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► To cite this version:

Raphaël Hanon, Marylène Patou-Mathis, Stéphane Péan, Sandrine Prat, Brigette F Cohen, et al.. Early Pleistocene hominin subsistence behaviors in South Africa: Evidence from the hominin-bearing deposit of Cooper's D (Bloubaan Valley, South Africa). *Journal of Human Evolution*, 2022, 162, pp.1013116. 10.1016/j.jhevol.2021.103116 . hal-03816450

HAL Id: hal-03816450

<https://hal.science/hal-03816450>

Submitted on 8 Feb 2024

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1 Early Pleistocene hominin subsistence behaviors in South Africa: Evidence from the hominin-
2 bearing deposit of Cooper's D (Bloubank Valley, South Africa)

3

4 Raphaël Hanon^{a,b,*}, Marylène Patou-Mathis^b, Stéphane Péan^b, Sandrine Prat^c, Brigitte F.
5 Cohen^{d,a}, Christine Steininger^{a,e}

6

7 ^a *Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, Wits 2050,*
8 *Johannesburg, South Africa*

9 ^b *UMR 7194, HNHP, MNHN/CNRS/UPVD, Alliance Sorbonne Université, Institut de*
10 *Paléontologie Humaine, 1 rue René Panhard, 75013 Paris, France*

11 ^c *UMR 7194, HNHP, MNHN/CNRS/UPVD, Alliance Sorbonne Université, 17 place du*
12 *Trocadéro, 75116 Paris, France*

13 ^d *National Museum of Bloemfontein, P.O Box 266, Bloemfontein, 9300, South Africa*

14 ^e *Centre of Excellence in Palaeosciences, Private Bag 3, Wits 2050, Johannesburg, South Africa*

15

16 *Corresponding author.

17 *E-mail address: raphael.hanon@edu.mnhn.fr (R. Hanon).*

18 **Abstract**

19 Evidence of the consumption of meat through hunting or scavenging by Early Pleistocene
20 hominins is scarce, particularly in South Africa. Moreover, the interpretations of taphonomic
21 evidence are subject to an important discussion commonly called the 'hunting-vs-scavenging
22 debate'. Until today, only the Swartkrans Members 1–3 site has yielded a butchered bone
23 assemblage large enough to permit reconstruction of carcass acquisition strategies by Early
24 Pleistocene hominins in South Africa. This leaves an information gap between 1.4 and 1.0
25 Ma. Here, we provide the first evidence of meat consumption by hominins during this gap,
26 based on the zooarchaeological study of the large mammal bone assemblage recovered from
27 the Cooper's D site, South Africa. Based on skeletal part representation, our results show
28 density-mediated attrition of bovid bones due to pre- and post-depositional destruction. We
29 argue that this attrition is the result of both abiotic (i.e., decalcification) and biotic (i.e.,
30 carnivore ravaging) processes. Bovid mortality profiles point out the involvement of ambush
31 predators such as large felids. Bone surface modifications also indicate that the assemblage
32 has been accumulated mostly by carnivores but with some hominin involvement as well. We
33 observe all the stages of animal carcass processing (skinning, disarticulation, defleshing,
34 marrow extraction) as well as the exploitation of a diversity of prey size classes at both
35 Swartkrans Members 1–3 and Cooper's D. Thus, our study shows the importance of the
36 Cooper's D bone assemblage for understanding Early Pleistocene hominin subsistence
37 behaviors. Moreover, this paper highlights the need for including long bone flake specimens
38 in the analysis of large bone assemblages from South African caves to better understand the
39 Early Pleistocene hominin bone damage record.

40

41 **Keywords**

42 Taphonomy; zooarchaeology; cut marks; carnivore; bone surface modifications

43 **1. Introduction**

44 *1.1. Background*

45 Identification of butchery marks on prey animal bones from Plio-Pleistocene
46 archaeological assemblages provides direct evidence of meat consumption by hominins. The
47 frequency, location and morphology of cut and percussion marks are used to reconstruct the
48 timing of access to carcasses by hominins (i.e., Binford, 1981, 1985; Potts and Shipman,
49 1981; Bunn, 1981, 1991; Shipman and Rose, 1983; Bunn and Kroll, 1986; Shipman, 1986;
50 Binford et al., 1988; Blumenschine, 1988, 1995; Potts, 1988; Blumenschine and Cavallo,
51 1992; Capaldo and Blumenschine, 1994; Selvaggio, 1994, 1998; Domínguez-Rodrigo, 1997;
52 Capaldo, 1997, 1998; Heinzelin, 1999; Lupo and O’Connell, 2002; Domínguez-Rodrigo and
53 Pickering, 2003; Pickering et al., 2004a, 2008; Egeland et al., 2004, 2014; Pickering and
54 Domínguez-Rodrigo, 2006; Domínguez-Rodrigo et al., 2007, 2009; Egeland and Domínguez-
55 Rodrigo, 2008; Pobiner et al., 2008, 2018; Thompson et al., 2015, 2019; Parkinson, 2018;
56 Pobiner, 2020). However, most of our knowledge about Plio-Pleistocene hominin subsistence
57 behaviors is based on the East African fossil record. Despite the richness of Plio-Pleistocene
58 faunal assemblages in South Africa, zooarchaeological studies on the timing of access to
59 carcasses by hominins are relatively sparse (Brain, 1981; Pickering et al., 2004a, 2007, 2008;
60 Pickering, 2006; Pickering and Brain, 2010). Many efforts have been made in the last fifteen
61 years to increase our understanding of hominin subsistence behaviors since the publication of
62 new data on the faunal assemblage from the Early Stone Age site of Swartkrans Members 1–3
63 (Pickering et al., 2004a, 2008). A total of 149 fossils have been identified as bearing butchery
64 marks, which the authors used to infer hominins primary access to animal carcasses
65 (Pickering et al., 2008).

66 Except for Taung and Makapansgat, most South African Plio-Pleistocene sites are located
67 in the Bloubaank Valley, Gauteng Province (previously Transvaal Province), about 40 km

68 northwest of Johannesburg, called the Cradle of Humankind. Through taphonomic studies of
69 the bone assemblages of Sterkfontein, Swartkrans, Kromdraai, Makapansgat and Taung,
70 Brain (1981, 1993) showed that hominins of the Late Pliocene and Early Pleistocene were
71 regularly preyed upon by large carnivores, especially felines such as the leopard (*Panthera*
72 *pardus*). These taphonomic studies identified predation on hominins, but not their subsistence
73 behaviors.

74 Swartkrans and Sterkfontein are the only sites to have yielded mammal bones with
75 butchery marks that link the Oldowan/Acheulean lithic industry to carcass exploitation by
76 hominins (Brain, 1981; Pickering, 1999, 2006; Pickering et al., 2004a, 2005, 2007, 2008;
77 Pickering and Domínguez-Rodrigo, 2006). However, there is a total absence of available data
78 on the patterns of faunal exploitation by hominins between 2.22 ± 0.09 Ma (Swartkrans
79 Member 1) and 1.3 Ma (Swartkrans Member 2) as well as between 1.3 and 0.96 Ma
80 (Swartkrans Member 3) in South Africa (Balter et al., 2008; Pickering et al., 2008, 2019;
81 Gibbon et al., 2014; Kuman et al., 2021). Thus, there is an apparent need for the study of
82 Early Pleistocene hominin subsistence behaviors and animal carcass exploitation from sites
83 covering these overlooked periods.

84

85 *1.2. The Cooper's D sedimentary deposits*

86 Cooper's D is situated in the Bloubank Valley, approximately 1.5 km northeast of
87 Sterkfontein, 1 km southwest of Kromdraai and located approximately 45 km northwest of
88 Johannesburg (Fig. 1). Archaeological sites in the Bloubank Valley occur on dolomites of the
89 Monte Cristo Formation (Malmani Subgroup, Transvaal Supergroup) and preserve fossils in
90 both calcified and decalcified breccia (Berger et al., 2003; de Ruiter et al., 2009). Regular
91 excavations at Cooper's D were conducted between 2001 and 2009 on decalcified sediment,
92 which yielded an abundant fossil assemblage ($n > 50,000$), stone tool material ($n = 49$) and

93 seven hominin remains, six attributed to *Paranthropus robustus* and one to indeterminate
94 Hominidae (Berger et al., 2003; de Ruiter et al., 2009; Val et al., 2014; Sutton et al., 2017).
95 The Cooper's D deposit has been dated by U-Pb to 1.526 ± 0.088 Ma for the basal speleothem
96 and ca. 1.4 Ma for the flowstone located in the middle of the sequence (Fig. 2; de Ruiter et al.,
97 2009). However, more recent U-Pb dating of the basal flowstone suggests an age of $1.375 \pm$
98 0.113 Ma (Pickering et al., 2019), making the deposit younger than 1.4 Ma. Using
99 biochronological data, Hanon and collaborators (2021) proposed a minimum age of 1.0 Ma.
100 Thus, an age bracket between 1.4 and 1.0 Ma is proposed for the whole faunal deposit.

101 The Cooper's Cave site has already been the target of several vertebrate paleontological
102 studies. This is notably the case for the order Primates (Berger et al., 1995; Steininger et al.,
103 2008; de Ruiter et al., 2009; DeSilva et al., 2013; Folinsbee and Reisz, 2013) and Carnivora
104 (Hartstone-Rose et al., 2007, 2010; O'Regan et al., 2013; Kuhn et al., 2017; O'Regan and
105 Steininger, 2017), and more recently also for the family Equidae (Badenhorst and Steininger,
106 2019). It has been noted that the Cooper's D bone assemblage is large and taxonomically rich
107 (Berger et al., 2003). More than 50,000 remains have been found in decalcified sediments (de
108 Ruiter et al., 2009).

109 The Cooper's D fossil assemblage has been the focus of three previous taphonomic
110 studies: on primates (Val et al., 2014), on a sample of large mammals (de Ruiter et al., 2009),
111 as well as on modifications attributed to the action of insects (Parkinson, 2016). According to
112 de Ruiter et al. (2009), the main accumulating agent of the assemblage was the brown hyena
113 (*Parahyaena brunnea*), although the leopard was also mentioned. Carnivores have also played
114 a significant role in the accumulation of the primate sub-assemblage at Cooper's D (DeSilva et
115 al., 2013; Val et al., 2014). Occupation of the cave, at least by Cercopithecidae, has been
116 inferred based on the low impact of carnivores on primate bones and the abundance of
117 cercopithecoid juveniles (Val et al., 2014).

118 In a previous paper, Cukrowska et al. (2005) mentioned the presence of possible cutmarks
119 on a specimen from Cooper's that was chemically cleaned of manganese coating. However,
120 they did not provide the number of the specimen or the identification of the bone element,
121 which justifies the need to study the long bone shaft fragments. Moreover, one definitive bone
122 tool has been recently described from Cooper's D (Hanon et al., 2021).

123 In this paper, based on several variables (i.e., faunal composition, skeletal part
124 representation, and the presence of bone surface modifications), we aim to provide the first
125 taphonomic study of the Cooper's D large mammal assemblage and to identify the most
126 probable agents involved in the bone accumulation.

127

128 **2. Materials and methods**

129 Our archeozoological study includes 21,193 remains from decalcified sediments excavated
130 between 2001 to 2009 (Berger et al. 2003; de Ruiter et al. 2009). All the specimens are
131 currently curated at the Evolutionary Studies Institute, University of the Witwatersrand,
132 Johannesburg.

133 The material studied includes all the remains of large mammals > 2 cm, both identifiable
134 and unidentifiable, as well as a randomized subsample of the unidentifiable remains smaller
135 than 2 cm ($n = 8405$).

136

137 *2.1. Skeletal part quantification*

138 The number of identified specimens (NISP) was used as the basic unit of quantification,
139 from which other units such as the minimum number of elements (MNE) or the minimum
140 number of individuals (MNI) were derived. The MNE is an estimate of the minimum number
141 of each skeletal element by taxon (Bunn, 1982; Gifford-Gonzalez, 2018). For long bones, as
142 advised by several authors (Marean and Spencer, 1991; Marean and Kim, 1998; Pickering et

143 al., 2003; Marean et al., 2004), we have calculated the MNE for each portion (proximal
144 epiphysis, diaphysis, distal epiphysis) using the method developed by Klein and Cruz-Uribe
145 (1984) and Marean and Spencer (1991). This method consists of measuring the percentage of
146 the complete circumference of a long-bone shaft piece, summing those percentages for each
147 calculated portion of a bone element, and then rounding up the fraction value. Although this
148 method slightly underestimates the MNE, it is relatively accurate (Lyman, 1994, 2008).

149 The MNI was calculated from both dental and long bone remains for three reasons: (1)
150 dental material provides a reliable basis for calculation of the MNI in the context of such large
151 paleobiodiversity; (2) teeth allow a much more accurate estimate of the age of individuals
152 than the post-cranial material; (3) because dental and long bone shafts are less subject to pre-
153 and post-depositional destruction. Indeed, dental material is less subject to fragmentation,
154 modification, and damage by carnivores (Brain, 1981), tends to be more conservative, and
155 therefore represents a more reliable tool for estimating the MNI. Thus, MNI values for
156 specimens identified to the genus or species level are based on dental material. However,
157 concerning specimens identified only to the family level (e.g. unidentified bovid size class I),
158 we provide an estimation of MNI based on long bone material. We further applied a MNI by
159 combination (MNIc), as defined by Poplin (1976), which presents the best represented
160 lateralized anatomical element in the assemblage for a given species, considering the age
161 estimation and other criteria in the count.

162 The minimum animal unit (MAU) was introduced by Binford (1978, 1984) and reports on
163 the differential preservation of bones. The MAU was obtained by dividing the MNE value of
164 a specific skeletal element by the number of times that element occurred in a skeleton. The
165 percentage of MAU (%MAU) was then obtained by dividing the MAU of each skeletal part
166 by the element with the highest MAU value (MAU max).

167 The percentage survival (% survivorship) of a skeletal element is a measure of differential
168 preservation, similar to MAU, but relates the MAU of that element to the number of expected
169 elements in the assemblage based on the minimum number of individuals. This calculation
170 was originally used by Brain (1969, 1976) and further developed by Lyman (1994):

$$171 \quad \frac{(MNEi) * 100}{MNI \text{ (number of times } i \text{ occurs in one skeleton)}}$$

172 Where *i* is a specific skeletal element or portion (i.e. scapula, proximal humerus, distal
173 femur...). All remains are identified to skeletal element but when that is not possible, we
174 record the element as a long bone shaft fragment or unidentified specimen. Each long bone
175 shaft fragment is also assigned to a limb segment according to Domínguez-Rodrigo (1997) as
176 upper (humeri or femora), intermediate (radio-ulna or tibiae), or lower (metapodials) limb
177 bone fragment. Using the method defined by Blumenschine (1988) and developed by
178 Domínguez-Rodrigo (1997), we attribute a long bone portion for each fragment as follows:
179 midshaft (diaphyseal part lacking proximal or distal articular surfaces), near-epiphyseal
180 (diaphyseal part with cancellous bone) and distal/proximal epiphysis fragments (articular
181 surface).

182 Long bone fragments are assigned to a dimension class, as follow: <2 cm; 2–3 cm; 3–4 cm;
183 4–5 cm; >5 cm. Circumferences of all specimens were recorded using the system originally
184 developed by Bunn (1983) and modified by Pickering et al. (2007): <25%; <50% but >25%;
185 <75% but >50%; <100% but >75%; 100% of original circumference preservation.

186 The system of bovid size classes defined by Brain (1981) was used in order to assign each
187 specimen to a body size group. We combine the size classes defined by Brain in three
188 different categories (Pickering et al., 2007) to facilitate comparison with other sites: small
189 (size class I), medium (size class II and III) and large (size class IV, size class V and size class
190 VI).

191 The preservation state of the bone assemblage was assessed using the fragmentation rate
192 which was calculated by taking the ratio of NISP and MNE. The impact of post-depositional
193 processes was estimated using published bone mineral density (BMD) estimates. The %MAU
194 values from Cooper's bovid elements were compared to computed-tomography-derived (CT)
195 BMD measures for an extant size class III bovid (*Connochaetes taurinus*; Lam et al., 1999).
196 Where possible, shape-adjusted values (BMD₂) were chosen over BMD₁ (not shape adjusted;
197 Lam and Pearson, 2004). The percentage MAU was log₁₀ transformed (Pickering and Carlson,
198 2002) and then compared with BMD values using the 'scatterplot' function in the RStudio
199 software v. 1.1.463 (RStudio Team, 2018).

200 Finally, carcass transport was measured by correlating the %MAU against the simplified
201 food utility index (SFUI). This index, introduced by Metcalfe and Jones (1988), estimates the
202 nutritional usefulness of each skeletal element. Bones with high nutritional potential will
203 mainly be transported by the predator, carnivore, or hominin. SFUI values were taken from
204 Metcalfe and Jones (1988) and were calculated from a single male caribou.

205

206 2.2. Age estimation

207 Age of individuals was estimated based on eruption stages and tooth wear patterns defined
208 by Bunn and Pickering (2010a) as follows: juvenile, prime, or old individual, which allowed
209 reconstruction of mortality profiles in the assemblage. It has been shown by some authors
210 (Bunn and Pickering, 2010a; 2010b), that young juvenile individuals could bias the
211 interpretation of mortality profiles in archaeological assemblages because they are less likely
212 to preserve than their larger counterparts. Therefore, we produced the mortality profiles of
213 Cooper's D Bovidae with and without the young juvenile individuals, although we retain
214 subadult individuals.

215 We provide a histogram where each bar represents the proportion of individuals in each
216 age class (Steele, 2005). Moreover, we applied ternary graphs developed by Stiner (1990,
217 1991), Steele and Weaver (2002), Bunn and Pickering (2010a), and Weaver et al. (2011). The
218 ternary graphs were produced with the Triangle v. 2.0 Program developed by Weaver et al.,
219 (2011), using the likelihood method. We compared our results with modern carnivores and
220 archaeological assemblages provided by Bunn and Pickering (2010a, 2010b).

221

222 *2.3. Analysis of bone surface modifications*

223 All specimens were carefully observed under binocular microscope Olympus SZ2-ILST
224 (10×–40×) to record bone surface modifications (rodent gnawing marks, root marks, acid
225 etching, carnivore tooth marks, cutmarks, percussion marks) and fracture patterns. Pictures of
226 bone surface modifications and tooth pit dimensions were taken using numerical microscope
227 Dino-Lite AD7013MTL (20×–100×) and DinoCapture v. 2.0 software (AnMo Electronics
228 Corporation, Taipei).

229 All long bone shaft fragments in the assemblage ($n = 5145$) have been included in this
230 analysis. It has been demonstrated that long bone fragments are high survival elements
231 (Marean and Cleghorn, 2003; Pickering et al., 2003) with a large amount of meat and/or
232 marrow making them one of the most useful bone portions for inferring hominin and
233 carnivore subsistence behaviors (Domínguez-Rodrigo, 1997). Indeed, experimental studies
234 have demonstrated that butchery marks (i.e. cutmarks and percussion marks) are most likely
235 to occur on long bone shaft fragments, which can provide insight into carcasses processing by
236 hominins (Domínguez-Rodrigo, 1997; Nilssen, 2000).

237 Surface preservation was assessed by attributing to each specimen a cortical preservation
238 stage (Pickering, 1999; Pickering et al., 2007; Daujeard et al., 2020): (1) the original surface
239 of the bone is preserved; (2) good preservation of the bone surface although slightly damaged

240 by taphonomic processes; (3) moderate preservation, some anatomical and taphonomic
241 criteria (e.g., profile of linear marks, circumference of pits) are no longer visible; (4) poor
242 preservation, the bone surface is no longer visible.

243 Carnivore, trampling, and stone tool modifications were identified and distinguished (from
244 each other) using the criteria developed by numerous authors (Potts and Shipman, 1981;
245 Shipman and Rose, 1983; Behrensmeyer et al., 1986; Patou, 1987; Blumenschine, 1988,
246 1995; Blumenschine and Selvaggio, 1988; Olsen and Shipman, 1988; Fiorillo, 1989; Lyman,
247 1994; Blumenschine et al., 1996; Patou-Mathis, 1997; Domínguez-Rodrigo et al., 2009, 2010;
248 Prat et al., 2011; Fernández-Jalvo and Andrews, 2016; Hanon et al., 2018). Percussion marks
249 were identified using the criteria described by Blumenschine and Selvaggio (1988) and
250 Blumenschine et al., (1996). Other bone surface modifications were identified on the basis of
251 published descriptions such as the action of carnivores (Binford, 1978, 1981; Maguire et al.,
252 1980; Brain, 1981; Cruz-Uribe, 1991; Pickering, 2002; Kuhn et al., 2010; Fourvel, 2012;
253 Bountalis and Kuhn, 2014), insects (Hill, 1987; Kaiser, 2000; Backwell et al., 2012; Huchet,
254 2014; Parkinson, 2016) and rodents (Binford, 1978; Brain, 1980, 1981; Maguire et al., 1980;
255 Shipman and Rose, 1983). We used both location and morphology of cutmarks to infer
256 butchery actions based on experimental data (Binford, 1981; Lyman, 1987; Valensi, 1991;
257 Patou-Mathis, 1997). Indeterminate marks are not included in our analysis. Weathering stages
258 were categorized following Behrensmeyer (1978) and abrasion stages after Fiorillo (1988).
259 Bone fragmentation patterns were recorded for long bone shafts following the methods of
260 Villa and Mahieu (1991).

261

262 *2.4. Statistics*

263 The bone flake length and bovid mortality distributions were compared to similar
264 distributions of archaeological and modern carnivore accumulations previously published

265 (Brain, 1981; Adams et al., 2007) through a Kolmogorov-Smirnov nonparametric test. We
266 applied the Monte Carlo permutation ($n = 10,000$) for $n < 30$ (Hammer et al., 2001). The
267 Spearman's r_s statistical test was conducted in order to measure the correlation between the
268 %MAU and the simplified food utility index (or SFUI) as well as the bone mineral density
269 (BMD). All the statistical tests have been performed with the PAST software v. 4.05
270 (Hammer et al., 2001).

271

272 **3. Results**

273 *3.1. Faunal assemblage*

274 More than 35% (7492/21193) of the bone material is identifiable to at least the family
275 level. The large mammal fauna of the Cooper's D deposit is rich (Table 1) and characterized
276 by the presence of 6 orders, 12 families, 37 genera and 32 species. Like the other sites in the
277 Cradle of Humankind, the assemblage is dominated by the order Cetartiodactyla and more
278 specifically by the family Bovidae in terms of both NISP (77%) and MNI (58%), followed by
279 Felidae (11% MNI) and Hyaenidae (7% MNI). Cercopithecidae and Canidae represent 7%
280 and 6% of the MNI respectively. Suidae were previously considered to be relatively abundant
281 in the Cooper's D assemblage (Berger et al., 2003), but according to our study represent only
282 4% of the MNI. In addition, Equidae and Giraffidae represent 1% and 2% of the MNI
283 respectively. Rhinocerotidae, Elephantidae and Orycteropodidae, represent less than 1% of the
284 total MNI.

285

286 *3.2. General preservation and fragmentation pattern*

287 The cortical surface preservation is characterized by an overrepresentation of stage 2 and 3
288 (Table 2). The large mammal bones are highly fragmented. More than 95% of all studied
289 remains ($n = 20,272$) are incomplete and 16,908 bones, approximately 97%, are less than 5

290 cm in length. The distribution of the length of remains of Cooper's D and Kromdraai B are
291 similar to each other ($D = 0.4$, p -value = 0.81). We also observe, through a series of
292 Kolmogorov-Smirnov tests, that the distributions of bone flake according to size classes from
293 the Cooper's D and Kromdraai B assemblages are statistically different from those observed
294 in carnivore accumulated assemblages (Table 3).

295 Fracture edges have been observed on 3,622 remains (about 17.1% of the total NISP).
296 More than 86% of fractures occurred on dry bone. Fractures on fresh bone represent only 7%
297 with the remaining fractures (6.4%) occurring after excavation.

298

299 *3.3. Skeletal part representation*

300 Bovidae is the most represented family at Cooper's D (in terms of MNI and NISP) and is
301 the most exploited taxon by both hominins and large carnivores. Moreover, most of the
302 taphonomic experimental studies focus on bovids. For these reasons, we focus on the skeletal
303 part representation of bovids by size and age class (Fig. 3; Supplementary Online Material
304 [SOM] Tables S1–S3). The hemi-mandibles, radii, metatarsals, and calcanei are the best-
305 preserved elements for small bovids (Fig. 3A). For medium-sized bovids, pelvis, cranial
306 bones, femur, and ulna are the best-preserved elements (Fig. 3B). The axis is the only bone
307 absent in both small and large bovids (Fig. 3A–B). The skeleton of large bovids is not well
308 preserved (Fig. 3C), and mostly represented by pelvis and foot bones (e.g. calcanei,
309 metacarpals).

310 The rate of fragmentation (NISP:MNE) of bovid bones varies, according to size classes,
311 between 1.49 and 1.74 when all bones are taken into consideration. This range widens, from
312 1.70 to 2.27, when we consider only the long bones. Juvenile bovids have a lower
313 fragmentation rate compared to the adults in any size class. This may be due to a

314 representation bias, as it is sometimes difficult to identify individual bone fragments in
315 juveniles.

316 We find a statistically significant positive correlation between %MAU and bone density
317 for each bovid size class (Fig. 3). There is no significant relationship between bovid %MAU
318 and simplified food utility index (SFUI) values (small bovids: $R_s = -0.20$, p -value = 0.31;
319 medium bovids: $R_s = -0.8$, p -value = 0.69; large bovids: $R_s = 0.10$, p -value = 0.61).

320

321 3.4. Ungulate mortality profiles

322 Small and large bovids are characterized by an absence of very old individuals (Fig. 4;
323 Supplementary Online Material [SOM] Table S4-S5). Medium sized bovids are represented
324 by older individuals and fewer juveniles. However, only one statistically significant difference
325 is found between small-sized and medium-sized bovids (Kolmogorov-Smirnov tests small vs.
326 medium: $D = 0.8$, p -value = 0.04; small vs. large: $D = 0.2$, p -value = 0.99; medium vs. large:
327 $D = 0.6$, p -value = 0.21).

328

329 Small-sized bovids (size classes 1 and 2) The 95% confidence interval of the Cooper's D
330 assemblage overlaps with both the lion (*Pan. leo*) and leopard (*Pan. pardus*) assemblages
331 (Fig. 5A), both of which are ambush hunters. The profile appears to be similar to a 'prime
332 dominated' model, which can also be observed within Swartkrans Members 1 to 3 (Fig. 5B).

333

334 Large-sized bovids (size classes 3 and 4) The large bovid assemblage is dominated by prime
335 adult individuals, which matches results obtained from small bovids. The pattern detected at
336 Cooper's D does not match the comparative data obtained from lion (*P. leo*) and hyena (*C.*
337 *crocuta*) accumulations (Fig. 5C). Large-sized bovids cannot be distinguished from
338 archaeological and comparative anthropic assemblages (Fig. 5D).

339

340 *3.5. Bone surface modifications*

341 Abiotic processes Most of the assemblage shows no sign of weathering (>73% stage 0, $n =$
342 15,576). Fifty-one specimens (0.2%) have blunt surfaces and edges, indicative of water
343 transport (Fig. 6). A deposit of manganese dioxide is visible on the surface of more than 96%
344 of the assemblage and more than 80% are covered on more than half of their surface ($n =$
345 17152). A total of 131 remains (0.5%) show modifications indicative of corrosion (Fig. 6)
346 namely alteration of the entire cortical surface and hollowing out the inside of the bone. The
347 medullary cavities are usually filled with sediment, and perforations are found at the edges
348 and collapsed into the bone. Fernández-Jalvo and Andrews (2016) indicate that these changes
349 are the consequence of high humidity in a closed environment and/or an acidic absorbent
350 sediment. Bacterial activity may also have an important role in the production of these
351 characteristics. In the case of Cooper's D, the fact that the assemblage comes from decalcified
352 sediments, and that there was an episode of significant erosion in the caves in the region,
353 leads us to favor the action of percolating water as a cause of corrosion. Within the Cooper's
354 D assemblage, we identify a total of 360 remains (1.7% of NISP) altered by decalcification.

355

356 Carnivore damages Modifications attributable to the action of carnivores are observed on
357 more than 5% of the remains at Cooper's D (Table 4). Pits (46%) and grooves (60%) are
358 mostly located on bovid bones (Fig. 7). Suidae ($11/467 = 2\%$ of the $NISP_{\text{suid}}$) and
359 Cercopithecidae remains ($20/491 = 4\%$ of the $NISP_{\text{Cercopithecidae}}$) have also been modified by
360 carnivores. The anatomical location of carnivore tooth marks (Table 5), especially pits, were
361 studied. The frequency of pits observed on the remains of medium-sized bovids is statistically
362 different from that of large bovids ($\chi^2 = 35.5065$, $ddl = 21$, $p\text{-value} = 0.02$). However, no
363 significant difference is observed between the small bovids and the other size classes. These

364 results should be interpreted cautiously because some NISP values are low ($n < 5$). As the
365 assemblage displays bone density-mediated attrition, we further tested whether the
366 distribution of the pits depends on the differential preservation of bovid bones by applying a
367 Spearman correlation test between pits by MNE and the total MNE by bovid size class. This
368 showed a statistically significant correlation between MNE and the number of pits per skeletal
369 element for small ($R_s = 0.44$, p -value = 0.04) and large bovids ($R_s = 0.50$, p -value = 0.01).

370

371 Rodent modifications Only eight remains present modifications attributable to rodent
372 activities (Fig. 7G–I). These marks are uncommon and form very small patches of linear
373 marks on edge bones (Fig. 7H–I). We note the presence of a rodent incise fragment on the
374 edge of a vertebrae fragment (Fig. 7G).

375

376 Trampling modifications Trampling by large mammals is characterized by bone fractures,
377 bone displacements (horizontal and vertical), as well as striations related to the rubbing of
378 sediment on bone surfaces. Given the context of the Cooper's D assemblage (collapsed cave
379 and decalcified sedimentary infill), it is difficult to attribute fractures to the unique action of
380 trampling. However, the superficial striations with non-preferential orientation, irregular
381 shapes, and trajectories are characteristic of this action. Within the Cooper's D large mammal
382 assemblage, we identify a total of 126 remains (0.59%) bearing trampling marks (Fig. 7). We
383 can thus consider, given the minimal impact of the modifications linked to trampling, that
384 movement inside the cave must have been relatively rare during the accumulation phases.

385

386 Anthropic modifications A total of 16 large mammal remains bearing cut marks (0.08%; Figs.
387 8–10), as well as 15 bearing percussion marks (0.07%) are observed, three of them with both
388 types of modification. Skinning marks, observed as a series of short and deep grooves with an

389 asymmetrical profile on each side of the bone surface, are visible on the surface of a proximal
390 phalanx attributed to a medium-sized bovid (CD.16947, Fig. 8). Two short, parallel striations,
391 with an asymmetrical profile and internal microstriations (Figs. 10A and 11A), were observed
392 on the proximal part of a metatarsal of a small bovid (CD.837). The same features are present
393 on the surface of a diaphyseal fragment of a large size bovid metapodial (CD.1643, Fig. 10B).
394 These marks were probably produced during disarticulation of the carcass. Finally, there are
395 two groups of marks located in areas that suggest that they were the result of defleshing . The
396 first consists of short, deep, V-shaped, oblique, asymmetrical marks (Fig. 9) that form sets of
397 superimposed marks visible on long bone shafts. The second group consists of long, thin,
398 longitudinal marks, visible on the diaphysis of long bones and the scapula (Fig. 11).

399 Over 80% ($n = 31$) of butchery marks are on long bone shafts. Of the sixteen bones bearing
400 cut marks identified at Cooper's D, thirteen are long bone fragments (small bovid = 4;
401 medium bovid = 6; large bovid = 3), and eleven of those are diaphyseal fragments. Similarly,
402 of the fifteen remains bearing percussion marks, fourteen are long bone fragments (small
403 bovid = 6; medium bovid = 6; large bovid = 2). Long bone remains bearing butchery marks (n
404 = 27; 25 on the diaphysis and 2 on the epiphysis) represent about 0.53% of all long bones
405 identified at Cooper's D (NISP long bones = 5122).

406 Butchery marks are concentrated around two anatomical regions (Figs. 12 and 13): the
407 stylopod (proximal segment of the limbs: humeri and femora) and the autopod (distal segment
408 of the limbs: basipod, metapod and acropod). The anterior limb appears to bear more
409 cutmarks than the posterior limb, especially in large bovids. At Cooper's D, midshaft
410 specimens bear the most cut marks (11:22 = 50%) while cut marks occur the least on
411 epiphyseal parts (2:22 = 9%). Cut marks occur with equal frequency on both upper limb and
412 lower limb bones (9:22 = 41%). The distribution of cutmarks differs according to bovid size
413 class (Fig. 13). Although most striae are localized on the long bones, there are a few special

414 cases. For small bovids, a cutmark is present on the surface of a rib. For medium-sized
415 bovids, several striations are visible on the proximal part of a phalanx. And finally, for the
416 large-sized Bovidae, a group of striations is observed on a scapula.

417 Anthropropic butchery marks are observed on the surface of small, medium, and large bovids.
418 Marks are more often observed on the bones of small bovids (1.37% of the NISP_{post-cranial})
419 compared to medium (0.7% of the NISP_{post-cranial}) and large bovids (0.78% of the NISP_{post-}
420 _{cranial}). The different stages of carcass processing have been inferred from several
421 characteristics (morphology, location, and orientation). We have identified three stages of
422 processing of small bovid carcasses: disarticulation, defleshing and bone marrow extraction.
423 Disarticulation is based on the presence of marks on the proximal part of a metatarsal (CD
424 837), while defleshing is identified from marks visible on stylopod shaft, the part richest in
425 meat (CD 8689; CD 7059; CD 2196). Finally, bone marrow extraction is shown by the
426 presence of a percussion mark on the cranial surface of a tibia and a humerus (CD 8078e; CD
427 7059; CD 2196). Skinning is also inferred based on the presence of cut marks on the proximal
428 part of a first phalanx. Large-sized bovids are distinguished from small and medium-sized
429 bovids by the identification of only two distinct stages: disarticulation (CD 1643) and
430 defleshing (CD 7665; CD 196; CD 13337).

431

432 **4. Discussion**

433 *4.1. Accumulation processes*

434 The original Cooper's D cave had two distinct sub-vertical entrances leading to the
435 formation of an accumulation slope (Berger et al., 2003; de Ruiter et al, 2009). These allowed
436 a variety of animals to move back and forth within the cavity. It leads us to reject the
437 hypothesis of a natural trap as a possible accumulation scenario of the large mammal fauna.
438 Moreover, the low number of weathered specimens indicates that bones were rapidly buried

439 and/or had been protected (e.g., forest cover) from the weather prior to burial. The significant
440 fragmentation of the bone material ($n > 95\%$ of the NISPt) reflects the impact of the
441 decalcification process. This observation is consistent with the results obtained by de Ruiter et
442 al. (2008) and Val et al. (2015), who found a significant difference in the degree of bone
443 fragmentation between calcified and decalcified breccia bone assemblages. In addition, the
444 presence of manganese dioxide deposits on most of the bone remains ($n = 96\%$ of the NISPt),
445 reflects a wet sedimentary environment. Although water was present, few bones show
446 abrasion related to water flow ($n = 0.2\%$ of NISPt), which is reinforced by the over-
447 representation of bone shafts smaller than 2 cm and the results of the sedimentological studies
448 (L. Bruxelles, pers. comm.).

449 Based on skeletal part representation, large-sized bovid carcasses appear to be less
450 complete than small and medium-sized bovids. Schoville and Otárola-Castillo (2014)
451 previously showed that, in general, distance is the most significant variable explanation for
452 transport variability among large prey animals. Thus, large bovid prey are less likely to be
453 transported into the cave by biotic agents (e.g. large carnivores and/or hominins). At Cooper's
454 D, small-sized bovids are mostly represented by foot and dental remains while medium-sized
455 bovid skeletons appear to be relatively complete. Transport distance does not explain skeletal
456 part distribution of small-sized prey as they tend to be transported complete in a wide variety
457 of distances (Schoville and Otárola-Castillo, 2014) and be stored in trees above caves by
458 leopards (Brain, 1981; Cavallo and Blumenshine, 1989). However, at Cooper's D, bovid
459 skeletal part representation reflects bone density-mediated attrition, which indicates pre- and
460 post-depositional destruction. The distribution of skeletal elements at Cooper's D is then
461 biased by biostratigraphic (carnivore ravaging) and/or diagenetic (decalcification) processes.
462 This pattern is not surprising in South African cave context where bone accumulations are
463 mostly the result of carnivore accumulation (e.g. Brain, 1981; Pickering et al., 2004b, 2008;

464 O'Regan and Reynolds, 2009; Adams, 2010; Reynolds, 2010; Fourvel et al., 2018) and are
465 highly impacted by post-depositional destruction (e.g. Adams et al., 2007; Val and Stratford,
466 2015; Val et al., 2015). The fragmentation pattern is mostly the result of post-depositional
467 destruction through decalcification process, as indicated by the difference of bone fragment
468 length distribution between Cooper's D, dominated by fragments smaller than 5 cm in size,
469 and modern hyena accumulations (Table 3). Thus, skeletal part representation of large-sized
470 carcasses most likely reflects transportability (Schoville and Otárola-Castillo, 2014), while the
471 small and medium-sized bone distribution pattern is likely the result of bone density-mediated
472 attrition.

473 We observe a 'prime dominated' mortality profile in both small and medium sized bovids.
474 Large bovids are characterized by an equal presence of juveniles and prime adults, with fewer
475 old individuals. This result is consistent with bone density-mediated attrition of more fragile
476 elements from small young individuals. The mortality profile of small-sized bovids (size class
477 I-II) from Cooper's D is similar to modern accumulations made by lion (*Pan. leo*) and leopard
478 (*Pan. pardus*). The same pattern is also observed at Swartkrans Members 1–3 (Bunn and
479 Pickering, 2010b) but also at Gondolin and Kromdraai A (Brain, 1981; Pickering et al., 2007,
480 2008; Bunn and Pickering, 2010b). This result supports the involvement of large felids, or
481 another large ambush predator, in the bone accumulation process at least for small bovid
482 carcasses. The mortality pattern of large-sized bovids from Cooper's D is different from
483 modern accumulations made by spotted hyena (*C. crocuta*) and lion (*Pan. leo*), but similar to
484 the distribution observed at FLK Zinj and Hadza-killed kudu (*Tragelaphus strepsiceros*).
485 Bunn and Pickering (2010b:402) state that this pattern "likely indicates a derivation from [...]
486 ambush hunting by early *Homo* at FLK Zinj, rather than any form of scavenging from felids".
487 Although this statement could be true at Cooper's D, the bone density-mediated attrition that

488 we observed, which leads to an under-representation of juvenile individuals, requires us to be
489 more cautious about the interpretation..

490 We identify only eight remains with rodent gnaw marks at Cooper's. Porcupine is known
491 to be an important accumulating and modifying agent of modern cave bone assemblages in
492 South Africa which can have 60% to 70% of remains showing evidence of gnawing when
493 porcupines are present (Brain, 1981), values which are much higher than observed at
494 Cooper's D ($n < 0.04\%$ of NISP). Therefore, it is unlikely that the Cooper's D cave was
495 occupied and used as a den by porcupines, although they may have visited the area around the
496 cave, as suggested by Adams et al. (2007) for the Gondolin 1 deposit.

497 At Cooper's D, the most common biotic agents responsible for bone surface modification
498 are carnivores. We report more than 5% of the NISP impacted by carnivore tooth marks. This
499 value is probably reduced by fragmentation of the bone material which increase the total
500 NISP. Our results suggest that the distribution of tooth pits reflects the differential
501 conservation of bone elements at Cooper's D. In the current state, it is not possible to use the
502 location of tooth marks as a tool to identify the responsible agent.

503 Occupation of the cave by brown hyena (*Par. brunnea*) is supported by the identification
504 of eight coprolite fragments (Val et al., 2014). The MNI of carnivores relative to ungulates at
505 Cooper's D (50:135 = 37%) is high, also consistent with a hyena den (Pickering, 2002). It is
506 higher than the archaeological deposits of Swartkrans Members 1 to 3 (Member 1 = 25%;
507 Member 2 = 19.51%; Member 3 = 23.74%), which correspond to mixed assemblages of
508 carnivores (Felidae and Hyenids) and hominins (Pickering et al., 2008; Adams and Rovinsky,
509 2018). Leopards (*Pan. pardus*) and hyenas (*C. crocuta* / *Par. brunnea*) are likely responsible
510 for the accumulation of animal carcasses, particularly those of bovids, in these caves
511 (Pickering et al., 2008). This is probably also the case at Cooper's D, but more investigation is
512 necessary, notably on the dimension and distribution pattern of carnivore tooth marks.

513

514 4.2. Early Pleistocene hominin subsistence behaviors in South Africa

515 One of the major results of our work is the identification of anthropic marks on the surface
516 of large mammalian bones. The presence of hominins in the assemblage is also supported by
517 the identification of *Paranthropus robustus* and Hominidae sp. indet. bone remains as well as
518 stone tools (Steininger et al., 2008; de Ruiter et al., 2009; Sutton et al., 2017). Despite the
519 small sample size, Cooper's D is still the second largest Early Pleistocene collection of
520 butchered bones in South Africa (Table 6). Our analysis shows that hominins were involved
521 in the accumulation of at least a part of the assemblage.

522 One of the major debates, around the interpretation of the hominin subsistence behaviors
523 during the Early Pleistocene concerns the modes of acquisition of the animal carcasses.

524 At Swartkrans (Fig. 14), the similar frequency of cut marks on meat-rich long bone shafts
525 (stylopod) between Members 1 to 3 suggests that hominins had primary access to animal
526 carcasses (Pickering et al., 2004a; 2007). The proportions of cutmarks are similar between
527 Cooper's D and Swartkrans Members 1 to 3 (<1% NISP of long bone); however, the
528 distribution profiles of the cut marks according to the three limb segments are quite different,
529 which could indicate a different exploitation pattern. The distribution profile depends on the
530 number of remains (of each element and of each size class) discovered within the different
531 deposits. There is no statistically significant difference between the distribution of cutmarks in
532 each bovid size class from Cooper's D. Thereby, we can conclude, as at Swartkrans (Pickering
533 et al., 2004a), that Cooper's D hominins exploited a diversity of bovid size classes, from small
534 to large antelopes.

535 It is currently not possible to rule out the genera *Australopithecus* and *Paranthropus* as
536 potential candidates for stone and bone tool-related behaviors or for the exploitation of animal
537 carcasses in South Africa. In East Africa, the discovery of lithic tools at 3.3 Ma (Harmand et

538 al., 2015) and probable butchery marks at 3.4 Ma (McPherron et al., 2010) allow us to
539 question the role of the genus *Homo* in the production of the first industries and the
540 exploitation of carcasses. The Drimolen Main Quarry site contains both *Paranthropus* and
541 early representatives of the genus *Homo* occurring in the same deposit along with stone and
542 bone tools (Backwell and d’Errico, 2008; Moggi-Cecchi et al., 2010; Stammers et al., 2018).
543 Moreover, new radiometric dates suggest that *Paranthropus robustus*, early *Homo*, and
544 *Australopithecus* were contemporaneous (Herries et al., 2020). Furthermore, morphological
545 evidence of enhanced manipulative ability has been inferred for *Australopithecus*
546 (*Australopithecus africanus* and *Australopithecus sediba*) and *Paranthropus robustus*
547 specimens (Susman, 1988; Kivell et al., 2011, 2015; Skinner et al., 2015). We argue that more
548 evidence is needed for attributed all Early Pleistocene butchery marks to the action of *Homo*
549 genus only.

550

551 **5. Conclusion**

552 The taphonomic analysis of the large mammal assemblage from Cooper’s D provides new
553 insights on the origin and history of the bone accumulation. The assemblage is composed by
554 an important diversity of mammals. The bones are highly fragmented and mostly covered by
555 manganese coating. At Cooper’s D, the bovid skeletal part representation reflects a density-
556 mediated attrition pattern. The attrition, based on the study of bone surface modifications, is
557 primarily the result of both pre- (carnivore) and post-depositional (decalcification) processes.
558 Indeed, carnivore tooth marks represent the most common bone surface modification at
559 Cooper’s D. However, hominin damage (e.g. cutmarks and percussion marks) was also
560 observed mainly on long bone cortical surfaces. The study of bovid mortality profiles
561 indicates the involvement of ambush predators, most likely large felids such as leopards.
562 Thus, our work highlights the involvement of both carnivores and hominins as taphonomic

563 agents in bone accumulation of Cooper's D. For now, even if the Cooper's D butchered bone
564 assemblage is the second largest one in South Africa, the relatively small sample size of
565 butchered bones ($n = 31$) does not permit speculation regarding the timing of access to
566 carcasses by hominins. However, we infer at both Swartkrans Members 1–3 and Cooper's D
567 (2.3–1.0 Ma) all the stages of animal carcass processing (skinning, disarticulation, defleshing,
568 marrow extraction) as well as the exploitation of a diversity of prey size classes. Thus, our
569 study shows the importance of Cooper's D and South African bone assemblages for
570 understanding Early Pleistocene hominin subsistence behaviors.

571

572 **Acknowledgments**

573 We would like to thank the three anonymous reviewers, the associate editor as well as
574 Clément Zanolli for their precious comments which undoubtedly contributed to improve the
575 quality of the paper. We thank Bernhard Zipfel from University of the Witwatersrand as well
576 as Stephany Potze, Mirriam Tawane, Heidi Fourie and Lazarus Kgasi from the Ditsong
577 Museum, Pretoria, for access to collections. C.S. acknowledges the funding contribution of
578 the Centre of Excellence in Palaeosciences (CoE-Palaeo) and the Palaeontological Scientific
579 Trust (PAST). R.H. would like to acknowledge the ATM MNHN “Paranthropus Diet. Régime
580 alimentaire et comportement de subsistance des Paranthropes sud-africains” (resp. S. Prat)
581 and the UMR 7194/MNHN for the funding support. R.H. addresses a special thanks to Tumi
582 Molefyane and Recognise Sambo for their help and support during the early stage of this
583 work.

584

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1003 **Table 1.** Updated faunal list from Cooper's D.

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1005 **Table 2.** Cortical surface preservation stage of bones from Cooper's D.

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1007 **Table 3.** Results of the Kolmogorov-Smirnov tests between bone flake size classes

1008 distribution of archaeological and carnivore assemblages.

1009

1010 **Table 4.** Observation frequency of the different bone surface modifications by the carnivores

1011 at Cooper's D. The percentages in brackets of the different stages of digestion were calculated

1012 on the total of digested bones observed.

1013

1014 **Table 5.** Anatomical distribution of the pits due to carnivore action identified on the surface

1015 of bovid bones from Cooper's D.

1016

1017 **Table 6.** Plio-Pleistocene sites of South Africa having delivered anthropic marks.

1018

1019 **Figure 1.** Localization of Cooper's Cave and other Early Pleistocene main sites in South

1020 Africa.

1021

1022 **Figure 2.** Geological scheme and plan of Cooper's D site (modified after de Ruiter et al.,

1023 2009).

1024

1025 **Figure 3.** Skeletal part representation of small (A), medium (B) and large bovids (C) from

1026 Cooper's D based on percentage of survivorship (%survivorship). Correlation between the

1027 percentage of minimum animal unit (%MAU) and the bone mineral density (BMD): A) $R_s =$

1028 0.49, p -value = 0.002; B) $R_s = 0.46$, p -value = 0.01; C) $R_s = 0.37$, p -value = 0.02. Marginal
1029 boxplots display the minimum, first quartile (Q1), median, third quartile (Q3) and the
1030 maximum value.

1031

1032 **Figure 4.** Bar plot of bovid mortality profiles from Cooper's D in percent of minimum
1033 number of individuals (MNI).

1034

1035 **Figure 5.** Ternary graph of bovid mortality profiles from Cooper's D. Small-sized bovids
1036 (size classes 1 and 2) compared to modern assemblages accumulated by carnivores (A) as
1037 well as with archaeological assemblages (B). Large-sized bovids (size classes 3 and 4)
1038 compared to modern assemblages accumulated by carnivores (C) as well as with
1039 archaeological assemblages (D). The ellipses represent a confidence interval fixed at 95%.
1040 Comparison data from Bunn and Pickering (2010b), see SOM Table S5. Numbers in brackets
1041 represent the MNI. Abbreviations: *G. thompsoni* = *Gazella thompsoni*; *C. gnou* =
1042 *Connochaetes gnou*; *C. taurinus* = *Connochaeste taurinus*.

1043

1044 **Figure 6.** Example of bone surface modifications observed at Cooper's D and interpreted as
1045 caused by the action of non-biological agents. A) water rounding. B) decalcification. C, D)
1046 cave corrosion.

1047

1048 **Figure 7.** Example of bone surface modifications observed at Cooper's D and interpreted as
1049 caused by the action carnivores (A–C), large mammal trampling (D–F) and rodents (G–I).

1050

1051 **Figure 8.** Linear marks identified as cutmarks made by hominins (skinning) visible on the
1052 surface of a medium-sized bovid phalanx (CD 16947) from Cooper's D. A post-excavation

1053 fracture can also be observed on the distal part. A and B) view of cutmarks on the dorsal side;
1054 D and E) view of cutmarks on the medial side; C and F) view of cutmarks on the ventral side;
1055 G–H) view of cutmarks on the lateral side.

1056

1057 **Figure 9.** Linear marks identified as cutmarks made by hominins visible on the surface of a
1058 small-sized bovid humerus shaft (CD 7059) from Cooper’s D. A–D) percussion marks; E–F)
1059 defleshing cutmarks.

1060

1061 **Figure 10.** Examples of cut marks observed on bone remains from Cooper’s D with a more
1062 closed-view by binocular microscope (A) and Dinolite microscope (B–E). A) small-sized
1063 bovid left metatarsal proximal fragment (CD 837). B) diaphyseal fragment of large bovid
1064 metapodial (CD 1643). C) indeterminate bone fragment (CD 7200). D) diaphyseal fragment
1065 of medium-sized bovid metatarsal (CD 1390). E) proximal left metacarpal fragment of
1066 medium-sized bovid (CD 5196).

1067

1068 **Figure 11.** Butchery marks observed on bone remains from Cooper’s D under the scanning
1069 electron microscope. A) small bovid left metatarsal proximal fragment (CD 837). B)
1070 diaphyseal fragment of medium-sized bovid metatarsal (CD 1390). C) diaphyseal fragment of
1071 a large right bovid humerus (CD 7665). D) proximal left metacarpal fragment of medium-
1072 sized bovid (CD 5196).

1073

1074 **Figure 12.** Butchery marks distribution observed on the surface of large mammal bones from
1075 Cooper’s D. Bovid size class is indicated between parentheses.

1076

1077 **Figure 13.** Distribution of the cut marks on the different bovid limb bones from Cooper’s D.

1078

1079 **Figure 14.** Distribution of the cut marks on the different bovid limb bones from Cooper's D
1080 and Swartkrans Members 1–3. Comparison data from Pickering et al. (2008).

Table 1

Order	Family	Taxon	NISP	MNI
Primate	Cercopithecidae	<i>cf. Dinopithecus</i> sp.	1	1
		<i>Gorgopithecus major</i>	5	2
		<i>cf. Gorgopithecus</i> sp.	1	-
		<i>Theropithecus oswaldi</i>	56	6
		<i>cf. Theropithecus</i> sp.	16	-
		<i>Papio</i> sp. indet	65	3
		indeterminate	31	-
		<i>cf. Cercopithecus</i> sp.	3	1
		<i>Chlorocebus</i> sp. indet	1	1
		indeterminate	312	-
	Hominidae	<i>Paranthropus robustus</i>	4	1
		<i>cf. P. robustus</i>	2	1
		indeterminate	1	-
	Indeterminate	indeterminate	144	-
Carnivora	Canidae	<i>Lupullela mesomelas</i>	29	2
		<i>Lup. cf. mesomelas</i>	16	1
		<i>Lupullela</i> sp.	70	3
		<i>Lycaon sekowei</i>	2	1
		<i>Lycaon cf. sekowei</i>	1	1
		<i>Lycaon pictus</i>	3	1
		<i>L. cf. pictus</i>	2	1
		<i>Lycaon</i> sp.	6	1
		<i>cf. Lycaon</i> sp.	6	-
		<i>Vulpes chama</i>	3	1
		<i>cf. V. chama</i>	5	1

	indeterminate	55	-
Felidae	<i>Dinofelis</i> cf. <i>aronoki</i>	11	2
	cf. <i>D. aronoki</i>	24	2
	cf. <i>Dinofelis</i>	-	-
	<i>Megantereon whitei</i>	7	3
	cf. <i>M. whitei</i>	4	1
	<i>Panthera leo</i>	4	1
	<i>Pan.</i> cf. <i>leo</i>	1	1
	<i>Panthera pardus</i>	15	2
	<i>Pan.</i> cf. <i>pardus</i>	7	1
	<i>Panthera</i> sp.	2	1
	<i>Caracal caracal</i>	3	2
	<i>Caracal</i> sp.	5	1
	<i>Felis lybica</i>	5	1
	<i>Felis sylvestris</i>	1	1
	<i>Felis</i> sp.	2	1
	<i>Acynonix jubatus</i>	3	1
	cf. <i>Acynonix</i>	1	1
	Machairodontinae	10	-
	indeterminate	151	-
Hyaenidae	<i>Chasmaporthetes nitidula</i>	1	1
	<i>Chasmaporthetes</i> sp.	2	1
	<i>Crocuta crocuta</i>	18	1
	<i>Crocuta ultra</i>	4	2
	<i>Crocuta</i> sp.	14	2
	<i>Parahyaena brunnea</i>	37	3
	<i>Par.</i> cf. <i>brunnea</i>	15	2

		<i>Hyaena</i> sp.	4	1
		<i>Proteles cristatus</i>	3	1
		<i>Proteles</i> sp.	7	1
		indeterminate	50	-
	Indeterminate	indeterminate	132	-
Artiodactyla	Alcelaphini	<i>Megalotragus</i> sp.	12	4
		<i>Connochaetes</i> sp.	60	7
		<i>Damaliscus</i> sp.	30	7
		medium-sized Alcelaphini	269	13
	Antilopini	<i>Antidorcas marsupialis</i>	50	11
		<i>Antidorcas recki</i>	45	8
		Antilopini indet.	82	7
	Hippotragini	<i>Hippotragus</i> sp.	13	3
	Tragelaphini	<i>Tragelaphus</i> cf. <i>strepsiceros</i>	1	1
		<i>Tragelaphus</i> cf. <i>oryx</i>	4	1
		<i>Tragelaphus</i> sp.	15	2
		Tragelaphini indet.	8	1
	Reduncini	<i>Redunca</i> cf. <i>fulvorufula</i>	2	1
		Reduncini indet.	37	8
	Peleini	<i>Pelea</i> sp.	10	4
	Neotragini	Neotragini indet.	26	3
	Cephalophini	Cephalophini indet.	7	1
	Bovini	<i>Syncerus</i> sp.	3	2
		Bovini indet.	1	1
	Indeterminate	Small-sized bovids	739	15
		Medium-sized bovids	1709	11
		Large-sized bovids	747	8

		indeterminate	1688	-
	Suidae	<i>Metridiochoerus modestus</i>	14	3
		<i>Metridiochoerus andrewsi</i>	20	5
		<i>Metridiochoerus</i> sp. indet	1	1
		indeterminate	432	-
	Giraffidae	<i>Sivatherium maurusium</i>	3	3
		<i>Sivatherium</i> sp. indet	1	1
		indeterminate	20	-
Perissodactyla	Equidae	<i>Equus capensis</i>	13	2
		cf. <i>E. capensis</i>	3	-
		<i>Eurygnathohippus cornelianus</i>	1	1
		indeterminate	40	-
	Rhinocerotidae	indeterminate	1	1
Tubulidentata	Orycteropodidae	<i>Orycteropus afer</i>	1	1
Proboscidae	Elephantidae	<i>Elephas</i> sp.	1	1
Indeterminate	Indeterminate	indeterminate	13701	-
		TOTAL	21193	204

Abbreviations: NISP = number of identified specimens; MNI = minimum number of individuals.

Table 2

Bone surface preservation	NISP	% NISP
Stage 1	866	4%
Stage 2	5 778	27%
Stage 3	12 997	61%
Stage 4	538	3%
Indeterminate	1 014	5%
Total	21 193	100%

Abbreviations: NISP = number of identified specimens.

Table 3

	Brown hyena	Spotted hyena Kalahari	Spotted hyena Kruger
Cooper's D	D = 1, <i>p</i> -value = < 0.01	D = 1, <i>p</i> -value = < 0.01	D = 1, <i>p</i> -value = < 0.01
Gondolin 1	D = 1, <i>p</i> -value = < 0.01	D = 0.8, <i>p</i> -value = 0.08	D = 0.8, <i>p</i> -value = 0.08
Kromdraai B	D = 1, <i>p</i> -value = < 0.01	D = 1, <i>p</i> -value = < 0.01	D = 1, <i>p</i> -value = < 0.01

Table 4

Carnivore modifications	NISP (%)
Pits	688 (3.2)
Grooves	207 (1.0)
Digestion	186 (0.9)
Stage 1	109 (58.6)
Stage 2	40 (21.5)
Stage 3	37 (19.9)
Total	1081 (5.1)

Abbreviations: NISP = number of identified specimens.

Table 5

Element	Small-sized bovids	Medium-sized bovids	Large-sized bovids
Cranium	0	1	0
Vertebrae	1	10	5
Ribs	6	9	8
Pelvis	2	6	6
Scapula	3	5	2
Humerus			
Hum EP	1	2	3
Hum DIA	0	5	0
Hum ED	2	2	2
Radius			
Rad EP	1	6	4
Rad DIA	5	5	2
Rad ED	2	2	3
Femur			
Fem EP	0	3	1
Fem DIA	0	9	0
Fem ED	1	0	3
Tibia			
Tib EP	1	0	2
Tib DIA	0	4	0
Tib ED	1	1	6
Carpals/Tarsals	6	5	7
Metapodials			
Met EP	1	6	4
Met DIA	10	26	4

Met ED	4	8	3
Phalanx	9	17	5
Total	56	132	70

Abbreviations: EP = proximal epiphysis; DIA = Diaphysis; ED = distal epiphysis.

1 **Table 6**

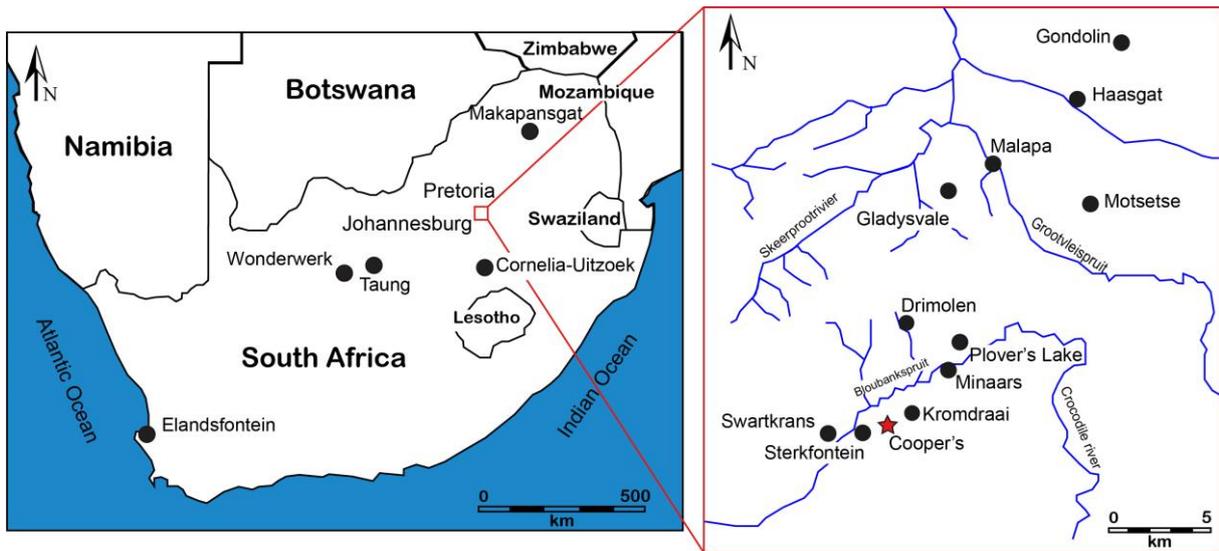
Sites	Deposits	Dates	Hominins	Industry	%BM	Faunal NISP	CT	PM	TM	References
Sterkfontein	Member 5 East Oldowan	2.18 ± 0.21 Ma	<i>P. robustus</i>	Oldowan	0.08%	1202	1	-	122	Brain (1981); Kuman (1994, 2007); Pickering (1999); Kuman and Field (2009); Granger et al. (2015)
	Name Chamber	2.18 Ma (?)	-	Oldowan	0.28%	5738	16	-	78	Stratford et al. (2012); Val and Stratford (2015)
Swartkrans	Member 1	2.22 ± 0.09 Ma	<i>P. robustus</i> <i>H. cf. erectus</i>	Oldowan	1.60%	824	10	3	143	Pickering et al. (2008, 2019); Kuman et al. (2021)
	Member 2	1.36 ± 0.29 Ma	<i>P. robustus</i> <i>H. cf. erectus</i>	Acheulean	5.90%	521	14	17	182	Balter et al. (2008); Pickering et al. (2008)
	Member 3	0.96 ± 0.09 Ma	<i>P. robustus</i>	Acheulean	7.80%	1350	60	45	475	Pickering et al. (2008); Gibbon et al. (2014)
Cooper's Cave	D deposit	1.375 ± 0.113–1.000 Ma	<i>P. robustus</i> Hominidae indet.	Indeterminate	0.15%	21193	16	15	895	De Ruiter et al. (2009); Pickering et al. (2019); Hanon et al. (in press); This study

2

3 Abbreviations: NISP = number of identified specimens; BM = butchery marks (percussion and cutmarks); CT = cutmarks; PM = percussion marks; TM =

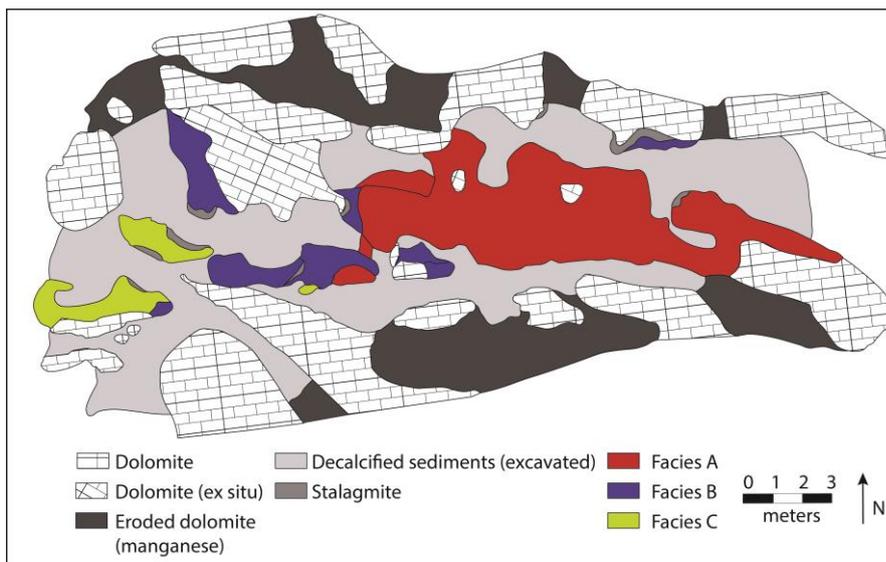
4 tooth marks.

5 Figure 1.



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7 Figure 2.



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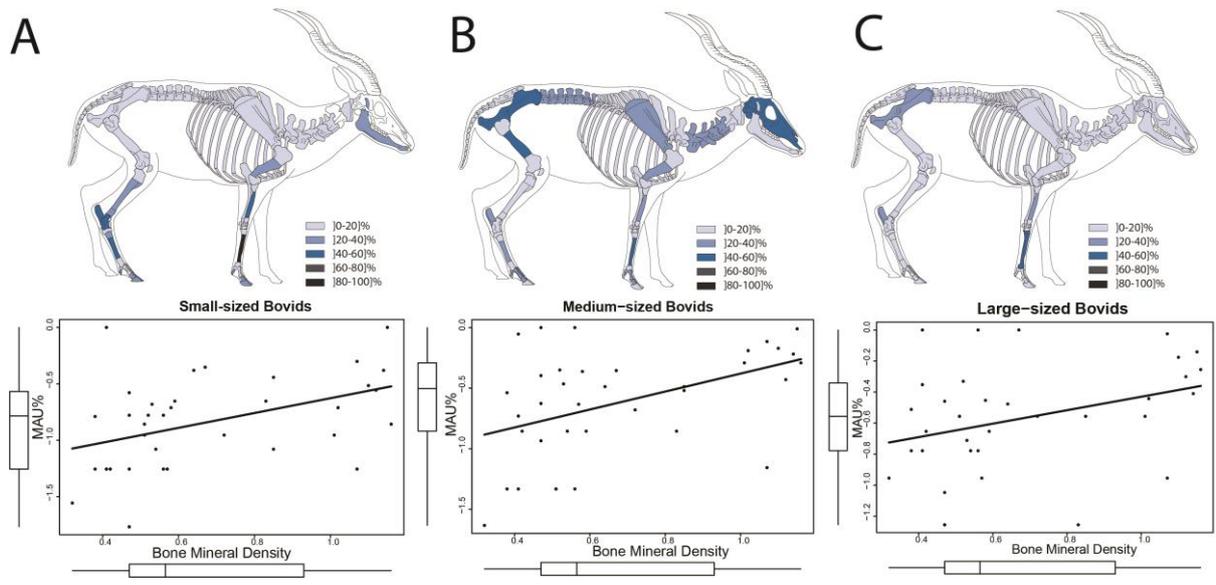
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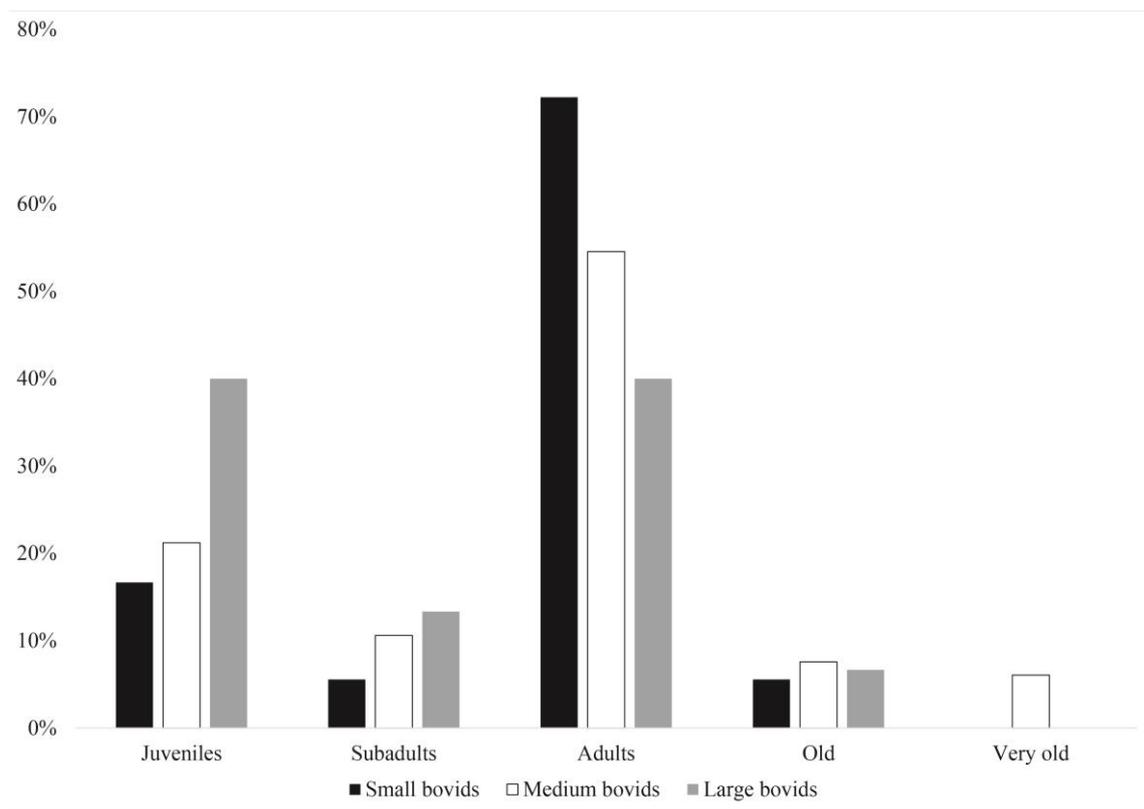
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16 Figure 3.



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18 Figure 4.



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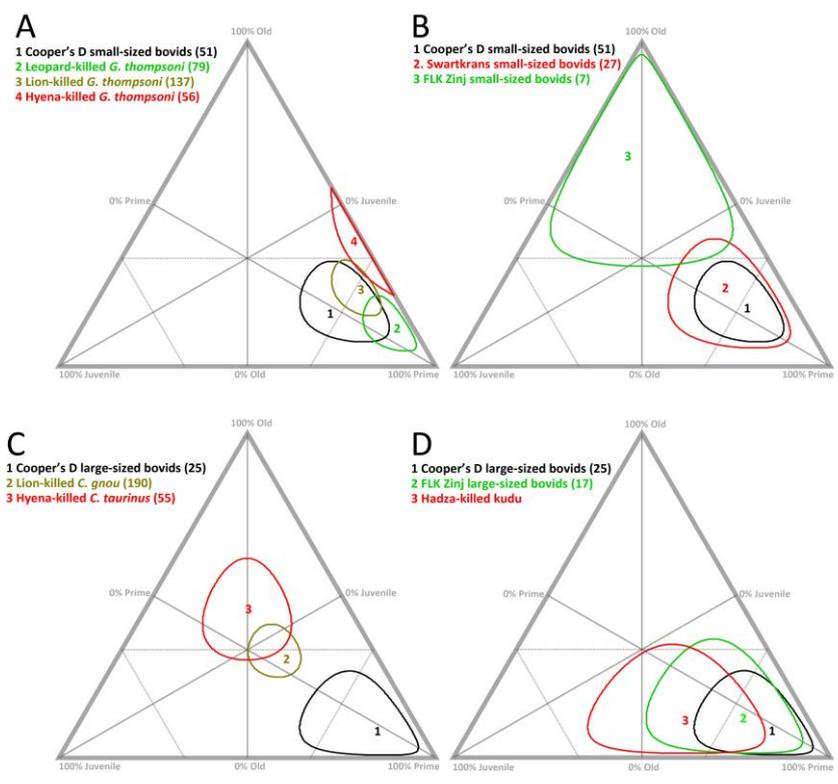
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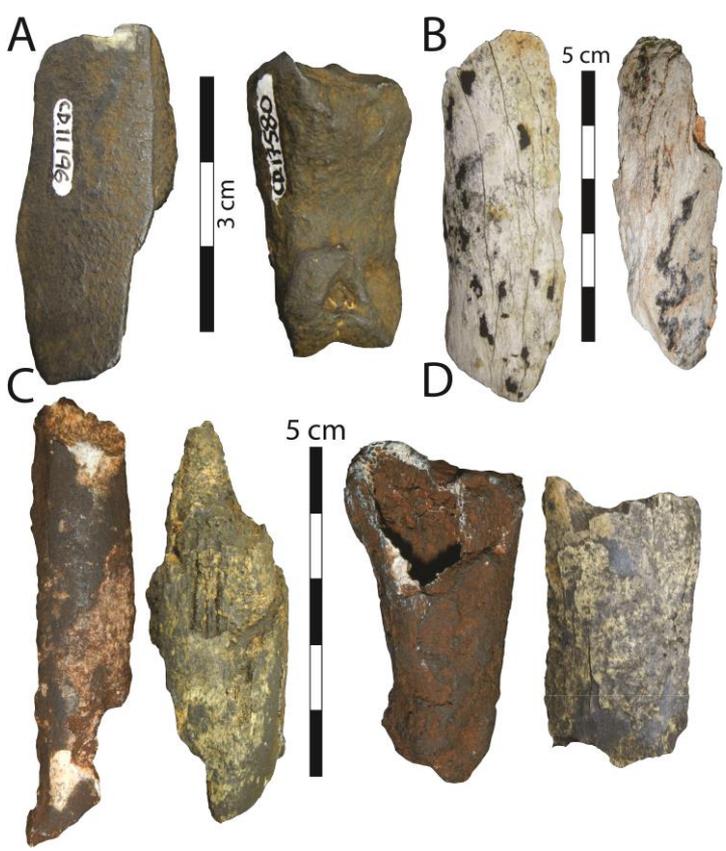
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24 Figure 5.



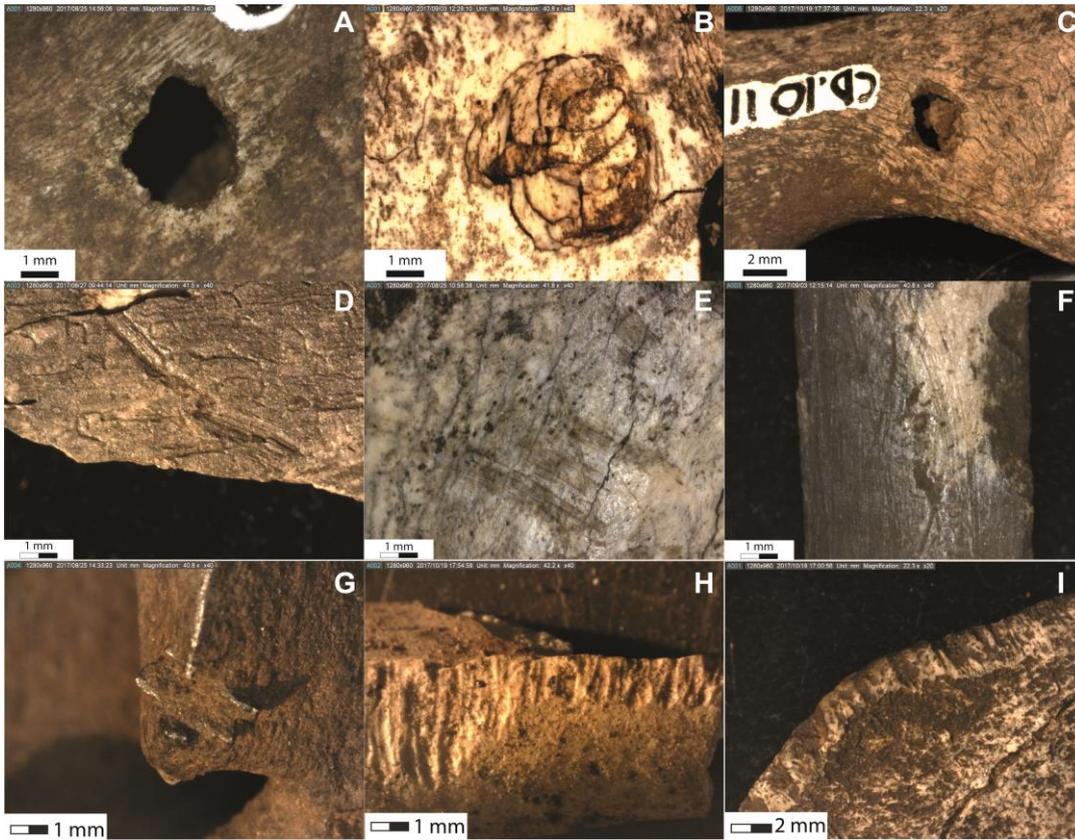
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26 Figure 6.



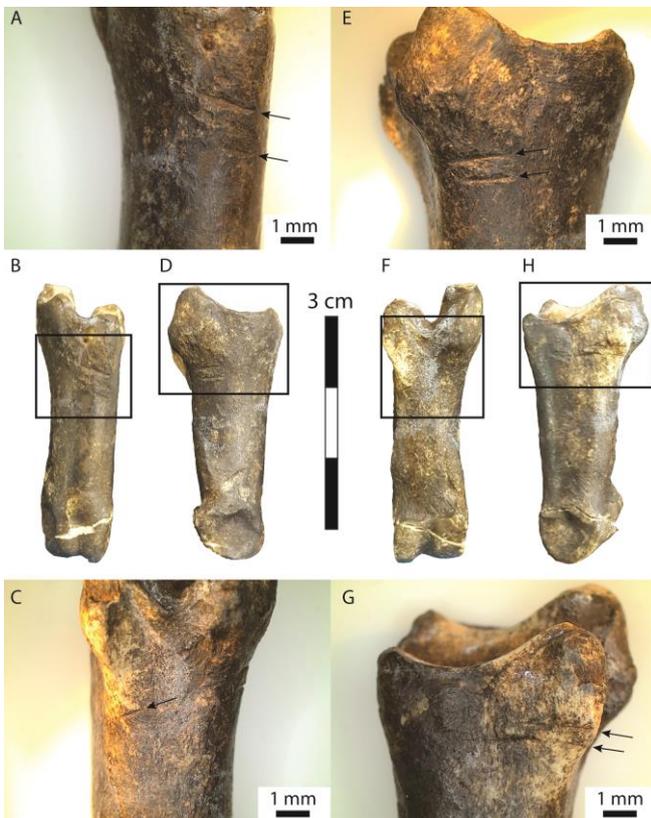
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28 Figure 7.



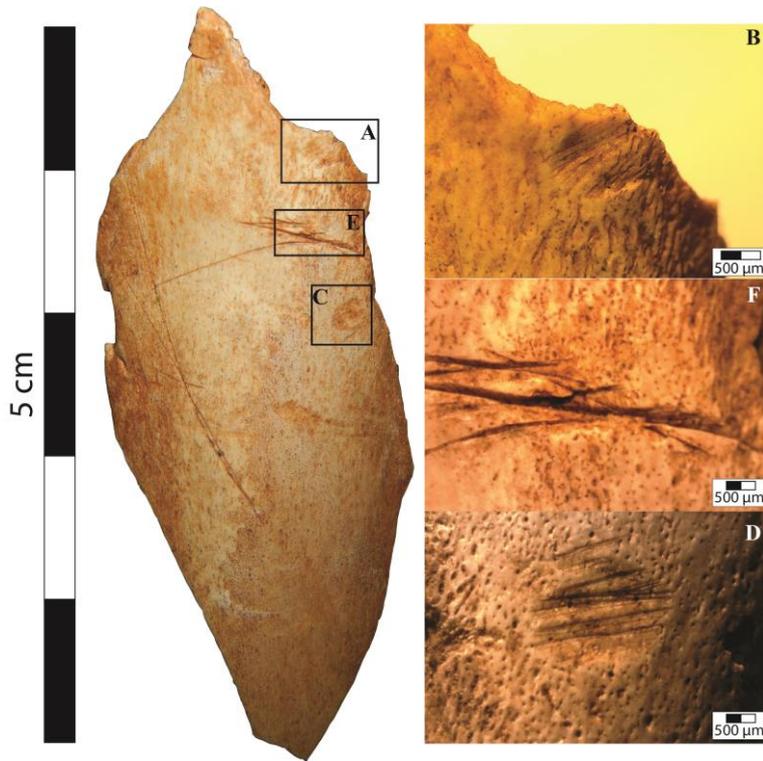
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30 Figure 8.



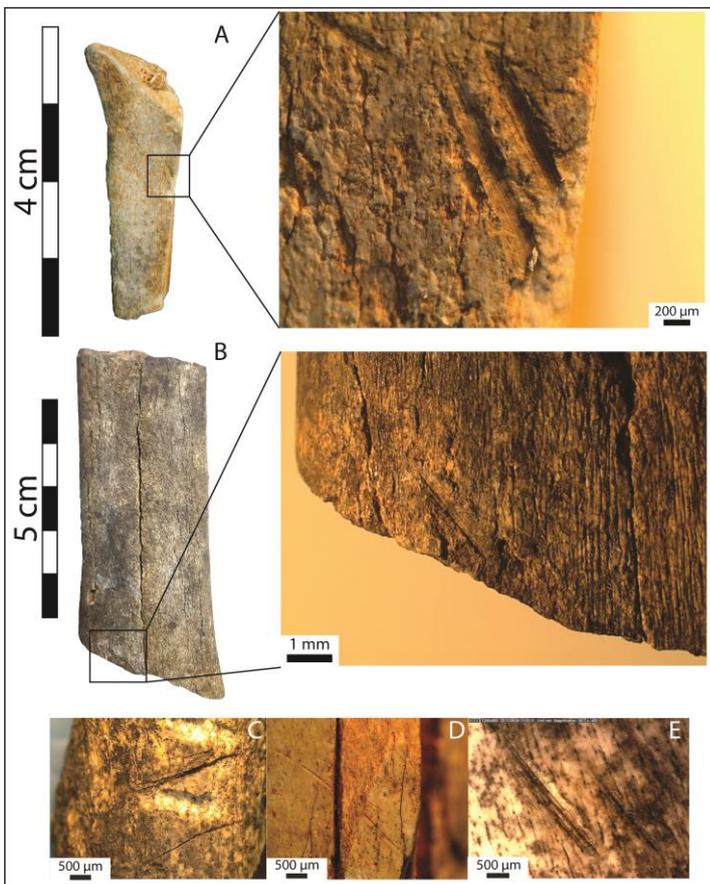
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32 Figure 9.



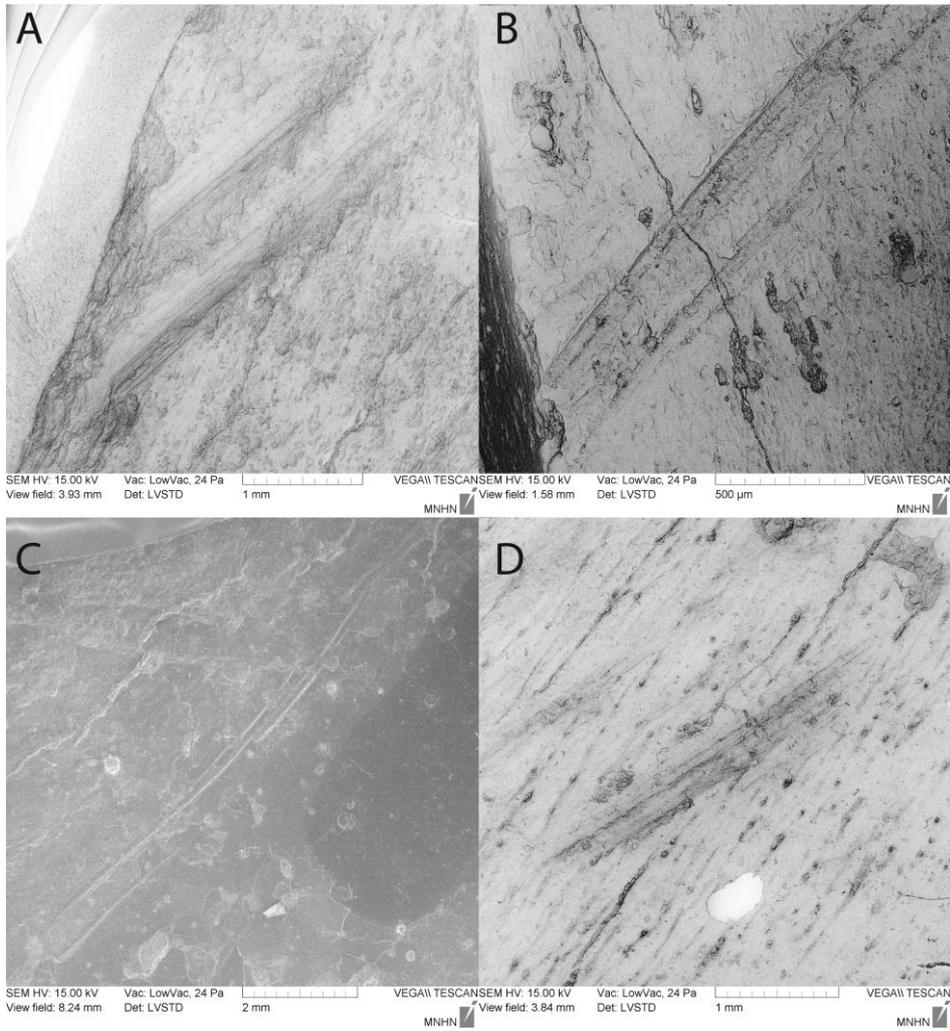
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34 Figure 10.



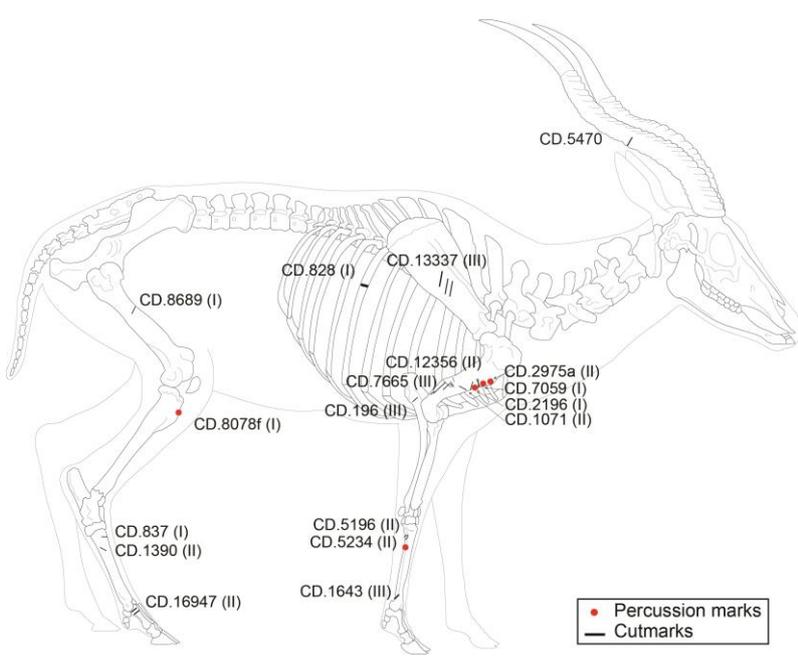
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36 Figure 11.



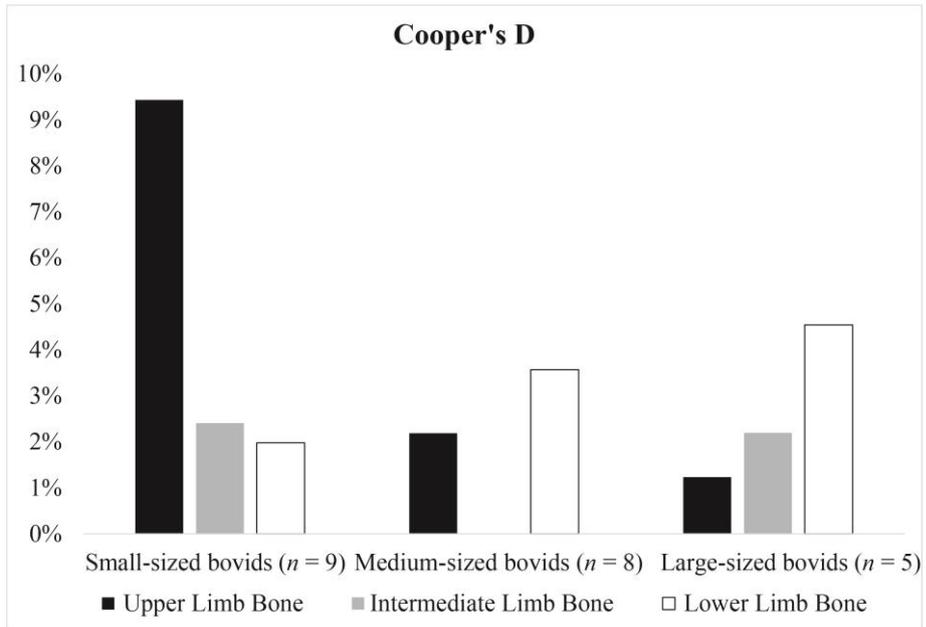
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38 Figure 12.



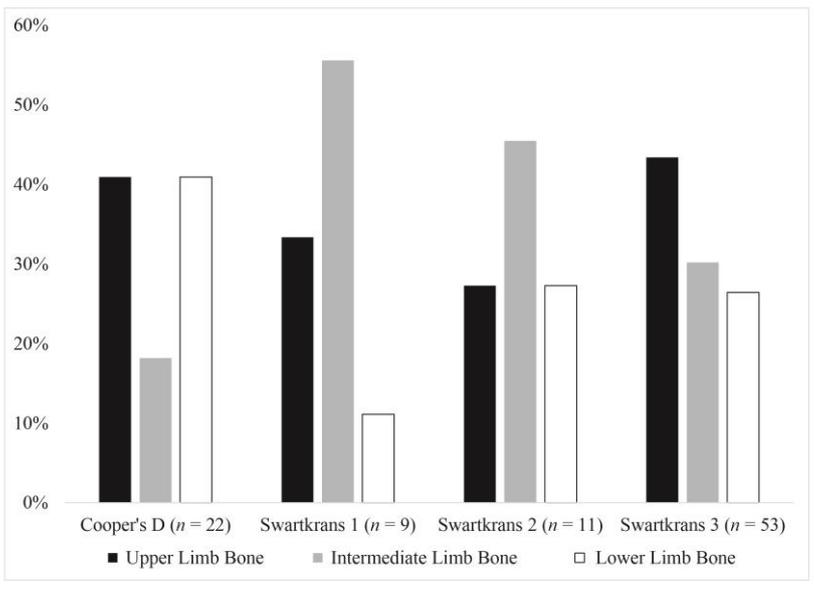
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40 Figure 13.



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42 Figure 14.



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