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The challenge of pollen analysis in palaeoenvironmental studies of hominid beds: the record from Sterkfontein caves

The search for pollen in carbonate-rich sediments from the hominid site Sterkfontein has been justified because previous investigations suggested that although pollen contamination is a problem, speleothems (e.g. travertines and stalagmites) are most likely to contain reliable assemblages. The new results confirm that, although they have some potential, most sediment types from the site, even speleothems, are usually not suitable for analysis and that they contain very low concentrations of pollen, if any. The extraction of pollen from them is complicated by the problem of contamination from the modern environment. Such contamination has shown up in many previous investigations at this and similar sites and judging from published literature, its significance has not been fully appreciated. Cave palynology can be a very valuable tool in palaeoenvironmental research but the caveats associated with palynology of different sediment types especially carbonate impregnated sediments must be emphasized.

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Introduction

Palynologists who have dealt with palaeo-anthropological excavation sites are aware of the pressure to provide an environmental picture from pollen data, even when the quality of pollen assemblages does not warrant reliable answers. The major taphonomic constraints and the potential for pollen analysis in these sites, especially in the case of sediments poor in organic matter, have not been satisfactorily assessed by palynologists, physical anthropologists and archaeologists. Although palynology has formed part of interdisciplinary research for decades, many interpretations of pollen assemblages in archaeological and palaeontological sites have gone too far in their claims as is suggested by Sánchez-Goñi (1994) and Carrión *et al.* (1995a).

We present new pollen results from carbonate rocks of the renowned australopithecine-bearing cave Sterkfontein,

Gauteng in South Africa (Clarke & Tobias, 1995). They support our view that palynology is not always applicable in these deposits because of poor pollen contents and the great chance of contamination. Sterkfontein, like other South African sites, is well placed for the recognition of recent pollen contamination in cave deposits because both the atmosphere (Cadman, 1991) and modern surface soil (Scott, 1995) contain a strong signal of recently introduced elements from the floras of other continents.

The cave deposits available for palynological investigations in solution cavities are limited. In this paper we are not dealing with the organic material like packrat middens or hyrax dung (Betancourt *et al.*, 1990; Scott, 1994), or with unconsolidated floor deposits in caves (Carrión, 1992), but with consolidated carbonate impregnated materials. The midden and dung deposits have their own problems but they are useful

because of their richness in pollen. Unconsolidated cave floor deposits can be problematic under conditions of dampness, oxidation and microorganism activity, but successful in arid areas where they can be ruled out (Davis, 1990; Carrión, 1992; Scott, 1987). The most typical and obvious consolidated sediments to experiment with in hominid caverns like Sterkfontein (Partridge and Watt, 1991), are the so-called breccias which consist of clastic elements including silt, sand, gravel and bone cemented together by carbonate crystals (Horowitz, 1975). The original aerated environment before the cementation process even started may not be good for pollen preservation. Cementation could have happened once or more often during the long history of cave sediments and may have involved several cycles of dissolution and recrystallization. Oxidation associated with these processes are likely to have destroyed the pollen grains which originally formed part of a breccia matrix. The resultant breccia rocks are often porous, which may allow percolation and incorporation of younger pollen through recrystallization (Scott, 1982a; Scott & Bonnefille, 1986). Breccias may contain coprolites (fossil dung pellets) that are capsules in which pollen may be protected from processes in surrounding matrix. However, those from Makapansgat were not productive and only coprolites from unconsolidated cave sediments e.g., those in Equus Cave, have proved to be useful (Scott, 1987, 1995). Flow stones or speleothems like stalagmites or travertines which consist of pure carbonate precipitated from flowing or drip-water, can trap pollen grains if the precipitation locality is in contact with the atmosphere outside the cavern (Bastin, 1979; Scott & Bonnefille, 1986; Burney *et al.*, 1994). If the original lamination is still visible, it is not likely that destructive processes such as recrystallization have affected the pollen.

The first palynological study at Sterkfontein was carried out by Horowitz (1975), from one big breccia sample of Member 5 of the Sterkfontein Formation (Partridge & Watt, 1991), which was compared with a sample of recent soil from the site. He processed almost 2.5 kg of travertine, recorded thousands of pollen grains in the slides, and suggested open Plio/Pleistocene grassland vegetation and dry climate for the time when the cave sediments were accumulated, and inferred a warmer and more humid climate for a subsequent phase of travertine consolidation. This amelioration was deduced from an assemblage reputedly containing *Podocarpus* (yellow wood) and *Euphorbia* (candelabra trees) pollen (Horowitz, 1975), an unusual combination from an ecological point of view. Further work by Scott (1982a) and Scott & Bonnefille (1986) drew attention to caveats associated with the palynology of the South African hominid deposits. Re-investigating the material from Sterkfontein, they showed that the pollen spectra had been subject to contamination, at least by *Pinus*, which is similar in appearance to *Podocarpus*. In addition, exposed travertines and breccias from Members 4 and 5 were investigated in the context of a wider study including similar hominid deposits nearby, namely at Kromdraai and Swartkrans. From Sterkfontein and Kromdraai, only rare samples were found to be relatively free of exotic pollen contaminants and suggested open grassland with some *Protea* woodland (Scott & Bonnefille, 1986; Scott, 1995). These samples comprise stalagmite and travertine material, and appear to be more suitable for pollen analysis than the breccias. They have low porosity, which diminishes the chances of post-depositional water percolation, fresh pollen penetration, recrystallization and oxidation of organic contents. Contaminants can be cemented to their outer surfaces, but are easy to remove.

Table 1 Samples from the Sterkfontein Formation

Grid	Member	Depth	Lab Number
Travertines from shed:			
M/64	Mb5	7'1"–8'2"	(2005)
M/64	Mb5	7'1"–8'2"	(2006a,b)*
M/64	Mb5	No2 SLB	(2004)
Travertines from excavation site:			
M/63	Mb5	8'4"	(2007)
R/65	Mb5	16'10"	(2008)†
J/46	Mb4	13'7"	(2009)
J/46	Mb4	13'7"	(2010)

*a=breccia piece.

†Included some breccia.

Since the results of Scott & Bonnefille (1986) and Scott (1995) suggested that travertines have potential, a series of these samples from borehole cores of the sediments, supplied by Partridge, were also examined (Partridge & Watt, 1991). No results of this work are reported here (Scott, unpublished data) because the samples proved to be unproductive, possibly because the travertines formed in underground chambers with no direct contact with the outside atmosphere and its microscopic dust and pollen. The negative results prompted us to investigate larger samples of travertine in order to see if this will improve the pollen counts.

Methods

Samples were taken for pollen from Members 4 and 5 of the Sterkfontein Formation. The locations according to the grid map of Kuman (1994) are shown in Table 1. The samples ranging in weight between ca. 150 g and 3.5 kg (Table 2) were broken from surface exposures. They consisted of pure white calcium carbonate with no visible porosity such as in breccias. Long-term trapping experiments have shown that it is possible to virtually eliminate pollen contamination within a labora-

tory if certain techniques are employed (Burney & Burney, 1993; D. Burney, pers. comm.). Although the processing was not done in a laboratory with positive air pressure as is recommended, it happened during winter when atmospheric pollen concentration is at its lowest. Routine palynological processing of fossil materials in this laboratory over several years suggested that pollen contamination is very rare but noticeable in the form of, for example, exotic *Platanus* pollen, derived from plants near the laboratory. In order to purify the samples, roughly the outer centimetre of sediment was dissolved by 10% hydrochloric acid. The resulting liquid contained palynomorphs that included fresh and light-coloured pollen grains with cell contents, a sure sign that they are derived from the modern environment. HCl treatment on the cleaned sample followed and because of the high calcium carbonate content of the sample and the big volumes treated, the procedure of dissolution took several days in a fume cupboard, in closed containers to avoid air contamination of pollen. The preparation followed the standard HF methods, with heavy liquid mineral separation using ZnCl₂ solution with a specific gravity of 2 (Gray, 1965). Acetolysis, the method which artificially "fossilizes" pollen, was not undertaken in order to distinguish possible contaminants.

Results

Given that, in most cases, a statistically valid pollen count was not obtained for calculating percentages, we present the original counts in Table 2. One of the samples (#2010) contained no pollen at all. Only one (#2004) exceeded a total of 200 pollen grains but these were mostly not well preserved. Palynomorph concentrations were extremely low: from 19 to 628 grains per kilogram (including cryptogam spores). However, we found considerable pollen diversity of taxa typical of the pristine South

Table 2 Palynological results from Sterkfontein travertines of Members 4 and 5

Sample no.	2004	2005	2006a	2006b	2007	2008	2009
Grid	M/64	M/64	M/64	M/64	M/63	R65	J/46
Member	5 (#2slb)	5	5	5	5	5	4
Weight (g)	3520	2179	148	250	3209	258	238
Palynomorphs/kg	130	40	331	240	19	318	628
Exotic plants							
<i>Pinus</i>	16	8	6	5	3	1	6
Cupressaceae	56	8			2		
<i>Cedrus</i>	5						
<i>Eucalyptus</i>	13						
Myrtaceae	5		2	1		4	
Trees and shrubs							
<i>Acacia</i>	2	1				1	
<i>Podocarpus</i>	1						
<i>Rhus</i>	22	1		1			
Sapotaceae			1				
Combretaceae	2						
<i>Diospyros</i>						1	
<i>Myrsine</i>			1				
<i>Myrica</i>			1	1		1	
Proteaceae				1			
Oleaceae				3		3	
Rhamnaceae			1				
Small shrubs and herbs							
Acanthaceae	3						
Poaceae	34	5	14	14		11	5
<i>Cerealia</i>						2	
<i>Eriocaulon</i>			1				
Ericaceae	5						
Restionaceae				2		1	
<i>Cliffortia</i>	2	1		1	1		
<i>Anthospermum</i>	3			4			
Asteraceae	5		2	7		10	
<i>Artemisia</i>	2		3	1	1	2	
<i>Gumera</i>			1			1	
Other herbs	16		4	5	2	8	8
Spores and other structures							
Fern spores	6						6
Moss spores	14						
<i>Glomus</i>	198	58			46	22	126
<i>Tilletia</i>	2	2					
<i>Gelasinospora</i>	3	1					
<i>Closterium</i>	2						
<i>Spirogyra</i>	2						
<i>Pseudoschizaea</i>	3	2			3		2
Type 229	8						
Unidentified	29	1	8	10	1	14	4
Total	460	88	47	60	62	82	149

African environment in the surroundings of the Gauteng province, e.g., Combretaceae, Sapotaceae, *Rhus*, *Diospyros*, *Acacia*,

Poaceae (Scott, 1982b). Pollen grains from exotic plants were found in comparatively high numbers (*Pinus*, *Cedrus*, Cupressaceae,

Eucalyptus, and other Myrtaceae). Likewise, there were indicators of water transport such as *Closterium* and *Spirogyra* zygospores, *Pseudoschizaea* shells (Scott, 1992), the algal Type 229 (van Geel *et al.*, 1989), and a diversity of fern spores including *Asplenium*-like sporomorphs. Indicators of organic matter decomposition such as *Gelasinospora* and some plant parasites like *Tilletia*, were present, but, among the fungi, the most abundant were the *Glomus* chlamidospores. In some archaeological beds, *Glomus* was shown to coincide with events of root activity, soil removal, and reworking of pollen assemblages (Carrión *et al.*, 1995b). They possibly represent recent processes, but the situation could be different in the carbonate strata of Sterkfontein where *Glomus* may well have been introduced by water and/or dust at an earlier time in speleothem history.

Discussion

As their quantities are relatively low and some of them showed cytoplasm, we cannot exclude the possibility that despite precautions, a number of exotic pollen grains settled in the samples out of the air during the lengthy laboratory processing. This is a problem that one would not expect in smaller and richer samples, like the material studied by Burney *et al.* (1994) from Drotzky's Cave. The contamination would imply even lower pollen concentrations for the travertines. The other possibility is that contaminants were already incorporated in the travertine layers and were not effectively removed by our pre-treatment. This would imply some recent localized decalcification and subsequent recrystallization of the sediment several millimeters below the surfaces of samples, and seems unlikely. Although precautions can minimize it, contamination can in fact come from anywhere and the main problem is to recognize it. Apparently some pollen grains in the studied travertines

are really of ancient origin but their numbers are low. The low concentrations may hypothetically be the result of deposition in chambers with no direct contact with the atmosphere outside the cave. It is difficult to know how far the studied sample localities were from the nearest ancient cave opening, what its size was, and if ventilation was enough to allow pollen and dust transport. Taphonomic evidence of pollen input in modern caves is restricted to a couple of studies in which Tauber traps (Burney & Burney, 1993) and sticky microscope slides (Coles & Gilbertson, 1994) were used. Burney & Burney (1993) showed that pollen influx decreases steeply toward the rear of caves, but more experiments are needed that relate pollen settlement in the inner cave surfaces with topographic features of differently shaped caves.

In view of the available results it is clear that, up to now, very little pollen data are available for reconstructing the palaeoenvironments experienced by Sterkfontein hominids. Most of the lithological members exposed in the present excavations and reported on in previous studies, especially breccia, seem to have been percolated by rainwater and recent pollen, which is likely because of its porosity. These carbonate-rich sediments either do not contain enough fossil pollen, or the concentration is very low and difficult to distinguish from contaminants. Increasing the sample size in the travertines is not an acceptable solution, as it is likely to amplify contamination (Scott, 1982a), while chronological control of such big samples poses another problem.

Responding to Scott & Bonnefille (1986), Horowitz (1992) questioned what share of known contaminants should preclude the use of an entire pollen spectrum. For instance, he does not agree that the whole spectrum of Sterkfontein breccia (Horowitz, 1975) should be discarded as contaminated. Some other papers reporting pollen diagrams from similar breccia deposits in the

australopithecine site, Makapansgat, in South Africa such as those by Cadman & Rayner (1989), Rayner *et al.* (1993) and Zavada & Cadman (1993) rest on the same principle and deal with contamination as a solvable problem. Based on low frequency, differences in pollen wall colour and preservation of the eucalypt and pine pollen, Zavada & Cadman (1993), for instance, attribute these forms to post-depositional contamination. These researchers offer palaeoclimatic interpretations after excluding what they consider to be contaminant pollen.

In our view, it is impossible to exclude all pollen contaminants because those that are from indigenous plants will not be recognizable except for a few containing fresh cell contents. Elimination of recognizable contaminants does not ensure that the rest of a spectrum is free of contamination. Further, it appears logical that if a pollen spectrum contains contaminants from the modern environment, it could also contain contaminants from different times during its history. Such contamination could, however, only have happened at such times when the cave was open to externally derived material, and only when cavernous conditions were amenable to the incorporation of pollen grains into soluble or porous layers. For instance, we know that modern exotics to South Africa, like pines and eucalypts, could only have been incorporated in sediments during recent times, but grass pollen may well have been incorporated at any time after deposition due to percolation or recrystallization. We do, however, believe that contamination from the modern environment is more likely, especially after sealed sediments have been opened and exposed by excavations.

We do not necessarily suggest that every breccia and travertine deposit within a cave sedimentary system is unsuitable for pollen analysis, although we believe breccias are more hazardous. Successful cases of stalag-

mite investigation have been reported (Bastin, 1979; Scott & Bonnefille, 1986; Brook *et al.*, 1990; Carrión, 1992; Burney *et al.*, 1994; Scott, 1995), showing that good potential exists. Stalagmites can be pollen traps, particularly if they are close to cave openings. At Wonderwerk Cave, South Africa, the position of a stalagmite in the cave entrance next to the surrounding vegetation outside, accounts for a reasonable pollen concentration (G. Brook & L. Scott, unpublished data). In the case of Sterkfontein and Kromdraai (Scott & Bonnefille, 1986), the presence of high proportions of *Protea* could well be a good indicator of an ancient origin for part of the pollen assemblages because these forms did not show up in modern surface samples at the site (Scott, 1995).

Despite the scarcity of pollen in carbonate rich cave sediments, preservation of macrobotanical remains has in fact been observed at Sterkfontein (Bamford, 1999). Although breccias from different members of the Sterkfontein Formation have been investigated for pollen, the precise locality in Member 4 which yielded macro-plant remains has not been tested for pollen. If this is found to be without pollen remains we will have to assume that fossil size played a role in preservation. It will be useful to continue looking for pollen in unusual inclusions of breccias, which may have preserved pollen more effectively, e.g., coprolites (Scott, 1987). Although some clay balls from the Member 2 breccia at Sterkfontein, which were provided by Dr Ron Clarke, were barren, the search for pollen in similar inclusions should be continued.

Unfortunately, low pollen concentrations and the presence of contaminants are typical in important palaeontological sites. This is the case for the Spanish sites of Cova Negra, Cueva del Salt, Cueva de Nerja, Cueva Victoria and Venta Micena (unpublished data). In another site at Atapuerca, analysis of a 6-meter section showed that a large part

of it is sterile while the rest is not rich in pollen (García-Anton & Sainz-Ollero, 1991). The absence of pollen, or poor concentrations, has also been confirmed by a more recent study (Y. Fernández-Jalvo & L. Scott, unpublished data). Here the possibility of contamination cannot yet be detected as easily as in the case of some South African sites, like Sterkfontein, where many exotic plants occur in the vicinity. At sites in regions not characterized by large-scale exotic plant introductions, contaminant pollen grains will be difficult to detect, especially if acetolysis treatment makes them indistinguishable from fossil grains.

In further studies, we must be alert to possible indicators of percolation, particularly if the deposits have been exposed to the elements for a long time before sampling. We recommend that, if possible, samples should be taken as soon as possible after opening the sections to avoid penetration of modern pollen into the exposed porous breccia. In view of the pitfalls in the palynological study of carbonate-impregnated cave sediments, and despite the arduous efforts involved in this work, we should be cautious about drawing palaeoecological conclusions from doubtful pollen assemblages, and excavators should not expect palynology to be a magic wand. Nevertheless, in some cases where careful consideration of the quality of cave pollen assemblages can eliminate the possibility of contamination, they may provide useful insights into past environments associated with hominids.

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References

- Bamford, M. (1999). Macroplants. In (T. C. Partridge & R. R. Maud, Eds) *The Cainozoic Geology of Southern Africa*, Oxford: Oxford University Press, in press.
- Bastin, B. (1979). L'analyse pollinique des stalagmites: une nouvelle possibilité d'approche des fluctuations climatiques du Quaternaire. *Ann. Soc. Géol. Belg.* **101**, 13–19.
- Betancourt, J. L., van Devender, T. R. & Martin, P. S. (1990). *Packrat Middens: The Last 40,000 Years of Biotic Change*. Tucson: University of Arizona Press.
- Brook, G. A., Burney, D. A. & Cowart, J. B. (1990). Desert palaeoenvironmental data from cave speleothems with examples from the Chihuahuan, Somali-Chalbi, and Kalahari deserts. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **76**, 311–329.
- Burney, D. A. & Burney, L. P. (1993). Modern pollen deposition in cave sites: experimental results from New York State. *New Phytol.* **124**, 523–535.
- Burney, D. A., Brook, G. A. & Cowart, J. B. (1994). A Holocene pollen record from the Kalahari Desert of Botswana from a U-series dated speleothem. *The Holocene* **4**, 225–232.
- Cadman, A. (1991). Incidence of atmospheric pollen in the Pretoria Witwatersrand-Vereeniging region during 1987/1988. *S. Afr. Med. Jour.* **79**, 84–87.
- Cadman, A. & Rayner, R. J. (1989). Climatic change and the appearance of *Australopithecus africanus* in the Makapansgat sediments. *J. hum. Evol.* **18**, 107–113.
- Carrión, J. S. (1992). Late Quaternary pollen sequence from Carihuella Cave, southeastern Spain. *Rev. Palaeobot. Palynol.* **71**, 37–77.
- Carrión, J. S., Dupre, M., Fumanal, M. P. & Montes, R. (1995a). A palaeoenvironmental study in the semi-arid southeastern Spain: the palynological and sedimentological sequence at Perneras Cave (Lorca, Murcia). *J. Archaeol. Sci.* **22**, 355–367.
- Carrión, J. S., Munuera, M. & Dupré, M. (1995b). Análisis polínicos en el sureste ibérico semiárido. *Cuaternario y Geomorfología* **9**, 17–31.
- Clarke, R. J. & Tobias, P. V. (1995). Sterkfontein Member 2 foot bones of the oldest South African hominid. *Science* **269**, 521–524.
- Coles, G. M. & Gilbertson, D. D. (1994). The airfall-pollen budget of archaeologically important sites: Creswell Crags, England. *J. Archaeol. Sci.* **21**, 735–755.

- Davis, O. K. (1990). Caves as sources of biotic remains in arid western North America. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **76**, 331.
- García-Anton, M. & Sainz-Ollero, H. (1991). Pollen records from the middle Pleistocene Atapuerca site (Burgos, Spain). *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **85**, 199–206.
- Gray, J. (1965). Palynological techniques. In (B. Kummel & D. Raup, Eds) *Handbook of Paleontological Techniques*, pp. 471–481. San Francisco: W. H. Freeman & Co.
- Horowitz, A. (1975). Preliminary palaeoenvironmental implications of pollen analysis of Middle Breccia from Sterkfontein. *Nature* **258**, 417–418.
- Horowitz, A. (1992). *Palynology of Arid Lands*. Amsterdam: Elsevier.
- Kuman, K. (1994). The archaeology of Sterkfontein—past and present. *J. hum. Evol.* **27**, 471–495.
- Partridge, T. C. & Watt, I. B. (1991). The stratigraphy of the Sterkfontein hominid deposit and its relationships to the underground cave system. *Palaeont. afr.* **28**, 35–40.
- Rayner, R. J., Moon, B. P. & Masters, J. C. (1993). The Makapansgat australopithecine environment. *J. hum. Evol.* **24**, 219–231.
- Sánchez-Goñi, M. F. (1994). The identification of European Upper Palaeolithic interstadials from cave sequences. *AASP Contr. Series* **29**, 161–182.
- Scott, L. (1982a). Pollen analyses of Late Cainozoic deposits in the Transvaal, South Africa, and their bearing on palaeoclimates. *Palaeoecol. Afr.* **15**, 101–107.
- Scott, L. (1982b). Late Quaternary fossil pollen from the Transvaal, South Africa. *Rev. Palaeobot. Palynol.* **36**, 241–278.
- Scott, L. (1987). Pollen analysis of hyena coprolites and sediments from Equus Cave, Taung, Southern Kalahari (S. Africa). *Quatern. Res.* **28**, 144–156.
- Scott, L. (1992). Environmental implications and origin of microscopic *Pseudoschizaea* Thiergart and Frantz ex R. Potonié emend. in sediments. *Journal of Biogeography* **19**, 349–354.
- Scott, L. (1994). Palynology of the Upper Pleistocene hyrax middens, southwestern Cape Province, South Africa: a preliminary report. *Historical Biology* **9**, 71–81.
- Scott, L. (1995). Pollen evidence for vegetational and climatic change in southern Africa during the Neogene and Quaternary. In (E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle, Eds) *Paleoclimate and Evolution with Emphasis on Human Origins*, pp. 65–76. Yale: Yale University Press.
- Scott, L. & Bonnefille, R. (1986). Search for pollen from the hominid deposits of Kromdraai, Sterkfontein and Swartkrans: some problems and preliminary results. *S. Afr. J. Sci.* **82**, 380–382.
- Van Geel, B., Coope, G. R. & Van der Hammen, T. (1989). Palaeoecology and stratigraphy of the Late-glacial type section at Usselo (The Netherlands). *Rev. of Palaeobot. Palynol.* **60**, 25–129.
- Zavada, M. S. & Cadman, A. (1993). Palynological investigations at the Makapansgat limeworks: an australopithecine site. *J. hum. Evol.* **25**, 337–350.