

# Orbital forcing and the spread of C<sub>4</sub> grasses in the late Neogene: stable isotope evidence from South African speleothems

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Received 4 November 2005; accepted 15 March 2007

## Abstract

Reconstructing Plio-Pleistocene African paleoenvironments is important for models of early hominin evolution, but is often hampered by low-resolution or discontinuous climatic data. Here, we present high-resolution stable oxygen and carbon isotope time series data from two flowstones (secondary cave deposits) from the South African hominin-bearing Makapansgat Valley. The age of the older of the two flowstones (Collapsed Cone) is constrained by magnetostratigraphy to approximately 4–5 Ma; the younger flowstone (Buffalo Cave) grew between 2.0–1.5 Ma, as determined by magnetostratigraphy and orbital tuning of the isotopic data.

The carbon isotope data is used as a proxy for the proportion of C<sub>4</sub> grasses in the local environment and the oxygen isotope data reflects monsoon rainfall intensity. The carbon isotope evidence indicates that in the late Miocene/early Pliocene, the local environment was dominated by C<sub>3</sub> vegetation, whereas, in the Plio-Pleistocene, it was composed of a mixture of C<sub>3</sub> and C<sub>4</sub> vegetation. This suggests that C<sub>4</sub> grasses became a significant part of the Makapansgat Valley ecosystem at approximately 4–5 Ma, towards the end of the late Neogene global expansion of C<sub>4</sub> grasses. After this initial expansion, South Africa experienced further fluctuations in the proportion of C<sub>3</sub> and C<sub>4</sub> vegetation during the Plio-Pleistocene, in response to regional and global climatic changes. Most notably, the Buffalo Cave flowstone provides evidence for C<sub>4</sub> grass expansion at ca. 1.7 Ma that we suggest was a response to African aridity caused by the onset of the Walker Circulation in the Pacific Ocean at this time.

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**Keywords:** Savanna; Monsoon; Walker Circulation; Precession; Hominin

## Introduction

Global climatic oscillations with Milankovitch periodicities are a dominant feature of the late Neogene and have been viewed as driving forces in the evolution of African mammalian faunas, including hominins (e.g., Bromage and Schrenk, 1995; Vrba, 1995a; Potts, 1998; Zeitoun, 2000; Bobe and

Eck, 2001; Barry et al., 2002; Bobe et al., 2002). In the absence of a long and detailed terrestrial record of global change, these models of climatically forced macroevolution have used the marine paleotemperature record (e.g., Shackleton, 1995) as the template onto which trends in mammalian evolution are fitted. The focus has been either on directional trends of global cooling (Vrba, 1992, 1995a) or on the magnitude and frequency of climatic variability (Potts, 1996, 1998). These global climatic trends have been held responsible for episodes of hominin speciation, extinction, and migration. While there

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are sound theoretical and empirical reasons to link events in hominin evolution to periods of climatic change (Vrba, 1995b), it is simplistic to assume that the late Neogene marine paleoclimate record is a faithful proxy for subtropical and tropical African paleoclimates. On the contrary, there is mounting evidence to show that tropical terrestrial climatic change is decoupled from the global ice volume record of deep-sea  $\delta^{18}\text{O}$  (e.g., Pokras and Mix, 1987; Clemens et al., 1991; Partridge et al., 1997; Trauth et al., 2005; Hopley et al., 2007). Previous proxy records of African climate change have been constructed from terrestrial components within marine sediment cores (deMenocal and Bloemendal, 1995; Dupont and Leroy, 1995) that produce space-averaged terrestrial records that cannot be linked to specific hominin habitats.

#### *Neogene spread of savanna grasses and the faunal response*

It is widely accepted that the mid-Miocene African faunas differ significantly from the Plio-Pleistocene African faunas in terms of their species composition and habitat preferences (e.g., Hill, 1987; Andrews, 1992; Vrba, 1995a), and that the interim period represents a gross restructuring of the African terrestrial communities in response to the developing savanna biome. However, refining the details of this transition from the mid-Miocene “C<sub>3</sub>-world” to the Plio-Pleistocene “C<sub>4</sub>-world” has been problematic. The Cerling et al. (1997) interpretation of the carbon isotope data from fossil herbivore teeth restricts the global expansion of C<sub>4</sub> biomass to one event between 8 Ma and 6 Ma. However, as noted by Köhler et al. (1998), this single pulse of C<sub>4</sub> grass expansion is not always accompanied by an increase in faunal turnover in the “C<sub>4</sub>-world”. Köhler et al. (1998) highlight the fact that faunal turnover events also occur in purely C<sub>3</sub> environments in the late Neogene, indicating that faunal turnover is not unique to tropical savanna-woodland mosaics.

Numerous episodes of increased rates of faunal turnover have been identified within terrestrial late Neogene mammalian sequences, each showing replacement of woodland fauna by more savanna-adapted species. These events occur at different times in different regions of the world and are uniformly distributed within the last ten million years. Examples of documented late Neogene faunal turnover events have been recorded at 10 Ma, 7.8 Ma, and 7.3–7.0 Ma in Pakistan (Barry et al., 2002; Patnaik, 2003; Raza et al., 2002); 10–9 Ma and 6.5 Ma in Spain (Pickford et al., 1995; Köhler et al., 1998); approximately 7.4 Ma–6.0 Ma in the Nawata Formation of the Lothagam succession, Kenya (Leakey and Harris, 2003; McDougall and Feibel, 2003); and between 2.8 and 2.3 Ma in the Omo sequence of Ethiopia (Bobe and Eck, 2001; Bobe et al., 2002). There is no global faunal turnover event significantly above background rates at 8–6 Ma (Köhler et al., 1998) that can be related to the rapid global expansion of C<sub>4</sub> grasses as described by Cerling et al. (1997). These studies indicate there was a series of turnover events in the late Neogene which, if they are linked with episodes of climatic change, are related to regional rather than global events.

#### *Southern African late Neogene paleoclimates*

The relative abundance of C<sub>3</sub> and C<sub>4</sub> plants in modern-day South Africa is strongly influenced by the existence of two seasonally distinct climate systems (Vogel et al., 1978; Lee-Thorp and Talma, 2000). C<sub>4</sub> grasses dominate the grassy vegetation of those areas receiving summer rainfall in the eastern and interior regions of South Africa, with the exception of the high mountains along the eastern escarpment (Vogel et al., 1978). C<sub>3</sub> grasses occur in the Fynbos region to the southwest of South Africa, which receives the majority of its rainfall in the winter. A mixture of C<sub>3</sub> and C<sub>4</sub> grasses is found in the transition zone between the winter and summer rainfall zones. A shift in the range and intensity of the dominant atmospheric circulation systems would, therefore, change the distribution of these two vegetation systems (Lee-Thorp and Talma, 2000). As a consequence of the C<sub>4</sub> photosynthetic pathway, the carbon isotope composition of C<sub>4</sub> plant matter is enriched in <sup>13</sup>C (O’Leary, 1981, 1988), enabling the presence of C<sub>4</sub> photosynthesis to be detected in organic and inorganic carbon species derived from biological processes. The proportion of C<sub>3</sub> and C<sub>4</sub> vegetation in past ecosystems can be determined in fossil teeth (e.g., Lee-Thorp et al., 1994, 2000) and sedimentary carbonates (e.g., Cerling et al., 1989), as long as the effects of diagenetic alteration can be discounted.

Data on the paleoenvironments of South African hominins are derived either from the fauna, flora, or geology of cave breccias. Many of the faunal specimens in the South African hominin sites were found in lime-dumps after the caves were mined in the early twentieth century, and lack stratigraphic context. In situ bone-breccias that survived the lime-mining intact tend to be poorly stratified, and represent unknown periods of deposition of tens- to hundreds-of-thousands-of years (McFadden et al., 1979; Herries, 2003). Both in situ and mined bone-breccias are given Member status within the stratigraphy of each cave deposit (e.g., Partridge, 1978, 1979) and are defined on broad differences in sedimentological and paleontological characteristics. Previous paleoenvironmental studies based on these bone-breccias have, therefore, lacked the temporal resolution required to investigate climatic change and early hominin paleoecology on the timescale of orbital cycles.

Stable carbon isotopes of fossil teeth from South African Plio-Pleistocene cave breccias have shown the presence of both C<sub>3</sub> and C<sub>4</sub> vegetation in the local environment of each faunal member studied (van der Merwe and Thackeray, 1997; Sponheimer et al., 1999; Lee-Thorp et al., 2000). However, as discussed in Kingston (1999), selective feeding and taphonomic factors (Vrba, 1980) make converting isotopic paleodietary data into meaningful paleovegetational reconstructions problematic. Fossil macrofloras have only been found in Sterkfontein Member 4 (Bamford, 1999) and fossil pollen studies have been hindered by modern-day contamination (Scott, 1995, 2002).

This study investigates the late Neogene paleoclimates of South Africa using time series of carbon and oxygen isotopes in flowstone sequences from the hominin-bearing Makapansgat Valley. In contrast to bone breccias, the speleothems offer a high-resolution and continuous stratigraphy.

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