Palynological analysis from a bush karoo rat (*Otomys unisulcatus*) lodge near Prince Albert, South Africa

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Abstract:

The "desertification" debate surrounding the Karoo Biome of South Africa has recently inspired much research in this region. The preservation of pollen in middens in arid environments from different parts of the world has great potential for the reconstruction of past vegetation. A lodge of the bush karoo rat (*Otomys unisulcatus*) was excavated near Prince Albert, South Africa, and the high numbers of well-preserved pollen grains was analysed. The vegetation reconstruction suggested that there was a decline in grasses over the whole sequence, while the vegetation experienced several short-term fluctuations throughout the time period. The ages within the lodge were uncertain, although the material is likely to be modern. The palynological analysis appear to be reliable and corresponds relatively well with other studies. The lodges of these species could therefore provide an exciting new source of historical pollen in the arid regions of southern Africa.

Introduction:

The vegetation of natural environments is dynamic over short-term and long-term time periods, especially arid/semi-arid regions, and the South Africa region of the Karoo is no different (Dean and Milton, 1999; Meadows and Watkeys, 1999). The Karoo contains a rich source of fossils that can be used to interpret change over longer periods, and palynological evidence shows that there have been many fluctuations in the vegetation of this region since the late Pleistocene (Bousman and Scott, 1994; Sugden 1989). The apparent drop in production potential of the land in the early 19th century (Scott and Bousman, 1990) has spurred much research, in an attempt to determine and understand the processes that have driven these changes (Roux, 1999; see Hoffman, 1995, for summary). Understanding how vegetation responds to climate change is of particular importance in the Karoo due to the large number of farmers that rely on both privately owned and communal farm lands (Meadows and Hoffman, 2002) thus the potential negative impacts of predicted climate change have strong economic significance for the region. However, the value of understanding vegetation change in the Karoo is not only economic, but also aesthetic, archaeological, and concerned with the issue of biodiversity, particularly preserving rare and endemic species. Therefore a knowledge and understanding of past vegetation changes in response to climate, will be invaluable for the management of the Karoo in the future.

Palynology, in conjunction with other palaeoecological methods, has proved to be an extremely useful method furthering the knowledge and understanding of vegetation change (Bousman and Scott, 1994; Scott and Bousman, 1990; Carrion *et al.*, 1999). The Karoo biome of South Africa has recently been the focus of extensive research as scientists try to decipher the history and ecological processes of this region (Dean and Milton, 1999), however, there is still little known about the ecological patterns and the driving forces of vegetation change. Nevertheless, much of what is presently known about the Karoo's fluctuating environment in the Late Quaternary is derived from pollen analysis and other related palaeoecological techniques (Meadows and Watkeys, 1999). The much-cited hypothesis of Acocks relating the advance of the unpalatable karroid vegetation into the grasslands further east, with the advent of the European settlers (Acocks, 1953), has not had much support from palynological evidence (Bousman & Scott, 1994; Hoffman and Cowling, 1990; Meadows and Watkeys, 1999). For example, Bousman and Scott (1994) showed that this vegetation change, or desertification as Acocks termed it, began before overgrazing would have had a chance to have an effect.

Several other studies have been conducted in response to Acock's "desertification" hypothesis using a variety of techniques. Bousman and Scott (1994) analysed pollen from two hyrax dung middens in the eastern Karoo and which demonstrated that numerous fluctuations have been observed continuously between karroid shrubs and grasses since the late Pleistocene. These changes appear to be driven by climate, although overgrazing may have had a minor role. The European farmers only settled permanently in the Karoo at the beginning of the twentieth century (Avery, 1992). In light of Acock's (1953) hypothesis, the timing of the most recent major decrease in grasses and increase in shrubs took place long before overgrazing would have had the chance to impact the vegetation (Bousman and Scott, 1994). Two studies by Avery (1991; 1992) used the remains of micromammals to reconstruct past vegetation in South Africa. Evidence from Abbot's Cave in the Cape Province showed that in the 18th century the conditions were equable with good scrub and grass cover. There were numerous fluctuations in the between grasses and shrubs in the 19th century. However, these were not long-term trends, nor a progressive degradation as a result of human impact (Avery, 1991). Avery (1991) concluded that the changes in this area appeared to be mainly driven by climate, but that there was no underlying directional trend. The second study by Avery (1992) involved sites from all over South Africa. The conclusion made here, was that the micromammalian community structure was relatively resilient to large climatic fluctuations, but the impacts of farming have been large (Avery, 1992).

Bond *et al.* (1994) also studied evidence from this period by looking at the isotopic signal of soil organic matter in the Karoo Biome. Most of the grasses in southern Africa that occur in the summer rainfall region have a C_4 photosynthetic pathway, while all trees and shrubs are C_3. These two photosynthetic pathways have different carbon isotopic signals, due to the different ratios of ^{13}C and ^{12}C that are characteristically reflected in the soil organic matter (Bond *et al.*, 1994). Although these results suggest that a change in land-use has caused the decline in grasses, all three authors came to the conclusion that the situation is considerably more complex than the earlier hypothesis by Acocks (1953) made it out to be. The general consensus was that the eastern Karoo is a transition zone and would naturally contain a mixture of grasses and shrubs (Hoffman, 1995). This therefore does not support Acock's (1953) hypothesis that the Karoo was an expansive grassland and is being irreversibly invaded by shrubs. Most research suggests that at some time in the past there was a higher percentage of grass cover than there is today, but it is important to remember that this region is, and has been, an ecotone with varying amounts of grasses and shrubs which fluctuated throughout this period (Hoffman, 1995; Meadows and Watkeys, 1999). It is likely that changes in the climate, particularly rainfall, were the driving force behind this "desertification", even though overgrazing would have had a certain amount of influence (Bousman and Scott, 1994).

Aims and objectives:

The primary aim of this research project was to determine if pollen of sufficient quality and quantity for palynological analysis was preserved in the lodges of the bush karoo rat, *Otomys unisulcatus*, in a site in the semi-arid Karoo. This is a preliminary investigation into the potential of the lodges of the bush karoo rat for pollen analysis. If proved to be feasible, the lodges of *O. unisulcatus* could provide an exciting new source of historical pollen for paleoenvironmental reconstruction in an area where such sources are rare.

Midden evidence for Holocene environments:

Arid and semi-arid environments, such as the Karoo, do not usually preserve pollen very well, in terms of both quality and quantity (Horowitz, 1992). It is therefore necessary to obtain fossil pollen preserved under more mesic situations, such as wetlands (Baxter and Meadows, 1999; Meadows *et al.*, 1996), pans, caves (Parkington *et al.*, 2000) and middens (Scott, 1996). Thus the prospect of a new source of fossil pollen, such as the lodges of the bush karoo rat, *Otomys unisulcatus*, in arid areas like the Karoo is exciting and could further knowledge in an area where pollen preservation is rare. Former studies on packrat middens in the United States (van Devender, 1990; Betencourt, 1990), stick-nest rat middens in Australia (Nelson *et al.*), and hyrax and dassie-rat middens in Africa (Scott and Bousman, 1990) have revealed much potential as palaeological indicators in arid/semi-arid regions (Betancourt, 1990; Betancourt *et al.*, 1990; Bousman and Scott, 1994; Nelson *et al.*, 1990; Scott, 1990; Scott, 1996; Scott and Bousman, 1990; Scott and Vogel, 1992; Spaulding, 1990). The discovery of a large, and potentially old, *O. unisulcatus* lodge near Prince Albert in the Karoo, Western Cape, South Africa (Richard Dean, pers. comm.) has lead to the suggestion that the lodges of the bush karoo rat, *Otomys unisulcatus*, may also preserve sequences of fossil plant material.

Packrat middens (*Neotoma*: Cricetidae) preserve plant fragments, pellets, and other debris as the packrat urine crystallises. This crystallised packrat urine is known as amberat, and its mineralogy renders the middens resistant to erosion and decay (Spaulding *et al.*, 1990). In the same way, plant macrofossils in the dassie-rat (*Petromus*: Petromuridae) and hyrax (*Procavia*: Procaviidae) middens are preserved as concentrated urine evaporates, in this case it is called hyracium (Scott, 1990). The stick-nest rat shelter consists of an external shell of sticks with an internal midden of organic matter cemented with urine and faeces (Nelson *et al.*, 1990). Pollen is also preserved in the middens of the former three genera, but as of yet there has been limited research in this field. There have been, however, various palynological studies of hyrax middens in Southern Africa (Scott, 1990; Scott and Bousman, 1990; Bousman and Scott, 1994) and a preliminary study of fossil pollen in a stick-nest rat midden in New South Wales (Green *et al.*, 1983).

Packrats inhabit a variety of habitats, and are therefore broadly distributed throughout North America, much of Western Canada, and throughout much of Mexico and Central America (Vaughan, 1990). The middens of the *Neotoma* thus allow reconstructions of past vegetation for a large area, but this is restricted to the Americas. Hyrax are found in most parts of Africa, except the northern and north western parts, and their distribution extends to Arabia, Israel, and Lebanon (Scott, 1990). The dassie-rats, on the other hand, are confined to the very arid zone of south western Africa (including parts of Namibia and parts of north-western South Africa) (Scott, 1990). The stick-nest rats are considered to be quite rare in Australia and several species are believed to be extinct (Nelson *et al.*, 1990). Nelson *et al.* (1990) suggest that the middens of the stick-nest rat are common in central Australia, and that there should be numerous ancient middens preserved. The bush-karoo rats are similarly restricted to the semi-arid Karoo and west coast regions of South Africa. However, the relatively limited distributions of the various genera becomes of less importance with the discovery of additional species/genera that inhabit different locations, thus information is accumulated to add to the knowledge of palynology and palaeoecology for regions all over the world.

The packrat, hyrax, dassie-rat, and stick-nest rat middens preserve plant macrofossils and pollen that is either carried or blown in. In the case of *O. unisulcatus*, the pollen rain that is trapped in the vegetative material on the surface of the lodge may be preserved due to the slightly moister conditions of the lodge relative to the surrounding air (Vermeulen and Nel, 1988). In this way, there is a vertical accumulation of pollen that forms a chronological sequence, the maximum length of which is not yet known. One of the factors that have contributed to the success of packrat middens as palaeoecological indicators is their age, as some packrat middens have been dated to 40,000 years (Webb and Betencourt, 1990). Even though the macro- and microfossil sequences from stick-nest rat, hyrax and dassie rat middens only extend as far back as about 2,000 years they can still contribute valuable palaeoecological evidence of conditions in the Holocene (Nelson *et al.*, 1990; Scott, 1990). Scott and Vogel (1992) suggest that these shorter sequences are also of value as comparative data and as a control for other fossil pollen studies.

Bush karoo rat:

O. unisulcatus (Muridae: Otomyinae) is endemic and widespread in the semi-arid Karoo and west coast regions of South Africa (Figure 1). There are currently eight species of Otomyinae that occur in Southern Africa (Vermeulen and Nel, 1988). The bush karoo rat builds dome-shaped stick shelters or lodges of an average height of about 1.45 m, usually with *Exomis micrphylla* var. *axyriodes*, as the supporting shrub (Vermeulen and Nel, 1988). *O. unisulcatus* is a generalist herbivore that brings the bitten-off foliage back to the entrance of the lodge to be consumed (du Plessis *et al.*, 1991). In addition, fresh, half-eaten leaves are commonly found on top of the lodges, although there is no evidence for the hoarding of food within the lodges (Vermeulen and Nel, 1988; du Plessis *et al.*, 1991). The hoarding of food is an important consideration, as it could potentially affect the pollen count and bias the results of the reconstructed vegetation. According to Vermeulen and Nel (1988) the lodges are composed of 70% grass, 18% shrub leaves, and 12% stems. Depending on the time at which the lodge was built, if the grasses brought in were carrying pollen this could influence the fossil pollen sequence. The effect of this is likely to be negligable, but is unknown at this stage.

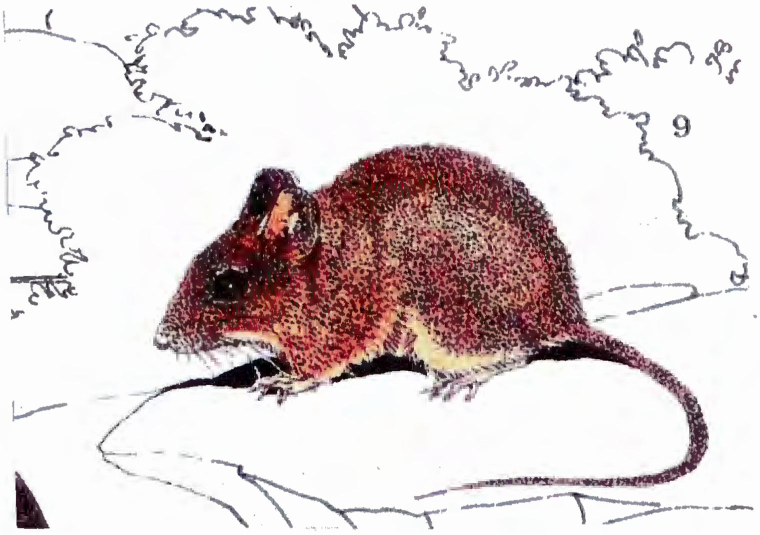

Figure 1: *Otomys unisulcatus*

<u>Limitations</u>:

Of course there are many factors to be cleared up regarding certain aspects of vegetation reconstruction from the plant microfossil and macrofossil evidence found in the *O. unisulcatus* lodge. A preliminary evaluation of the value of lodges of this species for palynological analysis can be made from one lodge. Further research should compare pollen analyses from several *O. unisulcatus* lodges and from other fossil pollen sources in the region to determine if the sequences are reliable. A comparison between the present vegetation, modern pollen rain and pollen found in modern lodges is also recommended. Additionally, the effect of regional pollen on the samples should be determined within this comparison.

In the study of this particular lodge, the pollen grains were identified only to family level, which always poses a problem when attempting to make inferences about the vegetation, as different species within a family often have different environmental affinities. There are already many assumptions made in the process of reconstructing vegetation from pollen, meaning that the identification to below family level would be very beneficial. The additional identification of macrofossils and spores would also increase the accuracy of the inferences. Packrat middens contain great variability in terms of plant macrofossil spectra, and there is still a lot of information that is missing and research that needs to be done (Spaulding *et al.*, 1990). An exploration of the possibilities of fossil pollen in packrat middens could also be interesting for future research, as Spaulding *et al.* (1990) mention that it is likely that dust and organic debris accumulate on the surface of these middens. Hyrax middens, on the other hand, do not seem to be so variable and are quite unbiased fossil pollen traps (Scott and Bousman, 1990). The reliability of the pollen sequences determined from the stick-nest rat and the dassie-rat middens have not yet been proved. In considering all the variables, such as the quality and quantity of the pollen, and the lodge-building characteristics of the *O. unisulcatus* species, it is likely that this source of fossil pollen can be considered to be relatively reliable.

Study Area:

The town of Prince Albert, 33°15'S and 22°5'E, and its surrounds, including the *O. unisulcatus* lodge of this study (Figure 2), occurs in the province of the Western Cape, South Africa, and is classified in Acocks (1975) as Karroid Broken Veld. This portion of the Koup Karoo has been described in detail by Milton *et al.* (1992). The study site is on the edge of the Great Karoo, about 5-10km north of the Swartberg mountain range, on the edge of the Sand River, at an altitude of 800m. The climate is arid and falls between the winter and summer rainfall regime, with 46% of the rainfall occurring in winter (April to September), while heavy rains are most likely to fall between the months of February and May (Milton *et al.*, 1992). The average rainfall is 167 mm, the mean annual temperature is 17.5°C, and the summer aridity index (SAI) is 4.8, with a month of drought often occuring between September and January (Milton *et al.*, 1992). The temperature range is extreme, as the daily maximum is greater than 30°C and the daily minimum is less than 0°C, on 90 days and 10 days per year respectively. The prevailing wind direction is from the south east in the summer and from the north west in the winter (Milton *et al.*, 1992). The geology of the area consists of underlying Ecca shales, Dwyka Hillite and Witteberg quartzite, while the Sand River Valley consists of a deposit of unstratified colluvium of at least 2 m in depth (Milton *et al.*, 1992). The dominant plant species on the site where the *O. unisulcatus* lodge is found are: *Pteronia pallens* and *Crysocoma ciliata* (Asteraceae), *Galenia africana* and *Ruschia spinosa* (Aizoaceae), *Diospyros lycoides* (Ebenaceae), *Rhus undulata* and other *Rhus* species (Anacardiaceae), *Lycium* sp. (Solanaceae), and *Acacia karoo* (Fabaceae) (Milton, pers. comm).

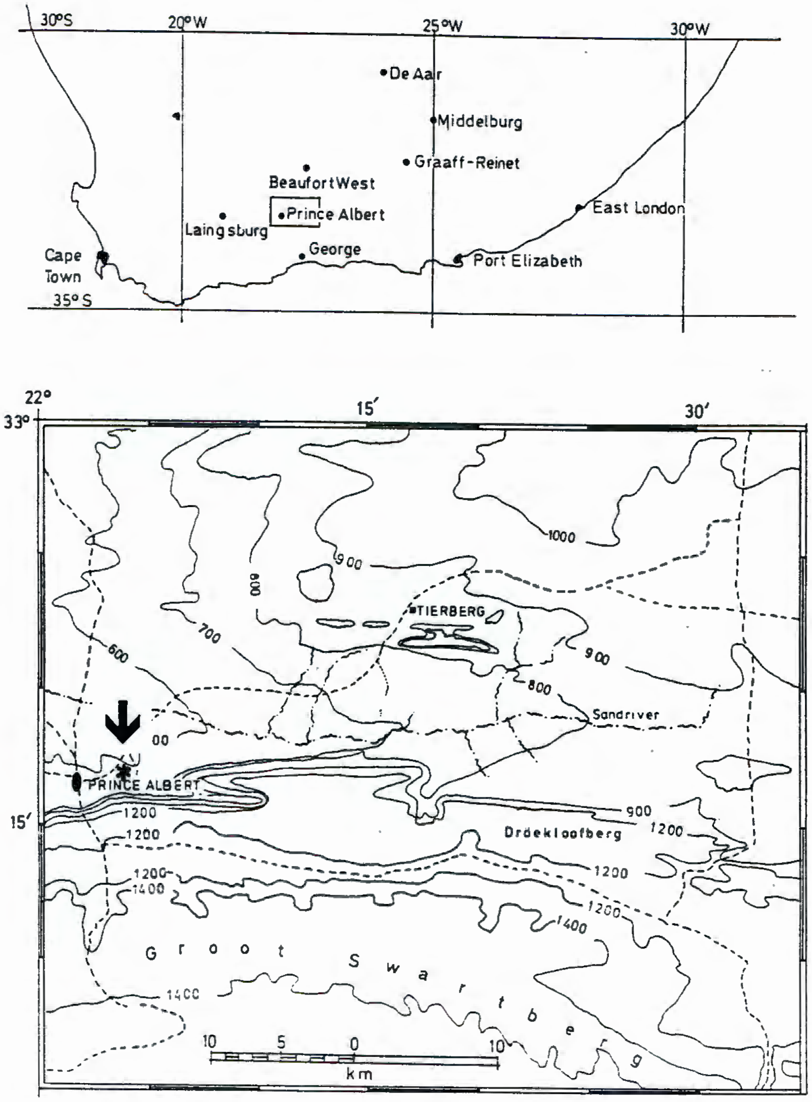

Figure 2: Position of the town of Prince Albert in South Africa, and the position of the study site of the bush karoo rat lodge (*).

Methods:

The studied lodge is approximately 5 km from the town of Prince Albert in an easterly direction. The *Otomys unisulcatus* lodge is constructed under a tangled bush (on the edge of a river bed, which was dry at the time of sampling) on the land of a farm called Prins Albert (Figure 3). The lodge is approximately 70cm high at the centre and highest point. In order to retrieve the actual sediments of the lodge, the covering branches were cleared away. The lodge was then cut in half with a spade to expose a cross-section of the centre (Figure 4a). The excavated cross-section revealed about 10 horizontal layers that were on average 5.2 cm thick (Figure 4b). The layers varied substantially in thickness, i.e. from 1 cm to 10 cm. The sediments appeared to be very rich in organic matter, and contained two twig layers; one between the top two sedimentary units (numbered 18 and 19) at 12 cm, and the second was between sedimentary units (14 and 15) at a depth of 37 cm. The edges of the lodge were observed to have experienced a flow of material, thus the samples were taken from the centre where the layers had experienced very little visible flow and where the sedimentary units lay horizontally. A sample was taken from each sedimentary layer by carefully inserting a trowel and removing approximately 5 x 5 x 2 cm of sediment from the centre. The samples were numbered from 10 to 19 (from bottom to top), and then tightly sealed in plastic bags and transported back to the laboratory so that the pollen could be extracted. In addition, organic material from 15 cm (sample 18) and 55 cm (sample 13) was dispatched for radiocarbon determination.

First, each of the approximately 5ml samples were treated with a 10% sodium hydroxide (NaOH) solution to remove the humic acids, and was then washed with distilled water until the supernatant became clear. The samples were centrifuged between each of the steps, and the supernatant was removed each time. Secondly, sodium pyrophosphate then added, then the course sand was removed from the samples by sieving with a 106 μm sieve. To get rid of the colloidal silicates and silica-fluorides, hydrochloric acid (HCl) was added. The samples were soaked in 40% hydrofluoric acid (HF) for three hours to remove the course fractions and fine siliceous matter, and were finally washed with HCl to halt the reaction. The extraneous organic matter was removed with the glacial acetic acid, then the acetolysis mixture was added, which consists of nine parts acetic anhydride and one part concentrated sulphuric acid. The introduction of glacial acetic acid after 3 minutes stopped the reaction. The 10 samples were then stained with aqueous safranine, and the pollen suspended in a few drops of glycerol phenol. The glycerol-phenol suspension was then transferred to 10 slides and sealed with glycerol jelly.

The question of how many pollen grains to count per sample has been a problem since the very early stages of palynology (Horowitz, 1992). It was decided that at least 200 pollen grains should be counted in each sample, not including the un-identified pollen grains. A pollen diagram showing the temporal changes in abundance for each family was created in the Tilia and Tilia Graph computer package. The families were divided into five groups, i.e. grasses, shrubs, succulents, trees and riparian vegetation

Figure 3: The *Otomys unisulcatus* lodge before excavation.

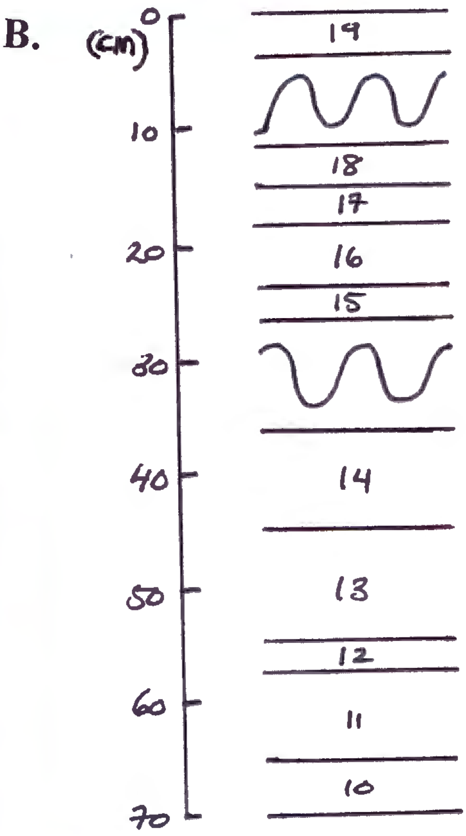

Figure 4: **A.** Cross-section of the bush karoo rat lodge after excavation.
B. Diagrammatical representation of a cross-section of the lodge.

Results:

Pollen diagram:

The *O. unisulcatus* lodge yielded a high density of relatively undamaged and good quality pollen. The density of pollen within each sample varied quite drastically, from 60.5 pollen grains per transect at 65 cm, to 250 pollen grains at 70 cm (Table 1). The percentages of unidentified pollen grains were relatively low – under 10% for each sample.

Table 1: Table showing the densities of pollen grains found in each sample.

Sample number	**Depth (cm)**	**Number of transects**	**Total number of pollen grains**	**Number of grains per transect**
19	3	2	500	250
18	15	4	242	60.5
17	18	2	308	154
16	23	3	289	96.3
15	27	1	242	242
14	45	2	302	151
13	55	3	221	73.7
12	57	1	222	222
11	65	3	223	74.3
10	70	2	438	219

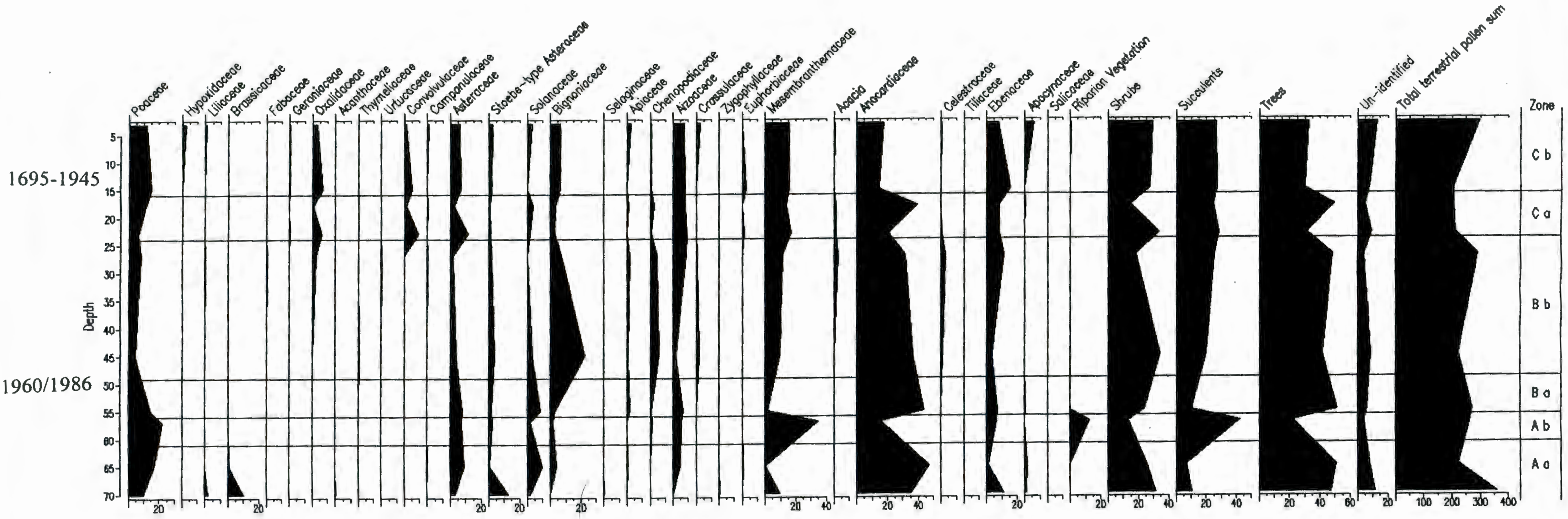

Figure 5: Pollen diagram from the bush karoo rat lodge near Prince Albert, South Africa.

The pollen diagram can be divided into six pollen assemblage zones (Figure 5). The zones occur at 62cm, 56cm, 49cm, 24cm and 16cm. A brief description of each pollen assemblage zone (PAZ) will follow: PAZ Aa contains an abundance of shrubs and trees, a low percentage of succulents, and a relatively high number of Poaceae. In PAZ Ab the riparian vegetation appears, there is also the climax of grasses and succulents, while the shrubs and trees exhibit a minimum. Zone Ba shows a decline in the Poaceae and trees and increase in shrubs and succulents. In Bb there is an increase in succulents and trees, while the Poaceae reach a minimum percentage and the shrubs reach one of three climaxes. PAZ Ca shows a high number of shrubs and trees, and the Poaceae are on the increase. In Zone Cb a low percentage of Cyperaceae appears, and the Poaceae, succulents and trees demonstrate minor changes.

The pollen diagram reveals the pattern documented by several palynologists (e.g. Bousman and Scott, 1994), i.e. the inverse fluctuation of the Poaceae (grasses) and karoo shrubs. This pattern is especially noticeable at the end and in the middle of the sequence, where there is a decrease in the grass cover and an increase in shrubs. The Poaceae increase from 70cm, and reaches a maximum at 57cm, from here the abundance of grasses decreases to a low at 45cm. Then there is another less marked increase in the percentage of Poaceae, finishing with a slow rate of decrease in the top sample to 8.0%. Conversely, the shrubs are abundant at the lowest depth of the sequence and then show a decrease until 57 cm. From here, mirroring the curve of the grasses, the proportion of karroid shrubs amplifies, reaching a maximum at 45 cm. Fluctuations follow, and the curve appears to level off at 15 cm, but still demonstrates a small rise in percentage. The overall trend appears to be a decrease in grasses and an increase in Karoo shrubs.

The succulent and tree families also reveal patterns of an inverse relationship. The proportion of succulents remain relatively stable throughout the sequence after the extreme peak of abundance at 57 cm. The minimum percentage of trees coincides with the maximum number of succulents. A rapid drop in the number of trees at 23 cm and increase at 18 cm, then another drop at 15 cm, is followed by a period of relative stasis. These recent changes in the tree data are mirrored by the succulent data, but to a lower degree. Cyperaceae is the only vegetation in the pollen sequence that is representative of riparian vegatation, appearing at 57cm and at 3cm. The presence of Cyperaceae at 57 cm coincides with a depth in the sample experiencing a greater grass cover, the maximum abundance of succulents, as well as the minimum percentage of Karoo shrubs.

Chronology:

There was a considerable amount of uncertainty surrounding the chronology within the midden. At a depth of 15 cm (second sample from the top) there were two possible ages, either 1960/1961 A.D. or 1986/1987 A.D. The lower sample at 55 cm revealed several possible dates, i.e. 1695 - 1724, 1816 - 1844, 1827 (1895, 1912, 1931) – 1931, or 1945 – 1955. The age of the *O. unisulcatus* lodge and of the layers within the lodge remain elusive due to the uncertain nature of the radiocarbon dates. The radiocarbon date for the sample at 15 cm appears to be relatively reliable, this layer is either 40 or 15 years old. At 55 cm the possible ages cover a period of 260 years. It is widely accepted that radiocarbon dating can be imprecise and involves some uncertainty. The period at which the lower samples ages fall coincide with the time when atmospheric ^{14}C rose dramatically after the atmospheric testing of thermonuclear bombs (Williams *et al.*, 1998). By 1963 the ^{14}C was two times the pre-1950 level in the atmosphere. Since then the atmospheric ^{14}C has been decreasing slowly, but the result is that modern organisms, living today, cannot be used as a basis for a modern standard (Williams *et al.*, 1998). A likely additional reason for the many potential ages lies on the calibration of radiocarbon dates with tree-ring sequences. There are many significant fluctuations in the relationship between the ^{14}C and tree-ring ages, meaning that at a given ^{14}C age there may be more than one calendar age as obtained from tree-ring data (Williams *et al.*, 1998). This means that the lodge could be 300 years or a mere 10 years old! It seems unlikely that the lodge is only 10 years old, and I would suggest that an age closer to the older suggested dates, i.e. early 1700s, is more likely for the sample at 55 cm. An additional problem is that the different sample layers within the lodge are extremely variable in thickness. This means that there is not a constant deposition of material, and therefore accumulation rate and time cannot be inferred for each layer. Despite the uncertainty surrounding the ages of the samples, one positive factor is that the radiocarbon dates indicate that there is a chronology, i.e. the older sample is found below the younger sample. It is also clear that this midden can be classified to be "modern".

Discussion:

The relevance of these fluctuations in percentages of the different vegetation groups is most likely related to moisture availability. The arid and harsh environment of the Prince Albert region amplifies the importance of moisture availability, in the form of rain to increase this, or evapotranspiration to decrease it. The sudden abundance of Cyperaceae in pollen assemblage zone Ab, which coincides with the maximum percentage of grasses suggests that there was great amount of moisture available at this time. The maximum in tree abundance takes place very soon after this, possibly reflecting a lag in response time for these larger plants, with a slower growth rate. The lowered percentage of grasses in pollen assemblage zone Bb is also likely to reflect a decrease in moisture availability, or the influence of another factor such as overgrazing.

Other studies looking at vegetation change occupying a similar time period show varied results, but overall they correspond with respect to past vegetation cover. Although the exact ages for each section of our pollen diagram are not known, they can be speculated. Carrion *et al.* (1999) inferred from pollen extracted from hyrax dung that the former eastern Orange Free State was open grassland in the first half of the 20th century, and from 1950 onwards there were many more trees present. The evidence from Prince Albert supports this as there is a dramatic increase in grasses somewhere near the beginning of the century, matched by a decrease in shrub cover. Just after the mid-1900s the abundance of grasses appears to begin a slow decline. The tree data, however, do not quite fit the proposed pattern of vegetation change experienced at this time. The aforementioned increase in grass cover corresponds with a peak in tree cover, which decreases rapidly as the grasses begin to decrease. Hoffman and Cowling (1990), and Scott and Vogel (1992) also suggest that there was a higher proportion of grasses later in the 20th century, compared to the early 1990s.

The 19th century appears to be characterised by short-term fluctuations between grasses and karroid shrubs (Avery, 1991; Hoffman and Cowling, 1990). The general trend at this time from the Prince Albert data, and from pollen evidence from a hyrax midden (Scott and Bousman, 1990), is a decrease in grasses with an inverse increase in shrubs. There are a couple of suggestions that this is a consequence of overgrazing (Hoffman and Cowling, 1990; Scott and Bousman, 1990). At the beginning of the 1800s palynological evidence (Bousman and Scott, 1884) and evidence from photographs (Hoffman and Cowling, 1990) points to a drier period, preceded by slightly ameliorated conditions with a combination of good grass and shrub cover (Avery, 1991; Hoffman and Cowling, 1990). There is, however, conflicting evidence for this period, including Prince Albert, which shows a low percentage of grasses but high numbers of trees and shrubs. The presence of the Cyperaceae family near the bottom of the Prince Albert pollen sequence does not seem to match with any other data available. In conjunction with this, the abundance of grasses and low counts of trees and shrubs indicate a "wetter" period where more moisture is available.

Conclusion:

The pollen evidence from Prince Albert does not show strong support for the "desertification debate" initiated by Acocks (1953). The abundance of grass cover is observed to undergo a slight decrease over the whole sequence, but there are short-term fluctuations throughout this time period, implying that there is no uni-directional invasion of shrubs. Acocks (1953) predicted an irreversible decline in productivity as shrubs invaded the grass-dominated Karoo Biome. Most contemporary studies, however, do not support this prediction, but there are many conflicting dates and forms of evidence making an unequivocal conclusion impossible at this stage. The research of many scientists also suggests that this decrease in the proportion of grasses began before overgrazing could have had an impact on the vegetation. The relative timing of the observed fluctuations is controversial at present, but forms an integral part of the answer to these questions.

The studied *Otomys unisulcatus* lodge shows enormous potential as a source of fossil pollen. The pollen grains are well preserved, with a low percentage of unidentifiable grains. In general, pollen preserved in this particular lodge appears to provide a reliable reconstruction of the past vegetation in Prince Albert. The environmental characteristics of arid/semi-arid zones usually results in poor pollen preservation (Horowitz, 1992), therefore the exciting discovery of this new source that can be used to reconstruct vegetation in the Karoo is invaluable, especially in light of the debate initiated by Acocks (1953) and the potential degradation of this region.

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