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Fossil hyrax dung and evidence of Late Pleistocene and Holocene vegetation types in the Namib Desert

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ABSTRACT: Pollen was derived from fossil dung of herbivorous hyraxes, deposited in a rock shelter on the highest mountain in Namibia, Dâures or Brandberg, situated on the Namib Desert margin. Radiocarbon dating ranging in age between modern times and 30 000 yr BP showed it represents the first empirical pollen evidence of continental palaeovegetation during the Late Pleistocene along the western escarpment of southern Africa. The initial results indicate Last Glacial Maximum vegetation differed totally from the current pattern as vegetation types were dominated by small Asteraceae shrubs, in contrast to those of the Holocene and modern times which show more succulents, grass and woody elements (arboreal pollen). The results suggest that Cape floral communities did not reach into the tropics along the western escarpment of Africa, despite such pollen types occurring in marine cores. Copyright © 2004 John Wiley & Sons, Ltd.

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KEYWORDS: palynology; Namibia; Restionaceae; Late Pleistocene; Last Glacial Maximum.

Introduction

Dâures, or the Brandberg Massif, is Namibia's highest mountain and well known for the extraordinary richness of its rock art (Kinahan, 1984), though it also recently attracted attention through the discovery of living specimens of a new insect order Mantophasmatodea (Klass *et al.*, 2002; Zompro *et al.*, 2003). The co-occurrence of other relict invertebrate taxa (Adlbauer, 2000; Evenhuis, 2001) indicated the need for a better understanding of African biogeographical evolution, particularly in groups sensitive to shifts in the aridity gradient. Marine records indicated possible migration of Cape fynbos vegetation to northern Namibia (Shi *et al.*, 2000, 2001) and geomorphic evidence apparently imply extreme aridity (Heine, 1998) along the desert margin during the LGM.

Dâures is situated in the transition zone between extreme desert and arid shrubland savanna along the western escarpment in Namibia (see Fig. 1). Its arid climate and granitic substrate, and that of Namibia in general, do not favour preservation of organic material, thus deepening the enigma of the origin and history of this inselberg's unique biodiversity. Reconstructions from the available organic deposits, e.g. those preserved in rock shelters (Kinahan, 1984), can be expected only to account for the most recent period as evidence is constantly being eroded and destroyed. Different forms of physical evidence about the Namib Desert's past have been forthcoming (Heine, 1998; Scott, 1995; Scott *et al.*, 1991; Brook *et al.*, 1999; Eitel *et al.*, 2002) but the environmental history remains poorly resolved. Local desert conditions and steep gradients in the Massif prevent the formation and preservation of deposits that are conventionally studied, e.g., lake or swamp deposits with reducing conditions that could preserve fossil plant material like pollen. Dâures also does not have limestone sink-holes and caves (Scott *et al.*, 1991; Brook *et al.*, 1999), river systems (Vogel, 1989; Eitel *et al.*, 2002) or dune-fields (Eitel *et al.*, 2002; Stokes *et al.*, 1997) where sediment records could provide proxy evidence of a more physical nature.

We report on initial results from an alternative source of fossil pollen for palaeoenvironmental reconstruction, viz. pollen analysis of mammalian herbivore dung deposits, i.e., those of hyraxes (Hyracoidea) like *Procavia*. Fossil hyrax dung is a potentially valuable source of palaeo-environmental information in areas where sources of proxy information are scarce or non-existent. Hyrax dung middens accumulate as hard crusts in shallow cave shelters in African deserts and semi-deserts, cemented together by quick-drying urine that seals off and preserves microscopic remains such as pollen grains derived either from aerial dust or through the herbivore's diet

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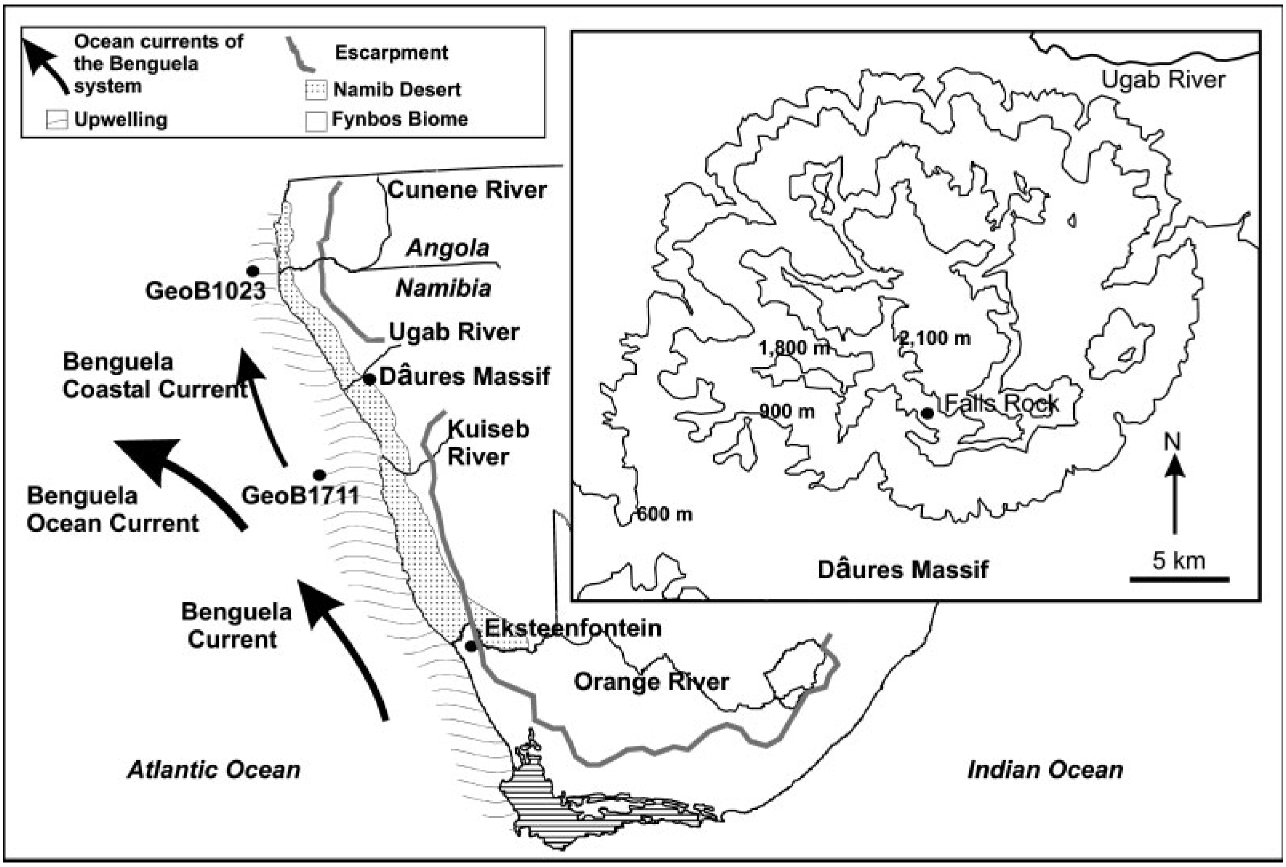

Figure 1 Geographical context of the Dâures Massif, with the Falls Rock hyrax dung site (inset), the western escarpment, significant marine palynological locations (GeoB1023, GeoB1711-4), Eksteenfontein spring pollen site, South Atlantic Ocean currents and the Namib Desert and Cape Fynbos Biomes

(Betancourt *et al.*, 1990). These remains are rich in pollen, but compared with packrat middens of the American Southwest or stick rat middens from Australia (Betancourt *et al.*, 1990), have relatively low concentrations of macrofossils. While the oldest radiocarbon dates reported previously for *Procavia capensis* dung is ca. 20 000 years for deposits from the Cape region in South Africa (Scott and Vogel, 2000), we sampled *Procavia welwitschii* dung ranging between modern times and 30 000 yr BP in age from Falls Rock Shelter (Kinahan, 1984) at ca. 1980 m altitude on the Massif. Despite the relative youthfulness of the record in relation to the mountain's antiquity (Miller, 2000), this age is remarkable. The record provides an insight into Late Pleistocene vegetation during extreme environmental benchmark periods (Partridge *et al.*, 1999) such as Oxygen Isotope Stage 3, the Last Glacial Maximum (LGM) and the Holocene on land in a desert area, including the more recent period during which human occupation on the Massif was reported (Kinahan, 1984). Our eventual aim is to obtain a chronologically continuous record of dung pollen spectra as was found to be possible in the South Western Cape (Scott and Vogel, 2000).

Methods

During 2002 we collected fossil hyrax dung from various sites at higher altitudes of Dâures. Pollen grains were extracted from four fossil dung samples and one modern dung-pellet sample by 10% KOH digestion and heavy liquid mineral separation. Three samples were radiocarbon dated by QUADRU (CSIR) in Pretoria, South Africa, and one by AMS in the Groningen Laboratory in the Netherlands.

Results

Uncalibrated ages of 2830 ± 40 (GrA-22033), 6400 ± 70 (Pta-8899), 17 000 ± 190 (Pta-8902) and 30 800 ± 650 yr BP (Pta-8887) were obtained. The pollen preservation and concentration ranged from poor in the 2830 yr BP sample, consisting of dung pellets in mineral-rich compacted sand (possibly a product of dung burning), to extremely rich and well-preserved in the older samples that consisted of almost pure dung and urine.

Pollen spectra (see Fig. 2) suggest a dramatic difference between vegetation conditions in the Pleistocene and Holocene periods. In comparison with the modern sample, which shows prominent succulent (Aizoaceae type) and Acanthaceae pollen typical of the modern desert, the 30 800 yr BP sample shows various Asteraceae forms, most notably of the *Pentzia* and *Stoebe* types. Comparable pollen assemblages with the *Stoebe* type are typical in modern transitional vegetation between Karoo and Cape fynbos flora or in high-lying vegetation of the southern African interior, e.g. in Lesotho, that include low shrubs like *Stoebe* or *Elytropappus*. In fossil records of glacial age such associations have been reported further to the north in the current savanna region of South Africa (Scott, 1982, 1989a). *Stoebe* type pollen was also more prominent in Mount Kenya during the LGM (Coetzee, 1967). Dâures is 200 km further to the north than the northernmost

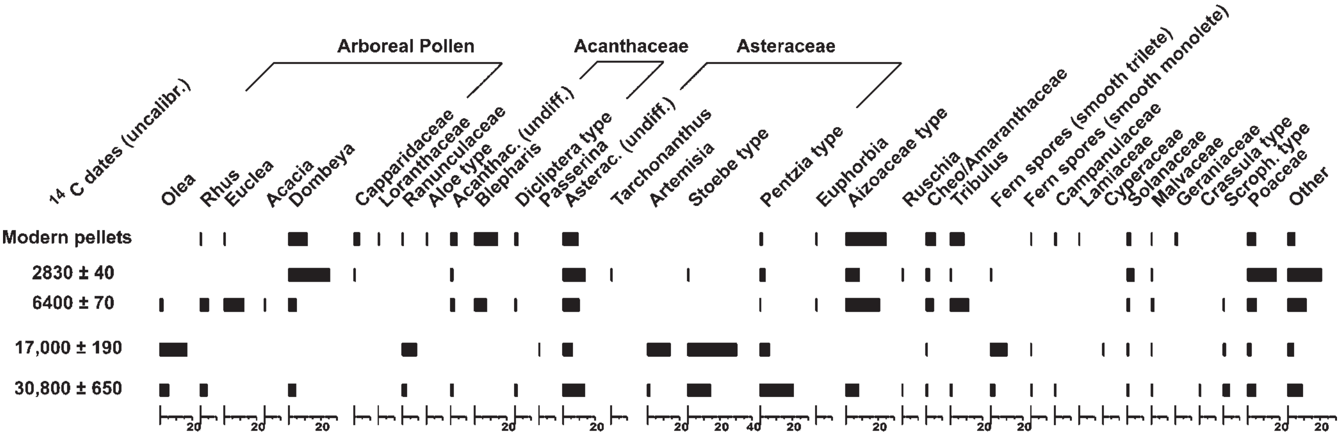

Figure 2 Hyrax midden palynology. Pollen percentages spanning 30 000 years from Dâures

record in eastern South Africa. In the sample representing the cool LGM at 17 000 yr BP *Stoebe* type pollen attains the highest values typical of LGM dwarf-shrubland. However, the associated presence of well-preserved but unidentified fern spores, *Olea,* and *Artemisia* suggest more moist conditions, possibly largely as a result of less evapotranspiration during the glacial period and not necessarily of increased rainfall. *Artemisia,* unlike Northern Hemisphere counterparts is not associated with dryness, and is no longer present on the mountain (Craven and Craven, 2000). Conditions during the LGM in the Namib were not likely to be constant and, although severe dryness (Heine, 1998) was probably included in extremes of variability, it is not reflected in our sample. The samples of 6400 and 2830 yr BP compare well with the modern assemblages but marked variations of grass (Poaceae), succulent (Aizoaceae type) and woody (*Dombeya* and *Euclea*) elements, call for investigation of secondary variation in Holocene vegetation and climate.

Discussion

Shi *et al.* (2000, 2001) did not differentiate *Stoebe* type during the LGM in offshore Atlantic pollen cores, thus we cannot compare Asteraceae subtypes from marine sediments with those in the Dâures samples. A strong increase of fynbos pollen in the Atlantic sediments during the LGM, including Restionaceae and some Ericaceae, led Shi *et al.* (2000, 2001) to suggest the possibility that some Cape floral elements migrated along the Namibian escarpment as far as the Cunene River, ca. 1500 km further north than their current occurrence in Namaqualand, South Africa (Linder, 2003). Our results, however, show no presence of Restionaceae and Ericaceae during the LGM on the Dâures Massif, midway along the proposed range extension to the north. The only Cape element is rare *Passerina* at 17 000 yr BP, a pollen type also recorded from the southern Kalahari during this period (Scott, 1989a). We therefore find no evidence for the northward migration (Linder, 2003) of Cape floral elements along the escarpment. There is also no fynbos pollen at Eksteenfontein (Scott *et al.*, 1995) before 12 000 yr BP in South Africa, ca. 800 km south of Dâures, but increased *Stoebe* type. Though cooler conditions and a slight shift in moisture seasonality towards winter (Stute and Talma, 1998) would have suited fynbos, northward migration during the LGM of Cape floral taxa through the Namib and of highland elements (Scott, 1982) through active Kalahari dunes (Partridge *et al.*, 1999; Eitel *et al.*, 2002) respectively, is difficult to imagine. At present no evidence exists for lagoons, estuaries or flats along the LGM coastline, when sea-levels were significantly lower, that could have served as stepping stones for coastal Restionaceae migration.

The prominence of Restionaceae in swamps from Rwanda and Burundi ca. 30 000 yr BP, and extant occurrences in central African mountains (Bonnefille *et al.*, 1990), indicate that tropical sources for the pollen in the Atlantic cannot be ruled out. The eastern inland sub-humid areas were known to have had upland fynbos vegetation, especially Ericaceae, during the LGM (Scott, 1982). Restionaceae pollen was present in low numbers in the high-lying parts of South Africa in the eastern Free State and the southern Kalahari, during the LGM (Scott, 1989b; G. A. Brook and L. Scott unpublished data) but it is unlikely that long-distance transported pollen from these areas accounts for the high numbers in the marine cores (Shi *et al.*, 2000, 2001). Other source areas for Ericaceae and Restionaceae pollen will have to be considered. An example is the moist Angolan highlands, but it difficult to see how pollen from this source could have been transported southwards as far as GeoB1711. Transport by wind, perennial river discharge and ocean currents may have to be re-examined. If aerial pollen can be transported for hundreds of kilometres by wind (Dupont and Wyputta, 2003), significant water transport of particles should also be possible. Shi *et al.* (2000) show prominent Restionaceae and Ericaceae from 21 000 to 17 000 cal. yr BP in the GeoB1023 core near the Cunene River and from 35 000 to 15 000 cal. yr BP in GeoB1711-4 near Walvis Bay (Shi *et al.*, 2001), corresponding in time with our uncalibrated dates of hyrax dung at 17 000 and 30 800 yr BP. In addition to higher concentrations in LGM levels, small numbers of these pollen types occurred throughout the Holocene until recently (Shi *et al.*, 2000, 2001). Given the absence of recent local source areas nearby, this might be a sign that upwelling of the Benguela system keeps pollen loads from the Cape area in suspension and transports them northward. Intensification of the Benguela during the LGM (Shi *et al.*, 2000, 2001; Romero *et al.*, 2003) might account for the higher fynbos input from such a source, hinting at considerable geographical bias of pollen distributions in marine sediments where upwelling is strong. Although fynbos pollen does not coincide with another strong upwelling event around 14 300 to 12 600 cal. yr BP (Shi *et al.*, 2000, 2001), the possibility of ocean transport should not be discounted unless a better explanation can be offered. It is clear that further studies of hyrax middens could help resolve these and other problems and could allow better land–ocean correlations.

The information presented here confirms that Cape floral indicator groups like Restionaceae and Ericaceae were not continuous along the western escarpment of southern Africa during the last 30 000 years. A more limited northwards extension of Restionaceae at higher altitudes in the escarpment to the south, or a westwards extension from sources in the Congo into the Angolan highlands, cannot be excluded yet, but we believe significant fynbos range extensions into the Namib region to be highly unlikely.

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