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Rock hyrax middens: A palaeoenvironmental archive for southern African drylands

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ABSTRACT

Like many of the world's subtropical regions, southern Africa is highly sensitive to changes in the earth's climate system, but a dearth of reliable palaeoenvironmental records means that relatively little is known about how regional environments have been affected over centennial to multi-millennial timescales. To a large extent this sensitivity is a function of the position of these regions at the interface between temperate and tropical circulation systems. The resulting seasonality and irregularity of rainfall have limited the development of suitable archives, such as lakes and wetlands, for the preservation of palaeoenvironmental proxies.

This paper reviews and evaluates the value of rock hyrax middens as novel palaeoenvironmental archives in southern Africa. Considered are (1) the contemporary taxonomy, distribution and ecology of hyraxes, (2) the mechanisms of hyrax midden development, their physical and chemical structure, rates of accumulation and age; and (3) the palaeoenvironmental proxies preserved within hyrax middens, including fossil pollen, stable isotopes and biomarkers. The interpretive constraints and opportunities offered by these various midden characteristics are assessed with a view to demonstrating the potential of these deposits, widespread as they are through arid and semi-arid southern Africa, in providing a more detailed and chronologically resolved view of late Quaternary palaeoenvironments across the subcontinent.

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1. Introduction

Southern Africa is a critical region for studying Southern Hemisphere climate and circulation dynamics. At the interface of the temperate and tropical moisture-bearing systems, the region is known to have experienced phases of significant environmental change driven by variations in hemisphere-scale atmospheric and oceanic circulation patterns. These large-scale changes in climate in

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the recent geological past have been conceptualised as taking place along three general axes: one extending northward from the Cape, where wet winter climates quickly grade to hyperarid conditions with rare summer rain; another extending eastward along the south coast where a progressive increases in summer rainfall create a year-round rainfall zone; and another that extends into the semi-arid interior of the continent across the modern NE—SW rainfall gradient (Fig. 1) (cf. Chase and Meadows, 2007).

Over glacial—interglacial cycles, climatic and environmental changes along these axes have been linked to latitudinal migrations of the winter westerlies and the intensity and amount of precipitation related to the Inter-tropical Convergence Zone (ITCZ)/Congo Air Boundary (CAB) (Lancaster, 1979; Meadows and Baxter, 1999; Chase and Meadows, 2007). Proxies from these regions are therefore

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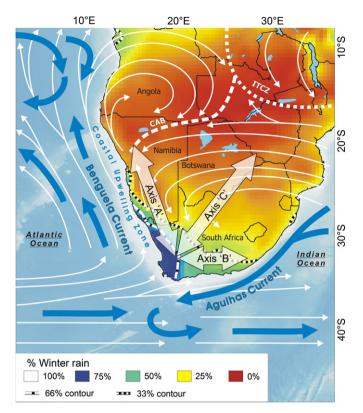


Fig. 1. Map of southern Africa showing seasonality of rainfall and sharp climatic gradients dictated by the zones of summer/tropical (red) and winter/temperate (blue) rainfall dominance. Winter rainfall is primarily a result of storm systems embedded in the westerlies. It has been postulated that these systems have expanded equatorward during glacial periods, increasing their influence eastward across the south coast and interior, as well as northward into the presently hyperarid regions of Namibia. Major atmospheric (white arrows) and oceanic (blue arrows) circulation systems and the austral summer positions of the Inter-tropical Convergence zone (ITCZ) and the Congo Air Boundary (CAB) are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

likely to preserve important information on long-term low latitude and temperate circulation dynamics, elucidate questions regarding the region's high levels of floral endemism and species richness (Goldblatt and Manning, 2002), and provide a context for interpreting southern Africa's rich archaeological record.

Despite southern Africa's sensitivity to climate change, and its position relative to hemispheric and global circulation systems, the environmental history of the region remains largely unknown. This is principally due to the region's topography and semi- to hyperarid climate, which are not conducive to the occurrence of lakes and wetlands that typically preserve long records of environmental change in temperate and tropical regions. In lieu of such traditional terrestrial palaeoenvironmental records, a variety of terrigenous proxies obtained from marine cores (Shi et al., 2000, 2001; Stuut et al., 2002; Dupont et al., 2006, 2007, 2011) and geomorphological records (Eitel et al., 2005; Srivastava et al., 2005; Chase and Thomas, 2007; Telfer and Thomas, 2007; Burrough et al., 2009; Stone et al., in press) have been analysed, but interpretations of their significance vary and have often been contradictory (Partridge et al., 1999; Lancaster, 2002; Thomas and Shaw, 2002; Scott et al., 2004; Chase and Meadows, 2007; Chase, 2009; Thomas and Burrough, 2012).

In this context, that is a region with a rich and dynamic environmental and human history, as well as a dearth of reliable palaeoenvironmental information, we present a palaeoenvironmental archive that is ideally suited to the reconstruction of dryland palaeoenvironments: the rock hyrax midden. Rock hyraxes (Procavia capensis) are herbivores that are common throughout southern Africa, and that have the particular habit of defecating in the same location over many generations (Scott, 1990a). These locations, often sheltered in caves, become covered in faecal pellets and accumulations of dried urine. Contained in these deposits are a range of palaeoenvironmental proxies that are protected from mechanical disruption and the wetting and drying effects typical of semi-arid environments. They may be preserved perfectly in this manner for upwards of 50,000 years (Sections 3.2 and 3.3 of this paper). Research carried out so far has produced reliable high-resolution records that have provided detailed information regarding past climate and vegetation change in southern Africa. When coupled with high-precision chronologies, these proxies provide sub- to multi-decadal records of rapid environmental change spanning thousands of years (Chase et al., 2009, 2010, 2011; Quick et al., 2011). Although hyrax middens are generally only preserved in dryland environments, their occurrence across the subcontinent dove-tails with the presence of permanent lakes in more mesic regions, and they are now providing the potential for a more balanced coverage of palaeoenvironmental records across southern Africa.

The aim of this paper is to review and evaluate the palaeoenvironmental significance of biogenic accumulations in hyrax middens. As such, we consider: (a) the contemporary taxonomy, distribution and ecology of the forming agents, (b) the mechanisms of hyrax midden development, their physical and chemical structure, rates of accumulation and age; and (c) the palaeoenvironmental proxies preserved within hyrax middens, including preserved pollen, stable isotopes and biomarkers. The interpretive constraints and opportunities offered by these various midden characteristics are assessed with a view to demonstrating the potential of these deposits to provide a more detailed and better resolved view of late Quaternary palaeoenvironments across the subcontinent.

2. Hyrax taxonomy, distribution, ecology and physiology

2.1. Taxonomy

Hyraxes (Procaviidae) are the only members of the order Hyracoidea, of which there are three extant genera: *Procavia* (rock hyrax), *Heterohyrax* (bush hyrax, or yellow-spotted rock hyrax) and *Dendrohyrax* (tree hyrax). It was thought that both *Procavia* and *Heterohyrax* are monospecific (*P. capensis* and *Heterohyrax brucei*, with 17 and 25 subspecies respectively (Wilson and Reeder, 1993)), but DNA evidence suggests that *Procavia* may in fact include two distinct species (Prinsloo and Robinson, 1992). There are two identified species of *Dendrohyrax*: *D. arboreus* (southern tree hyrax) and *D. dorsalis* (western tree hyrax), the latter of which includes six subspecies (Wilson and Reeder, 1993) (Fig. 2).

Considering that hyraxes are all furry, rabbit-sized animals, with small rounded ears and stubby tails, it is remarkable that their closest relatives are the Proboscidea (elephants) and Sirenia (sea cows) (Simpson, 1945; Kleinschmidt et al., 1986). Unlike their extant relatives, hyraxes are extremely adept climbers, an ability enhanced by the morphology and nature of their leathery footpads. Studies conducted by Adelman et al. (1975) suggest that this ability is, at least in part, linked to the occurrence of sweat glands in their footpads, which enable them to run up extraordinarily steep rock faces without slipping (Adelman et al., 1975).

2.2. Distribution

The distribution of hyraxes spans most of Africa; with the western and southern tree hyraxes inhabiting the western and

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