

An isotopic test of the seasonal migration hypothesis for large grazing ungulates inhabiting the Palaeo-Agulhas Plain

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Highlights:

- Isotopic sampling of ungulate teeth to test the hypothesis of an east-west migration across the Paleo-Agulhas Plain.
- We analyzed both carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes preserved in herbivore teeth from the site of PP30
- The nutrient rich Paleo-Agulhas Plain may have negated any necessity for herbivores to migrate, and was thus an ecosystem from which hunters could access animals roaming more locally

Keywords: archaeology, isotopes, migration, Middle Stone Age, South Africa, Pinnacle Point, Paleo-Agulhas Plain,

Abstract

The Middle Stone Age archaeological record from The Greater Cape Floristic Region (GCFR) of South Africa is critical for understanding the evolution of early modern humans (*Homo sapiens*). The now submerged continental shelf, exposed during periods of low sea level, formed its own ecosystem, the Palaeo-Agulhas Plain, that was crucial to the foraging of the early modern humans inhabiting sites on the south coast. It's hypothesized that grazing animals living on the plain migrated east and west in concert with the seasonally varying rains. Here, we test this east-west migration hypothesis by examining the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of serially drilled ungulate teeth, resting on previous observations that areas fed by summer rain to the east have more C_4 grasses while the winter rainfall area to the west have more C_3 grasses, and the summer and winter rains differ in $\delta^{18}\text{O}$. We analyze carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes preserved in herbivore teeth from the site of PP30 (a hyena den dating to ~151 ka) to track changes in diet and water during tooth formation, linked to these distinctions. The results demonstrate that while a few animals show vectored shifts in $\delta^{13}\text{C}$ across their tooth resembling an east-west, long distance migration, none of the animals have changes in $\delta^{13}\text{C}$ values statistically different from a taxon thought to have foraged locally through the year (Southern reedbuck, *Redunca arundium*). Overall, our data indicate that the Palaeo-Agulhas Plain could support herbivore populations year-round without substantial migration, providing an ecosystem ideal for human inhabitants.

1. Introduction

Africa is the epicenter for the evolution of our species (*Homo sapiens*), with the oldest genetic lineages present in South Africa, central Africa, and Tanzania (Skoglund et al., 2017). Archaeological sites located on the South African South Coast preserve a rich record of early evidence for complex behaviors by modern humans starting at 164 ka (Marean et al., 2014; Wadley, 2015). In addition to the deep genetic record and the early development of complex behaviors, evidence from sites like Blombos, Pinnacle Point (PP) 13B, PP5-6, Vleesbaai, and Klasies demonstrate that humans occupied sites in the South Coast region with varying intensity for nearly 200,000 years. This record makes it critical to understand the ecological context that allowed our species to survive and thrive in this location through the climatic changes of the Pleistocene.

Human and animal survival must have been linked to the availability of resources. The Greater Cape Floristic Region (GCFR) stretches from the southwest and southeast coasts of South Africa and is a biodiversity hotspot (Allsopp et al., 2014). Environmental reconstructions of the GCFR (explored in this issue) show that during globally cool phases in the Pleistocene this region remained ecologically rich, despite dramatic landscape changes. The Palaeo-Agulhas Plain (PAP) was instrumental to this richness (Marean et al., 2014). The coastal shelf of South Africa is shallow and was submerged during interglacials when global ice melted, moving the location of marine resources closer to the currently studied archaeological sites. During glacial cycles, ocean water receded exposing a vast PAP (van Andel, 1989; Fisher et al., 2010; Compton, 2011) providing grassland habitat for herbivores (Potts et al., this volume). Thus, over

time, carnivores and humans foraging across the landscape could access terrestrial and marine resources, with varying levels of ease in terms of foraging distance.

East-west trending foothills run across the South Coast as the continental shelf gradually increases in elevation rising to the Cape Fold Belt mountains. The southern edge of Cape coastal lowlands mark the current location of the coast and its intersection with the terrestrial zone, though this point of intersection was dynamic in the Pleistocene (Marean et al., 2014). In locations where resistant bedrock forms rocky headlands, it is common to find sea cliffs above the ocean. Millennia of erosion from ocean transgressions have opened caves and shelters within these cliffs creating ideal living spaces for humans. It is in this geological context that the PP cave and rock shelter complex is situated, preserving evidence of the activities of carnivores and humans for nearly 200,000 years. Archaeological discoveries at PP and the nearby open-air site of Vleesbaai have helped reconstruct how humans were moving on the landscape, collecting lithic raw material, creating tools, foraging, hunting, and butchering animals (Brown et al., 2009, 2012; Jerardino and Marean, 2010; Oestmo et al., 2014; Hodgkins et al., 2018). Yet, the seasonal availability of prey for hunters is still not fully understood.

It has been hypothesized that during glacial cycles hunters who used the PP shelters intercepted migratory prey as they moved east and west over the Palaeo-Agulhas Plain (Marean, 2010, 2016; Marean et al., 2014). This migration would have been driven by the seasonal availability of green plant forage that included a dominance of C₃ plants fed by winter rain in the west and C₄ plants fed by summer rain in the east. A study of the age at death of fossil remains of the blue antelope (*Hippotragus leucophaeus*) from a variety of sites of different ages concluded that there was evidence for seasonal movement (Faith and Thompson, 2013).

A recent strontium analysis ($^{87}\text{Sr}/^{86}\text{Sr}$) of herbivores hunted by humans at two sites in the GCFR (PP30 and PP 13B) found that prey species never ventured into the northern mountains, confirming the notion that they stayed on the PAP (Copeland et al., 2016). While the $^{87}\text{Sr}/^{86}\text{Sr}$ analysis was able to utilize geological changes in a north south axis it cannot track east west movements as the geology on the PAP is fairly homogeneous. However, if herbivores were shifting their diets between C_3 and C_4 plants as they moved between rainfall zones, then $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in teeth of young herd animals would have shifted in a pattered way reflecting their dietary changes. Thus, this study tests the hypothesis for an east-west migration by sampling $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in herbivore teeth at the site of PP30, a hyena den dated to 151 ka (MIS 6). If herbivores did undertake an east-west migration, their path would have been fairly unrestricted during MIS 6 when the plain ranged up to 89 km wide (Fisher et al., 2010), thus hunters utilizing the PP caves likely needed to travel to intercept prey. However, the route taken by species during interglacials would have been narrower as the ocean moved inland (Venter et al., this volume), placing the animals closer to the carnivore and human occupied shelters at PP. An alternative scenario is that the PAP, which was transected by meandering rivers (Cawthra et al., this volume) provided a resource rich environment allowing animals to roam on the plain but not undertake point to point seasonal movements. If this is the case, then during MIS 6 the PP shelters would have provided a homebase from which hunters could take advantage of animals that may have roamed more locally on the PAP.

We selected the paleontological site of PP30 for a first test of the east-west herbivore migration hypothesis. This cave site formed in a calcrete above the Pinnacle Point cliffs (Rector and Reed, 2010; Copeland et al., 2016). The preservation conditions of faunal remains from the

site suggest it was occupied for a relatively short time by brown hyenas (*Parahyaena brunnea*) at ~ 151 ka, thus minimizing issues related to time averaging (Lansing et al., 2009; Rector and Reed, 2010). *Parahyaena brunnea* is a species known to transport prey remains and ostrich eggs to cave sites for consumption and to provision their young (Skinner and Van Aarde, 1991; Skinner et al., 1998), and in keeping with this behavior the remains of grazers and ostrich eggs at this site are abundant (Rector and Reed, 2010; Hodgkins et al. 2018). At the time of hyena occupation, the PAP was near its maximum potential extent, providing a vast area for hunting (Fisher et al., 2010). Strontium analysis of ostrich eggs from PP30 provided values consistent with strontium measured from the ungulates, confirming that hyenas were focused on foraging on the PAP (Hodgkins et al., 2018).

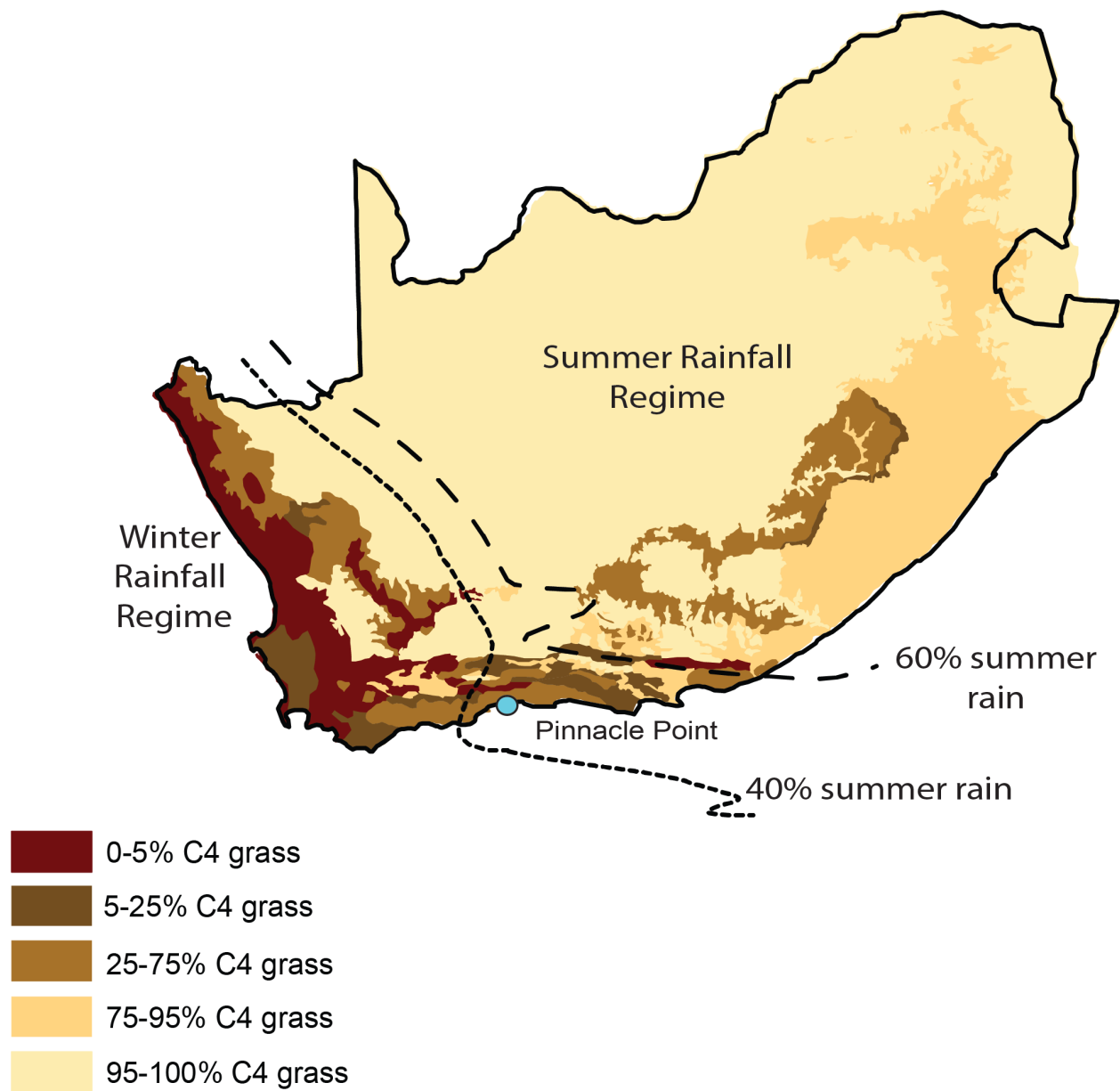


Figure 1. Map of South African isoscape showing the distribution of C4 grasses (modified from Vogel, 1978).

2. Background

2.1 Climate and environment isotopic background

The amount of rain that falls along the South Coast varies seasonally from east to west, creating summer, winter, and bimodal rainfall zones, which influence the plants that grow in each zone. Today, on the South Coast the summer rainfall zone occurs east of the GCFR and grasses in this region are primarily C₄ grasses. However, C₄ grasses also occur patchily throughout the Cape coastal lowlands of the southern and south-eastern GCFR (including the area inland of Pinnacle Point) on seasonally waterlogged soils and on north-facing slopes (Vogel et al., 1978; Cowling, 1983; Cowling and Richardson, 1995). The modern winter rainfall zone occurs in the western portion of the GCFR and the grasses are predominantly C₃. Both C₃ and C₄ grasses occur in the bimodal rainfall zone located in the southern GCFR where the PP sites are located. Speleothem records from PP have provided a long and well-dated record of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for this region (Braun et al., this volume, 2017, 2019; Bar-Matthews et al., 2010). Unfortunately, this sequence has a gap in the middle of MIS6 and thus does not cover 151 ka (Braun et al. 2018), the time of the accumulation of the PP30 fossils. During the first half of MIS 6 the speleothems suggest a mix of summer and winter rain and a mix of C₃ and C₄ vegetation, but not as strongly C₄ as is found in MIS 4 (Braun et al., this volume, 2017, 2019; Bar-Matthews et al., 2010).

Due to variation in how plants convert carbon dioxide (CO₂) to organic compounds, C₃ and C₄ plants differ in their isotopic $\delta^{13}\text{C}$ values—a value that expresses the difference in the $^{13}\text{C}/^{12}\text{C}$ ratio per mil of a sample compared to the Pee Dee belemnite limestone standard (Bender, 1971). C₄ plants have higher $\delta^{13}\text{C}$ values than C₃ plants. These differing $\delta^{13}\text{C}$ plant values are

taken up by herbivores who eat the plants and are stored in the animal's body tissue, including tooth enamel which provides a well-preserved record for inferring the diet of animals whose remains are preserved in the paleontological and archaeological record. Animals that consume purely C₃ plants have $\delta^{13}\text{C}$ values that are lower, typically $< -10\text{‰}$, those that consume mostly C₄ have higher values typically $> -7.5\text{‰}$, and those that consume both C₃ and C₄ have values between these ranges (Sealy et al., 2016).

Oxygen isotope ratios ($\delta^{18}\text{O}$) are also preserved in tooth enamel, providing another source of paleocological information from fossil and archaeological assemblages. The $\delta^{18}\text{O}$ of meteoric water are determined largely by fractionation occurring throughout the water cycle, driven by evaporation, condensation, and precipitation. Oxygen isotope values of meteoric water vary across landscapes along gradients that include altitude, distance from the coast, amount and season of rainfall, and temperature (Longinelli, 1984). The $\delta^{18}\text{O}$ measured in the tooth enamel of African ungulates reflects a fractionated version of $\delta^{18}\text{O}$ of meteoric water in animals that drink daily. As such, $\delta^{18}\text{O}$ can provide some signal of faunal mobility. Along the South African South Coast, rainwater from western winter rain systems is depleted in ^{18}O relative to rainwater from eastern systems with summer rain (Bar-Matthews et al., 2010; West et al., 2014; IAEA/WMO, 2015). At a sampling locality 6 km from Pinnacle Point, rainwater $\delta^{18}\text{O}_{\text{VSMOW}}$ during the 2006-2007 year varied from a mean of 0.1‰ in a summer month (January) to a mean of -6.1‰ in a winter month (July) (Bar-Matthews et al., 2010; Braun et al., 2017).

2.2 Isotopic Expectations for the Fossil Ungulates

The large mammal faunal remains from PP30 were reported on by Rector and Reed (2010). In the following sections, our characterizations of the behaviors of the herbivores rest largely on Estes (1991) and Kingdon (2015), except where we note specific details not found in those references and cite specific papers. We rely on Skead et al. (2011) for information on historical distributions of the mammals. The PP30 assemblage includes grazing herbivores that (based on modern behavior) can be highly migratory such as Cape Hartebeest (*Alcelaphus buselaphus*), wildebeest (*Connochaetes gnou*), and zebra (*Equus quagga*), but also grazing herbivores that do not tend to migrate. The southern reedbuck (*Redunca*) is a grazer that focuses on flood-plain grasslands, often tall grass, and is dependent on water. It will move off flood plains during the wet season, but never far and does not migrate. While individual animals vary in their behaviors and preferences, species that regularly move or migrate to find high quality forage, such as alcelaphines (e.g, hartebeest, wildebeest) and equids, should have consumed predominantly C₃ grasses in winter and predominantly C₄ grasses in summer if they were migrating from west to east across the PAP. This would be reflected in large shifts in intratooth $\delta^{13}\text{C}$ within their hypsodont molars (Balasse, 2002), but it is important to note that we do not have good comparative data on what the magnitudes of these shifts would be. Studies of this type are currently in the planning phase.

In bimodal rainfall regions such as the modern southern Cape Coast at Pinnacle Point, C₃ and C₄ grasses occur together in most vegetation types with their relative abundance and location varying as a function of season of rain, aspect, and other subtle factors (Vogel et al., 1978; Cowling, 1983). Non-migratory, local grazers such as the southern reedbuck (*Redunca*) should consume both C₃ and C₄ grasses resulting in bulk intermediate $\delta^{13}\text{C}$ values in its enamel. Such

animals may seasonally shift their consumption of C₃ and C₄ grasses as these grasses fluctuate in quality in reaction to seasonal changes in rainfall, potentially with more C₄ grass consumed during summer and more C₃ grass consumed during winter. However, the variations that result from forage switching should theoretically be smaller than those of a migratory grazer. Thus, species that are known to be grazers but not migratory, such as *Redunca* (reduncines), may act as indicators of the seasonal dietary fluctuation within one region of bimodal rainfall.

Within the species *Redunca arundinum*, two subspecies are recognized, the northern reedbuck (*Redunca arundinum occidentalis*) and the southern reedbuck (*Redunca arundinum arundinum*) (Du Plessis et al., 2016) of which the latter occurred in the GCFR (Klein, 1983). Skead (2011) considers the evidence for its occurrence in the GCFR as questionable. *Redunca* are grazers typically with >95% C₄ grass in their diets (Jungius, 1971; Gagnon and Chew, 2000; Codron et al., 2018). However, their diets sometimes contain a proportion of C₃ vegetation, likely sedges and wetland grasses (Venter and Kalule-Sabiti, 2016). *Redunca* are habitat specialists preferring wetlands with tall grass (Skinner and Chimimba, 2005; Brooke, 2018). The species is reported to be non-migratory, though anecdotal evidence suggests limited seasonal movement related to wetland water fluctuations (Holsworth, 1972). Thus, we expect that if non-*Redunca* animals were more mobile and ranging widely across the landscape (regardless of geographic directionality) into territories with different proportions of C₃/C₄ vegetation they will exhibit mean $\delta^{13}\text{C}$ values that differ significantly from that of the local *Redunca*. They should also have significantly wider ranges in $\delta^{13}\text{C}$ values across the tooth crowns within individuals. If that increased mobility included true migrations from one region to another, then we also expect them to show vectored (patterned) shifts in $\delta^{13}\text{C}$ values across tooth development rather than stochastic changes that might indicate a widely meandering range, but not a purposeful

movement that might be motivated by the need to follow rainfall from season to season. On the southern coast of South Africa, given that strontium isotope data from PP30 and nearby PP13B suggest little-to-no movement of herbivores into the interior (Copeland et al., 2016), patterned $\delta^{13}\text{C}$ changes would be most consistent with an east-west migration route.

Given that the cold, winter rainfall of the western region of the South Coast is depleted in ^{18}O relative to rainwater in the east (Bar-Matthews et al., 2010; West et al., 2014; IAEA/WMO, 2015), we would expect some variation in $\delta^{18}\text{O}$ for migrating animals moving along an east-west axis of the Paleo-Agulhas Plain (Bar-Matthews et al., 2010). However, animals staying in one location should also see some variation in rain-forced changes in $\delta^{18}\text{O}$. Additional complicating factors exist; for example, $\delta^{18}\text{O}$ can be substantially enriched in animals that obtain their water through the consumption of leaves or other foods rather than by drinking (Sponheimer and Lee-Thorp, 1999; Levin et al., 2006). Values can change from pre- to post-weaning (Fricke and O’Neil, 1996; Britton et al., 2015). Again, one way to mitigate these complications is to use the local and less mobile, non-migratory *Redunca* as a “control” group. As with the $\delta^{13}\text{C}$ values, we expect that if a species had a wide range (regardless of direction of movement), it will exhibit mean $\delta^{18}\text{O}$ values that differ significantly from the *Redunca* sample because it will have been drinking water from regions (beyond the local area surrounding PP30) supplied by differing proportions of summer versus winter rain. If that species was undergoing a true migration, it will also exhibit $\delta^{18}\text{O}$ values that show a vectored (patterned) shift in values across tooth development rather than a random changes. Such a vectored shift would suggest systematic movement from one area to another rather than a meandering movement back and forth between geographically disparate regions.

Table 1. Sampled taxa.

Taxon	Common Name	Feeding Classification	Propensity to Migrate	Number of individuals
<i>Alcelaphus buselaphus</i>	hartebeest	Grazer	Migratory	11
<i>Alcelaphus/Connochaetes</i>	species indeterminate	Grazer	Migratory	1
<i>Connochaetes gnou</i>	black wildebeest	Grazer	Migratory	5
<i>Antidorcas masupialis</i>	springbok	Mixed feeder	Migratory	8
<i>Antidorcas</i> sp. indet.	—	—	—	1
<i>Redunca arundinum</i>	southern reedbuck	Grazer	Non- migratory/limited movement	6
<i>Damaliscus pygargus</i>	bontebok	Grazer	sometimes migratory	4
<i>Hippotragus leucophaeus</i>	blue antelope	Grazer/Mixed feeder	Non-migratory	3

3. Methods

3.1 Fossil specimens

Studies of mammalian herbivores with known movement patterns show that geographical movements can be reflected in changing values of $^{87}\text{Sr}/^{86}\text{Sr}$, $\delta^{13}\text{C}$, and $\delta^{18}\text{O}$ across intra-tooth samples of enamel from individual animals (Balasse, 2002; Hoppe and Koch, 2007; Britton et al., 2009; Sealy et al., 2016). Hypsodont mammalian molars grow in a linear fashion from cusp to cervix over several months or years, incorporating carbon, and oxygen from the body pool into the enamel mineral lattice structure, resulting in a time-series (Passey and Cerling, 2002)). For example, experimental studies of the incorporation of carbon isotopes into sheep and cow enamel show that the changes between C_3 versus C_4 diets are clearly reflected in enamel $\delta^{13}\text{C}$, with some attenuation of the environmental signal (Balasse, 2002; Zazzo et al., 2010).

To reconstruct the diet and mobility of Pleistocene herbivores excavated from the paleontological site of PP30, teeth from 39 specimens identified to six herbivore taxa (Tables 1 and S1) were selected for stable isotope analysis (e.g., $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$). All the species studied have hypsodont teeth with molars mineralizing for a period of six months or more (Balasse, 2002; Zazzo et al., 2010; Copeland et al., 2016). We prioritized third molars as they form largely after weaning. Nursing has been found to enrich $\delta^{13}\text{C}$ values by an average of 2‰ during tooth development (Balasse, 2002). When third molars were not available or were poorly preserved, we sampled first and second molars instead. On maxillary teeth we sampled the distolingual lobe and on mandibular teeth we sampled the middle buccal lobe of the third molar or the distal buccal lobe on first and second molars.

3.2 Sampling procedures

To prepare teeth we mechanically removed all adhering dirt using a handheld drill (UP-200 model, KUPA Inc.) with a tungsten carbide diamond tipped drill bit, 0.5mm in diameter. After removing the dirt from the chosen lobe with the drill, the drilled surface was cleaned with cotton and alcohol and left to dry. Next, sequential samples of enamel were drilled using the same handheld drill and cleaned diamond drill bits following a sequence from the cervix to the apex of each tooth (Fig. 2). Each sample of enamel requires that a 2-4 mm horizontal band producing 4-6 mg of enamel powder is drilled into the tooth spanning the width of the lobe (Balasse, 2002). Enamel powder was collected in 2mL centrifuge tubes. The location of drilled enamel on each tooth was photographed using a Dino-Lite microscope with a calibrated scale.

3.3 Lab processing methods

All enamel powder was pretreated to remove secondary carbonate contaminants. This consisted of adding 0.1M acetic acid to each sample for 10 minutes, followed by another three rinses in purified H₂O. Following reaction with 100% phosphoric acid, gases evolved from the samples were analyzed to stable carbon and oxygen isotopic composition using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were calibrated against international standards IAEA NBS 18 ($\delta^{13}\text{C}$ -5.014 ± 0.032 ‰, $\delta^{18}\text{O}$ -23.2 ± 0.1 ‰), IAEA 603 ($\delta^{13}\text{C}$ $+2.46 \pm 0.01$ ‰, $\delta^{18}\text{O}$ -2.37 ± 0.04 ‰), IAEA CO8 ($\delta^{13}\text{C}$ -5.764 ± 0.032 ‰, $\delta^{18}\text{O}$ -22.7 ± 0.2 ‰), and USGS44 ($\delta^{13}\text{C}$ $= -42.1$ ‰) registered by the International Atomic Energy Agency and USGS. Overall measurement precision was studied through the measurement of repeats of MERCK CaCO₃ (n= 20, ± 0.2 ‰ for $\delta^{13}\text{C}$ and ± 0.2 ‰ for $\delta^{18}\text{O}$, $\delta^{13}\text{C} = \sim -40.6$ ‰, $\delta^{18}\text{O} = \sim -13.3$ ‰) and an equid tooth in house standard (n=10, ± 0.3 ‰ for $\delta^{13}\text{C}$ and ± 0.2 ‰ for $\delta^{18}\text{O}$).

3.4 Analytical approach and statistical tests

The formal statistical analyses described below test the first expectation of the east-west migration model, which is simply that when compared to the local *Redunca*, other herbivores should show evidence of greater mobility as evidenced by differences in their mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values suggesting that they were eating and drinking beyond the immediate region of PP30 in areas with differing proportions of C₃ and C₄ vegetation and summer versus winter rainfall. Such mobility should also be reflected in a wider range of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ within individual specimens. Run plots of the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values within individuals of each taxon were generated to assess the second expectation of the migration model, which is that the animals

should show vectored shifts in the intraindividual values indicating mobility consistent with seasonal movement between regions.

We conducted two formal statistical tests of the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data. First, we compared the means of taxa by way of a mixed-effects model with spherical correlation structure. This analysis addresses the question – do the species have significantly different $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ means? A mixed-effects model incorporates a fixed effect (in this case genus, being the factor of primary interest) along with nested random effects (the individual tooth specimens and the repeated sampling of each of those teeth). The correlation structure corrects for the autocorrelation caused by the repeated-measures nature of the data in which we have 39 specimens, each of which was sampled between two times and 15 times, giving 300 total measurements. This model allowed us to test for significant differences in the means among the genera without artificially inflating the model's degrees of freedom (which can give increased risk of Type I statistical errors) and accounted for the unequal variance and unbalanced sample sizes among the generic groupings. This approach yields benefits over a standard repeated-measures analysis of variance (ANOVA) using an ordinary least squares model. Importantly, a mixed-model can account for “missing data,” which is relevant in the current analysis because not all specimens in our dataset were sampled the same number of times. The mixed effects model was followed by a *post hoc* multiple comparison test using Dunnett contrasts (a “many-to-one” procedure) to compare the mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of each taxon against those of *Redunca* (the taxon used as the local control).

We also compared each taxon's total range of values to the range of values observed in *Redunca*. This was done to test the expectation that if animals had wider ranges than the local non-migratory control, then they should be expected to have larger ranges of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

within individual specimens than *Redunca*. Due to the fact that this approach collapses the repeated sampling of each specimen into a singular range value (and thus does not inflate the degrees of freedom), we opted to use a standard one-way least-squares model ANOVA followed by *post hoc* one-tailed Dunnett's contrasts to test the hypothesis that each of the expected migratory species has a greater range of isotopic ratios than the non-migratory *Redunca*.

4. Results

4.1 $\delta^{13}\text{C}$ isotopic ratios

Table 2 shows summary data of the $\delta^{13}\text{C}$ isotopic ratios for all specimens. Williams, (2015) presented $\delta^{13}\text{C}$ measurements on micromammals from PP30 and modern local samples, and all these show a stronger C_3 signal than the bovids measured here. We follow Sealy et al. (2016) in recognizing $\leq -10\text{‰}$ as a cutoff point between strongly C_3 diets and mixed C_3/C_4 diets. Based on this cutoff point of $\leq -10\text{‰}$, each specimen is assigned a grouping, presented in Table 2, based on its distribution of $\delta^{13}\text{C}$ values as sampled across the tooth: 1) all samples indicate a strong C_3 signal; 2) some samples indicate a strong C_3 signal; 3) no samples indicate a strong C_3 signal.

Within the “strong C_3 group” there are specimens with means ranging from -10.3 to -13.1‰. This grouping also shows relatively low ranges, with no specimens with ranges exceeding 1.3‰. In the “some strong C_3 group” the means range from -10.7‰ to -8.3‰. Within this group, the ranges are higher, with five specimens having ranges greater than 2.0‰ (one as high as 5.9‰). Within the “no strong C_3 group”, the means range from -9.3‰ to -5.8‰. Within this group, four individuals exceed a range of 2.0‰. *Redunca* are absent from the “strong C_3

group”, but present in the other groups, and never have a range that exceeds 1.2‰. *Hippotragus* shows low ranges never exceeding 1.6‰. *Alcelaphus* and *Connochaetes* are present in all the groups and vary in their ranges, with some having small ranges (.6‰), another set having ranges between 2.0‰ and 3.0‰, and a few having higher ranges (3.2‰ to 5.9‰). *Damaliscus* is present only in the “no strong C₃ group”, and one individual has a large range of 3.7‰ (the others have very few drillings, Table S1). *Antidorcas* is present in all the groups, and with the exception of one individual, its range never exceeds 2.0‰.

The results of the mixed effects model’s *post hoc* Dunnett’s contrasts analysis (Table 3) show no significant difference in the $\delta^{13}\text{C}$ isotopic ratios when each taxon is compared to *Redunca*. Similarly, the results of the one-way ANOVA shows no significant effect of taxonomic grouping on the total range of $\delta^{13}\text{C}$ isotopic ratio values ($F_{5,31} = 1.02$, $p = 0.43$) and one-tailed Dunnett’s contrasts show no significant differences between the *Redunca* control and any other taxonomic group ($p > 0.05$ for all pairwise comparisons). Figure 3 shows box-and-whisker plots of the $\delta^{13}\text{C}$ range values for each taxon with a gray box that encompasses the maximum and minimum ranges for the *Redunca* sample. The mean ranges of *Alcelaphus*, *Connochaetes*, and *Damaliscus* $\delta^{13}\text{C}$ differ the most from *Redunca*. However, there is considerable overlap and variability, such that the mean of *Redunca* falls within the bounds of the lower standard deviation of all non-reedbuck taxa.

Run plots (Fig. 3) show the shape of changes in $\delta^{13}\text{C}$ across enamel samples from every specimen. These plots document shifts in $\delta^{13}\text{C}$ across the development of the tooth from the cervix to apex (A-O in the figure). The top left plot in Figure 3 shows run plots for all specimens from all taxa combined. This plot illustrates the basic shape of change observed for all specimens and highlights the few specimens for which patterned changes, such as a bell-curve or staircase shape, were found. The remaining plots show the shape of changes in $\delta^{13}\text{C}$ for specimens within

their respective genus or likely taxonomic attribution. These plots contain fewer specimens and allow the reader to visually identify the taxonomic groups that contain individuals with patterned $\delta^{13}\text{C}$ changes. Note the considerable intrataxon variation (see Discussion below).

Table 2 Part 1. Summary data of the $\delta^{13}\text{C}$ samples for each tooth specimen with assigned dietary categories. *Strong C3 specimens (all samples strong C3) [N=10]*

<i>Strong C3 specimens (all samples strong C3) [N=10]</i>								
Specimen ID	Genus	N	Median	Mean	Std Dev	Min	Max	Range
66805	<i>Alcelaphus</i>	12	-10.7	-10.6	0.3	-11.2	-10.1	1.2
67502	<i>Alcelaphus</i>	6	-10.3	-10.3	0.3	-10.7	-10.0	0.7
	<i>Alcelaphus/</i>							
67710	<i>Connochaetes</i>	14	-12.0	-11.9	0.4	-12.3	-11.1	1.3
66674	<i>Antidorcas</i>	3	-11.7	-11.9	0.6	-12.6	-11.5	1.2
66674	<i>Antidorcas</i>	4	-11.3	-11.3	0.5	-11.8	-10.8	1.1
66693	<i>Antidorcas</i>	3	-12.0	-12.2	0.3	-12.6	-12.0	0.6
115250	<i>Antidorcas</i>	9	-11.9	-12.0	0.3	-12.5	-11.4	1.2
115426	<i>Antidorcas?</i>	7	-10.5	-10.6	0.2	-10.8	-10.3	0.5
67539	<i>Connochaetes</i>	4	-10.5	-10.6	0.6	-11.3	-10.0	1.3
66316.11	<i>Hippotragus</i>	6	-13.4	-13.1	0.5	-13.5	-12.3	1.3
<i>Specimens with some strong C3 samples [N=14]</i>								
66751	<i>Alcelaphus</i>	9	-7.9	-8.3	2.2	-11.4	-5.5	5.9
67099	<i>Alcelaphus</i>	15	-9.5	-9.4	0.6	-10.4	-8.3	2.1
67562	<i>Alcelaphus</i>	7	-9.8	-10.0	0.3	-10.6	-9.6	1.0
67798	<i>Alcelaphus</i>	13	-9.8	-9.1	0.5	-10.2	-8.6	1.6
115209	<i>Alcelaphus</i>	14	-10.0	-10.4	1.0	-12.7	-9.4	3.3
67129	<i>Antidorcas</i>	8	-10.6	-10.5	0.4	-11.1	-9.7	1.3
115358	<i>Antidorcas</i>	6	-10.8	-10.7	0.4	-11.2	-9.9	1.3
67367	<i>Connochaetes</i>	14	-9.3	-9.2	0.6	-10.4	-8.3	2.1
115227	<i>Connochaetes</i>	13	-8.8	-8.7	0.8	-10.1	-7.5	2.7
115248	<i>Connochaetes</i>	7	-9.5	-9.7	0.4	-10.6	-9.3	1.3
Specimen ID	Genus	N	Median	Mean	Std Dev	Min	Max	Range

67836	<i>Hippotragus</i>	8	-9.2	-9.3	0.6	-10.2	-8.6	1.7
67278	<i>Redunca</i>	7	-9.3	-9.4	0.3	-10.0	-8.9	1.2
67535	<i>Redunca</i>	4	-10.1	-10.0	0.2	-10.2	-9.6	0.7
115391	<i>Redunca</i>	11	-10.4	-10.3	0.3	-10.7	-9.6	1.1

Table 2 Part 2. Summary data of the $\delta^{13}\text{C}$ samples for each tooth specimen with assigned dietary categories.

<i>Specimens with no strong C3 samples [N=15]</i>								
Specimen ID	Genus	N	Median	Mean	Std Dev	Min	Max	Range
66613	<i>Alcelaphus</i>	9	-8.4	-8.4	0.2	-9.2	-8.1	0.7
66996	<i>Alcelaphus</i>	12	-8.5	-8.	0.5	-9.1	-7.5	1.6
67302	<i>Alcelaphus</i>	5	-8.1	-8.5	0.9	-9.9	-7.6	2.2
67317	<i>Alcelaphus</i>	11	-5.5	-5.9	1.1	-8.4	-4.9	3.5
66769	<i>Antidorcas</i>	4	-7.9	-7.7	0.9	-8.7	-6.5	2.2
115268	<i>Antidorcas</i>	3	-8.5	-8.5	0.3	-8.8	-8.1	0.6
67037	<i>Connochaetes</i>	2	-7.2	-7.2	0.1	-7.3	-7.0	0.2
66594	<i>Damaliscus</i>	3	-7.6	-7.6	0.4	-8.1	-7.1	0.9
67833	<i>Damaliscus</i>	2	-7.6	-7.6	0.2	-7.8	-7.4	0.3
115216	<i>Damaliscus</i>	12	-5.5	-5.8	1.1	-8.0	-4.3	3.7
115237	<i>Damaliscus</i>	4	-9.2	-9.2	0.5	-9.9	-8.5	1.3
67125	<i>Hippotragus</i>	13	-8.3	-8.3	0.3	-8.9	-7.6	1.2
65115	<i>Redunca</i>	4	-9.4	-9.3	0.1	-9.5	-9.1	0.3
66902	<i>Redunca</i>	4	-7.8	-7.8	0.5	-8.5	-7.3	1.2
115240	<i>Redunca</i>	8	-8.9	-9.0	0.3	-9.6	-8.5	1.1

Table 3. $\delta^{13}\text{C}$ *post hoc* Dunnett's contrast comparisons from a mixed effects model comparing all taxa to the *Redunca**

Pairwise comparison	Est.	SE	lowerCI	upperCI	Pr(> z)
<i>Alcelaphus-Redunca</i>	0.13	0.68	-1.68	1.93	1
<i>Alcelaphus/Connochaetes-Redunca</i>	-2.33	1.38	-5.98	1.33	0.4206
<i>Antidorcas-Redunca</i>	-1.18	0.75	-3.15	0.79	0.4901
<i>Antidorcas?-Redunca</i>	-1.05	1.46	-4.92	2.81	0.9774
<i>Connochaetes-Redunca</i>	0.2	0.82	-1.97	2.38	1
<i>Damaliscus-Redunca</i>	1.6	0.89	-0.76	3.96	0.3494
<i>Hippotragus-Redunca</i>	-0.62	0.95	-3.12	1.89	0.9872

* Est . is the estimated difference between taxon means; SE is the standard error of that estimated difference;

lowerCI/upperCI are the lower/upper 95% family-wise confidence intervals for the difference between taxon means;

Pr(>|z|) is the probability that there is no difference between means (with a significant alpha level of 0.05).

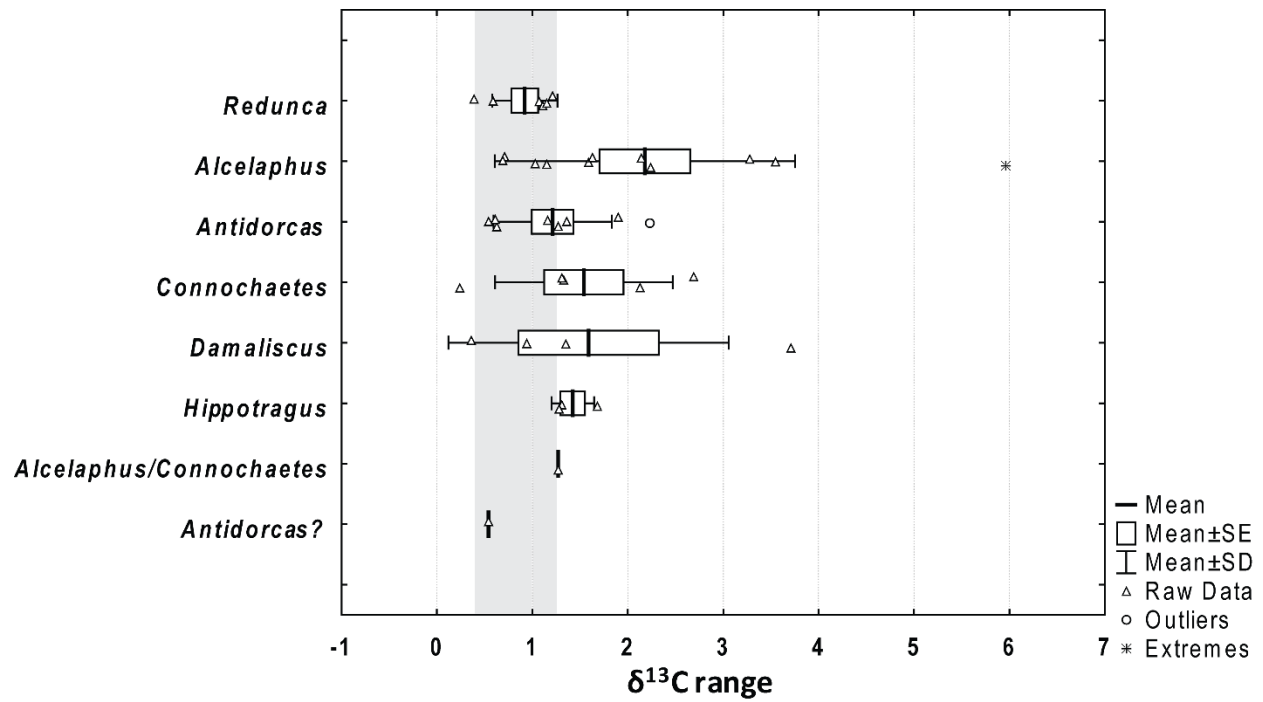


Fig. 3. Box-and-whisker plot of the total range of $\delta^{13}\text{C}$ isotopic ratio values for specimens from each taxon. The gray box encompasses the maximum and minimum ranges for the *Redunca* sample.

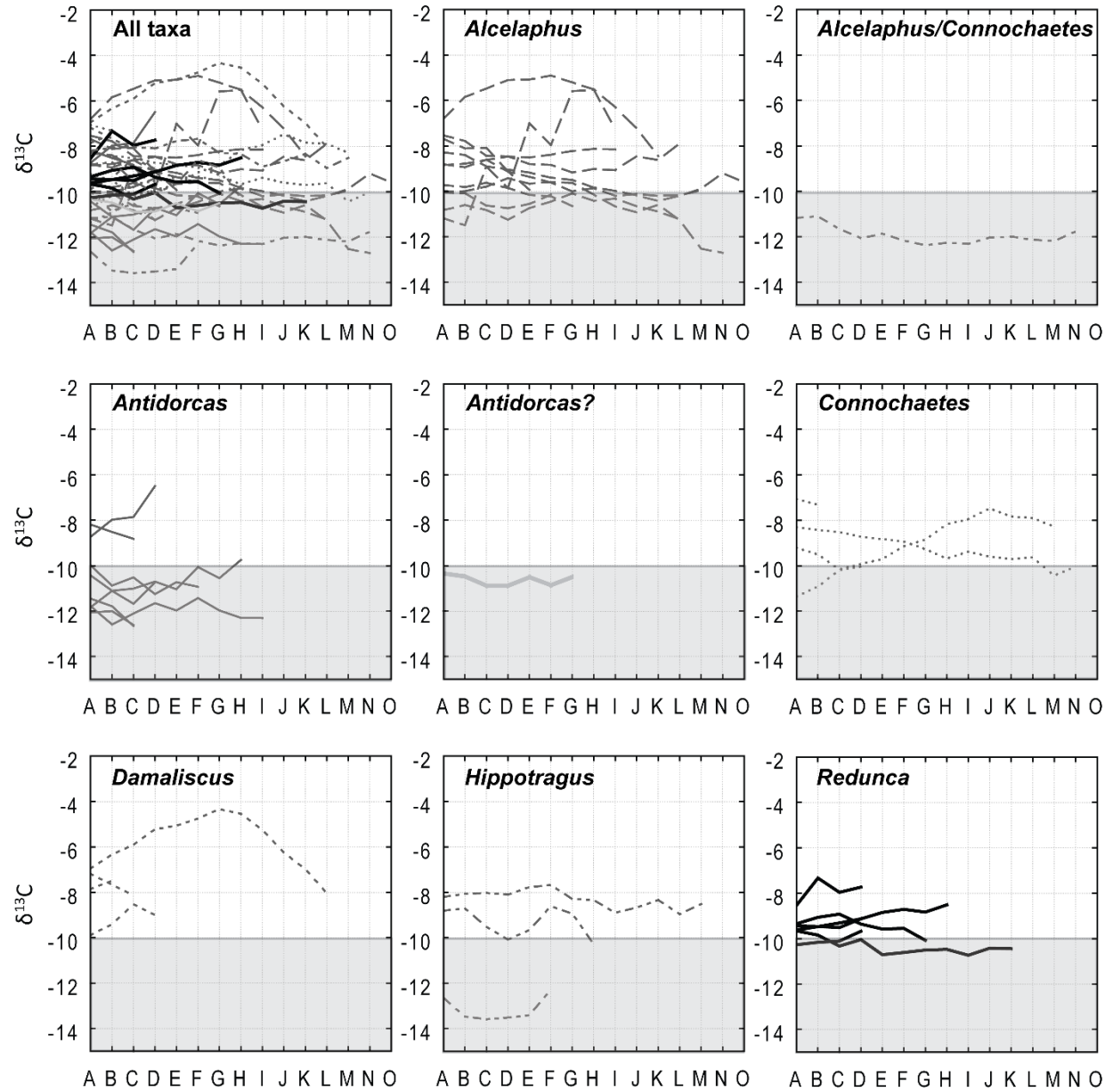


Fig. 4. Run plots of the $\delta^{13}\text{C}$ isotopic values. The dashed or solid lines represent individual teeth from a single specimen with the samples along the tooth provided in alphabetical order from cervix to apex. The type of dash in each individual taxon plot matches its counterpart in the “All taxa” plot. The translucent gray box indicates the zone of values for which a strong C_3 dietary signal is indicated ($\leq -10\text{‰}$).

4.1 $\delta^{18}\text{O}$ isotopic ratios

Table 4 part I and II show summary data of the $\delta^{18}\text{O}$ isotopic ratios for all specimens. The means of *Alcelaphus* specimens range between 0.6 to -3.0‰ with an average individual range of 3.7‰. One *Alcelaphus* specimen does have the highest $\delta^{18}\text{O}$ range (8.6‰) out of all specimens sampled. The mean $\delta^{18}\text{O}$ values for *Antidorcas* range between 0.2‰ and -3.5‰. Five individuals have ranges greater than 2‰ (one specimen with a range of 6.5‰). The means of *Connochaetes* specimens range from 2.3‰ to -2.0‰; all specimens have ranges greater than 2‰, with the highest individual range of 6.2‰. The mean $\delta^{18}\text{O}$ values for *Damaliscus* range between -0.3‰ and -1.8‰. Only one specimen of *Damaliscus* has a range greater than 2‰, at 3.4‰. The means of *Hippotragus* specimens range between 2.9‰ to -0.2‰ with the maximum range observed among individuals of 3.3‰. The mean $\delta^{18}\text{O}$ values for *Redunca* range between 0.5‰ and -1.4‰; four of the 6 specimens of *Redunca* have ranges greater than 2‰, with the greatest individual range at 5.3‰.

Similar to the $\delta^{13}\text{C}$ results, the $\delta^{18}\text{O}$ mixed effects model's *post hoc* Dunnett's contrasts analysis (Table 5) shows no significant difference in the $\delta^{18}\text{O}$ isotopic ratios when each taxon is compared to the southern reedbuck. The one-way ANOVA ($F_{5,31} = 1.18$, $p = 0.34$) and *post hoc* Dunnett's contrasts on the range values for the $\delta^{18}\text{O}$ isotopic ratio values also shows no significant difference between any taxon and *Redunca*. Box-and-whisker plots of the $\delta^{18}\text{O}$ range values for each taxon are provided in Figure 5, with a gray box that encompasses the maximum and minimum ranges for the *Redunca* sample. Note the extensive overlap in values among all taxa and that all specimens with the exception of three outliers (one each of *Alcelaphus*, *Antidorcas*, *Connochaetes*) fall within the range of values exhibited by *Redunca*.

Run plots (Fig. 6) show the shape of changes in the $\delta^{18}\text{O}$ across the samples for each tooth in all taxa combined and in each taxonomic grouping separately. The top left plot in Figure 6 shows run plots for all specimens from all taxa combined. These plots illustrate mostly random changes in $\delta^{18}\text{O}$ across the intraspecimen samples. One *Alcelaphus/Connochaetes* specimen and one *Damaliscus* individual might be interpreted as showing directional changes within a very limited range of values (possibly indicated movement from one rainfall regime to another), but overall the $\delta^{18}\text{O}$ data evince very few vectored shifts in the data.

Table 4 Part 1. Summary data of the $\delta^{18}\text{O}$ samples for each specimen.

Specimen ID	Genus	N	Median	Mean	Std. Dev	Min	Max	Range
66613	<i>Alcelaphus</i>	9	-2.1	-2.0	0.5	-3.0	-1.1	1.8
66751	<i>Alcelaphus</i>	9	-2.1	-2.1	1.7	-4.3	0.5	4.9
66805	<i>Alcelaphus</i>	12	-1.6	-1.6	0.7	-2.8	-0.3	2.5
66996	<i>Alcelaphus</i>	12	-3.2	-2.5	2.2	-4.2	4.4	8.6
67099	<i>Alcelaphus</i>	15	-1.2	-1.3	0.8	-3.4	-0.1	3.2
67302	<i>Alcelaphus</i>	5	0.4	0.6	1.1	-0.4	2.6	3.0
67317	<i>Alcelaphus</i>	11	0.0	-0.1	1.2	-1.7	1.7	3.5
67502	<i>Alcelaphus</i>	6	-2.2	-2.3	0.8	-3.4	-0.9	2.4
67562	<i>Alcelaphus</i>	7	0.4	0.4	1.2	-1.2	2.2	3.4
67798	<i>Alcelaphus</i>	13	-1.3	-0.6	1.4	-2.1	2.1	4.3
115209	<i>Alcelaphus</i>	14	0.0	0.0	0.8	-1.1	1.9	3.0
67710	<i>Alcelaphus</i> / <i>Connochaetes</i>	14	-3.1	-3.0	1.1	-4.7	-1.3	3.3
66674	<i>Antidorcas</i>	7	0.4	0.2	0.8	-0.7	1.5	2.3
66693	<i>Antidorcas</i>	3	-1.7	-3.5	3.6	-7.8	-1.2	6.5
66769	<i>Antidorcas</i>	4	-0.9	-0.8	0.8	-1.7	0.0	1.8
67129	<i>Antidorcas</i>	8	0.0	-0.2	1.0	-1.8	1.4	3.3
Specimen ID	Genus	N	Median	Mean	Std. Dev	Min	Max	Range
115250	<i>Antidorcas</i>	9	-1.0	-1.3	1.0	-2.9	0.1	3.0
115268	<i>Antidorcas</i>	3	0.1	0.1	0.7	-0.5	0.9	1.5
115358	<i>Antidorcas</i>	6	-0.9	-0.7	0.9	-2.0	0.5	2.5
115426	<i>Antidorcas?</i>	7	-0.3	-0.1	0.6	-0.7	0.7	1.4

Table 4 Part 2. Summary data of the $\delta^{18}\text{O}$ samples for each tooth specimen.

Specimen ID	Genus	N	Median	Mean	Std. Dev	Min	Max	Range
67037	<i>Connochaetes</i>	2	2.3	2.3	4.4	-0.8	5.4	6.2
67367	<i>Connochaetes</i>	14	-1.2	-1.3	1.1	-3.6	0.3	3.9
67539	<i>Connochaetes</i>	4	0.6	0.2	1.0	-1.2	1.1	2.4
115227	<i>Connochaetes</i>	13	-2.1	-2.0	1.0	-3.2	0.5	3.8
115248	<i>Connochaetes</i>	7	-1.6	-2.0	1.0	-3.6	-0.8	2.8
66594	<i>Damaliscus</i>	3	-0.3	-0.3	0.1	-0.5	-0.1	0.3
67833	<i>Damaliscus</i>	2	-0.7	-0.7	0.0	-0.7	-0.6	0.0
115216	<i>Damaliscus</i>	12	-1.5	-1.5	1.	-3.4	0.0	3.4
115237	<i>Damaliscus</i>	4	-1.8	-1.8	0.7	-2.7	-0.8	1.9
66316	<i>Hippotragus</i>	6	3.0	2.9	1.2	1.5	4.3	2.8
67125	<i>Hippotragus</i>	13	0.3	0.6	0.6	0.0	1.6	1.6
67836	<i>Hippotragus</i>	8	-0.2	-0.2	1.0	-2.0	1.3	3.3
65115	<i>Redunca</i>	4	0.4	0.5	0.3	0.2	0.9	0.7
66902	<i>Redunca</i>	4	-0.9	-0.8	0.9	-1.8	0.3	2.1
67278	<i>Redunca</i>	7	-1.4	-1.4	0.7	-2.8	-0.5	2.3
67535	<i>Redunca</i>	4	-0.9	-0.9	0.5	-1.5	-0.2	1.2
115240	<i>Redunca</i>	8	-0.3	-0.4	1.3	-2.5	1.5	4.0
Specimen ID	Genus	N	Median	Mean	Std. Dev	Min	Max	Range
115391	<i>Redunca</i>	11	-1.2	-0.5	1.8	-3.4	1.9	5.3

Table 5. $\delta^{18}\text{O}$ *post hoc* Dunnett's contrast comparisons from a mixed effects model comparing all taxa to *Redunca**

Pairwise comparison	Est.	SE	lowerCI	upperCI	Pr(> z)
<i>Alcelaphus-Redunca</i>	-0.5	0.63	-2.16	1.16	0.9601
<i>Alcelaphus/Connochaetes-Redunca</i>	-2.55	1.12	-5.5	0.39	0.1228
<i>Antidorcas-Redunca</i>	-0.48	0.73	-2.41	1.45	0.9852
<i>Antidorcas?-Redunca</i>	0.38	1.37	-3.23	3.99	0.9999
<i>Connochaetes-Redunca</i>	-0.54	0.76	-2.54	1.46	0.9773
<i>Damaliscus-Redunca</i>	-0.71	0.87	-3.02	1.59	0.9542
<i>Hippotragus-Redunca</i>	1.59	0.86	-0.66	3.85	0.3041

*Est. is the estimated difference between taxon means; SE is the standard error of that estimated difference;

lowerCI/upperCI are the lower/upper 95% family-wise confidence intervals for the difference between taxon means;

Pr(>|z|) is the probability that there is no difference between means (with a significant alpha level of 0.05).

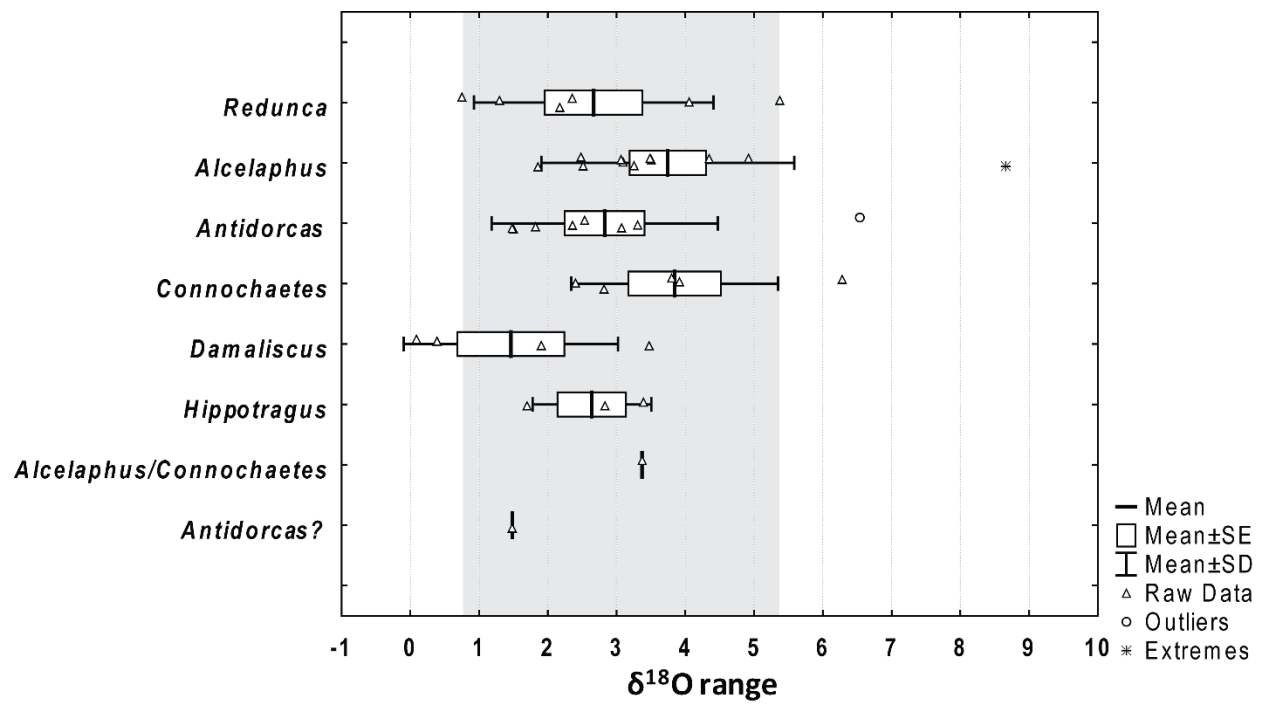


Fig. 5. Box-and-whisker plot of the total range of $\delta^{18}\text{O}$ isotopic ratio values for specimens from each taxon. The gray box encompasses the maximum and minimum ranges for the reedbuck sample (*Redunca*).

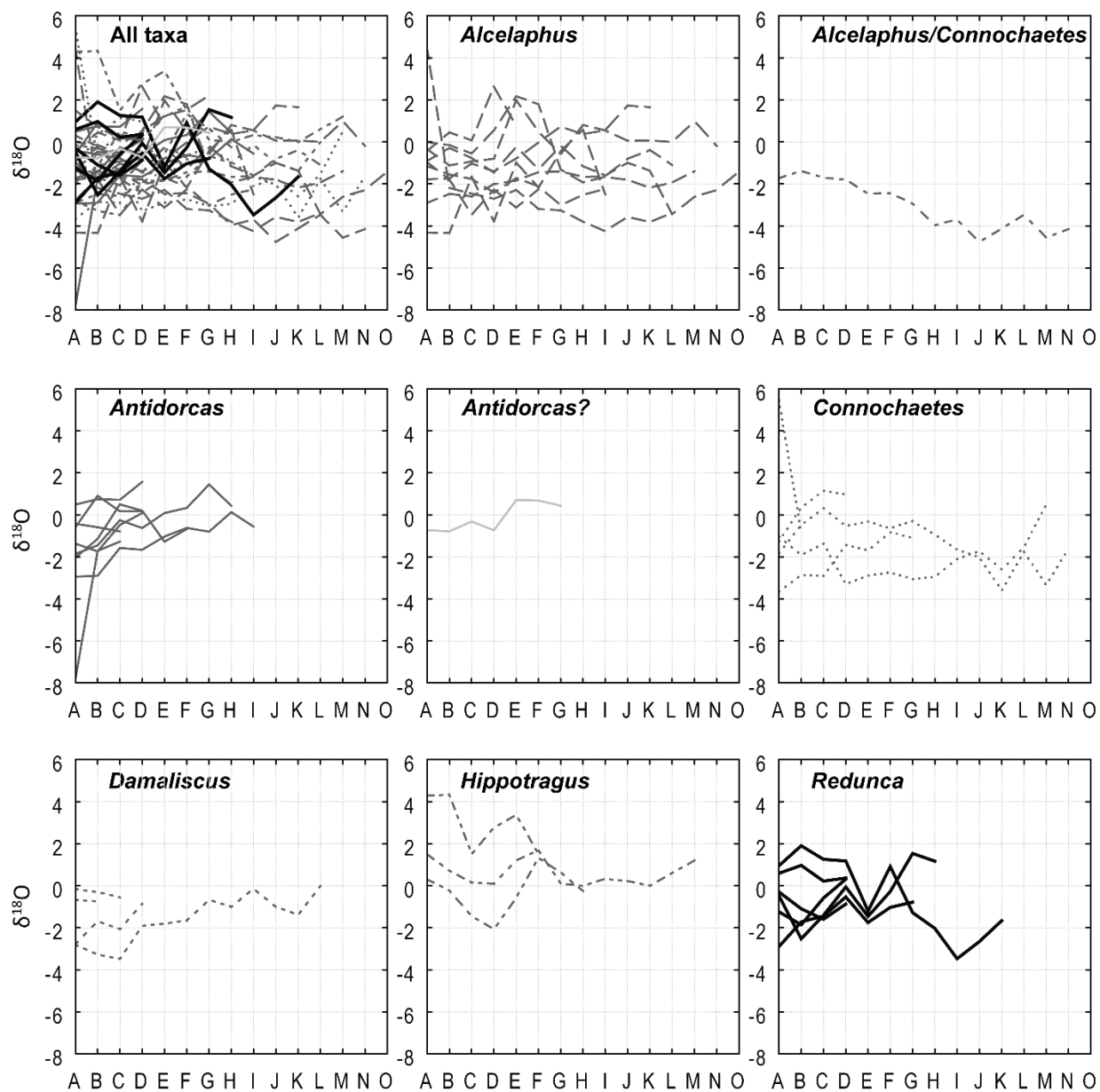


Fig. 6. Run plots of the $\delta^{18}\text{O}$ isotopic ratio values. The dashed or solid lines represent individual teeth from a single specimen with the samples along that tooth provided in alphabetical order from cervix to apex. The type of dash in each individual taxon plot matches its counterpart in the "All taxa" plot.

5. Discussion

5.1 $\delta^{13}\text{C}$ isotopic ratios

Results from the study show that herbivores from PP30 had a range of diets, with some individuals consuming a dominance of C_3 for their entire tooth development (all tooth samples $\leq -10\text{‰}$), others consuming a dominance of C_3 for part of their tooth development (enough C_3 to have some samples from the tooth be $\leq -10\text{‰}$), and still others consistently consuming a mix of C_3 and C_4 plants such that all tooth samples are $> -10\text{‰}$ (Table 2). None of the animals (on a taxon-wide basis) exhibit statistically significant differences in their $\delta^{13}\text{C}$ values (either the mean or range data) from the control taxon, *Redunca* (Table 3; Fig. 3). These analyses suggest that most of the animals were no more mobile than *Redunca* providing little evidence that they ranged beyond a fairly restricted local area surrounding PP30. Furthermore, most specimens either show little change in their $\delta^{13}\text{C}$ values ($< 2.5\text{‰}$) during tooth development indicating that there was little dietary shift across early life history (Fig.4). Moreover, the absence of clear vectored shifts in the values provides no strong evidence for migratory behaviors. However, the $\delta^{13}\text{C}$ values (both mean and range) for several individuals from various taxa fall well outside those found for *Redunca* and a few show patterns consistent with directional shifts. Here we consider the importance of intrataxonomic variation in $\delta^{13}\text{C}$ values for assessing herbivore mobility on the PAP and assessing the east-west migration model.

Redunca, the southern reedbuck (our control taxon), shows little variation in $\delta^{13}\text{C}$ within specimens ($<1.3\text{‰}$) (Table 2; Figs. 3 & 4). Given that *Redunca* are documented grazers consuming $>95\%$ C_4 grass (Jungius, 1971; Gagnon and Chew, 2000; Codron et al., 2018), it is interesting that at times the diet of three of our six specimens was composed of a mix of C_3 and C_4 plants, comparable to what was recorded by Venter and Kalule-Sabiti (2016), and at other

times focused on C₃ (Table 2; Fig. 4). The other three *Redunca* specimens in our sample consistently have a mixed C₃ and C₄ diet. These data suggest that we might be picking up some slight seasonal changes in the amount of C₃ and C₄ grass, as we would expect as the local rains shift from summer to winter through the year in this bimodal rainfall area of the southern Cape coast of South Africa. However, the modest changes are inconsistent with any significant changes in diet.

Redunca are known to eat C₃ sedges and wetland grasses (Venter and Kalule-Sabiti, 2016). Hyenas and humans transporting *Redunca* remains back to PP must have traveled to wetland grasslands to hunt them. The nearest floodplain, as reconstructed from the geophysics, would be roughly ~10-15 km to the east from PP in the Hartenbos River drainage. However, smaller drainages with floodplain grasslands may have been closer and provided *Redunca* habitat. Our results provide some information on the nature of those floodplain grasslands. These grasslands included both C₃ and C₄ grasses. The lack of major changes or any strong pattern of seasonally vectored change suggests that both C₃ and C₄ grasses were available year-round and *Redunca* fed on both all year. Most of the individuals hover around $\delta^{13}\text{C}$ values of -9 to -10, indicating that they were ingesting more C₃ grasses than C₄. Given that most grazers prefer C₄ grasses, this suggests that C₃ grasses were more common than C₄ on the floodplains. (Cawthra et al., this volume) show that floodplains were a dominant feature on the PAP, and (Marean et al., this volume) propose that *Redunca* may have been a major ungulate of the PAP.

Variation in $\delta^{13}\text{C}$ is similarly low in our *Hippotragus* specimens (Figure 3). This is a genus that includes three species: the extant sable antelope (*H. niger*), the extant roan antelope (*H. equinus*), and the extinct bluebuck (*H. leucophaeus*) (Skinner and Chimimba, 2005). The latter two occurred in the GCFR (Klein, 1983). Roan antelope went extinct in the GCFR ~10,000

years ago (Klein, 1983) but the bluebuck was still present in modern colonial times when it was hunted to extinction (Skead, 1980). Rector and Reed (2010) assigned the *Hippotragus* specimens to bluebuck and we follow those assignments here. Data on forage selection indicates roan are C₄ grazers or mixed feeders based on data from both extant animals and archaeological records (Schuette et al., 1998; Codron et al., 2018). Both extant species are known to be fairly water independent and occur far away from permanent water, avoiding competition from numerous water dependent herbivores and associated predation pressure (Harrington et al., 1999). There is no evidence to suggest that the extant species migrated in aggregations, though Faith and Thompson (2013) interpreted the age at death data of late Quaternary fossil specimens as being consistent with migration. Variation in $\delta^{13}\text{C}$ within specimens of *Hippotragus* is slightly greater than measured in *Redunca* but not by much (0.4‰). The diet within the individuals we sampled is varied, again consistent with behaviors reported for this group. One individual switched back and forth between a mixed diet to pure C₃, another individual's diet was purely C₃, and another had a consistently mixed diet (Table 2). These data are inconsistent with seasonal movement between the east and west. While our results are inconsistent with Faith and Thompson (2013), it is important to note that all our specimens come from a narrow window of time centered on ~151 ka, while their sample is spread widely in time.

Some specimens of Alcelaphines, a group that includes hartebeest (*Alcelaphus*), wildebeest (*Connochaetes*), and bontebok (*Damaliscus*), in particular show moderate vectored shifts between C₃ and C₄ over the course of tooth development (Fig. 5) as would be expected in a migratory situation in which animals' access to C₃ and C₄ plants changed as they moved east-west over the PAP. These vectored shifts may make sense for the documented behaviors of these genera both today and in the past as will be detailed below.

A total of eight extant *Alcelaphus* species are currently recognized (Venter and Child, 2016). One extant species, the red hartebeest (*Alcelaphus buselaphus caama*) (134 kg), was joined by the extinct giant hartebeest (*Megalotragus priscus*) (200 kg) in the GCFR, with the latter going extinct ~20 000 years ago (Klein, 1974, 1983; Brink et al., 1995, 2015). *Alcelaphus* are generally considered to be grazers with >75% of their diet consisting of grass (Gagnon and Chew, 2000). Current knowledge indicates that in the majority of cases *Alcelaphus* species (mainly red hartebeest) prefer C₄ grasses (Venter and Kalule-Sabiti, 2016; Codron et al., 2018; Vermeulen, 2018). They have long muzzles, an adaptation allowing them to feed on taller and coarser grass (Schuette et al., 1998; Venter et al., 2014). They are known to move significant distances in large groups, and aggregated seasonal migrations of red hartebeest have been recorded in arid Savanna systems (Verlinden, 1998; Harris et al., 2009). Within our sample, two specimens preserved $\delta^{13}\text{C}$ values consistently < -10 suggesting they ate primarily C₃ grass throughout tooth development. Five specimens switched between a mixed diet and strong C₃, and four specimens consistently ate a mixed diet (Table 2). These data again suggest the presence of C₃ grasses around PP and modest amounts of C₄ grass. Some of the *Alcelaphus* specimens resemble *Redunca* in their values (hovering around -9 to -10‰), their low maximum range (~1‰), and in not showing any distinct patterned change in their $\delta^{13}\text{C}$ values over time.

A second group of *Alcelaphus* individuals differs from the *Redunca* pattern. For example, specimen 66751 preserves a staircase like (up and down) shift from lower $\delta^{13}\text{C}$ values to more enriched $\delta^{13}\text{C}$ values (Fig. 4). For this specimen the total variation in $\delta^{13}\text{C}$ within the tooth is 5.96‰, the most variation recorded in our samples. The $\delta^{13}\text{C}$ values processed from specimen 67317 preserves a bell-shaped curve, with the total intra-tooth $\delta^{13}\text{C}$ variation equal to 3.55‰. These two specimens preserve the most variation in this taxon.

Within the genus *Connochaetes* two extant species, the black wildebeest (*Connochaetes gnou*) (132 kg) and blue wildebeest (*Connochaetes taurinus taurinus*) (189 kg) commonly occur in South Africa (Tambling et al., 2016; Vrahimis et al., 2016). The black wildebeest was present in the GCFR until ~6 000 years ago (Klein, 1983) and is a grazer with >80% of its diet composed of grasses, preferring short grass (Gagnon and Chew, 2000). Rector and Reed (2010) assigned the PP30 material to this species. It was thought to be primarily migratory though its movement systems were destroyed prior to being scientifically observed. Within our sample one specimen is assigned to *Alcelaphus/Connochaetes* sp. Indet. This individual ate a strongly C₃ diet, most likely C₃ grasses. Three specimens switched between mixed diets and strongly C₃, and one specimen consistently had a mixed diet (Table 2). All of these resemble the *Redunca* pattern. However, two of our specimens show a moderate to weak vectored shift: specimen 115227 preserves a long-tailed bell-curve with low intra-tooth $\delta^{13}\text{C}$ variation (2.69‰), and specimen 67367 preserves an overall trend of decreasing $\delta^{13}\text{C}$ values also with low intra-tooth variation $\delta^{13}\text{C}$ (2.13‰).

While the specifics of *Damaliscus* taxonomy are not yet fully resolved, it is generally accepted that two subspecies occur in South Africa: the bontebok (*Damaliscus pygargus pygargus*)(60 kg) and blesbok (*Damaliscus pygargus phillipsi*)(60 kg) (van der Walt et al., 2013). *D. p. pygargus* is endemic to the GCFR (Radloff et al., 2016). *Damaliscus* are mainly grazers with >95% grass in their diets (Gagnon and Chew, 2000; Kraaij and Novellie, 2010). The blesbok grazes mainly on C₄ grass (Codron et al., 2018), while the bontebok may consume more C₃ in Fynbos habitats; however, in Bontebok National Park this species mainly consumes *Cynodon dactylon* which is a C₄ short grass (Kraaij and Novellie, 2010), thus dietary flexibility is documented for this taxon. Within our samples, this is the only genus that had a consistently

mixed diet, with no pure C₃ signal. Records exist of migratory behavior for blesbok (Harris et al., 2009) but none for the bontebok. In our analysis, one specimen, 115216, preserves a bell curve pattern in $\delta^{13}\text{C}$ values with moderate intra-tooth variation $\delta^{13}\text{C}$ (3.71‰), which exceeds by 2‰ the variation detected in the southern *Redunca*.

With some individuals of *Alcelaphus*, *Connochaetes* and *Damaliscus* preserve vectored shifts in C₃ consumption (some with changes in $\delta^{13}\text{C}$ >2.5‰), it is interesting that clear shifts in diet are not observed in *Antidorcas*. Three extant subspecies of the genus *Antidorcas* are recognized. The common springbok (*Antidorcas marsupialis*) (29.5 kg) occurs in the GCFR (Anderson et al., 2016), and at least one extinct species, the southern springbok (*Antidorcas australis*) also occurred in the GCFR until ~20 000 years ago (Klein, 1983; Brink and Lee-Thorp, 1992). Data from both extant animals and archaeological records show common springbok are generally mixed feeders consuming both C₃ browse and C₄ grass (Codron et al., 2018). However, in some ecosystems they seem to prefer C₃ browse (Venter and Kalule-Sabiti, 2016; Vermeulen, 2018); for example, data of southern springbok from Swartkrans Member 1-3 indicates mainly a C₃ diet (Codron et al., 2018). Our analysis confirms that *Antidorcas* as a taxon has a flexible diet: four specimens and one difficult to identify specimen (*Antidorcas* sp.) ate pure C₃ diets, two switched between mixed and pure C₃, and two had mixed diets. Descriptions of massive aggregated seasonal migrations of common springbok in the Nama-Karoo of South Africa are common in records from colonial hunters and explorers (Skead, 1980; Skinner and Chimimba, 2005; Harris et al., 2009). At PP 30 the maximum change in $\delta^{13}\text{C}$ <2.5‰ argues against a seasonal east-west migration in this group.

Overall, the $\delta^{13}\text{C}$ results do not support an ecosystem model in which most herbivores were undergoing long distance point-to-point migrations that would be consistent with an east-

to-west migration system along the PAP. However, several individuals of various taxa diverge from the *Redunca* pattern. It is therefore possible that there was at least some intrataxon variability and that subgroups of each species were engaging in migratory behavior and that the hyena occupying PP30 were sampling from diverse populations that exhibited different behaviors. Time averaging could also have contributed to these results, since it is known that over relatively short time periods pressures can cause herbivores to change their migratory behavior (Wilson et al., 2018). It is also possible that these individuals were not undertaking point-to-point migrations but did range more widely at younger ages. This last scenario seems the most probable given the current results.

5.2 $\delta^{18}\text{O}$ isotopic ratios

There is no statistically significant difference in either the absolute mean $\delta^{18}\text{O}$ values (Table 5) or the intraspecimen ranges (Fig. 5) between *Redunca* and any of the taxon. Furthermore, none of the $\delta^{18}\text{O}$ run charts (Fig. 6) show strong vectored changes over the course of tooth development. The rainfall systems in South Africa, predominantly summer convective rainfall to the east and winter stratiform frontal or orographic rainfall to the west, have differing oxygen isotope characteristics. The winter rainfall is depleted relative to the summer (Bar-Matthews et al. 2010; Braun et al. 2017). This led us to hypothesize that oxygen isotopes may also preserve a signal related to pattern of movement, but our data suggest that they do not. Thus, the $\delta^{18}\text{O}$ data don't support the east west seasonal migration hypothesis for herbivores preserved at PP30.

Bar-Matthews et al. (2010) found a correlation between carbon and oxygen in the speleothems. This would be expected, because C₃ grasses are favored under winter rainfall while C₄ are favored under summer rainfall. Thus, serially drilled samples of enamel should show a more depleted oxygen signal at the same time as a more C₃ dietary signal, and conversely a less depleted signal associated with a more C₄ signal. Given that some individuals show $\delta^{13}\text{C}$ suggestive of at least high mobility (if not true migration), it is somewhat surprising that $\delta^{18}\text{O}$ values do not correspond with that pattern. To investigate this further, we calculated the correlation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ across the specimens in the sample. Such correlations were insignificant for all taxa except *Hippotragus* (Table 6). Thus, for most taxa the hypothesis that more depleted $\delta^{18}\text{O}$ would correlate with a stronger C₃ diet in herbivores, and more enriched $\delta^{18}\text{O}$ with a stronger C₄ signal is not upheld here. The significant correlation in *Hippotragus* deserves more attention in the future as no ecological explanation is immediately available. However, only three specimens of *Hippotragus* were available, making the statistical significance likely the result of sampling error. As we noted in the discussion above, the oxygen values for ungulates are subject to multiple causes, including a strong fractionation effect in plants; and increases and decreases in aridity (Brink, 2016) (an effect that would be pronounced over time at PP due to ocean transgressions and regressions). These factors may have overwhelmed any signal of movement in the $\delta^{18}\text{O}$.

Table 6. Correlation between $\delta^{13}\text{C}$ vs $\delta^{18}\text{O}$ within each taxon

	r^2	p
<i>Alcelaphus</i>	0.01	0.23
<i>Connochaetes</i>	0.08	0.08
<i>Antidorcas</i>	0.06	0.14
<i>Redunca</i>	0.02	0.44
<i>Damaliscus</i>	0.00	0.98
<i>Hippotragus</i>	0.36	<0.001

4.3 Implications for the Palaeoecology of the PAP

Our sample comes from a narrow time range when the PAP was expansive in size (Fisher et al. 2010) and conditions were relatively cold during the MIS 6 glacial. While the speleothem samples do not cover the dated accumulation phase of PP30 due to a hiatus, throughout MIS 6 the speleothem record suggests a mixed C_3 and C_4 vegetation cover. A comparison of bulk isotope values extracted from micromammals collected by owls and large ungulates collected by brown hyenas (Williams et al., this volume) show that the local vegetation was strongly C_3 , while the more expansive range covered by grazing large mammals was a mixed C_3 and C_4 vegetation system. These results, combined with the results presented here, allow us to make some tentative generalizations about the palaeoecology of the PAP in relation to the hunters who occupied the landscape.

Floodplain grasslands were a significant feature of the exposed PAP (Cawthra et al., this volume; Potts et al., this volume). The *Redunca* sampled here inhabited those floodplain grasslands, and our results suggest those grasslands were predominantly C₃ grass with modest amounts of C₄ grass. Thirteen of the sampled ungulates anticipated to utilize both the non-floodplain grasslands (Alcelaphines: *Alcelaphus*, *Connochaetes*, and *Damaliscus*), and the floodplains, show mixed C₃ and C₄ signals more toward C₃, without signs of seasonal changes in diet (< 2 ppm range). Four individuals show some moderate (2-3 ppm) seasonal switching between C₃ and C₄, and four show more substantial (> 3 ppm) seasonal switching between C₃ and C₄. This suggests that the Pinnacle Point region of PAP grasslands at ~151 ka experienced little seasonal variation, and maintained a mix of C₃ and C₄ grassland; otherwise, we would detect more substantial changes in the isotope values for *Redunca*. The ostrich eggshells from PP30 show a predominantly C₃ signal, which is consistent with the local grasslands being predominantly C₃ with some modest amounts of C₄ grass. The trends toward higher amounts of C₄ indicated by some of the alcelaphines suggest that some regions outside the Pinnacle Point region likely supported higher amounts of C₄ grass and were visited by these individuals. The mix of ranges of isotopic variation among the alcelaphines is consistent with an ecology where some tend to be resident and others tend to move seasonally. It is possible that the relatively colder temperatures of MIS 6 favored C₃ grasses, since an expanded C₄ grassland is indicated by the speleothems during the somewhat warmer MIS 4.

Ungulates such as *Alcelaphus* and *Connochaetes* normally move significant distances over the length of a year. Kingdon (2015) notes that the gregarious *Alcelaphus* persistently moves to get the best grass, and sometimes move up and down drainage lines in its pursuit. The black wildebeest (*Connochaetes gnou*) (before the destruction of its movement patterns and near

extinction in South Africa), summered in the Karoo then moved into the Highveld during the winter. Marean et al. (this volume) suggest that north-south movements on the PAP may have been an alternative to east-west movement when the plain was maximally exposed. The strongly dominant floodplain structure of the PAP may have imposed obstacles to east-west movement, but movements up and down the drainages to the coast and back may have been an alternative.

6. Conclusions

This analysis is a first attempt to use isotopic data as a test of the hypothesis that an east-west migration pattern was practiced by herbivores living on the PAP. We chose to test this hypothesis at PP30, a hyena den that preserves herbivore remains from a short accumulation period ~151 ka. At this time, the ocean had receded 91 km from the site of PP30, exposing a vast plain. Prior strontium isotope analysis of the ungulates from this site indicated that they all spent the vast majority of their lives on this plain rather than moving inland (Copeland et al. 2016), making them a good first test of the hypothesis. A combination of isotopic data from the majority of our ungulate sample and isotopic measurements from ostrich eggshell suggest that at ~151 ka in the Pinnacle Point region the grasslands, both floodplain and other, were predominantly C₃ with some C₄.

Results from this study do not substantiate the hypothesis that most ungulates were undertaking point-to-point migrations seasonally across the PAP. Some individuals exhibit a *Redunca* -like pattern, and these may have been resident in the area all year round. Some individuals exhibit more substantial dietary changes, but whether these were moving or not is unclear with the current sample. Environmental reconstructions presented in this issue demonstrate that paleo-rivers divided the PAP, creating a nutrient rich coastal plain that seems to have negated any necessity for herbivores to migrate. However, it is unlikely this situation

persisted through the many ocean transgressions and regressions of the late Pleistocene. It is possible, even probable, that the ocean transgression and the vanishing Paleo-Agulhas Plain triggered migratory behavior in herbivores, as they struggled to deal with loss of grazing territory. Future research will examine variations in the east-west migratory system across time and contribute to establishing the context within which early humans made a living in this environment.

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We have no conflicting interests.

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Supplemental Data

Table S1: The $\delta^{13}C$ and $\delta^{18}O$ values for each bulk sample of enamel drilled from each specimen.

Specimen	Distance from neck (mm)	Species	Mandible/ Maxilla		Molar	d13C	SD	d18O	SD
115250A- A	1.72	Antidorca	Maxilla	Right	M3	- 11.78	0.04	-2.94	0.07
115250A- B	3.04	Antidorcas	Maxilla	Right	M3	- 12.59	0.03	-2.90	0.06
115250A- C	5.43	Antidorcas	Maxilla	Right	M3	- 12.11	0.08	-1.57	0.06
115250A- D	7.21	Antidorcas	Maxilla	Right	M3	- 11.65	0.03	-1.66	0.10
115250A- E	9.53	Antidorcas	Maxilla	Right	M3	- 11.98	0.05	-1.03	0.03

115250A-F	10.76	Antidorcas	Maxilla	Right	M3	- 11.43	0.03	-0.62	0.05
115250A-G	13.35	Antidorcas	Maxilla	Right	M3	- 11.97	0.05	-0.80	0.06
115250A-H	15.45	Antidorcas	Maxilla	Right	M3	- 12.30	0.04	0.13	0.08
115250A-I	17.63	Antidorcas	Maxilla	Right	M3	- 12.31	0.03	-0.56	0.09
115268A-A	2.13	Antidorcas	Mandible	Right	M3	-8.19	0.05	-0.59	0.08
115268A-B	4.51	Antidorcas	Mandible	Right	M3	-8.52	0.05	0.91	0.03
115268A-C	6.41	Antidorcas	Mandible	Right	M3	-8.82	0.07	0.17	0.04

66693A-A	2.59	Antidorcas	Mandible	Left	M3	- 12.06	0.05	-7.81	0.09
66693A-B	4.48	Antidorcas	Mandible	Left	M3	- 12.00	0.08	-1.71	0.05
66693A-C	6.09	Antidorcas	Mandible	Left	M3	- 12.61	0.10	-1.27	0.06
66674A-A	1.95	Antidorcas	Mandible	Left	M3	- 11.83	0.07	0.49	0.04
66674A-B	3.82	Antidorcas	Mandible	Left	M3	- 11.11	0.10	0.75	0.03
66674A-C	5.41	Antidorcas	Mandible	Left	M3	- 11.67	0.07	0.72	0.04
66674A-D	7.68	Antidorcas	Mandible	Left	M3	- 10.75	0.05	1.57	0.04
66674B-A	1.40	Antidorcas	Mandible	Left	M2	- 11.46	0.06	-0.42	0.06

66674B-B	3.68	Antidorcas	Mandible	Left	M2	- 11.79	0.04	-0.59	0.06
66674B-C	5.38	Antidorcas	Mandible	Left	M2	- 12.66	0.08	-0.79	0.07
66769A-A	5.28	Antidorcas	Mandible	Left	M3	-8.73	0.06	-1.37	0.07
66769A-B	7.44	Antidorcas	Mandible	Left	M3	-7.98	0.04	-1.73	0.05
66769A-C	9.61	Antidorcas	Mandible	Left	M3	-7.86	0.10	-0.48	0.04
66769A-D	11.76	Antidorcas	Mandible	Left	M3	-6.50	0.11	0.09	0.13
67129A-A	2.25	Antidorcas	Mandible	Left	M3	- 10.43	0.17	-1.86	0.13
67129A-B	4.66	Antidorcas	Mandible	Left	M3	- 11.11	0.06	-1.45	0.06
67129A-C	7.47	Antidorcas	Mandible	Left	M3	- 11.01	0.13	-0.25	0.10

67129A-D	9.22	Antidorcas	Mandible	Left	M3	- 10.70	0.05	-0.63	0.06
67129A-E	11.70	Antidorcas	Mandible	Left	M3	- 11.04	0.08	0.09	0.05
67129A-F	14.24	Antidorcas	Mandible	Left	M3	- 10.06	0.07	0.33	0.06
67129A-G	16.77	Antidorcas	Mandible	Left	M3	- 10.55	0.06	1.45	0.05
67129A-H	18.75	Antidorcas	Mandible	Left	M3	-9.75	0.08	0.43	0.06
115358A-A	2.70	Antidorcas	Maxilla	Left	M3	-9.99	0.07	-2.04	0.09
115358A-B	4.78	Antidorcas	Maxilla	Left	M3	- 10.88	0.07	-1.14	0.07
115358A-C	7.47	Antidorcas	Maxilla	Left	M3	- 10.52	0.08	0.50	0.06

115358A-D	10.03	Antidorcas	Maxilla	Left	M3	- 11.25	0.07	0.20	0.09
115358A-E	12.70	Antidorcas	Maxilla	Left	M3	- 10.73	0.07	-1.28	0.06
115358A-F	15.29	Antidorcas	Maxilla	Left	M3	- 10.93	0.05	-0.68	0.07
67833A-A	4.18	Damaliscus	Maxilla	Right	M3	-7.85	0.09	-0.67	0.08
67833A-B	6.85	Damaliscus	Maxilla	Right	M3	-7.49	0.10	-0.76	0.05
115216A-A	4.26	Damaliscus	Mandible	Left	M3	-6.94	0.11	-2.81	0.09
115216A-B	6.73	Damaliscus	Mandible	Left	M3	-6.33	0.11	-3.29	0.12
115216A-C	9.78	Damaliscus	Mandible	Left	M3	-5.91	0.08	-3.48	0.11

115216A-D	12.83	Damaliscus	Mandible	Left	M3	-5.22	0.10	-1.91	0.06
115216A-E	15.55	Damaliscus	Mandible	Left	M3	-5.06	0.08	-1.80	0.09
115216A-F	18.35	Damaliscus	Mandible	Left	M3	-4.75	0.10	-1.66	0.08
115216A-G	20.73	Damaliscus	Mandible	Left	M3	-4.33	0.13	-0.66	0.05
115216A-H	23.76	Damaliscus	Mandible	Left	M3	-4.55	0.11	-1.01	0.07
115216A-I	26.24	Damaliscus	Mandible	Left	M3	-5.24	0.11	-0.13	0.07
115216A-J	28.75	Damaliscus	Mandible	Left	M3	-6.24	0.07	-1.01	0.10
115216A-K	31.29	Damaliscus	Mandible	Left	M3	-6.97	0.07	-1.38	0.09

115216A-L	34.34	Damaliscus	Mandible	Left	M3	-8.04	0.07	-0.01	0.08
115237A-A	3.41	Damaliscus	Maxilla	Left	M3	-9.9	0.1	-2.8	0.1
115237A-B	6.74	Damaliscus	Maxilla	Left	M3	-9.40	0.06	-1.70	0.05
115237A-C	10.15	Damaliscus	Maxilla	Left	M3	-8.53	0.10	-2.06	0.07
115237A-D	12.72	Damaliscus	Maxilla	Left	M3	-9.0	0.1	-0.9	0.1
66594A-A	3.60	Damaliscus	Maxilla	Left	M3	-7.19	0.06	-0.17	0.14
66594A-B	7.22	Damaliscus	Maxilla	Left	M3	-7.67	0.08	-0.31	0.07
66594A-C	10.77	Damaliscus	Maxilla	Left	M3	-8.13	0.06	-0.56	0.08
115248A-A	3.70	Connochaetes	Mandible	Right	M1/M 2	- 10.67	0.10	-3.65	0.09

115248A-B	9.17	Connochaetes	Mandible	Right	M1/M 2	- 10.18	0.10	-2.86	0.05
115248A-C	12.45	Connochaetes	Mandible	Right	M1/M 2	-9.66	0.10	-2.90	0.06
115248A-D	15.99	Connochaetes	Mandible	Right	M1/M 2	-9.52	0.11	-1.43	0.08
115248A-E	19.02	Connochaetes	Mandible	Right	M1/M 2	-9.38	0.10	-1.68	0.07
115248A-F	22.16	Connochaetes	Mandible	Right	M1/M 2	-9.34	0.09	-0.83	0.07
115248A-G	25.75	Connochaetes	Mandible	Right	M1/M 2	-9.49	0.11	-1.10	0.11
115227A-A	4.19	Connochaetes	Maxilla	Right	M3	-9.22	0.13	-1.03	0.07
115227A-B	7.38	Connochaetes	Maxilla	Right	M3	-9.51	0.11	-1.91	0.08

115227A-C	10.17	Connochaetes	Maxilla	Right	M3	- 10.16	0.09	-1.38	0.09
115227A-D	13.33	Connochaetes	Maxilla	Right	M3	-9.93	0.07	-3.29	0.14
115227A-E	16.27	Connochaetes	Maxilla	Right	M3	-9.70	0.09	-2.88	0.08
115227A-F	19.74	Connochaetes	Maxilla	Right	M3	-9.14	0.13	-2.73	0.10
115227A-G	22.48	Connochaetes	Maxilla	Right	M3	-8.85	0.10	-3.05	0.09
115227A-H	25.42	Connochaetes	Maxilla	Right	M3	-8.18	0.11	-2.96	0.04
115227A-I	28.28	Connochaetes	Maxilla	Right	M3	-7.95	0.08	-2.10	0.06
115227A-J	31.01	Connochaetes	Maxilla	Right	M3	-7.48	0.13	-1.72	0.06

115227A-K	34.22	Connochaetes	Maxilla	Right	M3	-7.85	0.14	-2.60	0.05
115227A-L	36.11	Connochaetes	Maxilla	Right	M3	-7.90	0.11	-1.53	0.07
115227A-M	39.56	Connochaetes	Maxilla	Right	M3	-8.28	0.12	0.51	0.05
67367A-A	8.05	Connochaetes	Mandible	Left	M1/M 2	-8.31	0.10	-1.81	0.15
67367A-B	11.48	Connochaetes	Mandible	Left	M1/M 2	-8.43	0.09	-0.48	0.16
67367A-C	14.37	Connochaetes	Mandible	Left	M1/M 2	-8.52	0.10	0.32	0.08
67367A-D	17.21	Connochaetes	Mandible	Left	M1/M 2	-8.72	0.06	-0.53	0.11
67367A-E	20.32	Connochaetes	Mandible	Left	M1/M 2	-8.83	0.08	-0.32	0.08

67367A-F	23.33	Connochaetes	Mandible	Left	M1/M 2	-8.93	0.10	-0.63	0.10
67367A-G	25.47	Connochaetes	Mandible	Left	M1/M 2	-9.28	0.11	-0.30	0.06
67367A-H	28.90	Connochaetes	Mandible	Left	M1/M 2	-9.69	0.13	-0.94	0.06
67367A-I	31.68	Connochaetes	Mandible	Left	M1/M 2	-9.39	0.12	-1.65	0.09
67367A-J	34.55	Connochaetes	Mandible	Left	M1/M 2	-9.60	0.16	-2.02	0.10
67367A-K	37.67	Connochaetes	Mandible	Left	M1/M 2	-9.71	0.14	-3.60	0.09
67367A-L	40.26	Connochaetes	Mandible	Left	M1/M 2	-9.63	0.18	-1.76	0.06
67367A-M	43.48	Connochaetes	Mandible	Left	M1/M 2	- 10.44	0.07	-3.33	0.04

67367A-N	46.82	Connochaetes	Mandible	Left	M1/M 2	- 10.03	0.08	-1.61	0.09
67539A-A	5.12	Connochaetes	Mandible	Right	M1/M 2	- 11.35	0.09	-1.27	0.10
67539A-B	7.78	Connochaetes	Mandible	Right	M1/M 2	- 10.92	0.08	0.35	0.10
67539A-C	10.66	Connochaetes	Mandible	Right	M1/M 2	- 10.20	0.08	1.14	0.09
67539A-D	12.91	Connochaetes	Mandible	Right	M1/M 2	- 10.04	0.12	0.97	0.13
67710A-A	10.48	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 11.16	0.08	-1.72	0.09
67710A-B	14.02	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 11.10	0.06	-1.38	0.13

67710A-C	15.93	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 11.65	0.09	-1.70	0.12
67710A-D	18.42	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 12.06	0.03	-1.79	0.07
67710A-E	20.66	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 11.87	0.06	-2.47	0.04
67710A-F	22.81	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 12.16	0.06	-2.44	0.09
67710A-G	24.70	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 12.37	0.07	-2.94	0.08
67710A-H	26.98	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 12.28	0.06	-3.96	0.08
67710A-I	29.10	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 12.31	0.07	-3.70	0.09
67710A-J	31.66	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 12.03	0.06	-4.76	0.08

67710A-K	33.46	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 11.99	0.08	-4.11	0.08
67710A-L	35.61	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 12.14	0.05	-3.46	0.06
67710A-M	37.32	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 12.19	0.06	-4.56	0.11
67710A-N	39.65	Alcelaphus/Con nochaetes	Mandible	Left	M1/M 2	- 11.77	0.04	-4.15	0.09
66751A-A	8.10	Alcelaphus	Mandible	Left	M1/M 2	- 11.18	0.06	-4.31	0.06
66751A-B	12.33	Alcelaphus	Mandible	Left	M1/M 2	- 11.49	0.03	-4.34	0.08
66751A-C	15.95	Alcelaphus	Mandible	Left	M1/M 2	-8.91	0.08	-1.65	0.07
66751A-D	19.18	Alcelaphus	Mandible	Left	M1/M 2	-9.85	0.06	-3.78	0.07

66751A-E	22.80	Alcelaphus	Mandible	Left	M1/M 2	-7.01	0.06	-0.99	0.09
66751A-F	25.77	Alcelaphus	Mandible	Left	M1/M 2	-7.96	0.06	-2.18	0.15
66751A-G	29.03	Alcelaphus	Mandible	Left	M1/M 2	-5.59	0.05	-0.43	0.10
66751A-H	32.40	Alcelaphus	Mandible	Left	M1/M 2	-5.52	0.12	0.58	0.08
66751A-I	35.58	Alcelaphus	Mandible	Left	M1/M 2	-7.25	0.06	-2.49	0.09
66805A-A	16.61	Alcelaphus	Maxilla	Right	M1/M 2	- 10.82	0.04	-2.90	0.05
66805A-B	18.15	Alcelaphus	Maxilla	Right	M1/M 2	- 10.60	0.05	-2.47	0.12
66805A-C	20.89	Alcelaphus	Maxilla	Right	M1/M 2	- 10.82	0.06	-2.59	0.09

66805A-D	22.56	Alcelaphus	Maxilla	Right	M1/M 2	- 11.25	0.06	-2.00	0.10
66805A-E	24.62	Alcelaphus	Maxilla	Right	M1/M 2	- 10.74	0.05	-1.84	0.07
66805A-F	26.93	Alcelaphus	Maxilla	Right	M1/M 2	- 10.45	0.05	-1.45	0.05
66805A-G	28.70	Alcelaphus	Maxilla	Right	M1/M 2	- 10.09	0.06	-1.40	0.10
66805A-H	31.08	Alcelaphus	Maxilla	Right	M1/M 2	- 10.41	0.07	-1.66	0.07
66805A-I	33.33	Alcelaphus	Maxilla	Right	M1/M 2	- 10.32	0.03	-1.64	0.09
66805A-J	36.67	Alcelaphus	Maxilla	Right	M1/M 2	- 10.66	0.04	-0.80	0.06
66805A-K	38.59	Alcelaphus	Maxilla	Right	M1/M 2	- 10.88	0.07	-0.38	0.11

66805A-L	42.18	Alcelaphus	Maxilla	Right	M1/M 2	- 11.23	0.06	-1.09	0.06
66613A-A	8.59	Alcelaphus	Maxilla	Right	M1/M 2	-8.84	0.06	-1.15	0.05
66613A-B	11.32	Alcelaphus	Maxilla	Right	M1/M 2	-8.78	0.05	-1.55	0.06
66613A-C	13.49	Alcelaphus	Maxilla	Right	M1/M 2	-8.61	0.04	-1.76	0.05
66613A-D	15.85	Alcelaphus	Maxilla	Right	M1/M 2	-8.47	0.02	-2.42	0.10
66613A-E	18.07	Alcelaphus	Maxilla	Right	M1/M 2	-8.50	0.02	-1.72	0.07
66613A-F	20.12	Alcelaphus	Maxilla	Right	M1/M 2	-8.39	0.04	-2.11	0.09
66613A-G	22.47	Alcelaphus	Maxilla	Right	M1/M 2	-8.22	0.05	-3.01	0.05

66613A-H	24.86	Alcelaphus	Maxilla	Right	M1/M 2	-8.13	0.07	-2.51	0.06
66613A-I	27.27	Alcelaphus	Maxilla	Right	M1/M 2	-8.15	0.05	-2.23	0.04
67099A-A	5.27	Alcelaphus	Mandible	Left	M1/M 2	-8.29	0.04	-0.90	0.06
67099A-B	7.89	Alcelaphus	Mandible	Left	M1/M 2	-8.40	0.04	-0.29	0.10
67099A-C	10.18	Alcelaphus	Mandible	Left	M1/M 2	-8.90	0.08	-0.77	0.07
67099A-D	12.28	Alcelaphus	Mandible	Left	M1/M 2	-9.04	0.03	-1.46	0.06
67099A-E	14.40	Alcelaphus	Mandible	Left	M1/M 2	-9.18	0.05	-0.23	0.07
67099A-F	16.95	Alcelaphus	Mandible	Left	M1/M 2	-9.40	0.04	-1.30	0.04

67099A-G	19.45	Alcelaphus	Mandible	Left	M1/M 2	-9.50	0.05	-0.18	0.03
67099A-H	21.69	Alcelaphus	Mandible	Left	M1/M 2	-9.83	0.05	-1.16	0.07
67099A-I	24.28	Alcelaphus	Mandible	Left	M1/M 2	-9.98	0.02	-1.60	0.07
67099A-J	26.82	Alcelaphus	Mandible	Left	M1/M 2	- 10.17	0.03	-1.00	0.06
67099A-K	28.98	Alcelaphus	Mandible	Left	M1/M 2	- 10.43	0.06	-1.38	0.09
67099A-L	31.41	Alcelaphus	Mandible	Left	M1/M 2	- 10.19	0.04	-3.43	0.05
67099A-M	33.88	Alcelaphus	Mandible	Left	M1/M 2	-9.88	0.06	-2.62	0.07
67099A-N	35.94	Alcelaphus	Mandible	Left	M1/M 2	-9.21	0.07	-2.28	0.09

67099A-O	37.86	Alcelaphus	Mandible	Left	M1/M 2	-9.58	0.02	-1.40	0.07
67317A-A	13.10	Alcelaphus	Maxilla	Left	M1/M 2	-6.80	0.07	-1.78	0.06
67317A-B	15.39	Alcelaphus	Maxilla	Left	M1/M 2	-5.84	0.08	-1.74	0.07
67317A-C	18.07	Alcelaphus	Maxilla	Left	M1/M 2	-5.47	0.05	-1.03	0.06
67317A-D	20.25	Alcelaphus	Maxilla	Left	M1/M 2	-5.11	0.03	-1.40	0.08
67317A-E	21.99	Alcelaphus	Maxilla	Left	M1/M 2	-5.07	0.05	-0.79	0.07
67317A-F	24.09	Alcelaphus	Maxilla	Left	M1/M 2	-4.90	0.07	-0.02	0.06
67317A-G	26.28	Alcelaphus	Maxilla	Left	M1/M 2	-5.20	0.06	0.72	0.07

67317A-H	28.22	Alcelaphus	Maxilla	Left	M1/M 2	-5.51	0.08	0.38	0.07
67317A-I	30.59	Alcelaphus	Maxilla	Left	M1/M 2	-6.29	0.05	0.56	0.08
67317A-J	32.58	Alcelaphus	Maxilla	Left	M1/M 2	-7.23	0.05	1.73	0.06
67317A-K	35.05	Alcelaphus	Maxilla	Left	M1/M 2	-8.45	0.04	1.65	0.06
67798A-A	2.73	Alcelaphus	Maxilla	Right	M1/M 2	-8.81	0.06	-0.01	0.05
67798A-B	5.33	Alcelaphus	Maxilla	Right	M1/M 2	-8.93	0.06	-0.15	0.09
67798A-C	7.51	Alcelaphus	Maxilla	Right	M1/M 2	-8.61	0.06	-0.55	0.11
67798A-D	9.82	Alcelaphus	Maxilla	Right	M1/M 2	-9.13	0.08	0.56	0.08

67798A-E	11.68	Alcelaphus	Maxilla	Right	M1/M 2	-9.36	0.06	2.17	0.08
67798A-F	14.27	Alcelaphus	Maxilla	Right	M1/M 2	-9.61	0.04	1.79	0.07
67798A-G	16.08	Alcelaphus	Maxilla	Right	M1/M 2	- 10.00	0.05	-1.32	0.08
67798A-H	18.13	Alcelaphus	Maxilla	Right	M1/M 2	-9.86	0.05	-1.92	0.04
67798A-I	20.29	Alcelaphus	Maxilla	Right	M1/M 2	- 10.20	0.08	-1.66	0.05
67798A-J	22.45	Alcelaphus	Maxilla	Right	M1/M 2	- 10.13	0.06	-1.81	0.08
67798A-K	24.22	Alcelaphus	Maxilla	Right	M1/M 2	- 10.19	0.07	-2.18	0.05
67798A-L	26.06	Alcelaphus	Maxilla	Right	M1/M 2	- 10.17	0.06	-1.94	0.08

67798A-M	27.81	Alcelaphus	Maxilla	Right	M1/M 2	-9.95	0.06	-1.39	0.11
115209A-A	11.31	Alcelaphus	Mandible	Right	M1/M 2	-9.99	0.05	-0.34	0.07
115209A-B	13.64	Alcelaphus	Mandible	Right	M1/M 2	-9.99	0.05	-1.11	0.08
115209A-C	15.61	Alcelaphus	Mandible	Right	M1/M 2	-9.79	0.06	-0.92	0.07
115209A-D	18.09	Alcelaphus	Mandible	Right	M1/M 2	-9.42	0.05	-0.80	0.06
115209A-E	20.11	Alcelaphus	Mandible	Right	M1/M 2	-9.66	0.08	1.98	0.07
115209A-F	22.25	Alcelaphus	Mandible	Right	M1/M 2	-9.59	0.07	0.48	0.07
115209A-G	24.47	Alcelaphus	Mandible	Right	M1/M 2	-9.63	0.05	-0.58	0.10

115209A-H	26.89	Alcelaphus	Mandible	Right	M1/M 2	- 10.15	0.06	0.81	0.06
115209A-I	28.74	Alcelaphus	Mandible	Right	M1/M 2	- 10.66	0.03	0.55	0.07
115209A-J	30.84	Alcelaphus	Mandible	Right	M1/M 2	- 10.92	0.04	0.06	0.06
115209A-K	33.26	Alcelaphus	Mandible	Right	M1/M 2	- 10.59	0.04	0.08	0.07
115209A-L	35.47	Alcelaphus	Mandible	Right	M1/M 2	- 11.27	0.07	-0.01	0.09
115209A-M	37.67	Alcelaphus	Mandible	Right	M1/M 2	- 12.53	0.06	0.99	0.09
115209A-N	39.43	Alcelaphus	Mandible	Right	M1/M 2	- 12.70	0.06	-0.19	0.10
66996A-A	2.73	Alcelaphus	Maxilla	Right	M1/M 2	-7.54	0.08	4.42	0.05

66996A-B	5.29	Alcelaphus	Maxilla	Right	M1/M 2	-7.78	0.04	-2.18	0.04
66996A-C	7.94	Alcelaphus	Maxilla	Right	M1/M 2	-8.44	0.05	-2.46	0.07
66996A-D	10.25	Alcelaphus	Maxilla	Right	M1/M 2	-8.46	0.08	-2.70	0.04
66996A-E	12.40	Alcelaphus	Maxilla	Right	M1/M 2	-8.79	0.07	-2.28	0.08
66996A-F	15.03	Alcelaphus	Maxilla	Right	M1/M 2	-8.83	0.06	-3.19	0.06
66996A-G	16.94	Alcelaphus	Maxilla	Right	M1/M 2	-9.17	0.07	-3.26	0.06
66996A-H	19.10	Alcelaphus	Maxilla	Right	M1/M 2	-9.01	0.09	-3.80	0.09
66996A-I	21.36	Alcelaphus	Maxilla	Right	M1/M 2	-9.07	0.07	-4.24	0.06

66996A-J	23.75	Alcelaphus	Maxilla	Right	M1/M 2	-8.46	0.09	-3.57	0.08
66996A-K	25.83	Alcelaphus	Maxilla	Right	M1/M 2	-8.62	0.06	-3.80	0.05
66996A-L	28.05	Alcelaphus	Maxilla	Right	M1/M 2	-7.88	0.06	-3.39	0.09
67502A-A	4.59	Alcelaphus	Maxilla	Right	M1/M 2	- 10.05	0.05	-0.97	0.05
67502A-B	6.66	Alcelaphus	Maxilla	Right	M1/M 2	- 10.08	0.05	-1.79	0.06
67502A-C	8.58	Alcelaphus	Maxilla	Right	M1/M 2	- 10.62	0.05	-3.45	0.08
67502A-D	10.97	Alcelaphus	Maxilla	Right	M1/M 2	- 10.74	0.04	-2.26	0.09
67502A-E	12.97	Alcelaphus	Maxilla	Right	M1/M 2	- 10.55	0.06	-3.12	0.09

67502A-F	15.15	Alcelaphus	Maxilla	Right	M1/M 2	- 10.15	0.04	-2.26	0.10
67302A-A	20.97	Alcelaphus	Maxilla	Right	M1/M 2	-7.69	0.04	-0.43	0.10
67302A-B	23.12	Alcelaphus	Maxilla	Right	M1/M 2	-8.11	0.05	0.46	0.08
67302A-C	25.44	Alcelaphus	Maxilla	Right	M1/M 2	-8.08	0.05	0.07	0.06
67302A-D	28.11	Alcelaphus	Maxilla	Right	M1/M 2	-9.12	0.02	2.64	0.06
67302A-E	30.18	Alcelaphus	Maxilla	Right	M1/M 2	-9.93	0.06	0.75	0.08
67562A-A	18.00	Alcelaphus	Mandible	Right	M1/M 2	-9.72	0.05	-1.26	0.08

67562A-B	20.83	Alcelaphus	Mandible	Right	M1/M 2	-9.81	0.05	-0.47	0.09
67562A-C	23.36	Alcelaphus	Mandible	Right	M1/M 2	-9.62	0.05	-0.67	0.05
67562A-D	25.63	Alcelaphus	Mandible	Right	M1/M 2	-9.85	0.07	0.50	0.05
67562A-E	27.92	Alcelaphus	Mandible	Right	M1/M 2	- 10.16	0.05	1.25	0.04
67562A-F	30.06	Alcelaphus	Mandible	Right	M1/M 2	- 10.22	0.06	1.53	0.06
67562A-G	32.82	Alcelaphus	Mandible	Right	M1/M 2	- 10.65	0.09	2.22	0.07
115391A-A	4.68	Redunca	Mandible	Right	M3	-9.66	0.12	0.95	0.15
115391A-B	7.07	Redunca	Mandible	Right	M3	-9.84	0.12	1.90	0.08

115391A-C	9.63	Redunca	Mandible	Right	M3	- 10.33	0.08	1.26	0.12
115391A-D	12.08	Redunca	Mandible	Right	M3	- 10.05	0.06	1.18	0.08
115391A-E	14.95	Redunca	Mandible	Right	M3	- 10.71	0.06	-1.21	0.15
115391A-F	17.31	Redunca	Mandible	Right	M3	- 10.61	0.07	0.91	0.10
115391A-G	19.94	Redunca	Mandible	Right	M3	- 10.50	0.11	-1.28	0.07
115391A-H	22.70	Redunca	Mandible	Right	M3	- 10.48	0.09	-2.03	0.11
115391A-I	24.57	Redunca	Mandible	Right	M3	- 10.73	0.12	-3.47	0.09
115391A-J	27.36	Redunca	Mandible	Right	M3	- 10.42	0.11	-2.65	0.14

115391A-K	30.21	Redunca	Mandible	Right	M3	- 10.45	0.07	-1.66	0.08
66902A-A	2.21	Redunca	Maxilla	Left	M3	-8.54	0.07	-1.25	0.13
66902A-B	4.31	Redunca	Maxilla	Left	M3	-7.33	0.07	-1.86	0.11
66902A-C	6.99	Redunca	Maxilla	Left	M3	-7.96	0.08	-0.59	0.10
66902A-D	8.84	Redunca	Maxilla	Left	M3	-7.73	0.12	0.31	0.09
115240A-A	2.49	Redunca	Mandible	Right	M3	-9.62	0.07	-0.48	0.10
115240A-B	5.00	Redunca	Mandible	Right	M3	-9.47	0.12	-2.52	0.05
115240A-C	7.67	Redunca	Mandible	Right	M3	-9.31	0.11	-1.41	0.11
115240A-D	10.04	Redunca	Mandible	Right	M3	-9.13	0.10	-0.06	0.10

115240A-E	12.63	Redunca	Mandible	Right	M3	-8.85	0.10	-1.46	0.12
115240A-F	15.36	Redunca	Mandible	Right	M3	-8.71	0.06	-0.28	0.11
115240A-G	17.96	Redunca	Mandible	Right	M3	-8.83	0.10	1.53	0.08
115240A-H	20.78	Redunca	Mandible	Right	M3	-8.51	0.10	1.17	0.10
67535A-A	3.57	Redunca	Maxilla	Left	M3	- 10.27	0.07	-0.30	0.09
67535A-B	6.09	Redunca	Maxilla	Left	M3	- 10.16	0.09	-1.10	0.10
67535A-C	9.34	Redunca	Maxilla	Left	M3	- 10.11	0.09	-1.59	0.13
67535A-D	12.08	Redunca	Maxilla	Left	M3	-9.68	0.12	-0.87	0.15

67278A-A	9.14	Redunca	Maxilla	Right	M3	-9.35	0.07	-2.89	0.08
67278A-B	11.67	Redunca	Maxilla	Right	M3	-9.06	0.09	-1.72	0.07
67278A-C	14.68	Redunca	Maxilla	Right	M3	-8.92	0.09	-1.44	0.09
67278A-D	17.24	Redunca	Maxilla	Right	M3	-9.36	0.05	-0.54	0.05
67278A-E	20.21	Redunca	Maxilla	Right	M3	-9.58	0.10	-1.75	0.11
67278A-F	22.83	Redunca	Maxilla	Right	M3	-9.55	0.06	-1.03	0.14
67278A-G	25.44	Redunca	Maxilla	Right	M3	-	0.07	-0.78	0.10
						10.07			
67836A-A	10.19	Hippotragus	Maxilla	Left	M3	-8.81	0.20	0.30	0.07
67836A-B	12.22	Hippotragus	Maxilla	Left	M3	-8.70	0.17	-0.23	0.11
67836A-C	14.71	Hippotragus	Maxilla	Left	M3	-9.52	0.12	-1.44	0.13
67836A-D	17.06	Hippotragus	Maxilla	Left	M3	-	0.16	-2.06	0.27
						10.07			
67836A-E	19.09	Hippotragus	Maxilla	Left	M3	-9.66	0.27	-0.56	0.11
67836A-F	21.24	Hippotragus	Maxilla	Left	M3	-8.61	0.13	1.33	0.10
67836A-G	23.35	Hippotragus	Maxilla	Left	M3	-8.94	0.23	0.62	0.09

67836A-H	25.38	Hippotragus	Maxilla	Left	M3	- 10.29	0.21	-0.25	0.10
66316.11 A-A	5.56	Hippotragus	Mandible	Right	M1/M 2	- 12.64	0.15	4.29	0.10
66316.11 A-B	7.26	Hippotragus	Mandible	Right	M1/M 2	- 13.47	0.15	4.33	0.08
66316.11 A-C	10.89	Hippotragus	Mandible	Right	M1/M 2	- 13.59	0.15	1.51	0.06
66316.11 A-D	13.31	Hippotragus	Mandible	Right	M1/M 2	- 13.51	0.16	2.76	0.10
66316.11 A-E	15.94	Hippotragus	Mandible	Right	M1/M 2	- 13.40	0.13	3.38	0.12
66316.11 A-F	18.09	Hippotragus	Mandible	Right	M1/M 2	- 12.28	0.15	1.50	0.11
67125A-A	3.25	Hippotragus	Mandible	Left	M3	-8.21	0.16	1.50	0.09

67125A-B	6.09	Hippotragus	Mandible	Left	M3	-8.07	0.16	0.72	0.08
67125A-C	7.93	Hippotragus	Mandible	Left	M3	-8.02	0.16	0.15	0.07
67125A-D	10.25	Hippotragus	Mandible	Left	M3	-8.09	0.12	0.10	0.09
67125A-E	12.76	Hippotragus	Mandible	Left	M3	-7.77	0.15	1.21	0.09
67125A-F	15.50	Hippotragus	Mandible	Left	M3	-7.68	0.16	1.70	0.10
67125A-G	18.00	Hippotragus	Mandible	Left	M3	-8.30	0.20	0.10	0.09
67125A-H	20.19	Hippotragus	Mandible	Left	M3	-8.34	0.18	0.00	0.09
67125A-I	22.49	Hippotragus	Mandible	Left	M3	-8.90	0.18	0.33	0.08
67125A-J	24.91	Hippotragus	Mandible	Left	M3	-8.67	0.14	0.22	0.09
67125A-K	27.50	Hippotragus	Mandible	Left	M3	-8.34	0.12	0.00	0.11
67125A-L	29.50	Hippotragus	Mandible	Left	M3	-8.96	0.13	0.61	0.10
67125A-M	31.84	Hippotragus	Mandible	Left	M3	-8.51	0.07	1.20	0.12
67037A-A	14.78	Connochaetes	Mandible	Right	M1/M 2	-7.08	0.18	5.44	0.07

67037A-B	17.64	Connochaetes	Mandible	Right	M1/M 2	-7.32	0.09	-0.84	0.10
65115A-A	2.59	Redunca	Mandible	Right	M3	-9.45	0.12	0.59	0.13
65115A-B	4.63	Redunca	Mandible	Right	M3	-9.46	0.14	0.97	0.11
65115A-C	6.85	Redunca	Mandible	Right	M3	-9.52	0.10	0.22	0.07
65115A-D	9.30	Redunca	Mandible	Right	M3	-9.13	0.09	0.37	0.11
115426A-A	3.05	Antidorcas?	Mandible?	Left?	M3	- 10.34	0.04	-0.73	0.06
115426A-B	5.55	Antidorcas?	Mandible?	Left?	M3	- 10.48	0.04	-0.78	0.08
115426A-C	8.45	Antidorcas?	Mandible?	Left?	M3	- 10.88	0.04	-0.31	0.07
115426A-D	11.03	Antidorcas?	Mandible?	Left?	M3	- 10.88	0.03	-0.73	0.06

115426A- E	13.95	Antidorcas?	Mandible?	Left?	M3	- 10.51	0.09	0.70	0.06	Table S1
115426A- F	16.56	Antidorcas?	Mandible?	Left?	M3	- 10.86	0.04	0.69	0.08	
115426A- G	18.80	Antidorcas?	Mandible?	Left?	M3	- 10.50	0.05	0.43	0.06	