

**A 12,000 year Record of Changes in Herbivore Niche Separation and Palaeoclimate
(Wonderwerk Cave, South Africa)**

Michaela Ecker^{1*}, James Brink^{2,3}, Liora Kolska Horwitz⁴, Louis Scott⁵, Julia A. Lee-Thorp¹

*1 Research Laboratory for Archaeology and the History of Art, School of Archaeology,
University of Oxford, UK*

*2 Florisbad Quaternary Research Department, National Museum, Bloemfontein, South
Africa*

*3 Centre for Environmental Management, University of the Free State, Bloemfontein, South
Africa*

*4 National Natural History Collections, Faculty of Life Sciences, The Hebrew University,
Jerusalem, Israel*

5 Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa

*Corresponding author: Michaela Ecker, Department of Anthropology, University of
Toronto, 19 Russell Street, Toronto, Ontario, M5S 2S2, Canada,
michaela.ecker@utoronto.ca

Abstract:

The large mammalian fauna of southern Africa today is characterised by strong niche separation into grazer and browser species, with few falling into the intermediate mixed-feeder niche. Moreover, the modern fauna is reduced in species diversity compared to the Pleistocene, following the extinction of several specialized grazers in the late Pleistocene and early Holocene. How did this state develop, and how might it be connected to climatic change during the Holocene? To better understand this development, we obtained extensive

carbon and oxygen stable light isotope data from herbivore tooth enamel samples from Wonderwerk Cave, South Africa, spanning about 12,000 to 500 cal. BP. This is a unique dataset since it is the only site in the southern Kalahari with a robust chronometric record and well-preserved faunal remains for the last 12,000 years without significant gaps. Combining the stable isotopes with pollen and micromammal data from Wonderwerk Cave, we have explored shifts in the proportions of C₃ and C₄ plants and moisture availability. Although climate remained generally semi-arid for much of this period, the results show significant hydrological and vegetation shifts in the sequence, particularly with the strengthening of summer rainfall in the mid-Holocene. The results for the sixteen herbivore species reveal a reinforcement of the grazer-browser niche partitioning through the Holocene and shows how niche specialization follows changes in local vegetation composition. In the light of this reconstruction of the local ecology we discuss grazer extinctions, human adaptations, and the drivers behind climatic changes in the summer rainfall zone of southern Africa.

Keywords: Holocene; Paleogeography; Southern Ocean; Stable Isotopes; ¹³C; $\delta^{18}\text{O}$; C₄ plants; summer rainfall; faunal turnover; Later Stone Age

1. Introduction

Ecological changes prevailed in faunal communities worldwide at the end of the Pleistocene. Although more muted, on the African continent the prevalent trend was an environmentally driven decline in species of grazers that began in the late Pleistocene (c. 13,000 BP) and continued into the early Holocene (c. 6000 BP), apparently without direct influence of humans (Faith 2011, 2013, 2014). In southern Africa, the change was marked with the replacement of the Florisian Land Mammal Age, which is defined by specialist grazers and wetland species, and a faunal community reduced in species diversity and

encompassing a higher percentage of generalists (e.g. Brink 2005, Faith 2013, Faith and Behrensmeyer 2013). Species that went extinct were mainly the highly specialized grazers, including *Equus capensis*, *Equus lylei*, *Syncerus antiquus*, *Megalotragus priscus*, *Damaliscus niro* and *Antidorcas bondi* (Brink 2005, 2016; Faith 2013, 2014). The mechanisms proposed as causes of this faunal turnover in southern Africa vary: increased aridification and reduced productivity of grasslands (Brink and Lee-Thorp 1992, Brink 2016), increased competition between grazer species (Thackeray 1984, 2015), increasing niche specialization (Codron et al. 2008), changes in the structure of grassland habitats (Faith 2014), or increased seasonality (Faith 2011), but are not mutually exclusive. Although it is clear that climate and environmental change impacted the faunal communities, the primary drivers behind this turnover remain unclear. To a large degree, this is due to a lack of clarity on the timing and nature of climate and environmental change through the Holocene.

The current climate in southern Africa is dry with strongly seasonal precipitation, which influences its biome structure (Fig. 1). Rainfall reaches the south-western Cape from the Atlantic Ocean mainly in the winter (June to August), whereas rain arrives from the Indian Ocean in northern and eastern southern Africa in summer (December to February). A small intermediate zone on the southern coast receives year-round rainfall, while the northern intermediate zone lies in a rain shadow. Holocene climate conditions in southern Africa are largely reconstructed from pollen records. Recent statistical models of pollen data show contrasting records in the summer rainfall zone. For example, in one set of records a modest increase in moisture availability is observed over the course of the Holocene (e.g. at Wonderkrater, Tswaing Crater), and another set shows dry periods 5-7 cal. BP (e.g. at Blydefontein, Braamhoek, Equus Cave, Lake Eteza) (Chevalier and Chase 2015; Scott 2016). A review of pollen records using principal component analysis demonstrates

decreased moisture at 7-8ka at several sites and slightly cooler temperatures after 6ka in the Holocene (Scott et al. 2012; Scott 2016). Around 2ka many records show drying and reduced summer rainfall (Nicholson 2001; Scott et al. 2012). The drawback of pollen records lies in that they cannot distinguish between temperature and aridity signals using principal components analysis. Another issue is the difficulty in establishing a robust chronology for pollen accumulation sites. Thus, in addition to pollen records, independent, chronologically sound environmental data is needed to mediate information on regional climate. However, palaeoclimatic records are extremely sparse for the arid interior of southern Africa. Finally, most pollen, and other proxy records such as speleothems, dune records as well as lake sediment cores represent short sequences, from disparate areas located at a significant distance from each other, that inevitably show a large degree of variability (e.g. Burrough and Thomas 2013) (Fig. 1) [insert Fig. 1].

In this paper we present carbon and oxygen stable isotope values for enamel from sixteen herbivore species from Wonderwerk Cave, located in the arid interior of South Africa. Our research represents the first detailed study of a single site in southern Africa that spans the entire Holocene from the late Pleistocene to historic periods (from ~12ka cal. BP to 500 cal. BP, Ecker et al. 2017). Moreover, the Wonderwerk Cave record offers a range of other environmental and climate proxies (microfauna, macrofauna, pollen, speleothems) with which to compare and contrast the isotopic results. Together, these records allow us to investigate regional trends through most of the Holocene and to discuss the drivers behind climatic changes in the summer rainfall zone.

1.1 Background to the Site

Wonderwerk Cave is located on the eastern flank of the Kuruman Hills in the Northern Cape Province of South Africa. It lies at the base of a 121m high conical hill overlooking

the Ghaap plateau (Fig. 1). The current climate is characterised by summer rainfall of <400mm MAP (mean annual precipitation) with dry winters where frost is possible (Beaumont 1990). Today the area falls within the Savannah biome and the local vegetation is defined as *Kuruman mountain bushveld* (Mucina and Rutherford 2006), with C₄ grasses and C₃ trees, shrubs and herbs. Historic records of European travellers in the 19th century describe a wide range of typical savannah herbivores and carnivores inhabiting the Kuruman Hills and surrounding region (Skead 1980; Thackeray 1981), but today's biomass is significantly reduced due to modern development and farming (Brink et al. 2016).

The cave is a ca. 140m long dolomitic cavity, which was initially explored and excavated in the 1930s and 1940s (for a review see Horwitz and Chazan 2015). The late Peter Beaumont undertook extensive excavations near the cave's entrance (known as Excavation 1) in 1978, to be joined in 1979 by Anne and J. Francis Thackeray, who were specifically interested in documenting the Holocene cultural, faunal and sedimentary record (Thackeray 1981, Thackeray 1984, Humphreys and Thackeray 1983, Beaumont 1990, 2004; Beaumont and Vogel 2006).

The Holocene archaeological strata in Excavation 1 comprise ca. 1 m of brown to reddish sandy deposits (Thackeray 1981, Thackeray 1984, Beaumont 1990, Ecker et al. 2017), which are dated by over 30 radiocarbon dates. A recent Bayesian radiocarbon model constrains the ages of the strata (Table 1; Ecker et al. 2017). *Strata 1* and *2a* represent periods of historic cave use and have yielded finds of metal, glass and European porcelain as well as sheep and cattle dung, indicating that these layers have been disturbed by anthropogenic activities. Small plain ceramic body sherds in *Strata 2b* and *3a* indicate the arrival of pottery in the region, while the lithic assemblage is similar to the underlying Wilton lithic industry levels; these strata, characterised by soft, dark-brown sand, have been attributed to the Ceramic Later Stone Age. *Strata 3b* and *4a-4c* represent the Later Stone

Age (LSA) Wilton industry, which is widespread in southern Africa. *Stratum 3b* was formed in soft dark-brown sand with pieces of roof spall, while *Strata 4a–4c* are characterized by red-brown sand. Shifts in both artefact types (from a dominance of scrapers and segments to backed artefacts) and dominant raw material (from banded ironstone to chert) occur within the Wilton in *Strata 4b to 4aLH* in the profile as a distinct convex hearth-like feature containing the richest material remains at the site (Thackeray 1981, Humphrey and Thackeray 1983, Beaumont 1990, Beaumont and Vogel 2006). *Stratum 4d* is made up of red-brown to orange sands containing ash lenses and roof spall and contains an Oakhurst-like assemblage, locally designated as the Kuruman Industry (Thackeray 1981). It differs from the overlying Wilton in artefact form, scraper morphology, raw material (local banded ironstone and dolomite) and tool types (scrapers with a few blades and retouched adzes) (Humphrey and Thackeray 1983).

Previous environmental studies of the Holocene strata in Excavation 1 at Wonderwerk Cave include abundance analysis and species identifications of macro-fauna (Thackeray 1984, 2015), micro-mammal (Avery 1981), pollen (Van Zinderen Bakker 1982, Brook et al. 2010, 2015, Scott and Thackeray 2015), in addition to speleothem growth data (Brook et al. 2010, 2015), stable carbon and oxygen isotope data for ostrich eggshell (Lee-Thorp and Ecker 2015) as well as carbon ($\delta^{13}\text{C}_{\text{collagen}}$ $n=16$; $\delta^{13}\text{C}_{\text{apatite}}$ $n=11$) and nitrogen ($\delta^{13}\text{C}_{\text{collagen}}$ $n=10$) isotope data for a limited number of Equid teeth (Thackeray and Lee-Thorp 1992). In general, these records show comparable trends of a semi-arid early Holocene, a possible expansion of C_4 grassland in a wetter mid-Holocene (Table 1) and subsequent increasing aridity thereafter.

1.2 Application of stable light isotopes to animal diet and environmental context

This study focuses on stable isotopes in the carbonate fraction of herbivore tooth enamel, as dentine collagen is for the most part poorly preserved. Enamel is a highly crystalline calcium phosphate mineral and resistant to diagenesis compared to bone and dentine. For this reason, it is an appropriate material for stable isotope analysis (Lee-Thorp and Sponheimer 2003). Carbon and oxygen isotopes are substituted in the carbonate of enamel during enamel formation incrementally from crown to base. Therefore, the bulk sampling method applied in this study reflects the animals' diet over several months to years in each tooth at the time of formation (Zazzo et al. 2005). *Pedetes capensis* is the only species in this study with ever-growing teeth, therefore reflecting the last months for this species (Skinner and Chimimba 2005).

Natural abundances of the isotopes of carbon ($^{12}\text{C}/^{13}\text{C}$) and oxygen ($^{16}\text{O}/^{18}\text{O}$) reflect the major pathways in vegetation and hydrology, respectively. The results for both isotopes are expressed as per mil (‰) in the delta (δ) notation versus the international VPDB and VSMOW standards respectively, as follows: $\delta^{13}\text{C}_{\text{VPDB}} = (\text{R}_{\text{sample}} - \text{R}_{\text{ref}}) / \text{R}_{\text{ref}} \times 1000$ where $\text{R} = ^{13}\text{C}/^{12}\text{C}$ and $\delta^{18}\text{O}_{\text{VSMOW}} = (\text{R}_{\text{sample}} - \text{R}_{\text{ref}}) / \text{R}_{\text{ref}} \times 1000$, where $\text{R} = ^{18}\text{O}/^{16}\text{O}$.

The main factor controlling ^{13}C depletion in C_3 plants is their photosynthetic pathway. In general, plants following the C_3 photosynthetic pathway have distinct isotopic values of -24‰ to -36‰, in contrast to plants following the C_4 photosynthetic pathway, with a mean value of -12.5‰ (Farquhar et al. 1989, Kohn 2010). We expect C_3 plant $\delta^{13}\text{C}$ values in our study region to be within the range of -13‰ to -30‰, without the extreme values for full desert or rainforest (Kohn 2010). The carbon isotopic signal reflects the CO_2 fixation in the plants. Therefore, the $\delta^{13}\text{C}$ values of herbivores indicate the proportions of C_3 and C_4 plant types in the animals' diet, making it possible to distinguish animals with a grazing, browsing or mixed-feeding diet. Isotope enrichment between enamel and diet is in the range of 11‰ (small rodents) to 14‰ (large-bodied bovids), depending, amongst others, on body

171 size and gut physiology (Passey et al. 2005). In this study, we have used 13‰ for
172 enrichment in carbon isotopes in all taxa for simplicity.

173 $\delta^{18}\text{O}$ enamel carbonate values are derived from blood biocarbonate, and therefore
174 ultimately from ingested water at the time of tissue formation, hence reflecting climatic
175 conditions (Dansgaard 1964, Longinelli 1984, Rozanski et al. 1993). Most mammals derive
176 a significant amount of the oxygen in blood biocarbonate from the vegetation consumed.
177 As plants undergo evapotranspiration, ^{18}O is unevenly distributed through the plant, with
178 leafwater becoming enriched in ^{18}O (Gonfiantini et al. 1965, Dawson et al. 2002).
179 Consumer $\delta^{18}\text{O}$ values are dependent on the plant parts preferentially consumed. For
180 instance, nocturnal feeders, or animals that feed mostly on underground storage organs of
181 plants, have depleted $\delta^{18}\text{O}$ values (Sponheimer and Lee-Thorp 1999). Browsers should
182 have enriched $\delta^{18}\text{O}$ values as they feed mainly on plant leaves compared to grazers and
183 carnivores who take in meteoric water on a daily basis (Kohn et al. 1996, Cerling et al.
184 1997, Sponheimer and Lee-Thorp 1999, Levin et al. 2006). In combination, ^{13}C and $\delta^{18}\text{O}$
185 isotopes in enamel provide a powerful tool for gaining insights about ecological niche
186 partitioning and its climatic drivers in the past.

Stratum	Age (Ecker et al. 2017)	Industry	Stable isotopes	Microfauna	Pollen	Macrofauna
1 and 2a	Historic	disturbed levels	C ₃ trees/shrubs with C ₄ grasses, semi-arid		High grass pollen count, arid	
2b and 3a	0.5-2.3ka cal. BP	Ceramic LSA	C ₄ grassland; maximum aridity	Open grass and scrub, arid	High grass pollen count, arid	Alcelaphini & Equids dominate
3b	2.8-4.5ka cal. BP	Wilton	C ₃ trees/shrubs with C ₄ grasses; arid	Slightly wetter and more trees/bushes	High grass pollen count, mesic	Similar percentages Alcelaphini & Tragelaphini
4a	5.3-4.6ka cal. BP	Wilton	C ₄ grassland; aridification trend starting	Open grassland, arid	High grass pollen count, mesic	Alcelaphini & Equids dominate, <i>Connochaetes gnou</i> present
4aLH	6.2-5.4ka cal. BP	Wilton	expansion of C ₄ grasses; fluctuating with at least one wet spell	Savanna grassland, arid	Increase in grass pollen, wet peak	Increase in Alcelaphini & Equids, <i>R. f. fulvorufula</i> & <i>A. marsupialis</i> first appear
4b	6.9-5.9ka cal. BP	Wilton	C ₃ trees/shrubs with C ₄ grasses; semi-arid at start then wetter	Savanna woodland, semi-arid	Reduced Asteraceae	Few Equids, equal percentages Alcelaphini & Tragelaphini
4c	9.4-6.8ka cal. BP	Wilton	C ₃ trees/shrubs with C ₄ grasses, semi-arid	Short grass with trees/bushes, semi-arid	High Asteraceae pollen count; arid	Few Equids, last appearance <i>M. priscus</i> & <i>A. bondi</i>
4d	11.8-10.4ka cal. BP	Oakhurst	C ₃ trees/shrubs with C ₄ grasses, semi-arid to arid	Open shrubland, arid	High Asteraceae pollen count; arid	Equal percentages Alcelaphini & Tragelaphini, few Equids- last appearance of <i>E. capensis</i>

188 Table 1: Holocene Strata in Excavation 1 of Wonderwerk Cave with modelled age ranges (based on Ecker et al. 2017) and associated lithic
189 industries (based on Beaumont 1990, 2004, Humphreys and Thackeray 1983). The local trends in vegetation and climate are a summary of stable
190 isotope analysis on enamel (this study) and ostrich eggshell (Lee-Thorp and Ecker 2015), microfauna analysis (Avery 1981), pollen analysis
191 (Brook et al. 2010, Scott and Thackeray 2015) and macrofauna abundances (this study, Thackeray 1984, 2015).

2. Material and Methods

Tooth enamel of sixteen herbivore species, including grazing, browsing and mixed-feeding species, were sampled from the Wonderwerk Cave faunal assemblage. Bovidae are the most abundant family present in all excavated strata at the site and tribes represented include Alcelaphini, Tragelaphini, Antilopini, Neotragini and Reduncini. Therefore, the whole range of modern southern African grazing, browsing and mixed-feeding bovids are found, as well as all size categories from the small *Raphicerus campestris* (steenbok) (~10 kg) to the largest bovid, *Taurotragus oryx* (eland) (~500 kg). Perissodactyla are represented by *Equus quagga* (Burchell's zebra). The two rodent species *Pedetes capensis* (springhare) and *Hystrix africaeaustralis* (porcupine) provides an opportunity to build a comparative isotopic sequence using smaller, less mobile mammals. Samples from the suid *Phacochoerus africanus* (warthog) and one *Procavia capensis* (hyrax) tooth complete the analysed assemblage.

Bulk samples were taken with a diamond-tipped drill along the whole length of the tooth crown following a cleaning sweep of the surface. The teeth are well-preserved and include complete teeth. Burned teeth, deciduous teeth or glued areas were avoided. Enamel pre-treatment followed a standard protocol, modified after Sponheimer (1999). Enamel powders were soaked in ~1.8 ml NaOCl solution (~2%) for 30 minutes to remove organics. Samples were centrifuged, decanted and washed with distilled water three times, before being soaked in 0.1M Acetic Acid (CH₃COOH) for ten minutes to remove any exogenous carbonate and again washed three times with distilled water. 2-3mg of the resultant dried powders were reacted with phosphoric acid at 70°C in a Finnigan Gasbench II, interfaced with a Thermo Delta V Advantage continuous flow isotope ratio mass spectrometer to release CO₂, for measurement of ¹³C/¹²C and ¹⁸O/¹⁶O ratios.

Analytical precision as determined from multiple replicates of the standards used (NBS 19, CO-1, CO-8 and three laboratory carbonate standards) was 0.1‰ for $\delta^{13}\text{C}$ and 0.2‰ for $\delta^{18}\text{O}$. To test for homogeneity of variance in the stable isotope results, a Levene's test was performed in R (R Core Team 2013, version 3.0.1), with the null hypothesis that all strata variances are equal. Statistical differences between all strata were tested for each species using one-way ANOVA with Tukey's HSD *post-hoc* test in R, with significance set as $p < 0.05$.

3. Results

Carbon and oxygen stable isotope results are listed by stratum and species in Table 2 and plotted in Figure 2 and 3 [insert Figure 2]. Appendix 1 gives the complete set of data.

The $\delta^{13}\text{C}$ values of enamel below -9‰ indicate a majority C_3 diet and $\delta^{13}\text{C}$ values of above -2‰ indicate a majority C_4 diet (Lee-Thorp et al. 2007) (Figure 3). The $\delta^{13}\text{C}$ values of all samples range from 100% C_3 diets (minimum value -14.1‰) to 100% C_4 diets (maximum value 3.9‰). For all samples, $\delta^{18}\text{O}$ values were expressed versus the SMOW standard and range from a minimum of 24.3‰ to a maximum of 42‰. Results are discussed in detail by family below:

Bovidae

Alcelaphini, which at Wonderwerk Cave include *Alcelaphus buselaphus* (Red Hartebeest), *Connochaetes* sp. (Wildebeest) and *Damaliscus* sp., comprise the largest group. *Alcelaphus buselaphus* is more flexible in habitat than other Alcelaphini as it is less specialized in habitat selection (Kingdon 1982, Skinner and Chimimba 2005). Of the wildebeest, the majority of the identified samples belong to *Connochaetes taurinus*, the blue wildebeest. Two samples (Strata 4a and 3b) are identified as possibly belonging to *Connochaetes gnou*, the black wildebeest, a species endemic to South Africa. Today the range of the two wildebeest

species is separate, with the black wildebeest inhabiting the grasslands of South Africa's interior and the blue wildebeest the northerly savannah areas of southern Africa (Brink 2005). The appearance of the black wildebeest in Wonderwerk Cave hints at a past biome shift. The third Alcelaphine species is *Damaliscus*. The sample (Stratum 3a) most likely belongs to *Damaliscus pygargus*, commonly known as the blesbok. It disappeared from this area in the mid-Holocene, but is widespread today in the neighbouring grassland highveld and the northern Karoo (Apps 2012). This is a second faunal indicator of biome shifts in the past.

In this study, Alcelaphini have mean $\delta^{13}\text{C}$ values between $-0.5 \pm 1.4\text{‰}$ (Stratum 1-2a, $n=2$) and $2.3 \pm 1.0\text{‰}$ (Stratum 4aLH, $n=8$) with the lowest individual value being -3.5‰ (Stratum 3b) and the highest individual value being 3.9‰ (Stratum 4b). As a general trend, $\delta^{13}\text{C}$ tend to be lower in earlier Strata (4d, 4c and 4b; mean values Stratum 4d $0.0 \pm 1.7\text{‰}$ ($n=4$) to Stratum 4c $1.8 \pm 0.8\text{‰}$ ($n=10$)) compared to the mid-late Holocene Strata 2b to 4LH which have mean values of $1.7 \pm 1.6\text{‰}$ (Stratum 3b, $n=20$) to $2.3 \pm 1.0\text{‰}$ (Stratum 4aLH, $n=8$) (Table 2 and Fig. 3) [insert Figure 3]. The mean $\delta^{18}\text{O}$ values range from $31.8 \pm 2.2\text{‰}$ in Stratum 1-2a ($n=2$) to $34.3 \pm 2.2\text{‰}$ in Stratum 4aLH ($n=8$), but individual values show a range over 10‰ . The $\delta^{13}\text{C}$ mean values for *Alcelaphus buselaphus* range from $0.8 \pm 2.1\text{‰}$ (Stratum 4b, $n=3$) to $2.4 \pm 0.5\text{‰}$ (Stratum 4a, $n=15$) and the $\delta^{18}\text{O}$ mean values from $33.0 \pm 1.9\text{‰}$ in Stratum 4a ($n=15$) to $34.4 \pm 2.1\text{‰}$ in Stratum 4b ($n=3$). The Wildebeest specimens (*Connochaetes taurinus* and *Connochaetes gnou*) have a tighter range of values. Their $\delta^{13}\text{C}$ mean values range between 1.2‰ in Stratum 3a ($n=1$) to $2.5 \pm 0.4\text{‰}$ in Stratum 3b ($n=2$) and are never below 0‰ . Wildebeest are consistent grazers reflected in their tight $\delta^{13}\text{C}$ range. Another specialist grazer in the Wonderwerk Cave assemblage is *Redunca fulvorufula fulvorufula* (Mountain Reedbuck) with $\delta^{13}\text{C}$ mean values ranging from between $1.1 \pm 1.2\text{‰}$ in Stratum 2b ($n=3$) to 3.5‰ in Stratum 4aLH ($n=1$).

265 For the Tragelaphini species, *Tragelaphus strepsiceros* (kudu) and *Taurotragus oryx*
 266 (eland), small differences have been reported in preferred browse, where the kudu
 267 concentrates on higher quality forage and the eland, being a generalist, includes some grass
 268 and dry forage in its diet (Gagnon and Chew 2000). This is reflected in modern published
 269 $\delta^{13}\text{C}$ values of around -13‰ for kudu and higher values of -8‰ to -11‰ for eland
 270 (Sponheimer et al. 2003, Codron et al. 2008). However, there is no statistically significant
 271 difference in the Wonderwerk Cave results in $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values between *Tragelaphus*
 272 *strepsiceros* and *Taurotragus oryx*. The differences between these species in eating habits
 273 as described above do not show up in the isotope data. Both Tragelaphini show mean $\delta^{13}\text{C}$
 274 values of $-10.0 \pm 0.6\text{‰}$ in Stratum 4d (n=4) to $-7.5 \pm 1.8\text{‰}$ in Stratum 4a (n=14), indicating
 275 a pure C_3 diet with a small C_4 intake. However, when values for bovid tribes are compared
 276 throughout the sequence, Tragelaphini and Alcelaphini have significantly different $\delta^{13}\text{C}$
 277 values (e.g. Stratum 4d Alcelaphini-Tragelaphini $p=0.02$), confirming the dietary
 278 separation of both tribes (Fig. 3).

279 Modern springbok (*Antidorcas marsupialis*) are mixed-feeders, ingesting more graze in
 280 summer and more browse in winter (Gagnon and Chew 2000, Apps 2012). In Wonderwerk
 281 Cave, *A. marsupialis* has $\delta^{13}\text{C}$ values between a pure C_3 diet and mixed-feeding with mean
 282 values range from $-9.8 \pm 0.8\text{‰}$ in Stratum 2b (n=3) to $-5.1 \pm 1.9\text{‰}$ in Stratum 4a (n=2). The
 283 extinct springbok species *Antidorcas bondi* (Bond's springbok) is also present but not
 284 abundant. The single specimen analysed gives a $\delta^{13}\text{C}$ value of -2.5‰ (Stratum 4c) and is
 285 in line with data obtained previously for this taxon (Brink and Lee-Thorp 1992).

286 Although the steenbok, *Raphicerus campestris*, has been classified as an intermediate
 287 grazer-browser by Gagnon and Chew (2000), it has been elsewhere shown to be
 288 predominantly a C_3 feeder. It consumes high-quality tubers, roots, leaves, flowers, pods
 289 and berries located near ground level and is largely water independent (e.g. Du Toit 1993).

The Wonderwerk $\delta^{13}\text{C}$ values are consistent with a predominantly C_3 diet, with mean values range from $-12.8 \pm 1.3\text{‰}$ (Stratum 3a, $n=2$) to $-9.1 \pm 1.0\text{‰}$ (Stratum 4b, $n=8$). Individual values range from a minimum of -14.1‰ (Stratum 3a), which is also the lowest individual carbon isotope value of the whole study, to a maximum individual $\delta^{13}\text{C}$ value of -7.6‰ (Stratum 4b). *Raphicerus campestris* has the lowest $\delta^{13}\text{C}$ and highest $\delta^{18}\text{O}$ mean values of any species in the Wonderwerk Cave assemblage, a result consistent with its ecological position as a water-independent browser. The other Neotragini in the assemblage, the klipspringer *Oreotragus oreotragus*, also consumed a C_3 diet ($\delta^{13}\text{C}$ -11.7‰ , Stratum 2b, $n=1$).

Pelea capreolus (grey rhebok) is a small bovid endemic to southern Africa. The limited sample ($n=3$) revealed in one Stratum a pure C_3 diet (Stratum 4aLH; $\delta^{13}\text{C}$ 11.9‰ , $n=1$) and in the other Stratum a more mixed diet (Stratum 4a; $\delta^{13}\text{C}$ $6.1 \pm 0.1\text{‰}$, $n=2$). Its $\delta^{18}\text{O}$ values (Stratum 4aLH $\delta^{18}\text{O}$ 35.2‰ $n=1$; Stratum 4a $\delta^{18}\text{O}$ $33.8 \pm 1.2\text{‰}$ $n=2$) are similar to the other small, water independent browsers, *R. campestris* and *O. oreotragus*, respectively. Their main source of water are leaves ingested as food. Compared to the larger browsers and the grazers, its $\delta^{18}\text{O}$ mean values are on average higher, but not statistically significant.

Perissodactyla

The two *Equus* sp. samples in Stratum 1 have lower $\delta^{13}\text{C}$ values than the other Holocene *Equus quagga* samples from the site with a mean of $-6.3 \pm 0.8\text{‰}$, reflecting mixed C_3/C_4 -feeding. Discounting the values for Strata 1 and 2a, as these levels possibly represent disturbed assemblages (Humphreys and Thackeray 1983), *Equus* $\delta^{13}\text{C}$ mean values in the rest of the sequence range from -1.6‰ (Stratum 3b, $n=1$) to 2.9‰ (Stratum 4aLH, $n=1$), reflecting clear C_4 diets. Equids are highly mobile, but dependent on frequent access to water. Their mean $\delta^{18}\text{O}$ values range from $30.4 \pm 2.1\text{‰}$ in Stratum 2b ($n=3$) to 37.1‰ in

314 Stratum 4aLH (n=1), with relatively little variability, reflecting that these animals were
315 regular drinkers. A non-significant difference is visible between the large grazer species,
316 with Equids tending to have lower $\delta^{18}\text{O}$ values than Alcelaphini.

317 Rodentia

318 *Hystrix africaeaustralis* (Cape porcupine) are nocturnal and feed on fruits, bulbs, roots,
319 bark and seeds (Apps 2012). Their mean $\delta^{13}\text{C}$ values range widely from -0.8‰ (Stratum
320 4b, n=1) to -11.6 ± 1.5 ‰ (Stratum 3a, n=2), with individual values between -0.2‰ for
321 Stratum 4a and -13.0‰ for Stratum 3a, thus spanning the complete C_3 to C_4 diet range.
322 Standard derivations within strata are large (up to 4‰). Mean $\delta^{18}\text{O}$ Holocene values are
323 28.7 ± 1.9 ‰ in Stratum 3b, n=4) to 31.5‰ (Stratum 4aLH, n=1), with individual values
324 ranging from 25.8‰ (Stratum 3b) to 31.8‰ (Stratum 4a). *Hystrix africaeaustralis* is clearly
325 a highly flexible mixed-feeder, with no clear trends in its diet apparent through time. Its
326 $\delta^{18}\text{O}$ values are lower than the large ungulates from the same strata.

327 *Pedetes capensis* (springhare) are also nocturnal and feed on the roots of grasses, as well
328 as seeds and sometimes grass leaves (Apps 2012). The *Pedetes capensis* specimens in
329 Wonderwerk have $\delta^{13}\text{C}$ mean values of -0.9‰ (Stratum 3b, n=1) to 0.1 ± 1.0 ‰ (Stratum 4b,
330 n=5), with individual values ranging between -2.3‰ (Stratum 4c) and 1.4‰ (Stratum 4b),
331 confirming a dominance of C_4 in their diet. Springhares obtain sufficient moisture from
332 rain drops, food and oxidation of hydrogen from ingested food (Skinner and Chimimba
333 2005). Oxygen isotope values (range $\delta^{18}\text{O}$ 27.2‰, Stratum 3b, to 31.5‰, Stratum 4aLH;
334 n=3), are similarly low as for *H. africaeaustralis* (25.8‰ to 31.8‰, see above). *P. capensis*
335 and *H. africaeaustralis* both have consistently lower $\delta^{18}\text{O}$ values compared to the other
336 species. Both are statistically significant different in $\delta^{18}\text{O}$ to Alcelaphini, Tragelaphini, *R.*
337 *campestris* and *R. f. fulvorufula* ($p < 0.000$). They are not significantly different from each

other ($p > 0.05$). This is most likely due to both being nocturnal animals that feed on the underground organs of plants.

Suidae

Five molars and one premolar of *Phacochoerus africanus* (warthog), from Strata 4a and 2b, were analysed. This diurnal Suid is mainly a selective grazer (Skinner and Chimimba 2005, Apps 2012), reflected in $\delta^{13}\text{C}$ mean values of 0.0‰ (Stratum 2b, $n=1$) and $1.0 \pm 0.5\text{‰}$ (Stratum 4a, $n=5$). Individual $\delta^{18}\text{O}$ values range from 30.5‰ to 37.2‰ (both Stratum 4a).

Hyracoidea

One tooth from a *Procavia capensis* specimen was analysed. Hyrax are opportunistic feeders, feeding on a mixed diet of grass, forbs, shrubs, fruit and berries (Skinner and Chimimba 2005, Apps 2012, Kingdon et al. 2013), which is reflected in the $\delta^{13}\text{C}$ value of -4.3‰ for a specimen from Stratum 2b. Hyrax are not water dependent if they can consume sufficient green food. Due to its water-concentrating physiology, $\delta^{18}\text{O}$ values are expected to be higher compared to large ungulates. The $\delta^{18}\text{O}$ value is 41.4‰ , which is the highest $\delta^{18}\text{O}$ value of any species analysed in the assemblage.

Comparing the results found in this study with $\delta^{13}\text{C}$ values from the literature on modern South African mammals (Sponheimer et al. 2003, Codron et al. 2008), most species in the mid-Holocene Strata of Wonderwerk are within the expected $\delta^{13}\text{C}$ ranges. Furthermore, based on $\delta^{13}\text{C}$ values, there is a clear separation of species into grazers and browsers. At the one extreme is the browser *Raphicerus campestris* with a diet of 100% C_3 plants (average $\delta^{13}\text{C}$ values of $< -12\text{‰}$). At the opposite end of the spectrum are hypograzers like *Connochaetes* sp. with 100% C_4 diet (average $\delta^{13}\text{C} > 2\text{‰}$). Few species fall into the mixed-feeder range (mean values of -9‰ to -3‰) (Figure 4), a characteristic noted for modern African ecosystems (Codron et al. 2008).

	Dietary behaviour	δ ¹³ C					δ ¹⁸ O				
Species		Mean	SD	Min	Max	n	Mean	SD	Min	Max	
Stratum 1-2a											
Alcelaphini	G	-0.5	1.4	-1.9	0.9	2	31.8	2.2	29.6	34.0	
<i>Equus</i> sp.	M	-6.3	0.8	-7.1	-5.4	2	31.0	0.6	30.5	31.6	
<i>H. africaeaustralis</i>	M	-6.7	0.6	-7.4	-6.0	4	30.3	0.9	29.2	31.7	
Stratum 2b											
<i>A. buselaphus</i>	G	2.0				1	32.4				
<i>C. taurinus</i>	G	1.5				1	31.5				
<i>A. marsupialis</i>	B	-9.8	0.8	-10.7	-8.8	3	31.7	0.4	31.2	32.2	
<i>R. fulvorufula</i>	G	1.1	1.2	-0.6	2.0	3	32.6	1.5	31.2	34.6	
<i>O. oreotragus</i>	B	-11.7				1	35.0				
Tragelaphini	M	-8.6	1.1	-10.3	-7.2	5	32.4	1.5	30.6	35.0	
<i>Equus</i> sp.	G	-0.8	0.8	-1.8	0.2	3	30.4	2.1	27.7	33.0	
<i>P. africanus</i>	G	0.0				1	31.5				
<i>Procavia capensis</i>	M	-4.3				1	41.4				
Stratum 3a											
Alcelaphini (all)	G	1.9	0.8	0.2	3.0	20	33.6	1.7	30.5	36.7	
> <i>A. buselaphus</i>	G	2.2	0.6	1.4	3.0	9	33.0	1.4	30.5	35.3	
> <i>C. taurinus</i>	G	1.2				1	31.6				
> <i>D. pygargus</i>	G	0.3				1	32.0				
<i>A. marsupialis</i>	M	-6.8	2.0	-9.0	-2.9	6	33.1	1.3	31.3	35.2	
<i>R. campestris</i>	B	-12.8	1.3	-14.1	-11.4	2	35.4	0.4	35.0	35.8	
<i>R. fulvorufula</i>	G	1.9	0.6	1.3	2.5	2	32.6	1.4	31.1	34.0	
Tragelaphini (all)	B	-9.8	1.0	-11.3	-8.1	9	32.9	2.5	28.1	36.5	
<i>Equus</i> sp.	G	-0.3	0.8	-2.1	0.9	9	31.7	1.2	29.9	33.6	
<i>H. africaeaustralis</i>	B	-11.6	1.5	-13.0	-10.1	2	28.7	0.4	28.3	29.1	
Stratum 3b											
Alcelaphini (all)	G	1.7	1.6	-3.5	3.5	20	33.5	2.1	29.2	36.5	

> <i>A. buselaphus</i>	G	2.0	0.6	1.1	2.8	8	33.2	2.5	29.2	36.1
> <i>Connochaetes</i> sp.	G	2.5	0.4	2.2	2.9	2	32.0	0.6	31.4	32.5
<i>A. marsupialis</i>	B	-9.8	1.0	-10.8	-8.9	2	32.7	1.8	30.9	34.5
<i>R. campestris</i>	B	-10.8	1.1	-12.8	-9.3	7	35.2	2.9	28.5	37.8
<i>R. fulvorufula</i>	G	2.1	0.8	1.1	3.1	4	33.2	1.3	31.6	35.1
Tragelaphini (all)	B	-9.1	1.0	-10.7	-7.4	18	34.0	1.7	31.3	38.1
<i>Equus</i> sp.	G	-1.6				1	33.7			
<i>H. africae australis</i>	B	-11.4	0.7	-12.3	-10.3	4	28.7	1.9	25.7	30.8
<i>P. capensis</i>	G	-0.9				1	27.2			
Stratum 4a										
Alcelaphini (all)	G	2.2	0.9	-1.2	3.7	36	33.5	2.4	29.7	39.2
> <i>A. buselaphus</i>	G	2.4	0.5	1.4	3.1	15	33.0	1.9	30.8	36.7
> <i>Connochaetes</i> sp.	G	2.3	0.9	0.6	3.7	7	33.6	1.0	32.0	35.0
<i>A. marsupialis</i>	M	-5.1	1.9	-7.1	-3.2	2	31.8	1.4	30.4	33.2
<i>P. capreolus</i>	M	-6.1	0.1	-6.2	-5.9	2	33.8	1.2	32.6	35.0
<i>R. campestris</i>	B	-9.3	0.9	-10.7	-7.9	10	34.4	1.8	31.1	37.0
<i>R. fulvorufula</i>	G	1.7	1.5	-1.6	2.9	6	34.6	2.4	31.3	37.9
Tragelaphini (all)	M	-7.5	1.8	-9.6	-4.3	14	34.1	1.9	31.6	38.1
<i>Equus</i> sp.	G	0.2	0.8	-0.9	0.9	3	33.0	1.3	31.7	34.7
<i>P. africanus</i>	G	1.0	0.5	0.4	1.9	5	33.0	2.4	30.5	37.2
<i>H. africae australis</i>	M	-6.8	4.0	-11.5	-0.2	5	29.9	1.5	28.1	31.8
<i>P. capensis</i>	G	-0.5	0.6	-1.2	0.3	8	28.6	1.8	24.3	30.3
Stratum 4aLH										
Alcelaphini (all)	G	2.3	1.0	0.0	3.3	8	34.3	2.2	31.0	38.3
> <i>A. buselaphus</i>	G	1.9	1.0	0.0	2.8	5	34.0	2.0	31.0	36.4
<i>A. marsupialis</i>	M	-7.0	0.1	-7.1	-6.9	2	31.0	0.4	30.6	31.4
<i>P. capreolus</i>	B	-11.9				1	35.2			
<i>R. campestris</i>	B	-11.4	0.4	-11.8	-11.0	3	36.1	4.2	32.9	42.3
<i>R. fulvorufula</i>	G	3.5				1	37.4			

Tragelaphini (all)	B	-9.2	1.1	-10.0	-7.4	4	35.3	2.4	32.6	38.1
<i>Equus</i> sp.	G	2.9				1	37.1			
<i>H. africaeaeaustralis</i>	B	-9.4				1	31.5			
<i>P. capensis</i>	G	-0.1	0.0	-0.1	0.0	2	30.6	0.9	29.7	31.5
Stratum 4b										
Alcelaphini (all)	G	1.5	2.0	-2.1	3.9	5	33.5	1.2	32.0	34.7
> <i>A. buselaphus</i>	G	0.8	2.1	-2.1	2.5	3	34.4	0.4	33.9	34.7
<i>A. marsupialis</i>	M	-7.7				1	35.0			
<i>R. campestris</i>	B	-9.1	1.0	-10.7	-7.6	8	34.5	2.9	31.7	39.5
Tragelaphini (all)	M	-8.1	1.0	-9.5	-6.5	5	34.4	1.8	32.7	37.8
<i>Equus</i> sp.	G	0.5	0.6	-0.2	1.1	2	33.0	1.4	31.7	34.4
<i>H. africaeaeaustralis</i>	G	-0.8				1	29.1			
<i>P. capensis</i>	G	0.1	1.0	-1.5	1.4	5	29.3	1.3	27.7	30.7
Stratum 4c										
Alcelaphini (all)	G	1.8	0.8	0.7	3.7	10	33.1	1.1	31.6	34.6
> <i>A. buselaphus</i>	G	2.3	1.4	0.8	3.7	2	33.3	1.3	32.1	34.6
> <i>C. taurinus</i>	G	1.9	0.1	1.8	2.0	3	33.5	1.3	31.6	34.4
<i>A. bondi</i>	G	-2.5				1	31.4			
<i>R. campestris</i>	B	-9.5	0.8	-10.7	-8.7	3	35.6	3.2	33.0	40.1
Tragelaphini (all)	B/M	-9.0	0.9	-10.9	-7.8	17	35.6	1.9	31.6	39.6
<i>Equus</i> sp.	G	0.7				1	33.0			
<i>H. africaeaeaustralis</i>	M	-8.0	1.7	-10.8	-6.1	4	29.7	1.0	28.9	31.4
<i>P. capensis</i>	G	-0.7	1.0	-2.3	0.6	6	29.0	1.1	27.5	30.5
Stratum 4d										
Alcelaphini (all)	G	0.0	1.7	-1.4	2.7	4	33.8	1.0	32.6	35.3
Tragelaphini (all)	B	-10.0	0.6	-10.5	-9.0	4	35.2	1.5	32.8	36.7
<i>H. africaeaeaustralis</i>	B	-9.2	1.5	-10.6	-6.9	4	29.4	1.6	27.1	31.4

362 Table 2: Descriptive statistics (mean values, standard deviations, minimum and maximum
363 values) of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel isotope results from Excavation 1 at Wonderwerk Cave.

Dietary behaviour divides the species into predominantly grazing (G, $\delta^{13}\text{C} < -3\text{‰}$), browsing (B, $\delta^{13}\text{C} > -9\text{‰}$) or mixed-feeding (M, $\delta^{13}\text{C} < -9\text{‰}$ and $> -3\text{‰}$) species after Lee-Thorp et al. 2007. N is the number of samples per species. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are expressed versus the VPDB and the SMOW standard, respectively.

4. Discussion

4.1 Vegetation and aridity during the Holocene

Combining the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ results, a complex picture of niche separation development in herbivores emerges for Wonderwerk Cave. In the following, the results are discussed in a local context before being compared to records from the wider region.

In the early Holocene strata at Wonderwerk Cave, several extinct species are present: *Antidorcas bondi* (Stratum 4c), *Megalotragus priscus* (Stratum 4c) and *Equus capensis* (Stratum 4d) (Thackeray 2015, Ecker et al. 2017). The Wonderwerk Cave specimen of *Antidorcas bondi* and *Megalotragus priscus* are possibly the youngest examples of their species (Faith 2014, Ecker et al. 2017). As both are specialist grazers, changes in the structure of grasslands due to aridification have been proposed as a likely explanation for their extinction (e.g. Brink and Lee-Thorp 1992, Faith 2014, Brink 2016). The $\delta^{13}\text{C}$ tooth-enamel record in Wonderwerk Cave indicates more C_3 plants in the local vegetation up to c. 7ka cal. BP compared to the mid- and late Holocene (Figure 4) [insert Figure 4]. Analysis of the Pleistocene Strata in Excavation 1 also show more mixed $\delta^{13}\text{C}$ tooth-enamel values (Ecker 2016). That could suggest that the faunal extinctions are most likely related to changes in the composition of local vegetation beyond a degree that could sustain specialist grazers in the long term. Enamel $\delta^{18}\text{O}$ results of the early Holocene across species are variable but suggest overall semi-arid conditions, as median values are consistently over 30‰ (except in rodents, see above). The span of individual $\delta^{18}\text{O}$ values has several values

substantially higher than the median values, suggesting that short arid phases were common (Fig. 3).

Only in the mid-Holocene (from Stratum 4aLH onwards, dated to 6.2-5.4ka cal. BP), do $\delta^{13}\text{C}$ values of tooth enamel in Wonderwerk Cave reach up to 4‰ and support at the same time both hypergrazers ($\delta^{13}\text{C} > 2\text{‰}$), as well as hyperbrowsers ($\delta^{13}\text{C} < -12\text{‰}$) (Fig. 3). *Antidorcas marsupialis* has individuals with a significant amount of C_4 plants in their diet only in Strata 4a and 3a. The results suggest increased C_4 growth in the local vegetation. Non-regular drinking species, which are covering their water requirements through water from digested plants, have their lowest $\delta^{18}\text{O}$ values in Stratum 4aLH (*R. campestris*, Tragelaphini, *A. marsupialis*). This suggests low evapotranspiration in this phase, which in turn can be an indicator of wetter conditions.

From Stratum 4aLH upwards, the specialized grazer *Redunca fulvorufula* reappears in the Wonderwerk Cave faunal assemblage. At the same time, *Connochaetes gnou*, today inhabiting the grassland biome to the east of the cave, is present, indicating biome shifts to open grassland for a limited time in the mid-Holocene. It was noted by Thackeray (2015) that in the Holocene faunal assemblages, frequencies of Equids and Alcelaphini rise from 35% of the total assemblage in the early Holocene to 45% in the Late Holocene. Comparing the abundances of large grazing bovids (Alcelaphini) and large browsing bovids (Tragelaphini), both tribes are found in low numbers in Strata 4d and 4b, with more Tragelaphini than Alcelaphini specimen in Strata 4c and 3b. Strata 4aLH, 4a and 3a show increased numbers of Alcelaphini, which could reflect more open grassland. However, since sample sizes are generally small these conclusions must be considered as only tentative. Equids are present in low numbers before the mid-Holocene Stratum 4a when their numbers rise, further pointing to an expansion of grassland from this point onwards

412 as demonstrated by other paleoenvironmental proxies from the cave (Avery 1981, Scott
413 and Thackeray 2015).

414 In the late Holocene at Wonderwerk Cave, (Strata 3a and 3b; dated to ~4.5ka cal. BP), $\delta^{13}\text{C}$
415 values for browsers like *R. campestris*, *H. africae australis*, Tragelaphini and *A. marsupialis*
416 shift even further into the C_3 range with lower carbon isotope values than found in the early
417 to mid-Holocene strata. *R. campestris* and the Tragelaphini have significantly higher $\delta^{18}\text{O}$
418 isotope values in Strata 3a and 3b compared to the early and mid-Holocene ($p < 0.05$),
419 possibly reflecting increased evapotranspiration. Other factors leading to increased $\delta^{18}\text{O}$
420 isotope values could be increased temperature, a change of water source or the (seasonal)
421 migration of the animals. Between Stratum 4a and 3a, which have the highest percentages
422 animals consuming a pure C_4 diet, Stratum 3b encompasses lower $\delta^{13}\text{C}$ values, e.g. in
423 Equids and Bovids. This indicates a period when C_4 grass expansion was not as strong as
424 before or afterwards (Figure 4). In general, the niche separation that is apparent between
425 grazers and browsers during the Holocene, is not driven by the C_4 grazer species alone.
426 Browsers also reacted to changing environmental conditions, but with two different
427 responses – in the mid-Holocene they take in more C_4 while in the late Holocene, they are
428 more distinct with an exclusively C_3 diet.

429 In the following section, the results are compared to other proxy results from Wonderwerk
430 Cave including stable isotopes in ostrich eggshell (OES). microfaunal composition and
431 results of the principal components analysis (PCA) of pollen data from Wonderwerk Cave
432 (Table 1) (Lee-Thorp and Ecker 2015, Scott and Thackeray 2015). The PCA method
433 follows the chronology in Scott and Thackeray (2015) and the same procedures used for
434 dry woodland as is explained in Scott et al. (2012).

435 The early Holocene pollen diagram obtained for Wonderwerk Cave by van Zinderen
 436 Bakker (1982) was re-interpreted by Scott and Thackeray (2015) as consisting of a
 437 moderate Asteraceae/grass ratio (SOM Figure 2). This suggests relatively moist conditions
 438 at first with higher ratios after c. 8ka indicating increasing aridity. In contrast,
 439 micromammal abundances in Wonderwerk Excavation 1, reflect a dry and open scrub
 440 landscape at the onset of the Holocene (Stratum 4d), which then slowly changed into a
 441 woodland savanna (Avery 1981, Thackeray 1984). The Wonderwerk Cave OES $\delta^{18}\text{O}$
 442 record indicates fluctuating early Holocene conditions and an arid to moist shift c. 6ka in
 443 Strata 4b/4aLH (~5.4-6.9ka cal. BP) (Lee-Thorp and Ecker 2015, Scott and Thackeray
 444 2015) (Fig. 5). A dry and open late Holocene is also evident in pollen and isotopic data
 445 from the large speleothem adjacent to Excavation 1 in the cave (Brook et al. 2010, 2015)
 446 and in isotopic data derived from OES (Lee-Thorp and Ecker 2015). Pollen and
 447 micromammals suggest a wetter Stratum 3b (4.4-2.8ka cal. BP), and in contrast an arid
 448 Stratum 3a (<2.3ka BP) (Avery 1981, Thackeray 1984, Scott and Thackeray 2015).

449 Other sites in the arid interior of Southern Africa indicate, in general, similar trends as those
 450 recorded at Wonderwerk Cave, although they are based on shorter or less detailed records.
 451 Rose Cottage Cave further to the eastern highlands and in the grassland biome (Fig. 1),
 452 shows some episodes with lower $\delta^{13}\text{C}$ values for large herbivore enamel in the early
 453 Holocene (Smith et al. 2002). In that case, because of the site's altitude (c. 1600m a.s.l.),
 454 the negative $\delta^{13}\text{C}$ shifts were interpreted as cool episodes. For 11.8 ka onwards, pollen
 455 records from various sites in disparate parts of the interior of South Africa indicate a dry
 456 phase. For example, localities in the Blydefontein Basin to the south-east in the Karoo
 457 (eastern Cape), indicate a dry start to the Holocene (until ca. 5ka) (Scott et al. 2005, 2012).
 458 Pollen from distant localities in the Savanna Biome to the east of Wonderwerk Cave, such
 459 as Wonderkrater, Rietvlei, Tata Vondo and Tswaing Crater, all indicate an expansion of

Kalahari Thornveld (Acocks 1953) around 9.4-7.2 ka, seen as an indicator of aridity (Scott 1993, 1999, 2008, 2016, Scott et al. 2008, Metwally et al. 2014).

The episode of increased mid-Holocene moisture is hinted at in several pollen and isotopic proxy records. For example, pollen evidence for an increased mid-Holocene spread of C₄ grasses comes from grassland pollen in records in the central Namibia (Windhoek) (Scott et al. 1991), from Blydefontein from 5.4ka onwards (Scott et al. 2005, 2012), and in the pollen record from Florisbad, although this sites' dating is based on only seven ¹⁴C dates on peat (Scott and Nyakale 2002, Scott et al. 2012). High $\delta^{13}\text{C}$ values for grazer tooth enamel from Rose Cottage Cave (Smith et al. 2002) further indicate a C₄ grass spread. Around 2-3ka, most interior records show a dry event with reduced summer rainfall (see reviews in Nicholson et al. 2001, Scott et al. 2012).

4.2 Climate in the Summer Rainfall Zone during the Holocene, and its drivers

The summer rainfall zone of South Africa currently receives rainfall during the austral summer, when low pressure attracts easterlies from the Indian Ocean. A review of current hypotheses on vegetation-independent drivers of rainfall suggests multiple forcing mechanisms in the past (Singarayer and Burrough 2015), including shifts of the rainfall zones in South Africa (Scott 1993, Lee-Thorp and Beaumont 1995, Chase et al. 2010, Zhao et al. 2016). Changing rainfall regimes, low CO₂ levels in the atmosphere, increasing aridity and disturbance by herbivory and fire have been proposed as possible explanations for the occurrence and expansion of C₄ plants during the Pliocene and Pleistocene (van Langevelde et al. 2003, Bond et al. 2005, Osborne and Beerling 2006, Schefuß et al. 2003, Dupont et al. 2013, Hare and Sealy 2013, Hoetzel et al. 2013). For the Holocene, the same drivers could have determined expansion of C₄ grasses.

483 With CO₂ values in the mid-Holocene reaching a low of <260 ppm (Fig. 5) [insert Figure
484 5] (Monnin et al. 2001), C₄ grasses had an advantage over C₃ plants at this point in the
485 Holocene. At the same time, the summer insolation at 30°S (Wonderwerk Cave lies at 27°S)
486 is on the threshold changing from minimum to maximum (Fig. 5), possibly further helping
487 the manifestation of the strong summer rainfall regime today, which might not have been
488 fully established earlier in the Holocene. Rising CO₂ levels would further explain the retreat
489 to more woody cover during recent times. The connection of rising CO₂ in the atmosphere
490 and tree cover in South Africa has been demonstrated in the laboratory (Kgope et al. 2010)
491 and in long-term outdoor experiments (Buitenwerf et al. 2012). Kgope et al. (2010)
492 demonstrated that C₃ plants showed increased stem growth and re-sprouting with higher
493 CO₂ levels, whereas C₄ grasses showed no reaction in productivity. A marine record from
494 the Namaqualand mudbelt (Zhao et al. 2016) suggested rainfall zone movements in the
495 Holocene. The record shows low grass pollen and low summer rainfall in the middle
496 catchment area of the Orange River during the early Holocene, and in the mid-Holocene a
497 change to a sub-humid savanna. This was interpreted as reflecting higher summer rainfall
498 in the mid-Holocene, while in the last 2,200 years the records suggests high aridity (Zhao
499 et al. 2016).

500 Regular fires have been suggested as a major factor of C₄ grasses replacing forests,
501 especially in savanna ecosystems (Bond et al. 2005). C₄ grassy ecosystems burn naturally
502 on a regular basis without anthropogenic ignition, although human influence cannot be
503 excluded (Bond et al. 2005). The above-mentioned marine sediment core off Namibia
504 (Zhao et al. 2016) contains a microcharcoal record which could support fire as a driver of
505 mid-Holocene changes to more C₄ grass environments in the summer rainfall zone. It has
506 high microcharcoal concentrations in the early Holocene at the same time as low summer
507 rainfall, but counts are reduced to their lowest in the mid-Holocene (7.6-5.9 cal. BP).

Gradual increase in microcharcoal afterwards (5.9-2.6 cal. BP) is interpreted as increasing fuel capacity due to abundant grasses (Zhao et al. 2016). The mixture of low CO₂ levels, insolation change, increased summer rainfall and increased fire could all explain the vegetation changes seen in the Wonderwerk Cave record, but it is impossible from our data to distinguish if one factor is the main driver and what feedback mechanism might be playing a role, or if a combination of several factors was necessary to drive vegetation change.

4.3 Implications for the Wonderwerk Cave cultural record

The earliest Holocene lithic industry, the Oakhurst, present in Stratum 4d, is significantly different in techno-typology compared to the overlying Wilton. While the Oakhurst has large scrapers of local banded ironstone, small microlithic scrapers and bladelets dominate the Wilton assemblage (Thackeray 1981, Humphrey and Thackeray 1983). Environmental proxies tentatively indicate more arid bush and scrub in Stratum 4d and more semi-arid savannah woodland in Stratum 4c, but it is uncertain how these shifts might have influenced the technology and other aspects of the human populations. A shift in the percentage of the dominant raw material and tool types appears in the mid-Holocene, whereas more bladelets on chert are found from Stratum 4aLH onwards, together with a higher artefact density (Thackeray 1981, Humphrey and Thackeray 1983). This change has been noted at other Wilton sites in South Africa, and attributed to the adoption of different hunting strategies during the supposed mid-Holocene climatic optimum (Deacon 1982). At Wonderwerk Cave, a wet episode followed marked by increasing grassland and an increase in grazing species, such as it might be connected to a change in hunting strategy or seasonal use of the cave. Strata 4aLH and 4a have the highest densities of cultural artefacts in any deposit at Wonderwerk Cave (Thackeray 1981, Humphrey and Thackeray 1983). The wet spell and expansion of grassland at this time probably improved resource availability for hunter-

gatherers at this time, such that they made more intensive use of the cave and/or increased their population numbers. Another development is the introduction of ceramics during the Wilton in Strata 3a and 2b (Thackeray 1981, Humphrey and Thackeray 1983), showing that the hunter-gatherers might have been in contact with herders, who spread from central to southern Africa during this period. Proxies from Wonderwerk Cave and other records show high aridity around 2-3ka BP, which would have influenced the resources available for hunter-gatherers as well as the herders and their livestock.

5. Conclusion

This extensive stable isotope study reveals a strengthening of the grazer-browser niche partitioning that developed during the Holocene at Wonderwerk Cave. It is, however, a dynamic period, whose changing nature is important for interpreting Pleistocene records. In summary, the early Holocene environment at Wonderwerk Cave was semi-arid to arid with more C₃ plant cover than the following mid to late Holocene, where grassland expansion reached a maximum after 6ka cal. BP and climate fluctuated, including short mesic events. The later Holocene shows a dominance of grazers and an overall trend of increasing aridification, but with fluctuations, reaching a peak around 2-3ka cal. BP. The Holocene was therefore not a stagnant period in the interior of southern Africa, but fostered the development of the modern niches of grazers and browsers and probably influenced the lifestyle of past human populations inhabiting the region.

Acknowledgements

We are grateful to David Morris (McGregor Museum Kimberley) for granting permission for stable isotope sampling and to Andy Gledhill (University of Bradford) for stable isotope measurements. All enamel samples were exported for analysis under a permit granted by

SAHRA. We thank Michael Chazan (University of Toronto) for constructive discussions of the Wonderwerk Cave Holocene sequence and the reviewer for their useful comments.

Funding: This work is part of a DPhil thesis by ME, for which funding was provided by the German Academic Exchange Service (DAAD), the Boise Fund Trust (University of Oxford) and a Quaternary Research Association (QRA) New Research Workers' Award. Research at Wonderwerk Cave, including on the fauna used in this study, is funded by grants from the Canadian Social Science and Humanities Research Council to Michael Chazan. LS was supported by the National Research Foundation of South Africa. Any opinion, finding, and conclusion or recommendation expressed in this material is that of the authors, and the NRF does not accept any liability in this regard.

Supplementary Online Material

T1 All individual $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ stable isotope results.

F1 Bar diagram showing loadings of pollen taxa at Wonderwerk Cave.

References

Acocks, J.P.H. 1953. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa*, 28, 1-192.

Apps, P. 2012. *Smither's Mammals of Southern Africa. A Field Guide*. Cape Town: Struik Nature.

Avery, D.M. 1981. Holocene microfaunal faunas from the northern Cape Province, South Africa. *South African Journal of Science*, 77, 265-273.

Beaumont, P.B. 1990. Wonderwerk Cave. In: Beaumont, P.B., Morris, D. (eds.), *Guide to the Archaeological Sites in the Northern Cape*, 1-70. Kimberley: McGregor Museum.

578 Beaumont, P.B. 2004. Wonderwerk Cave. In: Morris, D., Beaumont, P.B. (eds.),
579 *Archaeology in the Northern Cape: Some Key Sites*, 31-36. Kimberley: McGregor
580 Museum.

581 Beaumont, P.B., Vogel, J.C. 2006. On a timescale for the past million years of human
582 history in central South Africa. *South African Journal of Science*, 102, 217-228.

583 Berger, A. 1992. Orbital variations and insolation database. *IGBP PAGES/World Data*
584 *Center-A for Paleoclimatology Data Contribution Series*, 92(007).

585 Bond, W.J., Woodward, F.I., Midgley, G.F. 2005. The global distribution of ecosystems in
586 a world without fire. *New Phytologist*, 165(2), 525-538.

587 Brink, J.S. 2005. The evolution of the black wildebeest, *Connochaetes gnou*, and modern
588 large mammal faunas in central Southern Africa. Doctoral dissertation, University of
589 Stellenbosch.

590 Brink, J.S. 2016. Faunal evidence for mid- and late Quaternary environmental change in
591 southern Africa. In: Knight, J. and Grab, S.W. (eds) *Quaternary Environmental Change in*
592 *Southern Africa: Physical and Human Dimensions*. Cambridge University Press, pp. 286-
593 307.

594 Brink, J.S., Lee-Thorp, J. 1992. The feeding niche of an extinct springbok, *Antidorcas*
595 *bondi* (Antilopini, Bovidae), and its palaeoenvironmental meaning. *South African Journal*
596 *of Science*, 88(4), 227-229.

597 Brink J., Holt S., Horwitz L.K. 2016. The Oldowan and early Acheulean mammalian fauna
598 of Wonderwerk Cave (Northern Cape Province, South Africa). *African Archaeological*
599 *Review*, 33(3), 223–250.

600 Brook, G.A., Scott, L., Railsback, L.B., Goddard, E.A. 2010. A 35ka pollen and isotope
601 record of environmental change along the southern margin of the Kalahari from a
602 stalagmite and animal dung deposits in Wonderwerk Cave, South Africa. *Journal of Arid*
603 *Environments*, 74, 870–884.

604 Brook, G.A., Railsback, L.B., Scott, L., Voarintsoa, N.R.G., Liang, F. 2015. Late Holocene
605 stalagmite and tufa climate records for Wonderwerk Cave: Relationships between
606 archaeology and climate in southern Africa. *African Archaeological Review*, 32, 669-700.

607 Buitenwerf, R., Bond, W.J., Stevens, N., Trollope, W.S.W. 2012. Increased tree densities
608 in South African savannas: >50 years of data suggests CO₂ as a driver. *Global Change*
609 *Biology*, 18(2), 675-684.

610 Burrough, S.L., Thomas, D.S.G. 2013. Central southern Africa at the time of the African
611 Humid Period: a new analysis of Holocene palaeoenvironmental and palaeoclimate data.
612 *Quaternary Science Reviews*, 80, 29-46.

613 Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V.,
614 Ehleringer, J.R. 1997. Global vegetation change through the Miocene/Pliocene boundary.
615 *Nature*, 389(6647), 153-158.

616 Chase, B.M., Meadows, M.E. 2007. Late Quaternary dynamics of southern Africa's winter
617 rainfall zone. *Earth-Science Reviews*, 84(3), 103-138.

618 Chase, B.M., Meadows, M.E., Carr, A.S., Reimer, P.J. 2010. Evidence for progressive
619 Holocene aridification in southern Africa recorded in Namibian hyrax middens:
620 implications for African Monsoon dynamics and the “African Humid Period”. *Quaternary*
621 *Research*, 74(1), 36-45.

622 Chevalier, M., Chase, B.M. 2015. Southeast African records reveal a coherent shift from
623 high-to low-latitude forcing mechanisms along the east African margin across last glacial–
624 interglacial transition. *Quaternary Science Reviews*, 125, 117-130.

625 Cockcroft, M.J., Wilkinson, M.J., Tyson, P.D. 1987. The application of a present-day
626 climatic model to the late Quaternary in southern Africa. *Climate Change*, 161-181.

627 Codron, D., Brink, J.S., Rossouw, L., Clauss, M. 2008. The evolution of ecological
628 specialization in southern African ungulates: competition- or physical environmental
629 turnover? *Oikos*, 117, 344-353.

630 Dansgaard, W. 1964. Stable isotopes in precipitation. *Tellus A*, 16(4).

631 Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., Tu, K.P. 2002. Stable
632 isotopes in plant ecology. *Annual Review of Ecology and Systematics*, 33(1), 507-559.

633 Deacon, J.C.G. 1982. The Later Stone Age in the southern Cape South Africa. Doctoral
634 dissertation, University of Cape Town.

635 Du Toit, J.T. 1993. The feeding ecology of a very small ruminant, the steenbok (*Raphicerus*
636 *campestris*). *African Journal of Ecology*, 31, 35–48.

637 Dupont, L.M., Rommerskirchen, F., Mollenhauer, G., Schefuß, E. 2013. Miocene to
638 Pliocene changes in South African hydrology and vegetation in relation to the expansion
639 of C4 plants. *Earth and Planetary Science Letters*, 375, 408-417.

640 Ecker, M. 2016. Two million years of environmental change: a case study from
641 Wonderwerk Cave, Northern Cape, South Africa. DPhil thesis, University of Oxford.

642 Ecker, M., Brink, J., Chazan, M., Horwitz, L.K., Lee-Thorp, J.A. 2017. Radiocarbon dates
643 constrain the timing of environmental and cultural shifts in the Holocene strata of
644 Wonderwerk Cave, South Africa. *Radiocarbon* 59 (4), 1067-1086.

645 EPICA Community Members 2010. Stable oxygen isotopes of ice core EDML.
 646 doi:10.1594/PANGAEA.754444.

647 Faith, J.T. 2011. Ungulate community richness, grazer extinctions, and human subsistence
 648 behaviour in southern Africa's Cape Floral Region. *Palaeogeography, Palaeoclimatology,*
 649 *Palaeoecology*, 306, 219–227.

650 Faith J.T. 2013. Ungulate diversity and precipitation history since the Last Glacial
 651 Maximum in the Western Cape, South Africa. *Quaternary Science Reviews*, 68, 191-199

652 Faith, J.T. 2014. Late Pleistocene and Holocene mammal extinctions on continental Africa.
 653 *Earth-Science Reviews*, 128, 105-121.

654 Faith J.T., Behrensmeyer K.A. 2013. Climate change and faunal turnover: Testing the
 655 mechanics of the turnover-pulse hypothesis with South African fossil data. *Paleobiology*,
 656 39(4), 609-627.

657 Farquhar, G.D., Ehleringer, J.R., Hubick, K.T. 1989. Carbon isotope discrimination and
 658 photosynthesis. *Annual Review of Plant Biology*, 40(1), 503-537.

659 Gagnon, M., Chew, A.E. 2000. Dietary preferences in extant African Bovidae. *Journal of*
 660 *Mammalogy*, 81(2), 490-511.

661 Gonfiantini, R., Gratziu, S. and Tongiorgi, E., 1965. Oxygen isotopic composition of water
 662 in leaves. *Isotopes and Radiation in Soil-Plant Nutrition Studies*, 405-410.

663 Hare, V., Sealy, J. 2013. Middle Pleistocene dynamics of southern Africa's winter rainfall
 664 zone from $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of Hoedjiespunt faunal enamel. *Palaeogeography,*
 665 *Palaeoclimatology, Palaeoecology*, 374, 72–80.

666 Humphreys, A.J.B., Thackeray, A.I. 1983. *Ghaap and Gariep. Later Stone Age Studies in*
 667 *the Northern Cape*. Cape Town: South African Archaeological Society Monograph No. 2.

668 Hoetzel, S., Dupont, L., Schefuß, E., Rommerskirchen, F., Wefer, G. 2013. The role of fire
669 in Miocene to Pliocene C₄ grassland and ecosystem evolution. *Nature Geoscience*, 6(12),
670 1027-1030.

671 Horwitz, L.K., Chazan, M. 2015. Past and present at Wonderwerk Cave (Northern Cape
672 Province, South Africa). *African Archaeological Review*, 32(4), 595-612.

673 Kgope, B.S., Bond, W.J., Midgley, G.F. 2010. Growth responses of African savanna trees
674 implicate atmospheric CO₂ as a driver of past and current changes in savanna tree cover.
675 *Austral Ecology*, 35(4), 451-463.

676 Kingdon, J. 1982. *East African Mammals. An Atlas of Evolution in East Africa, Vol. 3*. New
677 York: Academic Press.

678 Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., Kalina, J. 2013.
679 *Mammals of Africa* (Vol. 1-6). A & C Black.

680 Kohn, M.J., Schoeninger, M.J., Valley, J.W. 1996. Herbivore tooth oxygen isotope
681 compositions: effects of diet and physiology. *Geochimica et Cosmochimica Acta*, 60(20),
682 3889-3896.

683 Kohn, M.J. 2010. Carbon isotope compositions of terrestrial C₃ plants as indicators of
684 (paleo) ecology and (paleo) climate. *Proceedings of the National Academy of Sciences*,
685 107(46), 19691-19695.

686 Lee-Thorp, J.A., van der Merwe, N.J. 1991. Aspects of the chemistry of modern and fossil
687 biological apatites. *Journal of Archaeological Science*, 18(3), 343-354.

688 Lee-Thorp, J.A., Beaumont, P.B. 1995. Vegetation and seasonality shifts during the late
689 Quaternary deduced from ¹³C/¹²C ratios of grazers at Equus Cave, South Africa.
690 *Quaternary Research*, 43(3), 426-432.

691 Lee-Thorp, J., Sponheimer, M. 2003. Three case studies used to reassess the reliability of
692 fossil bone and enamel isotope signals for paleodietary studies. *Journal of Anthropological*
693 *Archaeology*, 22(3), 208-216.

694 Lee-Thorp, J.A., Ecker, M. 2015. Holocene climate and environmental changes from stable
695 isotopes in ostrich egg shell at Wonderwerk Cave, South Africa. *African Archaeological*
696 *Review*, 32(4):793-811.

697 Lee-Thorp, J.A., Holmgren, K., Lauritzen, S.E., Linge, H., Moberg, A., Partridge, T.C.,
698 Stevenson, C., Tyson, P.D. 2001. Rapid climate shifts in the southern African interior
699 throughout the mid to late Holocene. *Geophysical Research Letters*, 28(23), 4507-4510.

700 Lee-Thorp, J.A., Sponheimer, M., Luyt, J. 2007. Tracking changing environments using
701 stable carbon isotopes in fossil tooth enamel: an example from the South African hominin
702 sites. *Journal of human evolution*, 53(5), 595-601.

703 Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R. 2006. A stable
704 isotope aridity index for terrestrial environments. *Proceedings of the National Academy of*
705 *Sciences*, 103(30), 11201-11205.

706 Longinelli, A. 1984. *Oxygen Isotopic Composition of Mammal Bones as a New Tool for*
707 *Studying Ratios of Paleoenvironmental Water and Paleoclimates*. Vienna: International
708 Atomic Energy Agency.

709 Metwally, A.A., Scott, L., Neumann, F.H., Bamford, M.K., Oberhänsli, H. 2014. Holocene
710 palynology and palaeoenvironments in the Savanna Biome at Tswaing Crater, central South
711 Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 402, 125-135.

712 Monnin, E., Indermühle, A., Dällenbach, A., Flückiger, J., Stauffer, B., Stocker, T.F.,
713 Raynaud, D., Barnola, J.-M. 2001. Atmospheric CO₂ concentrations over the last glacial
714 termination. *Science*, 291(5501), 112-114.

715 Monnin, E. 2006. EPICA Dome C high resolution carbon dioxide concentrations.
716 doi:10.1594/PANGAEA.472488.

717 Mucina, L., Rutherford, M.C. 2006. *The Vegetation of South Africa, Lesotho and*
718 *Swaziland*. Pretoria: South African National Biodiversity Institute.

719 Nicholson, S.E. 2011. *Dryland Climatology*. Cambridge: Cambridge University Press.

720 Osborne, C.P., Beerling, D.J. 2006. Nature's green revolution: the remarkable evolutionary
721 rise of C₄ plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
722 361(1465), 173-194.

723 R Core Team 2013. R: A Language and Environment For Statistical Computing. R
724 Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

725 Rozanski, K., Araguás-Araguás, L., Gonfiantini, R. 1993. Isotopic patterns in modern
726 global precipitation. *Climate Change in Continental Isotopic Records*, 1-36.

727 Rutherford, M.C. 1997. Categorization of biomes. *Vegetation of Southern Africa*, 91-98.

728 Schefuß, E., Schouten, S., Jansen, J.F., Damsté, J.S.S. 2003. African vegetation controlled
729 by tropical sea surface temperatures in the mid-Pleistocene period. *Nature*, 422(6930), 418-
730 421.

731 Scott, L. 1987. Pollen analysis of hyena coprolites and sediments from Equus Cave, Taung,
732 southern Kalahari (South Africa). *Quaternary Research*, 28(1), 144-156.

733 Scott, L., 1993. Palynological evidence for Late Quaternary warming episodes in southern
734 Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 101(3-4), 229-235.

735 Scott, L. 1999. Vegetation history and climate in the Savanna biome South Africa since
736 190,000 ka: a comparison of pollen data from the Tswaing Crater (the Pretoria Saltpan) and
737 Wonderkrater. *Quaternary International*, 57-8, 215–223.

738 Scott, L. 2016. Fluctuations of vegetation and climate over the last 75 000 years in the
739 Savanna Biome, South Africa: Tswaing Crater and Wonderkrater pollen sequences
740 reviewed. *Quaternary Science Reviews*, 145, 117-133.

741 Scott, L. Nyakale, M. 2002. Pollen indications of Holocene palaeoenvironments at
742 Florisbad spring in the central Free State, South Africa. *The Holocene*, 12(4), 497-503.

743 Scott, L., Lee-Thorp, J.A. 2004. Holocene climatic trends and rhythms in southern Africa.
744 In: Batterbee, R., Gasse, F. (eds), *Past Climatic Variability through Europe and Africa*,
745 691-699. Netherlands: Springer.

746 Scott, L. Thackeray, J.F. 2015. Palynology of Holocene Deposits in Excavation 1 at
747 Wonderwerk Cave, Northern Cape (South Africa). *African Archaeological Review*,
748 32(4):839-855.

749 Scott, L., Cooremans, B., De Wet, J.S., Vogel, J.C. 1991. Holocene environmental changes
750 in Namibia inferred from pollen analysis of swamp and lake deposits. *The Holocene*, 1(1),
751 8-13.

752 Scott, L., Bousman, C.B., Nyakale, M. 2005. Holocene pollen from swamp, cave and hyrax
753 dung deposits at Blydefontein (Kikvorsberge), Karoo, South Africa. *Quaternary*
754 *International*, 129(1), 49-59.

755 Scott, L., Neumann, F.H., Brook, G.A., Bousman, C.B., Norström, E., Metwally, A.A.
 756 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years
 757 in Southern Africa. *Quaternary Science Reviews*, 32, 100-118.

758 Singarayer, J.S., Burrough, S.L. 2015. Interhemispheric dynamics of the African rainbelt
 759 during the late Quaternary. *Quaternary Science Reviews*, 124, 48-67.

760 Skead, C.J. 1980. *Historical Mammal Incidence in the Cape Province*. Cape Town,
 761 Republic of South Africa: Department of Nature and Environmental Conservation of the
 762 Provincial Administration of the Cape of Good Hope.

763 Skinner, J.D., Chimimba, C.T. 2005. *The Mammals of the Southern African Subregion*.
 764 Cambridge: Cambridge University Press.

765 Smith, J.M., Lee-Thorp, J.A., Sealy, J.C. 2002. Stable carbon and oxygen isotopic evidence
 766 for late Pleistocene to middle Holocene climatic fluctuations in the interior of southern
 767 Africa. *Journal of Quaternary Science*, 17(7), 683-695.

768 Sponheimer, M. 1999. Isotopic ecology of the Makapansgat Limeworks fauna. PhD thesis,
 769 Rutgers University NJ.

770 Sponheimer, M., Lee-Thorp, J.A. 1999. Oxygen isotopes in enamel carbonate and their
 771 ecological significance. *Journal of Archaeological Science*, 26(6), 723-728.

772 Sponheimer, M., Lee-Thorp, J.A., DeRuiter, D.J., Smith, J.M., van der Merwe, N.J., Reed,
 773 K., Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberger, C., Marcus, W. 2003. Diets
 774 of Southern African Bovidae: Stable isotope evidence. *Journal of Mammalogy*, 84(2), 471-
 775 479.

776 Thackeray, A.I. 1981. The Holocene cultural sequence in the Northern Cape Province,
 777 South Africa. Ph.D. thesis, Yale University.

778 Thackeray, J.F. 1984. *Man, animals and extinctions: the analysis of Holocene faunal*
779 *remains from Wonderwerk Cave, South Africa*. Ph.D. thesis, Yale University.

780 Thackeray, J.F. 2015. Faunal remains from Holocene deposits, Excavation 1, Wonderwerk
781 Cave, South Africa. *African Archaeological Review*, 32(4):729-750.

782 Thackeray, J.F., Lee-Thorp, J.A. 1992. Isotopic analysis of equid teeth from Wonderwerk
783 Cave, northern Cape Province, South Africa. *Palaeogeography, Palaeoclimatology,*
784 *Palaeoecology*, 99, 141-150.

785 van Langevelde, F., Van De Vijver, C.A., Kumar, L., Van De Koppel, J., De Ridder, N.,
786 Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.
787 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84(2),
788 337-350.

789 van Zinderen Bakker, E.M. 1982. Pollen analytical studies of the Wonderwerk Cave, South
790 Africa. *Pollen et Spores*, 24, 235-250.

791 Zazzo, A., Balasse, M., Patterson, W.P. 2005. High-resolution $\delta^{13}\text{C}$ intratooth profiles in
792 bovine enamel: Implications for mineralization pattern and isotopic attenuation.
793 *Geochimica et Cosmochimica Acta*, 69(14), 3631-3642.

794 Zhao, X., Dupont, L., Schefuß, E., Meadows, M.E., Hahn, A., Wefer, G. 2016. Holocene
795 vegetation and climate variability in the winter and summer rainfall zones of South Africa.
796 *The Holocene*, 26(6), 843-857.

Figure captions

Fig. 1: Location of Wonderwerk Cave, as well as environmental records mentioned in the text. Rose Cottage Cave has a stable isotope record on enamel, all other records represent pollen data. The marine core GeoB8331 additionally has a microcharcoal record. The dashed lines mark the approximate boundary of the winter rainfall zone, and the approximate boundary of the year-round rainfall zone to the summer rainfall zone, respectively (Chase and Meadows 2007). Biome distribution after Rutherford (1997) and Mucina and Rutherford (2006).

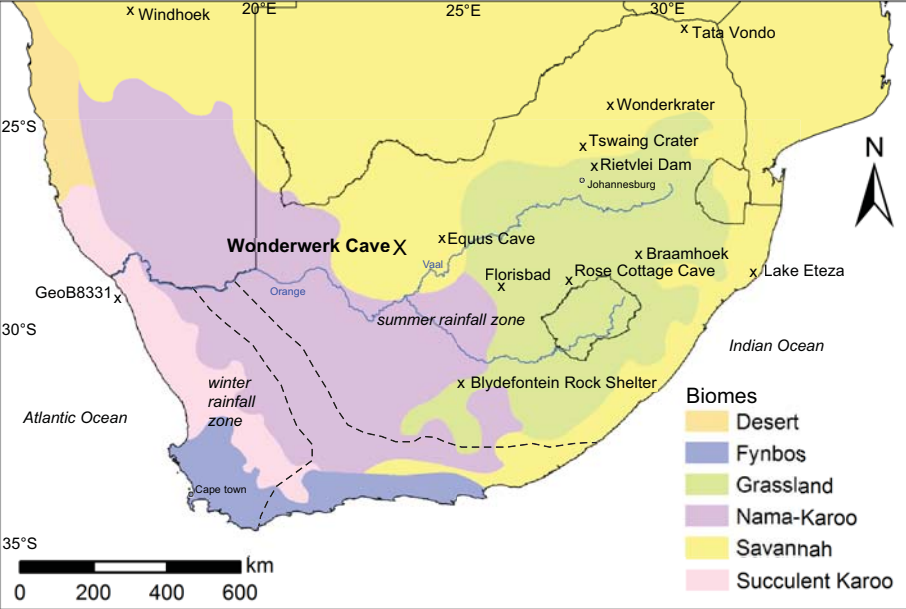
Fig. 2: Bivariate plot of individual enamel samples carbon (x-axis) and oxygen (y-axis) stable isotope results for Strata 1-4d of Excavation 1 at Wonderwerk Cave. Colours and symbol refer to the analysed species (see legend). Note how species predominantly show $\delta^{13}\text{C}$ values indicating a diet of C_4 or C_3 plants, with few mixed-feeding individuals.

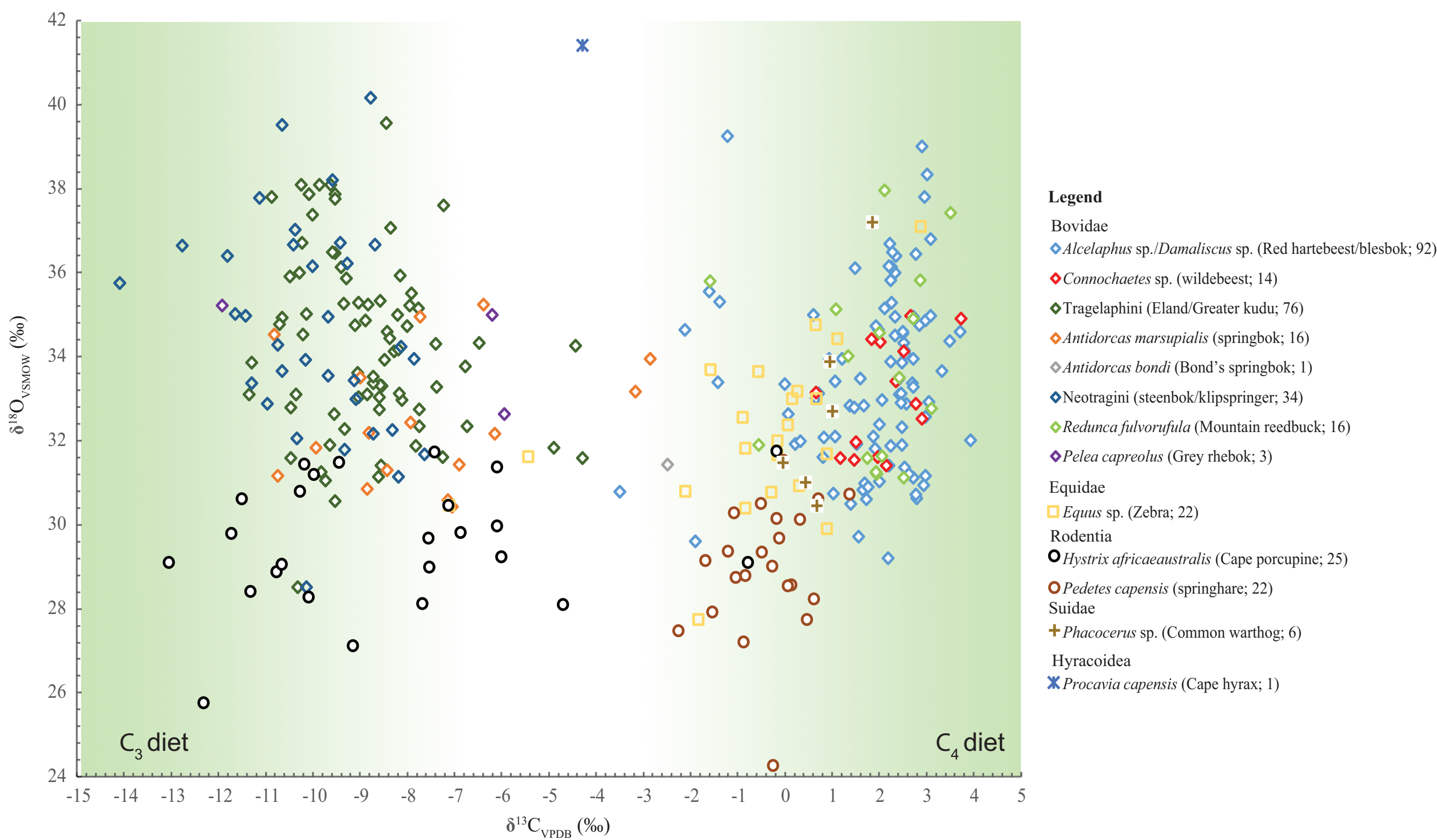
Fig. 3: Box and Whisker plots of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (x-axis) per Stratum (y-axis) of Excavation 1 at Wonderwerk Cave for Alcelaphini, *Hystrix africaeaustralis*, *Raphicerus campestris* and Tragelaphini. The box represents the third percentile with the median marked by a line; the points are the individual measurements. Open circles are outliers. In the middle part the radiocarbon age is given for each Stratum in cal. BP (based on Ecker et al. 2017).

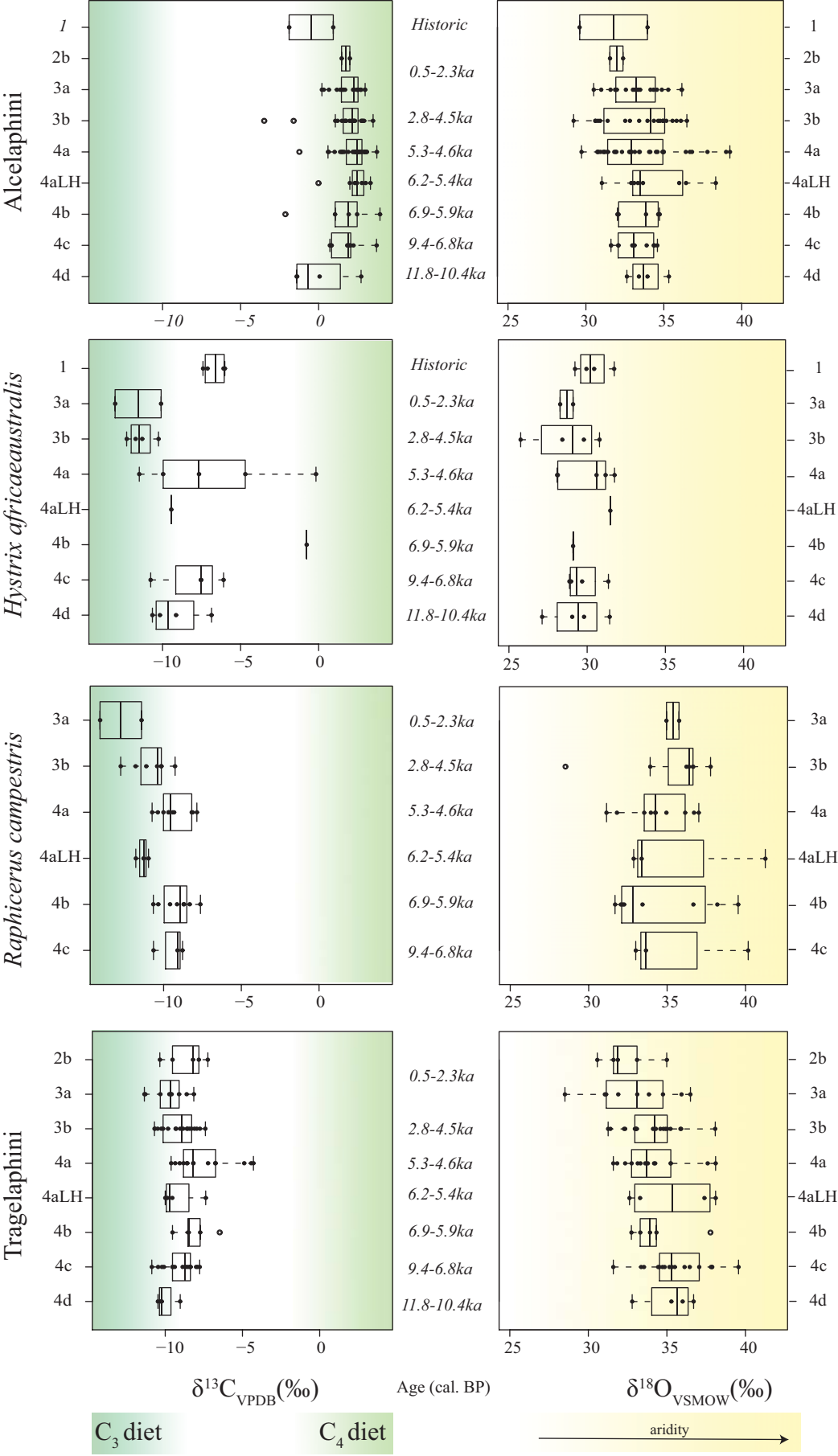
Figure 4: Percentage of C_3 , C_4 and mixed-feeding bovid specimen per stratum from oldest (Stratum 4d) to youngest (Stratum 2b) at Wonderwerk Cave, based on the individual measured $\delta^{13}\text{C}$ values. The definitions for the categories are: Browser $\delta^{13}\text{C} > -9\text{‰}$; Grazer $\delta^{13}\text{C} < -3\text{‰}$; mixed feeding $\delta^{13}\text{C} < -9\text{‰}$ and $> -3\text{‰}$ (after Lee-Thorp et al. 2007).

Fig. 5: Global climate parameters and Wonderwerk Cave data of the last 12ka years. (A) December insolation at 30°S (Berger 1992); (B) calculated $\delta^{18}\text{O}$ (‰) from the EDML ice core (EPICA community members 2010); (C) pCO_2 from EPICA Dome C ice core (Monnin

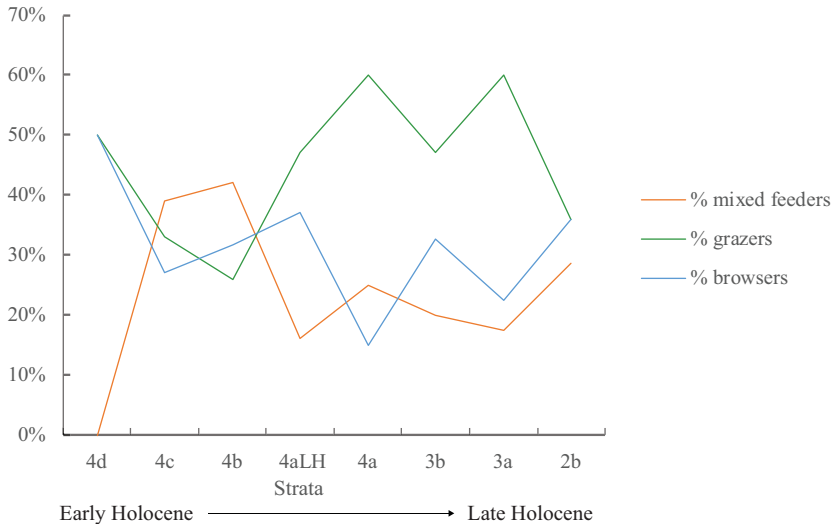
821 et al. 2006); (D) $\delta^{18}\text{O}$ (‰) from OES in Wonderwerk Cave as aridity indicator (Lee-Thorp
822 and Ecker 2015); Percentage of bovids with a predominant C_4 diet compared to the overall
823 bovid sample in this study; (F) PCA index based on pollen composition in Wonderwerk
824 Cave indicating moisture for the Holocene part of the sequence based on the data and
825 chronology used in Scott and Thackeray (2015). The shaded area marks the time of C_4
826 grassland expansion and wet spell in the mid Holocene, as indicated by enamel isotopes in
827 this study.

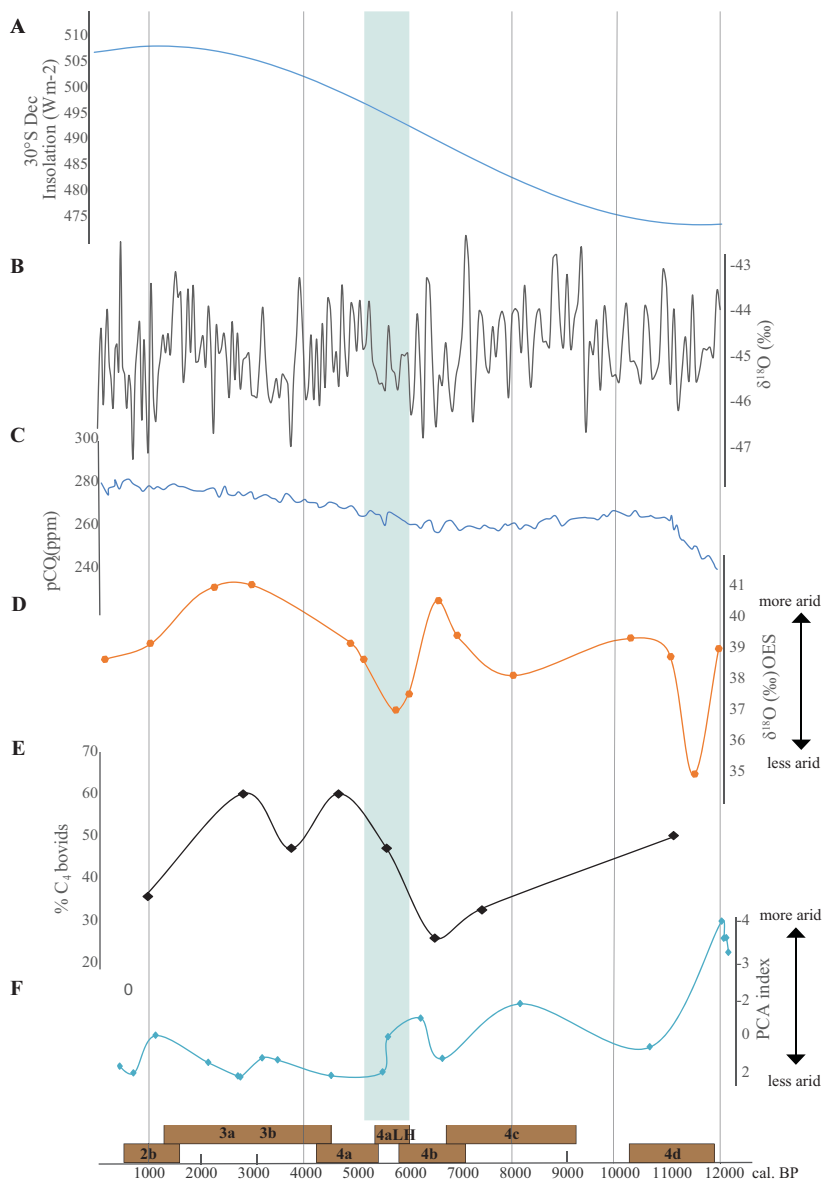






Percentage of full assemblage





A 12,000 year Record of Changes in Herbivore Niche Separation and Palaeoclimate (Wonderwerk Cave, South Africa)

Michaela Ecker^{1*}, James Brink^{2,3}, Liora Kolska Horwitz⁴, Louis Scott⁵, Julia A. Lee-Thorp¹

1 Research Laboratory for Archaeology and the History of Art, University of Oxford, UK

2 Florisbad Quaternary Research Department, National Museum, Bloemfontein, South Africa

3 Centre for Environmental Management, University of the Free State, Bloemfontein, South Africa

4 National Natural History Collections, Faculty of Life Sciences, The Hebrew University, Jerusalem, Israel

5 Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa

Supplementary Table 1: Stable isotope data for faunal enamel samples of Excavation 1 (Stratum 1-4d) at Wonderwerk Cave, indicating specimen number (SPF), species identification, sample origin and tooth type.

Sample	$\delta^{13}\text{C}_{\text{VPDB}}$ ‰	$\delta^{18}\text{O}_{\text{VSMOW}}$ ‰	SPF #	Square	Stratum	Species	Tooth
ME542	-1.9	29.6	8294	R22	1b	<i>A. buselaphus</i>	P ^{3/4}
ME525	2.0	32.4	8280	Q23	2bII	<i>A. buselaphus</i>	R M ₂
ME474	1.4	30.5	8258	S27	3aI	<i>A. buselaphus</i>	L M ₁
ME503	2.7	33.4	8259	S27	3aI	<i>A. buselaphus</i>	L M ^{1/2}
ME477	1.6	33.5	8232	S27	3aII	<i>A. buselaphus</i>	L M ₂
ME495	3.0	34.9	8264	T25	3aII	<i>A. buselaphus</i>	R P ₃
ME518	1.5	31.9	8267	T27	3aII	<i>A. buselaphus</i>	R M ²
ME505	2.3	31.9	8233	S27	3aIII	<i>A. buselaphus</i>	M ₂
ME441	2.2	35.8	8182	T28	3bI	<i>A. buselaphus</i>	R P ₃
ME442	1.5	36.1	8183	T28	3bI	<i>A. buselaphus</i>	R M ^{1/2}
ME 426	2.2	29.2	8214	T25	3bI	<i>A. buselaphus</i>	L M ¹
ME421	2.7	34.9	8199	T27	3bI	<i>A. buselaphus</i>	L M ¹
ME447	1.7	30.6	8212	T25	3bI	<i>A. buselaphus</i>	L M ₂

ME434	2.8	30.6	8407	T27	3bII	<i>A. buselaphus</i>	L M ^x
ME425	2.0	34.6	8198	S28	3bII	<i>A. buselaphus</i>	R M ¹
ME428	1.1	33.4	8202	T27	3bII	<i>A. buselaphus</i>	L M ₃
ME376	3.0	31.2	8428	P21	4a	<i>A. buselaphus</i>	R M ¹
ME342	2.6	32.9	8116	P21	4a	<i>A. buselaphus</i>	L M ₃
ME326	2.7	31.1	8119	P20	4a	<i>A. buselaphus</i>	L P ³
ME337	3.1	35.0	8129	O19	4a	<i>A. buselaphus</i>	R M ₃
ME338	2.4	33.5	8125	O22	4a	<i>A. buselaphus</i>	R M ³
ME341	2.5	31.4	8128	P19	4a	<i>A. buselaphus</i>	L M ₃
ME344	1.7	30.8	8124	O22	4a	<i>A. buselaphus</i>	R M ₂
ME381	1.9	31.8	8123	O22	4a	<i>A. buselaphus</i>	P ⁴
ME371	1.4	32.8	8089	T26	4aI	<i>A. buselaphus</i>	L M ¹
ME336	2.4	36.4	8088	T26	4aI	<i>A. buselaphus</i>	L M ³
ME334	2.3	34.5	8102	Q23	4aI	<i>A. buselaphus</i>	R M ₂
ME388	1.5	32.8	8155	Q22	4aII	<i>A. buselaphus</i>	L M ³
ME350	3.1	32.9	8139	S24	4aIV	<i>A. buselaphus</i>	M
ME360	2.9	30.9	8142	Q22	4aIV	<i>A. buselaphus</i>	L M ₁
ME301	0.0	33.3	8177	R25	4aLF	<i>A. buselaphus</i>	R M ¹
ME302	2.4	33.1	8172	R23	4aLH	<i>A. buselaphus</i>	L M ³
ME308	2.8	36.4	8176	S25	4aLH	<i>A. buselaphus</i>	L M ₂
ME309	2.0	31.0	8171	Q23	4aLH	<i>A. buselaphus</i>	R M ₂
ME271	1.9	34.7	8064	P23	4b	medium sized Alcelaphini	M _{2/3}
ME269	2.5	33.9	8056	P21	4b	<i>A. buselaphus</i>	L M ₂
ME275	-2.1	34.6	8037	S25	4bII	<i>A. buselaphus</i>	L P ₂
ME227	3.7	34.6	8309	P26	4c UP	<i>A. buselaphus</i>	R M ₁
ME216	0.8	32.1	8307	N26	4cI	<i>A. buselaphus</i>	R M ¹
ME485	3.0	32.6	8394	R24	3aI	<i>A. buselaphus</i> (cf)	M
ME489	2.5	33.1	8392	S21	3aI	<i>A. buselaphus</i> (cf)	M ^x
ME491	2.3	35.3	8403	T26	3aII	<i>A. buselaphus</i> (cf)	L P ⁴
ME400	2.2	36.7	8122	O20	4a	<i>A. buselaphus</i> (cf)	P ₂
ME310	2.3	36.0	8384	R23	4aLH	<i>A. buselaphus</i> (cf)	M ²
ME554	0.9	34.0	8435	S21	1a	Alcelaphini	M ^x

ME492	0.2	31.9	8397	T25	3aI	Alcelaphini	M
ME496	2.7	33.3	8391	R22	3aI	Alcelaphini	M
ME509	2.5	34.3	8257	T22	3aI	medium sized Alcelaphini	R M ³
ME511	2.3	36.1	8256	T22	3aI	Alcelaphini	M
ME512	2.5	34.2	8242	R22	3aI	Alcelaphini	M
ME513	1.7	31.0	8396	S22	3aI	Alcelaphini	M
ME519	2.5	34.6	8398	Q21	3aI	Alcelaphini	frag
ME484	2.2	36.2	8395	S27	3aII	Alcelaphini	M3
ME516	0.7	33.0	8224	T25	3aIII	<i>Damaliscus</i> sp.	M _{1/2}
ME433	3.5	34.4	8190	T26	3bI	Alcelaphini	M ^x
ME435	2.1	35.2	8185	T28	3bI	Alcelaphini	M ^x
ME444	-3.5	30.8	8420	Q23	3bI	Alcelaphini	M
ME456	2.3	35.0	8186	T28	3bI	Alcelaphini	M ^x
ME459	2.8	34.8	8210	R24	3bI	Alcelaphini	M
ME416	1.8	30.9	8408	T27	3bII	Alcelaphini	M
ME424	2.3	36.5	8413	S27	3bII	Alcelaphini	M
ME438	1.7	32.8	8205	T27	3bII	Alcelaphini	M _x
ME460	-1.6	35.6	8406	T28	3bII	Alcelaphini	M
ME335	1.6	29.7	8127	O24	4a	Alcelaphini	M _{2/3}
ME370	2.6	34.1	8112	P23	4a	Alcelaphini	M _x
ME384	2.5	32.3	8120	P20	4a	Alcelaphini	M
ME366	3.1	36.8	8091	T25	4aI	Alcelaphini	M _x
ME369	-1.2	39.2	8078	T28	4aI	Alcelaphini	M _x
ME383	2.5	34.6	8101	R24	4aI	Alcelaphini	M
ME393	2.5	31.9	8097	S21	4aI	Alcelaphini	M _x
ME327	3.0	37.8	8082	T26	4aI	Alcelaphini	M ^x
ME333	2.2	31.4	8083	T26	4aI	Alcelaphini	M _x
ME351	0.6	35.0	8150	T28	4aII	Alcelaphini	L M ₃
ME331	2.6	31.2	8165	S22	4aIII	Alcelaphini	M _x
ME347	1.0	30.8	8160	S23	4aIII	Alcelaphini	M ₃
ME367	2.9	39.0	8148	S24	4aIV	Alcelaphini	M
ME391	2.8	30.7	8146	S23	4aIV	Alcelaphini	R P ₄

ME303	3.3	33.7	8170	R25	4aLF	Alcelaphini	M _x
ME307	2.5	32.9	8181	R24	4aLF	Alcelaphini	M _x
ME311	3.0	38.3	8382	S25	4aLH	Alcelaphini	M _x
ME286	3.9	32.0	8385	O21	4b	Alcelaphini	P ₂
ME279	1.1	32.1	8039	S24	4bII	Alcelaphini (cf)	frag
ME220	0.8	31.6	8029	O24	4c	Alcelaphini (cf)	M
ME226	0.7	33.1	8026	P20	4c	Alcelaphini (cf)	P _x
ME221	2.2	33.9	8009	O25	4cI	Alcelaphini	M _x
ME225	1.9	32.1	8014	S25	4cI	Alcelaphini	P _x
ME217	2.1	33.0	8349	P26	4cI	<i>Alcelaphus/Damaliscus</i>	M
ME206	-1.4	35.3	8318	P25	4dI	Alcelaphini	frag
ME202	2.7	34.0	8000	T22	4dI	<i>Damaliscus</i> sp.	R M _{2/3}
ME207	-1.4	33.4	8332	S24	4dII	Alcelaphini	frag
ME205	0.1	32.6	8319	T22	4dII	Alcelaphini	frag
Antid.	-2.5	31.4	8346	K27 mix	4c	<i>A. bondi</i> (cf)	L M ₁
ME527	-8.8	32.2	8274	T25	2bII	<i>A. marsupialis</i>	L M ₃
ME537	-10.7	31.2	8439	T24	2bII	<i>A. marsupialis</i>	L M ₁
ME540	-9.9	31.8	8289	T24	2bII	<i>A. marsupialis</i>	L P ₄
ME475	-9.0	33.5	8253	T23	3aI	<i>A. marsupialis</i>	R M ₂
ME508	-6.2	32.2	8368	S23	3aI	<i>A. marsupialis</i>	R M ³
ME510	-7.9	32.4	8239	S26	3aI	<i>A. marsupialis</i>	L M _{2/3}
ME486	-2.9	34.0	8243	R22	3aI	<i>A. marsupialis</i> (cf)	M _x
ME515	-6.4	35.2	8399	Q21	3aI	<i>A. marsupialis</i> (cf)	frag
ME517	-8.4	31.3	8254	T23	3aI	<i>A. marsupialis</i>	L M ¹
ME420	-10.8	34.5	8216	T26	3bI	<i>A. marsupialis</i>	L M ₂
ME432	-8.9	30.9	8218	S27	3bI	<i>A. marsupialis</i>	M
ME396	-3.2	33.2	8131	O23	4a	<i>A. marsupialis</i>	L M ³
ME413	-7.1	30.4	8126	O23	4a	<i>A. marsupialis</i> (cf)	R P ₃
ME306	-7.1	30.6	8175	R23	4aLF2	<i>A. marsupialis</i>	L M ¹
ME305	-6.9	31.4	8174	R23	4aLH2	<i>A. marsupialis</i>	R M ₁
ME283	-7.7	35.0	8059	T27	4bI	<i>A. marsupialis</i>	L M ³

ME228	2.0	31.6	8311	P26	4c MID	<i>C./M. taurinus</i>	M ³
ME419	2.9	32.5	8217	S27	3bI	<i>C. taurinus</i>	R M ₃
ME230	1.8	34.4	8360	N27	4c UP	<i>C. taurinus</i>	M ^x
ME343	2.5	34.1	8099	T25	4aI	<i>Connochaetes</i> sp.	R M ³
ME339	2.7	35.0	8077	T24	4aI	<i>C. taurinus</i>	L M ³
ME377	1.5	32.0	8153	Q22	4aII	<i>C. taurinus</i>	L P ³
ME345	2.8	32.9	8144	Q23	4aII	<i>C. taurinus</i> (cf)	M ₃
ME427	2.2	31.4	8211	T24	3bI	<i>C. taurinus/gnou</i>	L M ²
ME340	2.3	33.4	8135	Q21	4aV	<i>C. taurinus/gnou</i>	R M ₃
ME523	1.5	31.5	8286	Q21	2bII	<i>C. taurinus</i>	L M ₃
ME480	1.2	31.6	8251	T28	3aI	<i>C. taurinus</i>	M ₃
ME330	3.7	34.9	8132	O23	4a	<i>C. taurinus</i>	M ^{2/3}
ME346	0.7	33.1	8136	T23	4aII	<i>C. taurinus</i>	L M ³
ME229	2.0	34.4	8310	P26	4c MID	<i>C. taurinus</i>	L M ^{2/3}
Blesbok	0.3	32.0	8238	T28	3aIII	<i>D. pygargus</i>	L M ₃
ME423	1.2	34.0	8201	S24	3bI	<i>Damaliscus</i> sp.	R M ₁
ME547	-5.4	31.6	8304	Q23	1	<i>Equus</i> sp	M ^x /P ^x
ME487	-0.6	33.6	8400	T27	3aI	<i>Equus</i> sp	frag
ME546	-7.1	30.5	8437	S27	1b	<i>Equus</i> sp.	M ^x
ME533	-1.8	27.7	8372	T21	2b	<i>Equus</i> sp.	R M _x
ME535	0.2	33.0	8276	S22	2b	<i>Equus</i> sp.	P ^x cf
ME538	-0.8	30.4	8275	T25	2bII	<i>Equus</i> sp.	M ₁
ME476	-0.2	32.0	8247	S25	3aI	<i>Equus</i> sp.	M _x /P _x
ME482	0.9	29.9	8390	T26	3aI	<i>Equus</i> sp. (cf)	P/M
ME488	-0.8	31.8	8245	T27	3aI	<i>Equus</i> sp.	M ^x /P ^x
ME504	-0.3	30.8	8388	T22	3aI	<i>Equus</i> sp.	M ^x
ME520	-2.1	30.8	8240	S26	3aI	<i>Equus</i> sp.	M ^x /P ^x
ME522	0.3	30.9	8393	R24	3aI	<i>Equus</i> sp.	L M ^{1/2}
ME521	0.1	32.4	8235	S27	3aII	<i>Equus</i> sp.	L P ₂
ME479	0.3	33.2	8236	S27	3aIII	<i>Equus</i> sp.	M ^x /P ^x
ME448	-1.6	33.7	8369	T26	3bI	<i>Equus</i> sp.	M _x
ME395	0.9	31.7	8427	P21	4a	<i>Equus</i> sp.	R M _{1/2}

ME361	0.7	34.7	8154	Q23	4aII	<i>Equus</i> sp.	M _x
ME382	-0.9	32.5	8161	Q23	4aIII	<i>Equus</i> sp.	P ^x /M ^x
ME304	2.9	37.1	8380	R23	4aLH	<i>Equus</i> sp.	M _x
ME267	1.1	34.4	8069	P22	4b	<i>Equus</i> sp.	R P ₂
ME270	-0.2	31.7	8076	O24	4b	<i>Equus</i> sp.	P/M
ME223	0.7	33.0	8021	T25	4cI	<i>Equus</i> sp.	P ^x /M ^x
ME532	-4.3	41.4	8374	S22	2b	<i>Procavia capensis</i>	P ^x /M ^x
ME550	-6.1	30.0	8295	R23	1b	<i>H. africae australis</i>	L M ¹
ME551	-7.1	30.4	8302	S22	1b	<i>H. africae australis</i>	L M ₃
ME552	-7.4	31.7	8300	R24	1b	<i>H. africae australis</i>	L M ¹
ME549	-6.0	29.2	8299	P24	2a	<i>H. africae australis</i>	L M ₃
ME494	-10.1	28.3	8249	R23	3aI	<i>H. africae australis</i>	L M ¹
ME507	-13.0	29.1	8227	T27	3aIII	<i>H. africae australis</i>	R M ²
ME449	-11.3	28.4	8196	R24	3bI	<i>H. africae australis</i>	L M ₁
ME430	-10.3	30.8	8405	T28	3bII	<i>H. africae australis</i>	M
ME437	-11.7	29.8	8220	T26	3bII	<i>H. africae australis</i>	R M ₂
ME463	-12.3	25.8	8197	T28	3bII	<i>H. africae australis</i>	L M ³
ME402	-7.7	28.1	8087	S25	4aI	<i>H. africae australis</i>	L M ²
ME403	-10.0	31.2	8104	S26	4aI	<i>H. africae australis</i>	M2cf
ME406	-0.2	31.8	8164	S22	4aII	<i>H. africae australis</i>	L M ¹
ME409	-4.7	28.1	8137	Q21	4aIV	<i>H. africae australis</i>	L M ³
ME322	-9.4	31.5	8173	R23	4aLF	<i>H. africae australis</i>	frag
ME408	-11.5	30.6	8133	R23	4aV	<i>H. africae australis</i>	R M ²
ME294	-0.8	29.1	8055	Q23	4bI	<i>H. africae australis</i>	R M ³
ME215	-6.1	31.4	8025	P22	4c	<i>H. africae australis</i>	P ₄
ME232	-7.5	29.0	8017	O21	4c	<i>H. africae australis</i>	R M ₃
ME233	-7.6	29.7	8315	O28	4c MID	<i>H. africae australis</i>	M ^x
ME234	-10.8	28.9	8008	P25	4cII	<i>H. africae australis</i>	L P ⁴
ME210	-6.9	29.8	8003	P24	4d	<i>H. africae australis</i>	R M ₂
ME211	-9.1	27.1	8001	O22	4d	<i>H. africae australis</i>	R P ⁴
ME212	-10.7	29.1	8004	S24	4dI	<i>H. africae australis</i>	R M ³
ME213	-10.2	31.4	8005	S24	4dI	<i>H. africae australis</i>	R M ³

ME536	-11.7	35.0	8373	R21	2b	<i>O. oreotragus</i>	L M ₁
ME440	-0.9	27.2	8203	T27	3bII	<i>Pedetes capensis</i>	M1
ME364	-1.2	29.4	8117	P23	4a	<i>Pedetes capensis</i>	M ₃
ME353	-1.1	30.3	8084	T26	4aI	<i>Pedetes capensis</i>	M1/2
ME356	-0.8	28.8	8093	T27	4aI	<i>Pedetes capensis</i>	M2/3
ME357	-0.3	29.0	8092	T27	4aI	<i>Pedetes capensis</i>	M2/3
ME365	-0.3	24.3	8085	T26	4aI	<i>Pedetes capensis</i>	M3
ME354	-1.0	28.7	8163	T26	4aII	<i>Pedetes capensis</i>	R M ^{1/2}
ME355	0.3	30.1	8158	S26	4aII	<i>Pedetes capensis</i>	L M ¹
ME363	0.2	28.6	8159	S26	4aII	<i>Pedetes capensis</i>	L M ₂
ME320	0.0	31.5	8179	S25	4aLF	<i>Pedetes capensis</i>	L M ₁
ME321	-0.1	29.7	8180	R24	4aLF	<i>Pedetes capensis</i>	R P ⁴ -M ²
ME296	0.5	27.7	8068	O21	4b	<i>Pedetes capensis</i>	R P ⁴
ME297	1.4	30.7	8065	P23	4b	<i>Pedetes capensis</i>	R M ¹
ME299	0.7	30.6	8067	O23	4b	<i>Pedetes capensis</i>	L M ^{1/2}
ME295	-0.5	29.3	8073	P22	4b	<i>Pedetes capensis</i>	M2/1
ME298	-1.5	27.9	8047	S23	4bI	<i>Pedetes capensis</i>	R M ₃
ME241	0.6	28.2	8018	O19	4c	<i>Pedetes capensis</i>	R M ^{1/2}
ME242	-1.7	29.1	8019	O19	4c	<i>Pedetes capensis</i>	R M _{1/2} cf
ME243	-2.3	27.5	8020	O19	4c	<i>Pedetes capensis</i>	M1/2
ME244	-0.2	30.1	8023	P24	4c	<i>Pedetes capensis</i>	L M ^{1/2}
ME245	-0.5	30.5	8024	O23	4c	<i>Pedetes capensis</i>	L M ^{1/2}
ME246	0.1	28.5	8033	O20	4c	<i>Pedetes capensis</i>	M1/2
ME314	-11.9	35.2	8169	R25	4aLF	<i>Pelea capreolus</i>	R M ₁
ME325	-6.2	35.0	8110	P21	4a	<i>Pelea capreolus</i> (cf)	M
ME389	-5.9	32.6	8107	O20	4a	<i>Pelea capreolus</i> (cf)	M _x
ME539	0.0	31.5	8285	S27	2b	<i>Phacocerus</i> sp.	M ₂
ME362	0.7	30.5	8121	O20	4a	<i>Phacocerus</i> sp.	M3
ME387	0.4	31.0	8114	P21	4a	<i>Phacocerus</i> sp.	M3
ME352	1.0	33.9	8098	S24	4aI	<i>Phacocerus</i> sp.	M3
ME401	1.9	37.2	8433	S27	4aII	<i>Phacocerus</i> sp.	P ₄
ME375	1.0	32.7	8145	S23	4aIV	<i>Phacocerus</i> sp.	M3

ME499	-11.4	35.0	8269	S27	3aII	<i>R. campestris</i>	R M ¹
ME501	-14.1	35.8	8402	S28	3aII	<i>R. campestris</i>	M _{1/2}
ME467	-12.8	36.6	8139	S28	3bI	<i>R. campestris</i>	L M ₃
ME443	-10.2	33.9	8219	S27	3bI	<i>R. campestris</i>	M ^{2/3}
ME469	-10.1	28.5	8191	T26	3bI	<i>R. campestris</i>	M ₃
ME436	-9.3	36.2	8208	S27	3bII	<i>R. campestris</i>	M _{2/3}
ME470	-11.8	36.4	8204	T27	3bII	<i>R. campestris</i>	R M ³
ME472	-11.1	37.8	8412	S27	3bII	<i>R. campestris</i>	L M ¹
ME466	-10.4	36.7	8207	S27	3bII	<i>R. campestris</i>	L P ³
ME411	-8.1	34.2	8113	P23	4a	<i>R. campestris</i>	RM _{2/3}
ME412	-9.7	33.5	8106	S26	4aI	<i>R. campestris</i>	M
ME414	-10.7	34.3	8426	S27	4aI	<i>R. campestris</i>	L P ₃
ME378	-7.9	34.0	8100	S28	4aI	<i>R. campestris</i>	R P ⁴
ME385	-8.2	31.1	8096	R21	4aI	<i>R. campestris</i>	M ^x
ME404	-9.3	31.8	8105	S26	4aI	<i>R. campestris</i>	M
ME405	-9.7	35.0	8095	T27	4aI	<i>R. campestris</i>	M _x
ME410	-9.4	36.7	8149	T24	4aII	<i>R. campestris</i>	L P ²
ME407	-10.0	36.2	8430	T22	4aII	<i>R. campestris</i>	M ¹
ME399	-10.4	37.0	8141	S24	4aIV	<i>R. campestris</i>	L M ³
ME319	-11.3	33.4	8167	T25	4aLH	<i>R. campestris</i>	M _x
ME317	-11.8	42.3	8168	R25	4aLH	<i>R. campestris</i>	R M ₁
ME318	-11.0	32.9	8166	S24	4aLH2	<i>R. campestris</i>	L P ₃₋₄
ME291	-9.1	33.4	8071	P22	4b	<i>R. campestris</i>	L M ₂
ME288	-9.6	38.2	8054	T25	4bI	<i>R. campestris</i>	M _{2/3}
ME285	-10.3	32.1	8061	T27	4bI	<i>R. campestris</i>	M ^{2/3}
ME289	-8.7	36.7	8052	Q25	4bI	<i>R. campestris</i>	L M _{2/3}
ME290	-10.7	39.5	8060	T27	4bI	<i>R. campestris</i>	L M ²
ME293	-8.3	32.3	8044	R23	4bI	<i>R. campestris</i>	L P ₃
ME292	-7.6	31.7	8035	T25	4bII	<i>R. campestris</i>	M
ME300	-8.7	32.2	8036	T25	4bII	<i>R. campestris</i>	M
ME247	-8.8	40.2	8015	O21	4c	<i>R. campestris</i>	M ^{2/3}
ME248	-10.7	33.7	8016	O21	4c	<i>R. campestris</i>	M ^{2/3}

ME249	-9.1	33.0	8031	O20	4c	<i>R. campestris</i>	M _{2/3}
ME529	2.0	34.6	8282	S23	2b	<i>R. fulvorufula</i>	L M ²
ME534	1.9	31.2	8281	S20	2b	<i>R. fulvorufula</i>	L M ³
ME528	-0.6	31.9	8288	Q21	2bII	<i>R. fulvorufula</i>	R M ₃
ME478	1.3	34.0	8263	T28	3aII	<i>R. fulvorufula</i>	L M ¹
ME500	2.5	31.1	8225	T25	3aIII	<i>R. fulvorufula</i> (cf)	L P ⁴
ME422	1.7	31.6	8215	T25	3bI	<i>R. fulvorufula</i>	R M ³
ME451	1.1	35.1	8195	S25	3bI	<i>R. fulvorufula</i>	M ^x
ME454	2.4	33.5	8187	T28	3bI	<i>R. fulvorufula</i>	L M ³
ME471	3.1	32.8	8404	T28	3bII	<i>R. fulvorufula</i>	P ³
ME386	2.7	34.9	8138	T22	4aIV	<i>R. fulvorufula</i>	L M ₁
ME313	3.5	37.4	8178	R24	4aLF	<i>R. fulvorufula</i>	P ⁴
ME380	1.9	31.3	8134	R23	4aV	<i>R. fulvorufula</i>	L M ¹
ME398	2.1	31.6	8115	P21	4a	<i>R. fulvorufula</i>	R P ⁴
ME390	-1.6	35.8	8103	T27	4aI	Reduncini indet.	R M _{2/3}
ME374	2.1	38.0	8143	Q22	4aIV	<i>R. fulvorufula</i>	L M ₁
ME397	2.9	35.8	8140	S24	4aIV	<i>R. fulvorufula</i>	R M _{2/3}
ME531	-10.4	33.1	8376	T23	2bII	<i>T. oryx</i> cf	P _x
ME473	-9.7	31.1	8365	T24	3aI	<i>T. oryx</i>	P ₄
ME455	-8.6	33.0	8423	T27	3bI	<i>T. oryx</i>	R M ¹
ME231	-9.5	37.9	8362	M26	4cII	<i>T. oryx</i>	R P ²
ME530	-9.5	30.6	8377	T23	2bII	<i>T. oryx</i> (cf)	M _x
ME273	-7.7	32.7	8386	O21	4b	<i>T. oryx</i> (cf)	R P ²
ME258	-8.9	34.9	8350	Q26	4c MID	<i>T. oryx</i> (cf)	M ^x
ME526	-8.2	35.0	8375	S24	2bII	Tragelaphini (cf)	frag
ME498	-11.4	33.1	8367	T26	3aI	Tragelaphini (cf)	M
ME502	-8.6	31.1	8389	R23	3aI	Tragelaphini	M
ME493	-9.1	34.8	8366	T28	3aIII	Tragelaphini (cf)	M ^x
ME481	-10.3	28.5	8401	T25	3aIII	Tragelaphini (cf)	frag
ME418	-9.3	35.9	8419	T26	3bI	Tragelaphini	M
ME446	-9.0	33.0	8416	T27	3bI	Tragelaphini	frag
ME450	-8.1	33.0	8415	T27	3bI	Tragelaphini	frag

ME458	-10.5	35.9	8414	T27	3bI	Tragelaphini	frag
ME379	-4.4	34.3	8151	T22	4aII	Tragelaphini	L M _x
ME328	-4.9	31.8	8429	T22	4aV	Tragelaphini	M
ME278	-8.5	33.9	8063	T27	4bI	Tragelaphini	frag
ME274	-8.5	33.3	8062	T27	4bI	Tragelaphini	P ^x
ME250	-8.6	35.3	8358	O28	4c MID	Tragelaphini	frag
ME251	-10.9	37.8	8338	M27	4c LR	Tragelaphini	M
ME252	-10.1	37.9	8363	L27	4c MID	Tragelaphini	frag
ME253	-8.0	34.7	8340	L27	4c MID	Tragelaphini	frag
ME254	-9.4	36.1	8361	L27	4c MID	Tragelaphini	M
ME255	-7.9	35.5	8359	Q26	4c UP	Tragelaphini	frag
ME256	-9.5	36.5	8364	Q26	4c UP	Tragelaphini	frag
ME201	-10.2	36.7	8331	O23	4d	Tragelaphini	frag
ME415	-8.4	34.6	8424	T27	3bI	Tragelaphini	M
ME429	-10.7	34.9	8425	T27	3bI	Tragelaphini	M
ME431	-8.6	31.4	8422	S28	3bI	Tragelaphini	M
ME462	-7.4	34.3	8209	R24	3bI	Tragelaphini	M
ME465	-9.8	31.3	8409	T27	3bII	Tragelaphini	M
ME417	-7.8	32.4	8421	S26	3bII	Tragelaphini	M
ME445	-9.3	32.3	8206	T27	3bII	Tragelaphini	frag
ME452	-8.3	34.1	8410	T27	3bII	Tragelaphini	M
ME461	-10.7	34.8	8411	T27	3bII	Tragelaphini	M
ME332	-9.6	38.1	8434	T24	4aIII	Tragelaphini	M ^x
ME358	-8.2	33.1	8431	S23	4aIV	Tragelaphini	M
ME316	-10.0	37.4	8383	Q23	4aLH	Tragelaphini	M
ME316	-9.9	38.1	8383	Q23	4aLH	Tragelaphini (cf)	M
ME272	-9.5	37.8	8387	O21	4b	Tragelaphini	M ^x
ME208	-10.3	36.0	8330	Q24	4dI	Tragelaphini (cf)	frag
ME209	-10.5	32.8	8333	P25	4dI	Tragelaphini (cf)	frag
ME524	-7.2	31.6	8277	S22	2bII	<i>T. strepsiceros</i>	M ^{1/2}
ME497	-9.6	36.5	8261	S24	3aI	<i>T. strepsiceros</i> (cf)	R P ^x
ME514	-9.6	31.9	8268	T27	3aII	<i>T. strepsiceros</i>	L M ²

ME483	-11.3	33.9	8221	S28	3aIII	<i>T. strepsiceros</i> (cf)	M frag
ME506	-8.2	35.9	8237	S27	3aIII	<i>T. strepsiceros</i>	M frag
ME453	-10.3	38.1	8200	T27	3bI	<i>T. strepsiceros</i>	L M ¹
ME464	-8.0	35.2	8213	T25	3bI	<i>T. strepsiceros</i>	M ^x
ME439	-10.1	35.0	8184	T28	3bI	<i>T. strepsiceros</i>	L M ₃
ME457	-8.8	33.1	8194	S26	3bII	<i>T. strepsiceros</i> (cf)	M ^x
ME392	-9.4	35.3	8118	P20	4a	<i>T. strepsiceros</i>	L P ₂
ME323	-6.8	33.8	8108	P21	4a	<i>T. strepsiceros</i>	M _x
ME324	-8.6	33.3	8109	P21	4a	<i>T. strepsiceros</i>	M
ME 348	-8.8	35.3	8086	T23	4aI	<i>T. strepsiceros</i>	M ^x
ME349	-8.6	32.8	8090	R23	4aI	<i>T. strepsiceros</i>	M ^{2/3}
ME372	-8.2	34.2	8081	T26	4aI	<i>T. strepsiceros</i>	M _x
ME368	-9.1	33.6	8094	T27	4aI	<i>T. strepsiceros</i> (cf)	M
ME359	-7.2	37.6	8156	S23	4aII	<i>T. strepsiceros</i>	M _x
ME394	-6.7	32.4	8162	Q21	4aIII	<i>T. strepsiceros</i>	M
ME373	-4.3	31.6	8432	Q21	4aIV	<i>T. strepsiceros</i>	L M ₂
ME268	-6.5	34.3	8075	O22	4b	<i>T. strepsiceros</i>	M ^x
ME265	-8.4	37.1	8341	N27	4c LR	<i>T. strepsiceros</i>	frag
ME266	-7.8	35.2	8336	P26	4c MID	<i>T. strepsiceros</i>	L M ¹
ME541	-7.8	31.9	8378	R23	2bII	<i>T. strepsiceros</i> (cf)	L M _{2/3}
ME312	-9.6	32.6	8381	R25	4aLH	<i>T. strepsiceros</i> (cf)	M _x
ME315	-7.4	33.3	8379	R24	4aLH	<i>T. strepsiceros</i> (cf)	M _x
ME264	-8.4	34.4	8306	M28	4c	<i>T. strepsiceros</i> (cf)	M _x
ME259	-8.7	33.4	8334	O28	4c MID	<i>T. strepsiceros</i> (cf)	M ^x
ME260	-10.2	34.5	8337	P26	4c MID	<i>T. strepsiceros</i> (cf)	M _x
ME261	-8.5	39.6	8342	K28	4c MID	<i>T. strepsiceros</i> (cf)	frag
ME262	-8.7	33.5	8347	K27	4c MID	<i>T. strepsiceros</i> (cf)	M ^x
ME263	-10.5	31.6	8352	N27	4cI	<i>T. strepsiceros</i> (cf)	M
ME203	-9.0	35.3	8328	P25	4dI	<i>T. strepsiceros</i> (cf)	M _x

Supplementary Figure 1: Bar diagram showing loadings of pollen taxa at Wonderwerk Cave (values are flipped to show increases as positive). The curve in Fig. 5 is based on PC2 (12.6% variance), while PC1 (not in Fig 5, 14.4%) is reflecting temperature rather than moisture.

