Using springbok (*Antidorcas*) dietary proxies to reconstruct inferred palaeovegetational changes over 2 million years in Southern Africa

L. Sewell[a,*], G. Merceron[b], P.J. Hopley[c], B. Zipfel[d], S.C. Reynolds[a]

[a] *Institute for Studies in Landscape and Human Evolution, Department of Archaeology, Anthropology and Forensic Science, Bournemouth University, Fern Barrow, Poole, Dorset, UK*
[b] *Laboratoire de Paléontologie, Évolution, Paléoécosystèmes, Paléoprimatologie (PALEVOPRIM; ex-iPHEP), UMR 7262 CNRS & Université de Poitiers, 86073 Poitiers Cedex 9, France*
[c] *Department of Earth and Planetary Sciences, Birkbeck College, University of London, Malet Street, London, UK*
[d] *Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa*

ABSTRACT

The reconstruction of past vegetation and climatic conditions of the Cradle of Humankind, Gauteng Province, South Africa, has been approached using various proxies (such as micromammals, speleothems, faunal and floral presence and stable carbon isotopes). Elisabeth Vrba's seminal studies (1974; 1975) on the fossil record of this region indicated dramatic faunal turnover based on species extinction and speciation data. This turnover was thought to have been driven by increasing aridity and spreading grasslands. These reconstructions however, are continuously being refined and adapted in light of advancing techniques (such as dental microwear textural analysis) and terrestrial proxies, such as speleothems.

However, more recent studies show varying proportions from wooded towards more grassland-dominated habitats, with the most common reconstruction being the heterogeneous 'mosaic' habitat. Here we re-evaluate the findings of a transition from woodland to grassland conditions in the fossil record from Member 4 Sterkfontein to Member 5 Sterkfontein and the deposits of Swartkrans. To approach the palaeovegetation changes through time via a different angle, we focus on the diet of the springbok (genus *Antidorcas*), represented throughout this temporal period from geological members dating from 2.8–0.8 Ma. We use detailed dietary methods (dental linear measurements, mesowear, microwear, and stable carbon isotope analysis) to explore past changes in diets of springbok that can be used to indicate the prevailing vegetation conditions. Our results presented here broadly agree with previous palaeoenvironmental reconstructions, in indicating increased grassland post ca 1.7 Ma, with some suggestion of more heterogeneous habitats for Swartkrans Member 2 (ca 1.65–1.07 Ma). We find that there is support for the implementation of a multi-disciplinary approach to produce more accurate and robust reconstructions of past diets and by extension, of palaeovegetation conditions, if the selected herbivore species is a mixed-feeder, like the springbok.

1. Introduction

Climatic aridification and spread of grasslands are a key feature of African Plio-Pleistocene environmental changes (e.g. Sepulchre et al., 2006; Ségalen et al., 2007; Hopley et al., 2007; deMenocal, 2011; Kaya et al., 2018), which are inferred to have caused dramatic habitat changes that impacted on our ancestors, as well as other fauna. There is broad agreement, from a range of different palaeoenvironmental proxies, (from climatic proxies such as deMenocal's (1995, 2004) marine sediment sequences to terrestrial habitat proxies such as Avery's (2001) micrommamals analyses, that Africa experienced gradually increasing aridity (Bobe and Eck, 2001; Bobe and Behrensmeyer, 2004;

Avery, 2001; deMenocal, 1995, 2004 amongst others) and a spread of grasslands through time after 5 Ma, with a resulting radiation in grassland-adapted taxa (Vrba, 1973, 1985). Yet recent studies cast doubt on this prevailing trend for east Africa (Blumenthal et al., 2017; Kaya et al., 2018), heralding the need to revisit this long-standing hypothesis.

An increasing number of hominin species are now known to have been present in the southern African region throughout this temporal period: *Australopithecus sediba* (Berger et al., 2010), *Australopithecus africanus* (Dart, 1925; Clarke, 2008) *Paranthropus robustus* (Broom, 1938), *Homo habilis* (Hughes and Tobias, 1977) and *Homo erectus/ergaster* (Leakey, 1960; Kuman and Clarke, 2000; Antón et al., 2014).

During this time of climate and habitat change, we see the disappearance of *Australopithecus* and the appearance of *Homo* and *Paranthropus*. What role, if any, did climate-driven habitat shifts have in the appearance and extinction of these hominins? Here, we are attempting to use dietary variations in other members of the faunal community for insights into wider patterns of vegetation and habitat change.

Within ecological proxies, the diversity of ungulate mammals and notably bovids has been frequently studied (e.g. Vrba, 1974; Spencer, 1997). Amongst bovids, the species of the genera *Antidorcas* is continuously present throughout this temporal period of interest in South Africa.

There are several *Antidorcas* species, of which only one remains today, *Antidorcas marsupialis*. Modern springbok are typically arid-adapted, mixed feeders, with a relatively wide habitat tolerance primarily in the more arid areas of south and southwestern Africa; South Africa, Namibia, Botswana and Angola (Lehmann, 2015; Castelló, 2016). Extant *A. marsupialis* will graze on young grasses when available, swapping to browse on low shrubs and succulents, when young grasses are not available. Springbok can survive without drinking water, as long as their food contains > 10% water content (Estes, 1991). Historic records make mention of the mass migrations of these animals in search of better quality grazing after the rains (Skinner and Louw, 1996). Social organization alters according to season, sex and age range of the individual springbok (Skinner and Chimimba, 2005). When considering dietary signals from fossil *Antidorcas*, social and migratory behaviour should be considered to account for the range of signals obtained (e.g. Nagy and Knight, 1994; Bednekoff and Ritter, 1997; Stapelberg et al., 2008).

Fossil springbok will henceforth be referred to by genus (i.e. "*Antidorcas*"). In the fossil record, there were several *Antidorcas* species; based on tooth enamel carbon stable isotopes, *A. recki, A. australis, A. bondi* and *A. marsupialis* appear to have been mixed feeders to varying degrees, with the exception of *A. bondi*, which was suggested to have been a specialist grazer (Brink and Lee-Thorp, 1992).

The earliest species, *Antidorcas recki* (Schwarz, 1932) was presumed to tend towards browsing (Luyt, 2001). It is assumed that *A. recki* is the species from which *Antidorcas australis* (Hendey and Hendey, 1968) and/or *Antidorcas marsupialis* (Zimmerman, 1780) and *A. bondi* (Cooke and Wells, 1951) descends. *Antidorcas bondi*, had a very specific small body-size and specialist dentition (with characteristically small, but very high-crowned, hyposdont teeth) and a unique dietary ecology (based on stable carbon isotope data) that enabled it to exist as part of a grazing succession in southern Africa prior to its extinction at the end of the Pleistocene/early Holocene (Brink, 2016; Brink et al., 2013; Brink and Lee-Thorp, 1992). Brink and Lee-Thorp (1992) proposed *A. bondi* to be the smallest member of a grazing succession feeding on new grass shoots whose growth was stimulated by the regular 'mowing' of grasses by extant and extinct species, such as the giant buffalo (*Pelorovis antiquus*), giant hartebeest (*Megalotragus priscus*), large equid (*Equus capensis*) and the medium-sized hartebeest (*Damaliscus niro*) in a similar way to that proposed for the Serengeti in East Africa by Gwynne and Bell (1968).

The presence and palaeoecology of *A. australis* as a potentially separate species, or a subspecies is debated, but remains unresolved (e.g. Gentry, 1978, 1992, 2011; Vrba, 1973). *Antidorcas australis*, was originally described from the Middle Stone Age (MSA) site of Swartklip (Cape Province, South Africa) by Hendey and Hendey (1968) as a transitional form of *Antidorcas* between the ancestral *A. recki* and the descendant *A. marsupialis*, consequently tentatively assigned as a subspecies of *Antidorcas marsupialis*. *A. australis* was subsequently elevated by Vrba (1973) to a separate species, supported by Hendey (1974) as a valid taxon, when found alongside *A. recki*. However, Vrba (1976) later doubted this elevation, suggesting *A. australis* was perhaps only a

southern Cape endemic form. Gentry (2010) suspects *A. australis* and *A. marsupialis* to be synonymous, but not all authors agree (e.g. Klein, 1980; Faith, 2014).

Initially all *Antidorcas* specimens are considered together as '*Antidorcas*' with no prior assumptions based on taxonomy and a second time, distinguishing specimens according to their assigned taxonomic category (see Table 1 and Fig. 1).

The number of species of *Antidorcas* in the past is important in understanding the overall function of the palaeoecosystem. If herbivore species can only coexist by species 'packing' into narrow niche spaces to reduce competition (e.g. Richie and Olff, 1999; Codron et al., 2008) then we should see that *A. australis* possesses indications of a distinct dietary niche, and or/different body sizes compared to other *Antidorcas* congeners. Can dietary signals from dental specimens of proposed *Antidorcas australis*, combined with contemporaneous *Antidorcas marsupialis*, establish the likelihood from dental and dietary evidence, of *Antidorcas australis* as a separate species?

From the dietary indicators of *Antidorcas*, we establish a broad palaoevegetation reconstruction. One way to reconstruct palaeovegetation cover would be to examine direct evidence of the plants themselves (fossil plants, pollen and phytoliths) preserved at sites like Sterkfontein and Swartkrans, Cradle of Humankind, Gauteng Province, South Africa. However, since plant fossils and pollen are not commonly preserved in the Cradle of Humankind sites (but see Bamford, 1999), we use the dietary evidence from a mixed feeding herbivore that is commonly preserved at these sites, and one which is relatively abundant. Herbivores are considered faithful reflectors of prevailing habitat conditions, over decades of detailed palaeoenvironmental research that used various aspects of herbivore palaeoecology (Vrba, 1974, 1975; Plummer and Bishop, 1994; Spencer, 1997; Reed, 1997; Bobe and Eck, 2001; amongst many others).

A key transition in the southern African fossil record is between Sterkfontein Member 4 (where *Australopithecus africanus* is abundant) and Member 5 (where we have no *Australopithecus*, but instead *Homo* and *Paranthropus*). The typical palaeoenvironmental story is one of wetter woodland and closed habitats up to and including Sterkfontein Member 4 (c. 2.8–2.0 Ma), with the area becoming more open with drier, grassland-dominated habitats by Sterkfontein Member 5 times which overlap with Swartkrans Members (2–0.8 Ma) (Bamford, 1999; Kuman and Clarke, 2000; Luyt, 2001). Mosaic habitats (Brophy, 2011; Reynolds et al., 2015) and local variations have been reported between the sites lying within the Cradle of Humankind, presumably due to the varying proximity to the Blaaubank River (Avery, 2001; Reynolds and Kibii, 2011). The cave stratigraphy and dating of these South African deposits have received much attention (e.g. Hopley and Maslin, 2010; de Ruiter et al., 2008) and a summary of the dates of the deposits are provided in Table 2. There are very few genera of herbivores that occur in both Member 4 and Member 5; which is chiefly characterized by a dramatic turnover in species (e.g. Vrba, 1974, 1975; de Ruiter, 2003a, 2003b; Reynolds and Kibii, 2011). We focus on the only single and successful lineage that is present in Member 4 (as *Antidorcas recki*) and in later Member 5 (as *A. marsupialis*).

The majority of previous studies typically employ only one or two methods (e.g. microwear and/or stable isotope analyis) to tackle aspects of palaeoenvironmental questions. Each method reveals important aspects relevant to the overall palaeoenvironmental picture, but these methods also have inherent limitations. For example, microwear indicates primarily the last few weeks as new micrometric marks occur after each meal eaten (Teaford and Oyen, 1989), mesowear requires observer experience and therefore large sample sizes to mitigate for this (Kaiser and Fortelius, 2003), and isotopes are informative only of a short window in the early years of life during enamel formation (Reade et al., 2015). Comparisons between species are also complicated by

Table 1

Features typical of each *Antidorcas* species found in Southern Africa, used to establish taxonomic assignment of fossil dentition. Characteristic features used to establish taxonomic assignment of fossil dental specimens (Vrba, 1973; Cooke and Wells, 1951; Gentry, 2010, 2011). Typical M² dimensions established according to the type specimens, from corresponding reference as stated in the table.

Species	*Antidorcas bondi*	*Antidorcas recki*	*Antidorcas marsupialis*	*Antidorcas* cf. *australis*
Reference	Cooke and Wells, 1951	Schwarz, 1932	Zimmerman, 1780	Hendey and Hendey, 1968
Figure	See Fig. 1, Images F-H	See Fig. 1, Images A-B	See Fig. 1, Image I	See Fig. 1, Images C-E
Characteristic dental features	• Upper: Strongly developed styles (are often basally (i.e. towards the body of the tooth) pinched, giving a more prominent impression). • Upper: Complicated folding of enamel walls of central cavities, with a greater tendency towards dumbbell- shaped central cavities and increased curvature • Extreme hypsodonty • Lower: a depression runs from occlusal surface to root between lingual molar lobes. Adjacent to these depressions the molar walls appear to "bow out", giving the whole lingual molar edge a wavy look (more similar to impala than the other *Antidorcas* species). • Lower: Sometimes present: lingual "rib" (metastylid) in the or depression between molar lobes. • Lower: Central cavities are centrally constricted, creating a dumbbell appearance. • Large M₃ metastyle. • Typically Retains PM₂ • PM₃ is larger and more complex than in *A. marsupialis*. • Lower: Buccal lobes are generally more pointed (less 'squaring'-where the anterior part of the lobe approaches the lobe in front), than is the case in the other *Antidorcas* species. • Lower: Occasionally goat folds/basal pillars are present. • Thickness of enamel; enamel walls, especially those surrounding central cavities typically appear thicker with respect to tooth size than is the case in other *Antidorcas* species.	• Unbent central cavities • Straight mandibular lingual molar face • Buccal lophs are V-shaped (more so than the more rounded ones of *A. marsupialis*) • Has styles on upper molars, which are more often V-shaped • Upper: Less strongly pronounced concave posterior part of lateral wall (than in *A. marsupialis/A. bondi*). • Upper: Stronger styles than *A. marsupialis*, with a flatter and even concave wall between mesostyle and metastyle. • P₂ is usually retained (sometimes absent). • Lower: Central cavities straighten in relatively early wear stages. • Large M₃ metastyle. • Typically Retains PM₂ • PM₃ is larger and more complex than in *A. marsupialis*. • Upper: concave labial walls behind their mesostyles	• Lower: Lingual walls are straight (less outwardly bowed than in the impala). • Lower: Central cavities straighten in relatively early wear stages • Large M₃ metastyle, with noticeably enlarge third (hypoconulid) lobes • Lacks PM₂ • Reduced PM₃	• Molars are bucco-lingually narrower in mesiodistal length (Vrba, 1973) than *A. marsupialis* (Vrba, 1970) • Lower: Central cavities straighten in relatively early wear stages • Large M₃ metastyle. • Lacks PM₂ • Reduced PM₃ • Narrower than *A. marsupialis* and appear more gracile (Vrba, 1970)
Mean M² dimensions	16mm × 9mm[a]	13.3 mm × 6.3 mm[b]	17.4 mm (Female) 18 mm (Male) × 10.9 mm[c]	12.5mm × 7.95 mm[d]

[a] Cooke and Wells, 1951; dimensions written as length × breadth (in mm).

[b] mesiodistal length × bucco-lingual width. Based on mean measurements taken of *A. recki* from Sterkfontein and Swartkrans by L. Sewell (2016).

[c] Vrba, 1970; mesiodistal length taken from the mesial surface of the parastyle to the distal surface of the metastyle × mean value from modern *A. marsupialis* specimens(measured by LCS).

[d] Based on mean measurements (by L. Sewell and Vrba, 1973) of specimens assigned to *A. australis*; mesiodistal length × buccolingual width.
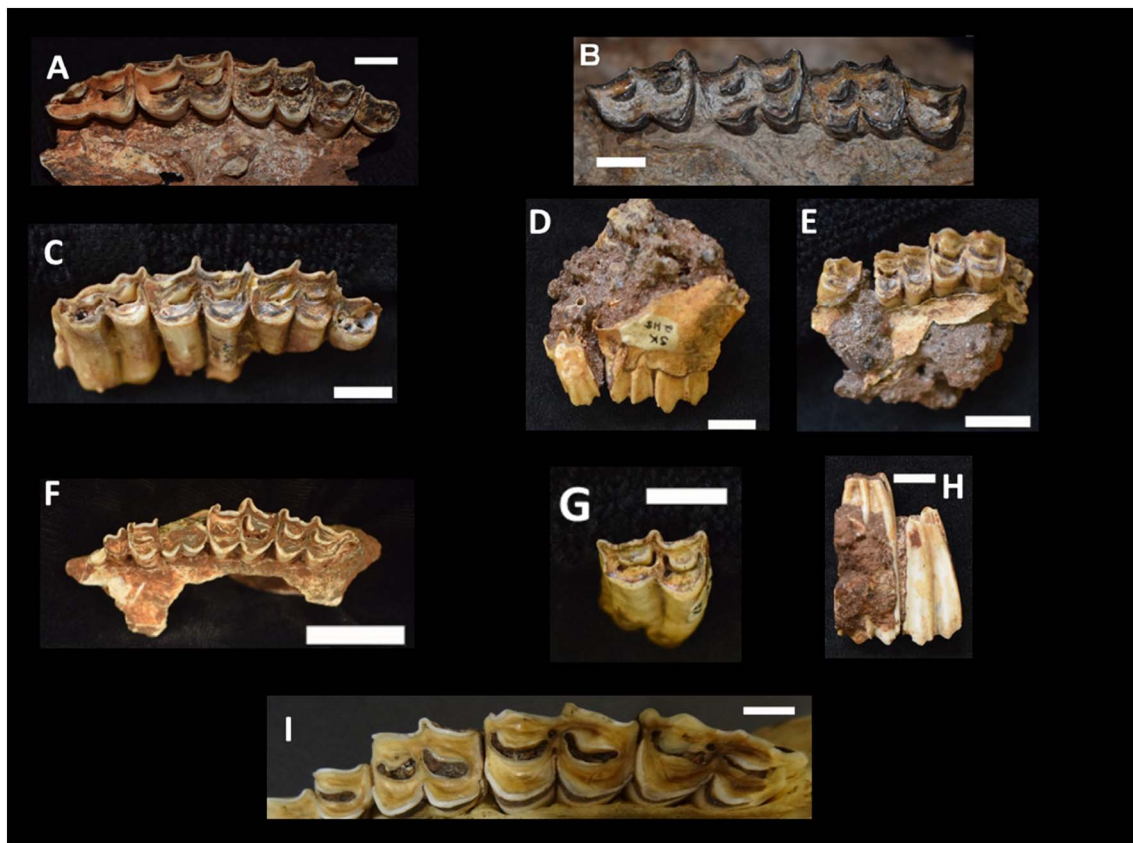
Fig. 1. Examples of *Antidorcas* maxillary (upper) dentition. All photographs taken by L. Sewell unless otherwise stated*. A-B: *Antidorcas recki* (A = KA2610; *B = KNM-ER 6–18), C–E: *Antidorcas australis* as identified by Vrba (1973): (C = SK 3055; D and E = SK 2115), F–H: *Antidorcas bondi* (F = SF 592; G = KA 2472; H = SK 2366), I: modern *Antidorcas marsupiualis*. [Key: KA = Kromdraai, KNM-ER = Kenya National Museum-East Rudolph [*photograph by Lucile Crété], SK = Swartkrans, SF = Sterkfontein]. Scale bars equal 10 mm.

tooth development varying inter-specifically (Reade et al., 2015). There is, therefore, support for a multi-disciplinary approach to produce more holistic, accurate and robust reconstructions of past diets (Schubert et al., 2006) and by extension, of palaeovegetation. Consequently, we take a multi-method approach here to understand when, and how, each method can be used. Our palaeoenvironmental picture obtained from measurements of dental molars, mesowear and microwear analyses, along with new stable isotope data (collected by SCR and PJH in 2002) are compared to the palaeoenvironmental signals gained from stable isotope analysis by Lee-Thorp et al. (2007).

In this paper, we report on our findings from each method; these methods are typical of much of the current research in palaeoanthropology. The results presented are a subset of results for the wider project underway, used here to reflect on the accuracy and limitations of each method. We use these datasets to address two main questions: 1) can palaeodietary information be used to reconstruct habitat conditions through time; and 2) what additional detail can we gain about the dietary differences between the different *Antidorcas* species in the fossil record?

2. Materials and methods

2.1. Materials

A sample of 287 fossil *Antidorcas* teeth from Sterkfontein and Swartkrans, Cradle of Humankind, Gauteng Province, South Africa were examined for this study. All species of *Antidorcas* present in the deposits are considered. Specimens are taxonomically identified following the criteria set out in Table 1.

Modern springbok specimens were also examined ($n = 33$ individuals). Only permanent upper and lower second molars (M^2 and M_2) were selected for study in the first instance. Where unavailable, permanent upper and lower first or third molars are used for use-wear analyses instead. Substitutions of the permanent molar teeth have been shown to produce comparable dietary signals (Scott, 2012; Ramdarshan et al., 2017 for dental microwear textural analysis, and Kaiser and Solounias, 2003 for dental mesowear analysis, respectively). Upper and lower second molar were separated for metric (linear dental measurements) analyses.

All statistical analyses were run in software package SPSS (v.23). All results presented here are used to showcase particular aspects of each methodology, highlighting where each method can be implemented to obtain the most accurate results. All data are rank transformed prior to analysis to mitigate for small and varying sample sizes.

2.1.1. Collections used

Sterkfontein Member 4 and 5 (Stw53 Infill, East and West), Swartkrans Member 031 (Lower Bank and Hanging Remnant), Member 2 and Member 3. Fossil collections are housed at the Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg and the Ditsong Museum of Natural History (DM), Pretoria, South Africa. Additional material from modern Mammalogy collections (wild caught) was studied to establish the anticipated range of variation. Modern collections are housed at the Natural History Museum (NHM), London and the National Museums Scotland (NMS), Edinburgh, United Kingdom and the Ditsong Museum of Natural History, Pretoria, South

Table 2
Dates ranges and methods used to obtain these dates for each member used. Maximum date ranges are indicated below each Member row. Member deposits ordered chronologically relative to one another (oldest to youngest) based on the dates provided in the table.

Member	Date	Method	Reference
Sterkfontein Member 4	2.8–2.4 Ma	Bovid biochronology	Vrba, 1976, 1980
	~2.5 Ma	Primate biochronology	Delson, 1988
	2.8–2.6 Ma	Mammalian biochronology	McKee, 1993
	~2.1 Ma	ESR (electron spin resonance)	
		Palaeomagnetism	Schwarcz et al., 1994
	2.15–2.14 Ma	Uranium-lead	
	2.65–2.01 Ma	ESR, and palaeomagnetism	Partridge, 2005
			Pickering and Kramers, 2010
	2.8–~2.0 Ma		Herries and Shaw, 2011
Date range: 2.8–2.0 Ma.			
Sterkfontein Stw infill	2.6–2.0 Ma	Biochronology	Kuman and Clarke, 2000
	1.8–1.4 Ma	Biostratigraphy	Herries et al., 2009
	1.8–1.5 Ma	ESR and palaeomagnetism	Herries and Shaw, 2011
Date range: 2.6–1.4 Ma.			
Sterkfontein M5 East	2.0–1.7 Ma	Biochronology and archaeology Dating seriation	Kuman and Clarke, 2000
	1.4–1.1 Ma	ESR, isotopes and	Herries et al., 2009
	1.4–1.2 Ma	palaeomagnetism	Herries and Shaw, 2011
Date range: 2.0–1.1 Ma.			
Sterkfontein M5 West	1.7–1.4 Ma	Biochronology and archaeology Dating seriation	Kuman and Clarke, 2000
	1.3–0.8 Ma	ESR and palaeomagnetism	Herries et al., 2009
	1.3–1.1 Ma		Herries and Shaw, 2011
Date range: 1.7–0.8 Ma.			
Swartkrans Member 1 LB	1.7 Ma	Biostratigraphy	Vrba, 1985; Churcher and Watson, 1993; de Ruiter, 2003a, 2003b; Brain, 1995, Vrba, 2000
	1.8 Ma	Biostratigraphy	
Swartkrans Member 1 HR	1.6 Ma	Biostratigraphy	Vrba, 1982, 1985; Delson, 1984; Brain, 1995; Berger et al., 2002; de Ruiter, 2003a, 2003b
Swartkrans Member 1	2.0–1.4 Ma	ESR	Curnoe et al., 2001
(combined)	2.0 (± 0.02) Ma	U-Pb bovid enamel dating	Albarède et al., 2006
Date range: 2.0–1.4 Ma.			
Swartkrans Member 2	1.36 (± 0.29) Ma (1.65–1.07 Ma)	U-Pb enamel dating	Balter et al., 2008
	1.44 ± 0.05	U-Pb enamel dating	Albarède et al., 2006
	1.7–1.1 Ma	Biochronology Dating seriation	Brain, 1995; Vrba, 1995a, 1995b; Herries et al., 2009
Date range: 1.7–1.07 Ma.			
Swartkrans Member 3	0.83(± 0.21)Ma (1.04–0.61 Ma) 0.988 ± 0.003	U-Pb enamel dating	Balter et al., 2008
	1.5–0.7 Ma	U-Pb enamel dating Biochronology	Albarède et al., 2006 Brain, 1993; Vrba, 1995a, 1995b; Herries et al., 2009
Date range: 1.5–0.61 Ma.			

Africa.

Additional modern collections were used for dental microwear textural analysis (DMTA). In addition to NHM and NMS, the following institutions' collections were used: MNHM Paris, France; Zoologisches Museum Berlin, Germany; Staatliches Museum für Naturkunde of Stuttgart, Germany; Senckenberg Naturkundemuseum of Frankfurt, Germany; NHM Basel, Switzerland.

2.2. Methods

Due to the uncertainty surrounding the taxonomic status of *A. australis*, (according to features in Table 1), *A. australis* and *A. marsupialis* fossil specimens were analysed together under 'Antidorcas sp.'

Other species of specific dietary preference, such as the grazing blesbok (*Damaliscus pygargus/dorcas*) are occasionally used to establish the fossil dietary parameters and understand the dietary signals gained from *Antidorcas*.

2.2.1. Linear measurements of teeth

Tooth dimensions obtained from measurements of mesiodistal length (MDL) and bucco-lingual width (BLW) are considered for this study. Measurements were taken in millimeters with carbon fiber composites digital calipers (resolution: 0.1 mm/0.001″).

2.2.2. Mesowear

Mesowear provides an indication of an individual's dietary signal through their lifetime. Mesowear scores are informative on the abrasiveness of the diet and can be used as a reflection of the grazing/browsing composition of diet. Grazers' molars typically exhibit low occlusal relief and blunter cusps due to the abrasive nature of a predominantly grazing diet. Browsers on the other hand, normally display higher occlusal relief, typically with sharper cusps (Fortelius and Solounias, 2000). Following the protocol established by Fortelius and Solounias (2000), numerical values are given to each tooth based on occlusal relief (High or Low) and cusp shape (Sharp, rounded or blunt) as set out in Fig. 2. The numerical value (score) is given as follows: Low Blunt:0, Low Rounded:1, Low sharp:2, High rounded:3, High sharp:4. Upper molars are used for mesowear analysis as lower molars have a tendency towards blunting and are consequently likely to be exhibiting a predominance of grazing signals (Kaiser and Fortelius, 2003).

2.2.3. Dental microwear textural analysis (DMTA)

Dental microwear textures provide insight into the diet over the last few weeks/days of an individual animal's lifetime (Teaford and Oyen,

Fig. 2. Mesowear scoring figure: Traditional mesowear scoring system.
Established by Fortelius and Solounias (2000), figure modified from Merceron et al. (2007).
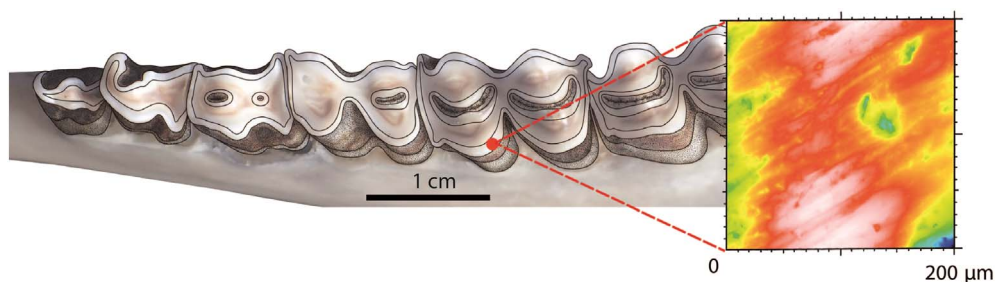
Fig. 3. DMTA image: Dental microwear texture analysis is run on the disto-buccal facets of the buccal cuspids along the lower arch.
(Modified from Merceron et al., 2016.)

1989; Schulz et al., 2013; Merceron et al., 2016; Ramdarshan et al., 2016). Upper and lower molars were used for microwear analysis to allow direct comparisons across species and deposits. Because values from all positions (M1 to M3) of permanent molars can be used together in statistical analysis as their dental microwear textures have been shown to be statistically similar (see Ramdarshan et al., 2017). Data on lower molars can be grouped with upper molars if specific facets are considered (see below; see Ramdarshan et al., 2017). This is beneficial when dealing with isolated fossil dentition that may not be as clearly identifiable to a particular tooth.

Dental microwear texture analysis (DMTA) was conducted according to Merceron et al. (2016). Molds of the dental enamel facets of interest, on the disto-buccal facets of the protoconid (or on the hypoconid if the former facet is broken), and on mesio-lingual facets of the protocone (Fig. 3), were created using polyvinvylsiloxane elastomer. Ramdarshan et al. (2017) have shown that there are significant differences in dental microwear textures between the disto-buccal facets of the protoconid on lower teeth and the lingual facet of the paracone on upper; but not with the protocone from upper molars (see discussion in Ramdarshan et al., 2017). This mold is cut to provide a relatively small and flat surface, for viewing under the surface profilometer (Leica DCM8 confocal profilometer). The prepared molds are placed under a Leica DCM8 confocal profilometer using white light confocal technology with a Leica 100× objective (Numerical aperture = 0.90; working distance = 0.9 mm). The lateral resolution is an (x, y) interval of 0.129 μm, with a vertical numerical step of 1 nm. Scans are taken in the centre of the facet, where possible, to ensure repeatability and to limit subjectivity. Scans are treated using LeicaMap to eliminate artefacts, such as abnormal peaks following procedures detailed in the supplementary material in Merceron et al. (2016). Data analyses for DMTA are run through Sfrax and Toothfrax software, as set out by Scott et al. (2006).

Complexity (Area-scale fractal complexity, *Asfc*) measures the roughness of the dental facet surface. Scale of maximum complexity (*Smc*) shows the scale range *Asfc* is calculated from (taking the steepest part of the relative area against the scale of the curve). Anisotropy considers the direction of wear and relative lengths of vectors (depth profiles), essentially providing a view of direction of wear and a glimpse into heterogeneity (Scott et al., 2006). Multiple scratches with no pitting would produce anisotropic surfaces with a high *epLsar* value, whereas a surface with scratches in opposing directions coupled with pits of varying depths and sizes would produce a complex (high Asfc)

ARTICLE IN PRESS

L. Sewell et al. *Journal of Archaeological Science: Reports xxx (xxxx) xxx–xxx*

and isotropic (low *epLsar*) surface and be more indicative of browsing diets (Scott, 2012; Scott et al., 2006). Homogeneity of wear is provided through *HAsfc* values (Heterogeneity of Area-scale fractal analysis). Higher *HAsfc* values indicate greater variation in diet. Homogeneity of diet tends to show in homogeneity of surface texture (i.e. lower HAsfc values) (Scott et al., 2006). *HAsfc* are calculated through a 9- and an 81-cell mesh over each scanned surface. *Tfv* (Textural fill volume) values represent the surface texture based on fill volume at different scales (i.e. the relief of the surface) (Scott et al., 2006). Considerable research has focused on the nature of microwear signatures in whether dust and grit cloud the dietary signals obtained. Ungar et al. (2016) and Merceron et al. (2016) show that overall, microwear data is informative of dietary preferences and thus, in this case also informative about palaeovegetation.

Data are rank transformed and a one-way ANOVA with post hoc Tukey's HSD and Fisher's LSD tests are performed, once to establish species dietary differences and a second time, to understand dietary differences (for all *Antidorcas* species combined) between members.

2.2.4. Stable carbon isotope analysis

Stable carbon isotope analysis was made possible via temporary export and destructive sampling permits granted by SAHRA (South African Heritage Resource Agency). Stable carbon isotope values provide a dietary signal from the early years of an individual animal's lifetime. The carbon values are reflective of the C_3/C_4 composition of the diet during the time of dental-enamel formation. Carbon isotopes indicate the photosynthetic pathways used by the vegetation and subsequently consumed by the animal sampled. C_3 plants (indicative of a predominantly browsing diet) are more depleted in carbon (δ^{13}C) than C_4 plants (indicative of a predominantly grazing diet) (Vogel, 1978; Luyt, 2001). Isotope analysis complements use-wear (mesowear and microwear) analysis. Isotopes contrast with microwear (meals of last days to weeks) and mesowear (averaged lifetime) results, by providing the early years (during dental enamel formation) signal. To obtain the isotopic information, approximately 5–10 mg of enamel powder was extracted from each tooth using a diamond-tipped drill bit, as a bulk sample. Samples were then cleaned using standard pre-treatment methods for the removal of organic and carbonate contaminants (Lee-Thorp et al., 1997; Van der Merwe et al., 2003). Carbon and oxygen isotopic measurements were obtained using a VG SIRA 12 mass spectrometer at the University of Liverpool (see Hopley et al., 2006 for further details). Long-term laboratory reproducibility (σ) is better than ± 0.1‰ for both isotope ratios.

3. Results

3.1. Linear measurements of teeth

Modern springbok are sexually dimorphic, with males having larger body size and larger, more robust horn sizes (e.g., Skinner and Chimimba, 2005; Brakora, 2014). To rule out sexual dimorphism, we tested modern *Antidorcas* data (of known sex) for significant differences in MDL and BLW measurements. No significant differences were found (Mann-Whitney *U* test $p > 0.05$ for occlusal length; $p > 0.05$ for bucco-lingual width). These results show that male and female springbok teeth do not differ significantly in size. Consequently, we consider that sexual dimorphism in the fossil species is unlikely to confound the potential size differences where they are observed in the fossil record.

Both *A. recki* and *A. bondi* can clearly be distinguished from *A. marsupialis* based on their consistently smaller size (Table 3). In contrast, there is considerable overlap between specimens previously assigned to *Antidorcas australis* (Vrba, 1973) compared to those assigned

Table 3
Mean M^2 measurements for each Antidorcas species. Measurements are separated according to deposit (site and Member). MDL = mesiodistal length; BLW = bucco-lingual width.

Species	Provenance	N	Mean MDL	Mean BLW
Antidorcas marsupialis/ australis	Swartkrans Member 1	3	14.1	9.6
	Swartkrans Member 2	1	14.7	9.4
	Swartkrans Member 3	22	14.8	9.4
	Cave of Hearths	5	15.0	11.3
Antidorcas marsupialis	Modern	44	16.3	11.7
Antidorcas recki	Sterkfontein Member 4	1	14.7	6.0
	Cooper's Cave (D)	1	14.7	10.4
Antidorcas bondi	Swartkrans Member 2	11	13.9	8.6
	Cave of Hearths	3	15.1	8.5
Antidorcas sp.[a]	Swartkrans Member 1	1	13.4	10.4
	Swartkrans Member 2	18	14.4	9.8
	Swartkrans Member 3	2	13.1	11.4

[a] In this table, *Antidorcas* sp. refers to specimens identifiable only to genus level.

to *Antidorcas marsupialis*. For example, in Swartkrans Member 1, the bucco-lingual width of *A. australis* ($n = 10$) ranges from 4.5–12.5 mm and *A. marsupialis* ($n = 3$) ranges from 5.5–10.2 mm.

Statistical analysis of mesiodistal length (MDL) and bucco-lingual width (BLW) (see Fig. 4) showed that *Antidorcas bondi* and *Antidorcas* sp. are significantly different for Swartkrans Member 2 (MDL $p = 0.014$; BLW $p = 0.08$), perhaps suggesting the presence of another *Antidorcas* species, other than *Antidorcas bondi*. BLW significantly increased (Kruskal-Wallis test) from Swartkrans Member 1 to Swartkrans Member 2 for specimens assigned to the following taxa: *Antidorcas* sp. ($p = 0.012$), *A. bondi* ($p = 0.005$) and *A. marsupialis* ($p = 0.004$). These results suggest the presence of two species of *Antidorcas* in Swartkrans Member 1 and Member 2, both of which exhibit dental size changes through time. Whilst some specimens are identifiable only to genus (*Antidorcas* sp.), we can assert that the bucco-lingual width increases for the *Antidorcas* genus from Swartkrans Member 1 to Swartkrans Member 2.

Antidorcas bondi second molar mesiodistal length significantly increases between Swartkrans Member 1 (1.7–1.1 Ma) and Swartkrans Member 2 (0.7–0.6 Ma). The mean mesiodistal length of the sample of *A. bondi* second molars significantly increased (Independent samples Kruskal-Wallis Test ($p = 0.018$), with post hoc independent samples *t*-test $p = 0.038$) from Member 1 times (mean length 12.9 mm) to Member 2 times (mean length 14.5 mm).

3.2. Mesowear

Mesowear scores from this study are given in Table 4. There is a good level of agreement with our data and the existing dietary inferences for each species.

Specifically, the extinct *A. bondi* differs from the modern *A. marsupialis* in having higher frequency of molars with low occlusal relief, together with rounded to blunt cusps. This is suggestive of more grazing dietary habits than the modern forms, as previously stated by Brink and Lee-Thorp (1992). Although low in sample size, *A. recki* exhibits a primarily browsing mesowear signature of high relief, with sharp cusps, thus supporting previous isotopic results by Luyt (2001) and other
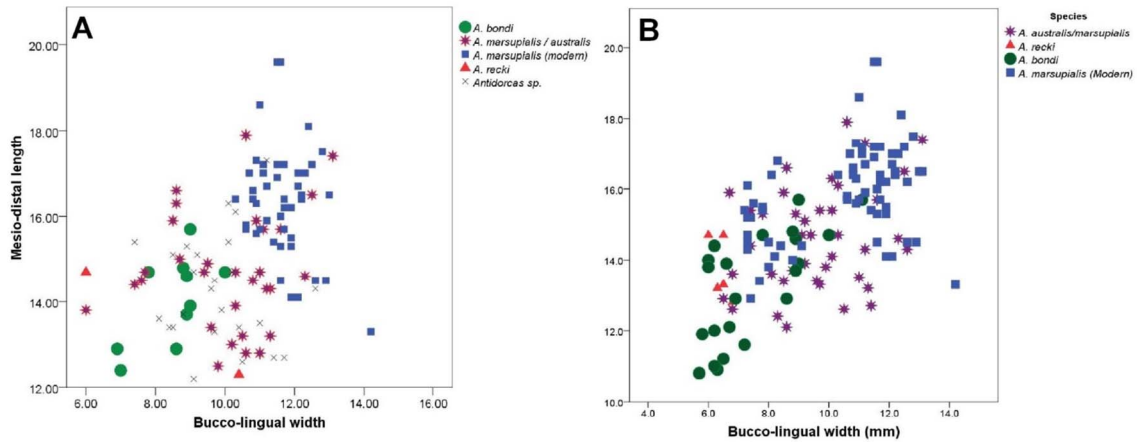
Fig. 4. Scatter plot of *Antidorcas* linear measurements. Morphological measurements of permanent A) lower second molars for all members (bucco-lingual width against mesiodistal length) according to species. (*Antidorcas bondi* n = 9, *Antidorcas recki* n = 5, *Antidorcas* sp. (*A. australis/marsupialis*) n = 28, modern *Antidorcas marsupialis* n = 36). Modern and fossil *A. marsupalis* and *A. australis* show significant overlap in dimensions. B) upper second molars for all members (bucco-lingual width against mesiodistal length) according to species.

Table 4
Antidorcas mesowear values. Relief (%high/low) and cusp shape (%sharp, rounded and blunt), 'N' = number of specimens Table A: Mesowear by species, B: Mesowear for all the *Antidorcas* genus through time, (ordered oldest to youngest according to member), C: Mesowear through time, separated for each *Antidorcas* species. *Antidorcas* sp. represents *Antidorcas* identifiable only to genus. "*Antidorcas marsupialis*" represents specimens taxonomically assigned to *A. australis* or *A. marsupialis* (with the exception of the modern specimens).

A: Species	N	% High	% Low	% Sharp	%Rounded	%Blunt
Antidorcas sp.	27	63	37	44	56	0
Antidorcas recki	4	75	25	100	0	0
Antidorcas bondi	58	43	57	43	47	10
Antidorcas marsupialis fossil	42	74	26	48	40	12
Antidorcas marsupialis modern	24	63	38	33	58	8

B: Provenance	N	% High	% Low	% Sharp	%Rounded	%Blunt
Sterkfontein (unstratified)	31	48	52	48	42	10
Sterkfontein Member 4	10	60	40	50	50	0
Sterkfontein Member 5 (west)	5	60	40	40	60	0
Swartkrans Member 1 (HR)	4	50	50	25	25	50
Swartkrans Member 1 (LB)	3	100	0	100	0	0
Swartkrans Member 2	22	64	36	36	59	5
Swartkrans Member 3	25	72	28	48	40	12
Cooper's Cave	4	75	25	100	0	0
Cave of Hearths	27	44	56	41	52	7
Modern	24	62.5	37.5	33	58	8

| C: Provenance	Species	N	% High	% Low	% Sharp	%Rounded	%Blunt
Sterkfontein (unstratified)	*Antidorcas* sp.	1	100	0	100	0	0
	Antidorcas bondi	25	40	60	52	36	12
Sterkfontein Member 4	*Antidorcas* sp.	10	60	40	50	50	0
Sterkfontein Member 5 (west)	*Antidorcas* sp.	5	60	40	40	60	0
Swartkrans Member 1 (HR)	*Antidorcas* sp.	1	100	0	0	100	0
	Antidorcas marsupialis	3	33	67	33	0	67
Swartkrans Member 1 (LB)	*Antidorcas* sp.	1	100	0	100	0	0
	Antidorcas marsupialis	2	100	0	100	0	0
Swartkrans Member 2	*Antidorcas* sp.	9	56	44	33	67	0
	Antidorcas bondi	11	64	36	36	55	9
	Antidorcas marsupialis	2	100	0	50	50	0
Swartkrans Member 3	*Antidorcas marsupialis*	25	72	28	48	40	12
Cooper's Cave	*Antidorcas recki*	4	75	25	100	0	0
Cave of Hearths	*Antidorcas bondi*	22	36	64	36	55	9
	Antidorcas marsupialis	5	80	20	60	40	0
Modern	*Antidorcas marsupialis*	24	62.5	37.5	33	58	8
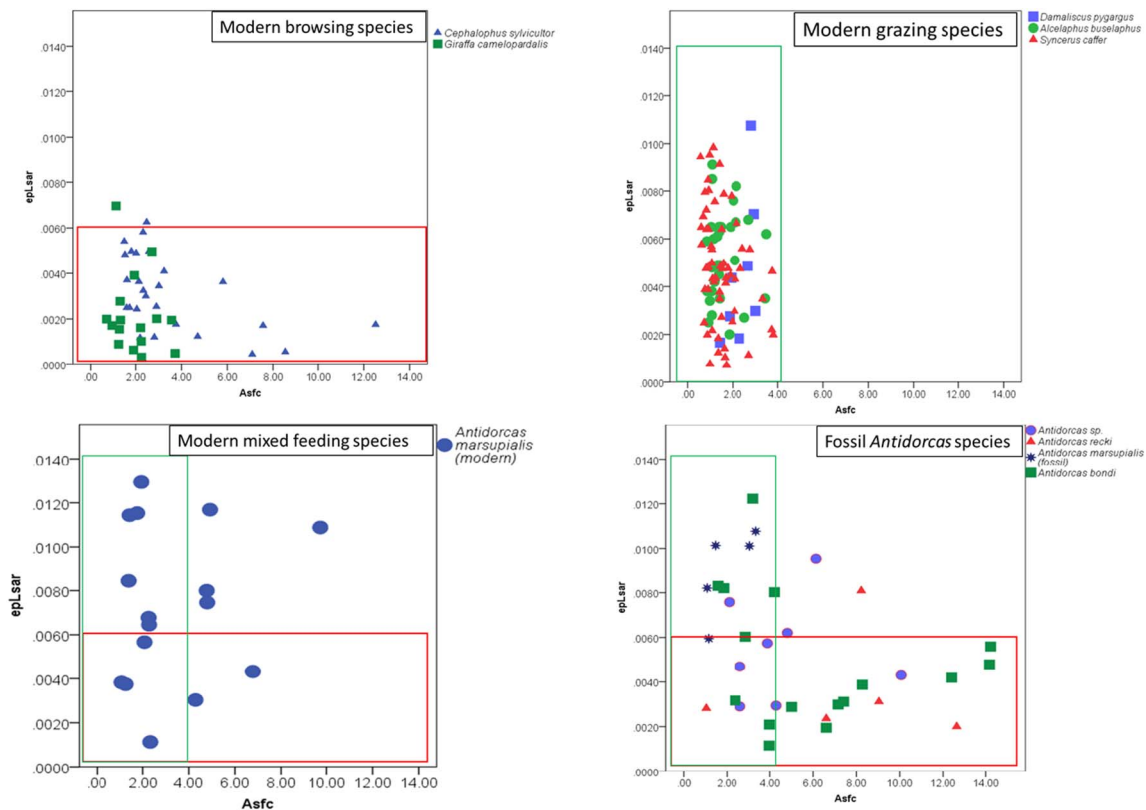
Fig. 5. Biplots (*Asfc* on X axis vs *epLsar* on Y axis) of modern ruminants and extinct species of *Antidorcas* from South African Cradle of Humankind sites. The two lower plots show overlap, and therefore mixed-feeding signatures, when compared to modern obligate browsing and obligate grazing species.

studies of postcranial ecomorphology of this species from Olduvai Gorge, Tanzania (Plummer and Bishop, 1994).

3.3. Microwear

The dental microwear textures of modern *A. marsupialis* display microwear values expected for mixed feeders with medium values in complexity and high values in anisotropy.

This data shows a wide *Asfc* and *epLsar* distribution for fossil *Antidorcas* also, indicative of mixed-feeding dietary habits, similar to modern springbok (Fig. 5).

As shown in Tables 5 and 6, significant differences between species emerge.

Tables 5 and 7 show that all extinct species of *Antidorcas* differ from

the modern grazing taxa-*Alcelaphus buselaphus* and *Syncerus caffer*, in having higher *Asfc*. All fossil *Antidorcas* differ from the leaf-browsing *Giraffa camelopardalis*, in having higher *Asfc*. All fossil *Antidorcas*, excluding *A. recki* have higher *epLsar* than the two modern species of browsing ruminants. Finally, all fossil *Antidorcas* species have higher *Tfv* than modern species (except modern springbok; Tables 5 and 7).

As indicated (Table 9), there are no significant differences for *Antidorcas* microwear texture parameters between Members (through time), suggestive of varying degrees of mixed habitats being available throughout this temporal period.

Considering Table 8, the highest *Asfc* and lowest *epLsar* values for Sterkfontein Member 4 could support the notion of greater woodland in the area, with *Antidorcas* including slightly more browse in the diet, than at Swartkrans (Member 2 and 3).

Table 5
Summary dental microwear texture parameter statistics. Mean (M), standard deviation (SD) and standard error of the mean (SEM) for all species. *Antidorcas* sp. refers to those identifiable only to genus level.

Species		N	Asfc			epLsar			HAsfc 9			HAsfc 81			TFV2		
			M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM
Fossil	Antidorcas sp.	7	4.61	2.79	1.06	0.00585	0.00221	0.00083	0.56	0.14	0.05	0.86	0.26	0.10	72,548.6	12,914.2	4881.1
	A.bondi	12	6.16	4.05	1.17	0.00479	0.00229	0.00066	0.52	0.34	0.10	0.85	0.44	0.13	63,763.9	8943.1	2581.6
	A.marsupialis/australis	10	3.98	3.79	1.20	0.00692	0.00395	0.00125	0.47	0.33	0.10	0.75	0.36	0.12	63,742.3	12,917.9	4085.0
	A.recki	5	7.51	4.25	1.90	0.00368	0.00250	0.00112	0.52	0.27	0.12	1.06	0.49	0.22	56,845.1	16,825.5	7524.6
Modern	Alcelaphus buselaphus	31	1.59	0.70	0.13	0.00536	0.00183	0.00033	0.34	0.21	0.04	0.59	0.22	0.04	50,449.0	8450.2	1517.7
	Cephalophus sylvicultor	27	3.50	2.63	0.51	0.00304	0.00173	0.00033	0.34	0.13	0.02	0.61	0.21	0.04	4.0349.2	8450.2	1517.7
	Giraffa camelopardalis	16	1.97	0.91	0.23	0.00217	0.00176	0.00044	0.40	0.33	0.08	0.68	0.49	0.12	27,251.7	19,050.1	4762.5
	Syncerus caffer	23	1.53	0.84	0.18	0.00456	0.00254	0.00053	0.32	0.19	0.04	0.57	0.28	0.06	46,026.2	8556.2	1784.1
	Damaliscus pygargus	8	2.38	0.58	0.21	0.00453	0.00308	0.00109	0.56	0.31	0.11	0.90	0.36	0.13	60,687.7	7822.0	2765.5
	Antidorcas marsupialis	16	3.32	2.40	0.60	0.00733	0.00360	0.00090	0.53	0.32	0.08	1.02	0.64	0.16	63,222.4	18,965.2	4741.3

Table 6

DMTA analysis of variance. One-way ANOVAs on dental microwear textural parameters to explore variations between modern and extinct species of ruminants. df: degrees of freedom, SS: sum of squares, MS: mean of squares.

	df	SS	MS	F	*p*
Asfc					
Sample	9	118,199.2	13,133.2	9.91	0.00000
Error	145	192,110.8	1324.9		
epLsar					
Sample	9	89,219.0	9913.2	6.50	0.00000
Error	145	221,091.0	1524.8		
HAsfc 9					
Sample	9	47,319.2	5257.7	2.90	0.00350
Error	145	262,990.8	1813.7		
HAsfc 81					
Sample	9	61,267.8	6807.5	3.96	0.00015
Error	145	249,042.2	1717.5		
Tfv2					
Sample	9	164,841.0	18,315.7	18.26	0.00000
error	145	145,469.0	1003.2		

3.4. Stable carbon isotopes

C_3 plants are more depleted in ^{13}C relative to C_4 plants (Vogel, 1978; O'Leary, 1981). Therefore, tooth enamel with higher carbon isotope values is indicative of the consumption of more C_4 plants. We assign each fossil enamel carbon isotope value to the dietary classifications of Lee-Thorp et al. (2007); see Tables 10, 11 & 12.

In line with results from the other dietary proxies, Table 11 shows *Antidorcas bondi* was generally eating a very different diet to other *Antidorcas* species and is more in line with *Damaliscus* (grazing) diets (other than during Swartkrans Member 2 times c.1.65–1.07 Ma). The higher mean carbon isotope values of *A. bondi* are indicative of C_4 plants being consumed, suggestive of a grazing and mixed feeding diet (Cerling and Harris, 1999). Of the 19 fossils classified as *Antidorcas* sp. (Table 8), two specimens (SK 14123 and SK11073) have carbon isotopic compositions consistent with *A. marsupialis*, and can be tentatively assigned to this species; the remaining specimens have higher carbon isotope values and are likely to belong to *A. bondi*.

The blesbok, *Damaliscus pygargus (dorcas)* is typically considered to be a grazing species and indeed, *Damaliscus* is expected to largely be a grazing genus (Estes, 1991). At Sterkfontein and Swartkrans, isotope data shows *Damaliscus* sp. to be true to expected dietary preferences and a small sample is included here to establish most-likely grazing parameters.

Stable carbon isotope results (Tables 11 & 12) support the dietary categories and vegetation signals obtained from use-wear (microwear and mesowear) analyses. However, *Antidorcas bondi* shows slight indications of more mixed feeding in Swartkrans Member 2, away from the specialized grazing signals apparent from the other methodologies. This perhaps lends support to the presence of more heterogeneous habitats for Swartkrans Member 2.

4. Discussion

This paper has used data from various dietary proxies of an abundant antelope to attempt a detailed reconstruction of the palaeovegetation conditions through time at the important hominin-bearing sites of the Cradle of Humankind. Each proxy, predictably, reflects a different aspect of the diets of the springboks. Combined, we have tried to use these datasets to address two main questions: 1) can palaeodietary

information be used to reconstruct habitat conditions through time; and 2) what additional detail can we gain about the dietary differences between the different *Antidorcas* species in the fossil record? In response to the first question, the dietary proxies from the *Antidorcas* examined in this study do yield palaeovegetation reconstructions that broadly agree with habitat reconstructions based on other palaeoenvironmental proxies. Our results suggest increased grassland post c.1.7 Ma, with some suggestion of more heterogeneous habitats for Swartkrans Member 2 (c.1.65–1.07 Ma). A reduced grassland presence in Swartkrans Member 2 is *potentially* indicated with the assumed-to-be grazing *Antidorcas* species, *A. bondi*, yielding a slightly mixed feeding dietary signal from stable carbon isotope values. Whilst it is only slightly indicative of more mixed feeding practices, *Antidorcas bondi* specimens from Swartkrans Member 2 do exhibit dietary behavioral difference when compared to *A. bondi* from other members, in which *A. bondi* is shown to be a more faithful grazer (from stable carbon isotope values). Lee-Thorp et al. (2007) suggested the lower $\delta^{13}C$ values were indicative of either a remnant component of C_3 vegetation or less specialized dietary taxa than their modern counterparts. However, dental microwear textures studied here suggest *A. bondi* had a more mixed-feeding diet than previously assumed.

The second question regarding dietary niches in the various fossil species of *Antidorcas* is more complex. Our dietary reconstructions indicate a wide dietary range represented within the *Antidorcas* lineage, as we would expect from a mixed-feeder that survived changing habitat and vegetation conditions.

In contrast to Brink and Lee-Thorp (1992) all the fossil species of *Antidorcas* display high values in dental microwear texture complexity (*Asfc*) which exclude grazing habitats. DMTA supports that all species of *Antidorcas* were mixed feeding, including herbaceous monocots and browse (shrubs and foliages with lignified tissues, possibly with seeds and fruit). *A. recki* displays a lower *epLsar* than the other *Antidorcas* species (see Table 5), and significantly lower than the fossil *A. marsupialis* (Table 7). The dental microwear texture for fossil *A. bondi* here shows it to have practiced greater mixed feeding than shown by the fossil *A. marsupialis* sample (Fig. 5). Dental microwear textures on *A. recki* are consistent with mesowear and isotopic analysis in all supporting a higher browsing component in the diet compared to the other *Antidorcas* species. Browsing is more likely to result in higher heterogeneity due to the nature and range of the browse vegetation consumed. Interestingly, both fossil *A. marsupialis/australis* and *A. recki* have higher heterogeneity of diet, indicative of more mixed feeding diets, higher than that of modern *Antidorcas marsupialis*, a known mixed-feeder. Indeed, all DMTA supports *Antidorcas* being a predominantly mixed-feeding genus.

In interpreting these diets and what they mean in the wider context of habitat changes and the faunal community, we must also consider the role of biotic factors within the faunal community. Codron et al. (2008) highlight the role that niche specialization can play on changing diets of herbivores within a community, with both environmental and biotic (competition) factors contributing to the forcing of dietary differentiation into specific niches (C_3 or C_4). *Antidorcas* may have been in competition with other herbivore species such as the impala (*Aepyceros melampus*).

Significant differences in tooth metrics analysed in this study indicate that the ancestral *A. recki* possessed smaller overall dental dimensions than modern *A. marsupialis*, supporting the results from previous studies (e.g. Vrba, 1970, 1973) and strongly suggesting that *A. recki* possessed a smaller body size (Gentry, 1978) than *A. marsupialis*. Body size can be informative of palaeoenvironmental conditions, and increases in body size can possibly be explained as an advantage in more seasonal environments where there is a longer period of fasting, a phenomenon known as fasting endurance (Millar and Hickling, 1990;

Table 7

Pairwise differences for microwear texture parameters between modern ruminants and extinct species of *Antidorcas* from South African fossil sites. Significance at $p < 0.05$ for a given variable is indicated by variable abbreviations below the diagonal for Fisher's LSD tests and above the diagonal for both Tukey's HSD and Fisher's LSD tests (see text for details). *Antidorcas* sp. represents specimens identifiable only to genus. Fossil '*Antidorcas marsupialis*' represents *Antidorcas marsupialis/australis*.

[Table 7 is a large rotated pairwise-comparison matrix. Columns and rows list, in order: Antidorcas bondi, Antidorcas sp, Antidorcas marsupialis, Antidorcas recki (Fossil); Alcelaphus buselaphus, Cephalophus sylvicultor, Giraffa camelopardalis, Syncerus caffer, Damaliscus pygargus, Antidorcas marsupialis (Modern). The matrix is repeated as four stacked blocks corresponding to variables asfc, epLsar, HAsfc (HAsfc 9 / HAsfc 81) and Tfv2; cells below the diagonal show Fisher's LSD results and cells above the diagonal show results agreeing for both Tukey's HSD and Fisher's LSD. Significant pairings are marked by the variable abbreviations (asfc, epLsar, HAsfc 9, HAsfc 81, Tfv2); the diagonal cells are filled black.]

LSD \ HSD tests		Antidorcas bondi	Antidorcas sp	Antidorcas marsupialis	Antidorcas recki	Alcelaphus buselaphus	Cephalophus sylvicultor	Giraffa camelopardalis	Syncerus caffer	Damaliscus pygargus	Antidorcas marsupialis
Fossil	Antidorcas bondi	■				asfc	asfc	asfc	asfc	asfc	asfc
	Antidorcas sp		■			asfc	asfc	asfc	asfc		
	Antidorcas marsupialis			■		asfc	asfc				
	Antidorcas recki				■	asfc	asfc				
Modern	Alcelaphus buselaphus	asfc	asfc	asfc	asfc	■					
	Cephalophus sylvicultor	asfc	asfc	asfc	asfc		■				
	Giraffa camelopardalis	asfc	asfc					■			
	Syncerus caffer								■		
	Damaliscus pygargus	asfc								■	
	Antidorcas marsupialis	asfc									■
Fossil	Antidorcas bondi	■					epLsar	epLsar			
	Antidorcas sp		■				epLsar	epLsar			
	Antidorcas marsupialis			■			epLsar	epLsar			
	Antidorcas recki				■			epLsar			
Modern	Alcelaphus buselaphus					■	epLsar	epLsar			
	Cephalophus sylvicultor	epLsar	epLsar	epLsar	epLsar	epLsar	■	epLsar	epLsar		epLsar
	Giraffa camelopardalis	epLsar	epLsar	epLsar	epLsar	epLsar	epLsar	■	epLsar	epLsar	epLsar
	Syncerus caffer						epLsar	epLsar	■		epLsar
	Damaliscus pygargus							epLsar		■	
	Antidorcas marsupialis						epLsar	epLsar			■
Fossil	Antidorcas bondi	■							HAsfc 9	HAsfc 9	
	Antidorcas sp		■			HAsfc 81	HAsfc 81	HAsfc 81	HAsfc 81		
	Antidorcas marsupialis			■							
	Antidorcas recki				■						
Modern	Alcelaphus buselaphus		HAsfc 81			■		HAsfc 9	HAsfc 9		HAsfc 81
	Cephalophus sylvicultor		HAsfc 81				■				
	Giraffa camelopardalis		HAsfc 81			HAsfc 9		■	HAsfc 9	HAsfc 9	
	Syncerus caffer	HAsfc 9	HAsfc 81			HAsfc 9		HAsfc 9	■		HAsfc 81
	Damaliscus pygargus									■	
	Antidorcas marsupialis					HAsfc 81			HAsfc 81		■
Fossil	Antidorcas bondi	■				Tfv2	Tfv2	Tfv2			Tfv2
	Antidorcas sp		■			Tfv2	Tfv2	Tfv2			Tfv2
	Antidorcas marsupialis			■		Tfv2	Tfv2	Tfv2			Tfv2
	Antidorcas recki				■	Tfv2	Tfv2	Tfv2		Tfv2	
Modern	Alcelaphus buselaphus	Tfv2	Tfv2	Tfv2	Tfv2	■					Tfv2
	Cephalophus sylvicultor	Tfv2	Tfv2	Tfv2	Tfv2		■				Tfv2
	Giraffa camelopardalis	Tfv2	Tfv2	Tfv2	Tfv2			■		Tfv2	Tfv2
	Syncerus caffer	Tfv2	Tfv2	Tfv2	Tfv2			Tfv2	■	Tfv2	Tfv2
	Damaliscus pygargus							Tfv2	Tfv2	■	
	Antidorcas marsupialis							Tfv2	Tfv2		■

11

Table 8
Dental microwear textural parameters (mean and standard deviation). All *Antidorcas* species are pooled together, with fossil *Antidorcas* separated by provenance (site and Member 'M'), where sufficient sample sizes allowed, to indicate the prevailing trend through time. 'Modern' represents the modern *Antidorcas marsupialis* sample.

Provenance	N	Asfc			epLsar			HAsfc 9			HAsfc 81			TFV2		
		M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM
Sterkfontein M4	5	7.51	4.25	1.90	0.00368	0.00250	0.00112	0.52	0.27	0.22	1.06	0.49	0.22	56,845.1	16,825.5	7524.6
Swartkrans M2	12	1.50	3.84	1.11	0.00589	0.00238	0.00069	0.50	0.21	0.06	0.80	0.26	0.07	69,556.8	11,937.3	3446.0
Swartkrans M3	7	2.80	1.19	0.45	0.00697	0.00336	0.00127	0.41	0.17	0.06	0.70	0.23	0.09	59,850.9	12,984.3	4907.6
Cave of Hearths	10	6.17	4.28	1.35	0.00482	0.00338	0.00107	0.59	0.43	0.13	0.93	0.53	0.17	65,679.1	9409.6	2975.6
Modern	16	3.32	2.40	0.60	0.00733	0.00360	0.00090	0.53	0.32	0.08	1.02	0.64	0.16	63,222.4	18,965.2	4741.3

Table 9
One-way ANOVAs on dental microwear textural parameters to explore variations between Members (Sterkfontein Member 4, Swartkrans Member 2, Swartrans Member 3, Cave of Hearths and Modern springbok). df: degrees of freedom, SS: sum of squares, MS: mean of squares.

	df	SS	MS	F	*p*
Asfc					
Sample	4	15,620.9	3905.2	1.42	0.242
Error	45	123,612.4	2746.9		
epLsar					
Sample	4	27,589.5	6897.4	2.02	0.107
Error	45	153,388.5	3408.6		
HAsfc 9					
Sample	4	1952.6	488.2	0.15	0.964
Error	45	151,665.9	3370.4		
HAsfc 81					
Sample	4	7396.2	1849.1	0.75	0.563
Error	45	110,802.2	2462.3		
Tfv2					
Sample	4	13,843.6	3460.9	1.64	0.181
error	45	94,932.1	2109.6		

Table 10
Dietary categories according to Stable carbon isotope values. Dietary distinctions according to $\delta^{13}C$ values and proportion of C3/C4 vegetation dominance in diet. Values from Lee-Thorp et al. (2007).

Dietary category	C3/C4 dominance	$\delta^{13}C$
Grazer	C_4	> −3.0‰
Mixed feeder	C_3 & C_4	< −3.0‰ > −9.0‰
Browser	C_3	< −9.0‰

Reynolds, 2007).

One of the outstanding problems in the fossil record is whether the extinct, *Antidorcas australis* is a valid species or not. The original species description emphasizes the difference in horncore shape, with *A. australis* having somewhat straighter horns than the lyrate form typical of *A. marsupialis* (Cooke and Wells, 1951). At present, we do not have enough data to definitively identify clear dietary distinctions between fossils assigned to *A. australis* and those assigned to *A. marsupialis*. The sample of fossil *Antidorcas marsupialis/australis* examined in this study does exhibit greater variation in measurements than modern *Antidorcas marsupialis*, which could be argued to lend support to the idea of the presence of multiple species (Brophy et al., 2014). Further landmark-based measurements and additional techniques, such as geometric morphometric analysis (to analyse shape changes) would be required to settle the question of this species distinction. It may be that the *A. australis* is differentiated only on its horncores and that dietary differences alone would not be sufficient to indicate distinctions between *A. australis* and *A. marsupialis*.

Another important aspect of modern springbok ecology is the migratory behaviour. Historic records show that springbok would trek in herds of thousands of individuals to seek out fresh grazing after the rains (Skinner and Louw, 1996). At present, there is little way to determine whether other extinct species of *Antidorcas* exhibited this behaviour or not. If so, *A. australis*, may have been a migrant to the Cradle region at various times. Certainly, migration would have helped reduce competition in grazing species.

As may be expected (e.g. Davis and Pineda-Munoz, 2016), there is some disparity between dietary signals from DMTA compared to those from stable carbon isotopes. DMTA indicates all *Antidorcas* fossil species were mixed feeders, whereas carbon isotopes indicate higher C4 signals (i.e. grazing) for these antelopes, particularly the case for *A. bondi*. This combination would support a mixed feeding dietary preference for *Antidorcas*, altering their dietary intake according to seasonal availability of resources. This suggests that the Cradle of Humankind region would have had seasonally available resources with significant amounts of both browse and graze. If severe seasonal droughts decimated the herbaceous layer (where grasses are abundant) then the antelopes may have switched to browse as tree/shrub roots go deeper in the soil to obtain water, compared to the herbaceous plants.

5. Summary

In this paper, we examined fossil *Antidorcas* dentition using a range of dietary proxies, from these results we attempted to infer the prevailing vegetation conditions between 2.8 and 0.8 Ma for the region where these *Antidorcas* lived and died, the Cradle of Humankind, South Africa. The majority of past research has used a single methodology on multiple species from assemblages, to address palaeoenvironmental questions. Here, we implemented a multiproxy analysis on a single mixed-feeding, herbivorous and abundant genus (*Antidorcas*) to provide a detailed palaeovegetation picture for the Sterkfontein and Swartkrans area through time. Aside from some subtle variations, preliminary conclusions from our study are found to be in broad agreement with those found through isotopic analysis by Lee-Thorp et al. (2007), of increased grassland presence in South Africa from ca 0.1.7 Ma.

Notably, we have been able to suggest from this multi-method approach, that methods can be reliably substituted for one another where time or cost constraints apply. Where methods such as mesowear, are non-destructive, quick and cheap to implement, these techniques can be used to accurately pinpoint where to concentrate the more time-consuming, expensive and destructive techniques, such as stable carbon isotope analysis. However, a more holistic, robust and detailed palaeovegetation reconstruction can be achieved by using complementary methodologies. The complementary use of methods such as mesowear analysis, stable isotope analysis and dental microwear texture analyses for instance, allows us to question whether *Antidorcas bondi* was typically a grazer or not. This approach could be implemented at other sites across the world for palaeovegetation reconstructions, where the

Table 11

Stable carbon and oxygen isotope data for *Antidorcas* fossils from Swartkrans. *Antidorcas* sp. indicates specimens only identifiable to genus level (specimens processed at the University of Liverpool).

Number	Species	$\delta^{13}C$	$\delta^{18}O$	Member
SK5882	*Antidorcas* sp.	1.6	−1.5	Swartkrans Member 2
SK5882	*Antidorcas* sp.	1.8	−0.8	Swartkrans Member 2
SK5990	*Antidorcas* sp.	−4.8	1.6	Swartkrans Member 2
SK10555	*Antidorcas* sp.	−1.1	0.1	Swartkrans Member 2
SK10555	*Antidorcas* sp.	−1.6	0.2	Swartkrans Member 2
SK4064	*Antidorcas* sp.	−0.6	0.6	Swartkrans Member 2
SK6118	*Antidorcas* sp.	1.1	0.6	Swartkrans Member 2
SK2264	*Antidorcas* sp.	−3.8	−0.9	Swartkrans Member 2
SK4083	*Antidorcas* sp.	−0.4	1.8	Swartkrans Member 2
SK4083	*Antidorcas* sp.	−0.4	1.5	Swartkrans Member 2
SK4080	*Antidorcas* sp.	−1.7	0.1	Swartkrans Member 2
SK2292	*Antidorcas* sp.	−5.9	−1.3	Swartkrans Member 2
SK4633	*Antidorcas* sp.	−0.6	−1.1	Swartkrans Member 2
SK11899	*Antidorcas* sp.	2.1	−0.8	Swartkrans Member 2
SK6106	*Antidorcas* sp.	−0.2	0.3	Swartkrans Member 2
SK11073	*Antidorcas* sp.	−12.7	−1.3	Swartkrans Member 2
SK 3014	*Antidorcas* sp.	−1.1	−0.8	Swartkrans Member 2
SK 14123	*Antidorcas* sp.	−12.7	0.8	Swartkrans Member 2
SK14070	*Antidorcas marsupialis*	−12.9	−1.9	Swartkrans Member 2
SK4054	*Antidorcas marsupialis*	−11.6	0.2	Swartkrans Member 2
SK 5958	*Antidorcas marsupialis*	−9.1	−0.8	Swartkrans Member 2
SK 4081	*Antidorcas marsupialis*	−10.3	0.4	Swartkrans Member 2
SK 2953	*Antidorcas marsupialis*	−15.0	−2.1	Swartkrans Member 2
SK 3055	*Antidorcas marsupialis/australis*	−11.0	2.1	Swartkrans Member 2
SK 2366	*Antidorcas bondi*	−5.2	−2.2	Swartkrans Member 2
SK 40592	*Antidorcas* sp.	−2.2	0.4	Swartkrans Member 5
SKX 41059	*Antidorcas australis/marsupialis*	−7.3	−1.1	Swartkrans Member 5

Table 12

Stable carbon isotope descriptive statistics for *Antidorcas and Damaliscus* species present in each member. References: where more than one value is given in original reference, a mean value has been calculated and used here. Luyt, 2001[1]; Van der Merwe et al., 2003[2]; Lee-Thorp et al., 2000[3]; Lee-Thorp et al., 1994[4]; New isotope data (this study)[5]; Vogel, 1978[6]; Sponheimer et al., 2003[7]. Dietary categories following category distinctions as set out in Table 6. *N.B. Modern *Antidorcas marsupialis* would be expected to be a mixed feeder. To aid comparison between the modern and fossil data, modern enamel values were increased by 1‰ to account for the post-industrial decrease in the $\delta^{13}C$ value of atmospheric CO_2 (Francey et al., 1999).

Species	N	Mean $\delta^{13}C$	Standard deviation	Minimum $\delta^{13}C$	Maximum $\delta^{13}C$	Dietary category
Sterkfontein Member 4						
Antidorcas recki	10 [1,2]	−11.4	1.063	−14.0	−5.0	Browser
Antidorcas bondi	2 [1,2]	−1.3	0.020	−1.0	−1.0	Grazer
Damaliscus sp.	9 [1]	−1.8	1.256	−7	3.0	Grazer
Sterkfontein Member 5						
Antidorcas recki	2 [1]	−11.7	0.945	−13.0	−11.0	Browser
Damaliscus sp.	5 [1]	−1.3	1.055	−5.0	1.0	Grazer
Antidorcas sp.	3 [1]	−5.4	3.133	−10.0	1.0	Mixed
Sterkfontein Member 5 East/Oldowan						
Damaliscus sp.	5 [1]	−2.7	0.965	−5.0	1.0	Grazer
Antidorcas sp.	1 [1]	−9.2	x	−9.2	−9.2	Browser-Mixed
Sterkfontein Member 5 West/Acheulean						
Antidorcas recki	2 [1]	−11.7	0.945	−13.0	−11.0	Browser
Damaliscus sp.	7 [1]	−0.9	0.540	−3.0	1.0	Grazer
Swartkrans Member 2						
Antidorcas recki	1 [4]	−12.9	x	−12.9	−12.9	Browser
Antidorcas bondi	9 [3]	−3.3	0.334	−5.0	−2.0	Mixed-Grazer
Antidorcas sp.	27 [4,5]	−5.1	1.076	−15.0	2.0	Mixed
Modern						
Antidorcas marsupialis	2 [6,7]	−13.1*	4.00	−17.0*	−9.0*	Browser

preserved faunal community is restricted in some way but where at least one continuous (mixed feeding) herbivore lineage is represented.

References

Albarède, F., Balter, V., Braga, J., Blichert-Toft, J., Telouk, P., Thackeray, F., 2006. U–Pb dating of enamel from the Swartkrans Cave hominid site (South Africa) by MC-ICP-MS. In: Goldschmidt Conference Abstracts. A7.

Antón, S.C., Potts, R., Aiello, L.C., 2014. Evolution of early *Homo*: an integrated biological perspective. Science 345 (6192), 1236828.

Avery, D.M., 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. J. Hum. Evol. 41 (2), 113–132.

Balter, V., Blichert-Toft, J., Braga, J., Telouk, P., Thackeray, F., Albarède, F., 2008. U–Pb dating of fossil enamel from the Swartkrans Pleistocene hominid site, South Africa. Earth Planet. Sci. Lett. 267 (1), 236–246.

Bamford, M., 1999. Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. S. Afr. J. Sci. 95, 231–237.

Bednekoff, P.A., Ritter, R.C., 1997. Adult sex ratio of a wild population of Springbok (*Antidorcas marsupialis*) at Nxai pan, Botswana. S. Afr. J. Wildl. Res. 27 (1), 22–24.

Berger, L.R., Lacruz, R., De Ruiter, D.J., 2002. Revised age estimates of *Australopithecus*-bearing deposits at Sterkfontein, South Africa. Am. J. Phys. Anthropol. 119 (2), 192–197.

Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M., Kibii, J.M., 2010. *Australopithecus sediba*: a new species of *Homo*-like Australopith from South Africa. Science 328, 195–204.

Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.P., Chritz, K.L., Harris, J.M., Jehle, G.E., Cerling, T.E., 2017. Aridity and hominin environments. Proc. Natl. Acad. Sci. 114 (28), 7331–7336.

Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 399–420.

Bobe, R., Eck, G.G., 2001. Responses of African Bovids to Pliocene climatic change. Paleobiology 27 (2), 1–48.

Brain, C.K., 1993. Structure and stratigraphy of the Swartkrans Cave in the Light of the new excavations. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Monograph. 8. Transvaal Museum, Pretoria, pp. 23–34.

Brain, C.K., 1995. The influence of climatic changes on the completeness of the early hominid record in Southern African caves, with particular reference to Swartkrans. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution With Emphasis on Human Origins. Yale University Press, New Haven, pp. 451–458.

Brakora, K., 2014. The ontogeny of sexual dimorphism in the skull of the springbok antelope (*Antidorcas marsupialis*) (918.7). FASEB J. 28 (1 Supplement), 917–918.

Brink, J.S., 2016. Faunal evidence for Mid-and Late Quaternary environmental change in southern Africa. In: Quaternary Environmental Change in Southern Africa: Physical and Human Dimensions. Cambridge University Press, Cambridge, UK, pp. 286–307.

Brink, J.S., Lee-Thorp, J.A., 1992. The feeding niche of an extinct springbok, *Antidorcas bondi* (Antelopini, Bovidae), and its palaeoenvironmental meaning. S. Afr. J. Sci. 88, 227–229.

Brink, J.S., de Beer, F.C., Hoffman, J., Bam, L., 2013. The evolutionary meaning of *Raphicerus*-like morphology in the dentitions and postcrania of *Antidorcas bondi* (Antilopini). Zitteliana 21.

Broom, R., 1938. The Pleistocene anthropoid apes of South Africa. Nature 142, 377–379.

Brophy, J.K., 2011. Reconstructing the Habitat Mosaic Associated With *Australopithecus robustus*: Evidence From Quantitative Morphological Analysis of Bovid Teeth. Doctoral dissertation. Texas A&M University.

Brophy, J.K., de Ruiter, D.J., Athreya, S., DeWitt, T.J., 2014. Quantitative morphological analysis of bovid teeth and implications for paleoenvironmental reconstruction of Plovers Lake, Gauteng Province, South Africa. J. Archaeol. Sci. 41, 376–388.

Castelló, J.R., 2016. Bovids of the World: Antelopes, Gazelles, Cattle, Goats, Sheep, and Relatives. Princeton University Press.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120 (3), 347–363.

Churcher, C.S., Watson, V., 1993. Additional fossil Equidae from Swartkrans. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum Monograph No. 8. Transvaal Museum, Pretoria, pp. 137–150.

Clarke, R.J., 2008. Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*. S. Afr. J. Sci. 104 (11−12), 443–449.

Codron, D., Brink, J.S., Rossouw, L., Clauss, M., 2008. The evolution of ecological specialization in southern African ungulates: competition-or physical environmental turnover? Oikos 117 (3), 344–353.

Cooke, H.B.S., Wells, L.H., 1951. Fossil remains from Chelmer, near Bulawayo, Southern Rhodesia. S. Afr. J. Sci. 47 (7), 205–209.

Curnoe, D., Grün, R., Taylor, L., Thackeray, F., 2001. Direct ESR dating of a Pliocene hominin from Swartkrans. J. Hum. Evol. 40 (5), 379–391.

Dart, R.A., 1925. *Australopithecus africanus*: the man-ape of South Africa. Nature 115, 195–199.

Davis, M., Pineda-Munoz, S., 2016. The temporal scale of diet and dietary proxies. Ecol. Evol. 6 (6), 1883–1897.

Delson, E., 1984. Cercopithecid biochronology of the African Plio-Pleistocene: Correlation among eastern and southern hominid- bearing localities. Cour. Forschungsinst. Senck. 69, 199–218.

Delson, E., 1988. Chronology of South African australopith site units. In: Grine, F.E. (Ed.), Evolutionary History of the 'Robust' Australopithecines, pp. 317–324.

Estes, R., 1991. The Behavior Guide to African Mammals, 20th Anniversary edition. University of California Press, Berkeley.

Faith, J.T., 2014. Late Pleistocene and Holocene mammal extinctions on continental Africa. Earth Sci. Rev. 128, 105–121.

Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. Am. Mus. Novit. 3301, 1–36.

Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E., Steele, L.P., 1999. A 1000-year high precision record of $\delta^{13}C$ in atmospheric CO_2. Tellus Ser. B Chem. Phys. Meteorol. 51 (2), 170–193.

Gentry, A.W., 1978. Bovidae. In: Maglio, V.J., Cooke, H.B.S. (Eds.), Evolution of African Mammals. Cambridge University Press, London.

Gentry, A.W., 1992. The subfamilies and tribes of the family Bovidae. Mammal Rev. 22 (1), 1–32.

Gentry, A.W., 2010. Bovidae. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, pp. 741–796.

Gentry, A.W., 2011. Bovidae. In: Harrison, T. (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context. Springer, Netherlands, pp. 363–465.

Gwynne, M.D., Bell, R.H.V., 1968. Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature 220 (5165), 390–393.

Hendey, Q.B., 1974. Faunal dating of the late Cenozoic of Southern Africa, with special reference to the Carnivora. Quat. Res. 4 (2), 149–161.

Hendey, Q.B., Hendey, H., 1968. New Quaternary Fossil Sites Near Swartklip, Cape Province. South African Museum.

Herries, A.I., Shaw, J., 2011. Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: implications for the age of the hominin fossils and stone tool industries. J. Hum. Evol. 60 (5), 523–539.

Herries, A.I., Curnoe, D., Adams, J.W., 2009. A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. Quat. Int. 202, 14–28.

Hopley, P.J., Maslin, M.A., 2010. Climate-averaging of terrestrial faunas: an example from the Plio-Pleistocene of South Africa. Paleobiology. 36 (1), 32–50.

Hopley, P.J., Latham, A.G., Marshall, J.D., 2006. Palaeoenvironments and palaeodiets of mid-Pliocene micromammals from Makapansgat Limeworks, South Africa: a stable isotope and dental microwear approach. Palaeogeogr. Palaeoclimatol. Palaeoecol. 233, 235–251.

Hopley, P.J., Marshall, J.D., Weedon, G.P., Latham, A.G., Herries, A.I.R., Kuykendall, K.L., 2007. Orbital forcing and the spread of C4 grasses in the late Neogene: stable isotope evidence from South African speleothems. J. Hum. Evol. 53 (5), 620–634.

Hughes, A.R., Tobias, P.V., 1977. A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. Nature 265 (5592), 310–312.

Kaiser, T.M., Fortelius, M., 2003. Differential mesowear in occluding upper and lower molars: opening mesowear analysis for lower molars and premolars in hypsodont horses. J. Morphol. 258 (1), 67–83.

Kaiser, T.M., Solounias, N., 2003. Extending the tooth mesowear method to extinct and extant equids. Geodiversitas 25 (2), 321–345.

Kaya, F., Bibi, F., Žliobaitė, I., Eronen, J.T., Hui, T., Fortelius, M., 2018. The rise and fall of the old world savannah fauna and the origins of the African savannah biome. Nat. Ecol. Evol. http://dx.doi.org/10.1038/s41559-017-0414-1.

Klein, R.G., 1980. Environmental and Ecological Implications of Large Mammals From Upper Pleistocene and Holocene Sites in Southern Africa. South African Museum.

Kuman, K., Clarke, R., 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. J. Hum. Evol. 38 (6), 827–847.

Leakey, L.S.B., 1960. Recent discoveries at Olduvai Gorge. Nature 188 (4755), 1050–1052.

Lee-Thorp, J.A., van der Merwe, N.J., Brain, C.K., 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. J. Hum. Evol. 27 (4), 361–372.

Lee-Thorp, J.A., Manning, L., Sponheimer, M., 1997. Problems and prospects for carbon isotope analysis of very small samples of fossil tooth enamel. Bull. Soc. Geol. Fr. 168 (6), 767–773.

Lee-Thorp, J., Thackeray, J.F., van der Merwe, N., 2000. The hunters and the hunted revisited. J. Hum. Evol. 39 (6), 565–576.

Lee-Thorp, J.A., Sponheimer, M., Luyt, J., 2007. Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites. J. Hum. Evol. 53, 595–601.

Lehmann, D., 2015. Dietary and Spatial Strategies of Gemsbok (*Oryx g. gazella*) and Springbok (*Antidorcas marsupialis*) in Response to Drought in the Desert Environment of the Kunene Region, Namibia. Doctoral dissertation. Freie Universität Berlin.

Luyt, J., 2001. Revisiting the Palaeoenvironments of the South African Hominid-bearing Plio Pleistocene Sites: New Isotopic Evidence From Sterkfontein. MSc Thesis. University of Cape Town.

McKee, J.K., 1993. Taxonomic and evolutionary affinities of Papio izodi fossils from Taung and *Sterkfontein*. Palaeontol. Afr. 30, 43–49.

deMenocal, P.B., 1995. Plio-Pleistocene African climate. Science 53–59.

deMenocal, P.B., 2004. African climate change and faunal evolution in the Pliocene-Pleistocene. Earth Planet. Sci. Lett. 220 (1), 3–24.

deMenocal, P.B., 2011. Climate and human evolution: climate change and its effects on African ecosystems may have played a role in human evolution. Science 331, 540–542.

Merceron, G., Schulz, E., Kordos, L., Kaiser, T.M., 2007. Paleoenvironment of Dryopithecus brancoi at Rudabánya, Hungary: evidence from dental meso-and micro-wear analyses of large vegetarian mammals. J. Hum. Evol. 53 (4), 331–349.

Merceron, G., Ramdarshan, A., Arthur Francisco, A., Denis Gautier, D., Boisserie, J., Milhet, X., Novello, A., Pret, D., 2016. Untangling the environmental from the dietary: dust does not matter. Proc. R. Soc. Lond. B Biol. Sci. 283 (1838), 20161032.

Millar, J.S., Hickling, G.J., 1990. Fasting endurance and the evolution of mammalian body size. Funct. Ecol. 4 (1), 5–12.

Nagy, K.A., Knight, M.H., 1994. Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. J. Mammal. 75 (4), 860–872.

O'Leary, M.H., 1981. Carbon isotope fractionation in plants. Phytochemistry 20, 553–567.

Partridge, T.C., 2005. Dating of the Sterkfontein hominids: progress and possibilities: aspects of hominid evolution. Trans. Roy. Soc. S. Afr. 60 (2), 107–109.

Pickering, R., Kramers, J.D., 2010. Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa. J. Hum. Evol. 59 (1), 70–86.

Plummer, T.W., Bishop, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. J. Hum. Evol. 27 (1–3), 47–75.

Ramdarshan, A., Blondel, C., Brunetière, N., Francisco, A., Gautier, D., Surault, J., Merceron, G., 2016. Seeds, browse, and tooth wear: a sheep perspective. Ecol. Evol. 6 (16), 5559–5569.

Ramdarshan, A., Blondel, C., Gautier, D., Surault, J., Merceron, G., 2017. Overcoming sampling issues in dental tribology: insights from an experimentation on sheep. Palaeontol. Electron. 20 (3), 1–19.

Reade, H., Stevens, R.E., Barker, G., O'Connell, T.C., 2015. Tooth enamel sampling strategies for stable isotope analysis: potential problems in cross-method data comparisons. Chem. Geol. 404, 126–135.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J. Hum. Evol. 32 (2), 289–322.

Reynolds, S.C., 2007. Mammalian body size changes and Plio-Pleistocene environmental shifts: implications for understanding hominin evolution in eastern and southern Africa. J. Hum. Evol. 53, 528–548.

Reynolds, S.C., Kibii, J.M., 2011. Sterkfontein at 75: review of Palaeoenvironments, fauna and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa). Palaeontol. Afr. 46, 59–88.

Reynolds, S.C., Wilkinson, D.M., Marston, C.G., O'Regan, H.J., 2015. The 'mosaic habitat' in human evolution: past and present. Trans. Roy. Soc. S. Afr. 70 (1), 57–69. http://dx.doi.org/10.1080/0035919X.2015.1007490.

Richie, M.E., Olff, H., 1999. Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400 (6744), 557–560.

de Ruiter, D.J., 2003a. Relative abundance, skeletal part representation and accumulating agents of macromammals at Swartkrans. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum Monograph No. 8. Transvaal Museum, Pretoria, pp. 265–278.

de Ruiter, D.J., 2003b. Revised faunal lists for members 1–3 of Swartkrans. Ann. Transv. Mus. 40, 29–41.

de Ruiter, D., Sponheimer, M., Lee-Thorp, J., 2008. Indications of habitat association of *Australopithecus robustus* in the Bloubank Valley, South Africa. J. Hum. Evol. 55 (6), 1015–1030.

Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E., 2006. Microwear evidence for Plio–Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 241 (2), 301–319.

Schulz, E., Piotrowski, V., Clauss, M., Mau, M., Merceron, G., Kaiser, T.M., 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. PLoS One 8 (2), e56167.

Schwarcz, H.P., Grün, R., Tobias, P.V., 1994. ESR dating studies of the australopithecine site of Sterkfontein, South Africa. J. Hum. Evol. 26 (3), 175–181.

Schwarz, E., 1932. Neue diluviale Antilopen aus Ostafrika. Zentralbl. Miner. Geol. Palaontol. B 1932, 1–4.

Scott, J.R., 2012. Dental microwear texture analysis of extant African Bovidae. Mammalia 76 (2), 157–174.

Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. J. Hum. Evol. 51 (4), 339–349.

Ségalen, L., Lee-Thorp, J.A., Cerling, T., 2007. Timing of C 4 grass expansion across sub-Saharan Africa. J. Hum. Evol. 53 (5), 549–559.

Sepulchre, P., Ramstein, G., Fluteau, F., Schuster, M., Tiercelin, J.J., Brunet, M., 2006. Tectonic uplift and Eastern Africa aridification. Science 313 (5792), 1419–1423.

Skinner, J.D., Chimimba, C.T., 2005. The Mammals of the Southern African Sub-region. Cambridge University Press.

Skinner, J.D., Louw, G.N., 1996. The springbok *Antidorcas marsupialis* (Zimmerman 1780). In: Transvaal Museum Monographs. 10. pp. 1–50.

Spencer, L.M., 1997. Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. J. Hum. Evol. 32 (2), 201–228.

Sponheimer, M., Lee-Thorp, J.A., DeRuiter, D.J., Smith, J.M., Van Der Merwe, N.J., Reed, K., Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberger, C., Marcus, W., 2003. Diets of southern African Bovidae: stable isotope evidence. J. Mammal. 84 (2), 471–479.

Stapelberg, H., Van Rooyen, M.W., Bothma, J.D.P., Van der Linde, M.J., Groeneveld, H.T., 2008. Springbok behaviour as affected by environmental conditions in the Kalahari. Koedoe 50 (1), 145–153.

Teaford, M.F., Oyen, O.J., 1989. In vivo and in vitro turnover in dental microwear. Am. J. Phys. Anthropol. 80 (4), 447–460.

Ungar, S., Scott, J.R., Steininger, C.M., 2016. Dental microwear differences between eastern and southern African fossil bovids and hominins. S. Afr. J. Sci. 112 (3/4) (5 pages).

Van der Merwe, N.J., Thackeray, J.F., Lee-Thorp, J.A., Luyt, J., 2003. The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. J. Hum. Evol. 44 (5), 581–597.

Vogel, J.C., 1978. Isotopic assessment of the dietary habits of ungulates. S. Afr. J. Sci. 74, 298–301.

Vrba, E.S., 1970. Evaluation of springbok-like fossils: measurement and statistical treatment of the teeth of the springbok, *Antidorcas marsupialis marsupialis* Zimmerman (Artiodactyla: Bovidae). Ann. Transv. Mus. 26 (13), 285–299.

Vrba, E.S., 1973. Two species of *Antidorcas* Sundevall at Swartkrans (Mammalia: Bovidae). Ann. Transv. Mus. 28 (15), 287–352.

Vrba, E.S., 1974. Chronological and ecological implications of the fossil Bovidae at the Sterkfontein australopithecine site. Nature 250, 19–23.

Vrba, E.S., 1975. Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. Nature 254, 301–304.

Vrba, E.S., 1976. The Fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. Ph.D. thesis. University of the Witwatersrand.

Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and predation patterns. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), Fossils in the Making. The University of Chicago Press, Chicago and London.

Vrba, E.S., 1982. Biostratigraphy and Chronology, Based Particularly on Bovidae, of Southern Hominid-associated Assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; Also Elandsfontein (Saldanha), Broken Hill (Now Kabwe) and Cave of Hearths. Proceedings of the 1st International Congress on Human Palaeontology 2. pp. 707–752.

Vrba, E.S., 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. S. Afr. J. Sci. 81, 229–236.

Vrba, E.S., 1995a. The fossil record of African Antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution With Emphasis on Human Origins. Yale University Press, New Haven, pp. 385–424.

Vrba, E.S., 1995b. On the connections between palaeoclimate and evolution. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution With Emphasis on Human Origins. Yale University Press, New Haven, pp. 24–45.

Vrba, E.S., 2000. Major features of Neogene mammalian evolution in Africa. Oxf. Monogr. Geol. Geophys. 40, 277–304.

Zimmerman, E.A.W., 1780. Antidorcas marsupialis. Geographische Geschichte des Menschen, und der vierf ssigen Thiere. Zweiter Band. Enth It ein vollstndiges Verzeichniss aller bekannten Quadrupeden. 2. Weygandschen Buchhandlung, Leipzig, Germany, pp. 427.