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High-throughput sequencing of ancient plant and mammal DNA preserved in herbivore middens

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ABSTRACT

The study of arid palaeoenvironments is often frustrated by the poor or non-existent preservation of plant and animal material, yet these environments are of considerable environmental importance. The analysis of pollen and macrofossils isolated from herbivore middens has been an invaluable source of information regarding past environments and the nature of ecological fluctuations within arid zones. The application of ancient DNA (aDNA) techniques to hot, arid zone middens remains unexplored. This paper attempts to retrieve and characterise aDNA from four Southern Hemisphere fossil middens; three located in hot, arid regions of Australia and one sample from South Africa's Western Cape province. The middens are dated to between 30,490 (±380) and 710 (±70) cal yr BP. The Brockman Ridge midden in this study is potentially the oldest sample from which aDNA has been successfully extracted in Australia. The application of high-throughput sequencing approaches to profile the biotic remains preserved in midden material has not been attempted to date and this study clearly demonstrates the potential of such a methodology. In addition to the taxa previously detected via macrofossil and palynological analyses, aDNA analysis identified unreported plant and animal taxa, some of which are locally extinct or endemic. The survival and preservation of DNA in hot, arid environments is a complex and poorly understood process that is both sporadic and rare, but the survival of DNA through desiccation may be important. Herbivore middens now present an important source of material for DNA metabarcoding studies of hot, arid palaeoenvironments and can potentially be used to analyse middens in these environments throughout Australia, Africa, the Americas and the Middle East.

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1. Introduction

The field of ancient DNA (aDNA) has, since its infancy, been largely restricted to the study of substrates from cool and frozen environments, which are deemed most amenable to long-term DNA preservation (Lindahl, 1993a,b). To date, a number of historical and ancient samples have been subject to genetic analyses, ranging from bone (Smith et al., 2001) and hair (Bonnichsen et al., 2001; Gilbert et al., 2004) to more complex, heterogeneous substrates such as coprolites (Kuch et al., 2001; Poinar et al., 2001) and sediments (Hofreiter et al., 2003b; Willerslev et al., 2003; Haile et al., 2009). A number of studies have also attempted the isolation of DNA from samples – including fossil rodent middens – collected in cool to cold, semi-arid or arid environments (Kuch et al., 2002; Hofreiter et al., 2003a) and at high altitudes (Poinar et al., 1998; Hofreiter et al., 2000; Poinar et al., 2003). The application of

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molecular aDNA techniques to hot, semi-arid or arid environmental samples has previously been considered unrealistic due to the extreme heat found in such areas and as such is somewhat rarer and controversial (Smith et al., 2003; Gilbert et al., 2005b; although see; Gilbert, 2011; Hekkala et al., 2011).

Hot, arid and semi-arid environments are often marked by periods of stasis fluctuating on the edge of environmental equilibrium (Moore, 1953; Van Devender, 1990), punctuated by potentially dramatic changes that are induced by various triggers (Friedel et al., 1993; Tausch et al., 1993). There exists a delicate ecological balance and complex interplay across various environmental and biological gradients in arid regions (Beadle, 1966; Hayward and Phillipson, 1979; Northcote and Wright, 1982; Ritchie, 1986), making them of considerable environmental and biological interest. Flora and fauna inhabiting such environments are often at the limits of their tolerance to various abiotic factors, including temperature and water conservation, and have evolved to cope with extreme environmental conditions (Tongway and Ludwig, 1990; Groves, 1994). The study of past and present arid zone environments – and the distribution of species within them – allows for the exploration of how they have adapted and shifted in response to both natural and anthropogenic mechanisms (Van Devender and Spaulding, 1979; Fall et al., 1990; Pearson and Betancourt, 2002). The study of arid environments, however, is extremely challenging owing to the costs of collection and analysis, paucity of research attention and the lower quantities of recovered macro- and microfossil material. Nevertheless, studies using herbivore middens show promise in examining temporal and spatial variation in arid zone climates and biota, and perhaps, in some cases, may be the only viable means of doing so (Scott, 1990; Pearson and Betancourt, 2002; Scott and Woodborne, 2007; Chase et al., 2009, 2011).

To date, the reconstruction of palaeoenvironments has involved the use of a variety of molecular and morphological techniques, usually applied to sediment cores. Such techniques have included macrofossil and pollen identification, stable isotope analysis and ^{14}C dating. The application of these techniques to middens, where pollen and macrofossils have been preserved for thousands of years (Pons and Quézel, 1958; Wells and Jorgensen, 1964; Van Devender and Spaulding, 1979; Fall et al., 1990; Pearson and Betancourt, 2002; Scott et al., 2004), has provided the bulk of palaeoecological information in arid environments, where macrofossils are sparse and continuous fossil pollen records are largely unattainable. Midden material has therefore played a large part in our understanding of arid zone ecology and environment and act as archives of valuable information. Midden accumulations, usually as organic-rich nests in the case of American and Australian middens and latrines in the case of the African rock hyrax middens (Fig. S1), consist of material from the surrounding environment for construction or dietary purposes by arid-zone adapted mammals, and for the most part, represent a localised picture of the flora and fauna (Dial and Czaplewski, 1990; Scott, 1990; Pearson and Dodson, 1993). In the case of American and Australian middens, the animals urinate and defecate on their nests during the course of habitation, and organic material such as plant and animal tissue, bone, hair and eggshell gathered from the local surroundings (Pearson et al., 2001), become cemented together by means of crystallised urine or amberat, solidifying the mass into a hard, impermeable amalgam, referred to as a midden. Individually, these middens are generally recognised as reflecting sub-centennial-scale periods of construction and habitation. Conversely, African rock hyrax middens are latrines composed nearly exclusively of excrement. They are excellent traps for microfossils (pollen, phytoliths, etc.) from both regional and local environments as these are respectively brought in by the wind or adhere to the midden agent's fur. Hyrax middens, however, contain very little non-dietary macrofossil material (for a fuller comparison and description of hyrax latrines and rodent nest middens see Chase et al., 2012). Increasingly, the hyrax middens that are collected for analysis are composed predominantly of urine, and have been shown to accumulate continuously over many thousands of years (Chase et al., 2009, 2011).

Genetic profiling has previously been applied to midden contexts, with two aDNA profiling studies retrieving reliable, seemingly authentic aDNA sequences from cold, arid zone (BWk – Köppen climate classification, see Peel et al., 2007) middens (Kuch et al., 2002; Hofreiter et al., 2003a). Since these studies, the fields of aDNA and environmental metabarcoding, whereby complex environmental samples are genetically audited (Valentini et al., 2009; Taberlet et al., 2012), have rapidly evolved. With the advent of affordable and accessible second generation high-throughput sequencing (HTS) it is now possible to genetically screen a wide range of complex modern and ancient substrates, with an unprecedented depth of sequence coverage (Shokralla et al., 2012). Through the use of material as diverse as sediment (Haile et al., 2009; Jørgensen et al., 2012), water (Rusch et al., 2007; Ficetola et al., 2008; Thomsen et al., 2012) and faeces (Deagle et al., 2009; Valentini et al., 2009; Murray et al., 2011) a wealth of data can be produced to aid in the understanding of pertinent ecological questions in relation to biodiversity (Andersen et al., 2011; Griffiths et al., 2011), dietary analysis (Pegard et al., 2009; Deagle et al., 2010) and anthropogenic impacts (Chariton et al., 2010; Vila and Borrelli, 2011). It is now possible, therefore, to bypass traditional molecular cloning and Sanger sequencing techniques through the use of new DNA technologies (HTS) to supplement morphological (macrofossils and palynology) methods of midden analysis, to allow an even fuller investigation of arid zone ecology.

Using HTS and environmental DNA metabarcoding techniques, this study attempts to recover aDNA from herbivore midden material collected from three hot, arid Australian sites and one site in South Africa (Fig. 1) that have been dated to between 30,490 ± 380 and 710 ± 70 cal yr BP. A comparison of the data obtained via HTS with complementary data on past and present species distributions, in addition to pollen and macrofossil analyses, allows for a critical examination and authentication of the genetic data. This study aims to demonstrate how genetic methods can be used to complement traditional methods of midden investigation for palaeoenvironmental reconstruction, to further our understanding of hot, arid environments.

2. Collection sites

Four Southern Hemisphere middens were sampled in this study; a single hyrax midden from South Africa's (RSA) Western Cape Province (Fig. 1A) and three herbivore middens from separate Interim Biogeographic Regionalisation of Australia (IBRA) regions (Thackway and Cresswell, 1995) within Western Australia (WA) (Fig. 1B–D). The three midden samples collected in Western Australia were from hot, arid zones (BWh Köppen climate classification, see Peel et al., 2007). The hot, arid zone collection sites are generally characterised by extreme hot summers and somewhat mild winters. Daytime summer temperatures average ~37–38 °C, but regularly exceed 40 °C. In winter, average daytime highs are ~21–25 °C, but can fall to ~6–7 °C at night. Winter nighttime temperatures at or close to freezing are extremely rare in these zones (climate data from Giles and Tom Price weather stations, WA). This contrasts markedly with previous midden genetic studies (Kuch et al., 2002; Hofreiter et al., 2003a) where average daily highs in summer are ~24–28 °C, although it can reach ~30 °C, and winter daily highs average ~16–21 °C, with nighttime

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