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1 Carnivores and hominins contributions to the Early Pleistocene bone accumulation of
2 Cooper's D, South Africa

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14 **Abstract**

15 Carnivores has long been identified as one of the most important taphonomical agent of the
16 Plio-Pleistocene hominin-bearing caves of South Africa. Cooper's D is an eroded cave deposit
17 dated between 1.3 – 1.0 Ma and has yielded an abundant and diverse large mammal faunal
18 assemblage. It has been previously argued that brown hyenas (*Parahyaena brunnea*) were the
19 main accumulator agent. However, more recently the involvement of hominins has also been
20 identified in the accumulation of at least a part of the assemblage. In this paper, we first describe
21 the composition of the carnivore paleoguild from Cooper's D, which permits to highlight an
22 important taxonomic diversity. The completeness indexes indicate a good retention of bone
23 material in our analysis. The carnivore ravaging index pointed out the relative moderate impact
24 of carnivores in the destruction of the bone assemblage. Through skeletal part representation,
25 mortality profiles and bone surface modifications, we argue that large felids, and especially
26 leopards, can in fact be identified as the most probable main taphonomic agents. Moreover, we
27 confirmed the involvement of hyenids but also canids in the accumulation and modification of
28 the assemblage. Based on the multiple carnivore taphonomic signal, we proposed that the cave
29 was not used as a carnivore den on a regular basis. Thus, we argue that Cooper's D faunal
30 assemblage is the result of the independent accumulations of both hominins and carnivores.

31 **1. Introduction**

32 Carnivores, and especially hyenas, have long been identified as one of the main taphonomic
33 agent of the accumulation and modification of Plio-Pleistocene large mammal assemblages.
34 Buckland (1822) was the first to characterize a prehistoric hyena den from the study of the
35 bone accumulation at Kirkland, Yorkshire, and therefore bring back to light the potential role
36 of carnivores in archaeological bone accumulations. His research was extended in Europe by
37 Zapfe (1939), Brunner (1944) and Thenius (1961), who recorded feeding traces left by hyenas
38 as well as bone fracture patterns. At the same time in South Africa, Dart (1956; 1957) was
39 conducted his research on the *Australopithecus* site of Makapansgat. He suggested that the
40 large mammal bone accumulation was the result of hominin rather than carnivore activity.
41 Some researchers were opposed to the hominin origin scenario for Makapansgat bone
42 accumulation proposed by Dart, and rather attributed the presence of bovid bones associated
43 with the hominin remains to the action of hyenas and other carnivores instead (Broom and
44 Schepers, 1946; Oakley, 1953; von Koenigswald, 1953). Even if Dart (1956) argued for an
45 anthropic origin of these assemblages, the first systematic taphonomic studies conducted by
46 Brain (e.g. 1969; 1978; 1981) pointed out that early Pleistocene hominins were more
47 susceptible to be hunted by large carnivores than accomplished hunters. From this point, most
48 of the South African Plio-Pleistocene large mammal bone assemblages were attributed to
49 carnivore activity: Gondolin GD2 (Adams, 2010), Sterkfontein Member 4 (Pickering et al.,
50 2004c), Kromdraai Member 2 (Fourvel et al., 2018b) and Swartkrans Members 1 to 3
51 (Pickering et al., 2008). Interestingly, most of the attention has been given to felids and hyenids,
52 leading to a gap of knowledge about the role of potential smaller carnivores such as canids,
53 viverrids or mustelids (Yravedra et al., 2014; Fourvel et al., 2018a).

54 Recent taphonomic investigations of South African caves have provided evidence for the
55 involvement of hominins in the accumulation of at least part of bone assemblage (Brain, 1993;
56 Pickering et al., 2004b; 2007; 2008). On one hand, based on the anatomical distribution of
57 butchery marks along limb bones, Pickering et al. (2007) argue that hominins did have an early
58 access to bovid carcasses during the Swartkrans Member 3 time period (0.96 ± 0.09 Ma; Gibbon
59 et al., 2014). On the other hand, carnivores were importantly active at this time in the cave,
60 specifically leopards and hyenids (Pickering et al., 2008). Similarly, Hanon (2019) and Hanon
61 et al. (2022) recently described the presence of hominin butchery marks at the Cooper's D site.
62 Moreover, one definitive bone tool has been described at Cooper's D (Hanon et al., 2021),
63 which reinforce the hypothesis of hominin involvement in the bone accumulation processes.
64 However, the relationship between these hominins and carnivores at that site remains
65 unexplored. This raises questions about faunal accumulations of early archaeological sites in
66 South Africa, the competition and interaction between hominins and carnivores at that time, as
67 well as Plio-Pleistocene hominin subsistence behaviours.

68 In this paper, we used multivariate taphonomic evidence obtained from the study of large
69 mammal assemblage of Cooper's D in order to explore the carnivores and hominins respective
70 contributions to the bone accumulation. Our study provides further conclusions on the hominin
71 subsistence behaviors during the Early Pleistocene of South Africa.

72 **2. The Cooper's cave site**

73 The Cooper's Cave site is situated in the Cradle of Humankind, approximately 45 km
74 northwest of Johannesburg (**Fig. 1**). Excavations were conducted by Berger and Steininger in
75 2001 (Berger et al., 2003; de Ruiter et al., 2009) and were focused on the decalcified
76 sediments of the D deposit. These excavations yielded an abundant assemblage of both micro
77 and macrofauna ($n > 50,000$), stone tools ($n = 49$) and seven hominin remains, six of them

78 attributed to *Paranthropus robustus*, the last one remains unidentified (Berger et al., 2003; de
79 Ruiter et al., 2009; Val et al., 2014; Sutton et al., 2017).

80 Cooper's D consists of two localities – Cooper's D East and West – which correspond to two
81 distinct parts of the cave (Berger et al., 2003; de Ruiter et al., 2009). The fossiliferous deposit
82 rests on dolomitic floor on which several types of speleothems formed before the cave opened
83 (ibid.). The western deposit (facies B and C), which makes up the lower major part of the
84 sequence, is made up of fine sand and contains an abundant assemblage of micromammals (de
85 Ruiter et al., 2009). The fossil breccia corresponds to an accumulation slope characteristic of
86 cave deposits with a vertical (or subvertical) opening. The deposit is separated in two by a
87 stalagmite floor. The presence of different calcite formations within the western deposit, such
88 as stalagmites, flows or floors associated with the low proportion of dolomitic clasts from the
89 collapse of the roof, indicates that the deposit accumulated when the cave was relatively well
90 closed. Cooper's D East is made up of large clasts, sometimes greater than 50 cm (facies A).
91 These dolomitic clasts originated from the collapsed roof. No preferential orientation of
92 dolomitic clasts or cherts is observed, while the bone remains seem to more or less align
93 horizontally (de Ruiter et al., 2009). Most of the large mammal bone remains have been
94 recovered from the finer-grained portions of the faces A and B.

95 The interbedded stalagmitic floors within the breccias of the West and East deposits have
96 been dated by the Uranium-Lead method (de Ruiter et al., 2009). The stalagmitic floor on which
97 all the deposits rests yielded an age of 1.526 ± 0.088 Ma. The horizontal layer cutting the
98 deposits into two sets has been dated to a minimum of 1.413 Ma and a maximum of 1.671 Ma.
99 Given the age of 1.526 ± 0.088 Ma of the basal floor, the age of the upper floor is dated between
100 1.413 and 1.526 ± 0.088 Ma (de Ruiter et al., 2009). All the sediments in the lower part of the
101 deposits must have accumulated between 1.5 and 1.4 Ma. Subsequently, a new study undertook

102 to recalculate the ages, in particular for the sample which provided the date of 1.526 ± 0.088
103 (CDD1). This sample is now estimated at 1.375 ± 0.113 Ma (Pickering et al., 2019). Based on
104 both radiometric dates and biochronological data, Hanon et al. (2022b) suggest that the faunal
105 assemblage from both West and East parts of the cave accumulated between 1.3 and 1.0 Ma.

106 Several paleontological studies have been conducted on the Cooper's D large mammal
107 fauna. This is the case for the Primates (Berger et al., 1995; Steininger et al., 2008; de Ruiter
108 et al., 2009; DeSilva et al., 2013; Folinsbee and Reisz, 2013), Carnivores (Hartstone-Rose et
109 al., 2007; 2010; O'Regan et al., 2013; Kuhn et al., 2017; O'Regan and Steininger,
110 2017), Equidae (Badenhorst and Steininger, 2019) and Bovidae (Hanon et al., 2022b).

111 In addition, with palaeontological studies, previous taphonomic studies have been
112 conducted on large mammal Cooper's assemblage (de Ruiter et al., 2009; Val et al., 2014;
113 Parkinson, 2016; Hanon, 2019). Based on the study of a sub-sample (NISP = 8488), de Ruiter
114 et al. (2009) identified the brown hyena (*Parahyaena brunnea*) as the main accumulating agent
115 of the assemblage, although the leopard is also mentioned. Through the study of large-bodied
116 non-hominin primates and the eight coprolite fragments recovered from Cooper's D, Val et al.
117 (2014) also suggest the role of brown hyena and felids.

118 Subsequently, Hanon et al. (2022a) has identified 31 bone remains bearing butchery marks.
119 Based on the study of the morphology and anatomical location of these marks, the authors
120 argued that hominins exploited a diversity of bovid size classes, from small to large animals
121 (Hanon, 2019; Hanon et al., 2022a). Moreover, Hanon et al. (2021) described the presence of
122 one definitive bone tool at the site, similar to those find at Sterkfontein, Swartkrans, Kromdraai
123 and Drimolen (Brain, 1993; Backwell and d'Errico, 2003; 2008; d'Errico and Backwell, 2003;
124 Val and Stratford, 2015; Stammers et al., 2018).

125 Thus, the faunal assemblage recovered at Cooper's D is characterized by an important
126 presence of diverse carnivores and also by a great impact of carnivores on at least a large part
127 of the bone assemblage as well as evidence of large mammal exploitation by hominins (de
128 Ruyter et al., 2009; Val et al., 2014; Hanon et al., 2022a). Here, through a multivariate
129 taphonomic approach, we seek to identify the respective role of carnivore taxa and hominins
130 in the accumulation and modification of the large mammal bone assemblage of Cooper's D.

131 **3. Material and methods**

132 The primary taphonomic data, upon which our analyses are based, derive from the study of
133 the Cooper's D large mammal assemblage (n = 21,193), which has been described in length
134 before (Hanon, 2019). Within that sample, 741 specimens are attributed to carnivores.
135 Moreover, 5,558 specimens are attributed to bovids and constitute the base of the skeletal
136 element and mortality profile analyses presented in this paper.

137 The collection comes from the excavations of decalcified sediments conducted from 2001
138 to 2009 by Lee R. Berger and Christine Steininger on both west and east side of the site (Berger
139 et al. 2003; de Ruyter et al. 2009). The Cooper's collection is stored and curated at the
140 Evolutionary Studies Institute of the University of Witwatersrand, Johannesburg. As a
141 comparative material, we used the modern and archaeological collections housed at the
142 Evolutionary Studies Institute of the University of Witwatersrand, Johannesburg, as well as the
143 collections of the Ditsong National Museum of Natural History of Pretoria.

144 *3.1. Quantification*

145 In this study, we use four quantification units (see Lyman, 1994 for a detailed description):
146 NISP (number of identified specimens), MNE (minimum number of elements), MAU
147 (minimum animal unit) and MNI (minimum number of individuals).

148 Our estimation of the MNE follows the method described by Marean and Spencer (1991)
149 which derived from the bone fraction record system developed by Klein and Cruz-Urbe
150 (1984:108). Thus, we recorded the bone portion (e.g. proximal epiphysis, proximal shaft, shaft
151 fragment, distal shaft, distal epiphysis) and the bone preservation fraction (e.g. < 0.25, 0.25-
152 0.5, 0.5-0.75, >0.75, 1) for each specimen. Then, we summed the fraction values for each
153 element and portion. The obtained value is rounded up to obtain an estimation of the MNE
154 (Lyman, 1994). This method has produced efficient results and has the advantage to take into
155 account long bone shaft specimens in the estimation (Marean and Spencer, 1991).

156 We obtain the MAU by dividing the MNE value of each specific bone element by the
157 number of times that element occurred in a complete skeleton (Binford, 1978; 1984). The
158 percentage of MAU (MAU%) is obtained by dividing the MAU of each bone element by the
159 highest MAU value.

160 The MNI is calculated by combination (MNIc) as defined by Poplin (1976). It represents
161 the most represented anatomical element in the assemblage for a given taxon, considering the
162 age estimation, the side and the size class.

163 *3.2. Animal size classes*

164 As described by Brain (1981), four bovid size-classes are commonly recognized: “Class I”
165 (less than 20 kg), “Class II” (from 20 to 100 kg), “Class III” (from 100 to 300 kg) and “Class
166 IV” (more than 300 kg). Following Fourvel et al. (2018b), we combined class III and IV into
167 one class (“large-sized bovids”) and considered the following distinction: “small-sized bovids”
168 (Brain’s class I), “medium-sized bovids” (Brain’s class II) and the “large-sized bovids”
169 (Brain’s class III and larger).

170 *3.3. Measure of completeness and degree of ravaging*

171 It has been previously shown that the Cooper's D faunal assemblage depicts a bone density
172 mediated attrition (Hanon et al., 2022a). For that reason, we conducted an estimation of the
173 assemblage completeness and of the carnivore ravaging. Marean et al. (2004) demonstrated
174 that completely retained faunal assemblages, which means that all the bone flakes have been
175 studied (retained), tend to have a high frequency of incomplete circumference long bone shafts.
176 In an incompletely retained assemblage, most of the shaft fragments are discard and the
177 assemblage is characterized by a high frequency of epiphysis with complete circumference
178 shaft attached to them. We first apply the circumference index using the long limb bone
179 circumference types used by Bunn (1983) as follows: (1) less than half circumference
180 preserved; (2) more than half circumference preserved; (3) complete circumference preserved.
181 We provide the distribution of long bone fragments (NISP) by circumference types and bovid
182 size classes to estimate the level of assemblage completeness.

183 Marean et al. (2004) also provided the "end versus shaft" index, by NISP, as a measure of
184 the completeness of an assemblage. Completely retained assemblages always preserve shaft
185 remains at higher rate than ends.

186 Moreover, we measure the carnivore ravaging process by applying the axial bones:limb
187 bones ratio by MNE (Domínguez-Rodrigo et al., 2007; Pickering et al., 2008). If a carcass has
188 been deposited complete and did not suffer from carnivore ravaging, then we expect to find
189 much more axial than appendicular remains. The ratio range between 4.25 (complete skeleton)
190 to 0 (completely ravaged skeleton).

191 *3.4. Skeletal part representation*

192 Skeletal part representation is commonly regarded as indicative of the impact of taphonomic
193 processes (e.g. Brain, 1981; Marean and Spencer, 1991; Stiner, 1991; 2002; Lyman, 1994;

194 Pickering et al., 2003; Domínguez-Rodrigo and Pickering, 2010). It has been previously
195 showed that the Cooper's D bone assemblage is biased by a bone-density mediated attrition
196 from pre- and post-depositional processes (Hanon et al., 2021). Here, we further analyze
197 skeletal part representation of preys in order to quantify the potential involvement of the
198 different carnivore taxa in the selection of bone elements. We study the relative distribution of
199 skeletal elements for each bovid size class according to NISP, MNE and MAU. It includes all
200 the specimens identified to a skeletal element and a bovid size class. For the purpose of the
201 analysis, we exclude unidentified specimens and isolated teeth. We compare our dataset to
202 modern carnivore assemblages provided by Domínguez-Rodrigo and Pickering (2010) using
203 multiple correspondence analysis (CA) for counted data (MNE). In order to test the results
204 obtained with the CA, we perform a hierarchical clustering analysis using the Ward's method,
205 which minimizes the sum of squares variance at each step of the process (Borcard et al., 2011).
206 The multiple correspondence and hierarchical clustering analyses are performed under the
207 PAST software version 4.05 (Hammer et al., 2001). The original dataset is provided in the
208 **Supplementary Material 1.**

209 *3.5. Mortality profiles*

210 We investigate prey mortality profiles through the ternary graph method developed by Stiner
211 (1990), Steele and Weaver (2002), Bunn and Pickering (2010), and Weaver et al. (2011). We
212 estimate age of individuals based on eruption stages and tooth wear patterns defined by Bunn
213 and Pickering (2010). Concerning the carnivores, we used a modified version of Mills, (1982),
214 where juveniles have unworn to well-worn deciduous premolars with erupting molars (classes
215 1 and 2), adults with a full permanent dentition (class 3) and old individuals with well-worn
216 permanent dentition (classes 4 and 5). We exclude young juvenile individuals as they could

217 biased mortality profiles (Bunn and Pickering, 2010b; 2010a). The ternary graphs are produced
218 with the Triangle version 2.0 Program using the likelihood method (Weaver et al., 2011).

219 *3.6. Bone surface modifications*

220 Each bone specimen was carefully observed under binocular microscope Olympus SZ2-
221 ILST (x10 – x40) in order to record bone surface modifications (rodent gnawing marks, root
222 etching, carnivore tooth marks, cut marks, percussion marks). The distinction between
223 carnivore, trampling and stone tools damage was made by using the criteria developed by
224 several researchers (Binford, 1981; Potts and Shipman, 1981; Shipman and Rose, 1983;
225 Behrensmeier et al., 1986; Blumenschine and Selvaggio, 1988; Olsen and Shipman, 1988;
226 Fiorillo, 1989; Lyman, 1994; Patou-Mathis, 1997; Blasco et al., 2008; Domínguez-Rodrigo et
227 al., 2009; 2010). Percussion marks were identified using the criteria described by
228 Blumenschine et al. (1996). We used the different criteria available in the literature for
229 identified carnivore tooth marks (Maguire et al., 1980; Binford, 1981; Brain, 1981; Cruz-Uribe,
230 1991; de Ruiter and Berger, 2000; Pickering, 2002; Pickering et al., 2004a; Domínguez-
231 Rodrigo and Pickering, 2010; Kuhn et al., 2010; Fourvel, 2012). We recorded punctures, pits,
232 crenulated edges, scoring, furrowing and digestion traces as defined by Fourvel (2012:151).
233 Digestion has been recorded as slight (stage 1: small digestion pits present), moderate (stage 2:
234 digestion pits cover most of the bone surface, edges are abraded and polished) or heavy (stage
235 3: original shape of the bone could not be determinable, digestion penetrates deep into the bone
236 which could create deep perforations). We recorded presence and absence of bone
237 modifications by bone section (e.g. proximal epiphysis, middle shaft, distal epiphysis).

238 We undertook to record the dimensions (maximum length and width) of 64 pits due to
239 carnivore bites visible at the bone surface using a digital DinoLite microscope (Dino-Lite
240 AD7013MTL) and the DinoCapture 2.0 software. If any mark is still ambiguous after a

241 carefully observation, we decided to record it as « indeterminate », and to not include it in our
242 analysis. Pits on epiphysis were not measured because it was shown that their dimensions were
243 much more variable than on the diaphysis and presented a strong overlap (Andrés et al., 2012).
244 We measured only well-preserved tooth pits visible on diaphysis of long bones (NISP = 64/143
245 = 45%). We compared our results with experimental data obtained from Selvaggio, 1994,
246 Domínguez-Rodrigo and Piqueras, 2003 and Pickering et al., 2004.

247 **4. Results**

248 *4.1. Composition of the carnivore paleoguild*

249 Carnivores are an important component of the Cooper's D faunal assemblage (25% of the
250 total MNI), representing the second most represented order after the Cetartiodactyla. At
251 Cooper's D, the order of carnivores is dominated by the felid family (MNI = 32%; **Fig. 2;**
252 **Table 1**), followed by the Canidae (MNI = 25%) and then the Hyaenidae (MNI = 22%).
253 Considering only medium to large-sized species (excluding all species smaller than *Lupullela*,
254 such as *Otocyon*, *Vulpes*, *Felis*, Herpestidae and Viverridae), these frequencies increase up to
255 40% MNI in felid, 31% MNI in hyenid, 27% MNI in canid and 1% MNI in mustelid. Carnivores
256 (**Table 2**) are mainly represented by adult individuals. However, we were able to identify post-
257 cranial remains of juvenile individuals in both Felidae and Hyenidae.

258 The Felidae are the most represented but also the most diverse carnivores at the Cooper's D
259 site. In terms of MNI, we observe that the *Panthera* genus (MNI = 6), especially leopard
260 (*Panthera pardus*, MNI = 2), is well-represented within the assemblage. Both the false saber-
261 toothed cat *Dinofelis* (MNI = 4) and *Megantereon* are also well represented (MNI = 4). The
262 other taxa are represented by only one individual.

263 Hyenids are very diverse at Cooper's D. Indeed, Kuhn et al. (2017) identify a minimum of
264 5 genera and 6 species. We can observe that the brown hyena (*Parahyaena brunnea*) is
265 represented by 3 individuals, including one juvenile. The extinct species *Crocota ultra* is
266 represented by 2 individuals. All the other taxa (*Chasmaporthetes*, *Crocota crocuta*, *Hyaena*,
267 *Proteles*) are represented by a single individual.

268 The Canidae are represented by 4 genera (*Lupulella*, *Lycaon*, *Vulpes* and *Otocyon*) and 4
269 species, 216 remains, representing a minimum of at least 17 individuals (Hartstone-Rose et al.,
270 2010; Fourvel et al., in prep.). At the genus level, *Lupulella* is the most represented carnivore
271 in the whole Cooper's large mammal assemblage (**Fig. 2**).

272 4.2. Estimating the post-depositional destruction

273 We applied the circumference and ends versus shafts indices (**Fig. 3**). Both show that,
274 regardless of the bovid size class, the shafts and the flakes preserving less than half of their
275 original circumference largely dominate the assemblage. This result indicates that the
276 assemblage is relatively complete and doesn't reflect analytical bias through element selection.

277 We obtain low values for the axial:appendicular ratios for each prey size classes, but not as
278 low as for Swartkrans Members 1 – 3 (**Table 3**). This result reflects the moderate role of
279 carnivore in the destruction of the bone assemblage at Cooper's D.

280 4.3. Prey skeletal part representation

281 Most of bovid skeletal elements are present at Cooper's D, even the most fragile and small
282 specimens such as ribs or patella (**Supplementary Material 1**) although they are not common
283 according to the axial:limb ratios calculated above. We observe a relatively similar distribution
284 pattern of skeletal elements between each bovid size classes (**Fig. 4**). However, through a series

285 of Kolmogorov-Smirnov tests, we find a statistically significant difference between small and
286 medium-sized bovids ($D = 0.62$, p -value = < 0.01) as well as between medium and large-sized
287 bovids ($D = 0.62$, p -value = 0.01). We do not find any significant difference of skeletal part
288 distribution between small and large-sized bovids ($D = 0.15$, p -value = 0.1). We note that
289 medium-sized bovids differ from small and large-sized bovids through the higher proportion
290 of ribs and a less proportion of some limb bone elements (i.e. radioulna, metacarpal and tibia).
291 This observation can explain the higher value of axial:limb bone ratios observed among
292 medium-sized bovids.

293 The correspondence analysis shows that all Cooper's D bovids, regardless of their size, have
294 a skeletal profile closer to the accumulations created by modern leopards than hyenas (**Fig. 5**;
295 **Supplementary Material 2**). We observe that leopard's accumulations are characterized by a
296 higher proportion of vertebrae and compact bones. In contrast, hyena's bone accumulations
297 include more long bones. The phenetic analysis performed on the row scores of the
298 correspondence analysis shows a clear distinction between a 'leopard-like' and 'hyena-like'
299 assemblage clusters. The Cooper's D material is once again closer to modern accumulations
300 made by leopards.

301 *4.4. Prey mortality profiles*

302 Each bovid size class is characterized by an 'adult-dominant' pattern of mortality profiles
303 at Cooper's D (**Fig. 6**). Small-sized bovid mortality pattern is statistically similar to large sized
304 modern felid (**Fig.6A**) and wild dog accumulations (**Fig.6B**). However, they differ from spotted
305 hyena accumulations. Large-sized bovids show a marked 'adult-dominant' mortality profile
306 which do not correspond to any of our comparative dataset, whether the assemblage is
307 accumulated by carnivore or natural flow (**Fig.6C-D**).

308 4.5. Carnivore tooth marks

309 We identified 1,081 specimens with carnivore tooth marks, which correspond to
310 approximately 5% of the total NISP (NISP = 1,081:21,193) and 11% of the post-cranial
311 assemblage (NISP = 1,081:9,534). We observed carnivore tooth marks on 318 identifiable
312 bovid bone specimens (**Table 4**). Carnivore tooth pits have been identified on small, medium
313 and large bovids (**Fig. 7; Table 4**). Among bone specimens bearing carnivore tooth pits, we
314 can observe that lower limb (28 to 45% NISP_{tooth-marked}) and axial bones (26 to 32% NISP_{tooth-}
315 _{marked}) are much more impacted, regardless of bovid size classes (**Fig. 8**).

316 Looking at more precisely the distribution of tooth marks on long bovid limb bones (**Fig. 9,**
317 **Table 4**), we observe that metapodials are much more impacted than intermediate and upper
318 limb bones. For both small and medium-sized bovids, tooth marks are more abundant on lower
319 limb bones. However, tooth marks on large-sized bovid bones are more frequently found on
320 intermediate limb bones. For the small-sized bovids, the most impacted long limb bone section
321 is the metapodial shaft, followed by the radio-ulna shaft. For the medium-sized bovids, the
322 metapodial shaft is also the more impacted by carnivore tooth marks, followed by humerus
323 shaft and both proximal radio-ulna and femur shaft. Large-sized bovids show a sparser pattern,
324 with the radio-ulna shaft, metapodials shaft and distal tibia bearing most of the tooth marks.

325 In order to test whether the distribution of tooth pits depends on the differential conservation
326 of bovid bones, we applied a Spearman's correlation test between the total NISP and the
327 number of tooth-marked elements by size class (**Supplementary Material 4**). This allowed us
328 to highlight a positive and statistically significant correlation between the skeletal
329 representation (in terms of NISP) and the number of pits per skeletal element for small ($r_s =$
330 0.62 , p -value = 0.01) and medium bovids ($r_s = 0.74$, p -value = 0.001). However, it is not the

331 case for large bovids ($r_s = 0.17$, p -value = 0.54). It therefore means that the distribution of the
332 tooth pits reflects differential bone preservation for small and medium sized bovids.

333 Overall, tooth marks are more abundant on long limb bone shafts than ends on small and
334 medium-sized bovids which differs from large-sized bovids, since we find more tooth marks
335 on their long limb bone ends than on their shafts (**Table 5**).

336 We measured a total of 64 tooth pits observed on bovid bones from Cooper's D (**Table 6**;
337 **Supplementary Material 5**). We compared our data to the measurements obtained from the
338 literature on archaeological and modern assemblages (**Fig. 10**). We note that carnivore tooth
339 pits are large, with a maximum mean width > 1.5 mm and a maximum mean length > 2 mm
340 for all bovid size classes. For all the bovid size classes, we observe that pits have dimensions
341 close to what we find in some modern spotted hyena or lion bone accumulations.

342 **5. Discussion**

343 *5.1. Which carnivore taxa are involved in the Cooper's D bone assemblage accumulation?*

344 In a previous taphonomic investigations of a large mammal sub-sample from Cooper's D,
345 de Ruiter et al. (2009) suggested that brown hyenas (*Parahyaena brunnea*) were the most
346 probable accumulated agent. This assumption was based on the high carnivores:ungulates ratio
347 (26%) and the relative high representation of small carnivores (viverrids, mustelids and canids).
348 Subsequently, Val et al. (2014) argued that, based on the attritional mortality profiles, large-
349 bodied primates were mostly occupying the cave. However, the dimensions and location of the
350 few carnivore marks observed on primate bones, as well as the presence of eight coprolites,
351 lead the authors to conclude that both leopards and hyaenas could be involved in part of the
352 accumulation and modification of the primate bone assemblages at Cooper's D.

353 By looking at some general characteristics of the Cooper's D bone assemblage (mainly
354 taxonomy and bone surface modification), it is obvious that carnivores contributed to the
355 taphonomic history of the large mammal assemblage. From a taxonomic point of view,
356 carnivores are well represented at Cooper's, and very diverse, representing the second most
357 abundant mammal order after Cetartiodactyla. The carnivore fauna is composed by both extinct
358 and extant felids, hyenids and canids.

359 At the Cooper's D site, two extinct felid species are present, *Megantereon whitei* and
360 *Dinofelis aronoki*. Several authors have hypothesized that saber-toothed cats participated in the
361 accumulation of the bones of large mammals from the Plio-Pleistocene caves of South Africa
362 (Vrba, 1975; Brain, 1981; 1993; Marean, 1989). The false saber-toothed cat *Dinofelis*
363 (estimated between 155 and 230 kg for the species *D. barlowi* and *D. piveteaui*) was probably
364 in competition with the lions (O'Regan and Reynolds, 2009). Nevertheless, it is stated that
365 *Dinofelis* species were less cursorial predators than modern lions and were probably ambush
366 specialized carnivores (Werdelin and Lewis, 2001). According to O'Regan and Reynolds
367 (2009) the most reasonable approach given the few individuals found on archaeological sites
368 would be to consider them as solitary animals. The study of their mode of locomotion, mainly
369 carried out via measurements of the bones of their limbs, indicates that the species of the genera
370 *Dinofelis* and *Megantereon* occupied the dense forests (Marean, 1989). Vrba (1974; 1975)
371 suggests that most bovids in cave sites in South Africa were too large for leopards to be the
372 source of their accumulation. This same argument has been made by Brain (1981). However,
373 current observations by de Ruiter and Berger (2000) have shown that leopards were able to
374 transport and accumulate large animals such as eland. Thus, they consider that the
375 accumulation capacity of leopards has been underestimated and that it is not necessary to
376 invoke the involvement of saber-toothed tigers in order to explain the accumulation of large
377 species in South African caves. Although this is correct, we believe here that their presence in

378 bone assemblages allows us to question their role in the large mammal bone accumulation.
379 Especially since, as suggested by Brain (1981), and on the basis of current observations of
380 leopard behavior, it is quite possible to consider that saber-toothed cats, as leopards themselves,
381 may have occupied the caves as a lair for the reproduction or feeding.

382 Hyenids are also well represented and diverse at Cooper's D. We can notice the presence of
383 the extinct hunting hyena *Chasmaporthetes*. However, the genera *Crocota* and *Parahyaenna*
384 are more abundant. Also, the only juvenile hyena individual recovered from Cooper's D is
385 attributed to the brown hyena (*P. brunnea*), based on post-cranial material. It is recognized that
386 hyenas occupy caves with their cubs, and that they frequently die in or near the den (Brain,
387 1981; Pickering, 1999; 2002; Kuhn et al., 2010). By principle of parsimony, we consider that
388 the hyenas occasionally came into the cave of Cooper's D. According to Kuhn et al. (2010),
389 spotted hyena dens are characterized by a carnivore:ungulate ratio of less than 13 %, that of
390 striped hyena over 30 %, and that of brown hyena around 20 %. At Cooper's D, the
391 carnivore:ungulate ratio is exceptionally high, up to almost 37% (Hanon et al., 2022a). In our
392 point of view, this could be a result of a taphonomical palimpsest, in which several carnivore
393 occupations blur the signal. Nevertheless, the presence of coprolites associated with juvenile
394 hyena remains strong evidence for a hyena den (Cruz-Uribe, 1991; Pickering, 2002; Kuhn et
395 al., 2010; Val et al., 2014). Furthermore, according to Brugal et al., (1997), Pleistocene hyenas
396 could accumulate larger ungulate carcasses than current felids and hyenas (size class 3 or
397 higher). It seems that felids can also leave digested bone fragments as well as bone cylinders,
398 which makes it difficult to identify with certainty a hyena den (Kuhn et al., 2010). However,
399 according to the review of all the criteria by Fourvel (2012), it appears that the presence of
400 coprolites associated with strongly digested bones is the only character really indicative of a
401 hyena den. Beyond the current hyenas, several extinct taxa such as the running and hunting
402 hyena *Chasmaporthetes* or the giant hyena *Pachycrocota* were probably able to contribute to

403 the formation of bone assemblage. Nonetheless, the characterization of their assemblage and
404 their ability to occupy a cave can only be speculative.

405 Cooper's D canids are incredibly abundant and diverse. This is particularly the case for
406 *Lupulella mesomelas*, the black-backed jackal, which are relatively abundant in the deposit and
407 for the large and robust extinct species *Lycaon sekowei* preserved at Cooper's D (Hartstone-
408 Rose et al., 2010). These canids present at Cooper's D, wild dogs (*Lycaon sekowei*) and jackals
409 (*Lupulella mesomelas*), are likely to have participated in the bone accumulation of large
410 mammals. Modern African wild dogs are gregarious hunters, with a body mass ranging from
411 20 to 25 kg (Creel and Creel, 1995). Although wild dogs' hunting ability is probably correlated
412 with pack size, a single individual appears to be able to hunt and consume prey as large as an
413 adult female kudu (Courchamp et al., 2002). According to the review by Hayward et al.,
414 (2006a), the current wild dogs have a preference spectrum for the body masses of their preys
415 of bimodal form, the first peak preferably located between 16 and 32 kg, the second between
416 120 and 140 kg. Nevertheless, Creel and Creel (1995) indicate that their major prey are
417 ungulates ranging from 15 to 200 kg. In general, the impala (*Aepyceros melampus*), the great
418 kudu (*Tragelaphus strepsiceros*), the bushbuck (*Tragelaphus scriptus*) and the Thompson's
419 gazelle (*Eudorcas thompsonii*) are the preferred prey (Hayward et al., 2006). Very little data is
420 available on the taphonomic signature of wild dog accumulations. They appear to have a
421 limited impact on the bones, with more than 50 % of the appendicular bones showing tooth
422 marks but no more than 10 marks per bones (Yravedra et al., 2014). They also produce fractures
423 and consume long limb bone shaft fragments (Fourvel et al., 2018a).

424 Thus, from a taxonomic point of view, it appears that all felids, hyenids and canids had the
425 ability to contribute to the bone accumulation of Cooper's D. Then, we have to investigate the
426 taphonomic signature of the fauna in order to identify which carnivore taxa were involved in

427 the taphonomic history of the assemblage. Previous skeletal element analysis of bovid
428 specimens indicated that Cooper's D bone assemblage is characterized by a density-mediated
429 attrition (Hanon et al., 2022). That result suggests the possible role of carnivore ravaging
430 process in the skeletal part representation and *in situ* destruction at Cooper's D (Cleghorn and
431 Marean, 2004). Our results obtained from carnivore ravaging ratio (axial:appendicular),
432 indicate a moderate carnivore ravage. Indeed, Cooper's D appears to be much less ravaged than
433 Swartkrans Members 1 – 3 (Table 3), which have been interpreted as both leopard (Member 1)
434 and leopard+hyena (Members 2 and 3) accumulations (Pickering et al., 2008). This relatively
435 moderate carnivore ravage observed at Cooper's D is much consistent with both leopard and
436 canid activities rather than hyenas. Thus, Cooper's D bovid bone assemblage is characterized
437 by bone-density mediated attrition, regardless of the bovid size class (Hanon et al., 2022), but
438 also by a relatively moderate carnivore ravage (axial:appendicular ratio). These observations
439 lead us to favor the hypothesis of a post-depositional destruction of bovid skeletal elements
440 rather than carnivore activity.

441 Through the study of the completeness of the assemblage, we observed a predominance of
442 long bone shaft fragments preserving less than half of their original circumference. This
443 indicates that our assemblage is relatively unbiased by selective retention (Marean et al., 2004;
444 Domínguez-Rodrigo et al., 2007). However, we noted that there is a fewer proportion of long
445 bone shaft (52%) identified for large-sized mammals compared to ends (48%). Moreover, large
446 animals are characterized by a good representation of complete circumference long bone
447 fragments (31%). These results indicate that large mammals tend to be better preserved at
448 Cooper's D which is consistent with our previous taphonomic study which pointed out a bone
449 density-mediated attrition (Hanon et al., 2022). Indeed, it seems that even if our assemblage
450 shows a good level of completeness, it has been largely impacted by post-depositional
451 processes. Our multiple taphonomic analysis of the prey skeletal part representation points out

452 similarity in Cooper's D bone preservation and modern leopard accumulations, regardless of
453 bovid size class. However, three cautionary remarks have to be made at this point. First, the
454 absence of comparative data on the skeletal part composition of an assemblage made by
455 African canids, such as wild dogs. Second, all the modern comparative data are setting in open
456 sites environments comparable with East African sites (Domínguez-Rodrigo and Pickering,
457 2010). Third, as pointed out before, it is highly probable that our bovid skeletal part
458 representation is the result of post-depositional destruction rather than carnivore activity.
459 Therefore, skeletal part representation cannot be used alone as a good indicator of the original
460 accumulator agent.

461 Regarding mortality profiles, Hanon (2019) already show the predominance of adult
462 individuals among the bovid assemblage at Cooper's D. Our results indicate a similarity in the
463 mortality distribution of small-sized bovids (size class 1 and 2) between Cooper's D and large
464 felid accumulations as well as wild dog accumulated assemblage. In contrary, mortality pattern
465 of large-sized bovids from Cooper's D (size class 3 and larger) differs from modern carnivore
466 and natural accumulations. The 'prime adult predominance' pattern is frequently observed in
467 archaeological contexts (Bunn and Gurtov, 2014) where it is often associated with
468 anthropogenic activity, especially when the proportion of adults exceeds 70% (Stiner, 1990;
469 Bunn and Gurtov, 2014). However, adult individuals also exceed 70% of the MNI in modern
470 leopard accumulation (Bunn and Pickering, 2010a). They also dominate in other South African
471 archaeological assemblages (**Supplementary Material 3**; Vrba, 1974; Adams, 2010; Fourvel
472 et al., 2018b), whether for small (Kromdraai Mb2 = 43%; Gondolin GD2 = 48%; Sterkfontein
473 Main Quarry = 50%; Swartkrans Mb1 = 57%; Swartkrans Mb2 = 49%) or large-sized bovids
474 (Kromdraai Mb2 = 64%; Sterkfontein Main Quarry = 52%; Swartkrans Mb1 = 60%). Ambush
475 or hunting predators (lion, leopard, probably *Megantereon*, *Dinofelis* and *Chasmaporthetes* for
476 the largest preys) also tend to create profiles similar to the structures of living populations, but

477 with a greater representation of adult individuals (Stiner, 1990). The bone density mediated
478 attrition observed at Cooper's D, associated with post-depositional bone surface modifications
479 (e.g. manganese coating, decalcification, abrasion and corrosion), indicate that most of the
480 fragile juvenile bones could have been discarded by post-depositional processes. It is also
481 highly probable that mortality profiles from other South African cave sites have been driven
482 by post-depositional processes rather than carnivore and hominin activities.

483 From the observation of bone surface modifications, it is convincing that carnivores
484 contributed to the accumulation and history of bone assemblage in large mammals at the
485 Cooper's D site. Indeed, more than 5% of the total NISP bear marks attributable to carnivores,
486 and up to 11% of the NISP if we exclude dental material. It is highly probable that the small
487 percentage of carnivore marks is the result of the important presence of manganese coating on
488 the bone surface (Hanon et al., 2022a), which is directly correlated to post-depositional
489 processes and altered the reading of most of the cortical surfaces. Our reanalysis of the
490 assemblage indicates that among specimens bearing carnivore tooth pits, we observed that most
491 of them are attributed to axial (28 to 45% $NISP_{\text{tooth-marked}}$) or lower limb bones (> 26 to 32%
492 $NISP_{\text{tooth-marked}}$), regardless of the bovid size class. Concerning long limb bones, tooth marks
493 (scores + pits) are found more frequently on metapodials shafts as well as on radio-ulna shafts.
494 Moreover, among limb bones, tooth marks are more abundant on shafts, except for large-sized
495 bovids. On one hand, the presence of tooth marks on both axial bones and metapodials is a
496 characteristic of hyenid scavenging damage (Pobiner and Blumenschine, 2003; Domínguez-
497 Rodrigo and Pickering, 2010). On the other hand, the scarcity of tooth marks and their presence
498 on intermediate limb bone shaft fragments can be attributed to felid type damage. However,
499 we also show that the distribution of tooth marks along bone elements reflects the differential
500 preservation. Then, it is difficult to make assumptions based only on tooth mark distribution.

501 Regarding to tooth pit dimensions measured on the small (size class I) and large (size class
502 III and IV) bovids at Cooper's D, although they fall within the range of variation of many
503 modern carnivore taxa (lion, leopard, cheetah, spotted hyena, jackals). According to Selvaggio
504 and Wilder (2001), a greater degree of variation than the overall dimensions of the cupules of
505 modern carnivores would indicate the action of several taxa. However, Domínguez-Rodrigo
506 and Piqueras (2003) demonstrated that there is no direct link between the strong variation in
507 the length:width ratio of the pits and the number of taxa involved in the accumulation of a bone
508 assemblage. According to Andrés et al. (2012), this variation could be explained by the small
509 sample size. We can however observe that the leopard (average ratio = 1.83, $\sigma = 0.73$), which
510 presents an average ratio close to that of the large sized mammals from Cooper's D (average
511 ratio = 1.65, $\sigma = 0.77$), also has a very strong variation like the *Dinofelis* genus (mean ratio =
512 2.84, $\sigma = 0.7$). However, the latter has a much higher average ratio than the leopard and the pits
513 observed on the surface of large sized mammal bones from Cooper's D. Although the leopard
514 sometimes hunts and consumes large bovids (kudu, eland or waterbuck), most of its diet
515 consists of small to medium prey (Pienaar, 1969; de Ruiter and Berger, 2000). According to
516 data collected by Brain (1981), size II antelopes represent between 44.8 to 83.1 % of the
517 leopard's diet, against 8.6 to 26.2% for those of size III. The carnivore pits observed on the
518 surface of the bones of medium-sized mammals (size class II) of Cooper's D are on average
519 smaller dimensions than those observed on small and large mammals. It should be noted that
520 the results obtained for medium-sized mammals are close to those obtained for medium-sized
521 mammals observed in Swartkrans member 3. Pickering et al (2004c) consider that they have
522 were mainly accumulated by leopards, unlike size III mammals, which have been accumulated
523 by several different taxa of carnivores (large canids, spotted hyena and lion).

524 Despite the difficulty of the identification of carnivore taxa using taphonomic modifications
525 (Selvaggio and Wilder, 2001), we attempt to discuss which carnivore taxa could be responsible

526 for the accumulation of ungulate at Cooper's D. Hyenas activity, and particularly brown hyena
527 (*Parahyaena brunnea*), is supported by the presence of juvenile individuals, bone surface
528 modifications, tooth pits dimension, the presence of some bone cylinder and by the coprolites
529 (Val et al., 2014). However, based on the current evidence, we can argue that large felids such
530 as leopard and extinct large felids, also contributed to the accumulation, at least for a part of
531 the ungulate remains, if is not for the main part. This is notably corroborated by the abundance
532 of felid remains (de Ruiter et al., 2009; O'Regan and Steininger, 2017), the skeletal part
533 representation, the bovid mortality profiles, bone surface modifications and the variation of
534 tooth pit dimensions.

535 It is important to note that the involvement of canid taxa cannot also be excluded for now.
536 In particular, a diet overlap has been demonstrated between black-backed jackals (*Lupullela*
537 *mesomelas*) and brown hyenas (*Parahyaena brunnea*) as they usually are in competition for
538 carcass scavenging (Merwe et al., 2009; Yarnell et al., 2013). Because of the important
539 presence of *Lupullela*, and canids in general, at Cooper's D, it is therefore expected that they
540 contributed to the accumulation or the modification of the bone assemblage. Moreover, based
541 on the faunal list and taphonomic alterations, Campmas et al. (2017) and Campmas and
542 Daujeard (2020) identified several north African Pleistocene sites as the result of large canid
543 activity. For the future, more attention should be given to the Canid assemblage in order to
544 identify if they play a role into the accumulation of South African fossil cave sites.

545 In summary, we argue that large felids (specifically leopard) should be regard as the main
546 accumulating agent of the bovid bone assemblage at Cooper's D. Hyenas (spotted and brown
547 hyenas), and probably canids, also contributed significantly to the constitution of the
548 assemblage as secondary agent, mostly through scavenging.

549

550 *5.2.Hominin and carnivore contributions at Cooper's D*

551 After Sterkfontein (Member 5 East Oldowan, Name Chamber; Pickering, 1999; Val and
552 Stratford, 2015) and Swartkrans (Members 1 – 3; Pickering et al., 2008), Cooper's D represents
553 only the third Early Pleistocene site in South Africa that provide hominin remains (NISP = 7;
554 de Ruiter et al., 2009) associated with stone tool industry (n = 49; Sutton et al., 2017) and
555 butchery marks (NISP = 31; Hanon, 2019). It makes this site a unique case for studying
556 hominin and carnivore respective contribution to the bone assemblage.

557 In this study, we noticed the absence of hominin and carnivore marks co-occurrence on large
558 mammal bones at Cooper's D. Moreover, we observe the presence of tooth marks preferentially
559 on axial skeleton and on lower limb bones (attributed to hyenid-like scavenging damage) and
560 less importantly on intermediate and upper limb bones (attributed to felid-like kill damage).
561 Whatever from who hyenas obtain their carcasses – natural death, felids or hominins kills – it
562 appears that carnivores did have early access to bovid carcasses at some point. Nevertheless,
563 Hanon (2019) describe the presence of hominin butchery marks (cut and percussion) on
564 ungulate bones from all size classes and note the absence of carnivore and hominin marks co-
565 occurrence on bone surfaces. By crossing these results, we can argue that Cooper's D large
566 mammal accumulation is the result of a relatively independent taphonomic signatures of both
567 carnivores and hominins. This hypothesis of distinct events of butchery and carnivore activity
568 has been previously proposed in other African Plio-Pleistocene sites, such as Swartkrans
569 Members 1 – 3 (Pickering et al., 2008), FLK “Zinj”, Olduvai (Domínguez-Rodrigo, Barba and
570 Egeland, 2007) or at the ‘Grotte des Rhinocéros’, Morocco (Daujeard et al., 2020).

571 We agree with Egeland et al. (2004) that this observation does not necessarily imply that the
572 hominin-carnivore competition was inexistent. Indeed, these authors observed an
573 independently derived hominin and carnivore component of bone accumulation at several Early

574 Pleistocene sites in Africa, especially at Swartkrans Member 3. The capacity of hominins to
575 avoid intense competition and to process a complete exploitation of ungulate carcasses can then
576 be explained by different non-exclusive hypotheses. (1) Hominins could have occupied
577 environments setting in a low competition context such as tree-covered woodland-like habitats.
578 Indeed, experimental studies point out that long limb bone remains can remain undisturbed for
579 several days (up to 16 days) in a riverine woodland (Blumenschine, 1988). Moreover, complete
580 limb bones are more frequently encountered in low competition areas (Blumenschine, 1989).
581 In this case, it could be easy for hominins to intensively exploit a carcass without being
582 preoccupied by the presence of scavengers. (2) Hominins could have developed specific
583 foraging strategies in order to reduce competition, such as body part transport in hiding places
584 (Blumenschine, 1991), refuge or “central places” model (Isaac, 1983). (3) The hominin toolkit
585 or technological advanced could have played a role in their ability to avoid carnivores. For
586 example, the use and domestication of fire could provide a “shift in the balance of power”,
587 allowing an optimal exploitation of the environments by hominins without the carnivore
588 competition pressure (Pickering et al., 2008). As indicated by Egeland et al. (2004), the
589 geological context of South African caves limited our ability to conclude about the origin of
590 independent hominins and carnivores taphonomic signatures. As in Swartkrans Member 3, the
591 Cooper’s D faunal assemblage derives from decalcified sediments which implies a secondarily
592 deposit of the material coming from the calcified bone breccia.

593 Hanon et al. (2022b) has showed through the analysis of bovid assemblage from Cooper’s
594 D that the environment surrounding the cave was probably a composite of grassland and sparse
595 covered habitat close to a water source which is consistent with the first scenario. Moreover,
596 the karstic environment of the Sterkfontein Valley provides an important source of hiding
597 places for food storage making the second hypothesis plausible.

598 In South Africa, evidence for a control of fire by hominins appears around 1 Ma at
599 Swartkrans Member 3 (Brain and Sillen, 1988; Pickering, 2012) and Wonderwerk (Berna et
600 al., 2012). It has been proposed that “the mastery of fire provided a “shift in the balance of
601 power”, allowing hominids to carry out activities in the cave for the first time unmolested by
602 predators”, and that the shift occurred at the Swartkrans Member 3 (Pickering et al., 2008).
603 However, based on the study of sub-samples from Swartkrans Members 1-3, Pickering et al.
604 (2008) has showed that there are no significant differences between large mammal exploitation
605 by hominins between the three deposits. Then, for these authors, the control of fire did not seem
606 to provide an important increase of success in carcass foraging. Moreover, the toolkit of
607 hominins at Cooper’s D is mainly composed by quartzite flakes and cores (Sutton et al., 2017),
608 which are unlikely to be used in the primary acquisition of ungulate carcasses, although they
609 can be used to cut pieces of carcasses for transport. Keeping a parsimonious approach of these
610 observations, we argue that the two first hypotheses, which are the low competition
611 environment and the adaptation of hominin foraging strategies in order to avoid competition,
612 are the most probable explanation for the independent taphonomic signals of both hominins
613 and carnivores observed at Cooper’s D.

614 **6. Conclusion**

615 In this paper, we provided the first taphonomic investigation of carnivore and hominin
616 contributions at the Early Pleistocene site of Cooper’s D. The aim was to explore the potential
617 role of carnivores in the origin of large mammal bone accumulation from Cooper’s D and to
618 characterize their relationship with hominins. Previous taphonomic studies permit to identified
619 mainly hyena, and possibly leopard, as the main accumulator agents of the large mammal
620 assemblage of Cooper’s D (Val et al., 2014; Hanon, 2019). Our results presented here permit
621 to better understand the taphonomic history of this assemblage. Based on taxonomic

622 composition, skeletal part representation and bone surface modifications, it appears that
623 leopards, or large felids, are the main accumulator agents of all-sized bovids. However, careful
624 investigation of the faunal list, the presence of coprolites and bone surface modifications also
625 permit to show the independent impact of both large canids and hyenids.

626 Compared with other Plio-Pleistocene archaeological assemblages, we argue that carnivores
627 and hominins did not interact directly at Cooper's D site but mostly visited the cave
628 alternatively. Thus, our work has demonstrated the role of three major taphonomic agents in
629 the bone accumulation of Cooper's D. The first is the leopard, or by extension the big cats.
630 Indeed, we cannot rule out with certainty the role that saber-toothed tigers may have played.
631 The seconds are the hyenas, probably the brown hyena (*Parahyaena brunnea*), and canids,
632 which accumulated and scavenged some carcasses and even briefly occupied the cave. Finally,
633 hominins constitute the third agent, but the time of access to the carcass remains uncertain for
634 now (Hanon et al., 2021). The large mammal assemblage of Cooper's D represents a
635 taphonomic palimpsest corresponding to a mixed accumulation by carnivores and hominins.

636 Then, we observe that both carnivore and hominins had a primary access to large mammal
637 carcasses. This interpretation of our results implies that carnivore and hominins were not
638 interdependent for each other. In other words, competition for food supply was not important
639 enough to avoid primary access. Our results are consistent with previous conclusions drawn
640 about hominin subsistence behaviours observed at other Plio-Pleistocene African deposits –
641 Swartkrans Members 1 – 3, South Africa (Pickering et al., 2008); FLK “Zinj”, Olduvai,
642 Tanzania (Domínguez-Rodrigo, Barba and Egeland, 2007); BK4b, Olduvai, Tanzania
643 (Domínguez-Rodrigo et al., 2014); FwJj14A, FwJj14B and GaJi14, Koobi Fora, Kenya
644 (Pobiner et al., 2008); Konso, Ethiopia (Echassoux, 2012); Kanjera, Kenya (Ferraro et al.,
645 2013); El-Kherba, Ain Hanech, Algeria (Sahnouni et al., 2013); Ain Boucherit, Algeria

646 (Sahnouni et al., 2018); ‘Grotte des Rhinocéros’, Morocco (Daujeard et al., 2020) – namely
647 that they already had access to a variety of animal carcasses. **Declaration of competing**
648 **interest**

649 The authors have no competing interests to declare.

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1017 **Table 1.** List of carnivore taxa identified at Cooper's D (after Hanon, 2019).

1018 **Table 2.** Large carnivore mortality profiles from Cooper's D.

1019 **Table 3.** Axial:Appendicular ratio values (in MNE) obtained for each bovid size class at
1020 Cooper's D. Comparative data for Swartkrans from Pickering et al., (2008).

1021 **Table 4.** Distribution of carnivore tooth marks (punctures, pits, furrowings and scorings)
1022 according to each bovid size class. Data represent NISP with at least one carnivore
1023 modification. Numbers in brackets represent percentage of the total NISP modified by
1024 carnivores.

1025 **Table 5.** Distribution of carnivore tooth marks (punctures, pits, furrowings and scorings)
1026 according to their location on each bovid limb bone part. Data represent NISP with at least one
1027 carnivore modification. Numbers in brackets represent percentage of the total NISP modified
1028 by carnivores.

1029 **Table 6.** Summary statistics of tooth pits dimensions according to the ungulate size classes
1030 from Cooper's D.

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1032 **Figure 1.** A: Location of Cooper's Cave and other Early Pleistocene main sites in South
1033 Africa. B: schematic plan of the Cooper's D deposit.

1034 **Figure 2.** Representation of the different large carnivore families and genera at Cooper's D.
1035 Viverridae, Herpestidae and Mustelidae are excluded here. NISP = 350, MNI = 52.

1036 **Figure 3.** Measure of the completeness of the Cooper's bone assemblage. (A) Percentage of
1037 circumference types (Bunns, 1983) on limb bone fragment for each bovid size class. (1) less

1038 than half circumference preserved; (2) more than half circumference preserved; (3) complete
1039 circumference preserved. (B) Percentage of shaft and end limb bone fragments for each bovid
1040 size class.

1041 **Figure 4.** Skeletal part representation (MNE) according to bovid size class at Cooper's D.
1042 Compact bones include all the foot elements (phalanges, carpals and tarsals). Based on data
1043 provided in the **Supplementary Material 1**.

1044 **Figure 5.** Correspondence analysis conducted on bovid remains (MNE) from Cooper's D
1045 compared with assemblages accumulated by modern leopard and spotted hyena. Hierarchical
1046 clustering analysis performed on the row scores of the correspondence analysis. Cooper's D
1047 bovid assemblages are in bold. *Compact bones include all the foot elements (phalanges,
1048 carpals and tarsals). Based on data provided in the **Supplementary Material 2**.

1049 **Figure 6.** Ternary graphs of mortality profiles for each bovid size class at Cooper's D. (A)
1050 Small-sized bovids from Cooper's D compared with modern assemblages accumulated by large
1051 felid. (B) Small-sized bovids from Cooper's D compared with modern assemblages
1052 accumulated by wild dog (*L. pictus*) and spotted hyena (*C. crocuta*). (C) Large-sized bovids
1053 from Cooper's D compared with modern assemblages accumulated by lion (*P. leo*) and spotted
1054 hyena (*C. crocuta*). (D) Large-sized bovids from Cooper's D compared with a living population
1055 and a modern assemblage created by natural flow. Ellipses represent the 95% confidence
1056 interval. Comparative data compiled from Bunn and Pickering (2010a). Based on the data
1057 provided in the **Supplementary Material 3**.

1058 **Figure 7.** Bone surface modifications attributed to carnivore activity observed on large
1059 mammal bones from Cooper's D. A: Puncture observed on an indeterminate juvenile pelvis
1060 fragment (CD.10117). B: Puncture observed on an indeterminate fragment (CD.198). C:

1061 Crushed pit observed on a thoracic vertebra of a medium-sized bovid (CD.6903). D: Crushed
1062 pit on a left scapula proximal fragment of a medium-sized bovid (CD.8188). E: Perforation on
1063 a complete proximal phalanx of a small-sized bovid (CD.3336). F: Perforation observed on an
1064 indeterminate fragment (CD.330). Photos and measurements taken with a Dino-Lite
1065 (AD7013MTL) and the DinoCapture 2.0 software.

1066 **Figure 8.** General distribution of carnivore tooth pits on bovid axial and appendicular
1067 anatomical region (NISP) according to bovid size classes at Cooper's D. NISP = 256.

1068 **Figure 9.** Distribution of carnivore tooth marks on bovid long limb bones according to size
1069 classes from Cooper's D. Percentage of tooth marks (furrows and pits) are calculated from the
1070 total of carnivore impacted long bone specimens (NISP). Data from **Table 5**.

1071 **Figure 10.** Carnivore tooth pit length:width ratios of modern carnivore on cortical bone
1072 compared to those observed at Cooper's D. Comparison data from (Selvaggio & Wilder, 2001;
1073 Domínguez-Rodrigo and Piqueras, 2003; Pickering et al., 2004a).

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Table 1

Family	Genus	species	NISP	MNI	Reference	
Canidae	<i>Lupulella</i>	<i>L. mesomelas</i>	46	4	This study	
		<i>L. cf. mesomelas</i>	16	1	This study	
		<i>Lupulella</i> sp.	70	3	This study	
	<i>Lycaon</i>	<i>L. sekowei</i>	2	1	Hartstone-Rose et al. (2010)	
		<i>L. cf. sekowei</i>	1	1	This study	
		<i>Lycaon</i> sp.	11	3	This study	
		cf. <i>Lycaon</i>	6	-	This study	
	<i>Vulpes</i>	<i>V. chama</i>	3	1	This study	
		cf. <i>Vulpes</i>	1	1	This study	
	<i>Otocyon</i>	<i>Otocyon megalotis</i>	1	1	This study	
		cf. <i>Otocyon</i>	1	1	This study	
	<i>Vulpes / Otocyon</i>	Indeterminate	2	-	This study	
	Indeterminate	Indeterminate	56	-		
	Felidae	<i>Dinofelis</i>	<i>D. cf. aronoki</i>	11	2	O'Regan and Steininger (2017)
			cf. <i>D. aronoki</i>	24	2	O'Regan and Steininger (2017); this study
<i>Megantereon</i>		<i>M. whitei</i>	7	3	Hartstone-Rose et al. (2007)	
		cf. <i>M. whitei</i>	4	1	O'Regan and Steininger (2017)	
<i>Panthera</i>		<i>P. leo</i>	4	1	O'Regan and Steininger (2017)	
		<i>P. cf. leo</i>	1	1	O'Regan and Steininger (2017)	
		<i>P. pardus</i>	15	2	O'Regan and Steininger (2017)	
		<i>P. cf. pardus</i>	7	1	O'Regan and Steininger (2017)	
		<i>Panthera</i> sp.	2	1	O'Regan and Steininger (2017)	
<i>Caracal</i>		<i>C. caracal</i>	3	2	O'Regan and Steininger (2017)	
		<i>Caracal</i> sp.	5	1	O'Regan and Steininger (2017)	
<i>Felis</i>		<i>F. lybica</i>	6	2	O'Regan and Steininger (2017)	
		<i>Felis</i> sp.	2	1	O'Regan and Steininger (2017)	
<i>Acynonix</i>		<i>A. jubatus</i>	3	1	O'Regan and Steininger (2017)	
		cf. <i>Acynonix</i>	1	1	This study	
Machairodontinea		Indeterminate	10	-	O'Regan and Steininger (2017); this study	
Indeterminate		Indeterminate	151	-		
Hyaenidae		<i>Chasmaporthetes</i>	<i>C. nitidula</i>	1	1	Kuhn et al. (2016)
			<i>Chasmaporthetes</i> sp.	2	1	Kuhn et al. (2016)
	<i>Crocuta</i>		18	1	Kuhn et al. (2016)	
	<i>Crocuta</i>	<i>C. ultra</i>	4	2	Kuhn et al. (2016)	
		<i>Crocuta</i> sp.	14	2	Kuhn et al. (2016)	
		<i>Parahyaena</i>	37	3	Kuhn et al. (2016)	
	<i>Parahyaena</i>	<i>P. brunnea</i>	15	2	Kuhn et al. (2016)	
		<i>P. cf. brunnea</i>	15	2	Kuhn et al. (2016)	
	<i>Hyaena</i>	<i>Hyaena</i> sp.	4	1	Kuhn et al. (2016)	
	<i>Proteles</i>	<i>P. cristatus</i>	3	1	This study	
<i>Proteles</i> sp.		7	1	Kuhn et al. (2016)		
Indeterminate	Indeterminate	50	-			
Herpestidae	<i>Herpestes</i>	<i>H. ichneumon</i>	5	5	Cohen et al. (2019)	
	<i>Ichneumia</i>	cf. <i>Ichneumia</i> sp.	1	1	Cohen et al. (2019)	
	<i>Atilax</i>	<i>A. paludinosus</i>	3	1	Cohen et al. (2019)	
	<i>Mungos</i>	<i>M. aff. Dietrichi</i>	1	1	Cohen et al. (2019)	
		<i>Mungos</i> sp.	3	1	Cohen et al. (2019)	
	<i>Galerella</i>	? <i>Galerella</i> sp.	3	2	Cohen et al. (2019)	
	Indeterminate	Large	3	-	Cohen et al. (2019)	
		Small	1	-	Cohen et al. (2019)	

		Indeterminate	9	-	Cohen et al. (2019)
Viverridae	<i>Propoecilogale</i>	<i>P. boliti</i>	1	1	O'Regan et al. (2013)
	<i>Civettictis</i>	<i>C. cf. civetta</i>	2	1	O'Regan et al. (2013)
		cf. <i>Civettictis</i> sp.	2	-	O'Regan et al. (2013)
Mustelidae	<i>Mellivora</i>	<i>M. capensis</i>	1	1	O'Regan et al. (2013)
Indeterminate	Indeterminate	Indeterminate	132		
Total			794	68	

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1079 **Table 2.**

Family	MNI	Juveniles	Adults	Olds
Canidae	17	2	15	0 ¹⁰⁸⁰
Felidae	22	5	17	0
Hyaenidae	15	1	13	1 ¹⁰⁸¹

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1084 **Table 3.**

Ratio	Cooper's D small-sized bovids	Cooper's D medium-sized bovids	Cooper's D large-sized bovids	Swartkrans Member 1	Swartkrans Member 2	Swartkrans Member 3
Axial	90	334	108	22	218	39
Appendicular	97	171	70	134	854	314
Axial:Appendicular	0.93	1.95	1.54	0.2	0.3	0.1

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1093 **Table 4.**

Skeletal element	Long bone section	Small-sized bovids	Medium-sized bovids	Large-sized bovids
Skull		0 (0)	1 (1)	0 (0)
Vertebrae		1 (2)	10 (6)	5 (5)
Ribs		6 (9)	9 (6)	8 (9)
Pelvis		2 (3)	6 (4)	6 (7)
Scapula		3 (5)	5 (3)	2 (2)
Humerus	Prox. Epi	1 (2)	6 (4)	4 (4)
	Shaft	2 (3)	12 (7)	3 (3)
	Dist. Epi	2 (3)	2 (1)	2 (2)
Radio-ulna	Prox. Epi	4 (6)	11 (7)	4 (4)
	Shaft	9 (14)	8 (5)	11 (12)
	Dist. Epi	2 (3)	4 (2)	3 (3)
Femur	Prox. Epi	3 (5)	7 (4)	2 (2)
	Shaft	1 (2)	11 (7)	2 (2)
	Dist. Epi	1 (2)	1 (1)	6 (7)
Tibia	Prox. Epi	1 (2)	0 (0)	3 (3)
	Shaft	1 (2)	8 (5)	2 (2)
	Dist. Epi	1 (2)	1 (1)	8 (9)
Metapodials	Prox. Epi	1 (2)	7 (4)	5 (5)
	Shaft	18 (28)	45 (28)	10 (11)
	Dist. Epi	6 (9)	8 (5)	5 (5)
Total		65 (100)	162 (100)	91 (100)

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1095 **Table 5.**

Part	Small-sized bovids	Medium-sized bovids	Large-sized bovids
Shafts	31 (58)	84 (64)	28 (40) 1096
Ends	22 (42)	47 (36)	42 (60) 1097
Total	53 (100)	131 (100)	70 (100) 1098

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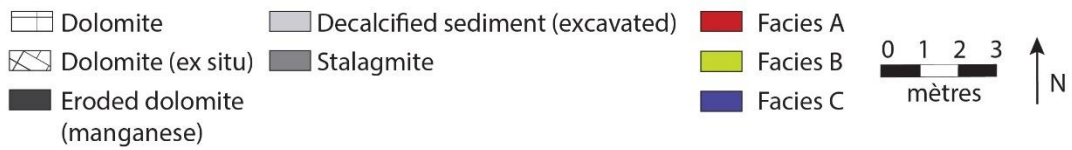
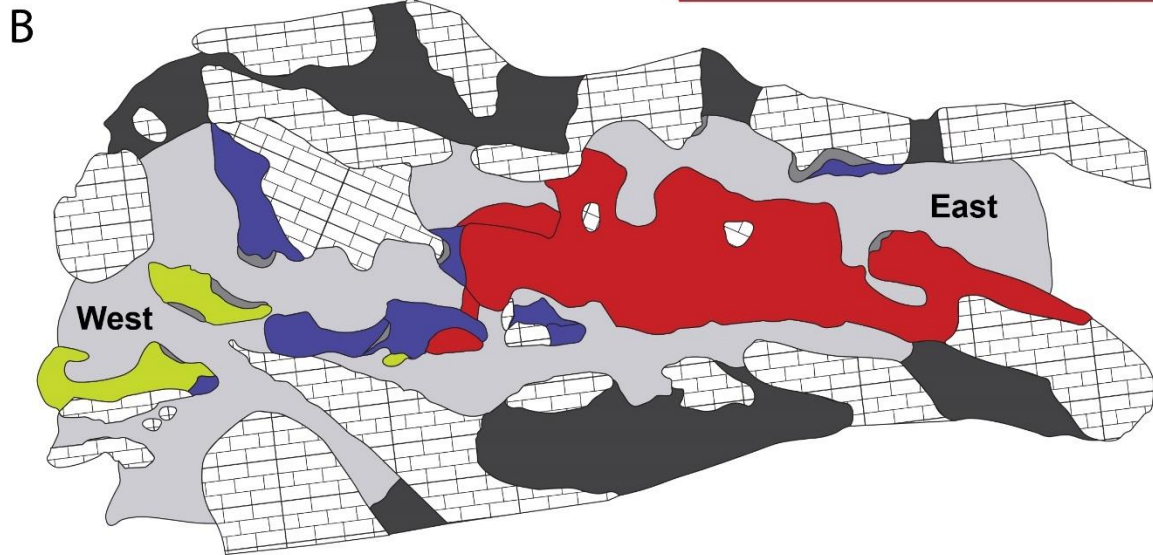
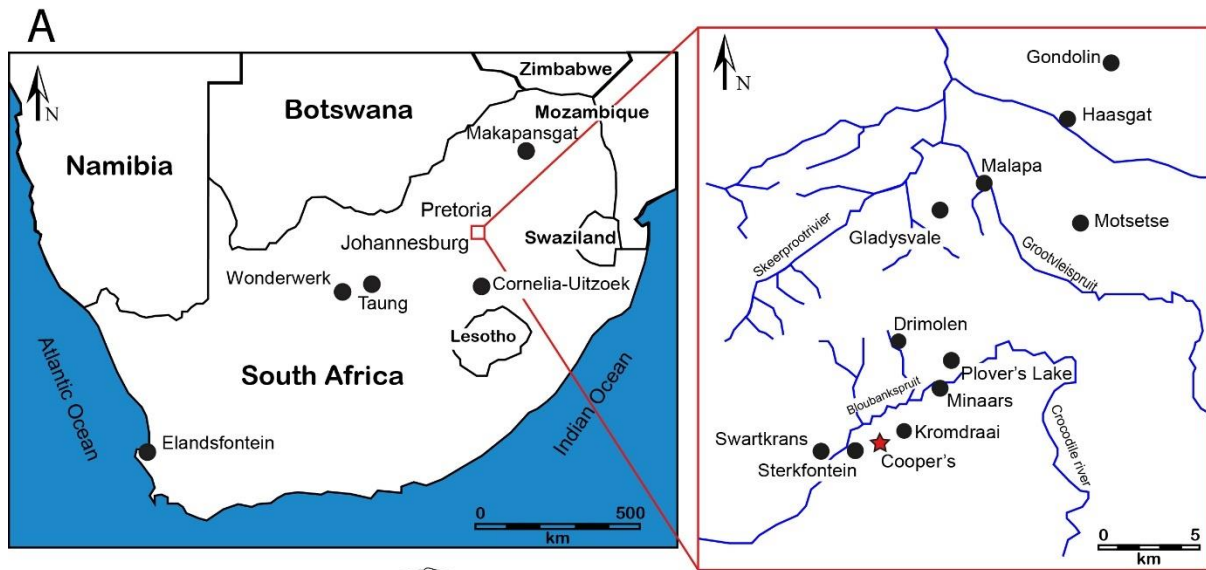
Table 6.

Sample	<i>n</i>	Mean ratio	s.d.	Mean length	s.d.	Mean width	s.d.
Small-sized bovids	23	1.66	0.30	2.64	1.17	1.62	0.73
Medium-sized bovids	23	1.41	0.40	3.35	1.83	2.44	1.40
Large-sized bovids	18	1.65	0.77	4.10	2.58	2.43	1.05

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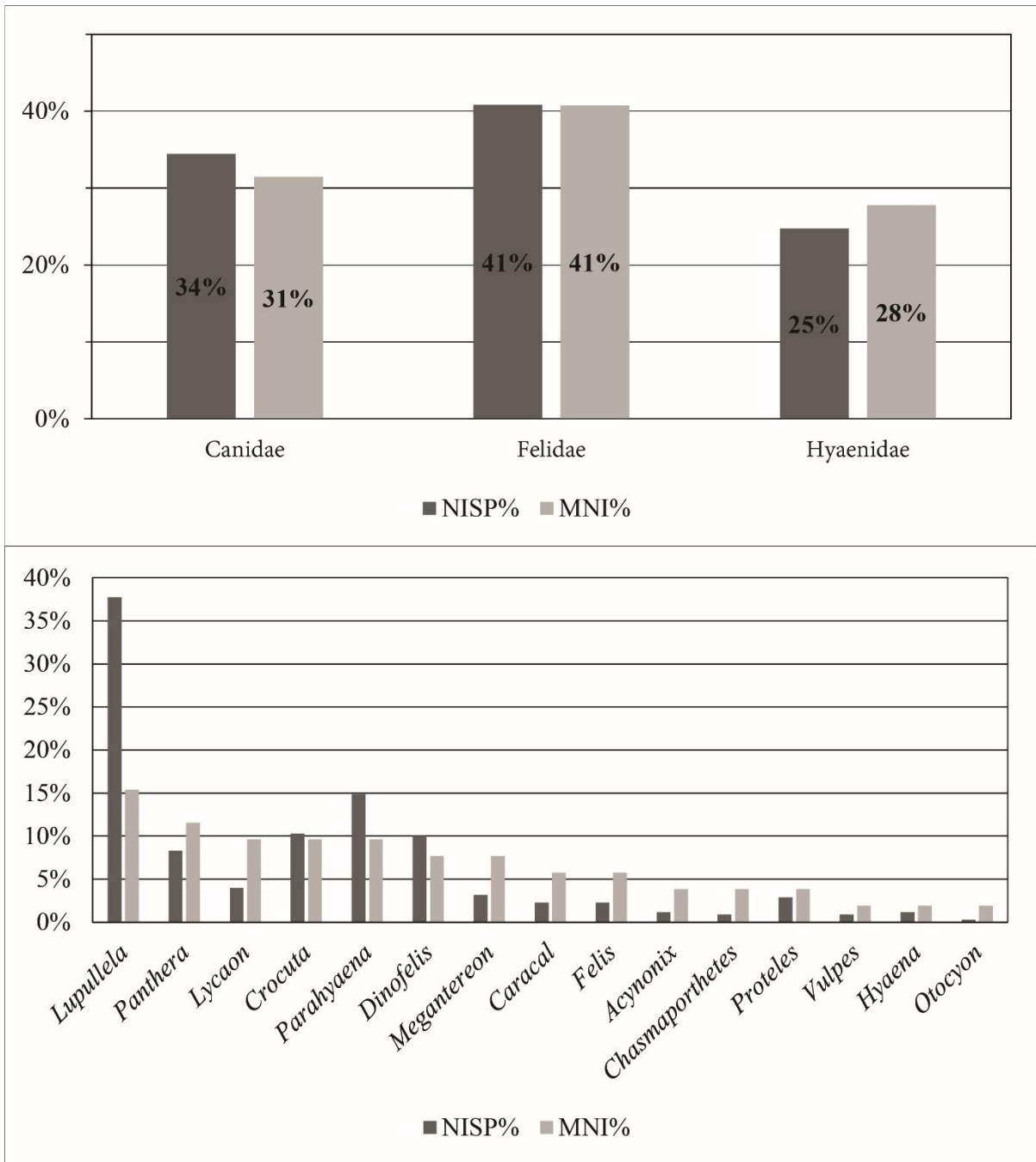
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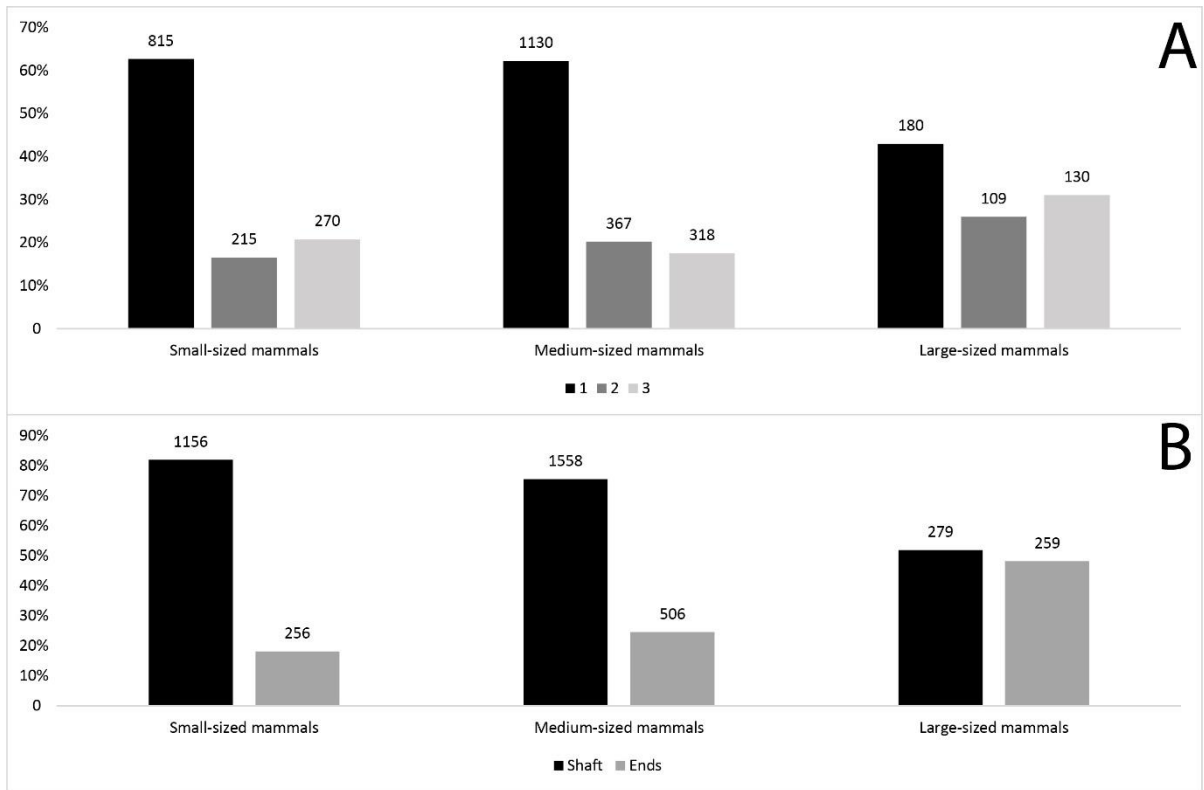
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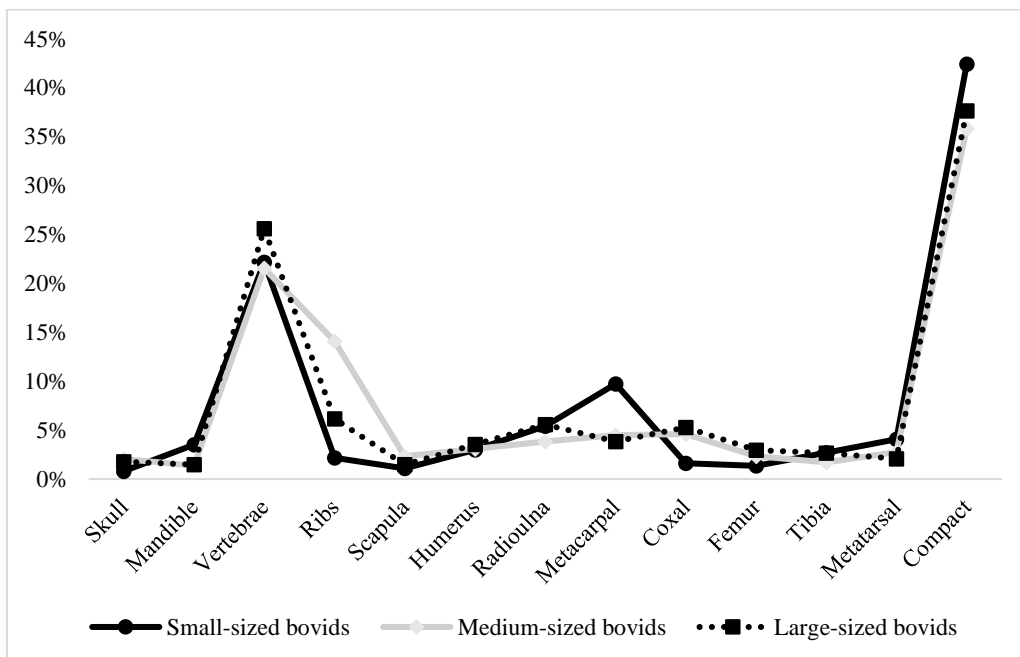
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1122 Figure 3.



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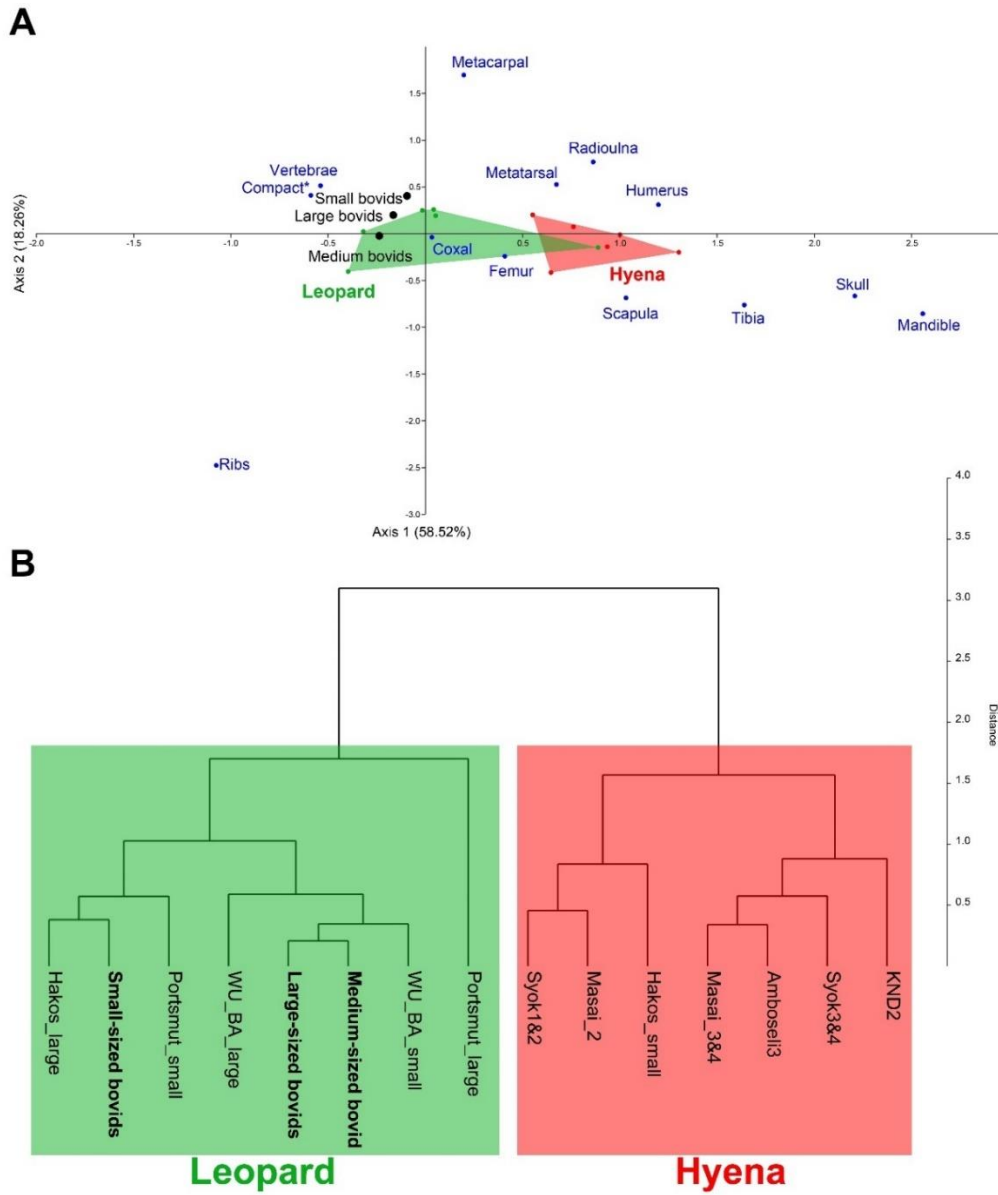
1124 Figure 4.



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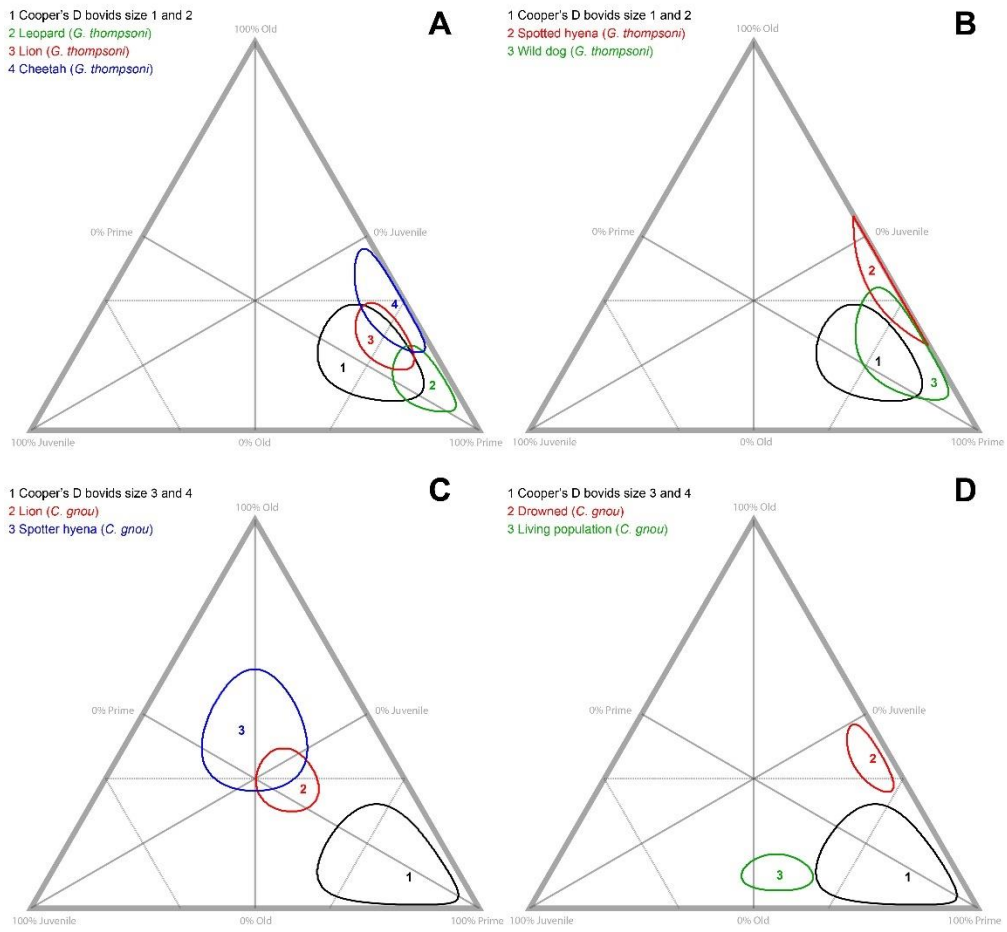
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1133 Figure 6.



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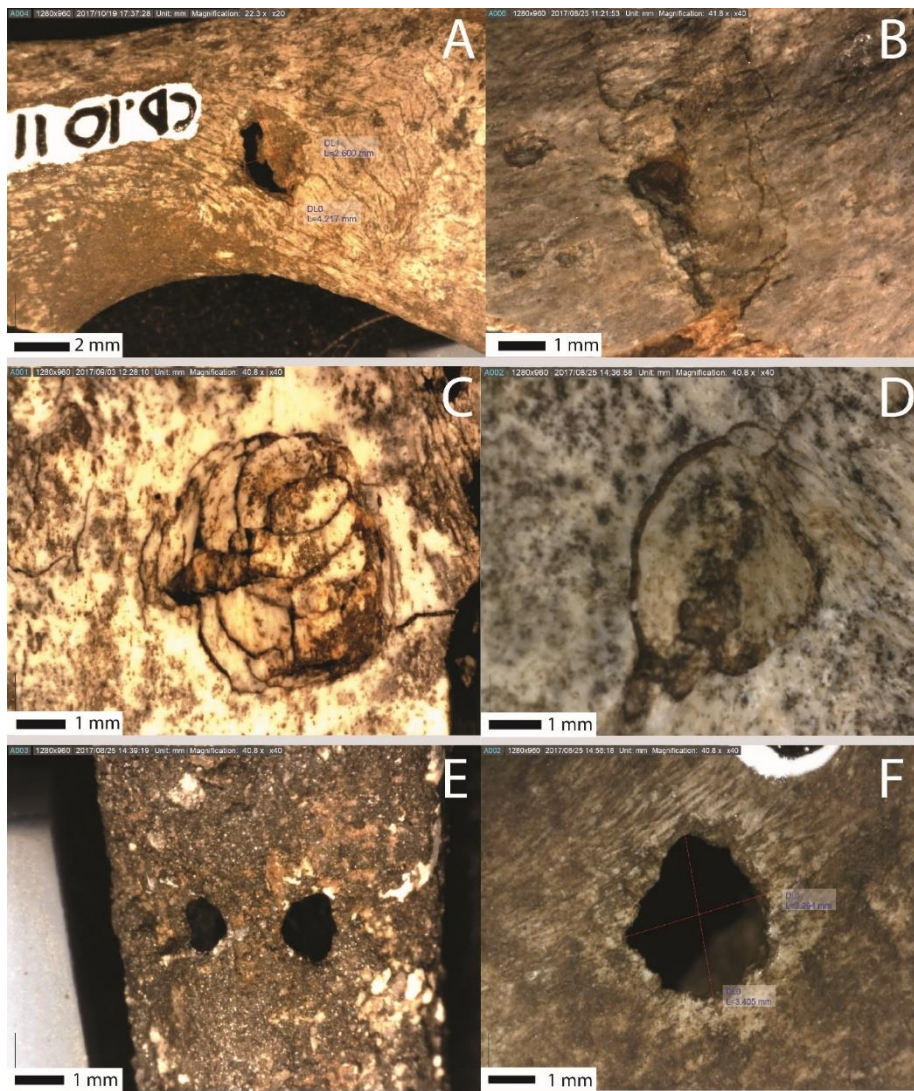
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1154 Figure 7.



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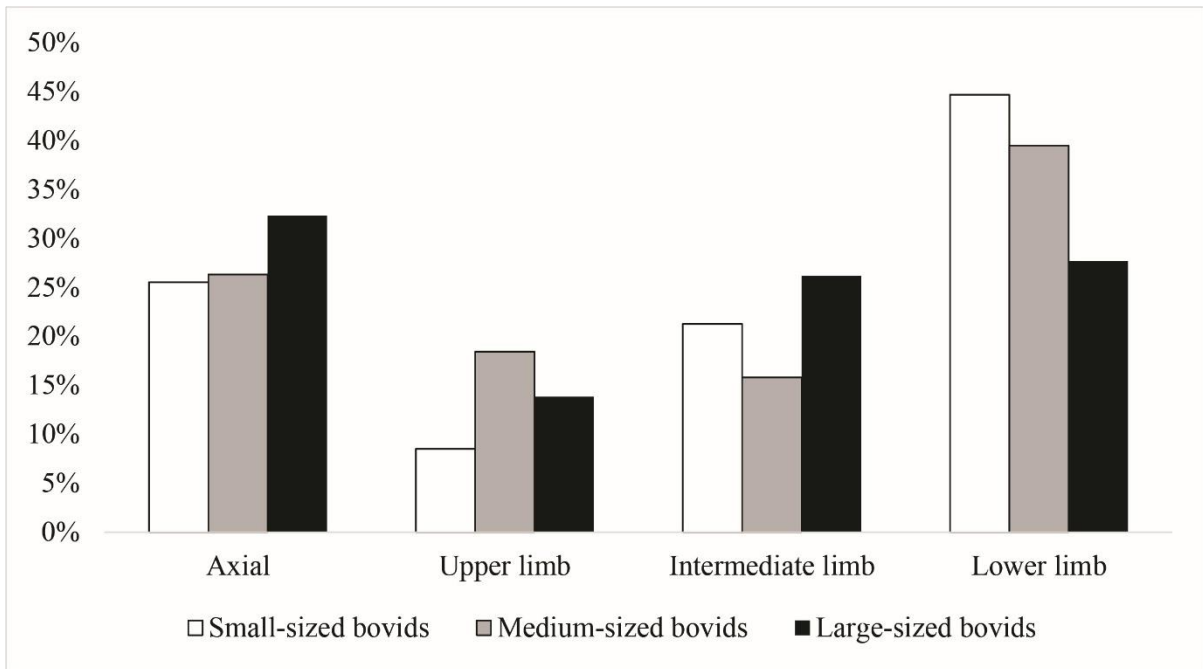
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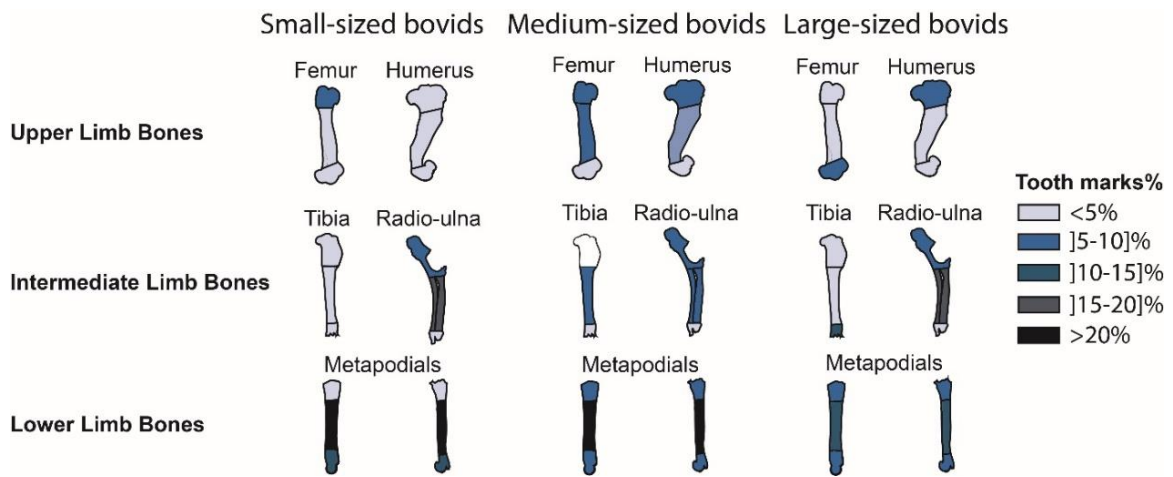
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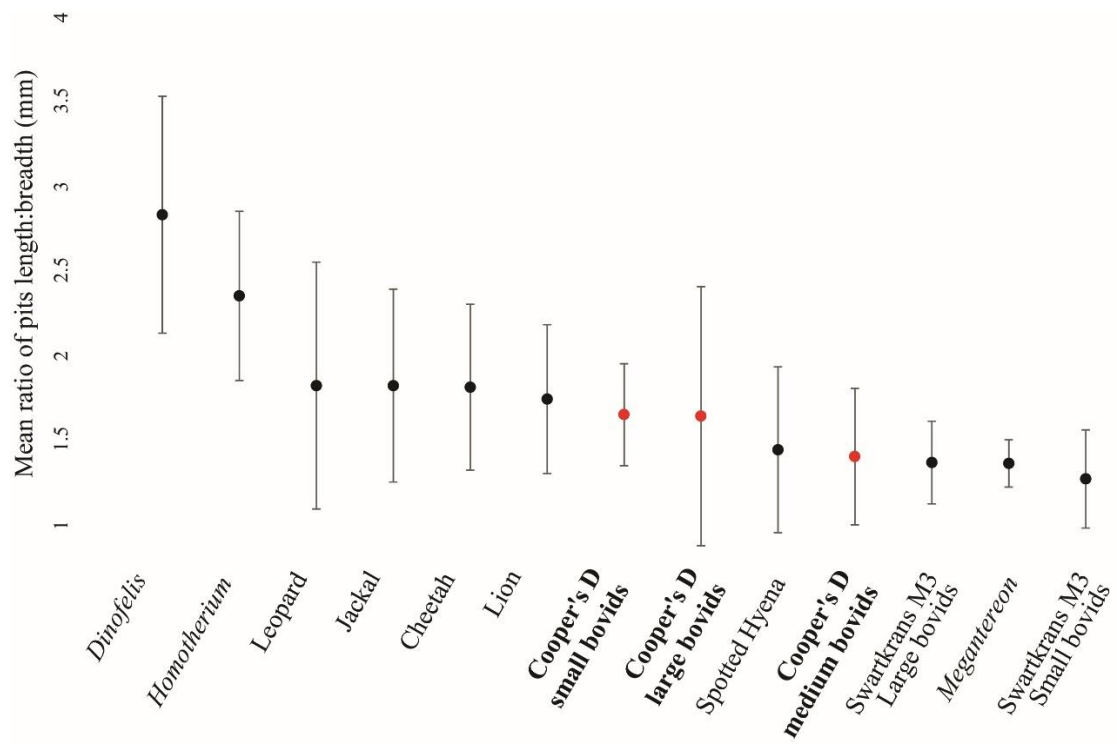
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1178 Figure 10.



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