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Palaeogeography, Palaeoclimatology, Palaeoecology 233 (2006) 235–251
PALAEO
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Palaeoenvironments and palaeodiets of mid-Pliocene micromammals from Makapansgat Limeworks, South Africa: A stable isotope and dental microwear approach

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Received 26 April 2004; received in revised form 14 September 2005; accepted 19 September 2005

Abstract

Savannah (C_4) grasses are first recorded at low latitudes in the mid-Miocene prior to their expansion towards mid-latitudes by approximately the Miocene–Pliocene boundary. In an attempt to determine the timing of the spread of savannah grasses into the South African highveld, a palaeoecological study of some of the oldest faunal deposits in the region (mid-Pliocene) was undertaken. The combination of carbon isotope and dental microwear analysis of micromammals from the Rodent Corner and the Exit Quarry repositories of the Makapansgat Limeworks has enabled the determination of the relative proportions of C_4 grass, C_3 grass and C_3 browse in the diets of two extinct herbivorous rodent species, *Otomys* cf. *gracilis* and *Mystromys* cf. *hausleitneri*. *M.* cf. *hausleitneri* is shown to have a similar diet to the extant *Mystromys albicaudatus* whereas *O.* cf. *gracilis* is shown to be less reliant on grazing than the extant *Otomys irroratus*, despite its specialised hypsodont molars. The lack of a grazing specialist amongst the most common species in the Makapansgat micromammal assemblages is suggestive of a local palaeo-environment that was more wooded than the present day woodland–savannah mosaic. The presence of C_4 grasses in the mid-Pliocene of Makapansgat indicates that the spread of C_4 grasses into the South African highveld occurred prior to this time.

Keywords: Isotopes; Carbon; Microwear; Rodent; South Africa; Pliocene

1. Introduction

A large-scale vegetation shift occurred when C_4 grasses began a global expansion between the mid-Miocene and early Pliocene (15–4 Ma; Cerling et al., 1997). It has been suggested that the origin and spread of the C_4 grasses was triggered by a decrease in atmospheric CO_2 levels to below 500 parts per million by volume (ppmv), which would have been of advantage to C_4 grasses which out-compete C_3 grasses under conditions of low atmospheric CO_2 and high temperatures (Ehleringer et al., 1991, 1997; Cerling et al., 1993, 1997). However, the evidence for a decrease in the partial pressure of atmospheric CO_2 (pCO_2) during the mid-Miocene is disputed (Pagani et al., 1999), and the ultimate cause for the spread of C_4 grasses remains unresolved. The C_4 global-expansion model (Cerling et al., 1997) predicts a latitudinal gradient in the proportions of C_4 versus C_3 plants, as is seen today and in the Quaternary (MacFadden et al., 1999), with C_4 grasses dominating over C_3 grasses in the low

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doi:10.1016/j.palaeo.2005.09.011

latitudes. Latitudinal gradients in C_4 grass distribution at any given time are a function of growing season temperature, with the magnitude of the gradient dependent on atmospheric pCO_2. The Cerling et al. (1997) model also predicts that the earliest records of C_4 grasses will occur in low latitudes and that the expansion of C_4 grasses into mid-latitudes will be accompanied by either an increase in global temperature or a decrease in pCO_2 (Cerling et al., 1997).

In support of the Cerling et al. (1997) model, there is evidence that the first record of C_4 grasses in mid-latitude sites can be as late as the Miocene–Pliocene boundary in Namibia (Segalen et al., 2002), China (Ding et al., 1997; Ding and Yang, 2000) and Northern North America (Cerling et al., 1997). The mid-Pliocene rodent faunas of Makapansgat (latitude 24° South) in South Africa offer the opportunity to determine the distribution of C_4 grasses close to the proposed transition from a C_3 to C_4 ecosystem for this region. The aim of this study is to use carbon isotopes in fossil micromammal teeth and combine this data with dental microwear analysis, to determine the approximate proportions of C_4 grasses, C_3 grasses and C_3 trees and bushes in the local palaeoenvironment.

1.1. Environment and palaeoenvironment of Makapansgat

The Makapansgat valley (see Fig. 1) is situated in the northeast of South Africa (latitude 24° South), at an altitude of approximately 1400 m. It is located within the summer rainfall zone and today has a mean annual temperature of 19 °C. The modern vegetation in the mountain range in the vicinity of the Makapansgat Valley is a mixture of riparian woodland, bushland and savannah grass. This region is transitional between Sourish Mixed Bushveld and North-Eastern Sourveld type as classified by Acocks (1953). The modern-day vegetation has also been classified as *Loudetia simplex–Diheteropogon filifolius* grassland (O'Connor and Bredenkamp, 1997) or Mixed-Savannah (Scholes, 1997). Both vegetation types are dominated by grasses using the C_4 photosynthetic pathway (Vogel et al., 1978). Tree and bush cover was greater prior to the deforestation of the valley by farmers (Maguire et al., 1985).

Previous faunal and palaeoenvironmental studies at the Makapansgat Limeworks have focused on the australopithecine-bearing bone breccias, Members 3 and 4 (late Pliocene). Palaeoenvironmental interpretations of these deposits have ranged from fairly shrub-like with open grassland nearby (Wells and Cooke, 1956) to sub-tropical forest (Rayner et al., 1993). However, in the light of recent ecomorphological and stable isotope data, these deposits have most recently been interpretated as representing a bush and woodland environment (Reed, 1998; Sponheimer et al., 1999). Therefore, despite the greater woodland cover in Member 3 times, it appears that the late Pliocene to Recent climate of Makapansgat and other regions of the South African highveld has been located within the summer rainfall regime and the vegetation has been a mix of C_3 and C_4 plants.

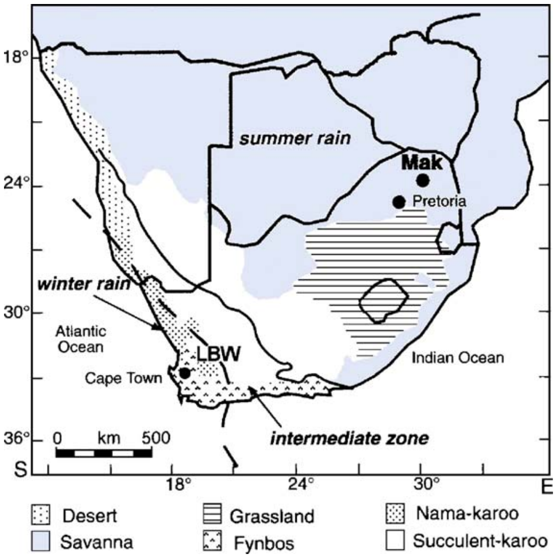

Fig. 1. Map of Southern Africa showing the present distribution of the main vegetation biomes, summer and winter rainfall regimes, and the position of Makapansgat (Mak) and Langebaanweg (LBW). Figure modified from Lee-Thorp and Talma (2000).

Dating of the South African Plio-Pleistocene cave faunas has been a problem since their first discovery. The Makapansgat Limeworks has been classified as one of the oldest of the South African cave deposits on the basis of faunal seriation (McKee et al., 1995; Mckee, 1995) and by palaeomagnetism which places Member 3 at 3.1–3.2 Ma (Partridge, 2000; Partridge et al., 2000). This is in broad agreement with faunal correlation with the radiometrically dated biostratigraphy of the Plio-Pleistocene of east Africa which places Makapansgat Member 3 at approximately 3 Ma (Vrba, 2000). The Makapansgat Rodent Corner *In Situ* pink Breccia (MRCIS) and the Exit Quarry basal Red Mud (EXQRM) microfaunas have traditionally been included within Makapansgat Member 4 (McKee et al., 1995). However, as discussed in Maguire et al. (1985), Latham et al. (1999) and (2003), Makapansgat Members 3 and 4 and the Rodent Corner and Exit Quarry deposits are best viewed as separate repositories with uncertain temporal relationships.