PHYTOLITHS AT SIBUDU (SOUTH AFRICA): IMPLICATIONS FOR VEGETATION, CLIMATE AND HUMAN OCCUPATION DURING THE MSA

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DECLARATION

I hereby declare that the work presented in this thesis is my original work based on research done by me and to the best of my knowledge has never been submitted for a degree at this or any other University or Institution of higher learning. All information from this thesis unless otherwise stated is based on my analysis and conclusions.

Signed Date

31st October 2017

May L. Murungi

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Contents

List of Acronyms

BP	Before Present (1950)
Ca.	approximate/around the time
HP	Howiesoons Poort
kya	thousand years ago
MSA	Middle Stone Age
SB	Still Bay
SRZ	Summer Rainfall Zone
WRZ	Winter Rainfall Zone
yr	year

ABSTRACT

Sibudu Cave is a rock shelter located in KwaZulu Natal at the east coast of South Africa and falls within the summer rainfall zone. Sibudu boasts well-dated deep Middle Stone Age deposits that have been studied to understand early human behaviour and their environment along the east coast of South Africa. Charcoal, pollen, seeds, carbon isotopes and faunal studies have contributed to understanding the past vegetation and climate at Sibudu during the MSA. However, little is known about the grassland composition during this period at Sibudu. This study presents a phytolith based reconstruction of palaeo-vegetation and palaeo-climate to understand early human-plant interactions and environment at the east coast of South Africa during the pre-Still Bay industry to the post-Howiesons Poort industry (ca. > 71, 000 to 48, 000 years ago).

Two studies were completed: archaeological samples and modern plant samples. Twenty eight archaeological samples were processed and compared with modern plant samples form the local area with additional modern plant material obtained from the herbarium at the Evolutionary Studies Institute, University of the Witwatersrand – specifically the sedges and rushes (total of more than 90 species). The main contribution of this study was to provide a modern phytolith reference collection for South African sedges for which hardly any information existed and for woody taxa for which no reference existed at the time.

MSA sediment records indicate a mix of grasses, sedges and woody taxa that were utilised at Sibudu. An important human activity occurred during the Still Bay (SB) and the Howiesoons Poort (HP), with an abundance of unique phytoliths in particular sediment layers that could not be confidently identified from the available literature. Given the high production of phytoliths in grasses, grass phytoliths in the MSA record were considered to occur in relatively lower than expected amounts. The phytolith study suggests that C4 grasses that are currently synonymous with the present-day vegetation in the Summer Rainfall Zone were likely the dominant grass type during the MSA at Sibudu. Specifically C4 tall grasses that favour warm mesic habitats are inferred in the Sibudu phytolith record as having been the most utilised grass type.

CHAPTER ONE

INTRODUCTION

1.0 General Introduction

South Africa today represents the epitome of human origins research on the continent, not only because of the several ground breaking discoveries of Plio-Pleistocene hominin remains (e.g. Clarke, 2008; Berger, et al., 2010, 2015; Stratford et al., 2016) but also the well preserved Late Pleistocene early human material culture that marks the development of cognitive and behavioural modernity, a character now attributed to the Middle Stone Age (MSA) of Africa (Klein, 1995; McBrearty and Brooks, 2000; Henshilwood and Marean, 2003). Archaeological interest in the MSA of South Africa has grown considerably in recent decades as evidenced by the rich body of research on its numerous MSA archaeological sites that goes as far back as the early 20th century (Goodwin and Van Riet Lowe, 1929; Deacon, 1976; Thackeray, 1992; McBrearty and Brooks, 2000; Lombard, 2005; Wadley, 2014, 2015). The MSA is not well defined but is thought to have started ca. 300,000 years ago (= 300 kya) and spanned the period ca. between 300 kya and 30 kya (McBrearty and Brooks, 2000; Wadley, 2015). The numerous excavated archaeological sites in South Africa play a key role in understanding biological and behavioural evolution of modern humans and their subsequent geographic expansion (McBrearty and Brooks, 2000; Lombard et al., 2012). Sediments containing archaeological remains are important sources of information for reconstructing early human use of prehistoric sites, their technologies and the climate they lived in as well as understanding modern human and landscape evolution (Avery, 1987; Schiegl and Conard, 2006).

Important MSA archaeological sites (Figure **1.0**) that have attracted attention and have been the focus of this extensive research in South Africa include: Blombos Cave (e.g. Henshilwood and Sealy, 1997; d'Errico et al., 2001; Henshilwood et al., 2001; Henshilwood et al., 2002), Sibudu Cave (e.g. Wadley and Jacobs, 2004, 2006; Allott, 2004, 2005; Cain, 2006; Sievers, 2006; Backwell et al., 2008; Wadley et al., 2009; Wadley et al., 2011; Hodgskiss, 2012), Rose Cottage Cave (e.g. Clark, 1999; Gibson et al., 2004; Wadley, 1997; Villa and Lenoir, 2006), Klasies River Mouth (e.g. Klein, 1976; Deacon et al., 1986; Avery, 1987; Thackeray, 1989; Wurz, 2002), Pinnacle Point Caves (e.g. Marean et al., 2004, 2007; Brown et al., 2012; Albert and Marean, 2012; Esteban, 2016); Umhlatuzana Rock Shelter (Kaplan, 1990; Lombard et al., 2010); Diepkloof Cave (e.g. Rigaud et al., 2006; Porraz et al., 2008; Texier et al., 2010;; Porraz et al., 2013); Border Cave (e.g. Klein, 1977; Villa et al., 2012); and Bushman Rock Shelter (e.g. Louw, 1969; Brain, 1969; Plug, 1981, 1982; Porraz et al., 2015). The various studies seek to understand early human behaviour and the environment they operated in. Most of these sites represent the later part of the MSA of southern Africa that includes the two distinct lithic technological industries – Still Bay (~71.9-71.0 kya) and Howiesons Poort (~65-60 kya) – that represent the important periods of the MSA that marked a period of enhancement of complex cognitive behaviour exhibited by early humans (Jacobs et al., 2008a). These study sites have provided evidence of innovations such as the use of pigment (ochre), symbolism such as engraved ostrich eggshells, personal ornaments such as shell beads, the use of adhesives for hafting stone and bone tools depicting improved hunting techniques, the use of medicinal plants as well as past climates at these sites (e.g. Avery, 1987; Henshilwood et al., 2002; Backwell et al., 2008; d'Errico et al., 2008; Texier et al., 2010; Wadley et al., 2011; Hodgskiss, 2012) that have allowed for the synthesis of detailed accounts of the MSA of South Africa (e.g. McBrearty and Brooks, 2000; Lombard et al., 2012; Wadley, 2014, 2015) and its key role in understanding the origins and behavioural evolution of *Homo sapiens*.

These important MSA sites are today distributed across the summer rainfall area (e.g. Sibudu Cave, Border Cave, Rose Cottage, Umhlatazana and Bushman Rock Shelters), the winter rainfall area (e.g. Blombos Cave and Diepkloof Cave) and the all year-round rainfall area (e.g. Pinnacle Point, Klasies River Mouth) of South Africa (Hall et al., 2014; Figure **1.0**). Klasies River, Blombos, Pinnacle Point and Diepkloof are some of the few sites with roughly the same span of occupation as Sibudu (Wurz, 2002; Henshilwood and Sealy, 1997; Marean, 2010; Porraz et al., 2013) and it is only Sibudu and Diepkloof that have so far been found to consist of both the Still Bay and Howiesons Poort technological industries within the same sequence in a single setting (Rigaud et al., 2006; Wadley, 2007; Porraz et al., 2013). However, these caves are located in the Winter Rainfall Zone (WRZ), within the Western Cape along the west coast near the Atlantic ocean (Blombos and Diepkloof) with Pinnacle Point and Klasies River in the all year-round rainfall region between the winter rainfall and summer rainfall regions in the Eastern Cape at the south coast, whereas Sibudu Cave is more than 1000 km away from the west coast, much farther north towards the east coast in the Summer Rainfall Zone (SRZ) (Figure **1.0**). Sibudu is 15 km from the Indian Ocean where environmental conditions are substantially different from those of the Western Cape/Eastern Cape (Wadley and Jacobs, 2006; Plug, 2006; Porraz et al., 2013).

Located in KwaZulu-Natal about 40 Km north of Durban (Figure **1.0**), Sibudu Cave has the potential to become one of the most important MSA sites in South Africa because of its deep, well-dated sequence that comprises one of the most complete later MSA sequences (Wadley and Jacobs, 2004, 2006; Wadley et al., 2011). Sibudu Cave is among the few sites in southern Africa with a long MSA that contains bone and plant preservation (Wadley, 2001). It provides evidence of early human occupation spanning ca. 37,000 years to >77,000 years with a long cultural sequence of pre-Still Bay, Still Bay (SB), Howiesons Poort (HP), post-Howiesons Poort, Late and Final MSA phases (Wadley and Jacobs; 2004; 2006; Jacobs et al., 2008a, b). Abundant lithic artefacts have been found at Sibudu and they provide detailed information on MSA technology during the different techno-complexes that form the primary basis for understanding early human techno-cultural variability during the late Pleistocene (e.g. Wadley, 2005; Lombard, 2005; Villa et al, 2005; Cochrane, 2006; Will et al., 2014; Soriano et al., 2015). Importantly, Sibudu consists of the SB and HP lithic technology industries that are important markers of technological and behavioural innovations of early humans that are linked to the geographic expansion of modern humans (Jacobs et al., 2008a). Because most of the important MSA sites are located on the south coast within the winter rainfall region (Chase, 2010), Sibudu Cave presents an opportunity to study the MSA within the summer rainfall region an area for which few environmental MSA records are available. Within the summer rainfall region, the Sibudu cultural sequence can be compared to few other sites such as Umhlatuzana Rock Shelter and Border Cave but not all their occupational phases are similar as what appears in one does not appear in another (Wadley and Jacobs, 2006). This means that they can only be compared for particular phases and worse still the sequence at Umhlatuzana is thought to have been mixed (Wadley and Jacobs, 2006).

It has been suggested that for South Africa, it is particularly important to study the past local climate for each ecosystem as the past climate of one cannot be extrapolated to represent other regions as South African past climate does not correlate with global inferences of past warming and cooling climates (Chase and Meadows, 2007; Chase, 2010). The need to study each site in its own context has been emphasised by studies that have shown that early humans occupied different sites at similar or different time spans and used lithic technologies during the MSA across South Africa creating similar technological records both at similar and at different time spans (Lombard, 2005; de la Peña et al., 2013; Porraz et al., 2013). Therefore, regional differences exist within similar techno-complexes and similarities exist within different complexes such as SB and HP (Wadley, 2001; Lombard, 2005). The techno-complexes described for South Africa such as HP are therefore not the same across archaeological sites in terms of timing and duration, and different ages exist for the same techno-complex (Lombard, 2005; Tribolo et al., 2013; Porraz et al., 2013). These studies have therefore disputed the current dates for South Africa's techno-complexes that suggest that the SB started around 71.9 ka and ended around 71.0 kya and the subsequent HP started around 64.8 kya and ended 59.5 kya (Jacobs et al., 2008a).

These aforementioned studies suggest that the MSA chronologies and cultural evolution models for these techno-complexes by Jacobs and Roberts (2008) and Jacobs et al. (2008a, b) do not delineate these industries in terms of the cultural technologies in which they occurred across South Africa as they are often taken to be homogenous in timing and technology across southern Africa by Jacobs and colleagues (e.g. Tribolo et al., 2013; Porraz et al., 2013). There are cultural evolution models by several other authors as well that suggest short intense occupation of several MSA sites by early humans and their subsequent abandonment and these have also been considered to be overly simplistic by recent studies (Lombard and Parson, 2010; Lombard, 2012; Porraz et al., 2013). There is a need for further investigation especially the chronological classifications that have been assigned to these techno-complexes to clearly delimit them and associated technological innovations (d'Errico et al., 2012). These recent concerns that have arisen from the naming and timings assigned to these lithic-based industries notwithstanding, the HP and SB of South Africa are the formally recognised industries across MSA sites in South Africa that also give the impression of being the most confidently defined across different sites. For purposes of fitting this study in the MSA context of other studies at Sibudu and the rest of South Africa, the informal terms that have been used to describe some industrial phases of the MSA assemblage at Sibudu are used in this thesis i.e. pre-SB and post-HP (Wadley, 2006; Wadley and Jacobs, 2006; Cochrane, 2006) along with the formal HP and SB industries as they are in the scope of this study. Therefore, this thesis acknowledges current on-going refinements of the lithic MSA technology of southern Africa that is the basis of naming and dating these techno-complexes but it does not concern itself with issues such as the new proposed techno-complex name for Sibudu i.e. the "Sibudan" for which the post-HP falls under (e.g. Conard et al., 2012; Will et al., 2014).

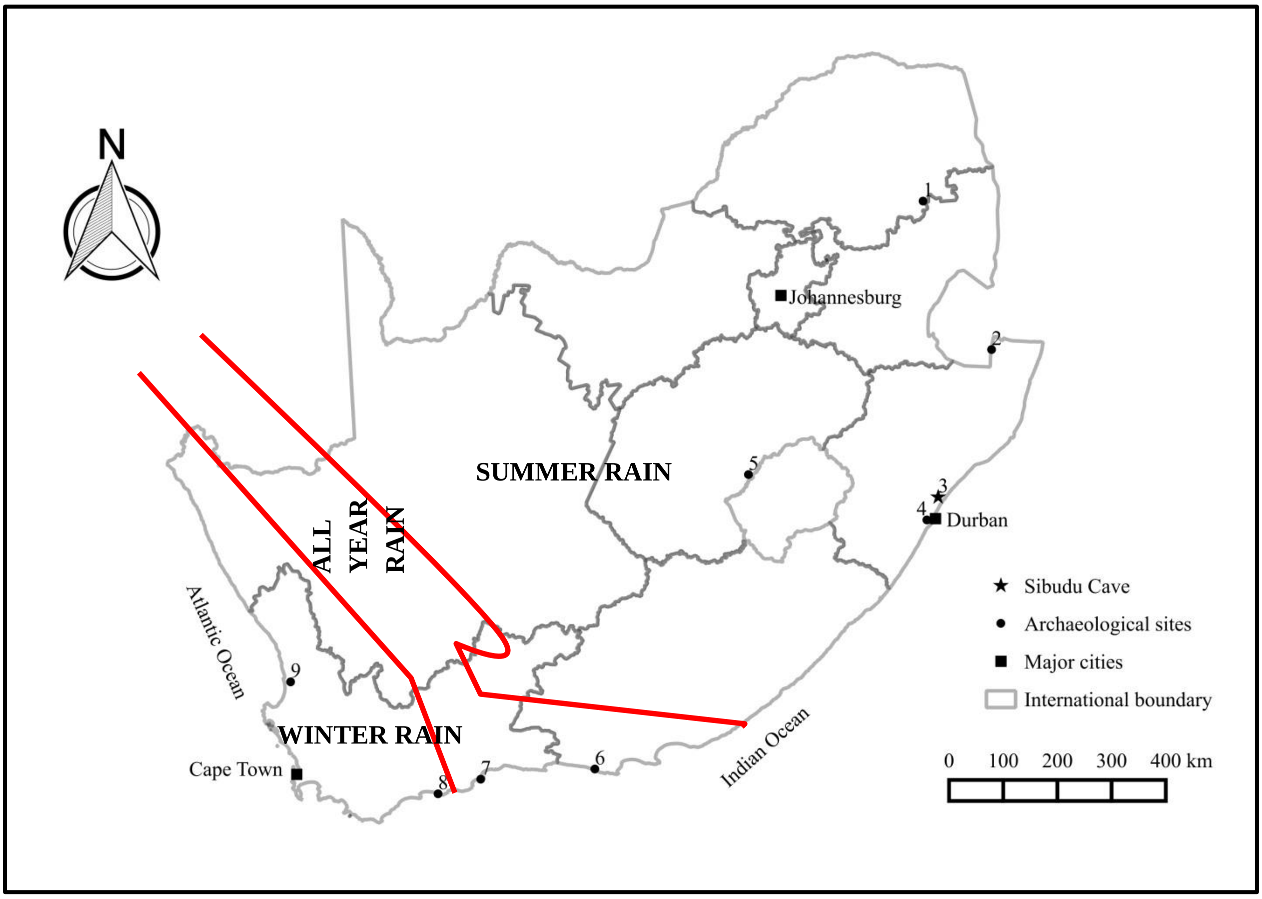


Figure 1.0 Location of Sibudu Cave and the archaeological sites mentioned in the text: 1) Bushman Rock Shelter, 2) Border Cave, 3) Sibudu Cave, 4) Umhlatazana, 5) Rose Cottage, 6) Klasies River Mouth, 7) Pinnacle Point, 8) Blombos Cave and 9) Diepkloof Cave. * The red lines illustrate the rainfall zone boundaries of South Africa - they have not been drawn to scale.

1.1 Phytoliths at Sibudu: a brief background

The account of early human settlement at Sibudu (in Wadley and Whitelaw, 2006 and studies therein) reveals occupation and abandonment of the site providing researchers with opportunities to study shifts in environmental conditions that may have affected their subsistence strategies as well as population density. Sibudu's long MSA cultural sequence has good organic preservation that has allowed for the analysis of phytoliths, charcoal, seeds, pollen (not well preserved) and bone (Schiegl et al., 2004; Allott, 2004, 2005; Sievers, 2006; Renaut and Bamford, 2006; Cain, 2006). Such organic material at Sibudu has not only provided information about human occupation e.g. the use of plant resources for wood, bedding and medicine but also palaeovegetation and palaeoclimate and their associated dynamics (Wadley, 2004; Allott, 2004, 2005; Sievers, 2006; Wadley et al., 2011; Bruch et al., 2012; Lennox and Bamford, 2015).

Whereas fossil plant remains provide valuable information about past vegetation and climatic conditions (Piperno, 2006), few palaeobotanical data are available from South Africa and southern Africa as a whole (e.g. Wadley, 2004; Allott, 2006; Sievers, 2006; Albert and Marean, 2012; Esteban, 2013). The few available plant remain studies in South Africa have focused on archaeological wood and seeds (e.g. Allott, 2004, 2005, 2006; Sievers, 2006; Sievers, 2013; Cartwright, 2013; Lennox et al., 2015). Although wood was burnt at most MSA sites, few show good charcoal preservation (Wadley, 2015) and the most extensive charcoal studies have been conducted at Sibudu and Diepkloof because of their excellent preservation (Allott, 2004, 2005. 2006; Cartwright, 2013; Lennox et al., 2015). Few studies have focused on fossil phytoliths in South Africa (Schiegl et al., 2004; Albert and Marean, 2012; Esteban, 2013). Most organic material studies at Sibudu have focused on the macrofossils of botanical (charcoal and seeds) and faunal (bones) remains (Wadley, 2004; Allott, 2004, 2006; Sievers, 2006; Plug, 2006; Cain, 2006; d'Errico et al., 2007; Sievers and Muasya, 2011; Val, 2016). A few studies have been done on the micro-botanical remains at Sibudu e.g. phytoliths and pollen (Schiegl et al., 2004; Schiegl and Conard, 2006; Renaut and Bamford, 2006). Some micro-botanical remains like phytoliths have also been observed in micromorphology studies at Sibudu (Goldberg et al., 2009).

Phytoliths from Sibudu MSA sediments were first presented by Schiegl and colleagues (Schiegl et al., 2004; Schiegl and Conard, 2006). Phytoliths were analysed from samples that were collected from recognisable hearths and their surrounding ashy layers

(Schiegl et al., 2004; Schiegl and Conard, 2006). The 20 samples analysed for their phytolith study were taken from various squares within layers that represent the later part of the MSA at Sibudu i.e. the post-HP, the late MSA and the final MSA (Schiegl et al., 2004). The phytoliths from hearths and the surrounding layers were found to be highly heat-altered and generally similar indicating that fires were intense and prolonged, and there may have been more fire at Sibudu than the visible hearth remains and black layers indicate (Schiegl and Conard, 2006). They also reported that phytoliths were abundant in the Sibudu sediments although several appear heat altered. This showed that phytoliths are a good indicator of past ash deposits or hearths in cases where the plant ash has been changed through diagenesis such that the original structures of fireplaces or ash dumps are not discernible at the site or have been heavily altered (Schiegl et al., 2004; Schiegl and Conard, 2006). Phytoliths at Sibudu are thought to have been brought to the site mainly through human activity but because Sibudu Cave is a high open shelter they suggested that some phytoliths could also come from decomposed plants that grew at the entrance of the shelter and some transported by air, water and through animal dung (Schiegl et al., 2004; Schiegl and Conard, 2006). Their phytolith study aimed at primarily differentiating between tree phytoliths, siliceous aggregates (SAs) that they attribute to trees and grass phytoliths to allow for the characterisation of wood ash deposits which would be dominated by tree phytoliths and SAs. It therefore provided insights into the prehistoric use of fire and taphonomic processes at the site (Schiegl et al., 2004; Schiegl and Conard, 2006).

A micro-morphological study also revealed that phytoliths are an important component of sediments at Sibudu sometimes being the sole component of a layer (Goldberg et al., 2009; Wadley et al., 2011). Goldberg and colleagues state that “many different types of phytoliths appear to be represented” (Goldberg et al., 2009). A general mention of the presence of phytoliths was made without specific type identification because the study’s aim was to study the site formation processes i.e. anthropogenic, biogenic, diagenetic and geogenic processes operating at Sibudu. Their study however, specifically identified sedge phytoliths and confirmed the presence of sedges brought to the site as bedding as previously suggested by seed studies at Sibudu (Sievers, 2006; Sievers and Wadley 2008). At Sibudu, intense heat and high pH conditions caused a significant proportion of the phytoliths to be morphologically altered (Schiegl and Conard, 2006). They found that this made quantitative phytolith analysis difficult and suggested that it could be overcome by analysing the proportions of phytoliths that show minor or no heating effects and this would provide important information for environmental interactions during the MSA (Schiegl and Conard, 2006).

The current phytolith study therefore set out to analyse phytoliths for purposes of understanding past environments during the MSA at the east coast of South Africa in terms of vegetation and climate. Importantly the specific types of plants that early humans utilised during the MSA can be identified through phytolith analysis (Piperno, 2006). Region-specific modern plant phytolith reference collections are necessary to make such meaningful identifications of phytoliths from the archaeological record (Bamford et al., 2006; Iriarte and Paz, 2009; Rossouw, 2009; Novello et al., 2012; Neumann et al., 2017; Collura and Neumann, 2017). Because few modern plant phytolith reference collections existed for South Africa (i.e. Rossouw 2009; Cordova and Scott, 2010), all of which focus on monocotyledonous plants mainly the grasses, this study also set out to create a modern plant phytolith reference collection for South Africa especially for woody taxa for which there was none at the time this study begun. A new modern reference collection that incorporated woody taxa has been recently added to the South African reference material (Esteban, 2016) and it focuses on plants from the WRZ of South Africa (Fig. **1.0**). The current phytolith study aimed at creating a modern reference collection of plants from the SRZ of South Africa (Fig. **1.0**). This reference collection adds to the few published modern phytolith reference collections and provided a standpoint on which to interpret the archaeological data at Sibudu and future archaeobotanical phytolith studies that are taking shape in South Africa.

1.2 Problem Statement

The previous phytolith study at Sibudu Cave focused on using phytoliths to identify tree phytoliths, siliceous aggregates (SAs) and grass phytoliths to characterise wood ash deposits with the primary aim of insight into prehistoric fires and taphonomic processes at the site (Schiegl et al., 2004; Schiegl and Conard, 2006). In so doing, several issues that are discussed here were clearly beyond the scope of their study. Firstly, the potential of phytoliths as a tool in archaeology has not been fully utilised at Sibudu by the previous phytolith study of Schiegl et al. (2004) as important phytolith morphotypes were not been identified to the highest taxonomic level possible. For example, grass phytoliths were classified and clustered together as ‘grass phytoliths’ by Schiegl et al. (2004). There is therefore no record of the type of grasses utilised at Sibudu by early humans. Identification of grasses to the subfamily level is important because different grass subfamilies with different photosynthetic pathways are adapted to different environmental conditions, for example, the analysis of C_3/C_4 grass composition is crucial to reconstruct past vegetation as it allows for making inferences of climatic conditions (Twiss, 1992; Piperno, 2006). For instance; abundance of C_3/C_4 tall grass species would suggest increased precipitation while C_4 short grass species would be associated with reduced precipitation (Singh et al., 2007).

The current study set out to make this grass distinction especially because of the paucity of C3/C4 grass data during the late Pleistocene at the east coast of South Africa compared to the west and south coast where several studies tend to concentrate (e.g. Bar-Matthews et al., 2010; Albert and Marean, 2012; Cordova, 2013; Cartwright, 2013; Esteban, 2016). Because the phytolith data of C3/C4 at archaeological sites such as Sibudu is as a result of human selection of plant types, it can be biased and may not be representative of past vegetation. However, at several archaeological sites, the assumption is made that early humans selected plants that were available in the vegetation and that the plants they selected offer a good representation of what was in their surroundings. This short coming is further over come by using various proxies at a given site to provide complementary or supplementary information as has been done at Sibudu (Wadley and Whitelaw, 2006 and studies therein). For example MSA phytolith data at Pinnacle Point at the south coast was correlated to Speleothem data (Albert and Marean, 2012). Most climate proxies for South Africa have been obtained from archeological sites (Chase, 2010; Wadley, 2015) and other rare proxies such as hyrax dung (Scott and Vogel, 2000) and their inferences are often placed into context of known climate phases of similar time occurrences for South Africa obtained from marine oxygen isotope data such as MIS 4 and MIS 5 to understand past climates (e.g. Wadley, 2004; Reynolds, 2006; Albert and Marean, 2012).

Moreover, phytoliths also have the potential to identify Cyperaceae (sedges), Arecaceae (palms) and some tree and herbaceous taxa that produce diagnostic phytoliths (Piperno, 1989; Ollendorf, 1992; Bamford et al., 2006; Piperno, 2006). In their phytolith classification system, Schiegl et al. (2004) show that grass phytoliths might have been grouped together with sedge phytoliths as they indicate the category ‘phytoliths from grasses and sedges’ in their phytolith classification in the methods but they make no mention of the sedge phytoliths percentage in their results and indicate only that of grasses. It is therefore not clear to what extent each of the two families contributes to this group or if sedge phytoliths were encountered at all. Furthermore, their phytolith classification (Schiegl and colleagues) is mainly based on identifications and classifications of a phytolith inventory by Runge (1999) on central African soils and the phytolith morphotype categories of Runge i.e. B1, B2, B3 that were identified at Sibudu were interpreted as belonging to 'dicotyledons' and they attributed them to trees in the Sibudu record.

The category B3 (spherical with big spines) was included in the 'dicot and tree' category in their classification system and no mention is made of its own percentage and yet according to Runge (1999), this morphotype is used to identify palms (Arecaceae), something that also their phytolith study indicated. This placement of this category (B3) is misleading since palms are monocots and are not essentially trees although many appear tree-like, and therefore would not contribute to the 'wood ash' in the sediments that was the aim of the Schiegl et al. (2004) study since they are not woody. It is also not clear from their results if this particular B3 morphotype was identified in Schiegl et al. (2004) since they grouped all the spherical phytolith types together. The extent to which these palms phytoliths occur at Sibudu is not clear from Schiegl et al. (2004) although the B3 morphotype was later mentioned in Schiegl and Conard (2006) seemingly as a one-time occurrence. It is important to categorically isolate palm phytoliths in any record as they are known as habitat-specific plants in archaeological and palaeoanthropological samples (Runge, 1999; Piperno, 2006; Bamford et al., 2006; Albert et al., 2009). More so, without presenting images of the phytoliths that they identified at Sibudu as is commonly done in contemporary phytolith studies, it remains generally difficult to comprehend the specific phytolith types previously identified at Sibudu and complicates comparison with other phytolith studies.

Finally, the way in which the previous phytolith study is being interpreted by other specialists to infer environmental change at Sibudu is problematic. For example Hall et al. (2014), interpret the reduction of grass phytoliths in some layers in Schiegl et al. (2004) as a reduction of grassland extent within the MSA environment at Sibudu. This kind of interpretation of the phytolith record at Sibudu is not justified as the study by Schiegl et al. (2004) cannot allow for this kind of environmental interpretation and neither did they imply it. Phytolith studies in South Africa are still rare and their application in South African archaeology is relatively new (Schiegl et al., 2004; Albert and Marean, 2012; Cordova, 2013; Esteban, 2016), and specialists of other archaeological proxies in archaeology may not be familiar with their application and interpretation. The study of Schiegl et al. (2004) was designed to use phytoliths to understand taphonomy and the use of fire at Sibudu but not to infer vegetation or environmental conditions and associated changes. The paucity of lake sedimentary archives in South Africa has led to the use of unconventional archives like cave deposits and fossil hyrax dung to infer palaeoenvironments in South Africa (Scott and Vogel, 2000; Scott, 2002). Because cave deposits can be almost entirely of anthropogenic origin as in the case of Sibudu, exercising caution is indicated when using them as climatic signals (Pickering, 2006; Goldberg et al., 2009). It was therefore necessary to study phytoliths at Sibudu in a context that allows to some extent for inference of past environmental conditions that include climate in a region for which few data exist.

1.3 Aims of the thesis

The aim of this thesis is to present a modern reference collection of phytoliths from important taxa that occur around present day Sibudu cave that are generally a good representation of the Summer Rainfall Zone vegetation. The focus was mainly on sedges and trees for which no data exists in the SRZ of South Africa. Modern grasses found at Sibudu were included in the study and although much smaller in comparison, contribute to the bigger study of Rossouw (2009). The modern reference collection was to guide the identification of the archaeological phytolith assemblage in this study and future phytolith studies for the region.

The second aim of this thesis is to present the environmental history of Sibudu archaeological site, South Africa, over the last > 71,000 to ca. 48,000 years ago. This period at Sibudu has been associated with several cultural and environmental changes including vegetation and climatic changes (e.g. Wadley, 2004; Allott, 2004; Sievers, 2006). Through phytolith analysis, the study involved identifying plant taxa that the early inhabitants of Sibudu utilised to understand their subsistence strategies and way of life. By identifying the taxa at the site, the like vegetation surrounding the site is suggested and the likely climate that prevailed during this MSA period. This study therefore aimed at providing supplementary and complementary data to other proxies at Sibudu Cave to improve and contribute to our knowledge of human occupation and their environment on the east coast of South Africa.

The study therefore intended to address the following specific research objectives:

1. To organise a reference collection of phytoliths from modern extant plants that are representative of vegetation of the Summer Rainfall Zone that are representative of plants that early humans utilised during the MSA at the east coast of South Africa.

2. To identify phytoliths in archaeological samples to a higher taxonomic resolution to identify the plant taxa mainly the grass subfamilies and other monocot components (i.e. sedges and palms) of the taxa that was utilised at Sibudu during the MSA.

3. To determine human-plant interactions at Sibudu during the MSA using phytoliths as a tool to understand early human subsistence strategies and occupation.

4. To reconstruct the past vegetation and infer climatic conditions around Sibudu.

1.4. Hypotheses

1. Phytoliths in the assemblage will provide evidence for early human-environmental interactions e.g. type of resources utilised for bedding and fire.

- According to Schiegl and Conard (2006), phytolith abundance at Sibudu is a good indicator of combustion of plant material which is supported by the large number of visible hearths and ash deposits. Phytoliths will be used to identify plant resources used during MSA occupation such as grasses, arboreal taxa and sedges.

2. Phytoliths in the assemblage will provide evidence of the vegetation and climate that existed around the cave and the region during the MSA.

- Assumption is made that most of the plants utilised by early humans at the site came from the surrounding cave environment. If few plant taxa are identified in the fossil phytolith assemblage, this will impede the proper reconstruction of past vegetation and inferring possible climate. This is because the site contains largely anthropogenic material, the record at Sibudu may contain plants selectively used by early humans and many surrounding taxa would be left out of the record. The assumption is made also that the plants during the MSA lived in conditions that are similar to those of that their modern counterparts live in today. Modern phytolith records from extant plants will be compared to those in the fossil record to determine possible climatic conditions.

1.5 Scope of the thesis

The primary focus of this thesis is to reconstruct the late Pleistocene environmental history of Sibudu Cave, South Africa within the context of the Middle Stone Age of South Africa. The study focuses only on the pre-Still Bay, the Still Bay, the Howiesons Poort and post-Howiesons Poort industries of Sibudu (> ~71 – ~48 kya). The research on which this thesis is based focused on the use of phytoliths as a potential proxy to reconstruct early-human plant interactions, their surrounding vegetation and the environment in which they operated.

1.6 Structure of the thesis

This thesis is arranged into nine chapters that are summarised below:

Chapter 1 – Introduction: It comprises the general introduction that places Sibudu in the context of South African archaeology and gives a brief background to Sibudu and the previous phytolith study at Sibudu. It briefly explains the usefulness of phytoliths and their potential to study past vegetation to understand early human-plant interactions and climatic conditions at Sibudu. It further introduces the need for a modern plant phytolith reference collection for South Africa. It states the gaps that this phytolith study sought to fill in the problem statement and comprises the aims and objectives of the study, the hypotheses and, the scope and structure of the thesis.

Chapter 2 – Background to the study: It gives the history of research at Sibudu Cave, the sources of evidence used in those studies with a particular focus on those that infer past vegetation and climate. It gives a brief description of the past environment at Sibudu as inferred by these proxies and early human culture during the MSA, describes the use of phytoliths as a tool to reconstruct past environments including their advantages and limitations and concludes with a brief history of phytolith research in Africa and a special mention of Cyperaceae (sedges) phytoliths.

Chapter 3 – Present-day Sibudu: It consists of a description of the present environment at Sibudu in terms of its geographic location, present-day climate and vegetation together with stratigraphy and chronology of the samples analysed in this study.

Chapter 4 – Methods: This chapter comprises of field based methods of sampling modern vegetation for the modern reference collection and sampling of archaeological samples as well as laboratory methods to extract phytoliths from them. It also presents the phytolith counting and classification criteria and a table showing the main morphotypes identified in this study and their taxonomic affiliation together with the statistics applied.

Chapter 5 – Results: Presents the results of the modern plant phytoliths – sedges, grasses, rushes and dicots that are mostly woody and photographs of their images.

Chapters 6 – Implications of the modern reference collection: It discusses the interpretations made from the modern reference collection in terms of their implications for taxonomy and archaeology. The results were used to characterise the MSA fossil phytolith results in the next Chapter (chapter 7). It therefore seeks to put into context chapter 7 in order to understand the background against which the taxonomical classifications used for the archaeological phytolith data were made.

Chapter 7 – Results: Presents the results of the MSA phytolith assemblage in terms of taxa utilised by early humans and the inferred past vegetation at Sibudu during the pre-Still Bay, Still Bay, Howiesons Poort and post-HP.

Chapter 8 – Discussion of the MSA: Comprises of the discussion of the past environment at Sibudu from the pre-SB to the post-HP (> 71,000 to ca. 48,000 yr BP), in terms of early human-plant interactions, vegetation and climate. It makes comparisons with other vegetation and climate data from Sibudu and gives an overview of the implication of the study for South African archaeology.

Chapter 9 – Conclusion: This chapter presents a summary of the main results and their implications and highlights the areas that need further investigation.

CHAPTER TWO

BACKGROUND TO THE STUDY

2.0 History of archaeological research at Sibudu Cave

Sibudu Cave was first excavated in 1983 by Aron Mazel of the Natal Museum with a small trial trench of about one metre-deep that revealed Iron Age (IA) deposits (Wadley and Jacobs, 2004). Major excavations of MSA deposits occurring immediately below the IA deposits begun in 1998 led by Prof. Lyn Wadley from the University of the Witwatersrand. Several multi-proxy studies were conducted to understand its environmental history and were published in Wadley & Whitelaw (2006) and several have since been published. As of 2005, deposits in the trial trench (squares B5 and B6) had reached a maximum depth of three metres with excavation of this trench ending at rocks that were thought to be boulders and not the actual bedrock while other squares yielded more than 4 metres of deposit without reaching bedrock (Wadley and Jacobs, 2006; Pickering, 2006). As of 2006, the Wadley team had excavated 21m^2 of MSA deposits (Wadley and Jacob, 2006). Excavations are on-going to date led by Nicholas Conard of Tübigen University since 2008 and several publications continue to emerge from both excavations.

The excavations have revealed deep sediments with good organic preservation that represent the pre-Still Bay (pre-SB), Still Bay (SB), Howiesons Poort (HP), post Howiesons Poort (post HP), late MSA and final MSA technological industries making Sibudu one of the most important archaeological sites in South Africa (Wadley and Jacobs, 2004, 2006). Most shelters contain relatively short sequences of human occupation and Sibudu is one of two that present a rare opportunity to investigate the MSA cultural evolution of SB and HP within a single stratigraphic sequence and setting (Jacobs and Roberts, 2008; Porraz et al., 2013). The rock shelter represents an important depositional site containing evidence of both human settlements and environmental conditions in the area during the Pleistocene and has provided evidence for the emergence of complex human behaviour (Wadley et al., 2009). The final Optically Stimulated Luminescence (OSL) ages for the well stratified layers at Sibudu are divided into pre-Still Bay (77 ka), Still Bay (70.5 ± 2.0 ka), Howiesons Poort (61.7 ± 1.5 – 64.7 ± 1.9 ka), post Howiesons Poort (58.5 ± 1.4 ka), late MSA (47.7 ± 1.4 ka) and final MSA (38.6 ± 1.9 ka) (Jacobs et al., 2008a, b).

MSA occupations at Sibudu lie directly below the Iron Age layers leaving no representation of Later Stone Age (LSA) remains (Wadley and Jacobs, 2006). The stratigraphic layers at Sibudu are clear and have been named according to the overshadowing colour of the predominant matrix and older layers have more conventional colours compared to the younger one (Wadley and Jacobs, 2006). Sediment deposits at Sibudu are composed mainly of anthropogenic materials such as ash and bone (Pickering, 2006). Ash is a major component of sediments and layers of hearths occur in parts of the shelter (Wadley and Jacobs, 2006). The MSA sequence at Sibudu has good organic preservation in which faunal remains show a presence of various mammals, birds and reptiles (e.g. Plug, 2004; Cain, 2006). This has provided evidence for occupation of skilled hunter-gatherers at the site. Botanical remains show plant use by early humans as bedding and firewood (Schiegl et al., 2004; Allott, 2004, 2005; Sievers, 2006).

More so, lithic artefacts at Sibudu have provided evidence of a long sequence of MSA technology (e.g. Lombard, 2004; 2006a; 2006b; Will et al., 2014) and residual analysis on stone tools provide evidence that early occupants processed plant material and used individual tools for multiple tasks (Williamson, 2004). Such studies from Sibudu have provided the environmental history of Sibudu allowing interpretation of human behaviour, human-environmental interactions, past vegetation and climate as well as site formation processes. Proxies that have been used in the multi-proxy and multidisciplinary research conducted at Sibudu to determine past environments in terms of climate and/or vegetation in particular are discussed below.

2.1 Sources of evidence at Sibudu

Firstly, a long sequence of lithic technology is represented throughout the MSA period at Sibudu that provides evidence for the emergence of complex human behaviour (Wadley et al., 2009). The sequence at Sibudu shows that the site was occupied and abandoned on several occasions (Cochrane, 2006). Several studies published in Wadley and Whitelaw (2006) document the lithic tools from Sibudu and subsequent publications have followed since then that continue to refine our knowledge of early human technologies (e.g. Conard et al., 2012; de la Peña et al., 2013; Will et al., 2014). In summary, lithic material present in samples older than ~ 60 Ka i.e. the Pre-Still Bay (unifacial points), the Still Bay (lanceolate points) and HP industry (blades and a bone point) while samples younger than ~ 60 ka i.e. Post HP (points, some bone), late MSA (unifacial ponts) and the final MSA contains more bifacial points than unifacial points, segments and hollow based points (Wadley and Jacobs, 2006). Microscopically analysed residues from stone tools from ~ 60 ka and 50 ka layers provide evidence of remains of hafting material that once attached the stone tools to bone or wooden shafts (Williamson, 2004; Lombard, 2006b). Similar results are observed in the Still Bay points (Lombard, 2006a) and Howiesons Poort segments (Lomabard, 2006b). In this section, I focus on discussing sources of evidence at Sibudu pertaining to environmental reconstructions of climate and vegetation as well as human-plant interactions.

Environmental history of Sibudu has been inferred from several multidisciplinary archaeological records that have allowed for the reconstruction of past environments especially for the HP and post-HP i.e. from about 65 to 58 ka (e.g. Allot, 2005, 2006; Sievers, 2006; Hall et al., 2014). Until recently, little has been known about the environmental conditions during the SB at Sibudu and few data is available e.g. the faunal study by Val (2016). Most studies are based on analysis of macrofossils (e.g. Allott, 2004, 2005, 2006; Wadley, 2004; Sievers, 2006; Cain, 2006; Plug, 2006; Backwell et al., 2008; Val, 2016) and a few on microfossils (e.g. Schiegl et al., 2004; Renaut and Bamford, 2006; Goldberg et al., 2009). Analysis of several micro and macro fossil proxies include: phytoliths (Schiegl et al., 2004), pollen (Renaut and Bamford, 2006), charcoal (Allott, 2004; 2005; 2006), seeds (Wadley, 2004; Sievers, 2006) and fauna (Cain, 2006; Plug, 2006; Val, 2016). The chemical composition of sediments and plant remains including minerals and isotopic content have also been used to reconstruct past environmental conditions at Sibudu (Schiegl et al., 2004; Hall et al., 2008, 2014). The use of data from different proxies together with improved dating control (Wadley and Jacobs, 2006; Jacobs and Roberts, 2008; Jacobs et al., 2008a, b) has led to an improved understanding of MSA environments and the possibility of further detailed palaeoenvironmental reconstructions. These archaeological sources of evidence from Sibudu are each briefly discussed here to show the extent of environmental research that has been conducted at Sibudu, showing their advantages and disadvantages were possible and their cultural and environmental interpretations are discussed later on.

Macrofauna at Sibudu occurring in the major age clusters are described in Plug (2004; 2006), Cain (2006) and Val (2016). The bird fauna assemblage at Sibudu is the largest MSA record for South Africa both in size and taxonomic diversity (Val, 2016). Several aquatic animals such as fish, crabs, frogs, crocodiles and fresh water birds in the record infer the presence of a water source at Sibudu throughout MSA (Plug, 2006; Val, 2016). Layers in the post-HP and late MSA (from ~58Ka and from ~48Ka respectively) were characterised by medium to large ungulates which include Zebra, giraffe, brown hyena, impala, waterbuck, blue wildebeest and roan (Plug 2004; Cain, 2006). Zebras are particularly well represented in the ca. 50,000 yrs layers along with brown hyena, giraffe, impala, klipspringer, grey waterbuck and red hartebeest (Plug, 2004; Cain, 2006). The macrofauna study has been complemented by microfauna data of Glenny (2006). These studies offer good interpretations of early human behaviour and to some extent environmental conditions at the site albeit rather limited in interpretation.

Archaeologically recovered charcoal has been analysed at Sibudu (Allott, 2004; 2005; 2006). Several tree taxa are deciphered from the record and offer valuable interpretations of the palaeovegetation and palaeoclimate and early human plant exploitation during the MSA. The study provides evidence of environmental change during the MSA at Sibudu and wood selection by early humans. The dynamics involved in tree taxa through the MSA may have been as a result of change in local vegetation, sample bias or simply a change in preference of wood source by early humans (Allott, 2006). According to Allott (2006), it is sometimes difficult to decipher the cause of changes observed in the charcoal assemblages and it is useful to have other proxy data such as phytoliths as changes may be a result of change in behaviour rather than climate. More so because charcoal can rarely be used to infer grasses at a site as it’s burnt beyond recognition in the record.

Carbonised and uncarbonised seeds have been recovered from Sibudu Cave (Wadley, 2004; Siever, 2006, 2011; Wadley et al., 2011). The seeds were first described by Wadley (2004) and sedge nutlets were first presented by Sievers (2006). These studies reveal tree species, shrubs, climbers, rushes and sedges throughout the MSA record. Sedges are thought to have been brought to the site by humans from the nearby Thongati River and carbonisation of their nutlets is thought to be a result of post depositional fires and deliberate burning of sedges by early humans for site maintenance (Sievers, 2006, 2011; Wadley et al., 2011). The sedges were interpreted as having been used as bedding or a working surface and this has been supported by micro-morphological studies by Goldberg et al. (2009). These sedge studies suggest the presence of a permanent water source during MSA of South Africa. Pollen from sedges and presence of aquatic remains in the Sibudu record support the presence of water from the Thongati River. (Renaut and Bamford, 2006; Plug, 2006; Val, 2016) Seeds from semi-deciduous and evergreen forest taxa throughout the MSA layers are described in Wadley (2004) and inferences about climate were suggested. These seeds are thought to have been brought to the cave by humans, animals, wind or could have fallen from trees on the cliff above the cave (Wadley, 2004). The forest taxa record by Wadley (2004) is supported by the charcoal record from Sibudu (Allott, 2004, 2005, 2006) for instance in terms of presence or absence of a particular taxon from the MSA layers. This seed method is not without problems, the main one being the inability to identify a large number of taxa as indicated by Sievers (2006) which leaves the inferred record rather incomplete. More so, not all layers have been sampled for charcoal (discussions of the seed data is largely complemented by charcoal data), this makes it difficult to interpret the results or explain the changes in the seed record according to Sievers (2006).

Sediment-based analyses at Sibudu have involved a study on pollen analysis. According to Renaut and Bamford (2006), most pollen studies in South Africa have concentrated on the Holocene with older studies not well fine-tuned. More so, pollen records from the east coast that are more applicable to Sibudu are limited (Renaut and Bamford, 2006). The pollen record at Sibudu was found to be poorly preserved and other organic material present in barren samples showed signs of damage and was amorphous. Although the pollen count is low it provides interpretations that support some of the seed (sedge), charcoal and phytoliths identifications from Sibudu (Renaut and Bamford, 2006). It is not surprising that the pollen record is not well preserved as pollen grains are not resistant to preservation but they deteriorate as a result of physical, chemical or biological attacks resulting in under representation in the pollen record (Lowe and Walker, 1997). This is supported by the finding at Sibudu that the pollen was destroyed by the prominent fires at the site hence the lack of preservation (Renaut and Bamford, 2006). Other than poor preservation, another problem with pollen is its inability to identify poaceae (grass) pollen beyond the family level making it impossible to differentiate between grass subfamilies as seen for Sibudu. However, such problems can be solved by additional sediment-based proxies such as phytoliths. The fossil botanical material from Sibudu mentioned above have been subjected to a GIS-based Coexistence Approach (CA_{GIS}) analysis and this method has presented a higher resolution of climatic conditions in terms of winter and summer for specific vegetation types during the MSA that were inferred from other studies at Sibudu (Bruch et al., 2012).

The stable carbon isotope (^{13}C) has been used to reconstruct past environments at Sibudu (Hall et al., 2008, 2014). Analysis of $\delta^{13}C$ values from C_3 plant charcoal of modern *Podocarpus* spp. and *Celtis* spp. (trees) and archaeological charcoal of the same were found to correlate well (Hall et al., 2008). They demonstrate that a palaeoenvironmental signal is preserved in archaeological charcoal described at Sibudu (Allott, 2004, 2005, 2006). Environmental shifts which fit well with climatic shifts from other proxies in the age clusters at Sibudu are reflected in the carbon isotope composition of the archaeological charcoal (Hall et al., 2008, 2014). There are problems involved in using ^{13}C from charcoal as several studies have produced contradicting values in carbon ratios of burnt and un-burnt plant material but others have shown the potential of charcoal ^{13}C values to record an environmental signal (Hall et al., 2008).

Finally, a magnetic susceptibility (MS) study that involves mineral magnetic analysis of sediments has provided evidence for climate change at Sibudu from the post-HP to the Iron Age (Herries, 2006) as will be discussed later. This method has been criticised by Goldberg et al. (2009) as the interpretations about the soil deposition at Sibudu are not the same as those found by the micromorphology study by Goldberg et al. (2009). They suggest that it is important to understand depositional processes and sediment components at Sibudu to aid interpretations of the MS study. Their study shows that soil components were brought to the site by humans and not conditions associated directly with climate change as suggested by the MS study (Goldberg et al., 2009). The MS readings therefore most likely do not represent climate change since the deposits at Sibudu are largely anthropogenic (Goldberg et al., 2009).

2.2 Summary of palaeovegetion and paleoclimate at Sibudu Cave during the MSA

The multidisciplinary studies above have enabled the reconstruction of past environments at Sibudu. Proxy evidence at archaeological sites might be biased and is problematic but several lines of evidence have been advanced for Sibudu (Hall et al., 2014). For example, it was impossible to decipher if the wood selection from the charcoal analysis was a result of choice by early humans or environmental availability but it is suggested that the charcoal is representative of the local woody vegetation that occurred at the site (Allott, 2006; Hall et al., 2014). Deposits at Sibudu cave are reported to have accumulated during periods within the Last Glacial and possibly earlier (Wadley and Jacobs, 2006). Significant global scale changes in climate and sea level are recorded for the last glacial but such climatic changes are not well-documented for archaeological sites in the summer rainfall region particularly KwaZulu-Natal (Allott, 2006; Chase, 2010). Most of the Sibudu MSA sequence falls within the Oxygen Isotope Stage (OIS) 3 and the final phase of OIS 4, periods in which seed and charcoal data point to variable and changing environmental conditions (Wadley, 2004; Allott, 2004, 2005, 2006; Sievers, 2006; Chase, 2010). The pre-SB, SB and HP layers (> 77 to 60 kya) fall within the OIS4, a period representing an overall cool climate while the post-HP, late MSA and final MSA fall within the OIS3 (~58-38 kya) with an overall warm climate (Wadley, 2004; Chase, 2010). Various accounts are given for the past climate and vegetation at Sibudu and the literature can be quite confusing and contradictory. Also the same occupation period can be presented with different environmental conditions in its layers (see Wadley, 2006; Hall et al., 2014). Therefore main broad environmental intepretations of the technocomplexes at Sibudu from various studies discussed below are summarised in Table **2.0**

Proxy environmental data for the pre-SB and SB is limited compared to the other industries but a recent faunal study suggests that the vegetation was that of evergreen and deciduous forest communities (Val, 2016). The pre-SB is associated with warm and moist conditions consistent with the end of an interglacial period (> 75 kya) that was followed by a colder phase that accompanied the first glacial maximum around 70 kya (Val, 2016). The presence of the Gambian giant rat in these earlier layers and in the succeeding HP layers is reported to indicate the presence of evergreen forest that is its habitat (Glenny, 2006).

Layers from the HP (~65-62 kya) suggest the dominance of evergreen forest taxa such as *Podocarpus* with high rainfall and more humidity than the post-HP occupations (Allott, 2006; Bruch et al., 2012; Hall et al., 2014). This warm and moist environment is similar to what is interpreted for the pre-SB (Val, 2016). Bruch et al. (2012) suggests that the winters were slightly colder and drier than present whereas the summer temperatures and precipitations were the same as those for today. The presence of sedge nutlets in all MSA layers suggests the presence of perennial water in the Thongati River (Sievers, 2006). These layers contain fern spores and sedge pollen indicating the presence of some moisture (Renaut and Bamford, 2006). The presence of reptiles, molluscs and fresh water birds confirms a permanent water source close to Sibudu (Plug, 2006; Val, 2016). Gypsum during the same period suggests that there was moisture at the time (Pickering, 2006; Schiegl and Conard, 2006). HP layers provide evidence for a variety of vegetation communities at Sibudu including forest, riverine vegetation and to a lesser extent drier bushveld vegetation (Allott, 2006). The presence of *Kirkia* tree species adapted to dry environments suggests mixed vegetation (Allott, 2006). Evergreen woody plants are thought to have been predominant during this period (Sievers, 2006). Fauna studies also suggest that the greatest percentage of mammals during this period was of those that are adapted to forested environments with a small percentage from open environments (Clark and Plug, 2008). The vegetation was interpreted as woodland savanna habitat growing close to a riparian forest in a warm environment (Allott, 2006).

The post-HP (~58 kya) layers are dominated by mainly evergreen, riverine forest taxa some of which suggest a shift to a cooler climate (Wadley, 2004; Allott, 2006; Bruch et al., 2012). Temperatures for the post-HP are said to have been similar as those of the HP (Sievers, 2006; Bruch et al., 2012) but the post-HP was slightly colder and represents the coldest phase with a climate colder and drier than today (Bruch et al., 2012). A shift to drier and colder than present climate with open savannas is inferred by Hall et al. (2014). Wadley (2004) and Sievers (2006) suggests an increase in deciduous taxa. These inferences are supported by Reynold (2006); and Glenny (2006) who suppose a combination of forest, riverine and open savanna. The period also registers a change of mammals adapted to closed forest or woodland to those in drier and more open savannas (Plug, 2004; Cain, 2006).

The late MSA (~ 48 kya), falls within OIS3 and is reported to have been a period with fewer evergreen forest taxa and more bushveld taxa that is common to drier areas (Allott, 2006). The seed and charcoal assemblages indicated an increase of deciduous wood species throughout the late MSA (Sievers, 2006; Allott, 2006). This period is therefore thought to have been drier and vegetation was more open than during the post-HP (Allott, 2006; Sievers, 2006). It is reported by other authors as a period of increased warming and humidity with an environment that is similar to that of today (Reynolds, 2006; Bruch et al., 2012; Hall et al., 2014). This warming is said to have continued into the final MSA (~ 38 kya) but most likely with drier conditions (Bruch et al, 2012). The magnetic susceptibility study (Herries, 2006) also suggested that there was an increase in warm conditions during the late MSA period. However, this interpretation has to be treated with caution since this interpretation has been questioned by Goldberg and colleagues specifically because the depositis at Sibudu are anthropoegenic and not climatically driven and thereofore such deductions cannot be made from this method (Goldberg et al., 2009). The faunal assemblage during this period shows the presence of a mixed environment with savanna/grassland and forest/woodland species (Plug, 2004; Cain, 2006). The study by Hall et al. (2014) also suggests mosaic vegetation around Sibudu that was a mix of grassland, savanna, woodland, evergreen and riverine forest and that moisture levels were higher than the post-HP.

The climate and vegetation of the final MSA (~ 38 kya) is thought to have been similar to that of today although drier (Allott, 2006). The warming trend from the late MSA is thought to have continued to the final MSA but possibly under drier conditions (Allott, 2006; Bruch et al., 2012). Charcoal analyses (Allott, 2004, 2005, 2006) and seed analyses (Wadley, 2004; Sievers, 2006) show that many taxa found in and around Sibudu today were also present when the site was occupied in the MSA because at least some conditions may have been similar to those of today. However, there are some plant taxa represented during the MSA that do not currently grow in the coastal environment of KwaZulu-Natal e.g. *Kirkia* spp. (Wadley, 2004, Allott, 2006). This implies that more northerly vegetation elements were once part of the region and that the local dry woodland component of the vegetation may have been larger than it currently is (Wadley, 2004; Allott, 2006). A general warming trend is suggested from the HP to the final MSA occupations at Sibudu (Jacobs et al., 2008a, b; Bruch et al., 2012) with increasing winter temperatures and stable summer temperatures (Bruch et al., 2012). Although the late MSA (from ~ 48 kya) and final MSA (~ 38 kya) environments have been described in this chapter, they are not in the scope of this study (See Chapter 1). This study sought to compare the implications of phytoliths in reconstructing past environments with those described above.

Occupation	**Vegetation**	**General Climate**	**Proxy**	**Refs**
Pre-SB **SB** **(> 71,000 – 65, 000)**	Evergreen and deciduous forest communities	Warm and moist, a colder phase around 70 kya	Fauna	Glenny, 2006; Val, 2016
HP **(65,000-62,000)**	Mixed - evergreen forest more dominant with *Podocarpus* spp as the dominant tree., riverine vegetation and drier bushveld to a lesser extent because of the presence of *Kirkia* spp. - wooded savannan close to a riparian forest	Warm and moist	Charcoal, seeds, fauna, gypsum	Allott, 2006; Glenny, 2006; Sievers, 2006; Pickering, 2006; Schiegl and Conard, 2006; Wadley, 2008; Clark and Plug, 2008; Hall et al., 2014
Post-HP **(58,000)**	Evergreen, riverine forest taxa with a marked increase in deciduous taxa – mixed forest, riverine, grassland	Warm similar to the HP but drier than the HP. Also the coldest period.	Charcoal, seeds, fauna	Plug, 2004; Cain, 2006; Glenny, 2006; Bruch et al., 2012
Late MSA (48,000)	Mixed - forest/woodland, savanna/grassland, increase of deciduous wood species. Less evergreen forest taxa like *Podocarpus* and more bushveld, more open than the HP	Warm and possibly dry but wetter than the post-HP	Charcoal, carbonised seeds	Allott, 2006; Sievers, 2006; Hall et al., 2014
Final MSA (38,000)	Deciduous and evergreen forest many similar to today. Presence of *Kirkia* spp. indicate dry habitats	Warm similar to today but drier	Charcoal	Allot, 2006

Table 2.0 Summary of broad proxy environmental evidence from Sibudu.

2.3 Occupation and culture at Sibudu Cave

Through these proxies used at Sibudu, the MSA record has contributed to the understanding of the evolution of early human behaviour and provides evidence for advanced cognitive functions with innovations that are thought to mark the emergence of anatomically modern humans in Africa (McBrearty and Brooks, 2000; Wadley, 2015). Occupation at Sibudu is thought to have occurred from > 77 kya ago to 37 kya ago during the MSA (Wadley and Jacobs, 2006; Jacobs et al., 2008a, b). To start with, most of the MSA cultural material at Sibudu is made from stone and shows changes in raw materials through time that define each techno-complex described for Sibudu (Wadley and Jacobs, 2006). Residue analysis on these stone tools revealed traces of ochre on some tools and this has provided evidence for the use of compound adhesives as hafting material to attach stone tools to wooden shafts or bone providing insights into the hunting techniques of early humans (Wadley et al., 2004; Lombard, 2005, 2006a, 2006b; Wadley et al., 2009). Evidence for hunting techniques is also from the use of bone tools during the HP at Sibudu that supports the hypothesis that important technological innovations occurred during the MSA in Africa (Backwell et al., 2008; d'Errico et al., 2012). Grindstones or their fragments found in the ca. 58,000 layers are thought to have been used in the processing of animal products and plants by early humans (Cochrane, 2006).

Perforated shell beads are an important component of the MSA of Africa as evidence for symbolism or personal ornamentation (Henshilwood et al., 2004; d'Errico et al., 2005). At Sibudu, a few perforated marine snail shells used as ornaments have also been described for Still Bay populations (ca. 70,000 years) at Sibudu but this activity seems to disappear in the Howiesons Poort layers. (d'Errico et al., 2008). The presence of ochre at Sibudu is also thought to have been used for symbolism, body paint and for decoration by early humans (Wadley, 2007; Hodgskiss, 2012). The presence of fish bones at Sibudu suggests fish was part of the early human diet during the MSA (Plug, 2006).

Numerous burned seeds of edible fruits at Sibudu also provide information on what the early humans ate (Wadley, 2004, 2006; Sievers, 2006). Evidence for the use of sedges as bedding (between 77 ka and 58 ka) by early humans has been presented by Sievers (2006, 2011); Goldberg et al. (2009) and Wadley et al. (2011). Because of the abundance of burnt sedge nutlets and the presence of sedge phytoliths, it is thought that sedges were harvested as whole plants and the different parts used for different purposes including bedding and food during the MSA (Sievers, 2006; Wadley et al., 2011). It is not clear if sedges were eaten by early humans but what seems clear is that sedge culms were laid on the floor to provide a surface for resting, sleeping or working (Sievers, 2011). It is also suggested that sedge culms were deliberately burnt to maintain their living area and probably to get rid of pests (Goldberg et al., 2009). Construction and maintenance of bedding through burning are behaviours not previously described for the MSA (Goldberg et al., 2009). The 77 ka old layers that had silicified sedge bedding were topped with leaves of the aromatic *Cryptocarya woodii* that are known to be insecticidal, providing the first evidence for bedding and medicinal plants (Wadley et al., 2011). This interpretation has been supported by the identification of the poisonous *Spirostachys africana* in a hearth at Sibudu that is thought to have been used as an insect repellent (Lennox et al., 2015). This has provided evidence that early humans were familiar with edible and medicinal plants (Sievers, 2006; Wadley et al., 2011).

There is evidence for intact hearths at Sibudu represented by numerous lenses of ashy and charcoal-rich units that are not observable at the site (Goldberg et al. 2009). Several hearths are visible in the Sibudu sequence and many more seem to have existed providing evidence for the extensive use of fire during the MSA (Wadley and Jacobs, 2006; Schiegl et al., 2004; Goldberg et al., 2009). Firewood must have been burned at most MSA sites in South Africa although charcoal preservation is poor in many (Wadley, 2015). Sibudu Cave is one of two sites that have provided evidence for firewood during the MSA because of its excellent wood preservation (Allott, 2004, 2005, 2006; Lennox et al., 2005; Wadley, 2015). The charcoal analyses demonstrate that good fuel wood was selected by the early humans and that their selection pattern varied through time in the MSA (Allott, 2006; Lennox et al., 2015).

2.4 Phytoliths as a tool for reconstructing past environments

Phytoliths are microscopic silica ($SiO_2.nH_2O$) particles that are produced when certain living plants absorb silicic acid (H_4SiO_4) from soil through their roots and deposit it as solid silica in plant tissues within their cells, cell walls and between cells (Carter, 1998; Lu and Liu, 2003; Piperno, 2006). They occur in stems, leaves, roots and inflorescences of higher plants and they have diverse and distinctive morphological characteristics (Piperno, 1988; Pearsall, 2000). When the plant decays, is burnt or digested, the organic material decomposes and phytoliths are released directly into the soil, creating an *in situ* record of the vegetation cover because released phytoliths become microfossils of the plants that produced them (Lu and Liu, 2003). The silica grains may be directly entrained into the sediment or transported either by water or air to the site of final deposition (Thorn, 2001). In many plant taxa (monocots, dicots and pteridophytes), these silica accumulations appear in various morphologies which are taxonomically unique in some allowing for for the discrimination of a wide range of taxa sometimes to genus level (Piperno, 1988, 1989). They are produced in many plant families but are more distinctive in a few families such as grasses (Poaceae), sedges (Cyperaceae), Asteraceae, Arecaceae, Marantaceae and some deciduous tress families such as Moraceae and Canabaceae. Grasses are abundant phytolith producers and their phytolith morphological variability and distinctiveness allows, to some extent, for identification of grasses to their subfamiliy level making phytoliths a reliable proxy tools for characterizing C_3 and C_4 grasses in fossil assemblages (Pearsall, 2000; Singh et al., 2007).

Of similar phytolith abundance are the sedges (Cyperaceae) which produce a phytolith morphotype that identifies sedges as a family with genera producing genus-specific phytoliths (Piperno, 1989; Ollendorf, 1992). Phytoliths also discriminate between forests (C_3 plants) and grasslands (C_3/C_4 grasses) in sediments (Piperno, 2006). Although phytoliths from C_3 trees and C_3 herbs are similar, according to Piperno (2006), there are taxa that are major indicators for both mature forest and successional herbaceous plant associations that make diagnostic phytoliths and would aid in identification of a particular vegetation type e.g. members of the Annonaceae, Arecaceae, Burseraceae, Chrysobalanceae, Magnoliaceae, Bambusoideae and many other plants that occur in older tropical forests. Phytoliths were initially used because of their diagnostic potential in plant taxonomy (e.g. Metcalfe, 1971; Palmer and Tucker, 1981) but attention was later given to their application in archaeological and palaeoecological studies (Piperno, 1985a, 1989).

Since its first application as a tool of environmental reconstruction in the 1970s and 1980s (e.g. Rovner, 1971; 1983; Pearsall, 1978; 1984; Piperno, 1985b; 1988), phytolith analysis has become increasingly important and widely used in the field of archaeology (e.g. Bowdery, 1998; Albert et al., 1999; Pearsall, 2000; Elbaum and Weiner, 2003; Albert and Bamford, 2012; Mercader et al., 2013) and palaeoecology (Alexandre et al., 1997; 1999; Barboni et al., 1999; Lejju, 2009; Mercader et al., 2000; Albert et al., 2006). Earlier archaeological studies e.g. Pearsall (1978), Pearsall and Trimble (1984), Piperno, (1985) successfully applied phytoliths to identify the presence of cultivated crops that contributed to understanding early plant domestication practices. In recent years, the application of phytoliths has enhanced recovery of data pertaining to human and plant relationships (e.g. Mbida, 2000; Mercader, 2000; Pearsall, 2000; Schiegl et al., 2004; Cabanes et al., 2010). Phytoliths have enabled the identification of the remains of plants, such as bananas, in sedimentary records that would otherwise not have been possible using pollen. Phytolith analysis thus offers additional information where the preservation of biological material is otherwise poor, and enables the reconstruction of vegetation history, for instance, in areas where arid and humid grass associations cannot be discriminated through pollen alone. For instance, it is possible to discriminate between forest (C_3 plants) and grasslands (C_3/C_4 grasses) in a sediment-based phytolith record (Alexandre et al., 1997; Barboni et al., 1999). Among the C_4 grasses, phytoliths can also be used to distinguish between members of the subfamily Chloridoideae (short grasses), which are adapted to warm and dry environments, members of the subfamily Panicoideae, which are adapted to warm and wet environments and members of the Pooideae (C_3 grasses), which are adapted to cool temperate and high altitude environments (Twiss, 1992; Alexandre et al., 1997; Pearsall, 2000; Barboni and Bremond, 2009).

Other than their role in reconstructing palaeovegetation and palaeoclimate, phytoliths play an important role in archaeological reconstruction because they can provide answers such as the availability and economic usage of wild plants and the characteristics of near-site landscapes and how cultures modified them (Piperno, 2006). This is so because the different structures of the plant body in a single phytolith-producing species will often contribute different types of phytoliths. The phytoliths record is therefore sensitive to the selective use of different portions of plants (Piperno, 2006). An example of application is presented in Cabanes et al. (2010) where plant preference by Neanderthals was deciphered from the phytolith record. In addition to phytoliths from sediments at prehistoric cultural occupations, phytoltihs from stone tools, dental remains and ceramics provide potential for stone tool function, diet as well as agricultural subsistence (Piperno, 2006; Henry et al., 2012). Dark-coloured or opaque phytoliths are related to high quantities of organic carbon occluded within or coating the surface and these are commonly produced when a plant is burned and can be an indication of vegetation fires (Thorn, 2004). Generally, Saddles are characteristic of light-loving grasses favouring open and arid habitats while Bilobates are characteristic of moisture-loving grasses favouring shade and/or mesic to hydric habitats and Trapeziform sinuate short cells are typical of high-elevation grasses of the Pooideae subfamily (Barboni and Bremond, 2009; Barboni et al., 2010).

2.4.1 Advantages of using phytoliths as a proxy and their limitations

Phytoliths are produced in many plant families but are distinctive and abundant in grasses and as mentioned this makes them useful proxies to differentiate between forest and grassland, a similar function of pollen. However, although grass pollen is produced in abundance and is well preserved in Africa, pollen from grasses is too morphologically similar to permit identification below the family level, (Livingstone and Clayton, 1980; Alexandre et al., 1997). This means that pollen can only indicate presence of the family Poaceae (grasses) but does not distinguish C_3 grasses versus C_4 grasses (Alexandre et al., 1997; Bremond et al., 2008) and this limits the reconstruction of tropical vegetation history. Therefore, although other proxies (such as pollen and carbon isotopes) can be used to infer past environments, none of these proxies are able to discriminate between C_3 and C_4 grasses in vegetation or trace grassland dynamics (Bremond et al., 2004). More so, carbon isotopes values can identify C_3 and C_4 vegetation but they do not discriminate between C_3 woody and C_3 grass species (Piperno, 2006).

Several studies suggest that phytoliths have an advantage over pollen because they are well preserved even in highly oxidizing environmental conditions and therefore resist decay unlike pollen (e.g. Bremond, et al., 2004; Barboni et al., 2010). According to Piperno (2006), chronological depth is great with phytoliths because they are stable through time in most sedimentary environments and this allows for detailed intra-site contrasts and different site comparisons of regional sequences are possible. This case is illustrated at Sibudu where the pollen record is poor throughout the record (Renaut and Bamford, 2006). Phytoliths also have an advantage over pollen in identifying agricultural crops as some of them are known to produce little or no pollen e.g. banana and those which do, produce a type very similar to that of non-domesticated plants e.g. cultivated grasses like maize and rice cannot be distinguished from native grasses using pollen (Piperno, 2006; Ball et al., 2016; Piperno et al., 2017). Also, phytoliths have an advantage over pollen in that they continue to be produced by plants that stop flowering because of stress following a cooling change of climate, (Carter, 1998). This means that unlike pollen, they would still be detected in sediment therefore providing a signal of past environmental conditions.

Despite the above advantages, phytoliths have limitations in reconstructing past environments e.g. only a limited number of taxa are reported to be capable of producing distinctive phytolith types (Piperno, 1988; Pearsall, 2000). More so, the interpretation of some of these distinctive phytoliths is still a problem (Runge, 1999). This is because the same plant species can produce different types/shapes of phytoliths (i.e. multiplicity) and many different species can produce the same phytolith types/shapes (i.e. redundancy) (Rovner, 1971), a problem that is constantly trying to be solved by researchers. This makes it difficult in some cases to assign a particular phytolith type to a particular species or plant taxon (Singh et al., 2007). For instance, in grasses, small amounts of Saddle (occurring in Chloridoideae, C_4), Cross and Bilobate (occurring in Panicoideae, C_3/C_4) short cell phytoliths can be produced by some species of Pooideae (C_3) and Arundinoideae (C_3) grasses in the Afro-alpine zone (Bremond et al., 2008). More so, some widespread Chloridoideae species (C_4) were found to have Rondel and Trapeziform phytolith types (occurring in Pooideae, C_3) and do not have the typical Saddle shapes and it is because of this redundancy that Rondel phytolith types in tropical East Africa may be interpreted as Pooideae and Chloridoid phytoliths (Bamford et al., 2006; Barboni and Bremond, 2009).

In addition to Rondels, Pyramidal and Trapeziform short cells (originally known to occur in C_3 Pooideae grasses as well) are redundant to some C_4 – xerophytic grasses of the Chloridoideae subfamily and some C_3 – high elevation grasses of the Pooideae and Danthonioideae subfamilies (Barboni and Bremond, 2009). Therefore there are difficulties that arise in attempting to quantify palaeoenvironments using phytoliths assemblages preserved in sediments since they do not always reflect the original plant communities precisely (Lu et al., 2007). According to Piperno (2006), not all individual kinds of short cell phytoliths present in a sediment assemblage can be assigned to a subfamily or below because of redundancy and proportions of different types of silica bodies may be needed in the reconstruction of grassland composition in order to confidently assume a particular subfamily. Barboni and Bremond (2009) describe the need for a combination of varying proportions of several phytoliths to confidently assume a particular subfamily and this shades some light to ease interpretation despite such redundancies. Pollen unlike phytoliths is more certainly linked to particular plants.

More so, some plant taxa produce few or no phytoliths at all (Pearsall, 2000) as shown by some Afromontane woody taxa leading to over-representation of grasses versus woody trees and shrubs phytoliths (Huang et al., 2005; Barboni et al., 2007; Bremond et al., 2008). This is confirmed by a more recent study at high altitude in which woody taxa are not well represented (Murungi, 2013). This means that for plants that do not accumulate phytoliths, their presence in the phytolith assemblages is not detectable. Finally, phytoliths morphologies generally do not facilitate aerial transportation and are normally deposited in sites close to the parent plant (Wallis, 2001; Pearsall, 2000). Therefore, unlike pollen, which is more likely to be blown in from distant sources, phytoliths may not be a good indicator of regional vegetation but are a good indicator of local vegetation. According to Wallis (2001), wind transport of phytoliths is known to be favoured by fire which serves to release phytoliths directly into the atmosphere and thereby enabling their lateral movement.

2.5 Phytolith research in Africa: a short history

Since their first appearance on the scholarly scene in the early 19th century Europe, phytoliths gained considerable attention from soil scientists, ecologists, agronomists and botanists primarily from the United States, United Kingdom and Australia in the 20th century in the late 1950s to the 1970s (Piperno, 2006). Several studies mostly anatomical analysed phytolith morphology in modern monocots especially grasses (e.g. Metcalfe, 1960, 1971; Blackman, 1968; Blackman and Parry, 1968; Twiss et al., 1969; Geis, 1978). It was Twiss et al. (1969) that developed the first grass phytolith classification system to discriminate among three grass subfamilies (i.e. Panicoideae, Pooideae and Chloridoideae), a classification that is still used today although with modification following several refinements in understanding phytolith production in grasses.

Studies also begun on deciduous trees and other dicotyledons e.g. Geis (1973); Klein and Geis (1978); Metcalfe and Chalk (1979). This was also a period of interest in using phytoliths as a tool to reconstruct vegetation history. A study by Rovner (1971) brought exposure to the significance of the use of phytoliths from living plants and soils in palaeoecological research. Several other studies on phytoliths in soils and living plants from the USA and South America were conducted during this period (Baker, 1959; Wilding, 1967; Wilding and Drees, 1971; Pearsall, 1978; Piperno, 1979). The 80s and 90s saw a major increase in phytolith research especially in America involving analysis in living plants and buried soils (e.g. Lewis, 1981; Mulholland, 1982; Piperno, 1984; Fredlund, 1986; Bozarth, 1986, 1987, 1990, 1992) and the spread to other parts of the world notably Asia, South America and the Middle East (e.g. Piperno, 1984; 1985a,b; Rosen, 1992; Kaplan et al., 1992; Piperno, 1994; 1995; Madella, 1995; Piperno and Becker, 1996; Kealhofer and Piperno, 1998) and numerous publications from around the world have since emerged in the 21st century.

Available literature suggests that concrete phytolith studies that involve phytolith extraction from plants and soils following standard procedures begun in the mid-1990s in Africa (J. Runge and Runge (1995); McLean (1995); Alexandre et al. (1997); Polcyn et al. (1997); F. Runge and Runge (1998); Runge (1999); Vrydaghs and Doutrelepont (2000) and several studies have since been conducted. Prior to that, anatomical studies of living East African grasses by Stewart (1965) and Palmer and colleagues (Palmer 1976; Palmer and Tucker, 1981, 1983; Palmer et al., 1985; Palmer and Gerbeth-Jones, 1988) were the early works of phytolith research in Africa that produced SEM images of grass short cells. The application of phytoliths to palaeoecological research in Africa started with grass cuticle anatomical studies by Palmer (1976) and phytoliths studies by J. Runge and Runge (1995); Runge (1995); McLean (1995); Alexandre et al. (1997) and Polcyn et al. (1997). In West Africa - where phytoliths studies have often been conducted on samples from more than one country at a time by the authors - phytoliths from modern plants to improve phytolith systematics and identification of palaeoecological phytolith records have been studied by Fahmy (2008); Eichhorn et al. (2010); Novello and Barboni (2015); Neumann et al. (2017) and Collura and Neumann (2017). Phytoliths in modern soils have also been studied to study their potential to determine plant physiognomy and use of phytolith indices as proxies of short versus tall-grass dominance, grass evapotranspiration and tree cover density (Bremond et al., 2005a, b) and palaeoenvironmental reconstructions (Polcyn et al., 1997; Neumann et al., 2009). Banana phytoliths from sites in Cameroon have led to critical discussion of agricultural evolution theories with the evidence of the first edible banana cultivation in Africa dated to ca. 2500 yr BP that predates the time they were known to have been introduced to Africa from Asia (Mbida et al., 2000, 2001).

Major phytolith studies in Africa started in Central Africa specifically the Congo and Central African Republic and involved study of modern soils and sediment profiles, modern plants and use of phytoliths for palaeoenvironmental reconstructions (Runge, 1995; J. Runge and Runge, 1995; Alexander et al., Runge, 1999; Mercader et al., 2000). Runge (1999) a phytolith inventory of soils in Central Africa and that was a major reference for phytoliths produced in monocot and dicot plants in Africa. Recent studies in Chad have also contributed to the modern reference collection of Africa grasses and sedges together with modern soil analogues (Novello et al., 2012; Novello and Barboni, 2015) as well one of few phytolith-based Miocene-Pliocene palaeoenvironmental reconstructions in Africa (Novello et al., 2015).

Other than the aforementioned SEM studies of East African grasses, available literature suggests that concrete phytolith studies in Eastern Africa begun in the late 1990s with paleoenvironmental reconstructions by Mworia-Maitima (1997) and Barboni et al. (1999) in Ethiopia. Several phytoliths studies have been conducted have been at Olduvai Gorge in Tanzania to understand the palaeoenvironments including vegetation that early hominins evolved in during the Plio-Pleistocene times (Albert et al., 2006; Bamford et al., 2006; Albert et al., 2009; Barboni et al., 2010; Rossouw and Scott, 2011; Albert and Bamford, 2012). Only two phytoliths studies have been conducted in Uganda to date (Lejju et al., 2003, 2005; Lejju, 2009; Murungi, 2013; Murungi et al., 2017). Phytoliths from modern soils in mountains in Kenya and Tanzania have provided evidence for the potential of grass indices to reconstruct past environments at high altitudes (Bremond et al., 2008). A few studies have extracted phytoliths from modern plants to improve palaeoenvironmental reconstructions in East Africa (Bamford et al., 2006; Albert et al., 2009; Murungi et al., 2017).

In Southern Africa, few phytolith studies generally exist for this vast region. Phytoliths have been applied to palaeoenvironmental reconstructions to understand Late Miocene/Early Pliocene, Pliestocene and Holocene environments (e.g. McLean and Scott, 1999; Grab et al., 2005; Scott and Rossouw, 2005; Rossouw et al., 2009; Parker et al., 2011), though several of them are stated as preliminary studies. They have also been applied in archaeology to understand early human-plant interactions at some MSA archaeological sites in the region (e.g. Schiegl et al., 2004; Albert and Marean, 2012; Mercader et al., 2013; Esteban, 2016). Phytoliths have also been used to study the diet of a recently discovered early hominid (Bamford et al., 2010; Henry et al., 2012). To improve phytolith identification from fossil sediments for palaeoenvironmental reconstruction, phytoliths from living plants have been studied by Rossouw (2009), Mercader et al. (2009, 2010), Cordova and Scott (2010) and recently Esteban (2016). Phytoliths from modern soils have also been studied by Cordova (2013), Esteban, (2016) and Esteban et al., (2017). Of these Southern Africa phytolith studies, those from South Africa are: McLean and Scott (1999), Schiegl et al. (2004), Scott and Rossouw (2005), Rossouw et al. (2009), Rossouw (2009), Cordova and Scott (2010), Bamford et al., 2010; Henry et al. (2012), Albert and Marean (2012), Cordova (2013), Esteban (2016) and Esteban et al. (2017).

Despite the wealth of archaeological sites in South Africa, archaeologists have clearly rarely enlisted the expertise of archaeobotanists and paleobotanists to study past vegetation. It is for this reason that few palaeovegetation reconstructions exist for South African archaeological sites that involve analysis of botanical remains (Wadley, 2015) a trend that is set to change as some sites such as Sibudu Cave, Diepkloof Rock shelter and Pinnacle Point Caves are setting the trend (Allot, 2004, 2005, 2006; Sievers, 2006, 2011, 2013; Renault and Bamford, 2006; Albert and Marean, 2012; Cartwright, 2013; Lennox et al., 2015; Esteban, 2016; Esteban et al., 2017).

2.6 Cyperaceae (sedges) phytoliths in this study: a brief background

Sedges are given special mention in this study because they were of major importance to early humans during the MSA at Sibudu (Sievers, 2006, 2011; 2013; Wadley et al., 2011). Sedges are of major economic and ecological importance and to date they are a source of income to rural communities in KwaZulu Natal (Gordon-Gray, 1995; Van Wyk and Gericke, 2000). Phytolith analysis is a valuable tool for their identification in the archaeological record (Chevalier, 2008; Iriarte et al., 2010). It was important to confidently discriminate between woody taxa phytoliths and sedges in the archaeological record and several sedge specimens were studied to this effect. Sedges are excellent phytolith producers producing phytolith types that are diagnostic to the family and in some genera, genus-specific bodies occur making them identifiable in the archaeological record as a family and as a genus (Piperno, 1989; Ollendorf, 1992).

Because most sedge phytolith studies have focused on the conventional identification of the classic cone/hat-shaped and/or achene phytoliths that are diagnostic of sedges (Mehra and Sharma, 1965; Metcalfe, 1971; Piperno, 1988, 1989; Ollendorf et al., 1987; Ollendorf, 1992), it was necessary to study the other important morphotypes produced by sedges that may be an important component of the archaeological record at Sibudu. This is because some recent studies have mentioned other phytoliths morphotypes found in sedges such as blocky parallelepiped morphotypes that are sometimes more dominant than the classic cone-shaped sedge phytoliths (Fernádez Honaine et al., 2009; Novello et al., 2012). These blocky phytolith morphotypes are often associated with woody species (e.g. Albert et al., 1999; Albert et al., 2003; Bamford et al., 2006) and they can occur in grasses and monocots (Novello et al., 2012; Collura and Neumann, 2016). Novello and colleagues found that a sedge species was identified by blocky parallelepiped morphotypes rather than the typical cones/hat-shaped phytoliths. The abundance of blocky phytolith morphotypes that were found in the MSA Sibudu sediments in this study led to the analysis of phytoliths from various sedge genera so as to identify phyoliths in sedges in specific terms beyond the classic cone/hatshape morphotype to make a more accurate attribution of the blocky morphotypes to sedges and/or to the woody species that are also noted as abundant from the charcoal and seed studies studies at Sibudu (Allott, 2005; 2006; Sievers, 2006; 2013; Lennox et al., 2015). Moreover, the classic cone-shaped phytoliths are reported not to preserve well in soils (Carnelli, 2002; Iriarte and Paz, 2009; Novello et al., 2012) and it is therefore necessary to determine other morphotypes of sedges that may contribute to the archaeological record.

Lastly it was hoped that this study can demonstrate the extent to which phytoliths from different genera can aid in sedge taxonomic classification. Some sedge fruit phytoliths (achene phytoliths) have been shown to be specific to species of the genera *Carex*, *Cyperus* and *Scirpus* (Piperno, 1989; Iriarte and Paz, 2009; Iriarte et al., 2010). Because sedges are morphologically diverse, classification to generic level was referred to as largely problematic (Metcalfe, 1971; Standley, 1990). Despite the many anatomical and DNA studies to improve sedge classification since then especially in South Africa (Gordon-Gray, 1995; Browning and Gordon-Gray 2011; Muasya et al., 2012), classification still remains problematic and species are constantly being moved from one genus to another with several species now representing segregate genera and major improvements continue to date (Gordon-Gray, 1995; Browning and Gordon-Gray, 2011; Muasya et al., 2009, 2012; Larridon et al., 2014; Global *Carex* Group, 2015).

Despite the archaeological, palaeobotanical and taxonomic importance of sedge phytoliths, few studies have set out to describe phytoliths from sedges as individual morphotypes in their entirety (i.e. Bamford et al., 2006; Fernádez Honaine et al., 2009; Novello et al., 2012) and they studied all major morphotypes found in the sedges analysed and not just the classic cone shaped phytoliths. It is against this background that 33 specimens of sedges (Table **4.1** in Chapter Four, Methods) were analysed for their major phytolith morphotypes to create a detailed modern phytolith reference for South Africa and Africa. Details of their morphotypes, their characteristics and microphotographs are presented in Chapters Four and Five.

CHAPTER THREE

PRESENT-DAY SIBUDU CAVE: SITE DESCRIPTION

3.0 SIBUDU CAVE: PRESENT-DAY

3.1. Geographical location

Sibudu cave is found in the north-eastern part of KwaZulu Natal province and is located 40 km north of Durban and about 15 km inland from the Indian Ocean (Wadley and Jacobs, 2006; Fig. **3.1**). Other Middle Stone Age sites in Sibudu's vicinity are Holley Shelter that is 60 km west of Sibudu, Shongweni and Umhlatuzana about 90 km south-west of Sibudu (Fig. **3.1**) and Border Cave 300 km to the north-east of Sibudu (Fig. **3.2**) (Wadley and Jacobs, 2006; Jacobs et al., 2008b). Today, Sibudu Cave is formed by a forested cliff overlooking the Thongati River (Fig. **3.4A**) and is boarded by sugar plantations that extend right to the edge of the cliff above the cave (Wadley, 2001; Wadley and Jacobs, 2004). Although often referred to as a cave, the site is in essence a rock shelter that is 55 m long and about 18 m wide (Wadley, 2001; Wadley & Jacobs, 2006; Fig. **3.4B**).

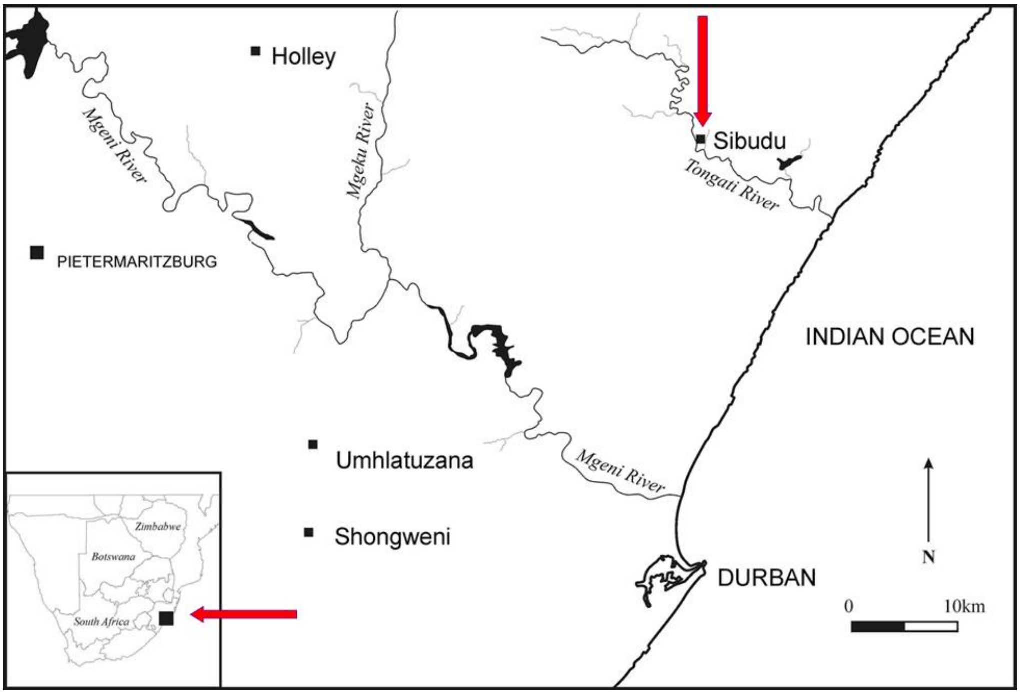


Figure 3.1 Location of Sibudu Cave above the Thongati River, 40 km north of Durban city and the three archaeological sites in the same province that is; Shongweni, Umhlatuzana and Holley Shelters. (Map by Wadley, 2001; Wadley & Jacobs, 2004).

3.1.1 Geology

The rock shelter is hosted in the sandstones of the Natal Group which are ca. 490 Ma and are mainly made of a thick sequence of sediments deposited on the stable platform from the erosion of the mainly granitic rocks (Pickering, 2006). At Sibudu, the sandstone is purple-red and consists of reddish quartz and feldspar-rich medium sand and some silt with some clay between the grains (Pickering, 2006). Sibudu cave is therefore a sandstone rock shelter that was formed by river erosion of the Natal Group sandstone when the river lowered its channel and eroded through the sandstone and shale cliff (Wadley and Jacobs, 2004, 2006; Seivers, 2006). The geology of the area has an influence on the lithic assemblage at the site and whereas there is evidence for the occasional use of sandstone to make tools, most tools at Sibudu are made of another finer grained rock than the one from the shelter wall (Wadley and Jacobs, 2006). A dolerite formation in the sandstone cliff a few hundred metres away from the shelter is thought to be the source of some of the dolerite that was used for knapping throughout the MSA (Wadley and Jacobs, 2006). Dolerite cobles, rare hornfels, quartzite and quartz also occur along the Tongati River below the shelter (Wadley and Jacobs, 2006).

3.1.2 Local climatic conditions

Firstly, it is important to mention that South Africa today is divided into three general climatic zones based on annual rainfall i.e. the summer rainfall region, the winter rainfall region and the all year-round rainfall region (Tadross and Johnston, 2012; Hall et al., 2014). 1) The summer rainfall season areas are; the eastern part of the country where annual rainfall is 500 mm and above as well as the central part and parts of the western area which are semi-arid to arid with late summer rain that varies from 500 mm to less than 100 mm; 2) the winter rainfall area is the cape fold mountains and the area between them and the sea in the west of the country; 3) and lastly the area with rainfall throughout the year in the more south-eastern parts of the country that ranges from 300 mm to more than 900 mm (Tadross and Johnston, 2012). See Figure **1.0** in Chapter 1 for an illustration of the three rainfall zones of South Africa. Using Figure **3.2** below, these three regions can be illustrated by the biomes of South Africa: the winter rainfall region is mainly represented by the relatively moist Fynbos biome in the west, the south-western and southern parts of the country, the drier Succulent Karoo biome in the west and the tip of the southern part of the Namib desert that covers a small area in South Africa while the summer rainfall region in the eastern and central interior is represented in the by the mostly summer rainfall Nama-Karoo biome, the Savanna biome in the north and east, the Grassland biome and the Gariep desert (Cowling et al. 1997; Rutherford et al., 2000; Rutherford et al., 2006; Neumann and Bamford, 2015). The south-eastern part of the country where rain falls at any time of the year is the area within the Fynbos biome for example where Klasies River is located in Figure **3.2** (Hall et al., 2014). These biomes are climatically distinct (Rutherford et al., 1997).

Sibudu Cave falls within the summer rainfall region and the present day climate of the Sibudu area receives an average summer rainfall of about 750 mm and an average winter rainfall of about 250 mm; with humid and hot summers that have mean January (mid-summer) temperatures of 22-25^{o}C and mean July (mid-winter) temperatures of 17-20^{o} C (Wadley, 2001; Wadley and Jacobs, 2004). The area is therefore one of high summer temperature and rainfall (minimum temperature 23^{o}C and maximum 33°C with about 1000 mm per annum) and mild winters (minimum temperature 16^{o}C and maximum 25°C) (Bruch et al., 2012). The high summer precipitation is due to the southward expansion of the easterly winds which carry moisture from the Indian Ocean on to the mainland while warm winters are caused the Warm Agulhas Current that transports heat from the ocean (Bruch at al. 2012).

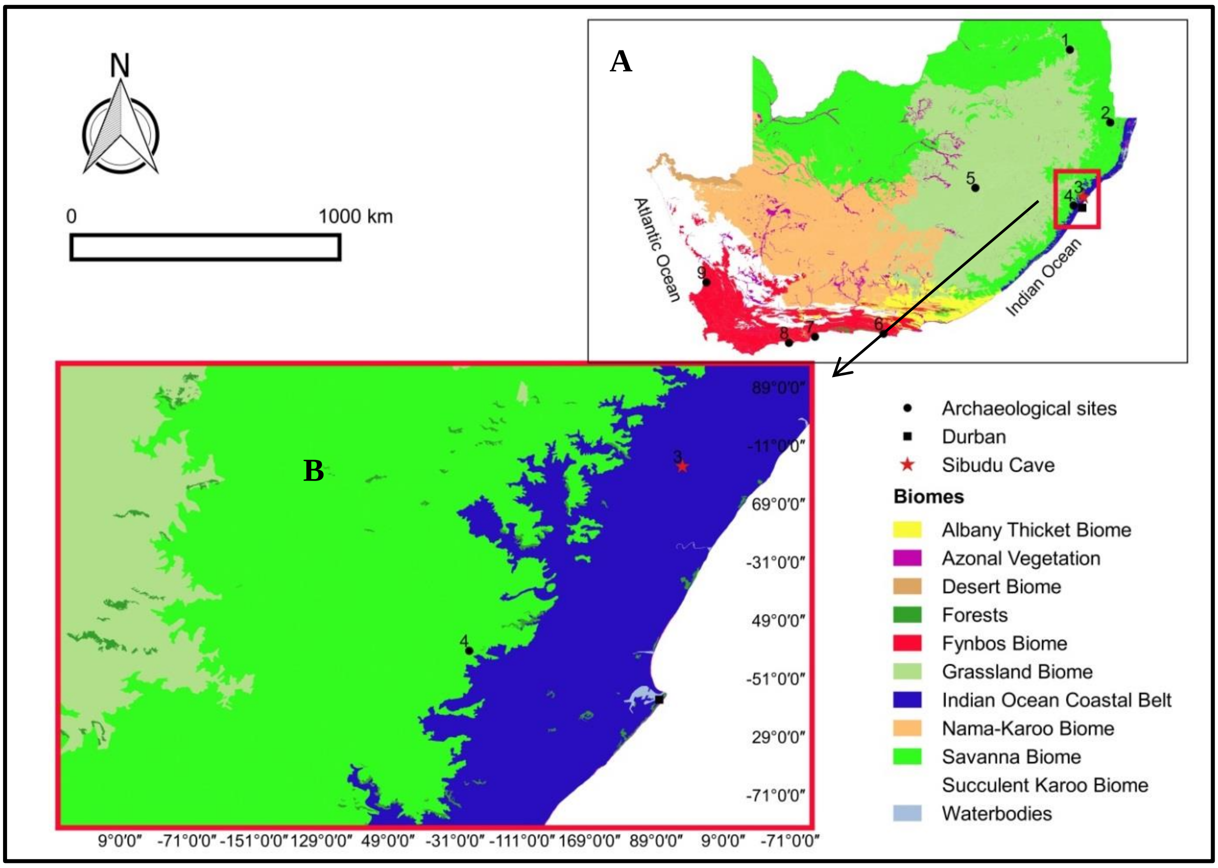


Figure 3.2 Vegetation map of South Africa showing the 8 biomes of Mucina and Rutherford (2006) and the location of Sibudu Cave and the archaeological sites mentioned in the text: 1) Bushman Rock Shelter, 2) Border Cave, 3) Sibudu Cave, 4) Umhlatazana, 5) Rose Cottage, 6) Klasies River Mouth, 7) Pinnacle Point, 8) Blombos Cave and 9) Diepkloof Cave.

3.1.3 Local vegetation

The varying climates of South Africa play a key role in determining the composition of South Africa’s flora (Rutherford et al., 2000). As aforementioned, South Africa has five spatially dominant biomes (Fynbos, Succulent Karoo, Nama-Karoo, Savanna and Grassland) and three biomes with a small geographic extent that is the Desert, Forest and Albany Thicket biomes (Rutherford et al., 2000; Rutherford et al., 2006). The biomes are defined on the basis of the most dominant plant life form and are climatically distinct (Rutherford, 1997). Sibudu cave falls within the Indian Ocean Coastal Belt bioregion a region that stretches from the east coast of South Africa near Port Elizabeth through Mozambique to East Africa and lies specifically in the Tongaland-Pondoland phytogeographical region that stretches along the east coast of South Africa from the mouth of the Limpopo River in Mozambique to Port Elizabeth in the south (Cowling and Hilton-Taylor, 1997; Wadley and Jacobs, 2004; Fig. **3.2**). The Tongaland-Pondoland Region is a subtropical regional vegetation mosaic consisting of subtropical forests, thicket, savanna and grassland (Cowling and Hilton-Taylor, 1997; Fig. **3.2**). Because its forest extent covers a very small, the Tongaland-Pondoland Region is included in the Savanna biome (Cowling and Hilton-Taylor, 1997; Rutherford et al., 1997). Therefore, this part of the greater Indian Ocean Coastal Belt that lies in South Africa is part of the Savanna biome. Its subtropical forests consist of five main types of forest described as; undifferentiated lowland forest, sand forest, dune forest, swamp forest and fringing forest by (Moll and White, 1978; White, 1983).

This forest vegetation is defined as the KwaZulu Natal Coastal Belt that is a part of the Indian Ocean Coastal Belt bioregion and together with the Cape Coastal forest form the KwaZulu-Cape Coastal forest mosaic ecoregion in the eastern and southern parts of the country (Fig. **3.2**) (Mucina and Rutherford, 2006; Olson et al., 2001). These forest patches are categorised in the subtropical Coastal Forest biome (referred to as Tropical and subtropical Moist Broadleaf Forests by Olson et al. (2001)) and represent the southernmost limit of the coastal forests of East Africa and are recognised as forming part of the Forest biome of South Africa, a biome that is made of up of scattered forests as islands along the eastern and southern margins of South Africa within larger biomes such as the Fynbos, Albany Thicket, Grassland and Savanna (Fig. **3.2** and clearly illustrated in Fig. **3.2B** for the eastern margin) (Mucina et al., 2006). Because of this, the transition between forests and adjacent biomes is abrupt (Neumann and Bamford, 2015).

The Sibudu area generally falls within the undifferentiated lowland forest on the border of Coastal and Riverine Ecozones (Wadley, 2001; Wadley and Jacobs, 2004) that is referred to as Coastal Forest by Acocks (1988) and Riverine Ecozone by Grant and Thomas (1998). Sibudu is therefore within the Forest biome. The forest at Sibudu is generally evergreen with proportions of deciduous and semi-deciduous species occurring particularly on the forest margins (Wadley, 2004; Wadley and Jacobs, 2006) and it develops from just above sea level to about 300 m a.s.l where rainfall is usually greater than 700 mm and temperatures are not extreme (Wadley and Jacobs, 2004). The existing original vegetation is a remnant of the original more extensive forest and the cave site today is partially hidden by the remnant forest on the steep slope (Wadley and Jacobs, 2004, 2006).

Local flora at Sibudu has been described by Wadley (2001) and Wadley and Jacobs (2004). They report that the forest has a diversity of taxa including canopy species such as: *Celtis africana* (Celtidaceae), *Celtis mildbraedii* (Celtidaceae), *Millettia grandis* (Fabaceae), *Albizia adianthifolia* (Fabaceae), *Harpephyllum caffrum* (Anacardiaceae), *Ficus lutea* (Moraceae), *Ficus natalensis* (Moraceae), *Ficus sur* (Moraceae), *Ficus ingens* (Moraceae), *Croton sylvaticus* (Euphorbiaceae), *Vepris lanceolata* (Rutaceae), *Zanthoxylum davyi* (Rutaceae), *Calodendrum capense* (Rutaceae); sub-canopy species such as *Teclea gerrardii* (Rutaceae), *Rawsonia lucida* (Achariaceae), *Diospyros natalensis* (Ebenaceae), *Cryptocarya woodii* (Lauraceae), *Ochna natalitia* (Ochnaceae), *Sideroxylon inerme* (Sapotaceae); forest margin species such as *Clerodendrum glabrum* (Lamiaceae), *Dichrostachys cinerea* (Fabaceae), *Rhus chirindensis* (Anacardiaceae), *Rhus gueinzii* (Anacardiaceae), *Crotalaria pallida* (Fabaceae), *Vangueria randii* (Rubiaceae) and woody lianas and climbers such as *Asparagus* spp., *Capparis tomentosa* (Capparaceae), *Cissus fragilis* (Vitaceae), *Rhoicissus digitata* (Vitaceae), *Rhoicissus tomentosa* (Vitaceae), *Dalbergia armata* (Fabaceae) and *Dalbergia obovata* (Fabaceae). Many of these were observed during fieldwork in April 2014 at the shelter and several were selected for phytolith analysis.

3.1.4 Human activities

Agricultural activities have influenced the current vegetation at Sibudu (Wadley, 2001; Wadley and Jacobs, 2004). The existing forest at Sibudu is a mere remnant as extensive deforestation to plant sugarcane has reduced the original forest and sugarcane plantations extend up to the edge of the cliff above the cave with the remaining forest spared because the rugged steep cliff on which it stands is not useful to farmers (Wadley, 2001; Wadley and Jacobs, 2004). However, this remnant forest is also under threat from encroaching exotic species, harvesting for firewood, stripping of tree bark for traditional medicine and illegal sand miners (Wadley, 2001; Wadley and Jacobs, 2004). Forest patches in KwaZulu Natal are indeed reported to be critically endangered because of agricultural practices, building damns, excessive water use for irrigation as well as local exploitation for forest products (Mucina et al., 2006).

3.2 MSA Sediments at Sibudu: stratigraphy and age chronology

The deposits at Sibudu are excavated in four separate 50 cm quadrants within a one metre square each i.e. squares A, B, C, D, E (Fig. **3.4B**) (Wadley, 2001; Wadley and Jacobs, 2006). There is a permanent datum line painted on the wall of the cave and depth of each excavation layer is measured from the datum line (Fig. **3.5**). Sediment deposits at Sibudu are predominantly anthropogenic and are made of material such as ash, abundant charcoal and bone and provide evidence for human settlement (Pickering, 2006; Goldberg et al., 2009). Ash is a major component of Sibudu sediments and in parts of the shelter hearths are built up on top of each other (Wadley and Jacobs, 2006). A mineralogical analysis of the sediments surrounding the hearths indicated ash as the major component of MSA layers at Sibudu (Schiegl et al., 2004). The mineralogical study suggests that phytoliths are an important component of the sediments and that the phytoliths and mineralogical composition of the ash deposits in the hearths are similar to those in the surrounding sediments (Schiegl et al., 2004). This provided evidence for the extent to which burning was conducted at the site with fire places destroyed after use and therefore numerous hearths that are not visible may occur at the site (Schiegl et al., 2004; Schiegl and Conard, 2006). Therefore, remnants of hearths and plant ash deposits form a considerable part of the MSA sediments (Shiegl and Conard, 2006). Because of this, mineralogical compounds such as calcium carbonate, apatite and gypsum occur in the sediments (Schiegl and Conard, 2006). At Sibudu, MSA occupation sediment layers lie directly below the Iron Age layers and therefore no Later Stone Age remains are present at the site and several hiatuses occur within the MSA layers (Wadley and Jacobs, 2006).

a) Stratigraphy

The site is excavated by natural stratigraphy and the Sibudu stratigraphy is complex but generally clear with thin coloured layers that have palimpsests of hearths and ash lenses occurring in them (Wadley, 2001; Schiegl et al., 2004; Wadley and Jacobs, 2006; Pickering, 2006) (Figure **3.3**). All the older layers have clear and conventional colours compared to the younger layers that are more complex with numerous ashy layers that have various colours (Wadley and Jacobs, 2006; Pickering, 2006). The layers at Sibudu have therefore been named according to the most conspicuous colour of the predominant matrix and sometimes they do not take into account the mottling observed in the younger layers (less than 60,000 yrs)

(Wadley and Jacobs, 2006). Stratigraphy of the differently walls at Sibudu that had so far been excavated at the time divided into a northern and eastern stratigraphy are described in detail in Wadley (2001) and Wadley and Jacobs (2004, 2006) with the name and abbreviations assigned to each layer as in Figure **3.5**. However, in summary; in the layers older than 60,000 ka, the names are simple and refer to the predominant colour of a clearly outstanding sediment matrix, for example the pre-SB layer LBG is an abbreviation for Light Brownish-grey (Wadley and Jacobs, 2006). Where the layers were deeper than about 10 cm, they were split, for example LBG, LBG2, LBG3 and LBG4 at the botton of the profile (Fig. **3.5**; Wadley and Jacobs, 2006).

Naming the layers in the younger layers was more complicated because of the mottling that created several colours and depict this ‘mottled deposits’ the abbreviation MOD was used and then OMOD, GMOD and BMOD were used to indicate that the mottled deposits have more orange, grey or brown matrix in them respectively (Wadley and Jacobs, 2006). In some layers, they do not only use the colour to denote the layers but also the chemical composition. For example, layers that are appended with Sp such as RSp, YSp and BSp refer to the speckling of white gypsum within a matrix that is reddish, yellow or brown respectively (Wadley and Jacobs, 2006). Table **3.1** shows an example of this kind of stratigraphy for the south profile of the C4 square from which phytolith samples were taken. The younger layers (from ~60,000 ka) have bright unusual colours that are thought to be a result of burning events of plant material but the presence of gypsum and small quantities of iron and manganese in the deposits may have influenced their colouration (Wadley and Jacobs, 2006). The contact between the different MSA layers is sharp and the ashy layers are well consolidated unlike those of the overlying Iron Age (Pickering, 2006).

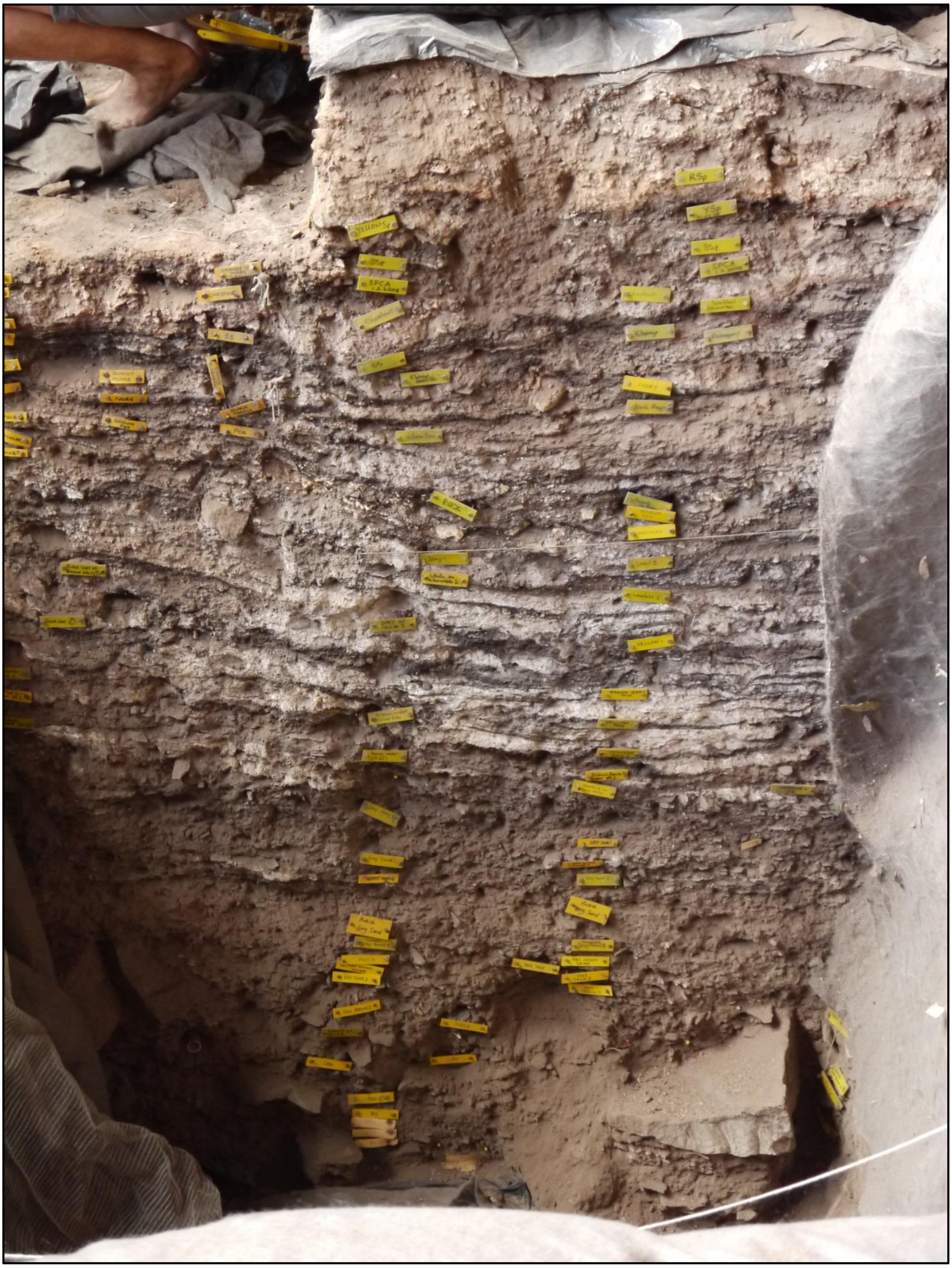


Figure 3.3: A north profile stratigraphy to illustrate what profiles at Sibudu look like. Photo by the Sibudu team of University of Tübingen.

b) *Chronology*

Recently obtained Optically Stimulated Luminescence (OSL) ages by Jacobs and colleagues have provided the age clusters for Sibudu deposits (Jacobs et al. 2008a, b) that supersede the previously published dates of Wadley and Jacobs (2006) that are slightly different. The OSL ages were obtained from a combination of single aliquot and single-grain analyses of sedimentary quartz and provide age clusters as weighted mean ages for each occupational phase at Sibudu i.e. pre-SB (>71 ka), SB (~71 ka), HP (~62) ka, post-HP (~58 ka), late MSA (~48 ka) and final MSA (~38 ka) (Jacobs et al., 2008a, Jacobs et al. 2008b). The pre-SB industry from the bottom (four layers, BS to LBG) followed by the SB (two layers, RGS2 and RGS), the HP (five layers, PGS to GR), the post-HP (25 layers, YA2 to BSp), the late MSA (12 layers, YSp to PB) and finally the final MSA (five layers, Mou to Co) at the top (Wadley and Jacobs, 2006; Wadley, 2006). Table **3.1** shows these layers and their associated ages from the pre-SB to post-HP where the phytolith samples were taken from and are the focus of this study. As excavations continue these layers may vary in publications that followed Wadley and Jacobs in 2006 and few more layers are mentioned in Wadley et al. (2011). The post-HP layers are the thickest and consist of ~ 28 layers (Jacobs et al., 2008b). The chronology supports that occupations at Sibudu seem to have been relatively short but intense and are punctuated by long hiatuses (Jacobs et al., 2008b). The last three phases were separated by two occupational hiatuses and their duration is estimated to be 10 ka for the hiatus between post-HP and late MSA and 9 ka for the hiatus between the late MSA and final MSA (Jacobs et al., 2008b). These hiatuses are not geologically recognisable as well as the hiatus between the upper most MSA layer and Iron Age (IA) which is of a longer duration (Jacobs et al., 2008b).

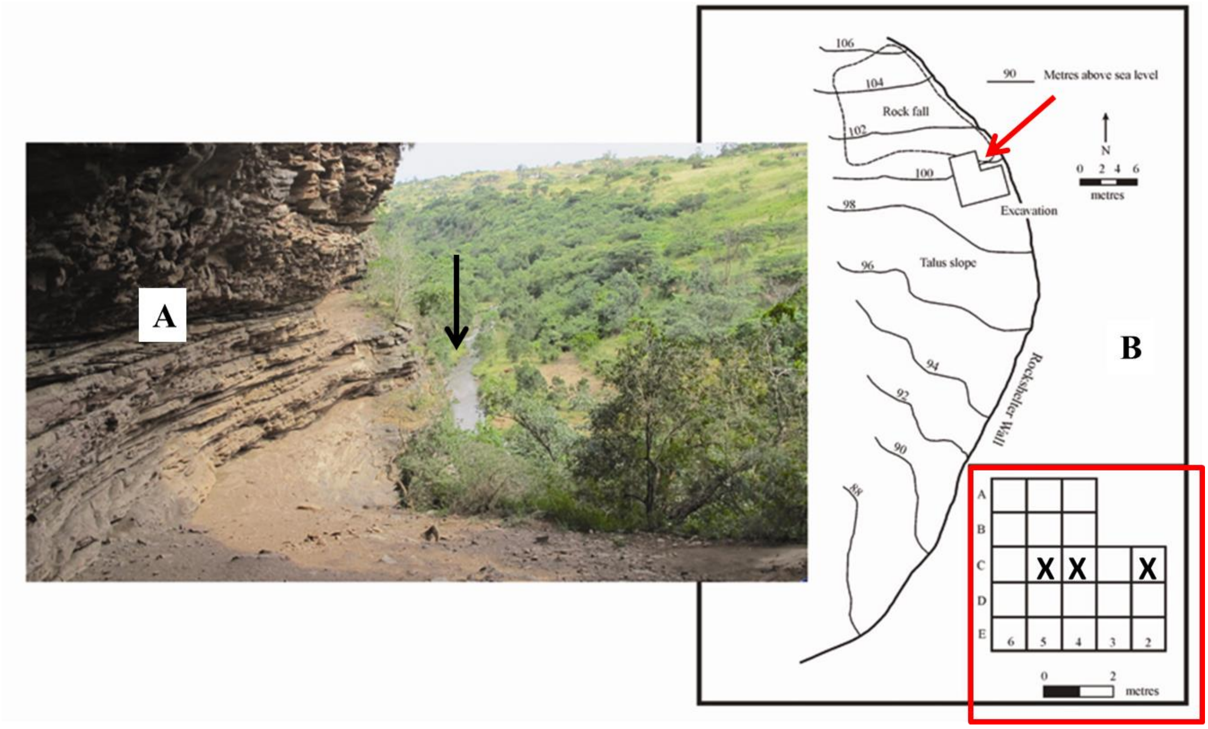


Figure 3.4: A) Sibudu Rock shelter wall facing the Tongati River (Wadley et al., 2011), **B)** Excavation Plan of the excavations led by Lyn Wadley (Wadley & Jacobs, 2004; Wadley et al., 2011) indicating squares C2 (one sample), C4 (26 samples) and C5 (one sample) where samples for phytolith analysis were collected.

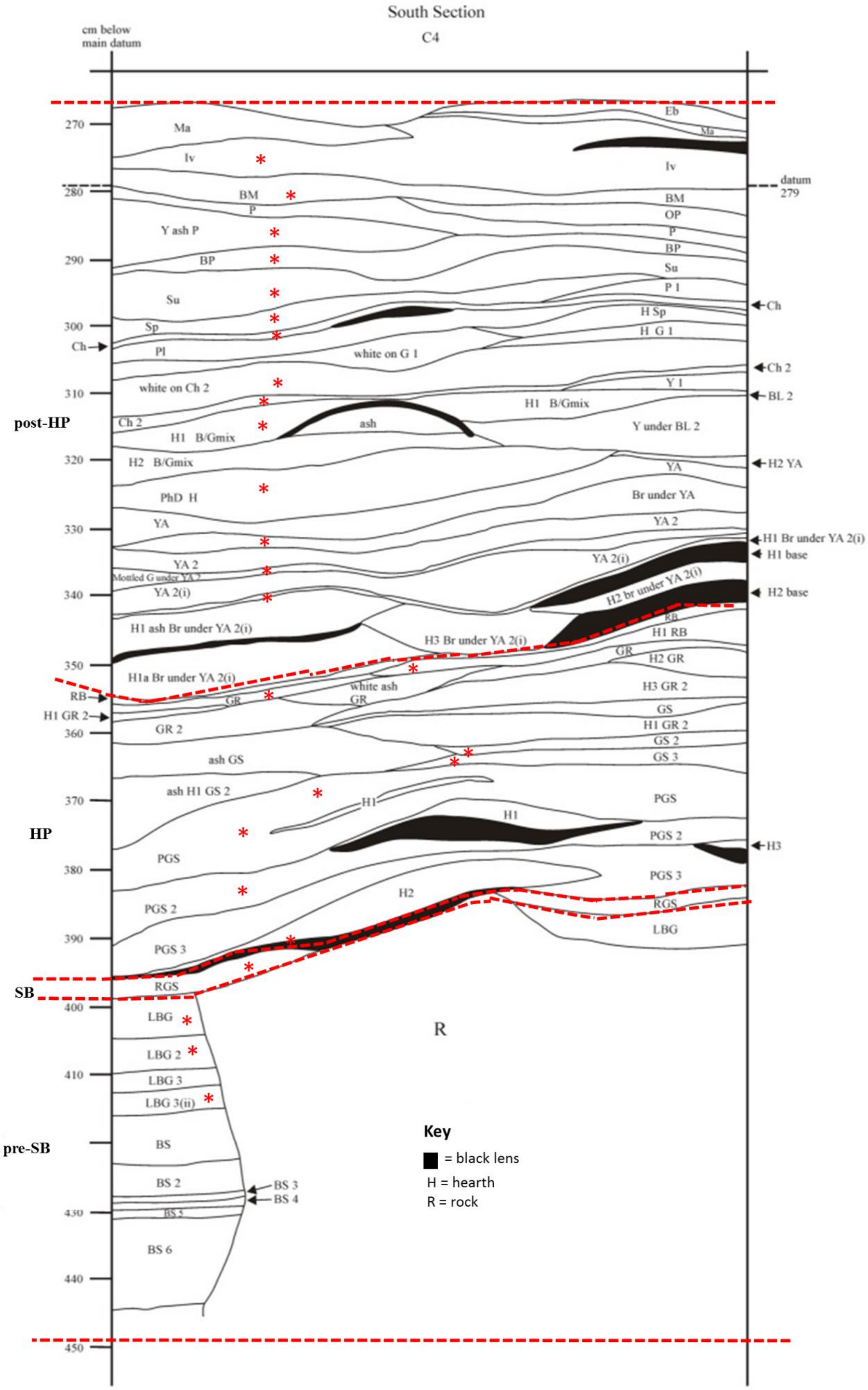


Fig. 3.5: Stratigraphy of the south profile of square C4 where 26 of the 28 samples were taken from the extreme left side of the wall (Wadley, pers. comm 2013).

Table 3.1: Sibudu Stratigraphy for square C4 South profile showing layers in which samples used in this present study were obtained, their OSL ages and lithic designation (Wadley and Jacobs, 2006; Jacobs et al., 2008a). All samples were taken from layers in square C4 apart from the two samples from the layers SPCA 2 and BS8 that were taken from squares C2 and C5 respectively.

Sample No.; Depth (cm below main datum)	**Layer abbrv.**	**Layer name**	**OSL age in Ka**	**Lithic designation**
367; 269	SPCA 2	Camel-coloured or grey-white sand that contains calcium carbonate		post-Howiesons Poort (post-HP, informal)
1; 278	Iv	Ivory (white ash)		
2; 282	BM	Black Magic (black ash)		
3; 287	**Y ash P***	Yellow ash in P (Pox)	59.0±2.2	
4; 291	BP	Brown Pox		
5; 295	Su	Sulphur		
6; 298	Sp	Speckled		
7; 302	Ch	Chocolate		
8; 304	White on Ch2	Chocolate 2		
9; 309	**Ch2***	Chocolate 2	58.3±2.0	
10; 313	**BG mix***	Brown/Grey mix	58.2±2.4	
11; 322	PhD H	PhD hearth is a hearth within BG/Mix		
12; 335	Br Under YA	Brown under Yellow Ash		
13; 342	Br Under YA2	Brown under Yellow Ash 2		

14; 348	H1 in Br Under YA2(i)	Hearth 1 in Brown under Yellow Ash 2(i)		
15; 354	H1 RB	Hearth 1 in Reddish Brown		Howiesons Poort (HP, formal)
16; 360	GR	Grey Sand		
17; 364	**GS2***	Grey Sand 2	63.8±2.8	
18; 367	GS3	Grey Sand 3		
19; 373	**PGS***	Pinkish-grey Sand	64.7±2.3	
20; 379	PGS	”		
21; 384	PGS2	Pinkish-grey Sand 2		
22; 391	BL (Black lens)	Black lens		Still Bay (SB, formal)
23; 397	**RGS***	Reddish-grey Sand	70.5±2.4	
24; 403	**LBG***	Light Brownish-grey	72.5±2.5	pre-SB (informal)
25; 411	**LBG2***	Light Brownish-grey 2	73.2±2.7	
26; 420	LBG3(ii)	Light Brownish-grey 3		
27; 420	BS8	Brown Sand	>77	

*Layers with OSL dates in the south profile are in bold (Jacobs et al., 2008a, b).

CHAPTER FOUR

MATERIALS AND METHODS

4.0 Field-based sampling and Laboratory-based analyses

4.1 Sampling of sediments

Sediment samples for phytolith analysis were collected from Sibudu Cave in March 2011 by Angela Bruch. Exposed MSA sediments from visually discernible layers in squares C2, C4 and C5 (Fig. **3.4B** in Chapter 3) were scraped at the surface to remove contamination. 26 sediment samples were collected following a column sampling approach from the extreme left of the south wall of the C4 square (Fig. **3.4B**) and the wall's stratigraphy is indicated in Figure **3.5** and names of stratigraphic layers and estimated ages are in Table **3.1** (in Chapter 3). One horizontal sample from the layer BS8 (Table **3.1**) that is contemporaneous with the oldest sample LBG3 (ii) in square C4 at 420 cm was taken from the bottom of the adjacent square C5 south profile at 420 cm (Fig. **3.4B**) for comparison between contemporaneous sediments in different squares. Another sample that was analysed in this study was from a younger post-HP layer SPCA 2 from the square C2 at a depth of 269 cm below the main datum and is the youngest sample in this study (Fig. **3.4B**). Sediments were scooped and placed in labelled plastic bags from each stratigraphic layer sampled (Table **3.1,** Chapter 3) and the samples were transported to the Evolutionary Studies Institute at the University of the Witwatersrand were they were stored.

4.2 Collection of voucher specimens and the rationale

Plant specimens for phytolith reference slides were collected from mature plants in the study area during field work in April 2014 with the expertise of Prof. Marion Bamford and Dr. Christine Sievers and transported to the Evolutionary Studies Institute and stored in the herbarium. Collection of the voucher specimens generally focused on plant taxa that have been identified by other botanical studies in the MSA record of Sibudu Cave. For instance, because sedges (Cyperaceae) were identified in the Sibudu record (Sievers, 2006, 2013; Wadley et al., 2011), the few sedge species found growing along or close to the Tongati river below the cave were collected and were supplemented by more sedge specimens of a bigger collection of mature sedges from the Free State province that is housed at the Evolutionary

Studies Institute herbarium (Table **4.1)**. A total of 33 sedge species were studied and all of them had their inflorescence (achenes) (Table **4.1**). The impetus to make a wide sedge phytolith reference collection was because no detailed sedge phytolith reference collection exists for South Africa and this study sought to make this contribution to provide more certainty in identifying phytoliths morphotypes in the MSA sediment record. Only five species of Cyperaceae from South Africa have been previously analysed for their phytolith composition (Cordova and Scott 2010). Grasses (Poaceae) and non-grass taxa mainly forest woody taxa that were identified in the MSA charcoal and seed record of Sibudu (e.g. Wadley, 2004; Allot, 2005; 2006;) growing around Sibudu and in the Springside Nature Reserve in KwaZulu Natal were sampled. At the time of this study, there was no modern reference collection for the eudicot plants of South Africa (see Esteban, 2016) and it was therefore important to create one especially for woody taxa that were an important component of the MSA of Sibudu (Schiegl et al., 2004; Allott, 2004). A total of 19 grass species and 42 eudicot species that are mainly woody (40) were studied (Tables **4.2** and **4.3** respectively). An extensive grass phytolith reference collection exists for South Africa (Rossouw, 2009) and this current study sought to make grass phytolith reference collection that is study area-specific – Sibudu Cave.

The family Juncaceae (rushes) - some of which occur at Sibudu - has been included in this study of South African sedge phytoliths (Table **4.1**) because its species are sometimes confused with sedges (Haines and Lye, 1983) and, because morphological, anatomical and phylogenetic studies have found sedges to be more closely related to rushes than they are to grasses (Metcalfe, 1971; Jones et al., 2007; Chase et al., 2000). They also occupy similar habitats and are used for similar economic purposes (Van Wyk and Gericke, 2000). More so, *Juncus* fruits were previously thought to have been identified in MSA deposits at Sibudu (Wadley et al., 2011), but a possibility of their utilisation by early humans at the site has not been completely ruled out (Sievers, 2013). However, the production of diagnostic phytoliths in Juncaceae is not clear and remains generally ambiguous (Pearsall, 2000; Piperno, 2006; Murungi et al., 2017) and Iriarte and Paz (2009) found no diagnostic morphotypes in the three species that they analysed. Three species of Juncaceae were studied (Table **4.1**). For all species studied, replicate specimen were not processed however, when more than one sample of a species was available, samples were taken from the different specimen of the species and mixed together for a good representation of the phytolith production. Replicates were not done since samples were collected from individuals growing under the same environmental conditions. They will have to be done with similar individulas from a different population.

This is a necessary step because some phytolith morphotypes have been found to vary within a species and this has been associated with differences in environmental factors (Piperno, 1998).

Species - Sedges	**Abbreviation**	**Sampling area**	**Slide No.**
Bulbostylis sp.	Bu.sp	Pullen farm, Mpumalanga	Cyp 32
Bulbostylis burchelli	Bub	Herbarium no. 85	Cyp 37
Cladium mariscus	Clm	Mpumalanga	Cyp 26
Cyperus albastriatus	Cya	Sibudu Cave	SIB 14 Monocot
Cyperus denudatus *	Cyd	Herbarium no. 15	Cyp 8
Cyperus rigidifolius	Cyr	Herbarium no. 22	Cyp 9
Cyperus fastigiatus	Cyf	Herbarium no. 2	Cyp 11
Cyperus haematocephalus	Cyh	Herbarium no. 23	Cyp 12
Cyperus obtusifloris	Cyo	Herbarium no. 24	Cyp 13
Cyperus semitrifidus	Cys	Herbarium no. 25	Cyp 14
Eleocharis sp.	El.sp	Herbarium no. 3	Cyp 5
Eleocharis caduca	Elc	Herbarium no. 13	Cyp 6
Eleocharis dregeana	Eld	Herbarium no. 26	Cyp 15
Fuirena pubescens	Fup	Herbarium no. 28	Cyp 16
Fuirena sp. 1	Fu1	Pullen farm, Mpumalanga	Cyp 30
Fuirena sp. 2	Fu2	Pullen farm, Mpumalanga	Cyp 27
Kyllinga pulchella	Kyp	Herbarium no. 14	Cyp 7
Kyllinga erecta	Kye	Herbarium no. 32	Cyp 18

Kyllinga sp. 1	Ky1	Sibudu Cave	SIB 27 Monocot
Kyllinga sp. 2	Ky2	Pullen farm, Mpumalanga	Cyp 31
Mariscus congestus (syn.: *Cyperus congestus*)	Mac	Herbarium no. 8	Cyp 4
Pycreus macranthus	Pym	Herbarium no. 33	Cyp 19
Pycreus sp.	Py.sp	Sibudu Cave	SIB 29
Schoenoxiphium sparteum	Scs	Herbarium no. 40	Cyp 2
Schoenoplectus sp.	Sc.sp	Pullen farm, Mpumalanga	Cyp 29
Schoenoplectus corymbosus	Scc	Herbarium no. 74	Cyp 38
*Schoenoplectus muricinux**	Scm1	Herbarium no. 75	Cyp 39
Schoenoplectus. Muriculatus	Scm2	Herbarium no. 37	Cyp 22
Scirpoides burkei	Scb	Herbarium no. 38	Cyp 24
Scleria natalensis	Scn	Sibudu Cave	SIB 17 Monocot
Scleria woodii	Scw	Herbarium no. 39	Cyp 25
Unidentified Cypereceae sp. 1 (later added to *Cyperus* see chapter 5 under *Cyperus*).	Cyp1	Sibudu Cave	SIB 23 Monocot
Unidentified Cyperaceae sp. 2 (later added to *Cyperus* see chapter 5 under *Cyperus*).	Cyp2	Sibudu Cave	SIB 30 Monocot
Species - rushes			
Juncus exertus	Juex	Herbarium no. 30	Cyp 20
Juncus oxycarpus	Juox	Herbarium no. 31	Cyp 21
Juncus effuses	Juef	Sibudu Cave	SIB 20 Monocot

*Analysed for their phytolith morphotypes but not counted.

Table 4.1: Voucher sedge (Cyperaceae) and rush (Juncaceae) plant materials collected in KwaZulu Natal, Mpumalanga and those housed at the Evolutionary Studies Institute herbarium from the Free State. Plant parts were analysed for their phytolith content as a whole from each specimen (i.e. all had achenes and culms and/or leaf blades).

Subfamily	**Species**	**Slide No.**	**Part analysed**
Aristidoideae	*Aristida* sp.	SIB 7 Monocot	C, L, I
Arundinoideae	*Phragmites australis*	SIB 19 Monocot	C, L, I
Chloridoideae	*Dactyloclenium* sp.	SIB 16 Monocot	C, L, I
	Eragrostis superba	SIB 4 Monocot	C, L, I
	Eragrostis sp.	SIB 24 Monocot	C, L, I
	Fingerhuthia sp.	SIB 11 Monocot	Whole plant
	Sporobolus africanus	SIB 18 Monocot	C, L
Panicoideae	*Digitaria* sp.	SIB 10 Monocot	C, L, I
	Digitaria sp. 2	SIB 21 Monocot	C, L, I
	Hyparrhenia hirta	SIB 28 Monocot	C, L, I
	Melinis repens	SIB 25 Monocot	C, L, I
	Monocymbium ceresiiforme	SIB 6 Monocot	C, L, I
	Odontyletrum sp.	SIB 5 Monocot	C, L
	Oplismenus sp.	SIB 26 Monocot	C, L, I
	Panicum maximum	SIB 8 Monocot	C, I
	Setaria pallide-fusca	SIB 13 Monocot	C, L, I
	Setaria megaphylla	SIB 22 Monocot	C, L, I
Pooideae	*Agrostis* sp.	SIB 12 Monocot	C, I
Unknown	Unidentified grass	SIB 3 Monocot	C, L

Table 4.2: Voucher grass (Poaceae) plant material collected from the area around Sibudu Cave and the plant part analysed. C = Culm, L = Leaves, I = Inflorescence.

Slide No.	**Family**	**Species**	**Plant habit**	**Part analysed**
31	Achariaceae	*Rawsonia lucida*	Woody	L, W
8	Anacardiaceae	*Protorhus longifolia*	Woody	L, W
14	Apocynaceae	*Carissa bispinosa*	Woody	L, W
19	Apocynaceae	*Tabernaemontana ventricosa*	Woody	L, W
6	Asteraceae	*Brachylaena discolour*	Woody	L, W
15	Cannabaceae	*Celtis africana*	Woody	L, W, F
36	Celtidaceae	*Celtis mildbraedii*	Woody	L, W
38	Ebenaceae	*Diospyros natalensis*	Woody	L, W
16	Euphorbiaceae	*Macaranga capensis*	Woody	L, W
39	Euphorbiaceae	*Acalypha glabrata*	Woody	L, W
41	Euphorbiaceae	*Clutia pulchella*	Woody	L, W
44	Euphorbiaceae	*Acalypha sonderiana*	Woody	L, W
17	Fabaceae	*Albizia adianthifolia*	Woody	L, W
23	Fabaceae	*Baphia racemosa*	Woody	L, W
32	Fabaceae	*Schotia bracypetala*	Woody	L,W
37	Fabaceae	*Millettia grandis*	Woody	L, W
40	Fabaceae	*Dichrostachys cinerea*	Woody	L, W, F
42	Fabaceae	*Acacia ataxacantha*	Woody	L, W
35	Lamiaceae	*Tetradenia riparia*	Herb	L, W
45	Lamiaceae	*Clerodendrum glabrum*	Woody	L, W
10	Lauraceae	*Cryptocarya woodii*	Woody	L, W
4	Meliaceae	*Ekebergia capensis*	Woody	L, W
7	Meliaceae	*Trichilia emetica*	Woody	L, W
21	Moraceae	*Ficus polita*	Woody	L, W
26	Moraceae	*Ficus* sp.	Woody	L, W
30	Moraceae	*Ficus ingens*	Woody	L, W
33	Moraceae	*Ficus sur*	Woody	L, W
20	Myrtaceae	*Eugenia capensis*	Woody	L, W

22	Myrtaceae	*Syzygium cordatum*	Woody	L, W
34	Ochnaceae	*Ochna natalitia*	Woody	L, W
28	Phyllanthaceae	*Bridelia micrantha*	Woody	L, W
1	Podocarpaceae	*Podocarpus latifolius*	Woody	L, W
24	Rhamnaceae	*Ziziphus mucronata*	Woody	L, W
27	Rubiaceae	*Vangueria infausta*	Woody	L, W
25	Rutaceae	*Teclea gerrardii*	Woody	L, W
29	Rutaceae	*Vepris lanceolata*	Woody	L, W
5	Sapindaceae	*Deinbollia oblongifolia*	Woody	L, W
2	Sapotaceae	*Mimusops obovata*	Woody	L, W
13	Sapotaceae	*Sideroxylon inerme*	Woody	L, W
47	Urticaceae	*Obetia tenax*	Woody	W
11	Vitaceae	*Rhoicissus rhomboidea*	Herbaceous	L
12	Vitaceae	*Rhoicissus tomentosa*	Herbaceous	L

Table 4.3: Voucher eudicot plant specimens studied from Sibudu cave and Springside Nature Reserve in KwaZulu Natal indicating their family and the plant parts analysed. L= leaves, W= wood, F= fruit.

4.3 Extraction of phytoliths from modern plant material

Phytolith analysis of the modern voucher specimens to make reference slides and of MSA sediments was conducted in the palynology laboratory at the Evolutionary Studies Institute, University of the Witwatersrand. The plant parts analysed for each specimen are indicated in the Tables 4.1, 4.2 and 4.3. Several studies have used different extraction methods to study phytolith morphotypes produced in plants (Rovner, 1971; Pearsall, 1978, 2000; Piperno, 1988; Runge, 1995; Albert et al., 1999; Albert and Weiner, 2001; Parr et al., 2001). There are mainly two methods that are used to extract phytoliths from plant material: 1) dry ashing and 2) wet oxidation (acid digestion) (Pearsall, 2000; Parr et al., 2001; Piperno, 2006). Comparative studies by Pearsall (2000) and Parr et al., (2001) demonstrated that the dry ashing technique is reliable at temperatures below 600°C. This study employed a combination of the dry ashing and wet oxidation method to extract phytoliths from the voucher plant specimens. For sedges, the initial weight of plant material targeted was 1 g but material used varied between 0.1 g and 1 gram subject to availability. 1 g was targeted for the grasses and after washing and drying, most samples ranged between 0.7 g to 0.9 g while 1 to 3 g was used for the eudicot plants. The plant parts of given taxa were processed together in this study to mimic what the archaeological record would look like as several plants were likely used as a whole. Grass infloresences were extracted together with the leaves/culms as they have been found to generally produce similar sets of grass short cells, only that infloresence tend to produce more rondels compared to leaves (Novello and Barboni, 2015). The procedure involved oven drying of freshly washed (quickly rinsed in soap solution and sonicated for 30 minutes) plant material at 105°C for 24 hours. The dried material was weighed and placed in porcelain crucibles and ignited in a muffle furnace at 500°C for 8 hours to break down the organic matter of the plant material. The samples were transferred to 50 ml plastic tubes and washed in about 5 ml of 10% hydrochloric acid (HCl) to remove carbonates, followed by about 20 ml concentrated nitric acid (HNO_3) and placed in a water bath for about 3 hours or until all the remaining organic material was digested (solid potassium chlorate ($KClO_3$) was added as a catalyst). The residue left was dried in acetone and weighted. Whenever possible, an equal fraction of phytoliths from dry samples for each plant group was mounted on microscopy slides with glycerol and observed under the microscope at x400 magnification. The remaining phytolith fraction was stored in Eppendorf tubes.

4.4 Extraction of phytoliths from archaeological sediments

Fossil phytoliths were extracted from sediment samples using a combination of standard procedures described in Piperno (1988, 2006), Pearsall (2000) and Thorn (2004). The procedure involved weighing approximately 4g of sediment and for the few samples that were slightly lumpy, gently spread out into finer particles in a crucible. The samples were placed in 50 ml plastic tubes and Sodium bicarbonate ($NaHCO_3$) was added and shaken with a manual shaker for 30 minutes to disaggregate the various mineral and organic constituents of the samples. They were centrifuged for 5 minutes at 3500rpm and treated with 10 ml of 10% HCl at about 70^0C in a warm water bath to remove carbonates, then centrifuged and decanted and washed three times using Millipore water. Approximately 3 to 5 ml of concentrated nitric acid (HNO_3) was added to each sample and placed in a hot water bath to digest the organic material until the reaction stopped. Potassium Chlorate ($KClO_3$) was added as a catalyst. The samples were then sieved through a 250 mesh sieve into 500 ml and 1000 ml beakers in order to remove sand and larger particles from the sample. To remove clays from the remaining sample, Millipore water added to the 250 ml mark in the 500 ml beakers and to the 500 ml mark in the 1000 ml beakers, stirred and left to stand for the silts to settle for about 1 hour or so. The supernatant was decanted and the procedure repeated several times until the supernatant was clear.

The residue was placed in centrifuge tubes and centrifuged at 3500rpm for 5 minutes to remove excess water. 10ml portion of heavy liquid of Sodium Polytungstate Solution (SPTS) at a density of 2.3 was added to the centrifuge tubes and centrifuged at 4000 rpm for 5 minutes to float the phytoliths. The floating phytolith material was carefully removed at the top of the test tube with a Pasteur pipette and transferred to another clean centrifuge tube. This procedure was repeated until no floating material was visible. Millipore water was added to each test tube containing the phytolith extracts in a ratio of 3:1 and vortexed to mix the heavy liquid and water. This lowered the density to less than 2.3, allowing phytoliths to settle at the bottom of the test tube. The samples were then centrifuged at 4000 rpm for 10 minutes and the supernatant decanted. The procedure was repeated twice to remove all the heavy liquid from the phytoliths. The remaining fraction containing phytoliths was dried in acetone by centrifuging each sample at 4000 rpm twice or thrice. An almost equal phytolith fraction was obtained from the dry material and was mounted on microscopy slides with glycerol.

4.5 Phytolith identification, classification and counting

For both the modern reference material and archaeological sediment samples, enumeration of phytolith morphotypes was done on mounted microscope slides observed under x400 magnification using an Olympus BX51 light microscope mounted with a camera. For the sedge voucher specimens, it was aimed to reach a maximum of 400 phytoliths per slide, for grasses it was aimed to reach 200 per slide while for the MSA sediments it was 300 phytoliths per slide. Therefore the number of phytoliths counted in the end across slides generally ranged from a minimum of 400 to a maximum of 450 for sedges phytoliths, a minimum of 200 to 250 for grasses and a minimum of 305 to maximum 413 in the MSA sediments. A minimum of 200 phytoliths has been recommended as sufficient to obtain reliable information (Albert and Weiner, 2001). However, a minimum of 400 was used for sedges as a count of 200 was often reached within few fields of view because of the abundance of the characteristic cone-shaped phytoliths appearing as if no other phytolith types were present. It was realised that when a count of 400 was used, the other phytolith morphotypes that they produce were encountered. For the MSA, 300 phytoliths were targeted because with only 200 of all morphotypes, grass silica short cells appeared to be more under represented. Grass phytolith morphotypes were identified according to the voucher specimens used in this study and different available published data (e.g. Twiss, 1992; Mulholland, 1992; Alexandre et al., 1997; Piperno, 2006; Barboni and Bremond, 2009; Rossouw, 2009; Cordova, 2013; Novello et al., 2012; Neumann et al., 2017) while non-grass phytoliths were identified according to Piperno (1989), Ollendorf (1992), Bozarth (1992), Runge (1999), Albert et al. (1999), Piperno (2006), Bamford et al. (2006), Mercader et al. (2009), Fernádez Honaine et al. (2009) among others as well as the voucher specimens. Phytolith data from this study is presented as counts and percentages and microphotographs of phytolith morphotypes are presented in the thesis.

4.6 Description of phytolith morphotypes and taxonomic interpretation

Phytolith morphotypes observed in the sediments and voucher specimens are described below (Table **4.4**) based on the standard descriptions of Madella et al. (2005), other published literature and on my own observations. The description is based on the morphological features that include shape, size and surface texture and identification to the lowest taxonomic level possible. Major phytolith morphotypes observed in the sediments and voucher specimens are described below based on the standard descriptions of Madella et al. (2005), other published literature such as Twiss et al. (1969); Twiss, (1992); Fredlund and Tieszen, (1994); Alexander et al. (1997) and on my own observations. The description is based on the morphological features that include shape, surface texture, sometimes size and identification to the lowest taxonomic level known possible.

Table 4.4 Summary of the main phytolith morphotypes and unique morphotypes identified in modern plant voucher specimens and archaeological MSA sediments from Sibudu and their morphological description or anatomical origin, and taxonomic attribution.

Phytolith morphotypes (Morphological or anatomical structures)	**Description**	**Main taxonomic attribution**	**Illustration** (In Chapter 5 & 7)	**References**
Acicular hair cell/ Scutiform	Needle-shaped/Point-shaped/shield-shaped	Poaceae	Fig. **5.2a**: aw-ax Fig. **7.2c**: am	Kaplan et al., 1992; Madella et al., 2005; Lu et al., 2006
Blocky parallelepiped	Thick four-sided phytolith in which opposite sides are parallel	Eudicots, Cyperaceae, Poaceae	Fig. **5.1c**: a-h; Fig. **5.3b**: t-v; Fig. **7.2c**: as-av	Eudicots: Albert, 2000; Mercader et al., 2009. Cyperaceae: Fernádez Honaine et al., 2009; Novello et al., 2012; This study
Bulliform cells – cuneiform or parallelepiped	Cuneiform shaped and parallelepiped shaped	Poaceae	Fig. **5.2a**: au-av; Fig. **7.2c**: an	Twiss et al., 1969; Twiss, 1992
Bulbous structures (Some are sclerieds)	Phytoliths with round enlarged bulbs at the	Eudicots, Cyperaceae	Fig. **5.1d**: w-ac; Fig. **5.3c**: e-h	Madella et al., 2005. Eudicots:

	end			Mercader et al., 2009. Cyperaceae: this study.
Bilobate-shaped cone phytoliths – leaf/culm type cones	Articulated cones that appear like two lobed phytoliths, sometime with more than two lobes (polylobate). Not easy to separate from the grass bilobate.	Observed only in *Bulbostylis* sp. (Cyperaceae)	Fig. **5.1a**: a-n	This study
Cone-shaped – leaf/culm type cones	Conical, widest at the base and tapering to the apex. Apices can be pointed or round or truncated and bodies smooth or with satellites	Cyperaceae	Fig. **5.1a**: o-aq	Metcalfe, 1971; Piperno, 1989; Madella et al., 2005; Fernádez Honaine et al., 2009
Cones – achene type (fruit)	Hexagonal or polygonal cones with smooth or stippled surfaces (i.e.	Cyperaceae	Fig. **5.1b**	Ollendorf et al., 1987; Piperno, 1989; Standley, 1990;

	‘scrobiculate’ of Madella et al., 2005).			Ollendorf, 1992; Piperno, 2006; Fernádez Honaine et al., 2009
Cork aerenchyma	Perforated plates - Tabular silicified tissue, various shapes with irregular perforations	Woody taxa	Fig. **5.3c**: a-b; Fig. **7.2c**: bf?	Collura and Neumann, 2016
Cystoliths	Large spherical and elliptical phytoliths with a verrucate or tuberculate surface. Sometimes they have a stalk	Woody taxa	Fig. **5.3a**: l-y Fig. **5.3b**: a-j	Bozarth, 1992
Echinate platelets (Celtis bodies)	Plates with echinate surface on one side, the other side smooth, with irregular outlines	In this study in *Celtis africana* only	Fig**.** **5.3b**: k-p	In other *Celtis* species: Bozarth, 1992; Piperno, 2006; Iriarte and Paz 2009
Elongate dendritic	Longer than it	Poaceae	Fig. **5.2a**: at	Piperno,

	is wide with dendritic margins – finely branched			2006; Novello and Barboni, 2015
Elongate psilate or echinate	Longer than wide rectangular rods with psilate or echinate margins	No taxonomic value, occur in monocots and eudicots. In this study, they are generally associated with monocots.	Fig. **5.2a**: ao	Runge, 1999; Thorn, 2001; Piperno, 2006
Elongate cells (Cyperaceae type)	Several articulated long cells forming two sets of parallel rows that are interconnected	Cyperaceae (*Eleocharis*, *Fuirena*)	Fig. **5.1d**: s-t	*Eleocharis*: Fernádez Honaine et al., 2009; this study. *Fuirena*: this study
Elongate crenate/pilate/columellate epidermal plates	Articulated elongate cells that have a dented margin or club-shaped or rod-like processes sometimes appearing contorted	Monocots. In the current study: in some Cyperaceae (crenate/pilate margin) and some Poaceae (columellate margin)	Fig. **5.1d**: a-d, g; Fig. **5.2a**: aq-as	Carnelli et al., 2004
Epidermal anticlinal cells	Phytoliths that resemble jigsaw puzzle	Eudicots	Fig. **5.3a**: ai-an	Piperno, 1988, 2006; Bozarth,

	pieces with wavy undulating or sinuous cell walls, often multicellular			1992; Mercader et al., 2009
Epidermal polyhedral cells	Silicified 4-8 sided epidermal cells, often multicellular	Eudicots	Fig. **5.3a**: g-k	Bozarth, 1992; Albert and Weiner, 2001; Strömberg, 2003; Bamford et al., 2006; Mercader et al., 2009
Epidermal polyhedral cells (with attached 'verrucate silica')	The same type as above but the cells are infused with silica particles creating a verrucate appearance, multicellular	Eudicots – *Ficus* leaves In this current study, also seen in *Millettia grandis* (Fabaceae) but with less silicification, therefore less verrucate surface	Fig. **5.3a**: j	Strömberg, 2003
Hemispherical and spherical echinulate bodies	Unique elliptical, hemispherical and spherical phytoliths with a granulate	Cyperaceae (*Scleria*, *Fuirena*)	Fig. **5.1d**: l-r	*Scleria*: Metcalfe, 1971; This study. *Fuirena*: Bamford et

	surface often in pairs with convex ends			al., 2006
Hair bases	Spheres with a circular protuberance in the centre – often embedded with cystoliths	Eudicots – appear diagnostic in some families in this study – e.g. Celtidaceae and Moraceae	Fig. **5.3a**: u-z; Fig. **5.3d**: i-n?	Piperno,1988, 2006; Watling and Iriarte, 2013
Polyhedral cavate	Polyhedral epidermal cells with a central cavity often multicellular	*Celtis africana* (this study), *Celtis mildbraedii* (same type in both species but *C. mildbraedii* has another unique type, this study)	Fig. **5.3a**: e-f. Fig. **5.3c**: c-d.	Collura and Neumann, 2016; This study
Polygonal epidermal cells (Cyperaceae)	Flat hexagonal cells that can appear netlike and like articulated cones in side view, multicellular	Only in *Scirpoides burkei* (Cyperaceae)	Fig. **5.1b**: al-am	This study
Irregular/sub globular granulate	Irregular to sub-globular bodies with numerous grain-like	Only in *Celtis africana*	Fig. **5.3b**: q-s	This study

	projections			
Globular psilate	Spherical phytoliths with a smooth or sub-smooth surface	Eudicots, mainly woody taxa	Fig. **5.3a**: a-d	Piperno, 1988; Kondo et al., 1994; Albert, 2000; Mercader et al., 2009; Iriarte and Paz, 2009
Sub-globular/irregular	Unique spherical bodies sometimes irregular, surface is lightly granulate produced similar to those produced by Restionaceae	Similar to Restionaceae type? Some may be sedges.	Fig. **7.2a**: p-v (some are likely sedge cones). Fig. **7.2b**: w-al.	Cordova and Scott, 2010; Esteban et al., 2017. Restionaceae - Esteban pers.comm, 2015.
GSSC – bilobate	With two lobes	Poaceae (Panicoideae, Aristidoideae)	Fig. **5.2a**: a-m	Twiss et al., 1969; Fredlund and Tieszen, 1994; Lu and Liu, 2003; Madella et al., 2005; Piperno, 2006; Fahmy (2008)
GSSC – cross	with four lobes	Poaceae	Fig. **5.2a**:	Pearsall,

	one at each of its ends, sometimes three lobes only	(Panicoideae)	o-t	2000; Piperno, 2006; Novello et al., 2012
GSSC –polylobate	cylindrical with more than two lobes linearly arranged	Poaceae (Panicoideae)	Fig. **5.2a**: n	Twiss et al., 1969; Madella et al., 2005; Rossouw, 2009; Mercader et al., 2010; Collura and Neumann, 2016
GSSC – rondel	Various - mainly trapezoidal phytoliths with circular base, top keeled, top truncated, conical, horned towers	Poaceae	Fig. **5.2a**: ab-am	Fredlund and Tieszen, 1994; Lu and Liu, 2003; Bamford et al., 2006; Novello et al., 2012; Cordova, 2013
GSSC - saddle	Saddle squat – convex edges longer than concave edges. Saddle tall – concave longer than convex edges, Saddle	Poaceae (Chloridoideae)	Fig. **5.2a**: v-aa	Twiss et al., 1969; Lu and Liu, 2003; Piperno, 2006

	plateau - trapezoidal with a saddle base and a smaller saddle-like top			
Stomata – Cyperaceae type	Elongate dome-shaped subsidiary cells that lie parallel to the stomatal pore	Cypereceae	Fig. **5.1d**: j	Carnelli et al., 2004; Watling and Iriarte, 2013
Stomata – eudicot type	Dicot type 'STO DIC' of Carnelli et al., 2004: 'guard cells with pore in the centre, 'appear spherical' – personal description	Eudicot	Fig. **5.3a**: aa-ae; Fig. **5.3d**: h	Carnelli et al., 2004
Stomata – Gramineae type	One of Gramineae type 'STO – GRAM' of Carnelli et al., 2004	Poaceae	Fig. **5.2a**: bc	Carnelli et al., 2004
Tabular elongate	Thin and flat, much longer than wide, margin psilate or echinate	Monocots, eudicots In the current study mainly in grasses and sedges	Fig. **5.2a**: ap	Madella et al., 2005; Bamford et al., 2006; Mercader et al., 2009

Tracheids	Silicified tracheary elements with spiral thickenings or rings, straight or branched	Woody eudicots, Monocots	Fig. **5.2a**:bd; Fig. **5.3c**: i-j; Fig. **7.2c**: bg	Bozarth, 1992; Runge, 1999; Iriarte and Paz, 2009

4.7 Statistics

4.7.1 Correspondence Analysis (CA): modern grass phytolith morphotypes

It has been suggested that CA is the most appropriate multivariate ordination method for comparing associations (columns) that containing counts of taxa (morphotypes) and rows containing the counted taxa (plant specimens) to deal with the major issues of multiplicity and redundancy (Neumann et al., 2017). CA was used to determine the relationships between modern grass phytoliths and known environmental and genetic factors (Barboni and Bremond, 2009; Rossouw, 2009). It was therefore used to determine similarities within the morden grass phytolith morphotypes by classifying grass species into different vegetation categories in the ordination diagram that signifies taxonomic and climatic preference of each vegetation category. Species that are similar in morphotype composition should appear close in the scatter plot (Neumann et al., 2017). The CA used was that of the statistical program PAST (Hammer et al., 2001). The scatter plot was presented in Figure **5.2e** in Chapter 5. The raw counts of individual phytolith morphotypes in grasses are indicated in the Appendix of the thesis in the Table **A4**.

4.7.2 Quantitative and Qualitative analysis: modern sedge phytoliths and eudicot phytoliths

Percentages of individual phytolith morphotypes in Cyperaceae were determined using Microsoft Excel and the data is shown in the Appendix of the thesis in Table **A1**. Cone size ranges of each sdege species are illustrated by a box and whisker plot (Fig. **5.1e**) and in Table **A2** in the appendix together with their silica content. Phytolith morphotypes in eudicot plants were enumerated qualitatively following the categories described in Wallis (2003) and Watling and Iriarte (2013) with some modification. The categories are: Abundant (A): a number of phytoliths observed in the majority of fields of view; Common (C): a small number of phytoliths observed in multiple fields of view; Rare (R): a small number of phytoliths observed with most fields of view containing no phytoliths (Watling and Iriarte, 2013). These results of this qualitative analysis are presented in Table **5.1** in Chapter 5. The modification that this study made was that of scanning the whole microscope slide not 'at least five transects' and therefore even when one phytolith of a given morphotype is encountered in the whole slide it is recorded as 'Rare'.

4.7.3 Construction of the archaeological phytolith assemblage diagram

To ease interpretation, the percentage phytolith data from the archaeological samples was displayed in a histogram (Figure **7.1** in Chapter 7) obtained using the computer program TILIA (Grimm, 2007), version 1.7.16. The horizontal axis of the histogram shows the phytolith morphotypes and their frequencies (%) while the vertical axis shows the depths (cm) of the different layers from which the different samples were obtained and their estimated age.

CHAPTER FIVE

PHYTOLITH ANALYSIS OF SELECT PLANTS FROM THE SRZ OF SOUTH AFRICA

5.0 Introduction

This chapter presents results obtained from the analysis of phytoliths in modern voucher specimens constituting 97 plant species representing 27 plant families that was conducted in order identify the phytolith types produced by plants typical of the summer rainfall region of South Africa. The 97 species consist of 33 sedges, 19 grasses, 3 rushes and 42 eudicot species and these were used as a reference to aid identification and interpretation of the Middle Stone Age phytolith record of Sibudu Cave (Chapter seven). Of the 27 families, Cyperaceae and Poaceae (monocots) yielded the most abundant and distinct phytoliths. Cyperaceae produced the diagnostic cone-shaped and achene phytoliths, and parallelepiped blocky phytoliths among others, while Poaceae mainly produced grass short-cell phytoliths. Juncaceae (monocot) yielded types that are non-diagnostic, mainly elongate and tracheid phytoliths that were abundant in only one species while phytolith production varied within species of the same family in the woody and non-woody taxa (eudicots) studied. However, eudicot families that generally showed good phytolith production were: Moraceae, Celtidaceae, Euphorbiaceae, Podocarpaceae, Fabaceae and Myrtaceae. Eudicots generally produced various phytolith morphotypes such as epidermal ground mass (multicellular polyhedral and anticlinal epidermal cells), globular types, hair bases, tracheid elements, stomata, cystoliths and irregular bodies. The Cyperaceae phytolith morphotypes are illustrated in Figures **5.1a - 5.1d**, the Poaceae morphotypes in Fig. **5.2a** and the dicots in Fig. **5.3a – 5.3d**. More images of phytoliths eudicot specimens studied here are in the appendix. The appendix shows the data sheets of the relative frequencies and row counts of various phytolith morphotypes in the Cyperaceae and Poaceae specimens analysed (Tables **A1** and **A4** respectively). Table **5.1** in this chapter shows the occurrence and abundance of phytolith morphotypes in the eudicot specimens.

5.1 Phytolith morphotypes in the family Cyperaceae (Sedges) and Juncaceae (Rushes) (Fig. 5.1a - 5.1d)

Results from the analysis of 33 species of sedges show that cone-shaped phytoliths are common in most species but can be hardly represented in a few species, with other morphotypes such as achene phytoliths, stomatal complexes, and tabular and/or blocky parallelepiped morphotypes being the most dominant. Some genera studied here produced known achene type phytoliths in their achenes that are sometimes genus-specific. These genus-specific achene phytoliths were observed in species previously not studied that have been moved by taxonomists from one genus to another, providing further support for the taxonomists' classification. The general silica content of species studied and the common morphotypes in each species are presented below according to their genus. The relative frequencies of sedge morphotypes in each species are detailed in Table **A1** and cone sizes and silica content of each species are shown in Table **A2** in the appendix.

5.1.1 Silica content

The silica content ranged from negligible to 2% in the samples analysed. The original weight of samples used ranged from 0.1 to 1.0 grams with only five species weighing above 0.5 grams. Only *Kyllinga* sp. *Schoenoplectus muriculatus*, *Schoenoplectus* sp. and *Scirpoides burkei* gave silica above 1%. Most of those with negligible silica content (final silica weight below 0.001 grams, the limit of the scale used in this study) gave a sufficient amount for analysis that matched the final weight used for the rest apart from *Cyperus fastigiatus*, *C. semitrifidus*, all the *Juncus* spp. and *Kyllinga pulchella* that all left an extremely small amount for analysis. *Cyperus denudatus*, *Bulbostylis humilis*, *Eleocharis dregeana* and *Schoenoplectus decipiens* left nothing requiring a repeat of the procedure. This repetition was not possible for *B. humilis* due to insufficient amount left of the original herbarium specimen.

5.1.2 Phytolith description

Bulbostylis

In the two species analysed, *Bubostylis* sp. and *B. burchellii*, leaf cones were the most abundant in their phytolith assemblage with 95.5% and 72% respectively (Table **A1**). Both species have two variants: those that are articulated and convex on both sides creating a bilobate/polylobate-like or bulbous appearance and are without satellites (Fig. **5.1a**: *a-n* in *B.* sp) and those that appear as ordinary cones with rounded bases with satellites (Fig. **5.1a**: *o* in *B. burchellii*). There is a visible variation in their assemblages as the articulated bilobate-like phytoliths are more conspicuous and abundant in *B.* sp. and rare in *B. burchellii*. Other morphotypes observed occur in very small numbers such as articulated tracheid elements (1.2%), elongate psilate (0.9%) and parallelepiped blocky psilate (0.9%) in *B.* sp. and parallelepiped blocky psilate (9.5%) and elongate psilate (6.8%) in *B. burchellii*. Polygonal cones typical of sedge achenes (here after generally referred to as achene phytoliths) were not observed in these species. Plates with articulated cells that are elongate with crenate or pilate margins that were not in the total count were observed in both species (Fig. **5.1d**: *a-d*, *g*). The cell margins are sometimes contorted. Going forward, these plates are referred to here as 'elongate crenate plates'.

Cladium mariscus

The most abundant morphotypes in this species were the typical leaf cones with articulated and isolated typical leaf cones contributing 62.9% and 26.2% respectively (Fig. **5.1a**: *p*, *q*, Table **A1**). Various sclereids that look like bulbous structures were common in this species contributing 4% (Fig. **5.1d**: *w*). Other types such as silica skeletons with cones only (1.9%), silica skeletons made up of cones with other morphotypes (1.5%) and elongate psilate (1.5%) occur in small numbers (Table **A1**). Diagnostic achene phytoliths were not observed in this species, but it has articulated polyhedral cells (Fig. **5.1b**: *ai*).

Cyperus

Of the nine species analysed, isolated and articulated typical leaf cone phytoliths were the most abundant morphotype in *Cyperus* sp. 1 (92.5%), *Cyperus* sp. 2 (69.3%), *C. albastriatus* (63.9%), *C. semitrifidus* (62%) and *C. obtusifloris* (48.3%) (Table **A1**). **Note:** *Cyperus* sp. 1

and 2 were initially ‘unidentified Cyperaceae 1 and 2’ (Table **4.1**, Chapter 4) before phytolith analysis. The other four species produced leaf cones in lower amounts contributing less than 30% of their phytolith assmeblage (27.7% in *C. fastigiatus*, 23.8% in *C. rigidifolius*, 20.4% in *Mariscus congestus* and 19% in *C. haematocephalus*) (Table **A1**). These cones of *Cyperus* species are illustrated in Fig. **5.1a:** *r–w*. However, *C. fastigiatus* and *C. rigidifolius* had the most abundant parallelepiped blocky morphotypes with 37.5% and 18.5% respectively (Fig**.** **5.1c**: *a*, *b*). All the nine species produce achene phytoliths (Fig. **5.1b**: *a-t*) albeit in small amounts of mostly 2.4% to 6.7%, apart from *C. congestus* (77.8%), *C. haematocephalus* (71.2%) and *C. semitrifidus* (33.4%). It is also these three species that have the biggest leaf cones in *Cyperus* (Fig. **5.1e**; Table **A2;** Fig. **5.1a:** *r–w*) and appear unique in *C. semitrifidus* (squared lightly echinate or smooth margins with large or minute apices). Also the achenes of *C. semitrifidus* have conspicuously large apices (Fig. **5.1b**: *q-s*), a character only seen in this species. All the species analysed produce achenes with a stippled surface (‘scrobiculate’, Madella et al., 2005) typical of *Cyperus* (Piperno, 1989) though not always exclusively (Fig. **5.1b**: *a-f, o, q-s*) apart from *C. haematocephalus, C. fastigiatus* and *C. denudatus* that had achenes with psilate surfaces only with echinate margins or sometimes broken margins (Fig. **5.1b**: *g-n*). It was because of the presence of these achene phytoliths with stippled surfaces that the previously unidentified Cyperaceae 1 and 2 in Table **4.1** were added to the genus *Cyperus*. *Cyperus denudatus* hardly yielded very little silica during extraction and phytolith counting was not done as phytoliths were extremely scanty under the microscope. However, it was made up of achene phytoliths with psilate surfaces, echinate margins and decorated apices that appear echinate in finer focus (Fig. **5.1b**: *g-i*), a character that was only seen in this species. In side view, these echinate apices look dendritic (Fig. **5.1b**: *h*). Facetate phytoliths occur in some *Cyperus* species e.g. Fig. **5.1c**: *t-u*.

Eleocharis

Four species were analysed in this genus. Articulated and isolated leaf cones were highest in the species *E. caduca* (55.8%) and *E. dregeana* (17.7%) but are hardly present in *E. cf. limosa* (1.5%) and *Eleocharis* sp. (0.8%) (Table **A1**). However, *Eleocharis* sp. has several line-like anticlinal structures that can sometimes give a cone-shaped impression that accounted for 9.8% of the assemblage counted (Fig. **5.1c**: *n-q*). They often appear like thin lines but sometimes they are fully silicified bodies with these lines along the body. These structures occur in all the species in low amounts and in *E. dregeana* they adhere to blocky parallelepiped phytoliths (Fig. **5.1c**: *f*). The assemblage of *E*. sp., the least abundant cone producer, was dominated by stomata complexes that account for 25.4% of the assemblage (Fig. **5.1d**: *k*). The stomata complexes are sometimes made up of stomata, long sinuous cells and cones. It also seems to be the only species that produces silica skeletons that are made up of cones only (16.7%). *E. cf. limosa*, another of the low cone-shaped phytolith producers, was dominated by parallelepiped blocky psilate phytoliths in its assemblage (72.6%), while *E. dregeana*, *E. caduca* and *E*. sp. produced 16.2%, 13.4% and 9.8% respectively of parallelepiped blocky psilate phytoliths (Fig. **5.1c**: *c-f*). They all produce parallelepiped blocky sinuate phytolith types in very low amounts mostly less than 2% (Table **A1**).

E. dregeana was dominated by articulated elongate cells (31.4%), several appearing like plates whose margins are lined with minute pores or serrations that are likely to be cones and were grouped under 'silica skeletons made up of cones and elongate cells or parallelepiped blocky or tracheids'. All the four species produce silica skeletons with elongate cells arranged in parallel rows (Fig. **5.1d**: *s*) in very low amounts and although they were not encountered in the total count of *E. cf. limosa*, they are also present. Achene phytoliths were generally not present in species of this genus however, *E. dregeana* seems to produce morphotypes with this polygonal shape in very small amounts (2.9%) but they appear faint as if with low silification (Fig. **5.1b**: *x*). The two species that produced a meaningful amount of cone-shaped phytoliths to allow the set number of cone measurements i.e. *E. caduca* and *E. dregeana*, gave a range of 4.52 to 9.99 µm and 4.25 to 12.51 µm respectively, making them the smallest cones in all sedge species examined in this study (Fig. **5.1e**; Table **A2** in appendix).

Fuirena

Fuirena pubescens contributed only 15.7 % of leaf cone phytoliths while *Fuirena* sp. produced up to 45.6% leaf cones in its phytolith assemblage. The two species produced 'elongate crenate plates' in their phytolith assemblages that were the most dominant phytolith morphotype in *F. pubescens* (Fig. **5.1d**: *b-d*, *g*). *F. pubescens* and the *F*. sp. had up to 55.6% and 27.4% respectively of these plates in their phytolith assemblage. The crenate plates in *F*. sp. were sometimes beset with large spherical bodies (Fig. **5.1d**: *d*) that are bases of hair cells when seen in finer resolution (Fig. **5.1d**: *e*) and another type of irregular hair bases (Fig. **5.1d**: *f*). Species in this genus are also marked by silica skeleton plates that often appear like dissolved articulated elongate cells that in fine focus are often arranged in parallel rows similar to those in *Eleocharis* species (Fig. **5.1d**: *t*). No achene phytoliths were observed in either species. They also produced other phytoliths types such as silica skeletons, blocky parallelepiped and tabular (Fig. **5.1c**: *g-i*), elongates and hairs in small amounts apart from *Fuirena* sp. that has the highest percentage of hairs seen in all sedge species analysed in this study (Table **A1**).

Juncus

Three species of this genus were analysed: *J. effusus*, *J. exertus* and *J. oxycarpus*. Of the three, only *J. effusus* produced a substantial amount of phytoliths and is made up of 60% tracheid phytoliths in its assemblage (Table **A1**). It also produces elongate phytoliths (25.8%) and a few unclear silica skeletons with several thread-like strands. *J. exertus* was generally devoid of phytoliths but an elongate and blocky phytolith were seen while *J. oxycarpus* had a few tracheid phytoliths mixed with elongate phytoliths. The few rondel-shaped morphotypes in *Juncus effusus* that are not always clear probably due to low silicification were thought to be a possible contamination.

Kyllinga

Four species of *Kyllinga* were studied: *K. pulchella*, *K. erecta* and two unidentified species referred to here as *K.* sp. 1 and *K.* sp. 2. Leaf cone phytoliths were the most common morphotype in species 1 and 2 (77.3% and 82.3% respectively) with *K.* sp. 1 having isolated cones as the highest contributor to the overall cone percentage (67.5%) while *K.* sp. 2 has articulated cones as the highest contributor at 57.6% (Table **A1**). On the other hand, *K. pulchella* and *K. erecta* produced fewer leaf cones (20.6% and 17.8% respectively) with parallelepiped blocky morphotypes well represented in them (24.6% and 36.0% respectively) while they were less frequent in species 1 and 2 (1.8% and 5.6% respectively). Silica skeletons made up of cone-shaped phytoliths only were only present in *K. pulchella* and *K. erecta*. Various other types were present in the four species such as silica skeletons, articulated cones with elongate cells on their base, elongate psilate and stomata in small amounts (Table **A1**). Achene phytoliths were observed in *K.* sp.1 (5.5 %) and *K. pulchella* (2.8%) while a broken achene was seen in *K.* sp. 2 and no achenes were recorded in the counts of *K. erecta* (Table **A1**). The achene phytoliths had stippled surfaces similar to those in *Cyperus* (Fig**. 5.1b**: *w*) and the few in *K. pulchella* were lightly stippled. The small amount of achene phytoliths in these species should be treated with caution as it is most likely associated with the small amount of achene structures available for analysis compared to other sedge genera.

Pycreus

P. macranthus and *P.* sp. showed variations in their phytolith assemblage. *P. macranthus* was dominated by 43.9 % of parallelepiped blocky phytoliths, followed by cone phytoliths (14.5%) of which isolated cones contribute only 2% (Fig. **5.1a**: *x-z*). A few articulated cones can appear tabular echinate but cone impressions on their surface are visible (Fig. **5.1a**: *z*). Silica skeletons composed of various phytoliths occur in much lower amounts (Table **A1**). Importantly, *P. macranthus* produced stippled achene phytoliths that are elongate shaped, occurring either isolated or articulated (Fig. **5.1b**: *y, z*) that look similar to some of the *Cyperus*/*Kyllinga* achene 'elongate' phytoliths in *Cyperus congestus* (Fig. **5.1b**: *b, e, f*). Rarely do their surfaces appear psilate (Fig. **5.1b**: *aa*). Sclereids that look like articulated bulbous structures were also observed in its assemblage (Fig. **5.1d**: *x*). On the other hand, *Pycreus* sp. is dominated by cone phytoliths (69.1%) with the articulated cones contributing the biggest percentage (53.3%) with elongate psilate and parallelepiped blocky phytoliths (Fig. **5.1c**: *j*) contributing 12.7% and 10.3% respectively (Table **A1**). Both have silica skeletons and cones with elongate cells on their base each contributing less than 2.5% to the counted assemblage. Both species have lightly facetate phytoliths in their assemblages (Fig. **5.1c**: *r, s*). *P. macranthus* seems to produce a few globular psilate phytoliths but these were not considered during the count.

Schoenoplectus

Four species were studied; *S. corymbosus, S. muricinux, S. muriculatus* and *S.* sp. but those in *S. muricinux* were only observed and not counted. *S. corymbosus* was dominated by bulbous structures and other large bulbous-like hollow structures (several bulbous are sclereids) that were grouped together (45.5%, Fig. **5.1d**: *y-aa*) followed by cone phytoliths (38.9%), while cone phytoliths were the most predominant type in *S. muriculatus* and *S.* sp. (71.3% and 78.5% respectively). Other common morphotypes observed were parallelepiped blocky phytoliths (12.2%) and elongate phytoliths (12.1%) in *S. muriculatus.* They all produce other morphotypes that occur in very small amounts (Table **A1**). *S.* sp. has large bulbous like structures similar to those seen in *S. corymbosus* contributing 5.7% (Fig.**5.1d**: ab). The abundance of bulbous structures in *S. corymbosus* is underestimated as the abundant isolated globular phytoliths were not counted; only the bulbous with an articulated larger appearance were counted (Fig. **5.1d**: *y-aa*). These globular phytoliths mostly appeared bulbous and were thought to be part of the bulbous structures. *S. muriculatus* and *S. muricinux* are some of the species with cones that appear big with most cones measuring above 13 µm giving a range of 5.07 to 27.41µm (Fig. **5.1a**: *aa-ai*) while those measured in *S.* sp. ranged from 5.52 to 18.20 µm (Fig. **5.1e**, Table **A2)**. Some articulated cones in *S. muriculatus* and *S. muricinux* appear rectangular forming what looks like elongate tabular phytoliths with echinate margins (Fig. **5.1c**: *ac* and Fig. 5.1c*: ai* respectively). Some isolated cone-shaped phytoliths in *S. muricinux* are truncated, appearing rondel shaped (Fig. **5.1a**: *ad*, *ae*) and some have echinate margins (Fig. **5.1a**: *af*, *ag*). The species analysed in this genus do not seem to produce achene phytoliths but an achene shaped phytolith was encountered in *S. muriculatus* (Fig. **5.1b**: *ah*).

Schoenoxiphium sparteum

The phytolith assemblage was mainly characterised by leaf cones i.e. articulated typical leaf cones (34.2%) and silica skeletons with cones only (15.6%), and isolated typical leaf cones (8.7%). It produces achene phytoliths that have slightly echinate margins and those with entire margins (4.7%) (Fig. **5.1b**: *ad-ag*) that contribute 4.7% to its phytolith assemblage. Other morphotypes observed were articulated or isolated parallelepiped blocky psilate/sinuate phytoliths (8.9%), articulated or isolated elongate sinuate/psilate (8.2%), hairs (5.5%), cones with other cells (5%), articulated cones with elongate cells on their base (2.2%) and tracheid phytoliths (1.5%), (Table **A1**). Most of the cones measured were bigger than 10µm and ranged from 5.48µm to 21µm (Fig. **5.1e**, Table **A2**).

Scirpoides burkei

This species appears to have the least diverse morphotypes and is represented almost entirely by leaf/culm cone phytoliths that account for 97.3% of its phytolith assemblage. The only other type observed are large structures made up of unique articulated polygons that can appear net-like with pointed edges (**Fig. 5.1b**: *al*) and in side view, look like articulated cones (**Fig. 5.1b**: *am*).

Scleria

Three species of this genus were analysed: *Scleria* sp., *S. natalensis* and *S. woodii*. Articulated and isolated typical leaf cones were the most abundant morphotype in *S.* sp. and *S. natalensis* (83.1% and 62.5% respectively, **Fig. 5.1a**: *aj-am*). *S. woodii* produced only 13.9% of leaf cones, 12.9% of which were articulated cones. Instead silica skeletons consisting of parallelepiped blocky phytoliths with other morphotypes mainly cones; and articulated parallelepiped blocky/tabular phytoliths (Fig. **5.1c**: *m*) were the most abundant morphotypes in *S. woodii* contributing 31.4% and 22.4% respectively. In addition, silica skeletons with unidentifiable cells accounted for 14.7% of the assemblage and it produced the other morphotypes such as elongate phytoliths in very small amounts (Table **A1**). *S. woodii* and *S.* sp. also produced ‘elongate crenate plates’ (0.8% and 1.6% respectively) similar to those seen in *Fuirena* species. However, the plates in *S. woodii* are beset with elliptical and spherical granulate/echinulate bodies that seem heavily infused with silica (**Fig. 5.1d**: *g*). These bodies also occur on their own in both *S. natalensis* and *S. woodii* and the elliptical granulate bodies in *S. natalensis* are often articulated with two or more bodies (**Fig. 5.1d**: *l-n*). Similar lightly decorated hemispherical convex bodies and spherical bodies, often occurring in pairs, were observed in *S. natalensis* (**Fig. 5.1d**: *o-r*).

S. natalensis also had some types of what appeared to be two articulated cones lying in parallel to another set of articulated cones (**Fig. 5.1d**: *u*, *v*). This arrangement of cones was only seen in this species. *S. natalensis* and *S.* sp. also appeared to have clearly truncated cones especially in *S. natalensis*, a character seen in only a few species analysed in this study (**Fig. 5.1a**: *aj*). In terms of cone size, *S.* sp. had the largest cones with most of those measured larger than 14µm and ranged from 5.76 to 25.76µm, those in *S. natalensis* ranged between 6.17 and 15.85µm while there were hardly any isolated cones to measure in *S. woodii* (Fig. **5.1e**, Table **A2**). It is not always easy to decipher which cones have satellites on them in all the specimens analysed in this study but *S.* sp. has conspicuous satellites on both isolated and articulated cones giving some cones an echinate appearance (**Fig. 5.1a**: *ak-am*).

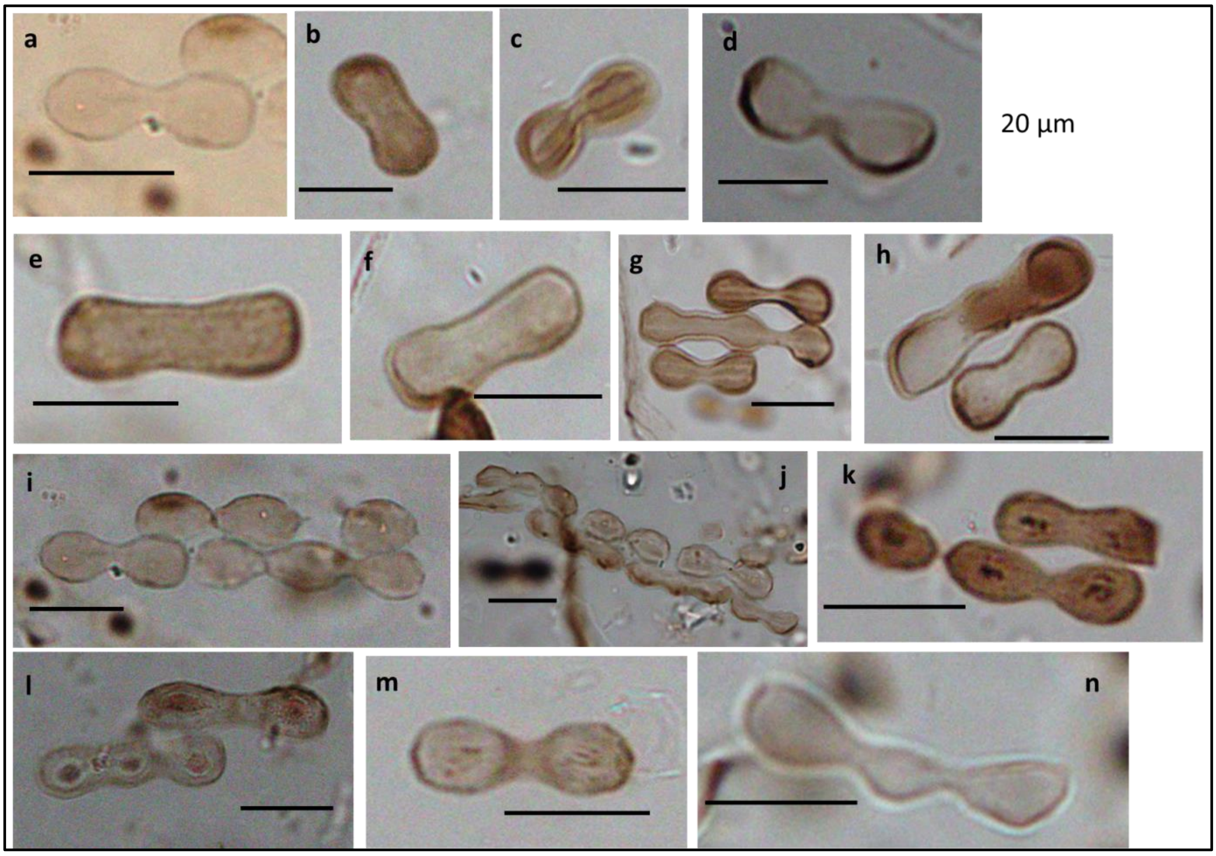


Figure 5.1a: Leaf/culm cone phytoliths that are bilo-/poly-lobate-like in *Bulbostylis* sp: **a-n**

Figure 5.1a Continued

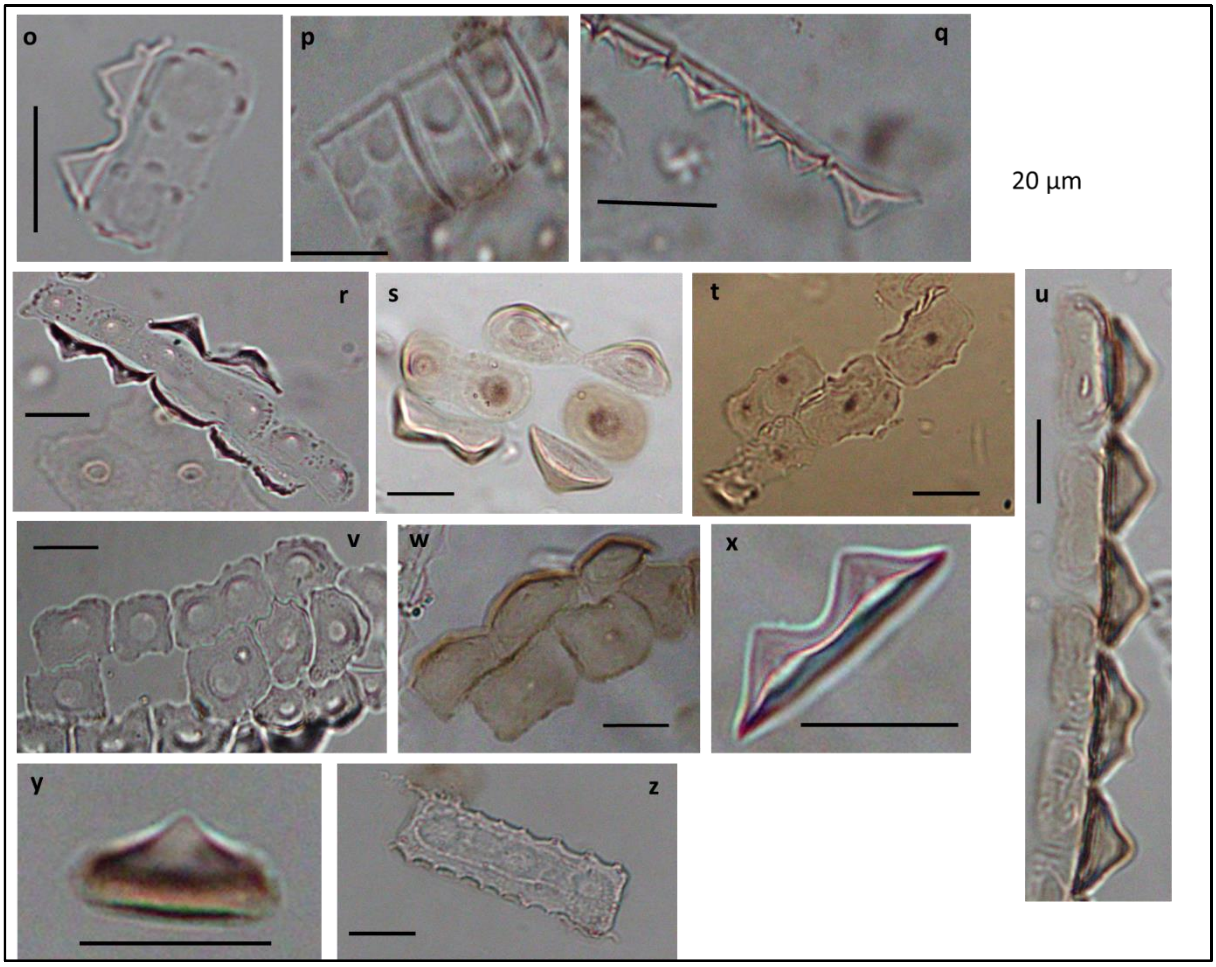


Figure 5.1a: Leaf/culm cone phytoliths: **o** *Bulbostylis burchellii*, **p-q** *Cladium mariscus*, **r** *Cyperus congestus*, **s** *C. haematocephalus*, **t-w** *C. semitrifidus*, **x-z** *Pycreus macranthus*.

Figure 5.1a Continued

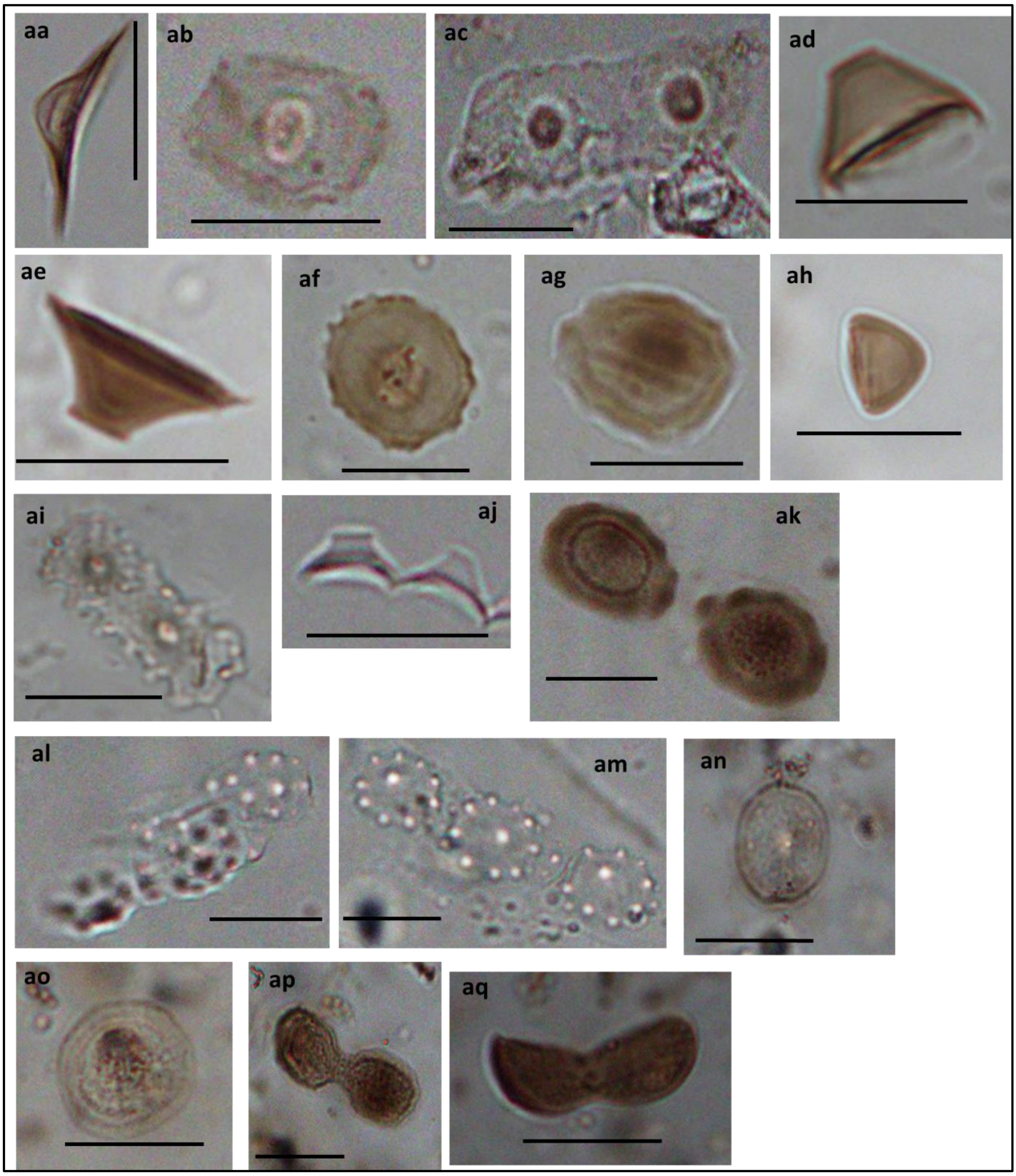


Figure 5.1a: Leaf/culm cone phytoliths: **aa-ac** *Schoenoplectus muriculatus*, **ad-ai** *S.muricinux*, **aj** *Scleria natalensis*, **ak-am** *Scleria* sp., **an-aq** *Scirpoides burkei*.

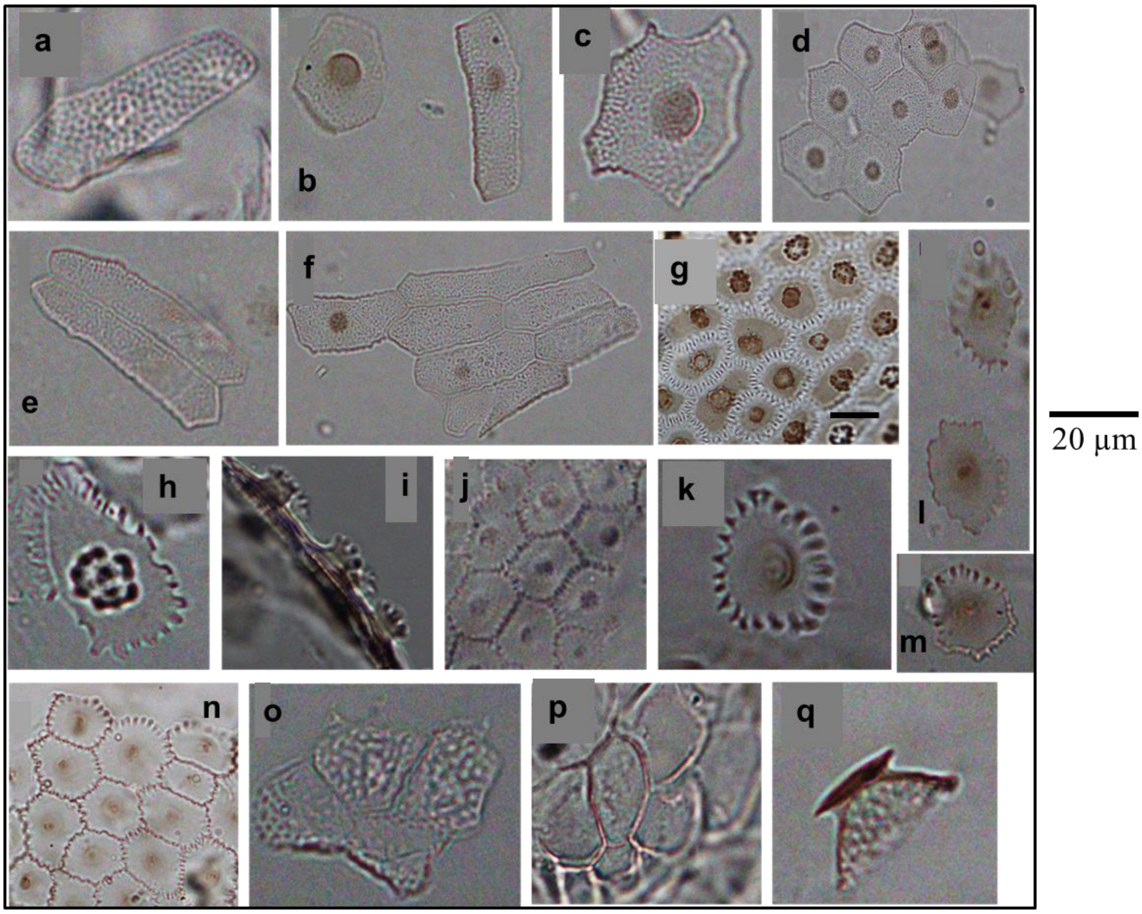


Figure 5.1b: Achene phytoliths/polygonal cones: **a** *Cyperus albastriatus*, **b-f** *C. congestus* (syn. *Mariscus congestus*), **g-i** *C. denudatus* (**h** is a high resolution of **g** and **i** is the side view), **j** *C. fastigiatus*, **k-n** *C. haematocephalus*, **o-p** *C. rigidifolius*, **q-s** *C. semitrifidus*.

Figure 5.1b Continued

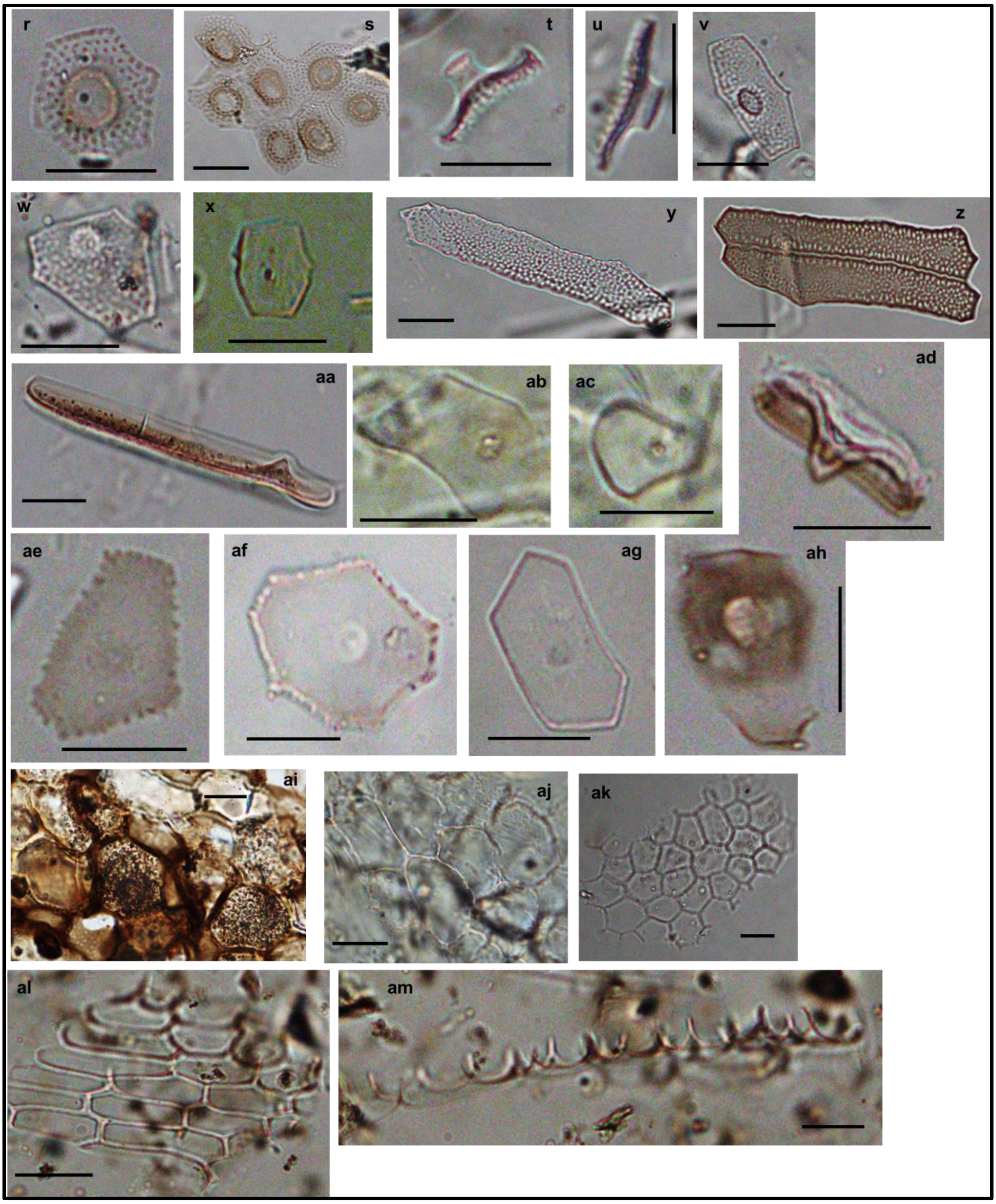


Figure 5.1b: t-v Unidentified Cyperaceae 2, **w** *Kyllinga* sp. 1, **x** *Eleocharis dregeana*, **y-aa** *Pycreus macranthus*, **ab-ac** *Pycreus* sp., **ad-ag** *Schoenoxiphium sparteum*, **ah** *Schoenoplectus muriculatus*. Polyhedral epidermal cells: **ai** *Cladium mariscus*, **aj** *Pycreus macranthus*, **ak** *Cyperus semitrifidus* **al-am** *Scirpoides burkei*.

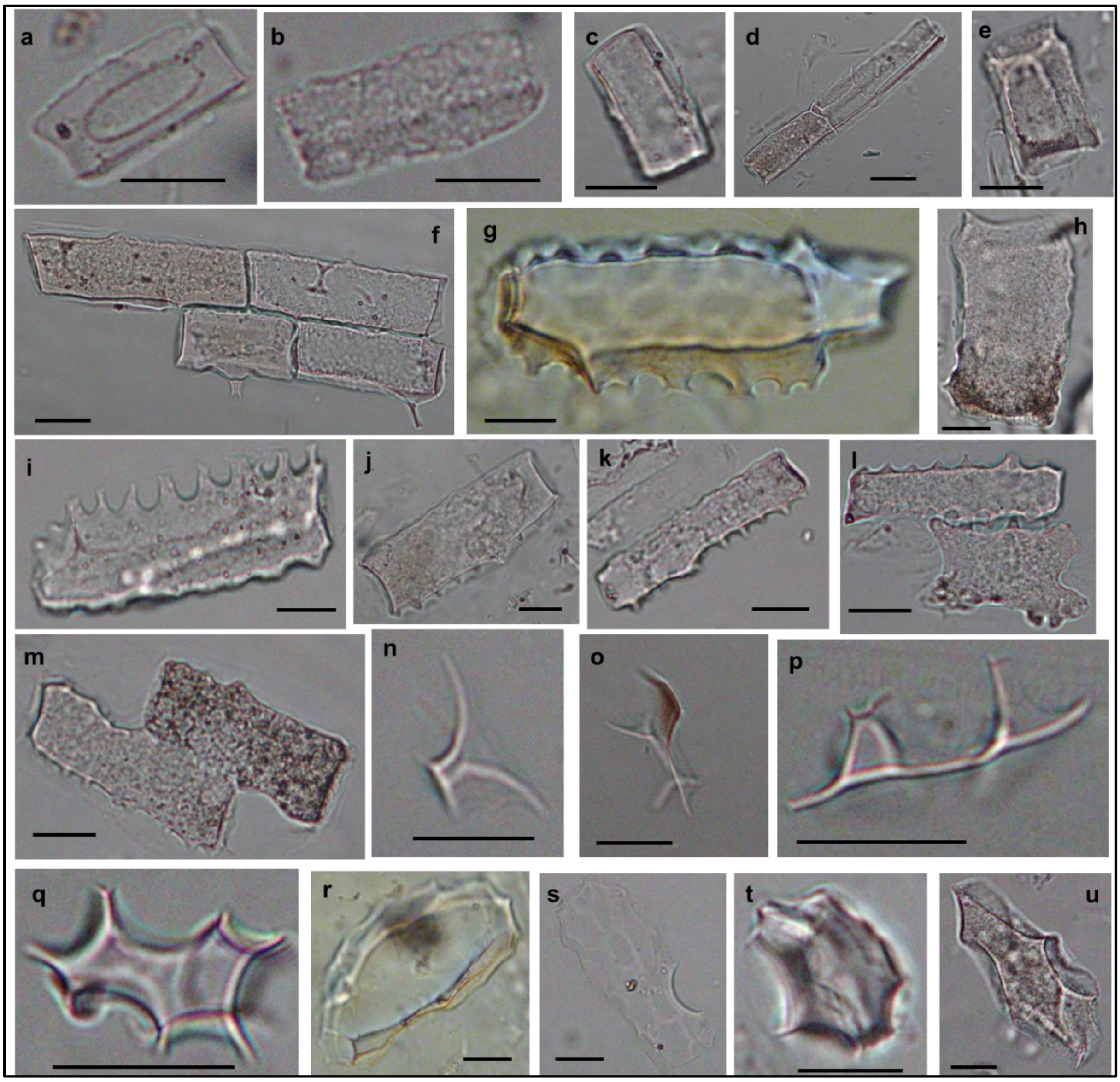


Figure 5.1c: Parallelepiped blocky and tabular phytoliths: **a** *Cyperus fastigiatus*, **b** *C. rigidifolius*, **c-d** *Eleocharis caduca*, **e** *E. dregeana*, **f** *E. cf limosa*, **g-h** *Fuirena* sp., **i** *F. pubescens*, **j** *Pycreus* sp., **k-l** *Scleria natalensis*, **m** *Scleria woodi*. Epidermal structures: **n-o** *Eleocharis* sp., **p-q** *E. caduca*. Facetate bodies: **r** *Pycreus* sp., **s** *P. macranthus*, **t-u** *Cyperus rigidifolius*.

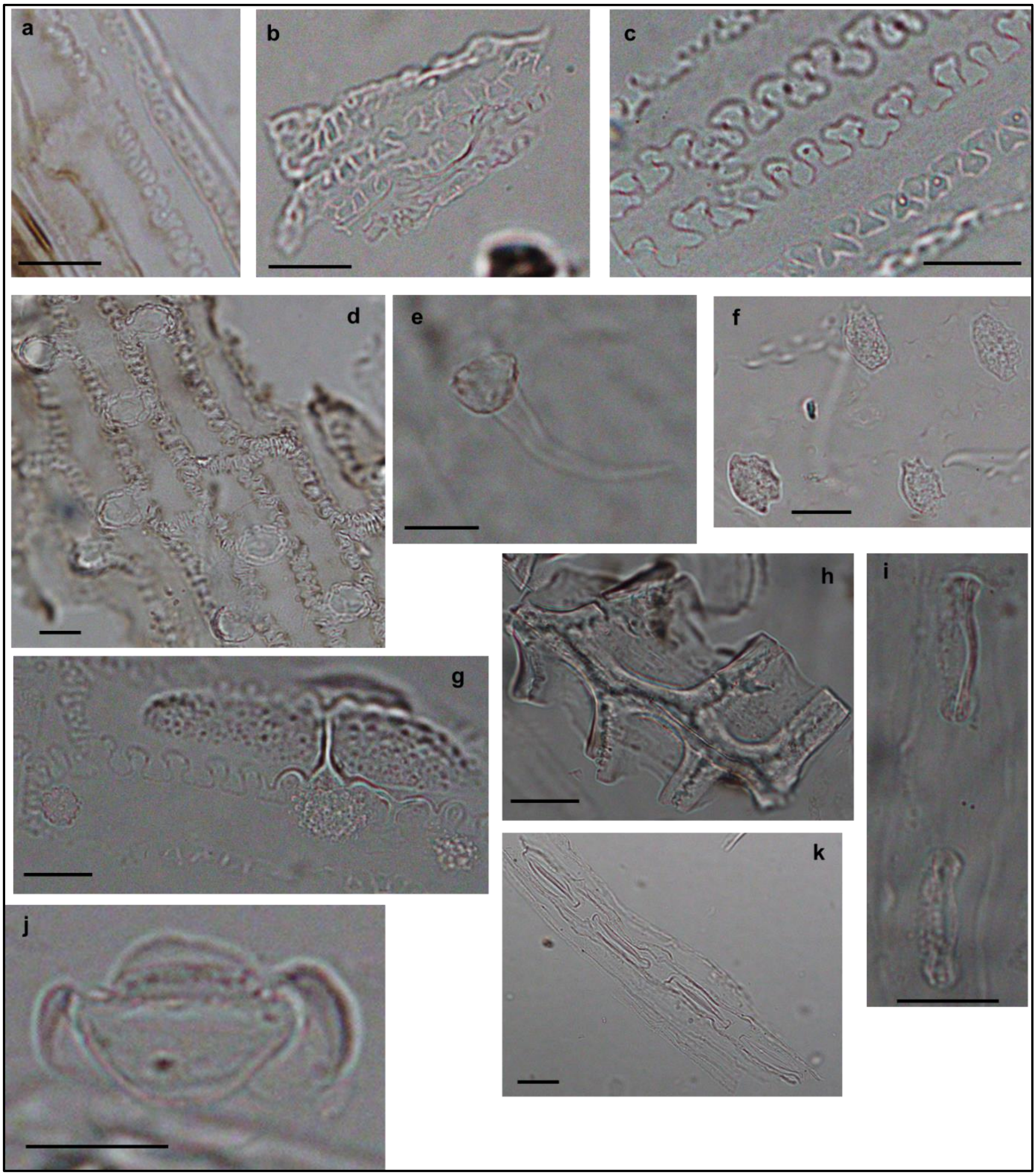


Figure 5.1d: articulated elongate crenate/pilate epidermal plates: **a** *Bulbostylis burchellii*, **b** *Fuirena pubescens*, **c**-**f** *Fuirena* sp. (**d** is embedded with spherical bodies that are hairs as seen in fine focus in **e** and another type of irregular hair bases in **f**), **g** *Scleria woodii* (beset with granulate bodies), **h** *S.* sp. Stomata: **i** *Scleria natalensis*, **j** *S. woodii*, **k** *Eleocharis* sp.

Figure 5.1d Continued

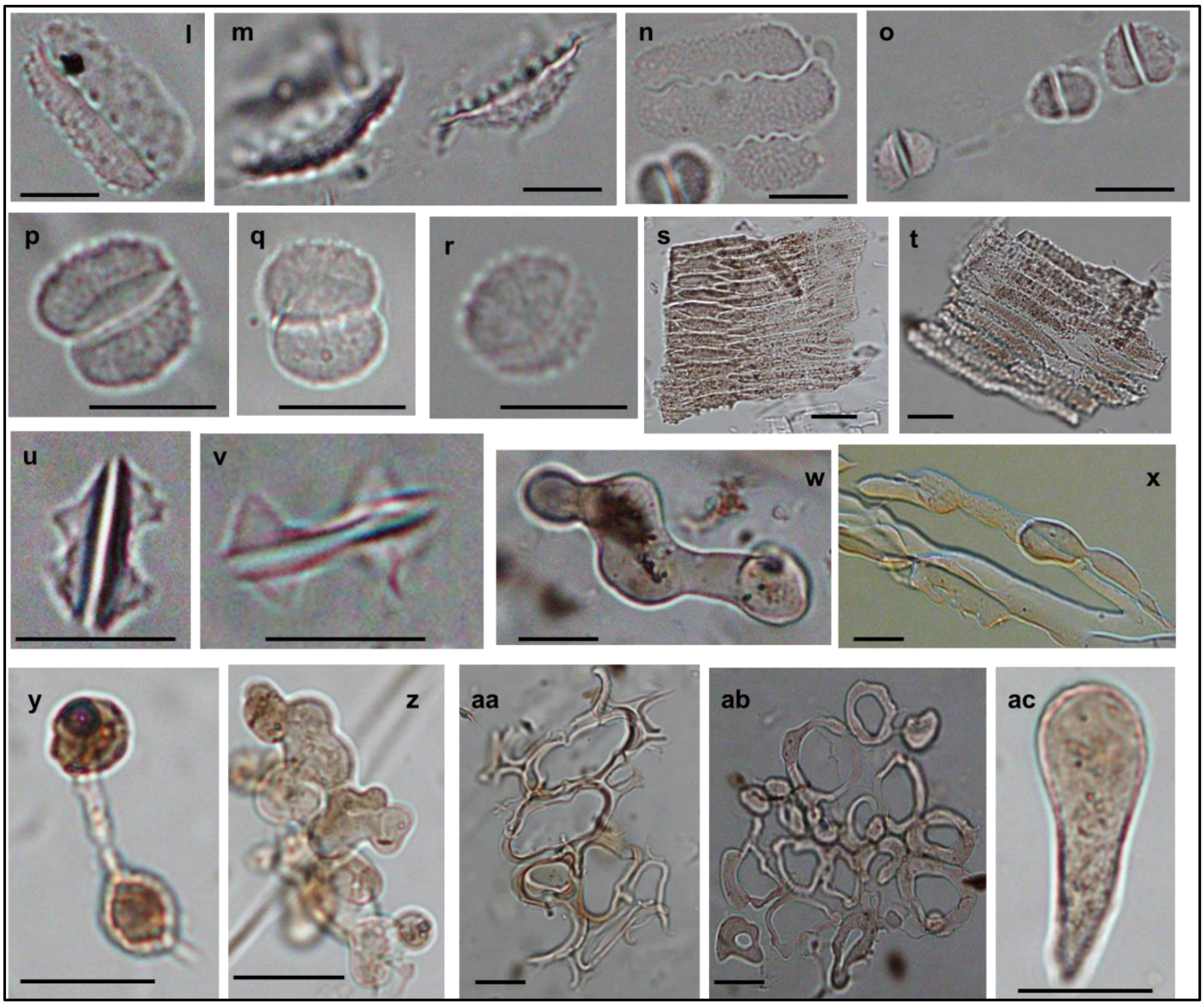


Figure 5.1d: Echinulate elliptical, hemispherical and spherical bodies: **l-r** *Scleria natalensis*. Elongate cells arranged in parallel rows: **s** *Eleocharis dreageria*, **t** *Fuirena pubescens*. Cones in parallel: **u-v** *Scleria natalensis*. Bulbous structures (some sclereids): **w** *Cladium mariscus*, **x** *Pycreus maranthus*, **y-aa** *Schoenoplectus corymbosus*, **ab** *Schoenoplectus* sp., **ac** *Schoenoplectus muricinux*.

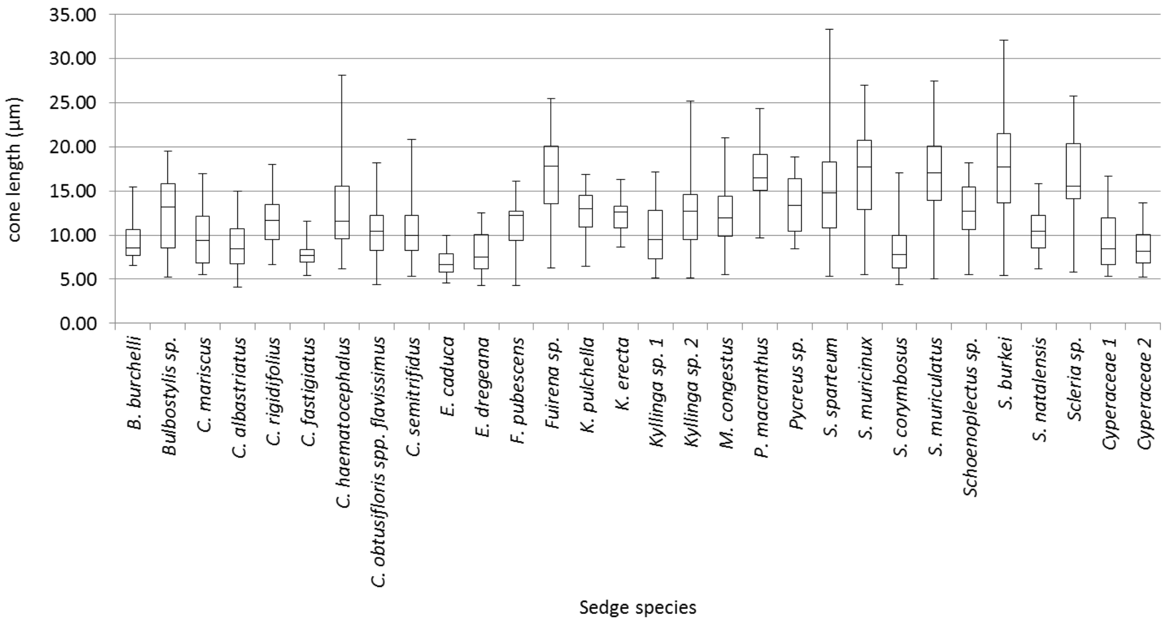


Figure 5.1e: A box and whisker graph showing the estimated cone size ranges (length of the longest axis of the base) from sampled cones in each species. The mean values (midlines), standard error± (boxes) and standard deviation (whiskers) are given for each of the species.

5.2 Phytolith morphotypes in the family Poaceae (grasses) (Figure 5.2a)

Phytoliths were observed in all of the 19 grass species studied that represent four grass subfamilies. All species were characterised by grass short cells that are typical for grasses and are illustrated in Fig. **5.2a**. Non-short cell phytolith morphotypes occurred in insignificant amounts in all species studied and examples of such morphotypes are shown in Fig. **5.2a**. The common morphotypes in each species and subfamily are presented below. Unless otherwise stated, percentages described here are those of grass short cell phytoliths only. The graphs in Figs. **5.2b**, **5.2c**, **5.2d** show the relative abundance of grass short cells in each grass species and overall subfamily. Their % of dry silica is shown in Table **A3** of appendix and it was above 5% in only one species i.e. *Oplismenus* sp. The raw counts of grass morphotypes in each species and subfamily are detailed in Table **A4** in the appendix.

5.2.1 Aristidoideae

This subfamily was represented by one *Aristida* sp. and its assemblage is made up of lobates (79.7%) and rondels (20.3%) (Fig. **5.2b**, **5.2c**). The lobates were made up of; 44.9% bilobates with short shanks and convex ends (BSCVX) (Fig. **5.2a**: *b*), 27.5% bilobates with long shanks and convex ends (BLCVX) (Fig. **5.2a:** *c*) and 7.2% of trapeziform bilobates (BT).

5.2.2 Arundinoideae

This subfamily was represented by one species - *Phragmites australis* - which in terms of grass short cells only, was made up of 93.5% rondel and 6.5% saddle phytoliths (Fig. **5.2b - 5.2d**). The other non-grass short cell morphotype observed in the count was the tabular echinate (Fig. **5.2a**: *ap*) which contributed only 1.5%. This species is made up of all kinds of rondels – those that are saddle-like, those that are conical, those that appear horned and those that are truncated (Fig. **5.2a**: ac-ak). Horned rondels (Fig. **5.2a**: *ad*, *ae*, *aj*) were most conspicuous in this species and were often tall (those that were sampled ranged from 15 to 19.94 µm in height). Its conical rondels (**5.2a:** *ak*) were also tall measuring up to 12.65 µm in those sampled. The saddles in *Phragmites australis* are illustrated in Fig. **5.2a**: *v*-*y* and often appear plateaued as in *v*.

5.2.3 Chloridoideae

Overall, the Chloridoideae subfamily was represented by rondel phytoliths (60.1%), followed by saddles (SAD) (20.2%) and lobates (19.7%) (Fig. **5.2b**). Other than *Fingerhuthia* sp., all the other species were dominated by rondel phytoliths with *Dactyloctenium* sp. having an equal amount of rondels and saddle phytoliths in its assemblage (50.2% and 49.3% respectively, Fig. **5.2c**). *Eragrostis superba* and *Sporobolus africanus* are largely represented by rondel phytoliths in their assemblage (96.4% and 89.3% respectively) with saddles (SAD) occurring in much smaller amounts of 3.6% and 8.3% respectively (Fig. **5.2a**: *z*, *aa*). Saddles (SAD) were only common in *Dactyloctenium* sp. (49.3%) and *Eragrostis* sp (41.3%) (Fig. **5.2c**). On the other hand, *Fingerhuthia* sp. was dominated by lobate phytoliths up to 81.1% (Fig. **5.2c**). These lobates are composed of mainly crosses (46.1%) (Fig. **5.2a**: *o-q*) and it also has special crosses that are H-shaped (*p*, *q*), a character only seen in this species. It was followed in abundance by bilobates with generally long shanks and concave margins and those with straight margins (BLCVE, BLSM) (35%), followed by rondels (18.9%) with no saddle phytoliths in the count.

5.2.4 Panicoideae

Panicoideae grasses produce abundant lobate morphotypes (69.1%), followed by rondels (30.4%), few saddles (0.4%) and trapeziform sinuate (0.1%) (Fig. **5.2b**). Bilobates are therefore the most dominate morphotype in eight species of the 10 species studied (Fig. **5.2c**). The remaining two species, *Setaria pallide-fusca* and *Panicum maximum* displayed a different tendency. *Setaria pallide-fusca* had bilobates that are in equal numbers as rondels each being almost 50% with 1.4% of trapeziform sinuate phytoliths while *Panicum maximum* was dominated by 91.1% of rondel phytoliths with only 8.9% of crosses that look like small bilobates (Fig. **5.2a**: *t*, *u*; Fig. **5.2c**), that sometimes appear trapezoidal (Fig. **5.2a**: *u*). Panicoideae grasses were made up of all types of known lobates but the most common types were crosses (15.1%), bilobates with short shanks and convex margins (BSCVX) (15.6%) and bilobates with short shanks with concave margins (BSCVE) (14.6%) (Fig. **5.2a**: *d-h*; **5.2d**). The other bilobate types occur in smaller amounts: bilobates with long shanks with concave margins (BLCVE) (7.4%), bilobate trapeziform (BT, 6.1%), (Fig. **5.2a**: *i-k*), bilobate short shanks with straight margins (BSSM) (3.6%), bilobate with generally long shanks with convex margins (BLCVX) (2.8%), bilobate nodular (BN) (1.6%; Fig. **5.2a**: *l*, *m*), polylobate (POLY) (1.6%; Fig. **5.2a**: *n*) and bilobate flared margins (BF) (0.1%). Polylobate phytoliths (POLY) (Fig. **5.2a**: *j*), were only observed in this subfamily and are very rare across the species and were only common in *Melinis repens* contributing 13% of its assemblage. Bilobate nodular phytoliths (BN) (Fig. **5.2a**: *l*, *m*) were also rare across the species but appeared more pronounced in *Melinis repens*. It is only in *Melinis repens* that two bilobates with a toothed or serrated width margin were observed and these were added to those with a concave margin.

5.2.5 Pooideae

This family is represented by only an *Agrostis* sp. Its phytolith assemblage is made up of lobates (44.1%), rondels (40.1%), saddles (11.9%) and trapeziform sinuate (4%) (Fig. **5.2b**, **5.2c**). The lobates are 23% bilobates and 21.1% crosses, with bilobates with short shanks and convex margins (BSCVX) being the most abundant bilobate type (10.6%; Fig. 5.2a: *a*) and other types occur in small amounts.

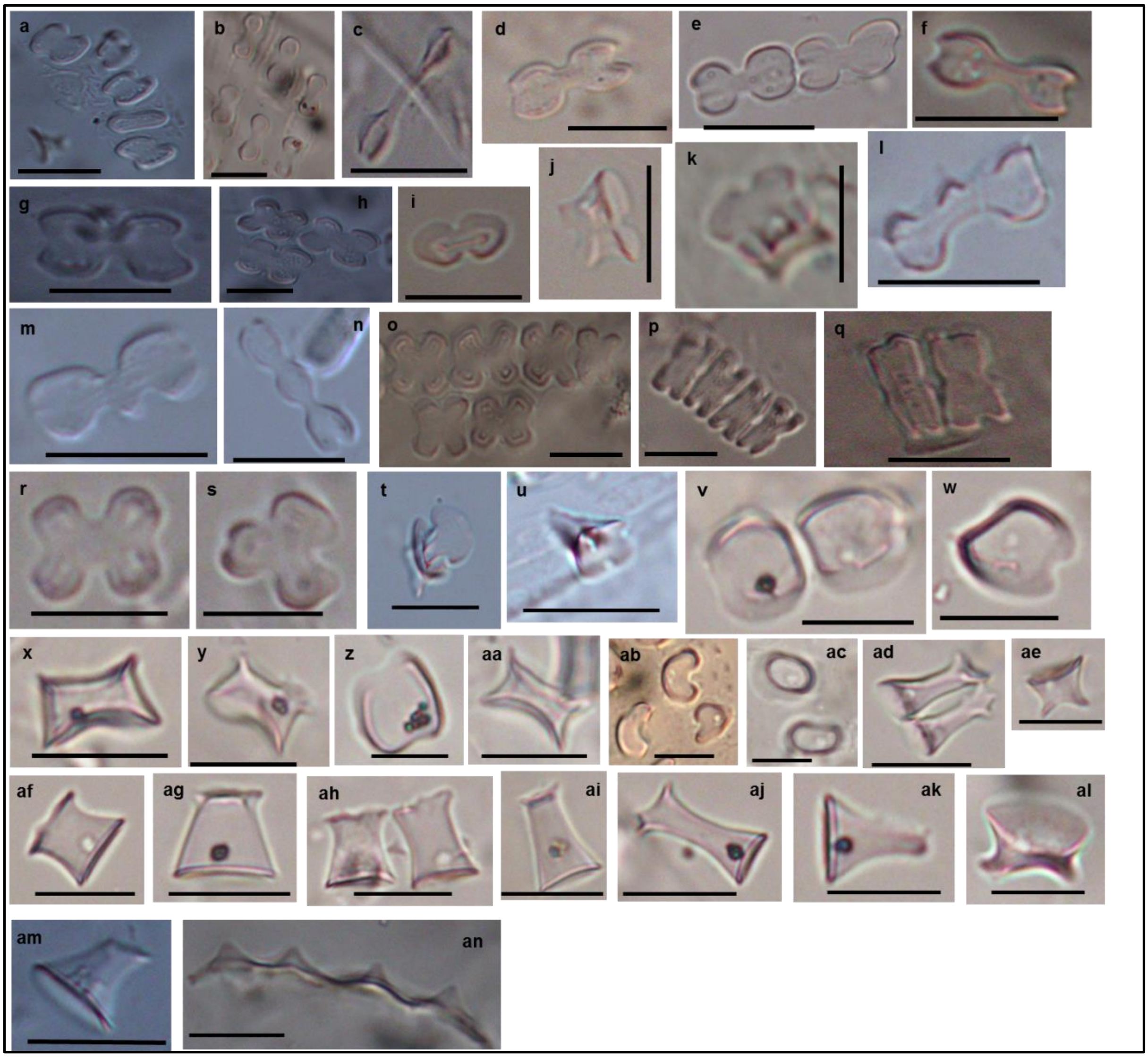


Figure 5.2a: Bilobate short and long shank convex ends: **a** *Agrostis* sp. (Pooideae), **b-c** *Aristida* sp. (Aristidoideae). Bilobate short shank concave/notched ends: **d-f** *Monocymbium ceresiiforme* (Panicoideae), **g-h** *Fingerhuthia* sp. Bilobate trapeziform: **i-j** *Monocymbium ceresiiforme*, **k** *Panicum maximum* (Panicoideae). Bilobate nodular: **l** *Odontelytrum* sp., **m** *Setaria megaphylla* (Panicoideae). Polylobate: **n** *Setaria megaphylla* (Panicoideae). Crosses: **o-q** *Fingerhuthia* sp. (**p** and **q** are unique H-shaped crosses), **r-s** *Monocymbium ceresiiforme*, **t-u** *Panicum maximum* (Panicoideae). Saddle: **v-y** *Phragmites australis* (Arundinoideae), **z-aa** *Eragrostis superba* (Chloridoideae). Rondel: **ab** *Aristida* sp., **ac-ak** *Phragmites australis* (Arundinoideae), **al** *Eragrostis superba* (Chloridoideae), **am** *Agrostis* sp. Cone-shaped: **an** *Digitaria* sp. 2 (Panicoideae).

Figure 5.2a Continued

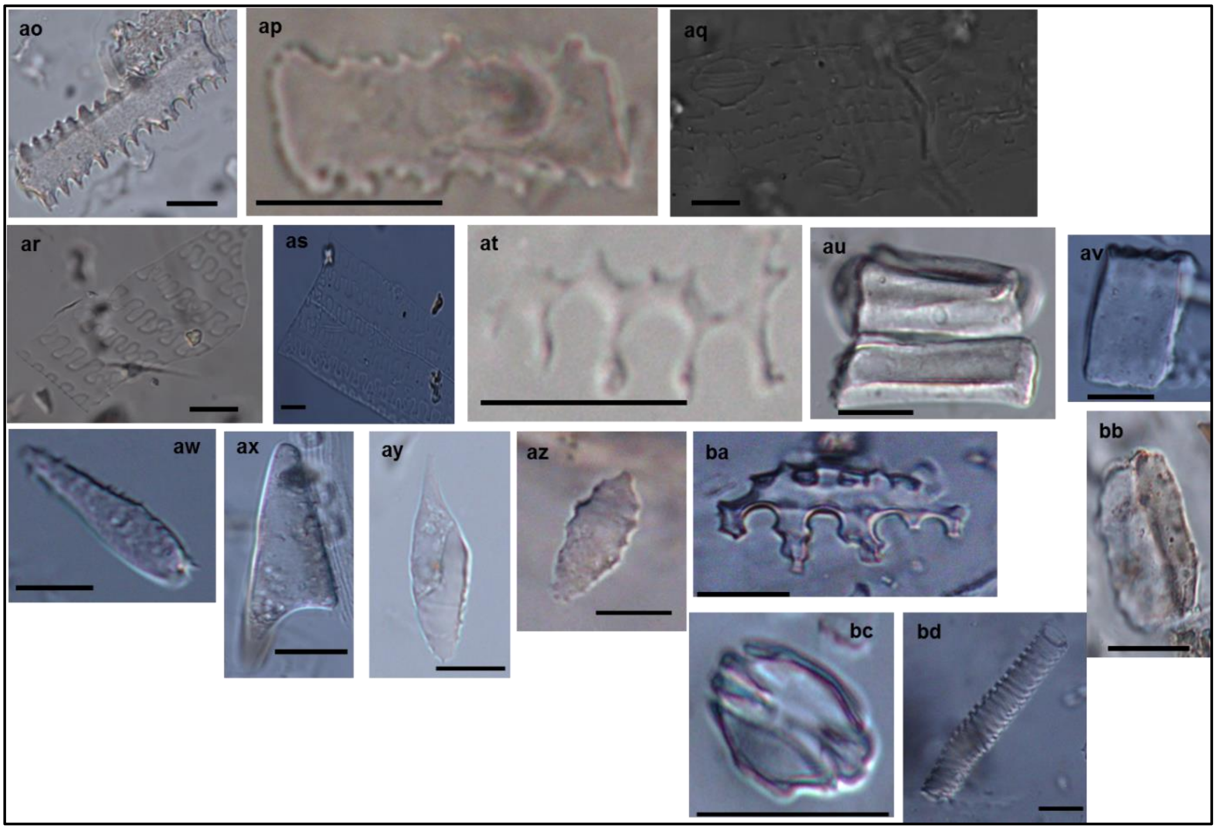


Figure 5.2a: Elongate echinate: **ao** *Odontelytrum* sp. (Panicoideae). Tabular echinate: **ap** *Phragmites australis* (Arundinoideae). Plates with elongate crenate/columellate cells: **aq** *Mellinis repens* (with stomata), **ar** *Setaria fusca pallida* (Panicoideae), **as** *Panicum maximum* (Panicoideae). Dendritic: **at** *Agrostis* sp. (Pooideae). Bulliform: **au-av** *Setaria megaphylla* (Panicoideae). Acicular: **aw-ax** *Setaria megaphylla*, **ay-az** *Panicum maximum*. Irregular: **ba** *Fingerhuthia* sp. Blocky parallelepiped: **bb** *Odontelytrum* sp. (Panicoideae). Stomata: **bc** *Setaria megaphylla* (Panicoideae). Tracheid: **bd** *Digitaria* sp. 2.

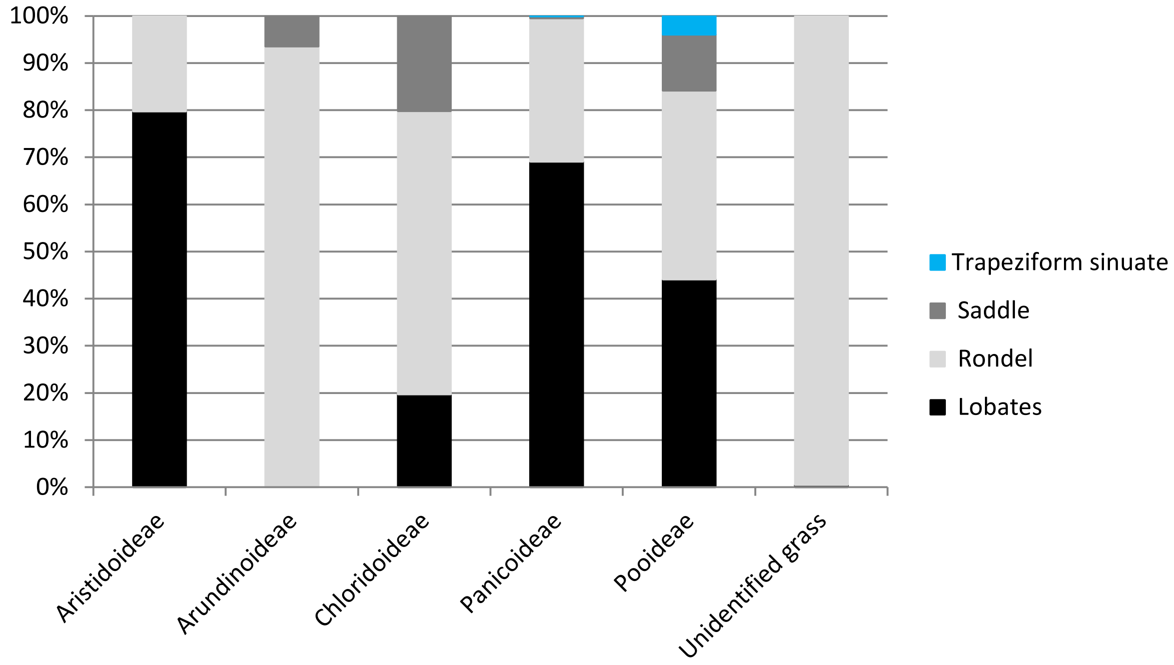


Figure 5.2b: Graph showing the relative dominance of main morphotype categories of grass silica short cells in each grass subfamily and in the unidentified grass.

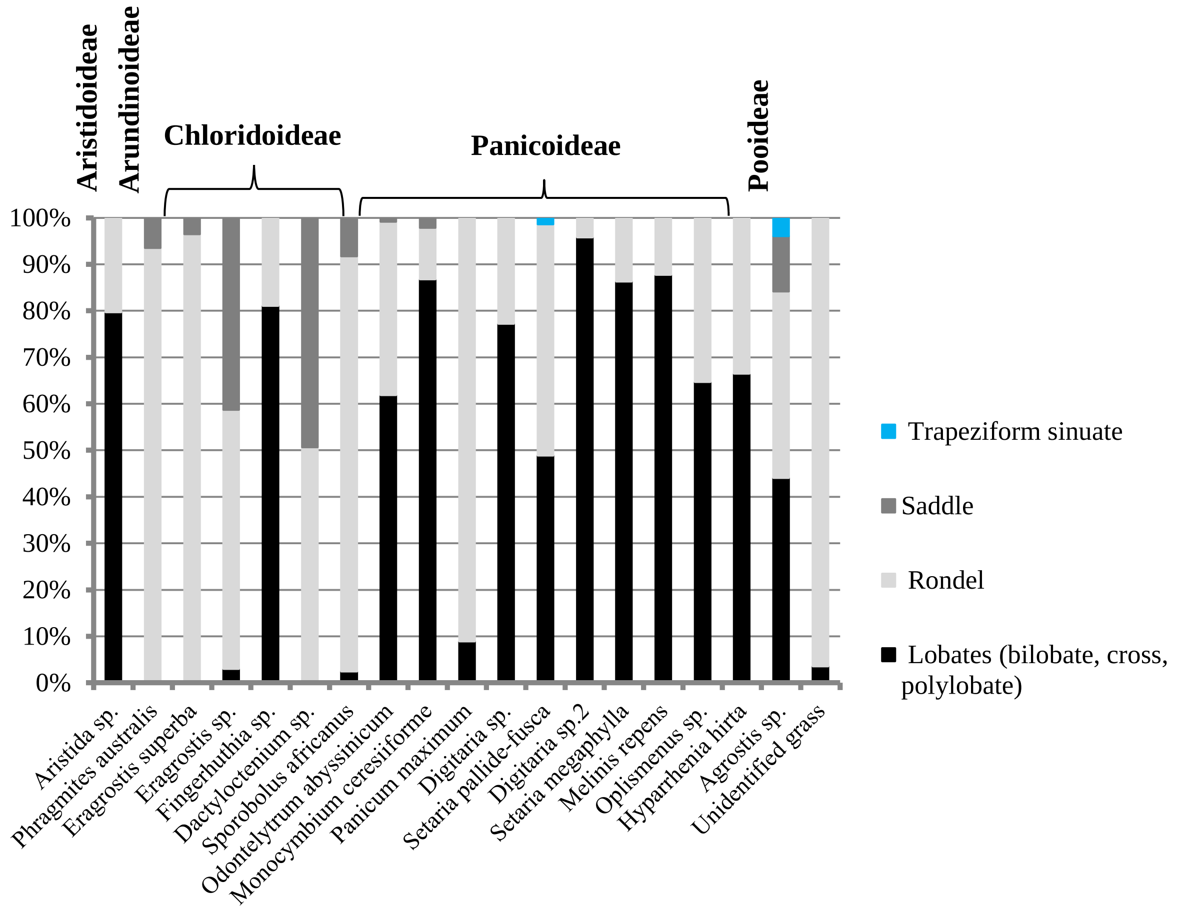


Figure 5.2c: Relative abundance of main morphotypes of grass silica short cells (Lobate, Rondel, Saddle and Trapeziform sinuate) in 19 grass species of KwaZulu Natal.

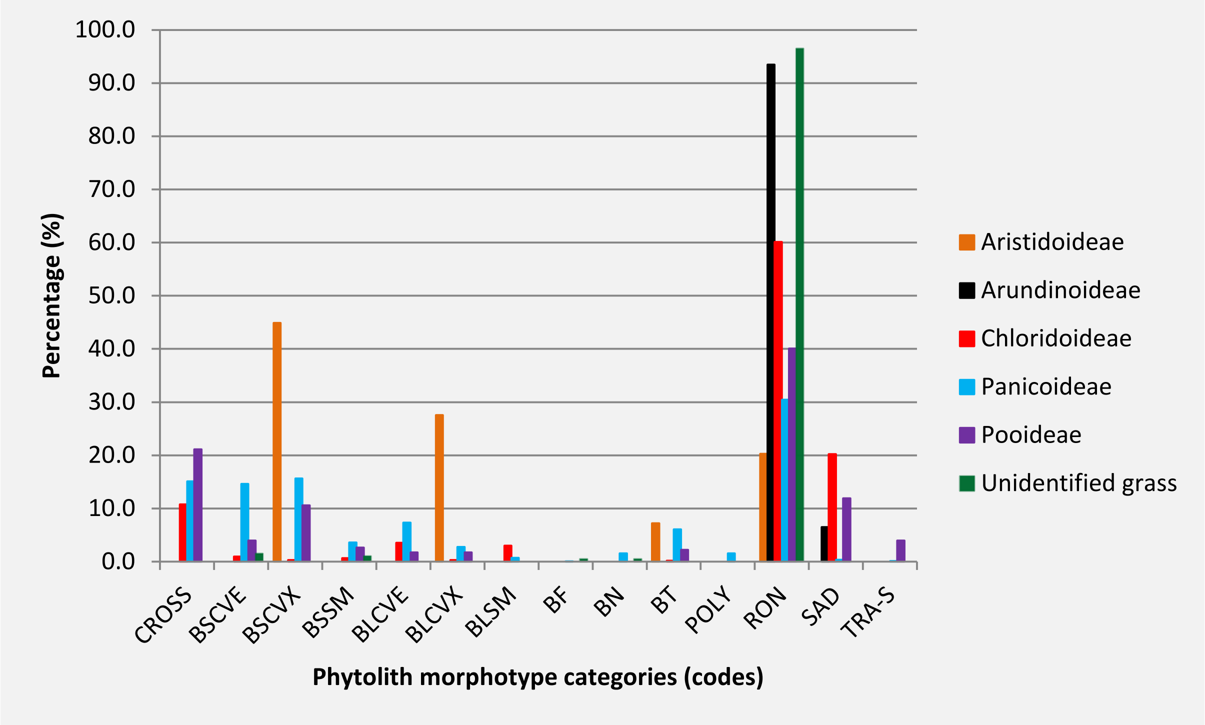


Figure 5.2d: Graph showing the relative dominance of specific morphotypes of grass silica short cells in each grass subfamily and in the unidentified grass.

5.2.6: Correspondence analysis (CA) among grass morphotypes

Figure **5.2e** presents results of the CA that was run for only grass short cells phytoliths to identify similarities among grass species. The first two axes account for 46.2% of the variability in the data with the first axis (eigenvalue 0.530) explaining 28.9% of the total variance and the 2nd axis (eigen value 0.317) explained 17.3% of the total variance. The distribution of morphotypes in the ordination diagram generally depicts the known relationship between grass subfamilies and their phytolith morphotype categories and environmental factors can be indirectly be inferred. It depicts the known separation of morphotypes among major subfamilies of Poaceae with some deviations i.e. Panicoideae, Chloridoideae, Pooideae and Aristidoideae while Arundinoideae falls in the redundant group as expected. However, Pooideae, Aristidoideae and Arundinoideae are each represented by a single species. Panicoideae grasses are predominantly identified by lobate phytoliths that are: cross, polylobate and bilobate of which are: bilobates with a trapeziform outline, bilobates with short and long shanks with concave margins, bilobates with short and long shanks with straight margins, bilobates with nodular shanks, bilobates with flared margins and bilobates with short and long shanks with convex margins. Only the Panicoideae species *Panicum* *maximum* did not appear in this group and fell in the redundant group that was represented by rondel shaped phytoliths. On the other hand, Aristidoideae is represented by bilobates with long and short shanks with convex margins only. Chloridoideae was represented by saddle shaped phytoliths in *Dactyloctenium* sp. and *Eragrostis* sp. with the exception of *Sporobolus africana* and *Egragrostis superba* that fell in the redundant rondel category while *Fingerhuthia* sp. was grouped with the Panicoideae subfamily. Pooideae, although closely placed to Panicoideae because of the abundance of bilobates present is placed on its own because of the presence of trapeziform sinuate phytoliths.

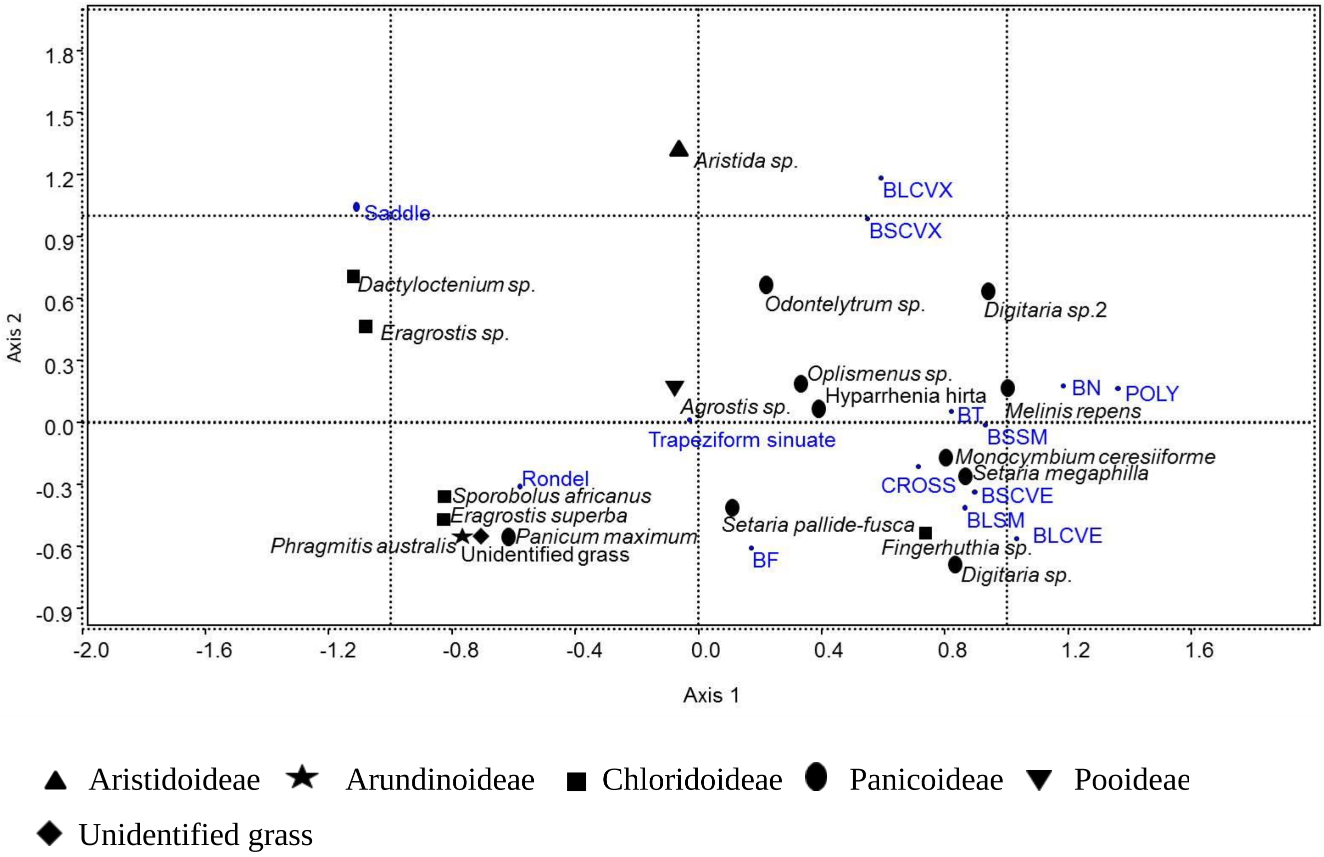


Figure 5.2e: Shows a scatter plot obtained from correspondence analysis of 14 phytolith morphotypes (blue) from 19 grass species (black).

5.3 Phytoliths in the eudicots (mainly woody plants) (Figure 5.3a – 5.3d)

The occurrence of morphotypes in the woody plants studied is detailed below in Table **5.1**. The main morphotypes are illustrated in Figures **5.3a**, **5.3b**, **5.3c** and **5.3d**. More morphotypes to further illustrate the variations of these eudicot morphotypes are presented at the end of the appendix for select species. The results presented here are from 42 species from 24 families of eudicots (see Chapter four). Although production is variable among species, eudicots generally exhibit the least phytolith abundance compared to grasses and sedges. Morphotypes observed in the dicots are mainly globular psilate, hair bases, epidermal polyhedrals, epidermal anticlinal, bulbous structures, cystoliths, tracheid elements, stomata, sclereids, irregular bodies, blocky and a few genus-specific bodies.

5.3.1 Phytolith production in eudicots families

Of the species studied, about 77% produced phytoliths with *Ficus polita* and *Ficus sur* (Moraceae) having the highest percentage of silica content by weight (6.3% and 5% respectively) and together with *Celtis africana* (Celtidaceae), *Trichilia emetica* (Meliaceae) and *Podocarpus latifolius* (Podocarpaceae) appeared to generally have the highest phytolith abundancy during microscopy. The only other species to yield silica above 5% of the dry weight was *Clerodendrum glabrum* (Lamiaceae). Other species that exhibited relatively high phytolith abundance under the microscope were: *Brachylaena discolor* (Asteraceae), *Deinbolia oblongifolia* (Sapindaceae), *Mimusops obovata* (Sapotaceae), *Macaranga capensis* (Euphorbiaceae), *Tabernaemontana ventricosa* (Apocynaceae), *Eugenia capensis* (Myrtaceae), *Vepris lanceolata* (Rutaceae), *Rawsonia lucida* (Achariaceae), *Celtis mildbraedii* (Celtidaceae), *Millettia grandis* (Fabaceae), *Acalypha glabrata* (Euphorbiaceae), *Dichrostachys cinerea* (Fabaceae), *Clutia pulchella* (Euphorbiaceae), *Acalypha sonderiana* (Euphorbiaceae), *Clerodendrum glabrum* (Lamiaceae), *Obetia tenax* (Urticaceae) and *Syzygium cordatum* (Myrtaceae). Those that exhibited relatively fewer phytoliths were *Acacia ataxacantha* (Fabaceae), *Diospyros natalensis* (Ebenaceae), *Tetradenia riparia* (Lamiaceae), *Baphia racemosa* (Fabaceae), *Rhoicissus tomentosa* (Vitaceae), *Cryptocarya woodii* (Lauraceae) and *Ekebergia capensis* (Meliaceae). Species that appear not to produce any phytoliths or had several tiny silica bodies that offer no taxonomic significance are: *Ochna natalitia* (Ochnaceae), *Schotia bracypetala* (Fabaceae), *Vangueria infausta* (Rubiaceae), *Teclea gerrardii* (Rutaceae), *Albizia adianthifolia* (Fabaceae), *Carissa bispinosa*

(Apocynaceae), *Protorhus longifolia* (Anacardiaceae) *Rhoicissus rhomboidea* (Vitaceae), *Sideroxylon inerme* (Sapotaceae), *Ziziphus mucronata* (Rhamnaceae).

All species that produced phytoliths consisted of morphotypes that have a consistent morphology that can be related to a specific plant tissue as in Piperno (2006) and Collura and Neumann (2017) or that can be clearly defined in the phytolith terms of Madella et al. (2005).

Table 5.1: Eudicots analysed, their phytolith morphotypes and their occurrence. *Species with diagnostic or unique morphotypes A = abundant; R = rare.

Family	**Species**	**Plant habit**	Globular psilate	Polyhedral	Anticlinal	Mesophyll tissue	Blocky PLP	Hair bases	Trichomes	Cystoliths	Tracheid	Sclereid	Blocky irregular	Irregular	Elongate	Elongate facetate	Ellipsoid	Stomata	Bulbous structures
Achariaceae	*Rawsonia lucida*	woody		**A**			**R**	**R**				**A**				**A**		**R**	**R**
Anacardiaceae	*Protorhus longifolia*	woody																	
Apocynaceae	*Carissa bispinosa*	woody																	
Apocynaceae	*Tabernaemontana ventricos*	woody	**R**	**A**														**A**	
Asteraceae	*Brachylaena discolour*	woody		**R**				**A**	**R**		**R**				**R**				**R**
Celtidaceae	*Celtis africana* *****	woody						**A**		**A**	**R**								
Celtidaceae	*Celtis mildbraedii* *****	woody	**R**	**A**	**A**			**R**							**C**			**C**	
Ebenaceae	*Diospyros natalensis*	woody					**R**				**R**				**R**				
Euphorbiaceae	*Acalypha glabrata*	woody		**C**	**A**		**C**	**R**			**R**		**A**						
Euphorbiaceae	*Acalypha sonderiana*	woody		**R**	**A**		**R**								**C**				
Euphorbiaceae	*Clutia pulchella*	woody		**C**		**R**		**R**	**R**		**A**		**R**	**R**					
Euphorbiaceae	*Macaranga capensis*	woody		**A**	**A**	**R**					**R**		**A**	**R**	**R**				
Fabaceae	*Acacia ataxacantha*	woody		**R**							**R**				**R**				
Fabaceae	*Albizia adianthifolia*	woody																	
Fabaceae	*Baphia racemosa*	woody	**C**												**C**				
Fabaceae	*Dichrostachys cinerea*	woody	**R**								**R**				**C**			**A**	
Fabaceae	*Milletia grandis*	woody		**A**	**A**						**R**				**A**				
Fabaceae	*Schotia bracypetala*	woody																	
Lamiaceae	*Clerodendrum glabrum*	woody		**R**		**R**		**A**			**C**							**R**	
Lamiaceae	*Tetradenia riparia*	herbaceous																	
Lauraceae	*Cryptocarya woodi*	woody									**A**								
Meliaceae	*Ekebergia capensis*	woody	**R**	**R**				**R**											
Meliaceae	*Trichilia emetica*	woody	**A**		**A**			**A**			**A**								
Moraceae	*Ficus ingens*	woody		**A**				**C**			**R**								
Moraceae	*Ficus polita* *****	woody	**A**	**A**			**R**			**A**					**R**				**C***
Moraceae	*Ficus sur*	woody		**A**				**C**			**C**								
Moraceae	*Ficus* sp.	woody		**A**															
Myrtaceae	*Eugenia capensis*	woody		**R**			**R**	**A**						**A**					**A**
Myrtaceae	*Syzygium cordatum*	woody	**C**			**R**	**R**	**R**			**R**							**A**	**C**
Ochnaceae	*Ochna natalitia*	woody																	
Phyllanthaceae	*Bridelia micrantha*	woody	**R**												**R**				
Podocarpaceae	*Podocarpus latifolius*	woody	**A**	**R**				**R**						**A***	**R**				**A**
Rhamnaceae	*Ziziphus mucronata*	woody																	
Rubiaceae	*Vangueria infausta*	woody																	
Rutaceae	*Teclea gerrardii*	woody																	
Rutaceae	*Vepris lanceolata*	woody	**A**															**A**	
Sapindaceae	*Deinbollia oblongifolia*	woody					**R**	**A**	**A**										
Sapotaceae	*Mimusops obvata*	woody	**A**																
Sapotaceae	*Sideroxylon inerme*	woody																	
Urticaceae	Obetia tenax	woody		**A**				**R**											
Vitaceae	*Rhoicissus rhomboidea*	herbaceous																	
Vitaceae	*Rhoicissus tomentosa*	herbaceous	**R**		**R**			**R**											**R**

5.3.2 Common and ubiquitous phytolith morphotypes

Morphotypes observed in the eudicots are mainly globular psilate types, hair bases, epidermal polyhedral and anticlinal structures, bulbous structures, tracheid elements, stomata, irregular bodies and; the more rare cystoliths and a few genus-specific bodies. Epidermal ground mass phytoliths (polyhedral and anticlinal structures that are often multicellular) are the most recurrent type with their occurrence varying from abundant to rare with the polyhedral type being more common. These epidermal multicellular structures occur in about 45% of the species studied. Common also were the globular psilate morphotypes and hair bases that were observed in 30% of the species studied. Stomata and tracheid elements were also relatively recurrent while blocky parallelepiped, elongate and sclereid morphotypes were less frequently encountered. In species that produced phytoliths, all species have various morphotypes or at least two morphotypes. Below are results of common phytoliths morphotypes and the species they occurred in.

Globular psilates (Fig. **5.3a**: *a-d*) were abundant to common in *Baphia racemosa*, *Ficus polita*, *Mimusops obovata*, *Podocarpus latifolius*, *Syzygium cordatum*, *Trichilia emetica* and *Vepris lanceolata*; and were rare in other species. Globular psilates are usually below 10 µm but larger sizes e.g. 13.43 µm were seen in some species such as *Vepris lanceolata*. Multicellular epidermal polyhedral (Fig. **5.3a**: *e-k*) were abundant to common in *Acalypha sonderiana*, *Clutia pulchella*, *Celtis africana*, *Celtis mildbraedii*, *Ficus* sp., *Ficus ingens*, *Ficus sur*, *Macaranga capensis*, *Millettia grandis*, *Rawsonia lucida*, *Obetia tenax* and *Tabernaemontana ventricosa*. These polyhedral types were generally abundant in the families: Euphorbiaceae, Fabaceae and Moraceae. Some multicellular epidermal polyhedral types shown in Fig. **5.3a**: *e, f* in *Celtis* spp. are presented further in section 4.3.3 under special phytoliths as they appear to be more genus specific.

Hair bases are abundant to common in *Brachylaena discolor*, *Celtis africana*, *Celtis mildbraedii*, *Clerodendrum glabrum*, *Deinbollia oblongifolia*, *Eugenia capensis*, *Ficus polita* and *Ficus sur*. Hair bases are often infused with cystoliths in some species such as *Ficus* (Fig. **5.3a**: *u-z*). Stomata (Fig. **5.3a**: *aa-ae*; Fig. **5.3d**: *h*) were common in *Dichrostachys cinerea*, *Syzygium cordatum*, *Tabernaemontana ventricosa*, *Trichilia emetic*a, *Deinbollia olongifolia* and *Vepris lanceolata*. More illustrations of various stomata can be found at the end of the appendix e.g. in plate p and q of *Tabernaemontana ventricosa* and *Trichillia emetica* respectively.

Spherical facetate bodies (Fig. **5.3a**: *af*, *ag*, *ah*) were observed in *E. capensis* and *Cryptocarya woodii*. Anticlinal structures (Fig. **5.3a**: *ai-an*) are common in *Acalypha glabrata*, *Acalypha sonderiana*, *Celtis mildbraedii*, *Millettia grandis* and *Trichilia emetica*. Blocky phytoliths (Fig. **5.3b**: *t-v*) are generally rare across species but were somewhat common in *Acalypha glabrata* and *Baphia racemosa*. The later however was contaminated with grass short cells.

Aerenchyma structures (Fig. **5.3c**: *a*, *b*) were present in *Celtis africana and Ficus polita*. Sclereid structures that tend to be bulbous (Fig. **5.3c**: *e-h*) are generally ubiquitous across species but occurred in varying abundance (Table **5.1**) and were abundant to common in *Eugenia capensis*, *Cryptocarya woodii*, *Rawsonia lucida* and *Podocarpus latifolius*. Tracheids (Fig. **5.3c**: *i*, *j*) were also ubiquitous and where abundant or common or rare across species (Table **5.1**). Tracheids were abundant or common in the species *Clerodendrum glabrum*, *Cryptocarya woodii* and *Trichilia emetica*. Abundant elongate facetted phytoliths (Fig. **5.3c**: *k*, *l*) and a few fibers and sclereid phytoliths (Fig. **5.3d**: *a*, *b*) were observed in *Rawsonia lucida*. Unique globular bodies were observed in *Ficus polita* (Fig. **5.3c**: *m*, *n*). Large globular bodies with central bodies (Fig. **5.3c**: *o-r*) were observed in *Acalypha glabrata*, *Cryptocarya woodii*, *Podocarpus latifolius*, *Deinbollia olongifolia*, *Syzygium cordatum*. Most of the morphotypes mentioned above are present in the species analysed, but only the abundance differs (Table **5.1**).

5.3.3 Special phytolith morphotypes

Some phytoliths morphotypes were only observed in specific families or species. These types were generally not included in Table **5.1** as they were limited to a few species. Some multicellular epidermal polyhedral types in *Celtis africana* and *Celtis mildbraedii* appear different from the more ubiquitous polyhedral epidermal cells as their cells appear a bit irregular, smaller and are cavate reffered to here as polyhedral cavate cells (Fig. **5.3a**: *e*, *f*).These have been previously reported in *Celtis mildbraedii* (Collura and Neumann, 2017). However, *Celtis mildbraedii* has another type of polyhdedral cavate cells that is unique to it and has not been encountered in the literature (Fig. **5.3c**: *c-d*). They are large tissue structures that give a first impression of being cork aerenchyma because of their polyhedral cavate cells that give a somewhat perforated impression as in aerenchyma.

Cystoliths or verrucate bodies (Fig. **5.3b**: *a-j*) were observed only in *Celtis africana* (Celtidiceae) and in *Ficus* species especially *Ficus polita* (Moraceae). Unique echinate bodies (Fig. **5.3b**: *k-p*) and unique granular bodies with granular projections (Fig. **5.3b**: *q-s*) were observed only in *Celtis africana*.

5.3.4 Grass phytolith contamination in sedges and eudicots

It is important to determine the extent to which grasses may have been introduced to the cave unitentionally by its inhabitats as it has been shown that grass phytoliths can adhere to the bark of wood (Albert and Weiner, 2000). In some species of sedges and eudicots, grass silica short cells (GSSCs) were encountered in their phytolith assemblage. Contamination was noted in some species of sedges and eudicots as they contained GSSCs phytoliths that are known to occur only in grasses (Piperno, 1988, 2006; Pearsall, 2000). In a few sedge species i.e. *Bulbostylis burchellii*, *Bulbostylis* sp., *Cyperus obtusifloris* spp. *flavissimus*, and *Schoenoxiphium sparteum*, grass short cells were encountered. A very small number of rondels (less than 20 ecountered in each when their total phytolith count was reached) was observed in *Bulbostylis* spp. while in the *Cyperus obtusifloris* spp. *flavissimus* and *Schoenoxiphium sparteum* it was copious amount of bilobates (above 50). In the later two species counting of bilobates was stopped when their count reached above 50 as bilobates were clearly a common occurrence in their assemblage. It was observed that the bilobates in *Cyperus obtusifloris* spp. *flavissimus* were often articulated. In eudicots, grass short cells were observed in species of *Baphia*, *Eugenia*, *Diospyros*, and *Syzygium*. None of the four produced a significant number of grass short cells and were all below 50. Tsartsidou et al. (2007) considered contamination of less than 50 phytoliths (phytoliths with a consistent morphology) as unreliable. One conical shaped phytolith was encountered in *Ficus polita* although it did not look exactly as those found in sedges with a more conical rondel appearance than dome-shape.

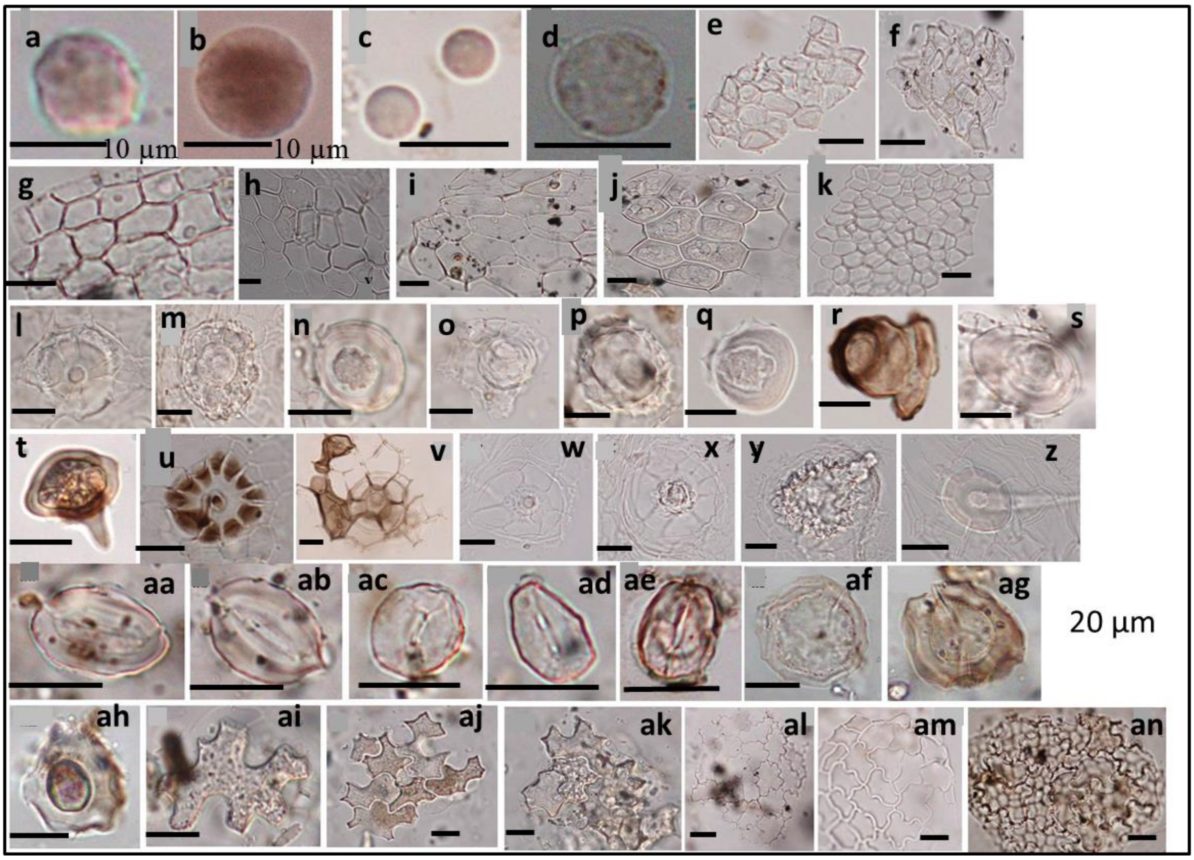


Fig. 5.3a: Globular psilate: **a** *Baphia racemosa*, **b** *Podocarpus latifolius*, **c** *Trichilia emetica*, **d** *Cryptocarya woodii*. Polyhedral epidermal cavate cells: **e** *Celtis africana*, **f** *Celtis mildbraedii*. Polyhedral epidermal cells: **g** *Celtis mildbraedii*, **h** *Ficus sur*, **i-j** *Ficus* sp., **k** *Millettia grandis*. Cystoliths/hair bases (most cystoliths are embedded in hair bases): **l-r** *Celtis africana*, **s-t** *Celtis mildbraedii*, **u** *Ficus ingens*, **v** *Ficus polita*, **w-z** *Ficus sur*. Stomata: **aa, ab** *Dichrostachys cinerea*, **ac-ad** *Vepris lanceolata*, **ae** *Rawsonia lucida*. Globular facetate bodies: **af-ah** *Cryptocarya woodii*. Anticlinial structures: **ai-aj** *Acalypha glabrata*, **ak** *A.sonderiana*, **al** *Celtis mildbraedii*, **am** *Millettia grandis*, **an** *Trichilia emetica*.

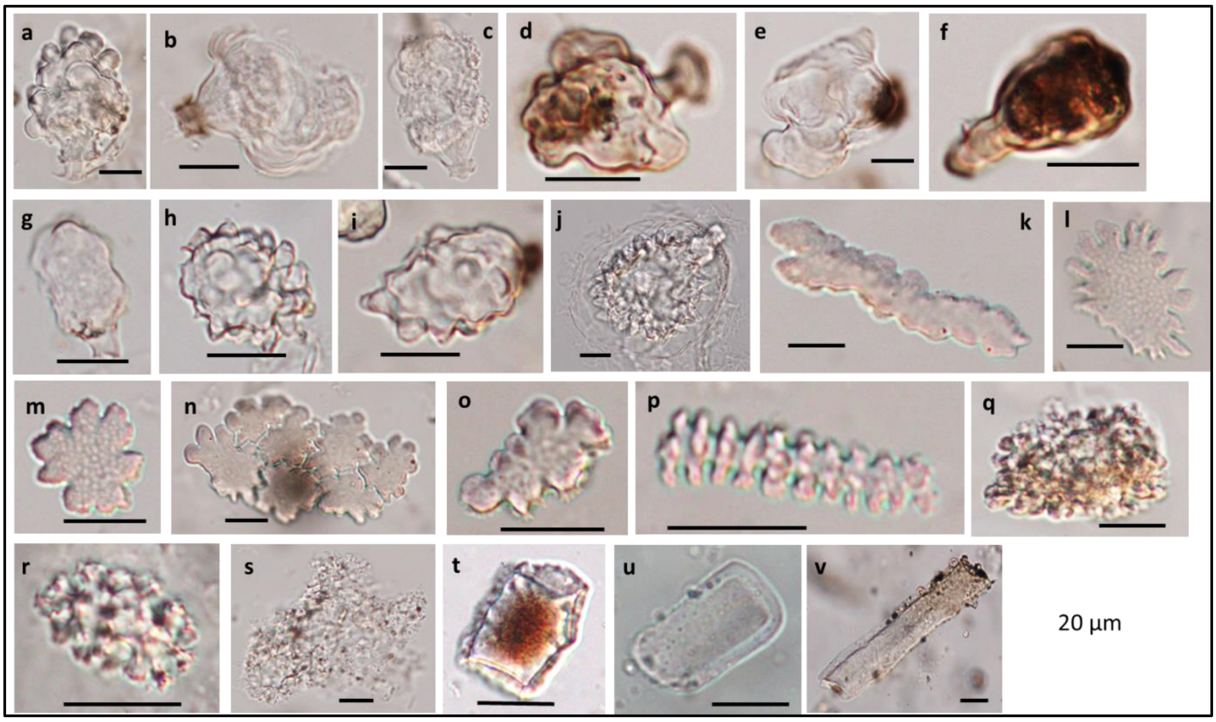


Fig. 5.3b: Cystoliths/verrucate bodies: **a-f** *Celtis africana*, **g-i** Ficus *polita*, **j** *Ficus sur*. Echinate platelets: **k-p** *Celtis africana*. Granular bodies with granular projections: **q-s** *Celtis africana*. Blocky: **t** **Baphia racemosa*, **u** *Cryptocarya woodii*, **v** *Celtis mildbraedii*. *Baphia racemosa – this species had contamination of grass short cells, therefore the blocky types cannot be interpreted with confidence.

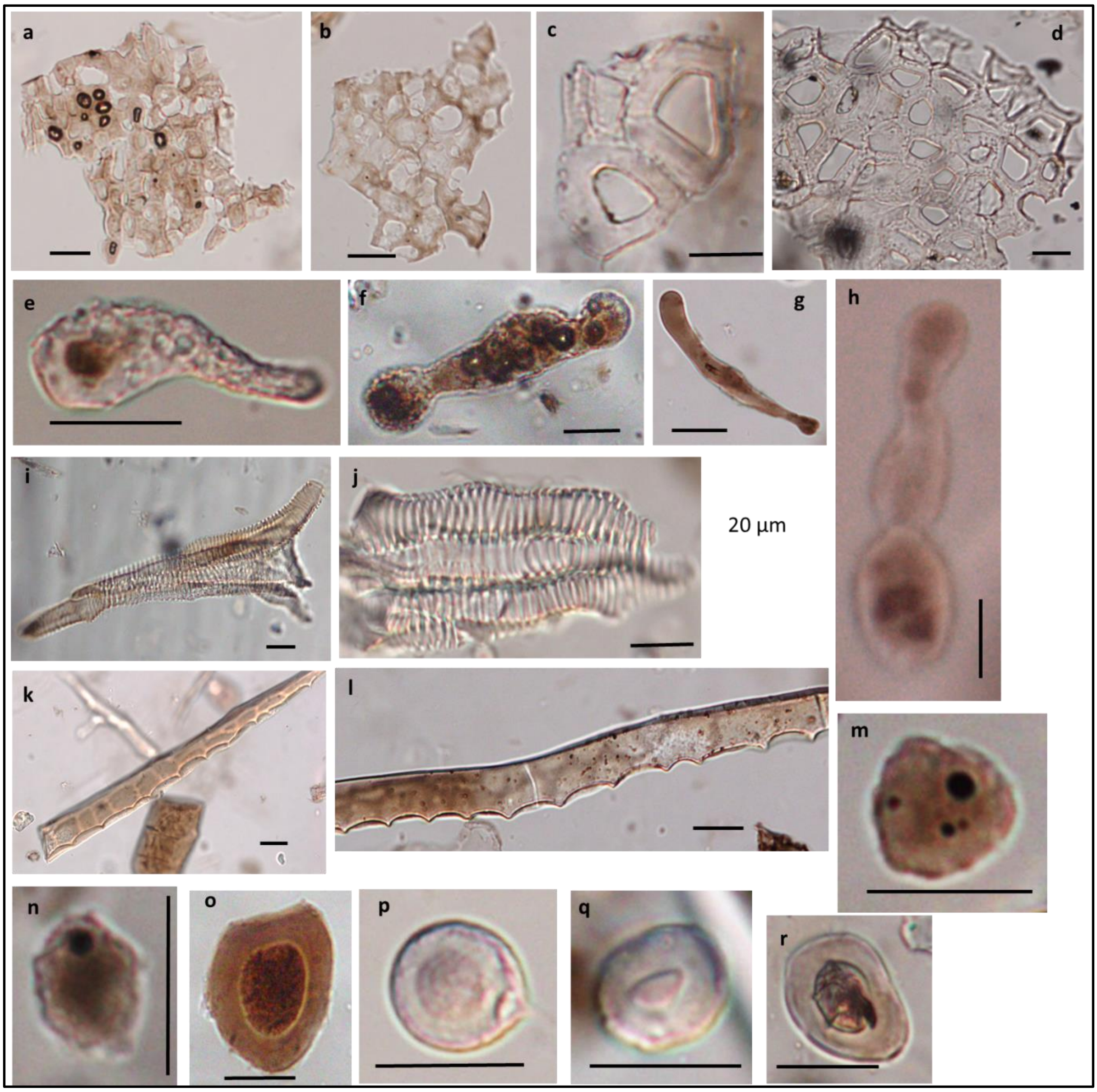


Fig. 5.3c: Aerenchyma structures: **a** *Celtis africana*, **b** *Ficus polita*. Polyhedral cavate: **c-d** *Celtis mildbraedii*. Bulbous structures (Sclereids?): **e** *Eugenia capensis*, **f** *Cryptocarya woodii*, **g** *Rawsonia lucida*, **h** *Podocarpus latifolius*. Tracheids: **i** *Cryptocarya woodii*, **j** *Trichilia emetica*. Elongate facetate: **k-l** *Rawsonia lucida*. Other globular type bodies: **m-n** *Ficus polita*, **p** *Acalypha glabrata*, **o** *Cryptocarya woodii*, **p** *Podocarpus latifolius*, **q** *Deinbollia oblongifolia*, **r** *Syzygium cordatum*.

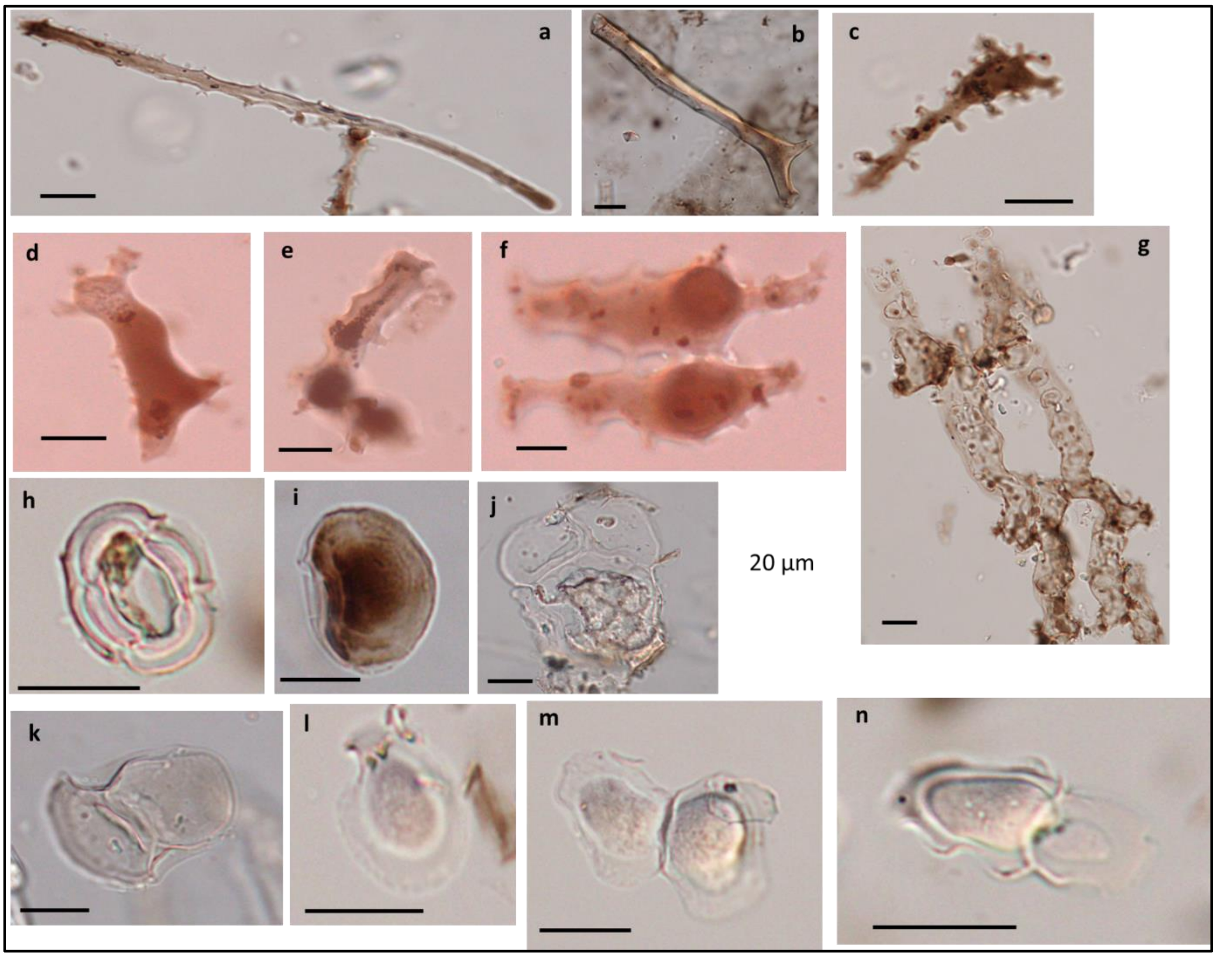


Fig. 5.3d: Fiber, Sclereid: **a-b** *Rawsonia lucida*. Spiny bodies/sclereids?: **c-g** *Podocarpus latifolius*. Stomata: **h** *Deinbollia oblongifolia*. Hair bases?: **i-k** *Deinbollia oblongifolia*, **l-n** *Clutia pulchella.*

5.4 Phytoliths in modern soils

The three soil samples collected from a small uncultivated grassland close to Sibudu did not produce abundant phytoliths. The ca. 200 phytoliths counted in each sample was reached with difficulty. Of the 200 for each sample, the grass silica short cells were only between 40 to 50 across the samples. In all samples however, rondels were the most common, followed by bilobates and then saddles. In the modern sample SIB M1, rondels were at 17.1%, bilobates at 4.1% and saddles at 1.8%. In SIB M2, rondels contributed 10.5%, bilobates 9.1% and saddles 4.1 while in SIB M3, rondels were 10.1%, bilobates 8.0% and saddles at 2.0% . In all three samples blocky parallelpiped phytoliths were the most dominant ranging from 43.3 to 50.3% followed by elongates that ranged from 19.6 to 26.7. These results are illustrated in the Figure 5.4 below.

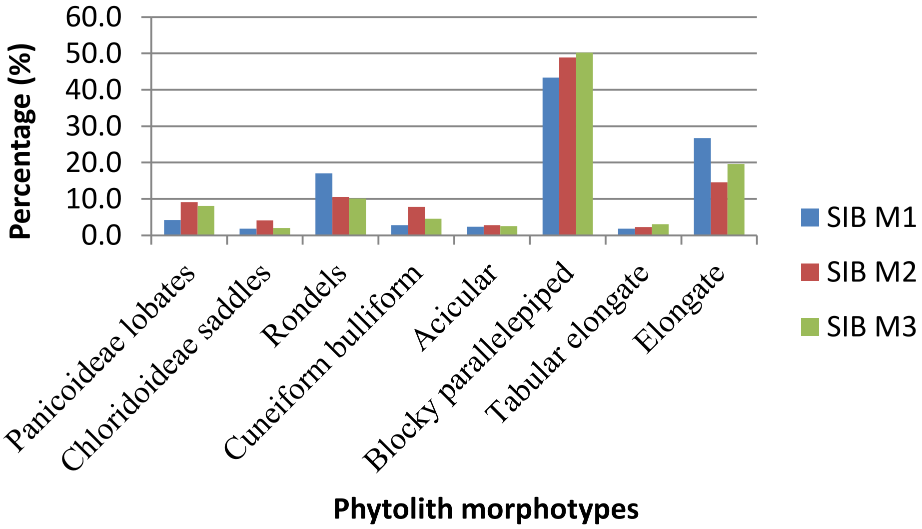


Figure 5.4: Percentage of phytolith morphotypes in modern soil samples, SIB M1, SIB M2 and SIB M3.

CHAPTER SIX

THE MODERN REFERENCE COLLECTION: IMPLICATIONS FOR TAXONOMY AND ARCHAEOLOGY

6.0 Introduction

This chapter provides a discussion of the phytolith data from the modern reference collection and its implications for taxonomic and archaeological interpretations such as those for the MSA phytolith data of Sibudu. It seeks to provide a context in which to understand the taxonomic phytolith classifications used in the next results chapter for the MSA phytolith data of Sibudu (Chapter seven). The role of phytoliths in plant taxonomy is discussed as the modern reference collection provided for taxonomic attribution of some plant taxa and their relevance in archaeological and palaeocological studies.

6.1 Modern Plant phytoliths from the Summer Rainfall Zone (SRZ) of South Africa

This study provides information on the phytolith morphotypes produced by modern South African plants from the SRZ, many of which constituted the landscape at Sibudu during the MSA and were available for early humans to utilise (Allott, 2004; Wadley, 2004; Sievers, 2006; Schiegl and Conard, 2006; Renaut and Bamford, 2006; Lennox et al. 2015). Not only is it an important component of the study because of the lack of modern plant phytolith data for South Africa, but also because it represents the first modern plant phytolith reference collection of eudicot plants (mainly woody) from the SRZ consisting of the largest woody phytolith reference collection for South Africa. More so, it also constitutes the first most comprehensive phytolith study of modern sedges (Cyperaceae) in Africa. It therefore provides a standpoint on which to interpret the ongoing archaeobotanical and palaeoecological studies in South Africa and adds to the few published modern phytolith references for South Africa that until recently were for grasses and other monocots only (Rossouw 2009; Cordova and Scott, 2010; Esteban 2016).

6.1.1 Sedges of South Africa: taxonomic potential of their phytoliths

Although numerous studies have been conducted in South Africa, problems remain within genera to date and their classification is constantly changing with several species being moved from one genus to another with several species' names being refined (Gordon-Gray, 1995; Browning and Gordon-Gray, 2011; Muasya et al., 2012). Other than sedges being an important component of the MSA of South Africa and of major economic importance in South Africa today especially in rural communities in KwaZulu Natal (Gordon-Gray, 1995; Van Wyk and Gericke, 2000; Sievers, 2006; 2011), this study secondarily aimed at establishing the extent to which phytoliths can be used to contribute to the discussion of the contemporary taxonomic issues of Cyperaceae in South Africa (Gordon-Gray, 1995; Browning and Gordon-Gray, 2011; Muasya et al., 2012).

The silica content of the samples analysed exhibited great variability within genera and a trend could not be determined across the samples analysed as many produced small amounts of silica. For instance, the different species analysed in the genus *Cyperus* showed that there is no correlation between the genus and silica amount with some having abundant amounts while others yielded small amounts with some like *C. denudatus* yielding almost nothing. It was clear that silica quantification of the sedges was of no taxonomic importance as observed by Fernádez Honaine et al. (2009). Higher amounts of silica content are reported by Honaine and colleagues with culms reaching 11%, leaves 13% and fruit achenes 18%. This current study achieved percentages far below this in these plant parts combined and might have been exacerbated by the fact that the original samples used were small. In addition to the lack of taxonomic implication for silica production in a genus, Fernádez Honaine et al. (2009) also observed major differences in silica content within a species further indicating that silica content is not taxonomically reliable.

As expected the typical sedge diagnostic cone-shaped phytoliths (leaf/culm cones) were present in all species but they were not necessarily the most dominant isolated morphotype in some species. In fact, in some species they were hardly represented and variations were observed across genera and within species of the same genus. Of the nine *Cyperus* species analysed, parallelepiped blocky phytoliths were the dominant type for *C. fastigiatus* while the cones in *C. rigidifolius* occurred in similar amounts as elongate phytoliths with the rest having cones (leaf or achene) as the dominant type. In the four species of *Eleocharis* analysed, only *E. caduca* has leaf cone phytoliths as the dominant morphotype while the others had different individual phytolith types dominating in their assemblage notably articulated blocky phytoliths in *E. cf limosa*, stomata complexes in *E.* sp and articulated long cells with minute pores along their edges in *E. dregeana*. *Eleocharis* therefore appears to be the genus that least identifies with leaf cone phytoliths in this study. Plates with elongate crenate/pilate cells were the most dominant type in *Fuirena pubesens* with cones occurring in much smaller amounts. Blocky phytoliths (mainly the parallelepiped type) were also the most dominant morphotypes in *Kyllinga erecta*, *K. pulchella* and *Pycreus macranthus* although they occurred in almost similar numbers as cone-shaped phytoliths in *K. pulchella*. Of the three species of *Scleria* analysed, *Scleria woodii* had a poor representation of single cone-shaped phytoliths and is dominated by articulated blocky phytoliths that usually have articulated cones attached to them. Blocky phytoliths were also reported to be an important component of some sedge species (Fernádez Honaine et al., 2009; Novello et al., 2012).

Phytolith morphotypes in the sedges studied are relatively diverse. However, a few species of *Cyperus*, *Bulbostylis*, *Kyllinga* and *Scirpoides* had little variation in the morphotypes they produce. *Scirpoides burkei* showed the least morphotype diversity with leaf cone phytoliths and polyhedral net-like silica skeletons that look like long pointed cones in side view as the only phytolith morphotypes in their assemblage. Globular psilates were not taken into account in this study. They were generally not well represented in this family and only conspicuous in *Schoenoplectus corymbosus* and to some extent in *Pycreus macranthus*. Several appear bulbous in *Schoenoplectus corymbosus* and may be part of the articulated bulbous structures in this species. This is in agreement with Novello et al. (2012) who report that globular psilates were produced in *Schoenoplectus roylei* and *Pycreus macrostachyos*.

Cone sizes were also varied across genera and within a species as observed by Ollendorf (1987) showing a general overlap in sizes with no genera falling in a unique category. For example, in *Cyperus* the largest cone size range of 6.21 µm to 24 µm was observed in *Cyperus haematocephalus* and the smallest size range of 5.38 to 11.56 µm in *Cyperus fastigiatus* with all other *Cyperus* species' cone sizes falling in the range of 4 to less than 21 µm. The species of *Pycreus* show variation in cone size with those of *P.* sp. ranging from about 8.50 to 18.85 µm while those in *P. macranthus* range from 9.72 to 24.37 µm. *Pycreus* species appeared to be the only species with cones that do not measure below 8 µm. A general trend can therefore be described for some species or genera. For example, in the

Eleocharis species that had leaf cones, they were very small and generally did not exceed 13 µm marking it as the genus with the smallest cones in agreement with the findings of Fernádez Honaine et al. (2009). Species that have some of the largest cones (above 26 µm) in their assemblage were *Schoenoplectus muriculatus, S. muricinux,* and *Scirpoides burkei* with those in *S. burkei* having the largest cones that measured up to 32 µm. Other than *Pycreus,* all the other genera have very small cones (4 – 8 µm) that occur in them rendering cone size generally of no taxonomic use especially for this size category. It is therefore difficult to assign taxonomic importance to cone size in sedges although it appears that some species cannot be associated with large sized cones while some cannot be associated with very small cones. Taxonomic inferences have been suggested from cone sizes (Fernádez Honaine et al., 2009) but overlap in sizes still remains a challenge to drawing very specific conclusions as shown in this current study that has a bigger data set. Important to note is that many articulated cones in *Bulbostylis* sp. have a convex bilobate-like or polylobate appearance typical of grasses, only that they appear larger in *Bulbostylis*, a character that so far appears unique or most conspicuous in this species.

It was not always easy to determine the presence of satellites on leaf cones in some species as noted by Metcalfe (1971) and Ollendorf (1987) because in some cases, they are very small or not easy to differentiate from a dissolution effect. Moreover, it was observed that cones with and without satellites occur within a single species as previously noted (Metcalfe, 1971; Piperno, 1989) and show variability within species of the same genus giving them less taxonomic value across genera. For example, satellites were conspicuous but not present on all cones in *Bulbostylis burchellii*, *B.* sp., *Scleria* sp. and yet rare in S. *natalensis* and absent in *S. woodii*. They seem to be a somewhat consistent character in species of some genera i.e. *Bulbostylis*, *Eleocharis*, *Pycreus*, *Scleria* (apart from *S. woodii*), *Schoenoxiphium* and *Schoenoplectus* although they were not always easy to determine in *Schoenoxiphium* and *Schoenoplectus*. They do not seem to occur in the species of the genera *Cyperus*, *Cladium*, *Fuirena*, *Scirpoides* and *Kyllinga* apart from *Kyllinga erecta*. In the species studied, cone apices were always pointed or rounded within a species and some truncated cones were certainly confirmed in *Cladium mariscus*, *Schoeonoplectus muricinux*, *Scleria natalensis* and *Scleria* sp. This too seems a redundant character when this study is compared with that of Fernádez Honaine et al. (2009) where truncated cone apices are seen also in species of the genera *Carex*, *Cyperus* and *Eleocharis*. Cone bases are generally round with some square or angular bases seen in related and unrelated taxa i.e. *Cyperus congestus, C. obtusifloris, C.*

semitrifidus, *Cladium mariscus*, *Kyllinga pulchella*, *Pycreus macranthus*, *Schoenoxiphium sparteum*, *Schoenoplectus* sp. and *S. muricinux*.

Cone-shaped phytoliths are redundant in Cyperaceae (Ollendorf, 1992; Vrydaghs et al., 2004), and several of their characters have proved to be redundant (Metclafe, 1971; Piperno, 1998; Fernádez Honaine et al., 2009; this study). A few unique characters were observed in some species although often in unrelated genera further suggesting that they are also generally taxonomically redundant. Although it was a rare character, *Cladium mariscus*, *Bulbosyltis* sp., the *Fuirena species*, *Schoenoxiphium sparteum* and *Scirpoides burkei* were the species that had some of their cones with two apices on one cone cell appearing unique in *Cladium mariscus* as the cone plates were squared (Fig. **5.1a**: *p*). Another unique feature was some of the cone-shaped phytoliths in *Cyperus semitrifidus* were big articulated square cones, sometimes with slightly sinuous bases with big or small apices (Fig. **5.1a**: *t*-*v*) and this particular type were only seen in this species. *Pycreus macranthus*, *Schoenoplectus muriculatus* and *S.muricinux* also had rectangular articulated cones that look more like tabular phytoliths but their light apices show that they are cones, a character that seems unique to them and those in *P. macranthus* and *S. muricinux* have an echinate margin appearing tabular echinate. Some cones with round and lightly sinuous bases were seen in *S. muricinux*. These sinuous bases are not unique to *Schoenoplectus* as they have been described in a species of *Scleria* by Watling and Iriarte (2013) where they are thought to have some diagnostic potential for the *Scleria* in the region they find them in.

A few more features that may be of some taxonomic significance that are not related to the typical cone-shaped Cyperaceae phytoliths were also isolated in some species. The species of *Eleocharis* and *Fuirena* produced silica skeletons with elongate phytoliths arranged in parallel in small amounts and are similar to those found in the *Eleocharis* species by Fernádez Honaine et al. (2009) but were not as abundant. Both species of *Fuirena* produce conspicuous neat plates with elongate cells that tend to appear dissolved but are elongate cells arranged in parallel in finer focus. This arrangement of elongate phytoliths in parallel is likely to be restricted to a few genera and may to some extent contribute to knowledge of the previously reported close relationship of *Fuirena* and *Eleocharis*. Phylogenetic studies have reported that *Fuirena* is closely related to *Eleocharis* than it is to other genera in the tribe Fuireneae (Muasya et al., 2009, 2012). *Fuirena pubescens* and *Fuirena* sp. produced crenate plates (plates with crenate/pilate or contorted margins) that are most likely the ‘plates with sinuations in the anticlinal walls for *Fuirena*’ referred to in Metcalfe (1971). These plates are well represented in *F. pubesens* and *F.* sp. and those in *F.* sp. tend to appear with more contorted margins than those in *F. pubesens*. The wavy plates in *F.* sp. are often beset with hair bases similar to Metcalfe (1971) who described hair bases in epidermis of leaves of *Fuirena*. Such crenate plates were also observed in *Scleria woodii* where they were beset with peculiar spherical and hemispherical bodies that are discussed next. The phytolith assemblages in *Scleria natalensis* and *S. woodii* are remarkable as they produced peculiar spherical and/or hemispherical/elliptical echinulate bodies that sometimes appear solitary or paired and sometimes are embedded in wavy plates. Metcalfe (1971) describes these echinulate bodies as being a distinguishing characteristic of *Scleria* from other genera in Cyperaceae although he reports that they were observed in three other genera two of which had only a few a species and belonged to the same tribe as *Scleria*. *Scleria natalensis* produces both the hemispherical echinulate bodies as well as spherical echinulate bodies although the latter occur in fewer amounts. This scenario was also described in a *Fuirena* sp. in Bamford et al. (2006) and are referred to as ‘hemispherical verrucate forms’ and ‘spherical with verrucate surfaces’. *Scleria woodii* produced mostly the spherical echinulate type but in small amounts. Other unique large structures of silicified tissue were seen in two species of *Schoenoplectus* only appearing different in *S. corymbosus* and *S.* sp., that were grouped under ‘bulbous’ and may be sclereids while one encountered in *S.* sp. is quite similar to aerenchyma cells seen in *Rhynchospora corymbosa* in Fernádez Honaine et al. (2009). Leaf cross-sections would be useful to determine what kind of tissue it is. Lastly, stomata complexes occur in some species and a copious amount occurs in *Eleocharis* sp. Carnelli et al. (2004) describe distinctive stomata types that are characteristic of Cyperaceae as elongated dome-shaped subsidiary cells that lie parallel to the stomatal pore. One complex of this type was observed in *Scleria eggersiana* by Watling and Iriarte (2013) and similarly in this study, it was observed in *Scleria woodi*. Several other stomata occur in the sedges that look different from this very type.

Unlike the leaf/culm cone-shaped phytoliths, achene phytoliths (polygonal cones) are still the morphotypes that provide better taxonomic potential at genus level and sometimes species (Piperno, 1989). In this study, genera which produced the achene phytolith type (polygonal cone) on top of the classic leaf cone phytoliths were: *Cyperus*, *Kyllinga*, *Pycreus*, *Schoenoxiphium* and may be *Schoenoplectus*. For *Schoenoplectus*, one polygonal cone was encountered in *Schoenoplectus muriculatus* suggesting that these types may occur in some species of the genus. It could be contamination as well. Interestingly, polygonal cones are indicated as present in the leaves of *Schoenoplectus roylei* in Novello et al. (2012) contrary to the fact that these types of cones are associated with achenes of sedges (Piperno, 1989; Fernádez Honaine et al., 2009). The current study cannot pronounce itself on this matter for *Schoenoplectus muriculatus* because the phytolith assemblage is mixed. Few morphotypes that looked like smooth achene phytoliths were observed in *Eleocharis dregeana*. Species so far studied in *Eleocharis* do not produce achene phytoliths (Piperno, 1989; Iriarte and Paz, 2009). We tentatively did not consider it as producing this type and the smooth polygons may well be epidermal polyhedral structures.

The achene phytoliths present in the five aforementioned genera are similar as expected in some species of *Cyperus* and *Kyllinga* as these genera are known to produce achene bodies that have a densely stippled surface that are diagnostic at the genus level. They are often referred to as the *Cyperus*/*Kyllinga* phytolith type as they cannot be differentiated (Piperno, 1989; Ollendorf, 1992). This affirms the problems often faced by systematists when classifying species from these genera and also the already known close relationship between the two genera by systematists that have long treated *Kyllinga* as a subgenus of *Cyperus* or among its various segregate genera (Haines and Lye, 1983; Piperno, 1989; Huygh et al., 2010) that have since moved species of the genus *Kyllinga* to *Cyperus* (Larridon et al., 2013, 2014). Of the nine *Cyperus* species studied, two collected from the area around Sibudu had not been identified and were initially referred to as Cyperecae 1 and 2 (Table 4.1, Chapter four). After phytolith analysis, they were found to produce this *Cyperus*/*Kyllinga* type of achene phytoliths and hence these species were then added to the genus *Cyperus* based on phytolith analysis. Phytoliths therefore have the potential to identify unknown sedges

. Furthermore, the stippled achene phytoliths of *C. denudatus* and those of *C. semitrifidus* were slightly different from the rest, with those in *C. denudatus* having echinate apices while those in *C. semitrifidus* had conspicuously large apices. The achenes with echinate apices in *C. denudatus* are similar to those presented in *C. reflexus* by Fernádez Honaine et al. (2009). Divergence from this densely stippled *Cyperus*/*Kyllinga* phytolith type was observed in *C. fastigiatus* and *C. haematocephalus* which produced only smooth surface achene phytoliths with echinate margins and rarely also produced smooth margin achenes. Piperno (1989) observed this divergence in *C. eculentas* and *C. ochraceus*. However, some species produces both types of achenes.

Important to note is how this phytolith study confirms several other known relationships between genera in other Cyperaceae studies involving morphology, anatomy and phylogeny and how it further affirms the difficulty that has long been faced by systematists when classifying species of Cyperaceae (Metcalfe, 1971; Piperno, 1989; Standley, 1990). For instance, some considered *Mariscus* as a genus but this lasted for a short time as several authors later treated it as a subgenus of *Cyperus* or placed *Mariscus* species under *Cyperus* (Lye, 1982; Vorster, 1983; Tucker, 1983; Huygh et al., 2010; Reynders et al., 2011). In this phytolith study, *Mariscus congestus* (now a synonym for *Cyperus congestus*), produced the highest number by far of the *Cyperus*/*Kyllinga* achene type phytoliths in all the *Cyperus* and *Kyllinga* species analysed. This phytolith study therefore confirms the long known relationship between the genus *Cyperus* and the genus *Mariscus*, a genus that has since become obsolete and its species firmly placed under *Cyperus* in South Africa (Archer and Goetghebeur, 2011). In addition, this phytolith study discovered achene phytoliths with a stippled surface in the assemblage of *Pycreus macranthus* that are similar to the *Cyperus*/*Kyllinga* type although many are more of elongate shaped than the usual polygons and sometimes with less clustered stipples. This phytolith study therefore confirms the long known close relation between *Cyperus* and *Pycreus* by taxonomists (Haines and Lye, 1983; Lye, 1997). The elongate shaped *Cyperus*/*Kyllinga* achene type found in *Pycreus macranthus* was similar to the elongate achenes in *Mariscus congestus* (syn. *Cyperus congestus*). In phylogenetic analyses, *Cyperus congestus* is thought to be associated with the early branching *Pycreus* lineages although there are no morphological characteristics between *C. congestus* and *Pycreus* to support this relationship (Larridon et al. 2013). This similarity in elongate stippled achene phytoliths may be of some contribution in understanding this relationship. *Pycreus* originally treated as a separate genus by some authors was considered as a subgenus of *Cyperus* by others (Haines and Lye, 1983; Lye, 1997). It was later left among the several segregate genera of *Cyperus* that include *Kyllinga* pending investigations to further understand their relationship with *Cyperus, sensu stricto* that was still unclear (Muasya et al., 2009; Huygh et al., 2010).

Recent investigations have led to *Pycreus* being formally included in the genus *Cyperus* and their species have been given new names in *Cyperus* (Larridon et al., 2014). There would probably then be no need to add ‘*Pycreus*’ to the term ‘*Cyperus*/*Kyllinga* phytolith type’ used in phytolith terminology (Piperno, 1989; 2006) since their species are now included in *Cyperus*. Since species of *Kyllinga* have also been moved to *Cyperus*

(Larridon et al., 2013, 2014), this term should probably be considered obsolete in phytolith research. This presence of the *Cyperus*/*Kyllinga* achene phytoliths of Piperno (1989) in *Pycreus* has to the best of my knowledge not been previously described for *Pycreus* although it was first presented in achene phytolith images of *Pycreus tener* (*See* Fernádez Honaine et al., 2009), although it was not categorically described as the *Cyperus*/*Kyllinga* type. The achene phytoliths illustrated for *Pycreus tener* have a stippled surface similar to that of phytolith achenes in *Cyperus* and *Kyllinga* (Fernádez Honaine *pers. comm*, 2016). Statistical analyses by Fernádez Honaine et al. (2009) show that *Pycreus tener* is closely related to *Cyperus* species. Further illustration of the taxonomic potential of phytoliths in this study is the presence of 4-7 sided smooth surface achene phytoliths with lightly jagged margins or lightly stippled margins in *Schoenoxiphium sparteum* that are similar to some of the types that are of diagnostic potential in the genus *Carex* (Piperno, 1989). This probably serves to support the taxonomic placement of the genera *Schoenoxiphium* and *Carex* in the same tribe (Cariceae) (Kukkonen, 1983) and better still the recent placement of the genus *Schoenoxiphium* under *Carex* (Global *Carex* Group, 2015). To the best of my knowledge, this '*Carex*' phytolith achene type is being described in *Schoenoxiphium* for the first time and further phytolith analysis of species originally under this genus would be necessary to confirm this assertion.

6.1.2 Phytoliths of KwaZulu Natal grasses and their taxonomic significance

A morphological classification for grass short cell phytoliths related to the grass taxonomy of three subfamilies was proposed by Twiss et al. (1969). This involved the classic categorizations of 'Panicoid' phytoliths (bilobates), 'Chloridoid' phytoliths (saddles) and 'Pooid' phytoliths (rondels) that identify the subfamilies Panicoideae, Chloridoideae and Pooideae respectively. With the ever growing body of research it is now known that due to the issue of phytolith redundancy and multiplicity (Rovner, 1971), these morphotypes only loosely identify these subfamilies as many deviations from the norm occur, with them also occurring in other grass subfamilies (Lu and Liu, 2003; Bamford et al., 2006; Piperno, 2006; Bremond et al., 2008; Barboni and Bremond, 2009; Cordova and Scott, 2010). Although this grass phytolith reference is much smaller than that of Rossouw (2009) that encompasses the many biomes of South Africa, it provides useful information specific to the study area. This study generally follows previously documented trends, with grasses yielding typical grass phytoliths and highlights the inherent problem of redundancy of some phytolith morphotypes.

In this study, the classic trend of bilobates as the most dominant or identifying morphotypes in Panicoideae grasses was corroborated (Twiss et al., 1969; Piperno, 2006; Fahmy, 2008; Rossouw, 2009; Cordova and Scott, 2010; Mercader et al., 2010; Esteban, 2016). The bilobates were of various margins (i.e. concave, convex and straight) without shanks or with their shanks short or long. The shank length categories used here were those recently recommended by Neumann et al., (2017) with short shank being less than 4 µm, long length shanks being between 4 – 7 µm and very long shanks above 7 µm. The presence of different margin types in this subfamily confirms Neumann and colleagues' assertion that separating bilobates according to the shape of their margin is of no taxonomic importance and only serves to increase redundancy of the isolated morphotype across subfamilies (Neumann et al., 2017). Bilobates with short shanks with concave margins and those with convex margins were the most common type in Panicoideae grasses in agreement with Mercader et al. (2010). The other lobates i.e. crosses and polylobates show affiliation to the subfamily Panicoideae especially the polylobate morphotype which was only observed in Panicoideae (Rossouw, 2009; Mercader et al., 2010; Neumann et al., 2017). Important to note is that rondels were a major component of most species of Panicoideae studied here, sometimes even occurring in equal or higher amounts in some species. In other South African studies, rondels were reported as present but not abundant in the subfamily Panicoideae in the south coast (Esteban, 2016) while they were reported as absent in Rossouw (2009).

Saddles most identify the subfamily Chloridoideae as expected (Twiss et al., 1969; Twiss, 1992; Piperno, 2006) but they are not always well represented in some of its species which instead produce abundant rondel phytoliths (e.g. Lu and Liu, 2003). In the genera *Eragrostis* and *Sporobulus*, rondel phytoliths were always the dominant type in their species although in the species of *Eragrostis*, the saddles were nearly as abundant as the rondels in agreement with previous studies in Africa (Bamford et al., 2006; Barboni and Bremond, 2009; Mercader et al., 2010; Novello et al., 2012; Cordova, 2013). This study is in agreement with that of Cordova (2013), who found rondels abundant in some Chloridoideae species in the WRZ of South Africa. This trend was not observed in West African grasses of this subfamily (Neumann et al., 2017), highlighting the importance of region specific data. On the contrary, rondels are absent in the Chloridoideae species of South Africa studied by Rossouw (2009). Peculiar also, is the fact that a *Fingerhuthia* sp. (Chloridoideae) was dominated by bilobate shaped phytoliths and rondels with no saddles. It was the only species of this subfamily to show an abundance of bilobates as the rest produced them in extremely low amounts or did not produce them at all. It must be noted that some of the bilobates with long shanks and concave margins in *Fingerhuthia* sp. look like saddles joined by a shank.

In Arundinoideae (*Phragmites australis*), rondels and saddles were the only grass short cells observed in agreement with Lu and Liu (2003) and Novello et al. (2012). However, in both these studies, saddles were the dominant type over the rondels while in this study it is the rondels that were the most dominant morphotype. We think this difference may be partly due to the difference in classification of the 'saddle-rondel' type that occurs in this species that will be discussed further shortly. Saddles were the only type in *P. australis* in Mozambican grasses (Mercader et al., 2010). In this study, all kinds of rondels occur in this species and many tend to be very long (up to 20 µm in height) making them conspicuous in this species and many are horned similar to Lu and Liu (2003). Others are flat rondels and conical rondels with pointed tops. Also the conical rondels that are often short in other species appear conspicuously long in *P. australis* reaching 12.65 µm. It is also made up of saddles that are plateaued (trapezoidal with a saddle outline base and a smaller saddle-like on top, Piperno, (2006)) and saddle-rondels/ellipsoid (appear rondel - oblong/suborbicular or orbicular with saddle tendencies, Lu and Liu, (2003)) (see images in chapter five). The latter type is taken to be the type referred to as 'saddle ovate' and defined for *Aristida* species in Mercader et al. (2010). The latter type has been grouped as rondel in this study as it appears more rondel than it is saddle unlike the plateaued saddles. We think that both these types are grouped together in the studies that show saddles as the most dominant type in *P. australis* as 'saddle-rondels' as it might not have produced this distinction their studies (e.g. Novello et al., 2012). Saddle-rondels alone are reported to be up to 39% in *P.australis* by Novello et al. (2012). Whereas this is mere speculation for the abundant saddles in other studies, either way in the current study, the typical rondels (e.g. horned and conical) were outrightly more dominant and conspicuous compared to the saddle-rondels. Plateau saddles are not necessarily a marker for *P. australis* as previously suggested (e.g. Lu and Liu, 2003; Piperno, 2006) as they occur in other subfamilies such as Chloridoideae (Neumann et al., 2017). Not only have saddle-rondels/ellipsoids been observed in *P. australis* in this study, they have also been observed in *Sporobolus africanus* and *Eragrostis superba* (Chloridoideae) in agreement with Novello et al. (2012) who found them in *Sporobolus cordofanus* (Chloridoideae).

Saddle-rondels/ellipsoids are also associated with the subfamily Aristidoideae in Southern Africa (Rossouw, 2009; Mercader et al., 2010).

The *Aristida* sp. was a single representative of the subfamily Aristidoideae and it also produces abundant bilobate and saddle-rondels/ellipsoid phytoliths in agreement other authors (Rossouw, 2009; Mercader et al., 2010). It produces bilobates with convex ends with short and long shanks. The long shanks fit the category 4 to 7 µm of Neumann et al. (2017) but it also has bilobates with longs shanks measuring above 7 µm which are categorised as having very long shanks (Neumann et al., 2017). It was therefore the only species to have some abundance of bilobates with convex margins and very long shanks, a phenomenon previously reported and this bilobate is often referred to as the '*Aristida* type' (Piperno, 2006; Rossouw, 2009; Mercader et al., 2010; Cordova, 2013; Neumann et al., 2017). This type occurred in very small numbers in some species of the subfamily Panicoideae in agreement with Rossouw (2009) and Neumann et al. (2017). The saddle-rondels in *Aristida* sp. are very small and mostly orbicular while those in *P. australis* are mostly oblong and blocky. The *Aristida* species is also made up of rondels with a reniform top similar to that referred to as 'Ro-5' in *P. australis* in Novello et al. (2012). This *Aristida* sp. is also made up of a bigger rondel reniform base type whose base is kidney-shaped with its body appearing like 'horned tower' rondels (Lu and Liu, 2003) and it is more common than the 'Ro-5'reniform type. These morphotypes were only observed in this *Aristida* sp, and 'Ro-5' and the 'kidney' shaped are thought to be variants of the same morphotype. Both these rondel types, the saddle-rondels/ellipsoid and the bilobates can appear clustered in the same silica skeleton. This species also produced rondels further highlighting the redundancy of rondels across grass subfamilies in South Africa (Cordova, 2013).

The subfamily Pooideae was represented by one *Agrostis* sp. which was dominated by rondel phytoliths as expected (Twiss, 1992; Barboni and Bremond, 2009). The cross-type lobates were common with a few saddles and bilobates. Bilobates appeared mostly conspicuously small compared to those in other grasses with no shanks. It generally did not present with the trapeziform sinuous type that is characteristic of high altitude C3 Pooideae grasses (Barboni and Bremond, 2009). Grasses from the WRZ of South Africa (an area dominated by C3 grasses) were found to produce lobates, saddles and rondels irrespective of their photosynthetic pathway and attribution to a particular pathway was made based on abundance (Esteban, 2016). C3 grasses were found to produce a higher amount of rondels compared to C4 grasses so rondels were then associated with C3 grasses (Esteban, 2016).

Similarly, rondels were also the most dominant morphotypes in the *Agrostis* sp. in this study however, the big number of cross-shaped phytoliths is strange and cannot be comparably discussed in line with available literature. Worsestill, only one grass species from the subfamily Pooideae was collected from the main study area. It is necessary to investigate to what extent these grasses occur in the study area, a region dominated by C4 grasses; and for more phytolith studies of the Pooideae subfamily from this area to ascertain phytolith production in these grasses. Until such a time, this study cannot confidently pronounce itself on the trend of phytolith production in C3 grasses specifically of the subfamily Pooideae that are typical for temperate climate/high altitude and this result is necessarily tentative.

Generally, saddles appear to be the least redundant phytolith morphotypes as they were absent or produced in very small amounts by species that do not belong to the subfamily Chloridoideae. Unique and, rare phytolith types that characterised individual species were encountered in the phytolith assemblage. *Fingerhuthia* sp. produced a unique type of H-shaped lobates together with the usual cross-shaped lobates. The typical four-lobed cross-shaped morphotypes (Piperno, 2006) appear as cross shapes in terms of the letter 'X' while some cross-shapes in *Fingerhuthia* are blocky with an 'H' shape. This 'H'- shaped lobate has its lobes long, straight and blocky. The other unique morphotypes are the cone shaped phytoliths that are difficult to separate from those typical for sedges that were observed in some species but the sedge resemblance was pronounced in *Digitaria* sp. because of the articulated cones and silica skeletons made up of cones only as in sedges. This particular character was observed only in *Digitaria* species. Although these cone shapes are termed as conical rondels and grouped under rondels in this study, some authors refer to them as 'papilla' in grasses and sedges (e.g. Ball et al., 1996; Novello et al., 2012). Those in grasses are reported as easy to confuse with sedge cones (Ball et al., 1996; Runge, 1999). This underscores the inherent problem of phytolith redundancy (Rovner, 1971). However, we note that they were only common in the *Digitaria* sp. and rare in other species.

The rare morphotypes were the non-GSSCs that occurred in very small amounts relative to the GSSCs i.e. tabular morphotypes, parallelepiped bulliforms, acicular, elongates, blocky parallelepipeds, tracheids and stomata. In particular, parallelepiped bulliform cells were the rarest type as they were absent in most grasses and rare in the few they were observed with only a significant amount of up to 7.1% in *Setaria megaphilla*. This species also had the highest number of acicular morphotypes. The cuneiform bulliform type typical for grasses (Piperno, 2006) was not observed in these grasses. It is the tabular and elongate morphotypes that were most likely to occur in every species.

In summary, inferences can be made that link grass short cells with the grass subfamilies that they are most affiliated to, supported by correspondence analysis. Therefore, the subfamily Panicoideae is characterised by bilobates with short and relatively long shanks with various margin types but the short shank type with concave and convex margins were the most dominant types. The other subfamily that is characterised by bilobate shaped phytoliths is Aristidoideae. Its bilobates are with short, long and very long shanks with convex margins only. The subfamily Chloridoideae is characterised by saddle-shaped phytoliths. This study cannot speak much to the phytolith morphotype dominance relationship with subfamily for Aristidoideae, Arundinoideae and Pooideae as each of them was represented by one species. Rondels are the most redundant phytolith morphotype as they occurred in all the five grass subfamilies studied here in agreement with previous studies (Novello et al., 2012; Cordova, 2013).

6.1.3 Eudicot plants of KwaZulu Natal: phytoliths and their taxonomic potential

In this study, eudicots (mostly woody taxa) produced the most variably phytolith morphotypes and it was difficult to associate a particular type with a given family in agreement with previous studies (Bozarth, 1992; Albert, 2000; Mercader et al., 2009; Collura and Neumann, 2017). This in agreement with Piperno (2006) that woody taxa may not be identified as individual plants but phytoliths will identify them as a vegetation component. Eudicots in this study area were mainly characterized by globular psilates, hair bases, epidermal ground mass (multicellular polyhedral and anticlinal epidermal cells), tracheids, elongates, irregular bodies, stomata, bulbous structures, and; the more rare blocky and sclereid morphotypes. They vary from abundant to rare in any given species that they occur in. These morphotypes have been previously associated with leaves or wood or bark of eudicots in many parts of the world (Geis, 1973; Bozarth, 1992; Runge, 1999; Albert et al., 2000; Albert and Weiner, 2001; Strömberg, 2003; Piperno, 2006; Mercader et al., 2009; Collura and Neumann, 2017). This is also in agreement with the recent study of eudicots from the WRZ of South Africa (Esteban, 2016). Of these morphotypes, it is the multicellular polyhedral and anticlinal epidermal cells, globular psilates, hair bases and to some extent stomata complexes that can be marked as the most common morphotypes of eudicot phytoliths in this study similar to other African modern phytolith studies (Mercader et al., 2009; Collura and Neumann, 2017; Esteban, 2016).

Multicellular polyhedral epidermal cells and globular psilate phytoliths appeared to be the most recurring phytolith types in the eudicots of this study. Globular psilate phytoliths are also reported to be the most recurring type in the wood of African woody taxa (Collura and Neumann, 2017; Esteban, 2016) while multicellular polyhedral epidermal cells were also found to be the most common type of dicot phytoliths by Bozarth (1992). Multicellular polyhedral and anticlinal epidermal cells are found in the leaves of many deciduous trees (Rovner, 1971; Bozarth, 1992). In our study, articulated polyhedral and anticlinal cells were also characteristic of many species with the polyhedral type appearing to be more common similar to Esteban (2016). Multicellular anticlinal structures were only abundant in *Acalypha glabrata*, *Acalypha sonderiana* (Euphorbiaceae), *Celtis mildbraedii* (Celtidaceae), *Millettia grandis* (Fabaceae) and *Trichillia emetica* (Meliaceae). Those in *C. mildbraedii* appear unique in their layout because they have uniformly sinuous cells and are often embedded with stomata, a character observed only in this species. Schiegl and colleagues also observed these multicellular anticlinal structures in *C. mildbraedii* in their burning experiment of the same species at Sibudu (Schiegl et al., 2004, Figure 8c). These morphotypes are associated with deciduous trees in humid environments (Geis, 1973; Bozarth, 1992). However, both types of multicellular epidermal cells occur in monocots and dicots in both arboreal and herbaceous taxa and are considered of little taxonomic value (Iriarte and Paz, 2009). Other than eudicots plants, few polygonal epidermal cells were also observed in sedges in the current study similar to Iriarte and Paz (2009). They observed also anticlinal cells in sedges but those observed in the sedges in the current study are different from those in eudicots. The epidermal ground mass in the form of multicellular spheroid/ellipsoid cells (mesophyll cells) also from the epidermis of dicot leaves (Bozarth, 1992; Albert, 2000; Strömberg, 2003) were generally a rare sighting in species studied here.

Following this reference collection that also included grasses and sedges, morphotypes that can be considered generally characteristic of eudicot plants are anticlinal and polygonal epidermal cells, sclereids, irregular bodies, hair bases and globular psilates. In addition, the stomata in the eudicots are different from those observed in sedges and grasses and are similar to the type referred to as ‘dicot stomata’ in Carnelli et al. (2004). Globular psilates are generally considered to be of little taxonomic value since they occur in a wide range of taxa including herbaceous monocots and arboreal taxa (Piperno, 2006). However, in this study they are considered more typical of eudicot plants as they cannot generally be associated with grasses and sedges in agreement with Runge (1999). This is also in agreement with Mercader and colleagues who found globular psilates more typical for trees and bushes than they are for grasses in Mozambican vegetation (Mercader et al., 2009, 2010).

Although the majority of species studied here can be considered phytolith producers (32 out of 42), many of them are single representatives of the family they belong to making it difficult to attest to phytolith production in the given family as a whole. More so, phytolith production was not consistent in most plant families. For example; species of the family Fabaceae showed variability in phytolith production with some species being high phytolith producers, others low producers or non-producers. This confirms Piperno's placement of this family under 'families whose phytolith production varies substantially among different subfamilies and tribes' (Piperno, 2006). Families that exhibited consistent phytolith production when they were represented by two or more species were: Celtidaceae (formerly Ulmaceae, APG: Cannabaceae), Euphorbiaceae, Moraceae and Myrtaceae marking them as good phytolith producers in agreement with previous studies. These families (apart from Myrtaceae) are among those whose reproductive structures are known to be good phytolith producers while Celtidaceae and Moraceae are grouped under families where phytolith production is usually high (Piperno, 1989, 2006; Watling and Iriarte, 2013; Collura and Neumann, 2017).

The two species of Myrtaceae studied here were relatively good phytolith producers but this family was grouped under those that have no phytoliths or production is rare (Piperno, 2006), confirming that phytolith production in many eudicot families is not always consistent at family level. Worth mentioning, is the family Podocarpaceae, the only non-eudicot taxon in this study represented by *Podocarpus latifolius* which was a very good phytolith producer although Podocarpaceae is among the families that are considered to be phytolith non-producers or in which production is rare (Piperno, 2006). It produced many globular psilates, bulbous structures and spiny irregular morphotypes that were unique to it and a quite similar to the unique 'blocky hairy' phytoliths that Mercader et al. (2009) found in *Podocarpus falcatus*. Some bodies in *P. latifolius* in this study do look hairy like hair bases but others were irregular with thicker projections that look more spiny than hairy and these are the spiny irregular bodies that are likely sclereids. These spiny bodies are somewhat similar to the 'knobby' bodies seen in the genus *Lepidoocarym* (Arecaceae) in Strömberg

(2003) and ‘bony’ bodies in *Protium guianense* (Burseraceae) (Watling and Iriarte, 2013). Important to mention also is *Brachylaena discolor*, the only Asteraceae species in this study. It produced various hair bases and some were the largest seen and look like polyhedral epidermal cells or as if embedded in them. This may be the same large type that has been described in *Melampodium camphoratum* (Asteraceae) by Watling and Iriarte (2013, Figure 5c). A blocky polygonal phytolith was observed in this species that is described as ‘irregular, ridged blocks with psilate surfaces’ by Watling and Iriarte (2013) who also observed them in *M. camphoratum* (Figure 5d). Blocky polygonal phytoliths ‘with a psilate to ridge texture’ are reported in *Brachylaena* spp. and occur in few dicot families (Mercader et al., 2009).

Of major interest were the genera *Celtis* and *Ficus* (Celtidaceae and Moraceae respectively) that produced diagnostic phytoliths or very specific phytoliths that made them stand out. Common to them is the presence of cystoliths (verrucate bodies sometimes with a stalk) and hair bases that are not necessarily present in all their species. This study conforms to previous studies that found cystoliths and hair bases common in Moraceae and Celtidaceae (formerly Ulmaceae) and stated their potential in taxa discrimination (Runge, 1999; Piperno, 2006; Watling and Iriarte, 2013). Cystoliths were observed in *C. africana* and *F. polita* and *F. sur*. Hair bases were observed in *C. africana*, *C. mildbraedii*, *F. ingens*, *F. polita* and *F. sur* and may indeed be of taxonomic value as they appear different for either genus and are also different from hair bases observed in all other families. Hair bases in *Celtis* tend to occur within multicellular polyhedral epidermal cells forming what Watling and Iriarte (2013) refer to as ‘hair base and polyhedral epidermal complex’. Only *Ficus* sp. did not follow either trend and was made up of only multicellular polyhedral phytoliths and large perforated structures that are similar to those seen in sedges of the genus *Schoenoplectus* and in the eudicot *Eugenia capensis* (Myrtaceae). The polyhedral epidermal cells of *Ficus* sp. (Moraceae) are mostly infused with silica creating thick globular bodies that give their surface a verrucate appearance, a phenomenon that was observed in leaves of a *Ficus* sp. and was referred to as ‘attached verrucate silica’ by Strömberg (2003). In this study, this character was also seen in the polyhedral epidermal cells of *Millettia grandis* (Fabaceae) albeit with less frequency and less silicification of this ‘verrucate silica’.

Distinct perforated plates were observed only in *C. africana* and *F. polita*. These plates are attributed to cork aerenchyma which is an air-filled tissue that is often found in humid forest trees although it can occur in species of drier habitats (Collura and Neumann, 2017). In their study, they found these plates in the bark of only 8.7% of the species that they studied and are reported in the three species of *Ficus* in their study. *Ficus polita* deserves special mention and further investigation because it had two microscope slides that produced different morphotypes. The multicellular polyhedral cells, globular psilate, hair bases and cystoliths were observed in one slide while the other had small globular verrucate bodies that were thought to be 'immature' cystoliths together with conspicuous brown globular bodies that are sometimes articulated in pairs and can appear slightly bulbous. These morphotypes were only observed in *Ficus polita* and are similar to those that are reported to be characteristic of Restionaceae plants in the unique Fymbos vegetation at the south coast of South Africa (Esteban, 2016; Esteban et al., 2017).

More specific for *Celtis* are phytoiths that are diagnostic of the genus. These are the numerous echinate sculptured platelets with irregular edges that occur in *C. africana* and have been previously identified in *C. occidentalis*, *C. spinosa* and *C. tala* (Bozarth, 1992; Piperno, 2006; Iriarte and Paz 2009). These echinate platelets can differ in shape and surface decoration among species and those observed in *C. africana* are most similar to those in *C. spinosa* in Piperno (2006) and *C. tala* in Iriarte and Paz (2009). Also present were unique conspicuous granular globular or irregular bodies occurring as isolated bodies or aggregates forming large grainy masses that were unique to *C. africana*. Various granular phytolith types are said to occur in few species and are diagnostic for wood (Collura and Neumann, 2017). Collura and Neumann observe unique globular bodies with cylindric projections in the bark of *Celtis adolfi-fridericii*. The unique granular bodies seen in *Celtis africana* also appear to be made up of very grainy projections that radiate from the centre of the body and unlike those of *C. adolfi-fridericii*, they have no globular body in their centre. Another special phytolith type in *Celtis* is made up of articulated polygonal-like cells that appear cavate and were observed in both *C. africana* and *C. mildbraedii*. This type is similar to the 'blocky cavate fimbriate' attributed to silicified cork observed in bark of *C. mildbredii* by Collura and Neumann (2017) but with thinner cell walls. The authors name this blocky cavate morphotype as diagnostic for *C. mildbraedii*. This type is also observed in the wood ash of burning experiments of *C. mildbraedii* and is presented as a silica skeleton in Schiegl et al. (2004) in Figure 5. In this current study, those observed in *C. africana* appear less silicified and several have spaces within them while those in *C. mildbredii* are always fully articulated with no spaces. However, conspicuous large thick plates with cavates occur in *C. mildbraedii* and this is the type that we found very unique to *C. mildbraedii*. The plates look like aerenchyma tissue because of the cavates that give an impression of regular perforations as in cork aerenchyma. These plates could not be easily interpreted from the available literature.

Lastly, it has been noted that some species presented in this study as without meaningful phytoliths or as generally lacking phytoliths may be presented in other studies with phytoliths in them. For example, phytoliths with a consistent morphology were present in *Sideroxylon inerme* in Esteban (2016) while they were absent in this study. This may be a result of the loss of the few phytoliths obtained during preparation given that eudicots are low phytolith producers compared to grasses and sedges (Piperno, 1988, 2006). The presence or absence of phytoliths in a particular species in this study should therefore be treated with caution. However, the aim of studying the modern eudicot species was to determine the relevant phytolith morphotypes that occur in them to aid environmental reconstruction from the archaeological record which was achieved.

6.1.4 Implications for archaeological and palaeoecology studies

One of the objectives of this study was to provide a standpoint from which to interpret the fossil phytolith assemblages in emerging archaeobotanical studies in South Africa. This was achieved by assessing phytolith production in ecologically and economically important plants from the SRZ of South Africa. The results of this study support what has been widely known about the application of phytolith analysis and phytolith morphologies established from taxa of other regions apply to South Africa. To this end, phytoliths from sedges follow the know function of identifying most sedges studied at family level and specific sedge genera identification in some. As previously documented, it is possible to identify in the archaeological and palaeoecological record the genera *Cyperus* and *Kyllinga* (Piperno, 1989; Ollendorf, 1992; Iriarte and Paz, 2009; Fernádez Honaine et al., 2009) and now *Pycreus* (Fernádez Honaine et al., 2009; this study). This study supposes that it may also be possible to identify the genus *Schoenoxiphium* from the palaeoenvironmental records although a distinction from *Carex* is likely not possible as its achene type is similar to one of the types found in *Carex* (see Piperno, 1989). At Sibudu cave, seed studies have confirmed the presence of *Schoenoplectus* and *Cladium* species during the MSA Sievers (2006, 2013), however in this study these genera did not produce diagnostic phytolith morphotypes that can identify them in the archaeological record other than the classic cone-shaped phytoliths.

Cladium mariscus appears to be the species with the highest amount of bulbous structures, a type that has been seen in sedges and eudicot plants in this study.

The unique hemispherical and spherical bodies observed in *Scleria* would also be useful in identifying this genus as suggested by Metcalfe (1971) as they were observed only in this genus. However, it is not clear from phytolith studies if this type preserves in soils as these bodies have been previously published in modern sedges only in Metcalfe (1971) and Bamford et al. (2006). Bamford et al. found these bodies in a species of *Fuirena* sp. but not in the fossil record. Further studies are needed to confirm the extent to which these unique bodies occur in *Scleria* and *Fuirena*. The presence of parallelepiped blocky morphotypes in the archaeological and palaeoecological record can also be attributed to a sedge origin as they have proven to be an important component of sedge phytoliths in most species in this study and in previous studies (Fernádez Honaine et al., 2009; Novello et al., 2012). They are reported to occur in grasses and woody taxa (Albert et al., 2000; Mercader et al., 2010; Collura and Neumann, 2017). Sometimes these parallelepiped bodies are not blocky but are tabular elongate and these are similar to those referred to as parallelepiped thin or elongate and were found to occur in sedges and other monocots (Bamford et al., 2006). In this study, they were also observed in sedges and grasses. Although their percentages may sometimes appear relatively low in some species due to the abundance of cone-shaped phytoliths, the numbers of blocky phytoliths recorded in any sedge species were often over and above those found in any grass and eudicot plant in this study.

More so, cone-shaped phytoliths are reported to not preserve well in modern soils compared to their abundance in living sedges (Carnelli, 2002; Iriarte and Paz, 2009; Novello et al., 2012). Blocky and elongate phytoliths were found to be the dominant types in modern soils where sedges were where the prevailing vegetation and cone-shaped phytolith remain very few even when sedges were the only plant taxa in the vegetation (Novello et al., 2012). Few cones are therefore expected to occur in the fossil record. Therefore even when cone-shaped phytoliths occur in low amounts in the archaeological record, an abundance of parallelepiped blocky phytolith may point to a sedge origin. However, making such an interpretation in the absence of the more family specific cone-shaped phytoliths would be problematic in itself (Novello et al., 2012).

Knowledge of possible vegetation types that existed in the past would allow archaeological studies to narrow down the most potential source of such ubiquitous phytolith morphotypes (Collura and Neumann, 2017). For example, blocky morphotypes can be attributed to grasses in open vegetation (Collura and Neumann, 2017). These morphotypes are generally redundant but as seen in this modern reference collection, parallelepiped phytoliths are more characteristic of sedges than they are of grasses and woody plants. These low numbers could be related to the fact that woody taxa are low phytolith producers compared to sedges as will be discussed later on. They were present in both grasses and eudicots but rarer in grasses compared to eudicots. This can only be speculated as it remains to be seen if this is the case across South Africa as modern phytolith reference collections for the region are still scanty. A new study from the south coast of South Africa indicates that blocky parallelepiped phytoliths occur in small numbers in woody taxa but mentions them as the second most recurring phytolith morphotype and does not mention them in grasses (Esteban, 2016). Blocky parallelepiped phytoliths are reported to specifically occur in the bark of woody plants (Collura and Neumann, 2017) however, this current study and that of Esteban (2016) did not concentrate phytoliths from bark alone but rather extracted phytoliths from wood samples with bark adhered to them. It is possible that this contributed to the low numbers of blocky morphotypes in the woody species in which they occurred since eudicots are generally low phytolith producers compared to grasses and sedges (Piperno, 2006).

The grass species in this study, although far less than the largest modern grass phytolith reference collection in South Africa (Rossouw, 2009), they followed the already established trend of grass phytolith morphology and high phytolith production (Twiss et al., 1969; Twiss, 1992; Piperno, 2006). The modern phytolith assemblages generally conform to the known major grass subfamily classifications especially for Panicoideae, Chloridoideae and Aristidoideae in agreement with Rossouw (2009). When bilobate phytoliths are abundant in the archaeological and palaeoecological record, they point to a Panicoideae and Aristidoideae origin with some morphological considerations that may separate the two while abundant saddles point to a Chloridoideae origin. The one Pooideae species (*Agrostis* sp.) analysed in this study could not allow for generalisations about this subfamily as it produced bilobates, saddles and rondels as seen in C3 grasses in the WRZ (Cordova, 2013; Esteban, 2016) and although rondels were the most dominant, it produced rather high amounts of bilobates and saddles not previously seen in this subfamily in African high altitude/cold climate C3 grasses (Bremond et al., 2008; Cordova, 2013, Esteban, 2016; Murungi et al., 2017). Unlike the WRZ, the SRZ is dominated by C4 grasses (Scott, 2002; Cordova, 2013) and during collection of voucher specimen it was the only species of Pooideae encountered.

C3 grasses in the SRZ are known to occur in a few high altitude areas (Cordova, 2013) and it will be necessary to study the extent to which they occur in the study area and their phytolith morphotypes so as to confidently discuss the type of phytoliths they will leave in the fossil record.

The other C3 grass subfamily studied was Arundinoideae which was represented by the species *Phragmites australis* which also showed redundancy of the rondels. It was dominated by various kinds of rondel phytoliths especially the ‘horned towers’ and long types that are similar to those seen in some Chloridoideae specie and this was also observed by Cordova (2013). Other than the unique ‘kidney-shaped’ rondels observed in *Aristida* sp. rondel phytoliths in this assemblage therefore lend themselves to no easy interpretation as they occur in all the subfamilies studied here. The abundance of these morphotypes in the fossil record at Sibudu was also precisely why this reference collection was conducted. Although no concrete answers have been obtained, it remains that the main morphotypes - bilobates and saddles - are informative of past vegetation and they will likely occur in the fossil record in combination with rondels as observed in the modern assemblage. In the WRZ, rondels were found in both C3 and C4 grasses and attribution to C3 grasses that dominate this region was based on them being most abundant in those grasses (Esteban, 2016). Generally this study shows that bilobates and saddles are the types to be related to grass subfamily identification when found in the fossil record and therefore make climatic inferences in the SRZ. This is in agreement with Esteban (2016) who also found bilobates and saddles as the most important morphotypes for C4 grasses in the WRZ of South Africa.

In woody plants (under eudicots), phytolith production was found to be unevenly distributed in most plant families studied in agreement with previous studies in Africa (Mercader et al., 2009; Collura and Neumann, 2017). More so, phytolith production in eudicot plants was found to be much lower compared to grasses and sedges as previously noted (Albert, 2000; Strömberg, 2003; Piperno, 2006; Mercader et al., 2009; Collura and Neumann, 2017) and more recently for South Africa (Esteban, 2016). It has been reported that only 10% of woody species globally contain silica in their wood making it difficult to detect the presence of wood in a fossil phytolith assemblage, more so because the morphotypes produced in wood such as globular psilates occur in other plant organs (Collura and Neumann, 2017). Their study separated bark and wood in the woody specimen studied and they found that they produce different phytoliths and that bark produces more phytoliths than wood. Several of the aforementioned studied also extract phytoliths from leaves and wood (with bark adhering) separately.

This current study did not focus on making this distinction in plant organs and different plant parts were studied as a whole to mimic the archaeological record as the interest was in understanding the kind of phytolith morphotypes they generally produce as plant groups for interpretation of the fossil phytolith record. It is unlikely that the early humans used the many firewood species identified from Sibudu (Allott, 2004, 2006) by first separating the wood and bark. Specifically, the incentive for this phytolith reference collection was the abundance of globular psilates and blocky parallelepiped phytoliths that occurred in the fossil phytolith assemblage of Sibudu. The focus of this reference collection therefore was to identify these two morphotypes in the modern vegetation so as to determine their plant origin with some level of confidence as they are sometimes considered to be ubiquitous while other studies have linked them with woody taxa (Runge, 1999; Albert, 2000; Piperno, 2006; Mercader et al. 2009, 2010). More so, the phytoliths that would be produced by different plant parts of eudicots have previously been documented (e.g. Piperno, 1989; Bozarth, 1992; Albert, 2000; Strömberg, 2003; Bamford et al., 2006; Piperno, 2006) and can still be identified in this kind of modern phytolith assemblage and their plant part origin determined.

To this end, their leaves are associated with tracheids, multicellular polyhedral and anticlinal structures, globular phytoliths, hairs/hair bases and the rare cystoliths; wood is associated with globular phytoliths (psilate and granulate) and the rare nodular and granular aggregate phytoliths; while bark is associated with sclereids, fibres, blocky types, cork aerenchyma and globular phytoliths (e.g. Bozarth, 1992; Alexandre et al., 1997; Strömberg, 2003; Bamford et al., 2006; Esteban, 2016; Collura and Neumann, 2017). Reproductive structures in various families tend to produce unique and sometimes diagnostic phytoliths (Piperno, 1989, 2006; Bozarth, 1992; Iriarte and Paz, 2009). Redundancy in plant parts is therefore still eminent with some types such as globular phytoliths occuring in leaves, seeds, wood and bark (Piperno, 2006; Mercader et al., 2009; Collura and Neumann, 2017). These morphotypes were found in the eudicots in this study and therefore taxa from this part of South Africa generally follow already established morphological trends from other parts of Africa and the rest of the world. Therefore among the aforementioned morphotypes, this study considered globular psilates, tracheids, multicellular polyhedral and anticlinal structures, hairs/hair bases, cystoliths, sclereids, blocky types, stomata and cork aerenchyma as the key morphotypes that indicate woody taxa in the fossil record. The non-woody eudicot *Rhoicissus tomentosa* produced anticlinal and globular morphotypes but they were very rare.

However, some of these morphotypes are known to occur in monocots as well i.e. tracheids, blocky types and globular psilates mainly (Piperno, 2006; Iriarte and Paz, 2009; Mercader et al., 2009). This was also confirmed by this study as tracheids were seen in sedges and rushes (Juncaceae) while blocky phytoliths were common in sedges and rare in grasses. Given that sedges produce a much higher number of phytolihs than eudicots, the parallelepiped blocky morphotypes in sedges are much more abundant compared to those in eudicots. They were generally not common across eudicot taxa but ranged from common to rare in taxa in which they occurred. Sedges were not part of the taxa studied in the WRZ of South Africa and parallelepiped blocky phytoliths are associated with woody taxa (Esteban, 2016). This current study supposes that it might be possible to separate the tracheids occurring in eudicots from those in monocots (grasses, sedges and rushes) as they appear much larger, thicker and can be branched, although the small sizes in monocots also occurs in eudicots. Basically the large complex tracheids seen in eudicots were generally not associated with monocots. Bozarth (1992) refers to these large types as ‘tracheids with spiral thickenings and a branched structure’ that are formed in leaves of many arboreal and herbaceous dicots. This possibility of separating tracheids in monocot and eudicot taxa needs to be further investigated to make more specific interpretation when they are found in the archaeological record.

Worthy of attention are the globular psilates which were common in the archaeological record at Sibudu that did not appear as redundant or ubiquitous in the modern plant reference collection as they are often considered (Piperno, 2006). Globular psilates were generally the most recurring type in eudicot plants as observed in South African and West African species although numbers among species vary from rare to abundant (Esteban, 2016; Collura and Neumann, 2017). In this reference collection, globular psilates are generally characteristic for eudicot plants (in particular the trees and shrubs) and were absent in grasses and rare in sedges in agreement with Runge (1999) who reports them absent in both taxa. Globular psilates were ranked last among the morphotypes produced in Mozambican grasses and were rather associated with woody taxa and bushes and were not mentioned in South African grasses (Mercader et al., 2009, 2010; Esteban, 2016). Globular granulates that can occur also in both monocots and eudicots but are often associated with trees (Alexandre et al., 1997; Barboni et al., 1999; Piperno, 2006) are absent in all the taxa studied here.

Lastly, it is important to mention that it is only the genus *Celtis africana* (Celtidaceae,) that can be identified in the archaeological record as it produced diagnostic stippled plates and granular aggregates while cystoliths might allow for the identification of some families i.e. Moraceae and Celtidaceae represented here by the genera *Celtis* and *Ficus*. Cystoliths are reported to be common in the leaves of Moraceae, Celtidaceae, Cucurbitaceae, Acanthaceae and Urticaceae (Runge, 1999). The hair bases of Moraceae and Celtidaceae also seem to be important in separating the two families in agreement with Iriate and Paz (2009). Several families in this study produce hair bases that tend to not always look similar and may be of some taxonomic importance. Species of the same family tend to show various hairs with some types common to them. For example, *Eugenia capensis* and *Syzygium cordatum* (Myrtaceae) produce various kinds of hair bases but they have a type that was similar in both and not observed in other species in agreement with Piperno (2006) that hair bases can be useful in taxa discrimination. Hair bases were only observed in eudicot taxa and it has been suggested that they may not be preserved in soils making them less useful in archaeological and palaeoecological studies (Piperno, 2006). Generally because few taxa produce silica in their wood, it is suggested that many may not leave a signal in the archaeological record making it difficult to trace wood in particular (Collura and Neumann, 2017). Wood phytoliths are mainly globular psilate or decorated morphotypes and the more rare diagnostic nodular/granular aggregate bodies (Collura and Neumann, 2017).

CHAPTER SEVEN

THE ARCHAEOLOGICAL PHYTOLITH ASSEMBLAGE

7.0 Introduction

This chapter presents results of the types of phytoliths and of plant taxa utilised by early humans obtained from the analysis of phytoliths preserved in 26 Middle Stone Age (MSA) sediment samples obtained from the south profile of square C4 and two from C2 and C5. They span the period from more than~71 ka to~48 ka representing the pre-Still Bay (>71 ka), the Still Bay (~71 ka), Howiesons Poort (~62 ka) and post-Howiesons Poort (~58 ka) techno-complexes or occupational phases (See Chapters 1 and 2). This chapter therefore presents an attempt at reconstructing the vegetation and inferred associated climatic conditions that prevailed at Sibudu during this period and human-plant interactions at the site.

7.1 The MSA phytolith assemblage

Phytoliths are abundant and diverse in the fossil assemblage of Sibudu and all the samples analysed produced statistically sufficient amounts that provided information regarding the type of plants utilised by early humans during the MSA. The fossil assemblage is largely made up of grass short-cells, blocky parallelepiped and elongate phytolith morphotypes (Fig. **7.1**). The other common morphotypes are globular psilates and other blocky types. Other types include tabular elongates, acicular phytoliths, Cyperaceae (sedge) phytoliths (cone and achene types) and several other types referred to as ‘Other’ that include articulated silica skeletons (that include polyhedral epidermal cells), bulbous structures, tracheids, stomata and sclereids. Those grouped under ‘Other’ are generally morphotypes commonly associated with eudicots in general and because they often occurred in small numbers individually, they were grouped together. Select examples of these morphotypes are illustrated in Fig. **7.2a**, **b**, **c**. Most of the phytolith terminology in this chapter follows that used in the modern reference collection (Chapter Five). Most of the morphotypes mentioned above were also observed in the modern phytolith reference collection, notably the grass short-cells, globular psilate, blocky parallelepiped, bulbous structures, cone and achene phytoliths, tracheids, polyhedral epidermal cells, tabular and elongate phytoliths. Few morphotypes observed in the modern specimens were rare or not observed in the fossil record such as cystoliths, hair bases and the diagnostic echinate bodies of *Celtis africana*.

7.2 Phytolith relative abundance and inferred plant taxa at Sibudu

Down-profile variations in the relative abundance of the fossil phytolith morphotypes are in the phytolith diagram Fig. **7.1** produced by the TILIA software (Grimm, 2007). Table **A6** in the Appendix shows the data sheet showing the relative abundance of each morphotype in each sample. The phytolith diagram is described below in terms of phytolith abundance and plant taxa identified and to ease interpretation, phytoliths zone boundaries have been adopted according to the techno-complexes/occupational phases described earlier in the thesis (Chapter 1 and 2), whose age clusters are described for Sibudu (Jacobs et al. 2008a, b) (Fig. **7.1**). Based on the modern phytolith reference collection in Chapter 5 and 6 and the literature, important fossil phytolith morphotypes are interpreted as follows: Phytolith short cells are associated with Poaceae (grasses) and in the fossil assemblage are represented by saddles, lobates (crosses, bilobates and polylobates) and rondels; while cone shaped and achene phytoliths are characteristic of Cyperaceae (sedges). A new group termed as 'sedge anticlinals' (Fig. **7.1)** that were observed in the fossil record (Fig. **7.2c**: bh-bj) that often appear line-like in a general conical shape were similar to those seen in the modern sedges studied and was therefore tentatively considered to be produced by sedges. Globular psilate morphotypes are associated with ligneous dicotyledons that include trees/shrubs and are interpreted as mainly representing forest taxa in this study following the modern reference material. Blocky parallelepiped morphotypes are generally considered redundant although most studies associate them with woody taxa (e.g. Albert, 2000; Mercader et al., 2009; Esteban, 2013) but their abundance in the Sibudu fossil record required an interpretation and from the modern reference collection they are associated with sedges and to a lesser extent, grasses and woody taxa. The major phytolith classifications used in the graph in Fig. **7.1** are based on results of the modern phytolith study and the literature. What follows is a description of the results of phytolith analysis following the known Sibudu techno-complexes and their chronology.

7.2.1 Pre-Still Bay (Pre-SB): >~71 ka

Four samples were analysed from this period in the lower part of the Sibudu deposits (layers BS8, LBG3 (ii), LBG2, LBG) (Fig. **7.1**). The samples yielded phytolith assemblages that are dominated by grass silica short cells (23.9 – 48.6%) that are composed mainly of lobates (1.2 – 25.3%) and rondels (11 – 20.9%). Other major morphotypes are elongates (8.7 – 27.6%), globular psilate (2.3 – 18.2%), blocky parallelepiped (3.1 – 15.6%), sedge phytoliths (cone shaped and achene types) (1.8 – 4.5%) and saddle shaped phytoliths (1.8 – 4.1%) (Fig. **7.1**). This period therefore suggests that various taxa were utilised at Sibudu and the vegetation in the vicinity was a mix of grass, sedge and woody plants.

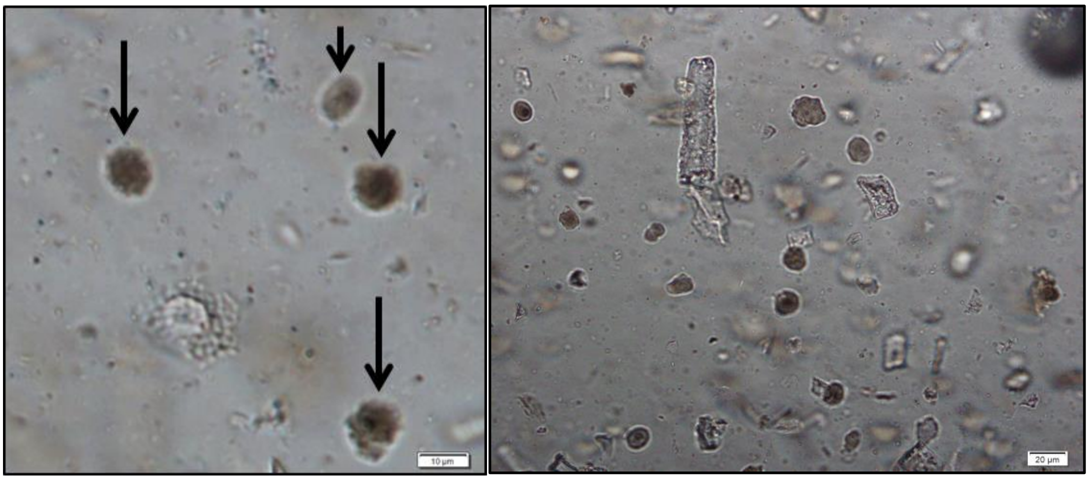
7.2.2 Still Bay (SB):~71 - 62 ka

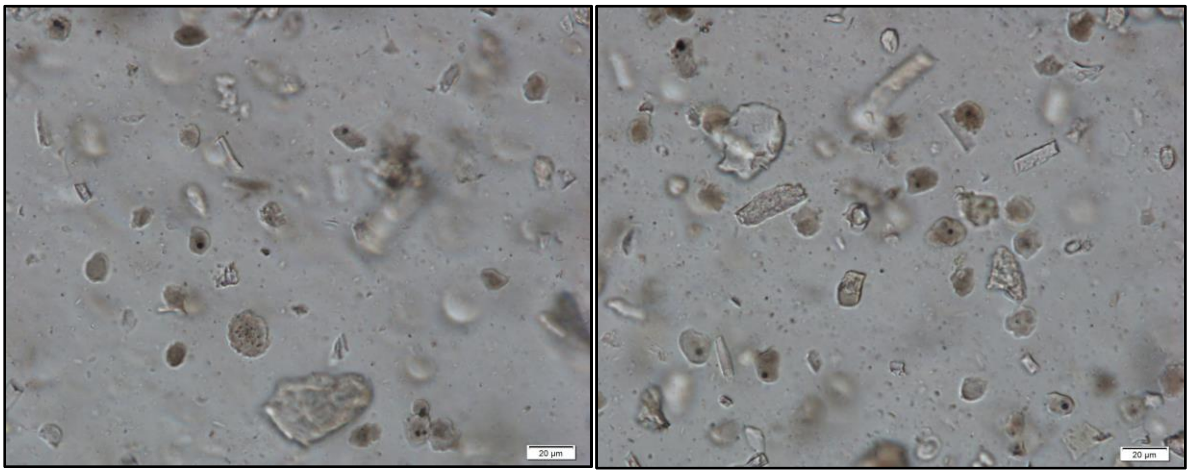
Two samples were analysed from this period from the layers RGS and a black lens. Lobates and rondels remain the most abundant grass silica short cells and occur in almost similar amounts as in the previous layers (1.8 – 20.3% and 12.6 – 22.9% respectively). Globular psilates remain low (1.1 – 11.7%), blocky parallelepiped remain constant (10.6 – 15.3%), saddles remain in insignificant amounts (0.6 – 1.1%) while sedge phytoliths (cones and achenes) increase slightly reaching 8.6% (Fig. **7.1**). This period therefore represents a mix of grass, sedge and dicotyledonous plants.

7.2.3 Howiesons Poort (HP):~62 - 58 ka

Seven samples were analysed from this section, Fig. **7.1** (Layers: PGS2, PGS1, PGS, GS3, GS2, GR, H1 RB). Grass silica short cells vary from 9.1 to 41.4% with rondels being the most dominant (6.8 – 24.8%) followed by lobates (1.8 – 12.5%). Saddle shaped phytoliths remain very low at less than 4.1%. Blocky parallelepiped phytoliths increase especially in the upper part of this section (9.8 – 22.9%). Globular psilate phytoliths vary between 4 to 17.9% while cone shaped and achene phytoliths account for 0.5 to 4.7% in the assemblages in this section. This section of the profile is peculiar because it was dominated by peculiar sub-globular to irregular bodies appearing lightly granulate that were always brown in colour, articulated or as single bodies (Fig. **7.2a**: *p-v* and **7.2b**: *w-al*). Most of those illustrated are from the GS layers. They are of varying forms and were all grouped together although some are thought to be Cyperaceae (sedge) cones given their presentation and size, which may have been weathered by some process (Fig. **7.2a**: *p*-*v*). The amount of sedge phytoliths is likely underestimated for this period but proper sedge phytoliths were commonly occuring with these peculiar bodies in the GS layers (Fig. **7.2a**: *a*-*o*, most of these are from the layer GS2 and GS3). These morphotypes occur in five layers and are most abundant in the layers GS2 and GS3 were they contribute 44.6% and 60.7% of the total count (Fig. **7.1**). They occur in lower amounts in the three preceding layers PGS, PGS1, PGS2 contributing 22.8%, 33.6% and 23.3% respectively (Fig. **7.1**). These sub-globular/irregular bodies are only somewhat similar to those seen in *Ficus polita* in the modern reference material (See Chapter Five, Fig. **5.3c**: *m*, *n*) but look similar to Restionaceae phytoliths of Cordova and Scott (2010) and Esteban et al. (2017). Researchers working with Restionaceae phytoliths in South Africa identified the ones in this study as restio types on seeing them (Esteban and Novello, pers. comm, 2015). These morphotypes suggests an important human activity during the HP. A scalloped phytolith (Figure **7.2c**: ba) was encountered in the layer GS2 during scanning for unique types after the set total phytolith count was reached and is therefore not part of the counts presented here. Scalloped phytoliths are associated with the family Cucurbitaceae (the gourd family) with the genus *Cucurbita* (squash) in parituclar (Bozarth, 1986, 1987; Piperno, 1989).

An *in-situ* illustration of the subglobular to irregular bodies that occur in HP layers.





7.2.4 Post Howiesons Poort (Post HP):~58 – 48 ka

This section is represented by a phytolith assemblage from 14 samples (Layers from H1 in Br under YA2 (i) at the bottom of the profile to Iv at the top (Fig. **7.1**)). GSSCs for this period range from 4.3 to 50.3% with rondel phytoliths contributing between 2 and 42.1%, lobate phytoliths varying between 0.9 and 13.9% while saddle shaped phytoliths remain very low (0 – 4.9%). Blocky parallelepiped phytoliths are most abundant in this section of the profile and reach their highest here (8.8 to 35.1%). Globular psilate phytoliths remain in amounts similar to the other periods but reach their highest in this period (4.3 – 25.6%). Elongate phytoliths are also most abundant in this section (12.3 to 32.9%). Cone shaped and achene phytoliths remain low varying between 0 and 4.4%. This period therefore represents a mix of grass, sedge and dicotyledonous plants in the surrounding vegetation. Similar to one of the HP layers, a scalloped phytolith was encountered in the layer Y ash P (Figure **7.2c**: az).

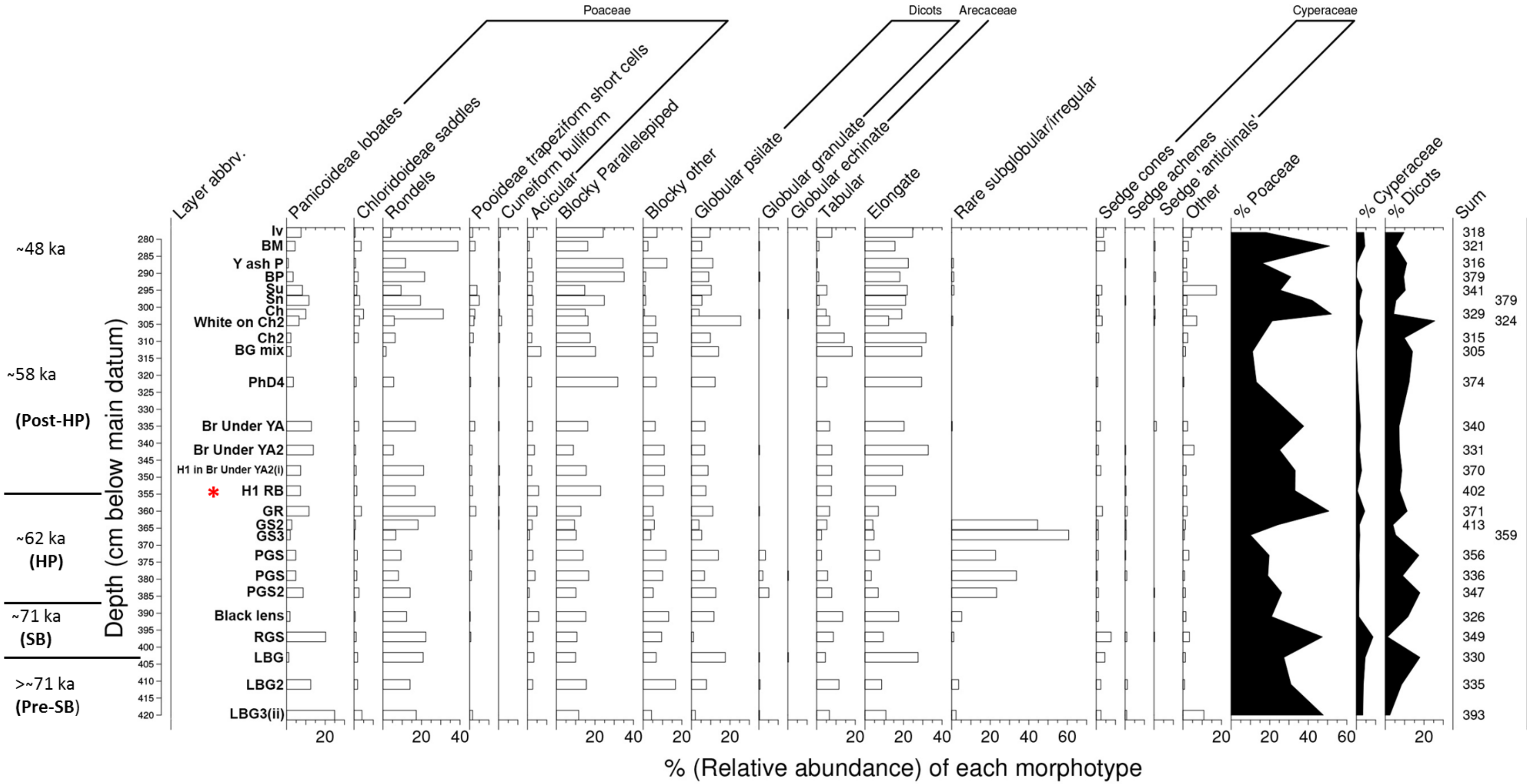


Figure 7.1: Phytolith histogram for Sibudu Cave showing the relative abundance of each morphotype expressed as a percentage of the total assemblage. * Recognisable hearth 1 which occurs in the two layers Br Under YA2(i) and RB.

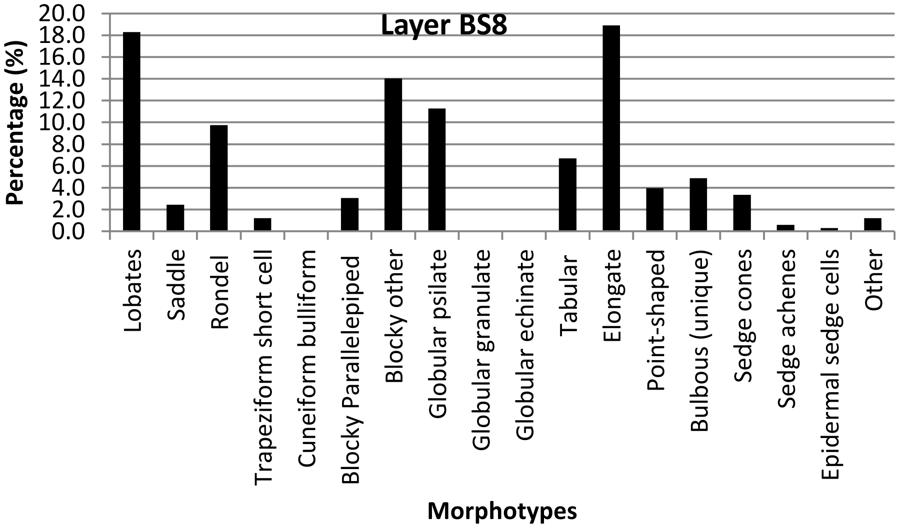
7.3 Reconstructing vegetation history and inferred climate during the MSA

The phytolith assemblage in the four techno-complexes of Sibudu cave is correlated to the modern phytolith reference collection and the literature to give an account of the vegetation during the MSA together with the inferred climatic conditions that prevailed. All samples had globular psilate phytoliths that were attributed to mainly the woody taxa which indicates the presence of trees and/or shrubs in the palaeovegetation (Fig. **7.1**). The presence of GSSCs that are diagnostic of Poaceae in all samples indicates the presence of grasses in the palaeovegetation. In all samples, the lobate (mostly bilobates) and rondel GSScs are the dominant morphotypes throughout the MSA period that these samples represent. In the modern reference collection, lobates were the most dominant in species of the Panicoideae subfamily and in the single species of the Aristidoideae subfamily that was studied, followed by rondels. Bilobates are typical for moisture-loving grasses that favour shade and/or mesic to hydric habitats (Barboni and Bremond, 2009). It is thought that these grasses were persistent at Sibudu because of the influence of the Tongathi River below the cave. Bilobates were abundant in the pre-SB and SB period occurring in almost similar amounts as rondels. During the HP and post-HP, bilobates reduce compared to rondels that remain dominant although the two types remain the most abundant all through and saddles do not exceed 5% at any one period.

On the other hand, rondel phytoliths are redundant offering no taxonomic interpretation as they are abundant in some C4 xerophytic grasses of the Chloridoideae subfamily, in C3 high altitude grasses of the Pooideae and Danthonioideae subfamilies and in some species of Aristidoideae (Bamford et al., 2006; Barboni and Bremond, 2009; Cordova, 2013). They were present in all the five subfamilies studied in Chapter Five further attesting to their redundancy across subfamilies. In the modern reference collection from Sibudu, rondel phytoliths were also an important component of Panicoideae grasses that are common in the in area. Saddle phytoliths that are typical for light-loving xerophytic Chloridoideae grasses that favour open habitats were very low throughout the MSA period of this study. In this study, they were observed in small amounts in the Arundinoideae, Panicoideae and Pooideae subfamilies and were most abundant in Chloridoideae. Phytoliths typical of sedges are present throughout the MSA and suggest the presence of sedges in the past vegetation which attests to wetland habitats at Sibudu as presented elsewhere (e.g. Sievers, 2006). Of the achene sedge phytoliths observed in the archaeological sediments, only the genera *Cyperus*/*Kyllinga* can be identified in this study. Consequently, the abundance of bilobate morphotypes suggests that the MSA at Sibudu for this period was dominated by moisture indicator grasslands growing under warm conditions and the climate is thought to have been warm and wet. The presence of sedge phytoliths suggests the presence of wetland habitats in the area and the utilisation of taxa close to the cave growing along the river and the grasses used may have been those along the river indicating a local phytolith record.

7.4 Phytoliths from the squares C2 and C5

The above analyses are based on the 26 samples taken from the square C4. Only two samples were available for analysis from two other squares; C2 and C5 i.e. from the layers SPCA 2 (post-HP) and BS8 (pre-SB) respectively. These two samples did not differ in phytolith content from the rest. They had the main morphotypes described in other layers and in both, bilobates and rondels were the most common grass silica short cells similar to the other samples from square C4. Although two samples is a small number, it is a step to suggest that the samples from the square C4 are a reliable indication of the MSA at Sibudu. In future samples from other samples should be analysed to support this.



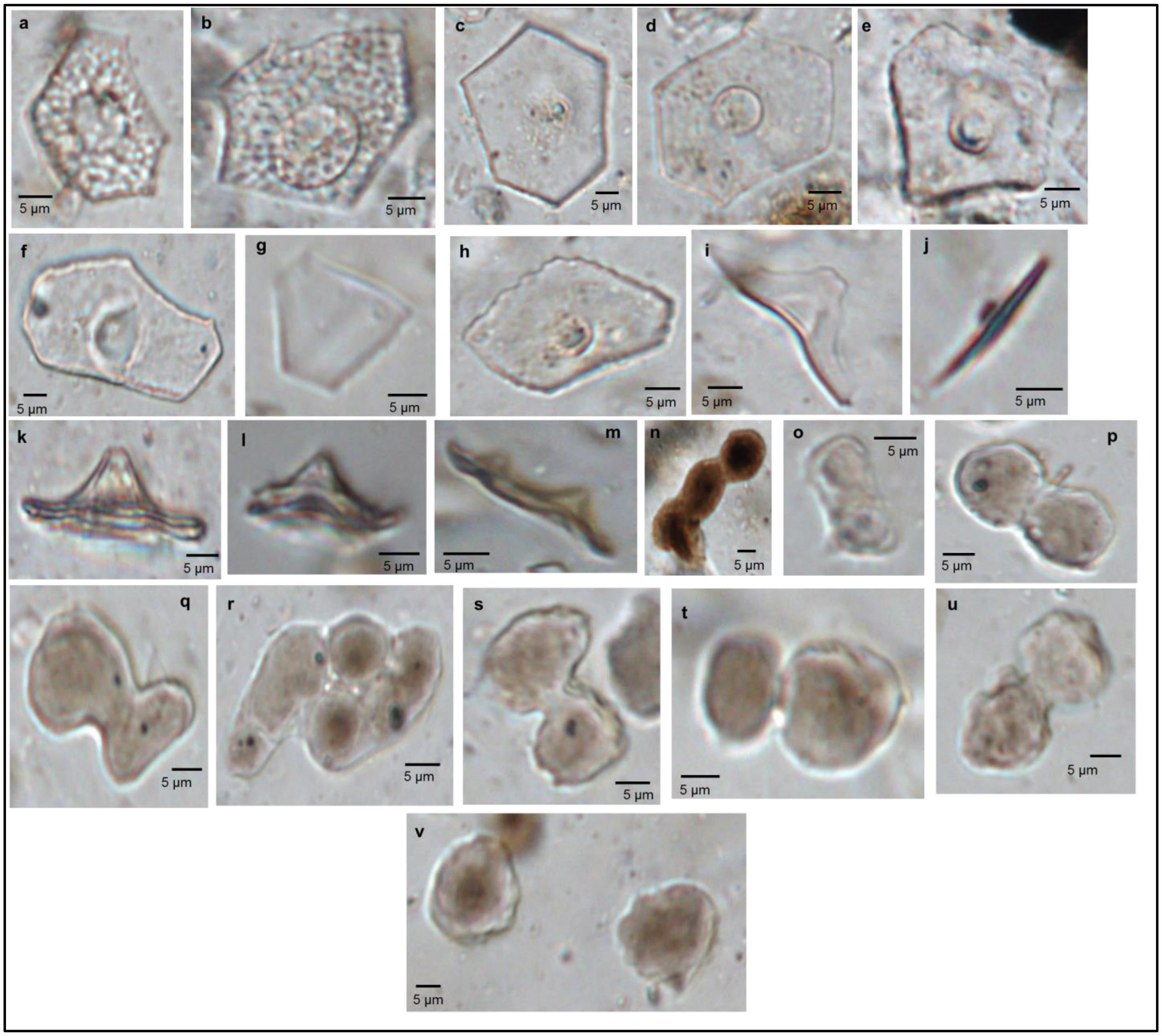


Figure 7.2a: Selected phytolith morphotypes from the MSA assemblage: Sedge phytoliths: **a-o**. Globular/subglobular bulbous phytoliths: **p-v** (several are likely weathered sedge cones).

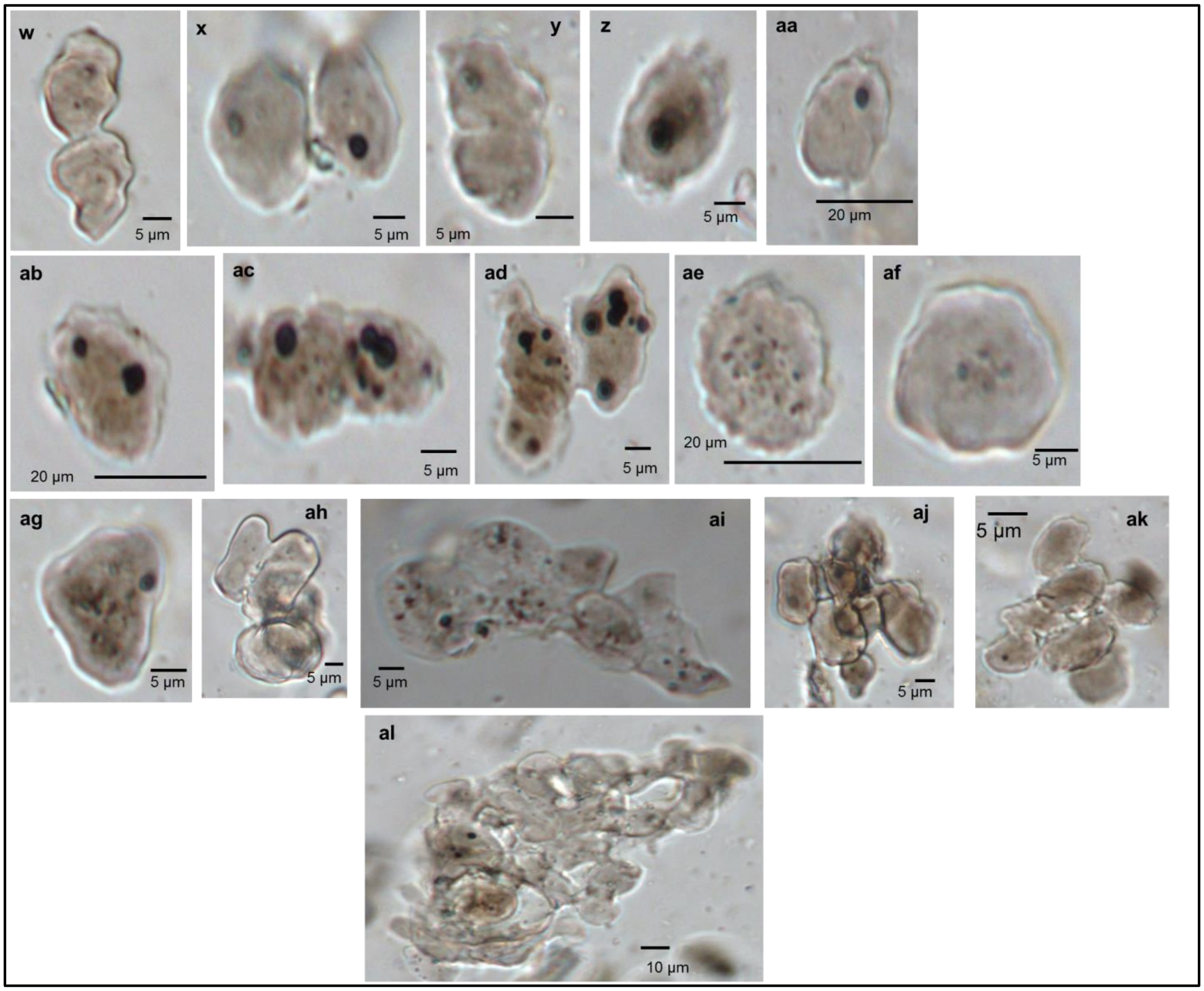


Figure 7.2b: Subglobular/irregular phytoliths (some bulbous): **w-al**

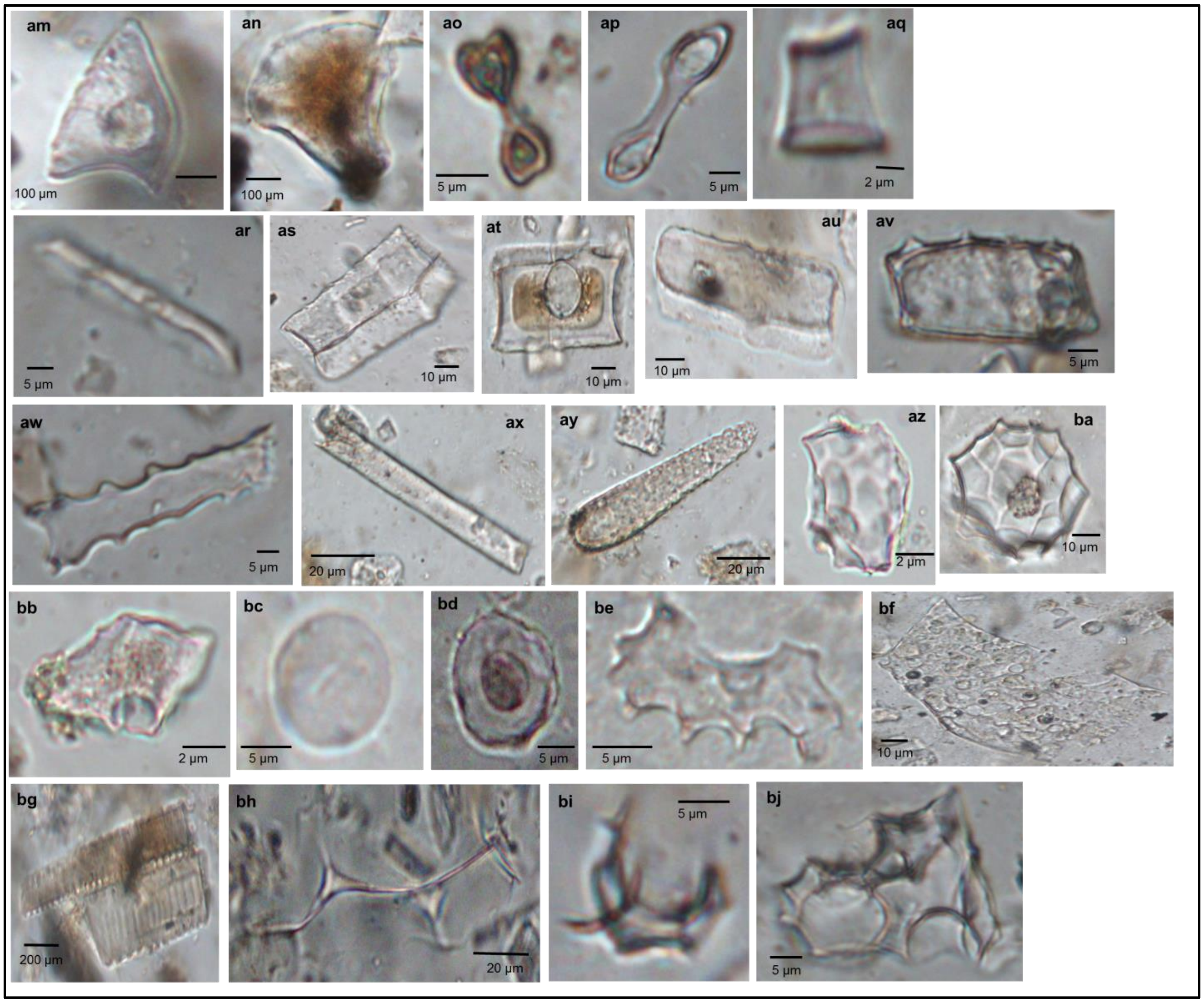


Figure 7.2c: Scutiform type: **am**. Bulliform: **an**. Bilobate grass short cell: **ao-ap**. Rondel grass short cell: **aq**. Trapeziform sinuate grass short cell: **ar**. Blocky parallelepiped: **as-av**. Elongate: **aw-ay**. Scalloped phytoliths (Cucurbitaceae type?): **az-ba**. Trough-like body: **bb**. Globular psilate: **bc**. Other globular type phytolith: **bd**. Irregular phytolith: **be**. Arenchyma?: **bf**. Tracheids: **bg**. Sedge 'anticlinals'?: **bh-bj**.

CHAPTER EIGHT

THE MSA AT SIBUDU: PLANT USE, VEGETATION AND CLIMATE

8.0 Introduction

This chapter provides an overview of the phytolith data from the MSA sediments within the context of Sibudu Cave and places the study in the regional context. It summarises the environmental history of Sibudu based on the phytolith assemblage presented in the previous chapter representing the period > 70,000 to ca. 48,000 yr BP and the plants that early humans utilised. Where possible, the archaeological phytolith assemblage is compared with phytoliths from the modern plants analysed and their climatic preferences or habitat is discussed. Phytoliths proved to be important in reconstructing past vegetation especially the type of grasses which in turn was an indirect proxy of the climatic conditions that prevailed during the MSA. The phytolith data is compared with other proxies at Sibudu and a few other sites in South Africa.

8.1 Phytoliths as an indicator of early human occupation, vegetation and climate at Sibudu ca. > 70,000 to 55,000 yr BP

8.1.1 The phytolith assemblage at Sibudu

The MSA phytolith assemblage in this study represents early human occupation from the Pre-Still Bay to the post-Howiesons Poort techno-complexes that span ca. > 70,000 to 55,000 yr BP at Sibudu cave. Of the 28 samples taken from 28 layers, only two were taken from a clearly recognisable hearth. Phytoliths are abundant and extremely diverse, in agreement with previous studies, and a variety of plants were utilised at Sibudu (Schiegl et al., 2004; Allott, 2004). In all samples, many phytoliths appear heat-altered, similar to Schiegl et al. (2004) who found heat-altered phytoliths in samples taken from hearths and in layers with no visible hearths. Whereas phytoliths are abundant and identifiable in the assemblage, in several samples they appear destroyed and unidentifiable providing evidence for the use of extensive fire at Sibudu as previously suggested (Schiegl et al., 2004). Phytoliths that are characteristic of woody taxa and grasses are well represented at Sibudu and the abundance of non-grass phytoliths confirms that wood ash is an important component of sediments at Sibudu and that they also often contain some grass phytoliths (Schiegl et al., 2004; Goldberg et al., 2009). It has been suggested that at archaeological sites where wood was the main plant utilised, eudicot plants might be underrepresented in the archaeological record because they are low phytolith producers especially in their wood (Albert, 2000; Collura and Neumann, 2017). This study found abundant phytoliths and although many are redundant morphotypes, they are not typical for grasses and are types that are often associated with wood, bark and leaves. More so, although grass short cell phytoliths can reach up to 50% of the phytoliths in few samples, their numbers can be considered lower than expected compared to non-grass phytoliths because of the high phytolith production in grasses compared to woody taxa that are very low phytolith producers (Piperno, 2006). Grasses are reported to produce up to about 20 times more phytoliths than wood/bark and that wood/bark are likely to be under represented compared to grasses in the archaeological record (Albert and Weiner, 2001).

This study set out to count approximately 300 phytoliths per sample, and this number was achieved, with ease in nearly all samples. The issue of how phytoliths entered the site and their preservation have already been discussed for Sibudu (Schiegl et al., 2004; Schiegl and Conard, 2006; Goldberg et al., 2009). Phytoliths were grouped into grass and dicotyledonous types in 19 sediment samples representing the post-Howiesons to the final MSA period (ca. 55,000 to 39,000 yr BP) (Schiegl et al., 2004). Their focus was mainly characterising the wood ash at Sibudu. This current study focused on discussing phytoliths in relation to early human-plant interaction, vegetation and climate during the MSA of South Africa. To achieve the latter, there was need to identify the grass phytoliths at Sibudu to a higher taxonomic resolution. Although grass phytoliths are preserved in the MSA assemblage at Sibudu, the assemblage is mainly dominated by the problematic rondel morphotypes that are often associated with C3 cold climate grasses of the subfamily Pooideae (Piperno, 2006; Cordova, 2013). Rondels are problematic because they have been found to be an important component of the modern phytolith assemblages of other subfamilies in Africa (e.g. Bamford et al., 2006; Cordova, 2013).

From the results in this present study, rondels are an important component of all grass subfamilies studied from the SRZ of South Africa, a region where grasses of the subfamily Pooideae are rare (Cordova, 2013). Rondels were found to also be the dominant morphotype in a potentially new MSA site in Limpopo also within the SRZ (Wadley et al., 2016). Rondels may therefore be an important part of grasses from this region. Their dominance in the archaeological record might also point to their high resistance to dissolution and fragmentation compared to other morphotypes. It has been found that smaller phytolith forms like rondels and trapezoids have less surface pitting than elongates or bulliforms due to less exposed surface (Osterrieth et al., 2009). It has also been suggested that phytolith with a more pure silica composition and less impurities from minerals like Calcicum and Iron tend to experience less dissolution (Osterrieth et al., 2009). Interpretations of the phytolith archaeological record in the current study are therefore based on combinations of rondels with another more diagnositic dominant grass short cell phytolith as suggested by the modern reference. The three modern soil samples analysed also suggest that rondels are the dominant grass short cell.

This study also set out to identify the dicotyledonous phytoliths to any highest resolution possible for specific plants that produced diagnostic phytoliths. Because sedges have been identified at Sibudu (Sievers, 2006, 2011, 2013), this study also set out to identify sedge phytoliths in the MSA assemblage. To enable identification and interpretation of the MSA assemblage, a modern plant reference collection was made to understand the phytolith morphotypes that can be expected for taxa from this region and that are likely to be found in the MSA assemblage. Important to note here is that phytoliths from various plants studied where found in the archaeological record but some important types from woody taxa do not seem to be preserved in the archaeological record. Hair bases that were common in woody taxa were hardly encountered in the archaeological record and the morphotypes that are diagnostic of *Celtis*, the only genus that was identifiable to that level, were not observed in the phytolith record. Piperno (2006) reported that hair bases may not be commonly preserved in sediments making them of less taxonomic value in phytolith analysis. In contrast, hair bases were indicated in the archaeological phytolith study at Sibudu by Schiegl et al. (2004).

Although plants at Sibudu were brought to the site by human activity and the sediments are largely anthropogenic (Goldberg et al., 2009), it is possible that some phytoliths found in the sediment layers may represent grasses that were not brought in intentionally. The modern plant reference collection showed that some grass phytoliths could have been deposited at the site through woody taxa and sedges. During analysis of woody taxa for their phytolith content, some species were found to contain some grass phytoliths in their assemblage i.e. *Baphia racemosa*, *Eugenia capensis*, *Syzygium cordatum* and *Diospyros natalensis*. A conical shaped phytolith was observed in *Ficus polita* but it appeared somewhat different from the sedge type to the eye. Although it was treated as contamination in this study, it is important to mention that Hart (1990) presented evidence for the redundancy of the sedge diagnostic cone shaped phytoliths as they were observed in three species of dicotyledonous families: *Acacia schinoides*, *Banksia oblongifolia* and *Casuarina distyla* and argues against their use as diagnostic to Cyperaceae at least for Australian vegetation. For the sedges, both the *Bulbostylis* spp. produced some grass phytoliths while two species produced a copious amount of grass short cell phytoliths mainly bilobates i.e. *Schoenoxiphium sparteum* and *Cyperus obtusifloris* spp. *flavissimus*. However, these four sedge species were not collected from the main study area (Sibudu). This study supports previous studies that suggest that this kind of grass phytolith deposition from other plants in the sediment is possible in archaeological sites although this kind of contamination is reported to be minimal (Albert and Weiner, 2001) and recently also in South African eudicots (Esteban, 2016). More so, a few phytoliths at Sibudu may also have been transported by wind, water or animals as suggested by Schiegl et al. (2004).

What follows here is how phytoliths have provided evidence for early human-plant interactions, and the prevailing vegetation and climate in which the early humans lived at Sibudu during the MSA. It is important to note that the phytolith data at Sibudu is most likely very local with forest taxa obtained from the forest around Sibudu and grasses subfamily types and sedges were influenced by the Tongati River. The phytolith morphotypes used to make these inferences and their abundance are shown in Figure **7.1** in Chapter seven. Lobates, saddles and rondels including trapeziform short cells represent grasses, while blocky parallelepiped and blocky other are associated with sedges and woody taxa, globular phytoliths are associated with woody taxa, cones and achenes are associated with sedges while elongate and tabular phytoliths are generally of little taxonomic value. Those grouped under ‘other’ are often associated with eudicot plants but can also occur in monocots and they were: tracheids, multicellular polygonal cells, sclereids, facetate bodies, bulbous structures and other various morphologies that did not occur in the modern grass and sedge phytolith assemblage.

8.1.2 Early human-plant interactions at Sibudu

The variety of phytoliths at Sibudu suggests that plant use at Sibudu was intense and involved combustion of various plant parts and taxa in agreement with Schiegl et al. (2004). As previously published for charcoal studies, the main source of fuel at Sibudu were woody plants (Allott, 2004, 2005; Lennox et al., 2015). Phytoliths indicative of woody taxa are present throughout the period of occupation. Grasses were also utilised by early humans throughout this period of occupation. Occurring together with wood, grasses are thought to have been used as tinder to start fires to burn the wood given their moderate numbers despite their known high phytolith production. This could be why grasses were conspicuously low in the non-hearth samples from the layers: white on Ch2, Ch2, BG mix and PhD4 that follow each other in stratigraphy during the post-Howiesons Poort. Conversely, a sample from a hearth embedded in the layer Ch2 by Schiegl et al. (2004) indicates an abundance of wood ash with a high amount of grass phytoliths suggesting grass could have been used to start fires in such fire structures. One other layer in the assemblage showed a very low number of grass phytoliths .i.e. Y Ash P in the upper layers of the post-Howiesons Poort. It is an ash layer that likely contained more woody taxa than grasses. Wood was therefore the preferred source of fuel at Sibudu as already registered in other studies (Schiegl et al., 2004; Schiegl and Conard, 2006).

Of the 28 layers examined in this current study, only two fall witinin a recognisable hearth i.e. hearth 1 in the layer RB (H1 RB) and hearth 1 in the Br under YA2(i) that are at the beginning of the post-HP. Grass short cell phytoliths reached nearly 50% of the total phytolith assemblage in only two layers and they were not hearths (the layers BM (black magic) and Ch (chocolate) that also belong to the post-HP. It is then possible that fire structures are more extensive at Sibudu than indicated by visible hearths as previously suggested by Schiegl et al. (2004) or grasses might have had other uses at Sibudu such as bedding.

The relatively low number of grass phytoliths can also suggest that grasses were only used in small portions as tinder and some could have been brought to the site unintentionally adhered onto other plants such as sedges and wood as seen in the plant reference material. The presence of grass and non-grass phytoliths throughout the occupation period in both hearths and layers without hearths, some of which are far separated from the recognised hearths may support that ash from hearth was spread to other layers through trampling or wind movement (Schiegl et al. 2004). It may also suggest that the use of fire at Sibudu was more extensive than what the visible hearths and ash layers indicate as suggested by previous studies (Schiegl et al., 2004; Schiegl and Conard, 2006). Phytoliths characteristic of grasses were mainly the grass short cell morphotypes from leaves and stems and those from their inflorescences were observed in insignificant amounts. This is also reported for the MSA at the south coast of South Africa (Esteban, 2016).

This study also provides evidence for the use of sedges by early humans throughout the period represented in agreement with previous studies (Sievers, 2006, 2011, 2013; Goldberg et al., 2009; Wadley et al., 2011). It provides evidence that sedges were utilised as early as the pre-Still Bay occupation (> 71, 000 yr BP) in agreement with Sievers (2011, 2013) and the highest number of sedge phytoliths in the whole assemblage was in the layer RGS (70.5±2.4 yr BP, the Still Bay). Sedges are thought to have been brought to the site by humans from the nearby Tongati River and carbonisation of their nutlets is thought to be a result of post depositional fires and deliberate burning of sedges by early humans for site maintenance (Sievers, 2006, 2011; Wadley et al., 2011). These sedge studies suggest the presence of a permanent water source during MSA of South Africa. Pollen from sedges (Renaut and Bamford, 2006) and presence of aquatic remains in the Sibudu record (Plug, 2006; Val, 2016), support the presence of water from the Tongati River that lies below Sibudu.

As aforementioned, phytoliths typical of sedges (cones) are not well preserved in soils and (Carnelli, 2002; Novello et al., 2012) they were indeed observed in fewer numbers in the MSA phytolith assemblage compared to their abundance in the modern material. However, the sedge modern reference collection showed an abundance of parallelepiped blocky phytoliths in this family. These phytoliths are among the most abundant in the archaeological phytolith assemblage at Sibudu. Although they were also observed in some woody taxa, they were not abundant. This study therefore suggests that a good number of parallelepiped blocky phytoliths may have originated from sedges. Moreover tabular elongate phytoliths were in the modern reference more common to grasses and sedges although they appear more abundant in sedges.

Although they are considered redundant in this study, some of them might have been produced by sedges. Therefore sedges are thought to be underrepresented in this fossil record (Fig. 7.1, Chapter seven). This study confirms the use of sedges of the genera *Cyperus*/*Kyllinga* that can be identified by phytoliths.

This phytolith study also points to the possible use of Cucurbitaceae plants (squashes and gourds) at Sibudu during the MSA. Two phytolith morphotypes that resemble those of Cucurbitaceae fruits were seen in HP layer GS2 and post-HP layer Y ash P (Bozarth, 1987; Piperno et al., 2000). It is possible that the early humans consumed their fruits and seeds or this also points to the possible earliest use of gourds (calabashes) dating as far back as the HP period around 60,000 years ago. Archaeological deposist from the Neotropics revealed the presence of Cucurbitaceae towards the end of the Pleistocene and early Holocene (Piperno et al., 2000). This submission needs more evidence at Sibudu as these phytoliths were observed rarely and were therefore not a significant component of the phytolith assemblage.

Two layers appear unique in the whole fossil assemblage studied here. These are GS2 and GS3 that represent the Howiesons Poort at 63.8±2.8 yr BP. The phytolith record suggests that a very specific plant was utilised by the early humans during occupation of this period. Brown globular bulbous like phytoliths are abundant in both layers. This abundance is illustrated in Figure **7.1** in Chapter seven under the phytoliths group ‘other’. This group was composed of a few morphotypes for each layer apart from these two layers because of the abundance of these conspicuous brown globular bodies making them the most dominant morphotypes in these samples. These bodies are very similar to those identified as characteristic of Restionaceae plants that are restricted to the present-day fynbos region at the south coast of South Africa with the WRZ (Cordova, 2013; Esteban, 2016; Esteban et al., 2017). Restionaceae plants have been identified in the MSA assemblage at the south coast and are thought to have been utilised by early humans as bedding, similar to sedges at Sibudu given their resemblance to sedges and similar in their use (Esteban, 2016). Today, relicts of fynbos vegetation in the SRZ occur at high elevation in Afromontane vegetation (Mucina et al., 2006) and existence of plants restricted to the WRZ in the SRZ have been reported from Pleistocene records from the SRZ (Scott et al., 2004). Restios do not occur in the area today and have not been identified in previous studies at Sibudu. Somewhat similar bodies that looked like small cystoliths were observed in *Ficus polita* in the modern reference collection. *Ficus* species have been identified in the HP and younger layers at Sibudu (Allott, 2006). It is not clear if these bodies can be associated to restio plants or *Ficus* trees. It can only be speculated, but they do seem to suggest a very specific activity by early humans given their abundance in both layers. These bodies tended to appear with sedge phytoliths and at first it was thought that they were associated with sedges before the modern reference collection was made. So far, this study cannot confidently associate them with a particular taxon. The Howiesons Poort is reported to also have been unique in the charcoal assemblage because of the abundance of *Podocarpus* charcoal (Allott, 2005).

8.1.3 Late Pleistocene vegetation and climate at Sibudu: a local and regional context

Significant global scale changes in climate and sea level are recorded for the last glacial and such climatic changes are often reported for archaeological sites in the WRZ and the all year rainfall zone (ARZ) at the east and south coast of South Africa (see Chase, 2010 and studies therein) but are not well-documented for archaeological sites in the SRZ of South Africa (Chase, 2010). Sibudu rock shelter is one of the archaeological sites in South Africa that has been studied following a multidisciplinary and multiproxy approach (Chapter two).

The environmental history of Sibudu has therefore been inferred from several archaeological records that have allowed for the reconstruction of past environments, especially for the Howiesons Poort (HP) and post-Howiesons Poort i.e. from about ˜62 to 58 ka and˜58 ka to 48 ka respectively (Jacobs et al., 2008a, b; Jacobs and Roberts, 2008; Hall et al., 2014). Until recently little was known about the pre-Still Bay (>71 ka) and Still Bay (~71 ka – 62 ka) industries at Sibudu since most studies have focused on the HP and post-HP (Sievers, 2011, 2013; Val, 2016). This study therefore also contributes to understanding vegetation and climate during the pre-SB and SB industries. The use of data from different proxies together with improved dating control (Jacobs and Roberts, 2008; Jacobs et al., 2008a, b) has led to an improved understanding of MSA environments and the possibility of further palaeoenvironmental reconstructions at Sibudu. Hall et al. (2014) warn that proxy evidence at archaeological sites might be biased and is problematic but affirm that several lines of evidence for past environments have been presented for Sibudu in regard to environmental reconstructions. For example, from the charcoal analyses, it was not possible to decipher if the wood selection at Sibudu was a result of choice by early humans or environmental change but it is suggested that the charcoal is at least representative of the local woody vegetation that occurred at the site (Allott, 2006; Hall et al., 2014).

This current phytolith study adds complimentary information to the previous phytolith study at Sibudu (Schiegl et al., 2004) and provides a higher taxonomic resolution of grasses found in the Sibudu phytolith assemblage so as to understand the past grassland composition and infer the possible climatic conditions that prevailed at Sibudu during the MSA. The phytolith record is generally able to identify eudicot plants as a whole but cannot reconstruct the presence of specific families, genera or species although a good number of exceptions occur (Piperno, 2006). Grasses respond quickly to environmental change and grass phytoliths provide a proxy to study such changes in terms of C3 and C4 grassland composition (Twiss et al., 1969; Twiss, 1992). Diagnostic grass phytolith short cells occurred in sufficient amounts at Sibudu and they are the basis on which inferences of the type of grassland in the vicinity of Sibudu, possible changes in grassland composition and climate condition are made. The grass short cells found in the archaeological sediments and their taxonomic attribution of grass type has already been discussed.

Phytoliths can generally identify the grass family Poaceae to its different grass subfamilies and can in turn distinguish C_3 from C_4 grasslands that occur under different environmental conditions and also further distinguish between C_4 grasslands dominated by grasses of the subfamily Panicoideae (warm humid/wet climate grasses) and those dominated by the subfamily Chloridoideae (warm/hot dry climate grasses) (Twiss, 1992; Barboni et al., 1999; Piperno, 2006; Barboni and Bremond, 2009; Rossouw, 2009). The main grass subfamilies that can be identified thorough phytolith analysis are: Panicoideae, Chloridoideae, Pooideae and Aristidoideae (Twiss, 1992; Piperno, 2006; Rossouw, 2009; Neumann et al., 2017). Therefore the past vegetation and inferred climate at Sibudu as inferred from the grass phytolith record are discussed below in relation to other studies at Sibudu and put in the context of the wider region specifically for the period ca. > 71,000 to 48,000 yr BP i.e. the pre-Still Bay to the post-Howiesons Poort.

The grasses identified at Sibudu during this MSA period are mainly C4 grasses that are presently characteristic of the summer rainfall region (Bar-Matthews et al., 2010; Scott, 2013). These C4 grasses mostly correspond to the grass subfamily Panicoideae (warm and wet climate grasses). C4 grasses of the subfamily Chloridoideae (hot and dry climate grasses) were rare throughout the phytolith assemblage. Because the saddle-shaped phytoliths characteristic of Chloridoideae occurred in small amounts, it is possible that were produced in the archaeological record by Panicoideae and Arundinoideae grasses which were found to produce them in very small amounts in the modern reference collection. It is therefore possible that Chloridoideae grasses may not have existed in the vicinity of Sibudu or the possibility that they were not selected could be a factor. C3 grasses of the subfamily Pooideae (cold climate grasses/high altitude) appear to have been present during this period but were most likely never dominant. Overall it appears that C4 grasses dominated this MSA period. C4 grasses are the dominant grass type in the strong summer rainfall region in the east of South Africa while C3 grasses dominate in the west where there is strong winter rainfall (Bar-Matthews et al., 2010). C3 grasses are reported to be generally absent today in the summer rainfall region of South Africa while C4 grasses can grow in Winter rainfall region (Cordova, 2013).This phytolith study finds no strong evidence of the dominance of C3 grasses during the MSA period and suggests that the present dominance of C4 grasses at Sibudu must have extended well into the late Pleistocene period. This study therefore suggests the dominance of grasses that are characteristic of humid climates that grow in warm mesic environments from the pre-SB to the post-HP period of occupation.

Proxy environmental data for the pre-SB and SB at Sibudu is limited compared to the other industries but a recent faunal study suggests that the vegetation was that of evergreen and deciduous forest communities (Val, 2016). Val (2016) associated the pre-SB at Sibudu with warm and moist conditions consistent with the end of an interglacial period (> 75 kya) that was followed by a colder phase that accompanied the first glacial maximum around 70 kya. The warm and moist conditions inferred for the pre-SB are consistent with the phytolith record. Layers from the HP (~65-62 kya) at Sibudu suggest the dominance of evergreen forest taxa such as *Podocarpus* with high rainfall and more humidity (Allott, 2006; Bruch et al., 2012) which supports the warm and wet conditions inferred by this phytolith study. Bruch et al. (2012) suggests that the winters were slightly colder and drier than present whereas the summer temperatures and precipitations were the same as those for today. This may be also suggested by the phytolith study which does not find evidence of an influence of winter rain on the grasses rather a dominance of grasses that are influenced by the summer rain and temperature as it is today.

Charcoal studies at Sibudu provide strong evidence for mesic forest vegetation that grew in warm conditions during the HP with evergreen forest dominating (Allott, 2004, 2005, 2006) in agreement with the phytolith record. The HP layers generally provided evidence for a variety of vegetation communities at Sibudu including forest, riverine vegetation and to a lesser extent drier bushveld vegetation (Allott, 2006). The presence of *Kirkia* tree species adapted to dry environments suggests mixed vegetation (Allott, 2006). The vegetation during this period was interpreted as warm woodland savanna habitat growing close to a riparian forest (Allott, 2006). This may affirm the phytolith study that suggests a dominance of warm and wet climate grasses and the possible presence of warm dry climate grasses in small amounts. Carbon isotope values from the charcoal of *Podocarpus* confirm also confirm that the HP was a period of high water availability (Hall et al., 2008, 2014). Evergreen woody plants are also thought to have been predominant during this period (Sievers, 2006). Fauna studies also suggested that the greatest percentage of mammals during this period is of those that are adapted to forested environments with a small percentage from open environments (Clark and Plug, 2008). Gypsum found in layers of this period also suggested that there was moisture at the time (Pickering, 2006; Schiegl and Conard, 2006).

The post-HP (~58 to 48 kya) layers are dominated by mainly evergreen, riverine forest taxa some of which are reported to suggest a shift towards a cooler climate (Wadley, 2004; Allott, 2006; Sievers, 2006; Bruch et al., 2012). Temperatures for the post-HP are said to have been similar to those of the HP (Sievers, 2006; Bruch et al., 2012). This is similar to the phytolith record that does not show a change in grass subfamily dominance or grassland composition between the HP and post-HP and that C4 warm and wet climate grasses remained dominant as it is today. Bruch et al. (2012) suggest that the post-HP was however slightly colder than the HP and represents the coldest phase with a climate colder and drier than today. A shift to drier and colder than present climate with open savannas is also inferred by Hall et al. (2014) for the post-HP. This consistent presence of moisture in the environment allowed C4 warm-wet climate grasses to flourish. These inferences are supported by Reynold (2006) and Glenny (2006) who suppose a combination of forest, riverine and open savanna. The period also registers a change of mammals adapted to closed forest or woodland to those in drier and more open savannas (Plug, 2004; Cain, 2006). Charcoal and seed analyses show that many taxa found in and around Sibudu today were also present when the site was occupied in the MSA because at least some conditions may have been similar to those of today (Allott, 2004, 2005, 2006; Sievers, 2006; Wadley, 2004; Lennox et al., 2015). The presence of sedge phytoliths in all the layers in this study confirms the presence of a nearby water body as suggested by previous studies. Sedge nutlets were also found in all MSA layers and suggested the presence of perennial water in the Tongati River (Sievers, 2006, 2011). These layers also contained fern spores and sedge pollen indicating the presence of some moisture (Renaut and Bamford, 2006). The presence of reptiles, molluscs and fresh water birds also confirmed the presence of a permanent water source close to Sibudu (Plug, 2006; Val, 2016).

Most of the Sibudu MSA sequence falls within the final phase of Oxygen Isotope Stage (OIS) 4 and the start of OIS 3, periods in which seed and charcoal data point to variable and changing environmental conditions at Sibudu (Wadley, 2004; Allott, 2004, 2005, 2006; Sievers, 2006). The pre-SB, SB and HP layers fall within the OIS 4, a period representing an overall cool and moist climate while the all post-HP layers falls within the OIS 3 (~58-38 kya) (Wadley, 2004; Jacobs et al., 2008a; Chase, 2010). Jacobs et al., (2008a) suggest that both the SB and HP of southern Africa occurred during a period of warming in global temperatures as inferred from Antarctica ice cores and argue the technological change observed in the two industries are not environmentally driven. The phtyolith record is in agreement with a warm climate during this period. However, it has been argued that the climate of southern Africa does not correspond to global changes in temperature (Chase, 2010). Chase (2010) notes that previously poorly dated archaeological sites that assigned their inferred climatic conditions and occupations based on global changes were problematic and the new ages by Jacobs et al. (2008a) have allowed for proper contextualisation of past climate in South Africa as they can now be correlated cores from the Indian Ocean.

The climate of South Africa is among other factors driven by Indian Ocean sea surface temperatures (SSTs) and changes in the SW Indian Ocean SSTs influence South Africa’s summer rainfall zone with warmer SSTs causing more precipitation on the continent (Chase, 2010). Marine data from the east coast of South Africa that represents these MSA periods are scarce and most studies are from the west coast (Chase, 2010). The marine record off the Namibian coast indicates that there was an increase in precipitation during the MIS 4 period from 72 ka to 58 ka (Stuut et al., 2002), a period within which the SB and HP of Sibudu fall (Chase, 2010). Following the synthesis of the available data, Chase (2010) concludes that warm tropical SSTs and increase in temperature caused more humid conditions during MIS 4 in South Africa’s winter and summer rainfall zones. It is suggested that tropical summer rainfall dominated the summer rain fall region at the MIS 4/3 boundary (Chase, 2010). The grassland composition that the phtyolith study infers for Sibudu confirms this interpretation and the conclusion that during the SB and HB industries, humid conditions prevailed at archaeological sites in South Africa along the south and east coast (Chase, 2010).

Isotope studies at Pinnacle Point Cave (south coast) suggest that between˜75 ka to 67 ka (the pre-SB and SB), C4 grasses prevailed in a cool environment in the ‘all year rainfall zone’ – ARZ of South Africa that sits at the C3/C4 grass boundary – an area that is the intermediary between the WRZ and the SRZ (Bar-Matthews 2010). From˜66 ka to 50 ka (the HP and the post-HP), more summer rain occurred and C4 grasses dominated (Bar-Matthews, 2010). Because this zone is influenced by both winter and summer rain, grasses vary between C3 and C4 depending on the dominant rainfall type (Bar-Matthews, 2010). The dominance of summer rain and C4 grasses in the ARZ during this period (HP and post-HP), would mean the same conditions occurred at the east coast which falls in the SRZ whose rain influences the ARZ. The C4 grassland inferred by this phytolith study at the east coast (Sibudu) during the pre-SB (only a small portion represented in this study), the SB, the HP and post-HP is consistent with the grasslands at the south coast of South Africa during these industries.

8.2 Implication of this study for South African archaeology

This study has provided a higher taxonomic resolution of grass phytoliths at Sibudu for a somewhat better environmental interpretation of grasses during the MSA and this has an implication for how archaeologists interpret the phytoliths from the previous phytolith study by Schiegl and colleagues at Sibudu (Schiegl et al., 2004; Schiegl and Conard, 2006). Numerous specialist studies exist for Sibudu to date (Chapter 1, 2) and in an attempt to understand the past environment at Sibudu, the phytolith study by Schiegl and colleagues has been interpreted in a way that is problematic by specialists of other proxies at Sibudu. A major example is in Hall et al. (2014; p. 18, 19):

"The frequency of grass phytoliths increases in the upper layers and this may reflect an increase in grasslands around Sibudu, but this interpretation must be made cautiously because grass could have been used for tinder in some of the fireplaces (Schiegl et al. 2004) and also in the plant bedding that was frequently laid on the shelter floor (Wadley et al. 2011)", referring to the post-HP environment and "The phytolith composition at this time shows an overall decrease in grass and an increase in trees (Schiegl et al. 2004) suggesting that grassland patches were reduced at the expense of woodland", referring to the Late MSA.

This interpretation of the phytolith record at Sibudu is not justified as the study by Schiegl et al. (2004) cannot allow for this kind of environmental interpretation and neither did they imply it. It is important to mention first that it is not clear how the 'upper layers' where the grass phytolith increase occurred during the post-HP referred to in Hall et al. (2014) were selected given that the study they drew from (Schiegl et al., 2004) had six samples that had an increase in grass phytoliths that were evenly distributed throughout the post-HP. That said, Schiegl et al. sampled 20 MSA sediment samples (from 11 squares) and of the 19 samples analysed, nine belonged to what was termed as type I sediments (wood ash and grass phytoliths) while ten belonged to what they termed as type II sediments (mainly wood ash). For the post-HP, six samples belong to type I sediments while five belong to type II sediments while for the Late MSA, three belong to type I and five belong to type II. It is probably this change from six samples of type I sediments in the post-HP to three samples in the Late MSA that Hall et al. (2014) deduce that an increase in grassland may have occurred in the post-HP, and a reduction of grassland and increase of trees in the Late MSA. The post-HP was represented by a total of eleven sediment samples while the Late MSA by eight samples. It is therefore from the eight Late MSA samples that only three were of the type I category, marking a reduction in grassland and increase in trees.

Important to note is that all these samples were taken from clearly recognisable hearths and their surrounding sediments and that sediments at Sibudu were reported to be predominantly anthropogenic (Schiegl et al., 2004; Goldberg et al., 2009). It is difficult therefore to make this interpretation from the phytolith data presented in Schiegl et al. (2004). Firstly, as acknowledged by Hall et al. (2014) that caution must be taken when making this interpretation because grass phytoliths may be from grasses that were used as tinder to start fire or that were carried in as part of bedding, is precisely why this interpretation cannot be made because Schiegl and colleagues describe the deposits at Sibudu as almost purely anthropogenic (Schiegl et al., 2004; Goldberg et al., 2009). Therefore whether early humans used grass as tinder or bedding or not, they brought them to the site. It is for this reason that even if phytolith abundance is presented chronologically as done in this current phytolith study (with all samples but one taken from the same square following the stratigraphy), a reduction or increase of grass phytoliths in the Sibudu phytolith assemblage can in no way imply a reduction or expansion of grassland in the vegetation during the MSA. What is most probable is that the phytolith record of the current study may suggest the type of grassland that existed in the region in terms of C3 or C4 grassland composition on assumption that the early humans collected grasses that were representative of the prevailing vegetation but not its expansion or reduction. This present study provides a basis on which grassland composition during the MSA can be inferred while the phytolith study by Schiegl et al. (2004) would only suggest the presence of grasses as a whole in the environment but in no way would it suggest their reduction or expansion during the MSA. The grass phytoliths are likely a result of the selection behaviour of early humans.

Secondly, among the layers that Schiegl and colleagues analysed, was a sediment layer referred to as BSp from the post-HP (with age of 57.6±2.1, Jacobs et al., 2008) that has four strata placed under it with hearths in them, three of which represent the same hearth (Schiegl et al., 2004; Schiegl and Conard, 2006). In these four strata, three were classified as type II sediments and one as type I sediments (Schiegl et al., 2004; Schiegl and Conard, 2006), can it then be inferred that there was a grassland reduction and increase in trees in parts of the post-HP since it shows variation of the two sediment categories in strata within the same layer? More so, Goldberg et al. (2009) report that the layers from YA2 to BSp (about seven layers of which all those used to describe the post-HP vegetation of Schiegl et al. (2004) fall) were formed in a short period of about 1,000 years by repetitive human activities. This means that layer BSp and its strata would have been formed in an even much shorter time and extreme changes in environment may not have occurred. These differences in phytolith composition in the sediments where likely due to the different burning activities taking place in each stratum or use of grass as bedding as would be the case for all other layers studied by Schiegl and colleagues and not a reduction of grass extent in the vegetation.

Not to belabour the point here but rather to further illustrate or speculate on a more probable if not the only environmental change interpretation that can be drawn from the previous phytolith study: It could be theorised that these reductions in grass phytoliths in sediments in Schiegl et al. (2004), were because of the unavailability of grasses to use as tinder or bedding in the vegetation as a result of changes in annual seasons. It could be that grasses disappeared during the winter or that during the rainy season, dry grass would not be readily available to use and so they would use available wood to start fires (creating an abundance of type II sediments). To suggest that the cause of increase in dicot phytoliths against grasses was a result of the reduction of grasses in the environment during the post-HP cannot be justified. Both these phytolith studies show that grasses were present throughout the MSA periods they represent and they were utilised and therefore phytoliths changes at Sibudu speak more for human behaviour than for environmental change.

Phytolith studies in South Africa are still rare and their application in archaeology is relatively new (Schiegl et al., 2004; Albert and Marean, 2012; Esteban, 2016), and specialists of other proxies in archaeology may not be familiar with their application and interpretation. The study of Schiegl et al. (2004) was designed to - among other objectives - use phytoliths to understand taphonomy and the use of fire at Sibudu but not to infer vegetation or environmental conditions and associated changes and, therefore, archaeologists should limit their interpretation of this study along those lines. The paucity of lake sedimentary archives in South Africa has led to the use of unconventional archives such cave deposits and fossil hyrax dung to infer palaeoenvironments in South Africa (Scott and Vogel, 2000; Scott, 2002). Because cave deposits can be almost entirely of anthropogenic origin as in the case of Sibudu, exercising caution is indicated when using them as climatic signals (Pickering, 2006; Goldberg et al., 2009).

The current study provides a much needed interpretation of the grass types in the sediments that may have prevailed during the MSA of Sibudu and suggests the climate that the early humans could have operated in based on the identified grass subfamilies and their known climatic preferences. It therefore contributes to the on-going discussion of palaeoenvironments at Sibudu in terms of vegetation and climate that prevailed during the MSA and if there were changes in grass subfamily composition in the vegetation but not a reduction or expansion of grasslands or forests. The way phytoliths were deposited at Sibudu cannot allow for the latter when both plant groups (grasses and trees) occur throughout the MSA sediments. Goldberg et al. (2009) have suggested that archaeology needs to be looked at beyond analysing major environmental shifts and that data must be studied in its proper anthropological context. This current phytolith study is better suited to contribute to the discussion of past environments including climate at Sibudu and the region.

CHAPTER NINE

CONCLUSIONS

9.0 Introduction

This chapter presents a summary of the findings of this thesis that had two main objectives: to develop a modern phytolith reference collection for the SRZ and to reconstruct the past vegetation and climate at Sibudu using phytoliths. Therefore, it presents the major outcomes of the modern plant phytolith study and highlights its contribution to taxonomy and palaeostudies. It also presents the main out comes of the phytolith analysis of archaeological sediments at Sibudu cave during the late Pleistocene in the period representing the pre-Still Bay, the Still Bay and the Howiesons Poort. It highlights the contribution this study made towards understanding the past vegetation and climate at Sibudu and the wider region and how it compliments or supplements previous studies at Sibudu. Areas that need further investigation are also highlighted in this study.

9.1 Summary of the modern plant phytolith assemblage

The full potential of utilising phytolith analysis to reconstruct past environments at Sibudu was made possible by the modern plant phytolith reference collection. It represents the first modern plant phytolith reference collection of eudicot plants (mainly woody) from the SRZ consisting of the largest woody phytolith reference collection for South Africa. More so, it also constitutes the first most comprehensive phytolith study of modern sedges (Cyperaceae) in Africa. It provided information on the phytolith morphotypes produced by modern South African plants from the SRZ, many of which constituted the landscape at Sibudu during the MSA and were available for early humans to utilise (Allott, 2004; Wadley, 2004; Sievers, 2006; Schiegl and Conard, 2006; Renaut and Bamford, 2006; Lennox et al. 2015). This information is summarised below:

1. The phytolith production in modern plants from the SRZ of South Africa and their morphology conform to patterns reported in Africa and elsewhere. Sedges

(Cyperaceae) and grasses (Poaceae) are the highest phytolith producers while eudicot plants show a lower frequency of phytoliths in their assemblage.

2. Sedges produce the characteristic cone-shaped phytoliths while some additionally produce achene phytoliths some of which are diagnostic in the genera *Cyperus*, *Kyllinga*, *Mariscus*, *Pycreus* and *Schoenoxiphium*. It provides some new information that confirms several morphological and phylogenetic classifications.

3. To the best of my knowledge, this study presents new evidence on the presence of *Cyperus*/*Kyllinga* achene type phytoliths in the genera *Pycreus* and *Mariscus* (now *Cyperus*). This *Cyperus/Kyllinga* type was first presented in micrographs of *Pycreus tener* in Fernádez Honaine et al. (2009) although they did not categorically refer to them as being the *Cyperus*/*Kyllinga* type. The rare elongate shaped *Cyperus*/*Kyllinga* type achenes found in *Pycreus macranthus* were seen only in *Mariscus congestus* (syn. *Cyperus congestus*). This similarity may offer some support to phylogenetic analyses that suggest that *Cyperus congestus* may be associated with the early branching *Pycreus* lineages although there are no morphological characteristics between *C. congestus* and *Pycreus* to support this relationship (Larridon et al. 2013).

4. This phytolith study therefore provides evidence of the long known relationship among the genera *Cyperus*, *Pycreus* and *Mariscus*; the latter a genus that has since been made obsolete in South Africa and its species placed in *Cyperus*. This current phytolith study and that of Fernádez Honaine et al. (2009) further illustrate the importance of phytoliths in taxonomy following the recent movement of species of the genus *Pycreus* to *Cyperus s.l.*

5. To the best of my knowledge achene phytoliths have not been previously described in the genus *Schoenoxiphium*. This study finds achene phytoliths in *Schoenoxiphium* that are similar to one of the achene types described for *Carex* by Piperno (1989; 2006) and may support the recent movement of this genus to *Carex*. This assertion needs further investigation of other species of *Schoenoxiphium* to confirm it.

6. Sedges are diverse phytolith producers and their classification in phytolith research should go beyond the classic cone-shaped and achene phytoliths of Piperno (1989, 2006) and Ollendorf (1992). Most species from various genera were found to produce a significant amount of parallelepiped blocky and tabular elongate phytoliths in agreement with Novello et al. (2012). For instance, in genera such as *Eleocharis*, blocky phytoliths form the biggest part of their phytolith assemblage and produce few cone-shaped phytoliths. This lends an alternative interpretation of blocky phytoliths in the archaeological record other than the common association with woody taxa.

7. Globular psilate phytoliths were generally not characteristic of sedges although some *Schoenoplectus* and *Pycreus* species have them in their assemblage. This is similar to observations made by Novello et al. (2012). They were not counted in the current study as they were thought to be associated with the bulbous structures in those species.

8. Several other unique types occur in some species such as *Fuirena* but important to note were the hemispherical and associated spherical echinulate bodies in the genus *Scleria* that have been reported to have potential to identify this genus (Metcalfe, 1971). Also lightly faceted bodies occur in some sedge species such as *Pycreus* spp and some *Cyperus* spp. and are similar to the multi-faceted bodies mainly associated with woody taxa in Watling and Iriarte (2013). Similar multi-faceted bodies referred to as terminal tracheids by Piperno (2006) were observed in *Cyperus rigidifolius*.

9. Of the three species of Juncaceae analysed (*J. exertus*, *J. effusus* and *J. oxycarpus*), only *Juncus effusus* produced abundant phytoliths and can contribute to the archaeological record although diagnostic morphotypes were not observed. It produces abundant tracheids and a relatively high number of elongate phytoliths. Its tracheids can be very long and tracheids as long as 317.79 µm were observed. It also produced thin threads that appear like articulated cones but are not bold enough or silicified to make sense of. A few rondels were observed and one bilobate and are

thought to be contamination. One blocky and one elongate were seen in *J. exertus* and *J. oxycarpus* produced a few tracheids mixed with long cells (elongates).

10. The grasses in this region produced the typical grass phytolith/silica short cells (GSSCs). Most of the grasses collected from the study site were found to be C4 grasses of the subfamilies Panicoideae and Chloridoideae. These subfamilies can be separated by their already known dominant phytolith morphologies i.e. lobates and saddles respectively. However, in both subfamilies rondel phytoliths were abundant and are dominant in some of their species. Rondel phytoliths are an important component of grasses from this region as all the subfamilies studies produced a significant amount of rondels in their assemblage. Even the phytolith assemblage in an unidentified grass species showed a more than 95% dominance of rondel phytoliths with the other small percentage from bilobate phytoliths.

11. From the modern grass phytolith assemblage, it was deduced that a high number of bilobates in combination with rondels are characteristic of the subfamily Panicoideae (warm, moist climate grasses) while a high number of saddles in combination with rondels are characteristic of Chloridoideae grasses (hot, dry climate grasses). The subfamily Arundinoideae was represented by only the C3 *Phragmites australis* and was dominated by rondel phytoliths and a few saddles.

12. The C4 Aristidoideae was represented by one *Aristida* sp. and was the only other subfamily to show abundant lobate phytoliths like Panicoideae. However, the *Aristida* sp. only produced lobates of the bilobate type and did not produce any cross or polylobate phytoliths that are more characteristic of Panicoideae. Particularly also, its bilobates are always with convex ends and their shanks often thin while those in Panicoideae are usually a mix of convex, concave or with straight margins. Rondels were relatively few in *Aristida* sp. and mainly conical shaped with pointed apices.

13. The only species of the C3 Pooideae subfamily (cold climate/high altitude grasses) was difficult to interpret as it had a combination of lobates, rondels and saddles, with

the lobates and saddles in unexpectedly high proportions. Rondels were also the dominant type. This also highlights the known redundancy and multiplicity in grasses and further investigation of the occurrence of this subfamily in the study area is necessary and their phytolith assemblages established from various species.

14. Eudicot plants were rather productive specifically the trees and shrubs (woody taxa). Phytolith production in eudicots was found to vary within species of the same family. In this study, morphotypes that were considered typical for woody taxa were: globular psilates, tracheids, multicellular polyhedral and anticlinal structures, hair bases, cystoliths, stomata and the rare sclereids and cork aerenchyma. The most common types were multicellular polyhedral cells, globular psilates and hair bases. Cystoliths and stomata were common in some species and can be the dominant morphotype. A few multicellular polyhedral structures (several thought to be polygonal cones) and anticlinal cells also occur in sedges but what this study considered as anticlinal cells in sedges are epidermal structures that are unique and different from those seen in woody taxa. Blocky parallelepiped phytoliths were classified as 'common' in a few species studied and were recorded as 'rare' or absent in most species.

15. Tracheids occur in all plant groups analysed in this study but those in woody taxa appear mostly large, thick and complex compared to those in the monocots (grasses, sedges and Juncaceae). Those in Juncaceae are not as complex but can be extremely long as seen in *J. effusus*. Cystoliths occurred in only species of *Celtis* and *Ficus* and they seem to occur in few families as previously suggested. *Celtis* was basically the only genus that exhibited several diagnostic morphotypes. This study combined the plant parts during phytolith extraction and did not separate parts as other studies but the results obtained here are similar in terms of the most abundant morphotypes in woody taxa and this study therefore gives information on woody taxa as a whole to mimic the archaeological assemblage.

16. Some woody taxa and sedges were found to contain grass phytolith short cells in their phytolith assemblage. They were insignificant in the woody taxa but copious amounts of bilobates were abundant in some sedge species. This suggests that a portion of grass phytoliths in the archaeological assemblage may be a result of unintentional deposit by early humans. Calculations have shown that such contamination in the archaeological record from South African woody taxa should be minimal (Esteban, 2016).

9.2 Summary of occupation, vegetation and climate at Sibudu > 70,000 to ca. 55,000 yr BP

Evidence of early human-plant interactions and vegetation, particularly grasslands, which prevailed at Sibudu during the MSA occupation, is reconstructed based on the phytolith morphotypes preserved in the archaeological assemblage. The findings of these environmental interpretations are summarised below:

1. This study corroborates previous studies at Sibudu on the extensive use of fire through burning woody and non-woody taxa with grass having been most likely used as tinder. It also corroborates the use of sedges at Sibudu by early humans. They are thought to have been used as bedding at Sibudu (Sievers, 2011; Wadley et al., 2011). The sedge genera that this phytolith study can differentiate in the archaeological record were *Cyperus* and/*Kyllinga*. This study suggests that Cucurbitaceae plants were also likely utilised by early humans.

2. An important early human activity is suggested during the Howiesons Poort and is concentrated in two subsequent layers GS2 and GS3. These are dominated by conspicuous brown sub-globular bodies that look very similar to phytoliths from Restionaceae plants that are presently restricted to the Winter Rainfall Zone of South Africa (Cordova, 2013; Esteban, 2016; Esteban et al., 2017). Their phytoliths have been found in the MSA record and interpreted as having been used for bedding by early humans as they resemble sedges and have a similar function (Esteban, 2016;

Esteban et al., 2017). The closest resemblance to these bodies in the reference collection was in the tree species of *Ficus polita*. These two layers at Sibudu appear to tell an important story that seems to start from older layers in the Still Bay and further phytolith analysis needs to investigate and confirm the origin of these sub-globular bodies. These bodies occur with sedge phytoliths and grass phytoliths among others several of which are trapeziform sinuate phytoliths when the whole slide is scanned through indicating a likely presence of C3 subfamily Pooideae grasses.

3. The vegetation at Sibudu is interpreted as having been dominated by C4 grasses throughout this period. C4 grasses of the subfamily Panicoideae were more likely to have been the dominant grass with C4 grasses of the subfamily Chloridoideae occurring in small amounts or were absent. Arundinoideae grasses like *Phragmites australis* may have been present during this period as a few very tall rondels were observed in the archaeological record. Because this grass produces a few saddles, the saddles in the fossil phytolith assemblage may originate from Arundinoideae and not Chloridoideae. During field work, it was collected from the uThongati River below the cave. Cold climate grasses of the subfamily Pooideae (C3) were present in the environment during this period as trapeziform sinuate phytoliths were encountered in very small amounts. It is suggested that C3 and C4 grasses co-existed with C4 grasses prevailing during the warm seasons and C3 Pooideae grasses increasing during cold seasons.

4. The phytolith record suggests that the climate during this period was warm and wet and this led to the dominance of C4 Panicoideae grasses. Grasses characteristic of hot and dry climate (Chloridoideae) may have existed but remained very low. Phytoliths characteristic of these hot climate grasses may have been produced by species such as *Phragmites australis* from the nearby river. This phytolith record at Sibudu suggests that the climate remained stable throughout this period but likely varied with cold periods as C3 Pooideae grasses seem to have existed in small numbers.

5. Woody taxa are well represented throughout this period and the vegetation at Sibudu is therefore interpreted as having been mixed.

6. The presence of sedges in the archaeological record suggests the presence of swampy vegetation and confirms the presence of the uThongati River during this period as corroborated by other studies.

REFERENCES

Acocks, J. P. H., 1988. Veld Types of South Africa, 3rd edition. Memoirs of the Botanical Survey of South Africa. 57, 1–146.

Albert, R. M and Marean, C. W., 2012. The exploitation of plant resources by early Homo sapiens: The phytolith record from Pinnacle Point 13B Cave, South Africa. Geoarchaeology: An International Journal 27, 363–384.

Albert, R. M., Bamford, M. K. and Cabanes, D., 2006. Taphonomy of phytoliths and macroplants in different soils from Olduvai Gorge (Tanzania) and the application to Plio–Pleistocene palaeoanthropological samples. Quaternary International 148, 78–94.

Albert, R. M., Bamford, M. K., Cabanes, D., 2009. Palaeoecological significance of palms at Olduvai Gorge, Tanzania, based on phytolith remains. Quaternary International 193, 41–48.

Albert, R. M. and Weiner, S., 2001. Study of phytoliths in prehistoric ash layers using a quantitative approach. In J.D. Meunier, and F. Coline (Eds.), Phytoliths: Applications in earth sciences and human history (pp. 251–266). Lisse: Balkema.

Albert, R. M., 2000. Study of ash layers through phytolith analyses from the Middle Palaeolithic levels of Kebara and Tabun caves. Unpublished PhD Thesis, Universitat de Barcelona, Barcelona.

Albert, R. M. and Bamford, M., 2012. Vegetation during UMBI and deposition of Tuff IF at Olduvai Gorge, Tanzania (ca. 1.8 Ma) based on phytoliths and plant remains. Journal of Human Evolution 63, 342-350.

Albert, R. M., Bar-Yosef, O., Meignen, L. and Weiner, S., 2003. Phytolith and mineralogical study of hearths from the Middle Palaeolithic levels of Hayonim Cave (Galilee, Israel). Journal of Archaeological Science 30, 461-480

Albert, R. M., Tsatskin, A., Ronen, A., Lavi, O., Estroff, L., Lev-Yadum, S., and Weiner, S., 1999. Mode of occupation of Tabun Cave, Mt Carmel, Israel during the Mousterian Period: A study of the sediments and phytoliths. Journal of Archaeological Science, 26, 1249–1260.

Alexandre, A., Meunier, J. D., Lézine, A. M., Vincens, A. and Schwartz, D., 1997. Phytoliths: indicators of grassland dynamics during the late Holocene in intertropical Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 136, 213–229.

Allott, L. F., 2006. Archaeological charcoal as a window on palaeovegetation and wood-use during the Middle Stone Age at Sibudu Cave. Southern African Humanities, 18, 173–201.

Allott, L. F., 2004. Changing environments in Oxygen Isotope Stage 3: reconstructions using archaeological charcoal from Sibudu Cave. South African Journal of Science 100, 179–184.

Allott, L. F., 2005. Paleoenvironments of the Middle Stone Age at Sibudu Cave, KwaZulu-Natal, South Africa: an analysis of archaeological charcoal, Unpublished PhD Thesis, University of the Witwatersrand.

Archer, C., and Goetghebeur, 2011. New names and new combinations in Cyperus for Southern Africa.

Avery, D. M., 1987. Late Pleistocene coastal environment of the southern Cape Province of South Africa: micromammals from Klasies River Mouth. Journal of Archaeological Science 14, 405-421.

Backwell, L., d'Errico, F. and Wadley, L., 2008. Middle Stone Age bone tools from the Howiesons Poort layers, Sibudu Cave, South African. Journal of Archaeological Science 35, 1566-1580.

Baker, G. 1959. Opal phytoliths in some Victorian soils and "red rain" residues. Australian Journal of Botany 7, 64-87.

Ball, T., Gardner, J. S. and Brotherson, J. D., 1996. Identifying phytoliths produced by the inflorescence bracts of three species of wheat (Triticum monoccocum L., T. dicoccum Schrank. and T. aestivum L.) Using Computer assisted Image and Statistical Analysis. Journal of Archaeological Science 23, 619-632.

Ball, T, Chandler-Ezell, ., Duncan, N., Dickau, R., Hart, T. C., Iriarte, J., Lentfer, C., Logan, A., Lu, H., Madella, M., Pearsall, D. M., Piperno, D. R., Rosen, A. M., Vrydaghs, L, Weisskopf, A.

and Zhang, J., 2016. Phytoliths as a Tool for Investigations of Agricultural Origins and Dispersals around the World. Journal of Archaeological Science, 68: 32-45

Bamford, M. K., Albert, R. M. and Cabanes, D., 2006. Plio–Pleistocene macroplant fossil remains and phytoliths from Lowermost Bed II in the eastern palaeolake margin of Olduvai Gorge, Tanzania. Quaternary International 148, 95–112.

Barboni, D. and Bremond, L., 2009. Phytoliths of East African grasses: An assessment of their environmental and taxonomic significance based on floristic data. Review of Palaeobotany and Palynology 158, 29-41.

Barboni, D., Ashley, G. M., Dominguez-Rodrigo, M., Bunn, H. T., Mabulla, A. Z. P. and Baquedano, E., 2010. Phytoliths infer locally dense and heterogeneous paleovegetation at FLK North and surrounding localities during upper Bed I time, Olduvai Gorge, Tanzania. Quaternary Research 74, 344-354.

Barboni, D., Bonnefille, R., Alexandre, A. and Meunier, J. D., 1999. Phytoliths as paleoenvironmental indicators, West Side Middle Awash Valley, Ethiopia. Palaeogeography, Palaeoclimatology, Palaeoecology 152, 87–100.

Barboni, D., Bremond, L. and Bonnefille, R., 2007. Comparative study of modern phytolith assemblages from inter-tropical Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 246, 454–470.

Bar-Matthews, M., Marean, C. W., Jacobs, Z., Karkanas, P., Fisher, E. C., Herries, A. I. R., Brown, K. S., Williams, H. M., Bernatchez, J., Ayalon, A., and Nilssen, P. J., 2010. A high resolution and continuous isotopic speleothem record of paleoclimate and paleoenvironment from 90 to 53 ka from Pinnacle Point on the south coast of South Africa. Quaternary Science Reviews, 29, 2131–2145.

Berger, L. R., Hawks, J., et al., 2015. *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. eLife 4:e09560

Berger, L. R., de Ruiter, D. J., Churchill, S. E., Schmid, P., Carlson, K. J., Dirks, P. H. and Kibii, J. M., 2010. *Australopithecus sediba*: a new species of Homo-like australopith from South Africa. Science 328, 195-204.

Blackman, E. and Parry, D. W., 1968. Opaline silica deposition in rye (secale cereale L). Annals of Botany, 32, 199-206.

Blackman, E., 1968. The pattern and sequence of opaline silica deposition in Rye (*Secale cereale* L.). Annals of Botany 32, 207-218.

Bowdery, D., 1998. Phytolith analysis applied to Pleistocene- Holocene archaeological sites in the Australian arid zone. BAR International series 695, Oxford OX2 7BP.

Bozarth, S. R, 1987. Diagnostic opal phytoliths from rinds of selected Cucurbita species. American Antiquity, 52, 607-615.

Bozarth, S. R., 1986. Morphologically Distinctive Phaseolus, Cucurbita, and Helianthus Annus Phytoliths. Proceedings of the 1984 Phytolith Workshop 1:56-66. North Carolina State University, Raleigh.

Bozarth, S. R., 1992. Classification of opal phytoliths formed in selected Dicotyledons native to the Great Plains. In: Rapp, G., Mulholland, S. C. (Eds.), Phytolith Systematics. Plenum Press, New York and London, pp. 193–214.

Brain, C. K., 1969. Faunal remains from the Bushman Rock Shelter, Eastern Transvaal. South African Archaeological Bulletin 24, 52–55.

Bremond, L., Alexandre, A., Hély, C. and Guiot, J., 2005a. A phytolith index as a proxy of tree cover density in tropical areas: calibration with Leaf Area Index along a forest– savanna transect in southeastern Cameroon. Global and Planetary Change 45, 277–293.

Bremond, L., Alexandre, A., Peyron, O. and Guiot, J., 2005b. Grass water stress estimated from phytoliths in West Africa. Journal of Biogeography 32, 311–327.

Bremond, L., Alexandre, A., Wooller, M. J., Hely, C., Williamson, D., Schafer, P.A., Majule, A. and Guiot, J., 2008. Phytolith indices as proxies of grass subfamilies on East African tropical mountains. Global and Planetary Change 61, 209–224.

Brown, K. S., Marean, C. W., Jacobs, Z., Schoville, B. J., Oestmo, S., Fisher, E. C., Bernatchez, J., Karkanas, P. and Matthews, T., 2012. An early and enduring advanced technology originating 71000 years ago in South Africa. Nature 491, 590-593.

Browning, J. B. M. and Gordon-Gray, K. D., 2011. Studies in Cyperaceae in Southern Africa 43: Scirpoides varius Browning - A New Name for Scirpus varius Boeck. ex. C.B. Clarke. South African Journal of Botany 77, 506–508.

Bruch, A. A., Sievers, C. and Wadley, L., 2012. Quantification of climate and vegetation from southern African Middle Stone Age sites: an application using Late Pleistocene plant material from Sibudu, South Africa. Quaternary Science Reviews 45, 7–17.

Cabanes, D., Mallol, C., Expo´sito, I., and Baena, J., 2010. Phytolith evidence for hearths and beds in the late Mousterian occupations of Esquilleu cave (Cantabria, Spain). Journal of Archaeological Science, 37, 2947–2957.

Cain, C. R., 2006. Human activity suggested by the taphonomy of 60 ka and 50 ka faunal remains from Sibudu Cave. Southern African Humanities 18, 241-260.

Carnelli, A. L., 2002. Long term dynamics of the vegetation at the subalpine – alpine ecocline during the Holocene: comparative study in the Aletsch region, Val D'Arpette, and Furka Pass, (Valais, Switzerland). University of Geneva, PhD thesis no.3378. Terre and Environnement, vol. 40, Imprimerie de la Sectionde physique, Gene`ve.

Carnelli, A. L., Theurillat, J.-P. and Madella, M., 2004. Phytolith types and type-frequencies in subalpine–alpine plant species of the European Alps. Review of Palaeobotany and Palynology 129, 39–65.

Carter, J. A., 1998. Phytoliths from CRP-1. Terra Antartica 5(3), 571-576.

Cartwright, C. R., 2013. Identifying the woody resources of Diepkloof Rock Shelter (South Africa) using scanning electron microscopy of the MSA wood charcoal assemblages. Journal of Archaeological Science 40, 3463–3474.

Chase, B. M., 2010. South African palaeoenvironments during marine oxygen isotope stage 4: a context for the Howiesons Poort and Still Bay industries. Journal of Archaeological Science 37, 1359-1366.

Clark, J. L. and Plug, I., 2008. Animal exploitation strategies during the South African Middle Stone Age: Howiesons Poort and post-Howiesons Poort fauna from Sibudu Cave. Journal of Human Evolution 54, 886–898.

Clarke, R. J., 2008. Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*. South African Journal of Science 104, 443-449.

Cochrane, G. W. G., 2006. An analysis of lithic artefacts from ~60 ka layers of Sibudu Cave. Southern African Humanities 18(1), 69–88.

Collura, L. V. and Neumann, K., 2017. Wood and bark phytoliths of West African woody plants. Quaternary International 434, 142-159.

Conard, N. J., Porraz, G., and Wadley, L., 2012. What is in a name? Characterising the 'Post-Howieson's Poort' at Sibudu. South African Archaeological Bulletin 67, 180–199.

Cordova, C. E. and Scott, L., 2010. The potential of Poaceae, Cyperaceae, and Restionaceae phytoliths to reflect past environmental conditions in South Africa. In: J. Runge (Ed.), Palaeoecology of Africa. CRC Press Taylor and Francis Group, Boca Raton, Florida.

Cordova, C. E., 2013. C3 Poaceae and Restionaceae phytoliths as potential proxies for reconstructing winter rainfall in South Africa. Quaternary International 293, 121-140.

Cowling, R. M., Richardson D. M., and Mustart, P. J., 1997. In R.M. Cowling, D.M. Richardson, and S.M. Pierce (Eds.), The vegetation of southern Africa (pp. 99–130). Cambridge: Cambridge University Press.

d’Errico, F., Backwell, L. and Wadley, L., 2012. Identifying regional variability in Middle Stone Age bone technology: the case of Sibudu Cave. Journal of Archaeological Science 39, 2479-2495.

d’Errico, F., Henshilwood, C. S., Vanhaeren, M. and van Niekerk, K., 2005. Nassarius kraussianus shell beads from Blombos Cave: evidence for symbolic behaviour in the Middle Stone Age. Journal of Human Evolution 48, 3-24.

d’Errico, F., Vanhaeren, M. and Wadley, L., 2008. Possible shell beads from the Middle Stone Age layers of Sibudu Cave, South Africa. Journal of Archaeological Science 35, 2675-2685.

de la Peña, P., Wadley, L., and Lombard, M., 2013. Quartz Bifacial Points in the Howiesons Poort of Sibudu. South African Archaeological Bulletin 68, 119–136.

Deacon, H. J., 1976. Where hunters gathered: a study of Holocene Stone Age people in the eastern Cape (No. 1). South African Archaeological Society.

d'Errico, F., Henshilwood, C. and Nilssen, P., 2001. An engraved bone fragment from c.70,000-year-old Middle Stone Age levels at Blombos Cave, South Africa: implications for the origin of symbolism and language. Antiquity 75(288), 309-318.

Eichhorn, B., Neumann, K. and Garnier, A., 2010. Seed phytoliths in West African Commelinaceae and their potential for palaeoecological studies. Palaeogeography, Palaeoclimatology, Palaeoecology 298, 300–310.

Elbaum, R., Weiner, S., Albert, R. M. and Elbuam, M. 2003. Detection of burning of plant materials in the archaeological record by changes in the refractive indices of siliceous phytoliths. Journal of Archaeological Science 30, 217 – 226.

Esteban, 2016. Reconstructing past vegetation and modern human foraging strategies on the south coast of South Africa. Unpublished PhD thesis, University of Barcelona.

Esteban, I., De Vynck, J. C., Singels, E., Vlok, J., Marean, C. W., Cowling, R. M., Fisher, E. C., Cabanes, D. and Albert, R. M., 2017. Modern soil phytolith assemblages used as proxies for paleoscape reconstruction on the south coast of South Africa. Quaternary International 434, 160-179.

Fahmy, A. G., 2008. Diversity of lobate phytoliths in grass leaves from the Sahel region, West tropical Africa: tribe Paniceae. Journal of Plant Systematics and Evolution. 270, 1-23.

Fredlund, G. G., 1986. A 620,000 Year Opal phytolith Record from central Nebraskan Loess. In plant phytolith Analysis in archeology and Paleoecology, Ed. I.Rovner, pp. 12-23. Occasional papers No.1 of The phy-tolitharien, North Carlifonia State University, Raleigh.

Fredlund, G. G. and Tieszen, L. T., 1994. Modern phytolith assemblages from the North American Great Plains. Journal of Biogeography 21, 321-335.

Geis, J. W., 1973. Biogenic silica in selected species of deciduous angiosperms. Soil Science 116, 113–119.

Geis, J. W., 1978. Biogenic opal in three species of Gramineae. Annals of Botany 42, 1119–1129.

Gibson, N. E., Wadley, L., and Williamson, B. S., 2004. Microscopic residues as evidence of hafting on backed tools from the 60 000 to 68 000 year-old Howiesons Poort layers of Rose Cottage Cave, South Africa. Southern African Humanities 16, 1–11.

Glenny, W., 2006. Report on the micromammal assemblage analysis at Sibudu Cave. Southern African Humanities 18(1), 279–288.

Global Carex Group, 2015. Making Carex monophyletic (Cyperaceae, tribe Cariceae): a new broader circumscription. Botanical Journal of the Linnean Society 179, 1–42.

Goldberg, P., Miller, C. E., Schiegl, S., Ligouis, B., Berna, F., Conard, N. J. and Wadley, L., 2009. Bedding, hearths and site maintenance in the Middle Stone Age of Sibudu Cave, KwaZulu-Natal, South Africa. Journal of Archaeological and Anthropological. Science 1, 95-122.

Goodwin, A. J. H. and van Riet Lowe, C., 1929. The Stone Age cultures of South Africa. Annals of the South African Museum 27, 1–289.

Gordon-Gray, K. D., 1995. Cyperaceae in Natal. Strelitzia 2, 1–218. Pretoria: National Botanical Institute.

Grab, S., Scott, L., Rossouw, L. and Meyer, S., 2005. Holocene palaeoenvironments inferred from a sedimentary sequence in the Tsoaing River Basin, western Lesotho. Catena 61, 49–62.

Grant, R. and Thomas, V., 1998. SAPPI Tree Spotting: KwaZulu-Natal Coast and Midlands. Jacana, Johannesburg.

Haines, R. W., and Lye, K., 1983. The Sedges and Rushes of East Africa. East African Natural History Society, Nairobi, Kenya.

Hall, G., Woodborne, S. and Scholes, M., 2008. Stable carbon isotope ratios from archaeological charcoal as palaeoenvironmental indicators. Chemical Geology 247, 384–400.

Hall, G.,Wadley, L. and Woodborne, S. 2014. Past environmental proxies from the Middle Stone Age at Sibudu, KwaZulu-Natal, South Africa. Journal of African Archaeology 12, 7–24.

Hammer, Ø, Harper, D. A. T., and Ryan, P.D., 2001. Past: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica, vol. 4, issue 1, art. 4: 9pp.

Hart, D. M., 1990. Occurrence of the 'Cyperaceae-type' phytolith in Dicotyledons. Australian Systematic Botany 3, 745-750.

Henry, A. G., Ungar, P. S., Passey, B. H., Sponheimer, M., Rossouw, L., Bamford, M., Sandberg, P., de Ruiter, D. J. and Berger, L., 2012. The diet of the Australopithecus sediba. Nature 487, 90-93.

Henshilwood, C., d'Errico, F., Marean, C., Milo, R. and Yates, R., 2002. An early bone tool industry from the Middle Stone Age at Blombos Cave, South Africa: implications for the origins of modern human behaviour, symbolism and language. Journal of Human Evolution 41, 631-678.

Henshilwood, C. S. and Marean, C. W., 2003. The origin of modern human behavior. Current anthropology 44(5), 627-651.

Henshilwood, C. S. and Sealy, J. C., 1997. Bone artefacts from the Middle Stone Age at Blombos Cave, southern Cape, South Africa. Current Anthropology 38, 890–895.

Herries, A. I. R., 2006. Archaeomagnetic evidence for climate change at Sibudu Cave. Southern African Humanities 18 (1), 131-147.

Hodgskiss, T., 2012. An investigation into the properties of the ochre from Sibudu, KwaZulu-Natal, South Africa. Southern African Humanities 24, 99–120.

Fernádez Honaine, M., Zucol, M. A. and Osterrieth, M., 2009. Phytolith analysis of Cyperaceae from the Pampean Region, Argentina. Australian Journal of Botany 57, 512-523.

Huang, F., Kealhofer, L., Xiong, S. and Huang, F., 2005. Holocene grassland vegetation, climate and human impact in central eastern Inner Mongolia. Science in China Ser. D Earth Sciences 48, (No.7), 1025-1039.

Huygh, W., Larridon, I., Reynders, M., Muasya, A. M., Govaerts, R., Simpson, D. A. and Goetghebeur, P., 2010. Nomenclature and typification of names of genera and subdivisions of genera in Cypereae (Cyperaceae): 1. Names of genera in the Cyperus clade. Taxon 59 (6), 1883–1890.

Iriarte, J., Glaser, B., Watling, J., Wainwright, A., Birks, J., Renard, D., Rostain, S. and McKey, D., 2010. Late Holocene Neotropical agricultural landscapes: phytolith and stable carbon isotope analysis of raised fields from French Guianan coasta savannahs. Journal of Archaeological Science 37, 2984-2994.

Iriarte, J. And Paz, E. A., 2009. Phytolith analysis of selected native plants and modern soils from southeastern Uruguay and its implications for paleoenvironmental and archeological reconstruction. *Quaternary International* 193, 99-123.

Jacobs, Z., Roberts, R. G., Galbraith, R. F., Deacon, H. J., Grun, R., Mackay, A., Mitchell, P., Vogelsang, R., and Wadley, L., 2008a. Ages for the Middle Stone Age of Southern Africa: implications for human behavior and dispersal. Science 322, 733-735.

Jacobs, Z., Wintle, A. G., Duller, G. A. T., Roberts, R. G. and Wadley, L., 2008b. New ages for the post-Howiesons Poort, late and final Middle Stone Age at Sibudu Cave, South Africa. Journal of Archaeological Science 35, 1790-1807.

Jones, E., Simpson, D. A., Hodkinson, T. R., Chase, M. W. and Parnell, J. A. N., 2007. The Juncaceae–Cyperaceae interface: a combined plastid sequence analysis. Aliso 23, 55–61.

Kaplan, J., 1990. The Umhlatuzana Rock Shelter sequence: 100 000 years of Stone Age history. Natal Museum Journal of Humanities 2, 1–94.

Kaplan, L., Smith, M. B. & Sneddon, L. A., 1992. Cereal grain phytoliths of southwest Asia and Europe. In (G. Rapp, Jr & S. C. Mulholland, Eds) Phytolith Systematics. Emerging Issues, Advances in Archaeological and Museum Science. New York: Plenum Press, pp. 149–174.

Kealhofer, L. and Piperno, D., 1998. Opal phytoliths in southeast Asian flora. Smithsonian Contribution to Botany 88, 39.

Klein, R. G., 1976. The mammalian fauna of the Klasies River Mouth sites, southern Cape Province, South Africa. South African Archaeological Bulletin 32, 14-27.

Klein, R. G., 1977. The mammalian fauna from the Middle and Later Stone Age (Late Pleistocene) levels of Border Cave, Natal Province, South Africa. South African Archaeological Bulletin 32, 14-27.

Klein, R. G., 1995. Anatomy, behavior, and modern human origins. Journal of World Prehistory 9 (2), 167-198.

Klein, R. L., Geis, J., 1978. Biogenic silica in the Pinaceae. Soil Science 126, 145–156.

Kukkonen, I., 1983. The genus Schoenoxiphium (Cyperaceae): a preliminary account. Bothalia 14, 819-823.

Larridon, I., Bauters, K., Reynders, M., Huygh, W., Goetghebeur, P., 2014. Taxonomic changes in C4 Cyperus (Cypereae, Cyperoideae, Cyperaceae): Combining the sedge genera Ascolepis, Kyllinga and Pycreus into Cyperus s.l. Phytotaxa 166 (1), 33-48.

Larridon, I., Bauters, K., Reynders, M., Huygh, W., Muasya, A. M., Simpson, D. A. & Goetghebeur, P., 2013. Towards a new classification of the giant paraphyletic genus Cyperus (Cyperaceae): phylogenetic relationships and generic delimitation in C4 Cyperus. Botanical Journal of the Linnean Society 172 (1), 106–126.

Lejju, J. B., 2005. A mid to late Holocene environmental history of Munsa archaeological site, Uganda. PhD thesis, University of Dublin, Trinity College, Ireland. Pg. 56-79.

Lejju, J.B., 2009. Vegetation dynamics in western Uganda during the last 1000 years: climate change or human induced environmental degradation? African Journal of Ecology 47, 21-29.

Lejju, B. J., Robertshaw, P. and Taylor, D., 2003. Vegetation history and archaeology at Munsa, western Uganda. Azania 38, 155-65.

Lennox, S. J. and Bamford. M. K., 2015. Use of wood anatomy to identify poisonous plants: charcoal of *Spirostachys africana*. South African Journal of Science 111(3/4), 43– 51.

Lennox, S., Wadley, L., and Bamford, M., 2015. Charcoal analysis from 49 000-year-old hearths at Sibudu: implications for wood uses and the KwaZulu-Natal environment. South African Archaeological Bulletin 70 (201), 36–52, 2015.

Lewis, R. O., 1981. Use of opal phytoliths in paleoenvironmental reconstruction. Journal of Ethnobiology 1(1), 175-181.

Livingstone, D. A., Clayton, W. D., 1980. An altitudinal cline in tropical African grass floras and its paleoecological significance. Quaternary Research 13, 392–402.

Lombard, M., 2004. Distribution patterns of organic residues on Middle Stone Age points from Sibudu Cave, KwaZulu-Natal, South Africa. Southern African Archaeological Bulletin 59, 37-44.

Lombard, M., 2005. Evidence for hunting and hafting during the Middle Stone Age at Sibudu Cave, KwaZulu-Natal, South Africa: a multianalytical approach. Journal of Human Evolution 48, 279-300.

Lombard, M., 2006a. First impressions on the functions and hafting technology of Still Bay pointed artefacts from Sibudu Cave. Southern African Humanities 18, 27-41.

Lombard, M., 2006b. Direct evidence for the use of ochre in the hafting technology of Middle Stone Age tools from Sibudu Cave. Southern African Humanities 18, 57-67.

Lombard, M. and Parsons, I., 2010. Fact or fiction? Behavioural and technological reversal after 60 ka in southern Africa. South African Archaeological Bulletin 65, 224-228.

Lombard, M. and Phillipson, L., 2010. Indications of bow and stone-tipped arrow use 64000 years ago in KwaZulu-Natal, South Africa. Antiquity 84, 1-14.

Lombard, M., Wadley, L., Deacon, J., Wurz, S., Parsons, I., Mohapi, M., Swart, J., and Mitchell, P., 2012. South African and Lesotho Stone Age sequence updated (I). South African Archaeological Bulletin 67, 123–144.

Louw, A.W., 1969. Bushman Rock Shelter, Ohrigstad, eastern Transvaal: a preliminary investigation, 1965. South African Archaeological Bulletin 24, 39–51.

Lowe, J. J. and Walker, M. J. C., 1997. Reconstructing Quaternary environments. 2nd edition. Longman Group Ltd.

Lu, H., Liu, K., 2003. Phytoliths of common grasses in the coastal environments of southeastern USA. Estuarine, Coastal and Shelf Science 58, 587–600.

Lye K. A., 1982. Studies in African Cyperaceae 21. New taxa and combinations in Kyllinga Rottb. Nordic Journal of Botany 1: 741–747.

Madella, M., 1995. A preliminary study of phytolith analysis, agriculture and uses of plants at Kot Diji (Sindh-Pakistan). Ancient Sindh 2, 93-108.

Madella, M., Alexandre, A. and Ball, T. 2005. International Code for Phytolith Nomenclature 1.0. Annals of Botany 96, 253–260.

Marean, C. W., 2010. Pinnacle Point Cave 13B (Western Cape Province, South Africa) in context: The Cape Floral Kingdom, Shellfish, and modern human origins. Journal of Human Evolution, 59(3–4), 425–443.

Marean, C. W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A. I. R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P. J., Thompson, E., Watts, I. and Williams, H. M., 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. Nature 449, 905–908.

Marean, C. W., Nilssen, P. J., Brown, K., Jerardino, A. and Stynder, D., 2004. Paleoanthropological investigations of Middle Stone Age sites at Pinnacle Point, Mossel Bay (South Africa): archaeology and hominid remains from the 2000 field season. Paleoanthropology, 14–83.

Mbida, C. M., 2000. Evidence for banana cultivation and animal husbandry during the first millennium BC in the forest of southern Cameroon. Journal of Archaeological Science, 27, 151-162.

Mbida, C. M., Doutrellepont, H., Vrydaghs, L., Swennen, R. L., Swennen, R. J., Beeckman, H., Langhe, E. and Maret, P., 2001. First archaeological evidence of banana cultivation in central Africa during the third millennium before present. Vegetation History and Archaeobotany, 10, 1-6.

Mbida, C., Van Neer, W., Doutrelepont H. and Vrydaghs, L., 2000. Evidence for banana cultivation and animal husbandry during the first millenium BC in the forest of southern Cameroon. Journal of Archaeological Science 27, 15 1-62.

McBrearty, S. and Brooks, A. S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behaviour. Journal of Human Evolution 39, 453-563.

McLean, B. and Scott, L., 1999. Phytoliths in sediments of the Pretoria Saltpan and their potential as indicators of environmental history at the site. In Tswaing-investigations into the Origin, Age and Palaeoenvironments of the Pretoria Saltpan, ed. T.C. Partridge, pp. 167–171. Council for Geosciences, Pretoria.

Mehra, P. N and Sarma, O. P., 1965. Epidermal silica cells in the cyperaceae. Botanical Gazette, 126, 53-58.

Mercader, J., 2009. Mozambican grass seed consumption during the Middle Stone Age. Science 326, 1680-1683.

Mercader, J., Astdillo, F., Barkworth, M., Bennett, T., Esselmont, C., Kinyanjui, R., Grossman, D. L., Simpson, S. and Walde, D., 2010. Poaceae phytoliths from the Niassa Rift, Mozambique. Journal of Archaeological Science 1953–1967.

Mercader, J., Bennett, T., Esselmont, C., Simpson, S. and Walde, D., 2009. Phytoliths in woody plants from the Miombo woodlands of Mozambique. Annals of Botany 104, 91–113.

Mercader, J., Bennett, T., Esselmont, C.,Simpson, S. and D. Walde, D., 2013. Phytoliths from Middle Stone Age habitats in the Mozambican Rift (105–29 ka). Journal of Human Evolution 64, 328–336.

Mercader, J., Runge, F., Vrydaghs, L., Doutrelepont, H., Corneille, E. and Juan-Tresserras, J., 2000. Phytoliths from archaeological sites in the tropical forest of Ituri, Democratic Republic of Congo. Quaternary Research 54, 102-12.

Metcalfe, C. R., 1960. Anatomy of Monocotyledons: I. Gramineae Claredon Press, Oxford.

Metcalfe, C. R., 1971. Anatomy of the Monocotyledons: II. Cyperaceae Claredon Press, Oxford.

Moll E. J. and White F., 1978. The Indian Ocean coastal belt. In Biogeography and Ecology of Southern Africa, ed. M.J.A.Werger, pp. 561–598.W. Junk, The Hague.

Muasya, A. M, Reynders, M., Goetghebeur, P., Simpson, D. A. and Vrijdaghs, A., 2012. Dracoscirpoides (Cyperaceae) – a new genus from Southern Africa, its taxonomy and floral ontogeny. South African Journal of Botany 72, 104–115.

Muasya, A. M., Vrijdaghs, A., Simpson, D. A., Chase, M. W., Goetghebeur, P. and Smets, E., 2009. What is a genus in Cypereae: Phylogeny, character homology assessment and generic circumscription in Cypereae. Botanical Review 75 (1), 52–66.

Mucina, L., Hoare, D. B., Lotter, M., du Preez, J. P., Rutherford, M. C., Scott-Shaw, C. R., et al., 2006. Grassland Biome. In: Mucina, L., Rutherford, M. C. (Eds.), The Vegetation of South Africa. Lesotho, and Swaziland, Strelitzia, vol. 19. South African National Biodiversity Institute, Pretoria, pp. 348-437.

Mucina, L., Rutherford, M. C., 2006. The Vegetation of South Africa, Lesotho, and Swaziland. Strelitzia, vol. 19. South African National Biodiversity Institute, Pretoria.

Murungi M. L., McGlynn, G. and Lejju, B. J., 2017. Alpine grassland palaeoecology of the Virunga Volcanoes, East Africa: a new phytolith record from Mt. Muhavura. Quaternary International 434, 102-116.

Murungi, M., 2013. Phytolith analysis and late Holocene environmental history of the Virunga Volcanoes, south-western Uganda. Unpublished MSc thesis, Mbarara University of Science and Technology, Uganda.

Naczi, R. F. C, and Ford, B. A. (Eds)., 2008. Sedges: Uses, Diversity, and Systematics of the Cyperaceae. Monographs in Systematic Botany from the Missouri Botanical Garden, 108. Missouri Botanical Garden.

Neumann, K., Fahmy, A., Lespez, L., Ballouche, A. and Huysecom, E., 2009. The Early Holocene palaeoenvironment of Ounjougou (Mali): phytoliths in a multiproxy context. Palaeogeography, Palaeoclimatology, Palaeoecology 276, 87–106.

Neumann, K., Fahmy, A.G., Müller-Scheessel, N. and Schmidt, M., 2017. Taxonomic, ecological and palaeoecological significance of leaf phytoliths in West African grasses. Quaternary International, 434, 15-32.

Novello, A., Barboni, D., Berti-Equille, L., Mazur, J., Poilecot, P. and Vignaud, P., 2012. Phytolith signal of aquatic plants and soils in Chad, Central Africa. Review of Palaeobotany and Palynology 178, 43-58

Ollendorf, A. L., 1992. Toward a classification scheme of sedge (Cyperaceae) phytoliths. In: Rapp, G. J., Mulholland, S. C. (Eds.), Phytolith Systematics. Emerging Issues. Plenum Press, New York, pp. 91– 111.

Ollendorf, A. L., Mulholland, S. C., Rapp, G.J., 1987. Phytoliths from some Israeli sedges. Israel Journal of Botany 36, 125–132.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. and Kassem, K.

R., 2001. Terrestrial ecoregions of the world: a new map of Life on Earth. BioScience 51, 933-938.

Osterrieth, M., Madella, M., Zurro, D., Fernanda Alvarez, M., 2009. Taphonomical aspects of silica phytoliths in the loess sediments of the Argentinean Pampas. Quaternary International 193, 70–79.

Palmer, P. G, Gerbeth, J. S., 1988. A scanning electron microscope survey of the epidermis of East African grasses, V, and West African supplement. Smithsonian Contributions to Botany 67: 157.

Palmer, P. G. and Tucker, A. E., 1981. A Scanning Electron Microscope Survey of the Epidermis of East Afiican Grasses. Washington: Smithsonian Contributions to Botany 49.

Palmer, P. G. and Tucker, A .E., 1983. A scanning electron microscope survey of the epidermis of East African grasses, II. Washington: Smithsonian Institution Press.

Palmer, P. G., 1976. Grass cuticles: a new palaeoecological tool for East African lake sediments. Canadian Journal of Botany 54, 1725–1734.

Palmer, P. G., Gerbeth-Jones, S. and Hutchison, S., 1985. A Scanning Electron Microscope Survey of the Epidermis of East African Grasses, III. Smithsonian Contributions to Botany, Washington. 136 pp.

Parker, A. G., Lee-Thorp, J., and Mitchell, P. J., 2011. Late Holocene Neoglacial conditions from the Lesotho highlands, southern Africa: phytolith and stable carbon isotope evidence from the archaeological site of Likoaeng. Proceedings of the Geologists' Association 122, 201–211.

Parr, J. F., Lentfer, C. J. and Boyd, W. E., 2001. A comparative analysis of wet and dry ashing techniques for the extraction of phytoliths from plant material. Journal of Archaeological Science 28, 875 – 886.

Pearsall, D. and Trimble, M., 1984: Identifiying past agricultural activity through soil phytolith analysis: A case study from the Hawaiian Islands. Journal of Archaeological science, 11, 119-133.

Pearsall, D. M., 1978. Phytolith analysis of archaeological site: Evidence for maize cultivation in formative Ecuador. Science, 199, 177 – 178.

Pearsall, D. M., 2000. Palaeoethnobotany - a Handbook of procedures 2nd edition, Academic Press, New York, p 695.

Piperno, D. R., 1979. Phytolith Analysis of Archaeological Soils from Central Panama. Master's thesis, Department of Anthropology, Temple University, Philadelphia.

Piperno, D., 1989. The occurrence of phytoliths in the reproductive structures of selected tropical angiosperms and their significance in tropical palaeoecology, palaeoethnobotany and systematics. Review of Palaeobotany and Palynology 61, 147–173.

Piperno, D. R., 1985a. Phytolith analysis and tropical paleoecology: Production and taxomic signicane of siliceous forms in New world plant domesticates and wild species. Review of palynology and Paleobotany, 45, 185-288.

Piperno, D. R., 1985b. Phytolith taphonomy and distributions in archaeological sediments from panama. Journal of Archaeological science, 12, 247-267.

Piperno, D. R., 1988. Phytolith analysis, an archaeological and geological perspective. San Diego: Academic Press.

Piperno, D. R., 2006. Phytoliths. A Comprehensive Guide for Archaeologists and Paleoecologists. AltaMira Press, Oxford.

Piperno, D. R. and Becker, P., 1996. Vegetational history of a site in the central Amazon Basin derived from phytolith and charcoal records from natural soils. Quaternary Research 45, 202–209.

Plug, I., 1981. Some research results on the late Pleistocene and early Holocene deposits of Bushman Rock Shelter, eastern Transvaal. South African Archaeological Bulletin 36, 14–21.

Plug, I., 1982. Bone tools and shell, bone and ostrich eggshell beads from BushmanRock Shelter (BRS), Eastern Transvaal. South African Archaeological Bulletin 37, 57–62.

Plug, I., 2004. Resource exploitation: animal use during the Middle Stone Age at Sibudu Cave, KwaZulu-Natal. South African Journal of Science 100, 151-158.

Polcyn, M., Polcyn, I., Rovner, I. and Neumann, K., 1997. Phytolith contribution to paleoenvironmental investigation in the Sahel of Burkina Faso, West Africa, In Pinilla, J. Juan-Treserras and M.J. Machado (eds), The State-of-the-art of Phytoliths in Soils and Plants. CSIC 4: 181-3.

Porraz, G., Texier, P.-J., Archer, W., Piboule, M., Rigaud, J.-P., and Tribolo, C., 2013. Technological successions in the Middle Stone Age sequence of Diepkloof Rock Shelter, Western Cape, South Africa. Journal of Archaeological Science 40, 3376–3400.

Porraz, G., Texier, P.-J., Rigaud, J.-P., Parkington, J., Poggenpoel, C., and Roberts, D. L., 2008. Preliminary characterization of a Middle Stone Age lithic assemblage preceding the ’classic ’ Howieson’s Poort complex at Diepkloof Rock Shelter, Western Cape Province, South Africa. South African Archaeological Society Goodwin Series 10, 105–121.

Porraz, G., Val, A., Dayet, L., de La Peña, P., Douze, K., Miller, C. E., Murungi, M. L., Tribolo, C., Schmid, V. C. and Sievers, C., 2015. Bushman Rock Shelter (Limpopo, South Africa): A Perspective from the Edge of the Highveld. South African Archaeological Bulletin 70 (202), 166–179.

Renaut, R., Bamford, M. K., 2006. Results of a preliminary palynological analysis at Sibudu Cave. Southern African Humanities 18, 235-240.

Reynders, M., Huygh, W., Larridon, I., Muasya, A. M., Govaerts, R., Simpson, D. A. and Goetghebeur, P., 2011. Nomenclature and typification of names of genera and subdivisions of genera in the Cypereae (Cyperaceae): 3. Names in segregate genera of Cyperus. Taxon 60 (3), 885–895.

Reynolds, S. C., 2006. Temporal changes in vegetation and mammalian communities during Oxygen Isotope Stage 3 at Sibudu Cave. Southern African Humanities 18, 301-314.

Rigaud, J-P., Texier, P-J., Parkington, J. and C. Poggenpoel, C., 2006. Le mobilier Stillbay et Howiesons Poort de l’abri Diepkloof. La chronologie du Middle Stone Age sud-africain et ses implications. Comptes Rendus Palevol. 5, 839–849.

Rosen, A. M., 1992. Preliminary identification of silica skeletons from Near Eastern archaeological sites: An anatomical approach. In G.R. Rapp, & S.C. Mulholland (Eds.), Phytolith systematics: Emerging issues, advances in archaeological and museum science 1 (pp. 129–147). New York: Plenum Press.

Rossouw, L. and Scott, L., 2011. Phytoliths and pollen, the microscopic plant remains in Pliocene volcanic sediments around Laetoli, Tanzania. In: Harrison, T. (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context, Geology, Geochronology, Paleoecology and Paleoenvironment, vol. 1. Springer Science + Business Media B. V., Dordrecht.

Rossouw, L., 2009. The application of fossil grass-phytolith analysis in the reconstruction of late Cenozoic environments in the South African interior, PhD Thesis. Bloemfontein: University of the Free State.

Rossouw, L., Stynder, D. D. and Haarhof, P., 2009. Evidence for opal phytolith preservation in the Langebaanweg 'E' Quarry Varswater Formation and its potential for palaeohabitat reconstruction. South African Journal of Science 105, 223-227.

Rovner, I., 1971. Potential of opal phytoliths for use in palaeoecological reconstruction. Quaternary Research 1, 343– 359.

Rovner, I., 1983. Plant opal phytolith analysis: major advances in archaeobotanical research. In: Schiffer, M.B.E., (Ed.), Advances in archaeological method and theory. Academic Press, London.

Runge, F., 1999. The opal phytolith inventory of soils in central Africa — quantities, shapes, classification, and spectra. Review of Palaeobotany and Palynology 107, 23–53.

Rutherford, M. C, Midgley, G. F., Bond, W. J, Powrie, L. W., Roberts, R. and Allsopp, J., 2000 Plant biodiversity In: Kiker, G. Climate change impacts in southern Africa. Report to the National Climate Change Committee, Department of Environment Affairs and Tourism, Pretoria.

Rutherford, M. C, Mucina, L. and Powrie, L. W., 2006. Biomes and Bioregions of Southern Africa. In: Mucina, L., Rutherford, M.C. (Eds), The Vegetation Map of South Africa, Lesotho and Swaziland. SANBI, Pretoria.

Rutherford, M. C. 1997. Categorization of biomes. In: (eds. Cowling, R.M., Richardson, D.M. and Pierce, S. M.). Vegetation of Southern Africa. Cambridge University Press, Cambridge. Pp 91-98.

Schiegl, S. and Conard, N. J., 2006. The Middle Stone Age sediments at Sibudu: results from FTIR spectroscopy and microscopic analyses. Southern African Humanities 18, 149-172.

Schiegl, S., Stockhammer, P., Scott, C. and Wadley, L., 2004. A mineralogical and phytolith study of the Middle Stone Age hearths in Sibudu Cave, KwaZulu-Natal, South Africa. South African Journal of Science 100, 185-194.

Scott, L., 2002. Grassland development under glacial and interglacial conditions in southern Africa: review of pollen, phytolith and isotope evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 177, 47-57.

Scott, L. and Rossouw, L., 2005. Reassessment of botanical evidence for palaeoenvironments at Florisbad, SouthAfrica. South African Archaeological Bulletin 60, 96–102.

Scott, L. and Vogel, J. C., 2000. Evidence for environmental conditions during the last 20000 years in Southern Africa from 13C in fossil hyrax dung. Global and Planetary Change 26 (1-3), 207-215.

Sievers, C., 2006. Seeds from the Middle Stone Age layers at Sibudu Cave. Southern African Humanities 18, 203-222.

Sievers, C., 2011. Sedges from Sibudu, South Africa: evidence for their use. In: A.G. Fahmy, S. Kahlheber, and A. C. D’Andrea (eds), Windows on the African Past: Current Approaches to African Archaeobotany. Proceedings of the 6th International Workshop on African Archaeobotany, June 13–15, 2009, Helwan University, Cairo, Egypt. Reports in African Archaeology 3, 225–241.

Sievers, C. 2013. What’s the rush? Scanning electron micrographs of Juncus (Juncaceae) seeds. Southern African Humanities 25, 207–16.

Sievers, C. and Muasya, A. M., 2011. Identification of the sedge Cladium mariscus subsp. jamaicense and its possible use in the Middle Stone Age at Sibudu, KwaZulu-Natal. Southern African Humanities 23, 77–86.

Sievers, C. and Wadley, L., 2008. Going underground: experimental carbonization of fruiting structures under hearths. Journal of Archaeological Science 35, 209-2917.

Simpson, D. A., 2008. Frosted curls to tiger nuts: ethnobotany of Cyperaceae. In R. F. C. Naczi and B. A. Ford (Eds), Sedges: Uses, Diversity, and Systematics of the Cyperaceae. Monographs in Systematic Botany from the Missouri Botanical Garden, 108. Missouri Botanical Garden.

Singh, V., Prasad, V. and Chakraborty, S., 2007. Phytoliths as indicators of monsoonal variability during mid-late Holocene in mainland Gujarat, western India. Current Science, Vol.92, No.12, 1754-1759.

Soriano, S., Villa, P., Delagnes, A., Degano, I., Pollarolo, L., Lucejko, J. J., Henshilwood, C. and Wadley, L., 2015. The Still Bay and Howiesons Poort at Sibudu and Blombos: Understanding Middle Stone Age Technologies. PLOS ONE, DOI:10.1371/journal.pone.0131127.

Standley, L. A., 1990. Anatomical aspects of the taxonomy of sedges (Carex, Cyperaceae). Canadian Journal of Botany 68, 1449-1456.

Stewart, D. R. M. 1965. The epidermal characters of grasses, with special reference to East African plains species: part 1. Botanische Jahrbucher 84, 63–116.

Stratford, D., Heaton, J. L., Pickering, T. R., Caruana, M. V. and Shadrach, K., 2016. First hominin fossils from Milner Hall, Sterkfontein, South Africa. Journal of Human Evolution 9, 167-173.

Strömberg, C. A. E., 2003. The Origin and Spread of Grass-dominated Ecosystems during the Tertiary of North America and How It Relates to the Evolution of Hypsodonty in Equids. Unpublished PhD dissertation thesis, University of California.

Tadross, M. and Johnston, P., 2012. Climate Systems Regional Report: Southern Africa.

Taylor D., Robertshaw, P. and Marchant, R, A., 2000. Environmental change and socio-economic upheaval in pre-colonial, Western Uganda. The Holocene, 10, 437-446.

Texier, J.-P., Porraz, G., Parkington, J., Rigaud, J-.P., Poggenpoel, C., Miller, C., Tribolo, C., Cartwright, C., Coudenneau, A., Klein, R., Steele, T. and Verna, C., 2010. A Howiesons Poort tradition of engraving ostrich eggshell containers dated to 60,000 years ago at Diepkloof Rock Shelter. South Africa. Proceedings of the National Academy of Science 107, 7621-7622.

Thackeray, J. F., 1992. Chronology of Late Pleistocene deposits associated with *Homo sapiens* at Klasies River Mouth, South Africa. Palaeoecology of Africa and the Surrounding Islands 23, 177-191.

Thorn, V. C., 2001. Oligocene and Early Miocene Phytoliths from CRP-2/2A and CRP-3, Victoria Land Basin, Antarctica. Terra Antartica 8(4), 407-422.

Thorn, V. C., 2004. Phytolith evidence for C4-dominated grassland since the early Holocene at Long Pocket, northeast Queensland, Australia. Quaternary Research 61, 168–180.

Tribolo, C., Mercier, N., Douville, E., Joron, J.-L., Reyss, J.-L., Rufer, D., Cantin, N., Lefrais, Y., Miller, C. E., Porraz, G., Parkington, J., Rigaud, J.-P., and Texier, P.-J., 2013. OSL and TL dating of the Middle Stone Age sequence at Diepkloof Rock Shelter (South Africa): a clarification. Journal of Archaeological Science 40, 3401–3411.

Tucker, G. C., 1983. The taxonomy of Cyperus (Cyperaceae) in Costa Rica and Panama. − Systemic Botany Monographs 2, 85.

Twiss, P. C., 1992. Predicted world distribution of C3 and C4 grass phytoliths. In: Rapp, G.R., Mulholland, S.C. (Eds.), Phytoliths Systematics Emerging Issues. Plenum Press,NewYork, pp. 113–128.

Twiss, P. C., Suess, E. and Smith, R. M., 1969. Morphological classification of grass phytoliths. Soil Science Society of America Journal, 33, 109–115.

Val. A., 2016. New data on the ovifauna from the Middle Stone Age layers of Sibudu cave, South Afica: Taphonomic and paleoenviromental implications. Quaternary International (2016).

Van Campo, E., Duplessy, J. C., Prell, W. L., Barratt, N., Sabatier, R., 1990. Comparison of terrestrial and marine temperature estimates for the past 135 kyr off Southeast Africa: A test for GCM simulations of palaecoclimate. Nature 348(6298), 209-212.

Van Wyk, B. E. and Gericke, N, 2000. People's plants: a guide to useful pants of southern Africa. Pretoria: Briza.

Villa, P., Delagnes, A. and Wadley, L., 2005. A late Middle Stone Age artefact assemblage from Sibudu (KwaZulu-Natal): comparisons with the European Middle Palaeolithic. Journal of Archaeological Science 32, 399–422.

Villa, P. and Lenoir, M., 2006. Hunting weapons of the Middle Stone Age and the Middle Palaeolithic: spear points from Sibudu, Rose Cottage and Bouheben. Southern African Humanities 18 (1), 89-122.

Villa, P., Soriano, S., Tsanova, T., Degano, I., Higham, T. F. G., d'Errico, F., Backwell, L., Lucejko, J. J., Colombini, M. P. and Beaumont, P. B., 2012. Border Cave and the beginning of the Later Stone Age in South Africa. Proceedings National Academy of Science 109, 13208-13213.

Vrydaghs, L. and Doutrelepont, H., 2000. Analyses phytolitariennes: acquis et prespectives In M. Servant et S. Servant-Vildary (eds.), Dynamique á long terme des écosystèms forestiers intertropicaux, pp. 389-98. Paris: UNESCO.

Vrydaghs, L., Cocquyr, C., Van de Vijve, T. and Goetghebeur, P., 2004. Phytolithic evidence for the introduction of Schoenoplectus Californicus Subsp. Tatora at Easter Island. Rapa Nui Journal 18 (2), 95-106.

Wadley, L., 1997. Rose Cottage Cave: archaeological work 1987 to 1997. South African Journal of Science 93, 439–444.

Wadley, L., 2001. Preliminary report on excavations at Sibudu Cave, KwaZulu-Natal. Southern African Humanities 13, 1-17.

Wadley, L., 2004. Vegetation changes between 61 500 and 26 000 years ago: the evidence from seeds in Sibudu Cave, KwaZulu-Natal. South African Journal of Science 100, 167-173.

Wadley, L., 2005. A typological study of the final Middle Stone Age stone tools from Sibudu Cave, KwaZulu-Natal. South African Archaeological Bulletin 60, 51-63.

Wadley, L., 2007. Announcing a Still Bay industry at Sibudu Cave, South Africa. Journal of Human Evolution 52, 681–689.

Wadley, L., 2015. Those marvellous millennia: the Middle Stone Age of Southern Africa. Azania: Archaeological Research in Africa 50 (2), 155-226.

Wadley, L., Hodgskiss, T. and Grant, M., 2009. Implications for complex cognition from the hafting of tools with compound adhesives in the Middle Stone Age, South Africa. Proceedings of the National Academy of Sciences 106, 9590-9594.

Wadley, L. and Jacobs, Z., 2004. Sibudu Cave, KwaZulu-Natal: background to the excavations of the Middle Stone Age and Iron Age occupations. South African Journal of Science 100, 145-150.

Wadley, L. and Jacobs, Z. 2006. Sibudu Cave: Background to the excavations, stratigraphy and dating. Southern African Humanities 18(1), 1–26.

Wadley, L., Murungi, M. L., Witelson, D., Bolhar, R., Bamford, M., Sievers, C., Val, A. and de La Peña, P., 2016. Steenbokfontein 9kr: A Middle Stone Age Spring Site In Limpopo, South Africa. South African Archaeological Bulletin 71 (204), 130–145.

Wadley, L., Sievers, C., Bamford, M., Miller, C., Goldberg, P., and Berna, F., 2011. Middle Stone Age bedding construction and settlement patterns at Sibudu, South Africa. Science, 334, 1388–1391.

Wadley, L. and Whitelaw, G. (eds), 2006. Middle Stone Age research at Sibudu Cave. Southern African Humanities 18(1), 1–341.

Wadley, L., Williamson, B.S. and Lombard, M., 2004. Ochre in hafting in Middle Stone Age southern Africa: a practical role. Antiquity 78, 661-675.

Wallis, L.A., 2001. Environmental history of northwest Australia based on phytolith analysis at Carpenter’s Gap1. Quaternary International 83-85, 103-117.

Watling, J. and Iriarte, J., 2013. Phytoliths from the coastal savannas of French Guiana. Quaternary International 287, 162-180.

White, F., 1983. The Vegetation Map of Africa. UNESCO, Paris. 356 pp.

Wilding, L. P., 1967. Radiocarbon dating of biogenetic opal. Science 156, 66-67.

Wilding, L. P., and Drees, L.R., 1971. Biogenic opal in ohio soils. Proceedings of the Soil Science Society of America 35,1004-1010.

Wilding, L.P. and Drees, L.R., 1971. Biogenic opal in Ohio soils. Soil Science Society of America Journal, 35, 1004–1010.

Will, M., Bader, G. D., and Conard, N. J., 2014. Characterizing the Late Pleistocene MSA Lithic Technology of Sibudu, KwaZulu-Natal, South Africa. PLOS ONE 9(5): e98359.

Williamson, B. S., 2004. Middle Stone Age tool function from residue analysis at Sibudu Cave. South African Journal of Science 100, 174–178.

Wurz, S., 2002. Variability in the Middle Stone Age lithic sequence, 115,000 – 60,000 years ago at Klasies River, South Africa. Journal Archaeological Science 29, 1001–1015.

APPENDIX

Table A1: Percentage of articulated and isolated phytolith morphotypes of sedge species

Abbreviations of species are given in Table 4.1, Chapter Four.

																Articulated															
Morphotypes	**Bu.sp%**	**%Clm**	**Cya%**	**%Cyr**	**%Cyf**	**%Cyh**	**%Cyo**	**%Cys**	**%Elc**	**%El.sp**	**%Ell**	**%Eld**	**%Fup**	**%Fu.sp**	**%Jue**	**%Kyp**	**%Kye**	**%Ky.sp1**	**%Ky.sp2**	**%Mac**	**%Pym**	**%Py.sp**	**%Scs**	**%Scm**	**%Scb**	**%Scn**	**%Scw**	**%Sc.sp**	**%Sc.sp??**	**%Cyp 1**	**%Cyp 2**
Leaf/culm cones	75.5	62.9	35.5	13.6	15.9	7.1	32.8	26.9	21.9	9.9	0.9	7.1	9.4	27.7	0.0	13.8	12.9	9.8	57.6	7.3	12.5	**53.3**	34.2	26.1	30.1	38.9	12.9	36.4	48.5	22.5	40.2
Achene cones	0.0	0.0	2.1	0.4	2.3	28.5	3.1	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	11.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0
Cones + elongate psilate on base	0.2	0.7	0.7	4.3	0.0	0.8	2.1	0.0	2.9	3.0	0.0	0.0	0.0	0.2	0.0	2.8	0.0	0.3	1.3	0.5	2.2	1.5	2.2	0.0	0.0	0.0	1.0	0.4	0.2	0.0	0.0
Cones + elongate/parallelepipedal/tracheid	0.0	1.5	0.5	4.9	2.8	0.2	0.5	0.7	8.0	3.5	8.8	31.4	2.3	0.2	0.0	4.5	5.9	0.3	0.4	0.0	12.5	0.4	5.0	1.5	0.0	8.5	31.4	0.0	0.9	0.0	0.0
Parallelepipedal/tabular psilate	0.0	0.7	1.1	1.0	5.5	0.0	0.0	0.0	0.7	2.1	54.9	2.9	0.6	1.6	0.0	3.0	5.9	0.0	1.6	0.0	13.0	0.4	0.2	0.9	0.0	1.3	4.4	1.1	0.5	0.9	0.4
Parallelepipedal/tabular sinuate	0.0	0.7	0.2	0.2	5.8	0.0	0.0	0.0	0.0	3.0	0.7	0.2	1.5	2.0	0.0	0.0	0.2	0.0	0.0	0.0	10.8	0.0	1.7	2.6	0.0	2.5	22.4	0.0	0.0	0.5	0.0
Tabular dendriform	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	4.4	0.0	0.0	0.0
Tabular decorated	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wavy plates	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	55.6	27.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	1.6	0.0	0.0	0.0
Elongate psilate	0.0	0.0	1.4	7.7	2.8	1.5	0.5	0.0	1.8	0.0	0.4	2.7	0.6	0.5	4.3	2.5	6.6	0.0	1.6	0.0	2.0	0.0	0.2	1.9	0.0	0.4	1.5	0.2	1.4	0.2	0.0
Elongate sinuate	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.2	1.1	0.4	0.2	0.0	0.8	0.0	0.0	0.0	0.0	1.0	0.0	5.5	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tracheid	1.2	0.7	0.7	6.9	3.0	0.2	2.8	0.2	0.2	3.2	1.8	1.3	1.5	0.2	20.6	1.5	0.2	0.0	0.7	0.5	0.7	0.0	1.0	0.4	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Bi-convex	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.0
Silica skeleton (cones only)	0.0	1.9	0.9	0.0	1.3	0.0	0.0	0.0	0.0	14.5	0.0	0.0	1.0	2.3	0.0	15.8	18.8	0.0	0.0	0.2	1.7	0.0	15.6	0.4	0.0	0.0	3.3	0.0	5.9	0.0	0.0
Silica skeleton	0.5	1.9	2.7	0.0	8.8	2.3	26.4	1.6	4.5	7.9	3.5	6.4	7.6	1.4	8.5	10.3	0.5	0.3	1.3	0.5	3.2	2.0	4.2	0.4	0.0	3.4	14.7	2.9	1.4	0.0	0.0
Silica skeleton platelets	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.1	4.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Silica skeleton (elongate arranged in parallel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stomata complex	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	25.4	0.0	5.1	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	3.1	1.5	0.2	0.0	0.0	0.0
Polyhedral epidermal	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.7	4.9	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.2	0.0	0.0	0.0
Anticlinal or cones?	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.9	0.2	0.0	0.9	0.2	2.8	0.0	1.8	0.4	0.0	7.1	3.9	0.0	1.1	0.0	0.2	1.5	0.0	0.5	4.4	0.2
																Isolated															
Leaf/culm cones	20.0	26.2	28.4	10.2	11.8	11.9	15.5	35.1	33.9	4.8	2.2	10.6	6.3	17.9	0.9	6.8	4.9	67.5	24.7	13.1	2.0	15.8	8.7	45.1	67.2	23.6	1.0	46.7	30.0	46.8	52.3
Achene cones	0.0	0.0	2.1	2.0	2.3	42.7	3.6	26.7	0.4	0.0	0.0	2.9	0.0	0.0	0.0	2.8	0.0	4.5	0.2	66.3	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	16.6	2.2
Parallelepipedal/tabular psilate	0.9	0.2	8.7	13.6	23.2	0.0	5.4	0.9	12.7	6.5	17.7	13.3	2.5	0.9	3.4	18.6	26.4	1.3	2.9	0.0	18.4	9.0	0.5	5.2	0.0	2.2	0.8	0.4	0.9	2.6	2.0
Parallelepipedal/tabular sinuate	0.2	0.7	3.9	3.7	3.0	0.4	1.0	0.0	1.8	1.2	1.3	0.2	3.6	0.0	0.2	3.0	3.5	0.5	1.1	0.0	1.7	0.9	6.5	3.5	0.0	4.0	0.8	1.1	2.1	0.2	0.2
Tabular dendriform	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	1.1	0.0	0.0	0.0
Elongate psilate	0.9	1.5	3.7	14.8	10.1	4.4	1.3	0.9	5.6	3.2	3.3	5.5	2.9	0.0	14.2	3.8	13.9	12.8	5.2	0.2	3.9	12.7	1.5	5.8	0.0	2.0	0.8	2.7	7.6	3.7	1.2
Elongate sinuate	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.9	0.0	0.7	1.3	0.0	0.2	7.3	7.0	0.0	0.0	0.2	0.0	1.0	0.0	1.0	1.9	0.0	1.8	0.3	0.2	0.0	0.2	0.0
Tracheid	0.0		0.2	2.2	1.5	0.0	0.0	0.0	0.7	3.9	2.2	2.0	0.4	0.0	40.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	1.5	0.4	0.0	0.0	0.3	0.2	0.0	0.0	0.8
Stomata	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polyhedral epidermal	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.4	7.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prickles/hairs	0.0	0.0	2.3	0.4	0.0	0.0	1.6	0.2	0.2	0.0	0.0	0.0	0.6	12.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4

Table A2: Estimated % silica in the dry weight of each species of Sedge and rushes, and the size of longest base axis of leaf/culm cone phytoliths from sedges.

Note: The weigh balance used for all species only measured up to three decimal places and therefore could not measuer weights below 0.001 g. Any measurements that were below 0.001 are written as zero or no data in this study.

Slide No.	**Species**	**Dry weight (g)**	**Post-acid (final) (g)**	**% Dry weight**	**length range of base axis (μm)**
	Subfamiliy Cyperaceae				
Cyp 32	*Bulbostylis burchelli*	-			6.51 – 15.48
Cyp 37	*Bulbostylis* sp.	0.35	No data		5.27 – 19.48
Cyp 26	*Cladium mariscus*	0.71	No data		5.47 – 16.91
SIB 14 Monocot	*Cyperus albastriatus*	0.755	0.028	3.7	4.12 -14.93
Cyp 8	*C. denudatus*	0.116	No data	0	Hardly productive
Cyp 9	*C. rigidifolius*	0.161	No data	0	6.45 – 18.01
Cyp 11	*C. fastigiatus*	0.153	No data	0	5.38 – 11.56
Cyp 12	*C. haematocephalus*	0.239	No data	0	6.21 – 28.13
Cyp 13	*C. obtusifloris* spp. *flavissimus*	0.172	No data	0	4.40 – 18.20
Cyp 14	*C. semitrifidus*	0.104	No data	0	5.28 – 20.85
Cyp 5	*E. caduca*	0.085	No data	0	4.52 – 9.99
Cyp 6	*Eleocharis* sp.	0.194	No data	0	- Hardly any single cones to measure

Cyp 15	*E. cf. limosa*	0.218	No data	0	- “
Cyp 16	*E. dregeana*	0.042	No data	0	4.25 – 12.51
Cyp 30	*Fuirena pubescens*	0.103	No data	0	4.24 – 16.07
Cyp 27	*Fuirena* sp.	0.8			6.12 – 25.49
Cyp 7	*Kyllinga pulchella*				6.43 – 28.48
Cyp 18	*Kyllinga erecta*	0.136	No data	0	8.64 – 16.33
SIB 27 Monocot	*Kyllinga* sp. 1	0.32	0.007	2.2	6.20 – 13.05
Cyp 31	*Kyllinga* sp.2	0.74			5.18 – 25.18
Cyp 4	*Mariscus congestus*	0.419	No data	0	5.48 – 21.00
Cyp 19	*Pycreus macranthus*	0.313	No data	0	9.72 – 24.37
SIB 29	*Pycreus* sp.	0.782	0.026	3.3	8.49 – 18.85
Cyp 2	*Schoenoxiphium sparteum*	0.151	No data	0	5.34 – 22.72
Cyp 29	*Schoenoplectus muricinux*	-			5.54 – 27.0
Cyp 38	*Schoenoplectus corymobosus*	-			4.38 – 17.04
Cyp 39	*Schoenoplectus muriculatus*	0.411	0.008	1.9	5.07 – 27.41
Cyp 22	*Scirpoides burkei*	0.376	0.006	1.6	5.42 – 32.04
Cyp 24	*Scleria natalensis*	0.816	0.017	2.1	6.17 – 15.86
SIB 17 Monocot	*S. woodii*	0.133	0.003	2.3	- no isolated cones to measure
Cyp 25	*Scleria* sp.	1.09			5.76 – 25.76
SIB 23 Monocot	*Schoenoplectus* sp.	1.00			5.52 – 18.20
SIB 30 Monocot	Cypereceae sp. 1	0.723	0.008	1.1	5.28 – 16.71
	Cyperaceae sp. 2	0.794	No	0	5.24 – 16.65

			data		
	Subfamily Juncaceae				
Cyp 20	*Juncus exertus*	0.238	No data	0	
Cyp 21	*Juncus oxycarpus*	0.44	No data	0	
SIB 20 Monocot	*Juncus effuses*	0.744	No data	0	

Table A3: Estimated % silica in each grass species studied.

Subfamily	**Species**	**Slide No.**	**Part analysed**	**Dry weight (g)**	**Post-acid (final) (g)**	**% Dry weight**
Aristidoideae	*Aristida* sp.	SIB 7 Monocot	C, L, I	0.838	0.018	2.1
Arundinoideae	*Phragmites australis*	SIB 19 Monocot	C, L, I	0.856	0.01	1.2
Chloridoideae	*Dactyloctenium* sp.	SIB 16 Monocot	C, L, I	0.72	0.015	2.1
	Eragrostis superba	SIB 4 Monocot	C, L, I	0.8	No data	
	Eragrostis sp.	SIB 24 Monocot	C, L, I	0.811	0.005	0.6
	Fingerhuthia sp.	SIB 11 Monocot	Whole plant	0.878	0.018	2.1
	Sporobolus africanus	SIB 18 Monocot	C, L	0.985	0.01	1.0

Panicoideae	*Digitaria* sp.	SIB 10 Monocot	C, L, I	0.85	0	0.0
	Digitaria sp. 2	SIB 21 Monocot	C, L, I	0.857	0.018	2.1
	Hyparrhenia hirta	SIB 28 Monocot	C, L, I	0.849	0.034	4.0
	Melinis repens	SIB 25 Monocot	C, L, I	0.821	0	0.0
	Monocymbium ceresiiforme	SIB 6 Monocot	C, L, I	0.829	No data	
	Odontyletrum sp.	SIB 5 Monocot	C, L	0.784	0.002	0.3
	Oplismenus sp.	SIB 26 Monocot	C, L, I	0.831	0.055	6.6
	Panicum maximum	SIB 8 Monocot	C, I	0.834	No data	
	Setaria pallide-fusca	SIB 13 Monocot	C, L, I	0.894	0.009	1.0
	Setaria megaphylla	SIB 22 Monocot	C, L, I	0.8	0.027	3.4
Pooideae	*Agrostis* sp.	SIB 12 Monocot	C, I	0.848	No data	
Unknown	Unidentified grass	SIB 3 Monocot	C, L	0.818	0.013	1.6

Table A4: showing the row counts of phytoliths from the grass species.

*Total count ca. 200 for each species

	CROSS	BSCVE	BSCVX	BSSM	BLCVE	BLCVX	BLSM	BF	BN	BT	POLY	Rondel	Saddle	TRA	Elongate	Tabular	Tracheid	Bulliform	PLPD	Bulbou	Dendritic	Subfamily
Unidentified grass	0	3	0	2	0	0	0	1	1	0	0	192	0	0	4	0	0	0	0	0	0	
Eragrostis superba	0	0	0	0	0	0	0	0	0	0	0	190	7	0	1	0	1	0	0	0	0	Chloridoideae
Eragrostis sp.	3	1	0	0	1	0	0	0	0	0	0	112	83	0	12	0	0	0	0	0	0	Chloridoideae
Fingerhuthia sp.	112	5	1	7	37	3	32	0	0	0	0	46	0	0	15	5	1	1	2	0	0	Chloridoideae
Dactyloctenium sp.	0	0	1	0	0	0	0	0	0	2	0	111	109	0	6	4	0	0	1	0	0	Chloridoideae
Sporobolus africanus	0	4	1	0	0	0	0	0	0	0	0	183	17	0	0	0	0	0	2	0	0	Chloridoideae
Odontelytrum sp.	25	0	115	2	0	0	6	0	3	0	0	91	2	0	0	7	0	1	0	1	0	Panicoideae
Monocymbium ceresiiforme	93	71	29	34	13	1	0	2	0	0	0	31	6	0	19	8	0	0	0	2	1	Panicoideae
Panicum maximum	0	18	0	0	1	0	0	0	0	0	0	195	0	0	4	2	0	0	0	1	3	Panicoideae
Digitaria sp.	5	59	1	0	88	2	0	0	1	8	2	49	0	0	6	1	0	0	2	0	0	Panicoideae
Setaria pallide-fusca	68	11	1	0	1	0	0	0	0	26	0	109	0	3	19	4	2	0	3	0	0	Panicoideae
Digitaria sp.2	23	35	75	0	32	33	0	0	0	30	0	10	0	0	9	1	0	0	0	0	7	Panicoideae
Setaria megaphilla	31	73	13	0	2	1	0	0	4	20	1	23	0	0	9	5	0	14	1	0	0	Panicoideae
Melinis repens	23	31	38	30	8	1	3	0	27	22	32	30	0	0	0	2	0	0	0	0	0	Panicoideae
Oplismenus sp.	28	18	34	5	15	24	3	0	0	12	0	76	0	0	5	8	0	4	1	0	0	Panicoideae
Hyparrhenia hirta	43	12	45	10	5	0	4	0	0	18	0	69	0	0	2	0	0	0	1	0	0	Panicoideae
Aristida sp.	0	0	93	0	0	57	0	0	0	15	0	42	0	0	18	0	0	0	1	1	1	Aristidoideae
Phragmitis australis	0	0	0	0	0	0	0	0	0	0	0	187	13	0	0	3	0	0	0	0	0	Arundinoideae
Agrostis	48	9	24	6	4	4	0	0	0	5	0	91	27	9	3	3	1	0	0	0	9	Pooideae

Table A5: Estimated % silica of each eudicot species studied.

Slide No.	**Family**	**Species**	**Part**	**Dry weight (g)**	**Post-acid (final) (g)**	**(%) Dry weight**
31	Achariaceae	*Rawsonia lucida*	L,W	2.652	0.059	2.2
8	Anacardiaceae	*Protorhus longifolia*	L,W	1.835	0	0.0
14	Apocynaceae	*Carissa bispinosa*	L,W	1.8	0	0.0
19	Apocynaceae	*Tabernamontana ventricosa*	L,W	1.819	0	0.0
6	Asteraceae	*Brachylaena discolour*	L,W	2.301	0	0.0
15	Celtidaceae	*Celtis africana*	L,W,F	2.385	0.012	0.5
36	Celtidaceae	*Celtis mildbraedii*	L,W	2.272	0.011	0.5
38	Ebenaceae	*Diospyros natalensis*	L,W	3.765	0.008	0.2
16	Euphorbiaceae	*Macaranga capensis*	L,W	2.05	0.037	1.8
39	Euphorbiaceae	*Acalypha glabrata*	L,W	3.725	0.008	0.2
41	Euphorbiaceae	*Clutia pulchella*	L,W	3.661	0.002	0.1
44	Euphorbiaceae	*Acalypha sonderiana*	L,W	2.712	0	0.0
17	Fabaceae	*Albizia adianthifolia*	L,W	1.007	0	0.0
23	Fabaceae	*Baphia racemosa*	L,W	1.458	0	0.0
32	Fabaceae	*Schotia bracypetala*	L,W	2.969	0.073	2.5
37	Fabaceae	*Millettia grandis*	L,W	2.452	0.033	1.3
40	Fabaceae	*Dichrostachys cinerea*	L,W,F	3.327	0.002	0.1
42	Fabaceae	*Acacia ataxacantha*	L,W	2.996	0	0.0
35	Lamiaceae	*Tetradenia riparia*	L,W	1.118	0	0.0
45	Lamiaceae	*Clerodendrum glabrum*	L,W	1.891	0	0.0
46	Lamiaceae	*Clerodendrum glabrum*	L,W	1.647	0.088	5.3
10	Lauraceae	*Cryptocarya woodi*	L,W	1.599	0	0.0
4	Meliaceae	*Ekibergia capensis*	L,W	1.66	0	0.0
7	Meliaceae	*Trichilia imetica*	L,W	3.095	0.004	0.1
21	Moraceae	*Ficus polita*	L,W	1.797	0.113	6.3
26	Moraceae	*Ficus sp.*	L,W	1.724	0.009	0.5
30	Moraceae	*Ficus ingens*	L,W	2.915	0.004	0.1

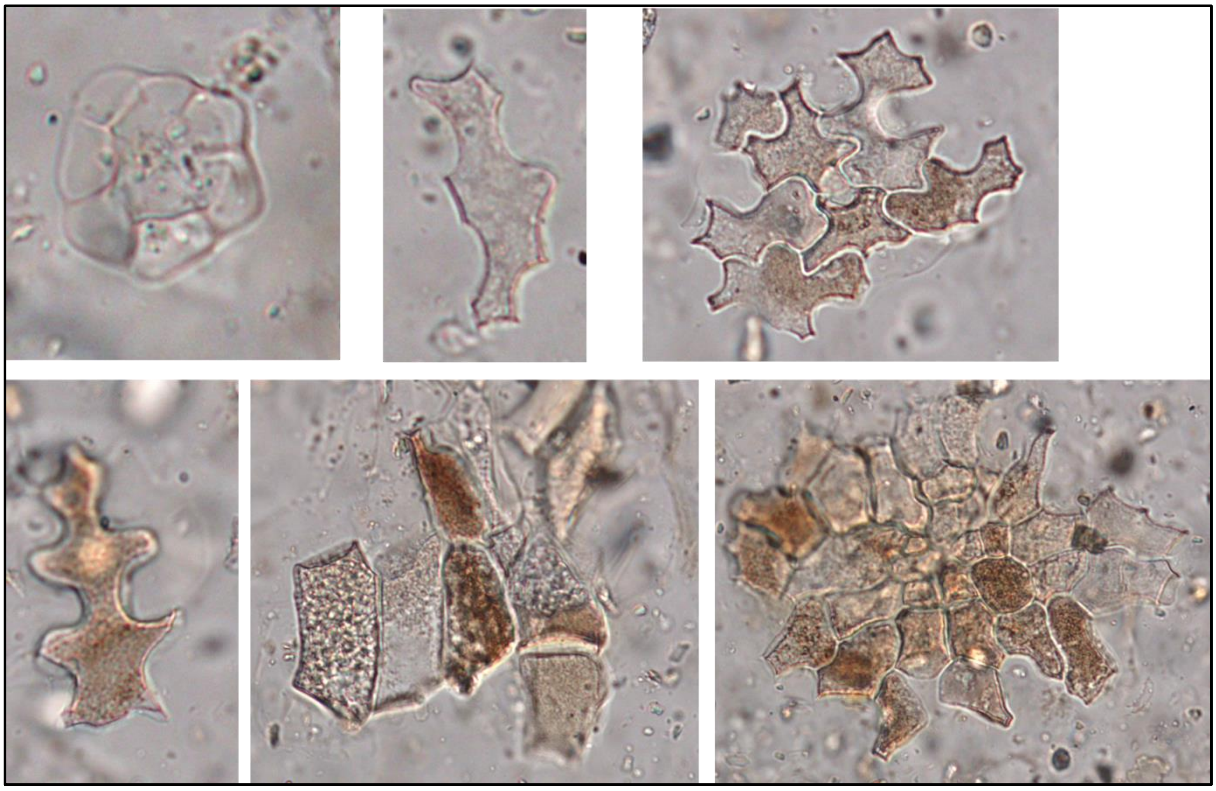
33	Moraceae	*Ficus sur*	L,W	2.607	0.13	5.0
20	Myrtaceae	*Eugenia capensis*	L,W	2.905	0	0.0
22	Myrtaceae	*Syzigium cordata*	L,W	1.497	0	0.0
34	Ochnaceae	*Ochna natalitia*	L,W	2.864	0	0.0
28	Phyllanthaceae	*Bridelia micrantha*	L,W	2.046	0.001	0.0
1	Podocarpaceae	*Podocarpus latifolius*	L,W	2.923	0	0.0
24	Rhamnaceae	*Ziziphus macronata*	L,W	1.349	0	0.0
27	Rubiaceae	*Vangueria infausta*	L,W	3.388	0.057	1.7
25	Rutaceae	*Teclea gerrardii*	L,W	1.73	0.007	0.4
29	Rutaceae	*Vepris lanceolata*	L,W	3.206	0	0.0
5	Sapindaceae	*Deinbolia oblongifolia*	L,W	1.499	0	0.0
2	Sapotaceae	*Mimusops obovata*	L,W	1.118	0	0.0
13	Sapotaceae	*Sideroxylon inerme*	L,W	1.74	0	0.0
47	Urticaceae	*Obetia tenax*	W	0.944	0.006	0.6
11	Vitaceae	*Rhoicissus rhomboidea*	L	1.417	0	0.0
12	Vitaceae	*Rhoicissus tomentosa*	L	1.249	0	0.0

Table A6: Showing the row counts of the phytoliths from the archaeological sediments

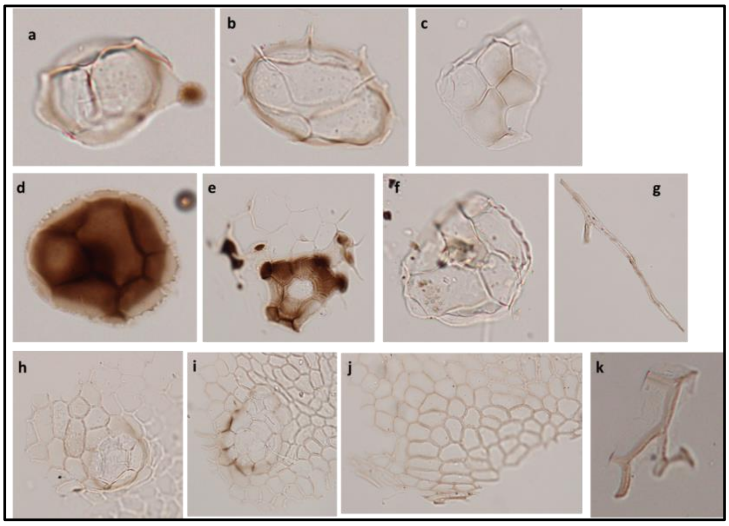
Sample No	Depth (cm)	Layer abbrv.	Lobates	Saddles	Rondels	Trapeziform	C. bulliform	Acicular	Blocky PLPD	Blocky other	G. psilate	G. granulate	G. echinate	T. elongate	Elongate	Unique' bodies	S. cones	S. achenes	S. 'anticlinals'	Other	Sum	% Poaceae	% Sedge	%Dico
1	278	Iv	7.5	0.6	4.1	1.6	0.9	3.1	24.2	7.2	9.7	0.0	0.0	7.9	24.8	0.0	3.8	0.0	0.0	4.4	318	17.9	3.8	9.7
2	282	BM	4.4	3.7	38.9	2.8	0.3	0.9	16.2	2.5	5.3	0.3	0.0	1.2	15.6	0.0	4.4	0.0	0.6	2.8	321	51.1	4.4	5.6
3	287	Y ash P	0.9	0.9	11.7	0.0	0.3	2.2	34.5	12.3	11.1	0.0	0.0	0.3	22.5	0.9	0.0	0.3	0.0	1.9	316	16.1	0.3	11.1
4	291	BP	3.4	2.1	21.6	0.0	0.8	2.9	35.1	1.3	9.0	0.5	0.0	1.1	18.2	1.1	0.0	0.0	0.8	2.1	379	30.9	0.0	9.5
5	295	Su	8.2	1.5	9.4	3.8	0.3	2.3	14.7	0.9	10.3	0.0	0.0	5.3	22.0	1.2	2.9	0.0	0.0	17.3	341	25.5	2.9	10.3
6	298	Sn	11.6	2.9	19.5	5.0	0.0	2.9	24.8	1.3	5.5	0.0	0.0	1.3	21.1	0.0	1.3	0.3	0.3	2.1	379	42.0	1.6	5.5
7	302	Ch	10.0	4.9	31.3	2.7	0.6	2.4	14.9	0.6	4.0	0.3	0.3	4.9	19.1	0.0	1.5	0.0	0.6	1.8	329	52.0	1.5	4.3
8	304	White on Ch2	6.5	2.8	5.9	2.2	1.5	2.5	16.4	6.5	25.6	0.0	0.0	6.8	12.3	0.6	3.1	0.0	0.3	7.1	324	21.3	3.1	25.6
9	309	Ch2	2.2	2.2	6.3	1.9	0.6	2.2	17.5	7.3	9.8	0.0	0.0	14.3	31.7	0.0	1.3	0.0	0.0	2.5	315	15.6	1.3	9.8
10	313	BG mix	2.3	0.0	1.6	0.3	0.0	6.9	20.3	5.2	14.1	0.0	0.0	18.4	29.5	0.0	0.0	0.0	0.0	1.3	305	11.1	0.0	14.1
11	322	PhD4	3.5	1.1	5.6	0.5	0.3	2.1	31.8	6.7	12.3	0.0	0.0	5.3	29.4	0.0	0.8	0.0	0.0	0.5	374	13.1	0.8	12.3
12	335	Br Under YA	12.9	2.4	16.8	2.6	0.3	2.6	16.2	6.2	7.1	0.0	0.0	6.8	20.3	0.3	2.1	0.0	1.2	2.4	340	37.6	2.1	7.1
13	342	Br Under YA2	13.9	0.9	5.4	1.2	0.0	3.6	8.8	10.9	6.9	0.3	0.0	7.9	32.9	0.0	1.2	0.3	0.0	5.7	331	25.1	1.5	7.3
14	348	H1 in Br Under YA2(i)	7.3	1.1	21.1	1.1	0.5	2.2	15.4	11.1	8.6	0.0	0.0	7.8	19.5	0.0	2.4	0.3	0.0	1.6	370	33.2	2.7	8.6
15	354	H1 RB	7.2	1.5	16.7	1.5	0.5	5.7	22.9	10.4	7.5	0.0	0.0	7.7	15.9	0.0	0.0	0.5	0.0	2.0	402	33.1	0.5	7.5
16	360	GR	11.6	3.8	27.0	3.2	0.3	4.9	12.7	5.1	11.1	0.3	0.0	6.7	7.0	0.0	3.2	1.1	0.0	2.2	371	50.7	4.3	11.3
17	364	GS2	2.7	0.7	18.2	0.0	0.2	2.4	9.4	5.8	3.9	0.0	0.0	5.3	4.1	44.6	1.0	0.5	0.0	1.2	413	24.2	1.5	3.9
18	367	GS3	1.9	0.3	6.7	0.0	0.0	1.1	10.3	3.9	5.3	0.0	0.0	2.5	4.7	60.7	1.1	0.6	0.0	0.8	359	10.0	1.7	5.3
19	373	PGS	4.8	1.7	9.3	1.1	0.0	2.8	13.8	11.8	14.0	3.4	0.0	2.5	7.6	22.8	1.1	0.3	0.0	3.1	356	19.7	1.4	17.4
20	379	PGS	4.8	1.5	8.0	0.9	0.0	3.9	16.7	10.1	6.8	2.1	0.3	5.7	3.3	33.6	0.6	0.9	0.0	0.9	336	19.0	1.5	8.9
21	384	PGS2	8.6	2.6	14.1	0.0	0.0	0.9	10.1	5.2	12.7	5.2	0.0	7.8	6.9	23.3	1.2	0.0	0.3	1.2	347	26.2	1.2	17.9
22	391	Black lens	1.8	0.6	12.3	0.3	0.0	5.8	15.3	13.2	11.7	0.0	0.0	13.5	17.5	5.2	1.2	0.0	0.0	1.5	326	20.9	1.2	11.7
23	397	RGS	20.3	1.1	22.3	0.6	0.0	2.9	10.6	9.5	1.1	0.0	0.0	8.6	9.5	1.1	7.7	0.9	0.3	3.4	349	47.3	8.6	1.1
24	403	LBG	1.2	1.8	20.9	0.0	0.0	3.3	10.0	6.7	17.6	0.3	0.3	4.5	27.6	0.0	4.5	0.0	0.0	1.2	330	27.3	4.5	17.9
25	411	LBG2	12.5	1.8	14.0	0.0	0.0	2.7	15.5	16.7	7.8	0.6	0.0	11.6	8.7	3.6	2.4	1.2	0.0	0.9	335	31.0	3.6	8.4
26	420	LBG3(ii)	24.9	4.1	17.3	1.5	0.0	0.0	11.5	4.3	2.0	0.3	0.0	6.6	10.9	2.3	2.5	0.8	0.0	10.9	393	47.8	3.3	2.3

A further illustration of select phytolith micrographs of eudicot species from South African woody taxa discussed in the text

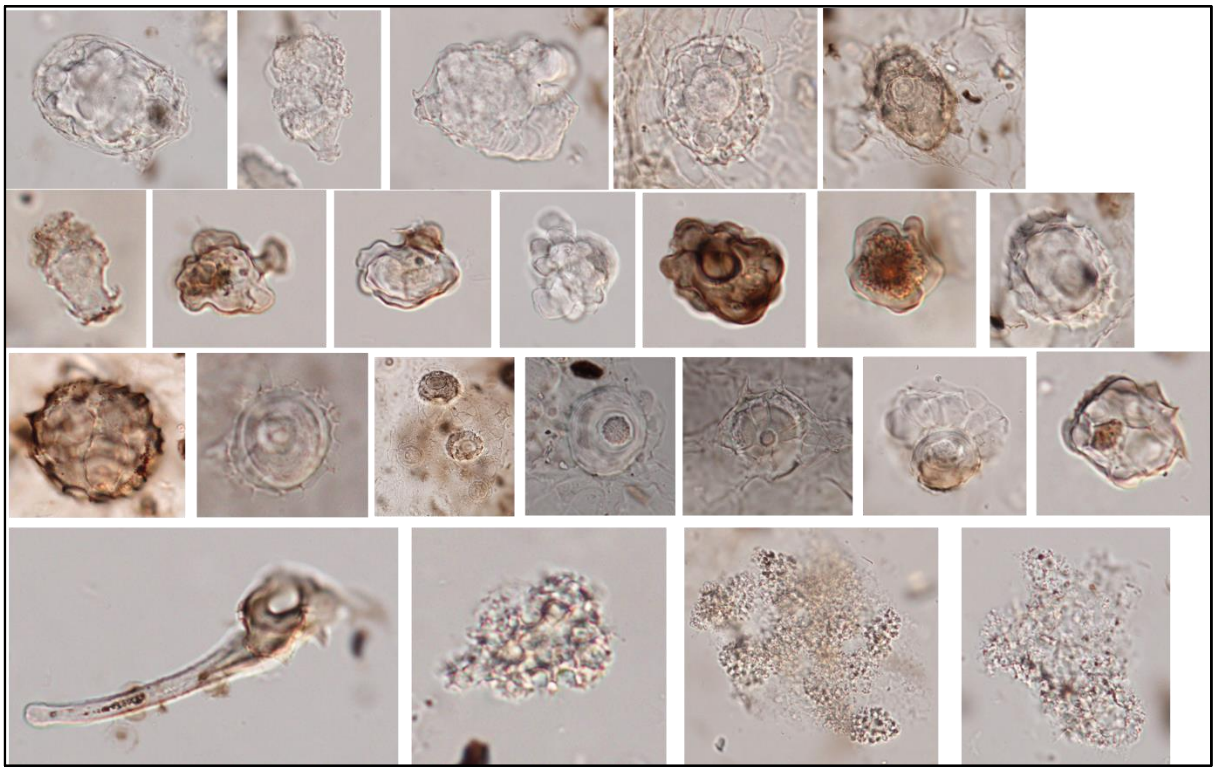
a) *Acalypha glabrata*



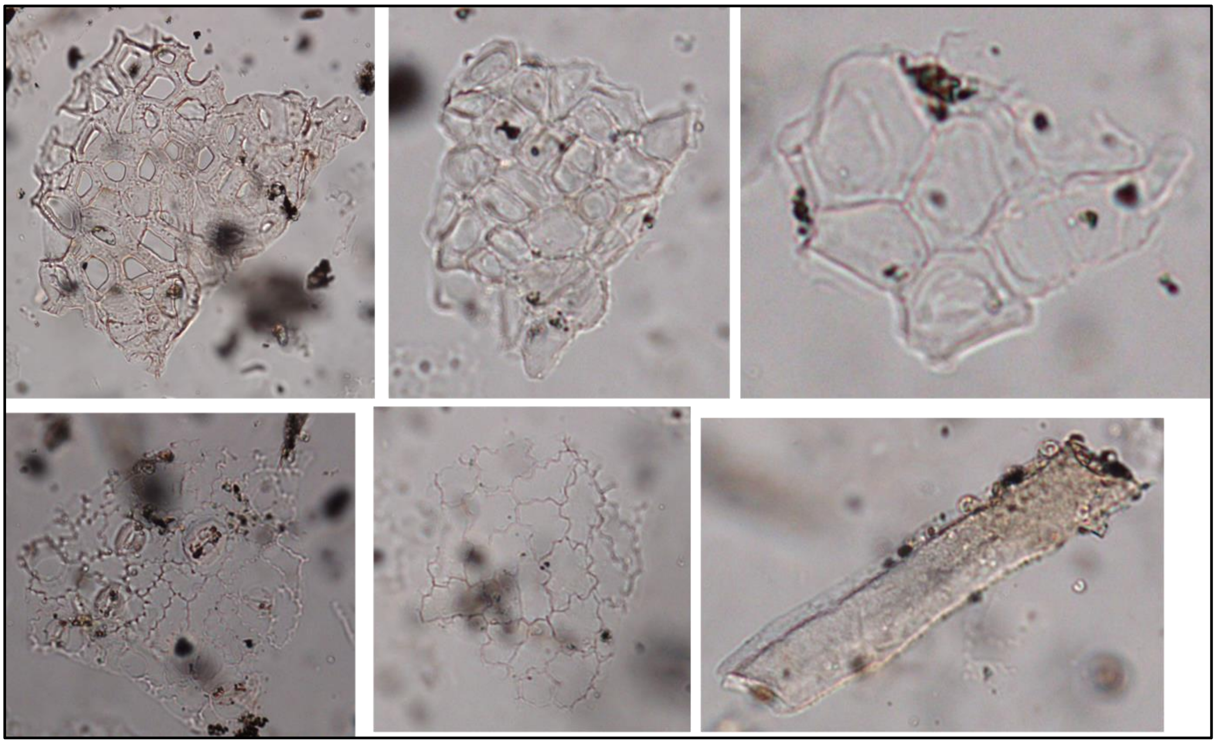
b) *Brachylaena discolor*



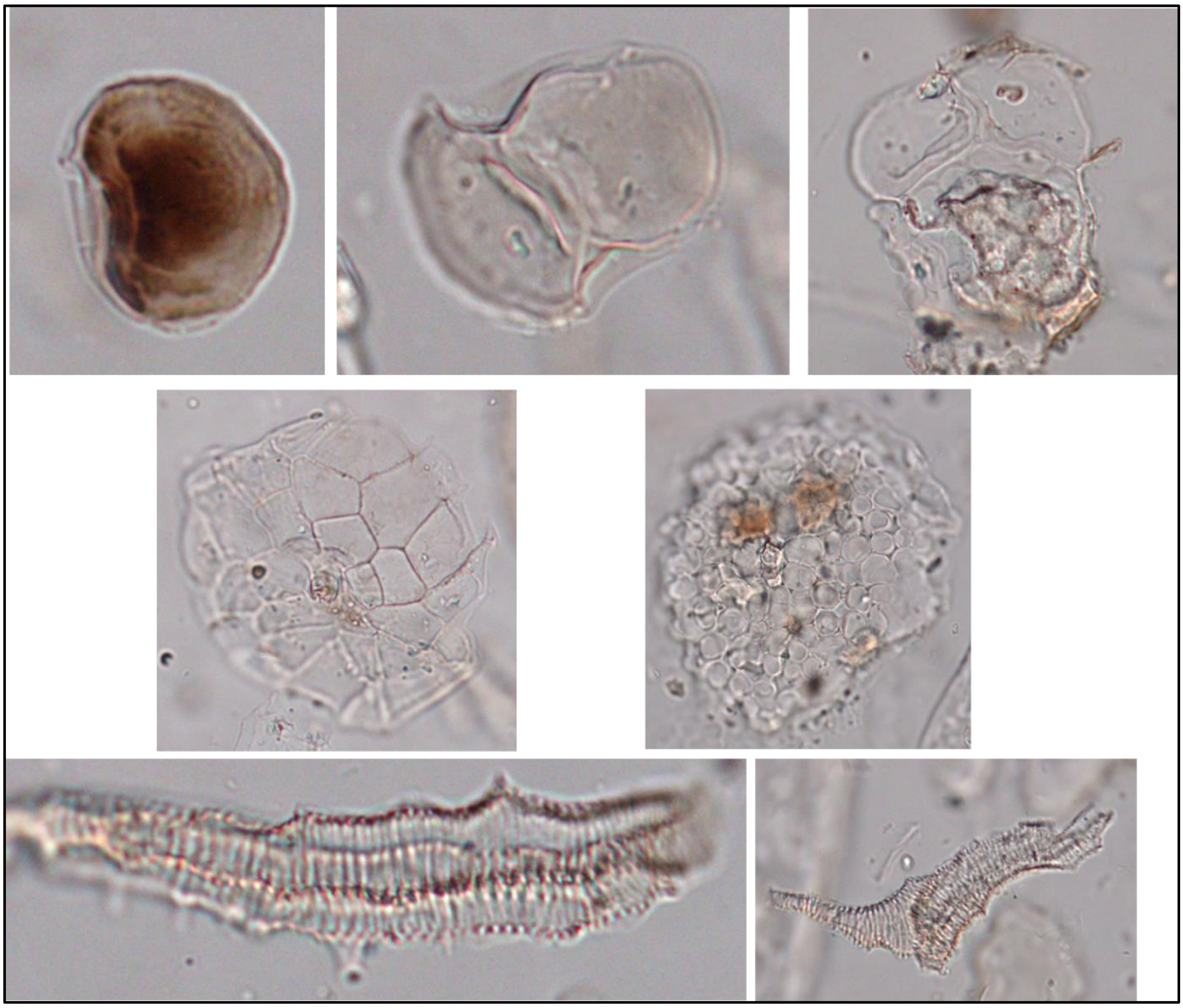
c) *Celtis africana*



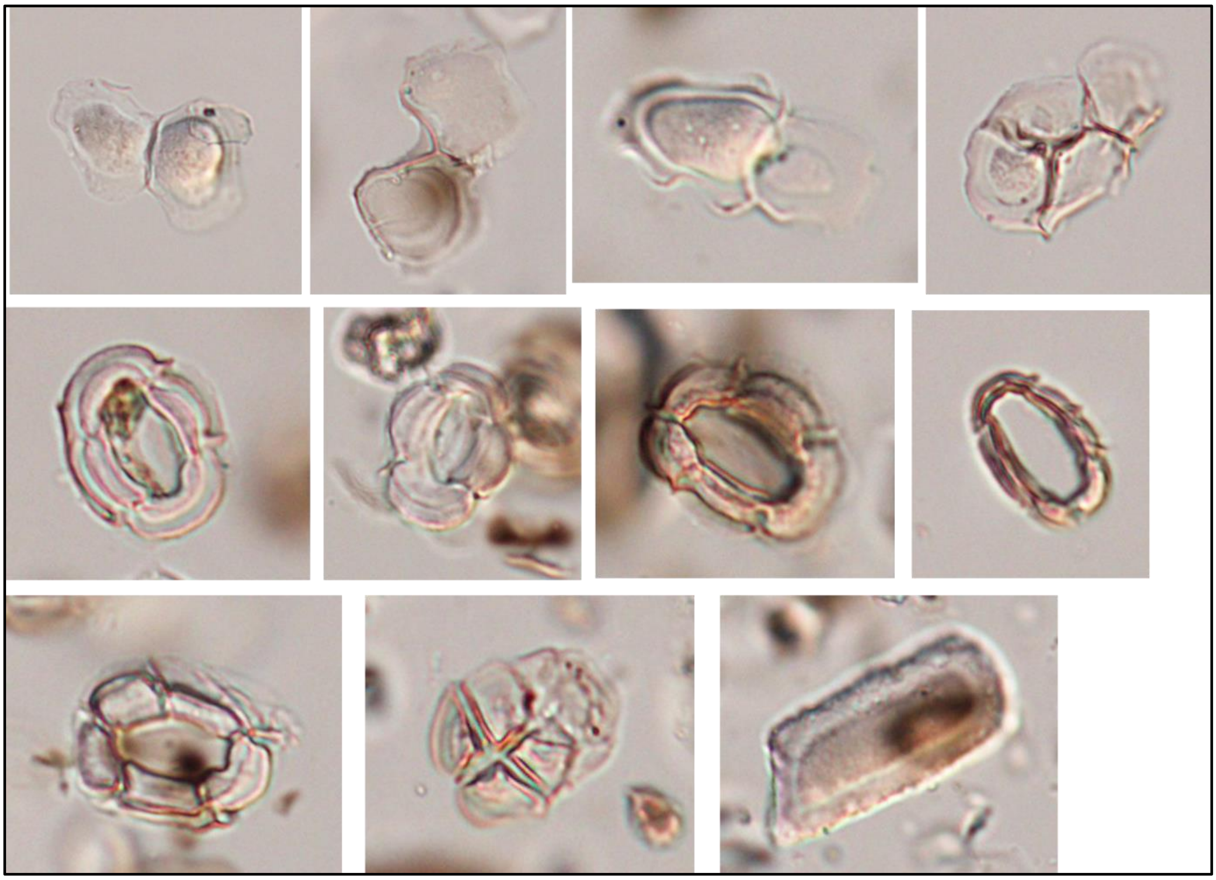
d) *Celtis mildbraedii*



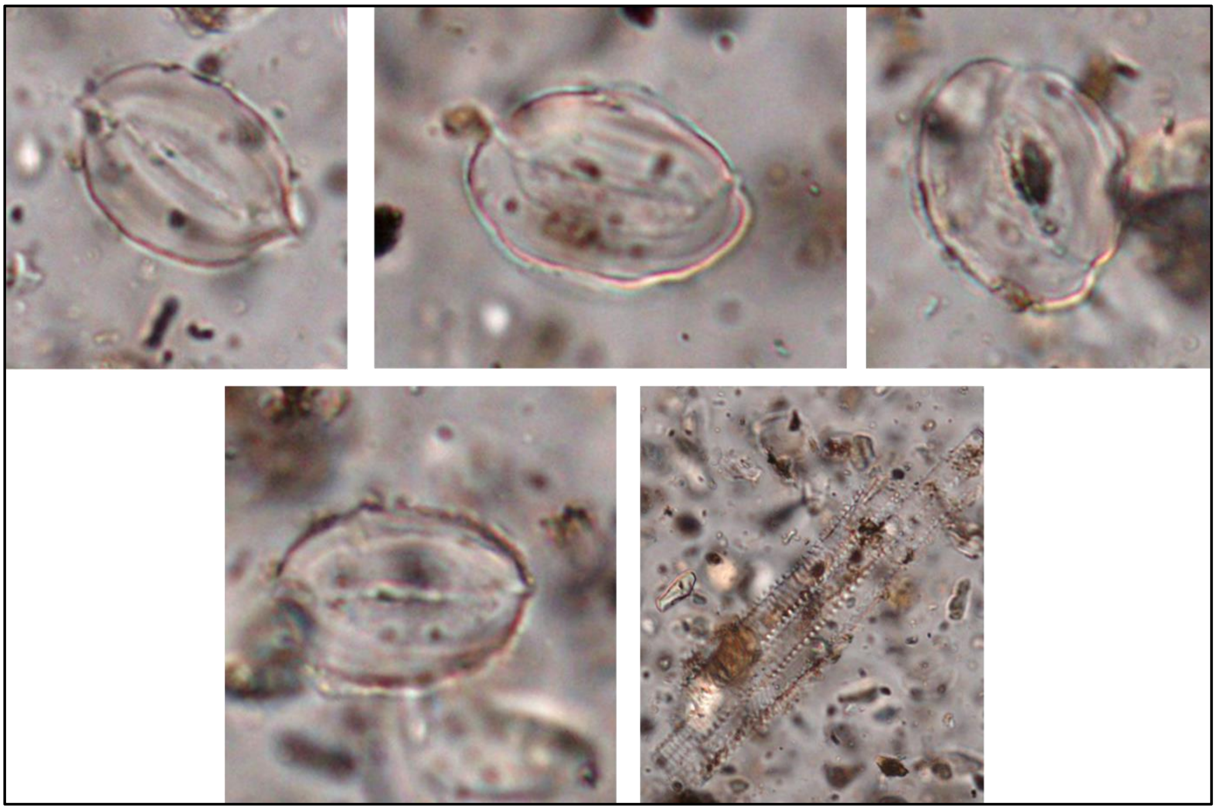
e) *Clutia pulchella*



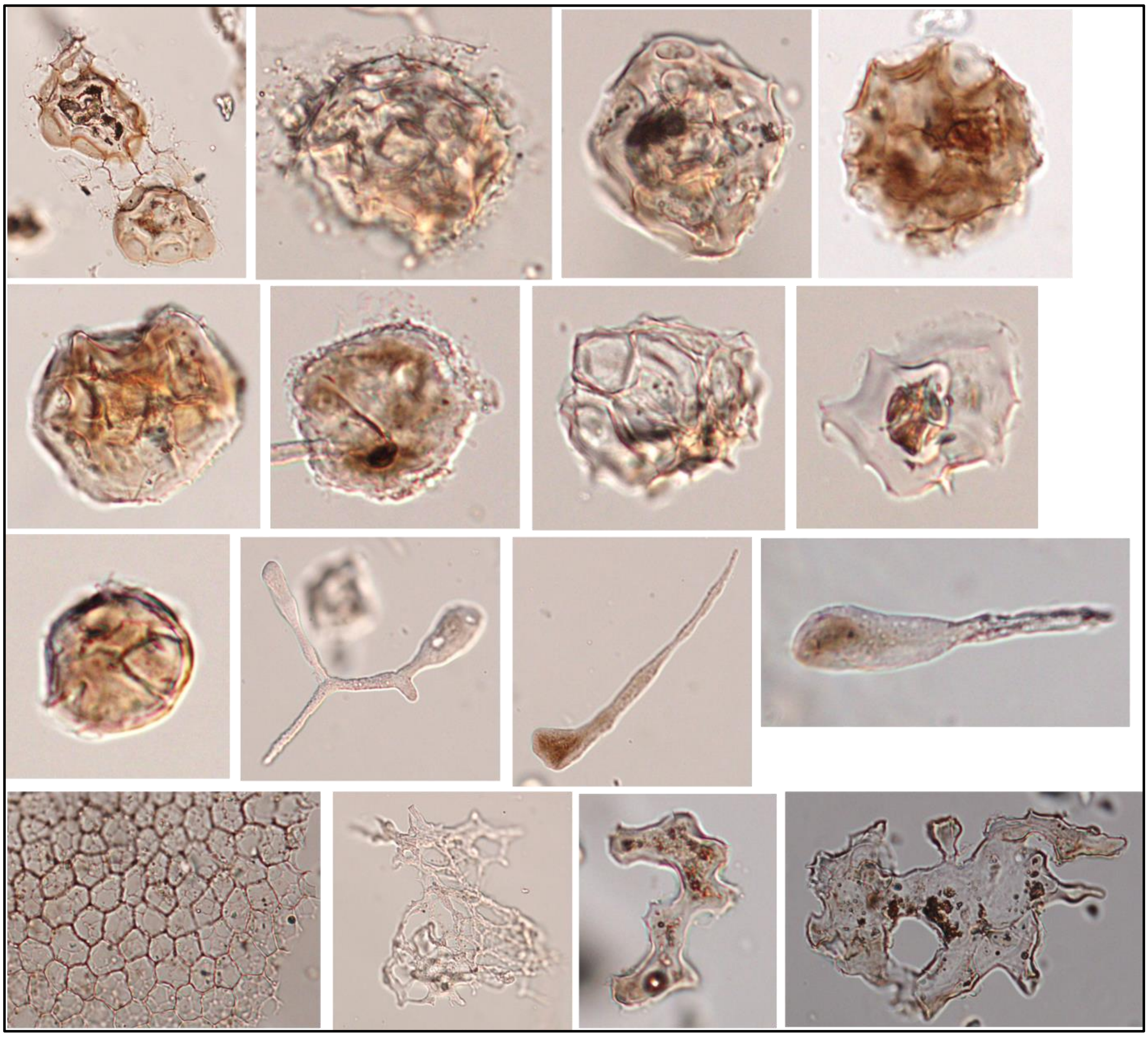
f) *Deinbolia oblongifolia*



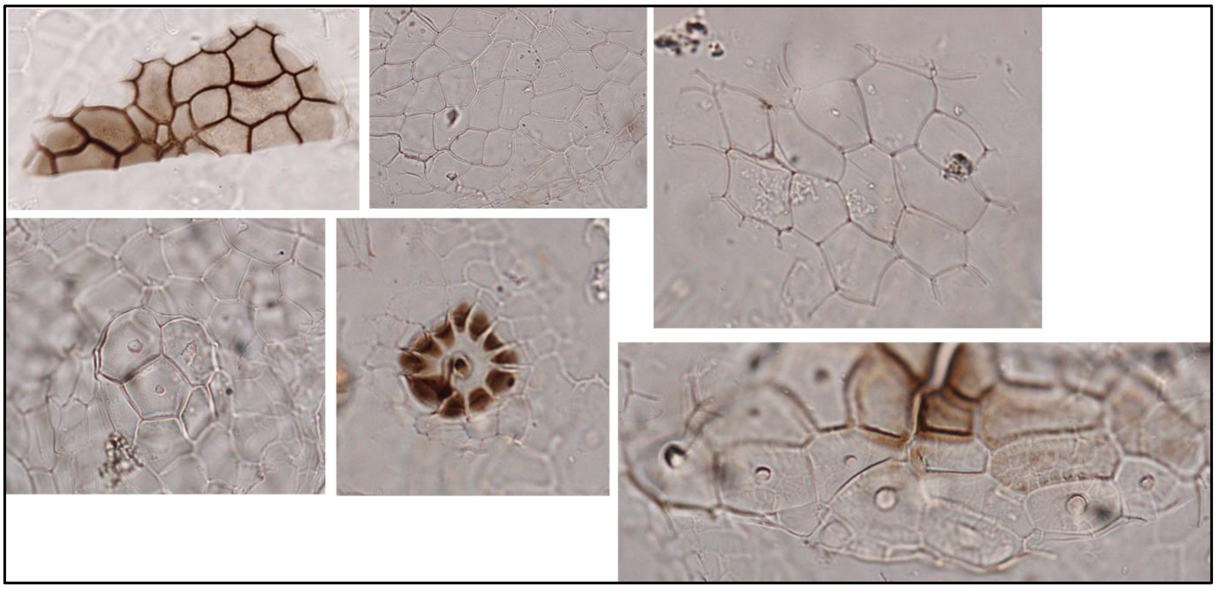
g) *Dichrostachys cinerea*



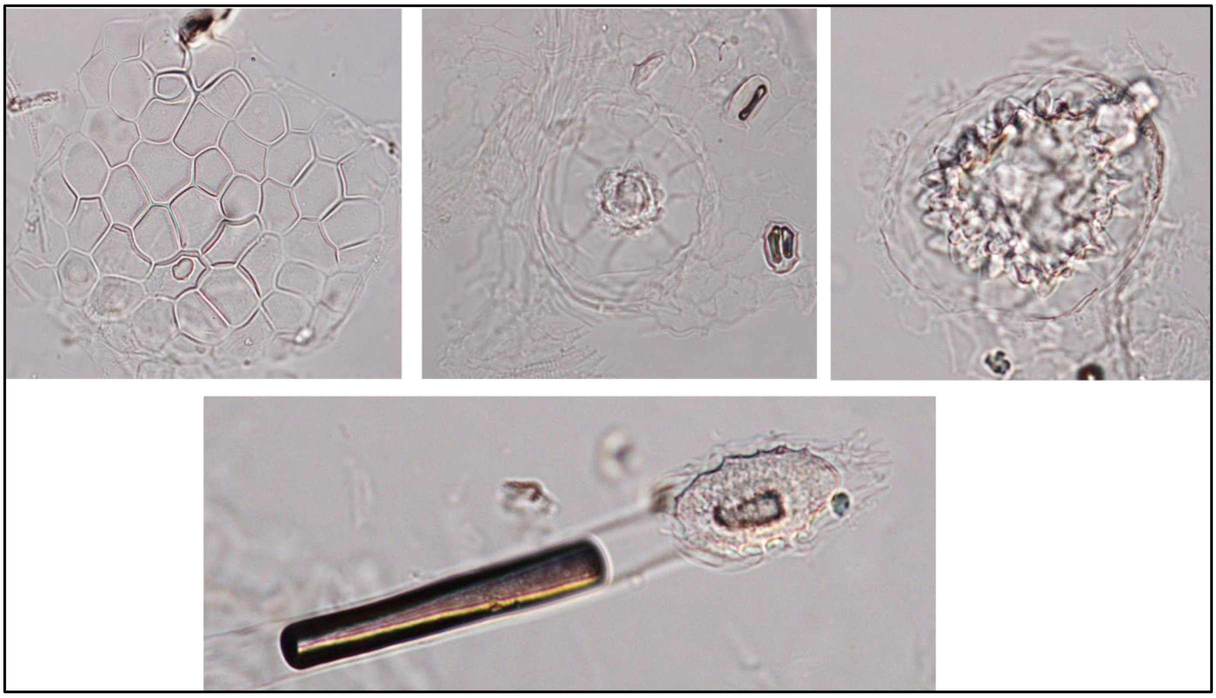
h) *Eugenia capensis*



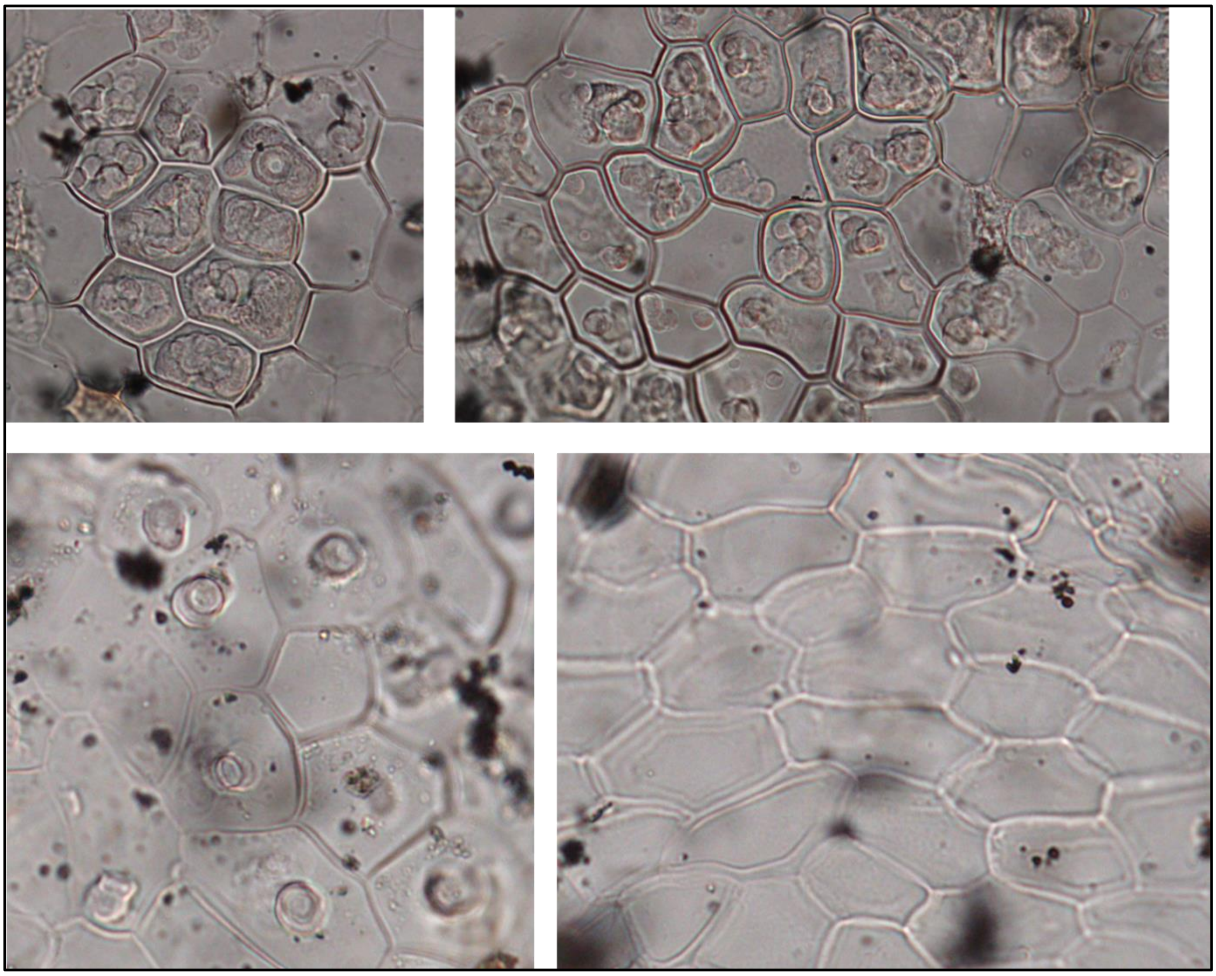
i) *Ficus ingens*



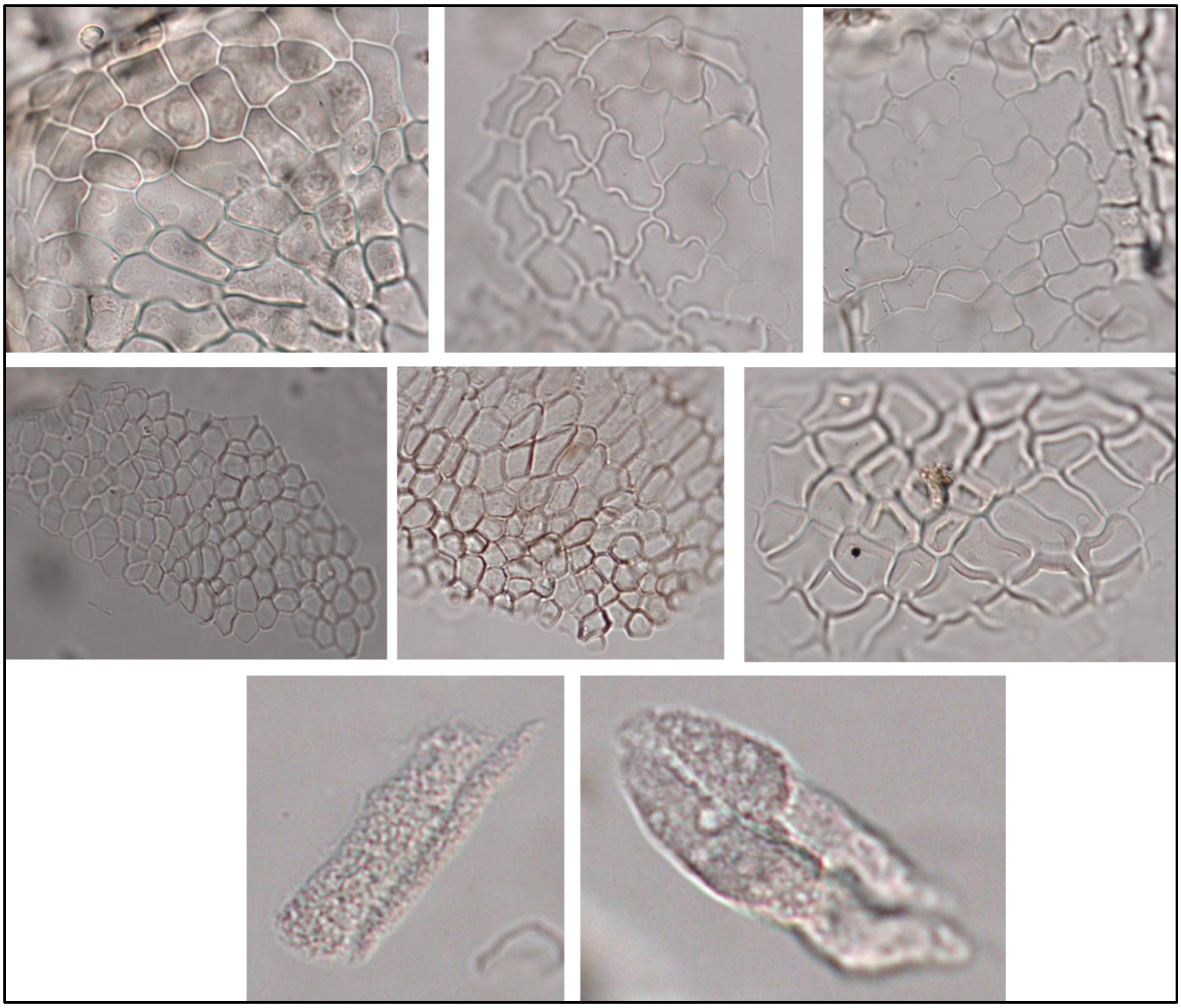
j) *Ficus sur*



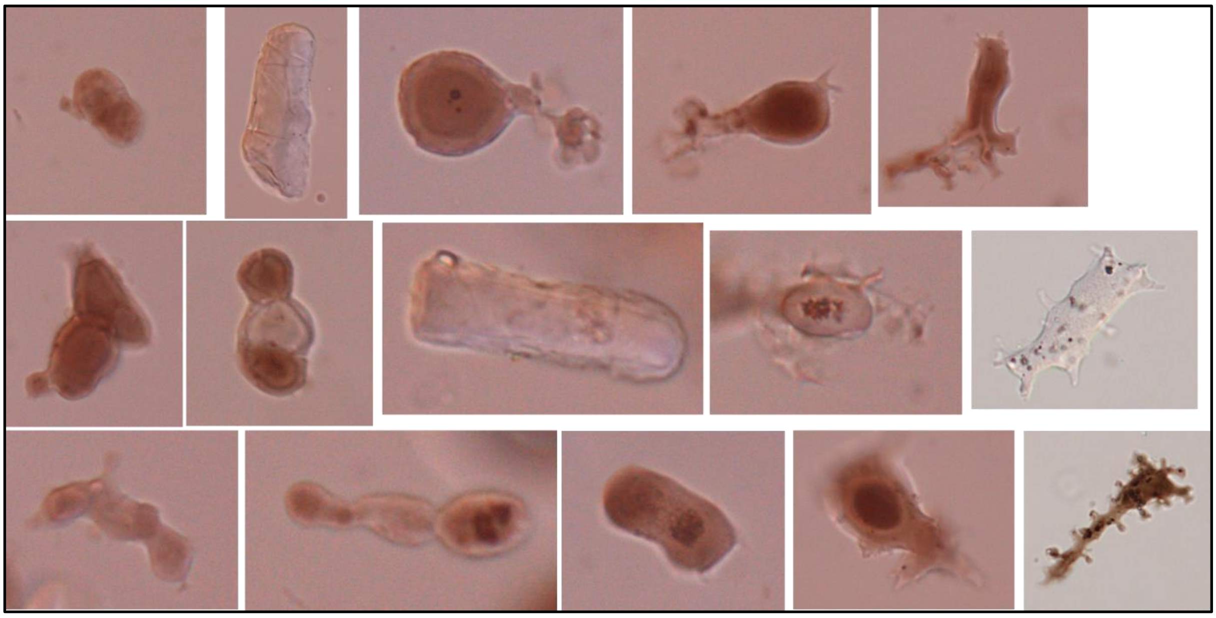
k) *Ficus* sp.



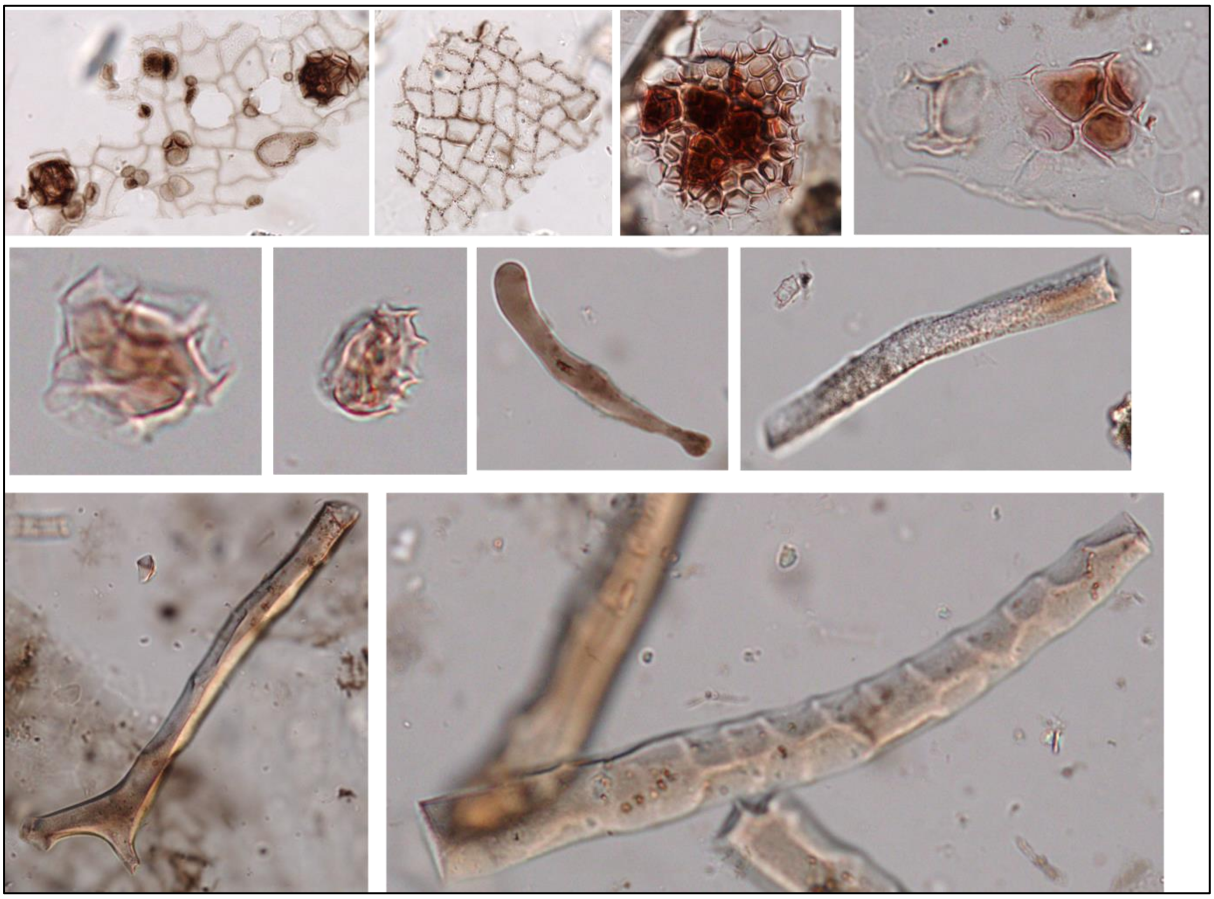
l) *Milletia grandis*



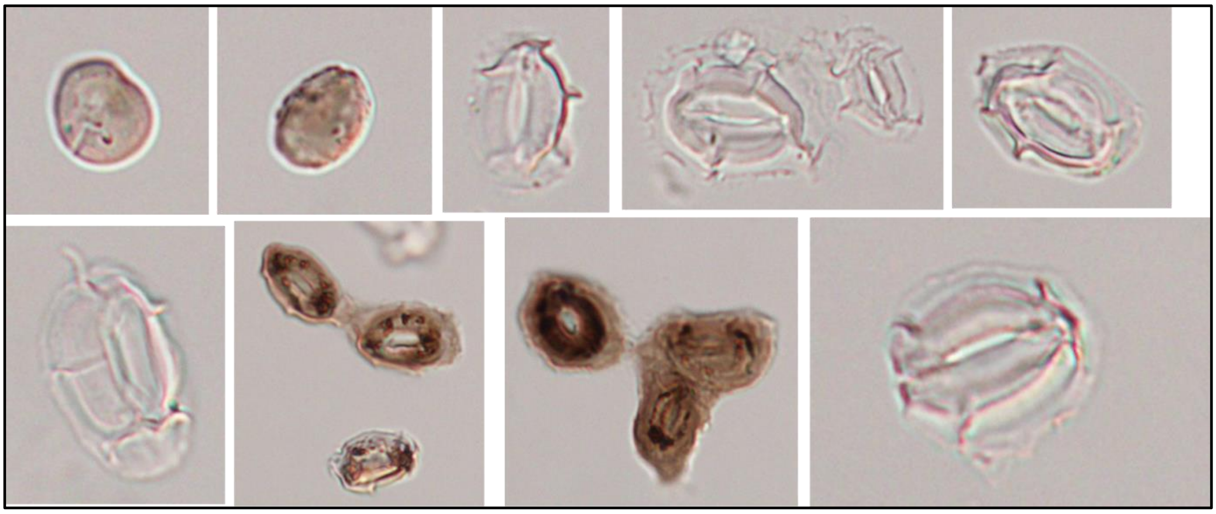
m) *Podocarpus latifolius*



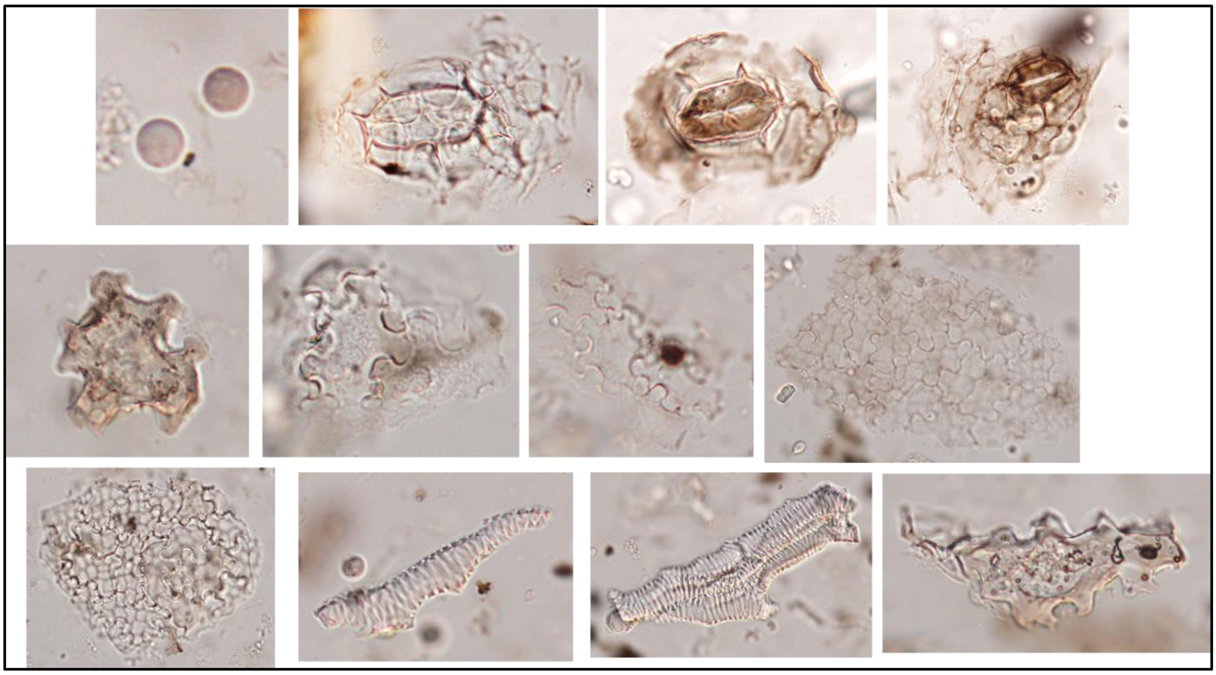
n) *Rawsonia lucida*



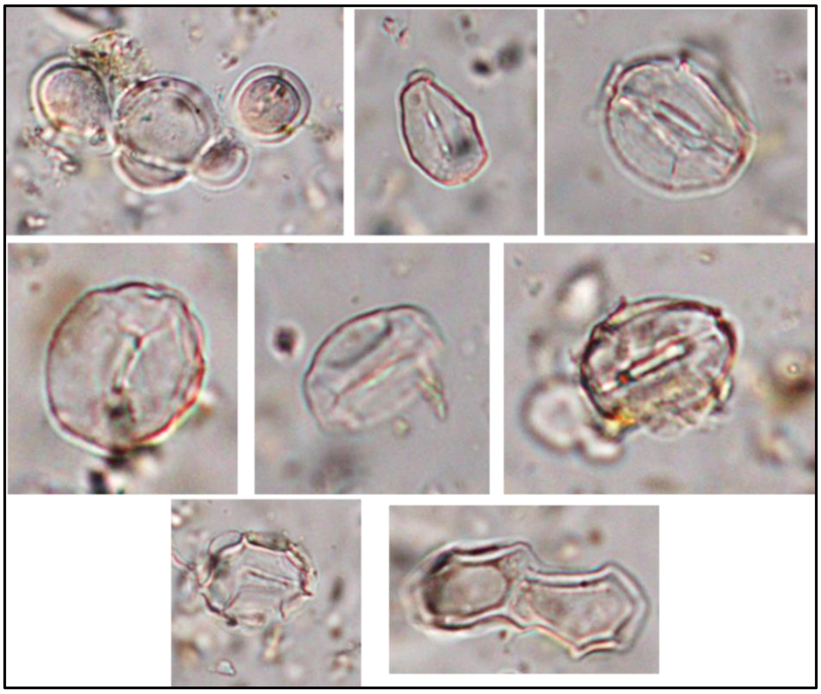
o) *Tabernaemontana ventricosa*



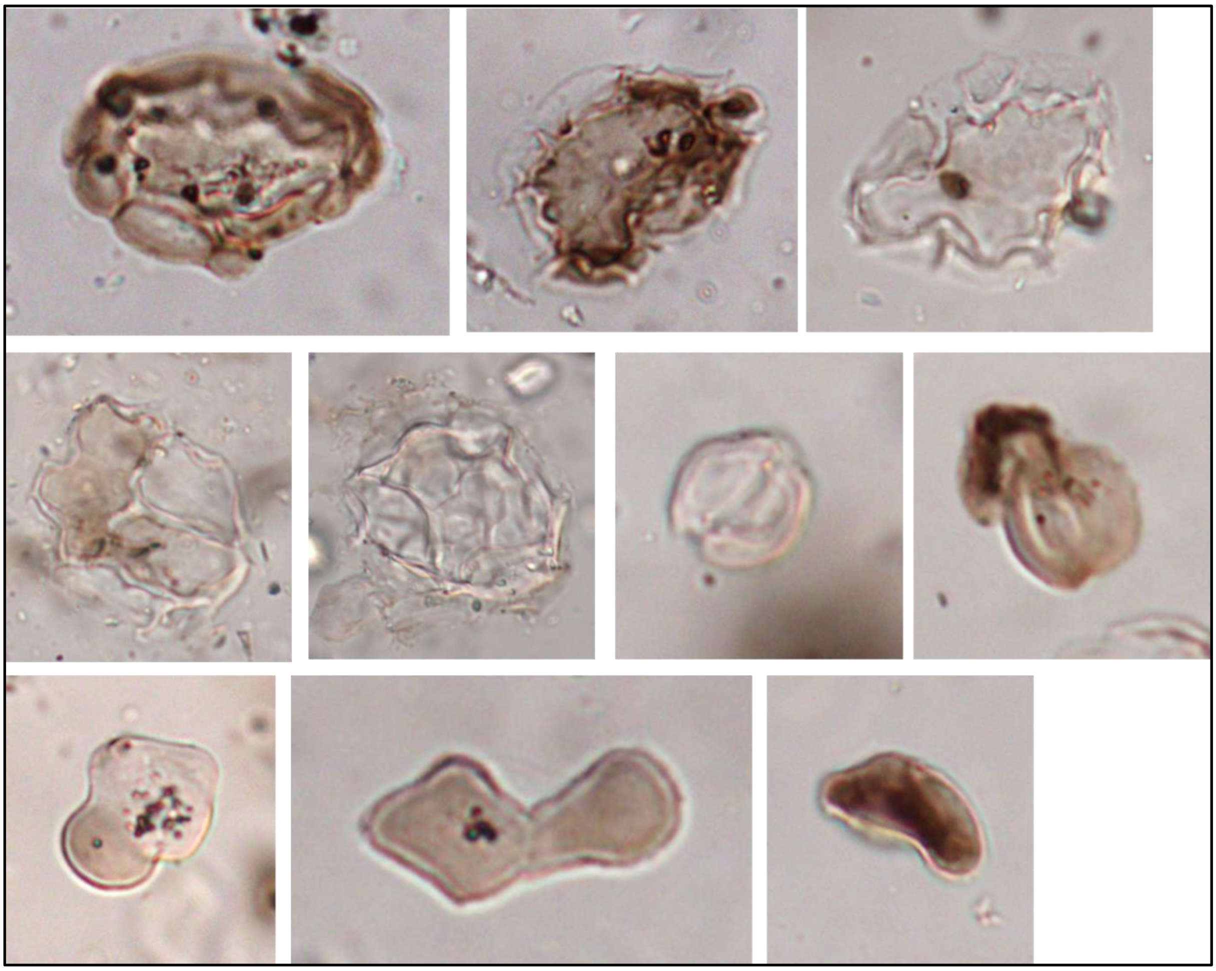
p) *Trichillia emetica*



q) *Vepris lanceolata*



r) *Syzygium cordatum*



s) *Macaranga capensis*