

***Late Quaternary environmental change in the Southern Cape, South Africa from stable carbon and oxygen isotopes in faunal tooth enamel from Boomplaas Cave***

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**Abstract**

Measurements of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in tooth enamel of 136 faunal specimens from the archaeological site of Boomplaas Cave, South Africa show significant shifts in the proportions of  $\text{C}_3$  and  $\text{C}_4$  vegetation from the earliest deposits, which probably date to MIS 5, to the late Holocene. Vegetation communities during the Last Glacial Maximum were strongly  $\text{C}_3$ -dominated, consistent with hypotheses of an expanded winter rainfall zone at this time. Winter rainfall and cooler temperatures, both of which favour  $\text{C}_3$  grasses, were clearly more important than lower  $p\text{CO}_2$  (which favours  $\text{C}_4$  grasses) in determining the nature of the vegetation. The intervals 40-35 and 18-14 ka supported substantial quantities of  $\text{C}_4$  grasses. These two intervals correspond with warmer climates as reflected in Antarctic ice cores, and are consistent with global climate models suggesting southward migration of the ITCZ and associated summer precipitation systems during periods of Antarctic ice retreat.  $\delta^{13}\text{C}$  of an as yet unnamed caprine, in combination with dental mesowear studies, indicate that these animals were primarily  $\text{C}_3$  grazers. The Pleistocene palaeoclimates and palaeoenvironments of southernmost Africa are important for understanding southern hemisphere climate dynamics and for reconstructing human evolution and early human settlement in this region.

**Keywords:** palaeoenvironment, palaeoclimate, glacial/interglacial,  $\text{C}_3$  vegetation,  $\text{C}_4$  grass

## Introduction

The Pleistocene palaeoclimates and palaeoenvironments of southernmost Africa are important in studies of southern hemisphere (and hence global) climates and in studies of human evolution. This region is located at the intersection of two major oceanic currents (the Benguela and Agulhas) (Lutjeharms et al., 2001; Rau et al., 2002) and is influenced by two major cyclonic systems that bring predominantly winter rain to the west and summer rain to the east (Schulze, 1972). Southern African climates are shaped by the interaction of these oceanic and atmospheric systems. The behaviour of these systems has shifted through time, particularly over glacial/interglacial cycles, contributing to changes in temperature, rainfall regime and other key climatic variables (Cockroft et al., 1987; Heine, 1982; Van Zinderen Bakker, 1976). In this part of the world, there is no consensus on the behavior of these systems through the Quaternary (Marean et al., 2014), and a better understanding of them will help refine models of southern hemisphere climate dynamics. In addition, climate and environment are important in understanding the biological and cultural evolution of humans. Archaeological sites in this region have yielded some of the best evidence in the world for the behaviour of early modern humans, including indicators of complex behaviours at unexpectedly early dates (Wadley 2013). This study is part of an ongoing effort to understand the environmental and climatic context for the emergence and development of these societies.

Boomplaas Cave (BPA) is an important archaeological site with a long sequence spanning most of the Late Pleistocene and Holocene. It is located at 33°23'22.60"S 22°10'58.66"E, on the southern slopes of the Swartberg mountains and on the edge of the Congo Valley (Fig. 1). The Swartberg form the northern boundary of an inter-montane basin known as the Klein Karoo, while the Outeniqua Mountains form the southern edge ~50 km south of the site. As a result, the cave lies in the rain shadow of the Outeniquas as moisture-bearing clouds move inland from the Indian Ocean, approximately 90 km to the south. The cave is formed in a dolomite seam that is exposed largely east-west. The well-known Congo Caves karstic system forms part of the same exposure. Rainfall at the nearby town of Oudtshoorn averages about 250 mm/year, falling at very low levels throughout the year. The Swartberg stands as the northern boundary of the Klein Karoo with the Great Karoo, the latter marking the transition to a summer rain dominant ecosystem and Paleo-Tropic vegetation.

The Klein Karoo is a floral biodiversity hot-spot that is highly endemic. The region is mostly assigned to the Succulent Karoo biome, comprising a complex patchwork of closely packed vegetation types (Bergh et al., 2014; Bradshaw & Cowling, 2014). The specific vegetation types are driven by subtle differences in soil and geology, moisture, protection from fire, and aspect (Vlok and Schutte-Vlok, 2010). The Succulent Karoo is part of the Greater Cape Floristic Region, and shares many taxa and vegetation types with the surrounding regions. In this area, fynbos, renosterveld, and sub-tropical thicket vegetation types are within a 10 km radius of the site. The small amounts of grass in this area today include both C<sub>3</sub> and C<sub>4</sub> types, with local variation depending on features such as slope aspect.

The site was selected for excavation by H.J. Deacon in part because the geology was likely to be conducive to good preservation of faunal remains (Deacon & Brooker,

1976; Deacon, 1979). One of the principal aims of Deacon's research programme was to investigate possible correlations between environmental change, as reflected in faunal remains and other palaeoenvironmental proxies, and human behavioural/cultural change – a goal that remains a priority today. Excavations were carried out from 1974 to 1979, uncovering a well-stratified sequence about five metres deep, spanning approximately the last 80 ka, although the lower portions of the site are not well dated relative to other major sites in South Africa (Table 1). Some depositional units derive from human occupation, while others are natural accumulations during periods of non-occupation by humans.

The large mammal fauna have been studied by Klein (1978, 1983) and more recently by Faith (2013a). Both report substantial variation in faunal composition through time. The base of the sequence (LOH-OLP) is dominated by small browsers and mixed feeders, including grey rhebok (*Pelea capreolus*), klipspringer (*Oreotragus oreotragus*), and grysbok/steenbok (*Raphicerus* spp.), with mountain reedbuck (*Redunca fulvorufula*) being the dominant grazer. This broadly parallels the Holocene deposits at BPA and indicates shrubland vegetation similar to the present, although rare examples of springbok (*Antidorcas* cf. *marsupialis*), blesbok/bontebok (*Damaliscus* cf. *pygargus*), and extinct long-horn buffalo (*Syncerus antiquus*) indicate a slightly more open and grassy vegetation component. From member BP until the end of the Pleistocene in CL (ca. 40 – 12 k cal a BP), a diverse community of grazers, including alcelaphine antelopes, zebras, and an extinct (and as yet unnamed) caprine first documented by Brink (1999) is dominant and indicates widespread grassland habitats. Ungulate community richness, which tracks annual precipitation in southern and eastern Africa today (Thackeray, 1980; Faith, 2013b), peaks during the LGM and suggests higher effective moisture and more productive terrestrial environments than at any other time in the sequence; the isotopic composition of the nearby Congo Caves speleothem (Talma and Vogel, 1992) suggest C<sub>3</sub> vegetation at this time. The onset of the Holocene occurs in member BRL and is associated with the replacement of the diverse grazer community by increasing frequencies of small browsers and mixed feeders, suggesting a return to shrubland-dominated habitats. Diversity declines and suggests a drying trend. The replacement of grazers by browsers and decline in diversity also occurs at other sites in the region such as Byneskranskop 1 and Nelson Bay Cave (Klein, 1972, 1983; Schweitzer and Wilson, 1982), indicating widespread vegetation change resulting in the loss of productive grassland habitats.

In this study we have measured the stable carbon and oxygen isotope ratios in tooth enamel of fauna from Boomplaas. We have analyzed mainly grazers, interpreting their  $\delta^{13}\text{C}$  values as an index of the proportion of C<sub>4</sub> grass in the region at the time. The proportions of C<sub>3</sub> and C<sub>4</sub> grasses depend upon the seasonality of rainfall, with summer rainfall favouring an increase in the C<sub>4</sub> component. Today, Boomplaas is in the year-round rainfall zone (Fig.1). If the proportion of summer rainfall were to increase, we would expect a corresponding increase in C<sub>4</sub> grasses. If, on the other hand, if summer rain were to be reduced and winter rainfall were to increase, we would expect more C<sub>3</sub> grasses. Shrubs and trees are overwhelmingly C<sub>3</sub>, regardless of rainfall regime.

Of the grazers available for analysis, *Redunca* (reedbuck - both *R. fulvorufula* [mountain reedbuck] and *R. arundinum* [southern reedbuck] have been identified at Boomplaas) are the most specific feeders. *R. arundinum* is rare and we sampled only

two specimens, both from unit BRL. *R. fulvorufula* is more abundant, spread more widely through the sequence, and we sampled 12 individuals. In Eastern and Southern Africa, these reduncines are almost exclusively grazers, with a strong preference for fresh new grass (Cerling et al., 2003; Skinner & Chimimba, 2005; Sponheimer et al., 2003). The overwhelming body of evidence from our region leads us to expect that, in this study, *Redunca* are likely to be obligate grazers, and shifts in  $\delta^{13}\text{C}$  of their tooth enamel will be an excellent indicator of changing proportions of  $\text{C}_3$  and  $\text{C}_4$  grass. Since *R. fulvorufula* is abundant and prefers grassy slopes, its values may also reflect changing grass ecologies in those locations.

The other grazers included in this study exhibit somewhat more flexible feeding behaviours. *Alcelaphus buselaphus* (red hartebeest), *Connochaetes gnou* (black wildebeest) and *C. taurinus* (blue wildebeest) and *Damaliscus pygargus* (blesbok/bontebok) are all predominantly grazers, preferring short grass, but will occasionally consume some browse especially in the dry season when grass is less palatable. Observational studies report that *Alcelaphus buselaphus* can consume significant proportions of dicots (Gagnon and Chew, 2000; Skinner and Chimimba, 2005) but these probably reflect short-term behaviour, because isotopic studies in both Eastern and Southern Africa indicate that the average diet of this species includes very little browse (Cerling et al., 2003; Sponheimer et al., 2003). *Syncerus caffer* (buffalo) and *Equus* (zebra) are also grazers. They will eat dry grass if necessary and are adapted to the consumption of large amounts of roughage (Skinner & Chimimba, 2005). Isotopic studies of modern fauna from Eastern and Southern Africa confirm that all of these species are overwhelmingly grazers. Populations in Southern Africa appear to consume slightly more  $\text{C}_3$  plants (browse) than those in East Africa, probably due to differences in the environment and thus in the most palatable species available. Even so, studies conducted to date indicate that these species do not consume more than 10% dicotyledonous plants (Cerling et al., 2003; Codron et al., 2007a,b; Sponheimer et al., 2003).

## Materials and Methods

Specimens included in this study were chosen from amongst bovid and equid teeth identified at least to genus level (or pairs of similar genera, e.g. *Connochaetes/Alcelaphus*). Some teeth were too brittle and fragile to be sampled; these were excluded. We analysed two browsers (*Oreotragus oreotragus*, the klipspringer, and *Pelea capreolus*, the grey rhebuck), chosen because they are the browsers which occur most consistently through the depositional sequence.  $\delta^{13}\text{C}$  results for these species provide a  $\text{C}_3$  baseline against which to evaluate the results for grazers. We also sampled all suitable specimens of the grazers *Equus*, *Alcelaphus*, *Connochaetes*, *Damaliscus*, *Syncerus* and *Redunca*. If the  $\delta^{13}\text{C}$  values of grazers overlap with the browser range, we infer that only  $\text{C}_3$  grasses were present; more positive grazer  $\delta^{13}\text{C}$  values indicate the presence of  $\text{C}_4$  grasses. In addition, we sampled a number of individuals of the extinct caprine identified by James Brink (1999). This animal is thought to have been a specialised grazer, since it has hypsodont teeth and a shortened premolar row (Brink, 1999). Other derived traits consistent with an adaptation to grazing include a posterior projection at the base of the maxillary M3, a feature typical of fossil and extant wildebeests (*Megalotragus* and *Connochaetes*) that prolongs the functional life of the tooth, coupled with the loss of

the mandibular dp2 and reduction of the dp3. Species known to have variable feeding behaviours ('mixed feeders') were not sampled.

Enamel surfaces were cleaned of any superficial debris and if necessary, surface discolouration removed by light burring using a diamond-tipped micro-drill. Enamel powder was removed along a line down the entire tooth crown from the occlusal surface to the cementum-enamel junction. This ensures that the sample includes enamel deposited over the entire period of formation of the tooth. Approximately 10 mg of powdered enamel was collected and transferred into a 1.5 ml plastic microcentrifuge tube with a snap cap. Where teeth were too brittle for this method to be viable, fragments were collected and powdered with a mortar and pestle before further processing.

Enamel powders were treated with 1 ml of 1.75% sodium hypochlorite solution for 45 minutes to remove organics, then rinsed three times with distilled water. Next, they were treated with 1 ml 0.1M acetic acid for 15 minutes to remove diagenetic carbonates, then again rinsed three times before being freeze-dried. For each sample, approximately two milligrams of prepared enamel was weighed into a 12 ml round-bottomed borosilicate glass vial and capped with an exetainer cap. The vials were placed in a Finnigan GasBench II, maintained at a temperature of 72°C, and flushed with helium before 7-8 drops of 100% phosphoric acid were injected into each vial. The resultant CO<sub>2</sub> was swept in a stream of helium into a Thermo Finnigan Delta Plus XP stable isotope mass spectrometer for measurement of <sup>13</sup>C/<sup>12</sup>C and <sup>18</sup>O/<sup>16</sup>O. All samples were reacted and analysed along with NBS 18, NBS 19, Carrara marble and in-house standard Cavendish marble. Results are expressed relative to VPDB. Repeated measurements (n=14) of in-house standard Cavendish marble yielded standard deviations of 0.1‰ for both δ<sup>13</sup>C and δ<sup>18</sup>O.

## Results

### Carbon isotopes

The results are listed in Table 2 and shown in Fig. 2. The browsers *Pelea* and *Oreotragus* all have δ<sup>13</sup>C between -10 and -14.5‰, with the exception of a single *Oreotragus* at -9.7‰ and a single *Pelea* at -8.6‰ (mean = -11.8 ± 1.3‰, n=36). From this sample, there is no discernible patterning in δ<sup>13</sup>C of these species through the stratigraphic sequence. These results provide a secure C<sub>3</sub> baseline against which to assess the results for grazing species.

*Redunca* yield the most consistently enriched δ<sup>13</sup>C values of all the species analysed. δ<sup>13</sup>C of 12 specimens of *Redunca fulvorufula* ranges from -1.1 to -5.6‰, with a single outlier at -9.6‰ (mean = -3.3 ± 1.8‰, n=11, excluding outlier). One *R. arundinum* has δ<sup>13</sup>C of -2.9‰, within the range of values for *R. fulvorufula* (Table 1); the other is slightly more positive at -0.4‰. The relatively positive δ<sup>13</sup>C values reflect the dietary specificity of *Redunca*: they are almost exclusively grazers, with a strong preference for fresh new grass (Skinner & Chimimba, 2005). *R. fulvorufula* prefers slope grasslands, while *R. arundinum* favours habitats close to water and around edaphic grasslands. In the southern Cape, C<sub>4</sub> grasses tend to grow on warmer, north-facing slopes (Cowling 1983, 1984) and *R. fulvorufula* may have grazed mostly on these.

Elsewhere in southern Africa, such as at Takatshwane in the Central Kalahari, *R. fulvorufula* also show a hyper-C<sub>4</sub> signal (Lee-Thorp and Sponheimer, 2005). It is not possible to assess changes through time on the basis of *Redunca* alone; this requires inclusion of results for other species.

$\delta^{13}\text{C}$  values for other grazing species are more scattered, as may be expected from their more flexible feeding behaviours. Fig. 2 shows results for *Damaliscus/Alcelaphus/Connochaetes* compared with those for the bulk grazers *Equus* and *Syncerus*. Not all species were recovered from all layers, which complicates comparisons.

The faunal sample from the oldest MSA levels of the site is small, so we were able to sample only a few animals, mostly browsers. These levels may also extend over a long time span encompassing significant climate and environmental change. Member LOH yielded one *Redunca fulvorufula* and one *Damaliscus* suitable for our purposes, both of which showed relatively enriched  $\delta^{13}\text{C}$  (-2.5 and -3.4‰ respectively) indicating a strongly C<sub>4</sub> diet. The overlying member OCH yielded five *Redunca fulvorufula*, including the outlier with the most negative  $\delta^{13}\text{C}$  for this species (-9.6‰), two *Damaliscus* (-7.5 and -9.6‰) and an *Equus* (-11.0‰). These values are substantially more negative than those from LOH, signalling that C<sub>3</sub> grass became relatively abundant during the formation of OCH. Despite the small number of specimens, taken together these results clearly indicate the presence of significant quantities of C<sub>4</sub> grass in LOH and C<sub>3</sub> grass in OCH times. OCH has an AAR age estimate of  $62.4 \pm 2$  ka (Miller et al., 1999) and the stone artefacts belong to the Howiesons Poort technocomplex, dated elsewhere in the southern Cape to ~65-60 ka (Brown et al., 2012; Jacobs et al., 2008). The underlying LOH is undated and may be late MIS5 (Deacon 1995).

We were able to analyse a single *Redunca fulvorufula* from the late Pleistocene member BP, but they are absent from YOL, LPC and LP. There is a single specimen from GWA/HCA (the time of the Last Glacial Maximum or LGM), but it was not suitable for isotope analysis. *Alcelaphus/Damaliscus/Connochaetes* are the most common grazing bovids in these levels. Specimens from member BP (ca. 35-40 k cal a BP) show significantly more positive  $\delta^{13}\text{C}$  values (mean  $-4.4 \pm 2.4$ ‰, n=7) than the single alcelaphine from YOL at -8.7‰, and *Alcelaphus/Damaliscus/Connochaetes* from LPC (mean  $-8.2 \pm 0.9$ ‰, n=8), LP (mean  $-7.4 \pm 1.7$ ‰, n=5) and GWA/HCA (mean  $-7.8 \pm 2.4$ ‰, n=11). Comparison of the values from BP with the four succeeding members (pooled) shows that the difference is statistically significant (Mann-Whitney Z-value = 2.76; p<0.0058). The small numbers of *Equus* (1-3 from each member) are insufficient to show any significant patterns. It is clear that grazers from BP ate substantially more C<sub>4</sub> grass than did animals in underlying or overlying layers. The consistent pattern in LPC, LP and GWA/HCA clearly shows that C<sub>3</sub> vegetation dominated the region during the LGM.

*Equus* and *Syncerus* are most abundant in the terminal Pleistocene member CL (ca. 18-14 k cal a BP), where many individuals analysed record high proportions of C<sub>4</sub> grasses, although there is a good deal of variation (mean  $\delta^{13}\text{C} = -4.6 \pm 3.7$ ‰, n=12). There were only a few *Alcelaphus/Damaliscus/Connochaetes* from this member, none suitable for isotope analysis.

In the early Holocene member BRL, three *Damaliscus* yielded  $\delta^{13}\text{C}$  values of -8.7 to -11.7‰, indicating strongly  $\text{C}_3$  diets.  $\text{C}_4$  grasses were, however, locally available, as shown by  $\delta^{13}\text{C}$  values of -1.5 to -2.8‰ for three *Redunca fulvorufula*. Later Holocene levels were dominated by browsing, rather than grazing fauna (Klein, 1978; Faith, 2013a). We were unable to obtain sufficient grazers to trace the proportions of  $\text{C}_3$  and  $\text{C}_4$  vegetation into this time period.

We also analysed a number of teeth of the extinct caprine, deriving from members LP to BRL. This species was particularly common in CL, a time when *Equus* and *Syncerus* show substantial intake of  $\text{C}_4$  grass. The majority of the thirteen caprines from CL, however, fall in the  $\text{C}_3$  feeder range (mean =  $-10.4 \pm 0.6\text{‰}$ ,  $n=10$ ), with just three individuals consuming significant quantities of  $\text{C}_4$  grass ( $\delta^{13}\text{C} = -3.7, -4.8$  and  $-5.8\text{‰}$ ). In the overlying BRL member, caprines have slightly more positive  $\delta^{13}\text{C}$  values (mean =  $-8.8 \pm 1.5\text{‰}$ ,  $n=6$ ).

### Oxygen isotopes

The  $\delta^{18}\text{O}$  values are scattered, and more difficult to interpret (Fig. 3). The ranges for the various species are similar, although browsers are significantly more enriched in  $^{18}\text{O}$  than grazers: mean  $\delta^{18}\text{O} = 3.1 \pm 1.4\text{‰}$  for browsers ( $n=36$ ) compared with  $1.5 \pm 1.6\text{‰}$  for grazers ( $n=76$ ) ( $t = 3.82$   $p = 0.05$  d.f. = 110). Only grazers have negative  $\delta^{18}\text{O}$  values.  $^{18}\text{O}$  enrichment in browsers compared with grazers has been documented in the literature (Sponheimer & Lee-Thorp, 1999; Levin et al., 2006; but see also Kohn et al., 1996) and is attributed to browsers obtaining much of their water from their food; plant leaves are enriched in  $^{18}\text{O}$  because of preferential loss of the lighter  $\text{H}_2^{16}\text{O}$  during evapotranspiration. The browsers in this study, *Pelea* and *Oreotragus*, are both independent of water, though they will drink if water is readily available (Skinner and Chimimba, 2005). Grazers tend to be more dependent on drinking regularly, so their  $\delta^{18}\text{O}$  more closely reflects that of meteoric water.

Amongst grazers, the  $\delta^{18}\text{O}$  values of *Equus* tend to fall at the negative end of the range of variation within each member. This is true also of fossil equids from Equus Cave in the Northern Cape of South Africa (Sponheimer and Lee-Thorp, 1999), where it was explained as the result of zebras feeding on large quantities of grass stems as well as leaves; stem water is depleted in  $^{18}\text{O}$  compared with leaf water (Yakir, 1992) because stems do not undergo evapotranspiration. In East Africa, Bocherens et al. (1996) found that zebra and buffalo (both bulk grazers) had lower  $\delta^{18}\text{O}$  than wildebeest. In other studies, however, zebras lie within the herbivore  $\delta^{18}\text{O}$  range (Kohn et al., 1996; Cerling et al., 2010).

It is difficult to detect patterning in  $\delta^{18}\text{O}$  through time. Given the difference between browsers and grazers identified above, possible temporal shifts should be evaluated within each group. *Alcelaphus/Damaliscus/Connochaetes* show a wide range of  $\delta^{18}\text{O}$ , perhaps partly due to the difficulty of distinguishing individual species. *Syncerus* in CL is highly variable in both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ . The numbers of other species are too small to draw any reliable conclusions. Mean values for grazers from the LGM (LPC to GWA/HCA) are not significantly different from other levels, but *Equus* and alcelaphines from these members show higher variance than at any other time in the sequence ( $F = 1.980$   $p = 0.088$ ; non-parametric Monte Carlo permutation test:  $p = 0.0584$ ) and compared with overlying levels ( $F = 3.332$ ,  $p = 0.064$ ; non-parametric

Monte Carlo permutation test:  $p = 0.0261$ ). These animals are obligate drinkers. It is possible that this variability relates to these species ranging more broadly across the landscape, perhaps even migrating, and thereby sampling different water sources, especially given that the  $\delta^{18}\text{O}$  of water from winter rainfall is likely to be different from summer rainfall (Bar-Matthews et al., 2010; Harris et al., 2010). In respect of their oxygen isotopes, the caprines do not cluster clearly with either browsers or grazers.

## Discussion

Below, we compare patterns in the isotope ratios of Boomplaas fauna with other records of palaeoclimate and palaeoenvironment, especially the Cango stalagmite (Talma & Vogel, 1992) and Antarctic ice cores. Such comparisons require reliable chronologies. There is scope for further work to obtain higher resolution chronologies for both the Boomplaas deposits and the Cango stalagmite, and some of this is already under way. Our reconstructions below are based on the dates available at present.

The  $\delta^{13}\text{C}$  values reported above shows that  $\text{C}_3$  vegetation dominated in LPC, LP and GWA/HCA, just prior to, and around the time of the Last Glacial Maximum, while the proportion of  $\text{C}_4$  vegetation increased in members BP and CL. The shift in member BP (c 35 – 40 k cal a BP) matches a positive excursion in the  $\delta^{13}\text{C}$  of the Cango stalagmite (Talma & Vogel, 1992) at the same time (note that the horizontal axis in Talma & Vogel's Fig. 6 shows uncalibrated radiocarbon years BP. Calibration shifts the peak appearing in that figure at ca 32 ka to match the age of BP).  $\delta^{18}\text{O}$  in the stalagmite increases slightly at the same time. Talma and Vogel (1992) interpreted this pattern as signalling an increase in summer rainfall. This is the strongest  $\text{C}_4$  signal recorded in Pleistocene growth increments of the stalagmite; it is not until the second half of the Holocene that comparable values occur again. Avery's (2004) analysis of size differences in molarats also indicated that BP was a wetter phase, with a greater proportion of summer rainfall. Faith (2013a) noted that member BP is the oldest of a series of members (extending up to CL) to show a larger proportion of grazers and that the degree of faunal change in BP compared with underlying (OLP) and overlying (YOL) levels is higher than at any other point in the sequence. BP stands out in that alcelaphines are especially common, including *Alcelaphus*, *Damaliscus* and both *Connochaetes gnou* and *C. taurinus* – the only *C. taurinus* in the site. Today, *C. taurinus* occur only on nutrient-rich  $\text{C}_4$  grasslands, and Faith (2013a) suggested that their presence in member BP may be linked to increased summer rainfall resulting in a greater proportion of  $\text{C}_4$  grasses. Our results are consistent with this scenario. Micromammalian assemblages from BP also differ from those in the underlying and overlying layers. Thackeray's (1987, 1990) factor analysis of micromammal species composition in relation to temperature and precipitation shows a warm peak in BP (especially in BP2). The presence of wood charcoal in BP indicates the presence of shrubby vegetation as well as grasses. One common (but unidentified) type of charcoal has features similar to that of plants in the family *Ericaceae* (Deacon et al., 1984). This plant no longer grows in the area.

The shift in the composition of the faunal assemblage and the presence of significant quantities of  $\text{C}_4$  grasses in member BP as observed in the grazer fauna and to a lesser extent in the stalagmite, are probably local manifestations of a much larger-scale palaeoclimatic event.  $\delta^{18}\text{O}$  records from Antarctic ice cores show a major warm event



(Antarctic Isotope Maximum 8) ca 40-36 k cal a BP (EPICA Community Members, 2006; Veres et al., 2013). AIM 8 was one of the most significant warm intervals of OIS 4-3 in terms of both degree of warming and duration. At the same time, there was a marked reduction in the intensity of SE trade winds (Stuut et al., 2002, 2004). During these warmer intervals, it has been hypothesized that the intertropical convergence zone moved southwards (Cvijanovic et al., 2013), bringing summer rain to more southerly latitudes. Moreover, concurrent warming of the Agulhas Current and increased influence of continental and sea surface temperature fluxes would increase the amounts of available moisture in these southerly regions and the importance of zonal precipitation drivers (Cook et al., 2004; Tierney et al., 2011). At approximately the same time, the northern hemisphere cold episode Heinrich Event 4 may have contributed to the southwards shift of the ITCZ, helping to bring more rainfall to southerly latitudes (Ziegler et al., 2013). In this scenario, summer rains extended further west across the Swartberg, increasing summer rainfall and thus the proportion of C<sub>4</sub> grass in the vicinity of Boomplaas.

The opposite scenario would have applied during the LGM, when Antarctic sea ice reached its maximum extent within the last glacial. Several authors have argued that greater ice volume would have led to increased pole-to-equator temperature and pressure gradients, shifting the oceanic and atmospheric fronts northwards (Stuut et al., 2004; Chase and Meadows, 2007). An equatorward shift of moist air masses, accompanied by an increase in storminess may have led to stronger winter rainfall, favouring C<sub>3</sub> vegetation at the expense of C<sub>4</sub>. We can see this in the strongly C<sub>3</sub> signal of LGM grazing fauna from Boomplaas and in the  $\delta^{13}\text{C}$  record from the Cango speleothem. The dominance of C<sub>3</sub> grasses around the LGM – in combination with lack of bushy cover – may explain the absence of *Redunca* from these layers.

We note, however, that  $\delta^{13}\text{C}$  values of grazing fauna indicate the presence of a greater component of C<sub>4</sub> grass in the vegetation of the LGM than was inferred from the Cango speleothem. Talma and Vogel wrote that the  $\delta^{13}\text{C}$  minimum in the speleothem near the LGM corresponded to “nearly complete C-3 cover” (1992:211).  $\delta^{13}\text{C}$  values of grazing fauna, however, remain distinct from (more enriched than) those of browsers, clearly indicating the availability of C<sub>4</sub> grasses at the LGM. The pattern of a stronger C<sub>4</sub> signal in grazer tooth enamel than in the stalagmite holds throughout the sequence. The range of  $\delta^{13}\text{C}$  values in the stalagmite is of the order of 3‰, while in grazer tooth enamel it is approximately 9‰. Carbon in stalagmites derives partly from humic matter in the soil, which is expected to track the proportions of C<sub>3</sub> and C<sub>4</sub> plants, but also partly from processes of respiration that occur within the soil. We also observe a stronger C<sub>4</sub> signal in grazer tooth enamel compared with pedogenic carbonates in soils (Lister, 2013), which has been attributed to animals’ selectivity in searching out preferred food plants. Details of the various carbon contributions to stalagmites and soil carbonates remain to be resolved, and are likely locally variable. This comparison between tooth enamel and the stalagmite record demonstrates the value of multiple proxies in palaeoecological and palaeoclimatic studies.

Low levels of atmospheric CO<sub>2</sub>, as existed during the last glacial, favour C<sub>4</sub> grasses over C<sub>3</sub> (Ehleringer et al., 1997). The C<sub>3</sub> signal during the LGM suggests that the dominance of winter rain and lower temperatures in the growing season swamped the effects of very low CO<sub>2</sub> in promoting C<sub>4</sub> vegetation at this latitude.

After the LGM, as post-glacial warming became established, the types of micromammals changed to more temperate-adapted species, and the presence of *Olea* charcoal in the deposit shows that trees were returning to the valley after being absent during the LGM (Deacon, 1995). C<sub>4</sub> grasses once again became a more important component of the vegetation. This is reflected in the relatively enriched  $\delta^{13}\text{C}$  values of some equids (up to -1.9‰) and *Syncerus* (up to +1.1‰) from member CL at Boomplaas (although there is considerable inter-individual variation).

In the early Holocene member BRL, the grazers show markedly divergent  $\delta^{13}\text{C}$  values with *Damaliscus* grazing mainly on C<sub>3</sub> grasses, while *Redunca* (as elsewhere in the sequence) focussed on C<sub>4</sub>. Earlier studies, based on the wood anatomy of charcoal, have suggested that this was a time of summer drought (Scholtz, 1986; Deacon & Lancaster, 1988) which would have favoured C<sub>3</sub> vegetation. *Redunca* likely sought out C<sub>4</sub> grasses in specific microenvironments.

The most continuous and high-resolution record of Late Quaternary palaeoclimates and palaeoenvironments in the southern Cape comes from isotope analyses of speleothems from Pinnacle Point near Mossel Bay dated between ~90-53 ka (Bar-Matthews et al., 2010). The pattern of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in this record has been interpreted as indicating that MIS4 had more summer rain and C<sub>4</sub> grass relative to late MIS5, and then returned to more winter rain and C<sub>3</sub> vegetation in early MIS3. At this time we do not have chronologically overlapping speleothem records from the coast and Klein Karoo. On a long-term (Pleistocene) timescale, it remains unclear whether there is a one to one relationship between glacials and interglacials and the spread and contraction of the winter rainfall region, since the glacials themselves are highly variable.

## Conclusions

Stable carbon and oxygen isotope analysis of 136 samples of tooth enamel from large mammals from the archaeological site of Boomplaas show shifts in the abundance of C<sub>3</sub> and C<sub>4</sub> vegetation during the Late Pleistocene. We have only a limited number of observations from the lowest units (LOH – OLP, ca. 80 – 44 ka) where the fauna was dominated by browsers (Klein, 1978, 1983; Faith, 2013a). Rather negative  $\delta^{13}\text{C}$  values for two *Damaliscus* and an *Equus* from unit OCH ( $62.4 \pm 2$  ka) indicate that the vegetation as a whole included a large proportion of C<sub>3</sub> grasses, although C<sub>4</sub> varieties were locally available, as shown by more positive values for *Redunca fulvorufula*. From units BP to CL, the overall faunal species composition shifted towards grazers.  $\delta^{13}\text{C}$  results indicate that C<sub>4</sub> grasses were most common at the beginning and end of this period, in units BP (ca 38-35 k cal a BP) and CL (18-14 k cal a BP). During the LGM, C<sub>3</sub> grasses dominated. This pattern is consistent with a more widespread winter rainfall zone at the LGM (Van Zinderen Bakker, 1976; Chase and Meadows, 2007). Summer rainfall, on the other hand, correlates with warm intervals as recorded in Antarctic ice cores, notably 38-36 and 18-14 k cal a BP.

$\delta^{13}\text{C}$  coupled with dental anatomy of the extinct caprine identified by Brink (1999) indicate that it was likely a specialized C<sub>3</sub> grazer. This may be linked to a preference for mountainous habitats, thus leading to dietary and ecological separation between this species and other contemporary grazers.

This study shows that palaeoenvironmental reconstructions based on stable isotope analyses of fauna need to take into account the dietary preferences of different species, rather than simply grouping them as ‘grazers’ and ‘browsers’. At Boomplaas, the most specialised grazer (*Redunca fulvorufula*) showed little change in  $\delta^{13}\text{C}$  over time, probably because its habitat specificity means that its isotope values reflect only a particular segment of the local environment (grasses on mountain slopes). More generalised grazers such as *Equus*, as well as *Alcelaphus*/*Damaliscus*/*Connochaetes*, provided a better record of shifts in the proportions of  $\text{C}_3$  and  $\text{C}_4$  grasses at a regional level since they are far more mobile and sample a wider range of habitats. Similar studies of other archaeological and fossil sites in this region will enable us to develop a more detailed picture of environmental change, and hopefully contribute to an understanding of underlying climate dynamics during the Late Pleistocene.

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## Figure and Table Captions

Fig. 1. Map showing localities mentioned in the text.

Fig. 2.  $\delta^{13}\text{C}$  values of various taxa analysed, by stratigraphic member. Grey shaded rectangle indicates approximate range of values for  $\text{C}_3$ -consuming browsers. The positive end of this range, at  $-10\text{‰}$ , is the error propagated  $1\sigma$  boundary of the predicted  $\delta^{13}\text{C}$  values of pure  $\text{C}_3$  consumers, based on  $\delta^{13}\text{C}$  values of modern  $\text{C}_3$  plants (Kohn, 2010), adjusted to a value of  $-6.84$  for atmospheric  $\delta^{13}\text{CO}_2$  (Leuenberger et al., 1992) (Hare & Sealy, 2013).

Fig. 3.  $\delta^{18}\text{O}_{\text{PDB}}$  values of various taxa analysed, by stratigraphic member.

Table 1. Radiocarbon, AAR and U-series dates for the stratigraphic sequence at Boomplaas A. Radiocarbon dates were all on charcoal, and were calibrated using OxCal 4.2 and SHCal13 (Bronk Ramsey, 2009). Dates from Deacon, 1984; Fairhall et al., 1976; Miller et al., 1999; Vogel, 2001.

Table 2.  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}_{\text{PDB}}$  values for tooth enamel of specimens analysed in this study.

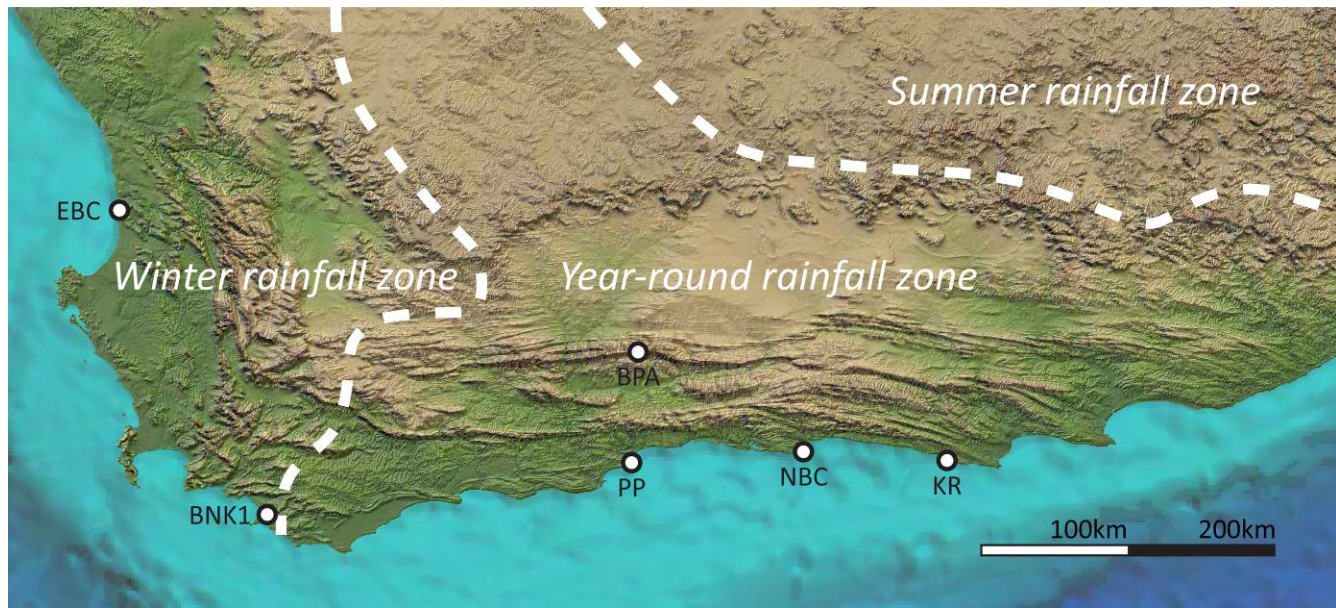


Fig 1

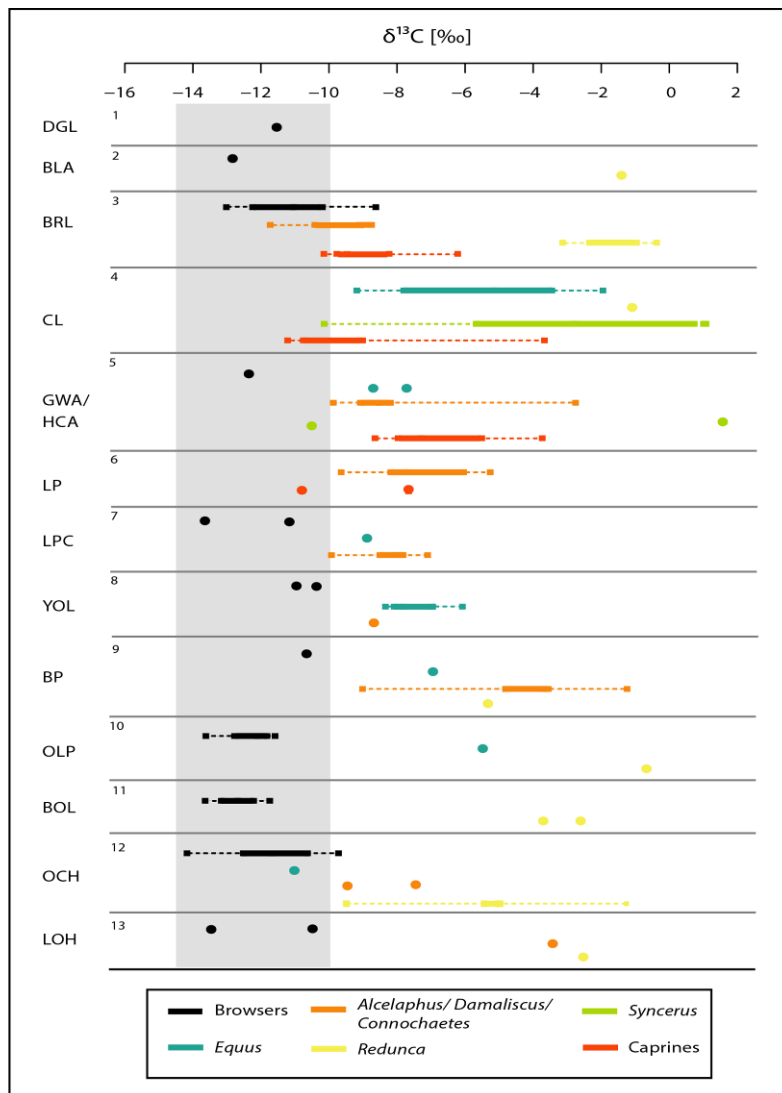


Fig. 2

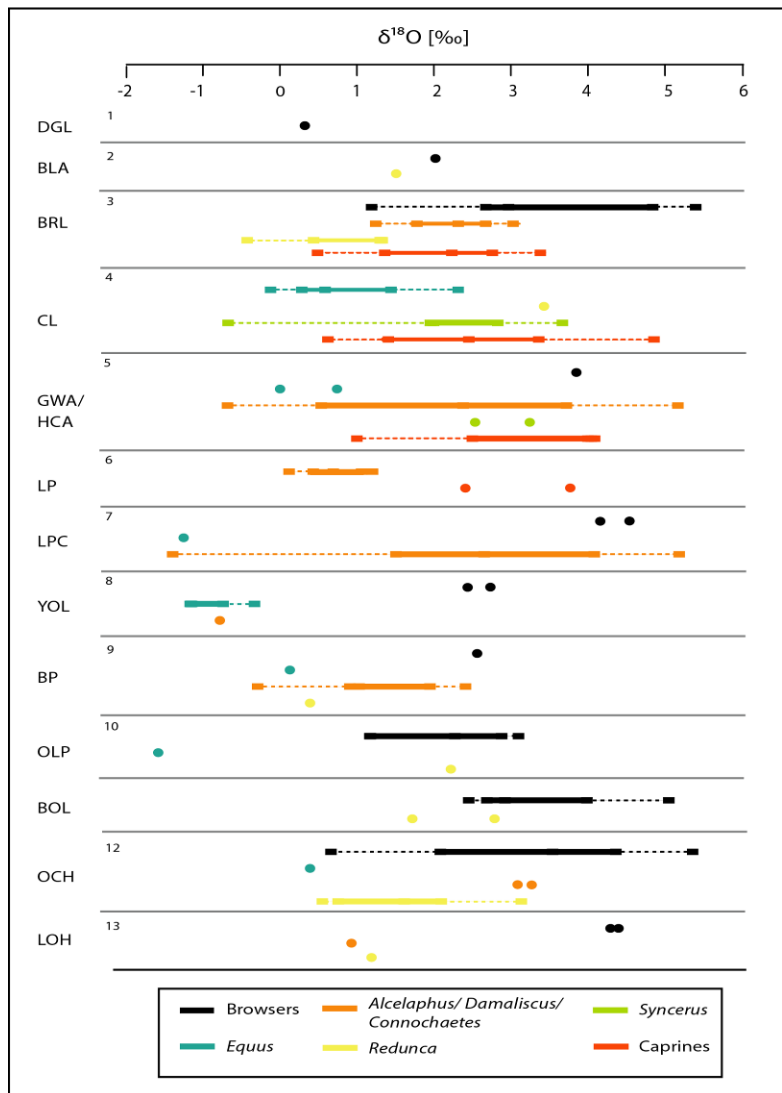


Fig. 3

Table 1

	Stratigraphic	Lab no	Date BP			Calibrated 2 $\sigma$ range
	Member					(cal yr BP)
LSA	DGL	UW-307	1510	$\pm$	75	1270-1535
		UW-337	1630	$\pm$	50	1365-1583
		UW-338	1700	$\pm$	50	1426-1702
	BLD	UW-336	1955	$\pm$	65	1713-2004
	BLA	UW-306	6400	$\pm$	75	7029-7434
	BRL	UW-410	9100	$\pm$	135	9744-10,570
		UW-411	10,425	$\pm$	125	11,775-12,645
	CL	Pta-1828	12,060	$\pm$	105	13,588-14,125
		UW-412	12,480	$\pm$	130	14,108-15,107
		UW-301	14,200	$\pm$	240	16,767-17,625
	GWA/HCA	Pta-3283	17,830	$\pm$	180	20,986-21,998
	LP		-			
	LPC	UW-300	21,110	$\pm$	420	24,346-26,196
		Pta-1810	21,220	$\pm$	195	25,090-25,895
	YOL		-			
MSA	BP	UW-304	32,400	$\pm$	700	34,986-38,369
			33,920	$\pm$	770	36,355-40,129
	OLP	Pta-1811	37,390	$\pm$	1370	39,355-44,542
			44,000	$\pm$	4000	(AAR)
	BOL		-			
	OCH		>49,000			(infinite radiocarbon age)
			56,000	$\pm$	6000	
			65,000	$\pm$	6000	(AAR)
			59,000	$\pm$	2000	(U-series)
			64,000	$\pm$	2000	(U-series)
			66,000	$\pm$	7000	(U-series)
	LOH		-			

Table 2

**Error! Not a valid link.**