The role of geophytes in Stone Age hunter-gatherer subsistence and human evolution in the Greater Cape Floristic Region

By

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Declaration

I, Elzanne Singels, hereby declare that the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university.

This thesis has been submitted to the Turnitin module, and I confirm that my supervisor has seen my report and any concerns revealed by such have been resolved with my supervisor.

Elzanne Singels (SNGELZ001)

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Abstract

It has been hypothesised that an adaptive shift to a starch-rich diet was an important driver in human evolution and supported the energetic requirements to sustain brain development throughout hominin evolution. Plants that possess underground storage organs (geophytes) have been put forward as the likely source of starch. Geophytes comprise a large portion of the plant diversity in the Greater Cape Floristic Region (GCFR), where significant archaeological evidence of the evolution of human modernity has been identified in the Middle Stone Age (MSA). It is thought that the resources available in this region during this time period fuelled the progression and development of complex language, art and tool production in early modern humans. The overall objective of this thesis is to determine the importance of geophytes in early modern human diets and the impact they might have had on human behaviour and cognition. The role of geophyte resources in Stone Age hunter-gatherer subsistence was evaluated by firstly creating an ecological and environmental framework of data to evaluate the geophyte resource base. Secondly, the archaeological evidence available on actual hunter-gatherer foraging behaviour was evaluated using this framework, together with novel methods of macrobotanical analysis and experimental archaeological methods. It was found that the nutritional quality of geophytes is high, even in comparison to domesticated crops such as potatoes. The desirability of geophytes to a forager would rely on many factors, apart from nutritional quality, however. Geophyte resources on the coastal plain of the GCFR are dense and diverse. This diversity encompasses variation in the quality of the nutrients contained in the USOs and the optimum time throughout the year they would be most profitable to harvest. Geophytes could have been available during a large portion of the year throughout the GCFR. The archaeological evidence shows just how widespread and complex geophyte foraging and processing were during the Holocene, although there is a relative lack of evidence in the MSA. The novel method presented to determine the energy cache offered by geophytes and the seasonality of geophyte foraging shows great promise to improve our understanding of foraging choices and hunter-gatherer mobility across the region. All Stone Age processing methods tested experimentally improved the nutritional quality of USOs, but veldfire produced the most profound nutritional quality improvements of all methods tested. Geophytes could have supplied the dense and predictable resource cache that made the GCFR a reliable environment for human evolution, despite climatic and vegetational shifts. The efficient exploitation of geophyte resources throughout the Stone Age could have altered early human behaviour and cognitive development.

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This thesis is the culmination of two decades of immersive and creative exploration of endemic plants of the Greater Cape Floristic Region. This, sometimes self-indulgent, exploration was possible due to the collaboration and input of a diverse range of academic colleagues, local communities and wild food activists and revivalists. I was able to use the rigorous scientific knowledge available, and access to the academics active in these fields, together with less formal explorations of the topic of wild food through experimentation in the kitchen, art and conversation. Without this complete immersion in both my professional and personal life in this topic, this thesis would no doubt have not contributed as much as I hope it will, to our understanding of how integral the Greater Cape Floristic Region was to the evolution of humans. I owe huge thanks to this entire community of colleagues that influenced my eventual interpretation of Stone Age subsistence.

From the sphere of academia, I must acknowledge the vital support I received from the entire Paleoscape Research team throughout my post-Graduate career. My co-supervisor, Prof. Karen Esler, makes up a part of this team; Karen, you originally opened the door for me to explore this topic and have supported my on-going efforts in doing so. Thank you so much for always being open to my ideas and helping refine them. Without the financial support you were able to obtain for the project costs, the field work could not have been as extensive as it was.

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I was able to gain access to archival material at the Iziko Museum and the Albany Museum by requesting access to research archaeological collections. Thank you to the friendly and helpful staff at both institutions. I wish to thank Louisa Hutton for her assistance in gaining access and navigating the archival archaeological material in the UCT collection, and friendship and support throughout my PhD journey. I was able to collect plant material for analysis from various SanParks nature reserves (Permit No.: SINE/AGR/036-2015) and CapeNature reserves (Permit No.0028-AAA008-00142).

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Lastly, but perhaps most importantly, I would like to acknowledge the ancient, historical, and modern cultures that formed part of this research. I have the extreme privilege of conducting research on the lifeways of humans. The artefacts they left behind are the primary source of information for our work in the field of archaeology, but it is important to be cognisant of the fact that these remains were part of a culture and generated by a group of people. I acknowledge my privileged position to have had access to this material through various museums and university affiliations. I have always tried to remain cognisant of the responsibility I carry in making inferences about these ancient peoples lives, in a conscientious way, from these resources. But of course, I welcome criticism to always improve on this matter. Furthermore, I based many of my interpretations of ancient human subsistence on the writings of early colonists regarding hunter-gatherers and herders (Ethnographic accounts). I acknowledge that the information from these resources is biased and written through the lens of white colonists. Lastly, descendants of these cultures persist. The cultural heritage described in my research is theirs and is present and ongoing. I hope that I have done justice to exploring aspects of hunter-gatherer lifeways that were eradicated by the systematic genocide that San and Khoi-khoin people were subjected to.

Glossary

USOs - Underground Storage Organs

Geophyte - A perennial plant that possesses an underground storage organ

kya - thousands of years ago

ya - years ago

GCFR - Greater Cape Floristic Region

MSA - African Middle Stone Age, a time period spanning roughly between 40 – 250 kya

LSA - African Later Stone Age, a time period spanning roughly between 40 kya to the colonial period in the 1600s

Holocene - A geological epoch which started after the last glacial maxima, 11 500 ya to present.

Pleistocene - A geological epoch spanning from roughly 2.6 million years ago, until 11 500 ya, which is categorised by repeated glacial phases.

Palatability –A categorisation of geophytes based on the sensory experience a person would have when eating the USOs of that geophyte. The palatability of geophytes is categorised as either palatable or unpalatable. Palatable species are pleasant to eat, while unpalatable species are unpleasant to eat, even if they may not be overtly toxic to eat. This categorisation was based on the anti-nutrient content of geophytes.

Edibility –A categorisation of geophytes species based on whether they could provide substantive nutrition in terms of calories, to hunter-gatherers. A clear distinction is made between those that might have been an important food source, used medicinally (or in other ways economically important), those that are dangerously toxic species and other species which might have been rendered edible by way of processing. Species categorised as edible were found to have likely been a food source to hunter-gatherers (even if processing might have been required to render them palatable), poisonous species are toxic, and unpalatable species are not overtly toxic, but inedible/unpalatable due to high anti-nutrient content.

Nutritional quality - The relative quality of geophyte species as a food source based on various variables which impact how nutritious and palatable their USOs would be to a human forager. USOs dense in fibre and other antinutrients are considered low quality while USOs dense in calories are considered high quality. A nominal ranking of nutritional quality (1-5) was generated for edible geophyte species based on various variables that were measured which impact their desirability to a human forager, from low quality (1) to high quality (5).

Resource quality – An estimate of the nutritional return rate possible from geophytes resources in a specific habitat. The estimate consists of an amalgamated rating of the individual geophyte species' which make up the geophyte community.

Relative carrying capacity - An estimate of how many people may be potentially sustained by the geophyte resources per hectare, for a day in specific habitats. These estimates are generated by extrapolating the data collected on the kilojoules per hectare (kJ/ha) divided by the daily caloric requirements of hunter-gatherers. These values provide a gauge of the geophyte resources in different areas, rather than a robust prediction.

Modern Human (Lineage) – The term 'modern human' is used in this thesis to refer to our recent ancestors who belong to the species *Homo sapiens*. Our modern human lineage refers to the evolutionary genetic history of our species which seems to have originated between around 160 – 195 kya.

Human modernity – This term refers to the traits in modern humans that have been described as characteristic of our modern human lineage like art, multi-step tool manufacture and complex language.

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Chapter 1: **Introduction**

1.1 Importance of geophytes in human evolution and Stone Age subsistence in South Africa

It has been hypothesised that an adaptive shift to a starch-rich diet was an important driver in human evolution (Perry *et al.*, 2007; Hardy *et al.*, 2015). The cooking of starch-rich foods would have made the nutrients contained in these foods easier to digest and up to 30 % more bioavailable for absorption by the human gut (Crittenden and Schnorr, 2017). The shift in diet from "low-quality foods" (dense in indigestible fibre), to a diet dense in "high-quality foods" (digestible carbohydrates and fats), could have fuelled the development of large brain size and enabled complex behaviour we associate with modern humans (Laden and Wrangham, 2005; Perry *et al.*, 2007; Carmody and Wrangham, 2009a). This hypothesis has been supported by the widespread prevalence of the Amylase gene in the human genome which allows us to digest starch efficiently (Perry *et al.*, 2007; Inchley *et al.*, 2016). These genes appear in the human genome as early as 300 kya (Inchley *et al.*, 2016).

Plants that possess underground storage organs (geophytes) have been put forward as one of the likely, reliable sources of starch that fuelled this development throughout human evolution (Hatley and Kappelman, 1980; Wrangham *et al.*, 1999; Ragir, 2000). It has been hypothesised that geophytes were an important part of the diet of our early hominid ancestors, such as *Australopithecus* and *Paranthropu*s (Yeakel *et al.*, 2007). Furthermore, evidence suggests *Homo erectus* cooked geophytes (Dominy *et al.*, 2008). Geophytes still comprise a significant portion of extant hunter-gatherer diets all over the world (up to 80 % of diet) (Eder, 1978; Hladik *et al.*, 1984; O'Connell and Hawkes, 1984; Hurtado *et al.*, 1985; Vincent, 1985; Hurtado and Hill, 1989a; Sato, 2001; Marlowe, 2005).

Geophytes comprise a large portion of the plant diversity in a region at the South-Western tip of Africa; the Greater Cape Floristic Region (GCFR) (Procheş, Cowling and Du Preez, 2005). The GCFR has the highest diversity of geophytes in the world (Procheş, Cowling and Du Preez, 2005), which can occur in dense resource patches (Youngblood, 2004; Singels *et al.*, 2016). Geophytes can comprise up to 40 % of the total plant cover in certain vegetation types in this region (Snijman and Perry, 1987).

Significant archaeological evidence of the evolution of human modernity has been identified in the GCFR during critical periods in the Middle Stone Age (period roughly between 40 - 250 kya: MSA) (Marean *et al.*, 2007; Brown *et al.*, 2009; Marean, 2010; Henshilwood *et al.*, 2018; Larbey *et al.*, 2019). For example, it is thought that the resources available in this region during this time period fuelled the progression and development of complex language, art and tool production in early modern humans (Marean *et al.*, 2014; Reynard and Henshilwood, 2017). It has been argued that geophytes could have been a large resource base for these early humans throughout the Stone Age (Deacon and Deacon, 1999; Marean, 2010).

Archaeological evidence from the Holocene (period roughly from 11 kya to present) corroborates the importance of geophytes in Stone Age hunter-gatherer diets and subsistence (Parkington, 1977; Deacon, 1993). Geophytes can comprise a large portion of the plant remains recovered from archaeological sites in the GCFR (Deacon, 1976; Parkington, 1976).

Exploring the prevalence of geophytes in the archaeological record to elucidate the possible impact this resource had on hunter-gatherer subsistence and early modern human evolution underpins the scope of this thesis. I have attempted to contextualise the geophyte remains found (or not found) in the archaeological record by quantifying how abundant, nutritious, and seasonal, geophyte resources are across the landscape in the contemporary environment. This can help develop our understanding of the impact this specific resource (geophytes) had on hunter-gatherer mobility across the region and the impact of this resource on the development of human behaviour and cognition.

The most prevalent and well-studied geophyte remains in the GCFR come from Holocene sites in the Western (Parkington, 1977; Liengme, 1987) and Eastern (Deacon, 1976, 1993) parts of the GCFR. The archaeological sites where significant geophyte remains have been found and analysed are Elands Bay Cave, Diepkloof Rock Shelter, De Hangen, Renbaan Cave, Andriesgrond Cave (Western section of GCFR), Boomplaas Cave, Klasies River, Scott’s Cave and Melkhoutboom Cave (Eastern section of GCFR) (see Figure 1.1). Sites, where important geophyte remains have been discovered outside of the GCFR, are Rose Cottage Cave, Strathalan Cave A/B, Sibudu and Border Cave. See the distribution of these sites and the biomes they occur in, in Figure 1.1. Note the prevalence of sites in the Fynbos and Succulent Karoo Biomes (which together, make up the GCFR).

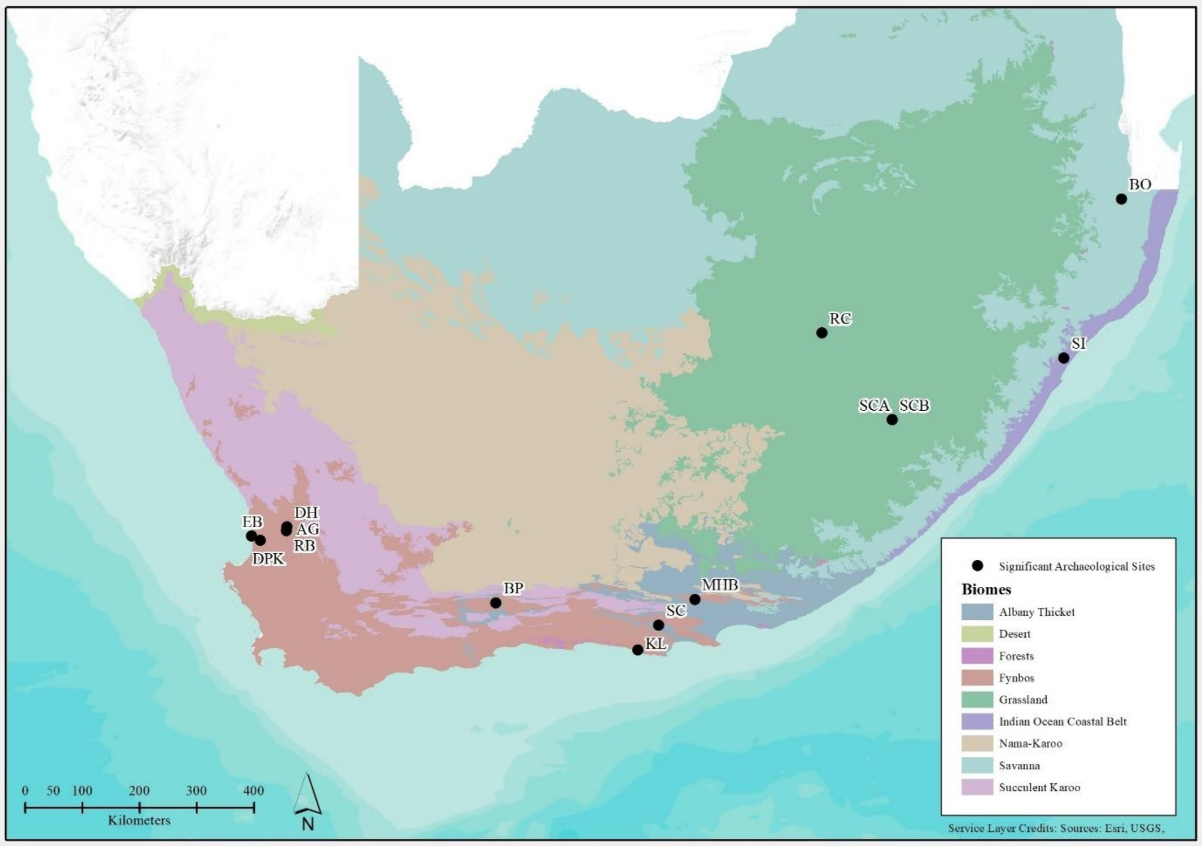

Figure 1.1 Significant archaeological sites where geophyte remains are well-reported and the biomes within which they occur. EB-Elands Bay Cave, DPK-Diepkloof Rock Shelter, DH-De Hangen, AG-Andriesgrond Cave, RB-Renbaan Cave, BP-Boomplaas Cave, KL-Klasies River, SC-Scott's Cave, MHB-Melkhoutboom Cave, SCA/SCB-Strathalan Cave A/B, RC-Rose Cottage Cave, SI-Sibudu, BO-Border Cave

The sites identified above are where geophyte remains have been well reported in the literature and systematically studied. The geophyte remains found at these sites, and the context of these critical sites is described briefly below. A comprehensive review of archaeological sites which contain geophyte remains will be presented in Chapter 6.

Three archaeological sites (Boomplaas Cave, Melkhoutboom Cave and Scott's Cave) in the Eastern part of the GCFR have been studied and excavated by Prof. Hilary Deacon and Dr Jeanette Deacon since the 1960s. Subsequently, the seminal work "Where hunters gathered" was published, which discussed in detail the significance of the plant remains identified during these excavations (Deacon, 1976). Geophytes comprised a significant portion of the botanical remains identified which predominantly dated to within the Holocene.

The bulk of the botanical material identified consisted of desiccated macro-botanical remains. Deacon made the following observation about the botanical remains identified at Scott's Cave: "Pressed under the weight of rocks overburden and kept dry in the shelter, the plant material is in a comparable condition to well curated herbarium specimens. Apart from chance inclusions due to wind drift and animal activities the remains are human imports, the selectively collected usable portions of plants rather that the complete specimens that botanists collect for reference purposes." (Deacon, 1993: 83). This type of preservation of botanical remains is a feature found in all the archaeological sites listed above where significant geophyte remains have been found.

The botanical remains often consisted of bedding patches, which were located along the back wall of the cave, which were hollowed out into the underlying deposit and filled with plant material (grass and geophyte material). Secondly, dense food waste patches are described which mainly consisted of a specific geophyte family: Iridaceae. Thirdly, some caves had special features such as storage pits, which would have been used to store food (Deacon, 1976). The difficulties in quantifying geophyte remains are discussed in depth, where it was argued that the number of geophytes which were foraged and the portion geophytes comprised of the total diet was difficult (if not impossible) to determine (Deacon, 1976).

During the same time that excavations were on-going in the Eastern Cape (1960s onwards), Prof. John Parkington was leading surveys and excavations in the Western section of the GCFR. Here, archaeological sites which were identified and subsequently excavated yielded similar significant botanical remains from Elands Bay Cave (Parkington, 1976), De Hangen (Parkington and Poggenpoel, 1971), Andriesgrond Cave (Robey, Von Schirnding and Flanagan, 1978), Diepkloof Rock Shelter (Silberbaur, 1974) and Renbaan Cave (Kaplan, 1984).

A seminal systematic botanical analysis was performed on the plant remains from the five sites in the Western sections of the GCFR (Liengme, 1987). This analysis also identified the quantification challenges of studying geophyte remains, while presenting compelling evidence of the seasonality of geophyte foraging, although only accurate to within broad seasonal categories (Liengme, 1987). The coastal or near coastal sites; Elands Bay Cave and Diepkloof Rock Shelter yielded good preservation of plant materials, and geophyte material was found in layers which dated to within the last 2000 years. In both sites, there was a prevalence of Iridaceae material which consisted of the coastal geophyte species unique to the vegetation of the area (Liengme, 1987). The remaining sites reported on in this study are located to the interior, in the Cederberg mountain range and comparable patterns of plant remains were found there. Similar to that reported from sites in the Eastern section of the GCFR, plant remains consisted of bedding patches along the back of the walls of caves, composed of grass and Iridaceae remains, Iridaceae food waste patches and storage pits filled with geophyte material which cut into the underlying layers (Liengme, 1987). All of this plant material dated to within the last 2000 years (Liengme, 1987). Following the publication of "Where hunters gathered" subsequent analysis and excavations in the Eastern section of the GCFR yielded further insight into the possible dynamics of geophyte foraging in the Stone Age. Significant finds from Boomplaas Cave are 74 storage pits (Deacon, 1982) and carbonised lenses associated with plant processing dating to between 12 - 14 kya; these features are some of the most ancient evidence of geophyte foraging (Deacon, 1979). Similarly, carbonised lenses identified at Klasies River have been interpreted as extensive geophyte processing and have been dated to between 70 – 120 kya (Deacon, 1995). Recently cooked geophyte starch particles have been identified in these layers seemingly confirming the interpretation that these layers represented extensive geophyte processing (Larbey *et al.*, 2019). The botanical remains excavated at Scott's Cave are more comparable with the West Coast sites due to the large amount of Iridaceae material that was identified and dated to within the last 2000 years (Wells, 1965). Melkhoutboom Cave had excellent preservation of botanical material which was found in layers dated to between 500 - 7500 ya and the species identified are similar to the species composition found at Scott's Cave (Deacon, 1967). Storage pits were found at Melkhoutboom Cave and were dated to within the past 3000 years. Similar to Boomplaas Cave, humified plant remains in older layers made identification of that material impossible, but the carbonised lenses observed were interpreted as extensive geophyte processing (Deacon, 1976). Iridaceae remains were again a common feature.

Due to the seasonal nature of geophyte resources, it has been argued that this resource would have influenced hunter-gatherer mobility in both the Western section of the GCFR (Parkington, 1972) and the Eastern section of the GCFR (Deacon, 1976), but in distinct ways. Based on the archaeological evidence of seasonal foraging of various resources in the Western Cape sites (including geophytes), Prof. Parkington presented the seasonal mobility hypothesis, a hypothesis of hunter-gatherer mobility (Parkington, 1972, 1976). The seasonal mobility hypothesis describes a scenario where hunter-gatherers migrated annually from the Cederberg interior along the Olifants River to the coast in early winter, where they utilized the coastal resources available at that time (Parkington, 1972). When geophytes became available and abundant in spring, he argued hunter-gatherers would have made their way back to the mountainous regions to utilise the abundant geophyte resources, completing the circular, annual migration (Parkington, 1976).

The interpretation of the seasonality of geophyte foraging in the Eastern section of the GCFR was quite different from the Western section of the GCFR. The geophyte genus which was found in almost every site in the Eastern Cape, *Watsonia*, can be visible year-round in that region and it was argued that this genus was targeted due to the long period of the year in which it could be foraged (Deacon, 1976). Further inferences of the seasonality of foraging were made based on when the geophyte species are most visible and abundant in the landscape in the Eastern section of the GCFR, which was interpreted as early summer (December-January).

Geophytes comprise a significant portion of the flora in other biomes in South Africa, apart from the GCFR. In the Grassland Biome geophyte remains from Strathalan Cave A/B, and Rose Cottage Cave have been dated back to the early LSA and terminal MSA. At Strathalan Caves, Iridaceae remains were found in layers which were dated to between 25 - 29 kya (Opperman and Heydenrych, 1990) and at Rose Cottage Cave charcoal geophyte starches were identified (Wadley, 1997). In the Indian Ocean Coastal Belt Biome, Sibudu Cave yielded substantial MSA deposits with remarkable preservation of macrobotanical remains in the form of bedding patches which contained sedge underground storage organs in layers which were dated to between 38 – 70 kya (Sievers, 2011; Wadley *et al.*, 2011). In the Savanna Biome, Border Cave yielded tools associated with geophyte foraging like grindstones and digging sticks from layers dated to 45 kya, the tools from these layers are comparable to the tools used by modern hunter-gatherers in southern Africa and illustrates the antiquity of this material culture (d'Errico *et al.*, 2012; Villa *et al.*, 2012). Recently cooked geophytes were identified which date to 170 kya (Wadley *et al.*, 2020). Although geophyte foraging predates the Holocene in this region it was focused on similar taxa and with a similar foraging method that is observed in the Holocene in the GCFR.

1.2 Problem Statement

The subsistence patterns of Stone Age hunter-gatherers in the GCFR have been extensively researched, and the significant role geophytes played in that subsistence has been shown from across the region. However, there are many facets of this portion of Stone Age life that are not well understood.

A great deal of information has been published based on the systematic analysis of geophyte remains from archaeological sites, which has contributed significantly in shaping our understanding of Stone Age hunter-gatherer subsistence. Many questions remain. Archaeological evidence of geophyte exploitation is predominantly identified dating to the Holocene (geophyte remains are rare in the MSA and early LSA). There is very little information available on how and which (if any) geophytes were foraged during these critical phases of human evolution. Furthermore, the archaeological evidence that does exist for geophyte plant use is not evenly spread over the region, and has not been addressed by the available literature. It is not known whether the lack of geophyte remains from archaeological sites in these regions translates to the interpretation that hunter-gatherers were not collecting geophytes. The impact of geophytes on seasonal mobility of hunter-gatherers is disputed (Sealy *et al.,* 1986) and could vary widely across the GCFR.

To help interpret and support the archaeological evidence of geophyte foraging we need a detailed understanding of the environmental and ecological factors that influence the geophyte resource base across the GCFR.

Studies conducted in recent years have attempted to quantify plant resources available to foragers in the contemporary southern Cape landscape (De Vynck, Cowling*, et al.*, 2016; Singels *et al.*, 2016; Botha *et al.*, 2020). These studies were designed to aid the modelling of large scale resource availability in the South Coast region as part of a bigger research project: the Paleoscape Project, which aims to reconstruct the conditions in the southern Cape region during critical periods of early human evolution throughout the MSA (Franklin *et al.*, 2015; Marean *et al.*, 2015). Although these studies have made great strides in describing the energetic benefits that would be possible from plant foraging in the contemporary landscape, no in depth quantification of the geophyte resource base has been made over the entire GCFR region which considers the quality of this resource and the seasonality of this resource. The nature of this resource would impact the dynamics and specific process of the exploitation of geophytes, which is not well understood.

The following key factors of the geophyte resource base are not well understood:

1. The array of geophyte species that were exploited by hunter-gatherers and the ways in which they were exploited;

2. Nutritional information of these geophytes;

3. Quantity and quality of geophyte resources available across the landscape;

4. Seasonal variation in geophyte resources across the landscape.

The challenge of compiling an in-depth description capturing the seasonal variation, carrying capacity or quality of geophyte resource within the GCFR is confounded by the unfortunate loss of traditional ecological knowledge surrounding geophytes in the region (De Vynck, Van Wyk and Cowling, 2016). No extant hunter-gatherer communities remain in the GCFR, which makes observational studies of hunter-gatherer behaviour impossible. As a result, there is limited potential to recreate foraging activities as they might have occurred in the distant past (as is done in other parts of the world where extant hunter-gatherer communities remain). Recreating, even if experimentally, the array of species and processing techniques that might have been employed by hunter-gatherers is near impossible using re-enacted foraging activity alone. Some of the most detailed evidence of geophyte exploitation and processing methods has been captured in historical accounts of early travellers to the Cape. A wealth of potential information about the array of geophyte species which were used by hunter-gatherers and the methods used to process them could be elicited from these resources. Attempts have been made to list all the potential plant species foraged by hunter-gatherers mentioned in these resources (Silberbaur, 1974; Parkington, 1976; Skead, 2009; Botha *et al.*, 2019), although no comprehensive analysis of the distribution, abundance or quality of these species has been attempted. Furthermore basic, high-quality data needed for such an evaluation (such as nutritional content of geophytes) is not available and only limited data have been published for a few species (Orthen, 2001; Singels *et al.*, 2016).

Along the east to west gradient across the GCFR a vast array of archaeological sites dated to within the MSA and LSA exist (Marean *et al.*, 2014). Within this wide geographic range, a wide range of rainfall regimes and edaphic environments lead to an array of geophytic communities (Procheş, Cowling and Du Preez, 2005). If the geophyte resources across this gradient are evaluated, an estimate of the availability of geophytic resources across a range of contemporary rainfall regimes and vegetation types can be made. By evaluating these data, estimates of the nutritional content within the current environment can be generated and compared to the archaeological record. These data could be invaluable to test previously untestable hypotheses and aid in on-going research projects (such as the Paleoscape Project) which require regional scale data that describes resources over a wide range of climates and habitats (Marean *et al.*, 2015).

Geophytism (the trait for plants to possess a USO) is an adaptation for drought and unpredictable rainfall. This life-history strategy leads to an array of phenological growth patterns (when plants are dormant, leaving, flowering or seeding) among the various geophyte species. These different patterns of growth determine when geophytes are in a growing phase with live biomass above ground and affect the composition of USOs (water and energy) throughout their growing season. These variations would have inevitably had a significant effect on the potential role of geophytes in human diets. No attempt has been made to describe the dynamics of how phenology might influence the nutrients available to foragers through the course of a year and as this might impact the nutritional content of geophytes this is essential information to assess geophytes as a possible human food source and the dynamics of how foraging could have occurred.

It is clear that there are many aspects of geophyte foraging that need to be explored further to understand the context of geophyte foraging in the Stone Age and the possible impact of geophyte exploitation on human evolution. The array of information still required to answer the remaining questions can be addressed from analysis of archaeological and anthropological data but must incorporate consideration of the environmental and ecological factors which impact geophyte resources across the entire GCFR.

1.3 Aims and Objectives

The overall objective of this thesis, then, is to determine the importance of geophytes in early modern human diets and evolution by evaluating the characteristics of this resource in the current GCFR landscape and the archaeological evidence of the foraging of geophytes by Stone Age hunter-gatherers. By creating an ecological and environmental framework of data, which evaluates the dynamics of the geophyte resource base, the archaeological evidence available on actual hunter-gatherer foraging behaviour can be evaluated. The evidence of geophyte exploitation, the value of geophytes as a food source and their possible nutritional contribution to human diets is investigated. The five main aims of this thesis are to;

1. ***Assimilate all the available information of geophyte use from existing literature from historical accounts of early travellers, compared to the evidence of geophyte exploitation presented in the available literature from the fields of archaeology, anthropology and ethnobotany.***
2. ***Access the nutritional composition of various edible geophyte species, by describing the macronutrient composition, energy content and anti-nutrient composition of various edible species.***
3. ***Determine the abundance and distribution of geophytes across the gradient of rainfall regimes in the GCFR, to help describe the biomass contained in these areas to generate an estimation of how many humans this resource could have sustained.***
4. ***Access the availability and nutritional quality of geophytes across the GCFR through the course of a year.***
5. ***Describe the geophyte remains identified in the archaeology and identify new methods to improve the analysis of these remains in the future.***
6. ***Determine the efficacy of Stone Age processing methods to improve the nutritional quality and palatability of USOs***

1.4 Study Area

In this thesis, I describe the spatial and temporal variation of geophyte resources, and geophyte remains in the archaeological record on the coastal plains of the GCFR. The Cape Fold Mountains are the dominant topographic feature of the GCFR, the interior slopes of which create the interior border of the GCFR (Figure 1.2) (Verboom *et al.*, 2009). This mountain range extends from the interior to the coast at False Bay (Hangklip), creating a natural, physical barrier between the West Coast and the South Coast. This feature is key to the biotic and climatic differences observed between the West and South Coast.

The region has been divided into three distinct study areas to describe the variation of geophyte resources and geophytes found in the archaeological record over the entire region. These areas capture the range of rainfall regimes over the coastal regions of the GCFR and from here on are referred to as the West Coast, South Coast and East Coast (see Figure 1.2). The West Coast encompasses the low-lying areas from Elands Bay to Mamre, from the coast to the foot of the Cederberg Mountains. The South Coast is defined as the low-lying areas of the coastal plain from Pearly Beach to Mossel Bay, from the coast to the foot of the Langeberg Mountains. The East Coast is a misnomer, as it technically falls in the southern Cape, but was so-called as it occurs to the east of the South Coast study area. This area encompasses the low-lying areas from Plettenberg Bay to Jeffrey’s Bay, from the coast to the foot of the Baviaans Mountains. The coastal regions of the northern extent of the GCFR were not sampled directly during ecological surveys.

The mean annual precipitation on the West Coast is considerably lower than that of the southern Cape. The northern reaches of the GCFR experiences lower levels of annual precipitation (Schulze, 1965). Elands Bay has a mean annual precipitation (MAP) of 165 mm per annum, where 75 % of this rain falls between the months of April-August (winter months). Mamre to the south has a MAP of 350 mm per annum, where 72 % of this rain falls in the winter months (see Figure 1.2). Pearly Beach has a MAP of 530 mm per annum, of which 62 % falls in the winter months. Mossel Bay has a MAP of 480 mm per annum, where 42 % falls in the winter months. Buffalo Bay has a map of 660 mm per annum which falls 38 % in the winter months, and lastly, Jeffrey’s Bay has a MAP of 530 mm per annum of which 43 % falls in the winter months.

The seasonality of rainfall in the GCFR will be discussed in greater detail in Chapter 2, but in general, the greatest proportion of rainfall in the West Coast falls within winter, while there are two peaks of rainfall in the South Coast during autumn and spring, and the East Coast receives rainfall roughly all year round.

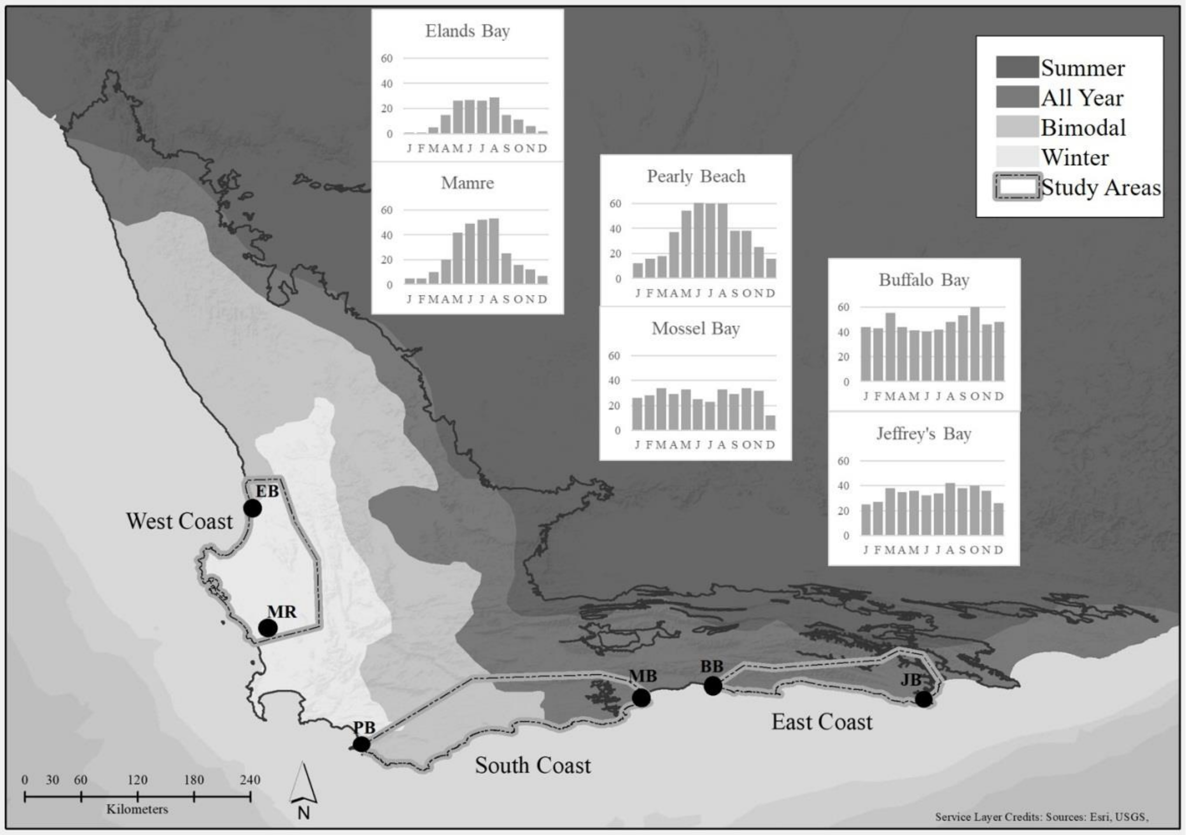

Figure 1.2 Map showing Rainfall regions and three study regions. Rainfall data adapted from Bradshaw & Cowling, 2014. Maps of a) rainfall seasonality in the GCFR (after Schulze 1997) and percentage winter (May-Oct) rainfall. The 50-year average rainfall observed in the three study areas for the towns at the terminal ends of study regions. Sourced from South African Weather Service. EB-Elands Bay, MR-Mamre, PB-Pearly Beach, MB-Mossel Bay, BB-Buffels Bay, JB-Jeffrey’s Bay

1.5 Methodology

Ethnobotany is the study of plant use by indigenous people of a region and focuses on describing the plant species that indigenous people use for daily life (Gerique, 2006). Palaeoethnobotany is defined as the analysis and interpretation of the direct interrelationships between humans and plants for whatever purpose, and as manifested in the archaeological record (Helbaek, 1969). The methodology and techniques used in this thesis were guided by the comprehensive guide of paleo-ethnobotanical research techniques presented by Pearsall (2016). To understand how ancient humans interacted with plants and were influenced by the ecosystem, a range of techniques and basic information from the fields of botany, archaeology and ethnobotany are required (Pearsall, 2016). Paleo-ethnobotanical research is guided by the direct evidence we find of plant use in the archaeological record by identifying, quantifying and exploring the processing and uses of plants identified. This information is then compared to the resource base of plants in the environment, which allows us to interrogate the human-plant relationship further by indirectly evaluating the choices that hunter-gatherers made, this method is called the ecological approach (Pearsall, 2016). In this approach, the contemporary distribution of resources in the immediate vicinity of archaeological sites is studied and compared to the botanical material found in the sites; this approach has been adopted in the GCFR in the sites discussed in section 1.1 (Deacon, 1976; Liengme, 1987). This is an effective method to interpret the resources that are available in the contemporary vicinity of specific cave sites. In this thesis, I am concerned with the broader patterns of geophyte resource use across the entire GCFR, how various climatic regions influence the distribution of these resources across the region, how seasonality affects the quality of the resources, and ultimately how this variation in the landscape (space) and across the season (time) would have affected hunter-gatherer subsistence and ultimately their evolution in the region.

To provide broader context, I conducted a review of the available information on how extant and extinct hunter-gatherers interacted with geophytes in the GCFR and across the world. From the available literature, I was able to extract information about specific geophyte species which allowed me to compile a comprehensive species list of geophytes which were used and processed in various ways. This information informs further interpretation of archaeobotanical material, such as how the geophytes identified in the archaeology were used (if at all) and is critical to any Paleo-ethnobotanical analysis of material found in the archaeology.

Secondly, I have developed a methodology of describing the contemporary distribution, quantity and quality of geophyte resources across the region, by conducting a spatial analysis of abundance, biomass and ultimately the relative carrying capacity of this resource across the region (Spatial Analysis). Relative carrying capacity is a unit of measurement that indicates the number of hunter-gatherers whose daily caloric requirements could be met, from the geophyte resources alone, per hectare of vegetation for a day. From the geophyte species identified in this analysis I conducted a nutritional survey of the various geophyte species identified in the region (Nutritional Analysis). In addition to these analyses, I conducted a survey of the variation of nutritional content throughout the growing season of a select group of geophyte species (Seasonal Variation Analysis).

Thirdly, I surveyed the botanical remains from archaeological sites across the region, to shed light on how humans exploited geophytes (Archaeological Analysis). For this analysis, I analysed macrobotanical (visible with the naked eye) archival material (almost exclusively from the Holocene) from sites that have been excavated in the past. Analysis of macrobotanical remains is the oldest and most simple technique used to identify plant remains from archaeological sites, and the basic, but effective methods presented by Pearsall (2016) were followed. These methods allowed investigation into the taxonomic, quantification and cultural implication of human-plant interactions.

My methodological contribution to the standard macrobotanical methods was to develop a proxy method to extrapolate seasonality of geophyte collection and energy content of individual USOs to material found in excavated assemblages. Additionally, experimental methods of replicating and testing the efficacy of Stone Age processing methods are presented.

All the information collected during these three steps is used to produce a synthesis of geophytes exploitation by Stone Age hunter-gatherers and the effects it might have had on human evolution in the region. Figure 1.3 presents an abstract representation of the methodological framework and flow of information presented in this thesis.

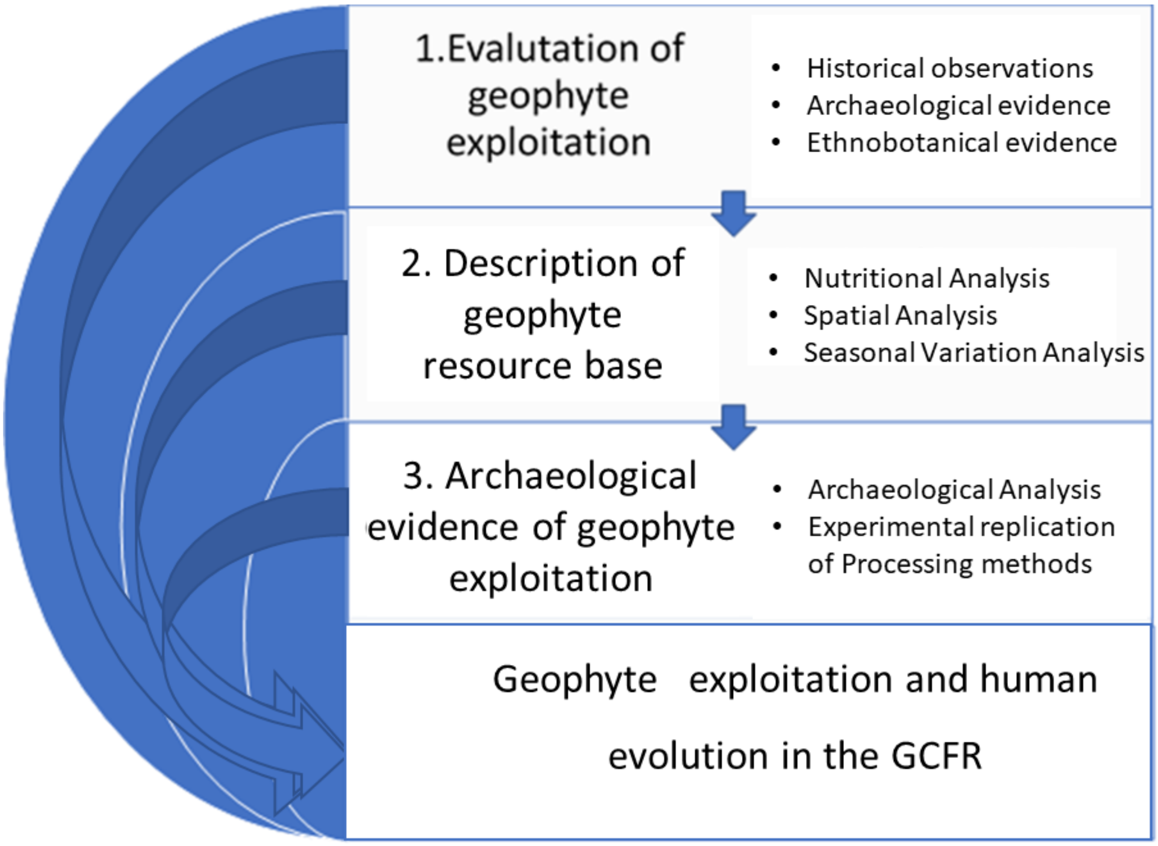

Figure 1.3 Methodological framework of this thesis

1.5.1 Evaluation of geophyte exploitation

The first step in understanding geophyte exploitation in the GCFR is to gather all the existing information on the exploitation of specific resources from the fields of anthropology, botany and archaeology. To evaluate the exploitation of geophytes in the GCFR, I conducted a review of the available information on how extant and extinct hunter-gatherers interact with geophytes in the GCFR and across the world (Chapter 2, Section 3). This allowed the compilation of a comprehensive species list of geophytes that were used and processed (Table 2.1, pg 47). This information is used in subsequent analyses and can be used to inform which geophytes make up the resource base and how the geophytes identified in the archaeological record were used (if at all).

1.5.2 Analysis of the geophyte resource base

Describing the geophyte resource base across the GCFR requires an understanding of the variation of this resource (if any). Understanding how climatic regions influence the distribution of these resources across the region, how seasonality affects the quality of this resource, and how this variation in the landscape (space) and across the season (time) would have affected hunter-gatherer subsistence and ultimately early human evolution in the region. This information together forms a description of the geophyte resource base (Chapter 4).

I structured the analysis of the geophyte resource base by performing three distinct analyses: Nutritional Analysis (Chapter 3), Spatial Analysis (Chapter 4) and Seasonal Variation Analysis (Chapter 5). The Spatial Analysis described the distribution, quantity and quality of geophyte resources across the region, by conducting an analysis of abundance, biomass and ultimately the relative carrying capacity of this resource across the region. From the geophyte species identified in this analysis, I was able to conduct a nutritional survey of the various geophyte species identified in the region (Nutritional Analysis). In addition to these analyses, I conducted a survey of the variation of nutritional content throughout the growing season of a select group of geophyte species and described the seasonal availability of geophytes in each of the study regions throughout the year (Seasonal Variation Analysis).

For all the nutritional analyses performed for this thesis the components which contribute to the energy content of USOs were measured (macro-nutrients) and components which would negatively impact the nutritional quality of USOs (anti-nutrients). Although micro-nutrients are an important component of the nutritional content of foods, testing for them was beyond the scope of this thesis. Additionally, no attempt was made to access the bioavailability or bioaccessibility of USOs to the human gut, as this too was beyond the scope of this thesis. It has been found that these factors can impact the amount of nutrients that are available for absorption (bioavailability), and are actually absorbed (bioaccessibility) by the human gut (Wollstonecroft *et al.*, 2008; Schnorr *et al.*, 2015).

See Figure 1.4 for an abstract layout of the factors that influence the geophyte resource base and which were investigated.

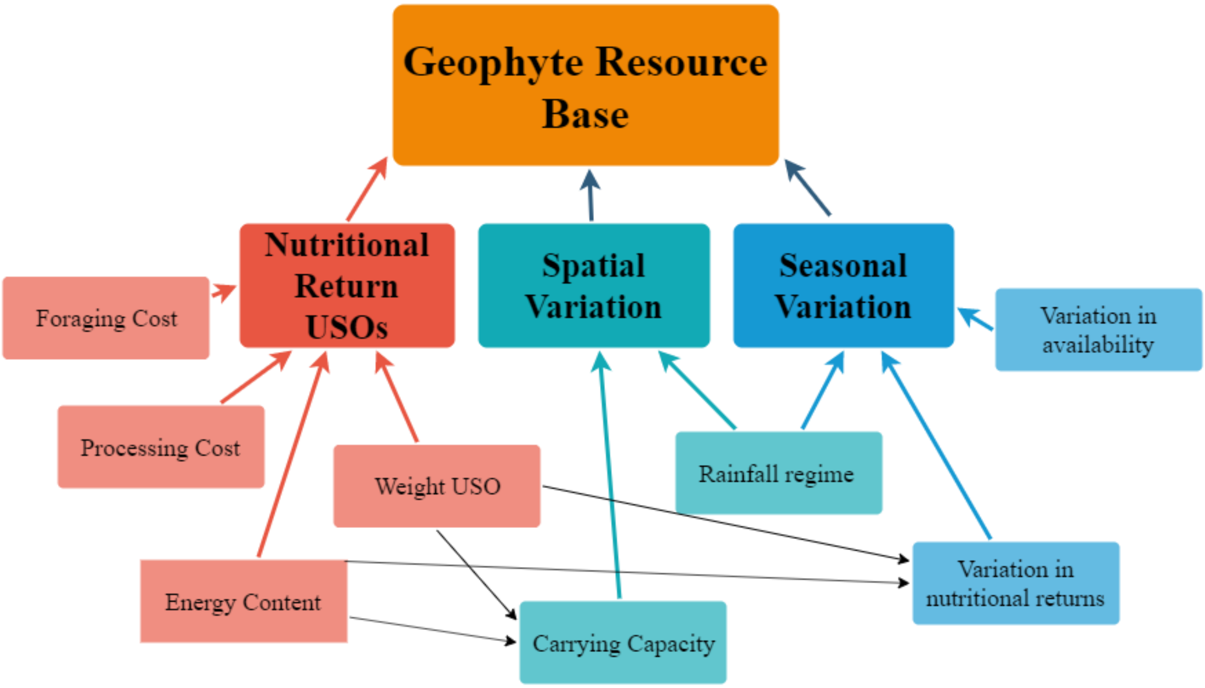

Figure 1.4 Layout of factors which impact the geophyte resource base and the various factors considered or measured during the three district analyses performed to evaluate the geophyte resource base.

1.5.3 Archaeological evidence of geophyte exploitation

To assess the archaeological evidence of geophyte exploitation I surveyed the botanical remains from archaeological sites across the region (Archaeological Analysis).

When considering the interpretation of any archaeological material one has to consider the pathways by which the remains were produced, deposited, preserved and eventually excavated (Pearsall, 1989). These factors are referred to as the depositional bias (what is introduced to the site and how), preservation bias (which deposited materials survive), and recovery bias (what is recovered from the site). Only once these biases have been considered can qualitative or quantitative analysis be attempted to help answer larger research questions (Pearsall, 1989; Marean *et al.*, 2015). Each archaeological site presents a specific environment, which should be analysed in unique ways and are deemed to be appropriate for each site. Because of the distinctive botanical remains at each archaeological site and the biases of each excavation there is no set default approach for botanical remains analysis (Pearsall, 2016).

In palaeoethnobotany, qualitative presentation of botanical remains usually requires the interpretation of the presence of plant remains at a site and in relation to a specific dated period (Pearsall, 2016). A species list, for various dates, although critically important, is the simplest form of analysis of botanical remains. The species composition of plant remains can give information about the ecological zones or vegetation types represented in the same deposits, patterns of foraging and even seasonal population movements.

Quantitative analysis of archaeological remains has allowed many high-quality interpretations of lithic and faunal assemblages from the archaeological record (Thackeray, 1988; Schoville and Brown, 2010). Quantitative analysis could be useful to determine the ratio of plant to animal food in hunter-gatherer diets for instance. Methodologically, a simple tabulation of frequencies is the starting point from where statistical analysis can be undertaken. These tabulations can be based on counts or weights of species. Most frequently the ratio between groups, or subsets of group is interpreted (Pearsall, 2016). However, there are various issues with comparing quantities in this way. For example, different techniques of obtaining plant remains will yield very different densities and overall biomass. Most commonly macrobotanical remains are sampled using various techniques (usually as a grab sample) and finer, organic material separated from other material using flotation. Flotation is a common technique used to separate organic matter from excavated material by submerging excavated material in water and filtering out organic matter by sorting material by its effective density and sieving it by effective size (Pearsall, 2016). Flotation results in the recovery of often fragmented material, while macroremains might be less dense because of the particulate size. What do the overall quantity and ratios tell us about the amount of food for example that may have been extracted? It is in some cases hard to argue that a certain weight of food is obtained from a certain weight of waste.

This is the case when it comes to geophyte remains, as geophyte species are structurally diverse and are certainly not functionally equivalent to other plant remains. This will be discussed in greater detail in Chapter 6. The amount of information that can be relayed from quantitative analysis of archaeological sites should be approached with caution and quantitative analysis should not require more rigor than the data are capable of sustaining (Pearsall, 1989)

Due to the fact that geophyte remains and even the material culture surrounding geophyte exploitation is perishable, archaeological evidence has limitations to test certain hypothesis (Hurcombe, 2008). Many of the processing methods used by hunter-gatherers during the processing of geophytes would be invisible in the archaeological record (for instance, cooking of geophytes, which are then eaten, would leave no visible evidence). It is difficult then to only rely on archaeological evidence to understand the possible processing methods that hunter-gatherers used to process geophytes. In order to test the possible processing methods that could have been used in the past, the efficacy of processing methods which were observed in the GCFR was tested experimentally (Experimental Archaeological Analysis).

By combining all of the information gathered about geophyte resources it was possible to form a synthetic view of geophyte exploitation in the Stone Age. This has key implications for human evolution in the GCFR, as we understand this area to have been important in the evolution of early humans, and the resources in the area likely enabled the survival and development of humans during critical periods in our evolution (Henshilwood and Marean, 2013). This is presented in the form of a synthetic chapter (Chapter 8) that combines the separate lines of evidence to interrogate the possible evolutionary impact geophytes had on early modern humans and the predicted foraging strategies hunter-gatherers had to optimise the exploitation of this resource in certain environments, at certain times of the year.

1.6 Thesis layout

The thesis follows the structure of the flow of information presented in the methodology section. This first introductory chapter is followed by a chapter that presents an ecological and behavioural framework of geophyte foraging in GCFR

The following three data chapters attempt to describe the geophyte resource base and are divided among the distinct analyses performed: Nutritional Analysis, Spatial Analysis and Seasonal Variation Analysis.

The next two data chapters present the archaeological evidence of geophyte foraging and are divided among the distinct analyses performed: Geophyte Remains Analysis and Experimental determination of the efficacy of USO processing methods.

The concluding chapter is a synthesis of the evidence presented and the implication for Stone Age hunter-gatherer subsistence and human evolution.

All the data chapters are written in article format: (Introduction, Methods, Results, Discussion, Conclusion), with all references used in the thesis appearing at the end, followed by the Appendices. Below is a schematic representation of the flow of the thesis (Figure 1.5).

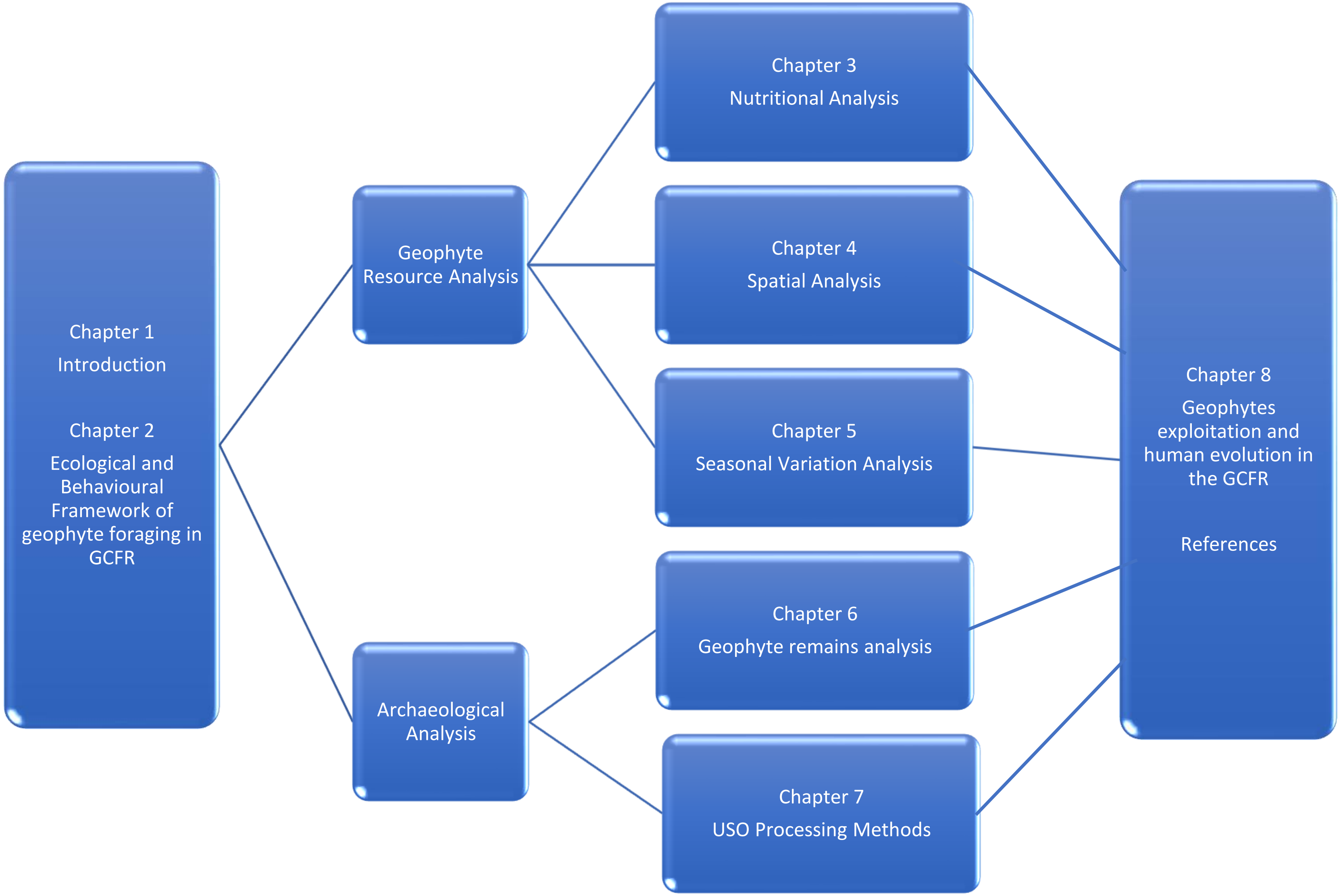

Figure 1.5 Thesis Layout

Chapter 2: **Environmental and behavioural context of geophyte foraging in the GCFR**

In this chapter, a framework of background information is presented from the available literature, which supplies the reader with the context required to understand the rest of the thesis. The reader is encouraged to refer back to this section if any of the information provided in subsequent chapters is unclear.

Section 1 will focus on the current and past climate and vegetation of the GCFR, followed by a short review of geophyte biology.

Section 2 will give a short review of human evolution and diet, followed by a brief overview of the people that have lived in the GCFR throughout the Stone Age.

Section 3 will serve as a literature review of the ethnography and ethnobotany of the GCFR and relevant literature from other parts of the world.

Section 4 will give a list of the economically important geophyte species in the GCFR that was identified from the litterature

2.1 The Greater Cape Floristic Region and geophytes

The Greater Cape Floristic Region is a phytogeographic region at the southwestern tip of Africa which is characterised by the presence of the floristic element of Fynbos, the heathland vegetation which dominates the region (Bergh *et al.*, 2014). The boundaries of this region are defined by assessing the distribution of "Cape elements" in this region. The Cape elements consist of the floral lineages which occur nowhere else in the world (endemic). The GCFR was recently defined and extends the boundaries of the Cape Floristic Region to include the winter rainfall regions of the succulent Karoo (Manning and Goldblatt, 2012; Bergh *et al.*, 2014). In this thesis, the focus is on the coastal lowlands of the GCFR.

2.1.1 Climate of GCFR

One of the prominent features of the GCFR is its distinct rainfall seasonality, where the most significant proportion of rain falls in winter (Winter rainfall region) (Bradshaw and Cowling, 2014; Engelbrecht *et al.*, 2014). This rainfall seasonality is unique among African climates, where the entire continent is subject to predominantly summer rainfall (Engelbrecht *et al.*, 2011). This unique rainfall pattern is governed by circumpolar, westerly frontal systems (Bradshaw and Cowling, 2014). The influence of these frontal systems is most pronounced in the extreme southwestern tip of the GCFR and decreases northward and eastward (Bradshaw and Cowling, 2014). This phenomenon results in a south-north, and west-east gradient of rainfall seasonality, where the proportion of rainfall experienced in winter decreases the greater the distance from the central south-western region of the GCFR (Engelbrecht *et al.*, 2011, 2014). In this thesis, the northern areas of the GCFR (Succulent Karoo) were not sampled, but the eastern extremes of the GCFR coastal regions were a prime focus area. Thus the west-east gradient of rainfall seasonality is more relevant.

Three main factors govern the climate over the west-east gradient;

1. The Cape Fold Mountains (which lie to the interior of the West and South Coast), meet at an angle at Hangklip, creating a barrier which blocks eastward penetration of the cold fronts which are common during the winter on the West coast (see Figure 2.1) (Bradshaw and Cowling, 2014).

2. The warmer ocean currents that flow off the South Coast also result in widespread rain (Cowling, Procheş and Partridge, 2009).

3. Cut-off lows and Tropical-temperate lows can deliver large rainfall events in Autumn and Spring, and they are exerted over the eastern part of the GCFR (Engelbrecht *et al.*, 2014)

These three factors together have resulted in the GCFR lowlands exhibiting the following rainfall patterns;

The West Coast has a strict winter-rainfall regime where 80 % of the annual rainfall falls in winter (Bradshaw and Cowling, 2014). The western part of the south coast has a bi-modal rainfall as a result of the cut-off lows delivering rain in Autumn and Spring while maintaining a high percentage of predictable winter rain (Engelbrecht *et al.*, 2014). The most eastern part of the GCFR (East Coast) exhibits an all-year pattern of rain with a more predictable summer component (Procheş, Cowling and Du Preez, 2005). See Figure 2.1 for distribution of rainfall regimes across the GCFR.

These variations in rainfall regime are not trivial and can be deterministic of the distribution of vegetation types across the GCFR (Bergh *et al.*, 2014). For instance, a significant decrease in species richness is observed along the west to east gradient along the GCFR (Cowling *et al.*, 2017). This decrease in diversity is observed among geophyte species richness as well (Procheş, Cowling and Du Preez, 2005) and could impact the geophyte resources available across the region.

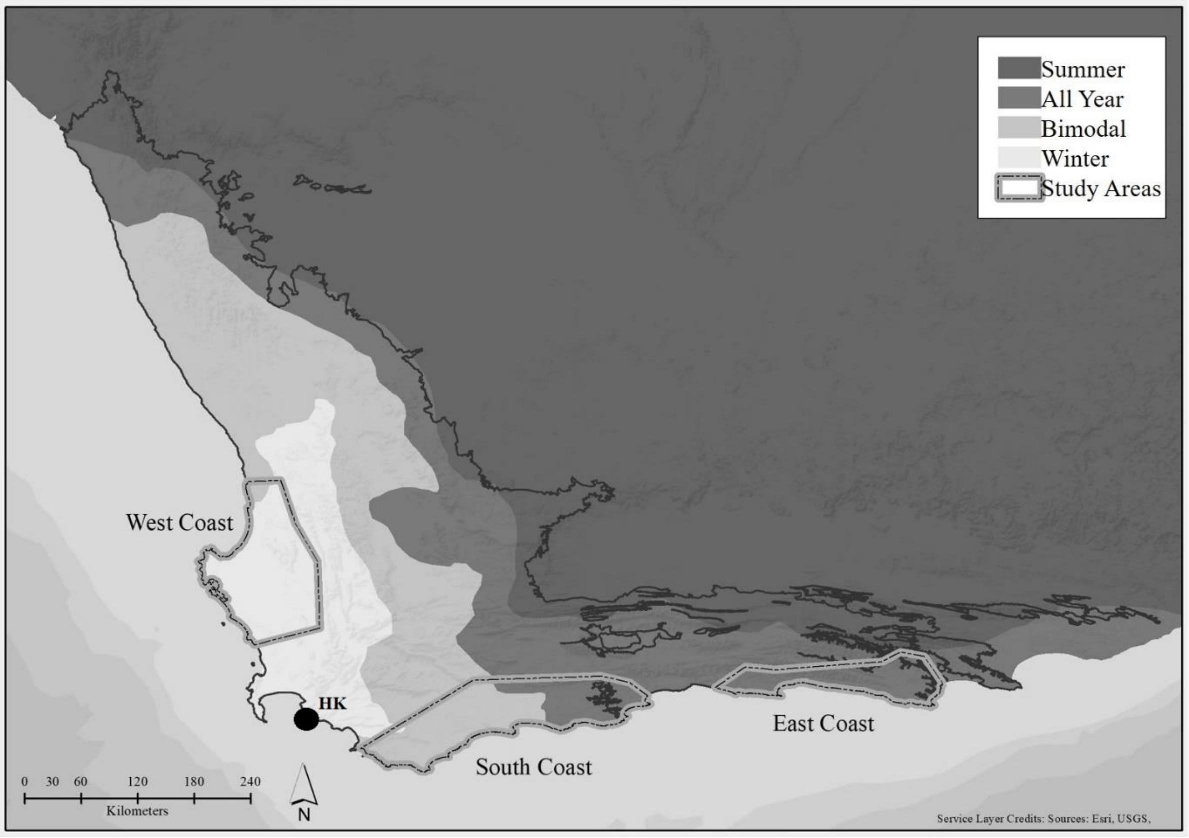

Figure 2.1 Rainfall seasonality across GCFR and three study areas. HK- Hangklip

2.1.2 Vegetation of GCFR

Although Fynbos vegetation and Fynbos elements are dominant in the GCFR, five distinct, broad vegetation types are recognised to occur in the GCFR namely; Fynbos, Renosterveld, Subtropical Thicket, Forest and Succulent Karoo (Bergh *et al.*, 2014). Each vegetation type has unique characteristics, but in general, all vegetation types, and the GCFR as a whole, contains a high proportion of geophyte species (Procheş, Cowling and Du Preez, 2005; Procheş *et al.*, 2006). Among the five different vegetation types however there are differences in the geophyte communities, and other characteristics, be they biotic or abiotic (Bergh *et al.*, 2014), which would affect the resources available to hunter-gatherers in those habitats. It is essential for the reader to understand the basic floristic and abiotic characteristics of the four broad vegetation categories contained in the GCFR which were sampled in the study areas (excluding Succulent Karoo) as defined by Mucina *et al.*, 2014. In the GCFR a few key factors influence the distribution and composition of vegetation types most strongly: fire, edaphic environment, rainfall amount and seasonality (Cowling, 1992; Allsopp, Colville and Verboom, 2014).

Fynbos vegetation is the dominant feature in the GCFR and hosts the highest number of species unique to the region (endemism). It is characterised as low growing heath shrubland. The composition of the flora is distinct from other types, and the dominant families are Ericaceae, Restionaceae and Proteaceae. Fynbos usually grows on soils derived from sandstone and thus occurs on nutrient-poor soils. The soil type on which the vegetation grows has a significant influence on the composition of the veld it supports. Fire is the second important abiotic factor determining the distribution and composition of Fynbos vegetation. Fire can be an agent that has forced speciation in Fynbos clades ever since it became a frequent and regular occurrence in Fynbos habitats in the Paleogene (Bytebier *et al.*, 2011; He, Lamont and Manning, 2016).

Renosterveld is the vegetation type most closely related to Fynbos (Bergh *et al.*, 2014), although it is distinct from Fynbos in the composition of species which occur in this vegetation type and set apart by the fact that it grows on nutrient-rich soils (Bergh *et al.*, 2014). Dominant families are Poaceae, Asteraceae and a higher component of geophytes than in Fynbos (Procheş *et al.*, 2006). The Renosterbos or *Elytropappus rhinocerotis* can be a dominant feature in some Renosterveld (Bergh *et al.*, 2014).

Subtropical thicket is a complex group of vegetation that extends in patches of varying sizes along the GCFR coastline, but its greatest extent lies in the dissected river valleys in the Eastern Cape (Albany Thicket) (Bergh *et al.*, 2014). It comprises spiny, sclerophyllous, broadleaved and/or succulent shrubs with an understory mostly comprising of geophytes. Strandveld is a vegetation type which falls under the Subtropical thicket complex which occurs in the Coastal lowlands. Although Subtropical thicket is associated with nutrient-rich soils, it can colonise any substrate if fire is absent. The vegetation type can prove to be good browsing for large game (Bergh *et al.*, 2014), which could have attracted hunter-gatherers (Klein, 2001). In this thesis, the Strandveld component of Subtropical thicket was defined by the substrate it grows on and is clearly delineated from Albany thicket which occurs to the east of the GCFR border.

Forest vegetation occurs in small fragments all over the GCFR mountains and large forests occur in Tsitsikamma/Knysna area on the coastal plain. These forests are dominated by large tree species that occur in dense stands which create a canopy that covers no less than 70 %. These forests occur in areas that receive high rainfall. Geophytes comprise a very small part of the overall diversity of this vegetation type.

Due to the importance of the edaphic environment in determining the distribution of vegetation types, vegetation subtypes are defined from one another by the substrate they grow on (e.g., Limestone Fynbos).

2.1.3 Climate and vegetation change in the GCFR in the Stone Age

The unique GCFR geology and climate history have resulted in the evolution of the unique flora, which is unprecedented in its biodiversity when corrected for surface area (Cowling *et al.*, 2017). The climate of this region has been relatively stable since the Miocene (5 - 23 million years ago) in comparison to other regions across Africa (Carrión *et al.*, 2003). This climate stability is caused by the prevailing Agulhas current and frontal systems associated with it, which have resulted in a region that could have been a refuge for early humans (Carrión *et al.*, 2003).

Winter rainfall, which was central to the evolution of the GCFR flora, first originated in the region in the Mid Miocene (Linder, 2003, 2005; Sauquet *et al.*, 2009). The stability of winter rain in the western part of GCFR since then, gave rise to the higher diversity of geophytes in this region, where these lineages have had more time to speciate (Procheş, Cowling and Du Preez, 2005; Cowling *et al.*, 2017). Phylogenetic evidence suggests that the core Fynbos flora speciated during the Cretaceous (66 - 145 million years ago) (Verboom *et al.*, 2014). Due to the shifting border between the rainfall regimes in the southern Cape throughout the Cretaceous, the flora had less time to speciate in comparison to the West Coast, which resulted in lower diversity (Verboom *et al.*, 2014).

Phylogenetic studies show that since the Cretaceous, the flora has been relatively stable (Linder, 2005; Verboom *et al.*, 2014). This pattern of stability and speciation is reflected in the phylogeny of geophyte taxa specifically (Goldblatt, Savolainen and Porteous, 2002). Thus, the geophyte species, which were present during the critical timeframes during our species' evolution in the Pleistocene, would have been similar to today.

However, the density, seasonality and distribution of these species across the GCFR would have been impacted by shifting rainfall regimes, fluctuations in CO_2 concentrations (Faltein *et al.*, 2019) and sea-level fluctuation, which were common during the various glacial phases that occurred during the Pleistocene (Carr *et al.*, 2006; Compton, 2011). Many paleoenvironmental studies have attempted to describe and model the variation of climate and vegetation in the region by using multi-proxy data (Chase and Meadows, 2007; Cartwright, Parkington and Cowling, 2014; Quick *et al.*, 2015; Carr, Chase and Mackay, 2016; Esteban *et al.*, 2017; Braun *et al.*, 2018). These studies show that there were various severe glacial phases throughout the Pleistocene during which time conditions would have been colder and drier in Africa (Carr *et al.*, 2006; Quick *et al.*, 2016). Deciphering the impact these glacial phases would have had on vegetation distribution is difficult, as different proxies taken from different areas can show different signals.

At present, there is no consensus of the regional scale vegetational and climatic variation across the entire GCFR. Presenting a review of all the available results is beyond the scope of this thesis. However, recent climatic and vegetational reconstructions show that Fynbos vegetational elements have been present in the region throughout the Pleistocene, with periodic intrusion of summer rainfall and vegetational elements driving fluctuations (Verboom *et al.*, 2014; Braun *et al.*, 2019; Esteban *et al.*, 2019). This affirms that the border of the rainfall seasonality over the southern Cape would have likely varied in response to glacial phases throughout the Pleistocene (Braun *et al.*, 2019; Esteban *et al.*, 2019; Cowling *et al.*, 2020).

The climate of the Holocene was relatively more stable than that of the Pleistocene; although small shifts in climate have been identified (Braun *et al.*, 2018). Studies from both the south and west coast, which use multi-proxy data, show that 7 – 10 kya was a relatively humid period (Quick *et al.*, 2016; Zhao *et al.*, 2016), while the period from 3 – 7 kya seems to have been more arid across the region (Carr *et al.*, 2006; Quick *et al.*, 2016; Zhao *et al.*, 2016) and relatively more humid again in the last 3ka (Quick *et al.*, 2016; Zhao *et al.*, 2016). The predicted changes in vegetation dynamics in these areas varies from study to study based on the proxy data used and the area of sampling. What is clear from these studies is that climate change did not have the same effect on vegetation dynamics across the entire region, where the areas in the south coast might have experienced the highest degrees of change in the GCFR (Cowling *et al.*, 1999; Cartwright, Parkington and Cowling, 2014).

The floristic composition of the vegetation types sampled in this study almost certainly changed in response to climate forcing during the Pleistocene (Avery, 1987). Although the overall distribution of vegetation types likely did not change significantly because their distribution is controlled primarily by edaphic factors (Bergh *et al.*, 2014). In this thesis, the assumption is made that sampling a range of vegetative units will capture the variation that might have occurred under a much different climate. For these reasons, I believe the current patterns of geophyte abundance and diversity in these vegetation types are a reasonable analogue for those throughout the Stone Age.

2.1.4 Geophyte biology

Geophytes are defined as plants with an underground storage organ which fulfils a function as a water and energy reserve (Procheş, Cowling and Du Preez, 2005; Procheş *et al.*, 2006). Geophyte plants are adapted to survive unfavourable conditions by storing these resources in their USOs (Ruiters and McKenzie, 1994). Geophytism has evolved independently in various taxa, which has led to a wide variety of geophyte forms that exist today. In broad terms, there are four main categories of geophytes, depending on the part of the plant that is the USO. These are; Bulbs, Rhizomes, Tubers and Corms (see Figure 2.2) (Procheş *et al.*, 2006).

Bulbs are adapted leaves, which consist of layers, like an onion, where each layer resembles a leaf. Bulbs are perennial structures that continue to grow throughout the lifetime of the plant (Procheş, Cowling and Du Preez, 2005). Both rhizomes and tubers are adapted stems that are perennial structures which can keep growing throughout the lifetime of the plant (Meyer and Hellwig, 1997), while rhizomes are horizontally thickened roots and tubers are thickenings at the tip of roots. Corms are adapted stems and comprise a solid USO which regenerates annually (Procheş, Cowling and Du Preez, 2005).

Geophytes have evolved the ability to survive unfavourable conditions (seasonal drought) by altering their phenology by inducing senescence or dormancy (Fenner, 1998; Khodorova and Boitel-Conti, 2013). Phenology refers to the cyclical growth of plants or animals (Fenner, 1998; Duchoslav, 2009;

Koch *et al.*, 2009) and the phenology of plants is determined by many factors, chief amongst these being the climate within which they grow and the physiology of that plant (Duchoslav, 2009; Park, 2016).

For the majority of species the phenological cycle progresses as follows:

At the commencement of the rainy season, the dormant phase ends and the USO will produce a new shoot of growth, which will form leaves; this is the leafing phase. For all USOs except corms, this shoot will remain attached to the perennial USO and continue to produce and store water and energy resources in the USO. In the case of cormous species, this phase is different; the new shoot develops from the dormant corm (old corm) and at the base of this new shoot, a new corm will form (Lopez-Corcoles *et al.*, 2015). This new corm will grow as the shoot grows and the water and nutrients in the old corm will be utilised by the new corm and shoot growth; by this process, the old corm is subsumed by the new season’s growth (Lopez-Corcoles *et al.*, 2015). The old corm is reduced to a thin, disc-like structure that remains under the new seasonal growth so that a mature plant can have multiple discs below the new seasonal growth (see Figure 2.2). In a few cormous species, the old corm does not get subsumed and remains viable to grow by itself; these corms are referred to as Pseudocorms (Manning and Goldblatt, 2012) (see Figure 2.2). Following the leafing phase, most geophytes will produce a flower (although not every single year), seed, and soon after seeding go into the dormant phase (senescence).

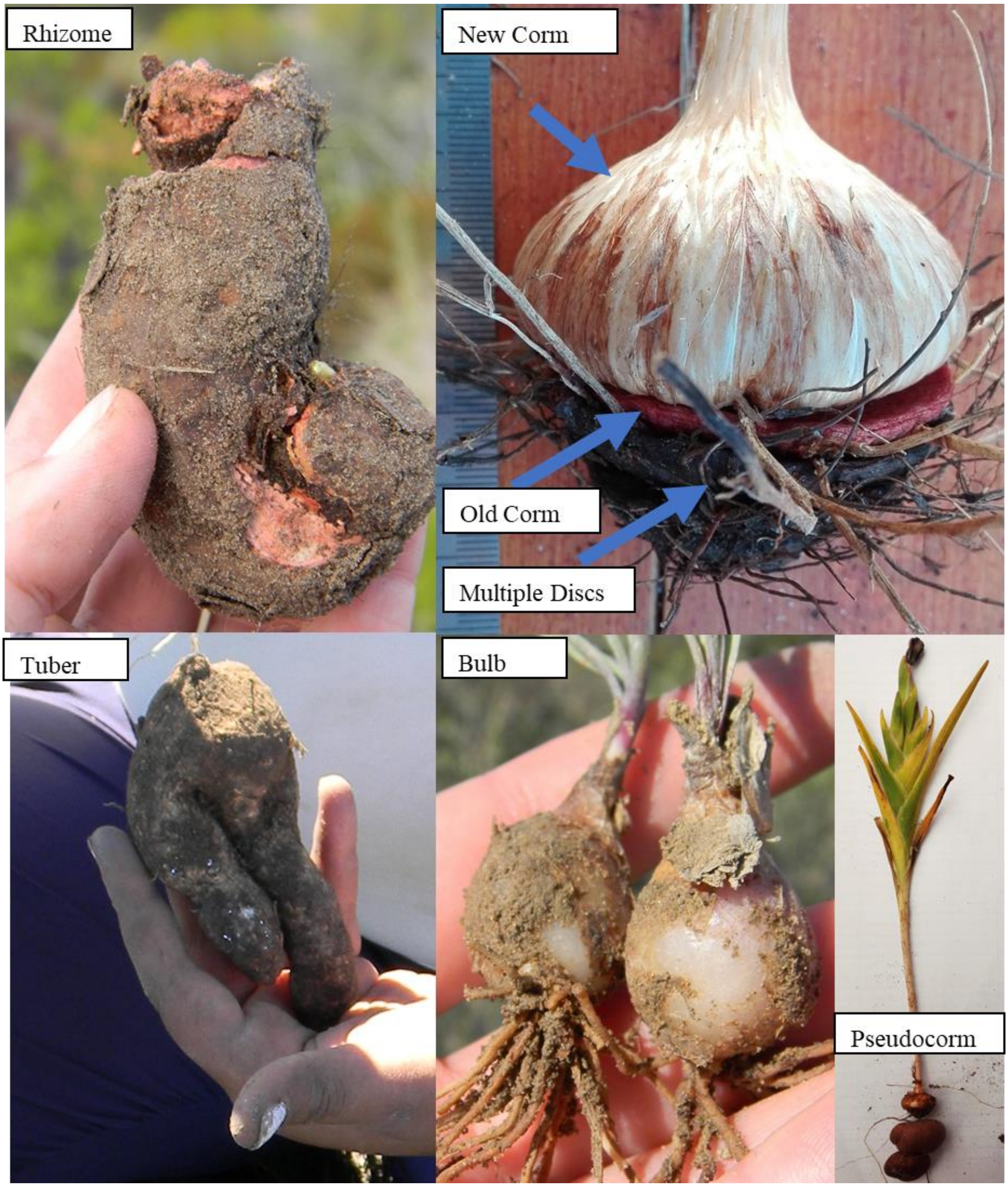

Figure 2.2 Underground storage organ types

The timing of the phenological cycle and the length of the various phases is determined by the predictability and amount of rainfall the plant is subjected to (Pierce, 1984). In the West Coast, the seasonal rainfall is low, yet predictable and in the South Coast and East Coast, there is considerable variation in rainfall seasonality and amount (Procheş *et al.*, 2006). The range of rainfall seasonality and predictability results in a peak in the geophyte phenology (when the largest amount of individual plants are flowering) between September and October in the West Coast, and extends from October to January in the East Coast (Johnson, 1992).

Some geophyte species have evolved another strategy which augments their phenological cycle to separate the time at which they produce leaves, and when they produce flowers, this is called hysteranthism (Marques and Draper, 2012). Hysteranthy is a strategy to optimise the resource allocation in different environments while avoiding competition for pollinators during the peak flowering season in spring (Procheş *et al.*, 2006). Synanthism is the normal state of geophytes, where geophytes produce leaves and flowers simultaneously (Dafni, Shmida and Avishai, 1981). Synanthous geophyte species comprise 69 % of the total geophyte species in the GCFR, while only 22 % are hysteranthous and a further 9 % are evergreen (Dafni *et al.*, 1981a). Evergreen species are restricted to areas where there is all year rainfall, such as the East Coast where evergreen geophytes in those regions can make up 20 % of the total geophyte species diversity (Dafni *et al.*, 1981a).

What effect would these cycles have had on hunter-gatherer subsistence?

Understanding the phenology and phenophases of geophytes is essential to understand how geophyte resources vary over time. Not only would these cycles determine when geophyte resources would have been available to foragers in the landscape, but these cycles could have determined the nutritional content and quality of USOs as carbohydrates and water reserves are built up throughout the growing period of the geophyte. Among hunter-gatherers across the world the cycling of nutrients caused by the phenology of geophytes influences hunter-gatherer behaviour directly (Vincent, 1985; Messner, 2011). Hunter-gatherers have been observed to understand these cycles intimately and strategically foraged these resources when USOs were at the peak of their nutritional quality (Messner, 2011). Additionally, understanding how different USO types grow and store energy throughout the phenological cycle would have affected the predictability of geophyte foraging. This is because there is low variation in USO weight between specimens of the same species which means that the size of USOs of cormous, tuberous and bulbous species is predictable based on species types (Procheş, Cowling and Du Preez, 2005). In rhizomatous species, however, USO weight can vary widely between specimens of the same species (Procheş, Cowling and Du Preez, 2005).

2.2 Human Evolution and Diet

Changes in diet have been hypothesised to have been one of the strong evolutionary drivers among hominids (Cerling *et al.*, 2011; Butterworth, Ellis and Wollstonecroft, 2016; Crittenden and Schnorr, 2017). A general trend of enlarged brain size, reduction in gut length, smaller jaws and teeth is observed and has been linked to an adaptive shift to the selection of a diverse range of high quality foods (Laden and Wrangham, 2005; Ungar, Grine and Teaford, 2006; Carmody and Wrangham, 2009a; Stahl *et al.*, 2014; Wrangham, 2017; Burini and Leonard, 2018). This improved dietary quality leads to improvements in cognition, which resulted in tool development and complex behaviour such as food processing, which increased the quality of foods even further (Milton, 1999; Wrangham *et al.*, 1999, 2009; Marshall and Wrangham, 2007).

The increase in behavioural complexity (tool production and control of fire) would have increased hominids ability to utilise a broader range of resources by rendering previously unavailable nutrients available (Butterworth, Ellis and Wollstonecroft, 2016). It has been argued that the use of fire by early hominids was one of the most significant technological advancements in human evolution as it enables the food niche available to expand greatly (Wrangham *et al.*, 1999; Carmody and Wrangham, 2009a; Wrangham, 2017). Cooking of food results in nonsomatic digestion (making food more digestible before ingestion) as it breaks down indigestible compounds into forms that are more bioavailable to the human gut for absorption and transforms food to a form which is easier to chew (Schnorr *et al.*, 2015; Wrangham, 2017). Protein, carbohydrates and lipids are the macronutrients contained in food which were the source of this high-quality nutrition; which types of foods are high in these energetically significant components?

Although amino acids (components of protein) are crucial for brain development (Speth and Spielmann, 1983; Carmody and Wrangham, 2009a; Tanaka *et al.*, 2009), a diet consisting of protein alone cannot sustain human metabolic function. This phenomenon has been observed among hunter-gatherer communities who starve when eating lean protein exclusively (Speth and Spielmann, 1983). This is because protein is a poor source of energy, as amino acids cannot be used in their unaltered state for energy production, but are essential in tissue building (Speth and Spielmann, 1983).

Hominins would have best fuelled their metabolic needs by food sources rich in energy which they could obtain either from lipids (fat) or carbohydrates (Speth and Spielmann, 1983; Milton, 1999). Most human organs, specifically the brain, require glucose (sugar) to meet the energy requirements of their metabolic function (Speth and Spielmann, 1983). While fat is the densest source of energy available to humans, lipids have to be transformed by the liver into a form that organs can use for metabolic function (Carmody and Wrangham, 2009b). Glucose (a type of carbohydrate) is readily dissolved in the bloodstream and used by organs and would have been vitally important for sustained brain development of early hominids (Milton, 2000).

A variety of USOs have been put forward as a likely high-quality food sources which could have fuelled the enlargement of our metabolically expensive brains, enabled the reduction of the gut, and with additional processing lead to the diminished size of our jaws and teeth (Hardy *et al.*, 2015; Butterworth, Ellis and Wollstonecroft, 2016; Wrangham, 2017).

2.2.1 Nutrition

Food that is consumed by humans has to cover the basal metabolic rate, metabolic response to food, the energy cost of physical activities and accretion of new tissue during growth and pregnancy (FAO, 2003). It is reasonable to estimate that a diet of 8000 – 8400 kJ is sufficient to support hunter-gatherer people of small stature and intense physical activity (Speth and Spielmann, 1983; Hurtado and Hill, 1989b; Lee, 1997). This estimated daily dietary requirement excludes the protein necessary for a balanced diet and normal metabolic functioning, which cannot be substituted by carbohydrates or lipids (Hurtado and Hill, 1989b; Lee, 1997).

The quality of food sources is impacted by the amount of energy contained in them, and the volume of food that consists of indigestible or even harmful substances. Fibre is one of these substances. Fibre is the portion of plant derived food that is indigestible in the human gut (Stahl, 1989). Fibre is made up of various compounds like non-starch polysaccharides, cellulose, lignin and hemicellulose (Uusiku *et al.*, 2010). Although fibre is promoted in our modern diets (due to a relative lack of fibre in our energy-dense diets), fibre would have lowered the quality of foods in hunter-gatherer diets (Milton, 1999). This is because the human gut is unable to digest fibre (Lambert, 1998; Milton, 2000b; Carmody and Wrangham, 2009a). Additionally, dietary fibre can affect the bioavailability of proteins and other minerals. Fibre may act as a complexing agent, reducing the bioavailability of minerals and can result in the lowered activity of pancreatic enzymes amylase and chymotrypsin (Stahl, 1989).

The most significant effect of fibre in human diets, however, is that it takes up volume in the gut that could have been available for the digestion of beneficial nutrients (Stahl, 1989; Milton, 2000b). Most types of fibre, especially the types common in USOs like lignin and hemicellulose, will increase the transit time of food through the gut and could diminish the complete absorption of nutrients (Stahl, 1989). Additionally, fibre could have hindered the sufficient absorption of minerals, vitamins and other macro-nutrients (Stahl, 1989). Finally, fibre makes foods harder to chew, as illustrated by the fracture strength of fibre-dense USOs (Dominy *et al.*, 2008), which makes fibre-dense food unpalatable to consume.

2.2.2 Human chemical ecology and antinutrients

Secondary metabolites are a by-product of a plants physiological processes that are harboured by the plant to deter herbivory (Waller and Nowacki, 1978; Johns, Harris and Hillman, 1989; Kaššák, 2012; Aniszewski, 2015). These compounds are diverse and can have a wide range of effects on human nutrition. Secondary metabolites can be extremely detrimental to mammal health and survival (Watt and Breyer-Brandwijk, 1932, 1962; Hawkes, 1989; Johns, Harris and Hillman, 1989).

Some secondary metabolites are overtly harmful to metabolic function and can cause organ failure, while others can reduce the absorption of other nutrients such as the example of fibre (anti-nutrients) (Mason, 1992). Tannins are one of the most common anti-nutrients found in plant foods (Mason, 1992) and these compounds can combine with protein, starch and digestive enzymes to form insoluble complexes which can reduce the digestibility of starch by 17 % (Stahl, 1989).

Humans have high sensory sensitivity to secondary metabolites and can sense them through smell, sight and especially taste, and most people are sensitive to the bitter tastes commonly produced by secondary metabolites (Johns, 1996, 1999). This sensitivity would have allowed humans to explore the edibility and other uses of various plants based on their chemical composition without incurring permanent harm to their health (Johns, 1996). Although secondary metabolites can impair nutrition, some have been shown to have medicinal properties (Messner, 2011), and are even used in modern medicine (Van Goietsenoven *et al.*, 2010). USOs can have high secondary metabolite content (McKey, 1979; Andersen and Anderson, 1987) and would reduce the quality of USOs or make them completely inedible/poisonous. It has however been observed that USOs with these compounds are consumed in higher frequency by extant hunter-gatherers during times when other foods are unavailable (Airaksinen *et al.*, 1986).

2.2.3 Modern humans and the GCFR

Recent genomic studies provide overwhelming evidence that the modern human lineage has an African origin (Ramachandran *et al.*, 2005; Ray *et al.*, 2005; Manica *et al.*, 2007; Blum and Jakobsson, 2011; Stoneking and Krause, 2011; Schlebusch *et al.*, 2012; Rito *et al.*, 2019). Most evidence points to our lineage emerging around 160 – 195 kya (Ingman *et al.*, 2000; Clark *et al.*, 2003; White *et al.*, 2003; McDougall, Brown and Fleagle, 2005; Reed and Tishkoff, 2006; Fagundes *et al.*, 2007; Tishkoff *et al.*, 2007; Behar *et al.*, 2008). The earliest archaeological evidence of anatomically modern humans is from sites in East Africa 150 – 190 kya (White *et al.*, 2003; McDougall, Brown and Fleagle, 2005; Tishkoff *et al.*, 2007).

The region in Africa where our species first evolved has been an issue of contention and speculations based on genetic, geographic, linguistic and archaeology suggests a northwest or East African origin

(Reed and Tishkoff, 2006; Stoneking and Krause, 2011). Recent genetic studies support the hypothesis that all modern humans originated from southern African hunter-gatherer communities (Henn *et al.*, 2011; Rito *et al.*, 2019). The deepest genetic divergence of contemporary humans is found between descendants of southern African hunter-gatherers and all other groups (Henn *et al.*, 2011; Stoneking and Krause, 2011; Schlebusch *et al.*, 2012). Recent genetic evidence suggests that humans migrated from southern Africa to eastern Africa and in this way gave rise to the early humans in those regions (Rito *et al.*, 2019).

Genetic data show that our species went through multiple genetic bottlenecks during the Pleistocene (Ambrose, 1998; Ramachandran *et al.*, 2005; Manica *et al.*, 2007; Stoneking and Krause, 2011). These bottlenecks might have been caused by climatic shifts during glacial periods when conditions in Africa were generally colder and drier (Partridge and Demenocal, 1997), which could have led to food scarcity (Petit *et al.*, 1999). The archaeological evidence from sites in the GCFR shows that humans were surviving in this region throughout these genetic bottlenecks and glacial phases (Singer, Wymer and Butzer, 1982; Henshilwood *et al.*, 2001; Marean, 2010). The earliest archaeological evidence of art (Henshilwood *et al.*, 2018), complex tool production (Brown *et al.*, 2012) and shellfish foraging (Marean *et al.*, 2007) have been found in the GCFR and has been interpreted as the possible site of origin of human modernity (Henshilwood and Marean, 2013; Marean *et al.*, 2014). Apart from the crucial archaeological evidence of human behaviour in the GCFR during genetic bottlenecks, the GCFR has the most continuous sequences of archaeological evidence throughout the Stone Age in Africa (Brown *et al.*, 2012; Lombard, 2012; McCall and Thomas, 2012; Marean *et al.*, 2014).

2.2.3.1 People of the GCFR

Who were the people who lived in the GCFR during the Stone Age, and what do we know about their subsistence?

At the time the first Europeans landed on the coast of the GCFR they noted that the first people of the GCFR were made up of various tribes, where their language and cultural practices defined every group's identity. The nomenclature used to describe the first people of South Africa has varied and has often been grounded in prejudice. According to the interpretation of the European colonists and later scholars the Stone Age people in this region consisted of two groups which had different subsistence practices; the pastoral Khoi-khoin and the hunter-gathering San (Van der Stel, 1932; Schapera *et al.*, 1933; Thom, 1952). The Khoi-khoin were referred to by early colonists as Hottentots (Schapera *et al.*, 1933), which is now known to be a derogatory term. Khoi-khoin is what some pastoralists in the region called themselves, meaning the real people (Schapera *et al.*, 1933). Hunter-gatherers were referred to as Bosjesman by the colonists (later Bushman), and the term San is used today to describe these people (Hitchcock, 2006).

Although these two groups are often presented as distinct groups due to the differences observed by the colonists among their lifeways, both have shared ancestry and descendants who exist in the South African demographic (Schlebusch *et al.*, 2012). These people are the most ancient surviving lineage of people on earth today, where their genetics diverged from other populations 100 kya (Gonder *et al.*, 2006; Schlebusch *et al.*, 2012). Skeletal remains from the GCFR in the MSA suggest that the people who inhabited the area throughout the Stone Age were anatomically similar to Khoi-khoin and San people (Pfeiffer and Sealy, 2006).

Although the shared ancestry of these groups is ancient, the archaeological evidence of the presence of Khoi-khoin cultures in the GCFR is more recent. Based on the dating of domesticated animal bones found at archaeological sites it seems that Khoi-khoin (or ancestors to the Khoi-khoin) entered the GCFR within the past 3000 years (Maingard, 1935; Smith *et al.*, 1991). The past 3000 years seems to have been a critical time frame within which geophyte foraging and is evident in the archaeological record (Deacon, 1976; Liengme, 1987).

With regards to the Khoi-khoin and San relationships to geophytes, both peoples were very reliant on these resources as a staple food source, and although Khoi-khoin people had livestock, they exhibited no typified agricultural practices surrounding plant foods (Schapera, 1930; Schapera *et al.*, 1933; Raven-Hart, 1967, 1971). They relied on the natural bounty of their environment for the vegetable portion of their diet, as did hunter-gatherers.

2.3 Ethnohistory of geophyte foraging in GCFR

To interpret botanical remains it is critical to study the available literature on the modern and historical behaviour of humans (ethnography, ethnobotany, historical accounts). We can glean valuable information from these sources to frame our interpretations and hypothesis about hunter-gatherer subsistence. This approach has been referred to as the Ethnographic Model (Hillman, 1989) and is commonly used in the field of Palaeoethnobotany (Harris and Hillman, 1989; Messner, 2011). The primary objective of this approach is not to represent hunter-gatherer behaviours (extinct or extant) as perfect analogues for past human behaviour, as every single situation is unique and no model could predict human choices perfectly. The intention of this approach is to showcase the diversity of strategies and choices humans have made regarding subsistence. This creates a framework of information, which can assist our interpretation of botanical remains.

In this section, I explore this approach by presenting the evidence of geophyte exploitation and role in subsistence among extinct and extant hunter-gatherers, to illustrate the strategies and behaviour that have developed to most efficiently utilise this resource. In later chapters, I will rely heavily on this framework to help interpret the results of analyses.

2.3.1 Ethnohistory and ethnobotany

In this section I have attempted to present relevant observations made of hunter-gatherer behaviour in the GCFR by European colonists and have searched these early traveller accounts for information about geophyte foraging and processing in the GCFR (Kolb, 1731; Sparrman and Forster, 1785; Thunberg, 1795; Burchell, 1822; Alexander, 1838; Livingstone, 1857; Dunn, 1873, 1931; Schultze, 1907; Bleek and Lloyd, 1911; Schapera, 1930; Schapera *et al.*, 1933; Vedder, 1938; Stow, 1964; Raven-Hart, 1967; Kannemeyer, 1992; Sponheimer *et al.*, 2005), and ethnobotanical surveys among extant hunter-gatherers across the world (Anderson, 1997; Eder, 1978; Hill *et al.*, 1987; Lee, 1969; Messner, 2011; O’Connell *et al.*, 1983; Tanaka, 1976; Vincent, 1985).

Almost every early traveller account refers to the staple vegetative food source of hunter-gatherers being an “underground nut” similar in size and taste to a chestnut (Sparrman and Forster, 1785; Thunberg, 1795; Thom, 1952; Stow, 1964; Raven-Hart, 1967, 1971; Skead, 2009), which was collected by women, eaten raw in some circumstance (if it was raining) (Skead, 2009), but most frequently roasted in embers, ground into flour (Raven-Hart, 1971) and even made into cakes and dried to enjoy later (Raven-Hart, 1967, 1971; Thunberg, 1986; Skead, 2009). This behaviour was observed throughout the colonisation of the Cape and was observed as early as 1616 through to the early 1900s (Raven-Hart, 1967, 1971). By this time very few hunter-gatherer communities remained who were able to roam across the landscape and most had succumbed to the colonists or illness, or been forced into servitude of the colonists as slaves (Raven-Hart, 1967, 1971; Skead, 2009).

The insights made during the time-frame of the 1600s to the 1900s are invaluable pieces of information to help us glimpse the possible ways in which hunter-gatherers utilised geophyte resources. The accounts predating the establishment of the refreshment station at Cape Town in 1652 hold extra weight as they were made at a time when the inevitable influence of colonists on hunter-gatherer behaviour was minimal, and the behaviour exhibited may have resembled the behaviours of hunter-gatherers in the Stone Age.

Although it is impossible to identify, to species level, every geophyte from accounts given by early traveller, some noteworthy expeditions were made by botanists and accompanied by very accurate descriptions of the characteristics of plants. These descriptions sometimes included paintings, etchings and drawings which were accompanied by accurate botanical descriptions of the plants (Sparrman and Forster, 1785; Thunberg, 1795; Evans *et al.*, 1969; Wilson, Van Hove and Van Rijssen, 2002; Skead, 2009). In this section, if a specific species is named, it is because an identification or synonym exists in the literature today that has been verified by modern botanists.

The cultural importance of geophytes in the lives of GCFR hunter-gatherers and the intricate knowledge that hunter-gatherers had about geophyte foraging is evident. In some accounts, detailed cultural fables/stories and songs were captured, which describe the intricacies of foraging and processing of certain geophytes, where their attributes, taste, growth pattern and cooking methods are central to the narrative (Bleek and Lloyd, 1911; Van Vuuren, 2013). Essential aspects of geophyte foraging to consider from these and other sources are the variety of species which were consumed, the effect seasonality has on geophyte foraging and subsistence pattern, the areas where foraging was focused (certain vegetation types or regions), the processes used to produce food from geophytes and the tools used during foraging and processing.

This framework of information can be used to interpret the archaeological record and hunter-gatherer subsistence patterns; although it will not predict past behaviour perfectly. Based on principles of foraging theory, archeologists have applied modeling options to reconstruct past human behaviour. (Marean *et al.*, 2015). Foraging theory underlies a field of research where foraging behaviour of animals (and humans) is predicted by a set of equations based on the assumption that foragers will maximise the net rate of return (of energy or nutrients) per unit of foraging time (Grayson and Cannon, 1999; Smith *et al.*, 1983). Optimal foraging models assume that caloric content of food sources is the primary incentive driving foraging decisions, but we know that there are many other factors which impact foraging choices, such as cultural norms or taste preferences (Pyke, 1984).

Major decision categories which impact the outcome of optimal foraging theory models include diet breadth (which and how many resource types are foraged), patch choice (which habitats are best for foraging and returns), time allocation (time spent foraging in different habitats or patches), foraging-group size and settlement location (Smith *et al.*, 1983). The equations presented for human foraging theory have been developed on the observed foraging behaviour and choices among extant hunter-gatherers (Hill *et al.*, 1987; Winterhalder *et al.*, 1988). Attempts have been made to recreate GCFR foraging behaviour with "Khoisan descendants" (Botha, 2019; De Vynck *et al.*, 2016; Singels *et al.*, 2016), where the assumption was that modern-day descendants of hunter-gatherer ancestors could function as a soft example of past hunter-gatherer behaviour, due to the vast amount of indigenous knowledge regarding edible plants which remains among these communities (De Vynck *et al.*, 2016). However, modern descendants of Khoi-khoin or San people's behaviour cannot be used as an analogue of Stone Age hunter-gatherer behaviour as these people, and their ancestors have been living modern lifestyles for centuries. The framework provided by optimal foraging theory was not used as the primary methodology in this thesis, however the categories of forager choice used in optimal foraging thoery models are still useful to understand possible hunter-gatherer behaviour where historical accounts do not accurately describe all geophyte foraging.

2.3.2 Dietary Diversity

The number of species or dietary diversity among extant San hunter-gatherers can be huge, with some groups foraging up to a hundred different plant species a year (Lee and DeVore, 1976; Tanaka, 1976). Species that contribute a significant portion of the diet and can be considered staples ranges from 10 to 23 species (Lee, 1969; Tanaka, 1976). This pattern is emulated in the archaeological record, where many sites with good preservation of botanical remains have a few dominant species which make up the bulk of botanical material (Deacon, 1976; Liengme, 1987; Hillman, 1989). In regions where both ethnobotanical surveys and archaeobotanical studies have been completed, the diversity of species identified in the archaeological record often outweigh the number of species which are observed to be foraged by modern communities (Messner, 2011; Botha *et al.*, 2019). This disparity begs the question: How can we access the species, which were foraged in the Stone Age without the presence of extant hunter-gatherers in the region?

The breadth of species available to include in a gatherer's diet would influence many aspects of the foraging activity. This is especially relevant when the diversity of edible geophytes is high, and the resources are not distributed evenly over the landscape (Singels *et al.*, 2016). Foraging theory states that when a gatherer encounters an edible geophyte, they have one of two options: to handle it (dig it out) or to search for another item of food (Hawkes and O'Connell, 1992; Smith *et al.*, 1983).

Geophyte species can be ranked in this theory by the nutritional returns and the predictability of the energy necessary to obtain USOs based on the likelihood that the species will be targeted when encountered during foraging (Hawkes and O'Connell, 1992; Smith *et al.*, 1983).

In reality, even if a species has high return rate on foraging, it does not necessarily mean it is foraged when encountered, examples of this are observed in many extant hunter-gatherer communities (Cane, 1984, 1989). Similarly, processing of geophytes could artificially increase the ranking of species (Carmody and Wrangham, 2009; Lambert, 1998), thus lower-ranked species can be targeted since humans are adapted for nonsomatic digestion (Milton, 1999). This behaviour would have increased the array of species which were available to a forager and could have decreased the time searching for geophytes as the chance of encountering one of the numerous lower-ranking species could be higher (Smith *et al.*, 1983). This adds another incentive for foragers to include an array of geophytes in their diet.

Unravelling precisely which species (out of more than 2000 geophyte species which occur in the GCFR) would have been targeted during foraging can result in misplaced specificity, and leads to a weak description of diet breadth (Grayson and Cannon, 1999). In Chapter 3, an attempt has been made to describe the diet breadth of geophytes that could have been included in Stone Age diets while trying to avoid the pitfalls of misplaced specificity. A ranking of geophyte species relative to one another is presented, in an attempt to address the diet breadth of geophytes that might have been included in hunter-gatherer diets. The ranking of species is based on ordinal level return-rate estimates based on the nutritional return possible (USO nutritional content and weight), how deep USOs grow below ground (an estimate of the effort to extract them) and an estimate of the level of processing that would have been required to render them palatable.

2.3.3 Patch Choice

In a megadiverse region such as the GCFR, where there is high turnover in the diversity of environment over the region, the areas foragers targeted for foraging could have significantly impacted their efficiency to obtain food. In such an environment, foraging theory predicts that "patch types" (areas with similar resources and density) are added to the foraging routine until the total time spent foraging is minimised (Smith *et al.*, 1983).

Geophyte resources would, of course, not have been the only consideration when targeting specific patches: protein resources were an additional critical consideration. In coastal environments, a high density of geophyte resources has been found in the GCFR, which is adjacent to shellfish resources (Singels *et al.*, 2016). Additionally, it has been argued that supplemental protein could have been supplied from territorial antelope (and other small game) that were caught in patches of dense geophytes (Deacon, 1993; Klein, 1981). It is logical that if one patch could satisfy all the dietary needs of a community for a while, most of the needed resources would be taken from this area to minimise inputs required to meet the dietary requirements of the group. Such patches, with the unique juxtaposition of a wide variety of resources, would have made a balanced diet easier to maintain.

Sedentary resources, such as geophytes, could have affected the mobility of hunter-gatherers and a pattern of moving to denser geophyte patches is not uncommon in extant hunter-gatherers (Hallam, 1996). For example, the Cuiwa of Venezuela will move closer to abundant patches of rhizomes during the dry season, as soon as they have exhausted nearby patches (Hurtado and Hill, 1987).

2.3.4 Seasonality

Plant foraging strategies are directly affected by seasonal changes (Tanaka, 1976). This is due to many factors, but the archaeological evidence suggests that the phenology of geophytes played a significant role in geophyte foraging (Parkington, 1977; Deacon, 1984). The /Xam San made a distinction between four seasons which determined the resource available from the veld based on the rainfall (Bleek and Lloyd, 1911). Among the Kung San, a ceremony was performed in early winter at the onset of the rainy season, where the head of the band would determine at which point the members of the tribe are permitted to forage for geophytes (Vedder, 1910). Observations of foraging of hunter-gatherers all over the world have shown that when resources are available, they are not necessarily targeted throughout the entire period they are available, but rather at a specific time when they are most easily obtainable and at their most nutritious or most palatable (Hallam, 1996). Among G/wi San in the Kalahari, rhizomes that are available throughout the year are only foraged during early summer when they are the main source of food (Silberbauer, 1972). Often it is noted that while new shoots of USOs are growing, the USOs are not harvested as it is thought this growth drains the USO of its nutrients (Hallam, 1996). Similar observation were made in the GCFR where certain geophytes were targeted after flowering by hunter-gatherers, as observed by colonists (Skead, 2009). Many geophytes were observed to have been foraged after flowering, when it was thought that the USOs were “most in order to eat” (Lichtenstein; 1930: 45).

The seasonal variation of geophyte resource availability and the effect of phenology on the nutritional quality of USOs are poorly understood in the GCFR, and very little information is available on the optimal time various geophyte species could have been targeted for foraging. In Chapter 4, an attempt has been made to address this lack of information by quantifying the effect seasonality has on the nutritional quality of USOs and the seasonal variation of the availability of this resource across the region.

2.3.5 Tools associated with geophyte foraging

Understanding the range of tools which were used for foraging, and processing of geophytes are critical to understanding the possible dynamics of geophyte foraging. The presence or absence of these tools in the archaeology can have been used as proxies of geophyte foraging and processing.

Digging sticks are the primary tools which would have been used during geophyte foraging, which consist of hardwood stick (approximately one meter in length), pointed and sharpened at one end. In areas with harder and rocky soil, the stick is often weighted with a bored stone (Skead, 2009) and sometimes tipped with buckhorn (Schapera, 1930; Dunn, 1931). The function of bored stones is presumably to act as a weight and was observed to have been used during geophyte foraging (Sparrman and Forster, 1785; Bell, 1876; Dunn, 1879; Bleek and Lloyd, 1911; Currlé and Péringuey, 1913), although this function has been disputed (Hromnik, 1984).

Bored stones are commonly portrayed in rock art (see Figure 2.3) (Lewis-Williams, 1987; Ouzman, 1997) and well represented in the archaeological record (Goodwin, 1929, 1947; Rudner, 1970; Mazel and Parkington, 1981); the oldest known examples are from Border Cave and date to 45ka (d’Errico *et al.*, 2012; Villa *et al.*, 2012). Significantly, the two bored stones from Border Cave were associated with other elements of modern San material culture, suggesting that the gathering of geophytes using these implements is ancient.

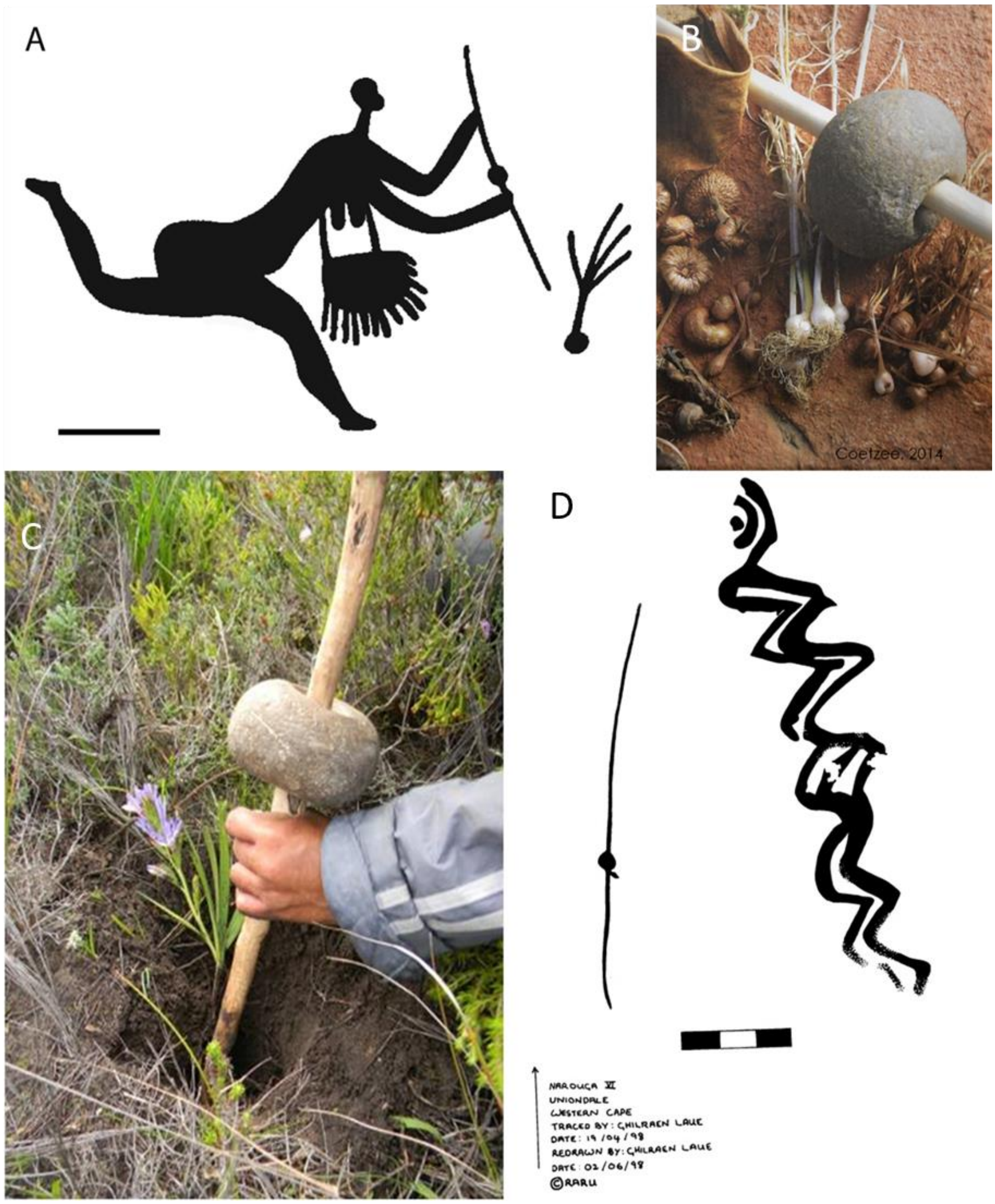

Figure 2.3 a) Rock art depicting a woman with a digging stick, mounted with bored stone and 'uintjiesakkie'. Adapted from Vinicombe,1976; Originally from the Mount Currie District, KwaZulu-Natal Scale bar = 30 mm. b) Digging stone and stick replica adapted from Coetzee, 2014. C) A replica digging stick produced for this thesis with iron wood branch (Olea capensis) and a digging stone loaned from the Stilbaai Archaeological Society. D) Traced image of rock art from Uniondale (adapted from Laue, 1999) showing a digging stick/bored stone complex, which clearly illustrates the digging stone, and a wooden peg which was used to affix the stone to the stick.

The cultural significance of the bored stone and digging stick seems evident from these various lines of evidence and the implements are sometimes charged with supernatural (Bleek and Lloyd, 1911; Deacon and Deacon, 1999) or symbolic properties (Ouzman, 1997; Lombard, 2002). Goodwin viewed bored stones as an archaeological signature of hunter-gatherer culture and therefore a tool for mapping Stone Age migrations (Goodwin, 1929). Another interpretation of the distribution of bored stones was that the variable soil conditions affect the availability and accessibility of plant foods, and therefore necessitate the use of a bored stone (Mazel and Parkington, 1981). Carrying a bored stone over a mean daily foraging distance of 8-10 km (Silberbaur, 1981; Lee, 1997) was not trivial; the average weight of bored stones is 1.45 kg (Goodwin, 1929). Thus, manufacturing and carrying a bored stone during foraging forays must have increased the net energetic cost of foraging. This cost would not have been expended if a substantial mechanical advantage did not offset it during digging, perhaps especially when soils are hard.

Digging sticks would have required regular sharpening, and the possible tool used for this is called an adze and has been suggested as a proxy of geophyte foraging in the archaeology (Mazel and Parkington, 1981), although this tool could have been used to work many wooden tools not associated with geophytes (see Figure 2.4). Wood shavings are often found in association with this tool.

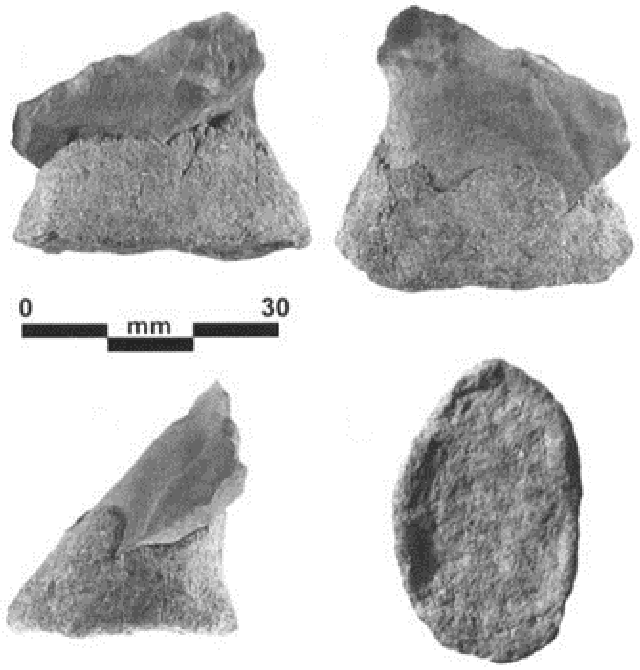

Figure 2.4 Adze with mastic, which would have been used to mount the adze to a wooden implement. Image reproduced from Jerardino, 1996

Processing implements

Certain artefacts found in the archaeology are associated with plant food processing specifically, namely grinding stones and pottery.

Grinding stones are used to grind various items, such as ochre, seeds, and USOs (Messner, 2011) and in the America’s USOs are ground with grinding stones by extant hunter-gatherers (Hillman, 1989; Messner, 2011). The residues left on grinding stones in the archaeology, has been identified as starch grains from geophytes (Hillman, 1989; Messner, 2011; Thoms *et al.*, 2014).

In the GCFR grinding stones have been suggested as a proxy of geophyte foraging (Mazel and Parkington, 1981). Although the importance of the association between grinding stones and geophyte processing has been challenged recently, as these implements had multiple functions (Eoin, 2016)

Pottery is a common feature in the archaeological record in the GCFR (Rudner, 1970). Pottery is most commonly found in association with the remains of domesticated animals, which were

Figure 2.5 Khoe-Khoen women holding a clay pot in one hand and 'uintjies'and digging stick in the other. Adapted from Raven-Hart,1971.

introduced to the GCFR in the past 2000 years (Rudner, 1970; Deacon, 1976, 1982). There are numerous historical accounts of clay pots being used for cooking of USOs in the GCFR (Kolb, 1731; Burchell, 1822; Alexander, 1838; Dunn, 1931; Schapera *et al.*, 1933; Stow, 1964; Raven-Hart, 1971). In one case an illustration even depicts women with 'Uintjies' in one hand and a pot in the other (Figure 2.5) (Raven-Hart, 1971).

2.3.6 Processing

Among extant hunter-gatherers, plant foods are often categorised as Sweet (Edible), Unpalatable (Bitter/Acrid) or Toxic (Jones and Meehan, 1989). By processing unpalatable or toxic USOs, early modern humans would have been able to extend the range of plant foods in their diets (Harris and Hillman, 1989; Carmody and Wrangham, 2009a). The nutritional quality of processed food can be significantly increased (Butterworth, Ellis and Wollstonecroft, 2016), while the harmful or unpalatable substances contained in the USOs are neutralised or removed (Stahl, 1989).

Although the niche expansion of humans would have been an active driver for the development of processing techniques, a survey of food processing among extant hunter-gatherers showed that processing was done for one of the following reasons (Johns and Kubo, 1988):

1. To modify otherwise inedible/toxic food into forms that are not only safe but easily chewed and digested;

2. To transform a single food source into many forms/tastes;

3. To make ingredients go further by processing them into a form that can be mixed and added with other ingredients;

4. To transform foods into a state that will preserve better.

Extensive processing can be required to render some USOs edible (Hawkes, 1989; Johns, Harris and Hillman, 1989; Butterworth, Ellis and Wollstonecroft, 2016). The following techniques would have a had a massive impact on the quality and variety of plant foods that could be exploited; cooking, pounding or grinding, leaching and fermentation (Harris and Hillman, 1989).

The effect processing could have had on the nutrition of GCFR hunter-gatherers is poorly understood. In the following section, I will describe the processing techniques that have been identified in ethnobotanical surveys of extant hunter-gatherers and the observations of processing methods that have been observed in the GCFR. In Chapter 6, I will present results on the effects of some of these Stone Age processing techniques on the nutritional quality of geophytes.

Grinding/Pounding

The purpose of grinding and pounding is to either remove undesirable component like fibre, or to alter the physical shape of the item (Stahl, 1989). Grinding will decrease the particle size making more nutrient available to be digested, or make detoxification methods more effective (Stahl, 1989). In some cases, the cell rupture that results from grinding is enough to expose harmful secondary metabolites contained in plants to oxidation, which renders them harmless and safe to consume (Stahl, 1989).

Another function of grinding as a processing method is to transform food into a form and state that can be stored, where "cakes" are formed from the flour produced by grinding and stored (Messner, 2011). In the GCFR this time-consuming processing method was performed on various geophytes and produced into a "cake/bread". The vernacular name of species which were targeted using this processing method is often called, 'Hottentot Brood' (Khoi-khoin Bread), notable examples are *Dioscorea elephantipes*, *Watsonia* spp., *Fockea* spp., *Grielum grandiflorum* (Schapera, 1930; Stow, 1964; Raven-Hart, 1967; Skead, 2009). The processing is described as follows: The USOs are roasted in embers, after which they are dried in the sun and then ground into a flour or paste (Schapera, 1930; Raven-Hart, 1967). In some cases, this flour was formed into a cake/bread which was then baked in embers and eaten immediately or stored for later (Stow, 1964; Raven-Hart, 1971; Skead, 2009) or the flour was mixed in with water to produce a porridge (Kolb, 1731; Stow, 1964). The flavour of this bread and porridge was compared to oatmeal by the early colonists in Cape Town (Skead, 2009).

Soaking/Leaching

Soaking and leaching might be employed as a processing technique for various effects, such as softening tissue, precipitating starch, to enable fermentation or detoxification (Stahl, 1989). Soaking is most effective in ridding food of indigestible compounds such as tannins or other toxic compounds and is a standard method of processing among extant hunter-gatherer communities (Chavan *et al.*, 1979; Stahl, 1989; Mason, 1992; Messner, 2011). It has been found that a soak of plant material in freshwater for 24 hours can remove more than a third of the tannin content (Chavan *et al.*, 1979; Zia-Ur-Rehman and Shah, 2001). The addition of other ingredients like salt, lime, ash or other chemicals that alter the alkalinity of the solution can facilitate detoxification even further (Khokhar and Chauhan, 1986) and even increase the nutrient content (Bressani and Scrimshaw, 1958). In some cases leaching might decrease the overall nutrient content by leaching out soluble nutrient, but these losses should be viewed holistically, by considering the decrease of harmful/unpalatable substances in relation to the addition of nutrients that other sources might bring (Stahl, 1989).

In the GCFR similar leaching techniques were observed by early travellers with two notable species being mentioned repeatedly (Sparrman and Forster, 1785; Thunberg, 1795; Coetzee, 2015): Wild Almond (*Brabejum stellatifolium*) and Varkblom (*Zantedeschia aethiopica*). The fruit of *Brabejum stellatifolium* was rid of its toxic compound (Cyanide) by steeping the nut in water. Following this leaching, the nuts were further processed by boiling and ground into flour (Thunberg, 1795). Similarly, the tuber of *Zantedischia aethiopica* was described as having a pungent taste that burns and cuts the tongue physically (Schapera *et al.*, 1933). These are attributes given by the secondary metabolites and crystals within this genus: oxalic acid, which physically cut the mouth and gut, causing severe irritation (Watt and Breyer-Brandwijk, 1932; Coetzee, 2015). The process by which these attributes were neutralised is described as follows: leaching of sliced USOs sometimes lasting three days, followed by cooking, which made the rhizome safe to eat (Kolb, 1731; Coetzee, 2015).

Fermentation

The base process which occurs during any fermentation is the chemical reduction of complex organic substances which can make complex molecules into a state that are more bioavailable for absorption by the human gut (Stahl, 1989; Butterworth, Ellis and Wollstonecroft, 2016; Di Stefano *et al.*, 2017). The processing of food by fermentation can lead to the improved shelf life of foods, improved palatability, detoxification and degradation of fibre (Stahl, 1989). Ionic bonding is often the primary measure by which tannins can be removed using this method (using ash or charcoal) which alters the pH of an organic compound and rendering the tannins soluble (Anderson, 2005; Etkin, 2008). Ash and clay have been known to be used to remove other secondary metabolites (Johns, 1996; Hart, 2004). Fermentation of honey was reported by almost every early colonist travelling in the GCFR, but none mention the fermentation of foods to remove anti-nutrients or toxins (Sparrman and Forster, 1785; Thunberg, 1795; Stow, 1964; Skead, 2009).

Heat Treatment/Cooking

The cooking of USOs can reduce the impact of certain toxins by destroying them (Stahl, 1989; Butterworth, Ellis and Wollstonecroft, 2016) and makes complex carbohydrates easily digestible in the human gut as mentioned in previous sections (Pennisi, 1999; Carmody and Wrangham, 2009b; Butterworth, Ellis and Wollstonecroft, 2016).

In the GCFR cooking was the most common method of processing of USOs which was observed (Kolb, 1731; Thunberg, 1795; Stow, 1964; Raven-Hart, 1967, 1971; Skead, 2009). In most cases, USOs were roasted in embers or boiled in pots (Kolb, 1731; Thunberg, 1795; Stow, 1964). In some cases, a complex earth oven was made by digging a hole in the earth, which was filled with a stone layer, and fire made on this stone layer. When coals formed, and the rocks were heated thoroughly, USOs were placed on the stones, topped with a fresh layer of stones, a fresh fire started above this and left to burn out. The USOs were then unearthed after the stones had cooled and eaten (Stow, 1964; Coetzee, 2015).

2.4 Economically important geophyte species of the GCFR

One of the important contributions of this thesis is to present a survey of the geophyte species in the GCFR to distinguish between those that might have been an important food source, used medicinally or in other ways economically important to Stone Age hunter-gatherers, whilst clearly distinguishing between dangerously toxic species and other species which might have been rendered edible by way of processing. There has been no such attempt made which takes archaeology, early traveller accounts, recent ethnobotanical surveys, nutritional data and pharmacological surveys into consideration. This information is presented in the table below (Table 2.1).

The geophyte species are defined, by listing their uses and processing, their edibility and when available their phytochemical composition. The economic importance of species is listed by defining how the species was used. Some species were foraged as food and the processing methods that were applied after harvesting are noted. Species that were important in hunter-gatherer subsistence other than a food source (medicine, glue source, poison source) are also noted.

I used 26 key references to compile this table (listed in Table 2.2). Historical accounts written by European colonists and travellers to the Cape, although written from the perspective of these colonists, are a particularly rich source of information on economically important geophyte species and how they were foraged and used by hunter-gatherers (Kolb, 1731; Sparrman and Forster, 1785; Thunberg, 1795; Barrow, 1801; Burchell, 1822; Bowie, 1830; Backhouse and Backhouse, 1844; Dragendorff, 1898; Schultze, 1907; Marloth, 1915; Schapera, 1930; Lichtenstein, 1930; Dunn, 1931; Van der Stel, 1932; Thom, 1952; Stow, 1964; Wilson, Van Hove and Van Rijssen, 2002; Skead, 2009; Coetzee, 2015). Modern ethno-botanical studies of species that remain important to extant hunter-gatherer subsistence and archaeological evidence of geophyte use were also a rich source of information of economically important geophyte species from the GCFR (Deacon, 1976; Parkington, 1977; Norwood Young and Fox, 1982; Liengme, 1987; Van Wyk and Gericke, 2000; Van Wyk, Van Heerden and Van Oudtshoorn, 2002). Lastly, information on the toxicity of geophyte species was sourced from the extensive review of pharmacology of South African plants, which determined the lethal doses of many geophyte species (Watt and Breyer-Brandwijk, 1932, 1962). The information collected from these references was later used to assess the edibility of geophyte species which were sampled during the field work for this study. Classification of species is according to Manning and Goldblatt, 2012.

The geophyte species which might have been important in hunter-gatherer subsistence are categorised as dietic (edible and contributing to diet), medicinal or other uses (Poison for arrows or glue for tool production). The lines between these uses can be very blurry as there was often no distinction made historically between food and medicine among hunter-gatherers in the GCFR (Thunberg, 1795). In this thesis the distinction between medicine and food is however critical, as some of the geophytes that are considered as medicinal are highly toxic, and the medicinal action is heavily reliant on the dose taken.

During the pharmacological experiments conducted by Watt and Breyer-Brandwijk, 1932, 1962, toxic compounds were identified in many medicinal species, rendering them lethal in high enough doses. In some cases a species might be proven to be toxic in its raw form, but we know that hunter-gatherer consumed those species after a lengthy processing methods which made the USO safe for consumption (Skead, 2009). These contradictions have been noted in Table 2.1.

As mentioned in this chapter, secondary metabolites in plants evolved to deter herbivory, these compounds often have a bitter taste, some of which can have beneficial effects in a low dose (medicinal effects), but in large quantities are described as either anti-nutrients (hindering absorption of other nutrients) or as toxic (cause organ failure and death) (Fekadu Gemede, 2014). Geophytes identified in Table 2.1 have been classified according to the compounds they contain as either non-toxic, toxic or bitter, depending on the phytochemical composition, similar to the methods employed in the surveys of geophytes in other studies (Bhandari and Kawabata, 2005; Poornima and RavishankarRai, 2009).

Some geophytes species were used for their medicinal properties exclusively and did not serve a dietic function, in this thesis this line is drawn between whether the species made any calorific contribution to the diet or not. The genus *Arctopus* is an excellent example of this (Skead, 2009), it is noted that a decoction is made from the exudate that is harvested from the root (Thunberg, 1795), *Kedrostis africana* was used in a similar way (Thunberg, 1795). These species contain high concentrations of unpalatable and toxic compounds however (Watt and Breyer-Brandwijk, 1962) and could not have contributed a significant amount of calories to stone age diets as that would have been lethal.

Table 2.1 Economically important geophyte species of the GCFR (see reference list in Table 2.2.)

Growth Form	**Family**	**Species**	**Phytochemical Category**	**Specific Phytochemical Profile**	**Edibility**	**Use**	**Reference**
Bulb	Hyacinthaceae	*Albuca* genus	Non-toxic		Edible	USO eaten as thirst quencher	18, 20, 21
Bulb	Hyacinthaceae	*Albuca maxima*	Non-toxic		Edible	USO eaten as thirst quencher	20, 21, 25, 26
Bulb	Alliaceae	*Allium dregeanum*	Acrid		Edible	USO eaten cooked	4
Corm	Colchicaceae	*Androcymbium eucomoides*	Toxic	Alkaloids	Inedible	Poisonous	25
Root	Apiaceae	*Annesorhiza macrocarpa*	Acrid		Edible	Root eaten cooked	10, 21
Root	Apiaceae	*Annesorhiza nuda*	Acrid		Edible	Root eaten cooked	5, 18, 21
Bulb	Amaryllidaceae	*Amaryllis belladonna*	Toxic	Alkaloids	Inedible	Medicinal	25
Rhizome	Aponogetonaceae	*Aponogeton distachya*	Non-toxic		Edible	USO eaten raw or cooked	2, 4
Root	Apiaceae	*Arctopus echinatus*	Acrid	Glycosides	Inedible	Medicinal	21
Corm	Iridaceae	*Babiana* genus	Non-toxic		Edible	Eaten as staple and found in various archaeological sites	11, 21
Corm	Iridaceae	*Babiana hirsuta*	Non-toxic		Edible	Found in archaeological site	11
Corm	Iridaceae	*Babiana hypogea*	Non-toxic		Edible	USO eaten raw or cooked	4
Corm	Iridaceae	*Babiana fragrans*	Non-toxic		Edible	USO eaten raw or cooked	7, 18
Corm	Iridaceae	*Babiana stricta*	Non-toxic		Edible	USO eaten raw or cooked	20
Corm	Iridaceae	*Babiana tubulosa*	Non-toxic		Edible	USO eaten raw or cooked	22, 26
Bulb	Amaryllidaceae	*Boophane disticha*	Toxic	Alkaloids	Inedible	Poison for arrows, used medicinally and as a wound dressing. Found in various archaeological sites	2, 10, 11, 21, 25
Bulb	Amaryllidaceae	*Boophane haemanthoides*	Toxic	Alkaloids	Inedible	Poison for arrows, used medicinally and as a wound dressing. Found in various archaeological sites	2, 10, 21, 25
Bulb	Amaryllidaceae	*Brunsvigia orientalis*	Toxic		Inedible	Poison arrows, Used medicinally	25
Bulb	Amaryllidaceae	*Brunsvigia* spp.	Toxic	Alkaloids	Inedible	Poison arrows, Used medicinally	2, 25
Corm	Iridaceae	*Chasmanthe* genus	Unknown		Unknown	Although the species has been identified in an archaeological site, the edibility of the species is not known. Extensive processing might render it edible	11
Root	Apiaceae	*Chamarea capensis*	Unknown		Edible	Root eaten cooked	5
Root	Aizoaceae	*Conicosia* spp.	Unknown		Edible	USO eaten as thirst quencher	18

Growth Form	**Family**	**Species**	**Phytochemical Category**	**Specific Phytochemical Profile**	**Edibility**	**Use**	**Reference**
Corm	Tecophilaeaceae	*Cyanella* spp.	Non-toxic		Edible	USO eaten raw or cooked	4, 5, 11, 21
Corm	Tecophilaeaceae	*Cyanella hyacinthoides*	Non-toxic		Edible	USO eaten raw or cooked	26
Corm	Tecophilaeaceae	*Cyanella lutea*	Non-toxic		Edible	USO eaten raw or cooked	25, 26
COrm	Tecophilaeaceae	*Cyanella orchidiformis*	Non-toxic		Edible	USO eaten raw or cooked	25, 26
Corm	Cyperaceae	*Cyperus genus*	Non-toxic		Edible	USO eaten raw or cooked	4, 5, 15, 25
Corm	Cyperaceae	*Cyperus esculentus*	Non-toxic		Edible	USO eaten raw or cooked	5, 25
Root	Cyperaceae	*Cyperus textillis*	Unknown		Inedible	Used for weaving	1, 4, 6, 17, 21
Corm	Cyperaceae	*Cyperus usitatus*	Non-toxic		Edible	USO eaten raw or cooked	4, 6, 15, 25
Tuber	Lobeliaceae	*Cyphia* genus	Non-toxic		Edible	USO eaten as thirst quencher	25, 26
Tuber	Lobeliaceae	*Cyphia digitata*	Non-toxic		Edible	USO eaten as thirst quencher	18, 25, 26
Tuber	Lobeliaceae	*Cyphia volubilis*	Non-toxic		Edible	USO eaten as thirst quencher	25, 26
Caudis	Dioscoreaceae	*Dioscorea elephantipes*	Acrid	Alkaloids, Tannin, Organic Acid	Edible	Called 'hottentotsbrood', it was eaten as staple after extensive processing: roasting, grinding into flour and forming into cake/bread	6, 8, 11, 14, 25
Bulb	Hyacinthaceae	*Dipcadi viride*	Non-toxic		Edible	USO eaten cooked	25
Bulb	Hyacinthaceae	*Drimia capensis*	Toxic	Alkaloids	Inedible	Medicinal	23, 24, 25
Tuber	Convallariaceae	*Eriospermum capense*	Acrid		Edible	Medicinal	16
Tuber	Ruscaceae	*Eriospermum* genus	Acrid		Edible	Some species are used in medicine, some instances the tuber is eaten, in other instances it has been proven to contain toxic alkaloids, but not identified to specific species in the GCFR	25
Tuber	Ruscaceae	*Eriospermum parvifolium*	Acrid		Edible	USO eaten as thirst quencher	25
Tuber	Ruscaceae	*Eriospermum pubescens*	Acrid		Edible	Medicinal	25
Corm	Iridaceae	*Ferraria* genus	Acrid		Edible	Although the species of this genus contain toxic compounds, they are known to be edible after processing	20, 25
Tuber	Apocynaceae	*Fockea* genus	Non-toxic		Edible	USO eaten raw or cooked. Extensive processing when cooked: ground to flower and made into cake. Thirst quenching when eaten raw	4, 8, 17, 21, 25, 26

Growth Form	**Family**	**Species**	**Phytochemical Category**	**Specific Phytochemical Profile**	**Edibility**	**Use**	**Reference**
Tuber	Apocynaceae	*Fockea angustifolia*	Non-toxic		Edible	USO eaten raw or cooked. Extensive processing when cooked: ground to flower and made into cake. Thirst quenching when eaten raw	4, 8, 17, 21, 25, 26
Tuber	Apocynaceae	*Fockea comaru*	Non-toxic		Edible	USO eaten raw or cooked. Extensive processing when cooked: ground to flower and made into cake. Thirst quenching when eaten raw	4, 8, 17, 21, 25, 26
Corm	Iridaceae	*Freesia corymbosa*	Non-toxic		Edible	USO eaten raw or cooked	6
Corm	Iridaceae	*Freesia viridis*	Non-toxic		Edible	USO eaten raw or cooked	26
Bulb	Amaryllidaceae	*Gethyllis afra*	Non-toxic		Edible	Seed pod eaten	5, 21
Corm	Iridaceae	*Gladiolus* genus	Non-toxic		Edible	USOs eaten raw or cooked. Identified in various archaeological sites	11
Corm	Iridaceae	*Gladiolus caryophyllaceus*	Non-toxic		Edible	USO eaten raw or cooked	26
Corm	Iridaceae	*Gladiolus permeabilis*	Non-toxic		Edible	USO eaten raw or cooked	4, 8
Root	Neuradaceae	*Grielum humifusum*	Non-toxic		Edible	Root eaten raw as thirst quencher	5
Bulb	Amaryllidaceae	*Haemanthus* genus	Toxic	Alkaloids, Organic Acid	Inedible	Medicinal	21, 24, 25
Bulb	Amaryllidaceae	*Haemanthus coccineus*	Toxic	Alkaloids, Organic Acid	Inedible	Medicinal	21, 24, 25
Root	Hypoxidaceae	*Hypoxis argentea*	Acrid		Edible	Scarcity food, corms dried and ground into flour	6, 25
Root	Hypoxidaceae	*Hypoxis villosa*	Acrid	Sapoginins, Organic Acid	Edible	Used medicinally, and as scarcity food	6, 25
Corm	Iridaceae	*Ixia* genus	Non-toxic		Edible	USO eaten raw or cooked	10, 17, 19
Tuber	Cucurbitaceae	*Kedrostis africana*	Toxic	Carbon bisulphide	Inedible	Medicinal, Poisonous	21
Bulb	Hyacinthaceae	*Lachenalia tricolor*	Non-toxic		Edible	Non-toxic	25
Corm	Iridaceae	*Lapeirosia jacquinii*	Non-toxic		Edible	USO eaten raw or cooked	26
Corm	Iridaceae	*Lapeirousia pyramidalis*	Acrid		Edible	Identified in archaeological sites	13, 25
Bulb	Hyacinthaceae	*Ledebouria* genus	Unknown		Edible	Identified in archaeological sites	11
Bulb	Hyacinthaceae	*Massonia bifolia*	Unknown		Edible	Eaten raw or cooked in stew	5
Corm	Iridaceae	*Moraea flaccida*	Toxic	Alkaloids	Inedible	Poisonous	24, 25

Growth Form	Family	Species	Phytochemical Category	Specific Phytochemical Profile	Edibility	Use	Reference
Corm	Iridaceae	*Moraea miniata*	Toxic	Alkaloids	Inedible	Poisonous	25
Corm	Iridaceae	*Moraea fugax*	Non-toxic		Edible	USO eaten raw or cooked	2, 9, 11, 17, 21,
Corm	Iridaceae	*Moraea polyanthos*	Toxic	Alkaloids	Inedible	Poisonous	25
Corm	Iridaceae	*Moraea polystachya*	Toxic	Glycosides	Inedible	Poisonous	25
Corm	Iridaceae	*Moraea setifolia*	Non-toxic		Edible	USO eaten raw or cooked	25
Bulb	Amaryllidaceae	*Nerine* genus	Toxic	Alkaloids	Inedible	Poisonous	25
Rhizome	Nymphaeaceae	*Nymphaea nouchali*	Unknown		Edible	USO eaten cooked	1
Rhizome	Menyanthaceae	*Nymphoides indica*	Unknown		Edible	USO eaten cooked	1
Bulb	Hyacinthaceae	*Ornithogalum* genus	Toxic	Alkaloids	Inedible	All species in this genus are highly toxic	25
Corm	Colchicaceae	*Ornithoglossum* genus	Toxic	Glycosides	Inedible	All species in this genus are highly toxic	25
Corm	Oxalidaceae	*Oxalis* genus	Acrid	Oxalic acid	Edible	Leaves and inflorescence eaten as source of vitamin C and thirst quencher. Corms eaten raw and cooked. Identified in various archaeological sites	5, 11
Corm	Oxalidaceae	*Oxalis capiosa*	Acrid	Oxalic acid	Edible	Leaves and inflorescence eaten as source of vitamin C and thirst quencher. Corms eaten raw and cooked. Identified in various archaeological sites	12
Corm	Oxalidaceae	*Oxalis flava*	Acrid	Oxalic acid	Edible	USO eaten raw or cooked	25
Corm	Oxalidaceae	*Oxalis incanata*	Acrid	Oxalic acid	Edible	USO eaten raw or cooked	12
Corm	Oxalidaceae	*Oxalis imbricata*	Acrid	Oxalic acid	Edible	Corms found in various archaeological sites	6
Corm	Oxalidaceae	*Oxalis lavida*	Acrid	Oxalic acid	Edible	USO eaten raw or cooked	12
Corm	Oxalidaceae	*Oxalis lawsonii*	Acrid	Oxalic acid	Edible	Leaves and inflorescence eaten as source of vitamin C and thirst quencher. Corms eaten raw and cooked. Identified in various archaeological sites	25
Corm	Oxalidaceae	*Oxalis pes-caprae*	Acrid	Oxalic acid	Edible	USO eaten raw or cooked	7, 12, 25
Corm	Oxalidaceae	*Oxalis purparata*	Acrid	Oxalic acid	Edible	Leaves and inflorescence eaten as source of vitamin C and thirst quencher. Corms eaten raw and cooked. Identified in various archaeological sites	25
Growth Form	**Family**	**Species**	**Phytochemical Category**	**Specific Phytochemical Profile**	**Edibility**	**Use**	**Reference**

Rhizome	Geraniaceae	*Pelargonium genus*	Unknown		Edible	USO eaten and used medicinally. Identified in various archaeological sites.	3, 11, 21, 25, 26
Rhizome	Geraniaceae	*Pelargonium carnosum*	Unknown		Edible	Root eaten cooked	26
Rhizome	Geraniaceae	*Pelargonium incrassatum*	Unknown		Edible	Root eaten cooked	5, 26
Rhizome	Geraniaceae	*Pelargonium rapaceum*	Unknown		Edible	Root eaten cooked	5
Rhizome		*Perlargonium triste*	Acrid		Edible	Medicinal and Edible, although described as acrid	7, 8, 21, 25
Root	Apiaceae	*Peucedanum* spp.	Unknown		Edible	Root eaten	18, 21
Tuber	Vitaceae	*Rhoicissus digitata*	Toxic		Inedible	Poisonous	25
Corm	Iridaceae	*Romulea* genus	Non-toxic		Edible	USO and seed capsule eaten. Found in the archaeological record	11
Corm	Iridaceae	*Romulea macowani*	Non-toxic		Edible	USO eaten raw	25
Corm	Iridaceae	*Romulea rosea*	Non-toxic		Edible	Seed capsule eaten	5
Tuber	Polygonaceae	*Rumex* genus	Acrid	Oxalic acid, tannin	Inedible	USO used medicinally and for tanning, but can cause poisoning	25
Tuber	Orchidaceae	*Satyrium bicorne*	Non-toxic		Edible	USO eaten and contain sweet mucilaginous and nutritious juice	8, 25
Tuber	Orchidaceae	*Satyrium candidum*	Non-toxic		Edible	USO eaten and contain sweet mucilaginous and nutritious juice	8, 25
Tuber	Orchidaceae	*Satyrium carneum*	Non-toxic		Edible	USO eaten and contain sweet mucilaginous and nutritious juice	8, 25
Tuber	Orchidaceae	*Satyrium erectum*	Non-toxic		Edible	USO eaten and contain sweet mucilaginous and nutritious juice	8, 25
Bulb	Amaryllidaceae	*Scadoxus puniceus*	Toxic	Alkaloids, Organic Acid	Inedible	Poisonous	21, 24, 25
Tuber	Asphodelaceae	*Trachyandra* genus	Non-toxic		Edible	Inflorescence eaten as vegetable	20
Corm	Iridaceae	*Tritonia securigera*	Non-toxic		Edible	Found in various archaeological sites	6
Bulb	Alliaceae	*Tulbaghia aliacea*	Unknown		Edible	Medicinal and USO eaten cooked	20, 21
Rhizome	Typhaceae	*Typha capensis*	Unknown		Edible	USOs and shoots eaten	5
Bulb	Amaryllidaceae	*Velthemia capensis*	Unknown		Inedible	Medicinal and Poisonous	11, 26
Growth Form	**Family**	**Species**	**Phytochemical Category**	**Specific Phytochemical Profile**	**Edibility**	**Use**	**Reference**

Corm	Iridaceae	*Watsonia* genus	Acrid	Tannins, Organic Acids	Edible	USOs found in very high frequency in Archaeological sites, and interpreted as a staple food source. Would require processing to remove acrid compounds	6, 11, 14
Corm	Iridaceae	*Watsonia angusta*	Acrid	Tannins, Organic Acids	Edible	USOs found in various archaeological sites, require processing or cooking	6, 25
Corm	Iridaceae	*Watsonia meriana var. bulbifera*	Acrid	Organic acid	Edible	USOs found in various archaeological sites, require processing or cooking	6, 25
Corm	Iridaceae	*Watsonia meriana var. meriana*	Acrid	Tannins, Organic Acids	Edible	USOs found in various archaeological sites, require processing or cooking	6, 25
Corm	Iridaceae	*Watsonia borbonica*	Acrid	Organic acid	Edible	USOs found in various archaeological sites, require processing or cooking	25
Corm	Iridaceae	*Watsonia tabularis*	Acrid	Tannins	Edible	USOs found in various archaeological sites, require processing or cooking	25
Corm	Haemodoraceae	*Wachendorfia paniculata*	Unknown		Unkown	Used as dye in tanning	8, 25
Corm	Haemodoraceae	*Wachendorfia thyrsiflora*	Unknown		Unkown	Used as dye in tanning	8, 25
Corm	Colchicaceae	*Wurmbea marginata*	Toxic		Inedible	Poisonous	25
Corm	Colchicaceae	*Wurmbea spicata*	Acrid		Edible	USO eaten raw or cooked	25, 26
Tuber	Araceae	*Zanthedischia aethiopica*	Acrid	Oxalate	Edible	Extensive processing required to render edible. Acrid compounds extracted by leaching multiple times, then roasting.	9, 25

Table 2.2 Key References used to determine the economically important geophyte species of the GCFR.

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Chapter 3: Characteristics of geophyte species which impact the nutritional quality of USOs

3.1 Introduction

In the previous chapter, I present a review of geophyte species observed to be important in hunter-gatherer diets, when they were foraged and how they were processed. Amongst extant San hunter-gatherers, there is a large number of species which are foraged (100 species), while only a few species comprise the majority of biomass which is consumed (10-23 species) (Lee, 1969). This is not to say that all 100 species are un-important in hunter-gatherer subsistence, as low-quality foods could have been consumed in lower quantities in times of drought and scarcity ensuring the survival of hunter-gatherers. The literature on this topic (Chapter 2) is sometimes based on casual observations made by European colonists and likely only captures a fraction of the possible complexity of hunter-gatherer subsistence and behaviours associated with geophyte exploitation that occurred in the GCFR. With the absence of extant hunter-gathers in the GCFR, we are left with an information gap and many questions remain unanswered about how hunter-gatherers made choices about which species to forage among the megadiverse group of edible geophytes available in the GCFR.

In this chapter, I attempt to describe all the characteristics of geophytes that would impact their attractiveness as a foraging item to hunter-gatherers, using this information a rating of attractiveness is generated for edible geophyte species. This provides an estimate of the diversity of geophytes which may have been included in hunter-gatherer diets. In this chapter (and throughout the thesis) I use the term *geophyte* when referring to the entire plant or a specific species, and *USO* when discussing an underground storage organ or USOs in general.

As discussed in Chapter 2, carbohydrates, protein and fat contribute to the energy content of food (Speth and Spielmann, 1983; FAO, 2003). Other compounds, such as water and fibre, do not contribute to the energy content of food (FAO, 2003). Fibre can diminish the nutrients available to the human gut for digestion and can make them unpalatable and difficult to consume (Milton, 1999). Similarly, the phytochemical composition of plant foods (anti-nutrients) can make them unpalatable (bitter) or poisonous (Stahl, 1989). These compounds together impact the palatability and energy content of plant foods available to the human gut for absorption (Crittenden and Schnorr, 2017). It stands to reason then that these are essential factors to consider when we want to understand the subsistence behaviour of hunter-gatherers and the effect the diversity of geophyte resources in the GCFR could have had on hunter-gatherer behaviour.

The energy contained in USOs is the simplest variable which will determine whether the effort to find, excavate, process, and eventually consume USOs provides significant rewards to a forager. The nutritional content of the USO is then a critical factor which will determine if a geophyte is foraged or not, greatly impacting the ‘attractiveness’ of a geophyte to a forager.

However, just as important as the possible energetic returns available from geophyte species, are the characteristics which will increase the amount of energy required to obtain the USO and render it palatable (Winterhalder, 1981; Metcalfe and Barlow, 1992). The substrate the geophyte grows in, the depth at which the USO grows below ground, and the required processing of the USO to render palatable/non-toxic can negatively impact the net return rate of energy from foraging certain USOs (Singels *et al.*, 2016).

Due to the complex array of characteristics which could positively or negatively impact the attractiveness of a geophyte species to a forager, I have found it helpful to simplify this complexity by borrowing the model of the fundamental equations used in optimal foraging theory: Net return rate of foraging (Stephens and Krebs, 1986). The energy content of USOs determines the net energetic return possible from foraging, minus the energy and time which will be required to forage the USO and render it palatable (Figure 3.1).

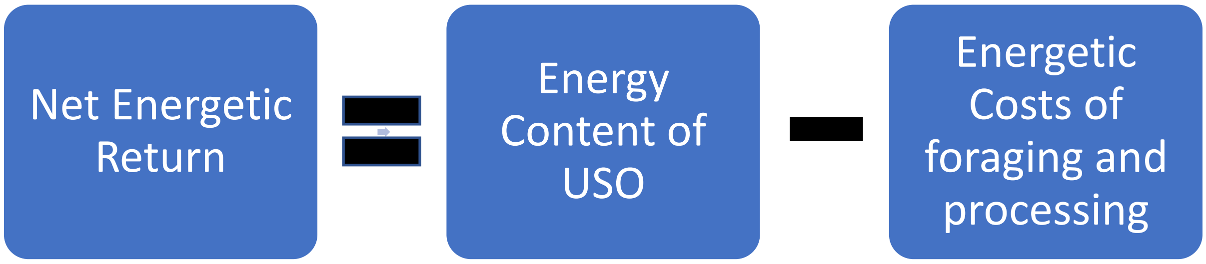

Figure 3.1 Simple interpretation of net energetic return rate of foraging for USOs

3.1.1 Energy content from USOs

3.1.1.1 The nutritional content of USOs

In general, the nutritional content of USOs (from all over the world) presents as follows:

USOs have high carbohydrate content; specifically, they contain large quantities of starch, one type of carbohydrate (Meyer and Hellwig, 1997; Orthen, 2001b; Almeida *et al.*, 2015). These compounds contribute most significantly to the overall energy content of USOs (Vincent, 1985; Youngblood, 2004; Marlowe and Berbesque, 2009). The fat and protein content of USOs is usually negligible

(Wehmeyer, 1986; Singels *et al.*, 2016). The water content of USOs is mostly high and the higher the percentage of water in a USO, the lower the percentage of compounds which contribute to the energy content, so in general the higher the water content of a USO the lower the available energy content. The micro-nutrient content of USOs is generally lower than other leafy greens or fruits (Wehmeyer, 1986).

There is limited information available of the nutritional content and quality of geophytes of the GCFR, only a few studies have focused on testing for specific energetic components in the hyper diverse group of plants, and fewer still have attempted to describe the total energy content. The carbohydrate content of a few geophyte species has been tested (Orthen, 2001a, 2001b; Orthen and Wehrmeyer, 2004), which provides very useful information on the most important energetic component of USOs. In other studies, the total energy content of GCFR geophytes has been determined by the "difference method", where carbohydrate content is not tested for directly, but determined by the difference between the total weight tested and the sum of the weight of all the other compounds tested (Wehmeyer, 1986; Youngblood, 2004). This method does not describe or test for all compounds contained in USOs and the results of the difference method can include compounds that are not carbohydrates (FAO, 2003). Furthermore, this method does not differentiate between different types of carbohydrates such as structural carbohydrates (which are not digestible by the human gut), and digestible carbohydrates (such as starch, mono and di-saccharides) (FAO, 2003). When carbohydrates are directly analysed, together with all other important components: moisture, fat and protein, a truer quantification of the energy content of USOs can be presented (FAO, 2003). This type of analysis has only been conducted for four geophyte species in the GCFR (Singels *et al.*, 2016).

In this chapter, the overall nutritional content, the various compounds which contribute to the energy content and quality of USOs is presented for 34 geophyte species and three leafy green species (as a comparison).

3.1.1.2 Size of USO

Different USO types (rhizome, bulb, corm and tubers) have a wide range of USO sizes (Procheş, Cowling and Du Preez, 2005). The size of a USO will impact the amount of energy obtainable from a specific plant. In studies describing the USOs foraged by extant hunter-gatherers, rhizomes and tubers are most often targeted and can weigh up to 3 kg (Eder, 1978; Vincent, 1985; Hurtado and Hill, 1987). Cormous species have far lower weight at as little as half a gram (Procheş, Cowling and Du Preez, 2005; Singels *et al.*, 2016). Because the size of USOs of different geophyte species will directly impact the amount of energy available in that USO, the weight of a USO is a crucial variable which will impact the attractiveness of a geophyte to a forager.

3.1.2 Energetic cost of foraging

3.1.2.1 Depth of USO below ground and the medium it grows in

The time and energy required to find and dig up USOs will vary for different environments and geophyte species. The abundance of geophytes in different habitats in the GCFR vary (De Vynck, 2014), as does the hardness of the soil (Singels, 2013). Additionally the depth needed to dig to obtain the USO differs for different geophyte species (Singels, 2013). The variation of energy and time inputs required to forage four geophyte species in four broad vegetation categories in the GCFR has been described (Singels *et al.*, 2016), and the time inputs required to find and dig up geophytes were magnitudes lower than measured among extant hunter-gatherer communities (5-15 times shorter) (Eder, 1978; Vincent, 1985; Sato, 2001; Singels *et al.*, 2016). However, the time required to dig up USOs was magnitudes longer in environments with rocky substrates (Singels *et al.*, 2016).

The aim of this chapter is to define how various factors (including the depth at which USOs grow) affect the attractiveness of geophyte species to a forager. In this way, a relative ranking of species is assigned based on the amount of time and energy required to forage them. The depths at which USOs grow below ground was recorded for all geophyte species identified in the various study areas and was included as a consideration of the relative ranking of geophyte species.

3.1.2.2 Anti-nutrient content of USOs

In modern diets fibre is revered as an overwhelmingly positive addition to one's diet, however, in Stone Age life, fibre would have taken up space in the gut that could have been filled by other compounds which contribute nutrients (Conklin-Brittain, Wrangham and Smith, 2002; Frassetto *et al.*, 2009). The fibre content of USOs could have negatively impacted the attractiveness of geophyte species to foragers and likely decreased their palatable by making USOs difficult to chew (Dominy *et al.*, 2008). The fibre content in USOs can differ widely (Singels *et al.*, 2016).

The anti-nutrient content of various geophyte species from the GCFR has been presented, but no quantification or comparison between species has been attempted (Watt and Breyer-Brandwijk, 1962). Among the hyper diverse range of phytochemical compounds present in plants, some can render the plant toxic or simply unpalatable (bitter) (Fekadu Gemede, 2014). Processing of USOs can render toxic USOs harmless or improve the palatability of USOs (Stahl, 1989). A specific group of compounds called tannins (phenolic compounds), which make plants unpalatable, are targeted most frequently during processing (Chavan *et al.*, 1979; Messner, 2011). In this chapter, the phenolic content of 34 geophyte species is presented. These data was used to rank species based on the effect the phenolic content would have on the amount of processing which would be required to render USOs palatable.

3.2 Methods

3.2.1 Collection of USOs samples

Common, numerous or archaeologically relevant geophyte species were collected for nutritional analysis. The tests conducted attempted to maximise the information collected about the overall nutritional quality of different geophytes and include the water, fat, protein, fibre, starch, sugar, and tannin content. Compounds tested that contribute to the energy content of USOs are the fat, protein, starch and sugar. Compounds tested that diminish the palatability and quality of USOs, were fibre and tannin content.

Toxic compounds were not tested for, directly due to the bewildering array of phytochemical compounds which render USOs toxic, as each compound must be tested for directly and individually (Watt and Breyer-Brandwijk, 1962). The toxic compounds in poisonous species are fortunately well studied due to the impact poisonous plants have on livestock farming, and these compounds have been described from the available literature for each species in Table 2.1 and later Table 3.5 (Watt and Breyer-Brandwijk, 1932, 1962)

During the spring and autumn of 2014-2016, Spatial Sampling occurred in the study regions. The aim of this sampling was to describe the variation of geophyte resources over the east-west rainfall seasonality gradient on the coastal plains of the GCFR. The methods and results of this sampling are described in detail in the next chapter (Chapter 4). When a new species was identified during sampling, it was categorised as either toxic, edible, or unpalatable, based on the available literature (see Table 3.5). If the species was categorised as edible 10-15 plants were excavated and the USO depth, length and biomass (wet weight) was recorded. The material that was harvested, if sufficient in weight (minimum of 100 g), was frozen and sent to laboratories for further testing.

Additional geophyte species, which were not sampled during the Spatial Sampling but deemed important, were sourced from growers and sent for analysis. These species include *Dioscorea elephantipes, Babiana stricta, Drimia exuviata,* and *Rumex lativalvis.* The nutritional content of one medicinal plant, *Arctopus echinatus*, was tested to explore the edibility of the species, as many medicinal plants are poisonous, or unpalatable, but could arguably offer nutritional benefits.

3.2.2 Nutritional testing

The nutritional content of USOs was determined by proximal analysis, where the following parameters are measured: moisture, ash, protein, carbohydrate, fat and fibre. These analyses were performed at Quantum Laboratory Services (Malmesbury) following protocols stipulated by the Association of Official Analytical Chemists or AOAC (Nielsen, 2003). Moisture content was determined by the oven-dry method (925.09, AOAC). Ash content was determined using test 923.03 (AOAC). Protein content was determined using the Kjeldahl method (955.04, AOAC), where the total nitrogen content of a sample is calculated and multiplied by 6.25 to determine the % protein. Fat content was determined by the Soxhlet test (920.85c, AOAC). Insoluble and soluble fibre content was determined by the crude fibre test (991.43, AOAC). The crude fibre method underestimates the true fibre content of a sample, because some hemicellulose, cellulose and lignins are not measured. During standard proximal analyses, carbohydrate content is calculated by difference, rather than being tested for directly. The carbohydrate content is calculated as the difference between the total weight of a sample (g/100 g) and all other constituents of the sample (percentage protein, lipid, water and ash). Instead of using this calculation, carbohydrate content was measured directly by determining the starch content (water insoluble) and the sugar content (water soluble) using two distinct methods. Starch content was measured by using the amyloglucosidase/α-amylase method (996.11, AOAC) and sugar content was determined by the Soluble carbohydrate test using the methods presented in Maness, 2010. Due to the cost of testing, no replicates were performed on each species. All nutritional data presented are percentages of wet weight. Nutritional data in wet weight allows the easy application of this data to the biomass data collected for USOs in the field, that in turn allows the estimation of the amount of energy contained in specific habitats

Kilojoule estimates were calculated using the conversion values of the Atwater General Factor System suggested by the FAO, where carbohydrates = 17 kilojoules per 1g of wet weight, protein = 17 kJ/g of wet weight and fat = 37 kJ/g of wet weight (FAO, 2003).

The content of a specific subclass of flavonoids known as flavanols (tannins) in USOs was determined by the Folin-Ciocalteu method as described in Nagel and Glories, 1991 at the Oxidative Stress Research Centre at the Cape Peninsula University of Technology. Triplicates were performed of each test and data are expressed as μmole Catechin per gram (μmole Catechin/g wet weight).

3.2.3 Statistical analysis

Two data sets are analysed and combined, with the end goal of creating a master list of geophyte species studied in this thesis, including the important factors influencing their desirability to a forager, their biology and taxonomy. The first data set comprises the nutritional content results of 34 geophyte species which were tested, with three indigenous leafy vegetables and four domesticated, crop geophytes included to serve as a comparison.

The second dataset comprises the depth and weight data that was collected for 153 geophyte species which were identified during fieldwork for this thesis. Of the 153 species that were identified in the study, 131 were found to be edible, 4 were found to have USOs which are not necessarily poisonous, but certainly unpalatable due to their high fibre or tannin content (see Table 3.5 for further detail). For one species, *Moraea tripetala*, I could find no references speaking to its toxicity or edibility, it is known that many *Moraea* species are poisonous. For this reason, it was categorised as unknown. *Moraea fugax* has two different morphotypes, exhibited in the form of a diminutive morph and a very large morph. For the sake of the measurements made of the USO size and weight, these are treated as two different species. Fifteen species are well known poisonous species. Since this thesis focuses on edible species, almost all analyses focused on the 131 edible species identified. However, some necessary, essential observations are made regarding poisonous species which could have helped hunter-gatherers identify these species even if they were unfamiliar with them.

Due to the costs associated with nutritional analysis, the red list conservation status of certain species (Raimondo *et al.*, 2009), and the number of plants that would be destroyed during the nutritional analysis, it was impossible to test the nutritional content of all species sampled during this study. For those species not sampled, an estimation method was applied to present an estimate of the nutritional content. If a species in a genus was not tested, the species closely related to it (genus and family level) that had been tested was used as a proxy for the nutritional content of the untested species. In cases where multiple species in a genus were tested directly for nutritional content, an average nutritional content for the genus was calculated and awarded to the untested species (See the master list: Table 3.5). This estimation method is supported by reported low variation in the overall energy content between geophyte species in the same genus (Wehmeyer, 1986; Theron and Jacobs, 1996; Orthen, 2001b, 2001a; Orthen and Wehrmeyer, 2004; Ranwala and Miller, 2008; Raccuia and Melilli, 2010).

Combining the two data sets allows us to understand better how these species compare to one another and how the characteristics of each species influence their desirability to a forager. These variables are analysed to assign a rating out of five (from low quality (1) to high quality (5)) to each species, as an indication of the desirability of a species. This rating was based on the assessment of kilojoule content, weight of USOs, depth at which the USO grow, and antinutrient content (fibre and tannin content).

All data were tested for normality and statistical differences using the following tests: Tukey HSD Post hoc test was used to determine the significant differences between group means in an analysis of variance setting.

3.3 Results

3.3.1 Nutritional quality

The nutritional content of the 34 geophyte species tested varied considerably in almost all aspects. The results presented under this sub-heading are in reference to Table 3.1. The species with the highest kilojoule content, are well known for their desirability to hunter-gatherers (Thunberg, 1795; Norwood Young and Fox, 1982; Skead, 2009). *Moraea fugax*, *Cyanella hyacinthoides* and *Babiana stricta* (613 - 650 kJ/100g) had nutritional contents twice that of potatoes (307 kJ/100g) while containing zero tannins and very little fibre. In fact, over half of the GCFR USOs tested had similar or greater nutritional content than domesticated USO species like lotus root, onion, potato and water chestnut, while containing no or few tannins. All species with a kilojoule content of more than 170 kJ/100g had total carbohydrate content similar to that of the highest-scoring domesticated species, the potato and the water chestnut.

The species that contained between 250 - 650 kJ/100g are distinguished from other species as usually having higher starch than sugar content. The highest scoring species are in the following genera: *Moraea*, *Babiana* and *Cyanella*, with up to 31 % of the total weight of USOs consisting of starch alone.

All USOs had greater energy content than the three leafy green species. *Babiana stricta* (650 kJ/100g) had 18 times greater kilojoule content than the highest scoring leafy green *Mesembryanthemum vanrensburgii* (36 kJ/100g). These differences are due to the high carbohydrate content of USOs in comparison to leafy greens, which contributed the majority of the energy content in all geophyte species.

Many species had zero tannin content. Low tannin content was also associated with USOs with low total kilojoule content. Species with a tannin content higher than 6 mg CE/g would require processing to render them palatable. The tannin content of 50 mg CE/g measured for *Arctopus echinatus* would have rendered this species inedible and bitter. *Watsonia galpinii* had an alarmingly high tannin content of 35 mg CE/g, which will be discussed further in subsequent chapters, as it gives us insights into the effect seasonality has on the palatability of USOs, as this species is evergreen and was collected in autumn.

Table 3.1 Nutritional results of species tested, in comparison to indigenous edible, leafy greens and four comparable, domesticated, geophyte crops. Percentages in wet weight.

USO Type	**Family**	**Species**	**Fat %**	**Fibre %**	**Moisture%**	**Protein %**	**Starch %**	**Sugar %**	**Carbs %**	**kJ/100 g**	**Tannin (mg CE/g)**
Bulb	Hyacinthaceae	*Albuca maxima*	0,12	2,22	88,00	1,08	0,10	6,11	0,10	128,18	0,00
Tuber	Apiaceae	*Arctopus echinatus*	0,21	2,87	70,37	1,08	5,96	1,70	7,66	156,28	50,00
Corm	Iridaceae	*Babiana ambigua*	0,35	0,46	59,79	1,35	22,58	1,75	24,33	449,51	1,14
Corm	Iridaceae	*Babiana hirsuta*	0,17	2,42	57,65	1,43	3,29	5,81	9,10	185,30	28,51
Corm	Iridaceae	*Babiana stricta*	0,38	0,89	47,22	2,21	30,96	4,26	35,22	650,37	0,00
Corm	Iridaceae	*Babiana tubiflora*	0,47	1,52	60,00	3,06	8,56	6,10	14,66	318,53	0,00
Corm	Iridaceae	*Chasmanthe aethiopica*	0,09	1,29	70,96	1,78	6,63	3,01	9,64	197,47	2,33
Rhizome	Aizoaceae	*Conicosia pugioniformis*	0,08	12,01	67,95	1,32	1,48	0,86	2,34	65,18	0,00
Corm	Tecophilaeaceae	*Cyanella hyacinthoides*	0,20	0,57	58,51	1,68	27,63	2,89	30,52	554,80	0,00
Corm	Tecophilaeaceae	*Cyanella lutea*	0,33	2,96	58,00	1,71	18,04	2,11	20,15	383,95	0,00
Tuber	Lobeliaceae	*Cyphia digitata*	0,13	2,84	84,00	0,58	0,82	5,40	6,22	120,33	0,00
Tuber	Dioscoreaceae	*Dioscorea elephantipes*	0,17	1,45	76,07	0,95	0,72	8,40	9,12	177,59	0,00
Bulb	Hyacinthaceae	*Drimia exuviata*	0,12	0,61	88,46	1,95	0,16	3,96	4,12	107,45	0,00
Tuber	Ruscaceae	*Eriospermum lanceifolium*	0,23	1,40	84,16	0,92	0,59	2,54	3,13	77,36	19,12
Corm	Iridaceae	*Ferraria crispa*	0,34	1,53	77,06	1,35	11,50	4,80	16,30	312,63	0,18
Corm	Iridaceae	*Ferraria densepunctulata*	0,25	1,98	64,38	1,74	16,09	2,74	18,83	358,94	0,00
Rhizome	Neuradaceae	*Grielum humifusum*	0,04	4,30	54,30	0,26	9,60	3,24	12,84	224,18	8,02
Tuber	Hypoxidaceae	*Hypoxis villosa*	0,06	1,33	84,26	0,82	2,16	1,25	3,41	74,13	0,00
Corm	Iridaceae	*Ixia monadelpha*	0,29	0,56	60,11	1,47	26,59	1,69	28,28	516,48	0,17
Bulb	Hyacinthaceae	*Lachenalia pustulata*	0,13	0,35	89,00	0,29	0,26	6,11	6,37	117,89	0,00
Corm	Iridaceae	*Moraea fugax*	0,06	0,50	54,45	1,58	30,72	3,65	34,37	613,37	0,00
Bulb	Oxalidaceae	*Oxalis versicolor*	0,97	1,24	75,28	1,26	3,96	0,56	4,52	134,15	17,08
Rhizome	Geraniaceae	*Pelargonium lobatum*	0,11	4,04	75,00	1,15	5,97	4,51	10,48	201,95	16,45
Rhizome	Geraniaceae	*Pelargonium triste*	0,07	2,07	62,81	1,24	4,07	4,49	8,56	169,19	18,89
Tuber	Orchidaceae	*Pterygodiumn volucris*	0,16	3,14	82,48	0,65	1,10	0,71	1,81	47,74	0,00

USO Type	**Family**	**Species**	**Fat %**	**Fibre %**	**Moisture%**	**Protein %**	**Starch %**	**Sugar %**	**Carbs %**	**kJ/100 g**	**Tannin (mg CE/g)**
Tuber	Polygonaceae	*Rumex lativalvis*	0,20	1,02	89,40	0,63	0,70	0,86	1,56	44,63	8,07
Tuber	Orchidaceae	*Satyrium carneum*	0,16	2,41	82,00	0,47	0,48	2,01	2,49	56,40	0,00
Tuber	Orchidaceae	*Satyrium princeps*	0,11	4,81	81,60	0,55	1,02	1,99	3,01	64,59	0,00
Rhizome	Haemodoraceae	*Wachendorfia paniculata*	0,32	1,45	74,24	0,90	6,44	2,10	8,54	172,25	0,54
Rhizome	Haemodoraceae	*Wachendorfia thyrsiflorius*	0,06	2,87	74,24	1,06	9,16	3,09	12,25	228,49	0,25
Corm	Iridaceae	*Watsonia fergusoniae*	0,24	2,39	58,00	3,31	6,26	4,50	10,76	248,17	11,05
Corm	Iridaceae	*Watsonia galpinii*	0,38	1,88	46,52	1,48	7,73	16,92	24,65	458,27	34,48
Corm	Iridaceae	*Watsonia knysnana*	0,08	0,62	77,96	1,42	7,70	1,92	9,62	190,64	6,51
Corm	Iridaceae	*Watsonia meriana*	0,16	0,66	67,15	0,64	6,60	3,60	10,20	190,20	2,33
Corm	Averages	*Babiana* average	0,34	1,32	56,17	2,01	16,35	4,48	20,83	400,93	7,41
Corm	Averages	*Ferraria* average	0,30	1,76	70,72	1,55	13,80	3,77	17,57	335,79	0,09
Bulb	Averages	Hyacinthaceae average	0,12	2,07	88,49	1,11	0,17	5,39	3,53	117,84	0,00
Tuber	Averages	Hypoxidaceae average	0,06	1,33	84,26	0,82	2,16	1,25	3,41	74,13	0,00
Corm	Averages	Iridaceae average	0,25	2,04	61,63	1,76	14,25	4,67	18,92	360,76	6,67
Tuber	Averages	Orchidaceae average	0,14	2,84	81,80	0,51	0,75	2,00	2,75	60,50	0,00
Rhizome	Averages	*Pelargonium* average	0,09	3,05	68,91	1,20	5,02	4,50	9,52	185,57	17,67
Tuber	Orchidaceae	*Satyrium* average	0,14	3,61	81,80	0,51	0,75	2,00	2,75	60,50	0,00
Corm	Averages	*Watsonia* average	0,22	1,39	62,41	1,71	7,07	6,74	13,81	271,82	13,59
Rhizome	Comparison	Lotus Root (*Nelumbo nucifera*)	0,11	2,00	80,69	2,11	6,40	9,70	16,11	276,14	3,33
Bulb	Comparison	Onion (*Allium cepa*)	0,10	1,70	89,11	1,10	0,00	4,24	4,24	94,48	
Tuber	Comparison	Potato (*Solanum tuberosum*)	0,09	2,10	79,25	2,05	15,00	0,82	15,82	307,12	
Corm	Comparison	Water Chestnut (*Eleocharis dulcis*)	0,10	3,00	73,46	1,40	7,00	4,80	11,80	228,10	
Leaf	Aizoaceae	*Mesembryanthemum crystallinum*	0,21	1,10	92,13	0,95	0,23	0,15	0,38	30,27	0,00
Leaf	Aizoaceae	*Mesembryanthemum vanrensburgii*	0,29	0,89	91,33	0,70	0,53	0,30	0,83	36,85	0,00
Leaf	Aizoaceae	*Tetrigonia decumbens*	0,22	0,73	93,40	1,35	0,11	0,12	0,23	35,00	0,00

3.3.1.1 USO type and nutritional content

A clearer pattern of the nutritional content of GCFR USOs emerges when USO type (namely bulb, corm, rhizome and tuber) is compared to the corresponding domesticated USOs and leafy greens (see Table 3.2). Fat and protein content are consistently low, with marginal differences being observable. One exception was the protein content of cormous wild species, that is slightly higher than other USO types, but remains a negligible energy component of the total USO weight (see Table 3.2). The fibre content in rhizomatous USOs was significantly higher than almost all USO types with the exception of tubers, which have a slightly elevated fibre content. The moisture content of bulbs and tubers was significantly higher than that of corms and rhizomes. Corms and rhizomes had significantly higher starch content compared to bulbs and tubers (see Figure 3.2). Sugar content, although similar in all USO types also contributed significantly to the overall energy content (see Figure 3.2). Overall, corms had by far the highest total carbohydrate content and energy content, almost double that of closest second, rhizomes. Tannin content did not differ significantly between USO types, but tubers and rhizomes had tannin content, which would require some kind of processing to render them edible.

Domesticated species had lower nutritional quality than wild species. The potato had the highest starch and kilojoule content, but the comparable wild tuberous species had very low carbohydrate content and overall kilojoule content (see Table 3.2). Lotus root had higher kilojoule content due to its high sugar content compared to wild rhizomatous species (see Table 3.2). Onion and water chestnut were similar in nutritional quality to the wild bulbous and cormous species, but the wild species consistently rated higher in starch and overall kilojoule content (see Table 3.2). Most notably wild cormous species had on average, double the amount of starch and one and a half times the number of kilojoules per unit weight (see Table 3.2). Leafy greens scored low on all variables which contribute to kilojoule content but had zero tannin content (see Table 3.2).

Table 3.2 Average nutritional content of USO types, compared to comparable domesticated species of the same USO type, compared to the indigenous leafy greens that were tested. Data are averages and standard deviation. Superscript letters denote significant differences between groups (rows). Groups with unique letters are significantly different from other groups, groups that share letters are not significantly different from one another. Bold data are highlighted in the discussion. Percentages in wet weight.

USO Type	n	Fat %	Fibre %	Moisture %	Protein %	Starch %	Sugar %	Carbohydrates%	kJ/100 g	Tannin (mg CE/g)
Bulb	4	0,3±0,4^{a}	1,1±0,8^{a}	**85,2±6,6^{a}**	1,1±0,7^{abc}	1,1±1,9^{a}	4,2±2,6^{a}	3,8±2,6^{a}	121,9±11,8^{a}	4,3±8,5^{a}
Onion	1	0,1	1,7	89,1	1,1	0,0	4,2	4,2	94,5	0,0
Corm	15	0,3±0,1^{a}	1,1±0,9^{a}	61,2±9,2^{b}	**1,7±0,7^{b}**	**15,4±9,9^{b}**	4,4±3,7^{a}	**19,8±9,3^{b}**	**375,2±159,6^{b}**	5,8±10,9^{a}
Water chestnut	1	0,1	3,0	73,5	1,4	7,0	4,8	11,8	228,1	0,0
Rhizome	6	0,1±0,1^{a}	**4,5±3,9^{b}**	68,1±8,3^{b}	1,0±0,4^{c}	**6,1±3,1^{ab}**	3,0±1,4^{a}	**9,2±3,8^{a}**	176,9±60,1^{a}	**7,4±8,6^{a}**
Lotus Root	1	0,1	2,0	80,7	2,1	6,4	9,7	16,1	276,1	3,3
Tuber	9	0,2±0,1^{a}	2,1±1,3^{ab}	**81,6±5,5^{a}**	0,7±0,2^{abc}	1,5±1,7^{a}	2,8±2,5^{a}	4,3±2,7^{a}	91,0±48,7^{a}	**8,6±16,8^{a}**
Potato	1	0,1	2,1	79,3	2,1	**15,0**	0,8	15,8	**307,1**	0,0
Leaf	3	0,2±0,0^{a}	0,9±0,2^{ab}	92,3±1,0^{a}	1,0±0,3^{abc}	0,3±0,2^{a}	0,2±0,1^{a}	0,5±0,3^{a}	**34,0±3,4^{a}**	**0,0±0,0^{a}**

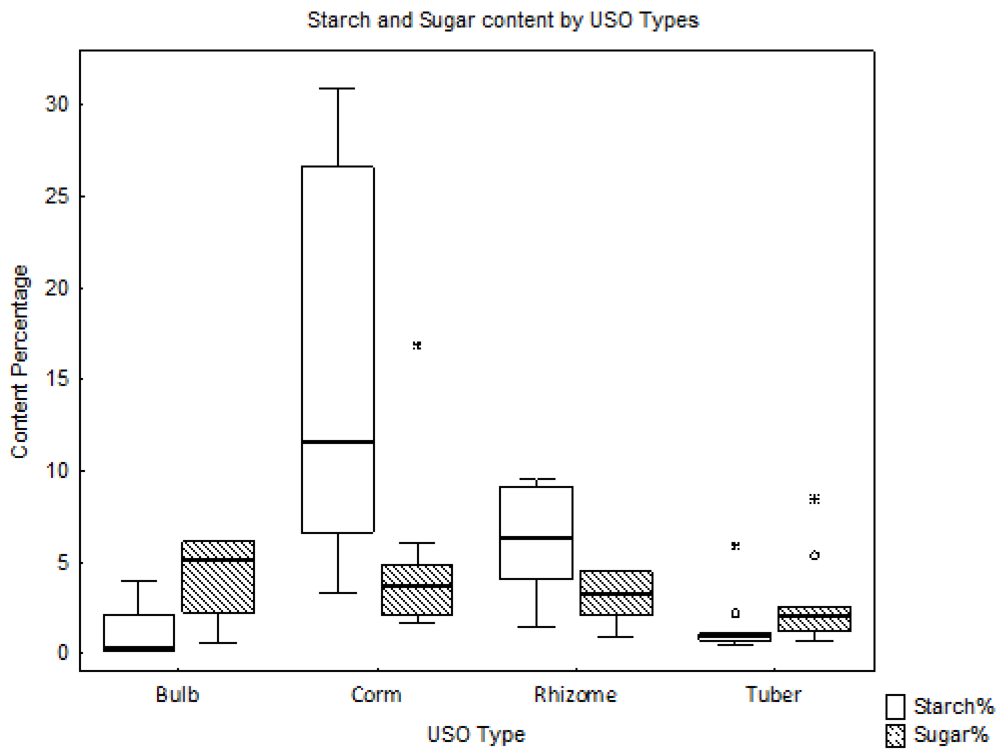

Figure 3.2 Carbohydrate content by USO type denoting sugar and starch. Box represents 75 % upper limit and 25 % bottom limit. Black bar denotes mean, whiskers denote the standard deviation, circles represent outliers, stars represent extremes. Percentages in wet weight.

3.3.1.2 Family level comparison of nutritional content

Family level comparisons are important, because the family Iridaceae often appear in ethnobotanical and archaeological literature as having contributed significantly to hunter-gatherer diets (Parkington, 1977; Liengme, 1987; Deacon, 1993; Van Wyk and Gericke, 2000). Regarding the important factors most impacting nutritional quality (starch, sugar, carbohydrate, kilojoule and tannin content), the important families to note are the Geraniaceae, Haemodoraceae, Hyacinthaceae, Iridaceae, Lobeliaceae, Neuradaceae and Tecophilaeaceae which all had high kilojoule, sugar or starch content (see Table 3.3). The families of Apiaceae, Geraniaceae, Iridaceae, Neradaceae, Oxalidaceae, Polyganaceae, Ruscaceae were highlighted as having high tannin content, all of which would have required some kind of processing to render palatable (see Table 3.3).

Table 3.3 Nutritional content by families. Where data are replicated, they are presented as means and standard deviation. Bold data are highlighted in the discussion Superscript letters denote significant differences between groups (rows). Groups with unique letters are significantly different from other groups while groups that share letters are not significantly different from one another. Percentages in wet weight.

Family	n	Fat %	Fibre %	Moisture %	Protein %	Starch %	Sugar %	Carbohydrates%	kJ/100 g	Tannin content
Aizoaceae	1	0,1^{a}	12,0^{a}	68,0^{abc}	1,3^{a}	1,5^{a}	0,9^{a}	2,3^{a}	65,2^{abc}	0,0^{a}
Apiaceae	1	0,2^{a}	0,5^{bc}	70,4^{abc}	1,1^{a}	6,0^{a}	1,7^{a}	7,7^{a}	156,3^{abc}	**50,0^{b}**
Dioscoreaceae	1	0,2^{a}	1,5^{bc}	76,1^{abc}	1,0^{a}	0,7^{a}	**8,4^{a}**	**9,1^{a}**	**177,6^{abc}**	0,0^{a}
Geraniaceae	2	0,1±0,0^{a}	3,1±1,4^{bc}	68,9±8,6^{abc}	1,2±0,1^{a}	**5,0±1,3^{b}**	**4,5±0,0^{a}**	**9,5±1,4^{b}**	**185,6±23,2^{abc}**	**17,7±1,7^{c}**
Haemodoraceae	2	0,2±0,2^{a}	2,2±1,0^{bc}	74,2±0,0^{abc}	1,0±0,1^{a}	**7,8±1,9^{b}**	2,6±0,7^{a}	**10,4±2,6^{b}**	**200,4±39,8^{a}**	0,4±0,2^{a}
Hyacinthaceae	3	0,1±0,0^{a}	1,1±1,0^{bc}	88,5±0,5^{a}	1,1±0,8^{a}	0,2±0,1^{a}	**5,4±1,2^{a}**	3,5±3,2^{a}	117,8±10,4^{abc}	0,0±0,0^{a}
Hypoxidaceae	1	0,1^{a}	1,3^{bc}	84,3^{abc}	0,8^{a}	2,2^{a}	1,3^{a}	3,4^{a}	74,1^{abc}	0,0^{a}
Iridaceae	13	0,3±0,1^{a}	1,0±0,8^{b}	61,6±9,8^{b}	1,8±0,7^{a}	**14,2±10,0^{c}**	**4,7±4,0^{a}**	**18,9±9,5^{c}**	**360,8±163,7^{b}**	**6,7±11,5^{ac}**
Lobeliaceae	1	0,1^{a}	2,8^{abc}	84,0^{abc}	0,6^{a}	0,8^{a}	**5,4^{a}**	6,2^{a}	120,3^{abc}	0,0^{a}
Neuradaceae	1	0,0^{a}	4,3^{abc}	54,3^{abc}	0,3^{a}	**9,6^{b}**	3,2^{a}	**12,8^{b}**	**224,2^{abc}**	**8,0^{ac}**
Orchidaceae	4	0,1±0,0^{a}	3,5±1,0^{ca}	82,0±0,4^{ca}	0,5±0,1^{a}	0,8±0,3^{a}	1,7±0,6^{a}	2,5±0,5^{a}	57,3±7,2^{ca}	0,0±0,0^{a}
Oxalidaceae	1	1,0^{a}	1,2^{abc}	75,3^{abc}	1,3^{a}	4,0^{a}	0,6^{a}	4,5^{a}	134,2^{abc}	**17,1^{ac}**
Polygonaceae	1	0,2^{a}	1,0^{abc}	89,4^{abc}	0,6^{a}	0,7^{a}	0,9^{a}	1,6^{a}	44,6^{abc}	**8,1^{ac}**
Ruscaceae	1	0,2^{a}	1,4^{abc}	84,2^{abc}	0,9^{a}	0,6^{a}	2,5^{a}	3,1^{a}	77,4^{abc}	**19,1^{ac}**
Tecophilaeaceae	2	0,3±0,1^{a}	1,8±1,7^{bc}	58,3±0,4^{bc}	1,7±0,0^{a}	**22,8±6,8^{c}**	2,5±0,6^{a}	**25,3±7,3^{c}**	**469,4±120,8^{bc}**	**0,0±0,0^{a}**

3.3.2 Geophyte Species Depth and Weight

When we compare the weight of USOs belonging to the various edibility categories an apparent pattern is illustrated, where poisonous species have very large USOs, which grow at or near the soil surface (see Table 3.4). The few exceptions are the poisonous species in the Colchicaceae family and the few poisonous species in the *Moraea* genus, which all have small corms and grow at depths of between five to fifteen centimetres below ground (see Table 3.4).

When the 131 edible species are analysed for the weight of their USOs by family we see that most families have small USOs; notably, the families which scored highest in nutritional value had very small USOs (see Table 3.4). The Geraniaceae (consisting of species in the genus *Pelargonium*) had the largest USOs followed by the rhizomes of *Typha capensis* in the family Typhaceae, a common wetland species. For each family, and in fact, for each species, there is a differing array of variability in the size and weight of USOs which depends on the USO type, where corms had the smallest USOs and rhizomes and tubers the largest. All edible USOs are situated in relatively shallow soil depths, with most USOs growing at a depth less than 15 cm. Rhizomes occurred at significantly deeper soil depths than other USO types.

Table 3.4 USO weight and depths of all species sampled, by edibility category. USO weight and depths by USO Type and Family (edible species). Data are presented as means and standard deviation. Bold data are highlighted in the discussion. Superscript letters denote significant differences between groups (rows). Groups with unique letters are significantly different from other groups while groups that share letters are not significantly different from one another. Percentages in wet weight.

Category	**n**	**Depth to USO (mm)**	**Total Depth (mm)**	**Weight (g)**
Edibility Category Comparisons of All species				
Edible	1588	52,1±47,2^{a}	79,2±57,2^{ab}	7,4±13,8^{a}
Poisonous	194	**27,8±34,0^{b}**	89,2±44,2^{a}	**361,9±619,6^{b}**
Unknown	14	53,1±8,4^{a}	64,3±9,8^{ab}	0,5±0,2^{a}
Unpalatable	46	36,3±14,2^{a}	59,7±14,7^{b}	7,9±8,3^{a}
USO Type Comparisons of Edible Species				
Bulb	251	40,0±35,1^{a}	61,5±37,9^{a}	5,6±7,4^{a}
Corm	894	62,3±51,3^{b}	81,5±55,7^{b}	**4,6±8,9^{a}**
Rhizome	168	40,3±45,5^{a}	109,7±87,1^{c}	**19,3±27,5^{b}**
Tuber	275	37,5±33,8^{a}	69,1±44,1^{a}	**10,8±14,7^{c}**
Family Level Comparisons of Edible Species				
Aizoaceae	9	0,0±0,0^{a}	44,9±13,0^{acd}	25,4±15,4^{bcd}
Alliaceae	15	21,3±6,0^{a}	100,7±25,5^{acd}	3,4±1,7^{ae}
Asphodelaceae	60	24,2±12,2^{a}	69,9±18,9^{ad}	7,0±3,9^{ae}
Campulaceae	42	79,2±57,5^{b}	132,2±57,9^{bc}	21,8±16,4^{c}
Convallariaceae	63	35,3±15,7^{a}	57,0±22,4^{ac}	10,5±16,6^{e}
Cyperaceae	31	32,6±18,4^{a}	43,2±21,8^{c}	1,2±0,8^{e}
Geraniaceae	44	44,1±42,8^{ac}	136,4±95,8^{b}	**38,3±43,7^{d}**
Haemodoraceae	24	34,6±23,0^{ac}	70,4±30,0^{acd}	9,7±9,0^{abe}
Hyacinthaceae	162	31,8±21,8^{a}	53,1±26,1^{ac}	7,7±8,4^{ae}
Hypoxidaceae	50	28,4±14,4^{a}	47,6±20,4^{ac}	6,2±15,8^{ae}
Iridaceae	786	63,6±51,5^{c}	83,1±55,9^{d}	**4,5±8,5^{e}**
Neuradaceae	21	52,9±41,4^{abc}	136,5±56,9^{bcd}	14,4±12,8^{c}
Orchidaceae	170	28,1±20,8^{a}	58,0±31,5^{cd}	8,1±12,1^{a}
Oxalidaceae	74	61,7±49,7^{ac}	72,1±51,9^{cd}	1,3±1,8^{ae}
Tecophilaeaceae	27	120,3±53,5^{d}	142,4±55,9^{e}	7,5±4,2^{ae}
Typhaceae	10	142,8±89,4^{d}	327,1±91,4^{e}	36,7±22,9^{d}

3.3.3 Master species list and ranking

One of the essential goals of this chapter was to create a “master list” of edible geophyte species based on their characteristics related to foraging (Table 3.5). This species list is used throughout the thesis.

The ranking of edible geophyte species identified in this thesis, the number of plants collected for measurements, the growth form of the USO, the family the species belong to, the depth of the USO below ground, USO weight, energy content, tannin content, archaeological visibility category (whether an inedible portion of the USOs could be found in the archaeology) and the references which note the use and phytochemical composition of species or genera are listed.

It was found that the nutritional quality of geophytes could be grouped into three distinct groups based on the energy they could provide a forager, while considering the palatability (tannin and fibre content) of the USO. These three groups correspond to the various ratings assigned to geophyte species. Some species had very high energy content, which always corresponded to high carbohydrate content, and low to zero anti-nutrient content. These species have been assigned a rating between 4 and 5 (differentiated by tannin content). Other species have high fibre and anti-nutrient content, and medium energy content. These species have been assigned a rating of between 2 and 3. Other species still had low energy content, and mostly consisted of water, while having zero antinutrient content. These species were assigned a rating of 1.

Table 3.5 Master species list of geophyte species identified in this study. Classification of species is according to Manning and Goldblatt, 2012. See Table 2.2 for list of references

n	**Growth Habit**	**Family**	**Species**	**USO Depth (mm)**			**USO Weight (g)**			**kJ/100g**	**Tannin content**	**Rating**	**Archaeological Visibility**	**Reference edibility**
6	Corm	Iridaceae	*Moraea tricuspidata*	225	±	69	6,0	±	2	613	0	5	Identifiable	13, 25
15	Corm	Iridaceae	*Moraea fugax greater*	240	±	63	5,3	±	1,8	613	0	5	Identifiable	13, 23
10	Corm	Iridaceae	*Moraea lewisiae*	144	±	22	2,8	±	1,4	613	0	5	Identifiable	13, 25
15	Corm	Iridaceae	*Moraea fugax diminutive*	197	±	70	1,6	±	0,7	613	0	5	Identifiable	13, 23
9	Corm	Iridaceae	*Moraea inconspicua*	130	±	61	1,6	±	1	613	0	5	Identifiable	13, 25
14	Corm	Iridaceae	*Moraea australis*	107	±	28	0,5	±	0,1	613	0	5	Identifiable	13, 25
12	Corm	Iridaceae	*Moraea setifolia*	50	±	20	0,1	±	0	613	0	5	Identifiable	13, 25
15	Corm	Tecophilaeaceae	*Cyanella hyacinthoides*	184	±	37	9,3	±	3,8	555	0	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Ixia paniculata*	85	±	31	3,1	±	1,5	517	0,2	5	Identifiable	13, 25
11	Corm	Iridaceae	*Ixia micrandra*	62	±	37	0,4	±	0,1	517	0,2	5	Identifiable	13, 25
9	Corm	Iridaceae	*Ixia orientalis*	41	±	12	0,3	±	0,2	517	0,2	5	Identifiable	13, 25
15	Corm	Iridaceae	*Ixia flexuosa*	25	±	6	1,4	±	0,8	517	0,2	5	Identifiable	13, 25
15	Corm	Iridaceae	*Babiana ambigua*	92	±	14	0,6	±	0,5	450	1,1	5	Identifiable	13, 23, 25
14	Corm	Iridaceae	*Babiana ringens*	121	±	21	3,9	±	1,2	401	7,4	5	Identifiable	13, 23, 25
6	Corm	Iridaceae	*Babiana patersoniae*	99	±	16	2,4	±	1,4	401	7,4	5	Identifiable	13, 23, 25
4	Corm	Iridaceae	*Babiana odorata*	61	±	13	2,5	±	0,4	401	7,4	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Babiana nana*	51	±	14	1,3	±	0,4	401	7,4	5	Identifiable	13, 23, 25
12	Corm	Iridaceae	*Cyanella lutea*	91	±	20	5,3	±	3,6	384	0	5	Identifiable	13, 23, 25

n	Growth Habit	Family	Species	USO Depth (mm)			USO Weight (g)			kJ/100g	Tannin content	Rating	Archaeological Visibility	Reference edibility
15	Corm	Iridaceae	*Gladiolus carinatus*	174	±	42	3,1	±	1,4	361	6,7	5	Identifiable	13, 23, 25
3	Corm	Iridaceae	*Gladiolus rogersii*	107	±	10	0,2	±	0,1	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Freesia fergusoniae*	121	±	24	3,2	±	1,5	361	6,7	5	Identifiable	13, 23
9	Corm	Iridaceae	*Gladiolus tristis*	101	±	19	3,6	±	1,1	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Freesia leichtlinii*	76	±	36	1,2	±	0,4	361	6,7	5	Identifiable	13, 25
15	Corm	Iridaceae	*Geissorhiza bracteata*	82	±	21	11,8	±	5,4	361	6,7	5	Identifiable	13, 26
16	Corm	Iridaceae	*Gladiolus miniatus*	70	±	22	1,9	±	1	361	6,7	5	Identifiable	13, 23, 25
9	Corm	Iridaceae	*Gladiolus wilsonii*	70	±	22	1,9	±	1	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Gladiolus stellatus*	58	±	18	0,2	±	0,1	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Romulea rosea*	60	±	11	0,7	±	0,4	361	6,7	5	Identifiable	13, 23, 24
15	Corm	Iridaceae	*Gladiolus floribundus*	66	±	14	4,5	±	2	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Gladiolus alatus*	53	±	17	0,5	±	0,4	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Gladiolus liliaceus*	53	±	8	1,3	±	1	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Gladiolus involutus*	46	±	15	0,2	±	0,1	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Sparaxis bulbifera*	81	±	19	4,3	±	1	361	6,7	5	Identifiable	13, 25
14	Corm	Iridaceae	*Hesperantha falcata*	48	±	30	2,5	±	0,8	361	6,7	5	Identifiable	25
15	Corm	Iridaceae	*Lapeirousia pyramidalis*	44	±	10	0,5	±	0,3	361	6,7	5	Identifiable	13, 25
15	Corm	Iridaceae	*Gladiolus cunonius*	44	±	20	0,5	±	0,7	361	6,7	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Freesia caryophyllacea*	56	±	8	2,2	±	1,2	361	6,7	5	Identifiable	13, 25
12	Corm	Iridaceae	*Geissorhiza aspera*	40	±	23	0,4	±	0,3	361	6,7	5	Identifiable	13, 25

n	Growth Habit	Family	Species	USO Depth (mm)	USO Weight (g)	kJ/100g	Tannin content	Rating	Archaeological Visibility	Reference edibility
15	Corm	Iridaceae	*Tritonia squalida*	37 ± 13	0,7 ± 0,3	361	6,7	5	Identifiable	13
11	Corm	Iridaceae	*Hesperantha radiata*	28 ± 5	0,4 ± 0,1	361	6,7	5	Identifiable	25
10	Corm	Iridaceae	*Melasphaerula graminea*	26 ± 9	0,5 ± 0	361	6,7	5	Identifiable	13, 25
14	Corm	Iridaceae	*Tritonia crocata*	35 ± 6	2,5 ± 0,6	361	6,7	5	Identifiable	13
15	Corm	Iridaceae	*Freesia grandiflora*	23 ± 6	0,6 ± 0,2	361	6,7	5	Identifiable	13, 24
11	Corm	Iridaceae	*Sparaxis villosa*	44 ± 10	0,8 ± 0,6	361	6,7	5	Identifiable	13, 25
15	Corm	Iridaceae	*Babiana tubiflora*	188 ± 26	1,6 ± 0,7	319	0	5	Identifiable	13, 23, 25
14	Corm	Iridaceae	*Babiana tubulosa*	112 ± 14	1,3 ± 0,5	319	0	5	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Babiana patula*	96 ± 16	2,9 ± 1,5	319	0	5	Identifiable	13, 23, 25
14	Corm	Iridaceae	*Ferraria densepunctulata*	102 ± 36	2,6 ± 1,1	359	0	4	Identifiable	25
5	Corm	Iridaceae	*Ferraria uncinata*	100 ± 22	9,4 ± 2,9	336	0,1	4	Identifiable	13, 25
15	Corm	Iridaceae	*Ferraria crispa*	164 ± 31	50,3 ± 17,5	313	0,2	4	Identifiable	23
6	Rhizome	Neuradacea	*Grielum grandiflorum*	207 ± 57	30,3 ± 14,1	224	8	4	Invisible	5
15	Rhizome	Neuradacea	*Grielum humifusum*	109 ± 23	8,0 ± 3,1	224	8	4	Invisible	5
13	Corm	Iridaceae	*Chasmanthe aethiopica*	96 ± 23	16,7 ± 7,2	198	2,3	4	Identifiable	14
13	Corm	Iridaceae	*Chasmanthe floribunda*	54 ± 14	12,5 ± 9,5	198	2,3	4	Identifiable	14
15	Corm	Cyperaceae	*Cyperus congestus*	58 ± 22	1,9 ± 0,5			4	Identifiable	13, 23, 25
8	Corm	Cyperaceae	*Cyperus esculentus*	29 ± 8	0,6 ± 0,3			4	Identifiable	13, 23, 25
9	Corm	Cyperaceae	*Cyperus usitatus*	29 ± 8	0,6 ± 0,3			4	Identifiable	13, 23, 25
15	Corm	Iridaceae	*Watsonia galpinii*	66 ± 13	2,0 ± 0,8	458	34,5	3	Identifiable	11, 14, 25

n	Growth Habit	Family	Species	USO Depth (mm)			USO Weight (g)			kJ/100g	Tannin content	Rating	Archaeological Visibility	Reference edibility
15	Corm	Iridaceae	*Watsonia aletroides*	62	±	12	0,8	±	0,7	272	13,6	3	Identifiable	11, 14, 25
15	Corm	Iridaceae	*Watsonia laccata*	50	±	9	0,3	±	0,2	272	13,6	3	Identifiable	11, 14, 25
15	Corm	Iridaceae	*Watsonia wilmaniae*	54	±	15	9,4	±	4,5	272	13,6	3	Identifiable	11, 14, 25
15	Corm	Iridaceae	*Watsonia coccinea*	47	±	9	1,2	±	0,8	272	13,6	3	Identifiable	11, 14, 25
5	Corm	Iridaceae	*Watsonia pillansii*	83	±	19	19,2	±	3,3	272	13,6	3	Identifiable	11, 14, 25
15	Corm	Iridaceae	*Watsonia fergusoniae*	65	±	8	16,9	±	5	248	11,1	3	Identifiable	11, 14, 25
15	Corm	Iridaceae	*Watsonia fourcadei*	42	±	10	4,8	±	1,3	248	11,1	3	Identifiable	11, 14, 25
9	Rhizome	Haemodoraceae	*Wachendorfia thyrsiflora*	52	±	37	11,9	±	13,4	229	0,3	3	Invisible	2
14	Rhizome	Geraniaceae	*Pelargonium carneum*	62	±	23	16,5	±	4,4	186	17,7	3	Invisible	13
15	Corm	Iridaceae	*Watsonia knysnana*	98	±	15	12,8	±	3,8	191	6,5	3	Identifiable	11, 14, 25
14	Corm	Iridaceae	*Watsonia meriana*	76	±	15	16,5	±	6,1	190	2,3	3	Identifiable	11, 14, 25
11	Rhizome	Geraniaceae	*Pelargonium triste*	223	±	103	44,4	±	45,2	169	18,9	3	Invisible	13, 23, 24
15	Rhizome	Geraniaceae	*Pelargonium lobatum*	169	±	66	49,3	±	36,9	202	16,5	3	Invisible	13
15	Corm	Iridaceae	*Babiana hirsuta*	202	±	36	8,8	±	1,7	185	28,5	3	Identifiable	11
15	Rhizome	Haemodoraceae	*Wachendorfia paniculata*	81	±	19	8,4	±	5,1	172	0,5	3	Invisible	2
11	Rhizome	Geraniaceae	*Pelargonium rapaceum*	53	±	33	31,1	±	60,4	186	17,7	3	Identifiable	13, 23
15	Corm	Oxalidaceae	*Oxalis versicolor*	132	±	83	4,0	±	2	134	17,1	3	Indistinguishable	13, 25
10	Corm	Oxalidaceae	*Oxalis obtusa*	59	±	30	0,2	±	0,1	134	17,1	3	Indistinguishable	13, 25
12	Corm	Oxalidaceae	*Oxalis pendulifolia*	59	±	30	0,2	±	0,1	134	17,1	3	Indistinguishable	13, 25
11	Corm	Oxalidaceae	*Oxalis polyphylla*	54	±	20	0,2	±	0,1	134	17,1	3	Indistinguishable	13, 25
13	Corm	Oxalidaceae	*Oxalis pes-caprae*	50	±	23	0,5	±	0,5	134	17,1	3	Indistinguishable	13

n	Growth Habit	Family	Species	USO Depth (mm)	USO Weight (g)	kJ/100g	Tannin content	Rating	Archaeological Visibility	Reference edibility
15	Corm	Oxalidaceae	*Oxalis hirta*	64 ± 22	1,7 ± 0,7	134	17,1	3	Indistinguishable	13, 25
12	Bulb	Hyacinthaceae	*Massonia echinata*	60 ± 17	9,1 ± 3,8	118	0	3	Indistinguishable	5
10	Bulb	Hyacinthaceae	*Massonia depressa*	44 ± 9	3,0 ± 1,1	118	0	3	Indistinguishable	5
15	Bulb	Hyacinthaceae	*Ledebouria ovalifolia*	41 ± 9	4,1 ± 4	118	0	3	Indistinguishable	24
15	Bulb	Hyacinthaceae	*Ledebouria revoluta*	33 ± 7	10,9 ± 6	118	0	3	Indistinguishable	24
15	Bulb	Hyacinthaceae	*Albuca flaccida*	76 ± 36	4,3 ± 1,8	128	0	2	Indistinguishable	13, 21, 25, 26
10	Bulb	Hyacinthaceae	*Albuca fragrans*	92 ± 59	19,8 ± 11,4	128	0	2	Indistinguishable	13, 21, 25, 26
12	Bulb	Hyacinthaceae	*Albuca canadensis*	51 ± 10	17,1 ± 9,9	128	0	2	Indistinguishable	13, 21, 25, 26
15	Tuber	Lobeliaceae	*Cyphia phyteuma*	178 ± 51	18,7 ± 14,3	120	0	2	Invisible	13
5	Tuber	Lobeliaceae	*Cyphia volubilis*	136 ± 49	14,3 ± 8,7	120	0	2	Invisible	13
15	Tuber	Lobeliaceae	*Cyphia digitata*	84 ± 24	30,9 ± 19,3	120	0	2	Invisible	13
14	Bulb	Hyacinthaceae	*Lachenalia rubida*	64 ± 22	13,9 ± 11,1	118	0	2	Indistinguishable	5
15	Bulb	Hyacinthaceae	*Lachenalia pustulata*	48 ± 22	1,0 ± 0,7	118	0	2	Indistinguishable	5
13	Bulb	Hyacinthaceae	*Lachenalia bulbifera*	49 ± 11	3,2 ± 3,1	118	0	2	Indistinguishable	5
10	Bulb	Hyacinthaceae	*Lachenalia aloides*	45 ± 11	2,0 ± 1,3	118	0	2	Indistinguishable	5
12	Bulb	Hyacinthaceae	*Lachenalia nervosa*	44 ± 9	2,1 ± 1,7	118	0	2	Indistinguishable	5
11	Bulb	Hyacinthaceae	*Lachenalia mutabilis*	48 ± 7	11,5 ± 9,3	118	0	2	Indistinguishable	5
10	Rhizome	Thyphaceae	*Typha capensis*	356 ± 165	36,7 ± 22,9			2	Invisible	2
10	Tuber	Ruscaceae	*Eriospermum brevipes*	94 ± 25	36,7 ± 30,8	77	19,1	1	Invisible	25
11	Tuber	Ruscaceae	*Eriospermum cordiforme*	52 ± 21	4,7 ± 3,3	77	19,1	1	Invisible	25

n	Growth Habit	Family	Species	USO Depth (mm)			USO Weight (g)			kJ/100g	Tannin content	Rating	Archaeological Visibility	Reference edibility
15	Tuber	Ruscaceae	*Eriospermum lanceifolium*	50	±	13	7,1	±	3,1	77	19,1	1	Invisible	25
15	Tuber	Ruscaceae	*Eriospermum breviscapum*	50	±	10	5,2	±	2,1	77	19,1	1	Invisible	25
14	Tuber	Ruscaceae	*Eriospermum pubescens*	50	±	10	5,2	±	2,1	77	19,1	1	Invisible	25
15	Corm	Hypoxidaceae	*Pauridia flaccida*	53	±	12	0,3	±	0,2	74	0	1	Identifiable	13, 25
12	Corm	Hypoxidaceae	*Empodium gloriosum*	46	±	9	0,5	±	0,5	74	0	1	Identifiable	25
11	Tuber	Hypoxidaceae	*Hypoxis villosa*	63	±	32	25,2	±	26,6	74	0	1	Identifiable	25
12	Corm	Hypoxidaceae	*Empodium veratrifolium*	29	±	4	1,7	±	0,6	74	0	1	Identifiable	25
9	Rhizome	Aizoaceae	*Conicosia pugioniformis*	302	±	300	25,4	±	15,4	65	0	1	Indistinguishable	5
4	Tuber	Orchidaceae	*Bonatea speciosa*	1125	±	84	6,5	±	4,1	61	0	1	Invisible	25
10	Tuber	Orchidaceae	*Satyrium acuminatum*	72	±	24	7,8	±	4,5	61	0	1	Invisible	25
4	Tuber	Orchidaceae	*Satyrium membranaceum*	61	±	13	6,0	±	1,4	61	0	1	Invisible	13, 25
11	Tuber	Orchidaceae	*Satyrium parviflorum*	51	±	6	2,2	±	0,8	61	0	1	Invisible	13, 25
14	Tuber	Orchidaceae	*Satyrium stenopetalum*	48	±	12	1,9	±	1,1	61	0	1	Invisible	13, 25
15	Tuber	Orchidaceae	*Satyrium longicolle*	79	±	17	14,2	±	13	61	0	1	Invisible	13, 25
15	Tuber	Orchidaceae	*Satyrium corrifolium*	56	±	15	5,1	±	3,1	61	0	1	Invisible	13, 25
15	Tuber	Orchidaceae	*Satyrium odorum*	93	±	13	18,2	±	12,9	61	0	1	Invisible	13, 25
12	Tuber	Orchidaceae	*Satyrium carneum*	103	±	16	34,2	±	22,4	61	0	1	Invisible	25
8	Tuber	Orchidaceae	*Satyrium princeps*	96	±	10	13,0	±	2,3	61	0	1	Invisible	13, 25
9	Tuber	Orchidaceae	*Holothrix villosa*	29	±	3	1,2	±	0,6	61	0	1	Invisible	25
7	Tuber	Orchidaceae	*Disa bracteata*	23	±	8	2,6	±	0,9	61	0	1	Invisible	25
14	Tuber	Orchidaceae	*Holothrix burchellii*	33	±	10	4,4	±	3,9	61	0	1	Invisible	25

n	Growth Habit	Family	Species	USO Depth (mm)			USO Weight (g)			kJ/100g	Tannin content	Rating	Archaeological Visibility	Reference edibility
15	Tuber	Orchidaceae	*Holothrix mundii*	13	±	4	0,4	±	0,3	61	0	1	Invisible	25
13	Tuber	Hyacinthaceae	*Pterygodium volucris*	32	±	11	0,5	±	0,1	48	0	1	Invisible	25
4	Tuber	Hyacinthaceae	*Pterygodium orobanchoides*	76	±	17	5,8	±	2,7	48	0	1	Invisible	25
15	Rhizome	Asphodelaceae	*Trachyandra falcata*	80	±	18	5,8	±	3,8			1	Invisible	13, 23
5	Rhizome	Asphodelaceae	*Trachyandra muricata*	93	±	14	7,9	±	2,4			1	Invisible	13, 23
10	Rhizome	Asphodelaceae	*Trachyandra revoluta*	62	±	12	9,5	±	4,6			1	Invisible	13, 23
15	Bulb	Alliaceae	*Tulbaghia alliacea*	101	±	26	3,4	±	1,7			1	Invisible	9, 21, 26
15	Rhizome	Asphodelaceae	*Trachyandra ciliata*	64	±	17	7,5	±	4,4			1	Invisible	13, 25
7	Rhizome	Asphodelaceae	*Trachyandra divaricata*	72	±	19	4,5	±	2,3			1	Invisible	13, 23
8	Rhizome	Asphodelaceae	*Trachyandra chlamydophylla*	57	±	14	6,8	±	2,5			1	Invisible	13, 25

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3.4 Discussion

A large variation exists in the resource quality between geophyte species in the GCFR, although the majority of species are edible. The few species classified as poisonous contain compounds which either make them poisonous or bitter. The variation in nutritional quality is impacted by the energy content of USOs, the anti-nutrient content, the size of USOs and the depths of USOs below ground.

What I hope to have achieved in this chapter, is to condense all of the variables that impact the desirability of USO species into a single rating, to enable grouping of species. These ratings can help us understand the choices hunter-gatherers would have made. In the absence of extant hunter-gatherers in the GCFR we are unable to evaluate the true choices foragers made. The ranking system presented can be a useful tool to guide our understanding of the choices faced by hunter-gatherer in the Stone Age. However, these rating alone are not enough; looking to the ethnobotanical work conducted on hunter-gatherers and the theories surrounding human evolution can help frame these ratings.

From all the variables measured for the geophyte species identified in this study, it seems that the USO type had the most significant effect on the size, depth, nutritional content, and ultimate rating of geophyte species. Although rhizomatous and tuberous geophyte species could have contributed significantly to hunter-gatherer diets, they consistently have lower rankings due to their high anti-nutrient content and average to low nutritional content. These species would not be preferred over the highest-ranking cormous species, which consistently ranked between three to five on this ranking system, which closely mimics their high nutritional content. The Iridaceae family contributes most significantly to this pattern with 61 species belonging to this family.

In San communities in southern Africa, there are hundreds of edible species foraged, but there is often a strong focus on foraging only a few species, especially when these resources are highly seasonal and only available for a short window of time (Lee, 1973, 1997; Tanaka, 1976). When these resources are available, they are always targeted; species in our study with a rating of five will fall in this category. It is important to note that the species which rank the highest, are Iridaceae species, commonly described in the archaeological record of the GCFR as the uintjies, i.e., *Moraea, Babiana* and *Cyanella* (Deacon, 1963, 1970, 1979; Opperman, 1978; Robey, 1984; Liengme, 1987).

Other species with lower rankings are, however, also found in the archaeological record. For example, the tuberous species *Dioscorea elephantipes* is commonly reported from archaeological sites from the West Coast and the Cederberg (Liengme, 1987). This species has a relatively low energy content and high anti-nutrient content. Other lower ranking species identified include species in the

Asphodelaceae, Oxalidaceae and Geraneaceae families. Although these taxa have lower ratings, they would still have been foraged periodically when conditions were such that the preferred highest-ranking species were not available (this will be discussed in detail in the following chapters). These species can be described as fallback foods (Lambert *et al.*, 2004; Laden and Wrangham, 2005; Marshall and Wrangham, 2007). While not preferred over higher-ranking species these species would still have been important in maintaining the nutrition of hunter-gatherers in times of the year when higher-ranked species are unavailable. The dietary adaptation of early humans to exploit fall back foods during times of relative scarcity is purported to have been one of the fundamental shifts which helped maintain brain development consistently and allowed hominids to utilise ever more marginal environments (Wrangham *et al.*, 1999, 2009; Hardy *et al.*, 2015; Butterworth, Ellis and Wollstonecroft, 2016).

Species with low tannin content, low nutritional content and high-water content are consistently ranked low. Although these species would require zero processing, they are unlikely to contribute significantly to fulfilling the dietary requirements of hunter-gatherers. These species could have been important sources of water in the field, however, and can be regarded as thirst quenchers.

Geophytes in the GCFR have far higher energy content than other above-ground plant food sources. However, above-ground plant foods would have been hugely important in micronutrient acquisition; minerals and vitamins (Ineke *et al.*, 2007; Uusiku *et al.*, 2010),

3.5 Conclusion

These results show that geophyte species in the GCFR are highly nutritious and in half of the species tested they were more nutritious than the domesticated potato, which has been selectively bred for hundreds of years. Geophytes are a hyper diverse group of plants that display huge variability in their nutritional content and quality. If hunter-gatherers understood the factors which made geophytes desirable to forage, they would have been able to selectively target species depending on the season and location. Geophytes would have been the densest source of complex carbohydrates, and thus energy, of any food source available to hunter-gatherers in the GCFR landscape.

Chapter 4: **Geophyte resource variation over time and space in the Greater Cape Floristic Region**

4.1 Introduction

The Greater Cape Floristic Region is defined as having: ‘similar biotic (vegetation and floristic) and physical features (landscapes and rock types) and processes at the regional scale (Mucina and Rutherford, 2006). However, there exists variation in the climatic and environmental conditions over this large area from West to East and North to South; this variation often presents as a gradient from high to low (temperature, precipitation, etc.). (See Chapter 1.)

One such gradient occurs along the coastal areas, where the diversity of conditions over the region would inevitably impact the resources that would have been available to hunter-gatherers. There are different patterns of botanical remains found in archaeological sites along the Cape coastal gradient (Wells, 1965; Deacon, 1967, 1976, 1979; Parkington and Poggenpoel, 1971; Liengme, 1987; Patrick, 1989; Orton *et al.*, 2011; Orton, 2014). This invokes the question - are these differences due to the variation in climatic and environmental conditions? Understanding how climate and environmental variation directly affects resources available to hunter-gatherers is fundamental to our interpretation of archaeological material and guides our attempts at reconstructing the possible lifeways of hunter-gatherers. The main objective of this chapter is to evaluate the nature of geophyte resources across the coastal plain of the GCFR during different seasons, across a large regional east-west gradient.

In the past, geophyte communities were surveyed in the immediate vicinity of archaeological sites, which included descriptions of their seasonal growth patterns and estimations of their nutritional content to assist the interpretation of geophyte remains found in archaeological sites in the GCFR (Wells, 1965; Parkington and Poggenpoel, 1971; Deacon, 1976; Liengme, 1987). This method makes valuable localised interpretation of geophyte remains possible but is limited in its ability to describe the impact geophytes could have had on larger patterns of hunter-gatherer subsistence and behaviour.

Seasonal movement of hunter-gatherers across vast landscapes in response to seasonal resource variation is one such larger pattern of hunter-gatherer behaviour that remains a topic of interest to archaeologists and paleoanthropologists (Sealy *et al.*, 1986; Parkington, 2001; Loftus *et al.*, 2019; Marean, Cowling and Franklin, 2020). The broad patterns of geophyte seasonality: when they are most abundant in the landscape (emergence in Spring in the West Coast, and Summer in the East Coast), has been used as partial evidence to support theories on seasonal mobility of hunter-gatherers (Deacon, 1976; Parkington, 1976). Arguably, just as important as the seasonal abundance of geophytes, is the cycling of seasonal scarcity of this resource. The seasonal unavailability of any resource might have been a limiting factor influencing hunter-gatherer subsistence and mobility strategies most profoundly. The data presented in this chapter are an actual assessment of seasonal variation of geophyte resources across the entire region. This data can be used to predict whether geophyte resources (or lack thereof during certain times) would have influenced hunter-gatherer mobility, which allows us to test previous hypotheses predicting patterns of hunter-gatherer mobility across the region.

The description of resources that would have been available to humans across the South Coast region has become an important tool to model past human behaviour during the emergence of human modernity in the MSA (Marean *et al.*, 2015; Marean, Cowling and Franklin, 2020). In this methodology all the resources available to hunter-gatherers in the current climate and environment are described, to construct a quantification of the resources in the landscape available to humans (De Vynck, Anderson, *et al.*, 2016; Botha *et al.*, 2020). The purpose of this detailed resource data is to form the baseline data to model past human behaviour under different climatic and environmental conditions in the past (Marean *et al.*, 2015; Marean, Cowling and Franklin, 2020). The reconstruction of the regional climate and environment to predict past human behaviour, relies on datasets that represent the largest possible variety of analogues habitats from the current environment (Marean *et al.*, 2015). The data presented in this chapter will serve as the widest array of data captured to date, on the geophyte resource across the current rainfall gradient that exists across the GCFR, over the biggest variety of geological substrata possible. Detailed data of any resources can help future modelling studies being conducted in the region, unravel the story of how human modernity emerged in the region and what role geophytes played in early modern human subsistence (Henshilwood and Marean, 2013).

4.1.1 Seasonality

In this chapter, the seasons are defined on a phenological basis where the physiology and morphology of plants are used to indicate seasonal cycling (Pierce and Cowling, 1984). When referring to specific seasons, they consist of the following months:

Summer: December-February, Autumn: March-May, Winter: June-August, Spring: September-November

As discussed in Chapter 1, in the GCFR, a predominantly winter rainfall regime exists, where the vast majority of the annual precipitation falls between May to October (Bradshaw and Cowling, 2014). This region can be further subdivided into temporal distribution of rainfall, where there exists a gradual transition from a strict Winter-rainfall regime in the West, to a bi-modal rainfall pattern on the South Coast, to an all-year rainfall pattern in the East Coast (Barrable, Meadown and Hewitson, 2002; Chase and Meadows, 2007; Bradshaw and Cowling, 2014) (Figure 4.1). The mean annual precipitation on the West Coast is considerably lower than that of the southern Cape.

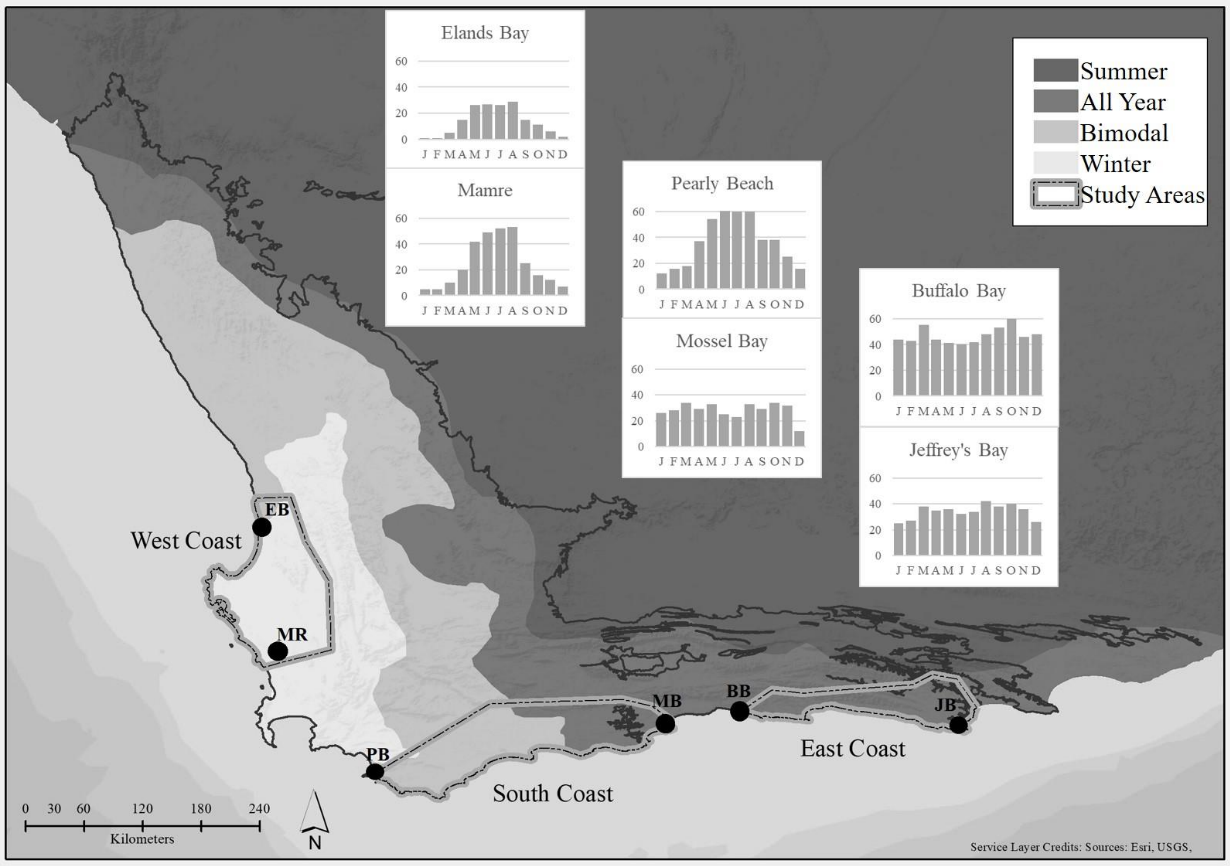


Figure 4.1 Map illustrating the rainfall seasonality across the GCFR and the annual precipitation within the three study regions. Map adapted from Bradshaw & Cowling, 2014 showing the rainfall seasonality in the GCFR (shading, after Schulze 1997) and percentage winter rainfall (May-Oct). Annual precipitation data are 50-year average rainfall observed in the three study areas, sourced from South African Weather Service.

4.1.2 Vegetation in the regions

The edaphic and geological environments within the GCFR have just as significant impact on the vegetation in the GCFR as rainfall (Bergh *et al.*, 2014, Table 4.1). The broad edaphic environments in each region and the vegetation categories which persist in each region are discussed below (as described in Mucina and Rutherford, 2006).

4.1.2.1 West Coast

A relatively broad, flat, coastal plain exists along the West Coast, built up through the erosion of sandstones in the Cape Fold Mountains since the Cretaceous period, depositing large sand belts (Truswell, 1977; Johnson, Anhauesser and Thomas, 2006). These ancient sands are interspersed with and, in some cases, underlain by shale (in the Swartland) and granite outcrops.

The different rocks in this region have eroded to develop unique soils, which support unique vegetation types. Shale developed to clay-rich soils, which support Renosterveld vegetation. Granite similarly erodes to clay-rich soil, which often has a high silica component, and usually supports Strandveld or Renosterveld vegetation. Cretaceous sands support Sand Fynbos, Strandveld and Dune Cordon vegetation. Other unique features of the West Coast are the meandering rivers and network of salt marshes over this region. Ancient inland lagoons, which have subsequently lost any connection to the ocean, have developed into Salt Marshes, such as Rocherpan north of Velddrif. Each vegetation type and its characteristics are described in Table 4.1.

4.1.2.2 South Coast

The South Coast consists of a broad coastal plain known as the Agulhas Plain, which contains similar Cretaceous sands to the West Coast. Shale is a far more dominant feature in this region, with Enon and Bokkeveld Shales being the most common (Johnson, Anhauesser and Thomas, 2006). These rocks have eroded into deep, clay-rich soils, which support intensive agriculture in that region. Historically, before the advent of agriculture, these areas would have supported Renosterveld vegetation. Extensive Limestone shelves exist parallel to the coast in this region which is often associated with Aeolianites, together these geological features produce a unique edaphic environment which has a relatively high pH, in comparison to the general acidic soils of the GCFR. These areas support unique Strandveld and Fynbos vegetation. (See Table 4.1 for further detail.)

4.1.2.3 East Coast

To the east of the Agulhas Plain, the Cape Fold Mountains protrude from the interior and stretch to within 10km of the coast. The steep slopes of this mountain range extend offshore on the continental shelf, which drops off steeply into the ocean, resulting in a very narrow coastal plain with heavily incised rivers. The Cape Fold Mountains consist primarily of Table Mountain Sandstone, which has eroded into sand, which dominates the GCFR coastal plains. Similar Enon and Bokkeveld Shales exist in the higher elevations of the coastal plain here, which support Renosterveld and Fynbos. In the ancient river courses and valleys of the East Coast, unique conglomerate sediments are found, which erode to clay-rich soils. These soils and geology most commonly occur in the highly eroded, incised rivers in the region, on these steep slopes a unique vegetation type is supported which technically belongs to a different biome: Albany Thicket. Thicket vegetation is defined as a semi-succulent thorny scrubland which is ecologically very different to vegetation types of the Fynbos biome, as it is not adapted to fire and subsequently many long-lived species occur in Thicket vegetation (Mucina and Rutherford, 2006). Another vegetation type that is unique to the East Coast is the coastal grasslands; this vegetation type is found on the plains, above the highly incised rivers, where deep clay soils support unique plant communities and species. See Table 4.1 for full descriptions of vegetation types.

Table 4.1 Vegetation types occurring in the study areas, with definitions according to Mucina and Rutherford, 2006.

Vegetation Types	**Regions**	**Description**
Coastal Grasslands	East Coast	Coastal Grasslands occur in the coastal regions of the Eastern Cape in the ecotone between Fynbos, Thicket and Strandveld. Due to the flat aspects of the terrain, where this vegetation type occurs, fires can be frequent. The high frequency of fire has led to the unique vegetation of Coastal Grasslands that has a high C4 and C3 grass component. This vegetation type occurs on the steps above highly incised rivers on the coastal plain in deep clay soils. Where fire is less frequent, and the slope becomes steep (due to dunes or incised rivers), shrub species that occur in Strandveld and Thicket can encroach. This vegetation type has a very high species diversity and abundance of geophytes. Areas, where this vegetation type occurs, are highly suitable for agriculture, and a high percentage of this vegetation has been transformed.
Dune Cordon	East Coast, South Coast, West Coast	Dune cordon vegetation comprises a floristically distinct form of subtropical thicket associated with recent (Holocene) marine sands that are found along a narrow coastal margin. Soils are deep but poorly developed, and highly alkaline. The associated dune thickets are not fire-prone. This vegetation can have dense patches of geophyte species which specialise on the alkaline and saline conditions in these soils.
Forest	East Coast	Forests in the GCFR are limited to areas that receive sufficient rainfall to sustain large tree growth, and where fires are less likely to occur. These environments are present in mountainous ravines, coastal dunes and on the coastal plain of the southern Cape. Famous Afromontane forests occur from Knysna to Humansdorp in the southern Cape. Forests are dominated by large trees, where the tree crowns overlap by no less than 75 %. Due to the litterfall from the canopy, the top layer of soil in these environments consists of nutrient-rich hummus. Most commonly, the underlying soil is sand. Common tree genera include *Podocarpus* spp., *Celtis* spp., and *Afrocarpus* spp.

Vegetation Types	**Regions**	**Description**
Granite Strandveld	West Coast	Strandveld is a mosaic of subtropical thicket and fynbos elements associated with old (late Cenozoic) dune sands. While Restionaceae (*Thamnochortus* spp.) are common, species richness of Proteaceae and Ericaceae is low. Owing to the low flammability of thicket species (Burger and Bond, 2015; Calitz, Potts and Cowling, 2015), and the low cover of other shrubs, Strandveld is less prone to fire than surrounding fynbos vegetation types. Granite outcrops on the West Coast give rise to a unique form of Strandveld, where the distinctly different soil that develops through the erosion of granite, and accumulation of plant matter, usually support a large geophyte community, many species are endemic to this vegetation type.
Limestone Fynbos	South Coast	Fynbos is the most widespread vegetation of the GCFR and is fire-prone evergreen shrubland; it is associated with nutrient-poor, sandy soils. Limestone fynbos grows on shallow, alkaline sands derived from late Cenozoic limestones, which sets it apart from other Fynbos vegetation which usually has acidic soils, while the limestone renders the soils of limestone fynbos alkaline.
Mountain Fynbos	East Coast, South Coast, West Coast	Mountain Fynbos occurs in the mountainous regions of the GCFR. Although no mountainous regions were sampled during this study, some areas within the coastal plains with high elevations were sampled. When these areas consisted of predominantly Table Mountain Sandstone outcrops, the vegetation was defined as Mountain Fynbos, as the structure and species composition was found to be similar to the true mountainous regions of the GCFR. This vegetation is similar in structure to other Fynbos types.
Renosterveld	East Coast, South Coast, West Coast	Renosterveld occurs on relatively fertile, clay-rich soils derived from shale and mudstone; it is a fire-prone, evergreen shrubland with an understory of grasses and high biomass and diversity of USO species (Procheş *et al.*, 2006). Renosterveld of the Cape south coast (south of Langeberg and Riviersonderend Mountains) is considered a distinct type with a high abundance of largely C4 grasses and between 50 – 70 % plant cover. West Coast Renosterveld may occur on granite derived soils, which often support many species of endemic geophyte species.

Vegetation Types	**Regions**	**Description**
Riparian vegetation	East Coast, South Coast, West Coast	Riparian vegetation is an azonal vegetation type associated with alluvial soils, in this case, fertile sandy loams, of the major rivers in the regions. Depending on the geology through which rivers cut Riparian vegetation can be very diverse. On the West Coast, the primary river system that was sampled belongs to the Berg River Catchment. Riparian vegetation along this catchment consists of primarily similar vegetation to the surround. In the South Coast, this vegetation comprises a tree or tall shrub component dominated by the winter-deciduous *Acacia karoo*. In the East Coast, due to the incised rivers, Riparian vegetation usually occurs on bedrock at a steep aspect. Exceptions are the alluvial plains, where deep clay soils sustain succulent-shrub vegetation related to Thicket vegetation. See below for further detail.
Salt Marsh	East Coast, South Coast, West Coast	Salt Marshes are associated with Inland saline vegetation. The salinity in these environments originates from salt-bearing substrates, mineral-rich aquifers or from other forms of water that evaporate to leave behind the high concentration of salt. These environments exist in areas with prolonged seasonal drought, with an endorheic (closed nature of drainage) system. On the West Coast, these Salt Marshes originated from coastal lagoons which became severed from the ocean. The Salt pans and marshes of the Agulhas Plain and East Coast originated from remnants of Pleistocene marine transgressions. Often the soils of these pans are deep clay, with origins from shale in the region. Most commonly the salt marshes and pans of the West Coast and South Coast are fringed by *Sarcocornia* and *Salicornia* species, which are semi-succulent, perennial shrubs. While in the East Coast Salt Marshes contain other halophile plants like *Typha capensis* and *Cyperus congestus*. There exist low geophyte abundance and diversity in this vegetation type.
Sand Fynbos	East Coast, South Coast, West Coast	Sand Fynbos is associated with deposits of leached, acidic, wind-blown sands. While appearing similar in structure to other fynbos types, these vegetation types have highly distinct flora, therefore treated them as different vegetation types.

Vegetation Types	**Regions**	**Description**
Strandveld	East Coast, South Coast, West Coast	Strandveld is a mosaic of subtropical thicket and fynbos elements associated with old (late Cenozoic) dune sands. While Restionaceae (*Thamnochortus* spp.) are common, species richness of Proteaceae and Ericaceae is low. Owing to the low flammability of thicket species (Burger and Bond, 2015; Calitz, Potts and Cowling, 2015), and the low cover of other shrubs, strandveld is less prone to fire than surrounding fynbos vegetation types. The dune cordon vegetation comprises a floristically distinct form of subtropical thicket associated with recent (Holocene) marine sands that are found along a narrow coastal margin. Soils are deep but poorly developed, and highly alkaline. The associated dune thickets are not fire-prone.
Thicket	East Coast, South Coast,	Thicket is defined as semi-succulent thorny shrub vegetation which occurs in the all-year rainfall, to summer rainfall areas of the Eastern Cape. Although it is not associated with any specific soil type, its selective force is rather fire, where the vegetation type often occurs and competes with Fynbos and Renosterveld vegetation. In areas where fire is less pervasive thicket can encroach upon Fynbos and Renosterveld. Thicket is then most commonly associated with refugia such as valleys. The succulent component of the vegetation is most commonly made up of *Euphorbia* spp. and ‘Spekboom’ (*Poritcularia afra*). It is a very variable vegetation type, but generally has a large C4 grass component and a biodiverse geophyte component.

4.2 Methods

4.2.1 Geophyte abundance and biomass

To capture seasonal and inter-annual variation in geophyte abundance, sampling was conducted over four years during autumn and spring between March to April, and August to November respectively in 2012, 2014, 2015 and 2016. Spring is a time of maximum apparency of geophytes in the study areas (Johnson, 1992; De Vynck, Cowling, *et al.*, 2016), whereas autumn is a time of minimum apparency of geophytes in the winter rainfall region (Pierce and Cowling, 1984). A hundred plots were sampled in each study area in spring, and 50 plots in each study area in Autumn. In total, 450 plots of 5×5 m^2 were sampled, with the percentage of randomly placed plots in each vegetation type roughly proportional to the area in which the vegetation types occur in the study area.

The species richness and abundance of visible, edible geophytes was surveyed within each plot. Voucher specimens of each species were collected and housed in the Ria Olivier Herbarium (Nelson Mandela Metropolitan University, Port Elizabeth) for the specimens collected in 2012 and the Bolus Herbarium (University of Cape Town) for those collected in 2014-2016. It must be noted that the GCFR experienced the worst drought in recorded history from 2014 to 2018. This will undoubtedly influence geophyte emergence during this time and the resulting data is likely an underrepresentation of the geophyte diversity and abundance in comparison to non-drought years. However, while absolute values of geophyte abundance and biomass may have been impacted, the patterns of geophyte abundance and biomass observed over a large regional scale are likely to reflect regional differences.

Edibility categories (edible, poisonous or unknown) were assigned to species encountered using the available ethnobotanical literature as presented in the master list: Table 3.5.

For each edible species, the first 10-15 plants found were excavated and the USO depth, length and biomass (wet weight) recorded. These values were used to generate a mean edible biomass per species; the plot-level species abundances were multiplied by these mean values to obtain an estimate of the biomass per plot.

In each plot the resource rating was estimated as an average rating of the edible geophyte resources observed in each plot. This average rating is derived from the ratings of species (presented in the previous chapter) contained in each plot.

4.2.2 Geophyte energy content and relative carrying capacity

The kilojoule content of USOs of each species presented in the previous chapter was used, together with the biomass per species, per plot, to determine the kilojoules contained in each plot (kJ/25 m^2). These values were extrapolated from the plot scale (25 m^2) to obtain an estimate of the kilojoules per hectare (kJ/ha). Once these values had been calculated they were divided by the estimated daily energetic requirement of a hunter-gatherer of small stature (8400 kJ/day) (Speth and Spielmann, 1983; Lee, 1997). These resulting values are an estimate of how many people may be potentially sustained by the geophyte resources per hectare, for a day. These values are termed the 'Relative Carrying Capacity', a value that provides a gauge of the geophyte resources in different areas, rather than a robust prediction.

4.2.3 Statistical analysis

As is often the case with ecological data, the data set analysed here was not normally distributed and often skewed. For this reason, the Konietschke's Test was used to analyse the variation in abundance, biomass, relative carrying capacity and quality of the geophyte resources across all regions, seasons and vegetation types.

The associations and interactions (in statistical terms) between region and type of vegetation were further analysed by performing correspondence analysis on two variables: the relative carrying capacity and the quality of the geophyte resources. During the correspondence analysis, the entire data set consisting of multiple variables can be summarised in two-dimensions. Each dimension captures multiple variables and presents a determinate proportion of the variability observed in the data (inertia). Correspondence analysis reveals the relative relationships between and within two groups of variables, based on data given in a contingency table. The contingency table (two-way table) compare the relative values between different variables, rather than comparing absolute values. Correspondence analysis allows predictions on the measure of strength of association between variables. This made it possible to determine statistically which variables had the most profound effect on relative carrying capacity and quality of geophyte resources.

4.3 Results

Geophyte abundance, biomass, relative carrying capacity and nutritional quality were highest in all regions during spring, whereas these values were considerably lower during autumn and highly variable across different vegetation types. The results on the regional and seasonal variation in geophyte resources will be discussed first, followed by the results on the variation of geophyte resources between vegetation types.

4.3.1 Regional and seasonal variation in geophyte resources

The highest values of relative carrying capacity (RCC) were recorded during spring in all regions where the average observed RCC was 221.6 Indv.ha^{-1} in the East Coast, 145.82 Indv.ha^{-1} in the South Coast and 141.37 Indv.ha^{-1} in the West Coast (see Table 4.2). There is no significant difference between the geophyte biomass, RCC and quality of the resource between the three regions during spring (see Table 4.2 and Figure 4.2). There is a significant difference between the abundance of geophytes in the South Coast and the East Coast, where the South Coast had a significantly higher abundance of geophytes, although this did not translate to significantly higher carrying capacity (see Table 4.2).

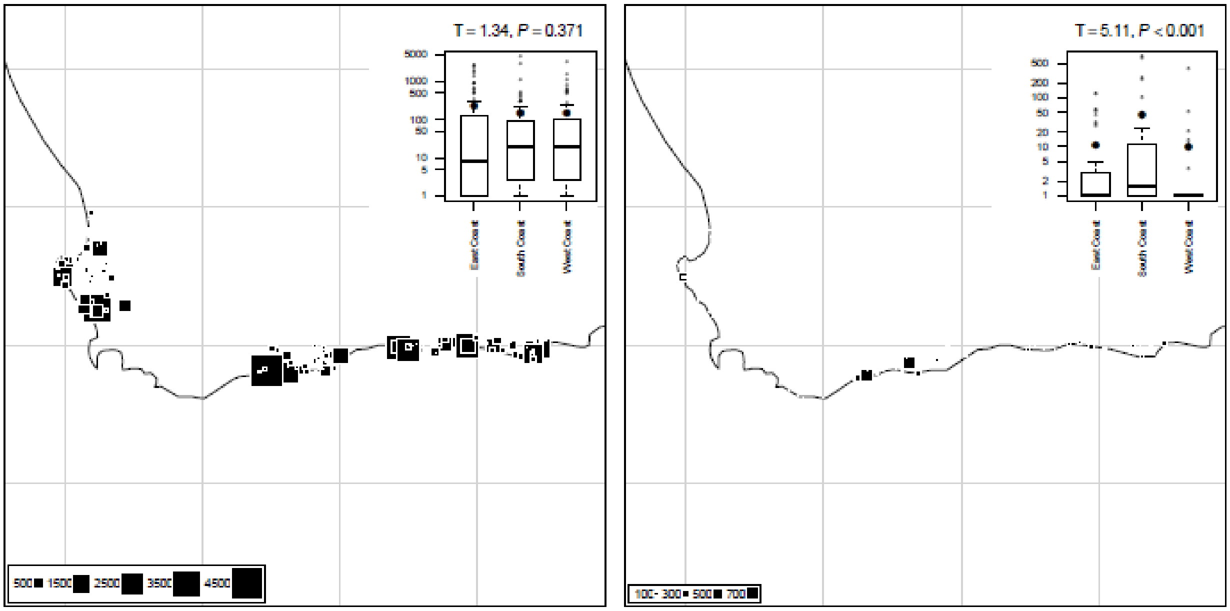
Geophyte biomass, RCC and resource quality dropped significantly in autumn in comparison to the high values observed during spring (see Table 4.2). The West Coast had the sharpest decline in relative carrying capacity from 141.37 Indv.ha^{-1} (spring) to a mere 9.40 Indv.ha^{-1} (autumn). The decline in the South Coast from 145.82 Indv.ha^{-1} to 43.73 Indv.ha^{-1} was less pronounced, but still significant. (See Table 4.2 and Figure 4.2.)

Patterns of abundance, biomass, RCC and quality of geophyte resource did not differ between the South Coast and East Coast during autumn. In the West Coast the values are significantly lower during autumn (see Table 4.2).

Table 4.2 Mean Values of Abundance(Abnd), Biomass (Bmss), Relative Carrying Capacity (rCrrC), and Resource Quality (Qlty) by Season, Type of Vegetation, and Region. Carrying Capacity Based on a Dietary Requirement Per Person of 8400 kJ d−1, Quality. (y Units for rCrrC and Qlty are Indv ha−1 and rCrrC USO−1 (equivalently, Indv ha−1 USO−1), where Indv represents individuals/people and USO represents underground storage organ. Empty cells represent vegetation types that do not exist in a region. Bold figures are highlighted in the text.

	East Coast					South Coast					West Coast				
	n	Abnd (#USO/25m^2)	Bmss (kg.ha^{-1})	rCrrC (indv.ha^{-1})	Qlty	n	Abnd (#USO)	Bmss (kg.ha^{-1})	rCrrC (indv.ha^{-1})	Qlty	n	Abnd (#USO)	Bmss (kg.ha^{-1})	rCrrC (indv.ha^{-1})	Qlty
Season															
Spring	100	45.72	535.38	**221.60**	2.28	100	93.47	652.86	**145.82**	1.41	100	69.58	259.79	**141.37**	1.61
Autumn	50	13.26	39.22	**10.88**	0.31	51	50.29	55.95	**43.73**	0.46	50	5.68	18.24	**9.40**	0.13
Vegetation Type															
Coastal Grassland	5	77.20	2873.45	**470.14**	**3.91**	0									
Dune Cordon	15	99.40	1173.14	**671.56**	**3.62**	14	60.93	623.43	**360.98**	1.59	18	22.67	56.15	22.21	0.45
Forest	21	31.57	258.17	87.59	1.31										
Granite Strandveld											12	150.58	379.11	**307.01**	2.03
Limestone Fynbos						24	42.79	124.81	67.62	1.22					
Limestone Strandveld											13	20.23	61.60	20.11	0.46
Mountain Fynbos	5	17.20	91.09	74.31	**3.09**	4	77.75	17.47	11.29	0.04	5	31.00	222.01	**236.30**	2.97
Renosterveld	11	7.82	49.24	27.77	0.49	39	120.51	475.94	72.94	0.68	27	73.30	226.33	117.60	1.49
Riparian	24	29.62	101.01	104.44	1.25	15	128.87	1621.79	54.13	0.40	13	108.85	751.87	**335.86**	0.83
Salt Marsh	4	111.75	1431.99	0.00	0.00	1	0.00	0.00	0.00	0.00	9	9.00	5.76	4.96	0.20
Sand Fynbos	34	16.03	58.14	35.13	1.34	33	53.27	40.71	69.70	0.91	26	14.23	27.98	20.88	1.33
Strandveld	15	48.40	449.30	**267.85**	2.61	20	66.00	557.86	**557.86**	2.53	27	28.30	102.04	35.25	0.99
Thicket	16	5.88	15.51	2.79	2.79	1	10.00	0.28	0.28	0.02					
Overall	150	34.90	370.00	151.36	1.63	151	78.89	451.26	111.34	1.09	150	48.28	179.27	97.38	1.11

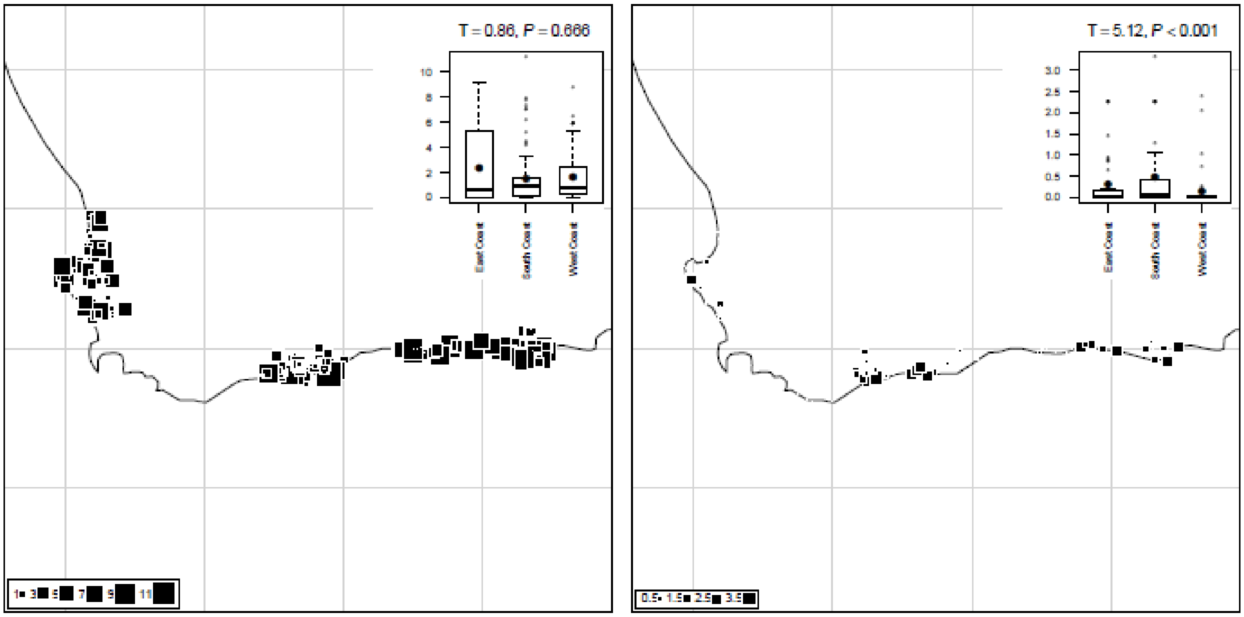
A map of the distribution of RCC over all the regions is presented in Figure 4.2 and illustrates how variable relative carrying capacity was over the regions, especially during autumn, where significant differences between the regions were observable.



(a) Spring. (b) Autumn.

Figure 4.2 Maps of the relative carrying capacity (Indv ha−1) of each region on a lat-long grid of the sites sampled. Inset boxplots show the distribution of the data in each region (Indv ha−1), (y-axis is nonlinear, the filled circle are the mean value); test statistics appear above the boxplots.

The resource quality was significantly higher in spring compared to autumn but did not differ significantly between regions during spring. During autumn the South Coast had a significantly higher quality of geophytic resources (see Table 4.2 and Figure 4.3) in comparison to the other regions which had very low quality of geophyte resources.



(a) Spring.

(b) Autumn.

Figure 4.3 Quality of USO resources (Relative Carrying Capacity USO−1) of each region on a lat-long grid of the sites sampled. Inset boxplots show the distribution of the data in each region (filled circle shows the mean value): test statistics appear above the boxplots.

4.3.2 Geophyte resource variation across vegetation types

Vegetation type seems to influence the quality of the geophyte resources found (see Table 4.2 and Figure 4.3). Coastal Grassland, Dune Cordon and Mountain Fynbos had high-quality geophyte resources in the East Coast, but these high values were not found in other regions, where Dune Cordon and Mountain Fynbos scored low ratings in other regions (see Table 4.2).

In spring, higher absolute values of all four variables were observed in most vegetation types when compared to autumn (see Table 4.3). Geophyte communities were consistent (in abundance and composition) within vegetation types that occurred across regions. In other words, the effect of vegetation type appeared to be stronger than the effect of region on geophytic resources.

In spring, Coastal Grasslands, Dune Cordon and Strandveld contribute the bulk of RCC observed in the East Coast (see Figure 4.4). Additionally, Coastal Grasslands and Dune Cordon had very high quality of resources (see Table 4.3). Similarly, in the South Coast, Dune Cordon and Strandveld contribute the bulk of the observable RCC (see Figure 4.4). Granite Strandveld, Mountain Fynbos and Riparian vegetation contributed the bulk of the RCC in the West Coast (see Figure 4.4)

In autumn the absolute values of RCC in the three regions were very different. Strandveld and Limestone Fynbos contributed most significantly to RCC during autumn in the South Coast while Dune Cordon and Sand Fynbos are secondarily important. Dune Cordon constituted the largest amount of RCC in the East Coast. Granite Strandveld contributed almost all the RCC during autumn on the West Coast (see Table 4.3 and Figure 4.4). Thicket and Salt Marshes contributed little to no geophyte resources in all regions (see Table 4.3)

Table 4.3 Two-way table of mean values of Relative Carrying Capacity. Values of zero indicate that no edible geophytes were found. Missing values indicate that the vegetation type was not sampled/does not occur in that region. Bold figures are highlighted in the text.

Vegetation type	East Coast		South Coast		West Coast	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
Coastal Grassland	**470.14**					
Dune Cordon	**1097.04**	**33.34**	**670.74**	**51.21**	31.73	3.17
Forest	122.51	17.73				
Granite Strandveld					**406.00**	**109.02**
Limestone Fynbos			52.53	**112.87**		
Limestone Strandveld					32.68	0.00
Mountain Fynbos	92.88	0.00	0.00	11.29	**295.37**	0.00
Renosterveld	43.09	0.95	107.59	11.06	186.06	1.21
Riparian	152.87	7.57	86.89	5.07	**545.77**	0.00
Salt Marsh	0.00	0.00	0.00	0.00	7.44	0.00
Sand Fynbos	50.62	6.75	42.59	33.73	31.93	0.00
Strandveld	**438.37**	12.09	**290.81**	**145.62**	47.46	0.36
Thicket	4.24	0.36	0.00	0.18		

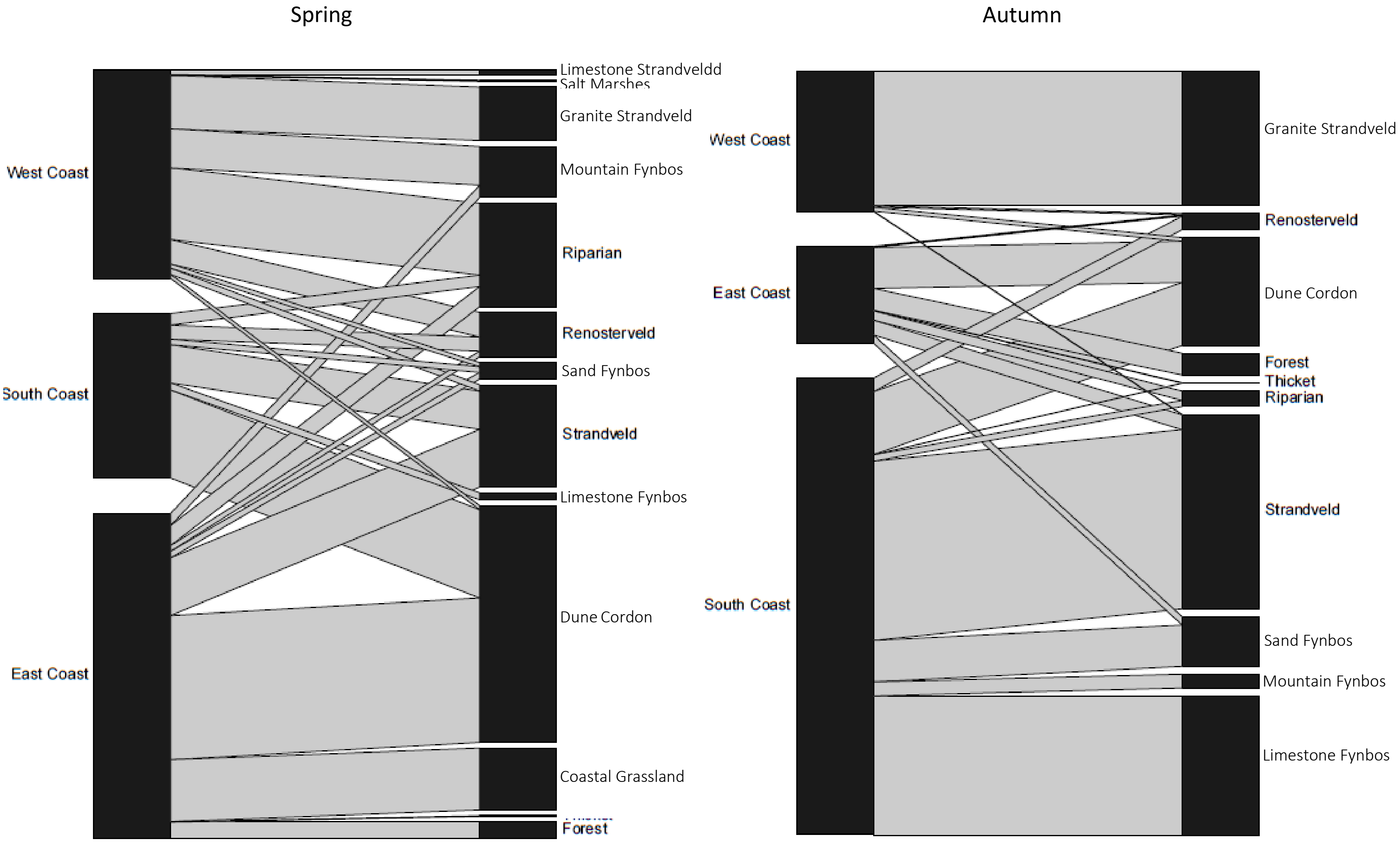


Figure 4.4 Web-plot of the partition (i.e., the proportional division) of the mean value of relative carrying capacity associated with each vegetation type, and region conditioned on season: spring and autumn respectively. Categories ordered based on the first dimension of the correspondence analysis. Black rectangles show the overall proportion of relative carrying capacity contributed by each region and vegetation type, while the grey rectangles show the proportion of relative carrying capacity each vegetation type contributes within each region.

When a correspondence analysis is performed on carrying capacity of geophytes, the vegetation types, regions or seasons which have similar or dissimilar geophyte resources can be identified. In Figure 4.5, these relationships are illustrated with a regression plot, where vegetation types, regions or seasons with similar patterns of geophyte resources are grouped together on this matrix, while vegetation types, regions or seasons that are dissimilar are far removed.

Broadly speaking, three groups of vegetation types emerge, which share similar patterns of relative geophyte carrying capacity. Within each of these groupings, there are further sub-divisions into two main sub-groups. Within these groups and sub-groups, relative carrying capacity changes in more or less the same way across the regional/seasonal combinations. This analysis delivers clear results that the vegetation types shared by the South Coast and East Coast mirror each other in the RCC between the seasons, indicating that RCC changes in a similar way across vegetation types, regardless of season (see Figure 4.5). The West Coast differs substantially to the other regions. During spring, the vegetation types that contain geophyte resources on the West Coast overlap to an extent with those that contain geophyte resources in the regions with a bimodal and all-year pattern of rainfall (i.e., South Coast and East Coast). During autumn the overlap is diminished, with only Granite Strandveld providing any geophyte biomass (109.02 Indv.ha^{-1}) (see Table 4.2).

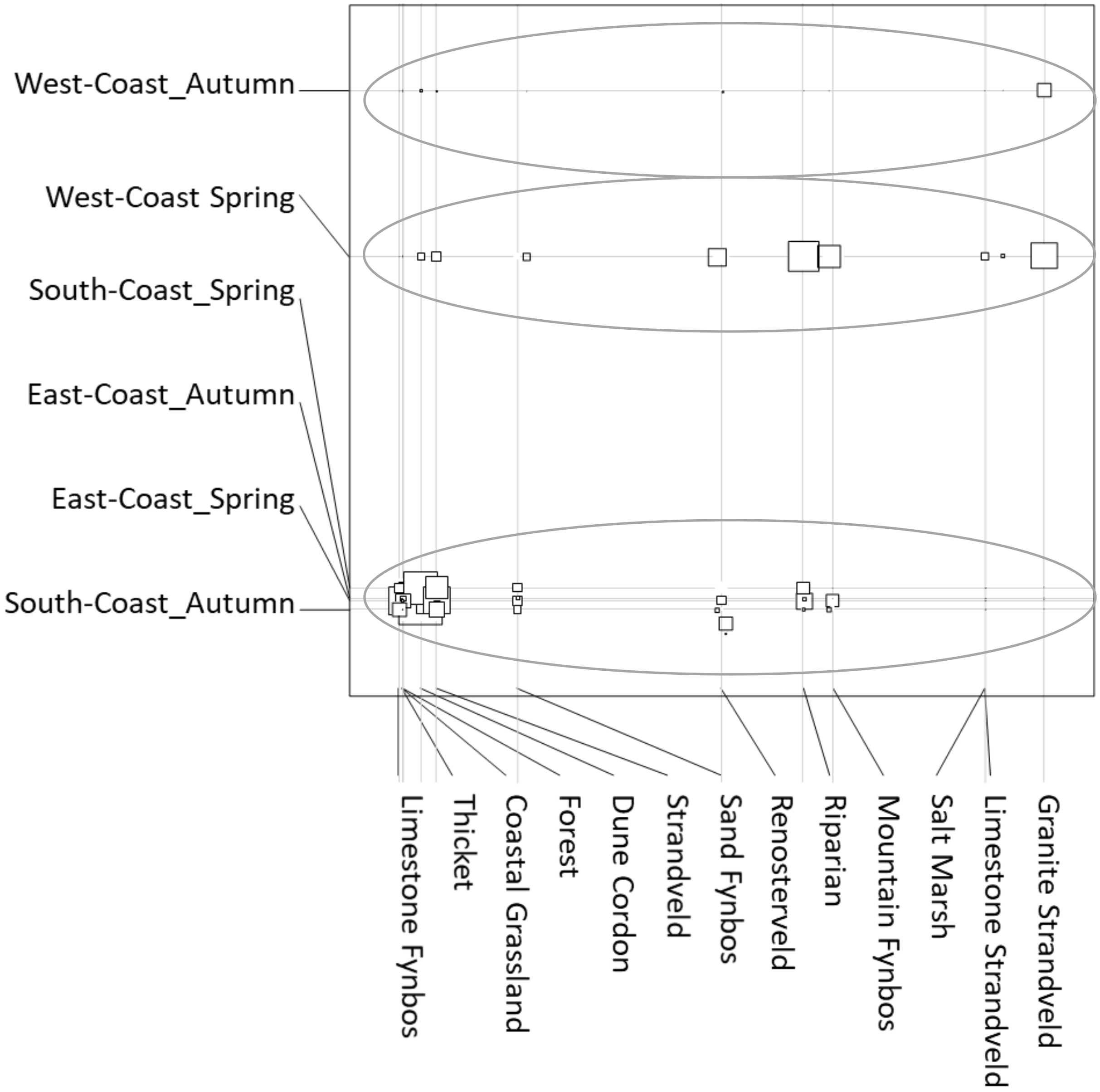


Figure 4.5 Regression plot of the first dimension (explains 56.96 % of the inertia) of correspondence analysis of mean values of the Relative Carrying Capacity by Vegetation Type and Region conditioned on Season. Blocks represent relative carrying capacity values of vegetation types, regions and seasons, where the size of the block indicated the relative carrying capacity values. The ovals circling three distinct groups, which have a similar pattern of relative carrying capacity.

This analysis also clearly highlights which vegetation types could offer high RCC, within which season and region. Six vegetation types cluster together tightly and are most important for geophyte resources in bimodal and all-year rainfall regions of the South Coast and East Coast. These are Limestone Fynbos, Thicket, Coastal Grassland, Forest, Dune Cordon, and Strandveld. The second clustering of vegetation types, distinct from the vegetation types important in the bimodal and all-year rainfall regions, are Granite Strandveld, Riparian vegetation, Mountain Fynbos, and Renosterveld.

The patterns of RCC in the different vegetation types that occur do not change substantially between spring and autumn (even if absolute values change considerably) because the East Coast and South Coast regions cluster together regardless of season. The same types of vegetation provide optimal foraging returns regardless of season.

4.4 Discussion

Geophytic resources in the GCFR can be very abundant, although patchy in space and time. Combined with information on species biomass and estimates of kilojoules yielded per species, relative carrying capacity (RCC; an estimate of how many people may be potentially sustained by the geophyte resources per hectare for a day), could be calculated at plot level. These data indicated that there are certain conditions within which the relative carrying capacity of geophytes is maximised and similarly certain conditions when geophytic resources are absent. In spring, regardless of region or vegetation type, geophyte carrying capacity and quality (palatability and nutritional value) are very high, but in autumn geophytic resources are restricted to certain regions and vegetation types and in far lower absolute values. Understanding the variation of geophytic resources in the time of relative scarcity of the resource is essential, as this might have been a limiting factor influencing hunter-gatherer subsistence and mobility strategies most profoundly. The discussion has been divided between the effect of region and season on geophyte resources and the variation between vegetation types.

4.4.1 Regional and seasonal variation in geophyte resources

The geophytic resource base differed between the study regions with the winter rainfall region being distinctly different from the bimodal and all-year rainfall regions, except during spring. The West Coast is unique in the types of vegetation that occur there, but the most profound difference in this study was the extreme seasonality of geophyte resources, with the majority being apparent in spring and almost entirely absent in autumn.

The strict winter-rainfall region leaves the West Coast a relatively desolate, dry place during the autumn months. In this region, hunter-gatherers would therefore have had to rely on other sources of food in the landscape during autumn or would have been forced to move to other areas (like the nearby mountainous regions) or onto coastal regions with shellfish resources seasonally. This seasonal movement of hunter-gatherer groups dictated by the availability (or absence) of food resources has been suggested by researchers studying the archaeology of the West Coast and Cederberg Mountains (Parkington, 1972).

In contrast to the West Coast, the South Coast and East Coast display distinctly different resource patterns and there are many similarities between these later two regions. In the bimodal and all-year rainfall regions, geophyte resources are less seasonal, and some even remain obtainable and relatively abundant in autumn. Furthermore, patterns of distribution of geophyte resources within vegetation types remain constant during spring and autumn in these regions, even if the absolute values are significantly lower in autumn compared to spring. Similar a-seasonality of resources has been described in other studies for the South Coast, where no significant differences in the return rate of foraging of edible plant resources was found between seasons (Botha *et al.*, 2020). Due to the relative predictability of geophyte resources across the seasons, foraging behaviour in these regions could have been similar in both spring and autumn.

Although it is helpful to consider the relative carrying capacity across the region and season, this variable does not fully capture how attractive these geophyte resources might have been to hunter-gatherers. The quality of resources measured in this study can tell us more about the relative palatability and nutritional quality of geophyte resource. When we consider variation in resource quality between seasons it is clear that the resource quality is considerably lower during autumn in all regions. The lower quality of geophyte resources in autumn is a result of the low quality of species available to foragers during autumn. Most of the species sampled in autumn were ranked lower (rankings 1-3) make up the bulk of the relative carrying capacity sampled during autumn. The higher ranked geophyte species (ranking of 4 or 5) were mostly observed in spring (See Table 3.5). The specific dynamics of the variation in geophyte phenology and the variation in the availability of geophyte resources seasonally will be discussed in further detail in Chapter 5.

What is clear from these results is that variation in rainfall seasonality has a significant impact on the seasonal availability of geophyte resources. Under the current climate, geophyte resources could have been a limiting factor in the winter rainfall region of the West Coast, which could have impacted hunter-gatherer mobility. The emergence of geophytes in great abundance in late spring has been argued to have driven the movement of hunter-gatherers to the interior mountainous regions of the West Coast (Parkington, 1972), however there would have been an abundance of geophyte resources available in the coastal region at this time. In the bimodal rainfall region of the South Coast geophyte resources are more a-seasonal and could have offered sufficient nutrition in both spring and autumn under the current climate. This is corroborated by recent parallel resource studies and modelling of hunter-gatherer mobility in the South Coast (Botha *et al.*, 2020; Wren *et al.*, 2020). It has been suggested that geophyte foraging occurred in summer in the East Coast, based solely on the phenology of certain taxa found in the archaeological record (Deacon, 1976). Based on the relative carrying capacity of geophyte resources presented in this chapter, geophytes could have been foraged year round in the all year rainfall region of the East Coast and would not have forced hunter-gatherer groups to move to other regions to exploit other more abundant resources.

These results also show that changes to the current distribution of rainfall seasonality due to glacial climate change could have affected the geophyte resources available to hunter-gatherers in the past. Throughout the MSA there were various glacial phases during which time early modern humans persisted in the region (Quick *et al.*, 2015; Braun *et al.*, 2018). It has been hypothesised that the resources available throughout the MSA supported early modern humans during the emergence of human modernity (Marean, Cowling and Franklin, 2020).

According to recent climate models it is predicted that the bimodal rainfall region likely narrowed in geographical range during the last glacial maximus (Engelbrecht *et al.*, 2019). The winter rainfall region would have expanded to the east and similarly the all year rainfall region would have expanded to the west, narrowing the extent of the bimodal region greatly (Engelbrecht *et al.*, 2019).

Additionally, during glacial phases the retreating coastline would have exposed novel landscapes and vegetation distributions on the now submerged coastal shelf which would have had different vegetation to the modern coastal plain (Cowling *et al.*, 2020). The modelling of the environs which might have persisted on the now submerged continental shelf show that the edaphic distributions would have been critical in determining the distribution of ancient vegetation that would have colonised the newly emerging land (Cowling *et al.*, 2020). Finding analogue environments on the current coastal plain of the GCFR enables the accurate modelling of geophyte resources available in the MSA. The data presented in this chapter represent the geophyte resource variation over the most diverse range of analogue environments that can be sampled under the current climatic conditions.

The results presented here show that geophyte resources are abundant in certain seasons and habitats, and if hunter-gatherers understood this variation, they could have had access to a large nutrient resource base across the entire region. The abundant archaeological sites in the West Coast and East Coast that contain evidence of geophyte foraging from the Holocene are evidence that hunter-gatherers did take advantage of this resource (Wells, 1965; Deacon, 1970, 1979; Parkington and Poggenpoel, 1971; Silberbaur, 1974; Parkington, 1977; Liengme, 1987; Anderson, 1991). The relative lack of archaeological sites in the South Coast that contain evidence of geophyte is at odds with the abundant geophyte resources that are available in the landscape currently. Based solely on the geophyte resources described for the South Coast region there should be far more abundant archaeological evidence of geophyte foraging in the South Coast. I would argue the relative lack of sites revealing this evidence in this region is not due to a lack of geophyte resources in the landscape, but other factors that will be discussed in subsequent chapters.

4.4.2 Geophyte resources in specific vegetation types

During spring, there are few notable differences between vegetation types of the different regions, and relative carrying capacity values are consistently high. The exceptions are Thicket and Salt Marshes, which had low relative carrying capacity in all regions.

When attention is focused on vegetation types that have high relative carrying capacity in autumn, the values and patterns of variation are similar in the bimodal and all-year rainfall regions. The same vegetation types could provide attractive foraging returns regardless of the season (Dune Cordon, Sand Fynbos and Strandveld), which correspond to the highest performing vegetation types for return rate of foraging of edible plant resources in the South Coast reported in other studies (Botha *et al.*, 2020). Hunter-gatherers would have been able to obtain geophytic resources in the bimodal and all-year rainfall regions of the GCFR throughout the year in these vegetation types, which together comprise a large surface area of the coastal lowlands in both regions. These vegetation types are also important vegetation types for foraging during spring.

Granite Strandveld was the only vegetation type on the West Coast with geophytic resources apparent and abundant during autumn. This vegetation type exhibited completely unique patterns of variability due to the unique geology and edaphic environments created by granite boulders. The dominant soil that is found among the large granite outcrops of this vegetation type are shallow calcareous sands (Mucina and Rutherford, 2006) and between the crevices of the large granite boulders shallow calcareous sand collects that is humus-rich. The shape of the granite boulders funnels any precious moisture during the dry summer and autumn months to these soils, which creates a micro-climate where plants can persist. Notably, these crevices support an abundance of geophytes, and this coastal vegetation type could be considered as island-like habitats surrounded by a sea of Sand Fynbos. The latter vegetation type supports low to no geophyte resources in summer and autumn. It was also found that the quality of the resources in this region is relatively high in comparison to the other regions during autumn. This is because Granite Strandveld exhibits some of the highest quality of geophytic resources for any vegetation type during autumn.

Vegetation types along the coast and river courses had high levels of relative carrying capacity in general. Across all regions, Dune Cordon, Strandveld and Riparian vegetation had some of the highest values of relative carrying capacity observed, although values varied. It is postulated that the attractiveness of these vegetation types to a forager could have been further bolstered by the juxtaposition of aquatic resources in river courses and the ocean. A similar pattern has been found for the energetic return rates of foraging of all plant resources in the South Coast region (Botha *et al.*, 2020). This variation has is predicted to have affected hunter-gatherer mobility in the Holocene according to agent based modelling (Wren *et al.*, 2020). Having access to an abundant plant and animal-based food source, paired with a water source, would have been advantageous to hunter-gatherers as it could have met a greater array of their needs simultaneously.

4.5 Conclusion

Findings indicate that if hunter-gatherers were able to discern and learn which environments to target, during which time of the year, geophyte foraging could have been an energetically profitable exercise. The consistent way in which geophyte relative carrying capacity varies among vegetation types in the South Coast and East Coast suggests that hunter-gatherers might have been able to forage efficiently for geophytes if they understood the dynamics of the climate and vegetation (under the current climate and distribution of geophytes).

Results highlight the seasonal nature of geophytic resources in the West Coast, where the strict winter rainfall regime forces geophytes to become dormant *en masse* during summer. If hunter-gatherers understood this pattern and the phenology of plants in that region, they would have known to target other resources or move to areas with more favourable resources. In the South Coast and East Coast however, geophyte resources would not have been a limiting factor forcing changes in hunter-gatherer subsistence or mobility in autumn. It is therefore postulated that environmental drivers such as rainfall patterns and the edaphic template drive geophytic resource availability, and this in turn has implications for forager behaviour and movement.

If there were substantial changes to the rainfall seasonality across the region during glacial phases in the MSA, geophyte resource seasonality and distribution would have likely been affected. If the winter rainfall region expanded the geophyte resources across the South Coast region could have become far more seasonal and could have become a limiting factor forcing changes in hunter-gather subsistence or mobility in autumn.

These results indicate that geophytes are an abundant resource over the entire region, understanding the variability of the quality and seasonality of these resources would have been key drivers in hunter-gatherer subsistence choices.

Chapter 5: The effect of phenology on the availability, foraging return and nutritional composition of geophytes across the GCFR

5.1 Introduction

In the previous chapter it was established that there is an abundance of geophyte resources in the GCFR, but there is also substantial variation in the geophyte resources available in different habitats and regions (spatially) and between autumn and spring (temporally). The relative carrying capacity of geophytes presented in the previous chapter offers two snapshots of the availability of geophyte resources across the GCFR i.e., in autumn and spring. These data, although useful to describe the broad variation in geophyte resources across the region, fail to describe how the cyclical, seasonal growth of geophytes (their phenology) could have impacted this resource and how it affected the optimal exploitation of this resource. Phenology refers to the expression of the seasonal cycles of plant processes, which are determined by seasonal climate variation (Zhang *et al.*, 2012). The phenological cycle of geophytes progresses through the following phenophases for the majority of species, as discussed in Chapter 2: emergence, leaving, flowering, seeding, senescence and dormancy (Dafni, Cohen and Noy-Mier, 1981).

It is poorly understood how the phenological cycle of geophytes impact when they are available to foragers and more importantly if their phenological cycle could impact their palatability or nutrition they could provide foragers.

In the past, broad phenological patterns of geophyte growth have been used to describe the seasonal availability of certain geophyte resources in broad terms (such as in late spring), together with estimates of time frames when certain geophytes could offer the optimal return rates upon foraging (after seeding), which was predominantly based on historical ethnographic observations of geophyte foraging (Parkington, 1977; Liengme, 1987; Deacon, 1993). Although the methods used in these studies were useful to evaluate broad patterns of subsistence, it leaves us with many questions about how the seasonal cycling of geophyte resource could have impacted hunter-gatherer subsistence patterns on a finer scale.

Understanding how geophyte resources vary annually (visibility/availability), how geophytes grow and allocate resources to their USOs and how the quality of the food source varies throughout the growing season has the potential to shed light on the finer scale impact this resource could have had on hunter-gatherer behaviour. Considering the staggering array of edible geophytes that are available across the GCFR, the interplay between these various factors could have impacted the foraging choices hunter-gatherers made. These choices might be detectable in the archaeological record and data of the seasonal cycling of geophyte resources could give us novel insights into the interpretation of archaeobotanical remains in the GCFR.

GCFR hunter-gatherers (and all hunter-gatherers) have been shown to have extraordinary taxonomic skills, showing in-depth understanding of the biotic and abiotic factors that influence food sources (De Vynck *et al.*, 2016; Van Wyk and Gericke, 2000; van Wyk, 2008). From the ethnographic accounts presented in Chapter 2 which describe geophyte foraging, it is clear that hunter-gatherers of the GCFR had a sophisticated understanding of where, when and how to forage specific geophyte species optimally (Thunberg, 1795; Burchell, 1822; Lichtenstein, 1930; Van Wyk and Gericke, 2000; Coetzee, 2015). A song has even been recorded that was sung by San people, describing the seasonality of *Moraea fugax* gathering and the optimum time to forage them (Van Vuuren, 2013). These accounts illustrate the deep understanding hunter-gatherers had of the growth patterns of geophytes, but they do not capture the complexity of variation of geophyte resources and how these dynamics over space and time would impact foraging and our interpretation of geophyte remains in the archaeological record.

The three main objectives of this chapter are to:

1. ***Evaluate the seasonal availability of geophyte species across the GCFR.***
2. ***Determine the effect of seasonal growth of geophytes (nutritional content and seasonal morphological changes) on the possible return rates of foraging.***
3. ***Evaluate the feasibility of using the seasonal growth patterns of USOs to analyse geophyte remains in the archaeological record***

5.1.1 Seasonal availability of geophytes across the GCFR

In the GCFR, studies describing the contemporary seasonal availability of plant resources in the southern Cape have been used to model past human behaviour which assist the interpretation of excavated assemblages from the region (De Vynck, Cowling, *et al.*, 2016; Singels *et al.*, 2016; Botha, 2019; Wren *et al.*, 2020). These studies have found that there are periods of time in the phenological cycle of plant species when they become most apparent and abundant in the landscape to foragers (De Vynck, Cowling, *et al.*, 2016). Despite these differences in the seasonal abundance of edible species, seasonality did not have a significant impact on the overall return rates of foraging geophytes in this region (Botha *et al.*, 2020). These results indicate that for this region, the individual phenological cycles of geophyte species have an impact on that individual species' availability to a forager (De Vynck, Cowling, *et al.*, 2016), however there seems to always be something to forage in this region, irrespective of season, resulting in the overall return rates of foraging remaining unchanged seasonally

(Botha *et al.*, 2020). These results correspond to the results in the previous chapter that showed that although the types of species that are available during different seasons differ in the South Coast region, geophytes could still provide significant carrying capacity irrespective of season.

Data on the effect of phenology on the availability and return rates of foraging geophytes described by De Vynck *et al.*, (2016) and Botha *et al.*, (2020) for the southern Cape are not available for the rest of the GCFR. For the East Coast and West Coast regions, the effect of phenology on geophyte foraging might be very different, as the results from the previous chapter showed that the seasonal availability of geophytes in those regions was markedly different to that in the South Coast. In this chapter, an attempt is made to describe the effect phenological cycles of individual geophyte species would have on the overall availability of geophyte resources seasonally, across the entire region.

5.1.2 Effect of phenology on energetic return rates of geophyte foraging

The phenology of geophytes not only influences when these plants are available to foragers, but it also influences the amount of beneficial and harmful compounds that are stored in the USO (Ruiters and McKenzie, 1994; Orthen, 2001b; Orthen and Wehrmeyer, 2004; Nikolić *et al.*, 2008). USOs store water and carbohydrates, which also make these USOs an attractive food source to humans (Perry *et al.*, 2007; Carmody and Wrangham, 2009b; Hardy *et al.*, 2015). However, they also contain other compounds that could affect their desirability negatively (anti-nutrients) like fibre and secondary metabolites (Ncube, Finnie and Van Staden, 2011; Kaššák, 2012; Di Giusto, Dounias and McKey, 2017) as described in detail in Chapter 2 and 3.

The amount and type of carbohydrates stored in USOs are dependent on the phase of plant growth: phenophase (Orthen and Wehrmeyer, 2004). Although the primary purpose of the USO is to store energy to allow survival of the plant in unfavourable conditions (throughout dormancy), the remaining energy is used to initiate growth at the start of the phenological cycle (following dormancy) as described in Chapter 2 (Orthen, 2001b; Lopez-Corcoles *et al.*, 2015). Following sprouting, these new leaves produce carbohydrates themselves, these resources are allocated back into the USO for storage, or to be used for further growth (Orthen and Wehrmeyer, 2004). The processes of storage below ground and plant growth above ground both require carbohydrate resources (Orthen and Wehrmeyer, 2004).

The type of non-structural carbohydrates produced and stored in the USO may vary. Polysaccharides like fructans and starches dominate the composition of most USOs (Ranwala and Miller, 2008). The composition and quantities of carbohydrates can vary throughout the growing season of the plant and would inevitably impact the nutritional content of the USO (Orthen, 2001a; Packer, 2011).

The carbohydrate content of USOs would impact their kilojoule content, which could have made them more or less attractive to human foragers. For instance USOs use carbohydrates to sustain growth during flowering, rather than store carbohydrates in USO (Waher, 1974; Zimmerman and Whigham, 1992; Orthen and Wehrmeyer, 2004). Flowering could have been a strong above ground signal for hunter-gatherers to indicate that the USO nutritional returns would be lower than that of a non-flowering plant.

Above ground signals such as flowering could similarly have indicated the antinutrient content of USOs, which might have made USOs more or less attractive to human foragers. Fibre content, and indeed presence of any anti-nutrients would have been a critical consideration for hunter-gatherers in making choices about which foods to target (Marshall and Wrangham, 2007). Fibre content does not diminish the nutritional returns of a geophyte, but neither does it contribute to the nutritional content. This is because fibre takes up volume in the gut without adding any caloric value to the diet (Conklin-Brittain, Wrangham and Smith, 2002; Schnorr *et al.*, 2015).

The anti-nutrient content of USOs can vary throughout the phenological cycle of geophytes based on the volume of other components (such as water and carbohydrates) or as anti-nutrients build up in USOs. During dormancy, for example, the plant uses the energetic and water reserves stored to survive (Orthen and Wehrmeyer, 2004), while metabolising and accumulating secondary metabolites (Waher, 1974; Ncube, Finnie and Van Staden, 2011; Kaššák, 2012; Di Giusto, Dounias and McKey, 2017). During dormancy it was found that corms have significantly higher fibre content and low energy content compared to any other phase of growth, rendering them unpalatable during dormancy (Singels, 2013). Similarly, the high tannin content identified in *Watsonia galpinii* collected in autumn (Chapter 3) (35 mg CE/g) is illustrative of such phenologically driven change in USO nutrient content. The increase anti-nutrient content is visible in *Watsonia* corms that turn bright orange/red when they enter the dormant phase (Singels, 2013) (see Figure 5.1).

Figure 5.1 Colour change in <u>Watsonia meriana</u> corms as they enter dormancy.

These colours have been argued to be a visual cue to foragers of high anti-nutrient content (Johns, 1999). In short, secondary metabolites build up and carbohydrate resources are depleted during the dormant phase (Waher, 1974; Orthen and Wehrmeyer, 2004; Kaššák, 2012; Singels, 2013; Di Giusto, Dounias and McKey, 2017), rendering USOs inedible, however it is not well understood how the concentration of anti-nutrient compounds vary during the leaving, flowering and seeding phases when plants would be visible above ground.

As described in Chapter 3, the USO weight is one of the most important characteristics to determine the energetic return rate possible when foraging a USO. Understanding how the dynamics of USO growth in different phenophases influences the nutritional returns (weight and nutritional composition) of geophytes can provide a unique insight into the availability, possible return rates and nutritional quality of geophytes. Additionally, if there exists some predictability in the pattern of cycling for these various factors, we might suspect that hunter-gatherers would have been able to discern these patterns and use this information in their arsenal of knowledge to navigate the resources that would have been available to them for survival.

5.1.3 Use of seasonal growth patterns of corms in the analysis of archaeological material

Seasonal morphological changes in various animal species have been used as proxy indicators of seasonal occupation of archaeological sites where the faunal remains of these species have been found in excavated assemblages in the GCFR (Parkington, 1972; Fletemeyer, 1977; Avery and Underhill, 1986; Woodborne, Hart and Parkington, 1995). In these studies, the patterns of growth of animal species were recorded from modern material and later compared to faunal remains found in excavated assemblages. In other parts of the world the seasonal morphological changes observed in geophytes have been used in the interpretation of remains found in excavated assemblages (Gill, 2014, 2016). Could the seasonal morphological changes of GCFR geophytes be used in a similar way to interpret the remains found in excavated assemblages?

Corm discs are one of the most prominent geophyte remains found in GCFR archaeological sites (Parkington and Poggenpoel, 1971; Deacon, 1976; Liengme, 1987). Understanding how the morphology of this debris varies seasonally could aid the interpretation of botanical remains. These discs are easily measurable and if a comparative collection of disc measurements were to be made of modern material, a correlative method can be developed to assess seasonality of collection of geophytes in the archaeological record, for instance.

In this chapter, a pilot study is presented which endeavoured to establish whether this method holds any promise to offer additional insights into geophyte remains. Preliminary equations are presented that could be used to determine the season of collection of geophytes, together with the estimated energy content of geophytes found in excavated assemblages. Although these results are preliminary, this method could help guide our interpretations of hunter-gatherer behaviour.

5.2 Methods

To address the three objectives of this chapter, three distinct groups of data were collected and analysed. Firstly, the phenological cycling of all species identified in the three study regions was studied and presented to illustrate when various geophytes would be visible to foragers. Secondly, four species were selected for time series measurements of nutritional content throughout the phenological cycle. Thirdly, an additional four cormous species which are commonly found in the archaeological record were selected, and measurements of the USO growth made throughout their phenological cycle.

5.2.1 Seasonal availability of geophytes across the GCFR

Species have a characteristic phenological cycle, where each phenophase occurs at roughly the same time each year. However, the timing of phenophases can vary between plant communities or even between individual plants in the same community, as phenology is influenced by abiotic factors (like precipitation and temperature) and biotic factors (like pollination ecology and genetic factors) (Gleeson, 1981; Fenner, 1998; Khodorova and Boitel-Conti, 2013). When the phenological cycle and the timing of phenophases are discussed, it is in reference to comparisons between taxa, not variation among communities or between individual plants.

To present the phenological cycling of the geophyte species identified in Chapter 3, the published dates of their phenological cycles were tabulated (Appendix A). Dates of timing of phenological events were generated from the available literature on the phenophases of geophyte species (Goldblatt, 1986, 1989, 1997; Van der Walt and Vorster, 1988; Perry, 1994; Goldblatt and Manning, 1998, 2007; Linder and Kurzweil, 1999; Procheş *et al.*, 2006; Manning *et al.*, 2010; Manning and Goldblatt, 2012). The dates for following phenophases were recorded: emergence, leafing, flowering, seeding, senescence and dormancy.

Phenological cycles of plants are commonly illustrated in a phenological curve where the x-axis represents the day of year (DOY), and the y-axis represents the abundance of individual plants visible that are exhibiting different phenophases (see Figure 5.2) (Zhang *et al.*, 2012). This convention was used to illustrate the phenological curves of all 131 edible species identified in this study.

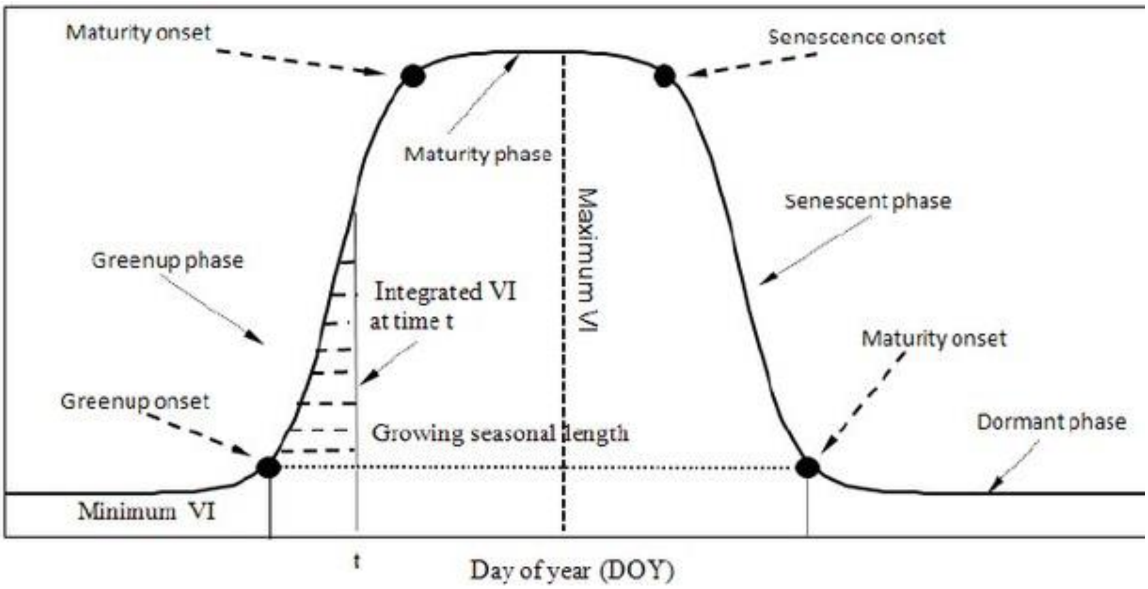


Figure 5.2 Example of a phenological curve, giving a visual representation of the species level phenophase development seasonally. The peak of the curve represents the time at which the greatest number of individuals of a species are in their mature phase, just before the onset of senescence. Adapted from Zhang et al., 2012.

The phenological curves for each species was generated from the published species level dates associated with different phenophases (x-axis, DOY), the onset of these phenophase was assigned a numerical value which is referred to as its relative apparency (y-axis). This value is to allow the visual representation of how the numerous geophyte species move through their phenological cycle annually and would be visible to a forager.

The dates at which the above-ground visible phases occur for each species were converted to numerical values (between 0-2) and plotted to produce a bell curve which roughly illustrated the phenological cycle of each species. Dormancy was awarded a value of 0. The highest amplitude of the curve was always awarded a numerical value of 2 and fell on the date immediately following flowering, at the onset of seeding. This date is treated as the culmination of flowering and seeding, after which senescence is initiated, and active growth of the plant ends. At the point of seeding the plant experiences the largest amount of above-ground biomass and would presumably be most visible to a hunter-gatherer, this date is defined as the “peak” of the species phenological cycle, when they might have been most apparent to a forager (maximum apparency). The curves that are generated using this method are meant to give an impression for how many months of the year a species is visible above ground, when it is dormant, and when it experiences the “peak” of its phenological cycle.

Of the 131 geophyte species identified across the study area, 128 species exhibit a synanthous phenological cycle where their phenophases follow the average sequence: emergence, leafing, flowering, seeding, senescence and dormancy. The remaining three species exhibit a hysteranthous phenological cycle, where their flowers and leaves are never present simultaneously. All three of these species belonged to the genus *Eriospermum*; *E. brevipes, E. breviscapum* and *E. lanceifolium* (as seen in Figure 5.3). Since hysteranthous species would be visible above ground to a hunter-gatherer twice in a year, they were treated as having two peaks in their phenology, during flowering and during leaving, which produced two bell curves in quick succession.

To clearly illustrate the broad patterns of phenology among geophyte communities, the phenological curves of species were grouped visually according to similar seasonal phenological cycles (for example autumn flowering species). A general trend line which represented the average combined curves of various species was generated using the average values of each species curve. These curves represented the general trends of phenology for various species. These graphs are meant as a general impression of the phenology of the entire geophyte community in the three study areas throughout the year.

5.2.2 Species selected for continual nutritional analysis and USO measurement

For the nutritional testing of USOs, each test carries high financial inputs, and a large quantity of test material is required for tests to be run successfully. For this reason, a sample of four species was chosen to perform nutritional testing across a full growing season. These four species were chosen to represent the diversity of edible geophyte species that have been identified in previous chapters. Further criteria used in selecting species for this testing included:

1. The species which were selected had to grow in large enough populations, in an area where collection was permitted and to enable subsequent collections to be carried out in the same plant populations to minimise variations induced by environment.

2. That the selected populations occur near Cape Town to allow regular and repeated observations to keep track of population phenology.

3. The selected species had large USOs, which would result in fewer plants being necessary to reach the target weight of 500g necessary for complete nutritional analysis.

One of the most significant differences among species of geophytes is that some have USOs that are perennial and others have USOs that regenerate annually (Dafni, Cohen and Noy-Mier, 1981; Ruiters and McKenzie, 1994). Tubers, rhizomes and bulbs most frequently have perennial storage organs, while corms regenerate annually.

The following species were selected for nutritional testing:

1. *Eriospermum lanceifolium*	Tuber	Perennial USO
2. *Ferraria crispa*	Corm	Perennial USO
3. *Pelargonium triste*	Rhizome	Perennial USO
4. *Watsonia meriana*	Corm	Annual USO

As described in detail in Chapter 3, tuberous species rarely generate a new tuber every year (or even over the lifetime of a plant), with the exception of ground Orchids that regenerate a tuber yearly (Johnson and Bytebier, 2015). The majority of tuberous plants (like the *Eriospermum lanceifolium* illustrated in Figure 5.3) store the resources produced by their leaves in the same tuber annually, causing it to grow increasingly larger as the plant ages. *Eriospermum lanceifolium* was used as an analogue for other tuberous species that have been identified in the ethnobotanical and archaeological record like *Cyphia* spp. a*nd Dioscorea* spp.

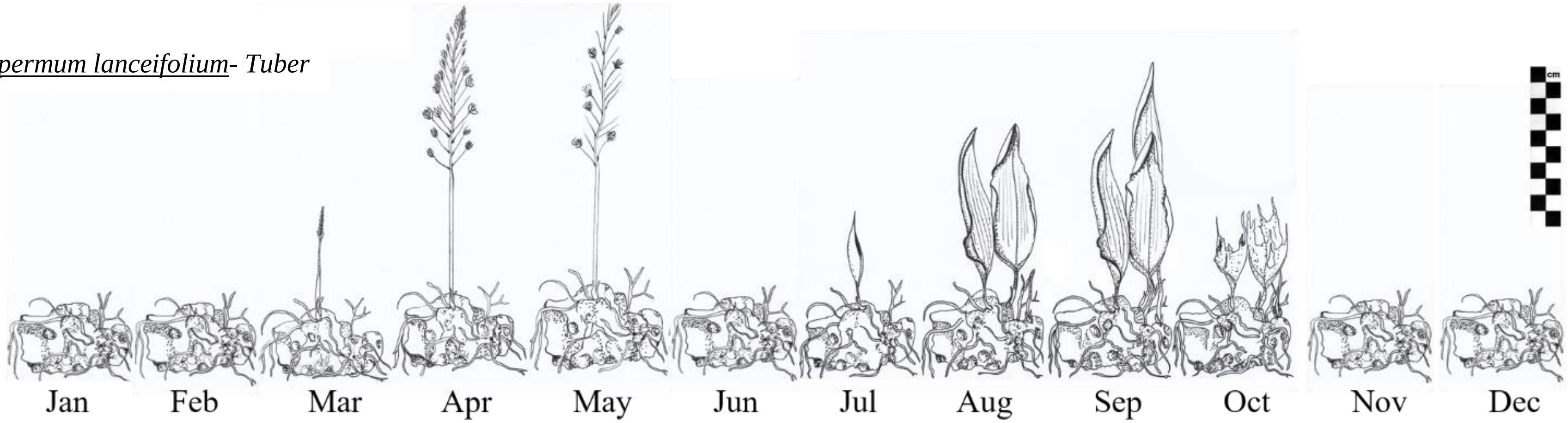
As discussed in Chapter 2, all cormous species produce a new corm annually, and in most cases, the old corms wither away. In some cases the old corms do not wither away, instead, they persist and are capable of growth themselves; these are called Pseudocorms (see Figure 5.3). Plants in the genus *Ferraria* are an excellent example of this type of growth. One *Ferraria* plant might have multiple corms attached to one another. This type of growth is rare, but this species was an analogue for the species that have been identified in the ethnobotanical and archaeological record that grow in this fashion (*Babiana hirsuta* and *Ferraria* spp.).

The rhizomatous geophyte *Pelargonium triste* has a perennial rhizome and resprouts from the same USO annually (see Figure 5.4). This type of growth is typical of other rhizomatous plants that have been identified in the ethnobotanical and archaeological record, and thus this species makes an excellent analogue for these rhizomatous species.

Most cormous species such as *Watsonia meriana* (Iridaceae) produce a new corm every season (see Figure 5.4). As the plant approaches dormancy towards the end of summer the aboveground portion of the plant withers and sometimes blows away. The corm that stays behind is then in its dormant phase and will survive under the ground until such a time that the winter rains trigger re-sprouting. This type of growth is typical of the vast number of cormous species that have been identified in the ethnobotanical and archaeological record like the Iridaceae family, and thus this species makes an excellent analogue for these cormous species. *Watsonia meriana var. meriana* was the specific subspecies sampled, which rarely produces seeds, but rather produces small cormlets on the inflorescence (see Figure 5.4).

Few bulbous species were identified in the ethnobotanical or archaeological record as being used as a food source (See Table 2.1, pg 47). Bulbs were rather used medicinally. A bulbous species was not chosen for repeated nutritional testing as a suitable, edible species could not be identified that met the criteria stated above. Even if one existed, it would not have represented any significant number of geophyte species, and testing thereof would have been a waste of resources.

Eriospermum lanceifolium- Tuber



Ferraria crispa- Corm

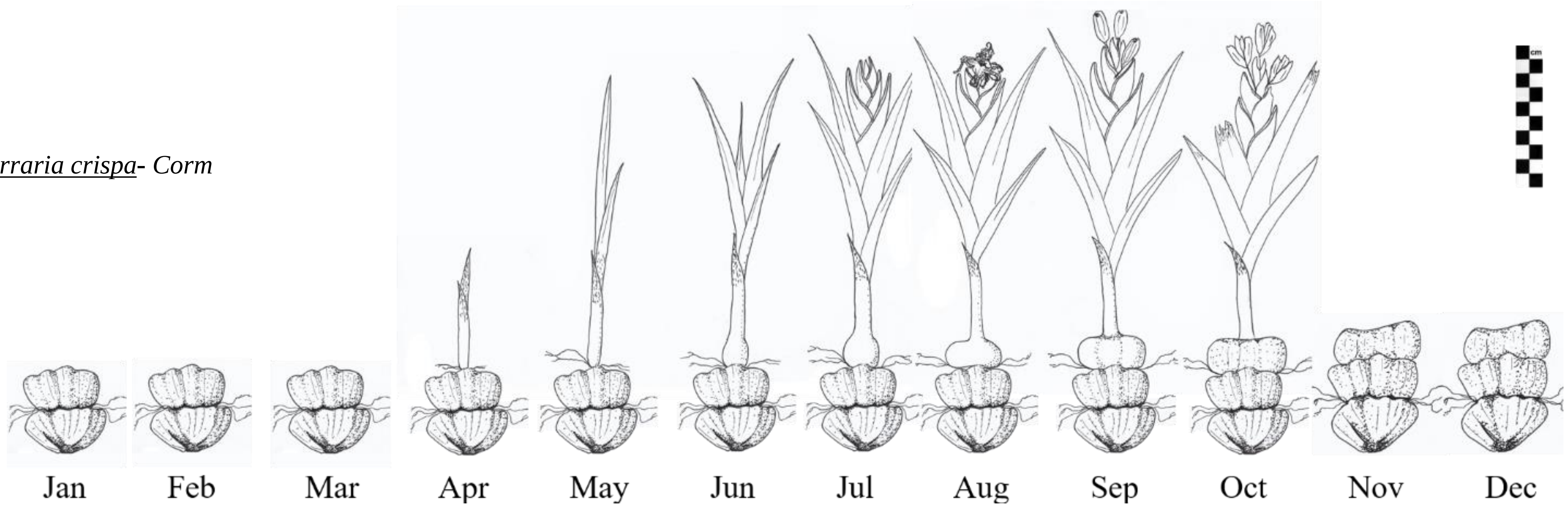
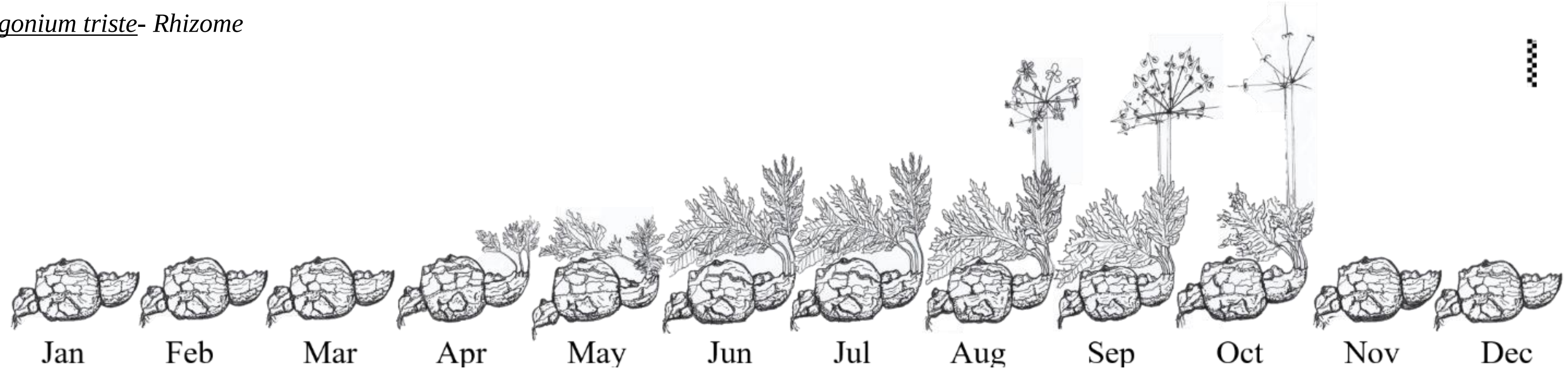


Figure 5.3 *Ferraria crispa* and *Eriospermum lanceifolium* seasonal growth cycle. Drawings by the author.

Pelargonium triste- Rhizome



Watsonia meriana- Corm

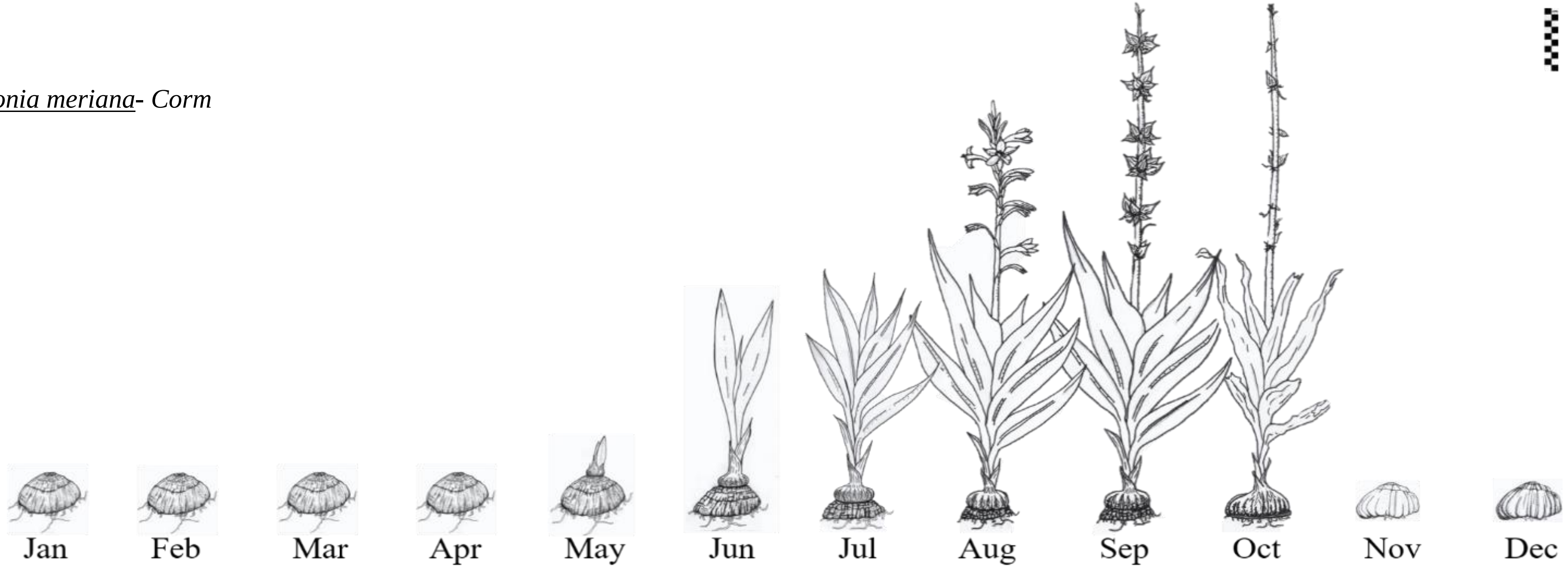


Figure 5.4 *Watsonia meriana* and *Pelargonium triste* seasonal growth cycle. Drawings by the author.

An additional four cormous species, which feature prominently in multiple archaeological sites, were sampled monthly and measurement taken of their USOs to describe the morphological changes they experience throughout their phenological cycle (see Figure 5.5). For all cormous species the weight of the corm was measured (A), the diameter of the disc (B), and the height of the disc (C). The date that the corm was harvested, and the phenophase it was in, were also recorded.

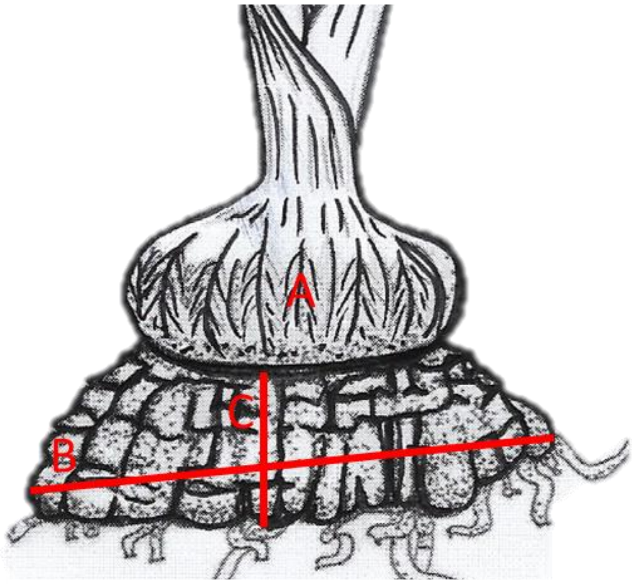


Figure 5.5 Diagram depicting measurements taken of all corms. A: the weight of the corm (g). B: Disc diameter (mm). C: Disc Height (mm)

Babiana ambigua, Cyanella lutea, *Moraea fugax* and *Watsonia meriana* (the latter species measurements were taken during the sampling of that species for the nutritional composition). Excluding *Watsonia,* the very small corm size of these species (sometimes 0.1 g) meant that thousands of individual plants would have been destroyed to reach the target of 500 g of material necessary for nutritional testing. This destruction of individuals was neither justified nor covered by the research permits obtained for this research.

5.2.3 Collection of species

During 2016 and 2017, eight target species were collected in the Cape Town area at four to six weekly intervals during their growing season, weighed, measured and tested for their nutritional composition. *Eriospermum lanceifolium* was collected in Cecilia Forest (-34.0075105, 18.4129606), where it grows in great numbers among Pine Plantations. *Watsonia meriana* and *Pelargonium triste* were collected from a dense population adjacent to the Kenilworth Racecourse Conservation Area (-34.002213, 18.480182). *Ferraria crispa* was collected in Cape Point Nature Reserve (-34.261130, 18.382584). The three additional species (*Cyanella lutea, Moraea fugax* and *Babiana ambigua*) which were collected solely for the monthly measurements of the USOs were collected at a site that was earmarked for development in Kommetjie (-34.142228, 18.348379). A search and rescue permit had been issued for this site and the work executed, in part, by these collections.

Collections were made at four-week intervals from the first day that plants were visible after emerging from dormancy. These plants were immediately cleaned and the external coatings /husks peeled. I attempted to collect 15 specimens of each species, or enough USO material to conduct nutritional composition testing on 500 g. The USO width, height, weight was then measured. The USO material was then frozen until such time that nutritional compositional tests could be conducted.

Nutritional testing occurred in the same laboratories and with the same methods as described in Chapter 3.

5.2.4 Statistical analysis

Data were rarely distributed normally, and non-parametric tests were therefore performed. Post hoc tests were used to determine the significant differences between group means in an analysis of variance setting. The Tukey HSD test is generally more conservative than the Fisher LSD test but less conservative than Scheffe's test when analysing non-parametric data and was thus chosen as the preferred test. Exponential regressions were performed to test correlations between disc height and the month of harvesting, and the disc width and the weight of corm.

5.3 Results

5.3.1 Geophyte seasonal availability over the GCFR

Figure 5.6 shows the broad patterns of geophyte phenology for all species sampled during the spatial analysis in the various study areas. The curves in colour capture the grouped phenological curves of species that have similar timing of their phenophases.

In the West Coast, USO phenological patterns mimic the rainfall patterns of the region, where a long-dormant phase occurs over the dry, hot summer. Most species experience the peak of their above-ground visibility during August and September, with some species experiencing the peak as late as October and November. A few species are winter flowering and experience their peaks from June to August. All species go dormant over the most extreme summer months, where an extensive period of visual absence of geophytes is experienced during summer and autumn.

In the South Coast, the pattern of geophyte phenology is distinctly different. The majority of species peak in their relative apparency over spring (66 of 83 species) (see Figure 5.6). There are a few species which experience their maximum apparency during winter, but a pronounced secondary spike is experienced during autumn, where 12 species were found to have their maximum apparency during March and April. These curves suggest that there are two peaks of geophyte apparency in the species identified from the South Coast: autumn and spring. The spring peak is broad while the autumn peak is narrow.

In the East Coast, the phenology curves of all the geophyte species have an erratic pattern, partly due to the evergreen species, which do not go dormant (having no bell curve, but a straight line). There is, however, still a definite peak of geophyte apparency over the spring months (August to October). There is a small peak of species apparency over summer and autumn respectively. This combination of peaks over the course of the year has led to geophyte species being present in some shape or form throughout the entire year, with no dormant phases universally identified.

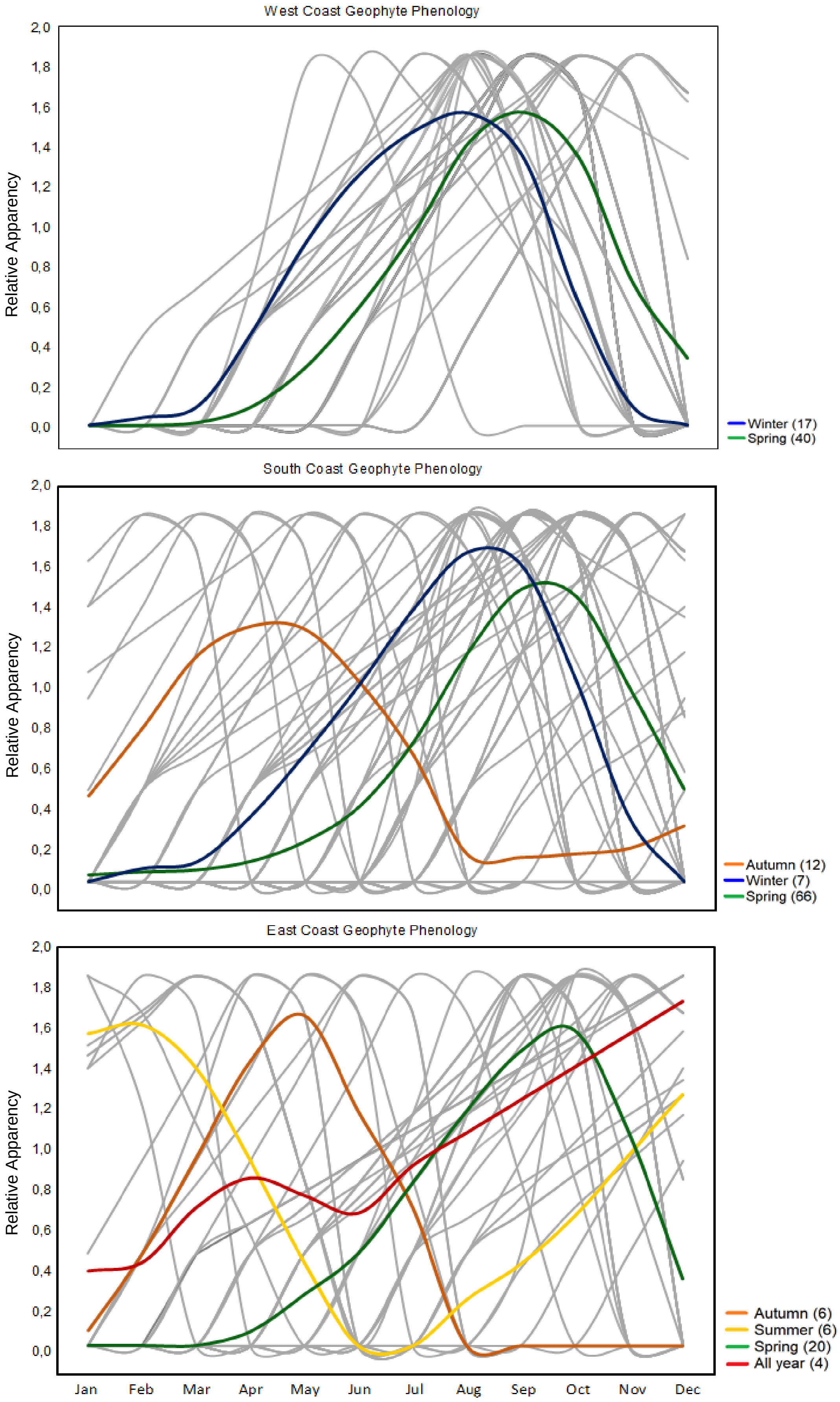


Figure 5.6 Phenology curves to illustrate periods of apparency and dormancy of geophyte species sampled in the West Coast, South Coast and East Coast study regions. Coloured lines are grouped curves, representing multiple species with similar timing of phenophases. Individual species phenological curves are represented in grey.

5.3.2 Effect of phenology on energetic return rates of geophyte foraging

5.3.2.1 Effect of geophyte phenology on nutritional composition of USOs

The four species measured had varying levels of nutrient content over time and across phenophases, but some compounds, including protein and fat content, remained proportionally similar throughout the growing season of the plant (see Table 5.1).

The overwhelming trend is that the carbohydrate content and thus, the energy content of USOs increased as the growing season progressed (see Figure 5.7 and Table 5.1). Starch content notably increased over the growing season, with a slight drop following flowering in *Pelargonium triste* and *Watsonia meriana*. Sugar content was higher in the first months of growth of the USOs and dropped off later in the growing season. There was almost zero fat content in all USOs regardless of the sample month and below 2 % protein.

The moisture content of all species was high, regardless of when they were collected, with a slight trend of the moisture content lowering later in the season, due to the relative accumulation of other compounds like starch (see Figure 5.8 and Table 5.1). The tannin content of most species was generally higher at the start of the growing season and tended to decrease towards the end of the growing season. The fibre content of all species was low.

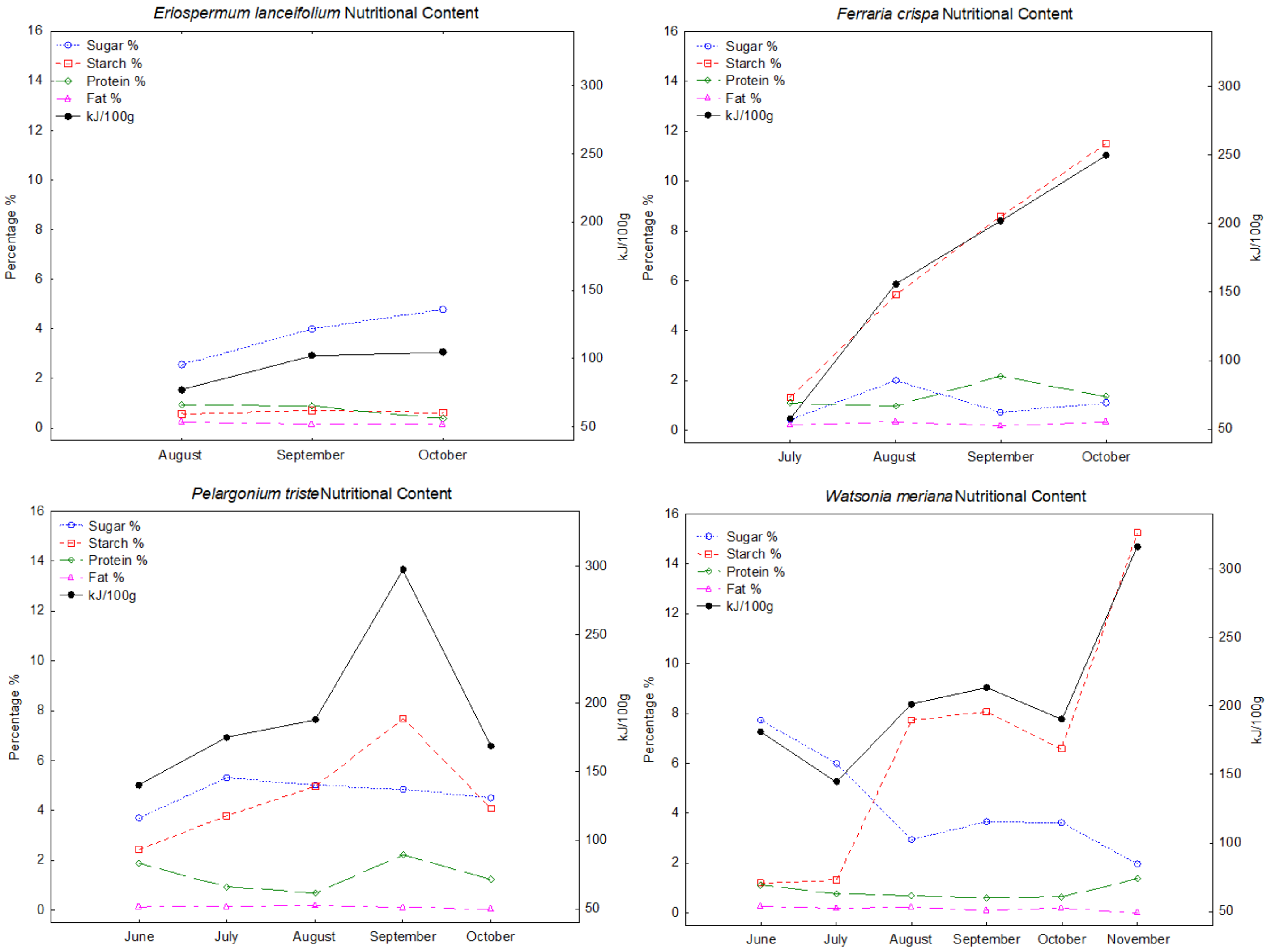


Figure 5.7 Nutritional composition of four geophyte species throughout their growing season (only components which contribute to caloric content)

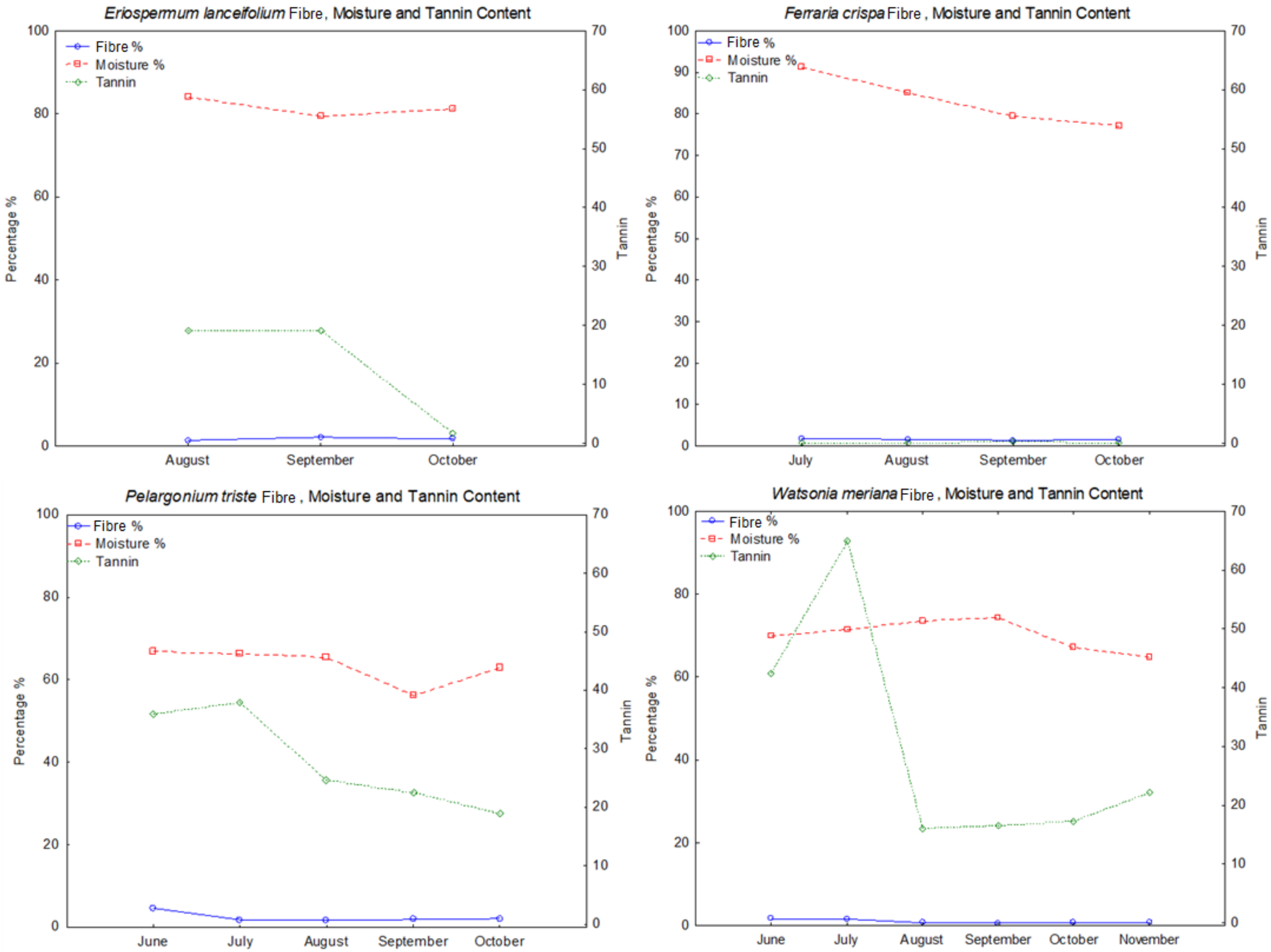


Figure 5.8 Nutritional compositions of four geophyte species throughout their growing season (fibre, moisture and tannin content)

Table 5.1 Nutritional composition of USOs over their seasonal growth. Data in wet weight.

Species	**Month**	**Starch %**	**Sugar %**	**Fat %**	**Protein %**	**Fibre %**	**Moisture %**	**Tannin**	**kJ/100 g**
Eriospermum lanceifolium	August	0.59	2.54	0.23	0.92	1.40	84.16	19.12	77.36
	September	0.73	4.02	0.16	0.91	2.15	79.47	19.16	102.14
	October	0.63	4.77	0.16	0.40	1.71	81.37	1.63	104.52
Ferraria crispa	July	1.34	0.44	0.23	1.10	1.84	91.17	0.00	57.47
	August	5.46	2.00	0.33	0.99	1.62	85.11	0.11	155.86
	September	8.60	0.73	0.17	2.19	1.42	79.58	0.18	201.98
	October	11.50	1.10	0.34	1.35	1.53	77.06	0.00	249.73
Pelargonium triste	June	2.43	3.70	0.12	1.88	4.58	66.87	35.98	140.61
	July	3.79	5.30	0.13	0.94	1.79	66.32	37.88	175.32
	August	4.99	5.02	0.16	0.69	1.74	65.42	24.70	187.82
	September	7.69	4.85	0.12	2.22	1.85	56.11	22.56	297.28
	October	4.07	4.49	0.07	1.24	2.07	62.81	18.89	169.19
Watsonia meriana	June	1.21	7.74	0.26	1.13	1.69	69.92	42.50	180.98
	July	1.31	5.99	0.20	0.77	1.62	71.40	65.02	144.59
	August	7.72	2.95	0.22	0.70	0.67	73.44	15.99	201.43
	September	8.07	3.64	0.11	0.61	0.62	74.27	16.55	213.47
	October	6.60	3.60	0.16	0.64	0.66	67.15	17.20	190.20
	November	15.22	1.98	0.01	1.39	0.68	64.73	22.11	316.47

5.3.2.2 Seasonal morphological changes of USOs over their seasonal growth

USO weight of perennial storage organs did not vary significantly over the growing season for *Eriospermum lanceifolium* (tuber) and *Pelargonium triste* (rhizome) (see Table 5.2). *Ferraria crispa* corm weight did, however, vary significantly over the growing season, where the corms were lighter in August compared to September. This difference was only weakly significant however, and there were no differences observed for the rest of the growing season.

Table 5.2 Weight of USO (g) of various geophyte species throughout their growing season. Superscript letters denote significant differences between months. Groups with unique letters are significantly different from other groups, while groups that share letters are not significantly different from one another.

		Eriospermum lanceifolium p=0.14		*Ferraria crispa* $p \leq 0.05$		*Pelargonium triste* p= 0.96
Month	n	Mean Weight Tuber	n	Mean Weight Corm	n	Mean Weight Rhizome
June					3	63.7±42.4^{a}
July			9	12.8±3.0^{ab}	3	84.0±43.3^{a}
August	6	88.2±44.3^{a}	11	17.1±7.5^{a}	3	56.3±24.8^{a}
September	5	75.2±52.3^{a}	10	10.2±2.6^{b}	3	56.0±29.5^{a}
October	5	110.6±54.4^{a}	7	13.2±4.7^{ab}	4	63.7±44.4^{a}
November	5	79.2±59.9^{a}			4	79.0±49.2^{a}
December	10	50.1±52.2^{a}			5	68.0±44.8^{a}
All	31	75.9±53.3	37	13.5±5.5	25	67.6±37.5

The cormous plants which were sampled monthly throughout their growth cycle displayed predictable patterns of growth (see Table 5.3). Specifically, the corm weight increased throughout the growing season, while the disc height decreased. The disc diameter remained the same.

Table 5.3 Average corm weight (g) and disc height (mm) of Babiana ambigua, Cyanella hyacinthoides, Moraea fugax and Watsonia meriana. Superscript letters denote significant differences between months. Groups with unique letters are significantly different from other groups while groups that share letters are not significantly different from one another.

Average corm weight and standard deviation by month $p\leq0.05$

Month	n	*Babiana ambigua*	n	*Cyanella hyacinthoides*	n	*Moraea fugax*	n	*Watsonia meriana*
June	10	0.2 ± 0.1^{a}					5	2.8 ± 0.8^{a}
July	8	0.3 ± 0.1^{ab}	8	0.8 ± 0.2^{a}			7	6.4 ± 2.6^{a}
August	15	0.5 ± 0.2^{b}	7	1.4 ± 0.4^{ab}	8	0.8 ± 0.5^{a}	10	9.2 ± 4.0^{ab}
September	15	0.4 ± 0.3^{b}	10	2.5 ± 0.7^{bc}	5	2.7 ± 1.3^{b}	19	16.7 ± 9.7^{ad}
October	7	1.0 ± 0.2^{c}	15	3.4 ± 1.1^{acd}	14	2.2 ± 1.4^{ab}	15	25.3 ± 7.9^{bd}
November	15	1.3 ± 0.2^{c}	7	3.8 ± 1.1^{d}	14	2.6 ± 1.4^{b}	21	22.7 ± 13.5^{a}
December							15	48.5 ± 24.3^{c}
All	70	0.6±0.5	47	2.5±1.4	41	2.1±1.4	92	22.3±18.5

Average disc height and standard deviation by month $p\leq0.05$

Month	n	*Babiana ambigua*	n	*Cyanella hyacinthoides*	n	*Moraea fugax*	n	*Watsonia meriana*
June	10	8.8 ± 1.2^{a}					5	29.0 ± 6.6^{a}
July	8	8.6 ± 1.2^{a}	8	11.4 ± 1.9^{a}			7	32.3 ± 3.1^{a}
August	15	2.1 ± 0.5^{b}	7	10.4 ± 2.8^{a}	8	8.0 ± 2.8^{a}	10	27.8 ± 4.6^{a}
September	15	1.2 ± 0.4^{c}	10	5.0 ± 1.5^{b}	5	7.8 ± 2.7^{a}	19	11.6 ± 7.7^{b}
October	7	1.2 ± 0.3^{bc}	15	1.4 ± 0.5^{c}	14	0.4 ± 0.3^{b}	15	9.3 ± 2.7^{b}
November	15	1.1 ± 0.4^{c}	7	1.1 ± 0.4^{c}	14	0.4 ± 0.3^{b}	21	10.4 ± 2.9^{b}
December							15	3.7 ± 0.8^{c}
All	70	3.3±3.3	47	5.1±4.5	41	2.7±3.8	92	13.9±10.2

When the flowering and non-flowering plants of *Watsonia meriana* were measured for the two variables corm weight and disc height, significant differences were observed monthly between the two groups (see Table 5.4). Flowering plants had significantly smaller corms throughout the growing season and significantly higher discs. This was especially true for the corm weight later in the season, after flowering had occurred, and for disc height at the start of the season when the old corm is actively diminishing.

Table 5.4 Corm weight and Disc Height of Watsonia meriana throughout its growing season of individuals flowering or not. Superscript letters denote significant differences between months. Groups with unique letters are significantly different from other groups while groups that share letters are not significantly different from one another.

Watsonia meriana		n	Corm Weight	Disc Height
September	Flowering	5	5.2 ± 1.5^{a}	22.0 ± 7.6^{a}
	Not flowering	14	20.8 ± 7.8^{a}	7.8 ± 2.6^{b}
October	Flowering	3	21.5 ± 5.4^{a}	13.0 ± 1.7^{a}
	Not flowering	12	26.2 ± 8.4^{b}	8.4 ± 2.0^{a}
November	Flowering	22	9.9 ± 2.8^{a}	9.1 ± 3.3^{a}
	Not flowering	19	27.6 ± 10.1^{b}	7.9 ± 2.6^{a}
December	Flowering	5	29.0 ± 13.4^{a}	3.2 ± 0.4^{a}
	Not flowering	10	58.2 ± 22.8^{b}	4.0 ± 0.8^{a}
All Groups	Flowering	35	12.9 ± 9.3^{a}	10.4 ± 6.6^{a}
	Not Flowering	55	31.1 ± 17.9^{b}	7.2 ± 2.7^{b}

The total energy content of USOs is determined by the kilojoule content per unit weight, multiplied by the weight of USOs. When the average weight of USOs (monthly), and the average kilojoule content per 100g of USO (monthly) are combined, one can determine what the potential kilojoule return would be of foraging various geophyte species. In general, the energy content of corms was higher than tubers and rhizomes, but if one considers the average weight of USOs and applies the kJ content, it is clear that in the first months of growth of cormous species the energetic returns are very low, but increase exponentially as the plant matures (see Table 5.5). The energetic returns for rhizomatous and tuberous species remain relatively constant due to their heavier weight irrespective of the phenophase they find themselves in (see Table 5.5).

Table 5.5 Energetic return rate of foraging different USO species throughout their phenological cycle

Species	**Month number**	**kJ/100g wet weight**	**Average weight of USO(g)**	**kJ per average USO weight**
Eriospermum lanceifolium	August	77.36	88.2±44.3	68.23
	September	102.14	75.2±52.3	76.81
	October	104.52	110.6±54.4	115.60
Ferraria crispa	July	57.47	12.8±3.0	7.36
	August	155.86	17.1±7.5	26.65
	September	201.98	10.2±2.6	20.60
	October	249.73	13.2±4.7	32.96
Pelargonium triste	June	140.61	63.7±42.4	89.59
	July	175.32	84.0±43.3	147.27
	August	187.82	56.3±24.8	105.74
	September	297.28	56.0±29.5	166.48
	October	169.19	63.7±44.4	107.77
Watsonia meriana	June	180.98	2.8±0.8	5.07
	July	144.59	6.4±2.6	9.25
	August	201.43	9.2±4.0	33.64
	September	213.47	16.7±9.7	35.65
	October	190.20	25.3±7.9	48.12
	November	316.47	22.7±13.5	71.84

5.3.3 Seasonal growth patterns of corms: Regressions of corm weight, disc height and disc diameter

To determine the relationship between the corm weight and disc height and diameter, exponential regressions were used. When regressions are performed for the corm weight, disc height and disc diameter against the time of year of collection, the resulting curves and r^2 values display high rates of correlation between all variables and the time of the year of collection.

If a possible interpretation of the predictability of the growth of archaeologically significant geophytes is to hold any water, illustrating the correlations between the disc height, disc diameter and the months within which that observation was sampled must be illustrated. These correlations will only be meaningful if the number of data points contributing to the correlations is substantial, and the r^2 value is over 0.64, meaning that the resulting equation represents 80 % of the data. This equation could then reasonably be used to infer from measurements taken from archaeological material when the geophyte was foraged. In this instance the unknown variable is time (month of collection).

Watsonia meriana and *Moraea fugax* showed moderate levels of correlation between disc height and the month of collection. *Babiana ambigua* and *Cyanella hyacinthoides* displayed very high levels of correlation between these two variables (see r values in Table 5.6 and Figure 5.9).

Due to the strong correlations (based on a minimum of 41 points of data), the resulting regression equations meet the above requirement and can be used to model the time at which one of these corms was collected (y) if the disc height is known (x) (see Table 5.6). In this case, due to their different physiological growth habits, each species requires a single equation to predict the month of collection of a corm most accurately.

Table 5.6 Regression equations and r values for various geophyte species correlation between disc height and the month of their collection

Species	n	r	Equation
Babiana ambigua	70	-0.8181	y= 10.0365-0.4171X
Cyanella hyacinthoides	47	-0.9086	y=10.5066-0.2678X
Moraea fugax	41	-0.8279	y=10.4923-0.2397X
Watsonia meriana	92	-.08089	y=11.6077-0.1379X

When the corm weight is correlated to the month of collection, the relationship is predominantly strong to moderate (see Figure 5.9). The corm weight correlation to the month of collection is weak for *Moraea fugax.*

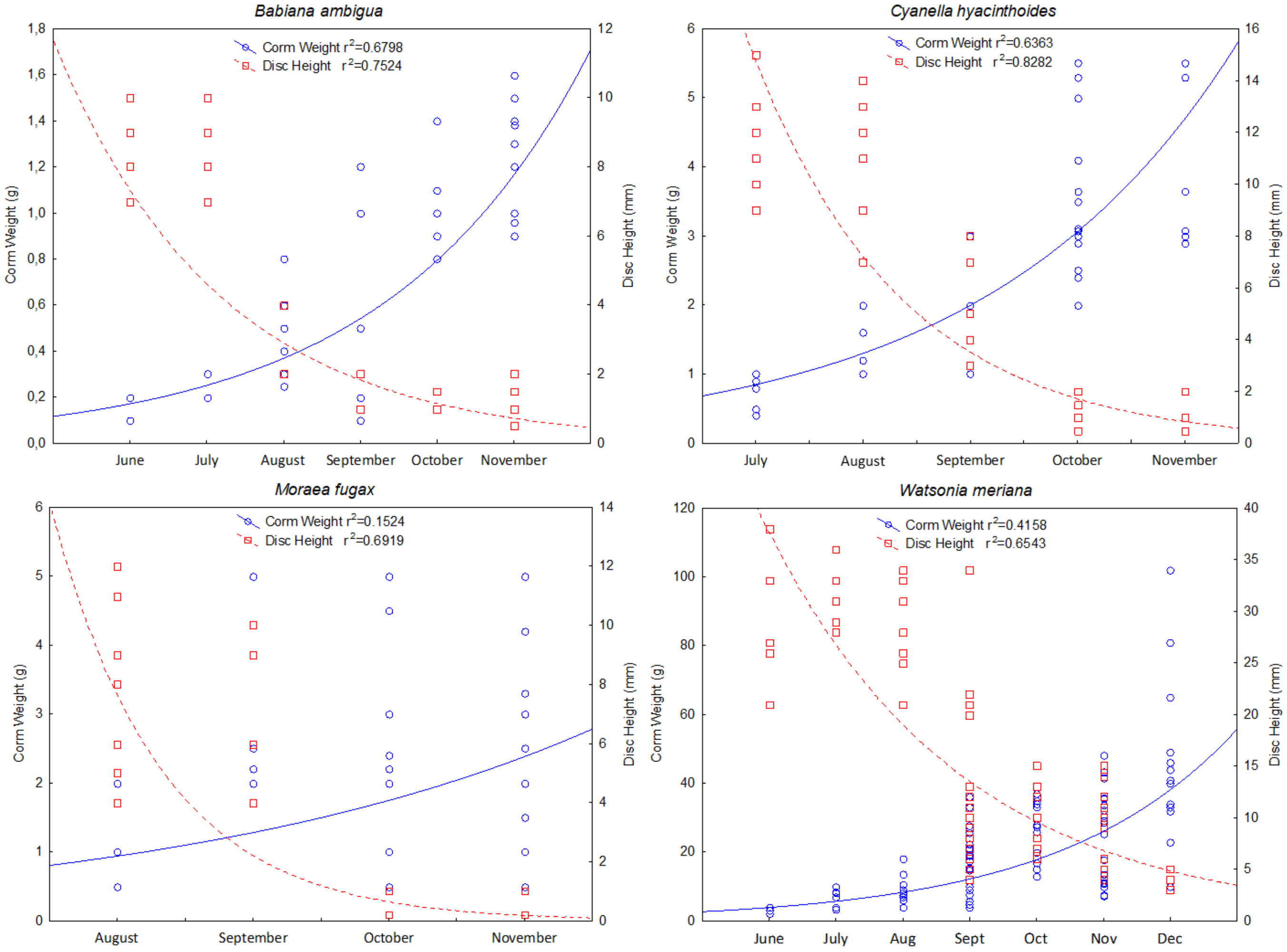


Figure 5.9 Corm weight and disc height regressions for various geophyte species

When the relationship between the disc diameter and corm weight is tested via a regression, the relationship is strong. This regression is based on 250 points of data (all four species grouped) which results in the r^2 value and equation carrying a high rate of reliability to predict the corm weight of plants when the disc diameter is known. For this regression if the diameter of the disc (x) is known, the corm weight (y) can be estimated with the equation (r= -0.85):

$$y=0.6923-0.0018x+0.0109x^2$$

5.4 Discussion

The results presented in this chapter provide both an overview of the seasonal availability of geophytes throughout the region, while simultaneously providing preliminary insights on the intricacies of how the nutritional quality and growth patterns of geophytes affect their overall nutritional return rates. The discussion of these results is divided among the objectives stated in the introduction, firstly discussing the broad patterns of availability of geophytes across the GCFR, the variation of growth and nutritional composition of geophytes throughout their growing cycle and lastly the results of the pilot study to evaluate whether the seasonal morphological changes of USOs can be used to interpret geophyte remains found in the archaeological record.

5.4.1 Seasonal availability of geophytes across the GCFR

The large-scale phenological patterns of geophytes over the GCFR tend to emulate the rainfall patterns that transition from the East to West along a gradient, as observed for other plant groups (Kruger, 1980; Pierce, 1984; Procheş *et al.*, 2006). In the winter-rainfall region of the GCFR geophytes would only be visible above ground in the winter and spring, with a pronounced peak of species evident during the spring months. This is what we would expect, as the short flowering peak in spring is well known for the core winter rainfall region (Pierce, 1984; Johnson, 1992). When we consider the phenological patterns of geophytes in the South Coast and East Coast, this pronounced peak is less obvious. In the South Coast, two peaks are observed, where the most pronounced peak still falls over spring, but an additional peak over autumn is observed. This pattern corresponds to recent studies describing the seasonal variability of plant resources in the South Coast (De Vynck, Cowling, *et al.*, 2016; Botha *et al.*, 2020). Furthermore, these broad phenological patterns support the results of Chapter 4, where the relative carrying capacity observed during the autumn months was significantly higher than that observed for the rest of the GCFR. In the South Coast many autumn flowering geophytes are known to grow (Dafni *et al.*, 1981a; Dafni *et al.*, 1981b; Ruiters and McKenzie, 1994), these autumn flowering species contributed the high relative carrying capacity observed for this region in autumn in the previous chapter.

When we observe the phenology of geophytes in the East Coast region, the patterns are even more complex, there are four main peaks: spring, autumn, summer, All year/Evergreen (in descending order of importance). Although there is still a pronounced peak of apparency over spring, it is far less prominent than in the other study areas. Importantly there are very few species that flower in winter; instead, there is a pronounced peak in summer. Additionally, some geophytes are evergreen and never go dormant (Pierce and Cowling, 1984). This array of phenological cycles results in a complex array of geophytes that are observable any time of the year, with no pronounced dormant phase. Despite this, the autumn relative carrying capacity of the East Coast was found to be significantly weaker than that of the South Coast, despite the presence of these summer flowering and evergreen geophyte species.

This disparity between regions is caused by the type of geophyte species that were found that contributed to the relative carrying capacity (Chapter 4). The biomass of geophytes observed in the East Coast during autumn did not translate to high relative carrying capacity, because the nutritional content of those species was poor. The autumnal flowering species from the South Coast were almost exclusively cormous Iridaceae species with exceptionally high nutritional content (Chapter 3).

When we observe the individual phenology curves for each geophyte species in the different seasons, what is evident is that many geophytes, experience staggered peaks of their phenology, throughout April-December (West Coast) and the entire year (South Coast and East Coast). This is a known phenomenon, where geophytes competing for the same pollinators, will avoid flowering at the same time, resulting in the staggering of flowering (Gleeson, 1981; Fenner, 1998; Procheş, Cowling and Du Preez, 2005). This phenomenon results in a very wide window of time, during the year, and across all study areas, when some species of geophyte are experiencing their maximum apparency.

Although the above-ground visibility of geophytes would have been critically important to hunter-gatherers during foraging, the nutritional returns possible from geophytes during the different phenophases would have been just as important to consider. In other words, does the maximum apparency or availability of geophyte resources translate to high return rates of foraging for those geophytes? The broad patterns of geophyte resource availability over the region do not describe the quality of the geophyte resources that are present at different times of the year. Does above ground visibility mean that a species can be foraged optimally? I will attempt to answer these questions below by evaluating the effect the phenological cycle has on the energetic return rates of geophytes.

5.4.2 Effect of phenology on energetic return rates of geophyte foraging

The results presented on the nutritional and growth variation of geophytes can attempt to start answering complex questions about how these seasonal changes would have affected hunter-gatherer behaviour; however, these data represent a small sample size from one single region and future replicate studies will be required to answer these questions definitively, for the entire region.

5.4.2.1 Nutritional composition of USOs across their seasonal growth

The weight of a USO does not equal the allocation of resources possible for the plants (Ruiters and McKenzie, 1994; Ruiters, 1995). In non-botanical terms, the amount of energy stored in the USO is not equal for all USO weights. We have to understand the nutritional content of USOs throughout their growing season to determine how much energy is actually contained in the weight discussed.

The nutritional composition of USOs will determine the possible energetic returns they can provide to hunter gatherers. The inedible or unpalatable portions would result in additional processing for a hunter-gatherer to render these plants edible, and therefore are likely to affect the energetic returns (as discussed in Chapter 3). These factors are thus not trivial to a forager and would influence which geophytes they would choose to forage at different times of the year (Hawkes, 1989; Stahl, 1989). Understanding how the various types of USOs store compounds in their tissue, in what quantities, throughout the growing season, is critically important to understand the choices hunter-gatherers made, and can assist the interpretation of the archaeological record.

Although the nutritional results presented in this chapter are from a small sample size, they present the largest data set to date capturing the nutritional variation throughout the phenological cycle of geophytes. From the results presented in this chapter it is clear that the nutritional content of especially cormous species increases toward the end of the growing season. This is in line with what is found for other geophytes (Almeida *et al.*, 2015; Orthen, 2001; Orthen and Wehrmeyer, 2004a; Ruiters, 1995). In general, there is a trend of increased energy content in USOs as the plant matures through the growing season, a trend especially evident in the cormous species tested. The biggest contributions to the energy content were carbohydrates; however, the type of carbohydrate actively being stored in the USO varied seasonally. For all species (except *Eriospermum lanceifolium)*, during the first two months of growth, it was mostly simple sugars like mono and di-saccharides that were stored in the USO. Initially low levels of starch were produced, but after the first month of growth the starch levels increased dramatically. Slightly elevated protein content was observed during the peak flowering months, although these levels were so low, they are unlikely to contribute to human daily requirements for proteins (below 2/100 g). Fat content in USOs was consistently negligible. *Eriospermum lanceifolium* had the lowest energy content in comparison to the other species. This is partly due to the low levels of starch observed for this species. This family has been shown to mostly store fructants and water in their USOs and very little starch (Orthen, 2001a).

The pronounced dip in energy content in *Pelargonium triste* and *Watsonia meriana* in the month of October is most probably due to the energetic cost of flowering which occurs during this time. As described in the introduction, during this month the starch being produced by leaves would be used to fuel the growth of the inflorescence and not stored in the USO(Waher, 1974; Zimmerman and Whigham, 1992; Orthen and Wehrmeyer, 2004). If hunter-gatherers were aware of this phenomenon, geophytes in flower might have been avoided during foraging forays.

The general trend of increased energy content of USOs as the growing season proceeds is underpinned by the variation in carbohydrate storage in the USOs. It has been found that different USOs store starches and fructants in different concentrations, depending on the physiology of the geophyte (Almeida *et al.*, 2015; Bülow *et al.*, 2010; Meyer and Hellwig, 1997; Orthen, 2001a, 2001b; Ranwala and Miller, 2008). During the initial growth of the plants, new growth is sustained from stored carbohydrates in the previous season corm; here starches are metabolized to form fructants which can sustain the new growth (Orthen and Wehrmeyer, 2004). Starch, an insoluble molecule that can be stored in the USO in a stable form, is only partitioned to the USO after the energetic requirements of the new growth and production of inflorescence has been satisfied (Orthen and Wehrmeyer, 2004). There is therefore an energetic advantage to forage perennial USOs later in the season, i.e., late spring. This matches the ethnographic observations made of hunter-gatherers foraging geophytes (Thunberg, 1795; Lichtenstein, 1930; Parkington, 1977).

The compounds that negatively affect the nutritional quality of USOs showed similar patterns of seasonal variation. USO fibre content was very low for all species, but water content very high. These two variables did not vary significantly throughout the growing season. The tannin content of the USOs however did. In all species except *Ferraria crispa* (which contained no tannins), tannin content was high during the first few months of the growing season, usually peaking in the second month of growth, and subsequently dropped significantly lower until the plant enters senescence and dormancy.

The changes in USO qualities linked to specific phenophases (sprouting and leaving) suggest that there would be an optimum time to forage a specific geophyte species. Phenological cues, which are visible above ground, could have been used to identify when geophytes are likely to yield the most palatable and nutritious harvest. Even if plants have a wide window of time during which they are visible above ground this does not mean that they would necessarily be palatable or profitable to forage for this entire window of time.

Although the conclusions we can draw from the small sample size of data are limited, what seems evident is that in general the quality of USOs increases through the growing season and reaches its peak shortly before senescence. Thereafter, the quality of the USOs drops throughout dormancy as secondary metabolites build up and carbohydrate resources are depleted (Waher, 1974; Orthen and Wehrmeyer, 2004; Kaššák, 2012; Singels, 2013; Di Giusto, Dounias and McKey, 2017). The staggering of geophyte phenologies across the study areas throughout the year shows that different species would experience this peak in their nutritive quality at different times. Early winter-flowering geophytes could experience the peak in their nutritive quality in early winter in the West Coast, with a pronounced peak in the number of species in spring, which can last until early summer. In the South Coast and East Coast there is almost always a geophyte species experiencing the peak of their nutritive quality. This is paired with various pronounces peaks in the number of species experiencing the highest nutritive quality in their cycles during autumn, spring, and even summer for the East Coast.

5.4.2.2 Seasonal growth patterns of different types of geophytes

The results presented on the variation of seasonal growth of different types of geophytes show how much the weight of USOs can vary throughout the growing cycle of geophytes. One of the most prominent factors that would influence the expected energetic returns from geophytes is whether the USO is perennial (most tubers, rhizomes and bulbs) or replaced yearly (most corms). This will affect the expected weight of USOs (i.e., return on foraging investment) at any point of seasonal growth. The results on seasonal growth are divided among the geophytes with perennial storage organs and those that replace their USO yearly.

Perennial Storage Organs weight

Some growth forms like rhizomes and tubers (and infrequently corms) do not replace their USOs seasonally but have what is called perennial storage organs (Dafni *et al.*, 1981a). How does this impact the possible variation of weight of the USO seasonally?

In the three species observed in this study there were no significant differences across the growing season of weights of USOs, apart from *Ferraria crispa* between the months of August and September. In these species it seems that the weight of USOs is determined by the age of the plant, not the phenophase it finds itself in. This resulted in the average weight of USOs not differing significantly over the growing season, however, there was very large variation of USO weight per month, which resulted in monthly means having standard deviation falling between 40 and 60 grams. This variation suggests that there is low predictability as to what the weight of the USO might be, judging solely from the above ground plant parts and the phenophase of the plant. The seeming unpredictability of USO weight would have resulted in unpredictable foraging returns for foragers. Despite the variability of the size of USOs of each species, the average weight of rhizomes and tubers was high. The average high weight of these species means that these species could deliver high nutritional return rates, but always present a gamble. These species can be considered as a high-risk foraging option for a hunter-gatherers, with low predictability of foraging return rates.

In the case of the cormous perennial storage organs of *Ferraria crispa*, the standard deviation of the weight of the corms was lower than the tuberous and rhizomatous species, suggesting there is some predictability in what a forager might find below ground if the plants are unearthed. This is because this Iris is a type of hybrid between a perennial storage organ and an annual storage organ. The plant grows a new corm yearly, but the old corms do not get “absorbed” by the new seasonal growth (Manning and Goldblatt, 2012). The overall effect on foraging might, however, be similar to the other perennial species: No matter the season of foraging, as soon as the above ground part of the plant is visible, there could be a USO of substantial weight lying below ground, depending on the age of the plant. For these species, what lies underground, and the energetic investment of foraging for it, is a gamble for the forager that could be handsomely rewarded, at any time that the plant is visible above ground.

Growth pattern of cormous species

Although the weight of corms can vary substantially, depending on the age of the plant, the general pattern of increased weight over the growing season is evident, although this pattern should be confirmed with more sampling. The low weight of corms in early phenophases (sprouting and leaving) is paired with the relatively lower energetic content in these early phenophases. This means that the energetic return rate of foraging cormous species shortly after they have sprouted was likely an energetically expensive endeavour, with very low rewards. There was a pronounced increase in the weight and energy content of corms in later phenophases, and the return rates of foraging are optimal just before the plant enters senescence.

Cormous plants that were in flower had smaller corms and lower energy content. When we observed the differences in the disc height and corm weight in plants that flowered in contrast to plants that did not, there were significant differences in the weight of the corm. The corm weight of non-flowering plants was significantly higher than flowering plants. Apart from the lower weight of corms during flowering, their energy content is also lower. In geophytes, flowering is an energetically expensive process (Waher, 1974; von Willert, Rossa and Steinberg, 1991) and for cormous geophytes that energy could have been stored in the corm to ensure survival during the dormant phase (Zimmerman and Whigham, 1992; Orthen and Wehrmeyer, 2004). Due to the competition between the storage of resources for dormancy and the urge to reproduce sexually (Orthen and Wehrmeyer, 2004) cormous plants might only flower as infrequently as every four years (Waher, 1974; pers. obs.).

The inflorescence of a geophyte is a strong above ground signal, which could have acted as another means for hunter-gatherers to predict what the returns of their energetic investment would have been in unearthing geophytes. This phenomenon, together with understanding what type of geophyte they encounter could have allowed them to make decisions about which individual plants and species to target, during which season, rather than randomly digging up geophytes that might require more energy to unearth than they might be able to supply.

These results show that if hunter-gatherers understood the fluctuations in nutritional quality of different geophytes species throughout their phenological cycles they would have been able to forage geophytes optimally for an extended time of the year, in all regions. This is not a unfounded assumption to make, as GCFR hunter-gatherers (and all hunter-gatherers) have been shown to have extraordinary taxonomic skills, showing in-depth understanding of the biotic and abiotic factors that influence food sources (De Vynck *et al.*, 2016; Van Wyk and Gericke, 2000; van Wyk, 2008). Ethnographic observation of geophyte foraging in the region also support the fact that specific species were targeted following flowering, before seeding (Thunberg, 1795; Bleek and Lloyd, 1911; Skead, 2009; Van Vuuren, 2013).

5.4.3 Use of seasonal growth patterns of corms in the analysis of archaeological material

The phenological and USO nutritional yield patterns described in this chapter indicate when geophytes could be optimally foraged in each region based on the parameters studied, but is there archaeological evidence that foragers targeted geophytes during these optimal timeframes in the various regions? To answer this question we would have to be able to determine when a geophyte found in the archaeological record was foraged in its phenological cycle.

The pilot study evaluating the feasibility of using corms as a proxy indicator tool shows promise. It is important to reiterate that these results should be considered preliminary, and any interpretation of the results should be confirmed by future studies and more sampling. There is, however, a clear relationship between corm weight, disc height and disc diameter. Since corm discs are one of the most prominent geophyte remains found in GCFR archaeological sites (Parkington and Poggenpoel, 1971; Deacon, 1976; Liengme, 1987), and because the discs are easily measurable, a correlative method can be developed to establish, using these relationships, the size and energy content of food collected by hunter-gatherers in the past. There is also potential to shed light on the seasonality of geophyte foraging.

At the crux of this potential proxy indicator method is the phenomenon observed that the height of discs decreases throughout the phenological cycle in a systematic way. This means that it might be possible to use the predictability of corm growth to interpret the discarded corm discs so commonly found in the archaeological record (Parkington and Poggenpoel, 1971; Deacon, 1976; Liengme, 1987).

The equation presented can be used to model the time of year when corms were foraged if the disc height is known, where x is the disc height and y is the corresponding month of extraction.

Although the correlation of disc height to the month of the collection was weaker for *Moraea fugax* and *Watsonia meriana* (likely due to the variation caused by flowering), *Cyanella hyacinthoides* and *Babiana ambigue* had remarkably high rates of correlation for these variables and would be prime candidate species to use in the execution of this method.

The other correlation that is critical to draw to interpret archaeological material is the diameter of the disc and the weight of the new corm. As cormous plants grow in a predictable way, the size of the previous season's disc (diameter) can help us approximate what the size of the corm was that was foraged (and presumably eaten), which will allow us to interpret the energetic returns of the geophytes that were collected by hunter-gatherers.

The regression performed on the disc diameter and corm weight for mature plants (August-October) found that the disc diameter had an excellent correlation to the weight of the corms, regardless of species. The equation presented can be used to model the corm weight if the disc diameter is known, where x is the disc diameter and y is the corresponding corm weight.

5.5 Conclusion

The availability and nutritional quality of the geophyte resource varies across the GCFR region and closely mimics the rainfall patterns observed for each region. The time frame during which some form of geophyte resources would have been available to foragers differs over the region. In the West Coast geophyte resources would have been highly seasonal, but available from early winter to early summer. In the South Coast and East Coast geophyte resource could have been available practically year-round. What is clear is that geophytes are available across the region for most of the year in some shape or form, which is surprising considering geophytes have always been considered a highly seasonal resource. This wide time frame of availability is due to the staggering diversity of geophytes that grow in the different regions, with different phenological cycles.

The preliminary results indicate that there is predictability in the variation of energetic return rates of corms. The nutritive quality of corms improves throughout the phenological cycle, as does the weight of corm and would offer optimum return rates before senescence and dormancy. For other growth forms the energetic return rates are less predictable based on the phenological cycle only. Tubers and rhizomes could potentially be foraged optimally for the entire time frame that they are visible above ground.

Archaeobotanical material is our primary line of evidence to decipher hunter-gatherer diet and foraging behaviour. Unfortunately, the interpretation of this material is complex and there are many limitations to the interpretation that can be developed from analysing this material. The geophyte remains in archaeological sites can be enigmatic windows into the precise time frame of when they were collected, processed, and consumed. Unravelling the information that we do have at our disposal (archaeological evidence and contemporary growth of plants), can help us understand at least what was possible or likely. The preliminary results imply that it might be possible to model the approximate time of collection of geophytes found in the archaeological record and what size the food package was that was foraged. If the sampling of this pilot study were replicated across the entire region, this method could allow us to improve our understanding of the decisions that were made in different environments, where resources in the landscape are not static, but vary seasonally. The novel method developed from this data will be applied to the data captured from 12 archaeological sites across the GCFR in the following chapter to evaluate the validity of this method and whether it is worth replicating in the future

Chapter 6: **Archaeobotanical evidence of geophyte exploitation in the GCFR**

6.1 Introduction

In this thesis, different lines of evidence were investigated to evaluate the impact of geophytes on hunter-gatherer subsistence in the Stone Age and human evolution. Archaeobotanical material remains the most direct resource available to study the actual subsistence patterns and foraging choices of Stone Age hunter-gatherers. The information on the geophyte resource base and ethnography of geophyte foraging presented to this point will provide a valuable framework to interpret the archaeological evidence of actual geophyte foraging by hunter-gatherers. In this chapter and the next, I will attempt to present compelling evidence of the diversity, temporal distribution, spatial distribution, and cultural complexity of geophyte foraging and processing found in excavated assemblages across the GCFR.

As discussed in Chapter 1, there are prominent archaeological sites across the GCFR which have shaped the prevailing hypothesis of the importance of geophytes in Stone Age hunter-gatherer diets. These sites are predominantly concentrated in the North-West of the GCFR (West Coast as defined in this thesis) and the east of the GCFR region (East Coast as defined in this thesis). See Figure 6.1 for the distribution of significant sites across the GCFR.

This strong relationship between Stone Age hunter-gatherers and geophytes is well presented from these sites in the following critical references, which include systematic analysis of geophyte material (Wells, 1965; Deacon, 1969, 1976, 1993; Parkington, 1972, 1976, 1984; Liengme, 1987). These studies broadly describe four categories of botanical remains identified in cave sites:

1. Grass-dominated deposits at the back of shelters, which are interpreted as sleeping hollows (bedding) which are scraped into the underlying deposits.

2. Iridaceae and USO-dominated deposits interpreted as food waste.

3. Special deposits such as storage pits.

4. Carbonised lenses, interpreted as extensive geophyte processing.

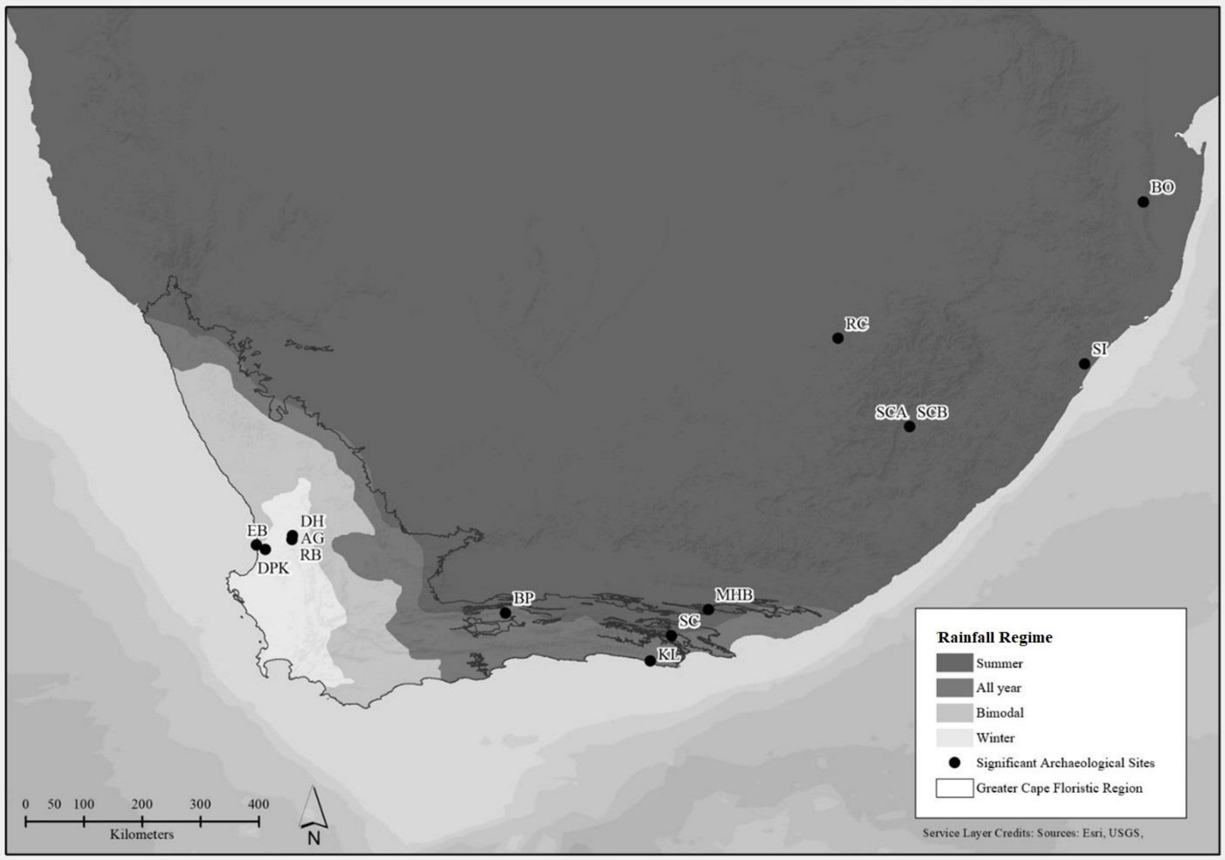


Figure 6.1 Significant Archaeological sites where geophyte remains are well reported, and the dominant rainfall regime within which they are found. Rainfall data adapted from Bradshaw & Cowling, 2014. EB-Elands Bay Cave, DPK-Diepkloof Rock Shelter, DH-De Hangen, RB-Renbaan Cave AG-Andriesgrond Cave, BP-Boomplaas Cave, KL-Klasies River, SC-Scott's Cave, MHB-Melkhoutboom Cave, RC-Rose Cottage Cave, SCA-Strathalan Cave A, SCB-Strathalan Cave B, SI-Sibudu , BO-Border Cave.

The primary objective of this chapter is to explore the spatial distribution of geophyte exploitation across the region. The reason for this focus is illustrated well by Figure 6.1. The distribution of archaeological sites where geophyte remains are well reported is concentrated in certain regions, despite the fact that the geophyte resources base is large across the entire region (as presented in Chapter 4). By evaluating the spatial distribution of geophyte remains across the GCFR, paired with qualitative analysis of the remains found in excavated assemblages, I hope to achieve the following objectives:

1. ***Determine the spatial distribution of geophyte remains across the GCFR***
2. ***Determine the temporal distribution of geophyte remains in the archaeological record in the GCFR***

3. ***Determine whether the diversity of geophytes found in the archaeology reflect the diversity and quality of the geophyte resources found in the contemporary landscape***
4. ***Test the applications of the proxy method develop in Chapter 5 to evaluate whether the seasonal growth patterns of corms can be used in the analysis of archaeological material***

This thesis and the archaeobotanical analysis presented in this chapter are reliant on the published archaeological literature available from the region and available archival material derived from excavations performed in the past. Although this range of information and material is expansive for this region (because archaeological research interest has been focused in certain regions), it cannot be viewed as a comprehensive, definitive representation of the archaeology of the region necessarily. Before the objectives listed above can be achieved, a discussion of the biases and selection forces which determine what food waste is preserved in the archaeology and later reported on is warranted. This will contextualise the archaeological evidence of geophyte foraging which is reported.

6.1.1 Selection forces determining where and what type of geophyte remains are reported

In this chapter I hope to evaluate the distribution of evidence of geophyte foraging across the GCFR by evaluating the presence or absence of sites in the landscape which show signs of geophyte foraging. The interpretation of this presence or absence is important to define, as the absence of evidence does not equate as evidence of absence of geophyte foraging. In other words, just because geophyte material is not found in excavated assemblages, does not mean hunter-gatherers did not forage geophytes. To better understand the distribution of sites where geophyte remains occur and what type of remains are uncovered, we have to investigate where and how these remains are found and how they are reported. There are various factors which influence how geophyte remains end up in archaeological sites and how they are later found and reported on. The factors and biases which determine what evidence of geophyte foraging is reported in the literature can be broadly defined under two categories: depositional bias and recovery bias (Pearsall, 2016). Depositional biases are factors which determine whether geophyte remains are preserved in the archaeological record, while recovery biases are factors which determine what remains are later found and reported by excavators (Pearsall, 2016).

6.1.1.1 Recovery Bias

There are many factors that enable or restrict archaeologists in the excavations they perform. The region where archaeologists focus surveys to identify new archaeological sites and eventually the excavation of these sites can be influenced by other supporting institutions such as University Departments and Museums, which facilitate the work. Where all of these resources are present, archaeological excavation can occur. The distribution of sites, especially in the GCFR, which report geophyte material seem to correspond to researchers based at the University of Cape Town, Stellenbosch University and Rhodes University (where there are supporting museums which aid in the curation of material excavated: the Iziko Museum and the Albany Museum, which have been important facilities historically).

The methods used during excavation, together with the process of archiving the material can also impact the results of excavations and future analysis of excavated material. Macrobotanical remains are retrieved from archaeological sites by three methods in most cases (Pearsall, 2016):

1. During excavation, in-situ macrobotanical remains are removed,

2. through screening of removed sediment,

3. by using water recovery techniques (such as flotation).

If standard protocol is followed, botanical remains from all three techniques will be weighed and measured and the volume and weight compared to the deposit that it came from, to allow some form of quantification. Often this method is only applied to certain samples to calculate average densities of plant remains in comparison to other materials. When these samples are analysed to provide identification of plants and other variables they are usually sorted and later stored. It is critically important that all information collected, all procedures of sorting and sifting need to be stored with archived material to enable future researchers to allow further analysis as new techniques are developed.

Using water recovery techniques can damage and even cause rapid decomposition of dry botanical material. Wet material will not be retrieved using this method as it will not float. Even screening could cause damage to delicate remains and depending on the mesh size, let important material pass through sieve holes. Even removing *in situ* macrobotanical material can damage the integrity of the remains.

6.1.1.2 Depositional biases

Certain regions produce conditions that are more conducive to botanical remains preservation. The areas where good preservation of botanical remains occur are in sites that are well protected from the elements (like rock shelters and caves as opposed to open-air sites). Apart from the climate, the topography and geology of a region will also determine where there are features that would have been suitable areas for shelter for Stone Age hunter-gatherers, which in turn determines where geophytes could have been processed and discarded. These abiotic factors have to be considered if we hope to evaluate the distribution of geophyte exploitation across the GCFR.

Most importantly, perhaps, are the biotic factors that determine if geophyte remains are found in archaeological sites. The distribution, density and quality of geophyte communities vary, and this would influence the types of geophytes that would have been foraged. I have attempted to describe these factors in the previous chapters, which will help us interpret the choices hunter-gatherers made in the landscape by evaluating if it would have been energetically profitable for them to forage geophytes in certain situations. The way in which geophytes were foraged and processed by hunter-gatherers determines what is discarded in archaeological sites. If geophyte processing took place in protected rock shelters and caves as opposed to open-air sites, the possibility of preservation of that material is far greater.

The debris that could be left in archaeological determines what evidence is preserved in the archaeological record. The fleshy part of USOs that was consumed (or used for other purposes), is usually absent in the archaeological record (Pearsall, 2016). Only if there is an inedible portion to the USO, which is brought back to a shelter, processed and discarded, can we expect to find this material in the archaeological record. This phenomenon sheds light on how important it is to understand human behaviour which produced archaeological material. Leaves, inflorescences, seeds and the outer covering of USOs (bark or tunics/husks) can be removed during processing of the collected geophytes and discarded as debris. Of the different types of USOs, different types of debris might be left behind, importantly, some will leave no debris in the archaeological record and are “invisible”. Furthermore, many USOs were cooked by roasting them in fire, in this process much of the possible debris that could have been preserved in the archaeological record can be lost (Pearsall, 2016).

6.1.2 How do we interpret the geophyte remains we do find?

Most systematic analysis of food debris has focused on identifying the diversity of animal/plant species which were hunted/gathered and the relative importance of those items in the diet. Quantifying the proportion of a particular food type made up of the total diet is a crucial component of understanding subsistence patterns. Quantification has often been attempted by evaluating the density values of certain food types or species; where the number or mass of that food type per unit volume of food debris/sediment is calculated (Treganza and Cook, 1948). These values have been used to estimate group sizes, subsistence shifts due to climate change and new resource use due to advances in technologies.

Could we evaluate the proportion of food debris that is comprised of geophyte remains to infer the importance of USOs in hunter-gatherer diets?

As outlined in Chapter 1, the quantification of geophyte remains is littered with pitfalls. The simple quantification method of comparing the volume of geophyte material to the volume of overall material will not generate an accurate representation of the proportion geophytes comprised of the entire diet. This is due in part to the different rates of sediment compression, which can make comparisons between different layers of the same site difficult (Jerardino, 1995). Additionally, not all geophytes foraged by hunter-gatherers will generate identifiable debris. Most importantly for most species, it is impossible to assign a specific weight of food to a certain weight or number of geophyte remains. For example, in the case of cormous species, they produce corms yearly, and the previous seasons' corms are reduced to flat discs which are stacked on top of one another underneath the new corm (I have observed as many as 12 discs to a single corm). Additionally, the outer covering of the corm consists of numerous layers of husks, which can be found intact or scattered into fragments. This debris that is found cannot be tied to a single corm, and certainly is not evidence of 12 corms.

In this thesis I have analysed archival archaeological material, which increased the difficulty of quantification even further as most of this material has been analysed or sorted previously. This results in material that is not necessarily representative of bulk samples of what was found in-situ during excavations. Furthermore, very detailed descriptions of each sample, how it was taken and the sorting process which it has undergone is not necessarily available for every single sample. Considering all of these confounding factors, the quantification of geophyte material was not possible for the analysis presented in this chapter. What information can be obtained from archival material?

Simple, yet useful information we can glean from archival material is the diversity of geophytes which were foraged across the region. This information was assessed in archival material from various sites across the region and was compared to the contemporary resource base across the region. The absence of certain species, which we expect to find in the archaeology was also assessed by evaluating the array of species which were foraged historically but would leave no identifiable debris.

Perhaps the most significant contribution of this thesis was the application of the proxi method presented in the previous chapter by using the patterns of growth of geophyte species to extrapolate the weight, energy content and seasonality of geophytes foraging in the Stone Age. In this chapter a preliminary test of this method was performed by evaluates the efficacy of applying the equations generated in the previous chapter on geophyte remains found in archival material from excavated assemblages. A preliminary evaluation of whether it is scientifically sound to extrapolate the weight, energy content and season of collection of certain geophyte species using this method is presented and recommendation on the use of this method in future studies are made.

To evaluate the spatial distribution of geophyte exploitation across the GCFR I will next present a review of all archaeological sites in the GCFR where evidence of geophyte foraging has been reported. The sites which were selected for further investigation will then be discussed in greater detail, before the results of the systematic botanical analysis of material from these sites are presented in the results section.

6.1.3 Review of presence or absence of geophyte remains in excavated assemblages

In an attempt to evaluate the geophyte remains present in archaeological sites all across the GCFR, all archaeological sites in or near the study regions were identified and the presence or absence of geophyte remains reported, investigated from the available reports and associated literature. In total fifty-nine sites were identified and evaluated. Of these sites, twenty-four were selected and the geophyte remains in archival material was systematically analysed. The presence or absence of geophyte remains in the fifty-nine sites is presented in Figure 6.2 and Table 6.1.

It is clear that geophyte remains are a very common occurrence across the entire region, with a dense concentration of sites in the West Coast and East Coast study regions.

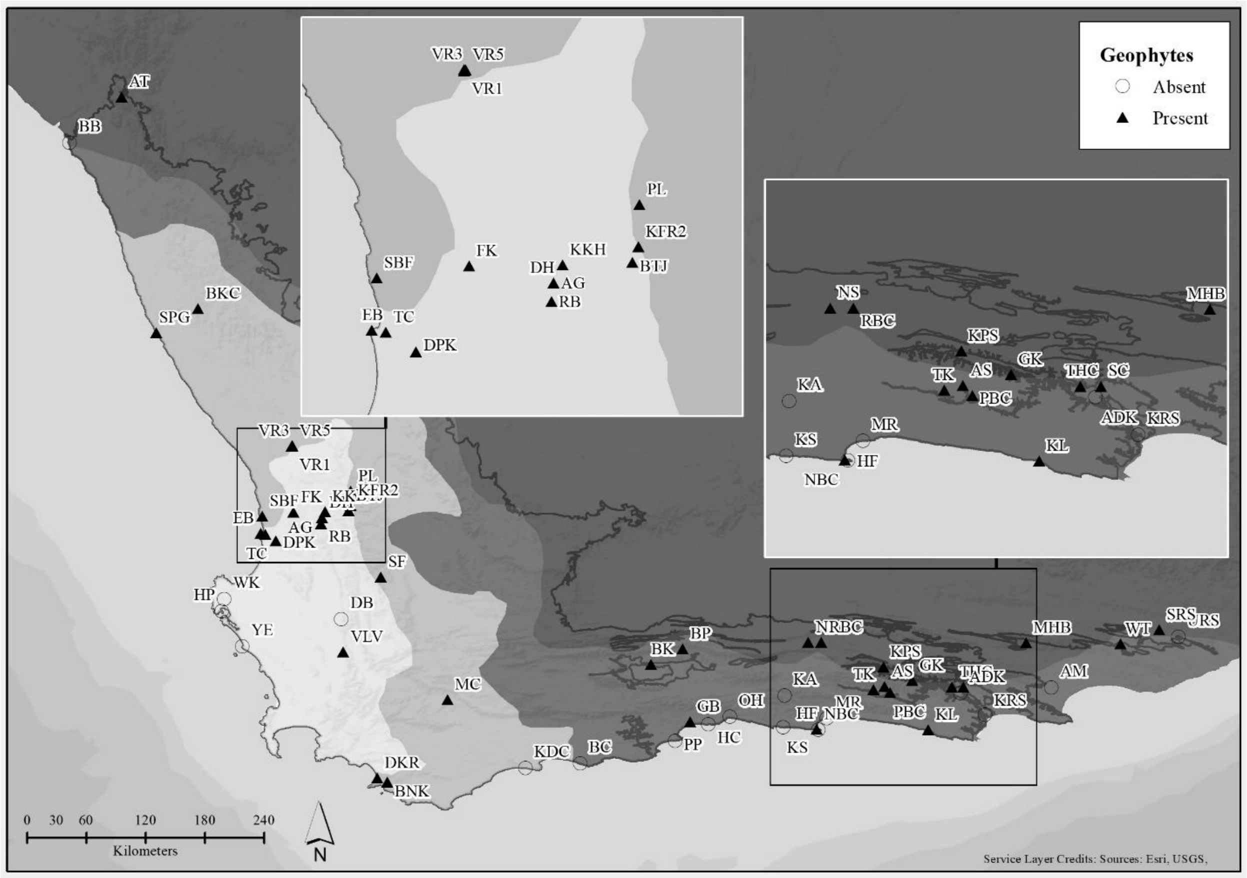


Figure 6.2 Distribution of archaeological sites where geophytes are present or absent in the excavated assemblages. See Table 6.1 for the Site names associated with abbreviations.

Table 6.1 All sites identified within GCFR and significant sites identified outside the GCFR. Sites in bold were included in the systematic botanical analysis

Locality	**Code**	**Dates (ya)**	**Reference**	**Region**	**Biome**	**Vegetation Type**	**Band**	**Geophyte absent or present. Site systematically analysed or not.**
Steenbokfontein	SBF	2200-6070	(Jerardino and Yates, 1996)	West Coast	Fynbos	Strandveld	Coastal plain	Not studied. Geophyte remains reported
Elands Bay Cave	EB	1000-13600	(Parkington, 1976; Orton, 2006)	West Coast	Fynbos	Strandveld	Coastal plain	Analysed. Geophyte material identified
Tortoise Cave	TC	760-8100	(Robey, 1984)	West Coast	Fynbos	Strandveld	Coastal Plain	Analysed. Geophyte material identified
Witklip	WK	500-3060	(Smith *et al.*, 1991)	West Coast	Fynbos	Strandveld	Coastal Plain	Not studied. No botanical remains reported
Hoedjiespunt	HP	80-130kya	(Marean *et al.*, 2014)	West Coast	Fynbos	Strandveld	Coastal Plain	Not studied. No botanical remains reported
Ysterfontein	YE	114-140ka	(Marean *et al.*, 2014)	West Coast	Fynbos	Strandveld	Coastal Plain	Not studied. No botanical remains reported
Faraoskop	FK	600-14000	(Manhire, 1993)	West Coast	Fynbos	Sand Fynbos	Coastal Plain	Analysed. Geophyte material identified
Diepkloof Rock Shelter	DK	390-1590, 45kya-130kya	(Silberbaur, 1974; Texier *et al.*, 2010)	West Coast	Fynbos	Sand Fynbos	Coastal Plain	Analysed. Geophyte material identified
Driebos	DB	none	(Smith *et al.*, 1991)	West Coast	Fynbos	Sand Fynbos	Coastal Plain	Not studied. No botanical remains reported
Voëlvlei	VL	373-1920	(Smith *et al.*, 1991)	West Coast	Fynbos	Sand Fynbos	Coastal Plain	Not studied. Geophyte remains reported
Andriesgrond Cave	AG	390-1640	(Anderson, 1991)	West Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte material identified
Renbaan Cave	RB	1150-5430	(Kaplan, 1984)	West Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte material identified
Klein kliphuis Shelter	KKH	1230-32300	(van Rijssen and Avery, 1992)	West Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte material identified
De Hangen	DH	90-450	(Parkington and Poggenpoel, 1971)	West Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte material identified
Boontjieskloof	BTJ	none	none	West Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte material identified
Putslaagte	PL	230-1900	(Halkett, 1990)	West Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte material identified

Locality	**Code**	**Dates**	**Reference**	**Region**	**Biome**	**Vegetation Type**	**Band**	**Geophyte absent or present Site systematically analysed or not.**
Klipfonteinrand 2	KFR2	1430-4279	(Nackerdien, 1989)	West Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte remains reported not found in archival material
Stompiesfontain	SF	none	none	West Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte material identified
Boegoeberg	BB	31-42ka	(Marean *et al.*, 2014)	West Coast	Succulent Karoo	Succulent Karoo	Coastal Plain	Not studied. No botanical remains reported
Spoegrivier	SR	1390-3520	(Webley, 1992; Vogel, 1997)	West Coast	Succulent Karoo	Succulent Karoo	Coastal Plain	Not studied. Geophyte remains reported
/Ai tomas	AT	320-1980	(Webley, 1984, 1992)	West Coast	Succulent Karoo	Succulent Karoo	Coastal Plain	Not studied. Geophyte remains reported
Bethelsklip Cave	BT	360-800	(Webley, 1984, 1992)	West Coast	Succulent Karoo	Succulent Karoo	Coastal Plain	Not studied. Geophyte remains reported
Varsche 1	VR1	828-21899	(Orton *et al.*, 2011)	West Coast	Succulent Karoo	Succulent Karoo	Coastal Plain	Analysed. Geophyte material identified
Varsche 3	VR3	220-1409	(Orton, 2012)	West Coast	Succulent Karoo	Succulent Karoo	Coastal Plain	Analysed. Geophyte material identified
Varsche 5	VR5	4551-5451	(Orton *et al.*, 2011)	West Coast	Succulent Karoo	Succulent Karoo	Coastal Plain	Analysed. Geophyte material identified
Die Kelder	DK1	1465-2020	(Schweitzer, 1979)	South Coast	Fynbos	Strandveld	Coastal Plain	Not studied. Geophyte remains reported
Byneskranskop	BNK	1480-3900	(Schweitzer and Wilson, 1982)	South Coast	Fynbos	Strandveld	Coastal Plain	Not studied. Geophyte remains reported
Klipdrift Cave	KDC	9700-11800; 59,4-65,5ka	(Henshilwood *et al.*, 2014)	South Coast	Fynbos	Strandveld	Coastal Plain	Not studied. No botanical remains reported
Blombos Cave	BC	1000-2000; 70-110ka	(Henshilwood *et al.*, 2001)	South Coast	Fynbos	Strandveld	Coastal Plain	Not studied. No botanical remains reported
Pinnacle Point	PP	90-130ka; 160ka	(Marean, 2010)	South Coast	Fynbos	Strandveld	Coastal Plain	Not studied. No botanical remains reported
Great Brak River Cave	GBRC	none	none	South Coast	Fynbos	Strandveld	Coastal Plain	Not studied. Geophyte remains reported

Locality	**Code**	**Dates**	**Reference**	**Region**	**Biome**	**Vegetation Type**	**Band**	**Geophyte absent or present Site systematically analysed or not.**
Heroldbay Cave	HC	70-125ka	(Marean *et al.*, 2014)	South Coast	Forest	Forest	Coastal Plain	Not studied. No botanical remains reported
Oakhurst	OH	2065-9100	(Patrick, 1989)	South Coast	Forest	Forest	Coastal Plain	Not studied. No botanical remains reported
Montagu Cave	MC	1100-5860	(Keller, 1973)	South Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. Geophyte remains reported
Buffelskloof Rock Shelter	BK	3840-6000	(Opperman, 1978)	South Coast	Succulent Karoo	Succulent Karoo	Cape Fold Belt	Not studied. Geophyte remains reported
Boomplaas Cave	BP	2000-14500	(Deacon, 1979)	South Coast	Fynbos	Renosterveld	Cape Fold Belt	Analysed. Geophyte material identified
Knysna Cave	KS	none	none	East Coast	Fynbos	Strandveld	Coastal Plain	Analysed. Plant remains identified. No geophytes remains identified
Nelson Bay Cave	NBC	4,8-12,5ka	(Inskeep, 1987)	East Coast	Fynbos	Strandveld	Coastal Plain	Analysed. Geophyte remains reported not found in archival material
Hoffman	HF	3310-4330	(Kyriacou, 2009)	East Coast	Fynbos	Strandveld	Coastal Plain	Analysed. Plant remains identified. No geophytes remains identified
Matjes River Rockshelter	MR	3555-10660	(Dockel, 1998)	East Coast	Forest	Forest	Coastal Plain	Not studied. No geophyte remains reported, but plant remains reported
Klasies River	KL	2525-4695; 70-125ka	(Deacon and Geleijnse, 1988; Binneman, 1995)	East Coast	Forest	Forest	Coastal Plain	Analysed. Geophyte remains reported not found in archival material
Kabeljous River Shelter	KRS	2450-5750	(Binneman, 1995)	East Coast	Fynbos	Riparian	Coastal Plain	Not studied. No botanical remains reported
Amanzi	A	ESA	(Inskeep, 1965)	East Coast	Albany Thicket	Riparian	Coastal Plain	Analysed. Plant remains identified. No geophytes remains identified
Kangkara	K	5355-12550	(Deacon, 1982)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. No botanical remains reported
Nuwekloof Shelter	NS	1140	(Binneman, 2000)	East Coast	Fynbos	Renosterveld	Cape Fold Belt	Not studied. Geophyte remains reported
Rautenbachs Cave	RBC	1620	(Binneman, 1995)	East Coast	Fynbos	Renosterveld	Cape Fold Belt	Not studied. Geophyte remains reported
Tierkloof	TK	2000	(Steyn, Binneman and Loots, 2007)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. Geophyte remains reported

Locality	**Code**	**Dates**	**Reference**	**Region**	**Biome**	**Vegetation Type**	**Band**	**Geophyte absent or present Site systematically analysed or not.**
Augussie Shelter	AS	4490	(Binneman, 1994)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. Geophyte remains reported
Paardeberg Cave	PBC	none	(Deacon, 1976; Binneman, 1995)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. Geophyte remains reported
Kleinpoort Shelter	KS	2000	(Binneman, 1995)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. Geophyte remains reported
Groot Kommandokloof	GKK	2000	(Binneman, 1999)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. Geophyte remains reported
The Havens Cave	THC	1280-9790	(Binneman, 1995)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. Geophyte remains reported
Andrieskraal	ADK	none	(Deacon, 1965)	East Coast	Albany Thicket	Thicket	Cape Fold Belt	Not studied. No botanical remains reported
Scott's cave	SC	360-1190	(Deacon, 1963; Wells, 1965)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Analysed. Geophyte material identified
Melkhoutboom Cave	MHB	250-15400	(Deacon, 1967, 1969)	East Coast	Albany Thicket	Thicket	Cape Fold Belt	Analysed. Geophyte material identified
Wilton	WT	2270-8260	(Deacon, 1995)	East Coast	Albany Thicket	Thicket	Cape Fold Belt	Not studied. Geophyte remains reported
Spring Rock Shelter	SRS	none	(Deacon, 1976)	East Coast	Nama-Karoo	Nama-Karoo	Cape Fold Belt	Not studied. Geophyte remains reported
Welgeluk	WG	510-4560	(Hall, 1990)	East Coast	Savannah	Savannah	Cape Fold Belt	Not studied. Significant sites outside GCFR that report geophyte remains
Uniondale Rockshelter	URS	2125-6300	(Leslie-Brooker, 1987)	East Coast	Fynbos	Mountain Fynbos	Cape Fold Belt	Not studied. No botanical remains reported
Highlands Rockshelter	HRS	4500	(Deacon, 1976)	Outside GCFR	Nama-Karoo	Nama-Karoo	Outside GCFR	Not studied. Significant sites outside GCFR that report geophyte remains
Strathalan Cave A	SCA	2470	(Opperman, 1996)	Outside GCFR	Grassland	Grassland	Outside GCFR	Not studied. Significant sites outside GCFR that report geophyte remains
Strathalan Cave B	SCB	20900-29249	(Opperman and Heydenrych, 1990)	Outside GCFR	Grassland	Grassland	Outside GCFR	Not studied. Significant sites outside GCFR that report geophyte remains

Locality	**Code**	**Dates**	**Reference**	**Region**	**Biome**	**Vegetation Type**	**Band**	**Geophyte absent or present Site systematically analysed or not.**
Sibudu	S	38,6-70,5ka	(Sievers, 2011; Wadley *et al.*, 2011)	Outside GCFR	Indian Ocean Coastal Belt	Indian Ocean Coastal Belt	Outside GCFR	Not studied. Significant sites outside GCFR that report geophyte remains
Rose Cottage Cave	RC	500-31300	(Wadley, 1997)	Outside GCFR	Grassland	Grassland	Outside GCFR	Not studied. Significant sites outside GCFR that report geophyte remains
Border Cave	BO	30-200ka	(d'Errico *et al.*, 2012; Villa *et al.*, 2012)	Outside GCFR	Savannah	Savannah	Outside GCFR	Not studied. Significant sites outside GCFR that report geophyte remains

The spatial and temporal distribution of geophyte remains will be discussed in the results section. Below is a short description of the sites which were included in the systematic botanical analysis for this study.

6.1.3.1 West Coast

Coastal Plain sites

Elands Bay Cave is located at the mouth of the Verlorenvlei on the coast. The most recent deposits, dated to within the Holocene, contained geophyte material (Parkington, 1976; Liengme, 1987). A large amount of geophyte material was analysed, which consisted of Iridaceae material predominantly. Numerous corm discs were identified and recording of measurements was possible during the systematic botanical analysis presented in this chapter. The species composition of geophyte material identified closely resembles the diversity of geophytes in the current landscape the site occurs in.

Tortoise Cave is located 3 km South East of Elands Bay on the banks of the Verlorenvlei. This site was occupied across a wide range of dates during the Holocene, from 1580 and 8100 ya with a midden- like occupation dated to 760 ya (Robey, 1984). Bedding layers were found along the back of the cave, but no other botanical material is mentioned in depth (Robey, 1984). During the systematic analysis geophyte material was identified, although not a large quantity.

Faraoskop is located in the Sandveld 30km east of Lamberts Bay. The excavation revealed a recent episodic occupation which was dated to between about 600 and 4000 ya (Manhire, 1993). Underlying the more recent deposits was earlier deposits dated to between 10 kya and 16 kya (Manhire, 1993). The site is best known for the burial of 12 humans. Most of the botanical remains recovered were dated to about 600 ya and between 2000 - 2500 ya (Manhire, 1993). No formal analysis had previously been performed on the botanical remains recovered during the excavation. Geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

Diepkloof Rock Shelter is located in an overhang on the border of the Verlorenvlei, about 18 km from Elands Bay. The excavation of this site revealed a shallow LSA deposit with a substantial MSA deposit under it (Silberbaur, 1974; Texier *et al.*, 2010). The site has excellent preservation of plant material and large amounts of geophyte remains were recovered from the Holocene layers which were dated to between 390 and 1590 ya (Silberbaur, 1974). A limited quantitative botanical analysis had previously been performed, together with species composition analysis (Liengme, 1987). A large amount of geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

Varsche River Sites: Reception Shelter (VR1), Buzz Shelter (VR5) and (VR3) are located in the Knersvlakte 43 km from the coast along the Varsche River and comprise of material mostly dated to within the LSA (Orton *et al.*, 2011). Although no systematic botanical analysis had been done on the material excavated, it was noted that there were well preserved macrobotanical material, a portion of which likely comprised of edible geophytes (Orton *et al.*, 2011; Orton, 2012). At VR1 deposits were dated to between 394 ya and 22 kya, at VR3 two dates were obtained of 220 ya and 1410 ya, and at VR 5 deposits were dated to between 324 ya and 13 kya (Orton, 2012). Geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

<u>Mountainous sites</u>

Renbaan Cave is located near the Olifants River near Clanwilliam (Kaplan, 1984). The deposits have been dated to between 1150 and 5430 ya (Kaplan, 1984). Quantitative and species composition analysis were performed on the botanical material from this site (Liengme, 1987). The site has various plant-rich deposits which consisted of bedding patches stacked above one another in various layers (Liengme, 1987). This material was dominated by corm husks as opposed to predominantly grass in other sites (Liengme, 1987). A large amount of geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

Andriesgrond Cave is located near the Olifants River near the Clanwilliam (Anderson, 1991). The deposits and botanical remains are similar to other sites in the region (Liengme, 1987). The botanical remains consisted of bedding patches along the back of the wall of the cave, composed of grass and corm casings and Iridaceaes food waste patches (Liengme, 1987). Storage pits filled with corm material which cut into the underlying layers were found, which is not typical of all sites in this region (Liengme, 1987). The various layers excavated were dated to between 390 and 1590 ya (Anderson, 1991). A large amount of geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

Klein Kliphuis Shelter is situated northeast of Clanwilliam (van Rijssen and Avery, 1992). The excavation yielded a shallow Holocene deposit which was dated to between 1230 and 1990 ya, below this was early LSA deposit which was dated to 32 kya (van Rijssen and Avery, 1992). In the initial report, two bedding layers were described, but only the upper layer contained identifiable plant material, which was described as consisting of grass (van Rijssen and Avery, 1992). Geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

De Hangen is located in the Olifants River valley near Clanwilliam (Parkington and Poggenpoel, 1971). The site yielded a shallow deposit which was dated to between 90 and 450 ya (Parkington and Poggenpoel, 1971). The site yielded valuable information about the spatial distribution of different domestic functions (Parkington and Poggenpoel, 1971). The site had excellent preservation of plant material and yielded large quantities of grass bedding, Iridaceae rich patches and storage pits (Liengme, 1987). The plant remains were collected as grab samples and bulk samples (Silberbaur, 1974) and only species composition analyses were described (Liengme, 1987). A large amount of geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

Boontjieskloof is situated over the Pakhuis Pass from Clanwilliam. No report was compiled of the excavations, but a large amount of archival material was retrieved for the systematic analysis. Numerous corm discs were identified and recording of measurements was possible.

***Klipfonteinrand 1 and* 2** occur within close proximity to Boontjieskloof and botanical remains were reported which consisted of grass and a number of corm cases (Thackeray, 1977; Nackerdien, 1989). Although not a large amount of plant material was recovered (Klipfonteinrand 2), it was interpreted as bedding material and was dated to 1800 ya (Nackerdien, 1989). There was no further formal analysis conducted on this material (Nackerdien, 1989). This material was not identified in the archival material from this site.

Putslaagte is a shelter at the northern end of the Cape Fold Belt along the Doorn River (Halkett, 1990). The deposits consisted of a large talus slope where the main units were dated to between 230 and 1900 ya. Geophyte remains were identified although no formal analysis had been performed on this material (Halkett, 1990). Geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were found and recording of measurements was possible.

Stompiesfontein is located in the southeastern border of the Cederberg. No report was compiled of the excavations, but a small amount of archival material was retrieved for the systematic analysis.

6.1.3.2 South Coast sites

Mountainous sites

Boomplaas Cave is located in the Cango Valley in the Swartberg 75 km from the coast and is well known for its excellent preservation of plant material which has been thoroughly studied and described (Deacon, 1976, 1982). The deposits in the cave are rich in humified plant remains and ashy hearths which were dated to between 1400 and 1700 ya. There were 74 storage pits found in this cave in various layers (Deacon, 1982). These pits were used to store *Pappea capensis* seeds and were lined with *Boophane disticha* bulbar leaves. Large amounts of geophyte material were identified in the recent layers and carbonized lenses associated with plant processing were identified and dated to between 12 kya and 14 kya. Although no macrobotanical analysis was possible on this material these lenses were interpreted as some of the most ancient evidence of geophyte use (Deacon, 1979). Geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

6.1.3.3 East Coast sites

Coastal Plain sites

Hoffmans Cave** and **Nelson Bay Cave are situated on the Robberg Peninsula near Plettenberg Bay (Kyriacou, 2009). Nelson Bay Cave yielded very deep deposits which have been extensively excavated and dated to within the past 20 kya (Deacon, 1982; Inskeep, 1987; Loftus, Sealy and Lee-Thorp, 2016). Artefacts from Nelson Bay Cave have been reported as highly significant to the interpretation of Stone Age subsistence patterns (Deacon, 1982). Geophyte remains were found in the late Holocene layers (Inskeep, 1987). The volume of these plant remains pale in comparison to the volume of shellfish and other cultural material. No botanical remains are reported for Hoffmans Cave and the stratigraphy was dated to between 3310 and 4330 ya (Kyriacou, 2009). Both Hoffmans Cave and Nelson Bay Cave archival material was investigated to identify plant remains during the systematic analysis, however the geophyte remains described were not found.

Klasies River are a series of caves near the Klasies River Mouth between Tsitsikamma and Cape St Francis (Deacon, 2001). The stratigraphy is complex and has revealed Holocene upper units dated to within 2525 and 4695 ya (Singer, Wymer and Butzer, 1982), while the MSA layers (70, 120 kya) have yielded carbonized lenses which have been interpreted as some of the most ancient evidence of geophyte exploitation (Deacon, 1995). Recently cooked geophyte starch particles have been identified from these layers confirming that they originated from cooked geophytes (Larbey *et al.*, 2019). During a lesser-known survey, geophyte remains (Iridaceae) were identified in the upper layers of Klasies River 5, and were dated to 1860 ya (Binneman, 1995). This material was not identified among archival material analysed during the systematic botanical analysis.

Mountainous sites

Scott's Cave is situated in the Gamtoos River, the site had excellent organic matter preservation, and systematic analysis of the plant remains found in this site was performed (Wells, 1965). The site consists of shallow Holocene deposits which have been dated to 360 and 1190 ya. A large quantity of geophyte remains was found, which comprised of predominantly Iridaceae material. Geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

Melkhoutboom Cave is situated in the Gamtoos valley (Deacon, 1969). The deposit consists of a very deep stratigraphy which was dated to between 250 and 15400 ya (Deacon, 1969). The site is famous for the exceptionally good preservation of botanical material which was found in layers dated to between 500 and 7500 ya. The species identified are similar to the species composition at Scotts Cave (Deacon, 1967). Storage pits are present which were dated to 2870 ya and are thought to have been used for storage of oil-bearing seeds similar to the function at Boomplaas Cave. Some storage pits were lined with *Boophane* bulb scales (Deacon, 1976). Humified plant remains in older layers made identification of that material impossible, but the carbonised lenses observed were again interpreted as the processing of large amounts of plant material (Deacon, 1976). Due to the sheer volume of plant remains at the site, the plant material was sampled in a systematic way to gain a representative sampled: unsieved bulk samples, sieved bulk samples and grab samples were collected (Deacon, 1976). The plant material had various geophyte species among it, but the husks and discs of *Watsonia* were the most common (Deacon, 1976). Geophyte material was identified in the archival material from this site and analysed for the systematic botanical analysis presented in this chapter. Numerous corm discs were identified and recording of measurements was possible.

6.2 Methods

6.2.1 Systematic botanical remains analysis

Due to the sheer number of archaeological sites which were identified which contain geophyte material, I decided to select only a few for further systematic botanical remains analysis. Archival botanical material from twenty-four archaeological sites was analysed systematically. These sites were selected based on the amount of archival material which was housed at Iziko Museum, UCT collections and Albany Museum, as the larger the volume of material the larger the sample size of measurements that could be made of corm material. The selection of sites was facilitated by the collaboration of the excavators who published reports on those sites, and they made excavation notes available to me, to assist the interpretation of material. For certain sites, archival botanical material mentioned in reports could not be found in Iziko Museum, UCT collections or the Albany Museum. In other cases, permission or access could not be provided to archival material.

To make the systematic analysis of archival botanical material possible, a comparative collection of the inedible portion of various geophyte species was made. The species included in this comparative collection were collected all over the GCFR during the fieldwork for previous chapters. Sixty-five geophyte species which are classified as producing identifiable inedible debris are included in the comparative collection. This material consisted of the unpalatable or inedible portion of material surrounding the USO that would potentially be found in archaeological sites. Geophyte species which are invisible archaeologically could not be included in the reference collection for the obvious reason that they do not leave identifiable debris in the archaeological record.

In most instances’ geophyte plant remains were identified to genus level and assigned an approximate species name such as *Babiana sp 1*. The diagnostic features of this species were then identified to facilitate the repeated and systematic identification of the species in subsequent layers and material.

Distinguishing between geophyte species in the same genus from one another in the archaeological material was possible. If more than one species in a genus was found it was assigned the next numerical value: *Babiana* sp 1, *Babiana* sp 2 etc. In very few cases was it possible to identify geophyte material to species level. For the purposes of addressing the objectives for this study however, genus-level identification should be sufficient.

Once archival material was called out of storage, all material was scoured for signs of any geophytic plant remains by sorting through all material systematically and comparing it to the reference collection. The geophyte material identified per sample (usually sorted into bags by layer and square) were then sorted into various genera. When a species was identified in a specific layer or square it was recorded. Due to the fact that this study was done on archival material, which had in some cases already undergone analysis and sorting it was not possible to perform quantification analysis of this material.

The distribution of the geophyte genera which are most frequently found in all archaeological sites identified was compared to the current distribution of common, widespread species of the same genera. In some cases where species-level identification of geophyte remains in the archaeology have been made, the distribution of that specific species was presented. This distribution data was obtained from iNaturalist.com, a public platform where users log observation of organisms, which are then identified by experts.

6.2.1.1 Evaluation of novel proxy method: Use of seasonal growth patterns of corms in the analysis of archaeological material

As described in the previous chapter, equations which predict the weight of cormous species and the time of year they would have been collected in, have been generated. The known variable that is required to extrapolate these factors are corm disc (corm base) dimensions of four archaeologically important species (*Watsonia meriana*, *Moraea fugax, Cyanella hyacinthoides* and *Babiana ambigua*). When intact corm bases belonging to the four archaeologically important genera (*Watsonia, Moraea, Cyanella* and *Babiana*) were identified, they were measured (diameter and height).

The relationship between disc diameter and the corresponding corm weight was found to be positively correlated, and the following equation was found to predict corm weight of the four taxa well (Chapter 5). The equation generated for the four important cormous taxa was as follows (where y is corm weight and x is disc diameter):

$$y=0.6923-0.0018x+0.0109x^2$$

When the disc diameter measurements were inserted in this equation, an estimate of the corm weight is generated, which can be used to determine the energy content of that corm when the nutritional content of that species is applied to the weight. This allows us to look at the weight and kilojoule content of corms that were foraged by hunter-gatherers and brought back to archaeological sites, where the corms were consumed, and the discs discarded.

As discussed, many seasons of discs of cormous species can be present for one individual plant, but the corm base/disc immediately below the new corm can be used to indicate when the corm was collected. If the disc is thicker than the average disc we can be sure that it is the most recent corm base/disc. Due to this pattern of growth of these plants, it was possible to identify signs that a corm was foraged earlier in the season. When the old corm has not been completely subsumed by the new seasonal growth and were found to have thicker than the average disc for the genera, it was noted, measured and recorded as a “signal of seasonality”.

As described in the previous chapter there was a significant difference found in the rate with which the height of the previous seasons’ corm thins. Throughout the seasonal growth of the plant and thus the height measurement of specific species can only be used to extrapolate the seasonality of foraging of the same species (equations are species specific). The four species identified in the archaeology to most closely resemble these species (or are likely the same species) and for which these equations can be used for extrapolation are *Moraea fugax, Watsonia* sp 1, *Cyanella* sp 1 and *Babiana* sp 1. Only at sites where these four species were identified can extrapolation of geophyte foraging seasonality be attempted. The equations used for the four species are as follows:

Table 6.2 Four equations which were used to extrapolate seasonality of geophyte collection for four archaeologically significant genera.

Species	n	r	Equation
Babiana ambigua	70	-0.8181	$y= 10.0365-0.4171^{X}$
Cyanella hyacinthoides	47	-0.9086	$y=10.5066-0.2678^{X}$
Moraea fugax	41	-0.8279	$y=10.4923-0.2397^{X}$
Watsonia meriana	92	-.08089	$y=11.6077-0.1379^{X}$

Once all of the measurements and observations were made, all material was returned to the packaging it was found in. In many cases where the packaging had disintegrated it was repackaged in zip lock bags, sealed and all information on previous packaging reproduced on the new packaging.

6.2.1.2 Assignment of dates to excavated material

The dating of geophyte material was done by obtaining the original dates supplied in-field report and published literature. Dates are reported as years before present, together with laboratory numbers, the type of material the sample consisted of that produced the date (charcoal, shell etc.) and the layer/square the sample was obtained from. Only in the case where a layer had been directly dated was the age applied to the geophyte material found in that layer. This excluded the possibility of dating the bulk of the observations made of geophytes identified in excavated assemblages but ensures that the dates reported for the material is reliable.

6.2.2 Taphonomy

An important aspect of the taphonomy of geophyte remains in the archaeology that has to be addressed pertains to the fact that both baboons and porcupines forage for geophytes, and both baboons and porcupines are known to frequent caves. During these visits, they are known to dig into the cave floor and are also known to leave scat behind. Baboons and porcupines are known to peel corm husks, removing the bulk of the inedible portion, before they consume the USOs (personal observations). Although, inevitably, baboons and porcupines can ingest fragmented corm husks, which could enter their intestinal tract and could finally be excreted in their scat in archaeological sites. Baboon scat was found on the surface layers of some cave sites which did contain fragmented Iridaceae husks (see Figure 6.3).

It could be argued that baboon scat is contained in the undisturbed/disturbed stratigraphy of cave sites below the surface, and due to decomposition in these layers are not recognizable as scat, but rather just as husk fragments. To assess what type of geophyte remains would be produced by decomposed or fragmented scat in the stratigraphy I collected porcupine and baboon scat in the Cederberg to describe the geophyte remains which are present in their scat which could be introduced to archaeological sites. The scat was softened in distilled water and the geophyte debris contained in them sifted out and photographed (see Figure 6.3). For both porcupine and baboon scat, the geophyte debris contained in scat was so fragmented that it would be impossible to distinguish them from other cormous species and is comprised of individual fibres. From these observations, it was decided that only intact, unfragmented geophyte material which has clearly not passed through the gut of a baboon or porcupine could be considered to possibly have been introduced by humans. See Figure 6.3 for an example of the intact corm husks which were considered to have been introduced by humans.

Figure 6.3 a) Fragmented Iridaceae husks recovered from modern porcupine scat (top left) and intact baboon scat, and corm husk fragments found when scat was dissolved (top right).
b) Intact Moraea fugax (bottom left) and Moraea sp 1 (bottom right) husk considered as introduced by humans, with the signature halving of the husk to access the corm inside.

A further issue of taphonomy which has not been addressed in detail in previous botanical analyses is the likelihood of certain geophyte species being preserved in the archaeological record, whereas other species, which were observed to have been foraged, are not found in the archaeological record.

Understanding the type of inedible debris which is generated by foraged geophyte species is crucial when analysing archaeological material, as this determines if these species are likely to be “visible” in the archaeological record. Similarly, understanding which edible species leave no debris behind at all is just as important. The characteristics of geophyte species debris have been classified into three different groups: identifiable, invisible and indistinguishable. Each species identified in the previous chapters contained in the master species list are described in Table 3.5 (pg 71) according to their inedible portion classification and the specific type of debris which would be created if it was foraged and processed. These classifications are defined in Figure 6.4 below.

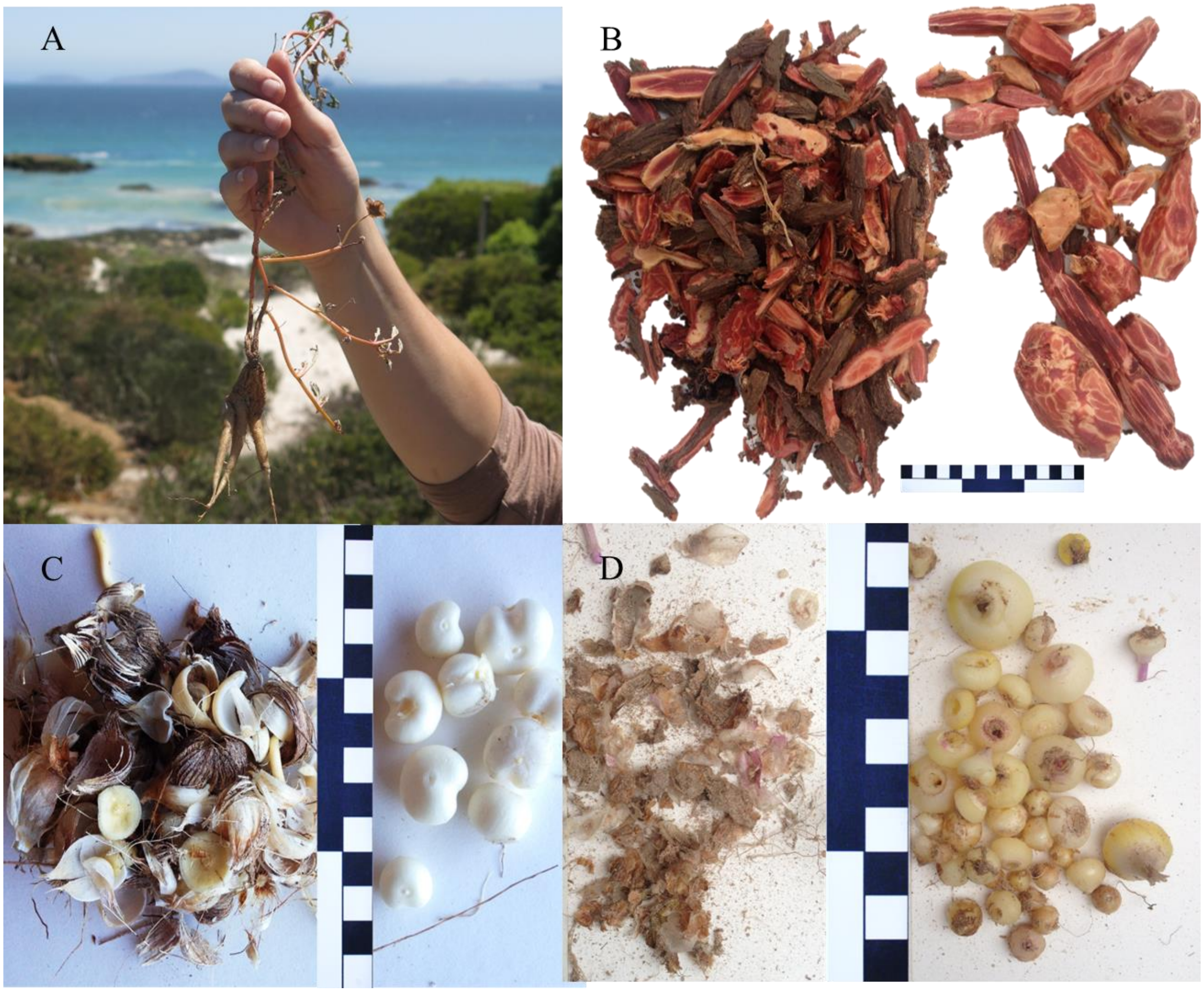


Figure 6.4 Geophyte inedible portion examples to illustrate the inedible portion classification that was assigned to all geophyte species identified in the master species list (see Table 3.5).

a) ***Invisible****: The edible tuber of* *Grielum humifusim* *would be completely invisible in the archaeology. Species which exhibit this phenomenon are classified as invisible in the species master list.*

b) ***Indistinguishable****: The edible portion of* *Pelargonium triste* *rhizomes on the right and the large amount of inedible portion (left). The bark which has to be peeled off the rhizome is almost indistinguishable from other tree bark and would be impossible to positively identify in the archaeology. Species which exhibit a similar inedible portion are classified as indistinguishable in the species master list.*

c) ***Identifiable****:* *Moraea fugax* *corms on the right and inedible portion on the left. Most Iridaceae species have very distinctive inedible portion (husks and discs) that are easily identifiable in the archaeology. These species are classified as identifiable in the species master list.*

d) ***Indistinguishable****:* *Albuca flaccida* *bulbs on the right, and the corresponding inedible portion on the left. Many bulbous species have very thin bulb sheaths that cover the edible bulb. These sheaths can be identified as being bulb sheaths in the archaeology, but they are not distinguishable from other bulb sheaths. These geophyte remains are classified as indistinguishable in the species master list.*

6.3 Results

6.3.1 Spatial distribution of geophyte remains across the GCFR

Geophyte remains are reported from an extensive range of sites all across the GCFR. In most cases, the material has not been systematically analysed and is briefly mentioned in most reports. Geophyte remains occur in a large proportion of sites all over the GCFR (40/59 sites: 68 %) (see Figure 6.2). There was a high concentration of sites where geophytes are present in the West Coast (18/25 sites: 72 %). Similar proportions of sites in the East Coast region were found to contain geophyte remains (14/23 sites:61 %). In the South Coast there were far fewer overall sites identified, and the proportion of sites which contained geophyte material was slightly lower but similar to the other regions (6/11 sites: 55 %).

6.3.1.1 West Coast

The densest concentration of archaeological sites where geophyte remains are reported from excavated assemblages is in the Northern Cederberg in the Cape Fold Belt (Andriesgrond Cave, Renbaan Cave, Klein Kliphuis Shelter, De Hangen, Boontjieskloof, Putslaagte, Klipfonteinrand 1 + 2, Stompiesfontein). Geophyte remains from these excavated assemblages are often described as a dominant feature, consisting of a large portion of Iridaceae material. Apart from Andriesgrond Cave, Renbaan Cave and De Hangen no formal analysis has been performed on the botanical remains from these sites. A fair amount of sites contained geophyte remains on the coastal plain with a few significant sites located in the Northern sections of the Sandveld (Steenbokfontein, Elands Bay Cave, Tortoise Cave, Faraoskop Rock Shelter, Diepkloof Rock Shelter). There is a relative scarcity of archaeological sites, where geophyte remains are reported, to the south of this region (Swartland), with the exception of Voëlvlei. In the Succulent Karoo section of the GCFR a large portion of the sites identified contained geophyte remains (Spoegrivier, /Aitomas, Bethelsklip Cave, Varsche 1 + 3 +5). The geophyte material reported from all sites was dominated by Iridaceae remains.

Arguably, one of the most important contributions which arose from the analysis of geophyte remains from the West Coast is the implications of geophyte foraging on seasonal mobility of hunter-gatherer groups in this region. Parkington (1972) has emphasised the role of seasonally restricted resources in patterning mobile economies: seasonal mobility hypothesis. Due to the extreme seasonality of geophyte resources (as shown in the previous chapter), Parkington argued that the timing of the availability of this resource could have dictated hunter-gatherer movement (Parkington, 1972, 1976). Using geophyte remains evidence and other remains evidence the argument was made the coastal plain sites were occupied during winter and early spring, while mountainous sites were occupied during the peak of spring and early summer when geophyte resources were at their peak (Parkington, 1976). It was argued that this seasonal migration would have allowed hunter-gatherers to forage and hunt for an array of resources while foraging the optimum range of geophytes.

See Table 6.1 for references, see Figure 6.5 for distribution of sites, see Appendix B.2 for full list of species identified for each site.

6.3.1.2 South Coast

Relatively fewer sites containing geophyte remains were identified in the South Coast (in comparison to the West Coast and East Coast). Sites which have contributed significant geophyte remains are located in the Cape Fold Belt (Boomplaas Cave, Montagu Cave and Buffelskloof Rock Shelter). The geophyte remains from Montagu Cave are the only material that has not been systematically analysed, but it was thoroughly described (Keller, 1973; Deacon, 1976; Opperman, 1978). The South Coast has a high concentration of highly significant MSA coastal sites (notable examples are Pinnacle Point and Blombos) where no plant material is reported. A small amount of Iridaceae material is reported for the following coastal sites: Die Kelders, Byneskranskop and Great Brak River Cave. The geophyte remains reported from these three coastal sites are only mentioned briefly and have never been systematically analysed. See Table 6.1 for references, see Figure 6.5 for distribution of sites, see Appendix B.2 for the full list of species identified for each site.

6.3.1.3 East Coast

The East Coast has a very large number of archaeological sites which contain geophyte material, most of which have not been systematically analysed or well reported. The topography of this region is of such a nature that the coastal plain is very narrow, which might have contributed to relatively few archaeological sites being identified on the coastal plain. The only coastal sites found to contain geophyte material were Nelson Bay Cave and Klasies River. These remains consisted of a small amount of Iridaceae material, which was only briefly mentioned in reports. The densest concentration of archaeological sites where geophyte remains were found, is in the mountainous regions in the Langkloof and Baviaanskloof (Nuwekloof Shelter, Rautenbachs Cave, Tierkloof, Augussie Shelter, Paardeberg Cave, Kleinpoort Shelter, Grootkommandokloof, The Havens Cave, Scott’s Cave, Melkhoutboom Cave, Wilton and Springrock Shelter). The geophyte remains from these sites are often reported as a dominant feature in the excavated assemblages. With the exception of Melkhoutboom Cave and Scott's Cave no systematic botanical analysis has been performed on the reported material. Deacon argued that Holocene hunter-gatherers focused on geophyte species "with a wide distribution and seasonal availability" (Deacon 1969: 162). See Table 6.2 for references, see Figure 6.5 for distribution of sites, see Appendix B.2 for the full list of species identified for each site.

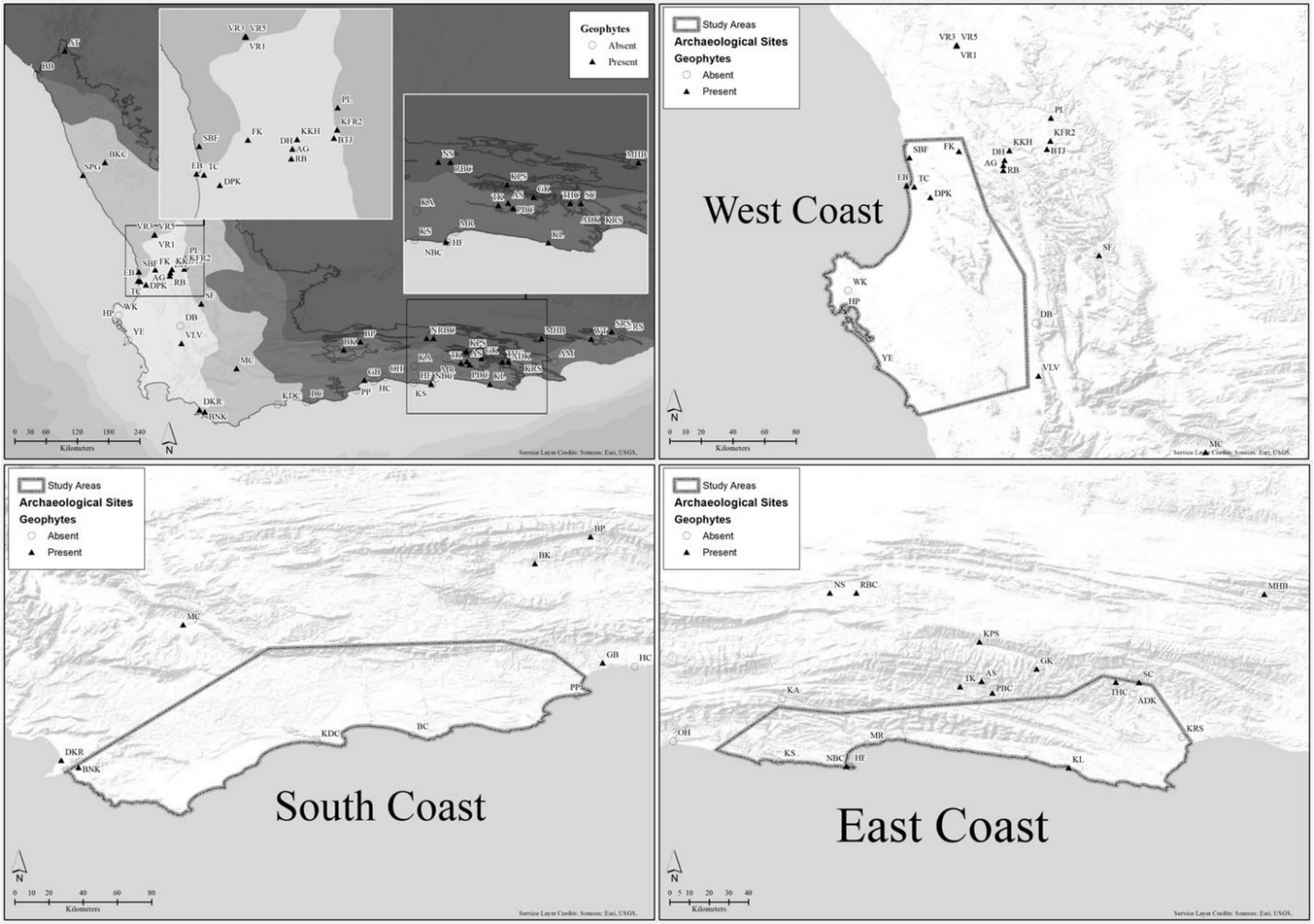


Figure 6.5 Distribution of archaeological sites across the GCFR where geophyte remains are present or absent in excavated assemblages.

6.3.2 Temporal distribution of geophyte remains across the GCFR

During the systematic analysis of archival plant material from 24 sites, 18 were found to contain geophyte remains, which could be studied further. In a few sites where geophyte remains are reported in the literature, the material was not found among the archival material that was made available for the systematic botanical analysis (Klipfonteinrand 2 (Nackerdien, 1989), Nelson Bay Cave (Inskeep, 1987) and Klasies River 5 (Binneman, 1995)). In other cases, the exploratory analysis of plant material collected from Hoffmans Cave and Knysna Cave did not yield any identifiable geophyte remains.

The geophyte material that was found and analysed came from layers which were radiocarbon dated to a wide array of ages. The bulk of observations of geophyte remains from the West Coast region were from layers which date to the past 3500 years (see Figure 6.6 and Table 6.3 for dates) with the exception of a few sites where dates stretch as far back as 11 500 ya. There was almost a complete lack of geophyte material in excavated assemblages from 6000-10 000 ya, despite the fact that almost all of these sites had layers which dated to within this period.

The geophyte remains from Boomplaas Cave (South Coast) came from layers mostly dated to within the last 3500 years. Some geophyte material came from layers dated to between 6000 and 12 000 ya.

Scott’s Cave and Melkhoutboom Cave in the East Coast yielded dates of 2000 ya and 6000 - 12 000 ya respectively. The big difference in ages between these two sites is partly because Scott’s Cave had a shallow deposit, the bottom of which was dated to 2000 years. Melkhoutboom Cave offered geophyte material from layers which dates to between 6000 – 8000 ya and older than 10 000 ya.

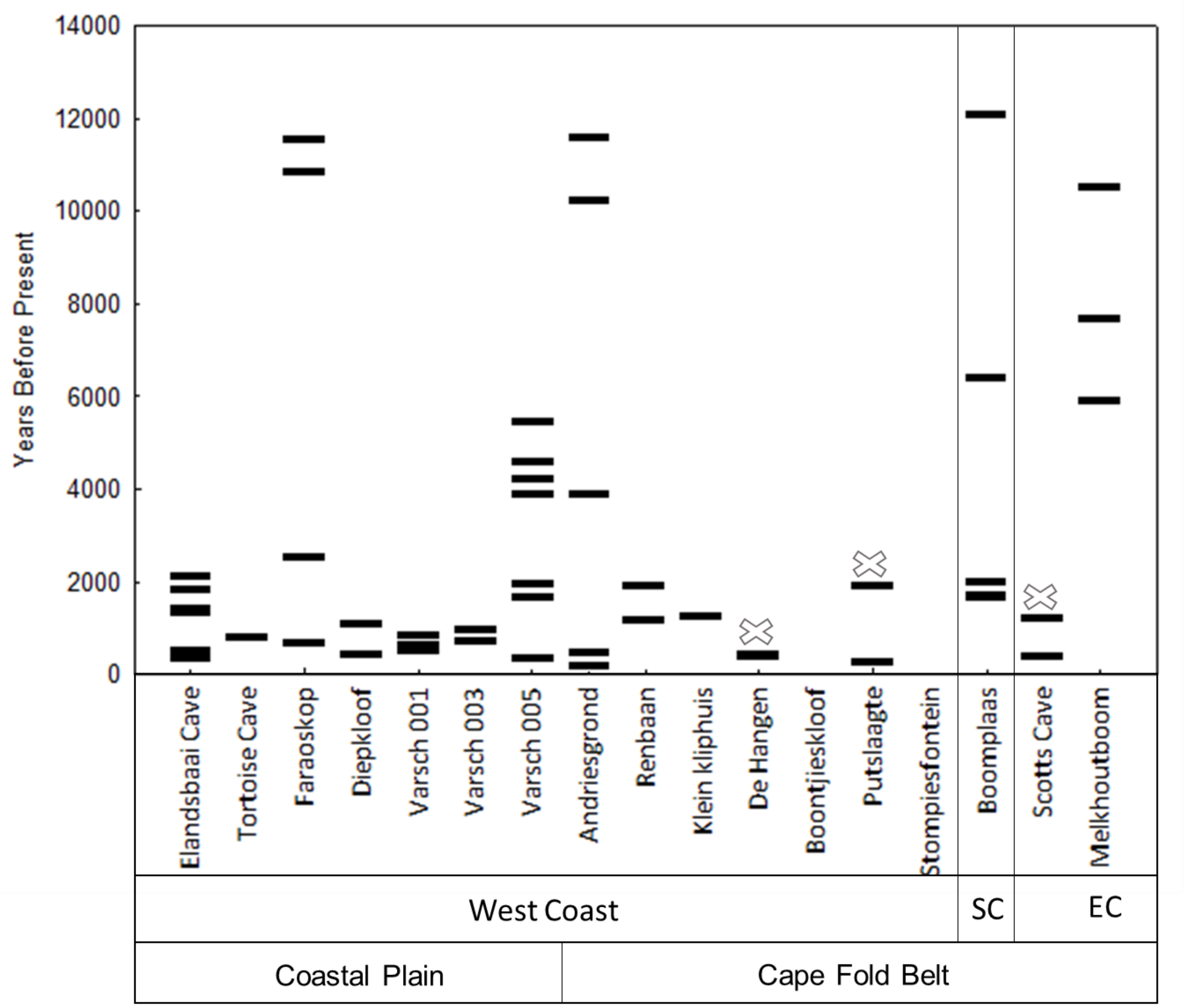


Figure 6.6 Dates of geophyte remains identified in various archaeological sites in the GCFR. All dates are collated from radiocarbon dates obtained from excavation reports for individual sites. X indicates the bottom of the assemblage.

Table 6.3 Dates obtained for layers where geophyte remains were identified in the archival material, from various archaeological sites. N indicates the number of samples which were identified from each layer.

Site	n	Layer age (Years before present)	Layer Name	Material Tested	Lab no.
Elands Bay Cave	10	320±50	Nkomo/A8	Charcoal	PTA-1815
Elands Bay Cave	3	500±45	MRSB/Y7	Charcoal	PTA-5813
Elands Bay Cave	4	1310±40	JECH/F7	Charcoal	PTA-5595
Elands Bay Cave	4	1660±50	BUTH/B1	Charcoal	PTA-5994
Elands Bay Cave	15	1790±50	POTA/X2	Charcoal	PTA-5820
Elands Bay Cave	1	2100±20	Kepler/X3	Charcoal	PTA-5611
Tortoise Cave	2	760±50	Fold up bedding/J3	Restio	PTA-3600
Faraoskop	22	670±50	GAS/D4,D5	Ash	PTA 4811
Faraoskop	5	2510±60	MAC(C)/D3	Ash	PTA 4954
Faraoskop	1	10810±100	CBA/D3	Ash	PTA-4816
Faraoskop	2	11550±120	ABS/D3	Ash	PTA-4817
Diepkloof	4	390±30	Second Bedding	Grass bedding	PTA 1055
Diepkloof	6	1050±80	Small hearth in bedding area	Grass bedding	GaK 4597
Varsche 001	19	474±22	Layer 5, middle (Y40/L11)	Stick	OxA-22982
Varsche 001	2	589±23	Layer 4, top (X90/L6)	Tortoise Bone	OxA-24513
Varsche 001	7	622±21	Layer 4, Middle (Y40/L7)	Charcoal	OxA-22876
Varsche 001	3	828±44	X40 NW L15a (TU1)	Tortoise carapace	AA899909
Varsche 003	4	701±23	I11 NW L2/4	Tortoise bone	OxA-25346
Varsche 003	1	932±24	I8 NE L3	Tortoise bone	OxA-25350
Varsche 005	3	324±22	Layer 3 base (N11NW/L7)	Grass	OxA-22877
Varsche 005	6	1646±25	Layer 2 (O11 SW L3a)	Tortoise bone	OxA-25352
Varsche 005	13	1921±25	Layer 3 top (O11 SW L4a)	Tortoise bone	OxA-24515
Varsche 005	6	3890±20	Layer 4 pit (N11 SE L10)	Grass	UGAMS-11683
Varsche 005	3	4185±31	Layer 5 (M11 NE L12)	Charcoal	OxA-22986
Varsche 005	42	4551±54	M11 NE/NW L9a (TU2)	Bone shaft fragment	AA89911
Varsche 005	10	5452±54	M11 SE/SW L15c (TU2)	Bone shaft fragment	AA89912
Andriesgrond	22	180±50	BED1	Ash	PTA-4026
Andriesgrond	24	430±50	MACO	Charcoal	PTA-2482
Andriesgrond	5	3850±80	BURY	Ash	OXA-457
Andriesgrond	2	10 200±180	LBSB	Tortoise bone	PTA-4222
Andriesgrond	2	11 590±190	BBSA	Ash	PTA-5545
Renbaan Cave	111	1150±50	Bedding Patch 3	Bedding	PTA-3768
Renbaan Cave	12	1910±60	Orange Speckle	Charcoal	PTA-3783
Klein kliphuis	7	1230±80	Bedding Unit	Charcoal	PTA-4672
De Hangen	22	350±50	Main ash concentration	Ash	PTA-126
De Hangen	166	390±50	Grass Layer	Bedding	PTA-346

Site	n	Layer age (Years before present)	Layer Name	Material Tested	Lab no.
Putslaagte	2	230±60	Bedding 1/G3	Bedding Material	PTA-4230
Putslaagte	4	1900±60	Brown Soil/G3	Charcoal	PTA-4229
Boomplaas Cave	2	1630±50	DGL/L13	Charcoal	UW-337
Boomplaas Cave	1	1700±50	BLD2/I14	Charcoal	UW-338
Boomplaas Cave	48	1955±65	BLD AM/P18	Charcoal	UW-336
Boomplaas Cave	1	6400±75	AF1 BRL/Q13	Charcoal	UW-306
Boomplaas Cave	2	12 060±105	CL1 AF1/O13	Charcoal	PTA-1828
Scott's Cave	1	360±80	Layer 3/J4	Charcoal	Y-1425
Scotts Cave	1	1190±100	Bedrock/H4	Charcoal	SR-82
Melkhoutboom	30	5900±90	Base of Main Bedding	Wood	PTA-680
Melkhoutboom	13	7660±80	Within Medium Brown series Unit	Charcoal	PTA-666
Melkhoutboom	2	10 500±190	Base of the Rockfall Unit	Charcoal	Gak-1538

6.3.3 Diversity of geophyte species in the archaeological record

Thirty-four species of geophyte were identified during the systematic analysis and the overwhelming bulk of the material consisted of Iridaceae species (18/34 species). See Appendix B for a description of the species identified in archival material.

Iridaceae species husks and discs dominated most plant material retrieved from archaeological sites, and the species which were most abundant in sites were often identified in the highest number of sites. See Figure 6.7 and Appendix B.2 for the full list of species identified per site.

A few species made up the bulk of the material in most assemblages and the frequency (number of samples which contained that taxa) with which species were identified closely resembles the number of sites they were identified in (see Figure 6.7). The important taxa which were identified frequently are *Cyanella* spp, *Dioscorea elephantipes, Oxalis* spp, *Pelargonium* spp, *Cyperus* spp. and *Watsonia* spp. The poisonous species *Boophane disticha* was equally common across the entire region. These species make up the most substantial proportion of observations made, with all other species being found far less frequently.

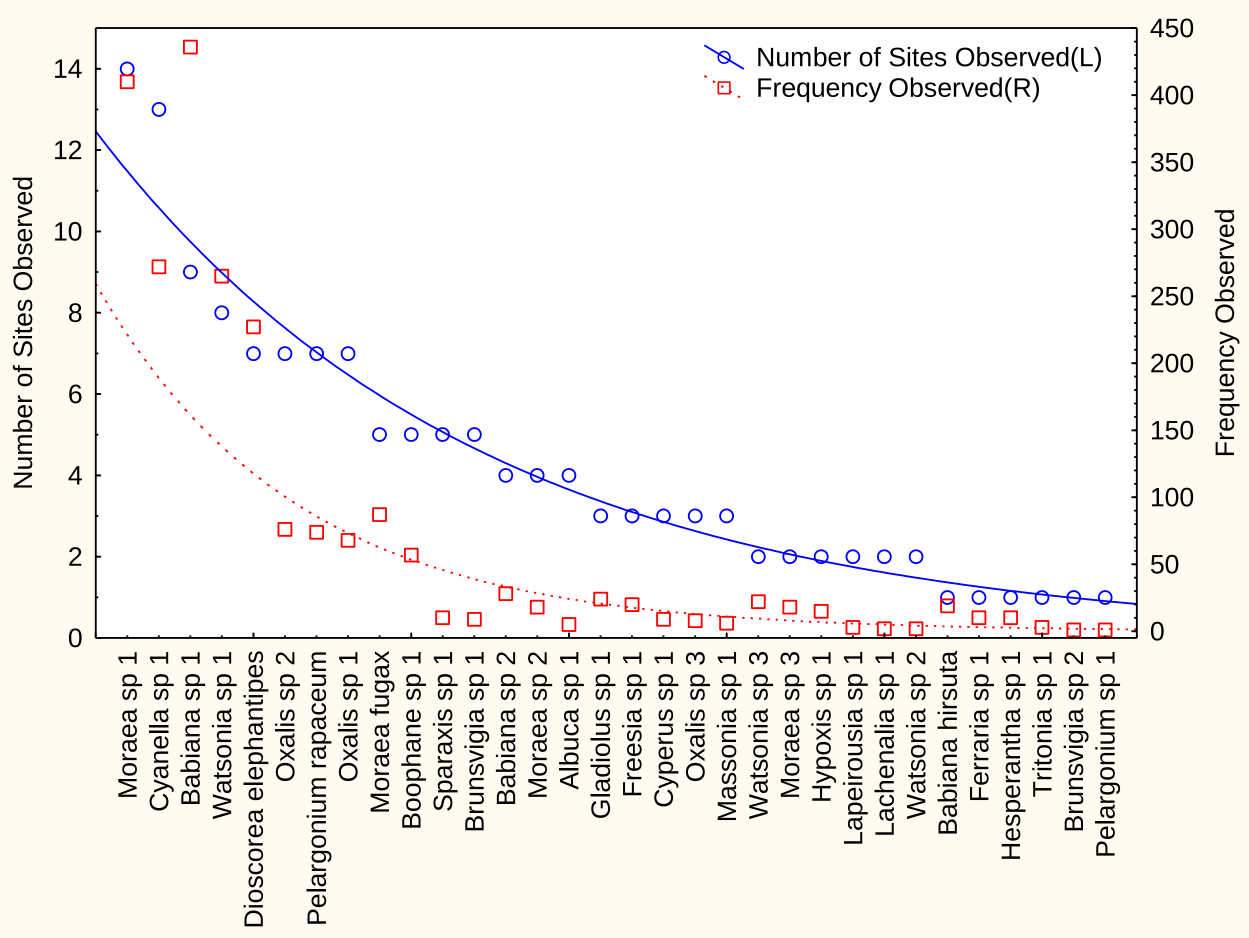


Figure 6.7 Frequency (number of samples which contained that species) of observations of species at sites and the number of archaeological sites where species were found

Across the entire region, for all sites investigated, a similar pattern is reported from the literature. There were seven families of geophytes identified, where Iridaceae was by far the most frequent number of species found (18 species), followed by Hyacinthaceae (6 species), Amaryllidaceae (3 species) and twenty-five genera were identified. *Moraea* spp. were identified in 24 sites, *Watsonia* spp. in 20, *Oxalis* spp. in 15, *Dioscorea elephantpes* in 14 sites, *Cyanella* spp. in 13 sites, *Freesia* spp. in 12 sites and *Boophane disticha* in 11 sites. See Appendix B.2 for a full list of species identified at all sites.

Per region, the most common species found in excavated assemblages differed in some respect, but Iridaceae remained a dominant feature across the entire region. The six most common genera for each region all included *Moraea* and *Watsonia* (see Table 6.4).

Table 6.4 Six most common genera identified in all archaeological sites investigated in the GCFR

West Coast most common genera	**No. sites identified**	**South Coast most common genera**	**No. sites identified**	**East Coast most common genera**	**No. sites identified**
Moraea	13	*Moraea*	4	*Watsonia*	11
Cyanella	12	*Watsonia*	2	*Freesia*	11
Oxalis	11	*Boophane*	2	*Dioscorea*	8
Babiana	9	*Cyanella*	1	*Moraea*	7
Watsonia	7	*Albuca*	1	*Cyperus*	7
Pelargonium	7	*Cyperus*	1	*Boophane*	6

The distribution of sites where the most common genera are found compares well to the current distribution of analogue species (see Figure 6.8 and 6.9). The notable exception of this trend is in the South Coast region, where all of these genera occur in the current landscape, but are not frequently identified in excavated assemblages.

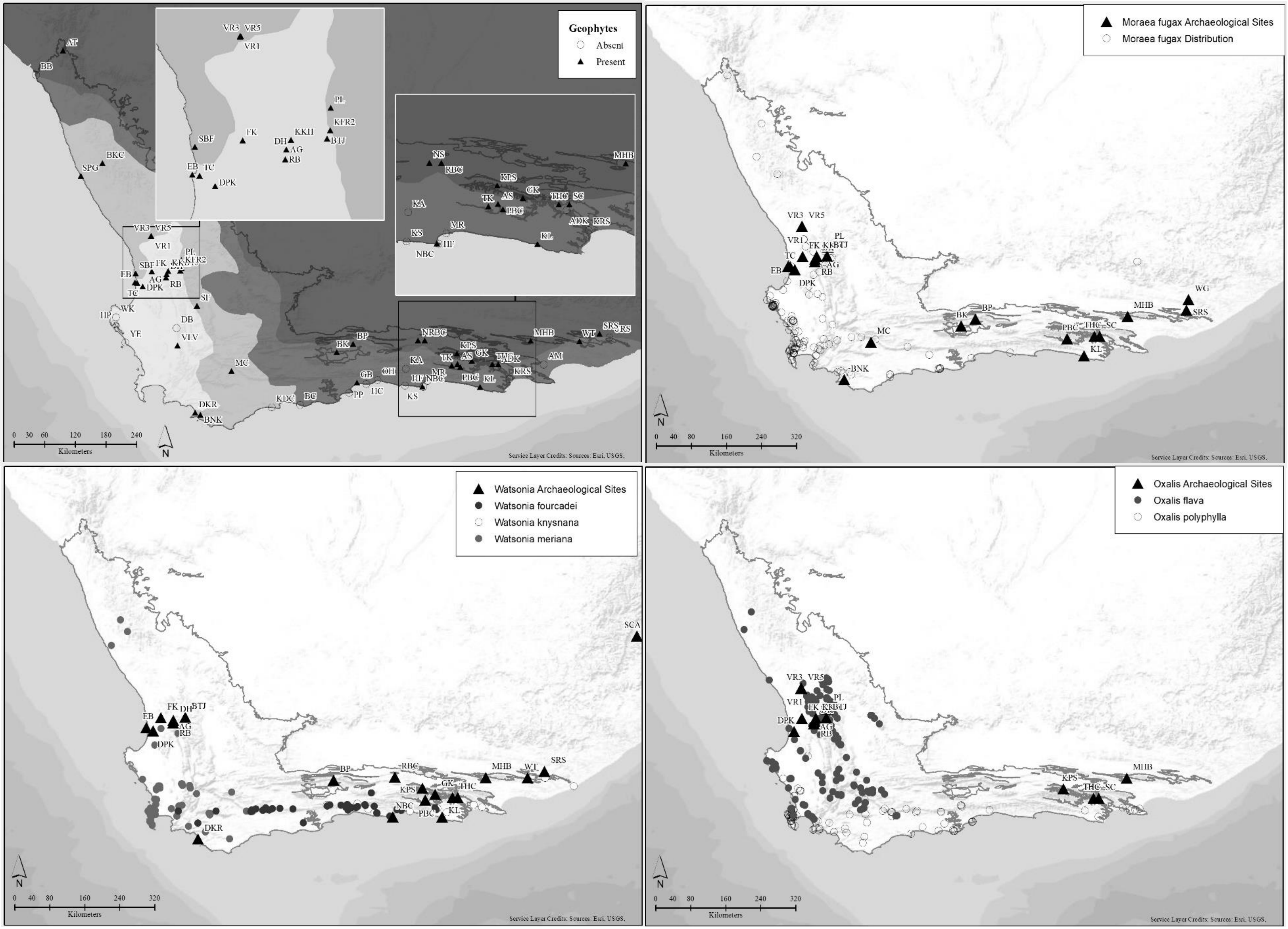


Figure 6.8 (Clockwise from top left) All sites in GCFR where geophyte remains were present or absent. The current distribution of Moraea fugax, Oxalis flava and Oxalis polyphylla, Watsonia fourcadei, Watsonia knysnana, Watsonia meriana (distribution data from iSpot) and the sites within which these genera where found in deposits

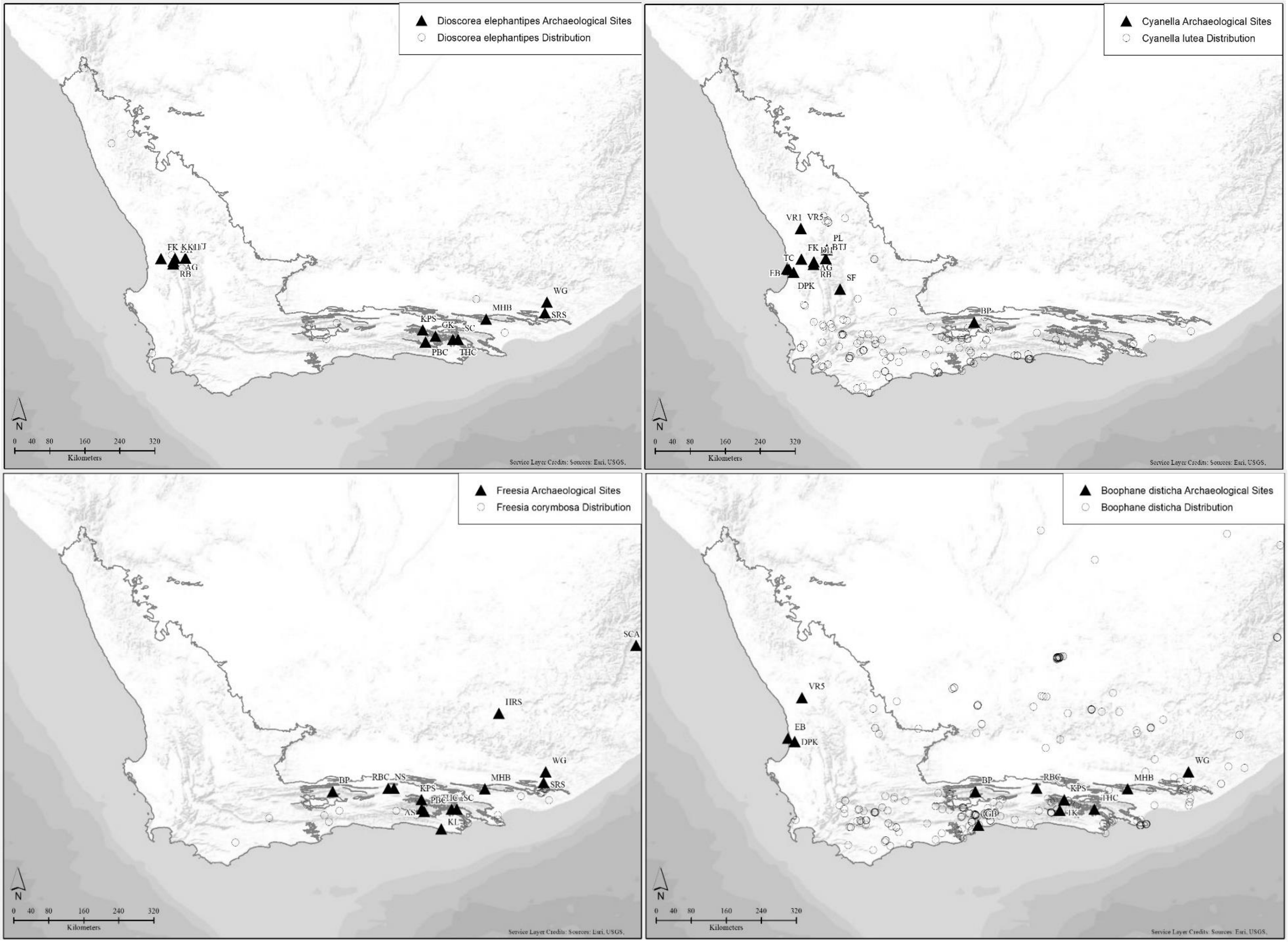


Figure 6.9 (Clockwise from top left) Current distribution of ***Dioscorea elephantipes****,* ***Cyanella lutea****,* ***Boophane disticha*** *and* ***Freesia corymbosa*** *(data from iNaturalist.com) and the distribution of archaeological sites where these genera were identified in deposits*

Just as telling as the distribution of identified geophyte species in the archaeology is the absence of geophyte species which occur in the region, but are not found in the archaeological record. From the total list of 131 edible geophytes which were identified in this study on the coastal plain of the GCFR, 70 are identifiable in the archaeology, and almost all of these species are cormous species in the Iridaceae family (see Figure 6.10). No bulbous species, one rhizomatous and one tuberous species would leave behind debris that could be identified in the archaeological record. Species which leave some form of debris in the archaeological record, but would be indistinguishable in the archaeology from other plant material are predominantly bulbous species (13/20). Species which would leave no inedible debris behind if they had been foraged, were numerous (39 species), and predominantly consisted of tuberous species (21) and rhizomatous species (14). See Figure 6.10 below and Table 3.5 (pg 71) for the full list of species and their archaeological visibility categorisation.

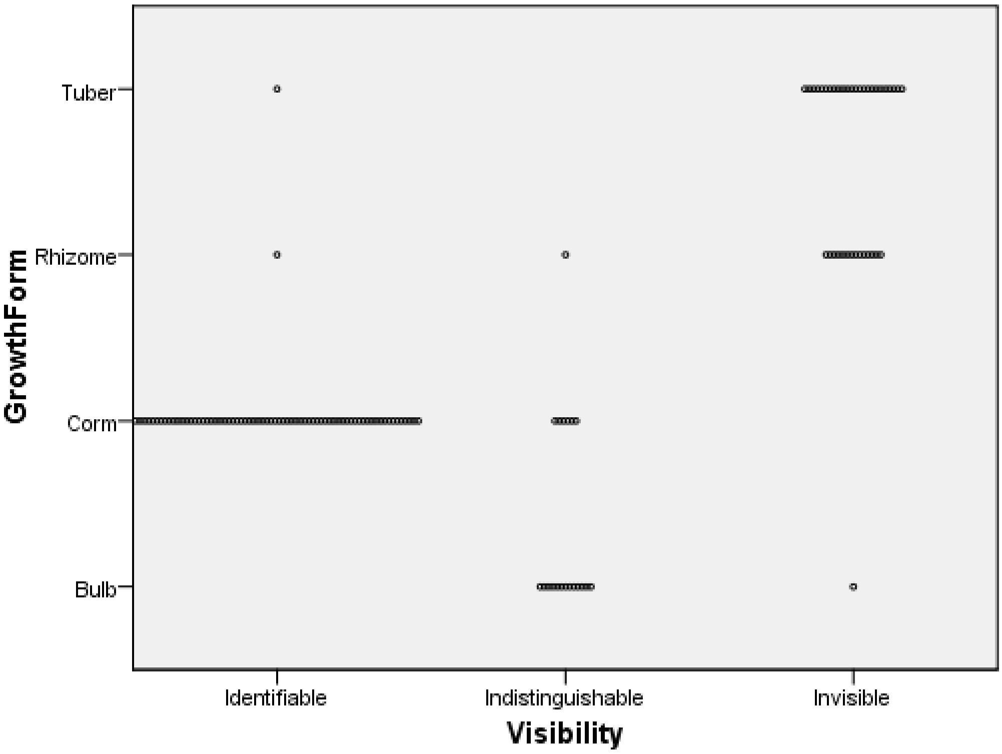


Figure 6.10 Number of species (of different growth forms) and their visibility in the archaeological record. Each dot represents a species.

6.3.4 Evaluation of novel proxy method: Use of seasonal growth patterns of corms in the analysis of archaeological material

During the systematic analysis of archival material more than 4000 intact discs of cormous species were identified and measured. From these measurements, we can extrapolate what the weight, energy content and seasonality of foraging was for the corms which were attached to the discs. These inferences are extrapolations and are not meant to be interpreted as an absolute value, but rather as a general indication of weight and energy content possible from cormous species found in the archaeology and the seasonality of when these corms were foraged.

6.3.4.1 Package size (weight) and energy content (kilojoules) of USOs in the archaeological record

The weight and energy content of corms of the four species for which extrapolations are possible are presented in Figure 6.11. Three genera (*Moraea, Cyanella and Babiana*) were found to have corms which could have weighed less than 5 g on average. These corms were some of the most frequently foraged geophyte species in various sites. *Watsonia* corms were the largest corm foraged by hunter-gatherers and extrapolations suggest they could have weighed up to 20 g.

Extrapolation of disc measurements suggest that even though *Moraea* corms were small they yielded the highest kilojoule content per corm, with up to 67 kJ per corm, which would be similar to a small potato (which weighs 20 g). *Watsonia* corms, which weighed the most, had a relatively low kilojoule content in comparison to the far smaller *Cyanella* and *Moraea* corms. Due to the variability in the weight of *Watsonia* corms found in the archaeological record, the kilojoule content varied substantially. The energy content of the larger corms of *Watsonia* is still comparable to that of a small potato. Extrapolation of the disc measurements of *Babiana* show that their corms, which were very low in weight (all measurements indicate a weight less than 3 g), delivered the lowest kilojoule content, which was on average 10 kJ per corm.

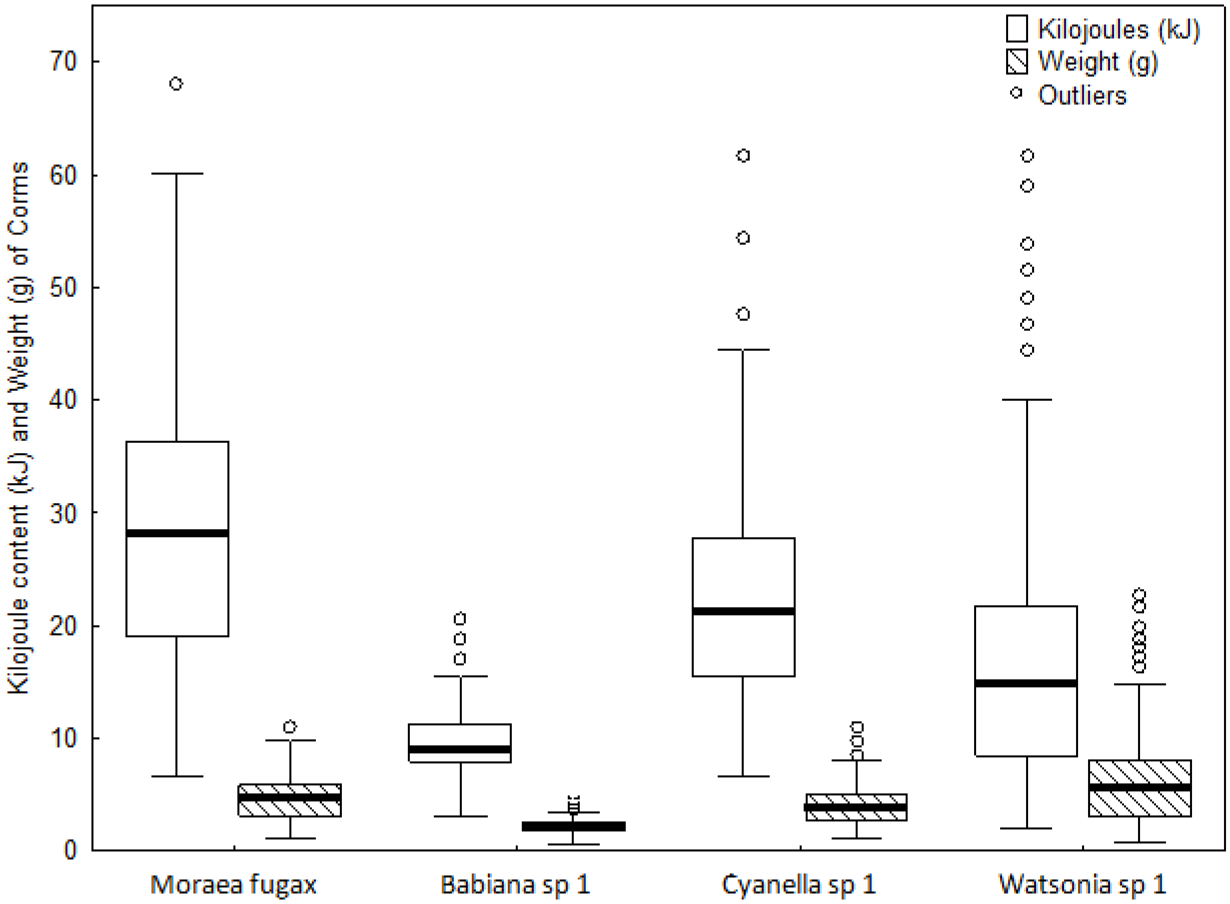


Figure 6.11 Kilojoule content and weight of corms collected by hunter-gatherers and returned to archaeological sites. Boxes represent upper limit 75 % of data, bottom limit 25 %. Mean denoted by black bar, whiskers represent the standard deviation, circles represent outliers.

6.3.4.2 Seasonality of geophyte foraging

The majority of discs found in the archaeological record did not show any signs of seasonality (many of these discs could have originated from the same plant). The majority of discs had height measurements of less than 1mm. At some sites, significantly higher rates of discs were found which were swollen and showed signs of being forage earlier in the season. These discs represent the most recent disc and likely represent only one plant. See Table 6.5 for the measurements and frequency of discs which were found to show no signs of seasonality (normal discs) and the sites where signs of early-season foraging are evident (swollen discs).

Table 6.5 Disc Height for swollen (showing signs of being foraged earlier in the growing season) and normal discs. Superscript letters denote significant differences between measurements for different sites. Superscript letters denote significant differences between groups (rows). Groups with unique letters are significantly different from other groups while groups that share letters are not significantly different from one another.

	n	Normal Disc Height (mm)	n	Swollen Disc Height (mm)
Elands Bay Cave	53	$1±0^{a}$		
Tortoise Cave	2	$1±0^{a}$	1	5.00^{b}
Faraoskop Rock Shelter	128	$1±0^{a}$		
Diepkloof Rock Shelter	23	$1±0^{a}$	7	$5.00±1.63^{bc}$
Varsche 001	48	$1±0^{a}$		
Varsche 005	145	$1±0^{a}$	5	$4.40±0.55^{c}$
De Hangen	1388	$1±0^{a}$	6	$4.17±1.72^{c}$
Klein kliphuis Shelter	12	$1±0^{a}$		
Boontjieskloof	48	$1±0^{a}$		
Andriesgrond	1008	$1±0^{a}$	161	$4.27±2.20^{c}$
Renbaan Cave	467	$1±0^{a}$	14	$3.29±1.33^{c}$
Putslaagte	21	$1±0^{a}$		
Stompiesfontein	6	$1±0^{a}$		
Boomplaas Cave	1	1		
Scott’s Cave	5	$1±0^{a}$	2	$6.50±0.71^{bd}$
Melkhoutboom Cave	570	$1±0^{a}$	93	$8.27±2.97^{bd}$

When these measurements are inserted into the equation generated in the previous chapter, an estimate of the month within which these corms were foraged is generated (see Figure 6.12). According to the extrapolations from this equation, it is predicted that the four taxa measured, were foraged during late spring (West Coast) and early summer (South Coast and East Coast). It is essential to note the frequency of outliers which are predicted to have been foraged as early as June at West Coast sites on the Coastal Plain and the Cape Fold Belt. For many sites, the time frame within which geophytes could have been foraged seems to be wide. In the case of Andriesgrond Cave (for which the largest amount of measurements was recorded), geophytes are predicted to have been foraged for as long as seven months. The greatest portion of the material is predicted to have been foraged between September and November in the West Coast, and October and December in the South Coast and East Coast.

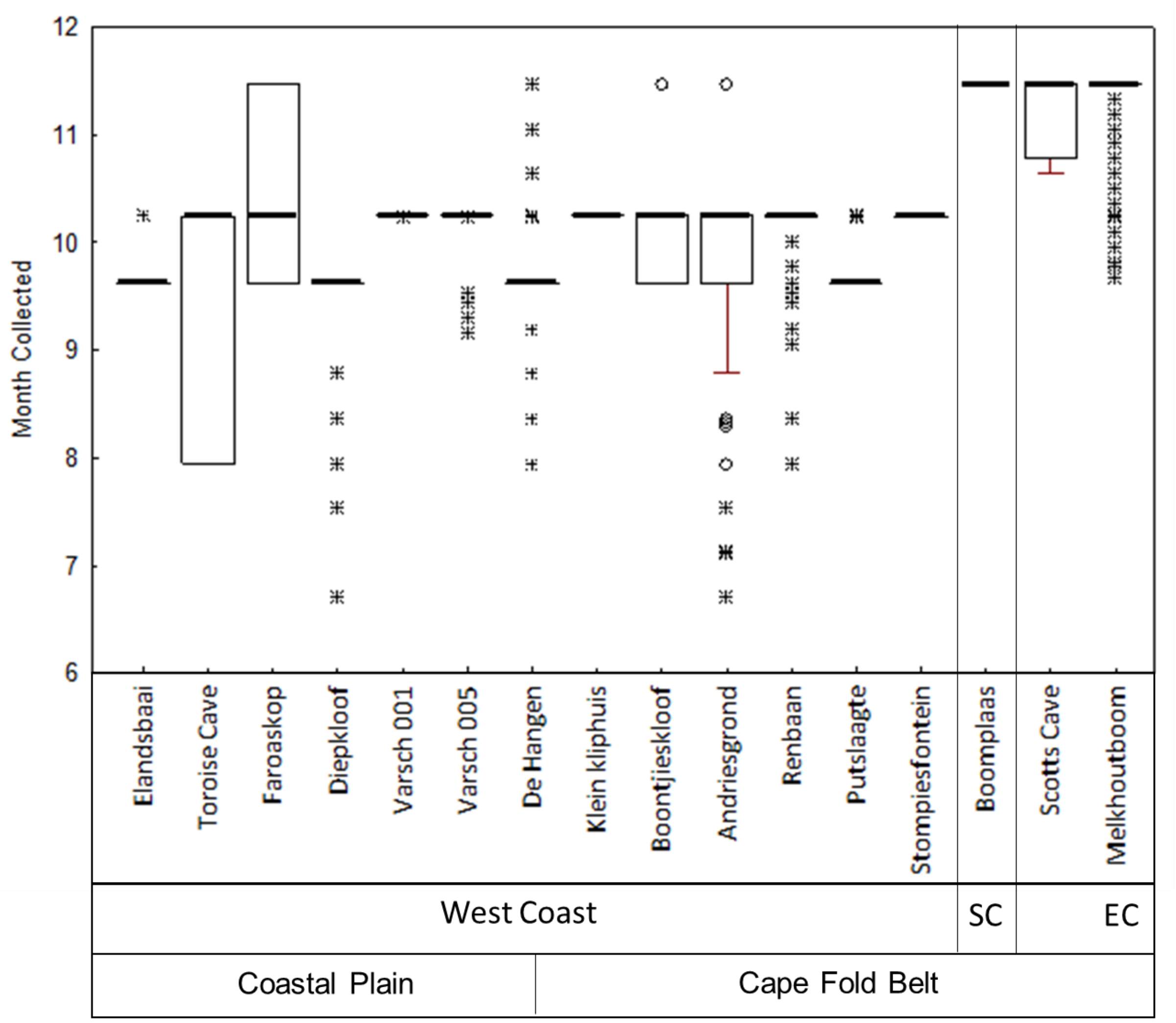


Figure 6.12 Extrapolation of the time of year when individual corms were foraged based on the height of corm discs found in the excavated assemblages. Boxes represent upper limit 75 % of data, bottom limit 25 %. Mean denoted by black bar, whiskers represent the standard deviation, circles represent outliers and stars extremes

6.4 Discussion

The results presented confirm the importance of geophytes in Holocene hunter-gatherer subsistence across the GCFR region. The results of the systematic geophyte remains analysis are similar to the results which have been published for selective sites in the region (Wells, 1965; Deacon, 1976; Liengme, 1987) and suggest that the patterns of geophyte exploitation which have been presented in these early works, is widespread across the region. The number of sites and wide distribution of sites where geophytes are found, presented in this chapter, has not been shown to such an extent before.

The results also support the overwhelming importance of Iridaceae species, which were present in large quantities in almost all archaeological sites where geophytes were identified. This corresponds to the high diversity, density and distribution of the Iridaceae family across the entire region, irrespective of diversity of climatic and environmental conditions that exist.

Apart from these general impressions of the importance of geophytes in Stone Age hunter-gatherer subsistence, the results presented make more detailed interpretations of geophyte exploitation possible. The interpretations presented are made possible by the novel methods applied, which can hopefully be used during future excavations and analysis of archival material. If these methods are used in future analyses, it could lead to an improved understanding of the dynamics of geophyte foraging in the Stone Age.

The specific objectives of the chapter are addressed one by one in the following four sections.

6.4.1 Spatial distribution of geophyte remains across the GCFR

Unravelling the interactions between humans and geophytes in the distant past is complex, where the artefacts we find in archaeological sites can be interpreted in any number of ways. Even the absence of certain artefacts or ecofacts (like geophyte remains) have been interpreted in a number of ways. The distribution and composition of geophyte remains over the GCFR landscape varies considerably. What does this variation mean and how do we interpret it in terms of hunter-gatherer subsistence?

The overwhelming concentration of sites where geophytes were identified falls within the interior of the West Coast region and the East Coast region. The South Coast region has a relative lack of sites where geophyte remains, or any plant remains are reported (Schweitzer and Wilson, 1978; Schweitzer, 1979) even when the surrounding vegetation is filled with geophyte resources as shown in previous chapters. The few sites along the South Coast coastline and coastal plain where geophytes are reported are certainly not well reported, and considerable effort was made to obtain these short mentions in excavation reports. From the informal observation reported of the small volumes of geophyte material (from these coastal sites), Iridaceae species are the only taxa specifically mentioned in reports (*Watsonia* spp. and *Moraea* spp. specifically). The presence of these taxa mirror the results of the West Coast even if the material is far sparser and less well reported. It is my belief that if future surveys of Holocene sites are conducted in the coastal plains of the entire GCFR coastal plain (but especially the South Coast), more geophyte remains could be discovered.

Apart from this relative shortage of archaeological sites containing geophytes in the South Coast region, there is a relative scarcity of any archaeological sites (rock shelters or caves) along the low-lying regions of the coastal plains of the West Coast and South Coast. This relative scarcity could possibly be due to the lack of suitable geology and topography in the coastal and coastal plain regions for the formation of rock shelters and caves that can create the herbarium like conditions that facilitate the desiccation and eventual preservation of macro-botanical material. This confounds the issue of preservation of plant material, which would already be challenging in the humid environments common along the coastline. The absence of geophyte remains along the coastal plain does not necessarily prove that hunter-gatherer did not forage geophytes in those regions but could rather be a function of geophyte processing not occurring in areas where plant remains can accumulate and be preserved. This illuminated an additional important consideration in understanding the distribution of sites which contain geophyte remains: Where did the processing of plant foods occur?

Foragers would have had the choice of processing geophytes in the field (peeling and cooking) or carrying them back to the cave site for processing (Metcalfe and Barlow, 1992; Pearsall, 2016). To justify the energy required to transport foraged geophytes to cave sites for processing would have required such activity resulting in an energetic/time-saving benefit. The choice between processing plants in the field or carrying the entire plant back to shelter for processing is influenced chiefly by two factors. These are the ratio between the weight of the whole plant, as opposed to the cleaned USOs, and the distance the foraging field is from the shelter where processing could be conducted (Metcalfe and Barlow, 1992).

In the case of the coastal plains which are lacking in rock shelters, it is possible that the distance of carrying geophytes back to a shelter and processing them there was cumbersome, and processing was rather done in the field. This would result in geophytes being invisible in the archaeology in these regions. This idea is further supported by the results presented in this thesis that shows the coastal plains have abundant and high-quality geophyte resources available for a large portion of the year.

6.4.2 Temporal distribution of geophyte remains across the GCFR

The overwhelming volume of geophyte material is found in layers dated to the past 3500 years, which consists of bedding layers, and food debris consisting of mostly corm husks of Iridaceae species. This pattern, along with the associated small ostrich eggshell beads, microlith blades and type of pottery found in association with these finds have been interpreted as originating from hunter-gatherer type activities (Parkington, 1984; Smith *et al.*, 1991). Pastoralists had entered the GCFR within the past 3000 years and could have influenced the patterns of hunter-gatherer mobility within this time frame (Smith, 1992). Despite the fact that both pastoralists and hunter-gatherers relied on gathered plants foods for the plant portion of their diet (and geophytes especially), the pattern in which they foraged and processed these foods could have differed substantially and thus affect the patterns we observe in the archaeological record. The cultural interaction between pastoralism and hunter-gatherer subsistence through the lens of geophyte foraging deserves better attention for this time frame, however an in-depth discussion of this topic is beyond the scope of this thesis and the results presented.

Determining the antiquity of geophyte foraging is not one of the primary goals of this thesis, as the potential of determining this is difficult using macrobotanical remains alone, which decompose quickly. However, based on the similarities of technological and subsistence changes observed in cultural material from various sites in the GCFR (and in some cases the presence and absence of geophyte remains) broad interpretations of the changes in hunter-gatherer subsistence pattern over the course of the MSA and LSA have been made (Klein, 2001). From the changes observed in the archaeological record during the period between 4000-8000 ya from Buffelskloof Rock Shelter, Boomplaas Cave, Byneskransop and Nelson Bay Cave it has been hypothesised that a climatic shift occurred during this time (Deacon, 1976; Opperman, 1978; Schweitzer and Wilson, 1978; Loftus, Sealy and Lee-Thorp, 2016). A shift in subsistence is thought to have occurred from a focus on large-bodied gregarious grazers, where hunting groups had large territories, to small-bodied animals and local geophyte resources, where groups were less mobile (Klein, 1981; Klein, 1983). During this time frame fever macrobotanical remains were found from sites in the West Coast, with the bulk of geophyte material found dating to the last 3500 years. Although geophyte remains were found which dated to periods throughout the Holocene.

The poor preservation of macrobotanical remains alone cannot completely account for the lack of geophyte remains in the terminal Pleistocene however. Could climatic shifts have caused geophyte resources to become less attractive to foragers, and thus lead to this apparent drop in geophyte remains that accumulated in archaeological sites during this time frame? This relative absence has been explained by climatic shifts in the past, focusing on the ecological models presented (Klein, 1983), where climatic shifts would have altered the resource base in areas and forced shifts in subsistence strategies.

During glacial phases throughout the terminal Pleistocene the now submerged Agulhas bank would have become exposed as the coastline receded, adding a novel landscape similar in extent to the contemporary GCFR (Marean, Cowling and Franklin, 2020). The resources that would have occurred on this novel landscape are predicted to have represented a very different resources base to the contemporary coastal lowlands and modeling of the possible resource available in this region during glacial phases is ongoing (Cowling *et al.*, 2020; Marean, Cowling and Franklin, 2020). Recent research shows that during glacial phases and resulting lower concentration of CO_2 in the atmosphere, geophyte growth and biomass accumulation could have been drastically lower than under current conditions (Faltein *et al.*, 2019). Despite this possible drop in geophyte biomass accumulation, we know that throughout glacial phases (from the late Miocene) the flora of the GCFR was relatively unchanged phylogenetically (Verboom *et al.*, 2014) due to the stability of the predominantly winter rainfall in the region which first appeared between 6.8 - 8 mya (Hoffmann, Verboom and Cotterill, 2015). Although the overall available biomass of edible geophytes might have been drastically lower during glacial phases, the GCFR environments would still have had the same or similar geophyte communities spread over the contemporary coastal lowlands.

This resource base could still have supported communities of hunter-gatherers if their mobility was of such a nature to allow them to move to new foraging fields when resources became stressed. Recent assessments of the regeneration of geophytes following intensive gathering show that this resource is remarkably resilient to foraging pressure (Botha, 2019). This shows that even if the available geophyte resources were at a tenth of the density they are today, and regenerated more slowly, this resource could still have been sufficiently robust to support small gathering communities. A plausible situation, however, is that other resources might have become more profitable to focus on as staples. Shellfish resources, for example, would have been mostly unchanged by climatic shifts and were gathered extensively during glacial phases throughout the terminal Pleistocene (Thackeray, 1988; Marean *et al.*, 2007; Langejans *et al.*, 2012).

It is rare to find well-preserved macrobotanical remains in terminal Pleistocene layers. Carbonised lenses from Matjes River, Boomplaas Cave, Melkhoutboom Cave and Klasies River, have been interpreted as extensive geophyte foraging and processing (Louw, 1960; Deacon, 1993), although only recently has this hypothesis been tested when these sediments from Klasies River were analysed and cooked rhizome starches were identified in layers dating to 70 and 120 kya (Larbey *et al.*, 2019). Additionally, the oldest evidence of geophyte processing has been identified at Border Cave (in Kwa-Zulu Natal) where cooked corms have been identified dating to 170 kya (Wadley *et al.*, 2020). Not only do these results indicate that hunter-gatherers were foraging geophytes during these dates in the Pleistocene, but that they were processing USOs. With the advances in microscopic techniques and improved excavation techniques, the number of sites that will yield evidence of geophyte foraging in the terminal Pleistocene is bound to expand in the coming years.

The discussion of the variation in the relative importance of geophytes in hunter-gatherer diets throughout the Pleistocene will remain open to debate until further research is conducted on microscopic plant remains from these timeframes. What is evident however from the results of this thesis and recent research on the nature of this resource is that it could have been sufficiently resilient to have been available to foragers throughout these critical periods in human evolution.

6.4.3 Diversity of geophyte species in the archaeological record

The number of species observed in the archaeology pales in comparison to the number of edible geophytes identified in the study regions. This corresponds to recent research conducted in the South Coast region which compared the contemporary ethnobotanical data to species identified in the archaeological record (Botha *et al.*, 2019). The species which rank high on the master list for their palatability and ease of foraging in Chapter 3 are most commonly found in the archaeological record. Although, some high ranked species do not necessarily appear, and this could be due to their "invisibility in the archaeological record". Half of the edible geophyte species identified in this thesis would not leave any trace in the archaeological record if they had been foraged.

The prevalence of Iridaceae and cormous species in the archaeological record corresponds well with the diversity, density and ranking of these species in the current landscape. Cormous species were, however, the most readily identifiable in the archaeological record and their importance could be over-represented due to this fact. It is reasonable to assume that many other geophytes were in fact foraged, processed and consumed by hunter-gatherers but are not identifiable in the archaeological record.

The diversity of geophyte species I was able to identify in the excavated assemblages analysed, corresponds well to the number of species which were observed to have been foraged in the GCFR (Parkington, 1976). Although many different geophyte species were identified, a few were found in very large volumes, in most sites. These species would have constituted staple food sources.

The distribution of the seven most common geophyte species identified in the archaeological record shows that most of these species are very common in the low lying regions of the West Coast and South Coast where there is a relative lack of archaeological sites. This illustrates the point that although these resources are currently available in these regions, they do not appear in the archaeological record necessarily. The taxa which were the focus of the most foraging activity in the various study regions were similar to the diversity of Iridaceae species which are found in the landscape, where the genera *Moraea* and *Watsonia* seem to have been foraged when they were available in the landscape. Additionally, a focus on other families like Cyperaceae and Hypoxidaceae in the East Coast corresponds to the distribution of these families in those areas.

6.4.4 Evaluation of novel proxy method: Use of seasonal growth patterns of corms in the analysis of archaeological material

The novel proxy method was conveniently applied to measurements captured of disc material from the archaeological record. This method produced extrapolated estimates which can aid in the interpretation of geophyte material in the future. The method does however require additional development and sampling to make it more robust and replicable to the entire region. Currently the reference measurements are based on a small sample size, exclusively collected from the West Coast. The results presented below are a representation of the interpretations that could be made possible using this method. Conclusions are impossible to be drawn from these preliminary results, but the results presented for the seasonality of geophyte foraging are most robust for the West Coast region and results presented for the South Coast and East Coast should be replicated as more reference data of modern plant material is made for those regions.

6.4.4.1 Package size (weight) and energy content (kilojoules) of USOs in the archaeological record

The extrapolations of weight and kilojoule content of corms that were foraged by hunter-gatherers show that the smaller corms of *Moraea fugax* and *Cyanella* sp 1 have higher nutritional content in some cases than larger *Watsonia* sp 1 corms. This gives us a direct insight into the choices hunter-gatherers made when choosing which species to target during foraging. Lower quality species like *Watsonia*, which would have required some form of processing to render palatable, can have similar nutritional content than far smaller species which are of very high nutritive quality, and easier to transport. In any regard, the kilojoule content of corms of these three species is all similar to that of a small potato. *Babiana* sp 1 corms were found to be under three grams generally (and as low as 0.5 g). This might seem to the modern observer like a minuscule amount of food to go to the effort of digging up and processing. However, *Babiana* were a dominant feature in many deposits and could have been considered a staple food source. This might be due to the early emergence of this species in comparison to the other species, where *Babiana* spp. emerge in early winter and the other genera in spring. Additionally, if *Babiana* spp. grow in a sandy medium the corms can be unearthed with minimal effort due to their shallow corm.

The insights offered by this novel method is that hunter-gatherers targeted an array of package sizes of corms. By doing so they could target a diversity of geophyte resources from early winter to late spring. They targeted high-quality small corms, lower quality larger corms, and even minute corms which are available earlier in the season.

6.4.4.2 Seasonality of geophyte foraging

The extrapolation of the seasonality of when four different geophyte species were foraged gives more direct and finer-scale estimates of when geophyte foraging occurred across the span of a year in the GCFR. These estimates suggest that the bulk of geophyte foraging was done in late spring in the West Coast, and early-summer in the East Coast.

In the West Coast, there were many data points which indicate that some geophytes were foraged as early as June. These sites were not limited to the coastal or near coastal sites as predicted by the seasonal mobility hypothesis, which argued that coastal sites were occupied during winter (Parkington, 1972). The bulk of material from coastal plain sites indicate that corms were foraged in late spring, by which time the seasonality mobility hypothesis predicts that hunter-gatherers had travelled to the interior to utilise the geophyte resources in the Cederberg (Parkington, 1972). These results suggest that geophyte exploitation in the coastal plain could have occurred over a wide seasonal range, from early winter to late spring. The results of the seasonality of geophyte foraging in the Cederberg region similarly indicate that geophyte foraging could have occurred in early winter, although the bulk of geophyte remains seem to have been foraged in late spring after most geophytes had flowered, which corresponds to the seasonal mobility hypothesis (Parkington, 1972).

The disparity between the seasonal mobility hypothesis and the results presented here could be due to the varied staggered peaks of phenological cycles of the geophyte species which occur on the West Coast. Although geophyte resources are strongly seasonal in the West Coast, there are species which experience the optimal nutritive quality of their USOs from early spring to early summer. One of the most common species found in excavated assemblages, *Babiana*, flower in winter, and could have been foraged optimally as early as June. From the results presented it seems there is a far wider window of time during the year when geophyte resources were foraged across the region, both in coastal sites and mountainous sites. I argue that based on these results for the West Coast, hunter-gatherers foraged geophytes opportunistically when species would offer the optimal nutritive returns. Due to the overwhelming number of geophytes experiencing this peak in nutritive returns in spring, the bulk of geophyte foraging was focused during this time.

Only one disc was measured from Boomplaas Cave in the South Coast and this is not sufficient to base any predictions of seasonality of geophyte foraging on. Had there been archival material available from the South Coast from which to extrapolate, I would hypothesise that there would be two peaks in the year when geophytes were foraged, which correspond to the two peaks of phenology when this resource might be available and at the peak of its nutritive quality. Genera which are commonly found in the archaeological record, such as *Freesia* and *Tritonia*, flower as early as March, and could have been foraged optimally in autumn, with a second peak of Iridaceae species in late spring.

Deacon predicted that geophyte foraging in the East Coast was focused on species which are available during a large portion of the year (such as the evergreen *Watsonia* species common in the region) (Deacon, 1976). Although many *Watsonia* species in this region are evergreen, there would only be a narrow time frame in early summer during which time they would be palatable. This was clearly illustrated by the high tannin content measured for *Watsonia galpinii* in autumn. The results presented in this chapter for the East Coast suggest that *Watsonia* corms were foraged during the time that their corms would be at the peak of their nutritive quality in early summer.

It is important to note that the strength of the extrapolation presented is subject to the species which were selected in this method. Common, early flowering, cormous species in the East Coast region such as *Freesia* spp. and *Tritonia* spp. were not included for example. These species would have given a wider array of data to base the extrapolation of the seasonality of geophyte foraging on. The strength of the results presented for the East Coast are then not as robust as for the West Coast. In future, as many cormous species, which are common in the archaeological record, as possible should be measured, which will improve the possible predictions. If this is done in the future, the predictions of seasonality of geophyte foraging will be more robust. If this is done I expect that the seasonality of geophyte foraging will be predicted to have occurred almost year round in the East Coast.

Many improvements could be made to the novel extrapolation methods to determine seasonality of geophyte foraging presented in this chapter. The method would be most effective if the extrapolation equations were determined for every single cormous species found in the archaeological record. This would entail monthly sampling of contemporary plants in the various regions, which would amount to the destruction of thousands of plants and more hours than there are in a day. The four species selected for this purpose in this thesis was in an effort to optimise the results possible, with the time and monetary resources available for this study. The burden of collecting this mountain of data does not have to fall on the shoulders of one researcher, but I hope that subsequent research can build on the dataset collected for this thesis (which I will make publicly available).

The results presented here, with all its flaws, do suggest that geophyte foraging was dictated by the phenological cycles of geophytes across the region. Geophyte resources are highly seasonal on the West Coast, although they seem to have been foraged as soon as early winter to early summer. Similarly, it is possible that geophyte foraging in the South Coast mimicked the two peaks of phenology observed in that region, although no data is available yet to base this prediction on. In the East Coast, evergreen species would only have been targeted during the time when their USO quality was highest, although other species which are available at various times of the year, could have made geophyte resources optimally forageable practically all year round.

6.5 Conclusion

The results reported in this chapter give a novel perspective on the intricacies of foraging behaviour of Stone Age hunter-gatherers and will hopefully lead to a renewed focus by archaeologists to sample plant material in the archaeological record, build robust comparative collections and collect relevant data on the distribution and nature of the resources in the contemporary environments. The novel methods of determining seasonality and the nutritional content of geophytes which were foraged can be applied to sites where geophyte remains have been identified previously, and during future excavations.

The strength of studies conducted on archival material are only as strong as the curation system that is implemented to store excavated material, which should include access to relevant information regarding the original excavations. These factors were a major constraint during the analyses performed for this chapter. Archival material has huge potential to help answer research questions as appropriate curation of this material can give future generations of researchers the opportunity to study material with the same vigor as was possible when the material was originally excavated.

Geophyte foraging seems to have been a very important part of Holocene hunter-gatherer subsistence over the entire GCFR. Although there are large scale subsistence strategy shifts observed in the macrofaunal assemblages throughout the terminal Pleistocene, the Fynbos assemblages, of which geophytes are a dominant component, have been stable throughout this era and geophyte would have been present in this region and available to foragers. The recent results providing micro and macroscopic evidence of geophyte cooking in the terminal Pleistocene, is a glimmer of hope that widespread evidence of geophyte exploitation will be uncovered in the future for this time period.

Chapter 7: **Processing of geophytes during the Stone Age**

7.1 Introduction

The exploitation of lower quality USOs or ‘fallback foods’ has been hypothesized to have allowed our human ancestors to exploit a resource base which was unavailable previously, during times of scarcity and supported the energetic requirements to sustain brain development throughout hominin evolution (Laden and Wrangham, 2005; Marshall and Wrangham, 2007; Marlowe and Berbesque, 2009). The exploitation of these resources was made possible by applying certain processing methods to the previously unpalatable resources, which decreased the anti-nutrient content and increased the bioavailability of the nutrients which remained (Wrangham *et al.*, 1999; Carmody and Wrangham, 2009b; Schnorr *et al.*, 2015). Elaborate processing of USOs is common among extant hunter-gatherers (Stahl, 1989). In the GCFR simple processing methods have been identified in the Pleistocene (Larbey *et al.*, 2019; Wadley *et al.*, 2020) and more complex methods in the Holocene (Raven-Hart, 1967; Skead, 2009). These processes seem to be focused on lower ranking geophyte species which contain toxins or acrid compounds, usually for the purposes of detoxification or improved palatability. These processing techniques enable the utilisation of a wider range of geophytes that would have been available to foragers, for a longer period throughout the year (Stahl, 1989).

Processing of USOs would have required hunter-gatherers to have made a complex set of decisions to develop effective methods to improve the nutritive quality. This complex process of developing processing techniques would have been pursued if it resulted in significant increase in the efficiency of food collecting and energy acquisition from the available resources in the landscape. Determining the efficacy of various methods of processing is crucial to understanding the possible benefits which hunter-gathers could have enjoyed and could shine light on the impact geophyte exploitation could have had on early human behaviour. Although early evidence of geophyte processing has been identified, there has been limited exploration into of the effectiveness of various Stone Age processing methods in the GCFR.

For our distant ancestors cooking USOs would have been the simplest yet effective method to increase the palatability and nutritional availability of USOs. The cooking hypothesis states that the cooking of USOs and other foods could have shaped our evolution for millions of years, although evidence of control of fire by early humans is limited to 400 kya (Wrangham, 2017). Cooking of lower ranking foods would have broken down fibre, which would have made mastication easier and increased the bioavailability of carbohydrates (Carmody and Wrangham, 2009b; Schnorr *et al.*, 2015). Cooking of geophytes in hot coals and ash is the most common method of processing observed in the GCFR, with almost every single early traveller accounting the cooking of ‘Uintjies’ in hot embers (Kolb, 1731; Stow, 1964; Raven-Hart, 1967; Thunberg, 1986). The array of complex methods of processing of USOs observed in the GCFR and across the world is however far more complex than this simple cooking of USOs and include physical processing, leaching and fermenting (Stahl, 1989).

The principle behind physical processing can have two purposes; rupture cell walls, exposing the content of the cells to further processing techniques, or to transform the USO into a form which is easier to incorporate in other foods or for storage. Grindstones would have been the primary tool used in the GCFR to perform physical processing of USOs. Grindstones have been used as a proxy of geophyte foraging and processing in the past (Mazel and Parkington, 1981; Parkington, Fisher and Tonner, 2009), although grindstones were used for a diverse range of tasks such as the production of paint, medicines and other plant food processing like grass grain (Thornton-Barnett, 2013; Eoin, 2016). Although grindstones seem to have been a multipurpose tool, one of their function was, however to process geophytes. Historical observations indicate that even the highest ranked USOs in the GCFR; 'Uintjies' were processed by grinding to produce a paste, which was used in that form or dried into flour (Burchell, 1822; Raven-Hart, 1967).

Leaching of anti-nutrients from USOs is one of the most common processing techniques used by extant hunter-gatherers (Eder, 1978; Headland, 1987; Wright, 1994) and among Stone Age hunter-gatherers (Messner, 2011). In this process fluid (usually water) is used, sometimes mixed with other binding chemicals such as charcoal, ash, clay or salt, to wash away toxic or antinutritive compounds (Stahl, 1989). Although this method can decrease the anti-nutritive content of USOs, increasing their palatability greatly, this method runs the risk of flushing away soluble nutritive compounds like sugars (Stahl, 1989). The holistic effect of this form of processing to improve the overall quality of USOs might make up for the potential loss of energy. In the GCFR the leaching of two important foods was observed historically: Wild Almonds (*Brabejum stellatifolium*) and Varkblom rhizomes (*Zantedischia aethiopica*) where in both cases the plant foods were leached in flowing rivers or steeped in water for up to three days (Sparrman and Forster, 1785; Schapera *et al.*, 1933; Thunberg, 1986).

Fermentation is a common method used to transform harmful molecules into a harmless state, or to make macronutrient more easily digestible and easily absorbed by the human gut (Stahl, 1989). Fermentation relies on the prolonged storage of USOs suspended in fluid for extended periods of time. In Samoan communities' plant foods processed by fermentation were stored in pits in the soil and could have a shelf life of up to two years (Cox, 1980). Although hunter-gatherers were observed to ferment honey in the GCFR (Skead, 2009), there were no observations of USO fermentation.

In many cases a combination of processing methods was observed with the following procedure reported in the GCFR: Corms were cooked in embers, (sometimes dried) then ground into flour, which was either mixed in with other food or formed into "cakes/bread" which was stored or eaten immediately (Kolb, 1731; Stow, 1964; Raven-Hart, 1967; Skead, 2009). Although these complex processing methods were observed historically in the GCFR and elsewhere, is there archaeological evidence which prove the antiquity of this complex behaviour?

Direct evidence of complex processing of USOs is surprisingly ancient in other parts of the world. In Australia there is evidence of leaching and grinding of USO from 38 kya (Hallam, 1996) and “bread” making from USOs has been identified from 14 kya in Egypt (Arranz-Otaegui *et al.*, 2018). These direct signs of complex processing are rare in the GCFR archaeological record. Signs of simple processing, such as cooking of geophytes, has been reported, although these interpretations are based on inedible debris that is charred which could have resulted after the USOs had been consumed raw. It is difficult to say that USOs were cooked, when the cooked portion is usually missing (as it was eaten). As discussed in Chapter 1, the cooked starches identified at Klasies River and cooked rhizomes at Border Cave from the middle Pleistocene are some of the most ancient evidence of USO cooking from the GCFR (Larbey *et al.*, 2019; Wadley *et al.*, 2020). The palatability and bioavailability of nutrients from these species could have been greatly improved by cooking alone. This evidence of processing of low ranking USOs in the middle Pleistocene shows that this behaviour could have greatly expanded the resource base available to early modern humans during the emergence of modernity in the GCFR.

The objectives of this chapter are:

1. ***Evaluate signs of processing and cooking present in excavated assemblages in the GCFR***
2. ***Evaluate the efficacy of various processing methods in improving the nutritive quality of geophytes***

To evaluate the evidence of processing of geophytes which occurred in the GCFR the evidence of cooking of geophytes was reviewed during the systematic botanical analysis performed for this thesis. The approach was taken to determine the efficacy of potential processing methods experimentally. This was done by replicating a range of scenarios that would have been possible using only Stone Age technologies, to determine the level of improvement to the quality of USOs. The experiments performed were guided by the observations made in historical accounts of USO processing by hunter-gatherers in the GCFR and the associated tools used during processing, together with the processing methods commonly used among extant hunter-gatherers across the world.

7.2 Methods

To determine the signs of cooking of geophyte remains in excavated assemblages any charring of geophyte material was noted during the systematic botanical analysis conducted on archival archaeological material, together with the type of material that was charred (husks, discs or corms).

To test the efficacy of possible processing methods to improve the nutritional quality of geophytes, two common *Watsonia* species found on the coastal plain of the GCFR were collected in November 2018 and exposed to various processing methods. A control of both species was collected, which consisted of fresh corms which were not processed. The macronutrient and tannin content were tested using the same methods as described in earlier chapters. The four processing methods which were tested are leaching, grinding, cooking and veldfire. For each treatment, 15 plants were collected per species.

To test the efficacy of leaching to remove antinutrient, corms were sliced in 1cm slices with a stone flake and set in an intertidal ocean pool for six hours. This process was repeated where corms were placed in a slow flowing river for six hours.

Figure 7.1 Left; Sliced corms and stone flake used to slice them. Middle; Corm slices placed in an intertidal pool to allow leaching of anti-nutrients. Right; the discoloration of water as tannins and other compounds leach out of the corms and oxidize, turning the water red.

To test the efficacy of the grinding of corms, the corms were ground with a traditional grindstone (raw) and steeped in fresh water for six hours then rinsed.

To test the effect of cooking corms, corms were placed under hot coals (whole) and ash for 30min.

Figure 7.2 Corms of Watsonia meriana and Watsonia tabularis roasting in hot ash and coals for 30 minutes.

Following a veldfire in the Cape Peninsula, *Watsonia tabularis* corms were collected and nutritionally tested. During this collection it was found that the corms had been cooked by the fire and the injured corms were exuding a glue which was also collected and used in other experiments. See Figure 7.3 for photo of corms following the veldfire.

Figure 7.3 Watsonia tabularis corms following a veldfire in the Cape peninsula. On the left the glue exuded by the corm is visible, in the middle the corms which show signs of being cooked by the fire, and on the right the charring of corm husks caused by the fire

7.3 Results

7.3.1 Evidence of processing and cooking in the archaeological record

There were various corms, discs, rhizome bark, tuber scales and husks that showed signs of charring in the archaeological record, which made it obvious that the plant material had been exposed to fire. Frequently the coverings of USOs or above ground parts of geophytes showed signs of charring. In one case the knotted together tops of geophyte plants were intact, but where the USOs would have been attached was charred off (see Figure 7.4). Intact husks of corms were found where only the outside layers of material had been charred (see Figure 7.4).

Figure 7.4 Knotted bunch of geophyte leaves with charring at base where USOs would have been attached (from Melkhoutboom Cave). b) Intact Moraea husk showing signs of charring (from De Hangen).

Other commonly charred material consisted of corm discs and the bark which covered USOs. In only a few cases intact corms were found which were completely charred, and in one instance a *Watsonia* corm which had a section removed, that almost looks like a bite mark, was found (see Figure 7.5). Frequently only the outside surface of husks, or bark (like *Dioscorea elephantipes* bark pictured in Figure 7.5) were charred while the inner surface was uncharred.

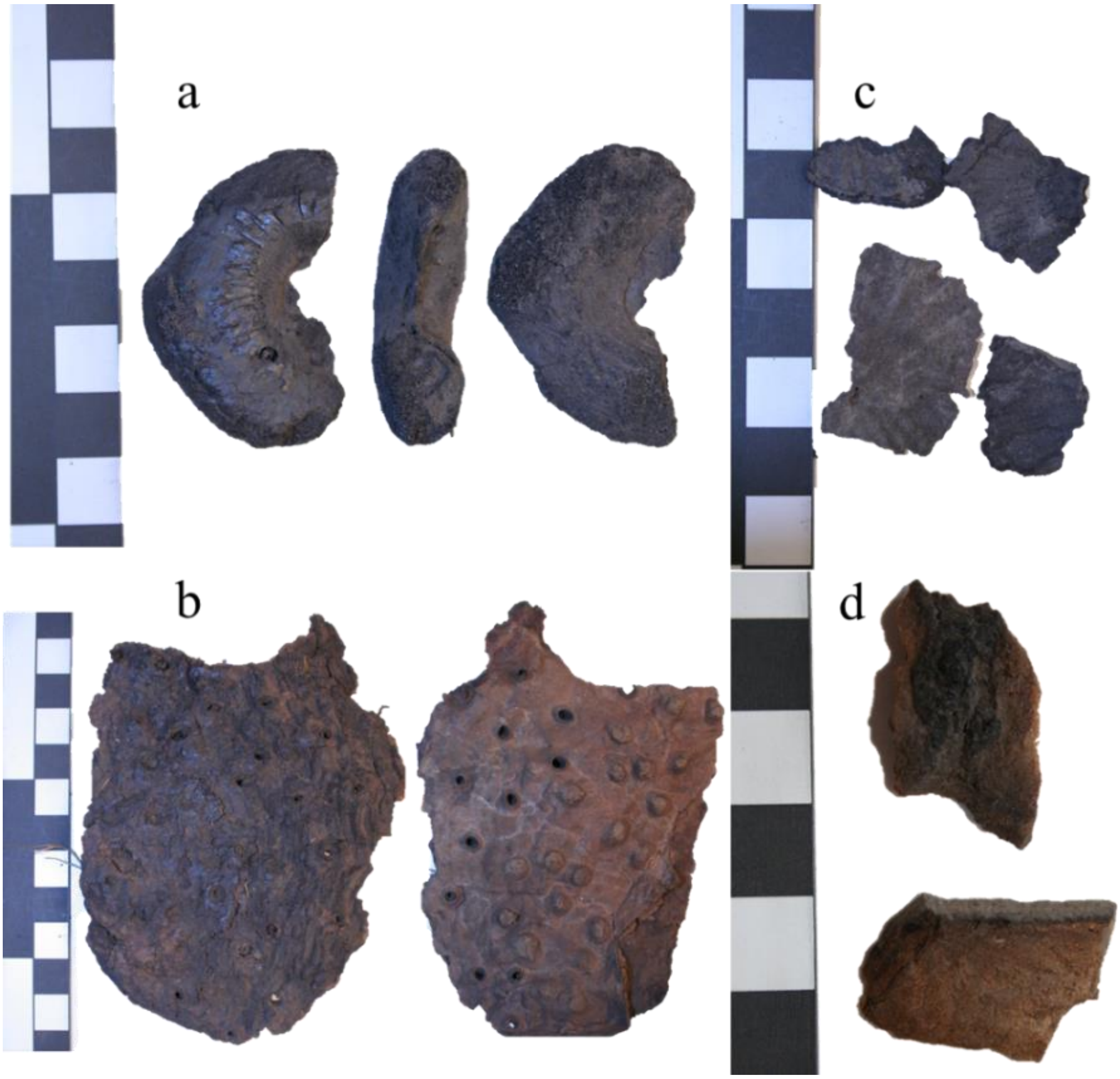


Figure 7.5 a) Watsonia corm, charred with section removed, b) Large Dioscorea elephantipes bark fragments which shows signs of charring on the outside surface. c) Fragmented Watsonia corm bases that are charred, d) Small Dioscorea elephantipes bark scale with sign

The species and sites which show signs of geophyte cooking show no discernable pattern over the landscape. Species which are edible raw were also found to show signs of being exposed to fire. There were no significant differences in the occurrence of burnt geophyte remains between sites (see Table 7.1). Similarly, the frequency of species that showed signs of charring is rather an indication of their overall frequency in the archaeology, where only the most common species were found to have any signs of charring (see Table 7.1).

Table 7.1 Frequency of charred geophyte remains observed for various Archaeological sites and species

Site where charred geophyte remains observed	Frequency observed	Species where charring was observed	Frequency observed
De Hangen	29	*Babiana* sp 1	17
Andriesgrond Cave	10	*Dioscorea elephantipes*	13
Faraoskop Rock Shelter	9	*Watsonia* sp 1	12
Boontjieskloof	7	*Moraea* sp 1	6
Renbaan Cave	2	*Cyanella* sp 1	5
Melkhoutboom Cave	2	*Babiana* sp 2	2
Varsche 005	1	*Watsonia* sp 3	2
		Moraea sp 2	1
		Ferraria sp 1	1
		Oxalis sp 2	1

7.3.2 Effectiveness of processing methods to improve USO quality

Every method of Stone Age processing tested lowered the tannin content of *Watsonia* corms significantly, except for leaching with fresh water (see Figure 7.6).

Leaching sliced corms in intertidal pools was equally as effective in removing tannins from corms as roasting corms in coals. Grinding corms and steeping them in fresh water was more effective still. The most effective method of removal of tannins was veldfire, which eliminated tannin content almost entirely (see Figure 7.6).

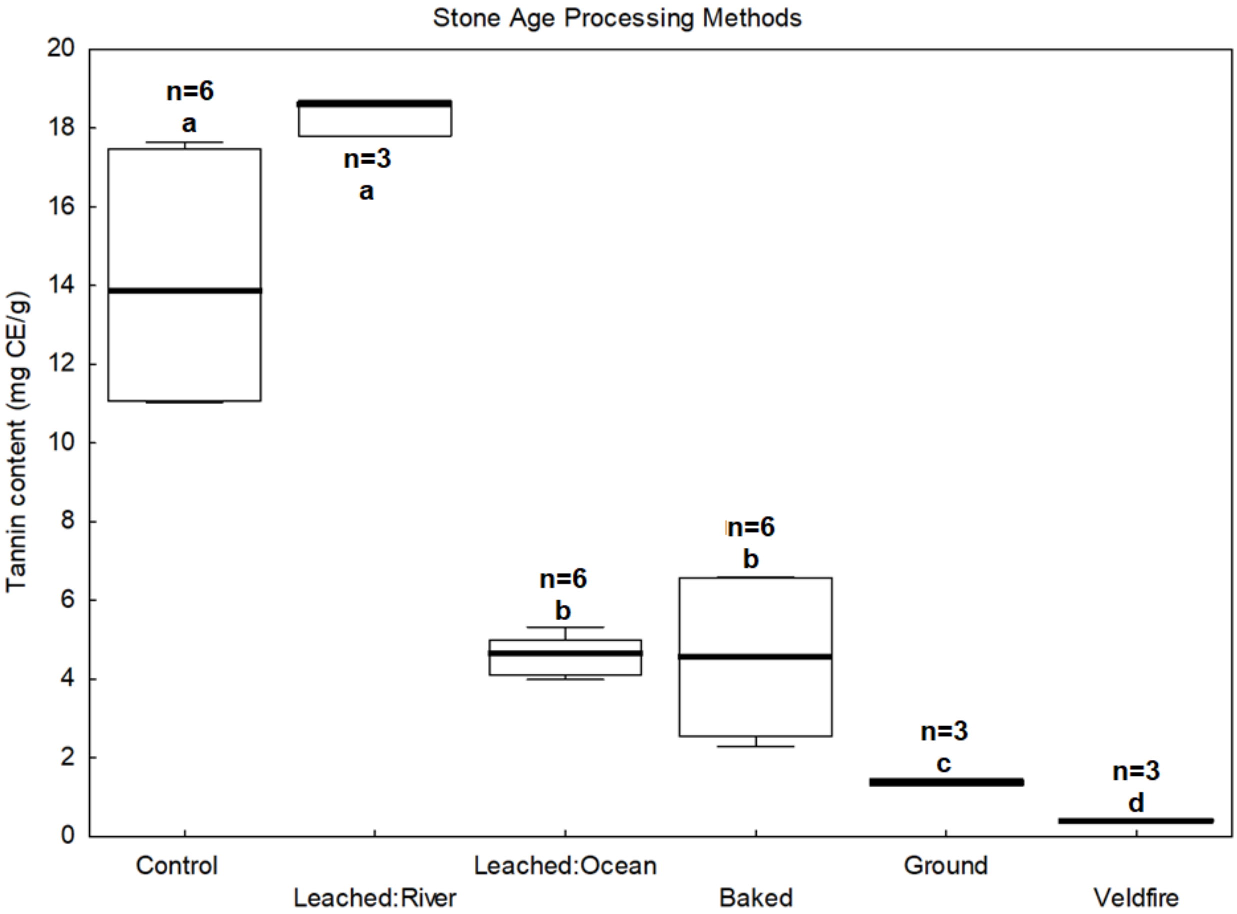


Figure 7.6 Tannin content of Watsonia meriana and Watsonia tabularis corms, after being processed using Stone Age methods. Boxes upper limit denote 75 % of data, bottom limit 25 %. Mean denoted by black bar, whiskers represent the standard deviation. Letters denote significant differences between groups. Letters denote significant differences between treatments. Treatments with unique letters are significantly different from other treatments while treatments that share letters are not significantly different from one another. N is the number of test replicates that were performed for each treatment.

The processing methods did not significantly change the nutritional composition of corms. Although methods that incorporate cooking significantly lowered the water content, which resulted in the remaining components making up a greater proportion of the weight than they did before. When this phenomenon is controlled for by evaluating the dry matter composition (which completely eliminates the water content of all samples), the carbohydrate content of leached corms was not significantly lower than the controls.

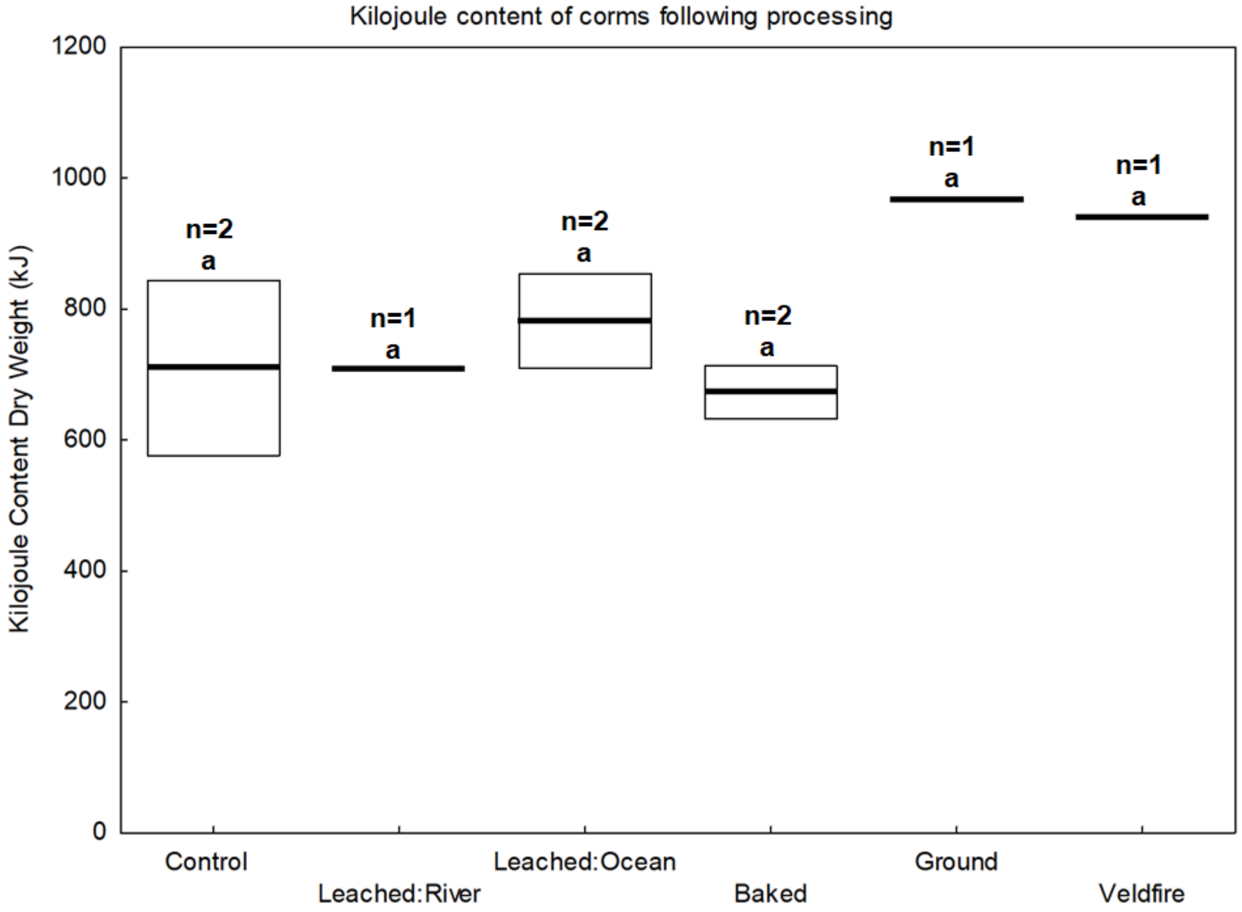


Figure 7.7 Kilojoule content of corms after processing (Dry matter). Boxes upper limit denote 75 % of data, bottom limit 25 %. Mean denoted by black bar, whiskers represent the standard deviation. Letters denote significant differences between groups. Letters denote significant differences between treatments. Treatments with unique letters are significantly different from other treatments while treatments that share letters are not significantly different from one another. N is the number of test replicates that were performed for each treatment.

7.4 Discussion

7.4.1 Evidence of processing and cooking in archaeological record

Many geophyte remains showed signs of charring, and although this charring could have been possible by debris from geophyte processing being strewn among burning coals in the domestic space, signs of deliberate cooking were identified. In many cases only the outside surfaces of husks, bark and other outer coverings of USOs are charred, and this was interpreted as a sign of deliberate cooking. Interestingly even species which are edible raw seem to have been cooked, which is possibly due to the increase digestibility of starch after cooking (Schnorr *et al.*, 2015).

7.4.2 Effectiveness of processing methods to improve USO quality

All the processing methods tested (except for leaching in fresh water) would have been effective in improving the nutritional quality of lower ranking USOs. The removal or neutralisation of anti-nutrients and toxins in USOs would not have been the only consideration for hunter-gatherers to develop and implement processes methods. Other factors which would have impacted their processing techniques are the effect processing had on the macronutrient composition (overall energy content), the energy and time required to execute a processing method and possible beneficial by-products of processing (such as glue exudates or increased shelf life).

The energy content of corms following processing treatments was not significantly different to that of the controls. This result is significant as loss of nutrients during processing of USOs can be significant, especially in processes which involve leaching (Stahl, 1989). The bulk of energy contained in corms is derived from carbohydrates and the primary carbohydrate content of corms consist of starches. Starch is insoluble in water and would not necessarily leach from corm material, whereas water soluble carbohydrates like mono- and disaccharides which can be prone to leaching comprise less than 3 % of the total weight of corms (see Chapter 3) and the loss of these nutrients would not significantly lower the total energy content of corms.

Although the crude nutritive composition of corms might not have been changed by processing, the bioavailability of carbohydrates could have been improved by cooking, which would not be reflected in the nutritive tests which were performed (Carmody and Wrangham, 2009b; Thoms *et al.*, 2014). This increased bioavailability of nutrients would have been a big incentive for USOs to have been cooked, apart from the effects cooking have on lowering the anti-nutrient content. This fits in with the observations that have been made historically that corms which do not contain anti-nutrients (‘Uintjies’), underwent extensive processing and were almost always cooked in embers (Stow, 1964; Raven-Hart, 1967).

Although almost all methods of processing showed significant improvements in the nutritional quality of USOs, the inputs required to perform these processes varied widely. Processes which involve grinding and leaching of USOs would have required a significant energy and time investment. This is contrasted by less time-consuming methods such as cooking of USOs, which might not be as effective in removing all anti-nutrients, but had other added benefits such as making the remaining nutrients more bioavailable during digestion. In other words, even though the USOs processed by cooking in embers might still be bitter tasting, due to remaining anti-nutrients, this method might be preferred due to the other benefits it holds in comparison to laborious methods such as grinding and leaching.

Some phytochemicals (such as tannins) have a complementary medicinal application to the functional food application, and these compounds are selectively targeted for this reason by extant hunter-gatherers (Johns, 1999; Mohd Noor *et al.*, 2019). Ancient human palettes would have been far more tolerant of bitter flavours and humans would have selectively ingested these compounds for their medicinal effects (in low concentrations) (Johns, 1996). If the processing methods were effective in reducing the anti-nutrient content to within safe levels, these compounds could have had beneficial medicinal effects (Johns, 1996).

Grinding and soaking of corms would have required a large, relatively immobile grinding stone, and a significant amount of energy and time to grind and soak the corms. If there exist other methods that are similarly effective in improving the nutritional quality of corms, and less energy and time consuming, why would this cumbersome method that requires a specialised, immobile tool be used? We know, however, that exceedingly complicated processing was observed in the GCFR historically as described in Chapter 2, which leads to the assumption that there are other added benefits to the extensive, complex processing of corms. As discussed in Chapter 2 (page 42) removing anti-nutrients is only one of four main goals of processing foods. The other goals are to transform a single food source into many forms/tastes, to make ingredients go further by processing them into a form that can be mixed with other ingredients and transforming ingredients into a state that will preserve better (Johns and Kubo, 1988).

Grinding of corms could have extended the shelf life of this food source while simultaneously improving the taste and number of functions the food could serve in dishes. As mentioned in Chapter 2, ground corms were observed to be recombined in different ways to produce a varied number of dishes and flavours. One of these intricate dishes that was observed to have been made in the GCFR are geophyte cakes. The grinding of geophytes into flour/cakes/bread would have resulted in a transportable, shelf-stable source of energy which could have lasted far past the date when this resource was available in the landscape. The appearance of storage pits in archaeological sites all over the GCFR in the later part of the Holocene shows that geophytes could have been stored in this form.

The interesting case presented by the results of the veldfire is significant and has far reaching implications. The corms which were cooked by the veldfire required absolutely no input (if the fire was passive) or minimal input (setting a piece of veld alight and collecting the corms later). This method showed the most drastic reduction of anti-nutrient content and produced a by-product; an exudate which could have served a functional use in other subsistence activities such as tool production. Composite tools usually consist of a haft (a wooden implement), a stone tool (like a flake) and adhesive to glue these components together and these tools are common features throughout the Pleistocene and Holocene (Lombard, 2004, 2012). The glue used during the manufacture of stone tools is not well studied and most glue currently identified on stone tools are produced by tree species like *Vachelia karoo* (*Acacia karoo* previously) and *Podocarpus* spp. (Lombard, 2004; Charrié-Duhaut *et al.*, 2016). *Podocarpus* and *Vachellia karroo* are not ubiquitous across the GCFR, where these known sources of glue are confined to river courses and the mountainous regions.   The exudate produced by Watsonia after the veldfire was used to produce composite stone tools illustrated in Figure 7.8.

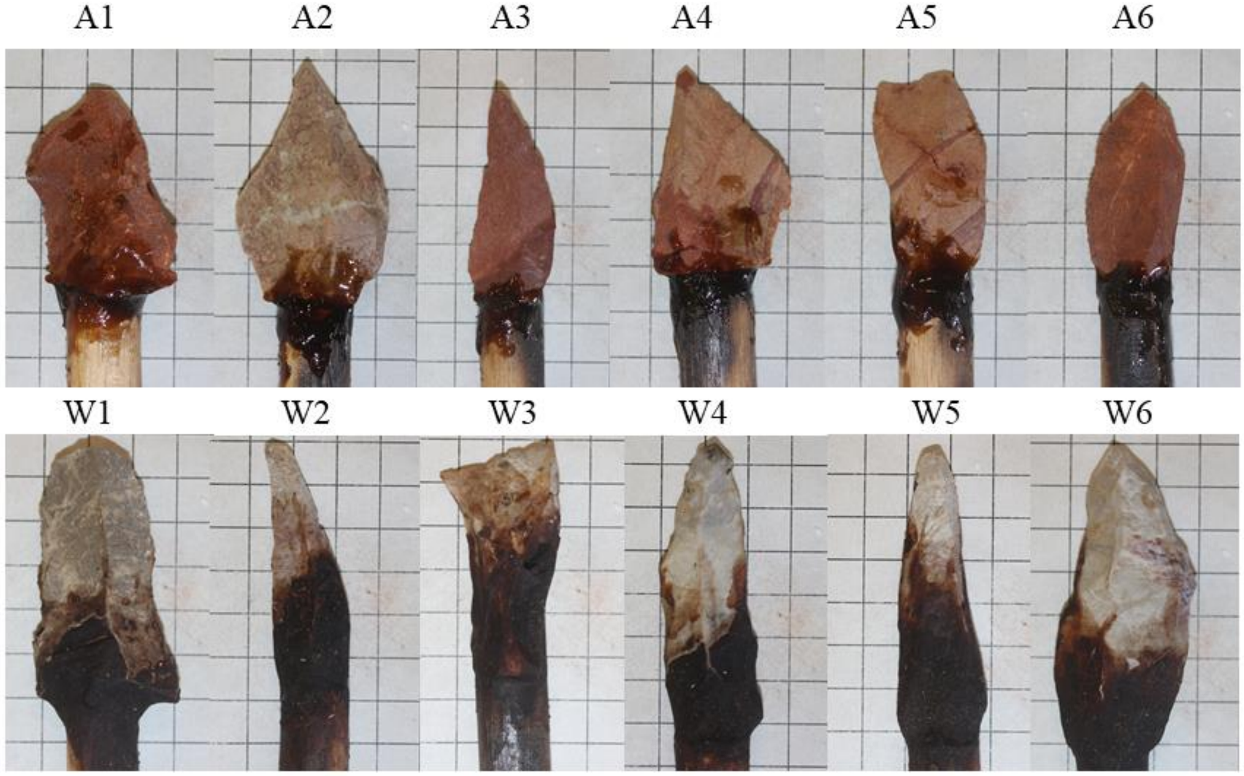


Figure 7.8 Composite stone tools made with Vachelia karoo resin (top) and Watsonia tabularis exudate (bottom). Image adapted from Singels & Schoville, 2018

The *Watsonia* glue was found to produce composite tools which would have been equally effective during hunting when compared to composite stone tools produced by the control glue (Singels and Schoville, 2018). A resource of glue which was widespread on the coastal plain would have been an important resource for hunter-gatherer living there, especially if the glue was a by-product of the foraging of *Watsonia* as a food source.

From the results presented here the occurrence of natural veldfire could have had many benefits for hunter-gatherers: corms were made easily accessible by the removal of all other above-ground plant material, the corms were cooked and the quality of the corms improved by the neutralisation of anti-nutrients and a source of glue was produced.

Apart from the effect of veldfires on *Watsonia* corms the entire ecosystem could have been altered to the benefit of hunter-gatherers. The management of geophyte resources by hunter-gatherers in the MSA and LSA by the deliberate burning of veld has been hypothesised (Deacon, 1993). This hypothesis was influenced by the observations made in Australia where "fire stick farming" is commonly observed among extant hunter-gatherers (Jones, 1980) and is thought to have been used as a resource management tool for millennia (Bird *et al.*, 2008). Similarly in the GCFR fire was observed to be used as a management tool of vegetation historically (Raven-Hart, 1967; Skead, 2009). These fires were intended to encourage plant growth, either for grazing or to invigorating growth of geophytes and aided hunting efforts by making the veld more traversable and game easier to spot (Schapera, 1930). In a recent simulated foraging study it was found that recently burnt veld had three times higher foraging return rates (Botha *et al.*, 2020), presumably due to the increased visibility and accessibility of remaining resources.

The resulting invigoration of plant growth would reach a peak in a few weeks following the fire and would have given hunter-gatherer groups an incentive to reap the benefits of the management of that area at that time, affecting their mobility. In some cases, as observed by Kaufmann among /Auin people, the person or people who conducted the active burning of a piece of veld had first choice over the resulting bounty of edible plants which emerged after burning, and gathering the bounty if you were not involved in the burning was seen as theft (Kaufmann, 1910). Similarly, women could stake claim to an especially abundant spot of geophytes and reserve the exclusive right to gather from that spot (Schapera, 1930). It is likely that a particularly well-managed patch of geophytes in the landscape could become a sedentary resource worth territorialising. Although this type of behaviour was never observed in hunter-gatherers.

Using fire as a resource management tool and a processing method for geophytes would have required the lowest energetic input of all processing methods suggested here, while the benefits which could arise from it are manifold. The prolonged management of resources could have altered ecosystems for the benefit of hunter-gatherers, sparked by the exploitation of lower-ranking geophytes which occur in this region. The benefits processing of USO as presented in this chapter could have resulted in the improved survival and fecundity of humans during the critical periods in modern human evolution.

Chapter 8: **The evolutionary context of geophyte foraging in the GCFR**

8.1 Conceptual implications of results

8.1.1 Co-evolutionary relationship between geophytes and humans

Co-evolutionary theory states that two or more species which have an association (symbiosis) can affect one another's evolution (Raven *et al.*, 2008). Species can either evolve to outcompete one another or form strong dependence on one another (mutualism) (Raven *et al.*, 2008). Early human hunter-gatherer activities constitute symbiotic relationships with the communities of animal and plant species which were targeted as food sources. Is it possible that early humans co-evolved with the vegetation and specific geophytes of the GCFR to maximise the benefits we gain from exploiting them? Additionally, could geophytes have benefitted from the human herbivory which they were exposed to?

Specialist relationships between geophytes and their mammalian herbivores have been explored for porcupine (Gutterman, 1987), baboons (Davidge, 1978) and mole rats (Lovegrove, 1989; Bennett and Jarvis, 1995; Barnett and Bennett, 2003). The fecundity of geophytes was increased in some cases by this herbivory as herbivores act as agents of dispersal of geophyte genetics. Geophytes are distributed by seed or specialised vegetative reproductive structure that get dislodged as the USO is disturbed and eaten (Gutterman, 1987). Additionally, during the foraging process soil within which geophytes grow is aerated, significantly increasing the rate at which plants can grow (Bragg, Donaldson and Ryan, 2005). During the fieldwork conducted for this thesis, the adaptations of geophytes to have improved fecundity as a result of herbivory were noted (see Figure 8.1). Vegetative reproductive structures consist of small USOs which are clones of the mother USO and attached to the USO. Bulblets growing on bulbous plants were frequently encountered (Hyacinthaceae, Oxalidaceae), cormlets (specialised vegetative reproductive structures of corms) growing on cormous species (Iridaceae) were encountered and resprouting clones from the inedible old corm growth (discs) were even observed in *Cyanella hyacinthoides* (see Figure 8.1). These adaptations would increase the fecundity of these species following herbivory, where even if the mother plant was destroyed, multiple clones might survive in the newly aerated soil.

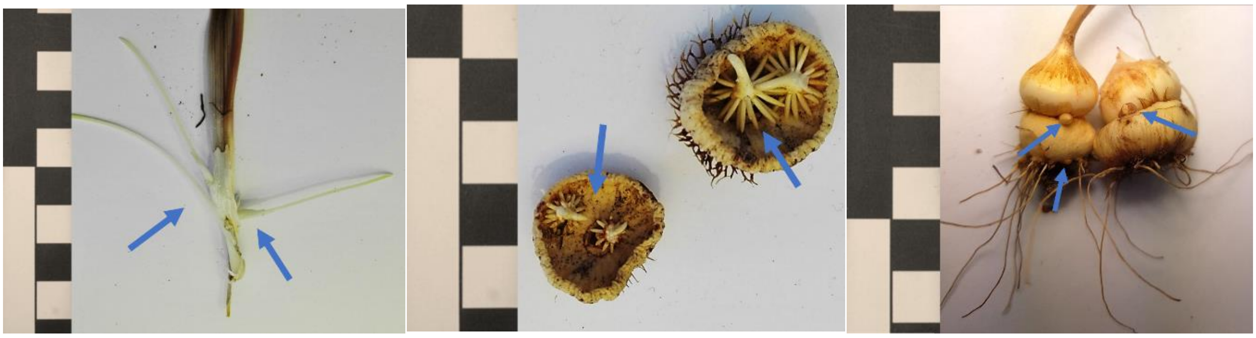


Figure 8.1 Herbivory adaptations observed in edible geophyte species in the GCFR, from left to right, Sprouting Bulblets on the stalk of Albuca flaccida, resprouting clones on the old corm growth (disc) of Cyanella hyacinthoides, cormlets attached to corms of Gladiolus carinatus

Other herbivory adaptations that have been discussed at length in this thesis are the secondary metabolites which geophytes produce. These compounds serve no metabolic function but are produced to deter herbivory due to their toxicity or unpalatability to potential herbivores (Johns, 1996). The high concentration of these compounds in USOs specifically (as opposed to the entire plant) shows that these adaptations occurred to deter herbivory of USOs (McKey, 1979; Andersen and Anderson, 1987).

Although using this strategy, geophytes can outcompete herbivores if the secondary metabolites cause harm to the herbivore, there would have been a huge evolutionary incentive for humans to overcome these compounds by way of processing. If humans could not develop these techniques, these resources would remain unavailable to them (Johns and Kubo, 1988). Discovering and developing these processing methods would have relied on chemical sensing of these compounds (by smell, taste or sight) before and after processing to determine if the process had resulted in the improved nutritional quality of USOs. This sensitivity and selection of plant foods based on their secondary metabolite content is common among primates (Glander, 1982; Huffman and Wrangham, 1994; Stoner, 1996). Humans too, have great sensitivity for sensing secondary metabolites in all three of these senses and we are particularly sensitive to bitter taste (Johns, 1996). Early modern humans would have been able to sense if the processing techniques they had employed had been effective, without causing harm to themselves (Johns, 1996). Additionally, the selection of medicinal plants based on their chemical composition was an important cognitive development and shaped how we sense chemical compounds (Johns, 1996). Again, parallels can be drawn to our primate relatives (Chimpanzees) who seek out certain plant foods for their medicinal properties (Koshimizu *et al.*, 1993; Huffman and Wrangham, 1994; Ohigashi *et al.*, 1994). The widespread occurrence of the highly toxic species *Boophane disticha* in the archaeological record shows that Holocene hunter-gatherers were actively choosing certain plants because of their toxic compounds.

Many primate species illustrate a high level of complexity in their foraging behaviour related to plant foraging (Koshimizu *et al.*, 1993; Huffman and Wrangham, 1994; Ohigashi *et al.*, 1994; Noser and Byrne, 2010). Among humans these complex behaviours would have been extended to include multi-step processing to make geophyte resources available as foraging items (as illustrated in the previous chapters). This could have included the use of tools and fire to render these resources available to human foragers. The series of steps and forethought involved in the efficient foraging and processing of geophyte species (for various uses) would have been a complex learning process and required complex knowledge transfer. If these hurdles were overcome a vast amount of geophyte resources, which were unavailable without processing methods, would have become available to early humans. It has been argued that the series of steps and forethought involved in stone tool manufacture may be evidence for advanced working memory, complex cognition and development of language (Wadley, 2010; Bradfield, Lombard and Wadley, 2015). I would argue that efficient geophyte foraging would have triggered the same advances in working memory, complex cognition and development of language in early modern humans.

This topic deserves further dedicated research to confirm that there is a co-evolutionary relationship between geophytes and humans, but I have little doubt that the optimal exploitation of this abundant resources partly shaped the trajectory of early modern human development and evolution.

8.1.2 Niche-construction

At an ecosystem level, it has been shown that hunter-gatherers can alter environments and ecosystems by their foraging and hunting activities (Terrel *et al.*, 2003). Hunter-gatherers can influence the resource base in their environment, which in turn determine their evolutionary survival and fitness. Through this cycle, early human hunter-gatherers could have unwittingly influenced their evolutionary trajectory: this phenomenon is referred to as niche construction (Smith, 2007, 2009). The effect of niche construction in the relationship between humans and geophytes has been shown in North America (Anderson, 2005) and among the Baka in Africa (Dounias, 2001), where foraging of geophytes increased the abundance of this resource over time (Anderson, 2005) .

Geophyte resources in the GCFR grow as dense resource patches, in a predictable way with predictable returns upon foraging, as shown in this thesis. These resources are surprisingly resilient to foraging and a patch that is foraged intensely can produce similar geophyte biomass available to foragers the following year (Botha, 2019). The shift to foraging for dense and predictable resources has been argued as an evolutionary milestone in humans and was driven by dense resources that are sedentary, this would foster economic reliance on this resource and can lead to the resource being defended and territorialised (Marean, 2016). This theory has been argued for aquatic resources in the South Coast (Marean *et al.*, 2007; Marean, 2016), but geophyte resources could have been territorialised in the same way.

When resource patches are territorialised, it creates an incentive for investment in that resource and could have led to the management of resources. It has been argued that by selectively foraging, starch-rich USOs early humans were managing this important resource (Stewart, 1992; Anderson, 1997, 2005). Furthermore, setting light to veld could have been a primitive yet highly effective form of resource management in the

GCFR, while significantly improving the nutritional quality of USOs and generating other useful by-products.

Despite these apparent benefits of territorialising geophyte resources, there is no archaeological or ethnographic evidence to support the notion of this behaviour. It is possible that the larder of resources in the GCFR was sufficient that territorialisation of resources was never necessary, and that the cost of sedentism outweighed the possible benefits in the GCFR.

The intricacies of niche construction driven by human exploitation of geophyte resources needs to be explored further, as geophyte resources are hypothesised to have been utilised by our hominin ancestors in ways that could have affected human evolution for millions of years (Laden and Wrangham, 2005). The advantages our early human ancestors could have gained by complex processing and foraging behaviour associated with geophyte exploitation would have affected their cognitive development in the same way that has been hypothesised for other technological developments.

8.2 Future work and importance of archaeobotany

The novel methods presented in this thesis to evaluate the energy content and season of collection of geophytes in the archaeological record can be applied to all cormous material available in archival material, and material from future excavations. It is my recommendation that this method should be applied in future research to determine the time of the year within which geophyte resources were in fact targeted. The effective application of this method is subject to the following stipulations being followed to be accurate and trustworthy; When geophyte remains are identified in future sites (or even from archival material), the first process is to identify and quantify the various species contained in different stratigraphic units. The species which occurs most commonly (or for which the largest sample of measurable discs is found) can then be further studied and measured. The comparative measurements for this species should be made of a species which occurs within close proximity of the site and which can be shown to be very similar in growth pattern and size if a direct identification of the species identified in the archaeology is not possible. At least 15 specimens should be unearthed and measured each month from the first emergence of the plants are visible (for most species this will be from April-November). This should then serve as a representative sample of the disc regression patterns from which correlations can be performed with discs measurements from the archaeology to determine the seasonality of geophyte foraging. The correlation of these regression curves needs to be high ($R^2>7.5$) to allow the extrapolations to be trustworthy. Additionally, it is advised that if possible, this method is performed with at least two species with differing phenological patterns to capture the broadest range of data possible: for instance *Babiana* species emerge April-September, while *Moraea* species emerge September-December.

Fully understanding the plant component of hunter-gatherer diets in the Stone Age (and especially the terminal Pleistocene) is one of the persisting areas of modern human evolution that is not well understood.

The plant-based component of early human diets will have had a profound effect on the trajectory of our species development and evolution. The sparse information we have available on the plant foraging behaviour in the Pleistocene is due to many factors, chief amongst which is the relatively poor preservation of botanical remains, which is contrasted by the overwhelming volume of remains and artefact contributed by the animal-based portion of human diets. Shells, bones and stone tools preserve well, and leave clear evidence of how hunting and gathering occurred.

Many edible geophyte species would leave no remains behind in the archaeological record, and most complex processing methods leave almost no trace. Residues resulting from the processing of geophytes are however detectable in some cases, and in the future microscopic techniques will improve even further, which will make the analysis of these microscopic residues even more powerful. Evidence of the emergence of human modernity is reported from important archaeological sites in the South Coast in the MSA (Marean *et al.,* 2007; Marean, 2011; Henshilwood and Marean, 2013). Currently very little information is available on plant use and plant remains from these critical sites. Residue analysis on sediments and artefacts from these sites might be our most direct line of evidence to understand the plant-human relationship during the emergence of modernity in our lineage.

8.3 Synthesis

In this thesis an in-depth assessment of the distribution, seasonality and quality of geophyte resources over the GCFR has been presented, together with the archaeological evidence of the exploitation of this resource across the region. Geophytes could have impacted hunter-gatherer subsistence significantly and likely influenced the trajectory of the evolution of early humans in the GCFR.

Although geophyte resources are widespread across the region there is considerable variation in the geophyte communities between the various study regions, primarily influenced by the variation in rainfall regimes, which influence the seasonality of the geophytes available to foragers. In the West Coast this resource is highly seasonal, available only in the latter half of the calendar year, while in the South Coast it is available during two peaks (autumn and spring) and in the East Coast it can be available year-round, with a peak in summer. This variation would have affected hunter-gatherer mobility in these regions as other resources would have been relied on when geophytes were not available. This variation must be taken into account when interpreting archaeological material in these regions.

What is striking from the results presented in this thesis is the diversity and extended time during the year that geophyte resources could have been available, and of high nutritive quality. In the West Coast and South Coast this resource could be foraged for up to eight months of the year, if lower ranking species were targeted during autumn. In the East Coast this time frame is extended to practically year-round. However, there would be an optimal time frame within which each geophyte species would reach the maximum energy content, size and lowest anti-nutrient content during its growth cycle. It would have been greatly beneficial for a forager to target species during this time frame. If the phenology of each species was understood well by a forager, the optimal nutritional return would have been possible with a high rate of predictability, especially for Iridaceae species. This predictability is predicated on the fact that hunter-gatherers understood the various factors which influence the net-return rate of geophyte foraging. This would have required a high level of botanical, nutritional and technological skills, shared through group learning.

The nutritional composition of the various geophyte species in these landscapes varies considerably, with some taxa ranking high in terms of every parameter which is important to the net return possible from foraging. It was found that these high ranking species are commonly found in the archaeological record. Lower-ranking species which are high in fibre, high in anti-nutrient content and lower in energy content were also commonly found in the archaeological record. This could be due to the increased quality of these geophytes after processing, and the wide time frame that these species are available. Lower ranked species or 'fallback foods' would have been an important food resource during times of scarcity when higher-ranking food items were unavailable. The nutritive quality of these lower ranking species could have been drastically improved by the processing methods tested, with minimal energetic input. When these processing methods are applied to lower ranking USOs they in effect increased the ranking of those USOs, garnering them similar return rates to even the highest ranked species. The prevalence of both highly ranked and lower ranked fallback species in the archaeological record across the region shows that hunter-gatherers certainly targeted both categories of species.

8.3.1 Predicted foraging strategies in the Holocene (under climatic conditions similar to contemporary conditions)

From all of the data collected which describe this dynamic resource, I predict the following foraging strategies would have been pursued in each region during the Holocene (starting from the start of the calendar year):

8.3.1.1 West Coast Strategy

Due to the highly seasonal nature of geophyte resource in the West Coast, and the diverse range of geophyte species which occur in this region, I predict that optimisation of geophyte foraging would have been a highly skilled activity which would take many years of experience to perfect. The knowledge required to forage this resource efficiently in this environment was likely passed on from generation to generation and involved a focused strategy to monitor and plan the seasonal exploitation of the myriad species with variable phenological cycles. There is a high degree of predictability in the cycling of this resource in this region, which would have allowed for the optimisation of this foraging strategy year after year.

In the West Coast, during the start of the year, hunter-gatherers would have had to rely on other resources, except geophytes, on the coastal plain to survive. What is more likely is that hunter-gatherer groups moved to the interior to utilise more abundant resources there during summer. Soon after the first autumn rains fell between March and April, however, hunter-gatherers could have started to forage for early flowering geophytes such as *Babiana* species (which are frequently identified in the archaeological record). Although targeting Iridaceae species earlier in their growing season was shown to yield far lower returns than targeting these species during the peak of their phenology, the archaeological evidence shows that hunter-gatherer likely did forage Iridaceae species earlier in their growing season opportunistically. Other lower quality species would have likely also been targeted as fallback foods (*Dioscorea* or *Pelargonium* species). These species were shown to have low predictability in their nutritive return rates, but could offer massive returns if a plant with a large USO was found. In general this results in a higher risk foraging strategy associated with geophytes that are described as fallback foods, with more unpredictable returns of foraging. Embarking on the gamble to forage geophyte in autumn with uncertain return rates might have seemed more alluring to a hunter-gatherer than the numbers on paper predict following the gruelling summer months.

As the winter rains continued and more and more geophyte species experience the peak in their phenology more geophyte species would have been added to the menu. Other species which might not offer high nutritional returns (such as bulbous Hyacinthaceae and Oxalidaceae species) might have been included in the diet as they could have been foraged opportunistically with minimal energetic input required, and consumed during foraging bouts in the veld.

As spring approached the majority of Iridaceae species would experience the peak in their abundance and nutritional quality. During this time geophyte foraging likely dominated women’s daily activities and likely became the staple part of the diet with a variety of highly ranked species being preferentially targeted, but lower quality species also being foraged. The veracity of geophyte foraging in spring likely continued until early December by which time even the latest flowering Iridaceae species have gone dormant.

During dormancy, even if geophytes are still visible above ground, geophytes were likely not foraged due to the reduction in their palatability (anti-nutrient build-up and loss of carbohydrates). Only geophyte species with perennial storage organs (such as *Pelargonium* or *Dioscorea* species) would have maybe remained edible, even if far more bitter than during active growth.

8.3.1.2 South Coast Strategy

In the South Coast there was likely two seasons of focused geophyte foraging corresponding to the bi-modal rainfall pattern. The array of information required to forage this resource optimally in this region was probably a similar barrier to that in the West Coast and likely required a high level of experience. The summer months were likely less gruelling than in the West Coast, with some a-seasonal rain supplying relief to the veld and plant resources available in the region. In general it seems that the region is more forgiving to hunter-gatherers during summer and a more relaxed foraging strategy could have been applied in this region, while not compromising the efficiency of geophyte foraging.

At the beginning of the year the South Coast is experiencing a relatively short, dry summer and very few geophyte species would be forgeable on the coastal plain (but a few persist). This period would persist for about two months and as early as February one of the bimodal rainfall peaks could rear its head, dousing the landscape in life giving rain. What is so astounding about the geophyte resources in the South Coast, is that the suit of species which flower during the first rainfall peak in this region are highly ranked Iridaceae species. Hunter-gatherers would have had a similar quality and palatability range of species to choose from, than during spring, although in lower absolute abundance. In other words, this region had a lower carrying capacity during the first rainfall peak, but with a similar pallet of choices offered to foragers than in spring. *Freesia, Babiana* and *Sparaxis* species could have been dominant foraging items that could have been foraged during the peak of their nutritional quality during the months of March-June. Other lower ranking species such as *Dioscorea, Pelargonium* and *Cyphia* species would have been targeted in a similar way to the West Coast: opportunistically as a fallback foods.

Winter might have presented a time of slightly lower abundance of high quality geophyte species in their peak of nutritional quality, but some lower ranking species could have been foraged opportunistically.

Spring would have been a similarly focused foraging period as predicted for the West Coast. Throughout the months of August-November various species would experience the peak in their phenology and would have been targeted as they reach this peak. *Watsonia* species were likely a dominant focus during this time, with other higher ranked species (which are less abundant) being targeted whenever encountered (like *Moraea* and *Gladiolus* species).

As most geophyte species enter their dormancy at the end of December, foraging focus would have been shifted to other resources or regions.

8.3.1.3 East Coast

The East Coast region has an almost all year pattern of rainfall and the geophyte resources in the region, as a collective, are similarly a-seasonal. I predict that geophyte foraging would have had to be extremely adaptable in this region, based on the conditions experienced annually which would have impacted geophyte resources. There would certainly still have been optimal time frames within which to target certain species in this region, but that time frame might have shifted based on the prevailing rainfall experienced in each year. The strategy surrounding geophyte foraging was likely a hyper responsive, opportunistic one in this region. This would have made it difficult to optimise geophyte foraging using a single strategy year after year, as it would have needed to be based on judgement of the multiple factors which govern this resource in this region and ongoing observation. Foraging strategy decisions were likely left to the most experienced of foragers who had experienced the greatest number of cycles to base their judgement on.

During the summer months many lower ranking species of *Watsonia* are experiencing the peak in their phenology and likely were a dominant foraging focus and staple in hunter-gatherer diets. Other geophyte species (of any ranking) experience the peak in their phenology during some time throughout the year and hunter-gatherer likely targeted species as they came into this peak and moved on to the next species as geophyte species moved into dormancy.

As in the other regions, spring certainly still is a time of maximum abundance of geophyte species experiencing the peak in their phenology. This would have, despite the general a-seasonality of geophyte resources in the region, been a time of focused foraging, with various geophytes likely comprising the bulk of hunter-gatherer diets. *Moraea*, *Freesia*, *Gladiolus* and *Watsonia s*pecies would have been targeted specifically, but other lower ranking Orchid and bulbous species (such as *Albuca*) could have been foraged opportunistically during foraging bouts.

Lower quality fallback foods such as *Pelargonium* and *Dioscorea* could have been opportunistically targeted year-round.

8.3.2 Geophyte resources in the terminal Pleistocene

Dramatic climatic shifts have been predicted to have shifted the boundaries of the current climatic zones over the GCFR throughout the terminal Pleistocene (Cowling *et al.*, 2020), which would have had an impact on hunter-gatherer behaviour to exploit this resource optimally. During glacial phases the extent of the bimodal rainfall regime in the South Coast region was likely contracted (Engelbrecht *et al.*, 2019). The West Coast and East Coast patterns of geophyte resources would have likely expanded over the current South Coast region during these phases. Human behaviour would have had to adapt accordingly to execute the most efficient foraging strategy possible in those regions. These fluctuations in foraging strategies might be visible in the archaeological record from the South Coast and could be identified in new archaeological sites, or existing sites re-examined with a focus on archaeobotanical analysis.

8.3.3 Conclusion

In this thesis the most comprehensive set of information to date of factors which impact geophyte resources quality and availability over the GCFR landscape is presented. This information makes predictions possible of when and how geophytes could be foraged optimally across the region. The archaeological evidence analysed corresponds well with this information and in general the bulk of geophyte foraging seems to have been focused on optimising the returns possible from geophyte foraging, per region. However, there were instances found where archaeological evidence suggests that not every single decision reached by hunter-gatherers was governed by optimizing return rates. It was found that some geophyte species were targeted earlier in their growing cycle when their nutritional return possible are not optimal, and the corm size was miniscule. Additionally, some geophytes which do not require additional processing were processed, which was an additional input of energy which was not necessarily recouped. These examples show us that other factors important to hunter-gatherers dictated choices in some cases. In autumn geophytes might have been opportunistically dug up just for variety in diet, even if they could not, at that stage, contribute significantly to the overall diet. Similarly, cooking of already nutritious corms could have been motivated by the improved taste, even if it had zero impact on the energetic returns presented.

In general geophytes are a widespread resource (temporally and spatially) across the region and it seems likely that hunter-gatherers would have attempted some sort of exploitation of this resource no matter where they found themselves. Although the individual foraging strategies likely varied across the region, the exploitation of this resource throughout the terminal Pleistocene and Holocene likely shaped a large part of the daily behaviour of hunter-gatherers.

Geophyte resources on the coastal plain of the GCFR are dense and diverse. This diversity encompasses variation in the quality of the nutrients contained in the USOs and the optimum time throughout the year they would be most profitable to harvest. Geophytes could have been available during a large portion of the year depending on the rainfall regime of the specific region. The archaeological evidence shows just how widespread and complex geophyte foraging and processing was during the Holocene, although there is a relative lack of evidence of this complexity during the critical periods of the emergence of human modernity in the Pleistocene.

Geophytes could have supplied the dense and predictable resource cache which made the coastal plains of the GCFR a reliable environment for human evolution, despite climatic and vegetational shifts. Additionally, geophytes could have had many other function in tool production, medicinal and ritualistic uses. The availability of this resource throughout the Pleistocene could have supplied an energy rich, predictable food resource that could have altered our behaviour and cognitive development to optimally exploit this resource in a complex and dynamic way.

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Appendix A. Numerical values assigned to generate phenological curves of species.

Numerical values generated for curves

To present the phenological cycling of the geophyte species identified in Chapter 3, the published dates of their phenological cycles are tabulated below. Dates of timing of phenological events were generated from the available literature on the phenophases of geophyte species (Goldblatt, 1986, 1989, 1997; Van der Walt and Vorster, 1988; Perry, 1994; Goldblatt and Manning, 1998, 2007; Linder and Kurzweil, 1999; Procheş *et al.*, 2006; Manning *et al.*, 2010; Manning and Goldblatt, 2012). The dates for following phenophases were recorded: emergence, leaving, flowering, seeding, senescence and dormancy. The below numbers are what numerical value attributed to plant throughout their phenological cycle for each calendar month to generate the pheno curve of each species.

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,"","","","","","","","","","","","","","","","","","","","","","","","","a","e","w","s"

Albuca canadensis,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","Bulb","s","s","s"

Albuca flaccida,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","Bulb","s","s","s"

Albuca fragrans,"0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","Bulb","","","s"

Babiana ambigua,"0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","1.62","1.44","1.26","1.08","0.9","0.72","0.54","0.36","0.18","0","0","0","0","0","Corm","a","s/a","s/a"

Babiana hirsuta,"0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0.9","0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0.9","0","Corm","","s",""

Babiana nana,"0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","Corm","","s","s"

Babiana odorata,"0","0","0","0.5","0.875","1.25","1.625","2","1.3","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","Corm","","s",""

Babiana patersoniae,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","Corm","s","",""

Babiana patula,"0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","0","Corm","","","s"
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Babiana ringens,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Corm","","","s"

Babiana tubiflora,"0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","0","Corm","","s","s"

Babiana tubulosa,"0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","Corm","","s",""

Chasmanthe aethiopica,"0","0","0.5","1.25","2","1.8","1.2","0.6","0","0","0","0","0","0","0.5","1.25","2","1.8","1.2","0.6","0","0","0","0","Corm","s","s","s"

Chasmanthe floribunda,"0","0","0","0","0.5","1","1.5","2","1.5","0.9","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","Corm","","s",""

Conicosia pugioniformis,"0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","Rhizome","","s",""

Cyanella hyacinthoides,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","Corm","","s",""

Cyanella lutea,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","Corm","","s","s"

Cyperus congestus,"1.57142857142857","1.78571428571429","2","1.8","0.9","0","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","1.57142857142857","1.78571428571429","2","1.8","0.9","0","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","Rhizome","","","s/a"

Cyperus esculentus,"0","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","Rhizome","s","s",""

Cyperus usitatus,"1.57142857142857","1.78571428571429","2","1.8","0.9","0","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","1.57142857142857","1.78571428571429","2","1.8","0.9","0","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","Rhizome","","","a"

Cyphia digitata,"0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","0","Tuber","","s","s"

Cyphia phyteuma,"0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","Tuber","","","s"

Cyphia volubilis,"0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","Tuber","","s","" Empodium gloriosum,"1.14285714285714","1.35714285714286","1.57142857142857","1.78571428571429","2","1.8","0","0","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","1.57142857142857","1.78571428571429","2","1.8","0","0","0","0.5","0.714285714285714","0.928571428571429","Corm","s","","s"

Empodium veratrifolium,"0","0","0","0.5","2","1.8","0.9","0","0","0","0","0","0","0","0","0.5","2","1.8","0.9","0","0","0","0","0","Corm","","s",""

Eriospermum brevipes,"1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","Tuber","a","","s"

Eriospermum breviscapum,"1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","Tuber","a","",""

Eriospermum lanceifolium,"0","0.5","2","1.8","1.35","0.9","0.45","0","0","0","0","0","0","0.5","2","1.8","1.35","0.9","0.45","0","0","0","0","0","Tuber","","s","s"

Ferraria crispa,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Corm","","s","s"

Ferraria densepunctulata,"0","0","0","0.5","1.25","2","1.8","1.35","0.9","0.45","0","0","0","0","0","0.5","1.25","2","1.8","1.35","0.9","0.45","0","0","Corm","","s",""

Ferraria uncinata,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Corm","","s",""

Freesia caryophyllacea,"0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","Corm","","","s"

Freesia fergusoniae,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","Corm","","","s"

Freesia grandiflora,"0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","Corm","s","",""

Freesia leichtlinii,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Corm","","","s"

Geissorhiza aspera,"0","0","0","0","0","0","1","2","1.3","0","0","0","0","0","0","0","0","0","0.5","2","1.8","0","0","0","Corm","","s","s"

Geissorhiza bracteata,"0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","Corm","s","",""

Gladiolus alatus,"0","0","0","0","0","0.5","1.25","2","1.8","0.9","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0.9","0","0","Corm","","s","" Gladiolus carinatus,"0","0","0","0","0","0","0.5","2","1.3","0.9","0","0","0","0","0","0","0","0","0.5","2","1.8","0.9","0","0","Corm","","s",""

Gladiolus cunonius,"0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","Corm","s","","s"

Gladiolus floribundus,"0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","Corm","","","s"

Gladiolus involutus,"0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","Corm","","","s"

Gladiolus liliaceus,"0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","Corm","s","",""

Gladiolus miniatus,"0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0","0","0","0","0","Corm","s","a",""

Gladiolus rogersii,"0","0","0","0","0","0","0.5","1.25","2","1.8","0.9","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0.9","0","Corm","","","s"

Gladiolus stellatus,"0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","Corm","","","s"

Gladiolus tristis,"0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","0","0","Corm","","s",""

Gladiolus wilsonii,"0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","Corm","s","",""

Grielum grandiflorum,"0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","Rhizome","","s",""

Grielum humifusum,"0","0","0","0","0.5","1","1.5","2","1.8","1.2","0.6","0","0","0","0","0","0.5","1","1.5","2","1.8","1.2","0.6","0","Rhizome","","s",""

Hesperantha falcata,"0","0","0","0","0","0.5","1.25","2","1.8","0.9","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0.9","0","0","Corm","s","s",""

Hesperantha radiata,"0","0","0","0","0","0","0.5","1.25","2","1.8","0.9","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0.9","0","Corm","","","s"

Holothrix burchellii,"0","0","0","0","0","0","0.5","1.25","2","1.8","1.2","0.6","0","0","0","0","0","0","0","0","0","0","0","0","Tuber","s","s",""

Holothrix mundii,"0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","0","0","Tuber","s","s",""

Holothrix villosa,"0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","0","Tuber","","s","s"

Hypoxis villosa,"2","1.8","1.2","0.6","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","1.2","0.6","0","0","0","0.5","0.8","1.1","1.4","1.7","Corm","","","s"

Ixia flexuosa,"0","0","0","0","0","0","0.5","2","1.8","0","0","0","0","0","0","0","0","0","0.5","2","1.8","0","0","0","Corm","","","s"

Ixia micrandra,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Corm","s","","s"

Ixia orientalis,"0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","Corm","s","",""

Ixia paniculata,"0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0","0","0","0","0","Corm","","s","s"

Lachenalia aloides,"0","0","0","0.5","1","1.5","2","1.8","1.2","0.6","0","0","0","0","0","0.5","1","1.5","2","1.8","1.2","0.6","0","0","Bulb","","s",""

Lachenalia bulbifera,"0","0.5","0.8","1.1","1.4","1.7","2","1.8","1.2","0.6","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","1.2","0.6","0","0","Bulb","","","s"

Lachenalia mutabilis,"0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","Bulb","","s",""

Lachenalia nervosa,"0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","Bulb","","","s"

Lachenalia pustulata,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","Bulb","","s","s"

Lachenalia rubida,"0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","Bulb","s","s","s"

Lapeirousia pyramidalis,"0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","Corm","","","s"

Ledebouria ovalifolia,"1.5","1.75","2","1.8","0.9","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0.9","0","0","0","0.5","0.75","1","1.25","Bulb","s","","s"

Ledebouria revoluta,"0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","0","Bulb","s/a","s/a",""

Massonia depressa,"0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","Bulb","s","","s"

Massonia echinata,"0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","Bulb","","","s"

Melasphaerula graminea,"0","0","0","0","0.5","1","1.5","2","1.3","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","Corm","","s","" Moraea australis,"0","0","0","0","0","0","0.5","1","1.3","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","Corm","s","",""

Moraea fugax,"0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","Corm","","s","s"

Moraea inconspicua,"0","0","0","0","0.5","1","1.5","2","1.3","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","Corm","","","s"

Moraea lewisiae,"0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0","0","0","0","0","Corm","","s","s"

Moraea setifolia,"0","0","0","0","0.5","1","1.5","2","1.3","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","Corm","","","s"

Moraea tricuspidata,"0","0","0","0","0","0","0.5","1.25","2","1.3","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","Corm","s","",""

Moraea tripetala,"0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0","0","0","0","0","Corm","s","s","s"

Oxalis hirta,"0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","Bulb","","s","s"

Oxalis obtusa,"0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0.9","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0.9","0","0","Bulb","","s","s"

Oxalis pendulifolia,"0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","0.5","1","1.5","2","1.8","0","0","0","0","0","0","Bulb","a","","a"

Oxalis pes-caprae,"0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0.9","0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0.9","0","0","Bulb","s","s","s"

Oxalis polyphylla,"0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","Bulb","s","","s"

Oxalis versicolor,"0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","1.2","0.6","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","1.2","0.6","0","Bulb","","s",""

Pelargonium carneum,"1.75","2","1.8","0","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","0","0","0","0.5","0.75","1","1.25","1.5","Rhizome","a","","a"

Pelargonium lobatum,"0","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","1.57142857142857","1.78571428571429","2","1.8","0","0","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","1.57142857142857","1.78571428571429","2","1.8","0","Rhizome","","s","s"

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Pelargonium rapaceum,"0","0","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","0","0","0","0","0","0","0","0","0","Rhizome","s","s/a","s/a"

Pelargonium triste,"0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","0","Rhizome","s","s","s"

Pterygodium orobanchoides,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Tuber","","s",""

Pterygodium volucris,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Tuber","","s",""

Romulea rosea,"0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0.9","0","0","Corm","","s","s"

Satyrium acuminatum,"0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0","0","0","0","0","0","Tuber","","s",""

Satyrium carneum,"0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","Tuber","","","s"

Satyrium corrifolium,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Tuber","","","s"

Satyrium longicolle,"0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0","0","0","0","0","Tuber","s","s",""

Satyrium membranaceum,"0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","Tuber","s","",""

Satyrium odorum,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","Tuber","","s",""

Satyrium parviflorum,"2","1.3","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","Tuber","","","s"

Satyrium princeps,"0","0","0","0","0","0","0","0","0.5","2","1.8","0","0","0","0","0","0","0","0","0","0.5","2","1.8","0","Tuber","s","",""

Satyrium stenopetalum,"0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0","0","0","0","0","0","Tuber","s","s",""

Sparaxis bulbifera,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","Corm","","s",""

Sparaxis villosa,"0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","Corm","","s",""

Spiloxene flaccida,"0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","Corm","","","s"
```

Trachyandra chlamydophylla,"0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","0","0","0","0","0.5","0.8","1.1","1.4","1.7","2","1.8","0","0","Tuber","","s",""

Trachyandra ciliata,"0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","Tuber","s","s","s"

Trachyandra divaricata,"0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","Tuber","s","s","s"

Trachyandra falcata,"0","0","0","0.5","0.875","1.25","1.625","2","1.8","1.2","0.6","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","1.2","0.6","0","Tuber","","s","s"

Trachyandra muricata,"0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","0","0","0","0","0.5","0.875","1.25","1.625","2","1.8","0","0","Tuber","s","",""

Trachyandra revoluta,"0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","Tuber","","","s"

Tritonia crocata,"0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","Corm","","","s"

Tritonia squalida,"0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","Corm","","","s"

Tulbaghia alliacea,"0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","Bulb","s","","s"

Typha capensis,"2","1.8","1.2","0.6","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","1.57142857142857","1.78571428571429","2","1.8","1.2","0.6","0","0.5","0.714285714285714","0.928571428571429","1.14285714285714","1.35714285714286","1.57142857142857","1.78571428571429","Rhizome","","s","s"

Wachendorfia paniculata,"0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0.9","0","Tuber","","s","s"

Wachendorfia thyrsiflora,"0","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","0","0","0","0","0","0","0","0","0","0","0","Tuber","","s",""

Watsonia aletroides,"0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","0","0","0","0","0","0","0","0.5","1.25","2","1.8","0","Corm","","","s"

Watsonia coccinea,"0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","Corm","","","s"

Watsonia fergusoniae,"0","0.5","0.6875","0.875","1.0625","1.25","1.4375","1.625","1.8125","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","0","0","Corm","s","s",""

```
Watsonia fourcadei,"0","0","0","0.5","0.6875","0.875","1.0625","1.25","1.4375","1.625","1.8125","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","Corm","s/a","s/a",""

Watsonia galpinii,"1.625","1.8125","2","1.8","0.9","0","0.5","0.6875","0.875","1.0625","1.25","1.4375","1.625","1.8125","2","1.8","0.9","0","0.5","0.6875","0.875","1.0625","1.25","1.4375","Corm","","","s/a"

Watsonia knysnana,"0","0","0.5","0.666666666666667","0.833333333333333","1","1.16666666666667","1.33333333333333","1.5","1.66666666666667","1.83333333333333","2","1.8","0","0","0","0","0","0","0","0","0","0","0","Corm","","s/a",""

Watsonia laccata,"0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","0","0","0","0","0","0","0.5","1","1.5","2","1.8","0","Corm","","","s"

Watsonia meriana,"0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","Corm","","s","s"

Watsonia pillansii,"0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0","Corm","s","",""

Watsonia wilmaniae,"0","0","0.5","0.666666666666667","0.833333333333333","1","1.16666666666667","1.33333333333333","1.5","1.66666666666667","1.83333333333333","2","1.8","0","0","0","0","0","0","0","0","0","0","0","Corm","","s",""

Zantedeschia aethiopica,"0","0","0","0.5","0.75","1","1.25","1.5","1.75","2","1.8","0.9","0","0","0","0","0","0","0","0","0","0","0","0","Tuber","","s/a",""
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Appendix B: Geophyte species identified in excavated assemblages, frequency and distribution of sites where they were identified

B.1. Geophyte species identified during the archaeobotanical analysis

Species identified in the archaeological record are described below and compared to the geophyte species in the comparative collection of modern geophyte samples. Material identified in the archaeology is compared to species in the comparative collection that share similar features. The purpose of this comparison was to identify species from the archaeological record to genus level (but in some cases it was possible to identify to species level).

Species are listed by family and all species belonging to that family are discussed under the heading of the family name. General features of each genus are described following the available literature on taxonomic features of the underground storage organs of plants. The conspectus of The Cape Flora of South Africa (Goldblatt and Manning, 2000) and subsequent revisions (Manning and Goldblatt, 2012; Snijman, 2013), were used as a primary reference, together with additional references of specific families or genera where available (see end of appendix for full reference list). Geophyte species identified in the archaeological record are described, with key features highlighted, with accompanying microscopic and macroscopic photographs of material found in the archaeological record in comparison to the material in the comparative collection, for each species.

Amaryllidaceae

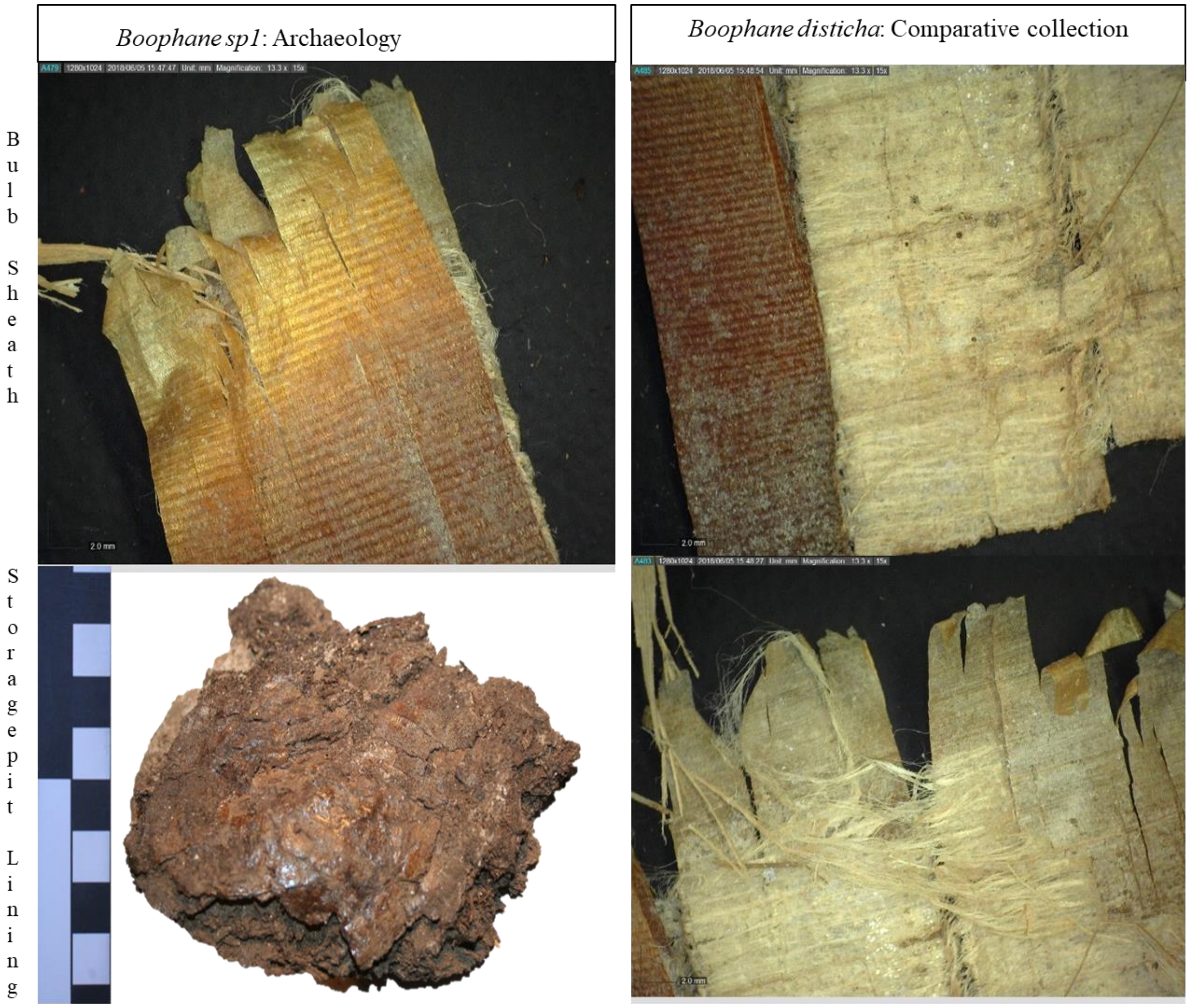
This is a large family of bulbous geophytes, most of which are poisonous (Watt and Breyer-Brandwijk, 1962). The bulbs are perennial and continue to grow through the lifetime of the plant (Duncan, 2016). Descriptions of Amaryllidaceae species are according to Duncan, 2016.

Boophane

This genus consists of two species with bulbs that are narrowly to broadly ovoid, 40-270mm in diameter, solitary or offset-forming, slightly strongly exposed, covered with many layers of papery, light grey or brown outer tunics, roots fleshy (Duncan, 2016).

*Boophane sp 1 (*comparable species *Boophane disticha)*

Large bulbs, densely covered by greyish parchment-like tunics (Duncan, 2016).. Tunics in many multiple layers, the outer surface is dark brown and has concentric, horizontal raised lines (Duncan, 2016).. The inner surface is pale in colour, soft and fibrous with fibres like cotton that are arranged horizontally. Mostly found in storage pit linings, tunics packed together on top of one another, with distinctive outer and inner surface present.



Brunsvigia

Genus with twenty plus species in southern Africa, all of which are bulbous geophyte that are solitary, or rarely offset forming, narrowly to broadly ovoid or globose bulb (Manning and Goldblatt, 2012). Vary in size from 15-200mm in diameter, mostly subterranean or partially to strongly exposed, sometimes produced into a thick neck (Duncan, 2016). Bulb, usually covered with tan, brittle tunic. Outer bulb scales leathery or papery, light to deep brown (Duncan, 2016)

*Brunsvigia sp 1 (*comparable species *Brunsvigia orientalis)*

Bulb ovoid, 120-200 mm in diameter, produced into a short neck 25-30mm long. Bulb sheath occur in multiple layers that are dense, membranous, light to dark brown (Duncan, 2016). The sheath outer surface has characteristic dark vertical striation and the inner surface of the sheath consist of soft, pale, cotton like strands that are arranged vertically (Duncan, 2016). *Brunsvigia sp 1* was identified at archaeological sites in the western part of the GCFR.

	Brunsvigia sp1: Archaeology	*Brunsvigia orientalis*: Comparative collection
Bulb Sheath		

*Brunsvigia sp 2 (*comparative species *Brunsvigia gregaria)*

Bulb ovoid, 40-70mm in diameter, solitary, neck absent or up to 10mm long, subterranean; outer tunic cartilaginous, dark brown, inner tunics membranous, light brown (Duncan, 2016). The outer layers of the bulb sheaths are dark orangy brown and are hard and brittle (Manning and Goldblatt, 2012). All layers have vertical striations. Inner layers have cotton like fibres that are tightly arranged vertically. This species was identified at archaeological sites in the Eastern part of the GCFR.

Cyperaceae (*Cyperus*)

In this family, only one genus was identified: *Cyperus*, which is a large genus consisting of almost 700 species wolrdwide (Manning and Goldblatt, 2012). A number of species in this genus are geophytic, these species usually have a perennial tuber or horizontal rhizomes with outer sheaths that are yellow-brown, and leathery (Manning and Goldblatt, 2012).

Cyperus sp 1 (comparable species *Cyperus congestus)*

Rhizome yellow with cataphylls that are papery and leathery (Manning and Goldblatt, 2012). Where they attach to the stem, they have a distinctive toothed pattern.

Cyperus sp 1: Archaeology

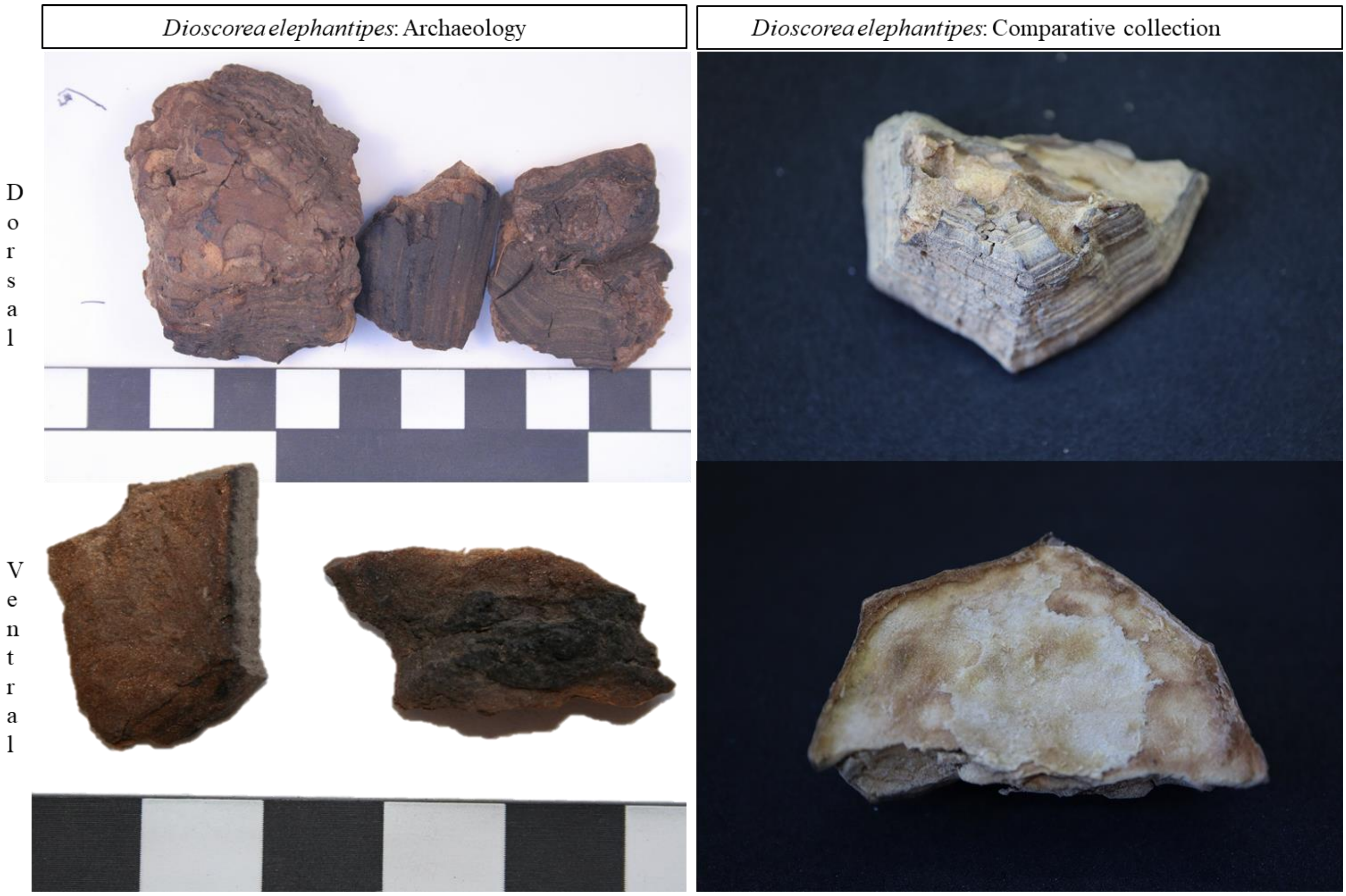
Cyperus congestus: Comparative collection

Dioscoreaceae (*Dioscorea*)

In this family, only one genus was identified: *Dioscorea,* which is a large genus of 400 species worldwide (Manning and Goldblatt, 2012). *Dioscorea* species have very large tubers, often sitting above the soil surface, exposed (Manning and Goldblatt, 2012). Tubers are covered in a distinctive arrangement of “armour plates” (Manning and Goldblatt, 2012).

Dioscorea elephantipes (comparable species *Dioscorea elephantipes)*

Surface covered in armour-plating which is reminiscent of tortoise shell scales (Manning and Goldblatt, 2012). Scales continue to grow seasonally as the tuber grows, which gives the plates distinctive concentric lines on the outer edges. The underside of the scales which attach to the tuber are soft textured, similar to cardboard.



Geraniaceae (*Pelargonium*)

In this family, only one genus was identified: *Pelargonium*. Pelargonium is a large genys of 250 species worldwide, many species in the *Pelargonium* genus are geophytic with tuberous or rhizomatous USOs (Van der Walt and Vorster, 1988). These USOs can vary considerably. They can be horizontal, large thickened roots with thick bark like covering, or tubers that are globose with leathery smooth coverings (Van der Walt and Vorster, 1988).

*Pelargonium rapaceum (*comparable species *Pelargonium rapaceum)*

Partially subterranean, acaulescent, cylindrical tuber that can be as large as a fist (Van der Walt and Vorster, 1988). The tuber is covered in a number of smooth, leathery, dark brown scales, with red brown edges. Diagnostic line of brown hairs towards the neck of the tuber where it meets the stem, which consist of a crown of dead bases of old petioles (Van der Walt and Vorster, 1988).

Pelargonium rapaceum: Archaeology

Pelargonium rapaceum: Comparative collection

Tuber covering

<u>Pelargonium sp 1 (</u><u>comparable species *Pelargonium triste)*</u>

Large, irregularly shaped rhizome covered in brown cracked bark, with red hue on edges (Van der Walt and Vorster, 1988).

Rhizome Bark

Pelargonium sp 1: Archaeology

Pelargonium triste: Comparative collection

Hyacinthaceae

Bulbous plants with membranous outer tunics or scales, often with glandular cells on surface of membranes (Manning and Goldblatt, 2012).

Albuca

Genus of 60 plus species worldwide, with globose, large bulbs, subterranean or partially exposed, the tunics sometimes only loosely overlapping, rarely fragmenting into triangular segments (Manning and Goldblatt, 2012).

*Albuca sp 1 (*comparable species *Albuca flaccida)*

Bulb tunics membranous, slightly fibrous above towards stem (Manning and Goldblatt, 2012).. Fibres vertically arranged, with irregular horizontal striations (Manning and Goldblatt, 2012).. Membranous windows between fibres dotted with white, raised spots (glandular cells) (Manning and Goldblatt, 2012).

Albuca sp 1: Archaeology

Albuca flaccida: Comparable collection

Lachenalia

Genus of 120 plus species in southern Africa, with pear-shaped, globose, or flattened bulbs, often forming bulblets at the base, usually with pale membranous outer tunics, sometimes the outer tunics papery and dark brown or black and then often forming a fibrous neck around the base of the stem (Manning and Goldblatt, 2012).

Lachenalia sp 1 (comparable species *Lachenalia pustulata)*

Outer tunics dark brown and papery, while inner tunics are membranous (almost see through) with frequent glandular spots toward the bottom of the pear-shaped bulbs (Manning and Goldblatt, 2012).


Lachenalia sp 1: Archaeology


Lachenalia pustulata: Comparative collection

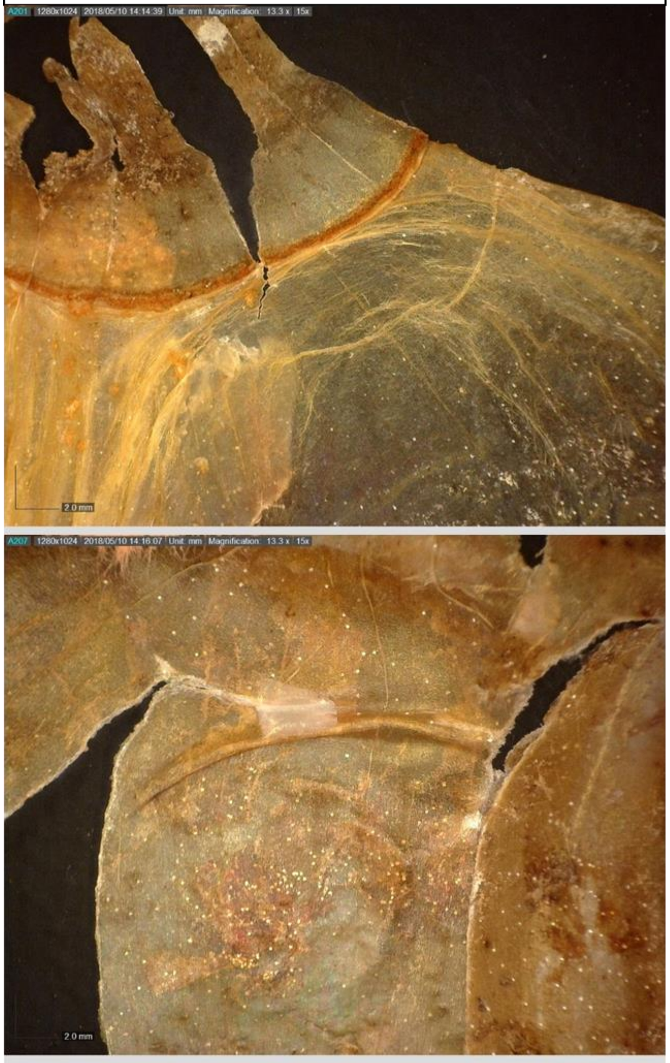
Massonia

A small genus of nine species from southern Africa that have globose bulbs with pale, papery or thinly leathery outer tunics (Manning, Goldblatt and Snijman, 2002). Bulb extended as a short neck towards stem where the tunics are lightly barred above with tubular membranous cataphyll (Manning, Goldblatt and Snijman, 2002).

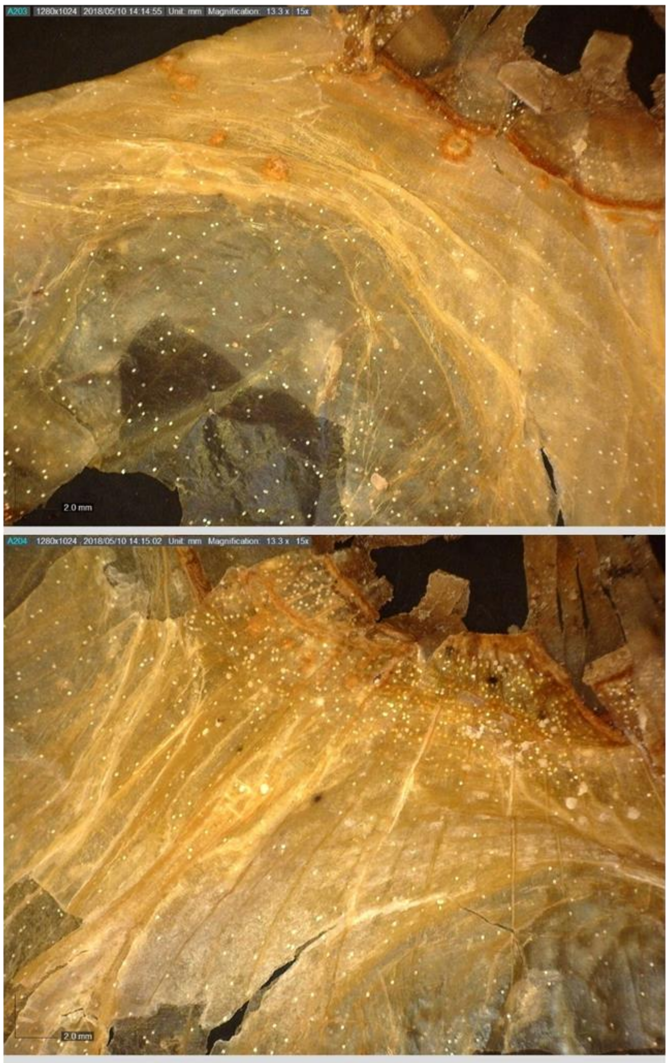
*Massonia sp 1* (comparable species *Massonia echinata*)

Thin membranous tunics, with dark barring above towards neck of bulb with regular granular spots (Manning and Goldblatt, 2012).

Massonia sp 1: Archaeology



Massonia echinata: Comparative collection



Hypoxidaceae (*Hypoxis*)

Hypoxis was the only genus identified in this family, which consists of 80 species worldwide (Manning and Goldblatt, 2012). Usually slow-growing vertical rhizome/corm, often large, sub-globose to elongated, often with yellow flesh (Manning and Goldblatt, 2012). Roots on USO are stout, contractile, present mostly in upper half of the USO (in mature plants) and to bottom of USO (in young plants) (Manning and Goldblatt, 2012).

*Hypoxis sp 1 (*comparable species *Hypoxis angustifolia)*

Corms often with a brown papery neck. Corm varies in shape depending on age of the plant (Manning and Goldblatt, 2012). When young the corm is small, elongated and globose with contractile roots at the bottom of the corm (Manning and Goldblatt, 2012). When plant matures the corm becomes more globose and roots are usually present mostly in upper half of corm (Manning and Goldblatt, 2012).

Iridaceae

Very large family with multiple genera identified in archaeological record. USOs are usually corms (in Cape species), typically with fibrous outer covering in multiple layers (Manning and Goldblatt, 2012). Corms are replaced seasonally and multiple seasons of growth can be visible in the form of discs (Manning, Goldblatt and Snijman, 2002). Corm tunics are very distinctive between genera and generally can be distinguished from one another with ease. Description following monographs for each genus (where available) and The conspectus of the Cape Flora of South Africa (Manning and Goldblatt, 2012).

Babiana

Genus of 92 species worldwide, which are small to medium-sized, with a globose corm rooting from below and basal in origin (Goldblatt and Manning, 2007). Corm tunics are characteristic of the genus in their pale, brown colour and tough, closely fibrous texture (Goldblatt and Manning, 2007). They are usually deep-seated, in many species buried over 10cm below ground level, and the tunics are usually extended upward, persisting as a collar around the underground part of the stem (Goldblatt and Manning, 2007). Genus is characterised by distinctive corms tunics with the vertical members thickened below and resembling claws, clubs or wishbones (see Figure C1.1) (Goldblatt and Manning, 2007).

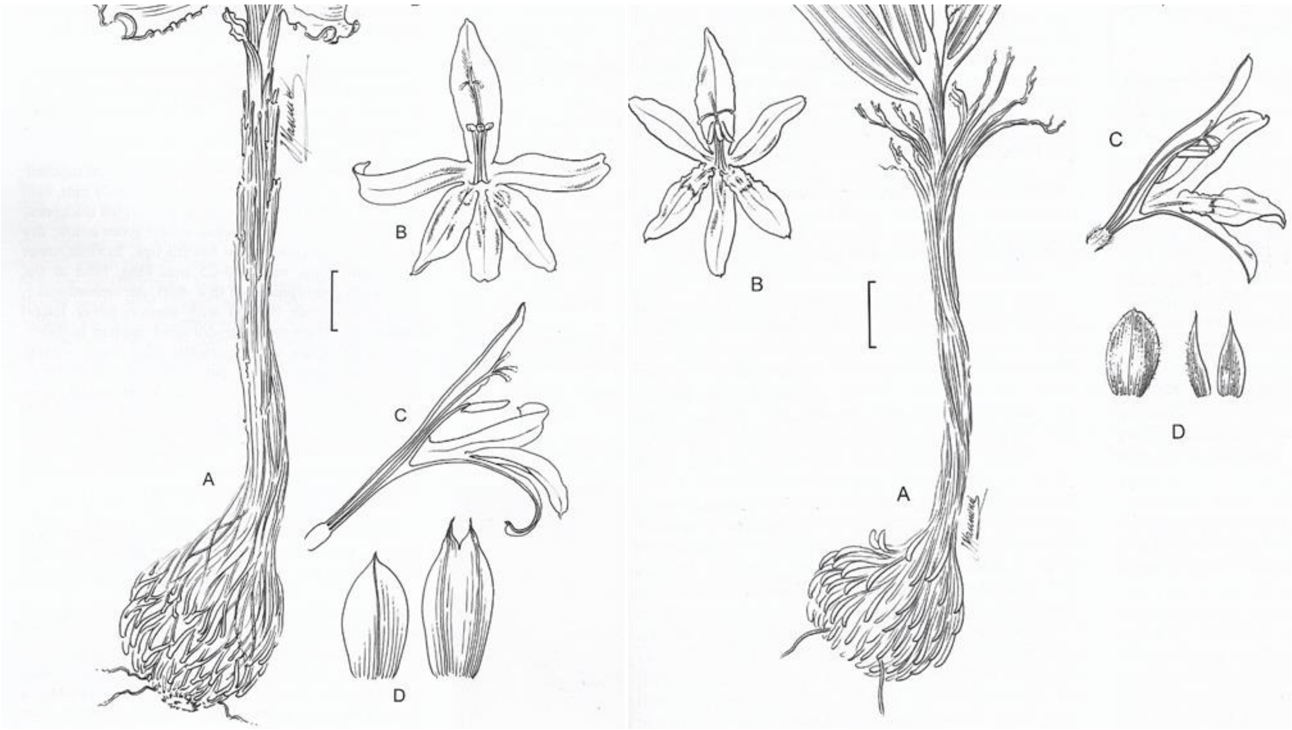


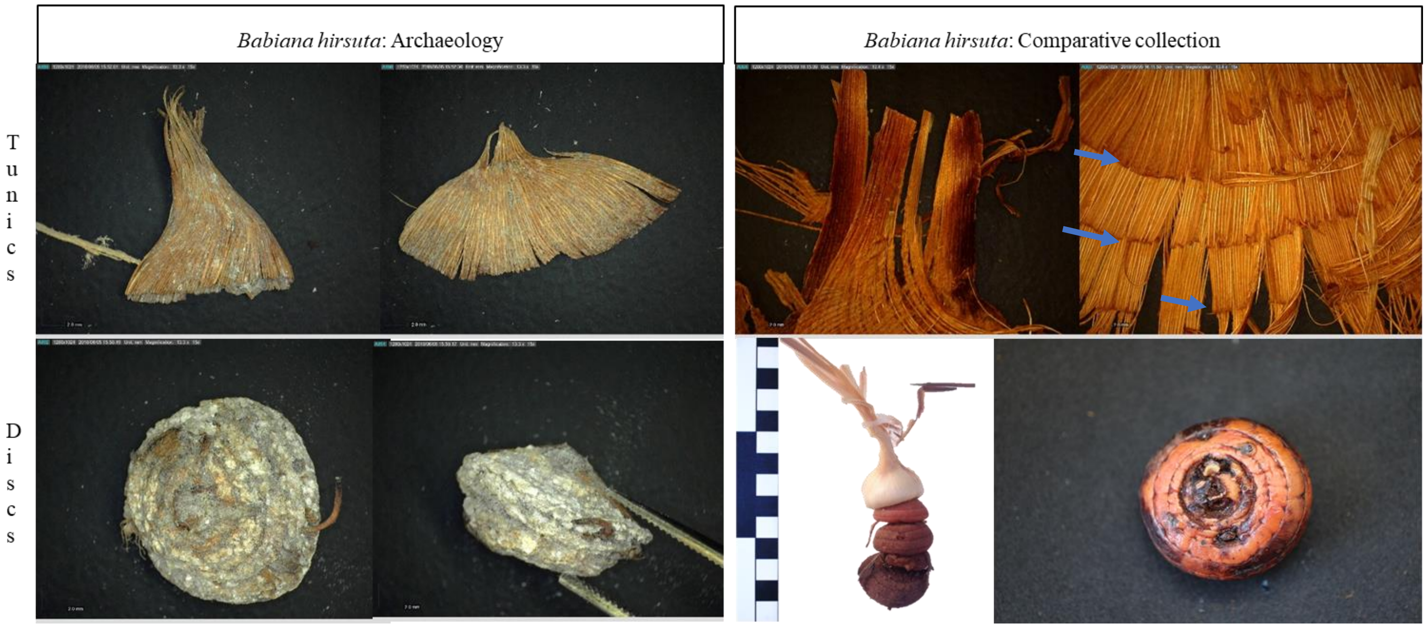
Figure B1.1 Left <u>Babiana cinnamomea</u> with distinct thickening of vertical members below resembling a wishbone; Right <u>Babiana toximontana</u> with distinctive thickening of vertical members below resembling clubs. Figure adapted from Goldblatt and Manning, 2007. Pg 30 and 73

Babiana hirsuta (comparable species *Babiana hirsuta*)

Globose corm rooting from below and basal in origin (Goldblatt and Manning, 2007).

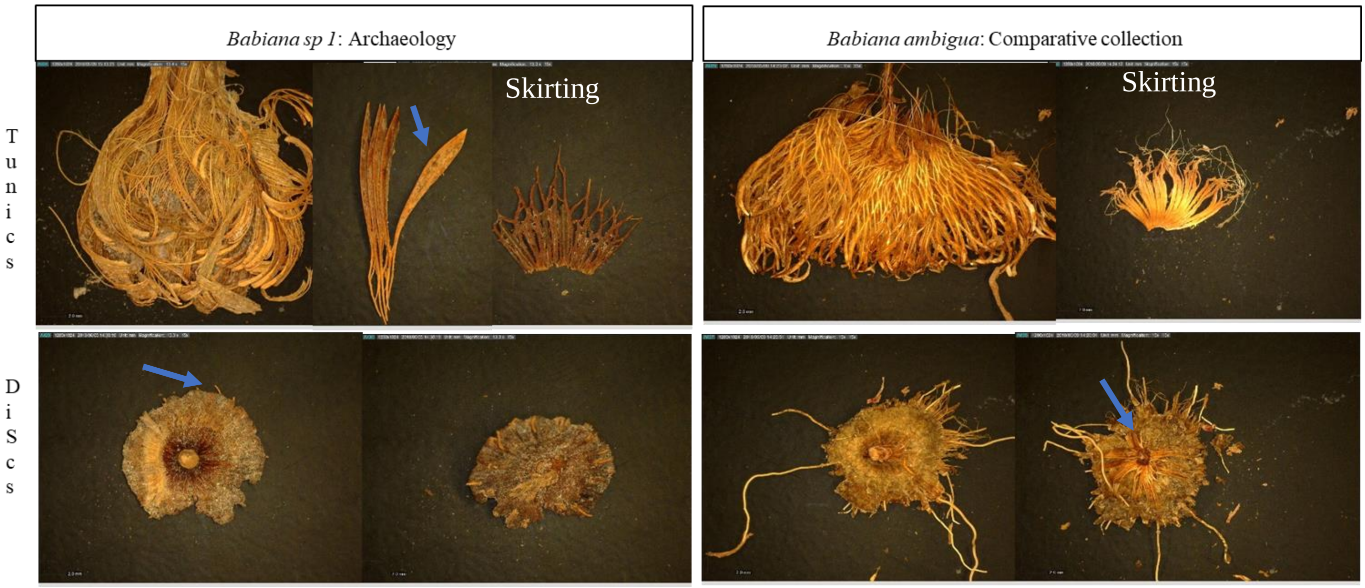
Due to the restricted distribution of this species (Dune Cordon from Velddrif to Elands Bay (Manning and Goldblatt, 2012)) and the distinctive tunics and discs it was possible to identify to species level. New corms are produced from the base of the flowering stem, older corms are not resorbed and accumulate below the current corm (Pseudocorms) (Goldblatt and Manning, 2007).

Husks are fibrous with very neat, tightly packed vertical members (Goldblatt and Manning, 2007). Layers of tunics overlay one another to form distinctive concentric, overlapping layers (Goldblatt and Manning, 2007).



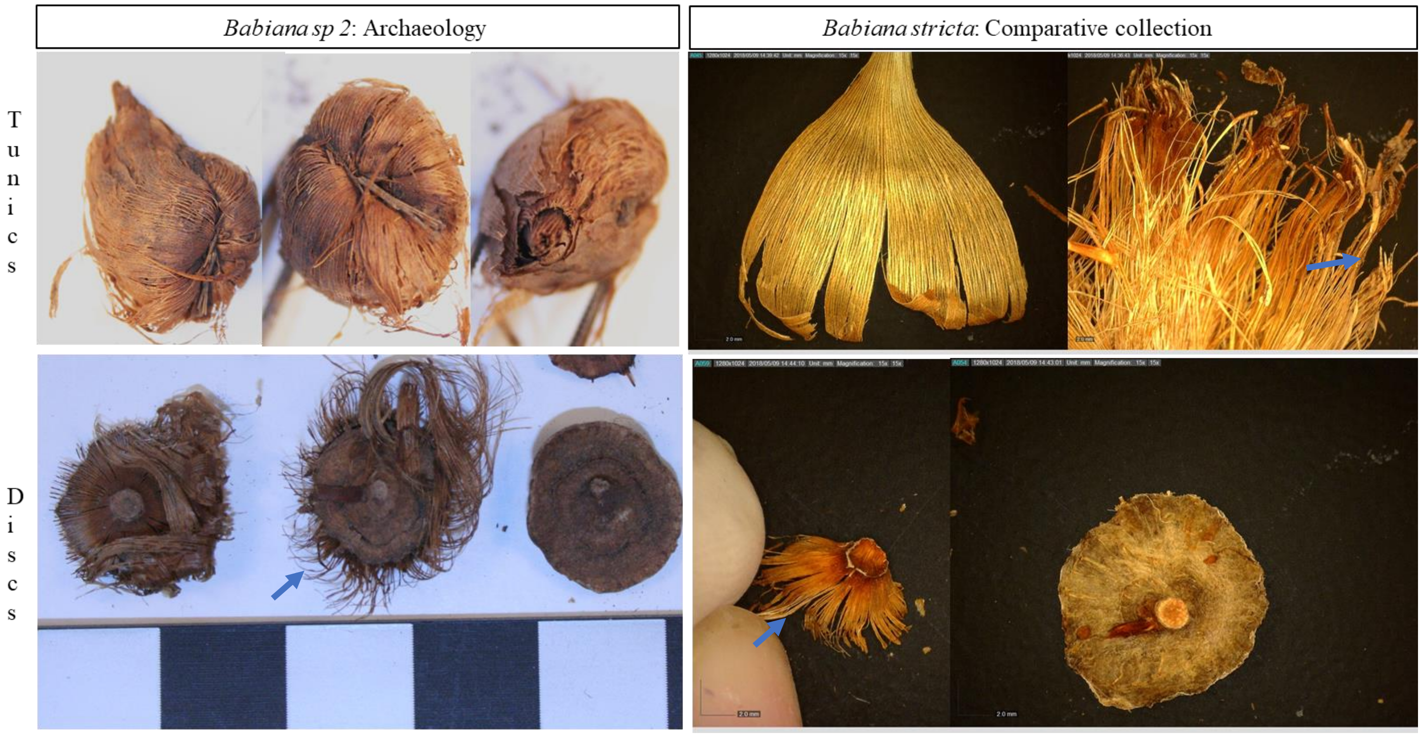
*Babiana sp 1 (*comparable species *Babiana ambigua)*

Globose corm rooting from below and basal in origin (Goldblatt and Manning, 2007). Stem underground or reaching shortly above ground level without neck of fibres, suberect or inclined, sparsely hairy (Goldblatt and Manning, 2007). Corm tunics netted with distinctive clubbed vertical members toward bottom (Goldblatt and Manning, 2007). Discs often have contractile roots (or evidence of where contractile roots were attached) and often have distinctive “skirting” or netting around the centre of the disc, which is found at the bottom of the corm.



*Babiana sp 2 (*comparable species *Babiana stricta)*

Globose corm rooting from below and basal in origin (Goldblatt and Manning, 2007). Corm tunics are typical of the genus in their pale, brown colour and tough, closely fibrous texture (Goldblatt and Manning, 2007). Tunics are fairly coarsely fibrous with vertical members with no thickening toward the bottom, which is distinctive from most *Babiana* species which have a pronounced thickening toward the bottom of the vertical members (Goldblatt and Manning, 2007). Furthermore, tunics are not netted as in other species, but striated, which is particularly evident in the skirting attached to discs.

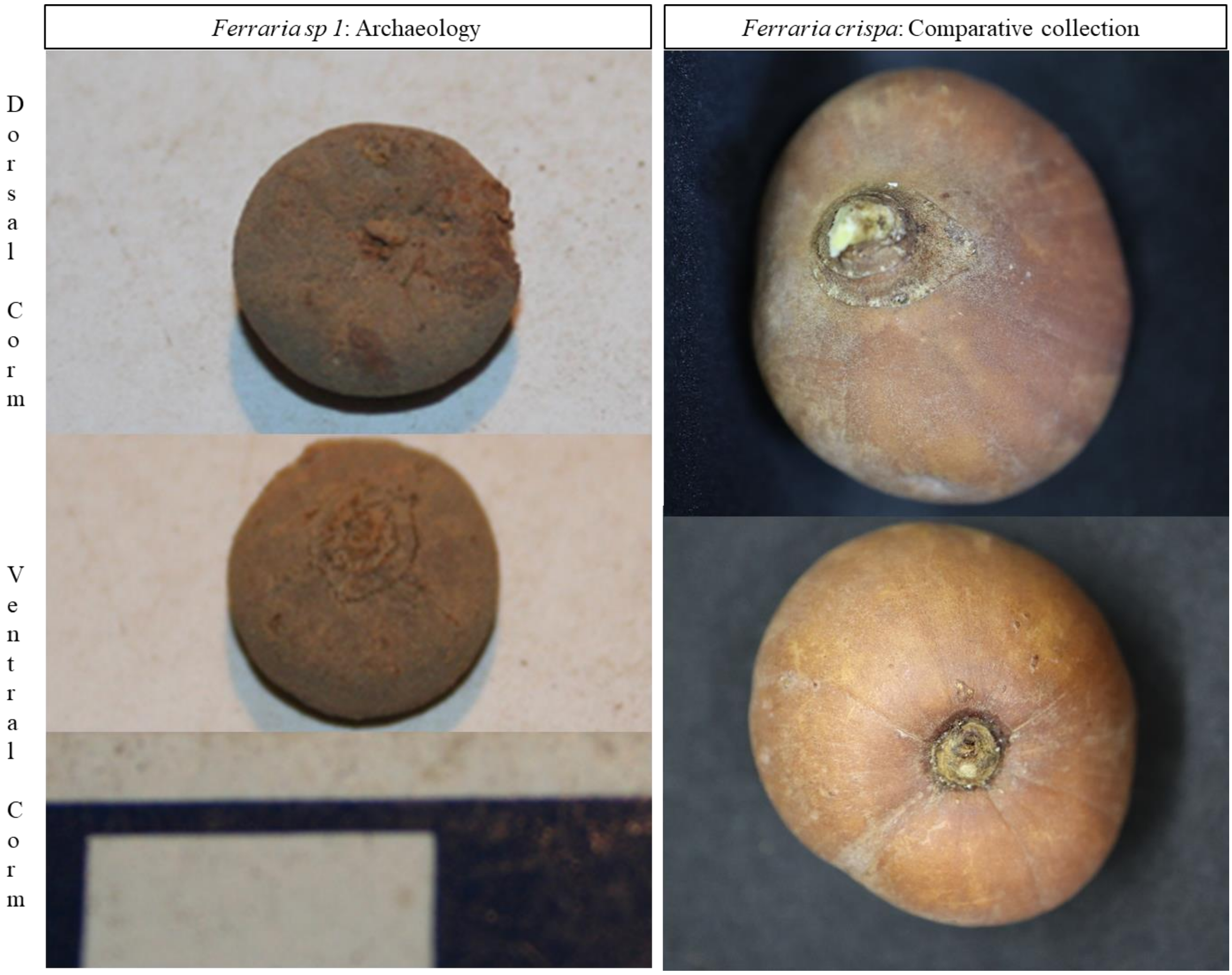


Ferraria

A smaller genus of eighteen species with corms that persist, are depressed-globose, apically rooting (Manning and Goldblatt, 2012). New corms are produced from the base of the flowering stem, older corms are not resorbed and accumulating below the current corm (Pseudocorms), the tunics are membranous soon disintegrating (Manning and Goldblatt, 2012).

<u>*Ferraria sp 1 (*comparable species *Ferraria crispa)*</u>

Smooth depressed-globose corm, that is dark brown (Manning and Goldblatt, 2012).



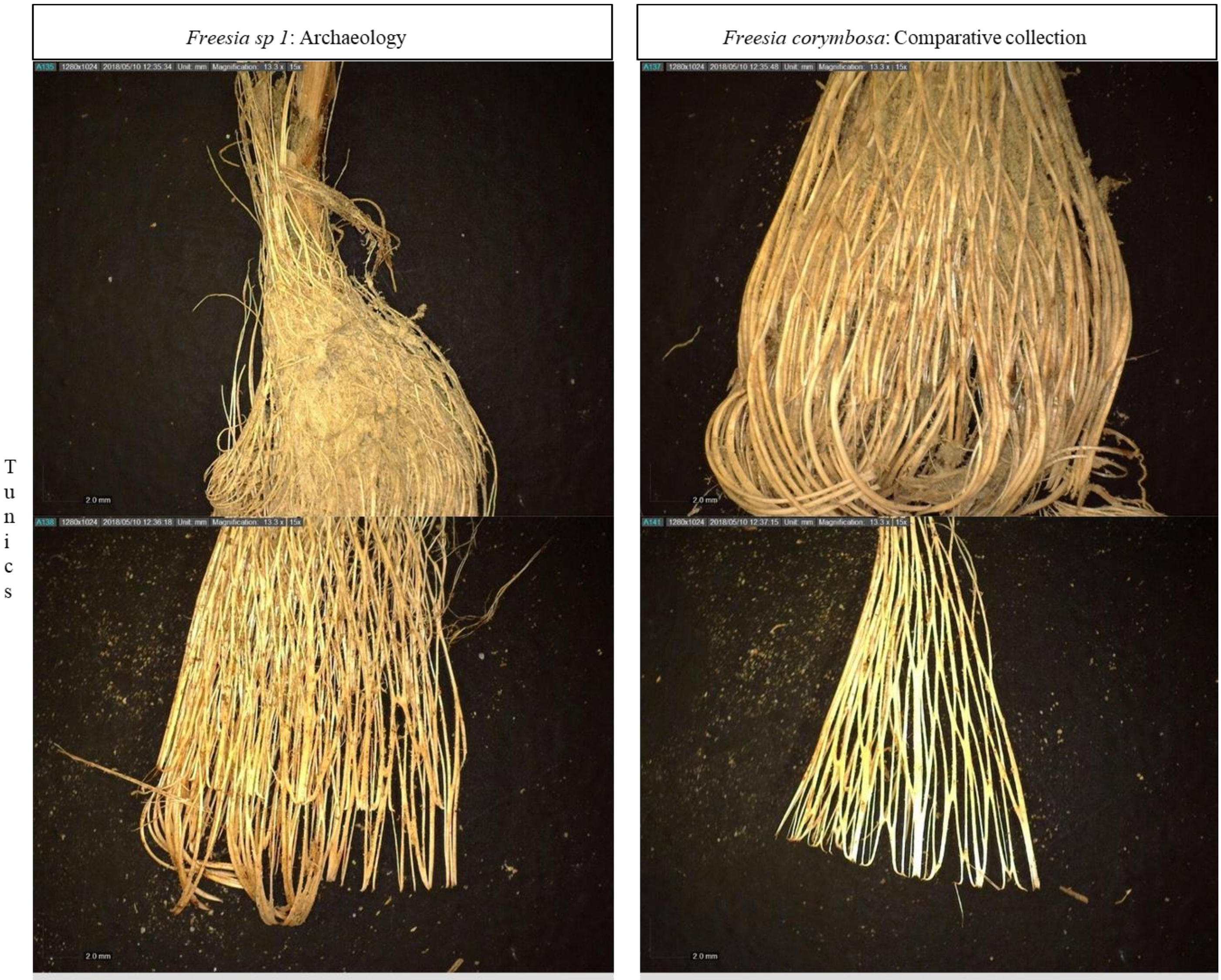
Freesia

A smaller genus of fifteen species with corms that are distinguished from other iris genera by the mostly conical (rather than globose) corms (Manning *et al.*, 2010).. Corms are small to moderate-sized, producing an underground corm that is replaced annually (Manning *et al.*, 2010). The outer tunics are characteristically pale in colour, and finely to somewhat coarsely fibrous, forming a regularly netted lattice as they decay (Manning *et al.*, 2010). Discs are not well developed and often only one diminutive corm is attached to the new seasons corm growth (personal observation).

Figure B1.2 Freesia corymbosa exhibiting the typical conical corm shape and fine, soft, light coloured, papery corm tunics. Note only one small fragment at bottom of corm which is the "disc" of previous seasons growth. Figure adapted from Manning & Goldblatt, 2010. Plate 6

*Freesia sp 1 (*comparable species *Freesia corymbosa)*

Corm conical with light brown tunics, of medium to coarse textured fibres, sometimes forming a neck (Manning *et al.*, 2010). Tunics consists of multiple layers that are finely fibrous with wide netted pattern (Manning *et al.*, 2010).. Tunics are conical shape to form around corm.



Gladiolus

A large genus of 250 species worldwide that have corms that are globose to depressed-globose, vary considerably in size from 4cm to 1cm in diameter, most species have tunics that are coriaceous to firmly papery (Goldblatt and Manning, 1998). Tunics are commonly brown and decay with age into irregularly broken fragments that sometimes become more of less fibrous (Goldblatt and Manning, 1998).

There is considerable variation in the tunics of different sub-sections of the genus (Goldblatt and Manning, 1998). Several species have tunics that are less woody and sometimes even quite soft-textured, so that on decaying the become softly fibrous, as in *Gladiolus carinatus*. (Goldblatt and Manning, 1998). Other species have membranous, extremely soft-textured tunics quite unlike those of most related species (Goldblatt and Manning, 1998). All this variation and identifying features are very well documented in the excellent monograph for the genus (Goldblatt and Manning, 1998). Discs are not well developed (similar to Freesia) and often only one diminutive disc is attached to the new seasons corm growth (personal observation).

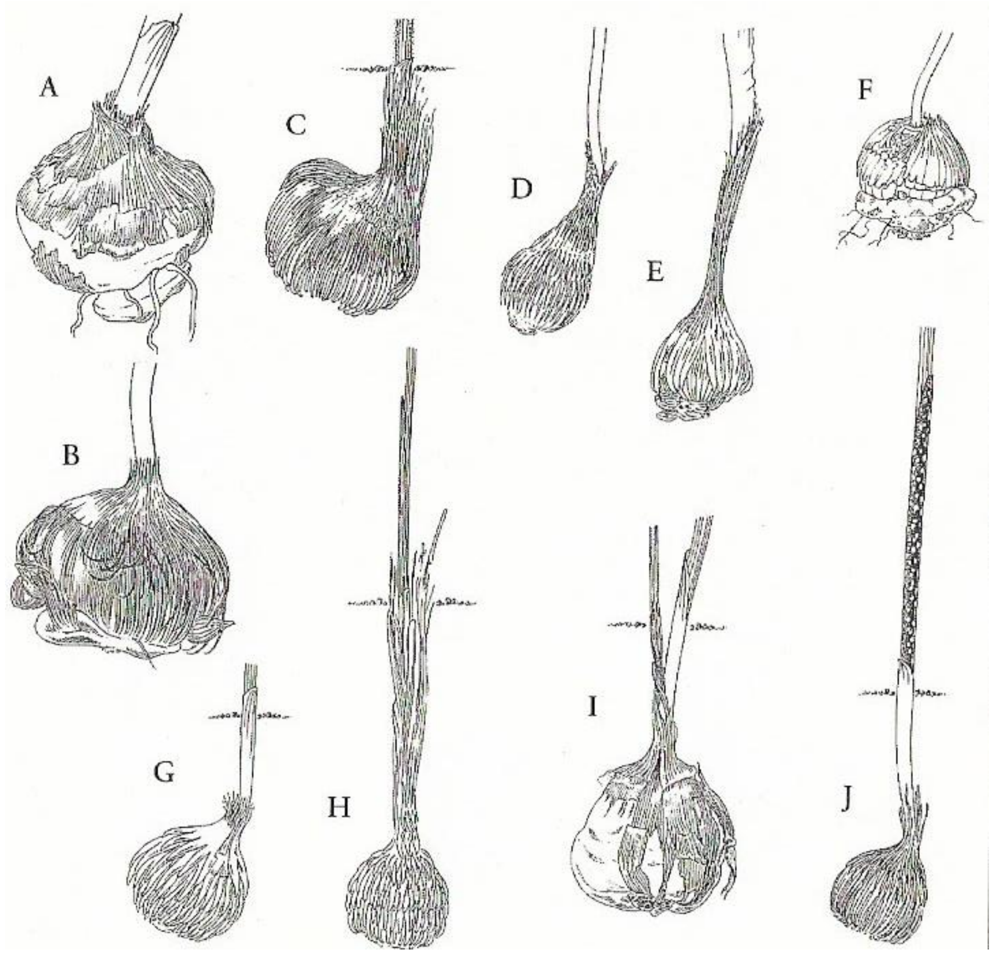


Figure B1.3 Corms of southern African Gladioli. Soft, papery corm tunics of G. aurantiacus (a) and G. dolomiticus (b). The firm-papery tunics of e.g. G hirsutus (c), decay with age into flat fibres. G. leptosiphon (d) with wiry tunics; G. scullyi (e) has coarse, woody tunics; G. arcautus (f) has softly membranous tunics. Hard, woody corm tunics are characteristic of section Homoglossum, e.g., in G. gracilis (g) and G. inflatus (h), the latter with the stem base enclosed in a thick, fibrous neck, in G. jonquilliodorus (i) the corm is moist and fleshy and the tunics consist of softly membranous layers; and in G. carinatus (j), which has characteristic mottled cataphylls, the fairly soft tunics decay into soft s. Adapted from Goldblatt & Manning, 1998 ,pg 16.

*Gladiolus sp 1 (*comparable species *Gladiolus carinatus)*

Corm globose, 12-18mm in diameter (Goldblatt and Manning, 1998). Tunics are woody in texture, and consist of concentric layers which fragment below, or completely with age into flat, vertical segments (Goldblatt and Manning, 1998). These may truncate basally or acute, and then are often thickened into claw-like ridges (Goldblatt and Manning, 1998). Cataphylls pale and membranous, the upper reaching 3-9 cm above the ground (Goldblatt and Manning, 1998).

Gladiolus sp 1: Archaeology

Gladiolus carinatus: Comparative collection

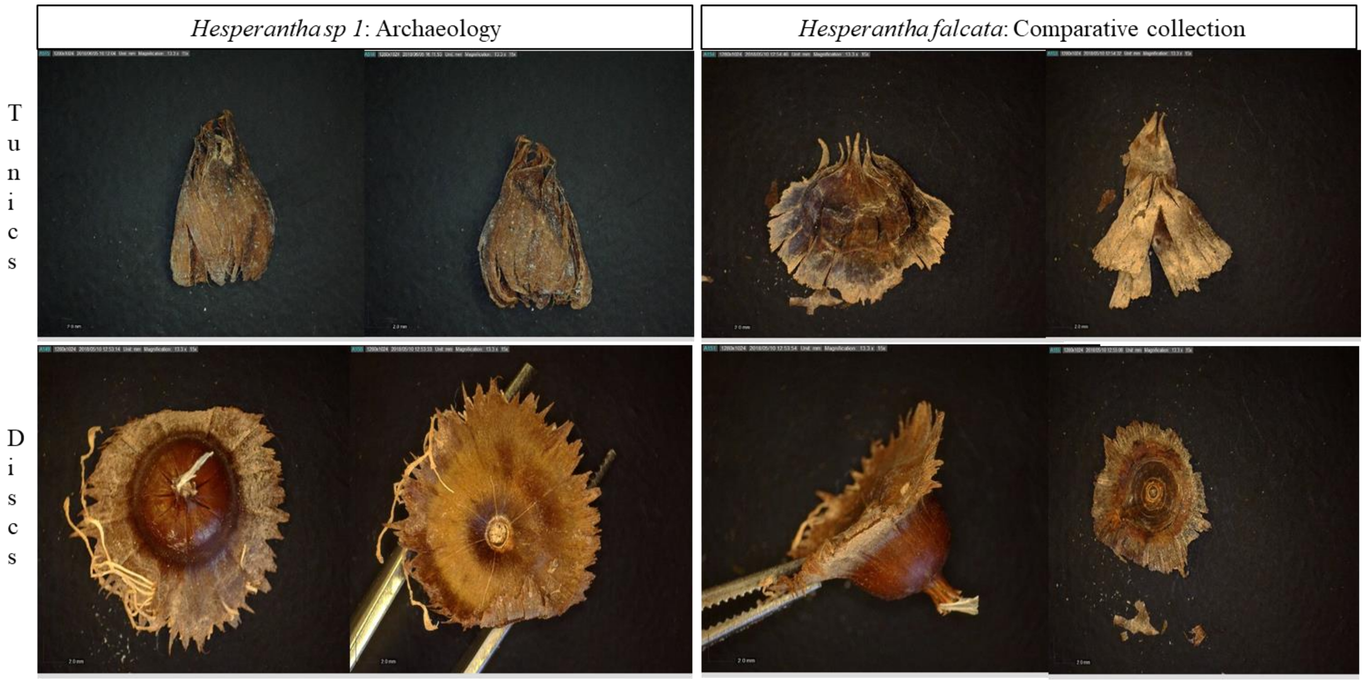
Tunics

Hesperantha

Genus of 82 species of cormous plants, that are globose to ovoid or bel-shaped with a flat base, sometimes with a basal ridge from which the roots emerge, basal in origin (Manning and Goldblatt, 2012). The tunics are woody or rarely firm-papery, concentric or overlapping and notched below (Manning and Goldblatt, 2012).

Hesperantha sp1 (comparable species *Hesperantha falcata)*

Corms bell-shaped with a flat base, tunics smooth and woody (Manning and Goldblatt, 2012). Concentric overlapping and then notched below (Manning and Goldblatt, 2012).



Lapeirousia

Genus of 42 species with bell shaped corms with a flat base, rooting from the edges, axillary in origin, the tunics of densely compacted fibres or woody (Manning and Goldblatt, 2012).

*Lapeirousia sp 1 (*comparable species *Lapeirousia fabricii)*

Corm tunics brown, with thickened, toothed to spiny margins (Manning and Goldblatt, 2012)..

Moraea

Genus of 220 species worldwide, plants with globose corms (Goldblatt, 1986). The tunics form a thick layer with characteristic appearance depending on the species, which has been very well described in a monograph of the genus (Goldblatt, 1986). The corm itself is renewed annually during the growing season and the old corm tissue is reabsorbed by the plant (Goldblatt, 1986). Discs can be well developed in some species and multiple seasons growth can be present below the new seasons corm (personal observation).

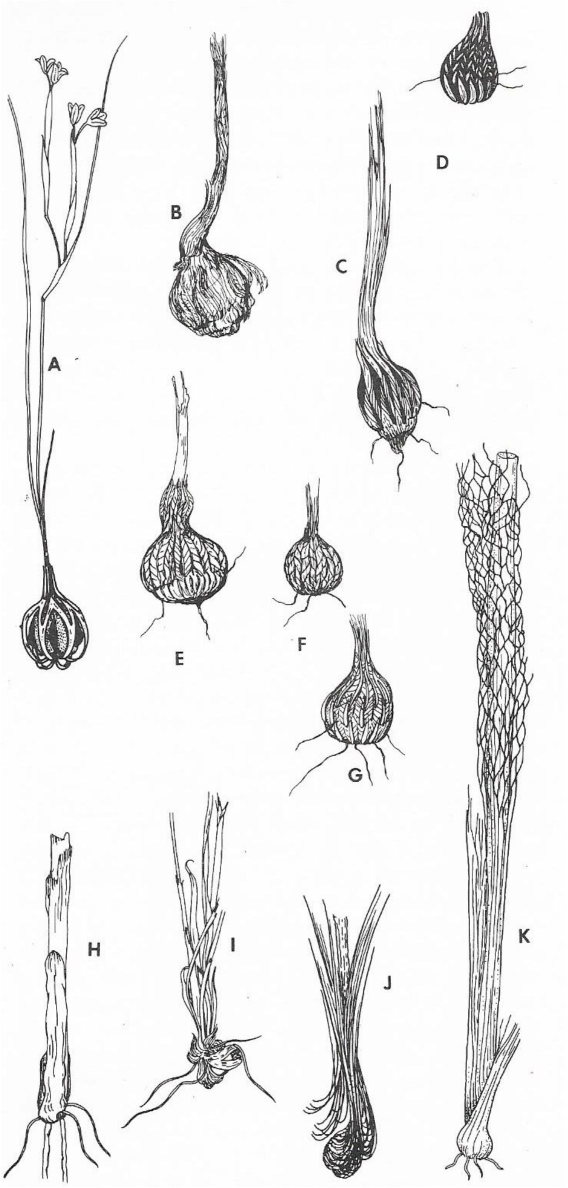


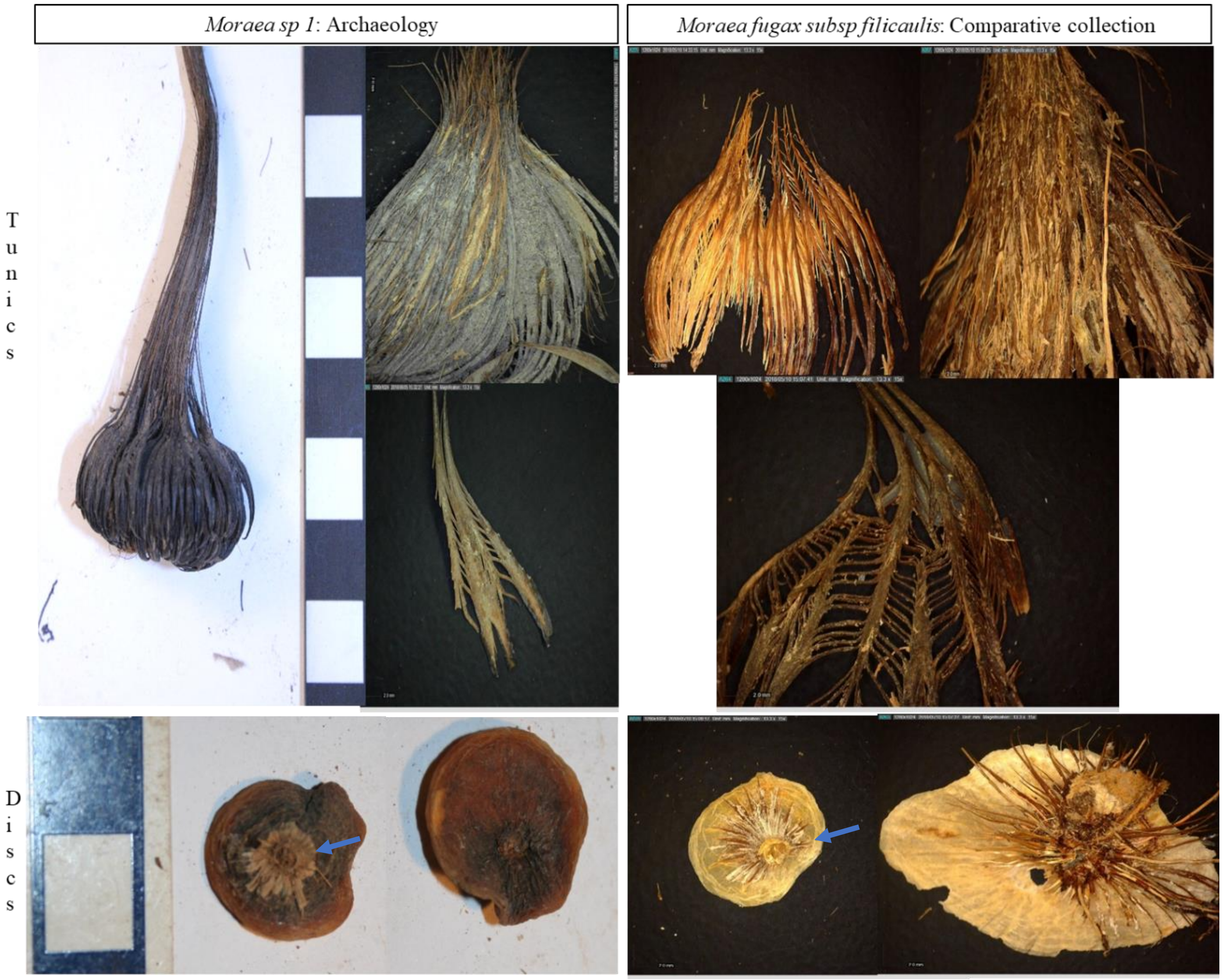
Figure B1.4 The variation in corms and cataphylls in Moraea. A. M lugubris; B. M. saxicola; C. M. margaretae; D. M. crispa; E. M. fugax; F. M. barkerae; G. M. lurida; H. M. graminicola; I. M. muddii; J. M. galpinii; K. M. alticola. Image adapted from Goldblatt, 1986 ,pg 9

*Moraea fugax (*comparable species *Moraea fugax* subsp. *fugax)*

Corm 3-5cm in diameter; tunics usually pale, rarely dark, of fine to medium fibres (Goldblatt, 1986).. Accumulated to form thick layer, with characteristic herringbone patterns visible on inner layers which are intact and woody (Goldblatt, 1986).. Cataphylls usually two, membranous, pale, becoming dry and brownish and often broken (Goldblatt, 1986). Discs are pale, smooth, oval and usually very thin.

*Moraea sp 1 (*comparable species *Moraea fugax* subsp. *filicaulis)*

Corms 7-16 mm in diameter (Goldblatt, 1986). Tunics consists of dark fibres, cataphylls brown and fibrous, forming a neck around the stem base, wiry reticulated fibres, accumulating to form thick layer and extending upward in a neck (Goldblatt, 1986). Discs often more irregularly shaped, but mostly oval (Goldblatt, 1986). Vary in colour, but often have a crown of adventitious roots sprouting from centre.



Moraea sp 2 (comparable species *Moraea lugubris)*

Corm small, 1-1.5 cm in diameter but enclosed in large basket-like tunics consisting of course open reticulum (Goldblatt, 1986). Cataphylls membranous and pale or brownish with tunics of coarse, often woody, claw like fibres (Goldblatt, 1986). No discs were found that could be associated with the tunics.

*Moraea sp 3 (*comparable species *Moraea polystachya)*

Corm 5cm in diameter, covered with black, coarsely reticulate to clawed tunics (Goldblatt, 1986). Cataphylls membranous, often disintegrating when dry (Goldblatt, 1986). *Moraea sp 3* was found in archaeological sites in the eastern part of GCFR. Discs similar diameter to corm (quite large in comparison to other species).

	Moraea sp 3: Archaeology	*Moraea polystachya*: Comparative collection
Tunics		
Discs		

Sparaxis

Smaller genus of sixteen species with corms of axial type in which the base of the stem thickens during development to become the new season’s corm (Goldblatt and Manning, 2013). The corm itself consists of several internodes with the apical shoot developed adjacent to the flowering stem (Goldblatt and Manning, 2013). Roots are produced form no fixed position on the lower portion of the sub-globose to obconic corm body (Goldblatt and Manning, 2013). Corm tunics are of two types. The more common in the genus consists of fine, relatively soft, netted fibres and the other of relatively coarse fibres with the vertical members thickened below and resembling claws (Goldblatt and Manning, 2013). The latter type of tunic is restricted to a small group of allied species *variegata, villosa, caryophyllaceae and meterlerkampiae* (Goldblatt and Manning, 2013).

Figure B1.5 Sparaxis variegata with distinctive wiry netting tunics with thickened vertical member resembling a claw. Figure adapted from Goldblatt & Manning, 2013, pg 59

Sparaxis sp 1 (comparable species *Sparaxis variegata*)

Corm 12-22mm diameter, tunics of coarse, hard fibres, with thickened vertical strands in lower half (Goldblatt and Manning, 2013).

Tunics

Sparaxis sp 1: Archaeology

Sparaxis variegata: Comparative collection

Tritonia

Genus of thirty species with globose corms, rooting from the base, the tunics are pale, composed of fine to coarse fibres (Manning and Goldblatt, 2012).

*Tritonia sp 1 (*comparable species *Tritonia crocata)*

Corm depressed-globose with tunics of fairly fine fibres, that are openly netted (Goldblatt and Manning, 2013).

	Tritonia sp 1: Archaeology	*Tritonia crocata*: Comparative collection
Tunics		

Watsonia

Genus of 52 species that are robust and tall, plants with depressed globose, large corms (5-15 cm) (Goldblatt, 1989). Tunics vary considerably between species and can be used to differentiate between the species, with the aid of the monograph of the genus that captures the distinctions in the underground parts of the different species (Goldblatt, 1989). Some species have papery tunics, some coarsely fibrous that are reticulated and wiry (Goldblatt, 1989).. Almost all species have multiple layers of husks and multiple discs usually present below corms (Goldblatt, 1989).

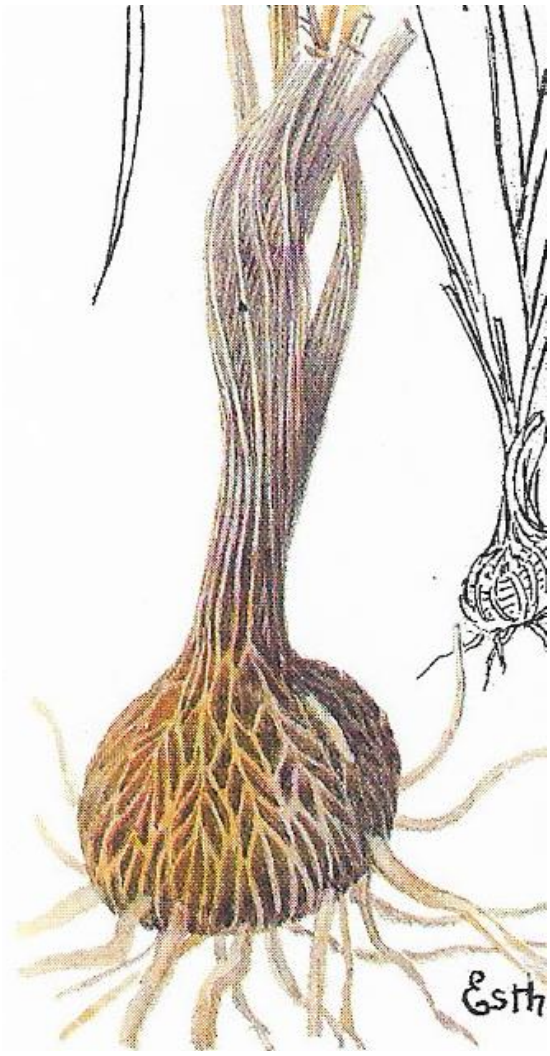


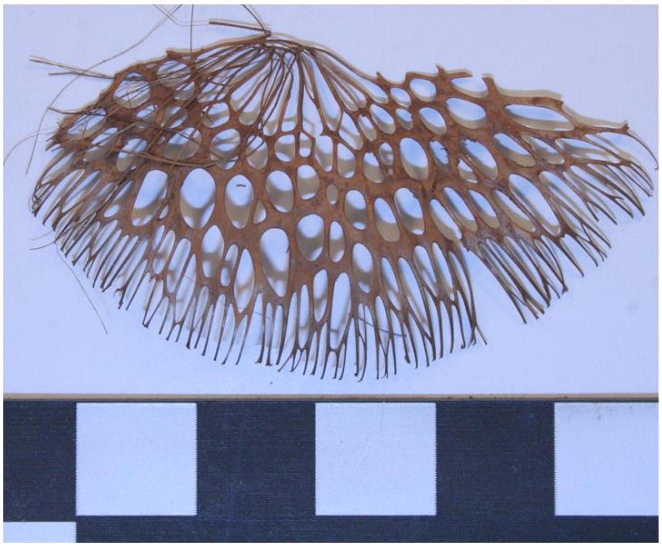
Figure B1.6 Watsonia meriana var. bulbifera corm showing distinctive reticulated, thick tunics. Figure adapted from Goldblatt, 1989. Plate 18

Watsonia sp 1 (comparable species *Watsonia meriana var. bulbifera*)

Corms depressed globose, 3-4.5cm in diameter, tunics grey-brown, coarsely reticulate (Goldblatt, 1989). Windows between netting are diamond shaped. Discs are dark red, to nearly black, with adventitious roots on the outer edge of irregular shaped disc. Scurting connected to dorsal side of disc is smooth, papery and orangy-brown.

*Watsonia sp 2 (*comparable species *Watsonia stokoei)*

Corms depressed globose, 20-30mm in diameter, tunics grey-brown coarsely reticulate, the outer becoming finely fibrous, inner often unbroken (Goldblatt, 1989).. Diagnostic feature is the shape of the windows between the netted fibres, which is smooth ovals, instead of characteristic diamond shape in other species. No discs were identified that could be associated to tunics.

	Watsonia sp 2: Archaeology	*Watsonia stokoei*: Comparative collection
Tunics		

*Watsonia sp 3 (*comparable species *Watsonia galpinii)*

Corm depressed globose, 3-4.5 cm in diameter, tunics grey-brown coarsely reticulate, inner layers often unbroken (Goldblatt, 1989). Discs are irregularly oval shaped from the dorsal view, and raised in the middle where the disc connected to the previous seasons growth. Adventitious roots are thick and originate from the raised central part of the disc.

Oxalidaceae (Oxalis)

One genus was identified within this family; *Oxalis*, which consists of 800 species worldwide. Many species in the genus are geophytic or weakly geophytic (Manning and Goldblatt, 2012). Some species have perennial bulbs that grows continually (Manning and Goldblatt, 2012). Some species the bulbs consist of various scales that overlap and are beaked at the apex (Manning and Goldblatt, 2012). Other species have multiple bulbs that develop annually on the root tips, with one plant having multiple bulbs (Manning and Goldblatt, 2012). The bulbs are mostly teardrop shaped with either woody, hard coverings or softer, papery scales that overlap (Manning and Goldblatt, 2012).

*Oxalis sp 1 (*comparable species *Oxalis livida (photo sourced from Pacific Bulb Society))*

Caulescent geophyte with stem to 20 cm, often branched, bulb not beaked (Manning and Goldblatt, 2012). Bulb is teardrop shaped with sharp tapering towards the top (Manning and Goldblatt, 2012). Bulb completely covered in hard, woody cover with vertically raised ridges (Manning and Goldblatt, 2012).

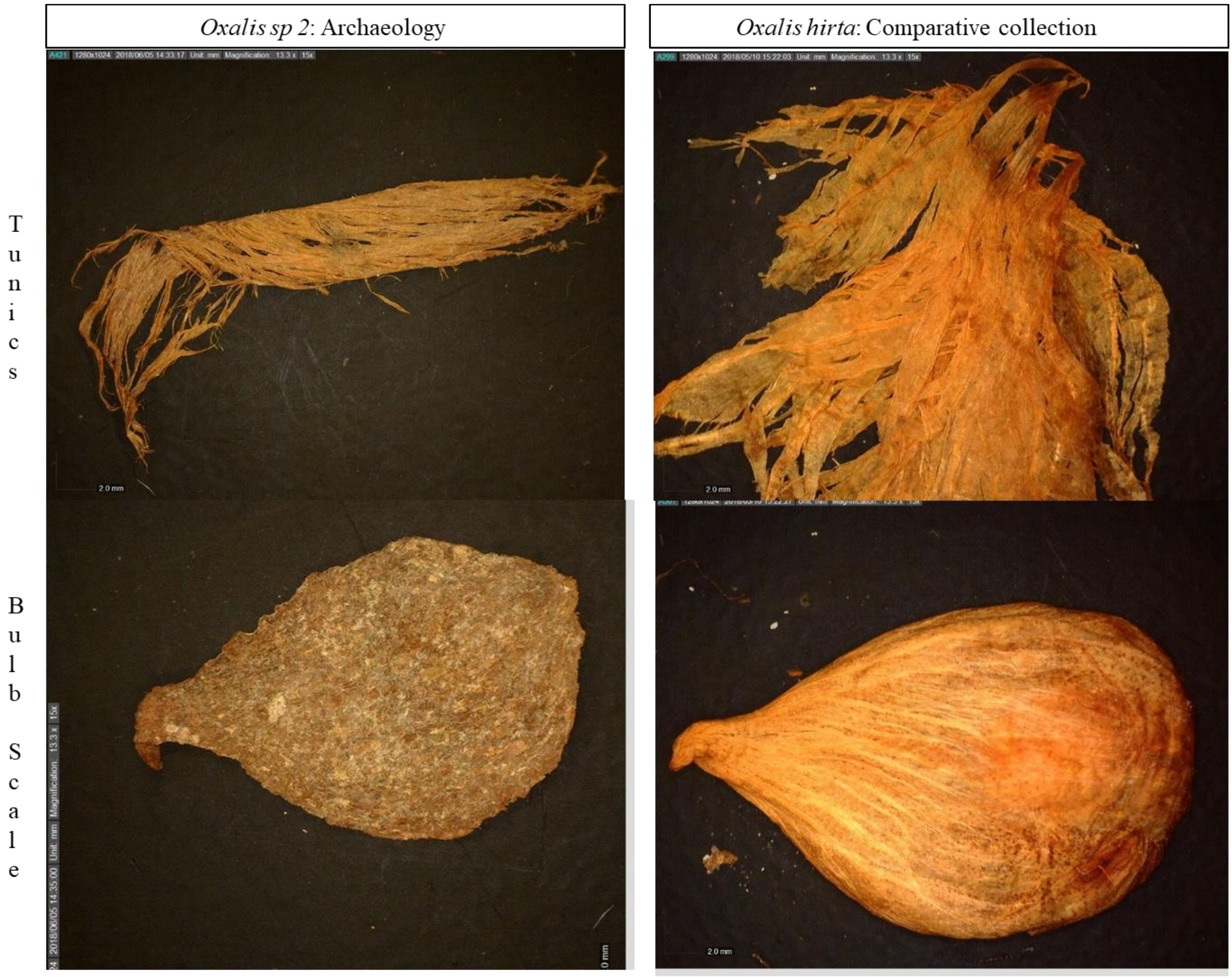
Oxalis sp 1: Archaeology

Oxalis livida: Comparative collection

Bulb Covering

Oxalis sp 2 (comparable species *Oxalis hirta)*

Caulescent geophyte, bulbs can be very large, up to 5 cm (Manning and Goldblatt, 2012). Bulb scales unprotected and often flaking away, covered loosely in orange, papery tunics that loosely overlap (Manning and Goldblatt, 2012).



Oxalis sp 3 (comparable species *Oxalis imbricata)*

Acaulescent geophyte with shallow, contorted bulb (Manning and Goldblatt, 2012). Loosely covered with papery tunics with vertical, slightly raised ridges (Manning and Goldblatt, 2012).

Tunics

Oxalis sp 3: Archaeology

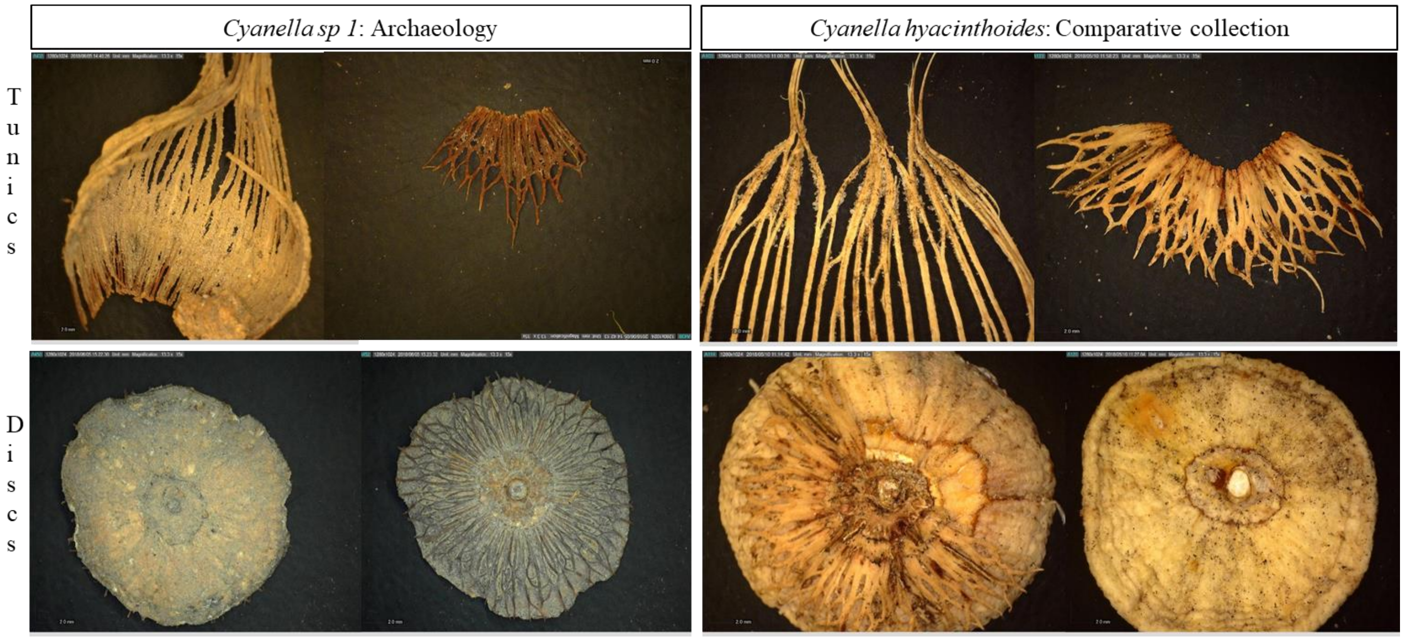
Oxalis imbricata: Comparative collection

Tecophilaeaceae (*Cyanella)*

One genus was identified within this family; *Cyanella*, which consists of nine species . Species in this genus have a deep-seated corm, which is depressed-globose and large (up to 5cm in diameter) (Manning and Goldblatt, 2012). Corms are covered in thick layer of netted fibres (Manning and Goldblatt, 2012). Discs are as broad as the corms (up to 5cm in diameter), generally very round, but domed, and can have multiple discs attached to the corm (personal observations).

*Cyanella sp 1 (*comparable species *Cyanella hyacinthoides)*

Globose-depressed corm with thick layers of tunics (Manning and Goldblatt, 2012). Outer layers broken and disintegrating, the inner layer tight, with thin membrane between thickened vertical members (Manning and Goldblatt, 2012). Bottom of corm has circular netted "skirt" which is present between every disc of the old seasons corm on the ventral surface.



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B.2. Distribution and frequency with which geophyte taxa and artefacts associated with geophyte foraging are found in various archaeological sites across the GCFR.

Locality Code for sites (in alphabetical orders):

/Ai tomas:AT, Amanzi:A, Andriesgrond Cave:AG, Andrieskraal:ADK, Augussie Shelter:AS, Bethelsklip Cave:BT, Blombos Cave::BC, Boegoeberg:BB, Boomplaas Cave:BP, Boontjieskloof:BTJ, Border Cave:BO, Buffelskloof Rock Shelter:BK, Byneskranskop:BNK, De Hangen:DH, Die Kelder:DK1, Diepkloof Rock Shelter:DK, Driebos:DB, Elands Bay Cave:EB, Faraoskop:FK, Great Brak River Cave:GBRC, Groot Kommandokloof:GKK, Heroldbay Cave:HC, Highlands Rockshelter:HRS, Hoedjiespunt:HP, Hoffman:HF, Kabeljous River Shelter:KRS, Kangkara:K, Klasies River :KL, Klein kliphuis Shelter:KKH, Kleinpoort Shelter:KS, Klipdrift Cave:KDC, Klipfonteinrand 2:KFR2, Knysna Cave:KS, Matjes River Rockshelter:MR, Melkhoutboom Cave:MHB, Montagu Cave:MC, Nelson Bay Cave:NBC, Nuwekloof Shelter:NS, Oakhurst:OH, Paardeberg Cave:PBC, Pinnacle Point:PP, Putslaagte:PL, Rautenbachs Cave:RBC, Renbaan Cave:RB, Rose Cottage Cave:RC, Scott's cave:SC, Sibudu:S, Spoegrivier:SR, Spring Rock Shelter:SRS, Steenbokfontein:SBF, Stompiesfontain:SF, Strathalan Cave A:SCA, Strathalan Cave B:SCB, The Havens Cave:THC, Tierkloof:TK, Tortoise Cave:TC, Uniondale Rockshelter:URS, Varsche 1:VR1, Varsche 3:VR3, Varsche 5:VR5, Voëlvlei:VL, Welgeluk:WG, Wilton:WT, Witklip:WK, Ysterfontein:YE

West Coast

Artefact or Geophyte Species	PL	KFR1	KFR2	SF	BB	SR	AT	BT	VR1	VR3	VR5	DK1	BNK	KDC	BC
Plant remains	y	y	y	y	n	y	y	y	y	y	y	n	Y	n	n
Geophyte Remains	y	y	y	y	n	y	y	y	y	y	y	n	y	n	n
Iridaceae Patches	y	y	y	y	n	y	y	y	y	y	y	n	Y	n	n
Systematically Analysed	n	n	n	y	n	n	n	n	y	y	y	n	n	n	n
Analysed For this Thesis	y	y	y	y	n	n	n	n	y	y	y	n	n	n	n
GCFR	y	y		y	y	y	y	y	y	y	y	y	y	y	y
Grinding stones	y	y	y												
Adzes	y	y	y						y						
Digging Sticks	y	y													
Mastic		y	y												
Storage Pits															
Perforated Stones															
Wood shavings															
Albuca genus															
Babiana genus	a														
Babiana hirsuta															
Boophane disticha											a				
Brunsvigia genus									a		a				
Bulbine alooides															
Chasmanthe genus															
Cyanella genus	a			a					a		a				
Cyperaceae genus															
Cyperus usitatus															
Dioscorea elephantipes															
Ferraria genus											a				
Freezia corymbosa															
Gladiolus genus															
Hesperantha genus															
Hexaglottis genus (now Moraea)													y		
Homeria genus (now Moraea)															
Hyacinthaceae family															
Hypoxis genus															
Lachenalia genus				a											
Lapeirousia genus															
Ledebouria genus															
Massonia genus									a		a				
Moraea genus	a								a	a	a		2		
Moraea fugax									y				y		
Oxalis genus	a								a	a	a				
Pelargonium genus				a							a				
Romulea genus															
Sparaxis genus											a				
Tritonia genus															
Tritonia/Freezia															
Velthemia glauca															
Watsonia genus												y			
Watsonia meriana															

West Coast Sites Continued

Artefact or Geophyte Species	PP	GBRC	HC	OH	MC	BK	BP
Plant remains	n	y	n	n	y	y	y
Geophyte Remains	n	y	n	n	y	y	y
Iridaceae Patches	n	y	n	n	y	y	y
Systematically Analysed	n	n	n	n	n	n	y
Analysed For this Thesis	n	n	n	n	y	n	y
GCFR	y	y	y	y	y	y	y
Grinding stones				y	y	y	
Adzes						y	
Digging Sticks		y					
Mastic							
Storage Pits		y					y
Perforated Stones							
Wood shavings							
Albuca genus							a
Babiana genus							
Babiana hirsuta							
Boophane disticha		y					a
Brunsvigia genus							
Bulbine alooides							
Chasmanthe genus							
Cyanella genus							a
Cyperaceae genus							a
Cyperus usitatus							y
Dioscorea elephantipes							
Ferraria genus							
Freezia corymbosa							a
Gladiolus genus							
Hesperantha genus							
Hexaglottis genus (now Moraea)							
Homeria genus (now Moraea)					y		
Hyacinthaceae family							
Hypoxis genus							a
Lachenalia genus							
Lapeirousia genus							
Ledebouria genus							
Massonia genus							
Moraea genus					2	1	a
Moraea fugax					y	y	y
Oxalis genus							
Pelargonium genus							
Romulea genus							
Sparaxis genus							
Tritonia genus							
Tritonia/Freezia							a
Velthemia glauca							
Watsonia genus							a
Watsonia meriana							

East Coast Sites

Artefact or Geophyte Species	KS	NBC	HF	MR	KL	KRS	A	K	NS	RBC	TK	AS	PBC	KS	GKK
Plant remains	y	y	n	n	y	n	y	n	y	y	y	y	y	y	y
Geophyte Remains	n	y	n	n	y	n	n	n	y	y	y	y	y	y	y
Iridaceae Patches	n	y	n	n	y	n	n	n	y	y	n	y	y	y	y
Systematically Analysed	y	n	n	n	n	n	n	n	n	n	n	n	y	n	n
Analysed For this Thesis	y	y	y	n	y	n	y	n	n	n	n	n	n	n	y
GCFR	y	y	y	y	y	y	y	y	y	y	y	y	y	y	y
Grinding stones		y		y											
Adzes		y		y											
Digging Sticks												y			
Mastic															
Storage Pits										y					
Perforated Stones		y		y											
Wood shavings															
Albuca genus															
Babiana genus															
Babiana hirsuta															
Boophane disticha										y	y			y	
Brunsvigia genus															
Bulbine alooides															
Chasmanthe genus															
Cyanella genus															
Cyperaceae genus									y	y				y	
Cyperus usitatus									y	y				y	
Dioscorea elephantipes													y	y	y
Ferraria genus															
Freezia corymbosa					y				y	y		y	y	y	
Gladiolus genus															
Hesperantha genus															
Hexaglottis genus (now Moraea)															
Homeria genus (now Moraea)															
Hyacinthaceae family															
Hypoxis genus														y	
Lachenalia genus															
Lapeirousia genus															
Ledebouria genus															
Massonia genus															
Moraea genus					1								1		
Moraea fugax					y								y		
Oxalis genus														y	
Pelargonium genus															
Romulea genus															
Sparaxis genus															
Tritonia genus															
Tritonia/Freezia					y							y	y		
Velthemia glauca															
Watsonia genus		y			y					y			y	y	y
Watsonia meriana														y	

East Coast Sites Continued

Artefact or Geophyte Species	THC	ADK	SC	MHB	WT	SRS	WG	URS
Plant remains	y	n	y	y	y	y	y	n
Geophyte Remains	y	n	y	y	y	y	y	n
Iridaceae Patches	y	n	y	y	y	y	y	n
Systematically Analysed	y	n	y	y	n	y	n	n
Analysed For this Thesis	n	n	y	y	n	n	n	n
GCFR	y	y	y	y	y	y	y	y
Grinding stones		y		y				y
Adzes		y		y				y
Digging Sticks				y				
Mastic				y				y
Storage Pits	y			y			y	
Perforated Stones		y						y
Wood shavings								
Albuca genus			a	a				
Babiana genus								
Babiana hirsuta								
Boophane disticha	y			a			y	
Brunsvigia genus				a				
Bulbine alooides								
Chasmanthe genus								
Cyanella genus								
Cyperaceae genus	y		a	a			y	
Cyperus usitatus	y		y	y			y	
Dioscorea elephantipes	y		a	y		y	y	
Ferraria genus								
Freezia corymbosa	y		a	a		y	y	
Gladiolus genus				y				
Hesperantha genus								
Hexaglottis genus (now Moraea)								
Homeria genus (now Moraea)								
Hyacinthaceae family				y				
Hypoxis genus	y			a				
Lachenalia genus								
Lapeirousia genus								
Ledebouria genus								
Massonia genus								
Moraea genus	1		a	a		1	1	
Moraea fugax	y			y		y	y	
Oxalis genus	y		a	a				
Pelargonium genus								
Romulea genus								
Sparaxis genus								
Tritonia genus				a				
Tritonia/Freezia			a	a		y	y	
Velthemia glauca								
Watsonia genus	y		a	a	y	y		
Watsonia meriana				y				

B.3. Frequency of species identified from archaeological record during the systematic botanical analysis and the number of sites species were identified in. Archaeological sites ordered from West to East gradient.

Species	Number of Sites Found	Frequency Observed	EB	TC	FK	DK	V1	V3	V5	AG	RB	KKH	DH	BK	PL	SF	BP	SC	MB
Moraea sp 1	14	410	**3**	**6**	**7**	**2**	**31**	**6**	**50**	**192**	**68**	**4**	**29**	**15**	**2**		1		
Cyanella sp 1	13	272	**5**	**9**	**10**	**1**	**4**		**11**	**45**	**47**		**102**	**32**	**2**	3	1		
Babiana sp 1	9	436	26	2	5	7				73	45		235	39	4				
Watsonia sp 1	8	265			16	2				7	8		176	53	1		2		
Dioscorea elephantipes	7	227			9					29	26	4	153	4				2	
Oxalis sp 2	7	76					3		11	15	3		38	4	2				
Pelargonium rapaceum	7	74			4				1	13	12		42	1		1			
Oxalis sp 1	7	68			4		9	2	30	15		1	7						
Moraea fugax	5	87	19						2	47	4		15						
Boophane sp 1	5	57	1						6				1				41		8
Sparaxis sp 1	5	10			4				2	1	1		2						
Brunsvigia sp 1	5	9	3				1		3	1		1							
Babiana sp 2	4	28	1							12	1		14						
Moraea sp 2	4	18			15			1		1			1						
Albuca sp 1	4	5								1							1	2	1
Gladiolus sp 1	3	24	19							1			4						
Freesia sp 1	3	20															1	13	6
Cyperus sp 1	3	9															2	5	2
Oxalis sp 3	3	8								1								6	1
Massonia sp 1	3	6					4		1			1							
Watsonia sp 3	2	22																6	16
Moraea sp 3	2	18																4	14
Hypoxis sp 1	2	15															2		13
Lapeirousia sp 1	2	3		1									2						

Species	Number of Sites Found	Frequency Observed	EB	TC	FK	DK	V1	V3	V5	AG	RB	KKH	DH	BK	PL	SF	BP	SC	MB
Lachenalia sp 1	2	2			1											1			
Watsonia sp 2	2	2											1	1					
Babiana hirsuta	1	19	19																
Ferraria sp 1	1	10							10										
Hesperantha sp 1	1	10								10									
Tritonia sp 1	1	3																	3
Brunsvigia sp 2	1	1																	1
Pelargonium sp 1	1	1										1							
Total density of sites			96	18	75	12	52	9	127	464	215	12	822	149	11	5	51	38	65