapnell et al., (1976) placed the lower boundary of the Podocarpus-Juniperus forest at ~2515 m a.s.l., while Isaac et al., (1972) suggested that the forest savanna interface was located further downslope between 2130 and 2140 m a.s.l. While the exact location of the boundary in recent times is complicated by the absence of detailed descriptions and differences in measurement between studies, the more detailed maps of Trapnell et al., (1976) suggest the elevations reported by Isaac et al., (1972) were an overestimation.

2.10 Chapter summary

The information presented in this chapter has discussed how: 1) present-day vegetation distributions in the Afromontane Biome are strongly controlled by climatic-elevational gradients on East African mountains; 2) how localised environmental conditions and can create further subdivision within broader vegetation types; and 3) that the crossing of environmental tipping points can result in rapid shifts between apparently stable vegetation states. This chapter began by quoting the adage that "the present is key to the past". While study of the contemporary situation can act as valuable tool for interpreting the palaeoenvironmental changes, it is also important to acknowledge that the species compositions, biogeographic, and ecological patterning of vegetation communities, that exist today, are the cumulative result of the long-term ecological-evolutionary processes which have shaped them. In order to interpret long term trends in palaeovegetation change it is necessary to understand the complex ways in which vegetation may have responded to large fluctuations in past climate. To do so is it imperative to combine our modern understanding of species-environmental relationship with long-term independent records of species and environmental changes. The palaeoelimatic and internal ecosystem dynamics that are thought to have played an important role in palaeovegetation changes in East Africa are discussed in Chapter 3.

Chapter 3 Late Quaternary palaeoenvironmental change in East Africa

3.1 Introduction

As presented in Chapter 1, the site of Prospect Farm has the potential to act as a key sequence in contributing to our understanding of variability in the MSA record, and the extent to which palaeoenvironmental fluctuations acted as a selective force in this process. This Chapter highlights the ambiguity surrounding the nature of palaeoenvironmental changes that occurred in the KCR relative to other areas of East Africa throughout the late Quaternary period. The 'late' Quaternary is an informal sub-division of the period not recognised by the ICS International Commission on Stratigraphy, but is defined in this thesis as covering MIS 6 to MIS 1 (capturing the penultimate and last glacial-interglacial cycles [the terminal Middle and Late Pleistocene]); from ~200 kya until present. Understanding the differential response of the Nakuru-Naivasha basins to past regional palaeoclimatic trends relative to adjacent areas and lake basins has important implications for establishing if, and if so when, the area acted as refugium for human groups. Elucidating these sub-regional bio-geographic patterns is currently impeded by the current lack of detailed local and regional palaeoenvironmental records from equatorial East Africa prior to the LGM. Understanding how regional palaeoclimate trends were expressed in the study area is further complicated by the intermediate position that the KCR occupies near to the centre of regional climatic zones. Its location means that the KCR is likely to have been influenced by different monsoonal systems, which adds a further degree of complexity to the task of understanding the underlying causes of palaeovegetation changes in the Nakuru-Naivasha Basin in response to broader palaeoclimatic trends.

In order to understand the mode and tempo of palaeovegetation changes that occurred at Prospect Farm it is necessary to not only place the records of vegetation change within the context of modern vegetation dynamics (as introduced in Chapter 2), but to do so against the backdrop of the wider patterns and processes of palaeovegetation changes associated with regional late Quaternary climate dynamics; as well as internal local ecosystem dynamics that occurred on orbital and suborbital timescales. This Chapter introduces palaeoclimatic and associated palaeovegetation changes that occurred across East Africa between MIS 6 (the penultimate glacial maximum) and early MIS 1 (the beginning of the Holocene period), with three main goals in mind. These goals are 1) To introduce the main factors forcing and pacing late Quaternary climatic change, as well as historical developments and current paradigms in studies of the region's palaeoclimate dynamics; 2) To provide an overview of the changing spatiotemporal patterning of palaeoenvironmental change across the region, and to place the study area within the context of this pattern; 3) To very briefly highlight how the multitude of complex feedbacks between climate, vegetation, topography and other biotic/abiotic factors, that affect the climate ecosystem balance over time, can result in localised non-linear responses of individual species and vegetation communities to the same overarching forcing factors/palaeoclimatic trends.

The temporal/stratigraphic nature of palaeosol sequences, such as those at Prospect Farm, is such that an individual soil profile may represent a few hundred, and upwards of 10s of millennia (i.e. over a full half-precession climatic cycles in equatorial Africa (sensu Trauth et al., 2003). Thus, they are polygenic, time averaged assemblages of palaeoenvironmental conditions which are unlikely to be resolvable to submillennial scales (see Chapters 6 and 7.2). Consequently, palaeovegetation signals in these archives are unlikely to be resolvable to sub-millennial scales. Potentially rapid late Quaternary shifts in vegetation changes associated with complex zonal interactions in moisture sources and circulation patterns are likely not be resolvable in the Prospect Farm record. Nevertheless, it is still important to introduce them here along with the main drivers of change that have contributed to the broader environmental signals from the site.

3.2 East African climate and orbital forcing during the late Quaternary Period

As introduced in Chapter 2.2, seasonal variations in the distribution of insolation around the globe are important in controlling moisture availability in East Africa via the monsoons, ITCZ and CAB. On orbital and suborbital timescales, variations in monsoon dynamics are also thought to be the main influence on spatial and temporal changes in past climates, and by extension palaeovegetation distributions and past human habitats of East Africa. In turn, the alteration of these systems has been linked to changes within, and interactions between, global and regional air and sea surface-temperature gradients, as well as glacial-interglacial atmospheric and marine boundary conditions (Dupont and Kuhlman, 2017). Major shifts between different equilibrium states of glacial and interglacial conditions in climate, are driven by orbital forcing (i.e. cyclical, long-term, high-amplitude changes in incoming solar radiation related to the distance and angle of the earth relative to the sun, known as "Milankovitch cycles" [Milankovitch, 1941]) (Hays et al., 1976; Berger and Loutre, 1997; Yin and Berger, 2012).

The orbital parameter that exerted the strongest control on tropical climate viability over the last million years is thought to have been eccentricity which has a 100 kyr periodicity and acts as the amplifier for obliquity and precession forcing cycles; that occur on 41 kyr and 23 kyr timescales respectively during the late Quaternary period (Trauth et al., 2003; Clement et al., 2004; Wang, et al., 2007; Kutzbach et al., 2008; Wang et al., 2008; Cheng et al., 2012). Precession paced (19-23 kyr) cycles of equatorial insolation, proposed by Kutzbach and Street-Perrott (1985), alter the meridional temperature gradient, resulting in latitudinal displacement of the tropical rainfall belt, ITCZ and zonal shifts in the CAB (Mohtadi et al., 2014; 2016; Tierney et al., 2011a; 2011b). As such, precession has been linked to the large oscillations in lake levels recorded across Africa throughout the late Quaternary. Precession is described as being sinusoidal (Trauth et al., 2010) (i.e. there are periods of ~8000 years that experience minimal changes in insolation, followed by Transition Periods of ~2500 years when ~60% of the changes in insolation and seasonality take place [Maslin et al., 2005; Trauth et al., 2010]). North and south of the Equator in the tropics, stable 'Wet' and 'Dry' periods correspond to both precession minima (associated with increased humidity and high lake levels) and maxima (associated with increased aridity and low lake-levels) (see Appendix 3, Figure 3.1 [A, I, M]). Trauth et al., (2010) report that during 'Wet' Periods, large, deep rift

lakes can buffer the effect of short-lived climatic perturbations (e.g. IOD and El Niño episodes and Heinrich and Dansgaard-Oeschger [D-O] Events on millennial timescales), while enhanced aridity and evaporation during stable Dry Periods limits the effect of extreme rainfall events. In contrast, Transitional Periods are more susceptible to the influences of global climatic changes, whereby small changes in moisture availability are amplified by the topography of the rift (see Chapter 1.7.2.1), resulting in high amplitude and rapid local environmental changes. Past precession-driven climatic environmental changes in East Africa have been linked to alternating phases of forest retreat and savanna expansion in Africa, and correspondingly in the mediation of migratory pathways and viability of isolated forest, savanna and lake-shore ecosystems to act as refugia for human and faunal communities.

It has been suggested that due to the geometry of precession at the Equator, changes in insolation (and thus humidity) experience a double maximum; occurring at a half-precession (hemi-precessional) frequency of 10-11 kyr during maximum equatorial insolation in March or September (Berger, 1978; Berger and Loutre, 1997; Trauth et al., 2003; Bergner and Trauth, 2004). Strong hemi-precession signals are present in records near the Equator, including the study area from Lake Naivasha and Ol Njorwa Gorge, lacustrine sedimentary sequences in the Nakuru-Naivasha Basin, (Trauth et al., 2003; Bergner and Trauth, 2004) and at lake Challa (Verschuren et al., 2009) (see Section 3.4).

3.3. 'hinge-zone' behaviour of the African monsoon during the late Quaternary period

Recently published late Quaternary climatic and vegetation reconstructions, that use isotopic hydroclimatic and vegetation proxies, have led to suggestions of the existence of a climatic 'hinge-zone' (c.f. Barker and Gasse, 2003), which divides African lake basins into those that show more linear responses to either northern hemisphere or southern hemisphere climate forcing (Singarayer and Burrough, 2015 and reference therein). This theoretical line is drawn immediately north of Lakes Malawi (Figure 3.1 [K]) and Masoko, below which several southern African records show a strong direct response to southern hemisphere obliquity insolation forcing (e.g. Dupont et al., 2011; Caley et al., 2011 [Figure 3.1 and Appendix 3, Figure 3.1 (D)]; Collins et al., 2014; Castañeda et al., 2016 [Figure 3.1 and Appendix 3, Figure 3.1 (L)]). Eccentricity modulates precession so that when eccentricity is high (e.g. during MIS 6 and MIS 5) the influence of precession forcing is increased in lower compared to higher latitudes across the globe. Precession forcing amplified by eccentricity has been associated with the signal of "megadroughts" and lake highstands at both low and high latitudes in Africa (Scholtz et al., 2007). Records, such as those from lake Malawi, that span the end of MIS 6 until MIS 4 (from 135 ka to 75 ka (Scholz et al., 2007; Konecky et al., 2011; Stones et al., 2011; Figure 3.1 and Appendix 3, Figure 3.1 [K]), indicate that aridity was more extreme here during the penultimate glaciation (MIS 6) than during the LGM. Refilling and stabilisation of lakes occurred after ~70 ka in eastern Tropical Africa, associated with the decreasing influence of eccentricity on precession, and the southern displacement of the tropical rainfall belt and ITCZ (linked to changes in glacial boundary conditions) delivering more moisture to the region (Tierney et al., 2008; 2010; Scholtz et al., 2007). At the same time, sites in equatorial East African lakes (e.g. Lakes Victoria and Naivasha) continue to show instability due to the ongoing influence of precession at the Equator, which becomes progressively reduced by the time of the LGM (see Appendix 3, Figure 3.1 [I]). In other words, the decreasing influence of equatorial forcing may have allowed Northern and Southern Hemisphere forcing factors to exert a stronger influence on regional climates across Africa (see Tjallingii et al., 2008; Brown et al., 2007; Kuechler et al., 2013).

During the LGIT several hydroclimatic records from East Africa indicated that as the influence of the West African monsoon expanded, that the rift barrier in the Ethiopian Highlands (which at present limit its modern eastern extent [see Figure 3.1]) was breached by air masses drawing their moisture from the Atlantic Ocean. This allowed for regular incursions or possibly a semi-constant supply of moisture from West Africa into East Africa, delivered via the Congo Air Boundary (CAB) (e.g. Tierney et al., 2011a; Tierney and Zander, 2017). However, whether the CAB may have played a part in providing moisture to equatorial East Africa and the Central Rift Valley during the last glacial period; by breaching the moisture barrier formed by the EARS to airmasses originating in West Africa, is presently unclear. This is due to the lack of records from this area that would allow for the source of precipitation associate with lake highstands to be determined (see Appendix 3.1.1, 3.2 and 3.3 for details). Modelling of MAP during the last interglacial and LGM indicate that the highland areas of the Nakuru-Naivasha Basin continued to receive more rainfall than other areas in the Central Rift Valley, remaining relatively climatically stable (see Figure 3.2). Additional information on regional, sub-regional, and local late Quaternary climate trends in Africa and East-Africa, and the Nakuru-Naivasha Basin respectively, are provided in Appendix 3.1.1-3.3 and Section 3.4 and discussed in relation to results of palaeoenvironmental reconstructions from the study site of Prospect Farm in Chapter 7.



Figure 3.1 Letters A to U indicate the locations of palaeoenvironmental records discussed in the text and shown in Figure 3.2. Also shown are the present-day latitudinal limits of the monsoon belts in East Africa and the position of the putative climatic 'hinge-zone'. Also show is summary climatology (monthly changes in precipitation and temperature) for lowland and highland areas of East Africa and eastern Tropical Africa, based on satellite emitted long-wave radiation for the period 1981–2010 (from IRI database: http://iri.columbia.edu); along a rough N-S transect of the course of the seasonal movement of the rainfall belt: 1) Chew Bahir Basin, Ethiopia; 2) Lake Turkana Basin, Kenya; 3) Nakuru-Naivasha Basin (study area); 4) Lowlands between Boma National Park and Lake Turkana, South Sudan; 5) Muhesi Game Reserve, Tanzania; 6) Malawi Basin, Malawi/Mozambique.



Figure 3.2 Modelled mean annual rainfall in Eastern Africa for (A) The last interglacial (Otto-Bliesner et al., 2006); (B) The LGM (Braconnot et al., 2007); (C) The present (Hijmans et al., 2005). Adapted from Shipton et al., (2018).

<u>3.4 Palaeohydroclimatic changes in the Nakuru-Naivasha Basin and their context within</u> current models of late Quaternary interhemispheric monsoon dynamics

As introduced in Section 3.1, large fluctuations in the lake level of Naivasha during the last glacial period and the Holocene recorded in Ol Njorowa Gorge sequences (Figure 3.1 [H]) appear to correspond to half-precession forcing. The sequence provides a well-dated record of lake level changes between 175-60 ka (see Figure 3.3) and suggests that moderately high lakes existed during MIS 9 (~336-305 ka) or MIS 7 (~237-228 ka) (not shown), and that large fluctuations in lake level (up to +150 m) are evident from the MIS 6-MIS 5 transition onwards (Trauth et al., 2003; Bergner and Trauth, 2004; Bergner et al., 2009). Lake highstand events occurred at 139 ka-133 ka, ~113 ka -108 ka, ~91 ka, ~81 ka, ~72 ka and possibly ~66 ka. These roughly correspond to humid periods matching maximum equatorial March or September insolation and hemi-precessional forcing (Trauth et al., 2003).



Figure 3.3 Comparison of Late Quaternary lake level change in the Nakuru-Naivasha Basin, and insolation changes. (A) Lakelevel change in the Nakuru-Naivasha Basin based on records from Lakes Nakuru, Elementaita (Richardson and Dussinger, 1986; Trauth et al., 2001; Trauth et al., 2003). Solid black squares indicate ⁴⁰Ar/³⁹Ar dating from the Naivasha Basin; squares with no fill indicate ⁴⁰Ar/³⁹Ar dating from the Nakuru-Elementaita Basin. Circles indicate ¹⁴C dates following the same scheme. (B) Equatorial insolation data from (Berger, 1978). Adapted from Trauth et al., (2003). ⁴⁰Ar/³⁹Ar ages are from dating of ignimbrites and lava flows from the Ol Njorowa Gorge fluvio-lacustrine sequence (see Figure 1.7), which overlies younger Olkaria lava flow deposits (dated to 320 ka; not shown but representing the first evidence of a closed basin in which a large and stable rift lake formed).

The chronology of maximum lowstands and the environmental conditions during these periods are less well constrained than during lake highstand events, largely due to erosion or burial of these low-lake and desiccation horizons; however, they are likely to have occurred at around 332 ± 20 ka, 60 ± 2 ka and 32.3ka. Minor lake transgressions at 21-17.5 ka are congruent with maximum March insolation, while a similar highstand at 30-28.5 ka and 10-6 ka are not. Trauth et al., (2003) suggest an alternative mechanism to explain these highstands, with increased moisture delivery to the areas possibly being related to maximum June-July insolation in the Northern Hemisphere. If this is correct then the record demonstrates a non-linear relationship between the magnitude of changes in insolation forcing and the amplitude of lake highstands, as well as a lack of coevality between the timing of high lakes and insolation maxima. Alternatively, these highstands may relate to other mechanisms, such as to the presently unquantified influence of moisture delivered to equatorial East Africa via the Congo Air Boundary (CAB) (e.g. Tierney et al., 2011a; Tierney and Zander, 2017), and/or to the ill-defined combination of Northern and Southern Hemisphere forcing factors that are supposed to have exerted a stronger influence on regional climates across Africa during the LGIT (see Tjallingii et al., 2008; Brown et al., 2007; Kuechler et al., 2013); and/or to other unknown factors controlling the climate of the region during this period.

A general correspondence exists between these humid phases and higher sea surface temperatures (SSTs) (inferred from alkenones; Bard et al., 1997) from the western Indian Ocean and in records from Lake Challa (Moernaut et al., 2010; Sinninghe Damsté et al., 2011) and Lake Tanganyika (Tierney et al., 2010). There may also be a connection to be drawn between lake highstands at the end of MIS 6 and warmer western Indian Ocean SSTs (Rostek et al., 1997), although this requires further testing. Significantly, lake highstands at Lake Naivasha are not in phase with those observed at Tanganyika, Challa, or Malawi. This is a result of the increased influence of hemi-processional forcing at the Equator where it is located. It appears that while precession-based equatorial insolation is the main factor in hydroclimate change in the Nakuru-Naivasha Basin, more explicit links between factors determining local annual total rainfall and rainfall seasonality over the basin during the last glacial cycle are lacking. As are the relative contributions of local and more remote atmospheric circulation to this signal are currently unclear.

3.5 Responses of vegetation in East Africa to late Quaternary climate changes

Sections 3.2 to 3.4 have highlighted that high amplitude, sometimes rapid, spatially and temporal nonlinear changes in hydroclimatic conditions have taken place across East Africa during the late Quaternary period. Palaeoecological records have also shown that these changes have cause major rearrangement of composition and distribution of vegetation Biomes and have affected the relative stability and functioning of past ecosystems, for which there are no present-day analogues. However, at present only a few terrestrial vegetation records from East Africa extend past 45 ka that can inform vegetation change over a full glacial cycle and provide proximal records for direct comparison to vegetation changes at Prospect Farm. In order to interpret past vegetation changes at Prospect Farm it is necessary to consider the primary sources of variation responsible for vegetation change at the site on orbital and suborbital timescales. The Prospect Farm Formation occupies a mid-elevation position (from 2000 to 2150 m a.s.l.) between present-day upland savanna and Afromontane forest, and it has been shown that vegetation belts have shifted their mean elevations by up to \sim 1000 m in response to late Quaternary climate fluctuations. As such, the factors controlling vegetation changes within and between forest and savanna Biome states are of significance to vegetation reconstructions in this thesis. While high-elevation sites above the upper tree line are not thought to have been inhabited by humans, records from these zones provide important insight into late Quaternary vegetation dynamics in East Africa.

3.5.1 Long-term drivers of vegetation change on East African mountains

A central tenet of vegetation ecology is that vegetation physiognomy and composition, and plant species richness, is modulated by climate via critical processes for plant growth (i.e. photosynthesis, respiration and transpiration) (Gritti et al., 2010 and references therein). Seminal work on treeline shifts in East Africa during the late Quaternary period using pollen data from mid to high elevation (~2000-3000 m a.s.l.) sites advocated changes in either MAT or MAP (e.g. Coetzee, 1967; Livingstone, 1975; Hamilton, 1982) or both (Bonnefille and Riollet, 1988) as the primary divers of expansion of montane forest downslope or encroachment of savanna plants at higher altitudes. These studies postulate that this climatic downturn (i.e the reduction in MAP and MAT) experience duting the LGM, caused Afroalpine vegetation (i.e. cool elevation grassland and heathers) to expand at the expense of Afromontane forest belt. This belt was predicted to have contracted and moved downslope (Jolly et al., 1998), causing a depression in the treeline of up ~1000 m.

3.5.2 pCO₂ variability and internal ecosystem dynamics as long-term drivers of vegetation change

As research has progressed it has highlighted that the length and intensity of the dry season (Vincens et al., 1999; Lézine et al., 2011), variation in in atmospheric carbon dioxide (pCO_2) (Ehleringer et al., 1997; Bremond et al., 2012) and local scale vegetation-climate feedbacks (Zeng et al., 1999; Claussen, 2009; Hély, and Lézine, 2014), are equally if not more important than MAP and MAT in diving vegetation change. However, most importantly, is the combination of these variables that constitute the fundamental long-term controls on vegetation change in the tropics. Furthermore, recent studies show that ecological inertia, and local environmental parameters (e.g. fire, soil, topography, geology) that interact with rainfall and pCO2, influence both vegetation distributions and creating dynamic, asynchronous responses to regional climate trends in montane zones of East Africa (e.g. Wooller et al., 2003; Street-Perrott et al., 2007; Rucina et al., 2009; Sinninghe Damsté et al., 2011; Nelson et al., 2012; Urban et al., 2015; Fer et al., 2016; Ivory and Russell, 2016). (see Appendix 3.4.1 for supporting information on the long-term drivers of vegetation change on East African mountains and Appendix 3.4.2 for an explanation of the factors controlling the competitive balance of C₃ vs. C₄ plants under contrasting glacial and interglacial climate conditions).

3.5.3 Regional patterns of vegetation change in East Africa during the LGM, LGIT and Holocene

Patterns of vegetation change during the LGM, LGIT and Holocene across East Africa reflect the general pattern of wider millennial scale vegetation responses to deglaciation (Olago, 2001; Kiage and Liu, 2006; Willis et al., 2013) - upon which sub-millennial local-scale shifts in vegetation are superimposed. Regional scale vegetation distributions across Africa during the LGM broadly correlate with the moisture balance model show in Figure 3.4. In equatorial East Africa, reductions in forest taxa are evident during the LGM, however, their response is muted relative to other East African records from further north and to the west (Willis et al., 2013). This suggests that stable climatic conditions in these areas allowed them to act as continuous refugium (e.g. Mumbi et al., 2008; Finch et al., 2009; Rucina et al., 2009; Schüler et al., 2012), perhaps supporting greater species diversity than more sporadic refugia elsewhere in East Africa. Details of the records from equatorial East Africa and eastern Tropical Africa that collectively inform this pattern are provided in Appendix 3.5.



Figure 3.4 NCAR CCM3 GC model of geographic disruption of annual-mean precipitation minus evaporation across Africa for the LGM relative to today, produced by Kim et al., (2008), overlain with LGM palaeoclimatic conditions inferred from lake level based and pollen-based reconstructions. Image adapted from Kim et al., (2008) and Tierney et al., (2011b). Mesic conditions are predicted for the Easterm Arc Mountains (EAM) and the Ethiopian highlands. Because of the levels of biodiversity found in EAM rainforest (Myers, 1990) and the considerable time-depth of the mountains' formation (~30 mya; Griffiths, 1993) the EAM has long been hypothesised to be a zone of endemism and refugia. Results from both palynostratigraphy and modelling (Platts et al., 2013) of the EAM over the last 60 ka lend support to the idea that climatic stability across these mountain ranges associated with long-term moisture stability, provided by their proximity to the Indian Ocean (Fjeldsa° and Lovett, 1997; Lovett et al., 2005), created ecological stable conditions (termed the ecosystem-stability model [Finch et al., 2014]), which allowed the accumulation of unique reticulate species.

3.5.4 Palaeovegetation studies from the Nakuru-Naivasha Basin

Palaeolake level and pollen records from Naivasha (Maitima, 1991; Lamb et al., 2003) and ¹³C/¹²C ratios in late Holocene palaeosols on Mt. Eburru (Ambrose and Sikes, 1991) (summarised in Appendix 3.6), follow similar broad trends in vegetation change across the LGIT to those reconstructed at other East African sites (see Section 3.5.3). However, marginally wetter conditions are proposed for the KCR at Naivasha (Maitima, 1991) and the Aberdares Range (Perrott, 1982); as well as to the southeast in coastal areas at Lake Challa (Tierney et al., 2011b) and the Eastern Arc Mountains (EAM) (Finch et al., 2014) (see Figure 3.4). HadCM3 models indicate dry conditions (open grassland) at 21 ka during the LGM at lakes Nakuru-Naivasha and Challa, with both sites simulated as relatively wet in the earliest LGM (25-22 ka) (Singarayer and Burrough, 2015). Other simulations suggest more mesic mosaic forest and savanna conditions at 21 ka (Chala et al., 2017; see Chapter 1.7.1.3 Appendix 1 – Figure 1.2 [C]). This highlights the sometimes-conflicting signals provided by different environmental proxies, but also that when taken together the proxy and model results indicate that the mechanism regulating rainfall across the region vary on different time scales, as well as by location duirng the same period (Singarayer and Burrough, 2015). As such, the mechanisms of rainfall across a region at a certain time are not necessarily mutually exclusive, and the expectation is that at times the Nakuru-Naivasha Basin matched regional signals of change and at other times did not. Records from the basin also demonstrate that large-scale altitudinal changes in forest and savanna vegetation occurred in the basin during the Holocene, associated with lake level variability on millennial to sub-millennial time scales (e.g. Verschuren, 1997). Mass-balance model outputs of lake highstands, that incorporate vegetation climate-feedbacks under interglacial climate conditions, indicate that vegetation could have had a significant impact on local climate conditions and lake levels (see Bergner et al., 2003). This finding is supported by studies that show links between climate change, anthropogenic forest clearance, reduced water discharge to lowlands, and reduced lake levels in the Nakuru-Naivasha Basin in recent times (e.g. Verschuren, 1997; Becht et al., 2006; Hesslerová and Pokorný, 2010; Stoof-Leichsenring et al., 2011). However, vegetation changes prior the Holocene in the Nakuru-Naivasha Basin lack chronological resolution, and related biotic and abiotic drives and feedback remain largely unresolved. Our lack of understanding of local vegetation response during the late Quaternary period are especially apparent periods of low lake levels and desiccation events, for which lake records are absent (e.g. during MIS 4 and MIS 3).

As deposits at Prospect Farm accumulated as a result of volcanic activity on Mt. Eburru and possibly other sites in the KCR (see Chapter 5), the role of volcanism if palaeovegetation changes at the sites is also of considerable importance. Volcanism can have direct catastrophic effects for vegetation communities, destroying vegetation during eruption, but repeat volcanism can also affect soil moisture and drainage. These factors can in turn influence fire frequency, as well as promoting the growth of fire-tollerant taxa, such as *Olea*, as well as plants such as grasses and *Artemisia* griwng in clearings created by fire (Proctor et al., 2007; Bond and Parr, 2010; Jacob et al., 2015; Ivory and Russle, 2016). The factors, including volcanism, controlling changes in palaeovegetation distributions on East African mountains

during the late Quaternary period are discussed in greater detail in Chapters 6 and 7 in relation to phytolith-based palaeovegetation reconstructions from Prospect Farm.

<u>3.6 Implications of different vegetation states in the Nakuru-Naivasha Basin for evolutionary geography/behavioural ecological models</u>

The topography of the EARS may have also contributed to local palaeoenvironmental changes in the Nakuru-Naivasha Basin by acting as an atmospheric barrier to dry airmasses originating in the tropical Atlantic. This may have isolated the study area from the more severe influence of northern hemisphere climate forcing associated with glacial boundary conditions experienced for example on the Horn of Africa (see Tierney and Zander, 2017) (see Chapter 2.2, Section 3.3 and Appendix 3.1.1). The existence of a stable supply of moisture to highland areas of East Africa is also central to the hypothesis that highland areas of East Africa acted as refugia for flora, fauna and humans; maintaining biodiversity, as well as potentially acting as a montane archipelago route of migration (Basel, 2008) (see Chapter 1.7.1). The existence of refugial conditions for Afromontane plants and the associated ecological stability and resilience of highland areas relative to lower elevation areas of East Africa and other regions of Africa, has been most reliably demonstrated for the Eastern Arc Mountains and Mt. Kilimanjaro; and to a lesser extent Mt. Kenya (Mumbi et al., 2008; Finch et al., 2009; Rucina et al., 2009; Schüler et al., 2012) (see Section 3.5.3). Palaeoenvironmental reconstructions from other areas of East and eastern tropical Africa, indicate that different drivers and local feedbacks (e.g. Rucina, et al., 2009; Ivory and Russle, 2016) could have a great effect on the area's ability to act as a refugium for savanna and forest taxa, as well as the individual and collective ability of these vegetation types to support human populations at different times. At present, it remains unclear if putative periods of relatively high lake levels in the Nakuru-Naivasha Basin during the LGM are primarily linked with more stable moisture supply from the Indian Ocean, as has been hypothesised for the site across the EAM (Finch et al., 2014). However the available records suggest that the basin apparently experienced a less severe LGM compared to other sites in or near to the KCR (Olago, 2001; Willis et al., 2013). Naivasha Basin lacustrine records indicate an intensifying drying trend from MIS 4-3 (see Section 3.4), similar to that observed in records north of Lake Challa in the Ethiopian Rift and Horn of Africa (e.g. Foerster et al., 2012; Tierney, 2013; Tierney and Zander., 2017). This suggests that the Nakuru-Naivasha Basin may have responded differently to coastal areas in the southeast that demonstrate greater ability to temper the effects of aridity associated with orbital forcing and glacial boundary conditions. Alternatively, the mechanism controlling precipitation in the Nakuru-Naivasha Basin may have been somewhat different to these sites. Furthermore, the designation of Lake Naivasha as an 'amplifier lake' (Street-Perrott and Harrison, 1985; Olaka et al., 2010; see Chapter 1.7.2.1) underlies the expectation that its lake level will be strongly controlled by highland precipitation. However, it is currently not known if locally steep altitudinal and rainfall gradients buffered the effect of aridity (e.g. during the penultimate glacial maximum ~ 140 ka, MIS 4 [71-57 ka] and during the LGM), and created forest refugium (sensu Basell, 2008; Blome et al., 2012) that were more resilient to periodic drought; or if the closed basin morphology of the Nakuru-Naivasha Basin amplified these changes, causing shifts in vegetation that roughly tracked lake level and

orbital precession. Additionally, the extent to which internal vegetation-hydrological feedbacks, local disturbance regimes, and lower pCO_2 contributed to climatic and vegetation changes is poorly constrained.

3.7 Chapter summary

Throughout the late Quaternary period East Africa has supported a spectacular range of terrestrial ecosystems, which display strong spatiotemporal differences in glacial and interglacial boundary conditions and regional climate changes, as well as highly non-linear responses to complex and varying combinations of environmental determinants on both orbital and sub-orbital timescales. Evidence of the dynamic response of vegetation to climate forcing and its mediation through local agents (e.g. fire topography, edaphics, atmospheric gas concentrations, grazing/browsing, volcanic activity and ecological inertia) has signalled a theoretical shift away from studies that seek to determine the monolithic drivers of vegetation, towards those that attempt to reconstruct and understand the multifarious elements that have contributed to the vegetation history of an area. Furthermore, partially coincident forcing factors and climate-vegetation feedbacks have been shown to be responsible for ecological threshold behaviour (i.e. the rapid shift between different ecological states [Scheffer and Carpenter, 2003; Maslin, 2004]). A major challenge for palaeoenvironmental research is to tease apart these interactions to overcome issues of differential response rates of elements within these systems, to external and internal forcing factors. This approach allows researchers to be more certain the underlying causes of specific environmental changes and the adaptive responses of humans to them (Maslin and Christensen, 2007; Trauth et al., 2007; Maslin et al., 2014). The research presented in the following Chapters 4-7 of this thesis report phytolith based reconstructions of local scale vegetation reconstructions from the MSA/LSA site of Prospect Farm. These aim to provide insight into the status of the site as a refugium, the movement of the savanna forest interface over time; as well as MSA habitat preferences and adaptations to past environmental change in the Nakuru-Naivasha Basin, in relation to testing MSA behavioural-ecological models (see Aims and Objectives: Chapter 1.9).

Chapter 4 Modern plant-phytolith studies, phytolith descriptions and classifications in the Afromontane zone

4.1 Introduction

Phytoliths are preserved in Prospect Farm MSA bearing sediments, providing us with an opportunity to establish local changes in past vegetation communities, and the palaeoenvironmental context of the occupation of the site over time. Interpretation of phytoliths in the fossil record relies upon comparison to phytoliths extracted from living plants, as well as to soil phytolith assemblages from different extant vegetation communities (see Chapter 5.6.6). No modern reference collection of phytoliths from woody plants exists for the Nakuru-Naivasha Basin within the Afromontane zone. To correct this deficit and to inform phytolith classifications used to interpret the phytolith record from Prospect Farm (see Chapter 6), Chapter 4 reports studies designed to establish phytolith morphological-taxonomic relationships in indicator and characteristic woody and herbaceous dicotyledon species from forest, woodland, and savanna vegetation communities in the study area. Classification schemes based on published records of variability in phytolith production across East African grass subfamilies that act as guide for interpreting phytolith types originating from Poaceae in the fossil record, are also outlined.

4.1.1 The utility of phytoliths in vegetation reconstructions from open-air archaeological sites.

After plants die and decompose, phytoliths are released into the soil, creating a polygenic assemblage that provides a generalised time-average picture of past vegetation (Strömberg, 2004; Piperno, 2006). Due to their resistance to decay, phytoliths are preserved in open-air sedimentary contexts as old as the Eocene (Strömberg, 2005), where organic botanical remains are usually destroyed. This is also the case in the Prospect Farm sequence, where other botanical remains (e.g. seeds, charcoal, and pollen) only rarely survive from the most recent Holocene phase of deposition (see Chapter 5.4.1). Phytoliths have been shown to be valuable proxies in local vegetation reconstructions in African Plio-Pleistocene and late Quaternary records. (see Appendix 4.1 for additional information on these studies and of phytolith production in plants). Arguably, the greatest utility of phytoliths in this respect is their ability to identify grasses to a subfamily level (see Section 5.6.5.6 and Appendix 5.4 - 5.9), that is unachievable using other vegetation proxies such as pollen. As grass subfamilies have been shown to follow altitudinal, ecological, and climatic gradients on East African mountains and to respond differently to changes in *p*CO₂ (see Chapters 2.6 and Appendix 3.4.1-3.4.2), the ability to identify changes in the relative supremacy of these groups in the Prospect Farm sequence is important in understanding vegetation responses at the site to past climatic changes (see Chapters 5.6 and 6.7).

4.1.2 Considerations and limitations of the use of phytoliths in palaeoenvironmental reconstruction

As stated, at a fundamental level, interpretation of phytoliths in the fossil record relies upon comparison with phytoliths from modern plants. Phytolith analysis is limited by inherent factors relating to the variable production and taxonomic classifications of phytoliths in different plant groups, as well as by the taphonomic processes affecting their preservation in various depositional environments (see Piperno [2006] and Appendix 4.2 for supporting information on general trends in phytolith production across different phylogenetic orders of plants). The greatest difficulty inherent in studying phytolith assemblages occurs because of their 'multiplicity'; the occurrence of different morphotypes within the same taxonomic groups, and 'redundancy'; the production of the same phytolith morphotype across different taxonomic groups in unrelated plants with similar vegetative tissues and cellular structures (Rovner, 1988; Collura and Neumann, 2017). Multiplicity and redundancy arise as the result of both genetic inheritance and high levels of convergent evolution in higher plants (Piperno, 2006). Ultimately, multiplicity, redundancy, and differential phytolith production rates in plants result in certain plants/plant groups being poorly represented in the sedimentary record which can hinder palaeobotanical reconstructions. These issues can be exacerbated by the polygenic nature of soils and taphonomic factors. Taphonomic processes that can bias vegetation reconstructions are considered in greater detail in relation to the depositional environments in the Prospect Farm sequence in Chapter 6.7.3.1. and 6.7.3.2.

4.1.3 Rationale and approach

Despite the limitations discussed in the previous section, phytoliths are useful indicators of vegetation composition and structure, particularly in tropical settings. However, to reiterate, robust palaeovegetation reconstructions are contingent upon understanding the relationships between phytolith production and morphology in living plants and vegetation types in a study area (e.g. Carnelli, 2001, Carnelli et al., 2004; Lu and Liu, 2003; Gallego and Distel, 2004; Tsartsidou et al., 2007). Both qualitative and quantitative information exists on phytolith production in various plants from the main phytogeographical zones of sub-Saharan Africa. These studies have tended to focus on phytolith production and morphology in grasses (e.g. the from Somalia-Masai and the Afromontane zones [Barboni and Bremond, 2009]; the Sudano-Sahelian [Fahmy, 2008; Novello et al., 2012; Novello And Barboni, 2015; Neumann et al., 2017], the Guineo-Congolian zone [Runge and Runge, 1997] and from across southern African [Cordova and Scott, 2010; Cordova, 2013; Novello et al., 2018]), instead of in species of woody dicotyledons. To date, systematic studies that provide quantitative taxonomies of phytolith production in woody plants exist from the Guineo-Congolian zone (focusing solely on the morphology of phytoliths from wood and bark [Collura and Neumann, 2017]) and from the Mozambiquean Miombo woodland of the Zambezian zone in eastern Tropical Africa (Mercader et al., 2009). These studies have highlighted the similarities but also the considerable differences which can exist in production rates of indicative morphotypes between different African vegetation zones. While studies of soil phytolith assemblages exist for the Afromontane zone (see Barboni et al., 2007; Bremond et al., 2008a and Chapter 5.6.6) and there is a small degree of overlap of species between the Zambezian and Afromontane zone, no studies to date have been carried out of taxonomic-morphological relationships of phytoliths in woody plants from the Afromontane zone.

As this thesis aims to better understand changes in forest cover over time within the Afromontane zone, identifying morphotypes from species in this zone that have taxonomic and ecological importance, as well as understanding levels of multiplicity and redundancy across key species, is important for the resolution of palaeoenvironmental reconstructions. Consequently, I attempt to determine variability in phytolith production, polymorphism rates, dissolution potential, type frequencies, and the identification of diagnostic morphotypes in characteristic and indicator species (mainly of ligneous and herbaceous dicotyledon) from vegetation types and ecological settings within the Afromontane zone. Species sampling focused on the vegetation zones that have been recorded in ethnographies and archaeological records of the Afromontane zone as having been visited by recent/extant hunter-gatherer and by MSA and LSA groups in the Nakuru-Naivasha Basin (see Appendix 1.7.1 - 1.7.5) (e.g. Afromontane forest, transitional forest/woodland and bushland types [Olea forest, Euphorbia candelabrum forest, Acacia woodland/forest] and savanna vegetation; including lakeside and riverine plant communities, but not the Afroalpine zone). Results are used to inform woody phytolith classifications for the study of fossil phytolith assemblages at Prospect Farm (see Chapter 6.7.6). As the phytoliths from the modern botanical samples from the study area do not capture the full range of phytoliths morphologies observed in the fossil assemblages, other published phytolith reference collections from Africa were also used to fill the gaps in morphotype classifications. While select samples of Poaceae and Cyperaceae samples were also collected from the Nakuru-Naivasha Basin, classifications of grasses rely on published comprehensive reference collections for the region (see Section 4.2.3). These modern samples of herbaceous monocots collected in the study area were not included in the analysis presented here, but instead acted as a practical guide for the author of these plant types and as a training resource for future researchers at the University of Cambridge choosing to carry out similar studies in the region. As such, they are not discussed here. One exception to this is a sample of Arundinaria alpina (Afromontane bamboo) that was collected to better clarify the prevalence of certain indicator phytoliths in this grass, that have been debated by different reference collection studies (see Sections 4.3.5, 5.6.5.6 and Appendix 5.4 - 5.9).

4.2 Materials and methods

4.2.1 Field collection and identification of botanical samples

A list of characteristic and indicator species of conifers, woody and herbaceous dicotyledons, and nongrass herbaceous plants was compiled for the Nakuru-Naivasha Basin based on vegetation types identified by the VECEA vegetation project (Lillesø et al., 2011 and references therein) and local vegetation surveys (Mutangah, 1994, Mutangah & Agnew, 1996; Dharani et al., 2009; Ng'weno et al., 2010) (see Chapter 2.9). Botanical samples were collected within the basin, primarily on Mt. Eburru, following the approach of Albert and Bamford (2012): Samples were collected in February, during the dry season, when the accumulation of phytoliths in plant tissue is expected to be highest (Mercader, 2009). Each botanical specimen was photographed in its growing context and again following collection. As many component parts of the plant (e.g. leaf, stem, bark, inflorescence, fruit etc.) as possible were sampled. When one or more of these elements were absent this was noted. Identification of woody plants relied upon field guides (e.g. Dale & Greenway, 1961; Dharani, 2011) and the knowledge of local guides. Identifications were confirmed with the aid of staff and reference material from the East African Herbarium in the National Museum of Kenya (NMK). In total 87 species from 40 different genera were collected and assigned to either forest, woodland, or savanna habitats. Botanical nomenclature followed Klöpper et al., (2007). The names, photosynthetic pathways used by each species, the parts of the plant collected and processed, as well as the light and water requirements of species within the habitats (based on the available literature), are provided in Table 4.1.

Family and subfamily	Species	Parts collected	W-R	L-R	C3/C4/cam VZ
Acanthaceae	Thunberoia alata Boier ex Sims	Stem, leaf, inflorecences	Me	O/S	C3 W
Amaranthaceae	Achyranthes aspera L.	Stem, inflorecences	Me	S	C3 G
Apocynaceae	Acokanthera oppositifolia (Lam.) Codd	Branch, leaf, inflorecences	Me M-	S	C3 W
Apocynaceae	Leptadenia hastata (Pers.) Decne	Stem leaf inflorecences	Xe	0/3	C3 G
Apocynaceae, Asclepiadoidea	Sareostemma viminale L.	Stem, leaf, inflorecences	S-Xe	Ŏ/S	Č3 Ā
Araliaceae	Cussonia arborea Hochst. ex A.Rich.	Branch, leaf	Me	O/S	C3 G
Arecaceae	Hyphaene compressa (H.Weld)	Bark, leaf, inflorecences, fruit	S-Xe	0	C3 G
Asteraceae	Aspilia mossambicensis (Oliv.) W ild Corvera sumetrensis (Retry) F. Walker	Stem leaf inflorecences	Me	\$/5	$C_3 W$
Asteraceae	Felicia muricata (Thunh.) Nees	Stem, leaf, inflorecences	Me	Ŏ/S	Č3 W
Asteraceae	Microglossa pyrifolia (Lám.) Kuntze	Stem, leaf, inflorecences	Me	S/O	C3 A
Asteraceae Compositae	Pluchea induca (L.) Less. Desiadia punctulata (DC.) Vathe	Branch, leaf, inflorecences	Me/He S Xe/Me	8/8	C3 W
Asteraceae	Tarchonanthus camphartus L.	Branch, leaf, inflorecences	Se-Xe/Me	ő	C3 W
Asteraceae	Vernonia auriculfera Schreb.	Branch, leaf, inflorecences	Me	O/S	C3 W
Asterales	Sphaeranthus suaveolens (Forssk.) DC. Diplovium hylothilum (Hieron) C.Chr	Stem, inflorecences	He	Q.	$C_3 = W$
Athyriaceae	Dryoathyrium borvanum (Willd.) Ching	Stem, inflorecences	Me	o/s	C3 A
Boraginaceae	Cordia africana Lam.	Branch, leaf, fruit	Me	Õ/Š	C3 G
Boraginaceae	Cordia monoica (Roxb.)	Branch, leaf, fruit	Me	O/S	C3 A
Capparaceae	W arourgin ugunaensis Sprague Boscia coriacea Pax	Branch, leaf, fruit	Me	0/8	
Capparaceae	Cadaha farinosa Forssk.	Stem, leaf, inflorecences	S-Xe	ŏ	C3 G
Capparaceae	Cadaba rotundifolia Forssk.	Stem, leaf, inflorecences, fruit	S-Xe	Ō.	C3 G
Capparaceae	Maerua triphylla A. Rich.	Branch, leaf, inflorecences	Me	O/S	C3 W
Celastraceae, Hippocrateaceae	Maytenus hetrophylla (Eckl. & Zeyh.) N.Kobson Terminalia hrownii Fresen	Branch, leaf inflorecences fruit	Me	0/8	C3 W
Compositae	Solanecio mannii (Hook.f.) C.Ieffrey	Branch, leaf, inflorecences	Me	s/o	C3 Ĝ
Cupressaceae	Juniperus procera Hochst. ex Éndl.	Branch, leaf, inflorecences	Me	O/S	C3 A
Ebenaceae Eucharbiageae Crotopoidea	Eluclea divinorum Hiern	Branch, leaf	Se-Xe/Me	O/S	C3 A C3 W
Euphorbiaceae	Euphorbia hussei var. kihwezensis	Branch, fruit	Me	O/s	C3 G
Euphorbiaceae	Euphorbia candelabrum Kotschy	Branch, inflorecences	Me	O)	C3 G
Euphorbiaceae	Neoboutonia macrocalyx Pax	Branch, leaf, inflorecences	Me	S/O	C3 G
Euphorbiaceae, Acalyphoideae	Crotalaria lebrunii Baker f	Branch leaf inflorecences pods	5-Ae/Me Me	0/8	C3 W
Fabaceae, Caesalpinioideae	Cassia didymobotrya (DC.) Irwin & Barneby	Branch, leaf, inflorecences, pods	Me	s/o	C3 W
Fabaceae	Bauhinia tomentosa L.	Branch, leaf, inflorecences	Me	O/S	C3 A
Fabaceae Fabaceae Faboideae	Crotalaria agatifolia Schweinf.	Branch, leaf, inflorecences, pods	Me	O/S	C3 G
Fabaceae	Notonia hildebrandtii (Vatke) Torre	Branch, leaf, pods	S-Xe/Me	0'3	C3 G
Fabaceae, Caesalpinioideae	Senna spectabilis (Fresen.) Irwin 🕉 Barneby	Branch, leaf, inflorecences, pods	Me	0	C3 W
Fabaceae	Sesbania seban (Jacq.) W. Wight	Branch, leaf, inflorecences, pods	S-Xe/Me	8	C3 W
Fabaceae	Acacia diepansohium (Harms ex Siöstedt) P.I.H.Hurter	Branch, leaf, inflorecences	S-Xe/Me	O/S	C3 G
Fabaceae, Mimosoideae	Acacia xanopholoea Benth. P.J.H.Hurter	Branch, leaf, inflorecences, pods	Xe/S-Xe	Ő/S	C3 G
Gentianaceae	Anthocleista zambesiaca Afzel. ex R.Br.	Stem, leaf	Me	O/S	C3 W
Lamiaceae	Leucas nepetifolia Benth	Stem leaf inflorecences pods	Me	0/5	C3 W
Lamiaceae	Leonotis nepetifolia (L.) R.Br.	Branch, leaf, inflorecences	Me	Ő/S	Č3 Ŵ
Lamiaceae	Ocimum gratissimum L.	Branch, leaf, inflorecences	Me	O/S	C3 A
Lamiaceae Lamiaceae Nepetoideae	Plectranthus barbatus Andrews Plectranthus cylindraceus Hochst ex Benth	Stem, leaf, inflorecences	Me	3/U	$C_3 W$
Lamiaceae, Viticoideae	Vitex doniana L.	Branch, leaf	Me	O/S	C3 Å
Malvaceae, Sterculiaceae	Dombeya burgessiae Gerr. ex Harv.	Branch, leaf	Me	O/S	C3 G
Malvaceae, Grewioidea	Grewia similis K.Schum. Hibiseus caluthullus Can	Branch, leaf, inflorecences	Me	0/8	CAM G
Melianthaceae	Bersama abyssinica Fresen.	Branch, leaf	Me	0/S	C3 G
Moraceae	Ficus cordata Vahl	Branch, leaf, fruit	Me	O/S	C3 G
Moraceae	Ficus successory I	Branch, leaf, fruit Branch, leaf	Me	8/8	$C_3 G$
Moraceae	Ficus thonningii Blume	Branch, leaf, fruit	Me	O/S	C3 Ğ
Moraceae	Ficus wakefeldii L.	Branch, leaf, fruit	Me	0	C3 W
Myrsinaceae	Kapanae nelanophleos (L.) Mez	Branch, leaf	Me Me	8/8	C3 G
Nolinoideae, Dracaenaceae	Dracaena steudneri Enel.	Branch, leaf, fruit	Me	O/S	C3 A
Ochnaceae	Ochna holstii Engl.	Branch, leaf	Me	O/S	C3 A
Oleaceae	Olea africana (Wall. ex G. Don) Cif.	Branch, leaf, fruit	Me	O/S	$\begin{array}{cc} C3 & A \\ C3 & C \end{array}$
Podocarpaceae	Podocarbus latifolius (Thunh.) R.Br. ex Mirh.	Branch, leaf	Me	O/S	C3 A
Polygonaceae	Rumex usambarensis Engl. ex Dammer	Branch, leaf	Me	O/S	C3 A
Pteridaceae	Pteris abyssinica Hieron.	Stem, inflorescences	Me M-	O/S	C3 A
Rutaceae	Colodendrum capense (I.f.) Thunh	Branch leaf	Me	0/8	C3 A
Rutaceae	Vepris simplicfolia (Engl.) Mziray	Branch, leaf	Me	š/ŏ	Č3 Ĝ
Rutaceae	Zanthoxylum gilletii (De Wild.) P.G.Waterman	Branch, leaf	Me	O/S	C3 G
Kutaceae, Toddalioideae Salvadoraceae	Zaninoxylum usumbarenses (Engl.) Kokwaro Salvadora persica Forssk	branch, leat Stem leaf inflorecences	Me	5/0	C3 G
Sapindaceae	Dodonaea augustifolia L.f.	Branch, leaf, inflorecences	S-Xe/Me	ŏ/s	C3 A
Solanaceae	Solanum aculeastrum Dunal	Branch, leaf, fruit	Me	O/S	C3 W
Solanaceae	Solanum incanum L.	Branch, leaf, inflorecences, fruit	Me Me	O/S	C3 W
Urticaceae	Obetia pinnatifida Baker	Branch, leaf	Me	O/S	C3 A
Urticaceae	Urtica massaíca Mildbr.	Stem, leaf	Me	O/S	C3 W
Verbenaceae	Lantana trifolia L. Libbia ignatica (Burnet) Streng	Stem, leaf, inflorecences	Me Me	O/S	C3 A
verbenaceae	Lappia javanica (Durm.j.) Spreng	Dranch, lear, inflorecences	TATC	0/3	CJ A

Table 4.1 Species list of botanical samples collected for phytolith extraction. VZ= Vegetation zone (A=Afromontane forest[2500-300 m a.s.l.], W=woodland [2000-2500 m a.s.l.], G=grassland [savanna] [1500-2000 m a.s.l.]). W-R=water requirements(Me=Mesophyte, Xe=Xerophyte, S-Xe=Semi-Xerophyte, He=Heleophyte. L-R= light requirements (open [O] or shaded [S]).

4.2.2 Extraction of phytoliths from botanical specimens

The extraction of phytoliths from modern plant specimens followed the dry ashing procedure developed by Parr et al., (2001), and adapted by Albert and Weiner (2001), with further modifications following Mercader et al., (2009) (see Appendix 4.3 for procedure details).

4.2.3 Phytolith identification and classification

Phytoliths were identified by scanning the full slide at $40 \times$ magnifications with an Olympus BX40F epifluorescence microscope. Photomicrographs of each morphotype were taken using ImagePro-Plus version 5.0. Phytoliths were identified, classified, and described according to criteria set out by the International Code for Phytolith Nomenclature 1.0 (Madella et al., 2005). For purposes of simplicity, the full range of morphologies, identified as having been produced by non-grass herbaceous and arboreal species and used for interpreting the fossil record at Prospect Farm, are presented here. This includes grass phytoliths and other morphotypes recorded in the Prospect Farm sequence (classified to taxonomic groups according to Runge (1999), Barboni et al. (1999), Strömberg, (2004), Albert et al., (2006), Neumann et al., (2009), Mercader et al., (2009), Kinyanjui (2011), Novello et al., (2015), Collura and Neumann (2017) and Novello et al., (2018), that are not recorded in the modern reference collection. For details of the sampling, extraction, and counting procedure used for phytoliths from sediment samples, the reader is directed to Chapter 5.6.2 and 5.6.3. When a morphotype was present in the Prospect Farm fossil assemblage but not in the Nakuru-Naivasha Basin reference collection, this is highlighted in both the descriptive tables and the images of that morphotype. Images of all morphotypes from woody and herbaceous dicotyledons, ferns and non-grass monocotyledons are found in Figures 4.1-4.7 (Plates 1-7). Appendix 4, Table 4.1 provides accompanying information to these morphotypes images. This table gives a description and the size of each morphotype, an associated plant group, the plant tissue from which the phytolith type is thought to originate, and key references from which each morphotype has been previously described where possible. Appendix 4, Table 4.2 provides greater detail on morphological-taxonomic associations of each morphotype (i.e. species in which the morphotype has been recorded in published studies and in this study's reference collection). Appendix 4, Table 4.3 gives the previous names use to describe each morphotypes when they have been identified in previous studies, as well as similar forms that may be confused with these phytoliths. Classifications of grass silica short cell (GSSC) phytoliths (extracted from the Prospect Farm sediments [see Chapter 5.5.2]) are based on Twiss et al. (1969), Mulholland (1989), Fredlund and Tieszen (1994), Piperno and Pearsall (1998), and Piperno (2006), and predominately follow morphological-taxonomic-environmental relationships recorded in East African grass phytoliths (e.g. Barboni et al., 2007; Barboni and Bremond, 2009; Mercader et al., 2010; Yost et al., 2018). These studies were augmented by other African grass phytolith studies (e.g. Neumann et al., 2009; Novello et al., 2012; Cordova et al., 2013; Novello and Barboni, 2015; Neumann et al., 2017). The full range of GSSC morphotypes recorded in sediment samples from Prospect Farm is shown in Figure 4.8. The same categories of accompanying information provided for woody plants are given for GSSC morphotypes in Appendix 4, Tables 4.4-4.6. However, GSSC data was gathered entirely from published reference collections. Together, morphotypes from woody plants and GSSCs were classified following a generalised approach into 98 morphotypes (52 from arboreal taxa and Cyperaceae, and 46 from Poaceae). These 98 morphotypes were then further reduced to 32 taxonomically-ecologically meaningful sub-classes for analysis and interpretation (see Chapter 5.6.3).



Figure 4.1 (Morphotypes - Plate 1) These morphotypes are produced by woody and herbaceous dicotyledons and in certain conifers, byrophytes and gymnosperms (see Appendix 4, Table 4.1. for details). (Aa-Ak) Blocky/ Tabular parallelepipedal. (Ba-Bd) Blocky facetate/ polyhedral facetate. (Ca-Cc) Blocky corniculate. (D) Blocky/Tabular decorated (including Blocky sulcate/ruminate, Blocky favose, Blocky lacunose). (Ea-Eh) Blocky/Tabular crenate-echinate-sinuate. (F) Blocky/Tabular radiating laminate. (Ga-Gc) Blocky/Tabular scutiform. (H) Blocky/Tabular tuberculate. (Ia-Ib) Tabular 'ridged'. (Ja-Jf) Blocky/Tabular cavate fimbriate.



Figure 4.2 (Morphotypes - Plate 2) These morphotypes are produced by woody and herbaceous dicotyledons and in certain gymnosperms and pteridophytes, unless otherwise stated (see Appendix 4, Table 4.1. for details). (Aa-Ab) Ellipsoid-elongate with regular or irregular projections. (B) Commelinid like types: (Marantaceae/Commelinaceae) (produced in Monoctyledon Commelinids). (Ca-Cb) Commelinid types: Pollia/Floscopa/Murdannia types. (Da-Db) Commelinaceae: *Cyanotis lanata* and *Cyanotis Longifolia* types. (Ea-Ed) Globular psilate. (Ea-Ed) Globular psilate large. (Ga-Gc) Globular granulate. (Ha-Hc) Globular decorated indifferent. (Ia-Ic) Globular tuberculate. (Ja-Jd) Globulose oblong tuberculate/verrucate. (K) Globular verrucate/ ruminate. (La-Lb) Globular pappilate (cysloiths). (M) Globulose sulcate-columellate (Anatomical origin unknown). (Na-Nc) Globular to sub-globular facetate. (O) Globulose favouse (found in monocotyledons and in mesophyll cells of certain woody dycotyledons). (Pa-Pb) Globular echinate (Arecaceae type) (produce in the woody monocot - Palmae). (Qa-Qc) Globular folded (found also in the bract of certain monocots, as well as in certain Cyperaceae). (R) Globular-sub-globular dark. (Sa-Se) Globular decorated compound (also found in certain herbaceous monocotyledons). (T) Obovate psilate. (Ua-Uc) Obovate scorbiculate/granulate.



Figure 4.3 (Morphotypes - Plate 3) These morphotypes are produced by woody and herbaceous dicotyledons and in some non-grass monocotyledons unless otherwise stated (see Appendix 4, Table 4.1. for details). (Aa-Ab) Cylindroid small (also found in certain Poaceae). (Ba-Bb) Cylindroid large. (Ca-Cf) Cylindroid large geniculate/ Cylindroid bulbous. (D) Asterosclereid (Non-specific). (E) Cylindroid corniculate (also found in gynosperms, and pteridophytes, as well as Cyperaceae and Poaceae). (Fa-Fg) Elongate faceted- Sclereid. (Ga-Gf) Cylindroic sulcate tracheid (vessel elements). (Ha-Hc) Elongate scalariform platelet.



Figure 4.4 (Morphotypes - Plate 4) These morphotypes are produced by woody and herbaceous dicotyledons and in some pteridophytes unless otherwise stated (see Appendix 4, Table 4.1. for details). (Aa-Ac) Epidermal jig-saw platelet. (Ba-Bg) Epidermal polygonal/ parallelogram/cork aerenchyma platelet. (C) Thin platelet irregular ruminate.



Figure 4.5 (Morphotypes - Plate 5). These morphotypes are produced by Poaceae and certain woody and herbaceous dicotyledons, bryophytes, Cyperaceae and Arecaceae (see Appendix 4, Table 4.1. for details). (Aa-Bg) Acicular and Fusiform/Ellipsoid/scutiform (Trichomes/Acicular hair cell). (C) Silica particles/ accumulation. (Da-Dd) Lanceolate.



Figure 4.6 (Morphotypes - Plate 6) These morphotypes are produced by Poaceae (most common) and certain bryophytes, Cyperaceae, Arecaceae, and woody/herbaceous dicotyledons (see Appendix 4, Table 4.1. for details). (Aa-Ae) Thin platelet elongate psilate. (Ba-Bt) Thin Tabular platelet echinate -sinuate-crenate-facetate. (Ca-Cb) Elongate decorated platelet (conical abraxial). (Da-Dc) Thin platelet dendritic.



Figure 4.7 (Morphotypes - Plate 7). (Aa-Am) Acicular and hair cells (produced in Poaceae and in certain dicotyledons). (Ba-Bd) Cyperaceae (sedge) type - hat shaped and papillae (produced in Cyperaceae).



Figure 4.8 Photomicrographs GSSC morphotypes (produced in Poaceae) described in Appendix 4, Table 4.4.

4.2.4 Phytolith counting and preservation potential in botanical samples

In order to assess the frequencies of phytolith production in the modern plant sampled, the presence and absence of each morphotype was recorded. Abundance was assessed though a semiquantitative approach (the Production Index) using three categories following Wallis (2003), Morris et al., (2009), Iriarte and Paz (2009): NP = non-producer (no phytoliths observed in any field of view), T = trace (a small number [n=2-3] of phytoliths observed on the entire slide, with most fields of view containing no phytoliths), C = common (a small number of phytoliths observed in multiple fields of view), and A = abundant (a large number of phytoliths observed in the majority of fields of view). I selected to forego the processes of extracting phytoliths from single plant parts in isolation and calculating absolute counts of phytoliths per gram of dry plant tissue from botanical specimens (e.g. Mercader et al., 2009) in favour of a semi-quantitative and descriptive approach. The approach adopted here placed emphasis on identifying diagnostic phytoliths from arboreal taxa and presence absence data of phytoliths from plants across the different vegetation zones of the Nakuru-Naivasha Basin. Similar approaches have been shown to still allow for identification of key species and for a general understanding of variability in phytolith production across plant groups, as well as being amenable to statistical analysis; while being significantly less time consuming than full quantitative approaches (e.g. Collura and Neumann, 2017). Following the procedure of Mercader et al., (2009), qualitative notes on phytolith morphotype preservation potentials were made based on whether a phytolith morphotype was partially silicified or thin, and thus more likely to be destroyed or altered through physical abrasion and chemical dissolution.

4.2.5 Statistical analysis (correspondence analysis and hierarchical clustering)

Both descriptive and multivariate statistical analysis was employed in order to evaluate correlations between morphotypes, taxonomic groups and ecological conditions (i.e. identifying important gradients in the data). Correspondence analysis (CA) and hierarchical clustering analysis were used as complimentary techniques. CA is a form of indirect gradient analysis (i.e. the factors influencing the data are identified but not directly measured) which has been widely used in ecological studies (see ter Braak, 1986; Legendre and Legendre, 2012) and in similar phytolith reference collection studies (e.g. Carnelli et al., 2004; Gallego and Distel, 2004; Marx et al., 2004; Barboni and Bremond, 2009; Neumann et al., 2017). Here, CA is primarily used to calculate and visualise the 'correspondence' between objects (species) and variables (phytolith morphotypes) in the multivariate dataset. Put another way, CA allows us to plot, in ordination space, the deviation from the null hypothesis that there is no association between objects and variables (Buttigieg and Ramette, 2014). Furthermore, CA is compatible with the use of binary and ordinal data and is generally effective in overcoming the 'double zero' problem, that is commonly encountered in presence/absence ecological datasets (i.e. zero values are not counted as true similarities between objects in CA) (Legendre and Legendre, 2012). CA is best suited to data in which variables have unimodal distributions across objects. However, it is also tolerant of bi- and multimodality (which is the case for some of the data here [see Appendix 4, Figure 4.1 and 4.2]). CA outputs are susceptible to the 'arch effect' and can be sensitive to outliers, that may affect interpretations (Buttigieg and Ramette, 2014). However, if these issues are identified, and if the ways in which they may affect interpretations is properly considered, then CA is still thought to be an effective way of identifying key trends in the data and assessing multiplicity and redundancy in this dataset. For this reason, as well as the fact that rescaling of the axes performed in Detrended Correspondence Analysis (DCA) result in the proximity among points and Scores along a detrended axis being rendered as meaningless (Legendre and Legendre, 2012), CA was preferred to DCA as the primary ordination technique. CA was performed on ordinal data (ranked 0-3 based on the relative occurrences of phytolith morphotype across species following the Production Index [see Appendix 4 Table 4.7]) using PAST software v.3.21 (Hammer et al., 2001). Initially, ecological data (e.g. light and water requirements) were included in the analysis as passive variables (i.e. they did not influence results). No 'significant' associations (i.e. high correspondence in ordination space) were intuitively observed between these conditions and individual/groups of morphotypes. Therefore, I opted to exclude these ecological variables from the analysis, as they are not thought to be important factors in structuring the data, and not to perform additional direct gradient analysis on the data.

Hierarchical cluster analysis was used as an additional means of identifying discrete groups in the data and to assess the degree of similarity between objects and variables (represented by a similarity matrix) using an agglomerative approach. For this analysis, an average-linkage method, the unweighted pairgroup method using arithmetic averages (UPGMA), and the Jaccard distance (where double zeros are ignored), thought to be most appropriate to the analysis of binary data were used (Legendre and Legendre, 2012). The significance of linkages further tested through bootstrapping (n= 9999, in PAST software v.3.21).

4.3 Results

4.3.1 Morphotypes recorded in plants from the Afromontane zone

Of the 87 species studied, 11 (12.6% of the total) produce no phytoliths in their tissues. 40 (45%) produced only trace amounts of phytoliths. In 29 species (33%) one or more morphotypes were observed as being common, and in 10 species (11.4%) one or more morphotypes were recorded as being abundant. Species that produce no, or only trace amounts of phytoliths were all dicotyledons. These findings indicate low silica concentrations in woody dicots observed by other studies (e.g. Epstein, 1994; Hodson, 2005; Mercader et al., 2009; Collura and Neumann, 2017). Figure 4.9 shows the morphotypes identified as being either 'common' or 'abundant' in certain species. Figure 4.10 shows the distribution of different morphotypes in plants as a percentage of all species studied. Arboreal species in the Nakuru-Naivasha Basin produce large phytoliths (>50 μ m) (e.g. blocky-tabular and cylindroid morphologies that commonly originate in parenchyma/cork cells in bark and leaves [see Appendix 4, Table 4.1]). These types are present in just over 70% of all species. Members of the Asteraceae and Fabaceae families, well known silica accumulators, were found to be high producers of these blocky-tabular morphotypes. Smaller globular types (usually <20 μ m), that commonly originate from wood and leaves, as well as in seeds and fruit, are a minority; as has been observed in similar studies of phytolith morphotype



Figure 4.9 Histogram of representation of morphotypes recorded as either 'abundant' or 'common' as a % of the total number of species (*n*=87) studied

As in the case of blocky morphotypes, globular psilate and decorated forms are found in higher relative frequencies in Asteraceae, but also in Athyriaceae and Ebenaceae. However, they only occur in trace amounts in Fabaceae and other families, except for in Urticaceae and Arecaceae where globular morphotypes that are specific at a family level are present (see Section 4.3.3).

Within the globular category the globular psilates are most common (occurring in 37.8% of species). This finding agrees with other studies of phytolith production of indigenous dicots from Africa. However, this morphotype is more frequently recorded across species in other studies; for example, Collura and Neumann (2017) report that these types are present in the bark/wood of 84.6% (22 of 26 species) of West African woody plants that they studied. A further divergent trend in the dataset presented here is that globular decorated types (in particular globular granulates), that are recorded as occurring at higher frequencies by other studies and in some cases are produced in abundance by certain families (e.g. in Apocynaceae and Musaceae in Miombo woodland samples [Mercader et al., 2009]), occur very infrequently in the species from the Nakuru-Naivasha Basin (see Figure 4.10). Polymorphism rates, shown in Table 4.2, are high across taxa, with an average of 12 morphotypes produced by any given species (range 1- 39). Only Myrsinaceae, Ochnaceae, and Ulmaceae produced trace amounts of a single, non-diagnostic morphotype (either elongate psilate or cylindroid). Of the 40 families studied, 14 stand out as producing a wide range of phytoliths, these are: the Asteraceae, Capparaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Melianthaceae, Moraceae, Nolinoideae, Oleaceae, Rosaceae, Rutaceae, and Salvadoraceae, Sapindaceae (see Table 4.2).



Figure 4.10 (A) Histogram of presentation potential of morphotypes as a % of the total number of species studied (n=87). Preservation potential was based on qualitative observations of whether a phytolith morphotype was partially silicified or thin, and thus more likely to be destroyed or altered through physical abrasion and chemical dissolution; or if they were robust and thus more likely to survive diagenetic processes operating in soils (following Mercader et al., 2009). (B 1 to 3) Phytolith morphotype preservation/dissolution as a % of [1] all; [2] the 10 most frequently observed; and [3] the 5 most frequently observed morphotypes identified from arboreal taxa (n=52).

Family	Species (n)	Morphotype (n)	Unique morphotypes present (yes=x, no=)
Acanthaceae	1	8	-
Amaranthaceae	1	14	-
Araliaceae	1	7	_
Apocynaceae	3	10	_
Arecaceae	1	7	X
Asteraceae	10	36	X
Athyriaceae	2	8	X
Boraginaceae	2	9	X
Canellaceae	1	11	—
Capparaceae	5	23	—
Celastraceae	1	13	—
Combretaceae	1	5	_
Compositae	1	NP	_
Cupressaceae	1	3	_
Ebenaceae	1	9	_
Euphorbiaceaee	1	14	X
Fabaceae	11	39	_
Hypericaceae	1	11	_
Lamiaceae	6	34	X
Malvaceae	2	24	-
Melianthaceae	1	15	_
Moraceae	5	19	_
Myrsinaceae	1	1	-
Myrtaceae	1	3	_
Nolinoideae	1	11	_
Ochnaceae	1	1	_
Oleaceae	2	18	_
Podocarpaceae	1	NP	_
Polygonaceae	1	12	_
Pteridaceae	1	3	-
Rosaceae	1	11	_
Rutaceae	3	23	_
Salvadoraceae	1	11	_
Sapindaceae	1	14	_
Solanaceae	1	6	-
Ulmaceae	1	1	-
Urticaceae	2	7	Х
Verbenaceae	2	9	-

Table 4.2 Phytolith polymorphism rates in local families studied.

4.3.2 Phytolith preservation/dissolution potential

Extensive examination of potential dissolution and preservation, under different taphonomic conditions, of the morphotypes encountered here are beyond the scope of this study. Qualitative predictions of phytolith destruction and survival (shown in Figure 4.10 [B]) suggest that 26% of all morphotypes in the assemblage, 60% of the 10 most frequently observed morphotypes, and 71% of the 5 most frequently observed morphotypes, and 71% of the 5 most frequently observed morphotypes, are likely to be preferentially destroyed in fossil assemblages. In particular, hair cells, asterosclereids, and thin elongate and epidermal platelet types, that are omnipresent and produced in high relative proportions in many species and taxa, are predicted to undergo high levels of destruction. The morphotypes that are predicted to have a better chance of preservation are: blocky-tabular, globular and cylindrical classes, in which some diagnostic and characteristic types are present (see Section 4.3.3 below).

4.3.3 Distinctive and unique phytoliths

Despite the fact that 35% of the genera studied produced a wide range of phytolith morphotypes, considerable redundancy in forms is present across families; with only 7 producing types unique to their genera. For example, some species of Lamiaceae (e.g. *Vitex doniana* and *Ocimum gratissimum*) produce a diverse range of blocky, cylindric, epidermal platelet, and acicular morphologies, sometimes in high numbers (see Appendix 4, Table 4.7). However, these forms are also present in other families at lower frequencies in this and other studies. In the case of the five *Ficus spp.* (Moraceae), that have previously been recorded as being high phytolith producers (Piperno, 2006; Collura and Neumann, 2017), distinctive epidermal polygonal/parallelogram platelets are common. However, very similar and indistinguishable forms are also common in Boraginaceae, Celastraceae, Lamiaceae, Malvaceae, and Rutaceae. Phytolith production in Malvaceae is highly variable (e.g. distinctive epidermal polygonal platelets that are common in *Dombeya burgessiae*, only occur in trace amounts in *Grewia similis*, and are not recorded in *Hibiscus calyphyllus*). This finding mirrors those similar studies of phytolith production in this family in West Africa (Collura and Neumann, 2017).

Six morphotypes were identified as being specific at a species/subfamily level or to a particular family. These types are (1) Cylindroid corniculate (sclereid) in *Ricinus communis* (Euphorbiaceae); (2) Globular favouse, in *Achyanthes aspera* (Amaranthacae); (3) Globular tuberculate (2 forms): similar but not identical forms are present in both *Urtica massaica* (Urticaceae) and in species of Athyriaceae; (4) Globular echinate – Arecaceae type, in *Hyphaene compressa*; (5) Blocky corniculate, in *Felicia muricate* and *Psiadia punctulata* (Asteraceae). Amongst the unique types, the production of unique globular echinate types in Arecaceae has been known for some time (e.g. Runge, 1999). The globular tuberculate forms recorded here have also been recorded by Mercader et al., (2009) in the leaves of *Ponzolzia mixta* (Urticaceae). Mercader et al., (2009) also reported the occurrence of globular tuberculates in *Dolichos kilimandscharicus* and *Acacia spp*. (Fabaceae). However, these types are more elongated than those recorded in members of the Urticaceae. Consequently, similar forms identified here are included in the 'globulose oblong tuberculate/verrucate' category instead. As such, I propose that globular tabulates (*sens. str.*) are

diagnostic of Urticaceae and Athyriaceae. As the species of ferns and nettles studied from these families usually occupy the same ecological niche (e.g. semi-shaded margins of wooded areas), the lack of differentiation between these types in the fossil record does not limit overall environmental reconstructions. Globular pappilate types were also recorded exclusively from Urticaceae in this study. However, these morphotypes, that originate in the outgrowths of cell walls of specialized cells (lithocysts), have also been widely recorded in certain species within Acanthaceae, Cucurbitaceae, Moraceae, Ulmaceae, and Cannabaceae (Runge, 1999).

In some instances, species in this study did not produce diagnostic phytoliths, whereas members of the same genus have been shown to do so in other studies of African woody dicots. For example, Mercader et al., (2009) report unique epidermal laminate morphotypes from an unknown Cassia spp. leaf. While Cassia didymobotrya sampled here did produce decorated blocky-tabular types, it did not produce this unique morphotype recorded from the Miombo woodlands. Similarly, diagnostic globulose bisected and cylindroid reticulate phytoliths observed in Miombo Solanum spp. were not observed in Solanaceae spp. (n=2) in this study (c.f. Mercader et al., 2009). In Miombo woodland samples, Podocarpus falcatus was recorded as producing unique blocky hairy morphotypes in low frequencies in its leaves (Mercader et al, 2009). In the Nakuru-Naivasha Basin Podocarpus latifolius, a key indicator species for Afromontane forest, did not produce any non-amorphous phytoliths. This divergence may be caused by variation between species or a lack of silica accumulation in specific plant cells associated with the formation of this blocky morphotype, that could be related to local growing conditions (i.e silica availability in the local environment). Even if Podocarpus latifolius does produce distinctive types with high taxonomic value under certain conditions, they were not identified here, and it is likely that it would do so in very low amounts. This makes it extremely unlikely that these idiosyncratic types would be identified in the fossil records without unrealistically high phytolith counts being undertaken. Similar issues are observed with inferring the presence of conifers based on the presence of blocky-tabular 'ridged' types, previously thought to be distinctive within the order Pinales (e.g. Carnelli, 2004; An, 2016). While this morphotype was recorded in Juniperus procera (Cupressaceae), it was also present in other taxa from the Nakuru-Naivasha Basin (see Appendix 4, Table 4.7) and is likely to originate in Parenchyma/Cork cells in needles and wood of multiple woody genera. Similarly, while members of the Capparaceae in this study produce some rare blocky decorated forms, they did not produce characteristic blocky echinate types observed in the West African taxa of this family (Collura and Neumann, 2017). Furthermore, the 'blocky multilayer' type, cited as diagnostic of Maerua crassifolia (Collura and Neumann, 2017) was not recorded the current study in other members of the genus. However, the multilayered appearance of this phytolith is often indistinguishable from some blocky decorated or radiating laminate types unless observed through SEM imaging.

Additionally, the blocky facetate morphotype recorded as unique to *Uapaca nitida* (Phyllanthaceae) in Miombo woodland samples, was recorded in trace amounts in 43 species and are produced in high frequencies in *Crotalaria agatifolia* (Fabaceae) and *Ocimum gratissimum* (Lamiaceae). This suggest that this morphotype is a good general indicator of more temperate East African woodland and forest habitats.
Other morphotypes considered to be diagnostic to species level by Mercader et al., (2009) e.g. epidermal laminate, tabular thin pilate, have also been observed in species from different families here (see Appendix 4, Table 4.7). These findings are in agreement with previous studies of woody dicots which often have recorded considerable unevenness in phytolith production at a family level (Piperno, 2006). These findings are also a reminder that types identified as unique to a subset of species or region may in fact be produced in a larger number of taxa in other areas.

I also make a distinction between the epidermal jig-saw phytoliths produced by ferns (Figure 4.4 [Aa and Ab]) and those produced in the leaves of woody dicots (Figure 4.4 [Ac]) based on the observation that the edges of the latter are often wavy rather than 'puzzle like'. In classification in this study, the types assigned to the epidermal jig-saw class by Mercader et al., (2009) are more consistent with the morphology of Epidermal polygonal/ parallelogram (Figure 4.1 [Bc]) with wavy edges. Hair cell and acicular types, recorded in most of the families studied here are generally indistinct, however in some species they show unique traits. Their taxonomic values in the archaeological records however is largely negated by the fact that there are not predicted to survive in these contexts and are not present in Prospect Farm fossil phytolith samples (see Chapter 6.7.6).

4.3.4 Differences in phytolith production in woody taxa across Afromontane vegetation communities

Figure 4.11 shows the distribution of indicator phytoliths in plants from different broad vegetation communities in the Nakuru-Naivasha Basin. Figure 4.10 (B) shows the distribution of all phytoliths across these communities. Figure 4.12 shows the distribution of all phytoliths recorded as 'abundant' and 'common' across these communities. Results indicate that the majority of phytoliths are found across two or more communities, thus limiting their use in distinguishing between these communities in the fossil record using a presence-absence approach. Redundancy in phytolith forms across taxonomic groups and vegetation zones is discussed in more detail in relation to the results of multivariate statistical analysis in Section 4.3.6. It is only in rare cases that a particular morphotype can be said to be unique to a particular community. For example, globulose oblong tuberculate/verrucate are only recorded in species from the savanna habitats in this study. Globulose favouse and globulose oblong tuberculate/verrucate are recorded in species that occupy either woodland, wooded grassland and submontane grassland by Mercader et al., (2009). As epidermal jig-saw types (sens. str.) are diagnostic of ferns, these types act as forest or montane woodland indicators, as do Arecaceae types for riverine forest. Cylindroid corniculate types are only found in transitional lowland woodland, however this is based on the presence of this morphotype in a single species. Globular granulate types are only recorded in transitional woodland samples, however, as discussed in Section 4.3.1, they have been recorded in a wide variety of arboreal families by other studies. Other species, that are either highly diagnostic of, or are indicator species of their vegetation zones, were not found to produce phytoliths (e.g. Hagenia abyssinica, Podocarpus latifolius), or were found to produce some characteristic types that are not unique to their families (e.g. Acacia spp., Olea spp., Ficus spp., Dodonaea augustifolia, and Juniperus procera).



■ Forest (n=10) ■ Lowland fores/woodleand (n=34) ■ Open savanna/dry woodland (n=35) ■ Riverine forest (n=8)

Figure 4.11 Distribution of indicator phytoliths and the associated habitat of the species in which these morphotypes occur. The Y axis records the number of species in which a given indicator phytolith occurs out of to the total number of species found in each habitat (show below the chart).



■ Forest (n=10) ■ Lowland fores/woodleand (n=34) ■ Open savanna/dry woodland (n=35) ■ Riverine forest (n=8)

Figure 4.12 Distribution of phytoliths identified as being either 'common' or 'abundant' in certain species and the associated habitat of the species in which these morphotypes occur. The Y axis records the number of species in which a given common/abundant phytolith occurs out of to the total number of species found in each habitat (show below the chart).

4.3.5 Phytoliths from Arundinaria alpina (Afromontane bamboo)

Barboni and Bremond (2009), suggested that the collapsed saddle morphotype is not diagnostic of closehabitat Bambusoideae as this morphotype is produced in Chloridoideae. More recently Sangen et al., (2011) and Yost et al., (2018) have proposed that large forms of collapsed saddle (>20 μ m long in lowland *Oxytenanthera abyssinica*, and >15 μ m long in Afromontane *Arundinaria alpina*), classified as "very long saddles" by Yost et al., (2018), are in fact diagnostic of this genus. In samples of *Arundinaria alpina* this morphotype (see Figure 4.13) was recorded as being present at trace levels, thus confirming that it can be used as indicator of bamboo in the study area.



Figure 4.13 Photomicrographs of morphotypes that were recorded as common in- and/or diagnostic of *Arundinaria alpina*: (A) Bulliform - top view; (B) Trapeziform sinuate smooth ('wavy' trapeziform)- top view; (Ca-Cb) Plateaued saddle. Trapeziform equidimensional to long (Sad-4) - top and oblique view; (D) Short, tabular, rounded convex lobes (Bi-2) – oblique view; (Ea) Rondel-conical, bevelled/spiked top (Ron-6) – side view; (Eb-Ec) Rondel-conical, top truncated to keeled (Ron-5) – side view; (F) Rondel with a small, keeled, tent-shaped body.(Ron-1) – side view; (G)Very tall saddle - oblique view.

4.3.6 Multivariate statistical results

CA and cluster analysis were run on the full dataset to identify trends in morphotype production across different species, families and orders. Ordination diagrams from CA analysis are shown in Figure 4.14. The variation captured by CA axes 1 and 2 (as a percentage of total inertia [heterogeneity of the dataset]) are 13.32% and 11.65% respectively (see Figure 4.14 [A]). The variation captured by other axes was small and was disregarded. In CA, distances in ordination space are not Euclidean but rather Chi-Squared: as such, they are not directly comparable, but the proximity of objects can be interpreted as indicating similarities in the distribution of values across variables. It is evident in the CA plot (Figure 4.14 [A]) that several species (Diplazium hylophilum and Dryoathyrium boryanum [Athyriaceae]; Pteris abyssinica [Pteridaceae]; Obetia pinnaitifida and Urtica massaica [Urticaceae]; Hyphaene compressa [Arecaceae]) are different in terms of the suite of photoliths they produce when compared to the rest of the species, that cluster closely near the axes' centroid. This difference relates to the fact that these ferns, nettles and palms all produce rare and distinctive phytoliths at a family level (e.g. epidermal jigsaw platelets and globular echinate Arecaceae types), that are not recorded in woody dicotyledon species. The CA exaggerates these differences resulting in their location away from other samples; forming outliers on the first and second axes. This suggests that species which cluster closely together at the centroid are poorly ordinated due to high levels of redundancy in phytolith morphotypes across these woody dicots. This is also reflected in the fact that axis loading scores suggest no single morphotype in this central group contributed greatly to the total

inertia. These differences are also reflected in the cluster dendrogram (Figure 4.14 [C]) in which several of the same species (e.g. Are1, At1, At2, Pt, Ur1, Ur2), that have long rescale linkage distances and cluster separately from the majority of samples, are separated from the larger cluster with shorter rescale distances in the centre of the dendrogram (which is comprised mainly of wood dicot species). Bootstrap resampling of rescale linkages indicate that divisions between these outer groups and the less distinct more tightly clustered groups is supported. However, the percentage of replicates where each node is supported for the central cluster, is often zero. This indicates that the high levels of compositional similarity (morphotype multiplicity and redundancy) that exist across taxonomically unrelated families in this sub-set of the data, creates high levels of uncertainty in clustering within this group. The range of distinctive blocky-tabular and cylindroid morphotypes produced by *Vitex doniana*, Lamiaceae (L6) result in its clustering away from other members of its family. Clustering of species within the same family is supported in some cases (e.g. of V1 and V2, As6 and As7, L2 and L5, M1 and M2). However, phytolith composition is often more similar in species from different families in the sample presented here.

Figure 4.14 [B] shows CA plots that focus on just the main body of closely clustered points. The distribution of phytolith morphotypes in these plots does not appear to clearly follow any taxonomic grouping or habitat divisions. The fact that blocky-tabular psilate morphotypes occupy an intermediate position on axis 2, away from all other morphotypes, reflects their ubiquity across species of woody dicots in the study area. The separation in ordination space of some herbaceous dicots, from certain species of Verbenaceae and Polygonaceae, indicates the presence of rarer obovate scrobiculate/granulate and cylindroid geniculate morphotypes in these species, while still being influenced by high levels of multiplicity and redundancy of other morphotypes within the assemblage. Additional CA and detrended correspondence analysis (DCA) (Hill and Gaugh, 1980) were also performed on this reduced dataset to determine if species and morphotypes were better ordinated when outliers were removed and axes were rescaled. However, these analyses did not reveal majorly different patterns to those observed in the original CA (see Appendix 4, Figures 4.3 and 4.4). Consequently, the arch-like right angle shaped distribution and tight clustering of points are thought to be accurate representations of high levels of multiplicity and redundancy in the dataset, with a few rare unique morphotypes occurring in certain, mainly herbaceous, species. In samples of plants from the Afromontane zone, CA and clustering results support the idea that a subset of plants (mainly herbaceous monocots and dicots and Polypodiopsida [ferns]) with rare phytoliths can be identified in the phytoliths record. However, results also indicate that in woody dicots, differentiation along taxonomic or ecological lines is not possible due to high levels of multiplicity and redundancy within this group.



Figure 4.14 (A) CA biplot comparing plant species to morphotypes using Type 1 scaling (i.e. ordinating species with accuracy). Species are coloured according to the habitat in which they are found. Open circles indicate open growth conditions while closed circles indicate close canopy conditions. (B) Zoomed plot of a subset of samples highlighted in box A. (C) Cluster dendrogram plotting the result of hierarchical cluster analysis. The values at nodes indicate the bootstrapping results for the formation of each node.

4.4 Key findings

This study has to some extent confirmed and reinforced previous studies' conclusions regarding phytolith production in indigenous arboreal woody eudicot taxa in Africa (e.g. Mercader et al. 2009; Collura and Neumann, 2017). Specifically, it was found that in general phytoliths produced in this group are highly polymorphic and their taxonomic power is limited due to high levels of redundancy (e.g. Bozarth, 1992). From these findings I have concluded the majority of woody taxa do not leave a phytolith signal that can be unambiguously identified in the fossil phytolith record, because of redundancy and the mixed nature of phytolith assemblages in soils. However, it is also the case that a few derived clades within the woody and herbaceous dicots (e.g. Urticaceae, Euphorbiaceae, Asteraceae, Boraginaceae, and Lamiaceae) produce uncommon or distinctive phytoliths that can add discriminatory values to palaeovegetation reconstructions. Several of these families (Asteraceae, Urticaceae, Euphorbiaceae) were recorded as also producing similar distinctive morphotypes as in arboreal taxa from the Miombo woodlands (Mercader et al., 2009). This indicates that these morphotypes are useful in identifying these families in palaeoecological contexts in East Africa. However, while Mercader et al., (2009) recorded distinctive morphotypes from Fabaceae, the ten different species of this family studied here from the Nakuru-Naivasha Basin were not found to produce any distinctive types. This finding reinforces the uneven nature of phytolith production at a subfamily level. This study has also recorded variation in phytolith production in species from the Afromontane zone from plant groups highlighted as known phytolith producers by previous studies, for example the Polypodiopsida (Athyriaceae and Pteridaceae) and woody/herbaceous monocots (e.g. Arecaceae) (Piperno, 2006; Albert et al., 2015). However, in most cases unique types occur only rarely (e.g. globular favouse and cylindroid corniculate types), thus the likelihood of detecting them in fossil soil phytolith assemblages is low. This is further complicated by the fact that in some cases where unique morphotypes are produced in high frequencies (e.g., globular tuberculates, and various platelets produced in epidermal tissues), they are also predicted to be unlikely to survive in fossil assemblage. This is because they are more susceptible to disarticulation and dissolution in terrestrial sedimentary deposits. This is reflected in low abundances of these types in the Prospect Farm records (see Chapter 6.7.6) and has already been underlined by other phytolith reference collections (Mercader et al., 2009) and taphonomic studies (see Chapter 6.7.3.1).

The most common morphotypes identified in woody dicots are blocky-tabular types (which originate from sclerenchyma, parenchyma and cork cells) rather than globular decorated types (shown to develop their shape regardless of cell form in wood [Collura and Neumann, 2017]). Globular decorated forms are recorded at higher frequencies in woody plants in Tropical African settings than blocky-tabular types (e.g. Mercader et al., 2009; Collura and Neumann, 2017). As such, they have been commonly used to infer the presence of arboreal taxa in palaeoecological studies and to track spatio-temporal changes in arboreal cover (see Chapter 5.6.5.1 and 5.6.5.2). While blocky-tabular morphotypes do have some taxonomic value, in the majority of cases taxonomic relevance is low in the species studied from the Nakuru-Naivasha Basin. It is however recommended that future studies of woody dicots focus on extraction of phytoliths from species of the subfamilies identified here as occasionally producing unique

types. It is unclear if low rates of production of globular decorated types in East African arboreal taxa is caused by environmental factors (e.g. lower rates of production in plants growing under more temperate climate conditions [e.g. Carnelli et al., 2004; Tsartsidou et al., 2007]) or is due to taxonomic factors (i.e. production is genetically controlled). Globular granulates were shown to be present in two species that grow in intermediate woodland habitats in one species from Afromontane forest, and in no species from savanna settings in the study area. However, the sample size here is low, such that higher silica accumulation in woody tissue in these settings requires further attention before any linkages between edaphic conditions or water availability and the production of these forms in different habitats can be proposed. Given the low production rates of globular morphologies in taxa of the Afromontane zone, it is recommended that future studies of soil phytoliths assemblages focus on the relative abundances of blocky-tabular types in relation to changes in plant biomass and arboreal cover across different plant communities.

Indicator and characteristic species selected for this study (mainly woody eudicots) did not in most cases produced diagnostic phytoliths that could allow us to discriminate between forest, woodland and savanna vegetation communities in the palaeoecological record. Furthermore, some distinctive morphotypes (e.g. cylindroid corniculates) are recorded in fossil samples but not in this or any other published reference collection. This is likely to relate to size limitations of the current dataset, whereby the 87 species studied here represent only 37% of all characteristic and indicator species for vegetation communities found in the Nakuru-Naivasha Basin as classified by the VECEA (Lilleso et al., 2011). As such, more diagnostic types may be discovered by future studies, which I recommend should focus on understory monocot shrubs and herbs; that may produce diagnostic types in greater abundances. In conclusion, studying phytolith production in plants from the Afromontane zone provides limited taxonomic value for palaeoecological reconstructions overall, but can act as a complimentary tool to soil phytolith assemblage-based approaches discussed in Chapters 5.6.4 and 6.7.

Chapter 5 Study site, materials, and methods

5.1 Introduction

Chapter 5 focuses on introducing the geological setting and excavation history of Prospect Farm, as well as the methods that allow its palaeosol sequence to be used to infer palaeoenvironmental conditions. Artefact density survey and mapping of Prospect Farm sequence stratigraphy were used to identify archaeological sites on the landscape. Local palaeoenvironmental reconstructions focus on phytolith analysis, which includes identification of specific vegetation and plants types based on comparisons with modern soil and botanical phytolith reference datasets. Geomorphologic, sedimentologic and pedologic investigations, focus on identifying depositional and taphonomic process to further constrain the environmental context of the sequence (e.g. by establishing the relative degrees of weathering between palaeosols horizons), and to infer landform evolution. Additionally, these investigations were conducted to better understand how these taphonomic factors affect the phytolith assemblages and thus vegetation interpretations. The investigative methods used include observations of field-based studies of sediment outcrops, in combination with lab-based studies of particle size analysis, sediment geochemistry, and phytolith preservation.

5.2 Geological background of the study area and the Prospect Farm Formation

5.2.1. Geological setting: Nakuru-Naivasha Basin

The Nakuru-Naivasha Basin is the highest lake basin within the KCR section of the EARS (Olaka et al., 2016). Lake Nakuru is located at 0°36'S, 36°08'E in the northern area of the basin at an elevation of 1758 m a.s.l., Lake Elementaita lies to the south west (0°45'S, 36°25'E) at 1670 m a.s.l., and Lake Naivasha is located to the south (0°55'S, 36°20'E) at 1890 m a.s.l. (Bergner et al., 2003). The location of the catchment at high elevation, its steep relief and closed morphology, all contribute to the area's classification as an amplifier lake (as introduced in Chapter 1.7.2.1). Figure 5.1 outlines the main geological units and the structural features of the catchment (described in more detail in Appendix 5.1). During the Plio-Pleistocene, volcanic deposits in-filling the inner rift were cut by younger N–S to NW–SW trending faults (Olaka et al., 2016 and references therein). Volcanic activity in the catchment continued during the Quaternary, including the Holocene, resulted in the development of smaller rhyolitic domes, pyroclastic deposits and basaltic lava flows, that formed volcanic edifices (including Mt. Eburru, on which the site of Prospect Farm is located). Quaternary volcanic activity segmented the inner rift into small sub-basins; bordered by fault scarps; a process which has continued into recent times. The last recorded major eruption in the basin - that altered the basin's morphology - is dated to 200 yrs BP from Olubutot volcano in the Olkaria area (Bergner et al., 2009 and references therein).



Figure 5.1 (A) Schematic profile of antithetic faulting, which divides the inner and outer rift after the Miocene (adapted from Bergner et al., [2009] after Clarke et al., [1990]). (B) Map of the Nakuru-Naivasha Basin showing the present-day location of the basin's main geological units, volcanic centres and tectonic features (adapted from a Bergner et al., (2009).

5.2.2 The Prospect Farm Formation

5.2.2.1 Geological setting of Mt. Eburru and the Prospect Farm Formation

The Eburru Volcanic complex (2859 m, 470 km²; Ren et al., 2006) forms an E-W trending ridge, creating a topographic barrier which separates the Nakuru and Naivasha sub-basins (Bergner et al., 2009; McCall 1967; Thompson and Dodson 1963a, 1963b). Figure 5.2 shows satellite imagery of the Eburru volcanic complex and the location of the main archaeological sites studied from the Prospect Farm Formation.



Figure 5.2 (A) Location of Mt. Eburru in the Nakuru-Naivasha Basin. (B) Satellite image of the Eburru volcanic complex showing the late-Pleistocene trachyte pyroclastic flows and rhyolitic lava flow extending from the northern and southern flanks of Mt. Eburru into the Nakuru and Naivasha Basins respectively. A yellow circle indicates the location of the main archaeological sites studied from the Prospect Farm Formation. These sites are located on the so-called Ridge 2 (eastern ridge) Anthony (1978). The western ridge is termed Ridge 1. Anthony (1978) recorded that uphill of the archaeological sites, Ridge 2 is cut on its southern end by a major fault, visible as a downward dipping surface of ca. 15 m.

Primary phases of Volcanic activity at Eburru are thought to have mainly occurred between ~1.2 and 0.4 Ma (Clarke et al. 1990; Ren et al. 2006), but continued into the Late Pleistocene and possibly early Holocene; with the area remaining thermally active in the present day (Thompson and Dodson 1963b). Clarke et al., (1990) divide the volcanic activity at Eburru into two phases: 1) The initial formation of the western rim structure; 2) The younger phase associated with the formation of the eastern rim and the deposition of the Eburru Trachyte Formation (EBT). The EBT has been subdivided into an Older, faulted (Ep1) and Younger, largely unfaulted (Ep2) member, and is characterised by feldspar-phyric trachyte lavas, welded pyroclastics, as well as pumice and scoria deposits (shown in Figure 5.3) (Clarke et al., 1990; Ren et al. 2006).



Figure 5.3 Map of main geological formations of Mt. Eburru and the location of the main sediment exposures recorded during survey and excavation of the Prospect Farm Formation. The geology of the Mau escarpment which flanks Eburru to the west, consists of welded and unwelded tuffs, minor rhyolites, basalts and trachytes underlying the upper and lower Mau sequences of the Mau pyroclastic series, otherwise known as the 'Mau ashes' (McCall, 1967; Leat, 1991; Olaka et al., 2016). The Mau ashes can be viewed as the counterpart to the pyroclastic series of the Prospect Farm Formation and were deposited during late Middle and Late Pleistocene. They record MSA and LSA bearing palaeosol-tephra sequences at sites such as Marmonet Drift, dating to MIS 7-MIS1 (Slater, 2016). Both the Mau escarpment and Mt. Eburru contain extensive deposits of highest quality obsidian (Merrick and Brown, 1984a; Merrick et al., 1994; Slater et al., 2016). Obsidian outcrops in the Er2 deposits (i.e. rhyolitic obsidian lava flows along N–S trending faults) were not formed until the Upper Pleistocene and Holocene and were unavailable to MSA groups at Prospect Farm. Figure adapted from Thomson and Dodson (1963a). Inset topographic map show the location of extent of the geological map. Black lines indicate maximum Holocene lake levels.

Pyroclastic series deposited on top of the Ep1 and Ep2 members form the 'Prospect Farm Formation' (Isaac 1972, Isaac et al., 1976) which contains multiple stratified MSA and LSA horizons and abundant surface scatters of predominantly obsidian artefacts. The volcanic foothills of the Prospect Farm Formation consist of pyroclastic tongues (Ridges 1 and 2) that extend northwards ~ 8 km from the western rim and represent the continuation of volcanic activity on Eburru during late Middle and Late Pleistocene. Deposits of the Prospect Farm Formation can be traced from ~2200 m a.s.l. and extend inward along the floor of the Nakuru Basin for ~ 6.5 km, where at elevations below ~ 1960 m a.s.l. pyroclastics become intercalated with lacustrine sediment. This point marks the southernmost extension of the Lake Nakuru-Elmenteita sub-basin (Thompson and Dodson 1963a, 1963b). The upper limit of the Prospect Farm Formation may be located at higher elevation on Mt. Eburru as mantling sediments transition to proximal volcanic deposits. However, the dense vegetation cover of Mt. Eburru obscures the upper limits of the distal ash and tuff deposits of the Prospect Farm sequence. Small (typically ~5 m tall) discontinuous escarpments, exhibiting minor E-W and NE-SW faulting (Thompson and Dodson 1963a, 1963b), cross cut these pyroclastic tongues, exposing pyroclastic deposits, that comprise of a series of lapillae tuffs, weathered colluvially redeposited tuffs, and several palaeosols (see Figures 5.4). Figure 5.5 and 5.6 outline the location of studied sediment exposures and excavation Localities of the Prospect Farm sequence.



Figure 5.4 Image of escarpment exposure at Prospect Farm Locality I. Photo taken looking north east towards Lake Elementaita. The outline of Ambrose's 2003 trench is visible behind the figures on the right side of the photo. The strata of the Prospect Farm sequence are generally horizontal but show a slight eastward downward dip (of \sim 7°) in sediments on the eastern margin of Ridge 2. The slope angle between Locality I and II is not steep at \sim 2.8° (5 %). Erosion of these sediments is ongoing during the rainy season. Studies of similar depositional environments have noted that physical weathering of mechanically weak pumice deposits, that have low physical shear strength and are susceptible to erosion and collapse (e.g. Capra et al., 2003), could have also contributed to the exposure of the sequence of Prospect Farm Formation sediments. Sediment stability is also compromised by low vegetation cover, dominated by *Tarchonanthus camphoratus* bushes.



Figure 5.5 Topographic maps of Mt. Eburru and the Prospect Farm Formation showing the location of main sediment exposures, sites and landscape features and maximum palaeolake shoreline position. (A-B) Map showing location of sites on northern slopes of Mt. Eburru. No sediment exposures were recorded above the upper points shown. This relates to both higher woody vegetation cover and associated lower rates of erosion above ~2200 m a.s.l. nearing the gazetted forest where sediments are stabilised by plant growth. (C-D) Areas where main exposures of the Prospect Farm Formation were identified on Ridge 1. Note: the steepness of the margins as these tongues increased in places where ephemeral streams that originate on Mt. Eburru down-cut through the sediments, creating small N-S trending river valleys where welded trachyte tuff deposits are exposed.



Figure 5.6 Topographic maps of the Prospect Farm Formation showing the location of main sediment exposures, sites and landscape features and maximum palaeolake shoreline position. (A) Map showing the GPS location of density survey polygons, localities excavated in the 1960s (Anthony [1978]) and presumed localities of artefact scatters mentioned by Anthony (1978), away from the main localities, shown in relation to sites and exposures investigated by this study. Countor lines in light grey, labour lines and tracks (in dark grey) and river courses (in blue) from Directorate of Overseas Surveys (1975). (B) Satellite image (Google Earth, 2018) with the extent of the main escapement features highlighted and the location of sites studied. The main escapement features are delineated by dashed white lines.

5.3 Research history and the archaeological sequence at Prospect Farm

5.3.1. Prospect Farm research history

The research history and information on the archaeological sequence presented here focuses on MSA and MSA-LSA sections of the Prospect Farm Formation. It does not cover late LSA or Pastoral Neolithic phases recorded in younger stratigraphic levels (Units 3-1) as they are not of direct relevance to the aims of this thesis, and have been covered in more detail elsewhere (e.g. Leakey 1947; Cole 1954; Anthony 1967; Cohen 1970; Wilshaw 2016; Van Balen et al., 2019). Investigations of the Prospect Farm Formation began in 1963 with excavations of two sites (Locality I [GsJi 7; 2102-2108 m a.s.l.] and Locality II [Gs]i 8; 2138-2140 m a.s.l), that are separated by ~0.7 km. Excavations focused on areas where significantly high amounts of surface lithics, assigned at the time as MSA (East African) Stillbay by Louis Leakey, were recorded eroding out of exposures. Early excavations at Locality II conducted by Barbara Anthony and Glynn Isaac were more extensive than those of Locality I, exposing a ~ 14 m deep stratigraphic sequence containing multiple archaeological horizons (Anthony 1978). These excavtions were the first to demonstrated the stratigraphic continuity with the upper levels of excavated sediments at Locality I. A further five interconnecting trenches at Locality II were excavated from 1963-1964. All trenches were cut back from the escarpment face with the exception of the 'pit-trench', which exposed the deepest stratigraphic levels. In 2003, excavations were reopened at both Localities by Stanley Ambrose of the University of Illinois (Ambrose, 2003: unpublished; NMK archive record no. 3201-3202 and 4310) (Van Balen et al., 2019).

5.3.1.1 Previous geological investigations of the Prospect Farm sequence

Stratigraphic divisions of the Prospect Farm Formation by Anthony (1978) are based on field observations made by Theisen (1964). Theisen's work established the main stratigraphic horizons and gave some detail of macroscale sedimentary structures in the sequence, but did not carry out more detailed analysis of sediments. These early investigations of the Prospect Farm sequence recognised that soil formation from tuffs has taken place, but that it was a problematic to identify former land surfaces from which weathering occurred based on field observations alone. Subsequent excavation by Ambrose (2003, unpublished; KNM archive records no. 4310 and 3201-320) identified four distinct palaeosols developing from volcanic deposits, based on pedogenic features identified in the field. However, no further analysis was conducted to clarify and further characterise the palaeosols.



Figure 5.7 Correlation of the stratigraphic units from Prospect Farm as defined by Anthony (1978), Ambrose (2003) and during the *In-Africa* project's 2016 fieldwork. Also shown are localities of phytolith samples (red dots) and micromorphology samples (red rectangles) collected from Locality I and re-excavation of Locality II. Units 35 and 36 recorded by Anthony (1978) were not exposed during renewed excavations.

5.3.2 The archaeological sequence at Prospect Farm

Figure 5.8 outlines the main archaeological horizons and character of MSA and LSA industries during Anthony's excavations. These are divided into occupation Phases I-IV (Anthony, 1978) which underlie stone bowl culture and Neolithic elements (see Appendix 5, Table 5.1 for an overview of existing dates for the Prospect Farm Formation). Attribute analysis of tools from the youngest MSA horizons at Prospect Farm (Phase IV), that directly overlies Phase III MSA material, indicates that this assemblage contains some LSA features. This suggests a gradual MSA-LSA transition occurring at the site (Michels et al. 1983). However, the overall characteristics of 'transitional' phase IV material are still considered to fall within the same range of variation as Phases I-III (Anthony 1978; Merrick 1975). Dating of the putative MSA-LSA transitional industry from Anthony's Unit 7/6, are only dated by obsidian hydration (OH), that places the industry to between $21,805 \pm 373$ and $32,483 \pm 568$ years ago (Michels et al., 1983). However, the exact stratigraphic position of the tools used for dating was not specified by Michels et al., (1983). The obsidian hydration method has been heavily criticised (Ridings et al., 1996; Stevenson et al., 1998; Anovitz et al. 1999; Rogers and Duke, 2014), and dates based on this method are often considered unreliable; and so are treated with caution. Four dates from Phase II (Anthony's Unit 15) range from \sim 14-88 ka and are considered unreliable as they show age reversal and are not coherent in terms of the age-depth relationship observed in other samples. No attempts have been made to date material from the lower sections (Phase I). With this in mind, the typology of the lithic assemblage and the published dates, suggest a tentative minimum age of ~120 ka (MIS 5) for Phase I and II. Michaels (1983) identified three Late Pleistocene MSA occupation phases within Phase III, based on obsidian hydration dates (see Figure 5.8). If this interpretation of Phase III is correct, and if the three distinct horizons identified by Anthony (1978) in Phase II are shown to constitute their own distinct occupation phases, then there are a minimum of five MSA occupation Phases and one 'transitional' phase that could be present in the Prospect Farm sequence.

Palaeosols (listed in descending stratigraphic order from youngest to oldest)	Stratigraphic units associated with palaeosol formation (after INAP 2016 excavations)	Stratigraphic units associated with archaeological horizons (after INAP 2016 excavations)	Associated archaeological phases (after Anthony 1978)	Associated archaeological phases (after 2016 INAP excavations)
Palaeosol 6 (PS6) (not part of PF Formation)	3B-1A	2B-1A	LSA and Pastoral Neolithic	N/A
Palaeosol 5 (PS5)	6-4A	4B-4A (Phase III) 4A-3B	Phase III (final MSA industries) and Phase IV (MSA-LSA 'transitional' industries)	Phase III (final MSA industries) and Phase IV (MSA-LSA 'transitional' industries) (a very small amount of archaeological material been reworked into unpedogenised Units 3F-3B)
Palaeosol 4 (PS4)	7C-7A	7A-5	Material not assigned to a phase	Phase II-C (MSA) (some archaeological material from PS4 has been reworked into the basal deposits of PS5 [Unit 5])
Palaeosol 3 (PS3)	9B-8A	9B-7C	Phase II (MSA)	Phase II-B (MSA) (a very small amount of archaeological material from PS3 has been reworked into the basal deposits of PS4 [Unit 7C])
Palaeosol 2 (PS2)	11B-10	10-9B	Material not assigned to a phase	Phase II-A (MSA) (a very small amount of archaeological material from PS2 has been reworked into the basal deposits of PS3 [Unit 9B])
Palaeosol 1 (PS1)	16-15A	16-15A	Phase I (earliest MSA)	Phase I (earliest MSA)

Table 5.1 Summary of the relationships between palaeosols identified in the PF sequence and archaeological occupation phases according to previous excavations of the site by Anthony (1978) and updated relationships based on INAP 2016 excavations and studies of sedimentology and stratigraphy.

5.3.1.2 Site formation and weathering trends identified by previous excavations

Given the horizontal nature of the strata and low slope angle, Anthony (1978) noted that artefact horizons in the Prospect Farm Formation were unlikely to be redeposited by high energy colluvial slope processes; and as such are likely to represent former land surfaces. However, at the contact between Units 3 and 4 most of the \sim 6700 artefacts recovered appear to be deposited horizontally, cross cutting these units, and did not show signs of dipping as might be expected if they had been deposited on top an undulating surface. As a result, Anthony (1978) concluded that it was difficult to identify a former surface on which the artefacts were deposited. Anthony placed the transition from Phase III to IV material as occurring in the Btb5-2 horizon (in Spit 15 [Anthony, 1978]). Following the transition to Unit 3, artefact densities and percentages are greatly reduced; with deposits recorded as sterile or near-sterile by Anthony in Units 3E-3B. Resolving the chrono-stratigraphic relationship between Phase III and Phase IV material is important, as it has direct implications for interpretation of the nature of the MSA/LSA transition at the site (i.e. if it is truly gradual, or if a significant break in occupation of the site exists between the two phases). It is also the case that while artefacts do form horizontal horizons, they can be dispersed vertically throughout a single sedimentary unit by up to 50 cm in some cases. In these cases, it is difficult to establish that artefact horizons represent a land surface, suggesting that some artefact horizons have been subjected to post-depositional reworking associated with the deposition of volcanic material, or physical reworking during pedogenesis.



Figure 5.8 (A) Relationship between archaeological phases, palaeosol phases identified during INAP 2016 excavations, the composite stratigraphy of Prospect Farm proposed by Anthony (1978), and published conventional ¹⁴C and Obsidian hydration dates for the Prospect Farm sequence (Michels et al., 1983). Anthony's identified four different phases within the Prospect Industry (from oldest to youngest: phases I-IV). Phases I and II are separated by several meters of pumice deposits that are archeologically sterile. Phases I-III show clear MSA affinities designated as a local expression of the (East African) Stillbay (Clark 1954; Cole 1954; Leakey 1931; Anthony 1967a, 1972, 1978); referred to by Anthony (1978) as the Prospect Industry. Phase IV shows affinities to both the MSA and LSA. In this thesis, Levallois and other prepared cores and flakes are considered as MSA; Lithics and soft hammer blade/bladelet and laminar cores (usually prismatic) technology as LSA. Lithic artefact drawings after Anthony (1978). (B) Percentage of obsidian I Phases III and IV from sources at different distances from Prospect Farm (data from Merrick et al., [1994] modified from Ambrose [2001]). Assemblage size indicated in parentheses in the figure key. Anthony (1978) suggested the archaeological horizons marked ?? were likely to belong to Phase II, but as artefact densities in these horizons were low, they could not be identified at both localities.

5.3.3 Raw material procurement in the Prospect Farm sequence

Obsidian is the preferred raw material in all archaeological levels of the site, followed by trachyte (mainly occurring in Phase III), and very low frequencies of chert and crystalline quartz. The local sources of this raw material accounts (at least in part) for the richness of the site in terms of artefact numbers. Obsidian is widely available in the Nakuru-Naivasha Basin and Prospect Farm is located near several outcrops; the nearest being ~3 km away (Merrick and Brown 1984a, 1984b; Merrick et al. 1994; Brown et al. 2013; Goldstein and Munyiri 2017). The geochemical composition of obsidian from Locality I, covering Phase III and IV, has been analysed by Merrick et al., (1990, 1994), but material from the earlier Phases I and II has not. Geochemical 'fingerprinting' identified 30 petrological groups in the area, of which 16 different obsidian groups, including several sub-groups, are represented at Locality I, as well as several unidentified sources (Merrick et al., 1994; Van Balen et al., 2019). Figure 5.8 (B) plots changes in obsidian sourcing with depth in Phases III and IV of the Prospect Farm sequence. These changes are discussed in more detail in Chapter 7.5 in relation to changes in palaeolandscape use patterns over time. In all three samples exotic obsidian artefacts are debitage products not tools. There is little difference in reduction intensity between exotic and local material, and obsidian does not appear to have been brought to Prospect Farm as finished tools (Ambrose 2001; Van Balen et al., 2019).

5.4 Renewed excavations at Prospect Farm (2014 and 2016)

A brief overview of the archaeological sequence and history of excavation at Prospect Farm place the Prospect Farm MSA horizons within the Eastern African MSA. However, the transitional character of the Phase IV artefacts, the sourcing of raw material in phases I and II, the age and duration of each phases, and their associated environmental conditions remain unanswered. To address these questions new full-scale excavations at both Localities I and II were carried out by the *In-Africa* Project between 2014 and 2016. The primary aims of this research were to produce a detailed description of the stratigraphic sequence, to establish the number of distinct archaeological horizons and relationships between tem, as well as to collect and analyse samples for dating and environmental analyses. A new density survey was also undertaken to better understand the spatial distribution of MSA versus LSA artefacts across the Prospect Farm Formation with the goal of reconstructing prehistoric land use patterns through time.

Archaeological excavations were conducted by senior project members Dr. Ann Van Balen and Dr. Alex Wilshaw and overseen by Prof. Marta Mirazón Lahr and Prof. Robert Foley. During the 2016 fieldwork two trenches (PF1-1 and PF1-2) were dug at Locality I (see Figure 5.9 [A]). This included re-exposing an older, pre-existing open-ended trench (trench PF1-1) by cutting down from the top of the escarpment to the flat area in front of it. This produced a 9 m long and 1.4 m wide trench with six steps, spanning a 6.1 m difference in elevation and exposing the upper part of the stratigraphic sequence. Secondly, the excavation of a completely new a four-walled stepped trench (trench PF1-2); aimed at exploring the lower stratigraphic levels - measuring 4.1 by 2.9 m, was dug at the bottom end of trench PF1-1. Starting from the flat area in front of the escarpment, the trench PF2-1 was slowly taken down into the

undisturbed underlying deposits. (see Figure 5.9 [C]). Three more trenches (PF2-1, PF2-2, and PF2-3) were excavated at Locality II (see Figure 5.9 [A]). These trenches (shown in Figure 5.9 [B]) have partially overlapping stratigraphic deposits, allowing the compilation of a vertical stratigraphic sequence spanning 10.4 m from the top of the escarpment (306.3 m) to the base of trench PF2-3 (295.9 m). Their excavation involved the cutting back of the pit trenches excavated by Anthony and Ambrose, to expose undisturbed archaeological material and fresh sections for sampling. The deposits were slowly excavated, exposing as many artefacts as possible. The sediment was (dry) sieved over 5 mm metal meshes and chips and fragments were selected from the sieve. When it was no longer possible to continue with the excavation because of the high number of exposed finds, the location of artefacts and the elevation of the exposed surface were recorded with the total station. 3D recording of all finds larger than 1 cm was conducted using a total station. Details on artefact position (horizontal, vertical or oblique) and orientation (dorsal or ventral face up, side up) were additionally recorded for each artefact. More detailed information relating to the methodology of the density survey and excavation practices at the site can be found in Van Balen et al., (2019) which is in press at the time of writing.

At present, dating of volcanic deposits by ⁴⁰Ar/³⁹Ar and the geochemical characterisation of tuffs (see Section 5.5.2) is being conducted to develop a new chronostratigraphic framework for the site and to facilitate the placement of the sequence within the developing tephrostratigraphic framework of the region (Blegen et al., 2016; Lane et al., 2016, 2017). New dating evidence as well as archaeological and geoarchaeological investigations have been carried out and are ongoing in order to verify existing obsidian hydration dates for Phase III and IV material. If this lithic material is confirmed as transitional in form and OH dates are confirmed as correct, then the Prospect Farm archaeological sequence covers a vital period in the development of MSA/LSA lithic variability over the MSA-LSA transition. Dating of the Phase I and II deposits and geochemical analysis of artefacts from these horizons, to establish patterns in obsidian sourcing during the earliest MSA at the site, is also ongoing. Once completed, new analysis of existing and newly excavated lithic material is expected to allow comparison of artefact traits and geochemistry throughout the Prospect Farm sequence to other East African sites (e.g. Brown et al., 2013; Tryon and Faith, 2013; Faith et al., 2015) (see discussion in Chapter 7.6).

5.4.1 Challenges of studying open-air MSA sequences

The preservation of organic material in such open-air MSA sites is poor. Test samples indicated that pollen was not preserved in these sediments and so a phytolith-based approach to vegetation reconstructions was adopted in this thesis. The depositional nature and lack of a high-resolution chronology from palaeosol and non-lacustrine open-air terrestrial tephrostratigraphic sections, means that the sedimentary resolution is typically too low within these deposits to identify fine-scale, temporally distinct phases of sediment accretion (e.g. Gatti et al., 2013). Consequently, it is necessary to constrain the depositional pathways and taphonomic process which result in the formation and post-depositional alternation of these deposits. By doing so it is possible to suggest how these factors might affect the coherence of the phytolith-based bio-stratigraphy (Madella and Lancelotti, 2012), the archaeological

stratigraphy; and ultimately, the reliability of combined analyses of past environmental conditions at the site and the archaeological sequence to make inferences about past human behaviour at the site.

5.5. Methods

5.5.1 Field descriptions of sedimentology, stratigraphic relationships and density survey

The density survey1 of the Prospect Farm Formation targeted six areas, totalling 0.486 km2 situated between ~1960 m a.s.l. and ~2215 m a.s.l. This area approximately spans the area noted by Isacc (1972) as covering the highest artefact densities at the site (see Van Balen et al., 2019 and Appendix 5.2.1 for survey methodology, artefact counts and attributions). In order to use the Prospect Farm sequence to reconstruct palaeoenvironmental conditions, outcrop locations across the Prospect Farm Formation were identified and their locations recorded using handheld DGPS. Archaeological excavations at Localities I and II exposed the near-complete Prospect Farm sequence identified by Anthony (1978), with bedding unaffected by modern process (i.e. surface washing, slumping and anthropogenic disturbances). These stratigraphic sequences were photographed, measured and described at the cm scale to establish bed thickness, geometry, induration and plasticity, bedding structure and features, unit boundaries, texture (size, sorting, rounding properties) colour and lithology (primary and inclusions). Pedogenic features (e.g. soil colour, structure, and mineral content) that inform the relative degree of weathering of deposits were described following the guidelines of the World Reference Base for Soil Resources (IUSS Working Group WRB, 2014). Palaeosol horizons were assigned following the criteria of Soil Survey Staff (1999), with adaptations by Retallack (1988, 1998), and palaeosol modifiers following Mack et al., (1993) (see Table 5.2). Exposures at Locality I and II acted as type-sequences from which to identify and correlate sedimentary horizons exposed at other locations across the Prospect Farm Formation, as well as to assess the degree of spatial variability in the stratigraphic sequence across the formation. This also provided the opportunity to reassess stratigraphic divisions made by Anthony (1978). Additional exposures away from the main localities were trenched where necessary to expose bedding.

¹ Note: The destiny survey was carried out by Alex Wilshaw, José Manuel Maillo and the author, and analyses were conducted by Ann Van Balen (see Van Balen et al., 2019).

(A) Paleosol taxonomic modifiers (Mack et al., 1993)		(B) Soil horizons		Adapted from soil survey Staff (1998)
Modifier	Features	0	Accumula which ma	ation of organic matter at the soil surface ay be underwater (peat, lignite, coal)
Albic	Presence of an eluvial (E) horizon [Fe and Al compounds accumulaed]	А	Organo-r	nineral horizon occurring at the surface
Allophanic	Presence of allophone or other amorphous Si and Al compounds		or under	O horizon
Argillic	Presence of illuvial [downward transported] clay	Е	Underlie	s an O and A horizon and is characterised
Calcic	Presence of pedogenic carbonate		by less of than the	rganic matter, less sesquioxides or less clay underlying horizon, usually light coloured
Concretionary	Presence of globules with concentric fabric	B Underlie enrichme organic r		s O, Λ or E horizon and show discernible ent in clay, carbonate, sesquioxides, or matter
Dystric	Low base status as indicated by relative paucity of chemically unstable grains such as feldspars and volcanic rock fragments			
Eutric	High base status as indicated by the abundance of chemically unstable grains such as feldspars and volcanic rock fragments	С	Subsurfa but lackir	ce horizon more weathered than bedrock ng degree of weathering of A, E, B
Fragic	Subsurface horizon that was hard at the time of soil formation (e.g., root traces and burrows terminate or are diverted at this horizon;	horizon characteristics Subordinate descriptors		
Gleved	nard pan) Evidence of periodic waterlogging such as drab hues, mottles of drab	b	Buried so	pil horizon
	colors and yellow, red, or brown, presence of pedogenic pyrite or siderite	c Con- iron,	Concreti iron, alur	ons or nodules enriched in minerals that contain ninium, manganese or titanium
Nodular	Presence of globules with undifferentiated internal fabric; typically	g	Evidence	e of strong gleying
Ochric	Presence of a light-colored A horizon	k	Accumul	ation of carbonates
e.E.	Described for a light-colored A horizon	m	Evidence	e of cementation, induration
Salic	Presence of pedogenic salts more soluble than gypsum (e.g., halite)	0	Residual	accumulations of sesquioxides
Vertic	Presence of decimeter-scale dessication cracks, wedge-shaped peds, hummock and swale structures (gilgai micro-relief), slickensides, or clastic dikes	88	Presence	of slickensides
		s	Illuvial a	ccumulations of sesquioxides
Vitric	Presence of relict or actual volcanic glass shards or pumice	t	Illuvial a	ccumulations of clay
		у	Accumul	ation of gypsum or crystal casts

Table 5.2 (A) Taxonomic modifiers and (B) palaeosols horizon classification used in this study

5.5.2 Sampling strategy

The archaeological trench at Locality I (see Figure 5.9 [C]) was chosen as the primary location for environmental and geoarchaeological sampling. The density survey had identified Locality I as containing the highest frequencies of MSA surface finds (and thus the most likely nucleus of MSA settlement activity) (see Chapter 6.1). 63 Samples for phytolith, particle size analysis and bulk geochemistry were collected at 5 cm intervals from cleaned sections in the lower MSA bearing levels of the sequences, and at wider intervals covering the main stratigraphic Units throughout upper LSA/Pastoral Neolithic levels. Sample locations are shown in Figure 5.7.

An additional 5 samples from the uppermost preserved horizons of palaeosol were collected from Locality II to allow for assessment of potential altitudinal variability in vegetation changes between the two main sites. Sampling equipment was cleaned between each sample to ensure no cross-contamination of sediment samples occurred in the field. A further 11 samples for micromorphology were collected at key archaeological horizons and inferred palaeosol profiles throughout the sequence, as well as across bed contacts (see Figure 5.7). These samples, along with an aliquot of sediment samples from the Locality II sampling column were sent to Prof. Hema Achyuthan (Anna Univ. Chennai, senior geologist *In-Africa* project) for X-ray Powder Diffraction (XRD) and magnetic susceptibility (χ) analyses. Pumice and tuff samples were studied with a hand lens in the field to establish the presence of feldspar crystals suitable for dating. Samples for ⁴⁰Ar/³⁹Ar and geochemical analysis were collected from pumice and tuff deposits and sent to Dr. Nick Blegen (Harvard Univ./Max Planck Inst.).



Figure 5.9 Examples of the main excavation locations and trenches at Prospect Farm. (A) 3D model of the locations of escarpment exposures showing Locality I (b: dark blue circle), Locality II (c: light green circle [trenches 1 & 2]; light grey circle [trench 3]) and the Prospect Farm trachyte quarry. In this model trachyte deposits (turquoise layer) are inferred to underlie the Prospect Farm formation (grey and brown layers). The main escarpment features are delineated by dashed white lines. (B) images, schematic representation of trenches, and topographic map using local coordinate system of Locality II. (C) images, schematic representation of trenches, and topographic map using local coordinate system of Locality I. (D) Images of Prospect Farm trachyte quarry.

5.5.3 Particle size and bulk geochemistry

For analyses of the bulk chemical composition of 10 major elements (Al, Si, Fe, Ti, Mn, K, Mg, Na, Ca and P), sediment samples were air-dried and sieved (<2 mm). A 1-g aliquot of the samples was digested with aqua regia (a mixture of concentrated nitric acid and concentrated hydrochloric acid; in a molar ratio of 1:3), prior to dilution with polished (HQ) deionised water, using the facilities in the Dept. of Geography, Univ. of Cambridge. Samples were analysed by inductively coupled plasma optical emission spectroscopy (IPC-OES) on the Perkin Elmer Optima 2100DV ICP-AES chemical analyser at 396.153 nm (Al); 251.612 nm (Si); 398.176 nm (Ti); 238.204 nm (Fe); 257.610 nm (Mn); 769.896 nm (K); 280.271 nm (Mg); 588.995 nm (Na); 317.933 nm (Ca); 214.914 nm (P). The emission spectra of samples were compared to those from a series of Perkin Multi-element Calibration Standards. Grain size distribution was performed on the Malvern Mastersizer 2000 laser particle size analyser at facilities in the Dept. of Geography, Univ. of Cambridge following the procedure of Gatti et al., (2013) (See Appendix 5.2.2) to determine coarse sand (2000-630 μ m), medium sand (630-200 μ m), fine sand (200-63 μ m), coarse silt (63-20 μ m), medium silt (20-6.3 μ m), fine silt (6.3-2 μ m) and clay (<2 μ m) fractions.

5.5.4 Approach to studying elemental changes across soil horizons

Absolute and relative changes in elemental concentrations, indicative of chemical alteration and pedogenic processes, were examined to test field classifications of palaeosol horizons and to provide insight into relative weathering, palaeosol formation and the sedimentary processes active during soil formation. Interpretations of palaeosols in the Prospect Farm sequence follow the premise that in the absence of additions of material through secondary sedimentary processes, and individual palaeosol should show less alteration (weathering) with depth; with their lower units consisting of less weatherd buried volcanic parent material.

Numerous elements can exist in sediment in multiple states of oxidation and valence, and compounds with difference in solubility, reducibility and extractability contribute to total element concentrations in palaeosols. For example, the clay size fraction is generally composed of multiple different minerals (e.g. mixtures of feldspars, Fe- and Al- oxyhydroxides and phyllosilicates) that are not readily disaffiliated from one another (Sheldon and Tabor, 2009). The elemental values reported in Chapter 6.4 are the total extractable values (inorganic and organic forms e.g. total exactable Iron [Fet] expressed in ppm). As such, the bulk geochemical result reported in Chapter 6.4 records these combinations of minerals rather than giving a direct measure of elemental oxides/mineralogical indicators of pedogenic conditions. This means that molecule weathering indices using major oxide ratios [see Sheldon and Tabor, 2009] and total elemental values for pedogenic minerals (e.g. goethite, hematite, and ferrihydrite in Fe [Fed] [e.g. Nordt and Driese, 2009]) were not established here. It is apparent from modern studies of their behaviour during weathering in volcanic ash (see Section 5.5.4), that total elemental values of some elements are more reliably associated with specific elemental states and weathering phases than others. For example, elements such as Ti and P and to a lesser extent Fe, indicate that it is difficult to assign dominant phases of transformation of mineral and organic particles during weathering and pedogenic process, to total

concentrations of these elements. However, where such relationships can be better established, relative changes between selected elements can reveal pedogenic processes following the same rationale of more widely used proportional wt% data that have ben used to calculate molecular weathering and pedogenesis ratios (see Sheldon and Tabour, 2009).

An advantage of studying total elemental values is that, unlike more widely used weathering indices, this approach does not assume advanced weathering (leaching and mineral accumulation); and thus may be better suited to identifying incipient pedogenesis in weakly formed palaeosols (Terhorst et al., 2014). Furthermore, relationships between total element content, oxalate-extractable forms and secondary crystalline extracts - recorded in modern soils developing on volcanic ash parent material - can be applied to the sediment sequence to make generalized inferences about pedogenesis.

5.5.4.1 Elemental weathering ratios applied to the Prospect Farm sequence

Table 5.3 shows the inferred relationship between variation in total elemental concentrations and pedogenic processes used in this thesis, including the rationale of these inferred linkages. Behaviour of individual elements and groups of elements with similar properties during weathering are discussed in more detail in Appendices 5.3-5.3.5. Ongoing mineralogy analysis (through XRD and micromorphology) of Prospect Farm sediments (being conducted by Prof. Hema Achyuthan) is expected to improve associations between total element values, weathering products of parent material; as well as the mobility of different elements, identification of specific authigenic indicators of pedogenesis, and additions of unweathered and non-pedogenic sedimentary material. While results of this ongoing work are expected to drastically alter the general inferences made about the palaeosol types, associated formation process, and climate conditions presented in this thesis.

Total and relative	Formula	Inferred pedogenic	Rationale
change in		and sedimentary	
elements		processes	
Hydrolysis (Mg, Na, Ca, K) decrease relative to Al	<u>ΣBases</u> (<u>Ca+Mg+Na+K)</u> Al	Hydrolysis	Al primarily reflects (Al _o) in volcanic soils (Shoji et al., 1993) and is less mobile than alkaline and alkaline earth elements, Si or Fe and Mn (Common rock-forming alkaline and alkaline earth elements are lost relative to Al during pedogenesis (Nanzyo et al., 2002a,b; Harsh, 2005; Sheldon and Tabour, 2009).
Base loss	Base/Ti	Leaching and additions of unweathered primary rock forming elements through colluvial or aeolian processes	Base cations (Ca, Mg, Na, K) should be leached during weathering under normal pH conditions and Ti accumulated (Sheldon and Tabour, 2009). Ti is less mobile than alkaline and alkaline earth elements, Si or Fe and Mn. Common rock-forming alkaline and alkaline earth elements increase relative to Ti when marginally weathered primary minerals are added through physical processes (Nanzyo et al., 2002a,b; Retallack, 2008). Accumulation of alkali earth elements relative to Ti and Al may also indicate alkanisation and/or salinization (Retallack, 2008).
Clayeyness (Al increases relative to Si)	Al/Si	Hydrolysis	Al is accumulated as clay minerals form.
Increases and decreases in total concentrations of Fe an Mn		Redox	Fe values in volcanic soils primarily reflect the sum of secondary Fe and Mn in Fe _o , Mn _o and Fe _d and Mn _d (Shoji et al., 1993; Nanzyo et al., 2002a,b; Mahaney et al., 2014). increased concentrations indicate oxidising soil conditions, decreased concentrations indicate reducing conditions (Sheldon and Tabour, 2009).

Table 5.3 Weathering and pedogenesis ratios and changes in total element concentrations applied to the Prospect Farm sequence.

5.6 Phytolith analysis

5.6.1 Phytolith extraction from sediments

Phytolith extraction from soils followed the procedure of Madella et al., (1998) and Calegari et al., (2013) with minor modifications (see Appendix 5.2.3 for procedure details).

5.6.2 Phytoliths identification and counting

Phytoliths were measured, identified, and counted according to morphology (shape and size) using an Olympus BX40F epifluorescence microscope at 400 × magnification with a µm eyepiece and graticule. Higher magnifications were used when identification was problematic and for some photomicrographs. Phytolith length was measured along the primary axis. A minimum 200 standardised index specific (ecologically meaningful) GSSC morphotypes were counted per sample: this threshold was chosen in order to ensure statistical confidence (set at 95% certainty [Lytle and Wahl, 2005]) that count error and chance error did not adversely affect numerical analyses and the robustness of explanations of habitat structure drawn from them (see Barboni et al., 1999; Strömberg, 2009a, 2009b, Alexandre and Bremond, 2009; Zurro et al., 2016). After this target was reached, the whole slide was also scanned for rare and diagnostic morphotypes. Qualitative observations of the presence of diatoms, sponge spicules, and tephra shards in samples were also noted. The preservation of phytoliths was noted following the combined preservation/alteration index developed by Fredlund and Tieszen (1997). The phytolith diagrams were prepared with the C2 programme (Juggins, 2007). Carbon coating and the very strong dark or opaque appearance of phytoliths, representing burning, was noted and used as rough indicator

of fires that reach over 600 °C (e.g. Yost et al., 2018); but is not taken as a precise indicator of fire frequency (see Chapter 6.7.4). Photomicrographs of all morphotypes identified were compiled using Photomicrographs of ImagePro-Plus version 5.0. The concentration of phytoliths per gram AIF was calculated following Albert and Weiner (2001); simplified into a single equation by Bates (2011):

$N \ge (A/a) \ge (P/p)$

AIF

N, is the number of phytoliths counted; A, the total slide area (calculated by dividing the area of the slide cover [22 x 40 mm = 880 mm²] by the area of the microscope field of view [3.14 (pi) x 0.275² mm = 0.237462 mm²]); *a*, is the area counted (number of microscope fields of view); *P*, is the weight of the dry silicate; *p*, is the weight of dry silicate on the slide; AIF, is the weight (g.) of the acid insoluble fraction of the dry sediment.

5.6.3 Phytolith descriptions and classifications

Phytoliths descriptions and classifications follow the scheme laid out in Chapter 4. A summary of the 32 key phytoliths morphotype classes used in this study for indices analysis and general interpretation is presented in Table 5.4 and Figure 5.10.

5.6.3.1 Considerations of regionally divergent trends in the taxonomic and environmental significance of phytoliths from East African flora

As introduced in Chapter 4.1.2, a major issue in phytolith analysis is the multiplicity and redundancy of phytolith morphotypes across different taxonomic groups. This needs to be taken into account when assigning taxonomic and ecological significance to different morphotypes. Multiplicity and redundancy (caused by inheritance and convergence), means that there are very few individual phytolith types that are explicitly diagnostic of (i.e. exclusively present in) a singular grass subfamily or woody/herbaceous dicotyledon. This is further complicated by the fact that phytolith morphological-taxonomic patterns show some regional variation; which means that regionally-specific phytolith reference collections cannot be uncritically applied to different ecological zones (see Section 5.6.5.6 and Appendix 5.5 - 5.9). However, important relationships between certain phytolith types, distinct plant functional types, and ecological conditions (in which they occur in high frequencies), means that morphotypes can generally be assigned to a group within the taxonomic hierarchy of plants (see Sections 5.6.5.3 - 5.6.5.6 and Appendix 5.5 - 5.9). The challenge of interpreting certain morphotypes that exist in different plants using different photosynthetic pathways and/or that occupy different ecological niches, is somewhat reduced when they are found in an assemblage with complementary morphotypes that collectively, as an assemblage, indicate a particular set of environmental conditions and vegetation community. How regionally specific environmental-taxonomic relationships of phytoliths from East African vegetation may affect vegetation interpretations are discussed below in Section 5.6.5. This dicussion includes adjustments made to widely used phytolith indices (developed for West African vegetation) so they are appropriate for use in East African settings; which is the focus of this study.



Figure 5.10 Photomicrographs of main ecologically important phytolith morphotype sub-classes in Prospect Farm fossil samples. Scale bar 10µm. (A) GSSC: (a) Cross 3 lobed; (b) Cross 4 lobed; (c) Bilobate - long shaft, rounded non-indented/sculpted lobes; (d) Bilobate long shank; (e) Bilobate short shank; (f) Bilobate asymmetrical/non-sculpted, trap.; (g) 'scooped bilobate'; (h) Bilobate 'stipa-type'; (i) Polylobate; (j) Trapezoid square; (k) Trapeziform short cell; (l) Rondel ('pooid', conical, keeled and pyramidal types); (m) Rondel - base ≥15um; (n) Saddle long/tall and collapsed types; (o) Saddle 'short/squat'; (p) Plateaued saddle; (q) Saddle equidimensional; (r) Tabular Trapeziform ('sinuate' or 'wavy' types)/polylobate. (B) Other Poaceae and family specific types: (a) Cuneiform bulliform indiff.; (b) Commelinaceae/Marantaceae types; (c-e) Cyperaceae types; (f) Globular echinate – Areaceae type. (C) Woody and herbaceous dicotyledons: (a-b) Sclereids; (c-f) blocky/tabular types. (D) Woody and herbaceous dicotyledons (globular types): (a) Globular psilate; (b) Globular granulate; (c) Globular verrucate oblong; (d) Globular founded; (e-g) Globular decorated; (h) Epidermal jig-saw platelet; (i) Epidermal polygonal/Cork aerenchyma platelet lrg.

Morphotype*	Morphotype code*	Taxonomic interpretation*	Plant functional type or group	Explanatory index use
Cross - 3 lobed	Cr-1	Chloridoideae	C4 Xerophytic grass	Ic, Iph, Fi-t ratio
Saddle 'short/squat'	Sad-2	Chloridoideae	C4 Xerophytic grass	Ic, Iph, Fi-t ratio
Bilobate short shank	Bi-1 to Bi-9	Panicoideae	C4 Mesophytic grass ^a	Ic, Iph, Fi-t ratio
Bilobate long shank	Bi-13 to Bi- 16, Bi-20	Panicoideae	C4 Mesophytic grass ^a	Ic, Iph, Fi-t ratio
Polylobate	Poly-1, 2	Panicoideae	C4 Mesophytic grass ^a	Ic, Iph, Fi-t ratio
Bilobate asymmetrical/non-sculpted, trap.	Bi-10, 11	Panicoideae	C4 Mesophytic grass ^a	Ic, Iph, Fi-t ratio
Bilobate - long shaft, rounded non- indented/sculpted lobes	Bi-17, 18	Panicoideae /Aristidoideae)	C4 Mesophytic grass ^a	Ic, Iph, Fi-t ratio
Plateaued saddle	Sad-4	Poaceae	Grass- indeterminate ^b	Ic, Iph, Fi-t ratio
Cross - 4 lobed	Cr-2 to Cr-4	Poaceae	Grass-	Ic, Iph, Fi-t ratio
Saddle equidimensional	Sad 1	Poaceae	Grass-	Ic Iph Fi-t
outure equilimensional			indeterminate	ratio
Saddle long/tall and collapsed types	Sad-3, Sad-5	Poaceae	Grass- indeterminate ^c	Ic, Iph, Fi-t ratio
Bilobate 'stipa-type'	Bi-19	Poaceae	Grass- indeterminate ^d	Ic, Iph, Fi-t ratio
Trapezoid square	Tra-1	Poaceae	Grass- indeterminate	Ic, Iph, Fi-t ratio
Trapeziform short cell	Tra-2	Poaceae	Grass- indeterminate	Ic, Iph, Fi-t ratio
Rondel ('pooid', conical, keeled and pyramidal types)	Ron-1 to Ron-7, Ron-9	Poaceae	Grass- indeterminate ^e	Ic, Iph, Fi-t ratio
Rondel - base ≥15um	Ron-8	Poaceae	C ₃ grass	Ic, Iph, Fi-t ratio
Bilobate deeply concave lobes, long and short shank "scooped bilobate"	Bi-12	Poaceaef	Grass - indeterminate	Ic, Iph, Fi-t ratio
Trapeziform wavy long (sinuate)/ polylobate	Tram-1, 2	Pooideae ^g	C ₃ grass	Ic, Iph, Fi-t ratio
Cuneiform bulliform indiff.	Bull-1	Poaceae	Grass- intermediate	Fs%
Blocky/Tabular types	Plate 1 Aa-Ib	woody/herbaceous dicotyledons	Woody/Arboreal and some Cyperaceae	Fi-t ratio
Globular echinate	Plate 2 Pa-Pb	Areaceae (palms)	Woody/Arboreal	Fi-t ratio
Globular psilate	Plate 2	woody/herbaceous	Woody/Arboreal	Fi-t ratio
	Ea-Ed	monocotyledons		

Globular granulate	Plate 2 Ga- Gc	woody/herbaceous dicotyledons	Woody/Arboreal	Fi-t ratio
Globular decorated	Plate 2 Ha- Ib, K, M, Na- O, R, Sa-Uc	woody dicotyledons and monocotyledons	Woody/Arboreal	Fi-t ratio
Globular verrucate oblong	Pate 2 Ja-Jd	woody/herbaceous dicotyledons	Woody/Arboreal	Fi-t ratio
Globular founded	Plate 2 Qa- Qc	woody/herbaceous dicotyledons	Woody/Arboreal	Fi-t ratio
Sclereids	Plate 3 Aa-Fg	woody/herbaceous dicotyledons	Woody/Arboreal	Fi-t ratio
Epidermal polygonal/Cork	Plate 4	woody/herbaceous dicotyledons	Woody/Arboreal	Fi-t ratio
aerencnyma platelet irg.	Ba-Bg			
Epidermal jig-saw platelet	Plate 4	dicotyledons/pteridophytes	Woody/Arboreal	
	Aa-Ac			
Opaque perforated platelets		Herbaceous	Asteraceae	
Commelinaceae/Marantaceae types	Plate 2 B-Db	Herbaceous	Commelinaceae/ Marantaceae	
Cyperaceae types	Plate 7	Cyperaceae ^h	Cyperaceae	
	Ba-Bd			

Table 5.4 Key phytolith morphotypes used in this study for indices analysis and interpretations following a general approach.

*References used for phytolith descriptions, names and taxonomic associations are provided in Chapter 4. Photomicrographs of the morphotypes are provided in Plates 1-7 Chapter 4. Corresponding Figure/morphotype codes are given in parenthesis.

a These morphotypes are found in high proportions in C_4 Panicoideae but are also present in small proportions in many species in other grass subfamilies. Bremond et al., (2008a) note that some Panicoids in close-canopy settings in montane areas of East Africa use C_3 photosynthesis (see Section 5.6.5.4 for discussion).

b 'Plateaued saddles' (Sad-4) have been assigned to Phragmites spp. (e.g. Yost et al., 2018) but are recorded in multiple subfamilies.

c 'Long' or 'tall' saddle have been recorded in Bambusoideae but are also present in Chloridoideae. Very tall' saddles (width $\geq 20\mu m$) have been identified by Piperno and Pearsall (1998) and Yost et al., (2018) as being exclusive to Bambusoideae (see Appendix 5.9 for details).

d "Stipa" type bilobates, previous though to be exclusive to C_3 grasses (Piperno, 2006) have been recorded in Panicoideae and Chloridoideae in East Africa (Barboni and Bremond, 2009).

e Rondels- Redundant across East African grass-subfamilies. Yost et al., (2018) assign rondel 'angular keeled' and 'keeled' types to Pooideae (Phalaris spp.). However, Barboni and Bremond (2009) have demonstrated that these morphotypes occur in multiple other grass subfamilies.

f Generally attributed to Ehrhartoideae and Bambusoideae (C₃) (see Piperno, 2006). However, assigned to indeterminate C₃ & C₄ based on the results of Barboni and Bremond (2009).

g Trapeziform sinuate morphotypes are produced in abundance by Pooideae but are also present in small proportions in several species within the Bambusoideae, Panicoideae and Chloridoideae subfamilies (Barboni and Bremond, 2009; Bremond et al., 2008a; Mercader, 2010).

h Yost et al., (2018) have identified previous unknown sedge type phytoliths with "hollow or tubular projections" SOM (Figs. S1eS6; Tables S3eS5) from Cyperaceae rhizomes that were not observed in Cyperaceae spp. from modern references collection in the Nakuru-Naivasha Basin or in palaeosols sample. As such, they are not considered here.

5.6.4 Indices and general approaches to studying East African phytolith assemblages

To reconstruct palaeovegetation change from the phytoliths record at Prospect Farm two complementary analytical approaches were employed. These have been defined as the 'indices' (specific) and 'general' approaches (Strömberg, 2003, 2004). The indices approach focuses primarily on comparing the ratio of a small number (n=8-13) of taxonomically significant short-cell GSSC phytolith groups (representative of specific grass subfamilies) and smaller phytoliths from arboreal taxa, calibrated using modern vegetation-climate training sets, commonly from West Africa (Neumann et al., 2009; Garnier et al., 2012). These indices act as a proxy for variables such as aridity, temperature and vegetation openness in Africa, and allow for tracking changes in major African vegetation types (i.e. in and between grassland and forest); based on quantitative measurements of changes in morphotype relative abundance within and between different vegetation types (Diester-Haass et al., 1973; Alexandre et al., 1997; Bremond et al., 2005a,b, 2008a,b; Aleman et al., 2012; Novello et al., 2012, 2015, 2017; Cordova et al., 2013; Esteban et al., 2017; Stewart et al., 2016; Arráiz et al., 2017a,b; Yost et al., 2018). The general approach takes all identified morphotypes into account when inferring past vegetation composition in Africa using changes in morphotype relative abundance that consider observed difference in the distribution of different plant types within and between different vegetation types; without relying on direct quantitative comparisons to modern phytolith-vegetation refrence sets (e.g. Runge, 1999, 2001; Mercader et al., 2000; 2013; Albert et al., 2006, 2009; Bamford et al., 2006; Albert and Bamford, 2012). In this thesis the data required to calculate phytolith indices and to compare these to published phytolith soil-surface assemblages across intertropical Africa, were extracted and summarised from the more detailed morphotype classification and count data produced through the general approach.

5.6.5 Phytolith Indices

Four phytolith indices (FI-t%, Iph%, Ic% and Fs%) were calculated to determine arboreal cover and the dominance of specific grass subfamilies in the Prospect Farm phytolith record.

5.6.5.1 Estimating arboreal vegetation cover using the D/P° index: benefits and limitations

The D/P index (Dicotyledons:Poaceae), first developed by Alexandre et al., (1997) and widely used in African phytolith studies to reconstruct changes in arboreal vegetation cover, tends to underestimate arboreal cover in East African habitiats (see Appnedix 5.4 for further details). Consequently, the Forest Indicator ratio (FI-t) was preferend.

5.6.5.2 Alternatives to the D/P index for reconstruction vegetation physiognomy. Estimating arboreal vegetation cover using the FI-t ratio.

Strömberg (2004) noted that it is often not possible to directly translate the relative abundance of phytoliths into the exact portions of differ plants types in a past ecosystem and instead proposed the use of the FI-t ratio as a rough indicator of relative balance of forest and grass cover: in other words, vegetation openness. This is calculated as the ratio of the total sum of all forest indicator (FI-t) phytoliths relative to the sum of FI-t plus the total of all GSSCs (Strömberg, 2004). In situations where the D/P index performs poorly, the FI-t ratio is more accurate but less precise (i.e. high values are interpreted

as closed habitats, and low values as open habitats as the FI-t ratio is not calibrated against detailed measurements of modern vegetation cover). (see Appendix 5.5 for an overview of the benefits and limitations of using this Fi-t ratio in East African settings).

Following this generalised approach, the FI-t ratio and relative abundance of FIs was calculated for each fossil sample and the relative abundances of blocky types, globular/special types, other woody indicators (e.g. sclereid/epidermal platelets are plotted stratigraphically with the relative abundances of xeric C₄ grasses, mesic C₄ grasses C_3/C_4 indeterminate grasses and *Cyperaceae*). These approaches allow for observations of the co-occurrence of general and specific indicators of woody plants and grass subfamilies that can share the same niche in modern settings, to infer broad vegetation types in the fossil record. Fossil phytoliths percentages from Prospect Farm were also compared to modern Miombo woodland samples (Mercader et al., 2013), as wetter Miombo vegetation types are physiognomically similar to some dry woodland/forest vegetation types of the Afromontane zone and share some common species (White, 1983).

5.6.5.3 Estimating short grass (xeric) vs. long grass (mesic) savannas using the Iph index

The Iph index was first developed by Diester-Haass et al. (1973) as a proxy for the shifts in the dominance of short grass (xeric) vs. long grass (mesic) North-West African savannas; based on the ratio of certain GSSC phytoliths from marine cores. It is calculated by dividing the sum of Chloridoideae GSSC phytoliths by the sum of Chloridoideae GSSCs plus Panicoideae GSSCs. C₄ mesic grass proportions shares a positive statistical relationship with increased summer precipitation and C₄ xeric grass proportions show a negative statistical relationship with increased summer precipitation (Yost et al., 2018). (see Appendix 5.6 for an overview of the benefits and limitations use of Iph index in East African settings).

<u>5.6.5.4 Estimating relative proportions of grass subfamilies to infer C_3 vs C_4 grass using the Ic index</u>

The Ic or climatic index, originally proposed by Twiss (1992), is calculated by dividing the sum of all GSSC phytoliths primarily produced in Pooideae, Bambusoideae and Arundinoideae by the sum of GGSC phytoliths primarily produced by Pooideae, Bambusoideae and Arundinoideae plus Chloridoideae and Panicoideae subfamilies (Diester-Haass et al., 1973; Watson et al., 1985; Twiss et al., 1987; Watson and Dallwitz, 1992; Alexandre et al., 1999).

Ic% = <u>Rondel + Trapeziform polylobate + Trapeziform short cell</u> Rondel + Trapeziform polylobate + Trapeziform short cell + Saddle + Cross + Bilobate

In East Africa Bremond et al., (2008a), demonstrated that a statistically meaningful relationship exists between the Ic index values and increases in C_3 grasses relative to C_4 grasses with increasing altitude. C_3 grass proportions share a positive statistical relationship with decreasing temperature and increasing soil moisture, while C_4 grasses abundance decrease linearly with increasing elevation and decreasing temperature. As such, the Ic index and the relative abundances of these groups in the fossil record can be used to infer changes in these climatic parameters. (see Appendix 5.7 for an overview of the benefits and limitations using the Ic index in East African settings).

5.6.5.5 Estimating grass water stress: The Fs index

Bremond et al., (2005b), drawing on observations that the production of bulliform phytoliths is a xeromorphic adaptation to dry climates, established a significant positive correlation exists between the percentage of fan shape bulliform phytoliths and increasing aridity and low water availability. The Fs index is the sum of bulliform cells divided by the sum of all classified phytoliths (see Appendix 5.8 for an overview of Fs values from different African vegetation types). It has, however, also been demonstrated that the abundance of bulliform cells is controlled but several other factors, such as silica availability in wetter areas where ponding of groundwater occurs (Sangster and Parry, 1969; Fernández Honaine and Osterrieth, 2012). Consequently, the assertion that higher proportions of bulliforms indicate increased aridity may not hold under certain conditions.

5.6.5.6 Summary of phytolith indices used in the study of Prospect Farm fossil phytoliths samples

A summary of the phytolith indices used for phytolith-based palaeovegetation reconstructions in Chapter 6 is provide in Table 5.5. Phytolith production patterns in East African grass subfamilies and the effect these trends have on phytolith indices values are discussed in greater detail in Appendix 5.9 and in relation to fossil phytolith results in Chapter 6.

Phytolith indices	Records changes in:	Proxy for changes in:
Fit-t	the relative abundance of all	Arboreal cover (higher values indicate
	forest vs non-forest indicator	increased arboreal cover)
	phytoliths	
Iph%	the relative abundance of xeric	discriminating
	C ₄ vs mesic C ₄ grass phytoliths	between xeric and mesic savannas
		(increased values indicate drier conditions)
Ic%	the relative abundance of All C ₃	Temperature and soil moisture (higher
	relative to C ₄ grass phytoliths	values indicate climatic cooling)
Fs%	The relative abundance of	Grass water stress as a result of changes in
	bulliform phytoliths	soil moisture (higher values indicate
		decease soil moisture and increase grass
		water stress)

Table 5.5 Summary of phytolith indices used palaeovegetation reconstructions in this thesis.

5.6.6 Modern soil phytolith reference samples

A modern phytolith dataset of 189 samples was collated from published surface soil samples from several phytogeographical zones and sub-zones defined by White (1983). Each contain vegetation types with different physiognomy and species composition. This data was used as comparative material against which phytolith relevant abundance and indices scores calculated from the Prospect Farm fossil phytolith assemblage were interpreted. Table 5.6 shows the distribution and grouping of samples across these zones and associated references. Appendix 5, Table 5.3 lists the relative abundance of phytoliths and the geographical coordinates of individual samples. Information on the phytogeographical zone (e.g.

Afromontane forest [AFMF]), vegetation zone (e.g. Montane forest), and local vegetation (e.g. Moist evergreen elevation forest) associated with each sample is provided in more detail in Table 5.6 and Appendix 5, Table 5.4. This dataset is primarily that which was compiled by Barboni et al., (2007) to test and refine the use of phytolith indices for differentiating between the vegetation zones of African and between vegetation types within these zones; but were also augmented by more recent studies (e.g. Garnier et al., 2012; Neumann et al., 2009; Novello et al., 2012; Bremond et al., 2016). Following the approach of Barboni et al., (2007), phytoliths were grouped into a smaller number of broad morphotype categories. This re-grouping of phytolith into broader (less specific) categories is necessary to ensure comparability between different published studies that can follow disparate phytolith classification schemes, while also allowing for the calculation of Ic and Iph indices. Long cell, bulliform and hair cell phytoliths were excluded from the original 13 morphotypes proposed by Barboni et al., (2007). This was because these types are ubiquitous in similar proportions in the plant group from which they originate, however, their inclusion was found by the authors to add no discriminatory value in differentiating vegetation types; instead adding 'noise' to the analysis. Rather, these types were found to add noise to the analysis. Therefore, the current analysis considers only 9 morphotype classes (see Figure 5.11). Phytolith counts from the detailed Prospect Farm fossil dataset were also combined into these 9 morphotype classes to ensure comparability when conducting statistical analysis and calculating phytolith indices values.



Figure 5.11 Phytolith percentage diagram of 9 morphotype classes from modern samples from the East African Afromontane phytogeographic zone, divided by vegetation type. Samples correspond to those listed in Table 5.6 and Appendix 5, Table 5.4.

5.6.7 Statistical analysis of phytolith data

5.6.7.1 Principal components analysis (PCA) of modern and fossil phytolith data

To determine if similarities existed between fossil samples and modern African vegetation and to infer changes in vegetation over time at Prospect Farm, fossil phytolith samples were compared to modern surface samples using principal components analysis (PCA). PCA aims to summarise the variance in
multivariate data within a reduced ordination space, while maximising the amount of variance explained (Jackson, 1993; ter Braak, 1994; Legendre and Legendre, 2012). In palaeoecological studies, PCA has been employed to provide a generalised picture of the key linear relationships between variables (in this case phytolith morphotypes) and objects (in this case phytolith soil samples). To does so by allowing the user to visualise key trends and groupings, outliers, and key variables structuring variability between the samples (Birks, 1995; ter Braak, 1994; Legendre and Legendre, 2012; Buttigieg and Ramette, 2014).

5.6.7.1.1 PCA: modern vs fossil of complete African dataset

PCA was conducted with Past software version 3.2.0 (Hammer et al., 2001). Initially PCA was carried out on the full dataset phytolith of relative abundances, scaling the data in two ways. Barboni et al., (2007) previously demonstrated the usefulness of phytolith assemblages in discriminating different African vegetation types using Type-2 scaling (i.e. the correlation biplot of Legendre and Legendre [2012]) on a slightly reduced dataset. Here PCA was performed on the correlation matrix (i.e. normalizing all variables using division by their standard deviations) to ensure comparability to the results of Barboni et al., (2007). Type-1 scaling (i.e. the distance biplot of Legendre and Legendre [2012]) was also used to evaluate similarities between modern and fossil samples.

5.6.7.1.2 PCA: modern vs fossil of East African dataset

Initial PCA results revealed overlap between Propect Farm fossil samples and a limited set of vegetation types represent by 36 samples primarily from East Africa (listed in Figure 5.11 and Table 5.11 and shown in Fig 5.12) as was expected [see Chapter 6.7.6.1]). Consequently, additional PCAs were conducted to compare these samples and fossil samples from Prospect Farm. Individual transformation bases PCAs (tb-PCA) were carried out on both the entire Prospect Farm dataset and on a reduced dataset of samples from the uppermost horizons (with the highest concentration of phytoliths) of the 5 Palaeosols identified in the Prospect Farm sequence. As PCA relies on the assumption of multivariate normality of data (i.e. that composition along the theoretical environmental gradient is not non-linear), tests were carried out to determine if appropriate transformations needed to be applied to the data prior to analysis. Both Mardia's Multivariate Normality Test (Mardia, 1974) and Shapiro-Wilks Test (Shapiro and Wilk, 1965) (see Appendix 5, Figures 5.1 and 5.2) (performed using the MVN package v 5.5 R [Korkmaz et al, 2014], for R version 3.4 [R core team, 2017]), indicated the data was non-normal. This was confirmed through detrended correspondence analysis (DCA) (Hill and Gauch, 1980) that indicated gradient length > 4 S.D (ter Braak and Prentice, 1988; Legendre and Birks, 2012) (performed using the vegan package version 2.4-3 for R [Oksanen et al., 2017]). As such, an ecologically motivated Hellinger transformation (Legendre and Gallagher, 2001) was performed (also using the vegan package) prior to PCA to compensate for the double zero problem that affects the dataset (Legendre and Legendre, 2012). As such tb-PCA was carried out on the variance-covariance matrix. tb-PCA was preferred to non-Euclidean (dis)similarity techniques such as Non-metric Multidimension Scaling (NDMS) and DCA, as it maintains the original Euclidean/Hellinger distances and is less sensitive to outliers. Furthermore, tests using NMDS did not show that this approach would yield result that would alter interpretations.



Figure 5.12 Images of selected biomes of mountainous areas of eastern Africa. The biomes and their associated VECEA vegetation types are those that exist in or near to the Central Rift Valley, Kenya today with the exception of the Miombo woodlands. The corresponding phytogeographical zones (PhytZ=zone code in Table 5.6) and vegetation types from which modern soil-phytolith sample assemblages have been published (listed in Table 5.6) and which act as a comparison sample to Prospect Farm fossil samples are provide as an approximate guide to the physiognomy of the vegetation from which these samples originate. All photographs are from Marchant et al., (2018): A) Afroalpine grassland (VECEA=A) [PhytZ=AFMS], Mt. Kilimanjaro. B) Afromontane rain forest (VECEA=Fa/Fb/Fe) [PhytZ=AFMF] surrounding swamp with tussock sedges and grasses, Mt. Kenya. C) Ericaceous vegetation (VECEA=E) [PhytZ=AFMS], Mt. Kilimanjaro. D and E) Epiphytic moist montane rain forest (Fa) [PhytZ=AFMF], Mt. Meru, Tanzania (similar to moist evergreen elevation forest and Evergreen upper forest [Hagenia-Hypericum]). F) Moist Afromontane forest (VECEA=Fa/Fe) [PhytZ=AFMF], Mt. Kenya. G) lower undifferentiated Afromontane forest (VECEA=Fb), Mount Longonot crater (no published soil surface samples exist from this Afromontane vegetation subtype, but it is most similar in species composition to moist evergreen elevation forest and Bamboo forest [PhytZ=AFMF]). H) Bamboo forest (VECEA=B) [PhytZ=AFMF], Mt. Elgon. I) Young deciduous woodland developing on basalt flow (VECEA=Fh/Be), Chyulu Hills, Kenya (no published soil surface samples exist from this vegetation type, but it shares some similarities with shrub savanna [PhytZ=AFMF/AFMSS]). J) Miombo woodlands (VECEA=Wm) [PhytZ=WOZA]. K) Wetland and Acacia forest embedded within the semi-arid savannah landscape, Selous (VECEA=wd) (no published soil surface samples exist from this vegetation type, but it is similar in appearance and physiognomy to drier open miombo woodland and Acacia wooded grassland) [PhytZ=WOZA/EDAP-Sah]). L) Grassland savannah with intermittent trees (shrub savanna) (VECEA=Be/wd) [PhytZ=AFMSS]). M) Northern Kenya Acacia woodland (VECEA=Bd/Wcd) [PhytZ=GRSO]. Northern Kenya acacia-Brachystegia shrubland-woodland (VECEA=Bd/Wcd) [PhytZ=GRSO]. I) Woody savannah pastoral landscape (no published soil surface samples but like PhytZ GRSO). VECEA vegetation code descriptions can be found in Table 5.6.

Phytogeographic zones (White, 1983)	zone	ne VECEA No.		zone	References					
	code	code	samples	map no.						
Afromontane forest*	AFMF	Fa/Fb/Fe/B	7	VIII	Bremond, 2003, et al.					
					2008a					
Afromontane shrubland/grassland*	AFMS	A/E	12	VIII	Bremond, 2003, et al.,					
					2008a					
Afromontane shrub savannah*	AFMSS	Fh/Be/wd	3	VIII	Bremond, 2003, et al.,					
					2008a					
Woodland (Zambezian)*	WOZA	Wm	6	II	Bremond, 2003, et al.,					
					2008a					
Semi-desert grassland (Somalia–Masaï)*	GRSO	Wcd/Bd	3d 3 IV Barboni et al.,							
					published)					
Sahelian edaphic grassland mosaics with	EDAP-	EDAP- 9 XVI Novello								
Acacia wooded grassland *	Sha									
Semi-desert grassland (Sahelian-	GRSA		7	XVI	Bremond et al., 2005b					
Saharan)										
Sahelian herbaceous swamp and aquatic	HSAS 10 XVI Novello et			Novello et al., 2012						
vegetation										
Sahelo-Sudanian savannah - floodplain	SFSS		12	III	Garnier et al., 2012					
Sudano–Sahelian gallery forest	GFSS		3	III	Neumann et al., 2009					
Sudanian edaphic grassland mosaics	EDAP-		3	III	Novello et al., 2012					
with Acacias/broad-leaved trees	Sud									
Dry Sudanian woodland - Shrub savanna	BUSA		24	III and	Bremond et al., 2005b					
with short grasses				XVI						
Dry Sudanian woodland - Tree/shrub	WOSU		32	III and	Bremond et al., 2005b (28);					
tall-grass savanna and undifferentiated				XVI	Novello et al., 2012 (4)					
woodland										
Guineo-Congolian lowland rainforest	EVF		20	I and XI	Bremond et al., 2016					
"Guineo-Congolian, semi-deciduous	MOSA		38	XI	Bremond et al., 2005a,b					
forests					(28); Bremond et al., 2016					
					(10)					

Table 5.6 Number and location (by phytogeographic zone) of published phytoliths from modern soil-surface across intertropical Africa used for comparison to Prospect Farm fossil phytolith samples through statistical analysis.*Samples collected from these phytogeographical zones corresponded to eastern African montane vegetation biomes shown in Corresponding Figure 5.12 VECEA vegetation codes: A=Afroalpine vegetation; Bd=Somalia-Masai Acacia-Commiphora deciduous bushland and thicket Be=Evergreen and semi-evergreen bushland and thicket; E=Montane Ericaceous belt; Fa=Afromontane rain forest; Fb=Afromontane undifferentiated forest; Fe=Afromontane moist transitional forest; Fh=Afromontane dry transitional forest; Wcd=Dry combretum wooded grassland; wd=Edaphic wooded grassland on drainage-impeded or seasonally flooded soils; Wm= Miombo woodland.

5.6.7.1.3 PCA and hierarchical clustering: expanded fossil dataset

In order to summarise relative changes in vegetation throughout the Prospect Farm fossil sequence, including the factors responsible for variation between phytolith assemblages from different palaeosols, samples were compared to one another through tb-PCA in addition to stratigraphic summary plots. These summaries use the expanded and more detailed generalised phytolith dataset that considers all ecologically meaningful morphotypes (i.e. the generalised approach). Multivariate normality tests (see Appendix 5, Figures 5.3 and 5.4) indicated that the Hellinger transformation was appropriate. tb-PCA on the variance-covariance matrix using Type-1 scaling was used to visualise similarities between samples. Several morphotypes were removed from the tb-PCA analysis due to *a priori* considerations of their ecological relevance in separating modern East African vegetation types due to redundancy and similarly high proportions of these morphotypes in all samples. The types excluded were various long cell platelets and acicular hairs cells, being ubiquitous in Poaceae and woody species, are ecologically uninformative (see Section 5.6.6).

Rondel morphotypes have been shown to discriminate alpine/highland elevation grassland/shrubland and Afromontane forest/shrub savanna in East African vegetation from lowland Central/West African vegetation. Within East African samples from the Afroalpine zone rondels on average constitute 72% of all phytoliths and they are the most important factor in distinguishing between samples from this zone from other East African vegetation (see Chapter 6.7.1). Predictably, the initial PCA comparing East African samples did not show an overlap between any fossil samples and Afroalpine grassland (see Chapter 6.7.6.1) (i.e. the percentage of rondels was too low to infer the existence of Afroalpine grassland at Prospect Farm, as expected). In vegetation types at elevations that could feasibly have existed in the past at Prospect Farm, such as Ericaceous shrubland, Afromontane forest/shrub savanna (above 1900 m a.s.sl) and grassland in the Somalia-Masaï zone (below 600 m a.s.l.), rondels range between 20-60% of the total assemblage irrespective of elevation (see Figure 5.11). This means that rondels alone do not provide a means of discriminating between these vegetation types or relative changes in C3 vs C4 grass subfamilies (Bremond et al., 2008a). Thus, while the rondel morphotypes may have large factor scores (0.6) and contribute 'significantly' to the structuring of the ordination space when included in the analysis, they add noise rather than discriminatory value. As such, the resulting patterns are ecological meaningless and potentially misleading. For this reason, rondel morphotypes (except those $\geq 15\mu m$ that are exclusive to C3 grasses) were excluded and other C3 indicators used to differentiate different approximated vegetation types. Additionally, stratigraphically constrained hierarchical clustering on fossil samples, using the dissimilarity based CONISS technique (Grimm, 1987; Bennett, 1996) in the rioja package for R (Juggins, 2017), was used alongside tb-PCA to find vegetation groupings.

5.6.7.2 Phytoliths indices comparisons: modern to fossil samples

To compare phytolith indices values from Prospect Farm palaeosol horizons to values from modern East African vegetation, and to assess altitudinal variation in these values between the two samples sites at Prospect Farm, descriptive statistics were calculated for each published vegetation types in East Africa and for each of the 5 palaeosol horizons from Locality I and II at Prospect Farm. Mean values for indices and standard error of the mean (SE) (which unlike the standard deviation considers sample size) at 95% confidence interval (1.96*SE) are reported as sample size is small.

5.7 Comparisons of key changes in geochemical, phytolith and grain size data.

Multivariate (PCA) and univariate analysis (linear regression) were carried out to summarise key changes in geochemistry and grain sizes throughout the Prospect Farm sequence and to provide insight into possible correlations between change in grain size and phytolith types, grain size and phytolith concentrations and grain size and sediment geochemistry. As the lack of current dates for the sequence currently make comparisons to regional environment records impossible, vegetation change could not be compared to independent environmental variables (e.g. pCO_2 , rainfall [inferred through lake level] and temperature), that are expected to have played a major role in driving vegetation change at the site over time. Direct gradient analysis was not considered appropriate for comparing geochemical data (as qualitative explanatory variables) to changes in the phytolith samples (unimodal response data). This was because while soil chemistry can influence vegetation type, there is no basis for suggesting that variation in soil geochemistry could be the primary driver of changes between vegetation type over time (i.e. no linear, <u>causal</u> relationship is expected to exist between the explanatory variables and the response data). For the PCA of geochemical data, grain size and phytolith concentrations the matrix was standardised using a z-score transformation (see Legendre and Legendre, 2012) to correct for differences in variable magnitudes and scales, thus aiding comparability.

Chapter 6 Results and interpretation: Palaeoenvironments of the Prospect Farm Sequence

The results present in Chapter 6 represent several elements of the geoarchaeological investigations of Prospect Farm including: field descriptions of sedimentology and stratigraphic relationships, particle size analysis and geochemical analysis, as well as phytolith-based vegetation reconstructions. Results and interpretations of palaeoenvironmental conditions in the Prospect Farm sequence are reported for individual occupation phases at the site. These interpretations form the basis of estimated projections of past vegetation distributions and climate conditions in the Nakuru-Naivasha Basin that are used to evaluate behavioural ecolgical models (e.g. the *Ecotonal Hypothesis*) in Chapter 7.

The Chapter is divided as follows: Sections 6.1-6.3 report the results of the artefact density survey, sedimentology and stratigraphy. Sections 6.4-6.7 report overall trends in grain size, major element concentrations and phytoliths within the Prospect Farm sequence. Section 6.8 reports field descriptions of sediments, evidence for pedogenesis, palaeosol characterization and changes in geochemistry and phytoliths throughout the six palaeosols in decreasing age/stratigraphic order (1-6).

6.1 Density survey - results

Results of artefact counting, and identification of surface finds in 387 squares indicated several key areas with high artefact densities across the Prospect Farm Formation. Results indicate a difference in the spatial distribution of diagnostic MSA and LSA artefacts. The two areas of highest density correspond directly with Localities I and II and generally support observations of earlier surveys by Isacc (1972). High concentrations of lithics are found ~2093 m a.s.l., 2103-2108 m a.s.l., ~ 2136 m a.s.l. and 2142 m a.s.l.; with some high-density occurrences also occurring downhill at lower altitudes from 2007-2038 m a.s.l. (see Figures 6.1 and 6.2 and Appendix 6.1.1 for additional information). Based on the result of the density surveys and field walking, excavation and environmental sampling focused on areas on highest MSA occupation intensity at Locality I and II (Van Balen et al., 2019).



Figure 6.1 (a) Map of the northern slope of Mt. Eburru showing the position of Anthony's Localities I and II and the results of the 2014 density survey. Contour lines are inferred from SRTM 1 arc-second global data (U.S. Geological Survey, http://eros.usgs.gov/find-data). Labour lines and tracks (in dark grey) and river courses (in blue) are taken from the Directorate of Overseas Surveys (1975). (b) Altitudinal transect (in m a.s.l.) depicting mean artefact densities per square meter. Orange polygons indicate the surveyed areas and yellow graduated symbols the total number of finds per square. (b) Altitudinal transect (in m a.s.l.) depicting mean artefact densities. White columns correspond to altitudes that were not surveyed. (c) Square meter showing example of obsidian artefact scatter. (d) Altitudinal transect with artefact density data per square m² as recorded by Isaac (after Isaac 1972: Fig. 1c, p. 166). (Figure from Van Balen et al., 2019).



Figure 6.2 (a-b) Map of the northern slope of Mt. Eburru showing the position of Anthony's Localities I and II and the results of the density survey. Orange polygons indicate the surveyed areas and yellow graduated symbols the total number of MSA or LSA finds per m². Contour lines are inferred from SRTM 1 arc-second global data (available from the U.S. Geological Survey, http://eros.usgs.gov/find-data). Labour lines and tracks (in dark grey) and river courses (in blue) from the Directorate of Overseas Surveys (1975). (c-d) Altitudinal transects (in m a.s.l.) depicting mean densities of MSA and LSA artefacts per m². The maximum number of artefacts per m² that can be securely assigned to MSA was 59 and or LSA was 17. Grey columns correspond to surveyed altitudes, white columns correspond to altitudes that were not covered by the survey. Figure from Van Balen et al., 2019.

6.2 Results: Sedimentology and stratigraphy

The Prospect Farm sequence records 6 palaeosols which developed on and are separated by volcanic deposits (airfall pumice, tuff and colluvially redeposited tuffs). The stratigraphic continuity of these deposits allows for the reconstruction of the landscape as a palaeocatena. *In-Africa* re-excavation of Localities I and II re-exposed all but the lowest two stratigraphic units (35 & 36) identified by Anthony (1978). Sedimentary units in this study were divided according to changes in depositional conditions identified in the field and later confirmed through laboratory analysis. Figure 6.3 shows the stratigraphic logs of six palaeosols horizons identified in the Prospect Farm Formation. Appendix 6, Table 6.1 provides a summary of field descriptions of the type section sediments from the Prospect Farm Formation. Figure 6.4 shows exposures of stratigraphic units and variations in bed thickness from the main escarpment exposures identified across the Prospect Farm Formation.



Figure 6.3 Measured stratigraphic sections from the measured type section at Locality I: showing the stratigraphic units and corresponding palaeosols horizons, pedogenic features, sedimentary structures, sediment colour, lithology and bed contacts.



Figure 6.4 Measured stratigraphic sections from escarpment exposures across the Prospect Farm Formation. (A) Correlation between stratigraphic units and variation in bed thickness. Coloured circles at base of stratigraphic sections correspond to topographic maps shown in (B-D).

6.2.1 The relationship between pyroclastic-airfall and pyroclastic-flow deposits of the Prospect Farm Formation

Previously unreported ignimbrite deposits were identified to the NW of Localities I and II, where \sim 6 m of sediments is exposed by downcutting of ephemeral streams and modern quarrying works (see Figures 6.4 and 6.5). The stratigraphic and temporal relationship between ignimbrite deposits and airfall tephra deposits exposed in the main Prospect Farm excavation sequence is currently unclear, as at no point on the landscape was evidence found of the main Prospect Farm sequence deposits or any other deposits overlying or becoming intercalated with the valley ignimbrites. (see Appendix 6.1.2 for a description of these deposits).



Figure 6.5 Sediment log and photographic examples of tuffaceous deposits recorded at Prospect Farm quarry.

6.3 Result: Lithics

Classification and geochemical analysis of lithics from the 2016 INAP excavation of Localities I and II are presently ongoing. As such, no absolute artefact frequencies exist for the sequences at present. However, the percentage of artefacts as a proportion of all lithic material excavated from each stratigraphic level, qualitative observations of variation in raw material types, and Anthony's (1978) records of artefact frequencies by stratigraphic level from Locality II are available for correlation with the environmental record. Figure 6.6 plots the available artefact data against the archaeological phases proposed by Anthony (1978) and observations of artefact frequencies. Lithic material from Phases II (Palaeosols 2-4) includes infrequent artefacts made from exotic raw material (white, green, and brown chert). Comparable lithologies were also observed in artefacts of Phase III (Palaeosol 5) but occurrences were noted as being more sporadic than in Phase II. No exotic raw material was recorded from material which corresponds to Anthony's Phase I (Palaeosol 1), in which all tools are made from obsidian bounders, from an undetermined source, that is presumed to be local (Anthony, 1978). Artefact percentages in our study show good agreement with the qualitative observations of artefact frequencies made by Anthony (1978), with the exception of only moderate artefact percentages being recorded in Phase II material; where Anthony noted abundant artefacts. This disparity reflects the higher amounts of non-archaeological lithic material associated with the formation of these sediments rather than lower artefact numbers (see Section 6.8.5.3). The highest artefact frequencies and percentages occur in Palaeosols 1, 3 and 5, form widespread floors of lithic material visible across sections of the landscape. Artefacts are present at lower frequencies in Palaeosols 2 and 4. Artefact distributions, relative frequencies and site occupation phases are discussed in relation to distinct palaeosol forming episodes in Section 6.8.



Figure 6.6 Stratigraphic plot of Prospect Farm locality I, comparing palaeosol horizons to down-profile changes in artefact percentages, archaeological phases and qualitative artefact frequencies according to Anthony (1978) and the same observations updated according to this study.

6.4 Results: Major element geochemistry trends

Geochemical trends in relation to individual palaeosol forming episodes are considered in more detail in Section 6.8, but several primary trends in major element concentrations in C, illuvial and eluvial horizons are identified in all palaeosols. Figure 6.7 shows key major element concentrations and weathering ratios plotted against depth from Locality I. Results are reported as mean concentration in ppm (mg/l) based on average of three replicate samples (see Appendix 6, Table 6.2). All samples were below the relative standard deviation (%RSD) cut-off point of 10%. Total element concentrations throughout the profile in general show higher values and similar stratigraphic distributions of transition metals (Fe, Mn and Ti) with Al and low concentrations of alkaline earth elements (Ca, Mg, Na and K), as well as P and Si. This relationship indicates that sediments have undergone extensive weathering, resulting in the formation of secondary minerals and is supported by over-all strong positive correlations between elements within these groups (see Table 6.1).

	Phytolits per gram AIF	Clay %	Silt %	Sand %	Al	Fe	K	Mg	Mn	Na	Р	Si	Ti	Ca
Phytolits per gram AIF														
Clay %	0.16225													
Silt %	0.02752	0.69750												
Sand %	-0.19353	-0.78377	-0.88388											
Al	-0.36080	-0.27044	-0.29183	0.30070										
Fe	-0.22952	-0.11708	-0.24805	0.21364	0.74464									
К	-0.21823	-0.078546	-0.05869	0.03718	0.77201	0.70402								
Mg	-0.39948	-0.15684	-0.19435	0.24636	0.74157	0.70870	0.80836							
Mn	0.14162	0.08625	-0.15981	0.11504	0.040871	0.53961	0.12171	0.20545						
Na	-0.30357	-0.51581	-0.43452	0.44981	0.66121	0.43458	0.52333	0.48768	-0.16982					
Р	0.34103	0.01098	0.01403	-0.037698	-0.52380	-0.31401	-0.64287	-0.65026	0.13707	-0.39698				
Si	-0.07675	0.63262	0.60525	-0.64044	-0.024508	-0.20263	0.10026	0.00014	-0.27359	-0.32087	-0.29734			
Ti	-0.18058	-0.29273	-0.40757	0.39194	0.72752	0.86990	0.63073	0.64020	0.40743	0.54083	-0.24848	-0.45395		
Ca	0.04855	-0.069482	-0.21787	0.18260	0.42803	0.53885	0.49140	0.48580	0.40385	0.25554	-0.084751	-0.37600	0.61046	

Table 6.1 Pearson's correlation coefficient (*R*) for selected sedimentology, geochemical, grain size data from the Prospect Farm record. Bold values indicate 99% confidence interval.

Peak Fe, Mn and Ti values occur in horizons that show physical signs of pedogenesis (i.e. these elements increase from less weathered parent material to the upper palaeosol horizons of individual palaeosols) as show in Figure 6.7. These weathering trends are in most cases supported by the Al/Si and Base cation ratios that indicates increased clay mineral formation in palaeosol horizons and increased concentrations of Base cations in less-weathered C horizons. However, exceptions do exist to these general trends. For example, it is apparent in Palaeosol 4, that alkaline earth elements increase relative to first transition metals and Al towards the top of the palaeosol profile. This is interpreted as indicating incipient to moderate weathering and mineral alteration of PS4 sediments, and possibly authigenic inputs of Si rich volcanic parent material (see Section 6.8.4 for a more detailed discussion). Variability in relative weathering intensity and development of soils is summarised in PCA outputs (see Figure 6.10).



Figure 6.7 Change in total element values (aqua regia ppm [mg/l]) and weathering ratios for the pedostratigraphic succession of the Prospect Farm sequence. Red dots indicate sampling depths.



Figure 6.8 Biplots comparing changes in selected element concentrations (that are associated with variability in redox conditions and increased chemical weathering) in samples from parent material (C horizons), eluvial horizons, and Bt horizons in Palaeosols 1-5. (A) Al vs Fe; (B) Mn vs. Fe; (C) Ti vs. Al; (D) Ti vs. Fe. In general, lower total concentrations of these elements in parent material indicate that they are less affected by weathering than the overlying palaeosol horizons. Low to intermediate concentrations of selected elements in eluvial horizons reflect depletion and movement of these elements to the illuvial Bt horizon.

Increases in Ti_t that are evident from lower to upper horizons observed in Palaeosols 1, 2, and 5, are taken primarily to indicate secondary enrichment of Ti associated with weathering products of secondary mineral phases, as suggested by Nanzyo et al., (2002a,b). This is supported by the generally strong positive correlations between Ti and Fe, and Ti and Al throughout the sequence (Figures 6.8 and 6.9). As such, spikes in total Ti are likely, in general, to be more reflective of the transformation (leaching and oxidation) of primary titanomagnetites in volcanic parent material into titanomagnetites and/or the formation of pseudorutile from weathering of ileminite (FeTiO₃).



Figure 6.9 Fe vs. Ti Ordinary Least Squares Regression. Blue line= 95% bootstrapped confidence intervals (N=1999). r²: 0.76379, Permutation p = 0.0001.



Figure 6.10 PCA correlation biplot of Prospect Farm sediment sample geochemistry. The upper horizons of Palaeosols 1-5 (PS1-5) are colour coded. PCA axis 1 reflects palaeosol weathering intensity and/or age associated with progressive palaeosol Bt horizon formation and ferruginisation. All elements, besides P and Si that are loaded to Axis 2, are positively loaded to Axis 1, with Al, Fe, Ti, Mg and K having the highest factor loading scores. Samples from Palaeosol 1, 2, 3 and 4 are mainly located at the negative end of Axis 1, indicating that they are less weathered than Palaeosol 5 which occupies the space at the positive end of Axis 1 and has a well-developed Bt horizon. Axis 2 is defined by higher Si values at its negative end and higher P values at its positive end. Axis 2 differentiates sediments with high and low proportions of unweather parent material. The weakly developed Palaeosol 4 is separated from all other palaeosols by its relatively higher Si content. Palaeosol 1 is the only palaeosol which displays elevated concentrations of P in its upper horizon (see Section 6.8.4 for details).

6.5 Particle size results

Figures 6.11 and 6.12 show key grain size variables plotted against depth from Locality I. A summary of the particle size analysis for Locality I is provided in Appendix 6, Table 6.3. Stratigraphic plots of changes in particle size values in the pedostratigraphic sequence indicate that the percentage of clay and silt size material generally increases relative to sand in B horizons of Palaeosols 1, 2, 3, 4 and 6. Sand content increases in eluvial E horizons in Palaeosols 1 and 2 and in the lower B/C horizons of all palaeosols. The higher percentage of sand-sized material in Palaeosol 5 partly reflects its development from pyroclastic flow deposits that have a higher coarse grain size fraction and inclusions of pebble size volcanic lithics (see Section 6.8.1). Similarly, a fining-upwards trend in Palaeosol 4 reflects the fine-grained nature of the airfall ash parent material, as well as clay production and translocation to the B horizons during palaeosol formation. It may also reflect the addition of fine material through post-depositional aeolian processes (see Section 6.8.4). Fine particle sizes reported for Unit 6 pumice deposits reflect laser particle size measurements of matrix material rather than the larger matrix supported pebble size pumice clasts recorded during field observations (see Appendix 6, Table 6.1 and Figure 6.5).

6.6 Combined sediment geochemistry, particle size, and phytolith concentration results

The PCA biplot (shown in Figure 6.13) summarises variation in geochemistry, particle size, and phytolith concentration values across all samples in the Prospect Farm sequence. Results of this analysis reinforce the differences between palaeosols highlighted in Sections 6.4 and 6.5. Additionally, the PCA shows that sediments interpreted as primary airfall tuffs, that have undergone minimal physical post-depositional reworking and chemical weathering (e.g. Units 2B-3E) and weakly developed palaeosols (e.g. PS4 [Unit 7]) and PS1 [Units 1A-2A]), are strongly positively correlated with fine particle sizes and higher Si content. Furthermore, these samples show a weak negative correlation with phytoliths per-gram AIF. This most likely reflects low vegetation cover and reduced phytolith production and deposition in sediments in which pedogenesis did not take place or was incipient. Total phytolith concentrations in the Prospect Farm sequence in comparison to those recorded in modern soils are discussed in Section 6.7 and in turn in relation to individual palaeosols in Section 6.8.



Figure 6.11 Key particle size variables and phytolith concentrations per-gram AIF down-profile for the Prospect Farm sequence, and particle size distributions in selected samples from Palaeosols 5 and 6 (red lines).



Figure 6.12 Key particle size variables and phytolith concentrations per-gram AIF down-profile for the Prospect Farm sequence, and particle size distributions in selected samples from Palaeosols 1 to 4 (darker grey lines).



Figure 6.13 PCA correlation biplot of Prospect Farm sediment sample geochemistry, phytolith concentrations, and key particle size variables (Sand%, Silt%, Clay%) and PhyteG (phytoliths per gram AIF).

6.7 Fossil phytolith assemblage results: occurrences, relative abundance, concentrations, preservation, taphonomy, evidence of alternation by fire, and comparison to modern vegetation samples

6.7.1 Phytolith occurrence and relative abundances

A total of 35508 phytoliths were counted across the 63 samples from the main sequence at Locality I. Absolute counts ranged from 84 - 3000 phytoliths per sample. In 22 samples from Locality I the minimum count size of 200 index specific GSSC phytoliths could not be reached before extracted material was exhausted (see Appendix 6, Table 6.4). An additional 3319 phytoliths were counted in five samples from the upper horizon of palaeosols at Locality II, that were identified in the field as representing lateral continuations of PS1-PS5 sampled from the main column at Locality I. Total phytolith counts are reported in Appendix 6, Tables 6.5 and 6.6. Percentage phytolith diagrams showing the relative frequency of all morphotypes from Locality I plotted against depth are shown in Figures 6.16 - 6.18. Phytolith percentage diagrams of ecological indicator types and summaries of ecological meaningful groupings of phytoliths with phytolith indices, preservation and concentrations plotted against depth, are shown in Figures 6.15 and 6.19. Ubiquitous morphotypes (e.g. Acicular types and square/rectangular psilate platelets) are the most abundant phytolith category when all morphotypes are

considered, accounting on average for 66% of the total assemblage. GSSC types account on average for 20%. Arboreal blocky, globular and cylindric types account for 10% on average. The remaining 4% comprises other types, such as bulliform, simple epidermal tracheids, and family specific types. When ecologically uninformative morphotypes are removed from the phytolith sum, GSSCs account for 54%, arboreal types for 40% and bulliform and family specific types for 6% of the total.

6.7.2 Phytolith distributions and estimated total concentrations in Prospect Farm palaeosol profiles

Summary bio-stratigraphic plots show that phytolith preservation and phytolith concentrations increase towards the upper horizons of palaeosols. An inverse trend is observed between phytoliths concentrations and the presence of sediments that are interpreted as being unpedogenised. The number of phytolith per gram of sediment AIF in B or B/A horizons range between 10,000,000 – 3,300,000 (average: 11,360,000). These values are comparable to those recorded in A/B horizons of modern soils (e.g. Fishkis et al., 2010; Madella and Lancelotti, 2012; McNamme, 2013; Strömberg et al., 2018) and palaeosols (e.g. Osterrieth et al., 2009, 2016). Phytolith concentrations are far lower in B/C horizons and in sediments that lack signs of pedogenesis: ranging from 0 (sterile) to 10,000,000 (average: 39,77,000). These classes of sediments are also generally associated with poor phytolith preservation and low total counts, resulting in phytolith index count targets not being reached.

6.7.3 Phytolith preservation in the Prospect Farm sequence

6.7.3.1 Factors potentially affecting phytolith preservation

Biogenic silica that forms phytoliths is generally stable in most soil conditions (Bartoli and Wilding, 1980). However, surface pitting that removes diagnostic features, physical breakage, and complete dissolution of phytoliths, occurs under certain conditions, which are not entirely understood (see Strömberg et al., 2018 and references therein and Appendix 6.2.1 for additional information). However, very generally, GSSC types seem more susceptible to destruction through physical damage than blocky types, while blocky types appear most vulnerable than GSSC types to dissolution (Cabanes and Shahack-Gross 2015).

6.7.3.2 Phytolith preservation and distribution trends in the Prospect Farm sequence

Like phytolith concentrations, phytolith preservation scores throughout the Prospect Farm sequence appear to vary according to the character of sediment in which they occur and in relation to their depth in a given palaeosol profile. Preservation is similarly high across all samples in the uppermost preserved horizons, with only very occasional pitting evidence on large blocky morphotypes and Al/Fe oxide coating on GSSC types. Figure 6.15 shows down-profile changes in preservation using the scale proposed by Fredlund and Tieszen (1997) shown in (Table 6.2). Visual comparisons of changes in total element concentrations compared to phytolith preservation does not indicate any obvious relationship between phytolith preservation and increases in Base cations (generally associated with more alkaline soil conditions) or increases in Al or Fe values (generally associated with more acidic soil conditions)

Scale	Description	Observable characteristics
5	Excellent	No pitting of bulliform cells or erosion of elongate forms
4	Good	Slight pitting of bulliform cells and erosion of elongates
3	Acceptable	Some pitting of bulliform cells and fragmentation of elongates
2	Poor	Significant pitting of bulliforms and destruction of elongates
1	Extremely poor	Extreme pitting of bulliforms; elongate cells absent
0	Absent	No phytolith preservation

Table 6.2 Scale used in evaluation of phytolith preservation (Table 4 pg. 211 [Fredlund and Tieszen, 1997]).

A linear regression model, comparing the number of morphotypes recorded per sample to the concentration of phytoliths per gram of AIF (Figure 6.14), does not indicate a strong correlation between increased phytolith concentrations and preservation with a wider range of phytolith morphotypes (c.f. Lancelotti, 2010). However, there is evidence to suggest that taphonomy has had a greater effect on the relative abundance of different morphotypes. For example, in Palaeosols 1 and 5 phytolith preservation



Figure 6.14 Ordinary Least Squares Regression: phytoliths per gram AIF (x axis) compared to number of morphotypes per sample (y-axis). Blue line=95% bootstrapped confidence intervals (N=1999), r^2 : 0.082298, Permutation *p*: 0.0348.

below the upper E and B horizons is poor and all phytolith types show some signs of surface alteration. These samples contain high proportions of blocky/tabular, globular, and bulliform morphotypes and lower proportions of GSSC morphotypes with signs of physical breakage. This suggest that these samples have been biased in favour of arboreal indicator types through taphonomic processes. As such, the evidence for vegetation change from these samples is considered unreliable (see Section 6.8.1 and 6.8.5). Comparisons of palaeosols samples to published modern soil phytolith assemblages from East African vegetation types through PCA analysis supports this interpretation (see additional information in Appendix 6.2.2). PS3 and PS4 are interpreted as having been formed under semi-humid to semi-arid climatic condition (see Sections 6.8.3 and 6.8.4). It may be the case that reduced biomass and slow or episodic (incipient) soil development caused phytolith preservation to be less variable in these palaeosols. This is because, in theory, phytoliths that are more rapidly detached from the terrestrial silicon cycle (through which phytoliths are reprocessed by plants in soil horizons where roots are active) are less affected by these taphonomic processes (Alexandre et al., 1997; Derry et al., 2005; Cabanes and Shahack-

Gross 2015). It may be the case that water percolation and burial compaction continues to have a postdepositional taphonomic effect on phytoliths in all palaeosol types before and after they are covered by overlying volcanic deposits (see del Carmen Gutiérrez-Castorena and Effland, 2010 and references therein; Madella and Lancelotti, 2012). Poor preservation and low concentrations of phytoliths in the unpedogenised airfall tuff of Unit 3 are interpreted as reflecting residual incorporations, during eruption, of phytoliths from vegetation of higher elevation forest on Mt. Eburru. It is also possible that small amounts of phytoliths were post-depositionally translocated into Unit 3 from overlying deposits. In summary, it may be tempting to interpret down-profile changes in phytoliths as indicating diachronic shifts in vegetation in the Prospect Farm sequence, particularly in palaeosols that are likely to encompass climatic changes and related ecological shifts that have been shown to occur over multimillennial timescales in Africa during the late Quaternary Period. However, low chrono-stratigraphic resolution and taphonomic factors affecting these palaeosols are likely to confound such interpretations. Consequently, phytolith samples from these lower palaeosol horizons are considered with caution in vegetation reconstructions.

Throughout the sequence Fs% results often contradict indications of climatic conditions inferred through other morphotypes. Bulliform phytoliths have very low relative abundances through the main Prospect Farm sequence (0-3%), which could affect the reliability of the Fs index. It may also be the case that this contradictory signal was generated by site specific local variation in preservation, relative humidity, or differences in grass species present at the two sites; resulting in artificially elevated Fs% in the samples from Locality II. Higher proportions of bulliforms at higher elevations compared to lower elevations are more compatible with findings that bulliform production is often in fact regulated by the availability silica which can increase under locally wetter conditions; where ponding of water occurred (Sangster and Parry, 1969; Fernández Honaine and Osterrieth, 2012), contra Bremond et al., (2005b). Low occurrences of most family specific types in the sequence are interpreted as primarily reflecting the dissolution potential of these more fragile types (i.e. those that are finely silicified and have delicate appendages) (see Appendix 6.2.3 for additional information on the preservation of family specific morphotypes). The influence of taphonomic processes affecting phytolith distributions and preservation bias is discussed on an individual basis for Palaeosols 1-5 in Section 6.8.

6.7.4 Evidence for fire in the Prospect Farm phytolith record

The high melting point of plant biogenic silica means that phytoliths do not generally show signs of alteration by fire (Wattez et al., 1990; del Carmen Gutiérrez-Castorena and Effland, 2010), except when fire temperatures rise above 600°C (Parr, 2006; Evett and Cuthrell, 2017). There is only very occasional evidence for phytoliths being altered by fire in the Prospect Farm record. When burnt phytoliths were recorded they are generally GSSC types and always constituted <0.5% of any given sample (see Figure 6.15). It is possible that the lack of evidence for fire may relate to low burning temperatures at the site. For example, Gowlett et al., (2017) have shown the temperatures in grass dominated savanna ecosystems in southern and East Africa rarely rise above 600°C and burn rapidly. When denser woody vegetation is

present temperatures reach higher values as increased fuel results in longer burning and more intense fires. Phytolith records that have shown evidence of repeat burning of vegetation of the Afromontane zone, supported by other independent records of fire (e.g. charcoal influx) (e.g. Wooller et al., 2000a, 2003; Yost et al., 2018), indicate that we would expect far higher frequencies of burned phytoliths in the Prospect Farm sequence; even if only local, low-intensity repeat fires occurred at the site. Furthermore, while studies indicate that burnt soil phytolith assemblages are slightly more unstable than unburnt assemblages (Cabanes et al., 2011), this difference in solubility is highly unlikely to explain the extremely low numbers of fire altered phytoliths recorded in the Prospect Farm sequence. Considering all these factors, burnt phytoliths from Prospect Farm are most likely to be residual exogenous additions to the assemblage caused by burning of non-local vegetation, but probably still within the Nakuru-Naivasha Basin. It is also possible that burnt phytoliths may also represent small-scale anthropogenic burning of vegetation at the site. However, no hearth features have been identified during INAP excavations or during previous investigations of the site's sedimentology.

6.7.5 Prospect Farm deposits: from phytolith assemblages to vegetation reconstructions: Temporal and spatial resolution of phytolith-based vegetation reconstructions

Sedimentological analysis of the Prospect Farm Formation indicates a pattern of deposition of volcanic material forming the parent material for palaeosol formation, and that this formation process occurred in low energy post-depositional environments. This suggest that sediments are preserved in-situ, with ground water and other post-depositional processes having no impact on the stratigraphic coherence of sediments and only a minor impact on the coherence of phytolith distributions. Studies of similar palaeosol sequences across ancient land surfaces from India (Blinkhorn et al., 2012) and East Africa (e.g. Ashley et al., 2010; Barboni et al., 2010; Diez-Martín et al., 2010; Barboni, 2014; Arráiz et al., 2017a,b) indicate that in low energy depositional environments, free from the influence of significant aeolian or fluvial inputs, phytoliths record a localised picture of standing vegetation. Similarly, modern soil samples from East African mountains, generally reflect standing vegetation within surrounding 5m² sampling plots accurately (Bremond et al., 2008a). As mentioned, a residual background phytolith signal is expected to be present in parent material due to incorporation of phytoliths into sediments during movement of volcanic material downslope prior to deposition or through burning in the surrounding area. However, these inputs are are minor enough that they are not considered to affect the ability of the samples to infer local vegetation dynamics at Prospect Farm. Comparisons of modern soil phytolith assemblages to standing vegetation indicate that phytolith assemblages can be highly polygenic (i.e. they do not record a single point in time, but instead represent a palimpsest of phytoliths accumulated from plants that were present during successive disturbance episodes (Strömberg, 2004; Piperno, 2006; Mercader et al., 2011; Pearsall, 2016). In cases where vegetation change was rapid or palaeosols were stable over decadal to millennial time scales, phytolith assemblages from a single palaeosol may record a combination of different successional vegetation changes and ecological trends (Mercader et al., 2011).

Phytoliths in the Prospect Farm sequence tend to be highly concentrated in the A/upper B horizons of soil where they are recycled and translocated to lower horizons through various taphonomic processes (see Section 6.7.3.2). Consequently, it can be misleading to interpret changes in phytoliths with depth as indicating even relative diachronic changes in vegetation. This means the Prospect Farm phytolith assemblages do not allow short-term seasonal or annual (reversible) changes to be detected. Instead, they provide a broader time-averaged summary of local vegetation dynamics. This low temporal resolution significantly limits our ability to understand changes in vegetation over time at the site and their relationship to regional environmental records. However, the polygenic nature of samples evident in Prospect Farm palaeosols has one advantage in that is likely to capture and amalgamation of spatial variation in vegetation (i.e. patch dynamics) over time within a given vegetation type of the Afromontane floristic zone, that can change over quite short distances. Consequently, extrapolating polygenic vegetation changes in the Prospect Farm sequence to environmental changes in the rest of the Nakuru-Naivasha Basin (using a single stratigraphic column/site approach [see Chapter 7.3.3]) is likely to be less prone to spurious vegetation interpretations than if the phytolith assemblages were assumed to reflect only very localised, spatially and diachronically delimited signals of vegetation change from a single vegetation patch (e.g. Blinkhorn et al., 2012).

6.7.6 Phytoliths from the Prospect Farm sequence: results and interpretation

A summary phytolith percentage plot of key phytolith groups and indices (Figure 6.15) shows that significant differences in phytolith assemblage composition and inferred vegetation communities evident across the 5 Palaeosol horizons (PS1-PS5) in the Prospect Farm sequence. For example, the oldest phytolith assemblage zone from PS1 (Unit 15A) is the only palaeosol in which high percentages (8-12%) of C₃ GSSC phytoliths occur in proportions comparable to those found in modern moist Afromontane forest. This indicates closed vegetation, locally cool moist climate conditions during the formation of PS5 and Phase I occupation of the site (see Section 6.8.1.4.6). By contrast in PS3 (Unit 8), very high percentages (24-32%) of C₄ xeric GSSC phytoliths are recorded, indicating open vegetation, arid conditions, and a likely increase in the length and intensity of the dry season during Phase II occupation of the site (see Section 6.8.2.4.3). The remaining palaeosol horizons in the Prospect Farm sequence show more mixed GSSC signals with varying contributions of phytoliths from woody dicotyledons indicating lower variability in arboreal cover relative to the differences observed between PS3 and PS5. The indeterminate C_3/C_4 GSSC group, that form a significant proportion of all GSSC types across all samples, is composed primarily of rondel morphotypes, that are redundant across many Poaceae subfamilies commonly found in the Afromontane zone (see Appendix 5.9and Figure 6.18).

More detailed discussion of phytolith-based vegetation reconstructions, that consider all samples as well as occurrences of tephra and diatoms, are reported in Section 6.8 for each palaeosol forming interval. Figure 6.20 plots summarise stratigraphic changes in FI results from Prospect Farm compared to the range of FIs in modern Miombo woodlands samples, as well as variation in selected key phytolith indices and morphotypes groups. Box plots comparing differences in phytolith indices values between samples from Prospect Farm Localities I and II are provided in Figure 6.21-6.24.



Figure 6.15 Phytolith percentage diagram of Prospect Farm sequence deposits showing summary phytolith groupings. Also shown are phytolith indices and preservation scores, as well as occurrences of diatoms, sponge spicules, burned phytoliths and micro-tephra. Abundances lower than 1% are represented by a dot.



Figure 6.16 Phytolith percentage diagram of Prospect Farm sequence deposits of all ligneous dicotyledon morphotypes.



Figure 6.17 Phytolith percentage diagram of Prospect Farm sequence deposits of other arboreal indicators, ubiquitous, and xeric and mesic GSSC morphotypes.



Figure 6.18 Phytolith percentage diagram of Prospect Farm sequence deposits of all indeterminate C₃/C₄ GSSC, C₃ GSSC, and other Poaceae morphotypes.



Figure 6.19 Phytolith percentage diagram of Prospect Farm sequence deposits of all ecologically important morphotypes.



Figure 6.20 Diagram showing down-profile variation in selected phytolith indices and morphotype groups. (A) FI % (green line) compared to the range and average (dashed line and box) of FI % of modern soil samples from the Miombo Woodlands, Tanzania. Black-fill circles indicate samples classified as 'dense' and clear circles as 'sparse' by Mercader et al., (2009). (B) change in % of globular granulate phytoliths. Dashed line at 15% marks point at which \geq 40% arboreal cover can be reliably inferred in Central African settings, according to Novello et al., (2017). (C) change in % of Mesic C₄ GSSC types plotted against % of indeterminate C₃/C₄ GSSC types. (D) change in % of Xeric C₄ GSSC types plotted against % of C₃ GSSC types. (E) Iph%. Dashed line indicates the value that divides moisture loving and arid adapted grasses. Solid grey horizontal bars delineate upper Palaeosol horizons. Pink bars indicate samples where phytolith preservation and concentrations were too low to calculate phytolith indices.



Figure 6.21 Box plots comparing Ic% values of published samples to fossil phytolith samples from palaeosol horizons from Prospect Farm Localities I and II. Values reported are the mean and SE. The floristic crossover between modern East African montane habitats in which C_3 grasses are more dominate than C_4 grasses is placed at 50% by Bremond et al., (2008a). WOZA=Woodland (Zambezian). AFMF=Afromontane forest. AFMS=Afromontane grassland/savanna. EDAP-Sah=Sahelian edaphic wooded grassland.



Figure 6.22 Box plots comparing Iph%*100 values of published samples to fossil phytolith samples from palaeosol horizons from Prospect Farm Localities I and II. Values reported are the mean and SE. The yellow box indicates the range of values across which the presence of arid adapted grasses can be inferred. The pink box indicates the range of values across which the presence of moisture loving grasses can be inferred (Alexandre et al., 1997; Bremond et al., 2005a; Novello et al., 2017). WOZA=Woodland (Zambezian). AFMF=Afromontane forest. AFMS=Afromontane grassland/savanna. EDAP-Sah=Sahelian edaphic wooded grassland.



Figure 6.23 Box plots comparing the relative abundance of FI plus CH as a % of all phytoliths counted in published samples to fossil phytolith samples from palaeosol horizons from Prospect Farm Localities I and II. Values reported are the mean and SE. WOZA=Woodland (Zambezian). AFMF=Afromontane forest. AFMS=Afromontane grassland/savanna. EDAP-Sah=Sahelian edaphic wooded grassland.



Figure 6.24 Box plots comparing Fs% index values of published samples to fossil phytolith samples from palaeosol horizons from Prospect Farm Localities I and II. Values reported are the mean and SE. WOZA=Woodland (Zambezian). AFMF=Afromontane forest. AFMS=Afromontane grassland/savanna. EDAP-Sah=Sahelian edaphic wooded grassland.
6.7.6.1 Comparison of fossil phytolith to modern phytolith reference samples: Africa-wide PCA results

PCA bi-plots comparing Prospect Farm fossil phytolith samples to modern soil phytolith assemblages from across inter-tropical Africa (Figure 6.25) show that Prospect Farm samples share ordination space with East African vegetation types (i.e. they have similar compositions: both having high proportions of rondels and trapeziform sinuate morphotypes [see Figure 6.25[B]). An exception to this trend is the overlap observed between Prospect Farm samples and those from sites of the Middle Awash subdesertic steppe in the Somalia–Masaï zone (< 600 m a.s.l.). These overlap in ordination space with Afromontane moist evergreen upland forest, grassland and, shrub savannah (Figure 6.25 [A]). This reflects the high number of rondel morphotypes produced by Poaceae found in the Afromontane zone, as discussed in Chapter 5.6.5.6 and Appendix 5.5 - 5.9. Two vegetation zones from outside of eastern Africa: Zambezian Woodland (WOZA) and Acacia wooded grassland from Lake Chad (EDAP-Sah) show a degree of overlap with Prospect Farm fossil samples. While the EDAP-Sah vegetation type is not expected to have been present in the Nakuru-Naivasha Basin in the past, it is structurally and compositionally similar to Edaphic wooded grassland on drainage-impeded or seasonally flooded soils (VECEA=Wd vegetation type) found in the basin today (see Chapters 2.9 and 5.6.7.1.2). This is supported by the overlap of EDAP-Sah samples with Afromontane shrub savanna (AFMS) (VECEA=Be/Wd) in the PCA, that share an ecotone with Wd vegetation types in the Nakuru-Naivasha Basin. As such, fossil samples that are compositionally similar to these types can be broadly taken to indicate wooded savannah and grassland environments, formed under higher temperatures and lower moisture availability than Afromontane forest.



Figure 6.25 (A) PCA distance bi-plot comparing Prospect Farm fossil samples to modern comparative samples from intertropical Africa. (B) PCA correlation bi-plot. As expected, the PCA largely demonstrates the same patterns as those from Barboni et al., (2007): PCA axes 1 explains 25% of variance and differentiates forested and non-forested sites. This is based on the negative loading of globular granulate and globular echinate morphotypes, associated with palms and woody species in West Africa, and positive loading of saddle, bulliform, bilobates and cross morphotypes produced in Poaceae, indicative of grasslands. PCA axes 2 explains 18% of the total variance and is characterized by positive loading of trapeziform short cell, trapeziform polylobate and rondel morphotypes which differentiate highland zones from lowland zones of East Africa (expect for the Middle Awash subdesertic steppe).

6.7.6.2 Comparison of fossil to modern comparative samples: East African PCA results

As introduced in Section 6.7.3.2, when taphonomic factors are considered, in general only the uppermost horizons of palaeosols in the Prospect Farm sequence are thought to record intelligible vegetation signals. This is because reworking of sediments is thought to have had a significant negative effect on the relative abundance of phytoliths in lower palaeosol horizons. This has resulted in a phytolith signal biased towards dominance of non-GSSC types without modern analogues in East Africa and which do not accurately reflect past vegetation. Figure 6.26 shows the PCA bi-plot of all East African and Prospect Farm fossil samples. The wide dispersion in ordination space of samples from lower palaeosol horizons compared to those from upper horizons, as well as their lack of overlap with samples from modern vegetation types, support the interpretation that these samples reflect taphonomic bias. For example, samples from Units 4B and 5 (Btsmb horizon PS5) that display similarly low proportions of GSSC and high proportions of globular morphotypes in Africa, are most similar to modern samples from the Miombo woodlands and the Guineo-Congolian semi-deciduous forest/savanna mosaic (see Figure 6.25), in which globular granulates form 50-80% of the assemblage. However, phytolith preservation of index specific GSSC types is far too low in these samples to reliably infer that similar vegetation types were present at Prospect Farm in the past.

Figure 6.27 shows the PCA bi-plot of all East African samples and Prospect Farm fossil samples for upper palaeosol horizons only. Results indicate that PCA is effective in separating Afroalpine samples from all other Afromontane zone vegetation, as well as from the EDAP-Sah and Somalia-Masaï zone. The PCA successfully captures the spatial continuum between modern vegetation with a mixed C_3/C_4 grass signal and vegetation with a dominant C_4 grass signal. However, it is important to note that because of redundancy of the 10 morphotypes used to characterize these samples, it fails to differentiate between Afromontane shrub savannah, Afromontane forest and bamboo communities and the ecotones between them at a fine scale. An additional limitation of this PCA is the inability of the 10 broad phytolith morphotype classes it uses, to reflect variation in arboreal cover across samples. It is apparent that redundancy of these 10 morphotypes confounds the complete differentiation of vegetation types of specific interest for this study. Variation in vegetation composition and structure over time at Prospect Farm between the two theoretical extremes of closed canopy Afromontane sclerophyll/bamboo forest at one end and open grass savannah on the other, cannot be inferred using these morphotypes alone. This is highlighted by the failure of the PCA to differentiate samples that are interpreted through a general approach as more similar to Afromontane forest with C₃ understory grasses (PS1), from open xeric grassland (PS3), when in reality these vegetation types differ greatly in terms of their structure, composition and underlying climatic and edaphic influences. Samples from PS1 (1f-3f) and PS3 (3d-5d) are both located at the negative end of Axis 1 and the positive end of axis 2. Although PS1 samples are located closer to bamboo samples than those from PS3, the PCA reflects shared abundances of all bilobate and all saddle morphotypes rather than the high proportions of wavy trapeziform and short/squat saddle morphotypes that differentiate these palaeosols using a general approach to phytolith analysis. This is highlighted in the PCA of the expanded morphotype dataset in Section 6.7.6.3. Due to the limitations of the PCA using reductive morphotype classes, as well as the wide range of variation evident within PS2 samples, it is impossible to determine through this analysis if phytoliths from PS5 reflect moist Afromontane forest, or Ericaceous shrubland/grassland, or variation between these two vegetation types. Of all the palaeosols, PS4 (1c-3c) can be most confidently assigned to a single vegetation type (Shrub savanna) within the Afromontane zone. The lack of overlap of PS3 and PS1 with any published samples is likely to reflect both the polygenic nature of palaeosols and a lack of modern samples in published datasets from drier Afromontane undifferentiated forest, as well as xeric upland savanna that can have a strong C4 Chloridoideae component.



Figure 6.26 PCA distance biplot of all samples from eastern Africa and Prospect Farm fossil samples, showing: (A) plot with explanatory variable (morphotype) vectors; (B) plot with range of variation in ordination space of modern samples from each vegetation type.



Figure 6.27 PCA distance biplot of all samples from eastern Africa and Prospect Farm fossil samples from upper palaeosol horizons. A broken stick model (Appendix 6, Figure 6.1) indicates that the first three components are significant in explaining variation in the dataset (Jackson, 1993). PCA axes 1 explains 26% of variance and displays positive loading all GSSC and negative loading of bulliform and other morphotypes (see Appendix 6, Table 6.7). This axis reflects a rough altitudinal and temperature gradient between highland and lowland zones of the region. Positive loading of all GSCCs to Axis 1 indicates their prevalence across all vegetation communities in the AFMF and AFMS vegetation zones (~2100 m a.s.l. - 4200 m a.s.l.). The positive end of PC1 is associated with lowland sites and warmer conditions. Weak negative loading of globular psilate and granulate types to Axis 1 are associated with mid-altitude Miombo woodlands sites (~880-910 m a.s.l.) that occupy an intermediate position along the gradient. These morphotypes occur in higher amounts here than in Afromontane forests (AFMF) and grasslands (AFMS). Bulliform phytoliths are associated with lowland vegetation types (GRSO, EDAP-Sah, and WOZA). This is likely to reflect water stress experienced by tall grass understory species during the long (5-7 months) dry season in these habitats (e.g. Ngulube et al., 1995). PC2 accounts for 17% of the explained variance and shows a gradient from C3 Poaceae dominated Afroalpine elevation grassland and ericaceous shrubland/grassland; to mixed C₃/C₄ Poaceae of evergreen forest and shrub savannah types; to C4 dominated GRSO and EDAP-Sah zones. However, there is clear overlap between phytoliths signals from different AFMF vegetation types below the pure C_3 elevation grasslands samples from Mt. Kenya. Additionally, trapeziform short cells do not appear to make any significant contribution to differentiating vegetation types.

6.7.6.3 Results: PCA of Prospect Farm fossil samples using an expanded morphotype dataset

PCA biplots and axes scores (plotted as a function of depth) are shown in Figure 6.28. A broken stick model (Jackson, 1993) indicates that the first 2 principal components, explaining 15.6% and 13.4%, can be taken as significant. Five phytolith assemblage zones were recognised using CONISS. In general, there is good agreement between CONISS zonation and the clustering of samples in ordination space. PCA axes loadings scores (see Appendix 6, Figure 6.2) show a strong positive correlation between PC axis 1 and mesic GSSC morphotypes, positive correlation of C₃ and xeric GSSCs, as well as weaker positive loading of epidermal jigsaw, epidermal decorated, globular granulate and globular echinate types.

A strong negative correlation exists between PC1 and blocky tabular, ellipsoid with outgrowths and sclereid phytoliths. C₃ GSSCs contribute to the second axis, which also show positive loadings of ligneous indicator phytoliths and strong negative loadings of xeric and mesic GSSC morphotypes. PC1 approximates shifts between grassland dominated habitats and habitats dominated by woody dicotyledons, and thus is a broad reflection of changes in vegetation openness (see Figure 6.29). This is supported by the similarity of PC1 scores trends and changes of FI% with depth (see Figure 6.20). PC2 scores are consistent with changes between xeric grassland habitats and mesic forested-wooded habitats with a C₃ grass dominated understory. As such, PC1 explains the main successional change in vegetation, with PC2 providing additional resolution.

An exception to these trends is that the first two PCA axes records two strong, opposite directions of change in the dataset, however both axes record the same strong positive change in samples 1f-3f (the only samples with significant proportions of C₃ GSSC morphotypes). This PCA is more successful than the PCA based on the reduced number of morphotypes, because it highlights the compositional dissimilarity of samples 1f-3f from the rest of the sequence. However, the positioning of these samples at the positive end of Axis 1 (that would suggest moist, open C₃ grassland) is misleading. This is because despite having high proportions of C₃ GSSC phytoliths (as would be expected in either Afroalpine grassland or Ericaceous shrub/grassland), the samples also have relatively high proportions of arboreal indicators (see Figure 6.15). This indicates that arboreal cover was more likely to have been present in PS1 and that C₃ GSSC phytoliths originated from understory or forest clearing grass species, rather than from C_3 species that occur in open, high altitude habitats. This interpretation is further supported by previous PCA results (see Section 6.7.6.2) and by the presence of GSSC morphotypes more commonly associated with Bambusoideae in PS1 (see Chapter 5.6.5.6). These findings are also more consistent with reconstructions of maximum past altitudinal shifts in vegetation zones that occurred on East African mountains during the late Quaternary period (see Chapter 3.5.1), which suggests that Afroalpine grassland is unlikely to have shifted downwards to the altitude of Prospect Farm. Furthermore, at least some degree of arboreal cover is consistent with the palaeopedological interpretation that PS1 developed under humid conditions (see Section 6.8.1). The PCA of Prospect Farm fossil samples using the expanded morphotype dataset highlights that the general phytolith approach provides more precise information on palaeovegetation. This allows samples to be better differentiated, resulting in the more parsimonious vegetation classifications to be reached (see Section 6.8 for vegetation classifications for PS1 through PS5 following a general approach). However, it is also apparent that modern comparative soil samples, which include a greater variety of both morphotypes and vegetation types in East Africa, would help to make less subjective, more precise vegetation classifications from Prospect Farm fossil samples (see Appendix 7.1).



Figure 6.28 PCA distance biplot of Prospect Farm fossil sample using the expanded morphotype dataset, showing: (A) explanatory variable (morphotype) vectors; (B) sample labels. Also shown are PC axis scores, PCA broken stick model and CONISS result divided into zones (with sample colours matched to PCA results shown in [A] and [B]) and in statigraphic order.



Figure 6.29 PCA distance biplot of Prospect Farm fossil samples using the expanded morphotype dataset. Palaeosol horizons are marked, as well as the hypothesised main gradients of change in vegetation that are explained by the first two principal components. CA was carried out on the same dataset which confirmed that PCA maintained the correct ordering of objects along the gradients (James and Mculloch, 1990). As such, it appears that the Hellinger transformation was successful in downweighting zero values to correct for the arch effect (i.e. when correlation coefficients in PCA identifying samples which contain many zeros as being similar) (Goodall, 1954; Swan, 1970; Legendre and Legendre, 2012). This indicates that the positioning of samples 1f-3f and 1b at the centre of the gradient (but separated in ordination space from other samples) accurately reflects their composition relative to other objects, rather being the result of the extreme curvature of dissimilar ends of a gradient.

6.8 Description and interpretation of individual palaeosol forming episodes and associated palaeoenvironmental conditions

6.8.1 Palaeosol 1 (Units 16-15A)

6.8.1.1 Field descriptions

Palaeosol 1 (PS1) has only been identified in excavated sections in the two pit trenches at Locality I and II at \sim 5 m below the present-day surface (see Figures 6.4 and 6.30). PS1 is not recorded elsewhere on the landscape because of burial by overlying sediments. As a result, determination of variation in bed thickness in PS1 across the Prospect Farm Formation was not possible. The type section for PS1 (described from Locality I) is divided into three soil horizons (corresponding to sedimentary units). From the base to the top of the profile these are interpreted as: CBcb1 (Unit 16), Btsocb1 (Unit 15B), and EBtsocb1 (Unit 15A). Features of PS1 horizons are described in detail in Appendix 6, Table 6.1. PS1 developed through the weathering of 'pink' tuff deposits. PS1 is tentatively interpreted as a Ferric Acrisol or Ferric Alisol with some hydromorphic properties, due to the sediments massive macrostructure, the presence of a ferruginous Ccb1 horizon with abundant Fe/Mn nodules, a clay rich (argillic) Btsocb1 subsurface horizon, and a whitish sandy albic Ebtsocb1 horizon. Cementation of PS1 matrix material is recorded as rising with increasing depth. Mn/Fe glabules (redox features and Fe/Mn nodules) are present in all horizons but were concentrated in higher amounts in the semi-cemented CBcb1 horizon and the more friable Ebtsocb1 horizon (see Figures 6.30 and 6.31). The sharp and erosional contact between Units 15A and 14E (see Figure 6.30 [A, B, E, G, F]) reflects erosion of the A horizon of PS1, leading to the formation of a truncated litho-profile.



Figure 6.30 Field photos of key features described in the main text and in Figures. 6.30, 6.32 and Appendix 6, Table 6.1 (A-C) Photos of Palaeosol 1 in sequence with overlying units. (E-D) photos of selected pedogenic features and artefacts from Palaeosol 1.

6.8.1.2 Grain size and geochemistry trends: Palaeosol 1

Particle size in PS1 varies between poorly to very poorly sorted and between coarse skewed, platykurtic and unimodally distributed to bimodally distributed, indicating dual sedimentary components. Most notably, concentrations of sand size particles increase in the EBtsocb1 horizon. There is a return to fine silt size material in the upper 5cm of this horizon at the bed contact with Unit 14E (see Figure 6.31[B]), where a thin band of clay (clay lens) is present (see Figure 6.30 [G]).

Al and Si concentrations are low and show little variability in PS1. Al behaves similarly to Na, Ca, K and Mn, as well as to Ti. Na, Ca, K and Mn occur in low concentrations throughout PS1 and show minor increases in the Btcb1h horizon. P also occurs in low concentrations but shows a steady increase towards the EBtsocb1 horizon, a strong positive correlation with phytolith concentrations (R = 0.82), and a strong negative correlation with Mg (R = -0.70) (see Table 6.3). Fe and Mn are positively correlated (R = 0.71) and are higher in the CBcb1 and EBtsocb1 horizons where the highest concentrations of Fe/Mn nodules occur.

	Phytolits per gram AIF	Clay	Silt %	Sand%	Al	Fe	К	Mg	Mn	Na	Р	Si	Ti	Ca
Phytolits per gram AIF														
Clay	-0.071283													
Silt %	0.45196	0.14489												
Sand%	-0.42879	-0.27896	-0.99059											
Al	-0.22847	-0.20369	0.0014291	0.02679										
Fe	0.2881	0.1397	0.10818	-0.12432	0.6266									
К	-0.42044	-0.30198	-0.025314	0.066342	0.90027	0.30968								
Mg	-0.61921	-0.30367	-0.14301	0.18081	0.83386	0.17292	0.96064							
Mn	0.093037	-0.00707	-0.25867	0.25203	0.50377	0.71923	0.31712	0.16585						
Na	-0.20156	-0.1294	-0.21403	0.22562	-0.3183	-0.43877	-0.2055	-0.0903	-0.3101					
Р	0.82189	-0.022434	0.41014	-0.39495	-0.3655	0.09501	-0.5296	-0.7045	0.17013	-0.3642				
Si	0.010828	0.54854	0.36539	-0.43051	-0.0707	-0.22014	-0.0035	-0.0095	-0.5247	-0.2663	-0.0655			
Ti	0.19831	-0.070396	-0.088588	0.095717	0.59637	0.42371	0.42501	0.32142	0.27959	-0.6076	0.0977	0.3461		
Ca	-0.48922	-0.49461	-0.18933	0.25218	0.79182	0.12882	0.94735	0.93988	0.28186	0.0122	-0.572	-0.178	0.2948	

Table 6.3 Pearson's correlation coefficient (R) for selected sedimentology, geochemical, and grain size data from Palaeosol 1 (sample No. 1f to 10f). Bold values indicate 99% confidence interval.



Figure 6.31 Stratigraphic changes in palaeoenvironmental proxies from Palaeosol 1. (A) Geochemistry, (B) particle size distributions and key particle size variables, (C) summary of phytolith groups and indices.

6.8.1.3 Phytolith distributions, preservation and grain size comparisons in Palaeosol 1

Phytolith distributions in PS1 are similar to those of modern soils that show decreases in phytolith concentrations and increases in partial-dissolution with increasing depth (Strömberg et al., 2018). High phytolith concentrations in PS1 point to a period of landscape stability. While there is still disagreement surrounding the movement of phytoliths in soils due to water seepage (see Madella and Lancelotti, 2012 and references therein), some studies indicate that downward translocation of phytoliths in soil could be as great as 4 cm per year (Fishkis et al., 2009, 2010). The increases in larger blocky/tabular arboreal phytoliths and decreases in more readily transported GSSC types with depth in PS1, suggest the preferential downward translocation of smaller phytoliths has not occurred. The lack of visual correspondence between phytoliths below 63 µm and particles below 63 µm supports the idea that bioturbation, shrink-swell processes, or particle size sorting during deposition, have not majorly impacted phytolith distributions in PS1. As such, phytoliths in PS1 are interpreted as having an approximately normal age-depth relationship. However, reduced preservation of GSSC phytoliths at lowered depths may reflect mechanical breakage and dissolution of phytoliths during pedogenesis and diagenesis under tropical weathering regimes. For example, in forest Latosols, the phytolith pool can be rapidly dissolved and absorbed by plants in depositional settings with high water availability and high pH [Bartoli, 1983; Alexandre et al., 1997; Fraysse et al., 2009; Madella and Lancelotti, 2012]). Thus, while the presence of arboreal vegetation cover can be inferred from the phytolith assemblage of Units 15B and 16, a more precise classification of vegetation types is confounded. As a result, successional vegetation changes from these units have not been inferred.

<u>6.8.1.4 Palaeosol forming processes, artefact distributions, palaeoenvironmental and palaeoclimatic interpretations: Palaeosol 1</u>

The following section provides the interpretation of the depositional and post-depositional, pedogenic and taphonomic processes operating during and after the formation of PS1, as well as climatic and palaeovegetation reconstructions.

6.8.1.4.1 CBcb1 horizon

The high concentrations of discrete Fe/Mn nodules (~1-3 cm in diameter) observed throughout all horizons in PS1 correspond to peaks in peaks Fe. Fe/Mn nodules are a common feature of many soil types and weathering profiles in tropical and sub-tropical environments (Amouric et al. 1986; Breuning-Madsen et al. 2007; Enze et al., 2014). These nodules can potentially form through several different pedogenic and post-depositional processes. Fe/Mn nodules in the profiles are more consistent with pedogenic formation than they are with secondary deposition of older eroded lateritic duricrusts or primary mafic rocks (see Appendix 6.3.1 for supporting information Fe/Mn formation in PS1). Ongoing micromorphological analysis of theses sediments are expected to help to establish a pedogenic or detrital origin for iron nodules in PS1 (see Section 6.9). Sporadic inclusions of lithic artefacts in the CBcb and Btsocb horizons may also be due to their downwards translocation through bioturbation and/or shrink swell action. Alternatively, lithics in the CB horizon may represent synsedimentary

incorporation of surface material into sediments during eruption or later through colluviation. Understanding the pathways by which artefacts entered the CB horizon is complicated by the lack of exposure of underlying sediments at the base of Unit 16. However, the fresh edges and unpatinated appearance of obsidian material from this horizon (Van Balen pers. comm.) suggest that it did not undergo significant weathering prior to deposition. Thus, post-burial vertical movement of material remains currently the most likely explanation for the sporadic occurrences of lithics in the CBcb1 horizon. This is supported by earlier excavation records which describe Unit 17 as a highly indurated 'red tuff' that is sterile (Anthony, 1978). High densities of iron nodules and a highly indurated matrix (forming a semi-cemented ferruginous pisolith in horizon CBcb1 [see Figures 6.30 [A, B, C, G] and 6.31) are consistent with hydromorphic soils with a medium to short hydroperiod (Veneman et al., 1976; Fanning and Fanning, 1989; Retallack, 1998). Increases in concentrations of Fe and Mn in CBcb1 and Btsocb1 horizons with Fe/Mn nodules indicate strong oxidising conditions during the formation of these features. Oxidising conditions could have existed either due to periodic perching of the water table or phreatic conditions (e.g. Mahaney and Fabey, 1988; Mahaney et al., 2014). While physical evidence of clay coatings was recorded in PS1, low Al values in all horizons, relative to other palaeosols in the Prospect Farm sequence, may indicate that weathering intensity was not sufficiently high enough for, or the weathering pathways were not conducive to the formation of Al rich clay minerals. Alternatively, low Al may indicate that Al was preferentially leached from the profile under more intense weathering conditions.

6.8.1.4.2 Btsocb1 horizon

Additional indicators of redox processes provide further evidence of seasonal saturation of soils. Clay cutans, dark grey drab mottling, and drab halo root traces in the Btcb1 horizon (see Figure 6.30) indicate illuviation of clays. These features are often linked to fluctuations of the water table, shifts in the zone of alteration, and the leaching and residual accumulation (illuviation) of (hydr)oxides of Fe, (Mn), and Al (ferralitization). These features are often observed when periodic (likely seasonal) saturation of soils occurs under a humid tropical weathering regime (van Breemen and Buurman, 2002). Such features are also often found in association with pedogenic iron nodules (McDaniel & Buol, 1991). Weak Fe/Mn rootlet traces and occasional and weak drab haloes are also present in the Btsocb1 horizon. These features provide further support for waterlogging of the rhizosphere but could also be contributed to by anaerobic decay of rootlets and other organics post-burial (Retallack, 1988). The presence of reducing conditions in the Btsocb1 horizon is supported by its geochemistry which shows decreases in Fe and Mn (Retallack, 1986) (see Figure 6.31 [A]).

As considered in Chapter 5.5.4 and Appendix 5.3.5, high Ti values and strong positive correlations between Ti and Fe and Ti and Al are thought to be indicative of the formation of titanomaghemites in association with Fe_0 and Al_0 . While these elements follow a similar trend in Palaeosol 1, it is possible that peaks in Ti may also represent inputs or translocation of less weathered material (e.g. titanomagnetite) to the Bt horizon. However, there is no obvious correlation between total element

values and a single grain size fraction. As Al values are typically expected to increase during weathering and clay formation, relatively low Al values in Palaeosol 1, are likely to relate to preferential mobilization and leaching of Al. Low Al values may also relate to lower Al concentrations in certain secondary silicate minerals (e.g. kaolinite and allophone) (Bache, 1986). Interpretations of the behaviour of Ti and Al in the PS1 profile are complicated by the fact that the base of deposits and thus the unweathered parent material was not uncovered during excavations. However, observations of lower Ti values in other pumice deposits in the Prospect Farm sequence of Units 12 and 6, relative to values in the overlying PS2 and PS5 respectively, indicates that Ti is generally enriched in the upper soil horizons relative to underlying volcanic deposits. Low levels of Si and moderately high levels of Ti and Fe suggest that extensive weathering and transformation of primary minerals to secondary phases and then to a predominantly crystalline phase occurred during the formation of Palaeosol 1 (i.e. the soil evolved through the Andosol phase to a more well-developed soil type). This conclusion is supported by macro morphological observations. However, at present, the current lack of mineralogy from the Prospect Farm sequence makes it difficult to identify specific oxide/mineral phases. It is likely that nodules in the CBcb1 horizon formed authigenically (as redox accumulations) but it is less clear how nodules in the EBtsocb1 horizon formed (see Appendix 6.3.1). The deposition of airfall pumice (Units 14-12) resulted in the truncation of the upper soil layer (upper EBtsocb1/A horizon) of PS1. Consequently, the phytolith signal of the final vegetation-state of PS1 is unknown.

6.8.1.4.3 EBtcb1 horizon

The albic EBtsocb1 horizon is characterized by high artefact densities (see Figures 6.6 and 6.31), lighter colouration, and sandy texture typical of desilication (liberation of Si from primary silicates). This process is associated with the eluviation and accumulation of silicate clays as coatings and mottles down-profile in the argic Bt horizon (Chittleborough, 1991). Increase in Fe and Al relative to the underlying Bt horizon adds further support to the interpretation of this unit as an albic, eluvial E horizon (Mack et al., 1993). Higher Fe and Mn values in this horizon are associated with high concentrations of Fe/Mn nodules, as in the CBcb1 horizon. Polygonal desiccation cracks in EBtsocb1 horizons (see Figure 6.30 [E, H]) are typical of shrink-swell processes that occur is soils under tropical climate regimes (i.e. cracks form during dry periods when the water table is lowered, clays shrink and tension occurs, and cracks are then infilled with coarse material, which becomes compacted during the rehydration phase [Chico., 1968; Bohn et al., 2005a,b; Tang et al., 2011]). In Latosols with abundant iron nodules, formation of bleached zones indicates the removal of silicates, but also a kaolinite rich matrix caused by de-ferrugination (Ghosh et al., 2015). The presence of these features in the EBtsocb1 horizon provides further evidence of seasonal saturation of sediments during the formation of PS1. This horizon is more permeable than the Btsocb1 horizon. As such, groundwater is expected to have accumulated in its lower levels. The green coloration of clay coatings in the EBtsocb1 horizon is likely to indicate the presence of relatively less stable short order range clays (SORC) such as allophone, or more stable crystalline (phyllosilicate) smectite or kaolinite clay minerals. Both can develop from vitric parent material at different phases of weathering in climates with marked seasonality where soils are subjected to periodic waterlogging (Sheldon and Tabor,

2009; Beverly et al., 2015a). Waterlogging in PS1 is further supported by the occasional occurrences of diatoms observed in this palaeosol (see Figure 6.15).

Signs of both illuviation and eluviation in the EBtsocb1 horizon suggest a complex history of development and of post-depositional alteration of these sediments. Groundwater currently reaches the EBtsocb1 horizon today due to the high permeability of the largely clast-supported overlying pumice deposits (Units 12-14). Therefore, it is possible that desiccation cracks may have formed post-burial of PS1 under phreatic conditions, and that significant post-depositional alteration of this palaeosol is still ongoing. Unfinished mineralogical and micromorpholgical analysis of sediments may help to more fully elucidate how post-depositional processes may have continued to affect PS1 since its burial (see Section 6.9). It seems likely that illuviation of green clays in the EBtsocb1 horizon, associated with the formation of desiccation cracks, occurred after the initial eluviation of this layer. Advances of the wetting front in shrink-swell clay soil (usually Vertisols) have been shown to cause uplift of coarse grains (Yaalon and Kalmar, 1978). This process may also have contributed to the coarse texture and homogenization of the EBtsocb1 horizon. In this case wet-dry cycles could have partially obliterated slickenside features, resulting in their weak appearance and diffuse distribution in this horizon. Elevated P values in the EBtsocb1 horizon may reflect the occlusion of P within phytoliths (e.g. Trinh, 2017) and/or sorption of phosphate Fe/Al oxides or clay minerals; and/or increase in organic P in organic matter at the former contact between the upper E horizon the A horizon.

6.8.1.4.4 Phytolith-based vegetation trends: Palaeosol 1

Woody dicotyledon indicators and indeterminate C4/C4 GSSCs occur in high percentages in the CBcb and Btscob horizons, where phytolith preservation is poor. The EB horizon contains a greater diversity of woody dicot morphotypes: globular granulates, globular echinate (Areaceae), cork platelets (epidermal polygonal types) and ellipsoids with irregular projections are all recorded. Cork platelets are produced in a variety of woody taxa but are more frequent in some genera (e.g. Ficus) (see Chapter 4.3.3). Ficus grow in semi-open, often drier conditions at forest margins and along river courses today. Similarly, ellipsoids with irregular projections are recorded in Stereospermum spp. in West Africa (Collura and Neumann, 2017) which occur in the dry margins of evergreen forests. However, there is no evidence currently to suggest that this morphotype is exclusive to the genus. All GSSC types increase in the EBtscocb horizon, with the most conspicuous feature being the highest percentage of C₃ GSSCs in the whole Prospect Farm sequence. This C3 GSSC grass signal is associated with very low Iph index values (Figures 6.15 and 6.22), and average Ic values (~45%) (Figures 6.21), as well as the presence of arboreal and mesic C_4 Poaceae indicators. This suggests the presence of C3 understory forest grasses and mesic growth conditions in PS1, instead of open Afroalpine grassland expected to occur at higher altitudes. While no vegetation soil samples exist for Mt. Eburru, these findings are consistent with modern observations of the relative abundance of C3 and C4 grass species in the Mau forest: Modern vegetation surveys show that 68% of grass species between 2500-3200 m a.s.l. belong mainly to C₄ Panicoideae (Tieszen et al., 1979). This interpretation is corroborated by other findings which also suggest that PS1 formed under humid climate

conditions and supported forest vegetation. Furthermore, high phytolith concentrations reflect higher biomass and an extended period of vegetation stability with limited erosion, allowing forest vegetation to become well-established. The co-occurrence of long saddles (2-3%) and collapse saddles (1-2%), bilobate stipa types (8 -10%), with more definitive GSSC C₃ Poaceae indicators, most likely indicates the presence of Bambusoideae and Pooideae. This gives further weight to the idea that PS1 supported an at least semi-shaded, predominately moist forested environment. Given the proportions of other Poaceae subfamily indicators, very low percentages (0-1%) of collapsed saddles in EB horizons samples are interpreted as reflecting Bambusoideae rather than Chloridoideae. It is not possible to say conclusively if high abundances of rondels are associated primarily with C₃ Panicoideae, Pooideae and Bambusoideae, or with C₄ Panicoideae, or both. Given the high abundance of other C₃ GSSC, a C₃ or mixed C₃/C₄ source appears most likely.

FI values and globular granulate percentages indicate a progressive reduction in the arboreal cover in PS1, with values falling below the threshold at which $\geq 40\%$ vegetation cover can be inferred (see Figures 6.20). Even though arboreal cover is likely to be underestimated at the site due to the representational biases that affect phytolith assemblages from Afromontane vegetation, overall, the phytolith assemblage points to drier undifferentiated Afromontane forest vegetation types. This variety of Afromontane forest, that is present on Eburru today, demonstrates high levels of variation in structure (i.e. changes from closed canopy conditions to forest clearings) over short distances (described in Chapter 2.9). Reduced FI% may reflect the polymorphic nature phytoliths in palaeosols but also an overall shift to drier, more seasonal conditions that contributed to vegetation openness in sample 1f. This is supported by slightly elevated Iph% compared to samples from those recorded in modern moister Afromontane forest (see Figure 6.22). However, Iph values are likely to be slightly artificially inflated by saddles that are, as mentioned, more likely to originate from C_3 subfamilies than from Chloridoideae in this case. Very occasional occurrences of burnt phytoliths, most probably indicating burning in adjacent vegetation communities or low frequency local fires, could have partially contributed to maintaining marginally more open forest. The lack of species specific morphotypes from woody dicots means that it is impossible to suggest whether this was mixed forest or if it was single species (e.g. Podocarpus or Juniperus) dominated forest. However, if drier Olea forest or other drier lowland forest/woodland types were present, such high proportions of C_3 grasses as those estimated for PS1 would not be expected.

6.8.1.4.5 Altitudinal variation in phytolith signals from PS1 at Prospect Farm Localities I and II Phytolith results from the PS1 EB horizon from Locality I and locality II indicate that FI-t ratio and FI+CH% values, Ic%, and Iph% values are very similar in both sites (see Figures 6.21-6.24). Fs% values are very slightly higher in the Locality II sample; however, values are still very close to the mean value of AFMF samples.

6.8.1.4.6 A preliminary model of Palaeosol 1 formation processes

Macromorphological features coupled with low Si, Al and high Fe and Mn values in PS1 point to a welldeveloped, moderately well-drained soil that supported Afromontane forest. Pedological features suggest a complex formation process involving extensive weathering under a rainfall regime in which precipitation outweighs evaporation. Root traces <1 cm wide (indicating herbaceous/wooded vegetation) in the Bt horizon are consistent with forested vegetation (Retallack, 2008). In highly weathered soils that develop on rhyolitic volcanic material it is expected that soils should transform from those containing non-crystalline material toward containing crystalline clay material. Ultimately this should result in the substitution of an Andosol with another soil order. Macro-descriptions of the soil profile indicate a soil similar to modern ferric Acrisols which support a variety of tropical forest vegetation (e.g. Bussmann, 2001; Epron et al., 2006). The absence of pedogenic carbonates in PS1 suggest that the moisture regime during the dry season was not sufficiently arid (below $\sim 100 \text{ cm MAP}$) to allow for secondary carbonate precipitation and accumulation (Cerling, 1984; Zamanian et al., 2016). Furthermore, the presence of clay coatings and some weak hydromorphic features suggest that palaeosol formation was long enough to reach a state of equilibrium with climate. Medium clay content (of $\sim 8\%$) in the Bt horizon also indicates that the soil is likely to have had a moderate water storage capacity and fertility. These general observations are corroborated by the phytoliths signal from the EBtsocb1 horizon that indicates PS1 supported well-established Afromontane forest vegetation. Palaeosols with similar features (e.g. Fe/Mn clay coatings, pedogenic clay minerals in which volcanic glass as been fully weathered and allophane content is low) from subtropical areas of Mexico, have been shown to take upwards of 4000 years, often over 10,000 years and up to 100,000 years to form (Sedov et al., 2009; Solleiro-Rebolledo et al., 2015). Ongoing micromorphology, mineralogy, y analysis, and ⁴⁰Ar/³⁹Ar dating of PS1 sediments are expected to help to determine the stability of mineral constituents of PS1 and whether it reached equilibrium with the ambient climate. A more complete understanding of the percentage of volcanic glass and clay mineralogy (e.g. proportion of silicate clays) in PS1 will ultimately help to achieve a more precise soil designation of PS1 as a ferric Acrisols, ferric Alisol, or albic Luvisol etc. (see Section 6.9). As results indicate that the EBtcb1 horizon may represent two separate phases of pedogenesis, this profile is considered to represent a pedocomplex; and may also have undergone postdepositional alteration following its burial. A tentative model of site formation for this Palaeosol is proposed base on existing evidence (shown in Figure 6.32).



Figure 6.32 Palaeosol formation model for Palaeosol 1. Note: Inferred changes in vegetation may have also been modified by other factors (e.g. changes in pCO_2) included in the model due to the lack of dates from the sequence from which comparisons can be made to independent climate records.

6.8.2 Palaeosol 2 (Units -11B-10)

6.8.2.1 Field descriptions

The sedimentary units forming Palaeosol 2 (PS2) were identified in section and outcropping in exposures at the base of the main escarpments at both Locality I and II (see Figure 6.33 [A, B]). PS2 was not identified at any other exposures across the Prospect Farm Formation (see Figure 6.4). The type section for PS2 (described from Locality I) is divided into three soil horizons (corresponding to sedimentary units). Described from the base to the top of the profile, these are interpreted as: Cb2 (Unit 11B), Btsb2 (Unit 11A), and Eb2 (Unit 10). Features of PS2 horizons are described in detail in Appendix 6, Table 6.1. PS2 is tentatively interpreted as a poorly developed Andosol with albic and argillic horizons and weak ferric properties, that developed from ash deposits of Units 11-10 that overlie the airfall pumice of Unit 12. This soil classification is based on the presence of a bleached eluvial E zone with prismatic structure and weak genetic features. This E horizon has a gradational contact with the underlying argillic Bts horizon which shows evidence of weak illuviation and Fe accretions and accumulation of clays (Figure 6.33 [B, F]). Despite the interpretation of PS2 as being relatively poorly-developed, pedogenic features and the thickness of the Bts horizon prevents it from being classified as a tephric Regosol (IUSS Working Group WRB, 2014). PS2 is ~50cm deep and the bed thickness of each horizon varies by up to 10 cm across exposures at Localities I and II. Artefact densities are relatively low in Units 11 and 10 compared to the rest of the Prospect Farm sequence (see Figure 6.6). Slight increases in artefact densities occur towards the top of the PS2 profile at the contact between Units 10 and 9B. Here lithics are clearly visible in-situ (see Figure 6.33 [E]). The very sharp contact between Units 10 and 9B suggests that the A horizon of PS2 was eroded during the deposition of Unit 9B pumice, creating a truncated litho-profile.



Figure 6.33 Field photos of key features described in the main text and in Figures. 6.34, 6.35 and Appendix 6, Table 6.1 (A-B) Photos of Palaeosol 2 in sequence with overlying units. (C and E) Photos of selected pedogenic features and artefacts from Palaeosol 3. (D) Profile of Palaeosols 3 and 4. (E-G) Photos of selected pedogenic features and artefacts from Palaeosol 2.

6.8.2.2 Grain size and geochemical trends: Palaeosol 2

Particle size distributions are coarse skewed, platykurtic and unimodally distributed to bimodally distributed; indicating dual sedimentary components (see Figure 6.12 and Appendix 6, Table 6.3). Skewness increases towards the top of the profile. Particle size varies between poorly and very poorly sorted with reduction in mean grain size and sand size material and increase in silt and clay sized material in the Bts horizon (see Figure 6.34). In the E horizon, sand sized material increases relative to silt and clay size material. Phytolith concentrations are highest in the B horizon, but also show quite high

concentrations in the C horizon. Variations in the relative abundance of grains below 63µm do not show a similar visual trend to changes in phytoliths in the same size class (mainly GSSC types).

All elements, besides P and Si, demonstrate increases from the base of the profile to the Btb2 horizon, followed by a reduction in their values in the Eb2 horizon. A strong positive correlation exists between Al and all other elements besides P, Mn and Si. Fe demonstrates a strong positive correlation with K, Mn, and Ti. Ti shows a strong positive correlation with Al, Fe, K, Mg, Mn, and Na. Ca is positively correlated with Al, K, Mn and Na (see Table 6.4). P values are very low in PS2, as in the rest of the Prospect Farm sequence, but do show a reduction from the C horizon to the Bts horizon and a slight increase in the upper E Horizon.

	Phytolits pre gram	Clay %	Silt %	Sand%	Al	Fe	K	Mg	Mn	Na	Р	Si	Ti	Ca
Phytolits pre gram														
Clay %	-0.30212													
Silt %	-0.023942	0.52165												
Sand%	0.04505	-0.5738	-0.99806											
Al	-0.069844	0.37804	-0.37081	0.32834										
Fe	0.3646	0.22833	-0.41047	0.37735	0.86465									
К	0.15475	0.010695	-0.61849	0.59294	0.8979	0.8885								
Mg	0.27026	0.23544	-0.47189	0.4358	0.89162	0.96835	0.93568							
Mn	0.53524	0.25139	-0.33034	0.29875	0.66362	0.90202	0.73817	0.90284						
Na	0.32494	0.51935	-0.104	0.061901	0.81267	0.88986	0.69984	0.83877	0.80865					
Р	0.19488	0.24014	-0.013869	-0.004227	-0.1521	0.17842	-0.1286	0.11548	0.31839	0.1843				
Si	-0.4533	-0.20304	0.18857	-0.16619	-0.26	-0.63457	-0.3405	-0.5349	-0.7203	-0.5655	-0.7874			
Ti	0.16325	0.5015	-0.27455	0.22692	0.9081	0.92499	0.82099	0.94275	0.8849	0.9001	0.1173	-0.521		
Ca	0.19117	0.32138	-0.42264	0.38224	0.92178	0.98007	0.89898	0.96207	0.85297	0.8946	0.1604	-0.602	0.9494	

Table 6.4 Pearson's correlation coefficient (R) for selected sedimentology, geochemical, and grain size data from PS2 (sample No. 4e to 12e). Bold values indicate 99% confidence interval.

6.8.2.3 Phytolith distribution, preservation and grain size comparisons in Palaeosol 2

The bimodal distribution of phytoliths between the C and E horizon in PS2 either relates to: i) their vertical translocation due to bioturbation; ii) incorporation of phytoliths into sediment during eruption and deposition of the tuff; or iii) secondary redeposition of this tuff on the landscape. Aggregation of ash in distal deposits remains poorly understood and could be the result of eruptive behaviour or postdepositional reworking (Folch et al., 2010; Gatti et al., 2013) (see Appnedix 6.3.2 for details). Tuffs of Units 11 and 10 lack distinct taphonomic bedding structures, have bimodal grain size distributions, poor sorting and inclusion of large clasts of weathered pumice, and increasing skewness towards the top of the profile (see Figure 6.48 [B]). These factors suggest that minor reworking of this tuff has occurred through bioturbation during pedogenesis and/or colluvial redeposition of the tuff. The lack of visual correspondence between variations in particles below 63 µm and phytolith morphotypes below 63 µm (see Figure 6.34 [B]), as well as the absence of macromorphological evidence of vertebrate or invertebrate burrowing, indicates that bioturbation is not likely to have been responsible for the moderate increases in phytolith concentrations in the C horizon. The moderate to low impact of root bioturbation in the redistribution of phytoliths is supported by the presences of < 5 mm root traces in PS2. These indicate that smaller plants (Sheldon and Tabor, 2009) (likely to be grasses, based on the phytolith signal) were better established in PS2 than in PS1.

When water seepage is the primary mechanism in the redistribution of phytoliths, many modern soils show uniform increases in phytoliths towards the top of the profile (Madella and Lancelotti, 2012) and not the bimodal pattern that is evident in PS2. Furthermore, there is no change in the combined preservation/alteration index across E and C horizons. This remains high, indicating that the reduction in phytoliths in the lower Bts horizon is unlikely to be due to chemical dissolution or physical abrasion (see Figure 6.34 [B, C]). It is possible that changes in water seepage, linked to climatic fluctuations and internal drainage during the formation of PS2, could have created the bimodal phytolith distribution. However, it is equally likely that phytoliths/plant material in the C horizon may have been incorporated into sediments during deposition of the tuff (e.g. Jones, 2010). Increases in sand and silt sized material in samples that also show a reduction in the relative abundance of blocky and tabular phytoliths (many of which are above 63 µm) in Palaeosol 2, gives the impression that the signal represents a true absence of ligneous morphotypes rather than their removal through sorting. Until the underlying cause of the binomial distribution of phytoliths in PS2 can be resolved, the phytolith-based record of vegetation is best considered as representing vegetation during the entire period of palaeosol formation.

6.8.2.4 Palaeosol forming processes, artefact distributions, palaeoenvironmental and palaeoclimatic interpretations: Palaeosol 2

6.8.2.4.1 Pedogenic processes PS2

Changes in major element concentrations and grain size in the PS2 profile support field-based distinctions between zones of eluviation in the E horizon and the illuvial accumulation of Fe/Mn oxides and clay minerals in the Bts horizon. Overall reduction in Fe, Mn and Ti, very low clay content, the lack of both gleying or oxidization/burial rubification, domed columnar peds, as well as the absence of root traces and clay skins in Unit 10, supports this units' classification as an albic horizon (Bestland and Retallack, 1993). Doming of columnar peds in some palaeosols has been associated with salinization (e.g. Northcote and Srene, 1972). While there are very minor increases in K and Na in the upper zone of Unit 10, Al and Fe also increase. This is more consistent with a zone of eluviation in which Fe and Al compounds accumulated. This finding, as well as strong positive correlations between first transition metals and alkaline earth elements, and a predominately mesic C₄ grassland phytolith signal with a minor xeric C₄ element (see Section 6.8.2.4.3), suggest that salinization did not occur. Instead, alkaline earth elements in PS2 were fixed to/retained by clay minerals with high Fe, Ti and Al formed during weathering.

Unit 11A shows evidence of redoximorphic features that indicate periodic poor drainage during palaeosol formation of PS2. Higher Al content in the Bt horizon than in PS1 is likely to reflect higher Al_o content (see Chapter 5.5.4 and Appendix 5.3.2) associated with Al release during the weathering of allophanes in the initial stages of Andosol formation (Solleiro-Rebolledo et al., 2015). Al increases in tropical soils have also been linked to the formation of Al-geothite. However, this seems unlikely as its formation only occurs under extreme weathering conditions (Fitzpatrick and Schwertmann, 1982). Clay coatings are present in the Bts horizon that are much weaker than those recorded in PS1. Such redox

features have been shown in some cases to form as quickly as a single wet season (Vepraskas and Richardson, 2001; Vepraskas and Faulkner, 2001; Beverly et al., 2015b). This suggests that climate was sufficiently wet, and drainage adequate to allow for redox activity to bring PS2 into equilibrium with climate and that the dry period was long enough to deposit illuviated clay coatings. However, illuviation may still have been short-lived (i.e. PS2 could have developed into and orchic, cambic or ferric Luvisol if continued weathering, had its development not been curtailed by the deposition of the Unit 9B pumice). High shrink-swell capacity may have resulted in the columnar structure of the E horizon (Dixon, 2009). A muted dry season in PS2 is also supported by the absence of carbonate features (as in PS1), as well as a predominantly mesic grassland phytolith assemblage.

6.8.2.4.2 Artefact distributions: Palaeosol 2

Sporadic artefacts are present in the Btsb2 of PS2, increasing slightly in the Eb2 horizon and at the boundary between the Eb2 and Unit 9B. Artefacts appear to have been discarded on the former land surface of PS2 and accumulated in its upper horizons, becoming reworked into Unit 9B during deposition of the pumice.



Figure 6.34 Stratigraphic changes in palaeoenvironmental proxies from Palaeosol 2. (A) Geochemistry, (B) particle size distributions and key particle size variables, (C), and summary phytolith groups and indices.

6.8.2.4.3 Phytolith-based vegetation trends: Palaeosol 2

Phytolith signals from PS2 are characterised by high percentages of mesic C₄GSSCs and indeterminate C_3/C_4 GSSCs that follow the same stratigraphic trend, as well as moderate to low percentages of xeric C_4 GSSCs, and the absence of C_3 GSSCs. FI values are slightly lower than those in PS1, indicating that arboreal vegetation was present, but less-well established than in PS1. This indicates that vegetation was semi-open, and that tree cover was unlikely to be $\geq 40\%$. Ic values (~40-50%) are most similar to modern samples from mesic EDAP-Sah savanna and Somalia-Masaï lowland (30% to 59%), but still overlap with Ic values from shrub savanna samples within the AFMF zone (see Figure 6.21). Despite the lack of C3 Poaceae indicators in PS2, high mesic GSSC proportions of mesic C4 indicators result in lower Iph values than in PS1. The lack of C_3 GSSC types in PS2 means that saddle types are most likely to represent Chloridoideae. Both the phytolith assemblage and pedogenic features of PS2 indicate the presence of mesic C_4 savanna with a strong woody element. It is expected that this vegetation developed under mesic climate conditions and a short dry season which was relatively longer and/or more intense than was specified for PS1. The lack of indicator phytoliths from PS2, combined with the fact that drier forest/woodland types at the transition between forest and savanna in the Nakuru-Naivasha Basin are poorly represented in modern soil comparative data, means that it is difficult to be more specific about the type of woody vegetation present. The lack of overlap between PS2 samples and samples from AFMS shrub savanna, EDAP-Sah, or GRSO Acacia bushland and thicket in the PCA, suggests that Prospect Farm samples may be more similar to vegetation types found in the Nakuru-Naivasha Basin not represented by modern samples (e.g. Olea and Euphorbia forest types which have grass understories and clearings dominated by Panicoideae).

<u>6.8.2.4.4 Altitudinal variation in phytolith signals from PS2 at Prospect Farm Localities I and II</u>

Phytolith results from the PS2 E horizon from Locality I and Locality II indicate that FI+CH%, Iph% values are similar at the two sites, while Ic% and Fs% values are marginally higher, (see Figures 6.21-6.24). This indicates that very similar vegetation conditions existed at the two sites.

6.8.2.4.5 Preliminary model of Palaeosol 2 formation processes

Phytolith based inferences about climatic conditions in PS2 suggest its formation under semi-humid conditions (~21-25 °C) with lower rainfall, a longer rainy season, and 5-6 dry months. This suggest similar precipitation values (~1000-1500 mm MAP) to those experienced during the present at this altitude in Kenya (Ehleringer et al., 1997; Barboni et al., 2007). This is dependent on the assumption that pCO_2 concentrations were the same as present-day levels, which requires further testing (see Chapter 7.4). Comparable Regosols-Andosols in Mexico have been shown to develop very rapidly, in ~50 years, under very humid conditions (22.5 °C MAT, 4000 mm MAP), whereas vitric Andosols develop more gradually (over ~600 yrs). Andosols, that have B horizons with evidence of clay accumulation (as in PS2), have been shown to form over 3000-6000 yrs under semi-humid conditions (Solleiro-Rebolledo et al., 2015). Several studies suggest that under humid conditions the Andosol formation stage ends, and

other soil types become established after ca. 10,000 yrs of development (Miehlich, 1991; Shoji et al., 1993; Sedov et al., 2001; Solleiro-Rebolledo et al., 2015). Current evidence indicates that the closest analogues to PS2 are soil that fall into a 3000-6000 year bracket. Further analysis is necessary to test this hypothesis (see Section 6.9), but if correct, this length of time would be more than enough for woody vegetation to become established. This would indicate that the lower levels of woody vegetation in PS2 than in PS1 was limited by climate rather than being a function of time.

While several aspects of the formation of PS2 are undetermined, pedofeatures, geochemical and phytolith results are interpreted as representing forming under semi-humid conditions over several millennia. PS2 is shown to have supported a mesic C_4 dominated grassland environment with limited arboreal cover. A tentative model of site formation based on existing evidence is shown in Figure 6.35.



Figure 6.35 Palaeosol formation model for Palaeosol 2. Note: Inferred changes in vegetation may have also been influenced by other factors (e.g. changes in pCO_2) that are not included in the model due to the lack of dates from the sequence from which comparisons can be made to independent climate records.

6.8.3 Palaeosol 3 (Units 9A-8A)

6.8.3.1 Field descriptions

The units forming PS3 were exposed in section and outcrops at both Localities I and II at the base of the main escarpments (see Figure 6.33 [A, B, C, G]). The type section for PS3 (described from Locality I) is divided into three soil horizons (corresponding to sedimentary units). Described from the base to the top of the profile, these are interpreted as: Cb3 (Unit 9A), Btsob3 (Unit 8B) and Bwb3 (Unit 8A). The features of PS3 horizons are described in detail in Appendix 6, Table 6.1. Weakly developed clay coatings and the prismatic structure of PS3 Bt horizon leads to its preliminary interpretation as a poorly developed vitric Andosol, developing from alteration of pumice and tuff deposits of Units 9A and 8. Following rain, the Btso horizon holds water and is slick, becoming hard once dry (see Figure 6.33 [A]).

PS3 is ~40 cm deep with minor (0-5 cm) changes in bed thickness evident across the Prospect Farm Formation. Both densities and percentages of artefacts, relative to unworked lithic material, are moderately high in Unit 9. They show a sharp increase in Unit 8 where they reach the highest values of the entire Prospect Farm sequence (see Figure 6.6). The sharp contact between Units 8A and 7C is interpreted as an erosional surface associated with the deposition of airfall tuff in Unit 7. Deposition of this ash is interpreted as having removed the A horizon of PS3, creating a truncated litho-profile. Medium to small gravel size matrix supported pumice grains that form a diffuse horizontally bedded band in Unit 9A and the fine, matrix supported pumice of Unit 9B, are both sub-rounded to rounded. Neither of these unit show obvious signs of pedogenesis.

6.8.3.2 Grain size and geochemical trends: Palaeosol 3

Sediments in Palaeosol 3 are poorly sorted and show little variation in sorting throughout the profile. Particle size distributions are coarse skewed (see Appendix 6, Table 6.3). Particle size distributions show very low proportions of clay size material. An increase in sand size material in the Cb3 horizon is associated with the coarse band of pumice (see Figures 6.33 [C, G] and 6.36 [B]). Sand % decreases relative to silt and clay in the Bt horizons. Phytolith concentrations increase progressively towards the top of the profile reaching a maximum in the Bw horizon after which their concentration and preservation becomes reduced in Unit 7C. There is no visible correlation between phytoliths below 63 μ m and particles below 63 μ m. All elements show very little variation throughout the profile from Unit 9B pumice through to the Bwb3 horizon. All elements in PS3 show reduced concentrations compared to other palaeosols besides P and Na, that still have low overall concentrations (see Figures 6.7 and 6.36 [A]). Very minor increases in Al, Fe, Ti, Mn, and Mg are observed in the lower Bt horizon. Slight increases in K, Na and Ca are evident in the Bw horizon. P shows a reduction in its concentration from the base to the top of the profile. Strong positive correlations (R = > 0.9) are observed between Mg and Mn with Fe, Al, K and Ti. Strong positive correlations are also evidence between Al and Mn, Al and Na and Al and Si. Ca is positively correlated with Fe, K, Mg and Mn (see Table 6.5).

	Phytolits per gram AIF	Clay	Silt %	Sand%	Al	Fe	К	Mg	Mn	Na	Р	Si	Ti	Ca
Phytolits per gram AIF														
Clay	-0.083487													
Silt %	-0.43429	0.87133												
Sand%	0.41571	-0.88592	-0.99953											
Al	-0.23528	-0.024213	-0.039367	0.03872										
Fe	-0.66901	0.24299	0.45757	-0.44766	0.78938									
К	-0.68507	0.12134	0.40978	-0.39491	0.59056	0.90897								
Mg	-0.62509	0.46047	0.65554	-0.64834	0.63416	0.94971	0.90169							
Mn	-0.65329	0.21435	0.50792	-0.49347	0.60567	0.93867	0.98169	0.94528						
Na	-0.014124	-0.23579	-0.27943	0.27882	0.73485	0.52701	0.60171	0.45347	0.52893					
Р	-0.072448	-0.3532	-0.24392	0.25257	0.70675	0.48159	0.27428	0.32011	0.34262	0.4089				
Si	-0.45335	0.20378	0.2456	-0.24485	0.90801	0.86357	0.60827	0.76804	0.65712	0.4982	0.6919			
Ti	-0.65693	0.27333	0.48287	-0.47346	0.79086	0.98421	0.83053	0.92151	0.88531	0.4166	0.5433	0.8994		
Ca	-0.60131	0.22582	0.42629	-0.41702	0.71418	0.94854	0.97264	0.93219	0.96659	0.6568	0.2995	0.7105	0.8813	

Table 6.5 Pearson's correlation coefficient (R) for selected sedimentology, geochemical, grain size data from the Palaeosol 3 (sample No. 3e to 1d). Bold values indicate 99% confidence interval.



Figure 6.36 Stratigraphic changes in palaeoenvironmental proxies from Palaeosol 3. (A) Geochemistry, (B) particle size distributions and key particle size variables, (C) and summary phytoliths groups and indices. Lithics located in Unit 10/9B are Phase II-A material. Lithics in Units 8/7C belong to Phase II-B (Anthony's original Phase II).

6.8.3.3 Phytolith distributions, preservation and grain size comparisons in Palaeosol 3

Phytolith distributions in PS3 follow the same broad patterns observed in PS1 and PS2. Good preservation of phytoliths in PS3 may be a function of its deposition under semi-arid conditions in a relatively shallow soil that typically experienced less intense chemical weathering and lower biological activity. The lack of evidence of bioturbation in PS3 means that phytoliths at lower depths are likely to have been vertically translocated through post-depositional water percolation. Larger arboreal indicator phytoliths show little change in their abundances at all depths. It appears the expected effect of the preferential translocation of smaller GSSC phytoliths to lower depths was likely to have been minimal. Therefore, sedimentary processes are not thought to have biased the relative abundances of different morphotypes in PS3. As it is likely that artefacts from Unit 10 have been incorporated into Unit 9B (see Section 6.8.2.4), it is also likely that some phytoliths that originated in Unit 10 could also be present at the base of PS3.

Crude horizontal bedding and rounding of pumice grains and limited variation in sorting in PS3 suggest that reworking of these sediments occurred during and/or immediately after deposition and before pedogenesis. However, this is likely to have been on a local scale that preserved the stratigraphic order of initial deposition (i.e. low energy sheet wash/slope processes, that redeposited sediments over short distances). Although it is likely that Units 9-8 represent a single phase of eruption, the length of the hiatuses between sub-phases of eruptions associated with these units (i.e. the recurrence rates of low-level volcanic activity) could have taken hours to millennia. The change in grain size and moderately sharp contact between the fine-grain lapilli tuff at the transition from Unit 9A to 8B may indicate short breaks in volcanic eruptions, which allowed for the minor reworking visible in these sediments to take place. However, in the absence of radiometric dates for these horizons, it is currently unclear how long any such hiatuses lasted. Although there are minor indications of phytolith mobility in PS3, there is a general uniformity in the distribution of phytoliths through soils and lack of indications of significant bioturbation in PS3. However, given the polygenic nature of soils, changes in the relative abundances of phytoliths with depth are not used to infer broad successional vegetation changes during the formation of PS3.

6.8.3.4 Palaeosol forming processes, artefact distributions, palaeoenvironmental and palaeoclimatic interpretations: Palaeosol 3

Low variability in total element concentrations and grain sizes, as well as similar trends between some alkaline earth elements (K and Mg) and first transition metals, suggest the pedogenic processes in these horizons have been minimal compared to other palaeosols in the Prospect Farm sequence. Low concentrations and similar down-profile trends of Ti, Al, Fe, Mn and Si indicate that weak to moderate weathering, low mobilization and secondary enrichment of these elements (through the weathering of volcanic glass to secondary oxide phases) occurred before burial of PS3 by the airfall tuff of Unit 7. K, Mg, and Ca follow the same trends as Ti, Al, Fe, Mn and Si in PS3. This suggests they were fixed/absorbed in resistate primary minerals or moderately unweathered parent material in PS3. This

also indicates that leaching was the dominant process during pedogenesis rather than physical additions of material in PS3. Low concentrations of alkaline earth elements also suggest that mobilization and hydrolysis occurred resulting in the loss of Base cations. Higher values of P and Na in PS3 are interpreted as reflecting higher concentrations of these elements in parent material, rather than their being enriched through weathering. The absence of well-developed Fe/Mn redox features and the existence of clay coatings in the Btso horizon implies that PS3 had a relatively short hydroperiod and developed in a climate with a longer or more intense dry season. The ability of the Btso horizon to hold water when wet is likely to be due to its colloidal properties (i.e. higher clay mineral content than other horizons) and columnar ped structure, that limit water peculation and result in a high shrink-swell capacity. The interpretation of PS3 as having formed under intermediate sub-humid to semi-arid conditions over a relatively short period of time (like that of PS2), is supported by the high relative abundance of xeric C_4 grass subfamily phytolith morphotypes and evidence of low woody vegetation cover (see Section 6.8.3.4.2). The absence of carbonate concretions in this horizon implies that MAP was not likely to be <100 cm (Cerling, 1984; Zamanian et al., 2016). This suggests that precipitation was probably still greater than evaporation, but that a climatic shift characterized by an increase in the length and/or intensity of the dry season occurred between the burial of PS2 and during the formation of PS3.

6.8.3.4.1 Artefact distributions in Palaeosol 3

The lack of macromorphological evidence for major bioturbation in this unit suggests that low to moderate densities of artefacts in Unit 9 are highly unlikely to be the result of vertical movement of lithics from the A horizon to the C horizon. Therefore, the extremely high artefact densities recorded in the upper part of the Bwb horizon in PS3 are interpreted as being deposited on the former land surface as the soil developed. Where Unit 8 is laterally exposed over large areas of the landscape through erosion, extraordinarily high densities of lithics carpet these floors (see Figure 6.37[A]). As Unit 9B pumice show some indications of physical reworking during or soon after deposition, it is likely that the sporadic and broken MSA lithics visible in this horizon (Figure 6.37 [B]) were incorporated into the sediment from the eroded A horizon of Unit 10. We anticipate that artefact orientation data from Unit 9B will help to further test this interpretation.



Figure 6.37 Field photos of (A) artefacts exposed through erosion of Unit 8 (Btsob3/Bwb3 horizons) and (B) artefacts in-situ in Units 9 and 10.

6.8.3.4.2 Phytolith-based vegetation trends: Palaeosol 3

The most notable feature of the phytolith assemblage from PS3 is the presence of high percentages of xeric C₄ GSSC phytoliths, very low percentages of arboreal indicator phytoliths compared to the rest of the Prospect Farm sequence, as well as the absence of C₃ GSSCs. PS3 is also characterised by high percentages of mesic C₄ GSSCs and indeterminate C_3/C_4 GSSCs, that follow inverse stratigraphic trends across the Btso/Bw horizons (see Figure 6.36). As in PS2, Ic values (35-40%) are most similar to samples from mesic EDAP-Sah savanna Somalia–Masaï lowland sample types, but still overlap with Ic values from shrub savanna samples within the AFMF zone (see Figure 6.21). Iph values are notably higher than those in PS1 and PS2 and overlap with those from EDAP-Sah samples (see Figure 6.20). FI% falls below the minimum values from open grass clearing Miombo woodland sites (see Figures 6.20 and 6.23). Both the phytolith assemblage and pedogenic indicators from PS3 point to the presence of open, mixed C₄ grassland communities with very low arboreal cover developing on poor quality shallow soils. The presence of a strong Chloridoideae element also indicates and increase in the length and/or intensity of the dry season relative to PS2.

While PS3 records the strongest signal of relative aridity in the Prospect Farm sequence (see Figure 6.29), very occasional occurrences of Cyperaceae phytoliths, in combination with mesic C₄ GSSCs, may also indicate that the local environment was periodically wet. However, Cyperaceae phytoliths were not identifiable to a specific genus; and while sedge normally grown in wet forest marginal environments or where pooling of water occurs, these phytoliths could represent fire tolerant sedges that occur in grasslands or specific edaphics (e.g. sandier soils) (Browning and Goetghebeur, 2017). The presence of Cyperaceae morphotypes in PS3 but not in PS1 and PS2 (that record mesic conditions) is likely to be the result of preservation of fragile silica bodies linked to rapid burial in shallower PS3 and associated lower biological activity. Contrary to indications of semi-arid conditions in PS3, Fs% are unexpectedly low, suggesting low grass moisture stress. Given the other collective indications of semi-arid conditions it may be the case that the Fs% is affected by preservation bias of bulliform types. However, good preservation of fragile phytolith types makes this a moot point. Disagreement between Fs% and climatic conditions evidenced by other morphotypes also occurs in other Prospect Farm palaeosol samples. The cause of this divergence remains unresolved, but it is notable that bulliform phytoliths have very low relative abundances through the main Prospect Farm sequence (0-3%) which could affect the reliability of the Fs index.

Samples from PS3 do not show any overlap with any published modern samples from East Africa (see Figure 6.27). However, the phytolith composition of PS3 samples resembles that of evergreen and semievergreen bushland and thicket (VECEA code: *Be*), Upland *Acacia* wooded grassland (*We*), Edaphic wooded grassland (*Wd*) (tree cover >10%), and Edaphic grassland (*g*) (tree cover <10%) that is present at lower elevations in the Nakuru-Naivasha Basin today (see Chapter 2.9). While these vegetation types both include mixed xeric/mesic C₄ grassland communities and can have very low local wooded vegetation cover, Be and We both develop under hotter, semi-arid conditions (500-850 mm MAP) with a short rainy season, whereas Wd develops under warm and semi-arid conditions (950-1250 mm MAP) with a longer rainy season. The lack of modern comparative phytolith soil samples from these vegetation types prevents more specific classifications of the PS3 fossil phytolith assemblage to these or other similar vegetation types. The lack of fire in the Prospect Farm record provide some evidence to suggest that MAP may have been above 800 mm. This suggests the occurrence of Wd vegetation is more likely. More open vegetation conditions in lowland areas of the basin generally at his time could have resulted in the long-distance aeolian transport of phytoliths (see Strömberg et al., 2018 and references therein). Consequently, the xeric grassland signal in PS3 may be less localised than in other palaeosols; in which higher arboreal cover is likely to have limited wind dispersal of phytoliths.

6.8.3.4.3 Altitudinal variation in phytolith signals from PS3 at Prospect Farm Localities I and II

Phytolith results from the PS3 Bwb/Btsob horizon at Locality I and Locality II show that FI +CH % are similar at the two sites, while Ic% values are slightly elevated and Iph values are slightly reduced at Locality II. This illustrates that arboreal vegetation cover was likely to have been similar between the two sites, but that mesic C_4 grasses were present in higher proportions than xeric C_4 grasses at higher elevations. This finding agrees with the modern-day altitudinal distributions of Poaceae subfamilies on East African mountains (see Chapter 2.6). Furthermore, these findings support the interpretation that vegetation physiognomy was characterised by open conditions across the Prospect Farm Formation.

6.8.3.4.4 A preliminary model of Palaeosol 3 formation processes

While several aspects of the formation of PS3 remain unresolved, pedofeatures, geochemical and phytolith results indicate its formation under intermediate sub-humid to semi-arid conditions; with a longer or more intense dry season than in PS2. A preliminary model of site formation for PS3 is shown in Figure 6.38).



Figure 6.38 Palaeosol formation model for PS3. Note: Inferred changes in vegetation may have also been modified by other factors (e.g. changes in pCO_2) not included in the model. This is due to the lack of dates from the sequence from which comparisons can be made to independent climate records.

6.8.4 Palaeosol 4 (Units 7C - 7A)

6.8.4.1 Field descriptions: Palaeosol 4

The units forming Palaeosol 4 are well exposed in section and in most escarpment exposures across the Prospect Farm Formation (see Figures 6.4 and 6.39 [A-E]). As noted by Anthony (1978), Unit 7A is particularly conspicuous across the landscape and acts as a key stratigraphic marker horizon for this section of the Prospect Farm sequence. The type section for PS4 (described from Locality I) is divided into three soil horizons (corresponding to sedimentary units). Described from the base to the top of the profile, these are interpreted as: Cb4 (Unit 7C), BwCb4 (Unit 7B) and Btskb4 (Unit 7A), developed from fine-grained silty ochreous coloured yellow airfall tuff. Features of PS4 horizons are described in detail in Appendix 6, Table 6.1. PS4 is characterised by a C horizon which is structureless and has limited signs of mottling and clay coatings, an intermediate BwC horizon, and a Bt horizon with redox features and occasional pedogenic calcite hypocoatings on ped faces (Figure 6.39 [E, G]). A moderately welldeveloped sub-angular shaped ped structure is also recorded towards the top of the profile (Figure 6.39 [C, D, E]), while in certain areas of Unit 7A peds appear somewhat prismatic. At the transition between Unit 7C and 7B, a thin band of diffuse weathered pumice is present in a zone (~5 cm thick) that defines the lower limit of redox features in the profile (see Figure 6.39 [H, F]). Based on these features and results of geochemical analysis (Section 6.8.4.2), PS4 is preliminarily identified as a tephric (vitric) Cambisol with ferralic, luvic, and calcic features. PS4 is ~1 m deep and shows evidence of slight, progressive reductions in thickness towards topographic low points on the landscape (i.e. towards valley edges) and marginal low angle dipping of beds towards the east at Locality I and II. The very sharp contact between Units 7A and 6 is interpreted as an erosional surface associated with the deposition of pumice of Unit 6. This was likely to have removed the A/O horizons of PS4, creating a truncated lithoprofile. Artefact densities in PS4 are sporadic, increasing slightly towards the top of the profile in the Btskb4 horizon (Unit 7A) and in Unit 6 (see Figures 6.6 and 6.40).



Figure 6.39 Field photos of key features described in Figures. 6.40, 6.41, and Appendix 6, Table 6.1. (A-B) Photos of the position of PS4 in Locality I step trench in the Prospect Farm sequence. (C-E and G) Photos of selected pedogenic and sedimentological features of Bt horizons in PS4. (F and H) Photos of selected pedogenic and sedimentological features at the contact between PS3 and PS4.
6.8.4.2 Grain size and geochemical trends: Palaeosol 4

Sediments in PS4 are poorly sorted and show limited variation throughout the profile. Particle size distributions are bimodal to unimodal with coarse skewness (see Appendix 6, Table 6.3). Particle size distributions show increases in clay and silt size material from the base to the top of PS4 (see Figure 6.40 [B]).

PS4 demonstrates divergent trends in total elemental values compared to other palaeosols of the Prospect Farm sequence. Al is high in the C horizon and gradually reduces towards the top of the profile. Si increases from the C to Btsk horizons and remains high into Unit 6 (see Figure 6.40 [A]). Fe, Ti, Mn, and P values a relatively low, with Fe slightly increasing in the Btskb4 horizon. Strong positive correlations (R = > 0.9) exist between Fe, Ti and Al. Base cations (Ca, Mg, Na, K) all increase from the C horizon to the top of the profile. Strong positive correlations also exist between several of these elements and clay % (see Table 6.6). Step-wise increases in phytolith concentrations occur from the base to the top of the profile and are sharply reduced in Unit 6. An apparent weak visible correlation between phytoliths below 63 µm and grain size below 63 µm is observed throughout most of the profile.

	Phytolits per gram AIF	Clay %	Silt %	Sand%	Al	Fe	K	Mg	Mn	Na	Р	Si	Ti	Ca
Phytolits per gram AIF														
Clay %	0.72315													
Silt %	0.60685	0.96827												
Sand %	-0.63029	-0.97839	-0.99902											
Al	0.19601	0.50719	0.51802	-0.51851										
Fe	0.29612	0.4104	0.43014	-0.42863	0.90196									
K	0.77177	0.89636	0.83078	-0.84627	0.6759	0.70163								
Mg	0.67174	0.86504	0.76815	-0.78889	0.74257	0.67476	0.96169							
Mn	0.14999	-0.2844	-0.24239	0.25096	-0.0885	0.34232	0.02879	-0.1722						
Na	-0.70851	-0.28604	-0.20494	0.22027	0.40257	0.36573	-0.1348	-0.0304	0.00673					
Р	-0.28964	-0.32112	-0.38864	0.37847	-0.7927	-0.80171	-0.4722	-0.4277	-0.1996	-0.0426				
Si	0.77548	0.56056	0.44147	-0.46464	0.60672	0.75662	0.85042	0.80887	0.35136	-0.1702	-0.5334			
Ti	0.37641	0.30149	0.32948	-0.32605	0.70143	0.93824	0.63612	0.52946	0.63418	0.2229	-0.7421	0.7801		
Ca	0.56348	0.92006	0.84851	-0.86514	0.55721	0.31681	0.78497	0.86166	-0.5903	-0.1811	-0.2529	0.4495	0.0984	

Table 6.6 Pearson's correlation coefficient (*R*) for selected sedimentology, geochemical, and grain size data from PS4 (sample No. 5c to 26b). Bold values indicate 99% confidence interval.



Figure 6.40 Stratigraphic changes in palaeoenvironmental proxies from PS4. (A) Geochemistry, (B) particle size distributions and key particle size variables, (C) and summary phytolith groups and indices. Lithics concentrated in Unit 7C belong to Phase II-B. Lithics concentrated in Unit 7A/6 belong to Phase II-C.

6.8.4.3 Phytolith distributions, preservation and grain size comparisons in Palaeosol 4

Phytolith distributions and preservation in PS4 are comparable to those of modern soils and those recorded in PS3. The lack of macromorphological signs of bioturbation in the C horizon suggest that low numbers of phytoliths in this horizon are the result of either post-depositional translocation via water percolation or incorporation of phytoliths into airborne ash occurring in the time from eruption to deposition. Close visual correspondence between phytoliths below 63 µm and particles below 63 µm in all Unit 7 samples, except No. 1C, may indicate that sediment sorting has influenced the phytolith assemblage. An inverse trend is also visible in the reduction in the abundance of large blocky morphotypes with decreasing sand percentage (see Figure 6.40 [B]). This suggest that grain size sorting could have potentially created an artificial increase in small GSSC phytoliths in finer sediments relative to larger morphotypes. Furthermore, clear vertical and horizontal cracking, associated with shrink-swell processes and the sub-angular blocky-prismatic structure of PS4, could also have resulted in the lateral and vertical movement of phytoliths throughout the profile. Additionally, it is currently not possible to rule out that phytoliths accumulated in the Btsk horizon partially through aeolian activity. In this case the phytolith signal from PS4 may in part reflect a more mixed regional picture of vegetation, rather than an exclusively local one. Based on the current evidence, it is appropriate for the time being to treat the phytoliths signal of PS4 as polymorphic and representative of all vegetation stages during the entire period of palaeosol formation, instead of following a well-defined age-depth relationship.

<u>6.8.4.4 Palaeosol forming processes, artefact distributions, palaeoenvironmental and palaeoclimatic interpretations: Palaeosol 4</u>

The homogenous appearance of sediments and limited variations in sorting and skewness of grains in PS4 imply that it is an airfall deposit in which minimal physical reworking occurred after deposition and during pedogenesis. Low concentrations of Fe, Ti and Mn suggest incipient to moderate weathering occurred (i.e. limited transformation of primary minerals to secondary oxides and minerals occurred insitu). Low to moderate weathering and periods of poor drainage are supported by macromorphological features (i.e. depletion of Fe and Mn within the matrix producing mottles and precipitation as Fe/Mn coatings in root channels, ped faces and cracks). Higher values of both Al and Si in the C horizon are likely to indicate the presence of silica rich allophanes or similar Al and Si compounds. These point to minimal alteration of volcanic parent material in the C horizon. This is supported by the roughly inverse relationship between clay % and Al. Therefore, in the case of PS4, the Al/Si ratio cannot be used to infer the accumulation of clay minerals.

Increases in the concentrations of Base cations and Si towards the top of the profile could be explained by alkalinisation. This is supported by the presence of weak carbonate hypocoatings in the Btskb4 horizon. Hypocoatings develop as water percolates the soil matrix and calcium carbonate precipitated around medium to large soil pores (Zamanian et al., 2016), or as a result of fluctuations in the water table (Durand et al., 2010; Zamanian et al., 2016). Moderately to poorly developed pedogenic features with diffuse boundaries suggest a relatively short period of pedogenesis. However, the presence of clay coatings indicates that pedogenesis operated for long enough to bring PS4 into equilibrium with the climate. It may be possible that if weathering was strong enough, the slight increases in Fe in the Btskb4 horizon could represent the release of Fe from ferromagnetic minerals; forming iron oxide mottles that can co-exist with carbonate hypocoatings under alkaline conditions. However, Mn concentrations do not follow the same down-profile pattern as Fe as would be expected if this was the case. Furthermore, pedogenic iron carbonates (e.g. siderite) tend to form in waterlogged soils under strong reducing conditions, where precipitation outweighs evaporation (Ludvigson et al., 2013); which are not observed in PS4.

The precipitation-evaporation balance has been shown to the primary control on the development of carbonate features in soils (Cerling, 1984; Borchardt and Lienkaemper, 1999; Candy and Black, 2009). The precipitation of CaCO₃ is often indicative of warm-dry climate conditions and can take place rapidly over weeks or months (i.e. within a single dry season). The co-occurrence of redox and carbonate features in the Btskb4 horizon implies increased seasonal differences in the precipitation-evaporation balance and that changes in the water table occurred during pedogenesis. However, redox features can also form over the course of a single wet-dry cycle. Therefore, it is not clear if the presence of both these features high seasonal variability during the entirety of the formation of PS4, brief enhanced seasonality, or the switching and overprinting of features formed under a climate with a longer wet season to one with a longer dry season.

The depth of carbonate leaching and precipitation in palaeosols have been shown to relate to the relative length and intensity of wet and dry season precipitation (e.g. Egli and Fitze, 2001) (Zamanian et al., 2016). While the A/O horizon of PS4 is interpreted as having been removed by erosion, the presence of hypocoatings at the top of the profile suggest that precipitation was <500 mm MAP and may have to been lower than <200 mm (see Retallack, 2005; Zamanian et al., 2016 [Fig. 9. Pg. 10]). Increases in the activity of Si and Base cations are often associated with the formation of pedogenic smectites. These are commonly found in association with calcite and hematite that form in xeric and monsoonal climates with strong seasonal precipitation (Borchardt, 1989; Sheldon and Tabour, 2009 and references therein). Increases in these elements in the Bt horizon in PS4 may indicate the presence of smectite clays or other phyllosicate minerals. Alternation(s) between semi-humid and semi-arid climate conditions during the formation of PS4 is further supported by ped structural features (e.g. prismatic structure and an argillic Bt horizon), that indicate evolution of an andic Cambisol towards a luvic Phaeozem (Shoji et al., 1993). It is also possible that hypocoatings were formed after the burial of PS4 and represent post-depositional diagenetic alterations (overprinting) during more recent arid episodes recorded in the study area (e.g. the Mid-Holocene dry phase ~4.5 ka [Ambrose and Sikes, 1991; Maitima, 1991]). However, the absence of these feature in overlying PS5 make this explanation less plausible. An alternative, albeit less likely, explanation for increases in Si and Base cations represents the addition of unweathered material into PS4 through aeolian processes, the presence of which would require further analyses to establish (see Section 6.9 and Appendix 6.4.1).

6.8.4.4.1 Artefact distributions: Palaeosol 4

The low artefact percentages and densities throughout Unit 7 is composed mostly of sporadic obsidian flakes. These finds are consistent with the interpretation off Unit 7 as an airfall tuff with minimal post-depositional reworking, into which very occasional accidental lithics and artefacts were incorporated during deposition. During the original excavation of Locality II, Anthony (1978), listed Unit 6 as sterile, however our excavations identified a slight increase in the percentage of lithic artefacts in this level. The existence of another archaeological level between Unit 7 and the "ferruginized tuffs" of Units 5 and 4 was recognised as likely by Anthony (1978), as artefacts are visible eroding out of escarpments between these units although they had not been located by previous excavations in section. Increases in artefacts in Unit 6 and at the transition from Unit 6 to 5 are likely to reflect redeposition of tools from the eroded Unit 7 A/O horizon during deposition of the pumice deposit of Unit 6. The same process is proposed for the slightly elevated artefact densities and percentages recorded at the transition from Unit 8A to 7C and from Unit 4A to 3F. Ongoing archaeological analysis will help to determine if material from Unit 7 should be assigned to Phase II or III material. For now, low artefact densities in Unit 7 and 6 are assigned to a sub-phase of Phase II (Phase II-C); and are likely to represent a short-lived occupation of the site or a period where activity at the site was less frequent.

6.8.4.4.2 Phytolith-based vegetation trends: Palaeosol 4

The phytolith assemblage from PS4 has a mixed vegetation signal, like that of PS2, but with some notable differences: Mesic C4 GSSC types form the largest proportion of Poaceae indicators, which are accompanied by high percentages of indeterminate C_3/C_4 GSSCs, moderate to low percentages of xeric C_4 GSSCs, and very occasional C_3 GSSCs. Ic values (~20-40%) are most similar to those recorded from EDAP-Sah and AFMF shrub savanna, as well as to those from PS2 and PS3 (see Figure 6.21). Iph values are the lowest observed throughout the Prospect Farm sequence and are similar to those from AFMF and AMFS, reflecting the dominance of mesic C_4 grasses (see Figure 6.22). FI values are higher in the BwCb and Btsb horizons than in PS1-3 but decrease towards the top of the profile; reaching a minimum in the Btskb horizon. In the Btsb horizon globular granulate percentages reach values that indicate tree cover $\geq 40\%$. This represents the only sample in the Prospect Farm sequence where this threshold is surpassed and in which poor preservation is not thought to have affected phytolith indices calculations (see Figures 6.20 and 6.23). However, when all woody indicator morphotypes are considered, FI values fall below the average of Miombo woodland samples. This suggest the presence in the local vegetation community of unknown woody species that produce high abundances of globular granulates. Globular granulates made up less than 5% species studied from Nakuru-Naivasha Basin but were found to be most common in those from drier woodland settings (see Chapter 4.4). Thus, both the phytolith assemblage and pedogenic indicators suggest that PS4 supported dry forest or woodland with moderate to low arboreal cover and a mesic C₄ grass understory. Diagnostic morphotypes from Cyperaceae and

epidermal jigsaw morphotypes, produced by pteridophytes, are present in low abundances in PS4. This indicates that damp conditions existed at least periodically, perhaps seasonally. The presence of ferns suggests semi-shaded conditions, possibly at woodland margins, or associated with patches of denser tree cover. PS4 is also the only palaeosol in which Commelinaceae (*Cyantois lantanta* type) phytoliths are recorded. This herbaceous species grows in a variety of habitats but is most common in shallow poorly developed soils and in seepage areas (Eichhorn et al., 2010). Taken together, these findings suggest strong seasonality was likely during the development of vegetation communities in PS4.

A broadly inverse trend is evident between decreases in arboreal phytoliths and increases in mesic and xeric C₄ GSSC abundances in PS4. As phytolith preservation is not thought to have strongly affected phytolith counts in PS4, it is tempting to interpret changes in phytolith types with depth as recording a reduction in tree cover over time. However, until taphonomic factors can be more fully resolved, the PS4 phytolith signal is best considered as polygenic. PCA and phytolith indices results show that the vegetation signal is most similar to AFMF shrub savanna. This vegetation type is found at the transition between Afromontane rainforest/undifferentiated forest and open grassland vegetation types, a position which is occupied by evergreen and semi-evergreen bushland and thicket (Be) in the Nakuru-Naivasha Basin today. Modern samples of AFMF shrub savanna come from Mt. Rungwe, Tanzania, within the Zambezian phytogeographic zone. Wooded vegetation communities (e.g. the Miombo woodlands) within this zone typically produce higher percentages of globular granulate forms than Afromontane forest. It may be the case that higher proportions of globular granulate morphotypes in PS4 relate to the presence of an increased number of broadleaved species in wooded grassland habitats, possibly like Combretum-Terminalia wooded grassland that is found widely across equatorial and eastern Tropical African today. In our study, globular granulate phytoliths were recorded primarily in species characteristic of modern transitional woodland habitats, species such as Terminalia brownii were not found to produce this morphotype (see Chapter 4.4). As in PS1-3, additional comparative samples are necessary to be more precise about the floristic and physiognomic nature of wooded grassland evident in PS4 samples. A more nuanced understanding of the nature of wet-dry cycles and of phytolith taphonomy will also help to ascertain if the phytoliths signal should be interpreted as representing climatic shifts over time, or as having been deposited under less changeable but more highly seasonal climate conditions (see Section 6.9).

6.8.4.4.3 Altitudinal variation in phytolith signals from PS4 at Prospect Farm Localities I and II

Phytolith results from the Btskb horizon from Locality I and Locality II indicate that FI+CH%, Ic% and Fs% are similar at the two sites (see Figures 6.21-6.24). Iph% values at Locality II are slightly lower than those recorded at Locality I and overlap with mean values form WOZA, as well as with AFMF and AFMS. These findings suggest that arboreal vegetation cover was likely to have been similar at, and in the area between the two sites, and that C_4 mesic grasses probably occurred in higher numbers than xeric C_4 grasses at lower elevations.

6.8.4.4.4 Preliminary model of Palaeosol 4 formation processes

Geochemical and phytolith results from Palaeosol 4 are interpreted as representing palaeosol formation under intermediate sub-humid to semi-arid conditions, similar to PS3 and with a longer or more intense dry season than in PS2. A preliminary model of site formation based on existing evidence is shown in Figure 6.41).



Figure 6.41 Palaeosol formation model for Palaeosols 4. Note: Inferred changes in vegetation may have also been modified by other factors (e.g. changes in pCO_2). These are not included in the model due to the lack of dates from the sequence from which comparisons can be made to independent climate records.

6.8.5 Palaeosol 5 (Units 6 - 4B)

6.8.5.1 Field descriptions: Palaeosol 5

The sedimentary units forming Palaeosol 5 (PS5) are generally well exposed in section and at all escarpment exposures across the Prospect Farm Formation (see Figures 6.4 and 6.42 [A, B, E]). The type section for PS5 (described from Locality I) is divided into three soil horizons (corresponding to sedimentary units). Described from the base to the top of the profile, these are interpreted as: C (Unit 6), argillic/eutric Btsmb5 (Unit 5) showing evidence of minor gleying, argrilic, eutric and nitric properties, and Btsob5 (subdivided into Btsob5-1 and 2 in Unit 4). At the base of Unit 5 (Btsmb5) there is a

moderately sharp, slightly undulating, and rapid (over 2-4 cm) contact with the unconsolidated pumice of Unit 6. This contact is best exposed at the base Escarpment No. 5 (see Figure 6.43 [A, B]). In the Locality I trench, Unit 6 is poorly exposed due to a localised topographic depression here (see Figure 6.42 [B, C]), but is well exposed across the rest of the Prospect Farm Formation and in section at Locality II (see Figures 6.4 and 6.42 [A, E]). PS5 is ~1.1 m deep and is characterised by a C horizon of ferrugenised bands. This is overlain by an indurated Btsmb5 horizon with inclusions of poorly bedded volcanic gravels, and abundant Fe/Mn redox features in its matrix (Figure 6.42 [C]). Distinctive clay accumulations (cutans) are also present in fissures in this horizon, that show clear signs of cracking and have a localised subangular blocky structure indicative of shrink-swell behaviour (see Figure 6.42 [D]). The cutans are 'dish-shaped' and extend vertically and horizontally, joining at approximately 70-90° angles; creating a roughly prismatic macrostructure. The indurated matrix material surrounding these cutans appears granular/nutty with inclusions of small gravels. At Locality II the dish-shaped features and boundaries between Units 5 and 4 are less distinct. Here sediments display a very crude blocky subangular structure. In places Unit 4 contains concave depressions which result in an undulating contact between Unit 4 and the units above and below it (see Figure 6.42 [C]). Btsmb5 grades into the Btsob5-1 horizon which has a crude prismatic to blocky subangular blocky structure. This horizon also shows increased lateritic soil properties (e.g. rubification [ferruginization] and Fe/Mn mottling), as well as increases in the size and frequency of gravels and pebble sized volcanic clasts (e.g. trachyte and obsidian). The Btsob5-1 in turn grades into Btsob5-2 that demonstrates a light reduction in rubification, mottling, and gravel content, as well as a stronger prismatic structure. The contact between Btsob5-2 and the buff yellow tuff of Unit 3 is abrupt but does not appear to be erosional. In section at Locality I this contact appears horizontal, but across escarpments at both localities it appears to undulate. In these cases, Unit 3 tuff infills depressions in Unit 4 that are up to \sim 30 cm deep, occurring roughly every 30-60 cm (see Figure 6.43 [C, D]). At Escarpments No. 5 and No. 1, the distinction between these units is less clear; their contact being horizontal and more gradational. This indicates that the undulating contact between these horizons is confined to mid-elevation sites across the Prospect Farm Formation. Variations in bed thickness of Unit 5 across the Prospect Farm Formation is low compared to Unit 4 that varies by up to 50 cm between Locality I and Escarpment No. 5 (Figure 6.43 [B, C]). At Escarpment No. 5, large gravel size material was not observed in either unit. As in PS4, PS5 shows evidence of reduction in bed thickness towards topographic lows, as well as low angle dipping towards the east at Locality I and II. For further descriptions of the features in PS5 see Appendix 6, Table 6.1. Due to the presence of argillic subsurface horizons, high-activity clays and features that indicate areas of high base saturation, PS5 is preliminarily identified as a well-developed cambric Luvisol with ferralic and minor nitic, eutric and vertic properties; that has developed from thin foot slope lahar deposits.



Figure 6.42 Field photos of key features described in Figures. 6.44, 6.46 and Appendix 6, Table 6.1 (A-B) Photos of position of Palaeosol 5 and 6 in Locality I step trench. (C, D, G, F) Photos of selected pedogenic and sedimentological features of Palaeosol 5. (E) Photos of contact between Palaeosols 4 and 5 In Trench 1, Locality II.



Figure 6.43 Field photos of Palaeosol 5: (A) bed contact between pumice deposits of Unit 6 and fine-grained lahar deposits of Unit 5 at Escarpment No. 5 where the base of Unit 5 is exposed as a horizontal surface. (B) Contact between Units 6 and 5 and between Units 5 and 4B in exposures at Escarpment No. 5. (C) The wavy contact between Units 4 and 3 in Trench 1, Locality II. (D) The wavy contact between Units 4 and 3 observed at Locality I. Note: large cobble to medium gravel size artefacts and non-archaeological lithics were observed imbedded in-section and eroding out of Unit 3 and 4.

6.8.5.2 Grain size and geochemical trends: Palaeosol 5

Sorting of sediments in PS5 varies between moderately to very poorly sorted. Particle size distributions are generally unimodal with a strong coarse skew (see Figure 6.44 and Appendix 6, Table 6.3). Particle size distributions show an increase in sand sized material from the C to Btsm horizon and a rough decrease in grain size up-profile. It is notable that the results of laser particles size analysis presented here only record variation in matrix material but does not capture variation in larger inclusions of gravels and pumice clasts in the C horizon. Phytolith preservation and concentrations are more variable in PS5 than in PS1-4. In the Btsm preservation is poor, horizon and concentrations are extremely low; In the Btso-1 horizon their values increase and are highest in the Btso-2 horizon; In the Btsm horizon, a broadly inverse relationship is evident between phytoliths blow 63 µm and mean grain size.

In PS5, Si values are high in the C horizon but low in others and show a positive correlation with clay (R= 0.59) and silt (R= 0.66), as well as a negative correlation with sand size material (R= -0.66) and Mn (R= -0.57) (see Table 6.7). Al, Fe, K, Mg, Na and Ti values are high, while P, Si and Mn values are low. Visually, most elements (Al, Fe, K, Mg, Na, Ca, and Ti) mirror one another up-profile. These elements increase from the C horizon into Btsmb5, before declining at the boundary with Btso-1 and increasing in Btso-1 and Btso-2; where they again decrease and remain relatively low. Positive correlations are

recorded between Al with K, Mn, and Na. Positive correlations also exist between K and other alkaline earth elements such as Mg and Na, but also with Ti. Mg is positively correlated with Mn and Na, Na with Ca, and Ti with Ca.

	Phytoliths per gram AIF	Clay %	Silt %	Sand %	Al	Fe	K	Mg	Mn	Na	Р	Si	Ti	Ca
Phytoliths per gram AIF														
Clay %	0.17183													
Silt %	0.070581	0.85366												
Sand %	-0.079019	-0.87364	-0.99921											
Al	-0.31617	-0.21514	-0.22636	0.22785										
Fe	-0.29423	-0.18128	-0.19498	0.19596	0.85265									
K	-0.12394	0.13929	0.20233	-0.19962	0.59015	0.69507								
Mg	-0.3625	-0.20998	-0.30989	0.30549	0.84473	0.83393	0.62743							
Mn	-0.22451	-0.33669	-0.3465	0.34934	0.55386	0.73495	0.2984	0.50325						
Na	-0.19649	-0.17446	-0.1707	0.17275	0.59922	0.72709	0.58316	0.60523	0.43442					
Р	-0.16223	-0.12848	-0.25416	0.24723	-0.3507	-0.24439	-0.3974	0.02828	-0.0229	0.0091				
Si	-0.18053	0.59184	0.66545	-0.66673	-0.0521	-0.23093	0.09991	-0.0905	-0.5729	-0.219	-0.2105			
Ti	-0.19103	-0.28137	-0.26002	0.26433	0.81861	0.9525	0.60996	0.68835	0.81433	0.6834	-0.3526	-0.378		
Ca	-0.25454	-0.17314	-0.14424	0.14793	0.79383	0.76758	0.67998	0.8647	0.49222	0.6418	0.0064	-0.089	0.6575	

Table 6.7 Pearson's correlation coefficient (R) for selected sedimentology, geochemical, and grain size data from PS5 (sample No. 25b to 1b). Bold values indicate 99% confidence interval.



Figure 6.44 Stratigraphic changes in palaeoenvironmental proxies from Palaeosol 5. (A) Geochemistry, (B); particle size distributions and key particle size variables, (C) Summary phytoliths groups and indices. Note: Lithics concentrated in Units 6/5 belong to Phase II-C. Lithics concentrated in Unit 4B/4A belong to Phase III. Lithics concentrated in Units 4A/3F belong to Phase IV.

<u>6.8.5.3 Palaeosol forming processes, artefact distributions, palaeoenvironmental and palaeoclimatic interpretations: Palaeosol 5</u>

6.8.5.3.1 Depositional and post-depositional processes in Unit 6

Particle size distributions, fabric, angularity, physical signs of weathering, colour, and geochemistry of pumice in Unit 6 are similar to those of the pumice beds described from Units 14-12 (see Section 6.2.1). As such, Unit 6 is also interpreted as a primary airfall deposit. Minimal evidence for physical reworking, and moderate evidence of chemical weathering in Unit 6 (e.g. higher Si and lower Fe, Ti and Mg values than overlying deposits), suggest Unit 6 was not exposed for a long period of time before burial by the overlying finer tuffs. Deposition of Unit 6-4 as part of the same eruptive episode is further supported by the gradual nature of the contact between Units 6 and 5, and 5 and 4.

6.8.5.3.2 Depositional processes, artefact distributions, frequencies, and phase attributions in Units 5, 4, and 3

The presence of both inclusions of gravel size volcanic material and the 'dish-shaped' clay-filled fissures in Unit 4 are most consistent with lahar and subsequent pedogenic processes, rather than with colluviation (see Appendix 6.3.3 and 6.3.4 for further detail). In these deposits the undulating contact between Units 4 and 5 are consistent with depositional processes related to tree stump moulds rather than hill slope processes (see Appendix 6.3.4 for further details).

Anthony (1978), recorded low artefact frequencies at the contact between Units 6 and the base of Unit 5, with only sporadic flakes recorded throughout the rest of Unit 5. Artefact densities increase dramatically in Unit 4; with the highest frequencies recorded in Unit 4A. Artefacts at the base of Unit 5 were assigned to Phase III by Anthony, but it was also noted that tool attributes showed little divergence from those in the bulk of Phase II material in Unit 8 (PS3). INAP excavations discovered small but previously unrecorded artefact levels from Units 7A (PS4) and in pumice deposits of Unit 6 (assigned by this study to a newly created Phase II-C [see Section 6.8.4.4.1]). It seems likely that the artefacts at the contact between Units 6 and 5 in fact originated in PS4 from Phase II-C rather than III, having been redeposited during the deposition of Unit 6 pumice; and possibly reworked again during deposition of Unit 5 pyroclastics. Artefact distributions and \sim 50 kyr gap in the age of artefacts between these in lower Unit 5 and Unit 4 suggested by obsidian hydration dates provisionally supports the suggestion that artefacts in these horizons were produced/deposited at different times by one or more groups. However, this difference could relate to errors in this dating technique (see Chapter 5.3.2), especially as evidence of fluctuations in hydrology and humidity, know to affect the reliability of the OH technique, are present in PS5. Artefacts in Unit 4B/4A have been attributed to Phase III by Anthony (1978), whereas those recorded at the contact between Unit 4A and 3F, as well as very sporadically throughout the rest of Unit 3, were assigned to Phase IV.

Unlike the other palaeosols in the Prospect Farm sequence, artefact densities increase in Unit 4 of PS5 while artefact percentages decline. This reflects the increase in non-archaeological gravel material in this

unit associated with lahar deposits. Due to the horizontal nature of artefact distributions across the wavy bed contact between Unit 4A and Unit 3F (the point at which the transition between artefacts Phase III and Phase IV occurs), it was unclear to Anthony if Phase III and IV material was deposited on the same former land surface. If they were it would suggest some level of continuity between these two phases. Alternatively, artefacts from these units may belong to distinct deposition episodes. The most parsimonious explanation of artefact distributions in these deposits is that Phase III material was deposited in PS5 prior to that of Phase IV material. Phase IV material was then subsequently reworked during the deposition of Unit 3 tuff. The low chronostratigraphic resolution of these palaeosol deposits means that it is not possible to determine if the occupation of the site was continuous during the shift from Phase III to Phase IV material, however there are no obvious stratigraphic breaks in artefact occurrences in Unit 4. This suggests that there was at least some level of continuity between these phases and that the groups that produce these tools occupied the same land surface, albeit potentially at different times and possibly under different environmental conditions. The horizontal orientation of artefacts across the undulating boundary between Units 4 and 5 discussed by Anthony (1978) is likely to be caused by a reduction in artefact inclination cause by sediment compaction following burial (see Appendix 6.3.6 for a detailed explanation).

6.8.5.3.3 Phytolith distributions, preservation and grain size comparisons in Palaeosol 5

Distribution and preservation of phytoliths in PS5 show a similar pattern to those recorded in modern soil (i.e. decreases in preservation and concentrations with increased depth). No discernible correlation is present between particle size and phytolith distributions in these sediments. As suggested for PS1, latosolization processes are likely to have contributed to the dissolution and degradation of the phytolith pool, through chemical and physical processes, in the lower soil horizons of PS5. The relationship between decreasing phytolith preservation and increased latosolization is supported by higher phytolith counts in the Btso-1 horizon, that has limited signs of this process. Low phytolith counts and physical damage (breakage) of phytoliths in Unit 5 (Btsmb horizon) are likely to have been caused by shrink-swell action and induration of these sediments. The much higher relative abundances of blocky morphotypes compared to GSSC types in Unit 5 is likely to represent better preservation of robust morphotypes over more fragile forms; biasing palaeovegetation reconstructions (see Chapter 4.3.2).

6.8.5.3.4 Phytolith-based vegetation trends: Palaeosol 5

The phytolith assemblage from PS5 demonstrates a comparable vegetation signal to those from PS2 and PS4, with the exception that indeterminate C_3/C_4 GSSCs and arboreal phytoliths are slightly more abundant (see Figure 6.44). Phytolith preservation is generally poor in the lower Btso and Btsmb horizons (Units 4B and 5). However, there are instances in which index specific counts were reached where high FI%, not thought to have been biased by taphonomic factors, are observed (e.g. Sample 11b). At no point do values from samples unaffected by preservation bias reach the levels that have been used in West/Central African studies to infer tree cover $\geq 40\%$ (see Figure 6.20). Iph values show considerable variability throughout the upper Btso horizon; indicating conditions in which either xeric

or mesic grasses were dominant (see Figure 6.22). Ic values are relatively more stable and are consistently above 50%. These values are similar to those from modern AFMF and AMFS samples (see Figure 6.21). PS5 records very low percentages of Aceraceae indicator types but no other family specific arboreal indicator morphotypes. PCA results show that PS5 samples have some similarities with AFMF, GROS and AFMS shrub savanna types. The intermediate position between forest and shrub/wooded grassland of PS5 samples in the PCA suggests a transitional vegetation type. Very low percentages of C₃ grass indicators and indicators of moderate tree cover suggest that in general the phytolith signal from PS5 is more consistent with shrub savanna and transitional woodland types, as inferred for PS4, than with either Afromontane forest or more open savanna vegetation. Pedogenic features, higher phytolith concentrations, arboreal indicator phytoliths, and index values, suggest a higher woody biomass, developing under marginal more humid conditions on more well-developed soils, than have been inferred for PS4.

High Ic% values in PS5 reflect the higher abundances of rondel phytoliths in the indeterminate C_3/C_4 GSSCs category. While both xeric C4 GSSC and C3 GSSC are present in low percentages in the Btso horizon, C_4 xeric types are more frequent and have slightly high proportions. Therefore, it is more likely that the very occasional C_3 GSSC types (e.g. wazy trapeziforms) were produced by Chloridoideae subfamilies in this instance; and that rondels and other indeterminant types (e.g. long and collapsed saddles, and Bilobate 'stipa' types) are more likely to have been produced by Panicoideae (see Barboni and Bremond, 2009). This could explain overinflated Ic values and contradictory Ic and Iph values in PS5. It is also possible that this signal represents the amalgamation of recurrent short-term shifts between semi-mesic to semi-xeric conditions; which are not resolvable in the bio-stratigraphic record. Alternatively, similarly high percentages of long and collapsed saddles, trapeziform short cells and bilobate 'stipa' types, as recorded in in PS1, may indicate the presence of lowland drought-resistant bamboo (Oxytenanthera abyssinica) thicket. This bamboo type is generally found below 1500 m a.s.l. today in savanna woodland, semi-arid wooded grassland, bushland and thicket (e.g. Combretum-Termitaria wooded grassland) where C_3 Pooideae grasses are absent. While Oxytenanthera abyssinica is not recorded in the Nakuru-Naivasha Basin today, it is a mass-flowering plant and thus can appear and spread rapidly before dying off (White, 1983, pg. 55). Neither of these competing interpretations affects the basic classification of PS5 as supporting a transitional woodland/wooded grassland environment, dominated by C4 grasses; developing under semi-humid to semi-arid conditions. Given the inferred longer timedepth of PS5 and polygenetic nature of most soils, while improbable, it is not possible to rule out an interpretation of the phytolith signal in PS5 as reflecting vegetation fluctuations between more humid conditions, in which C_3 understory grasses were periodically present, and drier conditions where more open vegetation and xeric C4 grasses dominated. On the other hand, it is also possible that decreases in FIs and increases in GSSC indicators towards the top of Btso horizon (Unit 4A) reflect a shift towards more open vegetation conditions over-time. If this was the case, then this shift occurs across the boundary of the transition of Phase III to Phase IV material in Unit 4A/3F, during the putative MSA- LSA transition at the site. These conflicting interpretations highlight the complexities involved in inferring successional vegetation change within individual palaeosols of the Prospect Farm sequence using a phytolith-based approach.

<u>6.8.5.3.5 Altitudinal variation in phytolith signals from PS5 at Prospect Farm Localities I and II</u>

Phytolith results from the PS5 Btso horizon from Locality I and Locality II demonstrate that FI+CH%, Ic% and Fs% are similar at the two sites. As in PS2-4, Iph% values at Locality II are slightly lower than those recorded at Locality I; indicating increases in C₄ mesic grasses relative to C₄ xeric grasses with increasing altitude. Very similar FI values in the upper Btos horizon (the Unit 4A-3F transition) at both sites suggest that more widespread opening of wooded savanna vegetation (at least across the lower slopes of Eburru) could have occurred at the transition between Phase III and Phase IV material.

6.8.5.3.6 Pedogenic and post-depositional processes in PS5: Palaeoenvironmental and palaeoclimatic interpretations

High Al values in PS5 suggest that residual accumulations of Al in highly crystalline material occurred under tropical climate conditions (i.e. latosolization took place after initial illuvial laterization) over several thousand years (Fanning and Fanning 1989). Increases in Base cation concentrations in PS5 are also likely to reflect the presence of more ordered, highly crystalline material or small fragments of unweathered primary volcanic material in the sediment matrix. For this reason, the Base loss ratio is not though to be informative in this palaeosol.

Well-developed hydromorphic and redox features in the Btsmb5 and the Btsob5 horizons (e.g. drab haloes, clay coatings on peds, and low chroma mottling of matrix material) indicate a hydrological shift that occurred during and possibly after pedogenesis. Clay desiccation cracks in fissures, clay coating on peds, and infilling of root and desiccation cracks with fine material (possibly tephra) are consistent with shrink-swell processes caused by wetting and drying of smectite in Vertisols (e.g. Beverly et al., 2015a; Lukens et al., 2017). The Btsob-5 horizons shares pedofacies (e.g. nut-shaped peds with gradual structure and shiny clay coatings [probably Fe oxides], a deep profile and deep rooting) with modern Nitisols of East African highland areas developing on trachytes and rhyolites. These Nitisols, that have kaolinite and 2:1 phyllosilicates, develop in tropical environments due to seasonal wetting and drying cycles (e.g. Retallack and Germán-Heins, 1994; Jacobs et al., 2005). However, clay content in this horizon is much lower than in modern analogues (De Wispelaere et al., 2015). Prolonged and/or more intensive weathering is reflected in the low Si values and high values of Fe, Al and Ti. This suggests alteration to more ordered mineral phases occurred in PS5, that is also reflected in the mirroring of Base cations and alkaline elements. Mirroring of these groups also means that Base loss weathering ratio is not applicable to this palaeosol. Given the inferred high base status of the soil and the presence of chemically unstable volcanic grains, this horizon can be described as eutric (Mack et al., 1993). Evidence for strong shrinkswell activity in these horizons make it likely that total element concentrations in PS5 represent intermixing of highly crystalline smectite clays (e.g. illite, montmorillonite) or chlorite clays with others

clay minerals, such as kaolinite (Nash et al., 1988). Complex mixtures of clay minerals in these horizons is consistent with weathering of more varied, multi-component parent material (i.e. containing volcanic glass and accidental lithics of trachyte, and highly felsic obsidian). It is also possible that elevated Fe and Al values indicate the presence of ferrihydrite but are more likely to be more stable iron and oxyhydroxide minerals (e.g. goethite, hematite and gibbsite), that often occur in kalolinite-dominated soils (Tardy et al., 1990; Sheldon and Tabor, 2009).

Both Unit 5 and 4 shows signs of well-developed redox features and similar geochemical values. The colour difference between these horizons (i.e. the rubification and lateritic appearance of Unit 4 and bleached appearance of Unit 5) and the presence of clay desiccation cracks in fissures in Unit 5 is attributed to changes in soil saturation with depth and the higher lithic content in Unit 4, rather than representing separate stages of soil formation (i.e. a pedocomplex). This is supported by the gradual contact between these horizons and reductions in all major elements (indicating a leaching zone) at the transition between Units 4 and 5. Drab hues and haloes, localised belching, cementation and low chroma mottling of matrix material and of clay infilling fissure (wetting fronts), points to gleying and periodic cessation of Bt formation. These features are interpreted as forming in one or more phases, in which there were prolonged periods of sediment saturation (ground water table rise) in Unit 5. These features occur in contrast to more seasonal indicators of wetting and drying cycles in Unit 4. When compared to the more cemented argillic Btsm horizon of Unit 5, ferralic properties in the relatively less cemented and more permeable Unit 4 suggests that periodic episaturation (perching of the water table) of this unit has occurred. Hydromorphic clay features in Unit 5 are also likely to be related to phreatic processes (i.e. subsurface groundwater flows) associated with large water-conducting pores (Vepraskas et al., 2012). Similar vertic features (e.g. curved vertic features, concave slickenslide or polygonal fractures) are often associated with wetland gilgai micro-relief in Africa (e.g. Beverly et al., 2015a; Diaz et al., 2016). However, in the case of PS5, the hummocky subsurface microtopography of clay features is more likely to reflect deformation due to tree rooting (as considered in Appendix 6.3.5), that may be localised at Locality I. In this case the spacing of clay bands/fissures could indicate the upwards migration of the water table and formation of these features at different depths over time. Vertically orientated root traces in Unit 5 (Btsm horizon) suggest that sediments were not cemented during the earlier phases of pedogenesis as roots would be expected to run horizontally to indurated surfaces (Retallack, 2008). Higher bulk density in similarly cemented/indurated horizons (e.g. fragipans) is often associated with shrink swell processes (Bryant, 1898).

Vertic features are present in Unit 5 but PS5 does not have decimeter scale desiccation cracks, wedgeshaped peds, clastic dikes or slickenslides characteristic of Vertisols, that usually develop under arid climate conditions. This supports the idea that PS5 formed under semi-arid or semi-humid conditions, not entirely dissimilar to present day conditions in the Nakuru-Naivasha Basin. This interpretation is further supported by the phytolith assemblage which indicates mesic wooded savannah vegetation with a minor xeric C₄ grass component. Root traces <5 mm wide indicate the growth of herbaceous plants in PS5, and drab haloes and root traces ~1 cm wide, penetrating to ~1m, are consistent with woody vegetation (Retallack, 2008). However, it is unclear if drab halo root traces have preserved their original dimensions. The co-occurrence of small and larger root impressions also supports phytolith-based interpretations that a wooded grassland environment was the main vegetation type of PS5. More detailed clay mineralogy is necessary to establish the precise extent of weathering in PS5. Nevertheless, Luvisols developed on pumice deposits under similar climate conditions as those inferred for PS5, have been shown to have a pedogenesis lasting more than 10,000 years (Solleiro-Rebolledo et al., 2015). Consequently, the formation of PS5 has the potential to have occurred under a range of different climatic conditions.

6.8.5.3.7 Site formation processes: Palaeosol 5

Geochemical and phytolith results from PS5 indicate that pedogenesis occurred under intermediate humid to sub-humid conditions over multiple millennia. Like PS1 but with a longer or more intense dry season. A preliminary model of site formation for PS5 base on existing evidence is proposed in Figure 6.45).



Figure 6.45 Palaeosol formation model for Palaeosol 5. Note: Inferred changes in vegetation may have also been influenced by other factors (e.g. changes in pCO_2). These were not included in the model due to the lack of dates from the sequence from which comparisons can be made to independent climate records.

6.8.6 Termination of the Prospect Farm sequence and Palaeosol 6

The lower most ~1.2 m of Unit 3 sediment (Units 3F-3D), containing very sporadic Phase IV LSA artefacts, represent the final phase of the Prospect Farm formation sediments. Sediments of Unit 3 are interpreted as a unpedogenised, poorly stratified, sub-aerial pyroclastic flow deposit; that has undergone only incipient weathering and minor reworking. Artefact percentages and densities recorded by Anthony (1978) are extremely low (see Figure 6.6) and are likely to have been sporadically incorporated into this unit during deposition of underlying Unit 4 ash. (see Appendix 6.5 for a more detailed account of theses deposits).

The remaining ~1.4 meters of the excavated trenches (Units 3C-1A) contain artefacts of the cultures that occupied the site during the LGIT and Holocene, and possibly during the LGM, but do not belong to the Prospect Farm Formation. Unit 3A/2 sediments are dated to between ~32 to ~10 ka via obsidian hydration and ¹⁴C samples (that show a number of age reversal [see Appendix 5, Table 5.1]). A younger phase of late Holocene soil formation (Unit 1) is also present which continues today. As these phases do not belong to the Prospect Farm sequence, they are not discussed in detail here. However, phytolith signals from a limited number of samples (No. 1a and 2a) suggest a vegetation signal with conditions not dissimilar to those hypothesized for PS2, PS4 and PS5, but with signs that this phytolith signal is likely to be affected by sediment mixing.

6.9 Future work

Ongoing micromorphological, mineralogical (by XRD), χ studies and ⁴⁰Ar/³⁹Ar dating, currently being completed by other INAP members, are expected to augment trends in major element geochemistry that will help to clarify weathering processes and their intensity, drainage conditions, taphonomic influences and climatic conditions during the formation, diagenetic processes and post-depositional alternation of palaeosol, as well as the timing of palaeoenvironmental changes. Ultimately this will improve soil characterizations and refining putative soil classifications and interpretations of palaeoenvironmental change throughout the Prospect Farm sequence. For detailed descriptions of ongoing and proposed future work see (Appendix 6.4.1 to 6.4.3).

6.10 Chapter summary

Results of geoarchaeological and phytolith-based vegetation reconstructions for the Prospect Farm sequence were presented. Findings indicate that there was considerable variability in the type of vegetation present at the site during different occupation phases in the past, but also that several factors hinder some aspects of vegetation reconstructions. These include: a current lack of dates for the site, the low temporal-stratigraphic resolution of palaeosols, and in cases the limited spatial resolution of sampling. Site formation processes and palaeovegetation changes are summarised for each occupation phase/palaeosol in Table 6.8.

Archaeological occupation phases (from oldest to youngest)	Related palaeosols	Palaeosol type classifications and dominant formation process and prevailing paleoclimate	Phytolith-based interpretation of palaeovegetation
Phase I (earliest MSA)	PS1	Ferric Acrisol or Ferric Alisol with some hydromorphic properties formed due to weathering of volcanic tuff under humid climate conditions (with a long and/or intense wet season	Closed-canopy Afromontane forest with a C ₃ grass understory
Phase II-A (MSA)	PS2	Poorly-developed Andosol with albic and argillic horizons and weak ferric properties formed due to incipient weathering of volcanic tuff under semi-humid conditions (with a wet and dry season of a similar length but in which aridity in dry season was not intense)	Mesic C ₄ dominated grassland (savanna) environment with limit arboreal cover
Phase II-B (MSA)	PS3	Poorly-developed vitric Andosol formed due to incipient weathering of pumice and tuff deposits under intermediate sub-humid to semi-arid conditions (where the dry and wet season were of a similar and intensity)	Edaphic wooded grassland (savanna very low arboreal cover)
Phase II-C (MSA)	PS4	Tephric (vitric) Cambisol formed due to incipient weathering of tuff deposits under intermediate sub- humid to semi-arid conditions (where the dry season was intermittently either longer or more intense that the wet season)	Transitional shrub savanna with possible fluctuation occurring between moderate to low arboreal cover
Phase III (final MSA)	PS5	Well-developed cambric Luvisol with ferralic properties formed due to weathering of thin foot slope volcanic lahar/colluvial deposits under semi-humid to semi-arid climate conditions (where the rainy season was longer and/or more intense that the dry season)	Transitional shrub savanna/woodland with moderate arboreal cover
Phase IV (MSA- LSA 'transitional' industry)	PS5	Well-developed cambric Luvisol with ferralic properties formed due to weathering of thin foot slope volcanic lahar/colluvial deposits under semi-humid to semi-arid climate conditions (it is possible that the rainy season became less intense than it was during the deposition of Phase III material)	Transitional shrub savanna/woodland, possibly with lower arboreal cover than is associated with Phase III material

Table 6.8 Summary of the relationship between occupation phases and associated episodes/related processes of palaeosol formation and local palaeovegetation reconstructions.

Chapter 7 summarizes interpretations of the environmental and climatic changes and major trends at the site in the context of the likely cliamtic pahse to which they belong. It also addresses the utility of the data in its current form to address the aims and objectives of this thesis (i.e. testing of evolutionary geographic models and the environmental setting of the MSA-LSA transition at the site). Limitations of the approach adopted here are also highlighted in Chapter 7 and Appendix 6.4.1 to 6.4.3.

Chapter 7 Discussion and conclusions

7.1 Introduction

Chapter 7 summarises and discusses the archaeological stratigraphy, depositional environments, weathering trends, and palaeoenvironmental changes in the Prospect Farm sequence. The discussion first focuses on the utility of the data generated to achieve the main objectives of this thesis (set out in Chapter 1.9.3). This includes extrapolations of generalised past vegetation distributions on Mt. Eburru to the rest of the Nakuru-Naivasha Basin and hypothesised vegetation-climate relationships (i.e to which MIS or MIS and/or MIS sub-stage each occupation phase and palaeosol is most likely to correspond). Secondly, it considers the implications of these habitat reconstructions and the available archaeological data for the central target of this thesis: to evaluate competing behavioural-ecological models of early modern human adaptations to past environmental change in highland areas of East Africa, and the environmental context of the MSA-LSA transition at Prospect Farm. Where ongoing and future work could improve interpretations, this is highlighted.

7.2 Depositional environments, palaeosol formation and weathering trends

The goal of Objective no. 1 was to develop site formation models for Prospect Farm and to identify the depositional processes and taphonomic biases that affect interpretations of the pedostratigraphy, archaeological stratigraphy, and phytolith assemblage. Overall, Objective 1 was accomplished. The results of geoarchaeological analysis of the Prospect Farm sequence indicated a pedostratigraphic framework consisting of a succession of palaeosols that developed from volcanic airfall material. Each palaeosol forming interval appears to follow a similar trend of soil development due to weathering of volcanic parent material and an associated vegetation succession. Vegetation presumably initially developed on largely unvegetated post-eruption land surface into vegetation communities, that then became established in reached an equilibrium with the prevailing climate. All soils then experienced partial erosion and burial by a subsequent stage of vocalic activity. While, the duration of palaeosol formation is variable, palaeosol development and associated occupation phases are interpreted as approximating the main MIS of the last interglacial-glacial cycle (MIS 5e – MIS 2), as will be discussed in Sections 7.4.1 - 7.4.1.1.2.

Within the palaeosol sequence the partial erosion of the upper soil horizons, as well as post-burial compaction and cementation, were recorded. Truncated palaeosol profiles, created as a result of high energy processes (e.g. pyroclastic- and lava-flows), have been observed in volcanic-palaeosol sequences elsewhere in East Africa (e.g. Graef et al., 1997; Claessens et al., 2016). This suggests the erosive capacity of sub-aerial density flow currents recorded in Prospect Farm sediments was strong enough to remove top layers of the palaeosols upon deposition, as recorded in volcanic palaeosols from other areas of the tropics (e.g. Solleiro-Rebolledo et al., 2015). Like other African MSA palaeosol sequences (e.g. Wright et al., 2017), laterization of sediments under tropical rainfall regimes have contributed to the formation of acidic soils and degradation of organic deposits and 'A' horizons in the Prospect Farm sequence.

Pedofeatures associated with pre-burial palaeosol formation (e.g. root traces, iron nodule formation, and clay coatings) are moderately well-preserved. All the palaeosols at Prospect Farm also show signs of various post-burial alteration effects (i.e. overprinting by diagenetic processes such as hematization, carbonisation, and illuviation). Results of sedimentological and geochemical analysis made it possible to make qualitative assessments of variation in the intensity and duration of weathering, as well as the prevailing climate conditions during the formation of palaeosols in the Prospect Farm sequence. Pedofeatures and phytolith analysis also suggest that indicators of increased chemical weathering correspond to forested/wooded habitats and humid climate conditions, during which palaeosol development was uninterrupted for long periods. Significant variability in the extent of weathering is visible between buried palaeosols with similar permeabilities in the Prospect Farm sequence. Furthermore, no simple relationship exists between the temporal-stratigraphic position of palaeosols and increased weathering (i.e. older palaeosols at the base of the sequence are not more weathered than those younger soils recorded above). These findings suggest that post-burial recharge through meteoric groundwater is not the only weathering process that affected the sequence. This contradicts Anthony (1978), who suggested that the degree of weathering in different strata is solely the result of postdepositional alteration following burial. Anthony viewed this process as being controlled by the clay content of the overlying strata, that creates differences in permeability and temporary water tables throughout the sequences. Instead, this appears to be only one of several mechanisms controlling palaeosol formation and indicates that weathering occurred when currently buried palaeosols were still exposed on the landscape. This is further supported by the agreement between palaeosol vegetation signals and the degree of individual palaeosol development. For example, poorly developed soils with minimal signs of alteration tend to support grassland communities. On the other hand, well-developed soils with signs of weathering, commonly observed in modern soils developing in humid forest (e.g. iron nodules), are associated with forest indicator phytoliths. Sedimentology, distributions and concentrations of artefacts and phytoliths in the Prospect Farm sequence suggest that while truncation of palaeosols did occur at points, due to volcanic processes, overall low energy slope processes have resulted in only minor post-depositional reworking of deposits. As such, the stratigraphic coherence of the deposits has not been significantly affected by taphonomic processes. Furthermore, the lateral continuity of deposits in the Prospect Farm Formation means that local palaeogeography (palaeotopography and vegetation distributions) were able to be inferred.

While artefacts are more highly concentrated in the upper horizons of palaeosols, they are not strictly vertically constrained to levels that could be defined as a 'floor', except in the case of Palaeosol 3. Relatedly, the signal of vegetation changes in a given palaeosol throughout the duration of its formation and existence as a former land surface before its burial by a volcanic event is a polygenic one. When this fact is considered in combination with observations that lithics are widely dispersed throughout the upper horizons of a given palaeosol, it becomes difficult to say precisely at what point during the course of a palaeosol's formation and related vegetation succession that hominins were present at the site (i.e. if they were present when the landscape was largely unvegetated following eruption, or if they only visited

the site when vegetation became well-established). Interpreting hominin occupation of the site is more problematic for palaeosols which encompass multiple millennia, in which vegetation communities have longer to develop, and within which vegetation shifts may have occurred. For example, in the forested environments of PS1, where closed-canopy forest became established but may also have undergone a subtle shift back to slightly more open forest conditions before it burial, it is difficult to say in which vegetation setting hominin occupation occurred or was more intense. In shorter-lived palaeosols where only incipient soil formation has taken place before burial (e.g. in PS3 where a strong xeric grassland signal is present in all samples), we can say with greater confidence that hominins lived in this type of habitat. When we turn our focus to the differences in palaeovegetation between palaeosols in the sequence then boarder inferences about the differences in the habitats that hominins inhabited are more easily made. For example, we can say that hominins inhabited a landscape of forest/woodland with high arboreal cover associated with the former land surface of PS1 (Phase I), whereas hominins inhabited the landscape of open xeric grassland associated with the former land surface of PS3 (Phase II-B).

While no stratigraphic break was recorded between Phase III MSA and Phase IV 'transitional' assemblages in PS5, ongoing micromorphological and lithic orientation analyses are expected to refine our understanding of this depositional environment, and the relationship between these assemblages. Results of artefact occurrences from Locality I, have been used to update the archaeological stratigraphy proposed by Anthony (1978). The updated scheme (see Chapter 6.3) reflects findings that archaeological material at the transition from Units 6 to 5 in fact originates from Unit 7A (see Chapter 6.8.4.4.1). Whether or not this material (re-designated as Phase II-C) is more similar in form to the original Phase II or Phase III material is expected to be resolved through ongoing lithic analyses.

7.3 Vegetation reconstructions from the Prospect Farm sequence

The goal of Objective 2, to develop an understanding of vegetation change at Prospect Farm, while considering geology, climatic controls and internal ecosystem dynamics, was divided into several sub-objectives.

7.3.1 Modern reference collection

The focus of Objective 2.1 was to establish if any previously undocumented, diagnostic phytoliths from ecologically informative modern plants in the Nakuru-Naivasha Basin (Afromontane phytochorion) could be used to aid palaeovegetation reconstructions. Overall findings of this study were similar to those of phytoliths from woody dicotyledons in West and eastern Tropical Africa (see Chapter 4.4), there being a high level of redundancy within this group of plants. Consequently, they were found to add little taxonomic resolution to vegetation reconstructions. This study was able to establish that several families of herbaceous dicotyledons and monocotyledons (typically understory and forest margin plants) tend to produce highly diagnostic phytoliths. However, these were identified as being more vulnerable to breakage and dissolution, which probably explains why they were not recorded in the fossil phytolith assemblage at Prospect Farm. As such, it is recommended that future work focus on phytolith extraction from living understory herbs and shrubs in the Afromontane zone. It is likely that diagnostic

morphotypes identified by this study could benefit palaeovegetation reconstructions from more recent time periods, or from depositional settings (e.g. lake sediments) that may better preserve these fragile morphotypes.

7.3.2 Comparison of fossil phytolith samples to modern phytolith samples from African vegetation types

Objective 2.2 proposed to compare fossil phytolith assemblages with modern phytolith assemblages using a reduced set of morphotypes, as well as to adjust existing phytolith indices to East African vegetation, based on phytolith-vegetation and ecological-taxonomic relationships specific to the region. Objective 2.3 focused on reconstructing the vegetation variables (e.g. vegetation distributions, composition and structure) thought to be the most important factors for understanding aspects of past human ecology (i.e. habitat preferences and mobility on the landscape).

By comparing the available fossil and modern comparative samples, using a combined generalised and index approach, it was possible to differentiate between forested palaeoenvironments with a C₃ grass understory and savanna palaeoenvironments with a C₄ grass understory. Dominance of xeric or mesic grass subfamily composition in savanna types were also able to be reconstructed. Phytolith analysis provides a semi-quantitative insight into changes in arboreal cover during different occupation phases at the site. Limitations of the comparative dataset, as well as the finding that phytoliths are a poor proxy for differentiating woody plant species/families (and thus woody vegetation communities), means that it is difficult to be more specific about the composition of woodland or dry forest vegetation communities present at the site. For example, the lack of comparative samples from vegetation subcommunities, such as Olea and Euphorbia forest, and drier undifferentiated Afromontane forest present in the Nakuru-Naivasha Basin today, means that groups of fossil samples cannot be easily assigned to a modern vegetation type. Furthermore, where fossil samples do show compositional similarities to samples from modern plant communities, the high level of overlap of phytolith signals in comparative samples from distinct savanna and forest vegetation types makes it difficult in some cases to definitively assign fossil samples to a specific vegetation type. These issues are compounded by the use of reductive phytolith categories in available published data for differentiating between modern vegetation types.

Comparing vegetation signals from the two main MSA localities at Prospect Farm provided some insight into the degree of uniformity in past vegetation at different elevations. When the polygenic nature of phytolith assemblages in palaeosols is considered, vegetation composition within the restricted altitudinal range at the site can be inferred for each occupation phase. This approach makes it possible to suggest the local habitats associated with the occupation of the site have revealed some consistent patterns (e.g. increased arboreal vegetation cover in samples taken from Locality II at a higher elevation). However, the lack of exposure of the same palaeosol horizons at higher or lower elevations that are recorded in the main Prospect Farm localities, make it difficult to infer the upper or lower limits forest and grassland vegetation bands, depending on which vegetation type is present at the localities. Furthermore, the lack of lateral exposures of palaeosol horizons recorded at Prospect Farm, at the same elevations in other areas of Mt. Eburru, make it difficult to determine whether significant lateral changes in vegetation occurred across the mountain. The low chronological resolution and polygenic signal of vegetation and climate variability from palaeosol samples at Prospect Farm and at other sites in the region (e.g. Zech et al., 2011; Beverly, et al., 2015a,b; Brandt et al., 2017), means that sub-millennial scale palaeoenvironmental changes are not resolvable in these records. Pollen-based records of Holocene vegetation distributions in the Naivasha Basin and isotope-based vegetation reconstructions from Mt. Eburru (see Chapter 3.5.4), as well as other records of recurrent environmental shifts between forest and open savanna conditions during the LGIT and Holocene in East Africa (e.g. Taylor, 1990; Marchant et al., 1997; Willis et al., 2013), act as a reminder of the rapidity with which vegetation could have changed on Mt. Eburru during the last glacial period. As palaeosols in the Prospect Farm sequence are estimated to have developed on multimillennial time scales, it is reasonable to suggest that palaeoenvironmental signals reconstructed from individual palaeosols are amalgamations that average multiple climatic and ecological shifts over time. The ability of vegetation reconstructions carried out at Prospect Farm and by other palaeoenvironmental investigations in the region to establish the relative ecological stability of sites and their roles as refugia (see Section 7.6), is limited by the fact that measurements of palaeovegetation change differ between studies. Consequently, records are often not directly comparable, and, in some cases, local drivers of change have the potential to be overrepresented (Finch et al., 2014). These problems are exacerbated in the Prospect Farm record by the limitations of low taxonomic and spatial resolution in vegetation reconstructions. In summary, the palaeovegetation reconstructions presented here are most heavily biased by temporal, followed by taxonomic, and to a lesser extent, spatial factors.

7.3.3 Palaeovegetation results from Prospect Farm as a basis for inferring wider palaeovegetation distributions in the Nakuru-Naivasha Basin

As introduced in Chapter 2.5, there are examples in the literature in modern settings of divergent responses of certain species and plant communities to local environmental factors and pressures (e.g. edaphics, herbivory, and the rain shadow effect etc.). The same is true of the long-term responses of plants and plant communities to late Quaternary climate changes that took place on East African mountains (i.e. forest ecosystems did not respond uniformly to the same external pressures). This resulted in heterogenous vegetation distributions and the existence of non-analogue plant communities in the past (e.g. Finch, 2009; Rucina et al., 2009: Zech et al., 2011; Ivory et al., 2016a). For example, during the LGM on Mt. Kenya, pollen records indicate that ericaceous zone taxa *Stoebe* and *Ericaceae* moved downslope while *Juniperus* and *Hagenia* persisted at the same altitude on the south-eastern side of the mountain (Rucina et al., 2009). This indicates that moist montane forest species continued to be present in reduced numbers here, and that Mt. Kenya acted as a refugium for these species during the LGM. However, despite these subtleties in ecosystem responses to a myriad of biotic and abiotic factors, it is also the case that modern studies and palaeovegetation reconstructions show that generalised zonation patterns have existed on equatorial East African mountains (see Chapters 2.5, 3.5.1, and

Appendix 3.4.1-3.4.2). Available palaeovegetation reconstructions also appear to show some broadly consistent patterns in vegetation responses to certain regional scale climatic trends of the last glacialinterglacial cycle (e.g. lowering of the forest belt and expansion of Afromontane heath /grassland under reduced ρCO_2 and temperatures during stadial phases [e.g. the LGM]) (see Chapter 3.5.1). As such, the presence of a vegetation type at a specific elevation can be used to suggest the presence of associated vegetation types above or below this zone, depending on the prevailing climatic conditions of the time. There are however exceptions to these trends, such as the relatively muted response of Afromontane forest in the EAM to LGM climate changes (see Chapter 3.5.2 and Appendix 3.4.1-3.4.2). Extrapolation of palaeovegetation distributions at Prospect Farm in order to suggest theoretical vegetation distributions in the rest of the Nakuru-Naivasha Basin during each occupation phase at the site is carried out in Sections 7.4.1.-7.4.1.5. These putative vegetation distributions rest on inferences about the likely MIS to which a given occupation phase plausibly belong. Links between occupation and likely coeval MIS are suggested based on a combination of existing obsidian hydration dates for the site, the character of archaeological assemblages, and broad climatic conditions inferred from palaeopedological and palaeovegetation studies. This approach has several inherent, considerable assumptions and limitations: 1) obsidian hydration dates are acknowledged as likely to be underestimations of the true age of the occupation phases; 2) Assigning archaeological phases to a specific MIS (based on the character of tool types) is inaccurate given the wide range of dates covered by the first emergence and last appearance of MSA and LSA tool kits in East Africa (see Chapter 1.3). Assigning an occupation phase to an MIS phase based on climatic conditions inferred from phytolith analysis and pedological indicators is problematic because similar vegetation distributions could result from a number of different climate scenarios (see Section 7.4). Furthermore, this approach is open to problems of circular reasoning. For example, assigning PS5 (Phase I) to an interstadial or interglacial period, based on indicators of semi-humid and semi-closed forest conditions during its formation and similar conditions being present on adjacent mountains during these periods, may be erroneous if in fact the Nakuru-Naivasha Basin responded differently to prevailing climate conditions and supported these conditions during stadial periods.

While the phytolith record provides some insight into the lack of influence of fire on vegetation changes at Prospect Farm, it is clear that the current lack of chronological control for the sequence somewhat undermines our ability to use global (e.g. pCO_2), regional (e.g. SSTs), and local records of palaeoenvironmental change (e.g. the Naivasha Lake level curve) to identify the main factors driving vegetation change at the site (Objective 2.5). This also limits our ability to determine if the Nakuru-Naivasha Basin responded differently than other sites in East Africa to overarching regional late Quaternary climate changes (Objective 2.4) (see Section 7.4.1.5). The lack of temporal control also somewhat negatively affects our ability to assess the capacity of the Nakuru-Naivasha Basin to have acted as a refugium for humans, and to determine regional connections with other archaeological sites (Objective 3) (discussed in Section 7.6), and whether the region acted as a 'pivot'; connecting different regions within a refugium network, as introduced in Chapter 1.6.1.1. This being said, it is also apparent

that assigning a palaeosols to a certain MIS and its associated climatic conditions in East Africa is more readily resolvable for some occupation phases rather than for others. For example, the linking PS5 (Phase III) to MIS 3 is not contentious, given the agreement between multiple lines of evidence that it belongs to this phase (e.g. that it shares a palaeoenvironmental signal with other montane vegetation records in the region from this stage, and both the character of the lithic assemblage and associated OH dates point to this period).

The absence of an age model for the site that would facilitate comparison with wider palaeoenvironmental records means that putative vegetation distributions presented in Section 7.4.1 on a palaeosol by palaeosol basis, are to some extent subject to equifinality and uncertainty. As such, these models and models of human adaptations to the environment of the Nakuru-Naivasha Basin (see Section 7.5) are best considered as working hypotheses (presenting likely alternative vegetation scenarios based on current evidence), that can be reconsidered once ongoing ⁴⁰Ar/³⁹Ar analysis for the sequence is completed. As such, each palaeosol and its associated vegetation signal can be thought of as a series of more or less probable or readily resolvable scenarios in terms of their age and the climatic factors which shaped them. Consequently, in some cases these links are used to conditionally suggest when the basin was most likely to have acted as a refugium for human groups. Confidence in these extrapolations to suggest vegetation distributions in the Nakuru-Naivasha Basin could be improved by additional sampling of lateral exposures of palaeosol horizon across the Prospect Farm formation, as well as at other MSA sites in the basin (e.g. Marmonet Drift [Slater, 2016]) that are likely to be of a similar age to Prospect Farm. The lack of exposure of the Prospect Farm sequence at higher or lower elevations on Mt. Eburru, as well as the deep burial of older sediments in the sequence, would require a large-scale excavation campaign to be undertaken to expose these deposits at other sites across the formation. More complete palaeovegetation reconstructions for the entire basin are also highly dependent on the dating of Prospect Farm, as well as other sites in the basin, and their integration into a chronostratigraphic framework. Suggestions of how future research may help to resolved some of these issues are outline in Appendix 7.1.

7.4 Timing and drivers of vegetation change at Prospect Farm, comparisons to local and regional archaeological and palaeoenvironmental records, and extrapolation of local vegetation reconstructions to the rest of the Nakuru-Naivasha Basin

As introduced in Section 7.3.3, the current lack of chronostratigraphic control for the Prospect Farm sequence means that Objective 2.4 (to compare vegetation change over time at Prospect Farm to local and wider palaeoenvironmental records) and Objective 2.5 (to identify and quantify drivers of vegetation changes in the Prospect Farm sequence through comparison to global, regional and local records) cannot be fully addressed at the time of writing. Despite the limitations imposed on our present ability to discern the main drivers of vegetation change in the Prospect Farm sequence, phytolith-based records do indicate that fire frequency was low on the lower slopes of Mt. Eburru and also that volcanism resulted in rapid vegetation change through destruction of existing plant communities. Consequently,

hypothesised alternative vegetation scenarios presented in Section 7.4.1 are most likely to be those in which past fire frequency was low or in which the effect of fire on vegetation was limited by feedbacks between other factors.

Section 7.4.1 proposes theoretical vegetation distributions on the watershed of Mt. Eburru, associated climatic conditions, and internal vegetation feedbacks for each occupation phase in the Prospect Farm sequence. Models of changes in environmental gradients that infer the positioning and steepness of ecotones are based on palaeovegetation and palaeoclimatic (seasonality, rainfall and temperature) conditions inferred from phytolith assemblages and palaeosol features. These are in turn guided by vegetation distributions and various associated vegetation-climate relationships, that have been proposed by other studies of multiple East African mountains during the late Quaternary period. Palaeovegetation and palaeoclimate records from Mt. Kenya, covering altitudes ranging from 1820 m a.s.l to 4595 m a.s.l. (Ficken et al., 1998; Olago et al., 1999; Huang et al., 1999; Wooller et al., 2000; Ficken et al., 2002; Wooller et al., 2003; Street-Perrott et al. 2004, 2007; Rucina et al., 2009), as well as and from Mt. Kilimanjaro, covering altitudes ranging from 1700 m a.s.l to 2800m a.s.l (Zech et al., 2011; Schüler et al., 2012), provide information on the shifts to the upper and lower boundaries of Afromontane forest and associated vegetation types during the last glacial period and Holocene. Further insights into shifts in the savannaforest interface are drawn from mid-low elevations (840 m a.s.l.) archives at Lake Challa (Sinninghe Damsté et al., 2011; van Geel et al., 2011; Nelson et al., 2012; Urban et al., 2015) and Lake Tanganyika (Tierney et al., 2010; Ivory and Russel, 2016) (see Chapter 3.5.2 and Appendix 3.4.1-3.4.2). These records, which have been subject to the same or analogous regional climate trends, act as a baseline for interpreting palaeovegetation changes in the Prospect Farm sequence.

7.4.1 Theoretical models of vegetation distributions at Prospect Farm and in the Nakuru-Naivasha Basin

Figure 7.1 provides idealised conceptual models of hypothetical changes in elevational vegetation zonation on Mt. Eburru (and by extension in the Nakuru-Naivasha Basin) under different climatic scenarios and considers different interactions between internal ecosystem parameters. This is intended to show how similar vegetation distributions could occur under different climatic conditions and modes of local climate-ecosystem balance. The most probable climatic stage and vegetation-climate scenario is suggested for each palaeosol and associated occupation phase in the Prospect Farm sequence, based on the available evidence.

7.4.1.1 Theoretical age and vegetation distributions: Palaeosol 1

PS1 is interpreted as having supported Afromontane forest vegetation, formed under semi-humid to humid climatic conditions with a strong wet season and hydromorphic pedogenetic conditions (see Chapter 6.8.1.4.6). Modern and palaeovegetation distributions on East African mountains suggest that Afromontane forest could have existed at the elevation of Prospect Farm (2100-2140 m a.s.l.) under different climatic states. The most probable scenario is that PS1 developed during a humid interval of

the penultimate or last interglacial (e.g. MIS 5e or MIS 7a [similar to the more recent African Humid Period {AHP}). It is unclear if OH dates systematically over- or underestimated ages of occupation phases in the Prospect Farm sequence. An age of ~120 ka associated with Phase III can be tentatively used to suggest a minimum age for underlying deposits. The associations made between MSA artefacts from PS1 and South African Stillbay industries by Anthony (1967, 1972, 1978) require further testing. However, assuming that Phase I material has aspects of both earlier MSA and some traits of Stillbay (e.g. bifacially retouched points), then the age of PS1 is more likely to be closer to MIS 5e than to MIS 7a.

7.4.1.1.1 Palaeoclimatic trends in equatorial East Africa during MIS 5 in relation to palaeovegetation reconstructions from PS1

Records across the region during MIS 5 (see Figure 7.2), indicate that high lake levels were common with lake highstands recorded in Lake Naivasha sediments during MIS 5e and 5d (see Chapter 3.4). During these intervals, elevated rainfall and pCO_2 are hypothesised to have tipped the competitive advantage of C₃ woody plants vs. C₄ grasses in favour of forest vegetation; allowing Afromontane forest to move downslope to elevations lower than are projected for the site under present-day climate conditions free from the influence of anthropic vegetation disturbances (see idealised model [E] in Figure 7.1). Under present day (interglacial) pCO2 levels, the change in dominance of C₃ over C₄ Poaceae subfamilies occurs at between 21°- 25° C (Ehleringer et al., 1997). As discussed in Chapter 6.8.1.4.4, the strongest evidence for fire in the local area in the Prospect Farm sequence comes from PS1. However, the occurrence of burnt phytoliths is still far too low to infer that frequent high intensity fires affected vegetation at the site. These results are consistent with climate and internal feedbacks in forest limiting fire (i.e. MAP exceeded 1500 mm) (see Chapter 2.7).

7.4.1.1.2 Palaeovegetation trends in the Afromontane zone in equatorial East Africa during MIS 5 in relation to palaeovegetation reconstructions from PS1

No vegetation records from East Africa currently cover humid intervals of the last interglacial period. However, palaeoclimatic records and models suggest widespread warm and humid conditions occurred across the region (see Chapter 3, Figure 3.2). On nearby Mt. Kenya, pollen and isotope records capture the last interglacial-glacial transition (115 to 110 kyr BP), where slightly drier conditions, cooler than today, and lower pCO_2 , have been inferred (see Figure 7.2 [P]) (Olago et al., 1999). This record indicates that the savanna forest ecotone, with a strong C₃ woody component, present around Sacred Lake (2350 m a.s.l.) today, was at this time higher upslope (by ~350 m). This suggest that forest vegetation at lower altitudes on Mt. Eburru (2100-2140 m a.s.l.) were likely to have occurred under moister climate conditions than today. These vegetation distributions are supported by mass-balance models of the predicted forest expansion ~135 kyr BP (MIS 6-MIS 5e transition) in the Nakuru-Naivasha Basin (Bergner et al., 2003), and pollen- and isotope-base models of forest expansion during Holocene lake high stand events, occurring at 17 ka, 15 ka, and 9.5 ka (Maitama, 1991; Ambrose and Sikes, 1991; Lamb et al., 2003; and summarised in Appendix 3.6). Palaeoenvironmental records across eastern Africa indicate that during arid periods of the last glacial cycle (e.g. the LGM), the elevational range of the Afromontane forest belt contracted and shifted to lower altitudes. This was generally accompanied by ericaceous zone vegetation

expansion at higher elevations and C₄ grassland expansion at lower elevations (see Chapter 3.5.1, 3.5.2 and Appendix 3.4.1-3.4.2). Records from Mt. Kilimanjaro suggest that during drier periods savanna vegetation expanded at lower elevations (840 m a.s.l.) (Urban et al., 2015) and moved upslope by at least 600 m (from 1400 to 2000 m a.s.l.) in some areas (Zech et al., 2011). Phytolith results suggest that it is unlikely that vegetation distributions inferred for PS1 occurred under similarly arid climate conditions. Slightly more open conditions inferred from phytoliths in the upper samples of PS1 could relate to either a climatic shift and/or to non-linear internal ecosystem interactions, that brought threshold behaviour into effect, and in which shifts between vegetation states, from open to closed conditions occurred (see Tierney et al., 2010; Ivory and Russell, 2016). See Tierney et al., (2010); Burrough and Willis, (2013) and Ivory and Russell, (2016) for examples of how internal ecosystem dynamics have influenced past forest communities in Tropical Africa.

An alternative scenario is that forest vegetation recorded in PS1 was present under cooler but still relatively humid conditions during an interstadial period of the last glacial cycle (e.g. MIS 3) (see idealised model in Figure 7.1 [B] 'Interstadial 2'). As previously mentioned, at present it is only possible to suggest the most likely vegetation-climate feedback relationships from several hypothetical scenarios based on relationships observed in published studies of vegetation distributions at Prospect Farm. The absence of dates for the Prospect Farm sequence means it is difficult to assess if the expansion of forest at lower elevations on Mt. Eburru at Prospect Farm reflects contraction and downwards migration of the forest belt, under lower pCO_2 levels during stadial or interstadial periods of the last glacial cycle, or under elevated pCO_2 levels during the last interglacial period (i.e. [B] 'Interstadial 2', or [E] 'AHP' Figure 7.1). Palaeovegetation signals, palaeosol properties, and estimates of the time taken for the formation of the remaining palaeosols in the Prospect Farm sequence (PS2-PS5), are more consistent with their formation having occurred during cooler, semi-humid or arid conditions over the last glacial period (see Sections 7.4.1.2-7.4.1.5). As such, PS1 is more likely to have formed during MIS 5e than during MIS 5d-a or 3. However, in the absence of dates from the site, the possibility that Mt. Eburru may not follow vegetationclimate trends observed on other mountains in the region during the later Quaternary period cannot be entirely ruled out. East African palaeoclimate trends during MIS 3 are discussed in more detail in relation to vegetation reconstructions from PS4 and PS5 (see Section 7.4.1.4), that are thought to be more likely to have formed during this marine isotope stage.



Figure 7.1 Simplified hypothetical models of the impact of abiotic (fire, rainfall and pCO_2) and biotic (megaherbivore browsing) on vegetation in the Nakuru-Naivasha Basin at selected time slices over a glacial-interglacial cycle, as well as the hypothesised feedback relationships between them. Arrows show the magnitude of change in parameters relative to the preceding climatic phases (e.g. slightly increased rainfall in A and B reflect inferred slightly higher rainfall during MIS 3 than in MIS 4 [not shown] which precedes it). Variation in vegetation zonation during a climatic stage, due to changes in one or more parameters, are represented by two alternative models (e.g. models A and B represent different vegetation distributions that could have occurred during MIS 5d-a or MIS3).

A) Interstadial period [1] (e.g. MIS 5d-a or 3): Rainfall was moderately low (~800 - 650 mm MAP), but higher relative to the preceding stadial. This, as well as slightly increased temperatures, is modelled initially to have encouraged woody growth. In time fire frequency increased due to more ignition sources provided by slightly higher rainfall, increasing biomass for burning. These factors combined with low pCO_2 and increased megaherbivore browsing to increase grass %, causing forest to contract (sensu Tierney et al., 2010; Ivory and Russell, 2016). These interactions could be further accentuated through weathering regimes (Ivory et al., 2016b). As such, a small change in climate could lead to a large change in vegetation via feedback mechanisms. The feedback between megaherbivore density and grass % was initially positive (i.e. if forest was opened enough by the combined effect of browsing and fire, plant species richness and thus herbivore density would be expected to increase). However, over time, assuming no major climatic change, more open conditions would allow rainfall and fire to exert stronger pressure on forest vegetation, leading to fewer trees and bamboo, and in turn reducing megaherbivore numbers in the area (producing a negative feedback). It is also possible that slightly higher temperatures and rainfall during MIS 3, relative to MIS 4, could have contributed to vegetation openness and heterogeneity though temperature-induced water stress and the promotion of fire tolerant taxa (Dupont et al., 2011; Ivory et al., 2016a). This is expected to have resulted in non-analogue vegetation communities (e.g. Gill et al., 2013; Ivory and Russel, 2016).

B) Interstadial period [2] (e.g. MIS 5d-a or 3): Change in a single factor, in this case fewer megaherbivores, is modelled to have resulted in decreased degradation of forest and woodland vegetation (i.e. canopy conditions remain relatively closed). This in turn is expected to have limited the effects of fire (i.e. internal buffering of forest occurs as it collects moisture in the highlands, while lower elevations are more arid). This is likely to have allowed contracted forest to remain even under lower rainfall and pCO_2 conditions. In this scenario, over time and with the absence of major internal disturbances (as in scenario A) and MAP above ~650 mm (Sankaran et al., 2005), a positive feedback would develop between forest vegetation and hydroclimate; in which vegetation change was gradual and hydrological change was rapid (Tierney et al., 2010). In this scenario, ecosystem threshold behaviour may have been active (i.e. rapid reversals between forest and more open wooded conditions would occur once gradual changes in pCO_2 , temperature, precipitation, and fire levels reached the tipping point, which then once again favoured drier, more open-woodland taxa). This represents the establishment of equilibrium between available moisture and C₃ plant composition (Shanahan et al., 2016). In turn this would have affected hydroclimate through water retention and albedo etc., and potentially contributed to accelerating climatic shifts (Tierney et al., 2010; Ivory and Russell, 2016).

C) Last Glacial Maximum [1]: Low pCO_2 , rainfall, and increased length of the dry season is modelled to have increased moisture stress and fire frequency- driving vegetation openness and expansion of C₄ grassland at lower elevations and C₃ and/or C₄ grassland at higher elevations. The range of Afromontane forest was greatly reduced and shifted to lower elevations. Increased frequency of fire at higher elevations is expected also to have led to the expansion of fire-tolerant taxa (e.g. Hagenia abyssinica) and of the ericaceous belt at the upper timberline (e.g. Rucina et al., 2009). The regenerative stability of forest was reduced to the extent that a positive feedback between fire and other factors, such as increased albedo, higher run-off, increased aridity, and nutrient deficiency (that favoured alpine grass expansion), was established. In this scenario fire became a major driver in maintaining grassland during the LGM (e.g. Wooller et al., 2000; 2003). In this case, as lowland areas of the rift have a higher precipitation/evaporation ratio, highland areas could have acted as 'water towers'; trapping moisture through occult precipitation and relief rainfall (Marchant et al., 2007). This created a threshold mechanism; in which rivers continued to be recharged, sustaining higher lake levels for a short period. Over time, a combination of enhanced moisture stress and lower pCO_2 , compounded via a positive feedback with fire, could have led to the expansion of C₄ grasses at low elevations, and ericaceous belt vegetation at higher elevations. This would have eventually reached a threshold at which the ability of Afromontane forests to collect moisture and transfer it to the lowlands would become sufficiently impeded, to lower lake levels, eacerbating arid conditions until a shift in climate occurred (i.e. during the climatic amelioration of the Holocene). Today rainfall at lower elevations in the Nakuru-Naivasha Basin is ~700- 600 mm MAP (see Chapter 2.3). On sub-millennial timescales, if MAP were t

D) Last Glacial Maximum [2]: Rainfall was reduced but was relatively higher than in LGM scenario [1] because of a more stable supply of moisture from the Indian Ocean. Aridity and low pCO_2 are modelled to have still limit C_3 woody growth but to a lesser extent than in LGM scenario [1].

Base image adapted from https://www.bbc.com/bitesize



Figure 7.1 (continued)

E) Interglacial humid period (e.g. the AHP, MIS 5e or MIS7a). High rainfall and high pCO_2 is modelled tas having promoted the expansions of woody C₃ vegetation. Rainfall > 800 mm MAP and a shortened dry season limited fire, as there was less time for grasses to dry and fuel fire and less potential for ignition. Closed canopy conditions and lower fire further suppressed C₄ grass expansion through biophysical feedback loops (e.g. by increasing shading and lowering temperature [see Chapter 2.8]). Threshold behaviour may have occured in such forest ecosystems in response to increased aridity (i.e. the effect of pCO_2 in stabilising these systems is reduced, causing rapid collapse and reversals to more open wooded or savanna conditions (Shanahan et al., 2016).

F) Interglacial arid phase (e.g. the Mid-Holocene dry phase) [1]: Moderately reduced rainfall, increased temperature and pCO_2 is modelled as having promoted the expansion of arid adapted C₄ grasses and C₃ shrubs at lower elevations which provided adequate fuel for repeat fire. In this scenario montane woodland and forest is hypothesised to have moved up-slope. Individual species responses may have been present (e.g. *Juniperus* may move upslope more quickly with increased warming, in contrast to Olea and Podocarpus, that are tolerant to a wider range of temperatures). If temperatures increased enough, and rainfall was further reduced, then fire would have been limited at lowered elevations.

G) Interglacial arid phase (e.g. Mid-Holocene dry phase) [2]: Large reductions in rainfall, and higher temperatures is modelled to have limited fire and promoted the expansion of xeric C₄ grassland at lower elevations. In this scenario, at mid and high elevations, drier (species poor) woodland and shrubland vegetation is modelled as having expanded and stabilised under elevated pCO₂ and reduced fire frequency. At very high pCO₂ levels, the advantage of C₃ plants over C₄ plants decreased (Cowling and Sage, 1998). This may have encouraged threshold behaviour if temperature reached a tipping point that favoured C₄ vegetation, that could have hypothetically led to the collapse of woodland (Shanahan et al., 2016).

H) Modern phase: Increases in rainfall relative to the Mid-Holocene arid phase is modelled as having resulted in reduced fire frequency and moderate expansion of forest, as well as more mesic savanna types.

Base image adapted from https://www.bbc.com/bitesize


Figure 7.2 Comparison of select palaeoclimatic time series across tropical and subtropical Africa, covering the last 150 kyr. Oceanic core records of terrigenous runoff: (F) Stable hydrogen isotopic composition of leaf waxes, corrected for ice volume contributions (δD_{wax-IV}) as an indicator of aridity (increasingly negative value indicates higher precipitation); data from the Gulf of Aden (core RC09-166) (Tierney and Zander, 2017). (L) The carbon isotopic composition of the C_{31} *n-alkane* ($\delta^{13}C_{wax}$). Higher values indicate increased inputs from C4 vegetation; data from core MD96-2048, Zambezi River outflow (Castañeda et al., 2016). Lacustrine δD_{wax} records: (J) δD_{wax} data corrected for changes in global ice volume (δD_{wax-IV} [% vs. _{VMSNOW}]) as an indicator of aridity (increasingly negative value indicates higher precipitation); data from Lake Tanganyika (Tierney et al., 2010). (K) δD_{wax-IV} data from Lake Malawi (Konecky et al., 2011). SST records: (B) SSTs (°C) based on Mg/Ca ratios on planktonic forams; data from the Gulf of Guinea (Weldeab et al., 2007). (C) Alkenone (UK'37)-based SSTs (°C); data from the western Indian Ocean (Bard et al., 1997). (D) UK37, Mg/Ca ratios of G. rubers.s.s, and TEX86 based SSTs (°C): data from the Zambezi River outflow (Caley et al., 2011). (E) SSTs (°C) based on Mg/Ca ratios on planktonic forams; data from the eastern Indian Ocean (Mohtadi et al., 2010). Insolation changes: (A) Mean insolation at 25°N during June-July-August (JJA) (Berger and Loutre, 1991). (I) Mean insolation at 25°N during March (red line) and September (black dashed line) (Berger and Loutre, 1991). Mean insolation at 25°N during December-January-February (DJF) (Berger and Loutre, 1991). (M) Mean insolation at 15°S during December-January-February (DJF) (Berger and Loutre, 1991). Lake levels: (G) lake level change based on seismic reflection profiles; data from Lake Challa (Moernaut et al., 2010). (H) Lake level data based on sedimentology and diatom analysis; data from Lake Naivasha (Trauth et al., 2003). Atmospheric trace gasses: (N) composite CO2 from Epica Dome C, Antarctica (Monnin et al., 2001; Eggleston et al., 2016). (O) CH4 data from Epica Dome C ice core, Antarctica (Monnin et al., 2001). Pollen records: (P) Mt. Kenya (Olago et al., 1999); (Q) Deva-Deva Swamp in the Uluguru Mountains (Finch et al., 2009); (R) Lake Naivasha (Mworia-Maitima, 1997); (S) Mt. Kilimanjaro (Schuler et al., 2012); (I) Rukiha Highlands Uganda (Taylor 1990); (U) Kashiru Swamp, Burundi (Bonnefille and Riollet, 1988).

7.4.1.2 Theoretical age and vegetation distributions: Palaeosol 2

PS2 is interpreted as having supported a semi-open woodland habitat with a predominately C4 mesic grass understory, formed under semi-humid to semi-arid conditions, with a longer wet season. The specific type of arboreal vegetation at the site could not be established (see Chapter 6.8.2.4.3), however it seems likely that it represents a drier forest or woodland, that acted as a former ecotone between savanna and forest vegetation. Signs of hydromorphic processes and weathering are reduced in PS2 compared to PS1. Relative to PS1, the time taken for PS2 to form was brief, halted by deposition of overlying ash deposits. The absence of a strong xeric C4 grass component and moderate woody cover in PS2 suggests that the balance between available moisture (i.e. the interaction between seasonality, drought intensity, and MAP) and pCO_2 levels was such that fire was limited and C₃ woody vegetation was maintained. In savanna grasslands, in low-elevation areas near Mt. Kilimanjaro, sub-millennial scale changes in C4 grass abundance during the LGM have been shown to be controlled by MAP and seasonality, rather than by pCO_2 or fire. Urban et al.'s (2015) record indicates that C₄ grass abundance in this area reached its maximum under intermediate rainfall conditions. Therefore, wooded vegetation and the dominance of mesic C4 grasses at this altitude at Prospect Farm is unlike the vegetation patterns observed on Mt. Kilimanjaro during arid stadial periods (e.g. MIS 6, MIS 4, or MIS 2). It is worth noting that Urban et al.'s study provides details on C_4 grass abundance and the competitive balance between C_3 and C₄ grasses but does not provide insight into mesic C₄ vs. xeric C₄ grass abundance.

7.4.1.2.1 Palaeoclimatic trends in equatorial East Africa during from MIS 5e to MIS 5d in relation to palaeovegetation reconstructions from PS2

Assuming that PS1 was formed during an interglacial phase (probably MIS 5e, but possibly MIS 7), the palaeovegetation signal at PS2 appears most likely to have formed during the last interglacial-glacial transition (i.e. from MIS 5e to MIS 5d [see idealised model in Figure 7.1 {A} Interstadial 1']). If ongoing dating reveals that PS1 in fact corresponded to MIS 7, then the age of the whole sequence would need to be pushed back. Under this model, PS2 should have formed during the earlier penultimate interglacial-glacial transition (MIS 7a to MIS 6). Alternatively, PS2 could relate to a brief, comparatively drier phase during either MIS 5e or MIS 7a (depending on the age of PS1 at the base of the sequence), similar to the mid-Holocene ~6-5 ka; with semi-humid to semi-arid climate conditions and pCO_2 concentrations similar to the present. Climate during these phases is expected to be relatively more arid than PS1 (see idealised model in Figure 7.1 [H] 'Late Holocene/Present'). As PS1 is considered most likely to represent MIS 5e and PS3 is thought to represent cooler parts of the last glacial (i.e. MIS 4 or 3) (see Section 7.4.1.3), the most parsimonious explanation for the age for PS2 is that it formed during MIS 5e or the MIS 5e-MIS 5d transition rather than during MIS 7a/MIS 6.

As discussed in relation to PS1, the sole East African pollen record of the last interglacial-glacial transition from Mt. Kenya (Olago et al., 1999) (Figure 7.2 [K]), indicates that transitional savanna forest vegetation was present at 2350 m a.s.l., similar to that inferred for PS2. The presence of cool-temperature adapted mesic C₄ grasses (e.g. *Themeda spp.* [Ludlow, 1976]) is consistent with a reduction in temperature

during the last interglacial-glacial transition (Bremond et al., 2012). Olago et al., (1999) noted that there is some evidence to suggest that pCO_2 lags temperature change by a few thousand years during this transition. This is reflected in SST records from the eastern Indian Ocean, that show a reduction in temperature that precedes pCO_2 and CH₄, when at the same time, during the early part of MIS 5d, low to intermediate palaeolake levels occur in the Naivasha Basin (Figure 7.2 [C, N, O, and H]). With this in mind, it is possible that vegetation distributions in PS2 reflect carbon cycling remaining in its 'interglacial' mode for a period. This could have limited water stress and allowed woody vegetation to remain relatively well established while mesic C4 grasses expanded at mid-altitude and low altitude sites. An inverse trend is observed during the LGIT on Mt. Kenva, associated with sustained lower SST (Street-Perrott et al., 2004). Contrary to these findings, records from Lake Challa indicate high lake levels during the early part of MIS 5d (see Figure 7.2 [F]). The low chronological resolution of SST and palaeolake records during this interval impedes assessment of leads and lags in these records. Consequently, it is difficult to be certain if divergent climatic conditions existed between inland and coastal equatorial eastern African at this time, and whether moist conditions persisted in the Nakuru-Naivasha Basin in a similar manner to at Lake Challa, that could have allowed for the continued growth of woody vegetation in PS2 at the same time as cold adapted mesic C4 grasses also become more prominent in the record.

7.4.1.2.2 Palaeovegetation trends in the Afromontane zone in equatorial East Africa during MIS 4 in relation to palaeovegetation reconstructions from PS2

As in PS1, low fire activity is inferred for PS2. This suggests the regenerative stability of forest cover was never reduced to the extent that a positive feedback between fire and other factors, such as increased albedo, higher run-off, increased aridity and nutrient deficiency, did not occur. As such, fire did not become a major driver in maintaining C₄ grassland at this time, in the way suggested for the upper treeline zone on Mt. Kenya and Mt. Kilimanjaro during the last glacial period (Wooller et al., 2000, 2003; Rucina et al., 2009; Zech et al., 2011). In modern settings, fire often has a strong influence on vegetation dynamics at the savanna-forest ecotone (see Chapter 2.8). Limited evidence for fire in PS2 and the rest of the Prospect Farm sequence may relate to a short dry season (i.e. less than 800 mm MAP) in the area that didn't allow enough time for plant fuel to dry.

Using Holocene vegetation distributions in the Nakuru-Naivasha Basin as rough analogues of those in previous interglacial periods, it can also be suggested that palaeovegetation distributions in PS2 may represent a short-lived semi-arid phase of MIS 5e or possibly MIS 7a, similar to present day conditions (e.g. idealised scenario Figure 7.1 [H] 'Late Holocene/Present'). In modern settings and during the last 5-6 kyrs of the Holocene, fire is limited to areas where MAP is below 800 mm (i.e. dry forest or woodland in low and some mid-altitude settings in the Nakuru-Naivasha Basin today). This has been associated with warmer conditions and prolonged seasonal droughts limiting fuel for burning (Nelson et al., 2012: Urban et al., 2015 and see Chapter 2.8). Several East African records indicate that a very long dry season, reduced temperatures and lower pCO_2 , can limit grass productivity, which in turn can lead to insufficient biomass for fire (e.g. Rucina et al., 2009; Zech et al., 2011). However, indicators of relatively more mesic

conditions from the PS2 phytolith assemblage and a lack of arid palaeopedological indicators (e.g. carbonate features), are inconsistent with increased aridity limiting fire under last glacial climate conditions. It appears more likely that a short dry season, and cool, semi-humid to semi-humid conditions, with pCO_2 slightly lower than during interglacial periods, limited fire in PS2. Limited sources of ignition may have also played a role in reducing the incidence of fire in the Prospect Farm record. In summary, the PS2 data appears to be more consistent with scenario [A] 'Interstadial 1' and is possibly associated with elevated palaeolake levels in the Nakuru-Naivasha Basin at ~113-108 ka (see Chapter 3.4). However, the formation of PS2 during a semi-arid phase of a previous interglacial cannot be ruled out at this juncture.

It is also not inconceivable that vegetation distributions, associated with mesic conditions in PS2, could represent the climatic amelioration at the transition from the penultimate glacial to last interglacial (MIS 6 to MIS 5e), roughly equivalent in climatic terms to the LGIT. During the LGIT forest expanded on many East African mountains as humidity and pCO_2 (see Figure 7.2 [O]) increased rapidly with deglaciation (see Chapter 3.5.3). If this alternative scenario were the case, then PS1 would correspond to MIS 7a, with no soil formation taking place during more arid conditions that are generally suggested for East Africa during most of MIS 6. However, if OH ages from PS1 of between 21,805 ± 373 to 32,483 ± 568 for early LSA (or Second intermediate) and 14,145 ± 874 to 14,452 ± 1350 for LSA (unidentified) are accurate, then this suggests that soil formation was likely to have occurred under similar conditions to MIS 6 during the LGM and LGIT at Prospect Farm. Therefore, a scenario in which soil formation did not occur during MIS 6 is deemed still possible, but less probable. As such, given current age estimates and palaeoenvironmental information for the site, this scenario appears less likely than those previous discussed above (i.e. that PS2 formed during the MIS 5e to MIS 5d transition).

7.4.1.3 Theoretical age and vegetation distributions: Palaeosol 3

PS3 is interpreted as having supported open grassland with low arboreal cover and a C₄ understory, with a strong xeric C₄ component. The phytolith assemblage and palaeopedological indicators suggest that PS4 formed under semi-humid to semi-arid conditions with a long and/or intense dry season. As in PS2, the period of weathering and palaeosol formation appears to have been relatively brief compared to PS1 before burial took place. PS3 also lacks evidence of fire. High xeric C₄ grass cover and low woody cover are consistent with low *p*CO₂, reduced rainfall and increased aridity, that limited woody cover and allowed C₄ grass to expand during stadial periods. Based on the hypothesised ages for the Prospect Farm sequence, PS3 is most likely to have formed during the stadial period of MIS 4 (idealised scenario Figure 7.1 [D] 'LGM 2'). During MIS 4, Indian and Atlantic Ocean SSTs were reduced (see Figure 7.2 [B, C, E, and F]), and low to intermediate lake palaeolake levels are recorded in Naivasha (see Figure 7.2 [H]). East African pollen records from Mt. Kilimanjaro and Mt. Kenya indicate cold and very dry conditions shifting to cold and semi-humid conditions during MIS4, and cool to semi-humid conditions during the MIS4 to MIS 3 transition (see Figure 7.2 [P and S]), that are also recorded in a pollen record from the Rukiha Highlands, Uganda (see Figure 7.2 [T]). It is also possible that PS3 vegetation distributions could represent MIS 6, a drier phase of MIS 3 Figure 7.1 [A] 'Interstadial 1', or a hyper arid phase of the last interglacial (Figure 7.1 [F] 'Mid-Holocene dry phase 1'), (equivalent to the Mid-Holocene Dry Phase in the Nakuru-Naivasha Basin [see Appendix 3.6, Figure 3.4 [E]).

As introduced in Section 7.4.1.2, C₄ grass abundance reaches a maximum under intermediate rainfall conditions during the LGM in some lowland areas of East Africa. In some LGM records, low rainfall has been shown to limit fire, although low temperatures (~22 °C) are not generally considered to have been a limiting factor (Nelson et al., 2012). However, at other low-mid elevation sites, fire was not limited during the LGM, but became limited by seasonal drought once temperatures rose during the Holocene (e.g. Sinninghe Damsté et al., 2011; Nelson et al., 2012; Urban et al., 2015). Similarly, to PS2, the absence of pedogenic carbonate features and the continued presence of C_4 mesic with xeric C_4 grasses in PS3, suggest that extreme aridity is unlikely to have been responsible for limiting fire during this interval at Prospect Farm. It is possible that if the dry season was intense but short-lived, the interaction between local moisture balance and pCO_2 was such that it produced enough C₄ grass biomass for burning, but that the drying periods were too short, thus limiting fire. If this were the case, it suggests that pCO_2 would have been the main limiting factor on woody vegetation growth at the site. Additionally, the limited time between eruptions may have contributed to reduced soil moisture which could have also acted to limit arboreal cover (Proctor et al., 2007; Jacob et al., 2015). It is also possible that there was insufficient time for trees to become established within the course of the vegetation succession before the burial of PS3. However, while PS3 is poorly developed, it most likely formed over several millennia, and forest has been shown to regenerate in as little as 25 years in some modern settings on East African mountains (Eshetu, 2002). Radiometric dates from these PS3 units are expected to clarify the duration of their soil forming episodes. They will also facilitate comparisons to local and regional records, to help establish the climatic, atmospheric, and internal vegetation-climate feedbacks influencing vegetation during PS3 (see Section 7.3.3). However, at the time of writing, it seems likely that PS3 formed under stadial climate conditions (e.g. MIS 5d-MIS 4).

7.4.1.3.1 Palaeoclimatic trends in equatorial East Africa during MIS 5d - MIS 4 in relation to palaeovegetation reconstructions from PS3

Relatively stable vegetation communities developing under semi-arid conditions in the Nakuru-Naivasha Basin thought to occur during MIS 5d-MIS 4 in PS3, are recorded in other palaeoenvironmental records from coastal and highland areas of equatorial East Africa. These records indicate that climate was relatively mild compared to eastern Tropical Africa during the early last glacial period (~117-70 ka). These so call "megadrought" signals (Scholz et al., 2007), that are pronounced in the Tropical region, are present but relatively muted at ~128 ka, as well as at ~114 ka and ~97 ka, in seismic reflection profiles from Lake Challa (Moernaut et al, 2010; Figures 3.1 and 3.2 [G]). Similar lowstands, for which dates are less certain, are also present in the Naivasha palaeolake record (see Figure 7.2 [H]). While there is some correspondence of these records with north western Indian Ocean SSTs (Figure 7.2 [C]), the strongest relationship with hydroclimatic changes in terrestrial palaeolake records prior to ~75 ka from equatorial

East Africa is with hemi-precessional insolation cycles (see Figure 7.2 [A]). Hydroclimatic changes tracking hemi-precessional cycles have also been observed in molecular proxies for aridity (δ Dwax-IV) in marine cores from the Gulf of Aden [Figure 7.2 [F]). It has been proposed that the reduction in amplitude of arid episodes detected in the Challa record (3°S) is related to climate variability in sites near to the Equator corresponding to an anti-phase pattern of changes in insolation (Berger and Loutre, 1991; Figure 3.2 [I]). This anti-phase pattern is hypothesised to have limited the most extreme effects of variation in precession on MAP (i.e. any variation in northern or southern hemisphere insolation, that negatively affected the intensity of either one of the NE and SE Indian monsoon, should be offset to some degree by amelioration of the other [Verschuren et al., 2009; Moernaut et al., 2010]). Relatedly, there is little evidence to suggest that glacial boundary conditions could have resulted in a shift of the tropical rainfall belt so far south during MIS 5d - MIS 4 causing the region to cease experiencing a bimodal pattern of annual rainfall. As such, it is possible that the Nakuru-Naivasha Basin could have offered refuge to plants and animals during this interval when increasingly arid conditions were experience in parallel basins.

7.4.1.3.2 Palaeovegetation trends in the Afromontane zone in equatorial East Africa during MIS 5d - MIS 4 in relation to palaeovegetation reconstructions from PS3

At mid-altitude sites on Mt. Kenya, from 110-62 ka, cool and dry conditions have been suggested for the areas surrounding Sacred lake (2350 m a.s.l). Vegetation here was dominated by C4 plants (probably drought-tolerant grasses) that were subject to frequent burning (Olago et al., 1999). Similarly, on Mt. Kilimanjaro the dominance of herbal taxa (e.g. Asteraceae and Poaceae) suggest dry but also stable conditions and low taxonomic diversity from 90-75 ka; with forest taxa and species diversity showing slight increases between 75-60 ka (Schüler et al., 2012). As introduced in Section 7.4.1.1, Zech et al., (2011), building on previous studies (e.g. Hemp and Beck, 2001; Zech, 2006), proposed that during this interval and the LGM, C₄ savanna grassland expanded up to at least 2000 m a.s.l.. This change was accompanied by ericaceous belt vegetation movement downslope by up to 1100 m relative to today, to elevations as low or possibly lower than 2600 m a.s.l.. Unfortunately, no published data is available from sites on Mt. Kilimanjaro below 2600 m a.s.l that allows inferences to be made about the precise nature of vegetation communities (e.g. C4 mesic vs C4 xeric grassland proportions) at lower altitudes on Mt. Kilimanjaro (Zech et al., 2011), or at other similar sites during this interval. To summarise, semi-arid conditions in PS3 are consistent with more stable conditions occurring in highland areas relative to lowland areas of equatorial East Africa during MIS 5d to MIS 3. This relative ecological stability, could also be related to the maritime climate affect, as suggested for other mountain sites and for PS2, and may corresponded with moderate lake level increase in the Nakuru-Naivasha Basin at either ~91 ka, ~81 ka, \sim 72 ka or possibly \sim 66 ka (see Chapter 3.4).

It is also possible that drier conditions recorded by phytoliths in PS3, could correspond to arid phases of MIS 3. These arid episodes are associated with positive stable isotope values on Mt. Kenya and have been linked to high altitude forcing (e.g. Heinrich events) (Olago et al., 1999); when the influence of low

latitude forcing on equatorial Africa was reduced after ~70 ka (see Chapter 3.3). However, pedogenic features (e.g. pedogenic carbonates associated with higher temperatures and drought in other East African palaeosol records [e.g. Beverly et al., 2015a,b]) are not present in PS3. Grasslands, most probably with a strong xeric C₄ Poaceae component as observed in PS3, have been recorded associated with drought episodes during the Holocene in the Nakuru-Naivasha Basin (see Appendix 3.6, Figure 3.4 [E]), and could have occurred during the last interglacial (MIS 5e). While palaeoenvironmental trends and existing dates from other palaeosols in the Prospect Farm sequence make it more likely that PS3 developed after MIS 5e, dates to constrain the timing of the formation of PS3 are necessary before its development under interglacial conditions can be ruled out (see Chapter 6.9).

7.4.1.4 Theoretical age and vegetation distributions: Palaeosols 4 and 5

PS4 and PS5 are interpreted as having supported woodland vegetation with moderate to high arboreal cover, with a predominately mesic C_4 grass understory. Periodically moist conditions are indicated by the presence of phytoliths from ferns and sedges in these palaeosols. While vegetation signals are similar in these two palaeosols, PS5 is considered to have taken over 10,000 years to form and displays stronger evidence of hydromorphic conditions. Phytolith and pedogenic results also suggest that strong seasonal shifts between semi-humid and semi-arid climate conditions occurred in PS4, (with short but intense dry seasons suggested by carbonate features and small but present xeric C_4 grass component). PS4 is interpreted as having undergone a relatively short period of pedogenesis prior to burial, and experienced incipient to moderate weathering. As in the other palaeosols of the Prospect Farm sequence, evidence of fire is weak in both palaeosols. The vegetation signal in PS4 and PS5 is similar to those reconstructed from mid-elevation sites on mountains in equatorial East Africa during interstadial periods (e.g. pre-LGM MIS 3) (see idealised scenario Figure 7.1 [A] 'Interstadial 1' and [B] 'Interstadial 2').

7.4.1.4.1 Palaeoclimatic trends in equatorial East Africa during MIS 3 in relation to palaeovegetation reconstructions from PS4 and PS5

Throughout the last glacial period the whole of Africa experienced a trend toward the widespread aridity of the LGM associated with glacial boundary conditions. These conditions were characterised by lower pCO_2 and CH₄ (see Figure 7.2 [N, O]), increased global ice volume, lower sea levels, and cooler global temperatures that influenced Eurasian and Afro-Asian monsoon circulation [Prell and Kutzbach, 1992]). While these conditions climax at the LGM, regional and sub-regional differences are evident during the last glacial cycle. Differences are apparent between West Africa, where records indicate a steady increase in aridity towards the LGM (e.g. Weldeab et al., 2007; Figure 7.2 [B]), and East Africa, where records also document cold but also relatively humid and stable conditions, particularly during the pre-LGM MIS 3. In some East African records, periodic rapid climatic downturns and ameliorations are also recorded despite the general trend towards increased hydroclimatic stability. For example, after 75 ka (MIS 4-2) the Lake Challa palaeolake curve indicates high lake levels, punctuated by brief climatic perturbations that are broadly synchronous with Henrich Events 2-6 (see Figure 7.2 [G]). The Naivasha palaeolake record indicates intermediate to low lake levels during MIS 5b, 5a and MIS 4, but lake levels from between 60 and 30 ka (Trauth et al., 2003), during MIS 3, have not yet been recorded in the sedimentary records of the basin. From ~60-10 ka (MIS 4-2), Naivasha failed to reach the levels previously recorded during MIS 5, after which highstand events are again recorded during the early- and mid-Holocene. As introduced in Chapter 3.3, lake levels in East, eastern Tropical and southern Africa show progressive stabilisation after ~70 ka, associated with the waning influence of eccentricity on precession forcing. However, lakes in equatorial Eastern Africa primarily appear to continue to follow hemi-precessional forcing cycles. Consequently, these records are not generally in phase with those north and south of the Equator. During interstadial periods several palaeoenvironmental records from eastern Tropical Africa (see Figures 7.2 [E, J, K, and L]) indicate periods of increase humidity (~60 ka, 55 ka, 45 ka, and 35 ka) set against a backdrop of regional aridity. These humid intervals have been partially associated with a southern shift in the tropical rainfall belt and ITCZ caused by glacial boundary conditions during the latter part of the last glacial period, but more so with vegetation-climate dynamics that have a strong positive feedback on regional hydrology (see Tierney et al., 2010; Burrough and Willis, 2015; Ivory and Russell, 2016). As during MIS 4, it is also highly improbable that the rainfall belt was displaced so far south during MIS 3 that it stopped delivering moisture to eastern equatorial Africa. This suggests that while precipitation was lower during MIS 3 compared to at previous highstand events during the last glacial and interglacial period, it was still sufficient to maintain wooded vegetation in the Nakuru-Naivasha Basin.

Dry conditions during MIS 3 have been inferred for lowland areas of equatorial East Africa, as well as on the Horn of Africa (e.g. Tierney and Zander, 2017). Palaeosol-based palaeoprecipitation reconstruction from the eastern side of Lake Victoria record a dry episode in the basin between 94 and 36 ka (Beverly et al., 2015a,b; 2017 and references therein). This period of aridity is supported by faunal data from the same area (Faith et al., 2012; 2015; 2016), and is consistent with a lake desiccation event in Lake Victoria of unknown length beginning at ~80 ka (Stager and Johnson, 2008). However, these records from the Victoria Basin cannot resolve climate change in the area on sub-millennial timescales. It has been suggested that the reduction in eccentricity associated with glacial boundary conditions, as well as a reduction in Indian Ocean SSTs could have resulted in low palaeolake levels in Naivasha during MIS 3; as has been suggested for similar lake lowstands in the Victoria Basin (Stager et al., 2011; Beverly, et al., 2017). Taken together records for equatorial East Africa suggest the existence of the East-West moisture gradient, characterised by increasing aridity further west and in lowland areas during MIS3.

Difference in hydroclimatic conditions observed in the records of Lake Challa and Lake Victoria are probably best explained by lower Indian SSTs (as suggested for lowstands at Victoria at 15 and 18 ka [Stager et al., 2011] and at Lake Naivasha), and/or large-scale atmospheric circulation (as proposed form the Horn of Africa [Tierney and Zander, 2017]), that weakened monsoonal circulations across inland equatorial East Africa. Both have been associated with stronger teleconnections with the Northern hemisphere. This model is consistent with studies that suggest aridity visible in the Victoria Basin records, the Gulf of Aden from 75 to 50 ka, and possibly in the Lake Naivasha record, cannot be explained by changes in eccentricity-modulated precession forcing alone (see Trauth et al., 2003; Tierney

and Zander, 2017). HadCM3 simulations also show that between ~80 ka and 12 ka variability in sea level is highly correlated with changes in rainfall over East Africa, and that a precession signal is still observed but that it was weakened (Singarayer and Burrough, 2015). This finding supports the idea that extratropical climate forcing (linked to changes in Northern Hemisphere summer insolation) exerted a stronger influence on East African climate from MIS 4 onwards. Given that in lowland areas such as Lake Victoria the Rift valley does not act as a physical barrier to sequester connections with West African climate, it is possible that drier conditions there were also linked to variability in West African Monsoon. (see Chapter 4.4.1.1). However, this link requires further testing. Indian Ocean SSTs are milder in general than global SST change during the last glacial period (1.5–2.0 °C lower than today; Farrera et al., 1999). During MIS 3 they are in fact relatively mild compared to those that occurred during MIS 4 and MIS 2 in the same records (Figure 7.2 [C, D, E]). Reduced SSTs in the Indian Ocean (linked to decreased rainfall across East Africa) during the last glacial, correspond to decreasing CO₂ and increasing ice volume. However, at the same time, lower sea levels in the Indo-Pacific would have exposed sections of the Sunda Shelf, causing convective uplift in this region, leading to increased precipitation in the western Indian Ocean and coastal East Africa relative to other areas of terrestrial Africa (DiNezio and Tierney, 2013; Singarayer and Burrough, 2015). This semi-continuous supply of moisture is thought to have buffered coastal and highland areas from the most severe effects of aridity; averting monsoonal collapse (Marchant et al., 2007; Moernaut et al., 2010).

7.4.1.4.2 Palaeovegetation trends in the Afromontane zone in equatorial East Africa during MIS 3 in relation to palaeovegetation reconstructions from PS4 and PS5

Multiple mountain sites in eastern Africa indicate a climatic amelioration occurring ca 50-30 ka, associated with cold and humid or semi-humid climate conditions. Open forested conditions (*Hagenia* forest with *Podocarpus*) are recorded prior to the abrupt shift to colder more arid climate during the LGM (Olago, 2001; Kiage and Liu, 2006; Gasse et al., 2008) (see Figure 7.2 [P, R, and S]). Sites west of the Victoria Basin, in and near the Albertine Rift, show a more mixed signal; with some sites indicating cool semi-humid conditions, and others cool and dry conditions (see Figure 7.2 [Q, T, and U]). During MIS 3, pollen records from Mt. Kilimanjaro suggest that the forest belt expanded and moved to higher altitudes relative to its extent in the preceding stadial period (MIS 4) but remained lower and more contracted than today (Zech et al., 2011; Schüler et al., 2012). The lack of samples from sites below 2600 m a.s.l. prior to the LGM on Mt. Kilimanjaro makes it difficult to determine the position of the lower boundary of Afromontane forest here during MIS 3 and 4. Similar cool and semi-humid climatic conditions recorded in the Sacred Lake core from Mt. Kenya during MIS 3 are associated with a treeline depression of at least 500 m (Coetzee, 1967; Olago et al., 1999). Under these conditions it is hypothesised that cooler temperatures, that are expected to have reduced evapotranspiration and increased soil moisture content, could have helped to maintained forest at lower altitudes.

Similar episodes of forest expansion and relative ecological stability are also evident in pollen records in the EAM (Finch et al., 2014). This stability is associated with the influence of the Indian Ocean as a source of long-term moisture stability in the region, as discussed in Section 7.4.1.4.1. The presence of

intermediate (cool-humid) conditions and associated transitional woodland types during MIS 3 at Prospect Farm, is consistent with its intermediate position (between Victoria and coastal areas) along the E-W moisture gradient across sites near to the Equator. In theory, reduction in woody cover in the upper horizons of PS5 could represent increases in aridity closer in time to the LGM. While feedbacks between rainfall, vegetation, and lake levels are unresolved during this interval in the Nakuru-Naivasha Basin, vegetation results from Prospect Farm suggest that lake levels in the study area could feasibly have been moderately high intermittently. Irrespective of whether Nakuru-Naivasha palaeolake levels were very low or intermediate during MIS 3, the palaeovegetation record from Prospect Farm suggests the vegetation communities of the rift margins surrounding the lake may have been more stable than in the lowland parts of the basin. Similar patterns have been observed during 'megadrought' intervals in Tropical African sites (e.g. Mercader et al., 2013; Wright et al., 2017). Parallels can also be drawn with findings from palaeoclimate and palaeovegetation records from Lake Tanganyika, eastern Tropical Africa, in which Afromontane forest appears to have been partially buffered against aridity by a southern shift in the ICTZ during periods of northern high-latitude climatic downturn. This resulted in a bimodal rainfall pattern over the region which increased the length of the wet season despite lower MAP (Vincens et al., 2007). However, local internal ecosystem feedbacks have been shown to have been more important in forest maintenance in the basin than hydroclimatic changes associated with shift in the tropical rainfall belt and ITCZ (Powers et al., 2005; Vincens et al., 2005; Tierney et al., 2008; 2010; Ivory and Russel, 2016). Under lower temperatures, forest vegetation moved downslope in the Tanganyika Basin to form dense forest in which fire was subdued (see Chapter 2.8). This increased organic acids and soil moistures at lower elevations, causing weathering to occur at similar rates to interglacial phases (Ivory et al., 2016b). Rainfall was likely to be lower and more variable in the Nakuru-Naivasha Basin than in the Tanganyika Basin during most of the latter part of last glacial period. This was due to the southern shift of the ranfall belt and possibly the ITCZ and the continued greater influence of precession forcing at the Equator (see Figure 3.2 [I]). However, it is possible that the buffering effect of marine climate in eastern Africa, involving the sustained transfer of moisture from the Indian Ocean to the KCR, and its interplay with internal disturbance regimes in the Nakuru-Naivasha Basin, could have had a similar effect on local moisture availability and forest stability as the shift in the rainfall belt and ITCZ and internal ecosystem buffering had for vegetation around Lake Tanganyika. At present this is the best explanation for similar vegetation distributions (i.e. wooded vegetation at lower elevations) at Prospect Farm during Phase III and IV with those that have been inferred on other East African mountains during MIS 3.

Given that vegetation results from Prospect Farm indicate intermediate levels of rainfall in the basin during MIS 3 rather than aridity, it is possible that the major erosional unconformity observed in the Naivasha palaeolake record, between 60 and 30 ka, may not represent a prolonged period of total lake desiccation (c.f. Beverly et al., 2017). Instead, it is possible that the putative low to intermediate (possibly fluctuating) lake levels of MIS 3 are not recorded as they have been eroded or obscured in sedimentary records. This could have been caused by subsequent, more spatially expansive and stable, lake highstand events and intense volcanic activity of the Olkaria Volcanic Complex that began ~20 ka (Trauth et al.,

2003). Erosion and limited exposure of former strandlines of palaeolakes at elevations lower than subsequent maximum highstands is recorded during the Holocene in the Nakuru-Naivasha Basin (e.g. Washbourn-Kamau, 1970; Richarson and Richardson, 1972; Butzer et al., 1972), as well as in other lakes in the Kenyan Rift system, such as Lake Turkana (e.g. Butzer et al., 1972; Owen et al., 1982; Garcin et al., 2012; Morrissey and Scholtz, 2014).

7.4.1.4.3 Existing dates for Palaeosols 4 and 5

Four OH dates (see Appendix 5, Table 5.1) from Units 10/9 (now associated with phase II-C material that originated in PS4 but was subsequently reworked into the C horizon of PS5), places this material from 119,646 \pm 1668 to 106,297 \pm 3163 yrs BP, during MIS 5e/5d. However, a further two dates from Unit 9 of 14.9 ka and 18.3 ka suggest that dates from these units are likely to be unreliable. Fifteen OH dates from the material in Units 8, 7, and 6 suggest that PS5 formed much later, between $51,308 \pm 4260$ and $45,670 \pm 236$ yrs BP. These dates are consistent with the palaeoenvironmental interpretation that PS5 formed during MIS 3. Nine OH dates from Units 2 and 1 ranging between $32,483 \pm 568$ to 10,460 \pm 173 kyr BP, indicate that PS6 encompasses the LGM and Early to Mid-Holocene periods (MIS 2 and 1). These OH dates are supported by a single conventional ¹⁴C date of 10,560 \pm 1650 uncal BP from Unit 1 (Anthony, 1978), and eleven AMS ¹⁴C dates on charcoal and bulk sediment samples between 55-15 cm in Units 2 and 1 (PS1). These samples were collected during earlier excavations of LSA levels at the site by the In-Africa project, that record ages of between ~20 to 5 ka (Wilshaw pers. comm.: not included in Appendix 5, Table 5.1). This suggests that OH dates from the Bt Horizon of PS6 are likely to be accurate; and provides further support that PS5 (Units 7 and 8), that is separated from PS6 by Unit 6-3 tuff deposits (which are largely archaeologically sterile and lack signs of pedogenesis), is likely to have formed during MIS 3. Despite indications that PS5 is most likely to have formed during MIS 3, it remains unclear if the difference in age (of ~50 kyr) between Phase II-C material from PS4 and Phase III/IV material from PS3 represents a true break in sedimentation or that the OH dating method overestimates the ages of phase II-C material from PS4. If it is revealed that a 50 kyr hiatus existed in palaeosol development following the deposition of the Unit 10 pumice, then the ages of the rest of sequence would be required to be pushed back. This means that palaeosols earlier in the stratigraphic sequence, such as PS1, would be more likely to correspond to MIS 7 than to MIS 5. Completing the dating programme at the site is necessary to test these competing models (see Chapter 6.9) and to confirm a MIS 3 age for PS5. However, the fact that semi-continuous soil formation from MIS 4 to the end of MIS 3 has been recorded in other drier lowland settings (Beverly et al., 2017) and in montane areas on volcanic terrain (Zech et al., 2006, 2011) in the region, suggests that climate is not likely to have been a limiting factor in palaeosol formation at Prospect Farm during this interval. It is my view that large age discrepancies in OH dates from Unit 9 are caused by longstanding issues with this dating technique. As such, these dates should be disregarded. On balance, while dates from PS4 are probably younger that MIS 5e, and its vegetation signal appears similar to that of PS5, it is difficult to say with any real certainty if PS4 can be placed within the same climate phase as PS5 (MIS 3), or if vegetation distributions in PS4 could represent a brief humid period that occurred from between MIS 5e to \sim 50 ka.

Vegetation distributions inferred from PS6 are not of direct interest to this study as they relate to later LSA assemblages. However, it is also important to note that age reversals of AMS radiocarbon ages in Units 2 and 1 (PS6) (Wilshaw pers. comm) indicate that these sediments have undergone significant mixing. This reinforces both the polygenic nature of the phytolith assemblages from palaeosols in the Prospect Farm sequence and their potential to encompass long intervals of time and different climatic phases. While sample resolution in PS6 is low, it shows a similar vegetation signal to PS4 and PS5. A mixed vegetation signal is most likely a reflection of its polygenic nature, covering a period in which large swings in vegetation are recorded elsewhere from the LGM to the Mid-Holocene (see Chapter 3.5.3). A mixed vegetation signal with relatively high arboreal cover during this period is also supported by pollen studies that indicate the LGM was relatively more humid (see idealised scenario Figure 7.1 [D]) in the Nakuru-Naivasha Basin compared to other sites in East Africa, where more arid conditions existed (see idealised scenarios Figure 7.1 [C]) (see Chapter 3.5.4).

7.4.1.5 Summary of theoretical age and climatic conditions recorded in the Prospect Farm sequence

In summary, likely climatic intervals can be suggested for palaeosols and associated occupation phases in the Prospect Farm sequence with varying degrees of confidence. The most secure associations exist between PS5 and cold but humid pre-LGM MIS 3 climate conditions reflected at other sites across East Africa. Due to known issues with the OH dating technique, indications of erroneous ages in PS4, and a lack on any dates from older palaeosols, the ages and climatic phases associated with PS1-PS4 are debatable. Interestingly, in contrast to studies at similar elevations on East African mountains, the role of fire in driving vegetation changes at Prospect Farm appears to have been minimal. This may have important implications for the highland areas of the KCR to buffer against woody vegetation degradation by fire through regional moisture sources of the Indian Ocean, as well as via internal rainfall-vegetation feedbacks which could have maintained locally higher moisture levels. As has already been noted, the lack of dates for the site, makes it difficult to compare Prospect Farm to regional and local records to assess whether the basin 'amplified' regional climate changes, and the affect on its vegetation.

It is possible that the suppression of frequent fire at lowered elevations on Mt. Eburru allowed the area to act as a refugium for woodland/forest plant species, that may have been attractive to human groups. The variety of habitats recorded in the Prospect Farm sequence (e.g. open grassland to closed Afromontane forest) allow us to test which habitats were more favourable to human groups at Prospect Farm, and how they relate to aspects of variability in human behaviour, such as by influencing residential mobility, raw material procurement strategies, and inter-group interactions within the basin. Doing so is central to establishing which behavioural-ecological models, outlined in Chapter 1.9.2, best explain variability in the archaeological record. As lithic and dating analysis is ongoing, placing Prospect Farm MSA assemblages within the regional patterns of lithic variability is currently not possible (see Objective no. 3, Chapter 1.9.3). Furthermore, the current lack of geochemical analysis of raw material in PS1-PS3, means inferences that can be made about past human behaviour in relation to palaeoenvironmental conditions during Phases 1, II-A, and II-B are more speculative than for PS5 (Phase III and IV [the

putative MSA-LSA transition]); for which ages are most secure, and raw material sourcing data exists. Habitat preferences and occupation intensity are also considered for palaeosols, (for which less archaeological information is available), to test aspects of competing behavioural-ecological models. Environmental trends in the Prospect Farm sequence are broadly explicable as a climatically driven succession of soil formation episodes that that approximate MIS of the last interglacial-glacial cycle and are periodically interrupted by volcanic activity. Table 7.1 summarises vegetation conditions inferred at Prospect Farm and across the rest of the basin, best estimate of the MIS for these conditions, and conditions recorded in other East African montane site during these stages. Figure 7.3 present this information visually, providing and overview of the Prospect Farm environmental record, hypothesises best estimates of MIS and linkages climatic trends in other key equatorial East African climate records for each palaeosol in the sequence following a visual signal matching approach in which the Prospect Farm record is floating in time. As such, this approach does not address potential leads and lags between the Prospect Farm and other palaeoenvironmental records. It is notable that parts of the sequence are more reliable assigned to a certain MIS or sub-stage than others based on current environmental and dating information. For example, it is difficult to confidently assign Phase II-B (PS3) and Phase II-C (PS4) to a specific point during MIS 5d to MIS 3.



Figure 7.3 Signal matching between the Prospect Farm palaeoenvironmental record, MIS and other East African palaeoenvironmental records. The upper panel shows changes phytolith-based vegetation indices by sample depth. Grey bars correspond to the upper horizons of palaeosols, yellow bars to sample where the phytolith signal is unreliable, and red 'H's to depositional hiatuses where unpedogenised volcanic deposits exits. Coloured arrows indicate which MIS in thought to be a best estimate for each palaeosols. The lower pane shows key East African climate records from MIS 6 to present with letters corresponding to their locations (see Figure 3.1): (H) Palaeolake Naivasha lake level curve (Trauth et al., 2003); (I) Mean insolation at 25°N during March (red line) and September (black dashed line) (Berger and Loutre, 1991); (P) Pollen record, Mt. Kenya (Olago et al., 1999); (S) Pollen record, Mt. Kilimanjaro (Schuler et al., 2012); (G) Palaeolake Challa lake level curve (Moernaut et al., 2010). (C) Alkenone (UK'37)–based SSTs (°C); data from the western Indian Ocean (Bard et al., 1997). (F) δDwax-IV record from the Gulf of Aden (Tierney and Zander, 2017). Note: (C) and (F) are not strictly East African records, but they are thought to broadly reflect changes in palaeomonsoon intensity across the region.

Archaeological occupation phases and palaeosols (from oldest to youngest)	Vegetation at Prospect Farm (~2100-2200 m.a.s.l.)	Inferred changes in vegetation distributions in the Nakuru- Naivasha Basin relative to the present day (A: in montane areas above Prospect Farm; B: in areas below Prospect Farm on lower scarps and the rift floor)	Likely MIS stage and climate conditions recorded from other coeval equatorial East Africa montane records
Phase I (carliest MSA) PS1	Closed-canopy Afromontane forest with a C ₃ grass understory	 A: Expansion of Afromontane forest and possibly <i>Hagenia</i> forest, and contraction of Montane ericaceous belt vegetation to higher elevations e.g. Figure 7.1 [E] B: Expansion of upland (moist) woodland and mesic savanna and lacustrine margins 	MIS 5e (~135-115 ka) No terrestrial pollen records from this interval exist from region. High lake levels are recorded in the lake Naivasha record ~135 ka. Climate models indicate warm and humid conditions and elevated <i>p</i> CO ₂
Phase II-A (MSA) PS2	Mesic C4 dominated grassland (savanna) environment with limit arboreal cover	 A: Contraction of the Afromontane forest belt and expansion of ericaceous belt vegetation Figure 7.1 [A]). B: Open mesic C₄ grassland expands and xeric C₄ grassland is likely present in areas on the basin floor at the lake margins 	MIS 5e to MIS 5d transition or MIS 5d (~115 -105 ka) Low lake levels in the Naivasha basin are broadly coeval with cold and dry conditions at 2350 m.a.s.l. on Mt Kenya, pCO ₂ is reduced, however high lake levels are recorded in Naivasha at the end of MIS 5d
Phase II-B (MSA) PS3	Edaphic wooded grassland (savanna with very low arboreal cover and a strong xeric C ₄ component)	 A: Major contraction of the Afromontane forest belt (i.e. existing as pockets) and expansion of ericaceous belt vegetation (e.g. Figure 7.1 [D]) B: Grassland at lower elevations is dominate by xeric C₄ grasses with very limited or no tree cover 	 MIS 4 (~71-57 ka) or colder/more arid period of MIS 5c, 5b, or 5a (~96-82 ka). Cold and very dry to cold conditions are present on Mt. Kilimanjaro and Mt. Kenya are indicated at points during this stadial period, low pCO₂
Phase II-C (MSA) PS4	Transitional shrub savanna with possible fluctuation occurring between moderate to low arboreal cover	 A: Contraction of the Afromontane forest belt and expansion of ericaceous belt vegetation (e.g. Figure 7.1 [A] and [B]). B: Open mesic C₄ grassland expands and xeric C₄ grassland is likely present in areas on the basin floor at the lake margins 	MIS 3 (~57-29 ka) Multiple mountain sites in eastern Africa indicate a climatic amelioration occurring ca 60-30 ka, associated with cold and humid or semi-humid climate conditions, with a trend towards increase climatic stability but with short-lived climatic perturbations
Phase III (final MSA) PS5	Transitional shrub savanna/woodland with moderate arboreal cover (possibly becoming reduced over time [i.e. in association with the MIS 3- 2 transition])	As in Phase II-C	As in Phase II-C
Phase IV (MSA- LSA 'transitional' industry) PS5	Transitional shrub savanna/woodland, possibly with lower arboreal cover than is associated with Phase III material	 A: Contraction of the Afromontane forest belt and expansion of ericaceous belt vegetation (e.g. Figure 7.1 [A] and [B]). B: Open mesic C₄ grassland expands and xeric C₄ grassland is likely present in areas on the basin floor at the lake margins 	Pre-LGM MIS 3 or MIS 3-2 transition (~29-27 ka) Cold and humid or semi-humid climate conditions becoming increasing cold and arid towards MIS 2. Lake level and pollen records from the Abredares, Lake Naivasha and the EAM display relatively humid conditions compared to other records during early MIS 2

Table 7.1 Summary of best estimates of corresponding MIS to each palaeosol in the Prospect Farm sequence and associated palaeovegetation distributions at the site, in the rest of the basin and in other montane zones of East Africa from which comparable and palaeoenvironmental records of a similar age are available.

7.5 Testing MSA-LSA behavioural-ecological models in the Nakuru-Naivasha Basin using palaeoenvironmental and archaeological data from Prospect Farm.

The following section attempts test behavioural-ecological models outlined in Chapter 1.9.2 by integrating records of palaeoenvironmental change at Prospect Farm with indicators of site occupation intensity and past mobility on the landscape from Prospect Farm (Objective no. 3). Recurrent occupation of Prospect Farm has occurred from at least MIS 5 onwards, associated with a variety of different habitat conditions. Palaeovegetation distributions in Phase II-A (PS2), Phase II-C (PS4), and Phases III and IV (PS5) are consistent with occupation at the ecotone between savanna and forest environments. Phase I (PS1) is associated with habitation of forest environments, and Phase II-B (PS3) with open grassland.

7.5.1 Raw material sourcing in the Prospect Farm sequence

Raw material sourcing information is important for understanding the past mobility of humans on the landscape, as well as more speculatively the scale and structure of inter-group connections (Brooks et al, 2018; Frahm and Tryon et al., 2018). Obsidian sourcing data from archaeological phases in the Prospect Farm sequence, that provide insight into these aspects of past hominin behaviour in Nakuru-Naivasha Basin, is only currently available for Phases II-C to IV. However, observations of raw material in PS1 indicate that obsidian boulders from a single source, that is likely to be local to Mt. Eburru (Anthony, 1978), were used for tool producing during this phase. A greater diversity of obsidian types is recorded in Phase II-A and II-B material (Van Balen pers. comm.), but the variety of obsidian, as well as the use of chert and trachyte is observed (Van Baelen pers. comm.). Figure 7.4 shows changes in obsidian sourcing behaviours from Phase II-C to IV (after Merrick and Brown, 1984; Merrick et al., 1994). These are set against best-fit idealised vegetation distributions in the Nakuru-Naivasha Basin, which are based on vegetation-climate reconstructions from the Prospect Farm sequence discussed in Sections 7.4.1.1 – 7.4.1.4.

Material assigned to the newly established Phase II-C from Units 9/10 comes mainly from unknown and probably local sources (within 10-15 km) of Prospect Farm, from upper Eburru sources, the Masai Gorge, and Cedar Hill in the Naivasha Basin (see Figure 7.4 and Appendix 7 Table 7.1). Idealised vegetation models for Phase II-C indicate ecotonal conditions at Prospect Farm, a depressed tree line, the expansion of ericaceous belt vegetation at higher elevations, and the expansion of predominantly mesic C₄ open savanna on rift floor. In Phase III (Units 9/8) obsidian is still largely derived from local sources, but there is a shift to the exploitation of obsidian outcrops 30-40 km away from the site; mainly in the Naivasha Basin and from the Njorwa Gorge and Ololeria (located on the western shore of presentday lake Naivasha). Idealised vegetation models for Phase III also indicate ecotonal conditions at Prospect Farm, but with reduced seasonality and increased arboreal cover, relative to Phase II-C. Under these conditions, forest is expected to have expanded to higher elevations, and woodland and wooded savanna vegetation are expected to have been more extensive at lower elevations on the rift scarps below Prospect Farm. At the same time, the rift floor is deemed to still have been mainly mesic C₄ grasslands. In Phase IV (Unit 8/7), sourcing of obsidian from intermediate outcrops outweighs those from local sources, with 49% of all analysed material originating from the Sonanchi crater; ~4 km west of modern lake Naivasha. This change occurs when idealised vegetation models indicate more open vegetation, in which ecotonal conditions are present at the site, and vegetation distributions are modelled as being intermediate between those suggested for Phase II-C and Phase III. However, it is notable that sedimentary time averaging, which disguises rapid sub-millennial scale shifts between more open and closed canopy conditions in the bio-stratigraphic record, may affect PS5 (Phase III and IV); and cannot be resolved at this juncture. In all three of these phases, obsidian sourcing from Kisanana (~75 km away from Prospect Farm) is recorded but makes up very low percentages of the total assemblage. The provenance of raw material for chert artefacts in Phase III and IV is not known. Slater (2016) notes that "small, thin irregular nodules and seams occur locally on Mt. Eburru", that are unsuitable for tool production. The closest outcrops of material amenable to flaking come from Basement System metamorphic rock regions from ~80 km south at Ol Doinyo Rasha, 130 km SE at Lukenya Hill, and \sim 140 km north in the Tugen Hills to the west of Lake Baringo. Other sources within the Rift valley are the Lake Baringo Basin (~140 km north) and the Lake Menengai Basin (~130 km south) (Ambrose, 2010; Slater, 2016). While provenancing of this material warrants further investigation, the presence of chert suggests that more regular long-distance transport of exotic material occurred during these occupation phases at Prospect Farm, as well as at other nearby sites such as Momonet Drift.



Figure 7.4 (A) Map of the Nakuru-Naivasha Basin showing locations of obsidian outcrops exploited during Phase II-C to IV in the Prospect Farm sequence, divided into local sources (10-15 km away from the site [dark grey ellipse]), intermediate sources (30-40 km away from the site [brown ellipse]), and non-local sources (over 75 km away from the site [blue ellipse]). The yellow circle denotes the location of Prospect Farm. Important raw material sources discussed in the main text are highlighted. (B) Pie charts showing the contribution of obsidian from different sources as a % of the total material in the assemblage during each of the Phases II-C to IV. (C) Maps of idealised models of vegetation distributions in the Nakuru-Naivasha Basin from Phase II-C to IV plotted against raw material sources. Large images show the most likely vegetation scenarios based on vegetation reconstructions, age estimates, and climatic associations for these phases. The smaller images below show alternative, secondary vegetation reconstructions that cannot be entirely ruled out at the site.

7.5.2 Implications of habitat preferences, landscape use, and technological organisation for MSA and LSA behavioural-ecological models in the Nakuru-Naivasha Basin

Resolving the drivers underlying variability in MSA assemblages at local and regional scales, as well as the causes of the MSA-LSA transition, requires explanatory models. These models often consider demographic factors (e.g. population size and stability, residential mobility and inter-group connectedness, competition, and isolation), as well as ecological factors (e.g. shifts in habitat preference, changes in foraging opportunities and subsistence risk) to be the most important and readily testable agents of change that shape variability in material culture (e.g. influencing technological organisation and 'emblemic' style [Wiessner, 1983]) (Tryon and Faith, 2013). These factors are closely connected and sometimes interdependent (e.g. Bird and O'Connell, 2006; McCall, 2007; Mackay et al., 2014; Marean, 2014, 2016). Of the two, palaeodemographic change is the more difficult to reliably reconstruct for the MSA and LSA periods using the archaeological record (French, 2016). Even in cases where high population sizes can be reliably inferred using lithic proxies, producing empirical measures of both population density and mobility, (thought to be equally important in controlling encounter rates and thus rates of cultural transmission [Grove, 2016: Premo, 2016]), has only been attempted by a handful of studies in Africa (e.g. Barut, 1994; Tryon and Faith, 2016). These efforts are further complicated by the fact that establishing that demographic change occurred does not always allow us to identify its underlying causes (Klein, 2003; Tryon and Faith, 2016).

By considering demographic and ecological factors in isolation, we cannot expect to fully explain variability recorded in the archaeological record; since other intrinsic factors, such as neurological-cognitive changes and the effects of cultural transmission, are inseparable from social, demographic and environmental changes; interacting with one another in a multitude of ways (see Thomson et al., 2018 and references therein). Therefore, the most instructive studies should consider multiple factors to identify primary drivers of change, as well as secondary mediating factors (e.g. Tryon and Faith, 2016; Thomson et al., 2018), that can be used to suggest the social-ecological network structures that are most consistent with a specific archaeological population (Grove, 2016).

As lithic material from Prospect Farm is still undergoing analysis, and because there are current chronological inconsistencies in the record, it is only possible at present to make speculative inferences about social network structures in the basin. More universal caveats of behavioural-ecological models that may affect interpretations of the archaeological record are summaries in Appendix 7.2. The abundance of high-quality raw material in the Nakuru-Naivasha Basin means that this is not assumed to have been a limiting factor in the occupation of Prospect Farm or in general to the production of specific tool types. Consequently, changes in occupation intensity of Prospect Farm are likely to relate to changes in the productivity of the local environment or to demographic factors.

7.5.2.1 Estimating past residential mobility and habitat preferences in the Prospect Farm record

Broader limitations of these models aside, it is still possible to focus on estimates of past changes in mobility on the landscape and habitat preferences in the Prospect Farm record in order to suggest which of the generalised behavioural-ecological models these estimates are most consistent with. These models are expected to show varying responses to the same underlying environmental and demographic pressures, which are not necessarily mutually exclusive (see Chapter 1.9.2). Changes in mobility are partially inferred through artefact densities acting as a proxy for occupation intensity, and through raw material sourcing data. In the absence of ages and quantitative assessments of artefact densities per m⁻³, occupation intensity was estimated as being either low, moderate, or high; based on qualitative artefact densities in a soil and the hypothesised duration of soil formation. Because of these limitations and considering the underlying assumptions of calculating occupation intensity in general (see Barton and Riel-Salvatore, 2014; Tyron and Faith 2016; French, 2016), these estimates are at present only useful for making generalised relative comparisons between different occupation phases at the site. In the MSA phases at Prospect Farm the earliest recorded occupation of the site by MSA using groups in PS1 (Phase I), is characterised by low occupation intensity and mixed vegetation, while PS3 (Phase II-B) is associated with high occupation intensity and a savanna habitat with low local woody vegetation cover.

7.5.3 Landscape and behavioural models for MSA levels at Prospect Farm

7.5.3.1 Mesic vs. xeric mobility models: Phase I (PS1)

In PS1, moderate to high occupation intensity, limited residential moves, and the use of a single local raw material source under mesic conditions, can be explained to an extent by risk-based behavioural ecological models (see Bamforth and Bleed, 1997) (e.g. the *Ecotonal hypothesis, Generalized and Seasonal Grassland Models,* and Tryon et al's *xeric grassland/lakeside model* [see Chapter 1.7.2.3, 1.7.3, and 1.7.3.4]). In the context of the Phase I occupation of Prospect Farm, forested environmental conditions with high lake levels could have allowed large structured populations to exist. In this scenario vegetation would have acted as a physical barrier to contact between groups and to the transfer of information between them. This would have resulted in local isolation of groups and higher rates of cultural boundary formation and within-group prosocial behaviour (Thomson et al., 2018). These models also predict that when seasonality was low and environmental conditions were relatively stable, there is a lack of ecological pressure on a group to develop more diverse, sophisticated toolkits. Further analysis of lithic reduction strategies, tool types and, retouch techniques is necessary to assess the level of diversity of Phase I material compared to other phases in the sequence.

Information on occupation duration (that can be estimated using the percentage of transported retouched tools [e.g. Kuhn, 1995; Barton and Riel-Salvatore, 2014; Frahm and Tryon, 2018]) and measures of regional group connectedness are not yet available for Phase I. However, the lack of evidence for both increased mobility on the landscape and procurement of non-local raw material during this phase are inconsistent with the *Amplifier Lakes Hypothesis* and the *Hydro-Refugium Hypothesis*. These models posit that increased rainfall, widespread forest vegetation cover, and high lake levels would have driven dispersals outside of the basin (see Chapter 1.7.2.1-1.7.2.2). The occupation of Prospect Farm when arboreal cover in the local habitat was high, is consistent with aspects of the *East African Refugium*.

hypothesies (see Chapter 1.7.1). However, there is limited evidence from Phase I to suggest expanded forest vegetation fostered intra-basin interactions, which in theory should have resulted in higher levels of innovation and cultural transmission (Derex and Boyd, 2016).

7.5.3.2 Best-fit mesic environment subsistence risk-based models: Phase I (PS1)

A scenario in which MSA hunter-gatherer subsistence was focused on local resource patches under mesic conditions, in which lake levels were intermediate to high, has also been suggested for MSA sites in south eastern Tropical Africa. Several studies in the Malawi Basin record exploitation of dense resource patches in riparian corridors and limited contact between groups in different areas of the basin (e.g. Wright et l., 2013, 2017; Mercader et al., 2013). These findings are echoed in LSA assemblages across the Nakuru-Naivasha Basin during the humid phases of the Holocene when lake levels were high. Under these conditions, sites, including Gamble's Cave (Frahm and Tryon, 2018), indicate increased occupation intensity at the ecotonal savanna-forest boundary, but also near lake shores (Wilshaw, 2013). As the lakeshore is inferred to have been in closer proximity (~3 km from Prospect Farm) during Phase I, the local carrying capacity is expected to have been high; with more diverse subsistence provisions available to groups locally. While the Phase I occupation is of Afromontane forest, which should have lower resource richness than that of mesic savanna, in practice the savanna vegetation would have been easily accessible by groups at the site. Other factors attracting groups to the site at this time are likely to have been favourable edaphics that attracted game, similar to those recorded today in the Eburru forest (e.g. high Ca, Mg, and P levels [Kübler et al., 2016]), as well as locally low frequencies of fire. At all times in the past Prospect Farm would have provided a good vantage point from which to survey the movement of people and animals in the Nakuru Basin. When palaeolake levels were high, as inferred for Phase I, the areas between Mt. Eburru and Lake Nakuru-Elmenteita would have provided easy access to the lakeshore and grazing areas (another being near Kariandusi, Gilgil area [Kübler et al., 2016]), while access to the lake in other areas was limited by steep escarpments. The Generalized Grassland Model suggests that under mesic conditions, the mobility of gregarious residential mammals would be low, and that large mobile game would move through predictable corridors in an environment more densely vegetated by woody plants. It is feasible that this was the case during Phase I at Prospect Farm, and that the site held a special strategic significance at these times when migratory game was likely to have been funnelled into this area of the sub-basin.

7.5.3.3 Demographic-ecological models: Phase I (PS1)

Thomson et al., (2018) note that the mesic conditions discussed above could eventually have encouraged demographic expansion, as proposed by the *Amplifier Lakes hypothesis* and the *East African Refugium hypothesis*. However, expansion is only expected to have taken place once groups had developed behavioural adaptations to these environments, in which the return from exploiting them outweighed their initial investment (e.g. Marean, 2016). At present, the information available from the archaeological record of PS1 is insufficient to evaluate regional connections and technological complexity and their possible contribution of demographic expansion to other areas. The habitation of forested environments

during Phase I is consistent with aspects of the East African Refugium hypothesis, but not with it's view that there were increased connections between groups within the Nakuru-Naivasha Basin. It is, as mentioned, not currently possible to test if these environmental conditions encouraged increased regional connections. Considering MSA records of the Malawi Basin, Wright et al. (2013) proposed that geographical isolation of populations, and low levels of technology exchanges, could also be partially influenced by competition with LSA groups that expanded across Africa during MIS 3. In this case technological conservatism is hypothesised to have been caused by low subsistence risk and competition with other groups. During the same period of demographic expansion, Eren et al., (2013) have also linked increased territoriality with the defence of dense, but spatially restricted resource patches that were present under mesic conditions at Mumba Rockshelter, Tanzania. In their model, mesic conditions and more competition for resources resulted in increased subsistence-risk, which in turn drove further complexity in tool kits (e.g. microlithisation). While completion with LSA populations during Phase I can be ruled out, it may be the case that archaeological patterns in Phase I relate, in part, to competition with other groups in the basin and control of the resources the site provided. Competition may have been caused by population expansions that are thought to have occurred across the continent during MIS 5 (see Chapter 1.3). These models differ from studies of the environmental drivers of the MSA-LSA transition, that posit increased risk was associated with resource unpredictability due to environmental deterioration. These models share a key factor (i.e. that increased risk drives technological complexity), that can have different underlying environmental or demographic causes. (see Section 7.5.4.2).

7.5.3.4 Summary of best-fit behavioural-ecological models for Phase I (PS1)

The archaeological-environmental patterns in Phase I are broadly reconcilable with risk-based models in which local isolation of groups occurred under mesic environmental conditions. It is possible that either or both low-subsistence risk and demographic pressure, could have resulted in what seems to have been the relatively isolated existence of groups during Phase I. However, at present it is difficult to further constrain the casual conditions without more robust archaeological information from Prospect Farm, and archaeological and ecological datasets from other sites within the basin, as well as from geographically connected areas.

7.5.3.5 Mesic vs. xeric mobility and risk-based models: Phases II-A (PS2) and II-B (PS3)

Low artefact densities and an increase in the diversity of obsidian types used in tool production in PS2 (Phase II-A) occurs in association with semi-humid to semi-arid climate conditions thought to correspond an interstadial phase of last glacial period. At this time temperatures and primary productivity are expected to have been lower and more seasonal (less predictable) than during Phase I (i.e. in an interglacial period). During Phase II-A open woodland was present at Prospect Farm and lake levels are thought to have been intermediate to low. In PS3 (Phase II-B), high occupation intensity is recorded in association with arid open grassland habitats at the site. PS3 is thought to have developed during a stadial

period of the last glacial cycle, when primary productivity is predicted to have been lower still than in PS2.

7.5.3.5.1 Mesic vs. xeric mobility and risk-based models: Phases II-A (PS2)

The ephemeral Phase II-A occupation at the ecotone between forest and savanna is compatible with the idea that Prospect Farm was primarily an area of tool discard or very short-lived tool production, rather than of prolonged occupation (Conard and Adler, 1997; Tryon et al., 2016). This pattern is broadly consistent with xeric grassland expansion risk-based models (e.g. the Ecotonal hypothesis and Tryon et al's xeric grassland/lakeside model). In these models we expect to see lower population densities, higher levels of residential mobility, more sporadic use of stone-tools across more sites on the landscape, and more complex tool kits, as an adaptation to increased ecological risk when groups focused on the tracking of large mobile herds of ungulates. Under these conditions, and provided that competition between groups was not a significant factor, a reduction in woody cover in savanna habitats on the valley floor during Phase II-A would have increased rates of inter-group contact and reduced rates of cultural boundary formation. It is also the case that lower occupation intensity at Prospect Farm is not necessarily mirrored in other sites within the basin. It is possible that activity was focused at other unknown more strategically advantageous and ecologically appealing sites that would display higher levels of occupation intensity. During Phase II-A, Prospect Farm probably lost some of its strategic significance as large areas of the basin floor became available for grazing. However, it could be argued that under mixed vegetation conditions in which a degree of arboreal cover was maintained on the basin floor, increased residential mobility and group interaction was encouraged (as predicted by the EARH and Amplifier Lakes hypothesis). This could have resulted in the reduction in occupation intensity that has been inferred for this phase. It seems likely that landscape use by groups during Phase II-A may fall somewhere between these two models. However, as in PS1, the lack of independent measures of past mobility on the landscape and of regional connections during Phase II, make it problematic to suggest the most suitable behaviouralecological model for this phase of occupation at the site.

7.5.3.5.2 Mesic vs. xeric mobility and risk-based models: Phases II-B (PS3)

Similar difficulties are encountered in relation to interpreting ecological-archaeological patterns in PS3 (Phase II-B). High occupation intensity in arid open grassland environments with low woody vegetation cover during Phase II-B can be said to be at odds with predictions of the xeric expansion models, as well as with studies that show increased mobility and cultural complexity in response to deteriorating environmental conditions during stadial periods (e.g. Elston and Brantingham, 2002; Goebel, 2002; Neeley, 2002; McCall, 2007; Mackay, 2009; Petraglia et al., 2009; McCall and Thomas, 2012). Instead, low residential mobility of groups in Phase II-B is more compatible with isolation of groups under arid climate conditions, as proposed by the *EARH*. Under these environmental conditions, this model predicts that activities would have been focused in a restricted area where resources could support a group. Additionally, regular movement to other areas of the basin is modelled to have been limited by the expansion of arid grassland that provides limited shelter; resulting in increased levels of cultural

boundary formation. In this model the proximity of Prospect Farm to Afromontane forest on Mt. Eburru could have provided an additional resource patch and source of fresh water when resources in other areas of the basin are predicted to have been scarce.

Alternatively, high occupation intensity at Prospect Farm during this Phase II-B could reflect regular visits by different mobile groups to the site. This could have occurred if water availability (provided by steams with sources on Mt. Eburru or ground springs in the forest itself) remained higher here relative to other areas of the basin, as suggested for certain sites in the Victoria Basin by Tryon et al's *xeric grassland/lakeside model*. Under such a model access to patches of USOs on well-drained slope but nutrient poor soils could have also encouraged regular visits to the site (e.g. Ichikawa, 1980; Marean, 1997; Tryon et al., 2016). Also, while Prospect Farm may have lost some of its strategic significance in exploitation of game compared to when lake levels were very high, it still provided a good vantage point for tracking movements of animals and people across the basin (Clarke, 2001).

At present, our data is insufficient to say with certainty which of these two models is the best-fit for Phase II-B. The *EARH* and *xeric grassland models* propose key differences in lithic reduction strategies, occupation duration, residential mobility, and the homogeneity in archaeological assemblages under these environmental conditions. Only by studying these factors in further detail from Prospect Farm and from other MSA sites in the basin dated to the same period (Ambrose and Lorenz, 1990; Tryon, et al., 2015), such as Mamonet Drift, Cartwrights' site, Lukenya Hill, Kilombe, and Prolonged Drift, will it be possible to provide the added detail necessary to evaluate which of these models fits the data best, if at all.

7.5.3.6 Possible refugial conditions and occupation of arid environment in Phase II-B

While population movement in response to climate change has been recorded during the MSA period across Africa (Blome et al., 2012 and see Chapter 1.3), recent studies from southern and eastern African have highlighted the ability of MSA groups to make specialised adaptations in marginal environments to overcome low temperatures, extreme aridity and ecological patchiness during the MSA in the Kalahari and Namib Deserts between 90 and 70 ka (e.g. Nash et al., 2016; Dewar and Stewart, 2016) and in mountain areas from 80 ka onwards (Stewart et al., 2012, 2016; Pargeter et al., 2017; Stewart and Mitchell, 2018). The presence of high-occupation intensity during Phase II-B at Prospect Farm associated with semi-arid conditions and xeric grasslands, suggest that lowland areas surrounding the basin may have experienced significant aridity at this time. Thus, it is possible the basin at this time acted as a refugium. Settlement strategies to cope with increased aridity in lowland areas such as the Kalahari are analogous to those records in the Victoria Basin (i.e. specialised hunting strategies, increased mobility and intergroup connections over long distances). In highland areas, archaeological and palaeoenvironmental records from Mochena Borago Rockshelter and open air sites on Mt. Damota (Brandt et al., 2012, 2017; Vogelsang and Wendt, 2018), agree with records of hunter-gatherer adaptations to the Afromontane zone during periods of climatic deterioration and unfavourable environmental conditions in general, in that they both suggest small scale movement between different ecozones on mountains to be the first response; limiting the need for long distance migration (Blome et al. 2012, Wright et al., 2015). However, the abandonment of sites is still recorded at several locations, (e.g. Lesotho [Stewart et al., 2016]) during extremely cold intervals such as the LGM.

At present without dates we cannot be certain if environmental conditions of Phase II-B occurred at the same time as hyper-arid in lowland areas, nor whether the site acted as refugium for groups in the region over the sequence (see Section 7.3.3). Assuming that this was the case, under the *EARH* we would expect that activity should have been focused at the ecotonal boundary between forest and savanna in order to provide ease of access to multiple resources; however, this is not the case for Phase II-B. It is possible that the reduction of Afromontane forest at this time made this niche less productive. Thus, the small-scale shifts in habitat preferences to cope with aridity identified in other montane records do not appear to follow a strict ecotonal model at Prospect Farm. Instead, I speculate that adaptations to more open grassland conditions in this instance are influenced by reduced investment in the forest niche. Furthermore, the inferred contraction of lake levels at this time could have stopped groups from shifting their home base to higher elevations, in favour of a base positioned nearer to the lake's resources and surrounding grassland. The habitation of xeric grassland may alternatively indicate the movement of a group from adjacent areas into the basin, who settled at the site, and had pre-existing adaptations to this habitat (see Section 7.5.3.7 below).

7.5.3.7 Demographic-ecological models: Phase II-B (PS3)

The inference that occupation intensity in PS3 was higher than in PS2, despite the fact environmental reconstructions indicate that subsistence-risk probably increased, suggests that migration, human agency, and associated demographic changes may have had a greater influence on landscape use during Phase II-B than that of environmental conditions. It is possible to explain the signal of low residential mobility and high occupation intensity in PS3 as reflecting increased population pressure within the basin. Population pressure is likely to have been mediated by regionally arid climatic conditions that are expected to have existed in surrounding lower elevation areas at this time. If regional aridity was severe enough, this could have forced groups and mesic adapted fauna from neighbouring basins to migrate to highland areas, as proposed by the EARH (see Section 7.5.3.7 above). This would in theory have increased local population densities and inter-group competition within the basin, resulting in competition over denser resource patches found here compared to adjacent areas.

One possible source area for the ostensive populations moving into the Nakuru-Naivasha Basin during II-B is the Victoria Basin. The transfer of raw material from the former to the latter demonstrates the connection of these regions since, at least, the Late Pleistocene onwards (e.g. Merrick and Brown, 1984a, 1984b; Faith et al., 2015; Blegen et al., 2017; Frahm et al., 2017; Frahm and Tryon, 2018). The paucity of dates from the Prospect Farm sequence make it difficult to say with confidence when PS3 was formed, although it seems likely it corresponds to MIS 4. At this time the Victoria Basin is recorded as being significantly drier than today. However, sites here indicate that it was still able support human populations (Beverly 2015a; Beverly 2017). Both the records from Prospect Farm and the Victoria Basin

indicate conditions more arid than the present (Beverly, 2017), however differences in the proxy methods used in this thesis and other studies, mean comparisons made to suggest which environments were more inhospitable to human groups lack equivalency.

It is possible that a 'push-pull' mechanism could have existed between the Afromontane zone and lowland areas during periods of aridity, similar to larger, regional scale ecological-demographic changes recorded in South Africa (Stewart et al., 2016; Stewart and Mitchell, 2018), infrequently between Tropical and equatorial East Africa (Blome et al., 2012), and more speculatively between the Turkana Basin and the Ethiopian highlands (Foester, et al., 2015; Brant et al., 2017; but also see Wright et al., 2015). However, during the Holocene, when these connections are easier to reconstruct, the movement of material by LSA groups is more closely linked to humid periods (e.g. the AHP), rather than arid episodes. Furthermore, there is currently no evidence to suggest that movement of raw material between the two areas was bidirectional. While the behaviours of LSA and MSA groups may have been different in response to environmental and demographic pressures, this suggests that other population sources for hypothetical migrations to the Nakuru-Naivasha Basin other than the Victoria Basin should be considered. Obvious candidates are the Turkana Basin and the southern Kenyan Rift, that lack direct palaeoenvironmental records during stadial phases of the last glacial period but are modelled as being extremely arid during MIS 4 (see Chapter 3. Figures 3.2 and 3.3). Connections between adjacent areas and the Nakuru-Naivasha Basin during the Late Pleistocene require further testing, with the only firm connection being with the Baringo Basin within the KCR, based on the movement of obsidian between the two areas (Brown et al., 2013; Blegen et al., 2017). Analyses of changes in technological complexity, local and regional site connections, and dating, need to be completed for the Prospect Farm sequence to further test these competing theories.

7.5.3.8 Acquisition of raw material as a factor in structuring the Prospect Farm archaeological record

Access to a high-quality source of raw material near the site during all occupation phases, may have made it more attractive than other sites in the area. It is possible that a cultural preference for raw material on Mt. Eburru may have outweighed the challenges of adapting to changing environments at the site and that the groups that settled at Prospect Farm may have needed considerable resilience in order to continue to access this material (see Section 7.5.4.1). Thus, control of this material may have been the main factor shaping changes in mobility and occupation intensity etc. at the site. Similar models have been suggested for LSA hunter-gatherer and pastoralists groups during the Eburran phase in the Nakuru-Naivasha Basin. For example, Frahm and Tryon (2018) have recorded the exclusive use of obsidian from Mt. Eburru by Elementian pastoralist groups, whose sites were located up to (~200 km away). On the other hand, Savanna Pastoral Neolithic groups only exploited obsidian sources near Lake Naivasha (Goldstein and Munyiri, 2017): they speculate that this pattern indicates controlled access to these two raw material sources, mediated by social or physical factors.

Information on obsidian sourcing at Prospect Farm and from other earlier MSA sites in the region demonstrates the occasional long-distance transport of material, indicating inter-basin mobility and likely the existence of wide exchange networks, but also an ongoing preference for material near to occupation sites Merrick and Brown, 1984a,b; Merrick et al., 1994; Deino and McBrearty, 2002; Negash and Shackley, 2006; Tryon and McBrearty, 2006; Blegen et al., 2017; Brooks et al., 2018). Merrick et al., (1994) note a trend toward the increased movement of obsidian from intermediate sources from the MSA to the LSA. Obsidian sourcing data from similar late MSA/MSA-LSA 'Transitional' assemblages from Prolonged Drift and Prospect Farm Phase IV (presumed to be of a comparable age), indicate that inhabitants of Prolonged Drift sourced ~90% of their material from Njorowa Gorge and the Sonanchi Crater (see Figure 7.4). These outcrops are located around \sim 30 km further away from the Prologue Drift than those on Mt. Eburru, which are more readily accessible source of high-quality raw material (Merrick et al., 1994). This indicates increased mobility and a preference for a particular type of raw material of groups at Prologued Drift at this time, but also suggest a deeper antiquity of the control of resource by groups on Eburru (i.e. it may not be solely an LSA or pastoral Neolithic phenomenon). The current lack of obsidian sourcing data from Phases I to II-B, means that it is not possible to rule out the possibility that at times of population and/or environmental pressure, the need for control of this resource had the greatest influence in structuring the archaeological record at Prospect Farm.

7.5.3.9 Summary of MSA behavioural-ecological models for MSA phases at Prospect Farm

Despite the signs of increased aridity in PS3, occupation intensity reached its highest levels during this period. By combining aspects of risk-based and specialised subsistence models with those that consider demographic factors, it is possible to make the argument that competition for dense resource patches and raw material sources in the mosaic environments, created by the rift topography, could have driven innovations that might have allowed larger populations to be maintained in the basin (e.g. Ugan et al., 2003). Further research is necessary to elucidate variability in MSA landscape use in response to shifts in environmental conditions at Prospect Farm and in the wider basin, and to overcome problems of equifinality and equivocal evidence that affects interpretations here. Comparison of the available, albeit limited, archaeological indictors of human behaviour with ecological data, indicates a move away from the strictly ecotonal based subsistence model of Phases I and II-B during Phase II-C, that anticipates the greater viability observed in landscape use patterns of MSA-LSA 'transitional' and LSA groups in the basin (see Wilshaw, 2013). The ability of MSA groups (presumably H. sapiens) to shift between the more generalised exploitation of broad niches and specialised exploration of narrow niches within them, at Prospect Farm, has been observed in an increasing number of MSA studies across Africa. This 'generalist specialist' behaviour has led to suggestions that this adaptation is a hallmark of our species (see Roberts and Stewart, 2018). These findings also support the idea that such an adaption could have helped hominin populations to survive by allowing groups move between refugium in East Africa that presented different ecological challenges, as is proposes by the refugium networks theory (Mirazón Lahr, 2013).

7.5.4 Landscape and behavioural models in later MSA and MSA-LSA 'transitional' levels of <u>Prospect Farm</u>

The archaeological record at Prospect Farm does not indicate a dramatic replacement of MSA by LSA traditions associated with a large population replacement event, or a rapid neurological-cognitive shift. Instead the more gradual introduction of LSA features (e.g. blade production and other innovative behaviours) into the assemblage has been recorded at other sites across the continent, where they have been linked to a variety of environmental, demographic, and social factors.

7.5.4.1 Mesic vs. xeric mobility models in the later MSA and MSA-LSA 'transitional' levels of <u>Prospect Farm</u>

Using a risk-based model of cultural change, Ambrose (2002) interpreted the lower proportions of more distant raw materials in MSA Phase III (which Ambrose assigned to the last interglacial period based on the character of lithics in this phase) as representing an ecotonal based model of settlement. Following the same reasoning, higher proportions of raw material from intermediate distances (~30 km) in Phase IV (~50 ka) were inferred as representing increased mobility under glacial climate conditions. Several studies suggest the increased production of microliths and points during the LSA, using fine-grained non-local raw materials, indicates the widespread development of projectile technology (Ambrose, 2002; Brooks et al. 2006; Shea et al., 2006; Tryon and Faith, 2013; Pargeter and Redondo, 2016). Following the *Ecotonal Hypothesis*, Ambrose (2001) linked the production of microliths (recoded in the Phase IV assemblage) to the exploitation of less predictable high-risk glacial environments.

Idealised vegetation models for Phase II-C to IV, that cover the final MSA and MSA-LSA 'transitional' assemblages at the site, record subtle shifts from semi-arid to semi-humid, and back to semi-arid conditions (see Section 7.4.1.4). These vegetation reconstructions show patterns similar to those observed at other pre-LGM MIS 3 sites in East Africa (i.e. short-lived and smaller scale fluctuations in climate conditions compared to the early part of the last glacial period are set against the backdrop of incresead climatic stabality from ~75 ka onwards and the comparative interstadial amelioration of climate before the onset of LGM aridity). It is also important to reiterate that while it appears that a change in vegetation structure towards more open conditions occurred during Phase IV, that this signal may be partially biased by the polygenic nature of phytolith assemblages in palaeosols; and could either represent the averaging of more extreme swings in vegetation conditions or rapid small scale vegetations changes (see Chapter 6.8.5.3.4).

Following the ideas laid out in the *Ecotonal Hypothesis* and other arid grassland expansion models, it could be argued that the shift towards more open savanna conditions, as climate moved towards full glacial conditions in Phase IV, was responsible for increased mobility on the landscape. This ecological shift could have mediated the spread of grassland associated LSA technological traditions and populations (Tryon et al., 2016), which could explain the high percentages of raw material from intermediate sources at this time in the Prospect Farm record (see Figure 7.4). Reassessment of the dates and palaeoenvironments of the Prospect Farm sequence makes it unlikely that Phase III material was produced during MIS 5 (see Section 7.4.1.4). However, it could also be argued the shift towards preLGM humid conditions in Phase III, associated with reduced residential mobility, supports arid grassland expansion models, rather than models in which mobility was encouraged by mesic conditions. Specifically, more wooded conditions on Mt. Eburru and surrounding the Masai Gorge could have limited access to raw material outcrops in the western, low elevation areas of the Naivasha Basin. It is however important to note that the vegetation changes that occur through the MSA-LSA transition at Prospect Farm do not constitute a major ecological shift and are less profound that those observed between earlier MSA occupation phases in the sequence. This suggests that climatic factors alone are not likely to have resulted in the independent emergence of LSA technology at Prospect Farm. However, as stated the long time-depth and potential for time averaging in PS5, means that rapid or large-scale shifts in climatic/environmental factors, that effected the local ecology at the site, cannot be entirely rule out as a driving factor in the MSA-LSA transition at the site.

7.5.4.2 Demographic-ecological models: Phase II-C to IV (PS4 to PS5)

Demographic changes, occurring under various climatic conditions, have been hypothesised to be at the heart of the MSA-LSA transition at sites across Africa (e.g. McBrearty and Brooks, 2000; Henshilwood et al., 2003; Kusimba, 2005; Powell et al., 2009; Eren et al., 2013; Mackay et al., 2014; Tryon and Faith, 2016). Increases in occupation intensity, residential mobility, and the emergence of LSA technology in Phase IV at Prospect Farm are consistent with higher rates of cultural transmission through expanded territories and inter-group connection. Elsewhere, the factors have been associated with the continentwide increase in population density during MIS 3. In this case, in terms of palaeodemography, the transition at Prospect Farm can be viewed as one example of the localised changes that formed the longterm MSA trend towards larger, more dense populations globally (Tryon and Faith, 2016). At Prospect Farm the initial increase in occupation intensity in Phase III is associated with more mesic conditions. If a growing human presence existed in the Nakuru-Naivasha Basin at this time, it is reasonable to suggest that it may have been rooted in the more widespread pre-LGM climatic amelioration. Assuming that population pressure remained high in Phase IV, as is denoted by continuing high estimates of occupation intensity, then we may argue that the emergence of LSA technology occurred as a consequence of increased contact with other groups already in or entering the basin. This contact could have been competitive or a more mutually constructive exchange of ideas. Limited evidence for changes in sourcing of raw material originating over 75 km away from Prospect Farm suggest that changes in demographic and environmental conditions did not significantly alter the behaviour of the occupants of the site in terms of their inter-basin mobility. This said, increases in chert tools in both Phase III and IV may indicate more long-distance transport or exchange (see Section 7.5.1). However, sourcing of this material is not certain enough to be more exact about any potential changes in mobility or expanded social networks that may have emerged during this period. In both scenarios it is likely that environmental change would mediate this shift rather than being the primary driver of it.

Similar patterns have been inferred across the MSA-LSA transition at Nasera Rockshelter [MIS 4-1] (Tryon and Faith, 2016) and at Mumba Rockshelter [MIS 5e, 4, 3] (Eren et al., 2013), both in Tanzania.

At these sites long distance procurement of raw material is also observed in late MSA and MSA-LSA transitional assemblages (Merrick and Brown, 1984; Mehlman, 1989; Merrick et al., 1994). At Nasera, lithic records indicate that significant declining residential mobility across the MSA-LSA transition in huntergatherer groups, 'crosscut' a habitat shift from drier more open to more mesic conditions that occurred across the LGIT. Tryon and Faith (2016) proposed that increasing population density may have reduced residential mobility in this case, as a response to sparser resources and the defence of territories. Faunal records from Nasera also indicate a shift towards more humid conditions prior to the LGM, set against a long-term trend of increased aridity, as observed in Phase III at Prospect Farm. It is feasible that the initial move towards the adoption of LSA technologies in Phase III at Prospect Farm is the result of increased territoriality and defence of more abundant resources, under locally more mesic habitat conditions as populations expanded. A similar model has been suggested by Eren et al., (2013) for the transition at Mumba Rockshelter. At Prospect Farm, increased territoriality appears to have been compounded as environmental conditions began to deteriorate into Phase IV. Increasing population pressure during Phase III is partially supported by the fact that mobility is notably lower in Phase II-C; with more focus on local raw material sources. These patterns are more consistent with earlier MSA phases in the sequence, as well as with differences observed between MSA and LSA raw material procurement strategies at other sites across East Africa. However, this interpretation is complicated by the sources of ~30 % of raw material from Phase II-C being unknown and feasibly related to other factors (e.g. MSA toolkits being less well adapted to the exploitation of grassland environments in the basin).

Regular trips for raw material away from the main site, in Phase III, and more so in Phase IV are consistent with trends observed in other sites across East Africa during the LSA, that record repeat trips to single distal sources, often located at the riparian zone (e.g. Pearl and Dickson, 2004; Tryon et al., 2010; Wright et al, 2015). At Prospect Farm, more regular trips to obsidian sources, near to the lake shore in the Naivasha Basin, may also indicate a move towards a more generalised subsistence strategy (i.e. that more completely exploited the mosaic habitats found within the rift setting, in which resources from lake shore settings constituted a more significant part). Similar multifaceted subsistence and raw material procurement strategies are observed in LSA groups in the basin (Ambrose, 2002; Wilshaw, 2013) and at other sites in East Africa (e.g. Tryon et al., 2010; Shipton et al., 2018).

As introduced in Section 7.5.3.8, a cultural preference and strategic control of raw material sources in the basin could have emerged earlier than previously thought, during the MSA. It is notable that between Phase III and IV groups at Prospect Farm shifted their raw material procurement strategy away from multiple sites in Naivasha towards a single intermediate source at Sonanchi crater. This site provided around half of the material at the site during Phase IV, with the other half coming from local sources. Sochanai is located near to both Njorwa Gorge and Ololeria (visited during Phase III). This suggests that local environmental conditions were not a constraining factor in access to these sources, or to a shift in obsidian sourcing across the MSA-LSA transition. As such, it seems more probable that demographic pressure, that may have been mediated by ecological conditions, intensified territorial behaviours during Phase IV. However, again, we must consider that the palaeoenvironmental signal from PS5 is not able to be fully resolved at this time.

Another model that requires consideration is that technology itself was the principal driver of demographic change across the MSA-LSA transition. For example, Kusimba (2005) envisages a positive feedback loop whereby microlithisation enhanced food procurement, that in turn increased population densities and supported further technological innovations, allowing hunter gatherers for the first time to fully exploit open grassland niches during the LSA (e.g. Shea [2011]) which resulted in extensive population expansions. While it could be argued that both climatic amelioration or deterioration set the conditions for such a feedback loop to become established, more evidenced is needed on the function of specific LSA tools in different environmental contexts, before this hypothesis can be tested.

7.5.4.3 Summary of behavioural-ecological models for MSA-LSA transitional phases at <u>Prospect Farm</u>

When all records of the MSA-LSA transition across East Africa, including the Prospect Farm sequence, are considered, it appears generally that lithic adaptations, increasing hunting efficiency, and migrations were all strategies used to cope with denser populations. It is also apparent that on a regional scale, palaeodemographic changes are likely to have been linked to both environmental deterioration and amelioration that affected primary productivity, the structure of resources on the landscape, and changes in sociality exercised through kinship and descent relationships. However, the precise underlying causes of the speculated demographic changes at these sites and Prospect Farm remain to be demonstrated. It is clear that further analysis of both Prospect Farm archaeological material and of other MSA/LSA sites within the Nakuru-Naivasha Basin, that provide more detailed information on palaeodemographic changes, mobility, intergroup connections, and the function of tools in specific environments, is necessary before a more nuanced understanding of the role of palaeoenvironmental and palaeodemographic shifts in driving and mediating the transition from MSA to LSA technology in this area of East Africa can be achieved.

7.6 Habitat preferences at Prospect Farm in the context of regional migrations and refugium networks

Recent comparisons of MSA and LSA archaeological assemblages to local signals of environmental change in East Africa (Robinson, 2017) and South Africa (Ziegler et al., 2013; d'Errico et al., 2017; Chase et al., 2018), that benefit from high temporal resolution of archaeological- and associated climate records, indicate that technological changes associated with the adoption of LSA technologies can sometimes be directly linked to abrupt, millennial-scale shift in climatic and local habitat conditions. However, these studies also underscore the fact that the trajectory of environmental and technological-behavioural changes varies between sites. These studies also reinforce the idea that the 'push-pull' factors associated with dispersals and movement in and out of refugia appear to have varied spatially and temporally over regional and sub-regional scales. This is perhaps best represented by the contrasting effects of aridity on Central African forest and the Sahara. In this case, aridity appears to have aided dispersals in the former

while creating a biogeographic barrier to contact in the Sahara (see Chapter 1.7.2.4). The converse is thought to be true during humid periods where burgeoning palaeohydrological networks in the Sahara facilitated increased contact between previously isolated groups (Scerri et al., 2014; Drake and Breeze, 2016). Several studies postulate a 'Green Sahara' as a pull mechanism that encouraged groups to leave Africa via vegetated riverine corridors (e.g. Drake et al., 2011; Timmermann and Friedrich, 2016). Others predict that hominin groups were 'pushed' out of Africa by a phase of aridity caused by North Atlantic Heinrich events occurring over several thousand years (e.g. Carto et al., 2009). More recent studies suggest that *H. sapiens* left Africa during transitions from humid to dry conditions during MIS 5a – MIS 4 and dry periods (MIS 4 and early MIS 3), with MIS3 being only marginally wetter than the present-day; suggesting a 'push' mechanism for these migrations (Tierney and Zander, 2017). An alternative way of viewing this pattern is that migrations and inter-regional connections may have increased during a period when climate was in a transitional phase (i.e. when two connected regions experienced similar climatic conditions) (e.g. Cohen et al., 2007; Scholtz et al., 2007).

The temporal resolution of climate change in the Prospect Farm record is too coarse to suggest if rapid, high amplitude climatic shift affected cultural trajectories at the site. Furthermore, until ongoing archaeological analysis can be completed, it is difficult to decide whether arid, mesic or transitional climate period migration models are most appropriate for different occupation phases. I suggest that further work should initially focus on comparing assemblage compositions from Phase II-C, III and IV material from Prospect Farm with lowland MSA sites such as Rusinga Island, Aringo and Kisaaka in the Victoria Basin, that have been shown to be of a similar age (~49-46 ka [Faith et al., 2015]) and have links to Naivasha (see Section 7.5.3.7). Particular attention should be paid to the environmental context of specific tool types at Prospect Farm (e.g. bifacial points), that have been linked to exploitation of grassland environments in lowland settings (Tryon et al., 2010, 2012, Faith et al., 2016). Such an approach may allow us to better understand the potential for environmentally mediated technological and environmental driven dispersals between these areas. Comparison should then be extended to other published sites in East Africa, as well as to other MIS 5-3 sites in the Turkana Basin, newly identified through the *In-Africa* project.

7.7 Thesis conclusions

The principal aims of this thesis have been to reconstruct habitat variability and human habitat preferences in the highland setting of the KCR. This was carried out to test competing behavioural-ecological models of human adaptations to past environmental change, and to refine our understanding of the role of forest highland refugia in supporting past human populations in East Africa. While past habitat preferences have been established, testing of behavioural-ecological models is complicated by chronological uncertainties and incomplete archaeological information from Prospect Farm. These limit the inferences that can be drawn from the variability evident in the archaeological assemblages. Comparisons with sites in other areas are similarly constrained. Nevertheless, it has been possible to identify tentative linkages between habitat preference, occupation intensity and residential mobility.

Findings suggest that palaeoclimatic factors played a secondary or mediating role in techno-cultural and mobility changes that occur across the MSA-LSA transition at Prospect Farm, rather than being a primary driver of them.

To the author's knowledge, the palaeovegetation record from Prospect Farm presented here is the only record that provides local palaeoenvironmental information from within the Afromontane zone of the KCR prior to the LGM. As such, it is currently the only record that can be directly used to establish changes in MSA habitat preferences in this key area of Africa contributing to our understanding this period of human evolution. Prospect Farm's litho- and bio-stratigraphic sequence records vegetation change on Mt. Eburru thought to correspond to local and regional changes in monsoon dynamics and glacial boundary conditions. The sequences from Prospect Farm show that MSA groups would have had to cope with frequent, significant and unpredictable changes in environmental conditions, as well as with alterations in the landscape in the basin, such as abrupt perturbations caused by volcanic events on Mt Eburru, producing ash fall and pyroclastic flows.

For the time being, the current data from Prospect Farm is only detailed enough to suggest which archaeological patterns are roughly compatible with certain climatic or demographic pressures. However, it has still been possible to identify important trends in changes in human habitat preferences at the site. In particular, new analyses from Prospect Farm presented in this thesis have revealed that changes in habitat preferences in the MSA phases at Prospect Farm indicate that the ecotonal subsistence and settlement strategy, proposed by earlier studies as a key MSA behavioural adaptation in rift settings, is not supported in all MSA occupation phases. Instead, behavioral-ecolgical models which appear to be a 'best-fit' for each occupation palse suggest that more complex senarios in which demographic likely to have been as important, if not more so, in influencing human land use practices and social networks that shape the archeolgical record of the site. A summary these 'best-fit' models are provided for each occupation phase in Table 7.2 that consider occupation intensity and mobility, climate variability across East Africa during the associated intervals, and broad changes in site frequency, as well as a related assessment of the potential of the basin to have acted as a refugium a during these periods.

Ongoing and future work is expected to improve our understanding of settlement and subsistence strategies themselves and of the direct links that existed between technological organisation and these strategies, and their relations to climate records. In doing so behavioural-ecological models at Prospect Farm and the mechanisms at the heart of trajectories of cultural change should be able to be more fully tested. Specifically, the lack of dates for Prospect Farm make it difficult to determine whether deposits at the site coincided with hyper arid phases elsewhere in East African, or in other cases whether they are absent from Prospect Farm. However, the record provisionally suggests that ecological conditions at the site remained relatively stable throughout the MSA and early LSA periods. Thus, Prospect Farm and the Nakuru-Naivasha Basin had the potential to have acted as a refugium over this period. To establish whether it fulfilled this role, a great deal of further work is necessary, not only at Prospect Farm but at other sites in the region, focussing on re-dating of existing sites, the excavation of new sites, and their

integration into a regional archaeological-environmental-chronological framework. The new palaeoenvironmental record from Prospect Farm presented in this thesis means that once archaeological and dating work from the site is complete, the sequence will be comparable to regional records, and the site will provide an important reference point to develop comparisons across the region. Consequently, the information presented here has the potential to make a significant contribution to our understanding refugium networks, human population change, the timing and routes of dispersal, and their underlying adaptations during one of the crucial stages in the evolution of *H. sapiens*.

In conclusion, greater variability in MSA settlement and subsistence strategies recorded in the Prospect Farm record suggest that the factors underlying them were more complex than have been suggested by earlier behavioural-ecological models (e.g. the *Ecotonal Hypothesis*), and that the responses of MSA groups to past environmental and demographic pressures are likely to have been more diverse and possibly more flexible than previously believed. The finding that the niches inhabited by hominins were more variable than previously documented for the basin, support the concept that behaviour flexibility was a key component of the human adaption within putative refugium networks. It may be that this behavioural flexibility has its roots in the topographic variability and habitat heterogeneity of rift settings in East Africa. These mosaic landscapes have been implicated in the evolution of specific traits in earlier hominin species (e.g. Bailey et al., 2011; Reynolds et al., 2011, Winder et al., 2013), and share some attributes with the mosaic environments found in coastal areas of Africa, where complex 'modern' behavioural indicators are more regularly recorded during the MSA. This pattern is compatible with the complex picture emerging from other sites, across the globe, of diverse populations of behaviourally flexible MSA hunter gatherers, which became gradually adapted to a wide range of terrestrial and coastal environments, using opportunistic survival strategies, that changed as and when circumstance demanded (Shipton et al., 2018). This is not to say that these groups strategies were always 'optimal' or successful, however it does appear that this plasticity in MSA behaviour was key to the success of H. Sapien dispersals within and out of Africa and led in our species' exploitation of the majority of terrestrial ecosystems on Earth.

Archaeological occupation phases, associated palaeosols, inferred level of residential mobility, local vegetation conditions	Likely MIS stage and regional climate conditions (from costal, montane and lowland areas)	Potential for refugial conditions to have existed in the basin	Best-fit environmental subsistence risk-based models for occupation phases based on palaeoenvironmental and archaeological records from PF and other East African sites
Phase I (earliest MSA PS1. Moderate occupation intensity and limited residential moves. Closed-canopy Afromontane forest with a C ₃ grass understory.	 MIS 5e (~135-115 ka). Records from Lake Challa (Moernaut et al., 2010) and Panga ya Saidi cave (Shipton et al., 2018) indicate stable humid conditions in coastal areas. Similar conditions and high lake levels are present in highland areas in the study are (Trauth et al., 2003), as well as on the Horn of Africa (Voight et al., 1990); Natron and Magadi (in southern Eastern Rift Valley) (Hillaire-Marcel et al., 1986). No records exist form inland lowland areas, but an oxygen isotope-pollen record from the Arabian sea (Van Campo et al., 1982) and δD_{wax-IV} record from the Gulf of Aden (Tierney and Zander, 2017), indicate generally warm and humid conditions across the NE of the region. 	Low	Most consistent with the <i>Generalized Grassland Model</i> . (i.e. moderate occupation intensity limited residential moves, and the use of a single local raw material source under mesic conditions). Demographic pressure, associated with the general pollution expansion that occurred across Africa during MIS 5 (Blome et al., 2012), may have also encourage isolation of groups at Prospect Farm as a result of competition with other MSA groups for control of the sites raw material and/or its favourable position in the landscape for hunting and gathering.
Phase II-A (MSA) PS2. Low occupation intensity higher levels of residential mobilit Mesic C ₄ dominated grassland (savanna) environment with lim arboreal cover.	 MIS 5e to MIS 5d transition or MIS 5d (~115 -105 ka). Low lakes levels at Lake Challa and a sedimentary hiatus at Panga ya Saidi cave indicate a shift towards cooler more arid conditions for the duration of MIS 5d in coastal areas. This is also reflected in 8D_{wax-IV} record from the Gulf of Aden indicate increased aridity during 5d and 5b that is muted compare to that of MIS 4 and 3. Naivasha and lake level and Mt. Kenya pollen records (Olago et al., 1999) in montane areas indicate cooler and more arid condition during early MIS 5d and amelioration towards the end of this sub-stage, suggesting climate conditions may have been more favourable in the KCR than in coastal areas during this interval. No records from the Victoria basin exist from this interval. 	Moderate	Neither xeric nor mesic risk-based expansion models alone adequately explain low occupation intensity during this phase. The lack of independent measures of past mobility on the landscape limit more definitive explanations of social structure and landscape use during this period. It does however appear that the phase is characterised by decreased investment in the forest niche.

Table 7.2 Summary of 'best-fit' models for each occupation phase in the PF sequence that consider occupation intensity and mobility, climate variability across East Africa during associated intervals, and broad changes in site frequency. A related assessment of the potential of the basin to have acted as a refugium a during these periods is given.
Archaeological occupation	Likely MIS stage and regional climate conditions	Potential	Best-fit environmental subsistence risk-based models for occupation
phases, associated palaeosols,	(from costal, montane and lowland areas)	for refugial	phases based on palaeoenvironmental and archaeological records from PF
inferred level of residential		conditions	and other East African sites
mobility, local vegetation		to have	
conditions		existed in	
		the basin	
Phase II-B (MSA) PS3.	MIS 4 (\sim 71-57 ka) or colder/more arid period of MIS 5c,	Moderate to	Consistent with elements of Tryon et al's xeric grassland/lakeside model (i.e. use of
	5b, or 5a (\sim 96-82 ka).	High	the site but different mobile MSA groups) but also with the isolation of groups
High occupation intensity low			under and climate conditions, as proposed by the EARH. Further information
residential mobility.	Climate was relatively stable in coastal areas during later		on lithic reduction strategies (that would suggest either decreased or increased
	MIS 5 and MIS 4, however NE marine records indicate		mobility) and other sites in the basin at the time is necessary to determine land
Edaphic wooded grassland	aridity during MIS 4 and arid episodes are present records in		use patterns in the basin at the time. Arid conditions in lowland areas and
(savanna with very low arboreal	coastal areas from Lake Challa during MIS 5c. Similarly, a		indications that site frequency declined at this time, led (Blome et al., 2012)
cover).	depositional hiatus, thought to represent the coldest period		suggest that refugial conditions may have increase subsistence risk and
	of MIS 4 occurs in the Panga ya Saidi cave record. Cold and		population pressure that may have had a strong influence on human behaviour
	very dry conditions are present on Mt. Kilimanjaro and Mt.		during this interval.
	Kenya in the earlier part of this stadial period, while the		
	Naivasha record shows low to intermediate lake levels were		
	present in the study area. These trends occur in contrast to		
	records from the Horn of Africa which show a brief wet		
	period occurring at the beginning of MIS 4 (Voight et al.,		
	1990). Palaeosol records for eastern part of the Victoria		
	basin indicate the onset of aridity from MIS 5b onwards.		
Phase II-C (MSA) PS4.	MIS 3 (~57-29 ka).	Low	There is no definitive support for either xeric and mesic risk-based expansion
			models as intermediate climate conditions are associated with intermediate levels
Low occupation intensity and	Climate was cool and humid to semi-humid and relatively		of residential mobility. However, low occupation intensity under more open
intermediate residential mobility.	stable in coastal areas as is also the case in pollen records for		conditions compared to PS1 support xeric grassland expansion models, such as
	Mt. Kenya and Mt. Kilimanjaro. Short-lived, probably rapid		the <i>Ecotonal Hypothesis</i> . Overall land use patterns indicate a move away from the
Transitional shrub savanna with	climatic reversals are also found in several records.		strictly ecotonal based subsistence model of Phases I and II-B during Phase II-C,
possible fluctuation occurring	Palaeosol records for eastern part of the Victoria basin		that anticipates the greater variability observed in landscape use patterns of
between moderate to low	continued aridity up until end of MIS 3. No lake record is		MSA-LSA 'transitional' and LSA groups in the basin.
arboreal cover.	present from Naivasha for this interval.		

Table 7.2 Continued.

Archaeological occupation phases, associated palaeosols, inferred level of residential mobility, local vegetation conditions	Likely MIS stage and regional climate conditions (from costal, montane and lowland areas)	Potential for refugial conditions to have existed in the basin	Best-fit environmental subsistence risk-based models for occupation phases based on palaeoenvironmental and archaeological records from PF and other East African sites
Phase III (final MSA) PS5. High occupation intensity and lower residential mobility than in Phase IV. Transitional shrub savanna/woodland with moderate arboreal cover	MIS 3 (~57-29 ka). As described for Phase II-C.	Low	Lower residential mobility (relative to Phase III) under more mesic conditions supports xeric grassland expansion models (e.g. The <i>Ecotonal Hypothesis</i> and of Tryon et al's (2016) <i>xeric grassland/lakeside model</i>) rather than models in which mobility was encouraged by mesic conditions (e.g. the <i>EARH</i> and <i>Amplifier Lake Hypothesis</i>). However, vegetation shifts across this phase is subtle, suggesting that demographic rather than physical environmental pressures played a greater role in driving intra assemblage variability and behavioural shifts (e.g. adoption of LSA technologies and repeat trips to single distal obsidian source near the lakeshore) that occur in Phase III and IV.
Phase IV (MSA-LSA 'transitional' industry) PS5. Lower occupation intensity and higher residential mobility compared to Phase III. Transitional shrub savanna/woodland, possibly with lower arboreal cover than is associated with Phase III material.	MIS 3 (~57-29 ka) or MIS 3-2 transition (~29-27 ka). Marine records indicate increase aridity during MIS 3-2 transition, however records from both Lake Naivasha and some other montane and costal sites (such as Panga ya Saidi cave) do not show extreme aridity present in the lowland terrestrial records of the Turkana and Victoria Basins during early MIS 2. This suggest that generally montane and coastal areas may be buffered from extreme aridity during this transition and the early part of MIS 2. Lake Challa does however record lake lowstand events during MIS 2.	Low during MIS3 but high during the LGM (MIS 2)	Land use patterns are broadly consistent with xeric risk-based expansion models. However, as site frequency shows steady increase during MIS 3 (Blome et al., 2012) across African and in the Nakuru-Naivasha Basin (Ambrose, 2003) despite increasing aridity towards the LGM, changes in land use are likely to be better explained by increased demographic pressure and associated heightened territoriality

Table 7.2 Continued.

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APPENDICES

APPENDIX 1

1.1 Background to the formation of the East African Rift System

The EARS has developed though an on-going process of divergence between the Somali and Nubian tectonic plates, which began during the Cenozoic era ~3 million years ago (Barker et al., 1972; Chorowicz, 2005), following more ancient rift structure that formed from the Precambrian onwards (Macdonald et al., 2001). Progressive faulting and uplift during the late Cenozoic to Plio-Pleistocene resulted in the formation of troughs in which large EARS fresh-water lakes have formed (e.g. Lake Turkana) (Tiercelin and Lezzar, 2002; Trauth et al., 2007). These fault troughs are generally elongate, tracking the major fault trends (Olaka et al., 2010). The Eastern Gregory Rift is generally >100 km wide, except at the northern end of the Turkana Basin and to the south in Tanzania, where it splays outwards to >300m and terminates (Chorowicz, 2005). The development of high-angle boarder faults on eastern side of the rift and a faulted flexural margin on the western side have resulted in the highland domes (with peaks between 1500 and 5100 m a.s.l.) of the rift and the closed-graben shaped basins (Sepulchre et al., 2006; Olaka et al., 2010; Trauth et al., 2007). During the Quaternary, the formation of volcanic edifices and internal segmentation of the rift has created smaller sedimentary basins within larger rift basins (Strecker et al., 1990; Bergner et al., 2003; Mortimer et al., 2007); in which small, predominantly saline lakes, currently exist (e.g. Ziway-Shalla, Awassa, Suguta, Baringo-Bogoria, Nakuru-, Magadi-Natron, and Manyara). Lakes Nakuru and Naivasha have been shown to increase their depth by + 180 m and + 110 m respectively during climatic optima.

1.2 The chronology and location of human fossils in Africa during the last 800 ka

Figure 1.1 summarises the chronology and location of human fossils in Africa during the last 800 ka (thousand years ago) (MIS 21 to MIS 1).



Appendix 1 - Figure 1.1. Geographic and chronological variability in African fossil hominins during the Middle and Late Pleistocene plotted against the marine δ^{18} O curve (Lisiecki and Raymo, 2005) with grey horizontal bars delineating warm approximate Marine Isotope Stages and white bars representing cold stages. Recent discoveries, thought to represent an early population of the *H. sapiens* clade, from Jeble Irhoud, Morocco, dated to 315 ± 34 (not shown, Richter et al., 2017), points to the potential earlier emergence regional complexity of the evolution of *H. sapiens* traits. The earliest evidence from East Africa is the Omo 1 specimen from Omo Kibish, Ethiopia, dated to 194 ka (McDougall et al., 2005). These fossils show some unique traits of modern human anatomy but there is still continuity with earlier species of homo (i.e. derived forms of *H. sapiens* groups in Africa, such as *H. naledi* (335 ka to 236 ka; Dirks et al., 2017) and other unknown populations of African hominins (e.g. Xu et al., 2017) means that interactions with other members of the genus, that may or may not involve the transfer of genetic information, should be considered in the process of the evolution and diversification of the earliest populations of *H. sapiens*. Figure from Mirazón Lahr and Foley (2016).

1.3 Evolutionary-ecological approaches to understanding the MSA and LSA

A myriad of different interconnected social and environmental factors feed back upon one another through niche construction processes (Banks et al., 2011; Odling-Smee et al., 2003; Foley and Mirazón Lahr, 2011; Riede, 2011) to bring about human behavioural changes. These are manifested to varying degrees in the archaeological record. The relationship between different socioecological factors is often difficult to tease apart and harder still to place within a relative causal hierarchy. Having said this, and while not supporting stringent environmental deterministic explanations for behavioural transitions, it is apparent that historic and contemporary hunter gatherer subsistence, land use, technology and some social behaviours demonstrate a direct relationship with environment (Kelly, 1995; Binford, 2001; Marlowe, 2005). As such, changes in MSA and LSA archaeological record have been increasingly interpreted in behavioural-ecological frameworks (Blome et al., 2012), often drawing from elements of optimal foraging theory; that emphasises the fitness-based trade-off decisions made by human groups in relation to variability in resources across a landscape as local environmental and demographic pressures changed (e.g. Ambrose and Lorenz, 1990; Marean, 1997; Kusimba, 1999; Marean et al., 2007; McCall, 2007; Tryon et al., 2016).

While it is the case that humans do not always behave optimally, evidence of human use of past landscapes is amenable to testing using the archaeological and environmental record. Therefore, an approach grounded within behavioural and evolutionary ecology, that provides an evolutionary perspective on culture, is arguably one of the best ways to tackle questions about the evolution of diverse behaviours in Africa during the late Quaternary period (McCall, 2007; Eren et al., 2013; Will et al., 2015; d'Errico et al., 2017; Thompson et al., 2018). These approaches provide the broad theoretical grounding for this thesis, which also draws on concepts in palaeoecology and vegetation ecology to understand human reposes to environmental changes at Prospect Farm.

Studies of MSA sites generally use stone tools as indicators of technological and social organization, mobility and demography. This is because these artefacts are the most continuous and often only source of information on biogeographical connections and estimates of the size of the physical (e.g. home ranges, habitat availability and site presence) and social landscapes (e.g. cultural boundaries, territorial ranges, trade and kinship networks) known to human groups (Will et al., 2015; Tryon and Faith, 2013; Tryon et al., 2016). Stone tools can also provide insight into specific behavioural adaptations (e.g. hunting and foraging behaviours, and raw material procurement strategies) through the combination of functional analysis of tools and concomitant palaeoenvironmental records (but see Villa and Lenoir, 2006).

1.4 The concept of a refugium and theoretical roots of hominin refugium models in East Africa

Both the distributions of MSA/LSA archaeological sites in relation to spatiotemporal patterns of palaeoenvironmental change and phylogenetic studies of late Quaternary animals suggest that past environmental shifts are likely to have been of central importance to East African biogeography and

population dynamics (i.e. population size, interconnectedness, densities and distribution) during the late Quaternary Period (Mirazón Lahr and Foley, 1998; Basel, 2008; Jacobs and Roberts, 2009; Blome et al., 2012). The concept of a refugium differs from that of a "bottleneck", in that it does not always imply continuity of a population following its retreat into a refugium. If environmental change is severe enough to reduce the capacity of a refugium to support a population, then it will become a zone of extinction. However, because refugium have been shown to remain stable over glacial-interglacial cycles they are often considered to be synonymous with a zone of species endemism (Bennett and Provan, 2008; Stewart et al., 2010; Keppel et al., 2012).

Several refugium models for hominins in Africa are rooted in earlier models of allopatric speciation (e.g. the *Forest Refuge Hypothesis*: Haffer, [1969] or the 'forest islands' model [Lönnberg, 1929; Moreau, 1933]), which posit that the existence of glacial forest refugia in highland areas, within the Afromontane phytochorion (White, 1978; Carbutt and Edwards, 2015), was a mechanism for the creation of genetic diversity as follows: On evolutionary time scales, species which were adapted to forested environments retreated into isolated forest refugia while lowland sites became largely uninhabitable. The divergent local ecological conditions within isolated refugia are hypothesised to have resulted in the emergence of derived traits, thus promoting genetic and phenotypic diversity. Subsequent expansions when conditions become more favourable led to both admixture and competition between species that further affected species diversity.

Phylogeographic studies, species-climate envelope modelling and modern distributions of plants and animals, support the idea that refugia created by the contraction and expansion of forest and savanna Biomes in sub-Saharan Africa had a major impact on population dynamics and the shaping of population genetic patterns during the late Quaternary (e.g. Menotti-Raymond and O'Brien, 1993; Kornas, 1993; Querouil et al., 2003; Bertola et al., 2016; Pozzi, 2016). Such studies have tended to focus on the geographical location of areas of high speciation and endemism in Afromontane organisms (e.g. Fjeldså and Lovett, 1997; Fjeldså and Bowie, 2008; Chala et al., 2017 and references therein; Mairal et al., 2017 and references therein). These indicate that both reticulate Afromontane species and mammals are concentrated in areas of proposed refugia (e.g. the Upper Guinea, the Cameroon Highlands, the Congo Basin, the Ethiopian Highlands, the Eastern Arch Mountains, and south-eastern South Africa) (Diamond and Hamilton, 1980; Crowe and Crowe, 1982; Mayr and O'Hara, 1986; Fjeldså and Lovett, 1997; Levinsky et al., 2013). Far fewer studies have focussed on the location of refugium for savanna species, although it has been suggested the Angola-Namibia area may have acted as a biodiversity hotspot for savanna species (Levinsky et al., 2013) and that less stable refugia for savanna ungulates, such as the common eland antelope, Taurotragus oryx, existed in East Africa (Lorenzen et al., 2010). Other studies indicate habitat loss associated with moister conditions and forest expansion caused regional extinctions in arid adapted species in the LVRM (Faith et al., 2015). These studies do not involve all faunal communities, nor are they a precise analogue for the location of human refugia. Aspects of the original Forest Refuge Hypotheses are no longer supported by more recent palaeoenvironmental reconstructions, which indicate that forest refugia occurred in both lowland (particularly Central Tropical Africa), as well as in highland zones (see Cowling et al., 2008; Cornelissen, 2016), and that Afromontane and Afroalpine plant species responded individually to late Quaternary climate fluctuations (Colinvaux et al., 2000; Ivory et al., 2016a; Ivory and Russell, 2016; Chala et al., 2017; Mairal et al., 2017). However, the fundamental principle that highland zones in equatorial East Africa were able to buffer the negative effects of climatic downturns, and acted as refugia for plants and animals, including hominins, during periods of habitat loss at lower altitudes, forms the basis of the East African Refugium Hypothesis, summarised in Chapter 1.7. Modern species distributions in the Nakuru-Naivasha Basin show that areas such as the Mau Escarpment, Mt. Eburru and the Aberdares Range act as refuges for some species today (e.g. the Mountain Bongo [Faria et al., 2011] and African Forest Elephants [Beale et al., 2013]), and so may have acted similarly in the past. This is supported by phylogeographic studies of plants, which imply that highland zones are centres of endemism and refugia for some species (Aldasoro et al., 2004; Ehrich et al., 2007; Gichira et al., 2017). Furthermore, palaeoenvironmental evidence for the Nakuru-Naivasha Basin suggest that forests may have remained here during the LGM (see Chapter 3.5.4).

1.5 Ecological basis for the exploitation of East African habitats by hunter-gatherers

Information that forms the ecological basis of models of hunter-gatherer subsistence in the different habitats is drawn from 1) the ethnographies of African hunter-gatherer groups; 2) contemporary observations of aspects of the ecology of habitats (e.g. carrying capacity, resource distribution and abundance); and 3) comparison between detailed archaeological records of land use and local palaeoenvironments. Optimal strategies detailed in these models set expectations about how different environments were exploited by MSA groups and potentially which were more favourable, or which were most fitness enhancing (a factor which could depend on pre-existing adaptations of a group to a specific niche). Generalised resources expectations for each of the main vegetation zone encounter in East Africa are listed in Appendix Table 1.1. These indicate that both mesic and arid savanna could have been productive environments for hunter-gatherer groups, but that they require different subsistence strategies and levels of mobility.

Vegetation zone	Resource expectations	
Desert	Minimal edible plant and animal resources. No/low human populations expected	
Sub-Desert/Sahel vegetation, generally of the Sudanian floristic zone	Small seeded grasses and forbs occur, while seeds and fruit of many trees and shrubs are available. Herds of herbivores occur but these are often of smaller herd size and/or body size than for Tropical savannah/woodland- grass mosaic	
Riverine corridors: marshes and gallery forests	Wild grains of grasses, sedges, and other aquatics as well as tubers are frequent. Small game, birds and fish are readily available, with some larger game, especially in dry season	
Tropical savannah/woodland grass mosaic [synonym: edaphic savanna]	Wild grass grains and other seeds are numerous, including wild progenitors of most tropical cereals; some tubers are available and numerous edible seasonal fruits. Large herbivore herds.	
Dry tropical woodland (e.g. Sudanian and dry miombo woodland) [synonym: eutropic savanna]	Numerous fruits, nuts and tubers. Edible seeds of herbaceous plants include wild pulses. Large herbivores are frequent but in small groups. Smaller game present but may be hard to catch.	
Moist tropical woodland and grassland mosaic (e.g Mosaic semi-deciduous forest and grassland [Guineo–Congolian] and wetter miombo woodland)	Wild grass grains and other seeds are numerous, including seasonal wild rice in local wetland; some tubers are available and numerous edible seasonal fruits. Large herbivore herds. Smaller game present but may be hard to catch.	
Moist tropical woodlands and rainforest (e.g. Evergreen forest [Guineo–Congolian])	Wild seeds are sparse in time and space; tree-nuts and fruits may be locally and seasonally abundant but are likely to be unpredictable in time and space. Larger game is rare and smaller game is harder to catch. Very low human population densities expected.	
Tropical montane vegetation (e.g. Afromontane forest)	Some edible fruits, seeds and tubers, but generally only localized and seasonal. Few large game, and hard to catch small game. Low human population densities expected.	

Appendix 1 – Table 1.1 Generalised resources expectations for the main vegetation types encountered by hominin groups in East Africa. After Bovin et al., (2013).

1.6 The East African Refugium Hypothesis: locations of refugia - supporting information

The steep-climatic and environmental gradients of African mountains, which create distinctive altitudinal ecological zones that change over short distances (see Chapter 2.5), have been proposed to be attractive environments for hunter-gatherer groups for several reasons. Firstly, palaeoenvironmental reconstructions suggest that when climate conditions in a given area were locally cooler and more arid, changes in precipitation and temperature have a more extreme impact on vegetation distributions in lowland areas due to both the lack of sharp topographic relief found in highland zones and the more continuous supply of moisture to highland areas. Furthermore, records suggest that in some areas of East Africa, a more continuous seasonal supply of monsoon rains from the Indian Ocean means water availability and habitats may have been more stable during climatic downturns, relative to northern and southern Africa (see Chapter 3.5.3). Additionally, the variety of habitats available to hominin groups in montane rift lake basin settings could have increased resource availability, which mitigated against resource unpredictability, thus lowering risk. Lakes themselves attract both migratory and residential mammals and provide predictable resources in the form of fish, a variety of edible fruits, sedges, and woody plant species that are less severely affected by seasonality. As such, lakes, particularly those in highland rift settings, are thought to have provided more stable habitats for hominin groups (Marean

and Assefa, 2005; Basell, 2008; Blome et al., 2012; Mercader et al., 2013; Foerster et al., 2015; Wright et al., 2017).

1.7 Evidence in support of behavioural-ecological models discussed in Chapter 1

1.7.1 Ethnographic basis for the exploitation of East African forest and mesic savanna environments by hunter-gatherer groups

There are relatively few ethnographic records of hunter-gatherer adaptation to montane forest environments from which to establish the ecological basis for the exploitation of these forest types, that might be tested against the archaeological record of East Africa. The Okiek provide the only ethnographic evidence of habitation of East African forest environments. This group historically occupied the Afromontane forest boundary in highlands areas on the Mau escarpment (see Figure 1.7). They practiced opportunistic, non-specialised hunting but specialised in the seasonal gathering of honey (Blackburn, 1982). While no ethnographic data exist for hunter-gatherer groups in mesic savanna habitats (i.e. in which there is high rainfall, high woody cover, and low biomass of large herbivores [see Section 1.7.3 for details of differences between savanna types]), there is strong evidence in the archaeological record for the exploitation of this niche by MSA and LSA groups. On a site-specific basis, archaeological records that suggest mesic conditions are often associated with reduced residential mobility (see Appendix 1.7.4). This finding is in opposition to the increased mobility and inter- and intra-regional connections under mesic conditions proposed in the EARH.

<u>1.7.2 The ecological basis for the exploitation of East African wooded environments and arboreal cover as a key component of the *EARH*</u>

The exploitation of forest biomes by MSA hunter gatherers is an intensely debated topic in human evolution (see Bailey et al., 1989; Roberts and Petraglia, 2015). MSA adaptations have generally been viewed as adaptations to grassland environments (see Finlayson, 2005), and it is thought that close canopy forest in West and Central Africa rainforest may have supported groups of hominins at low densities (Mercader, 2002; Barham, 2001; Taylor, 2016 and references therein). At present however, there is no conclusive evidence that MSA groups in Africa exploited true lowland tropical rainforest (Marean and Assefa, 2005; Banks et al., 2006). These highland (e.g. Afromontane forest, upland woodland, wooded savanna) and lake and river margin areas (e.g. riparian woodland/forest and wooded savanna) are also thought to have remained relatively stable during stadial periods (e.g. MIS 6, 4, 2) because of higher local moisture availability. This suggests that hominin groups may have been adapted to environments with arboreal cover that could have formed an important aspect of hunter-gatherer site selection and subsistence strategies in East Africa. Appendix 1 - Figure 1.2 maps MSA sites against vegetation and climate and species entropy model outputs during the stadial conditions (represented LGM models), and the humid phases of interstadials (e.g. MIS 5e) presented by mid-Holocene model outputs. There does not appear to be a strong relationship between any single period with a specific vegetation type, except for in the Horn of Africa, and in sites in eastern Tropical Africa near Lake Rukwa and Lake Malawi during MIS 3 (Basell, 2008, Blinkhorn and Grove, 2018). Recent studies from Panga

ya Saidi Rockshelter in coastal East Africa have revealed the occupation of humid tropical lowland coastal forest environments and the ecotone with grassland over the last ~78 ka, associated with novel symbolic and technological behaviours (Shipman et al., 2018). This occupation occurs at a time when East African palaeoevironmental records that indicate that coastal areas of East Africa were buffered against climatic downturns during MIS 4-1 due to a more continuous supply of moisture form the Indian Ocean (see Chapter 3.5.3). This finding highlights the potential for similar sites with mosaic habitation patterns being found in this Biome in the future.

While acknowledging the poor dating and local environmental records of sites on the Horn of Africa, Basell (2008) noted that there are a lack of sites corresponding to grassland environments in lowlands settings away from coastal zones. Basell (2008) recognised that such coarse-scale palaeoenvironmental comparisons are useful to explore regional connections, but that vegetation patterns and habitat preferences are likely to be more complex and changeable over shorter time scales at local (i.e. single lake basin) scales (see Chapter 3.5.3). Coarse scale reconstructions indicate that the likelihood of wooded vegetation located within the hominin group's home range, at sites such as K'One, Gademotta and Kulkuletti, was high, but the lack of local vegetation reconstructions from other MSA in rift settings sites during arid periods means that it is not possible to make connection with a specific arboreal vegetation type. Current dating evidence indicates both the KCR and Ethiopian Rift were occupied by hominins during both stadial and interstadial periods. However, many sites have not been dated using modern techniques and dates are either questionable, or the error ranges are sufficiently large so as to not be able to assign sites to a stadial or interstadial stage or both (see Figures 1.2 and 1.5).

If wooded or moist savanna environments were preferred by hominins (because they theoretically had higher moisture availability, adequate food, shade, and protection against predators), then it is possible that the expansion of arid grasslands (with low arboreal cover) may have acted as a barrier to dispersal for East African populations (Basell, 2008). The opposite may have been true if a population occupied and was already well-adapted to drier savanna environments (i.e. in this case the expansion of xeric savanna would have encouraged increase mobility as groups successfully expanded within the niche that their adaptations were already geared towards (see Section 1.7.3). It is important to reiterate the fact that *EARH* envisages occupation not just of woodland and forests but also of lowlands settings and savanna lake margins. In these generally drier settings, areas of woody vegetation, inselbergs, gallery forest and seasonally flooded are places of importance for human subsistence activities. Following the logic of a 'push-pull' mechanism for expansion, increased availability of these types of habitat (generally in mesic savanna) would have encouraged the demographic growth and expansion of hominin groups.



Appendix 1 - Figure 1.2 MSA site distributions plotted against modelled vegetation and richness residual maps of east Africa during the LGM (roughly representative of periods of extreme aridity during the last glacial) and the mid-Holocene (roughly representing humid periods during interglacial phases). White circles represent sites confined to stadial periods, black sites to interstadial periods and grey sites to either as they are not dated precisely enough to make this distinction. Several sites dated to stadial periods fall within areas of highland forest refugia, however the lakes and river margins appear to be equally important to hominins. (A) Water-energy modelled species richness of mammals subtracted from Maxent modelled during the LGM (B) Modelled annual precipitation (mm) during the LGM (Levinsky et al., 2013). (C) CCSM4 GlobCover vegetation model for the LGM (Chala et al., 2017). Closed forest: [Closed (>40%) broadleaved deciduous or needleleaved evergreen forest (>5 m)]. Open forest I: [Closed to open (>15%) broadleaved evergreen, semi-deciduous or deciduous forest or shrubland (>5 m); Open (15-40%) broadleaved deciduous forest/woodland (>5 m); Closed to open (>15%) mixed broadleaved and needleleaved forest (>5 m); Mosaic forest or shrubland (50-70%) / grassland (20-50%)]. Open forest II: [Open (15-40%) needleleaved deciduous or evergreen forest (>5 m); Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)]. Shrub/grassland I: [Mosaic vegetation (grassland/shrubland/forest) (50-70%)/cropland (20-50%)]. Shrub/grassland II: [Mosaic grassland (50-70%)/forest or shrubland (20-50%); Sparse (<15%) vegetation]. (D) LPJ-GUESS Mid-Holocene vegetation Biome distributions (Fer et al., 2016). Small black symbols indicate pollen sites, red site indicate where pollen records do not agree with the simulated biome.

1.7.3 Archaeological evidence for the exploitation of East African forest environments and highland refugia by hunter-gatherer groups.

Mochena Borago Rockshelter (Figure 1.5 Site No. 30) shows occupation and activity in an area inferred to have been Afromontane forest or deciduous closed woodlands during late MIS 4/early MIS 3, but continued occupation during periods of aridity is yet to be established (see Brandt et al., 2017; Vogelsang and Wendt, 2018). To date, the only direct evidence of MSA occupation of refugia during arid "megadrought" intervals comes from the MSA cave site of Ngalue (Figure 1.5, Site No. 36, 1400 m a.s.l) in highland zones of the Mozambican Rift that flank Lake Malawi. Here, phytolith-based vegetation reconstructions indicate the presence of moist Afromontane forest/woodland in highland areas exploited by hominins ~105 ka (Mercader et al., 2013). Occupation of Enkapune Ya Muto (Figure 1.5 site No.7) located at the present-day lower boundary of Afromontane forest on the Mau Escarpment (2400 m a.s.l.) by LSA during the mid-Holocene arid phases, records a subsistence strategy focused on the hunting of small forest bovids (possibly to avoid more dangerous, larger game [Marean, 1992]). This strategy differs from that used by the Okiek but does indicate that forest supported late LSA huntergatherer populations in small numbers, possibly in a similar way as it supports pastoralists today during episodic droughts. However, occupation of forest zone as refugium has not been demonstrated in the KCR for MSA groups.

1.7.4 Archaeological evidence in support of hunter gatherer dispersals in forest, and mesic woodland/savanna environments

There is currently no direct evidence that links the increase mobility or migration in MSA groups in equatorial East Africa with mesic savanna conditions. Contrary to the scenario proposed by the EARH, patterns observed between local environment and mobility, several MSA and LSA sites (e.g. Eren et al., 2013; Mercader et al., 2013; Wright et al., 2013; 2017) suggest opposite trends in mobility more consistent with the Generalised Grassland Model (see Chapter 1.7.3). Faunal evidence from the Kibish Formation, Southern Ethiopia, indicates the northward expansion of ungulates adapted to a range of mesic habitats from wooded grassland to dense woodland (e.g. the Miombo woodlands [eutrophic woodlands]) (Rowan et al., 2015; Faith et al., 2015). However, direct links between this expansion of ungulates and humans requires further testing. It has been argued that the same periods of glacial aridity that caused the expansion of arid grassland in the Lake Victoria Regional Mosaic resulted in the opening of closed canopy Guineo-Congolian rainforest forest to the west of the Albertine Rift in Central Africa. This removed north-south barriers to dispersal of ungulates and primates present during interglacial periods (Goldberg and Ruvolo, 1997; Goldberg, 1998; Arctander et al., 1999; Flagstad et al., 2001; Nyakaana et al., 2002; Alpers et al., 2004; Lorenzen et al., 2012). However, the nature of vegetation at the time is contested (i.e. open canopy forest [Cowling et al., 2008] or savanna and woodland biomes [Dupont et al., 2000; Cornelissen, 2002]) (see Taylor, 2016). If the association between open-canopy forest and human occupation of Central Africa (e.g. van Noten, et al., 1972; McBrearty, 1988) is confirmed, then this would provide tentative evidence that dispersal in open forested/wooded environments was

possible, as is suggested during MIS 5e (Foley and Mirazón Lahr, 1998). However, it is unlikely that these more open canopy conditions in rainforest during the LGM are a direct analogue for more extensive forest and woodlands that would have expanded under interstadial conditions in equatorial East Africa.

1.7.4.1 The Hydro-Refugia Hypothesis

The recognition that water availability is of fundamental importance in hominin habitat/site selection and landscape use (Kusimba, 1999) (also acknowledged by Basell [2008]), led to the modification of the Amplifier Lake Hypothesis by Cuthbert et al., (2017). This involved incorporation of modelled spatiotemporal changes in the recharging of springs and availability of potable water in highland areas during arid periods, when freshwater in lowland areas declined. As there is a generalised cause and effect relationship between higher rainfall that recharges springs and causes higher lake levels with increase arboreal cover (see Chapter 2), the resulting *Hydro-Refugia Hypothesis* broadly proposes the same 'pushpull' factors as Trauth et al., (2010) as an environmental framework in which to understand taxonomic diversity in East Africa. There is currently no direct evidence that links the increase mobility or migration in MSA groups in equatorial East Africa with mesic savanna conditions.

Appendix 1 - Table 1.2 Summary of models develop by Marean (1997) of Hunter-gatherer adaptations to tropical grassland environments. More recent, selected referces, that support the original findings of Marean (1997) have been added to the text where relevant.

Environment	Model and description	Ecological, ethnographic and archaeological basis for the model
Moist/dystrophic	The Generalized Grassland Model: hunter-	Based on ecological and LSA archaeological evidence: In moist/dystrophic savannas, low seasonal variability in the
savanna	gatherer groups would follow a 'routed' hunting	abundance of underground storage organs (USOs) and above ground plant foods (AGPs) found in woody plants are recorded
	strategy, targeting a wide range of species in	(Sept, 1994; Copeland, 2007). Moreover, in these moist grassland habitats, low mobility of gregarious residential mammals, and
	riparian woodland, salt licks and favourable	the more seasonal movement of mobile large game through predictable migratory routes is habitats. This means that moist savannas
	edaphics for grazing, and would have a high	are more stable year-round than more seasonal arid grasslands, that have similarly highly productive resource patches of USOs on
	proportion of plant foods in their diet. In this	inselbergs, gallery forest and seasonally flooded grassland at fluvial margins, (Vincent, 1985; Kusimba, 1999) but fewer residential
	case residential mobility would be low,	mammals due to fewer permanent water sources (Marean, 1997). In mesic savannas, residential and migratory mammals often
	excluding social interactions, because the lack	gather around permanent water sources or riparian corridors during the dry season and periods of sustained aridity. In regard of
	of more co-ordinated hunting of larger	past human adaptations to these settings, residential mobility is expected to be low, excluding social interactions, because the lack
	herbivores reduces the need for the	of more organised tactical hunting reduces the need for the congregation of groups in an area. The Generalized Grassland Model was
	congregation of groups in an area.	found to be most consistent with archaeological evidence that indicates the exploitation of moist savanna environment (i.e. upland
		tropical savanna with high woody cover) by LSA groups (Marean et al., 1997).
Arid/eutrophic	The Seasonal Grassland Model: groups were	Based on ethnographic, ecological, and LSA archaeological evidence: Ungulates in arid savannas occur in large herds
savanna	required to use highly co-ordinated hunting	forming a dense resource for hunter-gatherers, but one that was spatially and temporally unpredictable. In xeric savannas small
	statagies on a seasonal basis to exploit large	patches of plants are rapidly exhausted, encouraging more frequent residential moves, as observed in Kalahari San (Tanaka, 1980)
	mobile herds of ungulates at specific points on	and the Hadza (Woodburn, 1968; Marlowe, 2010) hunter-gatherers. In regard of past human adaptations to these settings, mobility
	the landscape	in hominin groups is expected to have needed to have been high to visit these points and to form larger hunting parties. Sites
		would have been focused on topographic highs that provide USOs on well drained slopes, vantage points for tracking game, at
		points with woody vegetation (e.g. lakes, topographic lows, springs, streams [Clark et al., 1984; Miller, 1979; Ambrose and Lorenz,
		1990; Marean, 1990; Tryon et al., 2010]). Use of open grasslands in this way would have resulted in large undefended territories.
		Both mobility and social and trade networks expanded as a result. The Seasonal Grassland Model was found to be most consistent
		with archaeological evidence that indicates the exploitation of arid savanna environment (i.e. lowland tropical savanna with high
		woody cover) by LSA groups (Marean et al., 1997).

1.7.5 Evidence in support of settlement patterns in MSA groups proposed by the *Ecotonal Hypothesis*

In contrast to the *Amplifier Lake Hypotheses*, Ambrose's model suggests that contact and movement between different areas was limited under mesic conditions, such as during interstadials, and that residential mobility was low as a result. As MSA groups are expected to focus on more predictable and abundant local resources under these conditions, as proposed by the *Generalized Grassland Model*, raw material use should reflect the main ecotonal site where resources were more stable and activity was focused. Ambrose (2001) proposed that higher proportions of non-local raw material in MSA assemblages during the last glacial period indicated a shift in settlement dynamics towards increased territory size, residential mobility, and regional interconnections. Ambrose correlates this putative change with less predictable environmental conditions during the expansion of drier grasslands environments (i.e. the *Seasonal Grassland Model*). The *Ecotonal Hypothesis* predicts that during stadial periods, residential sites should have higher frequencies of more distant raw material reflecting the abandonment of the "ecotonal" settlement strategy (Ambrose and Lorenz, 1990; Ambrose, 2001). This does not rule out the possibility that mobile groups still preferred to occupy the interface between savanna and forest during arid periods; but that groups would shift their elevational range to accommodate vegetation changes and were likelier to have occupied sites more sporadically and on a more seasonal basis.

The occupation of mid-elevation sites like Prospect Farm, on rift margins and near lakes by hominin groups has a deep history in the Nakuru-Naivasha Basin. Such occupations are recorded at the Acheulean site of Olorgesailie (1.2 to 0.499 ma old) (Brooks et al, 2018) and at other sites recording Acheulean, MSA and LSA material, such as Marmonet Drift (244 ka old) (Slater, 2016). Support for the "ecotonal" model comes from the pattern of MSA and LSA sites in a narrow elevational range in the Nakuru-Naivasha Basin, which does not appear to be an outcome by erosional biases (Isaac, 1972; Bower et al., 1977; Ambrose, 2001). Following Isaac's (1972) observation that MSA surface scatters at sites above 2400 m a.s.l. in the KCR were more numerous than below this datum, Ambrose (2001) found that permanent MSA settlement sites in the study area of the Nakuru-Naivasha Basin are generally located between 2000 and 2200 m a.s.l., and that this pattern conforms to an "ecotonal" model of MSA settlement dynamics (see Figure 1.7).

Prospect Farm records multiple MSA occupation phases as well as MSA/LSA transitional assemblages. The majority of raw materials were sourced locally from the Eburru Volcanic complex (Michels et al., 1983), with smaller amounts of material coming from further afield (~75 km away from Kisanana to the north of the site). The MSA sequence of Prospect Farm is imprecisely dated by the obsidian hydration method to ~120-50 ka (Michels et al., 1983; Merrick et al., 1994), and no dates or obsidian sourcing information currently exist for the two earliest MSA Phases (I and II) in the sequence (Van Balen et al., 2019) (see Chapter 5.3.3). Even though ages of MSA material from Phase III (dated to ~120 ka during the last interglacial) are likely to be overestimates of this assemblage true age. If correct this would support the *Ecotonal Hypothesis*. Ambrose (2001) does note however that lithic source patterns in all levels

of Prospect Farm are more alike than they are to sites such as Prolonged Drift. At Prolonged Drift, low surface densities of lithics and the lack of non-local raw material have been taken to indicate short lived occupations and higher mobility. When compared to sites like Prolonged Drift, Phases II and IV at Prospect Farm may still represent the tracking of ecotones, albeit in a manner consistent with increased but still intermediate levels of mobility over the landscape.

Sites are also known from higher altitudes, the highest recorded MSA occupation being in the KCR at 2540 m a.s.l at Uruu East in present day Afromontane forest. The only know MSA site on the KCR floor is Prolonged Drift, which is thought to be late MSA (younger than ~40 ka) (Merrick, 1975). Studies of settlement patterns on Mt. Damota (2908 m a.s.l.), in the Ethiopian highlands, record MSA and LSA landscape use between ~2000 and 2900 m a.s.l.. Here lithic densities are most highly concentrated around permanent settlements sites at ~2200 m a.s.l. (Vogelsang and Wendt, 2018). This range of elevation of MSA sites is consistent with Holocene vegetation records from Lake Naivasha (Maitima, 1991) and from on Mt. Eburru (Ambrose and Sikes, 1991), which indicate that the ecotonal boundary shifted by over 400 m in altitude in relation to climatic changes (see Appendix 3.6). The tracking of the ecotone between mesic savanna and forest by hunter-gatherers as it shifted between higher or lower altitudes under different climatic conditions, is partially supported by LSA record in the area (Ambrose 1986; Marean, 1992; Wilshaw, 2013). For example, Enkapune Ya Muto shows limited occupation during the earlier humid phases of the Holocene, when some sites were located at 1940 m a.s.l. on the rift floor. At the same site, increased occupation intensity is recorded during the mid-Holocene dry phases when lake desiccation occurred, Afromontane forest shifted to higher altitudes, and sites on the rift floor appear to have been abandoned. However, LSA responses to environmental change should not be uncritically back-projected onto the earlier MSA populations, and there is no categorical evidence to prove that LSA or MSA groups systematically tracked this boundary

1.7.6 Archaeological evidence in support of hunter-gatherer dispersals in xeric savanna environments

As in the *EARH*, Tyron et al's (2016) model proposes that the lake shore would have remained a focal point for hunter-gatherer groups in the Victoria region during both arid and humid intervals, and that fluctuation in shoreline locations acted as a mechanism for diffusion and contraction of hominin populations in a similar way to the ecotonal boundary between forest and savanna in upland basins. The sourcing of raw materials at MSA sites during the late Middle Pleistocene in East Africa provides insight into the mobility of groups and the development of intergroup exchange networks (e.g. Blegen et al., 2017; Brown et al., 2013). However, in most areas of East Africa the lack of local environmental records makes it difficult to determine if long distance obsidian transport was associated with a particular set of environmental conditions. The strongest evidence in support of settlement patterns predicted by the *Ecotonal Hypothesis* comes from recent studies of MSA sites from the eastern side of Lake Victoria in western Kenya.

Synthesis of multiple lines of archaeological and palaeoenvironmental evidence from sites such as Kurunga, Mfangano, and Rusinga Island on the eastern side of Lake Victoria indicate that during periods of expansion of xeric grassland habitats, between ~90-30 ka, shared technological affinities existed between sites south of the Equator in the LVRM near Lake Victoria and sites north of the Equator in the now distinct northern East Africa biogeographic zone SMCRE (e.g. Mocha Borago, Proc Epic, Kibish, Muguruk, Aduma, and Midishi) (Faith et al., 2015; Tryon et al., 2016; Beverly et al., 2017). Obsidian transport up to 250 km is also recorded to the north and possibly east of Lake Victoria (McBrearty, 1981; 1986; Merrick and Brown, 1984a; Merrick et al., 1994). Under Holocene and presentday climate conditions, allopatric arid adapted savanna ungulates form regionally distinct groups in East Africa, separated by the Central Africa rainforest and the East African forest belt. Palaeoenvironmental records and phylogenetic and biogeographic models of ungulates indicate that low lake levels and the coeval expansion of C₄ dominated grassland, as well as the fragmentation of forest in the past (Cowling et al., 2008), removed biogeographic barriers to expansion of arid adapted ungulates in the Victoria Basin. This encouraged range shifts and north-south dispersal of these species in East Africa to form nonanalogue, high biomass, large herbivore communities (Miller et al., 2011; Lorenzen et al., 2012; Faith et al., 2015; 2016; Tryon et al., 2016). The shared timing and directionality of changes in the archaeological and fauna record is interpreted as indicating diffusion of MSA groups in north East Africa into the Victoria Basin as they tracked herds of migration game (Tryon and Faith, 2013; Garrett et al., 2015; Tryon, 2015; Faith et al., 2016). As palaeoenvironmental reconstructions indicate that woodland in eastern Tropical Africa remained relatively stable after ~85 ka (see Chapter 3.3). It has also been suggested that more closed conditions may have limited dispersal of ungulates and humans from this area to equatorial East Africa and further north. While the model is also supported by findings from other MSA and LSA sites around Lake Victoria (e.g. Feathers and Migliorini, 2001; Prendergast and Lane, 2010). There are no MIS 5 records from the area that could provide insight into whether mobility and diffusion of MSA groups in the basin conform to a Generalised Grassland Model of subsistence; as predicted for interglacial periods. Contrary to the xeric expansion model, there is some limited evidence for the eastward diffusion of Lupemban technology occurred via wooded riverine corridors located around river courses, or during the expansion of the forest belt sometime during MIS 4-3 (McBrearty, 1988, but also see Taylor, 2016). However, the timing of this process is not well established and so does not allow any correlation to be made with specific environmental conditions.

APPENDIX 2





0 20 40 60 60 100 120 140 160 180 200 220 340 200 300 300 220 340 360 300 400 40 480 480 50 Precipitation (mm/month)

Appendix 2 - Figure. 2.1 Summary climatology of East Africa for August, November, January, and April, showing the seasonal movement of the tropical rainfall belt (shown as precipitation), ITCZ, and Congo Air Boundary (CAB). NE IWM: indicates the North East Indian Winter Monsoon, SE ISW: indicates the South East Indian Summer Monsoon. ITCZ: Intertropical Convergence Zone, CAB: Congo air boundary. L: low pressure area, H: high pressure area. The yellow marker indicates the location of the Nakuru-Naivasha Basin. Precipitation data are estimates of monthly precipitation (in mm/month) based on satellite emitted long-wave radiation over the period 1981-2010 (data from the IRI database: http://iri.columbia.edu). In East Africa, topography, vegetation, and large freshwater lakes (which influence surface albedo), as well as soil moisture and surface roughness, result in the differential heating of the land and cause the sinusoidal profile of the rainfall belt and ITCZ. Over contemporary seasonal timescales the ITZC; a zone of maximum convergence, cloudiness and rainfall); is thought to follows the sun's zenith (maximal insolation) (Holton et al., 1971; Nicholson, 2009). The WAM, associated with the CAB, transports moisture from the ocean, as well as trapping moisture over the humid tropical rain forest of the Congo Basin. The CAB is a wet westerly and south-westerly flowing air mass that is unstable where it merges with the ITCZ and East African monsoonal airmasses to form a N-S trending zone of convergence. The NE and SE Indian monsoons, which convect moisture from the Indian Ocean, are drier in comparison. The SE ISM transports moisture through reversed sun-meridional-flows away from East Africa, towards the low-pressure zone that exists over India during boreal summer. During boreal winter, the NE IWN is cooler and so convection over the Indian ocean occurs but is limited. Monsoon in East Africa is associated with a season of high rainfall from March to May (referred to as the "long rains") and a shorter, less intense, period of rainfall occurring between October and December (referred to as the "short rains") (Nicholson et al., 1996; Yang et al., 2014).



Appendix 2 - Figure. 2.2 Modern synoptic climatological sea surface temperature (SSTs) and mean surface air temperature data for East Africa, for August, November, January, and April and the seasonal movement of the ITCZ and CAB. NE IWM: indicates the North East Indian Winter Monsoon, SE ISW: indicates the South East Indian Summer Monsoon. ITCZ: Intertropical Convergence Zone, CAB: Congo Air Boundary. The yellow marker indicates the location of the Nakuru-Naivasha Basin. SST data are monthly climatological sea surface temperature (in °C) through the course of the year, based on Reynolds et al., (2002) OISST Version 2 data using the 1971-2000 base period. Surface air temperature data are UEA CRU TS2p1 climatology c7100 mean temp: Temperature (deg. C), from IRI database: http://iri.columbia.edu. It is apparent that surface air temperature over land varies according to altitude but demonstrates very little variation seasonally. In general, warm currents encourage rainfall in adjacent onshore areas; while the opposite is true for cold currents (Gasse, 2000; Barker and Gasse, 2003). Upwelling of cold sub-surface waters along the coast of Africa is dictated by the direction of the westerly trade winds and seasonal monsoon intensity, resulting in differential heating of surface waters off the east and west coasts of Africa (Schulz et al., 1998; Stuut et al., 2012). Inter-annual and sub-decadal rainfall is East Africa is strongly associated with variations in SSTs in the Indian Ocean, but also with the Atlantic Ocean (via teleconnections), which are associated with El Niño/Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) (Nicholson, 1996). Variations in the intensity of the rainy seasons relate to east-west changes in the position of the zonal Walker circulation, which in turn are controlled by India Ocean dipole and ENSO variability (Nicholson, 2000). Over decadal and multidecadal time scales, periods of severe drought and increases monsoon intensity in East Africa have been linked primarily to Indian Ocean SST anomalies (Nicholson, 2015): specifically changes in the state of the Indian Ocean dipole (IOD; Saji et al., 1999) (e.g. Bergonzini et al., 1997; Marchant et al., 2007; Bloszies and Foreman, 2015). They have also been linked to local alteration of the Walker circulation (Ummenhofer et al., 2009; Tierney et al., 2013; Tierney and Ummenhofer, 2015; Appelhans and Nauss, 2016) and to ocean-coupled phenomena such as El Niño-Southern Oscillation (ENSO) (see Hawinkel et al., 2016 and references therein).

2.1.2 Description of present-day vegetation distributions across East Africa

As shown in Figure 2.2, to the west of the Kenyan Rift, transitions from evergreen rain forest and tropical woodland to shrub and grass dominate savannah ecosystems of the LVRM follow latitudinal rainfall bands. Within the Kenyan and Ethiopian Rifts, the abrupt topography of the rift flanks creates steep orographic (altitudinal) rainfall and temperature gradients. This strongly influences vegetation distributions and has created Afromontane forest and Afroalpine habitats and predominantly wooded grassland highland savannah systems found on the valley floor (Edwards, 1940; Trapnell and Griffiths, 1960; Lillesø et al., 2011; Hawinkel et al., 2016). To the east of the eastern limb of the Central Rift Valley, in lowland areas of Somalia-Masaï zone, vegetation transitions into grass dominated savannah and thicket/shrubland. In low-lying basins (e.g. the Turkana Basin) within the rift, semi-desert vegetation predominates, while coastal mosaic vegetation (mangrove and lowland rainforest) exists in coastal areas. In southern Tanzania, the transition to the Zambezian zone (primarily in eastern Tropical Africa) occurs. Here vegetation consists of distinctive dry evergreen forest, dry deciduous forest, Miombo woodland, thicket and edaphic grassland (Edwards, 1940; White, 1983; Lillesø et al., 2011).

2.2 Present-day hydrology of the Nakuru-Naivasha Basin

It is thought that Lake Naivasha offsets its low precipitation vs. high evapotranspiration ratio to maintain a low pH through large freshwater inputs provided by the Gilgil and Malewa rivers, which drain the Kinangop Plateau and Aberdares Range. These rivers flow from the Aberdares Range in the east towards Naivasha and not in the direction of Nakuru-Elementaita because an En échelon fault is located at the eastern edge of the rift floor at Gilgil. This fault causes routeing of water from the highland zones southwards towards Naivasha. The nature of sub-surface drainage out of and between the basin are still largely undefined. It is estimated that Naivasha may lose 5-20% of its water though seepage; however, it may also regain this seepage from other areas (Gaudet and Melack, 1981; Hastenrath and Kuzbach, 1983). Sub-surface outflow may also allow the lake to maintain its low alkalinity levels (Gaudet and Melack, 1981; Ojiambo-Bwire and Lyons, 1996; Bergner et al., 2003).

Lake Nakuru and Elementaita are saline and are only fed by small seasonal rivers and a single minor permanent river each (the Ngosur and the Kariandusi respectively). Sub-surface seepage from Naivasha northward to the Nakuru Basin (hydraulic coupling of the two sub-basins) has been proposed as a mechanism by which these lakes maintain a positive water balance (Thompson and Dodson, 1963b; Bergner et al., 2003). Combined instrumental and sedimentological data from Lake Naivasha over the last two centuries has shown that levels have dropped at times by 3-5 m, becoming increasingly eutrophic, in relation to regional climate aridity and land clearance (Stoof-Leichsenring et al., 2011). Lake level fluctuations of over 20 m during the last 1000 years have been records from Naivasha, which have been broadly associated with periods regional drought linked to increased solar radiation (Verschuren et al., 2000, 2011).

2.3 Contemporary examples of divergent trends in plant distributions and community composition on East African mountains.

Extensive bamboo (C_3 Bambusoideae) zones are present on the majority of East African mountains between 2400 - 3000 m a.s.l. and between 1630 - 3200 m a.s.l. in favourable conditions (e.g. on Mt. Kenya): these cover 65,000 ha on the Aberdares, 51,000 ha on the Mau escarpment and 39,000 ha on Mt. Kenya (Hemp, 2006b; White, 1983). Bamboo zones develop under high annual rainfall [above 1250] mm], at temperatures of 10-15 °C, and with the presence of very deep volcanic soils, namely humic andosols, that develop on gentle slopes (Trapnell and Langdale-Brown, 1972; White, 1983; Bussmann, 2006). On Mt. Kilimanjaro the absence of a well-developed 'bamboo zone' (Hedberg, 1951; 1955) has been linked with a lack of suitable growing conditions on the dry northern slopes, as well as repeat destruction of the bamboo zone by megaherbivore (buffalo and elephant) grazing, as well as to unsuitable topographic conditions for growth on the wetter southern slopes (Hemp, 2006b). Small patches of bamboo (Arundinaria alpina) existed on the mountain in modern times (Greenway, 1965) but Zech et al., (2011) have inferred, using n-alkane biomarkers from palaeosols, that a bamboo zone was likely to have existed under wetter conditions on the northern slopes of the mountain at several stages of the late Quaternary period. The role of orographical constraints in accentuating vegetation diversity, such as leeward rain shadow effects, is also evident on many East African Mountains and creates conditions of increased aridity to the east of Mt. Kilimanjaro and Mt. Kenya (Trapnell and Griffiths, 1960; Nicholson, 1996; Bussmann, 2001; 2006; Sepulchre et al., 2006; Prömmel et al., 2013). For example, in the Kenyan and Ethiopian Rift Valleys, the rain shadow effect is associated with the distribution of drier undifferentiated Afromontane forest on leeward slopes and more humid Afromontane rainforest on windward sides of the rift (Trapnell and Griffiths, 1960; Friss et al., 1992; Lillesø et al., 2011). Other studies record significant shifts in floristic diversity (e.g. increased diversity of endemic plant such as ferns in upper montane forests above 1830 m), which correspond to orographic variations in rainfall and temperature (Schmitt et al., 2010).

As discussed in Section 2.5, the spatial ecological patterning of vegetation on East African mountains displays uniformity in terms of altitudinal zonation of vegetation types on mountains separated by hundreds of kilometers of lowland vegetation, but also individuality, in terms of the endemic species that are unique to isolated islands of forest vegetation. This biogeographic pattern, of isolated mountain refugia that share remarkably similar composition and patterning of vegetation, has long been recognised by phytogeographers (e.g. Hedberg, 1951; Bussmann, 2006). It is thought to be related to repeated episodes of expansion and contraction of the forest within the Afromontane Biome associated with late Quaternary climate change.

2.4.1 Primary environmental variables controlling C_3 vs. C_4 grass biogeography on tropical montane ecosystems in modern-times

Present-day distributions of C_3 vs. C_4 grasses on tropical mountains in relation to biotic and abiotic conditions have received attention from ecologists and palaeoecologists, as they can help in understanding the major shifts that have been observed in these vegetation types, as well as the factors

driving these changes. They can also contribute to studies on the ecological context of the evolution of C₄ photosynthesis. Furthermore, they can be used to forecast the response of tropical habitats to future climatic change (Bremond et al., 2012 and references therein). In general, the temperature optima for net CO₂ exchange is lower in many C₃ plants (10 - 25 °C) than in C₄ plants (30 - 45 °C) (Stowe and Teeri, 1978; Tieszen et al., 1979). Studies from tropical regions indicate that when mean July temperature temperatures drop below 10 °C, C₄ grass growth is limited for most species. From ~10 to 20 °C there is competitive overlap between C₃ and C₄ species, while above 20 °C C₃ grasses are present, but are generally found only in discrete ecological niches (Tieszen et al., 1979; Bremond et al., 2012). For example, in closed canopy tropical forests/woodland at mid-altitude sites, C₃ gasses occupy the understory (Rundel, 1980; Long, 1999). In shaded habitats, relatively low solar irradiance and leaf temperature below ~32 °C are thought to favour C₃ grasses where they exhibit higher quantum yields than C₄ grasses in the absence of other controlling factors (Ehleringer, 1978; Tieszen et al., 1979). Conversely, in open habitats with high irradiance above this temperature threshold, C₄ grasses dominate due to their highly efficient use of water (Sage et al., 1999; Bremond et al., 2012).

Tieszen et al., (1979) note trends in families of Poales in littoral/aquatic settings (e.g. in lowland swamps and lake margins self-shading C_3 Typha can dominate, while C_4 Cyperus papyrus can dominate in more open conditions), and that intensive herbivore grazing in East Africa is likely to have influenced C_3 vs C₄ occurrences by creating open canopy conditions in low and mid-elevation sites. There are some exceptions to theses general trends typified by the presence of C4 Panicoid tussock grasses (e.g. Andropogon amethystinus) at high altitudes (from ~3000 to 4000 m a.s.l.) on Mt. Kenya and the Aberdares Range (Schmitt, 1991). These C_4 tussock grasses are thought to locally outcompete C_3 (primarily Pooid) grasses around highland lake margins due to higher irradiance and an advantageous microclimate create by tussocks (Tieszen et al., 1979). Sub-alpine C₃ tussock grasses are not present on Mt. Eburru due to its lower maximum altitude (2850 m a.s.l) (see Chapter 2.9). However, studies of late Quaternary vegetation change on Mt. Kenya, indicate that C4 grass occurrences today are likely to be remnants of more widespread communities of C4 grasses, which thrived under past glacial environment conditions (e.g. lower pCO_2 and repeat burning). On Mt. Kenya, an altitudinal survey carried out by Tieszen et al., (1979) found minimum temperature, irradiance and soil moisture availability to be the dominant factor governing C_3 vs C_4 distributions on the open grass-dominated northern flanks. However, a later survey of the same area by Young and Young (1983) assigned greater importance to dry season soil moisture influencing the degree of vegetation openness. A further survey of the forested eastern and northwestern flanks revealed further divergent trends (i.e. C4 grasses located above the tree line) (Wooller et al., 2001a). Taken together, these surveys reinforce the idea that local variations in climatic, topographic and edaphic conditions can exert a strong influence on vegetation distributions over short distances on East African mountains. In summary, field-based studies and modelling of C₃ and C₄ grass biogeography, suggest that a suite of environmental determinants (e.g. temperature, rainfall, fire, pCO_2 , and edaphic conditions etc.) have an influence on the relative abundances of C₃ vs C₄ grasses in tropical ecosystems (e.g. Morgan et al., 2011; Higgins and Scheiter, 2012). These studies are of great utility in understanding the relative importance of these factors and how they feed back upon one another. However, this information is incomplete and observations of process operating over short periods cannot be extrapolated uncritically to a stadial-interstadial time scale under drastically different climate conditions (Urban et al., 2015). This is considered further in Chapter 3.5.1 and 3.5.2 and Appendix 3.4.1-3.4.2).

2.4.2 Differentiating between forest and savanna - additional information

It can be difficult to distinguish between mesic savanna, often defined by their continuous grass understory cover and sporadic nature of woody vegetation cover with a strong woody component, from similarly structured forest and true forest (House et al., 2003; Bond and Parr, 2010; Ratnam et al., 2011). Yet, it is important to distinguish between these two biomes, because despite sharing structural similarities (i.e. the external appearance and growth forms of dominant taxa) at their ecotone (e.g. tall trees at a high density), the resources they provide to hunter-gatherer groups through their species composition and associated faunal communities can be different (Bond and Parr, 2010 and references therein and see Appendix 1.5). Identifying, characterizing and mapping different stands of vegetation as separate units depends on our definition of plant communities or vegetation types, and how we draw boundaries between them. In vegetation ecology, current definitions emphasise that plant communities display both internal uniformity and external distinctiveness from the surrounding vegetation (see van der Maarel and Franklin, 2013 for details of current approaches to studying past plant communities). The concept of ecotones between two plant communities or vegetation biomes allows boundaries to be sharp or gradational, which is often a matter of scale.

Considering how best to distinguish high rainfall savanna and forest, due to structural similarities at their ecotonal boundaries, Ratnam et al., (2011) proposed a suite of physical environmental, species morphological, physiological and life-history traits, dominant in each system. These traits reflect the functional differences and divergent evolutionary and ecological histories, which can be used to differentiate between the two biomes. These traits are detectable to some extent through phytolith analysis (see Chapter 4) and are relevant on the scale of late Quaternary vegetation reconstructions using phytoliths, as listed in Appnedix 2 -Table 2.1.

	Mesic savanna	Forest
Environmental descriptors	High-light understorey	Low-light understorey
	Frequently burnt	Fires rare, catastrophic
Vegetation composition	Trees	Trees
	Herbs	C3 grasses
	C4 grasses	Herbs
Bark	Thick bark	Thin bark
Canopy	Lower specific leaf area	Higher specific leaf area
	Open crowns and higher light penetration through canopy	Dense crowns and lower light penetration through canopy

Appnedix 2 -Table 2.1 Selected physical environment, species composition and functional traits of dominant tree species found in forest and savanna ecosystems globally, which can be used to distinguish between the two systems (from Ratnam et al., (2011) pg. 654). Only those traits for which phytoliths can serve as a proxy are included from the original list. The utility and varying ability of phytolith analysis to reliably reconstruct variability in the traits listed above are discussed in Chapter 4 and Chapter 5.6.5

On a regional scale (across several degrees of latitude of Africa) shifts between savanna, grassland and woodland appear to be stable and clearly track climatic gradients (i.e. MAP) and regional edaphics (Sankaran et al., 2005); with topography and bioclimate factors (e.g. pre-existing vegetation structure and precipitation variability) affecting ecosystem sensitivity and woody cover on interannual scales (Field et al., 2005; Hawinkel et al., 2016). The relative position of different sub-types of East African savannas, including upland wooded savannas that exist in highland areas of Kenya today, vary in relation to gradients in soil texture and soil moisture availability (as shown in Figure 2.3). At ecotones between these stable vegetation states, blending of savannah sub-types, and savanna and forest vegetation occurs, creating mosaics and at the local level tree cover is highly heterogeneous (Sankaran et al., 2005; Favier et al., 2012). As such, savannas can be thought of as patch dynamic systems; stable across a range of environmental conditions at a coarse scale but containing multiple smaller sub-ecosystems (e.g. Sankaran et al., 2005; 2008; Weigand et al., 2005; Ssemmanda et al., 2014). On a more local scale, under the same regional climatic conditions, variations in savanna vegetation structure (changes in woody cover [see Figure 2.9]) and community (variations in species associations) are regulated by a suite of environmental biotic and abiotic determinants (e.g. edaphic factors such as geology and soil catena, soil depth and drainage, herbivory, fire, pCO_2 , and nutrient availability, etc.). These feed back on one another and reach thresholds under various disturbance regimes (e.g. Belskey, 1990 and references therein). For example, woody cover is inversely correlated with clay content in many savannas as roots find it difficult to penetrate compacted substrates. This allows grasses to outcompete trees locally; thus, clay content can act as a limiting factor in woody cover.

2.4.3 Disturbance regimes and tropical vegetation dynamics - additional information

A key feature of tropical savannas is that their understory is composed almost exclusively of C_4 grasses, while forests are dominated by C_3 grasses and herbs (Bond et al., 2003, Bond, 2008; Bond and Parr, 2010). C_4 grasses and trees have a low shade tolerance (Sage and McKown, 2006), as opposed to C_3 grasses and herbs that thrive in shaded habitats (Klink and Joly, 1989). C_4 savanna plants are tolerant to frequent fires (i.e. they have thick bark, underground storage organs and fast sprouting times that allow quick recovery following fire [Bond and Midgley, 2001; Cochrane, 2003; Hoffmann et al., 2004; Schutz et al., 2009]) while C_3 forest plants are largely fire intolerant (Uhl and Kauffman, 1990; Bowman, 2005; Bond and Parr, 2010). Furthermore, forest trees tend to have higher leaf areas than savanna trees, which lowers levels of solar irradiance (Hoffmann et al., 2005). Higher rainfall results in increased C_4 grass biomass, which during the dry season provides fuels for fires (Bond, 2008; Cardoso et al., 2008), this decreases canopy cover, which in turn prevents C_4 grass die-off from self-shading (Uys et al., 2004; Ratnam et al., 2011).

Both fire and tree growth rates have been observed as being of central importance to the maintenance of savanna forest boundaries (Hoffmann et al., 2009; Lehmann et al., 2011). When fires occur in tropical forest they usually do so at the boundary of savanna (Cochrane et al., 2003). This is because in mature forest, closed canopies and deep rooting systems increase moisture retention, bolstering resistance to
drought and lowering temperature and wind speed that would otherwise allow fire to spread (Cochrane et al., 2001; Murphy and Bowman, 2012). In mesic savannas, fire can often create sharp ecotones with forest areas, with few shared species across regularly burnt boundaries (Bond and Parr, 2010). This is due to moist forest leaf litter limiting the spread of fire; while fire inhibits invasive forest tree seeding in savanna (Ratnam et al., 2011). The resilience to prolonged drought and to fire is manifest in the persistence of forest in refugium during the late Quaternary period in East Africa (see Chapter 3.5.3). However, if biogeographic processes persist in the absence of fire, leading to the formation of plant communities ill equipped to resist its effect (Cochrane et al., 2003), and/or if a disturbance episode is severe enough, the forest canopy can open and become increasing vulnerable to disturbances. If such a bifurcation point is passed then rapid shifts between stable ecosystems states can occur (Scheffer and Carpenter, 2003; Hirota et al., 2011; Staver and Levin, 2012). Ratnam et al., (2011) note that in the absence of disturbances, forest trees are more likely to colonize savanna as they have a relatively greater range of light tolerances than savanna trees. As such, in the absence of fire we may expect forest to expand at the expense of savanna. This process is expected to be accelerated by conditions that favour forest growth (e.g. higher rainfall, development of nutrient rich deep moisture retaining soils, elevated pCO_2 etc.). The precise nature of the susceptibility of every every tropical forest to fire remains under study (Cochrane, 2003; Balch et al., 2008; Hoffmann et al., 2009). However, it is becoming increasingly clear that while fire reoccurrence rates are generally low (100-1000 years; Kauffman and Uhl, 1990; Cochrane, 2003) fire has played an important role in the long-term vegetation distributions during the late Quaternary on East Africa Mountains under different bioclimatic conditions (see Chapter 3.5.2 and Appendix 3.4.1-3.4.2).

The role of herbivory in controlling woody cover in African savannas has also been well demonstrated (e.g. Belsky and Canham, 1994; Staver et al., 2009), particularly during episodes of higher rainfall (Holmgren et al., 2013), including through research at Lake Nakuru National Park in the study area (Dharani et al., 2009). In forested environments grazing can favour increased woody biomass, while browsing has been shown to limit it. However, the impact of large herbivores on the boundary between forest and savanna and their distinct floral communities remains ambiguous (see Murphy and Bowden, 2012 and references therein).

2.5 PNV models for the Nakuru-Naivasha Basin and Prospect Farm: base data and key difference with vegetation distributions mapped from vegetation surveys

The PNV map shown in Chapter 2, Figure 2.10 combines floristic and physiognomic vegetation data (from published soil and vegetation surveys) with climatic, edaphic, and topographic information in order to digitize vegetation maps of new Potential Vegetation Type distributions; that are modelled as existing under present-day climate conditions without human land clearance and other anthropogenic disturbances. In inland areas of Kenya, the PNV composite map is based on the vegetation map and vegetation subclasses used by White (1983), as well as other maps: Trapnell et al., (1966), Trapnell et al.,

(1969), Trapnell and Langdale-Brown (1972), Trump, (1972), Trapnell et al., (1976), Trapnell and Brunt (1987), Herlocker, (1994), Kindt et al., (2005).

The PNV model maps a far more extensive bamboo zone on the Aberdares Range than exists today in an area currently used primarily for agroforestry. Several distinctive sub-types of vegetation that are recognised by other vegetation surveys but are grouped into Be and Fb by the VECEA are noteworthy: For example, Acacia woodland and forest (on the western border of Lake Nakuru at the base of the Mau Escarpment) is dominated by Acacia xanthophloea and reaches ~25 m in height, with an understory lianas, herbs, and dense shrubs (e.g. Cassia bicapsularis, Vernonia auriculifera, Erythroeocea bongensis, Grewia bieolor, Grewia similis, Pluebea bequaertii and Rhus natalensis) and herbs (e.g. Achyranthes aspera, Solanum incanum, and Urtica) in places; while smaller stands of Acacia seyal woodland lack a well-developed shrub understory (Mutangah, 1994). Olea forest (included in Fb) on the lower Mau Escarpment, is characterised by a closed canopy of Olea africana, ussonia holstii, Eulea divinorum, Olea africana and Teelea simplieifolia, with a mature understory of lianas, herbs and succulents (e.g. Notonia hildebrandtii, Plectranthus cylindraceus, Sareostemma viminale, Sansevieria parva, Senecio petitianus) and shrubs (e.g. Cordia ovalis, Grewia similis, Maytenus heterophylus). Also found at similar elevations to Olea forest is Euphorbia candelabrum forest (also included in Fb). This vegetation type has inclusions of Acacia xanthophloea, Cussonia holstii, Obetia pinnatifid and an understory of Hypoestes verticillaris and Achyranthes aspera. Tarchonanthus-Euphorbia candelabrum bushland (included in Be) is located on acidic well-drained soils with low fertility, that have developed on shallow volcanic and diatomaceous sediments (see Appendix 2.5, Figure 2.3). Burgeoning vegetation on lava outcrops (occurring within Be, and We) is variable and consists mainly of small trees and shrubs (e.g. Acacia spp, Clerodendrum myricoides, Heteromorpha trifoliata Maytenus heterophyllus, Rhus natalensis, Aspilia mossambicensis and the succulent Aloe seeundiflora) (Mutangah, 1994).

Vegetation surveys on Mt. Eburru (Trapnell et al., 1976; see Chapter 2, Figure 2.12) and field observations made by the author, indicate that the modern vegetation developing on top of the Prospect Farm Formation is evergreen and semi-evergreen bushland vegetation of probable forest origin (which falls within the range of the *Be* PNV type). This is interspersed with cultivated plots mainly of maize (*Zea*) and sugar cane (*Saccharum*). There is sparse C₄ grass cover (*Themeda triandra, Hyparrhenia hirta, Chloris gayana*) and scattered trees of broad-leafed savanna/forest species (e.g. *Dombeya burgessiae* and *Croton megalocarpus*). Occasional broadleaf trees are found bordering perennial rivers (e.g. *Newtonia hildebrandtii* and *Ficus thonningii*) and *Cyperus dives Cyperus laevigatus* occupy waterlogged areas. In open areas bordering agricultural plots and in semi-shaded areas low shrubs and herbs associated with overgrazing occur (e.g. *Achyranthes aspera, Leonotis nepetifolia, Solanum incanum, Lippia javanica, Psiadia punctulata, Pluchea indica, Ricinus communis, Aspilia mossambicense and Ocimum gratissimum*); as well as introduced exotics of the *Cactaceae* and trees (e.g. *Eucalyptus spp*). At ~2400 m a.s.l. (inside the Eburru forest boundary fence) Podo-Cedar forest and forest clearings (which fall within the *Fb* PNV type) are present. White (1983) reports that following fires *Fb* can be replaced by forest dominated by a single pioneer species, due to competition during colonisation (e.g. *Juniperus procera* forest [*Fb*], Afromontane single-dominant *Widdringtonia whytei* forest

[*Fc*] or Afromontane single-dominant *Hagenia abyssinica* forest [*Fd*]). In areas where MAP is between 700-1500 mm, and in areas of repeat fire, *Juniperus procera* typically dominate *Fb* (Wimbush, 1937; Bussmann, 2006). In more open stands of *Fbj*, C_3 Pooideae grasses (e.g. *Stipa dregeana* and *Brachypodium flexum*), herbs and low shrubs (e.g. *Berberis holstii*) are commonly found (Bussmann, 2006).



Appendix 2 - Figure 2.3 Map of the distribution of present-day soil conditions across the Nakuru-Naivasha Basin (after Sombroek et al., 1982: Kenya Soil Survey). Elemental analysis of soils and plant tissues across the Nakuru-Naivasha Basin was used by Kübler et al., (2016) to map favourable grazing conditions for herds of migratory animals in the basin during the Quaternary period. Their results indicate that soils around Lakes Nakuru, Elementaita and Naivasha, with high Ca, Mg, Na, K and F, support savanna vegetation (*Be* and *We*) and have moderately good edaphics. The deep well-developed fertile red humid Acrisols and Andolsos (Bussmann, 2006), with favourable edaphics (high Ca, Mg, and P levels) occur throughout the Nakuru-Naivasha Basin along the Sattima Escarpment; on Mount Kipipiri, on lower slopes of the Aberdares Range, as well as in the Mau forest (Kübler et al., 2016), on which *Fb* currently develops. Mt. Eburru was excluded from Kübler et al's (2016) analysis, as volcanism on Mt. Eburru was incorrectly reported as being restricted to the Holocene, and because soils on the lower slope today are poorly developed, having formed on top of pantelleritic ash falls and pumice (the Eburru pumice and trachyte formations) and more recent lava flows. However, it is not the case that soil quality was always poor on Eburru, and as discussed in Chapter 5; the palaeo-catena of Eburru was different during stages of the late Quaternary. At certain stages deep, fertile volcanic soils (which are now confined to the upper slopes of the Mau Escarpment and Mt. Eburru (supporting present-day Eburru forest vegetation communities) were present at lower altitudes on the mountain and supported montane forest (see Chapter 6).

2.6.1 Lower elevation vegetation (1750 - 2000 m a.s.l.) in the Nakuru- Naivasha Basin

The main PNV type which occurs at lower elevations along the rift margins and the valley floor of the Nakuru-Naivasha Basin is evergreen and semi-evergreen bushland and thicket (Be). This vegetation type typically forms an ecotone between undifferentiated Afromontane forest (Fb) and lowland deciduous

bushland (*Bd*). *Be* is characterized by C₄ grasses (of which *Themeda triandra* is the most dominant; typically growing between 0.8 - 1.2 m tall) and widely scattered trees (between 3 and 15 m tall). *Be* is quite varied with some areas of open grassland where trees are entirely absent. This dry savanna type is usually dominated by *Acacia* species with occasional broadleaved species (see Table 2.1) increasing in locally moist areas. In areas where rainfall is slightly higher *Be* is replaced by *Combretum* wooded grassland (*Wc*), in which *Acacia* spp. are present but occur less frequently than broadleaved trees (e.g. *Combretum*, *Terminalia*, *Ficus* and *Faurea*), and grasses grow taller (between 1.5-2.4 m) than in *Be* (Edwards et al., 1940; Lillesø et al., 2011).

Vegetation close to the shore of Lake Nakuru, growing on seasonally flooded soils (drainage impeded clay-loam [see Appendix 2.5, Figure 2.3]) with high alkalinity, is comprised of alkaline grasslands, Pluchea bushlands, or swamp vegetation (see Table 2.1). The area between Lake Nakuru and the lower northernfacing slopes of Mt. Eburru is covered by alternating stands of several different C_4 grassland types (Mutangah, 1994), as well as the Be savanna vegetation sub-type with a higher proportion of woody cover (see Table 2.1). Similar vegetation is found around Lake Elementaita and Lake Naivasha in Hell's Gate National Park (Trapnell et al., 1976). The density of Acacia increases in the park hinterland, at the base of the Mau escarpment in the west. Here, Tarchonanthus bushland changes into wooded bushland/woodlands near the lake and forms mosaics with dry forest/woodlands on the escarpment (Dharani et al., 2006). These communities are included in the Be vegetation type in the PNV projections (Figure 2.10) and are defined by Mutangah (1994) according to criteria of Pratt and Gwynne (1977) (i.e. woodlands: trees up to 20 m high with open canopy of >20%, forest: contiguous cover of trees, 10-40 m in height, with canopy interlacing [see Figure 2.9]). Similarly, the dry highland Olea forest located on the western escarpment is one of the few remaining of its kind in Kenya. Similarly, Euphorbia candelabrum forest; found on the escarpment on steep slopes and basalt ridges, are included in the Fb PNV vegetation type. Taken together Olea and Euphorbia forest types are similar to the less-studied dry transitional montane forest types described by Trapnell and Langdale-Brown (1972) that exist only as fragments today in areas which today receive ~800 mm MAP. In general, vegetation near river courses may show quite sharp transitions between Be and Riverine forest (R) where broadleaved trees (see Table 2.1) form denser stands of vegetation (Lillesø et al., 2011). Vegetation flanking the Makalia River and Nderit River, which has its headwaters on Mt. Eburru, is dominated by *Acacia* spp., but includes other semi-deciduous trees (see Table 2.1). Scattered trees of broad-leafed savanna/forest species and montane Acacia species, as well as very infrequent occurrences of Juniperus procera near the upper boundary of the Prospect Farm Formation, are most likely derived from montane sclerophyll forest (i.e. Fb) (Trapnell et al., 1976; and shown in Figure 2.12).

2.6.2 Higher elevation vegetation (2000 - 4000 m a.s.l.) in the Nakuru-Naivasha Basin

Afromontane forest, located in areas between ~ 2000 to 3000 m a.s.l in the Nakuru-Naivasha Basin is divided into drier undifferentiated Afromontane forest (*Fb*), found on leeward side of mountains, including Mt. Eburru, and more humid Afromontane rain forest (*Fa*), located on the windward site of mountains such as the Aberdares Range (covering ~ 35000 ha) and the Mau escarpment (Lambrechts et

al., 2003). A well-developed Afromontane bamboo zone occurs between 2400 and 3300 m a.s.l. on the wetter slopes of the Aberdares Range and is also present, discontinuously, on the Mau escarpment. Bamboo occur in small patches on the Eburru massive, where the native *Arundinaria alpina* is dominant (Schmitt, 1991). A moisture gradient running across the Mau forest complex, which covers 627960 ha, runs from west to east, with moist rainforest surrounding Lake Victoria grading into dry tropical forest (synonyms: Afromontane undifferentiated forest [*Fb*], Montane sclerophyll forest and Xeromorphic evergreen forest) on the western Mau escarpment and Mt. Eburru. This drier forest type, for which there are currently no detailed vegetation surveys on Mt. Eburru, is characterised by a mix of broadleaved and conifer species (e.g. *Podocarpus latifolius, Prunus africana* and *Juniperus procera*; and see Table 2.1 and Figure 2.12). On other East African mountains these are usually found growing between 1250 and 2500 m a.s.l., with a canopy height of ~20m (Trapnell, 1987; Beentje et al., 1994; Wass, 1995; Lillesø et al., 2011). In highland areas of the basin this mixed vegetation type develops where there are fertile soils (see Figure 2.10).

White (1983) observed that the structure and composition of Fb is highly mutable, and changes between closed canopy and open conditions can occur over short distances. For instance, areas of abundant large trees are often associated with a sparser canopy of smaller trees and an understory of pteridophytes (ferns), mosses, herbs, lianas and C₃ forest grasses. These can quickly transition into forest clearing scrub vegetation (see Table 2.1). Waterlogged grassland forest clearings within Afromontane forests on the Aberdares Range, the Mau forest and Mt. Kenya are commonly dominated by C3 sedges, while drier areas mainly support tufted C₄ Poaceae, (Georges, 1900; Edwards, 1940; Pringle, 1983; Wooller et al., 2003; Rucina et al., 2009). These generalised observations are in agreement with systematic surveys of C_3 vs C_4 distributions on East African Mountains (as introduced in Chapter 2.6). These record C_3 grasses present predominantly in shaded forest understories and increases in C₄ taxa in open areas and forest clearings. In lower transitional zones where intermediate Fb grades into drier woodland and savanna vegetation, tree species tend to be those that require lower available soil moisture (Bussmann, 2001; 2006). Fa is similar in appearance to tropical evergreen forests from central and western Tropical Africa and there is some overlap in species composition between the two (e.g. the presence of tropical tall palms *Phoenix reclinate*, and see Table 2.1). On the Aberdares Range, Fa replaces Fb on locally on more humid slopes. Fa is not present on Mt. Eburru today because of its drier climate conditions compared to the Mau Escarpment or the Aberdares Range. Elements of Fa are present of the western Mau escarpment which shares regional connections to the Lake Victoria Basin and by extension to Guineo-Congolian species of flora and fauna. This being the case, it may be possible that during humid intervals of the late Quaternary Period, Fa could have interspersed or replaced the relatively drier Fb forest type on Eburru. On the Kinangop Plateau (~2500 m a.s.l) an extensive area of C4 tussock grasslands growing on waterlogged ando-luvic phaeozem soils are found, characterised primarily by species of Panicoideae. It has been suggested this plateau was forested throughout much of the Holocene, but that grassland has formed as the result of a long history of grazing and burning (Lind and Morrison, 1974; Lamb et al., 2003). Similar C_4 grasslands are also present above the treeline on the eastern Mau escarpment and to a lesser extent on Mt. Eburru (Pringle, 1893; Gorges, 1900). Above *Fa* and *Fb* forest, and the bamboo zone, an extensive ericaceous belt (often referred to as 'moorland') and Hagenia-Hypericum vegetation, is followed by true Afroalpine vegetation and then the Nival zone with a few isolated grasses. While this altitudinal vegetation succession is present on the Aberdares Range, which has volcanic centres at Mt. Kinangop (3992 m a.s.l.) and Ol Donyo Lesatima (3999 m a.s.l), the comparatively diminutive Mt. Eburru (Ol Doinyo: 2856 m a.s.l.) does not possess the altitudinal, temperature and rainfall gradients to support these vegetation types under present day climatic conditions. The C₃ lawn and tussock grasses, some C₃ Danthonioideae, as well as occasional C₄ Panicoideae, that are found on the Aberdares (Gregory, 1894; Greenway, 1973; Schmitt, 1991), are not observed above the tree line in the Mau escarpment (3000 m a.s.l). As such, it seems less likely that alpine grasses extended their altitudinal range in the upper reaches of the Mau Escarpment and on to Mt. Eburru during cold intervals on the last glacial period, as has been inferred on other East African Mountains (see Chapter 3.5.1).

APPENDIX 3



Appendix 3 - Figure 3.1 Comparison of select palaeoclimatic time series across tropical and subtropical Africa, covering the last 150 kyr. Oceanic core records of terrigenous runoff: (F) Stable hydrogen isotopic composition of leaf waxes, corrected for ice volume contributions (δD_{wax-IV}) as an indicator of aridity (increasingly negative value indicates higher precipitation); data from the Gulf of Aden (core RC09-166) (Tierney and Zander, 2017). (L) The carbon isotopic composition of the C₃₁ n-alkane ($\delta^{13}C_{wax}$). Higher (less negative) values indicate increased inputs from C4 vegetation; data from core MD96-2048, Zambezi River outflow (Castañeda et al., 2016). Lacustrine δD_{wax} records: (J) δD_{wax} data corrected for changes in global ice volume (δD_{wax} -IV [100 vs. VMSNOW]) as an indicator of aridity (increasingly negative value indicates higher precipitation); data from Lake Tanganyika (Tierney et al., 2010). (K) δD_{wax-IV} data from Lake Malawi (Konecky et al., 2011). SST records: (B) SSTs (°C) based on Mg/Ca ratios on planktonic forams; data from the Gulf of Guinea (Weldeab et al., 2007). (C) Alkenone (UK'37)-based SSTs (°C); data from the western Indian Ocean (Bard et al., 1997). (D) UK37, Mg/Ca ratios of G. rubers.s.s, and TEX86 based SSTs (°C): data from the Zambezi River outflow (Caley et al., 2011). (E) SSTs (°C) based on Mg/Ca ratios on planktonic forams; data from the eastern Indian Ocean (Mohtadi et al., 2010). Insolation changes: (A) Mean insolation at 25°N during June-July-August (JJA) (Berger and Loutre, 1991). (I) Mean insolation at 25°N during March (red line) and September (black dashed line) (Berger and Loutre, 1991). Mean insolation at 25°N during December-January-February (DJF) (Berger and Loutre, 1991). (M) Mean insolation at 15°S during December-January-February (DJF) (Berger and Loutre, 1991). Lake levels: (G) lake level change based on seismic reflection profiles; data from Lake Challa (Moernaut et al., 2010). (H) Lake level data based on sedimentology and diatom analysis; data from Lake Naivasha (Trauth et al., 2003). Atmospheric trace gasses: (N) composite CO2 from Epica Dome C, Antarctica (Monnin et al., 2001; Eggleston et al., 2016). (O) CH4 data from Epica Dome C ice core, Antarctica (Monnin et al., 2001). Pollen records: (P) Mt. Kenya (Olago et al., 1999); (Q) Deva-Deva Swamp in the Uluguru Mountains (Finch et al., 2009); (R) lake Naivasha (Mworia-Maitima, 1997); (S) Mt. Kilimanjaro (Schuler et al., 2012); (I) Rukiha Highlands Uganda (Taylor 1990); (U) Kashiru Swamp, Burundi (Bonnefille and Riollet, 1988).



Appendix 3 - Figure 3.2 Select equatorial East African pollen and isotope records used to suggest general spatiotemporal changes in wetness and temperature across the region during the LGIT plotted relative to Norther Hemisphere climate trends (represented by the NGRIP $\delta^{18}O$ (‰) combined data [Scierstad et al., 2014]). AHP: African Humid period, YD: Younger Dryas, H1: Henrich Event 1. (A) Pollen record from Lake Naivasha [Figure 3.1 (R)] (Maitima, 1991). (B) Lake Challa [Figure 3.1 (G)] upper bar: Leaf Wax-Inferred δD_P (wetness) (Tierney et al., 2011); lower bar: pollen (van Geel et al., 2011). (C) Lake Victoria [-1.23'1.67''S 33°19'8.33''E] upper bar: δD_{wax} (wetness); lower bar TEX₈₆ (temperature) (Berke et al., 2012). (D) Pollen Mt. Kenya [Figure 3.1 (P)] (Olago et al., 1999). (E) Pollen, Rukiha Highlands Uganda [Figures3.1 (T)] (Taylor, 1990). The general trend visible in the data is of widespread cool conditions during the LGM across equatorial East Africa. Marginally wetter conditions are inferred during the LGM in the KCR from Naivasha and the Aberdares Range (record not shown) and to the southeast from coastal areas at Lake Challa and the EAMs [Figure 3.1 [Q]). In general, these vegetation changes are accompanied by widespread aridity at lower elevations indicated by desiccation events in many lakes across the region (e.g. Lake Turkana and Bogoria [Owen, 1981; Junginger and Trauth, 2013] and Lake Victoria [e.g. Talbot and Livingstone, 1989]). During the LGM, West Africa experienced major forest loss (see Figure 3.4), while in in East African forest extent was reduced but remained relatively stable (Hamilton, 1981). At the same time, pollen records from Tropical Africa [not shown] indicate cool but relatively wetter conditions.

Central Africa	Vegetation proxy records (Figure 3.4) shown evidence of much drier conditions occurring over
	severely depleted in the region during the LGM. Pollen records from west Africa indicate that forest cover was
	and Lézine, 2016), with some studies estimating a loss of up to 80% of rainforest in West and
	Central African (Anhuf et al., 2006). Forest loss in this region during the LGM are associated with
	decrease rainfall, higher levels of evaporation and a 47% decrease in pCO2 (to 180 ppm), as well
	as internal vegetation-climate reedbacks, that would have caused plants to experience neightened water stress (Cerling et al., 1997; Street-Perrott et al., 2004)
eastern Tropical	Both model and proxy data indicate dry, but relatively wetter conditions than other areas of the
Africa	continent, in eastern Tropical Africa during the LGM. Enhanced relative humidity has been
	associated with the southern displacement of the rainfall belt and ITCZ from 23-11 ka which
	change is reflected in palaeolake level and pollen records from Masoko (Garcin et al., 2007:
	Vincens et al., 2007) and Malawi (Beuning et al., 2011). Lake records from the Western Rift (e.g.
	Lake Tanganyika [Gasse et al., 1989; McGlue et al., 2008], Lake Rukwa [Talbot and Livingstone,
	1989], Lake Albert [Beuning et al., 1997] and see Street and Grove [1979]), indicate reduced lake
	show complete desiccation. Pollen records (e.g. Lake Tanganyika Ilyory and Russel 2016) and the
	Zambezi River catchment [Mercader et al. 2009; Ivory et al., 2012; Castañeda et al., 2016; Dupont
	and Kuhlmann et al., 2017) indicate the persistence of stable forest communities despite increased
	regional aridity associated with glacial boundary conditions, but that widespread forest at low
	Africa the LGT and Holocene saw the expansions of drought-tolerant Miombo woodland taxa
	as the ranfall belt and ITCZ shifted northwards (Garcin et al., 2006; Vincens et al., 2007; Ivory et
	al., 2012). During the same period in other areas of the continent, warm and drier conditions
	resulted in the expansion of grass dominated savanna landscapes (see Willis et al., 2013 and
equatorial East Africa	references therein). Both model and provy data indicate cold and dry but relatively more humid conditions occurring
equatorial Last Milea	in some coastal and highland areas of eastern Tropical Africa during the LGM relative to other
	areas of the continent; comparable to conditions in some areas of eastern Tropical Africa. Pollen
	records from the EAM from Dama Swamp in the Udzungwa Mountains (Mumbi et al., 2008) and
	al 2012) and Lake Challa (van Geel et al. 2011) display reductions in forest taxa during the LGM
	however their response is muted relative to other East African records from further north (e.g.
	Mt. Kenya [Olago et al., 1999; Rucina et al., 2009] and to the west (e.g. Uganda [Taylor, 1990] and
	Burundi [Bonnefille and Riollet, 1988]). This suggests that stable climatic conditions in these areas
	than more sporadic refugia elsewhere in East Africa. During the early last glacial period, low
	charcoal counts, low Erica pollen and the expansion of grasses in the Afroalpine zone on Mt.
	Kilimanjaro are thought to relate to very cool dry conditions limiting plant fuel. During the LGM
	on this mountain, forest declined but bushy ericaceous vegetation was not reduced to the same extent as during the early last glacial period (Schüler et al 2012). Similar conditions are observed
	in pollen records from Mt. Kenya (Olago et al., 1999; Appendix 3, Figure 3.1 [P]). This fits the
	model that climatic deterioration in East Africa was more severe during the penultimate Glacial
	Maximum and early last glacial period, when megadrought indicators are observed across the
	region (see Chapter 5.5), than during the LGM. Both amplifier and non-amplifier lakes in lowland areas in or near to the Kenvan Rift (e.g. II ake Turkana [Owen et al. 1982; Morrissey and Scholz
	2014], Lake Suguta [Garcin et al., 2009; Junginger and Trauth, 2013], Lake Victoria [Talbot and
	Livingstone, 1989; Johnson et al., 1996; Cockerton et al., 2015 experienced desiccation during the
	LGM (Gasse, 2000). In the Ethiopia Rift, Lake Abhé [Gasse, 1977] and Lake Chew Bahir (Foerster
	pollen records from Naivasha (Maitima, 1991), the Aberdares Range (Perrott and Street-Perrott.
	1982), and from Sacred Lake, Mt. Kenya (Rucina et al., 2009), suggest slightly wetter conditions
	on the Mau Escarpment and Aberdare Range relative to the inner rift and Mt. Kenya during the
	LGM. However, the low spatial resolution of model results and the issues associated with dating errors for these pollen records in the KCR binder definitive conclusions about the state of climate
	and vegetation in the Nakuru-Naivasha Basin during the LGM. Following the LGM, records
	generally show the rapid reestablishment of mesic forest taxa (e.g. Hagenia, Podocarpus, Polyscias,
	Schefflera etc.) associated with deglaciation. Severe regional droughts are recorded during the YD;
	nowever, these are not visible in the inatvasha pollen record. The two millennia following the YD (~12.4-10 ka) in East Africa was a period of significant climatic amelioration and environmental
	transition, related to rapid increases in temperature, pCO_2 , and humidity during the early Holocene
	Period and mid-Holocene AHP. In the Sahara the AHP saw large increases in woody vegetation
	and the migration of woodland \sim 500 km north. In montane settings this period is associated with
	expanded in highland areas there is evidence to suggest that these areas still experience episodic
	regional drought before the onset of widespread more continuous Holocene aridity ~4 ka in
	equatorial East Africa (Olago, 2001; Kiage and Liu, 2006; Willis et al., 2013).

Appendix 3 - Table 3.1 Regional palaeoclimatic and palaeovegetation changes during LGM, LGIT and Holocene in Africa.

3.1.1 The varying influences of the monsoons, CAB and ITCZ on East African hydroclimate during the late Quaternary period.

The early and long-held, but uncorroborated theoretical models of Tropical climate forcing (i.e. the premise of 'Interhemispheric asymmetry' [see Berger, 1978; Rudimann, 2006]), linked the continuous dominance of low latitude forcing throughout the Last Glacial cycle in East Africa to two factors: 1) Its positioning in a region of surface air convergence; 2) Rift Valley orogeny creating a physical barrier, that insulated the region from Tropical Atlantic Ocean climate dynamics, that created an east-west temperature gradient along the Equator. More recently, this idea has been revised to fit records near the Equator (e.g. Sepulchre et al., 2006), including those from East Africa, which show signs of being controlled to some extent by Northern Hemisphere (high latitude) forcing (e.g. Verschuren et al., 2009; Tierney et al., 2011a) as the influence of precession reduced towards the Last Glacial Maximum in the region (LGM; 26.5-19 cal kyr BP [Coetzee, 1967; Flenley, 1979]) (Singarayer and Burrough, 2015).

Records from Horn of Africa and the Turkana-Omo lowlands (see Appendix 3.2), indicate that when the influence of precession forcing was reduced (e.g. during the LGIT) and the influence of the West African monsoon broardened, that the rift barrier in the Ethiopian highlands was broken by Atlantic Ocean air masses. This would have allowed both the CAB and ITCZ to deliver moisture to the Horn of Africa, resulting in the synchronization of precipitation between the two areas at this latitude on orbital time scales. Today, rainfall is delivered to inland areas of East Africa primarily by the CAB via meso convection; with contributions also being made by the East African/Indian Ocean Monsoon and to a less extent the ITCZ (Nicholson, 2018). Palaeoclimatic records (see Appendix 3.2), indicate that, at times, the intensity of convergence of the WSAM and CAB appears to have even more important than at present than the East African/Indian Ocean Monsoon and ITCZ in delivering moisture to sites in the northern part of the Rift Valley on sub-millennial- and perhaps longer timescales. However, whether or not the influence of the CAB increased, such that it was the sole mechanism for providing moisture to equatorial East Africa and the Central Rift Valley during the last glacial period [when the influence of equatorial precession was both higher (during late MIS 6 and throughout MIS 5) and lower (during MIS 4-MIS 2)], is presently unclear. This is because of the lack of records from this area that allow for the source of precipitation associate with lake highstands to be determined (see Appendix 3.3 for details). Relatedly, this enhanced influence of the WAM is supported by palaeoclimate modelling and is readily visible in Last Glacial-Interglacial Transition (LGIT) and Holocene records from East Africa (see Appendix 3.1.2 - Figure 3.2 and Table 3.1). However, evidence of a strong northern mode of insolation from sites close to, and north of, the 'hinge-zone' in East Africa prior to the LGIT is more ambiguous. This lack of coherence on the finer details of palaeoclimate in the region arises from the paucity of well dated, high-resolution, long and contiguous records of climatic and associated environmental changes.

What has become apparent from studies employing molecular proxies of hydroclimatic variability from North Africa, subtropical West Africa, and eastern Tropical Africa, is that the zonal changes in moisture advection and their related forcing factors are not mutually exclusive and have interacted in the past on different spatial and temporal scales (Costa et al., 2014; Shanahan et al., 2015; Singarayer and Burrough, 2015). The result of these interactions may be divergent patterns of rapid or gradual change, which in turn can be amplified and accelerated, or muted and buffered, by local abiotic and biotic feedbacks. It is also likely that similar patterns of environment change across space and time can be created by the different overlapping forcing factors. As such, it is apparent that it will be necessary to develop multiple records from a region to differentiate changes in the position rainfall belts and changes in monsoon intensity relative to one another (e.g. Shanahan et al., 2015), if late Quaternary hydroclimatic changes in equatorial East Africa are to be resolved.

3.1.2 Simulated changes in the African rainfall belt over the last glacial cycle.

Recent HadCM3 general circulation climate models, simulating monsoon dynamics across Africa during the last glacial period (Singarayer and Burrough, 2015), support a direct response of hydroclimate to local insolation forcing in each month (at ~23 kyr intervals) as the dominant factor regulating the rainfall belt (e.g. Tierney et al., 2010) in equatorial East Africa and eastern Tropical Africa between 120 ka and 80 ka (MIS 5), and during the Holocene (e.g. Chevalier and Chase, 2015). This finding runs counter to studies (e.g. Tierney et al., 2008) that cite extratropical forcing of Indian Ocean SSTs as the central mechanism in modification of the Hadley circulation. Both Lake Challa and Malawi records show a relative stabilisation of climatic conditions from ~70 ka onwards as the influence of precession driven insolation forcing diminished. It does not appear that incursions of Atlantic moisture via meridional shifts in the CAB had a strong influence on high amplitude shifts in climate in eastern Tropical Africa, lack millennial East Africa during the early and middle parts of the last glacial period. However, at present SST from the western Indian Ocean [Appendix 3, Figure 3.2 [C]), proximal to East Africa, lack millennial scale chronological resolution (Bard et al., 1997) that could help to determine if changes in SSTs (linked either to local insolation forcing or controlled by northern extratropical forcing) were solely responsible for the hydroclimatic changes across the region.

3.2 late Quaternary palaeoclimatic trends on the Horn of Africa and the Turkana-Omo lowlands

Recently, stable hydrogen isotopic δD_{wax} records from marine core RC09-166 in the Gulf of Aden (Tierney and Zander, 2017; Figures 3.1 and Appendix 3, Figure 3.1 [F]) allow for examination of hydroclimatic change on the Horn of Africa (12°N) over the last 200 ka, in the early part of the last glacial, when the influence of orbital precession was greater. While there is some correspondence between this record and north-western Indian Ocean SSTs (Appendix 3, Figure 3.1 [C]) (but not Gulf of Aden SST's [not shown]), the strongest relationship with humid hydroclimatic intervals in this record is with insolation changes tracking maximum boreal summer insolation (June–August) on precessional timescales (see Appendix 3, Figure 3.1 [A]); and thus, with large-scale circulation patterns rather than

local SST variations. Support for the meridional locking in of hydroclimate at this latitude between West and Northeast Africa and the associated breaching of the rift barrier by the WAM, comes from the strong linear relationship observed in δ Dwax records from the Horn of Africa (Tierney, 2013; Tierney and Zander, 2017) with those from West Africa (Tierney and Pausata, 2017) during the AHP (when summer insolation peaked at 20°N, ~10-9 ka [deMenocal et al., 2000]).

Similarly, hydroclimatic records in the Turkana-Omo lowlands (Morrisey, 2014; Morrisey and Scholtz, 2014; Bloszies et al., 2015; Junginger and Trauth, 2013) and the Ethiopian Rift (Costa et al., 2014) appear to follow NH climate trends; and indicate the greater influence of the WAM over these areas in the past. However, it is also apparent from the RC09-166 record that Northeast Africa still experienced aridity during MIS 6, MIS 4, and MIS 3-MIS 2, and subdued aridity during MIS 5b and MIS 5d (Tierney and Zander, 2017). This pattern is consistent with the overarching influence of glacial boundary conditions on Africa mediating monsoon intensity (e.g. during MIS 3 rainfall is comparable to modern values and is wetter than MIS 4 but does not reach the levels of humid experienced during MIS 5a, 5c, 5e or the Holocene).

3.3. Hydroclimatic variability during LGIT in equatorial East Africa

Climate shifts during the LGIT and Holocene in equatorial eastern Africa are consistent with some high latitude sub-millennial scale climatic perturbations (e.g. [D-O] cycles and the Younger Dryas [YD]) (e.g. Stager et al., 2002; Marshall et al., 2011; Foerster et al., 2012). Climatic episodes which correspond with high latitude forcing in East Africa are thought to be expressed via the Atlantic Ocean Meridional Overturning Circulation (AMOC) and West African monsoon; with strong teleconnections between the North Atlantic and West Africa evident in records from the region on both suborbital- (millennial) (Gasse et al., 2000; Schefuß et al., 2005; Shanahan et al., 2015) and orbital time scales (e.g. Weldeab et al., 2007; Appendix 3, Figure 3.1 [B]) (Gasse et al., 2008). Records from Ethiopian Rift lakes (e.g. Gasse et al., 1977; Forester et al., 2012) appear to record Heinrich events and D-O cycles. However, these records do not provide evidence of origin of changes in moisture levels (i.e. it is unclear which monsoon has the strongest influence on hydroclimatic variability in these records), and their dating beyond ~20 ka is not secure. These factors limit testing of whether climate in the region was synchronised at times directly with Northern Hemisphere climatic changes. Similarly, there are comparatively few records from East Africa near the Equator that record detailed hydroclimatic changes beyond the LGIT, and even fewer over the full last glacial cycle.

3.4.1 Long-term drivers of vegetation change on East African mountains -additonal information

Temperature is generally considered to be relatively less important than rainfall in influencing tropical vegetation dynamics. This is due to the excess of incoming solar energy near the Equator (Köppen, 1936). This means that when increases in temperature occur which are not accompanied by increases in precipitation, plants experience water stress because enhanced photosynthesis (as the result of higher temperatures) is not supported if moisture availability is low (Field et al., 2005). Early pollen studies were

also used to argue that temperatures in Africa were $4\pm 2^{\circ}$ C lower than present and MAP was reduced by ~30% during the LGM (Bonfille et al., 1990; 1992; Vincens et al., 1993; see Saltré et al., 2013 and references therein). Many of these records document the continued presence of trees such as *Podocarpus* and *Olea* in low abundances as dry savanna vegetation expanded at low to mid altitude sites, indicating the localised survivals of both moist and dry forest types in highland refugia (Hamilton, 1982; Bonnefille and Riollet, 1988; Jolly and Haxeltine, 1997; and see Appendix 3, Figure 3.2).

Shifts in the relative abundances C_3 vs. C_4 plants in favour of C_4 plant at mid to low sites, and the expansion of cold adapted C_3 grasses above the upper timberline, recorded across East Africa during the last glacial period, were linked by earlier studies primarily to the contrasting effects of changes in pCO_2 on the quantum yields of photosynthesis in C_3 and C_4 plants (e.g. Ehleringer, 1978; discussed in greater detail in Appendix 3.4.2) under glacial climate conditions (i.e. reduced rainfall, temperatures, pCO_2 [Petit et al., 1999], and stronger seasonality [e.g. Jolly and Haxeltine, 1997; Huang et al., 1999; Street-Perrott et al., 1997]). On orbital time scales (i.e. during the transition from the last glacial to Holocene), multiple palaeoenvironmental records from Tropical, eastern and southern Africa, indicate that variations in atmospheric trace gasses (CH₄ and CO₂ [Appendix 3, Figure 3.1 (N, O)], associated with global climatic changes), are the primary driver of large scale shifts between forest and grassland vegetation types (Sinninghe Damsté et al., 2011; Tierney et al., 2010; Khon et al., 2014; Urban et al., 2015; Castañeda et al., 2016). Recent studies (e.g. Loomis et al., 2017) have also highlighted that the temperature lapse rate on East African mountains was sharper during last glacial and played a more significant role in vegetation change in East Africa than previously thought.

On sub-millennial timescales proxy- and model-based studies indicate that MAP, fire and the light and intensity of the dry season, exert a far greater influence on vegetation change, at both high and low elevations sites, than pCO₂ alone does (Wooller et al., 2000; Ficken et al., 2002; Wooller et al., 2003; Street-Perrott et al., 2004; 2007; Tierney et al., 2008, 2010; Rucina et al., 2009; Gritti et al., 2010; Sinninghe Damsté et al., 2011; Nelson et al., 2012; Ssemmanda et al., 2014; Urban et al., 2015; Fer et al., 2016; Ivory and Russell, 2016). Furthermore, these studies show that ecological inertia, and local environmental parameters (e.g. fire, soil, topography, geology), interact with rainfall, and pCO_2 to influence both vegetation distributions; and to creating dynamic, asynchronous responses to regional climate trends across the region. In particular, several recent studies of late Quaternary ecosystem dynamics have highlighted localised disturbance regimes (e.g. fire, mega herbivore browsing), internal vegetation climate feedbacks, and threshold behaviour, as being more important than regional climate in determine vegetation assemblage change (e.g. Felton et al., 2007; McGlue et al., 2008; Tierney et al., 2008; 2010; Burrough and Willis, 2015; Ivory and Russell, 2016; Shanahan et al., 2016). These studies provide evidence of decoupling of climatic changes from direct vegetation response, as well as in creating tipping points within ecosystems, which once breached, triggered large changes in vegetation communities. An additional finding of these, as well as other proxy- and model-based studies of palaeovegetation change on East African mountains, has been the importance of different physiological adaptations and

associated environmental tolerances (e.g. to temperature, water-stress and fire, controlling their distributions) in producing species specific, dynamic, non-linear of responses to environmental controls (Dupont et al., 2011; van Geel et al., 2011; Gill et al., 2013; Ivory et al., 2016a; Ivory and Russel, 2016). On Mt. Kenya, Mt. Kilimanjaro, and at sites across the EAMs, species specific responses to biotic and abiotic factors resulted in the mixing of species from vegetation communities located in district altitudinal zones today (Rucina et al., 2009; Schüler et al., 2012; Finch et al., 2014; Platts et al., 2013). These findings contradict the simplified model of the uniform movement of vegetation belts up or down slope, as proposed by early pollen-based studies (Bakker and Coetzee, 1988). It worth noting that modern approaches benefit from greater taxonomic, chronological and spatial resolution, as well as more detailed information on species ecophysiology, than earlier simplified, zonal models. These were intended to facilitate a broader understanding of palaeovegetation changes on a regional to continental scale, but relied on limited spatial resolution of pollen records to do so. They were also shaped by prevalent concepts in vegetation ecology of the time, that emphasised community responses and sharp ecotonal boundaries on a wider scale, in contrast to the more recent integration of individualistic (e.g. Whittaker, 1965) and community approaches (e.g. Wilson et al., 1998) (see van der Maarel, 2005; van der Maarel and Franklin, 2013).

<u>3.4.2 The competitive balance of C_3 vs. C_4 plants under contrasting glacial and interglacial climate conditions</u>

C3 and C4 plants are so defined by the two different CO2 fixing pathways (C3 [Calvin-Benson] and C4 [Hatch-Slack] cycles) they use during photosynthesis (Sage et al., 1999; Sage, 2001; Ehleringer and Cerling, 2002). The C₄ pathway is thought to have evolved as an adaptation to decreasing pCO_2 levels at ~7-6 Ma during the Miocene (see Cerling, 1999; Strömberg, 2011). In C₄ plants, CO₂ is pre-concentrated prior to fixation by the Rubisco enzyme, which gives them a competitive advantage over C_3 plants in arid climates (with increased photorespiration and physiological drought) (Sage and Kubien, 2007) and when pCO₂ is reduced (Ehleringer et al., 1997; Street-Perrott, 1994; Bremond et al., 2012), such as during the last glacial period (Petit et al., 1999). Furthermore, C_4 plants tend to have thicker leaves, with high stromal density and palisade-parenchyma cells containing more Rubisco [Crawford, 2008]) which make them better metabolically equipped (Körner et al., 1989) to deal with arid conditions. For these reasons, an inverse correlation has generally been shown to exist between C4 plant abundance and increasing soil moisture (e.g. Liu et al., 2005). Conversely, under humid conditions and increased pCO_2 (i.e. during interglacials), when favourable edaphic conditions (i.e. increased soil moisture and soil nutrients) were prevalent, the competitive balance is thought to have favoured C_3 plants. This is because C_3 plants require less energy during photosynthesis (Ehleringer et al., 1997) and lose less water due to transpiration. Consequently, when conditions became cooler (Harrison and Prentice, 2003), this allowed forest to expand at lowered altitudes; provided that rainfall was sufficiently high. As partial pressure of both CO₂ and O_2 reduces with altitude, the effects of low pCO_2 on East African montane vegetation is not expected to change with elevation (Sinninghe Damsté et al., 2011). The response mechanisms of forests to changing pCO_2 and drought are complex (see Bonal et al., 2016), but in general, increasing pCO_2 in modern times has caused shift from seasonal (mixed C_3/C_4 understory) to evergreen (predominantly C_3) forest. This has been associated with increased photosynthesis and efficiency of water use by evergreen woody taxa, which has enhanced vegetation growth and primary productivity (known as the fertilization effect in vegetation models [e.g. Hickler et al., 2008]) (Fer et al., 2016). However, real-world studies have demonstrated that transpiration is also reduced in C₄ grasses at higher CO₂ levels (Stock et al., 2005). C₄ plants require enough moisture in the warm season, and without considering the effects of other environmental factors. Collatz et al., (1998) argued that C₄ plants should outcompete C₃ plants in warmer more humid environments. Also, there is some evidence to suggest that high levels of pCO_2 may encourage tree recovery following fire (Bond et al., 2003). However, this is contingent on the local moisture balance (currently placed at 650 mm MAP: see Chapter 2.8) being high enough to maintain dense woodland and forests habitats (i.e. those that exclude a continuous grass understory) in the absence of the impact of herbivore grazing.

3.5 Examples of patterns of vegetation change in East Africa during the LGM, LGIT and Holocene

In eastern Tropical Africa both model and proxy data indicate that the southern displacement of the tropical rainfall belt and ITCZ from 23-11 ka created wetter conditions at 9°S in southern areas of eastern Tropical Africa. Multiproxy records from both Mt. Kenya (Olago et al., 1999; Rucina et al., 2009; and see Figure 3.1 and Appendix 3, Figure 3.1 [P]) and Mt. Kilimanjaro (Zech et al., 2006; Schüler et al., 2012; and see Figure 3.1 and Appendix 3, Figure 3.1 [P]) record cold but relatively moist condones during the LGM, under which Afromontane foresee contracted and Ericaceous belt vegetation moved downslope by over 1000 m, compared to present day vegetation distributions. Similar trends observed in many other East African records in montane sites in the western Albertine Rift (e.g. Rukiha Highlands Uganda (Figure 3.1 and Appendix 3, Figure 3.1 [T], [E]), and Kashiru Swamp, Burundi (Figure 3.1 and Appendix 3, Figure 3.1 [T], Segure 3.1 [Q]). Exceptions to this general trend come from sites in the EAM that show comparatively limited forest movement (of up to 100 m), which has been associated with the area's ability to mitigate widespread LGM aridity (Mumbi et al., 2008; Finch et al., 2009).

In Tropical Africa the LGIT and Holocene saw the expansions of drought-tolerant Miombo woodland taxa as the rainfall belt and ITCZ shifted northwards. In other areas of the continent warm and drier conditions resulted in the expansion of grass-dominated savanna landscapes. In equatorial East Africa, in montane settings, this period is associated with the establishment of more closed moist montane forest and bamboo communities in montane areas, which also experience marked episodes of regional drought. This period was followed by the onset of widespread Holocene aridity ~4 ka in equatorial Africa, and the establishment of current vegetation distributions (see Kiage and Liu, 2006; Hessler et al., 2010; Blome et al., 2012; Willis et al., 2013 for recent reviews). For a more detailed descriptions of regional vegetation change from the LGM to late Holocene see Appendix 3, Table 3.1

3.6 Palaeovegetation and palaeolake level changes in the Nakuru-Naivasha Basin since the LGM

Appendix 3, Figure 3.4 shows palaeolake level reconstructions for the Nakuru-Naivasha Basin for select time slices of the Holocene period based on lake core data (Richardson and Richardson, 1972; Richardson and Dussinger, 1986; Duhnforth et al., 2006), approximate vegetation distributions for the same periods inferred from pollen records from lake Naivasha (Maitima, 1991), and ¹³C/¹²C ratios in late Holocene palaeosol on Mt. Eburru (Ambrose and Sikes, 1991). Pollen and lake records from Naivasha just prior to the LGM indicate relatively cool and humid conditions, which are observed in other records across the region (e.g. higher lake levels [Lake Manyara and Lake Albert; Beuning et al., 1997, Lake Tanganyika; Felton et al., 2007, Lake Suguta; Casanova et al., 1988]) and higher abundance of Afromontane trees and ferns [e.g. Mt. Kenya; Olago et al., 1999, Aberdares Ranges; Perrott and Street-Perrott, 1982, Burundi Highlands; Bonnefille and Riollet, 1988, Eastern Arc Mountains; Mumbi et al., 2008; Finch et al., 2009]). Contrary to other lake records from the East African Rift Valley that show widespread aridity and low lake levels and desiccation events, the diatoms, ostracods and pollen data of Naivasha indicated intermediate but relatively higher lake levels during the LGM than other sites in East Africa (Richardson and Dussinger, 1986; Maitima, 1991). However, it is also the case that grassland appears to have expanded in the Nakuru-Naivasha Basin during this period. One possible explanation for this highland-lowland decoupling (i.e. were lake levels remained relatively high and grassland expanded during the LGM in the basin) is a change in temperature lapse rate. This involves a more pronounced precipitation: evaporation ratio in lowland areas; limiting the transfer of moisture from highland to lowland areas because of reduced tree cover at higher altitudes, associated lower occult precipitation (Rucina et al., 2009; Marchant et al., 2010).



Appendix 3 - Figure 3.4 Palaeovegetation and palaeolake extent maps for the Nakuru-Naivasha Basin based on published palaeolake level and pollen records from the area. Combined records suggest low lake levels and the expansion of savanna vegetation on the rift floor during the LGM (~20 to 17 ka; pollen Zone Ia) as well as from 15 to 12.3 ka (pollen Zone Ic); indicated by high percentages of Gramineae, Chenol/Am., Chenopodium, Compositae, and Sesbania and low percentages of Podocarpus and Olea. Vegetation distributions at these times are thought to approximate those displayed in [E]. However, the extent to which the Afromontane forest belt was lower during the LGM is unknown. It is however likely to have been lower under reduced pCO₂ conditions than is estimated during the Mid-Holocene Dry Phase (~2400 m a.s.l.). During other drier phases of the Holocene (e.g. at 10.5 ka [B], high levels of Artemisia pollen point to the expansion of dry shrubby montane grassland (Agnew, 1974) and the retraction to higher altitudes or local disappearance of montane forest (Maitima, 1991). Higher abundances of montane taxa (e.g. Podocarpus, Olea, Celtis, Anthospermum and Hagenia), between 17 ka and 15 ka (pollen Zone 1b) and at 8 ka (pollen Zone IIa) are associated with lake highstands and wetter conditions. During these periods of high lake levels, Rapanea (Myrsinaceae) and Pygeum pollen indicate the expansion of closed forest on the valley floor at ~2000 m a.s.l. During these highstands Lakes Nakuru and Elementaita became one large water body (as shown in [C]) but never merged with Naivasha due to the topographic high near Karterit volcano. At 9.5 ka, when the highest Holocene Lake Nakuru-Elementaita highstand occurred, there is no sedimentary evidence to suggest that Lake Nakuru-Elementaita breached a potential outflow at the Menegai caldera in the north of the basin, which sits at 1950 m a.s.l. Figure modified from Wilshaw (2013).

APPENDIX 4

4.1 Phytolith production in plants and their utility in palaeoecological studies – additional information

Soil soluble monosilicic acid [Si(OH)4] is ubiquitous in soils with a pH less than 9 (Iler, 1979; Haynes, 2014; Hodson, 2016). Si(OH)4 is transported in transpiration streams within the plants' xylem (Lewin and Reimann, 1969) and upon reaching areas of high sap content in the cells walls; cell lumen (commonly the epidermis and sheath cells of vascular bundles), it undergoes polymerisation to form silica dioxide [SiO₂]. This then solidifies and can constitute up to 10% of a plant's dry weight (Parry and Smithson, 1964; Kaufman et al., 1985; Epstein, 1994; Sangster et al., 2001; Snyder et al., 2007). The term 'phytolith' is reserved for solid silica with distinctive shapes (not amorphous forms), that are typically between 5 μ m to ~300 μ m in size.

Studies of phytoliths from African Plio-Pleistocene (e.g. Barboni et al., 1999; Albert et al., 2006; Bamford et al., 2006; Novello et al., 2015, 2017) and late Quaternary lacustrine and terrestrial sedimentary sequences, have shown that they can be of great utility as proxies for local vegetation in palaeoenvironmental reconstructions, where they are often found associated with archaeological and hominin fossil remains (e.g. Alexandre et al., 1997; Mercader et al., 2002, 2013; Wooller et al., 2003; Neumann et al., 2009; Albert and Bamford; Garnier et al., 2012; Wright et al., 2017; Novello et al., 2018; Arráiz et al., 2017; Yost et al., 2018). Phytoliths from these records provide information on the composition of past vegetation communities but do so at varying levels of taxonomic resolution (see Chapter 4.1.2). Comparison of the relative abundances of phytoliths in modern soil assemblages with fossil phytolith assemblages, (discussed in Chapter 5.6.6) has proved to be a useful approach to identifying the presence of different vegetation communities and variability in vegetation structure (e.g. changes in arboreal cover and canopy openness) in the past (e.g. Fredlund and Tieszen, 1997; Bremond et al., 2005, 2008, 2017; Albert et al., 2006; Mercader et al., 2011; Cordova and Scott, 2010; Dunn et al., 2015). However, it is also the case that large changes in the dominance of certain species within a vegetation community could have occurred due to late Quaternary climate fluctuations experienced in Africa (i.e. resulting in non-analogue vegetation communities in the past). Consequently, modern vegetation communities and associated phytolith assemblages may in some cases be limited in their ability to reconstruct vegetation communities that were present in the past, but which have no modern equivalent. This caveat makes establishing specific taxonomic-morphological relationships between phytoliths and specific plants important.

4.2 General trends in phytolith production across different phylogenetic orders of plants

Phytolith production shows high levels of variability across different phylogenetic orders of plants. However, general relationships do exist in phytolith production and morphology which allow us to differentiate between the plants responsible for their production at various taxonomic levels. In general, closely related taxa produce similar phytolith morphologies, and it is possible to differentiate between the phytoliths produced by many tropical and temperate plants at family and genus levels (e.g. Tomlinson, 1961; Runge and Runge, 1997; Piperno, 1998; Lentfer, 2004). As the majority of absorbed silica is deposited in the aerial structures of the plant (leaves) and reproductive parts (inflorescence, fruit and seeds and their protective tissues) (see Kondo et al. 1994; Runge and Runge 1997; Lentfer 2004; Pearsall et al., 2003; Kealhofer and Penny, 1998), plants with these structures (the angiosperms, gymnosperms, and pteridophytes), often produce numerous phytoliths.

Grasses (the Poaceae family) are by far the most studied group of plants when it comes to our understanding of phytolith production (e.g. Twiss et al., 1969; Piperno, 1998). Along with other monocots, this group were long believed to be the most prolific phytolith producers, generating a wider range of morphotypes. On the other hand, some plant groups produce no phytoliths at all (e.g. basal-monocots [Prychid et al., 2003]) (see Piperno, 2006; for an overview of phylogenetic variation and related patterns of phytolith production in different plant groups). Mercader et al., (2009) observed that in general more phytoliths are produced by lower phylogenetic orders of extant species, aside from basal monocots which produce no phytoliths (Prychid et al., 2003), and in some highly derived clades where production is high (Hodson, 2005). Genetic and environmental controls have also been shown to introduce variability in phytolith production at a family level (see Marschner, 1995; Piperno, 2006; Madella and Lancelotti, 2012), as well as between species of the same plant (Epstein, 1999; Piperno, 2006; Mercader et al., 2009). Piperno (2006) notes that while the evolution of silicon deposition systems in higher plants requires much additional research, it is likely that phytolith production evolved independently several times.

4.3 Extraction of phytoliths from botanical specimens - procedure

For each species its component parts (e.g. leaf, inflorescence, bark, stem) were cut into small pieces and processed together, using up to around 2 g of each component part. (1) Plant specimens were left for a day in 5% Sodium hexametaphosphate (NaPO₃)₆ solution on a shaker to remove any material that may have adhered to the specimen. (2) Specimens were then washed with distilled water placed in a sonic bath for 30 minutes to further clean them. (3) Samples were then dried overnight at a low temperature (100°C) in an oven, transferred to a muffled furnace and ashed at 500°C for 9 hrs. For some woody specimens the time was increased to achieve full combustion. (4) Dry ash was transferred to centrifuge test tubes and a solution of 10% Hydrochloric acid (HCL) was added. (5) Samples were placed in a water bath at 70°C for 20 minutes or until the reaction ceased. (6) Small pinches of solid potassium chlorate (KClO₃) were added to the test tube to speed up the reaction. (7) Samples were then centrifuged at 3000 rpm for 5 minutes and this process was repeated three times with distilled water to wash through the samples. (8) 10% peroxide (H₂O₂) was added and procedure 7 above was repeated. (9) 15% Nitric acid (HNO₃) was added and procedure 7 above was repeated. (10) An additional run of washes using distilled water was carried out to remove any remaining acid. Phytoliths residues were then pipetted onto slides and mounted using DPX® mountant.

Appendix 4 - Table 4.1 Description and the size of each morphotype from woody and herbaceous dicotyledons, ferns and non-grass monocotyledons are found in Figures 4.1-4.7 (Plates 1-7), an associated plant group, the plant tissue from which the phytolith type is thought to originate, and key references from which each morphotype has been previously described where possible. Phytolith morphotypes observed in woody/herbaceous dicotyledons (WHDS), pteridophytes (PDYT), Poaceae (POAC) and Cyperaceae (CYPE) specimens from Nakuru-Naivasha, (BYR) Bryophyte, (MONO) monocots, (HMON), herbaceous Monocots, (COMM) Commelinaceae, (GYN) Gymnosperms. When these are marked with and an asterisk this indicates that this morphotype was found modern plants form the study area (e.g. WHDS*). No asterisk next to a taxonomic association indicates that the morphotypes has been observed in this group in other studies but not in this group in the Nakuru-Naivasha reference collection. (S) indicates that the morphotype was present in Prospect Farm palaeosol samples. Fe=fruit/endocarp; I=inflorescence; L=leaves; R=roots; S=seeds; WS=wood/stem, B=Bark

Major Plant	Morphotype	Fig.	Size:	Morphotype	Observed in/plant part	Taxonomic	References (key African Studies)	References
Groups		code	length/di	description		association		(key global studies)
WHDS			-ameter of globular			(this study) based on published		
Class/Subcla			types µm			material		
ss			unless			and Ref.		
			stated			collection		
Δ	Blocky/Tabular	Dlate 1	20,200	Florente	(S) (WHDS*) (CVN*)	WHDS and	Ruppe 1000 (C2 and C3):	Strömberg 2004 (class
Parenchyma/	parallelepipedal	Aa-Ak	20-200	parallelepipedal	(3), (WIID3), (CIIV)	GYN	Mercader et al., 2000, 2009 (5a-n	E4. Fig.5 L pg. 259):
Cork (P/C)	Lanner L.L.			block with	S, L and occasionally the	0	pg 103); Albert et al., 2006 (2h pg.	2002 (Fig.3 16,17 pg.
(Palisade				smooth/lacunose/sli	exocarp or the legume case		84); Aleman et al., 2014 (2h,	83); Kondo et al.,
Parenchyma				ghtly scrobiculate	of woody dicotyledons. L		pg.276); Neumann et al., 2009;	1994; Kealhofer and
Mesophyll)				texture (often infilled	of certain conifers; L of		Novello et al., 2012 (Plate 2-	Piperno 1998; Bozarth,
				with occluded	shrubs, L, W of certain		2,3,6,7 pg.50); Collura and	1993.
				carbon (PhytC) [see	woody dicotyledon. Similar		Neumann, 2017; Novello et al.,	
				Alexandre et al., 2015]) Bostonoulor	in appearance to some		2017; Yost et al., 2018	
				(2D) /parallelepipeda	from Poaceae e.g.			
				1(3D) L/W < 2	Mercader et al 2010 (Fig 4			
				psilate, single and	20 pg. 1961) and see Plate			
				multicell (Collura	6			
				and Neumann,				
				2017).				

Blocky facetate/ polyhedral facetate	Plate 1 Ba-Bd	25–110	Single and multicell polyhedral or plate- like bodies with large facets. isodiametric with penta- to hexagonal faces, psilate with unsilicified elliptic cavities (Garnier et al., 2012; Collura and Neumann, 2017)	(S), (WHDS*), (GYN*) B, WS and L of woody dicotyledons and conifers. Very similar forms are recorded in Cyperaceae e.g. Thin facetate plates with raised ridges from woody rhizomes/sedge culms - Yost et al., 2018 (Fig.4 h, i pg. 84); Novello et al., 2018 (Plate I e2 pg.6). some Parenchyma/Cork cell Blocky polyhedrals (e.g. Collura and Neumann, 2017 [Fig.6 b	WHDS and GYN	Mercader et al., 2009 (5q pg.103); Aleman et al., 2014 (2f, pg.276); Neumann et al., 2009 (2a-b, j pg.92); Novello et al., 2012; Garnier et al., 2012 (3Ad pg. 5). Collura and Neumann, 2017 (4 c,d pg. 12); Barboni et al., 2010 (Fig.4- 26 pg. 348]); Esteban et al., 2017 (Fig.2 j pg. 9); Novello et al., 2017; Yost et al., 2018	Kondo et al., 1994 (Pl. 19a–c); Kealhofer and Piperno, 1998 (Fig.39 pg.18); Blinnikov et al., 2002 (Fig. 1,16); Strömberg 2003, 2004 (E4); Bozarth, 1993.
				pg.14]) can appear very similar to elongate psilate platelets from Poaceae			
Blocky corniculate	Plate 1 Ca-Cc	20–110	Ovate, rectangular, polygonal or irregular block with corniculate textures (Mercader et al., 2009).	(S), (WHDS*), (BYR) B and Fe of woody dicotyledons and L of Byrophytes	WHDS and BYR	Mercader et al., 2009 (Fig. 5-n, s pg. 103, Fig6-k pg. 104); Barboni et al., 2010 (Fig.4-32 pg. 348); Collura and Neumann, 2017 (Fig.4 k-l pg. 12)	Carnelli et al., 2004 (Plate VI 10,11 pg. 58)
Blocky/Tabular decorated (including Blocky sulcate/ruminate, Blocky favose, Blocky lacunose)	Plate 1 D	40-120	Elongate parallelepipedal block with sulcate, ruminate, scalloped (favose-like), lacunose texture. Rectangular (2D)/parallelepipeda l (3D), L/ W \leq 2, psilate, single and multicell (Collura and Neumann, 2017)	(S), (WHDS*) WS and B of woody dicotyledons and in some gymnosperms	WHDS	Mercader et al., 2009 (Fig. 5-n, s pg. 103, Fig6-k pg. 104); Barboni et al., 2010 (Fig.4-32 pg. 348]); Collura and Neumann, 2017	Carnelli et al., 2004 (Plate VI 10,11 pg. 58)

Blocky/Tabular crenate-echinate -sinuate	Plate 1 Ea-Eh	40-100	Elongate parallelepipedal block with wavy to scalloped edges, psilate and decorate texture. Rectangular (2D)/parallelepipeda $1 (3D), L/W \le 2$ (Collura and Neumann, 2017)	(S), (WHDS*), (POAC), (CYPE) L and WS of woody dicotyledons and gymnosperms. Also produced by Poaceae and Cyperaceae according to Novello et al., 2012	WHDS	Novello et al., 2012 (Plate.2 Blo-08 pg. 50); Mercader et al., 2009 (Fig.6 d pg. 104) Barboni et al., 2010 (Fig.4 22 [El-14] pg. 348)	Carnelli et al., 2004 (Plate.VII 3 pg. 59)
Blocky/Tabular radiating laminate	Plate 1 F	20-70	Orbicular to rectangular block with a surface covered by concentric layers (Mercader et al., 2009).	(S), (WHDS*), (GYN) L and WS of woody dicotyledons and gymnosperms	WHDS and GYN	Mercader et al., 2009 (Fig.5 u pg. 103); Collura and Neumann, 2017 (Fig.7 b pg. 15)	Carnelli et al., 2004 (Plate VI 12 pg. 57)
Blocky/Tabular scutiform	Plate 1 Ga-Gc	30-70	Shield-shaped block with psilate to scrobiculate texture	(S), (WHDS*) B of woody/herbaceous dicotyledons. Similar to Cuneiform bulliform types produced in leaves of Poaceae and Cyperaceae (Piperno, 1988; Kondo et al, 2004). In particular those produced in bambusoides (e.g. Lu et al., 2006 [Fig.3 Al pg. 950]) and Barboni et al., 1999 (Plate I 42 pg. 92)	WHDS	Collura and Neumann, 2017 (Fig.5 p pg.13)	_
Blocky/Tabular tuberculate	Plate 1 H	30-65	Blocky with tuberculate protrusions. Irregular block with lacunose/scrobiculat e/tuberculate texture (Mercader et al., 2009)	(S), (WHDS*) L and B of woody dicotyledons (Mercader et al., 2009; Collura and Neuman, 2016)	WHDS	Mercader et al., 2009 (Fig. 5 w pg. 103); Barboni et al., 2010 (Fig.4 30 pg. 348); Collura and Neumann, 2017 (Fig.4 n pg. 13)	_

4									
	Tabi	ular 'ridged'	Plate 1 Ia-Ib	40-70	Thin parallelepiped, orbicular to square, with surface covered by ridges (Mercader et al., 2009)	(S), (WHDS*) (POAC) L of woody/herbaceous dicotyledons. Very similar forms are recorded in Cyperaceae e.g. Thin facetate plates with raised ridges from sedge culms – (Yost et al., 2018 [Fig.4 h, i pg. 84]); (Novello et al., 2018 [Plate I e2 pg.6]). "grasses and non-grasses" (Runge, 1999)	WHDS	Mercader et al., 2009 (Fig.4 u pg. 102); Runge, 1999	_
	Bloc cava	cky/Tabular ate fimbriate	Plate 1 Ja-Jf	20-60	Elongate parallelepipedal block with singular internal cavity (Collura and Neumann, 2017) or centric depression" (Mercader et al., 2009)	(S), (WHDS*) L and B of woody/herbaceous dicotyledons	WHDS	Collura and Neumann, 2017 (Fig.7 g-l. pg. 15); Mercader et al., 2009 (Fig.5 o, s pg. 103)	
	Elliç with irreg proj	psoid-elongate n regular or gular jections	Plate 2 Aa-Ab	20-60	Blocky to ellipsoid to cylindric to ellipsoid with straight or knobby outgrowths, sometimes faceted (Garnier et al., 2012). Sometimes with pitted regular pattern (Collura and Neumann, 2017)	(S), (WHDS) Sclereids of tracheary elements of L of and B of woody/herbaceous dicotyledons.	WHDS	Collura and Neumann, 2017 (Fig.6 h-k. pg. 14) (Fig.3 l pg. 11)	

B. Commelinid types	Commelinid like types: (Marantaceae/Co mmelinaceae)	Plate 2 B	10-45	Basal part subcylindrical, lateral walls corniculate, loosely scrobiculate, proximal surface psilate; top polygonal- pyramidal to conical, psilate; with beaked projection (Eichhorn et al., 2010). Hexagonal to rectangular in side view, lower part with a finely echinate surface, upper part a truncated cone with psilate surface (Neumann et al., 2000)	(S), (COMM) Fe of Monoctyledon Commelinids Similar to those found in the Fruit and Seeds of Commelinaceae (e.g. similar to <i>Commelina</i> <i>forskaolii</i> type [Fig 6. e pg. 308]) Eichhorn et al. (2010). see also Novello et al. (2012), Granier et al., 2012)). Seeds of Marantaceae (Runge, 1999; Novello et al., 2009).	СОММ	Runge, 1999 (D2, Plate IV 4,5,6 pg.37). Mercader et al., 2000; Eichhorn et al., 2010 (Fig.6 i,e pg. 308). Neumann et al., 2009 (Fig.2 m pg. 92).	Piperno, 2006 (Fig2.16f, 1.17a pg. 198
	Commelinid types: Pollia /Floscopa/Murda nnia types	Plate 2 Ca-Cb	10-50	Basal part a planar elongated polygon [polygonal prism] in 2D view, upper part conical (orbilcular [conical] in 2D view), surfaces psilate	(S) Fe of Monoctyledon Commelinids	СОММ	Eichhorn et al. 2010 (Fig.3 c, e, g-i pg. 305); Garnier et al., 2012 (Fig.3 Dg pg. 420). Runge, 1999 (D2, Plate IV 6,7 pg. 37)	_
	Commelinaceae: <i>Cyanotis lanata</i> and <i>Cyanotis</i> <i>Longifolia</i> types	Plate 2 Da- Db	10-20	Basal part polygonal, psilate, slightly convex dentate margin, bent upwards; upper part conical, lateral walls concave, widest at top, top concave (Eichhorn et al., 2010)	(S) Fe of Monoctyledon Commelinids	СОММ	Eichhorn et al. 2010 (Fig. 3 l, m o, p pg. 305; Fig.6 e, g, h pg. 308); Garnier et al., 2012 (Fig.3 De pg. 420); Runge, 1999 (D2, Plate IV 6,7 pg. 37)	

C. Globular and globular aggregate types	Globular psilate	Plate 2 Ea-Ed	7-15	Spherioid with a sub- smooth texture (Mercader et al., 2009)	(S), (WHDS*), (PDYT), (HMON) (POAC) L, bark and fruit and WS of certain woody/herbaceous dicotyledons, monocotyledons, gymnosperms and pteridophytes. Produced in some Poaceae (see Mercader et al., 2010). Can be produced in independent of shape of cells in which they are formed and can also originate in ideoblasts (see	WHDS, HMON	Runge, 1999 (type B1/B7 Plate I 4 pg. 30); Neumann et al., 2009; Barboni et al., 1999 (Plate I 8 pg. 92); Mercader et al., 2009 (Fig.3 p,u pg. 100); Collura and Neumann, 2017 (Fig.3 a-c pg. 11); Barboni et al., 2010 (Glo-28, Fig.4 5 pg. 348); Mercader et al., 2010 (Fig.3 6 pg. 1960); Novello et al., 2017a; Yost et al., 2018	Hart, 1988; Kondo et al. 1994 (Pl. 10); Strömberg, 2004 (E7 Fig.5 f pg. 259)
	Globular psilate large	Plate 2 Ea-Ed	20-50	Large spheroid with a sub-smooth texture (Mercader et al., 2009)	Brilhante de Albuquerqueet al., 2013) (S), (WHDS*) L and WS of certain woody/herbaceous dicotyledons	WHDS	Mercader et al., 2009 (Fig.3 v pg. 100); Novello et al., 2017	
	Globular granulate	Plate 2 Ga-Gc	10-45	Spheroid with granular texture	(S), (WHDS*), (PDYT*), (GYN), (HMON) L and WS of certain woody/herbaceous dicotyledons, monocotyledons, gymnosperms and pteridophytes	WHDS, PDYT and HMON	Novello et al., 2012 (Plate II Glo- 2-4 pg. 50); Garnier et al., 2012 (Fig. 3B a-b pg. 420); Barboni et al., 2010 (Glo-3, Fig.4 4 pg. 348); Aleman et al., 2014 (Fig.2 Ba pg.276); Collura and Neumann, 2017 (Fig.3 e-g pg. 11); Mercader et al., 2009 (Fig.3 o pg. 100); Novello et al., 2017; Yost et al., 2018	Strömberg, 2003; Piperno, 2006 (Fig.2 13 pg. 196)

Globular decorated indifferent	Plate 2 Ha-Hc	10-50	Spherical to irregular ellipsoid with various surface decorations (scorbiculate, irregular, rugulate, columellate or nodular)	(S), (WHDS*) L, WS of certain woody/herbaceous dicotyledons (ray-cells [primarily parenchyma cells] Amos, 1952). Absent in Poaceae according to Runge (1999) and present according Sangster and Parry (1976)	WHDS	Barboni et al., 1999 (Plate I 6,7 pg. 92); Runge, 1999 (B2); Aleman et al., 2014 (Fig.2 b-e pg. 276); Garnier et al., 2012 (Fig.3 B-c pg. 420); Neumann et al., 2009 (Fig.2 d,e pg. 92); Novello et al., 2018; Yost et al., 2018	Piperno, 1988, 2006; Bowdery et al., 2001; Strömberg, 2004 (D1 Fig.5 d pg. 259)
Globular tuberculate	Plate 2 Ia-Ic	10–50	Spherical with tuberculate (smooth rounded projections)	(S), (WHDS*) L and WS of certain woody/herbaceous dicotyledons	WHDS	Neumann et al., 2009 (Fig.2 f pg. 92) Barboni et al., 2010; (Glo-20, Appendix A Fig.4 1 pg. 348); Mercader et al., 2009 (Fig.3 t pg. 100); Yost et al., 2018	Piperno, 1988, 2006
Globulose oblong tuberculate/ verrucate	Plate 2 Ja-Jd	50-70	Elongate sphere (obovate to ellipsoid) with tuberculate (smooth rounded projections)	(S), (WHDS*) Tracheary elements of Woody/herbaceous dicotyledons	WHDS	Mercader et al., 2009 (Fig.3 t pg. 100); Yost et al., 2018 (Fig.4p-q pg. 84)	—
Globular verrucate/ ruminate	Plate 2 K	10-35	Spheroid with verrucate (wart-like projections), ruminate (having a chewed appearance)	(S), (WHDS*) L and WS of certain woody/herbaceous dicotyledons	WHDS	Runge, 1999 (Plate IV, Type B8 pg. 37); Neumann et al., 2009 (Fig. 2 c pg. 92); Garnier et al., 2012 (Fig. 3B-d pg. 420); Collura and Neumann, 2017 (Fig3. f pg.11)	Kealhofer and Piperno 1998 (Figure 10, 11 pg. 8); Piperno 2006; Iriarte and Paz 2009 (Fig.2 a pg. 111); Strömberg et al., 2004 (Fig.5 d [class D1] pg.2590
Globular pappilate (cysloiths)	Plate 2 La-Lb	25-40	Spherical with papillae (minute rounded or acute) protuberances	(S), (WHDS*) Lithocyst of L and Fe of woody/herbaceous dicotyledons, common in Quercus, Ficus, Celtis, Urticaceae, Moraceae, Ulmaceae, Cucurbitaceae, Acanthaceae and Burseraceae.	WHDS		Tsartsidou et al., 2007

Globulose sulcate- columellate	Plate 2 M	40-50	Elongate sphere (obovate to ellipsoid) with sulcate (furrowed) decoration across the body and columellate edges	(S) Anatomical origin unknown			
Globular to sub- globular facetate	Plate 2 Na-Nc	25–35	Globular to sub- globular with facets	(S), (WHDS*) L and Fe of certain of woody/herbaceous dicotyledons, e.g. Annonaceae, Cucurbitaceae, Burseraceae, and monocoyledons e.g. <i>Marantaceae. Sclerenchyma.</i> In L of woody dicotyledons Kealhofer and Piperno, 1998 (figs. 28, 29, 39)	WHDS	Runge, 1999 (Type B4, Plate III 8 pg.34); Runge, 1996a,b; Neumann et al., 2009 (Fig.2 (B2) n pg. 92); Mercader et al., 2000 (Fig.4 d pg. 108); Mercader et al., 2009 (Fig.3 g,h pg. 100)	Kealhofer and Piperno, 1998 (Fig.28,29,29); Piperno, 1988, 2006 (Fig. 2.6 f pg. 192)
Globulose favouse	Plate 2 O	40-50	Spheroid with favouse surface texture	(S), (WHDS*) Fe of monocotyledons and in mesophylls of certain woody dycotyledons	WHDS	Runge, 1999 (Type B3, Plate III 7 pg.34); Neumann et al., 2009 (Fig.2 l pg. 92); Mercader et al., 2009 (Fig.3 c,d pg. 100); Barboni et al., 1999 (Plate I 1-3 pg. 92); Barboni et al., 2007 (Fig.2 11 pg. 457); Barboni et al., 2010 (Fig.4 6,7 pg. 348); Garnier et al., 2012 (Fig.3 D- c pg. 420); Novello et al., 2012 (Plate II Glo-1 pg. 50); Aleman et al., 2014 (Fig.2 C-a pg. 276); Albert and Bamford et al., 2012 (Fig.2 c,d pg. 346)	Dickau et al., 2013 (Plate I d pg.20); Piperno, 2006 (Fig2.8a pg.192); Tomlinson, 1961; Piperno, 1988; Iriarte and Paz, 2009 (Fig.2 b pg. 111); Strömberg, 2004 (Class C Fig.4 g pg. 258); Kealhofer and Piperno, 1998 (Fig.2 pg. 3)

Globular echinate (Arecaceae type)	Plate 2 Pa-Pb	5-25	Spheroid beset with prickles	 (S), (Arecaceae [woody MONO]) L, R of Palmae; (Arecaceae) Similar but not identical types are found in Bromeliaceae, Cannaceae, Marantaceae, Orchidaceae, Strelitziaceae, and Zingiberaceae (see Benvenuto et al., 2015) 	woody MONO	Runge, 1999 (Type B3, Plate III 7 pg. 34); Neumann et al., 2009 (Fig.2 1 pg. 92); Mercader et al., 2009 (Fig.3 c,d pg. 100); Barboni et al., 1999 (Plate I 1-3 pg. 92); Barboni et al., 2007 (Fig.2 11 pg. 457); Barboni et al., 2010 (Fig.4 6,7 pg. 348); Garnier et al., 2012 (Fig.3 D-c pg. 420); Novello et al., 2012 (Plate II Glo-1 pg. 50); Aleman et al., 2014 (Fig.2 C-a pg. 276); Albert and Bamford et al., 2012 (Fig.2 c d	Dickau et al., 2013 (Plate I d pg.20); Piperno, 2006 (Fig2.8a pg.192); Tomlinson, 1961; Piperno, 1988; Iriarte and Paz, 2009 (Fig.2 b pg. 111); Strömberg, 2004 (Class C Fig.4 g pg. 258); Kealhofer and Piperno, 1998 (Fig.2 pg. 3)
Globular folded	Plate 2 Qa-Qc	10-30	Sub-spheroid with extended, thickened rim (Mercader et al., 2009)	(S), (WHDS*), (CYPE), (HMON) L and Fe of certain woody/herbaceous dicotyledons, Bract of certain monocots, and in certain Cyperaceae (Novello et al., 2012)	WHDS and HMON	pg. 346); Novello et al., 2018 Mercader, 2009 (Fig.3 n pg. 100)	Piperno, 1988 (Plate 7 pg. 224); Kealhofer and Piperno, 1998 (Fig.1 pg. 3
Globular-sub- globular dark	Plate 2 R	10-50	Psilate spheroid to sub-spheroid with dark core (Mercader et al., 2009) (infilled with PhytC)	(S), (WHDS*) L, W, and Fe of woody/herbaceous dicotyledons	WHDS	Novello et al., 2012 (Plate II Glo- 5,Glo-8 pg. 50); Garnier et al., 2012 (Fig.3 B-f pg.420); Novello et al., 2018; Collura and Neumann, 2017 (Fig.3 d pg.11)	_
Globular decorated compound	Plate 2 Sa-Se	25-45	Globular decorated compound (see Garnier et al, 2012)	(S), (WHDS*), (HMON) L, W, and Fe of certain woody/herbaceous dicotyledons and certain herbaceous monocotyledons	WHDS	Garnier et al., 2012 (Fig. 3 B-c,g,h pg. 420); Aleman et al., 2014 (Fig.2 B-b-d pg.276); Collura and Neumann, 2017	Bowdery et al., 2001
Obovate psilate	Plate 2 T	30-35	Orbicular to oblong (ellipsoid) with smooth surface texture	(S), (WHDS*) W of woody/herbaceous dicotyledons	WHDS	Collura and Neumann, 2017 (Fig.3 j pg. 11)	_

	Obovate scorbiculate/ granulate	Plate 2 Ua-Uc	30-35	Orbicular to oblong (ellipsoid) with scorbiculate/ granulate surface texture	(S), (WHDS*) W of woody/herbaceous dicotyledons	WHDS	Mercader et al., 2009 (Fig.3 q pg. 100); Novello et al., 2018;	
D. Sclerenchyma Sclereid/meso phyll D1. Cylindroid types	Cylindroid small	Plate 3 Aa-Ab	20-40	Small cylindroid (elongate and circular in cross- section) commonly with a psilate texture	(S), (WHDS*), (HMONO*), (POAC) L of woody/herbaceous dicotyledons and C/L/I of certain Poaceae	WHDS, HMONO and POAC	Mercader et al., 2009 (Fig.2 a pg. 99); Mercader et al., 2010b (Fig.2 30 pg. 1959)	_
	Cylindroid large	Plate 3 Ba-Bb	80-120	Large cylindroid with smooth and pitted texture	(S), (WHDS*) (MONO) L of woody/herbaceous dicotyledons and non-grass monocotyledons	WHDS	Mercader et al., 2009 (Fig.2 g.j pg. 99); Aleman et al., 2014 (Fig.2 c-k pg. 276); Novello et al., 2012	—
	Cylindroid large geniculate/ Cylindroid bulbous	Plate 3 Ca-Cf	35-100	Cylindric curved to clavate to slightly straight psilate with a psilate to scrobiculate texture and irregular bulbous enlargements	(S), (WHDS*), (MONO) L of woody/herbaceous dicotyledons and non-grass monocotyledons	WHDS	Garnier et al., 2012 (Fig.3 Ab pg. 420); Albert et al., 2006 (Fig. 2 g pg. 83); Runge, 1999; Mercader et al., 2009 (Fig.2 c pg. 99, Fig.5 x pg. 103); Collura and Neumann, 2017 (Fig.4 f,g pg. 12)	Postek, 1981; Strömberg, 2004 (Fig.5 a pg. 259); Piperno, 1988; Kondo and Pearson, 1981; Postek, 1981; Kondo et al., 1994; Kealhofer and Piperno, 1998 (Fig.40 pg. 18)
	Asterosclereid	Plate 3 D	100-< 200	Stellate (star shaped) sclereid. Stellate element formed by a body of elongate cylindrical projections with pointed ends	(WHDS*) (GYN), (NYMP), (POAC), (CYPE) Non-specific	_	_	Blinnikov, 1999; Bonomo et al., 2009; Zucol and Bonomo, 2008; Fernández Honaine et al., 2009
	Cylindroid corniculate	Plate 3 E	45-50	Cylindroid (slightly elliptical) with horn like projections	(S) (WHDS*) Herbaceous dicotyledons (anatomical origin unknown)	WHDS	_	—

D2. Sclereid (palisade mesophyll or spongy mesophyll), vein leaf cells and terminal tracheids	Elongate faceted- Sclereid	Plate 3 Fa-Fg	40-150	Elongate cylindrical to parallelepipedal, often multi- facetated, sometimes brachiform "tapering ends, sometimes branched, faceted, or with knobs on surface (Strömberg, 2004)	(S) (WHDS*) Sclereid, terminal tracheid or silicified intercellular spaces in L of woody dicotyledons. B of woody/herbaceous dicotyledons, typical of lignified plants: diagnostic to woody plants	WHDS	Neumann et al., 2009 (Fig. 2 a pg. 92); Aleman et al., 2012 (Fig. 2 g pg. 276); Mercader et al., 2000 (Fig.4 a pg. 108); Mercader et al, 2009 (Fig. 6-d pg. 104); Runge, 1999 (Class A4, Plate III 6 pg. 34); Garnier et al., 2012 (Fig.3 Aa pg. 420); Collura and Neumann 2017 (Class A, Fig. 5 f,g.i pg. 13); Albert and Bamford, 2012 (Fig. 2f pg. 346); Esteban et al., 2017 (Fig.21 pg. 9); Neumann et al., 2017; Yost et al., 2018	Postek, 1981 (Fig.1,2,3,6 pg. 126, Fig.11-14 pg. 128); Piperno 1988, 2006 (Fig.2 6a pg. 191); Kondo et al., 1994 (Pl.19 a–c); Strömberg, 2004 (Type D2, Fig.5 a,c pg. 259)
E. Vessel elements/ Xylem Epidermal tracheid	Cylindric sulcate tracheid (vessel elements)	Plate 3 Ga-Gf	20-150	Elongate cylindroid, epidermal tracheid (Single-cell, fluid- conducting tissue [vessels of the xylem]) with furrowed/laminate texture	 (S), (WHDS*), (PDYT*), (POAC*), (CYPE*), (GYN), (HMON) L, R, B and WS of woody/herbaceous dicotyledons, gynosperms, and pteridophytes, as well as Cyperaceae and Poaceae (non-specific of plant or plant group) 	WHDS, PDYT, POAC and CYPE	Runge, 1999 (Plate III Type 2A 2 pg. 34); Aleman et al., 2014 (Fig.2 j pg. 276); Novello et al., 2012 (Plate II EL-4 pg. 50, Plate II Trac-1 pg. 50)	Iriarte and Paz, 2009 (Fig.5 d,e pg. 113); Strömberg, 2003 (Type E5 Fig.5 i pg. 259); Piperno, 2006 (Fig.2 18d pg. 1999); Strömberg et al., 2013
	Elongate scalariform platelet	Plate 3 Ha-Hc	40-200	"Elongate, with unsilicified elliptic cavities on the surface arranged perpendicular to the length of the body, reminding" (Collura and Neumann, 2017)	(S) (WHDS*) B and WS of woody/herbaceous dicotyledons	WHDS	Collura and Neumann, 2017 (Fig. 4 ab pg. 12); Mercader et al., 2009 (Fig.6 g pg. 104)	

F. Epidermal tissue F1. Leaf epidermis	Epidermal jig-saw platelet	Plate 4 Aa-Ac	~15 - > 250	Thin tabular epidermal cells with puzzle-like outline. Variable textures (Mercader et al., 2009). Occurring as articulated sheets and single plates	(S), (WHDS*), (PDYT*) L, of herbaceous/ woody dicotyledons and pteridophytes	WHDS and PDYT	Mercader et al., 2009; Runge, 1996 (pg. 334)	Rovner, 1971; Wilding and Drees, 1973; Kondo and Pearson, 1981; Piperno, 1985a, 1989; Bozarth, 1992; Kealhofer and Piperno, 1998; Strömberg, 2004 (Fig.5 e pg. 259)
	Epidermal polygonal/ parallelogram/cork aerenchyma platelet	Plate 4 Ba-Bg	~15 -> 250	Thin tabular epidermal polygonal cells, sometimes Isodiametrical with variable textures (from abraxial and adaxial surfaces). Occurring as reticulated sheets and single plates	 (S), (WHDS*), (PDYT*), (POAC), (HMON) L, R of herbaceous/woody dicotyledons, pteridophytes, occasionally produced in Poaceae (Piperno, 2006) e.g. Achillea spb. (Fig.2 Ia pg. 1160) (Frenandez Honaine et al., 2006); e.g. Pennisetum purpureum Schumach. (Culm/Leaf/Inflorescence) (Fig.4 16 pg. 1961) (Mercader et al., 2010) 	WHDS and PDYT	Runge, 1996; Mercader et al., 2009 (Fig. 2 k-o pg. 99)	Rovner, 1971; Wilding and Drees, 1973; Kondo and Pearson, 1981; Piperno, 1985a, 1989; Bozarth, 1992; Kealhofer and Piperno, 1999; Lentfer, 2004; Strömberg, 2004
F2. Achene epidermis	Opaque perforated platelet		40-70	Platelet with alternating amber- coloured and opaque stripes, regular perforations occur in the amber-coloured stripes only (Mercader et al., 2000)	(S) (HMON*) Inflorescences-achenes of some species of the Asteraceae (Piperno, 1988; Bozarth, 1992; Piperno, 2006)	HMON	Runge, 1999 (Plate V 4 pg. 38); Yost et al., 2018 (Fig.4 l pg. 84)	Piperno, 2006 (Fig.2 15b pg. 196); Iriante et al., 2010 (Fig. 3 s pg. 2987)
F.3 Undetermined epidermal tissue	Thin platelet irregular ruminate	Plate 4 C	40-70	Tabular platelet with ruminate texture and irregular edges	(S) Anatomical origin uncertain- likely epidermal tissue of woody dicotyledons	WHDS		

G.1 Non- diagnostic types: misc.	Acicular and Fusiform/Ellipsoi d /scutiform (Trichomes/Acicul ar hair cell)	Plate 5 Aa-Bg	25-40	Spindle shaped generally with psilate texture	 (S), (WHDS*), (HMON*) (POAC*) Trichomes of L and Seed bracts of Poaceae and of certain dicotyledons. Blocky forms may originate from Palisade Parenchyma (similar to bulliform cells from monocots) 	WHDS, HMON and POAC	Runge, 1999; Bremond et al., 2008a (Fig.2 7 pg. 214); Albert et al., 2006 (Fig.2 b pg. 84); Mercader et al. 2011 (Fig.2 m pg. 7)	Fullagar et al., 2006 (Fig.11 h-j pg. 610); Piperno, 2006
	Silica particles/ accumulation	Plate 5 C	_	Small irregular silica particles sometimes occurring aggregated, amorphous silica aggregations (Collura and Neumann, 2017)	(S), (WHDS*), (HMON*) W and B of woody dicotyledons	WHDS and HMON	Collura and Neumann, 2017 (Fig. 3 u pg. 11)	_
	Lanceolate	Plate 5 Da- Dd	30-70	Large tabular, psilate body shaped like a spear (Mercader et al., 2009), shaped like a lance-head, several times longer than wide, broadest above the base and narrowed to the apex	(S), (WHDS*), (HMON*) Non-specific of plant or plant group (possibly lactifier cells from leaves)	WHDS and HMON	Runge, 1999 (Plate III pg. 34) Mercader et al., 2009 (Fig.4 pg.102)	_
G.2 Non- diagnostic types: thin elongate platelets	Thin platelet elongate psilate	Plate 6 Aa-Ae	30-~120	Elongate tabular thin platelets with smooth texture	 (S), (WHDS*), (PDYT*), (POAC*), (CYPE*), (GYN), (HMON*) L and Fe of Poaceae (most common) certain bryophytes, Cyperaceae, Arecaceae, and stem of certain woody/herbaceous dicotyledons. Large rods (up to 250 µm) from "woody" culm from bamboo (Strömberg, 2003) 	WHDS, PDYT, POAC, CYPE, GYN, HMON	Barboni et al., 2010 (Fig.4 19 pg. 348); Albert et al., 2006 (Fig.2 o pg. 84); Mercader et al., 2009; Mercader et al., 2010; Collura and Neumann, 2017; Yost et al., 2018	Strömberg, 2004 (Class H1); Piperno, 1998

Thin Tabular platelet echinate - sinuate-crenate- facetate	Plate 6 Ba-Bt	30-~120	Thin elongate tabular platelet with slightly echinate or sinuate or crenate margins, and a psilate to sometimes slightly facetate surface	(S), (WHDS*), (PDYT*), (POAC*), (CYPE*), (GYN), (HMON*) L and Fe of Poaceae (most common) certain bryophytes, Cyperaceae, Arecaceae, and stem of certain woody/herbaceous dicotyledons. Similar to Tabular elongate columellate/crenate from <i>Resion triticieus</i> and <i>Helichrysum cymosum</i>	WHDS, PDYT, POAC, CYPE, GYN, HMON	Novello and Barboni, 2015 (Plate I B-a,b pg. 14); Aleman et al., 2014 (Fig.2 Ci pg. 276); Novello et al., 2012 (Plate II El-3 pg. 50); Barboni et al., 2010 (Fig.4 20-25 pg. 348); Mercader et al., 2010	Piperno and Pearsall, 1998; Stomberg, 2004 (Class H1); Piperno, 1998
Elongate decorated platelet (conical abraxial)	Plate 6 Ca-Cb	40-60	Elongate platelet with echinate (round nodular or conical) protuberances) surface forming a regular pattern	(Novello et al., 2018) (S), (POAC*), (CYPE*) (WHDS*) Likely to be produced in L and Fe of Poaceae and Cyperaceae, but may also be produced in woody/herbaceous diractivledoar	POAC, CYPE, WHDS	Novello and Barboni, 2015 (Plate I B-a,b pg. 14); Aleman et al., 2014 (Fig.2 Ci pg. 276); Novello et al., 2012 (Plate II El-3 pg. 50); Barboni et al., 2010 (Fig.4 20-25 pg. 348); Mercader et al., 2010; (Plate III, f pg. 8) Novello et al., 2018	Piperno and Pearsall, 1998 (Fig. 67 pg. 38)
Thin platelet dendritic	Plate 6 Da-Dc	50-65	Elongate tabular platelet with concave ends and dendriform to columellate edges	(S), (WHDS*), (HMON), (POAC*) Poaceae (possibly from seed bracts), dendritic long-cell phytolith from grass inflorescence tissue (Yost et al., 2018), as well as from epidermal tissue/Bark of woody dicotyledons	WHDS, HMON, POAC	Novello and Barboni, 2015 (Plate I pg. 14); Mercader et al., 2009 (Fig.6 f pg. 104); Yost et al., 2018 (Fig 3 w pg. 83)	Strömberg, 2004 (Class H1); Piperno, 1998

G.2 Non- diagnostic types: Acicular and hair cells	Acicular and hair cells	Plate 7 Aa- Am	15 ->150	Acicular and Fusiform/Ellipsoid /scutiform (Trichomes/Acicular hair cell), hair cells and hair cell bases	 (S), (WHDS*), (PDYT*), (POAC*), (CYPE*), (GYN), (HMON*) Non-diagnostic- smaller "prickles" more often associated with Trichomes of L and Seed bracts of Poaceae and in certain dicotyledons. Blockier forms may originate from Palisade Parenchyma (similar to bulliform cells from monocots) 	WHDS, PDYT, POAC, CYPE, GYN, HMON	Mercader et al., 2009 (Fig.4 a-g pg. 102); Albert et al., 2006 (Fig.2 b pg. 84); Bremond et al., 2008a (Fig.2 7 pg. 214); Mercader et al., 2010 (Fig.3 18 pg. 1960; Fig.2 m pg. 7); Novello and Barboni, 2015	Bozarth, 1992; Strömberg, 2003, 2004; Kealhofer and Piperno, 1988 (Fig. 25,26 pg. 10); Piperno, 2006 (Fig. 3.12 pg. 210); Baas et al., 1982; Fullagar et al., 2006 (Fig.11 h-j pg. 610)
H. Non-grass monocots: Cyperaceae types	Cypereaceae (sedge) type - hat shaped and papillae	Plate 7 Ba-Bd	15-35	Tabular, pentagonal or hexagonal, surface psilate or favose, with a central rounded cone. Epidermal plate with cone shapes ("papillae"; ICPN Working Group, 2005) (Strömberg, 2004), Tabular, pentagonal or hexagonal, surface psilate or favose, with a central rounded cone (Neumann et al., 2009). Polygonal sedge achene epidermis cells with central papilla (Yost et al., 2018)	(CYPE*) Leaf and inflorescence: Achene epidermis of Cyperaceae	CYPE	Runge, 1999 (G7/D5 [Plate V 5,7 pg. 38]); Albert et al., 2006; Barboni et al., 2007; Novello et al., 2012 (Plate II Pla-4 pg. 50); Garnier et al., 2012 (Fig.3 Da pg. 420); Novello et al., 2018 (Plate IV pg. 9); Yost et al., 2018	Metcalfe, 1971; Ollendorf et al., 1987; Ollendorf, 1992; Strömberg, 2004; Piperno, 2006 (Fig. 2,16a,b pg. 197)

Class/Subclass	Morphotype	Figure No.	Morphological-taxonomic association (representative taxa from published studies)	Morphological-taxonomic association (this study) primary producers (common to v. common – see Appendix 4, Table 4.7)
A. Parenchyma/ Cork (P/C) (Palisade Parenchyma Mesophyll)	Blocky/ Tabular Plate parallelepipedal Aa-A		Euphorbiaceae, <i>Sapium ellipticum</i> (Bark) (Fig. 6 b pg. 14), Annonaceae, <i>Anonidium mannii</i> (Bark) (Fig. 6 e pg. 14), Chrysobalanaceae, <i>Maranthes polyandra</i> (Fig. 6 f pg. 14), Euphorbiaceae, <i>Macaranga heudelotii</i> (Fig. 6 g pg. 14), Euphorbiaceae, <i>Macaranga heudelotii</i> (Bark) (Fig. 5 e pg. 15), Chrysobalanaceae, <i>Maranthes polyandra</i> (Bark) (Fig. 5 f pg. 15) (Collura and Neumann, 2017); Fabaceae, <i>Lonchocarpus capassa</i> (Stem), (Fig.4 q pg. 102), Solanaceae, <i>Solanum panduriforme</i> (Leaf), (Fig.4 r pg. 102), Fabaceae, <i>Acacia karoo</i> (Stem and leaf) (Fig.4 s pg. 102), Euphorbiaceae, <i>Uapaca nitida</i> (Stem) (Fig.4 t pg. 102), Amaranthaceae, <i>Celosia spp.</i> (Leaf) (Fig. 5 a pg. 103), Fabaceae, <i>Pterocarpus angolensis</i> (Stem) (Fig. 5 b pg. 103), Clusiaceae, <i>Pterocarpus angolensis</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus tinctorius</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus tinctorius</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus tinctorius</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus finctorius</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus capasa</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus tinctorius</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus finctorius</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus capasa</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus angolensis</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus angolensis</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus angolensis</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Pterocarpus angolensis</i> (Stem) (Fig. 5 d pg. 103), Fabaceae, <i>Psorospermum febrifugum</i> (Leaf) (Fig. 5 h pg. 103), Clusiaceae, <i>Psorospermum febrifugum</i> (Leaf) (Fig. 5 h pg. 103), Fabaceae, <i>Brachystegia spp.</i> (Stem) (Fig. 5 j pg. 103), Solanaceae, <i>Solanum panduriforme</i> (Leaf) (Fig. 5 j pg. 103), Fabaceae, <i>Piliostigma thonningii</i> (Stem) (Fig. 5 k pg. 103), Annonaceae, <i>Annona senegalensis</i> (Stem) (Fig. 5 l pg. 103), Annonaceae, <i>Celosia spp.</i> (Leaf) (Fig. 5 m pg. 103), Rubiaceae, <i>Pavetta crassipes</i> (Stem) (Fig. 5 n pg. 103), Mancardeae, <i>P</i>	Lamiaceae, Leonotis nepetifolia; Lamiaceae, Ocimum gratissimum; Fabaceae, Notonia hildebrandtii; Fabaceae, Senna spectabilis; Fabaceae, Sesbania seban; Euphorbiaceae, Ricinus communis; Capparaceae, Maerua triphylla; Asteraceae, Felicia muricata; Asteraceae, Aspilia mossambicense; Asteraceae, Felicia muricata; Sapindaceae, Dodonaea augustifolia
	Blocky facetate/ polyhedral facetate	Plate 1 Ba-Bd	Apocynaceae, <i>Ectadiopsis oblongifolia</i> (Stem) (Fig.5 t pg. 103) (Mercader et al., 2009); Bignoniaceae, <i>Kigelia africana</i> (Wood) (Fig.6 a pg. 14), Moraceae, <i>Morus mesozygia</i> (Bark) (Fig.6 c pg. 14), Moraceae, <i>Ficus sycomorus</i> (Bark) (Fig.6 d pg. 14) (Collura and Neumann, 2017)	Asteraceae, Microglosa pyrifolia; Capparaceae, Cadaba spp.; Fabaceae, Crotalaria agatifolia; Lamiaceae, Ocimum gratissimum
	Blocky corniculate	Plate 1 Ca-Cc	Meliaceae, <i>Pseudocedrela kotschyi</i> (Bark) (Fig 4 k pg. 12), Ochnaceae, <i>Lophira lanceolata</i> (Bark) (Fig.4 l pg. 12) (Collura and Neumann, 2017); Bryophyte, Changula (Leaf) (Fig.4 l pg. 102), Cucurbitaceae, <i>Cucumis spp.</i> (Rind) (Fig.5 p pg. 103) (Mercader et al., 2009)	Apocynaceae, Asclepiadoideae (Sareostemma viminale)
	Blocky/Tabular decorated (including Blocky	Plate 1 D	Rubiaceae, <i>Pavetta crassipes</i> (Stem) (Fig.5 n pg. 103), Euphorbiaceae, <i>Uapaca nitida</i> (Stem) (Fig.5 s pg. 103), Asteraceae, <i>Aspilia</i>	Asteraceae, Felicia muricata; Fabaceae, Dulbergia melanoxylon; Fabaceae, Crotalaria agatifolia; Fabaceae,

Appendix 4 - Table 4.2 Morphological-taxonomic associations of each morphotype from woody and herbaceous dicotyledons, ferns and non-grass monocotyledons identified in botanical samples from the Nakuru-Naivasha Basin and in fossil samples from Prospect Farm.
	sulcate/ruminate, Blocky		mosambicensis (Leaf) (Fig.6 k pg. 104) (Mercader et al., 2009).	Notonia hildebrandtii; Celastraceae, Hippocrateaceae,
	favose, Blocky lacunose)		Phyllanthaceae, Antidesma venosum (Bark) (Collura and Neumann,	Maytenus hetrophylla; Lamiaceae, Ocimum gratissimum;
			2017). May be confused with "Elongate onthogonal" from	Capparaceae, Cadaba spp.
			Poaceae, Cynodonteae tribe (Culm/Leaf/Inflorescence) (Fig.3 25	
			pg. 1960) (Mercader et al., 2010)	
	Blocky/Tabular crenate-	Plate 1	Fabaceae, Aeschynomene spp. (Leaf) (Fig.5 u pg. 103) (Mercader et al.,	Lamiaceae, Leonotis nepetifolia; Sapindaceae, Dodonaea
	echinate	Ea-Eh	2009); Pinaceae, Pinus mugo (Wood) (Plate VI 12 pg. 57) (Carnelli et	augustifolia; Fabaceae, Senna spectabilis; Nolinoideae,
	-sinuate		al., 2004); Capparaceae, Maerua crassifolia (Bark) (Fig.7 b pg. 15)	Dracaena steudneri
			(Collura and Neumann, 2017)	
	Blocky/Tabular radiating	Plate 1 F	Fabaceae, Aeschynomene spp. (Leaf) (Fig.5 u pg. 103) (Mercader et al.,	Lamiaceae, Vitex doniana; Lamiaceae, Ocimum gratissimum
	laminate		2009); Pinaceae, <i>Pinus mugo</i> (Wood) (Plate VI 12 pg. 57) (Carnelli et	
			al., 2004); Capparaceae, Maerua crassifolia (Bark) (Fig.7 b pg. 15)	
			(Collura and Neumann, 2017)	
	Blocky/Tabular scutiform	Plate 1	Moraceae, <i>Fucus sycomorus</i> (Bark) (Fig 5 p pg.13) (Collura and	Lamiaceae, Ocimum gratissimum
		Ga-Gc	Neumann, 2017)	
	Blocky/ labular tuberculate	Plate 1 H	Solanaceae, Solanum panduriforme (Leat) (Fig. 5 w pg. 103)	Lamiaceae, Ocimum gratissimum
			(Mercader et al., 2009); Cettis adolp-fridericii (Bark) (Fig.4 n pg. 13)	
		D1 + 1	(Collura and Neumann, 2016) $E_{1} = E_{2} + $	
	Labular ridged	Plate I	Ebenaceae, <i>Euclea crispa</i> (Lear) (Mercader et al., 2009) (Fig.4 u pg.	Rutaceae, Colodenarum capense; Euphorbiaceae, Croton
	DI 1 /T 1 1	1a-1b	$\frac{102}{10}$	megalocarpus
	Blocky/ Labular cavate	Plate I	Cannabaceae, Cettis mildoraedii (Bark) (Fig. / g-1 pg. 15) (Collura and	Celastraceae, Maytenus herrophyua; Asteraceae, Mucroglossa
	limbriate	Ja-Ji	Neumann, 2017); Bignoniaceae, <i>Kigeua ajricana</i> (Stem) (Fig.5 0, 8	pyrijolia
	Ellipsoid alongsto with regular	Diato 2	Bignopiagono Starastarmum hunthianum (Fig.6 h. pg. 14) (Bork)	
	en integular projections	Plate 2	Ellipsoid ophipate Coppension Reading suggleunic (Park) (Eig 2 1 pa	
	of inegular projections	ла-ло	11) (Collure and Neumann 2017)	—
B. Commolinid	Commolinid like types:	Dlato 2 B	Similar to those found in the Ervit and Seeds of Commelinatese	
D. Commennia	(Marantacana/Commolinacana)	Flate 2 D	a g similar to Commoling forshaelij type [Fig.6] a og 308] (Fighhorn	
types	(Marantaceae) Commennaceae)		et al. 2010) see also Novello et al. (2012) Grapier et al. (2012)	_
			Seeds of Marantaceae (Runge 1999: Novello et al. 2009)	
	Commelinid types: Pollia	Plate 2	Commelinaceae Eloscopa africana (Fig 3 g-i pg 305) (Fichhorn et	
	/Floscopa/Murdannia types	Ca-Cb	al 2010)	
	Commelinaceae: Cvanotis lanata	Plate 2	Commelinaceae Cyanotis lanata (Fig. 3 l m.pg. 305) (Eichhorn et	
	and Cvanotis	Da-Db	al. 2010)	_
	Longifolia types	5.20		
C. Globular and	Globular psilate	Plate 2	Fabaceae, Brachystegia boehmii (Stem) (Fig.3 p pg. 100): Proteaceae.	Asteraceae, Vernonia auriculfer; Ebenaceae. Eluclea
globular aggregate	1	Ea-Ed	Protea angolensis (Leaf) (Fg.3 u pg. 100) (Mercader et al., 2009);	divinorum; Rutaceae, Colodendsum capens; Celastraceae,
types			Sapotaceae, Malacantha alnifolia (Wood) (Fig.3 a pg.11);	Maytenus hetrophylla
· · ·			Burseraceae, Canarium schweinfurthii (Wood) (Fig.3 b pg.11);	, <u>, , , , , , , , , , , , , , , , , , </u>
			Sapotaceae, Pachystela brevipes (Wood) (Fig.3 c pg.11) (Collura and	

		Neumann, 2017); Melinis nerviglumis (Franch.) Zizka. (Culm/Leaf/Inflorescence) (Fig.3 6 pg. 1960) (Mercader et al., 2010)	
Globular psilate large	Plate 2 Ea-Ed	Euphorbiaceae, Uapaca sansibarica (Stem) (Mercader et al., 2009 (Fig.3 v pg. 100])	Hypericaceae, Hypericum revolutum
Globular granulate	Plate 2 Ga-Gc	Olacaceae, Olax subscorpioides (Wood) (Fig.3 e pg. 11), Anacardiaceae, Lannea acida (Wood) (Fig.3 g pg. 11) (Collura and Neumann, 2017); Fabaceae, Pterocarpus angolensis (Stem) (Fig.3 o pg. 100]) (Mercader et al., 2009)	Gentianaceae, Anthocleista, spp.; Euphorbiaceae, Acalyphoideae, Ricinus communis
Globular decorated indifferent	Plate 2 Ha-Hc	Cucurbitaceae, <i>Cucumis spp.</i> (exocarp) (Fig3. e pg. 100), Podocarpaceae, <i>Podocarpus falcatus</i> (Leaf) (Fig3. f pg. 100); Proteaceae, <i>Protea angolensis</i> (Leaf) (Fig3. w pg. 100); (Mercader et al., 2009); Zingiberaceae, <i>Zingiber spp.</i> (inflorescence) (Figure 8 pg. 7) (Kealhofer and Piperno, 1998); Alismataceae, <i>Ranalisrna rostratum</i> (Fig. 1 pg. 3) (Kealhofer and Pipero, 1988)	Fabaceae, Acacia seyal; Fabaceae, Crotalaria agatifolia; Polygonaceae, Rumex usambarensis; Amaranthaceae, Achyranthes aspera
Globular tuberculate	Plate 2 Ia-Bc	Urticaceae, Pouzolzia mixta (Leaf) (Fig.3 r pg. 100)	Urticaceae, Urtica massaica
Globulose oblong tuberculate/ verrucate	Plate 2 Ja-Jd	Unknown, Mchele (Leaf) (Fig.3 t pg. 100), Fabaceae, Acacia spp. (Stem and Leaf) (Fig.3 s pg. 100) (Mercader et al., 2009)	Lamiaceae, Ocimum gratissimum, Fabaceae, Acacia xanopholoea, Amaranthaceae, Achyranthes aspera
Globular verrucate/rumiante	Plate 2 K	Dioscoreaceae, <i>Dioscorea membranacea</i> (Leaf); Orchidaceae, <i>Dendrobium crumenaturn</i> (Leaf) (Kealhofer and Piperno, 1998 [Figure 10, 11 pg. 8]; Marantaceae, <i>Thalia multiflora</i> (Leaf) (Iriarte and Paz, 2009 [Fig.2 a pg. 111]); Phyllanthaceae, <i>Uapaca togonensis</i> (Wood) (Fig3. f pg.11) (Collura and Neumann, 2017)	_
Globular pappilate (cysloiths)	Plate 2 La-Lb	Similar to cystoliths, outgrowths of cell walls of specialized cells (lithocysts) e.g. in: Acanthaceae, Cucurbitaceae, Moraceae, Ulmaceae, Urticaceae (Runge, 1999). Urticaceae (Leaf), Cannabaceae (Leaf and Inforecence)	Urticaceae, Urtica massaica, Urticaceae, Obetia pinnaitifida
Globulose sulcate-columellate	Plate 2 M	—	—
Globular to sub-globular facetate	Plate 2 Na-Nc	Annonaceae, Anonidium mannii (Leaf) (Plate III, 8 pg. 34) (Runge, 1999); similar but not identical shapes observed in the rinds of Cucurbitaceae (Runge, 1999); Burseraceae, Annonaceae, Polyalthia suberosa (Leaf) (Fig. 39 pg. 18); Flacourtiaceae, Idesia polycarpa (Leaf) (Fig. 28 pg. 14); Fagaceae, Lithocurpus acuminatissima (Leaf) (Fig. 29 pg. 15) (Kealhofer and Piperno, 1998); Thymelaceae, Synaptolepis alternifolia (Leaf) (Fig.3 g pg. 100), Cucurbitaceae, Cucumis spp. Rind (exocarp) (Fig.3 h pg. 100) (Mercader et al., 2009); Annonaceae, Cucurbitaceae, Burseraceae (Leaf and Fruit); Burseraceae, Protium panamense (Fig. 2.6-f pg. 192) (Piperno, 2006).	Celastraceae, Maytenus hetrophylla

	Globulose favouse	Plate 2 O	Similar to flattened globular-granulate from Marantaceae,	Amaranthacae, Achyanthes aspera
			Stromanthe stromanthade (fruit bract) (Fig.3 R pg.5) (Chen and Smith,	
			2013); Similar to scalloped type from Cucurbitaceae, <i>Cucurbita</i>	
			maxima (Fig.3.6e pg.206]) and Cucurbitaceae, Sicana odorifera	
			(Fig.3.7e pg.206) (Piperno, 2006)	
	Globular echinate (Arecaceae	Plate 2	Arecaceae, Hyphaene spp. (Mature stem) (Fig.3 c,d pg. 100)	Arecaceae, Hyphaene compressa
	type)	Pa-Pb	(Mercader et al., 2009); Similar but not identical to globular	
			echinate phytolith from Arecaceae, Butia capitata (nut) (Fig.2 b pg.	
			111) (Iriarte and Paz, 2009)	
	Globular folded	Plate 2	Fabaceae, Afzelia quanzensis (Leaf) (Fig.3 i pg. 100); Rorola (Leaf)	Rosaceae, Hagenia abyssinica
		Qa-Qc	([Fig.3 j pg. 100); Bombacaceae, Adansonia digitata (Exocarp) (Fig.3	
			k pg. 100); Apocynaceae, Diplorhynchus condylocarpon (Leaf) (Fig.31	
			pg. 100); Bombacaceae, Adansonia digitate (Exocarp) (Fig.3 m pg.	
			100); Bombacaceae, Adansonia digitata (Exocarp) (Fig.3 n pg. 100)	
			(Mercader et al., 2009); Alismataceae, Ranalisrna rostratum (Leaf)	
			([Fig.1 pg. 3); Zingiberaceae, <i>Elettaria cardamomum</i> (Bract) (Fig.7 pg.	
			88) (Kealhofer and Piperno, 1998); Oleaceae, Ligustrum robustus	
			(Leaf) (Fig.14 pg. 10); Clusiaceae, Culophyllum burmanii (Leaf) (Fig.	
			20 pg. 11) (Kealhofer and Piperno, 1998)	
	Globular-sub-globular dark	Plate 2	Malvaceae, Cola cordifolia (Wood) (Fig.3 d pg.11) (Collura and	Asteraceae, Vernonia auriculfer, Ebenaceae, Eluclea
		R	Neumann, 2017)	divinorum, Rutaceae, Colodendsum capens, Celastraceae,
	Globular decorated compound	Plate 2	Phyllapthaceae Ustaca togonensis (Wood) (Fig 3 f pg 11) (Collura	Maraceae Ficus ludea Fabaceae Senna spectabilis
	Chobular decorated compound	Sa-Se	and Neumann, 2017)	Noraccae, 1 uns innuu, 1 abaccae, 5 china specialitas
	Obovate psilate	Plate 2	Anacardiaceae, Lannea acida (Wood) (Fig.3 j pg. 11) (Collura and	Lamiaceae, Leucas nepetifolia, Fabaceae, Acacia seyal,
	-	Т	Neumann, 2016)	Euphorbiaceae, Croton megalocarpus
	Obovate scorbiculate/	Plate 2	Fabaceae, Elephantorrhiza goetzei (Leaf) (Fig.3 q pg. 100) (Mercader	Urticaceae, Urtica massaica, Urticaceae, Obetia pinnaitifida
	granulate	Ua-Uc	et al., 2009)	
D. Sclerenchyma	Cylindroid small	Plate 4	Fabaceae, Dichrostachys cinerea (Leaf) (Fig.2 a pg. 99) (Mercader et	Oleaceae, Olea africana; Ebenaceae, Eluclea divinorum;
Sclereid/mesophyll		Aa-Ab	al., 2009); Bambusoideae, Oxytenanthera abyssinica (A.Rich) Munro.	Asteraceae, Felicia muricat; Cyatheaceae spp.; Malvaceae,
			(Culm/Leaf/Inflorescence) (Fig.2 30 pg. 1959) (Mercader et al.,	Sterculiaceae, Dombeya burgessiae
D1. Cylindroid			2010); Bewsia biflora (Hack.) Goossens. (Culm/Leaf/Inflorescence)	
types			(Fig.4 13 pg. 1959) (Mercader et al., 2010)	
	Cylindroid large	Plate 3	Verbenaceae, Vitex spp. (Stem) (Fig.2 j pg. 99) (Mercader et al.,	Malvaceae, Dombeya burgessiae; Euphorbiaceae, Ricinus
		Ba-Bb	2009); Myrsinaceae, Embelia schimperi (Leaf) (Fig.2 g pg. 99)	communis; Asclepiadaceae, Calotropis procera
			(Mercader et al., 2009)); Marantaceae, Monotagma plurispicatu (leaf)	
			(Fig.4 pg. 6) (Brilhante de Albuquerque et la., 2013)	
	Cylindroid large geniculate/	Plate 3	Proteaceae, Protea angolensis (Leaf) (Fig.2 c pg. 99) (Mercader et al.,	Asteraceae, Felicia muricata; Rutaceae, Colodendsum capense
	Cylindroid bulbous	Ca-Cf	2009); Moraceae, Ficus sycomorus (Bark) (Fig.4 f,g pg. 12) (Collura	
			and Neumann, 2017); Dipterocarpaceae, Monotes spp. (Stem) (Fig.5	

			x pg. 103) (Mercader et al., 2009); Annonaceae, Goniothalamus marcani (Leaf) (Fig.40 pg. 18) (Kealhofer and Piperno, 1998)	
	Asterosclereid	Plate 3 D	Pinaceae, <i>Pseudotsuga menziesii</i> (Fig.2 5c pg.191) (Piperno et al., 2006); Pinaceae, <i>Pseudotsuga menziesii</i> (Fig.3 a pg. 67) (McClune and Pellatt, 2013); Nymphea (Fig.a,b pg. 234) (Warner, 1989); Brassicaceae, <i>Alyssum desertorum</i> (Morris, 2008); Cyperaceae, <i>Rhynchospora corymbosa</i> (Fig.3 q,r pg. 517) (Honaine et al., 2009)	Nolinoideae, Dracaene steudneri
	Cylindroid corniculate	Plate 3 E	_	Euphorbiaceae, Ricinus communis
D2. Sclereid (palisade mesophyll or spongy mesophyll), vein leaf cells and terminal tracheids	Elongate faceted- Sclereid	Plate 3 Fa-Fg	Mesophyll of leaves (pg. 1116) (Metcalfe and Chalk, 1979); silicified terminal tracheids from Magnoliaceae, <i>Magnolia grandiflor</i> (Fig.1,2,3,6 pg. 126, Fig. 11-14 pg. 128) (Postek, 1981), or silicified sclereids (Piperno, 1988); Magnoliaceae, <i>Magnolia grandiflora</i> (Fig.2 6a pg.191) (Piperno, 2006); Fabaceae, <i>Albizia anthelmintica</i> (Leaf) (Fig. 6-d pg. 104) (Mercader et al., 2009); Burseraceae, <i>Canarium schweinfurtii</i> (Bark) (Fig.5 g pg. 13) (Collura and Neuamnn, 2016); Phyllanthaceae, <i>Uapaca guineensis</i> (Bark) (Fig.5 f,i pg. 13) (Collura and Neuamnn, 2016)	Nolinoideae, Dracaene steudneri; Malvaceae, Dombeya burgessiae; Sapindaceae, Dodonaea augistifolia; Fabaceae, Crotalaria agatifolia; Fabaceae, Cassia didymobotya; Apiaceae, Steganoteaenia spp.; Rutaceae, Vepris simplicfolia; Rutaceae, Colodendsum capense; Lamiaceae, Vitex doniana; Myrtaceae, Syzygium guineense
E. Vessel elements/ Xylem Epidermal tracheid	Cylindric sulcate tracheid (vessel elements)	Plate 3 Ga-Gf	Euphorbioideae, <i>Sebastiania brasiliensis</i> (Twig) (Fig.5 d pg. 113); Loranthaceae, <i>Tripodanthus acutifolius</i> (Twig) (Fig.5 e pg. 113) (Iriarte and Paz, 2009); Magnolianae, <i>Persea americana</i> (Fig.2 18d pg. 1999) (Piperno, 2006); Bambusoideae, <i>Oxytenanthera abyssinica</i> (A.Rich) Munro. (Culm/Leaf/Inflorescence) (Fig.4 1 pg. 1961) (Mercader et al., 2010)	Melianthaceae, Bersama abyssinica; Fabaceae, Cassia didymobotrya; Ebenaceae, Eluclea divinorum; Lamiaceae, Vitex doniana; Malvaceae, Dombeya burgessiae; Melianthaceae, Bersama abyssinica; Moraceae, Ficus cordata
	Elongate scalariform platelet	Plate 3 Ha-Hc	Cannabaceae, <i>Trema guineensis</i> (Bark) (Fig. 4 ab pg. 12) (Collura and Neumann, 2017); Apocynaceae, <i>Ectadiopsis oblongifolia</i> (Stem) (Fig.6 g pg. 104) (Mercader et al., 2009)	Cyatheaceae, Cyathea spp.; Nolinoideae, Dracaene steudneri
F. Epidermal tissue F1. Leaf epidermis	Epidermal jig-saw platelet	Plate 4 Aa-Ac	Fabaceae, <i>Albizia anthelmintica</i> (Leaf) (Fig 2. h pg. 99), Fabaceae, <i>Afzelia quanzensis</i> (Leaf) (Fig 2. i pg. 99) (Mercader et al., 2009); Marantaceae, <i>Donax grandis</i> (Leaf) (Fig.3 I pg. 5) (Chen and Smith, 2013)	Athyriaceae, Diplazium Genus, Euphorbiaceae, Ricinus communis; Fabaceae, Cassia didymobotrya; Senna spectabilis; Lamiaceae, Leucas nepetifolia, Plectranthus barbatus
	Epidermal polygonal/ parallelogram	Plate 4 Ba-Bg	Arecaceae, Hyphaene spp. (Leaf) (Fig. 2 k pg. 99), Fabaceae, Lonchocarpus capassa (Leaf) (Fig. 2 l pg. 99), Anacardiaceae, Sclerocarya birrea (Leaf) (Fig. 2 m pg. 99), Moraceae, Ficus spp. (Leaf) (Fig. 2 n pg. 99), Euphorbiaceae, Antidesma spp (Leaf) (Fig. 2 o pg. 99) (Mercader et al., 2009)	Asteraceae, Microglossa pyrifolia; Boraginaceae, Cordia africana; Celastraceae, Maytenus hetrophylla; Ebenaceae, Eluclea divinorum; Lamiaceae, Leucas nepetifolia; Malvaceae, Dombeya hurgessiae; Moraceae, Ficus wakefeldii; Moraceae, Ficus cordata; Moraceae, Ficus sycomorus
F2. Achene epidermis	Opaque perforated platelet		Asteraceae (Piperno, 2006). Platelet with alternating amber- coloured and opaque stripes, regularly perforated (Compositae?) (Runge, 1999)	Asteraceae, Microglossa pyrifolia; Asteraceae, Psiadia punctulata; Asteraceae, Vernonia auriculfera

F.3 Undetermined	Thin platelet irregular	Plate 4	_	
epidermal tissue	ruminate	С		
G.1 Non-	Acicular and	Plate 5	Asteraceae, <i>Pleiotaxis spp.</i> (Leaf) (Fig.4 a pg. 102), Asteraceae,	Asteraceae, Felicia muricata; Lamiaceae, Ocimum gratissimu,
diagnostic types: misc	(Trichomes/Acicular hair cell)	Аа-Вд	Aspitta spp. (Leaf) (Fig.4 b pg. 102), Ebenaceae, Diospyros spp. (Leaf) (Fig.4 c pg. 102), Albizia anthelminitica. (Leaf) (Fig.4 d,e pg. 102), Fabaceae, Afzelia quanzensis (Leaf) (Fig.4 f pg. 102), Bryophyte, Changula (Leaf) (Fig.4 g pg. 102) (Mercader et al., 2009); Panicoideae, Pennisetum unisetum (Culm/Leaf/Inflorescence) (Fig.3 18 pg. 1960) (Mercader et al., 2010); Fabaceae, Phaseolus vulgaris (Fig. 3.12 pg. 210) (Piperno, 2006)	Lamiaceae, Leucas nepetifolia; Rutaceae, V epris simpliciolia; Rutaceae, Colodendsum capense; Fabaceae, Caesalpinioideae; Senna spectabilis; Oleaceae, Olea africana; Fabaceae, Crotalaria agatifolia; Capparaceae, Cadaba spp; Urticaceae Urtica massaica
	Silica particles/ accumulation	Plate 5 C	Bignoniaceae, <i>Kigelia africana</i> (Bark) (Fig. 3 u pg. 11) (Collura and Neumann, 2017)	Lamiaceae, Leonotis nepetifolia, Ocimum gratissimum; Euphorbiaceae, Ricinus communis; Fabaceae, Crotalaria agatifolia, Senna spectabilis, Dulbergia melanoxylon; Capparaceae, Maerua triphylla; Asteraceae, Tarchonathus camphartus; Amaranthaceae, Achyanthes aspera
	Lanceolate	Plate 5 Da-Dd		Euphorbiaceae, Ricinus communis; Celastraceae, Maytenus hetrophylla
G.2 Non- diagnostic types: thin elongate platelets	Thin platelet elongate psilate	Plate 6 Aa-Ae	Acanthaceae, <i>Lepidagathis andersoniana</i> (Stem) (Fig.4 k pg. 102), Fabaceae, <i>Dalbergiella nyasae</i> . (Stem) (Fig.6 c pg. 104), Fabaceae, <i>Albizia anthelmintica</i> (Leaf) (Fig.6 d pg. 104) (Mercader et al., 2009). Also found in many grass taxa e.g. (Borrelli et al., 2010) (Fig.4 Class A pg. 990); <i>Sporobolus consimilis</i> (Culm/Leaf/Inflorescence) (Fig.5 8 pg. 1962); <i>Oxytenanthera abyssinica</i> (culm) (Fig.5 10 pg. 1962) (Mercader et al., 2010)	Found in the vast majority of families and species that produce phytoliths (non-specific)
	Thin Tabular platelet echinate -sinuate-crenate-facetate	Plate 6 Ba-Bt	Inflorescence of Bambusoideae, <i>Chusquea tongifolia</i> (Fig. 59 pg.36) (Piperno and Persall, 1998); Panicoideae, <i>Oplismenus spp.</i> (Culm/Leaf/Inflorescence) (Fig.4 15 pg. 1961) (Fig.5 5 pg. 1962), Chloridoideae, <i>Cynodon spp.</i> (Culm/Leaf/Inflorescence), (Fig.5 6 pg. 1962), Chloridoideae, <i>Eragrostis spp.</i> (Culm/Leaf/Inflorescence) (Fig.5 11 pg. 1962), Pharoideae, <i>Leptaspis cochleata</i> (Culm/Leaf/Inflorescence) (Fig.3 4 pg. 1960) (Mercader et al., 2010); <i>Helichrysum cymosum</i> (Plate III, f pg. 8) (Novello et al., 2018); .Crenate tabular, <i>Helichrysum cymosum</i> (Novello et al., 2018)	Found in the vast majority of families and species that produce phytoliths (non-specific)
	Elongate decorated platelet (conical abraxial)	Plate 6 Ca-Cb	Conical siliceous bodies emerging from the leaf epidermis of Bambusoideae, <i>Elytrostachys clanisera</i> (Fig. 67 pg. 38) (Piperno and Pearsall, 1998); Chloridoideae, <i>Chloris virgata</i> (Fig.4 3 pg. 1961) (Culm/Leaf/Inflorescence) (Mercader et al., 2010)	

	Thin platelet dendritic	Plate 6 Da-Dc	Panicoideae, <i>Bothriochloa laguroides</i> (Fig.4 a pg. 1162) (e.g. Frenandez Honaine et al., 2006); Similar but not identical to Achariaceae, <i>Hydnocarpus anthelmintheca</i> (Fig.14 pg. 27) (Kealhofer and Piperno, 1998). Similar to "Tabular thick dendritic", Bignoniaceae, <i>Kigelia</i> <i>africana</i> . (Stem) (Fig.6 f pg. 104) (Mercader et al., 2009). Similar but not identical to "dendritics" (Plate I C EL3d pg. 14) (Novello and Barboni, 2015);	Lamiaceae, Vitex doniana; Malvaceae, Dombeya burgessiae
G.2 Non- diagnostic types: Acicular and hair cells	Acicular and hair cells	Plate 7 Aa-Am	Asteraceae, <i>Pleiotaxis spp.</i> (Leaf) (Fig.4 a pg. 102), Asteraceae, <i>Aspilia spp.</i> (Leaf) (Fig.4 b pg. 102), Ebenaceae, <i>Diospyros spp.</i> (Leaf) (Fig.4 c pg. 102), <i>Albizia anthelmintica.</i> (Leaf) (Fig.4 d,e pg. 102), Fabaceae, <i>Afzelia quanzensis</i> (Leaf) (Fig.4 f pg. 102), Bryophyte, Changula (Leaf) (Fig.4 g pg. 102) (Mercader et al., 2009); Panicoideae, <i>Pennisetum unisetum</i> (Culm/Leaf/Inflorescence) (Fig.3 18 pg. 1960) (Mercader et al., 2010); Fabaceae, <i>Phaseolus vulgaris</i> (Fig. 3.12 pg. 210) (Piperno, 2006). Note: also recorded in many other subfamilies and species	Asteraceae, Aspilia mossambicense; Asteraceae, Vernonia auriculfera; Boraginaceae, Cordia africana; Fabaceae, Cassia didymobotya; Dulbergia melanoxylon; Lamiaceae, Vitex doniana
H. Non-grass monocots: Cyperaceae types	Cypereaceae (sedge) type - hat shaped and papillae.	Plate 7 Ba-Bd	Cyperaceae, <i>Rhynchospora corymbosa</i> (Plate V 7 pg. 38) (Runge, 1999); Albert et al., 2006; Barboni et al., 2007; Novello et al., 2012 (Plate II Pla-4 pg. 50); Garnier et al., 2012 (Fig.3 Da pg. 420). Found in all studied cyperaceae (Fig. 4) Yost et al., 2018	Cyperaceae, Cyperus papyrus, Kyllinya alba, Cyperus laevigatus, Cyperus dives, Carex elgonensis, Cyperus afroalpinus

Class/Subclass	Morphotype	Figure	Previous names and similar forms
A. Parenchyma/	Blocky/ Tabular	Code Plate 1	"Irregular shaped (C2 and C3) and elongate smooth
Cork (P/C) (Palisade Parenchyma Mesophyll)	parallelepipedal	Aa-Ak	rod with edges along the body (A3)" (Runge, 1999); "Parallelepiped forms" (Albert and Maurean, 2011 [Fig7. a-c pg. 376]); "parallelepiped blocky" (Albert et al., 2006; Barboni et al., 2010). "Large rod" (class H4) (Strömberg, 2005 [Fig 4. L pg. 258]). Similar in appearance to some elongate bulliform cells from Poaceae e.g. Mercader et al., 2010 (Fig.4 20 pg. 1961) and see Plate 6
	Blocky facetate/ polyhedral facetate	Plate 1 Ba-Bd	Not to be confused with; P/C Blocky polyhedral. Parenchyma/Cork (P/C) (Collura and Neumann, 2017 [Figure 6a]) classified by this study as polyhedral platelets. 3D Blocky polyhedron. Types Blo-1. to Blo- 5 (Strömberg, 2003 [Fig. 4.15b-f, pg. 319]) can also be included in this morphotype. Block polyhedral [Fig 5 (t) (Mercader et al., 2009). Elongate faceted (Neumann et al., 2009). Blocky polyhedron (Neumann et al., 2009). Elongate facetate (Collura and Neumann, 2017) and (Barboni et al., 2010 [Fig.4-26 pg. 348]); infilled "honeycombed mesophyll" or mesophyll aggregate (class E3) (Strömberg, 2004 [Fig.5 m pg. 259]). May be confused with elongate bulliform cells from Poaceae e.g. Mercader et al., 2010 (Fig.4 20 pg. 1961). Note: some Parenchyma/Cork cell Blocky polyhedrals (e.g. This study; Collura and Neumann, 2017 [Fig.6 b pg.14]) can appear very similar to elongate psilate platelets from Poaceae (see Plate 6). Also similar to <i>Schoenoplectus acutus</i> (Cyperaceae) woody rhizome phytoliths (Yost et al., 2018)
	Blocky corniculate	Plate 1 Ca-Cc	"Blocky irregular" (Collura and Neumann, 2017 [Fig.4-K, L pg. 12]). Potential to be confused with Cylindroid reticulate type (Mercader et al., 2009 [Fig.2- f pg. 99]). Blocky hexagonal with bulliform-type texture (Barboni et al., 2010 [Fig.4-27 pg. 348])
	Blocky/Tabular decorated (including Blocky sulcate/ruminate, Blocky favose, Blocky lacunose)	Plate 1 D	"Blocky irregular "(Collura and Neumann, 2017 [Fig.4 k-l pg. 12])
	Blocky/Tabular crenate- echinate -sinuate	Plate 1 Ea-Eh	
	Blocky/Tabular radiating laminate	Plate 1 F	"Blocky multi-layered" (Collura and Neumann, 2017 [Fig.7 b pg. 15]). "Polygonal" (Carnelli et al., 2004 [Plate VI 12 pg. 57])
	Blocky/Tabular scutiform	Plate 1 Ga-Gc	Sclereid psilate, Moraceae, <i>Ficus sycomorus</i> (Collura and Neumann, 2017 [Fig 5 p pg.13])
	Blocky/Tabular tuberculate	Plate 1 H	"Ovate, tuberculate surface" (Barboni et al., 2010 [Fig.4 30 pg. 348]); "Sclereid pitted" (Collura and Neumann, 2017 [Fig 5. n pg. 13])
	Tabular 'ridged'	Plate 1 Ia-Ib	"Elongate triangular psilate" (Aleman et al., 2014 [Fig.2 L pg.276]); "hexagonal with bulliform-type texture" (Barboni et al., 2010 [Fig.4-26 pg. 348]; "elongate smooth rod with edges along the body" (Type A3) (Runge, 1999 [Plate III 3 pg. 34])
	Blocky/Tabular cavate fimbriate	Plate 1 Ja-Jf	Similar to Commelinid types (see Plate 2)
	Ellipsoid-elongate with regular or irregular projections	Plate 2 Aa-Ab	"Ellipsoid with outgrowths, sometimes faceted" (Garnier et al., 2012 [Fig.3 f pg. 5]. Similar to Ellipsoid echinate (Collura and Neumann, 2017) [Fig.3 k,l pg.11]. Similar to trachery element with knoblike projections of Magnoliaceae, <i>Magnolia grandiffra</i> (Postek, 1981 [Fig. 15 pg. 129]). Also similar to substomatal cavity phytoliths of some Poaceae (Yost et al., 2018 [Fig. 3 a',b' pg. 83]). May also be confused in rare cases with irregular with tubular projections from sedge (Cyperaceae) roots (Yost et al., 2018 [SOM Fig. S5]).

"Elongate body with a 'head' and outgrowthe"
(Runge, 1999 [D2, Plate IV 4,5 pg.37]); Similar, but
not identical, to elongate body with a 'head' and
outgrowths along the 'body', probably from
Marantaceae seeds [Marantaceae type] Bears some
similarities with blocky types produced in the F, S of
Commelinaceae. Elongate body with a 'head' and
outgrowths along the 'body' (Runge, 1999).
Similar to Blocky cavate fimbriate (see Plate 1)
—
"Smooth/compound sphere" (Strömberg, 2004 [E7
Fig.5 f pg. 259])
—
Globular decorated (Collura and Neumann, 2017
[Fig.3 e,g pg.11]); Spherical with a rough (not smooth)
surface (Runge, 1999 [Plate IV, B2 pg. 37]; Small
rugulose sphere and sub sphere (Strömberg, 2003 [Cl-
7 Fig. 4.11c pg.314])
Glo-6 "Micro-echinate" (Novello et al., 2012 [Plate II
Glo-6 pg. 50]); Spooliform (Mercader et al., 2009
[Fig3. w pg. 100]); "spherical nodular" (Piperno, 1988
[Plate 5 pg. 224]); decorated ovoids (Kealhofer and
Piperno, 1998 [Figure 8 pg. 7])
_
Similar to (but more regular than) podular types
Similar to (but more regular man) notunar types
(Collura and Neumann, 2017 [Class G; Nodular Fig.3
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100])
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8,
 (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]).
 (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34])
 (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34])
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34])
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) — Similar to Annonaceae/Cucurbitaceae type (Neumann
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) — Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate"
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig.3 f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) — Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate
 (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) — Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate polyhedral" (Kealhofer and Piperno, 1998 [Fig.31 pg.
Similar to (our more regular than) notular types (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) — Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate polyhedral" (Kealhofer and Piperno, 1998 [Fig.31 pg. 15). similar but not identical to scalloped types
Similar to (our more regular than) notular types (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34])
Similar to (our nove regular that) fodular types (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34])
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(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) — Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate polyhedral" (Kealhofer and Piperno, 1998 [Fig.31 pg. 15). similar but not identical to scalloped types (Piperno, 2006 [Fig. 3.6a-3.6d pg. 205-206]) — Similar to "spherical nodulose" forms from Marantaceae, <i>Donax cannaeformis</i> (Runge, 1999 [Plate IV 2 pg.36]); Similar to "spherical spinulose phytoliths" from Arecaceae, <i>Butia capitata</i> (Piperno, 2006 [Fig. 2 ng. 102])
(Collura and Neumann, 2017 [Class G; Nodular types (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) — Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate polyhedral" (Kealhofer and Piperno, 1998 [Fig.31 pg. 15). similar but not identical to scalloped types (Piperno, 2006 [Fig. 3.6a-3.6d pg. 205-206]) — Similar to "spherical nodulose" forms from Marantaceae, <i>Donax cannaeformis</i> (Runge, 1999 [Plate IV 2 pg.36]); Similar to "spherical spinulose phytoliths" from Arecaceae, <i>Butia capitata</i> (Piperno, 2006 [Fig2.8a pg.192])
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(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) —— Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate polyhedral" (Kealhofer and Piperno, 1998 [Fig.31 pg. 15). similar but not identical to scalloped types (Piperno, 2006 [Fig. 3.6a-3.6d pg. 205-206]) —— Similar to "spherical nodulose" forms from Marantaceae, <i>Donax cannaeformis</i> (Runge, 1999 [Plate IV 2 pg.36]); Similar to "spherical spinulose phytoliths" from Arecaceae, <i>Butia capitata</i> (Piperno, 2006 [Fig2.8a pg.192]) "Subepidermal hemispherical clump" (Kealhofer and Piperno, 1998 [Fig.14 pg. 10]); "seed-like sphere from leaf sample" (Kealhofer and Piperno, 1998 [Fig.20 pg. 111): "Orbigular to contact spinulose
 (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34])
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) —— Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate polyhedral" (Kealhofer and Piperno, 1998 [Fig.31 pg. 15). similar but not identical to scalloped types (Piperno, 2006 [Fig. 3.6a-3.6d pg. 205-206]) —— Similar to "spherical nodulose" forms from Marantaceae, <i>Donax cannaeformis</i> (Runge, 1999 [Plate IV 2 pg.36]); Similar to "spherical spinulose phytoliths" from Arecaceae, <i>Butia capitata</i> (Piperno, 2006 [Fig2.8a pg.192]) "Subepidermal hemispherical clump" (Kealhofer and Piperno, 1998 [Fig.14 pg. 10]); "seed-like sphere from leaf sample" (Kealhofer and Piperno, 1998 [Fig.20 pg. 11]); "Orbicular to ovate, smooth, slightly curved" [Plate II Blo-9 pg.50])
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) —— Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate polyhedral" (Kealhofer and Piperno, 1998 [Fig.31 pg. 15). similar but not identical to scalloped types (Piperno, 2006 [Fig. 3.6a-3.6d pg. 205-206]) —— Similar to "spherical nodulose" forms from Marantaceae, <i>Donax cannaeformis</i> (Runge, 1999 [Plate IV 2 pg.36]); Similar to "spherical spinulose phytoliths" from Arecaeeae, <i>Butia capitata</i> (Piperno, 2006 [Fig2.8a pg.192]) "Subepidermal hemispherical clump" (Kealhofer and Piperno, 1998 [Fig.14 pg. 10]); "seed-like sphere from leaf sample" (Kealhofer and Piperno, 1998 [Fig.20 pg. 11]); "Orbicular to ovate, smooth, slightly curved" [Plate II Blo-9 pg.50])
(Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34]) —— Similar to Annonaceae/Cucurbitaceae type (Neumann et al., 2009 [Fig.2 (B2) I pg. 92]); "elliptical facetate" (Piperno, 2006 [Fig. 2.6-f pg. 192]); "multifacetate polyhedral" (Kealhofer and Piperno, 1998 [Fig.31 pg. 15). similar but not identical to scalloped types (Piperno, 2006 [Fig. 3.6a-3.6d pg. 205-206]) —— Similar to "spherical nodulose" forms from Marantaceae, <i>Donax cannaeformis</i> (Runge, 1999 [Plate IV 2 pg.36]); Similar to "spherical spinulose phytoliths" from Arecaceae, <i>Butia capitata</i> (Piperno, 2006 [Fig2.8a pg.192]) "Subepidermal hemispherical clump" (Kealhofer and Piperno, 1998 [Fig.14 pg. 10]); "seed-like sphere from leaf sample" (Kealhofer and Piperno, 1998 [Fig.20 pg. 11]); "Orbicular to ovate, smooth, slightly curved" [Plate II Blo-9 pg.50]) ——
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 (Collura and Neumann, 2017 [Class G; Nodular Fig.3 n-o pg. 11); Globular granulate oblong (Mercader et al., 2009 [Fig.3 t pg. 100]) "Micro-echinate fuzzy" (Glo-19) (Barboni et al., 2010 [Fig.4 3 pg. 348]); f. Globular decorated composed (Collura and Neumann, 2017 [Fig3. f pg.11]); Spheriod with 'nodular 'surface (Runge, 1999 [Plate V, Type B8, 2 pg.38]). Similar to (Runge, 1999 [Plate III, 10 pg. 34])
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D. Sclerenchyma	Cylindroid small	Plate 3	
Sclereid/mesophyll	5	Aa-Ab	
			_
D1. Cylindroid			
types			
**	Cylindroid large	Plate 3	"elongate smooth" (Aleman et al., 2014 [Fig.2 C-k pg.
		Ba-Bb	276])
	Cylindroid large geniculate/	Plate 3	Similar but not identical to "Tabular/parallelepipedal
	Cylindroid bulbous	Ca-Cf	bodies, pinched-point" (Novello et al., 2012 [Plate II
	-,		El-2 pg. 50]); Similar but not identical to "cyclindrical
			sclereid" (An, 2016 [Fig.3 aa pg.5]); "Elongate with
			globular parts" (Collura and Neumann, 2017 [Fig.4 f.g
			pg. 12]); "Clavate granulate" (Mercader et al., 2009)
			[Fig.5 x pg. 103])
	Asterosclereid	Plate 3	
		D	
	Cylindroid corniculate	Plate 3	Similar but not identical to "spiny phytolith" from
	5	Е	Pinaceae, Picea gluca (Bozarth, 1993), (Piperno 2006
			[Fig. 2.5b pg. 190])
D2. Sclereid	Elongate faceted- Sclereid	Plate 3	
(palisade mesophyll	0	Fa-Fg	
or spongy		0	_
mesophyll), vein			
leaf cells and			
terminal tracheids			
E. Vessel	Cylindric sulcate tracheid	Plate 3	"Rod with a ring- or spiral-shaped surface derived
elements/	(vessel elements)	Ga-Gf	from tracheids" (Runge, 1999 [Plate III Type 2A 2 pg.
Xylem Epidermal			34]); Similar to "Epidermal tracheid (Single-cell, fluid-
tracheid			conducting tissue)" (Mercader et al., 2009 [Fig.3 a pg.
			100])
	Elongate scalariform platelet	Plate 3	
	0 1	Ha-Hc	
F. Epidermal tissue	Epidermal jig-saw platelet	Plate 4	
1	1 ,0 1	Aa-Ac	_
F1. Leaf epidermis			
	Epidermal	Plate 4	—
	polygonal/parallelogram	Ba-Bg	
F2. Achene	Opaque perforated platelet		—
epidermis			
F.3 Undetermined	Thin platelet irregular	Plate 4	Similar but not identical to platelets from tabular from
epidermal tissue	ruminate	С	Strelitziaceae, Strelitzia reginae (Seed) (Chen and Smith,
0.4.11		D1 5	2013 [Fig. 4 Q pg. /])
G.I Non-	Acicular and	Plate 5	"silicitied prickle base from Poaceae" (Runge, 1999
diagnostic types:	Fusitorm/Ellipsoid/scutiform	Аа-Bg	[Plate V 8 Type G3])
misc.	(Irichomes/Acicular hair cell)	- D1 - F	
	Silica particles/ accumulation	Plate 5	—
	T 1.		
	Lanceolate	Plate 5	Similar but not identical to Phyllanthaceae, Uapaca
		Da-Dd	<i>Rirkiana</i> (Lear) (Mercader et al., 2009 [Fig.4 pg. 102]);
			similar but not identical to Type A5 from Poaceae
0.001	2111 1 . 1 . 1	DL	(Runge, 1999 [Plate III pg. 54])
G.2 Non-	I hin platelet elongate psilate	Plate 6	Type A1, "smooth rod without edges" (Runge, 1999),
diagnostic types:		Аа-Ае	"Smooth, straight long rods" (Rovner, 1971,
thin elongate			Stromberg, 2003, 2004)
platelets			
	Inin Tabular platelet echinate	Plate 6	Type A5, "elongate smooth rod with edges along the
	-sinuale-cremate-facetate	Da-Di	body, Type Ao, fod with short diagonal lines
			from the alit shared aits" (Punce 1000). Elements
			rectangular plates with smooth sinuous or spice
			adgas: loosa/sheets (Dicarrao, 1088, Stomborg, 2003
			2004) Note: Calegari et al. 2016 say that some
			echinate types are "parallelepipedal signate bulliform
			cell (Chusquea)" Fig 4 h pg 8)
	Elongate decorated platelet	Plate 6	Similar to epidermal tissue phytoliths of
	(conical abraxial)	Ca-Cb	Chloridoideae, Chloris gyana
	Thin platelet dendritic	Plate 6	
		Da-Dc	

G.2 Non- diagnostic types: Acicular and hair cells	Acicular and hair cells	Plate 7 Aa-Am	_
H. Non-grass monocots:	Cypereaceae (sedge) type - hat shaped and papillae	Plate 7 Ba-Bd	_
Cyperaceae types			

Appendix 4 - Table 4.3 Previous names use to describe each morphotype from woody and herbaceous dicotyledons, ferns and non-grass monocotyledons where they have been identified in previous studies, as well as similar forms that may be confused with these phytoliths.

Appendix 4 - Table 4.4 Description and the size of each morphotype from Poaceae found in Figure 4.8., associated grass subfamily, the plant tissue from which the phytolith type is thought to originate, and key references in which each morphotype has been previously described where applicable. (S*) indicates that the morphotype was present in Prospect Farm palaeosol samples. (ARIS) Aristidoideae, (BAM) Bambusoideae, (CHLO) Chloridoideae, (EHRH) Ehrhartoideae (PAN) Panicoideae, (POOI) Pooideae

Major Plant Groups GSSC and Bulliforms (Poaceae) Class/Subclass	Morphotype	Figure code	Size (length µm unless stated otherwi se)	Morphotype description	Observed in/plant part	Taxonomic association (this study) based on published material	References (key African Studies)	References (key global studies)
A. Bilobates (bodies with two lobes connected by a +/- long shank), size: L=10-2 μ m: "short" or L>25 μ m: "long", h \leq 5 μ m: "tabular" or h>5 μ m: "trapeziform / parallelepipedal" (Novello et al., 2012) A.1 Bilobate short shank	Bilobate 1	Bi-1	10-25	Short, tabular, truncated lobes (Novello et al., 2012)	(S*), (PAN) Culm/Leaf/Inflorescence most commonly of Panicoideae but also produced by Aristidoideae and other Poaceae subfamilies in low amounts (e.g. Ehrhartoideae and Bambusoideae)	Attributed to Panicoideae (C4)	Fahmy, 2008 (Fig.2 3,4 pg. 15); Cordova, 2013 (Fig.6 10-K pg. 127); Mercader et al., 2010 (Fig.3 15 pg. 1960); Novello et al., 2012 (Plate I. Bi-1 pg. 49); Neumann et al., 2017 (Fig.6 13 pg. 11)	Twiss et al., 1969 (Fig.2 3f pg. 111); Gallero and Distel, 2004 (Fig. 1 L h-j pg. 867); Piperno, 2006 (Fig.2.1a pg. 188); Lu and Liu, 2003 (Fig.2 C-1 pg. 79)
	Bilobate 2	Bi-2	10-25	Short, tabular, rounded convex lobes (Novello et al., 2012)	(S*), (PAN), (ARIS) Culm/Leaf/Inflorescence of Panicoideae and Aristidoideae and other Poaceae subfamilies (e.g. Bambusoideae) in low amounts but not identified in Bambusoideae in modern plant tissue in this thesis	Attributed to Panicoideae and Aristidoideae (C4)	Fahmy, 2008 (Fig. 2 15-19 pg. 15); Novello et al., 2012 (Plate I. Bi-2 pg. 49); Mercader et al., 2010 (Fig.3 1, 23,24 pg. 1960); Barboni et al., 1999 (Plate I 29 pg. 92); Bremond et al., 2017 (Fig.2 e-1 pg.4); Sagen et al., 2011 (Fig.2 h pg. 420); Novello et al., 2015 (Fig.3 5 pg. 92)	Twiss et al., 1969 (Fig.2 3d pg. 111); Gallero and Distel, 2004 (Fig. 1 L b-h pg. 867); Piperno and Pearsall, 1998 (Fig.6 pg 23, Fig.13 pg. 25); Mullholand, 1989 (Fig. 1 d pg. 500); Piperno, 2006 (Fig.2.1a pg. 188); Fredlund and Tieszen, 1994 (Fig.2 G pg. 326); Lu and Liu, 2003 (Fig.2 B1,B2 pg. 79)

Bilobate 3	Bi-3	17-25	Short, tabular, rounded lobes with thick outer margins and constriction between lobes (Neumann et al., 2017)	(S*), (PAN), (EHRH) Produced in Panicoideae (C4) but likely not be produced in Ehrhartoideae (C3) photosynthetic pathways. (not diagnostic to subfamily level)	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Neumann et al., 2017 (Fig.5 14 pg. 12)	_
Bilobate 4	Bi-4	17-20	Short, tabular, notched lobes - sometimes occurring with flared margins (e.g. 4a)	(S*), (PAN), (CHLO) Culm/Leaf/Inflorescence most commonly of Panicoideae but is produced by other Poaceae subfamilies in low amounts (e.g. Chloridoideae and Ehrhartoideae)	Attributed to Panicoideae (C4 mesic) but also occur in Chloridoideae	Fahmy, 2008 (Fig. 2 6-10 pg. 15); Barboni et al., 1999 (Plate I 27,28 pg. 92); Bremond et al., 2017 (Fig.2 e-3 pg.4); Mullholand, 1989 (Fig. 1 c pg. 500); Novello et al., 2012 (Plate I. Bi-8 pg. 49); Cordova, 2013 (Fig.6 10-W pg. 127); Aleman et al., 2014 (Fig.2 Ab pg. 276)	Piperno, 2006 (Fig.2.1a pg. 188); Twiss et al., 1969 (Fig.2 3f pg. 111); Gallero and Distel, 2004 (Fig. 1 M-k pg. 867); Lu and Liu, 2003 (Fig.4 5 pg. 82)
Bilobate 5	Bi-5	17-20	Short, tabular, notched lobes with flared margins	S*), (CHLO), (PAN) Culm/Leaf/Inflorescence most commonly of Chloridoideae but also Panicoideae and is produced by other Poaceae subfamilies (e.g. Danthonioideae and Bambusoideae)	Attributed to Chloridoideae (xeric C4)	(Mercader et al., 2010 (Fig. 3 11 pg. 1960); Barboni et al., 1999 (Plate.I 27 pg. 92)	Piperno and Pearsall, 1998 (Fig.10,14,15 pg. 24-25); Lu and Liu, 2003 (Fig.2 D-1 pg. 79, Fig.4 4 pg. 82); Strömberg, 2004 (Fig.4 j pg. 258)

Bilobate 6	Bi-6	10-25	Short, tabular, concave lobes	(S*), (PAN) Culm/Leaf/Inflorescence most commonly of Panicoideae but may be is produced by other Poaceae subfamilies (Ehrhartoideae, Aristidoideae) in low amounts	Attributed to Panicoideae (mesic C4)	Fahmy, 2008 (Fig. 2 11-14 pg. 15); Bremond et al., 2017 (Fig.2 e-2 pg.4); Novello et al., 2012 (Plate I. Bi-7 pg. 49); Barboni and Bremond, 2009 (Fig.1 8,11,12 pg. 33); Cordova, 2013 (Fig.6 10-X pg. 127); Neumann et al., 2009 (Fig.3 b pg.93); Aleman et al., 2014 (Fig.2 Ab pg. 276); Alexandre et al., 1997 (Fig.2 pg. 217)	Piperno, 2006 (Fig.2.1a pg. 188); Twiss et al., 1969 (Fig.2 3f pg. 111); Gallero and Distel, 2004 (Fig. 1 M- j pg. 867); Fredlund and Tieszen, 1994 (Fig.2 H pg. 326); Lu and Liu, 2003 (Fig.2 C-2,C-3 pg. 79, Fig.4 10 pg. 82)
Bilobate 7	Bi-7	10-25	Short, tabular, almost equidimension al, round- truncated lobes, missing shank (Novello et al., 2012)	(S*), (PAN), (CHLO) Culm/Leaf/Inflorescence most commonly of Panicoideae and Chloridoideae and is produced by other Poaceae subfamilies (e.g. Pooideae)	Attributed to Panicoideae (mesic C ₄)	Novello et al., 2012 (Plate I. Bi-9 pg. 49); Barboni and Bremond, 2009 (Fig.1 8,12,30e,30f pg.33); Fahmy, 2008 (Fig.2 19 pg. 15); Barboni et al., 1999 (Plate.I 30,33 pg. 92); Cordova, 2013 (Fig.6 3-K pg. 127)	Twiss et al., 1969 (Fig.2 Ib pg. 111); Gallero and Distel, 2004 (Fig. 1 M-d,M-l pg. 867); Cotton et al., 2012 (Fig 3 E pg. 93)
Bilobate 8	Bi-8	10-20	Parallelepipeda l, truncated lobes	(S*) Produced in both C3 and C4 Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Novello et al., 2012 (Plate I. Bi-10 pg. 49); Bremond et al., 2017 (Fig.2 e-1 pg. 4); Cordova, 2013 (Fig.6 4- J, 4-F pg.127); Novello et al., 2015 (Fig.3 7 pg. 92)	_
Bilobate 9	Bi-9	7-20	Short trapeziform, base bilobate, variable top, L>h (Novello et al., 2012)	(S*) Panicoideae, Ehrhartoideae, Aristidoideae according to Novello et al., (2012) and associated with aquatic species), and in Pooideae (Barboni ad Bremond, 2009) as well as other Poaceae subfamilies- non- diagnostic	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Novello et al., 2012 (Plate I. Bi-11 pg. 49)	Gallero and Distel, 2004 (Fig. 1 L-l pg. 867)

	Bilobate 10	Bi-10	15-25	Short, tabular, asymmetrical, 1 concave, 1 convex lobe	(S*) Culm/Leaf/Inflorescence of Panicoideae but also produced by other Poaceae subfamilies (e.g. Bambusoideae)	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Mercader et al., 2010 (Fig. 3 22 pg. 1960)	_
	Bilobate 11	Bi-11	7-25	Short Tabular staggered lobes in top/end view (Barboni and Bremond, 2009), sometimes lobes asymmetrical	(S*) Produced in both C ₃ and C ₄ Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Barboni et al., 1999 (Plate.I 26 pg. 92); Barboni and Bremond, 2009 (Fig.1 29a- c pg.33)	_
A.2 Bilobate Long/short shank	Bilobate 12	Bi-12	10-15	Bilobate with deeply concave lobes, long and short shank "scooped bilobate" (Barboni and Bremond, 2009; Neumann et al., 2017)	(S*), (EHRH) (BAM) (CHLO), (PAN) Culm/Leaf/Inflorescence of Ehrhartoideae, Bambusoideae, Chloridoideae and Panicoideae	Generally attributed to Ehrhartoideae and Bambusoideae (C ₃) (see Piperno, 2006). However, assigned to C ₃ & C ₄ based on Barboni and Bremond (2009)	Barboni and Bremond, 2009 (Fig.1 18a,18b pg.33); Mercader et al., 2010 (Fig.7 6-9 pg. 13)	Similar to Piperno, 2006 (Fig.2.2 Bam.3,4 and Ehrh.1 pg. 31); Similar to Prasad et al., 2011 (Fig.3 I,j pg. 4); Iriante, 2003 (Fig.1 a-c pg. 1087); Piperno and Pearsall, 1988 (Fig.50 pg.34, Fig.72 pg. 39); Lu and Liu, 2003 (Fig.2 D-1,D-2 pg. 79, Fig.4 11,12 pg. 82)

A.3 Bilobate long shank	Bilobate 13	Bi-13	20-30	Long shaft, flattened to slightly notched outer margin (Mercader et al., 2010), sometimes with nodular protrusion (knobs) on end lobes (Barboni and Bremond, 2009)	(S*), (PAN) Culm/Leaf/Inflorescence most commonly of Panicoideae but may be produced by other Poaceae subfamilies	Attributed to Panicoideae (mesic C4)	Barboni and Bremond, 2009 (Fig.1 6a,6b,9a,9b pg. 33); Garnier et al., 2012 (Fig.3 C-a pg. 5); Novello et al., 2012 (Plate I. Bi-3, Bi-6 pg. 49); Mercader et al., 2010 (Fig.3 10 pg. 1961); Neumann et al., 2017 (Fig.6 6,11-13 pg. 12); Fahmy, 2008 (Fig.2 1,2,11,12 pg. 15)	Twiss et al., 1969 (Fig.2 3e pg. 111); Gallero and Distel, 2004 (Fig. 1 O-j pg. 867); Piperno and Pearsall, 1998 (Fig.7 pg. 23); Novello et al., 2012 (Plate I. Bi-3 pg. 49)
	Bilobate 14	Bi-14	25-30	Long, tabular, notched lobes with flared margins (Mercader et al., 2010)	(S*), (PAN), (CHLO) Culm/Leaf/Inflorescence most commonly of Panicoideae but may be produced by Chloridoideae other Poaceae subfamilies (e.g. Pooideae)	Attributed to Panicoideae (mesic C ₄)	Cordova, 2013 (Fig.6 10-M pg. 127); Mercader et al., 2010 (Fig.4 10 pg. 1961); Barboni and Bremond, 2009 (Fig.1 5,11 pg. 33); Novello et al., 2012 (Plate I. Bi-5 pg. 49); Neumann et al., 2017	Piperno, 2006 (Fig.2.2 Pani-3 pg. 31, Fig.21.a pg. 188); Piperno and Pearsall, 1998 (Fig.5 pg. 23); Lu and Liu, 2003
	Bilobate 15	Bi-15	25-30	Long, tabular concave outer margin long shaft (Novello et al., 2012; Mercader et al., 2010) sometimes with one concave, one flattened end (see Neumann et al., 2017)	(S*), (PAN) Culm/Leaf/Inflorescence most commonly of Panicoideae but may be produced by other Poaceae subfamilies	Attributed to Panicoideae (mesic C ₄)	Neumann et al., 2017; Barboni et al., 1999 (Plate.I 31 pg. 92); Mercader et al., 2010 (Fig.2 21,22 pg. 1959); Fahmy, 2008 (Fig.2 14 pg. 15); Barboni et al. 2007 (Fig.2 4 pg. 457); Aleman et al., 2014 (Fig.2 Aa pg. 276)	Piperno, 2006 (Fig.2.2 Pani-1 pg. 3); Lu and Liu, 2003 (Fig.4 17,22,23 pg. 82)

	Bilobate 16	Bi-16	25-35	Long, tabular, round -convex ends, lobes, symmetrical	(S*), (PAN) Culm/Leaf/Inflorescence most commonly of Panicoideae but may be produced by other Poaceae subfamilies	Attributed to Panicoideae (mesic C ₄)	Novello et al., 2012 (Fig.1 Bi-4 pg. 49); Mercader et al., 2010 (Fig.2 16 pg. 1959, Fig.3 12 pg. 1960); Garnier et al., 2012 (Fig.3 C-c pg. 5); Fahmy, 2008 (Fig.2 15,16 pg. 15); Neumann et al. 2009 (Fig.3 a pg. 93)	Twiss et al., 1969 (Fig.2 3c pg. 111); Gallero and Distel, 2004 (Fig. 1 N-c pg. 867); Lu and Liu, 2003 (Fig.2 B-3 pg. 79)
	Bilobate 17	Bi-17	25-27	Long and narrow, flattened/trun cated end lobes, symmetrical	(S*), (PAN), (ARIS) Culm/Leaf/Inflorescence most commonly of Panicoideae (supertribe: Aristidoideae) but may be produced by other Poaceae subfamilies (e.g. Chloridoideae)	Attributed to Panicoideae (mesic C ₄) and Aristidoideae) (semi-xeric C ₄)	Mercader et al., 2010 (Fig.2 14 pg. 1959, (Fig.4 6 pg. 1961); Fahmy, 2008 (Fig.2 1 pg. 15); Neumann et al., 2017 (Fig.6 4 pg. 12)	Piperno 2006 (Fig.2.2 Aris-1 p. 31, Fig.2.1a pg. 188); Piperno and Pearsall, 1998 (Fig.8 pg. 23); Lu and Liu, 2003 (Fig.2 C-4 pg. 79);
	Bilobate 18	Bi-18	25-35	Long and narrow, rounded- convex end lobes, symmetrical to slightly staggered in top view	(S*), (PAN), (ARIS) Culm/Leaf/Inflorescence most commonly of Panicoideae (supertribe: Aristidoideae) but may be produced by other Poaceae subfamilies (e.g. Chloridoideae)	Attributed to Panicoideae (mesic C ₄) and Aristidoideae) (semi-xeric C ₄)	Mercader et al., 2010 (Fig.2 14 pg. 1959); Mercader et al., 2010 (Fig.2 14 pg. 1959); Neumann et al., 2017 (Fig.6 2 pg. 12)	Piperno and Pearsall, 1998 (Fig.8 pg. 23); Lu et al., 2003 (Fig.2 B4 pg. 79, Fig.4 15 pg. 82); Piperno 2006 (Fig.2.2 Aris-1 p. 31, Fig.2.1a pg. 188); Lu and Liu, 2003 (Fig.2 B-4 pg.79, Fig.4 15 pg. 82)
A.4 Bilobates (other)	Bilobate 19	Bi-19	10-12	Bilobate with convex ends, Constriction between the lobes, top a plateau ("Stipa type") (Neumann et al., 2017)	(S*), (POID), (BAM), (PAN) (CHLO) Culm/Leaf/Inflorescence most commonly of Pooideae but can also be produced by other Poaceae subfamilies (e.g. Panicoideae and Chloridoideae) in East African Poaceae [see Barboni and Bremond, 2009])	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Garnier et al., 2012 (Fig.3 Cd pg. 5); Fahmy, 2008 (Fig.2 19 pg. 15); Neumann et al., 2017 (Fig.6 9 pg. 12); Barboni and Bremond, 2009 (Fig.1 30a,30c,30d,30f,30g pg. 33); Cordova, 2013 (Fig.7 [8-B] pg. 128); Neumann et al., 2009 (Fig.3 e pg. 93)	Piperno, 2006 (Fig. 2.2 Pooid-7 pg. 31); Piperno and Pearsall, 1988 (Fig.11 pg. 26); Gallero and Distel, 2004 (Fig.1 A-b,E-b,L-b,M-b, E- d,M-d,L-d,A-e,L-e,M-e, L- f,M-f pg. 867); An, 2016 (Fig. 3 e pg. 5); Strömberg, 2004 (Fig.4 h pg. 258); Fredlund and Tieszen, 1994 (Fig.2 F pg. 326)

	Bilobate 20	Bi-20	17-30	Bilobate with extra-lobe on shank. Bilobates with one to several supplementary	(S*), (PAN) Culm/Leaf/Inflorescence of Panicoideae but also produced by other Poaceae subfamilies (e.g. Ehrhartoideae)	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Fahmy, 2008 (Fig.2 20-21 pg. 15); Mercader et al., 2010 (Fig.3 14 pg. 1960, Fig.4 8 pg. 1961); Garnier et al., 2012 (Fig.3 Cg pg. 5); Cordova, 2013 (Fig.6	Twiss et al., 1969 (Fig.2 3g,3j pg. 111); Gallero and Distel, 2004 (Fig.2 Ai,Bi,Bj pg. 868); Lu and Liu, 2003 (Fig.2 F-a pg. 79
				Novello et al., 2012) convex to truncated end lobes			al., 1999 (Plate I. 34 pg. 92); Novello et al., 2012 (Plate.I Bi-13 pg. 49)	
B. Polylobates	Polylobate 1	Poly-1	25-35	Polylobate ends rounded/conv ex to truncated, wide and short shank	(S*) Culm/Leaf/Inflorescence most commonly of Panicoideae but are produced by other Poaceae subfamilies (e.g. Pooideae) in low amounts	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Fahmy, 2008 (Fig.2 26-29 pg. 15); Novello et al., 2012 (Plate.I Poly-1 pg. 49); Neumann et al., 2017 (Fig.6 27,28 pg. 12); Barboni and Bremond, 2009 (Fig.1 32b, 34a pg. 33); Mercader et al., 2010 (Fig.3 21 pg. 1960); Garnier et al., 2012 (Fig.3 Ci pg. 5)	Twiss et al., 1969 (Fig.2 3i pg. 111); Gallero and Distel, 2004 (Fig.2 F-b,F-c,E-h); Piperno, 2006 (Fig.2.1a pg. 188); Lu and Liu, 2003 (Fig.2 F-b pg. 79,Fig.4 26 pg. 82)
	Polylobate 2	Poly-2	25-35	Polylobate- ends truncated/ concave, sometimes occurring with flared margins narrow and long shank	(S*), (PAN) Culm/Leaf/Inflorescence most commonly of Panicoideae but similar types are produced by other C4 Poaceae subfamilies (e.g. Arundinoideae)	Attributed to Panicoideae (mesic C ₄)	Fahmy, 2008 (Fig.2 27 pg. 15); Mercader et al., 2010 (Fig.3 27 pg. 1960, Fig.1 35 pg. 33); Neumann et al., 2017 (Fig.6 28 pg. 12); Aleman et al., 2014 (Fig.2 Ag pg. 276)	Lu and Liu, 2003 (Fig.4 25 pg. 82)

C. Crosses	Cross 1	Cr-1	8-12	Cross-3 lobed, Trapeziform	(S*), (CHLO) Culm/Leaf/Inflorescence most commonly of Chloridoideae but is also produced in Panicoideae and can be produced by other Poaceae subfamilies (e.g. Pooideae) in very small amounts	Attributed to Chloridoideae (xeric C4)	Novello et al., 2012 (Plate.I Cr-4 pg. 49); Garnier et al., 2012 (Fig.3 Ch pg. 5); Barboni and Bremond, 2009 (Fig.1 31a,31c,31d pg. 33); Neumann et al., 2017 (Fig.6 15 pg. 12); Neumann et al., 2009 (Fig.3 g pg. 93)	Twiss et al., 1969 (Fig.2 Ig pg. 111)
	Cross 2	Cr-2	8-15	Cross-4 lobed rounded, tabular	(S*), (PAN), (CHLO) Culm/Leaf/Inflorescence most commonly of Chloridoideae but is also produced in Panicoideae and can be produced by other Poaceae subfamilies (e.g. Bambusoideae) in very small amounts	Attributed to Panicoideae (mesic C ₄)	Novello et al., 2012 (Plate.I Cr-2 pg. 49); Cordovan, 2013 (Fig.6 11-A pg. 127); Garnier et al., 2012 (Fig.3 Ce,Cf pg. 5); Barboni et al., 1999 (Plate.I 35,36 pg. 92); Mercader et al., 2010 (Fig.2 25,26 pg. 1959); Neumann et al., 2017 (Fig.6 17 pg. 12); Barboni and Bremond, 2009 (Fig.1 31a,31c,31d pg. 33); Barboni et al., 2007 (Fig.2 5 pg. 457); Fahmy, 2008 (Fig.2 24 pg. 15); Neumann et al., 2009 (Fig.3 f pg. 93); Aleman et al., 2014 (Fig.2 e,f pg. 276)	Twiss et al., 1969 (Fig.2 3c pg. 111); Lu and Liu, 2003 (Fig.2 E-1 pg. 79, Fig.4 5- 7,113 pg. 82); Piperno and Pearsall, 1998 (Fig.16 pg 25); Gallero and Distel, 2004 (Fig.1 J-I,J-j,K-j pg. 867); An, 2016 (Fig. 3 c pg. 5)
	Cross 3	Cr-3	8-12	Tabular, 4- lobed angular, thin shank (Novello et al., 2012)	(S*), (PAN) Culm/Leaf/Inflorescence most commonly of Panicoideae but similar types are produced by other Poaceae subfamilies	Attributed to Panicoideae (mesic C ₄)	Novello et al., 2012 (Plate.I Cr-3 pg. 49); Fahmy, 2008 (Fig.2 25 pg. 15); Mercader et al., 2010 (Fig.2 23 pg. 1959)	Piperno, 2006 (Fig.3.1 Var.6 pg. 200, Fig.3.3b,3.3c pg.201)

	Cross 4	Cr-4	8-12	Trapeziform, 4-lobed, cross top (Novello et al., 2012) (Top tent-like arch to sloping trapezoids/rec tangular	(S*), (PAN) Culm/Leaf/Inflorescence most commonly of Panicoideae but similar types are produced by other Poaceae subfamilies	Attributed to Panicoideae (mesic C ₄)	Novello et al., 2012 (Plate.I Cr-5 pg. 49); Bremond et al., 2017 (Fig.2 f pg. 4); Neumann et al., 2017 (Fig.6 18,19,21 pg. 12); Aleman et al., 2014 (Fig.2 An pg.276); Novello et al., 2015 (Fig.3 10 pg.92)	Lu and Liu, 2003 (Fig.4 7 pg. 82); Piperno, 2006 (Fig.3.1 Var.5 pg. 200)
	Cross 5	Cr-5	10-12	Disarticulated obtuse-lobed cross, obtuse- lobed cross	(S*), (POID), (BAM), (EHRH) L of Bambusoideae, Ehrhartoideae, and Pooideae	Attributed to Bambusoideae, Ehrhartoideae, and Pooideae (C ₃)	—	Piperno, 2006 (Fig.3.1 Var.3/8/10 and other variants pg. 200); Yost and Blinnikov, 2011 (Fig.8 H pg. 1983, Fig.14 R pg. 1987)
D. Trapezoid	Trapezoid 1	Tra-1	12-15	Trapezoid- cubic/parallele pipedal body	(S*), (POID), (CHLO), (PAN), (PHAR) Culm/Leaf/Inflorescence of Pooideae, and Pharoideae, but also in Chloridoideae and Panicoideae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Barboni et al., 1999 (Plate.I 17 pg. 92); Cordova, 2013 (Fig.6 3A,3B pg. 127); Novello et al., 2012 (Plate.I Tra-1 pg. 49)	Piperno, 2006 (Fig.2.2 Phar- 1 pg. 31); Piperno and Pearsall, 1998 (Fig. 36 pg. 30); Gallero and Distel, 2004 (Fig.1 Ga,Gb,Gd pg. 867); Madella et al., 2005 (Table.1 pg. 255)
	Trapezoid 2	Tra-2	8-10	Trapezoid- short cell (top ridge/keeled)	(S*), (POID), (CHLO), (PAN) Pooideae but also recorded in Chloridoideae and Panicoideae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Barboni et al., 2007 (Fig.2 2 pg. 457)	Gallero and Distel, 2004 (Fig.1 Gh pg. 867)
E. Tabular Trapeziform	Trapeziform 1	Tram-1	25-40	Trapeziform sinuate	(S*), (POID), (BAM), (EHRH), (CHLO) Culm/Leaf/Inflorescence most commonly of Pooideae as well as Bambusoideae, and Ehrhartoideae. Also produced in low amounts by other Poaceae subfamilies (e.g. Chloridoideae)	Attributed to Pooideae (C ₃)	Barboni et al., 2007 (Fig.2 3 pg. 457); Cordova, 2013 (Fig.7 f [Type 4-K] pg. 128); Barboni and Bremond, 2009 (Fig.1 17a,17b pg.33); Mercader et al., 2010 (Fig.2 33 pg. 1959); Novello et al., 2015 (Fig.3 13a pg. 92)	Gallero and Distel, 2004 (Fig.2 Gc pg. 868); Yost and Blinnikov, 2011 (Fig.4 H pg. 1981); Fredlund and Tieszen, 1994 (Fig.2 D1 pg. 326); Piperno, 2006 (Fig2.2 Pooid- 3 pg. 31)

	Trapeziform 2	Tram-2	15-40	Trapeziform sinuate smooth	(S*), (POID), (BAM), (EHRH) Culm/Leaf/Inflorescence most commonly of Pooideae as well as Bambusoideae, and Ehrhartoideae.	Attributed to Pooideae (C ₃)	Barboni and Bremond, 2009 (Fig.1 16a,16b pg.33); Cordova, 2013 (Fig.7 d [Type 4-I],e [Type 4-H],g [Type 5-A] pg. 128); Nuemann et al., 2009 (Fig.3 o pg. 93); Twiss et al., 1969 (Fig.2 Ih pg. 111)	Strömberg, 2004 (Fig.4 d pg. 258); Piperno and Pearsall, 1998 (Fig.23 pg. 27); Yost and Blinnikov, 2011 (Fig.3 L- K pg. 1981, Fig.5 D pg. 1982); Fredlund and Tieszen, 1994 (Fig.2 D2 pg. 326); Xiaohong et al., 2015 (Fig. 3 r,s pg. 5); Piperno, 2006 (Fig.2.2 Pooid-1,2 pg. 31, Fig.21d pg. 188)
F. Saddles	Saddle 1	Sad-1	8-15	Tabular, equidimension al convex and concave edges	(S*), (CHLO), (ARIS), (EHRH) Culm/Leaf/Inflorescence most commonly of Chloridoideae but also produced in other Poaceae subfamilies (e.g. Aristidoideae and Ehrhartoideae)	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Cordova, 2013 (Fig.6 8-I pg. 127, Fig.7 n [Type 9-A] pg. 128); Bremond et al., 2017 (Fig.2 g-1 pg. 4); Novello et al., 2012 (Plate.I S-1 pg. 49); Barboni and Bremond, 2009 (Fig.1 39 pg. 33); Neumann et al., 2017 (Fig.6 31 pg.12); Mercader et al., 2010 (Fig.2 5-7 pg. 1959); Barboni et al., 1999 (Plate.I 21 pg. 92); Garnier et al., 2012 (Fig.3 C-m pg. 5)	Yost and Blinnikov, 2011 (Fig.6 D pg. 1982); Gallero and Distel, 2004 (Fig.1 H-I pg. 867); Fredlund and Tieszen, 1994 (Fig.2 E1 pg. 326); Piperno and Pearsall, 1998 (Fig.19 pg. 26)
	Saddle 2	Sad-2	8-12	Tabular short, convex edges longer than concave edges. "squat" saddle	(S*), (CHLO) Culm/Leaf/Inflorescence most commonly of Chloridoideae	Attributed to Chloridoideae (xeric C ₄)	Cordova, 2013 (Fig.6 9- F,9-H pg. 127); Novello et al., 2015 (Fig.11 pg. 93); Novello et al., 2012 (Plate.I S-3 pg. 49); Neumann et al., 2009 (Fig.3 h pg. 93); Barboni et al., 1999 (Plate.I 22-25 pg. 92); Garnier et al., 2012 (Fig.3 C-l pg. 5); Aleman et al., 2014 (Fig.2 Al pg. 276)	Twiss et al., 1969 (Fig.2a pg. 111); Fredlund and Tieszen, 1994 (Fig.2 E2 pg. 326); Piperno and Pearsall, 1998 (Fig.18,20 pg. 26); Piperno, 2006 (Fig.2.2 Chlo-1 pg. 31, Fig.2.1c pg. 188)

Saddle 3	Sad-3	10-15	Tabular long, convex edges shorter than concave edges. "Tall" saddle, elongrate or	(S*) Culm/Leaf/Inflorescence of C ₃ and C ₄ grasses, redundant across East African Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Garnier et al., 2012 (Fig.3 C-n,C-o pg. 5); Cordova, 2013 (Fig.6 9-A,9-C pg. 127); Barboni et al., 2007 (Fig.2 6 pg. 457); Barboni et al. 1999 (Plate L17-20)	Twiss et al., 1969 (Fig.2b pg. 111); Piperno and Pearsall, 1998 (Fig.21 pg.27, Fig.73 pg. 40); An, 2016 (Fig. 3 i pg. 5)
			thin saddle	Yost et al., (2018) note that in Bambusoideae, Yushania alpina (formerly Aguadiaaria alpina)	found in association with other Co CSSCs	pg. 92); Barboni and Bremond, 2009 (Fig.1 40a 40b pg 33): Bremond	
				"Very tall saddles" with width is ≥15 µm, are diagnostic of Bambusoideae grasses (Fig. S1a)	and forest indicators this morphotype is likely to originate from Bambusoideae	et al., 2017 (Fig.2 g pg. 4); Neumann et al., 2009 (Fig.3 I pg. 93); Neumann et al., 2017 (Fig.6 32 pg. 12); Mercader et al., 2010 (Fig.3 3,29 pg. 1960,Fig.4 17 pg. 1961)	
Saddle 4	Sad-4	8-10	Plateaued saddle. Trapeziform equidimension al to long, base oblong, round or vaguely constricted, saddle top (Novello et al., 2012)	(S*) Culm/Leaf/Inflorescence of C ₃ and C ₄ grasses, redundant across East African Poaceae Note: Yost et al., (2018) attribute these types to Phragmites.	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Cordova, 2013 (Fig.6 9-F pg. 127); Neumann et al., 2009 (Fig.3 j-l pg. 93); Novello et al., 2012 (Plate.I S-4,S-5 pg. 49)	Piperno and Pearsall, 1998 Fig.24 pg. 27, Fig.25 pg. 28, Fig.53 pg. 35Fig.60 pg. 36)

	Saddle 5	Sad-5	10-17	Saddle collapsed "i.e. very concave on one side in side view, but saddle-like in base view" (Barboni and Bremond, 2009)	 (S*), (CHLO), (BAM) Culm/Leaf/Inflorescence most commonly of Chloridoideae but may also be produced in other Poaceae subfamilies (e.g. Bambusoideae) Note: when found in association with other C₃ GSSCs and forest indicators this morphotype is likely to originate from Bambusoideae. When found in association with xeric C4 GSSCs mot likely to originate from Chloridoideae 	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Neumann et al., 2017 (Fig.6 33 pg. 12); Mercader et al., 2010. Barboni and Bremond, 2009	An, 2016 (Fig. 3 i pg. 5); Piperno, 2006 (Fig.2.2 Bam- 1,2,6,7); Piperno and Pearsall, 1998 (Fig.22 pg.27, Fig.26,27 pg. 28, Fig.30 pg. 2); Strömberg, 2004 (Fig.4 I pg. 258)
G. Rondels	Rondel 1	Ron-1	8-10	Rondel with a small, keeled, tent-shaped body. Rondel with irregular base and ridged top	(S*), (POID), (BAM), (EHRH), (PAN) Culm/Leaf/Inflorescence most commonly of Pooideae as well as Bambusoideae, and Ehrhartoidea but also present in all other Poaceae subfamilies	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate) Note: when found in association with other C ₃ GSSCs and forest indicators this morphotype is likely to originate from C ₃ forest grasses	Barboni et al., 1999 (Plate.I 13 pg. 92)	Piperno and Pearsall, 1998 (Fig.35 pg. 30); Gallero and Distel, 2004 (Fig.1 Be,Bf,Ce pg. 867)
	Rondel 2	Ron-2	h=8-15	Rondel- horned. Conical tall body, apex concave with acute outward apices (Mercader et al., 2010)	(S*) Culm/Leaf/Inflorescence of C ₃ and C ₄ grasses, redundant across East African Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Cordova, 2013 (Fig.6 5-J- 5-L pg. 127); Aleman et al., 2014 (Fig.2 A-j pg. 276); Neumann et al., 2009 (Fig.3 m pg. 93); Mercader et al., 2010 (Fig.5 17-19 pg. 1962, Fig.2 17-19 pg. 1959)	Fredlund and Tieszen, 1994 (Fig.2 B pg. 326); Xiaohong An, 2016 (Fig. 3 l pg. 5); Piperno and Pearsall, 1998 (Fig.74 pg.40)

Rondel 3	Ron-3	h=16- 20	Rondel- cylindric, base/top round/squared with +/- regular outlines ("chimney" or "volcano" bodies) (Novello et al.,	(S*) Culm/Leaf/Inflorescence of C ₃ and C ₄ grasses, redundant across East African Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Cordova, 2013 (Fig.6 3-J,5- A pg. 127); Novello et al., 2012 (Plate.I Ro-7 pg.49)	Fredlund and Tieszen, 1994 (Fig.2 C pg. 326); Piperno and Pearsall, 1998 (Fig.70 pg. 39)
Rondel 4	Ron-4	8-12	2012) Rondel- cylindric, constricted sides (Novello et al., 2012)	(S*) Culm/Leaf/Inflorescence of C ₃ and C ₄ grasses, redundant across East African Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Cordova, 2013 (Fig.6 2- L,5-G,5-P pg. 127); Novello et al., 2012 (Plate.I Ro-4 pg.49)	Piperno, 2006 (Fig.3.4e pg. 2003); Yost and Blinnikov, 2011 (Fig.12 F pg. 1985)
Rondel 5	Ron-5	8-10	Rondel- conical, top truncated to keeled	(S*) Culm/Leaf/Inflorescence of C ₃ and C ₄ grasses, redundant across East African Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Cordova, 2013 (Fig.6 5- B,5-G,5-H pg. 127); Aleman et al., 2014 (Fig.2 Ai pg. 276); Novello et al., 2012 (Plate.I Ro-1,Ro-2 pg. 49); Barboni and Bremond, 2009 (Fig.1 3a,3b pg. 32)	Piperno, 2006 (Fig.3.4e pg. 2003)
Rondel 6	Ron-6	h=8-12	Rondel- conical, bevelled/spike d top	(S*) Culm/Leaf/Inflorescence of C ₃ and C ₄ grasses, redundant across East African Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Aleman et al., 2014 (Fig.2 Ah pg. 276); Mercader et al., 2010 (Fig.3 8 pg. 1960); Cordova, 2013 (Fig.6 5-H pg. 127)	_
Rondel 7	Ron-7	h=8-10	Rondel- conical, top rounded to tapering	(S*) Culm/Leaf/Inflorescence of C ₃ and C ₄ grasses, redundant across East African Poaceae	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate)	Cordova, 2013 (Fig.6 1-A pg. 127); Novello et al., 2012 (Plate.I Ro-3 pg. 49)	An, 2016 (Fig. 3 k pg. 5)

	Rondel 8	Ron-8	base > 15	Rondel (multiple types) with base > 15 µm, ellipsoid in top view	(S*), (POID) Culm/Leaf/Inflorescence most commonly of Pooideae	Attributed exclusively to C ₃ Pooideae (based on Barboni and Bremond 2009)	Cordova, 2013 (Fig.6 5- O,5-P,6-A,6-B pg. 127); Novello et al., 2012 (Plate.I Ro-8 pg. 49); Bremond et al., 2015 (Fig.2 h pg. 4); Barboni and Bremond 2009	_
	Rondel 9	Ron-9	15-17	Rondel- carinate. Tent shaped with one sinuous edge	(S*), (BAM), (PHAR) Culm/Leaf/Inflorescence most of Bambusoideae and Pharoideae But also produced in small amounts by other Poaceae subfamilies	Attributed to C ₃ & C ₄ Poaceae (intermediate/ indeterminate) Note: when found in association with other C ₃ GSSCs and forest indicators this morphotype is likely to originate from C ₃ forest grasses	Barboni et al., 1999; Mercader et al., 2010 (Fig.2 27 pg. 1959); <i>Arundinaria</i> <i>alpina</i> (This study)	Twiss et al., 1969; Pearsall and Piperno, 1998 Carnelli et al. 2004
H. Bulliform	Cuneiform bulliform indiff.	Bull-1	30–100	Silicified bulliform cells- cuneiform/ "fan" shaped	(S*) Mainly in the leaf but also culm and inflorescence of all Poaceae subfamilies (Beal, 1886; Metcalfe, 1960)	Attributed to Poaceae but not to a particular GSSC category in this study	Alexandre et al., 1997; Barboni et al., 1999; Runge, 1999 (Plate V, 9b); Bremond et al., 2005, 2008ab; Mercader et al., 2010 (12: Fig. 3 [7,17,26]; Fig. 4 [12,20]); Novello et al., 2012 (Plate II, Blo-4 and Blo-5 pg. 50)	Twiss et al., 1969; Kondo et al., 1994

Appendix 4 - '	Table 4.5 Mo	orphological-taxone	mic associations	of each morphot	ype identified in I	Propose Farm p	alaeosols samples.

Class/Subclass	Morphotype	Figure No.	Morphological-taxonomic association (representative taxa from published studies)
A.1 Bilobate short shank	Bilobate 1	Bi-1	Panicoideae, <i>Brachiaria deflexa</i> (Leaf), Panicoideae, <i>Digitaria ciliaris</i> (Leaf) (Fig.2 3,4 pg. 15) (Fahmy, 2008); Panicoideae, <i>Melinis ambigua</i> (Culm/Leaf/Inflorescence) (Fig.3 15 pg. 1960) (Mercader et al., 2010). Similar to type 8-E (Fig.6 pg.127) and 10Q/10R (Fig.6 pg.127) predominet in C ₃ types (Cordova, 2013); Panicoideae, <i>Schizachyrium exile</i> (Fig.6 13 pg. 11) (Neumann et al., 2017); Ehrhartoideae, <i>Oryza sativa</i> , Bambusoideae, <i>Leersia hexandra</i> , Ehrhartoideae, <i>Zizaniopsis miliacea</i> , <i>Z. caduciflora</i> , Panicoideae, <i>Panicum amarum</i> (Fig.2 C-1 pg. 79) (Lu and Liu, 2003)
	Bilobate 2	Bi-2	 Panicoideae, Digitaria delicata (Leaf), Panicoideae, Brachiaria eruciformis (Leaf), Panicoideae, Brachiaria jubata (Leaf), Panicoideae, Digitaria lecardii (Leaf) (Fig.2 15-19 pg. 15) (Fahmy, 2008); Panicoideae, Aristidoideae, Aristida junciformis (Culm/Leaf/Inflorescence), Panicoideae, Pennisetum polystachion (Culm/Leaf/Inflorescence) (Fig.3 1, 23,24 pg. 1960) (Mercader et al., 2010); Similar to type Group III, 8-B,E (Fig.6 pg.127) predominant in C₃ types (Cordova, 2013); Bambusoideae, Chusquea longifolia (Leaf) (Fig.13 pg. 25), Panicoideae, Panicum fasciculatum (Leaf) (Fig.6 pg. 23) (Piperno and Pearsall, 1998); Panicoideae, Andropogonodae, Arundinella birta, A. setosa, Panicoideae, Eccoilopus cotulifer, Panicoideae, Eulalia speciosa, Panicoideae, Setaria faberi, Panicoideae, Pennisetum alopecuroides, P. purpureum, Panicoideae, Echinochloa crusgalli, Panicoideae, Aristida desmantha, Panicoideae, Echinochloa crusgalli var. mitis, Panicoideae, Andropogoneae, Saccharum sinensis, S. arundinaceum, Panicoideae, Sorghum vulgare, Panicoideae, Miscanthus floridulus, M. sinensis, Panicoideae, Cenchrus incertus (Fig.2 B1 pg. 79) (Lu and Liu, 2003); Ehrhartoideae, Oryza longistaminata, Panicoideae, Acroceras amplectens, and E. pyramidalis (Plate I. Bi-2 pg. 49) (Novello et al., 2012)
	Bilobate 3	Bi-3	Panicoideae, <i>Hyparrhenia rufa</i> (Fig.5 14 pg. 12) (Neumann et al., 2017). Similar to Bilobate-2 but with thicker outer margins. Similar but not identical to type 10-Z (Fig. 6 pg. 127 & Fig.7 S pg. 128) produced by Ehrhartoideae, <i>Ehrharta erecta</i> (Cordova, 2013)
	Bilobate 4	Bi-4	Panicoideae, Brachiaria jubata (Plate I 5 pg. 12) (Neumann et al., 2017); Panicoideae, Schizachyrium jeffreysii (Culm/Leaf/Inflorescence), (Fig.4 11 pg. 1961) (Mercader et al., 2010); Ehrhartoideae, Zizania caduciflora (Fig.4 5 pg. 82) (Lu and Liu, 2003); Ehrhartoideae, Oryza longistaminata, Panicoideae, Acroceras amplectens, and E. pyramidalis (Plate I. Bi-8 pg. 49) (Novello et al., 2012)
	Bilobate 5	Bi-5	Panicoideae, <i>Schizachyrium jeffreysii</i> (Culm/Leaf/Inflorescence) (Fig. 3 11 pg. 1960) (Mercader et al., 2010); Chloridoideae, <i>Eragrostis mexicana</i> (Fig.14,15 pg. 25), Bambusoideae, <i>Chusquea patens</i> (Fig.10 pg. 24) (Piperno and Pearsall, 1998); Similar but not identical to Ehrhartoideae type (Fig.2.2 Ehrh-1 pg. 31) (Piperno, 2006); Similar to Danthonioideae, <i>Merxmuellera decora</i> (Fig.7 q pg. 128); Bambusoideae, <i>Leersia oryzoides</i> , Ehrhartoideae, <i>Zizaniopsis miliacea</i> , Panicoideae, <i>Anthaenantia rufa</i> (Fig.2 D-1 pg. 79), Panicoideae, <i>Miscanthus floridulus</i> (Fig.4 4 pg. 82) (Lu and Liu, 2003)
	Bilobate 6	Bi-6	 Panicoideae, Panicum laetum (Leaf), Panicoideae, Pennisetum unisetum (Leaf), Panicoideae, Eriochloa nubica (Leaf), Panicoideae, Digitaria delicatula (Leaf) (Fig. 2 11-14 pg. 15) (Fahmy, 2008); Panicoideae, Melinis repens, Hyparrhenia spp., Schizachyrium jeffreysii (Culm/Leaf/Inflorescence) (Fig. 2 1-4 pg. 1959) (Mercader et al., 2010); Panicoideae, Anthephora elongata (Fig.1 8,12 pg. 33) (Barboni and Bremond, 2009); Panicoideae, Panicum bisulcatum, P. virgatum, Panicoideae, Spodipogon sibiricus, Panicoideae, Eriochloa villosa, Panicoideae, Bothriochloa ischaemum, Panicoideae, Capillipedium parvifibrum, Panicoideae, Anthephora elongata (Fig.2 C-2 pg. 79), Panicoideae, Saccharum officinarum, Panicoideae, Chasmanthium laxum, Panicoideae, Miscanthus rufloridulus, M. sinensis (Fig.2 C-2 pg. 79), Panicoideae, Digitaria sanguinalis var. ciliaris, Panicoideae, Dimeria ornithopoda, Panicoideae, Sorghastrum nutans, Panicoideae, Imperata cylindrica, Panicoideae, Themeda gigantea var. caudate, Panicoideae, Panicum virgatum (Fig.2 C-3 pg. 79), Panicoideae, Set (Fig.4 10 pg. 82) (Lu

			and Liu, 2003); Ehrhartoideae, Oryza longistaminata, Panicoideae, Acroceras amplectens, and E. pyramidalis (Plate I. Bi-7 pg. 49) (Novello et al., 2012)
	Bilobate 7	Bi-7	Panicoideae, Anthephora elongata, (Fig.1 8,12 pg. 33), Similar to "stipa types" Chloridoideae, Crypsis schoenoides (Fig.1 30e pg.33) and Panicoideae, Arundinella nepalensis (Fig.1 30f pg. 33) (Barboni and Bremond, 2009)
	Bilobate 8	Bi-8	Panicoideae, Antephora nigritana (Fig.6 10 pg. 12) (Neumann et al., 2017)
	Bilobate 9	Bi-9	Pooideae, Aira caryophyllea (Fig.1 30c pg.33) (Barboni and Bremond, 2009); Similar to Chloridoideae, Pappophorum subbulbosum (Fig.1 L-l pg. 867)
	Bilobate 10	Bi-10	Bambusoideae, Arundinaria alpine (Fig.3 2 pg. 1960), Panicoideae, Pennisetum polystachion (Culm/Leaf/Inflorescence) (Fig.3 22 pg. 1960) (Mercader et al., 2010)
	Bilobate 11	Bi-11	Panicoideae, Pennisetum purpureum, Oryzoideae, Humbertochloa greenwayi, Panicoideae, Hylebates chlorochloe (Fig.1 29a-c pg.33) (Barboni and Bremond, 2009)
A.2 Bilobate Long/short shank	Bilobate 12	Bi-12	Similar to Bambusoideae, Oreobambos buchwaldii, Bambusoideae, Olyra latifolia (Fig.1 18a,18b pg.33) (Barboni and Bremond, 2009); Similar to Ehrhartoideae, Oryza longistaminata (Fig.7 6,7,8 pg. 13) (Leaf), Ehrhartoideae, Oryza barthii (Fig.7 9 pg.13) (Leaf) (Mercader et al., 2010); Similar to Bambusoideae, Chusquea pittieri (Fig.50 pg.34, Fig.72 pg. 39) (Piperno and Pearsall, 1988); Bambusoideae, Leersia oryzoides, Ehrhartoideae, Zizaniopsis miliacea, Panicoideae, Anthaenantia rufa (Fig.2 D-1 pg. 79), Ehrhartoideae, Zizania caduciflora, Panicoideae, Microstegium vimineum var. imberbe, Chloridoideae, Leptochloa chinensis (Fig.2 D-2 pg. 79), Ehrhartoideae, Zizania caduciflora (Fig.4 11 pg. 82), Panicoideae, Themeda triandra var. japonica (Fig.4 12 pg. 82) (Lu and Liu, 2003)
A.3 Bilobate long shank	Bilobate 13	Bi-13	 Panicoideae, Anthephora elongata (Fig.1 6b,9b pg. 33), Panicoideae, Zonotriche inamoena (Fig.3 6a,9a pg. 33) (Barboni and Bremond, 2009); Panicoideae, Hyparrhenia spp. (Culm/Leaf/Inflorescence) (Fig.3 10 pg. 1961) (Mercader et al., 2010); Panicoideae, Sorghum aethiopicum (Fig.6 6 pg. 12), Panicoideae, Hyparrhenia involucrata (Fig.6 11,12 pg. 12), Panicoideae, Schizachyrium exile (Fig.6 13 pg. 12) (Neumann et al., 2017); Panicoideae, Digitaria horizontalis (Leaf) (Fig.2 2 pg. 15), Panicoideae, Cenchrus biflorus (Leaf), Panicoideae, Brachiaria stigmatisata (Leaf) (Fig.2 1,11,12 pg. 15) (Fahmy, 2008); Chloridoideae, Ctenium elegans (Plate I. Bi-3 pg. 49) (Novello et al., 2012)
	Bilobate 14	Bi-14	Panicoideae, <i>Pennisetum polystachion</i> (Culm/Leaf/Inflorescence) (Fig.4 10 pg. 1961) (Culm/Leaf/Inflorescence) (Mercader et al., 2010); Similar to Chloridoideae, <i>Enneapogon cenchroides</i> (Fig.1 5,11 pg. 33) (Barboni and Bremond, 2009); Panicoideae, <i>Andropogon leucbostachya</i> (Fig.5 pg. 23) (Piperno and Pearsall, 1998); Panicoideae, <i>Schizachyrium brevifolium</i> (Fig.4 16 pg. 82) (Lu and Liu, 2003)
	Bilobate 15	Bi-15	 Panicoideae, <i>Ischaemum spp.</i>, Panicoideae, <i>Hyparrhenia hirta</i> (Culm/Leaf/Inflorescence) (Fig.2 21,22 pg. 1959) (Mercader et al., 2010); Panicoideae, <i>Digitaria delicatula</i> (Culm/Leaf/Inflorescence) (Fig.2 14 pg. 15) (Fahmy, 2008); Panicoideae, <i>Themeda gigantea var. caudate</i>, Panicoideae, <i>Dimeria ornithopoda</i>, Chloridoideae, <i>Eragrostis japonica</i> (Fig.4 17,22,23 pg. 82) (Lu and Liu, 2003)
	Bilobate 16	Bi-16	Panicoideae, Pennisetum polystachyon, Panicoideae, Setaria pumila, Panicoideae, Hyparrhenia involucrata (Fig.6 7,8,11 pg. 12) (Neumann et al., 2017); Panicoideae, Digitaria delicata (Fig.2 15,16 pg. 15) (Fahmy, 2008); Panicoideae, Setaria glauca, Aristidoideae, Aristida desmantha, Panicoideae, Pennisetum alopecuroides, P. purpureum, Panicoideae, Panicum notatum (Fig.2 B-3 pg. 79) (Lu and Liu, 2003)
	Bilobate 17	Bi-17	 Panicoideae, Aristidoideae, Aristida spp. (Fig.2 14 pg. 1959), Panicoideae, Aristidoideae, Ischaemum spp. (Culm/Leaf/Inflorescence) (Fig.4 6 pg. 1961) (Mercader et al., 2010); Panicoideae, Cenchrus biflorus (Fig.2 1 pg. 15) (Leaf) (Fahmy, 2008); Panicoideae, Andropogon fastigiatus, Panicoideae, Loudetia togoensis (Fig.6 4 pg. 12) (Neumann et al., 2017); Panicoideae, Aristidoideae, Aristidoideae, Aristidoideae, Schizachyrium brevifolium, Chloridoideae, Eragrostis japonica, Chloridoideae, Eragrostis ferruginea (Fig.2 C-4 pg. 79) (Lu and Liu, 2003)
	Bilobate 18	Bi-18	 Panicoideae, Aristidoideae, Aristida orizaliensis (Fig.8 pg. 23) (Piperno and Pearsall, 1998); Similar to Panicoideae, Arundinella setosa, Panicoideae, Schizachyrium brevifolium, Panicoideae, Digitaria sanguinalis (Fig.2 B4 pg. 79), Panicoideae, Pennisetum purpureum (Fig.4 15 pg. 82) (Lu et al., 2003); Similar to Panicoideae, Aristidoideae, Aristidoidea

			Panicoideae, Pennisetum purpureum (Fig. 1 29a pg. 33) (Barboni and Bremond et al., 2009); Panicoideae, Arundinella setosa, Panicoideae,
A 4 D'1 1	D'1 1 40	D: 10	Schrzachyrum breujolium, Panicoideae, Digitaria sangunaus (Fig.2 B-4 pg.9), Pennsetum purpureum (Fig.4 15 pg. 82) (Lu and Lu, 2003)
A.4 Bilobates	Bilobate 19	B1-19	Panicoideae, Anaropogon gayanus (Fig. 6 9 pg. 12) (Neumann et al., 2017); Oryzoideae, Phyliorbachis sagittata, Pooideae, Arra caryophylica,
(other)			Pooldeae, Stipa aregeana, Panicoideae, Arunaneua nepalensis, Panicoideae, Crytococum multinode (Fig.1 504,505,506,500,509, pg. 5.5) (Barboni
			and Bremond, 2009); Bambusoideae, Macurolym reda (rig. 11 pg. 26) (Piperno and Pearsail, 1988); Pooldeae, Sipa carazu (Fig. 1 A-b,E-
			p,L-b,M-b pg. 86/), Poolacae, Stpa tenus (Fig.1 E-c,M-c,L-d pg. 86/), Poolacae, Stipa gynetrioides (Fig.1 A-e,L-e,M-e pg. 86/), $P_{\rm el}$
			Pooldae, <i>Stipa tenussima</i> (Fig.1 L-f,M-r pg. 867) (Gallero and Distel, 2004); Panicoideae, <i>Digitaria lecarai</i> (Fig.2 19 pg. 15) (Fanmy, 2008);
	D'1 1	D: 20	Pooldcae, Stipa capensis (Fig. / [8-B] pg. 128) (Cordova, 2013)
	Bilobate 20	B1-20	Panicoideae, Brachana xantholeuca, B. defexal (Fig.2 20-21 pg. 15) (Fahmy, 2008); Ehrhartoideae, Oryza punctata, Chloridoideae, Sporobolus
			africanus (Fig.1 2a,2b pg. 33) (Barboni and Bremond, 2009); Panicoideae, Bracharia Iata, Panicoideae, Sorghum aethiopicum (Fig.6 25,26 pg.
			12) (Neumann et al., 2017); Similar to Panicoideae, Melinis ambigua (Fig.3 14 pg. 1960) (Culm/Leat/Inflorescence) (Mercader et al.,
			2010); Anstidoideae, Aristida subulata, Panicoideae, Bothriochloa edwardsiana (Fig.2 Ai,Bi,Bj pg. 868) (Gallero and Distel, 2004);
			Panicoideae, Capillipedium assimile, Panicoideae, Panicum verrucosum (Fig.2 F-a pg. 79) (Lu and Liu, 2003).
B. Polylobates	Polylobate 1	Poly-1	Panicoideae, Brachiaria orthostachys, B. deflexa, Panicoideae, Pennisetum unisetum (Fig.2 26,28,29 pg. 15) (Fahmy, 2008); Panicoideae,
			Brachiaria lata, Panicoideae, Pennisetum pedicellatum (Leaf) (Fig.6 27,28 pg. 12) (Neumann et al., 2017); Arundinoideae, Crinipes abyssinicus,
			Panicoideae, Acritochaete volkensii (Fig.1 32b, 34a pg. 33) (Barboni and Bremond, 2009); Panicoideae, Melinis spp.
			(Culm/Leaf/Inflorescence) (Fig.3 21 pg. 1960) (Mercader et al., 2010); Panicoideae, Panicum fasciculatum (Fig.6 pg. 23) (Piperno and
			Pearsall, 1988); Panicoideae, Eulalia speciosa, Panicoideae, Rottboellia exaltata, Panicoideae, Capillipedium assimile, Panicoideae, Panicum
			verrucosum, Panicoideae, Oplismenus undulatifolius (Fig.2 F-b pg. 79) Panicoideae, Paspalum orbiculare (Fig.4 26 pg. 82) (Lu and Liu, 2003);
			Pooideae, Stipa clarazii, Pooideae, Piptochaetium napostaense, Pooideae, Stipa brachychaeta (Fig.2 F-b,F-c,E-h pg. 868) (Gallero and Distel,
			2004)
	Polylobate 2	Poly-2	Panicoideae, Brachiaria xantholeuca (Leaf) (Fig.2 27 pg. 15) (Fahmy, 2008); Panicoideae, Pennisetum polystachion (Fig.3 27 pg. 1960)
			(Mercader et al., 2010); Arundinoideae, <i>Elytrophoms globularis</i> (Culm/Leaf/Inflorescence) (Fig.1 35 pg. 33) (Mercader et al., 2010);
			Panicoideae, Pennisetum pedicellatum (Fig.6 28 pg. 12) (Neumann et al., 2017); Similar to Panicoideae, Sacciolepis myosuroides (Fig.4 25 pg. 82)
			(Lu and Liu, 2003)
C. Crosses	Cross 1	Cr-1	Chloridoideae, Apochiton burtii, Panicoideae, Setaria plicatilis, Panicoideae, Stenotaphrum dimidiatum (Fig.1 31a,31c,31d pg. 33) (Barboni and
			Bremond, 2009); Panicoideae, Hyparrhenia involucrata (Fig.6 15 pg. 12) (Neumann et al., 2017)
	Cross 2	Cr-2	Panicoideae, Melinis nerviglumis (Franch.) Zizka., Panicoideae, Coelorachis spp. (Culm/Leaf/Inflorescence) (Fig. 2 25, 26 pg. 1959) (Mercader
			et al., 2010); Panicoideae, Andropogon gayanus (Fig.6 17 pg. 12) (Neumann et al., 2017); Chloridoideae, Eragrostis macilenta, Bambusoideae,
			Olyra latifolia (Fig.1 31a,31c,31d pg. 33) (Barboni and Bremond, 2009); Panicoideae, Cenchrus biflorus (Leaf) (Fig.2 24 pg. 15) (Fahmy,
			2008); Panicoideae, Coix lacryma-jobi, Panicoideae, Zea mays, Panicoideae, Paspalum orbiculare, P. dilatatum, Panicoideae, Echinochloa crusgalli,
			Panicoideae, Brachiaria ramosa, Panicoideae, Themeda triandra var. japonica, Panicoideae, Panicum dichotomiforom, Panicoideae, Arundinella hirta,
			Panicoideae, Cyrtococcum patens, Panicoideae, Oplismenus compositus, Panicoideae, Bothriochloa ischaemum, Panicoideae, Echinochloa crusgalli va r.
			mitis, Saccharum sinensis, Panicoideae, Sorghum vulgare (Fig.2 E-1 pg. 79), Ehrhartoideae, Zizania caduciflora, Panicoideae, Zea mays,
			Panicoideae, Coix laryma-jobi (Fig.4 5-7,113 pg. 82) (Lu and Liu, 2003); Panicoideae, Zea may (Fig.16 pg 25) (Piperno and Pearsall, 1998);
			Chloridoideae, Pappophorum subbulbosum, Panicoideae, Bothriochloa edwardsiana (Fig.1 J-I,J-i,K-j pg. 867) (Gallero and Distel, 2004)
	Cross 3	Cr-3	Panicoideae, Sorghum arundinaceum (Fig.6 16 pg. 12) (Neumann et al., 2017); Panicoideae, Brachiaria eruciformis (Leaf) (Fig.2 25 pg. 15)
			(Fahmy, 2008); Panicoideae, Urochloa spp. (Culm/Leaf/Inflorescence) (Fig.2 23 pg. 1959) (Mercader et al., 2010)
	Cross 4	Cr-4	Panicoideae, Sorghum arundinaceum, Panicoideae, Brachiaria jubata, Panicoideae, Vossia cuspidata (Fig.6 18,19,21 pg. 12) (Neumann et al.,
			2017); Panicoideae, Zea mays (Fig.4 7 pg. 82) (Lu and Liu, 2003)

	Cross 5	Cr-5	Bambusoideae, Leersia oryzoides (Leaf), Ehrhartoideae, Zizania palustris var. palustris (Leaf) (Fig.8 H pg. 1983, Fig.14 R pg. 1987) (Yost and
			Blinnikov, 2011); Bambusoideae, Arberella dressleri (Fig.17 pg. 26) (Piperno and Pearsall, 1998)
D. Trapezoid	Trapezoid 1	Tra-1	Panicoideae, Dichanthium spp. (Appendix 2); Pooideae, Poa ligularis, Pooideae, Stipa clarazii, S. tenuis (Fig.1 Ga,Gb,Gd pg. 867) (Gallero
			and Distel, 2004); Pharoideae, Pharus spp. (Fig. 36 pg. 30) (Piperno and Pearsall, 1998)
	Trapezoid 2	Tra-2	Pooideae, Stipa brachychaeta, (Fig.1 Gh pg. 867) (Gallero and Distel, 2004)
E. Tabular	Trapeziform 1	Tram-1	Pooideae, Colpodium chionogeiton, Pooideae, Vulpia bromoides (Fig.1 17a,17b pg.33) (Barboni and Bremond, 2009); Pooideae, Agrostis
Trapeziform			lachnantha (Fig.7 f [Type 4-K] pg. 128) (Cordova, 2013); Pooideae, Glyæria grandis (Fig.4 H pg. 1981) (Yost and Blinnikov, 2011);
			Pooideae, Piptochaetium napostaense (Fig.2 Gc pg. 868) (Gallero and Distel, 2004)
	Trapeziform 2	Tram-2	Pooideae, Lolium temulentum, Pooideae, Helictotrichon elongatum (Fig.1 16a,16b pg.33) (Barboni and Bremond, 2009); Pooideae, Melica
			decumbens, Pooideae, Koeleria capensis, Pooideae, Agrostis lachnantha (Fig.7 d [Type 4-I],e [Type 4-H],g [Type 5-A] pg. 128) (Cordova, 2013);
			Pooideae, Triticum aestinum (Fig.23 pg. 27) (Piperno and Pearsall, 1998); Pooideae, Phalaris arundinacea (Fig.3 L-K pg. 1981), Pooideae, Poa
			palustris, (Fig.5 D pg. 1982) (Yost and Blinnikov, 2011); Pooideae, Stipa tenuissima, Stipa ambigua, Pooidae, Piptochaetium napostaense,
			Pooideae, Stipa tenuis, (Fig.2 Hf,Hg,Ic,Id pg. 868) (Gallero and Distel, 2004)
F. Saddles	Saddle 1	Sad-1	Oryzoideae, Humbertochloa greenwayi (Fig.1 39 pg. 33) (Barboni and Bremond, 2009); Chloridoideae, Eragrostis spp, Chloridoideae,
			Cynodonteae, Cynodon spp. (Culm/Leaf/Inflorescence) (Fig.2 5-7 pg. 1959) (Mercader et al., 2010); Chloridoideae, Schoenefeldia gracilis
			(Fig.6 31 pg.12) (Neumann et al., 2017); Aristidoideae, Aristida diffusa (Fig.7 n [Type 9-A] pg. 128) (Cordova, 2013); Chloridoideae,
			Muhlenbergia glomerata (Fig.6 D pg. 1982) (Yost and Blinnikov, 2011); Aristidoideae, Aristida subulata (Fig.1 H-I pg. 867) (Gallero and
			Distel, 2004); Chloridoideae, Muhlenbergii emersleyi (Fig.19 pg. 26) (Piperno and Pearsall, 1998)
	Saddle 2	Sad-2	Chloridoideae, Eragrostis macilenta (Fig.1 41 pg. 32) (Barboni and Bremond, 2009); Chloridoideae, Eragrostis racemosa (Fig.4 5 pg. 1961);
			Chloridoideae, Tragus racemosus (Fig.6 29 pg. 12) (Neumann et al., 2017); Chloridoideae, Chloris eiliara, Chloridoideae, Dactyluctenium
			aegpticum (Fig.18,20 pg. 26) (Piperno and Pearsall, 1998)
	Saddle 3	Sad-3	Chloridoideae, Eragrostiella bifaria, Chloridoideae, Rendlia altera (Fig.1 40a,40b pg.33) (Barboni and Bremond, 2009); Chloridoideae,
			Tetrapogon cenchriformis (Fig.6 32 pg. 12) (Neumann et al. 2017); Bambusoideae, Arundinaria alpine, Chloridoideae, Brachyachne spp.
			(Culm/Leaf/Inflorescence) (Fig.3 3,29 pg. 1960), Bambusoideae, Oxytenanthera abyssinica (Leaf) (Fig.4 17 pg. 1961) (Mercader et al.,
			2010); Bambusoideae, Guadua amplexifolia (Fig.21 pg.27), Micrairoideae, Isachne arundinaceae (Fig.73 pg. 40) (Piperno and Pearsall, 1998);
			Bambusoideae, Yushania alpina (formerly Arundinaria alpina) "Very tall saddles" with width is $\geq 15 \mu$ m, are
			assumed to be diagnostic of Bambusoideae grasses (Fig. S1a) (Yost et al., 2018).
	Saddle 4	Sad-4	Pooideae, Stipa dregeana (Fig.1 37b pg.33) (Barboni and Bremond, 2009); Chloridoideae, Sporobolus festivus (Fig.6 34 pg. 12) (Neumann et
			al. 2017); Arundinoideae, Phragmites mauritianus (Fig.24 pg. 27, Fig.25 pg. 28), Aristidoideae, Aristida recurrafa (Fig.53 pg. 35),
			Arundinoideae, Phragmites australis (Fig.60 pg. 36) (Piperno and Pearsall, 1998); Arundinoideae, Phragmites spp. (Yost et al., 2018);
			Chloridoideae, Pappophorum subbulbosum (Fig.1 I-l pg. 867) (Gallero and Distel, 2004).
	Saddle 5	Sad-5	Chloridoideae, Tetrapogon cenchriformis (Fig.6 33 pg. 12) (Neumann et al., 2017); Bambusoideae, Oxytenanthera abyssinica (Leaf) (Fig.4 17 pg.
			1961) (Mercader et al., 2010); Bambusoideae, Guadua amplexifolia (Fig.22 pg.27), Bambusoideae, Chusquea grandiflora (Fig.26,27 pg. 28,
			Fig.30 pg. 29) (Piperno and Pearsall, 1998)
G. Rondels	Rondel 1	Ron-1	Bambusoideae, Neurolepis pittiera (Fig.35 pg. 30) (Piperno and Pearsall, 1998); Pooideae, Stipa gynerioides, Stipa tenuissima (Fig.1 Be,Bf,Ce
			pg. 867) (Gallero and Distel, 2004)
	Rondel 2	Ron-2	Chloridoideae, Brachyachne spp., Chloridoideae, Sporobolus consimilis, Panicoideae, Pennisetum purpureum (Culm/Leaf/Inflorescence) (Fig.2
			17-19 pg. 1959), Bambusoideae, Oxytenanthera abyssinica, Panicoideae, Panicum spp. (Culm/Leaf/Inflorescence) (Fig.5 17-19 pg. 1962)
			(Mercader et al., 2010); Panicoideae, Gynerium saggitatum (Fig.74 pg. 40) (Piperno and Pearsall, 1998)
	Rondel 3	Ron-3	Similar to Panicoideae, Tripsacum lanceolatum (Fig.70 pg. 39) (Piperno and Pearsall, 1998)

	Rondel 4	Ron-4	Similar to Ehrhartoideae, Zizania palustris (Fig.12 F pg. 1985) (Yost and Blinnikov, 2011)
	Rondel 5	Ron-5	Chloridoideae, Eragrostis superba, Chloridoideae, Eragrostis spp. (Culm/Leaf/Inflorescence) (Fig.2 11,13 pg. 1959), Chloridoideae,
			Eragrostis racemosa, Bambusoideae, Oreobambos buchwaldii (Culm/Leaf/Inflorescence) (Fig.5 13,15 pg. 1962) (Mercader et al., 2010);
			Panicoideae, Arundinella nepalensis, Chloridoideae, Sporobolus africanus (Fig.1 3a, 3b pg. 32) (Barboni and Bremond, 2009); Pooideae,
			Phalaris spp. (Yost et al., 2018)
	Rondel 6	Ron-6	Panicoideae, Phragmites australis (Culm/Leaf/Inflorescence) (Fig.3 8 pg. 1960) (Mercader et al., 2010)
	Rondel 7	Ron-7	
	Rondel 8	Ron-8	East African Pooideae (Fig.1 pg. 32) (Barboni and Bremond, 2009)
	Rondel 9	Ron-9	Bambusoideae, Macharolyra feera, Bambusoideae, Pariana campestris (Fig.40, pg. 31; Fig.41 pg. 32) (Pearsall and Piperno, 1998).
			Bambusoideae, Arundinaria alpina (This study). Pharoideae, Leptaspis cochleata Nees exSteud (Fig.2 27 pg. 1959) (Mercader et al., 2010)
H. Bulliform	Cuneiform	Bull-1	Present in all subfamilies of Poaceae (Beal, 1886; Metcalfe, 1960)
	bulliform indiff.		

Class/Subclass	Morphotype	Figure code	Previous names and similar forms
A.1 Bilobate short shank	Bilobate 1	Bi-1	"Bilobate phytoliths with flattened outer margins" (Fahmy, 2008 [Fig.2 3,4 pg. 15]); "Dumbbell ends straight" (Palmer and Tucker, 1981). "Dumbbell, short shank, straight or concave ends" (Twiss et al., 1969 [Fig.2 3f pg. 111])
	Bilobate 2	Bi-2	"Dumbell, short shank" (Twiss et al., 1969 [Fig.2 3-d pg.111]); "Pancoid dumbell" (Mulholland, 1989 [Fig.1 d pg. 104]); "Dumbbell ends concave" (Palmer and Tucker, 1981). Some form with constricted shanks appear similar to "stipa type" bilobates (Bilobate morphotype 19)
	Bilobate 3	Bi-3	
	Bilobate 4	Bi-4	"Dumbbell, short shank, straight or concave ends" (Twiss et al., 1969 [Fig.2 3f pg. 111]); "Pancoid dumbell" (Mulholland, 1989 [Fig.1 c pg. 104])
	Bilobate 5	Bi-5	<u> </u>
	Bilobate 6	Bi-6	"Dumbbell, short shank, straight or concave ends" (Twiss et al., 1969 (Fig.2 3f pg. 111]); "Pancoid dumbell" (Mulholland, 1989 [Fig.1 c pg. 104])
	Bilobate 7	Bi-7	"Constriction between the lobes, top mirror-image" (Neumann et al., 2017 [Fig.6 10 pg. 12]). Could be confused with some "Stipa Types" (especially those in Barboni and Bremond 2009). Also, may be confused with medium saddle (see Barboni et al., 2007) Similar to "recatagular types" (Twiss et al., 1969 (Fig.2 Gd pg. 111]) "rectangle" (Barboni et al., 1999 [Plate.I 17 pg. 92]). more rectangular forms could be confused with trapezoids (Class D)
	Bilobate 8	Bi-8	—
	Bilobate 9	Bi-9	Similar to some "stipa type" bilobates (type 19)
	Bilobate 10	Bi-10	Shorter form could be confused with 3-lobed crosses (e.g. Ball et al., 2015 [Fig.1 Var1-1 pg. 4]). Sometimes called "simple lobates"
	Bilobate 11	Bi-11	—
A.2 Bilobate Long/short shank	Bilobate 12	Bi-12	Reported only in <i>Maltebrunia leersioides</i> (Palmer and Tucker, 1981, p.53), Ehrhartoideae, C ₃ , shade species. Assumed to be characteristic for Ehrhartoideae (Piperno, 2006), this type, however, is not observable in other African species of Ehrhartoideae (Palmer and Tucker, 1981). Barboni and Bremond, 2009 note also quite similar to crosses but slightly less elongate
A.3 Bilobate long shank	Bilobate 13	Bi-13	—
	Bilobate 14	Bi-14	—
	Bilobate 15	Bi-15	—
	Bilobate 16	Bi-16	"Dumbbell, long shank" (Twiss et al., 1969 [Fig.2 3c pg. 111])
	Bilobate 17	Bi-17	—
	Bilobate 18	Bi-18	—
A.4 Bilobates (other)	Bilobate 19	Bi-19	"Figure-eight" (Plamer and Tucker, 1981)
	Bilobate 20	Bi-20	"Crenate-vertical" (Plamer and Tucker, 1981); "Dumb-bell, nodular shank" (Gallero and Distel, 2004 [Fig.2 A-B pg. 868), (Twiss et al., 1969 [Fig.2 3g pg. 111])
B. Polylobates	Polylobate 1	Polv-1	"Complex dumbbell" (Gallero and Distel. 2004)
	Polylobate 2	Poly-2	
C. Crosses	Cross 1	Cr-1	"Oblong" (Twiss et al., 1969 [Fig.2 Ig pg. 111]); "Crossbody Short Cell" (Ball, 2002)
	Cross 2	Cr-2	"Crossbody Short Cell" (Ball, 2002); "Pancoid cross" (Twiss et al., 1969)
	Cross 3	Cr-3	"Rectangulars" (Piperno, 2006 [Fig.3.1 Var.6 pg. 200]); "Quadralobate/thin shank" (Fahmy, 2008 [Fig.2 25 pg. 15)

	Cross 4	Cr-4	"Sloping Trapezoids" (Piperno, 2006 [Fig.3.1 Var.5 pg. 200])
	Cross 5	Cr-5	"Nodules/Blocky Bambusoideae" and "Scooped/Concave Bambusoideae/Ehrhartoideae/Pooideae" (Piperno, 2006 [Fig.3.1 Var.3/8/10 and other
			variants pg. 200])
D. Trapezoid	Trapezoid 1	Tra-1	"Square" (Barboni et al., 1999 [Plate.I 17 pg. 92]); "Rectangular" (Gallero and Distel, 2004 [Fig.1 Ga,Gb,Gd])
	Trapezoid 2	Tra-2	"Trapeziform ridged top or keeled" (Ball, 2002)
E. Tabular Trapeziform	Trapeziform 1	Tram-1	"Oblong, sinuous" (Twiss et al., 1969 [Fig.2 Ih pg. 111]); "Polylobate trapeziform" (Novello et al., 2015), "Irregular, complex dumb-bell, convex end" and "Regular, complex dumbbell, straight end" (Gallero and Distel, 2004 [Fig.2 G pg. 868). "Trapezoid crenate" (Mercader et al., 2010 [Fig.2 33 pg. 1959]). Similar to Chloridoideae, <i>Bansia biflora</i> (Culm/Leaf/Inflorescence) (Fig.2 33 pg. 1959) (Mercader et al., 2010); Similar to elongate (>3 lobes) polylobates, ampliate basal lobes (Fig.13 K-M pg. 1986) (Yost and Blinnikov, 2011); "Elongated-sinuous" (Palmer and Tucker, 1981, 1983; Palmer et al., 1985; Palmer and Gerbeth-Jones, 1986); Similar to "Polylobate, ends truncated/concave, wide+short shank" (Fig.1 34c pg.33) (Barboni and Bremond, 2009)
	Trapeziform 2	Tram-2	"Oblong, sinuous" (Twiss et al., 1969 [Fig.2 Ih pg. 111]); "Elongated-smooth" (Palmer and Tucker, 1981, 1983; Palmer et al., 1985; Palmer and Gerbeth-Jones, 1986); "Oblong, sinuous" (Twiss et al., 1969 [Fig.2 Ih pg. 111])
F. Saddles	Saddle 1	Sad-1	"Saddle Short Cell" (Ball, 2002)
	Saddle 2	Sad-2	"Chloridoid Class" (Twiss et al., 1969 [Fig.2a pg. 111])
	Saddle 3	Sad-3	"Thin Chloridoid" (Twiss et al., 1969 [Fig.2b pg. 111]); "Oblong concave saddle" (An, 2016 [Fig. 3 i pg. 5]); 'long saddle' (Lu and Liu, 2003 and Mercader et al., 2010). 'collapsed saddle' (Barboni and Bremond, 2009)
	Saddle 4	Sad-4	"Saddle-rondel" (Strömberg, 2003); "Rondel base outline irregular" (Barboni and Bremond, 2009 [Fig.1 37b pg. 33). Often undisguisable from long saddle (Saddle 3) and "tall saddles", "very tall saddles" and "collapsed saddles" (Saddle 5) in top, oblique view.
	Saddle 5	Sad-5	"oblong concave saddle" (Xiaohong et al., 2015 [Fig. 3 i pg. 5]); short saddles" (Kondo et al., 1994; Lu et al., 2006)
G. Rondels	Rondel 1	Ron-1	"A small, wide, tent-shaped body" (Piperno and Pearsall, 1998 [Fig.35 pg. 30]) "Hat" and "Biconvex" (Gallero and Distel, 2004 [Fig.1 B,C pg. 867])
	Rondel 2	Ron-2	"Tower-horned" (Mercader et al., 2010). Also, included in this category are "Conical, tall body with tapering/flat apex; its base is at least three times wider than the apex" from (Mercader et al., 2010) as their tops are also horned.
	Rondel 3	Ron-3	"Pooid type rondel" (Twiss et al., 1969: Barboni et al., 1999 [Plate I 9-17 pg.92])
	Rondel 4	Ron-4	"Pooid type rondel" (Twiss et al., 1969: Barboni et al., 1999 [Plate I 9-17 pg.92])
	Rondel 5	Ron-5	"Pooid type rondel" (Twiss et al., 1969: Barboni et al., 1999 [Plate I 9-17 pg.92])
	Rondel 6	Ron-6	"Pooid type rondel" (Twiss et al., 1969: Barboni et al., 1999 [Plate I 9-17 pg.92])
	Rondel 7	Ron-7	"Pooid type rondel" (Twiss et al., 1969: Barboni et al., 1999 [Plate I 9-17 pg.92])
	Rondel 8	Ron-8	"Pooid type rondel" (Twiss et al., 1969: Barboni et al., 1999 [Plate I 9-17 pg.92])
	Rondel 9	Ron-9	"Pooid type rondel" "one sinuous and one sloping edge" and "irregular, complex short-cell" (Pearsall and Piperno, 1998). Similar to "rondel acutely angled on bottom/top view or Cross angular lobes" Micrairoideae, <i>Coelachne africana</i> (Barboni and Bremond, 2009 [Fig.1 1 pg. 32]).
H. Bulliform	Cuneiform bulliform indiff.	Bull-1	Similar to parallelepipedal/cubic blocky phytolith found in woody dicots (e.g. Mercader et al., 2009; Collura and Neumann, 2017; Novello et al., 2017a; This study) as well as blocky types from Cyperaceae (e.g. Carex aethiopica [Novello et al., 2012])

Appendix 4 - Table 4.6 Previous names use to describe each morphotype from Poaceae in early studies, as well as similar forms that may be confused with these phytoliths.



Appendix 4 - Figure 4.1 Histograms for each morphotype in the modern phytolith reference collection. Histograms indicate that the data appears to be non-normally- and in some cases bi-modally distributed



Appendix 4 - Figure 4.2 QQ (probability) plot showing the results of Mardia's Multivariate Normality Test for the modern phytolith reference collection. the non-linearity of points suggests that the data is non-normally distributed.

Appendix 4 - Table 4.8 Distribution and abundance of morphotype Abundance is measures on the following the Production Index: NP = 0 for CA used in Ca analysis is also show. Water- and light requirements commonly occurs is also provided. O=Open, S= Shaded.	es fi , T = of	:om = 1, eacl	m C n sp	ode = 2 peci	ern 2, A ies a	bo = (and	otani 3. P 1 th	ical lan e v	sar t fai eget	npl mily tatic	es in v ad on z	n th phy one	e N toli in	Jaku th n whie	ıru- norj ch t	Nai pho the s	vasl type spec	ha I es co cies	Basir odin mos	n. g st		n (Fricolmes/Aciular hair cell)				tate-dendritic	0
	Blocky/Tabular Blocky facetatee	Blocky corniculate	B/T deconted B/T cremate.echinate.sinuate	B/T radiating laminate	Blocky scutiform	Blocky tuberculate Tabular 'rideed'	B/T cavate	Globular psilate	Globular psiate large Globular granulate	Globular tuberculate	Globuale papillate	Globular to subglobular facetate Globulose favouse	Globular echinate (Arecaceae type)	Globular echinate Globular foukled	Globular decorated compound	Obovate psilate Obovate scorbiculate/granulate	Cylindroid	Cylindrod geniculate Cylindroid bulbous	A stero schlerid	Elongate faceted phytoliths	Cylindric sulcate tracheid	A cicular and Fusiform /Ellipsoid /scuitforn Lanceolate	Elongate scalariform platelet	Epidermal polygonal/parallelogram	Hair cell base/prickle/trichome/stomata Elongate psilate	Tabaular thin echinate-simuate-crenate-face	Elongate decorated platelet (conical abraxia

	Family-Species		Water	Light	Altitude /vegetatio																											
Family	coding for CA	Species	requirements	requirements	n zone	<u>6</u> ,	ų	P.	г C			CIV		7	ac	P.	, st	.a .	÷	.0 .	4	60				<u>م</u> ۲	(*	<u>c</u>	ę.			<u>c</u> .
				1		BT_	l 2	BL	2 2	B_s	8 8	1 8	5	5	ซี ซี	١J	ວ່ວິ	3	3 8	30	5 5	ີ່ປ	, ů	ປີ <	J	E S	2.	а ш ¹ с	a 2	ны	ιų.	a'
Acanthaceae	Ac	Thunbergia alata	Mesophyte	O/S	2000-2500 m (B)	ТТ	NP	NP N	JP T	NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP T	NP	NP N	P NP 1	NP T	NP N	P NP N	P NP	ТТ	TN	vР
Amaranthaceae	Am	Achyranthes aspera	Mesophyte	S	1500-2000 m (S)	ТТ	NP	Т	T NI	P NP	NP ′	T NF	РΤ	TN	NP NI	РТІ	NP NF	P T P	NP NP	NP N	P NP	ΤΊ	NP	NP N	P NP	T NP	NP N	P NP N	P NP	T N	P NP N	vР
Apocynaceae	-	Acokanthera oppositifolia	Mesophyte	S	2000-2500 m (B)	NP N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP N	P NP N	JP.
Apocynaceae, Asclepiadoideae	Ap1	Gomphacurpus fruticosus	Mesophyte	O/S	2000-2500 m (B)	ТТ	NP	NP '	T NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP 1	NP	NP N	P NP 1	NP NP	NP N	P NP N	РТ	NP T	TN	JP.
Apocynaceae	Ap2	Leptadenia hastata	Semi-xerophyte	0	1500-2000 m (S)	ТТ	NP	NP '	T NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP T	NP 1	NP NP	NP N	P NP	ΤN	P NP	NP N	P NP 1	NP NP	ΤN	P NP N	P NP	NP N	P NP N	1P
Apocynaceae, Asclepiadoideae	Ap3	Sareostemma viminale	Semi-xerophyte	O/S	2500-3000 m (A)	ТТ	Т	NP N	JP NI	P NP	NP '	T NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP 1	NP	NP N	P NP	T NP	NP N	P NP N	РТ	NP T	NP N	JP.
Araliaceae	Ar	Cussonia arborea	Mesophyte	O/S	1500-2000 m (S)	ТТ	NP	ΤN	JP NI	P NP	NP '	T NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP 1	Т	NP N	P NP	T NP	NP N	P NP N	P NP	NP N	P NP N	1P
Arecaceae	Arc1	Hyphaene compressa	Mesophyte	0	1500-2000 m (S)	T N	P NP	ΤN	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP	A NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	T N	P NP N	JP.
Asteraceae	As1	Aspilia mossambicensis	Mesophyte	O/S	2000-2500 m (B)	СТ	NP	Т	T NI	P NP	NP '	T NF	РТ	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	ТТ	NP	NP N	P NP	T NP	NP N	PTN	P NP	СТ	NP N	1P
Asteraceae	As2	Coryza sumetrensis	Mesophyte	S	2000-2500 m (B)	NP N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP T	NP N	1P
Asteraceae	As3	Felicia muricata	Mesophyte	O/S	2000-2500 m (B)	СТ	Т	Т	T NI	РТ	NP '	T NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP 1	NP	NP N	P NP	T NP	ΤN	P NP N	РТ	NP T	NP N	1P
Asteraceae	As4	Microglossa pyrifolia	Mesophyte	S/O	2500-3000 m (A)	C N	P NP	Т	T NI	РТ	NP '	т т	Т	TN	NP NI	P NP 1	NP NF	P NP 1	NP NP	TN	P NP	NP 1	NP	NP N	P NP	T NP	ΤN	P NP N	P C	ТТ	TN	1P
Asteraceae	As5	Pluchea indica	Helophyte	O/S	2000-2500 m (B)	NP T	NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP T	NP N	1P
Asteraceae, Compositae	As6	Psiadia punctulata	Semi-xerophyte	S/O	2000-2500 m (B)	ТТ	Т	Т	T NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP 1	NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP N	РТМ	ΔP
Asteraceae	As7	Tarchonanthus camphartus	Semi-xerophyte	0	2000-2500 m (B)	ТТ	NP	Т	T NI	P NP	NP N	JP NF	РΤ	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	TN	P NP	NP T	NP	NP N	P NP I	NP NP	NP N	PTN	РТ	ТТ	NP N	1P
Asteraceae	As8	Vernonia auriculfera	Mesophyte	O/S	2000-2500 m (B)	ТТ	NP	Т	T NI	P NP	NP N	JP NF	РТ	NP N	NP NI	P NP 1	NP NF	P NP 1	NP T	ΤN	P NP	NP 1	NP	NP N	P NP 1	NP NP	NP N	P NP N	РТ	СТ	NP N	1P
Asteraceae	As9	Sphaeranthus suaveolens	Helophyte	0	2000-2500 m (B)	T N	P NP	ΤN	JP NI	P NP	NP N	JP NF	РΤ	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP T	Т	NP N	P NP I	NP T	NP N	P NP N	РТ	NP T	NP N	1P
Athynaceae	At1	Diplazium hylophilum	Mesophyte	S	2500-3000 m (A)	T N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP	T A	NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP (СТ	NP N	P NP N	ΔP_
Athynaceae	At2	Dryoathyrium boryanum	Mesophyte	O/S	1500-2000 m (A)	NP N	P NP	ΤN	JP NI	P NP	NP N	JP NF	P NP	NP N	NP C	NP 1	NP NF	P NP 1	VP T	NP N	P NP	NP N	РТ	NP N	P NP I	NP NP	NP N	РТО	СТ	C N	P NP N	1P
Boraginaceae	Bo1	Cordia africana	Mesophyte	O/S	2500-3000 m (A)	T N	P NP	ΤN	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP T	NP	NP N	P NP 1	NP T	NP N	P NP N	P C	СТ	NP N	1P
Boraginaceae	Bo2	Cordia monoica	Mesophyte	O/S	2000-2500 m (B)	T N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP C	NP N	1P
Canellaceae	Can	Warburgin ugundensis	Mesophyte	O/S	1500-2000 m (S)	ТТ	NP	Т	T NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	ТТ	Т	NP N	P NP I	NP NP	NP N	P NP N	P NP	NP N	P NP N	1P
Capparaceae	-	Boscia conacea	Mesophyte	0	2000-2500 m (B)	NP N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP N	P NP N	1P
Capparaceae	Cap1	Cadaba farinosa	Semi-xerophyte	0	1500-2000 m (S)	ТТ	NP	ΤN	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP T	Т	NP N	P NP I	NP NP	NP N	P NP N	P NP	NP N	P NP N	1P
Capparaceae	Cap2	Cadaba rotundifolia	Semi-xerophyte	0	1500-2000 m (S)	ТТ	NP	ΤN	JP NI	P NP	NP N	JP NF	PΤ	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	ΤN	P NP	NP N	P NP 1	NP T	NP N	P NP N	P NP	ТС	TN	1P
Capparaceae	Cap3	Maerua triphylla	Mesophyte	O/S	1500-2000 m (S)	ТТ	NP	Т	T NI	РТ	NP N	JP NF	РΤ	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP 1	NP	NP N	P NP I	NP NP	ΤN	P NP N	P NP	NP T	NP N	1P
Celastraceae, Hippocrateaceae	Cel	Maytenus hetrophylla	Mesophyte	0	2000-2500 m (B)	ТТ	NP	NP N	JP NI	P NP	NP N	JP NF	PΤ	NP N	NP NI	P NP 1	NP T	NP 1	NP NP	NP N	P NP	ΤΊ	NP	NP N	P NP 1	NP T	ТТ	.' NP N	P C	ТТ	NP N	νP.
Combretaceae	Co	Terminalia brownii	Mesophyte	O/S	1500-2000 m (S)	ТТ	NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP T	NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP C	C (C _
Compositae	-	Solanecio mannii	Mesophyte	S/O	1500-2000 m (S)	NP N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP I	NP NP	NP N	P NP N	P NP	NP N	P NP N	1P
Cupressaceae	Cu	Juniperus procera	Mesophyte	O/S	2500-3000 m (A)	ТТ	NP	NP '	T NI	P NP	NP '	T NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP T	NP	NP N	P NP	т т	NP N	P NP N	РТ	ТТ	NP N	1P
Ebenaceae	Eb	Eluclea divinorum	Semi-xerophyte	O/S	2000-2500 m (B)	ТТ	NP	ΤN	JP NI	P NP	NP N	JP NF	Р С	ΤN	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP T	NP	NP N	P NP 1	NP C	NP N	P NP N	РТ	NP N	P NP N	1P
Euphorbiaceae, Crotonoideae	Eu1	Croton megalocarpus	Mesophyte	O/S	1500-2000 m (S)	NP T	NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	РТ	NP N	P NP	NP N	P NP	T NP	NP N	P NP N	P NP	NP N	P NP N	1P
Euphorbiaceae	-	Euphorbia bussei	Mesophyte	O/S	1500-2000 m (S)	NP N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP N	P NP N	1P
Euphorbiaceae	-	Euphorbia candelabrum	Mesophyte	0	1500-2000 m (S)	NP N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP N	P NP N	1P
Euphorbiaceae	-	Neoboutonia macrocalyx	Mesophyte	S/O	2000-2500 m (B)	NP N	P NP	NP N	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP I	NP NP	NP N	P NP N	P NP	NP N	P NP N	1P
Euphorbiaceae, Acalyphoideae	Eu2	Ricinus communis	Mesophyte	O/S	2000-2500 m (B)	СТ	NP	ΤN	JP NI	P NP	ΤN	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	TN	P NP	NP T	Т	NP N	PTI	NP T	NP T	.' NP 7	f NP	ТТ	TN	1P
Fabaceae	F1	Crotalaria lebrunii	Mesophyte	S/O	2000-2500 m (B)	ТТ	NP	NP N	JP NI	P NP	NP '	T NF	P NP	ΤN	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP	T NP	NP N	P NP N	РТ	NP N	P NP N	1P
Fabaceae, Caesalpinioideae	F2	Cassia didymobotrya	Mesophyte	O/S	2500-3000 m (A)	ТТ	NP	ΤN	JP NI	P NP	NP '	T NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	TN	P NP	NP 1	NP	NP N	P NP	Т Т	ΤN	P NP ?	ΓТ	СТ	TN	JP.
Fabaceae	F3	Bauhinia tomentosa	Mesophyte	O/S	1500-2000 m (S)	ТТ	NP	ΤN	JP NI	P NP	NP N	JP NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP N	P NP	NP N	P NP 1	NP NP	NP N	P NP N	P NP	NP N	P NP N	JP .
Fabaceae	F4	Crotalaria agatifolia	Mesophyte	O/S	1500-2000 m (S)	T A	NP	ΤN	JP NI	P NP	ΤN	JP NF	P NP	NP N	NP NI	P NP I	NP NF	P NP 1	NP NP	NP N	P NP	NP T	NP	NP N	P NP I	NP NP	NP N	P NP N	P NP	NP C	C (C _
Fabaceae, Faboideae	F5	Dulbergia melanoxylon	Semi-xerophyte	0	1500-2000 m (S)	ТТ	NP	ΤN	JP NI	РТ	NP N	JP NF	РΤ	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	ΤΊ	NP	NP N	P NP 1	NP NP	NP N	P NP N	РТ	A T	NP N	JP.
Fabaceae	F6	Notonia hildebrandtii	Semi-xerophyte	0	2000-2500 m (B)	C N	P NP	Т	T NI	РТ	NP '	T NF	P NP	ΤN	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	ΤΊ	Т	NP N	P NP	T NP	ΤN	P NP N	P NP	ТТ	NP N	JP .
Fabaceae, Caesalpinioideae	F7	Senna spectabilis	Mesophyte	0	2000-2500 m (B)	ТТ	NP	Т	т т	Т	NP '	T NF	P NP	NP N	NP NI	P NP 1	NP NF	P NP 1	NP NP	Т	Γ NP	NP T	NP	NP N	P NP	Т Т	T N	P NP ?	ΓТ	Т Т	TN	JP.
Fabaceae	F8	Sesbania seban	Semi-xerophyte	0	2000-2500 m (B)	C T	NP	TN	JP NI	РТ	ΤN	JP NF	РΤ	TN	NP NI	P NP 1	NP NF	P NP 1	NP NP	NP N	P NP	NP T	NP	NP N	P NP I	NP T	T N	P NP N	РТ	NP C	TN	vР

Blocky/Tabular
Blocky facetatee
Blocky corniculate
B/T decorated
B/T crenate-echinate-sinuate
B/T radiating laminate
Blocky scuttorm
Blocky tuberculate
Tabular 'ridged'
B/T cavate
Globular psilate
Globular psilate large
Globular granulate
Globular tuberculate
Globulose oblong tuberculate/verrucate
Globualr papillate
Globular to subglobular facetate
Globulose favouse
Globular echinate (Arecaceae type)
Globular echinate
Globular foulded
Globular decorated compound
Obovate psilate
Obovate scorbiculate/granulate
Cylindroid
Cylindrod geniculate
Cylindroid bulbous
Asteroschlerid
Cylindroid corniculate
Elongate faœted phytoliths
Cylindric sulcate tracheid
Acicular and Fusiform/Ellipsoid /scutiform (Tricolmes/Aciular hair cell)
Lanceolate
Elongate scalariform platelet
Epidemal jig-saw
Epidemal polygonal/parallelogram
Hair cell base/prickle/trichome/stomata
Elongate psilate
Tabaular thin echinate-simuate-crenate-facetate-dendritic
Elongate decorated platelet (conical abraxial)

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Family	Family-Species coding for CA	Species	Water requirements	Light requirements	Altitude/vegetatio n zone	BT_p	B_f	B_cor	b1_d	BT_d	B_s	B_t	T_r er	B1_cav	d p	G_g	j j	G_p	G_sgf	G_fa G_At	G_e	G_fo G_de	0_p	0_% C_%	6 6 C	£.	< °	E_fp	Ş Ç	L F en	13	E_pp H	E_P	T_t E_dp
Fabaceae	F9	Acacia seyal	Semi-xerophyte	O/S	1500-2000 m (S)	Т	Т	NP 1	Γ'N	P NF	ĊТ	NP	NP N	JP N	P NP	NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	Р Т I	NP NJ	ρNP	NP N	iP NP	NP	ΤТ	NP N	P NP	NP N	РΤ	NP NP
Fabaceae	_	Acacia diepansobium	Semi-xerophyte	O/S	1500-2000 m (S)	NP	NP	NP 1	ΓN	P NF	NP	NP	NP N	JP 1	Γ NP	NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP	NP T	NP	NP N	P NP	NP N	JP NP	NP N	P NP	NP N	РТ	NP NP
Fabaceae, Mimosoideae	F10	Acacia xanopholoea	Xerophyte	0	2000-2500 m (B)	Т	Т	NP 1	ΓN	P NF	РΤ	NP	ΤN	JP N	P NP	NP	NP '	Γ NP	NP 1	NP NI	P NP	NP NI	P NP	NP T	NP	NP N	P NP	TN	лр Т	NP N	P NP	т т	Т	NP NP
Gentianaceae	-	Anthocleista zambesiaca	Mesophyte	O/S	2000-2500 m (B)	NP	NP	NP N	IP N	P NF	NP	NP	NP N	JP N	P NP	P NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP	NP NJ	ΡNΡ	NP N	iP NP	NP N	JP NP	NP N	P NP	NP N	P NP	NP NP
Hypericaceae	Hy	Hypericum revolutum	Mesophyte	O/S	2000-2500 m (B)	Т	Т	NP 1	ΓΝ	P NF	Т	NP	T N	JP N	P NP	NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP I	NP T	NP	NP N	IP NP	TN	JP NP	NP N	P NP	NP T	NP	NP NP
Lamiaceae	LÍ	Leucas nepetifolia	Mesophyte	O/S	2000-2500 m (B)	С	Т	NP 1	ΓΝ	P NF	Т	NP	T N	JP 1	Γ NP	P NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	т	NP T	Т	ΤN	iP NP	Т	ΤТ	NP N	РТ	СТ	Т	T NP
Lamiaceae	L2	Leonotis nepetifolia	Mesophyte	O/S	2500-3000 m (A)	Т	Т	NP 1	ΓТ	ſ NF	Т	NP	T N	JP 1	Γ NP	P NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP	NP T	NP	ΤN	iP NP	Т	ΤТ	NP N	P NP	NP T	C	T NP
Lamiaceae	L3	Ocimum gratissimum	Mesophyte	S/O	2000-2500 m (B)	Т	С	NP 1	гт	гт	Т	Т	NP N	JP N	РТ	NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP I	NP T	NP	NP N	IP NP	NP N	JP T	NP N	P NP	т т	C C	C C
Lamiaceae	L4	Plectranthus barbatus	Mesophyte	O/S	2000-2500 m (B)	Т	NP	NP 1	гт	гт	Т	NP	T N	JP 1	F NP	NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP I	NP T	NP	NP N	IP NP	Т	T NP	NP N	РТ	т т	Т	T NP
Lamiaceae	L5	Plectranthus cylindraceus	Mesophyte	O/S	2500-3000 m (A)	NP	NP	NP N	IP N	P NF	P NP	NP	NP N	JP 1	Γ NP	P NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP I	NP N	P NP	NP N	JP NP	NP N	JP NP	NP N	P NP	NP N	P NP	NP NP
Lamiaceae, Viticoideae	L6	Vitex doniana	Mesophyte	O/S	1500-2000 m (S)	Т	NP	NP 1	ΓТ	r nf	NP	NP	NP N	JP 1	F NP	P NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP	NP T	NP	NP N	P NP	NP	C NP	NP N	P NP	ТС	NP	NP NP
Malvaceae, Sterculiaceae	Ma1	Dombeva burgessiae	Mesophyte	O/S	2500-3000 m (A)	Т	NP	NP 1	гт	[NF	РΤ	NP	NP 7	т 1	ΓТ	NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP I	NP T	Т	NP N	JP NP	NP	т т	NP N	P NP	СТ	NP	T NP
Malvaceae, Grewioideae	Ma2	Grewia similis	Mesophyte	O/S	1500-2000 m (S)	Т	Т	NP N	IP N	P NF	P NP	NP	TN	JP 1	гт	NP	NP N	P NP	NP 1	NP NI	P NP	NP NI	P NP 1	NP N	P NP	NP N	JP NP	Т	T NP	NP N	P NP	TN	P NP	NP NP
Malvaceae	_	Hibiscus calvohyllus	Mesophyte	O/S	1500-2000 m (S)	NP	NP	NP N	IP N	P NF	P NP	NP	NP N	JP N	P NP	P NP	NP N	P NP	NP 1	NP NI	P NP	NP NI	P NP 1	NP N	P NP	NP N	JP NP	NP N	JP NP	NP N	P NP	NP N	P NP	NP NP
Melianthaceae	Mc	Bersama abyssinica	Mesophyte	0/5	1500-2000 m (S)	т	т	NP N	рт	r ne	т	NP	NP N	JP 1	гт	NP	NP N	JP NP	NP N	NP NI	P NP	NP NI	P NP	NP T	NP	NP N	JP NP	NP	ст	NP N	P NP	тт	т	NP NP
Moraceae	M1	Ficus cordata	Mesophyte	O/S	1500-2000 m (S)	Т	NP	NP N	IP N	P NF	P NP	NP	NP N	JP 1	Γ NP	P NP	NP N	IP NP	NP 1	NP NI	P NP	NP NI	P NP	NP T	NP	NP N	JP NP	NP	C NP	NP N	PNP	C C	NP	NP NP
Moraceae	M2	Ficus ludea	Mesophyte	O/S	2000-2500 m (B)	NP	NP	NP 1	ΓN	P NF	P NP	NP	NP N	JP N	РТ	NP	NP N	P NP	NP 1	NP NI	P NP	NP NI	P NP 1	NP T	NP	NP N	JP NP	NP N	JP NP	NP N	P NP	TN	РТ	NP NP
Moraceae	M3	Ficus sycomorus	Mesophyte	0/5	1500-2000 m (S)	т	NP	NP	ΓN	P NE	NP	NP	NP N	JP 1	Γ NP	NP	NP N	JP NP	NP N	NP NI	P NP	NP NI	P NP	NP N	P NP	NP N	JP NP	NP	T NP	NP N	P NP	C C	NP	NP NP
Moraceae	M4	Ficus thonningii	Mesophyte	0	2000-2500 m (B)	т	NP	NP N	рт	r ne	P NP	NP	NP N	JP 1	Γ NP	P NP	NP N	JP NP	NP N	NP NI	P NP	NP T	NP	NP T	NP	NP N	JP NP	NP	T NP	NP N	PNP	тт	NP	NP NP
Moraceae	M5	Ficus wakefeldii	Mesophyte	0/8	1500-2000 m (S)	т	NP	NP N	IP N	P NF	P NP	NP	NP N	JP 1	Γ NP	P NP	NP N	JP NP	NP N	NP NI	P NP	NP NI	P NP 1	NP T	NP	NP N	JP NP	NP	тт	NP N	PNP	C C	Т	NP NP
Musinaceae	Mus	Rananae melanophleos	Mesophyte	0/5	2500-3000 m (A)	NP	NP	NP N	IP N	P NE	D NP	NP	NP N	JP N	P NP	NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP	NP NP	P NP	NP N	JP NP	NP N	JP NP	NP N	PNP	NP N	рт	NP NP
Myrtaceae	Myr	Syzygium guinense	Mesophyte	0/5	2500-3000 m (A)	Т	т	NP N	IP N	P NE	P NP	NP	NP N	JP N	P NP	P NP	NP N	JP NP	NP N	NP NI	P NP	NP NI	P NP	NP N	P NP	NP N	JP NP	NP N	JP NP	NP N	PNP	NP N	P NP	NP NP
Nolinoideae Dracaenaceae	N	Dracaena steudneri	Mesophyte	0/5	2500-3000 m (A)	NP	т	NP	гл	r ne	Т	NP	т	TN	P NP	P NP	NP N	JP NP	NP N	NP NI	P NP	NP NI	P NP	NP T	NP	NP '	ΓNP	TN	рт	NP N	PNP	NP N	РТ	C NP
Ochnaceae	Or	Ochna holstii	Mesophyte	0/5	2500-3000 m (A)	NP	NP	NP N	IP N	P NF	P NP	NP	NP N	JP N	P NP	P NP	NP N	JP NP	NP N	NP NI	P NP	NP NI	P NP	NP N	P NP	NP N	JP NP	NP N	JP NP	NP N	PNP	NP N	РТ	NP NP
Oleaceae	01	Olea africana	Mesophyte	0/5	1500-2000 m (S)	т	NP	NP	гл	r ne	т	NP	TN	JP 1	F NP	P NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP 1	NP T	NP	TN	JP NP	т	тт	NP N	PNP	NP T	. т	NP T
Oleaceae	0	Olea chrwophylla	Mesophyte	0/5	2500-3000 m (A)	т	NP	NP N	IP N	P NE	D NP	NP	NP N	JP N	IP NP	P NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP 1	NP N ^P	PNP	NP N	JP NP	NP N	JP NP	NP N	PNP	NP N	P NP	NP NP
Podocamaceae	_	Podocarous latifolius	Mesophyte	0/5	2500-3000 m (A)	NP	NP	NP N	IP N	P NF	P NP	NP	NP N	JP N	P NP	P NP	NP N	JP NP	NPN	NP NI	P NP	NP NI	P NP 1	NP N	P NP	NP N	JP NP	NPN	JP NP	NP N	PNP	NP N	P NP	NP NP
Polygonaceae	Po	Rumex usambarensis	Mesophyte	0/5	2500-3000 m (A)	т	NP	NP N	рт	r ne	D NP	NP	NP N	JP 1	F NP	P NP	NP N	IP NP	NPN	NP NI	D NP	T NI	D NP	тт	NP	NP N	JP NP	NPN	JP T	NP N	рт	тс	NP	NP NP
Pteridaceae	Pt	Pteris abassinica	Mesophyte	\$	2500-3000 m (A)	NP	NP	NP N	IP N	P NE	D NP	NP	NP N	JP 1	r np	> A	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP 1	NP N ^P	PNP	NP N	JP NP	NPN	JP NP	NP N	рт	NP T	NP	NP NP
Bosaceae	R	Hagenia abussinica	Mesophyte	0/5	2500-3000 m (A)	т	т	NP '	ΓΝ	P NE) Т	NP	NP N	JP N	P NP	NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP	NP T	NP	NP N	JP NP	NP N	лт	NP N	рт	A T	NP	NP NP
Butaceae	Ru1	Colodendrum capense	Mesophyte	0/5	1500-2000 m (S)	Ť	Ť.	NP	г 1	гт	NP	NP	TN	JP 1	гт	NP	NP N	IP NP	T 1	NP NI	D NP	NP NI	D NP 1	NP T	NP	TN	JP NP	т	ст	NP N	PNP	NP T	т	NP NP
Butaceae	Ru2	Venris simpliciolia	Mesophyte	\$/0	1500-2000 m (S)	Ť	Ť.	NP	г т	r ne	т	NP	TN	JP 1	r np	P NP	NP N	IP NP	NPP	NP NI	D NP	NP NI	D NP 1	NP T	NP	NPN	JP NP	TN	рт.	NP N	PNP	СТ	Ť	T NP
Butaceae	Ru3	Zanthoxylum gilletii	Mesophyte	0/8	1500-2000 m (S)	Ť	Ť	NP N	IP N	P NF	P NP	NP	TN	JP N	P NP	P NP	NP N	JP NP	NPN	NP NI	P NP	NP NI	P NP 1	NP N	P NP	NP N	JP NP	T	T NP	NP N	PNP	сī	Ť	NP NP
Butaceae Toddalioideae		Zanthoxylum usumbarenses	Mesophyte	\$/0	2500-3000 m (A)	NP	NP	NP N	IP N	P NE	D NP	NP	NP N	JP N	P NP	NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP	NP NP	P NP	NP N	JP NP	NP N	JP NP	NP N	PNP	NP N	P NP	NP NP
Salvadoraceae	Sa1	Salvadora persica	Semi-xerophyte	0	1500-2000 m (S)	т	т	NP	гл	r ne	D NP	NP	NP N	JP 1	F NP	P NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP 1	NP T	NP	NP N	JP NP	NP	T NP	NP N	PNP	тт	т.	NP NP
Sapindaceae	5.2	Dodonan aumstifolia	Macorbuta	0/5	2000 2500 m (b)	Ť	÷.	ND 7	г 1	r NIE	ND	ND	TN	JD N	D ND	ND	ND N	ID ND	ND	ND NI	ND	ND NI	D ND 1	ND T	ND	ND N	ID NE	т	тт	ND N	DND	т т	ċ	C C
Soloparaga	5a2 So1	Solonum aculeactrum	Mesophyte	0/5	2000-2500 m (B)	ND	ND	ND N	ID N	D NE	ND ND	ND	NDN	JD N	D ND	ND	NID N	ID ND	NDD	ND NI	D ND	ND NI	D ND 1	ND T	ND	ND N	ID NE	NDN	ID ND	ND N	DND	ND N	рт	TNP
Solanaceae	501 So2	Solanum incanum	Mesophyte	0/5	2000-2500 m (B)	NP	NP	NP N	IP N	P NE	D NP	NP	NP N	JP 1	F NP	P NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP 1	NP T	NP	NP N	JP NP	NPN	JP T	NP N	PNP	ТТ	' NP	NP NP
Umaceae	11	Celtis gomphophylla	Mesophyte	0/5	2500-3000 m (A)	NP	NP	NP N	IP N	P NE	D NP	NP	NP N	JP N	IP NP	P NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP 1	NP T	NP	NP N	JP NP	NPN	JP NP	NP N	PNP	NP N	P NP	NP NP
Urticaceae	Urt	Obetia pinpaitifida	Mesophyte	0/5	1500-2000 m (N)	т	NP	NP 1	F N	P NE	D NP	NP	TN	JP N	IP NP		NP N	IP C	NPN	NP NI	D NP	NP NI	D NP	СТ	' NP	NP N	JP NP	TN	JP NP	NP N	PNP	NP A	Т	NP NP
Urticaceae	Ur2	Urtica massaica	Mesophyte	0/5	2500-3000 m (A)	NP	NP	NP N	IP N	P NE	D ND	NP	TN	JP N	D ND	D NP	AN	IP C	NP	NP NI	D NP	NP NI	D NP 1	NP T	' ND	NPN	IP NP	- T N	JP ND	NP N	PNP	NP C	. т Т	NP NP
Verbenaceae	V1	Lantana trifolia	Mesophyte	0/5	2500-3000 m (A)	т	NP	NP N	IP N	P NE	ND	NP	NPN	JP 1	F ND	D NP	NPN	IP ND	NP	NP NI	D NP	NP NI	D NP 1	NP T	' ND	NPN	JP NP	NPN	JP ND	NP N	PNP	T A	ND	NP NP
Verbenaceae	V2	Linnia iavanica	Mesophyte	0/5	2000-2500 m (R)	Ť	NP	NP N	IP N	P NE	.ч	NP	NP N	JP N	IP NP	P NP	NP N	IP NP	NPN	NP NI	D NP	NP NI	D NP 1	NP T	' NP	NP N	JP NP	NP	тт	NP N	PNP	т A	NP	NP NP
· · · · · · · · · · · · · · · · · · ·	1.44	and a second sec	A 10	b/	manual marks of and the		- 14					- 14					- 24 - 41											- 14	- 4	- 14 - 13		- 42		



Appendix 4 - Figure 4.3 CA biplot of botanica data with outlier identified in CA (see Figure 4.14) removed. As in the initial CA analysis, tight cluster closely of points indicates that they are poorly ordinated due to high levels of redundancy in phytolith morphotypes across the woody dicots studied.



Appendix 4 - Figure 4.4 DCA biplot of botanica data with outlier identified in CA (see Figure 4.14) removed. As in the initial CA analysis, tight cluster closely of points indicates that they are poorly ordinated due to high levels of redundancy in phytolith morphotypes across the woody dicots studied.

APPENDIX 5

5.1 Geological history of the Nakuru-Naivasha Basin

The transformation of the Nakuru-Naivasha Basin from a half-graben to full-graben morphology occurred between 5.5 and 3.7 Ma, when a process of antithetical faulting (running from N-S along the basin) gradually transformed East-dipping normal faults (formed previously between 12 and 6 Ma). This process created the Aberdares escarpment (3999 m a.s.l.) and Mau escarpment (3080 m a.s.l.) which flank the basin (Baker and Wohlenberg, 1972; Barker et al., 1988; Bergner et al., 2009). The geology of the Mau escarpment is comprised primarily of unwelded tuffs, minor rhyolites, trachytes and basalts (Olaka et al., 2016 and references therein). Subsequent tectonic activity resulted in the creation of the two main depressions in the basin. After 2.6 Ma, further tectonic activity created the ~ 30 km wide Kinangop plateau at 2740 m a.s.l., bordered by Plio-Pleistocene fault scarps, and the inner rift depression which is \sim 40 km wide (Bergner et al., 2009). During the Quaternary period volcanic activity in-filled the basin with trachytic, comenditic, phonolitic, basaltic, and rhyolitic lava flows, tuffs, and volcanic air fall deposits that were cut then by a process of normal faulting along volcano-tectonic axes (Berger et al., 2009; McCall et al., 1967; Clarke et al., 1990). During the mid-Pleistocene, en échelon NNE striking normal faults, joined by complex transfer zones, were formed due to oblique extension of the preestablished rift structures. Obliquely slipping normal faulting in some cases re-activated older faults (as obliquely slipping normal faults/ local strike-slip faults), which are associated with the development of the volcanic centres of Menengai, Eburru and Longonot (Bergner et al., 2009 and references therein). The Menengai Caldera (2278 m a.s.l.) marks the northern limit of the basin. The volcanic massif of Mt. Eburru (2856 m a.s.l.) forms a ridge that extends across the KCR in an east-west orientation; separating the two Nakuru-Elementaita and Naivasha Sub-basins in the Gilgil area. At ~320 kyr BP rhyolitic lava flows originating from the Olikaria Volcanic Complex (2440 m a.s.l.) closed the basin in the south and southwest; cutting the basin and lake off from the trachytic Mt. Longonot volcano (2776 m a.s.l.) located to the south (Clarke et al., 1990; Trauth et al., 2010). Relatively recently in the basin's history, ~300 kyr BP, the inner rift floor rose to a point of maximum altitude (2010 m a.s.l.) in the Gilgil area which separates the two lake basins (Thompson and Dodson, 1963b; Bergner et al., 2003). Quaternary volcanic deposits on the rift floor are interbedded with lacustrine and fluviatile sediments associated with the development of Lakes Naivasha and Nakuru-Elementaita (Thompson and Dodson, 1963b). These deposits become more prominent in the sedimentary record after ~146 kyr BP when the basin has been shown to have regularly supported more stable extensive lakes (Trauth et al., 2001; Trauth et al., 2003; see Chapter 3.4). Studies of ground water connectivity between the Nakuru-Elmenteita and Naivasha Basins (which differ by ~ 100 m in altitude), indicate that the geomorphology of the west dipping fault block between Gilgil and Kariandusi directs water from the Kinangop Plateau water preferably towards Lake Naivasha; resulting in divergent lake conditions in the two sub-basins (i.e. the salinization of Lakes Nakuru-Elmenteita, while Lake Naivasha remains freshwater) (Olaka et al., 2010; Yihdego and Brecht; 2013; Olaka et al., 2015). It is these differences in elevational and ground water availability between the basins that result in their slightly differential responses to climate (Olaka et al., 2010).
Locality	Excavation campaign	Period	Phase	Stratum	Specimen	Date (BP)	Method	Sample type 2	Original interpretation	Reference
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13354	2,578 ± 80	ОН	Kenya B obsidian	Pastoral Neolithic, second occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13352	2,562 ± 129	ОН	Kenya B obsidian	Pastoral Neolithic, second occupation phase	Michels et al. 1983: table 3
3 (trench 5)	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	UCLA- 1234	2690 ± 80	14C	-		Berger & Libby 1968
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13345	2,815 ± 204	ОН	Kenya B obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13334	2,840 ± 161	ОН	Kenya B obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3	Cohen 1969	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation; Cohen's strata 3-4 which contain the main archaeological horizon	N-651	2910 ± 110	14C	-		Cohen 1970; Yamasaki et al 1970
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13338	2,930 ± 64	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13340	2,951 ± 107	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13339	2,994 ± 86	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13341	3,059 ± 154	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13342	3,080 ± 177	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3

Appendix - Table 5.1 Overview of dates for the Prospect Farm sequences and Pastoral Neolithic which stratigraphically overlie the sequence. OH= Obsidian Hydration.

3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13343	3,015 ± 175	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13336	3,102 ± 177	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13335	3,124 ± 245	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13346	3,146 ± 133	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13359	3,168 ± 133	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13344	3,168 ± 293	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13358	3,257 ± 250	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
3?	Anthony 1964	Pastoral Neolithic	-	colluvium overlying the Prospect Farm Formation	13337	3,279 ± 205	ОН	Kenya A obsidian	Pastoral Neolithic, first occupation phase	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	1	13363	$9,905 \pm 357$	OH	Kenya A obsidian		Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	1	13360	10,845 ± 144	OH	Kenya B obsidian		Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	2	13376	9,612 ± 470	OH	Kenya A obsidian		Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	2	13365	$9,905 \pm 535$	OH	Kenya A obsidian		Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	2	13366	$9,905 \pm 535$	OH	Kenya A obsidian		Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	2	13377	9,979 ± 622	ОН	Kenya A obsidian		Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	2	13364	$10,090 \pm 673$	OH	Kenya A obsidian		Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	2	13368	$10,277 \pm 445$	ОН	Kenya A obsidian		Michels et al. 1983: table 3

Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	2	13367	$10,460 \pm 173$	ОН	Kenya B obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA Eburran / Kenya Capsian	-	2-3 junction	13380	$10,522 \pm 224$	ОН	Kenya B obsidian	Michels et al. 1983: table 3
2 (trench 1)	Anthony 1964	LSA Eburran / Kenya Capsian	-	Eburran /Kenya Capsian horizon (base?); 14 to 20 inch below surface; in volcanic tuff	GX-224	$10,560 \pm 1650$	14C	-	Kruger & Weeks 1966; Anthony 1967
Unspecified	Anthony 1963-1964	LSA (unidentified)	-	1	13287	14,145 ± 874	ОН	Kenya B obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	LSA (unidentified)	-	1	13286	14,452 ± 1350	OH	Kenya A obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	early LSA (or Second intermediate)	-	2	13288	21,805 ± 373	ОН	Kenya B obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	early LSA (or Second intermediate)	-	2	13290	22,155 ± 329	ОН	Kenya B obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	early LSA (or Second intermediate)	-	2	13289	24,635 ± 696	ОН	Kenya B obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	early LSA (or Second intermediate)	-	2	13292	30,808 ± 762	ОН	Kenya A obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	early LSA (or Second intermediate)	-	2	13291	32,483 ± 568	ОН	Kenya A obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	MSA (transitional MSA to Second intermediate)	IV	5	13293	52,936 ± 836	ОН	Kenya B obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	MSA (transitional MSA to Second intermediate)	IV	5-6 junction	13294	49,586 ± 210	ОН	Kenya B obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	MSA (transitional MSA to Second intermediate)	IV	6	13296	52,106 ± 252	OH	Kenya B obsidian	Michels et al. 1983: table 3
Unspecified	Anthony 1963-1964	MSA (transitional MSA to Second intermediate)	IV	6	13295	53,553 ± 255	ОН	Kenya B obsidian	Michels et al. 1983: table 3

Unspecified	Anthony	MSA (transitional MSA to Second	IV	6 and 7	13297	49,621 ± 281	ОН	Kenya B		Michels et al.
	1903-1904	intermediate)						obsidiari		1965. table 5
Unspecified	Anthony	MSA (transitional	IV	7	13298	45,670 ± 236	OH	Kenya B		Michels et al.
	1963-1964	MSA to Second						obsidian		1983: table 3
		intermediate)								
Unspecified	Anthony	MSA (transitional	IV	7	13299	$47,816 \pm 2256$	OH	Kenya A		Michels et al.
	1963-1964	MSA to Second						obsidian		1983: table 3
		intermediate)								
Unspecified	Anthony	MSA (Stillbay)	III	8	13333	$46,538 \pm 1707$	OH	Kenya A	Phase 3 - third	Michels et al.
	1963-1964							obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	III	8	13306	$47,816 \pm 1295$	OH	Kenya A	Phase 3 - third	Michels et al.
	1963-1964							obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	III	8	13305	$48,160 \pm 1649$	OH	Kenya A	Phase 3 - third	Michels et al.
	1963-1964							obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	III	8	13301	$48,887 \pm 769$	OH	Kenya B	Phase 3 - third	Michels et al.
	1963-1964							obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	III	8	13300	$50,777 \pm 3322$	OH	Kenya A	Phase 3 - third	Michels et al.
	1963-1964							obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	III	8	13302	$51,843 \pm 4096$	OH	Kenya A	Phase 3 - third	Michels et al.
	1963-1964							obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	III	8	13304	$53,100 \pm 4145$	OH	Kenya A	Phase 3 - third	Michels et al.
	1963-1964							obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	III	8 and 9	13307	$51,308 \pm 4260$	OH	Kenya A	Phase 3 - third	Michels et al.
	1963-1964							obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	111	9	5.	14,900	OH	<u>ب</u>	Minimum age	Michels et al.
	1963-1964					10.000	0.11		201	1983: text
Unspecified	Anthony	MSA (Stillbay)	111	9	۲	18,300	ОН	۲	Minimum age	Michels et al.
	1963-1964				10010		0.11			1983: text
Unspecified	Anthony	MSA (Stillbay)	111	9	13310	$106,297 \pm 3163$	ОН	Kenya A	Phase 3 - second	Michels et al.
TT :C 1	1963-1964	A 50 A (0.111)		0	10000	107.001 0.100	OII	obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	111	9	13308	$107,201 \pm 3430$	ОН	Kenya A	Phase 3 - second	Michels et al.
TT :C 1	1963-1964	A FO A (O. 111		0	12200	100 (20 0017	OII	obsidian	occupation phase	1983: table 3
Unspecified	Anthony	MSA (Stillbay)	111	9	13309	$108,630 \pm 2917$	ОН	Kenya A	Phase 3 - second	Michels et al.
IIC. 1	1965-1964		TTT	0.10: / 6	12211	110.040 ± 1000	OU	obsidian	occupation phase	1985: table 5
Unspecified	Anthony	MSA (Stillday)	111	9-10 interface	15511	119,040 ± 1008	OH	Kenya A	Phase 5 - first	whichels et al.
2	1963-1964	MCA (Chille)	тт	15		14700	OU	ODSIGIAN	occupation phase	1985: table 5
2	Anthony	MSA (Stillday)	11	15	r	14,/00	OH	r	Minimum age	ivlichels et al.
	1903-1904									1985: text

2	Anthony	MSA (Stillbay)	II	15	5	24,500	OH	?	Minimum age	Michels et al.
	1963-1964									1983: text
2	Anthony	MSA (Stillbay)	II	15	?	81,800	OH	;	Minimum age	Michels et al.
	1963-1964									1983: text
2	Anthony	MSA (Stillbay)	II	15	?	88,400	OH	;	Minimum age	Michels et al.
	1963-1964									1983: text

5.2.1 Density surveys - methodology

Isaac (Isaac 1972; Isaac et al., 1972, 1976) reports on a density survey undertaken in the southern part of the Nakuru Basin. More specifically, a set of altitudinal south(east)-north(west) oriented transects between the top of Mt. Eburru and Lake Nakuru were surveyed, encompassing both the Prospect Farm Formation and the lacustrine deposits at the base of Mt. Eburru considered to form the lateral equivalent of the Prospect Farm Formation and assigned to Formation A (Isaac et al., 1972, 1976). Along these transects, artefact densities were calculated based on counts made in arbitrarily positioned squares of two by two meters. Isaac's results indicate that the highest densities with up to 198 artefacts per 4 m² occurred between 2070-2195 m a.s.l. on the northern slope of Mt. Eburru, close to the lower limit of the montane forest, and the position of Anthony's excavations. Densities recorded for these elevations are up to ten times higher than those obtained for the valley floor north of Mt. Eburru, where only one significant artefact concentration was found (GrJi 11). In order to better assess these areas with higher artefact densities and to improve our insight into the spatial distribution of MSA versus LSA artefacts, a new density survey was undertaken in 2014. Targeting six areas, totalling 0.486 km² situated between ~1960 m and ~2210 m a.s.l. on the northern slope of Mt. Eburru, the surveyed area also included the altitudes for which Isaac noted the highest artefact densities. Georeferencing of cartographic material produced by Isaac (Isaac, 1972) suggests that this new 3.7 km long altitudinal transect is located around 2 km east of Isaac's easternmost transect. Within each of the new areas, parallel transect lines separated by 20 to 50 m wide intervals were walked. Similar to the position and extent of the six selected areas, the width of the intervals between the transect lines was primarily determined by terrain accessibility. Every 20 m along the same transect line, a 1 by 1 m square was placed randomly on the ground and the following details on the surface finds present within that square meter were subsequently recorded: the total number of artefacts, the number of artefacts that could be securely assigned to either the MSA or the LSA, details on the size distribution of the finds per square (< 2 cm; 2-5 cm; > 5 cm in length), as well as details regarding other, non-lithic, find categories (if present). Based on these characteristics recorded for surface finds in 387 squares, this survey was able to identify a number of key areas showing markedly higher artefact densities and to demonstrate important differences in the spatial distribution of diagnostic MSA and LSA artefacts (Appendix 5, Table 5.2). As the survey did not reveal any fossil remains or pottery, the obtained densities exclusively reflect the distribution of lithic artefacts. Throughout the investigated areas, artefact densities per square meter range from zero to > 400.

5.2.2 Laser particle size analysis - procedure

Samples were processed as follows: (1) 1 gram of sediment was placed in 50ml plastic centrifuge tubes. (2) Tubes were topped up with 4.4% sodium pyrophosphate Na₄P₂O₇, placed in a water bath for ~3 hrs and stirred at ~1½ hours with a glass stirrer to deflocculate samples. (3) Samples were centrifuged (for 13 min at 3500 rpm) to separate the supernatant and cleaned with deionised water. Samples were then mixed with a whirly mixer and a few drops were pipetted into a glass beaker filled with water in which a vortex was created by the Malvern Mastersizer 2000. An obscuration value close to 15% (not greater 20% or lower than 10%) was achieved for each sample (Sperazza et al., 2004; Miller and Schaetzl, 2011). The average of four analyses per sample was used. GRADISTAT (Blott and Pye, 2001) was used to determine grain-size statistics (Folk and Ward, 1957).

5.2.3 Phytolith extraction from sediments - procedure

(1) 5 grams of sediment was sieved through a 2 mm sieve to remove the coarse fraction, transferred to clean 100 ml beakers dried at >100 °C to remove any moisture. Samples were left to cool and their dry weigh was recorded using a high-precision balance. (2) 25 ml of 10% solution of Hydrochloric acid (HCL) was added to the sample to remove carbonates and then placed in a sand bath for \sim 3 hours at 40 $^{\circ}$ C until the liquid was reduced to \sim 5ml and the reaction stopped. (3) The remaining liquid was transferred into 50 ml plastic centrifuge tubes and topped up with distilled water. (4) The sample was then agitated using a tube-shaker, then centrifuged from 3 minutes at 1500 rpm and the supernant was poured off. Two further rinses were carried out to ensure that all acid was removed from the sample. (5) If sediments appeared to be rich in Fe and Al oxides and hydroxides they were removed by adding 10 ml of tri-sodium citrate (88.4 g·l-1) and placing the mixture in a sand bath at 80°C for 1 hour. After the solution had cooled completely, 1 g of sodium dithionite (Na₂S₂O₄) was added and shaken gently for few minutes until the sediment turned grey (Calegari et al., 2013). Samples were then centrifuged for 2 min at 3000 rpm and the supernatant was carefully discarded into a separate container for disposal. The tubes were filled with distilled water, shaken and centrifuged for 2 minutes at 3000 rpm (repeated twice). (6) 15ml of 5% weight solution of Sodium hexametaphosphate ((NaPO₃)₆) was added to the sample to act as a deflocculant for clays, then left overnight. (7) The tubes were then shaken gently and centrifuged at 1500 rpm for 3 minutes, the supernant was discarded and tubes topped up with distilled water then centrifuged. This process was repeated twice. (8) 15 ml of 33% volume hydrogen peroxide (H₂O₂) was added to the tubes, shaken gently and left in a block heater at 40 °C to remove organics. (9) Step 6 was repeated, and samples transferred to an oven at 75 °C to remove any moisture which might affect the specific gravity (s.g.) of the Sodium polytungstate (SPT) (Na₆[H₂W₁₂O₄₀]) added in step 10. (10) 10 ml SPT solution at a s.g. of 2.35 g/cm³ was added to the tubes, shaken gently and centrifuged at 1500 rpm for 3 minutes. The floated fraction (containing the phytoliths) was recovered with a Pasteur pipette and transferred to a new tube. The remaining sample in the original tube was centrifuged again at 1500 rpm for 3 minutes and the floated material was again pipetted into the new tube. (11) 15 ml of distilled water was added to the new tube to recover the floating fraction and the sample centrifuged at 1500 rpm for 3 minutes, and the floating supernant poured off. This rinse was repeated twice to wash off any remaining SPT. (12) Empty glass vials were weighed using a high precision balance, samples were pipetted into them and dried in a muffle furnace at 70 °C for 2 days. Samples were then reweighed. (13) Glass slides were weighed and an aliquot of ~0.005 grams was added to the slide. The weight of the slide + the aliquot was recorded to calculate the number of phytoliths per gram of acid insoluble fraction (AIF%). Cargill Type-A optical immersion oil that facilitated rotation, 3D counting and identification of phytoliths was added to the slide and the aliquot was dispersed before a 22×40 mm = 880 mm² cover slips were added.

OBJECT	Point ID	Latitude	Longitude	Elevation (as inferred	Total	Chrono-cultural attributionArtefact sizeMSALSAUnidentified< 2 cm2-5 cm> 5 cm					
ID				from SRTM 30 m)		MSA	LSA	Unidentified	< 2 cm	2-5 cm	> 5 cm
1	PF1DS001	-0.604835	36.188668	2195	0	0	0	0	0	0	0
2	PF1DS002	-0.604747	36.188859	2199	12	0	1	11	11	1	0
3	PF2DS003	-0.604619	36.189014	2200	0	0	0	0	0	0	0
4	PF1DS004	-0.604502	36.189214	2200	8	0	2	6	8	0	0
5	PF1DS005	-0.604374	36.189350	2198	0	0	0	0	0	0	0
6	PF1DS006	-0.604598	36.189608	2205	8	0	0	8	7	1	0
7	PF1DS007	-0.604708	36.189379	2208	2	0	0	2	2	0	0
8	PF1DS008	-0.604798	36.189194	2205	3	0	0	3	3	0	0
9	PF1DS009	-0.604888	36.189055	2205	84	0	2	82	82	2	0
10	PF1DS010	-0.604997	36.188732	2196	34	0	5	29	28	6	0
11	PF1DS011	-0.605272	36.188970	2201	37	0	2	35	22	15	0
12	PF1DS012	-0.605154	36.189125	2207	12	0	0	12	12	0	0
13	PF1DS013	-0.605083	36.189311	2212	0	0	0	0	0	0	0
14	PF1DS014	-0.604980	36.189525	2212	0	0	0	0	0	0	0
15	PF1DS015	-0.604882	36.189707	2210	5	0	0	5	5	0	0
16	PF1DS016	-0.604364	36.189499	2198	0	0	0	0	0	0	0
17	PF1DS017	-0.604537	36.189285	2200	4	0	0	4	4	0	0
18	PF1DS018	-0.604709	36.189106	2205	99	0	12	87	67	28	4
19	PF1DS019	-0.604837	36.188905	2199	47	0	17	30	39	8	0
20	PF1DS020	-0.605115	36.188797	2200	16	0	4	12	14	2	0
21	PFDS001	-0.597347	36.181815	2132	0	0	0	0	0	0	0
22	PFDS002	-0.597176	36.181685	2135	2	0	0	2	2	0	0
23	PFDS003	-0.597022	36.181540	2135	24	0	0	24	23	1	0
24	PFDS004	-0.596836	36.181401	2135	0	0	0	0	0	0	0
25	PFDS005	-0.596673	36.181272	2135	0	0	0	0	0	0	0
26	PFDS006	-0.596482	36.181131	2138	2	0	0	2	2	0	0
27	PFDS007	-0.596282	36.181003	2137	3	0	0	3	3	0	0
28	PFDS008	-0.596105	36.180868	2137	56	0	1	55	56	0	0

Appendix 5 - Table 5.2 Density survey results: spatial distribution of diagnostic MSA and LSA artefacts across the Prospect Farm Formation (from Van Balen et al., 2019).

29	PFDS009	-0.595905	36.180753	2133	0	0	0	0	0	0	0
30	PFDS010	-0.595718	36.180626	2132	0	0	0	0	0	0	0
31	PFDS011	-0.595496	36.180514	2130	22	0	0	22	21	1	0
32	PFDS012	-0.595327	36.180400	2133	38	0	0	38	36	2	0
33	PFDS013	-0.595123	36.180289	2131	17	0	1	16	17	0	0
34	PFDS014	-0.594941	36.180163	2129	0	0	0	0	0	0	0
35	PFDS015	-0.594739	36.180047	2131	8	0	0	8	8	0	0
36	PFDS017	-0.594347	36.179864	2126	14	0	0	14	14	0	0
37	PFDS016	-0.594542	36.179938	2128	43	0	3	40	41	2	0
38	PFDS018	-0.594180	36.179766	2123	1	0	0	1	1	0	0
39	PFDS019	-0.594371	36.179394	2122	0	0	0	0	0	0	0
40	PFDS020	-0.594547	36.179521	2122	2	0	0	2	2	0	0
41	PFDS020	-0.594719	36.179635	2128	0	0	0	0	0	0	0
42	PFDS021	-0.594912	36.179744	2128	0	0	0	0	0	0	0
43	PFDS022	-0.595111	36.179837	2129	0	0	0	0	0	0	0
44	PFDS023	-0.595313	36.179945	2132	0	0	0	0	0	0	0
45	PFDS024	-0.595507	36.180032	2132	0	0	0	0	0	0	0
46	PFDS025	-0.595702	36.180134	2133	11	0	0	11	11	0	0
47	PFDS026	-0.595902	36.180240	2133	3	0	0	3	3	0	0
48	PFDS027	-0.596075	36.180374	2133	30	0	2	28	29	1	0
49	PFDS028	-0.596244	36.180473	2136	67	0	3	64	64	1	2
50	PFDS029	-0.596444	36.180615	2138	38	1	3	34	35	3	0
51	PFDS030	-0.596650	36.180773	2139	0	0	0	0	0	0	0
52	PFDS031	-0.596818	36.180915	2139	22	1	2	19	17	3	2
53	PFDS032	-0.596989	36.181044	2138	12	3	0	9	6	6	0
54	PFSD033	-0.597181	36.181124	2138	112	11	2	99	59	46	7
55	PFDS034	-0.597320	36.181270	2140	75	8	6	61	48	23	4
56	PFDS035	-0.597398	36.181388	2140	16	1	2	13	11	4	1
57	PFDS036	-0.597577	36.181528	2138	18	0	0	18	16	2	0
58	PFDS037	-0.597746	36.181164	2147	1	0	0	1	0	1	0
59	PFDS038	-0.597568	36.181029	2146	0	0	0	0	0	0	0
60	PFDS039	-0.597389	36.180936	2142	38	0	6	32	26	12	0

61	PFDS040	-0.597215	36.180797	2142	125	4	3	118	121	3	1
62	PFDS041	-0.597055	36.180687	2139	33	0	2	31	28	3	2
63	PFDS042	-0.596892	36.180571	2139	0	0	0	0	0	0	0
64	PFDS043	-0.596732	36.180485	2139	6	0	1	5	4	2	0
65	PFDS044	-0.596540	36.180357	2136	44	0	1	43	44	0	0
66	PFDS045	-0.596416	36.180282	2136	27	0	0	27	27	0	0
67	PFDS046	-0.596255	36.180153	2134	13	0	0	13	13	0	0
68	PFDS047	-0.596107	36.180026	2133	4	0	0	4	4	0	0
69	PFDS048	-0.595965	36.179904	2132	0	0	0	0	0	0	0
70	PFDS049	-0.595821	36.179752	2130	0	0	0	0	0	0	0
71	PFDS050	-0.595665	36.179666	2129	4	0	0	4	4	0	0
72	PFDS051	-0.595487	36.179579	2129	41	0	0	41	41	0	0
73	PFDS052	-0.595308	36.179523	2124	5	0	0	5	5	0	0
74	PFDS053	-0.595127	36.179478	2125	7	0	0	7	7	0	0
75	PFDS053	-0.594971	36.179382	2125	0	0	0	0	0	0	0
76	PFDS054	-0.594634	36.179281	2119	5	0	0	5	5	0	0
77	PFDS055	-0.594469	36.179198	2119	27	0	0	27	27	0	0
78	PFDS057	-0.595290	36.179085	2120	0	0	0	0	0	0	0
79	PFDS058	-0.595476	36.179203	2120	1	0	0	1	1	0	0
80	PFDS059	-0.595679	36.179380	2125	14	0	0	14	14	0	0
81	PFDS060	-0.595938	36.179553	2127	8	0	1	7	8	0	0
82	PFDS061	-0.596102	36.179708	2131	45	0	1	44	43	2	0
83	PFDS062	-0.596263	36.179799	2131	0	0	0	0	0	0	0
84	PFDS063	-0.596445	36.179915	2134	28	0	0	28	26	2	0
85	PFDS064	-0.596645	36.179981	2136	0	0	0	0	0	0	0
86	PFDS065	-0.596790	36.180067	2136	216	0	2	214	214	2	0
87	PFDS066	-0.596947	36.180178	2140	3	0	0	3	3	0	0
88	PFDS067	-0.597110	36.180265	2140	1	0	0	1	1	0	0
89	PFDS068	-0.597249	36.180369	2139	95	0	9	86	85	10	0
90	PFDS069	-0.597411	36.180458	2142	177	0	1	176	176	1	0
91	PFDS070	-0.597580	36.180535	2143	45	0	11	34	34	10	1
92	PFDS071	-0.597760	36.180680	2143	1	0	0	1	0	1	0

93	PFDS072	-0.597962	36.180783	2146	0	0	0	0	0	0	0
94	PFDS073	-0.598127	36.180423	2142	1	0	0	1	1	0	0
95	PFDS074	-0.597957	36.180330	2137	14	0	1	13	13	1	0
96	PFDS075	-0.597824	36.180233	2137	127	0	4	123	122	5	0
97	PFDS076	-0.597658	36.180137	2138	21	0	0	21	21	0	0
98	PFDS077	-0.597473	36.179988	2134	134	0	0	134	134	0	0
99	PFDS078	-0.597325	36.179880	2136	164	0	1	163	162	2	0
100	PFDS079	-0.597158	36.179798	2135	9	0	1	8	8	1	0
101	PFDS080	-0.597008	36.179713	2135	0	0	0	0	0	0	0
102	PFDS081	-0.596846	36.179620	2134	5	0	0	5	5	0	0
103	PFSD082	-0.596652	36.179468	2129	0	0	0	0	0	0	0
104	PFDS083	-0.596464	36.179356	2128	0	0	0	0	0	0	0
105	PFDS084	-0.596291	36.179245	2121	1	0	1	0	0	1	0
106	PFDS085	-0.596098	36.179111	2121	0	0	0	0	0	0	0
107	PFDS086	-0.595912	36.179004	2113	1	0	0	1	1	0	0
108	PFDS087	-0.595732	36.178895	2113	0	0	0	0	0	0	0
109	PFDS088	-0.595566	36.178804	2113	0	0	0	0	0	0	0
110	PFDS089	-0.595390	36.178682	2109	0	0	0	0	0	0	0
111	PFDS090	-0.595229	36.178567	2109	0	0	0	0	0	0	0
112	PFSD091	-0.595006	36.178463	2109	0	0	0	0	0	0	0
113	PFDS092	-0.595203	36.178119	2098	4	0	0	4	4	0	0
114	PFDS093	-0.595374	36.178275	2102	31	0	0	31	31	0	0
115	PFDS094	-0.595563	36.178396	2101	12	0	0	12	12	0	0
116	PFDS095	-0.595748	36.178512	2108	21	1	0	20	20	1	0
117	PFDS096	-0.595933	36.178634	2108	1	0	0	1	1	0	0
118	PFDS097	-0.596139	36.178756	2114	1	0	0	1	1	0	0
119	PFDS098	-0.596312	36.178877	2114	7	0	0	7	7	0	0
120	PFDS099	-0.596471	36.179000	2116	29	2	0	27	27	1	1
121	PFDS100	-0.596646	36.179135	2122	64	0	0	64	64	0	0
122	PFDS101	-0.596854	36.179262	2122	169	0	0	169	166	3	0
123	PFDS102	-0.597049	36.179367	2129	132	0	0	132	132	0	0
124	PFDS103	-0.597235	36.179465	2128	25	0	0	25	24	1	0

125	PFDS104	-0.597477	36.179615	2131	0	0	0	0	0	0	0
126	PFDS105	-0.597710	36.179730	2131	0	0	0	0	0	0	0
127	PFDS106	-0.597882	36.179849	2132	3	0	0	3	3	0	0
128	PFDS107	-0.598053	36.179957	2131	2	0	0	2	2	0	0
129	PFDS108	-0.598217	36.180063	2131	0	0	0	0	0	0	0
130	PFDS109	-0.598382	36.180134	2137	1	0	0	1	1	0	0
131	PF2DS001	-0.595334	36.180606	2130	27	0	1	26	26	1	0
132	PF2DS002	-0.595244	36.180990	2127	38	0	0	38	38	0	0
133	PF2DS003	-0.595068	36.180886	2124	3	0	0	3	3	0	0
134	PF2DS004	-0.594883	36.180809	2121	1	0	0	1	1	0	0
135	PF2DS005	-0.594664	36.180718	2120	32	0	0	32	32	0	0
136	PF2DS006	-0.594442	36.180652	2124	0	0	0	0	0	0	0
137	PF2DS007	-0.594281	36.180586	2121	158	0	0	158	158	0	0
138	PF2DS008	-0.594098	36.180524	2118	78	0	1	77	76	2	0
139	PF2DS009	-0.593908	36.180477	2118	34	0	1	33	31	3	0
140	PF2DS010	-0.593729	36.180441	2117	67	0	1	66	66	1	0
141	PF2DS011	-0.593538	36.180375	2117	78	0	1	77	75	3	0
142	PF2DS012	-0.593322	36.180312	2117	39	2	0	37	34	5	0
143	PF2DS013	-0.593113	36.180247	2113	72	3	0	69	68	4	0
144	PF2DS014	-0.592918	36.180172	2109	9	0	1	8	6	3	0
145	PF2DS015	-0.592767	36.180091	2114	1	0	0	1	1	0	0
146	PF2DS016	-0.592589	36.180003	2112	0	0	0	0	0	0	0
147	PF2DS017	-0.592435	36.179917	2110	0	0	0	0	0	0	0
148	PF2DS018	-0.592241	36.179805	2111	9	0	1	8	0	8	1
149	PF2DS019	-0.592060	36.179702	2108	0	0	0	0	0	0	0
150	PF2DS020	-0.591866	36.179642	2106	0	0	0	0	0	0	0
151	PF2DS021	-0.591668	36.179582	2106	0	0	0	0	0	0	0
152	PF2DS022	-0.591475	36.179537	2106	0	0	0	0	0	0	0
153	PF2DS023	-0.591283	36.179474	2102	0	0	0	0	0	0	0
154	PF2DS024	-0.591049	36.179426	2098	71	2	0	69	68	3	0
155	PF2DS025	-0.590866	36.179370	2098	86	6	0	80	78	7	1
156	PF2DS026	-0.590692	36.179322	2090	30	2	0	28	27	3	0

157	PF2DS027	-0.590636	36.179675	2092	32	2	0	30	30	2	0
158	PF2DS028	-0.590826	36.179733	2098	59	1	0	58	57	2	0
159	PF2DS029	-0.591017	36.179811	2098	10	2	0	8	8	0	2
160	PF2DS030	-0.591203	36.179921	2099	23	2	0	21	21	1	1
161	PF2DS031	-0.591380	36.179987	2102	30	2	0	28	27	2	1
162	PF2DS032	-0.591582	36.180018	2102	61	3	0	58	58	2	1
163	PF2DS033	-0.591755	36.180032	2105	117	6	0	111	108	8	1
164	PF2DS034	-0.591939	36.180062	2107	52	9	0	43	43	8	1
165	PF2DS035	-0.592107	36.180095	2107	112	16	0	96	91	13	8
166	PF2DS036	-0.592267	36.180141	2105	120	5	0	115	114	6	0
167	PF2DS037	-0.592427	36.180205	2105	104	4	0	100	95	8	1
168	PF2DS038	-0.592560	36.180328	2108	36	9	0	27	27	5	4
169	PF2DS039	-0.592705	36.180432	2105	0	0	0	0	0	0	0
170	PF2DS040	-0.592895	36.180539	2109	30	0	0	30	29	1	0
171	PF2DS041	-0.593078	36.180594	2113	1	0	0	1	0	1	0
172	PF2DS042	-0.590761	36.178966	2093	88	0	0	88	88	0	0
173	PF2DS043	-0.590951	36.179049	2096	58	1	0	57	57	1	0
174	PF2DS044	-0.591097	36.179116	2102	36	2	0	34	34	0	2
175	PF2DS045	-0.591290	36.179188	2102	0	0	0	0	0	0	0
176	PF2DS046	-0.591492	36.179242	2105	0	0	0	0	0	0	0
177	PF2DS047	-0.591671	36.179274	2108	0	0	0	0	0	0	0
178	PF2DS048	-0.591852	36.179327	2107	1	0	1	0	0	1	0
179	PF2DS049	-0.592048	36.179391	2109	0	0	0	0	0	0	0
180	PF2DS050	-0.592256	36.179447	2112	0	0	0	0	0	0	0
181	PF2DS051	-0.592446	36.179514	2112	0	0	0	0	0	0	0
182	PF2DS052	-0.592624	36.179566	2115	0	0	0	0	0	0	0
183	PF2DS053	-0.592827	36.179621	2117	1	0	1	0	0	1	0
184	PF2DS054	-0.593009	36.179679	2117	0	0	0	0	0	0	0
185	PF2DS055	-0.593205	36.179733	2117	1	0	1	0	0	1	0
186	PF2DS056	-0.593424	36.179791	2118	0	0	0	0	0	0	0
187	PF2DS057	-0.593610	36.179829	2120	0	0	0	0	0	0	0
188	PF2DS058	-0.593803	36.179912	2122	0	0	0	0	0	0	0

189	PF2DS059	-0.593988	36.179992	2124	0	0	0	0	0	0	0
190	PF2DS060	-0.594162	36.180066	2126	0	0	0	0	0	0	0
191	PF2DS061	-0.594337	36.180165	2124	0	0	0	0	0	0	0
192	PF2DS062	-0.594534	36.180254	2128	0	0	0	0	0	0	0
193	PF2DS063	-0.594721	36.180313	2129	0	0	0	0	0	0	0
194	PF2DS064	-0.594924	36.180413	2124	1	0	0	1	1	0	0
195	PF2DS065	-0.595109	36.180514	2126	58	0	3	55	56	2	0
196	PF2DS066	-0.595442	36.180174	2133	60	0	3	57	54	6	0
197	PF2DS067	-0.595232	36.180135	2131	32	0	1	31	31	1	0
198	PF2DS068	-0.595029	36.180110	2132	58	0	0	58	58	0	0
199	PF2DS069	-0.594844	36.180059	2131	79	0	1	78	77	2	0
200	PF2DS070	-0.594665	36.180005	2128	48	0	2	46	47	1	0
201	PF2DS071	-0.594491	36.179969	2128	75	0	1	74	74	1	0
202	PF2DS072	-0.594321	36.179926	2126	37	0	0	37	37	0	0
203	PF2DS073	-0.594122	36.179884	2124	3	0	0	3	3	0	0
204	PF2DS074	-0.593933	36.179834	2122	0	0	0	0	0	0	0
205	PF2DS075	-0.593744	36.179783	2120	0	0	0	0	0	0	0
206	PF2DS076	-0.593553	36.179731	2118	0	0	0	0	0	0	0
207	PF2DS077	-0.593299	36.179663	2117	0	0	0	0	0	0	0
208	PF2DS078	-0.593111	36.179605	2117	0	0	0	0	0	0	0
209	PF2DS079	-0.592923	36.179552	2118	1	0	0	1	1	0	0
210	PF2DS080	-0.592749	36.179513	2118	0	0	0	0	0	0	0
211	PF2DS081	-0.592547	36.179450	2115	1	0	1	0	0	1	0
212	PF2DS082	-0.592347	36.179379	2112	0	0	0	0	0	0	0
213	PF2DS083	-0.592140	36.179319	2109	1	0	0	1	0	1	0
214	PF2DS084	-0.591946	36.179224	2111	0	0	0	0	0	0	0
215	PF2DS085	-0.591752	36.179167	2108	0	0	0	0	0	0	0
216	PF2DS086	-0.591540	36.179101	2105	0	0	0	0	0	0	0
217	PF2DS087	-0.591358	36.178998	2106	0	0	0	0	0	0	0
218	PF2DS088	-0.591186	36.178896	2103	107	3	0	104	104	3	0
219	PF2DS089	-0.591056	36.178789	2099	54	0	0	54	54	0	0
220	PF2DS090	-0.590822	36.178617	2100	3	0	0	3	3	0	0

221	PF2DS091	-0.590951	36.178213	2100	1	0	0	1	1	0	0
222	PF2DS092	-0.591144	36.178284	2102	95	19	0	76	63	32	0
223	PF2DS093	-0.591318	36.178337	2102	32	11	0	21	16	12	4
224	PF2DS094	-0.591488	36.178406	2104	57	6	0	51	39	17	1
225	PF2DS095	-0.591686	36.178510	2108	90	10	0	80	71	17	2
226	PF2DS096	-0.591846	36.178558	2108	134	2	1	131	131	3	0
227	PF2DS097	-0.592036	36.178590	2110	3	2	0	1	1	1	1
228	PF2DS098	-0.592207	36.178684	2112	0	0	0	0	0	0	0
229	PF2DS099	-0.592388	36.178752	2114	6	0	0	6	6	0	0
230	PF2DS100	-0.592583	36.178812	2115	0	0	0	0	0	0	0
231	PF2DS101	-0.592758	36.178881	2116	1	0	1	0	1	0	0
232	PF2DS102	-0.592963	36.178931	2116	0	0	0	0	0	0	0
233	PF2DS103	-0.593147	36.178993	2115	0	0	0	0	0	0	0
234	PF2DS104	-0.593368	36.179070	2116	0	0	0	0	0	0	0
235	PF2DS105	-0.593599	36.179113	2117	0	0	0	0	0	0	0
236	PF2DS106	-0.593812	36.179196	2117	0	0	0	0	0	0	0
237	PF2DS107	-0.594002	36.179257	2118	1	0	0	1	1	0	0
238	PF2DS108	-0.594199	36.179300	2122	0	0	0	0	0	0	0
239	PF2DS109	-0.594380	36.179317	2122	0	0	0	0	0	0	0
240	PF2DS110	-0.594574	36.179339	2122	0	0	0	0	0	0	0
241	PF2DS111	-0.594792	36.179367	2124	0	0	0	0	0	0	0
242	PF2DS112	-0.594965	36.179416	2124	5	0	0	5	5	0	0
243	PF2DS113	-0.595150	36.179461	2125	2	0	0	2	2	0	0
244	PF2DS114	-0.595335	36.179511	2124	7	0	0	7	0	7	0
245	PF2DS115	-0.595559	36.179572	2129	0	0	0	0	0	0	0
246	PF2DS118	-0.594952	36.178964	2115	0	0	0	0	0	0	0
247	PF2DS119	-0.594767	36.178867	2115	0	0	0	0	0	0	0
248	PF2DS120	-0.594585	36.178795	2114	0	0	0	0	0	0	0
249	PF2DS121	-0.594318	36.178683	2109	0	0	0	0	0	0	0
250	PF2DS122	-0.594109	36.178632	2109	1	0	0	1	1	0	0
251	PF2DS123	-0.593884	36.178567	2109	0	0	0	0	0	0	0
252	PF2DS124	-0.593720	36.178506	2109	2	0	0	2	2	0	0

254Pi2DS126-0.50336436.178383210592019184.831255Pi2DS161-0.50547136.1784832107730271.06490256Pi2DS161-0.50562736.1794882119000 <t< th=""><th>253</th><th>PF2DS125</th><th>-0.593523</th><th>36.178433</th><th>2105</th><th>84</th><th>0</th><th>0</th><th>84</th><th>83</th><th>1</th><th>0</th></t<>	253	PF2DS125	-0.593523	36.178433	2105	84	0	0	84	83	1	0
255PH2D81270.93911430.17834321077302716490256PH2D8116-0.39562736.179148211900 </td <td>254</td> <td>PF2DS126</td> <td>-0.593336</td> <td>36.178385</td> <td>2105</td> <td>92</td> <td>0</td> <td>1</td> <td>91</td> <td>88</td> <td>3</td> <td>1</td>	254	PF2DS126	-0.593336	36.178385	2105	92	0	1	91	88	3	1
256PH2DS1160.59562736.179148211900 </td <td>255</td> <td>PF2DS127</td> <td>-0.593114</td> <td>36.178343</td> <td>2107</td> <td>73</td> <td>0</td> <td>2</td> <td>71</td> <td>64</td> <td>9</td> <td>0</td>	255	PF2DS127	-0.593114	36.178343	2107	73	0	2	71	64	9	0
257PF2DS1160.59562736.1791482119000000000000258PF2DS128-0.59223336.1782782108841007468160260PF2DS130-0.59274736.17827821082245901651141082261PF2DS131-0.59224736.17817321074404400366860262PF2DS133-0.59276736.178173210344042035229411000263PF2DS133-0.59267636.178173210344042035212411100264PF2DS133-0.59187336.17806210484110761221265PF2DS135-0.59147336.1778042102223019768100266PF2DS137-0.5912436.17780210222301921750267PF2DS137-0.5731836.17454197630122100268PF3DS004-0.5734836.1784519763052019422271PF3DS004-0.5778536.1754719702505219420272PF3DS06	256	PF2DS116	-0.595627	36.179148	2119	0	0	0	0	0	0	0
288Pf2DS128-0.59227136.1782/62210865406148170259Pf2DS120-0.59227136.1782/822108841007468160260Pf2DS130-0.59247336.1782/82210822450016.51141082261Pf2DS131-0.59247536.1781/72107440440366354860262Pf2DS132-0.59107636.1781/721034045203522941100263Pf2DS133-0.59163836.17802210487807361221264Pf2DS135-0.59147336.17964210487807368190265Pf2DS13-0.5914336.17802210487807968190266Pf2DS13-0.5914336.1780421006105420267Pf2DS10-0.5761836.1745419730122100270Pf3DS00-0.5766836.17507197502104194200271Pf3DS00-0.5776636.1750419719602104194200273Pf3DS00-0.5776636.175071976	257	PF2DS116	-0.595627	36.179148	2119	0	0	0	0	0	0	0
259PF2DS1290.50227136.1782782108841007468160260PF2DS1310.55224736.17823921082245901651141082261PF2DS1320.55224536.178137210344044003522941100262PF2DS1330.55926736.1781721034045203522941100263PF2DS1340.59145736.178042104177300147121551264PF2DS1340.59145736.1796421022230191775<	258	PF2DS128	-0.592923	36.178296	2108	65	4	0	61	48	17	0
260 PF2DS130 0.592477 36.178239 2108 224 59 0 165 114 108 2 261 PF2DS131 -0.592254 36.178183 2107 404 440 0 396 354 86 0 262 PF2DS133 -0.59167 36.17817 2103 404 52 0 352 294 110 0 263 PF2DS133 -0.591658 36.178026 2104 84 11 0 73 61 22 1 264 PF2DS136 -0.59144 36.177864 2103 87 8 0 79 68 19 0 266 PF2DS137 -0.59144 36.177807 2102 22 3 0 1 2 1 0 3 0 267 PF2DS137 -0.57163 36.175847 1976 3 0 2 1 0 3 0 269 PF3DS004	259	PF2DS129	-0.592771	36.178278	2108	84	10	0	74	68	16	0
261PF2D8131-0.59225436.17818321074404400396354860262PF2D8132-0.59027636.17811721034645203522941100263PF2D8133-0.59187236.1780421041773000147121551264PF2D8134-0.59145736.17802210484110736122.01265PF2D8137-0.59144736.1787021022230191750266PF2D8137-0.59102136.1787021022230191750267PF2D8137-0.59102136.17876210223012210268PF3D8001-0.5755536.174754197630121030270PF3D803-0.5757536.17567197725052019422271PF3D804-0.5766736.17567197668013991000274PF3D806-0.5774436.17639197668013220275PF3D806-0.5774436.1764919762013200274PF3D806-0.5784536.17849197620	260	PF2DS130	-0.592467	36.178239	2108	224	59	0	165	114	108	2
262Pf2DS132-0.5920766.67811721034045203522941100263Pf2DS134-0.59187236.178042104177300147121551264Pf2DS134-0.59185836.1780421048411073681900265Pf2DS136-0.59124436.17704210387801917.750266Pf2DS137-0.59124436.17700210222301917.750267Pf2DS137-0.5912436.17780821022230121030268Pf3DS00-0.5751536.174541976301210302270Pf3DS03-0.5757536.1767197025052019.4422271Pf3DS04-0.5768736.17507198210906103991002273Pf3DS05-0.57796136.1764919741960219419420274Pf3DS06-0.57795136.17448197540132201274Pf3DS07-0.57795136.178491976201322011101<	261	PF2DS131	-0.592254	36.178183	2107	440	44	0	396	354	86	0
263Pf2DS1330.5918723.61780x42104177300147121551264Pf2DS1340.5916583.61780x62104841107361221265Pf2DS1350.5914573.617964210387807968190266Pf2DS1370.5910213.61787021022250191750267Pf2DS1370.5910213.61743551977301221030268Pf3DS0010.575183.6174551977301221030269Pf3DS0020.575753.617516719702502103001730270Pf3DS0040.576673.617507198210906103991000271Pf3DS0050.577443.61763219766802194194200273Pf3DS0060.577443.6178491972013011100274Pf3DS0070.578953.617848197540132200275Pf3DS0100.578953.617844197300000000	262	PF2DS132	-0.592076	36.178117	2103	404	52	0	352	294	110	0
264Pf2D\$134-0.59165836.1780262104841107361221265Pf2D\$135-0.5914736.177964210387807968190266Pf2D\$137-0.59124436.17787021022230191750267Pf2D\$137-0.59124436.17780821006105420268Pf3D\$001-0.5751536.1745419730122103270Pf3D\$002-0.5757536.1751671970250520197422271Pf3D\$004-0.5768736.1751671970250520197302272Pf3D\$004-0.5768736.175071982197680219419420273Pf3D\$006-0.5776436.1759719741960219419420274Pf3D\$007-0.5795136.17818197540132200274Pf3D\$007-0.5788536.17818197540111100275Pf3D\$008-0.5788536.178181973000000000274Pf3D\$010-0.5788536.	263	PF2DS133	-0.591872	36.178084	2104	177	30	0	147	121	55	1
265Pf2DS135-0.59144736.17964210387807968190266Pf2DS136-0.59124436.1787021022230101750267Pf2DS137-0.59102136.1780821006105420268PF3DS001-0.5755336.174541977301221030270PF3DS03-0.5755336.17454197630520194.022271PF3DS04-0.5768736.17507198210906103991000272PF3DS05-0.5776636.17597198210906103991000273PF3DS06-0.5774436.17592197668056364000274PF3DS07-0.5785536.17418197540111000275PF3DS08-0.5785536.174181975201311000	264	PF2DS134	-0.591658	36.178026	2104	84	11	0	73	61	22	1
266PF2DS136-0.59124436.17787021022230191750267PF2DS137-0.59102136.17780821006105420268PF3DS001-0.57631836.174355197730122100269PF3DS003-0.5757536.17454197630210300270PF3DS004-0.5766736.175071970250520194420271PF3DS05-0.5776636.1758919741960219419420273PF3DS06-0.5774436.17632197668013220274PF3DS06-0.5789536.17818019764013220275PF3DS06-0.5789536.17818019762011100276PF3DS080-0.5789536.178180197620111000276PF3DS01-0.5789536.178441973000000000276PF3DS010-0.5789536.1784419730000000000277PF3DS010-0.5789536.17844 <td< td=""><td>265</td><td>PF2DS135</td><td>-0.591457</td><td>36.177964</td><td>2103</td><td>87</td><td>8</td><td>0</td><td>79</td><td>68</td><td>19</td><td>0</td></td<>	265	PF2DS135	-0.591457	36.177964	2103	87	8	0	79	68	19	0
267Pr2DS137-0.59102136.1780821006105420268Pf3DS001-0.57531836.17455197730122100269Pf3DS002-0.5755536.17457197630210302103003003003003003003003003003003003003003003003003000<	266	PF2DS136	-0.591244	36.177870	2102	22	3	0	19	17	5	0
268PF3DS001-0.57631836.174355197730122100269PF3DS002-0.57575536.17475419763021030270PF3DS03-0.5717536.1751719702505201942271PF3DS04-0.57668736.1750919821090610399100272PF3DS05-0.57766436.1758919741960219419420273PF3DS06-0.57746436.1758919741960219419420274PF3DS07-0.57745136.17418197568013220274PF3DS08-0.57785136.1781819754013220275PF3DS08-0.5788536.1781819752011110276PF3DS09-0.5788536.178181975200990000276PF3DS01-0.5789536.17841973000000000277PF3DS01-0.5789536.189221979145003142141400278PF3DS01-0.5810536.180331979 <td< td=""><td>267</td><td>PF2DS137</td><td>-0.591021</td><td>36.177808</td><td>2100</td><td>6</td><td>1</td><td>0</td><td>5</td><td>4</td><td>2</td><td>0</td></td<>	267	PF2DS137	-0.591021	36.177808	2100	6	1	0	5	4	2	0
269PF3DS002-0.5757536.174754197630210303270PF3DS03-0.57517536.1750719702505201942271PF3DS04-0.5766736.1750719821090610399100272PF3DS05-0.5776636.1754919741960219419420273PF3DS06-0.5774436.1653219766805636440274PF3DS07-0.5785836.1741819754013220275PF3DS08-0.5785836.1784019762011100276PF3DS09-0.57838536.1781819762011100276PF3DS09-0.57838536.178401976200000000277PF3DS01-0.57839536.17840197300000000000278PF3DS01-0.57839536.17840197414503142141400279PF3DS12-0.5802836.180241979145012210003141300<	268	PF3DS001	-0.576318	36.174355	1977	3	0	1	2	2	1	0
270PF3DS003-0.57157536.17516719702505201942271PF3DS004-0.57668736.17509719821090610399100272PF3DS005-0.57706036.17584919741960219419420273PF3DS006-0.57744436.175321976680132200274PF3DS007-0.57795136.17748197540132200275PF3DS008-0.57838536.17840197620111100276PF3DS009-0.57838536.178401976200090000276PF3DS009-0.57838536.1784019762000900000276PF3DS010-0.57839536.178401973000	269	PF3DS002	-0.575755	36.174754	1976	3	0	2	1	0	3	0
271 PF3DS004 -0.576687 36.17507 1982 109 0 6 103 99 10 0 272 PF3DS005 -0.577066 36.175849 1974 196 0 2 194 194 2 0 273 PF3DS006 -0.577444 36.17632 1976 68 0 5 63 64 4 0 274 PF3DS007 -0.577951 36.17418 1975 4 0 1 3 2 2 0 275 PF3DS008 -0.578355 36.178180 1976 2 0 1 1 1 0 0 276 PF3DS008 -0.578355 36.17874 1973 95 0 0 9 94 1 0 277 PF3DS010 -0.579393 36.179620 1973 0 0 0 0 0 0 0 0 0 0 1 1 0	270	PF3DS003	-0.575175	36.175167	1970	25	0	5	20	19	4	2
272PF3DS05-0.57706636.17584919741960219419420273PF3DS06-0.57744436.17653219766805636440274PF3DS07-0.57795136.17741819754013220275PF3DS08-0.57838536.17818019762011110276PF3DS09-0.57895336.17874419739500959410277PF3DS01-0.57939336.179620197300000000278PF3DS01-0.57993436.1802219791450314214140279PF3DS012-0.5806836.1808419822601252510280PF3DS014-0.5816436.18633197910028820281PF3DS015-0.5816436.1835019822003171730283PF3DS016-0.58150436.1835419783300333210284PF3DS017-0.5816936.18372197930033300302910	271	PF3DS004	-0.576687	36.175097	1982	109	0	6	103	99	10	0
273PF3DS006-0.57744436.17653219766805636440274PF3DS007-0.57795136.17741819754013220275PF3DS008-0.57838536.17818019762011110276PF3DS009-0.57830536.17874419739500959410276PF3DS010-0.57939336.17920197300000000277PF3DS011-0.57939336.18029219731450314214140278PF3DS012-0.58026836.18098419822601252510280PF3DS013-0.58076536.18163197910028820281PF3DS014-0.58116136.182311198034034343220282PF3DS015-0.58126436.18359019822003171730283PF3DS016-0.5810436.1834419783300333210284PF3DS017-0.58108936.18317219793000333210	272	PF3DS005	-0.577066	36.175849	1974	196	0	2	194	194	2	0
274PF3DS007-0.57795136.17741819754013220275PF3DS008-0.57838536.1781801976201110276PF3DS009-0.57880536.17878419739500959410277PF3DS010-0.57939336.179620197300000000278PF3DS011-0.57989136.1802219791450314214140279PF3DS012-0.5806836.18098419822601252510280PF3DS013-0.58076536.181663197910028820281PF3DS014-0.58116136.18231119803400343220282PF3DS015-0.5812636.18359019822003171730283PF3DS016-0.58150436.1834319783300333210284PF3DS017-0.58108936.1831721979300030302910	273	PF3DS006	-0.577444	36.176532	1976	68	0	5	63	64	4	0
275PF3DS008-0.57838536.17818019762011110276PF3DS009-0.57880536.17878419739500959410277PF3DS010-0.57939336.179620197300000000278PF3DS011-0.57989136.18029219791450314214140279PF3DS012-0.5806836.1808419822601252510280PF3DS013-0.58076536.18163197910028820281PF3DS014-0.58116136.18231119803400343220283PF3DS016-0.58150436.1833419783300333210284PF3DS017-0.5816936.18317219793000302910	274	PF3DS007	-0.577951	36.177418	1975	4	0	1	3	2	2	0
276PF3DS009-0.57880536.17878419739500959410277PF3DS010-0.57939336.179620197300000000278PF3DS011-0.57989136.18029219791450314214140279PF3DS012-0.58026836.18098419822601252510280PF3DS013-0.58076536.181633197910028820281PF3DS014-0.58116136.18231119803400343220282PF3DS015-0.58212636.18359019822003171730283PF3DS016-0.58150436.1833419783300302910284PF3DS017-0.58189936.18317219793000302910	275	PF3DS008	-0.578385	36.178180	1976	2	0	1	1	1	1	0
277PF3DS010-0.57939336.17962019730000000000278PF3DS011-0.57989136.18029219791450314214140279PF3DS012-0.58026836.18098419822601252510280PF3DS013-0.58076536.181663197910028820281PF3DS014-0.58116136.18231119803400343220282PF3DS015-0.58126436.18359019822003171730283PF3DS016-0.58150436.1833419783300333210284PF3DS017-0.58108936.18317219793000302910	276	PF3DS009	-0.578805	36.178784	1973	95	0	0	95	94	1	0
278PF3DS011-0.57989136.18029219791450314214140279PF3DS012-0.58026836.18098419822601252510280PF3DS013-0.58076536.181663197910028820281PF3DS014-0.58116136.18231119803400343220282PF3DS015-0.58212636.18359019822003171730283PF3DS016-0.58150436.1833419783300333210284PF3DS017-0.58108936.18317219793000302910	277	PF3DS010	-0.579393	36.179620	1973	0	0	0	0	0	0	0
279 PF3DS012 -0.580268 36.180984 1982 26 0 1 25 25 1 0 280 PF3DS013 -0.580765 36.181663 1979 10 0 2 8 8 2 0 281 PF3DS014 -0.581161 36.182311 1980 34 0 0 34 32 2 0 282 PF3DS015 -0.582126 36.183590 1982 20 0 3 17 17 3 0 283 PF3DS016 -0.581504 36.18354 1978 33 0 0 33 32 1 0 284 PF3DS017 -0.581089 36.18372 1979 30 0 0 30 29 1 0	278	PF3DS011	-0.579891	36.180292	1979	145	0	3	142	141	4	0
280 PF3DS013 -0.580765 36.181663 1979 10 0 2 8 8 2 0 281 PF3DS014 -0.581161 36.182311 1980 34 0 0 34 32 2 0 282 PF3DS015 -0.582126 36.183590 1982 20 0 3 17 17 3 0 283 PF3DS016 -0.581504 36.183590 1982 33 0 0 33 32 1 0 284 PF3DS017 -0.581089 36.183172 1979 30 0 0 30 29 1 0	279	PF3DS012	-0.580268	36.180984	1982	26	0	1	25	25	1	0
281 PF3DS014 -0.581161 36.182311 1980 34 0 0 34 32 2 0 282 PF3DS015 -0.58126 36.183590 1982 20 0 3 17 17 3 0 283 PF3DS016 -0.581504 36.183834 1978 33 0 0 33 32 1 0 284 PF3DS017 -0.581089 36.183172 1979 30 0 0 30 29 1 0	280	PF3DS013	-0.580765	36.181663	1979	10	0	2	8	8	2	0
282 PF3DS015 -0.582126 36.183590 1982 20 0 3 17 17 3 0 283 PF3DS016 -0.581504 36.183834 1978 33 0 0 33 32 1 0 284 PF3DS017 -0.581089 36.183172 1979 30 0 0 30 29 1 0	281	PF3DS014	-0.581161	36.182311	1980	34	0	0	34	32	2	0
283 PF3DS016 -0.581504 36.183834 1978 33 0 0 33 32 1 0 284 PF3DS017 -0.581089 36.183172 1979 30 0 0 30 29 1 0	282	PF3DS015	-0.582126	36.183590	1982	20	0	3	17	17	3	0
284 PF3DS017 -0.581089 36.183172 1979 30 0 0 30 29 1 0	283	PF3DS016	-0.581504	36.183834	1978	33	0	0	33	32	1	0
	284	PF3DS017	-0.581089	36.183172	1979	30	0	0	30	29	1	0

285	PF3DS018	-0.580578	36.182360	1974	0	0	0	0	0	0	0
286	PF3DS019	-0.580224	36.181743	1974	49	0	0	49	48	1	0
287	PF3DS020	-0.579860	36.181182	1978	0	0	0	0	0	0	0
288	PF3DS021	-0.579378	36.180324	1975	27	0	1	26	26	1	0
289	PF3DS022	-0.578915	36.179690	1973	34	0	0	34	34	0	0
290	PF3DS023	-0.578425	36.178868	1970	27	0	1	26	26	1	0
291	PF3DS024	-0.577966	36.178127	1972	1	0	1	0	0	1	0
292	PF3DS025	-0.577481	36.177402	1974	3	0	1	2	2	1	0
293	PF3DS026	-0.577010	36.176695	1972	5	0	0	5	5	0	0
294	PF3DS027	-0.576510	36.175947	1971	35	0	1	34	35	0	0
295	4	-0.576052	36.175333	1973	0	0	0	0	0	0	0
296	PF3DS028	-0.576051	36.175332	1973	1	0	0	1	0	1	0
297	PF3DS029	-0.575630	36.175854	1967	36	0	3	33	33	3	0
298	PF3DS030	-0.576045	36.176540	1965	3	0	1	2	2	1	0
299	PF3DS031	-0.576434	36.177310	1968	0	0	0	0	0	0	0
300	PF3DS032	-0.576836	36.178122	1966	0	0	0	0	0	0	0
301	PF3DS033	-0.577213	36.178859	1963	0	0	0	0	0	0	0
302	PF3DS034	-0.577721	36.179649	1965	2	0	0	2	2	0	0
303	PF3DS035	-0.578271	36.180504	1964	0	0	0	0	0	0	0
304	PF3DS036	-0.578912	36.181176	1972	0	0	0	0	0	0	0
305	PF3DS037	-0.579473	36.182171	1973	0	0	0	0	0	0	0
306	PF3DS038	-0.579816	36.183036	1971	0	0	0	0	0	0	0
307	PF3DS039	-0.580102	36.183762	1971	0	0	0	0	0	0	0
308	PF3DS040	-0.580475	36.184366	1972	0	0	0	0	0	0	0
309	PF3DS041	-0.584606	36.180443	2020	0	0	0	0	0	0	0
310	PF3DS042	-0.584858	36.180844	2019	5	0	2	3	1	4	0
311	PF3DS043	-0.585201	36.181411	2019	0	0	0	0	0	0	0
312	PF3DS044	-0.585563	36.182052	2021	162	0	1	161	159	3	0
313	PF3DS045	-0.585729	36.182454	2015	129	0	2	127	127	2	0
314	PF3DS046	-0.586409	36.181641	2027	105	0	1	104	104	1	0
315	PF3DS047	-0.585980	36.180637	2031	0	0	0	0	0	0	0
316	PF3DS048	-0.585508	36.179881	2031	134	2	0	132	131	2	1

317	PF3DS049	-0.585147	36.179092	2036	64	0	0	64	62	2	0
318	PF3DS051	-0.584219	36.178121	2035	0	0	0	0	0	0	0
319	PF3DS050	-0.585056	36.178528	2038	75	3	0	72	71	4	0
320	PF3DS052	-0.582441	36.176635	2019	0	0	0	0	0	0	0
321	PF3DS053	-0.582243	36.176331	2021	45	0	0	45	42	3	0
322	PF3DS054	-0.582236	36.176057	2020	106	0	3	103	103	3	0
323	PF3DS055	-0.582043	36.175598	2018	1	0	1	0	0	1	0
324	PF3DS056	-0.581511	36.177257	2008	0	0	0	0	0	0	0
325	PF3DS057	-0.581373	36.177082	2008	19	0	1	18	18	1	0
326	PF3DS058	-0.581291	36.176797	2006	10	0	0	10	8	2	0
327	PF3DS059	-0.581092	36.176636	2007	154	0	1	153	153	1	0
328	PF3DS060	-0.581005	36.176401	2006	0	0	0	0	0	0	0
329	PF3DS061	-0.580353	36.175406	2004	8	0	2	6	6	2	0
330	PF3DS062	-0.580290	36.175288	2005	0	0	0	0	0	0	0
331	PGDS01	-0.604206	36.178982	2185	0	0	0	0	0	0	0
332	PGDS02	-0.604174	36.178991	2185	7	0	0	7	6	1	0
333	PGDS03	-0.604103	36.179047	2178	4	0	0	4	3	1	0
334	PGDS04	-0.604057	36.179064	2178	0	0	0	0	0	0	0
335	PGDS05	-0.604044	36.179040	2178	0	0	0	0	0	0	0
336	PGDS06	-0.604111	36.179012	2183	37	0	0	37	36	1	0
337	PGDS07	-0.604165	36.178999	2185	6	0	0	6	3	3	0
338	PGDS08	-0.604183	36.178982	2185	0	0	0	0	0	0	0
339	PGDS09	-0.604199	36.178951	2185	0	0	0	0	0	0	0
340	PGDS10	-0.604170	36.178980	2185	4	0	0	4	2	2	0
341	PGDS11	-0.604110	36.179012	2183	22	0	0	22	22	0	0
342	PGDS12	-0.604030	36.179033	2178	0	0	0	0	0	0	0
343	PGDS13	-0.604119	36.178980	2183	8	0	0	8	8	0	0
344	PGDS14	-0.604171	36.178966	2185	2	0	0	2	2	0	0
345	PGDS15	-0.604119	36.178969	2183	9	0	0	9	8	1	0
346	PGDS16	-0.603935	36.178930	2183	8	0	0	8	8	0	0
347	PGDS17	-0.603876	36.178961	2183	6	0	0	6	5	1	0
348	PGDS18	-0.603799	36.178994	2181	5	0	0	5	5	0	0

349	PGDS19	-0.603792	36.178970	2181	1	0	1	0	0	1	0
350	PGDS20	-0.603858	36.178937	2183	3	0	0	3	3	0	0
351	PGDS21	-0.603904	36.178921	2183	18	0	0	18	18	0	0
352	PGDS22	-0.603896	36.178915	2183	9	0	0	9	8	1	0
353	PGP023	-0.603830	36.178947	2181	7	0	1	6	6	1	0
354	PGDS24	-0.603764	36.178978	2181	4	0	0	4	4	0	0
355	PGDS25	-0.603740	36.178956	2181	12	0	0	12	11	1	0
356	PCDS26	-0.603820	36.178898	2181	23	0	0	23	23	0	0
357	PGDS27	-0.603749	36.178929	2181	11	0	0	11	10	0	1
358	PGDS28	-0.603701	36.178998	2181	10	0	0	10	10	0	0
359	PGDS29	-0.603661	36.179041	2175	17	0	0	17	17	0	0
360	PGDS30	-0.603609	36.179089	2175	3	0	0	3	3	0	0
361	PGDS31	-0.603578	36.179050	2175	6	0	0	6	6	0	0
362	PGDS32	-0.603633	36.179012	2181	4	0	0	4	4	0	0
363	PGDS33	-0.603697	36.178954	2181	12	0	1	11	11	1	0
364	PGDS34	-0.603731	36.178919	2181	10	0	0	10	10	0	0
365	PGDS35	-0.603607	36.179001	2181	20	0	0	20	20	0	0
366	PGDS36	-0.603558	36.179028	2174	11	0	0	11	11	0	0
367	PGDS37	-0.603504	36.179071	2174	9	0	1	8	7	2	0
368	PGDS38	-0.603419	36.179111	2174	5	0	0	5	5	0	0
369	PGDS39	-0.603375	36.179139	2174	6	0	0	6	6	0	0
370	PGDS40	-0.603350	36.179116	2174	8	0	0	8	8	0	0
371	PGDS41	-0.603415	36.179033	2174	5	0	0	5	4	1	0
372	PGDS42	-0.603474	36.178974	2179	5	0	0	5	5	0	0
373	PGDS43	-0.603510	36.178948	2179	7	0	2	5	5	1	1
374	PGDS44	-0.603485	36.178936	2179	4	1	0	3	3	0	1
375	PGDS45	-0.603434	36.178995	2179	21	0	0	21	21	0	0
376	PGDS46	-0.603363	36.179074	2174	22	0	0	22	22	0	0
377	PGDS47	-0.603303	36.179112	2174	48	0	0	48	48	0	0
378	PGDS48	-0.603290	36.179093	2172	1	0	0	1	1	0	0
379	PGDS49	-0.603344	36.179044	2174	1	0	0	1	1	0	0
380	PGDS50	-0.603385	36.178977	2179	47	0	0	47	46	1	0

381	PGDS51	-0.603364	36.178974	2179	8	0	0	8	8	0	0
382	PGDS52	-0.603306	36.179040	2174	8	0	0	8	7	1	0
383	PGDS53	-0.603218	36.179075	2172	7	0	0	7	7	0	0
384	PGDS54	-0.603145	36.179092	2172	11	0	0	11	11	0	0
385	PGDS55	-0.603122	36.179069	2172	16	0	0	16	16	0	0
386	PGDS56	-0.603187	36.179008	2176	10	0	0	10	10	0	0
387	PGDS57	-0.603226	36.178987	2176	8	0	0	8	8	0	0

5.3 Behaviour of major elements during pedogenesis

Unconsolidated pyroclastic volcanic ash (tephra) and other volcanic ejecta (such as pumice) consist of comminuted minerals that contain a large amount of volcanic glass (Shoji et al., 1993). Volcanic glass is high in Si and Al (originating from primary minerals such as feldspar, hornblende, pyroxene, olivine, and bitotite, and silica minerals [e.g. SiO₂]) [Dahlgren et al., 1993; Nakagawa and Ohba, 2003]). Si and Al are rapidly leached during weathering under tropical climate conditions and precipitate in large amounts as noncrystalline material, as well as nanocrystalline material (Harsh, 2005). Chemical weathering of Si in volcanic soils is generally characterised by the formation of secondary noncrystalline and nanocrystalline SRO (short-range-ordered) oxide phases (e.g. allophane, imogolite, and opaline silica) as Si is rapidly leached by Fe and Al (hydr)oxide (e.g. amorphous ferrihydrite). Further weathering results in the formation of more crystalline Fe/Al oxides and aluminosilicate clay minerals, such as crystalline halloysite and kaolinite (Shoji et al., 1993; Walther, 1996; Hiradate et al., 2010; Jordanova, 2016).

5.3.1 Behaviour of alkali and alkaline earth elements Ca, Mg, Na and K during pedogenesis

The transformation of secondary mineral phases to crystalline mineral phases in volcanic soils during pedogenesis is highly dependent on the intensity of local weathering (e.g. increases in MAP and MAT and subaerial exposure and time). Weathering of primary minerals into in-situ secondary minerals and Fe and Mn oxides is associated with the removal of more mobile elements (e.g. alkali and alkaline earth elements such as Ca, Mg, Na and K [Chadwick et al., 1990]) through leaching and the enrichment of Al, Alo (e.g. all secondary Al products [Mahaney and Fahey, 1988]) and Sio (e.g. allophane), as well as Feo. Both Alo and Feo are thought to generally approximate amorphous/noncrystalline ferrihydrite in palaeosols (Parfitt and Childs, 1988; Mahaney et al., 2014) but can also indicate other Al and Fe (hydr)oxides. Decreasing total concentrations of alkali and alkaline earth elements generally reflect weathering of feldspars and other minerals and the removal of base cations (Nesbitt and Young, 1989; Sheldon and Tabour, 2009; Mohanty and Nanda, 2016). For example, loss of K can result from the breakdown of plagioclase feldspar, biotite and other minerals. As such, increased concentrations of this group of elements are interpreted in the Prospect Farm sediments as being most likely to signal additions of chemically unaltered parent material through physical weathering processes (e.g. incorporation of "fresh" material through removal of material from exposure upslope by colluviation or from proximal or distal sources through aeolian processes) (Kraus 1999; Retallack, 2008). Alternatively, the accumulation of alkali elements has also been shown to occur with increasing soil salinity in semi-desert and desert environments. Where alkaline earth elements increase with first transition metals and Al, this is likely to represent hydrolysis during later phases of weathering, and the formation of more ordered and complex clay minerals in the smectite chlorite and kaolinite-serpentine groups; such as montmorillonite, illite, halloysite and kaolinite (Neall, 2009).

5.3.2 Behaviour of Al and Si during pedogenesis

Al is generally considered to be more stable/immobile than Si during weathering but has been shown to become mobilised and removed under highly alkaline and acidic conditions (Chadwick et al., 2003;

Retallack, 2008). Modern volcanic soils and palaeosols in Japan, developing on tephra under humid conditions, show strong positive correlations between Si_o and Al_t and between Al_o and Al_t, whereas total Si content decreases with increased Al_o and Si_o (Nanzyo et al., 2002a,b). This demonstrates that: 1) Al generally has low mobility in volcanic soils; 2) higher total Si concentrations are generally reflective of unweathered primary crystalline material but are not a direct analogue for oxides of silicon (e.g. SiO₂); 3) Al_t acts as a rough indicator of Al_o and Si_o. It is however unclear to what extent increased Al_t is reflective of Al-humus complexes that occur in the A/O horizons of non-allophanic Andosols (Takahashi and Dahlgren, 2016). The ratio of Al₂O₃/SiO₂ in sediments is widely used as an indicator of clayeyness and hydrolysis, as Al₂O₃ is accumulated relative to Si as clay minerals form (Sheldon and Tabor, 2009). While Sit is not though to represent SiO₂, this ratio may still reflect clay mineral formation in the Prospect Farm sequence (i.e. changes from incipient to more advance weathering), provided that physical additions of unweathered material do not affect the ratio.

5.3.3 Behaviour of Fe and Mn during pedogenesis

Under tropical weathering regimes, concentrations of Fe and Mn in soils are primarily controlled by redox conditions as well as pH. Under reducing conditions mobile ferric FeO is present and under oxidising conditions ferrous oxides (e.g. hematite [Fe₂O₃]) are enriched (Sheldon and Tabour, 2009). Increases in the concentration of Fe_o (oxidation of primary ferrous iron) in late Quaternary palaeosols on Mt. Kenya with volcanic material have been interpreted as indicating strong reducing conditions and possibly fluctuations in the magnetic content of parent material (Mahaney and Fahey, 1988; Mahaney et al., 2014). Shoji et al., (1993) report that under accelerated weathering conditions both clay content, and the crystalline clay minerals and crystalline Fe-oxides (Fe_d [e.g. ferrihydrite, goethite and hematite]) increase, while Al_o , Si_o , and Fe_o generally decrease. This trend is also reflected in soil developing on basaltic material, in which decreases in total Fe are thought to be related to the pedogenic transformation of secondary weathering products (i.e. Fe_o) to crystalline iron oxyhydroxides; (i.e. Fe_d: the sum total of secondary Fe, from pedogenic mineral such as hematite and goethite) that are indicative of oxidising soil conditions [Nordt and Driese, 2010; Beverly et al., 2015a; Mohanty and Nanda, 2016]) (Thomson et al., 2011; Jordanova, 2016). Thomson et al., (2011) established that there is a systematic relationship between decreases in total Fe and increased precipitation under reducing conditions related to decreases in the crystallinity of the Fe-(oxy) hydroxide phases (Jordanova, 2016; Mahaney et al., 1991). As such, variations in Fet are interpreted as reflecting shifts between oxidising and reducing conditions during the initial formation phase of Feo as well as the subsequent formation of Fed.

5.3.4 Behaviour of P during pedogenesis

Variations in total P have been commonly related to the weathering, addition, removal or translocation of primary P bearing minerals such as apatite (Walker and Syers, 1976; Yang et al., 2013), that are abundant in rhyolitic and andesitic tephra. As P is released from primary minerals it is transformed to occluded P and absorbed by secondary minerals (e.g. Al and Fe oxides). Over time non-occluded P becomes occluded and in well-developed soils P primarily exists as occluded P with sesquioxides, and as

organic P with colloidal organic matter. During these intermediate and final stages of pedogenesis, P can be redistributed in the soil profile during translocation of these compounds (Yang et al., 2013; Fink et al., 2016). With increased weathering and pedogenesis, secondary mineral P, organic P and occluded P should increase, and total P decrease. In this case loss of total P can act as a rough measure of the relative strength of weathering (Leamy, 1975). Following the same logic and using Ti as an immobile element, Sheldon and Tabour (2009) proposed that that P/Ti ratios can be used as a rough guide to palaeo-fertility in soils with volcanic parent material. P concentrations in parent material in volcanic soil is typically ~ 1000 ppm (Gray and Murphy, 2002), but also typically only a small proportion of P is unbound to primary or secondary mineral forms where humic acids limits phosphorus absorption (see Fink et al., 2016 and references therein). Consequently, available P, occurring in organic forms and in solution in soils is expected to be low (Yang et al., 2013). Total P concentrations in Prospect Farm Formation sediments were found to be very low (raging between 0.3-1.5 ppm) (see Chapter 6.4). Such low values of P_t values and the fact that Al_t (though to primarily approximate Al_o) and P_t demonstrate a negative correlation (R = -0.5238: see Table 6.1) suggest that P_t may reflect very strong weathering of apatite, and the addition of small amounts of unweathered material through colluviation. Alternatively, P_t may be more reflective of available P in solution desorbed by Al-Fe oxides, or in organic forms, or of both, rather than occluded P absorbed by Al-Fe oxides. In summary, without accompanying mineralogy, it is difficult to identify and assign separate sources of changes in variations of total phosphorous (P).

5.3.5 Behaviour of first transition metals during pedogenesis

First transition metals (e.g. Fe, Mn, Ti) have been shown to be positively correlated with noncrystalline material content and show stronger correlation with Feo than Alo or Sio. This suggests that these metals are residually enriched during secondary phases and that they preferentially accumulate with ferrihydrite rather than with allophane-imogolite (Nanzyo et al., 2002a,b). TiO2 (rutile) is often considered to be resistant to weathering during pedogenesis and is thus viewed as relatively immobile. However, redistribution of TiO₂ can occur under highly acid conditions and through physical weathering (Cornu et al., 1999). Under increased or prolonged weathering conditions TiO₂ often increases relative to other elements when expressed in terms of weight percentage (i.e. when the increase in the concentration of an oxide is reflected as a relative decrease in others) (Sheldon and Tabor, 2009; Mohanty and Nanda, 2016). While both Ti and Al oxides are considered to be immobile compared to other elements, Al is removed more easily during chemical weathering than Ti, thus the Ti/Al ratio is commonly used as an indicator of provenance and acidification (Sheldon and Tabor, 2009). However, in Prospect Farm Formation palaeosols, the increase in Tit that is observed from lower to upper horizons (see Chapter 6.4) is taken primarily to indicate enrichment of Ti associated with weathering products of secondary phases, as suggested by Nanzyo et al., (2002a,b). In such cases, Ti accumulates with Al, Mn and Fe in more ordered mineral and secondary oxide phases. Enrichment of Ti has been shown to be as great as 10% in soil developing on Ti rich volcanic parent material under accelerated tropical weathering conditions (Gracin et al., 2006; Blume et al., 2015). This is supported by the generally strong positive correlations and mirroring between Ti and Fe and Ti and Al throughout the sequence (see Chapter 6.4).

In general, therefore, spikes in Ti reflect the transformation (leaching and oxidation) of primary titanomagnetites in volcanic parent material to titanomagnemites and/or the formation of pseudorutile from weathering of ileminite (FeTiO₃), as well as the precipitation of anatase (residual TiO_2 ; where Ti is partially exchanged for Fe). As such, the Ti/Al ratio is not thought appropriate for use in this study.

5.4 Estimating arboreal vegetation cover using the D/P° index: benefits and limitations

The D/P index (Dicotyledons:Poaceae), first developed by Alexandre et al., (1997) has been widely used in African phytolith studies to reconstruct changes in arboreal vegetation cover. The index uses the ratio of globular granulate phytoliths (produced in woody dicotyledons and monocotyledons), vs. grass phytoliths to differentiate between semi-deciduous forest/wooded savanna mosaics and open savanna/grassland environments. The D/P index was updated by Bremond et al., (2005a, 2008b) and Barboni et al., (2007) to the D/P° index. This involved the removal of bulliform, long cells, and trichome morphotypes from the count, as their abundances can be highly environmentally controlled (i.e. related to an aspect of their immediate growing environment such as water availability [water stress] or to the degree of shading [Bremond et al., 2005b; Dunn et al., 2015]). Bremond et al., (2005a) demonstrated that a very strong relationship exists between canopy openness (quantified through Leaf Area Index measurements) and D/P° along a modern soil-vegetation transect. The appropriate threshold value of the D/P° index used to distinguish between forest and savanna vegetation types varies slightly between different areas of West Africa and partly depends on the setting, scale of the study, and approach adopted. For example, while some studies used only globular granulate morphotypes to calculate D/P° (e.g. Bremond et al., 2008a; Garnier et al., 2012, Aleman et al., 2014; Bremond et al., 2017), other studies include all decorated globular morphotypes minus echinate types, and recalculate published data for comparison (e.g. Neumann et al., 2009), or focus on a more general approach that considers the percentage of globular decorate types as an alternative to the D/P° index (e.g. Novello et al., 2012; 2015; 2017). Despite these minor differences, in general a D/P° value of >2 distinguishes the modern western and central African rainforest's vegetation in the Guineo-Congolian floristic zone, from mixed/grassland vegetation in the Sudanian and Sahelian zones (Bremond et al., 2005a; Novello et al., 2017). The version of the D/P° given below is that of Neumann et al., (2009)

 $D/P^{\circ} =$ <u> Σ </u> <u>Globular decorated</u>

 \sum of Bilobate + Cross + Saddle + Rondel + Trapeziform polylobate + Trapeziform short cell

Using the D/P° to determine woody cover within tropical savanna settings has proven difficult. In these settings D/P° values are often very low (<<1), even when arboreal vegetation cover is high. This representational bias is caused by two factors: 1) Low production of globular granulate and decorated phytoliths in woody savanna taxa (e.g. Acaica spp.); and 2) high production rates of GSSCs in grassdominated savanna and lake shore settings disguising the woody vegetation signal (Barboni et al., 2007; Neumann et al. 2009; Aleman et al., 2012). Using modern comparisons between globular decorated morphotypes and field estimate tree cover from samples across West African forest and savanna settings,

Novello et al., (2012, 2015, 2017) report that when the abundance of globular decorated types in a sample falls below the threshold value of 15.3% (over which ligneous cover is $\geq 40\%$) woody cover cannot be reliably estimated. Similarly, the validity of the D/P° in non-West African settings (e.g. Strömberg, 2003, 2004), and in particular in high elevation settings in East Africa where drier deciduous rainforest environments exist, has been highlighted as problematic by Barboni et al., (2007) and Bremond et al., (2008a). It is apparent both from studies of modern phytolith in soils (e.g. Bremond et al., 2005a; Bremond et al., 2008a,b; Mercader et al., 2011) and phytoliths extracted from plant tissues (e.g. Mercader et al., 2009; Collura and Neumann, 2017; as well as this study [see Chapter 4.4]), that woody dicotyledons found in East African Afromontane forest do not produce globular granulate/decorated morphotypes in the same abundances as woody species in semi-deciduous West African rainforest. Similar issues have been encountered in temperate forest environments globally. These tend to be dominated by a higher proportion of conifers and other taxa with low phytolith production rates (Kerns et al., 2001; Strömberg, 2004). In intertropical lowland settings (e.g. at 800-900 m a.s.l. in semi-deciduous forest/woodland around Lake Masoko in southern Tanzania) D/P° values have been shown to slightly underestimate ligneous cover (ranging from 0.5 - 0.2). However, in montane forest samples from relatively close canopy conditions on Mt. Kenya and Mt. Rungwe (~2000-3400 m a.s.l.) D/P° values are consistently very low at <0.01 (Barboni et al., 2007; Bremond et al., 2008a). Therefore, in East African highland forest and savanna settings, low D/P° values may not necessarily reflect low ligneous cover. If total abundance of globular decorated types is above 15.3% then the presence of arboreal cover $\geq 40\%$ can be inferred. However, as this threshold is geographically controlled, values below this threshold in East African settings do not necessarily indicate arboreal cover <40%. Considering these factors, the D/P° values were not considered as reliable in this study. Instead, the Forest Indicator ratio (FI-t) and globular decorate percentages (discussed in Section 5.6.5.2 below) were calculated using fossil samples from Prospect Farm; samples were also compared to globular decorated percentage-based ligneous cover estimates from West and Central Africa following Novello et al., (2017). This approach in theory provides more reliable relative estimations of arboreal cover in highland settings in East Africa than the D/P° index.

5.5 Alternatives to the D/P index for reconstruction vegetation physiognomy. Estimating arboreal vegetation cover using the FI-t ratio: benefits and limitations

The limitations of the D/P index in geographic regions outside West Africa has led several alternative, more generalized, approaches to reconstructing vegetation physiognomy to be proposed. Strömberg (2004) noted that it is often not possible to directly translate the relative abundance of phytoliths into the exact proportions of different plants types in a past ecosystem; so instead proposed the use of the FI-t ratio as a rough indicator of relative balance of forest and grass cover: in other words, vegetation openness. It is argued that considering all FIs (e.g. palms, ferns, conifers, woody and herbaceous dicots and woody monocots) in situations where the D/P index performs poorly, is more accurate but less precise (i.e. high values are interpreted as closed habitats, and low values as open habitats as the FI-t ratio is not calibrated against detailed measurements of modern vegetation cover).

In African settings, Novello et al., (2017) have demonstrated that the ratio of all GSSCs, globular echinates (associated with palms) and globular decorated types (associated with woody dicots) can be used as a rough indicator of changes in ligneous cover in lowland settings. Mercader et al., (2013) compared the total percentage of arboreal phytoliths (which included globular psilate forms as well as sclereid, blocky/tabular and globular decorated morphotypes) relative to GSSCs phytoliths in a fossil assemblage, to the range of arboreal phytoliths in samples from modern Miombo woodland from the Zambezian floristic zone. While there is a general association between higher tree cover and blocky/tabular and globular decorated types in modern soils samples from the Zambezian phytogeographic zone (Mercader et al., 2011) and from the Afromontane zone (Laurent Bremond pers. comm.), previous systematic attempts to use phytoliths as a proxy of tree cover density in Africa have not considered these morphotypes (e.g. Bremond et al., 2005a, 2008a; Laurent Bremond pers. comm.). Thus, establishing a statistically significant correlation between these morphotypes and tree cover density in East African Afromontane forest and in grass dominate vegetation types, through more accurate counting of types from modern soil samples, remains to be demonstrated and should be an avenue of future research (Novello et al., 2017; 2018).

Bremond et al., (2005a), Aleman et al., (2014) and Novello et al., (2015, 2017) exclude globular echinate types from the woody indicators in their phytolith calculations, as they are overproduced in palms and thus may lead to overestimations of arboreal vegetation, particularly in lake shore settings where they can be the dominant vegetation type. As sites at palaeolake highstand events in the Nakuru Basin have never been shown to reach the elevation of Prospect Farm, they are not considered to have been lake shore setting at any point in the past. As such, globular echinate types were included in the FI-t calculations in this thesis. Low percentages of globular echinates recorded in fossil samples (see Chapter (6.7.1), that co-occur with C₃ grasses and forest indicator morphotypes, support the idea that globular echinate types in the Prospect Farm sequence do not represent palm grove sites (usually lake shores and springs); that have been shown to have roughly equal percentages of GSSC (37%), globular echinate (34%) and globular decorated (29%) phytoliths (Novello et al., 2017). Instead their presence is more likely to relate to either aeolian additions from nearby lake shores and river courses, or to the presence of isolated palms at the lower forest boundary as Areaceae species are not commonly found in Afromontane forest. Globular psilate morphotypes have been shown to originate mainly from dicotyledons but may also be produced in smaller proportions by herbaceous monocotyledons including some Poaceae (Piperno, 1988; Kondo et al., 1994; Yost et al., 2018). Their production in woody dicotyledons in modern reference collections and abundance in soil samples from East Africa (Bremond, 2003; Barboni et al., 2007; Mercader et al., 2009; and this thesis) suggests it is appropriate that this morphotype be included in the FI-t counts in fossil phytoliths samples from Prospect Farm.

5.6 Estimating short grass (xeric) vs. long grass (mesic) savannas using the Iph index: benefits and limitations

The Iph index, that is based on the taxonomic division of GSSCs proposed by Twiss et al., (1969) and Twiss (1992), has proven reliable in reconstructing changes in these grass subfamilies along an aridityhumidity gradient in lowland tropical savannas in West Africa (Alexandre et al., 1997; Bremond et al., 2005a). An Iph threshold of between 20 and 40% has been set by West African studies to distinguish between these grassland types (Alexandre et al., 1997; Bremond et al., 2005a; Novello et al., 2017). However, Bremond et al., (2008a) record that in modern phytolith soil assemblages from the Afroalpine grassland, Bamboo, Afromontane forest and Hagenia-Hypericum zones on Mt. Rungwe and Mt. Kenya, Iph values range from 0-30%. The Iph index assumes that saddles are dominant in the Chloridoideae. Anomalously high Iph values at sites where no Chloridoideae grasses were recorded in the botanical survey were linked to the production of 'collapsed', 'long' and 'short' saddle sub-types produced by C₃ Pooideae and Bambusoideae subfamilies that dominate these vegetation zones. Of these sub-types the abundance of 'short' ('squat') saddles is very low, only forming 8% (0.1% of sum of all classified phytoliths) in the Bamboo zone and 14% (0.5%) in Afromontane forest and the Hagenia-Hypericum zones, where Pooid grass are present and Bamboo is absent. The collapsed and long saddles types accounted for 51% (1.1%), 92% (2.1%) respectively in the Bamboo zone and 18.5% (1.2%) and 86% (6.5%) in the Afromontane forest and the Hagenia-Hypericum zones. The occurrence of these saddle morphotypes in Bambusoideae, Arundinoideae and in lower proportion in Pooideae led Bremond et al., (2008a) to caution that Iph cannot be used as a proxy of xeric vs. mesic grasses in highland zones of East Africa when vegetation is dominated by C3 grasses. More recent studies of the taxonomic and environmental significance of GSSC phytoliths in East African grass subfamilies by Barboni and Bremond (2009) has revealed that short/squat saddles [Figure 5.10 Ao], with long convex edges, are exclusive to Chloridoideae, while long saddles (Figure 5.10 An) are frequently recorded in Chloridoideae but are also present in lower frequencies in Bambusoideae, as highlighted in the studies of soils samples from the Bamboo zone. Other saddle types were found to be redundant across Chloridoideae and collapsed saddles were recorded in 5 of 67 species studied.

It is not possible to re-calibrate and validate the Iph index for modern East African samples to reflect the dominance of short/squat saddles, as raw counts of saddle and other GSSC classes recorded by Bremond et al., (2008a) are grouped together and not separated into sub-morphotypes. However, by adopting a generalised approach that considers the relative abundances of C_4 xeric vs C_4 mesic GSSC types that takes into account the presence of C_3 diagnostic types, it is possible to infer relative changes in these grass subfamilies that better reflect phytolith production in East African grass species. In doing so it is possible to flag instances when the Iph index may be biased. For example, only very rarely do shade loving forest or Afroalpine C_3 grasses have a floristic crossover with Chloridoideae in modern vegetation communities. In samples in which high frequencies of wavy trapeziform types (produced in abundance by C_3 grasses) and or other diagnostic C_3 types (e.g. alate, deeply concave lobed bilobates found only in shade loving Ehrhartoideae) are recorded in association with saddles (and low frequencies or no short/squat saddles are present); it is reasonable to infer that other saddle types (e.g. long saddles) originate from C_3 grasses. This is because while C_3 Arundinoideae (reed grasses e.g. *Phragmites* spp.) that produce long saddles may occur in association with Chloridoideae in wetland settings, they do not produce trapeziform sinuate morphotypes (Barboni and Bremond, 2009). Similarly, if short/squat saddle morphotypes are found in association with 3-lobed cross types that are recorded primarily in C_4 xerophytic, light loving open habitat Chloridoideae and Panicoideae grasses, then these vegetation types can be inferred (Barboni and Bremond et al., 2009).

<u>5.7 Estimating relative proportions of C_3 vs C_4 grass subfamilies using the Ic index: benefits and limitations</u>

Bremond et al., (2008a) recorded that Ic values were near zero in lowland areas such as lake shores. The Ic increased up to \sim 50% when Bambusoideae and Arundinoideae grasses were recorded in relative abundances similar to Panicoideae grasses at mid-elevation sites when floristic crossover of these subfamilies occurs (see Chapter 2.6). In the Afroalpine zone, where open C₃ grassland is dominated by C₃ Pooideae and Arundinoideae, Ic values range from 80-96% (Bremond et al., 2008a). The fact that Ic values do not reach 100% in the Afroalpine zone despite the near total dominance of C₃ grass subfamilies is explained by the multiplicity and redundancy of GSSC morphotypes (i.e. bilobates crosses and saddles are produced in small proportions in these subfamilies which affects the Ic index). At mid-elevation sites where overlap in the distributions of C₃ and C₄ grasses is observed (also see Chapter 2.6), Panicoideae grasses (in which 74% of species use the C₄ pathway) can be C₃ understory species. Consequently, in the case of closed forest conditions, the Ic index only reflects grass subfamily abundance and not C₃ vs C₄ grass abundance Bremond et al., (2008a).

5.8 The Fs index -values in different African vegetation types

Comparing phytolith soil assemblages across intertropical Africa, Barboni et al., (2007) recorded Fs index values of 10% for Sudanian grassland and 17% for Sahelian deciduous bushlands. However, Novello et al., (2012) calculated lower values of 3% and 10% respectively for the same vegetation types. Fs values for the Saharan steppe are 35% according to Barboni et al., (2007). In lowland and highland forest settings Fs% is low: mean values in Afromontane forest and shrubland/ bushlands are 6% and 7% respectively and 5% in Guineo–Congolian Evergreen forest.

5.9 Phytolith production patterns in East African grass subfamilies and its effect on phytolith indices

Global studies of phytolith production in Bambusoideae have suggested that collapsed and long saddle types are exclusive to specific species in this subfamily (e.g. Lu and Lui, 2003; Strömberg, 2004). Therefore, the use of saddle phytoliths assigned to C₄ grasses in the Ic index could potentially bias Ic values if they in fact mainly originated in C₃ Bambusoideae in certain settings. Studies of highland species *Arundinaria alpina* (commonly growing between 2200-2500 m a.s.l.), *Oreobambos buchalaldii* (found between 300-2000 m a.s.l.) and the lowland *Oxytenanthera* and *Leptaspis* genera from the Miombo woodlands by Mercader et al., 2010 have shown that "long" saddles form the highest proportion (36.25%) of all

phytoliths. In contrast, observation of phytoliths from the most common highland East African Bambusoideae species (*Arundinaria alpina* [synm. *Yushania alpina*]) (tribe Bambuseae) by Palmer and Tucker (1981), Bremond et al., (2008a), and Yost et al., (2018) show very low proportions of these morphotypes in *Arundinaria alpina* and this is reflected in low proportions in soil assemblages. These findings are confirmed by studies of *Arundinaria alpina* in this thesis (see Chapter 4.3.5), that recorded the "long" and "collapsed" saddle morphotype occurring in low frequencies in this species. Instead, in East African highland settings Bambusoideae were found to produce higher proportions of rondel "Pooid" types (~30%) and moderate proportions of bilobate (~15%) (Barboni and Bremond, 2009; Mercader et al., 2010). These findings suggest that the association of saddle types with C₄ species alone in East African highland settings is not thought to significantly affect the reliability of the Ic index. However, if the data of Mercader et al., (2010) is considered, then when high proportions of long saddles are recorded, especially in association with C₃ GSSC indicators, then it is likely that Bambusoideae species are present that affect the Ic index.

The fact that bamboo saddle morphotypes occur across several other grass subfamilies, particularly in Chloridoideae (Bremond et al., 2008a; Barboni and Bremond, 2008) means that if bamboos from lowland Oxytenanthera genera (not recorded in modern vegetation surveys of the Nakuru-Naivasha Basin) are present, then C₃ grass abundance could be underestimated in mid-low elevation settings or under different climate conditions in the past. High proportions of plateaued saddles in C₃ Arundinoideae swamp grasses (e.g. *Phragmites australis*) could also affect C_3 vs C_4 reconstructions but are less of an issue in differentiating between open grassland/lakeshore and woodland/forest vegetation types. Yost et al., (2018) suggest that "very tall" (very long saddles where the width is $\geq 20 \,\mu\text{m}$) are exclusive to Arundinaria alpina and Arundinaria gigantea. (Piperno and Pearsall (1998) have also suggested this is the dominant saddle type in Bambusoideae and should be used as a key indicator of all Bambusoideae, as they are not recorded in Chloridoideae. Low frequencies of this "very tall" morphotype were also observed in modern samples of Arundinaria alpina this thesis (see Chapter 4.3.5). The fact that very tall saddles were not observed in samples of Arundinaria alpina analysed by Barboni and Bremond, (2009) may relate to differences in counting methodology adopted (i.e. lower total counts in this study and by Barboni and Bremond (2009) may have resulted in these morphotypes not being identified during counting). Alternatively, it may be the case that production of this morphotype in this species is environmentally controlled (e.g. related to water stress) and thus only present in certain ecological settings.

Similar issues with C_3 vs. C_4 grass representation may be encountered in lowland settings because of the multiplicity and redundancy of rondel morphotypes across Poaceae subfamilies. Chloridoideae have high rates of production of rondel morphotypes (Bamford et al., 2006; Barboni and Bremond, 2009) (e.g. they account for 30% of all classified GSSC types identified by Mercader et al., [2010]). Rondel morphotypes were also present in 10 of 64 species of East African Panicoideae studied by Barboni and Bremond, (2009) and account for 15.05% of all classified morphotypes in 26 Panicoideae species from

the Miombo woodlands (Mercader et al., 2010). As the Ic index classifies all rondel morphotypes to C_3 , this may result in the slight overestimation of C_3 grass abundance in the zone of C_3/C_4 floristic overlap, and more significant overestimation at lower altitudes, or under climatic conditions where Chloridoideae species may have existed at higher altitudes in the past. Considering these findings and the fact that trapeziform sinuates were found to be present in 93% of C_3 grasses and saddles where recorded in 75% of C_4 grasses, Barboni and Bremond (2009) recalculated the Ic index, utilising the data of Bremond et al., (2008a), using only these morphotypes. However, they found that this new Ic showed less correlation ($r^2=0.53$) with elevation than the previous Ic index ($r^2=0.90$). The authors suggest that multiplicity and redundancy may introduce less bias when abundance rather than occurrence is considered when estimating grass subfamily classification (Barboni and Bremond, 2009). As mentioned, it is not common for C_3 Pooideae and Chloridoideae to share the same niche, so they are unlikely to both contribute to Ic index scores in the same sample, except where their presence is due to aeolian of fluvial inputs of phytoliths from other vegetation zones.

As with the Iph index, adopting a general approach that considers the association of main GSSC classes with key indicator GSSCs and other phytoliths types, is arguably the best means of identifying the presence of specific subfamilies. This contributes to more detailed and parsimonious vegetation reconstructions and estimates of relative change in vegetation types, and in doing so helps to suggest where biases in the Ic index values may arise. For example, wavy trapeziform, rondels with bases ≥ 15 μ m, Ehrhartoideae type bilobates, and very tall saddles are taken to represent the presence of C₃ grasses. When "stipa" and "scooped" type bilobates and long and collapsed saddles co-occur with these C₃ types they are also likely to originate from C3 grasses. When found in conjunction with relatively high abundance of FIs, C_3 grasses were interpreted as originating mainly from shade loving C_3 species. In samples with a low percentage of FIs and high percentages of C3 GSSCs (e.g. forest clearing environments), C3 GSSC counts were not divided into CH (closed habitat grasses) and POOID (openhabitat grasses) sensu Strömberg et al., (2007), as Pooideae grasses occur in closed forest settings in East Africa and the trapeziform morphotype common to Pooideae also occurs in Bambusoideae, Ehrhartoideae and Danthonioideae species. Where high proportions of saddles and rondels are present, confusion relating to the presence of C4 Chloridoideae, lowland bamboos or other xeric C4 indicators can be resolved. For example, if high proportions of squat saddle and 3-lobed crosses and lower proportions of plateaued saddles are identified in samples, then xeric grassland habitats can be inferred. In samples where high proportions of both plateaued saddles and long saddles, and thin bilobates are recorded, in association with other phytoliths originating from hydro- and helophytic plants (e.g. Cyperaceae types and rondel keeled types from *Phalaris* spp.), the presence of Arundinoideae grasses and waterlogged conditions can be inferred. Due to the redundancy and multiplicity of rondel morphotypes and relatively high rates of production of rondels across all subfamilies, these morphotypes (except rondels with bases $\geq 15 \,\mu\text{m}$) were classified as C_3/C_4 indeterminate under the general approach. Their likely origin from C_3 or C_4 grasses was then interpreted (but not reclassified) on a sample basis depending on associated phytolith types in the same sample rather than being automatically assigned to Pooideae.

Region	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
EA	МК	AFMS	Afroalpine zone	Elevation grassland	UAS 1–1	4111	37.16	-0.14	0.00	3.48	0.00	79.28	14.33	0.83	0.83	0.00	0.42	0.83	257	96.45	0.00	0.00	Bremond, 2003, et al., 2008
EA	МК	AFMS	Afroalpine zone	Elevation grassland	UAS 3-3	3951	37.16	-0.14	1.81	7.08	1.81	72.59	14.91	0.00	0.90	0.00	0.90	0.00	206	89.11	0.01	16.90	Bremond, 2003, et al., 2008
EA	МК	AFMS	Afroalpine zone	Elevation grassland	LAS 2-1	3614	37.16	-0.11	4.00	5.29	3.00	70.14	17.14	0.00	0.43	0.00	0.00	0.00	212	87.66	0.00	24.42	Bremond, 2003, et al., 2008
EA	МК	AFMS	Afroalpine zone	Elevation grassland	LAS 3-2	3570	37.16	-0.11	0.30	14.20	4.48	56.35	20.18	1.49	1.49	0.00	0.00	1.49	251	80.43	0.00	23.62	Bremond, 2003, et al., 2008
EA	MR	AFMS	Afroalpine zone	Grassland	RGW 27	2966	33.68	-9.17	0.00	4.72	0.00	86.23	7.83	0.40	0.40	0.00	0.00	0.40	248	95.24	0.00	0.00	Bremond, 2003, et al., 2008
EA	MR	AFMS	Afroalpine zone	Ericaceous shrubland/grassland	RGW 24	2600	33.7	-9.12	1.64	15.09	2.36	56.73	16.00	2.91	2.00	0.36	1.64	1.27	251	79.85	0.02	12.38	Bremond, 2003, et al., 2008
EA	MR	AFMS	Afroalpine zone	Shrubland	RGW 23	2300	33.73	-9.15	0.00	9.24	3.39	67.06	10.29	2.34	4.95	0.00	1.95	0.78	252	86.32	0.02	26.80	Bremond, 2003, et al., 2008
EA	МК	AFMS	Ericaceous zone	Ericaceous shrubland	ES 1-2	3527	37.15	-0.04	2.01	9.41	1.70	60.34	9.41	4.94	9.41	0.00	0.77	2.01	243	85.06	0.01	12.94	Bremond, 2003, et al., 2008
EA	МК	AFMS	Ericaceous zone	Ericaceous shrubland	ES 2-3	3353	37.17	-0.08	2.72	14.19	3.41	60.05	1.02	4.54	10.33	0.00	0.34	3.41	295	76.35	0.00	16.76	Bremond, 2003, et al., 2008
EA	МК	AFMF	Hagenia–Hypericum	Evergreen upper forest (Hagenia- Hypericum)	H 3–1	2945	37.15	-0.05	3.21	9.99	1.78	63.61	0.00	2.14	17.84	0.00	0.36	1.07	296	81.44	0.00	11.90	Bremond, 2003, et al., 2008
EA	МК	AFMF	Hagenia–Hypericum	Evergreen upper forest (Hagenia- Hypericum)	H 1–2	2928	37.15	-0.03	2.61	36.17	4.17	39.83	2.96	6.09	4.52	0.35	2.61	0.70	304	53.22	0.03	9.72	Bremond, 2003, et al., 2008
EA	МК	AFMF	Bamboo zone	Bamboo forest	B 1–2	2920	37.13	0	3.26	27.91	13.37	24.77	15.35	8.14	1.16	0.35	1.63	4.07	235	52.01	0.02	30.03	Bremond, 2003, et al., 2008
EA	МК	AFMF	Bamboo zone	Bamboo forest	B 2–3	2670	37.14	-0.03	7.09	41.20	5.59	23.06	1.64	1.64	3.96	0.00	13.51	2.32	130	32.82	0.17	10.38	Bremond, 2003, et al., 2008
EA	МК	AFMF	Mountain forest	Moist evergreen elevation forest	UM 1-2	2477	37.13	0	2.94	28.82	4.12	45.88	6.08	0.00	8.63	0.00	0.98	2.55	237	59.15	0.01	11.48	Bremond, 2003, et al., 2008
EA	МК	AFMF	Mountain forest	Moist evergreen elevation forest	UM 3–1	2193	37.13	1	4.51	33.33	13.97	35.52	0.00	0.00	10.33	0.00	1.16	1.16	287	40.67	0.01	26.97	Bremond, 2003, et al., 2008
EA	МК	AFMF	Mountain forest	Moist evergreen elevation forest	LM 1–2	1958	37.08	0.05	2.97	30.12	7.27	26.11	0.00	0.00	14.54	0.00	14.09	4.90	235	39.29	0.21	18.01	Bremond, 2003, et al., 2008
EA	MR	AFMS	Mountain forest	Grassland	RGW 19	2150	33.73	-9.17	0.00	36.17	10.15	34.54	0.00	0.00	17.04	0.00	0.35	1.75	301	42.71	0.00	21.91	Bremond, 2003, et al., 2008
EA	MR	AFMS	Mountain forest	Moist evergreen elevation forest	RGW 2	2113	37.16	-0.11	1.24	40.25	3.41	17.34	3.41	0.00	24.15	0.00	10.22	0.00	270	31.60	0.16	7.59	Bremond, 2003, et al., 2008
EA	MR	AFMSS	Mountain forest	Shrub savannah	RGW 4	2150	33.73	-9.17	3.04	54.37	9.89	20.91	0.00	0.00	3.04	0.00	2.66	6.08	263	23.71	0.03	14.69	Bremond, 2003, et al., 2009
EA	MR	AFMSS	Mountain forest	Shrub savannah	RGW 7A	2150	33.73	-9.17	3.90	24.68	3.46	55.41	0.00	0.00	11.26	0.00	1.30	0.00	231	63.37	0.01	10.81	Bremond, 2003, et al., 2010
EA	MR	AFMSS	Mountain forest	Shrub savanna	RGW 9	2150	33.73	-9.17	0.00	9.14	11.14	60.00	0.00	0.00	9.43	0.00	1.14	9.14	350	74.73	0.01	54.93	Bremond, 2003, et al., 2011

Appendix 5 – Table 5.3 (see caption at end of table)

Region	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
EA	MR	AFMS	Mountain forest	Grassland	RGW 17	2150	33.73	-9.17	0.00	54.98	15.54	7.57	0.00	0.00	18.33	0.00	1.99	1.59	251	9.69	0.03	22.03	Bremond, 2003, et al., 2012
EA	MR	AFMS	Mountain forest	Grassland	RGW 20	2150	33.73	-9.17	3.66	23.98	6.10	43.09	5.28	0.00	6.50	0.00	2.03	9.35	246	58.91	0.02	18.07	Bremond, 2003, et al., 2013
EA	ML	WOZA	Semi-deciduous forest	Moist miombo with tall-grasses (Uapaca) Uapaca semi-deciduous forest	MAS 1	898	33.76	-9.34	0.6	14.50	0.00	0.00	0.00	0.00	27.34	0.00	30.26	27.34	172	0.00	2.01	0.00	Bremond, 2003, et al., 2008
EA	ML	WOZA	Semi-deciduous forest	Moist miombo with tall-grasses (Uapaca) Uapaca semi-deciduous forest	MAS 3	885	33.76	-9.34	0.0	17.05	1.07	0.00	0.00	0.00	21.00	0.00	34.70	26.18	176	0.00	1.92	5.88	Bremond, 2003, et al., 2008
EA	ML	WOZA	Semi-deciduous forest	Moist miombo with tall-grasses (Uapaca) Uapaca semi-deciduous forest	MAS 7	901	33.75	-9.34	1.1	20.57	2.70	0.30	0.00	0.00	16.82	2.70	31.08	24.77	302	1.22	1.26	11.11	Bremond, 2003, et al., 2008
EA	ML	WOZA	Semi-deciduous forest	Moist miombo with tall-grasses Brachystegia–Isoberlinia semi-deciduous forest	MAS 8	881	33.75	-9.33	0.0	20.82	1.64	1.31	0.00	0.00	26.89	0.49	25.90	22.95	235	5.52	1.09	7.30	Bremond, 2003, et al., 2008
EA	ML	WOZA	Semi-deciduous forest	Moist miombo with tall-grasses Brachystegia–Isoberlinia semi-deciduous forest	MAS 9	909	33.76	-9.33	1.0	15.26	1.57	1.57	0.00	0.00	14.69	1.00	39.80	25.11	191	8.09	2.05	8.80	Bremond, 2003, et al., 2008
EA	ML	WOZA	Semi-deciduous forest	Moist miombo with tall-grasses Brachystegia–Isoberlinia semi-deciduous forest	MAS 14	878	33.75	-9.34	5.9	23.65	2.38	0.79	0.00	0.00	17.57	0.40	15.59	33.69	250	2.42	0.48	7.44	Bremond, 2003, et al., 2008
EA	МА	GRSO	Acacia–Commiphora scattered bushland, thicket and shrub steppe	subdesertic Steppe (under Acacia)	MA94-103	500	40.45	10.47	4.76	13.66	17.81	26.09	0.00	4.55	19.67	2.28	0.00	11.18	483	45.82	0.00	49.14	Barboni et al. 1999
EA	МА	GRSO	Acacia–Commiphora scattered bushland, thicket and shrub steppe	Tree savanna (along seasonal river)	MA94-106	600	40.43	10.52	8.40	25.82	7.38	8.81	0.00	9.22	18.65	1.02	0.00	20.70	488	30.24	0.00	17.73	Barboni et al. 1999
EA	МА	GRSO	Riverine Forest	Riparian forest swamp	MA94-101	500	40.5	10.45	3.11	14.15	9.75	8.36	0.00	6.65	11.36	0.00	0.00	46.62	933	35.71	0.00	36.11	Barboni et al. 1999
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.7	38	-15.99	14.79	0.00	45.21	2.05	0.00	0.00	0.00	34.25	0.68	7.53	10.27	146	0.00	0.16	4.35	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.5	7	-16.16	14.72	0.00	35.42	9.03	0.00	0.00	0.00	39.58	0.00	13.19	2.78	144	0.00	0.30	20.31	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-4	61	-16.5	14.7	6.00	38.50	8.00	0.50	0.00	0.00	24.50	4.50	16.50	1.50	200	0.94	0.31	15.24	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	82-77	54	-16.32	14.63	7.73	50.24	14.01	0.48	0.00	0.00	19.81	0.48	5.80	1.45	207	0.67	0.08	19.46	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	82-79	30	-16.1	14.17	7.03	65.95	16.22	0.54	0.00	0.00	7.57	0.54	0.54	1.62	185	0.60	0.01	18.18	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-75	61	-12.67	14.12	10.38	61.79	10.38	0.00	0.00	0.00	11.79	0.00	5.19	0.47	212	0.00	0.06	12.57	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	82-78	30	-16.05	14.08	4.91	72.08	8.30	0.00	0.00	0.00	4.53	0.75	7.55	1.89	265	0.00	0.09	9.73	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-70	61	-12.27	14.05	7.87	83.33	6.02	0.00	0.00	0.00	2.31	0.00	0.46	0.00	216	0.00	0.00	6.19	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-83	78	-13.32	13.97	9.38	79.46	6.25	1.79	0.00	0.00	2.68	0.00	0.45	0.00	224	1.84	0.00	6.57	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.84	61	-13.41	13.93	11.82	72.91	8.87	0.00	0.00	0.00	4.93	0.00	1.48	0.00	203	0.00	0.02	9.47	Bremond et al. 2005b

Regior	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-68	61	-12.25	13.88	7.25	73.43	5.80	0.97	0.00	0.00	6.28	0.48	4.83	0.97	207	1.10	0.06	6.70	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.118	40	-13.74	13.63	3.91	71.51	6.15	0.56	0.00	0.00	13.41	0.00	3.91	0.56	179	0.68	0.05	7.53	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.88	49	-13.56	13.6	2.31	71.76	13.43	0.00	0.00	0.00	7.87	0.46	2.31	1.85	216	0.00	0.03	15.34	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.91	62	-13.4	13.59	7.08	36.28	1.77	0.00	0.00	0.00	10.18	8.41	30.97	5.31	226	0.00	0.69	3.92	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-120	61	-13.83	13.48	4.35	76.52	4.78	0.00	0.00	0.00	5.22	0.43	6.09	2.61	230	0.00	0.07	5.58	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-122	30	-14.93	13.35	4.68	75.74	8.94	0.85	0.00	0.00	7.23	0.00	1.70	0.85	235	0.94	0.02	10.00	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.122	65	-13.94	13.35	7.30	67.88	9.49	0.73	0.00	0.00	14.60	0.00	0.00	0.00	137	0.85	0.00	11.21	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.93	58	-13.23	13.31	6.25	74.04	5.29	1.44	0.00	0.00	6.25	2.88	2.88	0.96	208	1.66	0.03	6.18	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-98	88	-12.83	13.08	9.58	81.44	2.99	0.00	0.00	0.00	1.20	0.60	3.59	0.60	167	0.00	0.04	3.18	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-127	38	-14.08	13.07	1.91	35.89	2.39	0.00	0.00	0.00	15.31	0.96	38.76	4.78	209	0.00	0.96	5.95	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.128	18	-14.1	13.03	0.00	61.78	4.71	0.00	0.00	0.00	19.90	0.52	3.66	9.42	191	0.00	0.06	7.09	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-100	110	-12.63	13.03	4.89	76.44	5.78	0.44	0.00	0.00	4.44	0.00	6.22	1.78	225	0.51	0.07	6.63	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	S.130	25	-14.17	12.92	6.67	60.67	8.67	0.00	0.00	0.00	19.33	0.00	3.33	1.33	150	0.00	0.04	11.40	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-103	198	-12.43	12.92	9.45	72.14	4.48	1.49	0.00	0.00	6.47	0.50	4.48	1.00	201	1.70	0.05	5.20	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree tall-grass savanna	S.138	34	-14.86	12.88	2.67	50.00	7.33	0.67	0.00	0.00	28.00	0.00	7.33	4.00	150	1.10	0.12	12.22	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree tall-grass savanna	S.136	7	-14.74	12.85	2.42	31.45	10.48	0.00	0.00	0.00	45.97	0.00	8.06	1.61	124	0.00	0.18	23.64	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree tall-grass savanna	83-116	145	-12.18	12.67	4.82	89.16	2.41	1.20	0.00	0.00	1.20	0.60	0.60	0.00	166	1.23	0.01	2.50	Bremond et al. 2005b
WA	SEN	WOSU	dry Sudanian woodland	Tree/shrub tall-grass savanna	83-115	297	-12.3	12.4	2.41	85.94	4.82	0.40	0.00	0.00	2.81	0.00	2.81	0.80	249	0.43	0.03	5.17	Bremond et al. 2005b
WA	MAU	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	83-35	25	-14.6	17	4.10	4.10	22.13	1.64	0.00	0.00	63.93	0.00	3.28	0.82	122	5.13	0.10	72.97	Bremond et al. 2005b
WA	MAU	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	RIM11	25	-15.2	16.93	0.00	24.46	22.28	0.00	0.00	0.00	50.54	0.00	1.09	1.63	184	0.00	0.02	47.67	Bremond et al. 2005b
WA	MAU	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	RIM10	25	-15.17	16.73	0.73	16.06	11.68	0.00	0.00	0.00	65.69	0.00	4.38	1.46	137	0.00	0.15	41.03	Bremond et al. 2005b

Regior	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
WA	MAU	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	RIM1	24	-15.97	16.68	0.59	20.59	2.94	1.18	0.00	0.00	57.06	1.76	10.59	5.29	170	4.65	0.42	12.20	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.33	15	-14.82	16.39	2.36	53.77	21.70	1.89	0.00	0.00	12.74	0.00	5.66	1.89	212	2.37	0.07	27.88	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.32	25	-15.35	16.29	4.24	40.68	18.64	0.00	0.00	0.00	31.36	0.85	0.85	3.39	118	0.00	0.01	29.33	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	83-30	61	-14.93	16.17	3.70	52.47	14.20	1.23	0.00	0.00	24.07	0.00	3.09	1.23	162	1.72	0.04	20.18	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.40	10	-13.89	16.1	1.99	36.82	29.85	0.00	0.00	0.00	22.39	0.00	7.46	1.49	201	0.00	0.11	43.48	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.29	45	-14.92	16.08	1.91	49.04	24.84	0.00	0.00	0.00	16.56	0.00	5.73	1.91	157	0.00	0.08	32.77	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	82-46	30	-14.95	16	2.77	58.50	12.25	1.19	0.00	0.00	18.18	1.19	4.74	1.19	253	1.59	0.06	16.67	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	82-47	30	-15.95	16	3.23	54.84	17.51	2.30	0.00	0.00	19.35	0.00	2.30	0.46	217	2.96	0.03	23.17	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.27	45	-14.86	15.92	4.81	55.61	28.34	1.07	0.00	0.00	9.63	0.00	0.53	0.00	187	1.19	0.01	31.93	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.44	92	-13.47	15.83	5.52	51.93	16.57	0.00	0.00	0.00	23.20	0.00	1.66	1.10	181	0.00	0.02	22.39	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.24	46	-14.99	15.69	0.56	72.07	18.99	0.00	0.00	0.00	7.26	0.00	0.56	0.56	179	0.00	0.01	20.73	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	83-46	61	-13.35	15.43	9.13	51.87	27.80	0.41	0.00	0.00	7.05	0.41	2.49	0.83	241	0.47	0.03	31.31	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	83-20	61	-15.12	15.42	6.45	43.78	35.48	2.30	0.00	0.00	7.37	0.00	3.69	0.92	217	2.62	0.04	41.40	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	83-15	61	-15.47	15.33	10.53	36.84	14.47	0.00	0.00	0.00	28.95	1.32	5.26	2.63	76	0.00	0.09	23.40	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.54	27	-12.99	15.31	1.88	60.00	15.00	0.00	0.00	0.00	20.00	0.00	1.25	1.88	160	0.00	0.02	19.51	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	83-48	61	-13.45	15.28	6.73	39.42	22.60	0.48	0.00	0.00	27.88	0.48	1.92	0.48	208	0.69	0.03	32.87	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.12	29	-15.17	15.21	1.34	48.32	12.75	0.00	0.00	0.00	16.78	2.01	10.74	8.05	149	0.00	0.17	20.43	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	S.58	31	-12.81	15.06	4.21	50.53	31.58	0.00	0.00	0.00	10.00	0.00	2.11	1.58	190	0.00	0.02	36.59	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	83-8	54	-15.85	14.9	4.26	40.43	22.55	0.85	0.00	0.00	20.00	3.83	6.38	1.70	235	1.25	0.09	33.54	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub savanna with short grasses	83-62	64	-12.33	14.85	11.39	36.08	30.38	0.63	0.00	0.00	17.09	1.27	1.27	1.90	158	0.81	0.02	39.02	Bremond et al. 2005b
WA	SEN	BUSA	dry Sudanian woodland	Shrub short-grass savanna	83-65	38	-12.25	14.75	6.51	64.65	22.79	0.47	0.00	0.00	2.79	0.00	2.33	0.47	215	0.49	0.02	24.26	Bremond et al. 2005b

Region	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
WA	MAU	GRSA	dry Sudanian woodland	Steppe (short grasses) with shrubs	RIM3	232	-13	21.53	0.00	20.69	6.90	0.00	0.00	0.00	59.77	2.30	4.60	5.75	87	0.00	0.17	25.00	Bremond et al. 2005b
WA	MAU	GRSA	dry Sudanian woodland	Steppe (short grasses) with shrubs	RIM8	298	-12.15	21.03	0.00	17.11	6.58	1.32	0.00	0.00	56.58	9.21	6.58	2.63	76	5.26	0.26	27.78	Bremond et al. 2005b
WA	MAU	GRSA	dry Sudanian woodland	Steppe (short grasses) with shrubs	MAU07	260	-12.2	20.93	0.79	29.13	8.66	0.00	0.00	0.00	44.09	1.57	7.09	8.66	127	0.00	0.18	22.45	Bremond et al. 2005b
WA	MAU	GRSA	dry Sudanian woodland	Steppe (short grasses) with shrubs	MAU06	350	-12.63	20.63	0.00	45.52	4.48	2.24	0.00	0.00	41.04	0.00	2.99	3.73	134	4.29	0.06	8.96	Bremond et al. 2005b
WA	MAU	GRSA	dry Sudanian woodland	Steppe (short grasses) with shrubs	MAU05	230	-13.03	20.4	3.61	31.33	6.02	1.20	0.00	0.00	53.01	1.20	1.20	2.41	83	2.86	0.03	14.71	Bremond et al. 2005b
WA	MAU	GRSA	dry Sudanian woodland	Steppe (short grasses) with shrubs	MAU04	350	-13.37	20.23	1.45	35.51	15.22	0.72	0.00	0.00	38.41	2.17	2.90	3.62	138	1.37	0.05	29.17	Bremond et al. 2005b
WA	MAU	GRSA	dry Sudanian woodland	Steppe (short grasses) with shrubs	RIM2	132	-14.08	19.93	0.00	9.20	2.30	1.15	0.00	0.00	71.26	3.45	5.75	6.90	87	9.09	0.45	20.00	Bremond et al. 2005b
WA	SEN	MOSA	Semi-deciduous forest	rain forest	S.155	33	-16.58	12.48	0.43	4.26	2.55	0.00	0.00	0.00	4.26	23.83	61.28	3.40	235	0.00	8.47	35.29	Bremond et al. 2005b
WA	SEN	MOSA	Semi-deciduous forest	rain forest	83-151	0	-12.30	12.4	0.81	3.25	0.00	0.00	0.00	0.00	2.03	21.95	64.23	7.72	246	0.00	15.80	0.00	Bremond et al. 2005b
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Dense tree/shrub savanna (Acacia), tall grass	CAM 26	640	13.72	4.33	0.34	29.93	0.00	0.00	0.00	0.00	18.37	1.36	50.00	2.04	294	0.00	1.65	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Dense tree/shrub savanna (Acacia), tall grass	CAM 25	640	13.72	4.33	1.12	37.54	0.00	0.00	0.00	0.00	7.28	1.96	52.10	1.40	357	0.00	1.35	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Dense tree/shrub savanna (Acacia), tall grass	CAM 24	640	13.72	4.33	1.46	42.70	0.00	0.00	0.00	0.00	4.01	1.82	50.00	0.00	274	0.00	1.13	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Dense tree/shrub savanna (Acacia), tall grass	CAM 23	640	13.72	4.33	0.38	38.93	0.00	0.38	0.00	0.00	5.34	0.76	54.20	0.76	262	0.96	1.37	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Dense tree/shrub savanna (Acacia), tall grass	CAM 22	640	13.72	4.33	2.53	30.06	0.63	0.63	0.00	0.00	6.33	1.27	58.54	3.16	316	1.87	1.73	1.90	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Pteridium ecotone	CAM 21	640	13.72	4.33	3.50	43.95	0.00	0.00	0.00	0.00	2.87	3.82	45.86	0.64	314	0.00	0.97	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Pteridium ecotone	CAM 20	640	13.72	4.33	1.73	53.47	0.00	0.58	0.00	0.00	14.74	0.58	28.90	0.29	346	1.04	0.52	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Pteridium ecotone	CAM 19	640	13.72	4.33	3.67	54.13	0.00	0.61	0.00	0.00	7.03	0.61	33.94	0.92	327	1.05	0.58	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Margaritaria ecotone	CAM 18	640	13.72	4.33	0.00	36.88	0.00	0.35	0.00	0.00	5.32	2.13	55.32	0.71	282	0.95	1.49	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Margaritaria ecotone	CAM 17	640	13.72	4.33	0.00	28.77	0.00	0.34	0.00	0.00	5.82	0.00	65.07	0.34	292	1.18	2.24	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Albizia)	CAM 16	640	13.72	4.33	0.00	23.16	0.00	0.37	0.00	0.00	5.51	1.10	69.85	1.10	272	1.56	2.97	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Albizia)	CAM 15	640	13.72	4.33	0.00	20.28	0.00	0.00	0.00	0.00	6.29	5.59	67.83	0.70	286	0.00	3.34	0.00	Bremond et al. 2005a
Region	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
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WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Albizia)	CAM 14	640	13.72	4.33	0.00	13.67	0.00	0.00	0.00	0.00	5.76	2.88	77.70	0.00	278	0.00	5.68	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Albizia)	CAM 13	640	13.72	4.33	0.00	7.46	0.00	1.12	0.00	0.00	10.45	0.00	80.97	0.37	268	13.04	9.43	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Albizia)	CAM 12	640	13.72	4.33	0.00	16.40	0.00	1.26	0.00	0.00	5.68	3.15	73.50	0.95	317	7.14	4.16	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Albizia)	CAM 11	640	13.72	4.33	1.09	8.39	1.09	0.73	0.00	0.00	4.01	23.72	60.95	2.19	274	6.45	5.39	10.34	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Albizia)	CAM 10	640	13.72	4.33	0.00	6.71	0.00	0.34	0.00	0.00	22.15	1.01	69.80	2.01	298	4.76	9.90	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Albizia)	CAM 9	640	13.72	4.32	0.00	13.03	0.00	1.41	0.00	0.00	5.28	3.17	77.11	1.76	284	9.76	5.34	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Rinorea)	CAM 8	640	13.72	4.32	2.08	7.50	0.83	0.00	0.00	0.00	2.50	20.00	67.08	1.67	240	0.00	6.44	8.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Rinorea)	CAM 7	640	13.72	4.32	0.00	13.56	0.00	1.36	0.00	0.00	6.78	3.39	74.92	0.68	295	9.09	5.02	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Rinorea)	CAM 6	640	13.72	4.32	0.00	5.79	0.41	0.41	0.00	0.00	1.24	11.57	80.58	2.48	242	6.25	12.19	6.67	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Rinorea)	CAM 5	640	13.72	4.32	0.00	7.38	0.37	0.00	0.00	0.00	5.90	0.37	85.98	2.58	271	0.00	11.10	4.76	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Rinorea)	CAM 4	640	13.72	4.32	0.00	6.11	0.38	0.00	0.00	0.00	11.07	0.76	81.68	2.67	262	0.00	12.59	5.88	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Rinorea)	CAM 3	640	13.72	4.32	1.20	2.81	0.00	0.40	0.00	0.00	5.22	13.25	77.11	0.80	249	9.09	17.45	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Semi-deciduous forest (Rinorea)	CAM 2	640	13.72	4.32	0.00	4.03	0.67	1.01	0.00	0.00	6.71	28.19	59.40	3.02	298	17.65	10.41	14.29	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian, semi-deciduous forests, savanna mosaic	Raphia swamp	CAM 1	640	13.72	4.32	0.00	2.77	0.00	1.04	0.00	0.00	4.15	75.09	16.96	2.42	289	27.27	4.45	0.00	Bremond et al. 2005a
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	stwooded savanna, on alluvium soils.	F15-1	-	-	_	5.09	44.55	8.20	0.99	0.00	0.00	0.00	3.54	35.79	1.84	707	1.68	0.61	14.18	Bremond et al. 2016
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	stwooded savanna, on alluvium soils.	F15-2	-	-	_	1.40	25.81	8.84	0.47	0.00	0.00	0.47	3.02	56.05	3.95	430	1.27	1.54	24.52	Bremond et al. 2016
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	stwooded savanna, on alluvium soils.	F15-3	-	-	-	0.31	4.59	2.14	0.00	0.00	0.00	0.31	14.37	74.62	3.67	327	0.00	10.61	30.43	Bremond et al. 2016
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	stwooded savanna, on alluvium soils.	F15-4	-	-	_	0.00	1.64	1.97	0.00	0.00	0.00	0.00	3.29	86.51	6.58	304	0.00	23.91	54.55	Bremond et al. 2016
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	stwooded savanna, on alluvium soils.	F15-5	-	-	-	0.00	2.04	0.00	0.00	0.00	0.00	0.00	25.66	69.39	2.92	343	0.00	34.00	0.00	Bremond et al. 2016
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	stwooded savanna, on alluvium soils.	F15-6	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.52	92.97	3.52	256	0.00	92.97	0.00	Bremond et al. 2016
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	stwooded savanna, on alluvium soils.	F15-7	_	_	_	0.00	1.35	0.00	0.00	0.00	0.00	0.00	17.57	80.07	1.01	296	0.00	59.25	0.00	Bremond et al. 2016

Region	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
WA	CAM	MOSA	Guineo-Congolian lowland rainford	estwooded savanna, on alluvium soils.	F15-8	-	-	-	0.00	0.41	0.00	0.00	0.00	0.00	0.00	7.85	91.74	0.00	242	0.00	222.00	0.00	Bremond et al. 2016
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	estwooded savanna, on alluvium soils.	F15-9	_	_	_	0.00	1.04	0.00	0.00	0.00	0.00	0.00	14.06	81.77	3.13	192	0.00	78.50	0.00	Bremond et al. 2016
WA	CAM	MOSA	Guineo-Congolian lowland rainfore	estwooded savanna, on alluvium soils.	F15-10	_	_	_	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	23	0.00	100.00	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest, on alluvium soils.	F19-1	_	_	_	0.00	1.38	0.92	0.00	0.00	0.00	0.46	0.46	96.31	0.46	217	0.00	41.80	40.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest, on alluvium soils.	F19-2	_	_	-	0.00	1.77	0.00	0.00	0.00	0.00	0.44	3.54	93.36	0.88	226	0.00	52.75	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest, on alluvium soils.	F19-3	_	_	_	0.00	1.31	0.44	0.00	0.00	0.00	0.00	6.11	90.83	1.31	229	0.00	52.00	25.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest, on alluvium soils.	F19-4	_	_	_	0.00	1.61	0.00	0.40	0.00	0.00	2.42	2.42	91.13	2.02	248	20.00	45.20	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest, on alluvium soils.	F19-5	_	_	-	0.00	2.21	1.47	0.00	0.00	0.00	0.37	9.56	84.93	1.47	272	0.00	23.10	40.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest, on alluvium soils.	F19-5	_	_	_	0.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	75.00	0.00	8	0.00	3.00	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	dense mixed terra firme forest (non-flooded) estwith Marantaceae giant herbs <i>Haumania</i> danckelmaniana	F7-1	_	-	-	0.00	0.00	0.90	0.00	0.00	0.00	0.00	0.45	95.95	2.70	222	0.00	106.50	100.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	dense mixed terra firme forest (non-flooded) estwith Marantaceae giant herbs Haumania danckelmaniana	F7-2	_	_	-	0.00	2.28	0.91	0.00	0.00	0.00	0.00	0.00	95.89	0.91	219	0.00	30.00	28.57	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	dense mixed terra firme forest (non-flooded) estwith Marantaceae giant herbs Haumania danckelmaniana	F7-3	_	_	_	0.00	1.23	0.82	0.00	0.00	0.00	0.00	0.00	97.95	0.00	244	0.00	47.80	40.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	dense mixed terra firme forest (non-flooded) estwith Marantaceae giant herbs Haumania danckelmaniana	F7-4	_	_	_	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	95.22	4.78	251	0.00	95.22	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	dense mixed terra firme forest (non-flooded) estwith Marantaceae giant herbs Haumania danckelmaniana	F7-5	_	_	-	0.00	0.00	0.00	0.30	0.00	0.00	0.30	0.00	89.91	9.50	337	100.00	303.00	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	dense mixed terra firme forest (non-flooded) estwith Marantaceae giant herbs Haumania danckelmaniana	F7-6	_	_	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	92.46	7.54	345	0.00	92.46	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	dense mixed terra firme forest (non-flooded) estwith Marantaceae giant herbs <i>Haumania</i> danckelmaniana	F7-7	_	_	-	0.00	0.00	0.96	0.00	0.00	0.00	0.32	0.00	86.50	12.22	311	0.00	89.67	100.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	dense mixed terra firme forest (non-flooded) estwith Marantaceae giant herbs Haumania danckelmaniana	F7-8	_	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	86.18	13.82	152	0.00	86.18	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest.	F17-1	_	_	-	0.00	2.81	2.11	0.00	0.00	0.00	0.00	1.05	92.98	1.05	285	0.00	18.93	42.86	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest.	F17-2	_	_	-	0.27	2.16	0.81	0.00	0.00	0.00	0.27	4.85	87.60	4.04	371	0.00	27.08	25.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest.	F17-3	-	-	-	0.82	3.55	1.37	0.27	0.00	0.00	0.27	15.85	74.32	3.55	366	4.55	12.36	23.81	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest.	F17-4	_	_	-	0.00	7.20	0.28	0.28	0.00	0.00	0.00	18.56	72.58	1.11	361	3.57	9.36	3.70	Bremond et al. 2016

Region	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
WA	САМ	EVF	Guineo-Congolian lowland rainfore	est Marantaceae forest.	F17-5	_	-	-	0.00	7.59	0.00	0.00	0.00	0.00	0.00	10.34	78.28	3.79	290	0.00	10.32	0.00	Bremond et al. 2016
WA	CAM	EVF	Guineo-Congolian lowland rainford	est Marantaceae forest.	F17-6	_	_	-	0.36	1.44	0.00	0.36	0.00	0.00	0.00	9.71	83.81	4.32	278	16.67	38.83	0.00	Bremond et al. 2016
CA	CHAD	Sahelian EDAP	Sahelian edaphic grassland mosaic with Acacia wooded grassland (uni 62)	s it Closed Acacia temporary herb-swam	54	297 m	16.29	13.55	2.0	15.4	10.7	32.2	0.0	1.3	20.8	1.3	3.4	12.8	149	54.35	0.05	38.10	Novello et al., 2012
CA	CHAD	Sahelian EDAP	Sahelian edaphic grassland mosaic with Acacia wooded grassland (uni 62)	s it Closed Acacia temporary herb-swam	53	295 m	16.29	13.5	0.0	17.3	6.7	23.1	0.0	0.0	23.1	0.6	6.1	23.1	165	49.03	0.13	27.85	Novello et al., 2012
CA	CHAD	Sahelian EDAP	Sahelian edaphic grassland mosaic with Acacia wooded grassland (uni 62)	s it Dwarf-shrub steppe	51	301 m	16.28	13.46	2.8	17.9	21.1	23.9	0.0	0.0	15.4	0.6	6.8	11.4	176	36.36	0.10	50.34	Novello et al., 2012
CA	CHAD	Sahelian EDAP	Sahelian edaphic grassland mosaic with Acacia wooded grassland (uni 62)	s it Closed Acacia temporary herb-swam	50	305 m	16.55	13.16	0.7	5.8	14.1	18.5	0.0	0.4	7.2	0.0	39.1	14.1	276	47.71	0.99	68.42	Novello et al., 2012
CA	CHAD	Sahelian EDAP	Sahelian edaphic grassland mosaic with Acacia wooded grassland (uni 62)	s it Tree and shrub steppe	52a	314 m	16.28	13.47	5.9	30.3	33.5	11.9	0.0	0.0	6.1	3.6	4.7	4.0	278	14.57	0.06	48.06	Novello et al., 2012
CA	CHAD	Sahelian EDAP	Sahelian herbaceous swamp and aquatic vegetation (Lake Chad) (unit 75)	Tree and shrub steppe	C1	283 m	14.44	13.25	2.8	19.7	11.3	10.3	0.0	0.3	11.3	15.7	26.3	2.2	319	23.94	0.59	33.33	Novello et al., 2012
CA	CHAD	Sahelian EDAP	Sahelian herbaceous swamp and aquatic vegetation (Lake Chad) (unit 75)	Tree and shrub steppe	C2	284 m	14.44	13.25	3.0	14.4	21.7	9.2	0.0	0.0	16.3	8.4	23.9	3.0	368	19.10	0.49	55.56	Novello et al., 2012
CA	CHAD	Sahelian EDAP	Sahel Acacia wooded grasslands and deciduous bushlands (unit 43)	Grass savanna	44	319 m	17.44	13.03	4.0	27.1	46.8	6.5	0.0	0.0	4.0	3.4	5.0	3.1	323	7.71	0.06	60.04	Novello et al., 2012
CA	CHAD	Sahelian EDAP	Sahel Acacia wooded grasslands and deciduous bushlands (unit 43)	Tree and shrub savanna	43	318 m	17.43	13.01	8.0	29.6	45.8	6.0	0.0	0.7	2.3	2.7	3.0	2.0	301	7.38	0.03	54.98	Novello et al., 2012
CA	CHAD	Sahelian	aquatic vegetation (Lake Chad) (unit 75) Lake Chad archipelago	Aquatic grassland and herb samp	В	275 m	14.44	13.26	8.0	22.5	7.5	13.6	0.0	0.5	15.5	7.5	21.6	3.3	213	27.03	0.41	19.75	Novello et al., 2012
CA	CHAD	Sahelian	aquatic vegetation (Lake Chad) (unit 75) Lake Chad archipelago	Aquatic grassland and herb swamp	A3	277 m	14.44	13.25	4.7	37.4	9.3	7.5	0.0	0.0	35.5	0.0	2.8	2.8	107	12.70	0.05	18.18	Novello et al., 2012
CA	CHAD	Sahelian	aquatic vegetation (Lake Chad) (unit 75) Lake Chad archipelago	Aquatic grassland and herb samp	A4	277 m	14.44	13.25	0.0	2.2	4.4	2.2	0.0	0.0	57.8	0.0	24.4	8.9	45	25.00	2.75	66.67	Novello et al., 2012
CA	CHAD	Sahelian	aquatic vegetation (Lake Chad) (unit 75) Lake Chad archipelago	Aquatic grassland and herb samp	A1	269 m	14.45	13.25	6.0	13.5	5.9	4.5	0.0	1.3	26.2	15.5	22.5	4.5	374	18.80	0.72	23.16	Novello et al., 2012
CA	CHAD	Sahelian	aquatic vegetation (Lake Chad) (unit 75) Lake Chad archipelago	Aquatic grassland and herb samp	A2	269 m	14.45	13.25	3.5	15.7	4.2	8.3	0.0	1.0	15.0	13.4	33.2	5.8	313	28.43	1.02	17.81	Novello et al., 2012
CA	CHAD	Sahelian	Sahelian herbaceous swamp and aquatic vegetation (Lake Chad) (unit 75) Lake Chad (south)	Aquatic grassland and herb samp	57a	298 m	14.35	12.56	17.0	41.4	8.0	26.0	0.0	0.0	2.8	0.3	1.2	3.4	327	28.15	0.01	11.98	Novello et al., 2012
CA	CHAD	Sahelian	Sahelian herbaceous swamp and aquatic vegetation (Lake Chad) (unit 75) Lake Chad (south)	Aquatic grassland and herb samp	57b	300 m	14.36	12.55	9.0	33.9	7.9	15.9	0.0	0.5	16.4	1.6	2.6	12.2	189	24.41	0.04	15.63	Novello et al., 2012
CA	CHAD	Sahelian	Sahelian herbaceous swamp and aquatic vegetation (Lake Chad) (unit 75) Lake Chad (south)	Aquatic grassland and herb samp	57c	299 m	14.37	12.55	6.2	31.0	11.9	22.5	0.0	0.0	12.8	3.7	4.6	7.3	218	31.41	0.06	24.30	Novello et al., 2012
CA	CHAD	Sahelian	Sahelian herbaceous swamp and aquatic vegetation (Lake Chad) (unit 75) Lake Chad (south)	Aquatic grassland and herb samp	57d	312 m	14.37	12.54	11.8	33.8	6.0	15.1	0.0	0.0	6.5	8.6	12.1	6.0	199	22.64	0.18	11.71	Novello et al., 2012
CA	CHAD	Sahelian	Sahelian herbaceous swamp and aquatic vegetation (Lake Chad) (unit 75) Lake Chad (south)	Aquatic grassland and herb samp	57e	n/a	14.37	12.54	12.8	39.5	4.1	29.4	0.0	0.0	4.6	2.1	3.3	4.1	242	34.22	0.04	7.33	Novello et al., 2012

Region	Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P*	Iph(%)	Reference
CA	CHAD	Sudanian EDAP	Sudanian edaphic grassland mosaics with communities of Acaci and broad-leaved trees (unit 63)	a Temporary aquatic grassland	2	360 m	15.42	9.59	19.4	59.1	5.9	14.1	0.0	0.0	0.6	0.0	0.9	0.0	340	14.33	0.01	6.97	Novello et al., 2012
CA	CHAD	Sudanian EDAP	Sudanian edaphic grassland mosaics with communities of Acaci and broad-leaved trees (unit 63)	a Temporary aquatic grassland	20	355 m	15.47	9.53	12.8	68.5	5.8	7.5	0.0	1.5	2.3	0.0	0.0	1.5	265	9.41	0.00	6.71	Novello et al., 2012
CA	CHAD	Sudanian EDAP	Sudanian edaphic grassland mosaics with communities of Acaci and broad-leaved trees (unit 63)	a Temporary aquatic grassland	19	357 m	15.48	9.44	9.4	59.5	8.8	14.8	0.0	0.0	4.2	0.6	0.9	1.8	331	16.04	0.01	11.31	Novello et al., 2012
CA	CHAD	WOSU	Sudanian undifferentiated woodlands (unit 29a)	Tree savanna	28	553 m	19.1	11.31	7.35	54.98	23.89	9.49	0.00	0.00	1.23	0.61	0.92	1.53	327	9.92	0.01	27.71	Novello et al., 2012
CA	CHAD	WOSU	Sudanian undifferentiated woodlands (unit 29a)	Woodland	9a	367 m	18.11	9.11	6.26	65.01	3.70	7.68	0.00	0.85	2.84	1.14	6.26	6.26	352	10.22	0.07	4.93	Novello et al., 2012
CA	CHAD	WOSU	Sudanian undifferentiated woodlands (unit 29a)	Temporary aquatic grassland	16	370 m	18.07	9.1	10.79	51.60	2.04	26.53	0.00	0.58	0.87	2.04	2.33	3.21	343	29.62	0.03	3.17	Novello et al., 2012
CA	CHAD	WOSU	Sudanian undifferentiated woodlands (unit 29a)	Tree savanna	7	434 m	18.03	9.04	4.57	30.51	4.24	5.87	0.00	0.00	3.92	0.00	49.27	1.63	307	13.00	1.09	10.79	Novello et al., 2012
WA	MALI	SFSS	Sahelo-Sudanian savanna	Seasonally flooded floodplain	OUN 1 376	_	-3.31	14.23	0.40	6.35	11.51	6.35	0.00	32.14	0.79	4.76	36.11	1.59	252	67.83	0.64	63.04	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	Yamé river bed	OUN 2 378	-	-3.31	14.23	2.07	11.11	21.96	10.08	0.00	27.91	1.03	4.13	19.64	2.07	387	51.94	0.27	62.50	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	drier floodplain, woody dicotyledons and Arecaceae	OUN 3 377	-	-3.31	14.23	0.29	8.93	20.17	10.66	0.00	25.94	5.76	8.07	19.60	0.58	347	55.46	0.30	68.63	Garnier et al., 2013

Regio	n Location	Phytogeographical Zone	Vegetation Zone	Local vegetation	Sample No.	Elevation m (a.s.l.)	Lon (°)	Lat (°)	Cross	Bilobate	Saddle	Rondel	Trapeziform polylobate	Trapeziform short cell	Bulliform	Globular echinate	Globular granulate	Globular psilate	Sum (classified phytoliths)	Ic(%)	D/P°	Iph(%)	Reference
WA	MALI	SFSS	Sahelo-Sudanian savanna	Ravin Sud Tibutary, sandstone plateau covered by savanna with Butyrospermum parkii, Adansonia digitata and Borassus aethiopum	OUN 5 217	_	-3.31	14.23	1.03	5.66	13.88	3.34	0.00	33.42	0.26	10.28	31.36	0.77	389	64.13	0.55	67.50	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	drier floodplain, woody dicotyledons and Arecaceae	DC 6 433	-	-3.31	14.23	0.33	3.16	3.32	1.33	0.00	73.42	1.50	3.49	13.29	0.17	602	91.65	0.16	48.78	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	Yamé river bed	DC 7 432	-	-3.31	14.23	1.02	19.73	23.13	15.99	0.00	18.71	1.36	3.40	16.33	0.34	294	44.16	0.21	52.71	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	drier floodplain, woody dicotyledons and Arecaceae	DC 8 431	-	-3.31	14.23	0.97	4.61	6.31	6.55	0.00	51.70	5.10	5.10	18.93	0.73	412	83.04	0.27	53.06	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	Dry soils located on the sandstone interfluves	DC 10 430	-	-3.31	14.23	0.00	12.16	22.64	16.55	0.00	30.41	1.69	2.03	14.53	0.00	296	57.44	0.18	65.05	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	drier floodplain, woody dicotyledons and Arecaceae	SP 11 387	_	-3.31	14.23	2.76	7.36	5.75	1.61	0.00	53.10	1.84	7.82	19.54	0.23	435	77.52	0.28	36.23	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	Yamé river bed	SP 12 528	-	-3.31	14.23	1.64	23.01	18.90	15.89	0.00	19.45	2.19	4.93	12.88	1.10	365	44.79	0.16	43.40	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	Pond, panicoid wetland	SP 13 366	-	-3.31	14.23	5.81	28.44	21.10	11.31	0.00	8.87	1.22	2.75	19.57	0.92	327	26.72	0.26	38.12	Garnier et al., 2013
WA	MALI	SFSS	Sahelo-Sudanian savanna	Seasonally flooded floodplain	SP 14 529	-	-3.31	14.23	2.43	25.95	29.46	17.84	0.00	10.81	0.54	2.43	10.27	0.27	370	33.13	0.12	50.93	Garnier et al., 2013
WA	MALI	GFSS	Sudano–Sahelian Dogon Plateau sa	monotypic stands of Schoenefeldia gracilis (annual Chloridoideae species)	134	_	-3.34	14.09	2.48	15.46	36.83	4.39	0.00	0.00	33.21	0.57	5.73	1.34	524	7.42	0.10	67.25	Neumann et al., 2009
WA	MALI	GFSS	Sudano–Sahelian Degraded gallery forest	closed woody vegetation Cola cordifolia, Khaya senegalensis, Saba senegalensis, Ceiba pentandra and Diospyros mespiliformis, and with v. ocassional wild	135	_	-3.35	14.1	7.45	17.19	23.21	9.46	0.00	0.00	24.64	1.43	13.75	2.87	349	16.50	0.24	48.50	Neumann et al., 2009
WA	MALI	GFSS	Sudano–Sahelian Undisturbed Ségué gallery forest	closed woody vegetation Cola cordifolia, Khaya senegalensis, Saba senegalensis, Ceiba pentandra and Diospyros mespiliformis, and with v. ocassional wild Oraza sercirs	138	_	-3.45	13.51	0.65	8.44	10.17	2.60	0.00	0.00	60.82	0.43	12.99	3.90	462	11.88	0.59	52.81	Neumann et al., 2009

Appendix 5 - Table 5.3 Detailed counts of phytolith types (in %), recovered from modern soil samples from published studied sites in East, West and North Africa. Vegetation zones according to White (1983). zone codes = AFMF: Afromontane forest, AFMS: Afromontane shrubland, AFMSS: Afromontane shrub savannah, WOZA: Woodland (Zambezian), GRSO: Semi-desert grassland (Somalia–Masai), EDAP-Sah: Sahelian edaphic grassland mosaics with Acacia wooded grassland, HSAS: Sahelian herbaceous swamp and aquatic vegetation, SFSS: Sahelo-Sudanian savannah - floodplain, GFSS: Sudano–Sahelian gallery forest, EDAP-Sud: Sudanian edaphic grassland mosaics with Acacias/broad-leaved trees, BUSA: dry Sudanian woodland - Shrub savanna with short grasses, WOSU: dry Sudanian woodland - Tree/shrub tall-grass savanna and undifferentiated woodland, EVF: Guineo-Congolian lowland rainforest, MOSA: Guineo-Congolian, semi-deciduous forests, savanna mosaic Location codes = MK: Mt. Kenya, MR: Mt. Rungwe, ML: Masoko lake, MA: Middle-Awash, SEN: Senegal, MAU: Mauritanie, CAM: Cameroon, CHAD: Lake Chad, MALI: Mali. Ic (%) = Pooideae phytoliths (Rondel+Trapeziform polylobate short cell +Trapeziform short cell) Vs. Pooideae phytoliths (Bilobate short cell+Cross+Saddle+Rons+Siddle+Rons+Siddle+Ross+Bilobate short cell)*100. D/P°=Ligneous dicotyledon phytoliths (Gaddle+Cross+Bilobate short cell+Cross+Saddle+Ross+Siddle+Ross+Siddle+Ross+Siddle+Ross+Siddle+Ross+Siddle+Ross+Siddle+Ross+Siddle+Ross, saddle, Rondel, Trapeziform polylobate short cell types)*100. D/P for Neumann (2009) samples = sum of globular decorated phytoliths (including nodular) minus the echinate type/Poaceae phytoliths (bilobate, cross, saddle, Rondel, Trapeziform polylobate short cell) (bilobate, cross, saddle, Rondel, Trapeziform polylobate short cell (bilobate, cross, saddle, Rondel, Trapeziform polylobate short cell). D/P for Neumann (2012) = saddle produced in Bambusoideae excluded from D/P as they produce a D/P which underestimates tree cover. Note on morphotype nomenclature: Rond



Appendix 5 - Figure 5.1 QQ (probability) plot showing the results of Mardia's Multivariate Normality Test on Prospect Farm fossil samples (reduced morphotype dataset) and modern phytolith samples across Africa. the non-linearity of points suggests that the data is non-normally distributed.



Appendix 5 - Figure 5.2 Histograms for each morphotype in Prospect Farm fossil samples (reduced morphotype dataset) and modern phytolith samples across Africa. Histograms indicate that the data appears to be non-normally distributed



Appendix 5 - Figure 5.3 QQ (probability) plot showing the results of Mardia's Multivariate Normality Test on Prospect Farm fossil samples (expanded morphotype dataset). the non-linearity of points suggests that the data is non-normally distributed



Appendix 5 - Figure 5.4 Histograms for each morphotype in Prospect Farm fossil samples (expanded morphotype dataset). Histograms indicate that the data appears to be non-normally distributed.

APPENDIX 6

Depth of samples	Sample No.	Units	Geometry and bed contacts with underlying unit	Textural characteristics: Field observations and laser particle size analysis	Sedimentary structures	Soil formations/ pedogenic features	Palaeosol Horizon	Depositional environment
10-30 cm	1a	1A	Tabular. Bed contact is horizontal and sharp with Unit 2A	Clay loam. Poorly sorted. Very friable	Bioturbation from invertebrates and modern rootlets	Granular peds. Accumulations of organic matter	PS6: A/O	Modern soil formation
30-90 cm	2a-3a	2B	Tabular. Bed contact with Unit 2B is undulating over 15 cm	Clay loam. Poorly sorted. Very friable	Bioturbation from invertebrates and modern rootlets	Granular peds. Accumulation of organic matter	PS6: Ab6	Buried A horizon of Holocene soil (possible Andic Vertisols)
90-50 cm	4a-5a	2B	Tabular. Bed contact is horizontal and moderately gradational with Unit 3A	Silt Loam. Poorly sorted. Moderately friable. Very occasional inclusions of well- rounded-weathered pumice from Unit 3A towards base of the unit	Bioturbation has resulted in modern fine rootlets impressions of grasses/forbs on ped faces	Angular blocky peds (2-3 cm wide, 3-6 cm tall). Well- developed at top of Unit becoming more diffuse towards the base. Fe/Mn redoximorphic redistribution in matrix (mottling) and infilling voids. Illuviated clay coatings on peds	PS6: Btb6	Buried B horizon of Holocene soil (possible Andic Vertisols)
150-235 cm	6a -3b	3A - 3F/4A	Tabular. Draping landscape with thickness of whole of Unit 3 varying from ~2.5 m thickness to 30 cm thickness following peaks and troughs. Bed contact is moderately sharp with Unit 4	Very poorly sorted silty sand. Moderately indurated	Massive and unwelded pyroclastic airfall tuff. Diffused horizontal banding of sub-angular to rounded pumice	Carbonate nodules (~3 cm in diameter)	Ps6: Bckb6 changing to Cb6	Weathered volcanic tuff. Buried BC horizon of Holocene soil (possible Andic Vertisols)

235-300 cm	4b-17b	3F/4A -4B	Tabular. Bed contact with Unit 5 is gradational and undulating (repeating concave depressions up to ~30 cm deep and occur roughly every 30-60 cm). Bed thickness is highly variable from ~20 cm to ~80 cm in the main sequence to ~1.2 m in exposures at the foot of the Prospect Farm Formation (~1980m a.s.l.)	Very poorly sorted clay silty sand with small- gravel sized inclusions (angular to sub angular and occasion large gravels) of obsidian and trachytes or trachyphonolites and rounded pumice clasts	Sub-angular to angular blocky structure. Diffuse bands of gravels ~ 10cm thick with very crude horizontal bedding. Alternating pockets of coarser and finer material	Granular structure. Complex of Fe/Mn glaebules and illuviated clay. Large (up to 2 cm wide) root channels infilled with sand, clay and Fe/Mn. Clay and Fe/Mn coatings on peds. Fe/Mn redoximorphic redistribution in matrix (mottling) and infilling voids. Fe/Mn rhyzocretions	PS5: Btsob5	Thin unconsolidated foot slope lahar deposit that has undergone subsequent weathering and ferruginisation and pedogenesis (latosolization) to form a cambric Luvisol with ferralic and minor nitic, eutric and vertic properties. Overlain by deposition of air-fall tuff (Unit 3)
305-340 cm	18b - 25b	5	Tabular. Bed contact with Unit 6 is moderately undulating and moderately gradational	Poorly sorted and highly indurated sandy silt size matrix. Poorly sorted sandy silt with clay sized material infilling 'dish shaped' fissures (~1.5 cm wide) with very occasional small gravel pumice and obsidian chips at contact with Unit 4B and sometimes within laminar fissures. Clay within fissures (clay cutans) has a angular structure (i.e. showing small horizontal and vertical cracking)	Matrix is massive. Individual laminar fissures are ~10 cm long and join to form a network of 'dish-shaped' horizontal and vertical cracks (most fissures are parallel to bedding plane) that appear prismatic in section (creating a broadly prismatic macrostructure). In section there is evidence of mild slumping. Occasional gravels inclusions show evidence of reverse grading throughout the Unit.	Fe/Mn redoximorphic redistribution in matrix (mottling) and infilling voids. Well-developed medium size (0.5 cm wide ~3-5 cm long) drab halo root traces. Fe/Mn root traces. Possible tephra infilled burrows or root channels	PS5: Btsmb5	Cemented Bt horizon of cambric Luvisol with hydromorphic features and with evidence of minor gleying, as well as argrillic, eutric and nitric properties

350-360 cm	26b-27b	6	Tabular. Bed contact with Unit 7 is sharp and erosional. Unit 6 unconformabley overlies Unit 7. Bed thickness varies from less than 10cm to \sim 50cm in places	Poorly sorted. Clast supported pumice. Pumice is angular (medium vesicularity), small to large pebble sized. Accumulations of fine sand to clay size matrix material along horizontal bedding planes forming red coloured bands/drapes: here pumice becomes matrix supported	Horizontal bedding, normal grading	Mildly ferruginous clay lenses relating to water percolation	PS5: Cb5	Pyroclastic airfall pumice
385-465 cm	1c-5c	7A-7B	Tabular. Bed contact with 7C is gradational. Bed thickness is quite uniform across entirety of the Prospect Farm Formation	Clayey silt loam. highly indurated, massive. Moderately to poorly sorted. Clay and silt size material accumulates towards the top of this unit	Sub-angular blocky peds (2-3 cm wise, ~ 5 cm tall) in Unit 7A. peds appear somewhat prismatic in certain areas of Unit 7A. Horizontal and vertical cracking continues into Unit 7B becoming more diffuse with increasing depth. At base of Unit 7B fine band of diffuse pumice occurs (not well exposed on landscape)	Fe/Mn redoximorphic redistribution in matrix (mottling) and infilling voids. Clay and Fe/Mn coatings on peds. Fe/M root traces. Occasional calcium carbonate hypocoatings on peds faces in the Btskb4 horizon. Likely illuvial accumulations of sesquioxides.	PS4: Btskb4 to BwCb4	Unwelded pyroclastic fall deposit, weathered to form palaeosol of which the A and O horizon are scoured and removed by deposition of Pumice deposit (Unit 6). A tephric (vitric) Cambisol with ferralic, luvic, and calcic features
485-505 cm	1d-2d	7C- 7C/8 A	Tabular bed contact with Unit 8A is moderately sharp	Fine silt loam, poorly sorted	Massive structureless tuff	None	PS4: Cb4	Unwelded pyroclastic fall deposits forming C horizon of Palaeosol 4

510-520 cm	3d-5d	8A-8B	Tabular. Bed contact with Unit 9 is moderately sharp. Low variability in thickness across the Prospect Farm Formation	Silty-sand loam. Highly indurated. Poorly sorted. Increase in clay and silt size material relative to pumice/ash parent in C horizon	Large columnar peds (~10 cm wide and up to 15 cm tall). Peds appear to be more well developed in the Bt than in Bw horizon. When wet following rain the Btso horizon holds water and is slick but is indurated when dry	Weakly developed clay illuviation cutans. Weak clay coatings on peds. Occasional small (< 5 mm root trances)	PS3: Bwb3/Bts oB3	Buried Bw and Bt horizons of Vitric Andosol developing on weathered tuff/pumice deposit
525-535 cm	1e-3e	9A-9B	Tabular. Undulating in places. Bed contact with Unit 10 is sharp and erosional. Bed thickness varies between 10 and 40 cm across the Prospect Farm Formation	Unit 9B is poorly sorted sandy silt material replaced by silty sand material in Unit 9A. Unit 9B is comprised of matrix supported small gravel size clast of sub- rounded pumice that are common throughout the horizon ("Kaki Pumice"). Grading into Unit 9A: diffuse band of matrix supported gravels size pumice (sub-angular to sub-rounded) forming diffuse undulating band	Crude horizontal bedding. Reverse grading of pumice in Unit 9B	None	PS3: Cb3	Pyroclastic airfall deposits. Rounding of grains suggest minor amount of epiclastic reworking prior to deposition. C horizon of Palaeosol 3
540-550 cm	4e-6e	10	Tabular and undulating by up to 30 cm in places (following palaeotopography). Bed contact with Unit 11 in gradational. Bed thickness varies from between ~10 cm to 20 cm across the Prospect Farm Formation	Increase in sand in this horizon relative to underlying Unit 11A. Sand-loam. Appears massive in section in the field by is very poorly sorted according to laser particle size analysis. Moderately indurated	Large columnar peds with doming (~15 cm in diameter). Massive, structureless	Bleached horizon	PS2: Eb2	Albic horizon ferric Andosol developing on tephra deposit of Units 11 and 12
555-565 cm	7e-10e	11A- 11B	Tabular. Contact with Unit 12 is highly gradational	Very poorly sorted sandy loam. Normal grading of beds- frequent pumice inclusions decrease with decreasing depth	Weak subangular- blocky structure	Weak clay coatings on peds. Occasional small (< 5 mm root trances). Weak clay cutans	PS2: Btsb2	Argrillic horizon of ferric Andosol

575-585 cm	9e-10e	11B- 12A	Tabular. Contact Unit 12B is highly gradational	Silty-sand loam. Normal grading of beds -frequent small pebble sized, matrix supported, gritty pumice inclusion decreases with decreasing depth	Fe/Mn banding. Sub angular to sub rounded pumice clast showing signs of weathering	Mildly ferruginised clay lenses relating to water percolation	PS2: Cb2	C horizon of ferric Andosol
595-625 cm	11e-12e	12B- 13E	Tabular. Bed contact with Unit 13 is moderately gradational. Bed contact with Unit 15A is sharp and erosional	Very poorly sorted. Angular to subangular pumice. Finer, more well-rounded material in Unit 12C is underlain by grey pumice with increased angularity and size of clasts. Units 12-14 show alternation between matrix and clast supported pumice beds as well as of uncemented coarse sand size ash material (Unit 13). Some small gravel sized inclusions of obsidian interbedded with pumice. Accumulations of fine sand to clay size matrix material along horizontal bedding planes forming red coloured Fe/Mn bands/drapes: here pumice becomes matrix supported. Very subordinate accidental lithics were recorded	Horizontal bedding. Horizontal Fe/Mn banding.	None		Air fall Pumice beds. Unit 12 has undergone weathering. Rest of unit alteration due to burial and ongoing percolation of groundwater throughout layers where overlying sediments have been removed by erosion. Large voids spaces allow for penetration of modern roots were this layer underlies the modern soil formation (as in pit trenches of Locality I and II)
855-865 cm	1f-3f	15A	Tabular Bed contact with Unit 6 is gradational	Very poorly sorted friable sandy loam. Well-rounded medium gravel size abundant Fe/Mn iron nodules. massive structure (excluding prismatic structure). Increases in silt and clay size material occur in top 5 cm of this unit	Large polygonal cracks (~40 cm wide when viewing the horizontal surface of the sediment). Cracks are infilled with fine, bleached sand sized material	Fe/Mn glaebules throughout Units 15 and 16: well- rounded discrete pedogenic Iron nodules (3-4 cm in diameter) throughout entire Unit. Unit 15A shows evidence of both bleach eluvial albic features as well as argrillic clay illuviation features	PS1: EBtsocb1	EBtsocb1 of ferric Acrisols or ferric Alisol, developed from tuffaceous material and undergoing laterization under a tropical weathering regime

870-890 cm	4f-8f	15B	Bed contact with Unit 15A is moderately gradational	Very poorly sorted silty clay loam. Occasional, well-rounded medium gravel size Fe/Mn iron nodules. Moderately indurated	Massive to very weak subangular-blocky structure	Fe/Mn redoximorphic redistribution in matrix (mottling) and infilling voids. Clay illuviation cutans on ped faces. Weakly developed drab haloes (~2cm in diameter) and rootlet traces (< 5 mm). Occasional discrete well-rounded pedogenic iron nodules	PS1: Btsocb1	Btsocb1 of ferric Acrisols or ferric Alisol developed from tuffaceous material and undergoing laterization under a tropical weathering regime
895-900 cm	9f-10f	16	Tabular. Bed contact with Unit 15B is gradational. Bed contact with underlying Unit (Barbara Anthony's Unit 35) was not reached by the INAP excavation	Massive. Very poorly sorted sandy silt loam. Well-rounded medium gravel size abundant Fe/Mn iron nodules. Moderately indurated	Moderately indurated dense iron nodules (pisolith). Nodules are distributed across the unit	Well-rounded medium gravel size abundant Fe/Mn nodules in a ferruginised matrix	PS1: CBcb1	Ccb1 of ferric Acrisols or ferric Alisol developed from tuffaceous material and undergoing laterization under a tropical weathering regime

Appendix 6 - Table 6.1 Summary of field descriptions and particle size analysis of type section from Locality I at Prospect Farm.

Appendix 6 - Table 6.2 Mean elemental concentration in ppm (mg/l) based on analysis of the	ee replicate samples.
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Sample	Al	Fe	К	Mg	Mn	Na	р	Si	Ti	Ca
1a	28.819	77.657	3.046	1.637	3.872	0.556	0.324	0.425	361.209	1.856
2a	29.188	76.219	3.310	1.742	3.772	1.538	0.237	0.366	356.776	1.603
3a	37.219	94.243	4.350	2.127	4.090	1.045	0.077	0.311	371.700	2.514
4a	52.986	82.850	5.624	2.671	2.681	1.001	0.109	0.393	266.690	2.495
5a	54.982	92.597	6.917	3.374	2.094	1.794	0.203	0.450	291.022	3.475
6a	41.338	79.720	6.114	3.047	2.776	1.512	0.200	0.365	242.612	3.229
7a	25.088	58.181	4.842	2.382	2.471	1.456	0.151	0.339	227.791	2.453
8a	30.907	75.151	5.809	2.598	3.505	0.982	0.112	0.274	298.573	3.264
1b	24.882	46.696	4.528	1.588	2.156	2.194	0.188	0.049	312.966	3.675
2b	44.428	85.779	6.414	2.610	3.851	3.269	0.156	0.050	608.434	4.264
3b	37.380	81.141	6.335	2.724	3.271	2.673	0.205	0.035	501.198	4.638
4b	44.073	93.535	5.563	2.712	3.968	2.457	0.120	0.059	622.916	4.305
5b	45.281	89.357	5.358	2.628	3.418	2.409	0.109	0.057	646.176	4.301
6b	25.036	60.933	4.302	1.982	2.833	1.726	0.160	0.027	396.219	2.961
7b	64.948	130.614	6.851	3.467	4.667	3.043	0.110	0.077	965.631	6.082
8b	45.531	110.276	6.490	3.481	3.252	4.766	0.244	0.067	719.254	4.786
9b	65.600	139.931	6.405	3.743	4.070	3.175	0.120	0.089	1040.71	4.643
10b	54.074	122.394	6.130	3.674	3.542	2.992	0.149	0.075	758.731	4.532
11b	76.545	157.742	7.878	4.403	4.461	3.843	0.131	0.082	1118.22	5.577
12b	71.815	156.171	7.494	4.350	5.267	3.871	0.131	0.040	1077.36	5.490
13b	63.238	130.528	6.230	3.676	5.060	3.636	0.158	0.067	1006.88	4.870
14b	36.586	92.905	5.012	2.778	4.201	2.332	0.222	0.040	625.715	3.475
15b	43.029	99.032	4.315	2.564	4.863	2.111	0.104	0.049	767.616	3.316
16b	60.438	132.414	6.415	3.644	6.445	2.981	0.208	0.020	972.435	5.480
17b	78.204	129.724	6.746	4.281	4.063	3.319	0.106	0.071	937.715	5.529
18b	89.074	140.587	6.854	4.676	4.966	3.577	0.142	0.061	1040.56	5.984
19b	75.130	120.708	5.454	3.741	5.386	2.744	0.138	0.049	972.586	4.904
20b	92.949	131.138	6.616	4.627	3.952	3.394	0.104	0.072	944.237	5.861
21b	48.998	85.740	4.501	3.318	2.736	2.328	0.168	0.032	518.005	4.068
22b	65.409	102.921	5.033	3.772	4.245	2.739	0.177	0.027	680.279	4.746
23b	31.765	66.887	3.380	2.568	3.288	2.199	0.351	0.058	334.714	3.698
24b	53.484	99.572	4.104	3.755	4.136	3.045	0.320	0.100	567.188	4.859
25b	56.828	106.739	4.609	3.927	3.558	3.201	0.286	0.120	612.763	5.834
1c	47.508	66.454	6.406	3.221	1.201	1.183	0.233	0.347	283.499	8.585
2c	29.488	62.716	5.029	1.781	2.615	1.309	0.301	0.279	306.761	3.096
3c	27.591	53.809	3.863	1.428	2.143	0.748	0.265	0.289	276.611	2.527
4c	52.734	81.673	5.033	2.337	2.248	2.435	0.171	0.350	330.348	3.484
5c	46.535	69.514	4.312	1.620	1.852	1.528	0.062	0.206	301.460	4.003
1d	23.724	41.509	2.587	0.821	1.369	1.905	0.443	0.040	229.296	2.614
2d	22.418	38.408	2.272	0.756	1.302	1.727	0.876	0.050	219.592	2.463
3d	32.039	56.896	3.160	1.027	2.042	2.502	0.842	0.059	309.568	3.462

4d	23.527	44.162	2.575	0.811	1.450	1.824	0.727	0.049	241.769	2.833
5d	40.498	66.868	3.061	1.087	2.032	2.221	0.965	0.080	407.743	3.457
1e	29.423	57.838	3.159	0.977	2.002	2.167	0.906	0.061	327.397	3.276
2e	26.929	58.416	3.094	1.011	2.075	1.810	0.844	0.056	344.532	3.307
3e	26.000	60.388	3.112	1.129	2.078	1.836	0.806	0.064	353.155	3.351
4e	29.270	73.673	3.566	1.244	2.822	1.837	0.999	0.061	417.136	3.622
5e	47.934	111.349	5.511	1.720	4.958	2.826	0.517	0.062	739.993	5.227
6e	41.420	91.702	4.149	1.385	3.707	2.295	0.504	0.096	606.158	4.272
7e	35.061	87.182	3.887	1.277	3.567	2.105	0.509	0.059	548.840	4.112
8e	85.262	127.525	6.259	1.959	4.891	3.295	0.385	0.080	1176.59	7.005
9e	44.573	91.096	4.649	1.339	3.060	2.383	0.635	0.052	528.602	4.866
10e	68.822	127.053	5.766	1.735	3.840	3.143	0.477	0.068	793.188	6.328
1f	15.416	72.651	3.063	1.340	5.775	0.421	1.444	0.038	481.293	4.051
2f	16.162	76.560	3.433	1.479	10.620	0.414	1.320	0.030	628.934	5.255
3f	21.138	129.143	3.616	1.531	6.571	0.599	1.246	0.062	615.561	4.524
4f	13.720	77.306	2.862	1.305	2.725	0.214	0.718	0.077	602.188	3.239
5f	18.761	54.024	4.266	2.427	2.646	0.376	0.572	0.058	480.049	6.135
6f	27.698	73.310	4.769	2.977	2.865	0.541	0.375	0.071	749.876	7.272
7f	14.377	45.178	3.352	1.801	2.284	4.710	0.284	0.033	381.843	5.323
8f	19.774	98.929	3.859	2.211	4.905	0.536	0.338	0.043	511.290	5.609
9f	25.333	113.046	4.459	2.461	13.843	0.472	0.507	0.057	593.610	6.406
10f	28.184	141.009	4.414	2.594	14.084	0.501	0.510	0.009	602.125	6.477

Sample	clay	fine silt	medium silt	coarse silt	fine sand	medium sand	coarse sand	d (0.5)	D [4, 3] - Volume weighted mean	inclusive mean	inclusive kurtosis	inclusive SD	inclusive skewness	% of particles below 63 µm
1a	11.02	18.34	16.21	37.71	14.76	1.84	0.12	18.42	38.30	6.00	1.15	2.31	-0.21	83.46
2a	7.76	14.43	13.53	40.49	20.61	2.91	0.26	26.98	50.47	5.48	1.11	2.13	-0.22	76.45
3a	4.41	10.33	9.58	36.71	32.84	5.03	1.10	46.03	77.06	4.75	1.14	2.03	-0.24	61.32
4a	7.26	18.81	13.36	27.29	17.11	8.69	7.49	26.41	117.77	5.05	0.93	2.80	0.07	66.85
5a	6.17	17.88	13.26	31.32	20.63	6.64	4.10	28.27	88.01	5.24	1.00	2.46	-0.03	68.82
6a	5.36	15.52	12.61	36.03	23.19	5.98	1.31	31.40	70.62	5.19	1.04	2.23	-0.12	69.74
7a	3.65	10.80	10.63	38.89	32.65	3.39	0.00	41.53	65.45	4.81	1.06	1.93	-0.21	64.24
8a	4.47	11.88	11.33	39.34	28.64	4.28	0.06	37.72	63.61	4.98	1.09	1.99	-0.21	67.29
1b	2.90	12.03	11.80	37.35	26.92	7.00	2.02	39.41	84.63	4.78	1.10	2.11	-0.08	64.31
2b	2.24	7.07	6.59	21.24	29.53	19.21	14.11	116.48	218.01	3.39	0.88	2.37	-0.24	37.30
3b	2.57	7.86	7.88	28.41	31.84	12.33	9.10	70.78	161.77	3.87	0.98	2.32	-0.10	46.93
4b	2.77	8.67	8.64	29.03	28.84	10.32	11.72	64.81	178.18	3.93	0.98	2.46	-0.04	49.31
5b	4.12	10.06	9.50	29.31	26.80	13.72	6.49	55.45	141.42	4.21	0.92	2.47	-0.09	53.18
6b	1.47	4.53	4.54	17.84	39.48	23.80	8.34	147.65	214.35	3.09	1.06	1.96	-0.32	28.53
7b	0.68	5.94	6.32	27.38	47.34	11.10	1.24	84.02	119.40	3.79	1.03	1.77	-0.24	40.56
8b	2.39	6.38	6.19	23.96	36.74	10.65	13.69	92.02	210.81	3.51	1.12	2.35	-0.10	39.13
9b	2.68	6.98	7.58	28.13	27.09	12.35	15.18	75.26	203.26	3.65	0.93	2.45	-0.04	45.58
10b	2.64	7.16	7.71	30.01	41.33	9.93	1.23	67.65	107.32	4.10	1.05	1.97	-0.23	47.76
11b	3.43	8.06	8.62	31.65	41.09	6.42	0.72	59.00	91.65	4.33	1.06	1.98	-0.25	52.02
12b	2.75	7.51	7.82	29.01	34.11	13.60	5.20	69.59	136.38	3.97	0.98	2.19	-0.15	47.31
13b	0.64	5.78	6.15	24.57	39.35	14.11	9.40	96.41	182.50	3.48	1.04	2.06	-0.12	37.34
14b	2.26	6.40	5.95	18.85	30.29	18.02	18.23	137.89	247.52	3.18	0.93	2.39	-0.26	33.61
15b	2.62	7.39	6.53	20.27	25.42	10.43	27.33	115.16	331.40	3.12	0.80	2.74	-0.11	36.99

Appendix 6 - Table 6.3 Laser particle size analysis results for samples from Prospect Farm Locality I. Values are the average of 3 repeat measurements of the same sample. Clay (0.03 -1.95 µm), fine silt (1.95-7.81 µm), medium silt (7.81-15.63 µm), coarse silt (15.63-62.5 µm), fine sand (62.5-250 µm), medium sand (250-500 µm), coarse sand (500-2000 µm).

1(1	120	1()5	12 42	22 47	25 (2	E (0	1.10	21.00	71 (0	E 1 E	0.07	2.10	0.11	(7.71
160	4.36	16.25	15.45	33.47	25.65	5.68	1.19	31.82	/1.60	5.15	0.96	2.19	-0.11	67.71
17b	2.23	6.97	5.78	16.65	30.86	17.75	19.76	153.94	274.07	3.09	0.96	2.48	-0.29	31.77
18b	2.18	6.62	5.80	17.21	27.94	14.80	25.44	169.14	299.89	2.96	0.88	2.51	-0.30	31.95
19b	0.49	4.27	3.95	14.28	36.49	21.72	18.79	191.35	276.69	2.67	1.09	1.99	-0.28	23.12
20b	1.92	6.28	5.67	18.82	29.06	16.92	21.33	138.29	276.80	3.08	0.91	2.42	-0.21	32.85
21b	1.35	4.60	4.23	14.41	22.28	13.68	39.44	306.77	433.32	2.27	0.84	2.37	-0.42	24.71
22b	0.55	4.61	3.92	12.51	20.68	16.05	41.68	374.84	445.85	2.10	0.90	2.24	-0.51	21.68
23b	2.30	7.23	6.01	17.66	25.69	16.93	24.19	160.49	306.58	3.03	0.88	2.59	-0.28	33.33
24b	2.90	9.26	8.16	24.01	26.73	18.05	10.90	81.20	181.97	3.77	0.84	2.48	-0.16	44.49
25b	1.74	6.16	5.47	14.75	19.41	20.80	31.67	282.82	372.84	2.57	0.88	2.51	-0.47	28.21
1c	4.72	12.69	12.63	42.54	20.94	4.76	1.72	30.99	68.10	5.15	1.20	2.07	-0.09	72.81
2c	5.56	13.07	10.42	40.79	20.92	7.19	2.06	36.14	104.43	5.11	1.32	2.28	-0.14	70.10
3c	2.98	11.36	9.26	26.60	31.68	18.13	0.00	61.98	129.90	4.22	0.90	2.37	-0.16	50.37
4c	3.83	12.60	10.58	30.51	31.84	10.63	0.00	46.03	94.35	4.63	0.93	2.26	-0.15	57.73
5c	4.93	13.25	11.46	39.18	24.12	7.05	0.00	34.83	71.06	5.07	1.13	2.14	-0.15	69.08
1d	2.27	6.93	8.83	32.33	32.95	13.11	3.57	61.62	124.16	4.05	0.94	2.09	-0.09	50.58
2d	1.53	4.90	6.00	21.98	21.96	16.22	27.40	169.00	333.08	2.81	0.79	2.46	-0.22	34.57
3d	1.90	5.89	6.97	26.23	27.48	13.28	18.26	90.08	246.60	3.38	0.88	2.43	-0.03	41.17
4d	1.93	6.12	6.48	24.79	31.99	12.66	16.03	93.39	243.33	3.41	0.99	2.40	-0.05	39.52
5d	2.08	7.09	7.59	27.68	35.20	13.47	6.88	76.18	150.19	3.83	0.98	2.17	-0.14	44.66
1e	0.54	5.02	5.54	20.65	26.66	11.19	30.40	153.79	342.87	2.78	0.77	2.37	-0.14	31.91
2e	1.92	10.02	10.07	32.37	29.76	8.58	7.29	53.35	126.80	4.26	1.06	2.24	-0.05	54.60
3e	3.37	15.98	15.28	35.84	22.24	5.52	1.77	28.03	71.69	5.16	0.98	2.12	-0.01	70.64
4e	3.55	9.45	8.79	27.65	31.15	9.60	9.80	63.89	166.96	4.09	1.02	2.48	-0.09	49.65
5e	2.72	7.37	7.10	24.70	27.51	11.45	19.15	88.09	245.98	3.46	0.92	2.59	-0.06	42.08
6e	2.87	8.05	7.11	22.11	32.92	16.08	10.85	95.32	192.31	3.66	0.97	2.42	-0.21	40.31
7e	3.35	13.26	11.84	31.03	25.08	11.97	3.47	41.68	109.15	4.56	0.91	2.40	-0.03	59.67
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8e	4.64	11.10	8.43	20.21	26.52	13.54	15.56	85.39	199.09	3.85	0.83	2.77	-0.21	44.51
9e	2.79	7.31	6.17	18.43	31.25	18.43	15.61	132.26	225.43	3.33	0.95	2.44	-0.30	34.85
10e	3.16	9.50	8.50	24.52	32.84	13.40	8.08	75.74	153.26	3.98	0.93	2.39	-0.20	45.85
1f	4.85	17.60	13.26	28.44	23.25	8.52	4.09	31.51	98.81	4.96	0.90	2.53	0.00	64.31
2f	3.06	8.97	7.35	18.58	15.30	12.92	33.83	200.52	344.42	3.03	0.74	2.80	-0.40	38.06
3f	5.42	19.96	14.45	32.03	19.35	7.08	1.71	24.89	72.94	5.37	0.95	2.36	-0.01	72.03
4f	7.59	13.23	8.31	17.30	20.03	15.05	18.48	82.69	245.11	4.03	0.77	3.16	-0.22	46.53
5f	4.52	16.59	11.65	25.83	27.20	10.71	3.51	39.96	105.39	4.77	0.84	2.54	-0.08	58.75
6f	3.43	13.92	9.93	22.91	22.91	10.70	16.20	61.87	229.23	4.06	0.82	2.88	-0.04	50.33
7f	4.46	13.15	8.83	17.72	21.80	18.96	15.08	93.86	215.72	3.89	0.73	2.83	-0.26	44.27
8f	4.34	15.02	10.03	21.69	28.74	10.23	9.95	58.84	146.06	4.39	0.81	2.66	-0.17	51.22
9f	7.05	14.16	9.81	21.87	19.96	15.23	11.92	52.31	182.56	4.38	0.78	2.98	-0.10	53.02
10f	3.82	10.39	7.33	18.64	27.14	15.55	17.13	110.17	243.90	3.61	0.88	2.77	-0.25	40.31

Appendix 6 - Table 6.4 Phytolith counts. The table lists the number of fields of view (F.O.V) that were required to reach the target of 200 index specific morphotypes. All slides were scanned for rarer types one this target has been reached. In cases where low amounts of phytoliths were present the whole slide was checked and the corresponding F.O.V = (i.e. the whole slide). *p* is the weight of the dry silicate. AIF is the Acid Insoluble Fraction.

Sample	F.O.V.	Number of phytoliths counted	р	<i>p</i> on slide	AIF	Phytoliths per gram AIF
1a	181	1664	1.0292	0.0014	4.0056	6252698.119
2a	342	985	1.5585	0.0008	4.3597	4769346.65
3a	3706	192	4.2561	0.0045	4.2222	43009.23689
4a	3706	174	2.0999	0.0008	3.9762	114865.5123
5a	3706	80	3.0554	0.0013	3.6371	51696.30073
6a	3706	44	3.0131	0.0013	3.9604	25750.3904
7a	3706	118	4.3068	0.001	4.2555	119422.4885
8a	400	910	0.5252	0.0005	0.6095	14529509.56
1b	81	513	1.8789	0.0012	4.8784	7532964.321
2b	83	442	2.6292	0.0013	4.8062	8304455.458
3b	248	695	3.4581	0.0017	4.8483	4357333.651
4b	160	629	2.2481	0.0013	4.8206	5226252.527
5b	229	685	2.4056	0.0002	4.389	30378860.43
6b	277	1013	1.2972	0.0007	4.7264	5313695.376
7b	310	856	0.5505	0.001	4.6378	1214635.385
8b	693	2371	0.89	0.0009	4.4361	2826396.196
9b	467	873	2.3085	0.001	4.208	3800494.092
10b	3706	99	2.2542	0.0017	4.4614	29424.39593
11b	605	3000	0.5943	0.0012	4.3489	2092663.954
12b	3706	96	1.3493	0.0011	4.4671	26360.97041
13b	749	1892	1.417	0.0009	4.2888	3436524.242
14b	535	2165	0.8384	0.0012	4.4427	2358390.438
15b	3706	221	0.8629	0.0009	4.5206	46872.07205
16b	3706	398	0.7413	0.0008	4.5081	81807.57969
17b	3706	110	1.3666	0.0012	4.38	28600.83714
18b	3706	128	1.6768	0.0011	4.2248	46184.09048
19b	3706	142	2.3876	0.0008	4.4123	96049.45267
20b	3706	242	3.1513	0.0015	4.2429	119825.9995
21b	62	495	3.014	0.0023	4.3442	8924988.414
22b	3706	108	2.9546	0.0016	4.4526	44790.79639
23b	3706	159	2.9943	0.0013	4.254	86089.77975
24b	3706	269	3.5209	0.0018	3.974	132405.371
25b	3706	255	2.8426	0.001	4.1744	173644.8352
1c	140	813	2.6382	0.001	4.1596	13649200.31
2c	125	771	3.056	0.0016	4.1219	10591777.08
3c	235	765	4.9053	0.0013	4.1483	10973222.57
4c	527	937	4.1362	0.0013	3.9163	5353030.919
5c	420	800	3.1307	0.001	3.5392	6244038.834
1d	3706	179	2.8981	0.0011	4.3335	108826.5626
2d	72	425	2.6827	0.0011	4.4619	11956513.98
3d	73	372	2.4315	0.0011	4.4502	9380169.582
4d	94	474	2.1165	0.0014	4.4151	6398655.542

5d	105	490	1.7751	0.0014	4.4121	4969867.073
1e	468	616	1.5123	0.0009	4.6538	1761209.979
2e	97	536	0.9413	0.001	4.3539	4427221.134
3e	167	942	0.9873	0.0016	4.8178	2677339.033
4e	69	187	1.3569	0.001	4.3262	3150085.315
5e	105	740	2.3908	0.0007	4.3288	20606709.93
6e	98	646	1.963	0.0009	4.0796	13060361.57
7e	72	605	1.7255	0.0012	3.6418	12295014.78
8e	431	992	1.2086	0.0109	4.0703	232355.3223
9e	243	850	1.7337	0.001	3.9549	5682502.63
10e	200	819	2.5936	0.0009	3.896	11224939.19
1f	33	361	2.1165	0.0013	4.3708	15100655.47
2f	39	431	2.0356	0.0009	4.3844	21127153.01
3f	46	614	1.0095	0.0013	4.4683	8596461.797
4f	47	272	1.0758	0.0008	4.4575	6470082.197
5f	61	149	4.1791	0.0017	3.9073	5695109.371
6f	32	84	2.5624	0.001	4.2382	5881435.48
7f	30	115	2.7232	0.0017	4.0327	5642867.312
8f	33	135	2.0076	0.0016	4.2639	4461270.669
9f	29	128	2.1211	0.0011	4.2715	7383946.999
10f	34	191	2.0271	0.001	4.217	10007245.95

Sample ID	Blocky/Tabular (pislate/decorated/corniculate/cavate)	Blocky irregular	Tabular parallepiped	Tabular thick dendritic/decorated	Blocky facetate	Globular echinate	Globular granulate	Globular psilate	Globular decorated	Globular psilate Irg	Globular granulate Irg	Globular verrucate oblong	Globular founded	Sub-globular dark	Globular aggregate	Ellipsoid psilate	Ellipsoid with outgrowths	Sclereids	Cork platelet lrg	Epidermal jig-saw/polygonal	Epidemal - dendric	Cylindroid psialte/decorated	Cylindroid bulbous/Clavate	Simple epidermal tracheids	Aciular hair cell	Thick Aciular types	Long cell psilate/decorated edges	Square/recatagular psilate	Irregular decorated platelets	Perforated platelet-pitted	Perforated platelet-columellate
1a	53	0	4	8	4	0	4	0	0	11	0	0	0	0	0	4	0	4	0	0	0	45	8	15	604	23	17 0	47 2	0	8	0
2a	18	0	0	0	0	0	0	4	0	4	0	0	0	7	0	0	0	4	0	0	0	33	4	22	400	4	73	21 1	0	0	0
3a	5	0	0	1	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	5	1	1	86	2	26	36	0	0	0
4a	5	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	4	0	0	77	1	18	41	0	0	0
5a	7	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	3	35	0	19	0	0	0	0
6a	25	0	0	28	1	0	6	15	0	6	0	0	0	0	0	0	0	6	0	0	3	32	0	0	72	13	31	99	0	0	0
7a	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	4	0	0	50	2	10	23	0	0	0

Appendix 6 - Table 6.5 Total phytolith counts of non-GSSC types form Prospect Farm.

8a	0	0	0	5	6	0	5	5	0	0	0	0	0	10	0	5	0	4	0	0	0	35	0	0	350	5	13 0	16 0	0	5	0
1b	23	0	0	5	1	0	4	7	0	2	2	0	0	2	1	7	1	4	0	0	0	10	5	1	90	13	56	43	0	3	0
2b	3	0	0	1	4	0	1	3	0	0	0	0	0	0	0	5	0	1	0	0	0	18	2	3	82	0	60	42	0	6	0
3b	16	0	0	3	9	0	11	10	1	3	0	0	0	7	1	17	0	0	0	0	0	17	2	2	157	17	68	99	9	6	0
4b	30	0	1	1	2	4	3	9	0	1	0	0	0	4	1	5	0	4	0	0	0	25	1	3	148	10	60	84	0	8	0
5b	29	0	0	4	6	1	8	3	0	1	0	0	0	6	5	7	4	4	0	0	0	28	1	0	166	10	80	76	0	8	0
6b	53	0	1	1	15	0	14	11	0	2	0	0	0	5	4	14	0	0	0	0	0	27	7	4	290	0	11 6	19 0	0	11	0
7b	58	0	0	2	8	1	7	2	0	4	0	0	0	3	3	10	2	7	0	0	0	23	13	2	224	18	85	15 9	0	2	0
8b	85	0	0	5	18	0	13	22	0	0	0	0	0	16	2	11	0	4	0	0	0	33	11	2	578	18	17 6	40 9	0	16	0
9b	12	0	0	0	0	0	6	6	0	0	0	0	0	0	0	12	0	0	0	0	0	73	12	0	267	36	18 2	55	0	0	0
10b	4	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	45	0	7	29	0	0	0
11b	209	0	42	33	42	0	14	19	0	9	0	0	0	0	0	9	5	37	0	0	0	28	33	0	633	79	30 7	55 8	0	0	0
12b	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	40	2	10	28	0	1	0
13b	57	0	6	0	17	0	8	23	0	8	0	0	0	6	0	11	2	9	0	0	0	57	4	4	764	17	28 3	40 8	0	0	0
14b	53	0	6	0	12	0	6	6	0	6	0	0	0	0	0	24	0	0	0	0	0	41	6	12	882	24	37 6	48 8	0	0	0
15b	9	0	0	0	0	0	0	1	0	0	0	0	0	1	0	3	0	1	0	0	0	1	0	0	94	2	25	79	0	1	0

16b	20	0	2	1	2	0	2	5	0	1	0	0	0	0	0	5	2	0	0	0	0	8	0	0	168	1	46	11 7	0	0	0
17b	3	0	0	0	1	0	0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	34	0	34	31	0	0	0
18b	5	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	2	61	1	10	42	0	0	0
19b	5	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	2	1	0	67	2	20	34	0	0	0
20b	11	0	0	0	2	0	2	1	0	0	0	0	0	0	0	0	1	2	0	0	0	4	0	0	101	2	24	90	0	0	0
21b	14	0	0	0	1	0	2	8	0	0	0	0	1	4	1	0	0	1	0	0	0	12	0	3	90	0	47	69	0	9	0
22b	2	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	48	6	41	0	0	0	0
23b	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	0	0	3	0	0	61	0	28	45	0	0	0
24b	8	0	0	2	0	0	0	4	0	0	0	0	0	2	0	0	0	0	0	0	0	11	0	0	124	1	41	56	0	0	0
25b	17	0	0	2	0	0	0	2	0	1	0	0	0	2	0	1	2	0	0	0	0	6	0	1	95	1	32	79	0	0	0
1c	13	0	1	1	0	0	2	7	0	0	0	0	0	0	0	5	0	0	0	0	0	32	2	9	295	2	14 0	78	0	0	0
2c	20	0	0	3	0	0	4	5	0	0	0	0	0	0	0	7	0	0	0	0	0	8	6	1	248	16	11 5	10 1	0	3	0
3c	16	0	6	5	0	0	5	0	36	0	0	0	0	0	0	11	1	0	0	0	0	18	7	0	251	24	12 9	49	0	1	0
4c	34	0	5	0	0	0	7	28	2	0	0	0	0	0	0	11	0	0	0	0	0	68	13	13	260	7	18 4	91	0	2	0
5c	35	0	3	1	0	0	13	38	3	0	0	0	0	0	3	9	0	0	0	2	0	47	3	7	178	8	13 5	95	0	5	0
1d	2	0	0	0	2	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	5	0	1	71	0	19	62	0	0	0
2d	3	0	0	1	1	0	2	8	1	1	0	0	0	0	0	2	0	0	2	0	0	11	2	0	88	0	41	42	0	8	0

3d	2	0	0	0	0	0	1	2	1	0	0	0	0	1	0	3	0	0	0	0	3	11	0	1	64	0	28	37	0	6	0
4d	1	0	0	2	2	0	3	10	0	0	0	0	0	2	0	4	0	0	6	0	0	10	1	2	84	0	50	74	0	6	0
5d	2	0	0	1	0	0	3	5	0	0	0	0	0	2	0	0	0	0	0	0	0	12	1	0	95	0	58	81	0	11	0
10	6	0	0	1	3	0	3	6	0	1	0	0	0	1	2	2	0	0	0	0	0	0	0	0	100	2	58	84	0	0	20
	0	0	0	1	5	0	5	0	0	1	0	0	0	1	2	2	0	0	0	0	0	10	0	0	1))	2	50	04	0	10	2)
2e	1	0	0	1	0	0	1	4	0	0	0	0	0	1	0	4	0	0	1	0	0	10	0	2	144	1	58	83	0	19	0
3e	6	0	0	0	2	0	0	6	0	0	0	0	0	2	0	4	2	0	4	0	0	21	0	2	375	2	10 7	17 8	0	29	0
4e	0	0	0	1	0	0	0	0	0	1	0	0	0	3	0	0	1	1	0	0	0	5	0	0	72	0	29	42	0	3	0
5e	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
6e	0	0	0	2	0	0	0	8	0	0	0	0	0	4	0	0	0	2	0	0	0	6	0	2	256	0	60	92	0	12	0
70	12	0	1	1	6	0	3	7	0	2	0	0	0	1	11	3	4	2	Ŭ,	0	0	12	1	5	185	1	50	52	0	22	3
10	12	0	1	1	0	0	5	/	0	2	0	0	0	1	11	5	4	2	0	0	0	12	1	5	105	1	57	52	0	22	5
8e	35	0	0	0	4	0	0	12	0	0	0	0	0	0	0	4	0	0	0	0	0	27	4	8	346	0	10 8	21 2	0	0	19
9e	18	0	0	0	0	0	4	14	0	7	0	0	0	0	7	0	0	7	0	0	0	32	4	0	279	4	10 0	14 6	0	0	25
10e	8	0	0	0	4	0	8	8	0	0	0	0	0	0	0	0	0	4	0	0	0	30	0	0	328	0	83	12 1	0	0	5
1f	3	0	0	0	0	1	3	1	0	2	0	0	0	0	0	0	6	0	0	0	1	12	1	0	55	4	25	32	0	0	0
2f	18	0	0	2	1	1	6	7	1	1	0	0	0	3	2	0	4	7	2	0	1	23	0	2	119	3	0	0	0	1	0
3f	21	0	2	6	4	0	7	6	2	3	0	0	0	2	2	3	8	6	0	0	2	13	2	8	131	3	48	10	0	0	0
																												3			
4f	6	0	1	1	0	0	1	2	0	2	0	0	0	2	0	2	2	0	0	0	0	11	0	0	92	2	43	78	0	0	0

5f	8	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	69	0	13	43	0	0	0
6f	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	2	1	0	38	1	13	23	0	0	0
7f	4	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	1	1	0	0	1	2	1	0	51	2	12	31	0	0	0
06	(0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	1	0	50	1	12	42	0	0	0
81	0	0	0	0	1	0	0		0	0	0	0	0	0		0	1	1	0	0	0	2	1	0	39	1	10	43	0	0	0
9f	3	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	2	0	0	0	0	3	0	0	48	4	17	41	0	0	0
10f	3	0	0	0	0	0	0	2	0	1	0	0	0	1	0	0	1	1	0	0	1	4	0	0	87	0	15	62	0	0	0
PS5 (4a) LO C 2	41	2	1	0	5	0	11	0	9	0	1	0	0	0	7	9	0	0	0	0	0	30	8	1	222	1	98	20 5	0	2	0
PS4 (7a) LO C 2	20	0	7	0	0	0	14	1	2	0	0	0	1	1	0	3	0	0	0	0	0	15	4	0	266	5	11 3	91	0	0	0
PS3 (8b) LO C 2	0	1	2	0	1	0	0	0	14	0	0	0	0	1	0	2	0	1	3	0	0	13	0	0	115	3	47	78	0	3	1
PS2 (10) LO C 2	0	0	1	0	0	0	0	0	13	0	0	0	1	1	0	0	0	0	1	0	0	9	1	0	211	0	83	12 3	4	3	0
PS1 (15B) LO C 2	26	1	1	3	0	2	6	3	10	2	0	0	1	0	4	1	0	12	3	0	0	14	1	0	130	2	0	0	0	0	0

Sample ID	Cyanotis type	Marantaceae type	Murdannia type	Cyperaceae	Cross	Cross (3 lobed)	Saddle short/squat (Chloridoideae type)	Bilobate short shank	Bilobate long shank	Polylobate	Bilobate asymetrical	Trilobate	Bilobate - Aristidoideae type	Bilobate- well defined, non-sculpted, trap, asyml	Plateaued saddle	Saddle long/tall	Saddle "collapsed"	Bilobate "stipa-type"	Trapeziform short cell	Trapeziform polylobate	Trapezoid square	Rondel (pooid, conical, keeled and pyramidal types)	Rondel base >15um (exclusive to Pooideae)	Bilobate -Ehrhartoideae type	Trapeziform wavy long (Pooideae)	Dendriform	Parallepiped Bulliform	Bulliform Fan-shaped
1a	0	0	0	0	8	0	26	83	4	0	0	0	0	0	8	11	0	4	11	0	0	45	0	0	0	0	8	15
2a	0	0	0	0	4	0	36	55	29	11	0	0	0	0	0	7	0	0	7	0	0	51	0	0	0	0	4	0
3a	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	2	9	0	0	0	0	3	1
4a	0	0	0	0	1	0	3	6	2	0	0	0	0	0	0	0	0	0	1	0	0	9	0	0	0	0	1	1
5a	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1
6a	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	1	3	0	0	2.	0	0	0	0	0	8
7.2	0	0	0	0	0	0	3	8	1	0	0	0	1	0	2	0	0	0	2	0	1	6	0	0	0	0	0	0
80	0	0	0	0	0	0	25	55	15	0	0	0	5	0	5	5	0	5	10	0	5	50	0	0	0	0	0	0
116	0	0	0	0	2	0	0	25	0	4	2	2	1	1	1	10	7	24	10	2	2	00	0	0	2	0	2	6
2b	0	0	0	1	4	0	10	34	17	3	0	0	1	0	3	10	0	14	19	2	4	83	0	0	0	0	4	4

 Appendix 6 - Table 6.6 Total phytolith counts of Commelinid and GSSC types form Prospect Farm.

 Image: Commelinid and GSSC types form Prospect Farm.

3b	0	0	0	0	7	0	6	32	0	5	0	4	0	0	4	7	1	37	19	2	5	89	0	0	1	0	10	10
4b	0	0	0	0	4	1	10	40	8	1	0	0	2	0	4	1	0	16	25	0	5	90	0	0	0	0	7	3
F1.	0	0	0	0	1	0	15	10	0	0	0	0	0	0	(0	0	27	20	1	6	107	0	0	2	0	15	4
50	0	0	0	0	1	0	15	10	0	0	0	0	0	0	0	0	0	21	20	1	0	107	0	0	2	0	15	4
6b	0	0	0	0	1	0	6	33	9	2	0	0	0	0	2	4	0	0	35	0	9	90	0	7	0	0	26	19
7b	0	0	0	0	0	0	0	31	8	1	0	0	0	0	3	4	0	14	35	0	5	98	0	0	0	0	11	13
8b	0	0	0	0	0	0	24	49	13	0	0	0	0	0	2	0	0	15	24	0	9	65	0	0	0	0	31	18
9b	0	0	0	0	6	0	12	36	6	0	0	0	0	0	6	6	0	0	18	0	0	109	0	0	0	0	12	0
10b	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	2	0	1	1	0	0	0	0	0	2
11b	0	0	0	0	0	0	19	14	0	0	0	0	0	0	9	0	0	5	37	0	5	112	0	0	0	0	93	47
12b	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	2
13b	0	0	0	0	0	0	2	58	11	0	0	0	0	0	2	2	2	21	21	0	4	77	0	0	0	0	2	8
14b	0	0	0	0	0	0	12	88	12	0	0	0	0	0	6	0	0	24	12	0	6	41	0	0	0	0	0	24
15b	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
16b	0	0	0	0	0	0	0	4	0	1	0	0	0	0	0	0	0	0	1	0	0	5	0	0	0	0	5	2
17b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1
18b	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	1	0
19b	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	4	0	0	0	0	1	0
20b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
21b	0	0	0	0	14	1	13	<u>8</u> 1	17	1	0	0	0	0	0	3	0	4	18	1	0	78	0	0	0	0	0	0
22b	0	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	3

	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	· T
23b	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	12	1
24b	0	0	0	0	1	0	1	4	1	0	0	0	0	0	0	0	0	0	2	0	1	7	0	0	0	0	0	1
25b	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	2	0	1	2
1c	0	0	0	2	0	0	11	135	15	5	0	0	0	0	0	4	3	3	6	0	2	34	0	0	0	0	2	4
20	0	0	0	1	12	0	15	94	0	0	0	0	0	4	0	1	1	8	0	0	11	56	0	1	3	14	5	8
20	0	0	0	0	0	0	0	52	21	2	0	0	2	0	0	1	4	0	2	0	0	20	0	0	0	1	4	0
<u> </u>	0	0	0	0	9	0	9		21	5	0	0	3	0	0	4	4	0	5	0	0	50	0	0	0	1	4	0
4c	1	1	0	0	5	0	2	111	3	0	0	0	0	0	0	3	0	7	10	0	2	59	0	0	0	0	0	2
5c	0	0	1	2	4	0	5	61	17	2	0	0	0	1	0	19	0	13	13	0	5	62	2	0	0	0	1	2
1d	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	1	0	0	0	4	0	0	0	0	1	2
2d	0	0	0	1	13	1	56	10	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0	0	0
3d	0	0	0	0	9	1	45	64	7	6	0	0	0	0	1	0	0	10	11	0	0	55	0	0	0	0	0	0
44	0	0	0	1	5	2	40	51	0	0	0	0	0	0	2	6	0	14	10	0	4	60	0	0	0	0	0	
40	0	0	0	1	5	2	40	51	2	0	0	0	0	0	2	0	0	14	10	0	4	09	0	0	0	0	0	
5d	0	0	0	0	4	1	56	45	8	1	0	0	0	0	1	5	0	7	0	0	0	81	0	0	0	0	0	2
1e	0	0	0	0	4	0	31	61	9	0	0	0	1	0	3	0	0	9	10	1	4	71	0	1	0	0	0	1
2e	0	0	0	0	1	0	34	59	6	1	0	0	0	0	1	0	0	5	8	0	3	88	0	0	0	0	0	0
3e	0	0	0	0	0	0	21	79	4	0	0	0	0	0	6	2	0	10	11	0	4	61	0	0	0	0	0	6
					0											_						0.		0				
4e	0	0	0	0	0	1	3	12	2	0	0	0	0	0	1	0	0	1	0	0	0	8	0	0	0	0	0	1
5e	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
6e	0	0	0	0	4	0	26	52	10	0	0	0	0	0	0	10	0	12	2	0	0	86	0	0	0	0	0	0
7e	0	0	0	0	4	0	20	76	13	3	0	2	0	0	3	3	0	8	6	0	1	71	0	0	2	0	0	0

8e	0	0	0	0	0	0	31	50	8	0	0	0	0	0	8	8	0	23	0	0	0	73	0	0	0	0	0	15
9e	0	0	0	0	0	0	36	82	14	0	0	0	0	0	0	0	0	7	0	0	0	61	0	0	0	0	4	0
10e	0	0	0	0	0	0	4	98	11	0	0	0	4	0	0	8	0	8	11	0	0	57	0	0	0	0	0	2
1f	0	0	0	0	1	0	2	51	11	0	0	0	1	0	4	7	4	35	5	1	0	77	3	4	8	0	0	0
2f	0	0	0	0	3	0	6	42	12	0	0	3	0	0	4	12	5	33	4	2	0	74	3	7	12	0	0	3
3f	0	0	0	0	3	0	5	36	14	0	0	0	2	1	7	17	2	0	9	2	0	57	2	10	18	0	1	1
4f	0	0	0	0	1	0	0	5	1	0	0	0	0	0	0	2	0	7	0	0	0	3	0	0	0	0	1	7
5f	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	6	0	0	0	0	2	1
6f	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
7f	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	3	0	0	1	0	0	0
8f	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0
9f	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4	1
10f	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	1	0	1	1	0	0	5	0	0	1	0	1	0
PS5 (4a) LOC 2	0	0	0	0	0	0	4	50	6	1	0	2	0	1	4	3	0	0	41	0	3	103	0	5	0	0	30	11
PS4 (7a) LOC 2	0	0	0	0	0	0	5	84	9	12	0	0	0	0	0	1	2	1	10	1	1	53	0	0	0	0	4	3
PS3 (8b) LOC 2	0	0	0	0	8	0	32	66	5	0	0	0	0	0	1	0	0	9	20	0	2	81	0	0	0	0	0	0
PS2 (10) LOC 2	0	0	0	0	7	0	19	49	13	3	1	0	0	0	0	9	0	6	4	0	1	103	0	0	0	0	4	1
PS1 (15B) LOC 2	0	0	0	0	0	0	3	30	12	1	0	0	0	3	0	18	7	41	6	5	2	94	7	11	24	0	3	4



Appendix 6 - Figure 6.1 Scree plot (broken stick model) for the PCA of Africa-wider modern referce phytolith samples and fossil samples from Prospect Farm. The model shows that the first 3 are significant in explaining variability on the data.

Morpho	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10
-type										
Crs	0.37839	0.37657	0.48562	0.015776	-0.49832	0.10515	0.41912	-0.16491	0.12922	8.81E-
Bbt	0.35498	0.53862	-0.39526	-0.53218	0.27578	0.16902	0.1799	-0.07577	-0.04128	0.00064
Sad	0.4433	0.59871	-0.11592	0.32434	-0.09569	-0.21173	-0.29624	0.3263	0.27962	0.00034
Ron	0.7289	-0.43238	0.3353	0.034922	-0.06277	-0.13297	-0.23973	-0.10519	-0.27919	0.00080
Trap	0.40802	-0.61409	0.14658	0.11122	0.29532	0.27259	0.29873	0.32307	0.25965	0.00021
Trap	0.099719	-0.09759	-0.60725	0.68418	-0.08772	0.21697	0.12732	-0.26534	-0.04793	0.00023
Bul	-0.71127	-0.30859	-0.14102	-0.07851	-0.07172	-0.51209	0.23919	-0.07935	0.20476	0.00063
Glo-e	-0.16988	0.46512	0.41408	0.42835	0.51463	-0.21339	0.23719	-0.03991	-0.17784	2.31E-
Glo-g	-0.6772	0.098291	0.36099	0.046307	0.13373	0.3794	-0.33166	-0.25365	0.25123	0.00044
Glo-p	-0.76216	0.12799	0.027827	0.067713	-0.25462	0.24329	0.085491	0.41859	-0.30138	0.00046

Appendix 6 - Table 6.7 Loading scores on morphotypes to PCA axes: for the PCA of Africa-wider modern referce phytolith samples and fossil samples from Prospect Farm.



Appendix 6 - Figure 6.2 PCA axis 1 loading scores loading scores using the expanded morphotype dataset of Prospect Farm fossil samples.

6.1 Density survery result and depositional processes in the Prospect Farm sequence

6.1.1 Density survey results - additional information

Density plots shown in Figures 6.1 and 6.2 indicate that LSA tools (that are smaller on average than MSA tools) have a wider spatial distribution than MSA types, and that MSA tools cluster in mid-altitude areas. The highest densities of MSA artefacts come from Locality I (2102-2108 m a.s.l.) where lithic material is found eroding out of a 140-300 m long escarpment. LSA finds are also present at this site but have higher densities upslope at Locality II (2138-2140 m a.s.l.). MSA finds also occur in high densities at Locality II but in lower densities than at Locality I. Only LSA artefacts have been identified at the northern end of the Prospect Farm Formation between ~1980 m a.s.l. and ~2190 m a.s.l. (Van Balen et al., 2019). Where the highest MSA densities are found stratigraphic Unit 8 (see Chapter 6.8.3.4) is exposed on the landscape. Unit 8 contains Phase II MSA material and produced the highest number of artefacts per m² during 2016 excavations (see Chapter 6.3). Roughly 160 m to the NW of Locality II a 100 m long crescent-shape escarpment feature exposes the same sequence of sediments as at Locality II, however the density survey does not record any MSA tools in this area despite evidence to suggest that it has been eroded at a similar rate to Locality II. This suggests that the high densities of MSA artefacts at Localities I and II relate to increased human activity at these locations and are not solely a factor of increased rates of erosion at these locations. While at Locality I and II we can be more certain that lithic densities are a true indicator of settlement intensity and not erosional bias, the lack of exposure of lower MSA bearing units at the highest (~2190 m a.s.l.) and lowest (~1980 m a.s.l.) escarpments (Only Units 1-7A and Units 1-4B are exposed at these elevations respectively) means that the absence of diagnostic MSA tools from these levels may be due to a lack of exposure through erosion rather than a true absence of past hunter-gatherer activity in these areas of the landscape. Having said this, the fact that younger

Phase III and IV bearing sediments are visible in both these exposures suggest that activities of MSA groups that would have left clear indicators in the lithic record over these areas was low, at least during the later MSA phases. Both Isacc (1972) and Ambrose (2001) note low occurrences of LSA surface scatters at altitudes ~2250-2260 m a.s.l. on the upper slopes of Mt. Eburru and below ~1960 m a.s.l. on the pedimont fan and alluvial-lacustrine plain sediments of the Nakuru Basin (at GrJi11 in stream channel deposits). However, neither of these surveys note any MSA material at these altitudes. Field walking at lower altitudes on pedimont fan and alluvial sediments by the INAP team did not identify any MSA sites between the Prospect Farm Formation and the Enderit River (located ~6 km NNW of Prospect Farm).

6.1.2 Description of pyroclastic-airfall and pyroclastic-flow deposits of the Prospect Farm Formation

Ignimbrite deposit (likely to be either welded trachytes or trachy-phonolite tuffs [Blegen pers. comm.]) are currently undergoing dating but are likely to be late Middle or Late Pleistocene in age. Pumice deposits (Units 14-12 [~2.5 m thick]) and 6 [~0.5 m thick]) exposed in the Prospect Farm sequence consist of alternations between horizontally bedded angular to sub-angular, moderately to well sorted medium size equidimensional pumice clasts, with moderate vesicularity. The lack of indication of physical post-depositional reworking or transport of the pumice deposits of Units 12-14 and 6 indicates that they are primary pyroclastic airfall deposits, rather than being epiclastic. Alternations between matrix supported and clast supported pumice in Units 14 and 12 (see Figure 6.3) and sediment colour changes in these within sub-units are interpreted as arising from variations in column height, magma composition and magma discharge rates during the eruption and emplacement of these units (e.g. Wilson and Sparks, 1980; Carey and Sparks, 1968; Fisher and Schmincke, 2012). Changes in eruptive behaviour are also likely to be responsible for the reverse grading of Unit 14, that indicates an increase in column height. Normal grading of Unit 12 indicates a reduction in column height as the eruption waned. Occasional accidental lithics in Unit 14, 12 and 6 signal that only minor erosion of the conduit/vent occurred. The gritty sand sized unconsolidated lapilli tuff of Unit 13 (that has a gradational basal contact with Unit 14) is likely to represent either ash settling out of the atmosphere during shutdown of the column and a hiatus in the main eruption, or a short-lived phreatomagmatic explosion event, rather than being the result of pyroclastic density currents. The lack of indicators of soil formation in Unit 13 suggest that if a hiatus in eruption did occur that it was brief.

Unit 6 airfall pumice deposits are well exposed and laterally continuous across the Prospect Farm Formation (see Figure 6.4). Due to their greater depth in the sequence the pumice deposits of Unit 14-12 are less well exposed that those of Unit 6 but are visible at Localities I and II and on the NE side of the Prospect Farm Formation near Locality II. Small volume gravity controlled pyroclastic flow deposits have been shown to preferentially infill topographic lows while airfall deposits typically have a more uniform thickness as they blanketed the palaeotopography (e.g. Walker, 1973; Cas and Wright, 2012). The pumice deposits which mantle the Prospect Farm Formation show evidence of lateral thinning out at the flanks of pyroclastic tongues towards the valleys and depressions. This may indicate that pumice and/or ash fall deposits of the main Prospect Farm sequence represent co-ignimbrite deposits which are

typical of the lower slope of rhyolitic volcanoes where they veneer the landscape in medial areas adjacent to ponds of pyroclastic-flows. Such deposits are observed in other late Quaternary sequences at rhyolitic dome volcanoes similar to Mt. Eburru, and trachytic caldera volcanoes (e.g. Menengai) of the central Kenya peralkaline province in the Nakuru-Naivasha Basin. On these volcanoes ash flow tuffs typically cover 10-30 km3 (McCall, 1967; Macdonald and Scaillet, 2006). Alternatively, ignimbrite deposits may represent large volume flows that formed sheets at lower elevations covering the landscape (e.g. Gibson, 1970; Claessens et al., 2015). In this case these deposits would correspond to an earlier phase of eruption that stratigraphically underlies the main Prospect Farm sequence, that are only exposed on the landscape when significant fluvial downcutting exposes them, as at the Prospect Farm Quarry.

6.2.1 Factors potentially affecting phytolith preservation

The biochemical and physical mechanisms that influence the stability of biogenic silica, as well as the differential dissolution potential of distinct phytolith morphotypes in soils over geological time scales are not completely understood (see Strömberg et al., 2018 and references therein). Multiple studies have recorded that pH and water availability can affect biogenic silica solidity; with dissolution increasing under alkaline conditions (e.g. Benayas Casares, 1963; Blecker et al., 2006; Fraysse et al., 2006; Piperno, 2006; Cabanes et al., 2011; Cabanes and Shahack-Gross 2015). Some studies report that Al impurities (e.g. Bartoli and Wilding, 1980; Fraysse et al., 2009) or specific surface area (e.g. Piperno, 2006; Osterrieth et al., 2009) are the main determining factors controlling phytolith preservation in soils. However, these findings contradict a larger body of evidence which indicates that geometric surface area is a key factor in the differential preservation of phytoliths (e.g. Wilding and Drees 1974; Bartoli et al., 1980; Fraysse et al., 2009; Cabanes and Shahack-Gross 2015). While GSSC phytolith types appear to be relatively resistant to dissolution, there is some evidence to suggest that larger blocky types (produced in the leaves and bark of woody dicotyledons as well as bulliform phytoliths from Poaceae) are more susceptible to dissolution because of their high geometric surface/bulk ratio than more compact GSSC and globular types (Wilding and Drees, 1974; Alexandre et al., 1997). However, in other studies dissolution rates are the same across a variety of different morphotypes (e.g. Fraysse et al. 2009). Other factors that have been shown to affect the preservation of the phytolith assemblage include: time, burial-rate and burial depth (Derry et al., 2005; Cabanes et al. 2011; Cabanes and Shahack-Gross 2015).

<u>6.2.2 Phytolith preservation and distribution trends in the Prospect Farm sequence – additional information</u>

In PCA results of palaeosols samples to published modern soil phytolith assemblages from East African vegetation types, samples from lower horizons of PS1 and PS5 have a heterogenous phytolith signature, that is not comparable to any modern analogues (see Section 6.7.6.2). Both palaeosols are highly indurated and show signs of repeat shrink-swell activity, bioturbation, and prolonged development under tropical climate conditions. They are interpreted as having supporting woodland or forest vegetation communities (see Section 6.8.1 and 6.8.5). This suggests that poor preservation of phytoliths appears to be related to physical mechanisms, sediment compaction, burial depth, and possibly changes in the water

table, rather than to soil pH or time. Low phytolith preservation in these palaeosols is consistent with observations that phytoliths are not rapidly buried, but instead are continually subjected to pedogenic processes: including shrink-swell and bioturbation, that has resulted in the translocation and physical damage of phytoliths, and which contribute to spatial and temporal averaging of the phytolith pool in soils (Cabanes et al., 2012; Cabanes and Shahack-Gross 2015; Strömberg et al., 2018). Furthermore, compaction of the lower parts of these palaeosol profiles may contribute to additional mechanical breakage of phytoliths in these horizons (Strömberg et al., 2018). While some studies suggest that GSSC types are more resistant to chemical dissolution than blocky types; and that thinner or silicified phytoliths are more susceptible to physical breakage than more robust forms (e.g. Jenkins, 2009; Cabanes et al., 2011), limited data is available on the differences in preservation of GSSC and blocky/tabular types when mechanical abrasion is the main taphonomic factor effecting the assemblage. However, in the Prospect Farm sequence, it appears that smaller and often thinner GSSC types are more susceptible to mechanical breakage than blocky/parallelepipedal forms.

In contrast, in Palaeosol 4, phytolith preservation is good and does not visibly change down-profile. PCA results indicate that samples from PS4 and the uppermost horizons of all other palaeosols (where higher concentrations and better preservation of phytoliths are recorded) generally cluster closely to samples from within the same unit in ordination space (i.e. samples have low compositional variance). Furthermore, these samples often fall within the range of variation recorded in phytolith assemblages from East African modern vegetation types (e.g. samples from Units 7A, Unit 8A-8C, Unit 9A-9B, Unit 10, Unit 11A, and Unit 15A). This suggest samples from these sedimentary settings are less affected by taphonomic bias, and that the relative abundances of phytoliths present a coherent picture of past vegetation.

6.2.3 Preservation bias of family specific morphotypes in the Prospect Farm phytolith sequence

Low occurrences and abundance of Cyperaceae morphotypes, epidermal polygonal, cork platelets and some globular decorated types (e.g. globular pappilates associated with *Utrica* [stinging nettles]) throughout the entire Prospect Farm sequence, is likely to reflect their potential for dissolution identified by previous studies and in this thesis (see Chapter 4.3.2). Low occurrences of other family specific types such as Commelinaceae, are confined to PS4. Similar preservation values are recorded in PS4 in other palaeosol horizons. However, as these counts are so low (single occurrences) it is difficult to be certain that the absence of these types in other palaeosol horizons reflects the true absence of this herbaceous family or instead reflects preservation bias. The occurrence of moderately thick platelet types with a similar theoretical preservation potential in these horizons suggest the former scenario is more likely. Similarly, infrequent occurrences and the low relative abundances of globular echinates (Areaceae types) are interpreted as reflecting the true absence of palm vegetation, due to the regular occurrence of other globular morphotypes with similar geometric and specific surface areas to Areaceae types, rather than to preservation bias. Furthermore, some globular echinates show evidence of carbon coating, indicating their alteration by fire. This suggest that they may be windblown additions to the assemblage, resulting from the burning of palm vegetation in the surrounding area.

6.3.1 The origin of Fe/Mn nodules in the CBcb1 and EBtsocb1 horizons

Fe/Mn nodules can occur as either pedogenic nodules (formed through authigenic processes) or as detrital material (accumulated through erosional processes). The chemical composition and distribution of both forms in a soil profile can be further altered through diagenesis. Detrital Fe/Mn nodules in soils have been associated with the weathering of laterite duricrusts and other iron rich sedimentary rocks, that are redeposited downslope through colluvial processes. Additional redistributions of nodules in the soil profile has also been shown to occur because of bioturbation. Where these processes are in operation, nodules tend to become concentrated in lower ferric horizons, while A horizons are relatively free of nodules due to burial (e.g. Beauvaisa and Tardyab, 1993; Löhr et al., 2013). Alternatively, subrounded Fe/Mn nodules can develop in soils systems under alternation between oxidizing states (where Fe and Mn are insoluble) and reducing states (where Fe and Mn are soluble) (Zhang and Karathanasis 1997; Vepraskas et al., 1999; Gasparatos et al. 2005; Chan et al., 2007). Redox conditions causing the translocation and oxidation of Fe and Mn result in the reprecipitation of these elements; that infill and line matrix pores (Gasparatos, 2012). Accumulations of iron are associated with water table fluctuations, capillary action and vertical leaching. In lateritic soils, where ferricretisation has occurred, Fe/Mn nodules generally form under oxidising conditions above the water table where ferrous iron is precipitated and re-crystallised (see Ghosh et al., 2015).

The distribution of nodules and features indicative of laterization processes in the CBcb1 horizon are commonly found in modern soils of forest environments in the tropics. Such soils typically develop on hillslopes with undulating topography where colluvium accumulates (Magnien, 1966; Bowden, 1987; Velde and Barré, 2009). In these settings, more Fe/Mn nodules accumulate at depth relative to other zones because tree roots and biotic activity tend to translocate material down the soil profile and concentrate material below the root-zone. In contrast, in tropical grassland, nodules accumulate nearer the soil surface (McFarlane, 1976; Velde and Barré, 2009). Continuous penetration of roots over time may have been accentuated by cracking caused by shrink-swell action and by the mass wasting of this palaeosol. This could have also contributed to the consolidation of iron nodules at lower depths. In summary, Fe/Mn nodules in the profiles are more consistent with pedogenic formation than they are with secondary deposition of older eroded lateritic duricrusts or primary mafic rocks. Lithologies of this type, that could be used to suggest that such material stratigraphically underlie the deposits of the Prospect Farm Formation (theoretically acting as parent material for iron nodule formation) are not presently exposed or found as surface material upslope in the area.

While is likely that nodules in the CBcb1 horizon formed authigenically (as redox accumulations) but it is less clear how nodules in the EBtsocb1 horizon formed: This could have occurred (i) in-situ (pedogenically) as the result of fluctuation in the water table and/or centripetal accumulation. In this
scenario, bioturbation could have buried nodules, concentrating them in the E horizon while moving fine material to the A horizon (e.g. Tardy, 1992; Breuning-Madsen et al., 2007); (ii) as the result of redistribution of pedogenic nodules in upper parts of the profile due to physical translocation associated with shrink-swell processes; (iii) due to physical weathering of previously exposures of the CBcb1 horizon upslope and re-deposition of nodules from this horizon in the EBtsocb1 horizon at Prospect Farm Localities I and II; or (iv) pedogenically following a shift from forest to more open grassland vegetation.

6.3.2 An overview of particle size distributions in primary and secondary airfall (tuff) deposits

Several studies of grain size distributions in primary and secondary ash deposits of the Youngest Toba Tuff in India (e.g. Lewis et al., 2012, Jones, 2010) propose several properties to be indicative of primary ash airfall deposits. These include good to moderate sorting, unimodal distributions, and high tephra content. Other indicators include: the absence of sedimentary structure (e.g. laminations) and non-volcanic detritus, that indicate mixing with other sediments before deposition. However, Gatti et al., (2013) more recently demonstrated that particle size alone cannot be used to differentiate primary airfall from secondary reworked tuffs. This finding is based on observations of shared grain size properties in proximal primary ash in India and distal samples of the Toba tuff in Malaysia. Variability in skewness of ash deposits has been primarily linked to variation in plume dispersion rather than to primary or secondary depositional processes. In this case, the upward trend towards very fine skewness (towards the right [see Figure 6.34 [B]) in PS2 (from pumice through to ash), is likely to reflect grain size change during eruption rather than post-depositional reworking. The lag-time from primary deposition of ash to redisposition and burial is highly site specific and dependent on the primary mechanism of reworking. Often this process occurs rapidly in geological terms, over the timescale of days to years (e.g. Jones, 2010; Blinkhorn et al., 2012; Gatti et al., 2013).

6.3.3 Depositional processes in Units 5 and 4

Inclusions of angular to sub-angular fine to medium gravels (weathered obsidian and trachyte) and occasional sub-rounded pumice in the Btsm and Btso horizons were not discussed in detail by Anthony (1978), who described the units as unconsolidated ferrugenized orange, red, and pink tuffs. Anthony (1978) ruled out the possibility of colluvial processes having controlled the deposition of artefacts or larger non-archaeological lithic material in these horizons. This conclusion was partly based on the assertion that the low slope-angle of deposits would have impeded high energy colluvial processes, as well as the fact that Anthony did not identified any exposures of trachyte or obsidian immediately upslope of Locality I or II that could act as a source for the gravel material in these horizons. However, the field survey carried out during INAP excavations did identify deep deposits of trachyte near the main Prospect Farm localities; in the valley between Ridge 1 and 2 (see Chapter 6.2.1). If formation of this trachyte deposit was coeval with the eruption of Units 6-4, it is possible that a thin veneer of this trachyte tuff could have blanketed the topographic high point of Ridge 1; providing a source for the coarse lithic material found in Units 4 and 5. If this thin trachyte deposit did exist, it could have been eroded and

moved downslope by colluvial or slope wash activity; and redeposited with ashes from which PS5 form prior to and during the pedogenesis of Units 4 and 5. In this case the undulating contact between Units 4 and 3 may represent some form of rilling and inter-rilling, as is visible today across the Prospect Farm Formation see Appendix 6, Figure 6.1. However, the morphology of individual concave features in the palaeo-sedimentary record is relatively more uniform than those observed in association with present day examples of these slope wash processes at the site (i.e. the localised nature of these features on the landscape at Prospect Farm today does not agree with the regularity nor the wider spatial extent of these features in the stratigraphic sequence). Furthermore, while colluvial processes may occur on slopes with gradients $>2^{\circ}$ (French, 2003), the transport of larger pebble sized clasts visible in Unit 4, would require high-energy flood events under low vegetation cover and low clay content conditions. Such events are expected to create greater spatial heterogeneity in the thickness and sorting of Unit 4 deposits than is recorded. As the properties of this part of the Prospect Farm sequence are relatively uniform across the formation it is unlikely that colluviation or slope wash were the main processes responsible for formation of these deposits (see Bertran and Texier, 1999; French 2003; Huggett, 2016).



Appendix - Figure 6.1 Examples of concentrated areas of rilling and small gully erosion affecting the Prospect Farm Formation today. These features are consistent with splash erosion and rill erosion processes that affect small slopes of "badland" areas across Africa (e.g. Reding et al., 1995; Römer, 2013a,b): (A) location of sites selected as possible modern analogues for dish-shaped features observed at the contact between Units 4 and 3. (B) An aerial view of minor gully erosions concentrated in a ~100 m wide × ~400 m long area. Larger gullies are also visible in the eastern area of the image. (C) An example of shallow gullying (~30 cm deep and up to ~70 cm wide) on the eastern slope of Ridge 1, ~50 m east of Locality II. The photo was taken looking uphill facing west. Satellite images are from Google Earth (2018).

6.3.4 Depositional processes of sub-aerial pyroclastic flow and lahar deposits and their possible relationship with the dish-shaped features in PS5

Poor sorting and very poor and discontinuous horizontal bedding of gravels of Unit 4 and 5 are consistent with a matrix supported sub-aerial pyroclastic or thin lahar deposit. High quantities of gravel in these units reflect inclusions of subangular accidental lithics during eruption. Further dispersal and aggregation of larger gravels within the palaeosol profile could have occurred through shrink-swell activity and bioturbation during pedogenesis, that along with chemical weathering altered and partially obscure primary volcanic bedding structures. The presence of small size gravel material in addition to large clasts are more consistent with lahar deposits rather than thin (diluted) flow or rain flush-ash deposits that often remove fine components (Walker, 1971; Fisher, 1979). A reduction in bed thickness is observed in Unit 5 at the northern limit of the Prospect Farm Formation where it reaches the valley floor (e.g. in Escarpment 5). Also, a reduction in larger gravel size material is observed in Unit 4 in this area. These features are likely to indicate a progressive fining and fanning out of flow deposits away from the vent at more distal areas of the formation. This typically occurs in lahar deposits on the lower slopes of volcanoes where slope gradient and flow velocity are reduced (Walker, 1971; Lavigne and Thouret, 2000; Allen, 2011). The unconsolidated nature, low pumice content, and presence of some sub-rounded clasts in Unit 4 and 5 sediments may suggest that these are 'cold' lahar (debris-flow) deposits, that may not be directly initiated by an eruption (see Fisher and Schmincke 2012; Veldkamp, et al., 2012) However, the angularity of some obsidian clasts in Unit 4 points to 'hot' lahar deposits.

The dish-shaped morphology (i.e. concave-upward interfaces that cross cut one another) of clay filled fissures in Unit 5 (Btm horizon) are reminiscent of dewatering features that form in water-saturated dilute hyperconcentrated flow (lahar runout) deposits in footslope zones (see Lowe and LoPiccoto, 1974; Scott et al., 1995; Boggs, 2006). Scott et al., (1995) note that continued development of these features can occur post-depositionally due to phreatic processes that would concentrate fine material within these cracks/fissures. However, these features are confined to Locality I. At other locations concentrations of fine clay in Unit 5 appear as relatively more irregular coatings on sub-angular blocky peds. These are interpreted as shrink-swell pedogenic features most commonly found in Vertisols. Whether or not these features indicate post-depositional alteration of dewatering features or other processes is unclear. As a result, the formation processes associated with dish-shaped structures at Locality I requires further testing.

6.3.5 Evidence for past vegetation and hillslope processes creating an undulating surface at the contact between Units 4 and 3

Anthony (1978) proposed that the hollows in the undulating bed contact between Units 4 and 3 may represent the past growth positions of tree or shrub trunks and the centrals stem of their root systems. The morphology and semiregular recurrence of these depressions is more consistent with trees stump moulds (e.g. Brand et al., 2014) than with erosion of unconsolidated material by rilling or other processes (e.g. pyroclastic base surge deposits that generally only create u-shaped channels on steep slopes nearer to vents (Fisher, 1977). It appears that trees at the site that were covered by Unit 3 ash deposits remained as buried stumps for a period that later decayed; allowing the depressions they left to be infilled.

On hillslopes, similar semi-regular concave features are recorded associated with tree uprooting and decay processes (e.g. tree fall, pit-mounding, root penetration, and root decay) (Norman et al., 1995; Šamonil et al., 2010 and references therein; Pawlik, 2013). On low relief hillslopes (< 5°), similar concavities have been shown to be accentuated through winnowing processes and subsurface interflow dynamics (e.g. spill and fill processes), that affect Bt, Bw, and fragipan horizons of soils (McDonnell, 2013; Du et al., 2016 and references therein). The semi-regular spacing of concavities in PS5 is consistent

with root systems creating a macropore network that could have controlled subsurface flow and connected these depressions (e.g. Tromp van Meerveld and McDonnell, 2006). Thus, it is reasonable to suggest that rooting and its associated palaeo-drainage network, as well as post depositional winnowing processes, created and maintained the morphology of these features after trees were destroyed by the deposition of pyroclastic material of Unit 3. The diameter (~ 0.3 -0.6 m) of these putative tree stump hollows suggest quite a wide range of potential tree heights of between ~ 10 -30 m, depending on the type of arboreal vegetation present (Mugasha et al., 2013). While the phytolith record suggests the presence of woody taxa at this time, the lack of taxonomic resolution does not allow us to suggest specific tree or shrub types that are consistent with the morphology of these depressions. Therefore, further evidence is necessary to link a specific type of vegetation to these features.

6.3.6 Artefact orientation and the former land surface of Palaeosol 5

The horizontal orientation of artefacts across the undulating horizon at the contact between Units 4 and 3 (immediately after the transition between Phase III and IV material) where sediments undulated forming infilled hollows, presents a further challenge to interpretation of these deposits. Anthony (1978) thought that the slope gradient was too shallow for high energy slope processes to operate that could have created these concave depressions, it was suggested that they could indicate the location of former tree/shrub trunks or main stems, that were infilled during the deposition of the Unit 3 tuff. The horizontal orientation of artefacts was also observed in lateral extensions of the excavation, where they could be more clearly separated into those occurring within Unit 4 or Unit 3, as well as where it was difficult to distinguish between these units and to which units the lithics belonged. As Anthony (1978) noted, the expectation is that if artefacts were deposited on the undulating surface that their long axes should be preferentially orientated at steep angles; following the local topography of the depressions. The small number of artefacts at the base of Unit 3 are likely to relate to the removal of topsoil and mixing at the bed contact between Units 4 and 3 during the deposition of the sub-aerial pyroclastic flow/air-fall deposit of Unit 3. Very occasional inclusions of artefacts and accidental lithics in the rest of Unit 3 are also best explained as becoming entrained in these deposits during the downslope propagation and deposition of Unit 3 sediments. However, the entrainment of lithics in a flow does not account for their horizontal orientation. The most likely explanation for their horizontal orientation is a postdepositonal reduction in inclination angles of lithics. This has been shown to occur in experimental sediment compaction conditions regardless of artefact size and shape (Andrews, 2000; Brantingham et al., 2007). Artefacts in PS5 are buried at depths of ~2.5 m, over twice that of those studied in these experiments. This indicates that changes in the orientation of upper Phase III and lower Phase IV artefacts could have been equal to or greater than the maximum changes in orientation of 22° recorded by Andrews (2000). As vertically and horizontally placed artefacts have been shown not to undergo changes in inclination under compaction (Andrews, 2000), it is likely that artefacts were not deposited vertically. This is likely to be because stone tools settled following redeposition before sediment became consolidated. More detailed total station data of artefact orientation from across Units 3 and 4, is expected to facilitate a more definite understanding of artefact orientation across this horizon.

6.4.1 Future work: improving our understanding of weathering intensity, weathering processes, and climatic parameters in the Prospect Farm sequence through XRD, χ , and micromorphological analysis

More detailed mineralogy (particularly of clays) will help to refine our understanding of weathering intensity, hydromorphism, and variability in climate and drainage during palaeosol formation in the Prospect Farm sequence. For example, the stability of mineral constituents in palaeosols and whether equilibrium was reached between the palaeosol and ambient climate will be able to be assessed. Mineralogical studies will also help to elucidate the relative contributions of noncrystalline and crystalline minerals/oxides across palaeosols horizons, that are presently inconspicuously reflected by changes in total element values (see Chapter 5.5.4). For example, the presence of iron and aluminium sesquioxoides in B horizons and the provenance of minor components K, Ca, Na, Mg in PS1-5 will be able to be tested. Identifying the proportions of amorphous colloidal material/Fe and Al (hydr)oxides (e.g. and allophane, imogolite ferrihydrite) relative to more crystalline material, that are formed under more intense weathering in Bt horizons, can be used as an indication of both soil formation time and climatic conditions (e.g. Mahaney et al., 1991). Additionally, XRD analysis could improve our understanding of chemical weathering with depth and incipient soil formation. For example, it could be possible to determine if high Ti concentrations represent primary lithogenic titanomagnetites, or alternatively, the formation of titanomaghemites with Fe_o (e.g. ferrihydrites) associated with orange and drab coloured redoximorphic features in the Bt horizons of PS1, PS2, PS4, and PS5. Furthermore, as the crystallinity of Fe-(oxy)hydroxide phases and γ have been shown to decrease and increase respectively with depth under higher rainfall (Thomson et al., 2011; Grison et al., 2015; Maxbauer et al., 2016; Jordanova, 2016), XRD and χ could also provide further insights into palaeoprecipitation values during palaeosol formation. The abundance of unaltered minerals and ferromagnetic minerals (e.g. titanomagnetite) is also expected to reveal whether inputs of unweatherd local and/or nonlocal material has been incorporated in the sequences through aeolian or colluvial processes, as may be the case in PS4.

The mineralogical characterisation of fine clay and silt size material in the upper 5 cm of PS1, associated with reductions in Fe, Mn and Ti, could help to determine if this material accumulated during palaeosol formation or post-depositionally; penetrating from higher levels and permeating through the overlying pumice layer. In highly weathered and well-drained soils with high soil water activity developing under warm humid conditions (as is proposed for PS1), we would expect to see the evolution of minerals from allophane or imogolite \rightarrow noncrystalline Fe/Al oxides \rightarrow goethite, hematite or crystalline ferrihydrite (Fe-oxides) \rightarrow crystalline phase clay minerals (e.g. kaolinite, allophone or smectite). During this evolution if the predominance of goethite over hematite were present in PS1, increased soil moisture and more acidic soil conditions could be inferred. Alternatively, higher temperatures, lower levels of soil saturation, and more neutral pH levels could be inferred if hematite is dominant (Kämpf and Schwertmann, 1983; Das et al., 2011; Maxbauer et al., 2016). Similarly, if weathering intensity and time were sufficient to result in the formation of crystalline clay minerals, then the identification of the predominance of kaolinite over smectite would reflect more humid conditions and better drainage during the morphogenesis of

buried palaeosols. On the other hand, increases in smectite or illite would help to establish whether drier conditions were present (Deepthy and Balakrishnan, 2005; Beverly et al., 2015a).

If magnetite is present in the Btsocb1 horizon of PS1, Fe values could be overestimated in these horizons due to oxalate-magnetite interactions (Walker, 1983; Mahaney et al., 2014). K, Ca, Na, Mg, Al and Ti decrease in the EB and C horizons relative to the Bt horizon. Fe and Mn are also generally lower in the Bt than in EB or C horizon, but show a slight increase in the BT horizon in sample No. 6f in line with other elements besides Na. Further mineralogical analysis may help to determine if: (i) weathering was insufficient to totally remove these alkaline earth elements and that they accumulated in the Bt horizon through illuviation; or (ii) increases in these elemental values in the Bt horizon represents additions, through colluvial processes or translocation during changes in the water table, of minimally weathered primary minerals (e.g. small gravel to sand sized particles of obsidian); or (iii) increase represent adsorption of small amounts of occluded forms of minor components K, Ca, Na, Mg in clay minerals (e.g. K in Illite).

Micromorphological analysis of iron nodules in PS1 may help to identify features that can be used to clarify their pedogenic origin (e.g. accretionary banding [White and Dixon, 1996; Gasparatos, 2012] and resistant quartz grains [Cescas et al., 1970]) or non-pedogenic formation. Furthermore, micromorphology could be used to assess if precipitation of pedogenic nodules under redox conditions was caused by abiotic activity (as indicated by macromorphology of these sediments that show signs of hydromorphism) or by microbial processes (e.g. Schwertmann and Taylor, 1989; Stiles et al., 2001).

In PS2 and PS4, the results of ongoing mineralogical analyses are expected to help establish the degree of transformation of allophane and imogolite to more crystalline phases (e.g. halloysite under semiarid conditions or kaolinite under more humid conditions [Shoji et al., 1993; Nanzoy, 2002; Sheldon and Tabor, 2009 and references therein]). The ascendency of Fe_0 or Fe_d (e.g. Sedov et al., 2003a,b; Singleton et al., 1989; Childs et al., 1991) could also be used to elucidate the degree of weathering, climatic and drainage conditions during evolution of the putative Andosol of PS2 toward other soil types, such as chromic Luvisols. In PS4, the inference that C and Bt horizons have undergone limited weathering will be able to be tested through establishing the presence or absence of allophane and smectite, as well as the form of Fe/Mn features (e.g. ferrihydrite or more stable goethite or hematite).

It is anticipated that micromorphology will provide insights into the morphology of carbonate crystals (i.e. well-shaped vs. anhedral) in the Btskb4 horizon of PS4. This could help to establish the level of aridity during their formation (Kuznetsova and Khokhlova, 2012; Zamanian et al., 2016). Moreover, micromorphology may better help to clarify the formative mechanisms and distribution of pedogenic carbonates (i.e. Perdescendum, Perascendum, or *in-situ* processes [Monger, 2002]), as well as the affect biotic processes may have had on carbonate formation. Micromorphology may also reveal the relative timing of the deposition of redox and carbonate features (i.e. the history overprinting). This could help to determine if carbonate features could be the result of seasonal or short-term (e.g. decadal) climate

oscillations (e.g. Beverly et al., 2015a, 2017) that occured within a broadly more humid climate phase, or if they are more likely to reflect a more heightened seasonal difference in climate during the majority of this palaeosol's formation.

It may be possible that increases in Si and Base cations was caused the addition of unweathered material into PS4 through aeolian processes. Under more arid climate conditions with lower vegetation cover, local and regional tephra deposits would be more susceptible to erosion and redeposition. In this case increases in Si would indicate the input of primary silicate minerals. Similarly, associated increases in Base cations would relate to the higher concentrations of this group of elements in unweathered volcanic material (e.g. Na and K indicate gradual accumulation of sodium- and potassium-bearing primary minerals common in trachytic-phonolitic rocks). Similar inverted weathering profiles are recorded in late Pleistocene Andosols on Mt. Kilimanjaro (Zech et al., 2006, 2011). However, in these palaeosols, topsoil element values are similar to those of unweathered tuff. This is not the case in PS4. This either means that inputs of unweathered material originated from other tuffs exposed on the landscape that had a distinct chemical composition, or that increases in the aforementioned elements relate primarily to pedogenesis. As Al and Na do not show steady progressive increases up-profile, as in the case of K, Mg, Ca and Si, it seems more feasible that increases in Base cations and Si primarily relate to pedogenesis, rather than to aeolian additions. If aeolian process were active during formation of PS4, determining whether the influx of aeolian tuffaceous material was constant or occurred intermittently may be difficult due to the low stratigraphic resolution of these sediments.

These analyses are also expected to allow for better determination of the colloidal properties and percentage of unaltered tephra (vitric content) of palaeosols; thus, improving their classifications. For example, the classification of PS2 as an Andosol (containing >60% tephra) with Cambric/Orchic properties (clay mineral content lower than 10%) (IUSS Working Group WRB, 2014) could be tested quantitatively. Furthermore, XRD and micromorphological analysis is expected to provide more insight into the abundance and distribution of volcanic glass (either in the matrix and/or infilling micro voids or burrows), as well as information on whether tephra could have limited the shrink-swell activity of smectites where they are identified, such as has been suggested for PS4.

<u>6.4.2 Future work: constraining the processes and duration of palaeosol formation and alteration through micromorphology and ⁴⁰Ar/³⁹Ar</u>

Micromorphological analysis is expected to help to establish the history of wet/dry climate oscillations and the phases of palaeosol formation by identifying where overprinting or obliteration of clay coatings has occurred. Additionally, the relative freshness and deformation of clay coatings could be used to assess if post-burial clay formation has occurred under phreatic conditions [e.g. Wright et al., 2017]). This analysis should also help to establish whether in each palaeosol soil formation ceased following their burial (i.e. they primarily record climate and drainage conditions during their formation) or if pedogenic features of buried palaeosol horizons have been and continue to be significantly altered by post-depositional groundwater processes. ⁴⁰Ar/³⁹Ar dating of Unit 7C, 9B, and 12 are expected to provide minimum and maximum ages for PS2, PS3 and PS4. Dating of Units 12 and 6 are expected to provide maximum and minimum ages for PS1 and PS5 respectively. Dating of Unit 4 or Unit 3 to provide a maximum age for PS5 may not be possible due to the nature of these sediments. As pumice deposits below PS1 were not exposed by INAP excavations, establishing a minimum age for PS1 will not be possible. Studying the percentage of clay coatings in palaeosols also has the potential to provide additional independent relative age estimates of the duration palaeosol formation (e.g. Ufnar, 2007; Beverly et al., 2015a).

6.4.3 Future work: constraining biological and physical processes affecting Prospect Farm sediments through micromorphology

Micromorphological indicators of biological activity (e.g. termite/earthworm burrowing and root networks that may be obscured by Fe/Mn coatings in the field), as well as of slope processes (see Bertran, 1993), are expected to help to confirm whether bioturbation contributed to artefact translocation and phytolith reworking (e.g. how pore space or burrowing impacted phytolith translocation). This analysis could help to identify any common primary pathways for phytolith movement in all palaeosols (i.e. if percolation was uniform throughout the matrix or if movement took place via larger voids such as cracks and root channels). Micromorphology should also provide insights into how diagenetic processes (e.g. compaction) have affected porosity and permeability of sediments, as well as the coherency of primary bedding structures. This may help to reveal the cementing agents and processes that have resulted in the increased induration of some palaeosols (e.g. of Unit 5 in PS5).

6.5 Termination of the Prospect Farm sequence and Palaeosol 6 - additional information

The interpretation of Unit 3 as a poorly-stratified sub-aerial pyroclastic flow deposit that has undergone only incipient weathering and minor reworking is based on several lines of evidence: Firstly, sediments of Unit 3 are structureless and have a vitreous texture apart two distinctive horizontal bands of crudely stratified discrete pumice (Units 3-E and 3A), that are consistent with pyroclastic flow deposits. Clay content does increase towards the top of the unit; however, sediments in general consist of homogenous silty-sand size material. Subtle differences are observed in colour between different sub-units of Unit 3 but the contact between them is not sharp. The pumice bands (consisting of small gravel size, subrounded grains) are consistent with accretionary lapilli that were not heavy enough to have significantly deformed underlying ash. Geochemistry of the lower sub-units of Unit 3 is characterised by high Si and Base cation values (i.e. high Base loss indices values [Figure 6.7]) and relatively low Al, Fe and Ti concentrations, indicating limited chemical weathering of these sediments has taken place. Shifts in these values (e.g. hydrolysis increases) are evident in Unit 3B and 3A associated with a further phase of palaeosols formation (PS6 [Units 3A-2A]). Artefact percentages and densities recorded by Anthony (1978) are extremely low (see Figure 6.6). As there is no indication of depositional hiatuses, changes in depositional processes or soil formation in (Unit 3F-3C), the most convincing interpretation of low artefact densities in Unit 3 is that they were sporadically incorporated into this unit during deposition of underlying Unit 4 ash. This same mechanism has been proposed for several of other older horizons in

the Prospect Farm sequence. Furthermore, the fact that Unit 3 sediments are fine and indurated make it less likely that sporadic artefacts in the lower parts of Unit 3 were translocated from Unit 3A and 2 into these lower horizons through winnowing processes. Reworking of material into Unit 3F from Unit 4 is further supported by moderately high phytolith concentrations in this horizon and only residual numbers of phytoliths in the rest of Unit 3. Additionally, obsidian hydration ages conditionally suggest that tools in Unit 3F-3C and Unit 4 are the same age (Merrick et al., 1994).

APPENDIX 7

7.1 Future work: improving palaeovegetation reconstructions and human resource distribution modelling

Future work should focus on better differentiating all modern vegetation types in the Afromontane zone through phytolith-analysis, by using a wider range of arboreal morphotype categories (e.g. blocky, sclereid, and decorated globular phytoliths) and indicator types. Also, future studies should focus on establishing if the relationship between arboreal morphotypes and modern measures of tree cover (e.g. by using satellite images and in-field measurements of canopy density along a transect covering close forest to open grassland [e.g. Bremond et al., 2005a, 2017]), as this would allow for more detailed quantitative inferences of vegetation openness from fossil phytolith assemblages. Plant biomarkers, that are preserved in most sedimentary settings and can provide more precise information on the ratio of woody vs. non-woody plants have recently been refined for the hindcasting of local palaeovegetation distributions (e.g. Magill et al., 2016). By combining plant biomarker evidence with a phytolith-based approach a more detailed picture of past arboreal cover and of inputs from aquatic plants, sedges and ferns should be attainable (see Jansen et al. 2010; Magill et al., 2016). Vegetation modelling approaches, based on palaeovegetation data (e.g. Bunting and Middleton, 2009; Reitalu et al., 2014; Broothaerts et al., 2018), or regionally downscaled climate-vegetation models (e.g. Platts et al., 2013), that are beyond the scope of this study, could help to imporve 'best fit' models of past vegetation distributions. These could improve on existing vegetation models for the Nakuru-Naivasha Basin produced by Bergner et al., (2003), that only consider vegetation zonation under interglacial climate conditions. Furthermore, species distribution models that take into account vegetation climate feedback, topographic, and edaphic factors (e.g. Franklin et al., 2015; Kübler et al, 2016), could facilitate a more complete understanding of the different microhabitats within the basin. Consequently, whether vegetation communities can be said to be 'mosaic' within the area directly surrounding the site and within a group's home range, could be more fully tested. The mosaic quality of habitats in rift settings is often cited as having been important in attracting humans to these areas, as viability in habitat types provides a smorgasbord of resources for humans to exploit (Bamford et al., 2006; Kingston et al., 2007; Bailey et al., 2011; Roberts et al., 2016). Such mosaic habitat conditions are often inferred uncritically, based on a single-sediment column sampling approach alone and from polygenic assemblages that are spatially integrated (Reynolds et al., 2015).

7.2 Caveats of behavioural-ecological models

The presence of LSA features (e.g. use of the faceted platform technique (Clark 1954; Cole 1954; Leakey 1931) in the MSA assemblage of Prospect Farm, which are also recorded at other sites in the Nakuru-Naivasha Basin, such as Deighton's Cliff and Marmonet Drift (Slater, 2016), indicate higher levels of technological complexity in East Africa than in eastern Tropical, West and Central Africa (Mirazón Lahr and Foley, 2016; Taylor, 2016; Thomson et al., 2018). This technological behaviour is comparable to that

recorded in southern Africa (Mackay, 2016), but is present as early as 230 ka, suggesting a possible East African origin for these traits (Tryon et al., 2008; Mirazón Lahr and Foley, 2016; Slater, 2016). However, the resolution of available archaeological data being as it is, means it is not possible currently to test if sophisticated composite tools developed primarily as a functional response to a particular set of ecological conditions (e.g. ecotonal settings, habitat instability, or due to a combination of the other factors mentioned including changes in demography). The former has been suggested for LSA geometric microliths, thought to be projectiles, only recorded from ecotonal environments in the basin (Wilshaw, 2013), but similar studies of MSA tools are yet to be completed. These limitations, as well as those inherent in the capacity of the archaeological and sparse fossil/genetic record in general (e.g. preservation and excavation biases) to reconstruct past human behavioural changes in their entirety remains a significant caveat. Additional caveats include the limited diversity of foraging strategies in extant huntergatherer groups on which these models are based (Marean, 1997; Marlowe, 2005; Pargeter and Redondo, 2016; Thomson et al., 2018; and see Chapter 1.7.1.2 and 1.7.2.4). Furthermore, genetic and fossil data indicates the late survival of 'archaic' humans across Africa into the later MSA (see Section 1.2). While the hominin groups that occupied Prospect Farm were most likely anatomically modern humans, we cannot presume equivalent capacities of different groups across Africa to develop these complex technologies, nor parity in the socio-behavioural contexts in which they were used (Thomson et al., 2018).

Source	Petro. group	Muguruk@ n (km)	Songhor@ c (km)	Mumba-Höhle@ c (km)	Nasera @ c (km)	X ₁ - 98.10-97.90	ke X ₁ - 98.50-98.45	Hill* (km)	P Spits 22-23 n	ospect Spits 1618 c	t Farm Spits 9–10 n	• (km)	Prolonged Drift* (kg	Cartwright's@ n(ke	Wetherall's@n(km)
						n	n								
Kisanana	8								2	1	1	(75)			
Highlands	12	-				26	15	(6)	-	-			-		1 (45
Kedong	14					8	3	(65)		-			-		
Sonanchi	19	1 (190)		· /	6 (230)	3	-	(125)	-	-	56	(30)	41 (40)	-	5 (38)
Njorowa Gorgo	20/25		1 (145)	14 (305)		3	23	(105)	2	25	1	(40)	45 (50)	20 (35)	16 (24
Oserian #2	21	-				1	1	(115)	1			(40)	-		
Kinangop	24	-				-	1	(125)	2	6	1	(30)	-	2 (5)	3 (12
Cedar Hill/Opuru	27/35	-				-	1	(135)	10	-	1	(10)			1 (35
Upper Eburru	29/31/40	1 (185)	-		1 (240)	3	1	(130)	5	24	9	(15)	+ (33)	-	5 (34
Masai Gorge	30/32		-	·	2 (240)	5	2	(135)	60	49	24	(15)	4 (30)	28 (16)	16 (25
Ololerai	38		•	-	•	•	-		•	14	-	(30)	-		-
Unknowns															
PF unkn-1									26	15	18		6	1	
PF unkn-2			1	1 1					6	-	-			1	
PF unkn-3									2	-	1		-		
PF unkn-4										2	-		-	1	
PF unkn-5									-	-	3		· ·		
TOTAL PIECES		2	1	14	9	49	47		116	136	115		96	50	47

@ non-random samples

Appendix 7 - Table 7.1 Obsidian source assignments for MSA sites in the Nakuru-Naivasha Basin. Straight line distances over land to the nearest known outcrops of the sources are given in parentheses. From Merrick et al., (1994, pg. 40).

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