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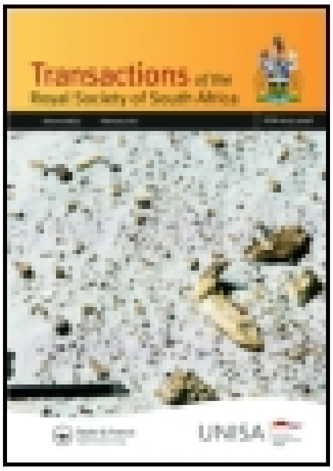

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Transactions of the Royal Society of South Africa
Publication details, including instructions for authors and subscription information:
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The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia

Eugène Marais[a], Louis Scott[b], Graciela Gil-Romera[c] & José S. Carrión[d]
[a] National Museum of Namibia, PO Box 1203, Windhoek, Namibia
[b] Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa
[c] Department of Geo-environmental Processes and Global Change, Pyrenean Institute of Ecology - CSIC, Campus de Aula Dei. Avda. Montañana 1005, CP 50159 Zaragoza, Spain
[d] Department of Plant Biology, University of Murcia, 30100 Murcia, Spain

Published online: 15 Jan 2015.

To cite this article: Eugène Marais, Louis Scott, Graciela Gil-Romera & José S. Carrión (2015): The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia, Transactions of the Royal Society of South Africa, DOI: 10.1080/0035919X.2014.999734

To link to this article: http://dx.doi.org/10.1080/0035919X.2014.999734

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Transactions of the Royal Society of South Africa, 2015
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The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia

Eugène Marais[1]*, Louis Scott[2], Graciela Gil-Romera[3] & José S. Carrión[4]

[1]National Museum of Namibia, PO Box 1203, Windhoek, Namibia; [2]Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa; [3]Department of Geo-environmental Processes and Global Change, Pyrenean Institute of Ecology – CSIC, Campus de Aula Dei. Avda. Montañana 1005, CP 50159 Zaragoza, Spain; [4]Department of Plant Biology, University of Murcia, 30100 Murcia, Spain
**Author for correspondence e-mail: marais.eugene@gmail.com*

Modern and fossil pollen grains extracted from bat guano in Arnhem Cave are evaluated for their potential as a palynological archive and the possible influence of insectivorous bat behaviour on the pollen contents of their dung. Four out of seven fossil guano samples from this cave were productive. The inconsistent preservation of pollen in bat guano layers may be due to deterioration through various mechanisms, including combustion. The samples that did contain pollen support previous conclusions, derived from pollen in spring deposits, about Holocene palaeoenvironmental changes in central Namibia. Two samples of modern bat dung yielded pollen spectra with a greater proportion of woody plant pollen than grass pollen in comparison with the fossil guano material, indicating denser tree cover than in the past, which may be due to the possible effect of modern farming practices. Differences in the pollen composition in dung of different bat species foraging in a relatively homogenous African savanna suggest that the behaviour of likely bat populations should be accounted for when using bat guano as a palynology source for environmental reconstruction.

Keywords: pollen, bat guano, cave sediments, Holocene, African savannah.

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INTRODUCTION

Insectivorous bat dung shows promise as a source of palynological records where appropriate caves are found (Maher, 1992, 2006; Bui-Thi & Girard, 2000; Navarro *et al.*, 2000, 2001; Carrión *et al.*, 2006; Leroy & Simms, 2006). Only a few additional investigators (e.g. Hunt & Rushworth, 2005; De Porras *et al.*, 2009; Geantă *et al.*, 2012) have augmented knowledge about this type of proxy environmental archive. These studies proved that bat dung may be useful in palaeoecology, although it may be less accessible than other tetrapod coprolites (Alcover *et al.*, 1999; Carrión *et al.*, 2000, 2001; Scott, 1987; Scott *et al.*, 2003) or other faecal materials like rodent and hyrax middens that are typical in certain arid and semi-arid regions (Davis & Anderson, 1987; Pearson & Betancourt, 2002; Scott, 1996).

The taphonomy of pollen in bat deposits has been discussed in detail in previous papers (Bui-Thi & Girard, 2000; Navarro *et al.*, 2000; Carrión *et al.*, 2006; Leroy & Simms, 2006; Maher, 2006; Geantă *et al.*, 2012). Maher (2006) and Leroy and Simms (2006) attribute the incorporation of pollen into bat guano to ingestion of pollen adhering to or taken in by prey insects (Pendleton *et al.*, 1996), that derived from skin and hair during grooming (Darnton *et al.*, 1999), and that brought in by air currents (Coles & Gilbertson, 1994). Carrión *et al.* (2006) suggest the spectra appear to reflect the vegetation more effectively than normal surface soil samples, though Hunt and Rushworth (2005) found that the foraging behaviour of bats may result in a bias where they hunt in complex, heterogeneous environments. We can expect that pollen assemblages from bat guano represent plants growing in the vicinity (Leroy & Simms, 2006; Carrión *et al.* 2006) but with the proviso that the behaviour and feeding habits of different bat species influence pollen spectra (Maher, 2006). Leroy and Simms (2006) suggest that bat guano may be a good tool for obtaining information on entomophilous plants otherwise under-represented in peat bogs and lake sediments, supported by the results of Carrión *et al.* (2006).

We investigated bat guano from Arnhem Cave near Windhoek, Namibia, in terms of different feeding strategies of species roosting communally in Arnhem Cave and the usefulness of its pollen contents for potential palaeoenvironmental reconstruction in the African savanna.

SETTING

Arnhem Cave (Figure 1) is situated at 22°42′ S 18°10′ E at an altitude of *ca.* 1590 m to the east of Windhoek in central Namibia. The cave entrance is located on a hill, representing the bulge of an anticline rising from below the surrounding Kalahari sand. The surrounding vegetation consists of open fine-leaved savanna (Giess, 1971) on a sandy substrate showing tree-grass co-dominance. The woody elements are either phanerophytes or microphanerophytes, which form an intermediate layer between trees and grasses. *Acacia* is the dominant tree genus, with *Acacia erioloba* and *Acacia mellifera* the main species, the latter being a shrub and an aggressive encroacher on overgrazed areas (Curtis & Mannheimer, 2005). Some Combretaceae trees, mainly *Terminalia sericea* on the plains and *Combretum apiculatum* on the hillsides, occur. *Commiphora* sp., adapted to scarcity in edaphic nutrients, are usually found on hill slopes (Curtis & Mannheimer, 2005) together with *Dichrostachys cinerea*, a pioneer tree in disturbed areas (Scholes, 1997). Perennial grasses dominate the understory, although some annuals occur during the annual wet season and years of above average rainfall.

Arnhem Cave, with a composite length of over 4500 m (Martini *et al.*, 1990), is the largest recorded cave in Namibia. It consists of a series of very large collapse chambers, connected to each other by spacious passages (Figure 2) that developed

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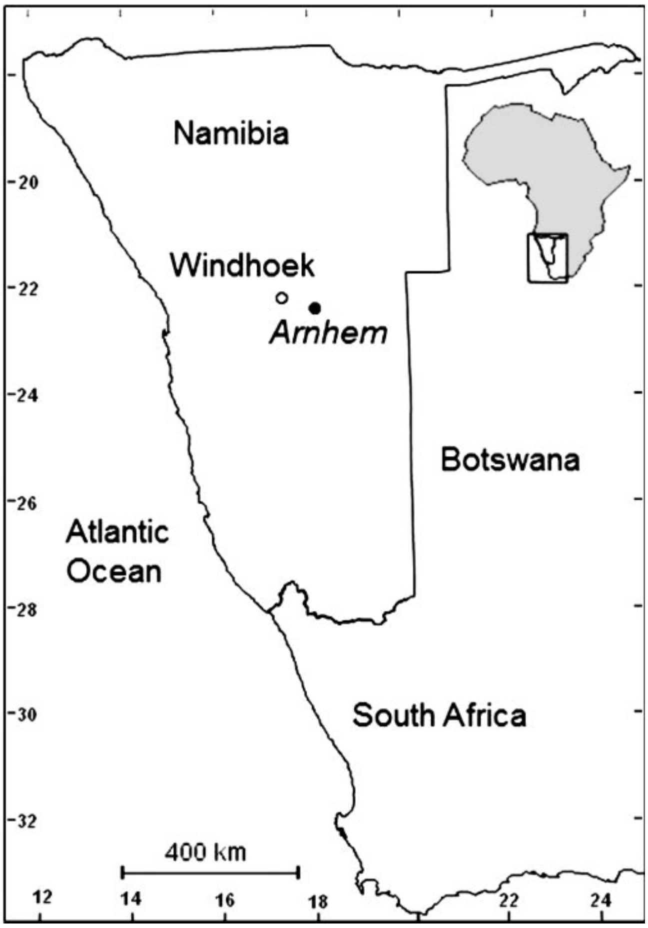

Figure 1. Location of Arnhem Cave and the Windhoek spring deposit in Namibia.

in Precambrian dolomitic rock. Commercial extraction of large quantities of bat guano from the cave occurred in the past, particularly between 1932 and 1943, for export to South Africa and Europe as a source of fertiliser, though sporadic exploitation continued until late in the 20th century. Arnhem Cave is now a tourist destination for its imposing chambers and hypogean ecology, with visitors guided along an unlighted underground route. Seven species of insectivorous bats roost regularly in the cave, often in large numbers: *Hipposideros caffer, Hipposideros commersoni, Miniopterus schreibersii, Nycteris thebaica, Rhinolophus clivosus, Rhinolophus darlingi* and *Rhinolophus denti* (Churchill *et al.*, 1997).

The average cave temperature is 24.5 ºC (with a temporal and spatial range of about 1ºC) and a relative humidity of about 70%. Conditions are dry enough to allow preservation of the bat guano and restrict microbial action and preserve pollen, which may not be the case in humid tropical caves. In some places, the guano deposits are more than a metre deep, even after guano mining took place, and according to some unpublished mining reports, some bat guano sequences may have been more than 5 metres thick. Thick sequences of bat guano may be subject to other processes, e.g. new minerals (Martini, 1994a) described from Arnhem Cave were proposed to originate from spontaneous combustion of thick guano assemblages (Martini *et al.*, 1990; Martini, 1994b). Some of these minerals came from the section between *ca.* 40 and 50 cm of the studied fossil dung sequence (Figure 4). Martini (1994b) suggested that guano fires are uncommon but have been reported from caves in Texas, California, Venezuela, East Africa, Namibia and South Africa.

MATERIALS AND METHODS

E.M. collected seven samples from a pit in a loose guano deposit some 500 m from the entrance of the cave (Figure 2A) and elsewhere in Arnhem in 1988. The samples were sealed in aluminium foil and archived in paper bags for future study. Three radiocarbon dates from profile A showed that its base is around 7700 cal yr BP old (Table 1). These dates were calibrated using the Clam 2.2 program (Blaauw, 2010) (Figure 3). Other dates of more than 10 000 cal yr BP were recorded at a site much deeper in the cave (Figure 2C) at the contact between bat guano and the underlying red sandy sediment. Three ostensibly organic-rich samples from sandy cave sediments from a section where extensive guano mining took place (Figure 2B) did not contain sufficient carbon to be dated (J.C. Vogel, personal communication 1991).

As a modern control for the fossil bat guano, we collected fresh dung from two places in the cave (Figure 2) in 2006. Bat dung I represents the roosting places of *Miniopterus schreibersii* (a slow aerial hawker) and *Nycteris thebaica* (a gleaner) and Bat

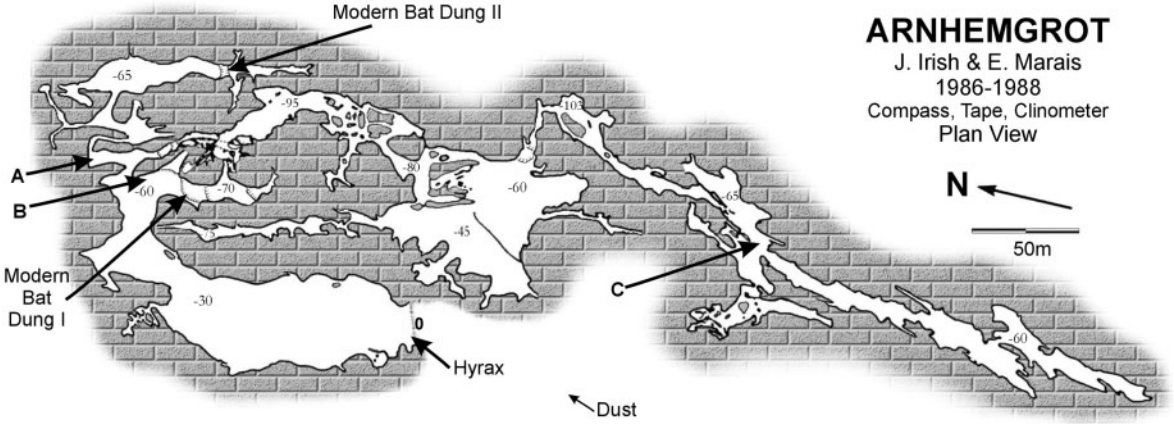

Figure 2. Simplified map of Arnhem Cave, Namibia. A, Sampling pit for fossil pollen; B, section of cave sediments (palynologically unproductive); C, contact section for fossil bat guano (palynologically unproductive) and cave sediments. The sources of modern surface dust, hyrax dung and two bat dung samples (Modern Bat dung I and II) are also indicated.

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Table 1. Radiocarbon dates from Arnhem Cave bat dung deposits at sites A and C.

Site and sample no.	Lab. no.	Depth (cm)	14C yr BP	Error	Cal yr BP (best)	δ13C
Arnhem A (1.16)	Pta-5460	36	1690	80	1538	−17.5‰
Arnhem A (1.11)	Pta-5474	74	5400	70	6117	−17.4‰
Arnhem A (1.9)	Pta-5475	84	6830	150	7649	−17.6‰
Arnhem C (1)	Pta-5326	40 (base)	9430	90	10606	−19.7‰
Arnhem C (2)	Pta-5259	50 (base)	9370	90	10504	−18.6‰

dung II was obtained from below a roosting place of *Hipposideros commersoni*, a bat that often specialises in hunting dung beetles (Taylor, 2000). These were compared to a surface control sample from outside the cave opening and some hyrax (herbivorous mammal) dung pellets from the cave entrance (Figure 2). Hyrax dung pellets are expected to give a good representation of pollen rain from the vegetation surrounding the cave (Scott, 1996).

The laboratory preparation techniques included HCl, HF and KOH digestion followed by mineral separation with a heavy liquid ($ZnCl_2$, density 2 g cm^{-3}). Glycerine jelly slides are housed in the pollen reference collection at the University of the Free State.

RESULTS

Only four of the seven guano samples analysed from the guano profile (Figure 2A) contained pollen but microscopic insect remains were usually present. Three cave sediment samples, two in this sequence and one from the contact between guano and basal sediment (Figure 2B), as well as two additional guano samples from very deep in the cave (Figure 2C) and dating to >10 000 cal yr BP (Table 1), were barren. Thus, in total, only four out of nine fossil guano samples were productive. The four productive fossil guano samples (Figure 4) of *ca.* 10 g each, yielded enough pollen grains to achieve a count of 250 with ease. Microscopic black charcoal pieces were observed in some preparations, e.g. at the 45 cm level, which lacked pollen.

Grass pollen is the dominant constituent in the fossil bat guano sequence, but the highest proportion of this pollen characterises the lower part of the sequence up to the 7650 cal yr BP level. Amaranthaceae pollen is recorded in the younger level dated to *ca.* 1540 cal yr BP, which, together with a lower grass proportion, possibly indicates drier conditions. Small numbers of arboreal pollen (AP), including Combretaceae and Tarchonantheae, suggest relatively low numbers of woody plant taxa on surrounding hill slopes. The fossil bat dung sequence as a whole, however, differs considerably from the modern pollen spectra, which contain lower grass pollen proportions and prominent arboreal pollen like Combretaceae, *Commiphora* and *Acacia*. Further, Aizoaceae and possibly Portulacaceae pollen indicates the presence of succulents.

DISCUSSION

Our results for fossil bat guano were obtained from unconsolidated layered deposits (Figure 4) in a 1.25 m deep pit (Figure 2A). We presumed that discolouration of the reddish-coloured natural weathering products of the host rock implied organic enrichment by bat dung, thus that darker discolouration would suggest greater pollen concentrations (Figure 4). An ash-white layer at 50–45 cm depth represented a spontaneous combustion event of bat guano (Martini, 1994b) sufficiently hot to have formed new geological minerals (Martini, 1994a). We have observed that gregarious troglophilic vertebrates such as baboons and porcupines do not venture far into the cave and did not find any indication of prehistorical human occupation. Pollen, dust and possibly microscopic charcoal could therefore only be introduced by bats to the profile due to the distance from the entrance (Figure 2) and the irregular internal topography and structure of Arnhem cave.

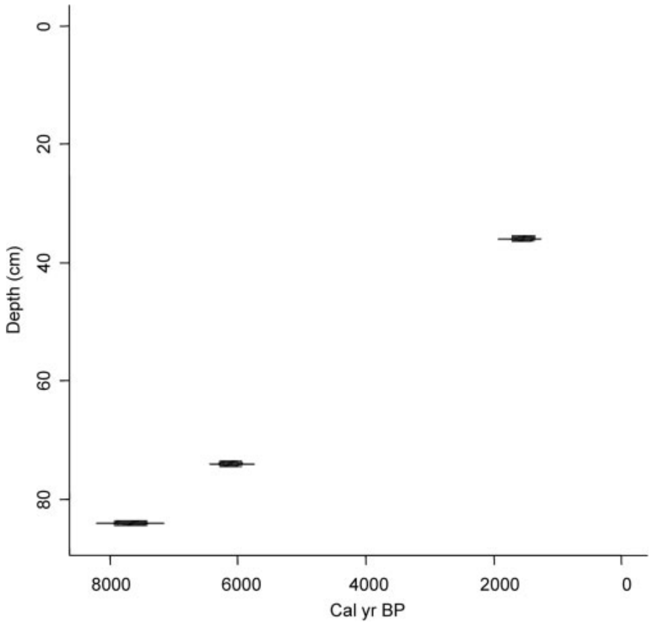

Figure 3. Age model of the Arnhem bat guano profile in pit (A) based on calibration with Clam 2.2 (Blaauw, 2010).

Colour seems to be a secondary characteristic not related to the degree of pollen preservation (Figure 4). The presence of microscopic black charcoal pieces in some preparations (e.g. at 45 cm depth) that show signs of combustion suggests that some dung layers have lost pollen through burning (Martini, 1994a), but dampness and oxidation could have destroyed pollen in others. The relatively low yield from this profile (four out of seven samples) and unproductive results from deep guano deposits elsewhere in Arnhem (Figure 2C) suggest long-term preservation of pollen in bat guano to be unreliable, possibly due to local factors such as guano combustion or others like high nitrate concentrations, low pH, dampness and oxidation. Absence of pollen in Southern African caves is not unusual, as indicated by the lack of pollen in eight bat guano samples from a 3 metre accumulation in Gcwihaba Cave in Botswana (G.A. Brook & L. Scott 1997, unpublished data).

The high proportion of grass pollen in the bat dung of *ca.* 7650 cal yr BP indicates a denser grass cover. Our pollen percentages give ratios and not absolute influx of pollen grains, therefore we interpreted this change in the tree-to-grass ratio as indicative of higher rainfall and not lower tree densities as there is no other evidence of climatic factors that may have affected trees, e.g. frost conditions or dryland

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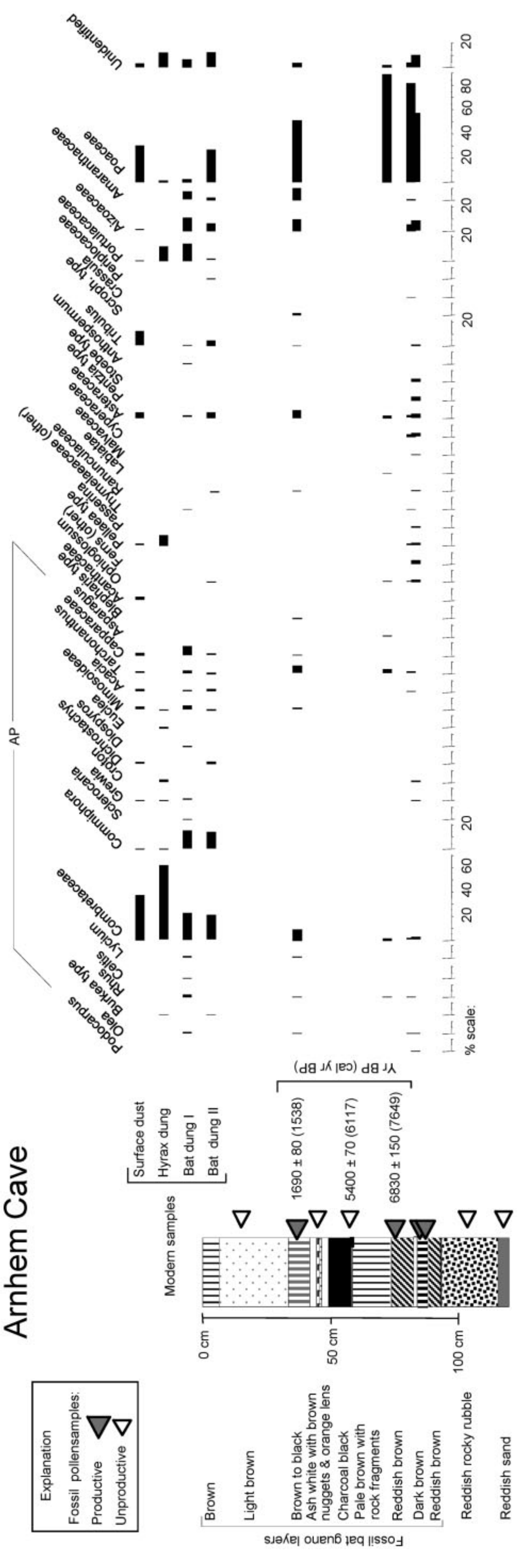

Figure 4. Stratigraphic profile of pit (A) in guano deposits and associated pollen diagram of fossil and recent bat guano and other samples from Arnhem Cave, Namibia (analyst L. Scott, 2005).

vegetation such as Amaranthaceae pollen. We suggest denser grass growth with increased pollen production may have obscured tree pollen presence. In the lowermost undated levels before 7660 cal yr BP, the presence of *Passerina* and *Stoebe* type pollen may, however, be indicative of vegetation elements and lower temperatures that were not yet fully ameliorated after the Last Glacial Maximum (Stute & Talma, 1998).

Long-term vegetation dynamics in savanna ecosystems are complex and insufficiently understood. The African savanna is a water-limited biome with a patchy distribution of rainfall where precipitation sufficient for tree germination are rare considering the longevity of woody plants (Wiegand *et al.*, 2006). Significant shifts in the tree-to-grass proportions would require a long-term and more homogeneous increment in rainfall, moderated by interspecific interaction, competition, fire cycles and herbivorous activity (Scholes, 1997). Some studies in savanna dynamics (Knoop & Walker, 1985; Scholes & Archer, 1997; Ward & Ngairorue, 2000) have shown grass production to decrease steeply with an increment in the tree biomass. The modern samples might therefore be pointing towards denser woodland (Rohde & Hoffmann, 2012), whereas the fossil pollen could depict a more open savanna in the past. However, it is not clear if the savanna tree-to-grass ratio is in a deterministic equilibrium (Scholes, 1997; Wiegand *et al.*, 2006), or if the savanna is the result of a combination of random, unstable disturbances like fire, which impede dominance by trees. Thus, the modern increase in arboreal pollen (average 16.6:1) in comparison with the fossil samples (average 0.12:1), may also be due to bush encroachment caused by fire suppression (Rohde & Hoffmann, 2012), overgrazing and lowered effective competition of grasses (Van Vegten, 1983; Skarpe, 1990; Perkins & Thomas, 1993). The current presence of taxa indicating edaphic disturbance, i.e. *Dichrostachys*, supports an argument for livestock impact. Recent anthropogenic induced change does not exclude a possible reduction in grass density resulting from a change in the rainfall pattern (Ward & Ngairorue, 2000) or increased CO_2 (Rohde & Hoffmann, 2012). Consequently a wetter past cannot be discarded since the Poaceae spectrum is over 50% in all of the four samples. Other taxa occurring only in the fossil samples such as Cyperaceae, *Passerina* and *Stoebe*-type confirm, to some extent, greater moisture availability or cooler growing conditions during the early Holocene.

Palaeoenvironmental information for the Holocene in central Namibia is scarce. A peak in excess air concentration in groundwater of the Stampriet artesian aquifer (Stute & Talma, 1998), which is recharged from a watershed 50 km southwest of Arnhem, was interpreted as a transition from drier to wetter conditions ~6500–7000 cal yr BP. However, other proxies from offshore deposits indicate high rainfall between 9000 and 8000 cal yr BP that reached a maximum ~6000 cal yr BP. Respectively, these interpretations are from clay minerals (Gingele, 1996) on the continental shelf off the Cunene River (~1000 km NW of Arnhem) and pollen (Dupont *et al.*, 2008) from cores off Angola (~1400 km NNW of Arnhem) that suggested increased river discharge and greater forest cover in the Angolan highlands. Such higher rainfall to the north was supported by highstand events at river endpoints in the Kalahari, e.g. ~6600 to ~6000 BP at Ngami ~540 km ENE of Arnhem (Burrough *et al.*, 2007). Rapid accumulation of an 18 m thick fluvial sequence at Homeb ~6000 BP suggested consistent discharge and high rainfall in the Kuiseb River

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catchment ~160 km west of Arnhem (Srivastava *et al.*, 2006). Previous palynological results from spring deposits, *ca.* 130 km to the west in Windhoek (Figure 1), suggest that grassy and waterlogged conditions prevailed between 8000 and *ca.* 6450 cal yr BP (Scott *et al.*, 1991). These Holocene deposits consist of diatomites and organic rich silts associated with the terminal swamp of a hot spring in Windhoek. If the grass increase *ca.* 8000 cal yr BP and earlier in the bat guano sequence is due to more rain, it supports the conclusions from the Windhoek spring deposits. Therefore, the guano samples appear to be yielding information consistent with other palaeoenvironmental proxies.

The hyrax dung sample from the cave opening (Figure 2) has a relatively lower diversity and higher proportion of Combretaceae pollen than the bat dung. This may reflect a more restricted feeding range of these herbivores on the slopes adjacent to the cave, which are vegetated by trees, mainly *Combretum apiculatum*. An interesting aspect of the pollen composition in the modern bat guano is that the pollen composition of the two samples, which represent roosting places of different bat species foraging in the same type of vegetation, seems to differ. It is likely that the activity of aerial hawkers and gleaners (*Miniopterus schreibersii* and *Nycteris thebaica*) around tree canopies (Aldridge & Rautenbach, 1987) might capture relatively more tree pollen in relation to grass pollen (Bat dung I, 20.3:1) than ground hunting activities of *Hipposideros commersoni* (Bat dung II, 1.6:1). These results from a typical African savanna mosaic are similar to those reported for patch landscapes in Wales (Leroy & Simms, 2006) and Borneo (Hunt & Rushworth, 2005), suggesting that the species of bat and roost selection within a cave (Churchill *et al.*, 1997) may be quite significant when examining pollen spectra from caves (De Porras *et al.*, 2009). However, it will be necessary to analyse additional samples in a controlled manner (e.g. *sensu* Carrión *et al.*, 2006) to evaluate the potential importance of different bat species in determining the pollen assemblage composition of cave guano.

Most insectivorous bats forage within a range of around 5 km of the roosting site (Whitaker, 1988), though large bats such as *Hipposideros commersoni* may range as far as 40 km from their roosts (Cotterill & Fergusson, 1999). Such general estimates are, however, moderated by seasonal changes in prey selection and foraging range of bats (Fenton *et al.*, 1993) that account for the availability, composition and activity of prey insects during the year. In addition, environmental changes during the Holocene are likely to have resulted in changes in the composition of the bat population in Arnhem Cave, e.g. its colony of *Hipposideros commersoni* is currently the southernmost breeding population of this tropical species, with several other cavern-inhabiting species occurring further north (Taylor, 2000). Since prey preferences, and therefore the pollen incorporated in bat guano, are related to the foraging strategy (Korine & Pinshow, 2004) and diet of resident bat populations, the composition and diversity of bat populations over time may affect the pollen spectra in bat guano.

Dung pellets of insectivorous bats may be identifiable from shape, size and prey remains, but rapidly lose cohesion and fragment after deposition due to hydration, biotic decomposition and activity of hypogean fauna, even in dry caves. Fragmentation is likely to homogenise variation caused by seasonal changes in bat behaviour, though reconstructing which bats may have been the aggregators of specific fossil guano assemblages requires site-specific explanation (e.g. Hunt & Rushworth, 2005) or experimentation (e.g. Carrión *et al.*, 2006). Gravity compaction and partial bonding due to bat urine nitrification and mineralisation may then result in stratified dung accumulations (e.g. Geantă *et al.*, 2012). We have observed that homogenisation and compaction increases with humidity, e.g. at Gcwihaba Cave in Botswana and other humid tropical caves. It seems, however, that pollen preservation may decrease under such conditions, e.g. no pollen was recovered from Gcwihaba Cave or the oldest guano assemblages in Arnhem Cave. We speculate that under more humid cave conditions, pollen preservation may be adversely affected by oxidation from K_2O or digested by microbial action or various organic acids filtering through dung deposits (Shahack-Gross *et al.*, 2004), while pollen preservation may improve under drier conditions (Navarro *et al.*, 2000; Geantă *et al.*, 2012) as a result of rapid surface nitrification of bat urine. However, even then long-term pollen preservation in bat guano may decline due to the cumulative effect of slow acid digestion, while episodes of wetter cave conditions may result in accelerated decomposition of pollen in some dung layers. Improved preservation of pollen from bat dung can be expected where pollen is incorporated in cave sediments such as stalagmites, flowstone, clays, sand etc. that buffer it from post-depositional decomposition. However, our speculation would require experimental validation or comparisons between deposits formed under different hypogean conditions.

CONCLUSION

Although bat dung deposits in many sites in southern Africa may have been lost through mining, remaining accumulations may be potentially useful sources of palaeopalynological information. Our study shows that pollen in fossil guano may not always be preserved, but where available its pollen composition is suitable for environmental reconstruction (Carrión *et al.*, 2006). However, as in any new source of information, due consideration has to be given to the taphonomy in order to interpret the stratigraphy and environmental conclusions of such sequences. Preservation depends on local post-depositional processes in cave sites, but these secondary taphonomic processes, including ignition of the organic material, oxidation by dampness, nitrification or slow acid digestion under low pH conditions should be investigated further to ascertain to what extent they affect the richness and composition of bat-derived pollen assemblages. We predict that in dry caves where oxidation through moisture, e.g. from drip-water or high humidity, is not a factor, pollen in bat deposits is more likely to be preserved as in other cave sediment (Davis, 1990; Scott, 2003). The data presented in this paper also show interesting changes in bat dung pollen composition, which seems to support indications for wetter conditions in the wider Windhoek region *ca.* 8000 cal yr BP.

ACKNOWLEDGEMENTS

Research in Arnhem Cave was facilitated by Jannie and Elmarie Bekker and initiated by John Irish.

DISCLOSURE STATEMENT

Any opinions, findings and conclusions are those of the authors and the National Research Foundation does not accept any liability in regard thereto.

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FUNDING

The Director of the Geological Survey of Namibia (R. McG. Miller) funded the radiocarbon dating by the late Dr J.C. Vogel, then Director of the Quaternary Dating Research Unit, CSIR, in Pretoria. The National Research Foundation funded the palynological research.

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