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Twentieth century changes in montane vegetation in the eastern Free State, South Africa, derived from palynology of hyrax dung middens

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ABSTRACT: The dating and pollen analysis of a hyrax dung deposit in a mountain rock shelter (Rooiberg Shelter II) are compared with that in a previous study from the same mountain range at the rural town Clarens, in South Africa. Calibration of radiocarbon measurements from the dung deposit provides different possibilities for the age of the sequence. Unlikely dates can be eliminated on the basis of pollen stratigraphy, comparisons with a previously studied accumulation from the last 30 yr, artificially increased radiocarbon levels in the upper samples as result of nuclear arms testing after 1954, the presence of historically introduced exotic elements, and the assumption of a relatively constant rate of dung accumulation. According to these considerations we suggest that the dung started accumulating at the beginning of the twentieth century. The pollen contents show marked changes in composition, indicating mainly open grass vegetation with fynbos in the first half of this century and woody vegetation in the second half. A first marked increase of the woody component is estimated to have occurred around 1950, but it only became permanent in the 1960s. The fluctuating pollen sequence can best be interpreted in terms of the combined effects of rainfall changes, fire and stock grazing, the latter of which increased together with town expansion in the area during the course of this century. Considering historical events recorded in the area and the region in general, the results suggest that pollen in hyrax dung is a good recorder of vegetation change. Copyright © 1999 John Wiley & Sons, Ltd.

KEYWORDS: hyrax middens; pollen analysis; grazing; palaeoecology; South Africa.

Introduction

Ever since the potential of deposits of faunal origin was realised for pollen analysis and palaeoecology, a variety of materials have been studied, especially North American packrat (*Neotoma*) middens (Van Devender, 1988; Thompson, 1985; Betancourt *et al.*, 1990). Although their macrofossil content has more regularly been relied upon, the use of pollen assemblages in these middens for reconstructing past vegetation changes is complicated by the taphonomical processes involved in their formation (Wells, 1976; Davis and Anderson, 1987; Ritchie, 1995). For different reasons, investigations of pollen in other faunal products are in their early stages. Materials studied include the following: sloth guano (Thompson *et al.*, 1980); goat droppings (O'Rourke and Mead, 1985); hyena coprolites (Scott, 1987); dung of large extinct mammals (Davis *et al.*, 1984; Davis, 1987; Minckley *et al.*, 1997); dassie-rat (*Petromus typicus*) middens (Scott, 1990; Scott and Cooremans, 1992); stick-nest rat (*Leporillus*) middens (McCarthy *et al.*, 1996); owl pellets (Fernández-Jalvo *et al.*, 1996); and bat guano (Dimbleby, 1985). In comparison with the North American packrats, hyrax dung middens have received relatively little attention (Pons and Quézel, 1958; Fall *et al.*, 1990; Scott and Bousman, 1990; Hubbard and Sampson, 1993).

Hyraxes (*Procavia capensis*) are rabbit-sized herbivores of rocky habitats with a generalist strategy in their dietary choice, which includes leaves, bark, flowers and fruits of

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most species represented in the local flora (Sale, 1965; Fourie, 1983; Barakat, 1995). Dung pellets of these animals become impregnated with urine and accumulate in certain dry rock shelters with rocky floors. It can be assumed that pollen in the middens is derived from different sources. Firstly pollen can be incorporated in hyrax diet either as pollen dust that settled on plant food, or through deliberate ingestion of flowers. Secondly, fresh sticky dung and urine trap pollen from the atmosphere and surroundings, including that derived from the fur of the animals. In other areas, comparison of modern soil pollen with fresh faecal pellet pollen, and a sequence of hyrax dung pollen with that in an adjacent pond sequence, suggests that the pollen composition in dung is close to that in the general surroundings (Scott and Bousman, 1990; Scott and Cooremans, 1992; Bousman and Scott, 1994). The implication is that the dietary bias in pollen spectra is not necessarily great, and that pollen in hyrax dung can give a good reflection of the surrounding vegetation. This is supported by a study of modern pellets, which indicates that seasonality of flowering may be reflected in pollen spectra in fresh pellets (Hubbard and Sampson, 1993). Seasonal behaviour of hyraxes relating to pollen trapping has, however, not been investigated yet.

A problem with pollen analysis of biogenic substances such as dung accumulations, is their stratigraphical and taphonomical contexts, and here we want to emphasise that hyrax middens differ from the nest middens of packrats (*Neotoma*) and dassie-rats (*Petromus typicus*) because they constitute stratigraphically coherent sections. Stratigraphy of the middens can, moreover, be established easily by radiocarbon dating. Although individual middens often represent short intervals of merely a few decades (Scott and Vogel, 1992) or less than 1000 or 2000 yr of age (Scott, 1996), long sequences of up to 20 000 yr have been assembled from different deposits in the same site (Scott, 1994). Another fact supporting the validity of pollen analysis of hyrax dung middens is the close correspondence between modern midden samples and adjacent plant community composition (Scott and Bousman, 1990; Scott and Cooremans, 1992). Like packrat middens, hyrax middens can be found in some arid lands where sites for conventional pollen analysis are scarce or absent. If these middens are well impregnated with dried urine (hyracium) their preservation of pollen is excellent. Rock hyraxes, such as *Procavia capensis*, are widespread in Africa and the Near East (Morris, 1965) and may thus be widely applicable to pollen analysis. A limitation of hyrax middens in comparison with packrat or dassie rat middens may be their relative lack of macrofossils. However Fall *et al.*, 1990, reported useful macrofossils from hyrax deposits in the Middle East, in contrast with Southern African examples, which were not found to be rich (Scott, 1994, 1996). The scarcity of macrofossils is the consequence of behavioural traits of the hyraxes, which are not known to collect nesting materials, like *Leporillus*, *Petromus* and *Neotoma*.

Because we feel that the palaeoecological potential of pollen analysis of hyrax dung has been underestimated, the main goal in this paper is to provide evidence that encourages future research. Although some studies have been carried out in the Middle East (Fall *et al.*, 1990), north Africa (Pons and Quézel, 1958; Thinon *et al.*, 1996) and Namibia (Scott, 1996), most of the published pollen data on hyrax dung come from South Africa. Even in this country, however, the reported sequences are bioclimatically and chronologically isolated, which precludes comparison. In the present study, we will describe a new twentieth century palynological record for hyrax dung from Clarens (South Africa) and its correlation with a previously published, partially coeval, sequence for the same area (Scott and Vogel, 1992). Afterwards, we will discuss the possible meaning of the pollen variations in terms of environmental variables, in the light of climatic and anthropological factors. The study of these middens of historical age is thought to be important in the application of pollen analysis of prehistoric middens.

Setting

The topography of the study area in the mountainous eastern Free State, South Africa, is characterised by large sandstone outcrops of the Clarens Formation, with overlying peaks of basaltic lava. Underlying the major sandstone unit, mudstones and sandstones are exposed along slopes of the deep valley of the Little Caledon River, running from east to west, south of the small town of Clarens. Quaternary alluvial deposits occur in the river basin (Scott, 1989). The Rooiberg II shelter with the midden material is situated on a south-facing slope north of Clarens (Fig. 1). The accumulated dung occurs in a shelter that is difficult to access. It has a vertical depth of ca. 40 cm and extends inward on a rock platform below a low roof, for ca. 1 m and has a width of about 1 m. Lobes of hyracium (dry urine) accumulate on the vertical surface below the platform. Some loose pellets occur on top of the midden but it is not sure if hyraxes presently use the midden site as a latrine. This new deposit (Rooiberg Midden II) lies on a slightly more inclined rock surface (Fig. 2) than the one studied previously (Rooiberg Midden I, Scott and Vogel, 1992).

The annual mean precipitation in the Clarens area is ca. 700 mm, occurring mainly in summer, but it increases sharply towards the east and southeast to more than 1400 mm within 50 km, along the Natal Drakensberg range. Towards the west of the study area the rainfall declines gradually to ca. 560 mm around Bloemfontein.

The vegetation of the area is dominated by grasses, experiences frost in winter, and lies within the grassland biome of South Africa (Fig. 1). On south-facing slopes and protected ravines, montane woodland is present, with forest edge species such as *Buddleja salviifolia*, *Leucosidea sericea*, *Clutia pulchella* and *Maytenus heterophylla*. Small ericoid fynbos satellites occur throughout the grassland, especially on nutrient-poor soils derived from aeolian sands of the Clarens Formation, and are restricted to localised areas protected from fire by virtue of topography (Du Preez, 1992). The fynbos on the south slopes, where Midden II was sampled, has a higher cover than on the eastern slopes surrounding Midden I. Asteraceae genera, including members of the *Pentzia* type group as defined on the basis of pollen morphology (Scott and Vogel, 1992), occur both in the grassland and *Erica*-dominated communities. Cyperaceae species abound among the grass-dominated communities under humid conditions. The scrub forest includes the liana *Clematis brachiata*. The region bordering the Caledon River has been farmed intensively with livestock and, in some places, cultivated lands occur. Especially around the town of Clarens, many exotic trees have been planted during this century, such as *Pinus, Eucalyptus, Platanus, Cedrus*, etc.

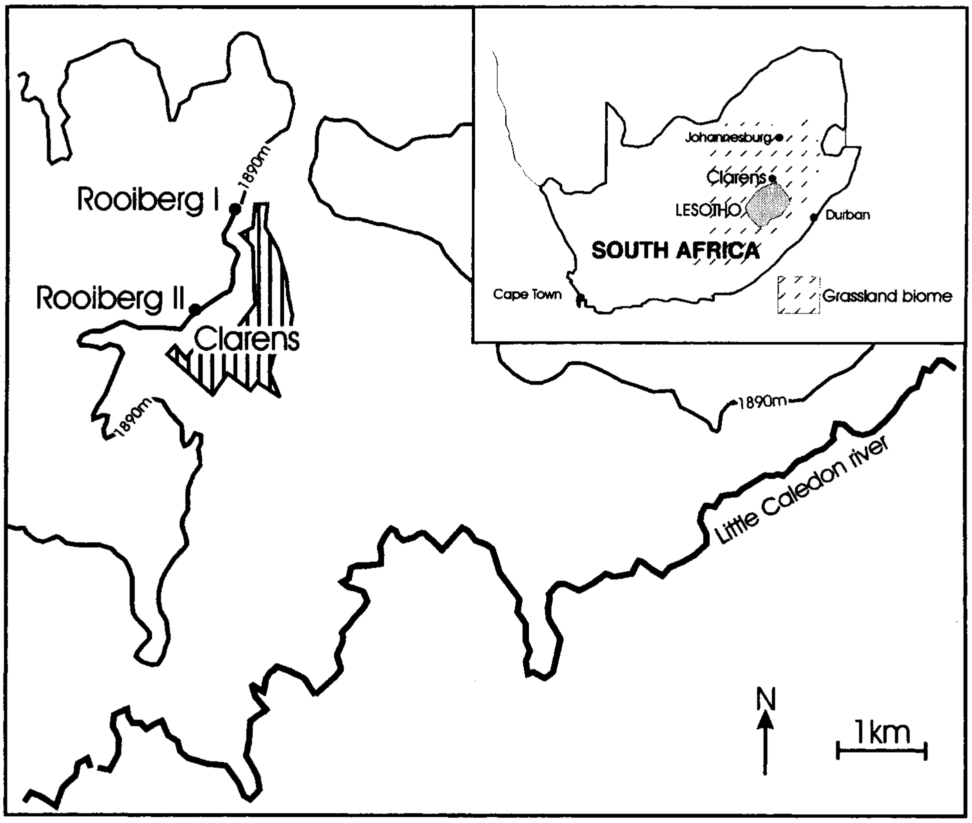

Figure 1 Map showing localities of the Rooiberg Shelters I and II in the Free State, South Africa.

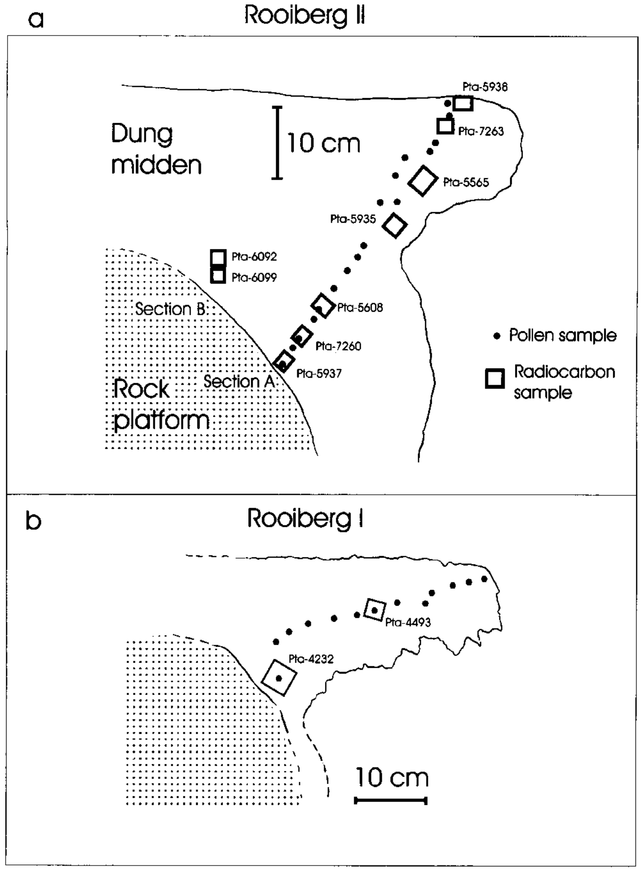

Figure 2 Schematic transects of the dung accumulations in Rooiberg Shelters I and II.

Dating

For radiocarbon dating, nine samples were studied at the Quaternary Dating Research Unit at Pretoria, where the results were also calibrated (Table 1). Between ca. 1900 and 1954 the ^{14}C content in the atmosphere decreased markedly as a result of the dilution caused by the addition of carbon dioxide from the combustion of fossil fuel. During this period ages can be determined quite accurately, but unfortunately the ^{14}C content will also correspond to one or more earlier dates. Assignment to the correct historic date can be achieved by comparison with the results of other samples in the same stratigraphic sequence.

After nuclear fusion bomb testing in 1954, the ^{14}C content in the air rose to some 65% above the normal in the Southern Hemisphere (Vogel, 1971). Since 1965 the value has been declining gradually, but even today still lies at 112% normal. Plants that grew during this time can be dated to ±1 yr, but there are again two possible interpretations of the result, depending on whether the sample belongs on the upward or downward arm of the environmental calibration curve. Which historic date applies can be determined from the position of the sample in the stratigraphy. The assignment of historic dates to the sets of dung samples from the hyrax middens in the two Rooiberg shelters is achieved with the use of the appropriate environmental calibration curves adapted for the Southern Hemisphere (J. C. Vogel, unpublished data).

A problem that does arise, however, is that the dates immediately above the rock platform in more than one section of the midden gave anomalous values, suggesting contamination with recent organic matter. One possibility to explain this is contamination by hyracium. Under relatively moist conditions at Clarens, urine can apparently

Table 1 Radiocarbon dating of the Rooiberg II shelter

Section	Laboratory number (Pta-)	Depth (cm)	$\delta^{13}C$ (‰ PDB)	^{14}C content (pMc)	^{14}C age (yr BP)	Calibrated date (AD)
A	5938	1.5	−28.8	127.5 ± 0.6	–	1981/1982
	7263	4.25	−29.0	137.6 ± 0.7	–	1976
	5565	10.5	−28.1	99.0 ± 0.5	80 ± 40	1900 or 1955
	5935	18.3	−27.9	97.1 ± 0.7	190 ± 60	1735, 1810 or 1944
	5608	30	−27.0	98.2 ± 0.6	150 ± 45	1830, 1878 or 1924
	7260	34	−27.0	99.9 ± 0.6	10 ± 45	1956
	5939	37.5	−26.3	99.8 ± 0.6	10 ± 45	1956
B	6092	24.5	−26.9	100 ± 0.6	0 ± 50	1956
	6099	27	−26.7	98.8 ± 0.6	90 ± 45	1900 or 1956

‰PDB = relative ^{13}C content with respect to the PDB reference standard.
pMC = percentage modern carbon with respect to the US NBS oxallic acid reference standard.
– = yr BP not applicable.

percolate through the midden and will tend to accumulate on the rock floor and crystallise out in the basal levels. The dung adjacent to the base can thus contain significant amounts of younger organic compounds, and if hyracium is not dissolved effectively during pre-treatment, dates of these levels will be too young. It is also possible that other organic material could have moved along the inclined rock platform, through seepage after heavy rains. Contamination could not have come from calcium carbonate, as the samples were pre-treated with hydrochloric acid.

The presence of pollen from exotic plants throughout the midden sequence (see below) indicate a young age and do not support the oldest calibration possibilities in Table 1 and Fig. 3. Exotic plants could only have been introduced to this part of the country during the latter half of the last century by settlers and probably multiplied only during the twentieth century as part of town expansion and commercial plantations. Previous results of Rooiberg Shelter I (Scott and Vogel, 1992) showed a relatively constant rate of dung accumulation and it is likely that this will also be the case in the Rooiberg II midden. The younger possible dates for the upper five samples (section A) form a virtually straight line that extrapolates to ca. AD 1900 at the base, and this linear accumulation rate during the twentieth century can be accepted with confidence (Fig. 3).

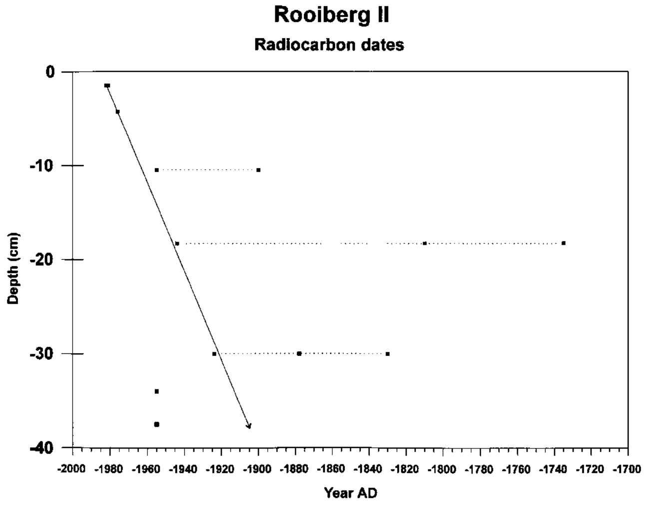

Figure 3 Calibration possibilities of radiocarbon dates in Section A versus depth in hyrax dung from Rooiberg Shelter II.

Methods

Sampling of the dung accumulation was carried out along a stratigraphical sequence as shown in Fig. 2. Between 1.4 and 4.1 g of sediment per sample were taken, of a thickness of 1–2 cm. With the dating model suggested it is considered that 2 cm of sample does not exceed a timespan of longer than 5 yr per sample. Samples were processed in the laboratory by KOH 10% digestion and heavy liquid mineral separation. Pollen concentrations were calculated by adding to each sample a known quantity of exotic *Alnus* pollen grains. The identifications were performed using the reference collection of the Palynological Laboratory at the University of the Orange Free State. The Tilia 1.12 and TiliaGraph 1.18 programs were used to make pollen diagrams and to define pollen zones. The pollen types described as Type 16A, Type 123 and Type 204 correspond to the descriptions by (Van Geel *et al.*, 1981, Van Geel *et al.*, 1983 and Van Geel *et al.*, 1989) (Figs 4–6). The nomenclature of taxa follows (Morris, 1965) for mammals, and (Arnold and de Wet, 1993) for plants.

Pollen stratigraphy and interpretation of the Rooiberg II section

The percentage pollen diagrams are shown in Figures 7–9 and a pollen concentration diagram is presented in Fig. 10. The main characteristics of the pollen zones are reflected in Table 2. The pollen of introduced plants mentioned above, including *Pinus* and Cupressaceae, occur consistently, *Cedrus* appears in B1 and B4, *Eucalyptus* in B3 and B4, other Myrtaceae in B1, B3 and B4, and *Platanus* in B3 (Fig. 7). Most samples showed wide taxa diversity, good pollen preservation and low quantity of unidentified palynomorphs (Fig. 10). Total concentrations are mostly higher than 3×10^5 grains g^{-1}, with maximum values in zones B3 (higher than 5×10^5 grains g^{-1}), and B4 (between 10^6 and 2×10^6 grains g^{-1}). They are higher than those found in the case of Rooiberg I, where the maximum was around 6×10^5 grains g^{-1} (Scott and Vogel, 1992). In comparison with other hyrax dung deposits and the middens of packrats and stick-

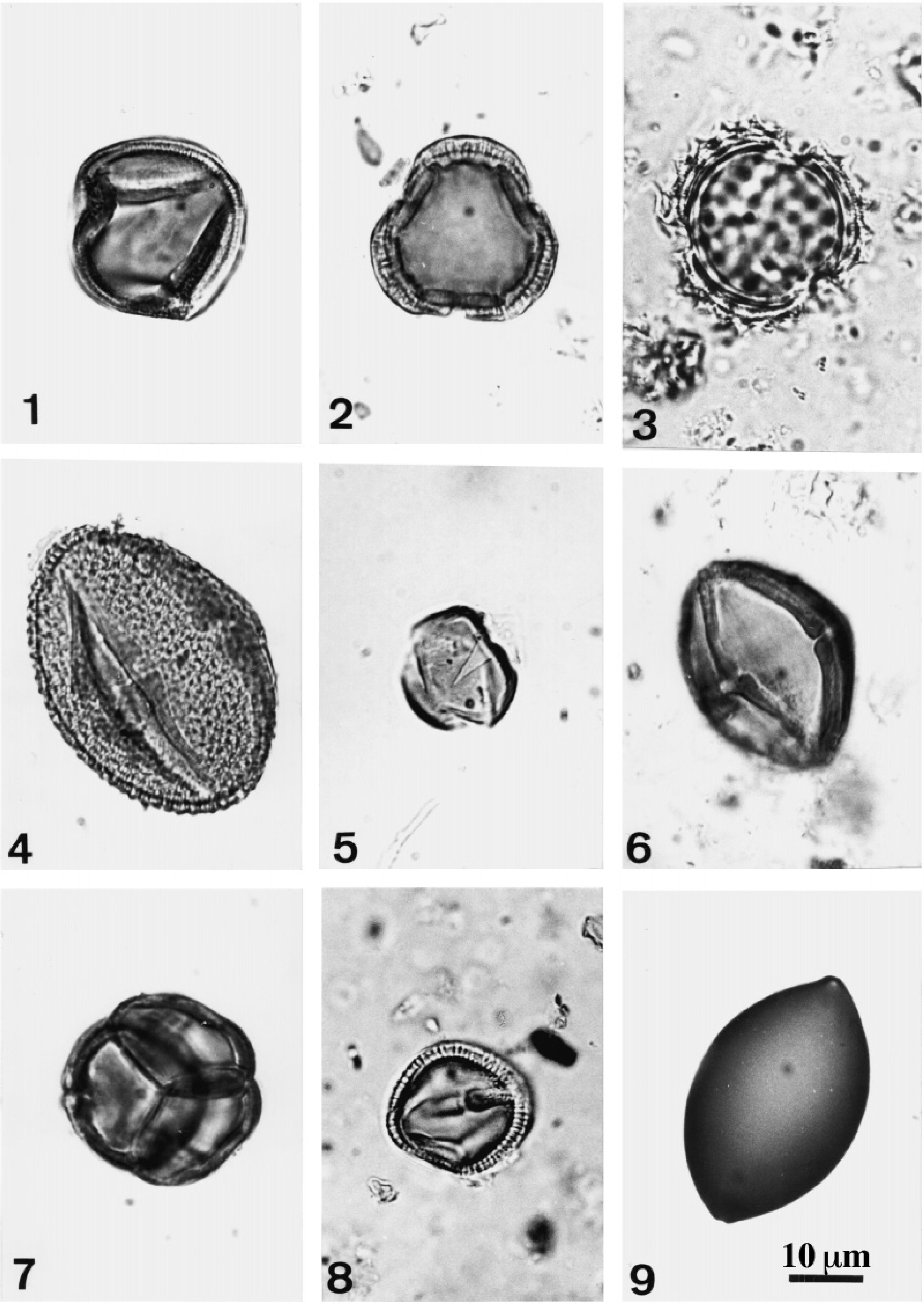

Figure 4 LM micrographs of pollen grains and spores in the hyrax dung of Rooiberg II. 1, *Leucosidea*. 2, *Anthospermum*. 3, *Pentzia* type. 4, *Clutia*. 5, *Buddleja*. 6, *Leucosidea*. 7, Ericaceae. 8, *Maytenus*. 9, Type 204.

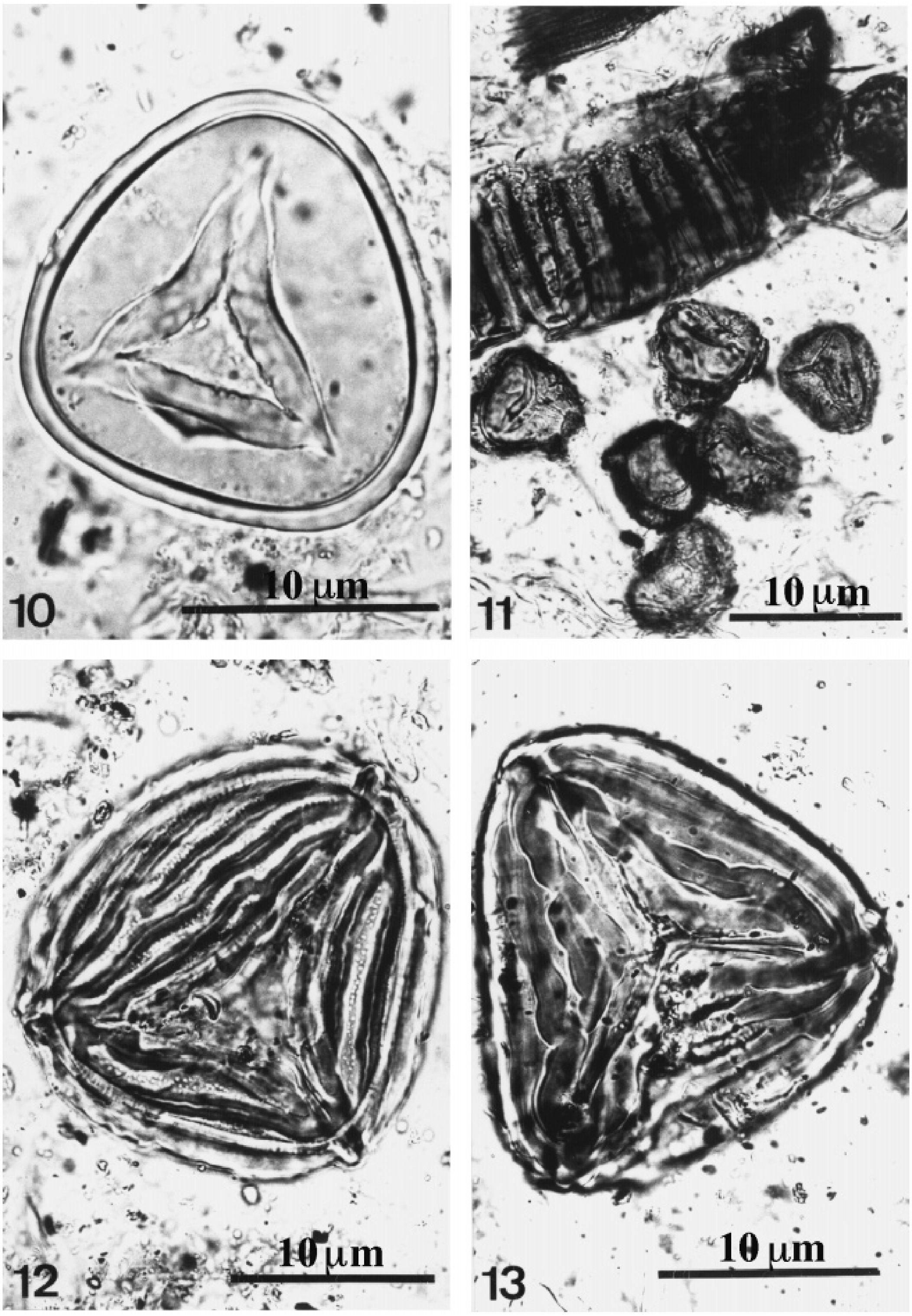

Figure 5 LM micrographs of spores in the hyrax dung of Rooiberg II. 10, *Pellaea* type. 11, Pteridophyta. 12 and 13, *Mohria*.

nest rats (Betancourt *et al.*, 1990), the samples of the present study show considerably higher pollen concentrations.

Major pollen contributors are Ericaceae, Poaceae, *Buddleja, Leucosidea*, *Clematis* type, *Pentzia* type and *Anthospermum*. Pollen grains of Cyperaceae and spores of *Pellaea* and Sordariaceae are also abundant. Among the shrubby components and arboreal pollen (AP) there are minor records of *Myrica*, *Myrsine, Passerina,* Ebenaceae, *Celtis, Clutia, Maytenus, Pittosporum,* and *Rhus*. A wide variety of heliophytes is also represented in low frequencies, such as Aizoaceae, Asteroideae, *Artemisia*, Chenopodiaceae, Lamiaceae, etc. In general terms, the present-day vegetation has a similar composition to the pollen assemblages.

There are two pulses of increased *Buddleja-Leucosidea* assemblages (Fig. 7), which are confirmed by the concentration curves (Fig. 10). The pulses coincide with zones B2 and B4, with the latter zone being more noticeable, particularly in the *Leucosidea* curve. In zone B4, the total pollen concentration and the number of taxa attain their highest values, and other woody elements such as *Maytenus*, *Rhus, Myrsine* and *Tarchonanthus* slightly increase. The rest of the sequence (zones A, B1 and B3) represents grassland spectra

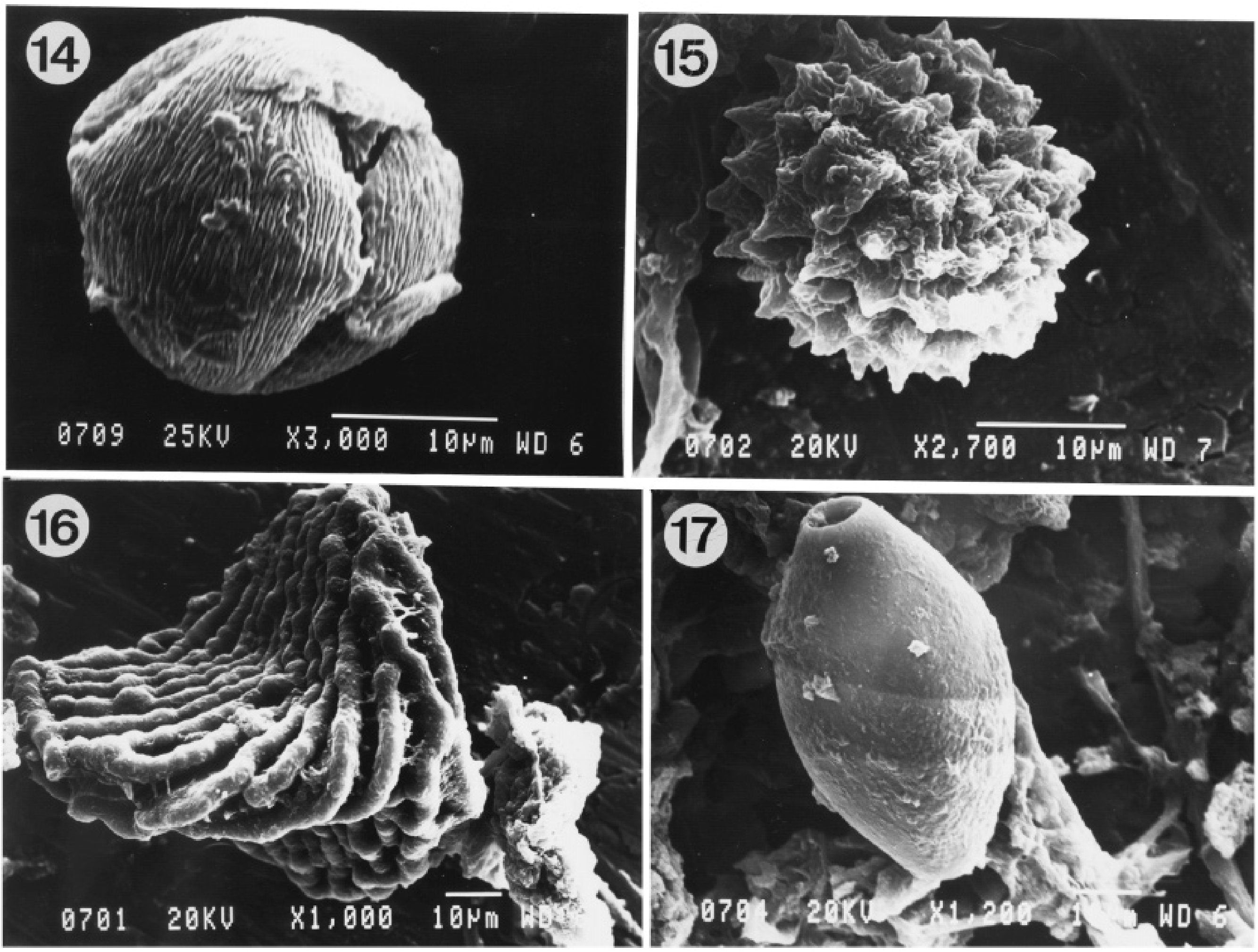

Figure 6 SEM micrographs of palynomorphs in the hyrax dung of Rooiberg II. 14, *Leucosidea*. 15, *Pentzia* type. 16, *Mohria*. 17, Type 204.

that is characteristic of the present-day vegetation in the region.

A previous survey (Scott, 1989) provides indications of the pollen production of the wider study area, including the slopes surrounding Clarens and the Little Caledon River Valley (Fig. 1). Modern sediment and midden samples from the eastern Free State, including two very close to the Rooiberg middens, show that Poaceae is almost exclusively the dominant pollen. Most of the remaining pollen taxa are represented in the local flora and, as for the grasses, their regional signal is difficult to isolate. Interestingly, pollen taxa such as *Buddleja* and *Leucosidea*, which display important cover in the present-day flora of the hills next to Clarens, have a minor pollen representation in the regional surface spectra. This suggests that their high percentages in the Rooiberg sequences reflect the dominance of the plants on these slopes.

Cyperaceae, *Salix*, and hydrophytes are most abundant in zone A, but they persist in younger zones (Fig. 9). The aquatics suggest that hyraxes visited water pools. *Callitriche* displays a constant presence, *Nuphar* is recorded in B1, B2, and B4, *Potamogeton* in A, B2 and B3, *Myriophyllum* in B2, and *Lemna* in B4. Towards the top there are moss spores that showed heavily perinated walls, such as those from xerophytic Pottiaceae (Carrión *et al*., 1993). Spores such as *Selaginella, Asterella*, *Pellaea*, *Mohria*, *Ophioglossum* and some unidentified fern types are more frequent in the bottom zone A, together with indicators of moisture, such as the zygospores of *Closterium* and *Spirogyra*, *Pseudoschizaea*, *Botryococcus* and *Arcella* (Van Geel *et al*., 1989; Scott, 1992).

Two clear indicators of the faecal origin of the sediments are Sordariaceae ascospores and the parasite eggs of *Trichuris* (Fig. 9). Their occurrence in the hyrax dung is not surprising, but they have not been mentioned hitherto in hyrax literature. *Chaetomium* species can also appear in dung, but not necessarily. They are fungi that decompose cellulose, occurring commonly on all kinds of plant remains (Van Geel *et al*., 1983). Altogether, Sordariaceae, *Glomus*, *Chaetomium* and the fungal types 16A, 123 and 204 (Figs 4 and 9) suggest aerobic conditions for organic matter decomposition.

Zone A is characterised by high proportions of hydrophytes, pteridophytes and fungi. This fact poses an interesting taphonomical problem, that of determining the pollen source for the very abundant water-related palynomorphs. Hypothetically, the source could have been either post-depositional water transport, or a diet including stagnant water. Roots were not noticed in the samples, although aeration by some other means, such as water transport, could have allowed fungal activity. In zone A, pollen grains of Ericaceae and Poaceae, for example, appear corroded and percentages of unidentified palynomorphs slightly increase, and pollen concentrations and the number of taxa diminish (Fig. 10). It is unlikely, however, that water moving along the rock slope into the basal part of the midden

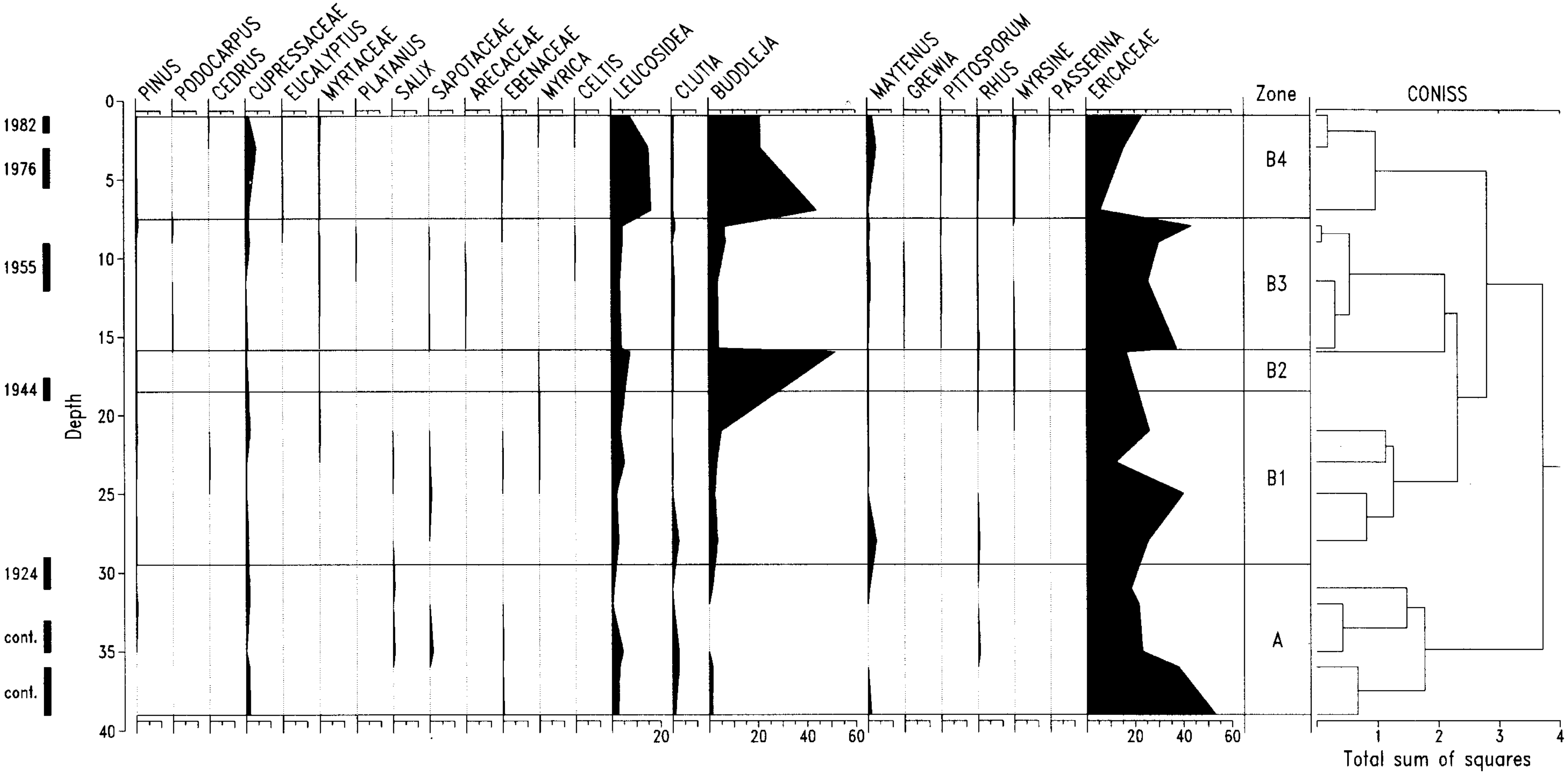

Figure 7 Diagram of tree and shrub pollen in dung from the Rooiberg Shelter II. CONISS zonation based on total spectra.

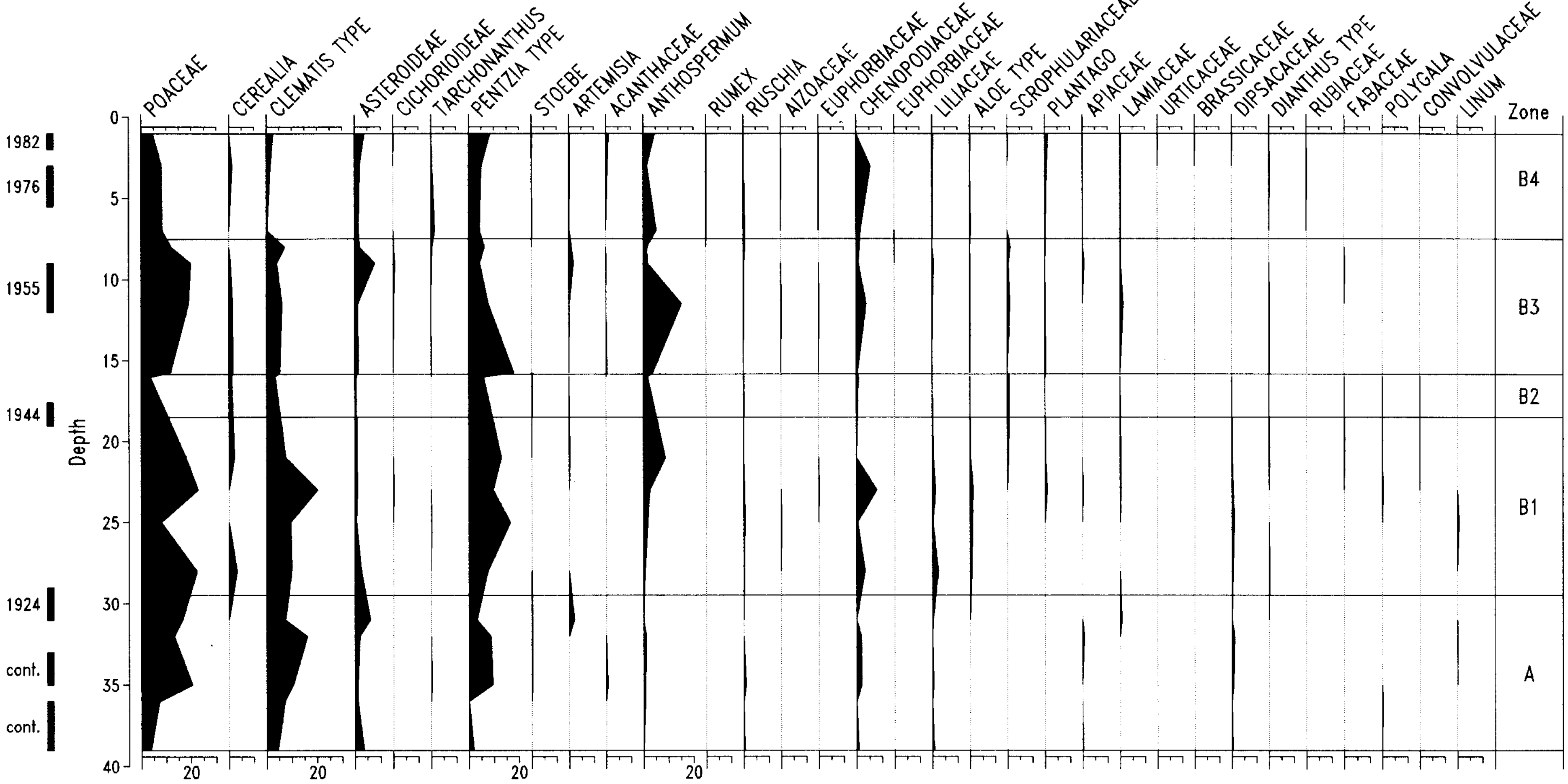

Figure 8 Pollen diagram showing percentages of some non-arboreal elements such as Poaceae.

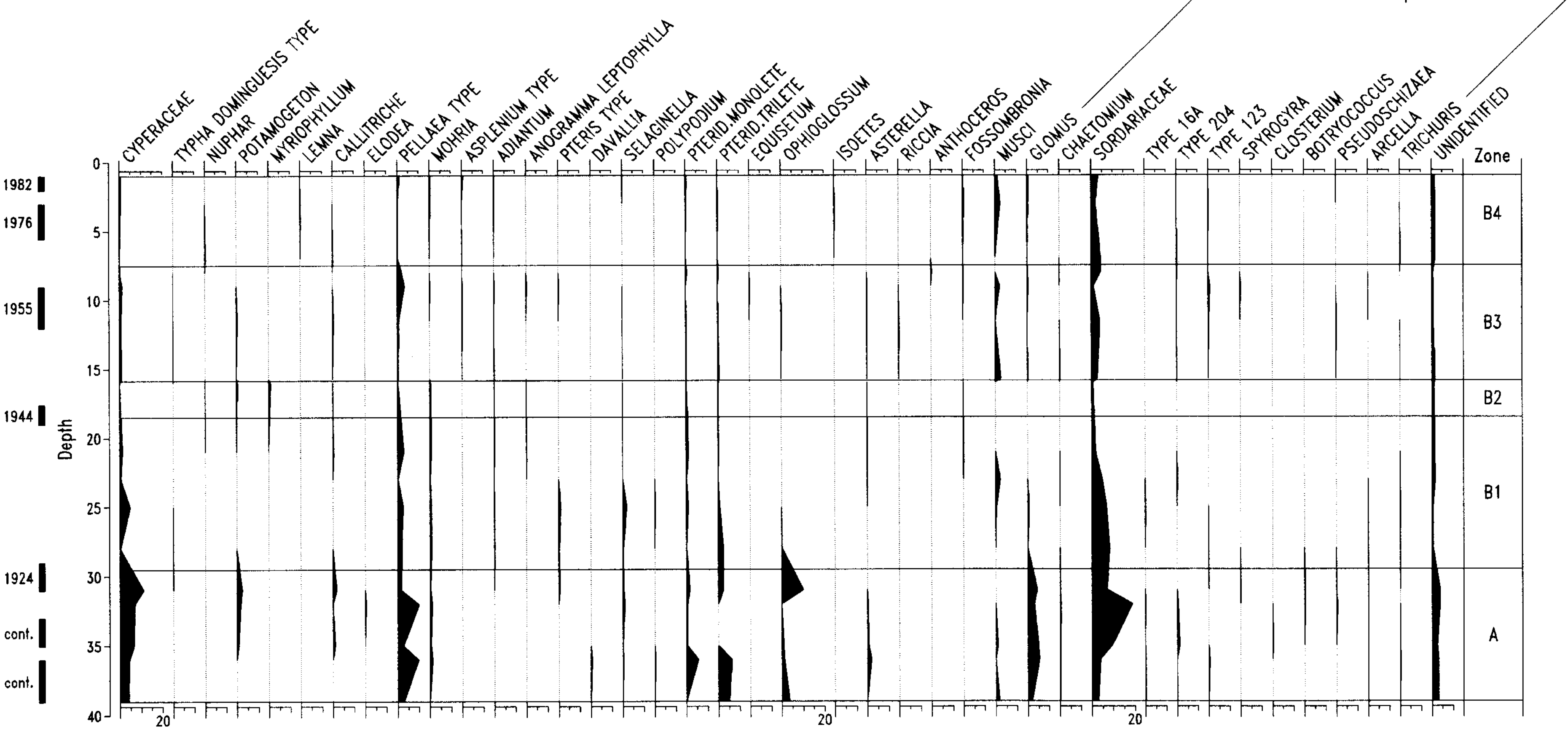

Figure 9 Pollen diagram showing percentages of other non-arboreal elements such as Cyperaceae and hydrophytes, including non-pollen palynomorphs.

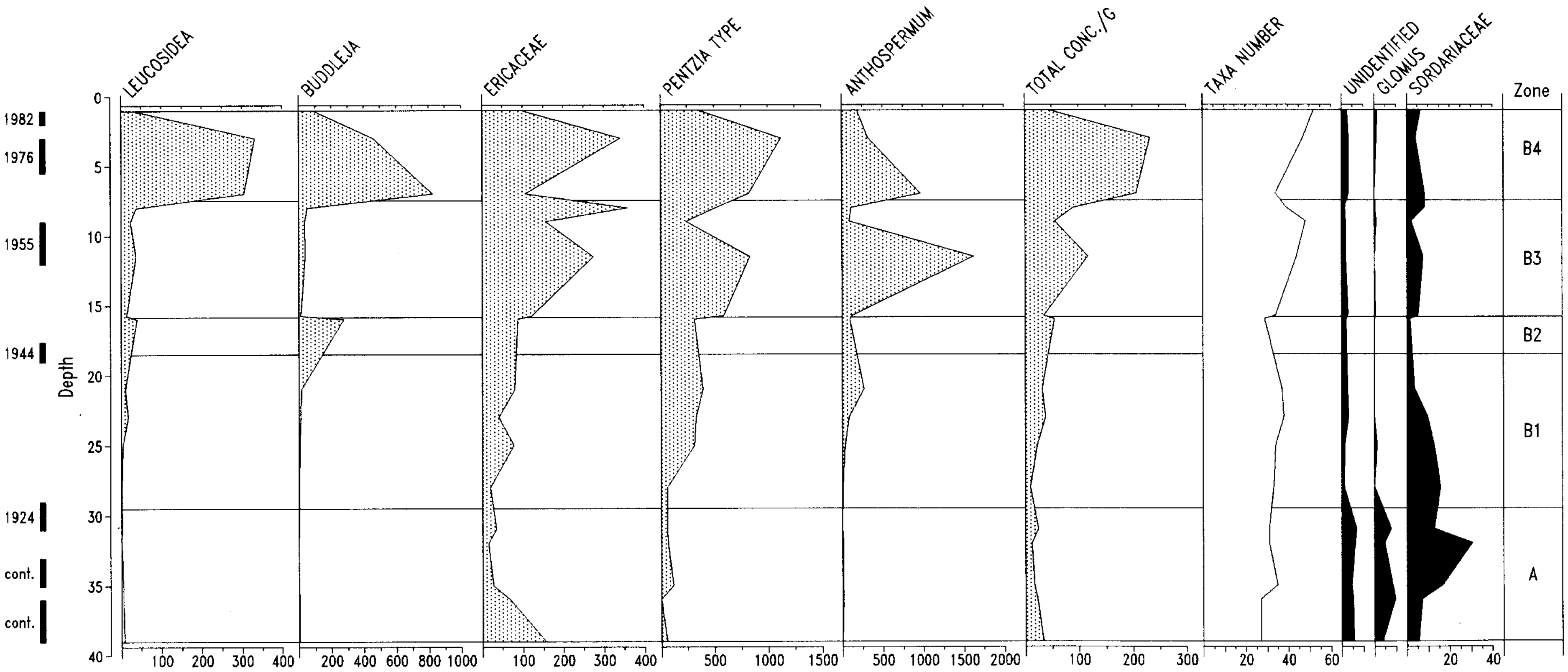

Figure 10 Pollen concentrations (shaded) of *Leucosidea*, *Buddleja* and Ericaceae (× 1000), and *Pentzia* type and *Anthospermum* (× 100) and total concentration (× 10 000), compared with taxa diversity (not shaded), and percentages (black) of unidentified pollen, and *Glomus* and Sordariaceae spores.

Table 2 Main characteristics of the Rooiberg II pollen zones

Zones	Characteristics
B4	*Buddleja* – *Leucosidea* – Ericaceae Increased *Maytenus*, *Rhus*, *Myrsine* and *Tarchonanthus* Highest pollen concentrations
B3	Ericaceae – Poaceae – *Pentzia* type – *Anthospermum*
B2	*Buddleja* – *Leucosidea* – Ericaceae
B1	Ericaceae – Poaceae – *Clematis* type – *Pentzia* type (increased) Decreases in Cyperaceae, hydrophytes, Pteridophyta and fungi
A	Ericaceae – Poaceae – *Clematis* type – *Pentzia* type Maxima Cyperaceae, hydrophytes, Pteridophyta and fungi Presence of *Salix*, *Closterium*, *Botryococcus*, *Spirogyra* and *Pseudoschizaea* Minimal pollen concentration Signs of pollen decay

has introduced some of the water-transported palynomorphs because the deep soils above would have filtered the water.

We know that although the hyraxes are active mostly close to their shelters, they can travel up to 650 m looking for drinking water (Matthews, 1977). Hyraxes therefore could have introduced water-related palynomorphs through drinking water from distant sources during generally dry conditions when the available moisture in their plant-tissue diet was not sufficient, but this seems unlikely because no increases of pollen indicators for desiccation, such as Chenopodiaceae and Asteraceae, have been noticed. Instead, Cyperaceae pollen attains maximum values in zone A, which is a good indicator of humidity. Another, more plausible, possibility is that hyraxes were directly ingesting more water, either deliberately or accidentally, simply because of increased availability. Hypothetical sources of water are not more than 100 m away from the shelter, at springs that are still active on the higher slopes above and in local watercourses draining towards the Little Caledon River. Our preferred explanation therefore is that zone A provides evidence for favourable moisture conditions in the first quarter of the century, which will be discussed below in a wider context in a comparison of the Rooiberg I and II pollen records.

Comparison of two middens and palaeoecological discussion

The Rooiberg I pollen record includes 16 midden pollen spectra that were dated to between ca. 1963 and 1990 by means of assessment of artificially increased radiocarbon levels as result of nuclear arms testing (Scott and Vogel, 1992). The most abundant pollen types are the same as those in Rooiberg II midden (Fig. 11). The sequence showed marked changes in composition, of arboreal pollen especially, which increased from less than 20% ca. 1963 to ca. 90% in 1974 and stayed relatively high despite temporary declines to ca. 30% and 10% in 1975 and 1988 respectively. During the early period before the *Buddleja-Leucosidea* increase, first *Penzia* type pollen, and later fynbos taxa, were relatively important, suggesting a succession of herbs and low shrubby vegetation. A series of air and other photographs of the Clarens area gave some visual evidence of the increase of woody plant density between 1964–1969 and afterwards, which is in keeping with the pattern in the pollen diagram (Fig. 11). It seems that the relatively open treeless situation which can be observed in the photographs of the study area during the late 1940s and early 1960s, is representative of relatively undisturbed veld.

To explain the declines in *Buddleja* and *Leucosidea* pollen recorded about 1976 and 1988 (Fig. 11), Scott and Vogel (1992) attributed it to the combined effects of climate change, domestic stock grazing and other local developments. According to the Clarens Town Council, intensive stock grazing occurred on the slope studied roughly between 1950 and 1985. This could have led to bush encroachment and the increase of woody elements, which is a typical phenomenon in overgrazed veld (O'Connor and Bredenkamp, 1996). Further, differential response and pollen production between woody and understorey species might have been related to rainfall cycles. During dry years, woody plant pollen showed up stronger as a result of the removal of the understorey by grazing, whereas during wet years the understorey pollen featured relatively prominently.

Tyson (1986) and Tyson and Lindesay (1992) postulated that wet and dry spells over the last 2000 yr in southern Africa alternated according to a regular cycle, and we can compare the recognised pattern with the pollen indicators for drought from the Rooiberg sequences. Palynozones B3–B4 of Rooiberg II correlate with Y–Z of Rooiberg I (Fig.11). Zones Y and B3, are characterised by Ericaceae, *Pentzia* type and *Anthospermum*, whereas zones Z and B4 display increases in *Leucosidea* and *Buddleja.* In both diagrams, the *Pentzia* peaks coincide, preceding those of *Anthospermum.* The date of the transition towards denser scrub and woody pollen production in both diagrams is indicated after 1965 but before 1970 (Fig. 12). The timing of important AP increases in the Rooiberge I sequence seems to correspond well with rainfall data from the nearby town Bethlehem (Scott and Vogel, 1992). The longer sequence of data in Rooiberg II also follows this pattern and it can be compared with twentieth century data presented by Tyson (1986), which indicate that the percentage of normal rainfall in the summer rainfall region was below normal in the 1960s, for instance (Fig. 13). The correlation of woody plant pollen with below average rainfall is also evident in the late 1950s, but not previously.

Up to the present, the main fluctuations of pollen spectra in hyrax midden sequences have been related to environmental change rather than to modifications in the hyrax diet (Scott, 1996). Considering the results of this paper, we think that although some changes in the hyrax diet could have influenced the palynomorph assemblages, they confirm associated environmental changes.

Before proposing an environmental hypothesis to explain the pollen records, it is worth considering some current ideas about vegetation dynamics in the grassland biome of South Africa. Grassland is considered to be dependent on climate, topography and soil type, although fire is a secondary determinant (O'Connor and Bredenkamp, 1996). In some cases, prolonged protection from fire can convert grassland to scrub forest, although this has for a long time been discounted by the hypothesis of Acocks (1953), who suggested that afromontane grasslands were anthropogenically

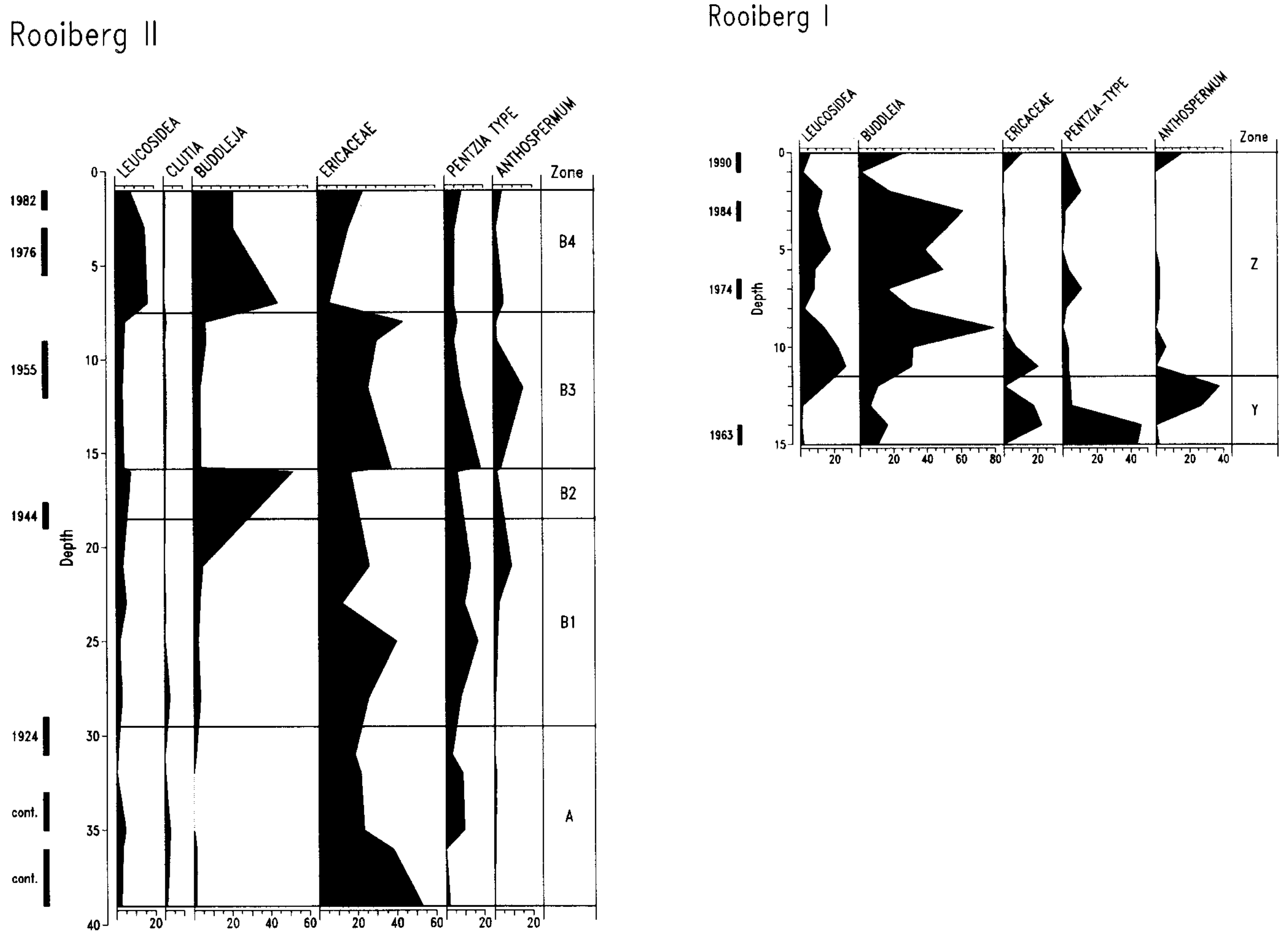

Figure 11 Pollen diagrams of Rooiberg Shelter I and II for correlation.

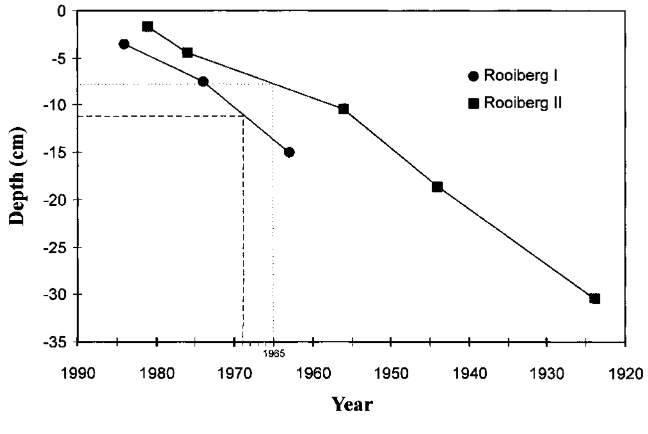

Figure 12 Dating results of the Rooiberg I and II sequences in relation to zones.

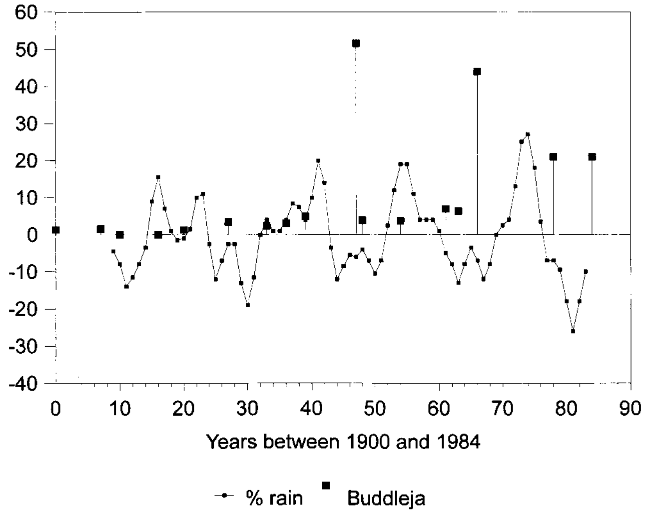

Figure 13 Comparison of *Buddleja* pollen percentages in the dung from Rooiberg Shelter II with the rainfall index of Tyson (1986), which presents a summary of regional weather data from South Africa.

derived in historical times and maintained by fire. Thus, the Quaternary pollen sequences of Elim, Cornelia, and Craigrossie provide evidence about the Late Quaternary environmental history of Clarens (Scott, 1989), and show that open grasslands were typical throughout the Late Pleistocene and Holocene. Expansions of small shrubs and increases in composites and chenopods probably occurred in the driest periods, whereas humid stages supported increased grass and Cyperaceae cover.

Ecological studies show that, as precipitation diminishes, scrub invasion tends to be initiated by heavy grazing rather than fire exclusion, and it is clear that grazing has a more immediate effect on community change in semi-arid than moist grassland (O'Connor and Bredenkamp, 1996). Moreover, for grasslands with high year-to-year variability in rainfall, there is now increasing evidence that grazing-induced changes are contingent upon rainfall patterns (O'Connor, 1985). In conclusion, the susceptibility to scrub invasion will be increased during the dry spells by grazing pressure and during the wet spells by fire reduction. Interestingly, both processes are known to have taken place in the area of Clarens since the middle twentieth century, and more intensively the former.

Although the aforementioned palaeoecological data show that grassland has been practically stable, it is likely that its floristic composition and palatability changed. It has been proposed by Meakins (1988) that swards suffering the simultaneous effects of prolonged drought, seasonal burning and overgrazing by cattle and goats would have replaced the nutritious 'sweet' species (sweetveld) by 'sour' grasses (sourveld) of *Eragrostis* species, with a palatability that is limited to the growing season. Furthermore, palatability of grasses in South Africa can be related to rainfall. Arid areas (contain more 'sweet' grass and) seem to be more palatable than that of the wetter more leached regions with 'sour' grass (Fuls *et al.*, 1992). Recent results (Scott and Vogel, in press) have evaluated dietary preferences of hyraxes and environmental conditions from the analysis of stable carbon isotopes in hyrax dung, which relate to ingestion of C3, C4, and CAM plant during the last 20 000 yr in southern Africa. For the eastern Free State, these data suggest that although both C3 and C4 grasses are numerous, hyraxes rely mainly on leaves of the woody plants while avoiding unpalatable sour grasses.

Bearing in mind the above considerations, we hypothesise that:

1. During zone A, ca. before 1924, local conditions were relatively wet in the area, and the vegetation that surrounded the Caledon River was dominated by grass communities rich in sedges, which would also have occupied wide spaces of what is nowadays covered by scrubs. Springs and streams were active, leading to the existence of bodies of stagnant water. The good water supply allowed aquatic and phreatic plants to find their way into the digestive systems of hyraxes. This phase was not necessarily related to an increased rainfall, but water availability could have been comparatively higher than in subsequent decades owing to a lower degree of human impact. It is interesting that the drought period of 1930 and earlier did not show an increase in pollen of woody plants. It is possible that the number of these plants were too small at the time and grazing was not intense enough, so that the natural resilience of the vegetation allowed good growth and pollen production of understorey elements, despite droughts.
2. During zone B1, ca.1924 to 1944, the vegetation changed little except that its wetness indicators progressively disappeared. Rainfall oscillations, as indicated by Tysons's index (Fig. 13), seem not to have affected the vegetation cover markedly and bush encroachment is not indicated during the drought period around 1930.
3. During zone B2, for a brief period between 1943 and 1953, an important scrub increase is indicated at the slopes around Rooiberg II shelter. It involves mainly a reduction in grassland cover, but also affected the fynbos. Woody elements, such as *Buddleja* and *Leucosidea*, in the vegetation were more important, possibly providing a palatable diet for hyraxes near the shelter. Increased stock grazing and progressively more fire protection by the local population over the previous decades probably enhanced bush encroachment and this effect only becomes noticeable in the pollen results of these levels. The AP increase is probably exaggerated in the pollen data due to relatively more understorey clearance as result of dry conditions along with grazing pressure at the time (Fig. 13).
4. During zone B3, ca. 1947 to 1965, *Leucosidea* and *Buddleja* pollen experience strong reduction. During this phase electricity was not yet common in the town and high fuel demand might have played a role. The AP decrease probably does not indicate a return to a more open landscape, but good understorey growth and pollen production of this stratum during the wet years which were experienced at that time (Fig. 13; Scott and Vogel, 1992). The increasing town population would have forced hyrax colonies to stay close to their shelters. It is well known that when they are hunted by indigenous people, which often happens, they become elusive (Roberts, 1954).
5. During formation of zone B4, from ca. 1965 to 1982, increased grazing pressure, fire control, and a smaller demand for natural fuel occurred. In combination with a drought period this could account for a new increase in the *Buddleja–Leucosidea* pollen assemblages, of which the parent plants continued to flourish on the slopes of the Rooiberge, as can be seen from the aerial photographs (Scott and Vogel, 1992). The hyrax diet composition would have been similar to that of B2.

Rainfall variability, grazing pressure, fire control and wood demand should therefore have interconnected to determine short-scale vegetation changes in the area for the last century. Although it is not possible to quantify the main factors controlling the observed changes precisely, we can propose a working hypothesis to explain these processes on the basis of the information available. We still need much more ecological research on the time of vegetation response in the grassland and its satellites. According to O'Connor and Bredenkamp (1996), 'community change depends on the influence of communities on the abiotic environment and on species attributes, but the response of species to environment is contextual rather than absolute'. Therefore, every observed event of local change is due to the interaction of different factors with different degrees of influence and for each the history should be determined individually. The topic is further complicated if we consider that, as has been demonstrated for most of the Holocene in the Northern Hemisphere (Bennett, 1997), the response of species has probably been individualistic. The old concepts of climax, potential vegetation, and intermediate stages where species change harmoniously to environmental changes have very much obscured our understanding of both the long-term and short-term climate–vegetation relationships because they have largely ignored the importance of historical processes.

The results of the Rooiberg hyrax dung study demonstrate that pollen assemblages recorded complex processes that took place in the area. Therefore, it is expected that new pollen research on hyrax dung will in future provide much needed palaeoenvironmental information about the Quaternary. Owing to the relatively high humidity in the area, Clarens lies on the limit of the rainfall gradient along which hyrax midden studies are feasible. In this area, where long-term preservation of dung occurs only in the driest, inaccessible rock shelters, most accumulations decompose due to leaching and natural decomposition. Fungal or other contamination in the lowermost layer of the midden, is therefore no coincidence. Over large dry parts of Africa where suitable rock shelters are available, especially in deserts and semi-arid areas, investigations on fossil dung show great promise. It is in these areas where we believe that the potential of hyrax dung studies as a tool in palaeoenvironmental reconstruction has been underestimated, possibly as a result of the relatively poor macrofossil content in these middens. In our view, projects such as the Kalahari Transect study (Scholes and Parsons, 1996) and part of the PEP (Pole-Equator-Pole) III study (Eddy, 1992), could gain from more pollen analyses of products of *Procavia* and other species.

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