

Stable isotopic composition of fossil mammal teeth and environmental change in southwestern South Africa during the Pliocene and Pleistocene



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ABSTRACT

The past 5 million years mark a global change from the warmer, more stable climate of the Pliocene to the initiation of glacial–interglacial cycles during the Pleistocene. Marine core sediment records located off the coast of southwestern Africa indicate aridification and intensified upwelling in the Benguela Current over the Pliocene and Pleistocene. However, few terrestrial records document environmental change in southwestern Africa over this time interval. Here we synthesize new and published carbon and oxygen isotope data of the teeth from large mammals (>6 kg) at Langebaanweg (~5 million years ago, Ma), Elandsfontein (1.0–0.6 Ma), and Hoedjiespunt (0.35–0.20 Ma), to evaluate environmental change in southwestern Africa between the Pliocene and Pleistocene. The majority of browsing and grazing herbivores from these sites yield enamel $\delta^{13}\text{C}$ values within the range expected for animals with a pure C₃ diet, however some taxa have enamel $\delta^{13}\text{C}$ values that suggest the presence of small amounts C₄ grasses at times during the Pleistocene. Considering that significant amounts of C₄ grasses require a warm growing season, these results indicate that the winter rainfall zone, characteristic of the region today, could have been in place for the past 5 million years. The average $\delta^{18}\text{O}$ value of the herbivore teeth increases ~4.4‰ between Langebaanweg and Elandsfontein for all taxa except suids. This increase may solely be a function of a change in hydrology between the fluvial system at Langebaanweg and the spring-fed environments at Elandsfontein, or a combination of factors that include depositional context, regional circulation and global climate. However, an increase in regional aridity or global cooling between the early Pliocene and mid-Pleistocene cannot explain the entire increase in enamel $\delta^{18}\text{O}$ values. Spring-fed environments like those at Elandsfontein may have provided critical resources for mammalian fauna in the mid-Pleistocene within an increasingly arid southwestern Africa ecosystem.

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1. Introduction

The Pliocene–Pleistocene climatic transition is marked by a global shift from relatively warm and stable climate conditions in the Pliocene to colder and more variable conditions in the Pleistocene (Imbrie et al., 1992; Zachos et al., 2001). Over the course of this transition African landscapes are considered to have become more arid (e.g., deMenocal, 2004; Dupont et al., 2013). In southwestern Africa, intensified upwelling

of cold bottom waters in the Benguela Current System has been linked with increased regional aridity and the onset, expansion and speciation of the endemic Cape flora since the Miocene (Marlow et al., 2000; Dupont et al., 2005; Dupont, 2011; Etourneau et al., 2009). While marine-based records indicate major changes in vegetation and climate in southern Africa, terrestrial-based records could provide a more local perspective of the hydrological setting, vegetation and climate of southwestern South Africa since the Pliocene; currently there are few archives of environmental change in this region during the last 5 million years (myr) (Roberts et al., 2011; Eze and Meadows, 2014).

Sedimentary strata from known Pliocene and Pleistocene fossil sites in southwestern South Africa have the potential to provide direct evidence for the local environmental response to climate change (Table 1). Sedimentary records indicate a transition from fluvial to

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Table 1

A summary of the terrestrial records of climate, vegetation and depositional environment from southwestern South Africa.

Age	Locality	Depositional environment	Substrate	Vegetation	Climate	Data sets	References
late Pleistocene (0.35–0.25 Ma)	Hoedjiespunt	Coastal	Sands	Shrubs and widespread grasslands	Glacial	Taxonomy ^a Stable isotopes ^a	Klein, 1983; Stynder, 1997; Hare and Sealy, 2013
mid-Pleistocene (~1.0–0.6 Ma)	Elandsfontein	Spring-fed and eolian	Eolian and marine sands, carbonate-leached sediments, pedogenically modified sands	Trees, shrubs, and seasonal grasses	Glacial and/or Interglacial	Taxonomy ^a Stable isotopes ^a Microwear ^a Sedimentology	Butzer, 1973; Klein, 1978; Luyt et al., 2000; Stynder, 2009; Braun et al., 2013
Pliocene (~5 Ma)	Langebaanweg	Fluvial and deltaic	Floodplain, marsh, and river channel deposits	Trees, shrubs, and seasonal grasses	Warm and wet	Taxonomy ^a Stable isotopes ^a Mesowear ^a Microwear ^a Sedimentology	Franz-Odenaal et al., 2002; Roberts et al., 2011; Stynder, 2011

^a Datasets that apply to teeth.

spring-fed and eolian deposition in southwestern South Africa (Roberts et al., 2011; Eze and Meadows, 2014). Data from pre-Holocene mammalian fossils suggest the presence of significant amounts of surface water and a vegetated landscape composed of a fynbos shrubland and grassland mosaic, interspersed with trees and broad-leaved bush, which contrasts the dry, eolian landscapes that are prevalent in southwestern South Africa today (e.g., Luyt et al., 2000; Franz-Odenaal et al., 2002; Stynder, 2009, 2011; Braun et al., 2013).

Here we use the carbon and oxygen isotopic composition of fossil herbivore tooth enamel obtained from paleontological and archeological sites in southwestern South Africa to investigate trends in regional climate and hydrology, vegetation and animal diet between the Pliocene and Pleistocene. Together with marine archives off the coast of southern Africa that record broader, regional-scale climate and vegetation, we use these terrestrial-based data to improve upon the understanding of how environments in southwestern South Africa responded to global climatic changes during the Pliocene and Pleistocene.

2. Background

2.1. South African climate and vegetation

South Africa is predominantly semiarid with three distinct rainfall zones and corresponding vegetation zones (Fig. 1; Cowling and Lombard, 2002). The winter rainfall zone of western South Africa encompasses an area of ~200-km² where ~65% of mean annual precipitation (MAP) occurs between April and September. The summer rainfall zone is affected by the warm Agulhas Current that flows along the eastern coast of South Africa. At the intersection of these two major meteorological zones, situated along the South Coast of South Africa, there is a region that receives rainfall during both the summer and winter. This annual rainfall zone spans from the southern coast of the Eastern Cape Province of South Africa into the Western Cape Province (e.g., Chase and Meadows, 2007).

Rainfall zones in South Africa partition zones of vegetation, which can be seen through the spatial distribution of the frequency of the

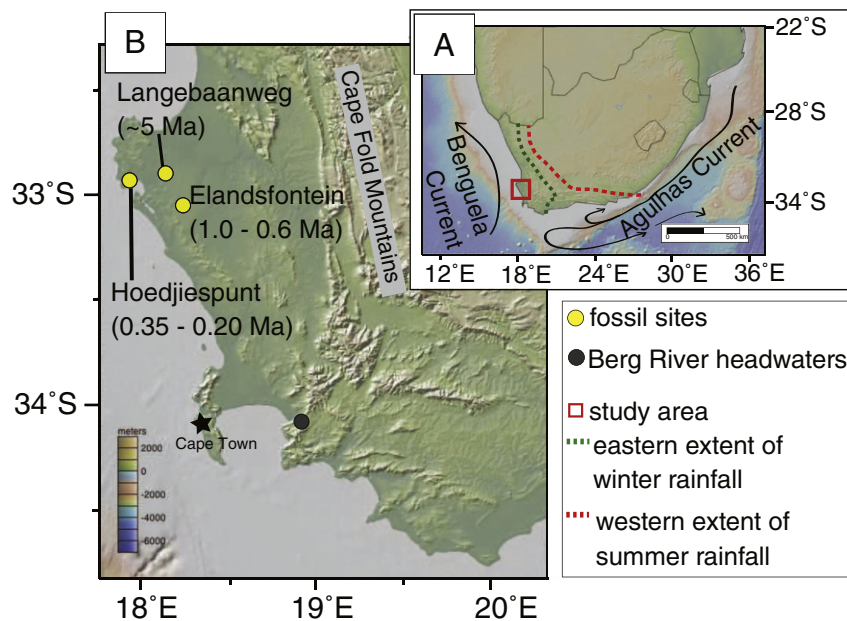


Fig. 1. Marine currents, climate zones and southwestern South African fossil sites discussed in text. A) A map of southern Africa indicating the location of the study area with a schematic of the present-day extent of the winter and summer rainfall zones, the Benguela and Agulhas Currents and present-day political boundaries (Chase and Meadows, 2007). B) A map of the study area denoting the fossil localities discussed in text (yellow circles), Cape Town, the Cape Fold Mountains and the headwaters of the Berg River. The color base maps indicating topography were generated using Global Multi-Resolution Topography from <http://www.geomapapp.org> (Ryan et al., 2009).

three main photosynthetic pathways: C₃, C₄, and Crassulacean Acid Metabolism (CAM). The distribution of these pathways is largely determined by environmental factors (Farquhar et al., 1989). C₄ plants thrive in environments with a warm growing season while C₃ plants grow primarily in regions with a cool growing season. CAM plants, such as cacti and succulents, are often found in semiarid to arid environments. The distribution of grass type is related to the seasonality of rainfall in South Africa; C₄ grasses mostly grow in regions with summer rainfall, C₃ grasses grow where there is winter rainfall, and both C₃ and C₄ grasses grow in the annual rainfall zone (Vogel et al., 1978; Cowling and Lombard, 2002; Bar-Matthews et al., 2010). Increased upwelling and latitudinal movement of the Benguela Current may modify the movement of warm waters along the coast of South Africa and this could impact the distribution of the rainfall zones (Chase and Meadows, 2007). The positions of the rainfall and vegetation zones are hypothesized to have shifted during the late Quaternary in response to the position and upwelling intensity of the Benguela Current (Lee-Thorp and Beaumont, 1995), however it is unclear whether they were stable in the Pliocene and mid-Pleistocene.

The paleontological and archeological sites that are the focus of this paper are within southwestern South Africa, west of the Cape Fold Mountains and stretch across 40 km of the coastal plain. These sites, Langebaanweg (~5 million years ago (Ma), early Pliocene), Elandsfontein (~1.0–0.6 Ma, mid-Pleistocene) and Hoedjiespunt (0.35–0.20 Ma, late Pleistocene), are within the winter rainfall zone (Fig. 1). Regionally the area is known as Strandveld (literally 'beach vegetation') and geomorphologically is dominated by a coastal plain variably covered by marine sands (Mabbutt, 1956; Roberts et al., 2011). Limited outcrops of granite to the south and west interrupt Cenozoic-aged eolian deposits that blanket much of the region. The western portion of the area is underlain by shales of the Malmesbury Group leading up to the Palaeozoic sandstones of the Cape Supergroup (Besans, 1972; Roberts et al., 2009). The contemporary vegetation in the study area is primarily composed of small-leaved, nutrient-poor taxa of the strandveld and fynbos families. C₃ grasses and trees are scarce in this area because of the nutrient-poor soils. It has generally been presumed that C₄ grasses are limited in the southwestern Cape by the long, hot and dry summers, however C₄ grasses are able to grow in areas that are well watered throughout the year (e.g., Cowling and Lombard, 2002; Cowling et al., 2005).

2.2. Pliocene and Pleistocene climate and vegetation in western South Africa

2.2.1. Marine records

Marine sediment records from cores off the coast of southwestern Africa span the past 4.5 myr and provide information about terrestrial responses to global climate change and the degree of ocean upwelling (Marlow et al., 2000; Dupont et al., 2005; Etourneau et al., 2009). Charcoal and plant waxes preserved offshore show that there was an increase in aridity, seasonality and fires to the north of the study area during the Miocene and Pliocene (Hoetzel et al., 2013). The drying trend continued across the Pliocene-Pleistocene climatic transition; offshore pollen records indicate a reduction in grass and an increased occurrence of fynbos and semi-desert vegetation (e.g., Dupont et al., 2005).

2.2.2. Terrestrial records

In contrast to the high-resolution, marine-based proxy records that extend into the Miocene, there are no terrestrial-based proxy records with a similar time span or resolution. However the numerous archives of eolian and riverine sedimentary sequences on the coastal plains of southwestern South Africa provide some details of late Cenozoic environments. There have been numerous studies of ancient environments in this region based on these records (e.g., Klein, 1978, 1982, 1983, 1991; Klein and Cruz-Urbe, 1991; February, 1992; Meadows et al., 1996). However, the vast majority of these studies have focused on

environments since the Last Interglacial (0.125 Ma). Langebaanweg, Elandsfontein and Hoedjiespunt are paleontological and archeological sites within the study area that date to within the last ~5 myr. These sites are well known for their contribution to our understanding of faunal change and human evolution in South Africa (e.g., Hendey, 1976; Klein, 1978; Berger and Parkington, 1995; Stynder, 1997; Stynder et al., 2001; Klein et al., 2007; Braun et al., 2013). The flora, fauna and sediment records at these sites provide a record of environmental change in the area from the Pliocene and Pleistocene (Luyt et al., 2000; Franz-Odenaal et al., 2002; Stynder, 2009; Roberts et al., 2011; Stynder, 2011; Braun et al., 2013; Hare and Sealy, 2013; Eze and Meadows, 2014). While these sites have been the focus of a variety of paleoecological studies (Table 1), currently there is no detailed, integrated record of the hydrological, ecological and climatic changes in southwestern South Africa over the past 5 myr.

2.3. Carbon and oxygen isotope composition of herbivore tooth enamel

C₃, C₄ and CAM plants have distinct stable carbon isotope values primarily due to different physiologies of the different photosynthetic pathways (e.g., Farquhar et al., 1989). Carbon isotope data of plants are traditionally presented using δ -notation, where $\delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000$ in per mil (‰) units and R_{sample} and R_{standard} are the ratios of heavy to light isotopes (in this case, ¹³C and ¹²C) of the sample and standard, respectively. $\delta^{13}\text{C}$ values are reported relative to Vienna Pee Dee Belemnite (VPDB). The $\delta^{13}\text{C}$ values of C₃ plants globally range from ~−31.7‰ to −23.1‰ (Kohn, 2010). The $\delta^{13}\text{C}$ values C₄ plants range from ~−14.0‰ and −10.0‰ (Hattersley, 1982). In southwestern South Africa the average $\delta^{13}\text{C}$ value of C₄ plants is $-12.8 \pm 1.3\%$ (Radloff, 2008), whereas $\delta^{13}\text{C}$ values of CAM plants range from ~−24‰ to −16‰ (Boom et al., 2014).

The $\delta^{13}\text{C}_{\text{enamel}}$ value reflects the proportion of C₃ and C₄ plants in an animal's diet such that the $\delta^{13}\text{C}_{\text{enamel}}$ values of fossil herbivore teeth can be used to determine the presence or absence of C₃ and C₄ grasses in the past. There is a +14.1‰ dietary enrichment of $\delta^{13}\text{C}$ values between the diet of large herbivorous mammals (>6 kg) and their enamel (Cerling and Harris, 1999) and as such the $\delta^{13}\text{C}$ value of tooth enamel ($\delta^{13}\text{C}_{\text{enamel}}$) reflects the isotopic composition of an animal's diet (see Kohn and Cerling, 2002 for review). Here we define large mammals as >6 kg because the smallest mammal included in this category is the grysbok, which is ~10 kg, whereas we refer to the mammals from Elandsfontein with body weights <6 kg as small mammals, which includes the rodent genera *Bathyergus* and *Otomys*. For fossil sites, in southern Africa, the presence or absence of C₃ and C₄ grasses in mammalian diet has been presumed to reflect the presence or absence of winter and summer rainfall (Luyt et al., 2000; Franz-Odenaal et al., 2002; Hare and Sealy, 2013). Within a C₃-dominated ecosystem, the isotopic composition of tooth enamel from large herbivores can be used to tease apart subtleties in the distribution of vegetation (e.g., Luyt et al., 2000; Franz-Odenaal et al., 2002; Hare and Sealy, 2013). For example, Hare and Sealy (2013) suggest that there was some C₄ grass in C₃-dominated grasslands in southwestern South Africa during the late Pleistocene because the $\delta^{13}\text{C}_{\text{enamel}}$ values of grazers were more enriched in $\delta^{13}\text{C}_{\text{enamel}}$ values than what is expected for a grazer consuming purely C₃ vegetation. CAM plants are not considered to have greatly influenced the $\delta^{13}\text{C}_{\text{enamel}}$ values because they do not comprise a major proportion of large mammalian herbivore diets (Cerling et al., 2003) and therefore they will not be further considered in this study.

The stable oxygen isotope composition of the carbonate component of herbivore tooth enamel is affected by a number of factors including the $\delta^{18}\text{O}$ value of ingested water, which is influenced by the $\delta^{18}\text{O}$ values of precipitation, surface and plant water, as well as animal physiology and behavior (as reviewed in Kohn and Cerling, 2002). All of these factors generally contribute to higher $\delta^{18}\text{O}$ values of enamel in more arid environments. The comparison of enamel $\delta^{18}\text{O}$ values between obligate

drinkers and non-obligate drinkers has been specifically used for evaluating relative aridity in terrestrial ecosystems (e.g., Levin et al., 2006).

The oxygen isotopic composition of enamel phosphate has also been used as a proxy for paleoclimate and is considered to be less susceptible to alteration than the oxygen isotope composition of the carbonate component of enamel because oxygen in the phosphate component is more tightly bound than in the carbonate component of enamel (Chenery et al., 2012). The offset between $\delta^{18}\text{O}$ values of the carbonate and phosphate components of enamel ranges from 7.2‰ to 10.6‰ in well-preserved teeth and has been used as a means to evaluate diagenetic modification of the $\delta^{18}\text{O}$ values of fossil teeth (e.g., Iacumin et al., 1996).

3. Materials and methods

3.1. Fossil enamel samples

We sampled mid-Pleistocene fossil teeth from two separate faunal collections at Elandsfontein. The first collection is housed at the Iziko South African Museums in Cape Town, South Africa. This faunal sample, known as Elandsfontein Main (EFTM), was predominantly collected from surface deposits over the course of several decades as described in Klein et al. (2007). The second collection derives from recent fieldwork conducted by the West Coast Research Project (WCRP) between 2008 and 2014. These materials are archived at the Department of Archaeology, University of Cape Town and include both surface samples and excavated teeth. All fossils that we sampled from the WCRP collection derive from the Upper Pedogenic Sand lithological unit that is part of the Langebaan Formation (Braun et al., 2013). We also sampled Pliocene teeth ($n = 10$) from the Varswater Formation at the Langebaanweg paleontological locality, which were obtained from the West Coast Fossil Park (Roberts et al., 2011). The teeth from Langebaanweg were sampled to provide a point of comparison in the evaluation of the diagenetic alteration of oxygen isotopes in tooth enamel from Elandsfontein. All tooth enamel was sampled with a diamond drill bit along the tooth growth axis. When possible, third molars were sampled. New data were compiled with previously published carbon and oxygen isotope tooth enamel data from the region, including 64 teeth from Langebaanweg (Franz-Odenaal et al., 2002), 18 teeth from Elandsfontein (Luyt et al., 2000), and 39 teeth from Hoedjiespunt (Hare and Sealy, 2013). This compilation does not include the isotope data of the fossil teeth from the “Bone Circle” at Elandsfontein that Luyt et al. (2000) published because we are uncertain of their context and relationship to the other fossils from Elandsfontein (Braun et al., 2013).

3.2. Isotopic measurements

We measured $\delta^{13}\text{C}_{\text{enamel}}$ values and $\delta^{18}\text{O}$ values of both the carbonate and phosphate components of fossil tooth enamel. We also measured $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values of surface and ground waters in the immediate vicinity of Elandsfontein and in the general Langebaan–Hopefield region.

3.2.1. Analysis of the enamel carbonate component

Fossil enamel was powdered, treated with 3% H_2O_2 to remove organic material and rinsed three times with deionized water. The resultant powder was rinsed with 0.1 M buffered acetic acid to remove secondary carbonate, rinsed three times with deionized water and dried overnight at 60 °C. Approximately 500 to 800 μg of each powdered sample were placed in a silver capsule then digested under vacuum in a common bath of 100% phosphoric acid at 90 °C and the resultant CO_2 was purified using a custom-built automated device (Passey et al., 2010). The CO_2 was analyzed for $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$ ratios using a dual inlet system on a Thermo MAT253 isotope ratio mass spectrometer in the Department of Earth and Planetary Sciences, Johns Hopkins University. The isotopic composition of the resultant CO_2 was determined with respect to a working CO_2

reference, calibrated using NBS-19, and monitored using working references of calcite and enamel. The precision of the working carbonate enamel standards over the course of the analyses made for this study was 0.4‰ and 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively. An acid fractionation factor of 1.00725 was used for determining $\delta^{18}\text{O}$ values of the carbonate component of fossil enamel digested at 90 °C (Passey et al., 2007). All $\delta^{13}\text{C}$ values are reported relative to VPDB (Vienna Pee Dee Belemnite) and $\delta^{18}\text{O}$ values are reported relative to VSMOW (Vienna Standard Mean Ocean Water).

3.2.2. Analysis of the $\delta^{18}\text{O}$ values of enamel phosphate

Forty-eight fossil teeth from Langebaanweg and Elandsfontein were analyzed for the $\delta^{18}\text{O}$ values of enamel phosphate, in addition to carbon and oxygen isotope analyses of enamel carbonate mentioned above. Samples were drilled and pretreated in the manner described above (Section 3.2.1). Phosphate-bound oxygen was isolated and extracted from enamel using a modified version of the batch Ag_3PO_4 precipitation method of O’Neil et al. (1994) followed by $\delta^{18}\text{O}$ analysis of approximately 400 μg of Ag_3PO_4 via high temperature pyrolysis to CO (TC/EA) on a continuous flow Delta Plus XL isotope ratio mass spectrometer at the Department of Geosciences, Princeton University.

Long-term performance (precision of the isotope ratio mass spectroscopy measurement and wet chemistry conversion from hydroxyapatite to Ag_3PO_4) was confirmed by repeat analysis of NBS120c, a phosphate rock with certified metal oxide abundances and distributed by the National Institute of Standards and Technology and the de facto standard for $\delta^{18}\text{O}$ in phosphate, with $\delta^{18}\text{O}$ values ranging from 21.3 to 22.6‰ VSMOW (e.g., Vennemann et al., 2002; Halas et al., 2011). Although precipitation yield varied using the modified O’Neil et al. (1994) batch precipitation method ($52 \pm 22\%$), repeat analysis of the NBS120c phosphate standard over 18 months averaged $22.36 \pm 0.48\%$ and showed no dependence of measured $\delta^{18}\text{O}$ values on precipitation yield, with the average value aligning well with published $\delta^{18}\text{O}$ values.

3.2.3. Analysis of the $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values of water

Samples of standing water and ground water ($n = 3$) were collected from a series of active springs in the vicinity (within an ~3 km to ~17 km radius) of the Quaternary deposits at Elandsfontein where fossil teeth were collected. Tap water from The Western Cape Fossil Park (which is in the general proximity of the study area) was also collected ($n = 1$). Samples were passed through a 0.45- μm filter in the field and sealed in a glass bottles with polycone seal lids and wrapped in parafilm to prevent evaporation. Samples were cleaned with activated charcoal to remove organics, filtered again and then analyzed by laser absorption spectroscopy on a Los Gatos Research Liquid-Water Isotope Analyzer at the Department of Earth and Planetary Sciences, Johns Hopkins University. The precision of the working water standard USGS48 over the course of the water analyses was 0.03‰ and 0.1‰ for $\delta^{18}\text{O}$ and $\delta^2\text{H}$ respectively. The $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values of water samples are reported relative to the VSMOW-SLAP scale, where SLAP is Standard Light Antarctic Precipitation.

3.3. Interpretation of stable isotope results

3.3.1. Influence of $\delta^{13}\text{C}$ values of atmospheric CO_2

The $\delta^{13}\text{C}$ value of atmospheric CO_2 has decreased over the past 5 myr (Tippie et al., 2010) and this decrease needs to be considered when using $\delta^{13}\text{C}_{\text{enamel}}$ values to determine the proportion of C_3 and C_4 plants in an animal’s diet. The $\delta^{13}\text{C}$ value of atmospheric CO_2 will influence the $\delta^{13}\text{C}$ values of C_3 and C_4 plants and as a consequence will influence $\delta^{13}\text{C}_{\text{enamel}}$ values of the tissues of the animals that eat these plants. We calculated the ranges in $\delta^{13}\text{C}$ values that we expect for C_3 and C_4 plants at the time periods representative of Langebaanweg (~5 Ma), Elandsfontein (~1.0–0.6 Ma) and Hoedjiespunt (0.35–0.20 Ma) to better determine what herbivore $\delta^{13}\text{C}_{\text{enamel}}$ values may indicate about the

distribution of C₃ and C₄ plants in the study area, considering the $\delta^{13}\text{C}$ values of atmospheric CO₂ reconstructed from benthic foraminifera (Tipple et al., 2010; see Table S1 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042> for details). Given changes in the $\delta^{13}\text{C}$ value of atmospheric CO₂, the maximum $\delta^{13}\text{C}_{\text{enamel}}$ values for large mammals with a pure C₃ diet are -7.6% for Langebaanweg and -8.4% for both Elandsfontein and Hoedjiespunt (Table S1 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>). If the $\delta^{13}\text{C}_{\text{enamel}}$ value of a grazer is higher than the reconstructed maximum $\delta^{13}\text{C}_{\text{enamel}}$ value for an animal eating a pure C₃ diet, then it implies the presence of C₄ grass in the animal's diet and, in turn, the growth of C₄ plants in the otherwise dry summer months in southwestern South Africa. As mentioned earlier, the presence of C₄ grass in southwestern South Africa is interpreted as the presence of rainfall during the summer months in this ecosystem. Alternatively, large mammals may be feeding around permanent water sources such as springs and rivers where C₄ plants may have grown.

3.3.2. Analysis of the $\delta^{18}\text{O}$ values of enamel phosphate

Low carbonate content of fossils, bones and sediments at Elandsfontein have led to hypotheses that carbonate has been leached from the fossil deposits at the Elandsfontein archeological site since initial deposition and burial (Luyt et al., 2000). This is in contrast to fossils from the sites Langebaanweg and Hoedjiespunt, which have been recovered from carbonate-rich sediments (Stynder, 1997; Roberts et al., 2011). To evaluate the potential influence of leaching on the $\delta^{18}\text{O}$ values of the carbonate component of tooth enamel at Elandsfontein and whether or not these $\delta^{18}\text{O}$ values can be used as indicators of paleoclimate, we compared the offsets in $\delta^{18}\text{O}$ values of the carbonate and phosphate of fossil teeth from Elandsfontein to those from Langebaanweg.

Oxygen in enamel phosphate is more strongly bound and more resistant to diagenetic alteration than in enamel carbonate. There is a consistent enrichment between the $\delta^{18}\text{O}$ value in enamel phosphate and carbonate and as such $\delta^{18}\text{O}$ values of the oxygen in the phosphate and carbonate component of tooth enamel are strongly correlated for modern and unaltered fossil enamel (Bryant et al., 1996; Iacumin et al., 1996; Martin et al., 2008). This enrichment, or epsilon (i.e., $\epsilon^{18}\text{O}_{\text{A-B}}$ where $\epsilon^{18}\text{O}_{\text{A-B}} = \left[\frac{1000 + \delta^{18}\text{O}_{\text{A}}}{1000 + \delta^{18}\text{O}_{\text{B}}} \right] \times 1000$ and where in this case A = CO₃ and B = PO₄), ranges from 7.2 to 10.6‰ for enamel that has not experienced significant diagenesis (Bryant et al., 1996; Iacumin et al., 1996; Martin et al., 2008). The $\epsilon^{18}\text{O}_{\text{CO}_3\text{-PO}_4}$ has been used to determine if the oxygen isotopic composition of the carbonate in bioapatite has been diagenetically altered (Iacumin et al., 1996). We compared $\epsilon^{18}\text{O}_{\text{CO}_3\text{-PO}_4}$ values of teeth at Elandsfontein to those from Langebaanweg and from compilations of modern teeth to evaluate the integrity of the $\delta^{18}\text{O}$ values of the carbonate component of teeth from Elandsfontein. If the $\epsilon^{18}\text{O}_{\text{CO}_3\text{-PO}_4}$ values at Langebaanweg and Elandsfontein are similar to one another and within the range expected for unaltered teeth, then the $\delta^{18}\text{O}$ values of the carbonate component of enamel from Elandsfontein can be used to reconstruct paleoenvironment.

3.3.3. Statistical comparison of isotopic values

All comparisons of isotope data from fossil teeth were performed using the JMP 11, a statistical analytical software program developed by the SAS Institute, and evaluated using the Tukey–Kramer HSD test. The \pm symbol is used throughout this paper to represent one standard deviation from the mean.

4. Results

4.1. Isotopic composition of fossil enamel carbonate from Elandsfontein

The compiled dataset for carbon and oxygen isotope data (carbonate component only) for large mammalian teeth from Elandsfontein is

comprised of two collections that represent the mid-Pleistocene, EFTM ($n = 71$; Luyt et al., 2000; this study) and WCRP ($n = 123$; this study). The EFTM and WCRP collections include fossil teeth from seven herbivore families: Bovidae, Elephantidae, Equidae, Giraffidae, Hippopotamidae, Rhinocerotidae and Suidae, in addition to a single tooth from the primate family, Cercopithecidae (see Table 2 and Table S2 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>). These samples likely all belong to the same stratigraphic unit, the mid-Pleistocene Upper Pedogenic Sand in the Langebaan Formation (Braun et al., 2013). The main difference between these collections is that fossils in the EFTM collection were collected from surface finds over decades (Klein et al., 2007), whereas the WCRP collection includes a combination of fossils recovered from surface surveys and excavations made with careful attention to stratigraphic context (Braun et al., 2013).

There are no differences in either the $\delta^{13}\text{C}$ values ($p > 0.9$) or $\delta^{18}\text{O}$ values ($p > 0.2$) of enamel carbonate, grouped by taxonomic family, from the EFTM collection data reported by Luyt et al. (2000) and the new EFTM data that we report in this study. When the isotopic data from teeth in the combined EFTM dataset (Luyt et al., 2000; this study) are compared to the isotopic data from fossils in the WCRP collection (this study only), we do not find any differences in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of fossil teeth from like families except for $\delta^{18}\text{O}$ values (enamel carbonate) of the suids (EFTM, $n = 5$, $26.3 \pm 2.6\%$; WCRP, $n = 3$, $32.1 \pm 0.6\%$, $p = 0.004$). We note that the sample size is small for several of the families analyzed at Elandsfontein (see Table 2 and Table S2 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>). From here on out, we discuss the isotope data from both the EFTM and WCRP collections together and refer to them as all from Elandsfontein, unless otherwise noted.

We classified the dietary behavior (i.e., grazer, browser or mixed feeder) of 104 teeth from the compiled collections for Elandsfontein using a combination of approaches, including mesowear, microwear and taxonomic analogy (Fig. 2; Table S2 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>; Stynder, 2009, 2011). The individual teeth fall into three groups: browsers ($n = 20$), mixed feeders ($n = 4$) and grazers ($n = 71$). *Theropithecus* at Elandsfontein has not yet been analyzed using mesowear or microwear to determine diet so we do not place it in one of these categories. We consider hippopotamids apart from the other taxa that we sampled and classify it as semi-aquatic because in modern African ecosystems *Hippopotamus amphibius* spends a significant amount of time immersed in water, unlike the other taxa in this dataset (e.g., Bocherens et al., 1996; Cerling et al., 2008). The $\delta^{13}\text{C}_{\text{enamel}}$ values of browsers, mixed feeders and grazers average $-11.6 \pm 0.8\%$ ($n = 20$), $-10.3 \pm 1.1\%$ ($n = 4$) and $-10.1 \pm 1.0\%$ ($n = 71$), respectively. The average $\delta^{13}\text{C}_{\text{enamel}}$ value of hippopotamids from Elandsfontein is $-12.3 \pm 1.1\%$ ($n = 9$). The $\delta^{18}\text{O}$ values of the carbonate component of enamel of browsers, mixed feeders, grazers and hippopotamids are $33.1 \pm 1.9\%$, $31.3 \pm 1.6\%$, $32.4 \pm 2.5\%$ and $29.7 \pm 1.5\%$, respectively. Hippopotamid $\delta^{18}\text{O}$ values of enamel carbonate are significantly lower than $\delta^{18}\text{O}$ values of browsers ($p = 0.002$) and grazers ($p = 0.005$).

4.2. Comparison of oxygen isotopic values between enamel carbonate and enamel phosphate

We analyzed the oxygen isotope composition of both the carbonate and phosphate components of a subset of tooth enamel from Elandsfontein and Langebaanweg to evaluate whether the $\delta^{18}\text{O}$ value of the carbonate component of enamel from fossil teeth at Elandsfontein is well enough preserved that it can be used as a proxy for conditions during the animal's life. The average $\epsilon^{18}\text{O}_{\text{CO}_3\text{-PO}_4}$ values of enamel are $9.2 \pm 0.7\%$ ($n = 38$) and $8.2 \pm 0.7\%$ ($n = 10$) for Elandsfontein and Langebaanweg, respectively; these values fit within the range observed for well-preserved teeth (7.2–10.6‰) (Bryant et al., 1996; Iacumin et al., 1996 and Martin et al., 2008; Fig. 3; Table S3 in the online version at

Table 2
 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of fossil tooth enamel from sites in southwestern South Africa, averaged by family and bovid tribe^a.

Taxon (family or tribe)	Dietary behavior ^b	$\delta^{13}\text{C}_{\text{enamel}}$ (‰ VPDB $\pm 1\sigma$)	$\delta^{18}\text{O}_{\text{enamel}}$ (‰ VSMOW $\pm 1\sigma$)	Number of samples
Hoedjiespunt (0.35–0.25 Ma)				
Alcelaphini	Grazer	-9.8 ± 1.3	31 ± 1.5	16
Bovini	Grazer	-7.1 ± 1.3	32.9 ± 0.6	2
Reduncini	Grazer	-10.2 ± 2.3	32.7 ± 2.0	2
Antelopini	Mixed feeder	-9.6 ± 1.1	31.2 ± 2.1	5
Neotragini	Mixed feeder	-8.4 ± 2.5	32.2 ± 1.3	3
Cephalophini	Browser	-10.4 ± 0.6	31.1 ± 1.5	3
Tragelaphini	Browser	-9.5 ± 1.3	31.2 ± 1.2	8
All Bovidae	–	-9.5 ± 1.5	31.4 ± 1.5	39
Elandsfontein (~1.0–0.6 Ma)				
Alcelaphini	Grazer	-10.3 ± 1.2	32.6 ± 1.9	19
Bovini	Grazer	-10.3 ± 0.8	33.8 ± 1.6	18
Reduncini	Grazer	-9.6 ± 0.7	33.3 ± 2.7	9
Hippotragini	Mixed feeder	-10.3 ± 1.3	31.3 ± 1.9	4
Neotragini	Browser	-12.3 ± 1.4	32.6 ± 0.7	2
Tragelaphini	Browser	-11.8 ± 0.5	34.6 ± 1.4	8
All Bovidae	–	-10.0 ± 1.3	33.2 ± 2.0	123
Elephantidae	Grazer	-8.5	30.8	1
Cercopithecidae	–	-10.2	31.2	1
Equidae	Grazer	-9.8 ± 0.7	32.7 ± 1.0	32
Giraffidae	Browser	-11.0 ± 1.3	32.5 ± 2.0	7
Hippopotamidae	Semi-aquatic	-12.3 ± 1.1	29.7 ± 1.5	9
Suidae	Grazer	-9.9 ± 1.4	28.0 ± 3.1	8
Rhinocerotidae	Grazer and browser	-11.0 ± 0.8	31.6 ± 1.8	13
Langebaanweg (~5 Ma)				
Alcelaphini	Browser to grazer	-10.8 ± 1.0	27.5 ± 1.5	7
Reduncini	–	-10.7 ± 0.0	28.0 ± 2.1	2
All Bovidae	–	-10.7 ± 0.8	28.7 ± 2.8	11
Equidae	Grazer	-10.7 ± 1.4	28.1 ± 2.4	8
Giraffidae	Browser	-11.4 ± 1.2	28.4 ± 2.0	29
Suidae	–	-11.8 ± 1.0	27.7 ± 0.9	4
Rhinocerotidae	Grazer	-10.9 ± 0.7	26.2 ± 1.4	4
Hippopotamidae	Semi-aquatic	-11.9 ± 1.5	25.4 ± 1.7	18

^a In addition to the new isotopic data, the isotopic data from previously published papers are included to determine the average $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ data for mammalian families and bovid tribes at each fossil site (Luyt et al., 2000; Franz-Odenaal et al., 2002; Hare and Sealy, 2013). See Table S2 for the compilation of data from individual teeth and the corresponding references.

^b References for the classification of dietary behavior are provided in Table S2.

<http://dx.doi.org/10.1016/j.palaeo.2016.04.042>). Based on the similarities in these offsets to what has been measured in well-preserved enamel, we consider the $\delta^{18}\text{O}$ values of the carbonate component of tooth enamel from Elandsfontein to be unaltered and to reflect the environmental and physiological conditions experienced by an animal during tooth formation.

Further data to support this conclusion comes from interspecific comparisons of $\delta^{18}\text{O}$ values of enamel carbonate. Numerous fossil and modern localities have documented that $\delta^{18}\text{O}$ values of hippopotamid enamel carbonate are lower than the $\delta^{18}\text{O}$ values of coeval taxa because they would be eating plants close to water and drinking water (e.g., Bocherens et al., 1996; Levin et al., 2006). Similar taxonomic distinctions found between ancient taxa in the Elandsfontein collection indicate that the unaltered biogenic signal of isotopic values is preserved in these specimens (Fig. 2b). Henceforth, we only discuss the $\delta^{18}\text{O}$ values from the carbonate component of tooth enamel and refer to them as $\delta^{18}\text{O}_{\text{enamel}}$ values.

4.3. Trends in $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ values from southwestern South Africa since 5 Ma

We compiled the new carbon and oxygen isotope data from tooth enamel produced in this study from Elandsfontein and Langebaanweg with the published data from Langebaanweg (Franz-Odenaal et al., 2002), Elandsfontein (Luyt et al., 2000) and Hoedjiespunt (Hare and Sealy, 2013) to examine environmental and climatic changes in southwestern South Africa over the past ~5 Myr. We used mesowear, microwear and taxonomic analogy to classify the dietary behavior of

taxa for samples from Langebaanweg and Elandsfontein (Sponheimer et al., 2001; Franz-Odenaal et al., 2004; Stynder, 2009, 2011). Dietary behaviors of Hoedjiespunt bovids are discussed in Hare and Sealy (2013). These data are compiled in Table S2 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>.

The $\delta^{13}\text{C}_{\text{enamel}}$ values of fossil teeth average $-11.3 \pm 1.3\text{‰}$ ($n = 74$) at Langebaanweg, $-10.6 \pm 1.3\text{‰}$ ($n = 194$) at Elandsfontein and $-9.5 \pm 1.5\text{‰}$ ($n = 39$) at Hoedjiespunt. The average $\delta^{13}\text{C}_{\text{enamel}}$ value of large mammals (>6 kg) at each site fall within the range of the $\delta^{13}\text{C}_{\text{enamel}}$ values expected for animals with diets comprised of purely C_3 vegetation (Fig. 4).

Comparisons of $\delta^{18}\text{O}_{\text{enamel}}$ values from each family from Langebaanweg and Elandsfontein indicate significant differences for like taxa ($p < 0.001$), where the $\delta^{18}\text{O}_{\text{enamel}}$ values for teeth from Elandsfontein are typically $\sim 4.5\text{‰}$ more positive than those from Langebaanweg (Tables 2; S2 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>, Fig. 4b). This distinction holds for $\delta^{18}\text{O}_{\text{enamel}}$ values of all taxa sampled from the two sites except for suids for which there is no difference in $\delta^{18}\text{O}_{\text{enamel}}$ values for Elandsfontein ($28.0 \pm 3.1\text{‰}$) and Langebaanweg ($27.7 \pm 0.9\text{‰}$) (Fig. 4b). However, we do observe an $\sim 4.4\text{‰}$ increase in suid $\delta^{18}\text{O}_{\text{enamel}}$ values between Langebaanweg and Elandsfontein when we only consider the suid $\delta^{18}\text{O}_{\text{enamel}}$ values from the WCRP collection at Elandsfontein ($32.1 \pm 0.6\text{‰}$, $n = 3$) and exclude the suid $\delta^{18}\text{O}_{\text{enamel}}$ values from EFTM from Luyt et al. (2000). The Hoedjiespunt enamel samples are limited to bovids and the comparison of $\delta^{18}\text{O}_{\text{enamel}}$ values for fossil bovids from the three fossil sites are distinct from one another ($p < 0.001$). Bovid $\delta^{18}\text{O}_{\text{enamel}}$ values average $28.7 \pm 2.8\text{‰}$ at

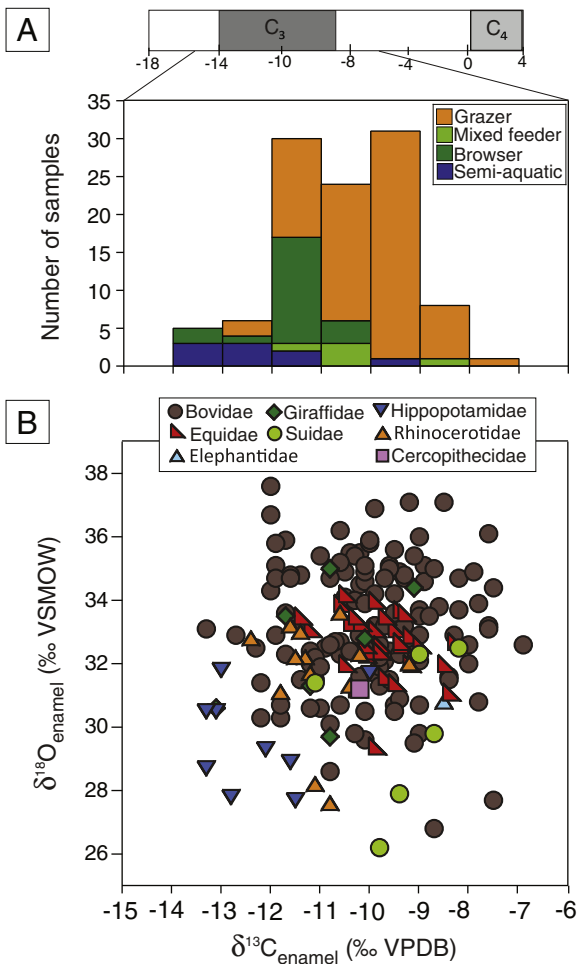


Fig. 2. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the carbonate component of fossil mammalian tooth enamel from the Elandsfontein collections EFTM and WCRP (Luyt et al., 2000; this study). A) Histogram of $\delta^{13}\text{C}$ values of teeth that can be categorized as browser ($n = 20$), grazer ($n = 71$), mixed feeder ($n = 4$) and semi-aquatic hippopotamid ($n = 9$) (Table S2 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>). The smaller plot above the histogram provides a guide for interpreting $\delta^{13}\text{C}$ values in terms of animal diet (pure C_3 and C_4 vegetation, gray bars). B) The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the carbonate component of tooth enamel are plotted for each fossil tooth, grouped by family.

Langebaanweg, $33.2 \pm 2.0\%$ at Elandsfontein, and $31.4 \pm 1.5\%$ at Hoedjiespunt.

5. Discussion

5.1. Vegetation trends in southwestern South Africa

Mammalian faunal and offshore pollen records indicate that the ecosystem of southwestern South Africa was different in the Pliocene and Pleistocene from today and that C_3 grasses were an important component of the physiognomic structure of these ecosystems at times during the last 5 myr (e.g., Dupont et al., 2005; Faith, 2011; Hare and Sealy, 2013). Today the vegetation community is composed of mostly woody, fynbos shrubs. Although rare in southwestern South Africa, grasses are more common inland where they grow on shale substrate, than they are on the marine sands typically found in the study area (Cowling, 1992).

The $\delta^{13}\text{C}_{\text{enamel}}$ values of large mammals from Langebaanweg, Elandsfontein and Hoedjiespunt show that herbivores had diets composed largely of C_3 vegetation (Luyt et al., 2000; Franz-Odenaal et al., 2002; Hare and Sealy, 2013; this study). Specifically, the $\delta^{13}\text{C}_{\text{enamel}}$ values of grazers indicate that the majority of the grasses consumed

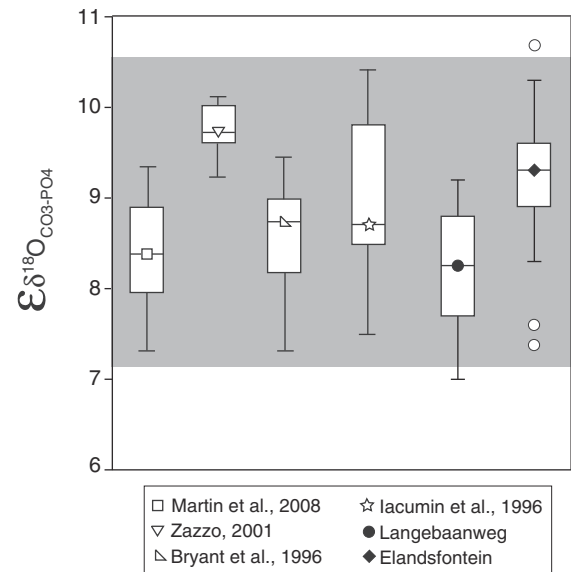


Fig. 3. Box plot of the offset of $\delta^{18}\text{O}$ values of enamel carbonate and enamel phosphate ($\epsilon\delta^{18}\text{O}_{\text{C03-P04}}$) for fossil enamel from Langebaanweg and Elandsfontein (closed symbols) and modern enamel from published studies (open symbols). The ends of the boxes represent the quartile values and the horizontal line within is the median, horizontal lines outside of the box indicate the range, and the outliers are plotted as circles. The gray bar denotes the maximum and minimum $\epsilon\delta^{18}\text{O}_{\text{C03-P04}}$ values measured for modern teeth (Bryant et al., 1996; lacumin et al., 1996; Zazzo, 2001; Martin et al., 2008).

were C_3 grasses. Although the presence of C_4 vegetation cannot be totally discounted at Elandsfontein and Hoedjiespunt (Luyt et al., 2000; Hare and Sealy, 2013; Patterson et al., 2016-in this issue), the $\delta^{13}\text{C}_{\text{enamel}}$ data presented here indicate that it was a relatively small component of the diets of large herbivores (Fig. 4).

The bovids at Elandsfontein are diverse and have a range of dietary behaviors such that the variation in the isotopic composition of bovid teeth may be used to develop a more detailed understanding of the nature of vegetation in the C_3 -dominated ecosystem of southwestern South Africa. For this reason, we compared the $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ values among different bovid tribes, classifying them as browsers, grazers or mixed feeders (see Table 2 and Fig. 4).

When split by tribe there are no distinctions among the $\delta^{13}\text{C}_{\text{enamel}}$ values of bovids from the other grazing and browsing taxa at Langebaanweg ($p > 0.8$). The $\delta^{13}\text{C}_{\text{enamel}}$ values of all fossil teeth at Langebaanweg (browsers, grazers and mixed feeders) are $>2\%$ more negative than the cutoff value for animals with a diet that includes any C_4 vegetation (-7.6% , refer to Section 3.3.1), indicating that all of the animals we sampled had diets composed of solely C_3 vegetation. At Elandsfontein, the $\delta^{13}\text{C}_{\text{enamel}}$ values of browsing taxa (Tragelaphini, Neotragini and giraffids) are significantly more negative than those of grazing taxa (Alcelaphini, Bovini, Reduncini and equids) ($p = 0.005$). In comparison, at Hoedjiespunt the $\delta^{13}\text{C}_{\text{enamel}}$ values of browsing and grazing bovids are not statistically different from one another ($p = 0.97$). In addition, we find that $\delta^{13}\text{C}_{\text{enamel}}$ values of browsing bovid tribes at Hoedjiespunt are $\sim 4\%$ more positive than those of the browsers at Elandsfontein (Fig. 4), whereas the $\delta^{13}\text{C}_{\text{enamel}}$ values of grazing bovids at Elandsfontein and Hoedjiespunt are not significantly different from one another in ($p = 0.2$). This might indicate that the browse vegetation at Elandsfontein was different from that at Hoedjiespunt, which could be related to a drier or less dense mosaic landscape (Kohn, 2010) at Hoedjiespunt compared with Elandsfontein. There are no clear trends that distinguish the $\delta^{18}\text{O}_{\text{enamel}}$ values among different bovid tribes at either Elandsfontein or Hoedjiespunt. There are some indications of C_4 vegetation in the diets of both browsers and grazers at Hoedjiespunt and of grazers at Elandsfontein, however there are no indications of C_4 in the diet among browsers at

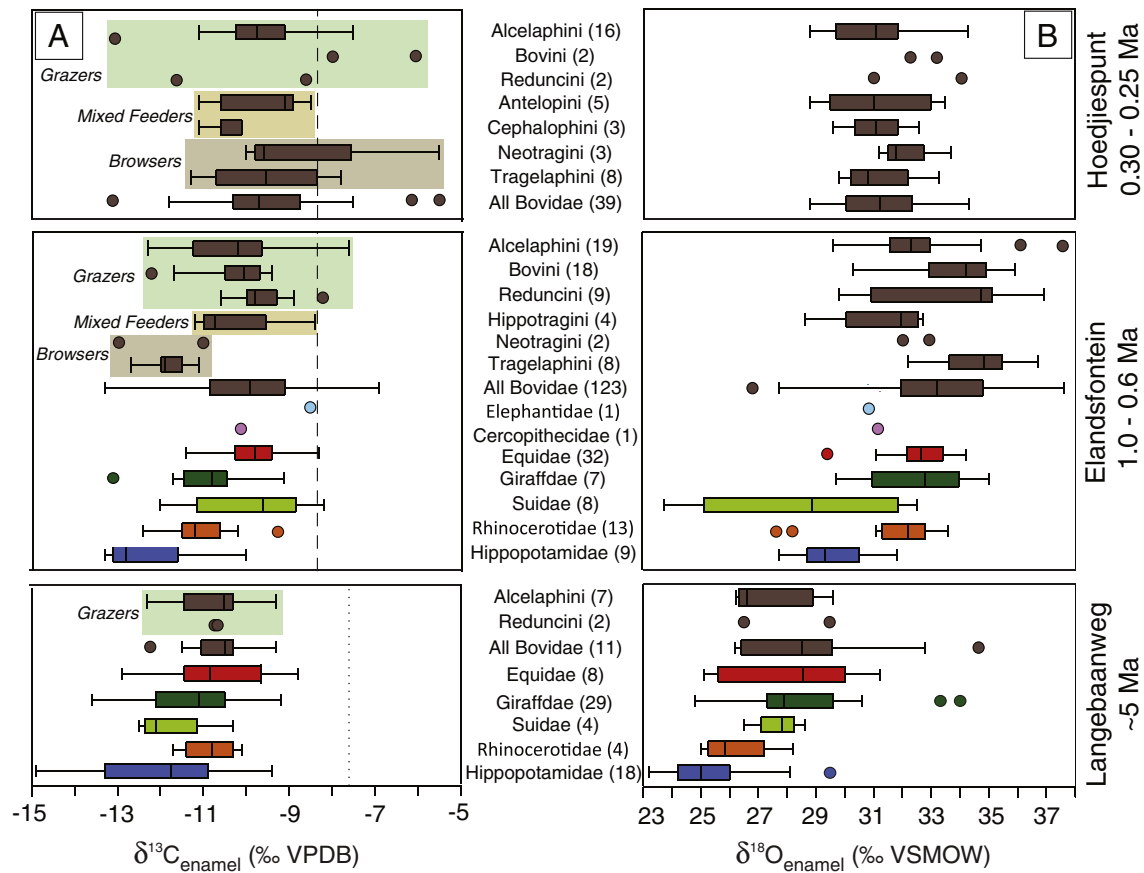


Fig. 4. Box plot of the compiled $\delta^{13}\text{C}$ values (A) and $\delta^{18}\text{O}$ values (B) of the carbonate component of tooth enamel data from this study and of published records of Pliocene and Pleistocene fossil teeth from southwestern South Africa (Luyt et al., 2000; Franz-Odenaal et al., 2002; Hare and Sealy, 2013; this study). Data are divided by family and bovid tribe. The number of individual analyses for each category is indicated in parentheses and when there are fewer than three isotopic values, analyses are presented as points. The dietary behaviors of bovids are divided into browsers, mixed feeders and grazers. See Table S2 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042> for the compilation of isotope data and source for dietary behaviors. A vertical line within the box marks median values. The ends of the boxes represent the quartile values, horizontal lines indicate the range, and the outliers are plotted as circles. The maximum $\delta^{13}\text{C}$ value of herbivores with a pure C_3 diet are represented by a vertical dotted black line (Langebaanweg) and a vertical dashed black line (Elandsfontein and Hoedjiespunt). These values are based on reconstructed $\delta^{13}\text{C}$ values of CO_2 (Tippie et al., 2010) in Table S1 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>.

Elandsfontein and any of the herbivores at Langebaanweg. There are no distinctions in $\delta^{13}\text{C}_{\text{enamel}}$ or $\delta^{18}\text{O}_{\text{enamel}}$ values among the bovids that were sampled and identified to tribe (Acelaphini and Reduncini) at Langebaanweg ($p = 1.0$).

The $\delta^{13}\text{C}_{\text{enamel}}$ values of grazers at Elandsfontein and Hoedjiespunt that are more positive than what is expected for a pure C_3 diet (-8.4‰ , refer to Section 3.3.1) could indicate the presence of some C_4 grasses, either in some seasons or on specific points on the landscape, like well-watered areas such as springs which is consistent with results from Patterson et al. (2016-in this issue). Hare and Sealy (2013) also suggest that the presence of some C_4 vegetation in the diets of grazing bovids from Hoedjiespunt might reflect the ability for C_4 plants to grow within a winter rainfall zone during low $p\text{CO}_2$ conditions that are characteristic of glacial intervals. Although low $p\text{CO}_2$ conditions might account for the presence of some C_4 vegetation in the diets of grazers at Elandsfontein, the resolution of the current age control on the deposits at Elandsfontein precludes us from assigning it to either a glacial or interglacial period (Braun et al., 2013).

The survival of large herbivores in southwestern South Africa would have required access to resources throughout the year. It is possible that there was an extended rainy season and that abundant food resources grew on nutrient-rich calcareous soils, which are no longer present at the fossil sites (Luyt et al., 2000). A year-round supply of palatable browse and graze would have required sufficient surface water and at Elandsfontein, this likely included springs (Braun et al., 2013).

5.2. Oxygen isotope record

The $\sim 4.5\text{‰}$ increase in $\delta^{18}\text{O}_{\text{enamel}}$ values between the Langebaanweg and Elandsfontein fossil localities (from ~ 5 to 1.0–0.6 Ma) occurs across a time of global cooling and aridification (Marlow et al., 2000; Etoirneau et al., 2009). $\delta^{18}\text{O}_{\text{enamel}}$ values can be influenced by a combination of factors including the $\delta^{18}\text{O}$ value of surface water, aridity and animal physiology (Kohn and Cerling, 2002). We do not think that physiological changes are responsible for the increase in $\delta^{18}\text{O}_{\text{enamel}}$ values as we observe it among multiple herbivore families and consider it unlikely that multiple disparately related herbivore families would converge upon identical physiological changes across this time span. Consequently, we must consider the influence of changes in the $\delta^{18}\text{O}$ value of surface water and changes in aridity on the observed increase in $\delta^{18}\text{O}_{\text{enamel}}$ values between the fossil teeth at Langebaanweg and Elandsfontein.

5.2.1. Oxygen isotopic composition of reconstructed surface water

In modern ecosystems $\delta^{18}\text{O}_{\text{enamel}}$ values of hippopotamids closely track the $\delta^{18}\text{O}$ values of meteoric water (Bocherens et al., 1996) and as such, fossil hippopotamid $\delta^{18}\text{O}_{\text{enamel}}$ values can be used to reconstruct the $\delta^{18}\text{O}$ values of meteoric waters (Levin et al., 2006). We used hippopotamid $\delta^{18}\text{O}_{\text{enamel}}$ values from Langebaanweg ($n = 18$) and Elandsfontein ($n = 9$) to estimate the $\delta^{18}\text{O}$ values of the surface waters in which these hippopotamids lived, which would reflect a combination

of the $\delta^{18}\text{O}$ value of regional precipitation and the hydrological condition of the local surface waters. We were not able to estimate the $\delta^{18}\text{O}$ values of the surface waters at Hoedjiespunt because there are no hippopotamid teeth preserved at the site (Stynder, 1997). We estimated $\delta^{18}\text{O}$ values of local surface waters from the hippopotamid $\delta^{18}\text{O}_{\text{enamel}}$ values by considering both the $5.4 \pm 1.3\%$ enrichment in $\delta^{18}\text{O}$ between local surface water and hippopotamid body water reported by Levin et al. (2006) for modern hippopotamids and the carbonate-water $^{18}\text{O}/^{16}\text{O}$ fractionation relationship reported by Kim and O'Neil (2005), assuming that tooth formation occurred at typical mammalian body temperatures of 37 °C.

Using this approach, we reconstruct the average $\delta^{18}\text{O}$ values of local surface water to $-3.9 \pm 1.6\%$ at Langebaanweg and $-0.3 \pm 1.5\%$ at Elandsfontein. For comparison, spring, tap and standing water nearby modern springs exhibit a mean $\delta^{18}\text{O}$ value of $-1.7 \pm 2.2\%$ ($n = 4$) (Table S4 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>). The similarity between the $\delta^{18}\text{O}$ values of the reconstructed mid-Pleistocene water and that of modern waters within the Elandsfontein vicinity indicate that hydrological conditions of waters near spring systems in the region may not have not changed greatly since the mid-Pleistocene. However, the $3.6 \pm 1.8\%$ increase in reconstructed surface water $\delta^{18}\text{O}$ values between Langebaanweg and Elandsfontein requires further explanation. The possible explanations for this $\sim 4\%$ increase include 1) a change in regional precipitation patterns as a result of changes in global climatic patterns that would affect precipitation $\delta^{18}\text{O}$ values and 2) a change in the type of surface waters (rivers vs. springs) that the hippopotamids were living in during the early Pliocene vs. the mid-Pleistocene. Here we review the potential roles of climate change and hydrological setting on the increase in $\delta^{18}\text{O}$ values of surface waters in southwestern South Africa between the early Pliocene and the mid-Pleistocene.

5.2.2. Global cooling

Decreased global temperatures and increased ice volume affected $\delta^{18}\text{O}$ values of precipitation globally between the Pliocene and Pleistocene with the onset of glacial and interglacial cycles (Zachos et al., 2001) but it is not clear how these oscillations affected $\delta^{18}\text{O}$ values of precipitation in southern Africa. A study of $\delta^{18}\text{O}$ values from speleothem carbonate from Buffalo Cave in South Africa (Hopley et al., 2007) that dates to the early Pleistocene (1.99 to 1.52 Ma) can provide perspective on the amplitude of change in the $\delta^{18}\text{O}$ values of meteoric water that we would expect between glacial and interglacial periods in southern Africa. Hopley et al. (2007) determine that there may be an $\sim 2\%$ increase in $\delta^{18}\text{O}$ values of regional precipitation between interglacials and glacials based on a combination of temperature and ice-volume effects. Despite some work that attributes the fossils at Elandsfontein to an interglacial interval based on the size of fossil carnivores (Klein et al., 2007), this assignment is less certain given more recent work at Elandsfontein (Braun et al., 2013). Regardless of whether the Elandsfontein fossils represent an interglacial or glacial interval, the maximum amount of change in $\delta^{18}\text{O}$ values of precipitation that we would expect between glacials and interglacials is $\sim 2\%$, which is not enough to explain an $\sim 4\%$ difference in $\delta^{18}\text{O}$ values of surface water between the early Pliocene and mid-Pleistocene.

5.2.3. Rainfall amount

The negative correlation between rainfall amount and the $\delta^{18}\text{O}$ value of rain is termed the “amount effect” (Dansgaard, 1964). This effect must be considered in the interpretation of the $\sim 4\%$ increase in $\delta^{18}\text{O}$ values of reconstructed surface waters. If southwestern South Africa became more arid between the early Pliocene and the mid-Pleistocene, as indicated by offshore archives (e.g., Marlow et al., 2000; Dupont et al., 2013), then we might expect to see indications of less rainfall in the reconstructed surface water $\delta^{18}\text{O}$ values. Modern precipitation data from Cape Town indicate that the “amount effect” is limited in southwestern South Africa (Midgley and Scott, 1994; Harris et al., 2010; West et al.,

2014); it is equivalent to $-10 \text{ mm}/1\%$ $\delta^{18}\text{O}$ for monthly winter rainfall (based on $\delta^{18}\text{O}$ values of monthly rainfall reported in Harris et al. (2010)) and thus very little of the variation in $\delta^{18}\text{O}$ values of precipitation in modern southwestern South Africa can be explained by amount of rainfall. In comparison, Panama (WGS-84 Lat/Long: 9.00970, -79.60324) has a strong “amount effect” with -35 mm rainfall for every 1% increase in the $\delta^{18}\text{O}$ value of rainfall (Higgins and MacFadden, 2004).

In addition, we do not expect to observe an “amount effect” in southwestern South Africa because this oxygen isotopic effect mostly occurs where temperatures are $>20^\circ\text{C}$ and where there is high humidity or significant rainfall (e.g., Rozanski et al., 1993), a pattern seen at collection sites globally (IAEA/WMO, 2001). The majority of rain in this region falls in the winter and it is associated with cold, westerly fronts; it is unlikely that average winter temperatures were $>20^\circ\text{C}$. If temperatures during the rainy season were $>20^\circ\text{C}$ during the Pliocene and Pleistocene, then it could have been warm enough for the growth of C_4 grass. The $\delta^{13}\text{C}$ values of fossil enamel from grazers, however, suggest that there was little C_4 grass in this region.

Although a change in the $\delta^{18}\text{O}$ values of rainfall related to moisture source may contribute to the increase in the $\delta^{18}\text{O}$ values of rainfall, it is unlikely that this would represent a substantial contribution to the full $\sim 4\%$ increase documented between the Pliocene and mid-Pleistocene. If there had been a change in the rainfall related moisture source from the east (i.e., contribution of summer rainfall), then we would expect to see the $\delta^{13}\text{C}_{\text{enamel}}$ values of some large mammalian herbivores to be more positive than what is calculated for a pure C_3 diet because they would be incorporating C_4 grasses that grow during the summer months into their diet. We find that the majority of $\delta^{13}\text{C}_{\text{enamel}}$ values are within the range expected for animals with pure C_3 diets and no change in $\delta^{13}\text{C}_{\text{enamel}}$ values between the fossil herbivores at Langebaanweg and Elandsfontein (Fig. 4). Furthermore, models of regional climate indicate that the source of atmospheric moisture, Atlantic water off the coast of southwestern South Africa, would have been constrained by relatively stable regional meteorological factors (e.g., ICTZ, Agulhas Current, Subtropical convergence zone and Benguela Current; McClymont et al., 2005) and thus would not have drastically changed between the early Pliocene and mid-Pleistocene.

5.2.4. Depositional mode and surface water

A change in the local hydrology and $\delta^{18}\text{O}$ value of surface water might be responsible for the increase $\delta^{18}\text{O}_{\text{enamel}}$ values between Langebaanweg and Elandsfontein. Today much of the coastal plain of southwestern South Africa is fed by ground water and many areas have standing water associated with artesian wells. The depositional environments of the Varswater Formation (i.e., the Langebaanweg fossil site) indicate the presence of fluvial and estuarine waters (Roberts et al., 2011). Various sedimentological studies indicate that the paleo-Berg River in the early Pliocene had a southerly trajectory and emptied into the embayment which is today the Saldanha Bay as opposed to emptying into the Atlantic Ocean in St. Helena Bay as the Berg River does today (e.g., Roberts et al., 2011; Fig. 1). Although a previous study of Elandsfontein suggested the presence of fluvial activity (Butzer, 1973), recent investigations document the complete lack of any sedimentary structures that would support a fluvial explanation for the sediments in which fossils at Elandsfontein have been found (Braun et al., 2013). Geomorphological reviews emphasize that large Cenozoic eolianites as well as granite outcrops act as barriers for any fluvial systems west of the Sout River and south of the Berg River (Mabbutt, 1952). As a result the main source of surface water in the region is provided by springs fed by the large underground Elandsfontyn and Langebaan Road aquifers (Brumfitt et al., 2013). Thus the $\delta^{18}\text{O}$ values of the enamel from large, mid-Pleistocene mammals at Elandsfontein likely reflect the $\delta^{18}\text{O}$ values of isolated springs distributed around the landscape. The waters from the Berg River headwaters have $\delta^{18}\text{O}$ values today that range from -6.0% to -4.0% (Weaver and Talma, 2005; West et al.,

2014), whereas $\delta^{18}\text{O}$ values of spring and tap waters surrounding the Elandsfontein vicinity today range from -3.6 to -1.9% (Table S4 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>; Midgley and Scott, 1994; West et al., 2014; this study). There is as much as a 4.1% difference in $\delta^{18}\text{O}$ values between surface waters sourced from the Berg River compared with waters from springs near Elandsfontein. Standing spring water at Elandsfontein has been evaporated and yields $\delta^{18}\text{O}$ value of 1.5%. Furthermore, the average $\delta^{18}\text{O}$ value of reconstructed surface water at Elandsfontein ($-0.3 \pm 1.5\%$) sits within the expected range of water near the Elandsfontein locality today. If offsets between $\delta^{18}\text{O}$ values of waters from the Berg River and from springs in the study area were consistent over the last 5 myr, then the $\sim 4\%$ increase in reconstructed surface water $\delta^{18}\text{O}$ values from tooth enamel between Langebaanweg and Elandsfontein fossil sites can be explained solely by a difference in local hydrology. At Langebaanweg, hippopotamids likely spent much of their time in waters that derived from the paleo-Berg River, whereas some 4 million years later, the hippopotamids from the Elandsfontein fossil deposits likely spent much of their time in water bodies that were fed by springs. The differences in the enamel $\delta^{18}\text{O}$ values of these two hippopotamid populations may be best explained by these local differences in the types of water bodies in which they wallowed.

5.2.5. Aridity

Aridity can have an effect on $\delta^{18}\text{O}_{\text{enamel}}$ values in multiple ways. Aridity can be the result of decreased rainfall amount which will affect $\delta^{18}\text{O}_{\text{enamel}}$ values due to a change in $\delta^{18}\text{O}$ values of precipitation that then contributes to the water that animals ingest. However, the degree of aridity may influence $\delta^{18}\text{O}_{\text{enamel}}$ values independent of any changes in the $\delta^{18}\text{O}$ values of precipitation via the ingestion of leaf water, which becomes greatly enriched in ^{18}O relative to ^{16}O in arid climates (Levin et al., 2006). The $\delta^{18}\text{O}_{\text{enamel}}$ values of animals that are not obligate drinkers (e.g., giraffes and oryx) may be sensitive to aridity in part because a large fraction of their body water may come from leaf water. The strong relationship between aridity and $\delta^{18}\text{O}_{\text{enamel}}$ values of these Evaporation Sensitive (ES) animals, taxa whose body water may be derived largely from leaf water, today can be used to evaluate aridity in the past by comparing $\delta^{18}\text{O}_{\text{enamel}}$ values of ES animals to those from Evaporation Insensitive (EI) animals, taxa whose body water is derived largely from ingested surface water (e.g., hippopotamids and elephants). The $\delta^{18}\text{O}_{\text{enamel}}$ values of EI taxa do not vary with aridity and can be used to control for changes in meteoric water $\delta^{18}\text{O}$ values (Levin et al., 2006). The $\varepsilon_{\text{ES-EI}}$ between $\delta^{18}\text{O}_{\text{enamel}}$ values of ES and EI taxa is greater in more arid environments than in less arid environments (Levin et al., 2006).

We evaluated whether increased aridity could explain the $\sim 4\%$ increase in enamel $\delta^{18}\text{O}$ values between the early Pliocene and mid-Pleistocene by comparing the $\varepsilon_{\text{ES-EI}}$ of $\delta^{18}\text{O}_{\text{enamel}}$ values of individual teeth from Langebaanweg ($n = 47$) and Elandsfontein ($n = 16$), where hippopotamids (i.e., *Hippopotamus*) are the representative EI taxa and giraffids (i.e., *Sivatherium*) are the representative ES taxa. Calculated $\varepsilon_{\text{ES-EI}}$ values are $+3.0 \pm 1.9\%$ and $+2.7 \pm 1.9\%$ for Langebaanweg and Elandsfontein, respectively. There is no large difference between the $\varepsilon_{\text{ES-EI}}$ values for the two populations, suggesting no change in aridity between the Pliocene and mid-Pleistocene environments in southwestern South Africa. However, we cannot simply evaluate aridity as outlined above if 1) there were changes in $\delta^{18}\text{O}$ values of surface water due to the differences in depositional setting between Langebaanweg and Elandsfontein and 2) if the behavior of EI and ES taxa was different during the Pleistocene and the Pliocene. First, $\delta^{18}\text{O}_{\text{enamel}}$ values from hippopotamids might not be closely tracking precipitation $\delta^{18}\text{O}$ values during the mid-Pleistocene in the same way as in the early Pliocene if hippopotamids from Elandsfontein wallowed in pools of evaporated spring water, whereas hippopotamids from the Langebaanweg collection spent time immersed in river waters. Our compilation of $\delta^{18}\text{O}$ values from modern waters in the region indicates

that spring-based water sources have more positive $\delta^{18}\text{O}$ values than that of river waters (Table S4 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>). Second, it is important to note that in this analysis we use the genus *Sivatherium* rather than *Giraffa* as the ES taxon. Although these two taxa are within the family Giraffidae, isotopic studies from eastern Africa indicate that *Sivatherium* underwent a major transition during the Pliocene and Pleistocene to incorporate more graze into their diet, while *Giraffa* did not (Cerling et al., 2015). Thus, it is feasible that sensitivity to aridity was different between these two taxa such that *Sivatherium* might not be an appropriate ES taxon to use in the $\delta^{18}\text{O}_{\text{enamel}}$ -based aridity index proposed by Levin et al. (2006).

While we cannot rule out the effects of evaporation on surface water $\delta^{18}\text{O}$ values, we do not think that aridity is the primary driver of the $\sim 4\%$ increase in reconstructed surface water $\delta^{18}\text{O}$ values between the early Pliocene and the mid-Pleistocene. It is unlikely that we would observe a uniform increase in the average $\delta^{18}\text{O}_{\text{enamel}}$ values of herbivore families from Langebaanweg and Elandsfontein because hippopotamids would have remained in the water, somewhat buffered from increased aridity, resulting in a smaller shift for hippopotamids than for other herbivore families. Furthermore, the $\sim 4\%$ increase in reconstructed surface water $\delta^{18}\text{O}$ values between fossil sites can be explained solely by a shift from riverine water to groundwater-fed springs as discussed in Section 5.2.4. Given the present data, we view this as the simplest way to explain the trends in the fossil $\delta^{18}\text{O}_{\text{enamel}}$ values we observe.

5.3. Theropithecus diet at Elandsfontein

The diet of fossil *Theropithecus* species from southern and eastern Africa have been evaluated to determine the partitioning of resources between primates and other mammalian species as well as to better define the influences that contributed to the success of *Homo* (e.g., Lee-Thorp et al., 1989; Codron et al., 2005; Cerling et al., 2013; Levin et al., 2015). A single *Theropithecus* mandible was excavated from Elandsfontein (WCRP collection) and this specimen has a $\delta^{13}\text{C}_{\text{enamel}}$ value of -10.2% , which is indicative of a diet composed of C_3 vegetation (Fig. 4; Table S2 in the online version at <http://dx.doi.org/10.1016/j.palaeo.2016.04.042>). This is the only $\delta^{13}\text{C}_{\text{enamel}}$ value of *Theropithecus* from Pleistocene southwestern South Africa. Contemporaneous *Theropithecus* $\delta^{13}\text{C}_{\text{enamel}}$ values from eastern Africa and in other locations in South Africa indicate that *Theropithecus* consumed C_4 graze (e.g., Codron et al., 2005; Cerling et al., 2013). The addition of carbon isotope data from *Theropithecus* at Elandsfontein shows that *Theropithecus* was able to survive on diets composed C_3 vegetation during the Pleistocene (whether it was browse or graze) if it lived in environments where C_3 vegetation was dominant, as with the modern gelada baboon (Levin et al., 2008).

5.4. Hominin paleoenvironment at mid-Pleistocene Elandsfontein

The sedimentary record at Elandsfontein provides unique insights into the ecology of southwestern South Africa during the mid-Pleistocene, which is not well documented elsewhere in southern Africa (Klein et al., 2007; Braun et al., 2013). The archives at Elandsfontein also provide evidence for some of the earliest hominin behavior in a winter rainfall zone in southern Africa. The association of the fossil fauna with Acheulean stone tools (i.e., hominin technology that indicate behavioral advances intersecting with the biological change) in an excavated context at Elandsfontein allows us to use inferences about paleoclimate from $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ values to develop an understanding of hominin ecology. This is especially important because of the age of this locality (~ 1.0 – 0.6 Ma) situates the site around the time of the mid-Pleistocene transition in climate dynamics (McClymont et al., 2005). Large mammalian remains at Elandsfontein indicate that there were both large browsing and grazing herbivore communities, suggesting that the landscape would have had

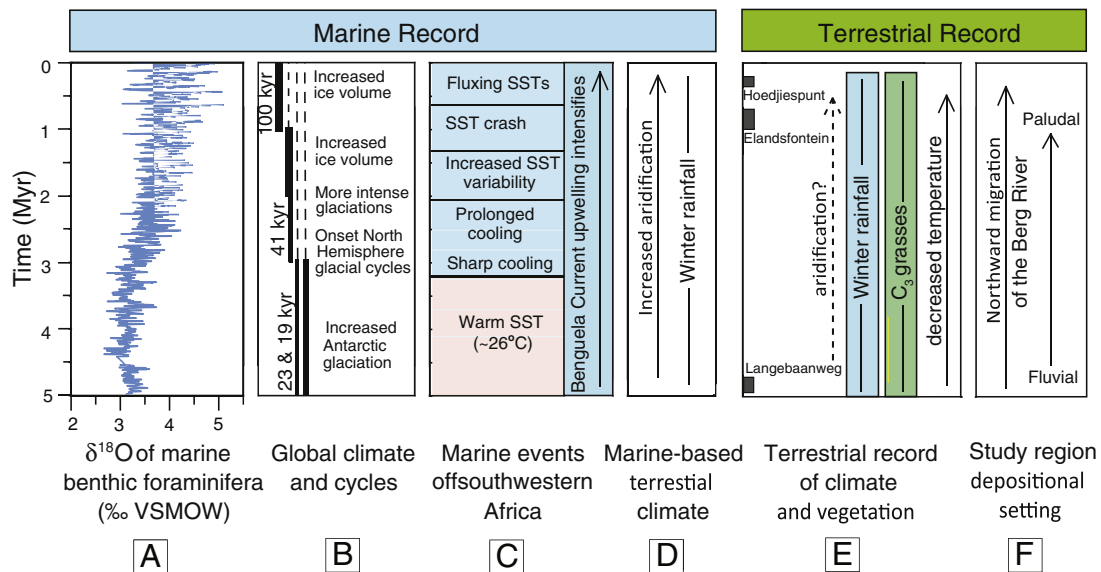


Fig. 5. A summary of Pliocene and Pleistocene records of global, regional, marine, and terrestrial changes relevant to southwestern Africa. A) The global benthic foraminifera $\delta^{18}\text{O}$ curve (Zachos et al., 2001) and B) a summary of major change in global climate (composite record based on data from Ruddiman et al., 1989; Shackleton et al., 1995). C) Summary of results from mid-latitude marine sediment cores off the southwestern Africa (Marlow et al., 2000; Dupont et al., 2005; Etourneau et al., 2009). D) Summary of data from terrestrial records including $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from fossil teeth and soil geochemistry from southwestern South Africa (Eze and Meadows, 2014; this study). E) Summary of depositional environments based on sedimentological data from Langebaanweg and Elandsfontein (Butzer, 1973; Roberts et al., 2011; Braun et al., 2013).

sufficient resources to assure the survival of these animals, in stark contrast to the modern ecosystems in this area. This ancient landscape clearly was a draw for hominins, as indicated by the thousands of stone tools recovered from this locality (Singer and Wymer, 1968; Klein, 1983; Braun et al., 2013) as well as fossil remains of early humans (Drennan, 1953). The springs at Elandsfontein (Braun et al., 2013) would have been a resource-rich environment for early humans, if Elandsfontein had been buffered from the regional aridification during the mid-Pleistocene. This is consistent with studies of Pleistocene archeological sites where springs and groundwater-fed areas have been considered to be important resource for hominins (e.g., Cuthbert and Ashley, 2014).

6. Conclusions

The results of this study add to a growing body of work, from both terrestrial- and marine-based archives, on how climate and vegetation in southwestern South Africa have changed over the last 5 Myr (Fig. 5). The main conclusions from this study are:

- 1) The $\delta^{13}\text{C}_{\text{enamel}}$ values of fossil teeth from southwestern South Africa indicate that both browsing and grazing herbivores had diets dominated by C_3 vegetation, which suggests the dominance of the winter rainfall season during the time intervals of fossil deposition at Langebaanweg, Elandsfontein and Hoedjiespunt. We cannot, however, totally discount the presence of C_4 grasses during the mid-Pleistocene and late Pleistocene.
- 2) There is an increase in reconstructed surface water $\delta^{18}\text{O}$ values from southwestern South Africa between the early Pliocene and mid-Pleistocene of $\sim 4\%$. We attribute the increase in $\delta^{18}\text{O}$ values of surface waters primarily to a shift in hydrology and depositional environments along the coastal plain of southwestern South Africa. The major source of water for animals during the Pliocene appears to have been a fluvial system whereas springs were likely the dominant surface waters in the mid-Pleistocene.
- 3) While increased aridity in southwestern Africa is indicated both by the marine- and terrestrial-based proxy records compiled in this study, it is not clearly evident in the isotopic record of large mammals presented here. The Elandsfontein archeological site may

have been buffered from regional mid-Pleistocene aridification as a result of the available surface water indicated by ancient spring deposits. If springs were annually active, then water and other resources associated with springs would have been available to mammals, such that the area may have served as an oasis of sorts within a relatively drier landscape.

- 4) This study highlights the importance of considering depositional environment and the local environmental setting when understanding how specific terrestrial environments responded to regional climate and environmental change.

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