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Preservation and interpretation of pollen in hyaena coprolites: taphonomic observations from Spain and southern Africa

Louis Scott[1], Yolanda Fernández-Jalvo[2], José Carrión[3] & James Brink[4]

[1]*Department of Plant Sciences, University of the Free State, P.O. Box 339, Bloemfontein, 9300 South Africa*
[2]*Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal, 2 28006-Madrid, Spain*
[3]*Department of Plant Biology (Botany), University of Murcia, 30100 Campus de Espinardo, Murcia, Spain*
[4]*National Museum, P.O. Box 266, Bloemfontein, 9300 South Africa*

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A survey of palynological research on hyaena coprolites from 10 fossil sites in southern Africa and 4 from Spain shows that coprolites from 10 out of the 14 sites contained fossil pollen. Pollen-bearing coprolites are generally richer in pollen than the surrounding sediments. Provisionally it seems that the sites with poor or no pollen in coprolites are relatively old or have been exposed to wet and dry moisture fluctuations, namely Makapansgat, Gran Dolina, Redcliff Cave and Erfkroon. This suggests that conditions during their long histories eventually destroyed pollen through oxidation associated with regular saturation of sediments. The composition of pollen spectra and preservation of pollen grains from coprolites is compared with that in fresh hyaena dung. SEM studies suggest that pollen grains in fresh dung and in fossil coprolites if preserved under suitable cave conditions, are generally well preserved with little damage. The damage traits require further systematic investigation in order to assess their taphonomic significance but selective destruction of pollen through ingestion, if any, seems to be light. Of particular interest to palaeoenvironmental studies is the observation that pollen assemblages preserved in hyaena dung are likely to provide relatively unbiased characterizations of vegetation representative of the wide surroundings in which the hyaenas were active. This implies that where pollen was relatively well-preserved in coprolites, it can provide palaeoenvironmental information extending beyond the immediate environs of the site in which they were found. Any possible bias introduced through behaviour-related pollen trapping is, however, difficult to exclude.

Keywords: palynology, hyaena coprolites, taphonomy, South Africa, Spain.

INTRODUCTION

Some hyaena coprolites contain rich pollen spectra, e.g. those from Equus Cave, South Africa and Las Ventanas Cave in Spain (Scott 1987; Carrión *et al.* 2001). In arid areas where pollen traps such as lakes and swamps do not occur, coprolite palynology can serve as an alternative to conventional pollen analysis (Scott 2000) although high resolution cannot be expected. When pollen is preserved in hyaena coprolites in caves, preservation often seems to be better there than in the associated sediment. Hyaena scats are durable (Bearder 1977) and probably insulate organic matter, including sporopollenin, more effectively from local oxidizing environments. Several questions arise when pollen from hyaena coprolites are considered as an indicator of palaeoenvironments. In this paper we assess the quality of preservation of pollen grains and their surfaces as well as pollen-assemblage composition in hyaena coprolites from sites in South Africa and Spain

*Author for correspondence. E-mail: scottl.sci@mail.uovs.ac.za

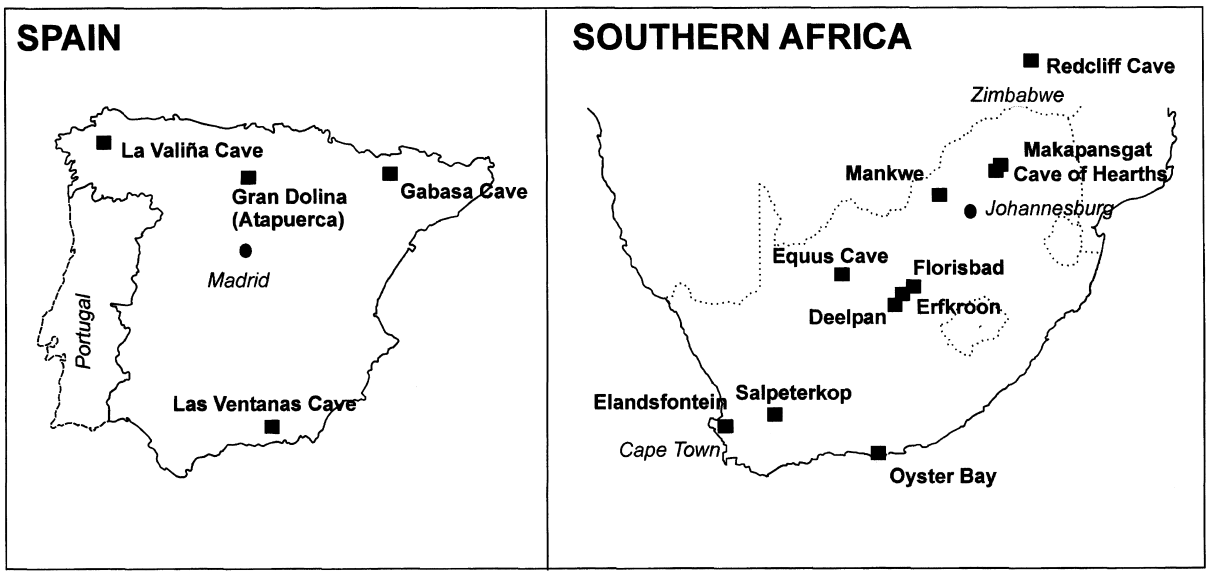


Figure 1. Locations of southern African and Spanish hyaena coprolite sites referred to in the text.

Table 1. Sites in southern Africa and Spain where palynology of hyaena coprolites was attempted.

Region	Site	Reference
Southern Africa	Equus Cave	Scott 1987
	Florisbad	Van Zinderen Bakker 1989; Scott & Brink 1992
	Deelpan	Scott 1987; Scott & Klein 1981; Scott & Brink 1987
	Makapansgat	Scott 1995
	Oyster Bay	Carrión *et al.* 2000
	Erfkroon	Churchill *et al.* 2000
	Cave of Hearths	L. Scott, unpubl. data
	Redcliff Cave	R.G. Klein and L. Scott, unpubl.
	Elandsfontein	Van Zinderen Bakker *in* Singer & Wymer 1968, and notes
	Salpeter Kop	G. Avery & L. Scott, in prep.
Spain	Ventanas Cave	Carrión *et al.* 2001
	La Valiña	Fernández-Rodríguez *et al.* 1995
	Gabasa Cave	González-Sampériz *et al.* 2003
	Gran Dolina	This paper

(Fig. 1). We look for signs of digestion and anomalies in the composition of pollen assemblages and for signs of selective pollen trapping. The investigation involved comparisons of modern and fossil spectra in hyaena dung and those from natural pollen rain in surface soils of the wider surroundings of a scat site. This paper briefly reviews previous studies on hyaena coprolite palynology and is a provisional assessment of its value in palaeoenvironmental studies.

TAPHONOMIC CONSIDERATIONS

An important question is how well pollen spectra in hyaena coprolites are preserved and how well they represent contemporary vegetation. Selective trapping of pollen in coprolites of different hyaena species can be due to behavioural differences. Unfortunately, coprolites cannot always be linked conclusively to particular hyaena species. We believe that, except for the older deposits of Makapansgat (Maguire *et al.* 1980), pollen-bearing coprolites and fresh hyaena dung investigated in this study are derived mainly from brown hyaena (*Parahyaena brunnea*) and spotted hyaena (*Crocuta crocuta*) (Table 1). Since the striped hyaena (*Hyaena hyaena*) occurs in the Middle East, India and North Africa but not southern Africa, we believe that coprolites of this species are not likely to be among the ones we studied. The Spanish materials we studied are all attributed to spotted hyaena. Palaeontological evidence can be useful to distinguish coprolite types where bones of a particular hyaena species together with coprolites give circumstantial evidence about the species involved. The three Spanish caves La Valiña, Las Ventanas and Gabasa have spotted hyaena bones and relatively large coprolites (Fernández-Rodríguez *et al.* 1995; Carrión *et al.* 2001; González-Sampériz *et al.* 2003; Table 1). The size and nature of the hyaena scats are diagnostic. For example, spotted hyaena scats (*c.* 35–44 cm) consist of pellets larger than those of brown hyaena (25–40 cm) and often include bone fragments (Skinner 1976) (Fig. 2). Distinction of scats of the two species on the basis of size can, however, be problematic because of possible overlap. This is even more problematic between coprolites of brown hyaena and the closely related striped hyaena.

Although spotted hyaenas may sometimes leave bones at open feeding sites (Dart & Craig 1959), they are also known to accumulate bones in caves and burrows (Kruuk 1972; Bearder 1977; Sutcliffe 1969, 1970). Although they include some fruits and seeds in their diet, brown and striped hyaenas often accumulate large numbers of bones in dens where their young are raised (Skinner 1976; Skinner *et al.* 1980; Skinner & van Aarde 1980; Siegfried 1984; Mills 1989).

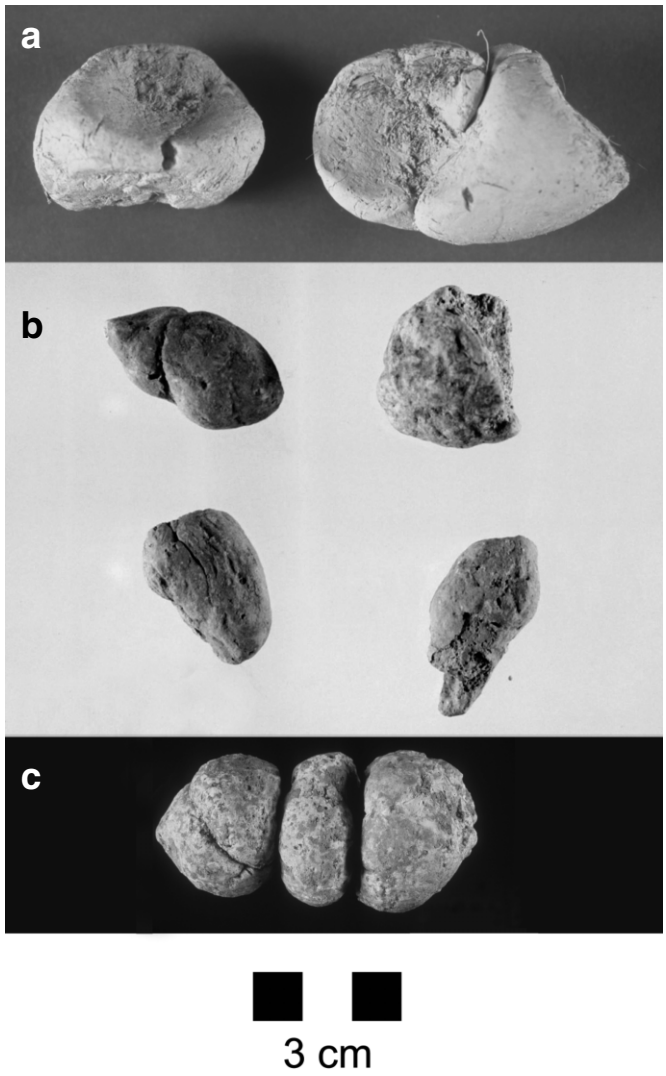


Figure 2. **a**, Fresh *Crocuta* dung from Laetoli; **b**, *P. brunnea* dung from Equus Cave; **c**, coprolite from Gran Dolina TD6, Atapuerca, Spain.

Table 2. Productivity and age of hyaena coprolites used in palynological analysis (for references see Table 1).

Site	Site type	Type of hyaena	Age or culture	Productive coprolites
Deelpan	Burrow	*P. brunnea*	~100–200 yr	5/5
Salpeter Kop	Cave	*P. brunnea*	100 yr	3/3
Equus	Cave	*P. brunnea*	Up to 27 ka	39/50
Las Ventanas	Cave	*C. crocuta*	~9.5–10.7 ka	10/25
Gabasa	Cave	*C. crocuta*	*c.* 40–50	8/12
La Valiña	Cave	*C. crocuta*	*c.* 35 ka	4/8
Oyster Bay	Burrow	*P. brunnea*	~70 Ka?	9/12
Florisbad	Spring	*C. crocuta*	> 250 ka	6/6
Erfkroon	Burrow	Unidentified	MSA	0/4
Redcliff	Cave	*C. crocuta*?	MSA	0/1
Cave of Hearths	Cave	*C. crocuta*	ESA	1/5
Elandsfontein	Surface	*P. brunnea*?	ESA (Midle Pleistocene)	14/?
Gran Dolina	Cave	*C. crocuta*	~780 ka	0/2
Makapansgat	Cave	*H. hyaena makapani*	2.6 million yr	0/23

The relative importance of different pollen sources cannot be easily determined in individual coprolites. It is important to know how pollen is trapped and what part of the assemblage was ingested accidentally or through feeding. The sources might include dust that settles on food before ingestion, dust that settles on dung after defecation, flowers in hyaena diets, or pollen contained in drinking water. All these possibilities probably occur and could potentially result in a biased pollen composition. Spotted hyaenas do not consume the rumen contents of herbivorous prey (Smithers 1983: 361) while rumen and viscera seem to be the least popular parts eaten by brown hyaenas (Bowland *et al.*, no date). A bias in pollen composition from this source therefore seems possible but probably not typical.

Previous studies suggest that hyaena coprolites in general are not markedly biased compared with the regional pollen rain (Scott 1987; Carrión *et al.* 2001). This suggests that much of the pollen in hyaena dung is accidentally ingested. For instance, leaves ingested by hyaenas are good pollen traps and reflect local vegetation both in terms of species composition and relative cover (Gutiérrez *et al.* 1998), but ingestion of pollen-rich flowers may cause a bias in composition. Massive over-representation of one pollen type in a coprolite may be a sign of ingestion of whole anthers, but this has not been obvious in previous studies of hyaena dung.

When coprolites have been consolidated with fixative glue, e.g. in some cases from Makapansgat, it sealed modern pollen contaminants from the time of excavation in cracks (Scott 1995). It is therefore essential first to remove the coprolite surface before extracting pollen. Cleaning in the laboratory before sample preparation may remove fossil pollen clinging to the original surfaces which might differ slightly in composition from ingested pollen. By removing the surface we are likely to obtain only the ingested portion of the pollen. If the pollen source is mainly through accidental ingestion, removal of the outside layer therefore would not affect pollen composition significantly. In view of the relatively better preservation evident in coprolites compared to the surrounding sediment matrices (Scott 1987; Carrión *et al.* 2001), it is likely that the surfaces of faeces would experience more unfavourable conditions for pollen preservation than interior parts. Therefore the loss of surface would not affect composition greatly.

Apart from individual pollen grains, other coprolite inclusions can provide information about hyaena behaviour, e.g. insect remains, parasites, fungi, hair and plant remains. The Las Ventanas Cave hyaena coprolite preparations showed algal zygospores possibly derived from drinking water (Carrión *et al.* 2001).

The amount of pollen in hyaena coprolites varies from nil to extremely rich (290 000 grains per gram) (Carrión *et al.* 2001). Primary factors such as seasonal pollen scarcity might affect numbers. Since it is unlikely that no pollen would be present, secondary factors such as selective preservation through gastric action or sediment conditions may play a role. Where pollen is consistently absent in several coprolites from the same site, unfavourable conditions for preservation over the long term are probably the cause. Good as well as poor fossil pollen preservation, including exine thinning, has been reported in coprolites from sites such as Equus Cave and Oyster Bay (Table 2) (Scott 1987; Carrión *et al.* 2000). This could either be attributed to gastric conditions in hyaenas or long-term conditions in the sedimentary environment. Sporopollenin is very resistant to corrosive acids, e.g. HCl and HF, and therefore it is unlikely that acids in hyaena stomachs will corrode pollen.

Experimentation to establish whether enzymatic corrosion as well as acid action in a hyaena's stomach is responsible for specific damage patterns on pollen is not the subject of this study. The procedure we follow is, first, to search for obvious signs of alteration in the morphological features of pollen grains by scanning electron microscopy, as in the case of pollen in modern owl pellets (Fernández-Jalvo *et al.* 1999). Second, we compare the pollen assemblage in a hyaena scat with the regional pollen composition to search for biases. Bias can, for instance, be introduced when local vegetation at a particular site differs from that of the wider surroundings and coprolite pollen spectra appear to generally reflect the latter (Scott 1987; Scott & Brink 1992). This suggests that pollen is

collected largely during hyaena movements away from dens. Furthermore, small dung pellets that are often recorded at dens may be those of young hyaenas. Since they do not venture far from their dens they may be more likely to represent the immediate surroundings. However, their food is brought in from wider surroundings and this would introduce a regional component. In addition, any atmospheric pollen rain, such as can be expected in coprolites, will represent a regional component.

PREVIOUS WORK

At least 10 hyaena sites in South Africa and four in Spain (Fig. 1) have been subjected to palynological examination of coprolites (Tables 1 & 2). Hyaena coprolites have also been studied in other regions such as Israel, Sicily, France and Britain (Sutcliffe 1969, 1970; Horwitz & Goldberg 1989; Larkin *et al.* 2000; M. Weinstein-Evron, J.A. López Sáez & A. Cinzia, pers. comm.) but published pollen records for these areas were not available to us. Information regarding the nature and age of sites containing coprolite and pollen yields are shown in Table 2. Five examples of hyaena coprolite palynology are discussed below.

Deelpan

Hyaena coprolites and bone accumulations were discovered in in-fillings of a hyaena burrow in Late Holocene lunette dunes on the eastern edge of Deelpan, a playa lake (Scott & Klein 1983). The rich bone assemblage indicates a brown hyaena den. The pollen assemblages were compared with surface pollen samples from the surroundings of Deelpan (Scott 1987; Scott & Brink 1992). The high proportion of grass pollen in the coprolites differed from the local pan spectra, suggesting that the hyaenas preferred the distant grassy surroundings of the pan using the burrow only for shelter and breeding. Although the bones from the den were thought to be Late Holocene, previously unpublished radiocarbon dating showed that they were surprisingly young (Scott & Brink 1992). The dates on bone collagen (120 ± 45 yr BP, Pta-6348; 150 ± 20 yr BP, Pta-6346) show that the den represents the period immediately before or during the first arrival of Boer settlers in the region. The fossil bones together with the coprolites are of interest because they give evidence of the environment in the western Free State just before farming disturbance and the introduction of cattle and sheep that largely replaced the original fauna.

Equus Cave

A rich accumulation of Late Pleistocene and Holocene bones and brown hyaena coprolites was collected from Equus Cave (Scott 1987; Klein *et al.* 1991). Compared with pollen in the surrounding sediment matrix, pollen spectra from the coprolites represent an open grassy environment. This suggests that the hyaena coprolites contained more pollen from the wider environment than from the slopes around the cave, which are naturally likely to have been more wooded than open areas (Scott 1987). The coprolite pollen yield is also richer than that recovered from the sediment matrix. The pollen sequence demonstrates a transition from cool Late Pleistocene vegetation with grass and small shrubs to the warmer environment of the Holocene containing more woody shrubs.

Oyster Bay

Several coprolites were discovered in a soil horizon on an open-air coastal site at Oyster Bay (Carrión *et al.* 2000). The size of the pellets suggests but do not prove that they relate to brown hyaenas. The soil possibly represents deflated remains of hyaena burrows and also contains vertebrate remains conforming to other early Last Glacial assemblages. Except for recently exposed specimens, the bones in the original soil did not show wind abrasion and therefore no signs of reworking. The association of these finds with Howieson's Poort-type artefacts is not clear but these possibly represent a surface broadly contemporaneous with the faunal burrows. The pollen contents of the coprolites, however, suggest an environment different from that along the present coast, indicating conditions typical of higher altitudes and therefore cooler conditions with the coastline not as near as at present. Sediments associated with coprolites were not tested for pollen but they appeared to be typically unproductive sands, while the original sedimentary context and burrow structure was probably lost.

Florisbad

Middle Pleistocene hyaena coprolites associated with a rich faunal assemblage and Middle Stone Age artefacts from spring sediments at Florisbad spring were attributed to spotted rather than brown hyaenas on the basis of size, the presence of bone fragments and taphonomical associations (van Zinderen Bakker 1989; Scott & Brink 1992). The grass-dominated pollen from the coprolites compared with the spring sequence that includes local pan halophytes (Chenopodiaceae) and spring sedges, suggests hyaena activity in the grassy surroundings of the spring and saltpan. The grass pollen represents one of the moist grassy phases in the sequence that shows strong variations between grass, sedge, Asteraceae and Chenopodiaceae (van Zinderen Bakker 1989; Scott & Brink 1992).

Las Ventanas

Thousands of coprolites and abundant bone remains of spotted hyaena (*Crocuta crocuta*) were found in association with bones of their prey in Las Ventanas Cave in Spain (Fig. 1). Coprolites were dated to between *c.* 9500 and 10 500 yr BP (Carrión *et al.* 2001). Despite the lack of pollen in some coprolites, ten of them showed good pollen preservation and diversity and concentrations of up to approximately 290 000 pollen grains per gram. The surrounding sediments were barren of pollen (Carrión *et al.* 2001). The coprolite pollen record is similar to that from Late Glacial sediments in an adjacent archaeological cave site and other regional pollen records.

MATERIALS AND METHODS

The pollen from two coprolites in Las Ventanas Cave and pollen from three modern brown hyaena pellets from Mankwe (Fig. 1), were studied by scanning electron

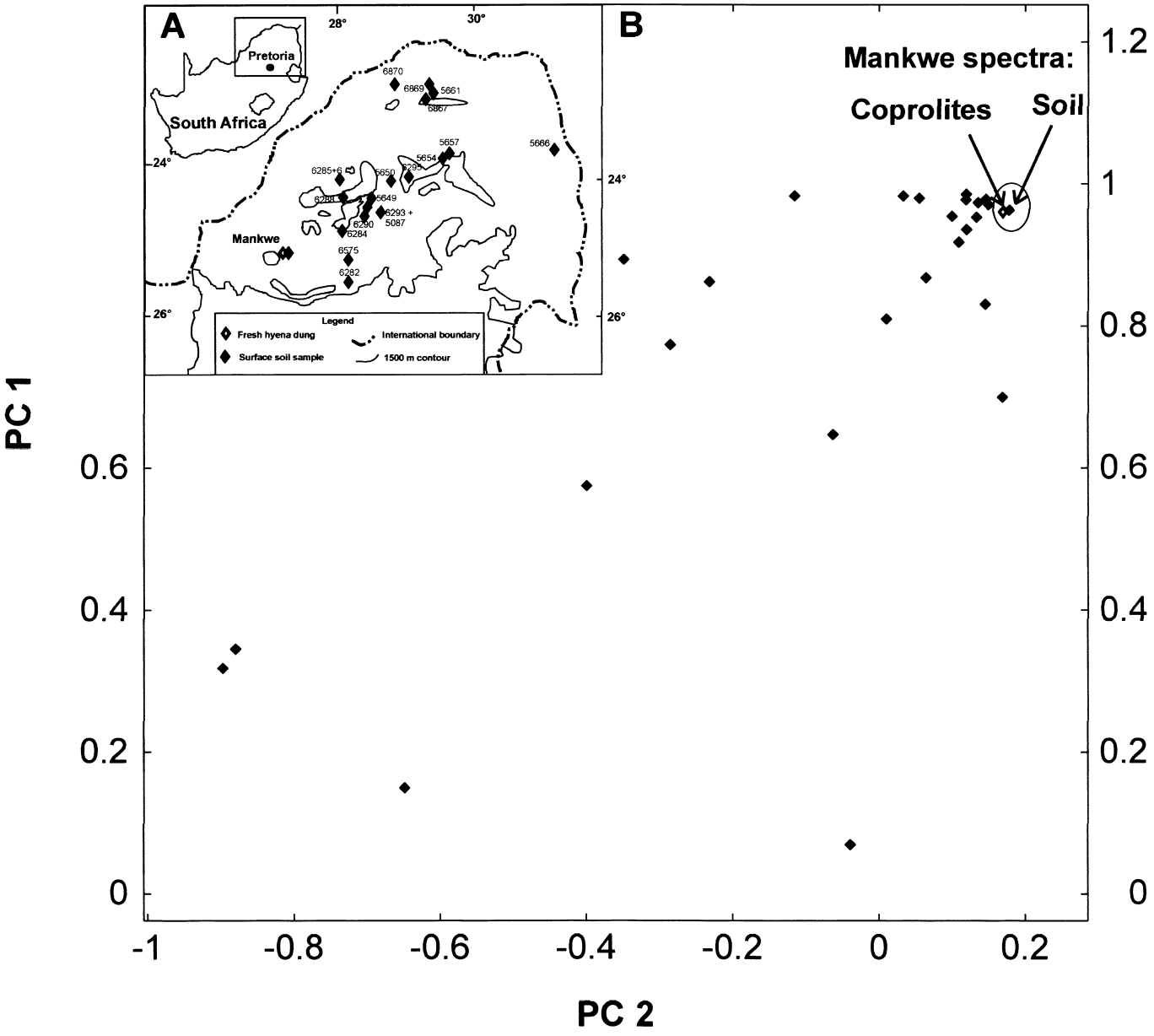


Figure 3. **A**, localities of surface pollen samples from Bushveld region and hyaena coprolites from Mankwe; **B**, PCA of dung and surface pollen spectra from bushveld region.

microscopy. Pollen types in the latter were counted under a light microscope. The samples from Mankwe (Fig. 1) and of five modern spotted hyaena dung samples from Laetoli (Serengeti, Tanzania) were processed for light microscopy. Since coprolites are destroyed during chemical extraction of pollen, we first tested fragments from two coprolites of the Grand Dolina site (Atapuerca, Spain). When they proved to be sterile we saved the better specimens for other purposes because it was likely that they also do not contain pollen (Fig. 2).

Before extraction of pollen from the coprolites and dung, pellets were thoroughly cleaned to remove their outer layers. The samples were then crushed and immersed in 10% HCl, followed by 40% HF treatment to break up coprolite matrices to release pollen. The samples then underwent mineral separation using $ZnCl_2$ solution with a specific gravity of 2. Pollen concentrations were determined according to the method of Stockmarr (1971). Pollen residues were mounted on stubs for SEM investigation, while some were mounted in glycerine jelly for light microscopy.

A modern pollen spectrum from local soil was obtained for comparison with the Mankwe dung material. These spectra were also compared with previously published modern spectra of surface soils from the wider savanna and grassland region (Scott 1982) (Fig. 3A). In order to look for differences between hyaena dung and soil pollen assemblages the total data set was subjected to principal components analysis (PCA).

RESULTS

Together with pollen, numerous other items, including plant fibres, fungal spores, microscopic charcoal, insect remains and unidentified objects were recorded. The minute spherical bodies (*c.* 2 μm) found in abundance in owl pellet preparations that might represent pigment

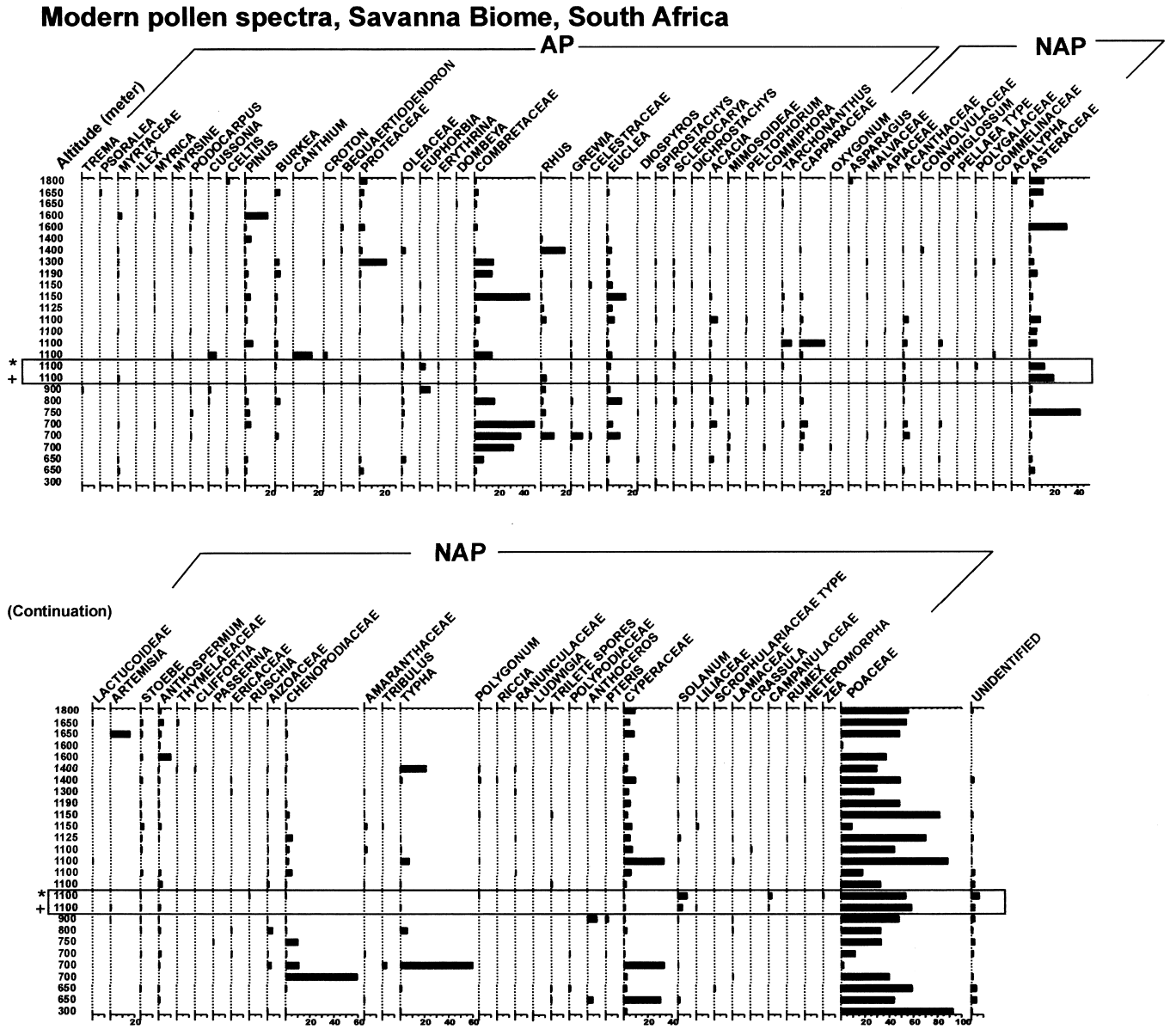


Figure 4. Comparison of modern pollen spectra from Mankwe dung (*) and soil (+) compared with soil pollen spectra from savanna and grassland samples in South Africa (Scott 1982). The dung spectrum was derived from counts on three pellets.

bodies from prey hairs (Fenández-Jalvo *et al.* 1999, unpubl. data) were not found in the hyaena dung. The resistant, transparent covering of owl pellet pollen, which is invisible under a light microscope, was also not found in hyaena coprolites. Relatively high pollen concentrations, ranging between 1300 and 93 000 grains per gram (Table 3) were recorded for modern dung pellets from Mankwe and Laetoli, respectively. No pollen could be found in the Early Pleistocene coprolite fragments from Gran Dolina, Atapuerca. Modern coprolite pollen assemblages in the hyaena dung from Mankwe are presented in Fig. 4 together with previously published surface pollen spectra (Scott 1982). It appears that the dung spectra show variability that places them within the range of surface pollen spectra. These results of PCA suggest that the coprolite pollen spectra conform well to the surface pollen data from the region, falling within the general cluster, albeit in a slightly peripheral position (Fig. 3B). This position cannot be considered to indicate a significant difference in view of the slightly out-lying geographical position of the Mankwe samples compared with other localities. Further, the Mankwe coprolite and soil-surface spectra show great similarity to each other and compared with pollen data from regional soils, suggest that coprolites give a good reflection of the regional pollen rain. The pollen grains in fresh spotted hyaena dung from Laetoli were not subjected to SEM investigation. Examination under a light

Table 3. Pollen concentrations in modern brown and spotted hyaena dung pellets from Mankwe and Laetoli.

Site and hyaena species	Pollen grains per gram
Mankwe, *P. brunnea*	30837
Mankwe, *P. brunnea*	48986
Mankwe, *P. brunnea*	8163
Laetoli, *C. crocuta*	1273
Laetoli, *C. crocuta*	1827
Laetoli, *C. crocuta*	92759
Laetoli, *C. crocuta*	4107

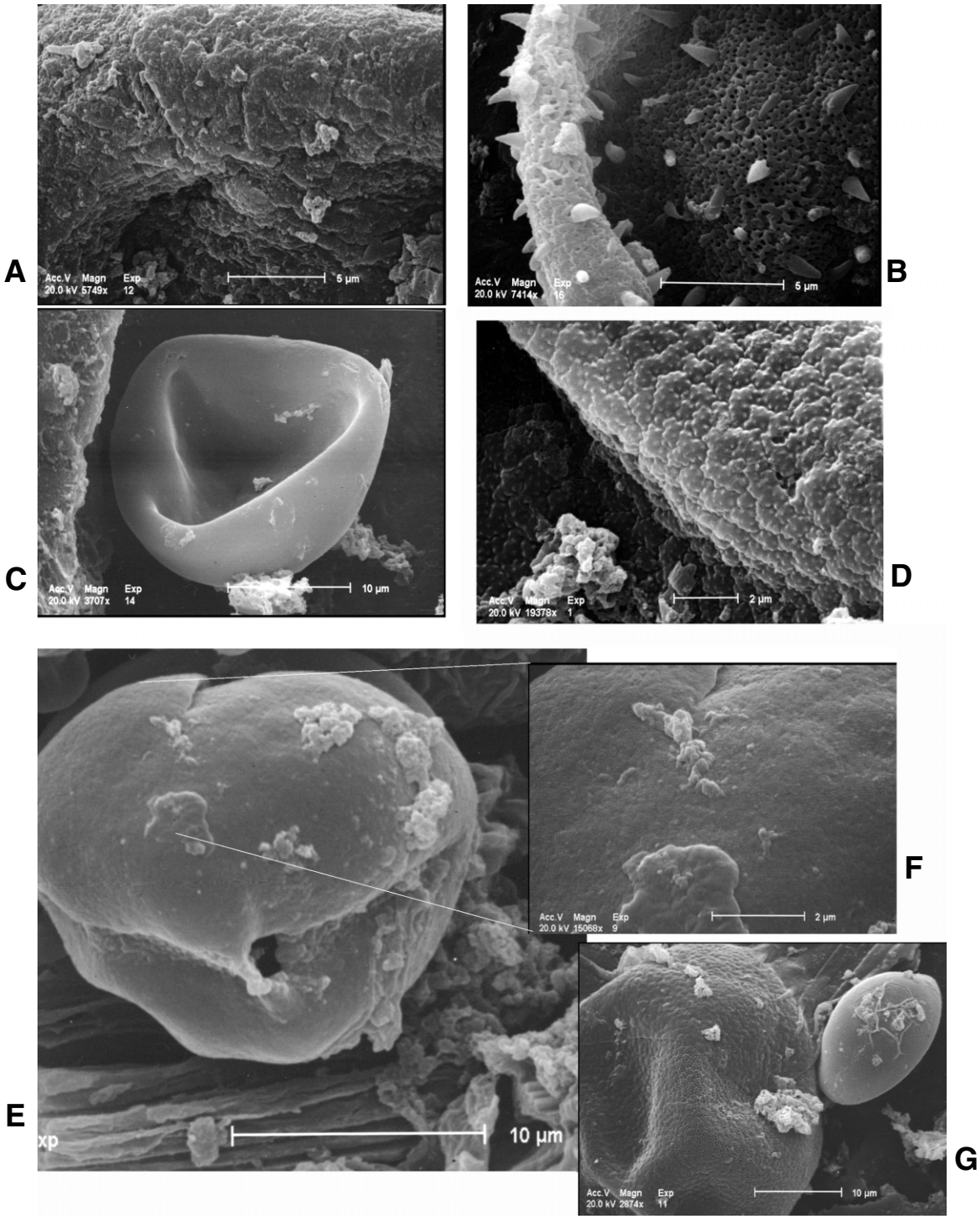


Figure 5. Palynomorphs (pollen and other microscopic objects) from fresh *Parahyaena brunnea* dung from Mankwe that show light signs of corrosion. **A**, an apparently corroded (flaked) surface of an unidentified pollen type. **B**, unidentified pollen with spine-covered surface showing an irregular reticulate pattern that might be a sign of corrosion. **C**, smooth structure, probably of fungal or algal origin, showing minute cracks. **D**, grass pollen grain surface showing generally good preservation except for a small area of pitting. **E**, a smooth colporate pollen grain (unidentified), showing a crack, a small cover patch and other minute loose debris (lines indicate area enlarged in F). **F**, detail of E. It is uncertain whether the cover patch (in E and F) is the remains of an outer layer, a swelling, or a foreign object. **G**, a grass pollen grain with well preserved surface, an unidentified elliptical structure (fungal spore?) showing narrow linear ridges, and loose debris.

microscope revealed their preservation to be excellent. The SEM results for modern brown hyaena coprolites from both Mankwe (Fig. 5 D,G) and spotted hyaena coprolites from 10 000-year-old sediments in Las Ventanas Cave (not illustrated) show generally well preserved pollen grains, although signs of limited damage can be seen. Some cases of fracturing are noticed on unidentified structures (probably fungal remains) from the scats (Fig. 5C) but we restricted our observations mainly to grains that could be identified as pollen. At least 15 of the more than 20 pollen grains in Mankwe scats and Las Ventanas Cave coprolites showed no signs of corrosion or damage, although some of the Las Ventanas specimens were severely folded or partly obscured by fine debris from the coprolite, rendering it difficult to assess the damage.

DISCUSSION AND CONCLUSIONS

Since coprolites in caves and burrows in some cases contain high numbers of pollen, e.g. those in Las Ventanas Cave, Spain, which yielded between 20 000 and 290 000 grains per gram (Carrión *et al.* 2001), it seems that high numbers in scats can be retained under favourable conditions. After being subjected to acid gastric environments, encapsulation of pollen in hyaena faecal material appears to aid preservation by affording protection against direct sunlight and moisture fluctuations until the scats disintegrate or are buried and preserved. The condition of pollen in modern hyena scats seems to be generally good judging from the preservation of pollen surfaces from Mankwe and of Laetoli, which show no abnormal signs of corrosion. Van Zinderen Bakker & Müller (1987) also made no mention of any such corrosion on pollen in similar dung from the Namib Desert. The condition of pollen grains in Las Ventanas Cave coprolites indicates that generally good preservation of pollen can be expected back to at least 10 000 years despite folding of pollen grains.

The small degree of fracturing and surface flaking that has been observed on pollen from the modern hyaena scats and fossil dung may be the result of gastric juice digestion. Experimental work on damage traits is needed to establish if they exceed the degree of natural damage of pollen in the environment. As yet no published statistical observations of corrosion and fracturing of natural pollen spectra are available for comparison. Exine thinning that we observed previously in Equus Cave and Oyster Bay pollen grains (Scott 1987; Carrión *et al.* 2000) may or may not have been caused by gastric action. Outer surfaces of pollen seem to be unaffected but we did not examine inside surfaces of pollen by SEM. If gastric thinning of exine did occur it might have happened on the inner (endexine) layer due to differential resistance, but as yet there is no evidence for this. An alternative explanation for exine destruction or thinning could, however, be long-term post depositional deterioration due to local conditions in sediments. It seems more likely to find pollen in relatively young fossils (Table 2). In contrast with the good pollen yields from 10 000-year-old coprolites from sites such as Las Ventanas Cave, no pollen has been recorded in coprolites from Gran Dolina, Atapuerca, which have been preserved *c.* 780 000 years since their burial (Parés & Pérez-Gonzalez 1999). Pollen is also missing from the 2.6-million-year-old coprolite-rich layer at Makapansgat (Scott 1995). The lack of pollen in coprolites from these older sites and the exposed site Erfkroon (Table 2) (Churchill *et al.* 2000) may be due to unfavourable local events such as moisture saturation and accompanying oxidation episodes in surrounding sediments at specific times during their long histories. On the other hand, the Middle Pleistocene pollen in coprolites from the Florisbad spring, which are possibly more than 200 000 years old (Scott & Brink 1992) is well preserved when viewed under a light microscope. This good preservation is probably due to reducing conditions in the spring deposits that also preserved rich pollen in the surrounding sediments. Pollen grains were extracted by van Zinderen Bakker from coprolites from Elandsfontein (Singer & Wymer 1968) that are of last glacial age but may be 400 000 years old. Unfortunately, there is no record of their exact provenance (G. Avery, pers. comm.).

It can be concluded that 1) although age appears to be related to the survival of pollen grains in coprolites, their preservation under reducing or moisture-free conditions rather than oxidizing conditions appears to improve their potential for long-term preservation. 2) Pollen spectra in hyaena dung are representative of the whole area in which hyaenas move around and not only that around the hyaena habitation site. 3) It must be kept in mind that hyaena behaviour, e.g. dietary preferences like ingestion of flowers, or consumption of viscera as proposed in the case of Las Ventanas Cave coprolites, might influence pollen spectra (Carrión *et al.* 2001). 4) Variability between individual coprolite pollen spectra and pollen rain needs to be investigated thoroughly to identify such effects. 5) In general, however, on account of good preservation of pollen in coprolites, and the apparently random pattern of palynomorph trapping, hyaena dung can potentially provide a good reflection of regional palaeoenvironments.

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