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African savanna elephants and their vegetation associations in the Cape Region, South Africa: Opal phytoliths from dental calculus on prehistoric, historic and reserve elephants

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ABSTRACT

This study tests the association between opal phytoliths in dental calculus on modern, historic, and prehistoric specimens of *Loxodonta africana* (African savanna elephant) with their local and regional vegetation. The modern samples were obtained from dental remains from deceased animals at the Addo Elephant National Park (Eastern Cape Province) and the Pilanesberg National Park & Game Reserve (Northwest Province) in the Republic of South Africa. The historic and prehistoric specimens, presumed to be free-roaming elephants, were sampled from museum collections in the Eastern Cape and Western Cape Provinces. In addition to comparing phytolith assemblages in dental calculus with those of the main vegetation associations, this study assesses the phytolith assemblage differences between free-roaming and park elephants.

The results show that: (1) the phytolith assemblages in dental calculus of park elephants show little variation among individual specimens and close resemblance to phytolith assemblages of soils inside their areas of confinement; (2) the free-roaming specimens have a much higher diversity of phytolith morphotypes than those in parks and reserves, exhibiting sometimes typical signatures of more than one biome; (3) free-roaming Cape elephants from fynbos areas have significant amounts of Restionaceae phytoliths, which suggests that grazing on restios in grass-poor fynbos types was important; (4) short saddles, typical of Chloridoideae grasses, are always the most abundant short-cell morphotypes in dental samples, even in areas where other grass subfamilies dominate, and (5) with some limitations, the study of phytoliths in herbivore dental calculus has a high, largely unexplored, potential in paleoecology and conservation ecology.

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1. Introduction

Opal phytoliths are microscopic particles of amorphous silica deposited in cellular and extra-cellular parts of plants by means of absorbed silica in soluble state from underground water (Piperno, 2006). Eventually, silica becomes solid and resistant to organic decay, being sometimes the only part of a plant surviving as fossils. Most of these particles take the form of characteristic cells and other parts of the plant, rendering these forms useful to identify particular taxonomic groups of plants. The opal phytolith approach

has strong applications in archaeology, and their usefulness in paleoecology has provided information on long-term vegetation structure (e.g. Alexandre et al., 1997; Blinnikov, 2005; Golyeva, 2007; Bremond et al., 2008; Neumann et al., 2009; Cordova et al., 2011), paleoclimates (e.g., Fredlund and Tieszen, 1994; Lu et al., 2006, 2007), and definition of stages of plant-herbivore coevolution in deep geologic time (e.g., Strömberg, 2004; Prasad et al., 2005).

In general, opal phytoliths can provide paleo-vegetation information including taxonomic details of C₃ and C₄ grasses (e.g., Twiss et al., 1969; Fredlund and Tieszen, 1994), graminoids, and a number of monocots and dicots (Runge, 1999; Piperno, 2006; Neumann et al., 2009; Mercader et al., 2010), as well gymnosperms and other groups of higher plants (e.g., Klein and Geis, 1978; Kondo and

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Tsumida, 1978; Blinnikov, 2005). Opal phytoliths provide a potential alternative proxy for paleovegetation reconstruction particularly in deposits where pollen grains are absent or do not preserve (Scott, 2002). However, it is important to bear in mind that phytolith records do not replace the type of information provided by pollen analysis, since they both represent different aspects of vegetation.

The research approach that uses opal phytoliths embedded in dental calculus (i.e., tartar) can provide relevant information on herbivore diets and their paleoenvironments. Unfortunately, this approach is still in its infancy, limited mostly to tests that emphasize its potential for paleodiet reconstruction (e.g., Armitage, 1975; Middleton and Rovner, 1994; Gobetz and Bozarth, 2001), particularly on specimens of extinct North American Pleistocene mega-herbivores (Bozarth and Hofman, 1998; Gobetz and Bozarth, 2001; Scott-Cummings and Albert, 2007; Cordova and Agenbroad, 2009). Nonetheless, the potential for its application to prehistoric and modern herbivores can be tested in modern and historical environments where fauna-vegetation relations are known, and studies of modern phytolith assemblages exist. Thus, the study presented here is an attempt to relate modern (reserve) and free-roaming (prehistoric and historic) African elephants with vegetation associations and biomes using phytoliths assemblages from soils and from dental calculus of a number of specimens.

The Republic of South Africa contains nine different biomes (Fig. 1a), and historical and archaeological evidence suggest that elephants once roamed in all of them (Ebedes et al., 1995), although not all of them are considered preferred elephant habitat (Boshoff and Kerley, 2001). At present, however, elephants in the Republic of South Africa are confined to parks and reserves (Fig. 1b). The study presented here focuses mainly on the southern part of the country, where reports of elephants and other megafauna go back to the mid-1600s, when the Dutch established a colony near the Cape of Good Hope and from where European settlement radiated into the interior and along the coast (Fig. 2). Thus Dutch settlers and explorers in the 17th and 18th century and later British settlers, missionaries, and explorers of the 19th century produced historical records all of which can be used to describe herds of elephants being exterminated (Skead et al., 2007; Boshoff and Kerley, 2010).

Based on historical records, elephants in the Greater Cape region existed in a mostly non-savanna environment, including various vegetation types of fynbos, renosterveld, coastal succulent scrub, forest, subtropical thicket, grassland, nama karoo and succulent karoo (Fig. 1a), although not all of these environments sustained elephants permanently (Boshoff and Kerley, 2001). The fact that the so-called “savanna elephant” (i.e., *Loxodonta africana* var. *africana*) adapted to non-savanna vegetation communities is an interesting topic discussed by several authors (Carter, 1970; Ebedes et al., 1995; Seydack et al., 2000; Boshoff and Kerley, 2001; Skead et al., 2007) and part of the present research.

Furthermore, the fact that some habitats in the Cape region provided permanent elephant habitats whereas others were only seasonal (per Boshoff and Kerley, 2001), meant that specific migration patterns would have existed. Some migratory routes could be hypothesized using proxies such as stable isotopes or in the case of this study through distinctive phytolith assemblages associated with particular flora. Within this contextual framework, the study presented here is a preliminary research project with the following objectives: (1) assess dietary differences between free-roaming and park elephants, (2) assess the diet of the savanna elephant in non-savanna biomes of temperate southern Africa, and (3) to assess the use of the opal phytoliths in dental calculus to study prehistoric elephant-vegetation interactions. Objective 1 is applied to the Addo Elephant National Park in the Eastern Cape Province coastal region and the Pilanesberg National Park & Game

Reserve in the Northwest Province. Objectives 2 and 3 direct attention to phytoliths in soil and dental calculus samples from a broad area in the Cape Region (Focus area in Fig. 1a and b).

2. Background information

2.1. Study areas

The focus area of this study comprises the southern part of the Western Cape and Eastern Cape Provinces south of latitude 32° S (Fig. 1b). In general terms, this area constitutes the southern part of the Greater Cape Floristic Region. Its physiography is dominated by landforms resulting from the tectonic and erosional evolution of Cape Fold structures and the African Escarpment (Partridge, 1998; Maud, 2012). The Cape Fold structures form a series of mountain systems parallel to the coast, which have created a series of interior valleys connected by antecedent stream valleys. Some of the mountain systems associated with the Cape Fold Belt include the Cederberg, the Hottentots-Holland, the Outeniqua Mountains and the Suurberg. The African Escarpment forms the edge of a plateau in the west forming a series of mountains such as the Roggeveldberg, the Nuweveldberg and the Sneeuweg (Fig. 2). Towards the east, the Escarpment is marked by the Drakensberg Mountains. Other erosional remnants of the retreating African Escarpment have formed minor mountain systems such as the Amatole Mountains in the Eastern Cape.

Between the Cape Fold Mountains and the African Escarpment lies a vast area of interior plains and lowlands drained by the Gamka, Groote and Sundays Rivers. The lithology of the Cape Fold Mountains includes sandstone and shale, with minor structures of granites, quartzite, conglomerates, and limestone. The Escarpment consists of even older rocks, mostly sedimentary, with a few of volcanic origin. The coastal areas in the west and south are dominated by plains and rolling hills of eolian sand, eolianites and alluvium of Late Cenozoic age.

The focus area of this study encompasses the southern part of South Africa's winter rainfall zone (WRZ), an area defined by more than the 60% in the winter months, the summer rainfall zone, with less than 40% of winter rain, (SRZ), and the all-year rainfall zone (ARZ), with between 40 and 60% of rain in winter (Fig. 1). The latter includes an area with rains uniformly distributed throughout the year on the south coast, and an area with two conspicuous rainfall concentrations (i.e., bimodal) in winter and summer rainfall. The Köppen climate types in the focus area include the Cs (Mediterranean) and Cf (temperate with rain all year) in the west and coastal south, BS (semiarid) in the interior, and Cw (temperate with summer rains) in the east. Temperatures in the focus area are highly modified by elevation, solar irradiation (dependent on cloud cover), ocean temperatures, and locally, on slope orientation and exposure. Areas of the south coast with frequent cloudy days tend to have less extreme temperatures, while those in the dry interior exhibit a wide range daily and seasonally. Winter snow is common at high elevations, usually above 1000 m in the west and 1800 m in the east.

Territories of seven of the nine biomes present in South Africa are included in the focus area (Fig. 1). The fynbos biome, which dominates the WRZ and parts of the ARZ, consists mainly of shrubby vegetation, which in some cases can be dominated by Proteaceae (proteoid fynbos), Ericaceae (ericoid fynbos), or Restionaceae (restioid fynbos) (Campbell, 1986). Grasses are rare in most fynbos types, except in types in the ARZ, where summer rainfall has higher incidence, particularly on quartzite or shale substrate (Rebello et al., 2006). Most fynbos associations thrive on nutrient-poor soils developed on sand, sandstone, granite, and limestone. In contrast, renosterveld (a type of fynbos association) develops on

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