

RECONSTRUCTING THE LATE PLEISTOCENE PALAEOENVIRONMENT OF THE RICHTERSVELD USING FOSSIL CHARCOAL

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ABSTRACT

The Succulent Karoo is recognised as an important biodiversity hotspot and many of the key plant lineages that characterise the biome are thought to have originated during the Pleistocene epoch. However, due to the paucity of palaeobiological proxy data available for the Succulent Karoo, relatively little is known about its environmental history and how an important core of this region, Namaqualand and its subregion the Richtersveld, may have responded to Pleistocene changes. Recent excavations at Spitzkloof Rockshelter A in the Richtersveld have provided a rare source of palaeoenvironmental data in the form of fossil wood charcoal assemblages that span a sequence from the last glacial maximum (LGM) to ~14 500 yrs BP. The present study analysed the fossil charcoal deposits from the rockshelter in order to reconstruct woody species assemblage patterns as a proxy for late Pleistocene palaeoclimate. Identification of the fossil charcoal specimens was achieved by anatomical comparison with transverse section photomicrographs of identified reference specimens of woody taxa currently growing at the site. Patterns in the charcoal data set were sought by assessing the changes in woody species assemblages over time. An assessment of the environmental correlates of the contemporary distributions of taxa found in the archaeological sequence provided the basis for palaeoenvironmental reconstruction. Based on the current generalisation for glacial climates in the winter rainfall zone (WRZ), it was hypothesised that the study region experienced an increase in rainfall at the LGM, and a steady aridification towards the terminal Pleistocene. However, Spitzkloof's charcoal records provide little evidence to suggest that the LGM supported a more mesic vegetation community than more recent time-periods. Instead, results suggest that the region experienced fairly limited climatic change as there is compelling evidence for the persistence of Succulent Karoo elements – namely *Stoeberia arborea*, *Hermannia disermifolia* and *Lycium spp.* - throughout the late Pleistocene. The localised appearance at the terminal Pleistocene (~14 ka) of all of the most abundant taxa at the site today is interpreted as a consequence of terminal Pleistocene changes in sea-level and CO₂ concentration within a persistent context of minimal climatic change. These results have important implications for the applicability of a generalised WRZ model of climate change to the Succulent Karoo and for hypothetical predictions of future climate change impacts in the biome.

INTRODUCTION

The Richtersveld, in the northern part of Namaqualand, is an important subregion within the Succulent Karoo biome (Midgley and Thuiller, 2007). It is a biome that is recognised as one of the most biologically rich ecoregions in the world (Midgley and Thuiller, 2007; Goldblatt and Manning, 2013). Indeed, it is the world's only desert biodiversity hotspot (Myers et al, 2000). The flora of Namaqualand is estimated to host a total of 2761 native species with 26.8% endemism (Goldblatt and Manning, 2013). Key Succulent Karoo plant lineages are thought to have originated fairly recently, during the Pleistocene epoch (2.58 million to 11 500 years BP) (Klak et al, 2004; Verboom et al, 2009).

Although explosive species diversification occurred in the Succulent Karoo during the Pleistocene, there is considerable debate as to what the environmental drivers of diversification may have been (Midgley and Thuiller, 2007). Two competing climate-history hypotheses have been proposed. It has been suggested (Midgley, 2001) that fluctuating conditions of enhanced moisture availability and increased aridity during the Pleistocene may have been instrumental in the rich diversification of the Succulent Karoo flora. An alternative viewpoint is that muted climate change and a moderate Pleistocene climate history allowed for the accumulation of plant species within the region (Midgley and Thuiller, 2007). This viewpoint is based on arguments made by Jansson (2003) that the global distribution of high endemic species richness is strongly related to regions that experienced limited glacial-interglacial climate change.

The muted climate-history hypothesis has prompted the suggestion that the Succulent Karoo may be particularly vulnerable to the effects of anthropogenic climate change. Indeed, early bioclimatic models identified the Succulent Karoo as the biome in southern Africa with the greatest vulnerability to climate change impacts, losing up to 100% of its suitable range by 2050 (Rutherford et al, 2000). However, the future vulnerability of the biome is a contested issue and contrasting predictions have been put forward in the recent literature (Driver et al, 2012). Based on downscaled climate scenarios for South Africa, Driver et al (2012) predict that even under worst-case scenarios, the Succulent Karoo is likely to maintain most of its current range by 2050. It is difficult to verify projected vegetation shifts in the Succulent Karoo, not only because climate change scenarios remain uncertain, but also because little is known about the Pleistocene climate-history of the region. An improved understanding about how an important core of this region, Namaqualand and its Richtersveld subregion, might have responded to Pleistocene changes may provide important insights into the resilience of the vegetation to climate variability.

Globally, Pleistocene climates have oscillated between cold glacial- and relatively warm interglacial-states driven by the cyclical growth and retreat of high latitude ice sheets (Cowling et al, 1999). At a global scale, glacial climates are understood to have been relatively dry due to the reduced water-holding capacity of the atmosphere (Chase and Meadows, 2007; Midgley and Thuiller, 2007). However, of relevance to much of the Succulent Karoo biome, is the suggestion that the winter rainfall zone (WRZ) along the western margin of southern Africa experienced fairly wet conditions during much of the last glacial (Chase and Meadows, 2007). It has been proposed that, with the expansion of Antarctic sea ice during glacial periods, the westerly rain-bearing anti-cyclonic weather systems associated with the WRZ may have been displaced equator-ward, bringing more frequent or intense winter storms to the region, even as far north as central Namibia (Chase and Meadows, 2007).

A growing number of palaeoenvironmental studies have outlined the late Pleistocene climate history for the west coast region of the WRZ. However, reconstructions have been hindered by the poor preservation of traditional palaeoenvironmental proxy data sources (Chase and Meadows, 2007). Unfortunately, due to prevailing semi-arid climatic conditions and a strongly seasonal rainfall regime, palaeoenvironmental data for the late Pleistocene is scarce for the Succulent Karoo biome, particularly for the Namaqualand region (Midgley and Thuiller, 2007). The current generalisation for the WRZ is that during the last glacial maximum (LGM; roughly 24 000 – 18 000 BP), conditions were around 5.2 - 6°C colder, and considerably wetter, than the present interglacial (Chase and Meadows, 2007). This interpretation is based on data from Namibia, a region currently influenced by summer rainfall zone (SRZ) climatic regimes, and from sites far to the south of Namaqualand, in the winter rainfall zone (WRZ) of the southwestern Cape. It therefore remains to be tested whether this model of Pleistocene climate change holds true for the Succulent Karoo.

Two main palaeobotanical proxies, in the form of fossil wood charcoal and pollen deposits, have been crucial for the reconstruction of a late Pleistocene climate history for the southwestern Cape. An analysis of pollen deposits from Elands Bay Cave in the southwestern Cape (Baxter, 1996) suggested that the LGM was moister than at present because maximum values of woodland taxa and minimum values of xeric karroid taxa were found in LGM deposition layers. In accordance with these findings, the fossil charcoal from the same deposits indicated a shift from drought-intolerant Afromontane forest species in the LGM, such as *Celtis africana* and *Grewia occidentalis*, to thicket and fynbos vegetation in the late Pleistocene (18 000- 11 500 BP) (Cowling et al, 1999). Recent analysis of the charcoal deposits at the nearby Diepkloof Rock Shelter reveals the same trend towards an increase in arid-adapted taxa after the LGM (Cartwright, 2013).

Further inland, in the mountains of the Cederberg, palynological evidence from rock hyrax (*Procavia capensis*) middens indicate a shift at 16 ka from glacial vegetation assemblages characterised by high-elevation *Stoebe/Elytropappus* shrubs and asteraceous fynbos to a mosaic of succulent karoo and thicket species (Scott, 1994). This shift has been interpreted as a signal of reduced rainfall availability during the last glacial termination (Scott and Woodborne, 2007a, b).

The palaeoenvironmental data from southwestern Cape provides compelling evidence in support of the generalised model of increased rainfall along the western margin of southern Africa during the LGM. However, the climate signals from Namibian sites are not as coherent and are somewhat contradictory. Two commonly cited palaeoenvironmental studies from Namibia lend credence to the suggestion that the equator-ward migration of the westerly frontal system during the last glacial would have resulted in the expansion of WRZ, bringing significantly enhanced rainfall to the Namib Desert. The first line of support comes from Scott et al's (2004) analysis of rock hyrax middens, situated as far north as Brandberg in the northern interior of Namibia. In samples dated to the height of the LGM (at 21 000 BP), Scott et al (2004) identified pollen from mesic-adapted taxa that are not present in the arid landscape today. Marine core data taken off the central Namibian coast corroborates these findings of a wetter LGM signal. Shi et al (2001) recorded a peak in Restionaceae pollen at the start of the LGM and a steep decline over the late Pleistocene, reaching negligible values by 15 ka. It has, however, been argued that marine cores may be of inadequate interpretive value due to the possible long-distance transport of pollen by wind or ocean currents (Scott et al, 2004; Chase and Meadows, 2007).

In a synthesis of the most reliable proxy evidence for palaeoclimatic change in Namibia, Lancaster (2002) argued that there is negligible evidence of enhanced rainfall in the Namib over the late Pleistocene. This suggests that the semi- to hyper-arid conditions of the Namib have remained fairly stable throughout the Quaternary. Indeed, palaeoenvironmental data from Apollo 11 Rockshelter in southern Namibia affirms this interpretation. Analysis of the faunal remains from excavations at the site revealed few taxonomic differences between Pleistocene and Holocene assemblages suggesting that glacial and interglacial climatic conditions were not dissimilar (Thackeray, 1979). However, the high 'mean ungulate body-mass' index of the last glacial assemblage hints at higher precipitation in the terminal Pleistocene (Thackeray, 1979). However, new data from a recent excavation of Apollo 11 could not confirm this signal (Vogelsang et al, 2010). Thus, it is not clear whether the glacial climatic conditions that characterised the southwestern Cape during the late Pleistocene extended as far north as Namibia. It is therefore possible that the westerly frontal system

associated with the WRZ did not expand, as suggested by Chase and Meadows (2007), into the contemporary SRZ during the LGM.

In the absence of available palaeobiological evidence for sites in the Namaqualand core region of the Succulent Karoo biome (Midgley and Thuiller, 2007), it is tempting to draw on a generalised model of WRZ palaeoclimatic change to reconstruct a late Pleistocene climate history for the region. However, given that the region is on the cusp of the interface between the current summer- and winter-rainfall zones, and that there does not appear to be a coherent late Pleistocene climate signal for the entire western margin of southern Africa, it is not clear that a generalised model would be applicable. Indeed, the high level of endemism associated with the biome may be a function of limited Pleistocene climate change (Midgley and Thuiller, 2007), rather than the steep glacial-interglacial shifts that characterise southwestern Cape records. The reconstruction of a palaeoclimatic history for the Succulent Karoo and Namaqualand requires a reliable proxy data source from a site within the region itself. Such a data source has recently become available in the form of fossil wood charcoal assemblages from Spitzkloof Rockshelter in the Richtersveld in the northern hinterland of Namaqualand.

Excavation of Spitzkloof Rockshelter was initiated in 2010 as part of a larger archaeological project called AMEMSA (Adaptations to Marginal Environments in the Middle Stone Age) (Dewar and Stewart, 2011). Preliminary analyses of the Spitzkloof charcoal assemblages were carried out in 2011 (Packer, 2011) and 2012 (Sobol, 2012). Results from these two studies did not provide a basis for making inferences about palaeoclimatic change as neither sampled a long enough sequence of charcoal material and analyses were conducted prior to radiometric dating of the site. Recently obtained radiocarbon dates suggest that the rockshelter was occupied during the LGM, at 19.5ka, and again at 16ka, 15ka and 14ka (Dewar and Stewart, 2013). This sequence provides the opportunity to renew attempts at reconstructing a late Pleistocene climate history for Namaqualand from Spitzkloof's charcoal assemblages.

The aim of the present study, therefore, was to analyse the fossil charcoal deposits from Spitzkloof Rockshelter A in order to reconstruct woody species assemblage patterns as a proxy for late Pleistocene palaeoclimate. Because of its location within the WRZ, it is hypothesised that Spitzkloof probably experienced an increase in rainfall at the LGM, and a steady aridification towards the terminal Pleistocene. Possible steady reductions in moisture availability over the period spanning the LGM to the late glacial (*sensu* Chase and Meadows, 2007) in the charcoal record should be manifested by a change from more mesic thicket

species to a greater predominance of arid-adapted taxa that characterise the contemporary Succulent Karoo vegetation of Namaqualand.

METHODS

Study area

Spitzkloof Rockshelter A (28° 51' 47.4" S; 17° 04' 39.162" E) is situated within the lower Gariiep Valley in the Richtersveld which forms the northern part of Namaqualand. The rockshelter is located roughly 30 km south of the Gariiep (Orange) River and 30 km inland from the Atlantic Ocean. Spitzkloof A is the largest of three consecutive caverns (labelled A-C) located on the valley slopes overlooking a dry tributary of the Holgat River (Figure 1) (Dewar and Stewart, 2011).

The landscape surrounding the site is a mosaic of undulating quartzitic gravel plains interspersed with rocky outcrops and sandy riverbeds that flow once a decade at most (Dewar and Stewart, 2011; Goldblatt and Manning, 2013). The area receives extremely low and erratic rainfall which arrives predominantly (>66%) in the winter months. In the desert areas of the Gariiep Valley, rainfall can be as low as 45 mm per annum. Precipitation increases towards the mountains of the central Richtersveld which can receive up to 200 mm per annum. The average annual rainfall for the low-lying plains is about 70 mm (Goldblatt and Manning, 2013). Maximum temperatures at the site typically exceed 30 °C in the summer while sub-zero temperatures typically characterise winter minimums (Dewar and Stewart, 2011).

The lower Gariiep Valley forms a corridor for cool moist air and fog to travel inland from the coast (Goldblatt and Manning, 2013). These coastal fogs, locally known as 'malmokkies', provide a crucial source of moisture to arid-adapted fauna and flora up to 90 km inland (Mucina and Rutherford, 2006; Dewar and Stewart, 2011). The vegetation of the Richtersveld forms part of the Succulent Karoo biome while the dominant vegetation type at Spitzkloof is described by Mucina and Rutherford (2006) as Lekkersing Succulent Shrubland. This vegetation unit is dominated by leaf-succulent shrubs such as *Stoeberia spp.* and non-succulent shrubs such as *Lycium cinereum* and *Hermannia spp.* while riverbeds and valleys can be densely wooded with trees and tall shrubs such as *Acacia karroo* and *Euclea pseudebenus*.

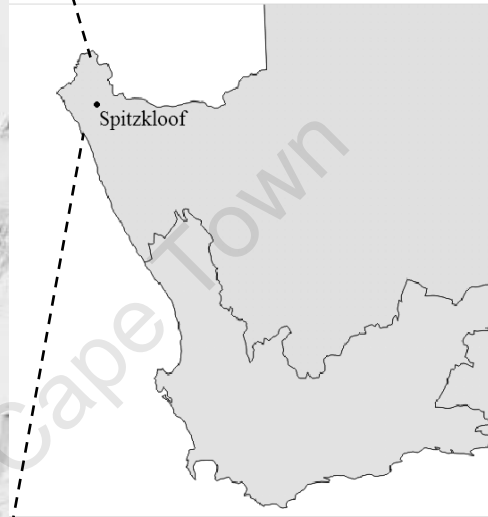
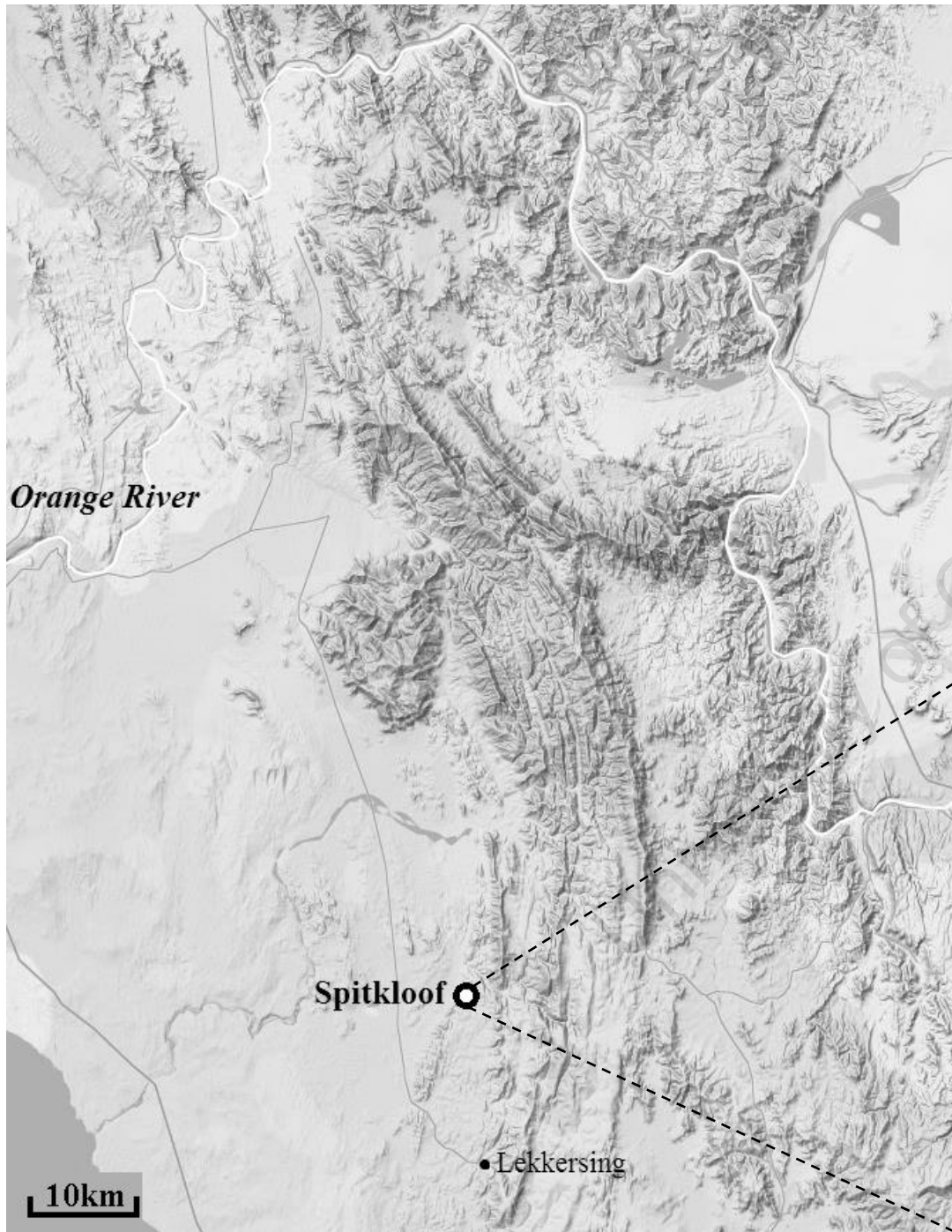


Figure 1: Map of South Africa (adapted from Packer, 2011) showing the location of Spitzkloof just below the Orange (Gariep) River and north of Lekkersing. The photograph below shows the three rockshelters (labelled A-C from right to left) and their position above the dry tributary.



Excavation of Spitzkloof Rockshelter A

Excavation of Spitzkloof Rockshelter A was initiated by the AMEMSA team in 2010 and continued in 2011 (Dewar and Stewart, 2011; Sobol, 2012). Care was taken to avoid the remains of modern-day camping fires in the establishment of the two-by-two m² excavation grid. In total, nine layers were excavated and 20 contextual changes were noted. Contexts were identified on the basis of changes in sediment texture and artefact inclusions. Artefactual material, including fragments of wood charcoal, was retrieved by means of dry-sieving sediment from each of the 20 contexts (Dewar and Stewart, 2011). Fragments were bagged on site and labelled according to the context of origin. Radiocarbon dates measured on ostrich eggshell from Spitzkloof A returned an age of $14\ 366 \pm 43$ ¹⁴C years BP for the upper-most context and ages of between $51\ 159 \pm 816$ and $52\ 139 \pm 794$ ¹⁴C years BP for the oldest datable contexts (Dewar and Stewart, 2013).

Reference charcoal collection

The collection of modern reference specimens necessary for the identification of charcoal from Spitzkloof Rockshelter began in 2011 (Packer, 2011) and continued in 2012 (Sobol, 2012) and 2013 (this study). Given that the two initial collections were limited to the immediate surrounds of the rockshelter and the widely-held view that hunter-gatherers typically acquired resources within a few hours walk of their base (Cartwright, 2013), the need arose to extend the sampling area.

In order to capture a more realistic collection area, a 2.3 km stretch of the dry river bed - starting at the valley opening 800 m downstream of the rockshelter and ending 1.5 km upstream of the shelter - was sampled. Along the course of the dry riverbed, woody taxa were documented, photographed and collected. Species identifications were made in situ and were later confirmed using published accounts (Goldblatt and Manning, 2013) and herbarium records. The percentage cover of each of the woody species growing within 100 m-long transects along the 2.3 km channel was recorded.

Modern wood samples from the initial localised collections made by Sobol (2012) and from the recent expanded collections were converted to charcoal - following methods described by February (1992) - to provide a basis for anatomical comparison with archaeological

charcoal specimens. Short fragments (up to 50 mm in length) of modern branch wood were wrapped in tin-foil and placed in a muffle furnace to char at 400 °C for two hours. This provided a total reference sample of 26 species (see Appendix 1).

Using standardised procedures (February, 1992), each charcoal fragment was manually fractured to expose the transverse surface for identification of anatomical features. Traditional archaeological charcoal analyses are typically based on the examination of transverse, tangential longitudinal and radial longitudinal sections of wood (Cowling et al, 1999; Cartwright, 2013). While this allows for more detailed anatomical characterisations, it is a relatively time-consuming process. Thus, in the interest of processing a larger number of charcoal fragments, only transverse sections of charcoal were analysed (sensu February, 1992). In order to initiate a clean transverse break in charcoal fragments with diameters exceeding 3 mm, a shallow ring was scored around the outside of the charred wood using a blade. Care was taken to avoid any disruption to the exposed transverse surfaces as anatomical features preserved in the charcoal are easily destroyed by the slightest disturbance.

Anatomical characteristics have been recorded for many South African woody taxa (Allott, 2006). However, none of the taxa from the Spitzkloof reference collection feature in the wood anatomy literature. As a result, before any identification of Spitzkloof charcoal fragments could commence, the anatomical features of each reference specimen needed to be characterised. The charcoal sections of each species were mounted on microscope slides and photographed using a Nikon Optiphot Darkfield Microscope (Japan) with a Nikon Coolpix camera attachment. Photographs were taken at magnifications of 50x and 100x. An anatomical characterisation of each of the reference species was compiled using descriptions and checklists from the International Association of Wood Anatomists (IAWA) (Wheeler et al, 1989; InsideWood; 2013). Species-specific descriptions were mainly based on characterisations of the shape and arrangement of vessels, rays and axial parenchyma (see Appendix 1).

Fossil charcoal identification

In a previous analysis of the fossil charcoal of Rockshelter A (Packer, 2011), the two uppermost archaeological layers or 'contexts' were sampled. The initial aim of the present study was to extend this analysis by sub-sampling 50 fragments of charcoal from each of the 20 excavated archaeological contexts. However, only ten of the contexts yielded charcoal that was suitable for analysis. The upper-most layers in the archaeological sequence were

generally more charcoal-rich, while many of the older contexts had very few usable charcoal remains. Indeed, in the three oldest layers (contexts 18 to 20), charcoal has degraded to charcoal-flecks and fine powder. In addition, a large proportion of the charcoal fragments from Rockshelter A has undergone calcification, making it impossible to examine anatomical features. As a result of these limitations, every single well-preserved charcoal fragment that was found in the ten contexts was included in the analysis. In addition, the 134 charcoal sections prepared by Packer (2011) were re-analysed and compared with the expanded reference collection.

Examination of the fossil charcoal was carried out by photographing the transverse sections of all fragments at magnifications of 50x and 100x. Anatomical comparisons were made with the transverse section photographs of the 26 reference specimens of woody taxa collected in 2011, 2012 and 2013. Most charcoals were identified to the species-level, however, identifications were made to genus-level in cases where species from the same genera displayed very similar anatomical features in the modern reference collection and could not be distinguished from each other. Fragments were classed as 'unknown' when no anatomical match could be made with specimens from the reference collection.

Data analysis

In order to provide a basis for comparing the ubiquity of taxa in the archaeological record with their ubiquity within the vegetation growing at the site today, the percentage-cover of each of the woody species growing within the 23 sampled river-channel transects was plotted. For ease of comparison, separate plots were created for tall shrubs and trees and for shrubs and sub-shrubs. Plots were also split into extant species that were found to occur within the fossil charcoal record and into species that did not show evidence of being present at the site in the past.

There is considerable debate in the charcoal analysis literature about the most appropriate means of quantifying the relative ubiquity of taxa in the archaeological record (Asouti and Austin, 2005). A major critique of early fossil charcoal studies relates to the perceived inappropriateness of basing quantitative analyses on percentage fragment counts (Rossen and Olson, 1985). It is argued that the practice of fragment-counting can lead to misinterpretation of taxon ubiquity due to the differential fragmentation properties of individual species. Some researchers have therefore promoted quantification by weight (Cowling et al, 1999; Cartwright, 2013). Given that this quantification method is more common in the recent South African literature, the ubiquity of each taxon in each of the Spitzkloof contexts was computed as its proportional contribution to the total weight for all the taxa in that context (hereafter referred to as a taxon's importance value, pi). Pattern in

the archaeological sequence was sought by plotting the importance values associated with individual taxa found within each of the ten sampled contexts.

There has been some contention that it is not necessary to weigh charcoal fragments. The Montpellier school, a major contributor to the development of early methodological approaches to charcoal analysis, has demonstrated that charcoal fragment counts and weight measurements represent co-varying parameters in almost all species (Asouti and Austin, 2005). As a result, interpretations based on charcoal fragment-counts should not differ from those based on fragment mass values.

In order to assess the appropriateness of the precautionary decision to quantify taxon ubiquity by weight, the degree of collinearity between mass and fragment-count was explored. Correlation analyses of context-specific fragment counts against the weight of those fragments per context were conducted for individual taxa. Only one species occurred commonly enough throughout the sequence to provide sufficient data points for statistical analysis.

Following Cowling et al (1999) patterns of diversity across the sequence were assessed by calculating the Shannon-Wiener function (H') for each context as follows:

$$H' = \sum p_i \log p_i \quad (1)$$

where, as described above, p_i is the importance value of an individual taxon. In order to test the hypothesis that the LGM was wetter than more recent time-periods, and thus potentially supported a greater diversity of woody taxa, the relationship between context-specific diversity and context age was explored using a simple linear regression. Only those contexts that have been radiocarbon-dated were included in the analysis. Context age was normalised by log-transformation.

All statistical analyses were conducted in *STATISTICA 12*.

Palaeoclimatic reconstruction

In order to reconstruct palaeoenvironmental conditions, published accounts and distribution maps were used to define a general set of environmental correlates of the contemporary distributions of taxa found in the archaeological sequence. This provided the basis for making inferences about past environments and climatic conditions.

RESULTS

Extant species

The dry riverbed at Spitzkloof supports ten tall shrub- and tree-species as well as eight smaller shrub species (Figure 1). The species with the highest overall percentage-cover include (in ascending order): *Tetraena* (formerly *Zygophyllum*) *prismatocarpa*, *Lycium* spp., *Acacia* *karroo*, *Stoeberia* *arborea*, *Searsia* (formerly *Rhus*) *populifolia*, *Calicorema* *capitata*, *Dyerophytum* *africanum* and *Euclea* *pseudebenus*. Most of these species are particularly abundant within a few hundred metres of Rockshelter A. Exceptions to this general observation include *Stoeberia* *arborea* and *Searsia* *populifolia*. These two species are most abundant 700 m upstream of the shelter (Figure 1).

All of the extant Spitzkloof species not occurring in the fossil charcoal record only begin to feature more prominently in the vegetation 600 m upstream of the shelter, and deeper into the river valley (Figure 1C and D).

Fossil charcoal identifications

Anatomical analysis of the charcoal record revealed eight identifiable taxa and six unknown species for which no comparative material could be found in the reference collection (Table 1).

In contexts 1-5, postulated to date between 14 366 and 14 417 yrs BP, the following species are present: *Tetraena* *prismatocarpa*, *Lycium* sp., *Acacia* *karroo*, *Stoeberia* *arborea*, *Hermannia* *disermifolia*, *Calicorema* *capitata*, *Dyerophytum* *africanum* and *Euclea* *pseudebenus*. Three unidentifiable species (Unknown 3, 4 and 6) are also present within this layer. Context 8 (~14 417 yrs BP) produced very few charcoal fragments and only one species, *Stoeberia* *arborea*, is identifiable. Two other species, Unknown 1 and 3, are also present. *Stoeberia* *arborea* and *Lycium* sp. are proportionately the most abundant species in contexts 9 (15 210 yrs BP) and 12 (16 244 yrs BP). The additional species present in context 12, Unknown 1 and 2 and *Hermannia* *disermifolia*, each contribute less than 5% to the total weight of all the species in the context (Table 1).

In the two contexts associated with the LGM, dated to 19 556 yrs BP (context 14) and 19 769 yrs BP (context 15), three species are identifiable: *Stoeberia* *arborea*, *Lycium* sp and *Hermannia* *disermifolia*. Two unknown species, Unknown 1 and 7 are present in context 14 (Table 1).

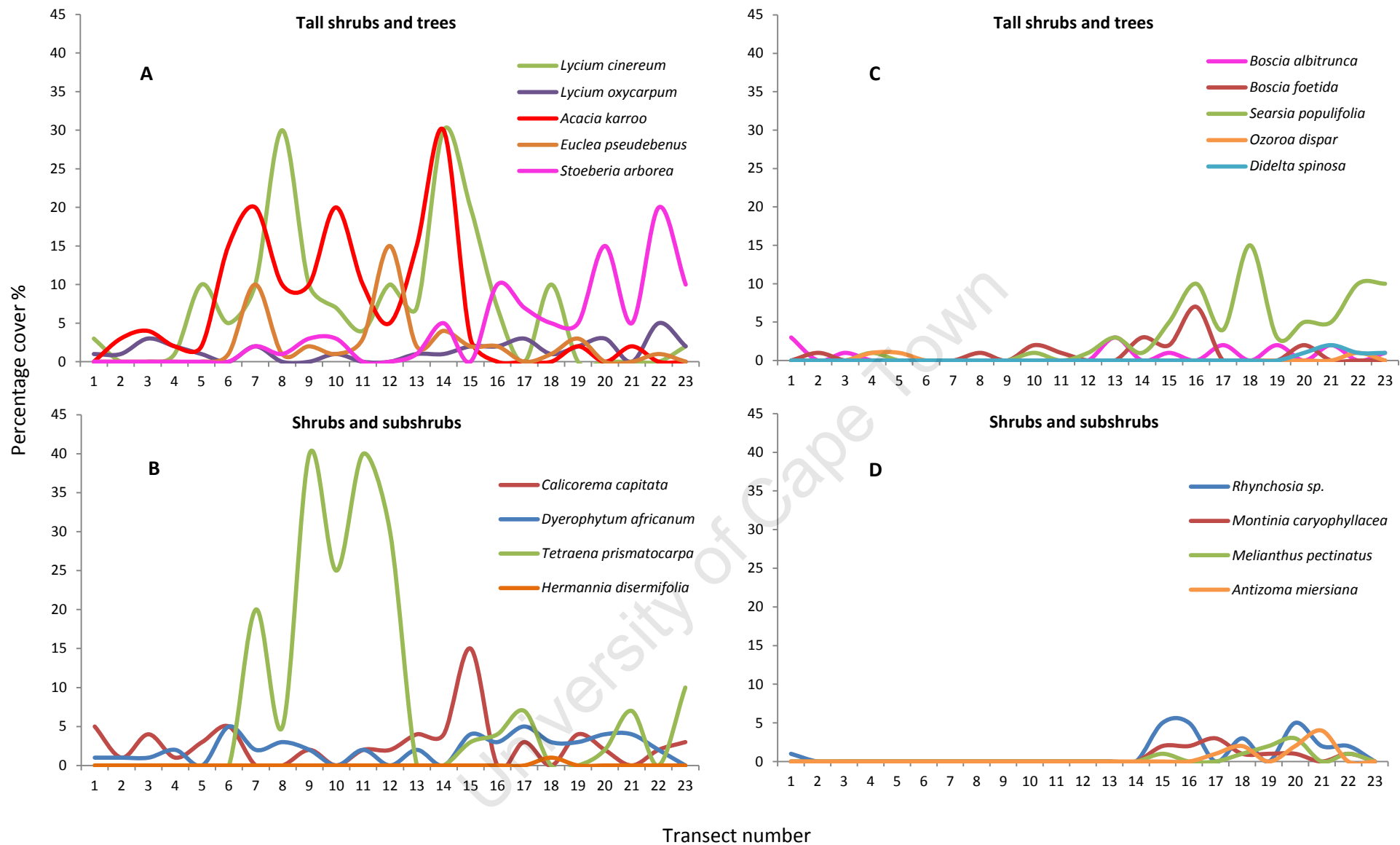
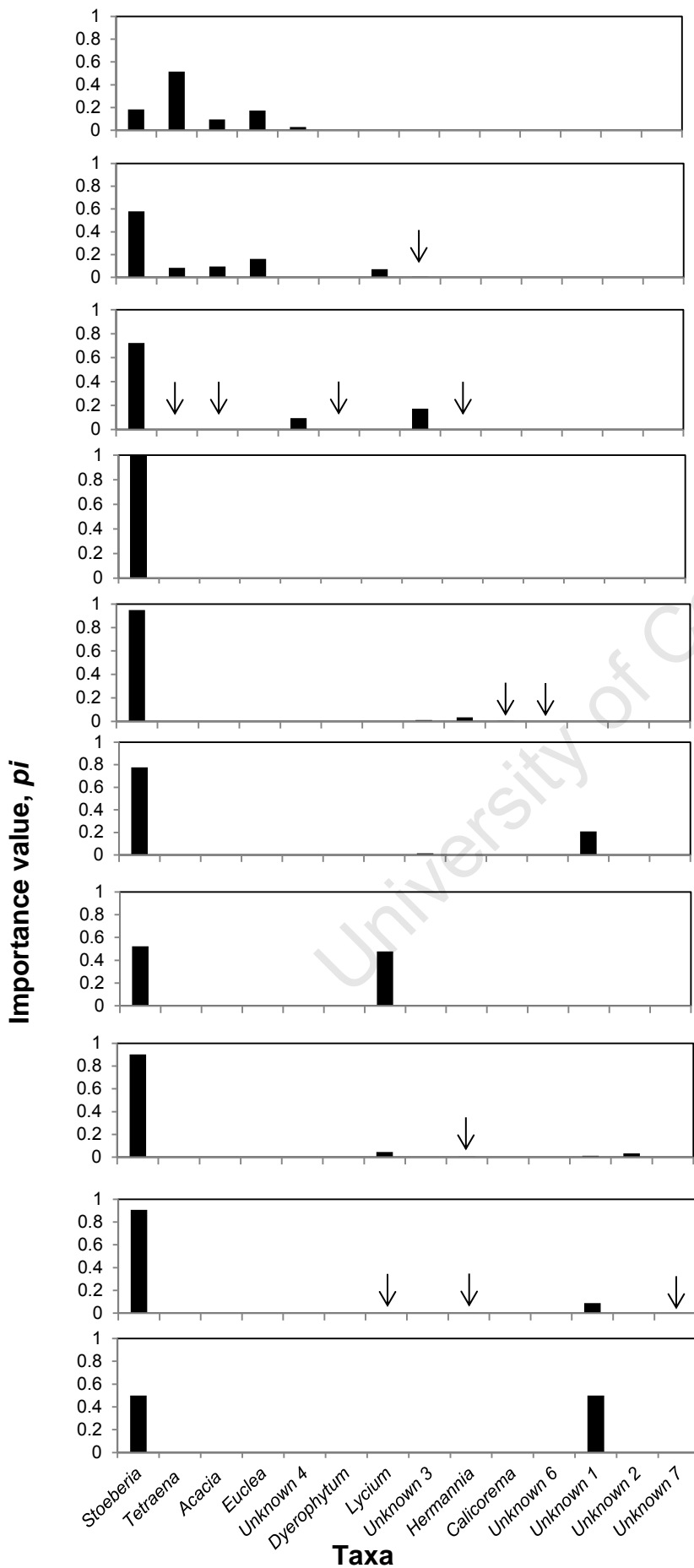


Figure 1. The percentage cover of woody species found within 23 100m-long river-channel transects at Spitzkloof. Transect 8 was taken directly opposite Rockshelter A. Transects 1-7 and 9-23 were taken downstream and upstream of the shelter respectively. Plots are split into extant species that were found to occur in the fossil charcoal record (A-B) and species that were not present in the charcoal record (C-D). A) and C) provide an indication of the relative abundances of tall shrubs and trees while B) and D) depict the abundances of shrubs and subshrubs.

Table 1. The relative importance of taxa identified within the fossil charcoal record of Spitzkloof Rockshelter A. Importance values represent a taxon's proportional contribution to the total weight (g) of all the taxa in a specific context. The identifiable taxa include: *Stoebertia arborea*, *Tetraena prismatocarpa*, *Acacia karroo*, *Euclea pseudebenus*, *Dyerophytum africanum*, *Lycium sp.*, *Hermannia disermifolia* and *Calicorema capitata*. Arrows have been inserted for species with $pi < 0.006$. Radiocarbon dates were obtained from Dewar and Stewart (2013).



CONTEXT	SAMPLE SIZE	¹⁴ C DATE (yrs BP)	PERIOD	
1	100	14 366 (± 43)	Post - LGM	
2	34			
3	36			
4	6			
5	34			
8	16	14 417 (± 61)		
9	17	15 210 (± 43)		
12	26	16 244 (± 45)		
14	12	19 556 (± 57)		LGM
15	38	19 769 (± 60)		

Relating the species that are present in the fossil record to their current importance within the vegetation at the site today revealed that all eight of the most abundant species (Figure 1), except for *Searsia populifolia*, are represented in the archaeological record (Table 1). In contrast, *Hermannia disermifolia*, a species that occurred in low proportions in LGM and post-LGM contexts (Table 1), is the least abundant woody species at Spitzkloof (Figure 1). Each of the eight identifiable species found in Rockshelter A's charcoal assemblage were represented in the 5 upper-most contexts. However, *Tetraena prismatocarpa*, *Acacia karroo*, *Calicorema capitata*, *Dyerophytum africanum* and *Euclea pseudebenus* were absent from all of the older contexts below this upper-most layer. *Stoeberia arborea* occurred throughout the archaeological sequence and was by far the most dominant species (by weight) in all of the contexts that pre-date context 1. *Lycium sp.*, which was present in contexts 1-5, was more prevalent in older contexts, and also occurred in the contexts associated with the LGM (Figure 1).

Quantifying ubiquity: weight versus fragment count

Correlation analysis did not reveal a strong relationship between fragment mass- and fragment count-measurements in the most ubiquitous species in the fossil charcoal record, *Stoeberia arborea* ($r=0.31$, $df=8$, $p=0.39$). However, the relationship was weakened by an outlying data point (5.6; 6) which was skewed by the presence of one partially calcified charcoal fragment in context 4 and was therefore uncharacteristically heavy. The data point corresponding to context 4 was consequently removed from the analysis. Removal of the outlying data point increased the R^2 value to 0.54, resulting in a significant positive relationship ($r=0.74$, $df= 7$, $p=0.02$) between fragment count and mass (Figure 2).

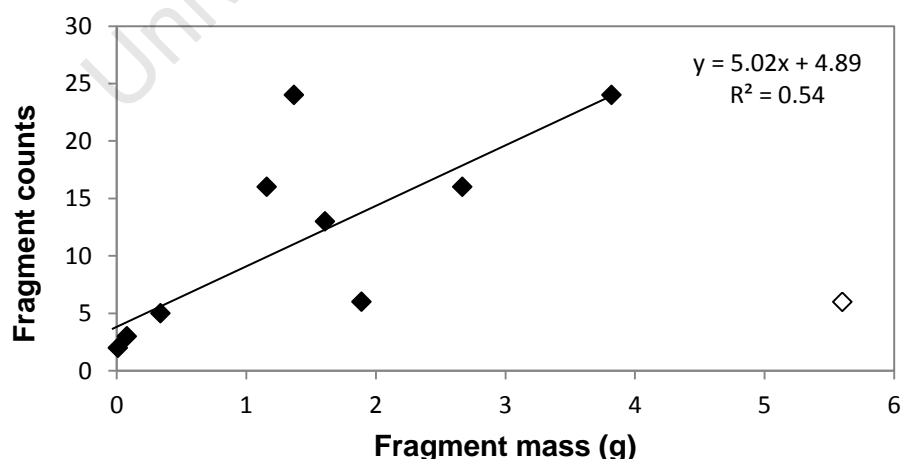


Figure 2. The correlation between charcoal fragment count- and fragment mass-measurements in *Stoeberia arborea*. Each data point represents one of the ten contexts sampled in the charcoal analysis. The unfilled marker corresponds to the data point for context 4 which was not included in the statistical analysis. Correlation statistics are as follows: $r=0.74$, $df= 7$, $p=0.02$.

Diversity

There was no significant trend in diversity in relation to context age ($t = -0.77$, $df = 4$, $p = 0.48$). However, context 1 contains a larger diversity of woody species than any of the other older contexts that have been dated (Figure 3 and Table 1).

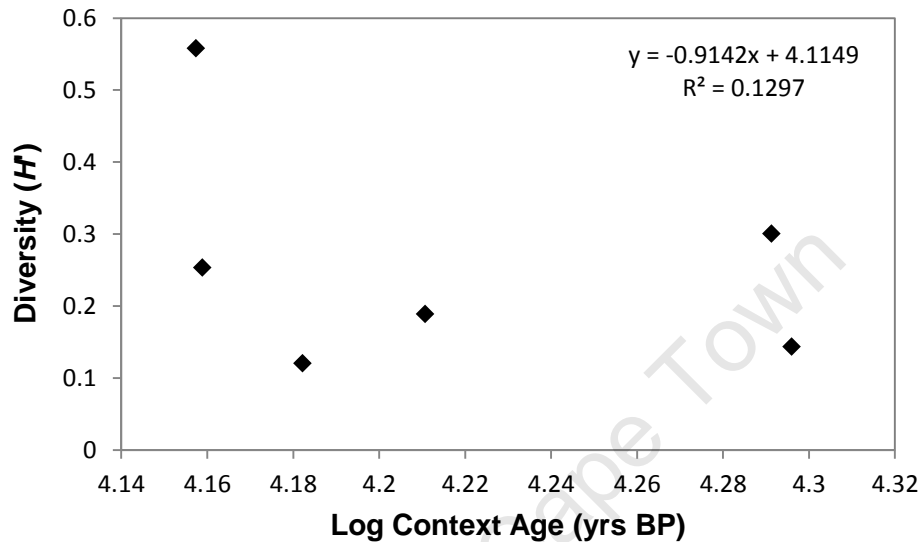


Figure 3. Relationship between species diversity of charcoals and context age. Diversity is computed as the Shannon-Wiener diversity function (H'). Regression statistics are as follows: $t = -0.77$, $df = 4$, $p = 0.48$.

DISCUSSION

The Spitzkloof charcoal assemblages enable important general inferences to be made about the history of vegetation and climate in the study region. These insights are valuable given the paucity of late Pleistocene palaeoenvironmental evidence available for the Succulent Karoo biome.

Analysis of the sequence of charcoal assemblages revealed two major patterns that are relevant to a reconstruction of Spitzkloof's palaeoenvironment. Of particular interest, is the persistence of three Succulent Karoo elements – *Stoeberia arborea*, *Lycium sp.* and *Hermannia disermifolia* - throughout much of the late Pleistocene, including both LGM and post-LGM environments. The contemporary environmental affinities of these three species (see Appendix 2) are highly suggestive of relative stasis in the environmental conditions in the Namaqualand region over the past 20 000 years. *S.arborea* and *H.disermifolia* are also both xerophytic shrubs that are endemic to the Namaqualand region. Although the

distribution of *Lycium* species is slightly more cosmopolitan, members of the genus (including *L.cinereum*) are known to favour arid environments that receive rainfall (between 160 -180 mm; Rubin and Palmer, 1996) that is within the range that characterises the average annual rainfall values of Namaqualand.

Assuming that the LGM represents the maximum expression of glacial environmental conditions, then the relatively limited variation between LGM charcoal assemblages and modern vegetation assemblages may be indicative of limited variations between Holocene/ inter-glacial and late Pleistocene/ glacial conditions in Namaqualand. This interpretation reinforces the suggestion that, given the high endemism associated with the Succulent Karoo, it is not likely that a core region in the biome, such as Namaqualand, experienced significant Pleistocene climate change (Midgley and Thuiller, 2007). Indeed, based on their modelled reconstructions of the palaeo-bioclimatic envelopes suitable for the Succulent Karoo biome, Midgley and Thuiller (2007) argued that even under peak glacial conditions of the LGM, the biome likely retained an important core range within the Richtersveld. If the muted climate-history hypothesis is indeed applicable to the Namaqualand region, then this may lend credence to the suggestion (Goldblatt and Manning, 2013; Midgley and Thuiller, 2007) that the Succulent Karoo may be particularly vulnerable to the effects of future climate change.

However, the vegetation-stasis signal apparent in the charcoal record could be alternatively interpreted as an indication of the resilience of Succulent Karoo to Pleistocene climatic changes. It is not easy to distinguish a vegetation signal indicative of muted climate change from a signal of vegetation-resilience to climatic variations. At this stage, both palaeoenvironmental interpretations may be equally inferable from Spitzkloof's charcoal assemblage. However, the presence of gypsum throughout the entire Spitzkloof A deposit (Dewar and Stewart, 2011) provides an additional line of evidence to support the muted climate change interpretation. Dewar and Stewart (2011) interpret the ubiquitous presence of the mineral as an indication of consistently arid to semi-arid conditions. Additional sources of palaeobiological proxy evidence from the late Pleistocene deposits at Spitzkloof will help to further disentangle the alternative interpretations.

A second climate-relevant pattern discernible from the charcoal sequence is the marked difference between the assemblages associated with the terminal Pleistocene (contexts 1-5 dated to 14 417 - 14 366 ¹⁴C yrs BP) and those of older LGM and post-LGM contexts. The fact that the terminal Pleistocene assemblages include all of the taxa that are most abundant at the site today, suggests that environmental conditions similar to those of contemporary Namaqualand may have been established as early as 14 ka. The abrupt appearance of five

additional Succulent Karoo species - *Tetraena prismatocarpa*, *Acacia karroo*, *Calicorema capitata*, *Dyerophytum africanum* and *Euclea pseudebenus* - is likely to reflect a shift from glacial conditions to conditions more characteristic of the Holocene. Indeed, at the terminal Pleistocene, a number of changes would have been taking place that are likely to have had some impact on the vegetation at Spitzkloof. Globally, temperatures would have been warming from LGM minima. An additional important consideration is that the 200 km coastal plain that had been exposed to the west of the Rockshelter during the LGM, would have been gradually submerged as sea levels rose from an LGM minimum of -120 m amsl to around -102 m amsl at the terminal Pleistocene (Dewar and Stewart, 2013). This shift in the relative position of the site from a terrestrial inland setting to a near-coastal setting, and the resultant increased influence of the moderating effects of the Atlantic Ocean, may have been an important factor in establishing conditions more conducive to the growth of certain Succulent Karoo elements that are present at the Spitzkloof site today. For example, the contemporary distribution of *Tetraena prismatocarpa* is largely confined to a broad coastal strip from Lüderitz to near Kleinsee (Goldblatt and Manning, 2013). Given its broad coastal affinity, it is possible that the species may only have been able to establish at Spitzkloof once the Namaqualand coastline had significantly advanced inland.

The localised appearance of two riparian woodland tree species, *Acacia karroo* and *Euclea pseudebenus*, in the terminal Pleistocene may be indicative of a late glacial moisture-regime shift. Both species are dependent on access to deep water sources (Jordaan and Theunissen, 1991) and, based on ethnographic studies by Archer (1994), in particularly arid areas of the northwestern Cape, the presence of these trees is taken to be an indication of subterranean water. The fact that these two species only appear in the charcoal record at around 14 ka and the fact that this time-period appears to have supported a relatively high species richness may suggest that the terminal Pleistocene was potentially more mesic than the LGM. Thackeray's (1979) findings of an enhanced 'mean ungulate body-mass' index for the late-glacial assemblage of Apollo 11, a site that is about 120 km north of Spitzkloof, supports the interpretation that the region experienced a peak in precipitation in the terminal Pleistocene. However, a more compelling argument is that this increase in woody biomass reflects a response to increased atmospheric CO₂ concentrations at the Pleistocene-Holocene boundary. A recent glasshouse experiment (Kgope et al, 2007) provides important insights into the growth responses of *Acacia karroo* saplings to increases in CO₂ concentrations above a baseline value of 180 μmol mol⁻¹, typical of the LGM. Photosynthesis and sapling growth rates were found to significantly increase in response to enhanced CO₂ concentrations. Indeed, Hoffman and Rohde (2011) suggest that the effects of CO₂ fertilisation may best explain the significant increase in phreatic woody species (particularly

Acacia karroo) that has occurred in the ephemeral streams of the Succulent Karoo region over the past few decades. By extending these ideas to the Pleistocene, it may be argued that the absence of *A.karroo* and *E.pseudebenus* from assemblages pre-dating the terminal Pleistocene relates to limiting atmospheric CO₂ concentrations. It has been suggested (Robinson, 1994) that LGM CO₂ concentrations may in fact have been low enough to be near the limit of effective C₃ photosynthesis. Drawing all the lines of interpretation together, it is argued that the establishment at 14 ka of a vegetation community entirely comparable to the woody assemblage at Spitzkloof today is likely to be a product of terminal Pleistocene changes in sea-level and atmospheric composition. Such environmentally-driven vegetation changes may have occurred within a context of minimal late-Pleistocene climatic change, with potentially little variation in moisture regimes. However, in order to fully dismiss the interpretation that a peak in precipitation is the primary driver of vegetation change in the terminal Pleistocene, additional sources of palaeoenvironmental proxy evidence will need to be explored. In addition, future analyses of Spitzkloof's charcoals may greatly profit from an expansion of the charcoal reference collection to include species characteristic of more mesic sites in Namaqualand. This may aid the identification of the 'unknown' taxa that have no analogues within the vegetation at Spitzkloof today. If the 'unknown' taxa in the most recent charcoal assemblages prove to be mesic-adapted species, then this strengthens the evidence in support of a wet terminal Pleistocene.

However, the value of charcoal analysis, specifically its reliability as a proxy for palaeoenvironmental change, has been brought into question (Asouti and Austin, 2005). It has been argued that the observed frequencies of individual species in the charcoal record may not reflect their exact proportions in past vegetation as they may be distorted by the influence of differential preservation characteristics and human selection (Asouti and Austin, 2005).

The Montpellier thesis argues that concerns about the potential distorting effects of differential fragmentation properties of species can be ruled out on the grounds that there is collinearity between fragment numbers and fragment mass (Asouti and Austin, 2005). In the case of *Stoeberia arborea*, the only species for which this study had sufficient data points, a strong collinearity between the two measurements was established. However, given that this relationship could not be established for other species, the conservative approach of quantification by weight was therefore an important precautionary means of avoiding distortion.

Preservation dynamics may well be a relevant consideration with regards to the absence of *Searsia populifolia* in the Spitzkloof charcoal assemblages. The absence of *Searsia*

populifolia, a species that is currently common in the immediate vicinity of the rockshelter, is somewhat perplexing and requires explanation given the argument that environmental conditions similar to those of contemporary Namaqualand may have been established as early as 14 ka. During the process of charring wood samples for the modern reference charcoal collection, it was noted that *Searsia* specimens typically cracked as a result of the combustion process. It is therefore possible that this species was not preserved in the archaeological record.

For any species in a charcoal assemblage, consideration has to be given to the possible filtering-effects of human selection. Based on an ethnographic study of the descendants of the Nama-speaking Khoi pastoralists of the Richtersveld, Archer (1994) argued that the collection of firewood is not a random process and that selection is based on factors such as burning properties, intended use (for cooking or warmth) and availability. Given that four of the species found in Spitzkloof's charcoal record – *Acacia karroo*, *Stoeberia arborea*, *Euclea pseudebenus* and *Tetraena prismatocarpa* - are considered to be popular choices for fuelwood (Archer, 1994), the significance of their presence (in terms of palaeoclimatic reconstructions) should be interpreted with a level of caution. However, given that the Spitzkloof charcoal assemblages accumulated over thousands of years, it is more likely that species presence patterns are a function of long-term environmental conditions rather than preferential selection by humans. Furthermore, even if *Stoeberia arborea* was preferentially collected, its presence throughout the entire charcoal sequence, in both LGM and post-LGM assemblages, provides compelling evidence to suggest that environmental conditions in the Succulent Karoo remained fairly constant over the late Pleistocene. In addition, the localised appearance of *Acacia karroo* and *Euclea pseudebenus* at 14 ka is more likely to reflect subtle shifts in environmental conditions than shifts in human-preference as it is hard to understand why people may have ignored the ample woody resources if these had been available in earlier assemblages. Thus, while the observed frequencies of individual species in the charcoal record may not reflect their exact proportions in past vegetation, it is argued that the broad patterns observed in Spitzkloof's charcoal sequence allow for relatively robust palaeoenvironmental interpretations.

Given Spitzkloof's location within the WRZ, it was originally hypothesised that the study region probably experienced an increase in rainfall at the LGM, and a steady aridification towards the terminal Pleistocene as has been inferred for other WRZ sites. However, the analysis of Spitzkloof's charcoal records has provided little evidence to suggest that the LGM supported a more mesic vegetation community than more recent time-periods. Instead, the region may have experienced fairly limited climatic change as suggested by the persistence of Succulent Karoo elements throughout the late Pleistocene. This has important

implications for the applicability of a generalised WRZ model of climate change to the Succulent Karoo and for hypothetical predictions of future climate change impacts in the biome. It is, however, acknowledged that additional proxy evidence from Spitzkloof will need to be explored in order to confirm or refute these interpretations. Nevertheless, the tentative interpretations that have been based on the wood charcoal assemblages from Spitzkloof Rockshelter A are extremely valuable given the paucity of palaeoenvironmental data available for the Succulent Karoo - an important biodiversity hotspot.

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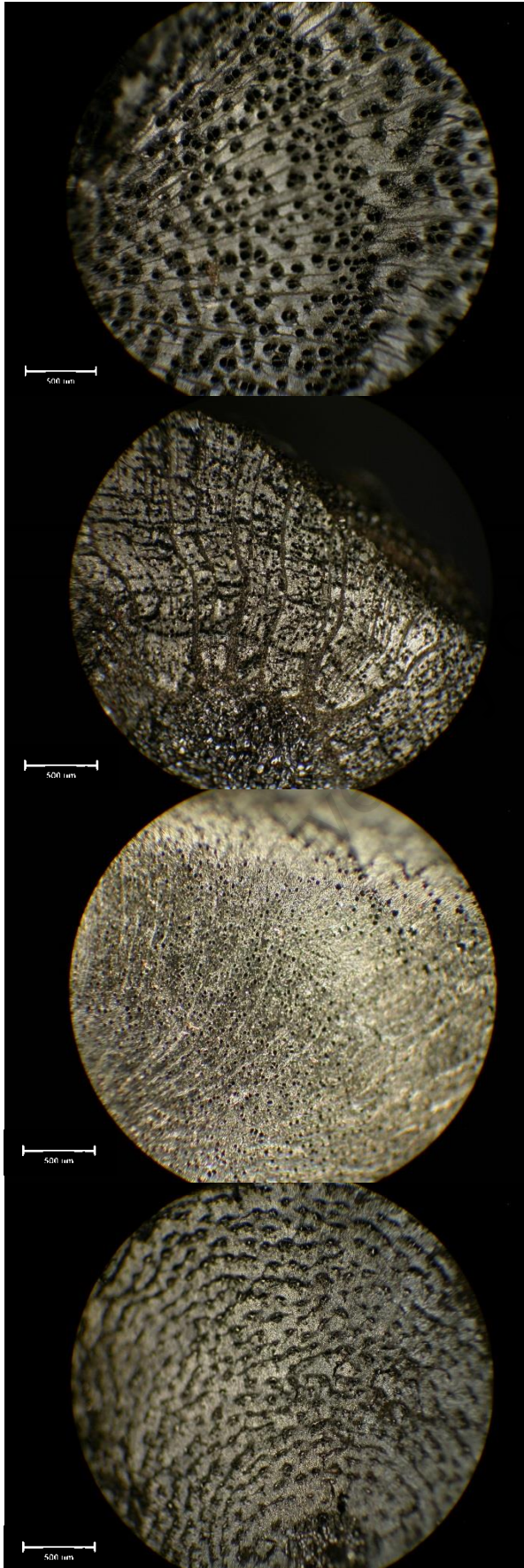
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APPENDIX 1

Transverse section photomicrographs (taken at magnifications of 50x and 100x) of the 26 reference specimens of woody taxa collected in the vicinity of Spitzkloof Rockshelter. Anatomical descriptions are based on checklists from the International Association of Wood Anatomists (IAWA) (Wheeler et al, 1989; InsideWood; 2013). Photomicrographs of *Boscia albitrunca*, *Hermbsstaedtia glauca* and *Lycium oxycarpum* were obtained from Packer (2011).



***Acacia karroo* (50x)**

Vessels solitary or in clusters of 2
Axial parenchyma vasicentric (forms complete sheath around vessel multiples)
Rays distinct (± 3 cells thick)

***Berkheya sp.*(50x)**

Vessels solitary/ in pairs/ radial groups
Axial parenchyma diffuse and wavy, scanty
paratracheal (occasionally surrounding vessels)

***Tetraena prismatocarpa* (50x)**

Wood ring-porous: earlywood is distinctly larger than latewood
Vessels round to oval in shape
Vessels mostly solitary
Axial parenchyma not always visible

***Stoeberia arborea* (50X)**

Vessels in distinct clusters of >3
Rays not visible



Boscia foetida (100x)

Vessels often solitary but radial multiples common
Axial parenchyma diffuse and in discontinuous

Searsia undulata (100x)

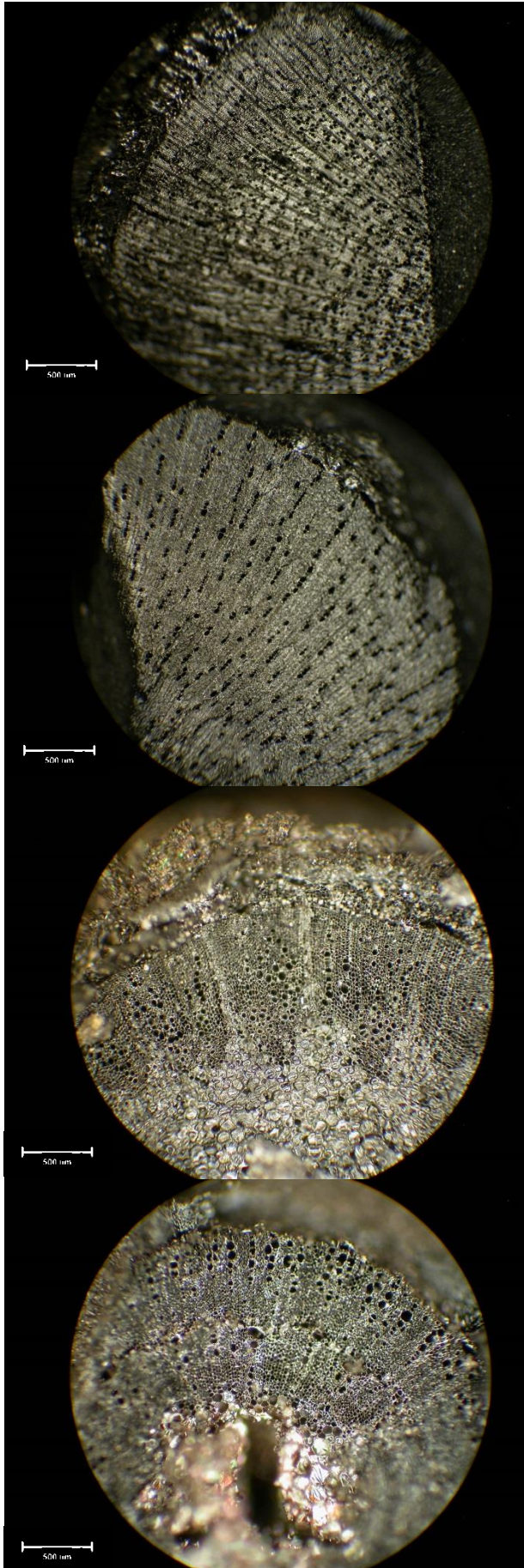
Wood semi-ring porous: gradual size transition from earlywood vessels to latewood vessels.
Vessels mostly solitary; some in clusters of 2-3
Vessels round when solitary
Axial parenchyma diffuse

Pteronia divaricata (100x)

Wood ring-porous
Vessels often in clusters of 3; sometimes with longitudinal extensions of smaller vessels
Solitary vessel outline angular
Rays wavy and surrounded by axial parenchyma

Montinia sp. (50x)

Vessels occasionally in radial associations of 2-3; mostly solitary
Solitary vessel outline angular
Distinct straight waves



Codon royenii (50x)

Rays distinct
 Vessels mostly solitary and in tangential lines parallel to rays

Euclea pseudebenus (50X)

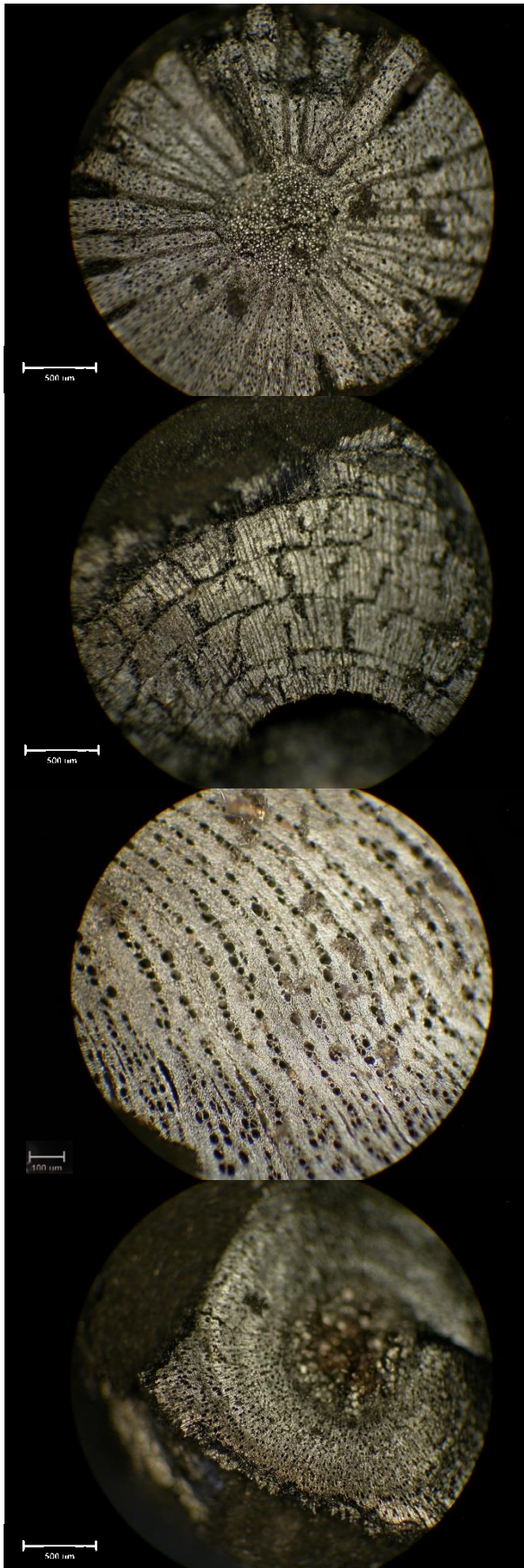
Axial parenchyma diffuse
 Vessels form radial groupings of ± 3
 Solitary vessels rare

Melianthus pectinatus (50X)

Vessels partly solitary, partly in radial multiples, or small clusters
 Solitary vessel outline angular
 Axial parenchyma in radial bands

Ozoroa dispar (50X)

Wood semi-ring porous
 Vessels form radial multiples of ± 4
 Vessels mostly solitary; angular in shape
 Rays distinct at magnifications of 100X



***Antizoma miersiana* (50X)**

Vessels mostly solitary;
occasional associations of 2
Aggregate rays of varying thickness

***Lycium cinereum* (50X)**

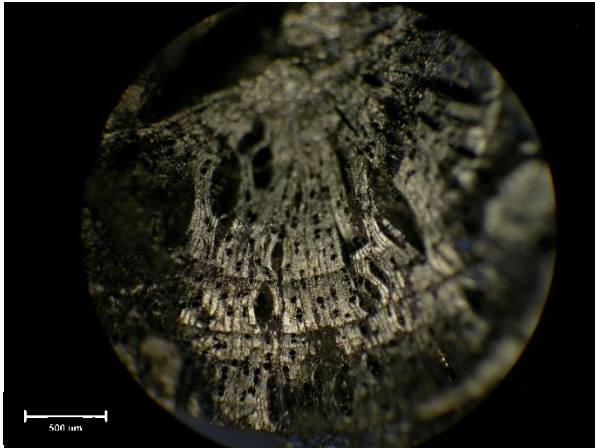
Vessels arranged in distinct dendritic pattern
Discontinuous radial lines of axial parenchyma

***Dyerophytum africanum* (100x)**

Adjacent vessels arranged in continuous radial files
Rays distinct

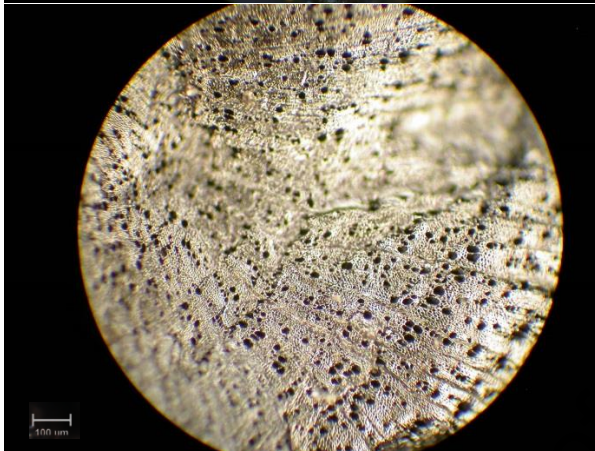
***Stachys sp.* (50X)**

Wood semi-ring porous
Vessels mostly solitary, occasionally forming associations of 3
Solitary vessels angular
Rays faint



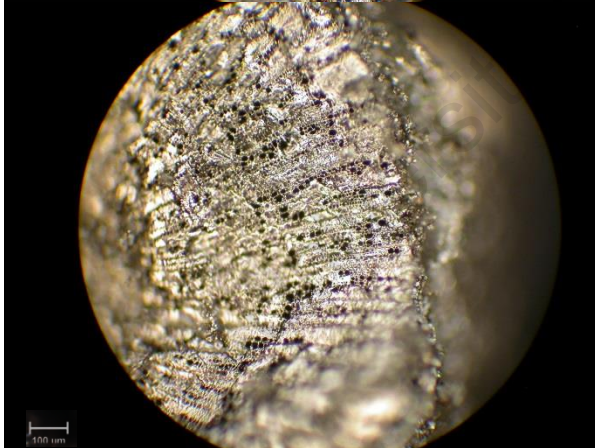
***Rhus populifolia* (50X)**

Vessels form radial associations of 3
 Rays 1 cell thick
 Wood often split (as shown in the photograph)



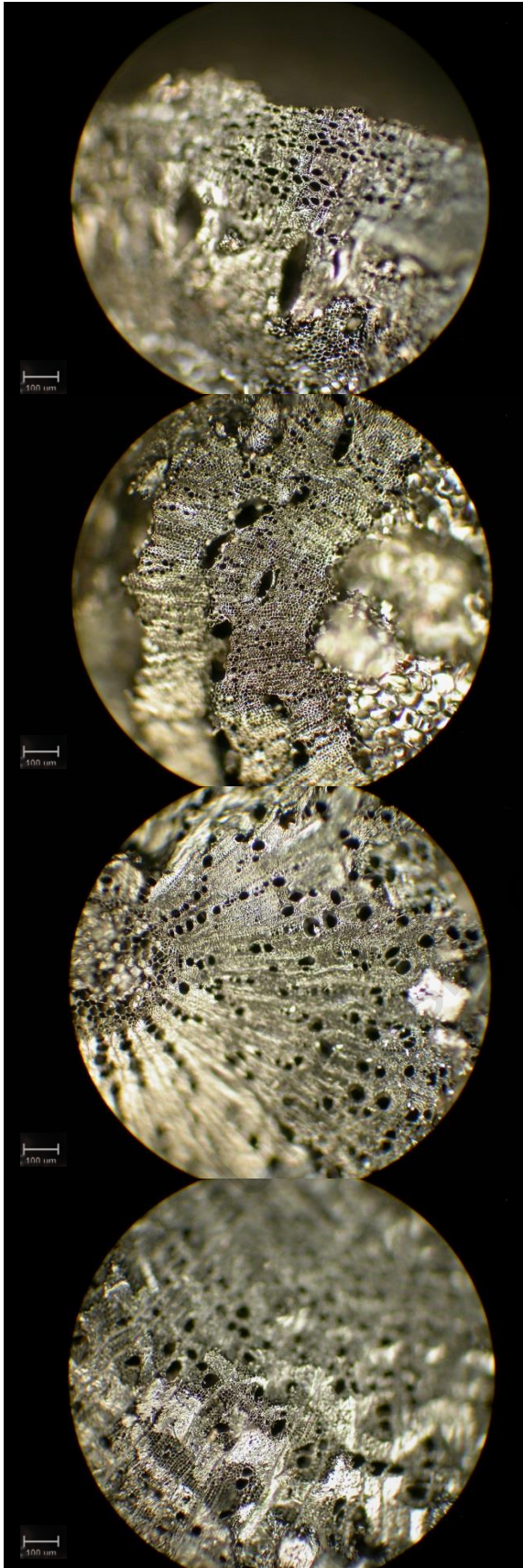
***Blepharis sp.* (100x)**

Vessels mostly solitary; occasionally clustered/ in
 tangential bands/ in radial groupings
 Solitary vessels angular
 Rays 1-2 cells thick



***Hermannia disermifolia* (100X)**

Vessels in tangential bands; radial multiples and
 clusters common
 Vessels rarely solitary
 Rays and axial parenchyma not visible



***Didelta spinosa* (100x)**

Vessels large and concentrated in outer tangential band
 Vessels typically share cell walls
 Vessel outline angular

***Calicorema capitatum* (100x)**

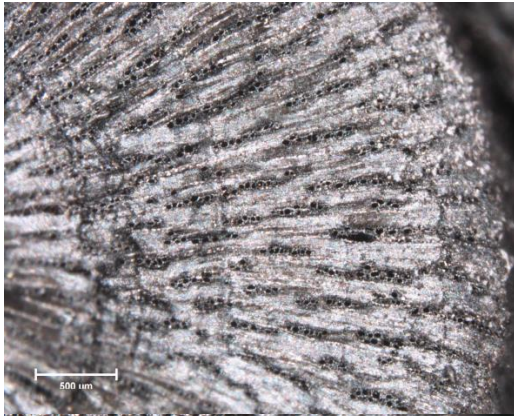
Vessels diffuse, often forming short radial multiples
 Solitary vessels angular
 Wood often split

***Rhynchosia sp.* (100x)**

Wood semi-ring porous
 Vessels in radial pattern
 Solitary vessels round to angular in shape
 Axial parenchyma diffuse

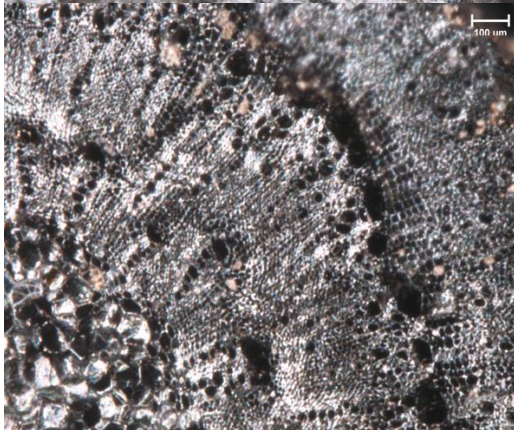
***Acacia erioloba* (100x)**

Vessels solitary or in clusters of 2-3
 Axial parenchyma vasicentric (forms complete sheath around vessel multiples)
 Rays distinct but thinner (± 1 cell thick) than those of *A.karoo*.



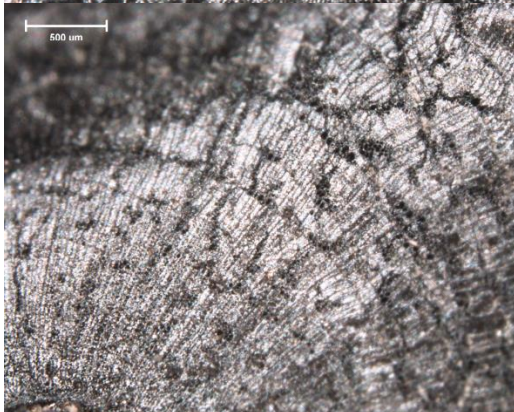
***Boscia albitrunca* (50X)**

Vessels form discontinuous radial chains
Axial parenchyma vasicentric (forming a sheath around vessel multiples)



***Hermbstaedtia glauca* (100x)**

Vessels form radial chains of ± 7
Solitary vessels round



***Lycium oxycarpum* (50X)**

Vessels arranged in distinct dendritic pattern
Discontinuous radial lines of axial parenchyma

APPENDIX 2

Table i. Information on the species identified within Spitzkloof's charcoal assemblages.

SPECIES	GROWTH FORM	ETHNOBOTANICAL INFORMATION (ARCHER, 1994)	HABITAT AND DISTRIBUTION (GOLDBLATT AND MANNING, 2013)
<i>Calicorema capitata</i>	Shrub		Occurs along dry washes and mountain slopes (Namibia and from eastern Richtersveld to Gordonia).
<i>Lycium cinereum</i>	Tall shrub		Namibia to lower Gariep valley, Steinkopf, Calvinia, Roggeveld Escarpment, Worcester and E. to Zimbabwe.
<i>Lycium oxycarpum</i>	Tall shrub	Berries eaten	Roggeveld Escarpment and Laingsburg to Little Karoo and Karoo.
<i>Dyerophytum africanum</i>	Shrub		Sandy beds of seasonal semi-desert streams (Angola through Namibia to northern and eastern Namaqualand and to Gordonia along Gariep Valley).
<i>Acacia karroo</i>	Tree	Popular firewood species	Often along rivers and streams throughout southern Africa to Zambia. Occupies a diverse range of habitats.
<i>Euclea pseudebenus</i>	Tree	Popular firewood species	Along watercourses and sandy depressions (Tropical W Africa, Angola, Namibia to Richtersveld to Gordonia).
<i>Tetraena prismatocarpa</i>	Shrub	Popular firewood species	On hills, ridges and dry riverbeds. (Luderitz to near Kleinsee).
<i>Stoeberia arborea</i>	Tall shrub	Recognised as a fine quality firewood which produces excellent coals	Southern Namibia, Richtersveld to Kamieskroon.
<i>Hermannia disermifolia</i>	Shrub		Richtersveld and Bushmanland to central Namaqualand.

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