Late Quaternary Palynological Studies at Lake St Lucia, KwaZulu-Natal

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Mkuze wetland, KwaZulu Natal

A Thesis submitted in fulfilment of the academic requirements for the degree of Doctor of Philosophy

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Declaration

I hereby declare that the scientific work described in this Thesis is my own work, except otherwise acknowledged. It was conducted at the Evolutionary Studies Institute under the supervision of Prof. Marion Bamford and Dr Frank Neumann for the purpose of acquiring a degree of Doctor of Philosophy in Science at the University of the Witwatersrand. This is my original work and has not been submitted previously to any University for the purpose of obtaining any degree.

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Abstract

Palynological studies were done on lacustrine sediments deposited during the last ~6300 and about ~2000 cal yrs BP in Mkhuze Swamp, which drains into the most northern part of Lake St Lucia located in the Indian Ocean Coastal Belt Biome of KwaZulu-Natal, eastern South Africa. The aim was to reconstruct the past vegetation and to infer past climate fluctuations as well as human disturbances to complement growing evidence from other disciplines about these questions in the area. Following standard palynological methods, samples from two cores Mkhuze River Delta (MKD-1, long core) and Mkhuze swamp (MK24-1, short core) were extracted and analyzed. Palynological results for both cores show a dominance of Poaceae (20-90%) suggesting a strong influence of grassy woodland savanna. *Spirostachys* pollen dominated the arboreal spectra of the pollen profile in MK24-1, but it dominated the arboreal pollen spectra for the last 2600 cal yrs BP in MKD-1 as *Podocarpus* pollen dominated the arboreal spectra from 6300-2600 cal yrs BP indicating a change from a forested environment to a more open woodland environment. The results also show that the mid Holocene was humid with high precipitation and high sea level while the late Holocene was warm, dry with Marine influence (more sea water flowing into the lake due to high evaporation and low fresh water supply caused by drought). Similar pollen fluctuations were observed in records from Lakes Eteza and Sibaya also located within the Indian Ocean Coastal Belt Biome. The presence of *Pinus* pollen at the top of the profiles suggests the onset of European settlement when pines were introduced for timber production. Other published pollen records from the region in the last ~7000 cal BP show a general trend from a mesic forested environment towards an open woodland environment with grasses which is due to climate change.

Key words: Holocene, Indian Ocean Coastal Belt Biome (IOCB), Lake St. Lucia, Mkhuze Swamp, Paleovegetation, Climate change, Human activities

Dedication

This work is dedicated to Professor **Margaret Bassey** and the many community women who have inspired me and helped make me the successful person I am today.

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My heartfelt gratitude goes to my two supervisors, Prof. **Marion Bamford**, and Dr **Frank Neumann.** They have encouraged, challenged, and supported me throughout this degree and have developed my academic writing. I am privileged to be mentored and guided by them. Without their mentorship, accompanied with patience and understanding, I wouldn’t be here today. They have both given me wings to fly and for that I am sincerely grateful.

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Chapter 1

Introduction

1.0 Background

Quaternary palynological studies have been carried out in South Africa and southern Africa at large and these studies involve the use of palynomorphs (pollen grains and spores) in the reconstruction of past vegetation and inferences of climate (Meadow, 2015). The study of past climate provides an important perspective for assessing the potential impacts of future climate on vegetation and other natural systems and it is important because humans and other organisms depend on these natural systems. Palaeoenvironment/palaeoclimate studies use geological and biological data (evidence) preserved in sedimentary archives (peat, bog, lakes) and other archives to reconstruct the past environment and climate (Neumann *et al*. 2010, 2008; Finch and Hill, 2008; House *et al*., 2022; Strobel *et al*., 2022).

Historically, Quaternary palynological studies started in the northern hemisphere where their environmental conditions are favourable for the preservation of palynomorphs (Meadows, 2015). The southern hemisphere started much later and in southern Africa, these studies began with van Zinderen Bakker in the late 1940's. He explored different sediment samples such as pan sediments, cave sediments and even coprolites and this was due to the paucity of suitable sedimentary environment and continuous lake and peat deposits in the southern hemisphere (Meadows, 2015; Scott and Lee Thorp, 2004).

In recent times, a few Quaternary palynological studies have been carried out in the different biomes in South Africa including the Indian Ocean Coastal Belt Biome (IOCB) which includes sites like Lake Eteza, Lake Sibaya (Neumann *et al*. 2010, 2008), the Mfabeni peatlands (Finch and Hill, 2008), Port Durnford (Scott *et al*., 1992; Ochadleus *et al*. 1996) and coastal areas of southern Mozambique (Ekblom, 2008; Ekblom *et al*., 2014) which are part of the IOCB.

Mazus (2000) studied a *Podocarpus* pollen sequence in Maputaland (IOCB), South Africa during the Quaternary which gives clues to the history of *Podocarpus* forest and concluded that there was a northward migration of *Podocarpus* forest along the Maputaland coastal plain during the Holocene. Neumann *et al.* (2010), in a study investigating core sediments at Lake Eteza which span c. 10 000 years, reported that the increase in forest trees (*Podocarpus*) in the mid Holocene was due to high sea levels, and the decrease in *Podocarpus* during the late Holocene and corresponding increase in Amaranthaceae and grasses coincide with a return to lower sea levels and drier conditions. Finch and Hill (2008) studied a pollen sequence from the Mfabeni peatland close to St. Lucia covering > 40 000 years. There is only one radiocarbon date for the Holocene and therefore the chronology is not robust. Finch and Hill (2008) reported that forest growth and expansion during the Holocene Altithermal (~8000–6000 cal BP) indicates warm, relatively moist conditions. The authors interpreted a mid-Holocene *Podocarpus* decline as evidence of deforestation during the mid-Holocene and that it is supported by the appearance of *Morella serrata,* suggesting a shift towards more open grassland/savanna, possibly due to burning. Neumann *et al.* (2008) in their study at Lake Sibaya suggested that the middle Holocene had warm humid condition while the early Iron Age had a moister climate. The increase in algae and Cerealia pollen from 300-150 years cal BP might reflect human activities. These studies show the Quaternary vegetation dynamics and changes of the different vegetation units in the IOCB but there is a shortage of Holocene climate history records in the region. This is not only due to a paucity of continuous lake and peat deposits but also to poor pollen preservation within the region’s Quaternary deposits (Scott 1984). Hence, late Quaternary palaeo-environmental studies of Lake St Lucia, in comparison with other palynological sites in the region, will further help to better understand not only the past vegetation but also the past climate of the Indian Ocean Coastal Belt Biome.

Also, from the previous palynological studies carried out in the IOCB, it can be seen that there is a wealth of palynological and ecological information on the IOCB Biome yet not a single fossil or modern pollen atlas of the region exists. Few other pollen atlases for South Africa exist, for example Scott (1982) produced a photographic record of 140 types of fossil palynomorphs from pollen analyses of spring deposits in the savanna biome with short discussions of their possible environmental indications, but no morphological descriptions. Scott (1982) focused on the palynoflora from the savanna biome hence the information is limited to that biome, e.g., many forest pollen taxa such as *Isoglossa*, or Arecaceae (*Phoenix*), as well as coastal vegetation like mangroves, are not represented. Van Zinderen Bakker (1953, 1956, 1959) published a series of descriptions of pollen grains and spores in South Africa, but the illustrations are pencil drawings, and the books are not easily accessible. Chevalier *et al*. (2022), discussed the climate sensitivities of 140 most abundant pollen morpho types from southern African Quaternary palaeoecological investigations. However, this information relies on only the Global Biodiversity Database Facility for parent plant distributions of pollen types to determine their climatic implications for reconstructions using the CREST method (Chevalier *et al*. 2014; Chevalier, 2022). They did not provide any photographs or give any information regarding other palynomorphs or non-pollen palynomorphs (NPP's) like cryptogam spores, fungal remains, algal cysts, etc.

Excellent pollen atlases for other regions in Africa, however, do exist. For example, for tropical West Africa (Gosling *et al.*, 2013), East Africa (Coetzee 1967; Riollet and Bonnefille, 1976; Schüler & Hemp, 2016) and Northern Africa (Reille, 1998, 1999). For individual countries, they include: (i) Chad (Maley, 1970), (ii) Ethiopia (Bonnefille, 1971a, b), (iii) Ivory Coast (Ybert, 1979), (iv) Madagascar (Straka, 1964-1983, 1983-1989), (v) Nigeria (Sowunmi, 1973,

1995) and (vi) Sudan (El Ghazali, 1993). In addition, there is an online African Pollen Database www.geo.arizona.edu/palynology/apd.html, (Lezine, 2005; Vincens *et al*. 2007) which has been re-launched recently https://africanpollendatabase.ipsl.fr/#/pollen-atlases. Other studies include the pollen dispersal qualities (Hamilton 1972, Hill *et al*. 2021), which depend on pollination mechanisms for which more data are required to refine palaeo-ecological interpretations in the future. In view of a demand for palaeoclimate studies to document the variation of fossil palynomorphs in sedimentary archives, their associated regional vegetation types, and their climatic implications during the Holocene, there is a need to create more especially regional fossil pollen atlases. From this study, we present a pollen atlas for the IOCB collating data from several sources. This will help Quaternary palaeo-ecologists in the region and in southern Africa at large, to identify palynomorphs and interpret ecological conditions.

This project is part of a broader project to study the vegetation and climate of southern Africa over the past ca 4 million years, i.e., since the evidence of humans in this part of Africa, and the evolution of the modern vegetation and biomes. It is particularly embedded in the German-South African project Tracing Human and Climate impacts in South Africa (TRACES), which focusses on investigating different proxies like biomarkers, chemical signatures of sediments and pollen, on the analyses of the combined effects of climate change and recent anthropogenic impacts on aquatic and terrestrial ecosystems in southeastern Africa during the last 250 years. Tracing Human and Climate Impacts in South Africa (TRACES) project number: 03F0798A is coordinated by Enno Schefuss and Mattias Zabel from the University of Bremen and sponsored by the German Federal Ministry of Education and Research (BMBF, Bonn, Germany). Other proxies are currently being investigated as some results are yet to be published.

Table 1: Summary of Vegetation dynamics and climate inferences in Palynological Sites in the IOCB

	Southern Mozambique (Nhaucati lake) Mozambique) Ekblom (2008)		Coastal forest and Miombo woodland of Vilankulo (Mozambique) Ekblom *et al*. (2014)		Mfabeni Peatland Finch and Hill (2008)		Lake Eteza Neumann *et al*. (2010)		Lake Sibaya Neumann *et al.* (2008)	
Age (cal ka/ka BP)	Vegetation dynamics	Climate inferences	Vegetation dynamics	Climate inferences	Vegetation dynamics	Climate inferences	Vegetation dynamics	Climate inferences	Vegetation	Climate inferences
0-250	Moraceae, *Celtis*, T*rema* and *Dialium* type declined by 5-10% *Alchornea* and *Cassine* types are in higher number.	Drought during the little ice age at Ca. 550 cal. yrs BP	Herbs and aquatic increased while grasses declined also, *Brachystegia* declined and disappeared	Cold dry periods			Neophytes, Poaceae, *Protea, Cliffortia*	Climate change induced by human activities and the onset of little ice age in Ca. 700 cal. yrs BP	Neophyte, *Zea mays*, Ericaceae grains	Climate change induced by human activities
250-550									*Spirostachys*, *Celtis*, *Stoebe*, *Manilkara* and *Rhus*	Humid climate
550-800	*Alchornea* type, Savannah is moderately represented by *Sclerocarya*, grassea and sedges also have their peak	Warm period	Increase in tree/shrubs and Cyperaceae, N*ymphaea*, *Typha* (riparian forest)						*Phoenix*, *Hyphaene*, monolete spore, Poaceae	
800-1200	Forest and riverine forest vegetation (*Celtis,Dialium* type, Moraceae and *Trema)*	Warm period	Myrtaceae (*Syzygium* and *Eugenia*), *Phyllanthus*, *Nymphaea*, *Brachystegia* is				*Phoenix*, Poaceae and Asteraceae	Drier, continued gradual decrease of SST, Sea levels drop.	*Olea*, *Manikara*, *Celtis*, *Bruguiera*	

			represented in low numbers.					Mangrove swamp forest decline		
1200-1600	Asteraceae, *Nymphaea* (dry bushveld savannah vegetation)	Dry period	Sterospermum, Combretaceae, *Myrsine africana*, *Alchornea*, Moraceae, *Trema* and *Brachystegia*	Dry periods					*Podocarpus*, Moraceae, *Morella*, *Ilex* and Asteraceae	
1600-3600										
3600-4600					*Acacia*, Cyanthaceae, *Ficus*, *Morella*, Myrtaceae, *Protea*, Rosaceae, *Podocarpus* declined		*Podocarpus*, *Isoglossa*, Mangroves, Aquatic ferns	High precipitation, High SST, relatively high sea level		
4600-6800										
6800-8000							*Isoglossa*, *Olea and Phoenix* declines, Poaceae increases and *Acacia gerardii* is represented	Relatively wet Ca. 10,000 cal. yrs BP becoming dry Ca. 8000-7000 cal. yrs BP increase SST/sea level	*Phoenix*, *Isoglossa*, *Manilkara*, *Celtis*	Warm moist conditions
8000-10,200					*Podocarpus* abundant forest, Anacardiaceae, Apocynaceae, Celastraceae, Fabaceae, Rosaceae, Rubiaceae	Moist cool climate				

1.1 Other Quaternary Paleoenvironmental Studies in South Africa

Other paleoenvironmental proxies have been used in the reconstruction of vegetation and climate such as isotopes, charcoal, geochemical records and diatoms. These studies on proxies are reviewed below. Not so much has been done in the IOCB hence, this review not only covers the IOCB but also the summer rainfall region where other paleoenvironmental studies using other proxies other than palynomorphs have been carried out.

Humphries *et al*. (2020) analysed the Mkhuze river delta core (MKD-1) and reconstructed the hydroclimate in Southeastern Africa during the past 7000 cal yrs BP using geochemical proxies. The authors reported a severe phase of drought at 4700-4200 and 3700-2600 cal yrs BP which they suggested was triggered by changes in the activity of El Niño-Southern Oscillation (ENSO). Humphries *et al*. (2020) also reported that rapid shifts in moisture availability were a characteristic feature of mid-late Holocene climate across the summer rainfall region of southern Africa. Similar hydroclimate reconstruction was reported by Humphries *et al*. (2019) working on sediment composition and diatom assemblage from Lake Muzi, only that drought phases were also recorded around 2100-1400 and 850-550 cal yrs BP.

Miller *et al*. (2019) analysed sediments of the Mfabeni peatland, using stable carbon and hydrogen isotopes of plant-wax and P_{aq} to reconstruct water table changes reported that drier conditions prevailed during the past 5000 cal yrs BP.

Johnson *et al*. (1997), working on late Quaternary paleoenvironment at Equus Cave South Africa using stable isotopes and amino acid racemization of Ostrich eggshell, reported that stable Nitrogen isotope data from Ostrich eggshell indicates that at 17000 cal yrs BP, mean annual precipitation was at a minimum (190±50mm/yrs) but increased steadily to modern values around 6000 cal yrs BP (600±150mm/yrs) and remained relatively unchanged still present. The authors also reported that stable Oxygen isotopes data combined with Nitrogen isotope data indicates that paleotemperatures were at a minimum between 14000-17000 cal yrs BP and reached their maximum in the latest Holocene.

Finally, House *et al*. (2022) working on charcoal from Holocene deposits at Wonderwerk Cave South Africa reported that most recovered and identified species were those that are tolerant to hot and dry conditions which signals an arid trend during the Holocene but wetter conditions prevailed during the mid-Holocene (6200-4500 cal yrs BP).

From all this studies, it can be deduced that the mid Holocene (7000-4500) had wet conditions with lower temperatures but around 4500-2600 was characterized by severe drought and latest Holocene (2600 cal yrs BP till present) was characterized by increase rainfall and temperature but lower water table.

1.2 Southern African Climate and Vegetation

In southern Africa, the position and extent of the circum-polar vortex and land-sea pressure gradients that modulate the advection of moisture from the tropical Atlantic and Indian Ocean have resulted in varied seasonal rainfall periods (Tyson and Preston-Whyte, 2000; Chase *et al*., 2020). Eastern South Africa experiences sub-tropical summer rainfall while the southwestern region experience winter rainfall from the temperate westerly systems during the winter seasons (Lindesay, 1998; Carr *et al*., 2006). This variation in seasonal rainfall periods in turn affects the vegetation hence, southern Africa has a wide range of biomes and vegetation types (Rutherford *et al*., 2006). The winter rainfall region consists of the Fynbos biome in the west and southwest, with the Succulent karoo biome inland of this. These two biomes form the smallest kingdom of the world’s floristic kingdoms (Takhtajan, 1986).

In the summer rainfall region, the north and east of the region is home to the savanna biome which represents the southern extension of the largest biome of Africa. The summer rainfall grassland Biome which houses a vast variety of species limited to southern Africa, is poorly represented elsewhere in Africa (Rutherford *et al*., 2006). The peculiar IOCB of South Africa (my study region) represents the southernmost extent of coastal subtropical forests of the wet, tropical and subtropical seaboard of east Africa (Rutherford *et al*., 2006). The southern African desert covers a small area and occurs in the northwest part and forms the southern tip of the winter-rainfall domain of Namib Desert as well as a summer rainfall Gariep desert with affinities to the central- north part of the Namib desert (Rutherford *et al*., 2006). The Albany thicket biome consists of plant forms intermediate between Savanna, Nama-karoo and Subtropical Forest hence it represents an uncommon structural, floristic and evolutionary ancient type of vegetation in southern Africa (Rutherford *et al*., 2006). The southern Africa Afrotemperate forests are characterized by their small and patchy occurrence over the wetter parts of the winter and summer rainfall as well as interannual rainfall areas and are part of the global warm-temperate forest biome (Rutherford *et al*., 2006).

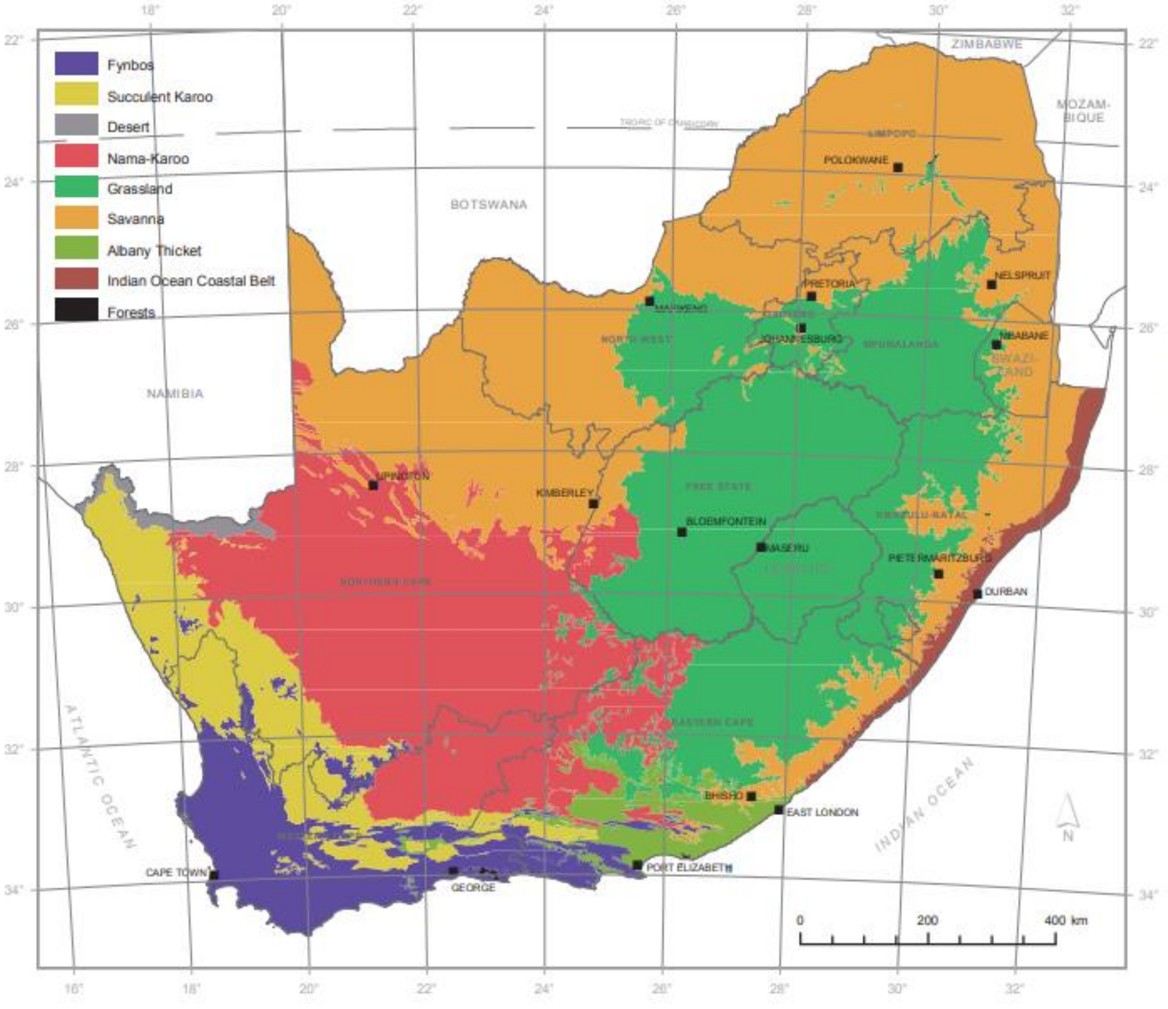

Figure 1: Map showing the Biomes of South Africa, Lesotho and Swaziland (after Rutherford *et al*., 2006).

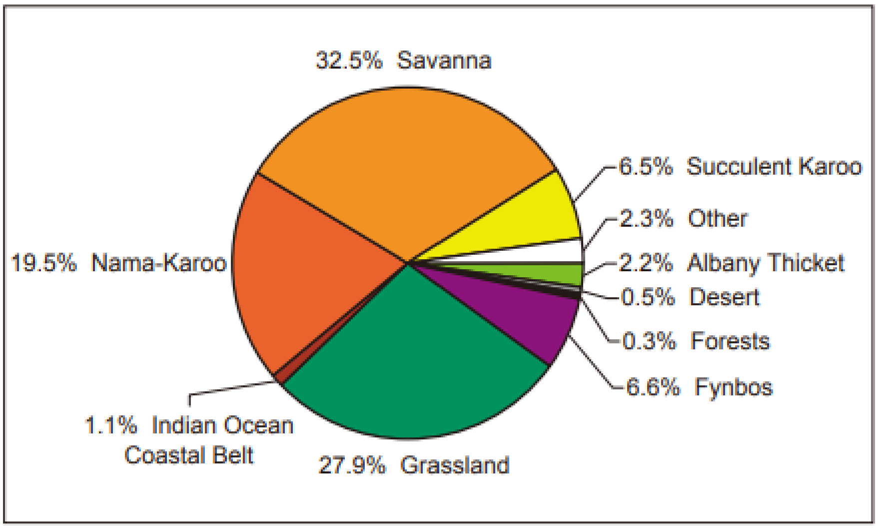

Figure 2: Percentage proportions of areas of the biomes (after Rutherford *et al*., 2006)

In view of a demand for palaeoclimate studies to document the variation of fossil palynomorphs in sedimentary archives, their associated regional vegetation types, and their climatic implications during the Holocene, there is a need to create more especially regional fossil pollen atlases. Also, Variability in rainfall in southern Africa during the late Quaternary has been debated because individual studies using different proxies give different information about the variability in rainfall, hence, there is little general agreement. Humphries *et al*. (2019a) working on the IOCB and using geochemical proxies reported series of drought phases as occurring between 4700-4200 and 3700-2600 cal yrs BP as opposed to Neuman *et al*., (2010) working in the same region (IOCB) but using palynomorphs proxies reported drought phases as occurring from 3600-700 cal yrs BP with severe drought (little ice age) occurring around 700 cal yrs BP. Finally, Miller *et al*. (2019) also working in the IOCB and using stable carbon and hydrogen isotopes of plant-wax proxies reported that drier conditions prevailed in the past 5000 cal yrs BP. Hence, there's little general agreement on the time periods when there was low rainfall leading to drought. The study of the palynomorphs in the IOCB which has a significant spatial heterogeneity as it has uneven distributions of plant species giving to its diverse ecosystems. Comparing the results with other study sites in the IOCB will give information about the late Quaternary climate variability within the IOCB and southern Africa at large. This study will also give information about vegetation types and changes in the IOCB of South Africa during the late Quaternary as climate is one of the major determinants of vegetation types. Hence, contributing to the understanding of the Quaternary paleoenvironment.

1.3 Sea level changes in Southern Africa since the Last Glacial Maximum

Cooper *et al.* (2018) using various archaeological, geomorphological, sedimentological and biological sea level indicators reported that a mid-Holocene highstand of +2 to +4m above the modern sea level is suggested between 7.3 and 6 cal ka BP. Also, between 13 and 7 cal ka BP, chronological and geomorphological evidence (submerged shoreline complexes) suggest several alternating periods of slow and rapid sea-level change (Fig. 3).

Also, Strachan *et al*. (2013) studied Sea level changes by analyzing foraminiferal from a salt-marsh peat sequence at Kariega estuary covering ~1200cal yrs BP and reported that sea level transgressed prior to 1100 cal yrs BP and the lowest record of sea level of -1±0.2m was reached between 800 and 600 cal yrs BP and that sea level has remained relatively stable after 300 cal yrs BP.

These sea level changes will affect local hydrology (water table) and vegetation. This is because a rise in sea level can bring about an increase in surface runoff from the coastal areas by raising the water table (Nuttle and Portnoy 1992). Also, as surface runoff increases, less rainfall will infiltrate into the ground and ground water discharge to the coast will also decrease (Nuttle and Portnoy 1992).

Changes in water table levels in turn affects vegetation as water table and ground water is one of the key mechanisms affecting the dynamics of wetlands plant ecosystems (Ridolfi *et al*., 2006) and tropical dunes (Moreno-Casasola and Vázquez, 1999). Also, emphasis have been made by numerous authors about the importance of water table dynamics on species composition and distributions in dune systems located in the temperate regions (Ranwell 1959, 1972; Burdick and Mendelssohn 1987; Olff *et al*., 1993; Boorman *et al*., 1997; Grootjans *et al* 1998; Moreno-Casasola and Vázquez, 1999) and on wetlands (Wierda *et al*., 1997; Ridolfi *et al*., 2006). Recently, Mansouri *et al*. (2021) conducted a research to check the effect of micro relief and water table on vegetation dynamics in silty loam saline soils of coastal areas of Iran and concluded that water table affects the physical and chemical properties of soil which in turn influences the vegetation structure and composition of the area.

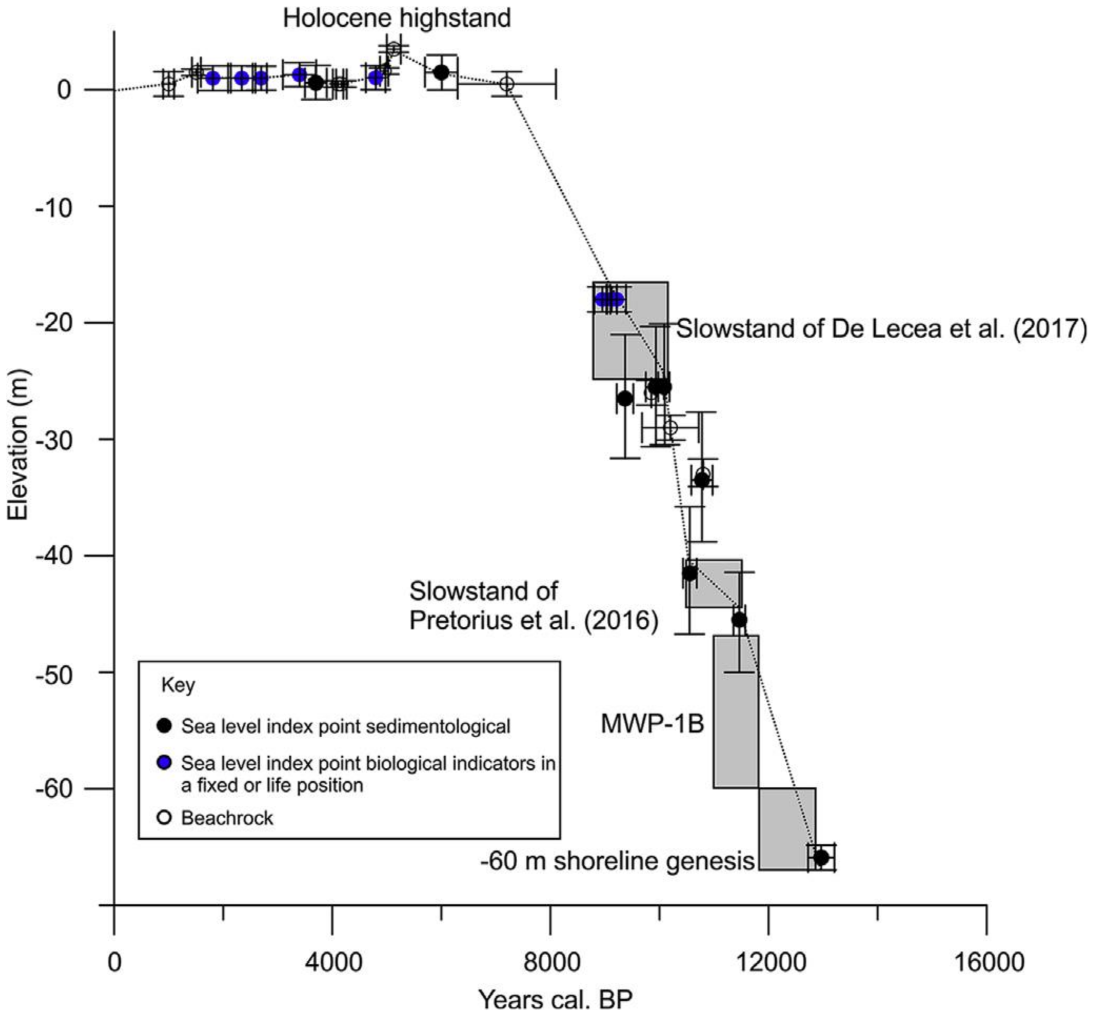

Figure 3: Sea-level curve 13 to 0 cal ka, showing index points and major stratigraphic/ sedimentological supporting evidence from the east coast of southern Africa. Grey blocks denote major sea level events recognised from the region (after Cooper *et al.*, 2018).

1.4 Palynology

This is the study of palynomorphs which are mostly pollen grains and spores.

Pollen grains are microscopic structures which bear the androecium which is a male reproductive organ in Angiosperms and Gymnosperms. It is otherwise known as the container in which the male gamete generation of angiosperms and gymnosperms are housed otherwise called the male gametophyte (Moore and Webb 1978). Spores, just like pollen, are microscopic structures of sexual or asexual reproduction in lower plants (Algae, Bryophytes and Pteridophytes) and Fungi. Higher plants, lower plants and fungi produce large quantities of pollen grains and spores but only a small portion of pollen fertilizes the ovum during pollination (Bennett and Wills 2001). Also, only a small portion of produced spores are used in reproduction, and the rest of the pollen grains and spores are dispersed and are deposited in the soil and water surfaces where taphonomic processes take place and they become part of the sedimentary records (Bennett and Wills 2001). Pollen grains and spores are usually well preserved and oftentimes retain their exine wall features because of the presence of chitin, for fungal spores, and sporopollenin which is a natural biopolymer present in the exine walls of pollen and spores of plant and is resistant to decay (Halbritter *et al*. 2018).

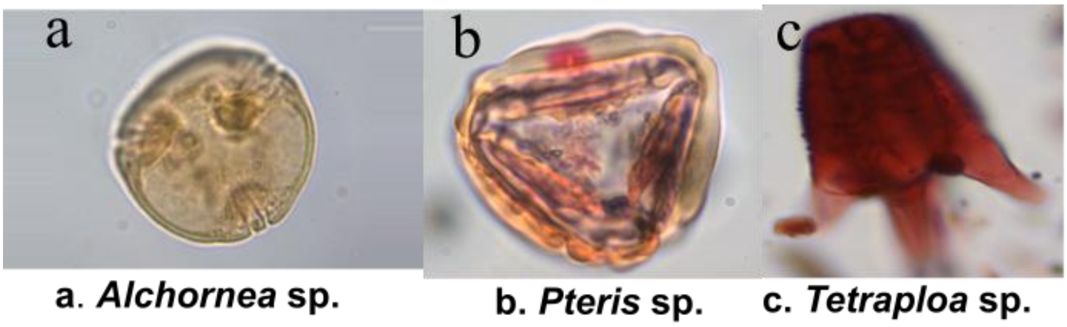

Figure 4: Examples of fossil pollen and spores from Lake St Lucia (a. is a pollen grain, b. is a Pteridophyte spore and c. is a fungal spore. see chapter 3 for more pollen and spores recovered from Lake St Lucia).

1.4.1 Pollen analysis

Pollen analysis is a scientific method that unveils the past vegetation history and climate changes (Kneller, 2009).It is also a process in which palynomorphs recovered from stratified sediments/ peat or other sources of palynomorphs such as dung are studied in order to ascertain the vegetation of the community from which they originated Pollen analysis together with stratigraphy and modern pollen-vegetation studies is, used to reconstruct the terrestrial vegetation of the past (Kneller, 2009). Pollen analysis can sometimes be referred to as stratigraphic palynology and is the most important branch of paleoecology for the late Pleistocene and Holocene (Roberts 1998).

Pollen and spores are important in paleoenvironmental studies because of the following reasons.

1. The presence of sporopollenin which makes them resistant to decay,

2. They are minute in size, dispersed to certain distances depending on their pollination mode, thus, they reflect a flora from a wider area of surrounding land and also reflect the vegetation of the environment at the time it was deposited.
3. They show vast diagnostic features that helps to delimit species.
4. They are produced in large quantities especially the wind pollinated forms; hence, a small portion of sediment is enough to recover a considerable number of palynomorphs.

after Bhattacharya *et al*., 2006, p.259

In pollen analysis, information from other disciplines such as Botany, Ecology, Geology, Archaeology, Geography and Climatology are required in order to understand and interpret results.

1.4.2 Problems and Limitations of Pollen Analysis

a. Pollen downwash through the soil (contamination): The downwash of pollen through the soil by water flowing downwards as suggested by Malmström (1922) may present a potential for contamination/error in the analysis of pollen. Sometimes, this happens when samples collected in wetlands or lakes either during or after coring. The water seeps or leaches downwards carrying palynomorphs from the top sediments down as will be seen in the short core MK24-1. It has been reported by Edrtman (1922) that the pollen downwash effect is correlative to the rate of formation of deposit and this error rarely occurs. Malmström (1923) later showed by direct experiment with *Lilium* pollen, that there is no notable pollen downwash. Nevertheless, the likelihood of such error must always be put into consideration when interpreting the presence of scattered pollen grains out of place in the general sequence of results of a regional analysis (Godwin, 1934).

b. Nature of depositional environment: Some sedimentary environments are not favorable for the preservation of pollen and spores. Sediments high in carbonate content are less favorable for pollen preservation (Groot and Groot 1966). Also, sediments with large pores such as sandy soil do not favor pollen preservation since the nature of the sediments allows for oxidation to occur hence destroying the pollen and spores.

c. Nature of palynomorphs: this really affects the identification of the palynomorphs. Strong deformation of pollen and spores in the sedimentary profile which may have been due to taphonomic or extraction processes will hinder the identification of the palynomorphs. Also, the difficulty of identification due to the complexity and similarities of pollen morphologies (Zhao *et al*. 2021). For example, Amaranthaceae are very difficult and sometimes impossible to delimit from Chenopodiaceae and these similar pollens may sometimes have different ecological zones and therefore questions the ecological deduction made. Other limitations include pollen production and dispersal agents that are not actively known. Unfortunately, there are few palynologists and not enough people (or funding) to produce comprehensive modern pollen references collections.

In summary, it is important to note that fossil palynomorph assemblages are not the exact production or representation of the detailed composition of local or regional vegetation but that they often reflect their essential characters.

1.5 Regional setting and study site

Samples were collected from Mkuze swamps by the Mkuze River which drains into the northern end of Lake St Lucia. Mkuze swamp, a wetland system of streams and floodplain pans developed along the lower reaches of the river, and they make up the Mkuze wetland with an area of 450km^2 (Ellery *et al*. 2003). The environmental heterogeneity and species richness of the Mkuze swamp and the fact that it has been relatively undisturbed by anthropogenic activities makes it an important ecosystem in the IOCB (Stormanns, 1987; McCarthy and

Hancox, 2000). The Lake St Lucia estuarine system forms the largest fluvial coastal plain in South Africa (Van Heerden 2011) and the largest estuary in Africa (Lück-Vogel *et al*. 2016). It is home to the highest biodiversity of wetland biota when compared to its size in the whole South Africa (Cowan 1999) and due to its temporal variability in rainfall, it experiences varied wet and dry cycles. These factors make it an ideal site to study the environment in order to understand the past and to predict the future.

1.5.1 Location

The St Lucia system is in the KwaZulu-Natal Province of the Republic of South Africa. The estuary of Lake St. Lucia is located at the southern end of the Maputaland coastal plain, which extends from northern KwaZulu-Natal to southern Mozambique and up to Maputo. The estuary is situated between 32°41’E and 28° 23’S, and covers ca 350 km^2, along a length of 60 km, with a width of 1–20 km, and an average depth of 0.9 m (Orme 1990).

Figure 5: Map of the Lake St Lucia showing the sampled locations (Source: Google earth map).

1.5.2 Climate

The climate at St Lucia is subtropical and lies in the summer rainfall region of South Africa with 60% of the rainfall in summer and 40% in winter (Potter and Blackmore,1998; Taylor *et al*., 2006). It has warm, moist summers (mean annual temperatures exceed 21°C), and mild dry winters. Rainfall at the coast varies from 1 200 - 1 300 mm per annum but drops to only 900mm per annum 10km to the west at Fanies Island (Taylor *et al*., 2006). This temporal changeability of rainfall gives rise to severe wet and dry periods in Maputaland (Taylor *et al*., 2006) which in turn affects the hydrology and salinity of the estuarine lake.

1.5.3 Hydrology and Salinity

Five rivers systems supply the estuarine lake with freshwater. These rivers are the Mkuzi, Hluhluwe, Mzinene, Impate and Nyalazi (Taylor *et al*., 2006). Variation in rainfall regionally and temporally affects hydrology and salinity at the St Lucia estuarine system (Taylor *et al*., 2005). Due to high surface area (350km^2) to volume ratio (about 0.9m average depth) in the estuarine lake (Orme, 1990), it is very sensitive to the impact of evaporation (Hutchison and Midgley, 1978). Hence, the hydrology of the lake changes. The quantity of water lost by evaporation exceeds the quantity received from rainfall even in years of moderate or above average precipitation (Potter and Blackmore,1998). Fresh water received from the streams and rivers mainly regulates the salinity of the overall system (Potter and Blackmore,1998). In periods were the amount of rainfall is moderate or above average, the salinity gradient ranges from a freshwater state near the river mouths to that of sea water (35 parts per thousand) in the estuary. In periods of drought, more water is lost from evaporation than enters the lake from river-flow and if the lake is open to sea at the mouth, then more sea water flows in resulting in an increase in salinity (Potter and Blackmore, 1998). Hence, during extended periods of drought, the lake becomes hypersaline.

From 1981-1994, on average, 50% of the estuary’s freshwater input was from direct rainfall, and around 45% was from inflow of river catchments in the North and East (Quibell 1996). During that same period, less than 10% of the estuary total fresh water was estimated as sourced from the groundwater input to the estuary (Quibell 1996). Thus, groundwater is of no great importance for the freshwater budget of the estuary during normal and wet conditions. Nevertheless, ground water from the eastern shores constitutes the only freshwater inflow into the estuary during extreme drought conditions when the rivers become dry and provide almost no recharge (Quibell 1996).

Since 1952, St Lucia has witnessed a drought condition (that has been monitored) which has led to hypersaline conditions in the inner part of the estuary at intervals of about ten years (Taylor *et al*., 2005). The salinity management strategy since 1952 has been to keep the estuary mouth artificially open by dredging, but in July 2002, the mouth of the estuary closed and has since been allowed to remain closed (Taylor *et al*., 2005). Due to the closed mouth, the water level fell to 0.8m biosafety level(bsl) in January 2004 and has been the lowest level on record with about 75% of the estuary bed being exposed (Taylor *et al*., 2005).

1.5.4 Geology and Geomorphology

The St Lucia System site comprises Cretaceous sedimentary rocks of the St Lucia Formation which are covered by the Maputaland Group sedimentary rocks of Neogene and Quaternary age (Potter and Blackmore,1998). The Cretaceous sedimentary rocks are rich in fossil remains and are exposed over extensive areas and the sediments have a shallow dip towards the east hence, the oldest rocks are exposed in the west in False Bay and the youngest along the western shores of Lake St Lucia (Potter and Blackmore,1998).

A high forested coastal barrier dune flanks the Indian Ocean coastline, and the dune cordon forms river estuaries and creates solitary coastal lakes and lagoons with limited marine influence along the coast of Maputaland (Miller, 2001; Wright *et al*., 2000). The forested dune system is a conspicuous landscape feature of the eastern edge of the coastal plain (Potter and Blackmore,1998).

The St Lucia Lake is connected to the Indian Ocean only in the south by a 22-km-long channel, with very limited tidal influence beyond the first 14km from the ocean (Taylor 1982; Wright 1995). The eastern shore which is a sandy region consisting of undulating dunes that separate the estuary from the coastal barrier dune, is characterized by a complex stratigraphy of mid Pleistocene to Holocene dune-sand units. These dune-sand units have resulted from the effects of coast-parallel prevailing winds (Potter and Blackmore,1998). The cliff along the western shoreline of St Lucia is supported by Cretaceous siltstone and the marine planed surface that is incised into the Cretaceous argillites dips seaward at a low angle (Davies and Partners, 1992; Kelbe *et al*.,1995; Miller, 2001).

Embomveni dune ridges (up to 70m asl) are formed beneath the coastal barrier extending inland. The Embomveni dune ridges are the mid to late Pleistocene Port Durnford and Kosi Bay Formations (Taylor *et al*., 2005).

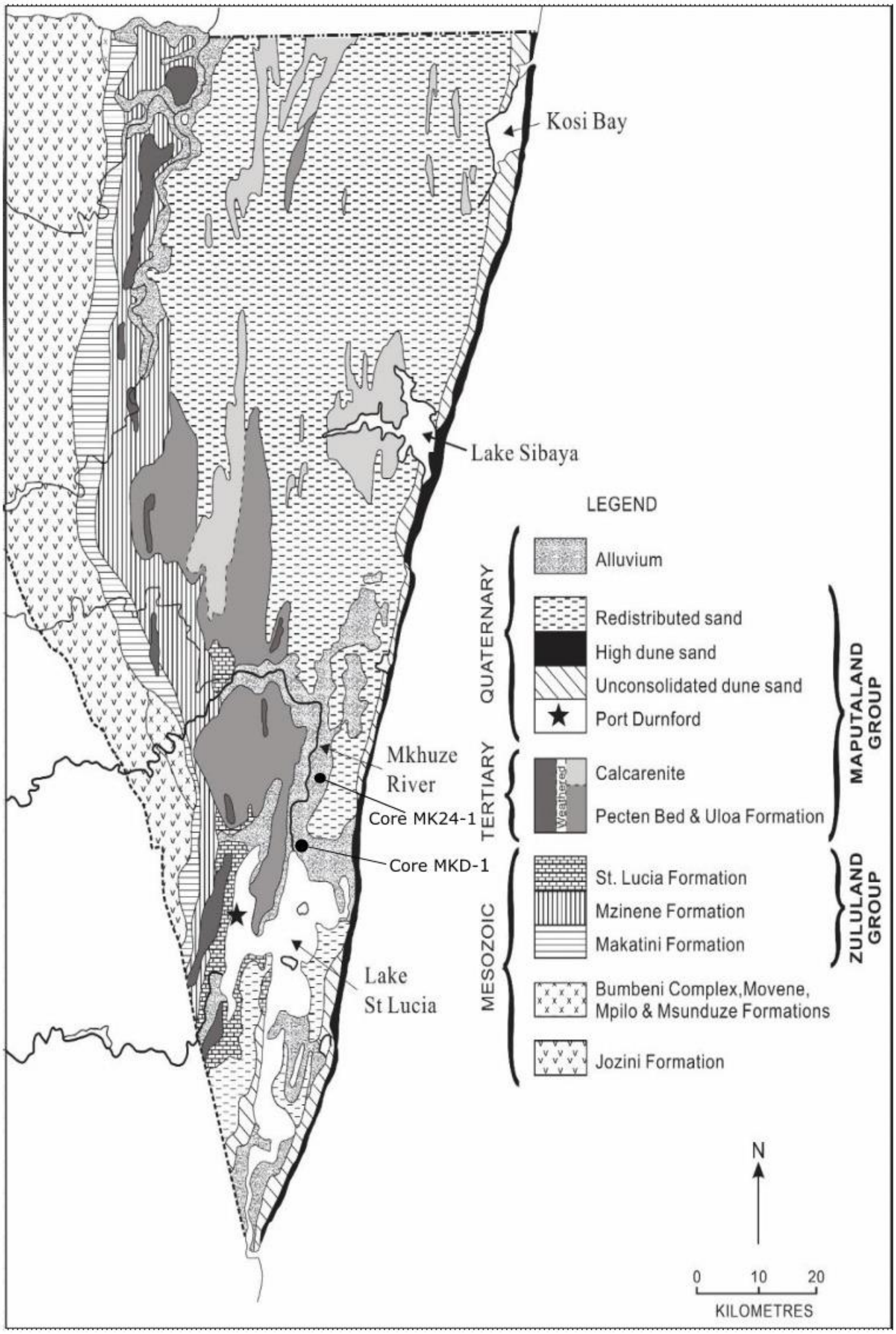

Figure 6: Regional map showing the Coring sites, main coastal waterbodies and geomorphologies on the northern KwaZulu-Natal coastal plain (after Wright *et al*., 2000).

1.5.5 Vegetation

Potter and Blackmore (1998) gave an elaborate classification of the vegetation at Lake St Lucia and divided it into six major groups based on their habitat and growth form. These groups are as follows:

1. Wetland types

   (a) Freshwater *Phragmites* and *Papyrus* swamp; characteristic species are *Cyperus papyrus* and *Phragmites australis*

   (b) Saline reed swamp; characteristic species is *Phragmites mauritianus*.

   (c) *Eleocharis* (Sedge) Swamp; characteristic species is *Eleocharis limosa*

   (d) Salt Marsh; characteristic species are *Sporobolus virginicus*, *Paspalum vaginatum Juncus kraussii*, *Salicornia* spp., and *Ruppia maritima*.

   (e) Submerged macrophyte beds; characteristic species are *Potamogeton pectinatus*, *Ruppia cirrhosa*, and *Zostera capensis*.

2. Grassland types

   (a) Hygrophilous grassland on sand; characteristic species are *Acroceras macrum* and *Ischaemum arcuatum*.

   (b) High-lying grasslands on sand; characteristic species are: *Aristida junciformis, Themeda triandra, Imperata cylindrica, Cymbopogon validus, Helichrysum kraussii, Diospyros villosa, Thesium* spp, *Cassytha filiformis* and *Smilax kraussiana*.

   (c) *Echinochloa* floodplain grassland; characteristic species are *Echinochloa pyramidalis, Eriochloa* spp., *Sorghum* spp., and various *Cyprus* species.

3. Swamp forest; characteristic species are *Ficus trichopoda, Voacanga thouarsii, Syzygium cordatum, Barringtonia racemosa, Phoenix reclinata, Macaranga capensis, Bridela micrantha, Psychotria capensis, Tarenna pavettoides,* and herbs *Psilotum nudum, Stenoclaena tenuifolia* and *Nephrolepis biserrata.*

4. Mangroves; characteristic species are *Bruguieria gymnorrhiza* and *Avicennia marina*.

5. Woodland types, characteristic species include….

a. Palm veld; characteristic species are *Hyphaene coriaccea, Phoenix reclinata* and grass species.

b. Riverine woodland; characteristic species are *Ficus sycomorus, Acacia xanthophloea, Rauvolfia caffra, Acacia schweinfurthii, Axima tetracantha, Panicum* spp., *Sporobolus* spp., and *Eriochloa* spp.

c. Coastal thicket on seaward-facing dune cordon slopes; characteristic species are *Eugenia capensis, Brachylaena discolor, Euclea natalensis* subsp. *rotundifolia, Diospyros rotundifolis, Mimusops caffra, Chrysanthemoides monilifera, Apodytes dimidiata, Erythroxylum emarginatum, Strelitzia nicolii and Hibiscus tiliaceus*. Dune pioneers include *Scaevola thunbergii, Rhoicissus digitata, Cynanchum obrusifolia, and Ipomoea wightii.*

6) Forest types

a. Coastal dune forest; characteristic species are *Mimusops caffra, Grewia occidentalis, Psychotria capensis, Peddiea africana, Ficus burtt-davyi, Diospyros natalensis, D. rotundifolia, D. inhacaensis, Euclea natalensis, Apodytes dimidiata, Brachylaena discolor, Ziziphus mucronata, Carissa bispinosa, Dracaena hookeriana, Isoglossa woodii, Panicum deustum, Digitaria diversinervis, Tragia durbanensis and Sansevieria hyacinthoides.*

b. Coastal lowland forest; characteristic species are *Strychnos decussata, S. gerrardii, Hymenocardia ulmoides, Canthium inerme, Scolopia zeyheri, Ekebergia capensis*, and the lianes *Monanthotaxis caffra, Dalbergia armata, Landophia kirkii,* and *Uvaria caffra.*

The conspicuous estuarine vegetation at Lake St Lucia was also divided into eight habitat units according to Rautenbach, (2015). These units are (a) permanently flooded macroalgae (b) submerged macrophytes (c) partly flooded reeds and sedges (d) salt marshes (e) mangroves (f) swamp forest (g) grass and shrub vegetation (h) floating macrophytes.

Table 2: Habitat units and their dominant species (after Rautenbach, 2015)

HABITAT UNIT	**DOMINANT SPECIES**	**DESCRIPTION**
Macroalgae	*Ulva intestinalis*, *Chaetomorpha* sp., *Cladophora* sp., *Bostrychia* sp. and *Polysiphoni*a sp	Found at estuary margins, as epiphytes and associated with mangrove pneumatophores
Submerged macrophytes	*Ruppia cirrhosa*, *Zostera capensis* and *Stuckenia pectinata*	Plants rooted in substrata whose leaves and stems are completely submersed.
Reeds and sedges	*Phragmites australis*, *Juncus kraussii* and *Schoenoplectus scirpoides*	Observed at sites with freshwater input at the margins, rooted in submerged substrata. *Juncus kraussii* is observed in the vicinity of the Forks and the Narrows.
Mangroves	*Avicennia marina* and *Bruguiera gymnorrhiza*	Observed in the brackish to saline intertidal areas at the Narrows and mouth area.
Grass and Shrubs	*Sporobolus virginicus*, *Paspalum vaginatum*, and *Stenotaphrum secundatum*	Sedge grass and shore slope lawn, observed in areas where there is no freshwater input, freshwater is provided by rainfall
Salt Marsh	*Sarcocornia* sp., *Salicornia meyeriana*, and *Atriplex patula*	Succulent species colonize exposed saline soils in False Bay and in the mudflats of North Lake and are not tolerant to long periods of inundation
Swamp forest	*Ficus trichopoda*, *Barringtonia racemosa*, and *Voacanga* sp	Observed on the banks of Mfolozi Estuary, in the vicinity of the back channel and Narrows and along the Eastern Shores under freshwater conditions
Floating Macrophytes	*Nymphaea nouchal*, *Azolla filiculoides*	Floating leaved species are commonly associated with submerged and deepwater aquatics and occur at water depths from 0.5 to 2 m

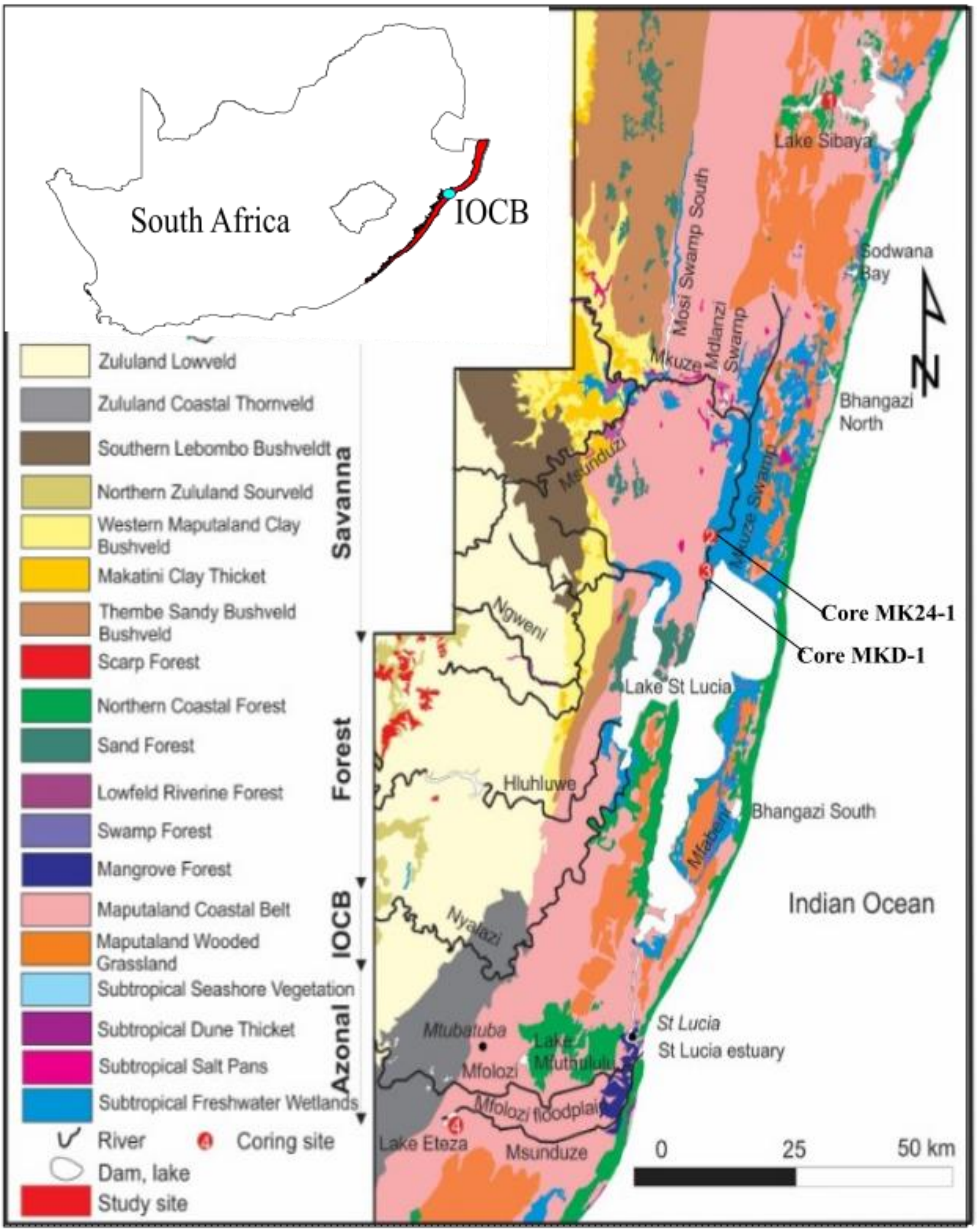

Figure 7: Map of Lake St Lucia; upper diagram: map of South Africa showing the Indian Ocean Coastal Belt Biome and study area, lower diagram: map of Lake St Lucia indicating current and previously sampled localities (Mkhuze River Delta). Red dot: Sites-1. Lake Sibaya (Neumann *et al*. 2008), 2. Core MK24-1 (this study), 3. Core MKD-1 (this study), 4. Lake Eteza (Scott & Steenkamp 1996, Neumann *et al*. 2010).

1.6 Contribution to Knowledge

In the Indian Ocean Coastal Belt biome (IOCB), agricultural activities, urbanization and climate change have brought about a reduction or loss in sedimentary environments such as wetlands (Kotze *et al*., 1995; Kotze and O'Connor, 2000). These wetlands are sources of proxy evidence of the past environment. The low number of Holocene climate history records in the IOCB is due to a scarcity of continuous lake and peat deposits (Scott and Lee-Thorp, 2004) and owing to poor pollen preservation within the region's Quaternary age deposits (Scott 1984). My research will contribute to the Holocene climate history records and present an improved understanding of Quaternary vegetation change in the IOCB. It will also give an overview of pollen, spores and other non-pollen palynomorphs from the region since no pollen atlas exists for the region. The photographic record of fossil pollen types recovered from my cores (Effiom *et al*., under review) will contribute to the understanding and identification of palynomorphs in the region and hence will aid in future palaeoecological studies in the region and world at large.

1.7 Study Aims and Objectives

The aims are to reconstruct the paleovegetation during the time period which is covered by the two cores (~6300 cal yrs BP), to infer the past climate of the environment, compare the pollen sequences with palynological results of relevant studies with robust chronologies in the region, e.g., Lake Sibaya and Lake Eteza and construct a regional pollen atlas. This will be carried out by

a. Retrieving suitable sediment samples from Mkuze swamp for pollen analysis and radiocarbon dating

b. Extraction and concentration of palynomorphs from the sediments

c. Counting and identification of the recovered palynomorphs

d. Determining the dominant ecological drivers responsible for the changes in palynomorphs composition throughout the period covered by both cores in order to decipher the past climate.

e. Establishing the chronology using the radio-carbon dates.

f. Taking photomicrographs of recovered palynomorphs from the studied cores in order to produce a pollen atlas.

1.8 Structure of the thesis

The introductory chapter presents the reader with the background of this study, exploring the need for pollen analysis in order to understand the past vegetation and the limitations of pollen analysis. It also explains South African climate and biomes, a summary of paleoecological studies within the Indian Ocean Coastal Belt Biome of Southern Africa. Finally, the chapter provides details of the regional setting of Lake St Lucia beginning with the location in the Indian Ocean Coastal Belt Biome (IOCB), geology, climate, hydrology and vegetation.

Chapter Two begins with the justification of the study site followed by a detailed discription of collection, extraction and analysis of the samples. This chapter also discusses the statistical methods used to explore my pollen dataset and radiocarbon dates.

Chapter Three gives an overview of pollen, spores and other non-pollen palynomorphs recovered from both sediment cores (MK24-1 and MKD-1) giving information about their morphology, plant growth habit, habitat and mode of pollination.

Chapter Four provides palynological results for the short core (MK24-1) giving information about the species composition and fluctuations in the different strata. It gives a summary of the palynomorphs composition plotted against depth (Pollen diagram)

Chapter Five provides results for the long core (MKD-1) also giving information about the species composition and fluctuations in the different strata. It gives a summary of the palynomorphs composition plotted against depth (Pollen diagram) for core MKD-1.

Chapter Six is the discussion of both cores in comparison with other study sites in the region and the final chapter provides a conclusion of the past vegetation change and the ecological factors that may have triggered the changes.

Chapter 2

Materials and Methods

2.0 Introduction

This chapter outlines the procedures followed in the collection, extraction, and analysis of sediment samples. In pollen analysis, standard methods have been developed over the years such as Erdtman 1969, Faegri and Iverson 1966. These methods have been used in the reviewed studies and allow for reproducible results and a more accurate comparison between review studies. These methods involve the separation of the palynomorphs from the sediments, concentration of the recovered palynomorphs, identification and understanding the ecological requirements of the recovered palynomorphs in order to reconstruct the paleo vegetation and infer climate.

2.1 Study Site Selection

Lake St Lucia being the largest estuary in South Africa (Moll *et al*., 1971; Turpie *et al*., 2012) and is part of the iSimangaliso Wetland Park, which is South Africa’s first UNESCO World Heritage Site. The estuarine lake has experienced a number of salinity fluctuations caused by wet and dry cycles which inturn controls the occurrence and growth of plants at a given time and locality (Taylor 1993). Hence, the necessity to study the past vegetation of Lake St Lucia in order to understand if the wet and dry cycles were naturally induced by climate or anthropogenic activity.

2.2 Field Work, Core collection, Sediment Analyses

Two core samples were taken from two different locations close to the Mkuze River Delta which is a contemporary bayhead delta that discharges into the most northern part of lake St Lucia. The Mkuze River is the largest contributor of sediment and freshwater to the northern basin of the lake.

Core MKD1: The core (27.8856 °S, 32.4853 °E) is 770cm long and spans ~6300 years. The core was retrieved in approximately 60 cm water depth using a barge mounted piston corer coupled to a percussion drill. Core sections were collected in PVC liners (63 mm diameter) and transported to the laboratory at the Department of Chemistry/Wits University (Dr Marc Humphries) where they were split longitudinally and described according to standard sedimentological procedures. Six sediment samples were submitted for radiocarbon dating, and radiocarbon ages were calibrated to calendar years using the Southern Hemisphere calibration SHCal20 (Hogg *et al.*, 2020); a Bayesian age-depth model was developed using Bacon 2.2 software (Blaauw and Christen, 2011) (Fig 9 and 14). The core was sub sampled for pollen analysis (total 81 samples). The samples were processed according to standard procedures (Erdtman,1969; Faegri and Iverson,1966).

Core MK24-1: Core *Swamp* (27°51.365'S 32°28,760'E) is 90 cm long and spans~2000 years according to radiocarbon dates. The core was retrieved in a swamp using a barge mounted piston corer coupled to a percussion drill. The core was sub-sampled by German collaborators Enno Schefuss and Mattias Zabel in the Framework of Tracing Human and Climate Impacts in South Africa (TRACES) project. A total of 30 subsamples were processed for pollen analysis according to standard procedures (Erdtman,1969; Faegri and Iverson,1966). Three sediment samples were sent for radiocarbon dating and radiocarbon ages were also calibrated to calendar years using the same method as for core MKD-1. The previous radiocarbon dates used were changed as they were for Core MK24-1 (coarse sediments) and not MK24-1 (fine sediment) but was wrongly sent to me by TRACES. Hence, the new date used are the correct dates for MK24-1.

2.3 Laboratory Work

Following the standard method of Erdtman (1969) and Faegri and Iverson (1966), the samples were treated systematically as stated below.

Treatment of Samples: The objective of this phase is to disaggregate the sediment and concentrate the fossil palynomorphs and this involves three steps:

a. Demineralization

Approximately 5g grams of each of the sediment samples were crushed in a pestle and mortar. 10% HCl was added to test for carbonates. The treated sample was centrifuged at 2500 r. p. m. and rinsed with distilled water to remove the acid.

The sample was later soaked in 40% HF overnight to dissolve silicates. After being soaked, centrifuged for about five minutes and the supernatant decanted, water washed thrice to neutralise the HF.

The sample was then treated with 10% KOH to remove humic acids as well as other organic materials. During this process, the sample was boiled for five minutes in a boiling waterbath then centrifuged and decanted; water washed thrice to remove the KOH.

(b) Heavy liquid separation

The purpose here is to separate the palynomorphs from the disaggregated silica. A solution of $ZnCl_2$ and HCl with specific gravity 2.0 was poured on the sample and thoroughly stirred. The mixture was centrifuged for 10 minutes at 2000 r.p.m. After this, the supernatant of organic matter (mostly pollen and spores) was poured into separate centrifuge tubes. This step was repeated to increase the concentration of pollen and spores in the residue. Finally, the concentrated pollen (residue) was water washed thrice to remove the $ZnCl_2$ and HCl solution.

(c) Acetolysis

This is done to make the pollen more translucent, and the exine structure more clearly visible as recommended by Sowunmi (1976), since the cellulosic materials will be destroyed. Glacial acetic acid was first added to the residue and left for 5 minutes to remove water. After this, it was subjected to the Erdtman (1969) acetolysis method. The acetolysis mixture of nine parts of acetic anhydride and 1 part of sulphuric acid (H_2S0_4) was prepared. This was introduced into tubes containing the residue and boiled in a water bath at 100°C for 3 minutes with occasional stirring with glass rods. The mixture was then centrifuged at 2000 r.p.m. for 5 minutes and the supernatant decanted. Glacial acetic was added to the residue to remove the acetolysis mixture before rinsing thrice with distilled water and a known volume of 100% glycerin was added. A well-labelled plastic vial was then used for storing the residue for microscopic study.

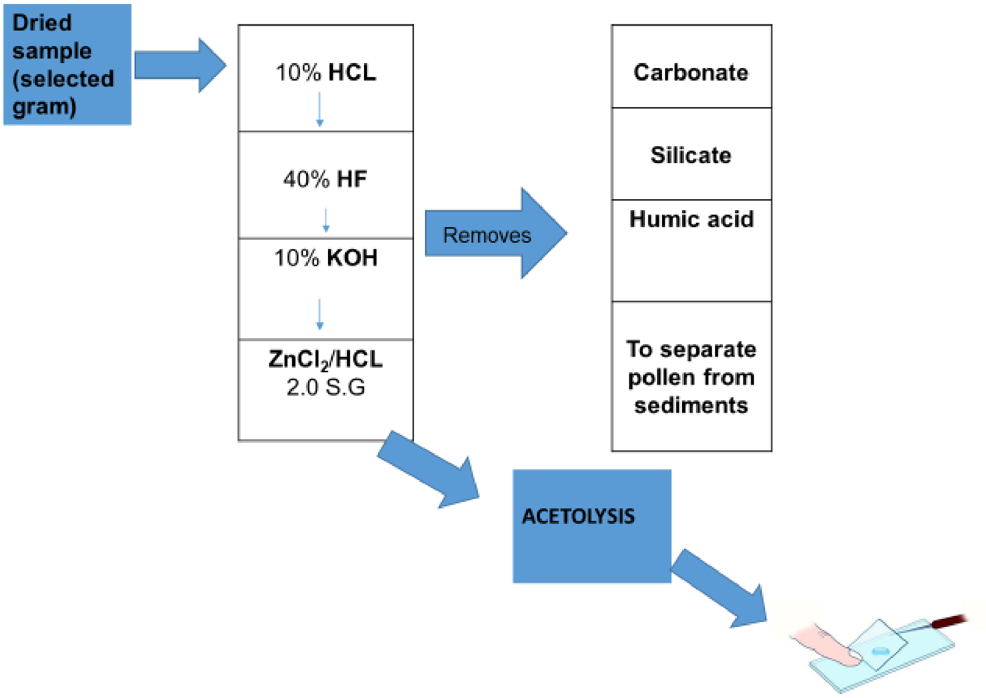

Figure 8: Summarized procedure of pollen preparation (after Faegri *et al*. 1989)

2.4 Microscopic study

Mounting

Two drops of glycerin jelly and two drops of the prepared residue were pipetted onto the same slide and was carefully stirred with the tip of the micropipette for even distribution. A cover slip was lowered on to the residue in a manner that avoids the formation of air bubbles.

Identification

The prepared semi-permanent slides were studied under a light microscope (Zeiss Axioscope 2, 1000 x magnification). Identification of the grains was done by comparison with modern pollen reference collections at ESI and Department of Plant Sciences, University of the Free State, and published pollen atlases such as Bonnefille and Riollet (1980) and Scott (1982). Documentation was done using the image analysis software of the light microscope at the Microscopy and Microanalysis Unit (MMU) at the University of the Witwatersrand. All grains were counted and were identified to family level (Faegri and Iverson, 1989) and some to generic level and a few to the species level. For grains that were deformed or badly damaged beyond recognition, they were grouped and termed indeterminate and were excluded from further analysis.

2.5 Data Analysis

Pollen spectrum: A pollen spectrum is the total assemblage of palynomorphs from one layer or stratum. Usually, a count of the pollen is done to know the percentage abundance of the different identified species, and this is done with the aim of identifying the dominant and ecologically significant species in the different layers (depth). Palynologists generally recommend 200 to 250 counts of pollen as it is statistically valid and reliable in percentage calculations (Barkley, 1934). Other palynologists have recommended a count of 150-500 ((Birks and Gordon, 1985; Erdtman, 2013). Birks and Gordon (1985) concluded that the count of palynomorphs comprising less than 1% of the total palynomorphs would not be reliable statistically hence, should be exempted from further analysis. During the pollen counts, the terrestrial pollen sum is usually calculated which is the total sum of all identified pollen in a layer (depth) excluding all wetland taxa and aquatics. About 100-250 pollen grains were counted for this study depending on the slides as some depth had paucity of pollen grains.

Phytoecological groupings (Sowunmi, 1981): Taxa with significant ecological limits were chosen for the phytoecological grouping. These groupings are made based on known present day natural distributions of their plant taxa. Works of Hutchinson and Dalziel (1954, 1958, 1963, 1968) and other more recent field guides, as well as the SANBI database, were consulted for the groupings. This grouping is meant to give more information about the ecological conditions of the past based on the plant taxa (pollen) recovered. It is known that the distribution changes of the plants match closely with climate model simulations suggesting that the migration of each species since the LGM has taken place as a response to climate change and that species have shifted their distribution ranges, rather than shifting their climatic optima and tolerance limits (Huntley *et al.*, 1997; Davis and Shaw, 2001). This grouping is done with the aim to infer past climate. This grouping also helps with Principal Component Analysis to understand temperature and moisture fluctuations over time (see table 5).

2.6 Statistical Analysis

Pollen Diagram: the compositions expressed as percentages of the pollen sum of each of the taxa that makes up an ecological grouping were used in the construction of the pollen diagram. This diagram was calculated using Strat. Plot in rioja which is designed for managing and graphing stratigraphic data especially paleontological data (Juggins 2012; 2022). The pollen diagram was further divided into Zones based on the internal variation within and between groups of palynomorphs at different depth/age using Constrained Incremental Sums of Squares (**CONISS)** which help to identify pollen assemblages and abundance or sparsity zones which in turn gives information about the changes in vegetation in the different cores.

Ordination Technique:

Principal component analysis (PCA) is a multivariate technique used in pollen analysis in describing the relationships of a set of species in an economical manner (Austin 1968). Often, in palaeoecological studies, PCA is used to monitor species sensitive to moisture and temperature fluctuations (Scott *et al*., 2012). It is often recommended that PCA be carried out on variance/covariance matrices (Seal 1964).

Using PCA which allows visual exploration of data, dataset was first calculated for percentages and the mean percentage determined. Species with a frequency below 1% of the total species occurrence for the different core samples were removed from further analysis because they are considered unreliable statistically (Birks, 2003) hence, those species are insignificant. The remaining species were explored for any changes in the pollen assemblages due to biotic and/ or abiotic factors with the goal of understanding overall trends within the pollen profile which might infer major drivers of the system.

Bayesian Age-Depth Modelling

In palaeoecological and environmental studies, not all sediment samples per depth are usually sent for radiocarbon dating due to the cost of dating and insufficient organic materials in sediments of some depth (Blaauw and Christen 2011). Hence, a few samples are usually selected for radiocarbon dating and the rest are interpolated using age-depth models. Bacon (Bayesian accumulation) model developed by Blaauw and Christen (2011) was preferred because Bacon explicitly incorporates, and models uncertainty as opposed to other age-depth models.

2.7 Conclusion

Analysis of sediments from a core following standard procedure allows for the separation of palynomorphs (pollen and spores) from the sediments and removal of cellulose from the pollen wall making it more translucent and easier to identify to family or even generic or species level hence, past environment can be reconstructed and past climate inferred.

Chapter 3

Results

3.0. **Morphology and ecological significance of Holocene palynomorphs from the Indian Ocean Coastal Belt Biome of South Africa**

3.1. Introduction

Results reported from this study are from two cores, Core MKD-1(27.8856 °S, 32.4853 °E) and Core MK24-1(27°51.365'S 32°28,760'E). Core MKD-1 and MK24-1 (~ 6300 and ~2000 cal yrs BP respectively) were both taken from the Mkuze wetland and about 100m apart with MK24-1 taken from the Mkuze swamp (see chapter 2). Palynomorphs recovered from cores MKD-1 and MK24-1 were identified, photographed and described. This is aimed at documenting the species and creating a platform for pollen identification which will aid future paleo-ecological studies in the region and in Southern Africa at large. This chapter is a manuscript currently under review.

3.2 Pollen Classification

Pollen taxa are first grouped according to the ecology of the parent plants and then in alphabetical order according to families and genera. Following South African National Biodiversity Institute (SANBI), recovered and identified taxa are named. In the photographic plates, pollen specimens are depicted from cores MK24-1 and MKD-1. A total of 156 palynomorph types were recovered from both cores and they consist of pollens, spores of pteridophytes, bryophytes and Fungi, algal cysts, phytoliths, cuticles and marine microfossils. Recovered palynomorphs represent a wide range of habits and habitats that are provided in detail below. From the total number of recovered palynomorphs, only a few pollen taxa were identified to species level because most genera are stenopalynous. Hence, the species are often difficult to delimit and are denoted as ‘type’ that may include different species within the genus and even similar species in other genera and families.

The pollen taxa are grouped into different ecological groups based on the extant plant species and it should be noted that the ecological subdivision is arbitrary because certain species are ubiquitous. The pollen and non-pollen photographs should not be viewed in the same sense of freshly prepared samples as they are fossil palynomorphs and therefore have been through taphonomic processes.

3.2.1 Arboreal and Shrub Pollen

3.2.1.1 Woody plants including trees and shrubs of forest, forest margins, along rivers, moderate to moist habitat

1. ***Metarungia* type Baden (Acanthaceae)** Plate 1, figure 1, Pollen grains prolate, tricolporate with pseudocopi, exine sculpture reticulate (Baden, 1995).

Habit and Habitat: Shrub in thickets and forests (Schmidt *et al*. 2002). *M. pubinervia* is widely distributed in eastern South Africa and often associated with Afrotemperate forests (Darbyshire *et al*. 2008). Using the South African National Biodiversity Institute (SANBI) report, only *M. pubinervia* is found in the IOCB because it was reported in KwaZulu-Natal which is part of the IOCB. Hence, the recovered pollen is likely that of *M. pubinervia*.

Pollination: species within the genera are mostly bird pollinated (Darbyshire *et al*. 2008).

2. ***Heteromorpha* type Cham. & Schltdl. (Apiaceae)** Plate 1, figure 2. Pollen grains are spheroidal to prolate spheroidal to prolate, trizonocolporate, exine sculpture reticulate with sexine thicker towards the pole creating a bone shaped outline which is a characteristic of Apiaceae (Baczyński *et al*. 2021).

Habit and Habitat: Trees and shrubs, often along streams in riverine woodland, in rocky bushveld or at forest margins (Retief and Herman 1997, Johannsmeier 2016).

Pollination: Insect pollinated (Johannsmeier 2016).

3. ***Rauvolfia caffra* Sond. (Apocynaceae)** Plate 1, figure 3. Pollen grains oblate-spheroidal, tricolporate with short colpi and a distinct fastigium, exine sculpture psilate (Rodrigues *et al*. 2016)

Habit and Habitat: Tree; grows along streams, at forest margins, in coastal or swamp forest (Coates Palgrave, 2002).

Pollination: Insect pollinated (Coates Palgrave, 2002). Pollen not well dispersed (Scott 1982).

4. ***Ilex mitis* (L.) Radlk. (Aquifoliaceae)** Plate 1, figure 4. Pollen grains prolate, tricolpate with long colpi, exine sculpture clavae (Beug 2004).

Habit and Habitat: Tall tree (up to 30m high) grows in riverine and Afromontane forests (Schmidt *et al*. 2002; Coates Palgrave, 2002); at low to high altitudes (10-2130 m); widespread in South Africa; monotypic family. (Germishuizen *et al*. 2006)

Pollination: *I. mitis* is insect pollinated (Johannsmeier 2016).

5. ***Phoenix reclinata* Jacq. (Arecaceae)** Plate 1, figure 5. Pollen grains are elliptic, Monocolpate, small (< 20µm), with thin exine and microreticulate sculpture, very similar to *P. dactylifera* (Roubik and Moreno 2018).

Habit and Habitat: Strongly ground-water-associated, up to 10m tall trees, often growing along rivers and streams in clumps or on coastal dunes and widespread at low to medium altitudes (Schmidt *et al*. 2002, Johannsmeier 2016). The pollen is said to represent *Phoenix reclinata* as it is the only species of *Phoenix* identified as occurring in South Africa by SANBI.

Pollination: Wind pollinated (Salomon-Torres *et al*. 2021).

6. ***Celtis africana* type Burm.f. (Cannabaceae)** Plate 1, figure 6. Pollen grains spheriodial to sub-oblate, triporate to pentaporate, with circular pores and annulus (Zarafshar *et al.*, 2010; Palazzesi and Pujana, 2007), exine sculpture scabrate (Palazzesi and Pujana, 2007). Sattarian *et al*. (2006) reported that other species of *Celtis* such as *C. gomphopylla* possess the same pollen morphology of *Celtis africana*.

Habit and Habitat: Deciduous tree that grows in dense forest, on rocky outcrops, in bushveld, in open grassland, on mountain slopes, on coastal dunes and along riverbanks and kloofs (Heywood *et al*. 2007; Mbambezili and Notten, 2008). *C. africana* is usually associated with higher rainfall areas but can also be drought resistant. However, it is more often found in moist environments (Scott 1982). *Celtis milbraedii* also occurs in the IOCB

Pollination: *Celtis africana* is insect (bee) pollinated (Mbambezili and Notten, 2008).

7. ***Trema* type Lour. (Cannabaceae)** Plate 1, figure 7. Pollen grains are ellipsoidal, bi-porate with slightly protruding pores on each end of an oblate body, exine sculpture is often granulate (Kodela, 2006).

Habit and Habitat: Evergreen trees that occur in a variety of habitat but usually found in moist soils at forest margins, in swamp forest, along rivers and streams, often in riverine fringe thicket, also in ravines and valleys (Malan and Notten, 2005).

Pollination: Insect pollinated (Malan and Notten, 2005).

8. **Celastraceae,** Plate 1, figure 8. Pollen grains sub-spheroidal, tricolporate, exine sculpture reticulate (Archer and Van Wyk, 2009). There is a wide overlap in the morphology of many species of this family (Scott 1982).

Habit and Habitat: Celastraceae are considered to represent several species and maybe herbs, vines, shrubs and small trees with a wide range of habitats (Scott 1982). These habitats range from mountains to forest and grasslands (Forester, 2005).

Pollination: Insect pollinated (Watson and Dallwitz, 1992).

9. ***Alchornea* type Sw. (Euphorbiaceae)** Plate 1, figure 9. Pollen grains prolate spheroidal to suboblate, isopolar (Yang *et al*. 2020; Bulalacao and van der Ham, 2003), tricolporate with operculate colpi, exine sculpture scabrate–perforate or psilate-perforate (compare Bulalacao and van der Ham, 2003).

Habit and Habitat: Monoecious or dioecious shrubs or trees growing in both primary and secondary forest, mountain forest, along roadsides (van Welzen and Bulalacao, 2007). Species include trees associated with evergreen (sub)tropical forests (Scott 1982).

Pollination: Wind pollinated (Watrin *et al.*, 2007; Serra Gamma *et al.*, 2019)

10. *Macaranga capensis* (Baill.) Benth.ex Sim. (Euphorbiaceae) Plate 1, figure 10. Pollen grains spheroidal, small (c. 20µm), tricolporate, exine sculpture psilate (Schüler and Hemp 2016).

Habit and Habitat: Medium-sized to tall tree, widely distributed in lowland forests in KwaZulu-Natal, often along streams (Johannsmeier 2016, Coates Palgraves 2002).

Pollination: Many species in *Macaranga* are wind pollinated (Schüler and Hemp 2016).

11. *Psoralea* type L. (Fabaceae) Plate 1, figure 11. Pollen grains oblate-spheroidal, tricolporate, exine sculpture coarsely reticulate (Scott 1982, Ferguson and Skvarla 1983, Retief & Herman 1997). *Psoralea* has been broken down into six genera: *Bituminaria, Cullen, Hallia, Otholobium, Orbexilum,* and *Psoralea* but pollen characters are not very significant at the generic levels (Stirton, 1989).

Habit and Habitat: Many trees, but also some shrubs and herbs (Scott 1982), in grassland or at forest margin and at streams (Retief and Herman 1997, Coates Palgrave 2002).

Pollination: Insect pollinated (Johannsmeier 2016).

12. ***Apodytes dimidiata*** **E.Mey. ex Arn. sub type** ***Dimidiate*** **(Icacinaceae)** Plate 1, figure 12. Pollen grains oblate, Amb triangular, 25-30µm, triporate, exine sculpture microreticulate (Schüler and Hemp 2016).

Habitat: Trees occur in South African coastal forests (Johannsmeier 2016, Coates Palgrave 2002).

Pollination: Insect pollinated (Johannsmeier 2016).

13. ***Myrsine africana*** **L. (Primulaceae)** Plate 1, figure 13. Pollen grains (sub)prolate-spheroidal, mostly 4 colporate, pores protruding at equator where colpi are slightly constricted, exine sculpture psilate to finely rugulate-granulate and reticulate (da Silva-Fourny *et al*. 2020; Kodela, 2006).

Habit and Habitat: The evergreen shrubs or small trees grow in thickets, Afrotemperate forests or on rocks (Schmidt *et al*. 2002).

Pollination: Wind pollinated (Otegui and Cocucci, 1999).

14. ***Eugenia*** **type P.Micheli ex L. (Myrtaceae)** Plate 1, figure 14. Typical pollen of this genus is oblate to peroblate, Amb triangular, 17-30µm in equatorial diameter, tricolporate, syncolpate (Van Wyk and Dedekind 1985). Pollen is dimorphic (pollen of the male *Eugenia* varies from the hermaphroditic species of *Eugenia*) but pollen from hermaphroditic flowers were not observed (compare Van Wyk and Dedekind 1985). Pollen grains of this genus are stenopalynous hence, it is difficult to delimit the species based on pollen characters (Van Wyk and Dedekind 1985).

Habit and Habitat: Trees; grow in riverine scrub or along forested rivers (Schmidt *et al*. 2002).

Pollination: Insect pollinated (Johannsmeier 2016).

15. *Syzygium* type P. Browne ex Gaertn. (Myrtaceae) Plate 1, figure 15. Pollen grains are oblate to sub oblate, small, tricolporate and sometimes tetracolporate, syncolpate, exine sculpture psilate or less commonly scabrate (Thornhill *et al*. 2012; Nacata *et al*. 2019). Soh and Parnell (2015) in their study of the genus *Syzygium* reported that it is difficult to delimit the species of *Syzygium* pollen grains. This morphology could include the neophyte pollen of *Eucalyptus* (Scott. 1982).

Habit and Habitat: Trees occur along stream banks, forest margins, riverine thicket, forest and sometimes in open grassy environments (Van Wyk and Gericke 2000)

Pollination: Self-compatible but has also been identified as insect pollinated (Hopper, 1980).

16. *Podocarpus* type L'Hér ex Pers. (Podocarpaceae) Plate 1, figure 16. *Podocarpus* and *Afrocarpus* pollen grains oblate to spheroidal, bisaccate, bilateral and vesiculate (Pocknall, 1981). The shape of the corpus varies from rhomboid to elliptic to spheroidal-cappa often smooth at the centre but may be irregular, finely rugulate at the margins; sacci are rounded to hemispherical and variable in size with reticulate sculpture often irregular to rugulate

(Pocknall, 1981). Pollen size varies depending on species, from 47µm in *P. acutifolius* to 107.8µm in *P. ferrugineus* (Pocknall, 1981). Often times, fossil *Podocarpus* species cannot be delimited because they share similar features, and pollen size that is the major delimiting factor is usually affected by taphonomic processes.

Habit and Habitat: Yellowwood trees grow naturally in mountainous areas and forests in the southern, eastern and northern parts of South Africa. They are also found on rocky hillsides and mountain slopes but do not grow so tall in exposed sites compared with in the forest (Coates Palgrave *et al.*, 1985; Mtsweni *et al.*, 2005).

Pollination: Wind pollinated. Pollen disposal is aided by the two air sacs. Just like other conifers, they produce pollen in large quantities, therefore they are easily over-represented in pollen spectra. Coetzee (1967) proposed that a presence of up to 10% of *Podocarpus* in the case of East African species suggested the absence of *Podocarpus* in the immediate environment, while <20% may indicate proximity of the trees, and higher numbers may point to the presence of *Podocarpus* forest.

17. *Cliffortia* type L. (Rosaceae) Plate 1, figure 17. Pollen grains sub-spheroidal, tricolporate with short colpi, apertures are operculate, exine sculpture microverrucate-verrucate (Hebda and Chinnappa 1994).

Habit and Habitat: Woody shrubs, often growing along streams (Schmidt *et al*. 2002).

Pollination: Wind pollinated (Fellingham 1999).

18. *Canthium* type Lam. (Rubiaceae) Plate 1, figure 18. *Canthium* s. str. sub type C (Tilney and Van Wyk 1997). Pollen grains oblate, Amb triangular with straight or slightly convex sides; diameter is 40-50 μm, apertures are 2-4-porate often 3-porate, exine sculpture perforate or punctate (Tilney & Van Wyk 1997). The identified pollen had 3 pores.

Habit and Habitat: Evergreen shrubs or small trees that grow in coastal forest, forest margins, rocky outcrops (Moll 1981). There are nine species of *Canthium* in South Africa (Tilney & Van Wyk 1997)

Pollination: Self-compatible and insect pollinated (Von Breitenbach, 1965).

19. *Vepris (Teclea)* type Comm. ex A. Juss. (Rutaceae) Plate 1, figure 19. Pollen grains sub-oblate to sub-prolate, tricolporate with a rhombic pore shape, striate exine sculpture (Gosling *et al.,* 2013).

Habit and Habitat: Trees occur in coastal dune bush, forest and riverine vegetation (Foden and Potter 2005).

Pollination: Insect pollinated (Foden and Potter 2005).

20. *Salix* type L., nom. cons. (Salicaceae) Plate 1, figure 20. Pollen grains prolate to spheroidal, tricolporate with sunken and circular pore, uneven reticulate exine sculpture (Shamso and Toshiyuki, 2012).

Habit and Habitat: Deciduous trees and shrubs often found along streams in wet to moist, open habitats (Judd *et al*. 2002, Coates Palgrave 2002). *Salix mucronata* is known as a riparian rheophyte (Jordaan 2002) and occur in the IOCB.

Pollination: Wind pollinated (Foden and Potter 2005).

21. ,

22. ,

23. *Mimusops* type L. (Sapotaceae) Plate 1, figure 21, 22, 23. Pollen grains prolate spheroidal or subprolate, 3 to 5-colporate, usually 4-colpate, rarely 6-colporate with endo-apertures usually more or less circular, exine sculpture psilate or scabrate (Harley 1991). Genera within the family Sapotaceae are difficult to delimit This group contains other genera such as *Manilkara*, *Englerophytum* amongst others. They have different habitats. Sapotaceae genera are stenopalynous (Harley 1991).

Habit and Habitat: Trees occur generally in hot but moisture rich areas, usually along the edge of swamp forest, in open woodlands, near dune forest, in valley grassland (Scott 1981, Mnxati 2013).

Pollination: Insect pollinated (Mnxati 2013).

a. Mangroves

24. *Rhizophora mucronata* Lam. (Rhizophoraceae) Plate 1, figure 24. Pollen grains oblate, spheroidal or sub-prolate, 3-zonocolporate with a long ectoaperture which is usually contracted at the equator, perforate-reticulate exine sculpture (Magalhães e Silver and Ribeiro dos Santos, 2008; Mohd-Arrabe and Noraini, 2014).

Habit and Habitat: Mangrove trees that occurs in tropical coastal regions, occupying intertidal zones and estuarine margins (Tomlinson, 1994).

Pollination: Self-compatible, but primarily wind pollinated (Tomlinson *et al.*, 1979) and secondarily insect pollinated (Katsuhiko *et al.*, 1987; Tomlinson *et al.*, 1979).

25. *Bruguiera* type Lam. (Rhizophoraceae) Plate 1, figure 25. Pollen grains oblate-spheroidal, 3-zonocolporate with short colpi and lalongate pore, exine sculpture is microreticulate to punctate (minute depressions) (Gupta *et al.*, 2008; Surya and Hari 2017).

Habit and Habitat: Mangrove trees occurring in the seaward side of estuaries, in well-watered and frost-free areas (Berjak *et al.*, 1997).

Pollination: Pollinated by birds (Katsuhiko *et al*. 1987).

3.2.1.2 Woodland trees and shrubs of relatively dry habitat and wide range of habitats

26. *Lannea* type A. Rich. in Guillem. (Anacardiaceae) Plate 1, figure 26. Pollen grains prolate-spheroidal, tricolporate with elliptic and lolongate pore, exine sculpture striate-reticulate (Gosling *et al*. 2013; Athavale 2014)

Habit and Habitat: Deciduous trees that occur in deciduous woodland, bushveld, in river valleys and on rocky outcrops (Fernandes and Fernandes 1966; Burrows *et al*. 2018).

Pollination: Insect pollinated (Gunjal *et al*. 2021; Singh and Singh 1992).

27. ***Sclerocarya* type Hochst. (Anacardiaceae)** Plate 1, figure 27. Pollen grains suboblate to prolate, tricolporate with colpus as long as the pollen, striated exine sculpture (Gosling *et al.*, 2013).

Habit and Habitat: Trees occurring in various woodlands, on sandy soil or sometimes sandy loam (Coates Palgrave 1983, 2002).

Pollination: Insect pollinated (Coates Palgrave 1983).

28. ***Searsia* type F. A. Barkley (Anacardiaceae)** Plate 1, figure 28. Pollen grains spheriodial to sub-spheriodal, tricolporate with colpi that are narrow and slightly constricted at the equator, exine sculpture striate with elongated striae (Heimsh, 1940; Ibe and Leis, 1979).

Habit and Habitat: Trees and shrubs occurring in scrub forest or on forest margins (Von Breitenbach 1974; Viljoen 2015) and in a wide variety of woodland types, some on rocky hills/slopes, in dry areas such as wooded grassland and bushveld (Scott 1982; Ngalo, 2016).

Pollination: Insect pollinated but it produces large amounts of pollen grains (Scott 1982).

29. ***Aloe* type L. (Aphodelaceae)** Plate 1, figure 29. Pollen grains more or less elliptic, monocolpate with colpus as long as the grains, exine sculpture with foveo-reticulate to microreticulate ornamentation, lumina rounded (Roubik and Moreno, 2018). It cannot be certain that some other genera are not included in this pollen type which is due to the wide overlapping in pollen characters of Liliaceae (Scott, 1982).

Habit and Habitat: Succulent herbs that are a prominent component of arid to sub-humid environment, occurring in succulent thickets, grassland and savanna (Bornman and Hardy 1972; Craib 2005; Smith and Van Wyk 2008).

Pollination: Both insect and bird pollinated (Bornman and Hardy 1972; Craib 2005; Smith and Van Wyk 2008).

30. *Hyphaene coriacea* Gaertn. (Arecaceae) Plate 1, figure 30. Pollen grains elliptic, Amb. Subcircular, monocolpate aperture, exine sculpture rugulate or perforate with supratectal gemmae (Ferguson *et al*. 1987).

Habit and Habitat: Evergreen trees occurring in a wide range of habitats; they are often found in bushveld and along swamps and coastal sand, occasionally in woodlands and on hard pan sites with short grasses (Moll 1972).

Pollination: Insect pollinated (Ferguson *et al*. 1987).

31. *Tarchonanthus* type L. (Asteraceae) Plate 1, figure 31. Pollen grains subspherical, sub-prolate to prolate-spheroidal (Cilliers, 1991), tricolporate, exine sculpture micro-echinate consisting of small warts that are spaces apart (Zavada and Lowrey, 2010). *Tarchonanthus* pollen type was found by Leins (1971) in four *Brachylaena* species (Cilliers, 1991).

Habit and Habitat: Trees, widely distributed in a variety of habitats in southern Africa including thickets of bushveld, grassland, forest and semi-desert (Herman, 2002) but some *Brachylaena* species are confined to coastal regions (Mucina and Rutherford 2006).

Pollination: Mostly insect pollinated (Herman, 2002).

32. *Commiphora* type Jacq. (Bursearaceae) Plate 1, figure 32. Pollen grains oblate spheroidal to prolate spheroidal, tricolporate with short colpi and pores that are often lalongate and rarely lolongate, exine sculpture often foveolate or reticulate spinulose and rarely scabrate spinulose (Harley *et al*. 2005; Harley and Clarkson, 1999).

Habit and Habitat: Shrubs and small trees occurring in dry deciduous forests but most species are found in arid and semi-arid conditions such as rocky habitats, mountain slopes, steep escarpments or hills and hardly ever found in coastal plains with deep soil (Alsherif, 2019; Hölscher, 2011). Generally, *Commiphora* is associated with warm, dry, rocky or sandy areas (Scott 1982).

Pollination: Insect pollinated (Farwig *et al*. 2004; Van der Walt, 1973; Hölscher, 2011).

33. *Combretum* type Loefl. (Combretaceae-Melastomaceae) Plate 1, figure 33. Pollen grains sub-prolate to prolate-spheroidal and sometimes prolate, heterocolpate, with three simple apertures alternating with three composite ones, exine sculpture is often psilate to micro-rugulate (El Ghazali, 2016). Pollen grains of this group belong mainly to about 18 species of *Combretum* and *Terminalia* (Scott 1982). It is difficult to delimit this group of pollen grains from that of *Dissotis* and *Memecylon* of the Melastomaceae (Scott 1982).

Habit and Habitat: Non-succulent trees and shrubs; Combretaceae occurs in widespread bushveld, woodland areas, often along rivers, in hot, dry areas, low to medium altitude (Carr, 1988; Le Roux, 2003).

Pollination: Combretaceae are predominantly pollinated by insects and birds (Gentry 1991; Valido *et al*. 2004).

34. *Euclea* type L. (Ebenaceae) Plate 1, figure 34. Pollen grains prolate to spheroidal, tricolporate with ora that are lalongate, exine sculpture psilate to granulate (Geeraerts *et al*. 2009; Wallnöfer, 2001).

Habit and Habitat: Shrubs and trees occurring in a wide range of habitats ranging from open rocky slopes, low hills with valleys, open Mopane, *Senegalia-Vachellia* woodland and along streams (Scott 1982; Voigt, 2013).

Pollination: Insect pollinated (Wallnöfer, 2001).

35. *Diospyros* type L. (Ebenaceae) Plate 1, figure 35. Pollen grains prolate to prolate-spheroidal, 3-zonocolporate with colpi that are narrow at the pole with granulate exine membrane around the colpus, exine sculpture psilate in southern African types but often striate and sometimes scabrate or perforate (Grygorieva *et al.*, 2013; Grygorieva *et al.*, 2017).

Habit and Habitat: Shrubs and trees growing in a wide range of habitats but mostly in woodland and savanna (Coates Palgrave 2002).

Pollination: Insect pollinated (Nakamura *et al.*, 2020).

36. *Spirostachys africana* type Sond. (Euphorbiaceae) Plate 1, figure 36. Pollen grains oblate-spheriodal to prolate, tricolporate with colpi that are wider at the equator and tapper towards the poles, pores are lalongate and swollen, exine Sculpture perforate-fossulate/scabrate (Park and Lee, 2013). Scott (2016) discusses the problem of distinguishing the pollen grains of *Spirostachys* (Euphorbiaceae) and *Kiggelaria* (Achariaceae) which have similar morphologies.

Habit and Habitat: Semi-deciduous trees growing in low-altitude bush, most often along rivers or stream banks (Scott 1982; Ndou 2004).

Pollination: Wind pollinated (Daru *et al.,* 2015)

37. *Euphorbia* type L. (Euphorbiaceae) Plate 1, figure 37. Pollen grains prolate to sub-prolate and prolate spheroidal, tricolporate with colpi wider at the equator and narrow at the pole, exine sculpture often reticulate but sometimes, granulate to perforate (Yang *et al*. 2020; Chaudhary and El-Ghazaly, 1994; El-Ghazaly, 1989). The sculpture pattern in zones adjacent to the colpi appear slightly different from that in the inter-colpate areas (Chaudhary and El-Ghazaly, 1994; El-Ghazaly, 1989).

Habit and Habitat: Trees, shrubs and herbs found in a variety of habitats ranging from grassy hills, outcrops and ridges, along river courses, bushveld and open savanna (Leistner, 2005). Because of the wide distribution and variety of life forms, *Euphorbia* pollen is of limited use in palaeoecological interpretations (Scott 1982).

Pollination: Insect pollinated but some species are also pollinated by lizards (Voigt, 2007; Traveset and Saez, 1997; Ehrenfeld, 1979).

38. ***Burkea africana*** **Hook. (Fabaceae)** Plate 1, figure 38. Pollen grains oblate spheroidal, trizonocolporate, exine sculpture perforate-rugulate (Banks and Lewis, 2009).

Habit and Habitat: Deciduous shrubs or trees growing in dry deciduous bushveld and woodlands (Nonyane and Masupa, 2010).

Pollination: Insect pollinated (Dry, 1993).

39. ***Dichrostachys cinerea*** **(L.) Wight & Arn. (Fabaceae)** Plate 1, figure 39. Pollen grains circular to spheroidal (Tantawy *et al*. 2005; Gosling *et al*. 2013), inaperturate with a verrucate exine sculpture (Raj and Reddy, 2019; Gosling *et al*. 2013). Pollen grains of this species are usually recorded in small numbers in sediments even when the parent plant is common because they are poorly dispersed (Scott, 1982).

Habit and Habitat: Small shrub or tree growing in thickets, often on sandy soil or encroaching in areas of mismanaged veld (Schmidt *et al*. 2002). They are also typical species of dry bushveld (Scott 1982).

Pollination: Bat-pollinated but can occasionally be insect pollinated (Orwa *et al*. 2009; Tchuenguem Fohouo *et al*. 2008).

40. ***Peltophorum africanum*** **Wight et Arn. (Fabaceae)** Plate 2, figure 40. Pollen grains oblate-spheroidal, tricolporate with long colpi, which are wider at the centre and narrow at the base, porus with pronounced annulus, coarsely reticulate exine sculpture (Orijemie 2018).

Habitat: Trees occurring in a wide range of habitats ranging from grassland, woodland, rocky places, highveld and bushveld plains and along wetland margins but are most often associated with savanna (Scott 1982, Chevalier *et al*. 2021).

Pollination: Insect pollinated (Mawdsley and Sithole 2010).

41. *Senegalia* type. Raf. (Fabaceae) Plate 2, figure 41. Pollen in the genus *Senegalia,* previously reported as *Acacia*, together with *Vachellia* (see below), are round to semi-round, polyads with 16 to 32 associated monads, porate, cullumelae absent, exine sculpture is often psilate-foveolate (Coetzee, 1955; Al-Watban *et al.,* 2013, Maslin *et al.,* 2003b).

Habitat: Shrub or small trees growing in a wide range of habitat ranging from coastal scrub, woodland, arid savanna, bushveld and highveld grasslands (Smit, 1999).

Pollination: Insect pollinated (Foden and Potter, 2005).

Phylogenetic studies of *Acacia* species have brought about a reclassification of African *acacias* as *Senegalia* and *Vachellia* (Kyalangaliwa *et al.,* 2013).

42. *Vachellia* type Wight & Arn. (Fabaceae) Plate 2, figure 42. Pollen grains are round to semi-round, polyad with 16 to 32 associated monads, colporate, collumelae present; exine sculpture is often psilate-foveolate and sometimes faintly reticulate, and characterized by conspicuous grooves (Coetzee, 1955; Al-Watban *et al.,* 2013, Maslin *et al.,* 2003b).

Pollen grains of *Vachellia* type together with *Senegalia type*, were previously reported as *Acacia*. Maslin *et al*. (2003b) reported that the major differences between the *Vachellia type* and *Senegalia* type pollen grains is in the presence of a colporate aperture and collumelae in the *Vachellia type* (described by Coetzee (1955) as grooves, and the presence of a porate aperture and absence of collumelae in *Senegalia* type Coetzee (1955). Scott (1982) divided *Acacia* pollen into two groups, "the polyad grains with grooves and polyad grains without grooves (Mimosoideae), which can tentatively be assigned to the *Vachellia*- and *Senegalia* types respectively. The Mimosoideae type without grooves may also include other legume species.

Habitat: Trees and shrubs occurring in a wide range of habitats ranging from coastal scrub, woodland, arid savanna, bushveld and highveld grasslands (Smit, 1999; Archibald and Bond, 2003).

Pollination: Insect pollinated (Foden and Potter, 2005).

43. *Loranthus* type. Jacq., nom. cons. (Loranthaceae) Plate 2, figure 43 Pollen grains often oblate and sometimes sub-oblate to sub-spheroidal, 2-3-4-colpate, often 3-syncolpate apertures, indistinctly granulate exine sculpture (Han *et al.,* 2004; Grimsson *et al.,* 2018).

Habit and Habitat: Hemiparasites growing on various host trees and found in a wide range of habitats, occurring as aerial branch parasites of plants (Grimsson *et al.*, 2018).

Pollination: Self-compatible, but pollination is mostly carried out by insects and birds (Vaknin *et al.*, 1996).

44. *Grewia* type L. (Malvaceae) Plate 2, figure 44. Pollen grains sub-prolate to prolate, tricolporate with long colpi, exine sculpture is reticulate (Shokefun *et al*. 2014).

Habit and Habitat: Shrubs or small trees occurring in a wide range of habitats ranging from arid karoo, dry savanna (especially *G. flava*), coastal dune bush, evergreen montane forest and wooded grasslands (e.g., *G. occidentalis*), but mostly associated with savanna (Venter and Venter 1996; Scott, 1982, Chevalier *et al*. 2021).

Pollination: Insect pollinated (Zietsman, 1991).

45. *Dombeya* type Cav. (Malvaceae) Plate 2, figure 45. Pollen grains spheroidal, ~45-60 µm, triporate, pori circular (4-5 µm) with broad annulus, exine sculpture echinate with short, pointed spines that are broader at the base (Schüler and Hemp 2016, Hamdy and Shamso, 2010). Pollen morphology in *Dombeya* is similar to that of other triporate Malvaceae like *Sphaeralcea.* However, the other Malvaceae pollen grains seem to have more closely spaced spines with better developed bases (Scott 1982).

Habit and Habitat: Mostly shrubs and more rarely trees or herbs (Schüler and Hemp 2016). Some species like *D. rotundifolia* are, in KwaZulu-Natal and Mpumalanga, more often growing in warmer, drier regions (Immelman *et al*. 1972, Coates Palgrave 2002). They are found in woodland, wooded grassland, rocky mountain slopes and forest margins (Foden and potter, 2005; Boon and Pooley, 2010).

Pollination: Insect pollinated (Yeo 1993, Schüler and Hemp 2016).

46. *Ficus* type L. (Moraceae) Plate 2, figure 46. Pollen grains often ellipsoidal, Amb. Triangular, 1-3-porate but often diporate apertures with circular and sometimes annulated pores; exine sculpture often psilate and sometime scabrate (Teleb and Salah-El-din 2014; Jago and Boyd 2003; Khan *et al.*, 2011).

Habit and Habitat: Shrubs or trees found in a variety of habitats depending on the species; habitats ranging from coastal scrub forest, low-altitude riverine forest, bushveld, rocky hillsides, rocky outcrops (Burrows and Burrows 2003, Chevalier *et al*. 2021).

Pollination: Insect pollinated (Burrows and Burrows 2003).

47. *Myrica* type L. (Myricaceae) Plate 2, figure 47. Pollen grains oblate to sub-oblate, triporate, circular to slightly elliptic pores with vestibulum, exine sculpture looks granulate with light microscope but micro-echinate or spinuliferous with scanning electron microscope (Punt *et al*. 2003; Coetzee and Praglowski 1984). Pollen morphology of *Myrica* is similar to *Casuarina* (Coetzee and Praglowski, 1984).

Habit and Habitat: Shrubs or trees found in a wide range of habitats from mountainous places along forests, coastal flats and dunes, streambanks (Polhill and Verdcourt, 2000; Scott 1982).

Pollination: Wind pollinated (Polhill and Verdcourt, 2000).

48. *Olea* type L. (Oleaceae) Plate 2, figure 48. Pollen grains often oblate spheroidal - sub prolate and less often sub oblate or prolate, tricolporate, exine sculpture reticulate with muri that are straight or curved with rounded or elongate knobs (Messora *et al*. 2017; Najmaddin, 2016). Pollen grains of *Olea* can sometimes be difficult to delimit from some Celastraceae pollen (Scott 1982).

Habit and Habitat: Evergreen trees occurring in a variety of habitats, often near water like the stream banks but sometimes in woodlands and on rocky hillsides (Scott 1982; Joffe, 2002).

Pollination: Self-compatible; hence it undergoes self-pollination (Bradley *et al*. 1961; Ayerza and Coates Palgrave, 2004) and insect pollinated (Green, 2002).

49. *Pseudolachnostylis* type Pax. (Phyllanthaceae) Plate 2, figure 45. Pollen grains spheroidal, 2-3 colporate, exine sculpture coarsely reticulate with a thick exine (Punt 1962). However, similar pollen types are recorded in some species of Celastraceae such as *Cassine burkeana* and *Maytenus senegalensis* and it is not unlikely that a few of these pollen types will be counted as *Pseudolachnostylis* type (Scott, 1982).

Habit and Habitat: Deciduous trees occurring in deciduous woodland, some species occur in sandveld (Ratshibvumo and Mutshinyalo, 2008), also in bushveld and rocky outcrops (Scott, 1982).

Pollination: Insect pollinated (Ratshibvumo and Mutshinyalo, 2008).

50. *Faurea* type Harv. (Proteaceae) Plate 2, figure 50. Pollen grains straight to slightly convex triangular shape (Amb), triporate with circular to ellipsoid-lolongate pore, exine sculpture is perforate on the sides and near the pores and semi-verruco-areolate at the poles (Sauquet and Cantrill, 2007).

Habit and Habitat: Deciduous trees occurring in dry, warm bushveld, *Brachystegia* deciduous woodland, wooded grassland (Von Breitenbach, 1965; Glen, 2008).

Pollination: *Faurea* species pollinator is unknown as the species have not been widely studied. Although, pollination is thought to be aided by rodents as the pentose sugar xylose produced by *Faurea*, is unfavourable to birds and insects (Mhlongo and Hankey, 2015). Rourke *et al*. (2013) also reported that *Faurea recondita* produces a yeasty odour that attracts diverse pollinating insects. Hence, their pollinators are likely to be insects.

51. *Ziziphus* type Willd. (Rhamnaceae) Plate 2, figure 51. Pollen grains spheroidal to prolate, Amb. Triangular, tricolporate with interapertural area sunken, exine sculpture rugulate to psilate (Dinesh, 2018). ***Ziziphus*** pollen is similar to other members of the family hence, Rhamnaceae is a stenopalynous family (Perveen and Qaiser, 2005).

Habit and Habitat: Shrubs or small trees. Generally, Rhamnaceae occur in a variety of habitats in southern Africa (Scott 1982). They are found in bushveld, along stream banks and in water courses, among rocks but even in xeric environments (Foden and Potter, 2005; Velembo, 2019; Chevalier *et al*. 2021).

Pollination: Insect pollinated (Johannsmeier 2016), sometimes wind pollinated (Devi *et al*. 1989; Zietsman, 1990).

52. *Zanthoxylum* type L. (Rutaceae) Plate 2, figure 52. Pollen grains prolate - sub-spheroidal, often tricolporate with long colpi, exine sculpture reticulate to striate-reticulate or striate-rugulate (Dutra and Gasparino, 2018; Cao *et al*. 2014).

Habit and Habitat: Shrubs, trees or woody climbers usually found in forested environments such as rainforest or evergreen forest, coastal thicket, woodland (Groppo and Pirani 2017)

Pollination: Insect pollinated (Kamiya *et al*. 2008).

53. *Gnidia* type L. (Thymeleaceae) Plate 2, figure 53. Pollen grains circular to spheroidal, pantoporate with small circular pores, exine sculpture is scabrate to reticulate (Schüler and Hemp 2016). Thymelaceae is a stenopalynous family (Schüler and Hemp 2016).

Habit and Habitat: Perennial herbs, shrublets or shrubs occurring in varied habitats from wooded grasslands, hillsides, forest margins and bushland (Schüler and Hemp 2016).

Pollination: Insect pollinated (Henning, 1984; Somanathan *et al*. 2004).

a. Neophytic trees

54. *Pinus* type L. (Pinaceae) Plate 2, figure 54. Pollen grains prolate or sub-prolate, elongated monosulcate aperture between two sacci, that were formed by expansion of the exine of the pollen (Song *et al*. 2012). The saccus exine sculpture ranges from rugulate to verrucate and reticulate (Song *et al*. 2012).

Habit and Habitat: Trees; primarily components of modern exotic forest plantations (Song *et al*. 2012) grown to produce timber but have become invasive and widespread in all areas in South Africa during the past century.

Pollination: Wind pollinated (Regal 1982) and abundance indicates a modern age in this country (Neumann *et al*. 2010).

3.2.2 Non-Arboreal pollen

3.2.2.1 Pollen of small shrubs/shrublets and herbs, moist, wide range of habitat

55. *Justicia* type (Forssk.) Vahl. (Acanthaceae) Plate 2, figure 55. Pollen grains prolate to prolate spheroidal, 3-colporate with ectocolpi showing lolongate or lalongate pores, exine sculpture granulate or microreticulate, and at the mesocolpium is microreticulate or reticulate with scattered granules in muri (Rueangsawang *et al.*, 2013).

Habit and Habitat: Herbs found in several different veld types especially in disturbed habitats (Baden *et al.*, 1995), while *Justicia campylostemon* occurs naturally in forest understorey and on forest margins and is tolerant of a wide range of rainfall and temperatures (Leistner, 2000). Twenty-three species of *Justicia* occur in Southern Africa where they are widespread (Leistner, 2000). Acanthaceae is more likely to represent the open veld rather than the swamp vegetation (Scott 1982).

Pollination: Insect pollinated (Fabian and Germishuizen, 1982; Pooley, 1998).

56. *Dicliptera* type Juss. (Acanthaceae) Plate 2, figure 56. Pollen grains prolate, Amb. Trigonal, tricolporate, colpi and pseudocolpi with perforate sculpture, exine sculpture reticulate, the brochi filled with small, meshed reticulum (Al-Hakimi *et al*. 2013).

Habit and Habitat: Herbs occurring in warm and tropical areas, bushveld, thornveld and highveld grassland (McQuillan, 2016). Some species are endemic to South Africa such as *Dicliptera cernua* (Manning and Goldblatt, 2012).

Pollination: Insect pollinated (McQuillan, 2016).

57. *Isoglossa* type Oerst. (Acanthaceae) Plate 2, figure 57. Pollen grain oblate, Amb. Circular (Darbyshire, 2009; Balkwill *et al*. 2017); biporate with pronounced marginal girdle (Darbyshire, 2009).

Habit/Habitat: Herbs or shrubs forming dense colonies in the understorey of sub-tropical to tropical moist forest including disturbed areas, along pathways and stream banks. The forest patches within which many species of *Isoglossa* occur are isolated within a matrix of grassland. *Isoglossa ovata* is the only species that grows in grasslands (Balkwill *et al*. 2017).

Pollination: Insect pollinated (Griffiths *et al.*, 2009)

58. Apiaceae type Plate 2, figure 58. Pollen grains within this family have only a few, closely related morphological pollen types (mostly strongly prolate with parallel flanks, equatorially elongated pore, tricolporate, often psilate, thick exine) which makes differentiation difficult (Beug 2004).

Habit and Habitat: Herbs, rarely trees (e.g., *Heteromorpha*) found in multiple habitats depending on the species, ranging from wooded grassland, mountain grassland, bushveld, forest margins, coastal scrub, fynbos, moist places close to streams and rivers (Hilliard and Burtt, 1986; Goldblatt and Manning, 2000; Manning and Goldblatt, 1996).

Pollination: Self-compatible (self-pollination), but most are insect pollinated (Koul *et al*. 1993).

59. *Cerastium* type L. (Caryophyllaceae) Plate 2, figure 59. Pollen grains circular to spheroidal, pantoporate with numerous circular annulated pori, exine sculpture is micro-reticulate (Schüler and Hemp 2016).

Habit and Habitat: Herbs occurring in grassland, bushland, forest margins, or on roadsides as weeds (Schüler and Hemp 2016)

Pollination: Insect pollinated (Willemstein, 1987)

60. *Commelina* type L. (Commelinaceae) Plate 2, figure 60. Pollen grains prolate to spheroidal, monosulcate (Salamma *et al.,* 2019; Halbritter and Buchner, 2016). Micro-verrucate exine sculpture (Halbritter and Buchner, 2016).

Habit and Habitat: Herbs typically found in moist forest and grasslands (Madau, 2007; Chevalier *et al*. 2021).

Pollination: Insect pollinated (Faden, 1998).

61. ***Drosera* type L. (Droseraceae)** Plate 2, figure 61. Pollen grains tetrads, and the tetrahedral disposition is more frequent than the square planar disposition of the tetrads (Rodondi *et al*. 2004), each monad is often globose in shape and with distinctive faces, 10-15 apertures (stephanoporate-like), exine sculpture echinate (Rodondi *et al*. 2004). Pollen colour varies for each species (Rodondi *et al*. 2004) and pollen possess a complex distal surface which is due to its echinate features (Beug, 1961; Erdtman *et al.*, 1961; Punt *et al.*, 2003).

Habit and Habitat: Herbaceous insectivorous plants that are found in very wet and sunny areas such as *Sphagnum* bogs, swamp, banks of marshes and dripping cliffs (D'Amato, 1998; McQuillan, 2008).

Pollination: They are self-compatible hence undergo self-pollination but are sometimes insect pollinated (McQuillan, 2008).

62. ***Erica* type L. (Ericaceae)** Plate 2, figure 62. Pollen grains tetrad, commonly isodynamoporous, and in tetrahedral to normal, compact and lobed arrangement, all four grains (monads) of the same size (Erdtman, 1952), exine sculpture rugulate to rugulate-granulate (Schüler and Hemp 2016; Van Zinderen Bakker, 1970).

Habit and Habitat: Shrubs found on mountains, in open forest, fynbos, grassland, often on rocky places and often grow together with *Stoebe*, *Artemisia* and *Protea* (Schüler and Hemp 2016).

Pollination: Self-compatible (self-pollination) but also undergoes cross-pollination which is aided by wind, insects and birds (Sarwar, 2007).

63. ***Acalypha*** **type L. (Euphorbiaceae)** Plate 2, figure 63. Pollen grains oblate-spheroidal to suboblate, small (c. 20µm), tricolporate with very short colpi, rugulate to microrugulate exine sculpture (Sagun *et al*. 2006).

Habit and Habitat: Herbs growing in a wide range of habitats depending on the species, *A. glabrata*, has a coastal distribution and can often be found in riverine thickets (Scott 1982, Schmidt *et al*. 2002). Other species can be found in grassland, forest margins, rocky and open wastelands, roadsides, bushveld (Radcliffe-Smith, 1998).

Pollination: Wind pollination (Sagun *et al*. 2006).

64. ***Geranium*** **type L. (Geraniaceae)** Plate 2, figure 64. Pollen grains prolate-spheroidal, tricolporate with round to lolongate pore, exine sculpture sculpture is cristato-reticulate (Verhoeven and Venter, 1992).

Habit and Habitat: Herbs or shrubs occurring in moist environments, floodplains and upland woodlands, savannas and rocky glades. Wild *Geranium type* is a typical species of mesic deciduous woodlands (Hilliard and Burtt, 1985). Most *Geranium* spp. can be found in montane grasslands (Chevalier *et al*. 2021)

Pollination: Insect pollinated (Hilliard and Burtt, 1985).

65. Liliaceae (others) Plate 2, figure 65. Pollen grains elliptic, monosulcate and are often difficult to delimit. Exine sculpture ranges from psilate to perforate to rugulate, scabrate and reticulate (Kosenko, 1999; Tekşen *et al*. 2010).

Habit and Habitat: Herbs found in a wide range of habitats from plains, steppes, alpine meadows to deciduous forest (Simpson, 2011; Patterson and Givnish, 2002).

Pollination: Insect pollinated (Sharma, 2009).

66. *Ammannia* type L. (Lythraceae) Plate 2, figure 66. Pollen grains prolate, sub-prolate to oblate-spheroidal, heterocolpate with elliptic apertures which are acute at the tips; exine sculpture are rugulate-striate or rugulate-fossulate rarely scabrate or subpsilate (Perveen and Qaiser, 2005).

Habit and Habitat: Herbs found in plains, moist or marshy environments, often in saline soil, along wetland margins or in fields (Lesica *et al*. 2012).

Pollination: Self-compatible (self-pollination) although outcrossing occurs, as evidenced by the hybrid nature of *A. coccinea* (Graham 1985).

67. *Sida* type L. (Malvaceae) Plate 2, figure 67. Pollen grains circular to spheroidal, >50 µm, polyporate, echinate with short, pointed, densely distributed spines, exine sculpture rugulate to micro verrucate (Schüler and Hemp 2016; Agwu *et al*. 2015). The genus is stenopalynous (El Naggar and Sawady, 2008).

Habit and Habitat: Shrubs found growing in dry habitat, grasslands, bushland and thicket, often in rocky places (Schüler and Hemp 2016).

Pollination: Insect pollinated (Dawar *et al*. 1994).

68. *Triumfetta* type L. (Malvaceae) Plate 2, figure 68. Pollen grains prolate to rhombic, tricolporate, exine sculpture reticulate (Schüler and Hemp 2016).

Habit and Habitat: Shrubs or small trees growing at forest margins, but also in dry hilly savanna, woodland and grassland (Schüler and Hemp 2016).

Pollination: Insect pollinated (Collevatti *et al*. 1998).

69. *Polygala* type L. (Polygalaceae) Plate 2, figure 69. Pollen grains often prolate-spheroidal, polyzonocolporate with 8-20 colpi, exine sculpture often psilate to granulate-rugulate, robust exine and polar fields often have lacunae (Beug 2004; Sarvi *et al*. 2022).

Habit and Habitat: Shrubs or herbs and cover a wide range of habitats ranging from forest edges, open woodlands, grassland and watercourses (Retief and Herman 1997).

Pollination: Insect pollinated (Westerkamp and Weber 1997, Johannsmeier 2016).

70. *Anthospermum* type L. (Rubiaceae) Plate 2, figure 70. Pollen grains oblate, sub-oblate, prolate-spheroidal or sub-prolate, tricolporate, exine sculpture rugulate (Robbrecht, 1982).

Habit and Habitat: Shrubs, sub-shrubs or herbs found in a wide range of habitats ranging from rocky outcrops in grasslands, rocky ridges, rocky sheets, on koppies, and krantzes (Puff 1986a; 1986b). *Anthospermum* pollen, when it occurs in association with ericaceous elements, may suggest cooler conditions (Livingstone, 1967; Morrison, 1968).

Pollination: Puff (1982) reports that *Anthospermum* is a wind pollinated genera.

71. *Oldenlandia* type L. (Rubiaceae) Plate 2, figure 71. Pollen grains sub-spheroidal, 3- to 4-colporate with long and narrow colpi, exine sculpture reticulate (Lewis, 1984).

Habit and Habitat: Herbs growing generally on moist disturbed soil, in swamps, along creek banks and beds, permanent water bodies in woodlands, forests and grasslands (Halford, 1992).

Pollination: Self-compatible (self-pollination) while some species are insect pollinated (Riveros *et al*. 1995; Raju and Krishna, 2018)

72. *Selago* type L. (Scrophulariaceae) Plate 2, figure 72. Pollen grains prolate spheroidal, trizonocolporate with long colpi, exine sculpture reticulate to micro-reticulate (Argue, 1993). It is referred to as *Selago* type instead of *Selago* because chances are that pollen of other Flacourtiaceae or other families could be included (Scott 1982).

Habit and Habitat: Shrubs and herbs that are widely distributed and represent an open veld vegetation (Scott 1982).

Pollination: Insect pollinated (Goldblatt and Manning, 2000).

73. *Passerina* type L. (Thymeleaceae) Plate 2, figure 73. Pollen grains spheroidal, pantoporate (18-44 composite, slightly protruding pores), Pori slightly bigger than lumina in the reticulum, exine sculpture reticulate (Bradenkamp and Van Wyk, 1996).

Habit and Habitat: Shrubs or shrublets occurring in different habitats depending on the species. Some species grow on the mountain crest like *P. montana* (Van der Schijff and Schoonraad, 1971). *P. corymbosa* grows in lowlands where dry fynbos, renosterveld and succulent karoo merge (Bean and John, 2005). *P. ericoides* occurs on littoral sand between rocks, or in coastal dune valleys between the primary and secondary dunes (Gunn and Codd, 1981). *Passerina* might indicate relatively cold conditions in the interior of South African Quaternary pollen records (Scott 1982).

Pollination: Wind pollinated (Bean and John, 2005).

3.2.2.2 Herbs and shrublets of relatively dry habitats and/or disturbance indicators

74. Aizoaceae type, Plate 2, figure 74. Pollen grains oblate-spheroidal to prolate-spheroidal, rarely sub-prolate, tricolporate with long colpi which tapers at the end, exine sculpture ranges from scabrate, spinulose, tubuliferous punctate and punctate-striate (Abo El-Naga *et al.*, 2014), often slightly thickened at poles. Aizoaceae have eurypalynous pollen and the morphology can be similar in other families like Portulacaceae (Scott 1982).

Habit and Habitat: Small shrubs or herbs occurring in diverse habitats such as dry subtropical deserts, wet tropical coasts and snow-covered subtropical mountains but most species and genera occur in semi-arid winter rainfall areas (Hartmann, 2001a).

Pollination: Insect pollinated (Peter *et al.*, 2004)

75. *Amaranthus* type L. (Amaranthaceae) Plate 2, figure 75. Pollen grains spheroidal, pantoporate, exine sculpture scabrate (Terzieva *et al.*, 2019).

Habit and Habitat: Herbs found in a wide range of habitats, from roadsides, public gardens to cultivated areas (Scott 1982; Iamonico and El Mokni, 2019)

Pollination: Self-pollination and cross-pollination which is aided by wind (Townsend, 1993).

76. *Alternanthera* type Forssk. (Amaranthaceae) Plate 2, figure 76. Pollen grains dodecahedric or circular to spheroidal, pantoporate (12-30 pores), the pore is surrounded by a rounded or elongate intectated flat ring area which is covered by nanospines, exine sculpture varies from perforate to micro echinate (Pino *et al.*, 2015).

Habit and Habitat: Herbs growing in different environments such as pastures, waste lands, also in wet environments such as marsh, irrigated agricultural land, along water courses either in a pure population or in association with other aquatic species such as *Cyperus*, *Polygonum*, *Rumex*, etc., (Tiwari *et al.*, 2015).

Pollination: Insect pollinated (Kubitzki *et al.*, 1994; Aluri and Chappidi, 2017).

77. ***Atriplex* type L. (Amaranthaceae)** Plate 2, figure 77. Pollen grains spheroidal to sub-spheroidal, pantoporate with many pores and numerous evenly distributed spinules, exine sculpture punctate (Olvera *et al.,* 2006). This morphology previously was typically placed under “Chenopodiaceae / Amaranthaceae”.

Habit and Habitat: Herbs, sub-shrubs or shrubs; just as other species in the family, *Atriplex* are facultative halophytes i.e., they grow in saline environments (Kelley *et al*. 1982). *Atriplex* can be found in deserts, semi-deserts, roadsides, any habitat rich in salt (Mandák and Pyšek, 1998).

Pollination: Predominantly wind pollinated (Blackwell and Powell, 1981).

78. **Tubuliflorae (Asteraceae)** Plate 3, figure 78. Pollen grains oblate spheroidal or prolate spheroidal, tricolporate, echinate exine sculpture with echinae that are longer than wide (Stanski *et al.,* 2013).

Habit and Habitat: Herbs, rarely shrubs and grow in varied habitats, but they form an important constituent of grassland and are important in the Karoo vegetation and macchia (Coetzee, 1967; Scott, 1982)

Pollination: Predominantly insect pollinated, but some are wind pollinated (Berry and Calvo, 1989).

79. **Liguliflorae, *Lychnophora* type Mart. (Asteraceae)** Plate 3, figure 79. Pollen grains prolate - spheroidal (Loecuille *et al* 2012), tricolporate with an echinate exine sculpture (Bolick and

Keeley, 1994). *Lychnophora* type is included in the type A pollen grains of the Vernonieae as designated by Keeley and Jones (1977; 1979).

Habit and Habitat: Shrubs adapted to shallow soils on quartzite and sandstones hence often are found in rocky grasslands (Bueno *et al*. 2017; Silva *et al*. 2014).

Pollination: Bird pollinated (Grant 1950).

80. Liguliflorae, *Vernonia* type Schreb. (Asteraceae) Plate 3, figure 80. Pollen grains oblate spheroidal, spheroidal or prolate spheroidal, 3-colporate with colpi interrupting the lophase that separate the poral lacuna from the abporal lacunae, pori lalongate to subcircular, echinolophate exine sculpture (Dematteis and Pire, 2008).

Habit and Habitat: Herbs, shrubs or small trees and are common in the summer rainfall grassland in southern Africa (Pooley, 1998)

Pollination: Insect pollinated (Nguimkeng *et al*., 2017).

81. Liguliflorae, *Vernonia*- E type Schreb. (Asteraceae) Plate 3, figure 81. Pollen grains spheroidal, 3-porate with pori more or less circular, psilolophate sculpture (Dematteis and Pire, 2008). The *Vernonia* type E differs from other *Vernonia type*s in the possession of porate aperture and a psilate lophase sculpture as compared to the colporate aperture and sub-echinate to echinate lophase sculpture possessed by others (Dematteis and Pire, 2008).

Habit and Habitat: Herbs, shrubs or small trees and are common in the summer rainfall grasslands in southern Africa (Pooley, 1998)

Pollination: Insect pollinated (Nguimkeng *et al.*, 2017).

82. *Stoebe* type *L. -Elytropappus.* Cass. (Asteraceae) Plate 3, figure 82. Pollen grains prolate-spheroidal to oblate-spheroidal, tricolporate, exine sculpture echinate with spines that are less than 0.3µm in length making the spines inconspicuous (Ingram, 2011). Both *Stoebe* and *Elytropappus* pollen possess this morphology (Scott, 1982).

Habit and Habitat: Herbs and shrubs; *Elytropappus* is endemic to South Africa and restricted to the winter-rainfall area hence, expected more often in the fynbos and ecotones to Karoo biomes or in the drier western parts; found on the rocky ridges of flat areas from sea level to 2200m (Koekemoer, 2002). *Stoebe* has a wider distribution in highveld or mountainous areas as far north as the East African mountains (Coetzee 1967; Scott, 1982). Coetzee (1967) recorded *S. plumosa* from near Aliwal North and suggested that the high number of *Stoebe* pollen in her late Pleistocene peat samples indicated cooler conditions during that period (Scott, 1982). Most species of *Stoebe* are pioneers on disturbed soil and they are prominent species to germinate after a fire (Koekemoer, 2002).

Pollination: It is not known how *Stoebe* and *Elytropappus* are pollinated, but the genera appear to be adapted to wind pollination, and genetic studies indicate that it probably outcrosses (does not self-fertilize) (Levyns, 1956).

83. *Artemisia* type L. (Asteraceae) Plate 3, figure 83. Pollen grains prolate to perprolate, Amb. spheroidal to triangular, tricolporate, with colpi wider at the equator and narrow at the pole, very short spines and conspicuous short columella (Ghahreman *et al.*, 2007), and relatively thick tectum. Scott (1982, 2016) suggests that there seems to be two types that differ in the thicknesses of columella and tectum layers, with the types found in the Holocene with equal thickness of these layers, and those of the Pleistocene more often with longer columella.

Habit and Habitat: Herbs; mostly distributed in the temperate regions of the world. In the wild it grows at altitudes between 202-440m on damp slopes, along streams and forest margins. Hamilton (1972) considers *Artemisia* pollen as a moderately well dispersed type in East Africa where *A. afra* is an important taxon in Ericaceous and Afro-alpine belts. In the late Pleistocene deposits of East Africa, *A. afra* is considered as an indicator of drier conditions than ericaceous belt species (Coetzee, 1967). In South Africa, *A. afra* occurs in high numbers in the eastern sub-humid mountainous areas while in the drier western parts it is found near water sources (Scott, 1982, 1988, 1989).

Pollination: Although many species are wind pollinated, there is evidence of insect pollination for some species (Tkach *et al.*, 2007; Vallés *et al*. 2001).

84. *Gerbera* type L. (Asteraceae) Plate 3, figure 84. Pollen grains prolate to subprolate, tricolporate with very large colpi, conspicuous columella and granulate sculpture (Xu *et al.*, 2018).

Habit and Habitat: Herbs; just as other Asteraceae these plants represent a wide variety of habitats and form an important constituent of southern African grasslands (Scott, 1982). Most species occur in grassland, but a few species are found in forests (Hilliard, 1977).

Pollination: Both self-pollination and cross-pollination occur in this genus. Cross-pollination is carried out by insects (Johnson, 2010).

85. *Dicoma* type. Cass. (Asteraceae) Plate 3, figure 85. Pollen grains suboblate or prolate, trizonocolporate with very conspicuous columellae and short echinae that are broader at the base (Coutinho *et al*, 2012).

Habitat: Herbs or shrubs found growing in the summer rainfall areas and occur in grasslands, hillsides or flat grasslands and in savanna (Eliovson, 1980).

Pollination: As a member of palaeotropical Asteraceae, potential pollinators of *Dicoma* include birds (Vogel, 2015).

86. *Pentzia* type Thunb. (Asteraceae) Plate 3, figure 86. Pollen grains oblate spheroidal or prolate spheroidal, tricolporate, exine scupture echinate with geniculum (Ingram, 2011).

Habit and Habitat: Shrublets found in Succulent Karoo, Nama Karoo, Renosterveld and Fynbos. *P. dentata* is endemic to South Africa (Trinder-Smith, 2003)

Pollination: Wind and insect pollinated (Vlok and Schutte-Vlok, 2010).

87. *Crassula* type L. (Crassulaceae) Plate 3, figure 87. Pollen grains prolate, tricolporate with long, narrow colpi and circular pore, exine sculpture psilate (Schüler and Hemp 2016).

Habit and Habitat: *Crassula* are succulents ranging from groundcover to shrubs or small trees. Occur in moist soil along streams and in wetlands, in upland forest, bushland and roadsides (Schüler and Hemp 2016). They also grow in fynbos and on mountains (Rowley, 2003).

Pollination: Predominantly insect pollinated (Rowley, 2003).

3.2.2.3 Grasses, including cultivars

88. Poaceae (25-40µm). Plate 3, figure 88. Pollen grains spherical to spheroidal to subprolate with a single annulated pore, exine sculpture ranges from psilate to granulate to scabrate. These are pollen grains of wild grasses, and they include numerous genera *Cynodon, Dactyloctenium, Diheteropogon* etc. (Schüler and Hemp 2016).

Habit and Habitat: Herbaceous grasses found in grassland, open bushland, deciduoud bushland, wooded grassland and savanna grassland (Schüler and Hemp 2016).

Pollination: Wind pollinated (Schüler and Hemp 2016).

89. Cerealia type (>40µm) **(Poaceae)** Plate 3, figure 89. Pollen grains spherical to spheroidal to subprolate with a single annulated pore, relatively large annulus with diameter greater than or equals 11µm (Joly *et al*. 2007; Beug, 2004). However, the pollen grains of several wild grasses species also show large diameters (Joly *et al*. 2007).

Habit and Habitat: Herbaceous grasses, includes cereal grasses whether cultivated or wild. The plants are found in varied habitats ranging from grassland, open bushland, deciduous bushland, wooded grassland and savanna grassland (Schüler and Hemp 2016).

Pollination: Some species of this group are self-compatible (Vuorela, 1975; Hicks, 1988). Some are insect pollinated while some are wind pollinated (Segerstrom, 1991; Vuorela, 1985).

Some cereal crops such as *Hordeum*, *Triticum* and *Avena* do not produce large quantities of pollen as they are to some extent self-pollinated (Vuorela, 1975; Hicks, 1988). These genera are short distance dispersed, like most pollen from insect pollinated cereals in cultivated lands, e.g., *Hordeum vulgare* (Segerstrom, 1991; Vuorela, 1985). Hence, small patches of cultivated land, used for a short period of time in a forested environment will seldom result in a strong signal of cereal pollen in palynological analyses.

90. *Zea mays* L. (Poaceae) Plate 3, figure 90. Pollen grains spherical to spheroidal and has the largest pollen size of the cereals (>70µm), monoporate with annulated pore, exine sculpture psilate (Sun and Liang, 1991).

Habitat: Large herbaceous grass; Maize is a versatile crop grown in varied habitats, in fact, the adaptability of maize to diverse environments is unmatched by any other crop hence the original habitat is obscure. It can grow on cropland, roadsides, grassland (Tripathi *et al*, 2011).

Pollination: Wind pollinated (Tripathi *et al*, 2011).

3.2.2.4 Herbs and shrublets, neophytic, crops and weeds

a. Aquatic plants

91. *Lemna* type L. (Araceae) Plate 3, figure 91. Pollen grains circular to spheroidal, monoporate with circular pore, exine sculpture spinulose to spinulate-punctate (Perveen 1999; Díez 1988).

Habit and Habitat: Herbaceous macrophytes found in small bodies of water such as ponds, pools, ditches and quiet streams (Ali *et al*. 2016).

Pollination: Self-compatible and may also be wind pollinated (Díez 1988).

92. *Myriophyllum* type L. (Haloragaceae) Plate 3, figure 92. Pollen grains sub-oblate to oblate, 3-5, zonoporate with annulation, exine sculpture micro-verrucate or micro or nano-echinate or micro-rugulate (Mathewes, 1978; Aiken, 1978).

Habit and Habitat: Herbaceous invasive macrophytes found in ponds, lakes, marshes, ditches, and slow running streams of lowland areas. It is invasive with only two species now naturalised in Southern Africa, i.e. *M. spicatum* and *M. aquaticum*. Both are thought to be introduced (Mendes, 1978). It is considered Africa's most invasive aquatic weed (Coetzee *et al.*, 2011).

Pollination: Wind pollinated (Cook, 1988).

93. *Utricularia* type L. (Lentibulariaceae) Plate 3, figure 93. Pollen grains sub-oblate to prolate-spheroidal, 10-19 zonocolporate, exine sculpture psilate (on mesocolpium), fossulate or perforate (on apocolpium) (Beretta *et al.*, 2014)

Habit and Habitat: Herbaceous macrophytes found in ponds, marshes, river, swampy areas, slow running water, wet areas in grassland and deciduous forest (Mishra and Kumar, 2020).

Pollination: Insect pollinated (Clivati *et al.*, 2013; Plachno *et al.*, 2019).

94. ***Persicaria*** **type Mill. (Polygonacaeae)** Plate 3, figure 93. Pollen grains spheroidal, pantoporate with reticulate exine sculpture Yasmin *et al*.2010). *Persicaria* type may include pollen grains of the pantoporate species of *Polygonum* which is difficult to delimit as fossils.

Habit and Habitat: Evergreen herbs found in moist to wet areas of riverbanks, roadsides and disturbed sites; it is abundant near springs, shores, ditches and stream banks (Ruffo *et al*. 2002).

Pollination: Insect pollinated (Shapiro, 2002).

b. Wetland plants

95. ***Hydrocotyle*** **type L. (Apiaceae)** Plate 3, figure 95. Pollen grains prolate-spheroidal to sub-prolate, tricolporate, exine sculpture reticulate to perforate and sometimes rugulate to foveolate (Jones and Pearce, 2015; Sangsuk *et al.,* 2021).

Habit and Habitat: Herbs, mostly found in marshes, ponds, at lake edges, margins of slow flowing watercourses, riverbanks, wetlands (McChesney 1994, Scott 1982).

Pollination: Self-compatible; hence they undergo self-pollination (Grime *et al*. 1988).

96. ***Ascolepis*** **type Steud. (Cyperaceae)** Plate 3, figure 96. Pollen grains triangular, 4-aperturate and exine sculpture scabrate to punctate (Sultan *et al*. 1994).

Habit and Habitat: Herbaceous sedge found in marshes and seasonally wet grassland (Mapaura and Timberlake 2004).

Pollination: Insect pollinated (Nagels *et al*. 2009; Goetghebeur, 1998).

97. *Carex* type L. (Cyperaceae) Plate 3, figure 97. Pollen grains subprolate, prolate-spheroidalal to suboblate, Amb often triangular with obtuse or elliptic apices in outline, 5-6 circular or elongated poroids (Wronska-Pilarek *et al*. 2010), exine sculpture often scabrate (Wronska-Pilarek *et al*. 2010). Pollen characters in *Carex* type are not diagnostic hence, are not considered as taxonomic tools to delimit within the genera and sub genera (Wronska-Pilarek *et al*. 2010). Tarasevich (1992) reported that it is impossible to recognize individual species of Cyperaceae based on pollen morphology.

Habit and Habitat: Herbaceous sedge; in southern Africa, Cyperaceae are found mostly in wetlands, marshes, swamps, along water courses, in moist grassland and along forest margins (Archer and Craven, 2004).

Pollination: Wind pollinated but a transition from wind to insect-pollination has been reported in some tropical sedges (Villa-Machio *et al.*, 2020).

98. *Sebaea* type Sol. ex R.Br. (Gentianaceae) Plate 3, figure 98. Pollen grains often spheroidal, tricolporate, with striato-reticulate to striato-rugulate and reticulate exine sculpture (Nilsson *et al.*, 2002).

Habit and Habitat: Herbs, in southern African often found growing in wet, disturbed habitats, depending on the species, they are found in a variety of habitats from open woodland to dense tropical forest, grasslands and savanna, marshes, wet rocks, or sandy riverbanks (Paive and Nogueira, 1990).

Pollination: Self-compatible, some species are insect pollinated (Kissling and Barrett, 2013).

99. *Phragmites* type Adans. (Poaceae) Plate 3, figure 99. Just like other Poaceae, *Phragmites* pollen grains are spherical to spheroidal, monoporate with annulus, exine sculpture psilate to granulate to scabrate (Clevering and Lissner, 1999). Usually, pollen of *Phragmites* are 15-25µm in size (Clark and Patterson 1985).

Habit and Habitat: Herbaceous grass found in wetlands, common on riverbeds and other wetland vegetation types (Gibbs Russell *et al*. 1990; Van Oudtshoorn, 1999).

Pollination: Self-compatible, but they often undergo wind pollination (Kettenring *et al*. 2011).

100. *Ranunculus* type L. (Ranunculaceae) Plate 3, figure 100. Pollen grains prolate to prolate-spheroidal and sometimes sub-spheroidal to spheroidal, tricolpate with colpi almost the length of the pollen, exine sculpture often distinctly granulate to scabrate (Kallajxhiu *et al.*, 2015; Erkul *et al.,* 2021).

Habit and Habitat: Herbs found in salt marshes, along stream banks, near ponds, grassy slopes near the mountain, meadows; generally, they grow at elevations of 950m a.s.l. and above and are tolerant to salt (Erkul *et al.,* 2021).

Pollination: Insect pollinated (Steinbach and Gottsberger, 1994).

101. ***Typha*** **type L. (Typhaceae)** Plate 3, figure 101. Pollen grains oblate-spheroidal to oblate, monoporate, reticulate to perforate exine sculpture (Hamdi *et al.*, 2010).

Habit and Habitat: Herbs found in aquatic and wetland environments, marshes, stream banks, dams and lakes (Grace and Wetzel, 1982).

Pollination: Self-compatible but are usually wind pollinated (Ahee *et al.*, 2015).

102. ***Gunnera*** **type L. (Gunneraceae)** Plate 3, figure 102. Pollen grains sub-oblate to spheroidal, tricolpate, reticulate exine sculpture (Wanntorp *et al.*, 2004).

Habit and Habitat: Herbs found at forest boundaries close to wetlands, stream-sides, at coastal cliffs, waterways, roadsides, and wet meadows (Williams *et al.*, 2005).

Pollination: Wind pollinated (Wanntorp and Ronse De Craene, 2005).

3.2.3 Cryptogams, marine elements and other plants and insect remains

3.2.3.1 Bryophytes and Pteridophytes

1. ***Anemia* type Sw. (Anemiaceae)** Plate 4, figure 1. Spore triangular to subcircular, tetrahedral, trilete, exospore sculpture cicatricose to canaliculate or reticulate and sclerine stratified with structured perine and thicker structured exospore (Dettmann and Clifford, 1991).

Habitat: They are found in open, well-drained areas, montane and highveld areas, river and riverbanks and are usually found occurring with savanna or shrubby vegetation (Dettmann and Clifford, 1991).

2. ***Mohria* type Sw. (Anemiaceae)** Plate 4, figure 2. Spores triangular to subtriangular, tetrahedral, trilete with a cicatricose (ribbed) sculptural pattern, (each rib may appear to be double barreled), sclerine stratified, comprising granular, stratified exospore (Dettmann and Clifford, 1991).

Habitat: Just like *Anemia*, they are found in open, well-drained areas, montane and highveld areas, river and riverbanks and are usually found occurring with savanna or shrubby vegetation (Dettmann and Clifford, 1991; Scott 1982).

3. ***Anthoceros* type L. (Anthocerotaceae)** Plate 4, figure 3. Spores sub-spheroidal to triangular, trilete with a distinct triradiate scar or mark, the exospore sculpture is spinulate on the distal surface and foveolate on the proximal surface (Villarreal *et al.*, 2017).

Habitat: *Anthoceros* occurs on bare ground along paths and on friable banks between 600 and 700m (Pressel *et al.*, 2016) in moist or seasonally moist settings.

4. ***Cyathea* type Hook. (Cytheaceae)** Plate 4, figure 4. Spores triangular to triangular concave, trilete with often psilate, granulate to scabrate exospore sculpture (Schüler and Hemp 2016).

   Habitat: These tree ferns occur in moist forest, often near streams, moist montane forest, riverine forest (Schüler and Hemp 2016). Although the spores detected in the cores often belong to *C. manniana* type, the species occurs in Zimbabwe and Mozambique but not in South Africa. Most likely, the spores were produced by a related taxon.

5. ***Lygodium* type Sw. (Lygodiaceae)** Plate 4, figure 5. Spores are subtriangular, tetrahedral-globose, with convex proximal face and hemispheric distal face, often trilete, exospore sculpture often verrucate to spheroid-tuberculate with perforated perine (Glacosa *et al*. 2012; Wang *et al*. 2001).

Habitat: They are climbers and are found in wet soil in wooded thickets, marshes, open woodlands, forested freshwater wetland and Mangrove communities (Munger 2005; Soti *et al*. 2014).

6. **Monolete spores.** Plate 4, figure 6. These are bean-shaped, and include all monolete, psilate pteridophyte spores whose perines were lost as result of taphonomy or extraction processes making it impossible to delimit them (Scott 1982).

Habitat: Generally, ferns occur in damp environments or seasonally damp environments, but Wei and Zhang (2016) reported that ferns producing monolete spores have a higher capacity to adapt to extreme habitats compared to ferns which produce trilete spores.

7. **cf. *Orthotrichum* type Hedw. (Orthotrichaceae, Bryophyta)** Plate 4, figure 7. Spores spheroidal to angular with verrucate to gemmate exospore sculpture (Savaroglu 2015).

Habitat: The saxicolous type occurs on rock surfaces while the corticolous type occurs as epiphytes on trees (Savaroglu 2015).

8. ***Polypodium* type L. (Polypodiaceae)** Plate 4, figure 8. Polypodiaceae produce both monolete and trilete spores. Spores often ellipsoidal, with psilate to scabrate, granulate, verrucate and fossulate sclerine (Roubik and Moreno, 1991)

Habitat: Polypodiaceae are mostly epiphytic, found in waterfalls or damp floors in evergreen forest, valley forest, woodland, riverine forest, or damp grassy slopes (Schüler and Hemp 2016).

9. ***Pteris* type L. (Pteridaceae)** Plate 4, figure 9. Spores triangular with rounded corners, tetrahedral, often trilete, although monolete and tetralete spores occur which are said to be abnormal (Chao and Huang, 2018). Exospore usually consists of two layers, exosporium verrucate to rugulate in the distal pole while its psilate in the proximal pole (Gonçalves de Freitas *et al.*, 2015). Cingulum on sides between corners, centrally thickened.

Habitat: The ferns occur in humid forest, on hills, creeks and river margins and shaded steep hills (Prado, 2005).

10. *Thelypteris* type Schmidel (Thelypterioideae) Plate 4, figure 10. Spores ellipsoidal, monolete with varied perine sculpture such as reticulate, verrucate to papillate (Tryon and Lugardon, 1991) and echinate (de León *et al*. 2008; Patel *et al*. 2019).

Habitat: The ferns are found in a variety of moist habitats, often shady, ranging from damp sandy thickets, swamps, to damp meadows, edges of marshes and bogs (Burrows, 1990; Jacobsen, 1983).

3.2.3.2 Algae-Acritarchs-Dinoflagellates

11. Centrales (diatom)

11a. Corroded Centrales, Plate 4, figure 11a.

11b. *Actinoptychus* sp. Ehrenberg Plate 4, figure 11b. A single specimen with moderate preservation was recovered, diameter of undulating valve c. 62µm, c. 8-10 sectors, which might belong to *A. splendens* (Lee & Chang 1995).

Habitat: Species are marine and globally distributed (Lee & Chang 1995).

12. Michrystidium Plate 4, figure 12. Globose, spinose acritarch cyst <20µm diameter (Truswell 1978).

Habitat: Marine (Truswell 1978).

13. Dinoflagellate cyst

***13a. Impagidinium* sp.** Plate 4, figure 13a. Cyst with smooth septa, triple junctions do not have processes (Zonneveld & Pospelova 2015).

Habitat: Common in (sub)tropical environments (Harland 1983).

***13b. Spiniferites* sp.** Plate 4, figure 13b**.** Cysts spherical to elongate, septa along sutures, long processes on triple junctions (Zonneveld & Pospelova 2015).

Habitat: Common in (sub)tropical environments (Harland 1983).

14. Pseudoschizaea Plate 4, figure 14. These algal cysts are circular to ellipsoidal, inaperturate, striate surface consisting of concentric striae (Gonçalves de Freitas *et al.*, 2015). Synonym of *Concentricites* (Christopher 1976).

Habitat: *Pseudoschizaea* is found in coastal environments where there is freshwater influence (Medeanic *et al*. 2008), also in stagnant and shallow water (Luz *et al.*, 2011).

Affinity and reproduction: *Pseudoschizaea* are generally thought to be of algal origin (Christopher 1976, van Geel 1976b) but Scott (1992) questioned this because it is not found in literature of living algae and instead he considered it to be the resting structures of unidentified organisms.

3.2.3.3 Miscellaneous

15. Phytoliths. Plate 4, figure 15. Some tissues of a plant can produce siliceous deposits (amorphous SiO_2) but these are especially common in Poaceae where they form various morphological types (Piperno 2006). The depicted phytolith is bilobate as produced by Panicoideae, Aristidoideae or Bambusoideae (Piperno 2006). Phytolith analysis was not undertaken for the current study.

Habitat: Poaceae are widespread in several biomes, especially the Grassland and Savanna biome (Mucina & Rutherford 2006).

***16.* Moth wing scales.** Plate 4, figure 16. Thin membrane consisting of chitin between network of more robust veins (Hunt 1971).

Habitat: Terrestrial, multiple environments.

***17.* Microforaminiferal linings *(*Ammonoid type)** Plate 4, figure 17. The term microforaminiferal linings has been applied to the organic inner linings < 150µm that are found together with pollen and spores following palynological acid preparation (Stancliffe 1989). The depicted type follows the coiled planispiral morphological type (Stancliffe 1989). A systematic analysis was not undertaken for the current study.

Habitat: Marine.

18. *Filinia longiseta* (eggs) Ehrenberg (Rotifera) Plate 4, figure 18. *Filinia longiseta* type comprises the resting eggs of two taxa, *F. longiseta* and *F. passa* which belong to the Rotifera (van Geel 2001).

Habitat: Plancktonic taxa in ponds, lakes but also in brackish water, cosmopolitan, warmth-demanding (van Geel 2001).

19. Scolecodont. Plate 4, figure 19. Scolecodonts are regarded as jaws of annelid worms (Schwab 1966). The illustrated specimen has > 15 denticles and saddles; an identification of scolecodonts was not undertaken.

Habitat: Shallow marine conditions (Schwab 1966).

20. Charred cuticle. Plate 4, figure 20. Cuticles consist of polymers and leaf waxes which reveal the underlying cell morphology often to a diagnostic level; often phytoliths are embedded or stomata are visible (Wooller 2002). Cuticles were charred and fragmented; an identification of cuticles was not undertaken.

Habitat: Terrestrial, multiple environments.

3.2.3.4 Fungi

Fungal spores and other fungal remains are described below, also adding the type numbers as far as provided by van Geel (1976a) and van Geel *et al*. (2011), for non-pollen palynomorphs (NPPs). Fungi can reproduce sexually as well as asexually by forming durable, chitin-rich and often dark coloured spores that can easily survive for long periods of time in sediments (McConnaughey 2007).

1. ***Vargamyces aquaticus*** Tóth. (**Amniculicolaceae)** Plate 5, figure 1. Conidia are elongated/fusiform, feature 5–8 septae, truncated at base, rounded apex, generally mid-brown, end cells are pale brown, psilate, 64–132 × 10–17 µm, base 2.5–5 µm (Hernandez-Retrepo *et al*. 2017). Specimen damaged.

Habitat: Grows on submerged, dead wood, freshwater fungus (aquatic hyphomycetes) (Hernandez-Retrepo *et al*. 2017).

2. ***Lasiodiplodia theobromae*** Griffon & Maubl. (**Botryosphaeriaceae)** Plate 5, figure 2. type HdV-1043: cf. *Lasiodiplodia theobromae* (Pat.) van Geel *et al*. 2011. Ellispodal ascospores feature 1 septum, c. 27×14 µm, with longitudinal furrows (Müller and von Arx, 1962).

Habitat: Plant pathogens with a wide range of hosts (Úrbez-Torres, 2008),

3. ***Cladosporium* sp. Link** (**Cladosporiaceae)** Plate 5, figure 3. Oval-spindle-like conidia often in chains of 3-4, psilate and light brown; >10 µm or more (Ellis & Ellis 1997).

Habitat: *Cladosporium* grows on leaves and fruits (Ellis & Ellis 1997)

4. ***Munkovalsaria donacina* (Niessl) Aptroot** (**Dacampiaceae)** Plate 5, figure 4. type HdV-1027 (van Geel *et al*. 2011). The ascospores are elliptical, c. 20µm long and c. 10µm wide (Aptroot 1995), thick-walled, have 1 septum, constricted at septum, one cell is slightly wider with a pointed end, the other cell is slightly longer with a rounded apex (Aptroot 1995, van Geel *et al*. 2011).

Habitat: Grows on a wide range of different plants (van Geel *et al*. 2011).

5. ***Spegazzinia deightonii* (S. Hughes) Subram.** (**Didymosphaeriaceae)** Plate 5, figure 5. type HdV-1041(van Geel *et al*. 2011). Conidia originally 8-celled but fossils always fragmentary. Separate cells ca. 12–16 μm in diameter, excluding the up to 5 μm long spines.

Habitat: Saprophytes on plants and soil (Seifert *et al*. 2011). *Spegazzinia deightonii* can grow on different host plants (Ellis, 1971).

6. 7. and 8. *Dictyoarthrinium* cf. *sacchari* (J.A. Stev.) Damon (**Didymosphaeriaceae)** Plate 5, figure 6,7,8. type HdV-1015A-C (van Geel *et al*. 2011). Conidia square, cruciately septate, flattened in one plane, verruculose, 10–16 μmin diameter. The three types (differing in the number of appendages, see Plate II) were in first instance recorded separately, but later grouped together and represented by one curve in Fig. 2 (van Geel *et al*. 2011).

Habitat: *Dictyoarthrinium sacchari* is reported from a variety of tropical plants (Ellis, 1971). In the Lake Challa record these conidia are rare in the Glacial and Late-Glacial sections, becoming more common during the Holocene (van Geel *et al*. 2011).

9. *Diporotheca* sp. C. C. Gordon& C. G. Shaw (**Diporothecaceae)** Plate 5, figure 9. type HdV-1245 (van Geel *et al*. 1986). Fusiform ascospores, >45 μm, both ends truncate with pore. Surface with dark brown/blackish anastomosing ribs (van Geel *et al*. 2011, own measurements).

Habitat: In Europe indicating eutrophic conditions (van Geel *et al*. 2011 and references therein). Parasitic on *Solanum* species (Mibey and Hawksworth, 1995, Hillbrand *et al*. 2012) but probably also on other wetland taxa like the wetland fern *Thelypteris palustris* (van Geel *et al*. 1986).

10. cf. *Mitteriella ziziphina* Syd. (Englerulaceae) Plate 5, figure 10. type HdV-1049 (van Geel *et al*. 2011). Fusiform conidia up to c. 40 µm, dark brown large middle cell with more pale end cells, 4-septate (van Geel *et al*. 2011).

Habitat: On leaves, e.g., *Mitteriella ziziphina* on *Zizyphus nummularia* (Gautam & Avasthi 2016).

11. *Glomus* sp. Tul. & C. Tul. (Glomeraceae) Plate 5, figure 11. type HdV-1103: ***Glomus* sp.** (van Geel *et al*. 1989). Spherical chlamydospores, 30–50 µm, distinctive hyphal attachment, often septate (van Geel *et al*. 2011).

Habitat: Endomycorrhizal fungi living on different root (Anderson *et al*. 1984). High abundance in sediments might indicate soil erosion (see van Geel *et al*. 2011).

12. *Diplocladiella* cf. *scalaroides* G. Arnaud ex M.B. Ellis (Hyphomycetes) Plate 5, figure 12. type HdV-1025 (van Geel *et al*. 2011). Conidia triangular, 2-horned, ca. 25 µm wide from horn tip to horn tip, horns 2-septate. The species was observed on dead wood in Europe (Ellis, 1976).

Habitat: Found occasionally in Lake Challa pollen record from southeastern Kenya (van Geel *et al*. 2011). The genus is an aquatic hyphomycete growing on submerged wood; conidia can be detected in foam in rivers (see Lee *et al*. 1998).

13. *Meliola* sp. Fr. (**Meliolaceae)** Plate 5, figure 13. type UG-1137 (Gelorini *et al*. 2012). Ascospores 3-4 septate, cylindric, cells deeply constricted (Mibey & Kokwaro 1999, Gelorini *et al*. 2012)

Habitat: In Kenya, species of *Meliola* grow on host plants including Asclepidiaceae (Mibey & Kokwaro 1999).

14. *Fusarium* sp. Link (**Nectriaceae)** Plate 5, figure 14. Macroconidia fusiform, often crescent-shaped, 5-7 septae, end cells tapering (Nelson *et al*. 1994).

Habitat: Growing on a wide range of substrates, often in soils where they are associated with plant roots, but also on aerial plant parts in a wide range of habitats from tropical to temperate but even in harsh environments like deserts (Nelson *et al*. 1994).

15. *Alternaria* sp. Nees (**Pleosporaceae)** Plate 5, figure 14. type HdV-1034 (van Geel *et al*. 2011)**.** Conidia 45–50μm long (van Geel *et al*. 2011), obclavate, tapering, wider at end, with transverse and longitudinal septa, verrucate sculpture (van Geel *et al*. 2011).

Habitat: The species are saprophytes on plants and in soils (Lee *et al*. 2015).

16. *Curvularia* sp. Boedijn (**Pleosporaceae)** Plate 5, figure 16. type HdV-1029A-B (Van Geel *et al*. 2011). Curved conidia, featuring ≥ septa, length c. 30 μm or more. End cells paler in colour than dark brown central cell (Ellis 1971, 1976, Ellis & Ellis 1998, Van Geel *et al*. 2011). Only the symmetrical type HdV-1029A was recovered.

Habitat: The taxon might be favoured by higher humidity (Van Gell *et al*. 2011).

17. *Drechslera* biseptata (Sacc. & Roum.) Richardson & Fraser (**Pleosporaceae)** Plate 5, figure 17. Conidia pale brown, smooth, 2-3 pseudosepta, c. 25µm (Ellis & Ellis 1997).

Habitat: Grows on dead plant material of e.g., *Avena*, *Dactylis* and *Triticum* (Ellis & Ellis 1997).

18. ***Epicoccum purpurascens*** **Ehrenb** (**Pleosporaceae)** Plate 5, figure 18. type HdV-1011 (van Geel *et al*. 2011)**.** Spherical, verrucate conidia, diameter 15- >30 µm, multiple septae in an often slightly hexagonal arrangement, brown,

Habitat: Cosmopolitan saprophyte on dead plant matter, in soil, on crops like potatoes and sugar beets (Ellis, 1971, Domsch *et al*. 1980). Moderate in MK 24 samples.

19. *Pleospora androsaces* **Fuckel** (**Pleosporaceae)** Plate 5, figure 19. type HdV-1046 (van Geel *et al*. 2011)**.** Spores large, dark brown, elliptic, many transverse and max. Five longitudinal septa (Ellis & Elli 1997; van Geel *et al*. 2011)

Habitat: On dead leaves, e.g., of *Silene acaulis* (Ellis & Ellis 1997).

20. *Gelasinospora* cf. *cratophora* R. S. Khan & J. C. Krug (**Sordariaceae)** Plate 5, figure 20. type HdV-1093: *Gelasinospora* cf. *cratiphora* R.S. Khan & J.C. Krug (van Geel *et al*. 2011)**.** Ellipsoidal ascospores, length c. 35 µm or more, dark brown with regularly spaced, small light pits (diameter c. 1 µm), no septae (van Geel *et al*. 2011), *G. cerealia* ascospores look similar, but their colour is described as red- brown (Ellis & Ellis 1997).

Habitat: Occurs on dung, charred particles and wood (Lundqvist 1972). *G. cerealia* grows on wheat grains (Ellis & Ellis 1997).

1. ***Gelasinospora* cf. *dictyophora* R.S. Khan & J.C. Krug** (**Sordariaceae)** Plate 5, figure 21. type HdV-1351: *Gelasinospora* cf. *dictyophora* R.S. Khan & J.C. Krug (van Geel *et al*. 2011). Ellipsoidal ascospores, length c. 35 µm or more, dark brown with regularly spaced, wide (diameter c. 3-4 µm) light pits, no septae (van Geel *et al*. 2011),

Habitat: Occurs on dung, charred particles and wood (Lundqvist 1972).

2. ***Sporomiella* type Ellis & Everh.** (**Sordariaceae)** Plate 5, figure 22. type HdV-113 (van Geel *et al*. 2003). Ascospores not multiseptated, but often isolated in samples, each cell (10-15 µm) has a narrow germslit running along its flank, identification to species level is challenging (see discussion in van Geel *et al*. 2011)

Habitat: Coprophilous fungi, regarded as a reliable indicator of herbivore activity including animal herding (van Geel *et al*. 2011 and references therein).

3. ***Tetraploa* sp. Berk. & Broome** (**Sordariaceae)** Plate 5, figure 23. type HdV-89 (van Geel, 1978, van Geel *et al*. 2011). Verrucate conidia verrucose, 4 columns of cells terminating in septate appendages (van Geel *et al*. 2011).

Habitat: *T. aristata* globally occurring in (sub)-tropics, on leaves and stems (Ellis, 1971; Farr and Rossman, 2009).

24. ***Aspergillus niger* van Tiegh.** (**Trichocomaceae)** Plate 5, figure 24. Conidia (c. 5 µm) either psilate, often verrculose or even echinulate (Ellis & Ellis 1997).

Habitat: Soil saprophytes, on decaying plant matter (Ellis & Ellis 19979.

25. ***Nigrospora sphaerica* (Sacc.) Mason** (**Trichosphoraceae)** Plate 5, figure 25. Conidia, black, measure 16-20 µm (Ellis & Ellis 1997)

Habitat: On dead grass stems (Ellis & Ellis 1997)

26. ***Urocystis* sp. Rabenh. ex Fuckel.** (**Urocystidaceae)** Plate 5, figure 26. type UG-1079 (Gelorini *et al*. 2012). Spores ellipsoid, flattened, hyaline-slightly brownish, minutely punctate, jacket cells surround spore (Chupp 1960).

Habitat: On leaf litter (Chupp 1960).

Uncertain affinity

27. **type HdV-1033** (van Geel *et al*. 2011). Plate 5, figure 27. Ascospores feature one septum, max. 40 µm, lower diameter in region around septum, finely verrucate-rugulate (Ellis & Ellis 1997)

Habitat: Unknown

28. **type HdV-1058** (van Geel *et al*. 2011). Plate 5, figure 28. Spores spherical, diameter 13–17 µm including 2–5 µm long appendage (van Geel *et al*. 2011).

Habitat: Unknown

Unidentified Fungal Spores

29. **type F1.** Plate 5, figure 29. Ellipsoid dark brown cell with two elongated, straight appendages (each > 30 µm long, c. 2 µm wide) (own observation).
30. **type F2.** Plate 5, figure 30. Spore c. 70 µm long, c. 30 µm wide, barrel shaped, 3 septae, cells constricted, end cells paler (own observation).

Further fungal material

31. **Fungal germling.** Plate 5, figure 31. Fungal spores germinate when attached, e.g., to suitable hosts and the conditions are favourable, e.g., humidity and nutrients (Brown & Howard 1994).

32. **Fungal fruit body.** Plate 5, figure 32. The often radially symmetric fruit bodies protect the meiotically derived spores (Busch & Braus 2007).

33. **Fungal hyphae.** Plate 5, figure 33. Abundantly found in sediments of core MK 24, fungal hyphae are fungal filaments with multiple septae and a psilate but also sometimes verrucate surface and brown colour (Ellis & Ellis 1997).
34. **Microsclerotium.** Plate 5, figure 34. Large cell cluster with outer layer (parenchyma cells) and inner layer (medulla cells), multiple septae, brown (Song 2018). Microsclerotia are forms of overwintering structures of many fungi in soil (Song 2018).

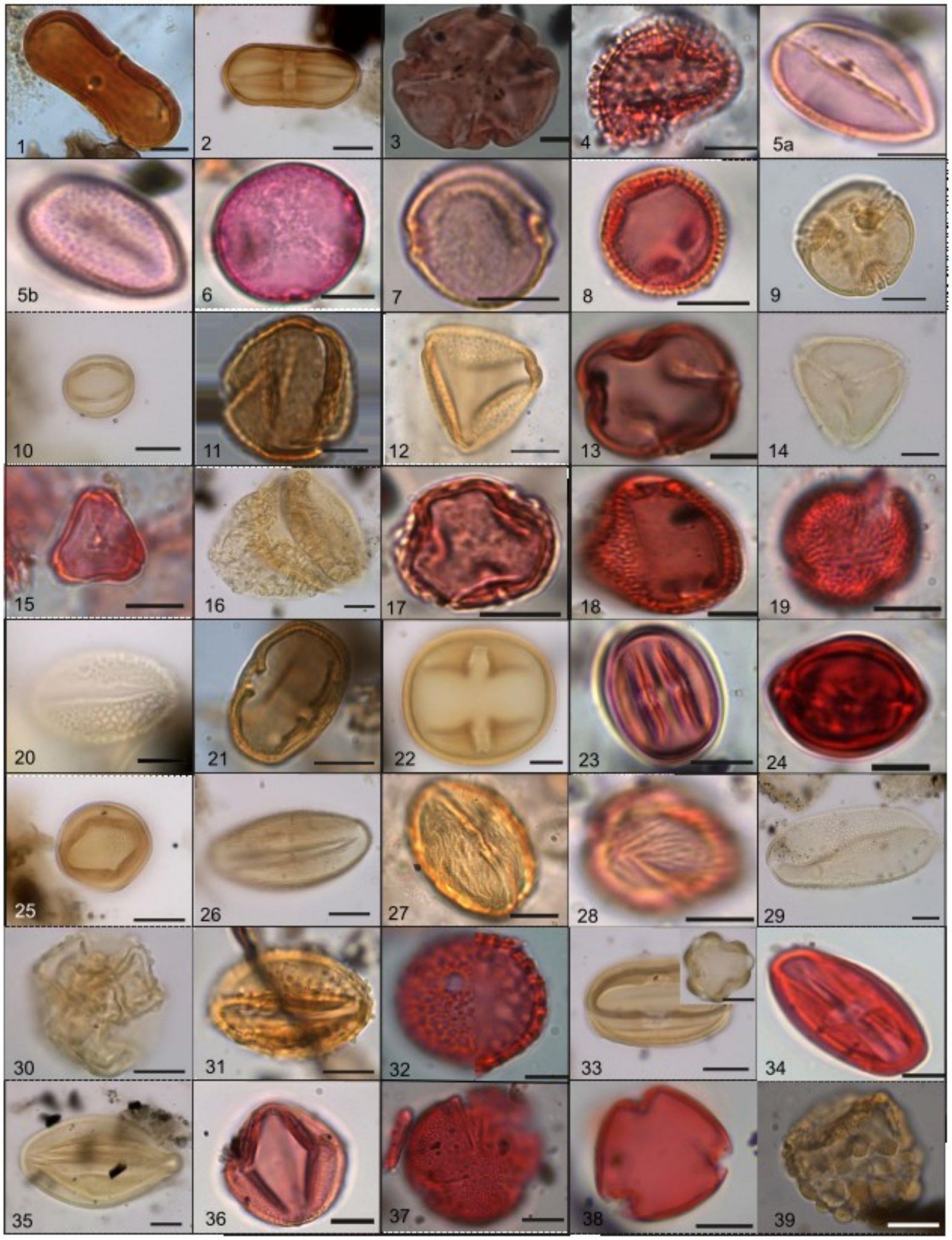
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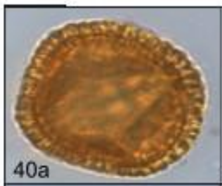
Plate 1**: Arboreal pollen from cores Mk24 and MKD-1**: 1. ***Metarungia* sp.**, 2. ***Heteromorpha* sp.**, 3. ***Rauvolfia caffra***, 4. ***Ilex mitis***, 5. ***Phoenix reclinata***, 6. ***Celtis africana***, 7. ***Trema* type**, 8. **Celastraceae,** 9. ***Alchornea* type,** 10. ***Macaranga capenis,*** 11. ***Psoralea* type**, 12. ***Apodytes dimidiate***, 13. ***Myrsine africana***, 14. ***Eugenia* type**, 15. ***Syzygium* type**, 16. ***Podocarpus* type,** 17. ***Cliffortia* type**, 18. ***Canthium* sp**., 19. ***Teclea* sp**., 20. ***Salix* sp**., 21,22,23 ***Mimusops*-type**, 24. ***Rhizophora mucronata***, 25. ***Bruguiera*-type**, 26. ***Lannea* type**, 27. ***Sclerocarya* type**, 28. ***Searsia*-type**, 29. ***Aloe* type**, 30. ***Hyphaene coriacea***, 31. ***Tarchonanthus-Brachylaena* type**, 32. ***Commiphora* type**, 33. ***Combretum* type**, 34. ***Euclea* type**, 35. ***Diospyros* type**, 36. ***Spirostachys africana* type**, 37. ***Euphorbia* type,** 38**. *Burkea africana***, 39. ***Dichrostachys cinerea*.** Scale bar = 10µm.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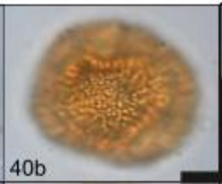
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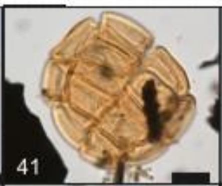
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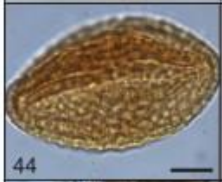
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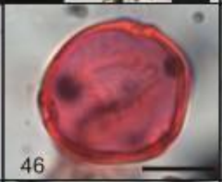
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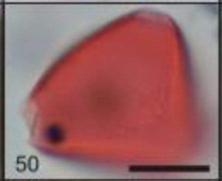
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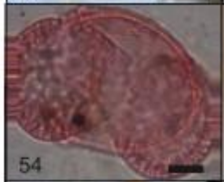
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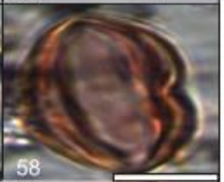
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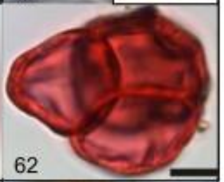
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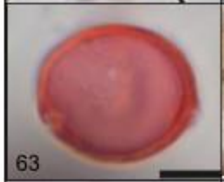
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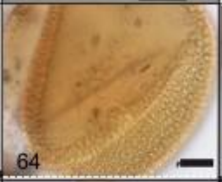
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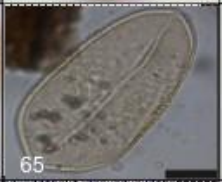
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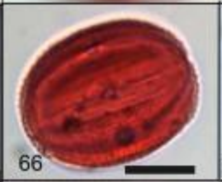
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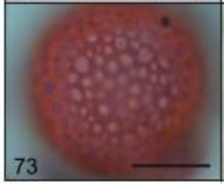
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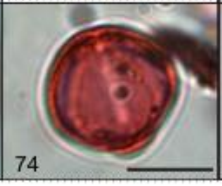
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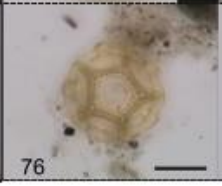
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Plate 2: Arboreal (41-58) and herb/shrublet pollen (59-80) from cores Mk24 and MKD-1: 40. ***Peltophorum africanum***, 41. ***Senegalia* type,** 42. ***Vachellia* type**, 43. ***Loranthus* type**, 44. ***Grewia* type**, 45. ***Dombeya* type**, 46. ***Ficus* type**, 47. ***Morella* type,** 48. ***Olea* type,** 49. ***Pseudolachnostylis* type,** 50. ***Faurea* type**, 51. ***Ziziphus mucronata***, 52. ***Zanthoxyllum* sp.**, 53. ***Gnidia* type**, 54. ***Pinus* type,** 55. ***Justicia flava* type**, 56. ***Dicliptera* type**, 57. ***Isoglossa* type**, 58. ***Apiaceae type***, 59. ***Cerastium* type**, 60. ***Commelina* type**, 61. ***Drosera* type**, 62. ***Erica* type**, 63. ***Acalypha* type**, 64. ***Geranium* type**, 65. **Liliaceae,** 66. ***Ammannia* type**, 67. ***Sida* type**, 68. ***Triumfetta* type**, 69. ***Polygala* type**, 70. ***Anthospermum* type.**, 71. ***Oldenlandia* type**, 72. ***Selago* type**, 73. ***Passerina* type**, 74. **Aizoaceae**, 75. ***Amaranthus* type**, 76. ***Alternanthera* type,** 77. ***Atriplex* type**, Scale bar = 10µm.


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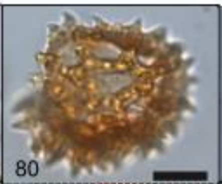
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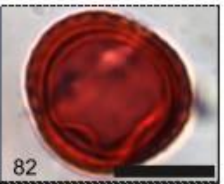
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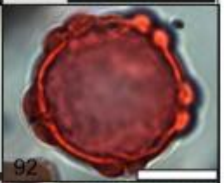
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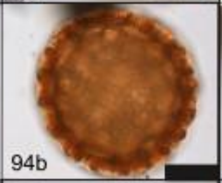
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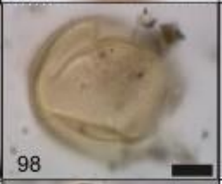
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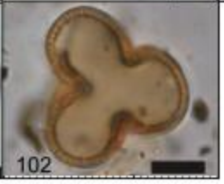
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Plate 3**: Herb/shrublet pollen continued (81-93), aquatics and wetland (94-105) from cores Mk24 and MKD-1**: 78. ***Tubuliflorae***, 79. ***Lychnophora* type**, 80. ***Vernonia* type,** 81. ***Vernonia* type E** , 82. ***Stoebe-Elytropappus* type**, 83. ***Artemisia* type**, 84. ***Gerbera* type**, 85. ***Dicoma* type**, 86. ***Pentzia* type ,** 87. ***Crassula* type,** 88. ***Poaceae*** (25-40µm), 89. ***Cerealia type*** (>40µm), 90. ***Zea mays***, 91. ***Lemna* type.**, 92. ***Myriophyllum-Laurembergia*-type**, 93. ***Utricularia* type.**, 94. ***Persicaria* type,** 95. ***Hydrocotyle* type**, 96. ***Ascolepis* type**, 97. ***Cyperaceae***, 98. ***Sebaea* type**, 99. ***Phragmites* type**, 100. ***Ranunculus* type**, 101. ***Typha* type**, 102. ***Gunnera* type.** Scale bar = 10µm.

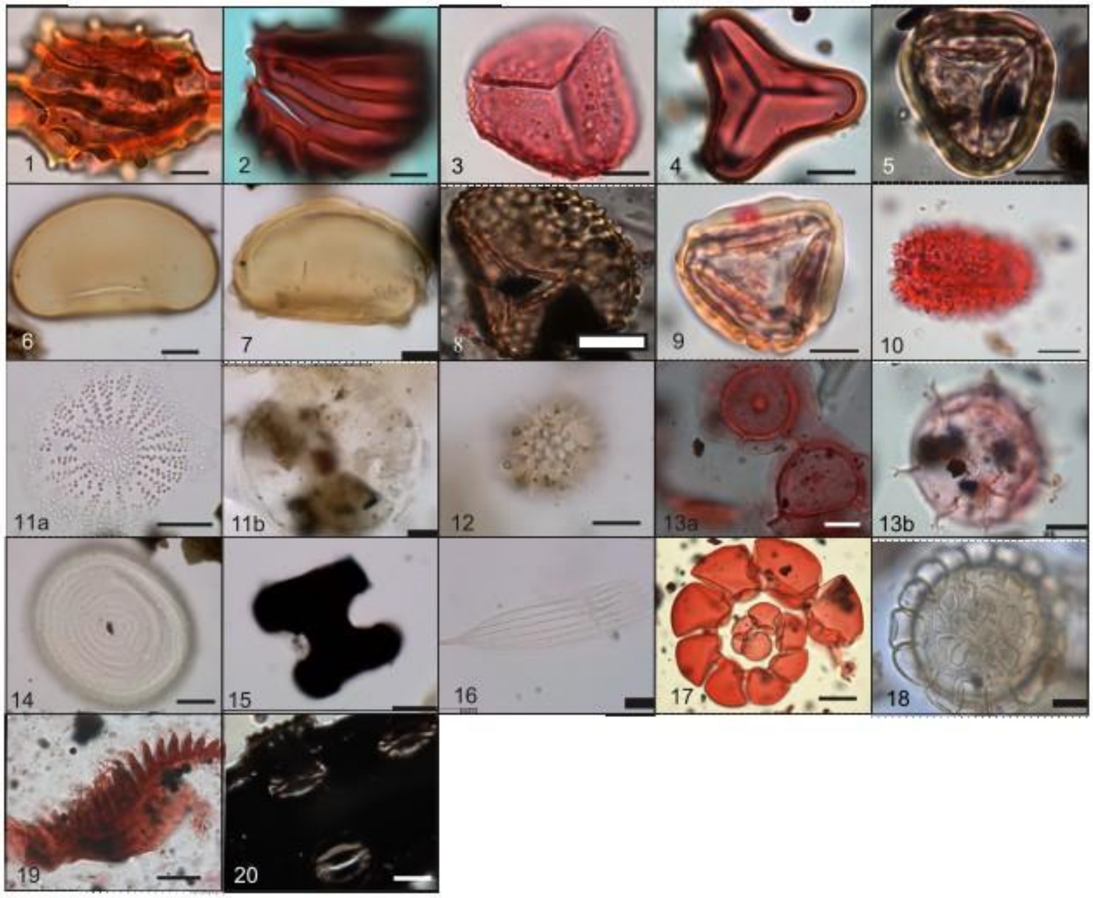
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Plate 4: Cryptogam spores (1-11), miscellaneous including marine indicators (12-21) from cores Mk24 and MKD-1: 1. ***Anemia sp.***, 2. ***Mohria sp.***, 3. ***Anthoceros sp.***, 4. ***Cyathea* type,** 5. ***Lygodium* type**, 6. **Monolete spore**, 7. **cf. *Orthotrichum* type**, 8. ***Polypodium* type**, 9. ***Pteris* type**, 10. ***Thelypteris* type,** 11a. ***Centrales (diatom)***, 11b. ***Actinoptychus* type**, 12. ***Michrystidium***, 13a. ***Impagidinium* type**, 13b. ***Spiniferites* type**, 14. ***Pseudoschizoaea***, 15. **Bilobate grass phytolith (charred)**, 16. **Moth wing scale,** 17. **Microforaminiferal lining,** 18. ***Filinia longiseta***, 19. **Scolecodont,** 20. **Charred grass cuticle with stomata**. Scale bar = 10µm.

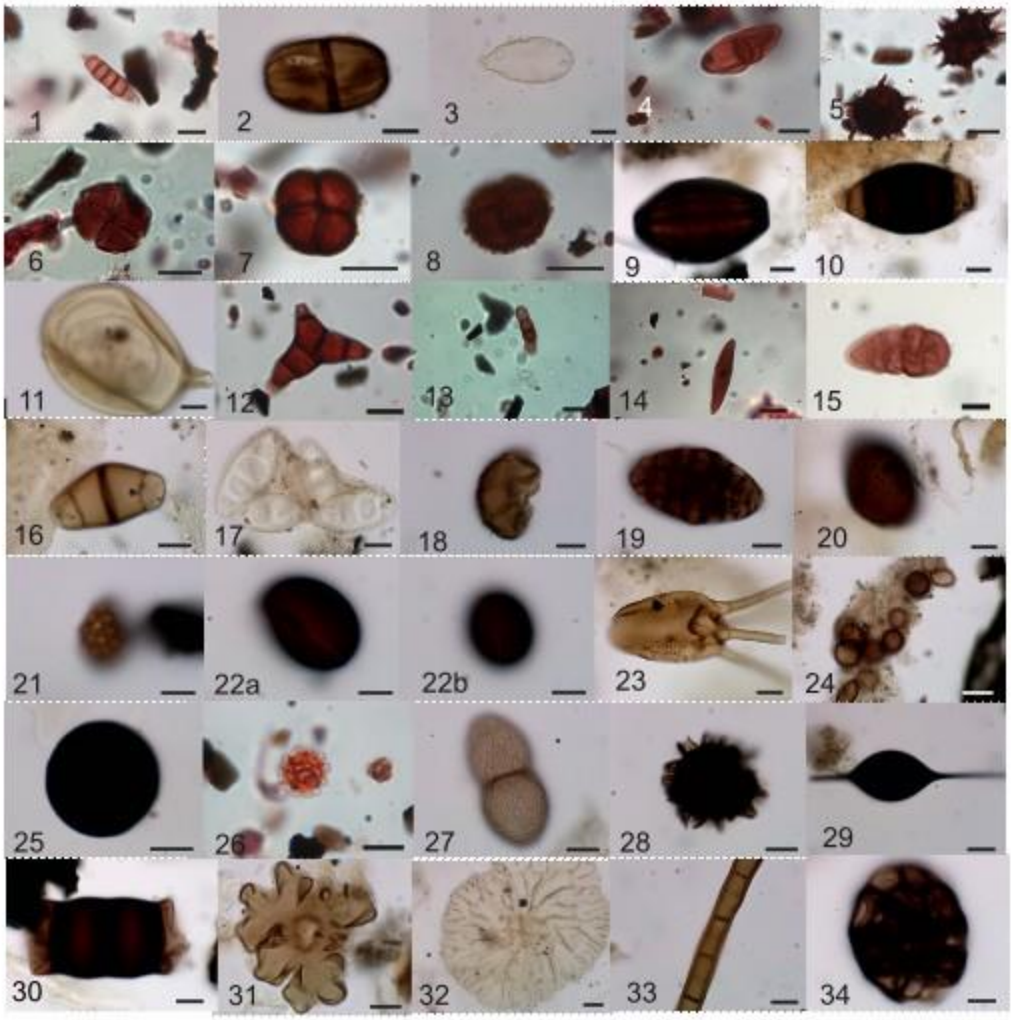
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Plate 5: Fungal spores and remains from cores Mk24 and MKD-1: 1. ***Vargamycetes aquaticus***, 2. ***Lasiodiplodia theobromae***-Type HdV 1043, 3. ***Cladosporium* sp**., 4. ***Munkovalsaria donacina***-Type HdV-1027, 5. ***Spegazzinia deightonii***-Type HdV-1041, 6. ***Dictyoarthrinium* cf. *sacchari***-Type HdV-1015A, 7. ***Dictyoarthrinium* cf. *sacchari***-Type HdV-1015B, 8. ***Dictyoarthrinium* cf. *sacchari*** -Type HdV-1015C, 9. ***Diporotheca* sp**.-Type HdV-1245, 10. **cf. *Mitteriella ziziphina***-Type HdV-1049, 11. ***Glomus* sp.-**Type HdV-1103, 12. ***Diplocladiella* cf. *scalaroides***-Type HdV-1025, 13. ***Meliola* sp**.-Type UG-1137 , 14. ***Fusarium* sp**., 15. ***Alternaria* sp**.-Type HdV-1034, 16. ***Curvularia* sp**.-Type HdV-1029A-B, 17. ***Drechslera* biseptata**, 18. ***Epicoccum purpurascens***-Type HdV-1011, 19. ***Pleospora androsaces***-Type HdV-1046, 20. ***Gelasinospora* cf. *cratiphor*a**-Type HdV-1093, 21. ***Gelasinospora* cf. *dictyophora***-Type HdV-1351, 22. ***Sporomiella*-type**-Type HdV-113, 23. ***Tetraploa* sp.-**Type HdV-89, 24. ***Aspergillus niger***, 25. ***Nigrospora sphaerica***, 26. ***Urocystis* sp**.-Type UG-1079, 27. Type HdV-1033, 28. Type HdV-1058, 29. Type F1, 30. Type F2, 31. Fungal germling, 32. Fungal fruit body, 33. Hypha, 34. Microsclerotium. Type numbers after van Geel *et al*. (2011), if not given otherwise in text. Scale bar = 10µm.

Chapter 4

Results

4.0 MKD-1

4.1. Dating and Sedimentation rate for MKD-1

Six radiocarbon dates were measured for MKD-1. The dates were measured at depths between 150cm and 970cm. The obtained radiocarbon dates (see table 3) were interpolated using Bayesian age depth modelling as seen in Fig 9.

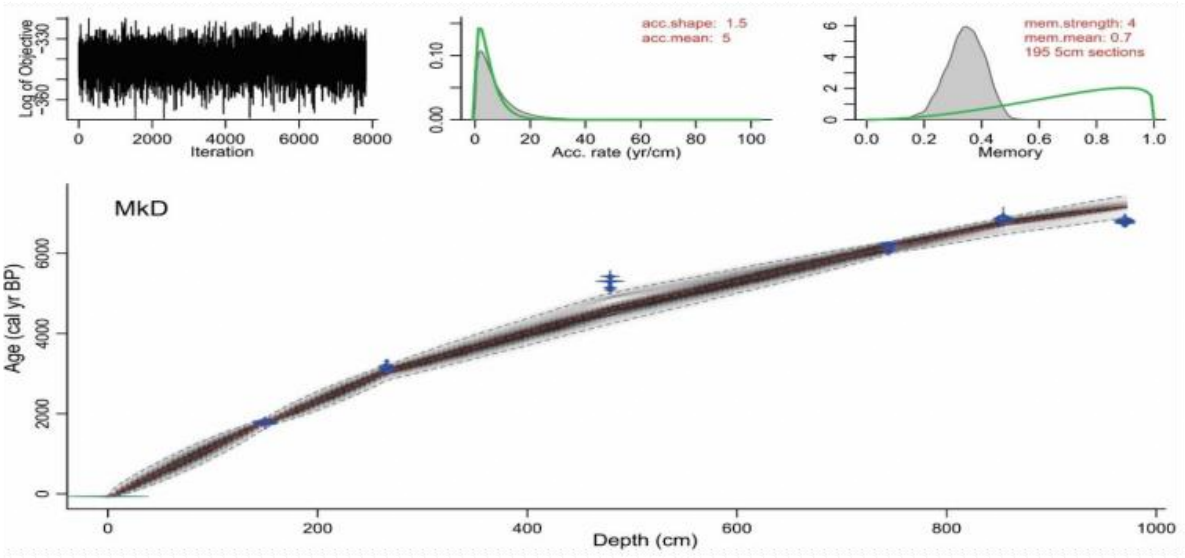

Figure 9: Age model using Bayesian statistics (Bacon software v2.2) for core MKD-1

Table 3: AMS radiocarbon analyses of material from core MKD-1. The SHCal20 Southern Hemisphere Calibration (Hogg et al., 2020) was used.

Lab-Code	**Depth (cm)**	**14C age (yr BP)**	**Calibrated Age (cal yr BP)**	**95% probability range**
Beta 439022	150	1890 +/- 30	1775 ± 64	Cal BP 1870 to 1852 (3.8 %) Cal BP 1839 to 1710 (91.6%)
Beta 439023	266	3020 +/- 30	3123 ± 123	Cal BP 3320 to 3308 (1.5%) Cal BP 3246 to 3005 (93.9%)
Beta 416422	479	4630 +/- 30	5299 ± 32	Cal BP 5450 to 5377 (26.4%) Cal BP 5330 to 5266 (40.6%)
Beta 416423	745	5420 +/- 30	6227 ± 55	Cal BP 6282 to 6171 (61.1%) Cal BP 6159 to 6103 (18.45) Cal BP 6082 to 6011 (15.8%)
Beta 416423	854	6060 +/- 30	6863 ± 87	Cal BP 6950 to 6775 (92.7%) Cal BP 6767 to 6750 (2.7%)
Beta 439024	970	6010 +/- 30	6787 ± 108	Cal BP 6895 to 6678 (95.4%)

Sedimentation rate for MKD-1 average ~0.1cm yr$_{-}^{1}$ from 292.2 cal. yrs BP to 4704.8 cal. yrs BP and 0.2cm yearly from 4704.8yrs cal. BP to 6283.1 cal. yrs BP.

4.2. Lithology of MKD-1

The lithological units of core MKD-1 are shown in Fig. 10.

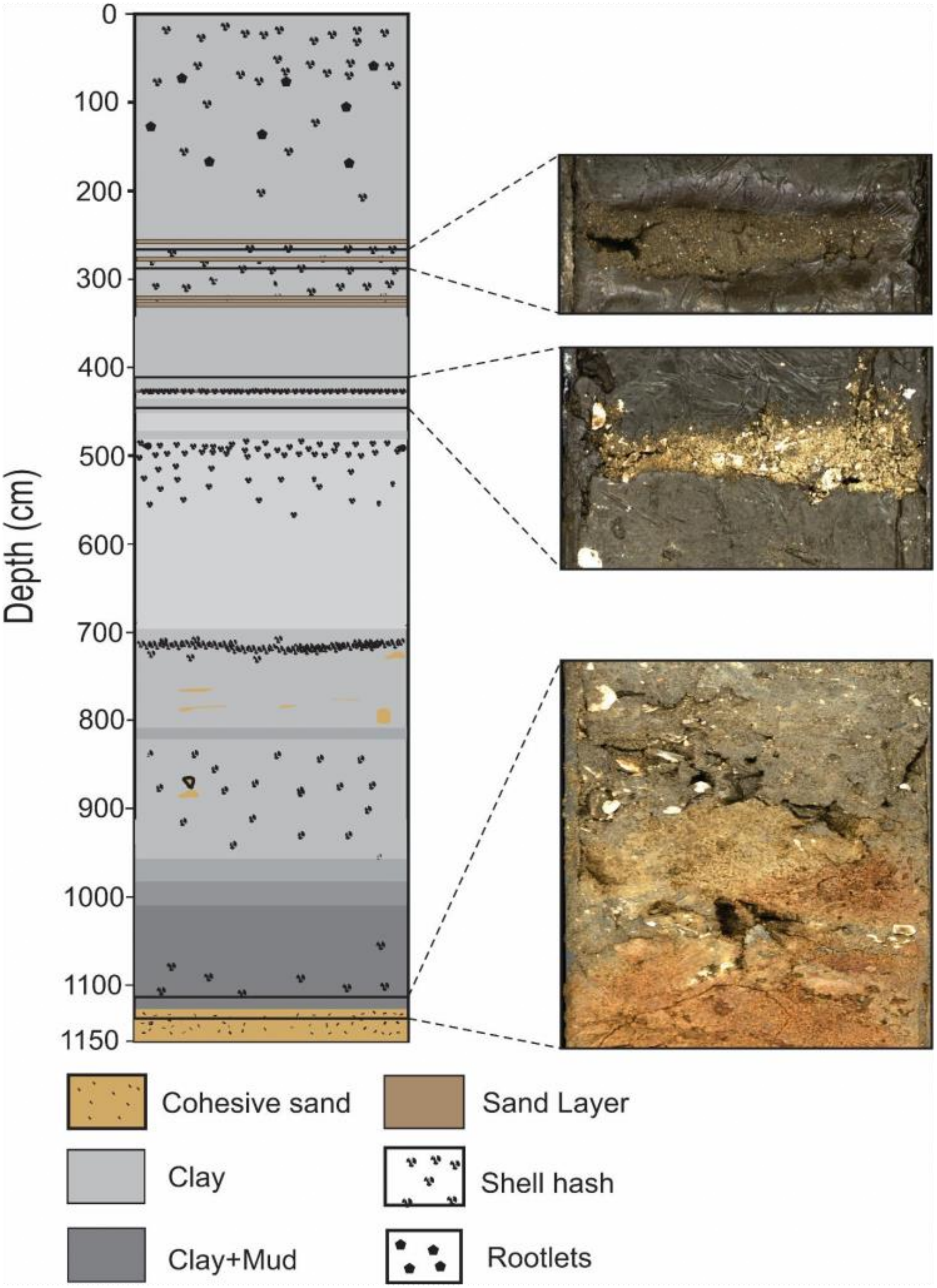

Figure 10: The lithological units of core MKD-1

The base of the core (1150-980cm) comprises cohesive orange-brown sand with isolated shell fragments. This deposit is sharply overlain by clay and silt dominated sediments that are characterized by smaller grain sizes and higher organic matter contents. From 980cm to the top of the core a few shell hash horizons that are evident, with significant accumulations occurring between 950-830cm, 570-490cm and at 150cm to the top of the core. Shell hash layers are usually associated with lower organic matter contents and an increase in grain size. Several discrete coarse-grained horizons are seen between 550cm and 250cm and are associated with frequent shell accumulation (see Fig 10). The upper 250cm of the sediment profile is characterized by generally finer textured material although variable grain sizes are observed within the uppermost 150cm. the material contains rootlets and occasional shell fragments.

Samples for pollen analysis were taken from 770-7cm depth and a total of 80 subsamples were analyzed (see appendix).

Pollen Analysis for core MKD-1

Generally, 7-300cm depth had poor pollen preservation as compared to the sediment between 350-770cm. Using Constrained Incremental Sums of Squares (CONISS), 6 pollen zone output were generated. Zone 6 differs from Zone 5 as Amaranthaceae peak was recorded with marine elements in Zone 6 and Zone 5 records an increase in *Podocarpus* and decline in Amaranthaceae. Zone 4 records a peak in *Podocarpus*, forest elements and Cryptogams while Zone 3 recorded a peak in *Spirostachys* at the beginning with Poaceae taking over at the middle, Zone 2 recorded the peak of *Phragmites*, Foraminifera linings and decline in Poaceae and Fungal spores. Finally, Zone 1 records the presence of *Pinus*, increase in fungal spores and presence of wetland elements.

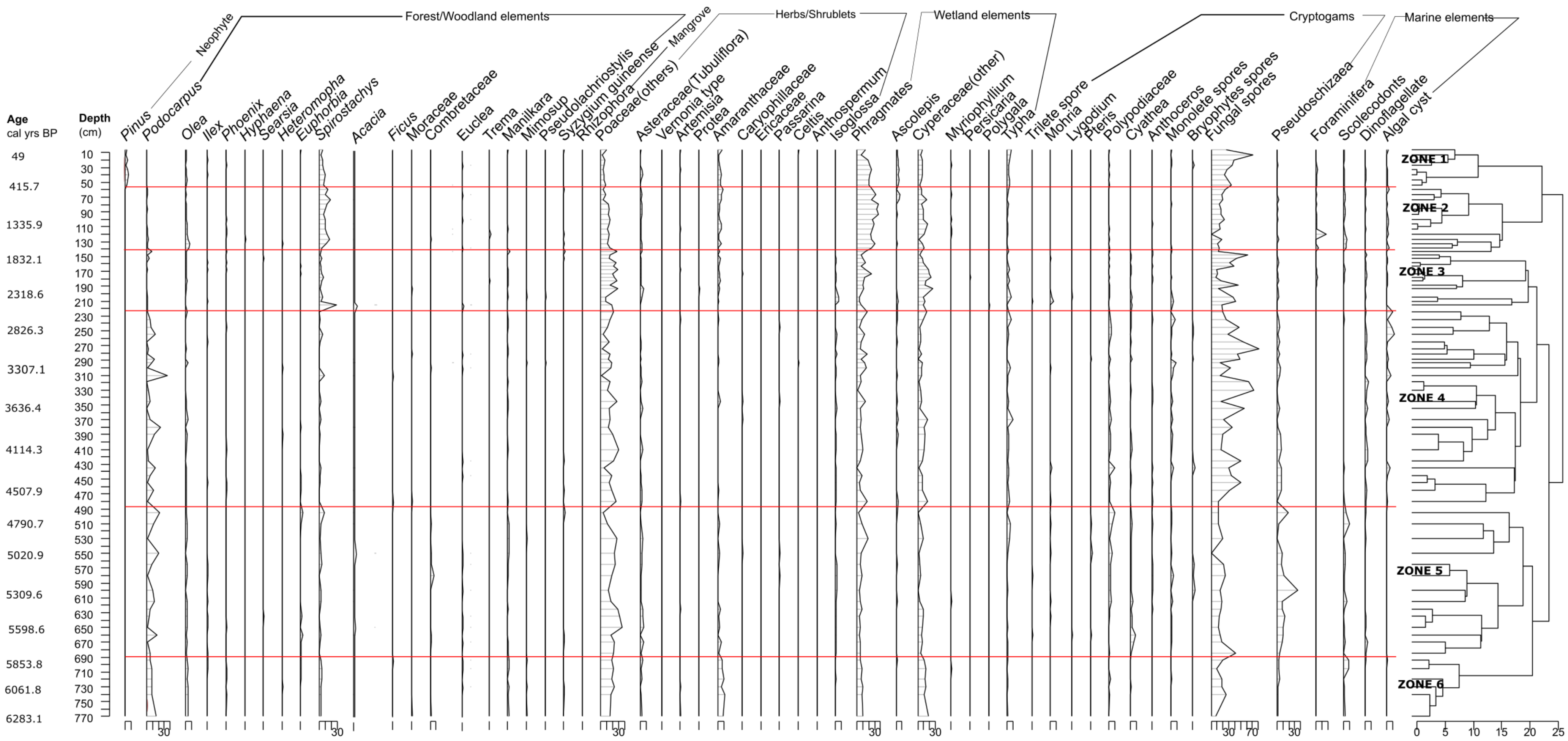

Figure 11: Pollen percentage Diagram for MKD-1 showing the six pollen zones and groupings

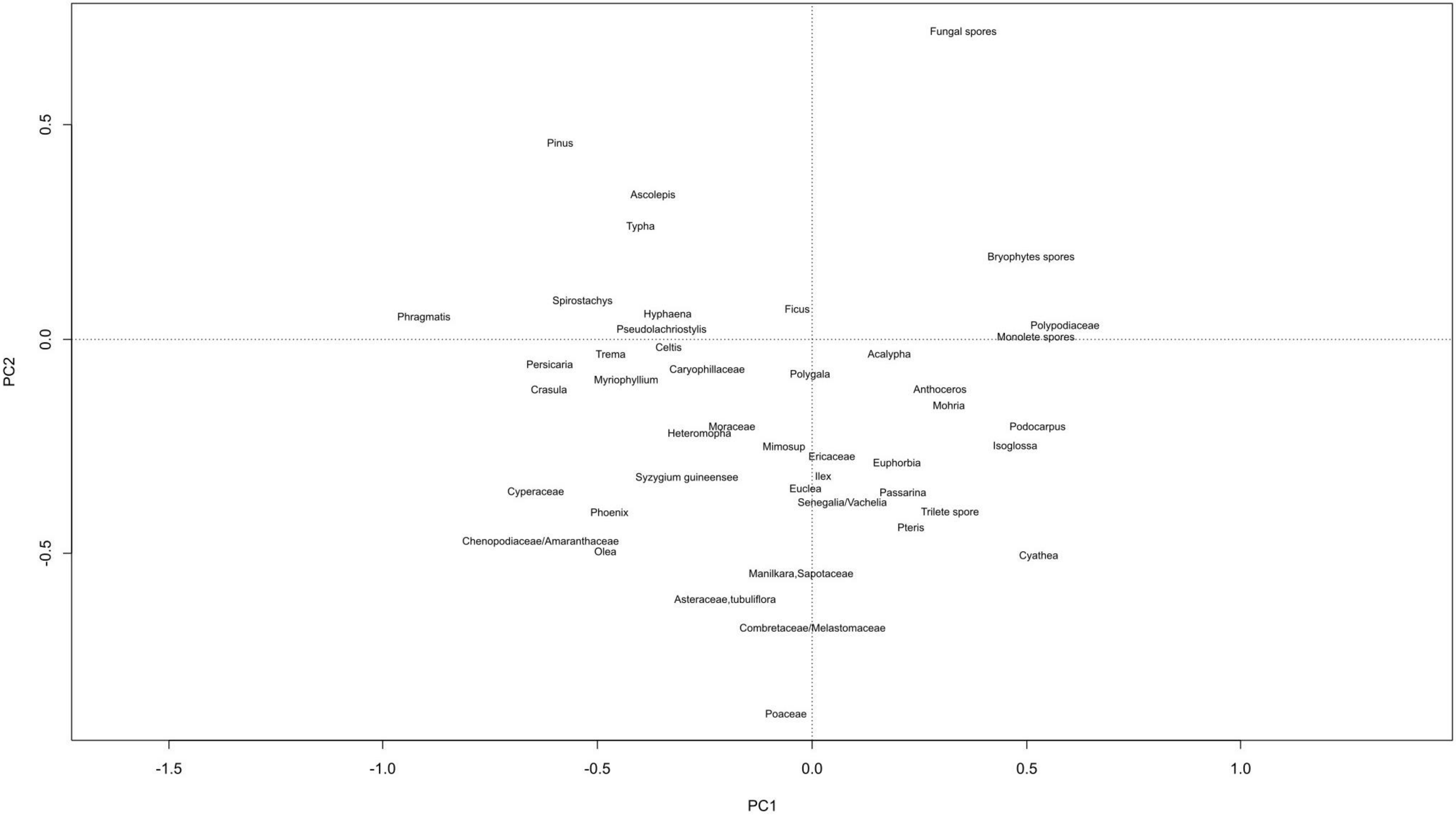

Figure 12: PCA Biplots for MKD-1 using CONNIS

4.3. Pollen zonation for MKD-1

Six pollen zones were derived from Constrained Incremental Sum of Squares (CONISS, R studio: http://www.rstudio.com/). The zonation of the pollen diagram is based on changes in composition and abundance of individual species (see Fig 12).

4.3.1. Zone 6 *Podocarpus,* Poaceae, Amaranthaceae, Cyperaceae and Scolecodonts. (6283-5800 Cal yrs. BP)

Peak of Amaranthaceae, High *Podocarpus*, Poaceae, Cyperaceae, and Scolecodonts, with little to no cryptogams (Pteridophytes and Bryophytes) was recorded.

4.3.2. Zone 5 *Podocarpus*, Poaceae, *Pseudoschizaea* and Cryptogams (5800-4680 Cal yrs. BP)

Increase in *Podocarpus*, Poaceae, Scolecodont and Cryptogams (Pteridophytes and Bryophytes) was recorded. Also, *Pseudoschizaea* reached its peak, and Ericaceae was also recorded in this zone.

4.3.3. Zone 4 *Podocarpus, Typha,* Poaceae, and Fungal spore (4680-2609.7 Cal yrs. BP)

Peak of *Podocarpus* and fungal spores, high Cryptogams, Poaceae, increase *Typha* and little to no marine elements was recorded in this zone.

4.3.4. Zone 3 *Spirostachys,*Cyperaceae, Poaceae and Fungal spore (2609.7- 2047 Cal yrs BP)

Podocarpus declined and disappeared at the beginning as *Spirostachys* increases and reached its peak but later declined as *Podocarpus* reappeared. Also, Poaceae decreased at the beginning as *Spirostachys* reached its peak but latter increased as *Spirostachys* declined. *Typha* was abundant in this zone and Foraminiferal linings appeared in.

4.3.5. Zone 2 *Spirostachys, Phragmatis* and Foraminiferal linings (2047-672.6 Cal yrs BP)

Spirostachys, Amaranthaceae increased as Poaceae declined. *Phragmites* and foraminiferal linings increased and reached its peak while fungi declined and little to no cryptogam spores (Bryophyte and Pteridophyte) was recorded in this zone.

4.3.6. Zone 1 Neophyte, *Spirostachys*, *Phragmites*, *Ascolepis* and Fungal spore (672.6 -0 Cal yrs. BP)

Presence of *Pinus* (Neophyte) at the top of the core (last 400 Cal yrs. BP), high abundance of fungi, pollrn of *Phragmates*. *Spirostachys* and Amaranthaceae present, low Poaceae pollen percentages, decline and disappearance of Foraminiferal linings.

4.4 Principal Component Analysis

Using a 1% sample threshold, pollen grains and spores were subjected to Principal Component Analysis, a representation of the principal component analysis is shown in Fig 13.

PC1 accounts for 52% while PC2 accounts for 42% of the variation in pollen and spores composition throughout the core. PC1 reveals strong positive loadings of ≥0.02 for *Podocarpus*, *Cyathea,* Polypodiaceae, *Isoglossa*, monolete bryophytes, *Mohria*, fungal spores, trilete spores, *Pteris*, *Anthoceros, Euphorbia, Acalypha, Passarina, Ilex*, *Polygala*, *Acacia*, *Euclea*, *Ericaceae*, *Ficus* and a strong negative loadings of ≥ -0.02 for *Phragmites,* Amaranthaceae, Cyperaceae, *Crassula*, *Pinus*, *Persicaria*, *Spirostachys*, *Olea*, *Trema*, *Phoenix*, *Myriophyllium*, *Ascolepis*, *Spaganium*, *Hyphaena*, *Pseudolachnostylis*, *Celtis*, Caryophyllaceae, *Syzygium*, *Heteromopha*, Asteraceae, Moraceae, *Manilkara*, Poaceae.

Chapter 5

Results

5.0 MK24-1

5.1 Dating and Sedimentation rate for MK24-1

Three radiocarbon dates were measured for MK24. The dates were measured at depths between 15.5cm and 70.5cm (see table 4). The obtained radiocarbon dates were interpolated using Bayesian age depth modelling as seen in Fig 14. Pollen analysis were done on sediments between 0.5cm and 91.5cm core MK24-1. Samples below 70.5cm were not dated due to shell deposits and was thought to be a hiatus but sediments above 80cm were subsampled, extracted and analyzed for palynomorphs.

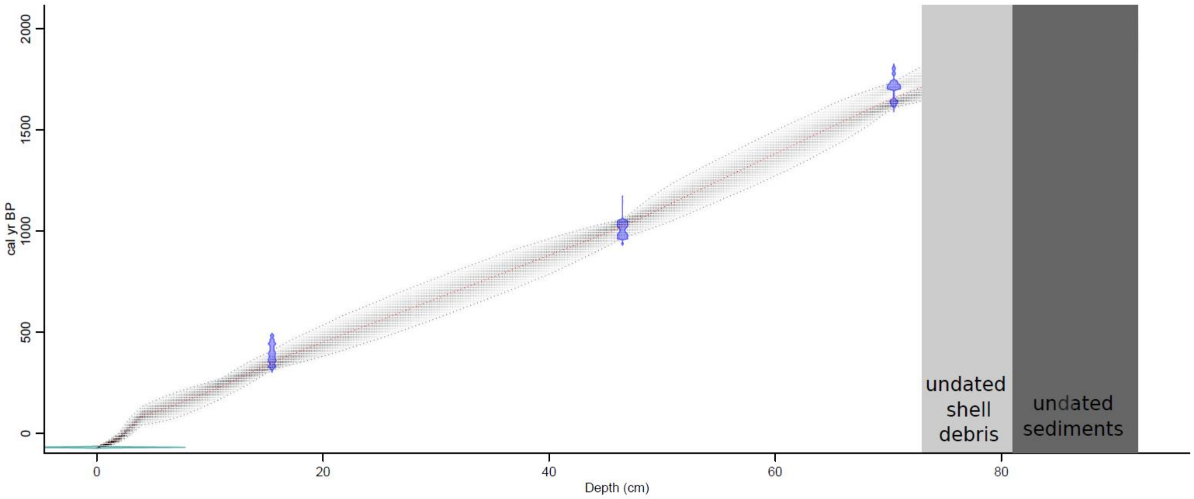

Figure 13: Age model using Bayesian statistics (Bacon software v2.2) for core MK24-1

Table 4: AMS radiocarbon analyses of material from core MK24-1. The SHCal20 Southern Hemisphere Calibration (Hogg et al., 2020) was used. The ages were calibrated with Calib 7.1 software (Stuiver et al. 2018).

Material	**Lab code**	**Depth**	**^{14}c uncalib.**	**Cal. Age yrs BP**		
	AWI	**(cm)**		**-2s**	**+2s**	**median**
fine fraction <150um	4286.1.2	15.5	375 ± 25 BP	487	319	391
fine fraction <150um	4288.1.2	46.5	1155 ± 24 BP	1059	958	1013
fine fraction <150um	4287.1.1	70.5	1833 ± 24 BP	1815	1612	1713

Sedimentation rate for MK24 average ~0.1cm yr^{-1} from 70.5cm to the top of the core.

5.2. Lithology

The lithological units of core MK24-1 are described in Fig 15.

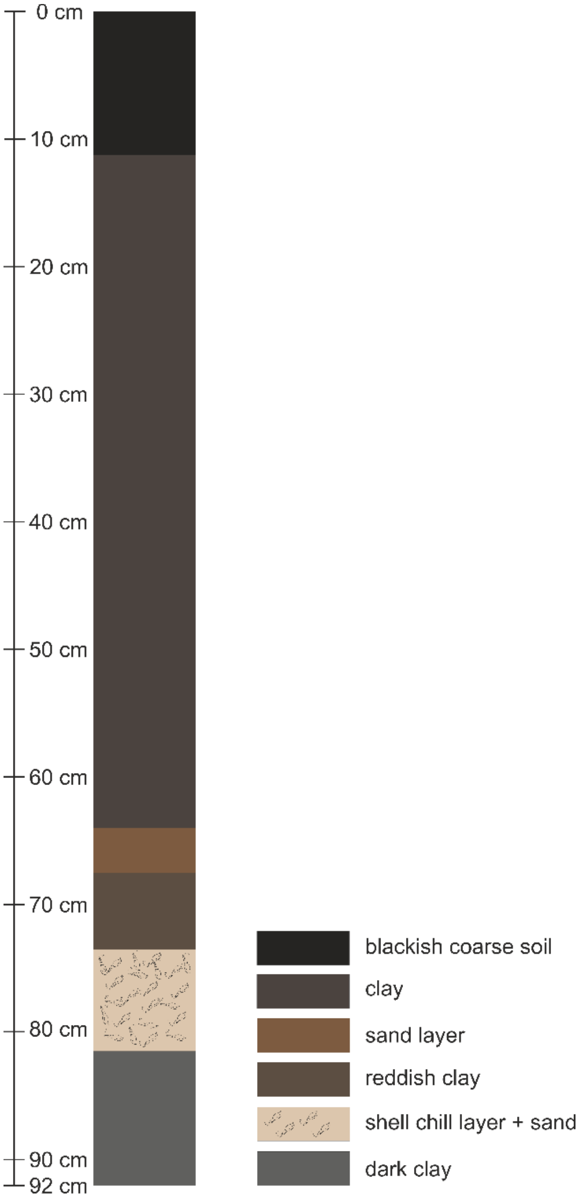

Figure 14: Lithology of core MK24-1

The base of the core (92-82cm) is made up of dark clayey sand and is overlain by sand and shell dominated sediments. 67-73cm is made up of reddish clay sediment which is overlain by sandy sediment layer and 65-12cm made up of a dark clayey sediment layer. The last 12cm comprises blackish coarse soil.

Pollen Analysis for core MK24-1

Generally, pollen preservation in all the studied depths was good and CONISS was used to generate 4 pollen zones. Zone 4 differs from Zone 3 as *Podocarpus* was recorded with low amount of *Spirostachys* in Zone 4 and *Spirostachys* became dominant in Zone 3. In Zone 2, all palynomorphs declined and only Amaranthaceae and charcoal increased and finally in Zone 1, wetland taxa and *Typha* increased and were abundant.

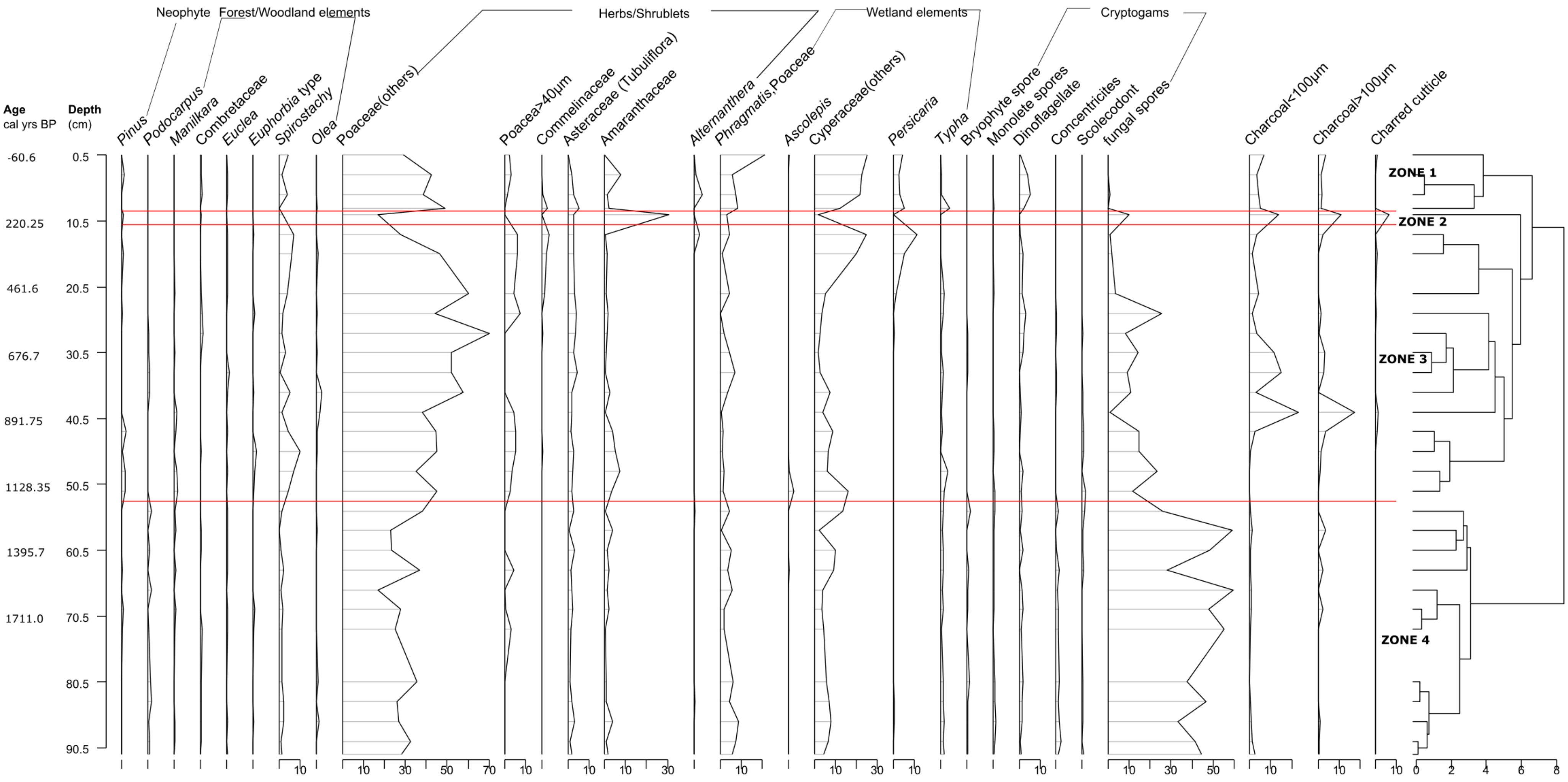

Figure 15: Pollen percentage Diagram for MK24-1 showing the six pollen zones and groupings

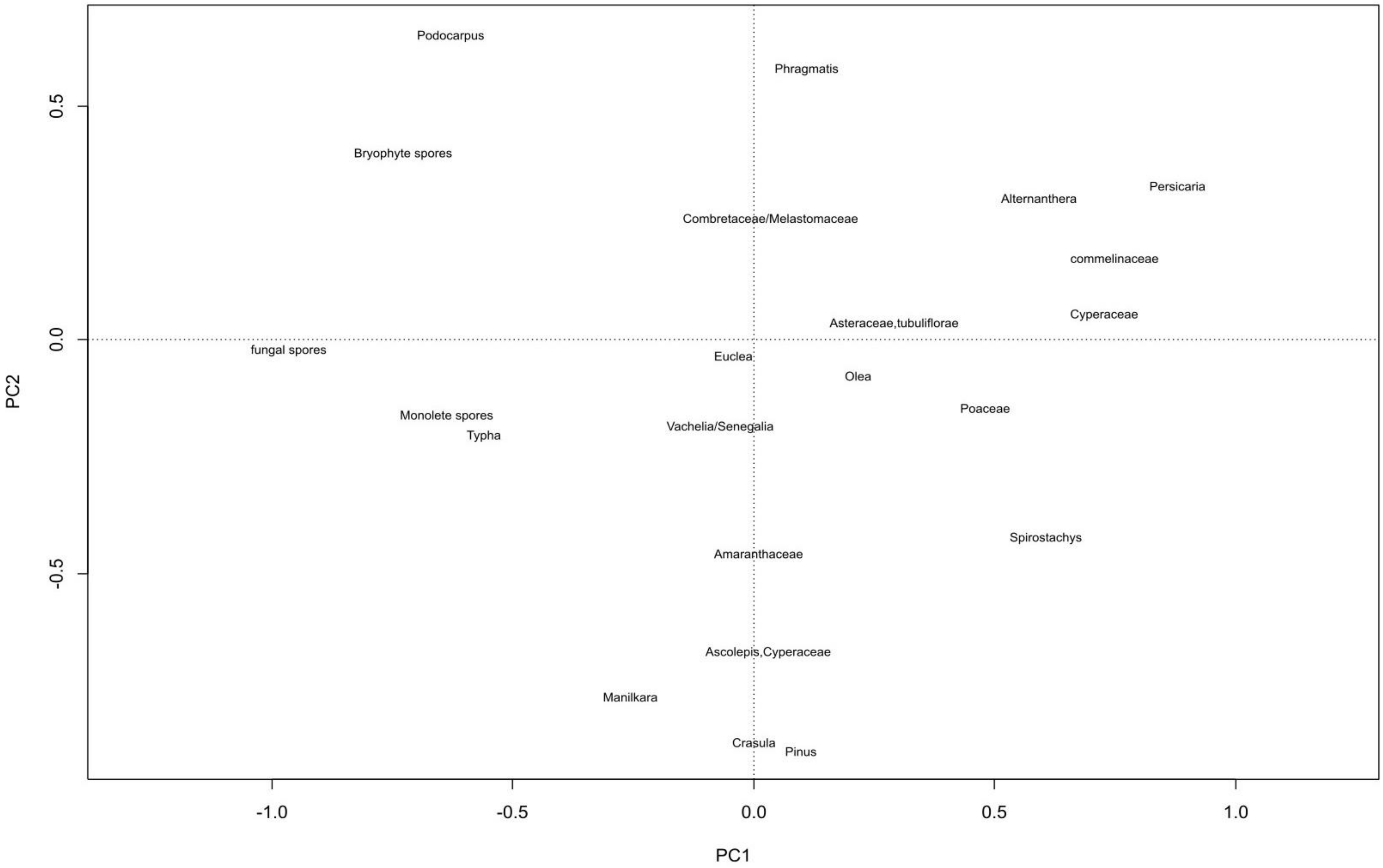

Figure 16: PCA Biplot for core MK24-1 using CONISS

5.3. Pollen Zonation for MK24-1

Four pollen zones were derived from Constrained Incremental Sum of Squares (CONISS, R studio: http://www.rstudio.com/). The zonation of the pollen diagram is based on changes in composition and abundance of individual species (see Fig17)

5.3.1. Zone 4 – *Podocarpus*, Cryptogams (1711.0- 1200 Cal yrs. BP)

Presence of *Podocarpus* pollen less than 5%, spores of ferns, bryophytes and fungi were recorded. High percentages of Poaceae (others) and *Phragmites* pollen and dinoflagellate cysts were also recorded.

5.3.2. Zone 3- *Spirostachys*, Poaceae and Charcoal (1200-280 Cal yrs. BP)

A peak in *Spirostachys* at the beginning which latter declined as charcoal increased and reached its peak accompanied by a return of *Podocarpus* in insignificant quantity. *Podocarpus* latter disappeared and *Spirostachys* increased towards the end. Also, Poaceae increased and reached its peak in this zone.

5.3.3. Zone 2 Amaranthaceae and Charcoal zone (280-200 Cal yrs. BP)

A peak in Amaranthaceae and increase in charcoal with a corresponding decline in forest element, wetland elements and grasses were recorded.

5.3.4. Zone 1 Phragmites, Cyperaceae and Dinoflagellate zone (200-0 Cal yrs. BP)

A peak of *Phragmites*, Cyperaceae pollen as well as dinoflagellate cysts with corresponding decrease in woodland elements and disappearance of forest elements, cryptogams and fungi were recorded.

5.4. Principal Component Analysis

Using a 1% sample threshold, pollen grains and spores were subjected to Principal Component Analysis, a representation of the principal component analysis is shown in Fig. 18.

PC1 accounts for 48% while PC2 accounts for 37% of the variation in pollen and spores composition throughout the core. PC1 reveals strong positive loadings of ≥0.01 for *Persicaria*, Commelinaceae, Cyperaceae, *Spirostachys*, *Alternanthera*, Poaceae, Asteraceae (tubuliflorae), *Olea*, *Phragmites*, Combretaceae, *Ascolepis*, Amaranthaceae and a strong negative loadings of ≥ -0.04 for fungal spores, bryophyte spores, monolete spores, *Podocarpus*, *Typha*, *Manilkara*, *Vachellia*/*Senegalia*, *Euclea*.

Chapter 6

Discussion

6.0 Pollen identification and Preservation

Palynomorph identification is an important part in many palaeoecological studies because without the correct identification of the recovered palynomorph, incorrect interpretations and inferences will be made. Hence, there is a need for regional pollen atlases and modern pollen reference collections that will aid in the identification of the pollen grains and spores and that can accompany pollen diagrams. It is also important to note that taphonomic processes to some extent can affect the size and shape as well as the preservation of pollen grains and spores. For example, in stenopalynous families where the size of the grains is a major delimiting factor between genera and species, it becomes difficult to distinguish the species. In these cases, they are referred to as "type" which includes all species within the family or genus and sometimes also in other families that share the same morphological features. In some fern spores, taphonomic or extraction processes can bring about a loss in the perine making it impossible to delimit the species, such as the monolete (laevigate) spores (Scott 1982).

It is also worthy to note that the abundance of a particular pollen in the pollen record does not necessarily indicate the abundance of the parent plant, therefore, the need to investigate their mode of production, dispersal and preservation potentials. For example, *Pinus,* is wind pollinated so even when it is not prominent in the local environment, it often dominates pollen assemblages (Campbell *et al*. 1999; Tyldesley 1973). In contrast, *Rauvolfia* species are usually underrepresented even when the trees are prominent in the local environment.

Apart from ecologically significant palynomorphs such as cryptogams, fungi, dinoflagellates, other microscopic particles such as charred cuticles, micro-charcoal and phytoliths also give additional information that may aid in palaeoecological interpretations. For example, cryptogams, fungi and dinoflagellates are important proxies that indicate changes in humidity or local water availability because pteridophytes, bryophytes and fungi require a humid environment. Their abundance suggests a humid local climate. Fungal spores give additional information such as the abundance of *Vargamyce aquaticus* suggests the presence of a water body (Hernandez-Retrepo *et al*. 2017). *Glomus* abundance can indicate soil erosion (Van Geel *et al*. 2011), the abundance of *Diporotheca* indicates eutrophication (Van Geel *et al*. 2011) and *Sporomiella* gives information about herbivore activities including animal herding (Van Geel *et al*. 2003). Micro-charcoal fragment sizes and abundance provide information about the different fire regimes (Conedera *et al*. 2009).

The holistic analysis of all microfossils found in palynological samples will improve palaeoecological interpretation of the past wetland dynamics, fire regimes, climate fluctuations and anthropogenic disturbances in the studied environment. This pollen atlas (see chapter 3) for a number of taxa occurring in the IOCB is a contribution to aiding and improving future work on Quaternary vegetation and climate and provides a visual comparison between palynomorphs and their sequences in future research endeavors.

Table 3: Fossil pollen taxa and their environmental indications (after Scott 1999; Finch and Hill, 2008)

Pollen types	**Vegetation**	**Environment**
Podocarpus	Forest	Relatively moist conditions
Isoglossa	Forest floor	
Proteaceae	Upland or mesic savanna	Wide range of temperature, sub-humid condition
Olea		
Combretaceae	Microphyllous or plains savanna	Relatively warm conditions, wide range of moisture condition; *Senegalia/ Vachelia* associated with relatively local deep soils
Spirostachys		
Euphorbia-type		
Peltophorum		
Senegalia/Vachelia		
Ficus		
Tarchonanthus	Kalahari thornveld savanna	Relatively dry conditions
Asteraceae	Shrubland	Relatively even seasonal moisture distribution
Artemisia		
Ericaceae	Fynbos	Cool, sub-humid conditions, relatively seasonal moisture distribution
Passerina		
Cliffortia		
***Stobe* type**		
Aizoaceae	Succulents	Relatively warm and/ or dry conditions
***Aloe* type**		
Amaranthaceae	Halophytes	Local? Evaporation
Persicaria	Semi-aquatics	Moist to damp or wet soil, indicates disturbances
Typha	Aquatics	Shallow freshwater conditions
Cyperaceae	Semi-aquatics	Local swamp, shallow water or damp soil
Poaceae	Grassland or savanna	Generally indicative of summer rainfall
Cyathea	Forest edges	Relatively warm and moist condition(humid)
Polypodiaceae		
Monolete/Trilete		

6.1 Vegetation History

Generally, core MKD-1 had a very low pollen preservation in terms of quantity but was better in terms of diversity of palynomorphs to core MK24-1. This may be due to the nature of the depositional environment as MKD-1 was taken closer to the mouth of the estuary lake so may be a good sedimentary environment as the materials are not just from the immediate environment but also from a larger catchment thus the higher diversity. Also, core MKD-1 which was retrieved from the estuary mouth has a higher salinity if compared to core MK24-1 which was taken from the freshwater swamp. Since the estuary lake has experienced series of wet and dry cycles that may have affected the preservation of pollen in the cores. Similar scenario was reported by Campbell and Campbell (1994) in their experiments of palynomorph preservation in saline and freshwater sediment that had undergone wet and dry cycles. Apart from the differences in pollen preservation, the vegetation histories derived from the pollen data from core Core MKD-1 and MK24-1 are similar.

The pollen record of Lake St Lucia is dominated by Poaceae (20-90%) suggesting a strong influence of grassy woodland savanna. Similar trends were described at Lake Sibaya and Eteza (Neumann 2008; 2010). *Spirostachys* pollen dominated the arboreal spectra of the pollen profile in MK24-1 which is about 2000 Cal yrs. BP at the base. The basal sample of MK24-1 (91.5cm) was not sent for radiocarbon dating as there were shell deposits between 75cm and 82cm hence, it was believed to be a hiatus but palynomorphs have been recovered from 80.5cm to 91.5cm depths. Hence, these depths are believed to be older than 1713 Cal yrs BP which is the last radiocarbon date at 70.5cm depth. In core MKD-1 which is about 6300 Cal yrs BP at the base, *Podocarpus* pollen dominated the arboreal pollen spectra from 6300- 2600 Cal yrs BP as *Spirostachys* pollen dominated the arboreal spectra from 2600 to 9 cal yrs BP. *Spirostachys* are trees found in woodlands and *Podocarpus* are forest trees and are fire-sensitive (Scott, 1999; Coates-Palgraves, 2002; Finch and Hill, 2008). *Phoenix* and *Hyphaene* palms also occurred in the MKD-1 sequence with *Phoenix* occurring more frequently than *Hyphaene*. They can be found along rivers, in forest and grassland (Pooley, 1993; Neumann *et al*., 2010). Ericaceae and *Passerina* which are fynbos elements were present although scanty with *Passerina* pollen occurring more abundantly in the MKD-1 sequence (see Fig. 15). This could be the coastal *Passerina* species (*Passerina rigida*) Pooley, 1993. Aquatics and semi-aquatic plants such as *Phragmites*, Cyperaceae, *Persicaria* and *Typha* dominated the topmost profiles.

6.2 Paleoenvironmental interpretations for MKD-1

6.2.1 Zone 6 (6280-5800 cal yrs. BP)

Forest trees such *as Podocarpus, Olea, Manilkara* were present with *Spirostachys* pollen occurring in very low quantities. An Amaranthaceae pollen peak, the presence of Cyperaceae, *Phragmites*, Scolecodonts, low abundancies of cryptogam spores (Bryophyte and Pteridophyte) and fungal spores were present during this period indicating a relatively warm and sub-humid forest with a wetland mosaic. The peak in Amaranthaceae points to a dry environment (local evaporation) or saline microenvironment such as coastal salt marshes (Dyer, 1975; Scott, 1999; Pooley, 2005). Cooper *et al.*, 2018 reported Holocene sea level high stand as occurring between 6000-7000 Cal yrs. BP. Which explains the presence of Scolecodonts because the increase in sea level would have led to a marine incursion which increased the water table and salinity of the soil hence, the presence of wetland plants such as Cyperaceae and *Phragmites*, and halophytic plants such as Amaranthaceae.

6.2.2 Zone 5 (5800-4680 cal yrs. BP)

Podocarpus, cryptogams (Pteridophytes and Bryophytes), and Poaceae increased; Ericaceae and *Passerina* were present in this zone. *Pseudoschizaea* increased and reached its peak, fungal spores were also present, *Typha* type became prominent. The presence of Ericaceae during this period suggests cold and sub-humid conditions with a relatively seasonal moisture condition (Scott 1999). As cryptogams increased, *Pseudoschizaea* peaked and *Typha* became prominent at around 5000 cal. yrs BP indicating a shift from a saline wetland to a freshwater condition (Scott, 1999; Neumann *et al*., 2010; Gonçalves de Freitas *et al*., 2015).

6.2.3 Zone 4 (4680-2600 cal yrs. BP)

Podocarpus reached a peak of about 30% at around 3380 cal. yrs BP but declined at 2600 cal. yrs BP. Abundant forest elements, increased cryptogams and *Typha* with little or no marine elements and Amaranthaceae suggesting a sub-tropical (relatively warm, moist and freshwater conditions) (Finch and Hills, 2008) typified this zone. This zone is wetter and more humid as compared to zone 5 which corresponds with the proposed 5-10% increase in precipitation in Maputaland during this period (Partridge, 1997).

6.2.4 Zone 3 (2600-2400 cal. yrs BP)

Podocarpus declined at about 2600 cal. yrs BP but finally disappeared at around 2390.1 cal. yrs BP. This decline was accompanied with a decline in other forest elements and cryptogams with a corresponding increase and peak of *Spirostachys* at around 2600-2390 cal yrs BP. *Spirostachys* later declined at after 2390 cal yrs BP with a corresponding increase in Poaceae, Amaranthaceae, Isoglossa and Cyperaceae. *Podocarpus* resurfaced again in very low quantity of less than 8% at around 1700 cal yrs BP as *Spirostachys* pollen levels were still low. Foraminifera lining appeared in this zone suggesting marine influence which may be due to high sea levels leading to marine incursion hence the increase in Amaranthaceae which might have spread along the shores of the lake. The decline in forest elements and cryptogams during this period and a corresponding increase in Poaceae signals to a change from a forested environment to a more open ecosystem which may be due to a drop in moisture levels (droughts). Similar *Podocarpus* forest retreat have been reported by Masus (2000) at around 3100 cal. yrs BP in Maputaland coastal area and Neumann et al. (2010) reported a similar *Podocarpus* retreat at around 3600 cal. yrs BP at Lake Eteza. Hence, it is suggested that this vegetation trend is a regional trend in the coastal area of the Indian Ocean Coastal Belt biome (see Fig.19). PCA results agrees with the changes reported as PCA results shows a strong positive loading of ≥0.02 for *Podocarpus* and cryptogams (forest and humid condition indicator) and a strong negative loading of ≥-0.02 for *Spirostachys* and Poaceae (woodland/ savanna indicator) meaning that an increase in *Spirostachys* brings about a reduction in the forest plant (*Podocarpus*) and cryptogams hence, a change from a humid forested environment to a dry open woodland vegetation.

6.2.5 Zone 2 (2400-670 cal. yrs BP)

Spirostachys pollen increases as Poaceae declined and *Podocarpus* declined and disappeared. Amarathaceae also increased and *Phragmites* increased and reached its peak. Foraminifera linings increased and reached a 20% peak at around 1500 cal yrs BP. During this period, Pteridophyte and

Bryophyte declined and disappeared, and fungal spores declined suggesting low moisture level (humidity) which signals to severe drought and marine influence leading to increase salinity in the environment which would have led to the disappearance of *Podocarpus* which is moisture loving (Scott 1999; Finch and Hill, 2008) and do not survive in highly saline environment as research such as Abiti (2019) reported that *P. latifolius* can survive low to moderate salinity but salinity or salt content >0.6M solution impede germination and is lethal. Also, another research by Zou *et al*. (2021) working on De novo transcriptome analysis of *P. macrophyllus* reported that salt treatment of *P. macrophyllus* significantly affected the photosynthesis system of the seedlings such as decreased chlorophyll content, altered chloroplast ultra-structure and reduced photosynthesis. Severe drought was also recorded during this period as reported by Humphries *et al*. (2019) through the analysis and interpretation of fossil diatoms from cores from lake Muzi.

6.2.6 Zone 1 (670-0 cal. yrs BP)

Typha increased together with fungal spores as fungal spores reached 60% with little to no foraminifera linings in the last 200 cal yrs BP suggesting a warm, sub-humid, less saline to freshwater environment in the last 200 cal yrs BP but 670-200 was still dry with marine influence as foraminifera linings were still present. The presence of benthic foraminifera linings in zone 2 and 1 could be due to severe drought leading to increase evaporation of water from the lake as it is very sensitive to evaporation due to its high surface area (350km^2) to volume ratio (about 0.9m average depth) (Orme, 1990; Hutchison and Midgley, 1978). Hence, as water is lost from the lake through evaporation, and less fresh water supplies due to drought, more sea water flows into the estuarine. *Pinus* pollen appeared in the last 400 cal yrs BP indicating disturbance by the European settlers (Neumann *et al*., 2008). This is because *Pinus* was introduced to South Africa by the

Europeans hence not indigenous. The increase and composition of fungal spores in the last 200 cal yrs BP also signals anthropogenic activities (Gelorini *et al*., 2012; Kettner *et al*., 2017; Li *et al*., 2018).

Table 4: Summarized Paleoenvironmental Interpretation for MKD-1

	Pollen character	**Age (cal. yrs BP)**	**Climate interpretation**
Zone 6	*Podocarpus*, Olea, Manilkara, and Cryptogams present High Amaranthaceae, Scolecodont	6280-5800	Warm, moist with Marine influence
Zone 5	Increase *Podocarpus*, Poaceae, Cryptogams appeared, presence of Ericaceae and *Passerina* Peak of *Pseudoschizaea*, and increase *Typha*	5800-4680	Cold, sub-humid with freshwater conditions
Zone 4	*Podocarpus* peak at 3300 cal. yrs BP. Increase Cryptogams, *Typha*	4680-2600	Relatively warm, moist with freshwater condition. Wetter and more humid than zone 4
Zone 3	Decline in *Podocarpus* and Cryptogams, Increase *Spirostachys* at the beginning but later declined as Poaceae increased .	2600-2400	Warm, drop in moisture level (drought) as *Podocarpus* and Cryptogams retreated
Zone 2	Increase *Spirostachys* as Cryptogams and *Podocarpus* declined but *Podocarpus* latter disappeared. Amaranthaceae, Scolecodont and	2400-670	Warm and dry (drought) with intense marine influence at 1500 cal. yrs BP This zone is drier than zone 3

	Foraminiferal lining increased and Foraminiferal lining peaked at 1500 cal. yrs BP		
Zone 1	Increase in *Typha* in the last 200 cal yrs BP, fungus spores increased and presence of *Pinus* in the last 400 cal. yrs BP	670- 0	Relatively warm and dry with increased precipitation in the last 200 cal yrs BP and disturbance from human activities

6.3 Paleoenvironmental interpretations for MK24-1

6.3.1 Zone 4 (1711-1200 cal yrs. BP)

The presence of forest elements and cryptogams in low quantities with *Podocarpus* less than 5% was recorded in this zone. Poaceae was 30-40%, *Phragmites* and Cyperaceae 7-8%, peak of fungal spore at 60%, *Pseudoschizaea* and *Typha* were also present indicating a warm environment with low moisture levels (humidity) and freshwater conditions. The presence of less than 5% *Podocarpus* and other forest elements suggest a low moisture (humid) environment as *Podocarpus* is moisture loving (Scott 1999; Finch and Hill, 2008). Neumann *et al*. (2010) reported a drier condition and a drop in sea levels leading to the decline of forest elements during this period. A comparable pattern in pollen sequence was seen at Lake Sibaya (Neumann *et al*., 2008) (see Fig. 20). PCA results shows strong positive loadings of ≥0.01 for *Persicaria*, Cyperaceae, *Phragmites*, *Ascolepis* (wetland elements with *Persicaria* indicating disturbances Scot, 1999) and *Spirostachys*, Commelinaceae, *Alternanthera*, Poaceae, Asteraceae (tubuliflorae), *Olea*, Combretaceae, Amaranthaceae (woodland/savanna elements), a strong negative loadings of ≥ -0.04 for fungal spores, bryophyte spores, monolete spores (high humidity) *Podocarpus*, *Manilkara* (forest element), *Typha* (fresh water conditions) suggesting a change from a humid forest with freshwater conditions to a disturbed woodland/savanna with wetland mosaic.

6.3.2 Zone 3 (1200-280 cal yrs. BP)

Spirostachys pollen grains increased and peaked at 10% around 980 cal yr BP, but they then began to drop between 810 and 515 cal yr BP with a corresponding increase and peak in Poaceae pollen at 70% and charcoal at 15%. Also, fungal spores, cryptogams, as well as pollen of *Typha*, *Pseudoschizaea* and *Phragmites* declined. A sharp increase in *Spirostachys* points to a more open woodland vegetation and the decline of fungal spores, cryptogams, *Typha*, *Pseudoschizaea* and *Phragmites* points to a drier environment with lower precipitation. The increase and peak of charcoal and Poaceae and corresponding decrease in *Spirostachys* between 816 - 515 cal. yrs BP may suggest anthropogenic activities which can be attributed to Iron Age farming as they were clearing the forest for grazing. Animal and crop farming started 1600 cal. yrs BP in the eastern South Africa (Hall, 1980; Bousman, 1998; Huffman, 2007) but it could also be due to the drier conditions of the environment (Ekblom 2008; Neumann *et al*., 2010). Towards the end of the zone, *Spirostachys* increased again together with Cyperaceae and *Persicaria* as Poaceae declined at about 284.7 cal. yrs BP indicating a relatively warm environment with disturbed swamp mosaic. *Pinus* is also present in this zone, which is a contamination due to pollen seepage (Malmström, 1922; Erdtman, 1922). This error can easily be identified and resolved during interpretations by comparing with regional pollen sequence (Godwin 1934) which has been done and is seen even in core MKD-1 sequence, Lake Eteza and Sibaya that *Pinus* didn't appear until about 400cal yrs BP.

6.3.3 Zone 2 (280-200 cal yrs. BP)

The increase and peak of Amaranthaceae at 30% with increase charcoal and charred cuticle during this period, along with the decline in Poaceae, herbs, shrubs, wetland elements and disappearance of forest elements, indicates drought leading to high evaporation and the drying out of the swamp hence, the abundance of Amaranthaceae as they point to a dry or saline environment (Dyer, 1975; Scott, 1999; Pooley, 2005). The increase in macro and micro charcoal and charred cuticles suggest local fire which may be caused by the dry climate conditions. Ekblom (2008) reported that there have been repeated dry spells associated with the "Little Ice Age" (250-500 cal. yrs BP) in the Indian Ocean Coastal Belt biome. Hence, this could be part of the dry spells period. Compared to zone 3, this period is drier because Amaranthaceae peaked while Poaceae, woodland, and wetland components declined drastically.

6.3.4 Zone 1 (200- 0 cal yrs BP)

The presence of *Spirostachys* and *Pinus* pollen and the increase in Poaceae, *Phragmites*, Cyperaceae, *Persicaria*, and *Typha* during this period indicates a relatively warm environment with increased precipitation and disturbed wetland mosaic indicated by the presence of *Persicaria* and other wetland taxa (Scott, 1999). *Pinus* indicates disturbances by the European settlers as they introduced and grew large Pine plantations in coastal areas of the Indian Ocean Coastal Belt biome since 1928–1929 and in the St. Lucia region since 1957 (Marwick, 1973; Thamm *et al*., 1996).

Table 5: Summarized Paleoenvironmental Interpretation for MK24-1

	Pollen character	**Age (cal. yrs BP)**	**Climate interpretation**
Zone 4	Presence of *Podocarpus*, forest elements and Cryptogams in very low percentages Presence of *Pseudoschizaea* and *Typha*	1711-1200	Warm with freshwater condition and low moisture level
Zone 3	Increase *Spirostachys* at 1168.5 cal. yrs BP Decline of *Spirostachys*, fungal spores, cryptogams, *Typha*, *Pseudoschizaea*, *Phragmites* and increase in Poaceae at 816.4-515.4 cal. yrs BP	1200-280	Warm with very low moisture level (Drought) Drier than zone 4
Zone 2	Decline in Poaceae, Wetland elements Increase and peak of Amaranthaceae, charcoal and charred cuticles	280-200	Drought leading to local fire Drier than zone 3
Zone 1	Presence of *Spirostachys* Increase Poaceae, *Phragmites*, Cyperaceae, *Persicaria* and *Typha* *Pinus* present	200-0	Relatively warm with increase precipitation and disturbance from human activities

6.4 Comparison of cores MKD-1 and MK24-1

From the pollen diagrams and summary of paleoenvironmental interpretations, it is clear that both cores have undergone similar vegetational changes, such as low *Podocarpus* assemblages in the last 2000 cal yrs BP (see Fig. 17 and 18) and a matching increase in *Spirostachys*, which later declined as Poaceae increased. The cores also show different evironmental changes: MK24-1 recorded a local fire caused by a severe drought between 280 and 200 cal yr BP, which allowed for the recovery of charcoal and charred cuticles, but MKD-1 showed little to no evidence of charcoal in the core. This may be because inland freshwater wetlands are more likely to be affected by changes in temperature, precipitation patterns, and severe drought while estuarine lakes still receive supplies from the sea during times of drought and may most likely experience hyper-salinity. So, the swamp core was more affected by drought leading to local fire. Finally, disturbances from human activities can be seen in both cores over the past 200 cal years BP.

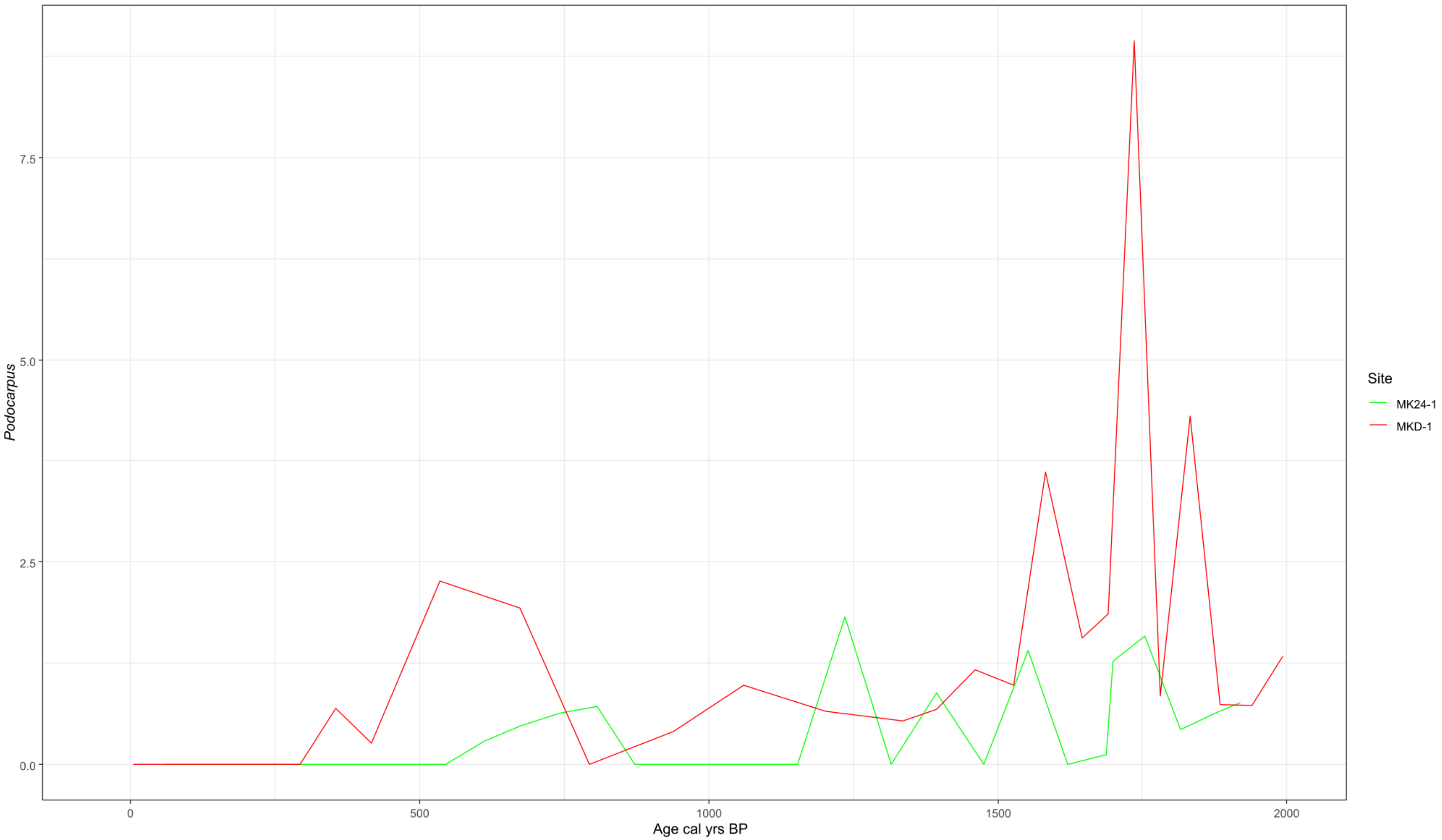

Figure 17: *Podocarpus* trends in core MKD-1 and MK24-1 showing lower percentages in the last 2000 cal yrs BP

Figure 18: *Spirostachys* trends in core MKD-1 and MK24-1 showing higher percentages in the last 2000 cal yrs BP

6.5 Regional Comparison

Regionally, vegetation history varies among the various sites, but Lake Eteza, Lake Sibaya, and Lake St. Lucia (MKD-1 and MK24-1) shared a similar vegetation history because they are all close to the Indian Ocean and reflect coastal vegetation, while the others are inland, with an exception of the coastal forest and Miombo woodland of Vilankulo in Mozambique. It is important to remember that local biogeography is influenced by elements other than climate, such as soil nutrients, soil type, topography, etc. Even though the vegetation history varies, consistent climate inferences based on palynological data were recorded in the various sites at different times (see tables 8&9). Other paleoenvironmental proxies in the area that extends to the South African summer rainfall zone provide varying climate deductions on drought phases but agreed that moist and wet climate prevailed between 7000 cal yrs BP to 4500 cal yrs BP but phases of drought were reported to last about 4700-2800 cal yrs BP based on geochemical and diatom studies in Lake St Lucia (MKD-1) and Lake Muzi (Humphries *et al*., 2020; Humphries *et al*., 2019). Although drought phases were also recorded around 2100-1400 and 850-550 cal yrs BP for lake Muzi (Humphries *et al*., 2019). In contrast, drought phases for Lake St Lucia using palynomorphs were recorded between 2600-200 cal yrs BP with intense drought between 600-200 cal yrs BP.

Early Holocene (10200—7000 cal. yrs BP): This period is characterized by moist climate as *Podocarpus* and other forest elements are present and abundant in Mfabeni peatland and Lake Eteza (Finch and Hill, 2008; Neumann *et al*., 2010). This present study does not cover this period and therefore cannot provide additional insights.

Mid Holocene (7000-2600 cal. yrs BP): The mid Holocene climate is characterized by high sea levels leading to a marine incursion and high precipitation (fresh water conditions) and high moisture content hence, the presence of moisture loving plants (*Podocarpus* forest, cryptogams and fungi) marine elements such as scolecodonts and freshwater indicators such as *Pseudoschizaea* and *Typha* in Lake St Lucia (Core MKD-1and Core MK24-1), Lake Sibaya and Eteza (Neumann *et al*., 2008; 2010).

Late Holocene (Last 2600 cal. yrs BP): Regional vegetation characteristics during the last 2600 cal. yrs BP is said to denote a warm and dry climate as the *Podocarpus* forest retreated as *Spirostachys* increased in Lake Sibaya, Lake Eteza (Neumann *et al*., 2008; 2010) and Lake St Lucia (Core MKD-1and Core MK24-1). Additionally, in the Nhaucatic Lake, Coastal forest, and Miombo woodland, an increase in bushveld savanna pollen, Asteraceae, and Brachystegia was noted (Ekblom 2008; Ekblom et al., 2014). It became more drier regionally leading to drought around 700-250 cal. yrs BP hence, the decline in *Brachystegia* in Miombo woodland, decline in bushveld trees in Nhaucatic Lake, Reduction in *Spirostachys* in Lake St Lucia (Core MKD-1and Core MK24-1) and Lake Eteza (see Fig. 21) (Ekblom 2008; Ekblom *et al*., 2014; Neumann *et al*., 2010). Marine influence was seen in MKD-1 between 1500-200 cal yrs BP which can be explained as increase in the flow of sea water into the estuarine due to the drying out of the lake (evaporation) and less supply of freshwater from the rivers caused by drought.

6.5.1 *Podocarpus*/*Spirostachys* trends in the Indian Ocean Coastal Belt Biome (IOCB)

Lake Eteza and Lake St. Lucia exhibit high *Podocarpus* percentages, despite fluctuations between 7000 and 2600 cal yr BP (see Fig. 19). *Podocarpus* decreased as *Spirostachys* increased in Lake Eteza, Sibaya, and Lake St. Lucia between 2600 and 670 cal yr BP. The drop in *Podocarpus* percentages as *Spirostachys* percentages increases is as a result of a drop in moisture content (Humidity) in the last 2600 cal yrs BP. *Podocarpus* has therefore been forced to retreat because of how sensitive they are to changes in moisture content and how strongly their distribution depends on high moisture availability (Chevalier et al., 2021).

In the past 670 cal yrs BP, *Podocarpus* was still present in Lake Eteza and Lake Sibaya as they attempted to recover, but it vanished from the Lake St. Lucia pollen record (see Fig. 19). *Podocarpus* is fire-sensitive (Scott, 1999; Coates-Palgraves, 2002; Finch and Hill, 2008), hence its disappearance in Lake St. Lucia cores may have been caused by the local fire that resulted from extreme drought in Core MK24-1 (see table 7). In core MKD-1, the soil in the surrounding environment may have become hypersaline as a result of the extreme drought. *Podocarpus* can only survive in slightly saline environment as studies like those by Abiti (2019) and Zou et al. (2021) have demonstrated that hypersaline soils kill or impede the germination and growth of *Podocarpus* seedlings.

In conclusion, the Indian Ocean Coastal Belt Biome (IOCB) experienced considerable moisture availability during the mid-Holocene (7000-2600 cal yrs BP), as demonstrated by the abundance of *Podocarpus* in Lake Eteza, Sibaya, St. Lucia, and even Mfabeni peatland. The late Holocene witness low moisture availability as *Podocarpus* retreated and in the last 670 cal yrs BP, extreme drought was experienced in Lake St Lucia leading to the disappearance of *Podocarpus* (see Fig. 20).

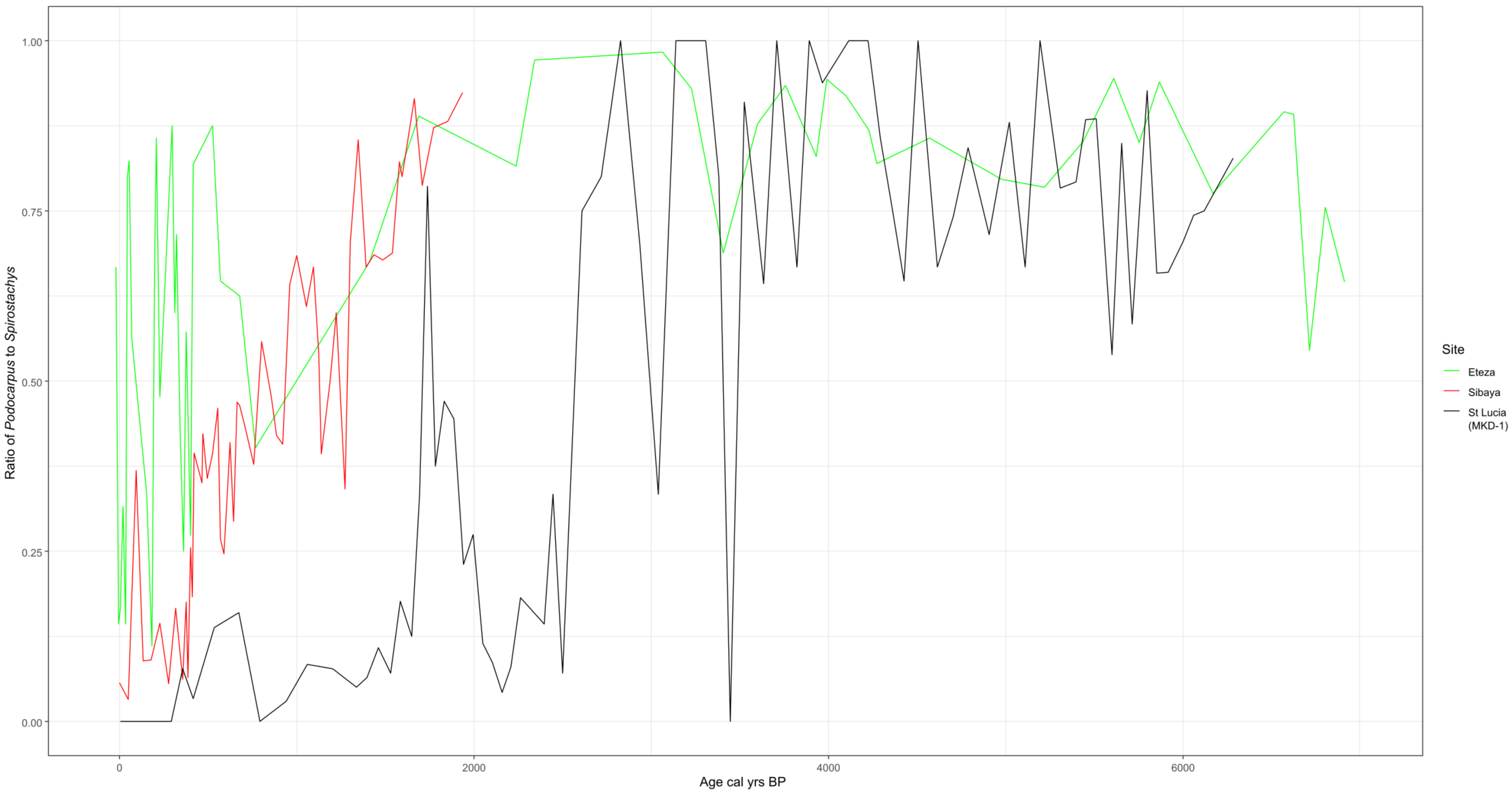

Figure 19. *Ratio of Podocarpus to Spirostachys pollen in the IOCB showing a decline in Podocarpus in the late Holocene*

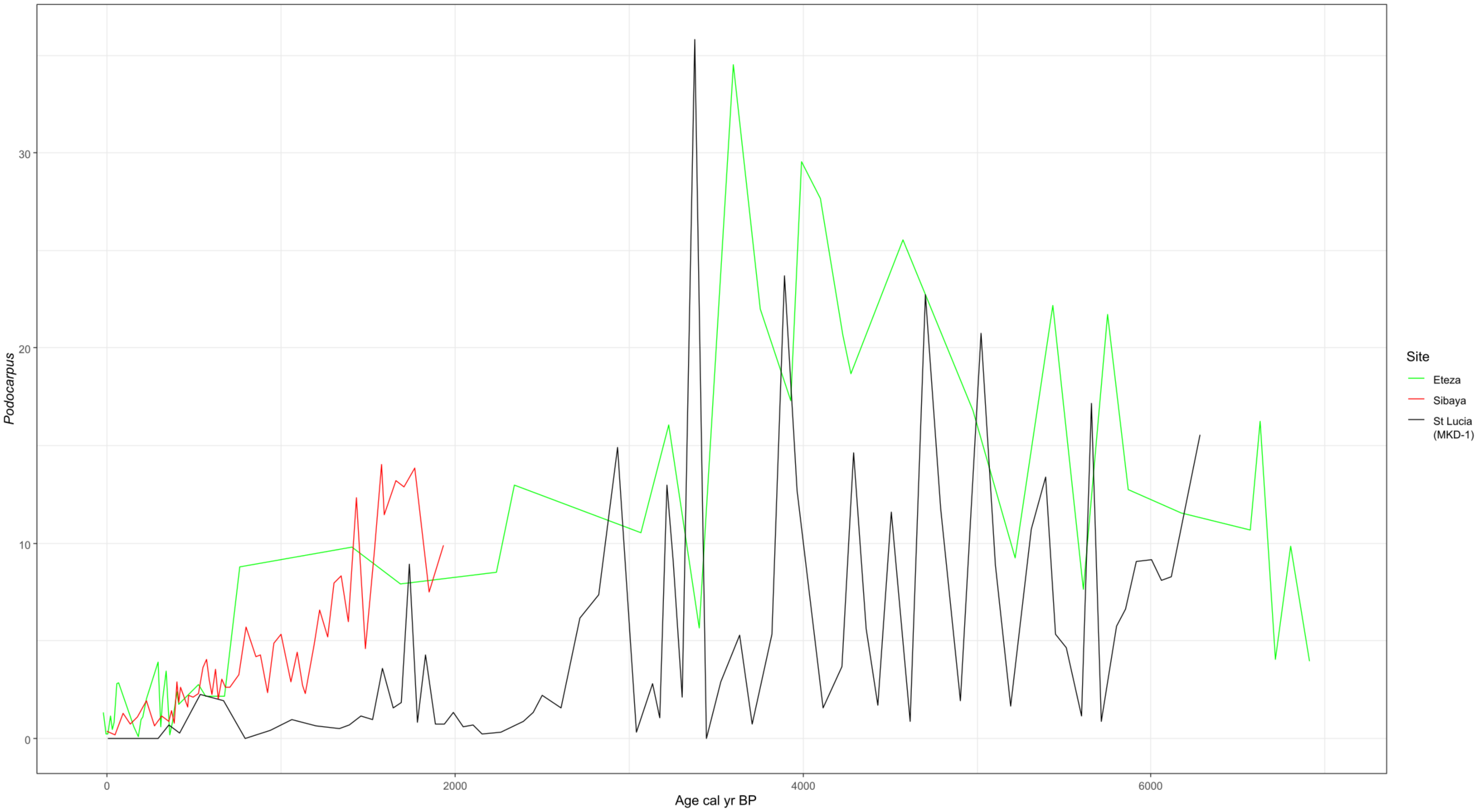

Figure 20. *Podocarpus* trends in the IOCB, showing a decrease in *Podocarpus* pollen in the late Holocene

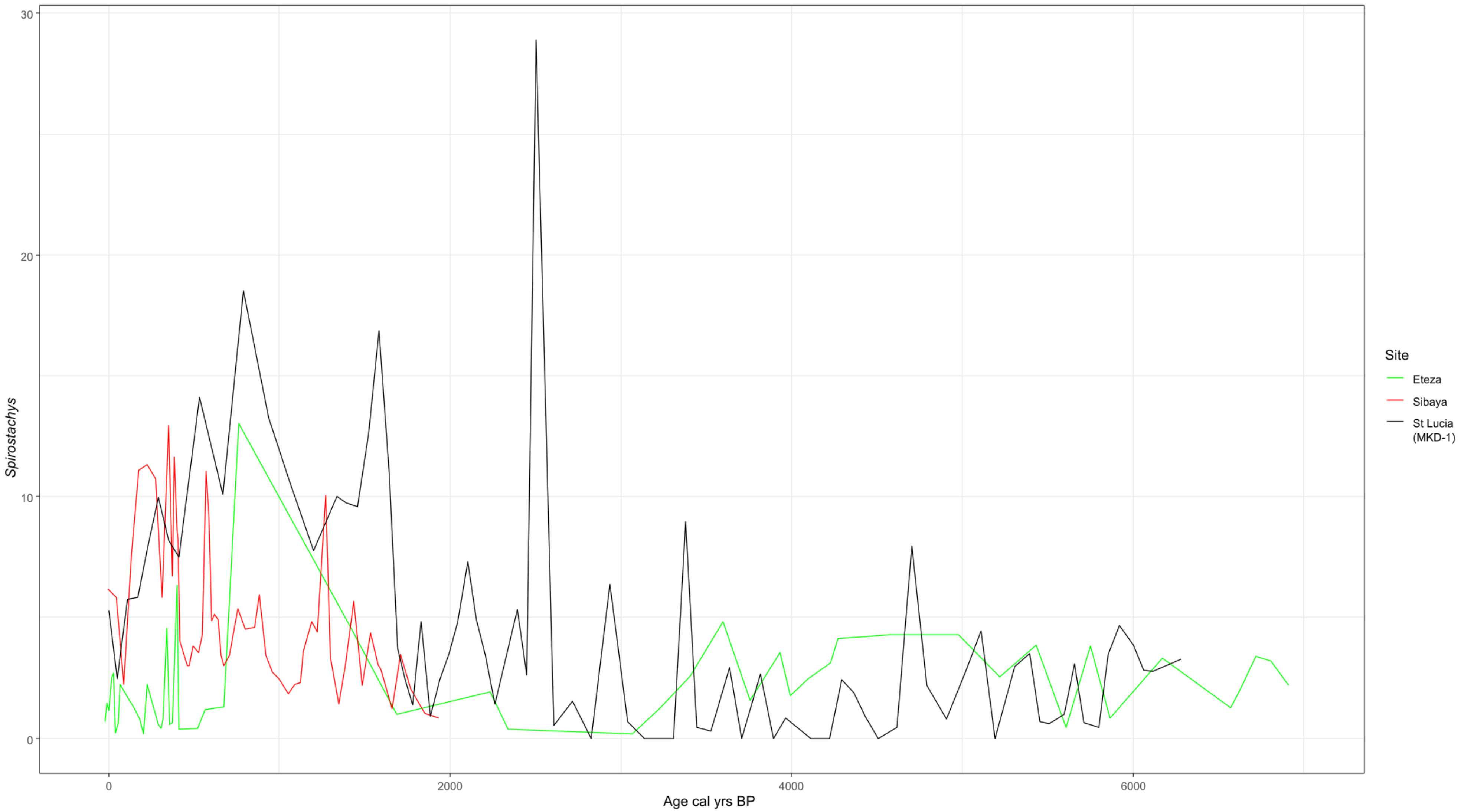

Figure 21. *Spirostachys* trends in the IOCB, showing an increase in *Spirostachys* in the late Holocene

Table 6: Regional Comparison of Palynological Results

	Southern Mozambique (Nhaucati lake) Mozambique) Ekblom (2008	Coastal forest and Miombo woodland of Vilankulo(Mozambique) Ekblom *et al*. (2014)	Mfabeni Peatland Finch and Hill (2008)	Lake Eteza Neumann *et al*. (2010)	Lake Sibaya Neumann *et al*. (2008)	Lake St Lucia Core MKD-1	Lake St Lucia Core MK24-1
Age (cal ka/ka BP)	Climate inferences	Climate inferences	Climate inferences	Climate inferences	Climate inferences	Climate inferences	Climate inferences
0-250	Drought during the little ice age at Ca. 550 cal. yrs BP	Cold dry periods		Climate change induced by human activities and the onset of little ice age in Ca. 700 cal. yrs BP (Drought)	Climate change induced by human activities	Relatively warm with high precipitation in the last 200 cal yrs BP and lots of human disturbances	Relatively warm with high precipitation and human disturbances in the last 200 cal yrs BP Intense Drought between 280-200 cal. yrs BP
250-550					Humid climate		
550-800	Warm period					Warm and dry with marine influence at 1500 cal yrs BP	Warm and dry
800-1200	Warm period			Drier, continued gradual decrease of SST, Sea levels drop Mangrove swamp forest decline			
1200-1600	Dry period	Dry periods					Warm with freshwater condition
1600-3600						Warm and dry	
3600-4600				High precipitation, High SST, relatively high sea levels		Warm, moist with freshwater condition	

4600-6800						Cold, subhumid with freshwater condition at 5800-4600 cal. yrs BP but warm and moist with high sea levels at 6280-5800 cal. yrs BP	
6800-8000				Relatively wet Ca. 10,000 cal. yrs BP becoming dry Ca. 8000-7000 cal. yrs BP increase SST/sea level	Warm moist conditions		
8000-10,200			Moist cool climate				

Table 7: Summarized Regional Paleoenvironmental Results

Periods	Southern Mozambique (Nhaucati lake) Mozambique) Ekblom (2008	Coastal forest and Miombo woodland of Vilankulo (Mozambique) Ekblom *et al*. (2014)	Mfabeni Peatland Finch and Hill (2008)	Lake Eteza Neumann *et al*. (2010)	Lake Sibaya Neumann *et al*. (2008)	Lake St Lucia Core MKD-1	Lake St Lucia Core MK24-1
Late Holocene (last 2000) cal. yrs BP	Warm and dry	Cold and dry		dry		Warm and dry with marine influence	Warm and dry
Mid Holocene (7000-2000) cal. yrs BP				High precipitation/ high sea levels		High precipitation/ High sea levels and High humidity	

6.6 Summary

Scott *et al.* (2012), in a recent review of Quaternary vegetation and climate changes in South Africa, studied terrestrial fossil pollen evidence of climate change during the last 26 thousand years in southern Africa using Principal Components Analysis (PCA) to monitor taxa sensitive to moisture and temperature fluctuations. The authors reported that marked but non-parallel moisture changes occurred in different sub regions during the Holocene suggesting that climatic forces were not uniform over the region.

Palaeoenvironmental studies in the Indian Ocean Coastal Belt Biome of South Africa reveal that moisture content varied within the region during the Holocene but generally, there has been a change from a humid climate with high sea level during the mid-Holocene to a warm and dry climate during the late Holocene.

Chapter 7

Conclusion

7.0 Main findings from the study

According to the pollen analysis of two Lake St. Lucia cores, the environment was warm, sub-humid to dry with local evaporation or saline microenvironment, such as coastal salt marshes, between 6280 and 5800 cal. yrs BP. This was due to an increase and peak in Amaranthaceae and very low cryptogams (Pteridophytes and Bryophytes). Based on the occurrence of Scolecodonts, there were high sea levels during this time. Cryptogams, *Ericaceae*, *Passerina*, *Typha*, and *Pseudoschizaea*—the latter of which was common—are evidence that the environment between 5800 and 4680 cal. years BP became cooler, sub humid, with freshwater conditions. Cryptogams and *Podocarpus* proliferated and peaked when the climate warmed and became more humid between 4680 and 2600 cal yrs BP. Between 2600 and 670 calendar years ago (cal. BP), the environment became warmer, there was low moisture levels (drought), and there was a greater influx of sea water into the estuarine Lake as a result of the lake's high rate of evaporation and low freshwater input caused by drought. Hence, the presence of foraminfera linings around 1500 cal yrs BP in core MKD-1 and the retreat of *Podocarpus* in the last 2600 cal yrs BP. Charcoal fragments, charred cuticles, and an Amaranthaceae peak were noted together with the decline/disappearance of other species in core MK24-1 between 670 and 200, when the climate grew warmer and dry leading to a local fire. A relatively warm environment with high precipitation, wetland mosaic and human disturbances was in the last 200 cal. yrs BP which is seen with the presence and increase in *Typha*, *Persicaria*, *Pinus*, *Phragmites* and Cyperaceae.

In conclusion, findings show a change from a humid forested environment with high precipitation and high sea levels (6280-2600 cal yrs BP) to a warm and dry open woodland environment (2600-200 cal yrs BP), with Principal Component Analysis (PCA) confirming this assertion. Findings also demonstrate that plants respond to climate change and that species have a bioclimatic range within which they can thrive but may not do so outside of it, as demonstrated by *Podocarpus*' decrease and eventual extinction in the investigated cores. The mid-Holocene is marked by moisture-loving plants (forest components), while the late-Holocene is marked by drought, which led to a decline in forest trees. These regional climate changes can be seen in the last 6300 cal yr BP.

7.1 Review of Study Objectives

7.1.1 Retrieving suitable sediment samples from Mkuze swamp for pollen analysis and radiocarbon dating

Two core samples were retrieved from two different location at the Mkuze with MK24-1 directly from Mkuze swamp. The core was sub-sampled, and the subsamples were analyzed for pollen and some sent for radiocarbon dating of which 6 radiocarbon dates were gotten from MKD-1 and 3 radiocarbon dates for MK24-1 and the rest interpolated through the use of Bayesian statistics. See chapter 2, 4 and 5 for more information

7.1.2 Extraction and concentration of palynomorphs from the sediments

The sub-sampled material was subjected to standard palynological laboratory processing method for pollen extraction from sediments

7.1.3 Counting and identification of the recovered palynomorphs

The recovered palynomorphs were counted, a minimum of 100 counts were done for MKD-1 as it had paucity of pollen at some depth between 300 to 7cm and a minimum of 250 count was done for MK24-1. The recovered palynomorphs were identified using Pollen Atlases, online pollen data bank and modern pollen reference collections at the Evolutionary Studies Institute, University of the Witwatersrand, and the Department of Plant Sciences, University of the Free State and a pollen atlas for the IOCB was generated see chapter 3.

7.1.4 Determining the species frequency and composition in the different strata

Changes in species assemblages both quantitatively and qualitatively was noted at the different depth which gave information about the changes in environment. This can be seen in the pollen diagrams in chapters 4 &5.

7.1.5 Determining the dominant ecological drivers responsible for the changes in species composition throughout the period covered by both cores in order to decipher the climatic indication

This was done by checking the species composition per depth/age and noting when the species composition changes as this signals to a change in environmental conditions and using the present day environmental requirement of the recovered species, a conclusion was reached on the major ecological drivers as in this case, humidity and aridity were the major drivers. See table 7 in chapter 6.

7.1.6 Comparison of findings from the study site to other palynological records

This was done by comparing the findings from core MKD-1 and MK24-1 with the reviewed palynological records (Lake Eteza and Sibaya) in the Indian Ocean Coastal Belt Biome of South Africa and result shows a good correlation especially with Lake Eteza (Neuman *et al*., 2010) (see Fig 19, 20,21).

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Appendices

MKD-1 PCA Scores

SPECIES	PC1		SPECIES	PC2
*Phragmites*_Poaceae	-0.85016		Poaceae_others	-0.87091
Amaranthaceae	-0.63023		Combretaceae_Melastomaceae	-0.67269
Cyperaceae_other	-0.60972		Asteraceae_Tubuliflora	-0.60405
*Crasula*_Crassulaceae	-0.53188		*Manilkara*_Sapotaceae	-0.54413
*Pinus*_Pinaceae	-0.52938		*Cyathea*_Cyatheaceae	-0.50303
Persicaria_Polygonaceae	-0.52734		Olea_Oleaceae	-0.49281
*Spirostachys*_Euphorbiaceae	-0.44852		Amaranthaceae	-0.46858
*Olea*_Oleaceae	-0.42282		*Pteris*_Pteridaceae	-0.42118
*Trema*_Ulmaceae	-0.40793		*Phoenix*_Aracaceae	-0.40234
*Phoenix*_Aracaceae	-0.40597		Trilete_spore	-0.39201
*Myriophyllium*_Myriophyllaceae	-0.33722		*Acacia*_Fabaceae	-0.37688
Ascolepis_Cyperaceae	-0.29851		*Passarina*_Thymeliaceae	-0.36298
*Sparganium*_Sparganiaceae	-0.27765		Cyperaceae_other	-0.3536
Hyphaena_Aracaceae	-0.26991		*Euclea*_Ebenaceae	-0.34723
*Pseudolachriostylis*_Phyllanthaceae	-0.26059		*Ilex*_Aquifoliaceae	-0.32907
*Celtis*_Cannabaceae	-0.25005		*Syzygium guineense*_Myrtaceae	-0.32107
Caryophillaceae	-0.24536		*Euphorbia*_Euphorbiaceae	-0.28782
*Syzygium guineense*_Myrtaceae	-0.23657		Ericaceae	-0.27088
*Heteromopha*_Apiaceae	-0.20342		*Mimosup*_Sapotaceae	-0.25004
Asteraceae_Tubuliflora	-0.19629		*Isoglossa*_Acanthaceae	-0.24597
Moraceae	-0.18722		*Heteromopha*_Apiaceae	-0.21795
*Manilkara*_Sapotaceae	-0.02271		*Podocarpus*_Podocarpaceae	-0.20341
Poaceae_others	-0.02008		Moraceae	-0.19966
Combretaceae_Melastomaceae	0.004696		*Mohria*_Schizaeaceae	-0.15365
*Mimosup*_Sapotaceae	0.006821		*Anthoceros*	-0.1143
*Ficus*_Moraceae	0.02791		*Crasula*_Crassulaceae	-0.10169
Ericaceae	0.033292		*Myriophyllium*_Myriophyllaceae	-0.09238
*Euclea*_Ebenaceae	0.054447		*Polygala*_Polygalaceae	-0.07996
*Acacia*_Fabaceae	0.064598		Caryophillaceae	-0.06859
*Polygala*_Polygalaceae	0.076948		*Persicaria*_Polygonaceae	-0.05695
*Ilex*_Aquifoliaceae	0.094345		*Acalypha*_Euphorbiaceae	-0.03253
*Passarina*_Thymeliaceae	0.238708		*Trema*_Ulmaceae	-0.02384
*Acalypha*_Euphorbiaceae	0.269931		*Celtis*_Cannabaceae	-0.01702
*Euphorbia*_Euphorbiaceae	0.288251		Monolete_spores	0.006917
Anthoceros	0.298578		*Pseudolachriostylis*_Phyllanthaceae	0.025426

*Pteris*_Pteridaceae	0.302942		Polypodiaceae	0.033271
Trilete_spore	0.325142		*Phragmites*_Poaceae	0.053595
Fungal_spores	0.356014		*Hyphaena*_Aracaceae	0.05914
*Mohria*_Schizaeaceae	0.402592		*Ficus*_Moraceae	0.072196
Bryophytes_spores	0.515257		*Spirostachys*_Euphorbiaceae	0.090647
Monolete_spores	0.525652		Bryophytes_spores	0.194513
*Isoglossa*_Acanthaceae	0.551497		*Sparganium*_Sparganiaceae	0.264081
Polypodiaceae	0.590327		*Ascolepis*_Cyperaceae	0.338065
Cyathea Cyatheaceae	0.607337		*Pinus*_Pinaceae	0.457556
*Podocarpus*_Podocarpaceae	0.618274		Fungal_spores	0.718104

MK24-1 PCA Scores

Species	PC1		Species	PC2
fungal_spores	-0.96151		*Pinus*	-0.87719
Bryophyte_spores	-0.72386		*Crasula*	-0.85724
Monolete_spores	-0.63429		*Manilkara*	-0.7604
Podocarpus	-0.6285		*Ascolepis* Cyperaceae	-0.66571
Typha	-0.55947		Amaranthaceae	-0.45296
Manilkara	-0.25509		*Spirostachys*	-0.42052
Vachelia/Senegalia	-0.06547		*Vachelia/Senegalia*	-0.18297
Euclea	-0.0414		*Typha*	-0.1657
Crasula	0.000258		Monolete_spores	-0.15875
Amaranthaceae	0.010697		Poaceae	-0.14211
Ascolepis, Cyperaceae	0.033086		*Olea*	-0.07307
Combretaceae_Melastomaceae	0.038437		*Euclea*	-0.03005
Pinus	0.097741		fungal_spores	-0.01933
Phragmites	0.109274		Asteraceae_tubuliflorae	0.03856
Olea	0.218221		Cyperaceae	0.05684
Asteraceae_tubuliflorae	0.294258		commelinaceae	0.17716
Poaceae	0.47974		Combretaceae_Melastomaceae	0.2616
Alternanthera	0.593341		*Alternanthera*	0.30695
Spirostachys	0.605356		*Persicaria*	0.33222
Cyperaceae	0.728275		Bryophyte_spores	0.40026
commelinaceae	0.748603		*Phragmites*	0.58248
Persicaria	0.878847		*Podocarpus*	0.65409

Depth and Calibrated ages

MKD-1		MK24-1	
depth (cm)	Age (cal yr BP)	depth (cm)	Age (cal yr BP)
		in cm	age BP
7	-4.6	0	-70
13	49	1	-51.2
20	110.7	2	-21
27	174.1	3	33.7
33	229.1	4	89.1
40	292.2	5	105
47	355.2	6	123.3
53	415.7	7	143.4
60	534.8	8	164.5
67	672.6	9	186.4
73	792.6	10	208.6
80	938.9	11	231.9
86	1060.2	12	257.9
93	1201.4	13	284.7
100	1335.9	14	311.9
106	1394.6	15	338.5
113	1461.3	16	363
120	1526.8	17	386.2
126	1583.4	18	408.2
133	1646.7	19	429.5
138	1691.6	20	450.9
143	1736.5	21	472.3
148	1781.7	22	494.1
153	1832.1	23	515.4
158	1884.9	24	536.8
163	1939	25	558
168	1992.9	26	579.7
173	2047	27	601.6
178	2102.1	28	623.1
183	2156.6	29	644.5
188	2210	30	665.8
193	2264.2	31	687.6
198	2318.6	32	708.7
205	2395.1	33	730.3
210	2447.9	34	751.8
215	2501.9	35	773.2
225	2609.7	36	794.6

235	2717.2	37	816.4
245	2826.3	38	837.9
255	2934.3	39	859
265	3042	40	880.9
275	3137.8	41	902.6
282	3174.4	42	924.1
288	3218.2	43	945.8
293	3255.2	44	967.2
300	3307.1	45	989
310	3380.1	46	1011.7
318	3438.6	47	1036.1
319	3445.9	48	1061.7
330	3525.5	49	1088.3
345	3636.4	50	1115
355	3709.6	51	1141.7
370	3820.4	52	1168.5
380	3893.3	53	1195.9
390	3967.4	54	1222.4
410	4115.3	55	1249.2
425	4222	56	1276.1
435	4292.2	57	1302.7
445	4364.7	58	1329.2
454	4428.9	59	1355.9
465	4507.9	60	1382.6
480	4615.8	61	1408.8
495	4704.8	62	1435.6
510	4790.9	63	1462.5
530	4905.7	64	1489.1
550	5020.9	65	1515.8
565	5108	66	1542.2
580	5193.7	67	1568.3
600	5309.6	68	1594.6
615	5395.7	69	1620.8
625	5453.1	70	1646
635	5511.5	71	1669.2
650	5598.6	72	1690.3
660	5656.3	73	1711
670	5714.9		
685	5801.2		
694	5853.8		
705	5917.6		

720	6004.5
730	6061.8
740	6118.9
770	6283.1

Podocarpus and *Spirostachys* percentages in Core MKD and MK24

ID	REFERENCE	Core	Age cal yrs BP	*Spirostachys*	*Podocarpus*	RATIO
1	1	MK24	-52	4.842615	0	0
2	2	MK24	60.3	1.426025	0	0
3	3	MK24	133.8	4.347826	0	0
4	4	MK24	177.5	0	0	0
5	5	MK24	200	2.200489	0	0
6	6	MK24	272.7	7.845579	0	0
7	7	MK24	347	6.782946	0	0
8	8	MK24	480.55	4.173623	0	0
9	9	MK24	545.6	1.845638	0	0
10	10	MK24	611.1	1.126761	0.28169	0.2
11	11	MK24	675.8	3.782506	0.472813	0.111111
12	12	MK24	741	0.625	0.625	0.5
13	13	MK24	806.6	5.486726	0.707965	0.114286
14	14	MK24	871.75	2.392344	0	0
15	15	MK24	937.15	4.942339	0	0
16	16	MK24	1005.15	10.78014	0	0
17	17	MK24	1076.55	7.432432	0	0
18	18	MK24	1153.35	4.308797	0	0
19	19	MK24	1235.25	1.459854	1.824818	0.555556
20	20	MK24	1315.2	0	0	0
21	21	MK24	1394.7	0.656455	0.875274	0.571429
22	22	MK24	1475.35	2.209302	0	0
23	23	MK24	1552.1	0.936768	1.405152	0.6
24	24	MK24	1620.3	1.960784	0	0
25	25	MK24	1687.25	1.261468	0.114679	0.083333
26	26	MK24	1698.8	1.150748	1.265823	0.52381
27	27	MK24	1754.1	2.107482	1.580611	0.428571
28	28	MK24	1816.85	2.23152	0.41841	0.157895
29	29	MK24	1879.05	0.642055	0.642055	0.5
30	30	MK24	1919.35	1.086957	0.76087	0.411765
31	1	MKD	4.6	5.275229	0	0
32	2	MKD	49	2.456647	0	0
33	3	MKD	110.7	5.753425	0	0
34	4	MKD	174.1	5.813953	0	0
35	5	MKD	229.1	7.808564	0	0
36	6	MKD	292.2	9.976798	0	0
37	7	MKD	355.2	8.205128	0.683761	0.076923

38	8	MKD	415.7	7.49354	0.258398	0.033333
39	9	MKD	534.8	14.12429	2.259887	0.137931
40	10	MKD	672.6	10.09615	1.923077	0.16
41	11	MKD	792.6	18.51852	0	0
42	12	MKD	938.9	13.25301	0.401606	0.029412
43	13	MKD	1060.2	10.67961	0.970874	0.083333
44	14	MKD	1201.4	7.76699	0.647249	0.076923
45	15	MKD	1335.9	10	0.526316	0.05
46	16	MKD	1394.6	9.731544	0.671141	0.064516
47	17	MKD	1461.3	9.565217	1.15942	0.108108
48	18	MKD	1526.8	12.62136	0.970874	0.071429
49	19	MKD	1583.4	16.86747	3.614458	0.176471
50	20	MKD	1646.7	10.9375	1.5625	0.125
51	21	MKD	1691.6	3.703704	1.851852	0.333333
52	22	MKD	1736.5	2.439024	8.943089	0.785714
53	23	MKD	1781.7	1.396648	0.837989	0.375
54	24	MKD	1832.1	4.83871	4.301075	0.470588
55	25	MKD	1884.9	0.914077	0.731261	0.444444
56	26	MKD	1939	2.41838	0.725514	0.230769
57	27	MKD	1992.9	3.502415	1.328502	0.275
58	28	MKD	2047	4.771784	0.622407	0.115385

Podocarpus and *Spirostachys* percentages in Lake St Lucia (MKD), Lake Eteza and Lake Sibaya

id	Reference	Site	Age Cal yr BP	Spirostachyl, Euphorbiaceae	*Podocarpus*	Ratio
1	1	StLucia	4.6	5.275229	0	0
2	2	StLucia	49	2.456647	0	0
3	3	StLucia	110.7	5.753425	0	0
4	4	StLucia	174.1	5.813953	0	0
5	5	StLucia	229.1	7.808564	0	0
6	6	StLucia	292.2	9.976798	0	0
7	7	StLucia	355.2	8.205128	0.683761	0.076923
8	8	StLucia	415.7	7.49354	0.258398	0.033333
9	9	StLucia	534.8	14.12429	2.259887	0.137931
10	10	StLucia	672.6	10.09615	1.923077	0.16
11	11	StLucia	792.6	18.51852	0	0
12	12	StLucia	938.9	13.25301	0.401606	0.029412
13	13	StLucia	1060.2	10.67961	0.970874	0.083333
14	14	StLucia	1201.4	7.76699	0.647249	0.076923
15	15	StLucia	1335.9	10	0.526316	0.05
16	16	StLucia	1394.6	9.731544	0.671141	0.064516
17	17	StLucia	1461.3	9.565217	1.15942	0.108108
18	18	StLucia	1526.8	12.62136	0.970874	0.071429
19	19	StLucia	1583.4	16.86747	3.614458	0.176471
20	20	StLucia	1646.7	10.9375	1.5625	0.125
21	21	StLucia	1691.6	3.703704	1.851852	0.333333
22	22	StLucia	1736.5	2.439024	8.943089	0.785714
23	23	StLucia	1781.7	1.396648	0.837989	0.375
24	24	StLucia	1832.1	4.83871	4.301075	0.470588
25	25	StLucia	1884.9	0.914077	0.731261	0.444444
26	26	StLucia	1939	2.41838	0.725514	0.230769
27	27	StLucia	1992.9	3.502415	1.328502	0.275
28	28	StLucia	2047	4.771784	0.622407	0.115385
29	29	StLucia	2102.1	7.300116	0.695249	0.086957
30	30	StLucia	2156.6	4.928806	0.219058	0.042553
31	31	StLucia	2210	3.407407	0.296296	0.08
32	32	StLucia	2264.2	1.410658	0.31348	0.181818
33	33	StLucia	2395.1	5.309735	0.884956	0.142857
34	34	StLucia	2447.9	2.631579	1.315789	0.333333
35	35	StLucia	2501.9	28.88889	2.222222	0.071429
36	36	StLucia	2609.7	0.529101	1.587302	0.75

37	37	StLucia	2717.2	1.538462	6.153846	0.8
38	38	StLucia	2826.3	0	7.377049	1
39	39	StLucia	2934.3	6.382979	14.89362	0.7
40	40	StLucia	3042	0.671141	0.33557	0.333333
41	41	StLucia	3137.8	0	2.824859	1
42	42	StLucia	3174.4	0	1.052632	1
43	43	StLucia	3218.2	0	12.96296	1
44	44	StLucia	3255.2	0	9.090909	1
45	45	StLucia	3307.1	0	2.12766	1
46	46	StLucia	3380.1	8.955224	35.8209	0.8
47	47	StLucia	3445.9	0.469484	0	0
48	48	StLucia	3525.5	0.290698	2.906977	0.909091
49	49	StLucia	3636.4	2.932551	5.278592	0.642857
50	50	StLucia	3709.6	0	0.749064	1
51	51	StLucia	3820.4	2.666667	5.333333	0.666667
52	52	StLucia	3893.3	0	23.68421	1
53	53	StLucia	3967.4	0.847458	12.71186	0.9375
54	54	StLucia	4115.3	0	1.569507	1
55	55	StLucia	4222	0	3.664921	1
56	56	StLucia	4292.2	2.439024	14.63415	0.857143
57	57	StLucia	4364.7	1.875	5.625	0.75
58	58	StLucia	4428.9	0.923077	1.692308	0.647059
59	59	StLucia	4507.9	0	11.60059	1
60	60	StLucia	4615.8	0.433526	0.867052	0.666667
61	61	StLucia	4704.8	7.954545	22.72727	0.740741
62	62	StLucia	4790.9	2.205882	11.76471	0.842105
63	63	StLucia	4905.7	0.779727	1.949318	0.714286
64	64	StLucia	5020.9	2.830189	20.75472	0.88
65	65	StLucia	5108	4.433498	8.866995	0.666667
66	66	StLucia	5193.7	0	1.652893	1
67	67	StLucia	5309.6	2.97619	10.71429	0.782609
68	68	StLucia	5395.7	3.503185	13.3758	0.792453
69	69	StLucia	5453.1	0.701262	5.329593	0.883721
70	70	StLucia	5511.5	0.608519	4.665314	0.884615
71	71	StLucia	5598.6	0.981997	1.145663	0.538462
72	72	StLucia	5656.3	3.067485	17.17791	0.848485
73	73	StLucia	5714.9	0.628141	0.879397	0.583333
74	74	StLucia	5801.2	0.45977	5.747126	0.925926
75	75	StLucia	5853.8	3.457447	6.648936	0.657895
76	76	StLucia	5917.6	4.678363	9.064327	0.659574
77	77	StLucia	6004.5	3.846154	9.171598	0.704545

78	78	StLucia	6061.8	2.8125	8.125	0.742857
79	79	StLucia	6118.9	2.763819	8.291457	0.75
80	80	StLucia	6283.1	3.26087	15.57971	0.826923
82	1	Eteza	-19	0.669643	1.339286	0.666667
83	2	Eteza	-7	1.463415	0.243902	0.142857
84	3	Eteza	5	1.160093	0.232019	0.166667
85	4	Eteza	19	2.514507	1.160542	0.31579
86	5	Eteza	32	2.684564	0.447427	0.142857
87	6	Eteza	43	0.208768	0.835073	0.8
88	7	Eteza	55	0.603622	2.816901	0.823529
89	8	Eteza	67	2.222222	2.857143	0.5625
90	9	Eteza	154	1.188119	0.594059	0.333333
91	10	Eteza	182	0.799201	0.0999	0.111111
92	11	Eteza	195	0.479616	0.959233	0.666667
93	12	Eteza	207	0.186916	1.121495	0.857143
94	13	Eteza	225	2.226721	2.024292	0.47619
95	14	Eteza	294	0.561798	3.932584	0.875
96	15	Eteza	309	0.40404	0.606061	0.6
97	16	Eteza	321	0.8	2	0.714286
98	17	Eteza	340	4.533333	3.466667	0.433333
99	18	Eteza	359	0.554529	0.184843	0.25
100	19	Eteza	374	0.625	0.833333	0.571429
101	20	Eteza	402	6.349206	2.380952	0.272727
102	21	Eteza	414	0.3861	1.737452	0.818182
103	22	Eteza	524	0.395257	2.766798	0.875
104	23	Eteza	567	1.192843	2.186879	0.647059
105	24	Eteza	675	1.287554	2.145923	0.625
106	25	Eteza	764	13.03258	8.77193	0.402299
107	26	Eteza	1409	4.710145	9.782609	0.675
108	27	Eteza	1686	0.990099	7.920792	0.888889
109	28	Eteza	2238	1.937984	8.527132	0.814815
110	29	Eteza	2342	0.387597	12.9845	0.971015
111	30	Eteza	3066	0.188324	10.54614	0.982456
112	31	Eteza	3226	1.234568	16.04938	0.928571
113	32	Eteza	3406	2.564103	5.641026	0.6875
114	33	Eteza	3600	4.819277	34.53815	0.877551
115	34	Eteza	3756	1.554404	22.02073	0.934066
116	35	Eteza	3932	3.549061	17.32777	0.83
117	36	Eteza	3991	1.771654	29.52756	0.943396
118	37	Eteza	4099	2.464789	27.64084	0.918129
119	38	Eteza	4227	3.131524	20.66806	0.868421

120	39	Eteza	4274	4.133858	18.70079	0.818966
121	40	Eteza	4572	4.291845	25.53648	0.856115
122	41	Eteza	4977	4.285714	16.78572	0.79661
123	42	Eteza	5219	2.540416	9.237875	0.784314
124	43	Eteza	5435	3.865979	22.16495	0.851485
125	44	Eteza	5610	0.448431	7.623318	0.944444
126	45	Eteza	5752	3.818616	21.71838	0.850467
127	46	Eteza	5868	0.823045	12.7572	0.939394
128	47	Eteza	6171	3.333333	11.53846	0.775862
129	48	Eteza	6572	1.257862	10.69182	0.894737
130	49	Eteza	6626	1.984127	16.26984	0.891304
131	50	Eteza	6717	3.378378	4.054054	0.545455
132	51	Eteza	6805	3.203661	9.839817	0.754386
133	52	Eteza	6913	2.186879	3.976143	0.645161
134	53	Eteza	7554	0.847458	3.389831	0.8
135	54	Eteza	7884	0.952381	4.761905	0.833333
136	55	Eteza	8011	0.813008	4.471545	0.846154
137	56	Eteza	8168	0	4.731183	1
138	57	Eteza	8324	1.652893	4.338843	0.724138
139	58	Eteza	8385	5.294117	5.294117	0.5
140	59	Eteza	8464	2.522936	4.12844	0.62069
141	60	Eteza	8651	1.412429	8.19209	0.852941
142	61	Eteza	8888	2.257336	4.063205	0.642857
143	62	Eteza	9224	4.532578	2.266289	0.333333
144	63	Eteza	9329	1.609195	8.735632	0.844444
145	64	Eteza	9485	5.555555	3.921569	0.413793
146	65	Eteza	9743	1.574803	3.149606	0.666667
147	66	Eteza	10022	2.105263	6.31579	0.75
148	67	Eteza	10175	2.973978	3.717472	0.555556
149	68	Eteza	10274	1.388889	3.703704	0.727273
151	1	Sibaya	-52	5.9369	0.7421	0.111111
152	2	Sibaya	-1	6.1914	0.3752	0.057143
153	3	Sibaya	48	5.8252	0.1942	0.032258
154	4	Sibaya	91	2.2181	1.2939	0.368421
155	5	Sibaya	134	7.4954	0.7313	0.088889
156	6	Sibaya	177	11.1111	1.0955	0.089744
157	7	Sibaya	225	11.3244	1.9194	0.144928
158	8	Sibaya	274	10.7595	0.6329	0.055556
159	9	Sibaya	316	5.8140	1.1628	0.166667
160	10	Sibaya	353	12.9310	0.8621	0.0625
161	11	Sibaya	373	6.7073	1.4228	0.175

162	12	Sibaya	387	11.6233	0.8016	0.064516
163	13	Sibaya	401	8.5595	2.9228	0.254545
164	14	Sibaya	410	8.2474	1.8557	0.183673
165	15	Sibaya	420	4.0241	2.6157	0.393939
166	16	Sibaya	462	3.0023	1.6166	0.35
167	17	Sibaya	471	3.0060	2.2044	0.423077
168	18	Sibaya	493	3.8055	2.1142	0.357143
169	19	Sibaya	526	3.5565	2.3013	0.392857
170	20	Sibaya	551	4.2735	3.6325	0.45946
171	21	Sibaya	570	11.0701	4.0590	0.268293
172	22	Sibaya	587	9.2369	3.0120	0.245902
173	23	Sibaya	605	4.8780	2.2358	0.314286
174	24	Sibaya	623	5.1383	3.5573	0.409091
175	25	Sibaya	641	4.9180	2.0492	0.294118
176	26	Sibaya	662	3.4483	3.0426	0.46875
177	27	Sibaya	678	3.0181	2.6157	0.464286
178	28	Sibaya	708	3.4413	2.6316	0.433333
179	29	Sibaya	757	5.3537	3.2505	0.377778
180	30	Sibaya	801	4.5187	5.6974	0.557692
181	31	Sibaya	856	4.6000	4.2000	0.477273
182	32	Sibaya	883	5.9305	4.2945	0.42
183	33	Sibaya	921	3.4188	2.3504	0.407407
184	34	Sibaya	959	2.7290	4.8733	0.641026
185	35	Sibaya	998	2.4641	5.3388	0.68421
186	36	Sibaya	1056	1.8595	2.8926	0.608696
187	37	Sibaya	1091	2.2177	4.4355	0.666667
188	38	Sibaya	1124	2.2965	2.7140	0.541667
189	39	Sibaya	1140	3.5714	2.3109	0.392857
190	40	Sibaya	1189	4.8263	4.8263	0.5
191	41	Sibaya	1222	4.3825	6.5737	0.6
192	42	Sibaya	1270	10.0580	5.2224	0.341772
193	43	Sibaya	1302	3.3613	7.9832	0.703704
194	44	Sibaya	1347	1.4257	8.3503	0.854167
195	45	Sibaya	1389	2.9880	5.9761	0.666667
196	46	Sibaya	1436	5.6555	12.3393	0.685714
197	47	Sibaya	1484	2.1978	4.6154	0.677419
198	48	Sibaya	1537	4.3478	9.5652	0.6875
199	49	Sibaya	1579	3.0550	14.0530	0.821429
200	50	Sibaya	1593	2.8689	11.4754	0.8
201	51	Sibaya	1661	1.2397	13.2231	0.914286
202	52	Sibaya	1708	3.4843	12.8920	0.787234

203	53	Sibaya	1770	2.0408	13.8322	0.871429
204	54	Sibaya	1851	1.0163	7.5203	0.880952
205	55	Sibaya	1933	0.8230	9.8765	0.923077
206	56	Sibaya	7105	8	25	0.757576
207	57	Sibaya	7131	5	14	0.736842
208	58	Sibaya	7143	4	19	0.826087
209	59	Sibaya	7162	5	31	0.861111