

50,000 years of vegetation and climate change in the Namib Desert

Sophak Lim

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Paléobiologie

École doctorale GAIA

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50,000 YEARS OF VEGETATION AND CLIMATE CHANGE IN THE NAMIB DESERT

Présentée par Sophak LIM

Le 24 novembre 2017

Sous la direction de Brian CHASE

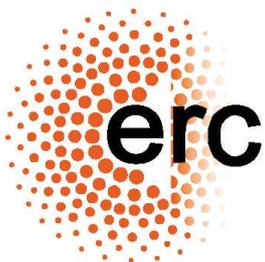
Devant le jury composé de

Prof. David J. Nash, Professeur, University of Brighton
Dr. Andrew Stephen Carr, PhD, University of Leicester
Prof. Adam A. Ali, Professeur, Université de Montpellier
Dr. Graciela Gil-Romera, PhD, Institute of Ecology-CSIC
Dr. Brian Chase, DR2, Université de Montpellier

Rapporteur
Rapporteur
Examineur (Président de jury)
Examineur
Directeur de thèse



**UNIVERSITÉ
DE MONTPELLIER**



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ABSTRACT

This thesis presents fossil pollen and microcharcoal data spanning the last 50,000 years from a north-south transect of sites from the Namib Desert. The arid environment of the Namib precludes the development of permanent wetlands, and as a result few palaeoenvironmental records exist from the region and understanding of past vegetation and climate change is limited. In this study, we employ rock hyrax middens – fossilised accumulations of the faecal pellets and urine of the *Procavia capensis*. Hyrax middens from three sites were selected for analysis: from the southern Namib (Pella), the eastern margin of Namib Sand Sea (Zizou), and the central Namib (Spitzkoppe). All of these sites occur in extremely arid environments (mean annual rainfall of 100-150 mm/yr), and rainfall regimes are characterized by high annual and inter-annual variability. As a result, all of the sites lie along the ecotone between the Desert and Nama-Karoo Biomes, with the Savanna Biome lying to the east. The ecotone is thought to be potentially highly sensitive to changes in region climate systems. Of specific interest in the assessment of the records from these terrestrial sites is the extent to which they may corroborate or conflict with findings from pollen records obtained from marine sediments off the Namibian coast; in particular, inferences that abundances of pollen from taxa dominant in the Fynbos Biome of the Cape may indicate a significant northward expansion of the Cape flora during cooler glacial periods.

According to the selected study sites, the primary findings of this work are as follows:

The **Pella** hyrax middens provide the first continuous pollen record from the southern Namib Desert spanning the last 50,000 years, and are used to reconstruct vegetation change and quantitative estimates of temperature and aridity. Results indicate that the last glacial period was characterised by increased water availability at the site relative to the Holocene. Changes in temperature and potential evapotranspiration appear to have played a significant role in determining the hydrologic balance. The record can be considered in two sections: 1) the last glacial period, when low temperatures favoured the development of more mesic Nama-Karoo vegetation at the site, with periods of increased humidity concurrent with increased coastal upwelling, both responding to lower global/regional temperatures; and 2) the Holocene, during which time high temperatures and potential evapotranspiration resulted in increased aridity and an expansion of the Desert Biome. During this latter period, increases in upwelling intensity created drier conditions at the site.

Considered in the context of discussions of forcing mechanisms of regional climate change and environmental dynamics, the results from Pella stand in clear contrast with many inferences of terrestrial environmental change derived from regional marine records. Observations of a strong precessional signal and interpretations of increased humidity during phases of high local summer insolation in the marine records are not consistent with the data from Pella. Similarly, while high percentages of Restionaceae pollen has been observed in marine sediments during the last glacial period, they do not exceed 1% of the assemblage from Pella, indicating that no significant expansion of the Fynbos Biome has occurred during the last 50,000 years.

The **Zizou** hyrax midden record highlights vegetation changes on the eastern margin of the Namib Sand Sea since 38,000 cal BP. Results show the different vegetation compositions between the last glacial period and the Holocene. Glacial vegetation characterised with relatively high percentages of Asteraceae pollen, particularly cool climate taxa such as *Stoebe*-type and *Artemisia*. Similar to the data from Pella, with the onset

of Holocene warming grass pollen comes to dominate the assemblage, suggesting an expansion of the Desert Biome. We suggest that the climate during the last glacial period was more humid, and supported the development of shrubs/small trees through the long-term development of more reliable groundwater resources. The increased humidity between ~ 34 – ~18 cal kBP was likely a response to cooler temperature and thus less drought stress during the LGM. Arid conditions during the Holocene saw the depletion of this resource, and the development of grasslands that could exploit the rare rains that the region experiences today. Also in common with the Pella record, no elements of the Cape flora are found in the Zizou middens.

The **Spitzkoppe** hyrax middens record vegetation changes in the central Namib during the last 32,000 years. Results show that glacial pollen assemblage characterised by the abundance of *Olea*, *Artemisia*, *Stoebe*-type, higher microcharcoal influx, and the modest proportions of grease noticeably during the LGM. The Holocene vegetation characterised by higher grasses with warmer arboreal species which also present in current vegetation at study site such as *Dombeya*, *Commiphora*, *Croton*, *Euclea*, etc.. We suggest that last glacial period was cool and more humid than in Holocene supporting mesic savanna woodland and shifted to xeric savanna woodland in Holocene in respond to warm and increased aridity. The increased humidity during the last glacial period occurred in majority under lower temperatures and evapotranspiration in which make any amounts of precipitation more effective for vegetation. Compared our pollen data with stables isotopes at the same site suggesting that a progressive aridification throughout Holocene with wetter early Holocene. After ~ 3 cal kBP, a rapidly increased aridity shifted vegetation at the study site toward Desert Biome.

At all sites, although significant variability is observed during both the last glacial period and the Holocene, cooler glacial conditions appear to be characterised by increased water availability along our transect. Indeed, acknowledging limitations imposed by the low resolution of some portions of the records, the timing and nature of climate and vegetation change seems to have been largely synchronous, suggesting that variations in each record are primarily determined by large-scale regional and extra-regional process and mechanisms. According to pollen data at all sites, cooler temperatures during the last glacial period have appeared to play an important part in increasing humidity as important as the precipitation at the region. Contrary to the findings in the marine records, our records indicate no significant expansion of the Fynbos Biome, with only trace amounts of the Restionaceae pollen being found in the southern-most site at Pella (not exceed 1%), and none being observed at either Zizou or Spitzkoppe.

Key words: palaeoenvironment, palaeoecology, fossil pollen, climate change, vegetation change, rock hyrax middens, Namib Desert

RESUME

Cette thèse présente les données des pollens et micro-charbons fossiles couvrant la période des 50 000 dernières années à partir de sites sélectionnés transversalement nord-sud du désert de Namib. Comme le climat aride dans le désert du Namib empêche la présence des zones marécageuses, il existe très peu de données palaeo-environnementaux dans la région et la compréhension du changement de la végétation et du climat est très limité. Dans le cadre de cette thèse, on utilise le rock hyrax middens, l'accumulation des boulettes et des urines fossilisées du *Procavia capensis*, représentant une excellente archive pour archives pour la préservation des pollens et micro-charbons à long-terme. Trois sites des hyrax middens ont été sélectionnés pour l'analyse: au sud du désert de Namib (Pella), la marge est des dunes de sable de Namib (Zizou) et le centre de la Namib (Spitzkoppe). Tous ces sites se trouvent dans des environnements extrêmement arides (la précipitation moyenne annuelle est entre 100 mm et 150 mm). En plus, le régime pluvial de ces sites se caractérise par une forte variabilité annuelle et interannuelle. En conséquence, tous ces sites se situent au long de l'écotone du Désert et du biome Nama-Karoo, ainsi qu'à l'est (biome de Savane). Alors que ces sites sont répertoriés dans des écosystèmes similaires, l'écotone, lui, est considéré comme une zone potentiellement très sensible au changement du système climatique régional. La distribution de ces sites permet d'identifier les différences spatiales en regard de la nature de la réponse au changement climatique à long terme. Un intérêt spécifique de ces enregistrements terrestres est pour évaluer s'ils corroborent ou s'opposent avec les résultats provenant ceux des sédiments marins de la côte namibienne, en particulier la conclusion : l'abondance des taxa dominants du Fynbos Biome du Cape peut indiquer significativement une expansion vers le nord de la flore du Cape pendant les périodes plus froides glaciaires.

Selon les sites d'études sélectionnées, les conclusions principales de ce travail sont les suivantes:

Les hyrax middens de **Pella** fournissent le premier enregistrement pollinique continué au sud du désert de Namib durant la période des 50 000 dernières années. Ces données polliniques ont permis de reconstruire le changement de la végétation et d'estimer la température et l'aridité. Les résultats indiquent que la période glaciaire se caractérise par une augmentation de la disponibilité de l'eau sur le site par rapport à l'Holocène. Les changements de la température et de l'évapotranspiration potentielle semblent avoir joué un rôle important dans la détermination de l'équilibre hydrologique. L'enregistrement peut être considéré en deux temps: 1) la dernière période glaciaire, lorsque des températures basses ont favorisé le développement de la végétation plus mesic de Nama-Karoo sur le site correspondant la période plus humide, en concurrent avec la remonté des eaux côtières (upwelling), a répondu à la fois à la baisse de températures globales ou régionales; et 2) l'Holocène, la période pendant laquelle des hautes températures et évapotranspiration potentielle sont résultant d'une augmentation de l'aridité et une expansion du biome du Désert. Au cours de cette dernière période, l'augmentation plus intense des upwellings se établie des conditions plus aride sur le site.

Considérant dans le contexte des discussions au sujet des forçages des mécanismes du changement climatique régional et la dynamique environnementale, les résultats de Pella ont montrés des contradictions avec des conclusions de nombreux changements environnementaux terrestres provenant des enregistrements marins. L'observation d'un fort signal de précession et les interprétations de l'augmentation de l'humidité se correspondent aux phases d'insolation estivale locale élevée proposés par les enregistrements marins ne sont pas

cohérents avec les données de Pella. De la même façon, lorsqu'on a observé des pourcentages élevés de pollen du Restionaceae pendant la dernière période glaciaire dans les carottes marines, on a pu constater que ce type de pollen ne dépasse pas 1% de l'assemblage pollinique de Pella. Ceci indique qu'aucune expansion significative de la végétation du biome de Fynbos a été présente au cours des derniers 50 000 ans.

L'enregistrement de **Zizou** hyrax midden met en évidence des changements de la végétation à la marge l'est des dunes de sable depuis 38 000 ans cal BP. Les résultats montrent qu'il existe différentes compositions de la végétation entre la dernière période glaciaire et celle de l'Holocène. La végétation de la période glaciaire se caractérise par les pourcentages relativement élevés des Astéracées pollen, et plus particulièrement par des taxa du climat plus froid: *Stoebe*-type et *Artemisia*. En accord avec les données de Pella, le réchauffement au début de l'Holocène indiqué par la dominance de pollen des graminées dans l'assemblage pollinique suggère une expansion du biome de Désert. Nous proposons que le climat au cours de la dernière période glaciaire était plus humide et que ce climat humide favorise le développement des arbustes et des petits arbres grâce à un développement à long terme de ressources en eaux souterraines plus fiables. L'augmentation de l'humidité de ~34 – ~18 cal kBP était plutôt dû à la réponse aux températures plus fraîches et donc il y avait moins des stress de sécheresse pendant la période glaciaire maximale. Les conditions arides pendant l'Holocène sont vues par l'épuisement de la ressource en eau et le développement des graminées qui pourraient exploiter les pluies rares qu'on observe actuellement dans la région. Le point commun avec l'enregistrement de Pella, aucun élément de flore du Cap n'est trouvé dans le Zizou middens qui aurait pu nous donner les preuves d'une expansion significative de la végétation du type Fynbos au cours de la dernière période glaciaire.

Les hyrax middens de **Spitzkoppe** enregistrent les changements de la végétation dans le centre du désert de Namib au cours des 32 000 dernières années. Les résultats montrent que la végétation de la dernière période glaciaire se caractérise par l'abondance de *Olea*, *Artemisia*, *Stoebe*-type, l'influx de micro-charbon plus élevé et relativement peu de graminées surtout dans la période glaciaire maximale. Pendant l'Holocène, des graminées ont plus augmenté au début de l'Holocène et espèces arborescentes taxa comme *Eculea*, *Dombeya*, *Commiphora*, et *Croton*. Ce changement de la végétation suggère le climat plus froid et plus humide dans la dernière période glaciaire relativement à l'Holocène. La baisse de température et d'évapotranspiration jouent semblent avoir joué un rôle important dans les phases humides pendant la période glaciaire. En comparant les données polliniques avec les isotopes stables dans le même site, les résultats montrent que l'Holocène climat se caractérise par l'aridification progressive s'installe depuis début Holocène. Après ~ 3 cal kBP, une augmentation rapide de l'aridité a déplacé la végétation de site d'étude vers le biome du Désert.

Dans tous ces sites, une variabilité significative a été observée à la fois dans la dernière période glaciaire et l'Holocène. Les conditions plus froides de l'ère glaciaire semblent être caractérisées par une augmentation de la disponibilité de l'eau le long de la totalité de notre zone d'étude. En effet, compte tenu des limites imposées par la faible résolution de certaines parties des enregistrements, le temps et la nature de changement climatique, le changement de la végétation semble avoir été synchronisés en grande partie. Ceci suggère que les variations de chaque enregistrement sont déterminées principalement par des processus et des mécanismes à la grande échelle régionale et extrarégionale. Selon les données polliniques provenant de ces trois sites d'études, les températures plus fraîches pendant la période glaciaire semble avoir aussi joué un rôle

important que la précipitation sur l'augmentation de l'humidité dans la région. Au contraire des résultats provenant des carottes marines, nos enregistrements indiquent aucune expansion de la végétation de Fynbos biome, et seulement des traces de Restionaceae pollen dans le site extrêmement au sud à Pella (pas plus de 1%), mais aucun trace de ce pollen n'ayant été observé à Zizou ainsi qu'à Spitzkoppe.

Mots clés : paléoenvironnement, paléoécologie, pollen fossile, changement climatique, changement végétale, rock hyrax middens, désert du Namib

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Chapter I: Introduction

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General context

Climate, more than any other factor, controls the broad-scale distributions of plant species and vegetation in general. As a result, the current vegetation patterns are the outcomes of long-term past climatic changes, both natural and human-induced (Emanuel et al., 1985; Sykes, 2001). The impacts of climate change on vegetation are complex because there are other factors influencing the presence or absence of a species, such as local environmental conditions including microclimate, soil nutrient status, and water-holding capacity, as well as the intra- and interspecific interactions, for example, competition for resources (light, water, and nutrients) (Sykes, 2001). A rapid or extreme change in temperatures and precipitation directly affects species and can therefore influence the course of competition among the species. The degree of climate change is unlikely to be uniform over the globe, and drylands seem to be the most sensitive areas to climate change. Land temperatures over Africa are projected to rise faster than the global land average, particularly in the more arid regions (IPCC, 2014). Over southern Africa a reduction in late austral summer precipitation has been reported over its western parts, extending from Namibia through to Angola during the second half of the 20th century (Hoerling et al., 2006; New et al., 2006). Desertification is defined by the United Nations Convention to Combat Desertification (UNCCD) as land degradation in the drylands (land falling within arid, semi-arid, and dry sub-humid areas) resulting from various factors, including climatic variations and human activities (Reynolds et al., 2007; Huang et al., 2016). Under a scenario of global warming, the arid regions are expected to undergo significant changes (Lioubimtseva, 2004).

Palaeoecology is the study of long-term vegetation patterns and encompasses a number of palaeoenvironmental techniques used to investigate past changes in the terrestrial environments, and pollen analysis (palynology) is one of the most established methods (Twiddle, 2012). Palynology helps to unlock the role of vegetation in the earth system process over time, for example the global models used to predict future climate changes are often validated by using palaeoenvironmental data, such as fossil pollen data (Gaillard et al., 2010; Anderson et al., 2017).

In southern Africa, palynological research was begun by van Zinderen Bakker in the 1950s. However, his study sites covered only the tropics of southern Africa where climate conditions favoured the preservation of pollen fossil, more so than the western arid region of

southern Africa (Deacon and Lancaster, 1988). At first, as elsewhere, pollen analysis in southern Africa was based on the classic sediment cores from lakes or swamps. Later, new sources of pollen preservation materials were discovered, such as pan sediments, valley fills, dung (hyena coprolite, cow dung, bat dropping), and rock hyrax middens. The rock hyrax midden is currently known to be a palaeoenvironmental archive for dryland in southern Africa (Scott & Vogel, 2000; Scott et al., 2004; Gil-Romera et al., 2007; Chase et al., 2012; Chase et al., 2013). The Namib Desert has, at present, very few terrestrial pollen records, in particular no long continuous records extending back to the last glacial period. Most of the pollen records in this arid region are only dated from the mid- to late Holocene (Scott et al., 1991; Scott, 1996; Gil-Romera et al., 2006; Gil-Romera et al., 2007), and only records from the Brandberg hyrax midden (Scott et al., 2004) provide the snapshots of glacial-age vegetation in the Namib Desert. As a result, the long and continuous climate and vegetation history relies heavily on marine records which are believed to provide climate and vegetation change for the adjacent continent (Shi and Dupont, 1997; Shi et al., 1998, 2000; Shi et al., 2001; Daniau et al., 2013). Therefore, the results from the later archive appear to be more contradictory to the findings from the few available terrestrial records in the region. While these sequences contain long, continuous records of terrestrial sediments (Gingele, 1996; Stuut et al., 2002; Pichevin et al., 2005; Weldeab et al., 2013), pollen (Shi and Dupont, 1997; Shi et al., 1998, 2000; Shi et al., 2001), charcoal (Daniau et al., 2013) and biomarkers (Rommerskirchen et al., 2003; Collins et al., 2011; Collins et al., 2014) the intense atmospheric and oceanic circulation systems dominating the southeast Atlantic basin - particularly along the southwest African margin and the potential for significant aeolian and fluvial sediment contributions, have raised questions regarding the taphonomy, and thus significance, of the records obtained (cf. Scott et al., 2004; Chase and Meadows, 2007). Unlike marine records, pollen recovered from hyrax middens reflect more local/regional vegetation changes responding to global and regional climate change.

This thesis presents pollen records derived from three hyrax midden sites situated longitudinally from southern to the central Namib Desert. The results of pollen fossils and microcharcoal from this thesis will help to improve the palaeoenvironmental reconstruction of the region following the signal of vegetation changes from the southern to central Namib Desert during the last 50,000 years.

This manuscript-based thesis is composed of three main articles with the results from each site considered. The Pella middens chapter is a published article: “50,000 years of

vegetation and climate change in the Southern Namib Desert, Pella, South Africa” (2016), in *Palaeogeography, Palaeoclimatology, Palaeoecology*. The articles describing the Zizou midden and Spitzkoppe middens are in the draft stage in preparation for future publication. Thus, the interpretation and discussion of pollen data may require refinement to meet the international scientific journal standard.

There are seven chapters in this thesis:

- Chapter I: General introduction.
- Chapter II: Description of study area (geography, climate, and vegetation).
- Chapter III: Material and methodology used in this thesis. This chapter provides detail information of material (rock hyrax midden), palynological method, and the climatic reconstruction method.
- Chapter IV: 50,000 years of vegetation and climate change in the Southern Namib Desert, Pella, South Africa.
- Chapter V: Fossil pollen and micro-charcoal evidence of the last 38,000 years in the central Namib Desert, Zizou midden, Namibia.
- Chapter VI: A record of vegetation changes during the last 32,000 years at the eastern margin of central Namib Desert from Spitzkoppe middens.
- Chapter VII: Conclusions and perspectives.

1.1. Climate and palaeoenvironment of the Namib Desert during the last 50,000 years

The Quaternary period is known as a time of great change in the Earth's climate system, and scientists have focused on collecting a diverse range of evidence in order to refine scenarios for future climate change (Anderson et al., 2007). The Quaternary also represents the time in which people have become a dominant environmental agent in the subcontinent; southern Africa has played a crucial role in the evolution of hominids and their development has been influenced strongly by accompanying environmental changes (Meadows, 2001). During the last 50,000 years, there are some key time periods related to remarkable changes in climatic conditions, such as the Last Glacial Maximum (LGM), the last glacial-interglacial transition, the Holocene and the Holocene Altithermal (HA), and the Little Ice Age, etc. Up to the present, there are more studies elucidating climatic conditions during those time periods in the Northern Hemisphere than the Southern Hemisphere. During the LGM (24-19 kBP), the Earth was dustier and received less precipitation, as well as changes in wind strength (Anderson et al., 2007). The last glacial-interglacial transition is characterized by events of rapid environmental change linked to the oceanic circulation change, for example, the Younger Dryas (12,900-11,700 year BP) was clearly evidenced in the Northern Hemisphere as the cooling phase with drier climate conditions over much of the temperate Northern Hemisphere (NOAA, 2008). In the Southern Hemisphere, the Antarctica Cold Reversal (14,700-13,000 year BP) coincides with the Bølling-Allerød warm stage in the North Atlantic, providing an example of inter-hemispheric coupling of abrupt climate change, referred to as the bipolar seesaw (Pedro et al., 2015). The Holocene is defined as an interglacial period, which covers approximately the last 11,500 years. The HA represents the warmest phase during the Holocene in southern Africa (8000-6000 cal BP) and is characterised by wetter conditions (Partridge et al., 1999).

In southern Africa, the temperature reconstructions during the LGM show a coherent signal with a decrease of 5-6 °C over the region (Heaton et al., 1986; Talma and Vogel, 1992; Stute and Talma, 1998; Truc et al., 2013; Chevalier and Chase, 2015). However, the precipitation reconstructions have been more disparate (Partridge et al., 1999; Chevalier and Chase, 2015). In South Africa, summer rainfall changes in response to summer insolation resulting from orbital precession suggested that LGM precipitation was decreased, and biome reconstruction indicated expansion of the Desert biome over most of southern Africa during

the LGM (see references within Partridge et al., 1999). The HA is indicated by warmer temperatures of 1-2 °C more than the present day and the excess air in the Stampriet Aquifer, Namibia, suggested a wetter climate (Stute and Talma, 1998), as well as pollen evidence in Namibia with increasing percentages of grasses (Scott et al., 1991; Scott, 1996; Gil-Romera et al., 2006; Gil-Romera et al., 2007) . The biome reconstructions show that vegetation during this period represent current biomes (see references within Partridge et al., 1999).

Situated at the interface of the tropical, subtropical, and temperate systems as well as oceans, the climate of the Namib Desert is influenced by a wide variety of atmospheric and oceanic systems (Chase and Meadows, 2007). Present-day climate in the Namib is characterised by very little summer rain in central to northern regions, associated with seasonal shift of the Intertropical Convergence Zone (ITCZ) and Congo Air Boundary (CAB), while the southern Namib receives some winter rainfall from temperate frontal systems embedded in the westerlies (Tyson and Preston-Whyte, 2002). Late Quaternary climate conditions in the Namib were likely influenced by these systems across cycles of global warming and cooling periods. It has been hypothesised that with the expansion of Antarctic sea ice during the last glacial periods, the westerlies would be displaced equatorward, influencing the climate of the subcontinent both more frequently and with greater intensity, thereby increasing humidity and the proportion of winter rainfall during the last glacial periods in southwestern Africa (van Zinderen Bakker, 1976; Stuut et al., 2002; Gasse et al., 2008). The tropical systems rely on high sea surface temperature (SSTs) and strong summer warming of the continent to create robust convection cells. These conditions are more fully developed during warmer interglacial periods and are generally curtailed during cooler glacial periods (Bowler et al., 2001). Related to this, a hypothesis was proposed that the ITCZ was displaced southward to its current position as the result of larger Northern Hemisphere continental ice sheets, which brought more tropical rainfall (increased monsoon strength) and direct insolation forcing (Southern Hemisphere summer insolation maxima), which resulted in increased summer rainfall in the southern African continent during the last glacial periods (Partridge et al., 1997; Collins et al., 2014).

Summer rainfall reconstructions from pollen data in the southeast African summer rainfall suggests heterogeneous summer precipitation to different sites in the region. Long-term trends of increasing summer rainfall in the northeast sites (Mozambique Channel) are

determined by sea-surface and continental temperature trends, revealing a positive relationship between temperature and rainfall. This long-term pattern appears to be primarily driven by higher northern latitude mechanisms, with direct local insolation being subordinate. Further south, in central South Africa, rainfall variability appears to be influenced by the latitudinal position of the Southern Hemispheric westerlies, which combined with tropical flow to create a tropical-temperate trough, advecting moisture into the interior (Chevalier and Chase, 2015). This calls for consideration of findings from marine records off the Namibia coast that suggest humid conditions during the glacial period were associated with the enhancement of Southern Hemisphere insolation causing increased summer rainfall (Daniau et al., 2013; Collins et al., 2014). Stable isotopes data from Spitzkoppe suggest that drier conditions are positive correlated with coastal upwelling activities (Chase et al., 2009). Decreased upwelling in the early Holocene suggests wetter conditions in central Namib, while phases of drier conditions are concurrent with increased coastal upwelling. The reconstructions of past SSTs as indicators of upwelling activity suggest that it was intensified during the last glacial period (Little et al., 1997; Kirst et al., 1999). During the glacial period with increasing intensity of upwelling, the climate at southwest Africa was humid (Stuut et al., 2002). Alternative evidence of the wet period during the last glacial in the Namib Desert is due to increased runoff from the east in the Great Escarpment rather than increased rainfall in the Namib Desert itself (Lancaster, 2002).

An alternative idea to explain increased humidity during the last glacial period is the influence of temperature (Scott et al., 2004; Chevalier and Chase, 2016). As the aridity index is a function of precipitation and temperature, increasing humidity during the last glacial period may be due to lower temperatures. Lower temperature reduces the atmospheric water demand resulting in lower evapotranspiration. When temperature increases, the rate of evapotranspiration also increases resulting in increasing aridity if the precipitation remains relatively constant.

In summary, despite the conflicts of mechanism driven aridity, the review of regional datasets seem to generally indicate: 1) more humid conditions during the last glacial period in the Namib, in particular during the marine isotope stage (MIS) 4 (71-59 ka) and during MIS 3 and early MIS 2 (35-24 ka), and 2), and relatively drier conditions during the Holocene (Chase and Meadows, 2007).

1.1.1. Terrestrial pollen analysis in the Namib Desert

Pollen analysis in the Namib Desert is limited to the mid- to late Holocene due to the lack of long and continuous records. Most of the available terrestrial pollen records are dated to the late Holocene (Scott et al., 1991; Scott, 1996; Gil-Romera et al., 2006, 2007). At the southernmost section, near the border of Namibia and South Africa, in Succulent Karoo Biome, pollen analysis from spring deposits at Eksteenfontein provided evidence from ~15 to 9.5 cal kBP (Scott et al., 1995; Scott et al., 2012). This record suggests that vegetation in the oldest period was abundant, dominated by *Stoebe*-type Asteraceae, indicating cooler temperatures than in the Holocene, when vegetation was dominated by an increase in grasses, woody plants, and succulents.

In the inselbergs area of Namibia, pollen analysis in hyrax midden at the Brandberg mountain provided a snapshot of vegetation changes since the late Pleistocene (30 ¹⁴C-kBP, uncalibrated dates) (Scott et al., 2004). The LGM vegetation differed entirely from the current vegetation pattern, i.e. vegetation types were dominated by small Asteraceae shrubs (including *Stoebe*-type), in contrast to those of the Holocene and modern times in which pollen assemblage show more succulents, grasses, and woody plants. The highest abundance of *Stoebe*-type are accompanied by *Artemisia*, *Olea*, and spore of ferns indicating cooler and more moister conditions under the lower evaporation condition rather than increasing rainfall (Scott et al., 2004). Similarly, annual temperature, summer precipitation, and the aridity index reconstructed from 13 pollen sites in eastern southern Africa suggest an important role of temperature in determining long-term aridity, e.g. increased humidity during the last glacial period despite lower precipitation (Chevalier and Chase, 2016). Stable isotopes at Spitzkoppe suggest progressive aridification throughout the Holocene, with wetter periods in the early Holocene and a rapid increased of aridity after ~3.5 cal kBP (Chase et al., 2009). The Holocene pollen records in Namibia suggested that the middle Holocene was wetter than present day, indicated by higher grass percentages over the trees/shrubs (Scott et al., 1991; Scott, 1996; Gil-Romera et al., 2006; Gil-Romera et al., 2007). Gil-Romera et al. (2006) suggested that the wetter conditions during mid-Holocene were associated with increased, more effective rainfall.

Pollen analysis in the marine cores off the Namibia coast provide longer, continuous records of vegetation at the adjacent continent in the region (Shi and Dupont, 1997; Shi et al.,

1998, 2000; Shi et al., 2001). The evidence from these records suggest the northward expansion of winter-vegetation during the last glacial period according to the findings of high percentages of Restionaceae pollen in their records. In contrast to these findings, the longest existing pollen records from the continent provide no evidence of this pollen type further north than its current distribution (Scott et al., 1995; Scott et al., 2004). The pollen analysis of Holocene sediments from the Namaqualand mud belt were interpreted as indicating an antiphase relationship between summer and winter rainfall systems. The ratio of Poaceae/Asteraceae was used as the indicator of summer rainfall (Zhao et al., 2016). Microcharcoal analysis off the Namib coast from MD96-2098 represents the biomass burning and fire activity in southern Africa (Daniau et al., 2013). The results from this analysis show that burning activity increased during the wetter and cooler climatic conditions, which contrasts with the general concept of increasing fires under warm temperatures and increased drought. The analysis of biomarkers from marine cores off the Namibia coast, MD08-3167, found that lower-leaf wax δD and higher $\delta^{13}C$ (more C_4 grasses) during the last glacial period indicated a wetter Southern Hemisphere concurrent with a period of SH insolation maxima (Collins et al., 2014). However, the terrestrial fossil pollen evidence only suggested higher grass percentages during the Holocene (Scott et al., 1995; Scott et al., 2004).

The summary of evidence from both pollen analyses in terrestrial and marine records shows contradictions in interpretations. As a result, the palaeoenvironment reconstruction in the Namib Desert remains complicated. Thus, additional long, continuous terrestrial records of vegetation changes are required to improve the understanding of the past environmental change in this region.

1.1.2. Hyrax middens: a new palaeoenvironmental archive

The arid environment of the Namib Desert precludes the development of lakes or any permanent wetlands, presenting an obstacle to finding long, continuous sediments sequences to study vegetation and climate change in this region. The discovery of a new palaeoenvironmental archive, the rock hyrax midden, sheds light on reconstruction of palaeoenvironment in the Namib Desert (Scott, 1990). This pollen in middens may be preserved perfectly for upwards of 50,000 years (Chase et al., 2012). Hyrax middens are demonstrated to be very useful and important pollen and microcharcoal traps (Scott and Bousman, 1990). The advantage of pollen spectra from middens over the wetland pollen

spectra is that they may reflect more terrestrial vegetation without a high proportion of aquatic taxa found in wetland sequences (Chase et al., 2012). However, while hyrax middens preserve pollen well, dietary bias is a consideration, as the animals may ingest whole flowers resulting in an over-presentation of some taxa in some pollen samples.

1.2. Objective of thesis

The objective of this thesis is to use fossil pollen extracted from rock hyrax middens in the Namib Desert to determine how the vegetation and environments of the Namib Desert have changed in response to changes in global and regional scale circulation and climate dynamics over the last 50,000 years.

To fulfill the objective, we have set up some key research questions, as follows:

- How has the vegetation responded to changes in climatic conditions at the biome scale during the past 50,000 years?
- Was there any northward winter-rain vegetation expansion during the last glacial period, as suggested by marine cores?
- What were the climatic conditions like during the last glacial period, the last glacial-interglacial transition, and the Holocene?
- What was the regional climate response to insolation forcing?
- How has the global climate influenced regional climate?

Chapter II: Description of study area

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2. The Namib Desert

2.1. Geography

The Namib Desert extends for over 2000 km along the west coast of southern Africa from Olifants River in South Africa (32°S) to the Carunjabamba River (14°S) in Angola (Stone and Thomas, 2013; Lancaster, 2002) (Figure 2. 1A). In the southern Namib, much of the area is extensively rocky and sand covered plains extend coastward from the escarpment, with low hills at the interval (Lancaster, 2002). The Namib Sand Sea area lies between the Lüderitz and Kuiseb River and has an area of some 34,000 km² (Lancaster, 1989). The central Namib Plains spread from Kuiseb River to the Brandberg mountain. This area is characterized by the rocky plains with low ranges of hills and isolated inselbergs (cf. in Lancaster, 2002). Most of the rivers in the Namib are ephemeral rivers, with the exception of the Orange River at the Namibia-South African border and the Cunene River along the Angolan border, both of which flow into the Atlantic Ocean (Figure 2. 1B).

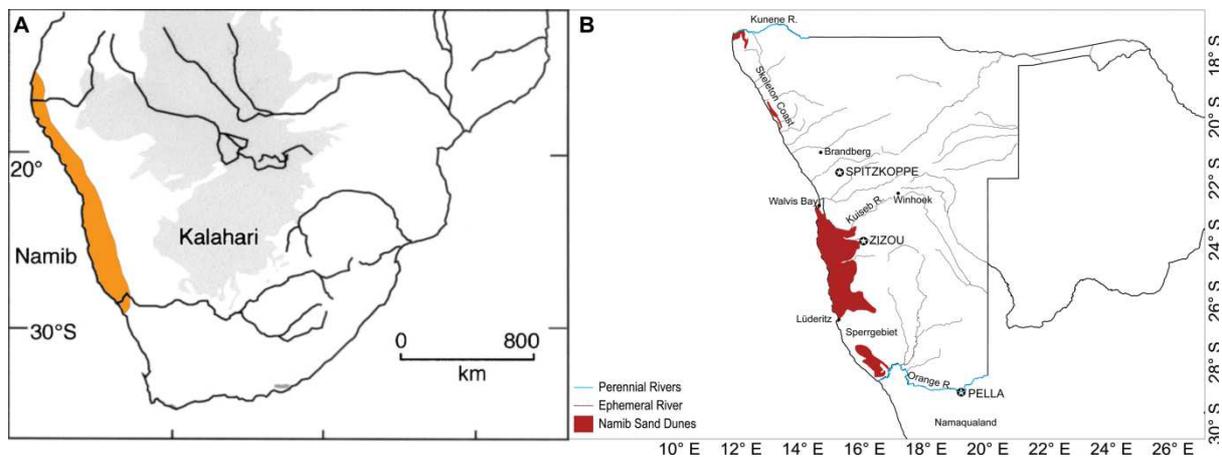


Figure 2. 1: Location of the Namib Desert (in the yellow) modified from (Lancaster, 2002), (b): Namib Sand Dune areas, ephemeral, and perennial rivers (in blue colour) (modified from ACACIA, 2002).

In this thesis, we have chosen to study three sites: one from the southern Namib (Pella), one from the margin of the Namib Sand Sea (Zizou), and one from the central Namib (Spitzkoppe). All sites lie along the eastern margin of the Namib Desert biome.

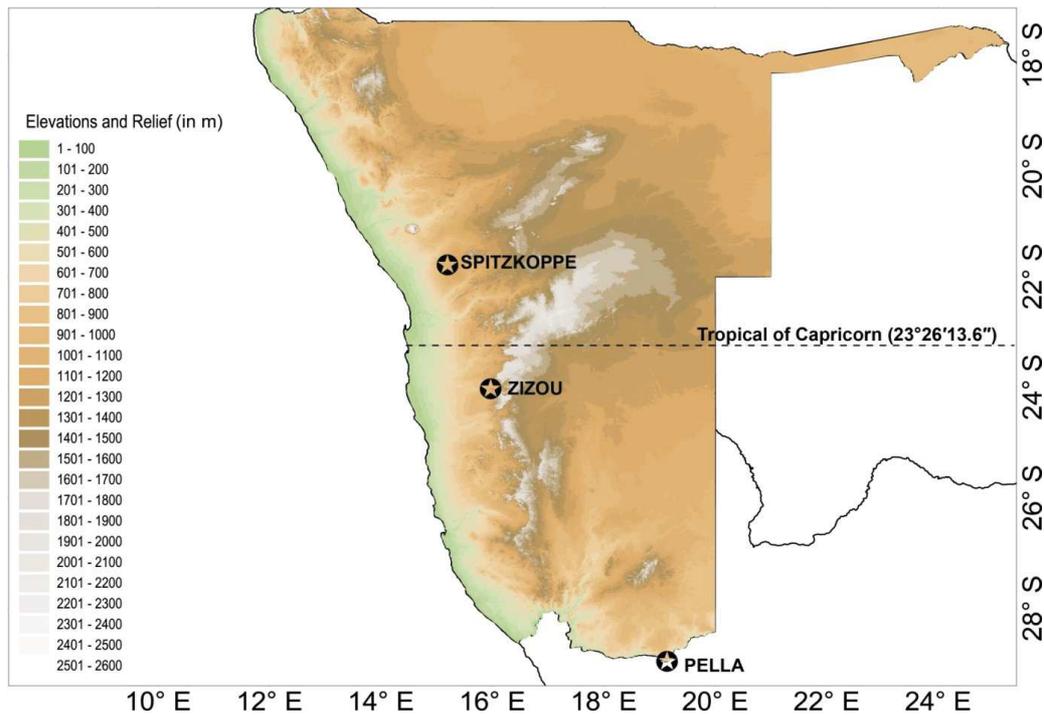


Figure 2. 2: Altitudinal map of Namibia.

From the Atlantic coast eastward, the Namib Desert gradually increases in elevation from sea level up to the foot of the Great Escarpment (100-200 km farther inland) in which the altitudes rise up to 1500-2500 m (Lancaster, 1989) (Figure 2. 2). Topography also plays an important part in the reduction of the humidity, as much of the moisture is derived from the Indian Ocean, and much of this moisture is lost in passing the Great Escarpment.

2.2. Climate

The climate of the Namib ranges from arid to hyper-arid. The aridity of the Namib Desert is the results of the permanent, but not stationary, South Atlantic high-pressure cell, and the effect of cold Benguela Current along the coast (Eckardt et al., 2013; Stone and Thomas, 2013; Lancaster, 2002).

At the equator, high insolation warms the near-surface air, causing it to rise. As this heated air rises it gradually cools, diverges poleward aloft and sinks at the $\sim 30^\circ$ latitude in both hemispheres (Figure 2. 3). This descending air inhibits convection, the formation of clouds, and thus results in reduced precipitation (Anderson et al., 2007). Most of the world deserts are situated in those regions.

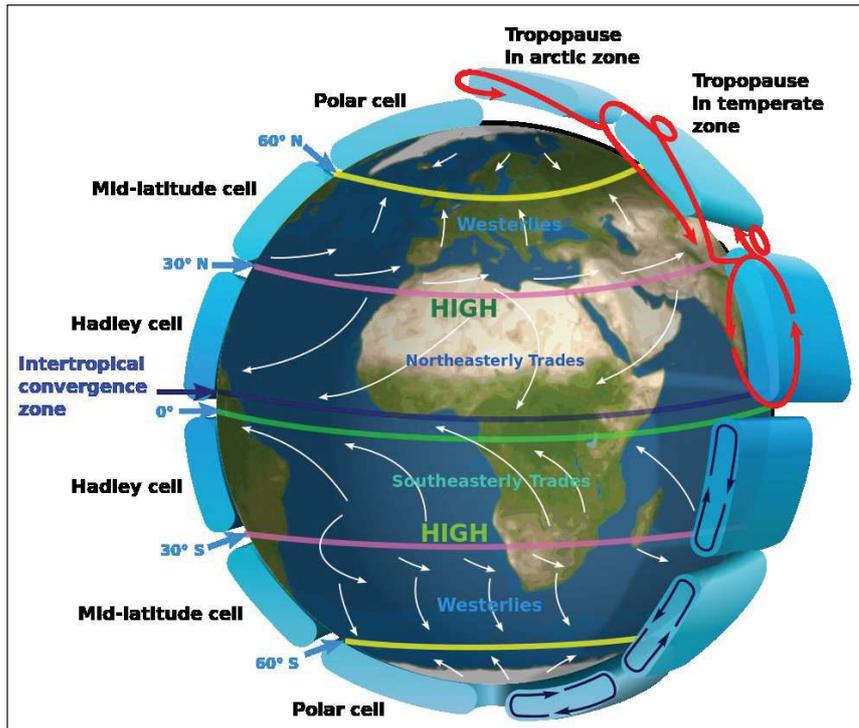


Figure 2. 3: Global Earth's atmospheric circulation (Wikipedia 2016, https://en.wikipedia.org/wiki/Hadley_cell).

The cold Benguela Current flows northward along southwestern Africa and it is part of the subtropical gyre (Fennel, 1999). It is driven by large-scale wind patterns associated with the South Atlantic Anticyclone (Garzoli and Gordon, 1996). The Benguela Current plays an important role in surface-water transportation from the southern to the northern hemisphere. The Benguela Current splits into two currents at 30°S: a northwestward-flowing main current (Benguela Ocean Current) and a wide sluggish flow along the continental margin (Benguela Coastal Current) into the Angola Basin (Peterson and Stramma, 1991). The latter current includes the Benguela upwelling system, which stretches from the southern tip of Africa to about 15°S - 16°S, where it is bounded by the Angola front that separates the warm Angola current and cold Benguela Current (Fennel, 1999). Coastal upwelling within this system varies seasonally (Shannon and Nelson, 1996). Depending on the variations, the Benguela upwelling system is divided into the Northern Benguela Region (NBR; winter maximum) and the Southern Benguela Region (SBR; summer maximum). Between these two regions is the zone of maximum upwelling intensity (centered around 26-27°S (Lüderitz)), which is characterized by the most persistent upwelling (Little et al., 1997).

The cold waters of the Benguela Current and coastal upwelling activity lower the evaporation from the Atlantic Ocean and induce a strong temperature inversion between cool humid air overlain by the hot and dry easterly air after passing the continent, which limits convection and minimizes the precipitation in the near-coastal zone of Namibia (Tyson, 1986). The northern boundary of the upwelling zone is coincident with the northern boundary of the Namib Desert (~14-15°S). The age of the Namib Desert is related to the origin of the present oceanic and climatological patterns, which, it has been suggested, could only develop after cold water produced in the Southern Ocean was able to penetrate northward, beginning in the early Oligocene (van Zinderen Bakker, 1975).

2.2.1. Precipitation and rainfall seasonality

Situated at the interface of the tropical, subtropical and temperate climate systems, as well as the Indian, Atlantic and Southern Ocean, precipitation across southern Africa is influenced by the variety of atmospheric and oceanic circulation systems. The north and the east of southern Africa receive summer rainfall (>66% of mean annual precipitation falling between October-March) (Figure 2. 4), climate is driven by the seasonal interplay between subtropical high-pressure cells and the migrations of easterly flows associated to the Inter-Tropical Convergence Zone (ITCZ) and the Congo Air Boundary (CAB) that bring rain to the tropic. The southern and western coasts are characterized by a Winter Rainfall Zone (WRZ) (>66% of mean annual precipitation falling between April -Sept) where rainfall results from the temperate frontal system embedded in the westerlies (see reference in Chase and Meadows, 2007). In between these two rainfall zones, which receive both winter and summer precipitation, there is a zone called the Year-round Rainfall Zone (YRZ).

In the Namib, rain falls mainly during the austral summer months of January- April, but the southern parts of this desert receive some winter rainfall. The sources of the summer rainfall derive from the moist air masses (easterly) from the Indian Ocean during the summer months and the advection moisture tropical air mass from the Atlantic Ocean associated to the seasonal movement of Inter-Tropical Convergence Zone (ITCZ) and the Congo Air Boundary (CAB). During austral summer ITCZ and CAB located to its southernmost and bring along the rainfall (Nicholson, 2000).

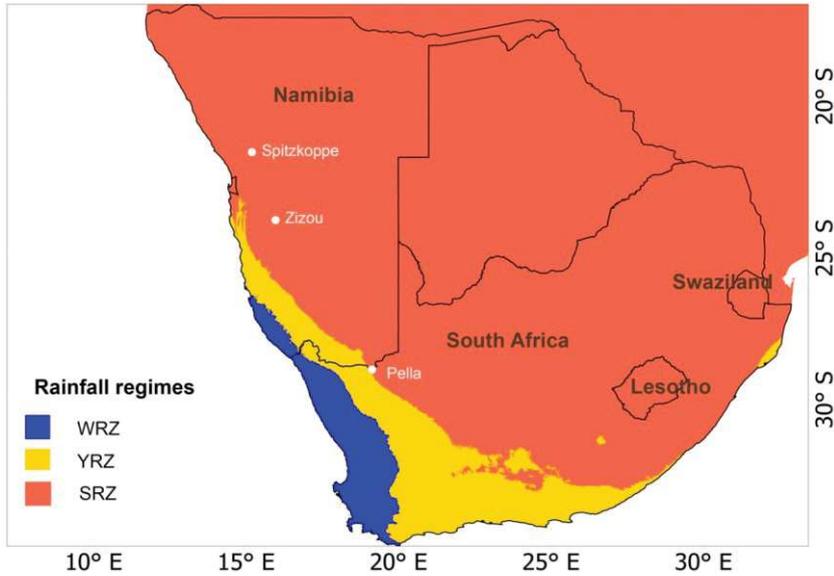


Figure 2. 4: Rainfall zones in southern Africa. The orange colour corresponds to the summer rainfall zone, the yellow colour to the year-round rainfall zone and the blue colour to the winter rainfall zone.

Rainfall gradients in Namibia follows a west-east increasing pattern and also one from north to south (ACACIA, 2002). The Namib Desert occupies a narrow range of mean annual rainfall $< 100 \text{ mm yr}^{-1}$. The annual rainfall is particularly low in the coastal area ($< 15 \text{ mm yr}^{-1}$) and it increases inland near the Great Escarpment ($80 - 100 \text{ mm yr}^{-1}$) (Lancaster et al., 1984). Maximum rainfall is observed in the northeast of Namibia due mostly to the effects of the easterly flow from the Indian Ocean that brings rainfall in the summer months. Three midden sites included in this thesis are located along the eastern margin of the Namib Desert with annual precipitation ranges from 100 to 150 mm yr^{-1} (Figure 2. 6). Inter-annual rainfall variability in the Namib is very high and it increases in the same way as aridity gradient, i.e. the area of the greater aridity is characterised by the greater rainfall variability (WWF, 2017). There are two principal causes of low rainfall in the Namib Desert. Firstly, the easterly trade winds emerging over the Indian Ocean lose their humidity when rising over the eastern Great Escarpment. These air masses become warm and dry when they reach the western Escarpment and continue to move down onto the low-lying Namib and produce the extremely hot and dry winds. Secondly, the cold and humid air cooled by the Benguela Current along the west coast move inland overlain by the warm, lighter air. This prevents the convective rise of cool and humid air and thus no cloud is formed (Von Willert et al., 1992).

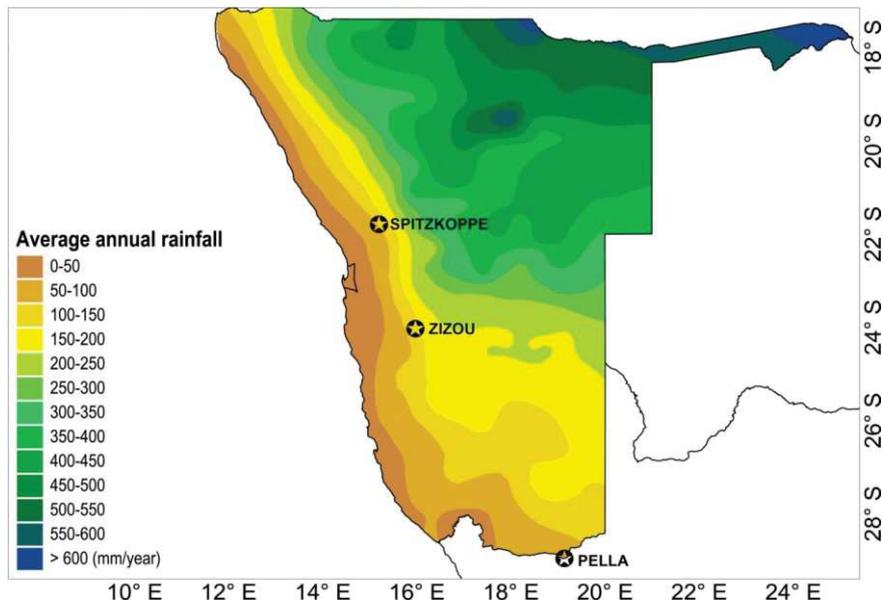


Figure 2. 5 :Average annual rainfall map showing the west-east increasing pattern (ACACIA, 2002).

2.2.2. Non-rainfall moisture

Advective fogs resulting from the cooling of moist oceanic air, and the cold Benguela Current effect, reach as far as 100 km inland (Oliver, 1995). This fog precipitation is known as an alternative moisture source for biota (both plants and animals) in the Namib (Henschel and Seely, 2008; Seely, 1978). However, the ways of how desert plants derive the moisture from fog precipitation are unclear. The effect of fog precipitation on plants could be negligible at our three study sites because the numbers of the fog-day at those sites range are around 5- 10 days per year (ACACIA, 2002) (Figure 2. 6).

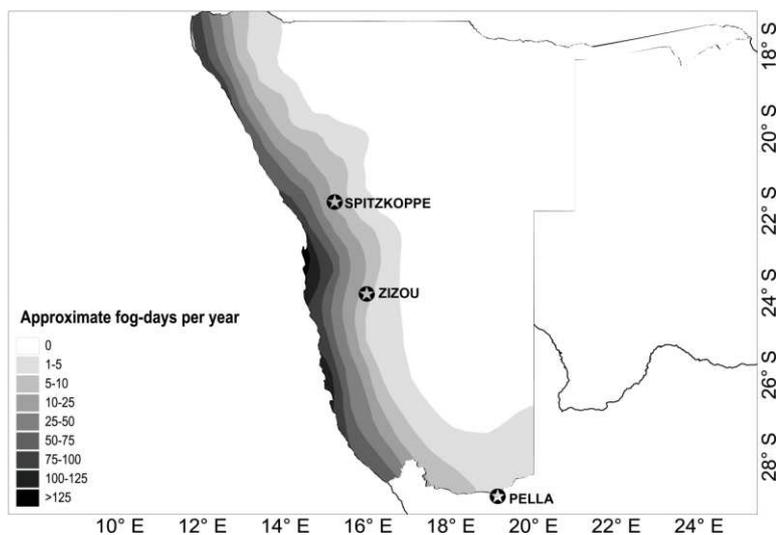


Figure 2. 6: Approximate number of fog-day per year (ACACIA, 2002).

2.2.3. Evaporation rates

The evaporation is another factor influencing the aridity. The evaporation rate in Namibia is lower in the coastal area and increases inland but it does not follow any north-south nor east-west gradient as the rainfall does (Figure 2. 7A). The evaporation rates are higher on the continent due to the continentality. The extraction of mean annual precipitation by evaporation rate provides the water deficit. All three midden sites are located in high water deficit area (2100-2500 mm) and this condition creates less water available for plants growth (Figure 2. 7B).

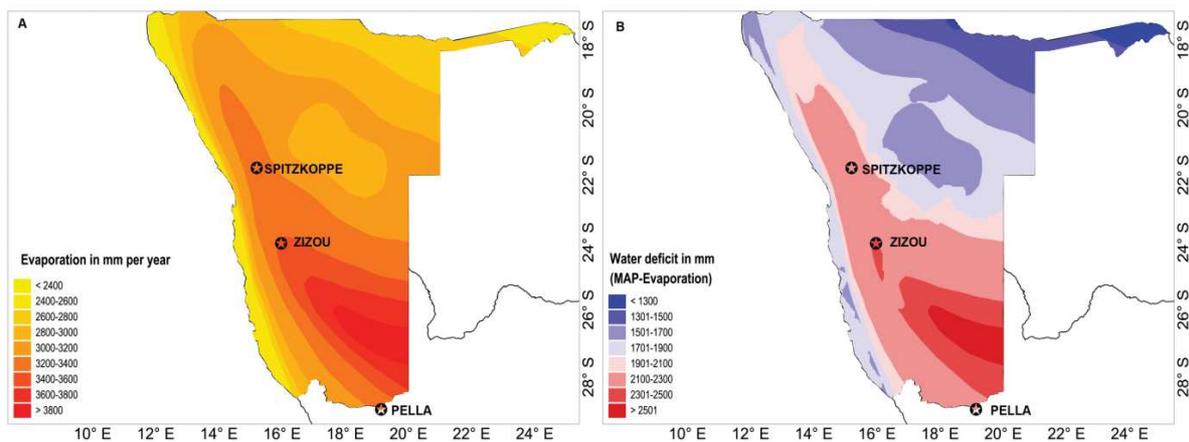


Figure 2. 7: Evaporation rates map (a) and Water deficit map (b) of Namibia, modified from ACACIA, 2002.

2.2.4. Temperature

Temperatures in the Namib are moderate in comparison with many other desert regions due to the influence of the cold ocean offshore. Mean annual daily maximum temperatures range from 17°C at the coastal areas to 28-33°C inland, while minimum daily temperatures are in average 13-16°C throughout the region (Lancaster, 2002). The average temperature at the coast is less than 16°C and it increases to >22 °C farther inland (Figure 2. 8).

There are four major characteristics in the distributions of the mean annual temperature. First, the expected overall temperature which increases towards the equator. Second, the effect of the cold Benguela Current. Third, the temperature irregularities which are induced by the topographic variation, for example, the lower temperature at the Escarpment (<14 °C) and higher temperature along the Orange River valley (>22 °C). Fourth,

the highest mean annual temperatures which occur in the area characterized by highest continentality effects (Dean and Milton, 1999).

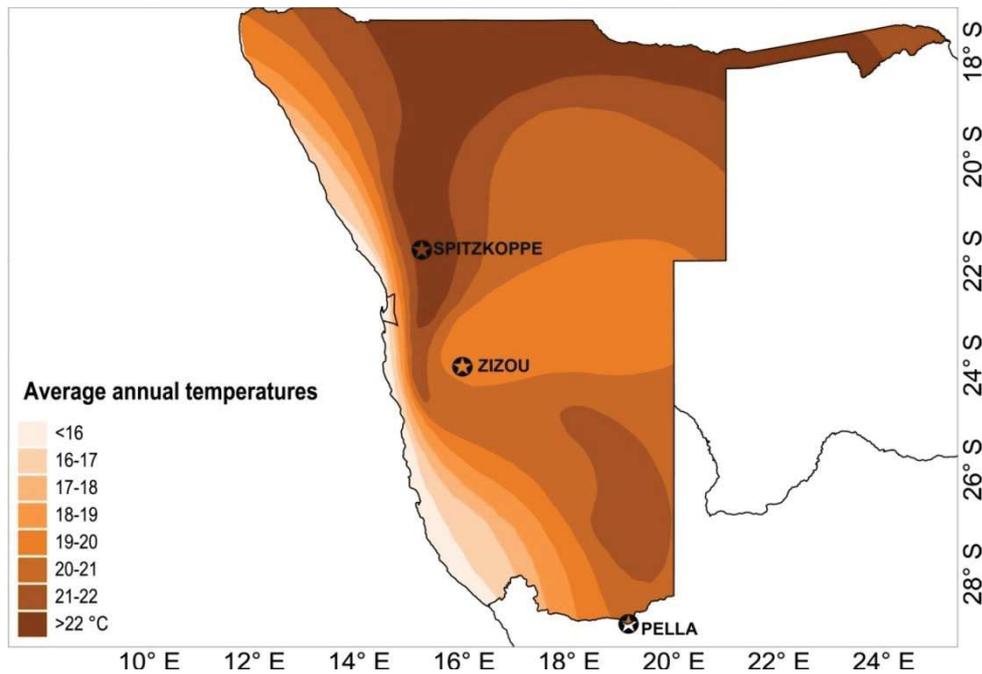


Figure 2. 8: Average annual temperature in Namibia (ACACIA, 2002).

2.2.5. Aridity index

There are several numerical aridity indices suggested to quantify the degree of dryness of a climate at a given location, and thus define the climate zones (Maliva and Missimer, 2012). Considering aridity here (mean annual precipitation divided by mean annual evapotranspiration), it is clear that the coastal area is significantly drier (Figure 2. 9) (Trabucco and Zomer, 2009). As aridity is a function of both precipitation and evapotranspiration, it is important to understand the pattern of these two variables in the Namib desert. Firstly, the east-west increasing aridity gradient seems to primarily follow the east-west increasing rainfall gradient. At the coastal area, the aridity index is the highest due to minimum rainfall. The evapotranspiration is the amount of transfer of water to the atmosphere via the evaporation and the plant transpiration. This factor is mainly influenced by the temperature. Lower temperature reduces the evapotranspiration while increased temperature leads to increased evapotranspiration.

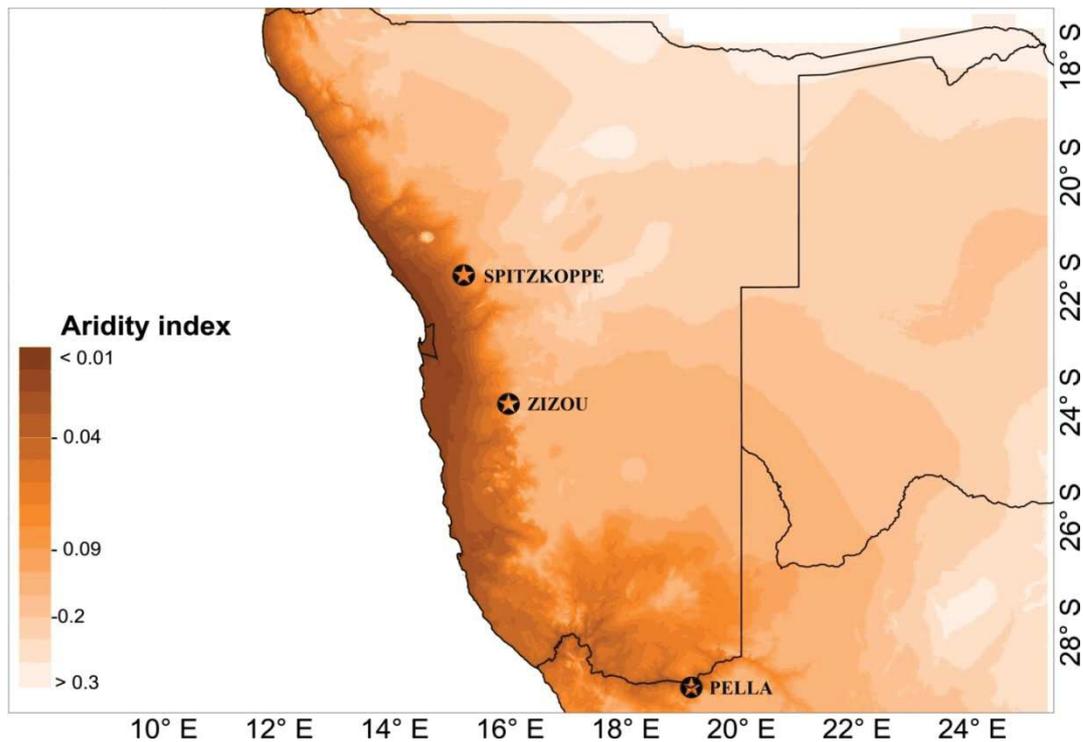


Figure 2. 9: Aridity index from WorldClim (Trabucco and Zomer,2009).

2.3. Vegetation

Vegetation patterns are primarily controlled by climate variables, for example, rainfall, temperatures, aridity etc. (Hoetzel et al., 2015). Some variables such as rainfall—amount, variability, duration, time— all play an important role in determining vegetation types. Temperatures are another climatic limiting factor for plant growth and development. Humidity available for plant growth is influenced both by rainfall and temperature. In Namibia, for example, we observed that landscape varies from regions devoid of vegetation to a dense ground layer of herbs, grass, and dwarf shrubs, taller shrubs and small trees following the humidity gradient from the coastal to further inland. Rutherford and Westfall (1994) mapped the vegetation in southern Africa into seven biomes: Savanna, Ticket, Grassland, Forest, Fynbos, Nama-Karoo, Succulent Karoo and Desert. Biomes broadly correspond with the climatic regions, although other environmental controls are sometimes also important. The Namibian biome map indicates four biomes: Savanna, Nama-Karoo, Succulent Karoo, and Desert (Figure 2. 10).

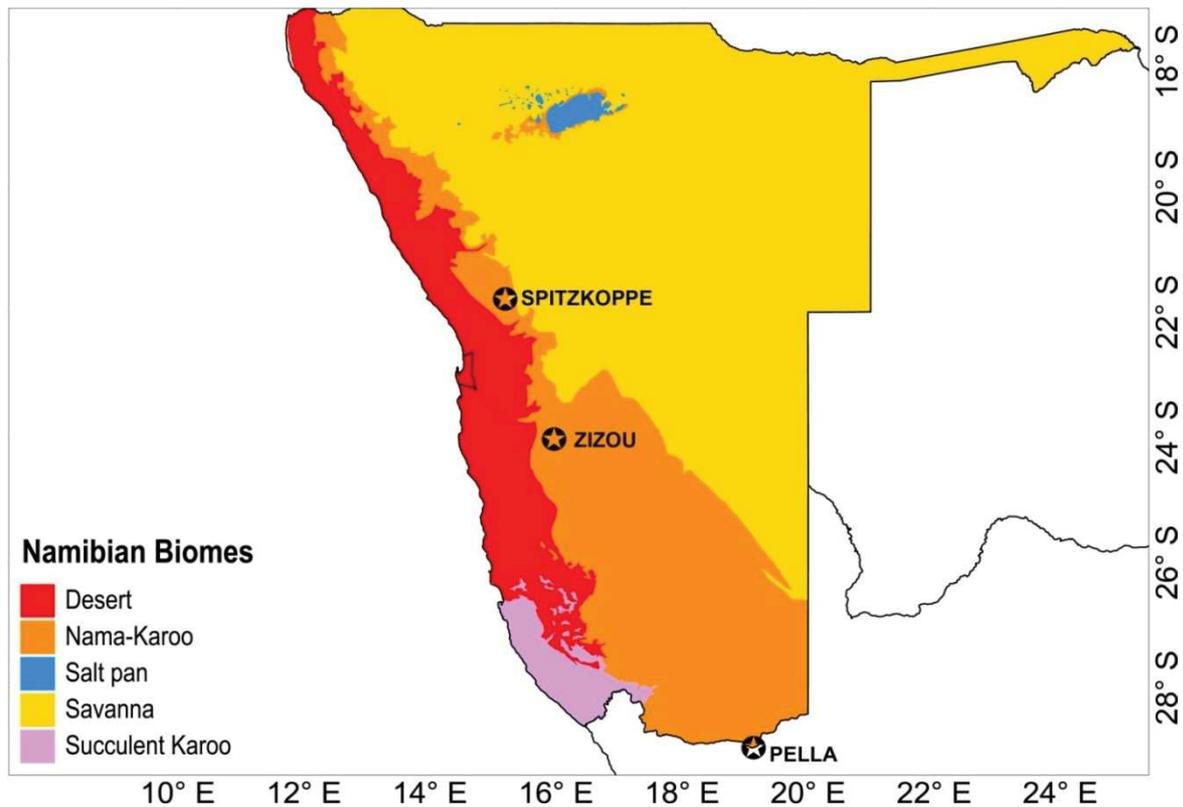


Figure 2. 10: Biome map of Namibia, ACACIA 2002.

The Savanna Biome is the largest biome in southern Africa as well as the dominant biome in Namibia (Mucina and Rutherford, 2006). This biome is characterised by a grassy (C_4 grass) ground layer and the upper layer composed of woody plants (Figure 2. 11c). The dynamics of the vegetation in this biome are associated with the rainfall (~250-1000 mm/yr), fire, and grazing. The major factor delimiting the biome is the lack of sufficient rainfall which prevents the upper layer from dominating, coupled with fires and grazing, which keep the grass layer dominant. The summer rainfall is essential for the grass dominance, which, with its fine material, fuels near-annual fires. C_4 grass in this biome is at an advantage where the growing season is hot. The shrub-tree element may come to dominate the vegetation in areas which are being overgrazed (Cowling et al., 2004; Mucina and Rutherford, 2006).

The Nama-Karoo lies to the west of the Savanna Biome (Figure 2. 10). This is the second largest biome in the region where rain mostly falls in summer months and varies between 60 and 400 mm/yr (Cowling et al., 2004). The dominant vegetation is a grassy and dwarf shrubland (Figure 2. 11a). Most of shrubs are deciduous in response to rainfall events (Mucina and Rutherford, 2006). Grass in both Savanna and Nama-Karoo is C_4 grass,

favoured by summer rainfall when there is a hot growing season. The dominant plant families of this biome are Asteraceae, Poaceae and Fabaceae (Shimida, 1985). Grazing activity rapidly increases the relative abundance of shrubs. The amount and nature of the fuel load are not sufficient to carry fires so fires are rare within the biome (Mucina and Rutherford, 2006).

At the southernmost as part of the southern Namib, the Succulent Karoo is primarily determined by the presence of low winter rainfall and extreme summer aridity (Mucina and Rutherford, 2006). During the summer, temperatures above 40°C are common. Fog is common nearer the coast. The entire Succulent Karoo receives its rainfall from weather systems associated with disturbances in the westerly stream (Dean and Milton, 1999). The altitude is mostly below 800 m, but in the east, it may reach 1500 m. This biome characterised by the highest species richness and endemics (> 50% of species). The biome is dominated by dwarf-leaf succulent plants such as Mesembryanthemaceae and Crassulaceae (Figure 2. 11d) (Cowling et al., 2004). Many other families are common including Asteraceae, Amaranthaceae, Euphorbiaceae and Zygophyllaceae. Grass is rare in Succulent Karoo except in some sandy areas but is of the C₃ type.

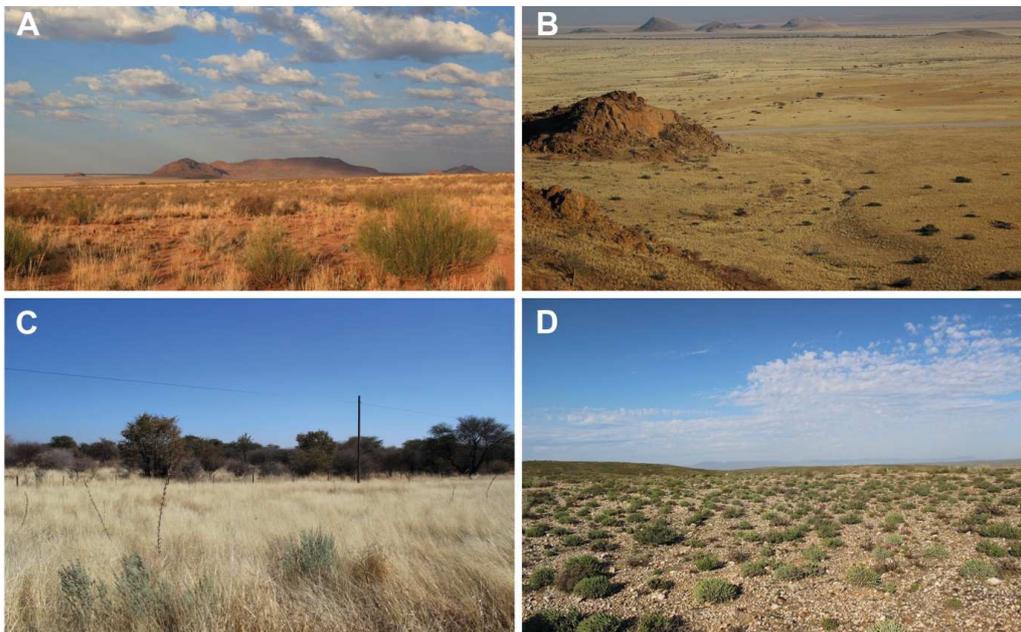


Figure 2. 11: Images of Namibian biomes; (a) Nama-Karoo, (b) Desert, (c) Savanna, and (d) Succulent Karoo.

The Desert Biome occupies the dry southern and coastal margins of Namibia. Climates are characterised by occasional summer rainfall with high levels of summer aridity.

Mean annual rainfall ranges from approximately 10 mm/yr in the west to 70-80 mm/yr on the inland margin of the desert. In addition, the rainfall is highly variable from year to year (Mucina and Rutherford, 2006). This results in vegetation dominated by the annual plants, especially grasses (**Error! Reference source not found.**b). We have observed that after a season with rarely abundant rains, desert plains can be covered with a sea of short annual grass whereas, in drier years, the plains appear bare with the annual plants persisting in the form of seed. The perennial plants are encountered in specialized habitats which are associated with local concentrations of water, for example, broad drainage lines or washes.

All three study sites included in this thesis are located at the ecotone of Nama-Karoo, lying between Savanna and Desert biome. The ecotone area is known as an effective monitor of global climate change because vegetation dynamics at such area are more sensitive to climatic variation than the main bodies of adjacent ecosystems (Noble, 1993). The relationship between ecotone dynamics and climate change, however, is made complicated by the individualistic response of species, the interaction of species, as well as time-lag of vegetation development during climate change. As we have noticed that each biome is characterized by a specific climate and dominant vegetation, we would expect to see the vegetation changes in between the adjacent biomes at all sites. Pella in the Orange River Valley, is characterised as a rocky desert area and this study site is at the border of the Nama-Karoo whose current climate and vegetation are different from the Desert Biome (see the description above). Zizou is at the eastern margin of the Namib Sand Sea near the foot of Great Escarpment zone. The vegetation at this site is currently classified in the narrow Nama-Karoo Biome (desert grassland) in between Desert and Savanna Biome (Rutherford, M.C. and Westfall, 1994). Spitzkoppe is at the eastern margin of the central Namib Plains where most of the isolated inselbergs are found in this part of the Namib Desert. Present-day vegetation at the site is characterised as xeric savanna woodland.

CHAPTER III: MATERIALS AND METHODOLOGY

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3. Materials and methods

Palynology is the branch of science concerned with the study of the pollen, spores, and similar palynomorphs, living and fossil. It plays an important role in the investigation of ancient climates, particularly through studies of deposits formed during glacial and interglacial stages (Windley and Harbaugh, 2016). Study of a sequence of spore- or pollen may reveal successive climatic changes, as indicated by changes in types of spores and pollen derived from the different vegetative complex. In seed plants, pollen grains are the male microgametophytes in which produce male gametes (sperm cells). Pollen grains have a hard coat made of sporopollenin that is highly resistant to most forms of decay other than oxidation, pollen-extraction procedure including strong acids, bases, acetolysis and density separation (Erdtman, 2013). This special characteristic allows pollen grains to be well preserved in a variety of archives as fossilized form. In palaeoecology and palaeoclimatology, fossil pollens are extracted from different sedimentary sources such as peats, lakes, and marine core.

In arid regions, such as the Namib Desert, the general lack of permanent wetlands due to arid climate limits the availability of suitable sediment archives for fossil pollen studies. Recently, a new palaeoenvironmental archive, the rock hyrax midden, has been shown to be an exceptional material for the preservation of fossil pollen in the arid regions of southern Africa (Chase et al., 2012; Chase et al., 2013; Gil-Romera et al., 2007; Scott et al., 2004; Scott & Vogel, 2000).

3.1. Materials

3.1.1. Rock hyrax middens

Rock hyrax middens are the accumulation of fossilized faeces and urine of the animal *Procavia capensis*, (Figure 3. 1) (Chase et al., 2012; Gil-Romera et al., 2007; Scott, 1990; Scott and Cooremans, 1992a). This species is commonly found over the greater portion of the subtropical dryland in southern Africa and being abundant from sea level to more than 2500 m. In addition, their ranges are included the hyper-arid region with precipitation less than 100 mm/yr and in the moister forested parts of the subcontinent, where rainfall exceeds 1500 mm/yr (Figure 3. 2).



Figure 3. 1: Rock hyraxes (*Procavia capensis*).

These wide climatic ranges suggest that past climate change may not affect their distribution during the Quaternary. The published data show that hyrax midden ages may be as old as 50,000 cal yr BP or more (Chase et al., 2012). Hyraxes are mix feeders consuming grasses, shrubs and forbs, but they have a preference for new shoots, buds, fruits and berries. Hyraxes are not thought to feed further than 60-500 m from their shelter and are unselective feeders suggesting that pollen registered in hyrax midden reflect the local vegetation. A study found that rock hyraxes consumed 79 species of plants with most of their time grazing during the wet season (78%) when grasses are available and only browsing (57%) during the dry season or dry year (Hoeck, 1975). Rock hyraxes live as a colony in the rocky shelters and the colony size ranges from 25 to 40 individuals (Kingdon,1971). A rock shelter can be continuously occupied by successive generations of hyrax colonies, accumulating hyraceum over thousands of years.

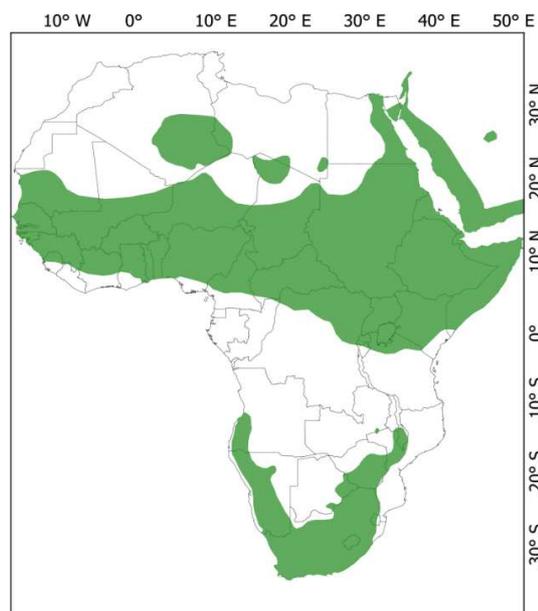


Figure 3. 2: The distribution of *Procavia capensis* (in the green colour) (IUCN, 2016).

The rock hyrax middens contain the pellets and urine, the latter of which we refer to hyraceum in its fossilized state (Figure 3. 3). The preservation of the middens depends on the shelter in which they are found, as they are susceptible to degradation by humidity. No consolidated middens have been found in the coastal situations where humidity prevents their development/preservation.



Figure 3. 3: The hyraceum of hyrax midden (left), the pellets of hyrax midden (right).

The accumulation rates of hyrax middens can vary based on the relative proportion pellets and hyraceum. Hyrax midden composed of mainly pellets accumulate much more quickly than hyrax middens composed primarily of hyraceum (generally between 200 and 500 years/cm) (Chase et al., 2012). Examinations of the internal and external structure of the middens suggest flow/deposition dynamics similar to speleothems (cave deposits, e.g. stalactites), with the fresh urine flowing across the surface of the midden, then drying and crystallizing, preserving the stratigraphic integrity of the midden (Figure 3. 4) (Chase et al., 2012).

Hyrax middens contain well-preserved microbotanical material including pollen, which is sealed in the hyraceum. Hyraceum protects pollen from microbial activity and decay. However, the degradation of pollen grains has been observed in loose pellets. Middens are excellent traps for pollen derived from the local and regional surrounding either via the alimentary channel of the animal



Figure 3. 4: Stratification of hyrax midden (Chase et al., 2012).

(excreted in pellets) or via deposition on the middens (Chase et al., 2012). The airborne pollen rains is incorporated by (1) collecting on the surface of the midden, (2) being brought in on the fur of the hyraxes, or (3) being ingested as dust on dietary items such as plants leaves or drinking water (Scott, 1990; Scott and Cooremans, 1992b). Some dietary components may also present when animals ingest the flowers, which may result in the occasional over-representation of the pollen of certain plant species in the pellet fraction of certain middens. The advantage of midden pollen spectra over wetland pollen spectra is that they may more clearly reflect the terrestrial vegetation without the high proportions aquatic elements found in the wetland sequences. Compared to other available palaeoarchives in the regions, such as fluvial sediments or paleosols, pollen record from peat bog and lakes, middens contain high fossil pollen concentration even in the poorly productive ecosystem such as the Namib Desert margin (Gil-Romera et al., 2007). In arid regions, fossil pollen in the hyrax midden reflects primarily local vegetation in the landscape (Figure3. 5)(Gil-Romera et al., 2010).

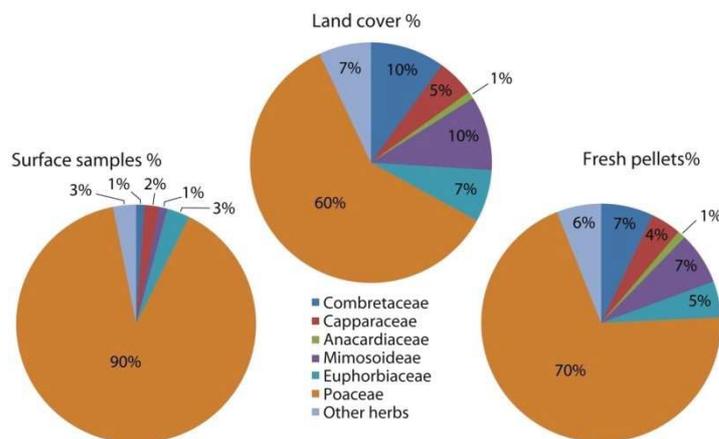


Figure3. 5: Pie diagrams showing the vegetation composition cover (in percentage) at Dewachaga, Ethiopia (top), the pollen abundance of the surface samples (left) and the hyrax pellets (right) (Gil-Romera et al., 2010).

While pollen recorded in middens can provide palaeoenvironmental information, however, diverse taphonomic vectors can complicate interpretations if they are not adequately considered. For example, pollen spectra from pellets may reflect the animal's dietary preferences on a particular day and they may contrast strongly with pollen spectra preserved in the hyraceum, which is primarily brought to the midden via the fur of hyraxes and the wind (Chase et al., 2012). Although structured studies to improve the interpretations of pollen preserved in hyrax middens remain to be done, the pollen analyses in fossil hyrax middens provide a unique opportunity to study long-term vegetation dynamics in the hyperarid such as the Namib Desert (Scott et al., 2004).

3.1.2. Fieldwork

We have selected three sites - Pella, Zizou, and Spitzkoppe - from the border of South Africa to the central of Namibia. The sites (a):

- encompass a latitudinal range from south to north in order to observe the coherent of regional vegetation and climate change, (b)
- are in the similar ecosystems both climate and vegetation (ecotone between Nama-Karoo and Desert), and (c)
- are in the summer rainfall zone of southern Africa.

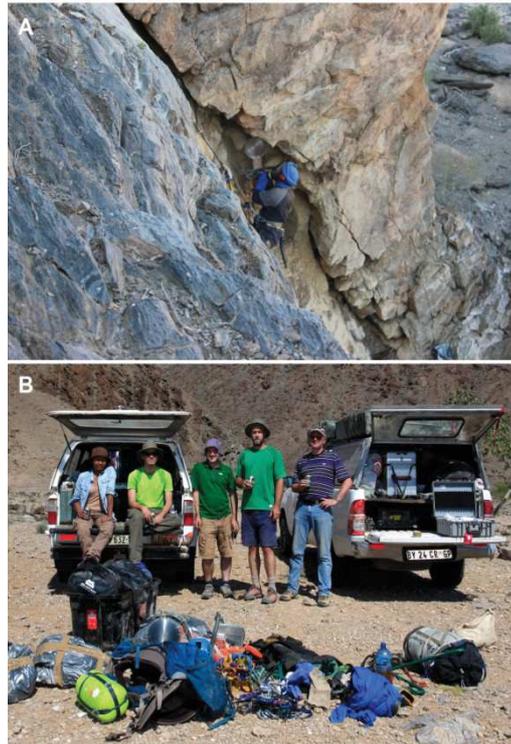


Figure3. 6: Images of fieldwork in Namibia: (a) collecting midden from the shelter, (b) equipment needed for collecting middens.

3.1.3. Sampling

Middens from the three selected sites were sampled for the pollen and micro-charcoal analysis (Figure3. 7). Table 3.1 indicates the number of sections, pollen and microcharcoal samples, and radiocarbon samples for each midden site. The pollen/micro-charcoal samples were from the section using a 2 cm diameter circular diamond saw blade. Depending on the friability of the section, samples range in thickness from 2-12 mm.

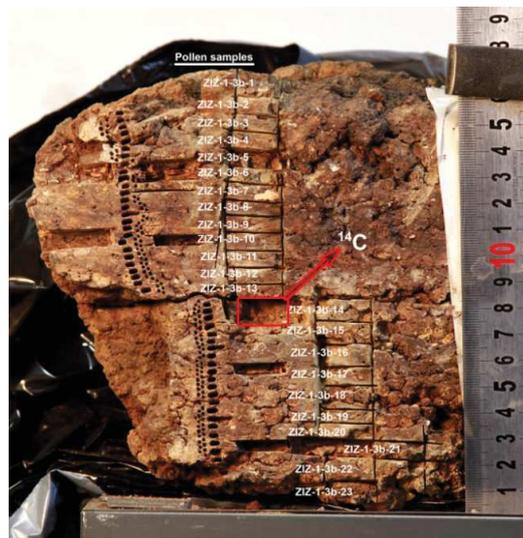


Figure3. 7: Image of a sampled midden section in the laboratory. The pollen samples were indicated in label white and several samples were taken for radiocarbon dates (all big square holes).

Table3. 1: Hyrax midden sites and number of pollen samples.

Midden sites	Sections	Number of samples	Radiocarbon samples
PELLA	PEL-1-1	38	10
	PEL-1-4a	21	6
ZIZOU	ZIZ-1-1	26	9
	ZIZ-1-3b	23	11
SPITZKOPPE	SPZ-2012-1-1	85	25
	SPZ-2012-1-2 top	15	8
	SPZ-2012-1-2 bottom	28	9
	SPZ-2013-1	47	13

Pollen and microcharcoal samples were sampled continuously, with independent samples being taken for radiocarbon dating (Table3. 1). The proportion of pellets affects midden stratigraphic integrity. Layers of pellets may create substantial pore-spaces which are or can be filled with hyraceum and in such cases, it may be difficult to determine the correct age of any given samples from those middens. This is an important criterion for selecting middens for analysis. The middens that are composed more completely or entirely of hyraceum better preserve the stratigraphic integrity and it is easier and more reliable to determine the age of samples (Chase et al., 2012). The middens used in this study were selected on this basis.

3.2. Methods

3.2.1. Pollen extraction

Pollen samples were prepared with standard physical (600 μm sieving and decanting) and chemical (HCl, KOH, HF and acetolysis) methods (Moore et al., 1991). *Lycopodium* tablets were added to the weighed sample to estimate pollen concentrations (Stockmarr, 1971). Each *Lycopodium* tablet (Batch 1031) that we used contains ~20,848 *Lycopodium* spores. The procedure of the extraction is outlined in Figure 3. 8.

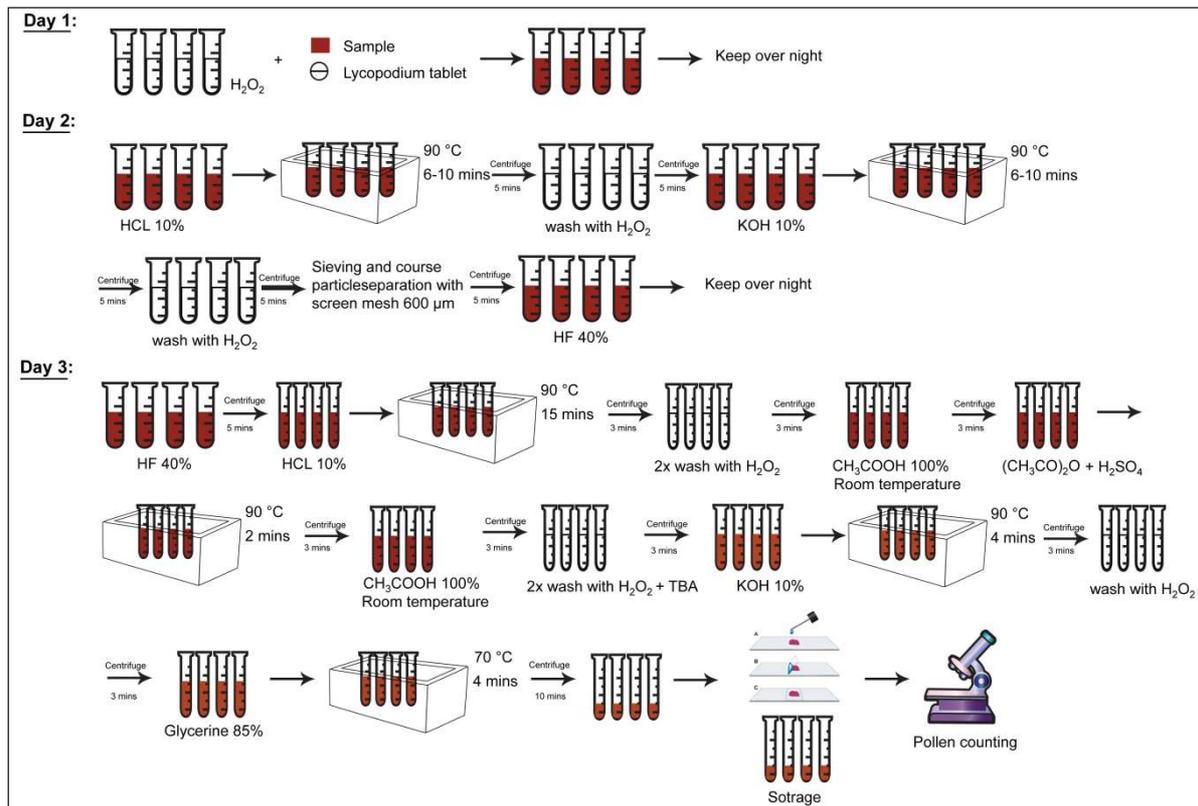


Figure 3. 8: Laboratory treatment procedure of pollen and microcharcoal extraction.

3.2.2. Pollen identification

Even though pollen grains may exhibit the specific characteristic of each plant species, these can generally not be observed using a standard optical microscope. Instead, palynologists are usually restricted to family or generic level identifications, depending on a region's flora.

Several sources of documents are used to help in identifying pollen in southern Africa such as the literature (Louis Scott, 1982a; van Zinderen Bakker, 1956, 1953; van Zinderen Bakker and Coetzee, 1959), and photographic and slides reference collections at the University of the Free State, University of Cape Town, and pollen collection at University of Montpellier.

Microscopic charcoal particles were identified as black, completely opaque, angular fragments that occurred in the pollen slides (Clark, 1988). Only charcoal particles $>75 \mu m^2$ (or longer than $10 \mu m$) were counted under a light microscope at $\times 400$ magnification. Charcoal particles which exceed the mesh-width size of $600 \mu m$ are missing from the microscopic charcoal record. Charcoal is deposited in hyrax midden mainly via wind

transport. Therefore our charcoal signal is related primarily to the regional fire signal, with specific local fires (large particles) and remote, extra-regional fires (<10 µm particles) being excluded.

3.2.3. Pollen counting

A minimum pollen sum of 400 grains was counted in each sample at a magnification of ×400 under a light microscope. Then the counting data were transformed into percentages. A minimum count of 200 items including exotic makers was used (Finsinger and Tinner, 2005). The pollen and microcharcoal concentration were calculated based on the *Lycopodium* added to each sample using the following equations:

$$\text{Pollen concentration (grains/gram)} = \left(\frac{\text{Lycopodium added}}{\text{Lycopodium counted}} \right) * \left(\frac{\text{Total number of pollen}}{\text{weight of sample}} \right)$$

$$\text{Micro charcoal concentration (particles/gram)} = \left(\frac{\text{Lycopodium added}}{\text{Lycopodium counted}} \right) * \left(\frac{\text{particles counted}}{\text{weight of sample}} \right)$$

3.2.4. Pollen diagram

We used Tilia program to create the pollen diagram. Tilia is software designed for managing and graphing paleontological data and metadata, especially stratigraphic data. The pollen zones are determined by the CONISS method (Constrained Incremental Sums of Squares)(Grimm, 2011). This method is based on the constrained cluster analysis; the dissimilarity square of Euclidian (Grimm, 1987).

Chapter IV: 50,000 years of vegetation and climate change in the Southern Namib Desert, Pella, South Africa (Lim et al., 2016)

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50,000 years of vegetation and climate change in the Southern Namib Desert, Pella, South Africa



Sophak Lim^{a,*}, Brian M. Chase^a, Manuel Chevalier^a, Paula J. Reimer^b

^aCentre National de la Recherche Scientifique, UMR 5554, Institut des Sciences de l'Evolution de Montpellier, Université de Montpellier, Bat. 22 CC061, Place Eugène Bataillon, 34095 Montpellier cedex 5, France

^bSchool of Geography, Archaeology and Palaeoecology, Queen's University Belfast, Belfast BT7 1NN, Northern Ireland, UK

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Corresponding author at: Institut des Sciences de l'Evolution de Montpellier (UMR 5554), Université Montpellier 2, Bat. 22 CC061, Place Eugène Bataillon, 34095 Montpellier cedex 5, France. Tel.: +33 04 67 14 39 25.

E-mail address: sophak.lim@univ-montp2.fr

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Abstract

This paper presents the first continuous pollen record from the southern Namib Desert spanning the last 50,000 years. Obtained from rock hyrax middens found near the town of Pella, South Africa, these data are used to reconstruct vegetation change and quantitative estimates of temperature and aridity. Results indicate that the last glacial period was characterised by increased water availability at the site relative to the Holocene. Changes in temperature and potential evapotranspiration appear to have played a significant role in determining the hydrologic balance. The record can be considered in two sections: 1) the last glacial period, when low temperatures favoured the development of more mesic Nama-Karoo vegetation at the site, with periods of increased humidity concurrent with increased coastal upwelling, both responding to lower global/regional temperatures; and 2) the Holocene,

during which time high temperatures and potential evapotranspiration resulted in increased aridity and an expansion of the Desert Biome. During this latter period, increases in upwelling intensity created drier conditions at the site.

Considered in the context of discussions of forcing mechanisms of regional climate change and environmental dynamics, the results from Pella stand in clear contrast with many inferences of terrestrial environmental change derived from regional marine records. Observations of a strong precessional signal and interpretations of increased humidity during phases of high local summer insolation in the marine records are not consistent with the data from Pella. Similarly, while high percentages of Restionaceae pollen has been observed in marine sediments during the last glacial period, they do not exceed 1% of the assemblage from Pella, indicating that no significant expansion of the Fynbos Biome has occurred during the last 50,000 years. These findings pose interesting questions regarding the nature of environmental change in southwestern Africa, and the significance of the diverse records that have been obtained from the region.

4.1. Introduction

Palaeoenvironmental evidence, and particularly palynological data, from the Namib Desert region are notably scarce (cf. Chase and Meadows, 2007; Lancaster, 2002), and as a result very little is known about long-term climate and vegetation dynamics surrounding the hyperarid core of southwestern Africa. The arid environment has precluded the preservation of organic material, and most palaeoenvironmental records have been obtained from a diversity of geomorphic features such as dune sediments (Bateman et al., 2003; Blümel et al., 1998; Bristow et al., 2007; Chase and Thomas, 2006; Chase and Thomas, 2007; Eitel et al., 2002; Stokes et al., 1997; Stone and Thomas, 2008; Telfer, 2007; Thomas et al., 1998; Thomas et al., 1997), fluvial deposits (Blumel et al., 2000; Bourke et al., 2003; Eitel et al., 2002; Eitel and Zöller, 1996; Heine, 2004; Heine and Heine, 2002; Heine and Völkel, 2009; Lancaster, 2002; Srivastava et al., 2006; Stone et al., 2010; Vogel, 1982) and fragmentary lacustrine records (Cooke and Heine, 1979; Deacon and Lancaster, 1988; Heine, 1978, 1982; Lancaster, 1979, 1984; Lancaster, 1986; Lancaster and Teller, 1988; Teller and Lancaster, 1985; Teller and Lancaster, 1986; Teller et al., 1990; Ward, 1984). Many of these, while being potentially valuable indicators of landscape dynamics (Thomas, 2013), are of debatable palaeoclimatic significance (Chase, 2009; Chase and Brewer, 2009; Lancaster, 2002; Stone et al., 2010; Thomas and Burrough, 2012), and a coherent environmental context for their

development remains to be established. In terms of palaeoecological records, while some Holocene age pollen records have been recovered from western Namibia, they are generally restricted to the mid- to latest Holocene (Gil-Romera et al., 2006; Gil-Romera et al., 2007; Scott, 1996; Scott et al., 1991), with only records from the Brandberg (Scott et al., 2004) providing snapshots of glacial-age vegetation in the Namib Desert.

This lack of terrestrial records has led to a reliance on records obtained from marine cores (cf. Chase and Meadows, 2007). While these sequences contain long, continuous records of terrestrial sediments (Gingele, 1996; Pichevin et al., 2005; Stuut et al., 2002; Weldeab et al., 2013), pollen (Shi and Dupont, 1997; Shi et al., 1998, 2000; Shi et al., 2001), charcoal (Daniau et al., 2013) and biomarkers (Collins et al., 2014; Collins et al., 2011; Rommerskirchen et al., 2003) the intense atmospheric and oceanic circulation systems dominating the Southeast Atlantic basin - particularly along the southwest African margin and the potential for significant aeolian and fluvial sediment contributions, have raised questions regarding the taphonomy, and thus significance, of the records obtained (cf. Chase and Meadows, 2007; Scott et al., 2004).

Despite the conflicts presented by these records and their interpretation, the regional dataset seems to generally indicate: 1) more humid conditions in the Namib during the last glacial period, particularly during marine isotope stage (MIS) 4 (71-59 ka) and during late MIS 3 and early MIS 2, from ~35-24 ka, and 2) relatively drier conditions during the Holocene (synthesised in Chase and Meadows, 2007). The mechanisms driving the differences in glacial and interglacial climates remain unclear. While Chase and Meadows (2007) suggested that the prevalence of southwest African sites indicating increased humidity during the last glacial period may support prevailing conceptual models relating wetter glacial conditions to equatorward shifts in the westerly storm track (e.g. van Zinderen Bakker, 1976), it has also been suggested that more extensive Northern Hemisphere ice sheets would have resulted in a southward displacement of the African rainbelt (cf. the Intertropical Convergence Zone (ITCZ)), bringing more tropical rain to the region during the summer (Butzer, 1984; Butzer et al., 1978; Lancaster, 1979; Lewis et al., 2010). Quantifications of summer precipitation amounts in eastern South Africa (Chevalier and Chase, 2015; Truc et al., 2013) suggest that while some evidence exists to indicate increased tropical precipitation during the last glacial period (Schefuß et al., 2011; Thomas et al., 2009; Wang et al., 2013), this was restricted, at least in the east, to a narrow belt south of Lake Malawi, and that any zone of enhanced tropical rainfall was likely more restricted than some general circulation model (GCM) simulations suggest (cf. Lewis et al., 2010). A further

consideration is the role of temperature on the regional hydrologic budget. Regardless of changes in the position or intensity of the regions' dominant moisture-bearing systems, indications are that temperatures in southern Africa were as much as 5°C to 6°C lower during the last glacial period (Chevalier and Chase, 2015; Kulongoski and Hilton, 2004; Stute and Talma, 1997; Stute and Talma, 1998; Talma and Vogel, 1992; Truc et al., 2013). This would have significantly reduced potential evapotranspiration (PET), and may have thus strongly influenced records derived from proxies sensitive to evaporation and water availability rather than purely rainfall amount (Chevalier and Chase, in press).

Here we present: 1) the first continuous pollen records from the southern Namib Desert and South Africa's Desert Biome spanning the last 50,000 years, and 2) quantified reconstructions of changes in aridity and mean annual temperature based on these data. The pollen records were obtained from two sections of a rock hyrax midden complex recovered from mountains near the town of Pella, South Africa (a full description of rock hyrax middens can be found in Chase et al., 2012). Through this analysis we seek to investigate: 1) the coherence between marine and terrestrial pollen records, 2) the extent that the former may be used as reliable indicators of changes in terrestrial ecosystems, and 3) the hypothesis that mediterranean Fynbos Biome expanded far to the north during the last glacial period as a result of an equatorward shift of the westerly storm track (e.g. Chase and Meadows, 2007; Shi et al., 2000; Shi et al., 2001).

4.2. Study region and site description

The Pella midden site (29°00'04"S, 19°08'06"E, 490 m amsl.) is located 3 km NNW of the town of Pella, on the South African southern flank of the Orange River valley, 4 km from the river (Figure 4. 1). Lower than the surrounding plains, which receive c. 200 mm yr⁻¹ of rainfall, the climate of the Orange River valley is arid to hyperarid, with the midden site receiving only c. 70 mm yr⁻¹ of rainfall (Hijmans et al., 2005). Most (66%) of what little rainfall the region receives falls during the late summer, placing the site on the border of the western margin of southern Africa's summer rainfall zone (SRZ; sensu Chase and Meadows, 2007). Compounding the effects of low rainfall and strong seasonality, inter-annual variability of precipitation is high, and the region may go for several years with no rainfall.

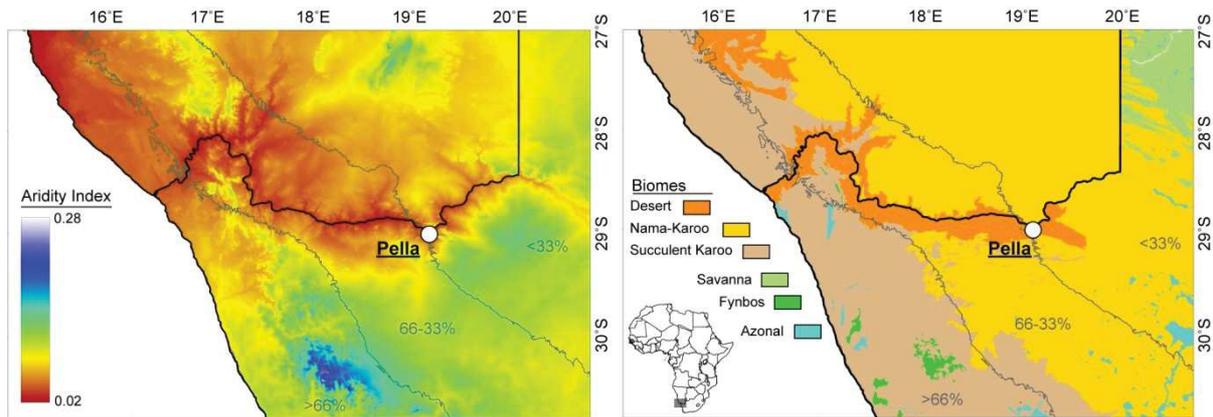


Figure 4. 1: Maps of aridity index (left) and the biomes of the southern Namib Desert region (right) with location of the Pella rock hyrax midden site. The data for vegetation type is derived from two separate sources for Namibia ('ACACIA', 2002) and South Africa (Mucina and Rutherford, 2006b). As the data differ in resolution and methodology, the desert region in Namibia was extended along the Orange River based on regional aridity index values (<0.04) (Trabucco and Zomer, 2009) to be comparable with the South African data. The boundaries of the winter, year-round and summer rainfall zones (defined as $>66\%$, $66\%-33\%$ and $<33\%$ winter Apr-Sept rainfall; (defined as $>66\%$, $66\%-33\%$ and $<33\%$ winter Apr-Sept rainfall; sensu Chase and Meadows, 2007) are indicated by the grey NW-SE trending lines.

The vegetation at Pella (Figure 4. 1) is classified as Eastern Gariep Rocky Desert, with the plains immediately to the south hosting Eastern Gariep Plains Desert vegetation (Mucina and Rutherford, 2006a), representing an extension of the hyperarid – arid extension of the Namib Desert across the more humid Succulent Karoo and Nama-Karoo biomes (Figure 4. 1). Indeed, vegetation on the rocky slopes around the site is extremely sparse. As the site is found in a structure created by a drainage line (Figure 4. 2, d), some larger shrubs (e.g. *Searsia* (a.k.a. *Rhus*) sp. (Anacardiaceae)) are found in close proximity (Figure 4. 3). While no *Aloe* were observed at the site, they are an important tree/shrub element of the ecoregion, as are species of *Acacia*, *Boscia*, *Euclea*, *Maerua* and *Pappaea*. Smaller shrubs include *Commiphora* sp., *Ruschia*, *Mesembryanthemum*, *Tylecodon*, *Zygophyllum*, *Diospyros*, *Eriocephalus*, *Hermannia*, *Justicia*, *Monechma* and *Petalidium*, and *Tribulus* is one of the primary perennial herbs. The surrounding plains host somewhat denser vegetation (Figure 4. 2c; Figure 4. 3), dominated by species of *Stipagrostis* grass and *Euphorbia* and *Zygophyllum* shrubs as well as localised stands of *Aloe dichotoma* (Mucina and Rutherford, 2006a). In this and drier regions of the Desert Biome (e.g. Figure 4. 2a), grasses are best adapted and most prevalent as they can withstand extended drought periods and respond quickly when rain does fall. Woody shrubs may be found along drainage lines or other locations that store groundwater (Figure 4. 2d; Figure 4. 3), but these situations become increasingly rare in drier environments.

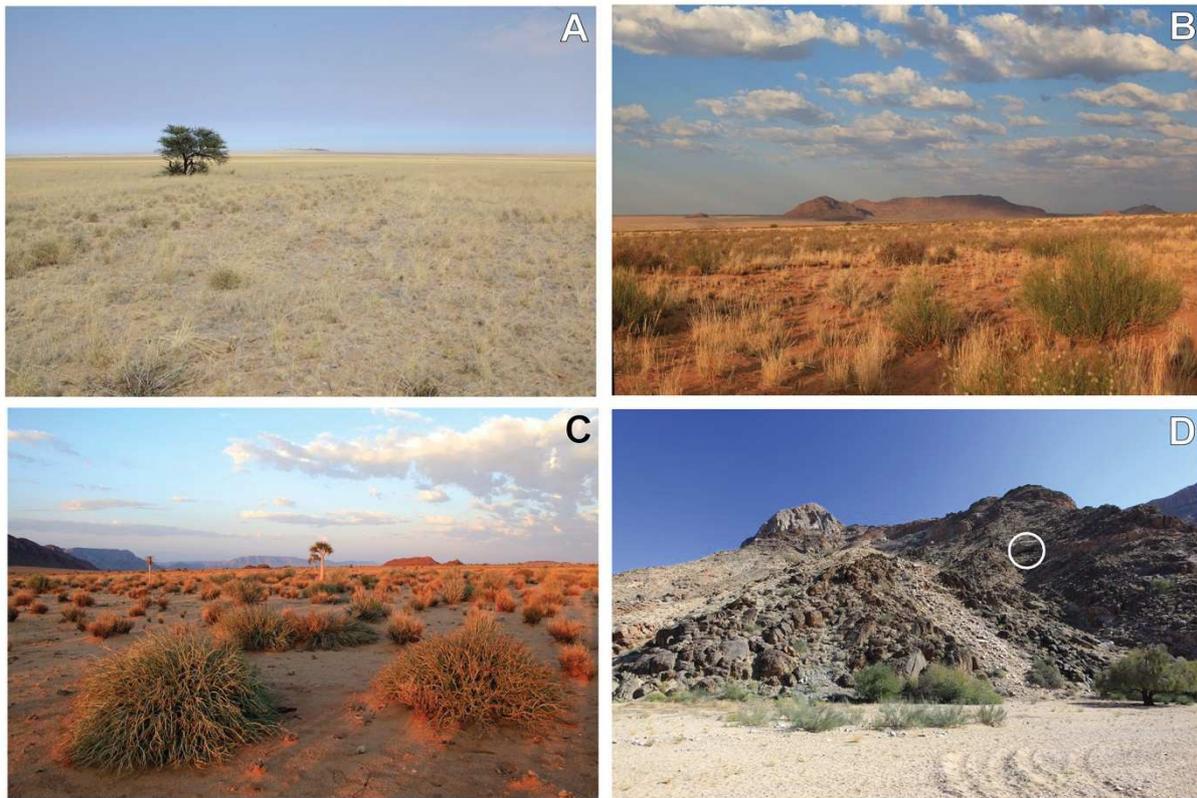


Figure 4. 2 : Images of the grassy plains of the Desert Biome (a), the Bushmanland Arid Grassland vegetation of the Nama-Karoo Biome (b), the Eastern Gariiep Plains Desert (c) and the Eastern Gariiep Rocky Desert, with the Pella midden site indicated within the white circle (d).

Approximately 20-30 km to the south of the site, increased rainfall supports Bushmanland Arid Grassland vegetation of the Nama-Karoo Biome (Mucina and Rutherford, 2006a) (Figure 4. 2, b). As a whole, the Nama-Karoo is distinguished from the adjacent Succulent Karoo Biome to the west by seasonality of rainfall (summer as opposed to winter rainfall dominance), and its relatively low plant diversity, with Asteraceae and Poaceae being the dominant families (Mucina and Rutherford, 2006a). A significant gradient in rainfall amount exists across the Nama-Karoo from east (c. 500 mm yr⁻¹) to west (c. 70 mm yr⁻¹). In the west, nearer to Pella, succulents of Aizoaceae, Crassulaceae and Euphorbiaceae become more common, reflecting the drier climate and the transition with the Succulent Karoo and Desert biomes. The Bushmanland Arid Grassland is similar in many respects to the Eastern Gariiep Plains Desert described above, with a dominance of *Stipagrostis* grasses. Species of *Aristida* and *Eragrostis* grass also occur, and the tree species *Acacia mellifera* and *Boscia foetida* are found along drainage lines. Shrubs such as *Lycium*, *Pentzia*, *Barleria*, *Berkhya*, *Blepharis*, *Eriocephalus*, *Hirpicium*, *Aizoon*, *Monechma*, *Solanum* and *Zygophyllum* are most

common, and *Tribulus* is again a common herb (Mucina and Rutherford, 2006a). Generally, grass dominates in the Nama-Karoo under two opposing climate regimes: 1) along its most arid margins, where there are insufficient groundwater resources to support perennial shrubs, and 2) with increasing rainfall, which becomes more regular/abundant to the east, where the Nama-Karoo grades into the Grassland Biome.

4.3. Materials and Methods

4.3.1. The Pella rock hyrax middens

Rock hyrax middens are stratified accumulations of urine and/or faecal pellets that are deposited as successive layers, often over thousands of years (see Chase et al., 2012). The midden at Pella formed in several distinct lobes (Figure 4. 3c). For this study, sections of two of the lobes of the midden complex were sampled for pollen analysis: PEL-1-1 (22 cm thick) and PEL-1-4a (13.5 cm). The samples from each (PEL-1-1 n=38; PEL-1-4a n=21) midden are contiguous, with each consisting of a block of material 2-5 mm thick and weighing between ~0.3 g and 1.0 g. For a full description of hyrax middens, their development and the sampling and

analytical methodologies for the proxies they contain, see Chase et al. (2012).



Figure 4. 3: Images of the view from the Pella rock hyrax midden site, looking east (a), the overhang sheltering the midden site (b) and the Pella rock hyrax midden, with PEL-1-1 and PEL-1-4a lobes labelled (72 mm camera lens cover for scale) (c).

Radiocarbon analysis was performed on 16 samples from the midden section (PEL-1-1, n=10; PEL-1-4a, n=6). The samples were pretreated with 2% HCl for one hour at room

temperature to remove carbonates and dried at 60°C. They were then weighed into quartz tubes with an excess of CuO, sealed under vacuum and combusted to CO₂. The CO₂ was converted to graphite on an iron catalyst using the zinc reduction method (Slota et al., 1987). The ¹⁴C/¹²C ratio and ¹³C/¹²C were measured by accelerator mass spectrometry (AMS) at the ¹⁴CHRONO Centre, Queen's University Belfast.

All the radiocarbon ages were calibrated (Table 4. 1) with the Southern Hemisphere calibration data (SHCal13, Hogg et al., 2013; Reimer et al., 2013) and chronologies were estimated with the Bacon v2.2 model (Blaauw and Christen, 2011). Bacon produces robust estimations of the probability density function (*pdf*) of the uncertainties associated with our pollen samples. That information, referred to as *pdf_{age}*, was extracted and integrated in a framework to derive robust quantitative climate reconstructions (more details below and in Chevalier and Chase, 2015).

4.3.2. Pollen and microcharcoal analysis

Pollen samples were prepared with standard physical (600 µm sieving and decanting) and chemical (HCl, KOH, HF and acetolysis) methods (Moore et al., 1991). *Lycopodium* tablets were added to the weighed sample to estimate pollen concentrations (Stockmarr, 1971). A minimum pollen sum of 400 grains was counted at a magnification of ×400 under a light microscope, and identified with the help of the literature (Scott, 1982a; van Zinderen Bakker, 1953, 1956; van Zinderen Bakker and Coetzee, 1959), and photographic and slides reference collections at the University of the Free State, University of Cape Town, and University of Montpellier. Microcharcoal particles were identified as black, completely opaque, angular fragments that occurred in the pollen slides (Clark, 1988). Only charcoal particles >75 µm² (or longer than 10 µm) were counted under a light microscope at ×400 magnification (Mooney and Tinner, 2011; Patterson et al., 1987). A minimum count of 200 items (given by the sum of charcoal particles and exotic marker grains) was used. Charcoal particles which exceed the mesh-width size of 600 µm are missing from the microscopic charcoal record and particles of ca. <10 µm were not counted in order to ensure correct identification (Mooney and Tinner, 2011). Therefore, our charcoal signal is related primarily to the regional fire signal, with specifically local fires (large particles) and remote, extra-regional fires (<10 µm particles) being excluded.

The TILIA program was used to construct the pollen diagrams, and pollen zones are determined by the CONISS method (Grimm, 2011).

4.3.3. Climate reconstruction from fossil pollen

To derive more specific palaeoclimatic information, we used the CREST software package (Climate REconstruction SofTware; Chevalier et al., 2014) to analyse the fossil pollen data from Pella. In this paper, we focus on the reconstruction of an aridity index (AI) and mean annual temperature (MAT).

The method is based on the use of *pdfs*. Modern plant distributions, obtained from the South African National Botanical Institute (Rutherford et al., 2012; Rutherford et al., 2003; SANBI, 2003), are correlated with AI (Trabucco and Zomer, 2009) and MAT (Hijmans et al., 2005) data to define climatic envelopes for plant species and fit species *pdfs* (pdf_{sp}). These pdf_{sp} are then combined according to the individual species that comprise each fossil pollen type identified in the sequence to create a pollen *pdf* (pdf_{pol}). Finally, the pdf_{pol} for each sample are weighted and multiplied to produce a curve that represents the likelihood of AI/MAT based on the coexistence of the different taxa (pdf_{AI} / pdf_{MAT}).

The CREST method has been shown to be sensitive to the number of taxa used (Chevalier et al., 2014). Juggins et al. (2015) and Chevalier and Chase (2015) have also shown – for different reconstruction methods – that selecting a subset of sensitive taxa was preferable to ensure robust quantifications from pollen data. Using the CREST software package and its diagnostics tools (based on assessments of the shape of the pollen *pdfs* (e.g. number of modes, kurtosis) and the modern correlation between plant distributions and climate gradients, we selected a subset of sensitive taxa for: 1) AI (Aizoaceae, *Aizoon* type, Amaryllidaceae, Anacardiaceae, Apiaceae, Caryophyllaceae, Celastraceae, *Crassula*, *Forsskaolea*, Menispermaceae, *Montinia*, *Pappea*, *Pentzia*-type, *Petalidium*, *Stoebe*-type, *Tribulus*, Rhamnaceae and *Zygophyllum*) and 2) MAT (Amaryllidaceae, Apiaceae, *Berkheya*, Capparaceae, Caryophyllaceae, *Crassula*, Ericaceae, *Forsskaolea*, *Hermannia*, *Justicia*, *Montinia*, Moraceae and *Stoebe*-type). Species-rich taxa such as Asteraceae, Poaceae and Scrophulariaceae cannot be used due to the saturation effect of the CREST method (further details available in Chevalier et al., 2014).

To enhance the signal over noise ratio of our reconstructions, we used the two-step Monte-Carlo framework presented in (Chevalier and Chase, 2015). Each sample is associated with quantified uncertainties from: 1) the CREST reconstruction (pdf_{AI} / pdf_{MAT}), and 2) the *pdf* of the age uncertainties derived from the age-depth model (pdf_{age}). To interpolate the reconstructions and integrate these two sources of uncertainty, different scenarios are built by

sampling pdf_{AI} / pdf_{MAT} and pdf_{age} for each sample. The accumulation and combination of 100,000 of those scenarios produces a robust interpolated curve that integrates uncertainties from the age-depth model and the reconstruction process. The interpolated curves are then stacked together (centred using their overlapping sections between 100 and 1300 cal BP (calibrated radiocarbon years before AD 1950)) with a second round of Monte-Carlo sampling to produce a single reconstruction. This process generates high-frequency, low-amplitude white noise that has no climate or environmental significance, and which is filtered out with a 1000-yr moving average.

4.4. Results

4.4.1. Age-depth models and midden accumulation rates

The radiocarbon analyses of the Pella middens PEL-1-4a and PEL-1-1 indicates that each lobe accumulated continuously, although with significant changes in accumulation rate (Figure 4. 4). An exception may be at ~15.75 cm in PEL-1-1 where a sharp decrease or cessation of accumulation may have occurred. Accumulation rates range from extremes of 4.9 yr/mm in PEL-1-4a to 780 yr/mm in PEL-1-1, with average accumulation rates of 230 yr/mm (PEL-1-1) and 9 yr/mm (PEL-1-4a). This identifies minimum and maximum resolutions of 10 and 2358 cal year per sample, and average resolutions of 950 ± 515 (PEL-1-1) and 40 ± 10 (PEL-1-4a) cal year per sample.

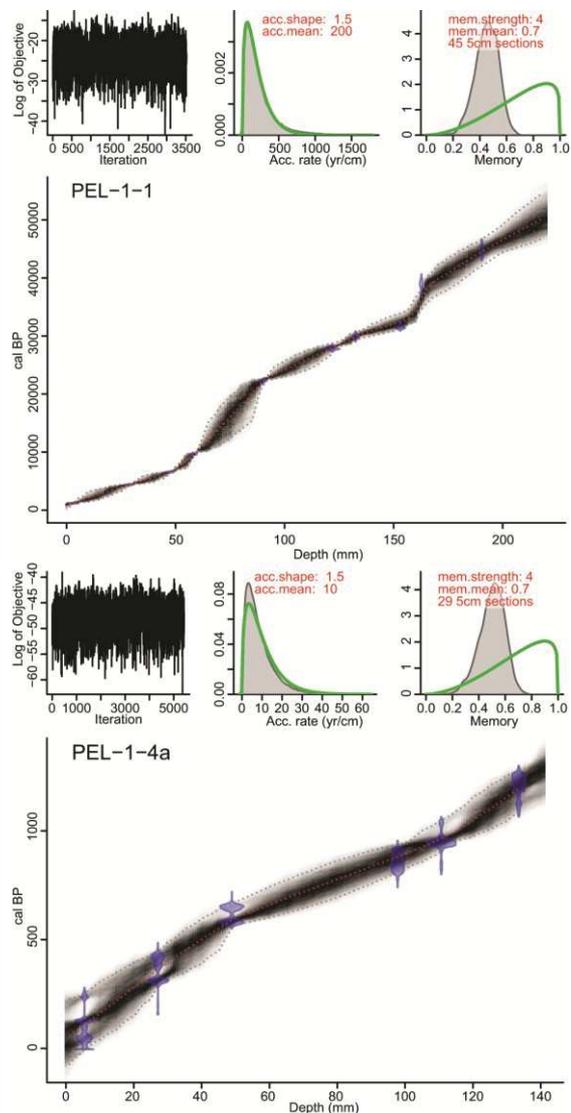


Figure 4. 4: Age models for the Pella rock hyrax middens PEL-1-1 and PEL-1-4a.

4.4.2. Vegetation dynamics inferred from pollen record

The Pella middens (PEL-1-1 and PEL-1-4a) are integrated into a single record (one sample from PEL-1-1 at ~630 cal BP with PEL-1-4a), with a total of fifty-one identified taxa being divided, and samples being clustered into seven statistically significant pollen zones spanning the last 50,000 years (Figure 4. 5). Poaceae and Asteraceae are the most common and persistent pollen types occurring, with Asteraceae being most prevalent during periods of the late Pleistocene (particularly from 50 – 39 cal kBP and 32 – 15 cal kBP (thousand calibrated radiocarbon years before AD 1950)) and grasses along with certain succulents and woody elements becoming more dominant during the Holocene.

4.4.2.1. Pleistocene vegetation composition and dynamics

The lowermost pollen zone (PEL-I; ~50 – ~39 cal kBP) is characterised by early peaks in Menispermaceae, *Olea*, Anacardiaceae (incl. *Searsia/Rhus*-type) and Cyperaceae pollen, followed by a general dominance of Asteraceae until 42 cal kBP, when it is replaced by consecutive peaks of *Zygophyllum*, Anacardiaceae and Cyperaceae pollen (Figure 4. 5). Trilete psilate spores are also consistently present, and even abundant during PEL-I. Pollen zone PEL-II (~39 – ~32 cal kBP) is defined by relatively low percentages of Asteraceae pollen, and significant increases in Anacardiaceae, *Dicliptera*-type and Scrophulariaceae pollen. Subsequently, zone PEL-III (~32 – ~27 cal kBP), is characterised by the disappearance of Anacardiaceae and *Dicliptera*-type pollen, the appearance of *Pappea* and spikes in *Zygophyllum* pollen (comprising as much as 91% of the pollen assemblage). PEL-IV (~27 – ~17 cal kBP) is dominated by Asteraceae pollen types. This increase in Asteraceae in PEL-III and PEL-IV is accompanied by the more regular abundance of succulents such as Aizoaceae, *Aizoon*-type and *Euphorbia*. In PEL-IV, Poaceae pollen becomes notably less abundant. Menispermaceae pollen declines and disappears across this period, and more generally, arboreal pollen is largely absent, particularly between ~24 – 17 cal kBP.

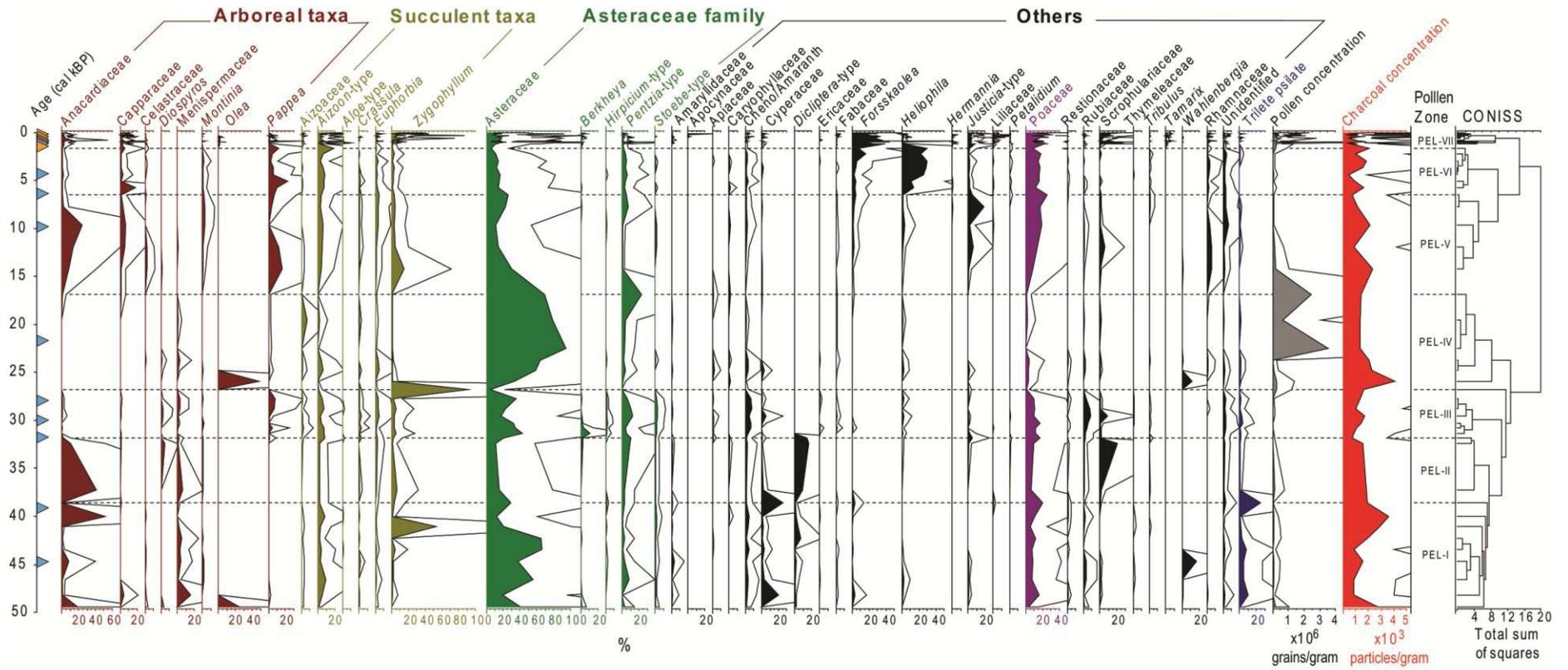


Figure 4. 5 : Diagram of pollen percentage and microcharcoal concentration data (5x exaggeration) from the Pella rock hyrax middens PEL-1-1 and PEL-1-4a. Triangles represent 14C dates (PEL-1-1 in blue, PEL-1-4a in orange).

4.4.2.2. Deglacial and Holocene vegetation composition and dynamics

Pollen zone PEL-V, from ~17 – 6.5 cal kBP, spans the last glacial-interglacial transition (LGIT) and the early Holocene. Beginning at ~14 cal kBP, marked increases in arboreal pollen (particularly *Pappea* and Anacardiaceae, but also Celastraceae in lower percentages) are apparent, as is a sharp decline in Asteraceae pollen types (Figure 4. 5). Poaceae pollen percentages also increase across this zone, reaching a maximum between ~9.6 – 6.5 cal kBP. This increase in Poaceae is paralleled by a decline in the aforementioned arboreal taxa, with Anacardiaceae being reduced to trace levels after ~7 cal kBP. Pollen zones PEL-VI and PEL-VII (~6.5 – 1.7 cal kBP and ~1.7 cal kBP to present, respectively) are most clearly defined by significant increases in *Heliophila* and *Forsskaolea* pollen. *Pappea* pollen percentages increase for a short time in early PEL-VI (peaking at ~5.1 cal kBP), but declines again after ~4.5 cal kBP. Poaceae pollen percentages remain high from ~9.6 cal kBP throughout PEL-VI and PEL-VII. PEL-VII is similar to PEL-VI, although of significantly higher resolution (a result of the higher accumulation rates of the PEL-1-4a midden). Notable are increases in *Forsskaolea* pollen between ~1.5 – 0.8 cal kBP, followed by its decline, and increase in *Zygophyllum* pollen after ~0.8 cal kBP and an increase in Scrophulariaceae pollen from ~0.5 cal kBP until the end of the sequence.

4.4.3. Pollen-based climate reconstructions

Reconstructions of temperature from the Pella pollen data indicate a predictable pattern of cooler glacial and warmer interglacial conditions (Figure 4. 6a). The absolute quantitative accuracy of the pollen-based reconstruction is limited by the number of true temperature dependent taxa (relying heavily on *Stoebe*-type and *Forsskaolea* pollen percentages), which is reflected in the low amplitude of variability. Taking the reconstructed values as relative index, however, it is apparent that the transition from cool glacial-age conditions to near-modern temperatures in the Holocene began at ~19 cal kBP and continued until ~9 cal kBP.

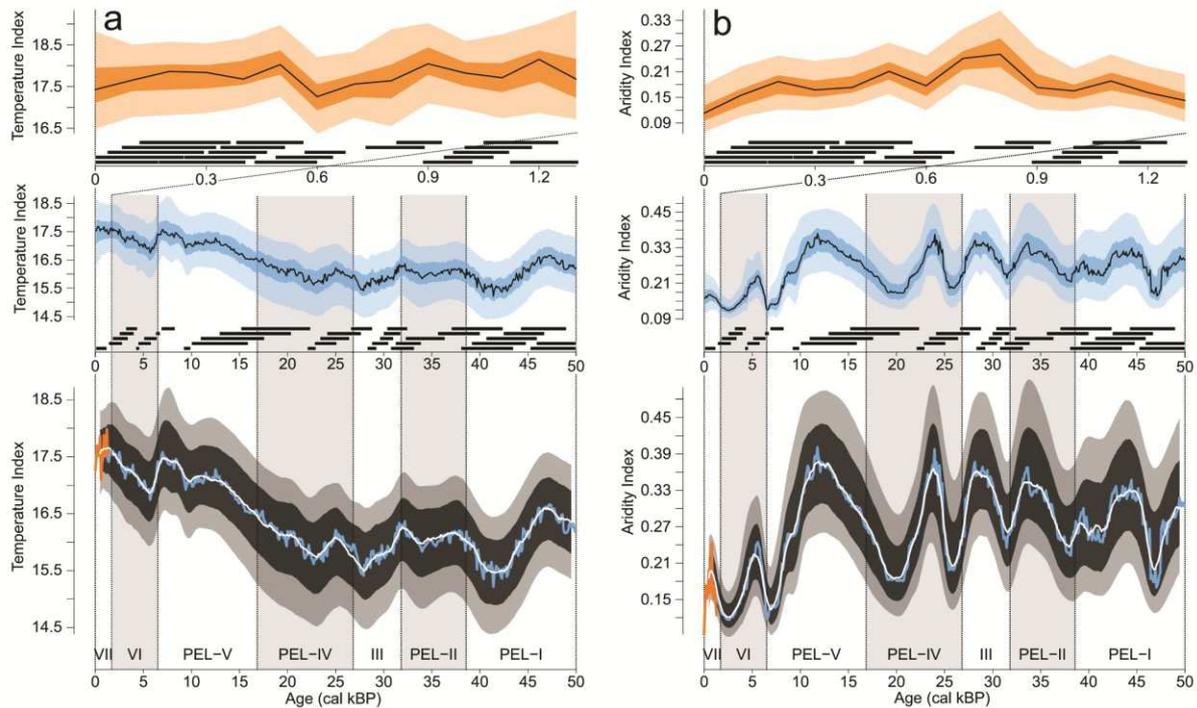


Figure 4. 6: Reconstruction with 30% and 50% errors of mean annual temperature (T_{meanAnn}) (a) and aridity (AI) (b) at Pella derived from the PEL-1-1 and PEL-1-4a pollen data using the CREST software package (Chevalier et al., 2014). Black bars indicate the age range of each pollen sample analysed.

The AI reconstruction (Figure 4. 6b) highlights the major trends inferred from the pollen record, with each of the seven pollen zones generally being associated with specific climate states and/or variability. During the 50,000 years covered by the Pella record, the AI reconstruction presents three different modes. In the oldest section (PEL-I to PEL-IV), the climate is relatively humid but highly variable, with alternating wet (~50, 44, 34, 29 and 24 cal kBP) and dry (~47, 38, 32, 26 and 20 cal kBP) phases. Conditions during the LGM ~24-18 cal kBP appear to be more stable, and relatively dry in comparison with the rest of the glacial period, but reconstructions around the LGM should be treated with some caution as during this period midden accumulation rates were low (with high temporal uncertainties), and the vegetation was dominated by Asteraceae, with a limited number of taxa available for the reconstruction (Figure 4. 5 & Figure 4. 8). PEL-V spans the LGIT and is marked by a broad phase of increased humidity from ~16 - 10 cal kBP followed by a sharp aridification that - with the exception of a relatively wet event around 6 cal kBP - continues across PEL-VI. Conditions were most arid at the end of PEL-VI (~2.5 cal kBP), while the last two millennia (PEL-VII) are associated with increased humidity in the region.

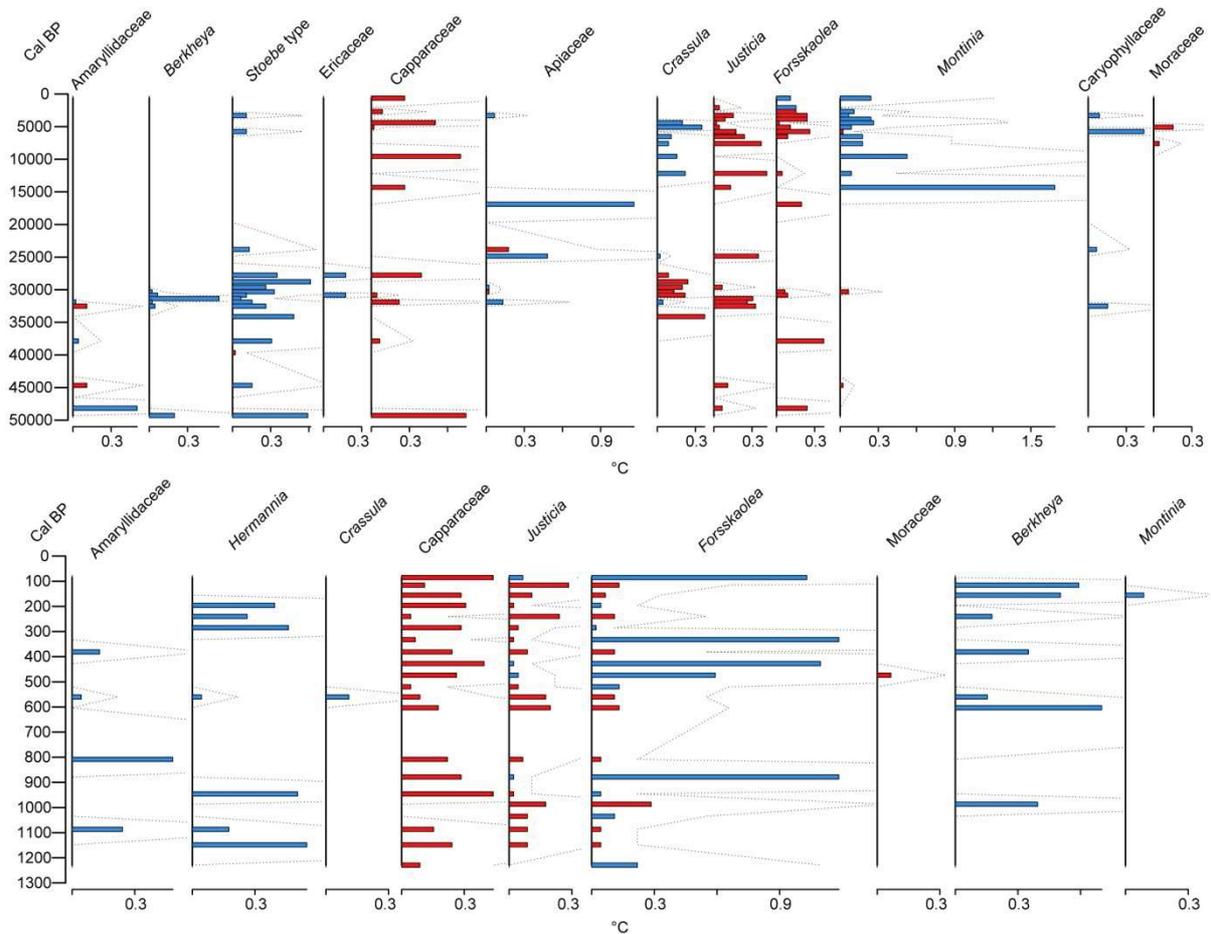


Figure 4. 7: Results of the leave-one-out cross-validation (LOOCV) analysis of the PEL-1-1 and PEL-1-4a pollen sequences for the temperature reconstructions. The importance of the pollen types for the reconstruction is indicated by the length of the bars, as is their influence in terms of reconstructing colder (blue bars) or warmer conditions (red bars) for a given sample.

The influence of each pollen type on the MAT and AI reconstructions is measured by a Leave-One-Out (LOO) approach, which consists of performing reconstructions without the given taxon. The difference between the reconstructions with and without the taxon provides insight into its climatic significance, both in term of sign and amplitude (Figure 4. 7 & Figure 4. 8). It should be noted that the sign of the signal – whether it is negative or positive is relative, depending on the other taxa observed in the assemblage, and the reconstructed climatic context (*e.g. Pentzia*-type is a wet indicator during the Holocene and a dry indicator during the last glacial period, Figure 4. 8).

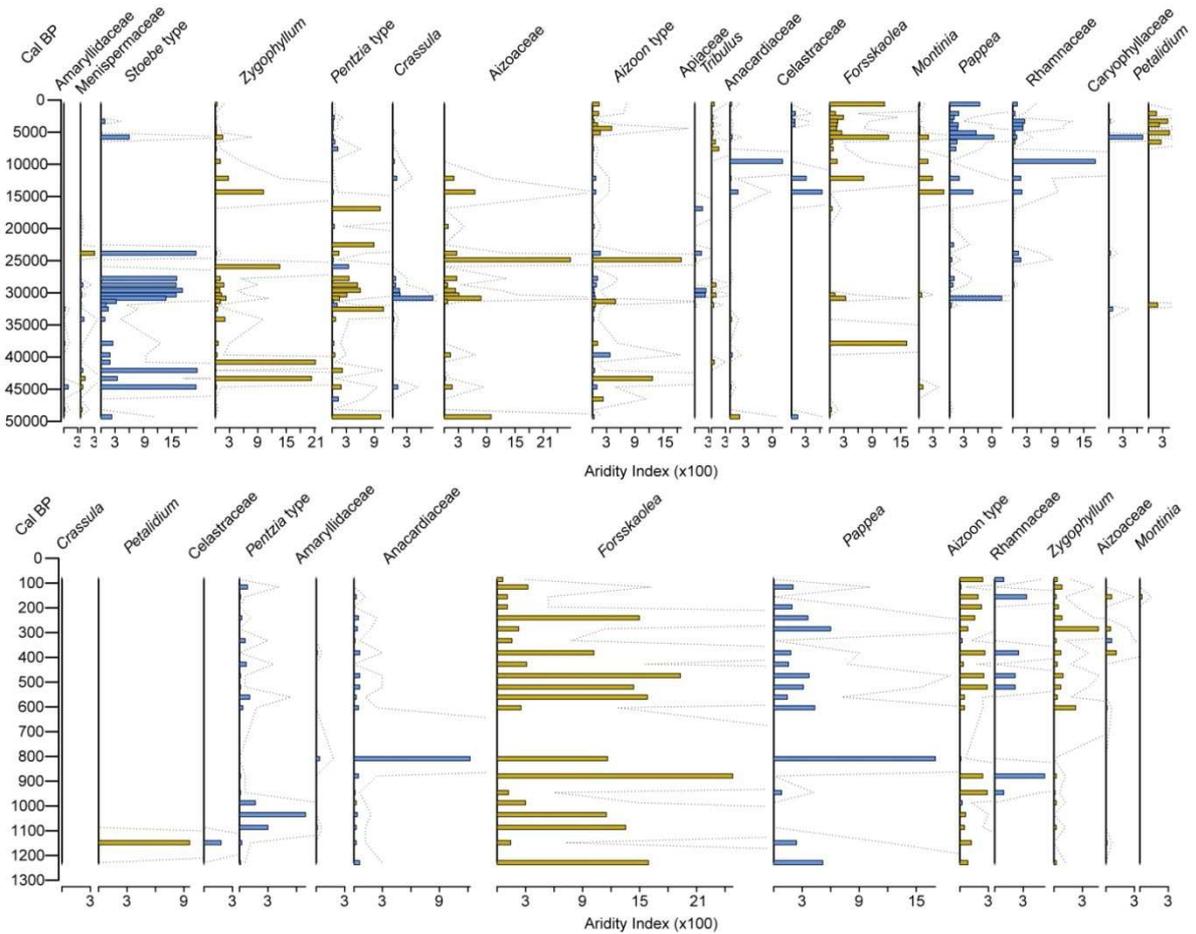


Figure 4. 8: Results of the leave-one-out cross-validation (LOOCV) analysis of the PEL-1-1 and PEL-1-4a pollen sequences for the Aridity Index reconstructions. The importance of the pollen types for the reconstruction is indicated by the length of the bars, as is their influence in terms of reconstructing wetter (blue bars) or drier conditions (brown bars) for a given sample.

4.5. Discussion

4.5.1. Climate and vegetation at Pella

The pollen records from the Pella rock hyrax middens show marked changes in the vegetation at the site, indicating substantial variability in moisture availability and temperature. Using the CREST method (Chevalier et al., 2014) described above, we have quantified these changes by reconstructing AI and MAT, creating records of climate change spanning the last 50 cal kBP.

4.5.1.1. The last glacial period (~50 – 12 cal kBP)

Considered as a whole, the last glacial period at Pella was characterised by cool climates and generally significantly greater moisture availability (Figure 4. 6 a & b). The temperature index reconstructed here shows marked similarities with the palaeotemperature record obtained from the Stampriet Aquifer (Stute and Talma, 1998), with both indicating that deglacial warming began immediately after the LGM, at ~19 cal kBP (Figure 4. 9). It is likely that changes in temperature had an influence on moisture availability (Chevalier and Chase, in press), at least at the scale of glacial-interglacial variability, but differences between the two reconstructions suggest that changes in rainfall amount may have also played a significant role over shorter timescales (Figure 4. 9).

The pollen data and AI reconstruction indicate relatively high amplitude fluctuations in moisture availability during marine isotope stage (MIS) 3 (24 – 59 ka). This is reflected in increased percentages of *Pappea*, Celastraceae and Anacardiaceae pollen during wetter phases, and more abundant succulents such as Aizoaceae and *Aizoon*-type pollen during relatively drier phases. It cannot be clearly differentiated from the pollen data whether the dominant vegetation at the site during this period was Nama-Karoo or Desert, but 1) its position on the modern ecotone, 2) the indications for increased humidity and 3) the abundance of Asteraceae pollen would suggest an expansion of the Nama-Karoo during this time. While Asteraceae and Poaceae are too widespread to be used for the reconstruction of specific palaeoclimatic variables, they are the dominant elements of the Nama-Karoo vegetation, and their relative abundance may in a broad sense, within this biome be considered as proxy for general aridity. Across the Nama-Karoo, Poaceae (Asteraceae) becomes more dominant with increasing humidity (aridity), with the Nama-Karoo grading into the Grassland Biome as rainfall increases to the east in South Africa. During the last glacial period, the humid conditions before ~27 cal kBP promoted the general development of grasses, and a relatively mesic Nama-Karoo vegetation. This is likely the result of more/more regular rain or a reduction in potential evapotranspiration, which resulted in increased water-availability for shallow rooting grasses. The increased aridity during the LGM sees a significant decline in grasses, along with most arboreal taxa, leaving a predominantly asteraceous vegetation, similar to drier regions of the Nama-Karoo. The humid period following the LGM is marked by the recurrence of arboreal taxa such as Anacardiaceae, Celastraceae, Capparaceae and *Pappea*, and a clear increase in grasses as Asteraceae pollen percentages decline sharply.

It is interesting to note that this phase of increased humidity correlates with a major period of dune activity in the adjacent southwestern Kalahari, which has been identified as occurring between 15 – 9 ka (Telfer and Thomas, 2007). These dune data, and inferences based on marine pollen records (Shi et al., 2000), had been thought to indicate drier conditions during this period, but these conclusions are inconsistent with the findings in this paper, and those from other terrestrial sites along the southwest African margin (Chase et al., 2015; Chase et al., 2010; Chase et al., 2009), and other marine records that indicate reduced wind strength/upwelling at this time (Farmer et al., 2005; Kim et al., 2003; Pichevin et al., 2005; Stuut et al., 2002). This apparent contradiction has been highlighted by Chase et al. (2010), who have suggested that the “aridification” (Shi et al., 2000) observed in the marine records may be dominated by a reduction in pollen source area as a function of reduced wind strength (resulting in a preponderance of arid Namib Desert pollen), and that the elevated number of dune ages from this period in fact reflects a cessation of dune activity similarly related to reduced wind strength and the subsequent preservation of these sediments in the more stable Holocene landscape (Chase and Thomas, 2006).

Comparing mean climate states for the glacial and interglacial periods, glacial AI values are substantially higher (0.28 for the period from 10 – 50 cal kBP, and 0.18 for the Holocene). While the reconstructed AI value for the Pella site is ~0.1 higher than the values derived from the data of Trabucco and Zomer (2009), this may be explained by either microclimatic/hydrologic factors related to the east-facing aspect of the site, its architecture and position in a shallow drainage feature (Figure 4. 3 & Figure 4. 2d), or reflect complications in the reconstructions as the log-normal pdf_{sp} reach 0. Correcting for this, moisture availability in the Pella region during the last glacial period was apparently more akin to the relatively humid eastern Nama-Karoo, with phases of peak humidity (AI values of ~0.35) perhaps even approaching the transition to the Grassland Biome.

One aspect of glacial vegetation dynamics in this region has been the question of whether the mediterranean Fynbos Biome expanded into the region as a result of an equatorward shift of the westerly storm track and regional ‘winter-rainfall zone’ driven by an expanded circumpolar vortex (Chase and Meadows, 2007; Cockcroft et al., 1987; van Zinderen Bakker, 1976). In the absence of long, continuous terrestrial sequences, fossil pollen recovered from marine cores (Shi et al., 2000; Shi et al., 2001; Urrego et al., 2015) has been used to infer vegetation change in southwestern Africa across the last glacial-interglacial cycle, with conclusions generally supporting the early conceptual models (e.g. van Zinderen Bakker, 1976). The significance of these data, however, remains a subject of debate, with

points of contention relating to: 1) the choice of taxa that are considered as fynbos indicators, and 2) the taphonomy of the pollen sequences.

The Fynbos Biome experiences a predominantly winter rainfall regime and a cool growing season. As such, it is characterised by taxa with affinities for lower temperatures such as Ericaceae, Restionaceae, Proteaceae, *Artemisia*, *Stoebe*-type and *Passerina*. This has led some researchers to consider elevated percentages of these taxa in glacial-age sediments from Namibian marine cores as evidence for expansions of the Fynbos Biome (Shi et al., 2000; Shi et al., 2001; Urrego et al., 2015). It must be kept in mind, however, that these taxa are not restricted to the Fynbos Biome. Rather, particularly in the case of *Artemisia* and *Stoebe*-type (*Stoebe* and *Elytropappus rhinocerotis*) (Urrego et al., 2015), these plants occur across southern Africa where there is enough moisture to meet their requirements, and temperatures during the wet season are below 21°C (Rutherford et al., 2012; Rutherford et al., 2003; SANBI, 2003; Urrego et al., 2015). A temperature depression of 4 – 6°C during the last glacial period, as estimated from regional palaeotemperature records (Chevalier and Chase, 2015; Kulongoski and Hilton, 2004; Stute and Talma, 1998; Talma and Vogel, 1992; Truc et al., 2013), would have led to a significant increase in the prominence and spatial distribution of these taxa, as is indicated in pollen records from across the subcontinent (Coetzee, 1967; Scott, 1982b, 1989, 1999; Scott et al., 2004; Scott et al., 2012).

Of the taxa that are considered to be fynbos indicators, Restionaceae is the closest to being exclusive to the biome. As such, it has been considered to be a key element in determining possible palaeo-expansions of the Fynbos Biome by Shi et al. (2000; 2001). However, Restionaceae are wind pollinated, and data from surface samples indicate that it can represent a significant percentage of the total pollen rain far downwind of the plant's distribution (Rutherford et al., 2012; Rutherford et al., 2003; SANBI, 2003). Unlike the pollen assemblages from the marine sequences, wherein Restionaceae pollen is abundant, Scott et al. (2004) found no pollen of these taxa in similar age hyrax middens from the Brandberg of central Namibia. This discrepancy between terrestrial and marine records led Scott et al. to suggest that the intensification of the atmospheric and oceanic circulation systems associated with the Benguela Upwelling System during the last glacial period (cf. Farmer et al., 2005; Little et al., 1997; Pichevin et al., 2005; Stuut et al., 2002) would have increased the long-distant transport of pollen from the Fynbos Biome, and that the biome itself did not expand significantly. While it could be argued that as the Brandberg is ~1000 km north of the present limits of the Fynbos Biome, and a significant expansion of the biome may still have occurred, the data from the Pella middens, as well as that from the

Richtersveld mountains to the west (Scott et al., 1995), suggests that this was not the case. Only ~150 km northeast of the northern fynbos remnants in the Kammiesberg mountains, Restionaceae pollen at Pella never exceeds 1% of the pollen assemblage (Figure 4. 5). This indicates that any expansion of the Fynbos Biome must have been very restricted, and that the elevated percentages of ‘fynbos’ pollen observed in marine cores more likely reflects: 1) generally cooler continental conditions, and 2) an increase in the long-distance transport of pollen with increased atmospheric and oceanic circulation intensity during the last glacial period.

4.5.1.2. The Holocene (12 cal kBP to present)

Interestingly, while the vegetation of the last glacial period seems to be broadly characterised by dynamics predicted for the Nama-Karoo Biome, the relationship between climate and key pollen types such as Asteraceae and Poaceae changes fundamentally during the Holocene. The increase in Poaceae pollen and decrease in Asteraceae pollen during the period of increased humidity following the LGM (from ~16 – 10 cal kBP) may be interpreted as an increase in water-availability following the above-described model. However, despite the abrupt aridification after 10 cal kBP, and the significantly drier conditions of the Holocene (observed also at Eksteenfontein in the nearby

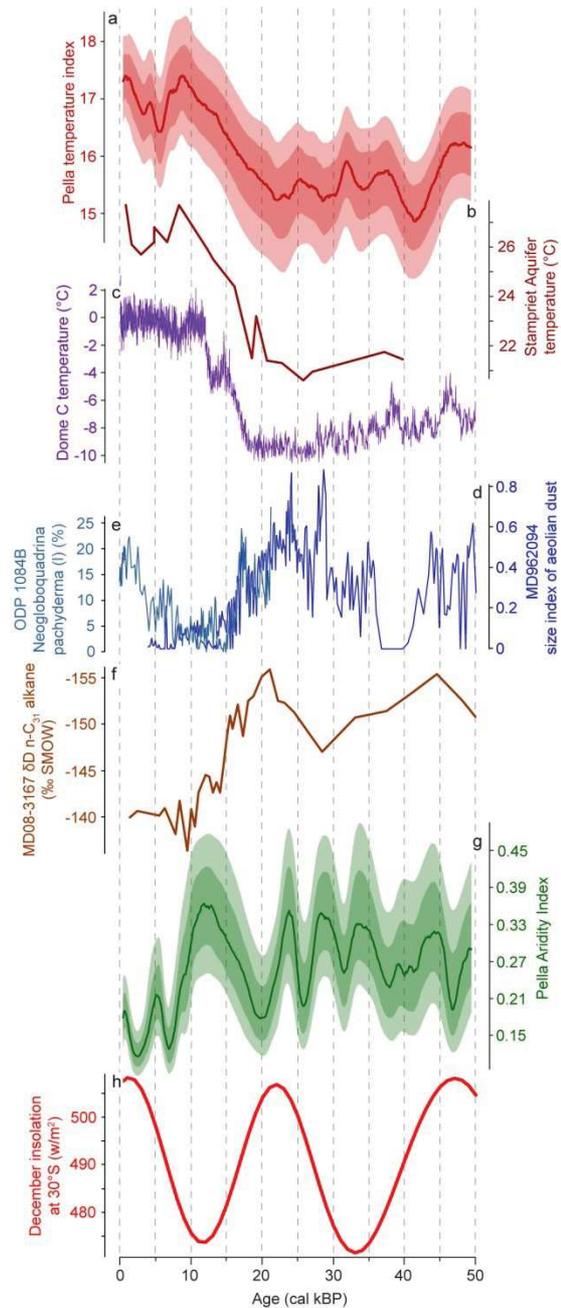


Figure 4. 9: Comparison diagram of the Pella temperature index (a), the palaeotemperature record from the Stampriet Aquifer (b; Stute and Talma, 1998), the palaeotemperature record from the Dome C Antarctic ice core (c; Jouzel et al., 2007), marine records of wind strength in the Benguela Upwelling System derived from foraminifera (d; Farmer et al., 2005) and particle size data (e; Stuet et al., 2002), the δD record from marine core MD08-3167 (f; Collins et al., 2014), the Pella Aridity Index record (g), and December insolation at 30°S (h; Berger and Loutre, 1991).

Richtersveld (Scott et al., 1995)), Poaceae pollen percentages remain at high level throughout the last 10,000 years. To explain this apparent inconsistency, the full environmental gradient across South Africa needs to be considered. As mentioned, with increased precipitation eastward in South Africa the Nama-Karoo becomes increasingly grassy, eventually transitioning into the relatively humid Grassland Biome. To the northwest of the Pella site precipitation declines sharply, and there are insufficient groundwater resources to support the widespread development of shrubs such as the Asteraceae that define the arid eastern Nama-Karoo. As this component of the vegetation disappears, grasses once more become dominant in the Desert Biome (Figure 4. 2 a), exploiting the rare rains that do fall.

Considered from this perspective, it appears that the arid conditions that began at the beginning of the Holocene resulted in a shift in the Desert - Nama-Karoo ecotone, with the Desert Biome expanding along the Orange River Valley from its core along the coast. During this period, increases in Asteraceae pollen may indicate slightly more humid conditions, as indicated by the AI reconstructions, and at least minor expansions of the Nama-Karoo.

4.5.1. Palaeoenvironmental history of the southern Namib

Considered in their regional context, results obtained from the Pella hyrax middens shed considerable light on the timing and mechanisms of climate change in the southern Namib Desert during the last 50,000 years. Despite the limited amplitude of the temperature reconstruction, as discussed above, the major temperature trends are consistent with the data from the nearby Stampriet Aquifer (Stute and Talma, 1998). Indications of increased humidity between 32 – 26 cal kBP, 25 – 20 cal kBP and 14 – 10 cal kBP from fragmentary wetland and lacustrine sediments from further north and west in the Namib Desert and Richtersveld (Lancaster, 1984; Lancaster, 1986; Lancaster, 2002; Scott et al., 1995; Teller and Lancaster, 1985; Teller and Lancaster, 1986) are generally consistent with phases of increased humidity at Pella, with the caveat that such correlations remain duly speculative, in light of the nature of the records and the low resolution of the Pella record during the LGM. A key question regarding these findings is what drove this glacial-age increase in humidity. While such changes are often considered to be the result of increased rainfall amount, studies from eastern South Africa have shown that temperature may be at least as important as rainfall amount in regulating water availability (Chevalier and Chase, in press; Scott and Thackeray, 1987; Truc et al., 2013). First order changes across the last 50,000 years certainly

appear to fit this model, with cool, humid conditions during the last glacial period, and warm, arid conditions during the Holocene. Environmental variability in the broader region within the last glacial period has been attributed to direct insolation forcing following the precessional cycle. Originating in findings from the Tswaing Crater (Partridge et al., 1997), studies of pollen (Urrego et al., 2015), charcoal concentrations (Daniau et al., 2013) and leaf-wax δD and $\delta^{13}C$ (Collins et al., 2014) from Namibian marine cores have also observed precessional cycles in their records, and inferred phases of increased humidity. In comparison, the data from Pella show no such correlation with the precessional cycle, with, if anything, a tendency for phases of increased humidity to occur during phases of reduced insolation (Figure 4. 9). These findings challenge the assertion that the marine records reflect continental conditions and climate dynamics, indicating that they either reflect conditions in particular subregions, or that taphonomic rather than climatic controls are dominant determinants of the observed signals, as described above.

As direct insolation forcing does not adequately account for the significant AI variability observed at Pella during either the last glacial period or the Holocene, we compare our results with other indicators of changes in regional circulation systems. Of these, coastal upwelling, through the suppressed convection and the blocking of moisture-bearing systems from the east, has been shown to be an important factor in determining late Quaternary climate change in southwestern Africa (Chase et al., 2010; Chase et al., 2009). Comparing the Pella data with grain size analyses of Stuut et al. (2002) and the foraminifera data of Farmer et al. (2005), a complex, but coherent relationship can be observed. Throughout MIS 3 and the LGM (50 – ~18 cal kBP), phases of increased humidity at Pella occur when atmospheric circulation intensity – and thus upwelling – increases (Figure 4. 9). Of these episodes, those between 35 – 50 cal kBP correlate strongly with temperature changes record in the Antarctic ice core from Dome C (Jouzel et al., 2007), with cooler periods being characterized by stronger winds (Farmer et al., 2005; Stuut et al., 2002). This relationship between cool conditions and increased upwelling continues until the beginning of the Holocene, although the link appears to be more generalized between 20 – 35 cal kBP. As increased upwelling is expected to have an aridifying influence in southwestern Africa, we surmise that either its influence did not extend this far inland and/or the related changes in temperature reduced potential evapotranspiration during these periods, counteracting any reductions in precipitation. The period between 16 – 10 cal kBP deviates from the pattern of humid periods occurring under cooler conditions. After 17 ka, the warming recorded at Dome C, the

Stampriet Aquifer and Pella is paralleled by a sharp decrease in Benguela upwelling intensity (Figure 4. 9). Pella experiences an increase in humidity during this transitional period between glacial and interglacial modes, likely as a result of dramatically reduced upwelling, allowing for increased local convection and the incursion of easterly air masses, while conditions were still relatively cool, limiting potential evapotranspiration. During the Holocene, high temperatures resulted in significantly more arid environments. Under these conditions, increases in upwelling strength are seen to intensify the arid conditions at Pella, with periods of enhanced upwelling and aridity occurring between $\sim 8 - 6$ cal kBP and $\sim 3.5 - 1.5$ cal kBP (Figure 4. 9).

4.6. Conclusions

Analyses of fossil pollen data from subsections of a rock hyrax midden from Pella, South Africa provide a 50,000-year record of vegetation and climate change from the southern Namib Desert. Key findings include:

- The last glacial period was characterised by increased, but variable, water availability relative to Holocene, with changes in temperature and potential evapotranspiration playing a significant role in the hydrologic balance.
- During the last glacial period, the site was within the Nama-Karoo Biome, wherein increased aridity is reflected by an increase in Asteraceae pollen and a decrease in grasses.
- Episodes of increased humidity during the last glacial period occur during periods of increased upwelling. As increased upwelling has generally been found to increase aridity along the southwest African coast, concurrent declines in temperature and potential evaporation are implicated as significant drivers in these changes in the regional water balance.
- Low Restionaceae pollen percentages ($\leq 1\%$) indicate no significant expansion of Fynbos Biome during the last 50,000 years.
- The last glacial-interglacial transition ($\sim 16 - 10$ cal kBP) is characterised by increasing temperatures, markedly reduced upwelling, and increased water availability at Pella. While increasing temperatures would have resulted in increased drought stress, the influence of low upwelling intensity may have counteracted this by allowing for increased local convection and the incursion of moisture-bearing air masses.

- As temperatures reached Holocene maxima, conditions became significantly drier, and the Desert Biome expanded to encompass the Pella region.
- Under warm Holocene conditions, phases of increased aridity occur during periods of enhanced upwelling intensity.

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Appendix

Table 4. 1: Radiocarbon ages and calibration information for the Pella-1-1 and Pella-1-4a hyrax middens.

Sample	Avg. depth (mm)	¹⁴ C age yr BP	1 sigma error	calibration data	95.4 % (2σ) cal age ranges	relative area under distribution
PEL-1-1						
UBA-22377	2.99	1302	26	SHCal13	cal BP 1156 - 1270	0.752654
					cal BP 1091 - 1153	0.247346
UBA-22378	28.38	3950	29	SHCal13	cal BP 4235 - 4435	0.998603
					cal BP 4194 - 4195	0.000652
					cal BP 4185 - 4186	0.000745
UBA-22379	46.96	5767	33	SHCal13	cal BP 6434 - 6635	0.978573
					cal BP 6414 - 6426	0.021427
UBA-22380	57.89	8720	39	SHCal13	cal BP 9538 - 9747	0.994191
					cal BP 9753 - 9761	0.005809
UBA-22381	89.75	18408	94	SHCal13	cal BP 21942- 22446	1
UBA-22382	121.76	23725	163	SHCal13	cal BP 27501 - 28086	1
UBA-22383	132.6	25785	194	SHCal13	cal BP 29409 - 30539	1
UBA-22384	153.04	27717	239	SHCal13	cal BP 31062- 32043	1
UBA-22385	162.75	34526	533	SHCal13	cal BP 37632- 40279	1
UBA-22386	190.49	41451	785	SHCal13	cal BP 43380- 46159	1
PEL-1-4a						
UBA-21248	5.46	59	27	SHCal13; SHZ1_2	*cal BP -6 - -5	0.151
					*cal BP 31 - 56	0.554
					*cal BP 122 - 132	0.295
UBA-22397	27.11	314	23	SHCal13	cal BP 365- 443	0.527392
					cal BP 292- 331	0.472608
UBA-22398	48.92	716	23	SHCal13	cal BP 360- 668	0.522551
					cal BP 564- 600	0.477449
UBA-22399	97.78	998	25	SHCal13	cal BP 800- 922	1
UBA-22400	110.67	1084	24	SHCal13	cal BP 918- 979	0.998805
					cal BP 1039- 1040	0.001195
UBA-21249	133.51	1320	27	SHCal13	cal BP 1171- 1278	0.906224
					cal BP 1095- 1144	0.093776

*Ages calibrated with Southern Hemisphere Zone 1 and 2 bomb curve extension; 1σ ranges given

PDFs of taxa used for temperature reconstructions

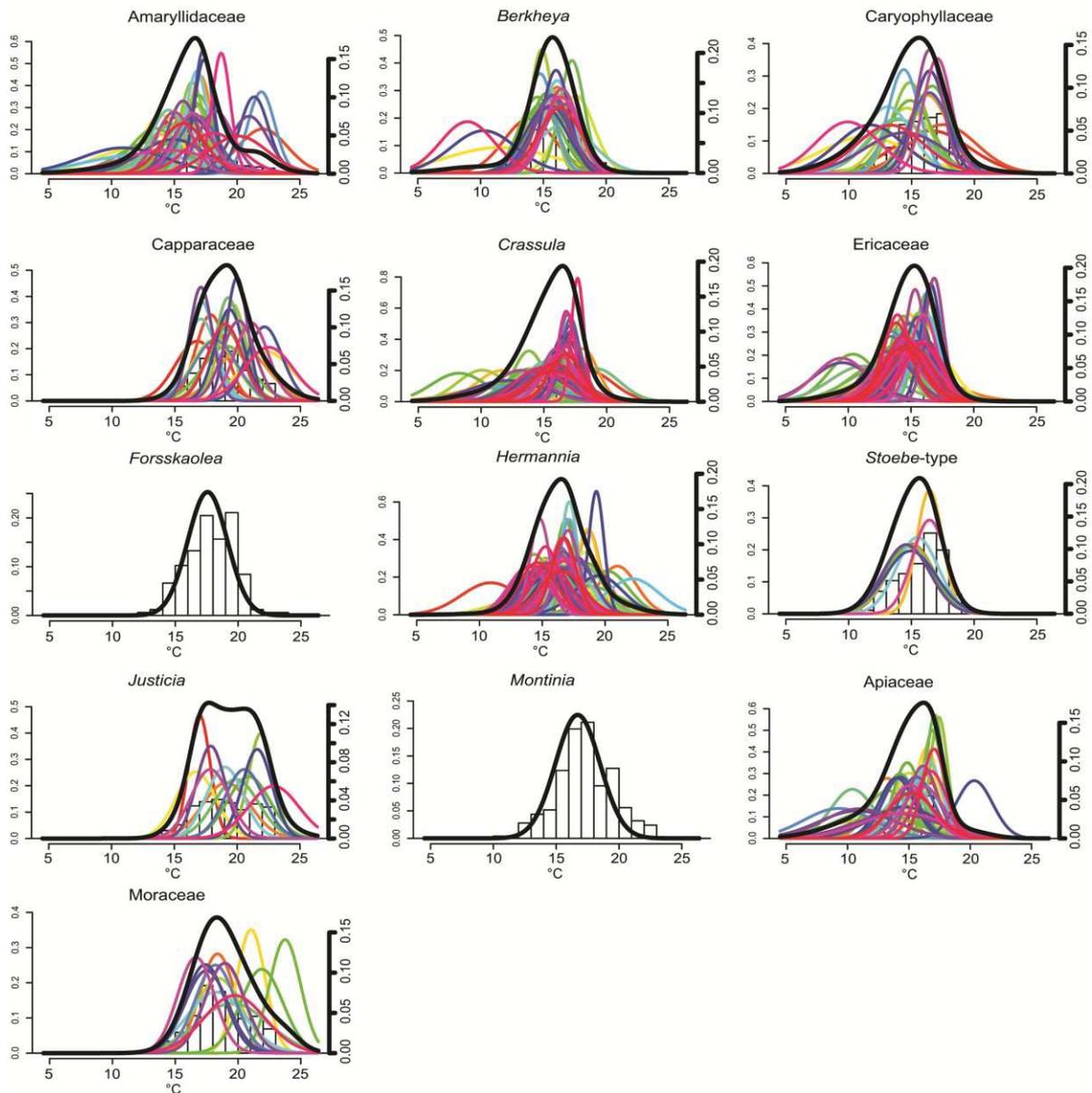


Figure 4. 10: PDFs of taxa used for temperature reconstructions.

PDFs of taxa used for Aridity Index (AI) reconstructions

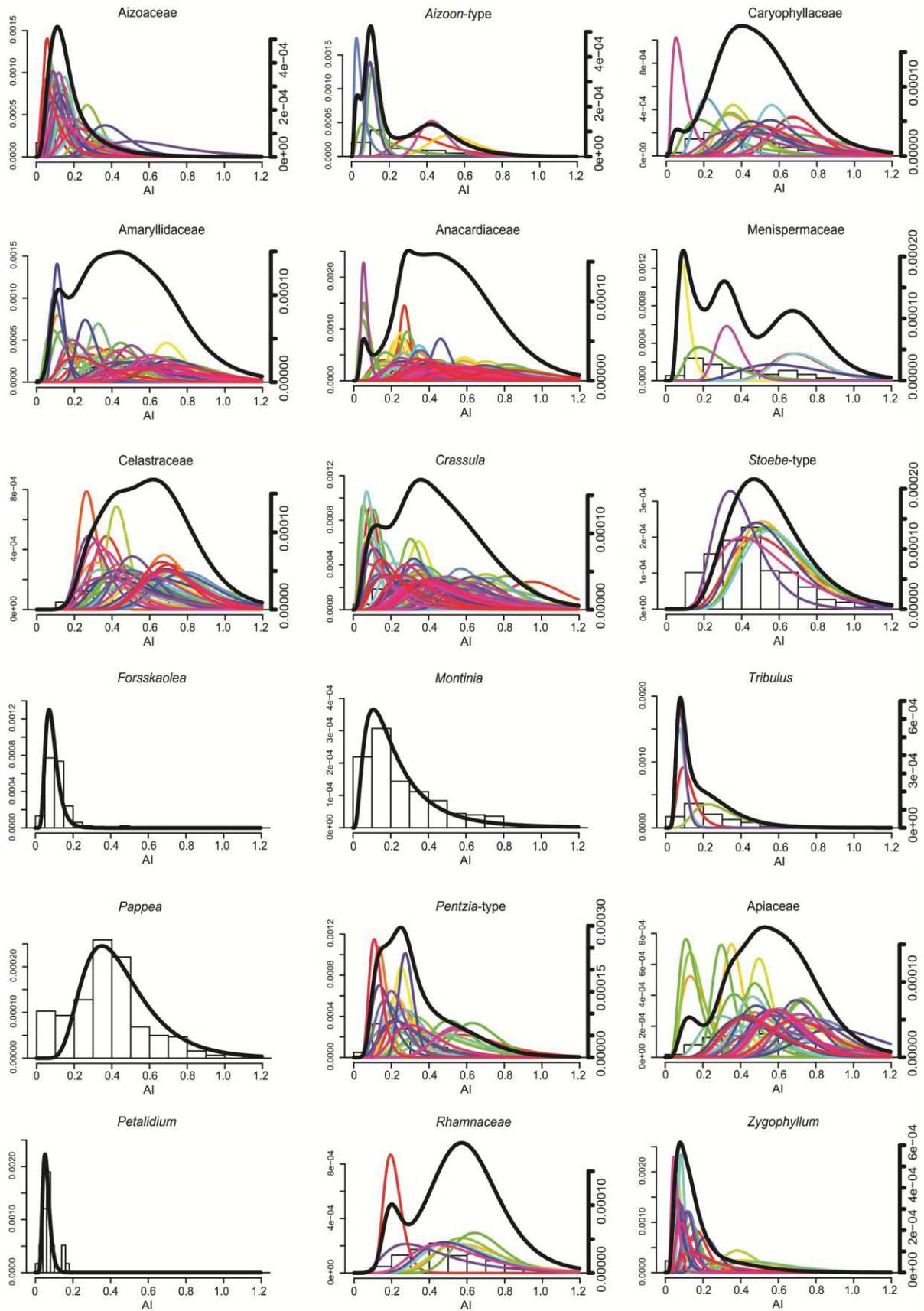


Figure 4. 11: PDFs taxa used for Aridity Index (AI) reconstructions.

Chapter V: Fossil pollen and micro-charcoal evidence of the last 38,000 years in the central Namib Desert, Zizou midden, Namibia

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Abstract

This paper presents the first continuous pollen record from the central Namib Desert spanning the last 38,000 years. Two rock hyrax middens were radiocarbon dated and sampled for pollen and microcharcoal analysis. The results show significant differences between glacial-age and Holocene vegetation types. During the last glacial period, Asteraceae pollen (including *Stoebe*-type and *Artemisia*-type) is prevalent, with higher pollen accumulation rates. This vegetation is similar to current karroid vegetation type located to the east of study area. After ~18 cal kBP, there is a clear shift towards the grass dominance observed at the site today, characteristic of the sparse grasslands of the Namib Desert Biome. These results indicate that the climate during the last glacial period was more humid, and the occurrence of shrubs/small trees was enabled by the existence of accessible groundwater resources. We consider that increased humidity between ~34 – ~18 cal kBP was likely a response to cooler temperatures and thus less drought stress during the LGM, as indicated by greater numbers of *Stoebe*-type. As with other terrestrial records from the Namib, no elements of the Cape flora are found to support the hypothesis of a significant expansion of Fynbos vegetation during the last glacial period.

5.1. Introduction

The central Namib Desert is characterised by arid to hyperarid climates, and the vegetation is often sparse or absent. Palynological data from the Namib Desert region are notably scarce (cf. Chase and Meadows, 2007; Lancaster, 2002), and as a result very little is known about long-term climate and vegetation dynamics in the region. The region's environment has precluded the preservation of organic material and thus most palaeobotanical and microcharcoal data have been obtained from marine cores (Shi and Dupont, 1997; Shi et al., 1998, 2000; Shi et al., 2001; Daniau et al., 2013; Dupont et al., 2006; Dupont et al., 2004; Dupont, 2004). It has been suggested that winter-rain vegetation may have expanded as north as 21°S during the Last Glacial Maximum based on higher percentages of temperate elements such as Asteroideae (tuboliferous composites), Ericaceae, and Restionaceae (Shi et al., 2000; Shi et al., 1998). During the same period, Shi et al. (2000) suggested that abundant pollen of desert, semi-desert, and temperate plants show arid, cold conditions in southwestern Africa due to enhanced upwelling. However, pollen transport into the marine sediments involves wind, rivers, and ocean currents. These pollen transportation agents could have modified the pollen source areas. Unlike marine cores, terrestrial pollen archives more clearly reflect local/regional vegetation depending on the type of archives, for instant, lake sediments, spring deposits or hyrax middens. In the arid Namib Desert, hyrax middens are an important palaeoenvironmental archive because they contain several palaeoenvironmental evidences such as stables isotopes, plants biomarkers, microcharcoal and pollen (Chase et al., 2012).

In terms of terrestrial palaeoecological records, while some pollen records have been recovered from Namibia, they are generally restricted to the mid- to latest Holocene (Gil-Romera et al., 2006; Gil-Romera et al., 2007; Scott, 1996; Scott et al., 1991), with only records from the Brandberg mountain (Scott et al., 2004) providing snapshots of glacial-age vegetation in the Namib Desert. Recently, pollen data from the southern Namib, at Pella, South Africa, indicate more humid condition during the last glacial period, favouring the development of Name-Karoo vegetation, while increasing warmth and aridity led to an expansion of the Desert Biome during the Holocene (Lim et al., 2016). The Brandberg pollen record suggested that vegetation during the last glacial period was characterised by higher percentages of Asteraceae elements (including *Stoebe*-type, *Artemisia*-type, *Pentzia*-type) and *Olea* whereas grasses, woody elements (*Dombeya*, *Euclea*), and succulent taxa (Aizoaceae-type) were more important during the Holocene (Scott et al., 2004). Maximum percentages of

Stoebe-type accompanied by high percentages of *Olea*, *Artemisia*-type, spores of ferns during the Last Glacial Maximum (LGM) suggest moister conditions, possibly as result of lower evapotranspiration during last glacial period and not necessarily increasing rainfall. Higher *Stoebe*-type was also recorded in spring deposit in Succulent Karoo Biome during the late Pleistocene and it was suggested that this pollen type is an indicator of cooler past temperatures (Scott et al., 2012; Scott et al., 1995).

The interpretation of pollen data from southern African remains problematic, due to the differences in pollen identification resolution as well as the different perspectives of how palynologists use pollen taxa as climate indicator. For instant, both marine and terrestrial records found the high percentages of Asteroideae during the last glacial period, but they interpreted it differently (Scott et al., 1995; Scott et al., 2004; Shi et al., 2001; Shi et al., 1998). The issue is that Asteraceae family in southern Africa contains hundreds of species and palynologists do not identify pollen of this family in the same way. Some identify this family into different pollen types and others record it as simply as Asteraceae undifferentiated. Dupont (2011) defined Asteraceae as semi-desert taxa and Poaceae as an indicator of Savanna vegetation in order to infer changes in vegetation patterns in southern Africa. These different perspectives have created a significant debate regarding the interpretation of individual records, and what information they may provide regarding past vegetation and climate change in the region.

We present here the first continuous pollen records from the central Namib Desert spanning the last 38,000 years. Considering the similarities between the ecosystem at Zizou and that at Pella midden site in the southern Namib (about 600 km apart from each other) (Chapter IV), it is interesting to compare how the vegetation at these two midden sites have shifted during the last glacial period and the Holocene. We aim to investigate how has vegetation responded to changes in climatic conditions at biome scale and were there any expansions of winter-rain vegetation at the site, e.g. Restionaceae in last glacial pollen assemblage at Zizou if there was an expansion northward of Fynbos biome during the cool and humid glacial period in the Namib desert.

5.2. Study regions and site description

The Zizou midden site (24°04'17.83"S, 15°58'11.50"E, 1121 m amsl.) is located 20 km south of the town of Solitaire, on the eastern margin of the Namib Sand Sea (Figure 5. 1a). This midden site is located near the foot of the Great Escarpment and it is approximately 150 km from the Atlantic Ocean. Mean annual rainfall at study area is around 130 mm /yr. To the west, precipitation decreases steadily towards the coast, and in the uplands immediately to the east it increases to ~200-250 mm/yr (Hijmans et al., 2005). Most of the rain falls during summer months (JFM) (Figure 5. 2 c). According to Chase and Meadows, 2007, our study area is in summer rainfall zone. Temperatures at the site presently ~18°C (Hijmans et al., 2005) are moderated by the effect of cold Benguela current near the coast, and increase inland. The evaporation rates at Zizou midden site are high, ranges from 3400 to 3600 $\text{mm}\cdot\text{y}^{-1}$ (ACACIA, 2002). The measurement of water deficit (mean annual precipitation minus evaporation rate) is also high at the study area. Aridity index values indicate that study area is located in arid region (AI, ~0.05, Figure 5. 2b)

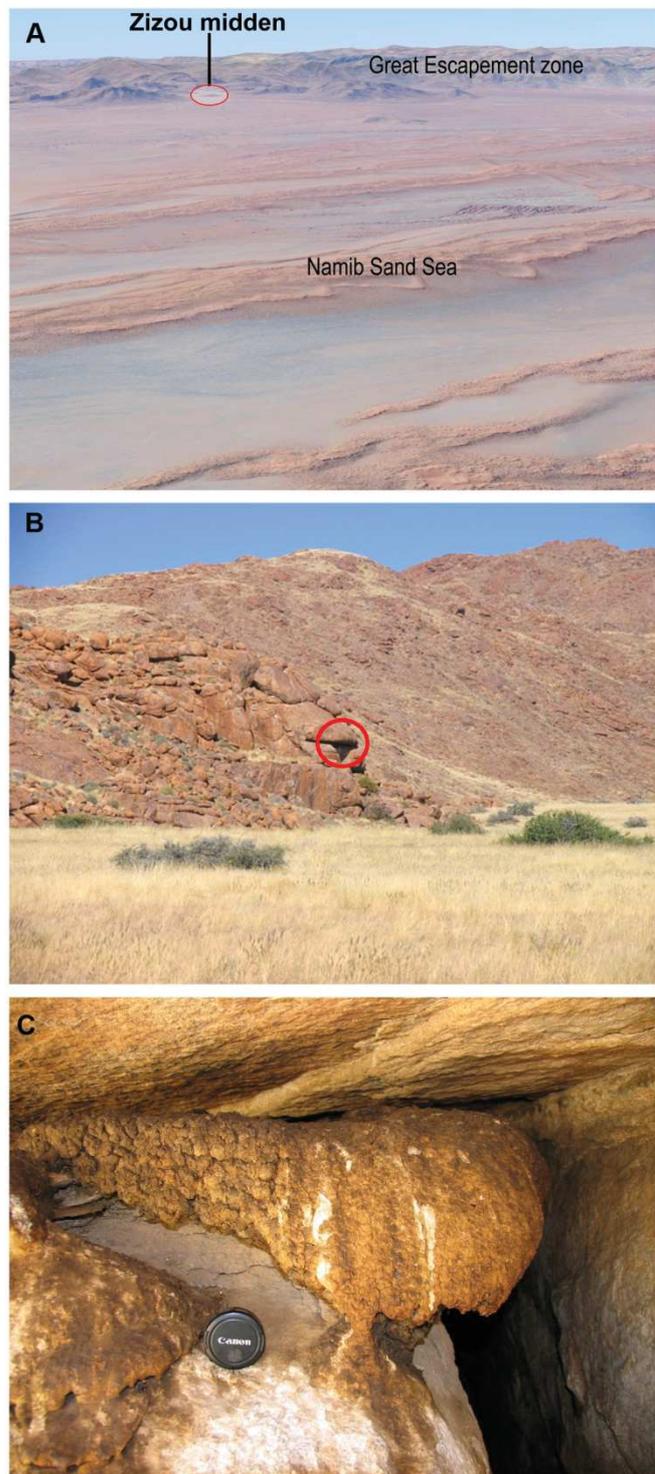


Figure 5. 1: Images of location of study area between the Namib Sand Sea and Escapement zone (a), the closer view of Zizou midden (red circle indicates location of midden) from the west (b), Zizou midden (ZIZ-1-1) with 72 mm camera lens cover for scale (c).

(Trabucco and Zomer, 2009).

Zizou (Figure 5. 6a) is located at the ecotone between the Namib Desert and Nama-Karoo biomes, making it an ideal site to study past vegetation change. In general, Nama-Karoo vegetation is characterised by dwarf shrubs, particularly Asteraceae, and grasses. In the Namib Desert, annual grasses dominate the vegetation because there is very little rainfall to support perennial growth forms (Figure 5. 3c). To the east, where mean annual precipitation exceeds ~ 250 mm/yr savanna vegetation, characterised by mixed tree and grass cover, develops.

The Zizou midden site itself is classified as being in Namibian Savanna Woodland according the WWF's ecoregions classification (WWF, 2017). The vegetation in this ecoregion is divided into three parts: Mopane savanna (north), semi-desert and savanna transition (central) and dwarf shrub savanna (south). At the southern part, the vegetation became more open with grasses and the Karoo shrubs. Arboreal species such as *Acacia giraffae*, *A. karoo*, *Tamarix usneoides*, *Euclea pseudebenus*, *Searsia lancea*, and others found along the rivers. Typical species in this vegetation type

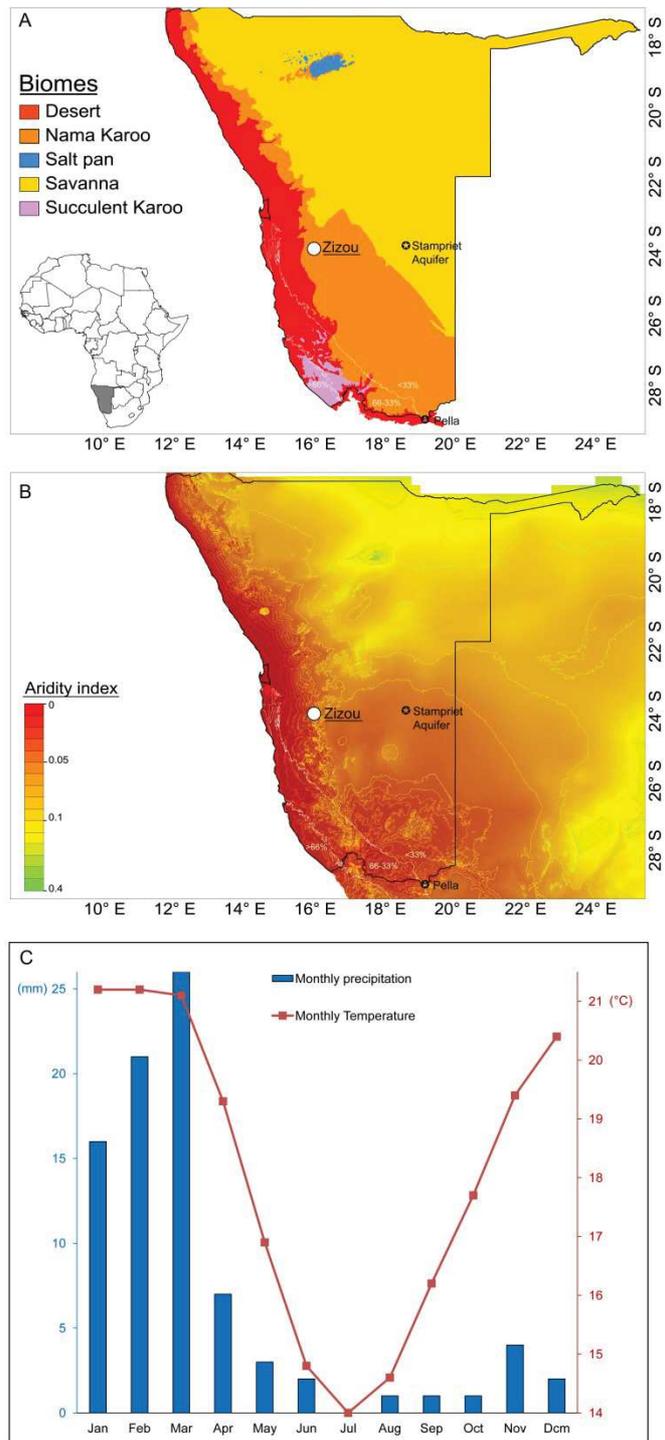


Figure 5. 2: Map of the biomes of Namibia with location of the Zizou rock hyrax midden site (a). The data for vegetation type is derived from Namibia ('ACACIA', 2002). Aridity index (Trabucco and Zomer, 2009) (b). Graphic indicates the monthly precipitation and temperature (c).

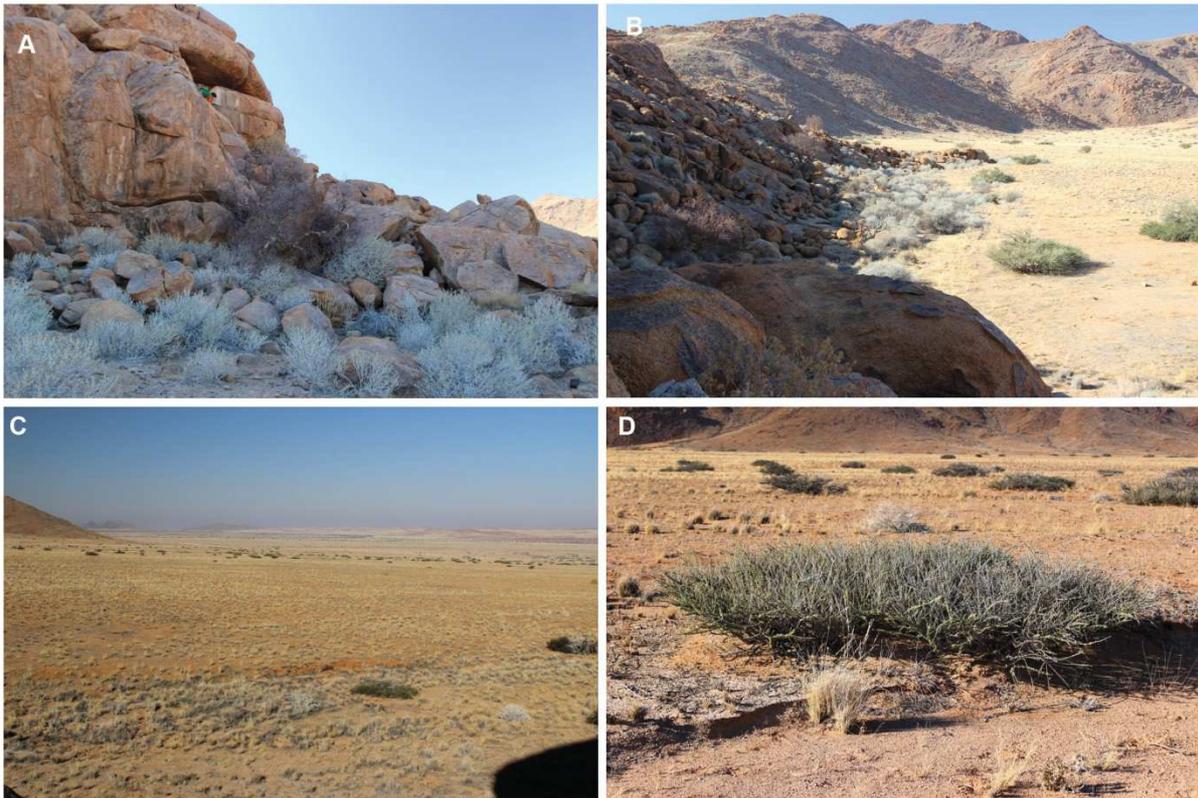


Figure 5. 3: Images of vegetation view at Zizou midden site. Vegetation below the midden site (a), east looking of midden site (b), plains vegetation at the west looking to midden site (c), Capparaceae bushes at the plains (d).

are *Rhigozum trichotomum*, *Parkinsonia africana*, *Acacia nebrownii*, *Boscia foetida*, *B. albitrunca*, *Catophractes alexandri* and some smaller Karoo bushes such as *Pentzia*, *Erioccephalus* (WWF, 2017). The vegetation at Zizou currently falls on the drier end of this spectrum, dominated by arid grasses, especially *Stipagrostis*, with scattered bushes of Capparaceae (*Boscia*, *Maerua*), few *Acacia* trees at the plain, and some other arboreal species such as *Searsia (Rhus)*, *Commiphora* along the rocky slopes (Figure 5. 3, field observation).

5.3. Material and Methods

5.3.1. The Zizou rock hyrax middens

Rock hyrax middens are finely laminated urino-fecal deposits (Chase et al., 2009). Two sections of Zizou midden were sampled: ZIZ-1-1 (19.8 cm), and ZIZ 1-3b (16 cm). From these midden sections, we collected samples for fossil pollen and microcharcoal analysis, as well as radiocarbon dating (Figure 5. 4). The samples from each (ZIZ-1-1 n=26, samples; ZIZ-1-3 n=23 samples) midden are contiguous, with each consisting of a block of material 3-12 mm thick and weighing between ~0.5 g and 3.94 g. For a full description of hyrax middens, their development and the sampling and analytical methodologies for the

proxies they contain, see Chase et al. (2012). ZIZ-1-1 accumulated as a series of horizontal laminae, while ZIZ-1-3b accumulated vertically. This explains the different accumulation rates of each section.

Radiocarbon analysis was performed on 20 samples from the middens (ZIZ-1-1, n=9; ZIZ-1-3b, n=11). The samples were pretreated with 2% HCl for one hour at room temperature to remove carbonates and dried at 60°C. They were then weighed into quartz tubes with an excess of CuO, sealed under vacuum and combusted to CO₂. The CO₂ was converted to graphite on an iron catalyst using the zinc reduction method (Slota et al., 1987). The ¹⁴C/¹²C ratio and ¹³C/¹²C were measured by accelerator mass spectrometry (AMS) at the ¹⁴CHRONO Centre, Queen's University Belfast.

All the radiocarbon ages were calibrated (Table 5. 1, Appendix) with the Southern Hemisphere calibration data (SHCal13, Hogg et al., 2013; Reimer et al., 2013) and chronologies were estimated with the Bacon v2.2 model (Blaauw and Christen, 2011).

5.3.2. Pollen and microcharcoal analysis

Pollen samples were prepared with standard physical (600 µm sieving and decanting) and chemical (HCl, KOH, HF, and acetolysis) methods (Moore et al., 1991). *Lycopodium* tablets were added to the weighed sample to estimate pollen concentrations and calculating the pollen accumulation rates (PARs) (Stockmarr, 1971). A minimum pollen sum of 400 grains was counted at a magnification of ×400 under a light microscope, and identified with the help of the literature (L Scott, 1982; van Zinderen Bakker, 1956, 1953; van Zinderen

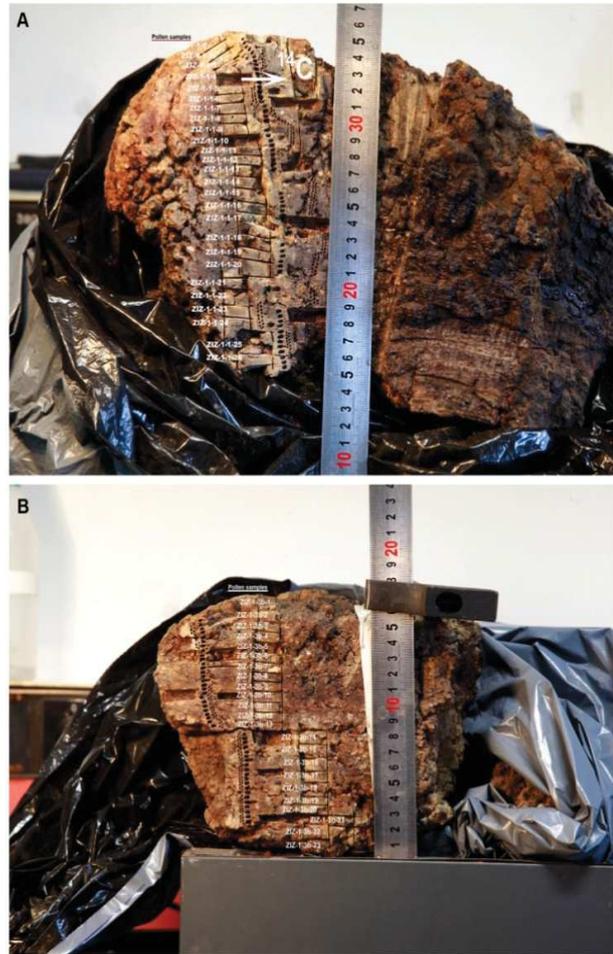


Figure 5. 4: Sampling of Zizou middens in each sections; ZIZ-1-1 (a), ZIZ-1-3b (b).

Bakker and Coetzee, 1959), and photographic and slides reference collections at the University of the Free State, University of Cape Town, and University of Montpellier. Microcharcoal particles were identified as black, completely opaque, angular fragments that occurred in the pollen slides (Clark, 1988). Only charcoal particles $>75 \mu\text{m}^2$ (or longer than $10\mu\text{m}$) were counted under a light microscope at $\times 400$ magnification (Mooney and Tinner, 2011; Patterson et al., 1987). A minimum count of 200 items (given by the sum of charcoal particles and exotic marker grains) was used.

Charcoal particles which exceed the mesh-width size of $600 \mu\text{m}$ are missing from the microscopic charcoal record and particles of ca. $<10 \mu\text{m}$ were not counted in order to ensure correct identification (Mooney and Tinner, 2011). Therefore, our charcoal signal is related primarily to the regional fire signal, with specifically local fires (large particles) and remote, extra-regional fires ($<10 \mu\text{m}$ particles) being generally excluded.

The TILIA program was used to construct the pollen diagrams, and pollen zones are determined by the CONISS method (Grimm, 2011). The palynological richness was estimated using the rarefaction analysis which standardized sample size and does not consider abundances of different pollen type (Birks and Line, 1992). This richness can be used as the presentation of the floristic richness, but its relationship is not an exact relationship due to the influences such as landscape structure, openness, pollen source area and pollen production (Birks et al., 2016).

Pollen concentrations (C_p) of each taxa were used for PAR calculations of each taxon by multiplying the concentration values by the sedimentation rate (S) of each sample:

$$P = C_p \times S$$

where P is the PAR value of each taxon (grains/gram/mm/year), C_p is pollen concentration of each taxon (number of grains/gram), and S is sedimentation rates expressed as mm/year. This calculation was also applied on microcharcoal to obtain to microcharcoal influx (particles/gram/mm/year). The calculation of PAR values here are not referred to infer the changes in population size of each taxon, but it aims to standardized percentages pollen data along the sequences due to changes in the accumulation rates in the middens. This prevents the erroneous interpretation of pollen percentages data that may result from changes in accumulation rates along the sequences.

5.3.3. Pollen types and climate indications

Zizou is at the ecotone area of Nama-Karoo and Desert Biome, a sensitive site to study vegetation changes at the adjacent ecosystems in respond to global climate change. While the vegetation at the site was classified into different Nama-Karoo Biome Rutherford and Westfall, 1994) or Namibian Savanna Woodland ecoregion (Barnard, 1998), the present-day vegetation at the site is more similar to the arid Desert Biome than the more humid Nama-Karoo Biome and Savanna Biome. Changes in moisture would have affected the vegetation of the site, for example, a decline in moisture would decreased the vegetation density and resulted low taxa diversity, characteristic of the Desert Biome. Changes in precipitation seasonality also lead to changes in vegetation types, for instance, the Succulent Karoo and Fynbos biomes receive winter rainfall whereas Nama-Karoo, Desert, and Savanna biomes receive mostly precipitation during the summer months.

In southern African, some pollen types can be used as climatic indicators. For example, Restionaceae is a typical pollen type of Fynbos Biome/winter-rain vegetation. *Stoebe*-type (*Stoebe* and *Elytropappus*) is an indicator of cooler growing conditions in southern Africa (Scott et al., 2017; Rutherford et al., 2012; Rutherford et al., 2003; SANBI, 2003). Grasses are dominant vegetation in the Desert Biome is associated to the insufficient rainfall to support the permanent growth forms such as shrubs and trees. Grasses and Asteraceae are widespread in the southern Africa either arid or humid climate (Rutherford et al., 2012; Rutherford et al., 2003; SANBI, 2003). The interpretation of grass pollen as a moisture indicator is complicated. In the Nama-Karoo Biome, grasses increase and shrubs (Asteraceae) decrease with increasing aridity at the eastern margin, where it grades into grassland. In the Desert Biome, over shorter time scales, increasing grass percentages may indicate the humid condition as grasses grow faster after the rainfall events and very little rainfall is enough for the establishment of grasses (Scott et al., 1991; Scott, 1996; Gil-Romera et al. 2006; Gil-Romera et al., 2007). Over longer time scale, however, increasing grass percentages without the presence of other shrubs/trees may indicate drier conditions while there is insufficient groundwater to support the perennials plants.

5.4. Results

5.4.1. Age-depth models and midden accumulation rate

The radiocarbon analyses of the ZIZ-1-1 and ZIZ-1-3b indicate that each section accumulated continuously, although with significant changes in accumulation rates (Figure 5. 5). ZIZ-1-1 was dated back from ~ 3 to ~ 35 cal kBP and ZIZ-1-3b was dated from ~ 20 to ~ 38 cal kBP. Accumulation rates range from 40 yr/mm to 436 yr/mm in ZIZ-1-1 with average accumulation rates of 159 yr/mm and 28 yr/mm to 505 yr/mm in ZIZ-1-3b with average accumulation of 176 yr/mm. We observed different accumulation rate between two midden sections during the overlap sections time period. For example, $\sim 18 - \sim 25$ cal kBP the accumulation rate indicates faster in ZIZ-1-1 with range of 50-85 yr/mm than ZIZ-1-3b with the accumulation rate ranges from 140 to 568 yr/mm. The differences of accumulation rate in both sections may be explained by

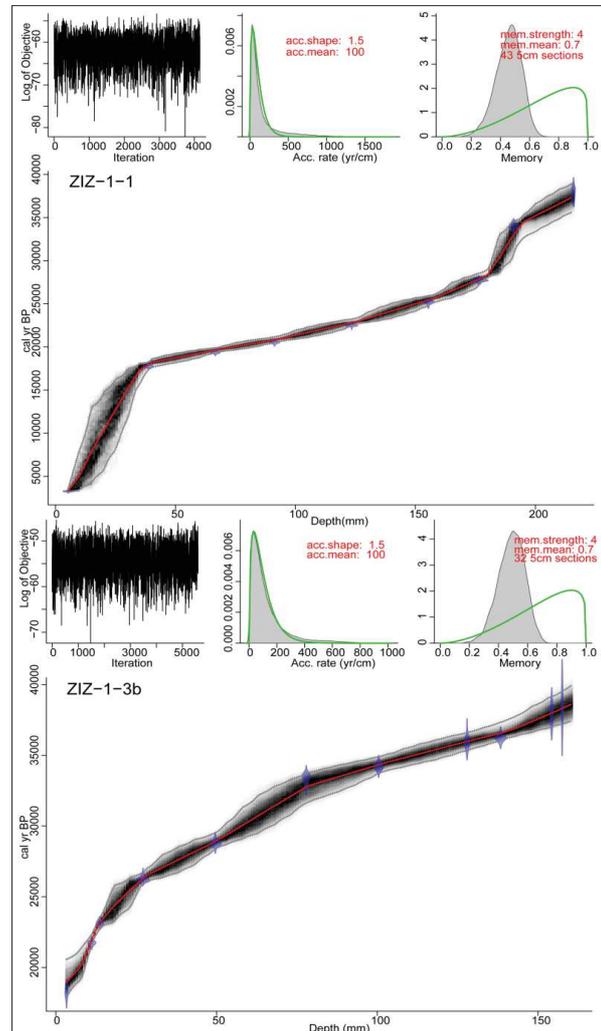


Figure 5. 5: Age models for the Zizou rock hyrax middens ZIZ-1-1 and ZIZ-1-3b.

different mode of accumulation as mentioned above in the methodology as well as the characteristics of the midden structures. In general, we observed that the accumulation rate is much slower during the Holocene (347 yr/mm) than the last glacial period.

5.4.2. Vegetation dynamics inferred from pollen record

The Zizou middens (ZIZ-1-1 and ZIZ-1-3b) are combined into a single record based on the calibrated ages of each sample. Two samples of ZIZ-1-1 (topmost dated to ~ 3 cal kBP and bottommost sample dated back to ~ 34 cal kBP) contained no pollen and were excluded from the pollen diagram. There are a total of fifty identified taxa divided into six statistically

significant pollen zones spanning from 6 to 38 cal kBP (see in appendix). Table 5.2 summarized the vegetation changes in each pollen zone (see in appendix).

Total pollen and microcharcoal concentrations are higher during the last glacial period relative to the Holocene. Poaceae pollen represents almost a half of total pollen assemblages indicating low diversity of other growth forms such shrubs and trees. Poaceae, Asteraceae, Capparaceae, and *Zygophyllum* are the most common and persistent pollen types throughout the record. Asteraceae is most prevalent during the late Pleistocene (from ~33 cal kBP and continue to occurs until ~18 cal kBP) with Capparaceae (~37 – ~35 cal kBP, ~22 – ~20.9 cal kBP, and peaked at ~19 cal kBP). Poaceae was particularly abundant from ~18 cal kBP to the end of the record (~ 6 cal kBP).

5.4.3. Pollen accumulation rates

Percentage pollen records provide general evidence about the occurrence of taxa, the general composition of vegetation, but these data are interdependent, i.e. the values of individual taxon are dependent on the abundance of the other plant taxa, and changes in abundance of one species will always lead to changes in the percentages of other pollen types (Seppä et al., 2009). Additionally, this issue is amplified by the differences in pollen productivity between different plant taxa. Unlike percentage data, the PAR value of a given taxa is directly dependent on the abundance of this taxa at study site. For example, percentage pollen diagram shows higher percentages of Poaceae in the Holocene, but the PAR values indicate the lowest values of Poaceae (Figure 5. 6 A and B). Without the Poaceae PAR values, we may interpret higher percentages of this taxon during the Holocene with the increased abundance of grasses at the site. As a matter of fact, higher Poaceae percentages during the Holocene indicate reduction of abundance of other taxa rather than an increased abundance of Poaceae.

Pollen concentrations are generally higher (average = $\sim 67 \times 10^3$ grains/gram) during the last glacial period compared to the Holocene (average = $\sim 35 \times 10^3$ grains/gram). Accumulation rates are also higher during last glacial period (highest from ~38 to ~32 cal kBP, relative high from ~ 24 to ~ 18 cal kBP) than during the Holocene (after ~18 cal kBP). Similarly, the total pollen accumulation rates during last glacial period are higher (average = ~ 938 grains/g/mm/y) than in the Holocene (average = ~ 81 grains/gram/mm/year) (Figure 5.

6 B). The lowest accumulation rates and PAR values after ~ 18 cal kBP suggest a reduction of vegetation density induced by an increased aridity at the study site.

Microcharcoal influx indicate higher values from ~ 38 to ~32 cal kBP and ~ 24 to ~18 cal kBP, encompassing the LGM and coinciding with the phases of increasing total pollen accumulation rates. After ~18 cal kBP, lower microcharcoal influx occurred in phase with the reduction of pollen accumulation rates. This suggests a positive relationship between fire and vegetation cover (the importance of fuel biomass to support fire). In arid regions, on the one hand, under increased aridity, longer or more frequent droughts may promote burning in ecosystems that are not fuel limited. On another hand, vegetation shifts toward fuel limited ecosystem may reduce fire activity in the same region. This later case may explain the shift of ecosystem at Zizou site across the last glacial-interglacial transition. More fires at Zizou during the last glacial occurred in non-fuel limited ecosystem (Nama-Karoo or Savanna Biome) while absence of fire during the Holocene suggest the vegetation at the site shifted into fuel limited ecosystem (Desert Biome).

5.4.3.1. Pleistocene vegetation composition and dynamics

Z-I (~38 – ~32 cal kBP), vegetation composed of different grow forms (arboreal species, succulents, Asteraceae small shrubs, and grasses). *Stoebe*-type and *Artemisia* were present with low numbers during this interval, indicating relatively warm temperatures. The pollen spectra variations suggest the increased, but variable, water availability in this period. In addition, the microcharcoal influx show some peaks at ~36 cal kBP and ~34 – ~32 cal kBP. For instance, from ~38 to ~34 cal kBP, the pollen data show prominent succulent taxa including Aizoaceae, *Crassula*, *Euphorbia*, and *Zygophyllum*, accompanied by some arboreal taxa such as *Rhus*-type, Capparaceae, and Menispermaceae, indicating relatively drier conditions. From ~34 to ~32 cal kBP, the record shows prominent shrubby Asteraceae (including *Felicia*) and grasses, indicating an increase in moisture (Figure 5. 6).

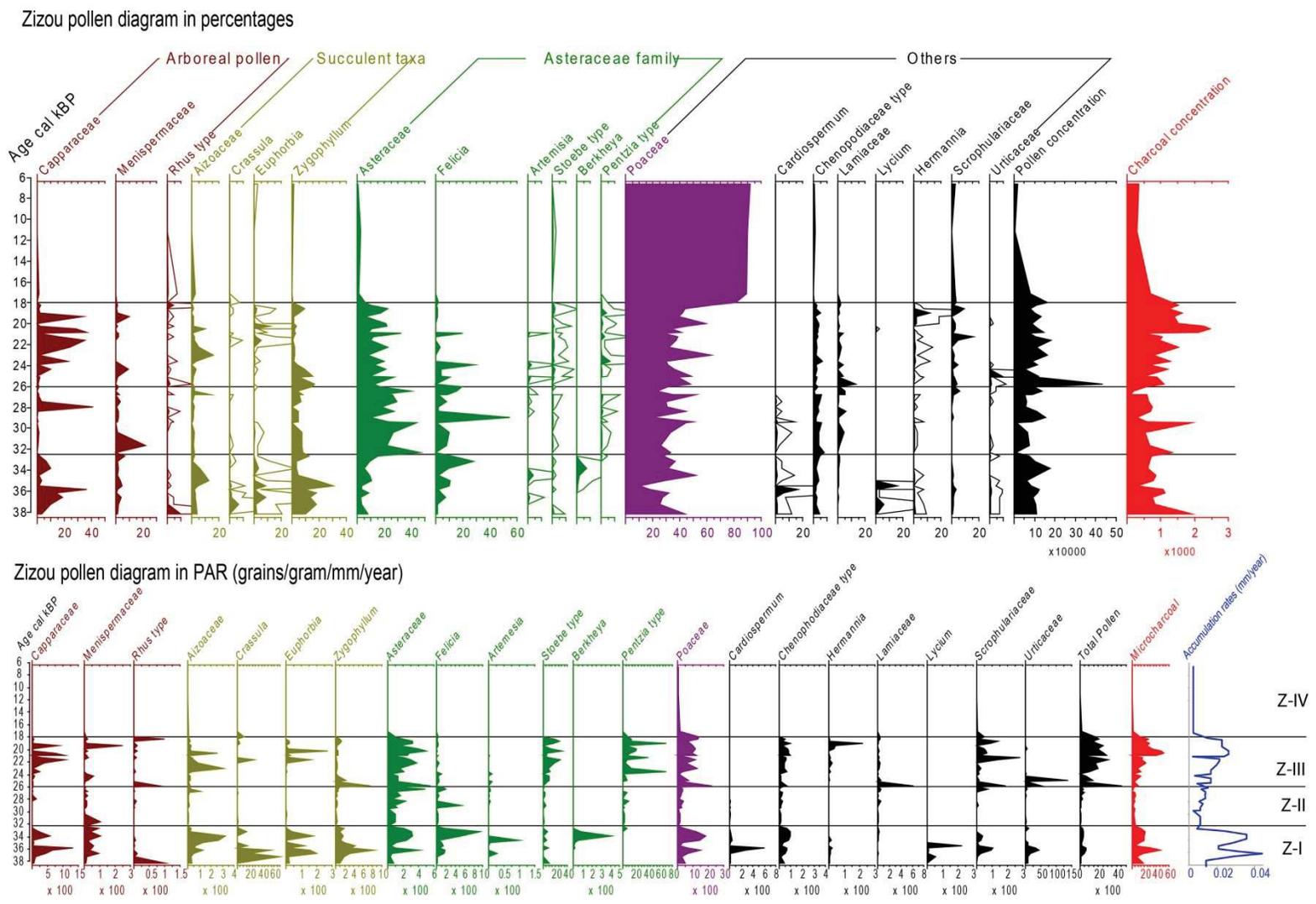


Figure 5. 6: Pollen diagram in percentages (A) and Pollen accumulation rates (grains/gram/mm/year) (B) at Zizou midden.

Z-II (~32 – ~26 cal kBP), the PAR data show covariation between Asteraceae pollen and grasses, but their PARs values were lower than previously. Fewer numbers of arboreal taxa, *Stoebe*-type, and *Artemisia* were observed in this interval while *Felicia* peaked at ~30 cal kBP (Figure 5. 6). These suggest cooler temperature than earlier periods of the record. Low accumulation rates, followed by lower total pollen accumulation rates and microcharcoal influx, and increased of Asteraceae suggest less variable climate conditions shifting from wetter to drier conditions.

Z-III (~26 – ~18 cal kBP), pollen data show an increase of *Stoebe*-type, a cool taxa, to its maximum values in particular from ~22 to ~18 cal kBP. This indicates the cooler temperature during the LGM. The accumulation rates were slightly increased from previous ages and the total PAR values were the highest of the record. At the same time, microcharcoal influx show the positive relationship with grasses and the total PAR values. Higher taxa diversity was observed in this interval including arboreal taxa, shrubby of Asteraceae (including *Pentzia*-type), succulent taxa, and grasses (Figure 5. 6). All these evidences suggest the increase moisture under cooler temperature, with some periods of droughts indicating by more frequency of microcharcoal influx and occurrence of succulent taxa.

Consistent to the other terrestrial records, there was not any winter-rain taxa (e.g. Restionaceae) in the Zizou pollen record during the last glacial period.

5.4.3.2. Deglacial and Holocene vegetation composition and dynamics

During Z-IV (~18 to ~6 cal kBP), lower pollen accumulation rates occur during lower midden accumulation rate phases, indicating low vegetation density at the site. Vegetation is characterized by the exclusively abundant of grass pollen in which reached its maximum (63-92% of total percentages). However, the PAR values of grass during this phase were very low. Consequently, the dominant of grass during this phase indicates the increased aridity at the site as temperature increased during the Holocene. At the same time, microcharcoal concentrations declined significantly to their minimum level of the record while grasses increase markedly (Figure 5. 6). This reflects the shift of vegetation towards the Desert Biome, in which fire is rare or almost absent due to insufficient fuel biomass to burn. We interpret the grass abundance here as indicating drier conditions because grasses thrive seasonally after rain, but also remain dominant in the long-term during the driest phases.

5.5. Discussion

5.5.1. Vegetation and climate change at Zizou

The fact that Zizou site is situated in a narrow belt of Nama-Karoo in which sandwiched between the Desert and Savanna Biome, the major climatic changes could result in vegetation fluctuation between those biomes during the last 38 cal kBP. The pollen records from the Zizou rock hyrax middens show a clear vegetation change particularly between the period of late Pleistocene and the Holocene. Pleistocene pollen assemblages were composed of different growth forms such as arboreal taxa (Capparaceae, *Rhus*-type, Menispermaceae), succulent taxa (Aizoaceae, *Zygophyllum*), Asteraceae (including *Stoebe*-type, *Pentzia*-type, *Felicia*, and *Artemisia*), and Poaceae. This vegetation type is more common in more humid Nama-Karoo Biome rather than present-day vegetation at study site. The last glacial Asteraceous-rich vegetation type were also reported elsewhere in southern Africa during the late Pleistocene (Lim et al., 2016; Scott, 2016; Scott et al., 2004). In contrast, this vegetation type disappeared from the Zizou pollen record during the Holocene. The disappearance of *Stoebe*-type and *Artemisia* after ~18 cal kBP suggests cooler temperature during the last glacial period and the deglacial warming after this time. This is coherent with the temperature index from pollen data in the southern Namib (Lim et al., 2016) and palaeotemperature estimates obtained from the Stampriet Aquifer (Stute and Talma, 1998). Similar to the Pella pollen record, last-glacial pollen and microcharcoal evidences at Zizou suggest that climate condition at the site were characterized by increased water availability, however, the moist conditions were variable, with evidence of wet and dry phases. After ~18 cal kBP, high grass pollen percentages, lowest microcharcoal influx, low pollen and midden accumulation rates suggest that the site became part of an expanding Desert Biome. However, very low pollen resolutions do not allow us to infer significant climatic variability during this period.

Present-day fire activity is absent from desert and semi-desert region due to the insufficient fuel biomass (Daniau et al., 2013). Only in the arid savanna and grassland that support surface fire. The surface fires occur mainly during the peak of the dry season and are highly dependent on the rainfall of the previous two years, and the influence of rainfall seasonality (Archibald et al., 2010). Assuming that microcharcoal influx indicates regional fire, however, as sources of microcharcoal in the hyrax midden are not well understood. Daniau et al., 2013 suggested that grass-fuel biomass burning is an important source of charcoal and maxima increased of biomass burning from grass occurred during the cooler climate conditions in southern Africa. Since we did not identify microcharcoal morphology,

we could not rule out whether microcharcoal in Ziou midden derived from grass or other growth forms. In general, however, it seems that there was more vegetation cover during the last glacial period and a drastically reduction of vegetation after ~18 cal kBP.

5.5.2. The last glacial period (~38 – ~18 cal kBP)

Pollen sequences at Zizou indicate some pollen types that only occurred during the last glacial period and disappeared during the Holocene. *Stoebe*-type pollen (*Stoebe/Elytropappus*) was used as the past temperature indicator in southern Africa (Lim et al., 2016; Scott et al., 2012, 2004). This pollen type is also recorded as being abundant in other terrestrial records in southern during the last glacial period (Scott et al., 2017, 2004, 1995; Lim et al., 20016). The presence of this pollen type in the Namib Desert also suggests slightly more humid local conditions, particularly when accompanied by *Artemisia* (Scott et al., 2017). At Zizou, higher PARs of *Stoebe*-type were recorded from ~ 22 to ~ 18 cal kBP indicating cooler temperature during the LGM and increased effective moisture (Figure 5. 7). This finding is coherent with terrestrial pollen records at Brandberg mountain and Mirabib Hill (Scott et al., 2017, 2004).

The occurrence of arboreal taxa such as Capparaceae was also observed in Ziou midden during the last glacial period. There are two phases increased of Capparaceae in Zizou record, ~ 36 – ~35 cal kBP and ~22– ~21 cal kBP and a peak at ~19 cal kBP. Species of Capparaceae such as *Maerua* sp. and *Boscia* are well adapted to aridity. For example, at study site presently, species are found as bushes with their umbrella architecture to collect any water drops from rainfall and to keep near the surface, creating their own microhabitats. Present-day vegetation show that phanerophytes are more commonly found at the hills with a strong root system to penetrate cracks in the bedrock to access water, e.g. *Commiphora*, *Rhus*. On the flat plains, bushes species of Capparaceae and rare *Acacia* trees are found along drainage lines where groundwater are concentrated. In the pollen record, the first phase of increased Capparaceae from ~ 38 – ~35 cal kBP, together with some succulent taxa such as Aizoaceae, *Crassula* and *Zygothellum* and lower grass and Asteraceae suggest dry conditions at the site. The second phase of increased Capparaceae from ~22 – ~19 cal kBP, encompassing the LGM, appeared again with presence of Aizoaceae and higher microcharcoal influx suggesting at least some period of drier conditions.

The pollen sequences from both Zizou and Pella show similar vegetation type indicating by abundant of Asteraceae during the last glacial period (Figure 5. 7). These two families are dominant elements of the Nama-Karoo Biome and their relative abundance can, in general, be used to indicate the aridity within this biome. Previous palynological works at the transition of Nama-Karoo and Grassland biome, Florisbad and Aliwal North, in South Africa suggested that grass-dominated pollen assemblage during the glacial period was associated to cooler and moister climate whereas higher percentages of Chenopodiaceae and Asteraceae pollen were more indicative of aridity (Coetzee, 1967; van Zinderen Bakker, 1989). Pollen from the Pella hyrax middens, at the transition of Nama-Karoo and Desert biome, show the reserved relationship between Poaceae and Asteraceae along the whole record during the last 50 cal kBP (Lim et al., 2016). The authors interpreted the data as indicating increasing humidity during the last glacial period, promoting the general development of grasses, and relatively mesic Nama-Karoo vegetation. This vegetation type is result from more/more regular rain or a reduction in potential evapotranspiration, which resulted in increased water-available for shallow rooting grasses. Arid conditions during the LGM are indicated by more abundant Asteraceae and a reduction of Poaceae (Lim et al., 2016). The reconstructed aridity index at Pella shows increased, but variable, water availability during the last glacial period relative to the Holocene. During the last glacial period, Pella site was within Nama-Karoo Biome, wherein increased aridity is reflected by an increase in Asteraceae pollen and a decline in grasses. As temperature reached the Holocene maxima, climate conditions became significantly drier, and the Desert Biome expanded across Pella region. During this period, increases in Asteraceae are interpreted as indicating wetter conditions, and ephemeral expansions of the Nama-Karoo into the region. Thus, interpretations of grass pollen as a moisture indicator needs to be considered in terms of the biome context.

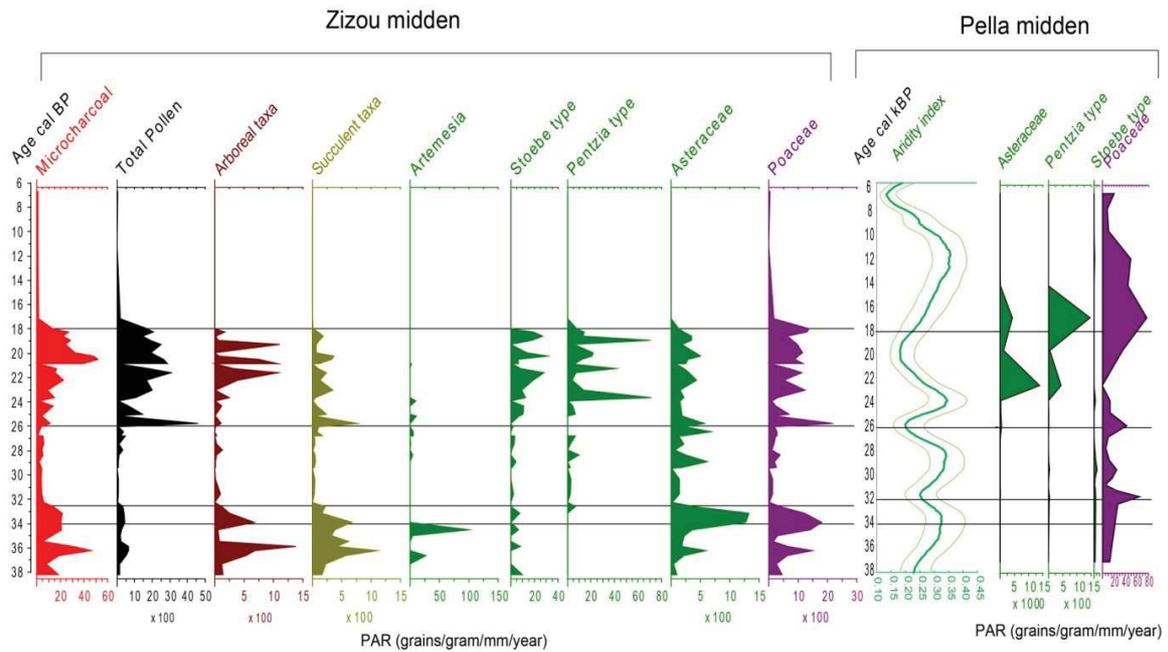


Figure 5. 7 : Comparison pollen records at Zizou with aridity index and pollen at Pella.

At Zizou, both Asteraceae and Poaceae were abundant during the last glacial period, but the reversed relationship between these two elements are not as clearly observed as they are at Pella (Figure 5. 8). The Zizou pollen data show covariation between Poaceae and Asteraceae across much of the last glacial period, except during the LGM. This may be due to the Zizou site is located at the ecotone area in which vegetation fluctuations could result in shifts between the Nama-Karoo, Savanna, and Desert biomes. The pollen and micro-charcoal data at Zizou suggest that from $\sim 38 - \sim 34$ cal kBP and from $\sim 26 - \sim 18$ cal kBP vegetation at the site was similar to Nama-Karoo-Savanna transition, indicated by more arboreal elements and more frequent fire. Today, fire activity in the Savanna Biome is more common than in Nama-Karoo Biome (Cowling et al., 2004). Climatic conditions maybe more variable, but the pollen sample resolution does not allow us to investigate whether increased fire activity was associated with increased amount rainfall or to seasonal changes in rainfall. From $\sim 34 - \sim 26$ cal kBP, a reduction of arboreal elements, co-occurrence of Asteraceae and grass, and lower microcharcoal influx suggest that the site was part of the Nama-Karoo Biome. Prior to ~ 26 cal kBP, we observed that periods of increased humidity at Pella coincided with phases of increased grasses at Zizou (Figure 5. 7). This suggests more/more regular rainfall or lower temperature prior to ~ 26 cal kBP, supporting the development of grasses and more mesic Nama-Karoo vegetation at Zizou (Figure 5. 8).

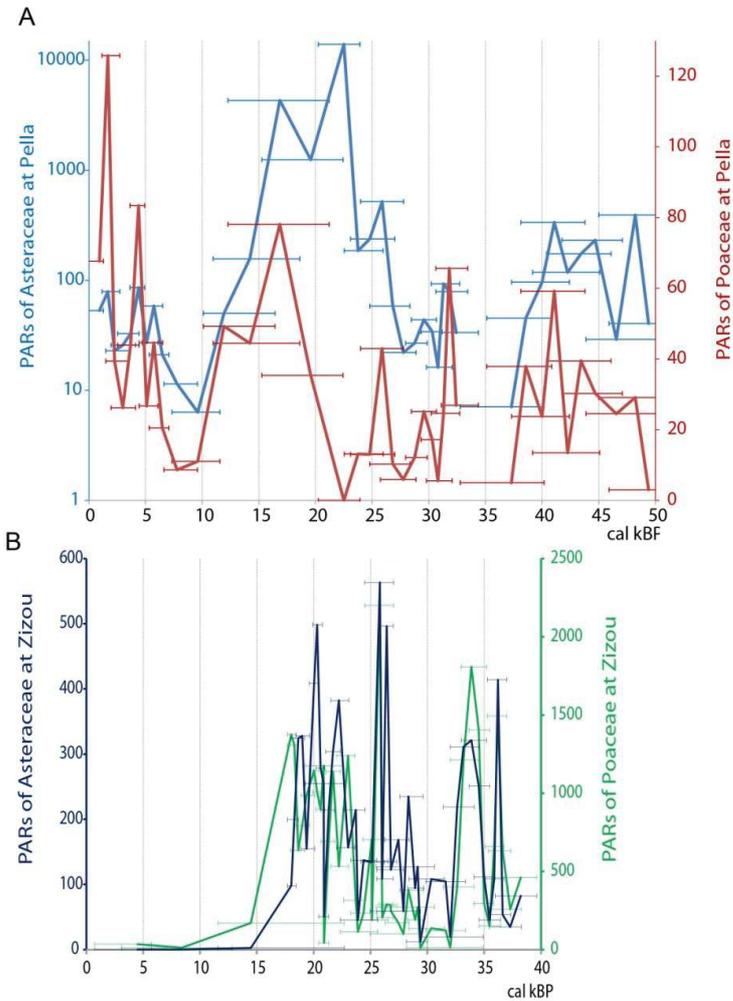


Figure 5. 8: PAR values of Poaceae and Asteraceae at Pella and Zizou midden.

Climate conditions, in general, were characterized by increased, but variable, moisture during the last glacial period at Zizou. However, a phase of warmer and drier conditions is inferred from pollen and microcharcoal data for the oldest part of the record, $\sim 38 - \sim 34$ cal kBP. Similar findings of warmer and drier conditions are also evidenced in Brandberg pollen data at c. 39 ka (Scott et al., 2017). Unfortunately, there are no samples from $\sim 34 - \sim 26$ cal kBP in the Brandberg record so we could not compare with pollen data at Zizou. At Pella, in the southern Namib, aridity index reconstructions indicate the occurrence of wetter phases at 34, 29 and 24 cal kBP, and drier phases at 38, 32, 26 and 20 cal kBP (Lim et al., 2016). Low percentages of cool taxa such as *Stoebe*-type suggest that increased humidity during these former intervals maybe related to an increase in rainfall. The greater numbers of *Stoebe*-type and *Pentzia*-type $\sim 22 - \sim 18$ cal kBP suggest the extreme cooler temperature than older ages.

The inference of increasing winter rainfall during the glacial period has largely been derived from pollen associated with the Cape flora (e.g. Restionaceae) in marine cores from

the southeast Atlantic (Shi et al., 2001; Shi et al., 2000). However, terrestrial pollen records indicate no evidence of such an expansion (Scott et al., 2004; Lim et al., 2016). Chase and Meadows, 2007 have discussed in detail to explain whether rainfall or wind is the dominant control of higher percentages of Restionaceae pollen in the marine record. The absence of this pollen type at Brandberg may be due to the edaphic affinities of Restionaceae species, which prefer nutrient poor sandy soils and are unlikely to have colonised the rich granite soils, perhaps favouring the sandier substrate found the west (Chase and Meadows, 2007). If Restionaceae had expand far northward, we might expect to find some Restionaceae pollen grains in Zizou midden because the site is located at the transition of the sandy substrate and Restionaceae pollen are wind-pollinated. However, similar to previous terrestrial pollen record in the region (Scott et al., 2004; Lim et al., 2016), there is no Restionaceae pollen found in the Zizou middens over the last 38 cal kBP. This finding supports the other terrestrial records, indicating no significant expansion of the Cape vegetation as proposed by the evidence from marine records.

5.5.3. The last glacial-interglacial transition and Holocene (~18 – ~6 cal kBP)

The vegetation at Zizou is dominated by grasses after the LGM, with a decline of midden and pollen accumulation rates and microcharocal influx (Figure 5. 6). We consider the very slow accumulation rates of Zizou midden during the Holocene to likely be a function of reduced colony size under more arid climates. The increased of aridity during this period may have led to a reduction in vegetation density at the site. At Zizou midden, grasses increased from ~18 cal kBP to the end of the record (at ~6 ka) without the presence of *Stoebe*-type and *Artemisia*-type. Additionally, there is an abruptly decline of shrubs (Asteraceae) that were abundant in last glacial period. The abundance of grasses reflects the current Desert Biome vegetation at the site. Thus, the dominance of grasses after ~18 cal kBP in pollen record is thought to be the result of increasing aridity and an expansion of the Desert Biome, as was observed at Pella (Lim et al., 2016). Low microcharcoal influx are also observed during the Holocene, suggesting insufficient fuel biomass for significant burning. The low accumulation rates and sample resolution in Zizou midden, and over-representation of Poaceae pollen during the Holocene do not allow us to investigate the short-term climate variability during this period.

5.6. Conclusions

Pollen and microcharcoal analyses of rock hyrax middens from Zizou, at the eastern margin of central Namib Desert, provide a 38,000-year record of vegetation in response to the past climate change.

Key findings include:

- The last glacial period was characterized by increased water availability with the vegetation being composed of different growth forms such as shrubs/trees, succulents and grasses and a higher diversity of taxa, similar to the Nama-Karoo Biome, which is presently found in more humid regions to the east of the site.
- Phases of increased humidity at the site during LGM occurred under cooler temperature, leading to more effective moisture. However, some drier phases also occurred during this period, indicated by increased Capparaceae pollen and microcharcoal influx.
- After ~18 cal kBP, increasing warmth and aridity resulted in an expansion of the Desert Biome, as indicated by a predominance of grasses and lower pollen diversity.
- Consistent with other terrestrial records, no evidence for an expansion of the Cape flora is observed during the last glacial period.

This study provides additional palaeobotanical data from an arid region where long records are rare. The vegetation at the study area shows patterns of change over the last 38,000 years that are consistent with those observed in the southern Namib, at Pella (Lim et al., 2016). Low midden accumulation rates and sample resolution during the Holocene limits the potential for climate reconstruction during this period, as does the pollen diversity of the record, wherein Poaceae represents more than 90% of total pollen assemblage. Despite this, we can conclude that the vegetation change reflects a regional pattern of humid glacial conditions and a more arid Holocene.

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Appendix

Table 5. 1: Radiocarbon ages and calibration information for the Zizou-1-1 and Zizou-1-3b hyrax middens.

Sample	Avg. depth (mm)	¹⁴ C age yr BP	1 sigma error	calibration data	95.4 % (2σ) cal age ranges	relative area under distribution
ZIZ-1-1						
UBA-24433	5.381356	3099	21	SHCal13	cal BP 3205- 3356 cal BP 3179 - 3203	0.933919 0.066081
UBA-24434	38.55932	14626	50	SHCal13	cal BP 17584- 17949	1
UBA-24435	66.61017	16081	53	SHCal13	cal BP 19168- 19557	1
UBA-24436	91.31356	17059	58	SHCal13	cal BP 20305- 20721	1
UBA-24437	123.4746	18670	82	SHCal13	cal BP 22323- 22712	1
UBA-24438	155.3814	20942	104	SHCal13	cal BP 24883 - 25566	1
UBA-24439	176.3983	23594	135	SHCal13	cal BP 27460- 27900	1
UBA-24440	190.9322	29929	287	SHCal13	cal BP 33532- 34532	1
UBA-24441	215.8898	33763	447	SHCal13	cal BP 36669- 39074	1
ZIZ-1-3						
Pta-9680	3.311949	15030	341	SHCal13	cal BP 17407- 18930	1
UBA-24442	11.18792	17985	78	SHCal13	cal BP 21469- 21965	1
UBA-9433	13.65169	19230	70	SHCal13	cal BP 22875- 23417	1
UBA-24444	27.10143	22034	118	SHCal13	cal BP 25944- 26518	1
UBA-24445	49.59845	24777	155	SHCal13	cal BP 28405 - 29156	1
UBA-24446	77.91158	29339	263	SHCal13	cal BP 32863- 33969	1
UBA-24447	100.449	30173	259	SHCal13	cal BP 33758- 34649	1
UBA-24448	127.9543	32063	386	SHCal13	cal BP 35010- 36744	1
UBA-9211	138.3748	32358	159	SHCal13	cal BP 35792- 36571	1
UBA-24449	154.2883	33703	570	SHCal13	cal BP 36397- 39258	1
Pta-9686	157.5599	34250	1600	SHCal13	cal BP 35137- 41669	1

Table 5. 2: Summary of each pollen zone shows some descriptions of vegetation changes.

Zone	Number of samples	Age range (cal BP)	Dominant taxa (zone mean)	Additional information
ZIZ-I	6	35467.8-38214.9	Poaceae (26%), <i>Zygophyllum</i> (16%), Capparaceae (14%), Asteraceae & <i>Felicia</i> (10%), <i>Stoebe</i> -type (0.2%), Artemisia (0.2%)	Vegetation composed of different growth forms such as grasses, succulent, arborescent, shrubs.
ZIZ-II	4	32626.4- 35467.8	Poaceae(33%), Asteraceae & <i>Felicia</i> (26%), <i>Zygophyllum</i> (7%), Menispermaceae (5%), <i>Stoebe</i> type (0.2%), Artemisia (0.2%), Pentzia type (0.2%)	Similar vegetation composition to the previous zone but showing the increasing proportion of shrubs elements (Asteraceae).
ZIZ-III	6	29145.4 - 32626.4	Asteraceae & <i>Felicia</i> (36%), Poaceae(35%), <i>Zygophyllum</i> (6%), Menispermaceae (5%), <i>Stoebe</i> type (0.1%), Pentzia type (0.3%)	Shrubs continue to increase gradually. Vegetation composition remains the same to the previous zone.
ZIZ-IV	13	23888.1-29145.4	Poaceae(36%), Asteraceae & <i>Felicia</i> (32%), <i>Zygophyllum</i> (6%), Capparaceae (5%), <i>Stoebe</i> type (0.4%), Artemisia(0.5%), Pentzia type (0.3%)	No significant vegetation changes from the previous zone apart from the reappearance of Capparaceae.
ZIZ-V	13	18293.8-23888.1	Poaceae(41%), Asteraceae & <i>Felicia</i> (18%), Capparaceae (16%), <i>Zygophyllum</i> (3%), <i>Stoebe</i> type (0.7%), Artemisia (0.1%), Pentzia type (1.4%)	Slight reduction of shrubs, but increasing of grasses and Capparaceae. <i>Stoebe</i> -type known as cold indicator, reaches its maximum in this zone. Micro-charcoal also peaks during the zone.
ZIZ-VI	5	4492.7-18293.8	Poaceae(88%), Asteraceae & <i>Felicia</i> (3%), <i>Stoebe</i> type (0.07%), Pentzia type (0.1%)	Completely different vegetation composition from other previous zones with the grassiness abundant. This vegetation type reflects the current vegetation composition at the study area.

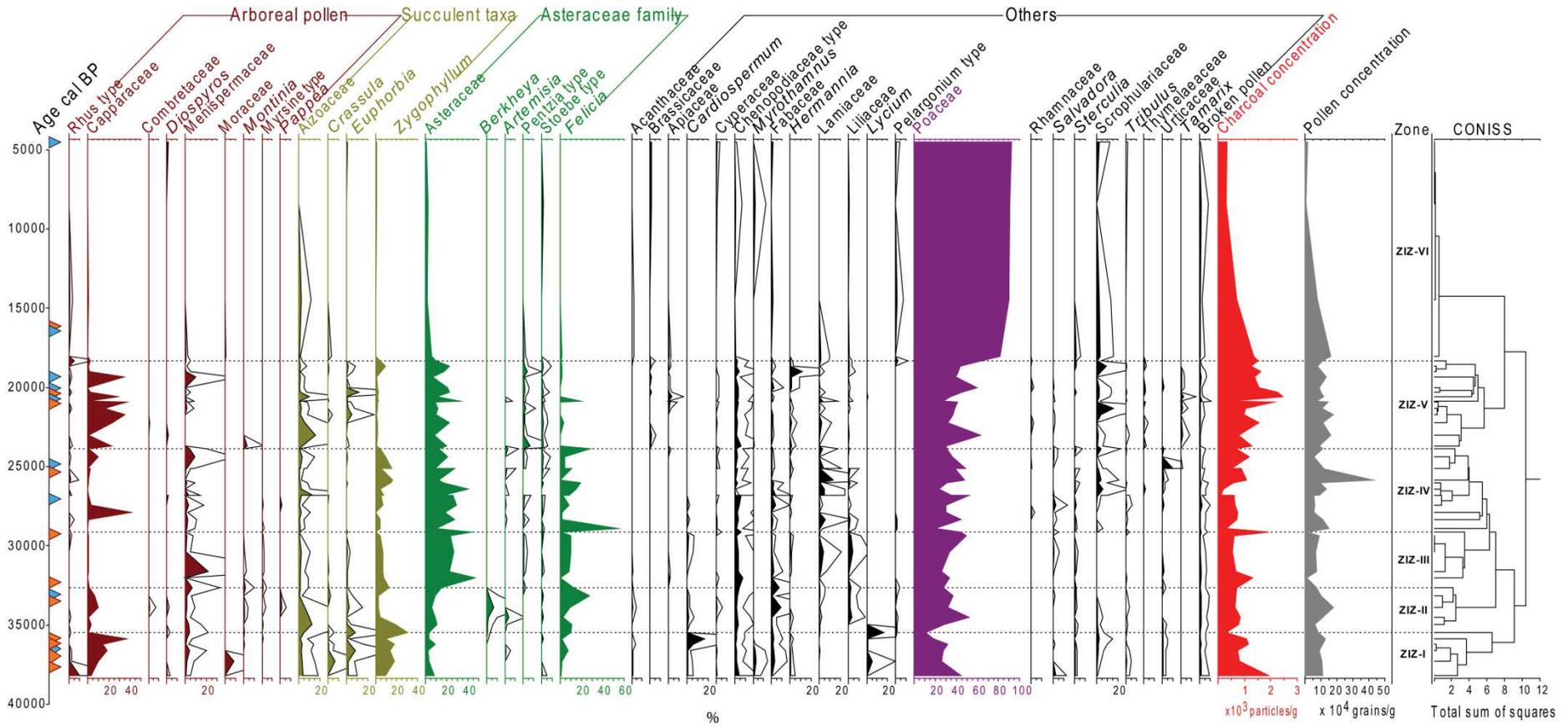


Figure 5. 9 : Diagram combining pollen percentage and microcharcoal concentration data from the Zizou rock hyrax middens ZIZ-1-1 and ZIZ-1-3b. 5 times exaggeration was applied to some lowered percentage taxa to clearly see their presence. Triangles indicate radiocarbon dates, ZIZ-1-1 (blue triangles) and ZIZ-1-3b (orange triangles).

Chapter VI: Spitzkoppe: a record of vegetation change over the last 32,000 years from the eastern margin of central Namib Desert.

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Abstract

Presented here are a series of high-resolution of pollen records from the Spitzkoppe hyrax middens on the eastern margin of the central Namib Desert. These records span the last ~32 cal kBP, with the exception of a hiatus from ~15 – ~12 cal kBP. Results of fossil pollen and microcharcoal suggest the generally cool and increased moisture conditions at study site during the last glacial period relative to the Holocene. Last glacial pollen assemblage shows an abundance of *Olea* (wild olives), Asteraceae (including *Artemisia*, *Stoebe*-type, *Pentzia*-type), higher microcharcoal influx, and the modest proportions of grasses noticeably from ~22 to 17 cal kBP. This vegetation corresponds to mesic savanna woodland with karoo shrubs suggesting cooler condition and more effective moisture. The increased humidity in this phase is likely due to cooler temperatures leading to lower evapotranspiration rather than an increase in precipitation. During the last glacial-interglacial transition (~17 – ~15 cal kBP), grass pollen increased to its maximum values concurrent with a reduction of cool taxa, suggesting increasing temperature and humidity at the site. The Holocene pollen assemblage (~12 cal kBP – present) indicates that grass pollen continues to increase from ~12 – ~7 cal kBP along with different arboreal species compositions from the last glacial period. While the prevalent arboreal taxa during last glacial period were *Olea*, *Rhus*-type, Menispermaceae, the Holocene arboreal taxa are *Euclea*, *Rhus*-type, *Croton*, *Dombeya*, *Commiphora*, taxa that are currently present at the study site. This vegetation reflects the current xeric savanna woodland indicating warmer and a progressive aridification throughout the Holocene, although wetter conditions were evidenced at early Holocene from ~12 – ~7 cal kBP. While rapidly increased aridity after ~3 cal kBP, a positive correlation between grasses and aridity indicates that vegetation shifted toward Desert Biome.

6.1. Introduction

Terrestrial fossil pollen records from the Namib Desert dating back the last glacial period are scarce (Lim et al., 2016; Scott et al., 2017, 2004; Van Zinderen Bakker, 1983; Marais et al., 2015) with many of the records covering only the mid- to late Holocene (Gil-Romera et al., 2007, 2006; Scott, 1996; Scott et al., 1991). Pollen spectra at Sossusvlei have been interpreted as indicating that vegetation in the region has changed very little over the last 18 kyr (van Zinderen Bakker, 1983). Van Zinderen Bakker concluded that the northern part of the Namib Sand Sea did not receive significantly more rainfall over the last 18 kBP which run counter to the penetration of more than usual winter rainfall in the region (van Zinderen Bakker, 1976). It is important to notice that the chronology of this record is problematic, and less reliable because the ^{14}C dates are from calcareous silt materials. Pollen records from other terrestrial sites in the region, however, indicate clear differences between vegetation types of the last glacial period and the Holocene (Lim et al., 2016; Scott et al., 2004; Zizou middens in chapter 5). Sites located to the south of the Spitzkoppe middens, at Zizou and Pella, indicate that glacial vegetation types were dominated by Asteraceae shrubs (including *Stoebe*-type, *Artemisia*) (Lim et al., 2016; Chapter 5 of this thesis), while to the west of Spitzkoppe, middens from the Brandberg indicate that glacial vegetation types were dominated by Asteraceae shrubs (including *Stoebe*-type, *Artemisia*), and *Olea* (wild olives) (Scott et al., 2004). A strong presence of Asteraceae pollen at Pella and Zizou middens in last glacial period suggests a Nama-Karoo Biome vegetation, while present-day vegetation at these sites is more similar to the Desert Biome. The annual temperature and aridity index reconstructed from pollen data at Pella middens suggest the cooler and more humid conditions during the last glacial period (Lim et al., 2016). Scott et al., 2004 suggested that a dominant of *Stoebe*-type, *Artemisia*, and *Olea* accompanied by spore of ferns indicating cool and moist condition at c. 21 ka. A recently published work of pollen analysis from two hyrax midden sites dating to MIS 3 and MIS 2 suggests significant changes in moisture and temperature between 50 ka and 20 ka in the central Namib Desert (Scott et al., 2017). Holocene vegetation types are characterised by increased grasses and succulents (Lim et al., 2016; Scott et al., 2004) and an exclusively abundant of grasses at Zizou middens located near the western margin of desert grassland in the Namib Desert (see chapter 5).

The palaeoenvironmental history of the Namib Desert remains poorly resolved due to the region's semi-arid to hyperarid climate. These climates limit the development of traditional palaeoenvironmental archives resulting in poor understanding of vegetation and

climate change especially at glacial-interglacial time scales (Chase et al., 2010, 2009, Gil-Romera et al., 2007, 2006; Scott et al., 2004). Very few terrestrial palaeoenvironmental records have been recovered from the region, and many of these are discontinuous or have problems with their chronologies (Chase and Meadows, 2007; Scott et al., 2012). As a result, the history of past vegetation change in the region has relied on pollen sequences derived from marine sediments (Shi and Dupont, 1997; Shi et al., 2001, 2000, 1998). The reliability of the results from these marine pollen sequences, however, are believed by some to be complicated by the large-scale mixing of pollen from the diverse sources and do not clearly reflect terrestrial environments (Scott et al., 2012; Scott et al., 2004; Lim et al., 2016).

Fossil hyrax middens (fossilized latrine of the rock hyrax (*Procavia capensis*)) have been shown to be valuable sources of the palaeoenvironmental information in arid region such as the Namib Desert where sources of proxy information are scarce or non-existent (Chase et al., 2012, 2009; Gil-Romera et al., 2006; Scott, 1996, 1990; Scott et al., 2004). The accumulation of hyrax middens provides long, continuous records for the study of long-term vegetation and climate change. Pollen grains are deposited in the hyrax middens from aeolian vectors but also possibly through the animal's fur and diet. The pollen assemblages in the hyrax midden sequences reflect primarily the local vegetation cover from within the animal's primary feeding range (Chase et al., 2012; Gil-Romera et al., 2010).

We present here a fossil pollen and microcharcoal record spanning the last ~32 cal kyr BP from the Spitzkoppe hyrax middens on the eastern margin of the central Namib Desert. The previous palaeoenvironmental history derived from stable isotopes in hyrax middens were published at Spitzkoppe, however, these records only cover the Holocene. This provides the opportunity to compare our pollen data with the stable isotopes proxy. Pollen data from this work contribute to the better understanding of the long-term climate and vegetation changes at the region. We aim to investigate how has the vegetation responded to the climate changes at the biome scale spanning the last ~32 cal kBP. We also seek to evaluate the hypothesis of northward expansion of Fynbos vegetation during the last glacial period as suggesting by marine sediment cores (Shi et al., 2001, 2000).

6.2. Study regions and site description

The Spitzkoppe midden site (21°49'54.19"S, 15°11'43.80"E, 1120 m amsl.) is located on the south-facing flank of Klein Spitzkoppe, in western-central Namibia (Figure 6. 2a). The site lies between the eastern fringe of the Namib Desert and the Great Escarpment to the east. It is approximately 100 km inland from Atlantic coast. The area is characterised by granite inselbergs that rise to an elevation of 1784 m.a.s.l., ~700 m from the surrounding plains. The annual temperature at the site is approximately ~20°C with the average maximum temperature in summer of ~30°C and an average minimum temperature in winter of ~8°C (Hijmans et al., 2005) (see in Table 6. 2, appendix). The global aridity index indicates the value of ~0.06 at Spitzkoppe in which is relatively more humid than the hyper-arid core of the Namib Desert to the west (Trabucco and Zomer, 2009). Rainfall is unpredictable and highly spatio-temporally variable (Burke, 2001). The site currently receives ~106 mm of rainfall per year under a strongly seasonal regime in which >70% falls between January and March (Hijmans et al., 2005) (Figure 6. 1, top). This middle and late summer rainfall maximum is controlled by 1) shifts in the Inter-Tropical Convergence Zone (ITCZ) and Congo Air Boundary (CAB), which respond to changes within and between the continent and adjacent oceans as a function of seasonal changes in insolation and temperature, and 2) the variation in coastal sea-surface temperatures (SSTs) which are primarily determined by marine upwelling intensity driven by the position and strength of the South Atlantic Anticyclone (SAA) (Nicholson, 2000).

The vegetation at Spitzkoppe is classified in Namibian Savannah Woodland (Barnard, 1998) (Figure 6. 1, bottom). This ecoregion covers the narrow escarpment belt lying inland of the Namib and Kaokoveld desert ecoregions and broadens gradually towards the south. The vegetation is varied in structure, physiognomy and species distribution. This ecoregion has diverse topographic, soil and microclimatic factors. According to Geiss' vegetation map of Namibia (1971), Spitzkoppe is located in the semi-desert and savannah transition vegetation type. This vegetation zone is characterised by a great variety of species, many of which are endemic (Burke, 2001). Typical species of this area are *Euphorbia guerichiana*, succulent stems of *Cyphostemma* sp., *Adenolobus* sp., *Aloe dichotoma*, and *Moringa ovalifolia*.

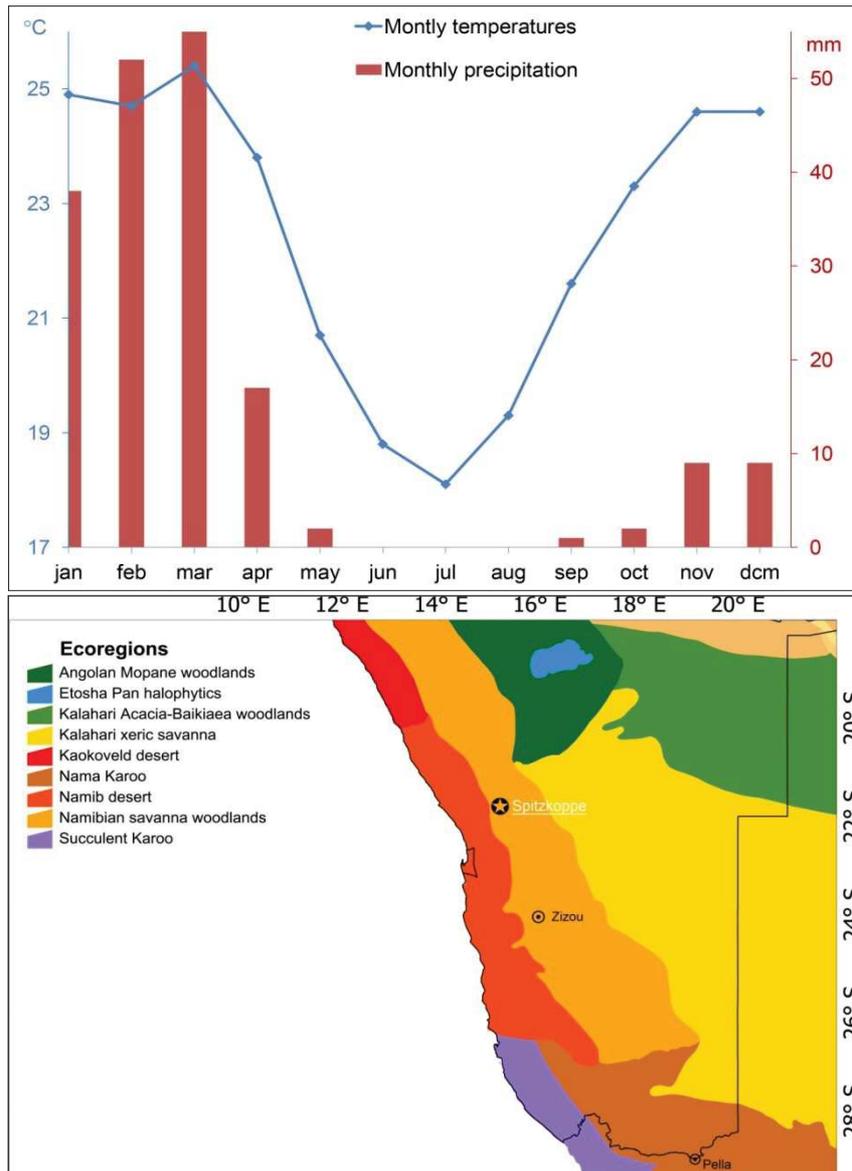


Figure 6. 1 : (Top) Monthly temperatures and precipitation from WorldClim (Hijmans et al., 2005). (Bottom) Eco-region map showing that SPZ middens are located in Namibian Savanna Woodlands in between the Desert and Savanna biome.

Vegetation on the rocky slopes surrounding the midden site is characterised by woody species such as *Searsia* sp. (aka *Rhus* sp.), *Ozora crassinervia*, *Euclea undulate*, *Dombeya rotundifolia*, *Croton gratissimus*, *Commiphora* sp., *Cysphostemma currorii*, *Ficus* sp., shrubs of the Scrophulariaceae, Asteraceae and Euphorbiaceae families, and a mixture of grasses (field observation) (Figure 6. 2d). On the surrounding plains, the vegetation is dominant by grassland with some important C₄ grass species such as *Stipagrostis uniplumis*, *Eragrostis nindensis*, *Schmidtia kalahariensis*, and *Stipagrostis hochsterteriana*. Woody

species are another important component of vegetation on the plains such as *Senegalia senegal*, *S. reficiens*, *Adenolobus garipensis* and *Blepharis pruinosa*, *B. gigantean*, and Capparaceae (Figure 6. 2b). Drainage off the inselbergs concentrates rainfall along drainage lines and more mesic vegetation, such as Oleaceae and Vitaceae, is present in favourable microclimates on the lower-most slopes (Carr et al., 2010).



Figure 6. 2: Spitzkoppe middens (highlight in red) (a), the vegetation at the surrounding plains (b), northern view of Spitzkoppe midden (c), and the granite outcrop vegetation (d).

At the biome scale, we observe that the climate-vegetation relationship can be summarized broadly as following: 1) to the west of study site (in the Desert Biome) where rainfall is low and aridity is high, the vegetation is characterized by the abundance of grass and few numbers of permanent shrubs/trees, 2) moving eastward following an increase in rainfall and humidity, a mixture of grass and shrub growth forms develops (the Nama-Karoo Biome), and 3) moving farther eastward (the Savanna Biome), higher rainfall and lower aridity promote the occurrence of the more abundant woody species. The Spitzkoppe midden site is located at the Nama-Karoo-Desert ecotone, which is known as an effective monitor of global climate change because vegetation dynamics at this area are more sensitive to climate fluctuation than the main bodies of adjacent ecosystems (Noble, 1993). The relationship between ecotone dynamics and climate change, however, is complicated by the

individualistic response of species, the interaction of species, as well as time-lag of vegetation development to climate change. Additionally, non-climatic factor such as soil, topography and aspect also contribute to vegetation dynamics because they can effects on local climate at the study site (Liu et al., 2001). The current vegetation at Spitzkoppe site is similar to the Desert Biome. However, the inselberg habitat favours the occurrences of more mesic woody species. Changes in moisture or temperature would affect the vegetation at the site, with an increase in moisture promoting more mesic vegetation, such as is found in the Savanna or Nama-Karoo biomes, and a decline in moisture would result in a dominance of grass, as is found in the Desert Biome.

6.3. Material and Methods

6.3.1. The Spitzkoppe rock hyrax middens

The Spitzkoppe middens are located in a rock crevice and composed of several sections (Figure 6. 2a). We sampled three sections for pollen and microcharcoal analysis: SPZ2012-1-1 (50.6 cm thick), SPZ2012-1-2 (36.3 cm), and SPZ2013-1(38.3 cm). SPZ2012-1-2 is divided into two sub-sections; SPZ2012-1-2-top (12.5 cm) and SPZ2012-1-2-bottom (14.7-36.3 cm). The samples from each (SPZ2012-1-1 n=85; SPZ2012-1-2-top n=15; SPZ2012-1-2-bottom n=28; SPZ2013-1 n=46) midden are contiguous, with each consisting of a block of material 4-11 mm thick and weighing between ~0.3 g and 2.55 g. For a full description of hyrax middens, their development and the sampling and analytical methodologies for the proxies they contain, see Chase et al. (2012).

The chronology was based on the radiocarbon dates of 55 samples from the midden sections (SPZ2012-1-1, n=25; SPZ2012-1-2-top, n=8; SPZ2012-1-2-bottom, n=9; SPZ2013-1, n=13). The samples were pretreated with 2% HCl for one hour at room temperature to remove carbonates and dried at 60°C. They were then weighed into quartz tubes with an excess of CuO, sealed under vacuum and combusted to CO₂. The CO₂ was converted to graphite on an iron catalyst using the zinc reduction method (Slota et al., 1987). The ¹⁴C/¹²C ratio and ¹³C/¹²C were measured by accelerator mass spectrometry (AMS) at the ¹⁴CHRONO Centre, Queen's University Belfast.

All the radiocarbon ages were calibrated (Table 6. 3, see the appendix) using the Southern Hemisphere calibration data (SHCal13, Hogg et al., 2013; Reimer et al., 2013) and chronologies were estimated with the Bacon v2.2 model (Blaauw and Christen , 2011).

6.3.2. Pollen and microcharcoal analysis

Pollen samples were prepared with standard physical (600 μm sieving and decanting) and chemical (HCl, KOH, HF and acetolysis) methods (Moore et al., 1991). *Lycopodium* tablets were added to the weighed sample to estimate pollen concentrations (Stockmarr, 1971). A minimum pollen sum of 400 grains was counted at a magnification of $\times 400$ under a light microscope and identified with the help of the literature (Scott, 1982; van Zinderen Bakker, 1956, 1953; van Zinderen Bakker and Coetzee, 1959), and photographic and slides reference collections at the University of the Free State, University of Cape Town, and University of Montpellier. Microcharcoal particles were identified as black, completely opaque, angular fragments that occurred in the pollen slides (Clark, 1988). Only charcoal particles $>75 \mu\text{m}^2$ (or longer than 10 μm) were counted under a light microscope at $\times 400$ magnification (Mooney and Tinner, 2011; Patterson et al., 1987). A minimum count of 200 items (given by the sum of charcoal particles and exotic marker grains) was used. Charcoal particles which exceed the mesh-width size of 600 μm are missing from the microscopic charcoal record and particles of ca. $<10 \mu\text{m}$ were not counted in order to ensure correct identification (Mooney and Tinner, 2011). Therefore, our charcoal signal is related primarily to the regional fire signal, with specifically local fires (large particles) and remote, extra-regional fires ($<10 \mu\text{m}$ particles) being excluded. The TILIA program was used to construct the pollen diagrams, and pollen zones are determined by the CONISS method (Grimm, 2011).

Pollen concentrations (C_p) of each taxon were used for PAR calculations of each taxon by multiplying the concentration values by the sedimentation rate (S) of each sample:

$$P = C_p \times S$$

where P is the PAR value of each taxon (grains/gram/mm/year), C_p is pollen concentration of each taxon (number of grains/gram), and S is sedimentation rates expressed as mm/year. This calculation was also applied on microcharcoal to obtain to microcharcoal influx (particles/gram/mm/year).

6.4. Results

6.4.1. Age-depth models and midden accumulation rates

The radiocarbon analyses of the Spitzkoppe middens indicate that each section accumulated continuously, although with different changes in accumulation rate in each section (Figure 6. 3). Accumulation rates range from extremes of 1.70 yr/mm in SPZ2012-1-1 to 157.68 yr/mm in SPZ2012-1-2top. The oldest sections, SPZ2013-1, covers the last ~22 – ~32 cal kBP with an average of accumulation rate ~27 yrs/mm. The SPZ2012-1-2 bottom section is dated back from ~15.7 to ~21.3 cal kBP with an average of accumulation rate of 28 yrs/mm. The SPZ2012-1-2-top section is dated back from 0.9 to ~12 cal kBP with an average of accumulation rates of 97 yrs/mm. There is a hiatus in Spitzkoppe middens from ~15 - ~12 cal kBP. The youngest section, SPZ2012-1-1 is dated back from the present to ~9 cal kBP with an average of accumulation rate of 18 yrs/mm. The overlapped ages between the SPZ2012-1-2-top and SPZ2012-1-1 section centred from 0.9 to 9 cal kBP (Figure 6. 3).

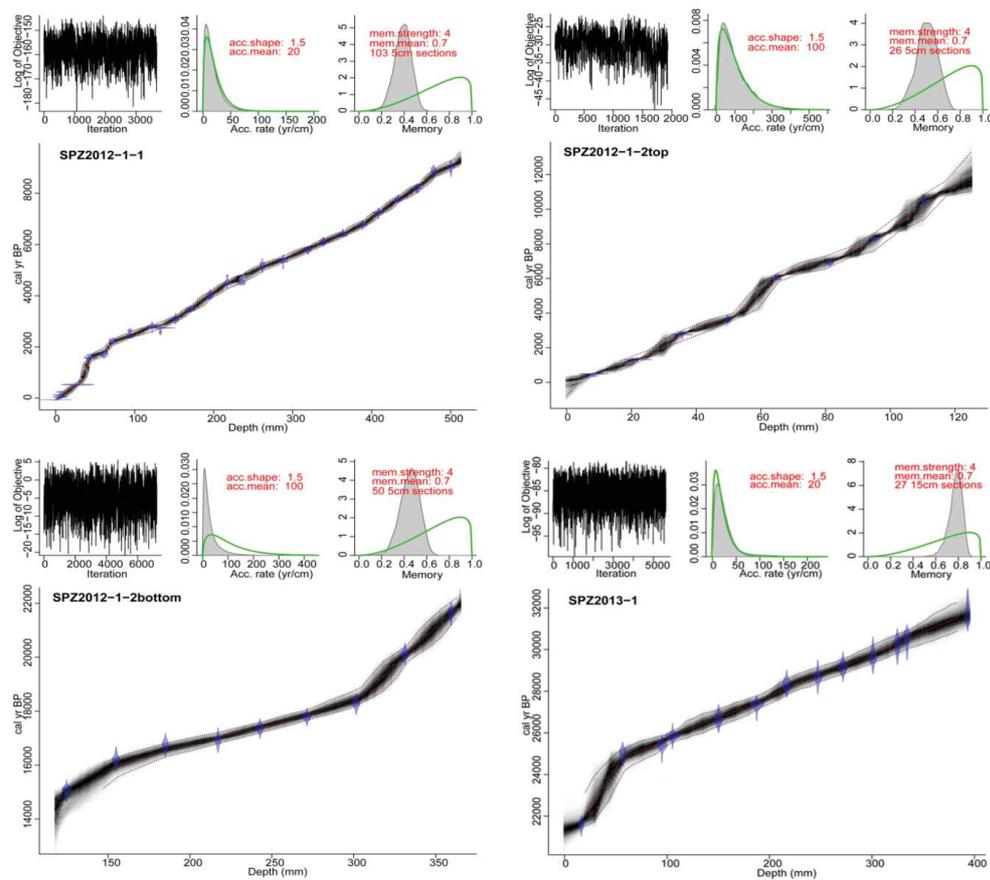


Figure 6. 3: Age models of Spitzkoppe rock hyrax middens SPZ2012-1-1, SPZ2012-1-2top, SPZ2012-1-2bottom, and SPZ2013-1.

6.4.2. Vegetation dynamics inferred from pollen record

The pollen and microcharcoal analysis of the Spitzkoppe middens provide evidence of vegetation change over the last ~32 cal kyr BP. We combined the results of all Spitzkoppe midden sections (SPZ2012-1-1, SPZ2012-1-2 top, SPZ2012-1-2-bottom, and SPZ2013-1) into a single pollen diagram based on the calibrated age order of each sample (Figure 6. 4). This summary pollen diagram shows only the major taxa that can be used to infer the climatic information. Detailed pollen diagrams of each section can be seen in the appendix. PAR diagrams also present here in order to consider the impact of changes in midden accumulation rates. Overall, we observe that the vegetation compositions during the last glacial period differ from the Holocene. The arboreal taxa during the last glacial period were mainly *Rhus*-type, *Olea*, and Menispermaceae while those in the Holocene were similar to present-day woody species such as *Rhus*-type, *Euclea*, *Commiphora*, *Capparaceae*, *Croton*, *Dombeya*, *Moraceae*, and *Senegalia* (Figure 6. 4).

According to the marked variations of pollen data, we have determined some pollen zones throughout the whole record. SPZ-I (~32 – ~26.2 cal kBP), SPZ-II (~26.2 – ~22 cal kBP), and SPZ-III (~22 – ~17 cal kBP) represent the last glacial vegetation, SPZ-IV (~17 – ~15 cal kBP) represent the deglacial period, all derived from SPZ2013-1 and SPZ2012-1-2 bottom section (Figure 6. 4). SPZ-V and SPZ-VI are included the samples from SPZ2012-1 and SPZ2012-1-2 top section representing the vegetation changes from ~12 cal kBP to present. However, the sample resolution in SPZ2012-1-1 section is higher (in average ~100 years/sample) than SPZ2012-1-2 top section (in average ~800 years/sample). SPZ2012-1-1 provides the finer resolution of vegetation fluctuations (multi-decadal to centennial time scale) while SPZ2012-1-2-top provides multi-centennial to millennial vegetation fluctuation during the Holocene. Despite the differences in sample resolution, similar age samples from SPZ2012-1-1 and SPZ2012-1-2-top indicate comparable trends of vegetation change (see detail pollen diagram in appendix).

Pollen and microcharcoal concentrations may be affected by several factors such as differences in midden accumulation mode, hyrax dietary preferences and local conditions of preservation (Chase et al., 2012; Scott et al., 2017). In general, pollen concentrations in middens are higher than other palaeoarchives in the region even in less productive ecosystem such as Namib Desert margins (Gil-Romera et al., 2007, 2006). On one hand, it is possible that slower accumulation rate phases in middens are expected to have the higher pollen

concentrations because there is more time for pollen to deposit into the middens and vice versa for faster accumulation rate phases (in the same ecosystem). On another hand, lower pollen concentrations could occur also during slower midden accumulation phases if there is a reduction in pollen sources (reduction in vegetation density) as well as a reduction in hyrax colony size. SPZ pollen sequences indicate that last glacial pollen concentrations and pollen accumulation rates are higher than those in Holocene. We could not interpret the total pollen accumulation rates to represent the vegetation density, but it is likely that a reduction both pollen concentrations and pollen accumulation rates in the Holocene maybe related to a reduction in vegetation density at Spitzkoppe site.

The microcharcoal in the hyrax middens has helped to shed some light on the interpretations of vegetation dynamics and it may contribute to multi-proxy approaches to paleoclimate reconstructions. In southern Africa, microcharcoal obtained from middens has provided insights of fire history in some biomes such as Fynbos and Savanna Biome (Gil-Romera et al., 2011; Quick et al., 2011). Microcharcoal influx at SPZ indicate a positive relationship with the total pollen accumulation rates along the whole record, and with some pollen taxa such as Poaceae, *Stoebe*-type, *Artemisia*, *Olea*, and *Croton*. This suggests that phases of cool and moisture conditions favour the fire. During the last glacial, a phase of increased microcharcoal influx is observed from ~22 to ~17 cal kBP (Figure 6. 4).

The pollen diagram below focus only on the main taxa in which present continuously and show the remarkable variations along the record. In addition, among those taxa, some of them can be used as an indicator of climatic condition changes such as *Olea*, shrubs of Asteraceae (including *Stoebe*-type, *Artemisia*, *Pentzia*-type), grasses, and succulents of Aizoaceae. *Olea* is an evergreen shrub/tree. *Olea europaea* is found in Namibia with only subspecies of *Olea africana* (Mannheimer and Curtis , 2009). This species is previously reported as a significant contributor to rock hyrax diet (Fourie, 1983). *Olea europaea ssp africana* is a frost and drought tolerant species that at first glance could signal a cool and arid landscape. Alternatively, the co-occurrence of this pollen type with *Stoebe*-type and *Artemisia* indicates a cool and moist condition in the Namib Desert (Scott et al., 2017, 2004). *Stoebe*-type (including *Stoebe* and *Elytropappus*) and *Artemisia* currently occur across southern Africa where there is enough moisture to meet their requirements, and are favoured by cool-growing seasons (Rutherford et al., 2012, 2003; SANBI, 2003). The current arboreal taxa commonly found at the site including *Rhus*-type, *Euclea*, *Commiphora*, Capparaceae,

Croton, *Dombeya*, Moraceae, and *Senegalia*. Among the arboreal taxa, some prefer hot growing seasons, for example, *Dombeya*, *Commiphora*, and Moraceae.

The interpretation of grasses in terms of moisture is site specific depending on which ecosystem grasses being found. For example, in the Namib Desert, grasses grow seasonally after rain but also became a dominant vegetation during long-term droughts in the Namib Desert (Scott et al., 2017). In contrast, in the Nama-Karoo Biome, an increase of grass versus small shrubs may indicate a wetter conditions (Coetzee, 1967; Lim et al., 2016). In the Namib Desert, from mid- to late Holocene, low grass to arboreal pollen ratios may indicate dry conditions that do not favour the shallow-rooted grasses cover, thus pollen from deep-rooted trees became dominant in pollen assemblage (Gil-Romera et al., 2007; Scott, 1996).

6.4.2.1. Last glacial vegetation composition and dynamics

SPZ-I covered from ~32 to ~26 cal kBP indicates the remarkable pollen variations within this period (Figure 6. 4). Very few numbers of cool taxa such as *Stoebe*-type and *Artemisia* were recorded in this interval suggesting a relatively warm, variable conditions. From ~32 – ~30 cal kBP, the pollen assemblage indicates an abundance of succulent Aizoaceae, Liliaceae, and very few numbers of grasses as well as very low pollen accumulation rates. After ~30 cal kBP, an increase of *Rhus*-type occurs, suggesting changes from drier to wetter conditions. From ~30 – ~28 cal kBP, grasses and Asteraceae (including *Pentzia*-type) increased progressively along with *Olea*, *Rhus*-type, and Menispermaceae suggesting the development of karroid vegetation at site. Higher numbers of *Dombeya*, Capparaceae in this interval suggest relatively warm conditions. From ~28 – ~26 cal kBP vegetation is characterised by abundant of Liliaceae, Aizoaceae, *Zygophyllum*, Menispermaceae, and *Olea* while grasses and Asteraceae declined suggesting dry conditions (Figure 6. 4).

SPZ-II (~22 to ~26 cal kBP), vegetation was characterised by *Olea* and a peak of *Artemisia* at ~26 cal kBP and little *Stoebe*-type, suggesting relatively cool and humid conditions. The vegetation then shifted with an increase in Asteraceae (*Pentzia*-type, and *Felicia*), relatively high number of grasses, and higher microcharcoal influx centred at ~25 – ~26 cal kBP suggest the return of karroid conditions. From ~25 – ~22 cal kBP, Asteraceae declined dramatically while grasses decreased slightly. At the same time, Capparaceae, Urticaceae, and *Zygophyllum* increased slightly suggesting drier conditions (Figure 6. 4).

The vegetation fluctuations suggest relative warmth and high amplitude moisture fluctuations. Vegetation shifted from relatively warm and dry karroid conditions at ~32 – ~26 cal kBP with the absence of *Artemisia* and *Stoebe*-type (except some wet spells from ~30 – ~28 cal kBP), toward cool and more humid from ~26 – ~25 cal kBP indicating by more occurrence of *Artemisia* and *Olea* with higher grass proportion.

SPZ-III (~22 – ~17 cal kBP) is characterised by higher numbers of cool taxa such as *Artemisia*, *Stoebe*-type suggesting much cooler temperature and relatively moist conditions during the LGM. Therefore, a declined in grasses and higher numbers of arboreal pollen such as *Olea*, *Rhus*-type, accompanied by increased in microcharcoal influx suggesting that some period of droughts also occurred during this interval (Figure 6. 4). The reduction of grasses during this interval may be explained by lower precipitation and periods of prolonged drought, however, moist conditions occurred under the lower evaporation due to the cooler temperature.

Table 6. 1: Summary of main pollen fluctuation at Spitzkoppe middens.

Age (cal kBP)	Environment	Indicator pollen types
SPZ-VI (0-7)	Warmer, drier condition towards desert condition	<i>Dombeya</i> , <i>Commiphora</i> , lower grasses ratio to arboreal pollen
SPZ-V (12-7)	Warmer, wet condition	<i>Dombeya</i> , <i>Rhus</i> -type, higher grasses ratio to arboreal pollen
SPZ-IV(17-15)	Relatively warm and wet condition	<i>Artemisia</i> , <i>Stoebe</i> -type, <i>Rhus</i> -type, higher grasses
SPZ-III(22-17)	Cooler and moist conditions	<i>Artemisia</i> , <i>Stoebe</i> -type, <i>Olea</i> , <i>Rhus</i> -type
SPZ-II (26-22)	Cool, moist karroid conditions	<i>Artemisia</i> , <i>Stoebe</i> -type, <i>Olea</i> , Asteraceae, grassy
SPZ-I (32-26)	Karroid conditions with some dry and wet spells	Asteraceae, Aizoaceae, Liliaceae

Chapter VI: Spitzkoppe middens, central Namib Desert

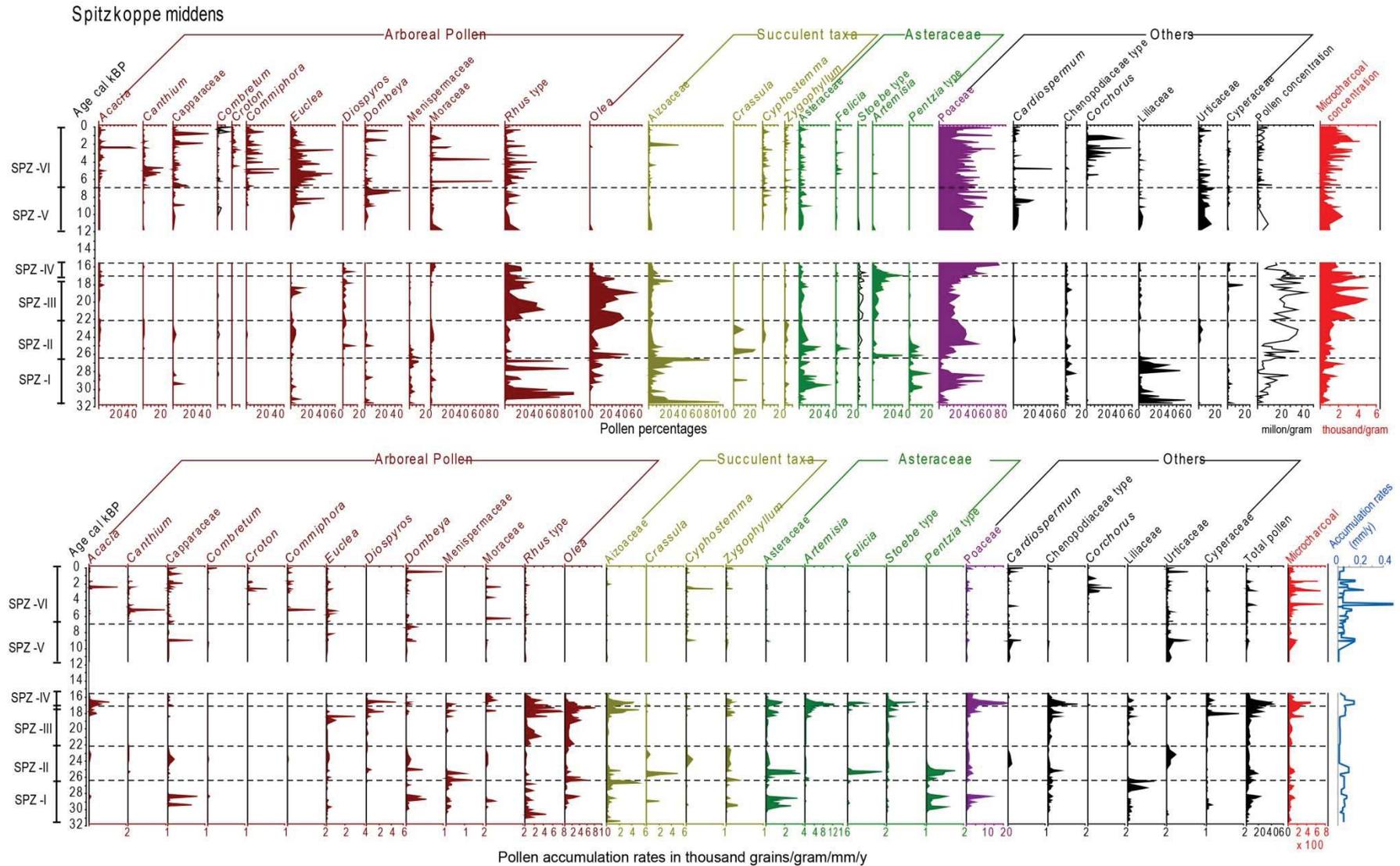


Figure 6. 4:A summarized pollen diagram in percentages and in PARs from all Spitzkoppe midden sections.

6.4.2.2. Deglacial vegetation composition and dynamics

SPZ-IV (~17 – ~15 cal kBP) spans the early portion of the last glacial-interglacial transition (Figure 6. 4). Grasses increased gradually and reached its maximum at ~15.7 cal kBP followed by increasing PARs of *Rhus*-type. In contrast, *Stoebe*-type, *Artemisia*-type and *Olea* were relatively higher at ~17 cal kBP but decreased to lower value at ~15.7 cal kBP. The increase of grasses with the existence of some cool taxa suggest the increased humidity under increased temperature during the deglacial period. The cessation of accumulation was observed from ~15 to ~12 cal kBP in SPZ middens record.

6.4.2.3. Holocene vegetation composition and dynamics

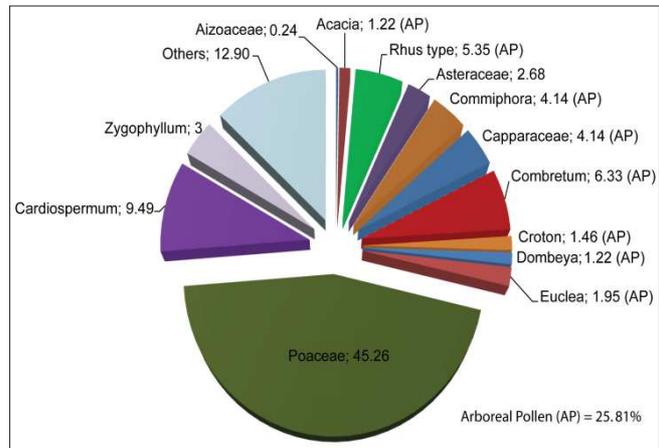
SPZ-V (~12 – ~7 cal kBP), grasses are consistently present with lower arboreal pollen, however, the arboreal species composition in the Holocene differs from arboreal taxa during last glacial period. Arboreal pollen which occurred together with *Artemisia* and *Stoebe*-type during the last glacial period such as *Olea* was replaced by other arboreal taxa such as *Dombeya*, *Euclea*, Capparaceae, and Moraceae. *Rhus*-type was present in both the last glacial period and Holocene (Figure 6. 4). At the same time, Urticaceae became more important in pollen assemblage from the early Holocene. Opposite to the glacial period, Asteraceae shrubs became less important and some cool indicator taxa such as *Artemisia* and *Stoebe*-type diminished across the Holocene. Pollen concentration and pollen accumulation rates reduced dramatically compared to the last glacial period. The combination of a reduction in pollen accumulation rates and the pollen assemblage during this period indicate the warmer and drier conditions during the Holocene compare to the last glacial period. This climate supports the currently xeric savanna woodland vegetation as reflected by the pollen assemblage. However, the generally constant levels of grasses suggest wetter conditions at early Holocene and a progressive increased aridity throughout the Holocene.

SPZ-VI (~7 cal kBP to present) indicates a reduction of grasses and relatively increased of dry arboreal taxa such as *Commiphora*, *Dombeya*, *Euclea*, Capparaceae, *Croton*, and *Senegalia* (Figure 6. 4). These arboreal taxa reflect the present-day woody species at the study site commonly found on the hill slopes near midden shelter, while grasses are more common on the surrounding plains. The presence of arboreal pollen taxa in this period reflects warmer and drier condition than the early Holocene.

6.5. Discussion

6.5.1. Climate and vegetation dynamics at Spitzkoppe

The uppermost sample in SPZ2012-1-1 indicates that grasses represent almost half of the total pollen sum (45.26%) following by the arboreal taxa (AP, 25.81%) such as *Rhus*-type, *Commiphora*, *Combretum*, *Croton*, *Dombeya*, *Capparaceae*, *Euclea*, and *Senegalia* (Figure 6. 5). These arboreal



taxa are currently present near the midden site. The isotopic analysis from Figure 6. 5: Uppermost samples indicating pollen percentages.

previously published work at Spitzkoppe suggested that C_3 plants (shrubs and trees) contribute significantly to the animals' diet (~56% in May 2013 and ~77% in July 2014) (Carr et al., 2016; Chase et al., 2009). A lower percentage of AP (25.81%) in the uppermost sample could be explained by higher pollen production and the wind-transport pollen of grasses over the arboreal taxa. The isotopic signal reflects primarily the alimentation of animals whereas pollen data in our samples more broadly represents the local/regional vegetation because it reflects animal diet, airborne pollen, and pollen that is brought to the midden on the animals' fur.

Fire in the arid western part of Nama-Karoo and Desert Biome is extremely rare due to insufficient accumulated fuel to support fire (Mucina and Rutherford, 2006). In the eastern Nama-Karoo Biome, occasional fires may occur after successive years of good rainfall in combination with light grazing, resulting in an increased fuel load (Palmer et al., 1999). Fire is more common in the Savanna Biome and it is one of the important factors for maintaining the ecology of the savanna. Fire and grazing helps to prevent the dominant of woody elements in the savanna ecosystem because grasses are generally more tolerant of fire than shrubs and woody elements. The regional microcharcoal derived from marine sediment cores off the Namibia suggest that phases of increased fire occurred under wetter and cooler climates, owing to a shift in rainfall amount and seasonality (Daniau et al., 2013). Unfortunately, the chronology from this core ended at ~30 cal kBP so that we cannot

compare microcharcoal influx from our study to this record. Microcharcoal influx at Spitzkoppe middens show higher values from ~22 cal kBP to ~17 cal kBP while the total pollen accumulation rates were also high. Microcharcoal concentrations are high both in Wonderkrater and Tswaing sites after c. 27 cal kBP suggesting the burning is more intense (Scott, 2016). In relatively dry areas, good moisture conditions may provide more plants growth and fuel, which may result in more natural and human-induced fires during seasonal biomass drying (cf. Scott, 2002). A prolonged annual dry season combined with relatively rapid rates of fuel accumulation creates conditions conducive to frequent fire in southern Africa (Archibald et al., 2009). An interesting question to address is the relationship between fuel availability and fire frequency, assuming that lush grass cover caused more fires. To answer to this hypothesis, we compared grasses pollen with microcharcoal influx for the whole record. Results suggest that periods of higher microcharcoal influx are in phase with period of higher grasses pollen ($r= 0.45$, $p < 0.05$) (Figure 6. 6). In addition, microcharcoal influx also show a strong positive relationship with some cool and moist taxa such as *Artemisia*, *Stoebe*-type, *Rhus*-type, and *Olea* during the last glacial period. During the Holocene, microcharcoal influx show a positive relationship with grasses ($r= 0.44$, $p < 0.05$) as well as warm and dry arboreal taxa such as *Croton* ($r= 0.52$, $p < 0.05$).

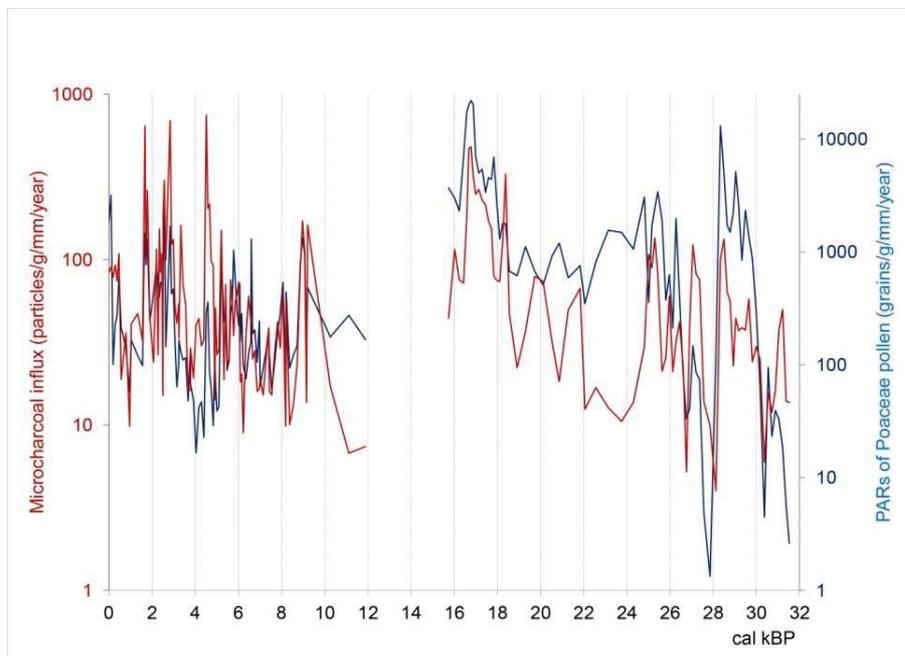


Figure 6. 6: PARs values of Poaceae and microcharcoal influx at Spitzkoppe.

We cannot distinguish whether the microcharcoal influx was derived primarily from regional or local fires, but they both seems coherent with previous studies suggesting that fire was more intense after c. ~27 cal kBP (Scott, 2016; 2002). A positive relationship of grass

pollen and microcharcoal is also indicated by pollen and microcharcoal data at the Zizou midden site. The microcharcoal influx at this site was higher from ~24 to ~18 cal kBP in phase with higher total pollen accumulation rates, accompanied by peaks of dry arboreal taxa such as Capparaceae and moderate numbers of grasses (see in chapter 5). Similar to Zizou, the microcharcoal influx at Spitzkoppe show a positive trend with total accumulation rates and grass pollen, suggesting that phases of more fire occurred during periods of increased fuel availability (Figure 6. 7). During the last glacial period, the maximum microcharcoal influx is concurrent with higher numbers of cool and moist taxa such as *Stoebe*-type, *Artemisia*, and arboreal taxa such as *Rhus*-type and *Olea*. The present-day fires in the Savanna Biome occur during the dry winter season, when grass biomass becomes dry and flammable (Scott, 2002). An increase of grass biomass in the Savanna or Nama-Karoo biome is believed to be linked to increasing rainfall amounts in the previous two years. However, we cannot draw any conclusions about this due the sample resolution. After all, grass biomass is an important source for fire ignition and phases of intense fires occurred cool and moist conditions from ~22 to ~17 cal kBP at Spitzkoppe as well as at Zizou. Our results show a coherent signal of regional fire history, suggesting that phases of increase fire activity occurred under cool and moist conditions (Figure 6. 7).

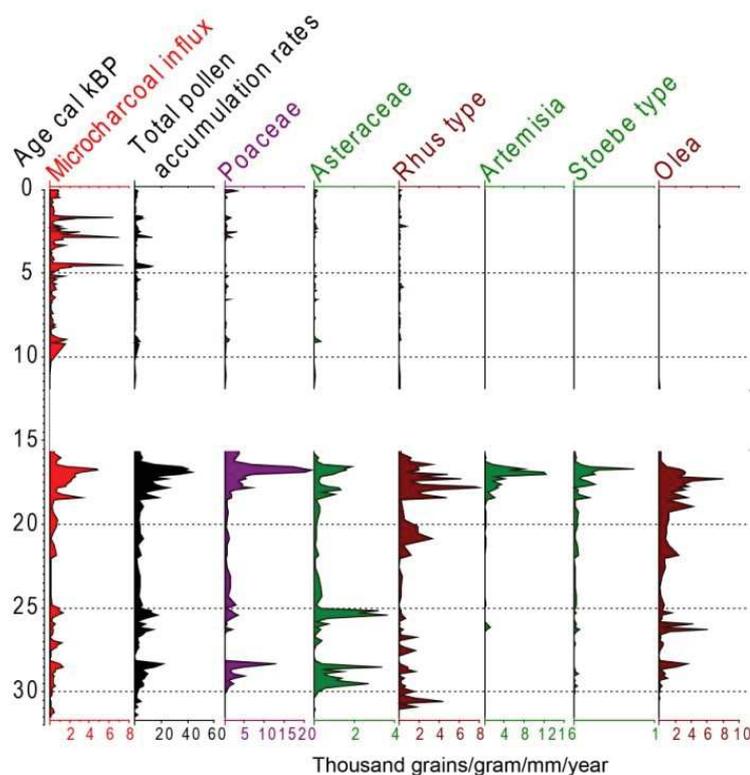


Figure 6. 7: Microcharcoal influx and some main taxa at Spitzkoppe middens.

6.5.1.1. Last glacial climate and vegetation dynamics (~32 - ~15 cal kBP)

Fossil pollen data from the Spitzkoppe middens suggest that climate conditions were characterised by a generally cooler temperatures and more humid conditions during the glacial period relative the Holocene. These results are coherent with other available terrestrials pollen records from southwestern African (Lim et al., 2016; Scott et al., 2017, 2004, 1995). *Stoebe*-type is known as a reliable temperature indicator for past climate reconstruction in southern Africa (Chevalier and Chase, 2015; Lim et al., 2016; Scott et al., 2012). This pollen type was also reported elsewhere in southern Africa during the last glacial period (Scott, 2016). Recently, Scott et al. (2017) suggest that the presence of this pollen type in the Namib Desert indicates lower temperatures in addition to improved moisture availability, given its modern distribution (Figure 6. 8). Spitzkoppe pollen sequences show that some taxa only occurred during the last glacial period and then disappeared in the Holocene, such as *Artemisia*, *Stoebe*-type, and *Olea*. The modern distribution of these taxa indicates that they are more common in the more humid areas, thus their occurrence at the study site from ~22 – ~17 cal kBP suggest cool and moist conditions (Figure 6. 8). From ~32 – ~24 cal kBP, higher numbers of warm arboreal taxa such as *Dombeya* and only trace amounts of *Artemisia* and *Stoebe*-type suggest relatively warm conditions. Pollen analysis from elsewhere in the Namib Desert also suggests relative warm conditions during MIS3 (Scott et al., 2017). During the last glacial-interglacial transition (~15 – ~17 cal kBP), *Stoebe*-type and *Artemisia* sharply declined, suggesting increased temperatures toward the Holocene (Figure 6. 8). In the early Holocene, increased warmth conditions at the study site leads to the disappearance of these cool taxa. In addition, greater numbers of warm taxa like *Dombeya*, *Commiphora* became more important in Holocene pollen assemblage. Cool glacial and warm Holocene conditions inferred from Spitzkoppe pollen assemblages are consistent with regional temperature reconstruction in southern Africa, e.g. pollen (Lim et al., 2016; Scott et al., 2017, 2012, 2004, 1995; Chevalier et Chase, 2015; Truc et al., 2013), and noble gasses from the Stampriet Aquifer (Stute and Talma, 1998).

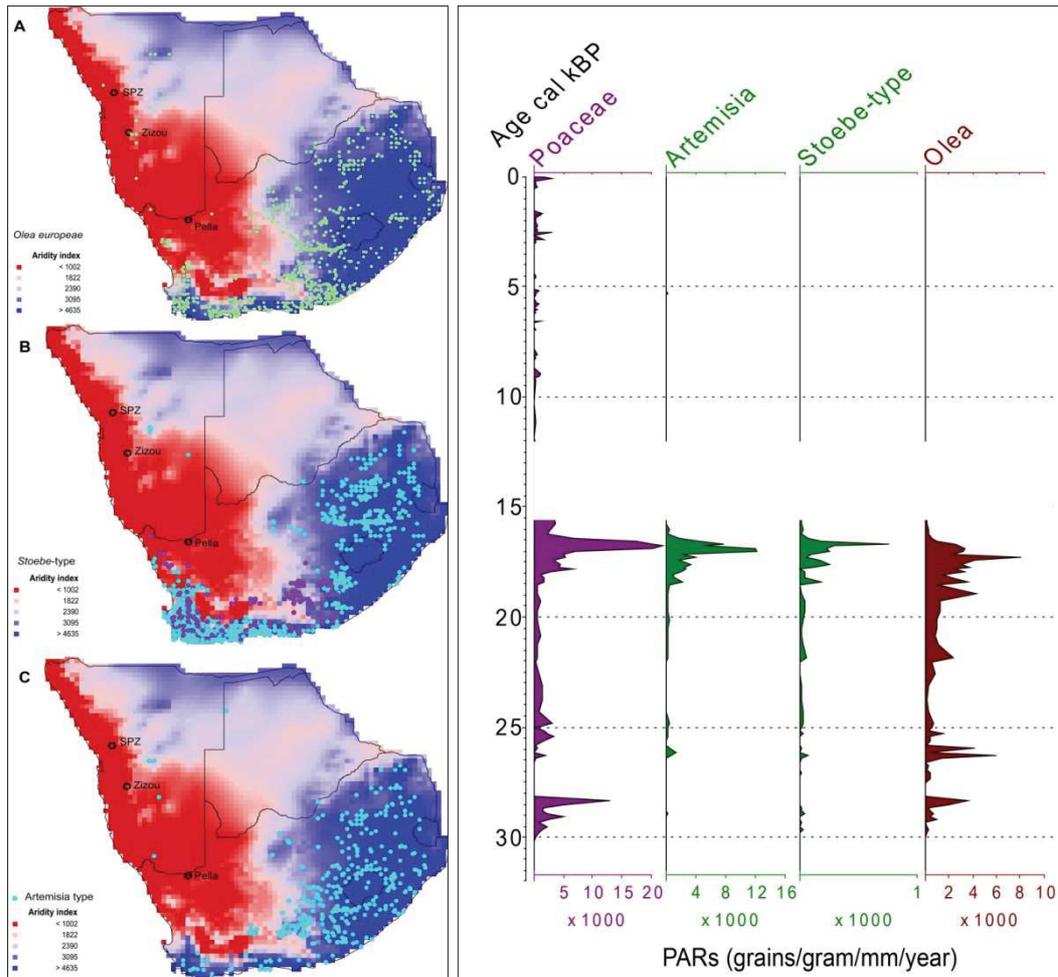


Figure 6. 8: Pollen accumulation rates of *Poaceae*, *Olea*, *Artemisia* distribution along aridity gradient map (except *Poaceae*)(Trabucco and Zomer, 2009).

The water availability is generally considered as the greatest limited factor of plant growth and distribution (Woodward, 1987). In an arid region, precipitation –amount, time, and space– are the important factor controlling successful of plants germination and establishment (Gil-Romera et al., 2006). Therefore, the inference of moisture changes from fossil pollen data is more complicated than temperature, because temperatures has a direct influence on plant survival. Beside changes in precipitation amount, the moisture availability for plant growth is also influenced by temperatures. For instant, moisture availability is higher under the lower temperatures at a given amount of precipitation. In addition, the capacity of plant species to adapt to changes in moisture as well as species interactions and competitions also could modify the moisture reconstructions from fossil pollen assemblages, especially in regions with very few modern vegetation ecology studies like the Namib Desert. The available terrestrial pollen records dated back to MIS 3 and MIS 2 from two sites; Brandberg and Mirabib (west of Spitzkoppe), suggesting relatively moist conditions during

MIS2 and MIS3 (Scott et al., 2017). It is interesting to compare the Spitzkoppe pollen sequences with Brandberg and Mirabib's, but there are no samples between ~37.2 to ~21 cal kBP at the latter two sites. At ~21 cal kBP, lower temperatures and increased moisture availability are inferred from the greater number of *Stoebe*-type in Brandberg pollen sequence. The authors inferred that increased moisture in this period occurred under lower temperature resulting from lowered evapotranspiration, making any precipitation more effective (Scott et al., 2017). Similarly, the reconstruction of summer rainfall, annual temperature, and aridity index values from pollen data in southeast Africa also suggested that there was elevated humidity in last glacial despite lower precipitation during the last glacial period (Chevalier and Chase, 2015; 2016). At Spitzkoppe, similar pollen types are registered in pollen sequences with increased abundance of *Stoebe*-type, *Artemisia*, and *Olea* ~22 to ~17 cal kBP. The occurrence of *Olea* and *Artemisia* during the last glacial period may be associated with colder, more humid conditions under lower evaporation due to lower temperatures, as suggested by Scott et al. 2004 and 2017.

In savanna ecosystem, the fluctuation between grass and woody elements can be linked to the changes in the rainfall amount. Spitzkoppe site is classified in the Namibian Savanna Woodland, but the vegetation aspects at the site currently look like the Namib Desert, so, the interpretation of fluctuation between growth forms such as trees/shrubs and grass as the influence of changes in rainfall amount need to take into account the differences of these growth forms in response to rainfall in adjacent ecosystems. In the Nama-Karoo Biome, grass dominates under two opposing climate regimes: 1) along its most arid regions, where there are insufficient groundwater to support perennial shrubs, and 2) with increasing rainfall or more regular rainfall to the east at its transition to the Grassland Biome (Lim et al., 2016). In the Desert Biome, grass thrives seasonally after rains, but also remain dominant in the long-term even during the driest phases (Scott et al., 2017). In the xeric Savanna Biome according to rooting-niche separation model (Knoop and Walker, 1985), over shorter timescale, more and/or more frequent rains would favour the development of shallow-rooting grasses in the landscape that is otherwise characterised by protracted droughts, and thus the prevalence of trees that are able to exploit deeper water resources. Over longer timescale, however, the development of shrubs/trees takes place under humid conditions (Chase et al., 2010). In arid ecosystems, such as the study area, rainfall events may generate new grasses but trees cover seems not change due to the fast-growing capacity of grasses. We hypothesis

that if there were significant changes in humidity, there would be changes in tree species compositions.

The Spitzkoppe pollen sequences show the different arboreal species compositions between the last glacial and interglacial periods (Figure 6. 4). This may be caused by likely changes in humidity. The main arboreal species occurring in the last glacial period were *Rhus*-type, Menispermaceae, and *Olea*, accompanied by *Artemisia* and *Stoebe*-type. In the Holocene, arboreal elements are *Rhus*-type, *Euclea*, *Dombeya*, *Commiphora*, *Senegalia*, Capparaceae etc. (Figure 6. 4). These woody taxa are known to be well adapted to the arid conditions. Additionally, higher diversity of growth forms are observed in glacial pollen assemblages such as trees, shrubs, geophytes (Liliaceae), succulents, and grasses. In short, last glacial vegetation compositions suggest more mesic climatic conditions and the vegetation shifted into xeric savanna as the climatic conditions became warmer and drier during the Holocene.

In fossil pollen data, we must recognise the fact that the tree/grass pollen ratios are relative and we do not know the actual cover of either (a decline in one may result in higher percentage of other) (Gil-Romera et al., 2007). Moreover, we observed that current vegetation at the site is characterised by woody species on rocky slopes (closer to hyrax shelter) and grasses are only dominant on the surrounding plains (further from hyrax shelter). Hyraxes have restricted feeding ranges (~60 m of their shelter (Sale, 1965)). While grasses produce large amounts of pollen and are wind-pollinated, it is possible that grass pollen from the surrounding plains is also deposited into the middens. Thus, the grass-rich pollen assemblages in our Spitzkoppe midden cannot be distinguished whether grasses increased on the rocky slopes closer to hyrax shelter or on the surrounding plains. During the last glacial period, increased grass percentages occur at ~30 – ~28 cal kBP and ~26 – ~22 cal kBP. Increased humidity prior to ~26 cal kBP promoted the development of grass and more mesic vegetation at the site. This is possibly the result of more and/or more regular rains or a reductions in potential evapotranspiration that favour the shallow rooting-grasses. The increased moisture from ~22 – ~17 cal kBP was more likely the result of cooler temperatures rather than an increase in precipitation due to a decline in grasses and dominance of arboreal taxa (*Rhus*-type and *Olea*). The slight reduction of precipitation during the LGM is due to lower sea-surface temperatures (SSTs) in cold Benguela Current (Farmer et al., 2005; Kim et al., 2002). These cooler SSTs limited moisture transport from the Atlantic to Namibian

coastal plains. Our results are not consistent with findings from marine core in which suggested that grasses were abundant during last glacial period concurrent with the Southern Hemisphere (SH) insolation maximum indicating wetter conditions (Collins et al., 2014). In contrast, phases of increased grass proportions during the last glacial period at Spitzkoppe occurred in SH insolation minima. This suggests that lower temperatures during the SH insolation minima also play important role in the increased humidity. A clear vegetation shift is evidenced at the glacial-interglacial transition ($\sim 17 - \sim 15$ cal kBP) with the dramatic decline of cool and humid taxa such *Olea*, *Artemisia*, and *Stoebe*-type (Figure 6. 8). These taxa almost disappeared from the records throughout the Holocene. In contrast, grass pollen increased remarkably and reached its maximum percentage in this period. The increased grass pollen during last glacial-interglacial transition is also recorded in other midden sites in Namibia, at Pella (Lim et al., 2016), Zizou midden (see in chapter 5) and the Brandberg (Scott et al., 2004). The increase of grass pollen and the decline of Asteraceae from 16 – 10 cal kBP in Pella midden was associated with the increasing water availability under the increasing temperature and the influence of low upwelling intensity, allowing for increased local convection and the incursion of easterly air masses (Lim et al., 2016). This phase of increasing rainfall under increasing temperature resulted in increasing humidity, which supported the development of grasses at Spitzkoppe.

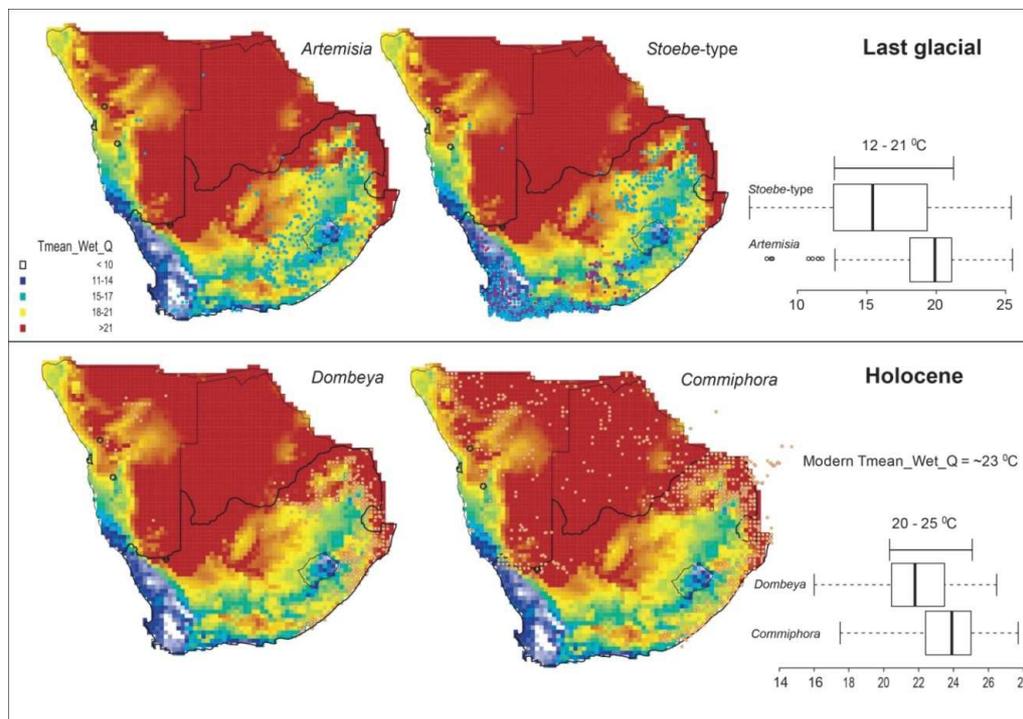


Figure 6. 9: Taxa showing a different temperature of growing season between last glacial and Holocene.

The phenology of present-day vegetation at Spitzkoppe is predominantly determined by summer rainfall. Scott et al., 2017 stated that the inference of rainfall seasonality from pollen data is complicated. Temperature during the growing season also plays important role in vegetation development, e.g. germination, photosynthesis, reproduction, etc.. It is observed that during last glacial period, the growing season is cooler, supported by the occurrence of *Stoebe*-type and *Artemisia*. During the Holocene, warmer growing seasons support the development of *Dombeya* and *Commiphora* and the disappearance of cooler taxa (Figure 6. 9). Therefore, we could not rule out if this different growing season is related to changes in rainfall seasonality (from winter to summer rain) or it is because of lower temperatures in general during the last glacial period. The cooler temperatures during the last glacial may facilitate water-use efficiency (limit water loss) for vegetation development, which means more effective rainfall for vegetation growth in an ecosystem. The winter-vegetation (*Restionaceae* pollen as suggested by Shi et al., 2000,2001) was absent during the last glacial period in Spitzkoppe pollen sequences. This finding supports the evidence from all available terrestrial pollen records in the region (Scott et al., 2004, 2017; Lim et al., 2016). In short, the inferences of northward migration of winter-rain vegetation during the last glacial period from marine sediment cores needs to be reconsidered

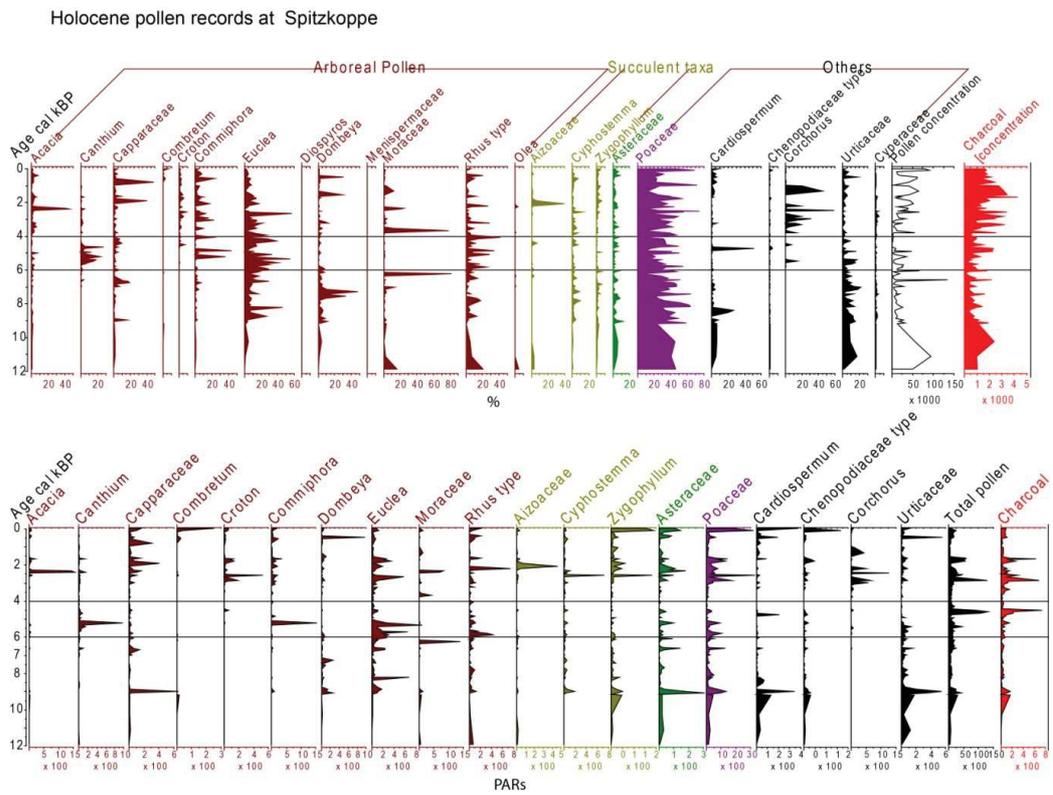


Figure 6. 10: The Holocene pollen diagram in percentages and in PARs at Spitzkoppe.

6.5.1.3. Holocene climate and vegetation dynamics (12 cal kBP–present)

The tree:grass ratio can be used as a climatic indicator particularly the moisture availability in the environment in savanna ecosystems (Gil-Romera et al., 2007, 2006). In Namibia, some studies have interpreted higher grass pollen as the indicator of increasing rainfall during the mid-Holocene (Gil-Romera et al., 2007, 2006; Scott et al., 1991). Gil-Romera et al., 2006 suggested higher than modern moisture availability at the edge of the northern Namib Desert between ~6 - ~1 cal kBP. In north-western Namibia, at the transition of the Nama-Karoo and Desert biomes, pollen records from hyrax midden suggested more frequent precipitation than present from ca. 6 to 4 cal kBP and 1.6 to 1.2 cal kBP with high values of grasses (Gil-Romera et al., 2007). Our records from ~6 to ~4 cal kBP show variability of grass proportion, but the trend seems to show a reduction of grasses from this period and increased arboreal pollen (Figure 6. 10).

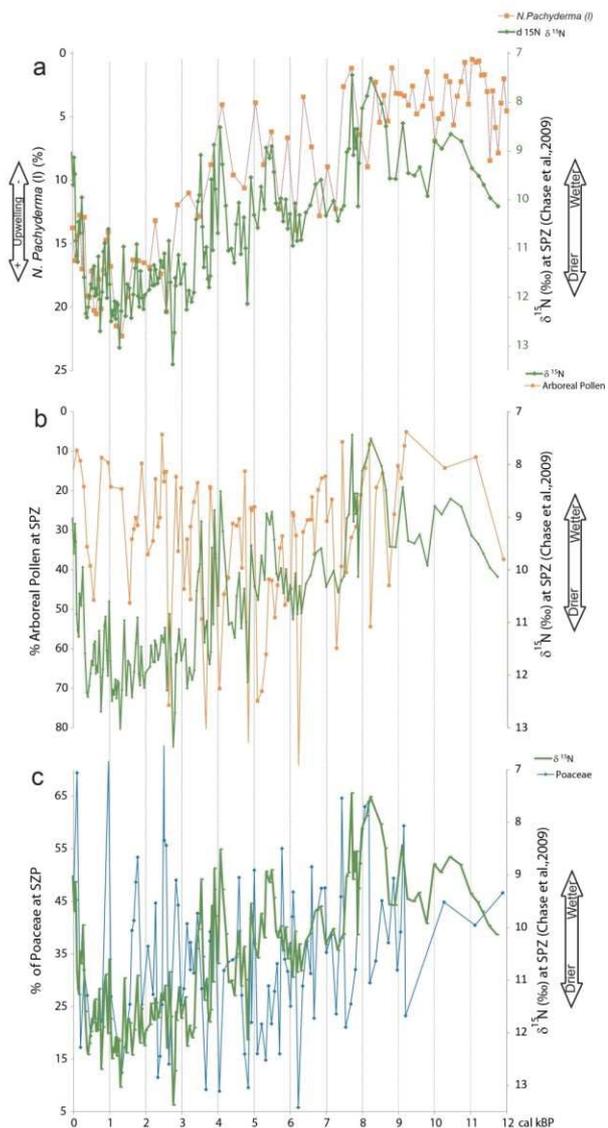


Figure 6. 11: Comparison (a) $\delta^{15}\text{N}$ stable isotopes from the same middens (Chase et al., 2009) with *Neogloboquadria pachyderma* percentages from Benguela upwelling region (Farmer et al., 2005), (b) Arboreal pollen, and (c) Poaceae.

The ^{13}C data from the Spitzkoppe middens suggested a progressive aridification from c. 6 – 2.5 cal kBP with the progressive reduction in grass-derived organic matter inputs into animal diets (Chase et al., 2009; Carr et al., 2010). This is consistent with a slight reduction of grasses and increased of arboreal pollen in our Spitzkoppe pollen sequence from ~7 to ~3 cal kBP (Figure 6. 10). A strong positive correlation between the midden $\delta^{15}\text{N}$ data and coastal upwelling intensity is also identified (Figure 6. 11, a). As a more sensitive and direct proxy for water availability, $\delta^{15}\text{N}$ values indicate phases of increased humidity 8.7 – 7.5 cal

kBP, 6.9 – 6.7 cal kBP 5.6 – 4.9 cal kBP and 4.2 – 3.5 cal kBP. We compare grass and arboreal pollen percentage to see the increasing moisture trend during the Holocene (Figure 6. 11, b & c). Grasses show a positive relationship with most of the increased humidity phases from early Holocene to ~6 cal kBP except at 5.6 – 4.9 cal kBP. These differences could be linked to dietary bias or differing sampling resolutions. We observed that the relationship between grass pollen and $\delta^{15}\text{N}$ changes between the early and mid-Holocene. From ~12 – ~7 cal kBP (wetter) pollen spectra shows more grasses, while from ~7 – ~3 cal kBP (drying) grasses decrease. After ~3 cal kBP (significantly drier) the proportion of grasses increases (Figure 6. 11). This latest phase likely represents a Desert Biome dynamic, with reduced groundwater precluding the development of trees/shrubs (cf. Lim et al., 2016).

6.6. Conclusions

The Spitzkoppe midden provides a record of vegetation change during the last ~32 cal kyr BP in the central Namib. The main results we found in this study are:

- A colder glacial period (~32 – ~17 cal kBP), indicated by the abundance of *Artemisia* and *Stoebe*-type in pollen assemblage.
- Glacial-age conditions supported more mesic arboreal taxa such as *Olea* and Menispermaceae, shrubs of the Asteraceae family including *Artemisia*, *Stoebe*-type and *Pentzia*-type. Relatively higher humidity during this period supports the shrubby grassland with karoo shrubs and wild olives.
- Phases of increased microcharcoal influx took place under cooler and moister conditions favouring the development of more vegetations at the site. Fires were more intense under phases of increased biomass.
- The last glacial-interglacial transition (~17 – ~15 cal kBP) experienced increasing water availability, with maximum grass development.
- Maximum Holocene humidity occurred between ~12 – ~7 cal kBP, followed by a trend of increasing progressive aridity throughout the Holocene. This trend is evident in the pollen record and is confirmed by isotopic data from the same midden site.
- The vegetation at the site shifted to the xeric savanna woodland, represented by present-day woody species compositions.

- Rapidly increased aridity at the site after ~3 cal kBP enabled the increase of grasses in the study area. The vegetation dynamics in this period are similar to the condition in the Desert Biome to the west of study site.

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Appendix

Table 6. 2: The current climate data at study site (Hijmans et al., 2005; Trabucco and Zomer, 2009)

Climatic variables	Value
Tmean_ann	20.2 °C
Tmax_Warm_M	30.7 °C
Tmin_Cold_M	8.1 °C
Tmean_Wet_Q	22.8 °C
Tmean_Dry_Q	16.8 °C
Tmean_Warm_Q	22.8 °C
Tmean_Cold_Q	16.8 °C
Prec_ann	106 mm
Prec_Warm_Q	80 mm
Prec_Cold_Q	0 mm
Aridity	556

Table 6. 3: Radiocarbon ages and calibration information for the SPZ2013-1, SPZ2012-1-2 top, SPZ2012-1-2 bottom, and SPZ2012-1-1 hyrax middens.

Sample	Depth (mm)	¹⁴ C age yr BP	1 sigma error	calibration data	95.4 % (2σ) cal age ranges	relative area under distribution
SPZ-2012-1-1						
surface	0	-62	5	SHCal13; SHZ1_2	*cal BP -6.24- -5.95	0.825
					*cal BP -6.75 - -6.67	0.175
SPZ2012-1-1-5	5.898	111	19	SHCal13; SHZ1_2	*cal BP 26 - 59	0.597
					*cal BP 115- 137	0.346
					*cal BP 232-238	0.055
					*cal BP -6- -6	0.001
					*cal BP -5- -5	0.000
SPZ1-1.005	27.983	547	26	SHCal13	cal BP 506-548	1

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SPZ-1-1.05	43.964	1728	24	SHCal13	cal BP 1535-1619	0.779076
					cal BP 1653-1698	0.220924
SPZ1-1.15	61.111	1836	36	SHCal13	cal BP 1611- 1758	0.74146
					cal BP 1761- 1823	0.25854
SPZ-1-1.1	72.633	2250	23	SHCal13	cal BP 2153- 2316	1
SPZ1-1.25	93.964	2458	27	SHCal13	cal BP 2349- 2517	0.772888
					cal BP 2821- 2843	0.260516
					cal BP 2633- 2698	0.1633
					cal BP 2588- 2616	0.052305
SPZ-1-1.2	122.084	2726	39	SHCal13	cal BP 2744- 2866	1
SPZ-1-1.3	132.578	2643	22	SHCal13	cal BP 2707- 2778	0.995802
					cal BP 2622- 2627	0.004198
SPZ1-1.35	151.645	2974	26	SHCal13	cal BP 2965-3174	1
SPZ-1-1.4	171.124	3290	24	SHCal13	cal BP 3397- 3561	1
SPZ1-1.45	195.678	3732	39	SHCal13	cal BP 3900- 4104	0.895764
					cal BP 4106- 4149	0.104236
SPZ-1-1.5	217.215	4077	33	SHCal13	cal BP 4418- 4616	0.964513
					cal BP 4765- 4784	0.035487
SPZ1-1.55	235.527	4100	27	SHCal13	cal BP 4424- 4629	0.905113
					cal BP 4762- 4798	0.085872
					cal BP 4637- 4642	0.00457
					cal BP 4683- 4687	0.004444
SPZ-1-1.6	261.522	4570	35	SHCal13	cal BP 5046- 5205	0.638606
					cal BP 5210- 5312	0.361394
SPZ1-1.65	287.996	4680	30	SHCal13	cal BP 5341- 5467	0.793406
					cal BP 5302- 5339	0.206594
SPZ-1-1.7	319.341	5098	31	SHCal13	cal BP 5713- 5909	0.994273
					cal BP 5667- 5671	0.005727
SPZ1-1.75	338.682	5367	32	SHCal13	cal BP 5992- 6211	0.980318

Chapter VI: Spitzkoppe middens, central Namib Desert

					cal BP 6248- 6264	0.019682
SPZ-1-1.8	363.442	5658	32	SHCal13	cal BP 6307- 6472	1
SPZ1-1.85	388.408	5980	32	SHCal13	cal BP 6669- 6859	0.985127
					cal BP 6871- 6879	0.014873
SPZ-1-1.9	408.641	6363	29	SHCal13	cal BP 7167- 7317	1
SPZ1-1.95	433.470	6975	36	SHCal13	cal BP 7674- 7852	0.994066
					cal BP 7908-7913	0.005934
SPZ-1-1.10	458.092	7424	38	SHCal13	cal BP 8151- 8332	0.867449
					cal BP 8048- 8099	0.092554
					cal BP 8101- 8121	0.026377
					cal BP 8131- 8141	0.01362
SPZ1-1.105	478.257	8062	39	SHCal13	cal BP 8720- 9020	1
SPZ2012-1-1-6	500.411	8137	39	SHCal13	cal BP 8968- 9137	0.883624
					cal BP 8781- 8832	0.047708
					cal BP 8862- 8919	0.041067
					cal BP 9176- 9203	0.013837
					cal BP 9220- 9241	0.010717
					cal BP 8954- 8962	0.003048
SPZ2012-1-2top						
SPZ2012-1-2-1	8.287	448	22	SHCal13	cal BP 450- 508	0.939187
					cal BP 339- 353	0.060813
SPZ-1-2_1.0.5	21.917	1460	24	SHCal13	cal BP 1289- 1358	1
SPZ-1-2 1.1	35.684	2700	28	SHCal13	cal BP 2742- 2844	1
SPZ-1-2_1.1.5	49.725	3429	37	SHCal13	cal BP 3549- 3742	0.925853
					cal BP 3491- 3534	0.045337
					cal BP 3795- 3818	0.024236
					cal BP 3483- 3489	0.003875
					cal BP 3755-3756	0.000699
SPZ-1-2 1.2	64.725	5277	26	SHCal13	cal BP 5915-6027	0.798536

Chapter VI: Spitzkoppe middens, central Namib Desert

					cal BP 6077- 6117	0.11438
					cal BP 6151- 6176	0.059541
					cal BP 6046- 6066	0.027543
SPZ-1-2_1.2.5	81.369	6091	37	SHCal13	cal BP 6780- 7006	0.990047
					cal BP 7133- 7140	0.005921
					cal BP 6757- 6762	0.004032
SPZ-1-2 1.3	95.068	7517	31	SHCal13	cal BP 8199- 8373	1
SPZ-1-2_1.3.5	110.342	9308	42	SHCal13	cal BP 10281- 10571	1
SPZ2012-1-2bottom						
SPZ-1-2 1.4	124.725	12727	48	SHCal13	cal BP 14839- 15288	1
SPZ-1-2 1.5	154.930	13519	66	SHCal13	cal BP 15989- 16487	1
SPZ2012-1-2-2	184.999	13886	57	SHCal13	cal BP 16491- 17007	1
SPZ-1-2 2.1	217.122	13992	54	SHCal13	cal BP 16636- 17149	1
SPZ-1-2 2.2	242.738	14309	52	SHCal13	cal BP 17155- 17570	1
SPZ-1-2 2.3	271.437	14657	50	SHCal13	cal BP 17615- 17975	1
SPZ-1-2 2.4	301.505	15088	63	SHCal13	cal BP 18050- 18458	1
SPZ-1-2 2.5	331.300	16731	64	SHCal13	cal BP 19919- 20364	1
SPZ2012-1-2-3	359.519	17918	72	SHCal13	cal BP 21409- 21886	1
SPZ2013-1						
SPZ2013-1 1	16.325	17866	84	SHCal13	cal BP 21311- 21864	1
SPZ2013-1-1.1	56.658	20805	97	SHCal13	cal BP 24593- 25347	1
SPZ2013-1 2	95.070	21102	119	SHCal13	cal BP 25110- 25692	1
SPZ2013-1 3	105.377	21618	126	SHCal13	cal BP 25630- 26076	1
SPZ2013-1-3.1	150.319	22426	130	SHCal13	cal BP 26261- 27100	1
SPZ2013-1-3.2	187.515	23073	128	SHCal13	cal BP 27089- 27592	1
SPZ2013-1 4	216.773	24344	170	SHCal13	cal BP 27928- 28707	1
SPZ2013-1-4.1	247.118	24693	175	SHCal13	cal BP 28267- 29096	1
SPZ2013-1-4.2	271.702	25133	157	SHCal13	cal BP 28751- 29520	1
SPZ2013-1-4.3	301.024	25542	161	SHCal13	cal BP 29152- 30195	1

Chapter VI: Spitzkoppe middens, central Namib Desert

SPZ2013-1 5	324.839	26024	211	SHCal13	cal BP 29625- 30759	1
SPZ2013-1 6	334.314	26365	222	SHCal13	cal BP 29982- 31005	1
SPZ2013-1 7	393.405	27883	321	SHCal13	cal BP 31119- 32589	1

*Ages calibrated with Southern Hemisphere Zone 1 and 2 bomb curve extension; 1 σ ranges given

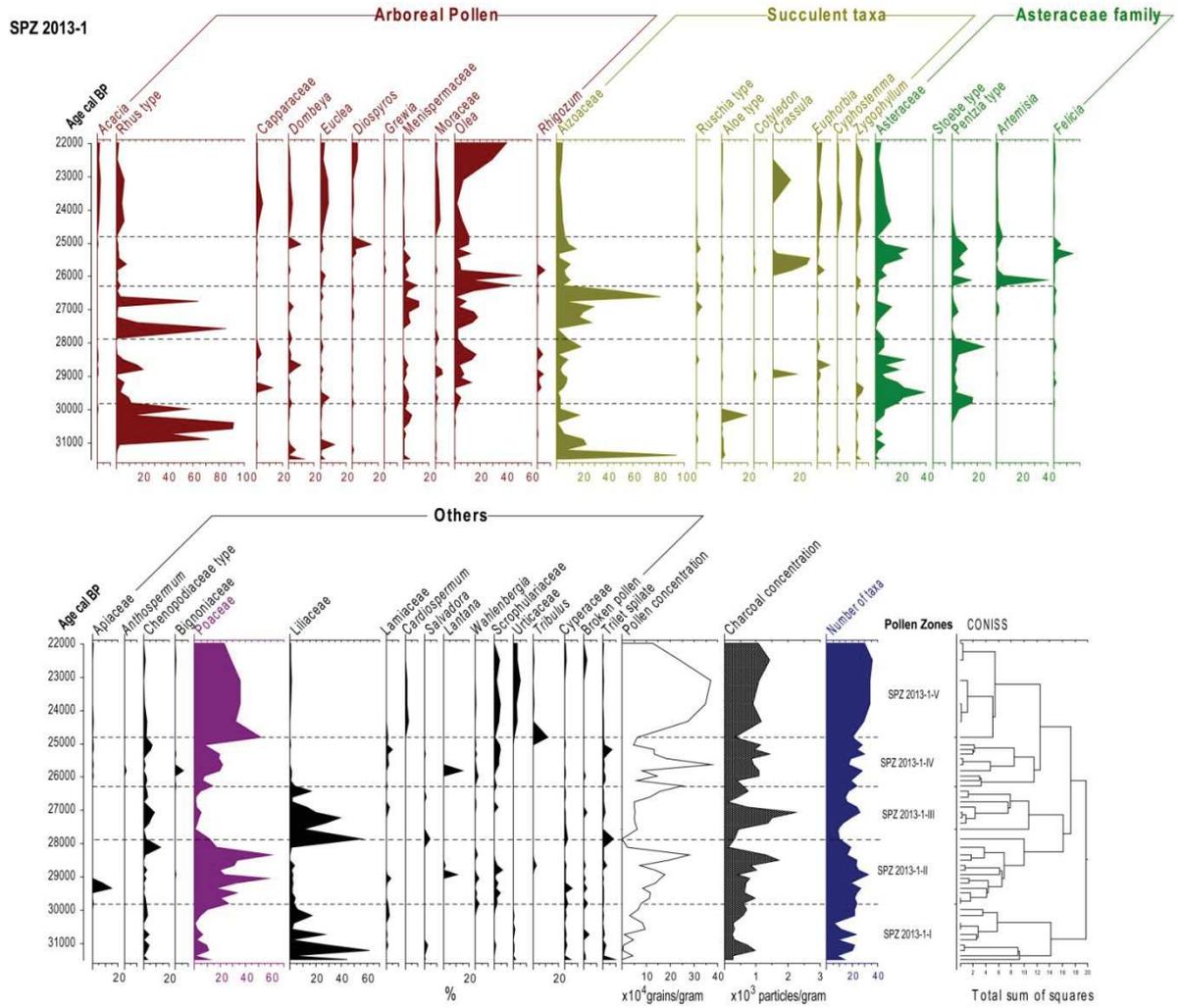


Figure 6. 12:: Diagram percentage pollen and microcharcoal concentration of SPZ2013-1.

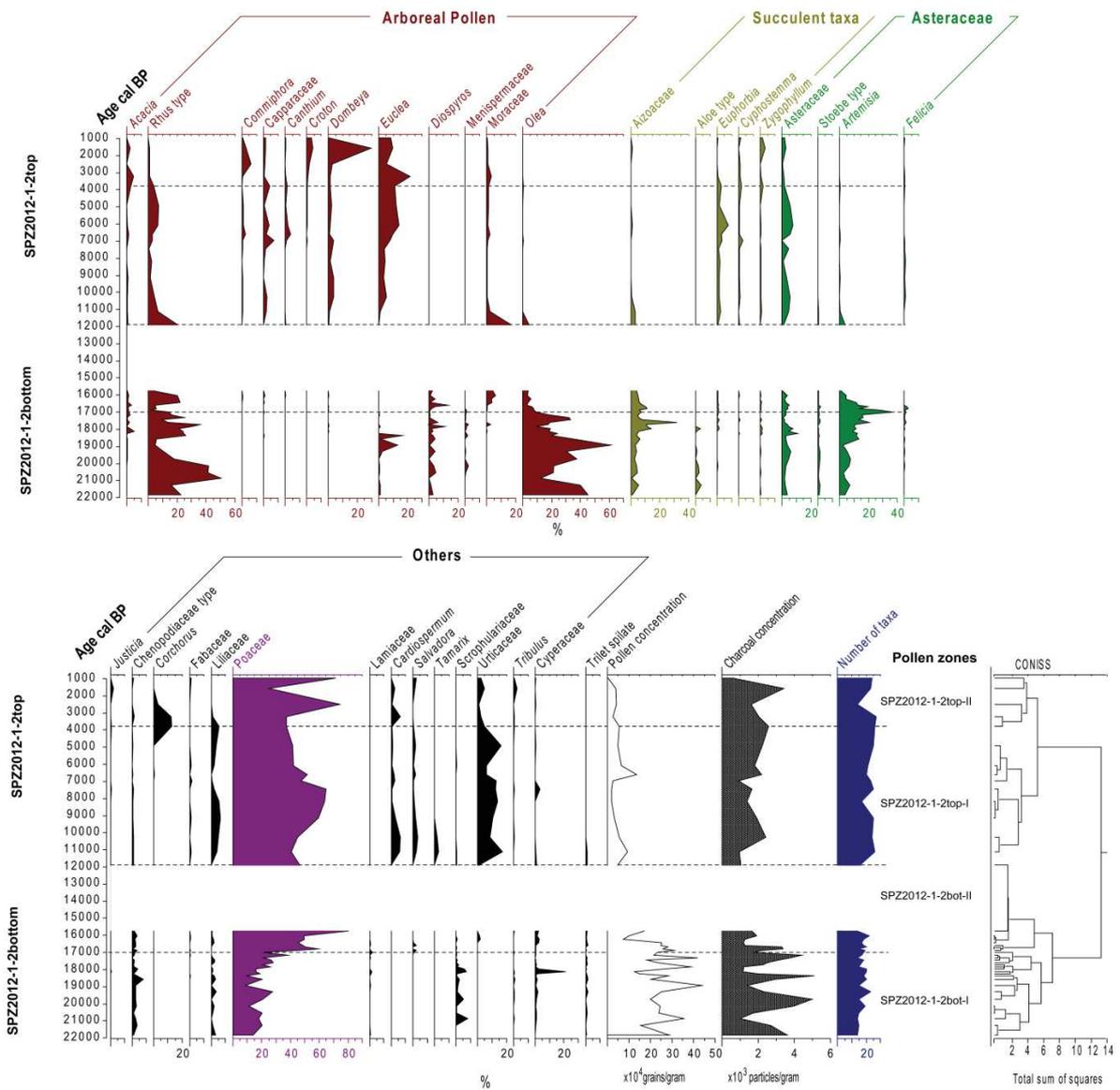


Figure 6. 13: Diagram percentage pollen and microcharcoal combining of SPZ2012-1-2 top and SPZ2012-1-2 bottom section.

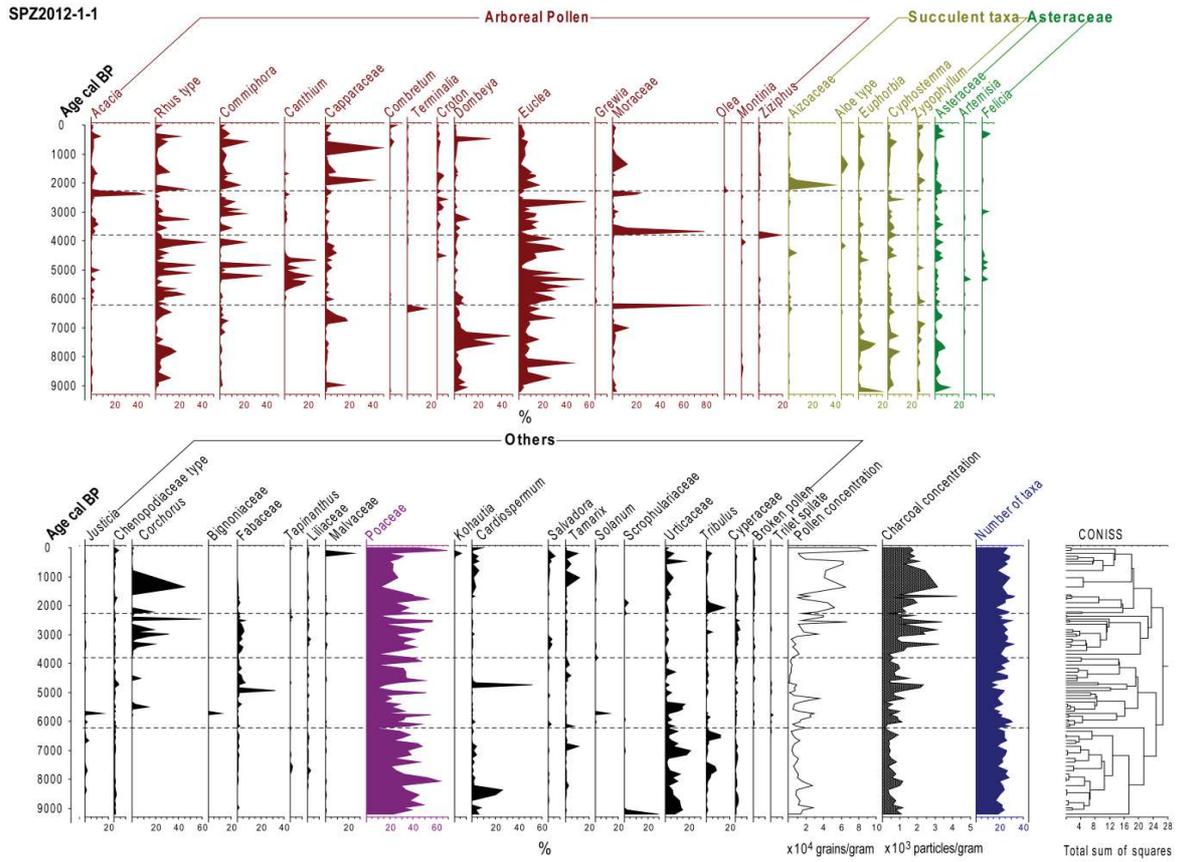


Figure 6. 14: Diagram percentage pollen and microcharcoal concentration of SPZ2012-1-1.

Chapter VII: Conclusions and Perspectives

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The objective of this thesis is to use fossil pollen extracted from rock hyrax middens in the Namib Desert to determine how the vegetation and environments of the region have changed in response to changes in global and regional scale circulation and climate dynamics over the last 50,000 years. Long pollen records in the Namib Desert are scarce due to the hyper-arid and arid climate preventing the development of permanent wetlands or lacks. Thus, the history of vegetation change in the region has relied primarily on the pollen evidence derived from the marine records. These marine records, however, may reflect the large-scale mixing of pollen from diverse sources and therefore may not be clear reflections of terrestrial environments. Unlike marine records, pollen from rock hyrax middens primarily reflects local vegetation change, and the data can be considered to be reliable indicators of vegetation and climate change at the site. The chronologies of the midden sites considered in this thesis indicate generally continuous accumulation, except for potential hiatuses in the PEL-1-1 midden at 15.75 cm and at Spitzkoppe from ~15 - ~12 cal kBP. Results of fossil pollen and microcharcoal analyses from all three midden sites show coherent vegetation changes during the last 50,000 years in the Namib Desert along the south-north transect.

We recall here the key research questions that were asked in the first chapter of this thesis:

- How has the vegetation responded to changes in climatic conditions at the biome scale during the past 50,000 years?
- Was there any northward winter-rain vegetation expansion during the last glacial period, as suggested by marine sediment cores?
- What were the climatic conditions like during the last glacial period, the last glacial-interglacial transition, and the Holocene?
- What was the regional climate response to insolation forcing?
- How has the global climate influenced regional climate?

7.1. The vegetation history in the Namib Desert during the last ~50 cal kBP

- How has the vegetation responded to changes in climatic conditions at the biome scale during the past 50,000 years?

The first two sites, Pella and Zizou midden are located at the ecotone between the Desert and Nama-Karoo biomes while last site, Spitzkoppe is located in a narrow swath of the Nama-Karoo Biome in between the Desert and Savanna biomes (Cowling et al., 2004).

The vegetation at this later site is classified as xeric Namibia Savanna Woodland (Barnard, 1998), although the present-day vegetation aspect is similar to drier end of the Desert Biome rather than the more humid Savanna Biome to the east. In addition, the elevated inselberg on which the site is located has favoured the development of some higher-rainfall woody species at the site while the surrounding plains are dominated by grasses, with some shrubs and trees. We recall some characteristics of the regional biomes that are reflected in the fossil pollen at all three sites.

The Nama-Karoo Biome is the second largest biome in southern Africa with rain mostly falling in summer months and varying between 60 and 400 mm/yr (Cowling et al., 2004) following a west-east gradient. The variability of rainfall is higher at the area of low rainfall. Lower rainfall is being observed in the western part of this biome at the transition with the Desert Biome. Similarly, the Desert Biome also receives summer rainfall, but the amount of rainfall is very low (10 mm in the west, to 70 or 80 mm on the inland margin of the desert) and highly variable from year to year. As a result, aridity in the Desert Biome is generally higher than in the Nama-Karoo Biome. This higher aridity in the Desert Biome has resulted in insufficient groundwater resources to support permanent growth forms such as shrubs and trees, and thus the vegetation is dominated by grasses. Unlike the Desert Biome, the Nama-Karoo vegetation is dominated by low (dwarf) shrubs (mainly Asteraceae) intermixed with grasses, succulents, geophytes, and forbs. It is too dry in summer for dominance by perennial grasses alone, and the soil is too shallow and the rainfall is too low for trees (Palmer, 2006). The Savanna Biome is the largest biome in southern Africa as well as the dominant biome in Namibia (Mucina and Rutherford, 2006). This biome is characterised by grassy (C_4 grass) ground layer and the upper layer composed of woody plants. The dynamics of the vegetation in this biome are associated with the rainfall (~250-1000 mm/yr), fire, and grazing. The major factor delimiting the biome is the lack of sufficient rainfall which prevents the upper layer from dominating, coupled with fires and grazing, which keep the grass layer dominant. Summer rainfall is essential for the grass dominance, which, with its fine material, fuels near-annual fires. C_4 grass in this biome is at an advantage where the growing season is hot. The shrub-tree element may come to dominate the vegetation in areas which are being overgrazed (Cowling et al., 2004; Mucina and Rutherford, 2006).

Fire activity both in the Nama-Karoo and Desert biomes is rare due to the insufficient fuel biomass to support fires (Archibald et al., 2010). In the more mesic eastern part of the Nama-Karoo Biome, grazing and highly variable rainfall result in low and discontinuous fuel load with only localised burning (Palmer, 2006). Occasional fires may occur after successive years of good rainfall in combination with light grazing, resulting in an increased fuel load (Palmer et al., 1999). Fire is potentially more common in the east along the southwestern edge of the Grassland Biome including the interface with this biome on the eastern mountains. In the Savanna Biome, fire occurs more frequently, in particular during the period of prolonged annual dry season combined with relatively rapid rates of fuel accumulation. Fire is considered a major determinant of the ecology and distribution of Africa's savanna and grassland vegetation types (Archibald et al., 2009). The majority of fires in southern Africa are surface fires, fuelled by grass and litter.

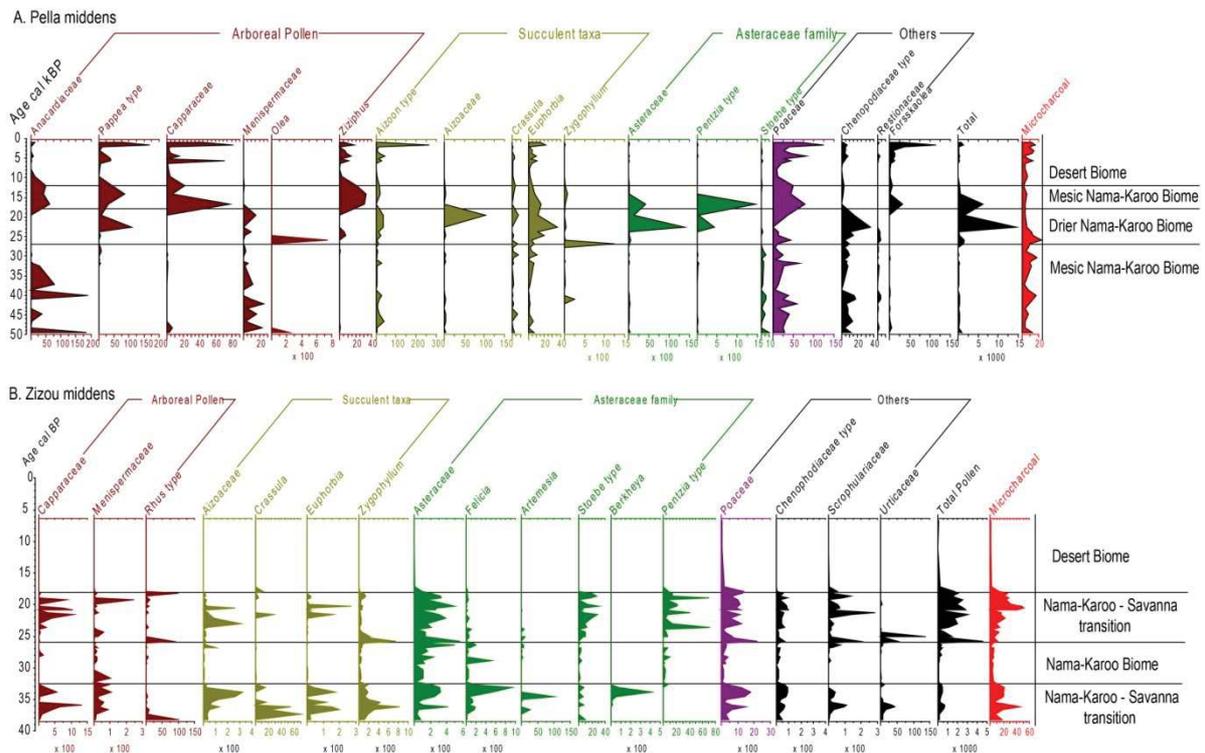


Figure 7. 1: Synthesis fossil pollen accumulation rates and microcharcoal influx diagram at (a) Pella and (b) Zizou middens.

We compare the fossil pollen and microcharcoal influx among sites including in this thesis in order to investigate the variability in vegetation fluctuations between adjacent biomes both local and regional scale during the last 50 cal kyr BP (Figure 7. 1). According to the similar ecosystems between Pella and Zizou middens sites, these two records provide

what might be considered a generalised history of vegetation changes between Nama-Karoo and Desert Biome.

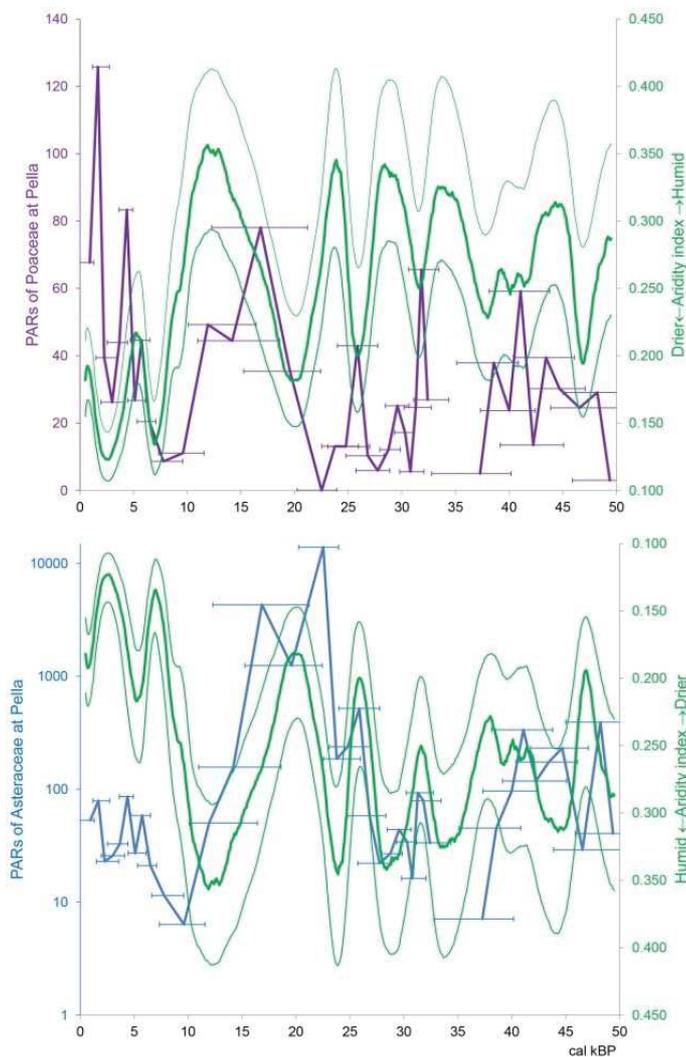


Figure 7. 2: Comparison grass (top) and Asteraceae pollen (bottom) with Aridity index at Pella.

Pella, southern Namib Desert: present-day vegetation is characterised as Eastern Rocky Desert representing an extension of hyperarid – arid Namib Desert across more humid Succulent and Nama-Karoo biome. Under cool and increased water availability (with variable) during the last glacial, the vegetation dynamics inferred from pollen data indicates that the site was within Nama-Karoo Biome, wherein increased aridity is reflected by an increase in Asteraceae pollen and a decrease in grasses (Figure 7. 2). Before ~27 cal kBP and at the glacial-interglacial transition (16 – 10 cal kBP), the increased humidity at the site favoured the development of grasses and mesic Nama-Karoo vegetation while increased aridity during the LGM resulting in increased Asteraceae and a decline of grasses (Figure 7. 2, a). However, the pollen resolutions for this period limit the investigation of vegetation

variability. At the beginning of Holocene (after ~10 cal kBP) as the temperature reached Holocene maxima, and climate condition became significantly drier. An inverted climate-vegetation relationship from last glacial, e.g. grasses increased and Asteraceae declined as aridity increased, indicating the expansion of Desert Biome at Pella region (Figure 7. 2). During this period, increases in Asteraceae occur under slightly more humid conditions and grasses increased under drier conditions.

Zizou, central Namib Desert: present-day vegetation is characterised as transitional Nama-Karoo and Desert biome, dominated by grasses. The last glacial period was characterised by increased water availability with the vegetation composed of different growth forms such as shrubs/trees, succulents and grasses and more diversity of taxa, similar to the Nama Karoo Biome, which is presently found in more humid regions to the east of the site. As expected, the proportions of grasses in Zizou pollen sequences are higher than in Pella pollen sequences. The microcharcoal influx at Zizou is also higher than at Pella. Microcharcoal influx indicate higher values during period of which there were higher vegetation covers (higher total pollen accumulation rates)/more vegetation connectivity at the site promoting the intense fires (Figure 7. 1, b). The vegetation during the last glacial period was displaced in Nama-Karoo Biome and perhaps developed toward Nama-Karoo-Savanna transition during phases of increased, but variable, water availability, indicating by higher peaks of microcharcoal influx (~38 – ~32 cal kBP, and ~26 – ~18 cal kBP). From ~32 – ~26 cal kBP, climate conditions were less variable, and vegetation developed toward Nama-Karoo Biome with minimum microcharcoal influx and lower vegetation covers/discontinuous fuel loads (indicating by lower total pollen accumulation rates) (Figure 7. 1, b). The vegetation at the site composed of higher dwarf shrubs (Asteraceae) and lower grasses. After ~18 cal kBP, increasing warmth and aridity resulted in an expansion of the Desert Biome, as indicated by a higher percentage of grasses (but lower PAR values), minimum microcharcoal influx, and lower pollen diversity. This vegetation dynamics reflect the Desert Biome, wherein grasses thrive seasonally after rains, but also remain dominant for longer-time periods even during the driest phases. The reduction of vegetation covers at the site after ~18 cal kBP limited the fire activity due to insufficient fuel load as being observed in present-day Desert Biome. The vegetation at the study site shows patterns of change over the last 38,000 years that are consistent with those observed in the southern Namib, at Pella.

Chapter VII: Conclusions and Perspectives

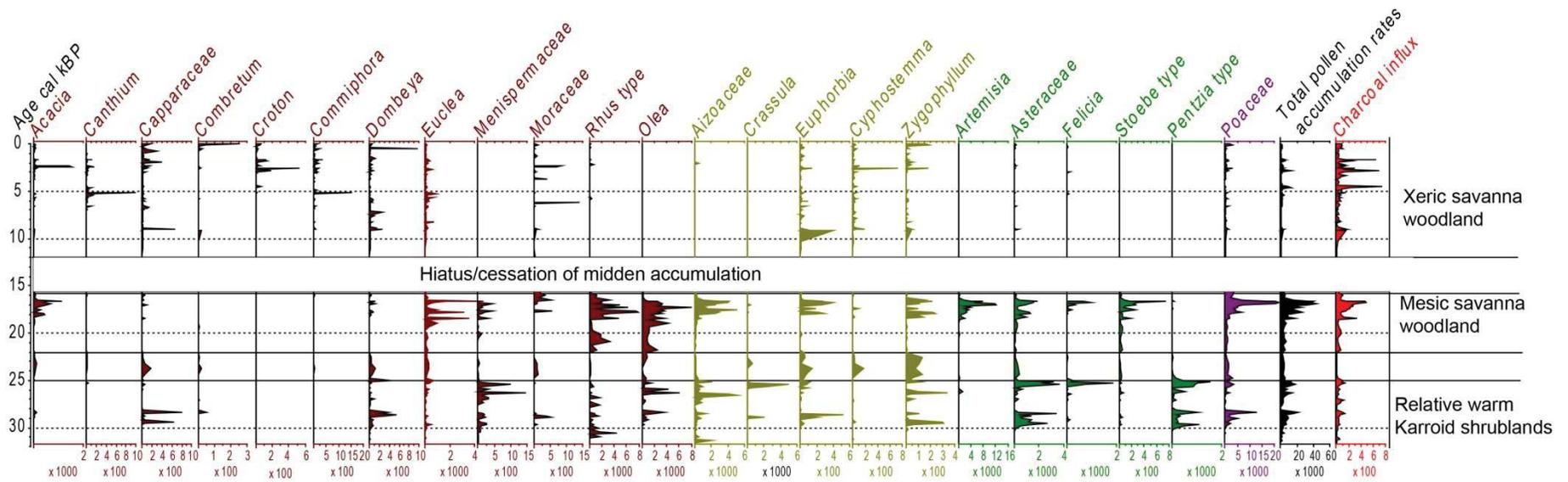


Figure 7. 3: Pollen and microcharcoal diagram at Spitzkoppe indicating vegetation changes at biome scale.

Spitzkoppe, eastern margin of central Namib: present-day vegetation is characterised as xeric savanna woodland with more arboreal species at rocky slopes while grasses are commonly found at the surrounding plains (Barnard, 1998). The last glacial vegetation (~32 – ~25 cal kBP) was characterised by shrubby vegetation of Asteraceae family, grasses, with some numbers of *Olea* (wild olives), *Dombeya*, and *Rhus*-type, accompanied by moderate microcharcoal influx suggesting relative warm grassy karroid shrubland (Figure 7. 3). From ~22 – ~16 cal kBP, vegetation was dominated by cool and moist karroid shrubs (including *Artemisia* and *Stoebe*-type), grass, and higher numbers of *Olea* (wild olives) and *Rhus*-type, as well as higher microcharcoal influx suggesting more mesic savanna woodland. We observe that PARs of grasses and microcharcoal influx are generally higher than previous two sites; Pella and Zizou middens. Some coherent vegetation fluctuations during the last glacial period may be observed between the Zizou and Spitzkoppe sites. For instance, from ~32 – ~26 cal kBP Nama-Karoo vegetation developed at both sites, suggesting an expansion of the Nama-Karoo over the xeric savanna woodland. Holocene arboreal species composition is similar to present-day's suggesting a xeric savanna woodland at the site (Figure 7. 3). Spitzkoppe vegetation shifted from more mesic savanna woodland to xeric savanna woodland across the last glacial-interglacial transition. After ~3 cal kBP, carbon and nitrogen stable isotopes suggest a rapid increased aridity, and vegetation dynamics reflect a shift towards the Desert Biome, wherein grasses increase under drier conditions, as observed at Pella and Zizou during the Holocene.

In summary, pollen data at all sites suggest the interplay of different vegetation types related to the adjacent biomes during the last 50 cal kyr BP. At Pella and Zizou, increased humidity favoured the development of vegetation typical of the Nama-Karoo Biome during the last glacial period, while increased warmth and aridity during the Holocene resulted in an expansion of the Desert Biome. The aridity index at Pella suggests increased humidity during the last glacial period, vegetation develop toward more humid eastern Karoo at the transition with the Grassland Biome. During the LGM, increased aridity supported more xeric Nama-Karoo vegetation, as seen today in the western part of the Nama-Karoo, at the border to the Desert Biome. At Spitzkoppe, where present-day vegetation is slightly different from other two sites, fossil pollen and microcharcoal records suggest that vegetation fluctuated between karroid shrubland (Nama-Karoo Biome) and more mesic savanna woodland during the last glacial period. The increased warmth and reduction in moisture during across the Holocene enabled the expansion of xeric savanna woodland at the study site. Changes in grass

proportions in fossil pollen records are sensitive indicator of humidity, but ecosystem specific and must be considered in the context of shifting ecosystem. Some taxa such as *Stoebe*-type and *Artemisia* are sensitive temperature indicators and their presence in the Namib Desert could also used as increased effective moisture due to their modern distributions.

- Was there any northward winter-rain vegetation expansion during the last glacial period, as suggested by marine sediment cores?

Another aspect of glacial vegetation dynamics in the region has been the question of whether the mediterranean Fynbos Biome expanded into the region as a result of an equatorward shift of the westerly storm track. Conceptual models suggest that the northward shift of this temperate climate system resulted in an increased winter rainfall in the Namib region (cf. Chase and Meadows, 2007). Evidence for this was obtained from the pollen analysis of marine sediments off the Namibian coast. Elevated Restionaceae pollen in the marine cores was cited to suggest that Fynbos Biome had indeed extended northward during glacial periods (Shi et al., 2001, 2000, 1998; Urrego et al., 2015). In contrast, our records indicate no significant presence of Restionaceae or other fynbos taxa, with only trace amounts of the Restionaceae pollen being found in the southern-most site at Pella (not exceeding 1%, as is found today) (Figure 7. 1), and none being observed at either Zizou or Spitzkoppe (Figure 7. 1 and Figure 7. 3). The trace amounts of this pollen type in Pella pollen sequences is not consistent with a significant shift of the Cape flora (Shi et al., 2001, 2000, 1998; Dupont et al., 2008). Another hypothesis stated that Restionaceae prefer the sandy substrate along the west coast, and thus we might expect to see this pollen type at Zizou because this site is located at the margin of the Namib Sand Sea. Pollen sequences at Zizou show no trace of this pollen type during the last ~38 cal kyr BP. Our pollen records are consistent with other terrestrial pollen records from the region (Scott et al., 2017, 2004, 1995; Lim et al., 2016). The elevated percentages of fynbos vegetation in the marine sediment cores more likely reflects an increase in the long-distance transport of pollen with increased atmospheric and oceanic circulation intensity during the last glacial period. The Restionaceae pollen in marine cores may be transported via river or winds into the Atlantic ocean from the Cape region, where the Fynbos Biome is currently established. After moving into the Ocean, this pollen type could have been transported northward especially during period of increased wind strength in the late Pleistocene (Farmer et al., 2005; Stuut et al., 2002).

7.2. Climate history in the Namib Desert during the last ~50 cal kBP

- What were the climatic conditions like during the last glacial period, the last glacial-interglacial transition, and the Holocene?

The quantitative climatic reconstructions (temperature and aridity index) from pollen data at Pella middens in the southern Namib desert indicate the cooler and increased, but variable, water availability during the last glacial period relative to the Holocene (Figure 7. 4). Some warmer phases are observed during the MIS 3 (~50 – 45 cal kBP at Pella, ~38 – ~35 cal kBP at Zizou, and ~32 – ~26 cal kBP) (Figure 7. 4). However, the conditions during these intervals were not as warm as during the Holocene. Cool taxa were higher during the last glacial and disappeared from all pollen sequences during the warmest periods of the Holocene. In conclusion, temperature trends are consistent with data from the Stampriet Aquifer, with deglacial warming starting immediately after the LGM, at ~18 cal kBP (Figure 7. 4).

The aridity index from Pella suggests more humid glacial-age conditions especially from ~35 – 24 cal kBP (Figure 7. 4). In the central Namib, pollen assemblages from the Zizou middens indicate a dominance of Asteraceae (including *Stoebe*-type and *Artemisia*), with higher pollen diversity, whereas grasses dominate the vegetation during the Holocene, as found in the modern Desert Biome. This is similar to the pattern observed at Pella, suggesting cool, relatively humid conditions during the glacial period relative to Holocene. The humidity inferred pollen data show some variability between sites. For example, the aridity index indicates that the LGM at Pella was drier but pollen and microcharcoal records at Zizou and Spitzkoppe suggest cool and increased moisture indicating by higher numbers of cool and moist taxa such as *Stoebe*-type, *Artemisia*. At Zizou, *Stoebe*-type was at its maximum numbers from ~24 – ~18 cal kBP, accompanied by dry taxa such as Capparaceae (~22 – ~19 cal kBP) and higher microcharcoal influxes, suggesting some periods of drought also occurred during the wetter phases. Similarly, Spitzkoppe pollen sequences show higher numbers of *Stoebe*-type, *Artemisia*, *Olea*, grasses and *Rhus*-type, suggesting cooler and moister conditions from ~19 – ~17 cal kBP. From ~24 – ~19 cal kBPm vegetation was dominated by *Olea* and *Rhus*-type and a reduction of grasses. According to our records, the increased moisture during the LGM is unlikely related to an increase in precipitation, but

more likely an increase in effective moisture under cooler temperatures. The precipitation reconstructions from the summer rainfall region of eastern South Africa suggest a reduction in precipitation under the colder atmospheric and oceanic conditions (Chevalier et al., 2017; Chevalier and Chase, 2015; Truc et al., 2013). Colder SSTs along the Benguela current during LGM (Kim et al., 2002) may limit the moisture transport from the Atlantic to the Namibian coastal plain. The synthesis in Chase and Meadows, 2007 suggest that majority of the evidence supports the conceptual model of increased rainfall along the western margin of southern Africa resulting from the expansion of Antarctic sea ice, and the influence of more frequent/intense frontal systems associated with the westerlies during the last glacial period. Our results, on the other hand, show that lower temperatures induced lower potential evapotranspiration also play important part in increased water availability in an environment as being suggested by (Chevalier and Chase, 2016). Episodes of increased humidity during the last glacial at Pella occur during the periods of increased upwelling (Farmer et al., 2005; Stuut et al., 2002). As increased upwelling has generally been found to increase aridity along the southwest African coast, concurrent declines in temperature and potential evaporation are implicated as significant drivers in these changes in the regional water balance. For this reason, changes in temperature and potential evapotranspiration appear to have played a significant role in determining the hydrologic balance. It is also noted that some climatic changes may be muted in the pollen records due to the lack of species-level pollen identification, for example, Asteraceae pollen type composed of many species and this pollen type was abundant during the last glacial period. The seasonality changes are difficult to infer from pollen data alone because lower temperature during summer might have same effect as winter rainfall.

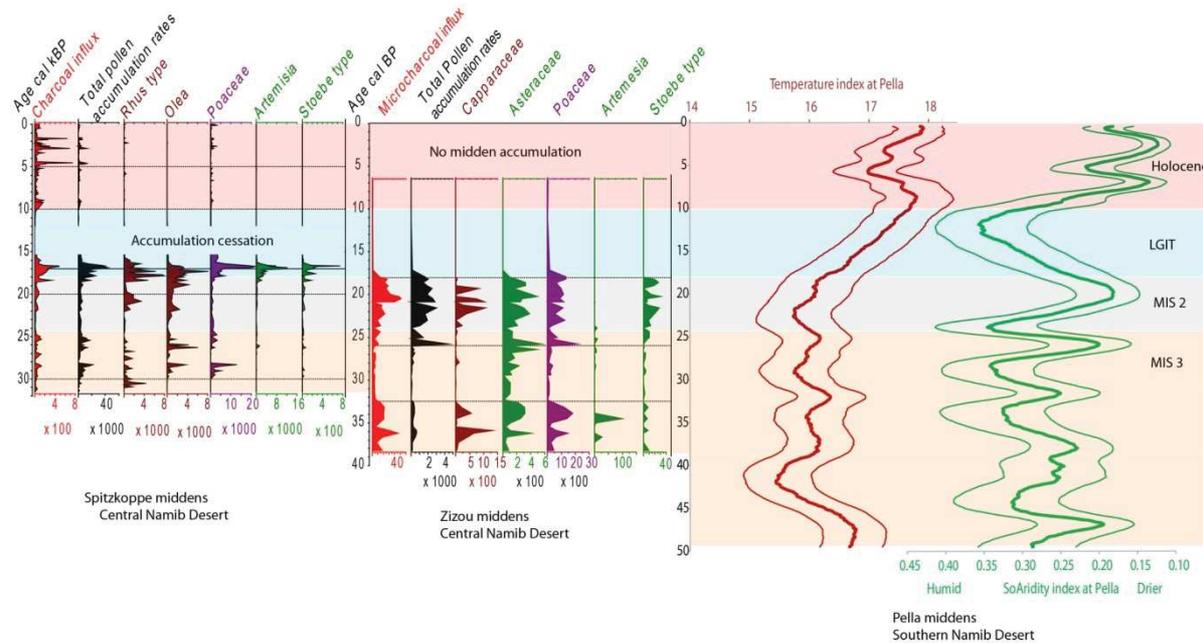


Figure 7. 4: Synthesis pollen diagram at Spitzkoppe, Zizou, and temperature and aridity index at Pella.

The last glacial-interglacial transition (~16 – ~10 cal kBP) is characterised by increasing temperatures, markedly reduced upwelling, and increased water availability at Pella. While increasing temperatures would have resulted in increased drought stress, the influence of low upwelling intensity may have counteracted this by allowing for increased local convection and the incursion of moisture-bearing air masses. At Zizou, high levels of Poaceae pollen (more than 90%) during the Holocene limits the potential for climate reconstruction during this period. However, we suggest that vegetation at the site shifted toward the Desert Biome throughout the Holocene in response to increased warmth and aridity, evidenced by the disappearance of *Stoebe*-type from the records. Pollen at Spitzkoppe suggest the increased temperature and humidity indicating by reduction of cool taxa such as *Stoebe*-type and *Artemisia* and maximum grass proportions at study site (~17 – ~15 cal kBP). These results are consistent with the Pella middens, suggesting increased humidity during the LGIT coincided with phases of reduced intensity of upwelling at the Benguela System (Farmer et al., 2005). In the southeast Atlantic, the strengthening of the South Atlantic Anticyclone and southeasterly trade winds would result in the intensification of coastal upwelling cells and enhanced aridification the Namib region. The warming oceans surrounding southwestern Africa (Kim and Schneider, 2003) and poleward shift of Subtropical Fronts resulting in a reduction of strength and position of the South Atlantic

Anticyclone modified the Angola-Benguela Front allowing more convection moisture from Atlantic ocean to the Spitzkoppe site.

During the Holocene, high temperatures and potential evapotranspiration resulted in increased aridity at Pella. Increasing upwelling intensity across the Holocene also created drier conditions during this time, in contrast with the last glacial period. The record from the Zizou middens ends at ~5 cal kBP, but the Holocene pollen assemblage suggests drier climates supporting desert grassland vegetation. The combination of lower pollen accumulation rates, lower microcharcoal influx and lower midden accumulation rates suggest drier climate during the Holocene. At Spitzkoppe, higher temperatures and increased aridity throughout the Holocene are indicated by the disappearance of cool taxa such as *Stoebe*-type and *Artemisia* and their replacement by warm arboreal species and grasses. Comparing grass and arboreal pollen to stable isotope data at Spitzkoppe and proxy for coastal upwelling in southeast Atlantic (Chase et al., 2009; Farmer et al., 2005), the Holocene aridification is positively correlated with coastal upwelling at Spitzkoppe site. This is coupled with findings at Pella site confirming the importance of upwelling in the control and maintenance of the regional climate.

- What was the regional climate response to insolation forcing?

The findings from a long sedimentological record from Lake Tswaing in southeastern Africa suggest that precipitation increased during Southern Hemisphere summer insolation maxima due to an enhancement of the southern African monsoon (Partridge et al., 1997). Some palaeoenvironmental data from the southwestern Africa have been interpreted as suggesting that the phases of increased humidity occur during summer insolation maxima (Collins et al., 2014; Danian et al., 2013; Urrego et al., 2015). In terms of forcing mechanisms of the regional climate change and environmental dynamics, the results from Pella middens stand in clear contrast with many inferences of terrestrial environmental change derived from regional marine records. Collins et al., 2014 suggest wetter conditions during the LGM due to an increase in monsoonal precipitation. The reduction of precipitation during the LGM in the summer rainfall zone is indicated by precipitation reconstruction from pollen data (Chevalier and Chase, 2015). LGM pollen assemblages at Spitzkoppe and Zizou show higher numbers of cool and more humid local conditions such as *Stoebe*-type and *Artemisia* and slightly reduction in grass proportions. Lower temperatures during the SH summer insolation minima might play important role in increased humidity under lower

potential evapotranspiration. Thus, increasing humidity during the phases of high local summer insolation – as suggested by marine records - is not consistent with the data from the Namib midden sites. The limitations imposed by the low resolution of some portions of our records notwithstanding, the timing and nature of climate and vegetation change across the Namib midden sites seems to have been largely synchronous, suggesting that variations in each record are primarily determined by large-scale regional and extra-regional process and mechanisms.

- How has the global climate influenced regional climate?

The pollen data and climate reconstructions presented in this thesis show that past global climate change has had great influences on regional climates, hydrological systems and vegetation. The regional temperature trends are consistent with cooling glacial and warming interglacial cycle. The regional climate was characterised by more humid conditions during cooler glacial periods and drier conditions during the warmer Holocene. Fossil pollen and microcharcoal data from the three midden sites considered suggest that in addition to changes in precipitation amount, temperatures play an important role in determining humidity at the region. Lower temperatures during the last glacial period resulted in lower potential evapotranspiration and increased water availability. Increased temperatures during the Holocene lead to higher evapotranspiration and less water availability for plant growth. From these data, it is predicted that a future increase in temperature will result in drier conditions in the Namib desert, and an expansion of the Desert Biome.

7.3. Perspectives

While we have answered some key questions related to vegetation and climate change in the Namib desert during the last 50,000 years, further works remain to be done. This includes:

- Increased resolution of pollen samples in some parts of the midden record, for examples, in the Pella middens for the Last Glacial Maximum. Lacking the higher pollen resolution in those time periods, it is hard to draw any conclusion about climatic variability registered in the pollen records.

- Apply quantitative reconstruction methods - such as the use of the CREST method to reconstruct other climatic variables (such as precipitation seasonality) that could provide more information to explain regional climatic system dynamics.

- Improve pollen identification potential for regional vegetation types, as pollen references collections are limited for the Namib.

- Identifying new middens from the region to provide more evidence for past vegetation and climate change, and integrate those results into scenarios of future climate change.

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Résume thèse en français

CHANGEMENT DE LA VEGETATION ET DU CLIMAT AU COURS DES DERNIERS 50 000 ANS EN DESERT DE NAMIB

Les structures de cette thèse se composées en sept chapitre :

- Chapitre I: l'introduction
- Chapitre II: la description de la zone d'étude (la géographie, le climat, et la végétation)
- Chapitre III: les matériels et les méthodes
- Chapitre IV: le changement de la végétation et le climat au sud de Namib, Pella, au cours les 50 000 dernières années (article publié)
- Chapitre V: Zizou middens, à la marge des dunes de sable de Namib (article en préparation).
- Chapitre VI: Spitzkoppe hyrax middens, à la marge est du désert du Namib central (article en préparation)
- Chapitre VII: Conclusions et perspectives

I. CHAPITRE I: INTRODUCTION

A cause des contraintes climatiques, il existe très peu d'analyses polliniques en Namibie et ces enregistrements couvrent seulement la période à partir de mi-Holocène ([Gil-Romera et al., 2006](#); [Gil-Romera et al., 2007](#); [Scott, 1996](#); [Scott et al., 1991](#)), sauf un enregistrement à Brandberg qui couvre la période de 30 000 ans BP (dates non-calibrées) mais les résolutions des échantillons pour les analyses polliniques sont très faibles. En conséquent, les reconstructions de la végétation et du climat dans la région dépendent des carottes de sédiments marins ([Shi and Dupont, 1997](#) ; [Shi et al.,1998, 2000](#); [Shi et al., 2001](#); [Daniau et al. , 2013](#)). Néanmoins, les résultats provenant des carottes marins donnent les conclusions contradictoires en comparant avec les résultats trouvés par les enregistrements terrestres. Par exemple, dans les carottes marins, ils ont trouvé les grands pourcentages de Restionaceae (la végétation de la zone de précipitation hivernale, la flore de Cape) pendant la période glaciaire (Shi et al., 1998; Shi et al. ,2000; Dupont et al., 2007).

Comme le climat aride dans le désert du Namib empêche la présence des zones marécageuses, il existe très peu de données palaeo-environnementales dans la région et la compréhension du changement de la végétation et du climat est très limitée (Scott et al., 2004; Chase and Meadows, 2007). Dans le cadre de cette thèse, on utilise le rock hyrax

middens – l'accumulation des boulettes et des urines fossilisées du *Procavia capensis*, qui sert comme une excellente archive pour conserver des pollens et des micro-charbons à long-terme (Chase et al., 2012; Scott et al. 2004; Gil-Romera et al. 2007; Gil-Romera et al. 2006).

L'objectif de cette thèse est d'utiliser les pollens fossiles extraient de rock hyrax midden dans le désert du Namib pour déterminer comment la végétation et l'environnement du désert du Namib ont changé en répondant aux changements de la circulation atmosphérique et océanique à l'échelle globale et régionale et aussi le changement dynamique du climat au cours des 50 000 ans.

Les questions scientifiques principales pour cette thèse sont les suivantes:

- Comment ont été les conditions climatiques au cours de la dernière période glaciaire , la transition de la période glaciaire-interglaciaire ?
- Comment la végétation à l'échelle de biome a réagi aux changements des conditions climatiques au cours des dernières 50 000 années ?
- Est-ce qu'il y avait une expansion de la végétation de Cape vers le nord au cours de la dernière période glaciaire comme les évidences provenant des carottes marines ?
- Comment le forçage d'insolation a l'influencé sur le climat régional ?
- Comment le climat global a l'influencé sur le climat régional ?

II. CHAPITRE II: DESCRIPTION DE LA ZONE D'ETUDE

Le désert du Namib s'étire sur près de 2 000 km de longueur entre l'Olifants River dans la province sud africaine de Cap (32°S) et la Carunjamba en Angola (15°S) (Lancaster, 2002 ; Stone & Thomas, 2013) (Fig. 1). En Namibie, il n'y que deux fleuves pérennes : la Cunene au nord et l'Orange au sud. La géographie de Namibie se caractérise par les zones côtières avec la plus fréquentée de la présence des dunes de sable jusqu'à plus de 1 000 m au

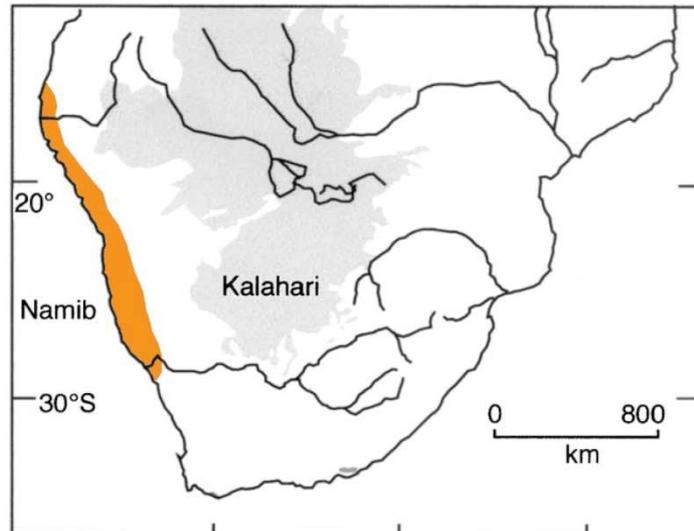


Fig. 1 : Location géographique de désert du Namib (en jaune se trouve le désert du Namib).

pied des Grands Escarpements. Selon l'aspect géographique, le désert du Namib peut être divisé en quatre zones principales : le Sud du Namib, la mer du sable du Namib, les plaines centrales du Namib et le nord du Namib (Lancaster, 2002).

L'existence du désert côtier du Namib associe avec sa location dans les zones de la haute pression atmosphérique (Hedly cells) et la présence du courant de Benguela (Eckardt et al., 2013; Lancaster, 2002; Stone & Thomas, 2013). Les cellules de Hadley se situent entre l'équateur et 30 degrés N et S. L'air chaud et humide converge à l'équateur (la zone de haute pression) se déplace vers les zones des basses pressions. Quand les parcelles d'air chaud et humide atteignent la tropopause (à environ 12 à 15 km d'altitude), elles sont repoussées vers le nord ou le sud de l'équateur. En se déplaçant vers les Pôles, l'air se refroidit (plus sec) par échange avec l'environnement et commence à descendre à environ de 30 degrés N et S. On se trouve plus souvent les déserts vers ces latitudes. Le courant de Benguela est traditionnellement associé à la présence d'eaux froides: à leur contact, l'air, refroidi à sa base, acquiert une grande stabilité au-dessous d'une forte inversion thermique qui interdit tout le développement vertical des nuages qui en restent au type stratiforme. Le vent soufflant parallèlement à la côte fait remonter les eaux plus froides de la profondeur de l'océan vers la surface l'océan, ce phénomène s'appelle *upwelling* qui est responsable de l'anomalie thermique négative. Le courant de Benguela et les *upwellings* font baisser l'évaporation de

l'eau de l'océan Atlantique et créent l'inversion de la température, par conséquent il y a très peu de précipitation dans la zone côtière.

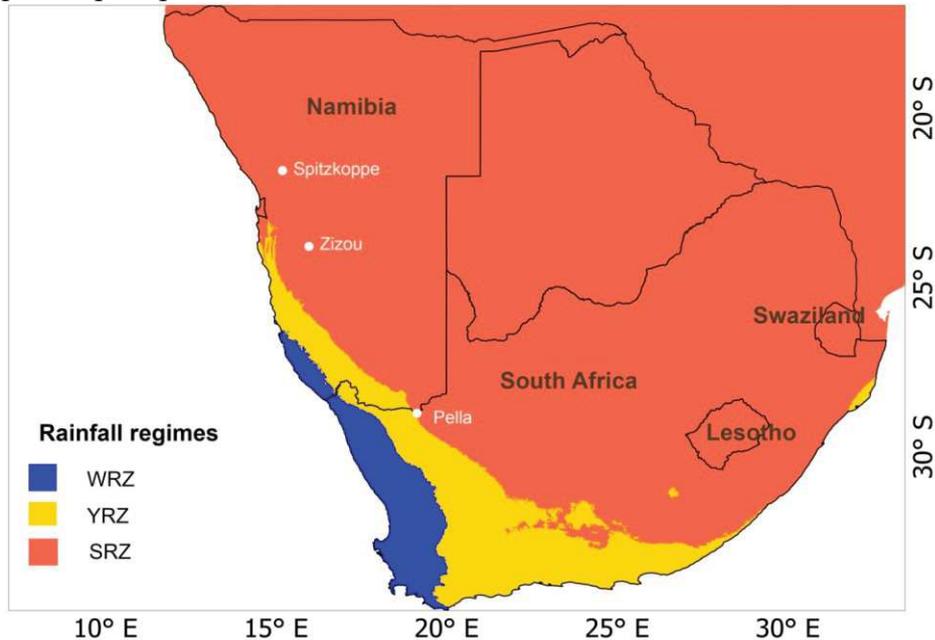


Fig. 2 : Les saisonnalités de la précipitation de la zone d'étude. En rouge indique la zone de précipitation estivale, en bleu celle de hivernale et en jaune est la zone qui reçoit à la fois hivernale et estivale.

Les gradients de précipitation se présentent en deux directions : l'est-ouest et le nord-sud gradients (Stone and Thomas, 2013). A l'ouest, la moyenne de la précipitation annuelle est moins que 15 mm par an et à l'est vers le pied du Grand Escarpement, elle augmente entre 80-100 mm par an (Lancaster et al., 1984) dans le désert du Namib. En plus, le régime pluvial dans le désert du Namib se caractérise par une forte variabilité annuelle et interannuelle. Sous l'influence de la circulation atmosphérique et océanique, le régime de précipitation de l'Afrique australe se caractérise par une importante variabilité saisonnière. Au nord et à l'est de l'Afrique australe se trouve le " Summer Rainfall Zone" qui reçoit plus de 66 % des précipitations annuelles entre octobre et mars (Fig. 2). L'humidité provient principalement de l'Océan Indien qui, lorsqu'il se réchauffe, charge l'air en humidité par évaporation. Cet air chaud et humide est ensuite transporté vers le continent par les vents d'est tropicaux. Au nord de Namibie, sous l'influence de déplacement au sud de la zone de convergence intertropicale (ZCIT) pendant l'été austral, permet l'advection d'humidité de l'océan Sud Atlantique vers le continent. Au sud-ouest de l'Afrique australe se trouve dans la "Winter Rainfall Zone" (WRZ) qui reçoit plus de 66% des précipitations annuelles entre avril et septembre. Ces pluies hivernales proviennent de l'humidité générée au-dessus de l'Atlantique sud, lors de la rencontre entre les masses d'air chaud subtropical et les masses d'air froid polaire. Cette humidité est transportée par les vents d'Ouest, lorsque la ceinture de circulation se déplace vers le Nord en hiver (Tyson,

1986). Entre les deux zones de régime précipitation, se trouve la "Year-round Rainfall Zone" (YRZ), recevant à la fois des pluies estivales et hivernales. Le sud du désert de Namib reçoit un peu la pluie hivernale par l'influence de vent d'ouest du système frontal.

Les gradients températures en désert du Namib caractérisées par les moyennes températures annuelles très basses sur la zone côtière et elles augmentent vers le continent. Le courant froid de Benguela favorise les températures basses sur la côte namibienne.

En terme de végétation en Namibie, il y a quatre biomes concernant la végétation de Namibie: le Savane, le Nama-Karoo, le Succulent Karoo et le Désert.

III. CHAPITRE III: LES MATERIELS ET LES METHODES

Nous choisissons donc trois sites des hyrax middens: au sud du désert de Namib (Pella), la bordure Est des dunes de sable de Namib (Zizou) et le centre de Namib (Spitzkoppe). Tous ces sites sont caractérisés par le climat extrêmement aride (la précipitation moyenne annuelle est entre 100 mm et 150 mm) (ACACIA, 2002). En plus, le régime pluvial de ces sites se caractérise par une forte variabilité annuelle et interannuelle. Par conséquent, ces sites se trouvent le long de l'écotone du Désert et du biome de Nama-Karoo, avec le biome de Savane qui se situe à l'est (Rutherford and Westfall, 1994). Bien que ces sites se localisent dans des écosystèmes similaires, l'écotone est considéré comme une zone potentiellement très sensible au changement du système climatique régional et leur distribution est élaborée pour identifier les différences spatiales de la nature de réponse au changement climatique à long terme (Neilson, 1993).

Ce tableau résume le nombre d'échantillon pour des analyses polliniques et des micro-charbons, le nombre des échantillons pour la datation du ^{14}C de chaque section des hyrax middens.

Midden sites	Sections	Nombre d' échantillons	Echantillons pour la datation ^{14}C
PELLA	PEL-1-1	38	10
	PEL-1-4a	21	6
ZIZOU	ZIZ-1-1	26	9
	ZIZ-1-3b	23	11
SPITZKOPPE	SPZ-2012-1-1	85	25
	SPZ-2012-1-2 top	15	8
	SPZ-2012-1-2 bottom	28	9
	SPZ-2013-1	47	13

L'extraction des pollens et des micro-charbons fossiles suivent la méthode standard de Moore et al. 1991. Les échantillons ont été filtrés avec le maille de 600 µm pour séparer les grandes parties végétatives et ont été traités avec les produits chimiques comme : HCl, KOH, HF et acétolyses. Une fois le traitement chimique terminé, on monte les lames et compte des grains des pollens et des micro-charbons. On compte au minimum 400 grains de pollen par chaque échantillon. On a utilisé le logiciel Tilia pour créer les diagrammes polliniques. Pour la reconstruction de la température et l'indice d'aridité, on a utilisé le logiciel CREST (Chevalier et al., 2014).

IV. CHAPITRE IV : LE CHANGEMENT DE LA VEGETATION ET LE CLIMAT AU SUD DE NAMIB, PELLA, AU COURS LES 50 000 DERNIERES ANNEES (article publié dans le revue scientifique international)

Les hyrax middens de **Pella** fournissent le premier enregistrement pollinique continué au sud du désert de Namib durant la période des 50 000 dernières années et ces données polliniques ont été utilisées pour reconstruire le changement de la végétation et pour estimer quantitativement la température et l'aridité. Les résultats indiquent que la période glaciaire se caractérise par une augmentation de la disponibilité de l'eau sur le site lié à l'Holocène. Les changements de la température et de l'évapotranspiration potentielle semblent avoir joué un rôle important dans la détermination de l'équilibre hydrologique. L'enregistrement peut être considéré en deux parties : 1) la dernière période glaciaire, lorsque des basses températures ont favorisé le développement de la végétation plus mésique de Nama-Karoo sur le site avec la période plus humide coïncident avec la remontée des eaux côtières, a répondu à la fois à la baisse de températures globales ou régionales ; et 2) l'Holocène, la période pendant laquelle des températures et évapotranspiration potentielle étaient élevées provoquent d'une augmentation de l'aridité et d'une expansion du Désert biome (Fig. 3). Au cours de cette dernière période, l'augmentation de l'intensité des upwellings établissent des conditions plus arides sur le site.

Considérant dans le contexte des discussions des forçages des mécanismes du changement climatique régional et la dynamique environnementale, les résultats de Pella ont montré des contradictions avec des conclusions de nombreux changements environnementaux terrestres provenant des enregistrements marins. L'observation d'un fort signal de précession et les interprétations de l'augmentation de l'humidité correspondent aux phases d'insolation estivale locale élevée proposées par les enregistrements marins qui ne sont pas cohérents avec les données de Pella (Fig. 3). De la même façon, lorsqu'on a observé des pourcentages importants de pollen du Restionaceae dans les carottes de sédiments marins pendant la dernière période glaciaire, ce type de pollen ne dépasse pas 1% de l'assemblage pollinique de Pella. Ceci n'indique qu'aucune expansion significative de la végétation du biome de Fynbos au cours des 50 000 dernières années. Ces résultats posent des questions intéressantes concernant la nature du changement environnemental au sud-ouest de l'Afrique et l'importance des différents enregistrements qui ont été obtenus dans la région.

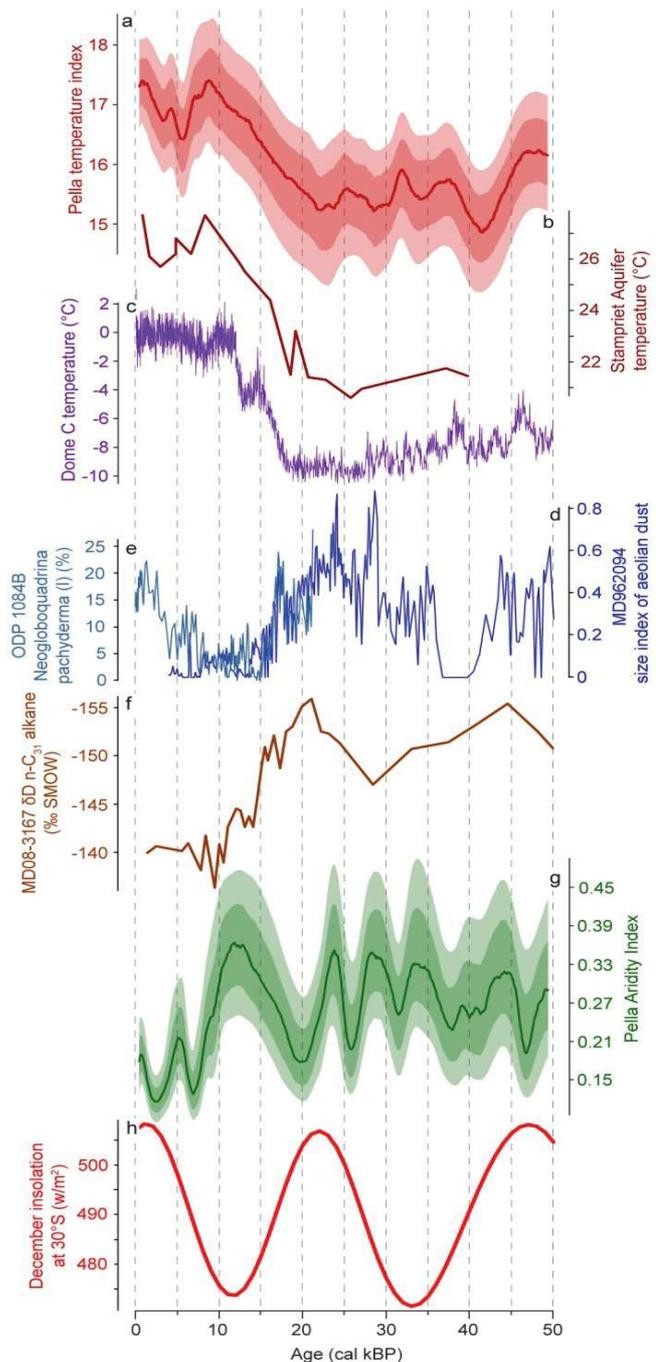


Fig 3: Comparaison l'indice de température a Pella (a), la palaeo-température de Stampriet Aquifer (b; Stute and Talma, 1998), la palaeo-température de Dome C de carotte glacée d'Antarctique (c; Jouzel et al., 2007), l'intensité de vents de Benguela Upwelling System (d; Farmer et al., 2005) et les données des grains de sédiment marin (e; Stuut et al., 2002), le δD de carotte marin MD08-3167 (f; Collins et al., 2014), l'indice aridité de Pella (g), et insolation en décembre à 30°S (h; Berger and Loutre, 1991).

V. CHAPITRE V : ZIZOU MIDDENS

L'enregistrement de **Zizou** hyrax midden met en évidence des changements de la végétation à la bordure de l'est des dunes de sable depuis 38.000 ans cal BP. Les résultats montrent qu'il existe différentes compositions de la végétation entre la dernière période glaciaire et celle de l'Holocène. La végétation de la période glaciaire se caractérise par les pourcentages relativement importants des Astéracées pollen, particulièrement par le climat plus froid de taxa : *Stoebe*-type et *Artemisia*. Pareillement avec les données de Pella, l'augmentation de température et l'aridité au début de l'Holocène est indiqué par la dominance de pollen des graminées dans l'assemblage pollinique, la diminution des les taux d'accumulation des pollen totale et la diminution des mirco-charbon, ce qui suggère une expansion du Désert biome. Nous constatons que le climat au cours de la dernière période glaciaire était plus humide et que ce dernier favorisait le développement des arbustes et des petits arbres grâce au développement à long terme des plus fiables ressources en eaux souterraines. Les conditions arides pendant l'Holocène sont vues par l'épuisement de cette ressource et le développement des graminées qui pourraient exploiter les pluies rares qu'on observe actuellement dans la région. Le point commun avec l'enregistrement de Pella est aussi aucun élément de flore du Cap qui est trouvé dans le Zizou middens pour donner les preuves d'une expansion significative de la végétation du type fynbos au cours de la dernière période glaciaire.

VI. CHAPITRE 6 : SPITZKOPPE MIDDENS

Les hyrax middens de Spitzkoppe enregistrent les changements de la végétation dans le centre du désert de Namib au cours des 32 000 dernières années. Les résultat montre que la végétation de la dernier période glaciaire caractérise par abondamment de *Olea*, *Artemisia*, *Stoebe*-type et relativement peu de graminées. Pendant l'Holocène, des graminées ont plus élevé au début de l'Holocène et espèces l'arborescentes taxa comme *Eculea*, *Dombeya*, *Commiphora*, et *Croton*. Ce changement de la végétation suggère le climat plus froid et plus humide dans la dernier période glaciaire relativement à l'Holocène. La baisse de température et d'évapotranspiration jouent semblent avoir joué un rôle important dans les phases humides pendant la période glaciaire. En comparant les donne polliniques avec les isotopes stables dans le même site, les résultats montrent que l'Holocène climat caractérise par l'aridification progressive s'installe depuis début Holocène. Après ~ 3 cal kBP, une augmentation plus rapide d'aridité a déplacé la végétation de site d'étude vers le biome de Désert.

VII. CONCLUSIONS ET PERSPECTIVES

Selon les sites d'études, des analyses des pollens fossiles et des micro-charbons, et les constructions des variables climatiques à partir des données polliniques, les conclusions principales de cette thèse sont les suivantes :

- ✓ Les conditions plus froides de la glaciaire semblent être caractérisées par une augmentation de la disponibilité de l'eau au long des sites d'études sélectionnés. La période plus humide coïncide avec la remontée des eaux côtières (des upwellings), a répondu à la fois à la baisse de températures globales ou régionales.
- ✓ Le climat plus froid et plus humide favorise le développement de la végétation plus mesic du biome de Nama-Karoo (pourcentages élevés des Astéracées). Les ressources d'eau souterraines permettent de maintenir le développement des petits arbres et des arbustes.
- ✓ La période de l'Holocène est caractérisée par l'augmentation des températures et la diminution de la disponibilité de l'eau. Au cours de cette période, l'augmentation de l'intensité des upwellings a établi des conditions plus arides sur le site.
- ✓ Le climat plus chaud et plus aride favorise l'expansion du biome de désert, indiquée par l'augmentation des pourcentages des graminées (Poaceae). Les graminées répondent plus rapidement aux pluies rares qu'on observe actuellement dans la région.
- ✓ En effet, en reconnaissant des limites imposées par une faible résolution de certaines parties des enregistrements, le temps et la nature de changement climatique, le changement de la végétation semblent avoir été synchronisés en grande partie. Ceci suggère que les variations de chaque enregistrement soient déterminées principalement par des processus et des mécanismes à la grande échelle régionale et extra-régionale.
- ✓ Contrairement aux résultats provenant des carottes de sédiment marin, nos enregistrements n'indiquent aucune expansion de la végétation de Fynbos biome, avec seulement des traces de Restionaceae pollen dans le site extrêmement au sud à Pella (ne pas dépasser 1%), mais aucune trace de ce pollen n'ayant été observée à Zizou ainsi qu'à Spitzkoppe.

Pour améliorer les connaissances sur le changement climatique et la végétation dans le désert du Namib, futures recherches seront importantes comme la construction des variables climatiques telles que la saisonnalité de précipitation. En plus, les collections de références de

actuel pollens dans la region sont aussi important pour mieux identifier des grains pollen fossil car actuellement il n'y a pas beaucoup de references des pollen en Namib.

Journal publication

- B.M. Chase, A. Boom, A.S. Carr, M. Chevalier, **S. Lim**, M.E. Meadows, P.J. Reimer: *Drivers and responses of late Quaternary southern African palaeoenvironments*. Quaternary International 06/2016; 404. DOI:10.1016/j.quaint.2015.08.187
- S. Lim**, Brian M. Chase, Manuel Chevalier, Paula J. Reimer: *50,000-years of vegetation and climate change in the Southern Namib Desert, Pella, South Africa*. Palaeogeography Palaeoclimatology Palaeoecology 06/2016; 451. DOI:10.1016/j.palaeo.2016.03.001
- Brian M. Chase, **S. Lim**, Manuel Chevalier, Arnoud Boom, Andrew S. Carr, Michael E. Meadows, Paula J. Reimer: *Influence of tropical easterlies in southern Africa's winter rainfall zone during the Holocene*. Quaternary Science Reviews 11/2014; 107. DOI:10.1016/j.quascirev.2014.10.011
- S. Lim**, Marie-Pierre Ledru, Francisco Valdez, Benoît Devillers, Alfred Hougnon, Charly Favier, Laurent Bremond: *Ecological effects of natural hazards and human activities on the Ecuadorian Pacific coast during the Late Holocene*. Palaeogeography Palaeoclimatology Palaeoecology 12/2013; 415. DOI:10.1016/j.palaeo.2013.12.021

Annexes

Annexe 1: FOSSIL POLLEN PREPARATION METHOD: STANDARD METHOD BERN

I. Materials:

- Samples (hyrax midden)
- Distilled water & water bath
- Water bath temperature: 90 °C (samples in Glycerine lower it to 70 °C)
- Centrifuge speed: 3000-3500 r.p.m
- Duration of centrifuge: Big test tubes (5 minutes) and small test tubes (3 minutes). Samples in Glycerine centrifuge in 10 minutes.
- Rods for stirring samples. Samples are stirred time to time in water bath
- *Lycopodium* tablet was added to each sample as marker.
- Balance, HCL (10%), KOH (10%), HF (Hydrofluoric acid) 40%, Acetic acid (C₂H₄O₂), Acetic acid anhydride (CH₃CO)₂ O & Sulphuric acid (H₂SO₄) 96%, Glycerine 85% (C₃H₈O₃), small porcelain dishes, mesh 0.6 mm.

Precaution: Fume cupboard ventilator should be always turn on if you use the water bath in order to prevent activating fire/vapour alarm detector and if you work with the chemical substances.

FH-treatment: please do not use **GLASS** and work inside the fume cupboard. Use the protective clothes, gloves, eye shield and waterproof shoes as any skin contact with this substance is very dangerous. Put the sign in order to attract the attention of others working in laboratory.

II. Procedure

DAY 1:

Each sample was weighed in order to calculate the pollen and microcharcoal concentration. At least 12 hours before starting the preparation, soak the *Lycopodium* tablet in a Polypropylen test tube with distilled water and sample. The amount of water should be used just to cover the tablet so that the chemical used afterwards will not be so much diluted.

DAY 2:

Add few amount of the HCL (10%) and wait until the reaction stops. If the reaction is too strong stop the bubbles formation with the alcohol before it overflows. Place samples in the water bath for 6-10 minutes. Then centrifuge the samples --> decant--> dispose the chemicals. Wash samples with distilled water by adding 3/4 test tubes with water then stir each sample and centrifuge them again. Dispose water in the drain.

KOH digestion: breaks up the matrix and dissolves the humic materials, producing a brown solution. Add the solution of KOH (10 %) in each sample test tube up to 3/4 then mix it well with samples and place all test tubes in the water bath for 6 minutes. Then centrifuges the samples--> decant--> dispose the chemicals.

Wash samples with distilled water as the process using in washing after HCL treatment.

Sieving: the purpose of this procedure is to remove the large particle matters, for example, plant fragments and grains. The process is as following:

- Put the mesh on the top of the porcelain dish. Add little amount of distilled water into each samples. Stir sample well and pure to the sieve. Repeat the action until the entire material sample has been taken. The large particles remain on the mesh, wash it out.

- Stir sample in the porcelain dish gently and swirl the content by moving the dish in circular motion, stop it for 3-5 seconds so in the centre of the dish, mineral & organic material bigger than 0.6 mm can settle down (pollen floats at least 20 seconds). Gently pure the liquid into the test tube leaving the minerals & plant materials in the dish. Repeat this step if necessary, then centrifuge the samples --> decant --> dispose water.

HF-40% treatment: remove the siliceous and clay materials. Pure 90 ml of HF into the plastic beaker (for 16 samples). Divide it evenly into each sample, stir the sample well. Place the samples in the safety place. Keep the samples in HF for whole night before restart the manipulation the day after.

DAY 3:

- Centrifuge the samples in FH for 5 minutes then --> decant--> disposal chemicals

HCL-10% treatment: adding few amount of solution HCL into the test tubes and transfer each sample into the small test tubes. Repeat the step in order to take the entire

sample from the bigger test tubes. Place the samples into the water bath for 15 minutes. Stir the samples time to time. Centrifuge --> decant--> disposal chemicals. Wash samples with distilled water two times (adding water--> mix well--> centrifuge--> decant). If observe that there are some residual floating on the surface while adding distilled water, please add TBA (tert-Butyl alcohol) in order to make the pollen that float on the surface sink to the bottom.

Acetolysis: removes the protoplasm and leaves the exine. Remove the outer part of the pollen wall exclusively sporopollenin (exine of pollen that well preserve in the soils & sediments). Some pollen types in certain families are destroyed with this procedure such as Cannaceae, Juncaceae, Lauraceae, and Musicales. Some characteristics of pollen grains may be lost under the acetolysis treatment such as spines. This process help to make the pollen grains are clearly observed with the light microscope. This step helps to remove the non-pollen materials. The process is as following steps:

1- Dehydrate the samples: this step is not to be forgotten otherwise the explosion could be taken place if you add directly the acetolysis solution. Fill half of test tubes with the glacial acetic acid --> stir it well --> centrifuge--> decant (no water bath)

2- Acetic acid anhydride (CH_3CO)₂O & Sulphuric acid (H_2SO_4) 96% in ratio 9:1 by volume (3:1 times for laboratory at ISEM). Please make sure that there is no water contacted with the solution because it will create the explosion. Pure those two elements in the glass beaker and gently swirl the beaker in order to mix these two elements well. Add even amount of this solution into each sample and place it 2 minutes in the water bath. Stir samples time to time. Centrifuge--> decant.

3- Repeat the dehydrate step as indicating in the first step. Then wash 2 times with distilled water and add TBA if necessary to make sure that we do not lost any pollen grains that float on the surface.

KOH 10%: preparation for staining (remove the remains of organic material). Add half of the test tubes with the solution of KOH (10%), stir them and place in water bath for the 4 minutes then centrifuge--> decant. Wash samples with distilled water 1 time (2 or 3 time if samples are in clumps).

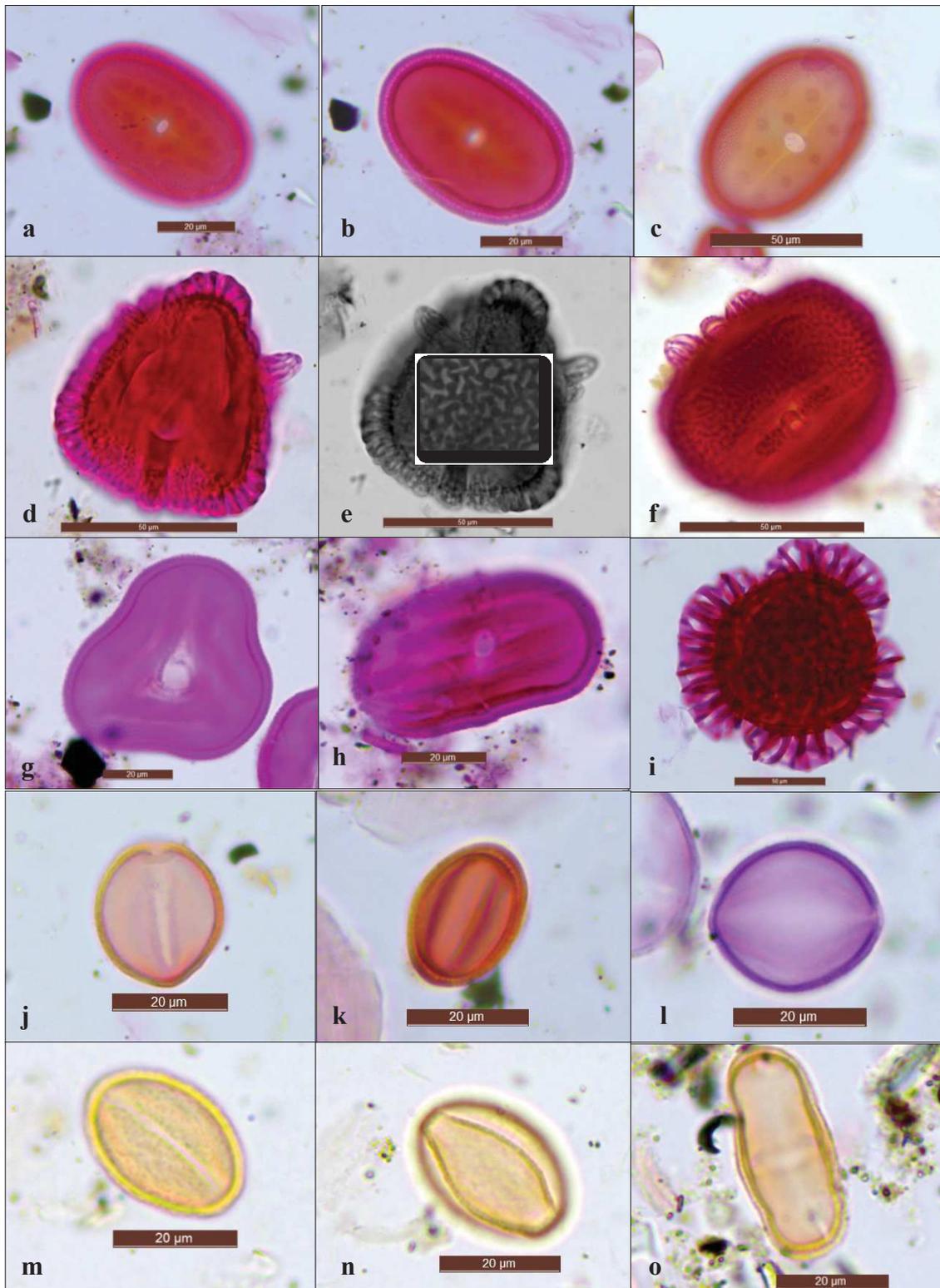
Glycerine 85% ($\text{C}_3\text{H}_8\text{O}_3$): Storage

- Fill 1/3 of test tubes with the Glycerine, stir then add more up to 2/3. Place samples in the water bath by lower the temperature to 70 °C for 4 minutes. Centrifuge the samples for 10 minutes --> decant. If the supernatant is dark, repeat the step by adding new Glycerine each time.

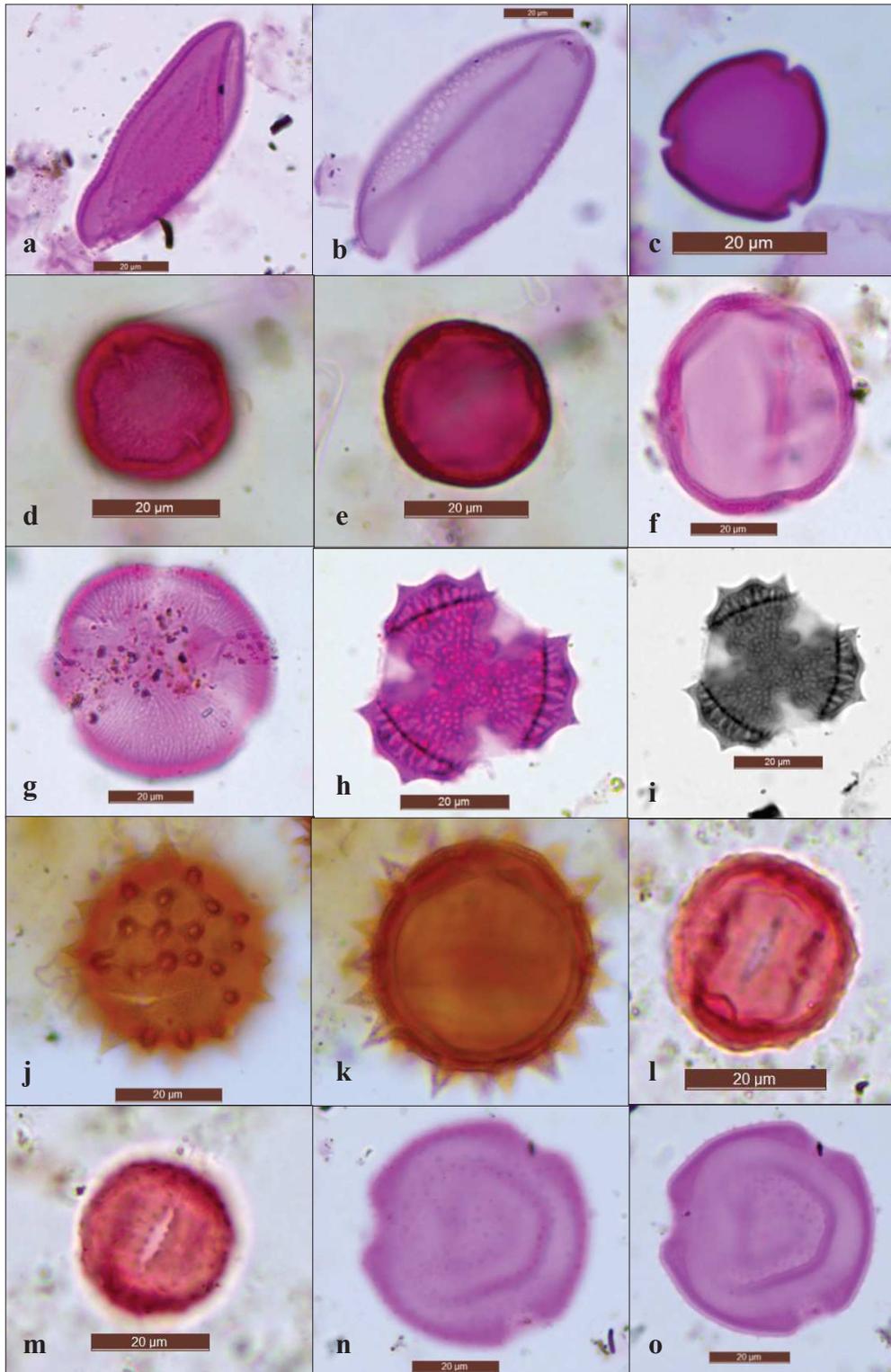
Pollen Atlas

PELLA midden

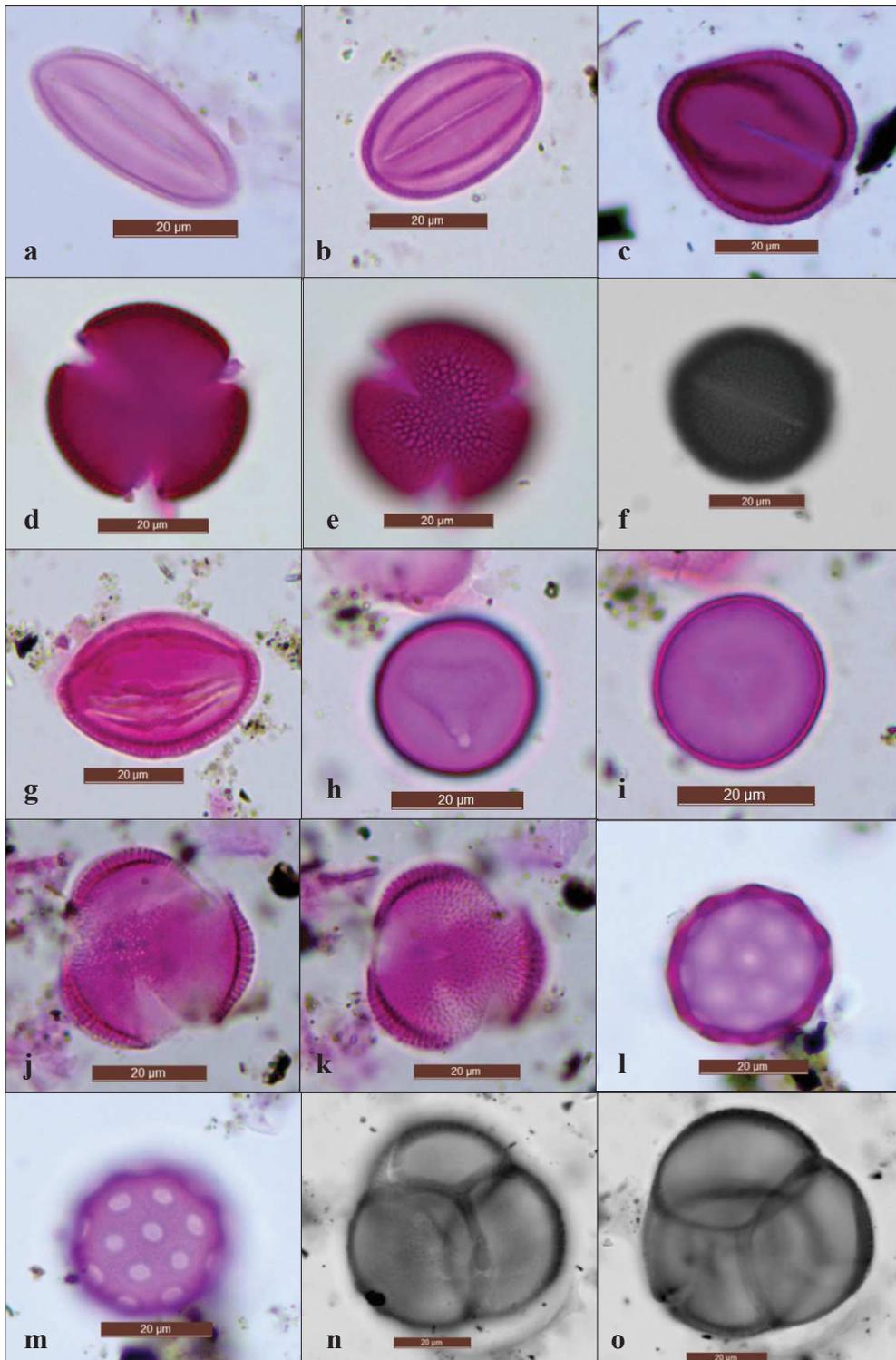
ACANTHACEAE *Justicia*-type (a-c) *Petalidium* (d-f), *Decliptera*-type (g-h), *Barleria* (i),
 AIZOACEAE (j-n), APIACEAE (o)



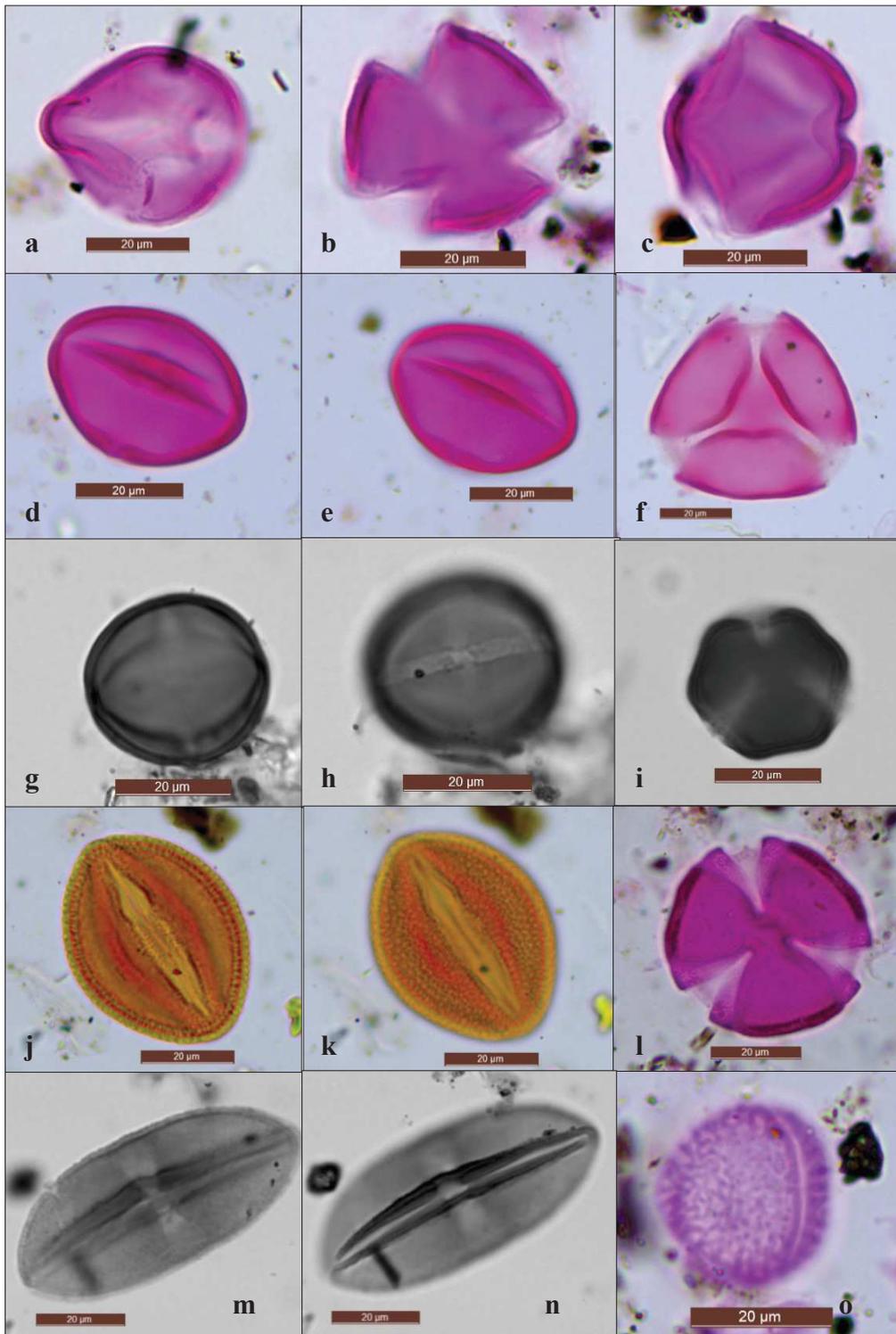
AMARYLLIDACEAE (a-b), APOCYNACEAE (c), ANACARDIACEAE (d-g),
 ASTERACEAE (*Pentzia*-type, h-e), *Berkheya*-type (j-k), *Stoebe*-type (l-m),
 CAMPANULACEAE (*Wahlenbergia*, n-o)



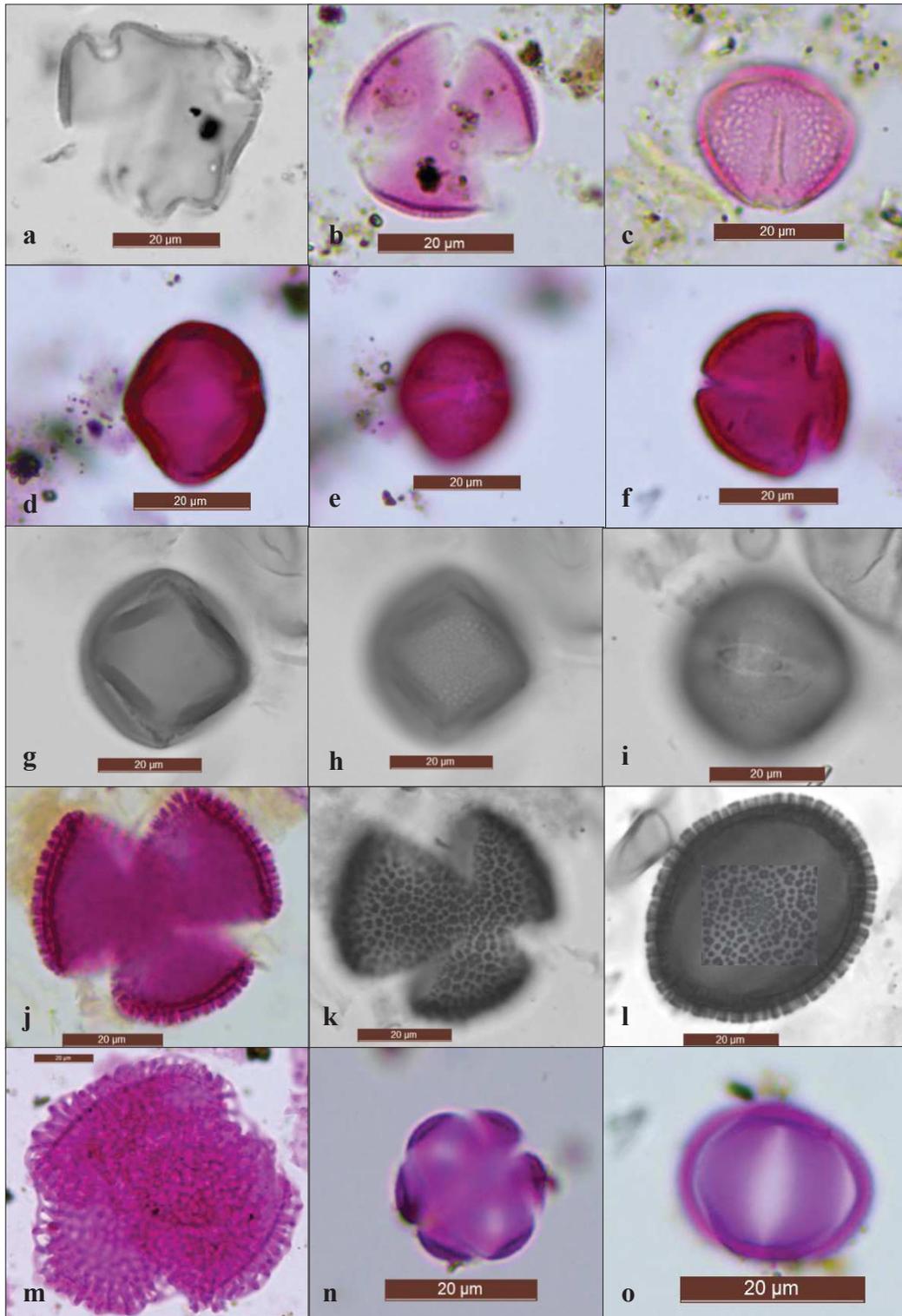
BRASSICACEAE (*Heliophila* , a-b), BRASSICACEAE (c-f), CAPPARIDACEAE (g),
 CUPRESSACEAE (h-i), CELASTRACEAE (j-k),
 CHENOPODIACEAE/AMARANTHACEAE (l-m), ERICACEAE (n-o)



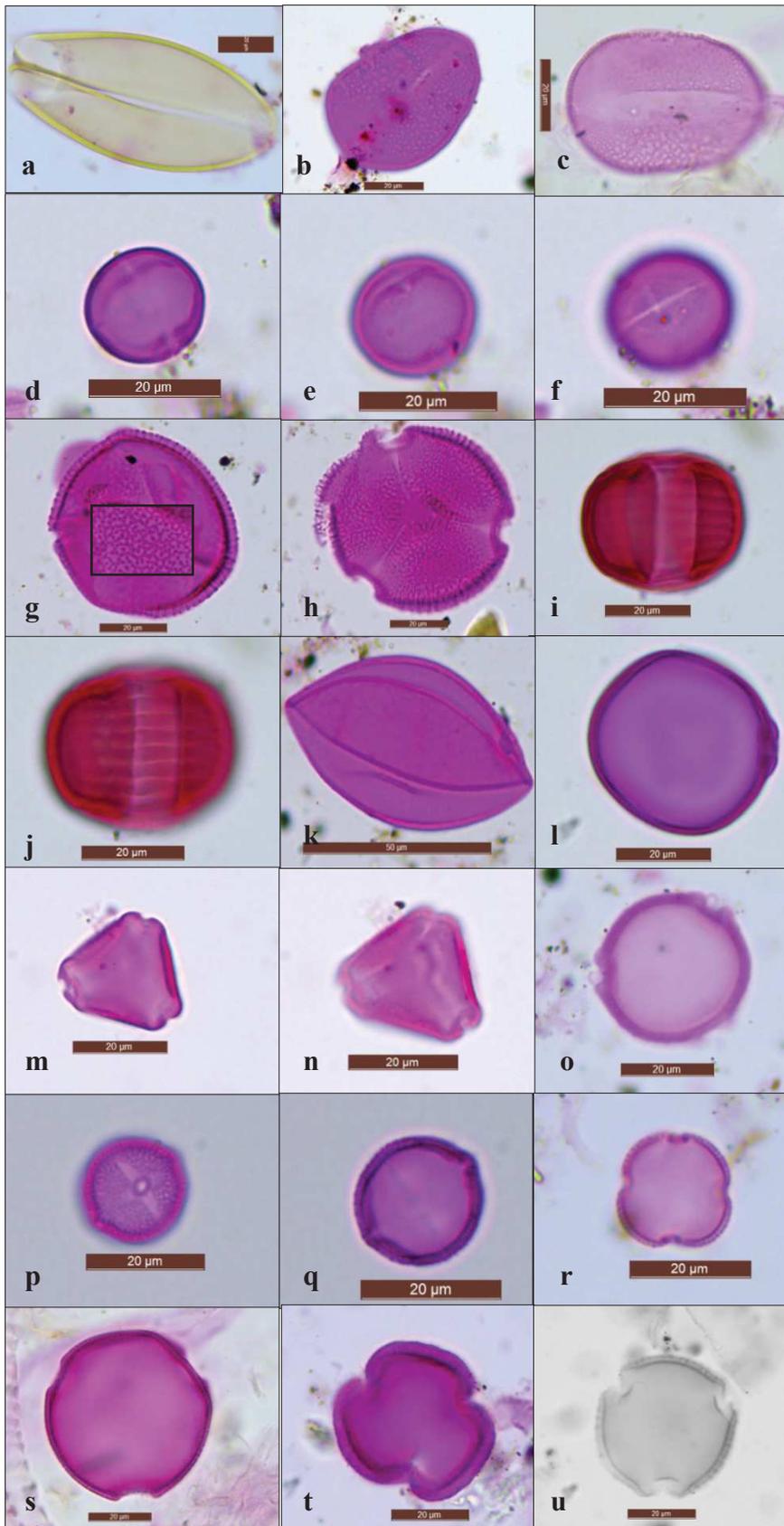
CRASSULACEAE (*Cotyledon* a-c), EBENACEAE (d-i), EUPHORBIACEAE – *Euphorbia* (j-l), *Hyeronima* (m-n), MENISPERMACEAE (o)



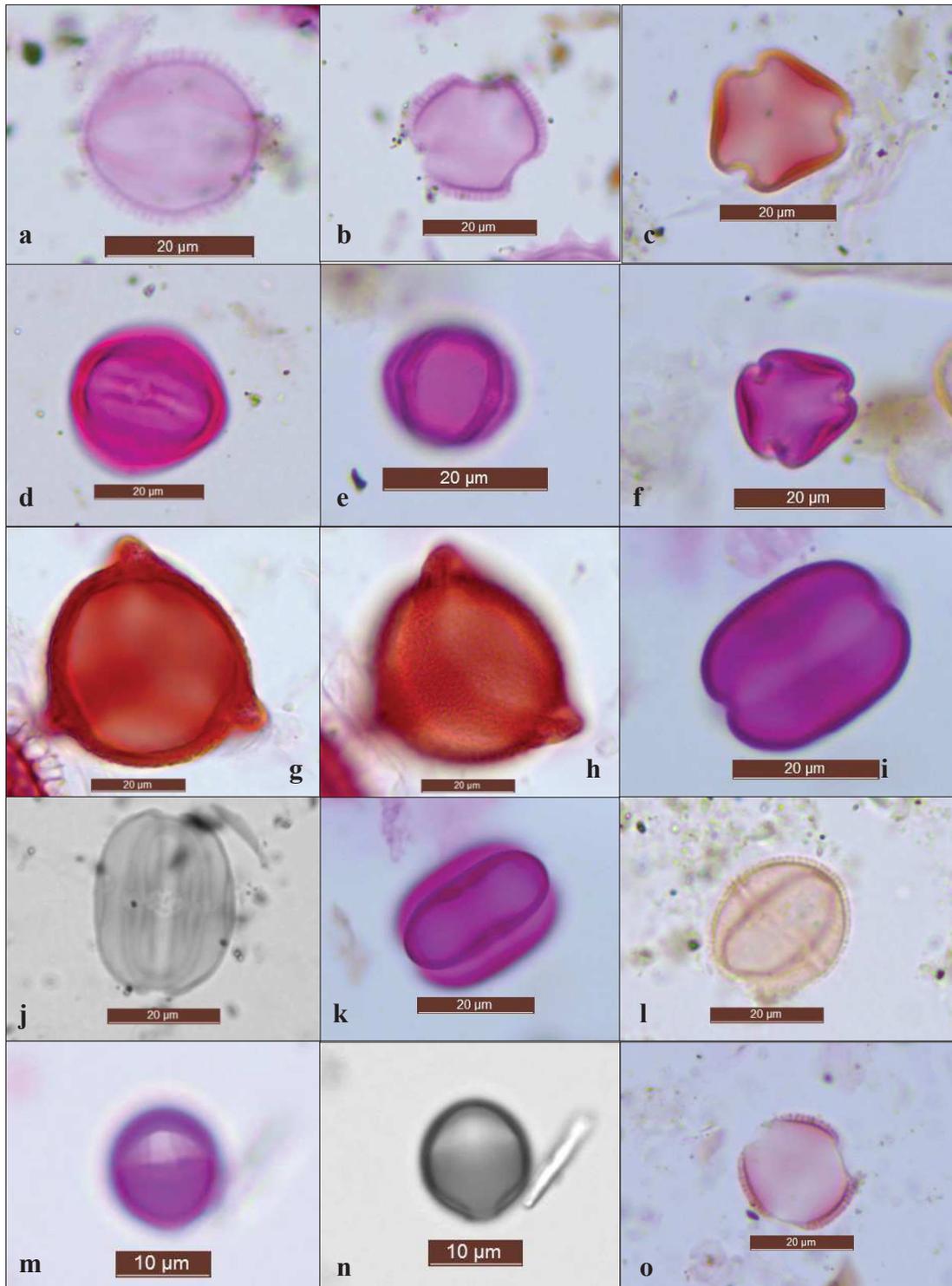
FABACEAE(a-i), GENARIACEAE (Pelargonium, j-l & Geranium, m), LAMIACEAE _
Minthostachys (n-o)



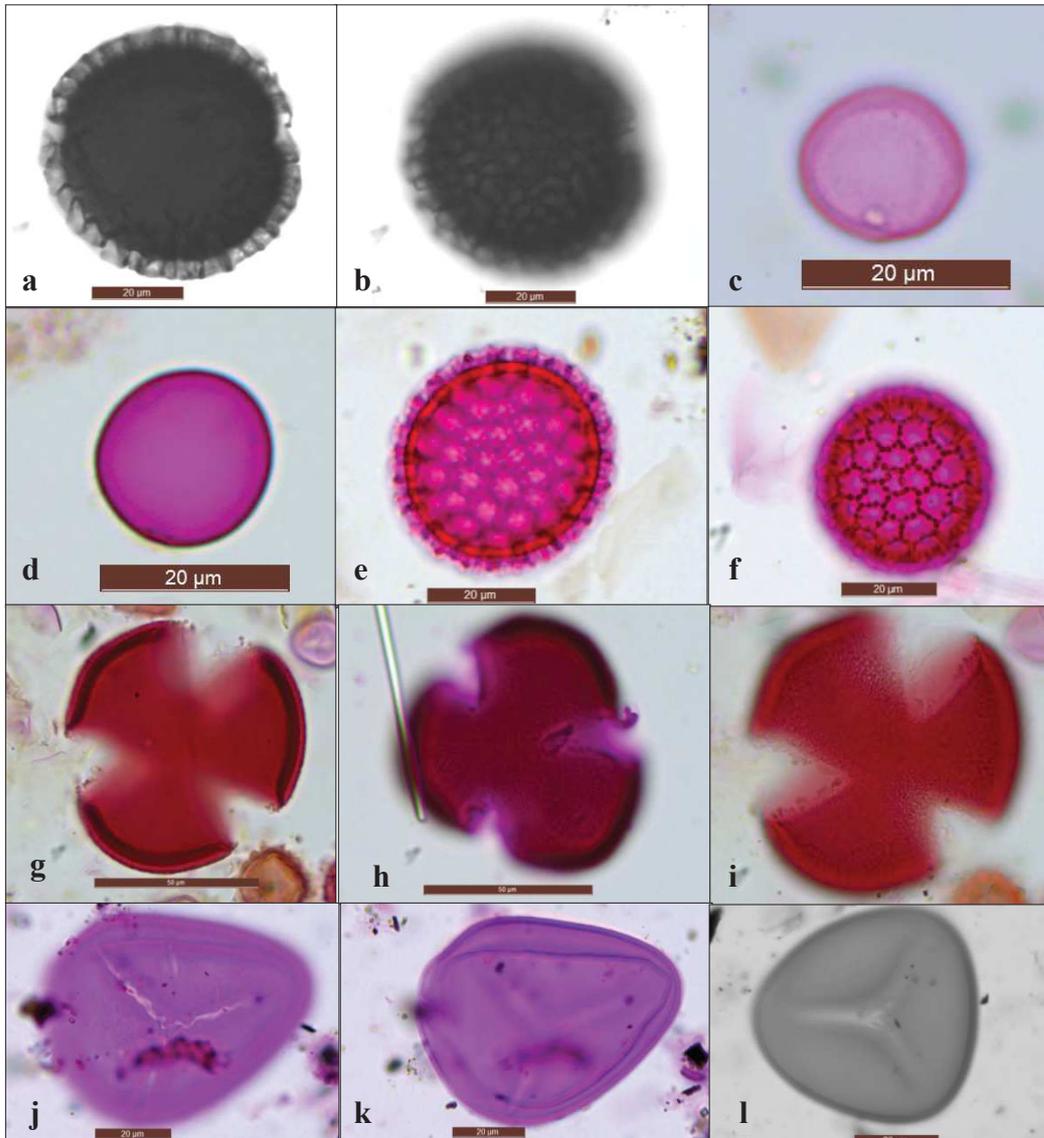
LIALIACEAE (a), *Aloe*-type (b-c), MALVACEAE (*Hermannia*, d-f), MONTINIACEAE (*Montinia*, g-h), POLYGALACEAE (i-j), POACEAE (k-l), RHAMNACEAE (m-n), ROSACEAE (o), RUBIACEAE (*Kohautia*, p-r), RUBIACEAE (s-u)



OLEACEAE (*Olea*, a-b), SAPINDACEAE (*Pappea*,c-f), *Cardiospermum* (g-h),
 SCROPHULARIACEAE (*Anticharis*, i-k), *Selago* (l), *Scrophulariaceae*-type (m-n),
 TAMARICACEAE(o)

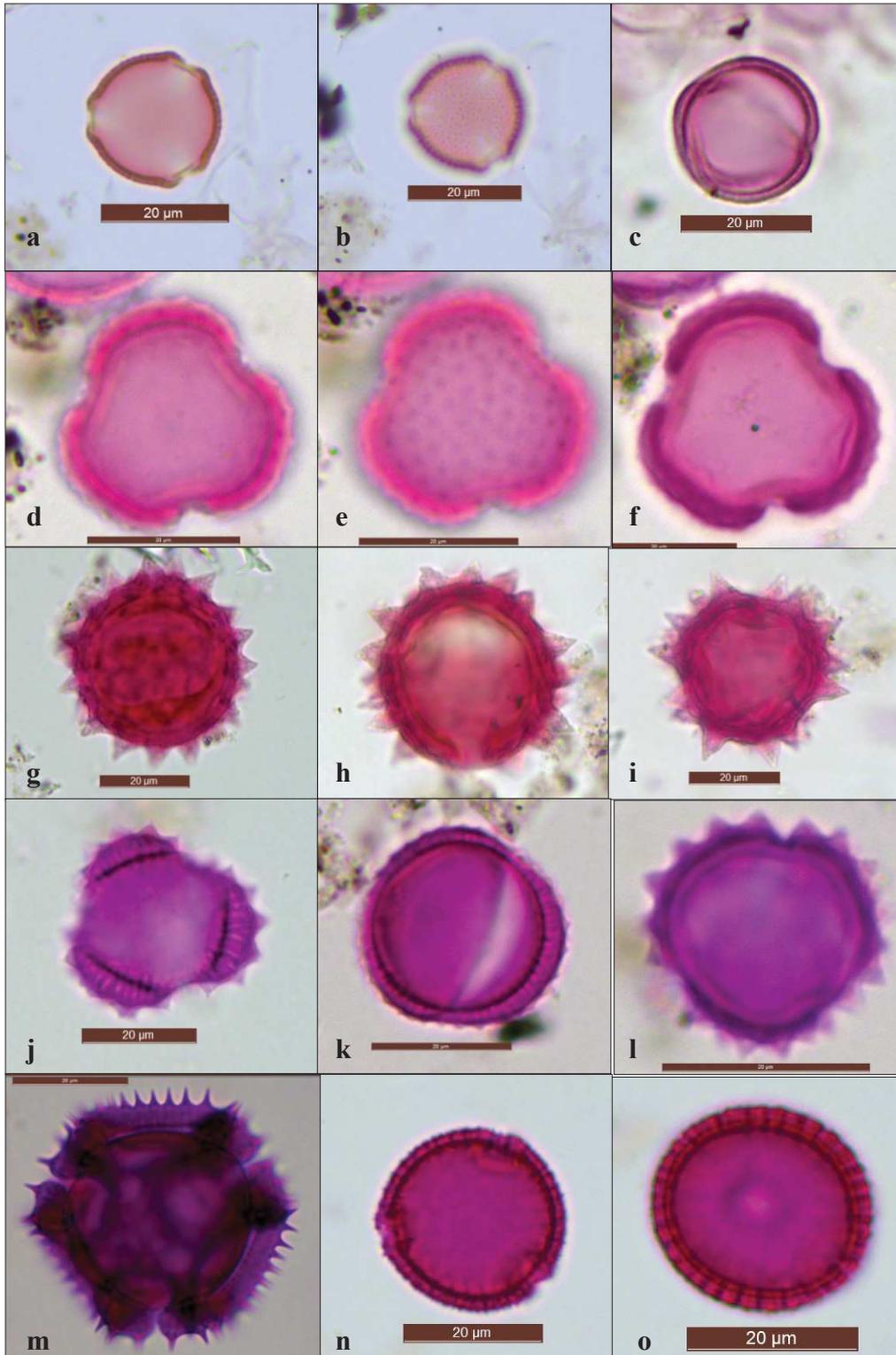


SIMAROUBACEAE(*Kirkia acuminata* , a-b), URTICACEAE (c-d),
 ZYGOPHYLLACEAE, *Tribulus*(e-f), *Sisymbrium* (g-h), SPORES (j-l)

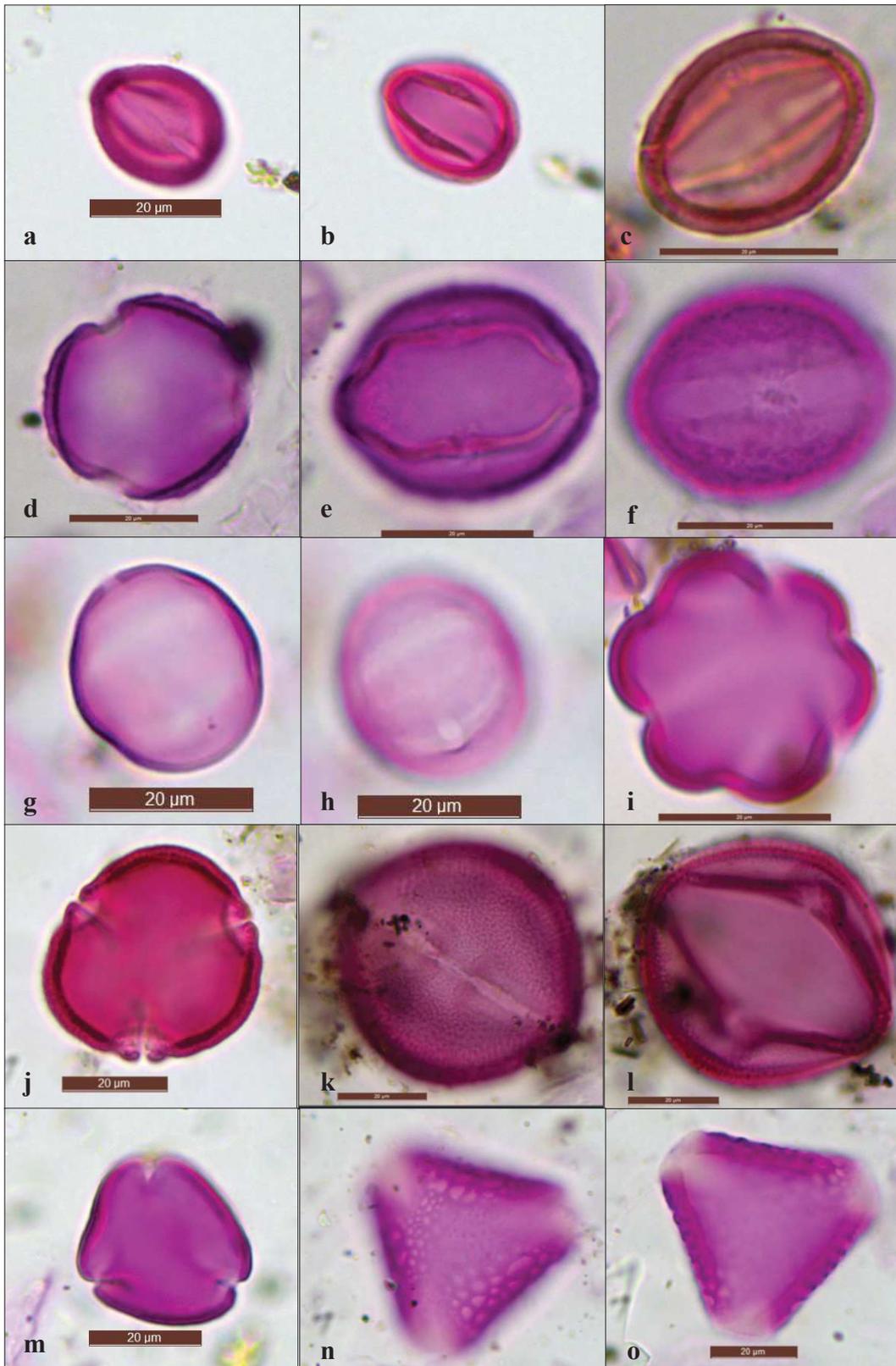


Zizou pollen

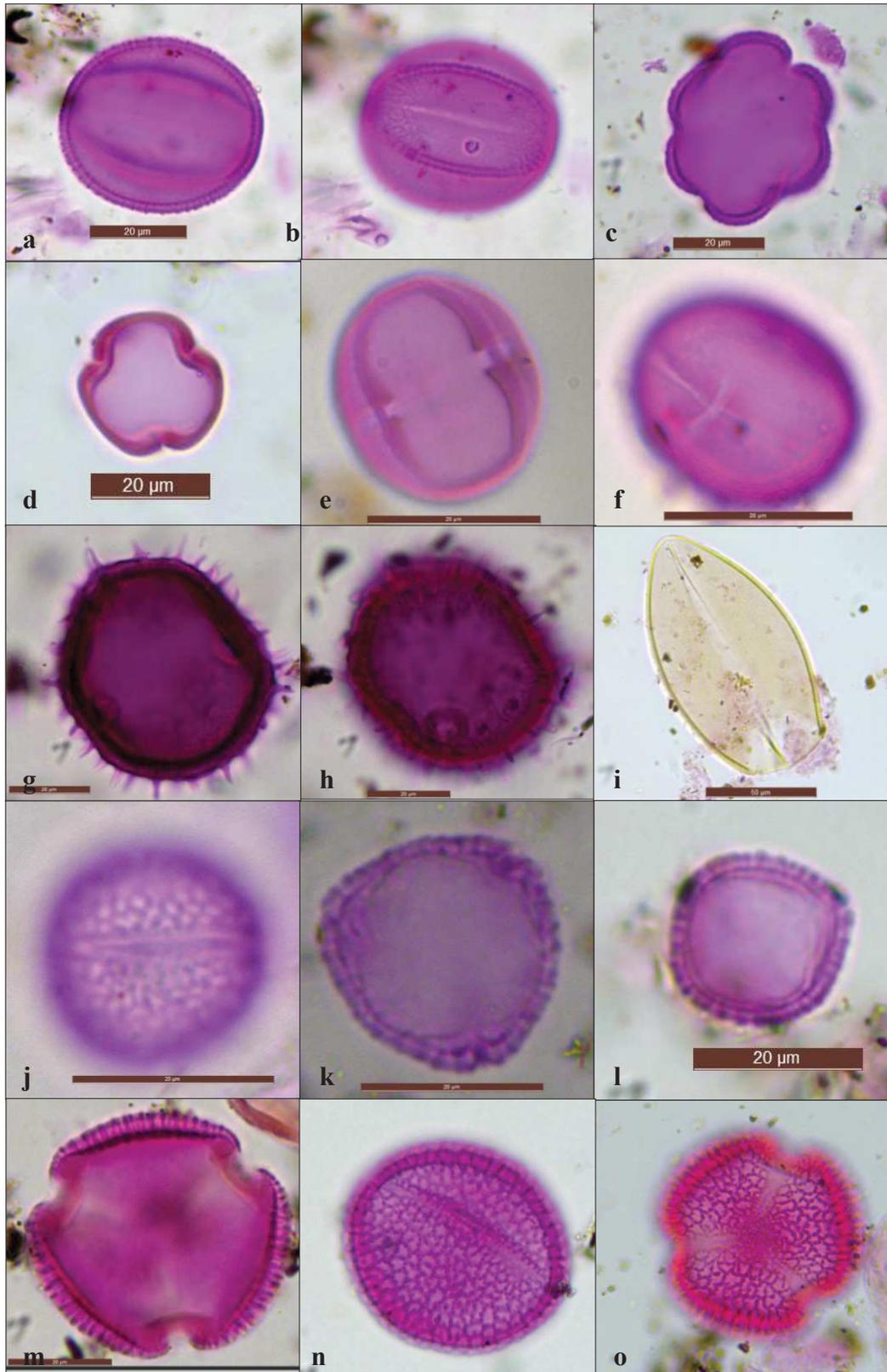
Aizoaceae (*Ruschia*-type, a-c), Aizoaceae (c), Asteraceae (*Stoebe*-type, d-f), Asteraceae (*Burkheya*, g-i), *Pentzia*-type (j-k), *Felicia* (l), Lactucoideae (m), *Commiphora* (n-o)



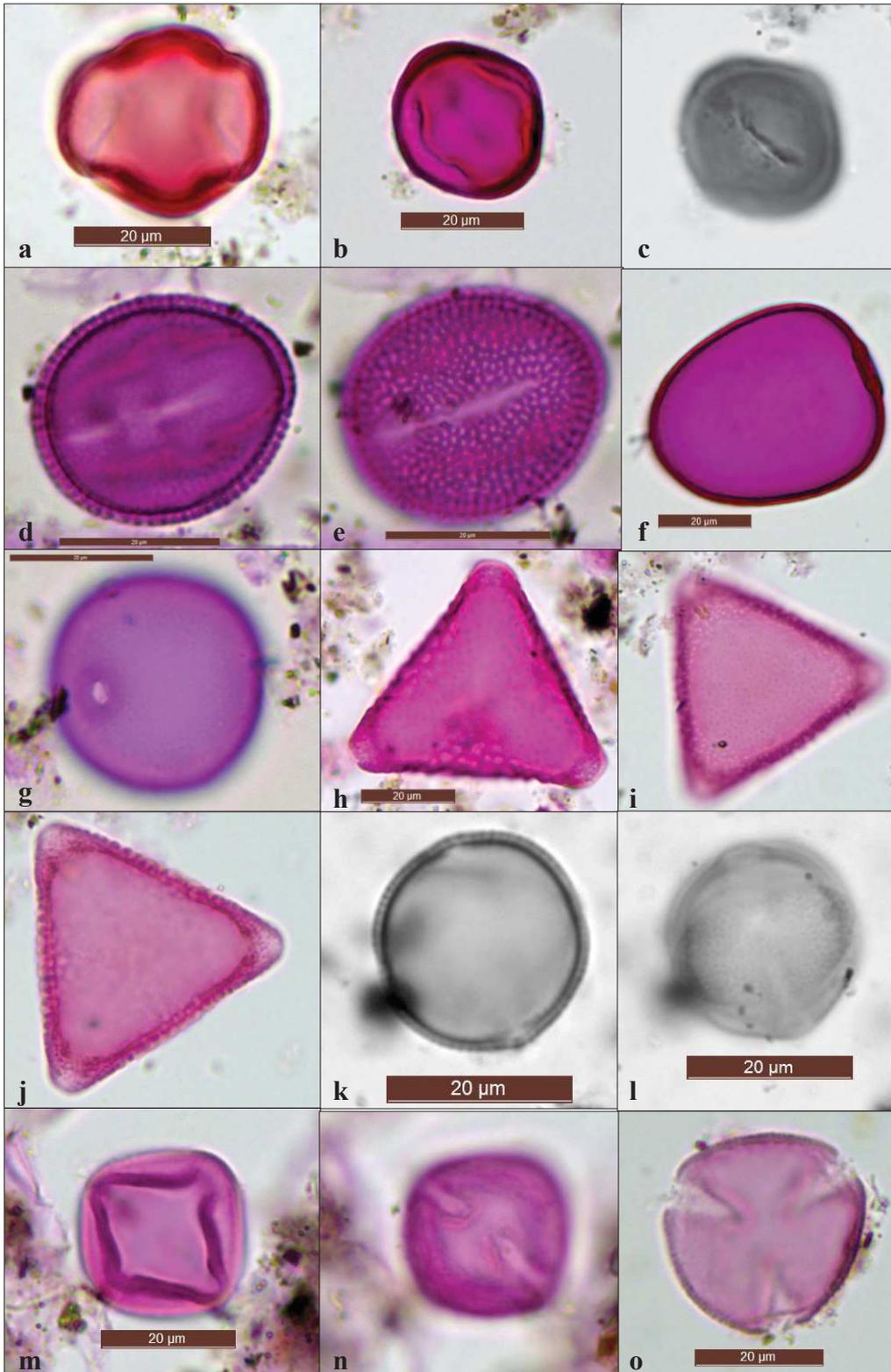
Capparaceae (a-f), Combretaceae (g-i), *Euphorbia* (j-l), Fabaceae (m), *Erythrina* (n-o)



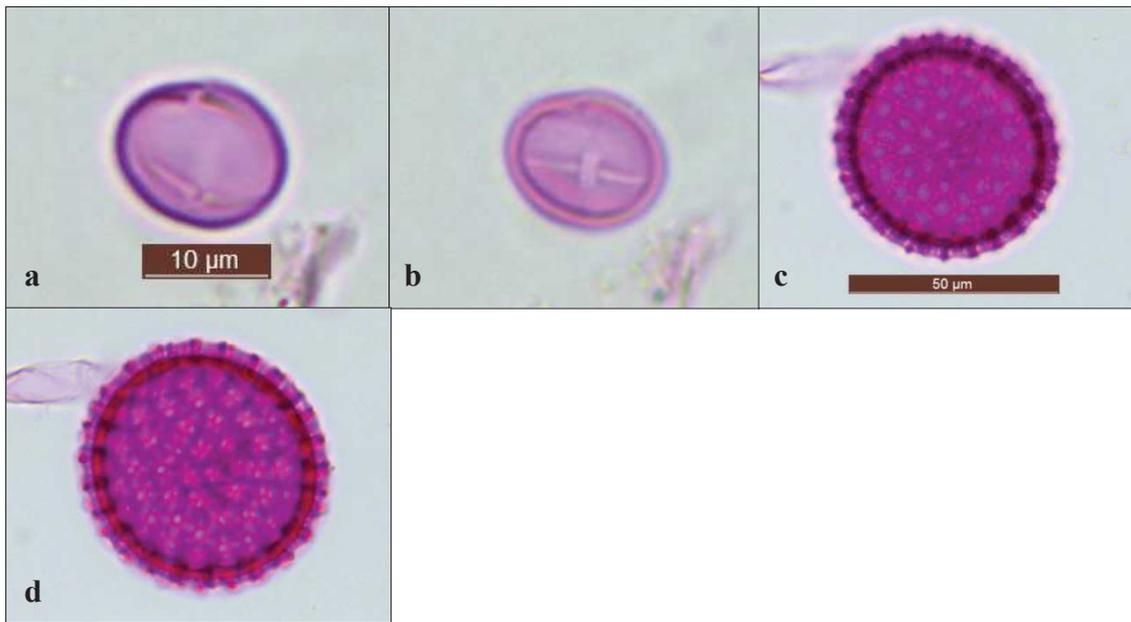
Laminaceae (a-c), Malvaceae (*Hermannia*, d-f), Malvaceae (g-h), Liliaceae (i),
 Menispermaceae (j-l), *Montinia* (m-o)



Myrsinaceae (*Myrsine*, a-c), Oleaceae (*Olea*, d-e), Poaceae (f-g), *Cardiospermum* (h-j),
 Scrophulariaceae (k-l), *Lycium* (m-o)

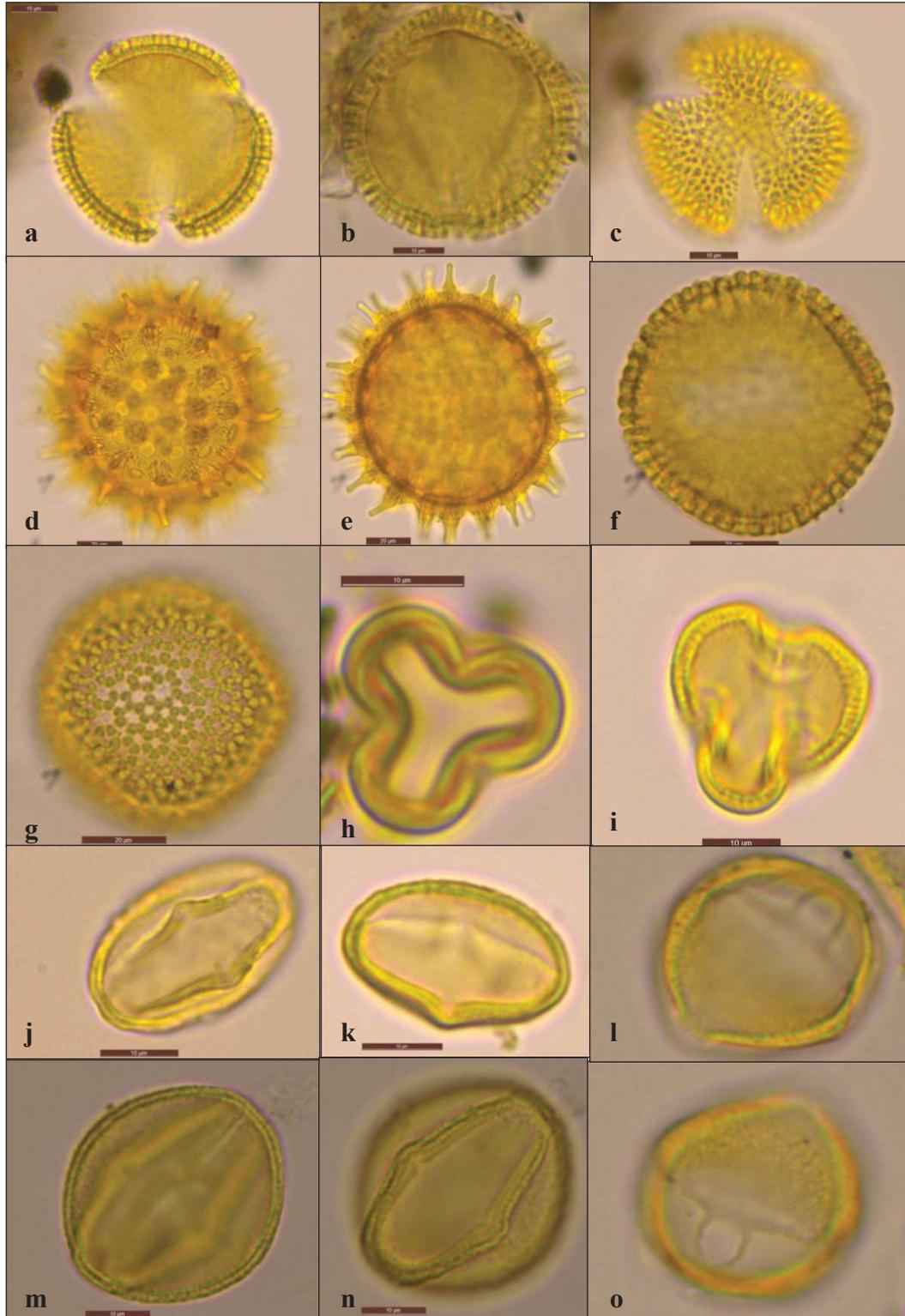


Zygophyllaceae: Zygophyllum (a-b), Tribulus (c-d)

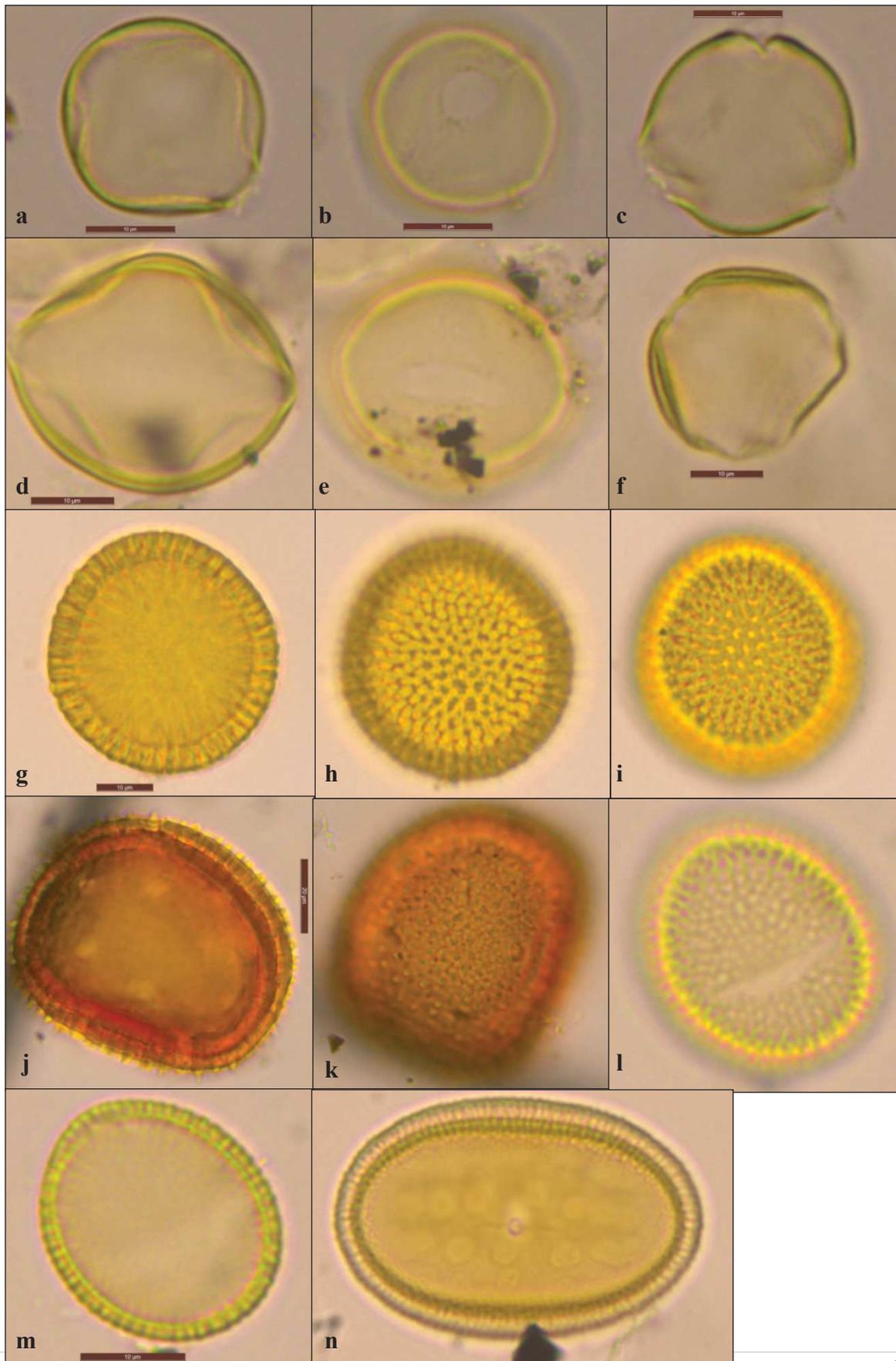


Spitzkoppe midden

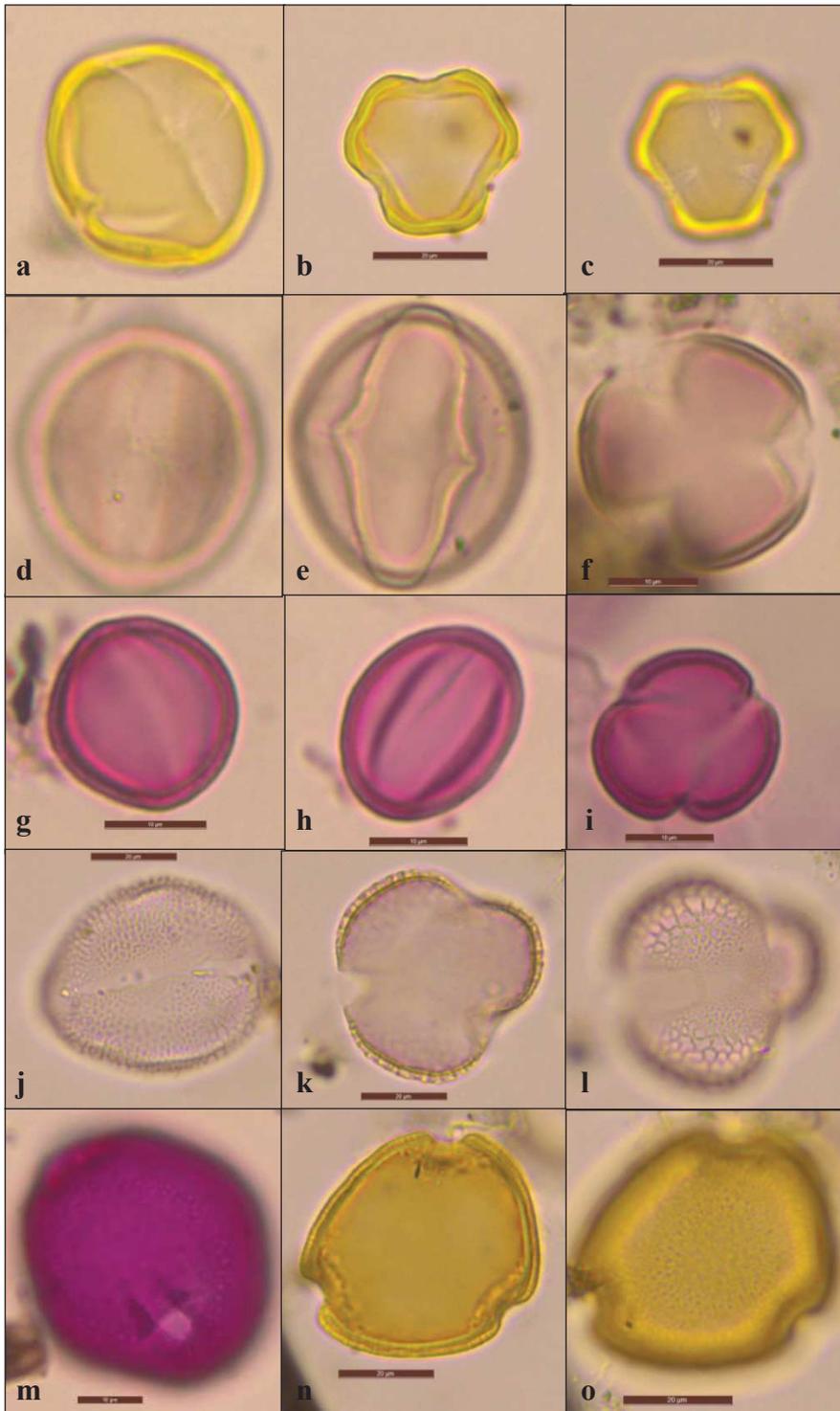
Olea (a-c), *Dombeya* (d-e), *Croton*-type (f-g), Euphorbiaceae (h-i), *Corchorus* (j-k),
Fabaceae (l-o)



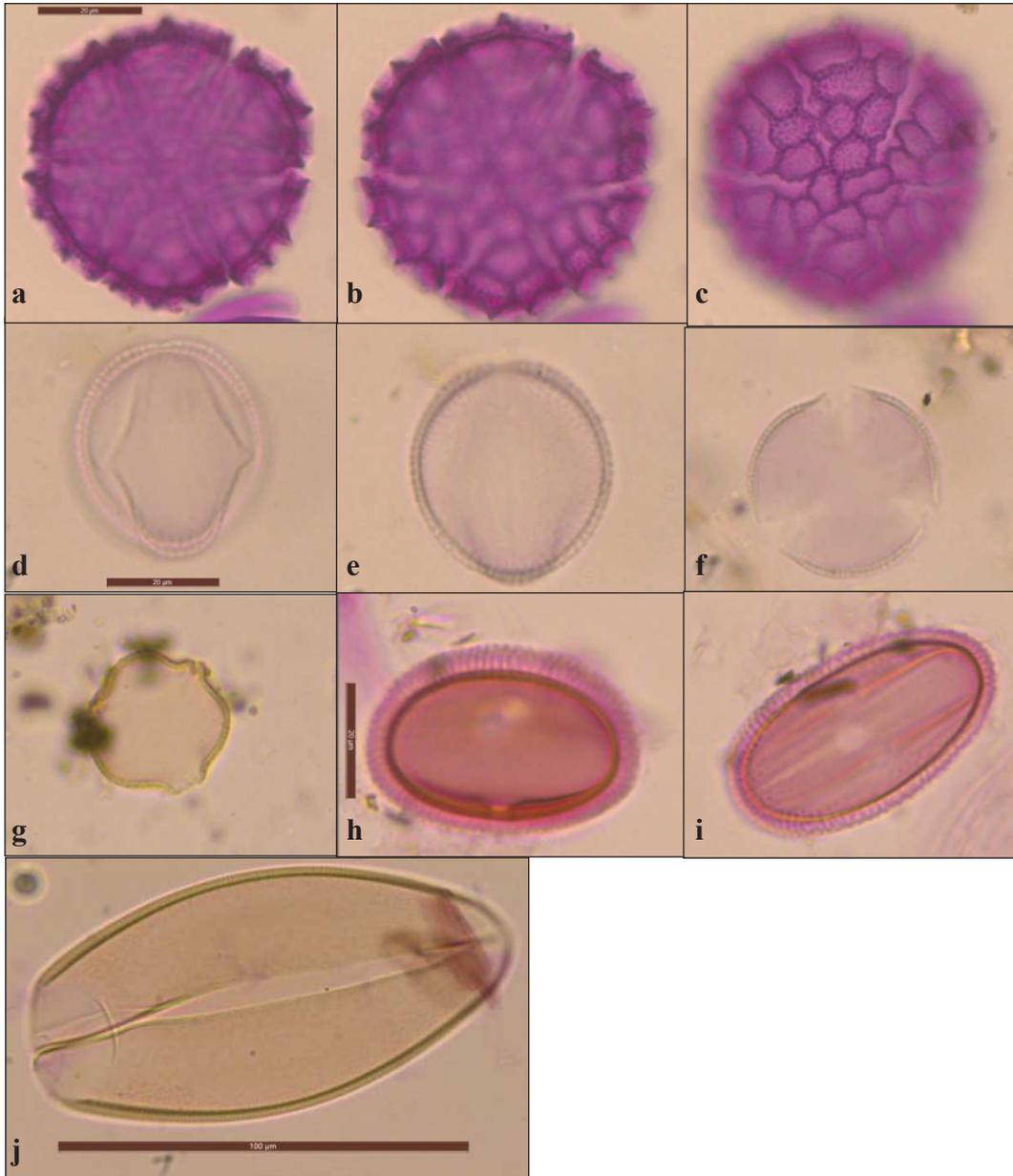
Fabaceae (a-f), Thymelaeaceae (g-i), Nyctaginaceae (j-k), Tamarix (l-m), Justicia (n)



Euclea (a-f), Aizoaceae (g-i), Bignoniaceae (j-l), Canthium-type (m-o)



Lamiaceae -*Ocimum* (a-c), Scrophulariaceae (d-f), *Ruschia* (g), Acanthaceae -*Hypoestes* (h-i), Liliaceae (j)



Brassicaceae *Farsetia* (a-c), Verbanaceae *Lantana* (d-f), Crassulaceae (g-i)

