The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia

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The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia

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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; Geantá 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) 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.

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

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 antidune 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. Conociphora 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...
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...
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 troglobiphilic 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.

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

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

<table>
<thead>
<tr>
<th>Site and sample no.</th>
<th>Lab. no.</th>
<th>Depth (cm)</th>
<th>14C yr BP</th>
<th>Cal yr BP (best)</th>
<th>3C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arnhem A (1.6)</td>
<td>Pta-5460</td>
<td>36</td>
<td>1690</td>
<td>1538 +17.5%</td>
<td></td>
</tr>
<tr>
<td>Arnhem A (1.11)</td>
<td>Pta-5474</td>
<td>74</td>
<td>5400</td>
<td>6117 +17.4%</td>
<td></td>
</tr>
<tr>
<td>Arnhem A (1.9)</td>
<td>Pta-5475</td>
<td>84</td>
<td>6830</td>
<td>7649 +17.6%</td>
<td></td>
</tr>
<tr>
<td>Arnhem C (1)</td>
<td>Pta-5326</td>
<td>40 (base)</td>
<td>9430</td>
<td>10606 -19.7%</td>
<td></td>
</tr>
<tr>
<td>Arnhem C (2)</td>
<td>Pta-5259</td>
<td>50 (base)</td>
<td>9370</td>
<td>10504 -18.6%</td>
<td></td>
</tr>
</tbody>
</table>

Eugène Marais et al.: The palynological potential of bat dung
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 & T alma, 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 (Ván 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 CO₂ (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 & T alma, 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.

![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).](image)
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. 6430 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 hawksers 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 Carrion 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 & Ferguson, 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. Carrion 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 K2O 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 palaeo-palynological 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 (Carrion 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.

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