1 TITLE: **USING SPRINGBOK (*ANTIDORCAS*) DIETARY PROXIES TO RECONSTRUCT INFERRED**

2 **PALAEOVEGETATIONAL CHANGES OVER 2 MILLION YEARS IN SOUTHERN AFRICA**

3

4 RUNNING TITLE: Dietary palaeoecology of Plio-Pleistocene *Antidorcas*

5

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31 **ABSTRACT**:

32    The reconstruction of past vegetation and climatic conditions of the Cradle of Humankind,

33 Gauteng Province, South Africa, has been approached using various proxies (such as

34 micromammals, speleothems, faunal and floral presence and stable carbon isotopes).  Elisabeth

35 Vrba's seminal studies (1974; 1975) on the fossil record of this region indicated dramatic faunal

36 turnover based on species extinction and speciation data. This turnover was thought to have

37 been driven by increasing aridity and spreading grasslands.  These reconstructions however, are

38 continuously being refined and adapted in light of advancing techniques (such as dental

39 microwear textural analysis) and terrestrial proxies, such as speleothems.

40    However, more recent studies show varying proportions from wooded towards more

41 grassland-dominated habitats, with the most common reconstruction being the heterogeneous

42 'mosaic' habitat.  Here we re-evaluate the findings of a transition from woodland to grassland

43 conditions in the fossil record from Member 4 Sterkfontein to Member 5 Sterkfontein and the

44 deposits of Swartkrans.  To approach the palaeovegetation changes through time via a different

45 angle, we focus on the diet of the springbok (genus *Antidorcas*), represented throughout this

46 temporal period from geological members dating from 2.8-0.8 Ma. We use detailed dietary

47 methods (dental linear measurements, mesowear, microwear, and stable carbon isotope

48 analysis) to explore past changes in diets of springbok that can be used to indicate the

49 prevailing vegetation conditions.  Our results presented here broadly agree with previous

50 palaeoenvironmental reconstructions, in indicating increased grassland post ca 1.7 Ma, with

51 some suggestion of more heterogeneous habitats for Swartkrans Member 2 (ca 1.65-1.07 Ma).

52 We find that there is support for the implementation of a multi-disciplinary approach to

53 produce more accurate and robust reconstructions of past diets and by extension, of

54 palaeovegetation conditions, if the selected herbivore species is a mixed-feeder, like the

55 springbok.

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**1. INTRODUCTION:**

Climatic aridification and spread of grasslands are a key feature of African Plio-Pleistocene environmental changes (e.g. Sepulchre *et al.* 2006; Segalen *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 & 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). Among 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

88   habitat tolerance primarily in the more arid areas of south and southwestern Africa; South

89   Africa, Namibia, Botswana and Angola (Lehmann 2015; Castelló 2016). Extant *A. marsupialis* will

90   graze on young grasses when available, swapping to browse on low shrubs and succulents,

91   when young grasses are not available. Springbok can survive without drinking water, as long as

92   their food contains more than 10% water content (Estes 1991). Historic records make mention

93   of the mass migrations of these animals in search of better quality grazing after the rains

94   (Skinner and Louw, 1996).  Social organization alters according to season, sex and age range of

95   the individual springbok (Skinner & Chimimba 2005). When considering dietary signals from

96   fossil *Antidorcas*, social and migratory behaviour should be considered to account for the range

97   of signals obtained (e.g. Nagy and Knight 1994; Bednekoff and Ritter 1997; Stapelberg, *et al*.

98   2008).

99   Fossil springbok will henceforth be referred to by genus (i.e. '*Antidorcas*'). In the fossil

100  record, there were several *Antidorcas* species; based on tooth enamel carbon stable isotopes,

101  *A. recki*, *A. australis*, *A. bondi and A. marsupialis* appear to have been mixed feeders to varying

102  degrees, with the exception of *A. bondi,* which was suggested to have been a specialist grazer

103  (Brink and Lee-Thorp 1992).

104  The earliest species, *Antidorcas recki* (Schwarz 1932) was presumed to tend towards

105  browsing (Luyt 2001). It is assumed that *A. recki* is the species from which *Antidorcas australis*

106  (Hendey & Hendey 1968) and / or *Antidorcas marsupialis* (Zimmermann 1780) and *A. bondi*

107  (Cooke & Wells 1951) descends. *Antidorcas bondi*, had a very specific small body-size and

108  specialist dentition (with characteristically small, but very high-crowned, hyposdont teeth) and

109  a unique dietary ecology (based on stable carbon isotope data) that enabled it to exist as part

110  of a grazing succession in southern Africa prior to its extinction at the end of the

111  Pleistocene/early Holocene (Brink 2016; Brink *et al*. 2013; Brink and Lee-Thorp, 1992). Brink and

112  Lee-Thorp (1992) proposed *A. bondi* to be the smallest member of a grazing succession feeding

113  on new grass shoots whose growth was stimulated by the regular 'mowing' of grasses by extant

114  and extinct species, such as the giant buffalo (*Pelorovis antiquus*), giant hartebeest

115  (*Megalotragus priscus*), large equid (*Equus capensis*) and the medium-sized hartebeest

116 (*Damaliscus niro*) in a similar way to that proposed for the Serengeti in East Africa by Gwynne
117 and Bell (1968).

118     The presence and palaeoecology of *A. australis* as a potentially separate species, or a
119 subspecies is debated, but remains unresolved (e.g. Gentry 1978, 1992, 2011; Vrba 1973).
120 *Antidorcas australis*, was originally described from the Middle Stone Age (MSA) site of Swartklip
121 (Cape Province, South Africa) by Hendey and Hendey (1968) as a transitional form of *Antidorcas*
122 between the ancestral *A. recki* and the descendant *A. marsupialis*, consequently tentatively
123 assigned as a sub-species of *Antidorcas marsupialis*. *A. australis* was subsequently elevated by
124 Vrba (1973) to a separate species, supported by Hendey (1974) as a valid taxon, when found
125 alongside *A. recki*.  However, Vrba (1976) later doubted this elevation, suggesting *A. australis*
126 was perhaps only a southern Cape endemic form. Gentry (2010) suspects *A. australis* and *A.*
127 *marsupialis* to be synonymous, but not all authors agree (e.g. Klein, 1980; Faith 2014).

128

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

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

140

141     From the dietary indicators of *Antidorcas*, we establish a broad palaoevegetation
142 reconstruction. One way to reconstruct palaeovegetation cover would be to examine direct
143 evidence of the plants themselves (fossil plants, pollen and phytoliths) preserved at sites like
144 Sterkfontein and Swartkrans, Cradle of Humankind, Gauteng Province, South Africa.  However,

145  since plant fossils and pollen are not commonly preserved in the Cradle of Humankind sites (but

146  see Bamford, 1999), we use the dietary evidence from a mixed feeding herbivore that is

147  commonly preserved at these sites, and one which is relatively abundant.  Herbivores are

148  considered faithful reflectors of prevailing habitat conditions, over decades of detailed

149  palaeoenvironmental research that used various aspects of herbivore palaeoecology (Vrba

150  1974, 1975; Plummer and Bishop 1994; Spencer 1997; Reed, 1997; Bobe and Eck, 2001;

151  amongst many others).

152     A key transition in the southern African fossil record is between Sterkfontein Member 4

153  (where *Australopithecus africanu*s is abundant) and Member 5 (where we have no

154  *Australopithecus*, but instead *Hom*o and *Paranthropus*). The typical palaeoenvironmental story

155  is one of wetter woodland and closed habitats up to and including Sterkfontein Member 4 (c.

156  2.8-2.0 Ma), with the area becoming more open with drier, grassland-dominated habitats by

157  Sterkfontein Member 5 times which overlap with Swartkrans Members (2-0.8 Ma) (Bamford,

158  1999; Kuman and Clarke 2000; Luyt 2001).  Mosaic habitats (Brophy 2011; Reynolds *et al*. 2015)

159  and local variations have been reported between the sites lying within the Cradle of

160  Humankind, presumably due to the varying proximity to the Blaaubank River (Avery 2001;

161  Reynolds and Kibii, 2011).  The cave stratigraphy and dating of these South African deposits

162  have received much attention (e.g. Hopley and Maslin 2010; de Ruiter et al. 2008) and a

163  summary of the dates of the deposits are provided in Table 2.  There are very few genera of

164  herbivores that occur in both Member 4 and Member 5; which is chiefly characterized by a

165  dramatic turnover in species (e.g. Vrba 1974, 1975; deRuiter, 2003a, b; Reynolds and Kibii,

166  2011). We focus on the only single and successful lineage that is present in Member 4 (as

167  *Antidorcas recki*) and in later Member 5 (as *A. marsupialis*)

168        The majority of previous studies typically employ only one or two methods (e.g

169  microwear and/ or stable isotope analyis) to tackle aspects of palaeoenvironmental questions.

170  Each method reveals important aspects relevant to the overall palaeoenvironmental picture,

171  but these methods also have inherent limitations. For example, microwear indicates primarily

172  the last few weeks as new micrometric marks occur after each meal eaten (Teaford & Oyen

173  1989), mesowear requires observer experience and therefore large sample sizes to mitigate for

174    this (Kaiser & Fortelius 2003), and isotopes are informative only of a short window in the early

175    years of life during enamel formation (Reade et al. 2015). Comparisons between species are

176    also complicated by tooth development varying inter-specifically (Reade et al. 2015). There is,

177    therefore, support for a multi-disciplinary approach to produce more holistic, accurate and

178    robust reconstructions of past diets (Schubert et al. 2006) and by extension, of

179    palaeovegetation. Consequently, we take a multi-method approach here to understand when,

180    and how, each method can be used. Our palaeoenvironmental picture obtained from

181    measurements of dental molars, mesowear and microwear analyses, along with new stable

182    isotope data (collected by SCR and PJH in 2002) are compared to the palaeoenvironmental

183    signals gained from stable isotope analysis by Lee-Thorp *et al.* (2007).

184    In this paper, we report on our findings from each method; these methods are typical of much

185    of the current research in palaeoanthropology. The results presented are a subset of results for

186    the wider project underway, used here to reflect on the accuracy and limitations of each

187    method. We use these datasets to address two main questions: 1) can palaeodietary

188    information be used to reconstruct habitat conditions through time; and 2) what additional

189    detail can we gain about the dietary differences between the different *Antidorcas* species in the

190    fossil record?

191

192    **2. MATERIALS AND METHODS**

193    2.1 MATERIALS

194    A sample of 287 fossil *Antidorcas* teeth from Sterkfontein and Swartkrans, Cradle of

195    Humankind, Gauteng Province, South Africa were examined for this study. All species of

196    *Antidorcas* present in the deposits are considered. Specimens are taxonomically identified

197    following the criteria set out in Table 1.

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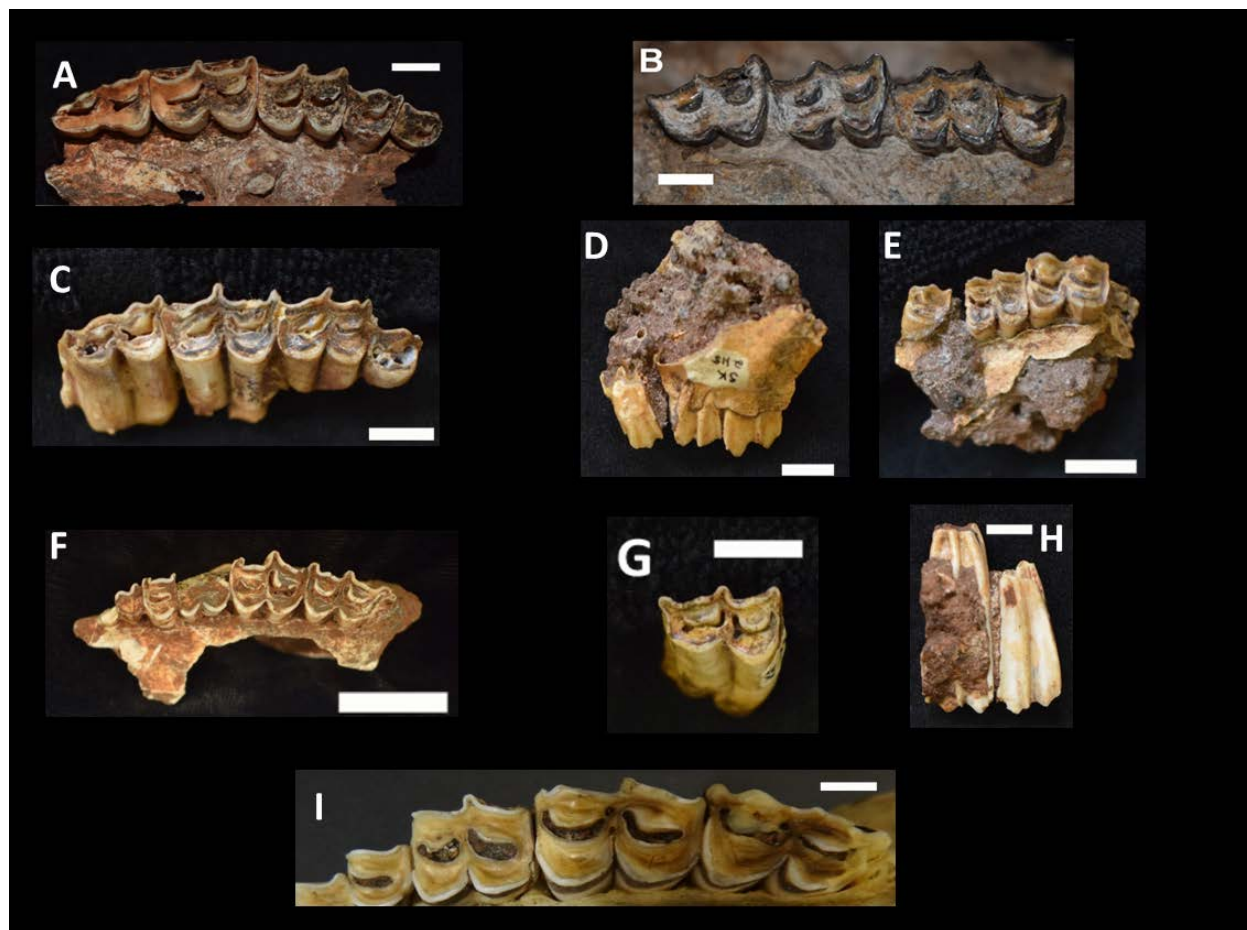


199

200 Figure 1: Examples of *Antidorcas* maxillary (upper) dentition. All photographs taken by L. Sewell

201 unless otherwise stated*. A-B: *Antidorcas recki* (A=KA2610; B=KNM-ER 6-18), C-E: *Antidorcas*

202 *australis* as identified by Vrba (1973): C=SK 3055; D and E=SK 2115), F-H: *Antidorcas bondi* (F=SF

203 592; G=KA 2472; H=SK 2366), I: modern *Antidorcas marsupiualis*. [Key: KA= Kromdraai, KNM-

204 ER=Kenya National Museum-East Rudolph [*photograph by Lucile Crété], SK= Swartkrans, SF=

205 Sterkfontein]. Scale bars equal 10mm.

206

207    Modern springbok specimens were also examined (n=33 individuals). Only permanent upper

208    and lower second molars ($M^2$ and $M_2$) were selected for study in the first instance. Where

209    unavailable, permanent upper and lower first or third molars are used for use-wear analyses

210    instead.  Substitutions of the permanent molar teeth have been shown to produce comparable

211    dietary signals (Scott 2012; Ramdarshan et al. 2017 for dental microwear textural analysis, and

212    Kaiser & Solounias 2003 for dental mesowear analysis, respectively). Upper and lower second

213    molar were separated for metric (linear dental measurements) analyses.

214    All statistical analyses were run in software package SPSS (v.23).  All results presented here are

215    used to showcase particular aspects of each methodology, highlighting where each method can

216    be implemented to obtain the most accurate results. All data are rank transformed prior to

217    analysis to mitigate for small and varying sample sizes.

218

219

| Species | *Antidorcas bondi* | *Antidorcas recki* | *Antidorcas marsupialis* | *Antidorcas cf. australis* |
|---|---|---|---|---|
| Reference | Cooke & Wells 1951 | Schwarz 1932 | Zimmermann 1780 | Hendey & Hendey 1968 |
| Figure | See Figure 1, Images F-H | See Figure 1, Images A-B | See Figure 1, Image I | See Figure 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).<br>• Upper: Complicated folding of enamel walls of central cavities, with a greater tendency towards dumbbell-shaped central cavities and increased curvature<br>• Extreme hypsodonty<br>• 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).<br>• Lower: Sometimes present: lingual "rib" (metastylid) in the or depression between molar lobes.<br>• Lower: Central cavities are centrally constricted, creating a dumbbell appearance.<br>• Large $M_3$ metastyle. | • Unbent central cavities<br>• Straight mandibular lingual molar face<br>• Buccal lophs are V-shaped (more so than the more rounded ones of *A. marsupialis*)<br>• Has styles on upper molars, which are more often V-shaped<br>• Upper: Less strongly pronounced concave posterior part of lateral wall (than in *A. marsupialis/ A. bondi*).<br>• Upper: Stronger styles than *A. marsupialis*, with a flatter and even concave wall between mesostyle and metastyle.<br>• $P_2$ is usually retained (sometimes absent).<br>• Lower: Central cavities straighten in relatively early wear stages.<br>• Large $M_3$ metastyle.<br>• Typically Retains $PM_2$<br>• $PM_3$ is larger and more complex than in *A. marsupialis.*<br>• Upper: concave labial walls | • Lower: Lingual walls are straight (less outwardly bowed than in the impala).<br>• Lower: Central cavities straighten in relatively early wear stages<br>• Large $M_3$ metastyle, with noticeably enlarge third (hypoconulid) lobes<br>• Lacks $PM_2$<br>• Reduced $PM_3$ | • Molars are bucco-lingually narrower in mesiodistal length (Vrba 1973) than A. *marsupialis* (Vrba 1970)<br>• Lower: Central cavities straighten in relatively early wear stages<br>• Large $M_3$ metastyle.<br>• Lacks $PM_2$<br>• Reduced $PM_3$<br>• Narrower than *A. marsupialis* and appear more gracile (Vrba 1970) |

| | | behind their mesostyles | | |
|---|---|---|---|---|
| | • Typically Retains PM$_2$<br>• PM$_3$ is larger and more complex than in *A. marsupialis.*<br>• 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.<br>• Lower: Occasionally goat folds/basal pillars are present.<br>• 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. | | | |
| **Mean M$^2$ dimensions** | [1]16mmx9mm | [2]13.3mmx6.3mm | [3]17.4mm(Female)18mm (Male)x 10.9mm | [4]12.5mmx7.95mm |

220 Table 1: Features typical of each *Antidorcas* species found in Southern Africa, used to aid in species identification of fossil dentition.

221 Characteristic features used to establish taxonomic assignment of fossil dental specimens (Vrba 1973; Cooke & Wells 1951; Gentry

222 2011, 2010). Typical M$^2$ dimensions established according to the type specimens, from corresponding reference as stated in the

223 table. [1] Cooke &Wells 1951; dimensions written as length x breadth (in mm). [2] mesiodistal length x bucco-lingual width. Based on

224 mean measurements taken of *A. recki* from Sterkfontein and Swartkrans by L.Sewell (2016). [3]Vrba 1970; mesiodistal length taken

225 from the mesial surface of the parastyle to the distal surface of the metastyle x mean value from modern *A. marsupialis*

226 specimens(measured by LCS). [4] Based on mean measurements (by L.Sewell and Vrba 1973) of specimens assigned to *A.australis;*

227 mesiodistal length x buccolingual width.

228 COLLECTIONS USED: Sterkfontein Member 4 and 5 (Stw53 Infill, East and West), Swartkrans Member 1 (Lower Bank and Hanging

229 Remnant), Member 2 and Member 3. Fossil collections are housed at the Evolutionary Studies Institute (ESI), University of the

230 Witwatersrand, Johannesburg and the Ditsong Museum of Natural History (DM), Pretoria, South Africa. Additional material from

231 modern Mammalogy collections (wild caught) was studied to establish the anticipated range of variation. Modern collections are

232 housed at the Natural History Museum (NHM), London and the National Museums Scotland (NMS), Edinburgh, United Kingdom and

233 the Ditsong Museum of Natural History, Pretoria, South Africa.

234 Additional modern collections were used for dental microwear textural analysis (DMTA). In addition to NHM and NMS, the following

235 institutions' collections were used: MNHM Paris, France; Zoologisches Museum Berlin, Germany; Staatliches Museum für

236 Naturkunde of Stuttgart, Germany; Senckenberg Naturkundemuseum of Frankfurt, Germany; NHM Basel, Switzerland.

237

| Member | Date | Method | Reference |
|---|---|---|---|
| Sterkfontein Member 4 | 2.8-2.4 Ma | Bovid biochronology | Vrba 1976, 1980 |
| | ~2.5 Ma | Primate biochronology | Delson 1984, 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,b; |
| | 1.8 Ma | Biostratigraphy | Brain 1995, Vrba 2000 |
| Swartkrans Member 1 HR | 1.6 Ma | Biostratigraphy | Vrba 1982, 1985; Delson 1984; Brain 1995; Berger et al. 2002; de Ruiter 2003a,b |
| Swartkrans Member 1 (combined) | 2.0-1.4 Ma | ESR | Curnoe et al. 2001 |
| | 2.0 (±0.02) Ma | U-Pb bovid enamel dating | Albarede 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 | Albarede et al. 2006 |
| | 1.7-1.1 Ma | Biochronology Dating seriation | Brain 1995; Vrba 1995a,b: 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 | Albarede et al. 2006 Brain 1993; Vrba 1995a,b; Herries et al. 2009 |
| **Date range: 1.5-0.61 Ma.** | | | |

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

241

242    2.2. METHODS

243    Due to the uncertainty surrounding the taxonomic status of *A. australis*, (according to features

244    in Table 1), *A.australis* and *A.marsupialis* fossil specimens   were analysed together under

245    '*Antidorcas* sp.'

246         Other species of specific dietary preference, such as the grazing blesbok (*Damaliscus*

247    *pygargus /dorcas*) are occasionally used to establish the fossil dietary parameters and

248    understand the dietary signals gained from *Antidorcas*.

249
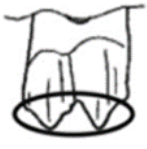
250    **2.2.1 Linear Measurements of Teeth**

251    Tooth dimensions obtained from measurements of mesiodistal length (MDL) and bucco-lingual

252    width (BLW) are considered for this study. Measurements were taken in millimeters with

253    carbon fiber composites digital calipers (resolution: 0.1mm/0.001").

254

255    **2.2.2. Mesowear**

256    Mesowear provides an indication of an individual's dietary signal through their lifetime.

257    Mesowear scores are informative on the abrasiveness of the diet and can be used as a

258    reflection of the grazing/browsing composition of diet. Grazers' molars typically exhibit low

259    occlusal relief and blunter cusps due to the abrasive nature of a predominantly grazing diet.

260    Browsers on the other hand, normally display higher occlusal relief, typically with sharper cusps

261    (Fortelius and Solounias 2000). Following the protocol established by Fortelius and Solounias

262    (2000), numerical values are given to each tooth based on occlusal relief (High or Low) and cusp

263    shape (Sharp, rounded or blunt) as set out in Figure 2. The numerical value (score) is given as

264    follows: Low Blunt:0, Low Rounded:1, Low sharp:2, High rounded:3, High sharp:4. Upper molars

265    are used for mesowear analysis as lower molars have a tendency towards blunting and are

266    consequently likely to be exhibiting a predominance of grazing signals (Kaiser and Fortlius

267    2003).

| | | | |
|---|---|---|---|
|  |  | Steep valley between cusps | HIGH Occlusal Relief |
| |  | Shallow valley between cusps | LOW Occlusal Relief |
|  |  | Sharp cusps | SHARP Cusp Shape |
| |  | Rounded cusps | ROUNDED Cusp Shape |
| |  | No distinct facets | BLUNT Cusp Shape |

268
269 FIGURE 2: Mesowear scoring figure: Traditional mesowear scoring system, established by
270 Fortelius and Solounias (2000), figure modified from Merceron et al. (2007).
271

272 **2.2.3. Dental Microwear Textural Analysis (DMTA)**

273 Dental microwear textures provide insight into the diet over the last few weeks/days of an
274 individual animal's lifetime (Teaford & Oyen 1989; Schulz et al. 2013; Merceron et al. 2016;
275 Ramdarshan et al. 2016). Upper and lower molars were used for microwear analysis to allow
276 direct comparisons across species and deposits. Because values from all positions (M1 to M3) of
277 permanent molars can be used together in statistical analysis as their dental microwear
278 textures have been shown to be statistically similar (see Ramdarshan et al. 2017). Data on
279 lower molars can be grouped with upper molars if specific facets are considered (see below; see
280 Ramdarshan et al. 2017). This is beneficial when dealing with isolated fossil dentition that may
281 not be as clearly identifiable to a particular tooth.

282

283 Dental microwear texture analysis (DMTA) was conducted according to Merceron et al. (2016).
284 Molds of the dental enamel facets of interest, on the disto-buccal facets of the protoconid (or

285  on the hypoconid if the former facet is broken), and on mesio-lingual facets of the protocone

286  (Figure 3), were created using polyvinvylsiloxane elastomer. Ramdarshan et al. (2017) have

287  shown that there are significant differences in dental microwear textures between the disto-

288  buccal facets of the protoconid on lower teeth and the lingual facet of the paracone on upper;

289  but not with the protocone from upper molars (see discussion in Ramdarshan et al. 2017). This

290  mold is cut to provide a relatively small and flat surface, for viewing under the surface

291  profilometer (Leica DCM8 confocal profilometer). The prepared molds are placed under a Leica

292  DCM8 confocal profilometer using white light confocal technology with a Leica 100x objective

293  (Numerical aperture = 0.90; working distance = 0.9 mm). The lateral resolution is an (x, y)

294  interval of 0.129 µm, with a vertical numerical step of 1 nm. Scans are taken in the centre of the

295  facet, where possible, to ensure repeatability and to limit subjectivity. Scans are treated using

296  LeicaMap to eliminate artefacts, such as abnormal peaks following procedures detailed in the

297  supplementary material in Merceron et al. (2016). Data analyses for DMTA are run through

298  Sfrax and Toothfrax software, as set out by Scott et al. (2006).
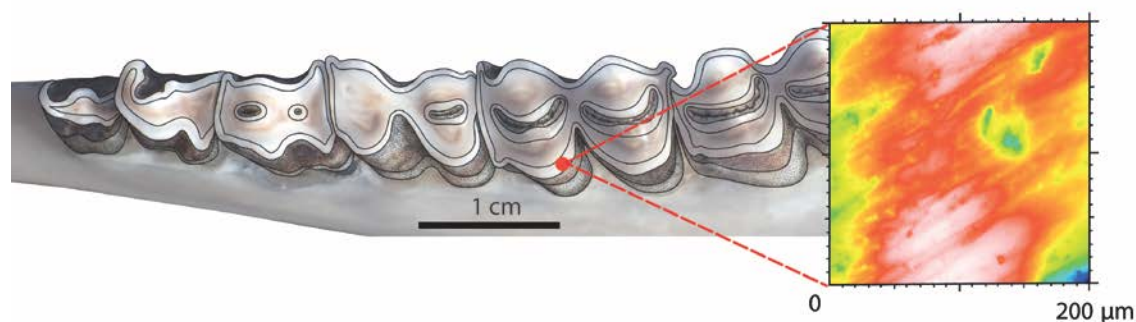


299

300  FIGURE 3: DMTA image: Dental microwear texture analysis is run on the disto-buccal facets of
301  the buccal cuspids along the lower arch (modified from Merceron et al. 2016).

302

303       Complexity (Area-scale fractal complexity, *Asfc*) measures the roughness of the dental

304  facet surface. Scale of maximum complexity (*Smc*) shows the scale range *Asfc* is calculated from

305  (taking the steepest part of the relative area against the scale of the curve). Anisotropy

306  considers the direction of wear and relative lengths of vectors (depth profiles), essentially

307  providing a view of direction of wear and a glimpse into heterogeneity (Scott et al. 2006).

308  Multiple scratches with no pitting would produce anisotropic surfaces with a high *epLsar* value,

309 whereas a surface with scratches in opposing directions coupled with pits of varying depths and

310 sizes would produce a complex (high Asfc) and isotropic (low *epLsar*) surface and be more

311 indicative of browsing diets (Scott et al. 2012, 2006). Homogeneity of wear is provided through

312 *HAsfc* values (Heterogeneity of Area-scale fractal analysis). Higher *HAsfc* values indicate greater

313 variation in diet. Homogeneity of diet tends to show in homogeneity of surface texture (i.e.

314 lower HAsfc values) (Scott et al. 2006). *HAsfc* are calculated through a 9- and an 81-cell mesh

315 over each scanned surface. *Tfv* (Textural fill volume) values represent the surface texture based

316 on fill volume at different scales (i.e. the relief of the surface) (Scott et al. 2006). Considerable

317 research has focused on the nature of microwear signatures in whether dust and grit cloud the

318 dietary signals obtained. Ungar *et al.* (2016) and Merceron *et al*. (2016) show that overall,

319 microwear data is informative of dietary preferences and thus, in this case also informative

320 about palaeovegetation.

321

322 Data are rank transformed and a one-way ANOVA with post-hoc Tukey's HSD and Fisher's LSD

323 tests are performed, once to establish species dietary differences and a second time, to

324 understand dietary differences (for all *Antidorcas* species combined) between members.

325

326 **2.2.4. Stable carbon isotope analysis**

327 Stable carbon isotope analysis was made possible via temporary export and destructive

328 sampling permits granted by SAHRA (South African Heritage Resource Agency). Stable carbon

329 isotope values provide a dietary signal from the early years of an individual animal's lifetime.

330 The carbon values are reflective of the $C_3/C_4$ composition of the diet during the time of dental-

331 enamel formation. Carbon isotopes indicate the photosynthetic pathways used by the

332 vegetation and subsequently consumed by the animal sampled. $C_3$ plants (indicative of a

333 predominantly browsing diet) are more depleted in carbon ($\delta^{13}C$) than $C_4$ plants (indicative of a

334 predominantly grazing diet) (Vogel 1978; Luyt 2001). Isotope analysis complements use-wear

335 (mesowear and microwear) analysis. Isotopes contrast with microwear (meals of last days to

336 weeks) and mesowear (averaged lifetime) results, by providing the early years (during dental

337 enamel formation) signal. To obtain the isotopic information, approximately 5-10 mg of enamel

338  powder was extracted from each tooth using a diamond-tipped drill bit, as a bulk sample.

339  Samples were then cleaned using standard pre-treatment methods for the removal of organic

340  and carbonate contaminants (Lee-Thorp et al. 1997; van der Merwe et al. 2003). Carbon and

341  oxygen isotopic measurements were obtained using a VG SIRA 12 mass spectrometer at the

342  University of Liverpool (see Hopley et al., 2006 for further details). Long-term laboratory

343  reproducibility ($\sigma$) is better than ± 0.1 ‰ for both isotope ratios.

344

345  **3. RESULTS:**

346  3.1. LINEAR MEASUREMENTS OF TEETH

347  Modern springbok are sexually dimorphic, with males having larger body size and larger, more

348  robust horn sizes (e.g., Skinner and Chimimba 2005; Brakora 2014).  To rule out sexual

349  dimorphism, we tested modern *Antidorcas* data (of known sex) for significant differences in

350  MDL and BLW measurements. No significant differences were found (Mann-Whitney U test

351  P>0.05 for occlusal length; P>0.05 for bucco-lingual width).  These results show that male and

352  female springbok teeth do not differ significantly in size. Consequently, we consider that sexual

353  dimorphism in the fossil species is unlikely to confound the potential size differences where

354  they are observed in the fossil record.

355      Both *A. recki* and *A. bondi* can clearly be distinguished from *A. marsupialis* based on

356  their consistently smaller size (Table 3).  In contrast, there is considerable overlap between

357  specimens previously assigned to *Antidorcas australis* (Vrba 1973) compared to those assigned

358  to *Antidorcas marsupialis*. For example, in Swartkrans Member 1, the bucco-lingual width of *A.*

359  *australis* (n=10) ranges from 4.5-12.5mm and *A. marsupialis* (n=3) ranges from 5.5-10.2mm.

360

| 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* | Modern | 44 | 16.3 | 11.7 |

| | | | | |
|---|---|---|---|---|
| *marsupialis* | | | | |
| *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* | Swartkrans Member 1 | 1 | 13.4 | 10.4 |
| | Swarktrans Member 2 | 18 | 14.4 | 9.8 |
| | Swartkrans Member 3 | 2 | 13.1 | 11.4 |

361 Table 3: Mean $M^2$ measurements for each *Antidorcas* species. Measurements are separated
362 according to deposit (site and Member). MDL=mesiodistal length; BLW=bucco-lingual width. *In
363 this table, *Antidorcas* sp. refers to specimens identifiable only to genus level.

364

365 Statistical analysis of mesiodistal length (MDL) and bucco-lingual width (BLW) showed that

366 *Antidorcas bondi* and *Antidorcas* sp. are significantly different for Swartkrans Member 2 (MDL

367 p=0.014; BLW p=0.08), perhaps suggesting the presence of another *Antidorcas* species, other

368 than *Antidorcas bondi*. BLW significantly increased (Kruskal-Wallis test) from Swartkrans

369 Member 1 to Swartkrans Member 2 for specimens assigned to the following taxa: *Antidorcas*

370 sp. (p=0.012), *A. bondi* (p=0.005) and *A. marsupialis* (p=0.004). These results suggest the

371 presence of two species of *Antidorcas* in Swartkrans Member 1 and Member 2, both of which

372 exhibit dental size changes through time. Whilst some specimens are identifiable only to genus

373 (*Antidorcas* sp.), we can assert that the bucco-lingual width increases for the *Antidorcas* genus

374 from Swartkrans Member 1 to Swartkrans Member 2.

375



376
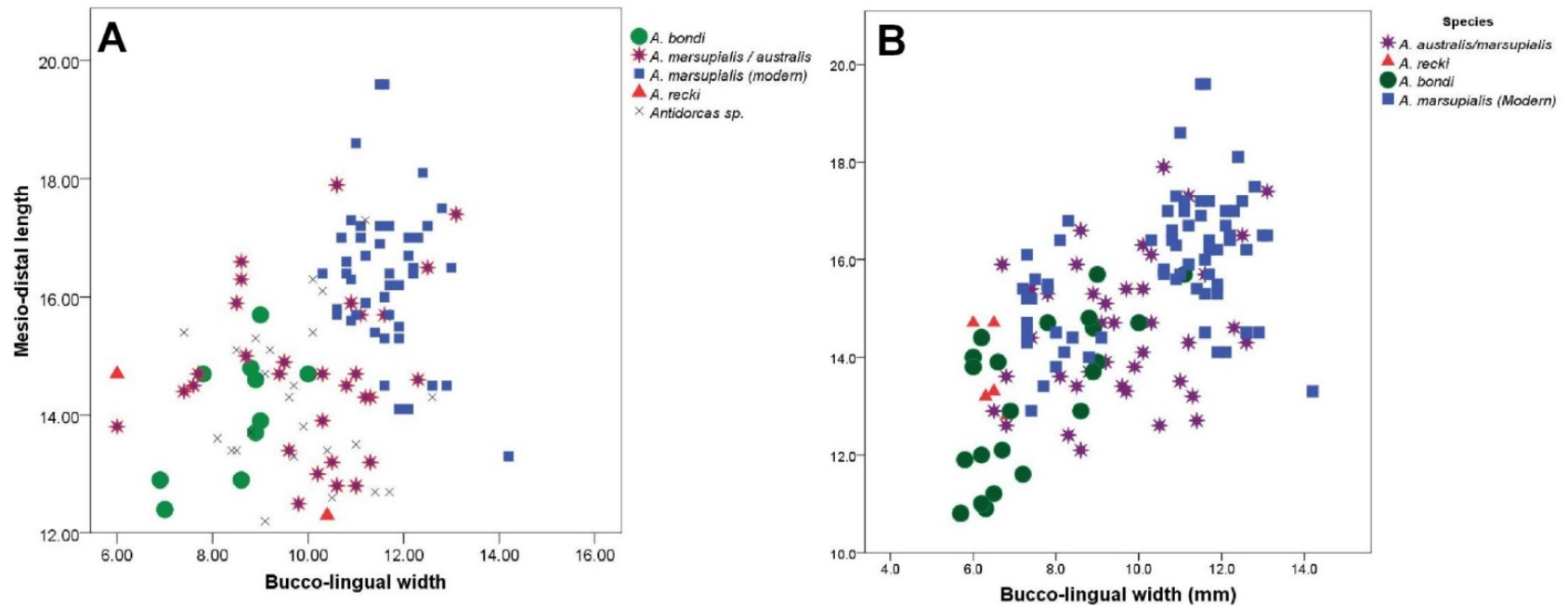
FIGURE 4: Scatter plot of *Antidorcas* linear measurements. Morphological measurements of permanent A) lower second molars for all members (bucco-lingual width against mesiodistal length) according to species. (*Antidorcas bondi* n=9, *Antidorcas recki* n=5, *Antidorcas* sp. (*A. australis/marsupialis*) 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.

382    *Antidorcas bondi* second molar mesiodistal length significantly increases between Swartkrans

383    Member 1 (1.7-1.1 Ma) and Swartkrans Member 2 (0.7-0.6 Ma). The mean mesiodistal length of

384    the sample of *A. bondi* second molars significantly increased (Independent samples Kruskal-

385    Wallis Test (p=0.018), with post-hoc independent samples t-test p=0.038) from Member 1 times

386    (mean length 12.9mm) to Member 2 times (mean length 14.5 mm).

387

388    3.2 MESOWEAR

389    Mesowear scores from this study are given in Table 4.  There is a good level of agreement with

390    our data and the existing dietary inferences for each species.

391    Specifically, the extinct *A. bondi* differs from the modern *A. marsupialis* in having higher

392    frequency of molars with low occlusal relief, together with rounded to blunt cusps. This is

393    suggestive of more grazing dietary habits than the modern forms, as previously stated by Brink

394    and Lee-Thorp (1992). Although low in sample size, *A. recki* exhibits a primarily browsing

395    mesowear signature of high relief, with sharp cusps, thus supporting previous isotopic results

396    by Luyt (2001) and other studies of postcranial ecomorphology of this species from Olduvai

397    Gorge, Tanzania (Plummer and Bishop, 1994).

398

| 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 |

399

| 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 |

| | | N | | | | | |
|---|---|---|---|---|---|---|---|
| | *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 |

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).

405     3.3 MICROWEAR

406     The dental microwear textures of modern *A. marsupialis* display microwear values expected for

407     mixed feeders with medium values in complexity and high values in anisotropy.

408     This data shows a wide *Asfc* and *epLsar* distribution for fossil *Antidorcas* also, indicative of

409     mixed-feeding dietary habits, similar to modern springbok (Figure 5).

410
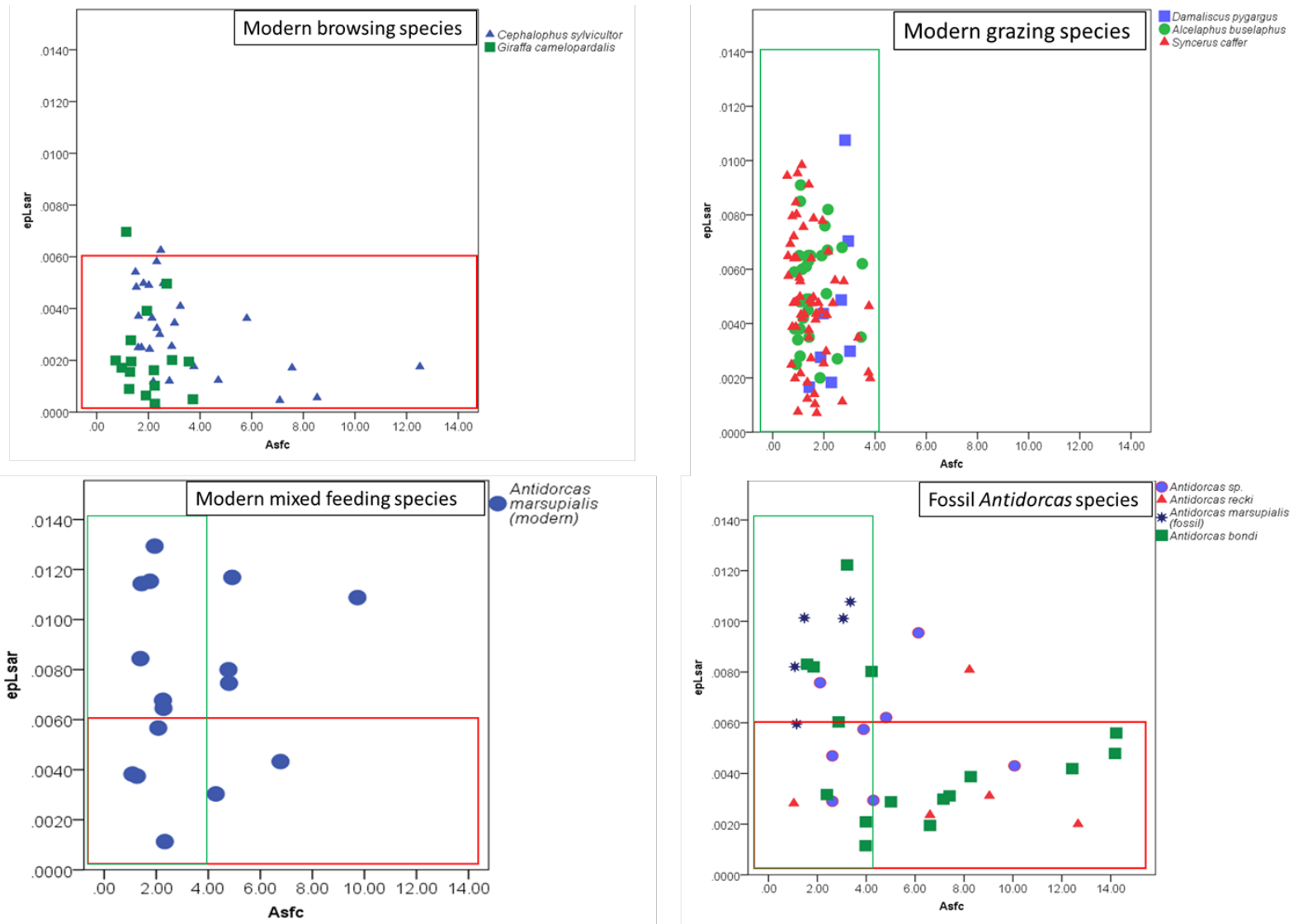
FIGURE 5. Biplots (*Asfc* on X axis vs *epLsar* on Y axis) of modern ruminants and extinct species of *Antidorcas* from South African Cradle of Humankind sites. The two lower plots show overlap, and therefore mixed-feeding signatures, when compared to modern obligate browsing and obligate grazing species.

415

| 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 | 72548.6 | 12914.2 | 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 | 63763.9 | 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 | 63742.3 | 12917.9 | 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 | 56845.1 | 16825.5 | 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 | 50449.0 | 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 | 27251.7 | 19050.1 | 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 | 46026.2 | 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 | 60687.7 | 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 | 63222.4 | 18965.2 | 4741.3 |

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

418

| Asfc | df | SS | MS | F | p |
|---|---|---|---|---|---|
| Sample | 9 | 118199.2 | 13133.2 | 9.91 | 0.00000 |
| Error | 145 | 192110.8 | 1324.9 | | |
| **epLsar** | | | | | |
| Sample | 9 | 89219.0 | 9913.2 | 6.50 | 0.00000 |
| Error | 145 | 221091.0 | 1524.8 | | |
| **HAsfc 9** | | | | | |
| Sample | 9 | 47319.2 | 5257.7 | 2.90 | 0.00350 |
| Error | 145 | 262990.8 | 1813.7 | | |
| **HAsfc 81** | | | | | |
| Sample | 9 | 61267.8 | 6807.5 | 3.96 | 0.00015 |
| Error | 145 | 249042.2 | 1717.5 | | |
| **Tfv2** | | | | | |
| Sample | 9 | 164841.0 | 18315.7 | 18.26 | 0.00000 |
| error | 145 | 145469.0 | 1003.2 | | |

419  Table 6: DMTA Analysis of Variance. One-way ANOVAs on dental microwear textural parameters to explore variations between

420  modern and extinct species of ruminants. df: degrees of freedom, SS: sum of squares, MS: mean of squares.

421

422

| 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 | | |
| | *Antidorcas sp* | | ⬛ | | | asfc | | asfc | asfc | | |
| | *Antidorcas marsupialis* | | | ⬛ | | asfc | | | asfc | | |
| | *Antidorcas recki* | | | | ⬛ | asfc | | | asfc | | |
| Modern | *Alcelaphus buselaphus* | asfc | asfc | asfc | asfc | ⬛ | asfc | | | | asfc |
| | *Cephalophus sylvicultor* | | | | | asfc | ⬛ | asfc | asfc | | |
| | *Giraffa camelopardalis* | asfc | asfc | asfc | asfc | | asfc | ⬛ | | | |
| | *Syncerus caffer* | asfc | asfc | asfc | asfc | | asfc | | ⬛ | | asfc |
| | *Damaliscus pygargus* | asfc | | | | asfc | | | asfc | ⬛ | |
| | *Antidorcas marsupialis* | asfc | | | | asfc | | | asfc | | ⬛ |
| Fossil | *Antidorcas bondi* | ⬛ | | | | | | epLsar | | | |
| | *Antidorcas sp* | | ⬛ | | | | | epLsar | | | |
| | *Antidorcas marsupialis* | | | ⬛ | | | epLsar | epLsar | | | |
| | *Antidorcas recki* | | | epLsar | ⬛ | | | | | | |
| Modern | *Alcelaphus buselaphus* | | | | | ⬛ | epLsar | epLsar | | | |
| | *Cephalophus sylvicultor* | epLsar | epLsar | epLsar | | epLsar | ⬛ | | | | epLsar |
| | *Giraffa camelopardalis* | epLsar | epLsar | epLsar | | epLsar | | ⬛ | | epLsar | epLsar |
| | *Syncerus caffer* | | | | | | epLsar | epLsar | ⬛ | | |
| | *Damaliscus pygargus* | | | | | | | epLsar | | ⬛ | |
| | *Antidorcas marsupialis* | | | | epLsar | | epLsar | epLsar | epLsar | epLsar | ⬛ |
| Fossil | *Antidorcas bondi* | ⬛ | | | | | | | | | |
| | *Antidorcas sp* | | ⬛ | | | | | | HAsfc 9 | | |
| | *Antidorcas marsupialis* | | | ⬛ | | | | | | | |
| | *Antidorcas recki* | | | | ⬛ | | | | | | |
| Modern | *Alcelaphus buselaphus* | | HAsfc 9 | | | ⬛ | | | | | |
| | *Cephalophus sylvicultor* | | HAsfc 9 | | | | ⬛ | | | | |
| | *Giraffa camelopardalis* | | HAsfc 9 | | | | | ⬛ | | | |
| | *Syncerus caffer* | HAsfc 9 | HAsfc 9 | | | | | | ⬛ | | |
| | *Damaliscus pygargus* | | | | | HAsfc 9 | | HAsfc 9 | HAsfc 9 | ⬛ | |
| | *Antidorcas marsupialis* | | | | | HAsfc 9 | | HAsfc 9 | HAsfc 9 | | ⬛ |
| Fossil | *Antidorcas bondi* | ⬛ | | | | | | | | | |
| | *Antidorcas sp* | | ⬛ | | | | | | | | |
| | *Antidorcas marsupialis* | | | ⬛ | | | | | | | |
| | *Antidorcas recki* | | | | ⬛ | | | | | HAsfc 81 | |
| Modern | *Alcelaphus buselaphus* | | HAsfc 81 | | HAsfc 81 | ⬛ | | | | | HAsfc 81 |
| | *Cephalophus sylvicultor* | | HAsfc 81 | | HAsfc 81 | | ⬛ | | | | |
| | *Giraffa camelopardalis* | | HAsfc 81 | | HAsfc 81 | | | ⬛ | | | |
| | *Syncerus caffer* | HAsfc 81 | HAsfc 81 | | HAsfc 81 | | | | ⬛ | | HAsfc 81 |
| | *Damaliscus pygargus* | | | | | HAsfc 81 | HAsfc 81 | HAsfc 81 | HAsfc 81 | ⬛ | |
| | *Antidorcas marsupialis* | | | | | HAsfc 81 | HAsfc 81 | 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 | | | | |
| Modern | *Alcelaphus buselaphus* | Tfv2 | Tfv2 | Tfv2 | | ⬛ | | Tfv2 | | | Tfv2 |
| | *Cephalophus sylvicultor* | Tfv2 | Tfv2 | Tfv2 | Tfv2 | Tfv2 | ⬛ | | | Tfv2 | Tfv2 |
| | *Giraffa camelopardalis* | Tfv2 | Tfv2 | Tfv2 | Tfv2 | Tfv2 | | ⬛ | Tfv2 | Tfv2 | Tfv2 |
| | *Syncerus caffer* | Tfv2 | Tfv2 | Tfv2 | | | Tfv2 | Tfv2 | ⬛ | Tfv2 | Tfv2 |
| | *Damaliscus pygargus* | | | | | Tfv2 | Tfv2 | Tfv2 | Tfv2 | ⬛ | |
| | *Antidorcas marsupialis* | | | | | Tfv2 | Tfv2 | Tfv2 | Tfv2 | | ⬛ |

423

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*.

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

429     Tables 5 and 7 show that all extinct species of *Antidorcas* differ from the modern grazing taxa-

430     *Alcelaphus buselaphus* and *Syncerus caffer*, in having higher *Asfc*. All fossil *Antidorcas* differ

431     from the leaf-browsing *Giraffa camelopardalis*, in having higher *Asfc*. All fossil *Antidorca*s,

432     excluding *A. recki* have higher *epLsar* than the two modern species of browsing ruminants.

433     Finally, all fossil *Antidorcas* species have higher *Tfv* than modern species (except modern

434     springbok; Tables 5 and 7).

435

436

437

| 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 | 56845.1 | 16825.5 | 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 | 69556.8 | 11937.3 | 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 | 59850.9 | 12984.3 | 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 | 65679.1 | 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 | 63222.4 | 18965.2 | 4741.3 |

438 TABLE 8: Dental microwear textural parameters (mean and standard deviation). All *Antidorcas* species are pooled together, with

439 fossil *Antidorcas* separated by provenance (site and Member 'M'), where sufficient sample sizes allowed, to indicate the prevailing

440 trend through time. 'Modern' represents the modern *Antidorcas marsupialis* sample.

441

| Asfc | df | SS | MS | F | p |
|---|---|---|---|---|---|
| Sample | 4 | 15620.9 | 3905.2 | 1.42 | 0.242 |
| Error | 45 | 123612.4 | 2746.9 | | |
| **epLsar** | | | | | |
| Sample | 4 | 27589.5 | 6897.4 | 2.02 | 0.107 |
| Error | 45 | 153388.5 | 3408.6 | | |
| **HAsfc 9** | | | | | |
| Sample | 4 | 1952.6 | 488.2 | 0.15 | 0.964 |
| Error | 45 | 151665.9 | 3370.4 | | |
| **HAsfc 81** | | | | | |
| Sample | 4 | 7396.2 | 1849.1 | 0.75 | 0.563 |
| Error | 45 | 110802.2 | 2462.3 | | |
| **Tfv2** | | | | | |
| Sample | 4 | 13843.6 | 3460.9 | 1.64 | 0.181 |
| error | 45 | 94932.1 | 2109.6 | | |

442 Table 9: One-way ANOVAs on dental microwear textural parameters to explore variations

443 between Members (Sterkfontein Member 4, Swartkrans Member 2, Swarktrans Member 3,

444 Cave of Hearths and Modern springbok). df: degrees of freedom, SS: sum of squares, MS: mean

445 of squares.

446

447 As indicated (Table 9), there are no significant differences for *Antidorcas* microwear texture

448 parameters between Members (through time), suggestive of varying degrees of mixed habitats

449 being available throughout this temporal period.

450 Considering Table 8, the highest *Asfc* and lowest *epLsar* values for Sterkfontein Member 4 could

451 support the notion of greater woodland in the area, with *Antidorcas* including slightly more

452 browse in the diet, than at Swartkrans (Member 2 and 3).

453

454 3.4 STABLE CARBON ISOTOPES

455 $C_3$ plants are more depleted in $^{13}C$ relative to $C_4$ plants (Vogel 1978; O'Leary 1981). Therefore,

456 tooth enamel with higher carbon isotope values is indicative of the consumption of more $C_4$

457 plants. We assign each fossil enamel carbon isotope value to the dietary classifications of Lee-

458 Thorp et al. (2007); see Tables 10, 11 & 12.

459 In line with results from the other dietary proxies, Table 11 shows *Antidorcas bondi* was

460 generally eating a very different diet to other *Antidorcas* species and is more in line with

461 *Damaliscus* (grazing) diets (other than during Swartkrans Member 2 times c.1.65-1.07 Ma). The

462 higher mean carbon isotope values of *A. bondi* are indicative of $C_4$ plants being consumed,

463 suggestive of a grazing and mixed feeding diet (Cerling et al. 1999). Of the 19 fossils classified as

464 *Antidorcas* sp. (Table 8), two specimens (SK 14123 and SK11073) have carbon isotopic

465 compositions consistent with *A. marsupialis*, and can be tentatively assigned to this species; the

466 remaining specimens have higher carbon isotope values and are likely to belong to *A. bondi*.

467

| 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‰ |

468   TABLE 10: Dietary categories according to Stable carbon isotope values. Dietary distinctions according to $\delta^{13}C$ values and proportion

469   of C3/C4 vegetation dominance in diet.  Values from Lee-Thorp et al. (2007).

470

| 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 |

471 TABLE 11: Stable carbon and oxygen isotope data for *Antidorcas* fossils from Swartkrans. *Antidorcas* sp. indicates specimens only
472 identifiable to genus level (specimens processed at the University of Liverpool).
473
474

**Sterkfontein Member 4**

| Species | N | Mean $\delta^{13}$C | Standard deviation | Minimum $\delta^{13}$C | Maximum $\delta^{13}$C | Dietary category |
|---|---|---|---|---|---|---|
| *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**

| Species | N | Mean $\delta^{13}$C | Standard deviation | Minimum $\delta^{13}$C | Maximum $\delta^{13}$C | Dietary category |
|---|---|---|---|---|---|---|
| *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**

| Species | N | Mean $\delta^{13}$C | Standard deviation | Minimum $\delta^{13}$C | Maximum $\delta^{13}$C | Dietary category |
|---|---|---|---|---|---|---|
| *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**

| Species | N | Mean $\delta^{13}$C | Standard deviation | Minimum $\delta^{13}$C | Maximum $\delta^{13}$C | Dietary category |
|---|---|---|---|---|---|---|
| *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 |

| Species | N | Mean $\delta^{13}$C | Standard deviation | Minimum $\delta^{13}$C | Maximum $\delta^{13}$C | Dietary category |
|---|---|---|---|---|---|---|
| *Antidorcas sp.* | 27 [4,5] | -5.1 | 1.076 | -15.0 | 2.0 | Mixed |
| **Modern** | | | | | | |
| Species | N | Mean $\delta^{13}$C | Standard deviation | Minimum $\delta^{13}$C | Maximum $\delta^{13}$C | Dietary category |
| *Antidorcas marsupialis* | 2 [6,7] | -13.1* | 4.00 | -17.0* | -9.0* | Browser |

475  TABLE 12: Stable carbon isotope descriptive statistics for *Antidorcas and Damaliscus* species present in each member. References:
476  where more than one value is given in original reference, a mean value has been calculated and used here. Luyt 2001[1]; van der
477  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.
478  2003[7].  Dietary categories following category distinctions as set out in table 6. *N.B. Modern *Antidorcas marsupialis* would be
479  expected to be a mixed feeder. To aid comparison between the modern and fossil data, modern enamel values were increased by 1
480  ‰ to account for the post-industrial decrease in the $\delta^{13}$C value of atmospheric $CO_2$ (Francey et al., 1999).

481     The blesbok*, Damaliscus pygargus (dorcas)* is typically considered to be a grazing species

482     and indeed, *Damaliscus* is expected to largely be a grazing genus (Estes 1991). At Sterkfontein

483     and Swartkrans, isotope data shows *Damaliscus sp.* to be true to expected dietary preferences

484     and a small sample is included here to establish most-likely grazing parameters.

485     Stable carbon isotope results (Tables 11 & 12) support the dietary categories and

486     vegetation signals obtained from use-wear (microwear and mesowear) analyses. However,

487     *Antidorcas bondi* shows slight indications of more mixed feeding in Swartkrans Member 2, away

488     from the specialized grazing signals apparent from the other methodologies.  This perhaps

489     lends support to the presence of more heterogeneous habitats for Swartkrans Member 2.

490

491     **5.  DISCUSSION**

492

493     This paper has used data from various dietary proxies of an abundant antelope to attempt a

494     detailed reconstruction of the palaeovegetation conditions through time at the important

495     hominin-bearing sites of the Cradle of Humankind.  Each proxy, predictably, reflects a different

496     aspect of the diets of the springboks.  Combined, we have tried to use these datasets to address

497     two main questions: 1) can palaeodietary information be used to reconstruct habitat conditions

498     through time; and 2) what additional detail can we gain about the dietary differences between

499     the different *Antidorcas* species in the fossil record? In response to the first question, the

500     dietary proxies from the *Antidorcas* examined in this study do yield palaeovegetation

501     reconstructions that broadly agree with habitat reconstructions based on other

502     palaeoenvironmental proxies.  Our results suggest increased grassland post c.1.7 Ma, with

503     some suggestion of more heterogeneous habitats for Swartkrans Member 2 (c.1.65-1.07 Ma). A

504     reduced grassland presence in Swartkrans Member 2 is *potentially* indicated with the assumed-

505     to-be grazing *Antidorcas* species, *A. bondi*, yielding a slightly mixed feeding dietary signal from

506     stable carbon isotope values. Whilst it is only slightly indicative of more mixed feeding

507     practices, *Antidorcas bondi* specimens from Swartkrans Member 2 do exhibit dietary behavioral

508     difference when compared to *A. bondi* from other members, in which *A. bondi* is shown to be a

509     more faithful grazer (from stable carbon isotope values). Lee-Thorp et al. (2007) suggested the

510    lower $\delta^{13}C$ values were indicative of either a remnant component of $C_3$ vegetation or less

511    specialized dietary taxa than their modern counterparts.  However, dental microwear textures

512    studied here suggest *A. bondi* had a more mixed-feeding diet than previously assumed.

513

514    The second question regarding dietary niches in the various fossil species of *Antidorcas*

515    is more complex.  Our dietary reconstructions indicate a wide dietary range represented within

516    the *Antidorcas* lineage, as we would expect from a mixed-feeder that survived changing habitat

517    and vegetation conditions.

518    In contrast to Brink & Lee-Thorp (1992) all the fossil species of *Antidorcas* display high

519    values in dental microwear texture complexity (*Asfc*) which exclude grazing habitats. DMTA

520    supports that all species of *Antidorcas* were mixed feeding, including herbaceous monocots and

521    browse (shrubs and foliages with lignified tissues, possibly with seeds and fruit). *A. recki*

522    displays a lower *epLsar* than the other *Antidorcas* species (see Table 5), and significantly lower

523    than the fossil *A. marsupialis* (Table 7). The dental microwear texture for fossil *A. bondi* here

524    shows it to have practiced greater mixed feeding than shown by the fossil *A. marsupialis* sample

525    (Figure 5). Dental microwear textures on *A. recki* are consistent with mesowear and isotopic

526    analysis in all supporting a higher browsing component in the diet compared to the other

527    *Antidorcas* species. Browsing is more likely to result in higher heterogeneity due to the nature

528    and range of the browse vegetation consumed.    Interestingly,  both fossil *A.*

529    *marsupialis/australis* and *A. recki* have higher heterogeneity of diet, indicative of more mixed

530    feeding diets, higher than that of modern *Antidorcas marsupialis*, a known mixed-feeder.

531    Indeed, all DMTA supports *Antidorcas* being a predominantly mixed-feeding genus.

532    In interpreting these diets and what they mean in the wider context of habitat changes

533    and the faunal community, we must also consider the role of biotic factors within the faunal

534    community.  Codron and colleagues (2008) highlight the role that niche specialization can play

535    on changing diets of herbivores within a community, with both environmental and biotic

536    (competition) factors contributing to the forcing of dietary differentiation into specific niches

537    ($C_3$ or $C_4$).  *Antidorcas* may have been in competition with other herbivore species such as the

538    impala (*Aepyceros melampus*).

539     Significant differences in tooth metrics analysed in this study indicate that the ancestral *A.*

540     *recki* possessed smaller overall dental dimensions than modern *A. marsupialis*, supporting the

541     results from previous studies (e.g. Vrba 1970, 1973) and strongly suggesting that *A. recki*

542     possessed a smaller body size (Gentry 1978) than *A. marsupialis*.  Body size can be informative

543     of palaeoenvironmental conditions, and increases in body size can possibly be explained as an

544     advantage in more seasonal environments where there is a longer period of fasting, a

545     phenomenon known as fasting endurance (Millar and Hickling 1990; Reynolds 2007).

546     One of the outstanding problems in the fossil record is whether the extinct, *Antidorcas*

547     *australis* is a valid species or not.  The original species description emphasizes the difference in

548     horncore shape, with *A. australis* having somewhat straighter horns than the lyrate form typical

549     of *A. marsupialis* (Cooke and Wells, 1951).   At present, we do not have enough data to

550     definitively identify clear dietary distinctions between fossils assigned to *A. australis* and those

551     assigned to *A. marsupialis*.  The sample of fossil *Antidorcas marsupialis/australis* examined in

552     this study does exhibit greater variation in measurements than modern *Antidorcas marsupialis*,

553     which could be argued to lend support to the idea of the presence of multiple species (Brophy

554     et al. 2014). Further landmark-based measurements and additional techniques, such as

555     geometric morphometric analysis (to analyse shape changes) would be required to settle the

556     question of this species distinction.  It may be that the *A. australis* is differentiated only on its

557     horncores and that dietary differences alone would not be sufficient to indicate distinctions

558     between *A. australis* and *A. marsupialis*.

559     Another important aspect of modern springbok ecology is the migratory behaviour.

560     Historic records show that springbok would trek in herds of thousands of individuals to seek out

561     fresh grazing after the rains (Skinner and Louw, 1996). At present, there is little way to

562     determine whether other extinct species of *Antidorcas* exhibited this behaviour or not.  If so, *A.*

563     *australis*, may have been a migrant to the Cradle region at various times.  Certainly, migration

564     would have helped reduce competition in grazing species.

565

566      As may be expected (e.g. Davis & Pineda-Munoz 2016), there is some disparity between

567     dietary signals from DMTA compared to those from stable carbon isotopes. DMTA indicates all

568    *Antidorcas* fossil species were mixed feeders, whereas carbon isotopes indicate higher C4

569    signals (i.e. grazing) for these antelopes, particularly the case for *A. bondi.* This combination

570    would support a mixed feeding dietary preference for *Antidorcas*, altering their dietary intake

571    according to seasonal availability of resources. This suggests that the Cradle of Humankind

572    region would have had seasonally available resources with significant amounts of both browse

573    and graze.  If severe seasonal droughts decimated the herbaceous layer (where grasses are

574    abundant) then the antelopes may have switched to browse as tree/shrub roots go deeper in

575    the soil to obtain water, compared to the herbaceous plants.

576

577    **SUMMARY**

578    In this paper, we examined fossil *Antidorcas* dentition using a range of dietary proxies, from

579    these results we attempted to infer the prevailing vegetation conditions between 2.8-0.8 Ma

580    for the region where these *Antidorcas* lived and died, the Cradle of Humankind, South Africa.

581    The majority of past research has used a single methodology on multiple species from

582    assemblages, to address palaeoenvironmental questions. Here, we implemented a multiproxy

583    analysis on a single mixed-feeding, herbivorous and abundant genus (*Antidorcas)* to provide a

584    detailed palaeovegetation picture for the Sterkfontein and Swartkrans area through time. Aside

585    from some subtle variations, preliminary conclusions from our study are found to be in broad

586    agreement with those found through isotopic analysis by Lee-Thorp *et al*. (2007), of increased

587    grassland presence in South Africa from ca .1.7 Ma.

588

589        Notably, we have been able to suggest from this multi-method approach, that methods can

590    be reliably substituted for one another where time or cost constraints apply.  Where methods

591    such as mesowear, are non-destructive, quick and cheap to implement, these techniques can

592    be used to accurately pinpoint where to concentrate the more time-consuming, expensive and

593    destructive techniques, such as stable carbon isotope analysis. However, a more holistic, robust

594    and detailed palaeovegetation reconstruction can be achieved by using complementary

595    methodologies. The complementary use of methods such as mesowear analysis, stable isotope

596    analysis and dental microwear texture analyses for instance, allows us to question whether

597  *Antidorcas bondi* was typically a grazer or not. This approach could be implemented at other

598  sites across the world for palaeovegetation reconstructions, where the preserved faunal

599  community is restricted in some way but where at least one continuous (mixed feeding)

600  herbivore lineage is represented.

601

614

615

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