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

Raphaël Hanon, Jean-Baptiste Fourvel, Christine Steininger

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

Raphaël Hanon[a,b,*], Jean-Baptiste Fourvel[c], Christine Steininger[a,d]

[a] *Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa*

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

[c] *Aix Marseille Université, CNRS, Ministère de la Culture, UMR 7269 LAMPEA*

[d] *Centre of Excellence in Palaeosciences, Private Bag 3, WITS 2050, Johannesburg, South Africa*

*Corresponding Author:

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

Abstract

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

1. Introduction

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

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

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

2. The Cooper's cave site

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

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

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

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

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

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

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

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

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

3. Material and methods

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

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

3.1.Quantification

In this study, we use four quantification units (see Lyman, 1994 for a detailed description): NISP (number of identified specimens), MNE (minimum number of elements), MAU (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-Uribe
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*

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

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

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

3.4.Skeletal part representation

Skeletal part representation is commonly regarded as indicative of the impact of taphonomic 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

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

3.6.Bone surface modifications

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

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

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

4. Results

4.1.Composition of the carnivore paleoguild

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

The Felidae are the most represented but also the most diverse carnivores at the Cooper's D site. In terms of MNI, we observe that the *Panthera* genus (MNI = 6), especially leopard (*Panthera pardus*, MNI = 2), is well-represented within the assemblage. Both the false saber-toothed cat *Dinofelis* (MNI = 4) and *Megantereon* are also well represented (MNI = 4). The 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 *Crocuta ultra* is
266 represented by 2 individuals. All the other taxa (*Chasmaporthetes*, *Crocuta 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% $NISP_{tooth\text{-}marked}$) and axial bones (26 to 32% $NISP_{tooth\text{-}}$
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 find 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

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

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

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

5. Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Hanon et al. (2022b) has showed through the analysis of bovid assemblage from Cooper's D that the environment surrounding the cave was probably a composite of grassland and sparse covered habitat close to a water source which is consistent with the first scenario. Moreover, the karstic environment of the Sterkfontein Valley provides an important source of hiding 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 Swarktrans 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

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

The authors have no competing interests to declare.

Acknowledgments

We thank Bernhard Zipfel from University of the Witwatersrand as well as Stephany Potze, Mirriam Tawane, Heidi Fourie and Lazarus Kgasi from the Ditsong Museum, Pretoria, for access to collections. C. S. acknowledges the funding contribution of the Centre of Excellence in Palaeosciences (CoE-Palaeo) and the Palaeontological Scientific Trust (PAST). R. H. would like to acknowledge the ATM MNHN "*Paranthropus* Diet. Régime alimentaire et comportement de subsistance des Paranthropes sud-africains" (resp. S. Prat) and the UMR 7194/MNHN for the funding support. RH would like to address a special thanks to Camille Daujeard for her comments on an early draft of the paper.

659 **Bibliography**

660 Adams, J.W., 2010. Taphonomy of the Gondolin GD 2 in situ Deposits and its Bearing on
661 Interpretations of South African Plio-Pleistocene Karstic Fossil Assemblages. Journal
662 of Taphonomy 8, 79–114.

663 Andrés, M., Gidna, A.O., Yravedra, J., Domínguez-Rodrigo, M., 2012. A study of
664 dimensional differences of tooth marks (pits and scores) on bones modified by small
665 and large carnivores. Archaeological and Anthropological Sciences 4, 209–219.
666 doi:10.1007/s12520-012-0093-4

667 Backwell, L., Errico, F. d', 2008. Early hominid bone tools from Drimolen, South Africa.
668 Journal of Archaeological Science 35, 2880–2894. doi:10.1016/j.jas.2008.05.017

669 Backwell, L.R., Errico, F. d', 2003. Additional evidence on the early hominid bone tools
670 from Swartkrans with reference to spatial distribution of lithic and organic artefacts.
671 South African Journal of Science 99, 259–267.

672 Badenhorst, S., Steininger, C.M., 2019. The Equidae from Cooper's D, an early Pleistocene
673 fossil locality in Gauteng, South Africa. PeerJ 7, e6909. doi:10.7717/peerj.6909

674 Behrensmeyer, A.K., Gordon, K.D., Yanagi, G.T., 1986. Trampling as a cause of bone
675 surface damage and pseudo-cutmarks. Nature 319, 768–771.

676 Berger, L.R., Pickford, M., Thackeray, F., 1995. A Plio-Pleistocene hominid upper central
677 incisor from the Cooper's site, South Africa. South African Journal of Science 91,
678 541–542.

679 Berger, L.R., Ruiter, D.J. de, Steininger, C.M., Hancox, J., 2003. Preliminary results of
680 excavations at the newly investigated Coopers D deposit, Gauteng, South Africa.
681 South African Journal of Science 99, 276–278.

682 Berna, F., Goldberg, P., Horwitz, L.K., Brink, J., Holt, S., Bamford, M., Chazan, M., 2012.
683 Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk
684 Cave, Northern Cape province, South Africa. Proceedings of the National Academy
685 of Sciences 109, E1215–E1220. doi:10.1073/pnas.1117620109

686 Binford, L.R., 1978. Nunamiut Ethnoarchaeology, Academic Press. ed. New York.

687 Binford, L.R., 1981. Bones: Ancient men and modern myths. Academic Press, New York.

688 Binford, L.R., 1984. Butchering, sharing, and the archaeological record. Journal of
689 Anthropological Archaeology 3, 235–257. doi:10.1016/0278-4165(84)90003-5

690 Blasco, R., Rosell, J., Fernández Peris, J., Cáceres, I., Vergès, J.M., 2008. A new element of
691 trampling: an experimental application on the Level XII faunal record of Bolomor
692 Cave (Valencia, Spain). Journal of Archaeological Science 35, 1605–1618.
693 doi:10.1016/j.jas.2007.11.007

694 Blumenschine, R.J., 1988. An experimental model of the timing of hominid and carnivore
695 influence on archaeological bone assemblages. Journal of Archaeological Science 15,
696 483–502. doi:10.1016/0305-4403(88)90078-7

697 Blumenschine, R.J., 1989. A landscape taphonomic model of the scale of prehistoric
698 scavenging opportunities. Journal of Human Evolution 18, 345–371.
699 doi:10.1016/0047-2484(89)90036-5

700 Blumenschine, R.J., 1991. Hominid carnivory and foraging strategies, and the socio-
701 economic function of early archaeological sites. Philosophical Transactions of the
702 Royal Society B: Biological Sciences 334, 211–221.

703 Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new
704 diagnostic of hominid behaviour. Nature 333, 763–765.

705 Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer New York,
706 New York, NY. doi:10.1007/978-1-4419-7976-6

707 Brain, C.K., 1969. The Probable Role of Leopards as Predators of the Swartkrans
708 Australopithecines. The South African Archaeological Bulletin 24, 170.
709 doi:10.2307/3888296

710 Brain, C.K., 1978. Interpreting the bone accumulations from the Sterkfontein Valley caves: A
711 case study in quaternary research. Southern African Humanities 23, 465–468.

712 Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy.
713 University of Chicago Press, Chicago.

714 Brain, C.K., 1993. Swartkrans. A Cave's Chronicle of Early Man. Transvaal Museum,
715 Pretoria.

716 Brain, C.K., Sillen, A., 1988. Evidence from the Swartkrans cave for the earliest use of fire.
717 Nature 336, 464–466. doi:10.1038/336464a0

718 Broom, R., Schepers, G.W.H., 1946. The South African fossil ape-men: the
719 Australopithecinae. Transvaal Museum Memoirs 2, 1–272.

720 Brugal, J.-P., Fosse, P., Guadelli, J.-L., 1997. Comparative study of bone assemblages made
721 by recent and Pleistocene hyenids. In: Hannus, L. A., Rossum, L,. and Winham, R.P.,
722 (Eds.), Proceedings of the 1993 Bone Modification Conference, Hot Springs, South
723 Dakota. Archaeology Laboratory, Augusta College: Sioux Falls, pp. 158–187.

724 Brunner, J., 1944. Beobachtungen zu den Lebensspuren der Hyänen an den Knochen der
725 Huftiere aus dem Unterpliozän von Pikermi. Palaeobiologica 8, 120–126.

726 Buckland, W., 1822. Account of an assemblage of fossil teeth and bones of Elephant,
727 Rhinoceros, Hippopotamus, Bear, Tiger, and Hyaena, and siwteen other animalx;
728 Discovered in a cave at Kirkdale, Yorkshire, in the year 1821: with a comparative
729 view of five similar caverns in various parts of England, and others on the continent.
730 Philosophical Transactions of the Royal Society B: Biological Sciences 112, 171–236.

731 Bunn, H.T., 1983. Comparative analysis of modern bone assemblages from a San Hunter-
732 gatherer camp in the Kalahari desert, Botswana, and from a spotted hyena den near
733 Nairobi, Kenya. In: Animals and Archaeology: Hunters and Their Prey. British
734 Archaeological Reports, Oxford, pp. 143–148.

735 Bunn, H.T., Gurtov, A.N., 2014. Prey mortality profiles indicate that Early Pleistocene *Homo*
736 at Olduvai was an ambush predator. Quaternary International 322–323, 44–53.
737 doi:10.1016/j.quaint.2013.11.002

738 Bunn, H.T., Pickering, T.R., 2010a. Bovid mortality profiles in paleoecological context
739 falsify hypotheses of endurance running–hunting and passive scavenging by early
740 Pleistocene hominins. Quaternary Research 74, 395–404.
741 doi:10.1016/j.yqres.2010.07.012

742 Bunn, H.T., Pickering, T.R., 2010b. Methodological recommendations for ungulate mortality
743 analyses in paleoanthropology. Quaternary Research 74, 388–394.
744 doi:10.1016/j.yqres.2010.07.013

745 Campmas, E., Michel, P., Costamagno, S., El Hajraoui, M.A., Nespoulet, R., 2017. Which
746 predators are responsible for faunal accumulations at the Late Pleistocene layers of El
747 Harhoura 2 Cave (Témara, Morocco)? Comptes Rendus Palevol 16, 333–350.

748 Campmas, E., Daujeard, C., 2020. Co-évolution Hommes-Canidés en Afrique du Nord-Ouest
749 : une longue histoire. Boudadi-Maligne M. and Mallye J.-B. (eds.) Relations hommes
750 – canidés de la Préhistoire aux périodes modernes. UN@ Éditions, 15–36. 978-2-
751 38149-012-0. ⟨10.46608/DANA3.9782381490120.3⟩.

752 Cleghorn, N., Marean, C.W., 2004. Distinguishing selective transport and in situ attrition: A
753 critical review of analytical approaches. Journal of Taphonomy 2, 43–67.

754 Courchamp, F., Rasmussen, G.S., Macdonald, D.W., 2002. Small pack size imposes a trade-
755 off between hunting and pop-guarding in the painted hunting dog *Lycaon pictus*.
756 Behavioral Ecology 13, 20–27.

757 Creel, S., Creel, N.M., 1995. Communal hunting and pack size in African wild dogs, *Lycaon*
758 *pictus*. Animal Behaviour 50, 1325–1339. doi:10.1016/0003-3472(95)80048-4

759 Cruz-Uribe, K., 1991. Distinguishing Hyena from Hominid Bone Accumulations. Journal of
760 Field Archaeology 18, 467–486. doi:10.2307/530408

761 Daujeard, C., Falguères, C., Shao, Q. et al. Earliest African evidence of carcass processing
762 and consumption in cave at 700 ka, Casablanca, Morocco. Sci Rep 10, 4761 (2020).
763 https://doi.org/10.1038/s41598-020-61580-4Dart, R.A., 1956. The myth of the bone-
764 accumulating hyena. American Anthropologist 58, 40–61.

765 Dart, R.A., 1957. The osteodontokeratic culture of *Australopithecus prometheus*. Transvaal
766 Museum Memoirs 10, 1–105.

767 DeSilva, J.M., Steininger, C.M., Patel, B.A., 2013. Cercopithecoid primate postcranial fossils
768 from Cooper's D, South Africa. Geobios 46, 381–394.
769 doi:10.1016/j.geobios.2013.07.001

770 Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa
771 in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass
772 processing behaviours. Journal of Archaeological Science 30, 1385–1391.
773 doi:10.1016/S0305-4403(03)00027-X

774 Domínguez-Rodrigo, M., Pickering, T.R., 2010. A Multivariate Approach for Discriminating
775 Bone Accumulations Created by Spotted Hyenas and Leopards: Harnessing
776 Actualistic Data from East and Southern Africa. Journal of Taphonomy 8, 155–179.

777 Domínguez-Rodrigo, M., Barba Egido, R., Egeland, C.P., 2007. Deconstructing Olduvai: A
778 Taphonomic Study of the Bed I Sites, 1. Ed. ed, Vertebrate Paleobiology and
779 Paleoanthropology. Springer Netherland, Berlin.

780 Domínguez-Rodrigo, M., Juana, S. de, Galán, A.B., Rodríguez, M., 2009. A new protocol to
781 differentiate trampling marks from butchery cut marks. Journal of Archaeological
782 Science 36, 2643–2654. doi:10.1016/j.jas.2009.07.017

783 Domínguez-Rodrigo, M., Pickering, T.R., Bunn, H.T., 2010. Configurational approach to
784 identifying the earliest hominin butchers. Proceedings of the National Academy of
785 Sciences 107, 20929–20934. doi:10.1073/pnas.1013711107

786 Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Baquedano, E., Uribelarrea, D.,
787 Pérez-González, A., Gidna, A., Yravedra, J., Diez-Martin, F., Egeland, C.P., Barba,
788 R., Arriaza, M.C., Organista, E., Ansón, M., 2014. On meat eating and human
789 evolution: A taphonomic analysis of BK4b (Upper Bed II, Olduvai Gorge, Tanzania),
790 and its bearing on hominin megafaunal consumption. Quaternary International 322–
791 323, 129–152.

792 Echassoux, A., 2012. Comportements de subsistence et modifications osseuses à l'aube de
793 l'Acheuléen à Konso, Ethiopie. L'Anthropologie 116, 291–320.

794 Egeland, C.P., Pickering, T.R., Domínguez-Rodrigo, M., Brain, C.K., 2004. Disentangling
795 Early Stone Age palimpsests: determining the functional independence of hominid-
796 and carnivore-derived portions of archaeofaunas. Journal of Human Evolution 47,
797 343–357. doi:10.1016/j.jhevol.2004.08.004

798 Errico, F. d', Backwell, L.R., 2003. Possible evidence of bone tool shaping by Swartkrans
799 early hominids. Journal of Archaeological Science 30, 1559–1576.
800 doi:10.1016/S0305-4403(03)00052-9

801 Ferraro, J.V., Plummer, T.W., Pobiner, B.L., Oliver, J.S., Bishop, L.C., Braun, D.R.,
802 Ditchfield, P.W., Seaman III, J.W., Binetti, K.M., Seaman Jr., J.W., Hertel, F., Potts,
803 R., 2013. Earliest archaeological evidence of persistent hominin carnivory. PLoS
804 ONE 8(4): e62174. doi:10.1371/journal.pone.0062174

805 Fiorillo, A.R., 1989. An experimental study of trampling. In: Bonnichsen, R., and Sorg, M.
806 H., (Eds.), Bone Modification. University of Maine, pp. 61–98.

807 Folinsbee, K.E., Reisz, R.R., 2013. New craniodental fossils of papionin monkeys from
808 Cooper's D, South Africa: Papionin Monkeys from Cooper's D. American Journal of
809 Physical Anthropology 151, 613–629. doi:10.1002/ajpa.22317

810 Fourvel, J., Magniez, P., Moigne, A., Testu, A., Joris, A., Lamglait, B., Vaccaro, C., Fosse,
811 P., 2018a. Wild dogs and their relatives: implication of experimental feedings in their
812 taphonomical identification. Quaternaire 21–29. doi:10.4000/quaternaire.8578

813 Fourvel, J.-B., 2012. Hyénidés modernes et fossiles d'Europe et d'Afrique : taphonomie
814 comparée de leurs assemblages osseux. Université de Toulouse Le Mirail, Toulouse.

815 Fourvel, J.-B., Thackeray, J.F., Brink, J.S., O'Regan, H., Braga, J., 2018b. Taphonomic
816 interpretations of a new Plio-Pleistocene hominin-bearing assemblage at Kromdraai
817 (Gauteng, South Africa). Quaternary Science Reviews 190, 81–97.
818 doi:10.1016/j.quascirev.2018.04.018

819 Gibbon, R.J., Pickering, T.R., Sutton, M.B., Heaton, J.L., Kuman, K., Clarke, R.J., Brain,
820 C.K., Granger, D.E., 2014. Cosmogenic nuclide burial dating of hominin-bearing
821 Pleistocene cave deposits at Swartkrans, South Africa. Quaternary Geochronology 24,
822 10–15. doi:10.1016/j.quageo.2014.07.004

823 Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software
824 Package for Education and Data Analysis 4, 9.

825 Hanon, R., 2019. Comportements de subsistance des hominines du Pléistocène inférieur
826 d'Afrique du Sud : analyse archéozoologique du site de Cooper's D (Bloubank
827 Valley). Muséum National d'Histoire Naturelle, Paris.

828 Hanon, R., Errico, F. d', Backwell, L., Prat, S., Péan, S., Patou-Mathis, M., 2021. New
829 evidence of bone tool use by Early Pleistocene hominins from Cooper's D, Bloubank
830 Valley, South Africa. Journal of Archaeological Science: Reports 39, 103129.
831 doi:10.1016/j.jasrep.2021.103129

832 Hanon, R., Patou-Mathis, M., Péan, S., Prat, S., Cohen, B. F., Steininger, C., 2022a. Early
833 Pleistocene hominin subsistence behaviors in South Africa: Evidence from the
834 hominin-bearing deposit of Cooper's D (Bloubank Valley, South Africa). Journal of
835 Human Evolution 162, 103116. https://doi.org/10.1016/j.jhevol.2021.103116

836 Hanon, R., Péan, S., Patou-Mathis, M., Prat, S., Rector, A., Steininger, C., 2022b. Fossil
837 Bovidae from the Hominini-bearing site of Cooper's D (Bloubank Valley, South
838 Africa): implications for *Paranthropus robustus* and early *Homo* habitat preferences.
839 Comptes Rendus Palevol 21 (21), 431–450.

840 Hartstone-Rose, A., Ruiter, D.J.D., Berger, L.R., Churchill, S.E., 2007. A sabre-tooth felid
841 from Coopers Cave (Gauteng, South Africa) and its implications for *Megantereon*
842 (Felidae: Machairodontinae) taxonomy. Palaeontologia africana 42, 99–108.

843 Hartstone-Rose, A., Werdelin, L., De Ruiter, D.J., Berger, L.R., Churchill, S.E., 2010. The
844 Plio-Pleistocene ancestor of wild dogs, *Lycaon sekowei* n. sp. Journal of Paleontology
845 84, 299–308. doi:10.1666/09-124.1

Hayward, M.W., O'Brien, J., Hofmeyr, M., Kerley, G.I.H., 2006. Prey preferences of the African wild dog *Lycaon pictus* (Canidae: Carnivora): ecological requirements for conservation. Journal of Mammalogy 87, 1122–1131. doi:10.1644/05-MAMM-A-304R2.1

Isaac, G.L., 1983. Bones in contention: competing explanations for the juxtaposition of early Pleistocene artifacts and faunal remains. In: Clutton-Brock, J., Grigson, C. (Eds.), Animals and Archaeology: I. Hunters and Their Prey, BAR British Series. Oxford, pp. 3–19.

Klein, R.G., Cruz-Uribe, K., 1984. The Analysis of Animal Bones from Archeological Sites, University of Chicago Press. ed. Chicago.

Koenigswald, R. von, 1953. The Australopithenicae and *Pithecanthropus*. Proceedings Koninklijke Nederlandsche Akademie van Wetenschappen 56, 403–413.

Kuhn, B.F., Berger, L.R., Skinner, J.D., 2010. Examining criteria for identifying and differentiating fossil faunal assemblages accumulated by hyenas and hominins using extant hyenid accumulations. International Journal of Osteoarchaeology 15–35. doi:10.1002/oa.996

Kuhn, B.F., Werdelin, L., Steininger, C., 2017. Fossil Hyaenidae from Cooper's Cave, South Africa, and the palaeoenvironmental implications. Palaeobiodiversity and Palaeoenvironments 97, 355–365. doi:10.1007/s12549-016-0247-y

Lyman, R.L., 1994. Vertebrate Taphonomy, Cambridge University Press. ed, Cambridge manuals in archaeology. Cambridge.

Maguire, J.M., Pemberton, D., Collett, M.H., 1980. The Makapansgat limeworks gray breccia: hominids, hyaenas, hystricids or hill wash. Palaeontologia africana 23, 75–98.

Marean, C.W., 1989. Sabertooth cats and their relevance for early hominid diet and evolution. Journal of Human Evolution 18, 559–582. doi:10.1016/0047-2484(89)90018-3

873 Marean, C.W., Spencer, L.M., 1991. Impact of Carnivore Ravaging on Zooarchaeological
874 Measures of Element Abundance. American Antiquity 56, 645–658.
875 doi:10.2307/281542

876 Marean, C.W., Domínguez-Rodrigo, M., Pickering, T.R., 2004. Skeletal Element Equifinality
877 in Zooarchaeology Begins with Method: The Evolution and Status of the "Shaft
878 Critique." Journal of Taphonomy 2, 69–98.

879 Merwe, I. van der, Tambling, C.J., Thorn, M., Scott, D.M., Yarnell, R.W., Green, M.,
880 Cameron, E.Z., Bateman, P.W., 2009. An Assessment of Diet Overlap of Two
881 Mesocarnivores in the North West Province, South Africa. African Zoology 44, 288–
882 291. doi:10.3377/004.044.0217

883 Mills, M.G.L., 1982. Notes on age determination, growth and measurements of brown
884 hyaenas *Hyaena brunnea* from the Kalahari Gemsbok National Park. Koedoe 25: 55–
885 61.

886 Oakley, K.P., 1953. Dawn of man in South Africa. Royal Institute Weekly Evening Meeting
887 20.

888 Olsen, S.L., Shipman, P., 1988. Surface modification on bone: Trampling versus butchery.
889 Journal of Archaeological Science 15, 535–553. doi:10.1016/0305-4403(88)90081-7

890 O'Regan, H.J., Reynolds, S.C., 2009. An ecological reassessment of the southern African
891 carnivore guild: a case study from Member 4, Sterkfontein, South Africa. Journal of
892 Human Evolution 57, 212–222. doi:10.1016/j.jhevol.2009.04.002

893 O'Regan, H.J., Steininger, C., 2017. Felidae from Cooper's Cave, South Africa (Mammalia:
894 Carnivora). Geodiversitas 39, 315–332. doi:10.5252/g2017n2a8

895 O'Regan, H.J., Cohen, B.F., Steininger, C.M., 2013. Mustelid and viverrid remains from the
896 Pleistocene site of Cooper's D, Gauteng, South Africa. Palaeontologia africana 48,
897 19–23.

898 Parkinson, A.H., 2016. Traces of Insect Activity at Cooper's D Fossil Site (Cradle of
899 Humankind, South Africa). Ichnos 23, 322–339.
900 doi:10.1080/10420940.2016.1202685

901 Patou-Mathis, M., 1997. Les marques de boucherie au Paléolithique. Revue Médical
902 Vétérinaire 148, 959–968.

903 Pickering, T.R., 1999. Taphonomic interpretations of the Sterkfontein Early Hominid site
904 (Gauteng, South Africa) reconsidered in light of recent evidence. University of
905 Wisconsin, Madison.

906 Pickering, T.R., 2002. Reconsideration of criteria for differentiating faunal assemblages
907 accumulated by hyenas and hominids. International Journal of Osteoarchaeology 12,
908 127–141. doi:10.1002/oa.594

909 Pickering, T.R., 2012. What's new is old: Comments on (more) archaeological evidence of
910 one-million-year-old fire from South Africa. South African Journal of Science 108.
911 doi:10.4102/sajs.v108i5/6.1250

912 Pickering, T.R., Marean, C.W., Domínguez-Rodrigo, M., 2003. Importance of limb bone
913 shaft fragments in zooarchaeology: a response to "On in situ attrition and vertebrate
914 body part profiles" (2002), by M.C. Stiner. Journal of Archaeological Science 30,
915 1469–1482. doi:10.1016/S0305-4403(03)00042-6

916 Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2004a. Beyond
917 leopards: tooth marks and the contribution of multiple carnivore taxa to the
918 accumulation of the Swartkrans Member 3 fossil assemblage. Journal of Human
919 Evolution 46, 595–604. doi:10.1016/j.jhevol.2004.03.002

920 Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2004b. New data and
921 ideas on the foraging behaviour of Early Stone Age hominids at Swartkrans Cave,
922 South Africa. South African Journal of Science 100, 215–219.

923 Pickering, T.R., Clarke, R.J., Moggi-Cecchi, J., 2004c. Role of carnivores in the
924 accumulation of the Sterkfontein Member 4 hominid assemblage: A taphonomic

925 reassessment of the complete hominid fossil sample (1936-1999). American Journal
926 of Physical Anthropology 125, 1–15. doi:10.1002/ajpa.10278

927 Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2007. Carcass foraging
928 by early hominids at Swartkrans cave (South Africa): a new investigation of the
929 zooarchaeology and taphonomy of member 3. In: Pickering, T. R., Schick, K., and
930 Toth, N., (Eds.), Breathing Life Into Fossils: Taphonomic Studies in Honor of C. K.
931 (Bob) Brain, Stone Age Institute Publication Series. Gosport, pp. 233–253.

932 Pickering, T.R., Egeland, C.P., Domínguez-Rodrigo, M., Brain, C.K., Schnell, A.G., 2008.
933 Testing the "shift in the balance of power" hypothesis at Swartkrans, South Africa:
934 Hominid cave use and subsistence behavior in the Early Pleistocene. Journal of
935 Anthropological Archaeology 27, 30–45. doi:10.1016/j.jaa.2007.07.002

936 Pienaar, U. de V., 1969. Predator-prey relationships amongst the larger mammals of the
937 Kruger National Park. Koedoe 12, a753.

938 Pobiner, B.L., Blumenschine, R.J., 2003. A Taphonomic Perspective on Oldowan Hominid
939 Encroachment on the Carnivoran Paleoguild. Journal of Taphonomy 1, 115–141.

940 Pobiner, B.L., Rogers, M.J., Monahan, C.M., Harris, J.W.K., 2008. New evidence for
941 hominin carcass processing strategies at 1.5 Ma, Koobi Fora, Kenya. Journal of
942 Human Evolution 55, 103–130.

943 Potts, R., Shipman, P., 1981. Cutmarks made by stone tools on bones from Olduvai Gorge,
944 Tanzania. Nature 291, 577–580. doi:10.1038/291577a0

945 Ruiter, D.J. de, Berger, L.R., 2000. Leopards as Taphonomic Agents in Dolomitic Caves—
946 Implications for Bone Accumulations in the Hominid-bearing Deposits of South
947 Africa. Journal of Archaeological Science 27, 665–684. doi:10.1006/jasc.1999.0470

948 Ruiter, D.J. de, Pickering, R., Steininger, C.M., Kramers, J.D., Hancox, P.J., Churchill, S.E.,
949 Berger, L.R., Backwell, L., 2009. New *Australopithecus robustus* fossils and
950 associated U-Pb dates from Cooper's Cave (Gauteng, South Africa). Journal of
951 Human Evolution 56, 497–513. doi:10.1016/j.jhevol.2009.01.009

952 Sahnouni, M., Rosell, J., van der Made, J., María Vergès, J., Ollé, A., Kandi, N., Harichane,
953 Z., Derradji, A., Medig, M., 2013. The first evidence of cut marks and usewear traces
954 from the Plio-Pleistocene locality of El-Kherba (Ain Hanech), Algeria: implications
955 for early hominin subsistence activities circa 1.8 Ma. Journal of Human Evolution 64
956 (2), 137–150. https://doi.org/10.1016/j.jhevol.2012.10.007.

957 Sahnouni, M., Parés, J.M., Duval, M., Cáceres, I., Harichane, Z., van der Made, J., Pérez-
958 González, A., Abdessadock, S., Kandi, N., Derradji, A., Medig, M., Boulaghraif, K.,
959 Semaw, S., 2018. 1.9-million-and 2.4-million-year-old artifacts and stone tool–cut
960 marked bones from Ain Boucherit, Algeria. Science 362 (6420), 1297e1301.
961 https://doi.org/10.1126/science.aau0008.Selvaggio, M.M., 1994. Carnivore tooth
962 marks and stone tool butchery marks on scavenged bones: archaeological
963 implications. Journal of Human Evolution 27, 215–228.

964 Selvaggio, M.M., Wilder, J., 2001. Identifying the Involvement of Multiple Carnivore Taxa
965 with Archaeological Bone Assemblages. Journal of Archaeological Science 28, 465–
966 470. doi:10.1006/jasc.2000.0557

967 Shipman, P., Rose, J., 1983. Early hominid hunting, butchering, and carcass-processing
968 behaviors: Approaches to the fossil record. Journal of Anthropological Archaeology
969 2, 57–98. doi:10.1016/0278-4165(83)90008-9

970 Stammers, R.C., Caruana, M.V., Herries, A.I.R., 2018. The first bone tools from Kromdraai
971 and stone tools from Drimolen, and the place of bone tools in the South African
972 Earlier Stone Age. Quaternary International 495, 87–101.
973 doi:10.1016/j.quaint.2018.04.026

974 Steele, T.E., Weaver, T.D., 2002. The Modified Triangular Graph: A Refined Method for
975 Comparing Mortality Profiles in Archaeological Samples. Journal of Archaeological
976 Science 29, 317–322. doi:10.1006/jasc.2001.0733

977 Steininger, C., Berger, L.R., Kuhn, B.F., 2008. A partial skull of *Paranthropus robustus* from
978 Cooper's Cave, South Africa. South African Journal of Science 104, 143–146.

979 Stiner, M.C., 1990. The use of mortality patterns in archaeological studies of hominid
980 predatory adaptations. Journal of Anthropological Archaeology 9, 305–351.

Stiner, M.C., 1991. Food procurement and transport by human and non human predators. Journal of Archaeological Science 18, 455–482.

Stiner, M.C., 2002. On in situ Attrition and Vertebrate Body Part Profiles. Journal of Archaeological Science 29, 979–991. doi:10.1006/jasc.2001.0798

Sutton, M.B., Kuman, K., Steininger, C., 2017. Early Pleistocene stone artefacts from Cooper's cave, South Africa. South African Archaeological Bulletin 72, 156–161.

Thenius, E., 1961. Hyänenfraßspuren aus dem Pleistozän von Kärnten. Ein Beitrag zur Frage der sog. "osteodontokeratischen Kultur" des Australopithecinen (Hominidae). Carinthia II, Naturwissenschaftlicher Verein fuer Kaernten 88–101.

Val, A., Stratford, D.J., 2015. The macrovertebrate fossil assemblage from the Name Chamber, Sterkfontein: taxonomy, taphonomy and implications for site formation processes. Palaeontologia Africana 50, 49–58.

Val, A., Taru, P., Steininger, C., 2014. New taphonomic analysis of large-bodied primate assemblage from Cooper's D, Bloubank Valley, South Africa. South African Archaeological Bulletin 69, 49–58.

Vrba, E.S., 1974. The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. Transvaal Museum Memoirs 21, 1–166.

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

Weaver, T.D., Boyko, R.H., Steele, T.E., 2011. Cross-platform program for likelihood-based statistical comparisons of mortality profiles on a triangular graph. Journal of Archaeological Science 38, 2420–2423. doi:10.1016/j.jas.2011.05.009

Werdelin, L., Lewis, M.E., 2001. A revision of the genus Dinofelis (Mammalia, Felidae). Zoological Journal of the Linnean Society 132, 147–258. doi:10.1111/j.1096-3642.2001.tb02465.x

Yarnell, R.W., Phipps, W.L., Burgess, L.P., Ellis, J.A., Harrison, S.W.R., Dell, S., MacTavish, D., MacTavish, L.M., Scott, D.M., 2013. The Influence of Large

1008 Predators on the Feeding Ecology of Two African Mesocarnivores: The Black-
1009 Backed Jackal and the Brown Hyaena. South African Journal of Wildlife Research 43,
1010 155–166. doi:10.3957/056.043.0206

1011 Yravedra, J., Andrés, M., Domínguez-Rodrigo, M., 2014. A taphonomic study of the African
1012 wild dog (*Lycaon pictus*). Archaeological and Anthropological Sciences 6, 113–124.
1013 doi:10.1007/s12520-013-0164-1

1014 Zapfe, H., 1939. Die Lebensspuren der eiszeitlichen Höhlenhyänen. Die urgeschichtliche
1015 Bedeutung der Lebensspuren knochenfressender Raubtiere. Forschungen und
1016 Fortschritte 15, 269–270.

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.

1031

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

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

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

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

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

Figure 7. Bone surface modifications attributed to carnivore activity observed on large mammal bones from Cooper's D. A: Puncture observed on an indeterminate juvenile pelvis 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). Date 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).

1074

1075 **Table 1**

1076

Family	Genus	species	NISP	MNI	Reference
Canidae	*Lupulella*	*L. mesomelas*	46	4	This study
		L. cf. *mesomelas*	16	1	This study
		Lupulella sp.	70	3	This study
	Lycaon	*L. sekowei*	2	1	Hartstone-Rose et al. (2010)
		L. cf. *sekowei*	1	1	This study
		Lycaon sp.	11	3	This study
		cf. *Lycaon*	6	-	This study
	Vulpes	*V. chama*	3	1	This study
		cf. *Vulpes*	1	1	This study
	Otocyon	*Otocyon megalotis*	1	1	This study
		cf. *Otocyon*	1	1	This study
	Vulpes / Otocyon	Indeterminate	2	-	This study
	Indeterminate	Indeterminate	56	-	
Felidae	*Dinofelis*	*D.* cf. *aronoki*	11	2	O'Regan and Steininger (2017)
		cf. *D. aronoki*	24	2	O'Regan and Steininger (2017); this study
	Megantereon	*M. whitei*	7	3	Hartstone-Rose et al. (2007)
		cf. *M. whitei*	4	1	O'Regan and Steininger (2017)
	Panthera	*P. leo*	4	1	O'Regan and Steininger (2017)
		P. cf. *leo*	1	1	O'Regan and Steininger (2017)
		P. pardus	15	2	O'Regan and Steininger (2017)
		P. cf. *pardus*	7	1	O'Regan and Steininger (2017)
		Panthera sp.	2	1	O'Regan and Steininger (2017)
	Caracal	*C. caracal*	3	2	O'Regan and Steininger (2017)
		Caracal sp.	5	1	O'Regan and Steininger (2017)
	Felis	*F. lybica*	6	2	O'Regan and Steininger (2017)
		Felis sp.	2	1	O'Regan and Steininger (2017)
	Acynonix	*A. jubatus*	3	1	O'Regan and Steininger (2017)
		cf. *Acynonix*	1	1	This study
	Machairodontinea	Indeterminate	10	-	O'Regan and Steininger (2017); this study
	Indeterminate	Indeterminate	151	-	
Hyaenidae	*Chasmaporthetes*	*C. nitidula*	1	1	Kuhn et al. (2016)
		Chasmaporthetes sp.	2	1	Kuhn et al. (2016)
	Crocuta	*C. crocuta*	18	1	Kuhn et al. (2016)
		C. ultra	4	2	Kuhn et al. (2016)
		Crocuta sp.	14	2	Kuhn et al. (2016)
	Parahyaena	*P. brunnea*	37	3	Kuhn et al. (2016)
		P. cf. *brunnea*	15	2	Kuhn et al. (2016)
	Hyaena	*Hyaena* sp.	4	1	Kuhn et al. (2016)
	Proteles	*P. cristatus*	3	1	This study
		Proteles sp.	7	1	Kuhn et al. (2016)
	Indeterminate	Indeterminate	50	-	
Herpestidae	*Herpestes*	*H. ichneumon*	5	5	Cohen et al. (2019)
	Ichneumia	cf. *Ichneumia* sp.	1	1	Cohen et al. (2019)
	Atilax	*A. paludinosus*	3	1	Cohen et al. (2019)
	Mungos	*M.* aff. *Dietrichi*	1	1	Cohen et al. (2019)
		Mungos sp.	3	1	Cohen et al. (2019)
	Galerella	?*Galerella* 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	*Propoecilogale*	*P. bolti*	1	1	O'Regan et al. (2013)
	Civettictis	*C.* cf. *civetta*	2	1	O'Regan et al. (2013)
		cf. *Civettictis* sp.	2	-	O'Regan et al. (2013)
Mustelidae	*Mellivora*	*M. capensis*	1	1	O'Regan et al. (2013)
Indeterminate	Indeterminate	Indeterminate	132		
Total			794	68	

1077

1078

1079 **Table 2**.

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

1080

1081

1082

1083

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

1085

1086

1087

1088

1089

1090

1091

1092

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)

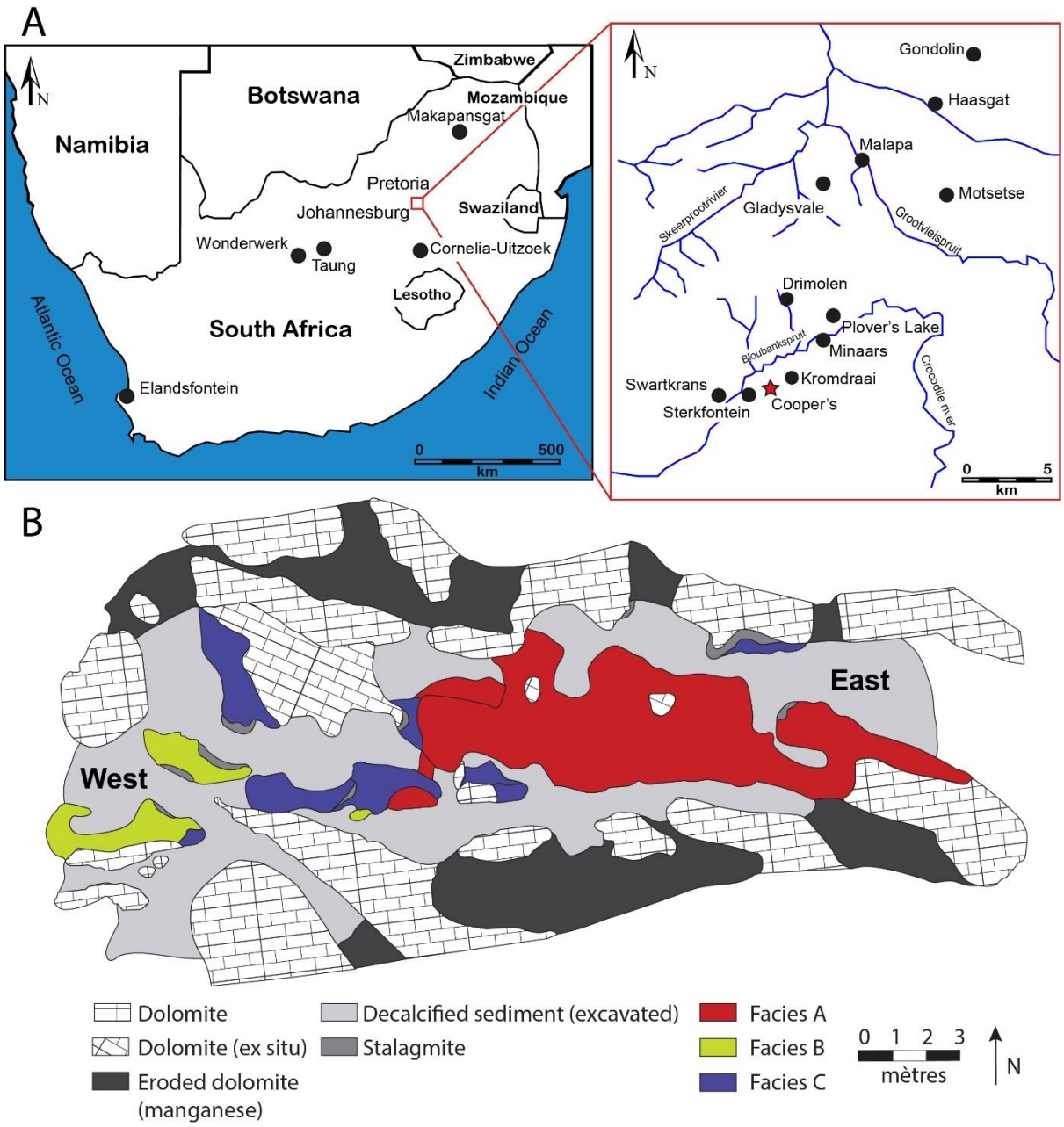
Table 5.

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

Table 6.

Sample	*n*	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

1106 Figure 1.



1107

1108

1109

1110

1111

Figure 2.

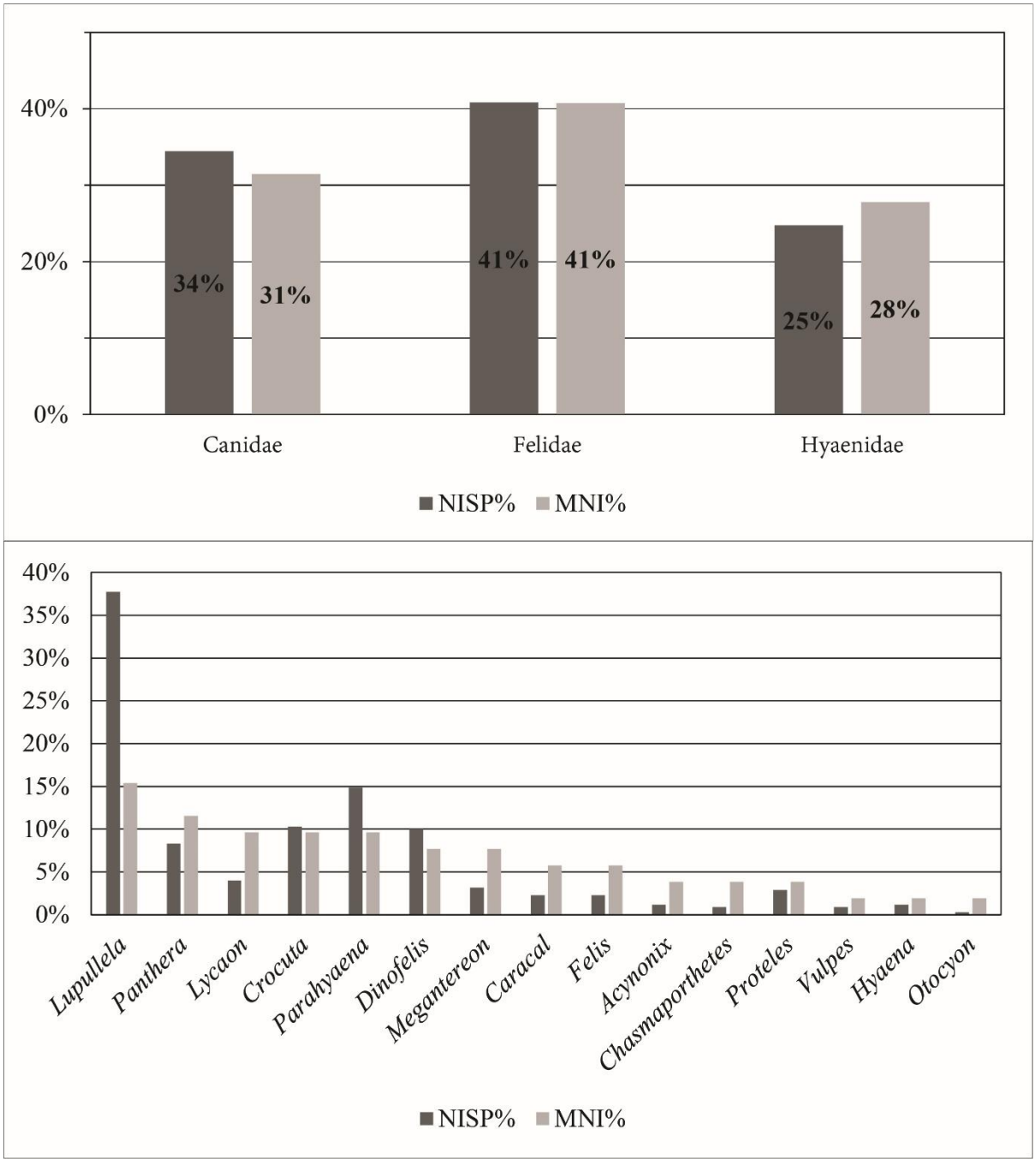

40%
20%
0%
34%
31%
41%
41%
25%
28%
Canidae
Felidae
Hyaenidae
NISP%
MNI%
40%
35%
30%
25%
20%
15%
10%
5%
0%
Lupullela
Panthera
Lycaon
Crocuta
Parahyaena
Dinofelis
Megantereon
Caracal
Felis
Acynonix
Chasmaporthetes
Proteles
Vulpes
Hyaena
Otocyon
NISP%
MNI%

Figure 3.

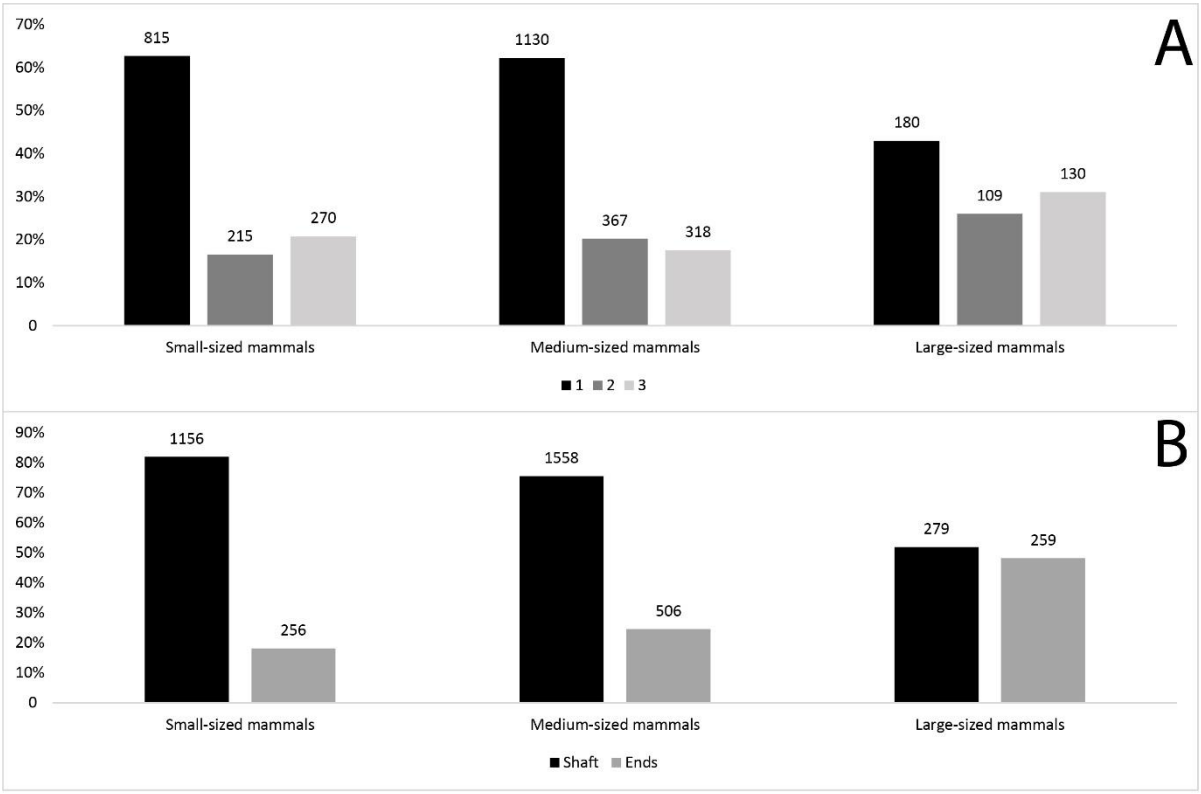


Figure 4.

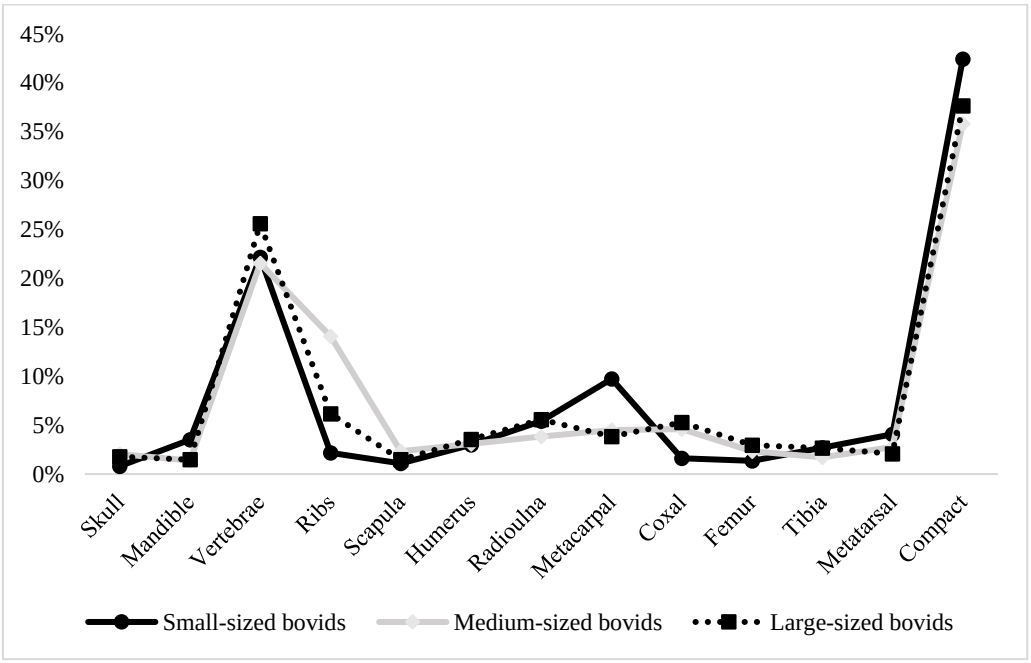


Figure 5.

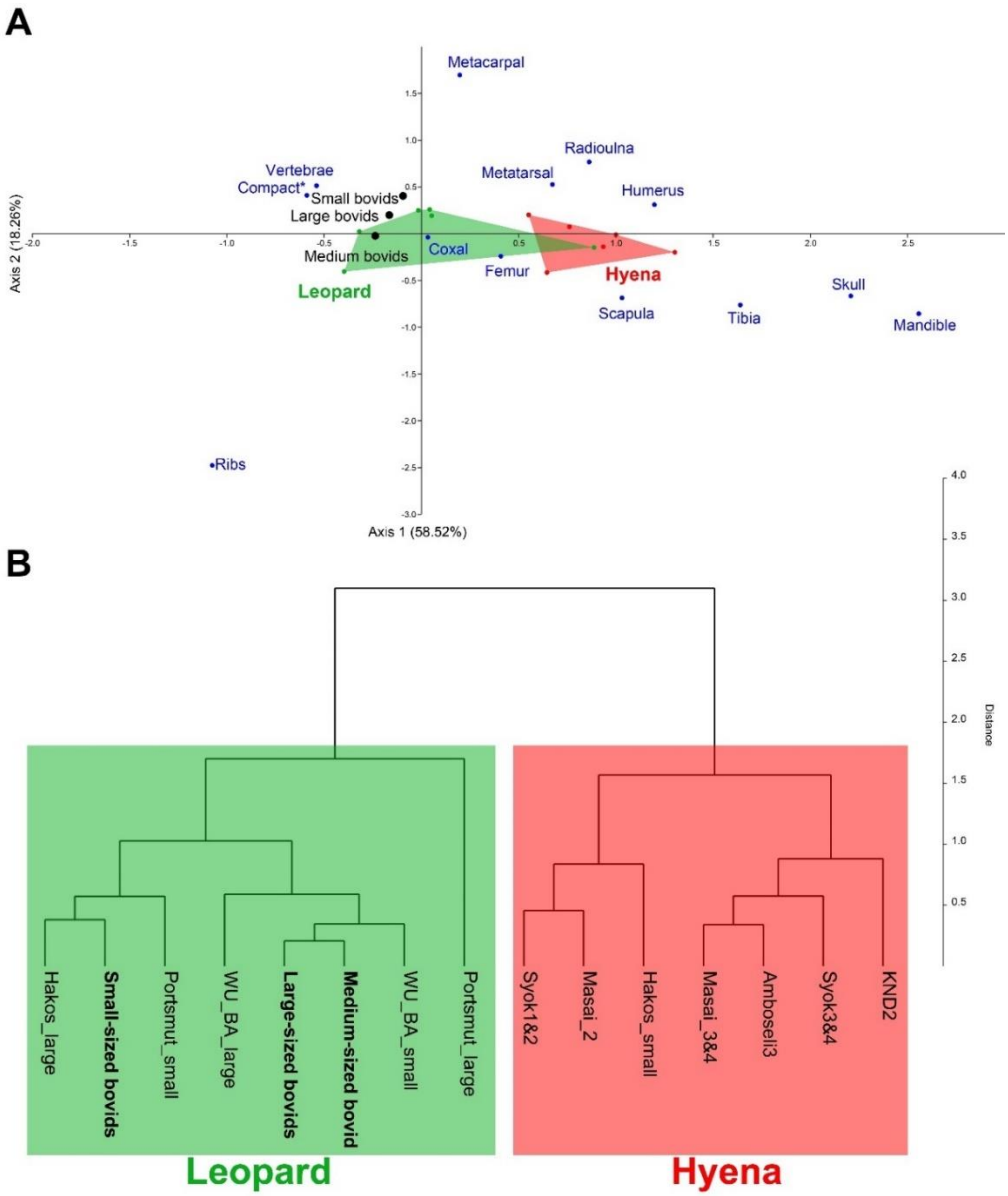

A
Metacarpal
Radioulna
Vertebrae
Compact*
Small bovids
Large bovids
Metatarsal
Humerus
Medium bovids
Coxal
Femur
Hyena
Leopard
Skull
Scapula
Tibia
Mandible
Ribs
Axis 2 (18.26%)
Axis 1 (58.52%)
B
Distance
Hakos_large
Small-sized bovids
Portsmut_small
WU_BA_large
Large-sized bovids
Medium-sized bovid
WU_BA_small
Portsmut_large
Syok1&2
Masai_2
Hakos_small
Masai_3&4
Amboseli3
Syok3&4
KND2
Leopard
Hyena

Figure 6.

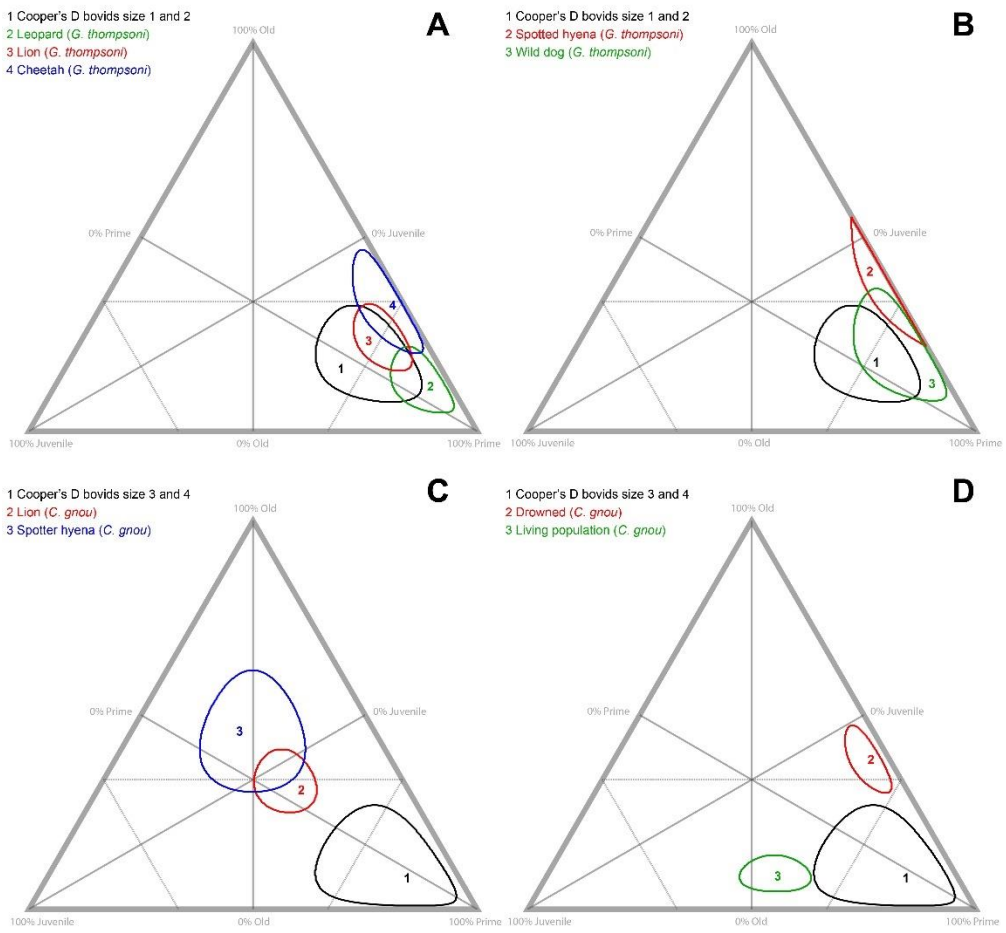
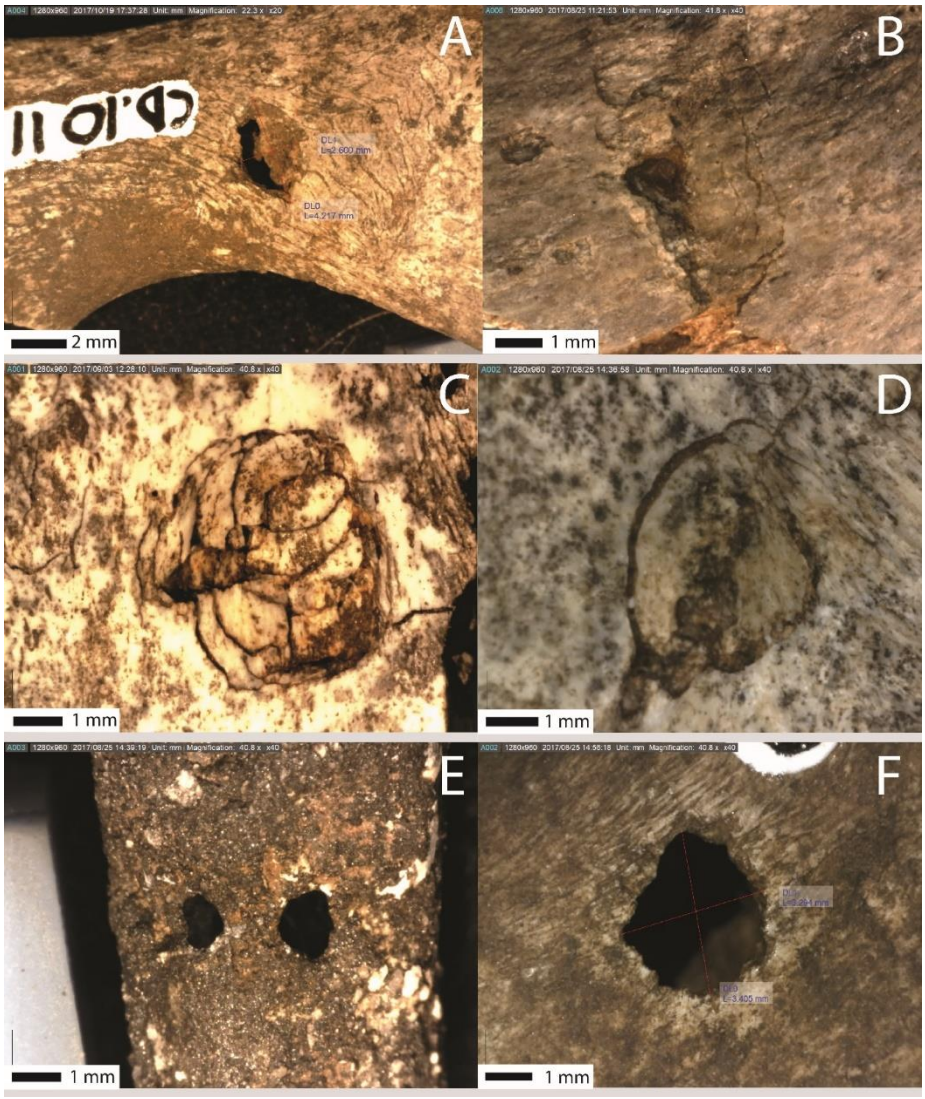
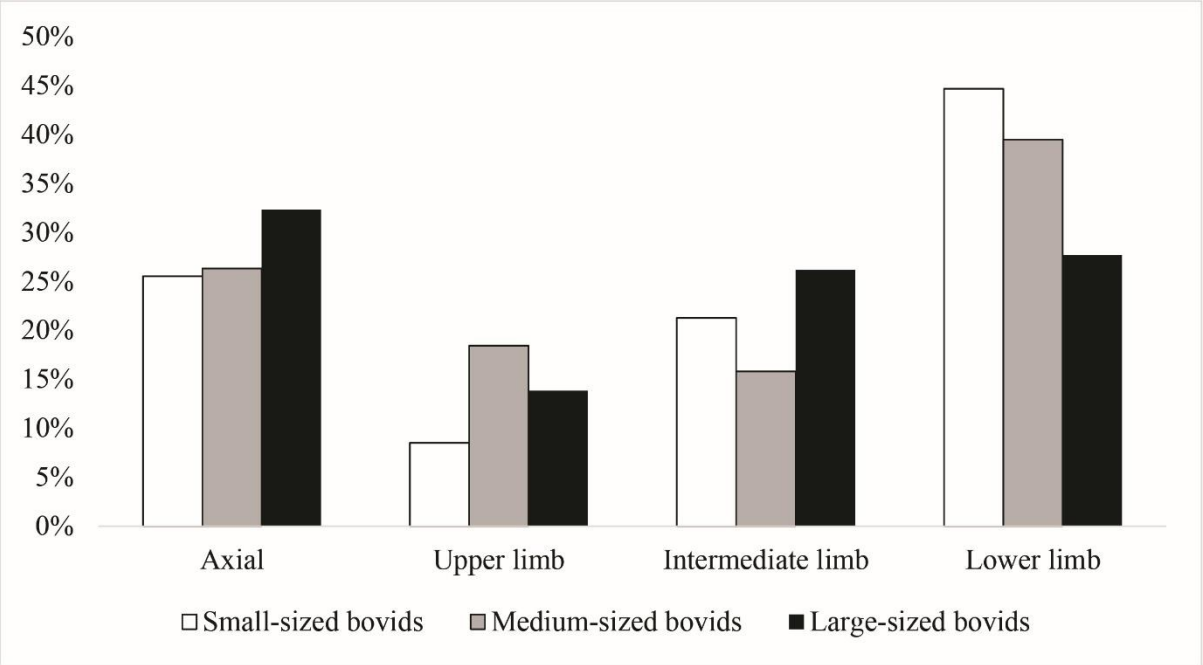

1 Cooper's D bovids size 1 and 2
2 Leopard (G. thompsoni)
3 Lion (G. thompsoni)
4 Cheetah (G. thompsoni)
A
100% Old
0% Prime
0% Juvenile
100% Juvenile
0% Old
100% Prime
1 Cooper's D bovids size 1 and 2
2 Spotted hyena (G. thompsoni)
3 Wild dog (G. thompsoni)
B
1 Cooper's D bovids size 3 and 4
2 Lion (C. gnou)
3 Spotter hyena (C. gnou)
C
1 Cooper's D bovids size 3 and 4
2 Drowned (C. gnou)
3 Living population (C. gnou)
D

Figure 7.

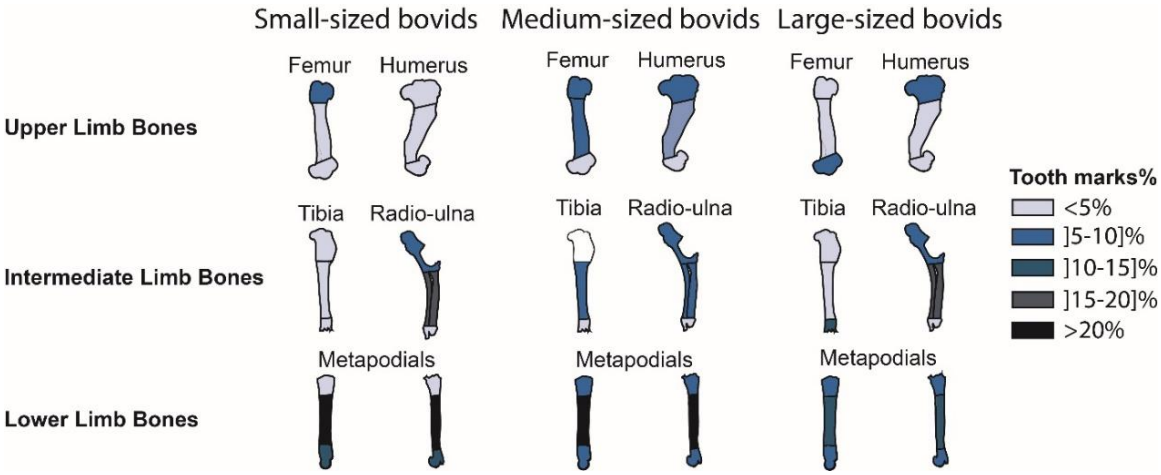


1171 Figure 8.



1172

1173 Figure 9.



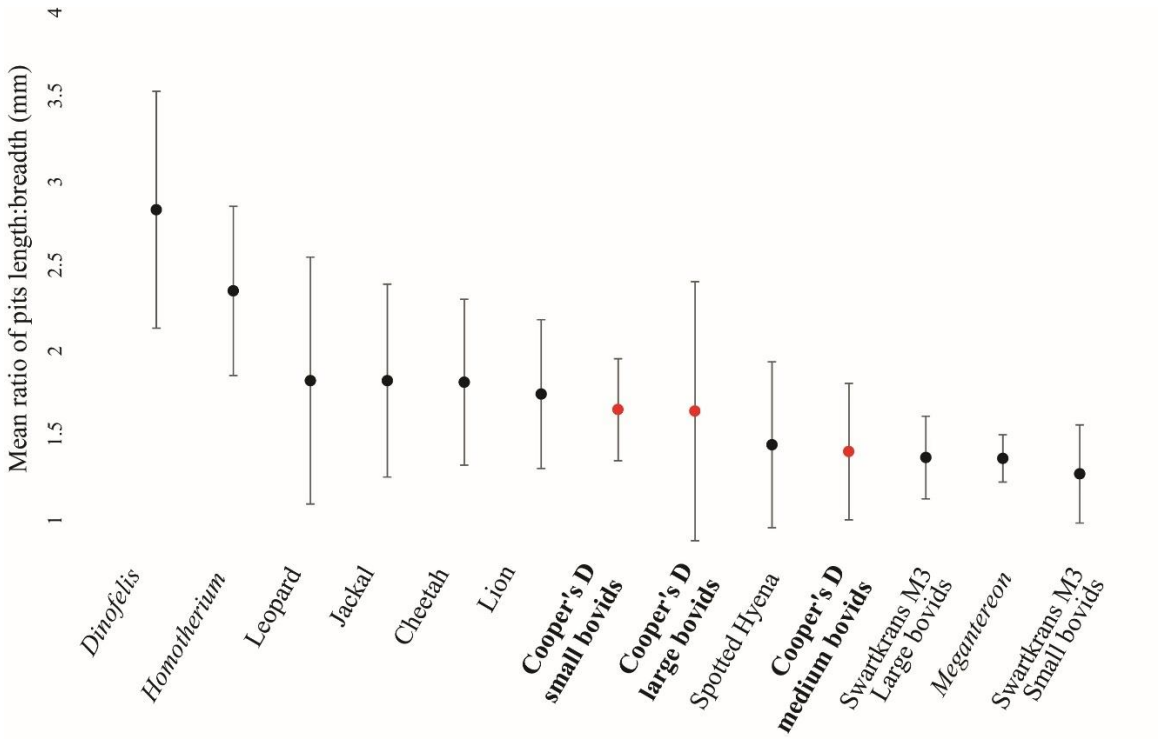
1174

1175

1176

1177

1178 Figure 10.



1179