

# Macromammalian faunas, biochronology and palaeoecology of the early Pleistocene Main Quarry hominin-bearing deposits of the Drimolen Palaeocave System, South Africa

Justin W Adams, Douglass S Rovinsky, Andy IR Herries, Colin G Menter

The Drimolen Palaeocave System Main Quarry deposits (DMQ) are some of the most prolific hominin and primate-bearing deposits in the Fossil Hominids of South Africa UNESCO World Heritage Site. Discovered in the 1990s, excavations into the DMQ have yielded a demographically diverse sample of *Paranthropus robustus* (including DNH 7, the most complete cranium of the species recovered to date), early *Homo*, *Papio hamadryas robinsoni* and *Cercopithecoides williamsi*. Alongside the hominin and primate sample is a diverse macromammalian assemblage, but prior publications have only provided a provisional species list and an analysis of the carnivores recovered prior to 2008. Here we present the first description and analysis of the non-primate macromammalian faunas from the DMQ, including all 826 taxonomically identifiable specimens catalogued from over two decades of excavation. We also provide a biochronological interpretation of the DMQ deposits and an initial discussion of local palaeoecology based on taxon representation.

The current DMQ assemblage consists of the remains of minimally 147 individuals from 9 Orders and 14 Families of mammals. The carnivore assemblage described here is even more diverse than established in prior publications, including the identification of *Megantereon whitei*, *Lycyaenops silberbergi*, and first evidence for the occurrence of *Dinofelis* cf. *barlowi* and *Dinofelis* aff. *piveteaui* within a single South African site deposit. The cetartiodactyl assemblage is dominated by bovids, with the specimen composition unique in the high recovery of horn cores and dominance of *Antidorcas recki* remains. Other cetartiodactyl and perissodactyl taxa are represented by few specimens, as are *Hystrix* and *Procavia*; the latter somewhat surprisingly so given their common occurrence at penecontemporaneous deposits in the region. Equally unusual (particularly given the size of the sample) is the identification of single specimens of giraffoid, elephantid and aardvark (*Orycteropus* cf.  *afer*) that are rarely recovered from regional site deposits.

Despite the diversity within the DMQ macromammalian faunas there are few habitat- or

biochronologically-sensitive species that provide specific ecologic or age boundaries for the deposits. Recovered species can only support the non-specific, mixed open-to-closed palaeohabitats around Drimolen that have been reconstructed for the other penecontemporaneous South African palaeokarst deposits. The identified *Equus quagga* ssp. specimens recovered from the floor of the current excavation (~-4.5-5m below datum) suggests that most, if not all the DMQ specimens, were deposited after 2.33 Ma. Simultaneously, the identification of *D. cf. barlowi* and *L. silberbergi* are consistent with earlier Pleistocene deposits and a pre- 2.0-1.8 Ma deposition for at least some of the DMQ fossil assemblage.

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2 Quarry hominin-bearing deposits of the Drimolen Palaeocave System, South Africa

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25

26 **Abstract**

27

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29 hominin and primate-bearing deposits in the Fossil Hominids of South Africa UNESCO World  
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32 cranium of the species recovered to date), early *Homo*, *Papio hamadryas robinsoni* and  
33 *Cercopithecoides williamsi*. Alongside the hominin and primate sample is a diverse  
34 macromammalian assemblage, but prior publications have only provided a provisional species  
35 list and an analysis of the carnivores recovered prior to 2008. Here we present the first  
36 description and analysis of the non-primate macromammalian faunas from the DMQ, including  
37 all 826 taxonomically identifiable specimens catalogued from over two decades of excavation.  
38 We also provide a biochronological interpretation of the DMQ deposits and an initial discussion  
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47 cores and dominance of *Antidorcas recki* remains. Other cetartiodactyl and perissodactyl taxa are  
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59 the floor of the current excavation (~-4.5-5m below datum) suggests that most, if not all the  
60 DMQ specimens, were deposited after 2.33 Ma. Simultaneously, the identification of *D.* cf.  
61 *barlowi* and *L. silberbergi* are consistent with earlier Pleistocene deposits and a pre- 2.0-1.8 Ma  
62 deposition for at least some of the DMQ fossil assemblage.

63

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65 KEYWORDS: *Chasmaporthetes*; *Dinofelis*; *Lycyaenops*; *Megantereon*; *Paranthropus*; *Homo*

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**75 Introduction**

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77 The Drimolen fossil site was discovered in 1992 during survey of the region for a sinkhole by Dr  
78 A.W. Keyser (then with the Geological Survey of South Africa; since 1993 known as the  
79 Council for Geoscience, one of the National Science Councils of South Africa) (Figures 1 and 2).  
80 During his third site visit a hominin tooth was found from one of the ‘Main Pinnacles’, which led  
81 to ad-hoc calcified sediment collection and mechanical preparation of fossil specimens from  
82 1992 to mid-1994. In October 1994, a five-by-five metre alphanumeric grid was erected in the  
83 Main Quarry along with three fixed theodolite stations; shortly thereafter excavations into the  
84 decalcified material began that led to the recovery of the DNH 7 and 8 *Paranthropus robustus*  
85 specimens from the ‘Eurydice Pinnacle’ (Keyser et al., 2000). From 1995 until 2009, the site was  
86 excavated for 10 months out of the year, during which time changes to the grid system (e.g.,  
87 numeric) and calcified sediment extraction methods (e.g., feather-and-wedge vs. drilling) were  
88 introduced. Although greatly reduced excavation seasons (~6 weeks per year) have been  
89 employed from 2010 to the present, this nearly 25-year history of sampling the Main Quarry  
90 deposits has led to the recovery of a substantial assemblage of *Paranthropus robustus* and *Homo*  
91 sp. remains, as well as non-hominin primate and other faunal remains (Keyser et al., 2000;

92 Gommery, Senut & Keyser, 2002; Lockwood et al., 2007; O'Regan and Menter, 2009; Moggi-  
93 Cecchi et al., 2010; Gallagher and Menter, 2011)

94

95 These excavations into the Main Quarry, and progressive exposure of the Drimolen Palaeocave  
96 System, has established that the site consists of a single large cavern in-filled with three main  
97 types of sedimentary deposits (speleothem, breccia, siltstone/sandstone) that often grades from  
98 one to the other laterally across the exposures (Figure 2; Keyser et al., 2000). The base of the  
99 sequence consisted of a thick flowstone speleothem deposit that was extensively mined at the  
100 turn of the 20<sup>th</sup> century. This formed an undulating basal floor onto which all the other deposits  
101 and fossil were deposited. This basal speleothem consists of clast-poor layers of flowstone with a  
102 sharp contact to the overlying fossil-bearing sediments. As such, it formed a significant time  
103 before an entrance formed allowing the clastic deposits to enter the cave.

104

105 In the centre of the Main Quarry a thick clast-supported, fossil-bearing breccia (referred to by  
106 Keyser et al. [2000] as the 'Blocky Breccia') occurred that represents the opening and  
107 subsequent collapse of a vertical entrance to the cave forming a central debris cone. This is best  
108 preserved against the western wall of the cavern where the deposits remain indurated (Figure 2).  
109 The eastern part of this debris cone has suffered from collapse due to undercutting by lime  
110 miners removing the basal speleothem; as a result, the very eastern part of the Main Quarry was  
111 filled with mining debris and removal has accelerated the decalcification of these deposits.

112

113 During phases of flooding, the fine-grained fraction within the blocky breccia was then  
114 winnowed to the edges of the cavern to form a series of interstratified siltstone and sandstone

115 deposits (referred to by Keyser et al. [2000] as ‘Cave Siltstone’). As a result, these two  
116 sedimentological deposits are contemporary and the clast-supported breccia of the central debris  
117 cone grades through a matrix-supported breccia and into the laminated siltstone and sandstone  
118 deposits towards the edge of the cavern. This exact sequence of formation can be seen at the  
119 nearby Wonder Cave active karstic system. The oldest siltstone and sandstone deposits in-filled  
120 the southern area of the Main Quarry. As the debris cone began to grow upwards and expand  
121 laterally it became less steep and matrix supported breccia became more prevalent. It is possible  
122 that at this time the original vertical shaft entrance, that would have initially restricted the access  
123 of certain animals to the cave, may have become so in-filled with sediments that entry became  
124 more accessible via a shallow talus cone into the fine-clastic sediment floors at the edge of the  
125 cavern. The southern area of the Main Quarry had become completely in-filled during this early  
126 phase due to the presence of a stepped cave roof, leading to concentrated deposition of the fine-  
127 grained siltstone and sandstone in the northern area of the cavern. It is notable that macrofaunal  
128 remains have not been recovered from the oldest southern siltstone and sandstone deposits, but  
129 are instead recovered either from the northern siltstone and sandstone deposits or from the  
130 central talus cone, suggesting that they could have been washed into the cave or that animals  
131 inhabiting the cavern stayed in the daylight zone around the entrance. Despite this there is little  
132 to suggest that the two periods are separated by any significant time interval, other than a series  
133 of thin (<2cm) flowstones forming during the deposition of the northern siltstone and sandstone  
134 deposits.

135

136 Despite the decades of excavation into the Drimolen Palaeocave System, to date only a basic  
137 listing of macromammalian taxa recovered from the first years of Main Quarry deposits (Keyser

138 et al., 2000) and a more comprehensive analysis of the Order Carnivora (O'Regan and Menter,  
139 2009) have been previously published. This analysis provides the first primary description of the  
140 entire macromammalian (e.g., all Orders other than Macroscelidea, Insectivora, and Rodentia  
141 [exc. Family Hystricidae]) faunal assemblage excavated from the Drimolen Main Quarry since  
142 palaeontological sampling began in the early 1990s. We only present data on the fossil  
143 specimens attributable to at least Order as the taxonomically non-diagnostic remains from the  
144 deposits form the basis for a separate study reconstructing the taphonomy of the Main Quarry  
145 deposits. As we note below, to avoid unnecessary duplication of previously published data we  
146 also do not present primary descriptions on the previously described Main Quarry carnivores  
147 (O'Regan and Menter, 2009) or non-hominin primates (Nieuwoudt, 2014).

148

## 149 **Materials and Methods**

150

151 The Drimolen Main Quarry (DMQ) fossil assemblage is curated in the Evolutionary Studies  
152 Institute at the University of the Witwatersrand and consists of 1380 specimens derived from  
153 excavation of decalcified sediments and processed calcified sediment blocks (Keyser et al.,  
154 2000). Since the start of the excavations, the Drimolen Main Quarry decalcified material has  
155 been excavated in one-by-one meter (or smaller) squares in 10 cm increments and all material  
156 has been sieved through three different mesh sizes (the smallest being ~1 mm). The sieving  
157 regimen, though, has undergone some changes over the years with wet sieving of the smallest  
158 mesh size from 1997 along with all these “fines” being sorted at a sorting table and not just  
159 quickly “over the sieve”. Since 2014, we have also wet sieved the medium fraction via a water  
160 pump and all the “fines” are now sorted in the lab over the following year. Prior to 2003, the

161 only provenience for the decalcified material was by its grid square and 10cm level boundaries.  
162 Since 2003, a total station theodolite has been permanently used at Drimolen allowing  
163 identifiable specimens or fragments larger than 2 cm to be directly piece-plotted in reference to a  
164 three-dimensional model of the deposits created via a Trimble laser scanner in 2012 (via the  
165 University of Cape Town Zamani Project) and again in 2015 with a Leica Nova MS50  
166 multistation (from La Trobe University).

167

168 All calcified breccia blocks have been removed from the Main Pinnacles through standard  
169 feather-and-wedge techniques. Most of the calcified material was removed in the 1990s with no  
170 drilling of breccia after this period. Prior to 1997, this calcified material was either surveyed with  
171 a theodolite (without electronic distance meter) or at the very least the Pinnacle number or plane  
172 table location was recorded on the block. Since 1997, all calcified blocks were only sampled  
173 when a total station was available and were surveyed with at least six survey points. Breccia  
174 blocks within a decalcified excavation square were also recorded in this manner. The only other  
175 sampling of calcified material has been removing blocks that are decalcifying from the ‘Eurydice  
176 Pinnacle’. This material is prepared mechanically until close to the bone and then the reduced  
177 block is prepared via acetic acid processing.

178

179 For this analysis we only considered specimens preserving sufficient morphology to be identified  
180 at least to Order level and are not presenting data on indeterminate mammalian elements or  
181 fragments. We have also not undertaken an analysis of the 554 primate craniodental and  
182 postcranial specimens, as this collection has recently been partially analysed (see Nieuwoudt,  
183 2014) and a full publication of this substantial assemblage will be forthcoming. We have also not

184 duplicated the primary description of the Main Quarry carnivores of O'Regan and Menter  
185 (2009), but we have re-evaluated the previously published *Dinofelis* and *Chasmaporthetes*  
186 specimens because of their bearing on biochronological interpretations and present data on  
187 carnivore specimens catalogued since publication of that study.

188

189 The taxonomic and/or element attributions were made in direct reference to the extant mammal  
190 skeletal materials of the Department of Vertebrates (Large Mammal, Small Mammal and  
191 Archaeozoology Sections) collections of the Ditsong National Museum of Natural History  
192 (Pretoria, South Africa), previously described fossil specimens in the Plio-Pleistocene Section of  
193 the Ditsong Museum and Evolutionary Studies Institute of the University of the Witwatersrand  
194 (Johannesburg, South Africa). All measurements of specimens reported here were taken using  
195 Mitutoyo 150 mm calipers with a direct digital input, including dental (**MD**: mesiodistal, **BL**:  
196 buccolingual; taken at the level of occlusion unless otherwise noted) and horn core metrics (**AP**:  
197 anteroposterior, **ML**: mediolateral; taken at the level of the pedicle unless otherwise noted).  
198 Three-dimensional (3D) surface scans were captured with an Artec Spider (Artec Group,  
199 Luxembourg) to facilitate morphological comparisons of some of the specimens following  
200 methods described in Adams et al. (2015). In some cases, external specimens were examined  
201 using a Dino-Lite Edge AM4815ZTZ microscope (AnMo Electronics Corp.).

202

203 In order to facilitate discussion and integrate the DMQ assemblage within the broader South  
204 African late Pliocene and Pleistocene fossil record, we draw from the extensive published  
205 literature on the well-described penecontemporaneous South African fossil deposit faunal  
206 assemblages (e.g., Bolt's Farm, Gondolin, Haasgat, Kromdraai, Swartkrans, Sterkfontein). To

207 facilitate comparisons of the proportion (based on the minimum number of individuals, MNI) of  
208 mammals in the DMQ deposits relative to other South African assemblages we have also  
209 calculated the McIntosh evenness statistic (McIntosh, 1967). We would note, however, that such  
210 direct comparisons of faunal assemblages assume that the taphonomic histories of these deposits  
211 (from predepositional processes and time-averaging to excavation/sampling methodologies) have  
212 not introduced substantial biases in the faunal representation or abundance; an assumption that  
213 may not always be warranted as each deposit has an idiosyncratic depositional history (see  
214 discussions in Brain, 1981; Reed, 1996; Pickering, 1999; Adams, 2006). As a comprehensive  
215 taphonomic analysis of the DMQ assemblage is still ongoing, we will not address the role  
216 taphonomic processes had in shaping the faunal presence/absence/abundance with the Main  
217 Quarry deposits at this time. We also largely do not consider the more recently described faunal  
218 assemblages (e.g., Motsetse [Berger and Lacruz, 2003], Hoogland [Adams et al., 2010], Malapa  
219 [Dirks et al., 2010; Kuhn et al., 2012]) as the faunal data from these localities is based on  
220 extremely small sample sizes and generally limited to simple listings without primary  
221 descriptions or supporting data.

222

## 223 **Results**

224

225 The current listing of identified non-hominin specimens (number of individual specimens, NISP;  
226 MNI) from the Drimolen Main Quarry is provided in Table 1, including previously published  
227 primate specimens described in Nieuwoudt (2014) and carnivore specimens described in  
228 O'Regan and Menter (2009).

229

230 **Systematic Palaeontology**

231

232 Order CARNIVORA Bowditch, 1821

233 Family FELIDAE Batsch, 1788

234

235 Subfamily MACHAIRODONTINAE Gill, 1872

236

237 Genus DINOVELIS Zdansky, 1924

238 Type species *Dinofelis abeli* Zdansky, 1924

239

240 *Dinofelis cf. barlowi* Broom, 1937

241

242 **Referred specimens.** DN 2791, right partial maxillary canine.

243

244 **Description.** This single partial canine is the first specimen from the site to be considered  
245 comparable to *Dinofelis barlowi* (Figure 3A). The canine exhibits greater transverse crown  
246 compression than present in pantherines like extant and contemporaneous *Panthera pardus*  
247 Linnaeus, 1758 canines from Swartkrans Member 1 (e.g., SK 349 [0.77], SK 354 [0.75]) (Table  
248 3; Figure 4). The size and transverse crown compression of DN 2791 is consistent with the  
249 machairodonts *Dinofelis piveteaui* Ewer, 1955a KA 61 type specimen (0.59; BL: 12.12 mm /  
250 MD: 20.48mm) and *Dinofelis barlowi* BF-55 22 specimen (0.59; BL: 14.52 mm / MD: 24.54  
251 mm). In contrast to the canines of the KA 61 *D. piveteaui* specimen, the DN 2791 specimen is  
252 both more curved from root to crown, more oval in cross-section, and lacks the well-developed

253 distal carina. The DN 2791 specimen is, however, identical to BF-55 22 in root-to-crown  
254 curvature, the ovoid cross-sectional shape, and the development of the mesial and distal carinae.  
255 Based on these comparisons we provisionally attribute the canine to *D. cf. barlowi*. We discuss  
256 the significance of this novel specimen relative to the previously published DMQ *Dinofelis* aff.  
257 *piveteaui* craniodental and postcranial specimens (O'Regan and Menter, 2009) below.

258

259

260 Genus MEGANTEREON Croizet and Jobert 1828

261 Type species *Megantereon cultridens* Cuvier, 1824

262

263 *Megantereon whitei* Broom, 1937

264

265 **Referred specimens.** DN 976, left partial P4; DN 3254, left mandibular symphysis and corpus  
266 with partial canine.

267

268 **Description.** Two specimens represent the machairodont *Megantereon whitei* from the Drimolen  
269 Main Quarry deposits. The DN 976 left P4, while broken and reglued with slight distortion on  
270 the lingual aspect, preserves part of the protocone, paracone and metastyle (Figure 3B; Table 2).  
271 The protocone is extremely small and grades smoothly into the upright paracone. There is a deep  
272 notch separating the paracone and bulbous metacone, and a distinct notch on the metastyle. This  
273 morphology is shared with the KA 64 *Megantereon whitei* P4 to the exclusion of other  
274 machairodonts (e.g., *Dinofelis piveteaui*, *Dinofelis barlowi*), similarly-sized extant felids (e.g.,

275 *Panthera pardus*, *Acinonyx jubatus* Schreber, 1775), or the indeterminate Main Quarry felids  
276 (DN 530, 4300, 5498) described below.

277

278 The DN 3254 left partial mandible preserves part of the symphysis and alveolus for the i1-i3, the  
279 canine alveolus with part of the canine root, and the diastema (Figure 3C). Although this  
280 specimen preserves the anterior portion that does not overlap other South African *M. whitei*  
281 mandibles (e.g., KA 64, TM 856, STS 1588; Ewer, 1955a; Turner, 1987a), several  
282 morphological features align the specimen with *M. whitei*; the most diagnostic of these features  
283 is the presence of a mandibular flange on the anterolateral border of the corpus adjacent to the  
284 canine alveolus. The root of the canine indicates the tooth was small (length: 12.5, breadth: 7.1)  
285 and consistent with other African and Eurasian *Megantereon* specimens (Palmqvist et al., 2007).  
286 Finally, the diastema is sharply margined and elongated given the absence of any premolar  
287 alveolus despite the preserved length of the corpus.

288

289

290

Felidae gen. et sp. indet.

291

292 **Referred specimens.** DN 530, right P4; DN 558, left proximal ulna; DN 2236, terminal phalanx;  
293 DN 2701, left partial mandible; DN 2937, indet. maxillary incisor; DN 3291, right calcaneus;  
294 DN 4300, right P4 (probable antimere to DN 5498); DN 4354, two associated indet. mandibular  
295 incisors; DN 4590, right partial astragalus; DN 5498, left P4 (probable antimere to DN 4300).

296

297 **Description.** A small collection of carnivore craniodental and postcranial specimens are  
298 attributable to the Family Felidae but are not considered sufficiently diagnostic to attribute to  
299 genus or species. The DN 558 left proximal ulna preserves part of the olecranon process and  
300 articular surface and is derived from a large, *Dinofelis*-sized felid but is too damaged to  
301 confidently attribute. Also likely derived from a larger felid is the DN 3291 partial calcaneus and  
302 DN 4590 partial astragalus, with the latter similar to the previously described DN 2149b *D. aff.*  
303 *piveteaui* astragalus (O'Regan and Menter, 2009: 338). In contrast the DN 2236 phalanx is from  
304 a smaller felid species that appears slightly larger than extant caracal (*Caracal caracal* Schreber,  
305 1776) and preserves a robust volar surface. The DN 2937 maxillary incisor is tall, pointed, and  
306 distinctly tricusped, preserving parts of two discrete lingual accessory cusps and is consistent  
307 with derived machairodont incisors (e.g., BF-55 23 *D. barlowi*, KA 61 *D. piveteaui*, KA 64  
308 *Megantereon whitei*; Biknevicius, Van Valkenburgh & Walker, 1996; Christiansen and  
309 Adolfssen, 2007); the similarly-shaped DN 4354 mandibular incisors are also likely derived from  
310 a machairodont felid, perhaps the same individual, given their shared size and distinct  
311 morphology.

312

313 Four of the indeterminate felid craniodental specimens may ultimately be attributable below the  
314 level of Family with additional analysis beyond this primary description. The DN 2701 left  
315 mandible preserves the posterior portions of the corpus, including gonion and the condylar and  
316 coronoid processes. The masseteric fossa is deep and exhibits robust scarring both dorsal and  
317 ventral to the margins. The specimen is much smaller than *D. barlowi* (BF-55 23) and *D.*  
318 *piveteaui* (KA 62, KA 63) mandibular remains, but similar in size to both *M. whitei* (KA 64, STS  
319 1588) and *P. pardus* (extant comparative and SK 349) mandibles. However, in contrast with

320 extant *P. pardus* mandibles (and SK 349) the DN 2701 coronoid process is shorter, narrower  
321 anteroposteriorly, and less robust. In addition, the DN 2701 gonion exhibits less lateral flare and  
322 the condyle is more robust and angled relative to the axis of the corpus. The DN 2701 coronoid  
323 process is also smaller and less robust than that of the KB 5224b *M. whitei* mandible from  
324 Kromdraai B (Turner, 1987a), but shows a similar condylar morphology to both the KB 5224b  
325 and KA 64 specimens. Unfortunately, this region is poorly preserved or absent in other South  
326 African *Megantereon* mandibles to assess potential variability in coronoid process morphology  
327 that may eventually provide for a more confident attribution of the DN 2701 specimen.

328

329 The DN 530, 4300 and DN 5498 maxillary fourth premolars all preserve similar cusp  
330 morphologies (DN 4300 and DN 5498 are probable antimeres based on shared morphology and  
331 spatial position in the deposits) and are likely derived from the same felid species (Figure 5A).  
332 The DN 530 specimen exhibits damage to the crown elements, and the DN 5498 P4 was broken  
333 in three places and reglued; however, the latter retains some of the maxillary alveolar bone  
334 including the alveolus for the M1, which indicates a robust, ovoid and possibly double-rooted  
335 M1 in life. All of these specimens exhibit weakly-developed protocones that grade smoothly into  
336 the paracone, and a deep cleft dividing the paracone and metastyle. They are all larger than  
337 extant *Acinonyx jubatus* and *Panthera pardus* (comparative measurements in Turner, 1984;  
338 Table 2) and also differ in protocone size (e.g., more developed than in *A. jubatus*, less separated  
339 from the paracone and more distally positioned than in *P. pardus*). None of these specimens can  
340 be accommodated into *Dinofelis* based on their size and morphology of the parastyle and  
341 metastyle (Table 2). The closest metric and morphological match for these Main Quarry  
342 specimens is the KA 64 *Megantereon whitei* P4; however, the DN specimens exhibit a parastyle

343 more distinct from the paracone, a more rudimentary ectostyle, no buccolingual pinching of the  
344 metastyle, and a flared posterior lip of the metacone (Figure 5A). Lacking a strong  
345 morphological match for these specimens, we have deferred a more specific taxonomic  
346 attribution of the specimens pending further analysis.

347

348

349 Family HYAENIDAE Gray, 1821

350

351 Genus LYCYAENOPS Kretzoi, 1938

352 Type species *Lycyaenops rhomboideae* Kretzoi, 1938

353

354 *Lycyaenops silberbergi* Broom in Broom and Schepers, 1946

355

356 **Referred specimens.** DN 974, right P3.

357

358 **Description.** A primary description of the DN 974 specimen was provided in O'Regan and  
359 Menter (2009), although we differ in treating the DN 974 specimen as a right P3 rather than a  
360 right P2 based on size and morphology (Figure 5B; Table 3). In the original description,  
361 O'Regan and Menter (2009: 343-344) allocated DN 974, and the DN 404 partial cranium, to  
362 *Chasmaporthetes nitidula* Hay, 1921 based on dental metrics and interpretation of mesial  
363 accessory cusp and P4 morphology relative to the Swartkrans Member 1 *C. nitidula* specimens  
364 (specifically SK 305, 306, and 307) and previously published descriptions by Broom (1948) and  
365 Ewer (1955b).

366

367 In contrast to the prior taxonomic attribution, the preserved morphology of the DN 974 specimen  
368 is most consistent with the type specimen and other African specimens of *Lycyaenops*  
369 *silberbergi*. The DN 974 right third premolar preserves a tall paracone and a large distal  
370 accessory cusp, but no mesial accessory cusp and only a modest mesial cingulum. The crown is  
371 rectangular in outline, has a distally-shifted lingual shelf well-separated from the paracone, and  
372 the paracone is separated from the distal accessory cusp by a distinct ‘waist’, particularly well-  
373 developed on the labial aspect. This morphology is shared with the *L. silberbergi* P3 type (STS  
374 130) and other specimens from Sterkfontein Member 4 (STS 127, 130, 135; SF 369/372,  
375 383/373, 408) and the *Lycyaenops* cf. *L. silberbergi* from Laetoli (NHM AS 7.VI.35, LAET 75-  
376 494) (Turner, 1986, 1990; Werdelin and Dehghani, 2011). It differs from the *C. nitidula* P3s  
377 from Swartkrans Member 1 (SK 305, 306, 309, 312, 313) and Member 3 (SKX 29205) in the  
378 development of the strong waist on the labial aspect and generally in mesial accessory cusp  
379 morphology (Ewer, 1955b; Brain, 1981; Turner, 1993). We echo prior publications that there is  
380 some variability in mesial accessory cusp expression across *C. nitidula* maxillary premolars (e.g.,  
381 Brain, 1981: 234 ‘type A, primitive’ and ‘type B, advanced’; Werdelin and Peigné, 2010);  
382 however, only SK 305 and 306 preserve a more reduced mesial accessory cusp (the former is  
383 damaged in this region) and both have more developed mesial cusps than that seen on DN 974.  
384 As noted by O’Regan and Menter (2009) the DN 404 dentition is damaged, but the P3 has a  
385 distinctly oval profile and smooth labial contour; the mesial and lingual aspects of the crown are  
386 somewhat crushed and offset, prohibiting confident morphological assessment but likely  
387 exhibited a modest mesial accessory cusp (and is closely resembling the ‘type A, primitive’  
388 Swartkrans Member 1 SK 306 partial maxilla).

389

390

391

Hyaenidae gen. et sp. indet.

392

393 **Referred specimens.** DN 2864, partial right scapula; DN 2973, partial right P4; DN 3281,  
394 partial right P2.

395

396 **Description.** In addition to the four indeterminate hyaenid craniodental and postcranial  
397 specimens described by O'Regan and Menter (2009), three further elements can be attributed to  
398 the family. The DN 2864 scapula preserves a very large infraglenoid tubercle relative to the size  
399 of the preserved glenoid fossa and is derived from hyaenid smaller than extant *Parahyaena*  
400 *brunnea* Thunberg, 1820. The DN 2973 right P4 preserves the complete protocone and lingual  
401 aspect of the anterior accessory cusp and paracone with little occlusal wear. There is some  
402 buccolingual swelling on the paracone that is shared with extant *P. brunnea* P4s and the SK 327  
403 *P. brunnea* P4 from Swartkrans Member 1 (although smaller than the latter), and there is no  
404 evidence for buccolingual compression or a ridge leading to the trigon basin as in *Crocota*  
405 *crocota*. This specimen, along with the DN 2321 P4 fragment described by O'Regan and Menter  
406 (2009: 344), support the occurrence of a hyaenid individual distinct from *Lycyaenops* and  
407 *Chasmaporthetes* in the Main Quarry deposits. In contrast, the DN 3281 right P2 preserves the  
408 anterior margin of the crown and half of the anterior root that lacks the cingulum distinctive for  
409 *P. brunnea* dentition. The specimen preserves strong labial ridging and a flattened lingual aspect,  
410 and is too buccolingually expanded to represent *Chasmaporthetes* or *Lycyaenops*. The closest

411 extant morphological match is *Crocota crocuta*; minimally suggesting an additional hyaenid  
412 distinct from *L. silberbergi*, *C. nitidula*, and the DN 2973/2321 individuals.

413

414

415 Order CETARTIODACTYLA Montgelard et al., 1997

416 Family BOVIDAE Gray, 1821

417

418 Tribe ALCELAPHINI de Rochebrune, 1883

419

420 Genus CONNOCHAETES Lichtenstein, 1814

421 Type species *Connochaetes gnou* Zimmermann, 1780

422

423 *Connochaetes* sp.

424

425 **Referred specimens.** DN 704, left maxillary third molar; DN 1111a, right maxillary second  
426 molar.

427

428 **Description.** Only two of the identifiable alcelaphin specimens represent the genus  
429 *Connochaetes* in the Main Quarry sample. The DN 704 third molar, derived from decalcified  
430 sediments, is a complete crown (ML: 29.80 mm, BL: 19.02 mm) that exhibits moderate occlusal  
431 wear. The DN 1111a molar is also a complete crown (ML: 25.47 mm) with moderate occlusal  
432 wear but is set within a partially mechanically processed aggregation of indeterminate  
433 postcranial fragments. As isolated teeth the specimens cannot be confidently attributed below the

434 generic level. Both specimens are consistent in cusp morphology, central cavity complexity and  
435 overall size with extant comparatives and fossil *Connochaetes* sp. specimens from Swartkrans  
436 Members 1 Hanging Remnant (e.g., SK 2482, 3008, 3102, 14120x) (linear metrics in Vrba,  
437 1976).

438

439

440 Genus DAMALISCUS Sclater and Thomas, 1894

441 Type species *Damaliscus dorcas* Pallas, 1766

442

443 *Damaliscus* sp.

444

445 **Referred specimens.** DN 2790, right horn core; DN 4778, right horn core.

446

447 **Description.** Two partial right horn cores, representing two adult individuals, are attributed here  
448 to the genus *Damaliscus*. The most complete of the cores, DN 2790, preserves the pedicle  
449 (infiltrated by an extensive sinus) to approximately  $\frac{3}{4}$  of the body of the core, which exhibits a  
450 small amount of torsion approaching the broken margin (Figure 6A). The base of DN 2790 core  
451 is mediolaterally compressed (AP: 35.25 mm, ML: 26.34 mm) and there is a deep medial groove  
452 on the body. The DN 4778 specimen preserves the body of the core in two articulating pieces,  
453 with a third associated fragment lacking a clear contact point. While mechanical preparation  
454 damage to DN 4778 prohibits confident metric comparison it exhibits analogous mediolateral  
455 compression to the DN 2790 specimen.

456

457 Both the DN cores exhibit similar size, curvature and mediolateral compression to extant  
458 *Damaliscus dorcas* comparative specimens and the SK 14206 specimen attributed to *Damaliscus*  
459 cf. *dorcas* by Vrba (1976) (ML: ~24 mm). Both Main Quarry specimens contrast with previously  
460 described *Damaliscus niro* Hopwood, 1936 horn cores (including the Swartkrans Member 2  
461 specimen SK 2862) in size (e.g., SK 2862, AP: ~44 mm, ML: ~36 mm; Vrba, 1976; published  
462 metrics from Olduvai and Cornelia in Gentry and Gentry, 1978), the onset of torsion and the  
463 absence of transverse ridging (see also Cooke, 1974; Gentry, 2010). Although these two  
464 specimens are morphologically close to *D. dorcas*, we agree with Gentry (2010: 786) that a  
465 comprehensive revision of smaller *Damaliscus* from Pleistocene localities is critical before  
466 attributing specimens like the Main Quarry horn cores to a species within the genus.

467

468

469 Genus MEGALOTRAGUS van Hoepen, 1932

470 Type species *Megalotragus priscus* Broom, 1909

471

472 *Megalotragus* sp.

473

474 **Referred specimens.** DN 748a, right M2; DN 748b, right M3; DN 856, left M2 (?); DN 4807,  
475 left M2.

476

477 **Description.** Four isolated alcelaphin maxillary molars exhibit dental dimensions that exceed  
478 extant *Connochaetes* comparatives with analogous occlusal wear and are consistent with fossil  
479 specimens attributed to the extinct genus *Megalotragus*. The two associated right molars (DN

480 748a, b) preserve complete crowns (DN 748a ML: 27.90 mm, BL: 19.20 mm; DN 748b ML:  
481 36.02 mm, BL: 19.41 mm) and moderate-heavy occlusal wear (Figure 6B). Both DN 4807 and  
482 DN 856 are left M2s (with the DN 856 position in the tooththrow only tentative) with moderate  
483 occlusal wear. While DN 4807 is missing the lingual enamel surface and is somewhat distorted,  
484 DN 856 preserves a nearly complete probable M2 crown (ML: 31.64 mm, BL: 24.42 mm) (with  
485 regluing and minor enamel damage). All four of these specimens are directly comparable in size  
486 and cusp morphology to *Megalotragus* maxillary remains from Swartkrans Member 1 Hanging  
487 Remnant (e.g., SK 2245, 2432, 3031) and Member 2 (e.g., SK 14120, 14218) (linear metrics in  
488 Vrba, 1976).

489

490

491

Alcelaphini gen. et sp. indet.

492

493 **Referred specimens.** DN 3, left deciduous P3; DN 41, left maxillary molar; DN 42, left  
494 maxillary molar (associated with DN 41); DN 82, left M3; DN 90, left deciduous P3; DN 255,  
495 horn core fragment; DN 259, right m1; DN 309, left M1 or M2; DN 446, right m1; DN 475, right  
496 deciduous p4; DN 529, right mandible with deciduous p3-p4; DN 719, right P3; DN 722, right  
497 m1 or m2; DN 831, right (?) horn core fragment; DN 837, mandible fragment; DN 863, cranial  
498 fragment; DN 878, horn core fragment; DN 1001, left (?) horn core fragment; DN 1006, right  
499 deciduous p3; DN 1007, left m3; DN 1013, right horn core fragment; DN 1015, left mandible  
500 with deciduous p2-p4; DN 1021, right P3; DN 1025, deciduous P4; DN 1026, left m1 or m2; DN  
501 1043, horn core fragment; DN 1061, left M2; DN 1065, right deciduous p3; DN 1099, left (?)  
502 horn core fragment; DN 1143, left mandible with deciduous p2-p4; DN 1156, indet. side M2 or

503 M3; DN 2053, horn core pedicle fragment; DN 2157, right M1 or M2; DN 2161, horn core tip  
504 fragment; DN 2168, tooth fragment; DN 2854, right m3; DN 2992, left mandibular molar  
505 fragment; DN 4321, horn core fragment; DN 4466, right deciduous p4; DN 4514, right  
506 deciduous p4; DN 4526, left m3; DN 4647, molar fragment; DN 4653, left mandible with p3-p4;  
507 DN 4779, right M3; DN 4780, left m3.

508

509 **Description.** Because of either incomplete preservation and/or the metric and morphological  
510 overlap in the isolated dentition of extant and extinct alcelaphin genera and species, a total of 45  
511 Main Quarry specimens could not be confidently attributed below the level of the Tribe. Within  
512 this sample, 11 specimens (DN 259, 529, 722, 863, 878, 1099, 1156, 2157, 2161, 2992, and  
513 4653) are derived from minimally four larger size class III individuals (e.g., within the size range  
514 of extant *Connochaetes* or larger); all adults excepting DN 529, which is an extremely young  
515 individual with the deciduous premolars just erupting. The remaining specimens are derived  
516 from minimally 9 larger class II and smaller class III alcelaphin individuals (e.g., within the size  
517 range of extant *Damaliscus* and *Alcelaphus*), including at least seven immature individuals  
518 retaining their deciduous dentition (e.g., DN 1015; Figure 6C).

519

520 At present we include in this group five partial horn cores that may ultimately be attributable to  
521 the generic or specific level; however, the paucity of horn cores from penecontemporaneous South  
522 African fossil deposits (particularly relative to the eastern African record) limits our ability to  
523 confidently diagnose the specimens. The DN 4321 horn core exhibits a very large sinus within an  
524 expanded pedicle, but supporting a very compressed core body that somewhat resembles the  
525 morphology of extant *Sigmoceras lichtensteinii* Peters, 1849 (alt. *Alcelaphus buselaphus*

526 *lichtensteinii sensu* Gentry, 2010; Kingdon and Hoffman, 2013b). DN 1043 is a left, likely  
527 immature horn core (AP: 39.31 mm) that is derived from a smaller alcelaphin and somewhat  
528 resembles the immature cores of extant *Damaliscus lunatus* Burchell, 1823 as well as the SK  
529 14008 indeterminate bovid horn core from the Member 1 Hanging Remnant.

530

531 The three remaining horn cores (DN 255, 381, and 1013) appear to exhibit the same morphology  
532 and are likely derived from the same alcelaphin species. The most complete of these, DN 1013,  
533 is a ~10 cm portion of a right horn core pedicle and body (Figure 6D). The base of the horn core  
534 lacks bossing as in extant *Alcelaphus* or *Connochaetes*, and the strong anticlockwise torsion  
535 eliminates attribution to extant *Damaliscus* (as well as the Swartkrans Member 1 SK 3211b  
536 *Numidocapra porrocornutus* Vrba, 1971 specimen, and *Parmularius braini* Vrba, 1977 or  
537 *Damaliscus gentryi* Vrba, 1977 specimens from Makapansgat Member 3). Amongst the  
538 previously described alcelaphin fossil horn cores, the closest comparative specimen is the SK  
539 14183 *Beatragus* sp. Heller, 1912 from Swartkrans Member 2 (Vrba, 1976). When oriented  
540 relative to SK 14183, DN 1013 exhibits features previously used by Vrba (1976) when  
541 attributing the SK specimen to *Beatragus*: anteroposterior flattening of the core ~3cm above the  
542 base, anticlockwise torsion, a modest mesial keel, foramina along the anterolateral border, and  
543 slight swelling on the posterolateral aspect (which is compromised by surface damage) that may  
544 indicate the origin of a posterolateral keel. We note, however, that the DN 1013 specimen is  
545 smaller (AP: 37.78 mm, ML: 45.35 mm) than the SK 14183 *Beatragus* specimen (AP: 45.15  
546 mm, ML: 51.18 mm) and the torsion is more exaggerated; potentially reflecting ontogenetic,  
547 demographic or phylogenetic differences.

548

549

550

Tribe ANTILOPINI Gray, 1821

551

552

Genus ANTIDORCAS Sundevall, 1847

553

Type species *Antidorcas marsupialis* Zimmermann, 1780

554

555

*Antidorcas recki* Schwarz, 1932

556

557 **Referred specimens.** DN 224, left adult male horn core; DN 879, left male horn core; DN 884,  
558 right immature male horn core; DN 890, right adult male horn core; DN 938, left adult female  
559 horn core; DN 990, right (?) immature male horn core; DN 995, left adult female horn core; DN  
560 1014, right sub(?)adult female horn core; DN 1022, left adult male horn core; DN 1048, indet.  
561 side female horn core; DN 1055, right (?) immature male horn core; DN 1058, left sub(?)adult  
562 male horn core; DN 1060, right adult male horn core; DN 1068, left adult male horn core; DN  
563 1071, left sub(?)adult male horn core; DN 2483a left adult female horn core; DN 2483b right  
564 adult female horn core; DN 2789, indet. side male horn core; DN 3033, indet. side female horn  
565 core; DN 3294, right immature male horn core; DN 4438, right adult female horn core; DN  
566 4690, left immature male horn core (possible antimere of DN 884); DN 4698, indet. side female  
567 (?) horn core; DN 4777, right male horn core; DN 4796, left adult female horn core.

568

569 **Description.** At present, this collection of 25 *Antidorcas recki* horn core specimens from at least  
570 16 individuals is the largest described sample for the species from the Cradle (and outside the  
571 Olduvai Bed deposits) (Gentry, 1966; Gentry and Gentry, 1978; Cooke, 1996). It is also the most

572 demographically diverse from the South African deposits, with minimally eight males (three  
573 adult, 2 probable subadult, 3 immature) and eight females (seven adult, 1 probable subadult)  
574 recorded in the sample.

575

576 The morphology of the horn cores largely conform to the description of male and female *A. recki*  
577 specimens from Olduvai (Gentry, 1966; Gentry and Gentry, 1978) and Bolt's Farm Pit 3 (Cooke,  
578 1996) (and contrasts with extant *Antidorcas marsupialis* horn cores) in the vertical rise of the  
579 horn core from the sinus-filled pedicle, degree of mediolateral compression, strong posterior  
580 angulation within the short body, and a lack of lateral divergence or torsion (Figure 7A and 7B;  
581 Table 4). The adult and immature male DN specimens contrast with those of *Gazella vanhoepeni*  
582 Wells and Cooke, 1956 from the Makapansgat Member 3 deposits (e.g., M 412, 415, 2224, 2717,  
583 8245, 8384, 9006, 9026) in the less pronounced mediolateral compression, core body size, and  
584 the sharper posterowards curvature in the core (Figure 7A). We do note, however, that none of  
585 the male DN horn cores exhibit the strong transverse ridging present on the Bolt's Farm Pit 3  
586 male cranium (UCMP 69521), which aligns the DN specimens with some of the noted *A. recki*  
587 variants from Olduvai and Peninj described by Gentry and Gentry (1978: 429). The substantial  
588 sample of female *A. recki* horn core specimens in the Main Quarry sample provides further  
589 evidence for the presence of strong sexual dimorphism in this skeletal feature within the species  
590 (Cooke, 1996). The DN female cores are substantially smaller, straighter, and exhibit a far more  
591 rounded cross-section than the male counterparts (Figure 7B); consistent with the morphology of  
592 the Bolt's Farm Pit 3 UCMP 80168 and 80169 specimens (Cooke, 1996; Table 4).

593

594

*Antidorcas cf. recki*

595

596 **Referred specimens.** DN 140, right indet. maxillary molar; DN 175, right m1 or m2; DN 308,  
597 right m3; DN 401, left P4; DN 447, right m1; DN 989, right P3; DN 1002, right mandible with  
598 p4-m2 (associated with DN 2283); DN 1034, right m1 or m2; DN 1054, right M1 or M2; DN  
599 1059, indet. side male (?) horn core; DN 1115, right immature horn core; DN 1116, right m3;  
600 DN 1135, left P4; DN 2175, indet. side m1 or m2; DN 2270, left mandible with p4 and m2; DN  
601 2271, right P4; DN 2283, right m3; DN 2307, right immature horn core; DN 2328, left p4; DN  
602 2554, left M2; DN 2614, right mandible with deciduous p2-p4 and m1-m2; DN 3009, left P3;  
603 DN 3287, right m2; DN 3346, left m1 or m2; DN 4185, right M2; DN 4290, right m3.

604

605 **Description.** In addition to the attributed *Antidorcas recki* horn cores, a collection of 26  
606 *Antidorcas* craniodental specimens have also been recovered from the Main Quarry deposits.  
607 This sample of isolated teeth display similar crown morphology with other previously attributed  
608 *Antidorcas recki* dentition from Bolt's Farm (see above; Cooke, 1996), Kromdraai A (e.g., KA  
609 964B, 1002, 1111, 1093) and dissimilar to both extant *Antidorcas marsupialis* Zimmerman, 1780  
610 and the hypsodont *Antidorcas bondi* Cooke and Wells, 1951 specimens from Swartkrans  
611 Member 2 (Vrba, 1976). Furthermore, most of these isolated specimens were recovered  
612 interspersed within the decalcified Main Quarry sediments alongside the diagnostic *A. recki* horn  
613 core specimens; and in the case of DN 3346 and 4185, were recovered from just adjacent to the  
614 DN 3033 and 3294 horn cores. We do, however, recognise and support the caution expressed by  
615 Gentry (2010) regarding the separation of remains of *A. recki* from early remains of *A. bondi* and  
616 *Antidorcas australis* Hende and Hende, 1968/*A. marsupialis*. In keeping with a more

617 conservative approach to these fragmentary craniodental remains, we treat them as provisionally  
618 attributable to *A. recki*.

619

620

621 Genus RAPHICERUS C.H. Smith, 1827

622 Type species *Raphicerus campestris* Thunberg, 1811

623

624 *Raphicerus* sp.

625

626 **Referred specimen.** DN 591, right p3.

627

628 **Description.** The single right mandibular third premolar is a complete crown (ML: 7.68mm, BL:  
629 3.10mm) with only superficial occlusal wear. The tooth is very mesiodistally elongate, exhibiting  
630 the gracile cusp morphology and weak-development of distal elements (e.g., hypoconid,  
631 entoconid/entostylid barely developed and fused) that is similar to the equivalent tooth preserved  
632 in the KA 710 *Raphicerus campestris* mandible from Kromdraai A (Vrba, 1976) and extant *R.*  
633 *campestris* comparatives.

634

635

636 Tribe OREOTRAGINI Pilgrim, 1939

637 Genus OREOTRAGUS A. Smith, 1834

638 Type species *Oreotragus oreotragus* Zimmermann, 1783

639

640 *Oreotragus* sp.

641

642 **Referred specimens.** DN 290, left mandible with deciduous p3; DN 400, right m2; DN 432,  
643 right m1 (associated with DN 400); DN 438, right mandible with m1-m3; DN 590, left M1 or  
644 M2; DN 710, right mandible with deciduous p3; DN 857, left mandible with m3; DN 910, right  
645 mandible with m1-m3; DN 965, right mandible with deciduous p3; DN 1008, right mandible  
646 with deciduous p3; DN 1046, left M1 or M2; DN 4773, left m2.

647

648 **Description.** The 12 mandibular specimens attributed here to *Oreotragus* are derived from at  
649 least nine individuals (five adults with occluded third molars, four immature individuals  
650 retaining their deciduous premolars). The more complete DN 438 (m2 MD: 11.96 mm, BL: 5.82  
651 mm; m3 MD: 16.02 mm, BL: 5.66 mm; Figure 7C), DN 857 (m1 MD: 9.53 mm, BL: 6.15 mm;  
652 m2 MD: 11.79 mm, BL: 6.42 mm; m3 MD: 19.34 mm, BL: 6.45 mm) and DN 910 (m1 BL: 5.79  
653 mm; m2 MD: 13.31 mm, BL: 6.49 mm; m3 MD: 15.41 mm, BL: 6.51 mm) specimens preserve  
654 relatively complete corpora and molars. The dental measurements of the DN *Oreotragus*  
655 specimens place them roughly in the narrow zone of overlap between the smaller-bodied fossil  
656 *Oreotragus* populations from Gondolin GD 2 and the larger-bodied *Oreotragus* from Haasgat  
657 HGD and Makapansgat Member 3 (see Adams, 2012a for comparative *Oreotragus* dental  
658 metrics). As noted in Adams (2012), a comprehensive revision of the fossil record of the genus is  
659 essential to establish the significance of the metric variability in *Oreotragus* across South  
660 African Plio-Pleistocene deposits.

661

662

663 Tribe REDUNCINI Knottnerus-Meyer, 1907

664 Genus REDUNCA C.H. Smith, 1827

665 Type species *Redunca redunca* Pallas, 1767

666

667 *Redunca cf. fulvorufula* (Afzelius, 1815)

668

669 **Referred specimens.** DN 111, right partial horn core and orbital margin; DN 2573, right partial  
670 horn core; DN 4775, right partial horn core.

671

672 **Description.** The most complete of the reduncin horn core specimens attributed to *Redunca cf.*  
673 *fulvorufula* is DN 111, which preserves the right horn core pedicle as well as part of the right  
674 superior orbital margin and cranial vault. The two other right horn cores, while retaining less  
675 adhering cranial vault portions preserve the same core morphology as DN 111. The angle of horn  
676 core insertion, absence of sinuses in the pedicle, and development of the postcornual fossa are  
677 consistent with members of the tribe, and the size, insertion angle and cross-sectional shape of  
678 the core excludes attribution to genus *Kobus* Smith, 1840. Among extant and extinct *Redunca*  
679 species, the DN specimens are smaller than, and exhibit more upright and rounder horn cores,  
680 than both the extinct *Redunca darti* Wells and Cooke, 1956 from Makapansgat Member 3 (e.g.,  
681 M 446 [type specimen], M 453, M 461, M 464, M783) and extant *Redunca arundinum* Boddaert,  
682 1785 comparative specimens (see also discussion of *Redunca* horn cores in Adams, 2006). The  
683 DN horn cores are similar in these morphological features to extant *Redunca fulvorufula* and the  
684 Gondolin GD 2 *Redunca* sp. horn cores (Adams and Conroy, 2005; Adams, 2006), but are from  
685 distinctly smaller-bodied individuals than the population sampled in the Gondolin GD 2

686 assemblage. Although the evolutionary relationships of South African Plio-Pleistocene *Redunca*  
687 and the diversity of reduncins during the Neogene remain unresolved (see Adams and Conroy,  
688 2005; Adams, 2006, 2012; Adams et al., 2010; Gentry, 2010), the morphology expressed by the  
689 Main Quarry specimens is most comparable with extant *R. fulvorufula*; a species present in the  
690 Cradle by at least the mid-Pleistocene (e.g., Gladysvale External Deposits; Lacruz et al., 2002).

691

692

693 Tribe TRAGELAPHINI Blyth, 1863

694 Genus TRAGELAPHUS de Blainville, 1816

695 Type species *Tragelaphus scriptus* Pallas, 1766

696

697 *Tragelaphus* sp.

698

699 **Referred specimens.** DN 120, right mandible with p2-m3; DN 163, left m3; DN 164, left m1;  
700 DN 165, left m2; DN 399, right p3; DN 1011, left M1; DN 1027, associated right p3, p4, and  
701 m1-m2 in a mandibular corpus; DN 2788, left maxilla with deciduous P4 – M2; DN 4112, right  
702 m1 or m2.

703

704 **Description.** The Drimolen Main Quarry *Tragelaphus* sample includes at least two different  
705 species. At least one species of large *Tragelaphus* is represented by the DN 399 and DN 2788  
706 specimens. The crown of the DN 399 p3 is complete and unworn, but the roots are incompletely  
707 formed. The crown is brachydont and the morphology of the paraconid, metaconid and entoconid  
708 are consistent with extant *Tragelaphus strepsiceros* Pallas, 1766 comparative specimens. The

709 DN 2788 maxilla retains the deciduous p4 and the M2 is just reaching the occlusal plane. Like  
710 the DN 399 specimen, the brachydonty and loph morphology is consistent with the genus, and  
711 size of the dentition is within the range of extant *T. strepsiceros*. Although these two specimens  
712 could potentially be derived from the same immature individual, we consider them as  
713 representing minimally two different individuals based on provenance: the DN 399 specimen  
714 was recovered from decalcified sediments (-2.3m below datum; MBD) whereas the DN 2788  
715 specimen was mechanically recovered from a surface-recovered *ex situ* calcified sediment block.

716

717 The remaining specimens are derived from at least one smaller species of *Tragelaphus*, likely  
718 representing minimally four individuals of *Tragelaphus pricei* Wells and Cooke, 1956 or the  
719 *Tragelaphus scriptus* lineage; however, lacking horn cores we cannot provide a more specific  
720 attribution. The most complete of these specimens are the DN 120 and DN 1027 right mandibles  
721 (Figure 6C). Both specimens exhibit similar dental metrics, corpus depths, premolar morphology  
722 (including paraconid-metaconid fusion on the p4) and buccal lophid rounding to the *T. pricei*  
723 holotype (M 18) and paratype (M 17, M 19) specimens from the Makapansgat Member 3  
724 deposits (Wells and Cooke, 1956). The evolutionary relationships between the South African *T.*  
725 *pricei* and other smaller fossil *Tragelaphus* (e.g., *Tragelaphus nkondoensis* Geraads and Thomas,  
726 1994) and extant *T. scriptus* is not resolved (see Gentry, 2010), and further assessment of the  
727 African record may eventually permit a more specific diagnosis of the Main Quarry specimens.

728

729 *Tragelaphini* gen. et sp. indet.

730

731 **Referred specimens.** DN 1193, right m1 or m2 with associated tooth fragment in matrix.

732

733 **Description.** Two associated craniodental specimens (catalogued as DN 1193) are  
734 morphologically consistent with a large-sized tragelaphin but are not attributable to generic level.  
735 The associated tooth fragment is a partial molar (probably a lower buccal loph), while the more  
736 complete tooth is a damaged right lower molar lacking the lingual enamel surface. The angled  
737 buccal lophids and brachydonty of the lower molar is consistent with the tribe, and the size  
738 places the specimen within the range of extant *Tragelaphus strepsiceros* and smaller  
739 *Taurotragus oryx* individuals.

740

741

742

Bovidae gen. et sp. indet.

743

744 **Referred specimens.** 538 specimens (see Supplemental Table 1)

745

746 **Description.** The majority of the indeterminate bovid specimens from the Main Quarry deposits  
747 are postcranial elements (n = 365), with only 173 craniodental specimens (primarily  
748 nondiagnostic enamel fragments, mandibular incisors or poorly preserved horn core fragments)  
749 not attributed below the Family level (Supplemental Table 1). Although these remains are  
750 undiagnostic, we would note that there is no indication of additional bovid taxa in the Main  
751 Quarry deposits beyond those established by the other referred specimens above. The one  
752 exception is the DN 647 partial left maxillary molar, which exhibits hypsodonty consistent with  
753 alcelaphins, but also resembles some of the smaller ovibovin remains potentially attributable to

754 *Makapania* Wells and Cooke, 1956 from Swartkrans Member 1, Gladysvale, and Haasgat HGD  
755 (Vrba, 1976; Lacruz et al., 2002; Adams, 2012a).

756

757

758 Family GIRAFFIDAE Gray, 1821

759

760 Giraffidae gen. et sp. indet.

761

762 **Referred material.** DN 1097, right humerus.

763

764 **Description.** The DN 1097 specimen is an extremely large right cetartiodactyl humerus that  
765 preserves the medial portion of the condyle, supracondylar region, and the diaphysis to the distal-  
766 most portion of the humeral crest (Figure 8A). Although no standard metrics could be gathered,  
767 the preserved length of the specimen is ~26 cm and the length of the medial epicondyle to  
768 midsagittal of the condyle is ~6.5 cm, indicating an approximate epicondylar width of ~12-13  
769 cm. In addition to the size of the preserved specimen, several morphological features align DN  
770 1097 to extant giraffid comparative specimens (e.g., *Giraffa camelopardalis* Linnaeus, 1758) to  
771 the exclusion of a large bovid (e.g., extant *Syncerus caffer* Sparrman, 1779). The supracondylar  
772 diaphysis is ovoid (anteroposteriorly compressed, mediolaterally wide) rather than triangular  
773 from a more robust humeral crest. The medial articular surface of the condyle is  
774 anteroposteriorly flattened and cylindrical, and lacks a strongly developed sagittal ridge laterally.

775

776 Unfortunately, there is a paucity of fossil giraffid postcranial from the South African  
777 palaeokarstic deposits, with only small collections described from Makapansgat Member 3 and  
778 the Swartkrans Members 1-3 deposits (Reed, 1996; Watson, 1993). Only a single humerus  
779 attributed to the extinct *Sivatherium* Falconer and Cautley, 1836 has been described from  
780 Swartkrans Member 1 Hanging Remnant (SK 3172), but this left humerus preserves only the  
781 non-overlapping proximal region. The penecontemporaneous eastern African record is more  
782 substantial, with postcranial samples from Koobi Fora, Olduvai, Omo-Shungura and Laetoli  
783 (Harris, 1976; Leakey and Harris, 1987; Harris, 1991; Robinson, 2011). The features that would  
784 allow for confident attribution of the DN specimen as either giraffine or sivatherine (e.g.,  
785 elongation of the diaphysis, relative compression and width of the distal epiphyses) cannot be  
786 ascertained in the preserved state; and the humeri of Plio-Pleistocene giraffid species overlap  
787 significantly in simple linear metrics (Leakey and Harris, 1987; Harris, 1991; Robinson, 2011).  
788 Given these limitations, we treat this specimen as indeterminate below the Family level.

789

790

791

Family SUIDAE Gray 1821

792

793

Suidae gen. et sp. indet.

794

795 **Referred material.** DN 2850, right third metatarsal.

796

797 **Description.** The DN 2850 specimen is a nearly complete right third metatarsal from a juvenile  
798 suid, preserving a notably immature proximal articular surface (missing part of the medial

799 articular surface) and an unfused distal metaphyseal surface (Figure 8B). The diaphysis of the  
800 element is visibly robust (ML: 12.07 mm, dorsoventral depth: 10.05 mm) given its overall length  
801 (53.18 mm). Metric comparisons of the proximal articular and distal metaphyseal surfaces of DN  
802 2850 against the third metatarsals of extant *Phacochoerus aethiopicus* Pallas, 1766 and  
803 *Potamochoerus porcus* Linnaeus, 1758 place this very immature element outside or just within  
804 the measured ranges of even fully adult *P. aethiopicus* and *P. porcus* individuals with complete  
805 proximal articular surface development and distal metaphyseal fusion (Table 5). The size of the  
806 specimen at its developmental stage would therefore seemingly preclude attribution to either of  
807 these extant genera.

808

809 Comparable fossil suid third metatarsals are extremely rare within African Plio-Pleistocene  
810 deposits (Bishop, 1994); however, a partial right third metatarsal of *Metridiochoerus andrewsi*  
811 (G 8105) has been described from the Gondolin GD 2 assemblage (Adams, 2006). The G 8105  
812 specimen only preserves the proximal articular surface and part of the diaphysis and is derived  
813 from a more developmentally mature individual (or full adult), and the single comparable  
814 measurement reflects the larger body size of the species compared to the extant suids (Table 5).  
815 While the overall shape of the proximal articular surface and robusticity of the diaphysis appears  
816 shared between DN 2850 and G 8105, the significant ontogenetic differences prohibit confident  
817 attribution of the Main Quarry specimen to the same genus or species based solely on these  
818 broad similarities. Similarly, while other suid genera (e.g., *Notochoerus*, *Kolpochoerus*) are less  
819 frequently recovered than remains of *Metridiochoerus* in South African Plio-Pleistocene  
820 deposits, we also lack equivalent postcrania for these lineages to allow for direct comparisons. At

821 present, we can only state that this specimen is derived from an extinct suid lineage that  
822 exhibited larger adult body size than extant or attributed fossil *Phacochoerus* or *Potamochoerus*.

823

824

825 Order PERISSODACTYLA Owen, 1848

826 Family EQUIDAE Gray, 1821

827 Genus EQUUS Linnaeus, 1758

828 Type species *Equus caballus* Linnaeus, 1758

829

830 *Equus cf. quagga* ssp. (Boddaert, 1785) (*sensu* Klingel, 2013)

831

832 **Referred material.** DN 3424, left distal tibia; DN 4525, intermediate phalanx; DN 4781, partial  
833 ungual phalanx.

834

835 **Description.** The DN 3424 specimen preserves part of the distal metaphysis and articular surface  
836 from a left tibia, from the medial malleolus to the midline. There is no indication of persistence  
837 of a metaphyseal line indicating full closure of the distal growth plate and skeletal maturity of the  
838 element. Unfortunately, no standard metrics could be taken from the specimen to facilitate  
839 comparisons, but the element is directly comparable to extant *E. quagga* ssp. tibiae in size and  
840 morphology and is visibly smaller than the *Equus capensis* Broom, 1909 distal tibiae previously  
841 described from Swartkrans Members 1 Lower Bank (SKX 9596) and 2 (SKX 2390) (Churcher  
842 and Watson, 1993), as well as the *Equus* sp. specimen from the Haasgat HGD deposits (HGD  
843 1015; Adams, 2012a).

844

845 The DN 4525 intermediate phalanx preserves the proximal epiphysis (ML: 45.89 mm,  
846 dorsoventral depth: 32.97 mm) and most of the diaphysis, but lacks the distal articular surface  
847 and some of the anterior face of the distal metaphyseal/diaphyseal region. The articular surfaces  
848 as preserved appear fully mature, there is no indication of a persistent metaphyseal line. As is the  
849 case with the DN 3424 tibia, the intermediate phalanx is consistent with extant *E. quagga* ssp.  
850 intermediate phalanges in size and morphology and smaller than previously described *E.*  
851 *capensis* specimens from Swartkrans Member 3 (SKX 39182: proximal ML: 50 mm [min.],  
852 proximal dorsoventral depth: 36 mm [min.]) and Haasgat HGD (HGD 1099, proximal ML: 53.49  
853 mm, proximal dorsoventral depth: 33.84 mm) (Churcher and Watson, 1993; Adams, 2012a).

854

855 The DN 4781 specimen preserves only a partial proximal articular facet and part of the volar  
856 surface of an equid ungual phalanx. The specimen is visibly larger than the hipparionin ungual  
857 phalanges previously described from Swartkrans Member 1 (SKX 9166), Member 2 (SKX  
858 2626), and Gondolin GD 2 (G 4218) (Churcher and Watson, 1993; Adams, 2006), and there is no  
859 indication of multiple nutrient foramina on the volar surface or posterior projection of the  
860 articular surface consistent with that tribe. The specimen appears to fall within the size range of  
861 extant *E. quagga* ssp. comparative specimens, and was recovered in close spatial proximity to  
862 the DN 3424 and 4525 specimens (see below). Collectively, this supports allocating this  
863 specimen to both *E. quagga* ssp. and potentially to the same individual as the other equid  
864 remains from the Main Quarry decalcified deposits.

865

866

867 Order PROBOSCIDEA Illiger, 1811

868 Family ELEPHANTIDAE Gray, 1821

869

870 Elephantidae gen. et sp. indet.

871

872 **Referred material.** DN 4335, maxillary incisor fragment.

873

874 **Description.** A single tusk fragment (DN 4335) recovered from the decalcified sediments can be  
875 attributed to an indeterminate genus and species of elephantid (Figure 9A). The recovery of this  
876 specimen, while relatively rare within other palaeokarstic deposits from the region, is not  
877 unexpected given the presence of minimally two separate elephantid tusk portions within the  
878 unexcavated calcified sediments of the Drimolen Main Quarry. The fragment exhibits both  
879 surface pitting and break-edge rounding, and it is uncertain whether the specimen preserves the  
880 most external, cortical enamel lamina or a more internal layer of enamel. The inner surface of the  
881 fragment exhibits fresh exposure of enamel that highlights the light longitudinal banding of the  
882 enamel, which under magnification is matched on the external, pitted surface of the specimen.  
883 The DN specimen is similar in laminar enamel thickness and suggested cross-sectional area and  
884 shape to the Swartkrans Member 1 Lower Bank specimens that have been previously attributed  
885 to *Elephas* sp. Linnaeus, 1758 (SKX 45691, 45692b; Watson, 1993); however, as a single tusk  
886 fragment we remain conservative in our attribution until further remains are recovered.

887

888

889 Order HYRACOIDEA Huxley, 1869

890 Family PROCAVIIDAE Thomas, 1892

891 Genus PROCAVIA Storr, 1780

892 Type species *Procavia capensis* Storr, 1780

893

894 *Procavia* sp.

895

896 **Referred material.** DN 552, left m1 or m2; DN 2365b, right I1; DN 2971, right and left I1  
897 (antimeric); DN 3072, right distal femur; DN 4219, right I1.

898

899 **Description.** In contrast to the faunal samples recovered from most other South African  
900 palaeokarstic localities and deposits there is only an extremely small sample of hyrax remains at  
901 the Drimolen Main Quarry deposits (see Churcher, 1956; Brain, 1981). The collection of six total  
902 specimens are largely isolated central incisors. The antimeric pair (DN 2971) are most likely  
903 from a male individual given the sharp, centrally-positioned keel, while the DN 2365b and 4219  
904 specimens exhibit the more rounded contour and mesial position of the central keel consistent  
905 with being from females (Churcher, 1956). None of the recovered teeth are metrically consistent  
906 with *Procavia transvaalensis* Shaw, 1937 (see comparative measurements in Churcher, 1956).  
907 Similarly, the DN 3072 distal femur is homologous to extant *Procavia capensis* Pallas, 1766  
908 comparative specimens and visibly smaller than the *P. transvaalensis* distal femur from Haasgat  
909 HGT (HGT 1004; Adams, 2012a). As the composition of the sample does not allow us to  
910 diagnose whether the sample is derived from the extinct *Procavia antiqua* Broom, 1934 (see also  
911 Schwartz, 2007) and/or extant *P. capensis*, we can only attribute the Main Quarry specimens to a  
912 species of *Procavia* that is not *P. transvaalensis*.

913

914

915

Order LAGOMORPHA Brandt, 1855

916

Family LEPORIDAE Fischer von Waldheim, 1817

917

918

Genus PRONOLAGUS Lyon, 1904

919

Type species *Pronolagus crassicaudatus* Geoffroy, 1832

920

921

*Pronolagus* sp.

922

923 **Referred material.** DN 2823, right mandible preserving the p3-m2.

924

925 **Description.** Only one of the 38 identified leporid remains could be identified as representing as926 species of *Pronolagus* in the Drimolen Main Quarry deposits. The overall size of the specimen is927 significant smaller than in extant *Lepus capensis* Linnaeus, 1758, and the p3 exhibiting both

928 anterior reentrants and no evidence of the posteroexternal reentrant extending nearly to the

929 lingual border of the tooth as in *Lepus*. Amongst extant analogues, the overall mandibular930 morphology is similar to *Pronolagus rupestris* Smith, 1834 but the dentition and corpus is931 somewhat smaller than both male and female *P. rupestris* comparatives. Given the currently

932 limited data on the South African leporid record (Winkler and Avery, 2010), we retain the

933 specimen at the generic level pending a more comprehensive review of the South African Plio-

934 Pleistocene lagomorphs.

935

936

937

Leporidae gen. et sp. indet.

938

939 **Referred material.** DN 771, right immature proximal tibia; DN 1083, left calcaneus; DN 2104,

940 right calcaneus; DN 2155, left distal scapula; DN 2256, left immature proximal tibia; DN 2330,

941 left mandibular corpus; DN 2333, right maxillary premolar or molar; DN 2341, left calcaneus;

942 DN 2342, left calcaneus; DN 2365c, left distal humerus; DN 2571, right immature distal femoral

943 epiphysis; DN 2715a, right distal humerus; DN 2715b, left proximal ulna; DN 2736, right

944 immature calcaneus; DN 2798, right proximal tibia; DN 2800, right immature distal femoral

945 epiphysis; DN 2805, right immature distal femoral metaphysis (articulates with DN 2800); DN

946 3059, left immature distal femoral epiphysis; DN 3304, left distal scapula; DN 4114, left

947 proximal ulna; DN 4116, left distal humerus; DN 4118, left calcaneus; DN 4120, associated set

948 of three lumbar vertebrae and sacrum; DN 4127, right immature proximal ulnar metaphysis; DN

949 4208, right distal humerus; DN 4225, left distal humeral metaphysis; DN 4226, left distal tibia;

950 DN 4227, right distal scapula; DN 4228, left proximal ulna; DN 4229, partial edentulous

951 maxilla; DN 4257, left immature calcaneus; DN 4381, left immature distal femoral epiphysis;

952 DN 4399, indet. side immature distal femoral epiphysis; DN 4531, left proximal tibial

953 metaphysis.

954

955 **Description.** The indeterminate leporid sample includes 34 numbered specimens (representing

956 36 total elements). Other than fragmentary and indeterminate craniodental remains (DN 2333

957 and DN 4229), the current collection is comprised of postcranial remains from what are likely

958 two different species. The majority of the remains are derived from a lagomorph somewhere in

959 body size between extant *Lepus capensis* and *Pronolagus rupestris*. A smaller lagomorph that  
960 had adult and immature postcranial elements smaller than adult extant *P. rupestris* is represented  
961 by DN 2104, 2155, 2715a&b, 2800, 2805, 3059, 4120, and 4228.

962

963

964

Order RODENTIA Bowdich, 1821

965

Family HYSTRICIDAE Fischer de Waldheim, 1817

966

Genus HYSTRIX Linnaeus, 1758

967

Type species *Hystrix cristata* Linnaeus, 1758

968

969

*Hystrix* sp.

970

971 **Referred material.** DN 2760, left maxillary molar (M2?)

972

973 **Description.** Only a single identifiable left maxillary molar can be attributed to an indeterminate  
974 species of porcupine (Figure 9B). The presence of both mesial and distal interstitial wear facets  
975 indicate that the specimen is either an M1 or M2; we favour the latter based on both the size and  
976 occlusal outline but cannot confidently attribute the position. Metrically, the specimen (MD: 8.19  
977 mm, BL: 9.27 mm [min. given minor enamel flaking]) falls within the range of extant *Hystrix*  
978 *africaeausustralis* Peters, 1852 maxillary M1s and M2s and is smaller than both *Hystrix*  
979 *makapanensis* Greenwood, 1958 and *Xenohystrix crassidens* Greenwood, 1955 (Adams, 2012b).  
980 We would note, however, that the current metric range for *H. makapanensis* M1 and M2 is based  
981 on an extremely small sample from the Gondolin GD 2 assemblage (e.g., derived from two

982 individuals; Adams, 2012b). As an isolated tooth lacking other diagnostic features we elect to  
983 retain the specimen at the generic level.

984

985

986 Order TUBULIDENTATA Huxley, 1872

987 Family ORYCTEROPODIDAE Gray, 1821

988 Genus ORYCTEROPUS Geoffroy Saint-Hilaire, 1796

989 Type species *Orycteropus afer* Pallas, 1766

990

991 *Orycteropus cf. afer*

992

993 **Referred material.** DN 1062, right proximal radius.

994

995 **Description.** The DN 1062 right proximal radius preserves a nearly complete head with articular  
996 surfaces and radial tuberosity, but very little diaphysis distal to the tuberosity (Figure 9C).  
997 Although there is minor abrasion damage to the cortex around the radial head, the minimum  
998 linear dimensions are 17.06 mm mediolaterally and 12.50 mm dorsoventrally. The articular  
999 surface morphology of the specimen is diagnostically orycteropodid (to the exclusion of  
1000 similarly sized carnivores, primates, *Hystrix* and *Smutsia* [Order Philodota]) in the well-  
1001 developed medial articular facets for contact with the lateral coronoid process of the ulna Figure  
1002 8C). The DN specimen is identical to extant *Orycteropus afer* radii available to us for direct  
1003 comparison in both morphology and size, and exhibits excellent joint congruence with the

1004 capitulum of the *Orycteropus cf. afer* distal humerus from Swartkrans Member 1 (SKX 14261)  
1005 (Lehmann, 2004).

1006

1007

## 1008 **Biochronology**

1009

1010 Fauna from the site has been recovered from both calcified and decalcified deposits in the Main  
1011 Quarry using a variety of techniques over the years. A small portion of the collections from the  
1012 early 1990s was developed from blocks recovered from the limeminers dumps just outside the  
1013 Main Quarry. While these blocks have always been assumed to come from the Main Quarry  
1014 deposits due to their proximity, the recent excavation of a new, older (~2.6 Ma) 50 m west of the  
1015 Main Quarry (the Drimolen Makondo; Rovinsky et al., 2015; Herries et al., in review) does mean  
1016 that this *ex situ* material could be mixed from more than one age of deposit. However, these two  
1017 different deposits are not stratigraphically intertwined as is the case for deposits like Members 4  
1018 and 5 at Sterkfontein (Herries and Shaw, 2011) or Swartkrans Members 1-3 (Herries and Adams,  
1019 2013). This is currently no indication that similarly-aged Pliocene deposits exist in the Main  
1020 Quarry itself.

1021

1022 Although there is notable diversity in the recovered Drimolen Main Quarry faunas, the majority  
1023 of the specimens provide limited biochronological data for interpreting the age of the deposits.  
1024 As is typical for South African palaeokarstic deposits in the region, the recovery of *Equus cf.*  
1025 *quagga* ssp. from the *in situ* deposits indicates that at least part of the assemblage formed after  
1026 2.33 Ma given the first appearance of the genus in African early Pleistocene deposits (Geraads,

1027 Raynal & Eisenmann, 2004). The remainder of the ungulate specimens identified from the Main  
1028 Quarry are either not specifically attributable, are members of long-surviving Plio-Pleistocene  
1029 lineages, or have poorly secured first appearance (FAD) and last appearance dates (LAD) in  
1030 South Africa. The largest bovid sample in the assemblage, *Antidorcas recki*, has been recovered  
1031 from eastern and South African deposits spanning the late Pliocene (e.g., Shungura Formation B-  
1032 H; Gentry, 2010; McDougall et al., 2011; Brown et al., 2013) to the >1.07 Ma (or <0.780 Ma)  
1033 Olduvai Bed IV (Tamrat et al., 1995) and the 1.07-0.780 Ma Elandsfontein deposits (Gentry,  
1034 2010; Braun et al., 2013). The differences in the transverse ridging of the horn cores with the  
1035 previously described Bolt's Farm Pit 3 specimens may or may not reflect a temporal difference  
1036 in depositional age.

1037

1038 Although this analysis has not addressed the non-hominin primates from the Drimolen Main  
1039 Quarry, data reported in Nieuwoudt (2014) and reproduced in Table 1 suggests a fairly  
1040 homogenous sample of cercopithecoids relative to other nearby early Pleistocene palaeokarstic  
1041 deposits that typically record greater taxonomic diversity (Brain, 1981; Jablonski and Freedman,  
1042 2010). The specifically attributable DMQ specimens have been allocated to either the extinct  
1043 papionin subspecies *Papio hamadryas robinsoni* Freedman, 1957 (alt. *Papio robinsoni*; Gilbert  
1044 et al., 2015) or the extinct colobin species *Cercopithecoides williamsi* Mollett, 1947. Both of  
1045 these species have FADs in the late Pliocene (a constrained FAD for *Papio* somewhat less clear,  
1046 see Jablonski and Frost, 2010 and Gilbert et al., 2015) and are common in post ~2 Ma early  
1047 (potential to mid-) Pleistocene South African deposits (e.g., Swartkrans, Sterkfontein Member 5,  
1048 Kromdraai, Cooper's D, Gladysvale; Jablonski and Frost, 2010). As such, neither primate  
1049 provides strong biochronological constraints on the depositional age of the Main Quarry deposits

1050 beyond being consistent with species recovered from other nearby early Pleistocene localities  
1051 (e.g., Sterkfontein Members 4 and 5, Swartkrans Members 1-3, Kromdraai A and B) (Brain,  
1052 1981; Jablonski and Frost, 2010).

1053

1054 The carnivoran specimens provide a more constrained depositional age. Remains of the genus  
1055 *Chasmaporthetes* have been recovered across African localities, with *C. nitidula* described from  
1056 South African deposits ranging from Sterkfontein Jacovec Cavern and Members 2 and 4 (<2.46-  
1057 2.01 Ma; Herries et al., 2013) to as late as Swartkrans Member 3 (sometime between 1.3-0.6 Ma;  
1058 Herries, Curnoe & Adams, 2009). However, *Lycyaenops silberbergi* has been recovered from a  
1059 far narrower range of terminal Pliocene and early Pleistocene deposits of Laetoli (as *Lycyaenops*  
1060 cf. *L. silberbergi*; Werdelin and Dehghani, 2011) in East Africa and Sterkfontein in South Africa  
1061 (~3.8–2.02 Ma; Turner, 1990, 1997; Werdelin and Lewis, 2005; Werdelin and Peigné, 2010;  
1062 Herries and Shaw, 2011; Herries et al., 2013). A single mandibular specimen (SK 300) of  
1063 *Lycyaenops silberbergi* has been described from Swartkrans Member 1 (Ewer, 1955b), and  
1064 although questions over provenience has been raised it is still considered derived from these  
1065 deposits (see discussion in Turner, 1987b); this effectively establishes an LAD for the species  
1066 within these deposits of 1.96-1.80 Ma (Pickering et al., 2011a; Herries and Adams, 2013).

1067

1068 The identification of *Dinofelis* cf. *barlowi* from the DMQ also argues for a late Pliocene-early  
1069 Pleistocene deposition. This apparently endemic South African machairodont has been  
1070 definitively recovered from a temporally narrow range of deposits spanning approximately 2.7–  
1071 1.98 Ma (Werdelin and Lewis, 2001; Lacruz, Turner & Berger, 2006; Herries, Curnoe & Adams,  
1072 2009; Werdelin and Peigné, 2010; Herries and Shaw, 2011; Pickering et al., 2011b; Kuhn et al.,

1073 2012). What cannot be determined at this point is the biological relationship of this specimen to  
1074 the previously described *Dinofelis* aff. *piveteaui* specimens, as no maxillary canine was  
1075 recovered or described in association with the craniodental remains. As discussed by O'Regan  
1076 and Menter (2009), the basis for classifying the DMQ *Dinofelis* remains as *D.* aff. *piveteaui* is  
1077 based largely on P4 morphology. The protocone of the DN 1012 P4 is reduced; not as reduced as  
1078 *D. piveteaui* specimens from Kromdraai A or Motsetse but yielding a buccolingually-narrower  
1079 tooth than is present in *D. barlowi*. Simultaneously, the P4 metastyle blade is only slightly  
1080 mesiodistally elongated relative to *D. barlowi* and lacks the elongation exhibited by South  
1081 African *D. piveteaui* P4 specimens. As with much of the anatomy of fossil taxa established from  
1082 small sample sizes, it is difficult at present to establish whether these P4 features reflect sexual  
1083 dimorphism, individual, or chronological variation within either *D. barlowi* or *D. piveteaui*. And  
1084 while further craniodental specimens could ultimately link the DN 2791 canine with these other  
1085 DMQ *Dinofelis* remains, there is no apparent morphological affinity to *D. piveteaui* maxillary  
1086 canines to support treating the specimen as derived from the same population.

1087

1088 Ultimately, if these previously described remains cannot be accommodated with either species  
1089 *sensu stricto* we posit four potential interpretations of the DMQ *Dinofelis* material assigned to *D.*  
1090 aff. *piveteaui* by O'Regan and Menter (2009) that will require further analysis to test whether: 1)  
1091 they represent a derived *D. barlowi*; 2) they represent a primitive *D. piveteaui sensu stricto*; 3)  
1092 they are derived from a discrete population undergoing anagenesis from a more primitive  
1093 *Dinofelis* (e.g., *D. barlowi* [O'Regan and Menter, 2009] or *Dinofelis aronoki* [Werdelin and  
1094 Lewis, 2001]) to *D. piveteaui* in the early Pleistocene; or 4) they represent a separate, previously  
1095 unrecovered species of *Dinofelis* in the African record (which we view as less likely). If the

1096 DMQ *Dinofelis* aff. *piveteaui* remains represent a novel species, they would ultimately contribute  
1097 little to interpreting deposit biochronology. As *D. barlowi* does not occur in South African  
1098 deposits after 1.98 Ma, if the DMQ *Dinofelis* aff. *piveteaui* remains are a derived *D. barlowi* they  
1099 would likely indicate deposition after 1.98 Ma – but would similarly lack an established FAD or  
1100 LAD. Finally, given the recovery of the *D. piveteaui* type specimen from the (tentatively dated)  
1101 1.89-1.63 Ma Kromdraai A deposits (Herries, Curnoe & Adams, 2009) and in east Africa by 1.61  
1102 Ma (Werdelin and Lewis, 2005; McDougall et al., 2011), then if representing a primitive *D.*  
1103 *piveteaui* or transitional *Dinofelis* then the DMQ *Dinofelis* aff. *piveteaui* specimens would  
1104 suggest a depositional date prior to ~1.6 Ma and/or the Kromdraai A assemblage.

1105

1106 In sum, the DMQ faunal assemblage includes species only occupying the South African  
1107 landscape after 2.33 Ma (*Equus* cf. *burchelli* ssp.), and includes the remains of carnivore species  
1108 whose currently reconstructed LADs within the early Pleistocene indicate at least some of the  
1109 deposits formed prior to (or near) 2.02 Ma (*Lycyaenops silberbergi*) to 1.98 Ma (*Dinofelis* cf.  
1110 *barlowi*).

1111

## 1112 **Discussion**

1113

1114 This first description and analysis of the macromammalian fossil specimens from the Drimolen  
1115 Main Quarry assemblage has documented remarkably high taxonomic diversity (9 Orders, 14  
1116 Families) relative to sample size (NISP: 1390, MNI: 147). While deposits like Swartkrans  
1117 Member 1 record a somewhat greater range of taxa (9 Orders, 17 Families), the number of non-  
1118 hominin taxonomically identifiable specimens underlying this diversity is substantially higher

1119 (NISP: 4583, MNI: 103; Watson, 1993). Despite this diversity, the McIntosh evenness statistic  
1120 for the DMQ is low (0.71) and one standard deviation below the mean (0.80; range 0.60-0.93;  
1121 s.d. 0.087) for South African early-mid Pleistocene localities (Table 6) and close to the value of  
1122 the Haasgat HGD *ex situ* assemblage (0.72; Adams, 2012a). This low value reflects the high  
1123 proportion of *Papio hamadryas robinsoni* individuals relative to all other taxa recovered from  
1124 the DMQ deposits. With the inclusion of *Cercopithecoides williamsi* and indeterminate  
1125 specimens, 38.4% of the DMQ assemblage come from the Family Cercopithecidae; equal to the  
1126 proportion (38.4%) of the second largest taxonomic group, the Family Bovidae. In this respect,  
1127 DMQ is also similar to Haasgat HGD where non-human primates make up 35.1% and bovids  
1128 make up 40.9% of the assemblage (Adams, 2012a); although we would reinforce that we are  
1129 only considering the non-hominin components of the DMQ assemblage in comparison to the  
1130 Haasgat HGD assemblage that lacks hominin remains.

1131

1132 The composition of the Drimolen Main Quarry bovid assemblage is not taxonomically unique  
1133 relative to other penecontemporaneous South African fossil assemblages, but the numerical  
1134 dominance of *Antidorcas recki* relative to other taxa is somewhat unusual. The only other site  
1135 with a similar sample size of *A. recki*, Kromdraai A (NISP: 44, MNI: 13), has a far more  
1136 substantial collection of alcelaphins (NISP: 220, MNI: 51) and only represents 11.5% of the total  
1137 bovid assemblage (Brain, 1981). What stands in rather strong contrast to the typical element-  
1138 wise representation of bovid elements is the high frequency of horn cores in the DMQ  
1139 assemblage (see Brain, 1981; Watson, 1993; Pickering, 1999), particularly in the case of *A. recki*,  
1140 where very few teeth have been recovered alongside a substantial number of horn cores.  
1141 Interpreting the origin and significance of this pattern of element preservation in the bovid

1142 sample compared to other palaeokarstic deposits is beyond the scope of the present paper, but  
1143 will potentially be informative on the taphonomic processes underlying the Drimolen Main  
1144 Quarry deposit formation.

1145

1146 The only other substantially represented taxonomic group in the DMQ assemblage is the Order  
1147 Carnivora, which comprises 13% of the faunal assemblage and is biased towards the Family  
1148 Felidae (57.9% of the Carnivora and 7.5% of the overall faunal assemblage). This positions the  
1149 DMQ assemblage as particularly carnivore-rich, with only Kromdraai B (15.8%), Swartkrans  
1150 Member 3 (16.85%) and the Sterkfontein Member 5 deposits (West: 30.65%; Olduvan Infill:  
1151 13.64%; STW 53 Breccia: 13.33%) having higher proportions of carnivores amongst the  
1152 penecontemporaneous South African palaeokarstic assemblages. The proportion of carnivores in  
1153 the DMQ assemblage is also substantially less than the recently described Drimolen Makondo  
1154 deposits (25%; Rovinsky et al., 2015; Herries et al., in review), although the limited faunal  
1155 sampling of the Makondo to-date (like other provisionally described faunal assemblages such as  
1156 Motsetse [Berger and Lacruz, 2003], Hoogland [Adams et al., 2010], Malapa [Dirks et al., 2010;  
1157 Kuhn et al., 2012]) necessitates further sampling to ensure these proportions are not artefacts of  
1158 sample size. The co-occurrence of large predatory felids (with minimally three subfamilies and  
1159 five genera represented in the deposit) - for example, *Panthera*, *Dinofelis* and *Megantereon* – is  
1160 not uncommon in South African early Pleistocene deposits (Brain, 1981; Werdelin & Peigné,  
1161 2010). What is unusual is the potential sympatric occurrence of two species of *Dinofelis* recorded  
1162 by the DMQ *Dinofelis* cf. *barlowi* and *Dinofelis* aff. *piveteaui*, specimens. While it has been  
1163 noted that temporal overlap of two *Dinofelis* species may have been relatively common, at least  
1164 in East Africa (e.g., Lewis and Werdelin, 2007), this current study would represent the first

1165 strong evidence of such contemporaneous overlap within a single deposit (Werdelin and Lewis,  
1166 2001, 2013; Werdelin and Peigné, 2010).

1167

1168 The Drimolen Main Quarry faunal assemblage is also unique relative to most  
1169 penecontemporaneous South African karstic deposits in the under-representation of porcupine  
1170 (Family Hystricidae) and hyrax (Family Procaviidae) remains in the deposits. These two families  
1171 only comprise 2.7% of the total DMQ faunal assemblage, which falls below even the low  
1172 proportions of these taxa at Sterkfontein Member 4 (4.2%; Brain, 1981) and Kromdraai A (9%;  
1173 Brain, 1981), and strongly contrasts the representation of these families in the Swartkrans  
1174 Member 1 (21.4%; Watson, 1993) and Haasgat HGD (19.5%; Adams, 2012a) faunal  
1175 assemblages. There are a number of geologic (e.g., entrance morphology, deposit time-  
1176 averaging), ecologic (e.g., immediate habitat and resource distribution) and/or taphonomic  
1177 factors (e.g., pre-, peri- and postdepositional) that could underlie this low representation of these  
1178 karst-utilising taxa that will require further analysis to assess.

1179

1180 In sum, this comprehensive accounting of the Drimolen Main Quarry faunal assemblage allows  
1181 us to provide some initial comments on the palaeohabitats of the Drimolen region during  
1182 deposition; although we note that a more comprehensive palaeoecological interpretation and  
1183 analysis integrating stable isotopic results from the assemblage will be forthcoming. The overall  
1184 vegetative communities and landscape ecology suggested by the taxon presence and abundance  
1185 recovered from the DMQ deposits is largely consistent with the mixed, open-to-closed  
1186 palaeohabitats that have been reconstructed for the other regional, penecontemporaneous South  
1187 African palaeokarst deposits (Vrba, 1976, 1995; Brain, 1981; Benefit and McCrossin, 1990;

1188 McKee, 1991; Rayner, Moon & Masters, 1993; Brain, 1995; Schmid, 2002; Elton, 2007; see also  
1189 summaries in Reed, 1996; Kuman and Clarke, 2000; Adams, 2006). In part this reflects the broad  
1190 habitat types that most of the specifically identifiable taxa from the DMQ deposits can occupy.  
1191 Both previously attributed primate taxa are larger-bodied and terrestrial (*Papio hamadryas*  
1192 *robinsoni*, *Cercopithecoides williamsi*) and may have been sympatric, niche-partitioned primates  
1193 adapted to the progressively more open habitats of the early Pleistocene (Elton, 2007; Jablonski  
1194 and Frost, 2010). However, the composition and resource availability of these more open  
1195 habitats, and how they contrast with earlier palaeoecosystems that supported cercopithecoids like  
1196 *Parapapio* (that disappear from the record in the early Pleistocene), remains unresolved. Even  
1197 the more unusual species recovered from the Drimolen Main Quarry deposits (indeterminate  
1198 elephant, giraffe, and aardvark [*Orycteropus cf. afer*]) can unfortunately provide few constraints  
1199 on the palaeohabitat types, distribution or proportions near the site. Neither the elephant or  
1200 giraffe individual specimens could be confidently attributed below the level of Family, and  
1201 extant aardvark populations occupy highly variable habitats across Africa with the only  
1202 limitation being access to social insects (Kingdon and Hoffman, 2013a).

1203

1204 The dominance of *Antidorcas recki* in the bovid sample does not provide any specific evidence  
1205 for reconstructing the overall vegetative community structure around Drimolen without further  
1206 isotopic analysis. Although prior analyses of Sterkfontein and Swartkrans specimens have  
1207 reconstructed the diet of this antilopin as a browser (Lee-Thorp and van der Merwe, 1993; Lee-  
1208 Thorp, van der Merwe & Brain, 1994; van der Merwe et al., 2003), a single specimen from  
1209 Gondolin was interpreted as a mixed feeder (Adams, 2012a) and sampled individuals from  
1210 Olduvai have documented greater dietary flexibility and an increase in graze in the species

1211 through the Bed I deposits associating them more with bushland to grassland palaeohabitats  
1212 (Plummer et al., 2009). The only bovid taxa recovered from DMQ with specific habitat  
1213 requirements are the mountain reedbuck (*Redunca cf. fulvorufula*) and klipspringer (*Oreotragus*  
1214 sp.). Extant mountain reedbuck graze primarily in montane grasslands on rocky, hilly and/or  
1215 broken terrain (Irby, 1976; Kingdon and Hoffman, 2013b); klipspringer exhibit a suite of  
1216 musculoskeletal, physiological and behavioural adaptations to browsing on pair-defended rock  
1217 outcrops (Norton, 1980; Kingdon and Hoffman, 2013b). The presence of some uplifted  
1218 topography and/or local kopjes with montane grasses and browse near Drimolen during the  
1219 formation of the Main Quarry assemblage is further reinforced by the recovery of hyrax  
1220 (*Procavia* sp.) and rock hare (*Pronolagus* sp.) (Kingdon et al., 2013; Happold, 2013).

1221

1222 The extinct DMQ large carnivores are similarly reconstructed as adapted for hunting within a  
1223 range of open and closed palaeohabitats. Both *Dinofelis* and *Megantereon* have been  
1224 reconstructed as ambush predators preferring a closed-mixed habitat (Marean, 1989; Lewis,  
1225 1995a, b, 1997; Palmqvist et al., 2003; Christiansen and Adolfssen, 2007; Palmqvist et al. 2008).  
1226 In its postcranial anatomy, the smaller-bodied *Megantereon* is reminiscent of the extant jaguar  
1227 (*Panthera onca*), with relatively short, heavily muscled, and powerful limbs (Lewis, 1995b,  
1228 1997; Christiansen and Adolfssen, 2007). Isotopic analyses of European *Megantereon* support  
1229 the preference for a closed-mixed habitat, suggesting that the genus predated on browsers and  
1230 mixed-feeders (Palmqvist et al., 2003, 2008). *Dinofelis* has been shown to have had greater  
1231 flexibility in the forelimb than seen in the other African machairodonts (i.e. *Homotherium*,  
1232 *Megantereon*; Lewis, 1995a, b, 1997) and a trend in the larger-bodied species toward a more  
1233 *Panthera*-like cranial and postcranial anatomy, suggesting that although it seems to have been an

1234 ambush grappler much like *Megantereon* it may have been able to exploit a larger range of  
1235 habitats than the other African sabertooth genera (Lewis, 1997; Lewis and Werdelin, 2007).  
1236 Although postcranial remains of African *Lycyaenops* and *Chasmaporthetes* species are extremely  
1237 rare (see Rovinsky et al., 2015), cursorial adaptations within the hunting-hyaena lineage supports  
1238 more open habitats in the region, in contrast to the felids (Khomenko, 1932; Galiano and Frailey,  
1239 1977; Berta, 1981; Tseng, Li and Wang, 2013). Amongst the extant carnivores identified by  
1240 O'Regan and Menter (2009) modern populations of Cape fox (*Vulpes chama*), yellow mongoose  
1241 (cf. *Cynictis penicillata*), and meerkat (aff. *Suricata suricatta*) typically occupy open, semi-arid  
1242 to arid ecosystems (Kingdon and Hoffmann, 2013a). Interestingly, the extensive burrowing  
1243 behaviour of meerkat and yellow mongoose also imply the presence of deep soils, with the latter  
1244 avoiding rocky and hard soil regions for burrow construction (Kingdon and Hoffman, 2013a).

1245

## 1246 **Conclusions**

1247

1248 This first description of the non-primate faunas of the Drimolen Main Quarry provides an insight  
1249 into the macromammalian community structure of a previously undescribed part of the Cradle of  
1250 Humankind during the Early Pleistocene of South Africa. The fauna recovered suggests a  
1251 community of great taxonomic breadth. Amongst the sampled Order Carnivora in particular  
1252 there is a surprising amount of diversity, with a minimum of four large species of felid present  
1253 alongside at least four hyaenid species, including the first strong evidence of two species of  
1254 *Dinofelis* recovered from a single deposit (but see Lewis and Werdelin, 2013). Although there is  
1255 a large amount of taxonomic diversity amongst the fauna, non-hominin primates comprise a  
1256 significant percentage of the assemblage - a disparity that will only increase when the substantial

1257 Drimolen hominin sample is included in the overall faunal picture. As this publication provides  
1258 the primary description of the recovered DMQ faunas, further analyses will need to be  
1259 undertaken to understand the idiosyncrasies of the site, ranging from the taphonomic processes  
1260 shaping the assemblage (particularly the large number of bovid horn cores and concomitant  
1261 paucity of dental and postcranial remains) to a more integrated palaeoecological analysis of the  
1262 Main Quarry.

1263

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1265

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1276

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**Table 1** (on next page)

List of macromammalian species from the Drimolen Main Quarry deposits

Table 1. List of macromammalian species from the Drimolen Main Quarry deposits

Taxon	NISP	MNI
Order Primates <sup>1</sup>		
Family Cercopithecidae		
Tribe Colobini		
<i>Cercopithecoides williamsi</i>	22	8
Tribe Papionini		
<i>Papio hamadryas robinsoni</i>	260	45
Cercopithecidae indet.	272	4
Order Carnivora <sup>2</sup>		
Family Canidae		
<i>Vulpes chama</i>	1	1
cf. <i>Vulpes chama</i>	1	-
Canidae indet.	5	1
Family Felidae		
Subfamily Machairodontinae		
<i>Dinofelis</i> aff. <i>piveteaui</i>	17	2
? <i>Dinofelis</i> sp.	1	-
<i>Dinofelis</i> cf. <i>barlowi</i> *	1	1
<i>Megantereon whitei</i> *	2	1
Machairodontinae indet.	1	1
Subfamily Pantherinae		
<i>Panthera pardus</i>	5	1
cf. <i>Panthera pardus</i>	3	1
<i>Panthera</i> sp.	1	-
Subfamily Felinae		
cf. <i>Caracal caracal</i>	1	1
<i>Felis silvestris lybica</i>	3	1
cf. <i>Felis silvestris lybica</i>	4	2
Felidae indet.*	31	-
Family Herpestidae		
aff. <i>Suricata suricatta</i>	1	1
cf. <i>Cynictis penicillata</i>	3	1
Family Hyaenidae		
<i>Chasmaporthetes nitidula</i> *	1	1
<i>Lycyaenops silberbergi</i> *	1	1
Hyaenidae indet.*	7	2
Carnivora indet.	15	-
Order Cetartiodactyla		
Family Bovidae		
Tribe Alcelaphini		
<i>Connochaetes</i> sp.	2	2
<i>Damaliscus</i> sp.	2	2

<i>Megalotragus</i> sp.	4	2
Indeterminate (Class II/III)	34	9
Indeterminate (Class III)	11	4
Tribe Antilopini		
<i>Antidorcas recki</i>	25	16
<i>Antidorcas</i> cf. <i>recki</i>	26	2
<i>Raphicerus</i> sp.	1	1
Tribe Oreotragini		
<i>Oreotragus</i> sp.	12	9
Tribe Reduncini		
<i>Redunca</i> cf. <i>fulvorufula</i>	3	3
Tribe Tragelaphini		
<i>Tragelaphus</i> sp.	11	6
Indeterminate	2	-
Bovidae indet.	538	-
Family Giraffidae		
Giraffidae indet.	1	1
Family Suidae		
Suidae indet.	1	1
Order Perissodactyla		
Family Equidae		
<i>Equus quagga</i> ssp.	3	1
Order Proboscidea		
Family Elephantidae		
Elephantidae indet.	1	1
Order Hyracoidea		
Family Procaviidae		
<i>Procavia</i> sp.	5	3
Order Lagomorpha		
Family Leporidae		
<i>Pronolagus</i> sp.	1	1
Leporidae indet.	36	5
Order Rodentia		
Family Hystricidae		
<i>Hystrix</i> sp.	1	1
Order Tubulidentata		
Family Orycteropodidae		

<i>Orycteropus cf. afer</i>	1	1
Total	1380	147

<sup>1</sup>Taxonomic attributions, specimen counts, and MNI values as reported by Nieuwoudt (2014).

<sup>2</sup>Taxonomic attributions, specimens counts, and MNI values as reported by O'Regan and Menter (2009) except where amended here (amended taxa and/or counts marked with an asterisk).

1

**Table 2** (on next page)

Measurements (in mm) of Drimolen Main Quarry Felidae gen. et sp. indet and comparative maxillary fourth premolars body.

Table 2. Measurements (in mm) of Drimolen Main Quarry Felidae gen. et sp. indet and comparative maxillary fourth premolars

Specimen	Deposit	MD	BL	Wpc	PaL	MtL
<i>Felidae</i> gen. et sp. indet.						
<b>DN 4300</b>	<b>Drimolen Main Quarry</b>	<b>29.8</b>	<b>11.6</b>	<b>9.4</b>	<b>11.8</b>	<b>12.3</b>
<b>DN 5498</b>	<b>Drimolen Main Quarry</b>	<b>30.2*</b>	<b>11.6*</b>	<b>9.3</b>	<b>11.1*</b>	<b>11.9</b>
<i>Megantereon whitei</i>						
<b>DN 976</b>	<b>Drimolen Main Quarry</b>	<b>23.4*</b>	<b>11.2*</b>	<b>9.6</b>	<b>10.0</b>	<b>10.6</b>
KA 64	Kromdraai A	29.7	11.1*	9.7*	9.6	10.8
<i>Dinofelis piveteaui</i> and aff. <i>piveteaui</i>						
<b>DN 1012</b>	<b>Drimolen Main Quarry</b>	<b>36.5</b>	<b>13.9</b>		<b>13.5</b>	<b>14.3</b>
KA 61	Kromdraai A	41.0	13.0			17.8
MT 1986 <sup>1</sup>	Motsetse	38.8	12.8			16.5
<i>Dinofelis barlowi</i>						
BF 55-22	Bolt's Farm Pit 23	37.0*	16.5			14.0
SF 5855 <sup>1</sup>	Sterkfontein Member 4	35.2	15.5		13.0	13.7*

\*Minimum value given damage to measured region.

<sup>1</sup>Measurements of Motsetse and Sterkfontein Member 4 specimens derived from Lacruz et al. (2006).

**Table 3** (on next page)

Regression equations and metrics for the Felidae canine shape groups in Figure 4. Maxillary canine MD length and BL width (in mm), along with the canine compression ratio (BL/MD).

Table 3. Regression equations and metrics for the Felidae canine shape groups in Figure 4. Maxillary canine MD length and BL width (in mm), along with the canine compression ratio (BL/MD).

Canine Morphology	Regression Equation		R <sup>2</sup>
Conical-toothed	$y = 0.7533x + 1.2559$		0.95666
False Saber-toothed	$y = 0.7119x - 2.0968$		0.90962
Saber-toothed	$y = 0.495x - 0.01$		0.87541
	MD Length (mm)	BL Width (mm)	Compression Ratio
<b>Conical-toothed Felids</b>			<b>0.83</b>
<i>Puma concolor</i> (n = 28) <sup>a</sup>	12.85	11.70	0.91
<i>Neofelis nebulosa</i> (n = 18) <sup>a</sup>	11.49	8.24	0.72
<i>Panthera uncia</i> (n = 12) <sup>a</sup>	11.85	11.06	0.93
<i>Panthera tigris</i> (n = 28) <sup>a</sup>	24.28	19.74	0.81
<i>Panthera onca</i> (n = 20) <sup>a</sup>	19.12	15.92	0.83
<i>Panthera pardus</i> (n = 26) <sup>a</sup>	14.72	12.44	0.85
<i>Panthera leo</i> (n = 17) <sup>a</sup>	23.30	18.29	0.78
<b>False Saber-toothed Felids</b>			<b>0.61</b>
<i>Dinofelis petteri</i> (n = 2) <sup>b</sup>	20.95	12.65	0.60
<i>Dinofelis aronoki</i> <sup>b</sup>	20.40	12.80	0.63
<i>Dinofelis barlowi</i> (n = 4) <sup>b</sup>	24.08	14.60	0.61
<i>Dinofelis piveteaui</i>	20.48	12.12	0.59
<i>Dinofelis cf. diastemata</i> (n = 2) <sup>b</sup>	20.20	11.85	0.59
<i>Dinofelis cristata</i> (n = 2) <sup>b</sup>	25.25	16.85	0.67
<i>Dinofelis palaeoonca</i> <sup>b</sup>	18.60	11.70	0.63
<i>Dinofelis</i> sp. <sup>b</sup>	24.80	15.10	0.61
<b>DN 2791</b>	<b>23.22</b>	<b>14.09</b>	<b>0.61</b>
<b>Saber-toothed Felids</b>			<b>0.51</b>
<i>Homotherium serum</i> <sup>a</sup>	34.56	15.78	0.46
<i>Megantereon cultridens</i> (n = 27) <sup>a,c</sup>	22.56	11.56	0.51
<i>Megantereon whitei</i> (n = 8) <sup>c</sup>	24.06	12.28	0.51
<i>Smilodon fatalis</i> <sup>c</sup>	44.22	24.65	0.56
<i>Smilodon populator</i> <sup>c</sup>	42.83	19.03	0.44

<sup>a</sup> Christiansen, 2007; <sup>b</sup> Werdelin and Lewis, 2001; <sup>c</sup> Palmqvist et al., 2007.

**Table 4** (on next page)

Comparative measurements (mm) of African fossil *Chasmaporthetes* and *Lycyaenops* maxillary premolars.

Table 4. Comparative measurements (mm) of African fossil *Chasmaporthetes* and *Lycyaenops* maxillary premolars

Specimen <sup>1</sup>	Deposit	P2		P3		P4	
		MD	BL	MD	BL	MD	BL
<i>Chasmaporthetes nitidula</i>							
SK 305	Swartkrans Member 1	15.8*	10.7	20.3*	12.9	32.7	15.3
SK 306	Swartkrans Member 1			19.6	13.6	32.4*	14.8
SK 307	Swartkrans Member 1					32.4	14.5
SK 309	Swartkrans Member 1			21.1	14.6		
SK 310	Swartkrans Member 1	18.8	11.9				
SK 311	Swartkrans Member 1	18.4	12.5				
SK 312	Swartkrans Member 1			21.9	14.0		15.8*
SK 313	Swartkrans Member 1			20.8	14.4		
SK 379	Swartkrans Member 1	19.5	12.0				
SKX 29205	Swartkrans Member 3			22.4	12.8*		
SKX 22992/72	Swartkrans Member 3					30.8*	15.8
SF 363	Sterkfontein Member 4						15.4
<i>Lycyaenops silberbergi</i>							
<b>DN 404</b>	<b>Drimolen Main Quarry</b>			<b>20.2*</b>	<b>11.6*</b>	<b>31.5</b>	<b>13.3</b>
<b>DN 974</b>	<b>Drimolen Main Quarry</b>			<b>20.4</b>	<b>13.5</b>		
STS 130	Sterkfontein Member 2 <sup>2</sup>			23.8	14.5*		
STS 135	Sterkfontein Member 4			19.6	11.9		
SF 383/373	Sterkfontein Member 4			22.6			
SF 369/373	Sterkfontein Member 4			22.8			
SF 408	Sterkfontein Member 4			20.3			
SF 463	Sterkfontein Member 4	17.1	11.0				
<i>Lycyaenops cf. L. silberbergi</i>							
NHM AS 7.VI.35	Laetoli (Laetolil Beds, Upper Unit)			17.7	12.5		
LAET 75-494	Laetoli (Unknown level)	19.1	11.0				

\*Minimum value given damage to measured region.

<sup>1</sup>All measurements reported are by the authors except those for Sterkfontein (SF) premolars reported by Turner (1987) and Laetoli premolars reported by Werdelin and Dehghani, (2011).

<sup>2</sup>The stratigraphic origin of the STS 120 *L. silberbergi* type specimen from Sterkfontein is uncertain but may be derived from Member 2 or 3 (Brain, 1981).

**Table 5** (on next page)

Linear dimensions (mm) of the Drimolen Main Quarry *Antidorcas recki* horn cores.

Table 5. Linear dimensions (mm) of the Drimolen Main Quarry *Antidorcas recki* horn cores.

DN Specimen	Anteroposterior depth	Mediolateral width
<i>Male</i>		
224	43.56	28.05
890	40.53	28.01
1060	42.16	28.86
3294	35.69	
<i>Female</i>		
995	17.51	14.59
2483a	18.19	16.08
4438	17.92	15.16

**Table 6** (on next page)

Comparative measurements (mm) of the DNH 2850 *Metridiochoerus* sp. right immature third metatarsal and fossil and extant adult suid third metatarsals.

Table 6. Comparative measurements (mm) of the DN 2850 Suidae gen. et sp. indet. right immature third metatarsal and fossil and extant adult suid third metatarsals.

Measurement	DN 2850	G 8105	<i>Phacochoerus aethiopicus</i>				<i>Potamochoerus porcus</i>			
			Mean	Min.	Max.	<i>n</i>	Mean	Min.	Max.	<i>n</i>
Proximal dorsoventral depth	<b>21.99</b>	30.03	19.56	18.11	20.92	6	22.12	21.32	23.30	4
Distal mediolateral width	<b>16.24</b>	-	15.40	13.67	16.92	5	15.69	14.33	16.90	4
Distal dorsoventral depth	<b>17.04</b>	-	15.48	14.63	16.49	6	16.49	15.72	17.70	4

1

**Table 7** (on next page)

McIntosh evenness statistic values for the Drimolen Main Quarry and comparative South African fossil assemblages.

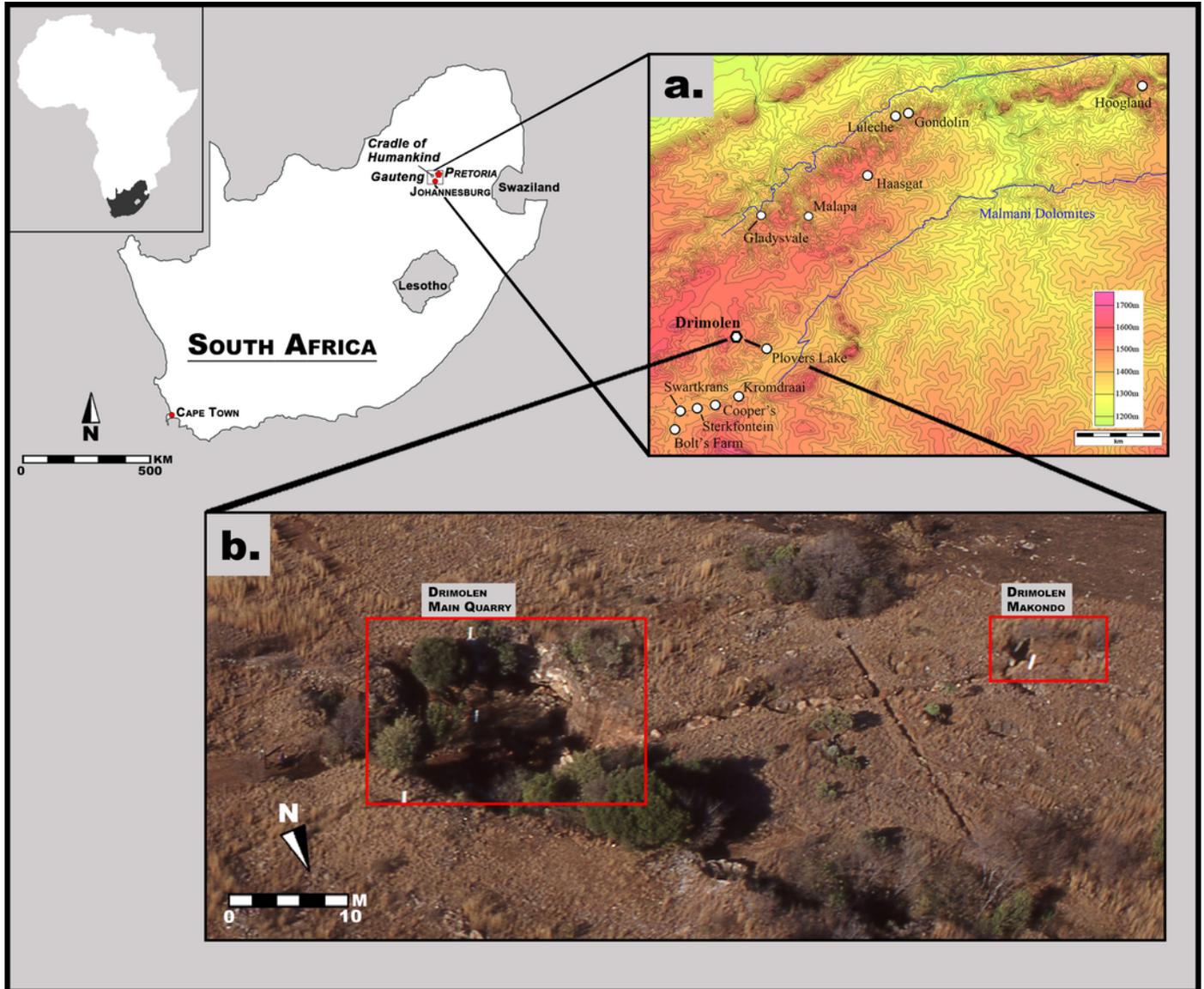
Table 7. McIntosh evenness statistic values for the Drimolen Main Quarry and comparative South African fossil assemblages.

	Site*	Evenness
1	Drimolen Main Quarry	0.71
	GD 2	0.60
	Gladysvale	0.92
	Haasgat HGD	0.72
	Kromdraai A	0.83
	Kromdraai B	0.76
	Makapansgat 2	0.93
	Makapansgat 3	0.81
	Makapansgat 4	0.84
	Makapansgat 5	0.78
	Sterkfontein Member 4	0.67
	Sterkfontein 53 Breccia	0.86
	Sterkfontein Olduwan Infill	0.74
	Sterkfontein Member 5 West	0.84
	Swartkrans Member 1 Lower Bank	0.83
	Swartkrans Member 2	0.86
	Swartkrans Member 3	0.84

\*Data from sources listed in Adams (2006, 2010) but modified to exclude hominin taxa from the calculation.

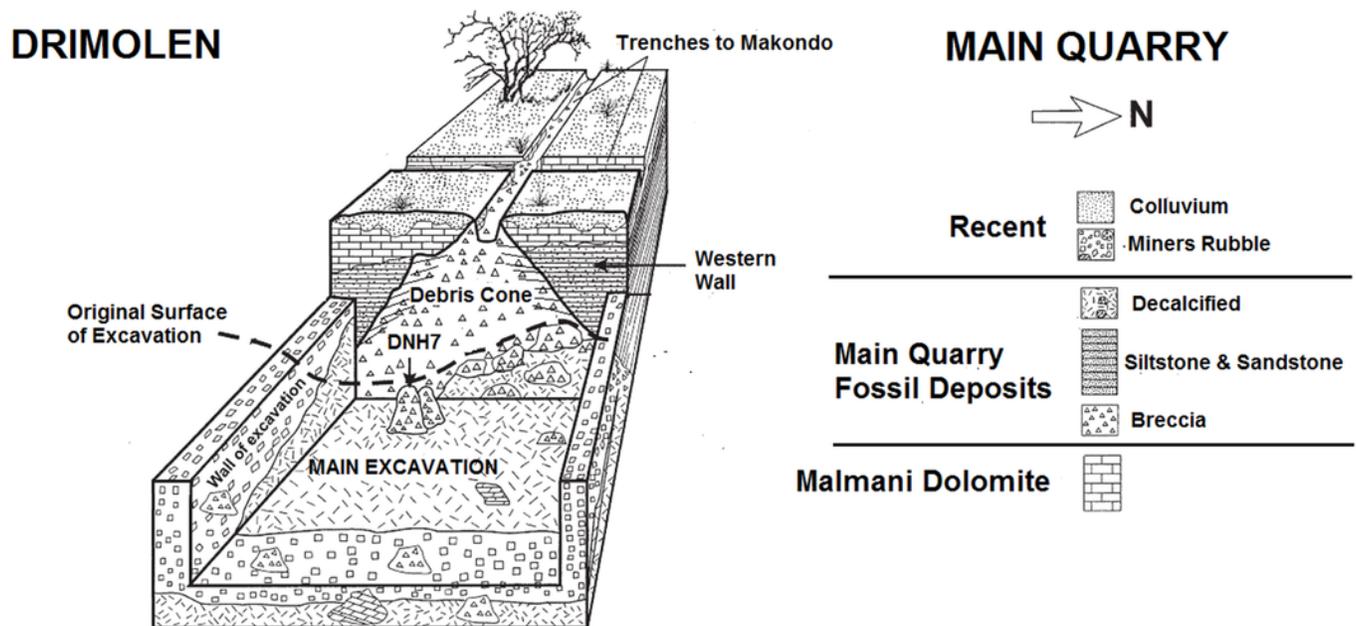
1

Aerial photograph and map of the Drimolen Palaeocave System relative to other penecontemporaneous South African fossil sites.



2

Schematic plan of the Drimolen Main Quarry excavation area and deposits.

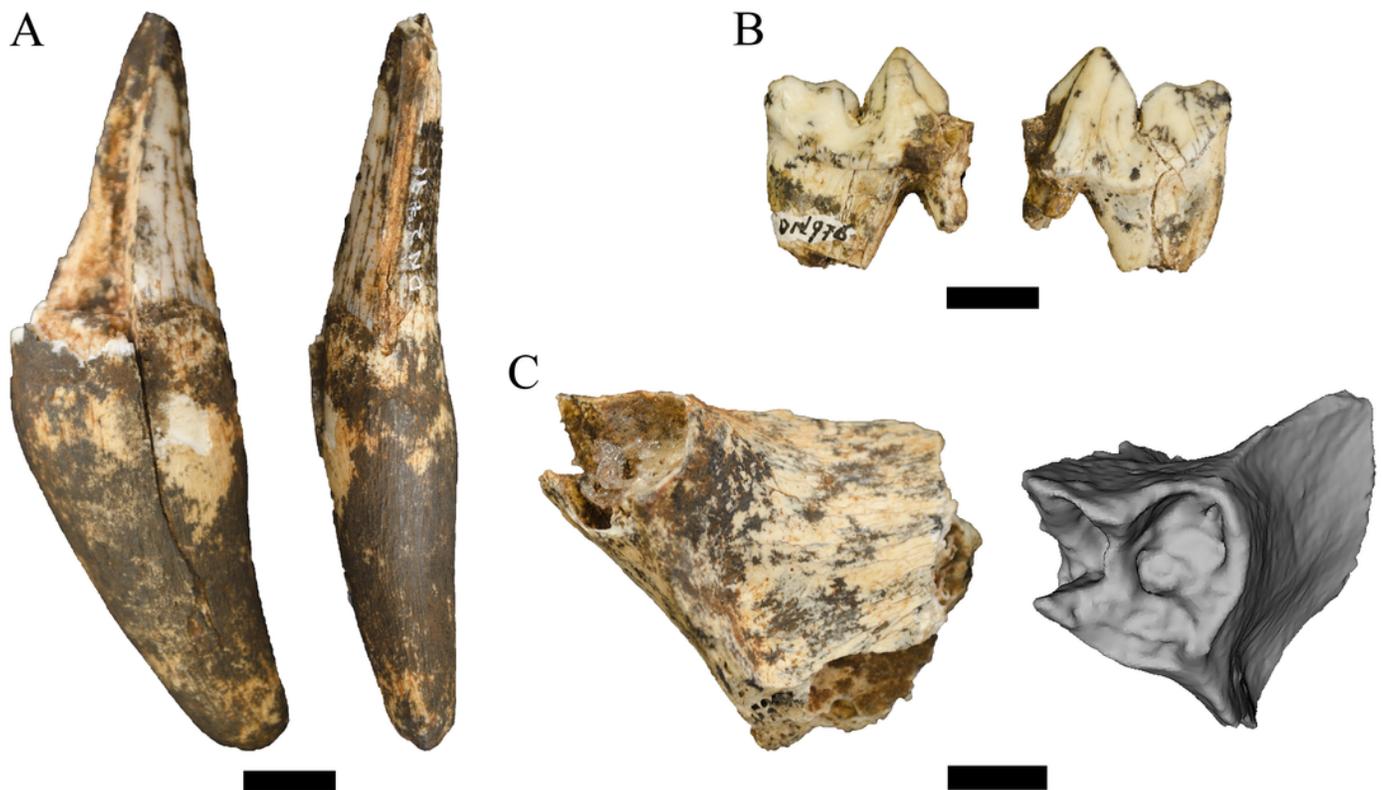


(after Keyser et al., 2000) not to scale

## 3

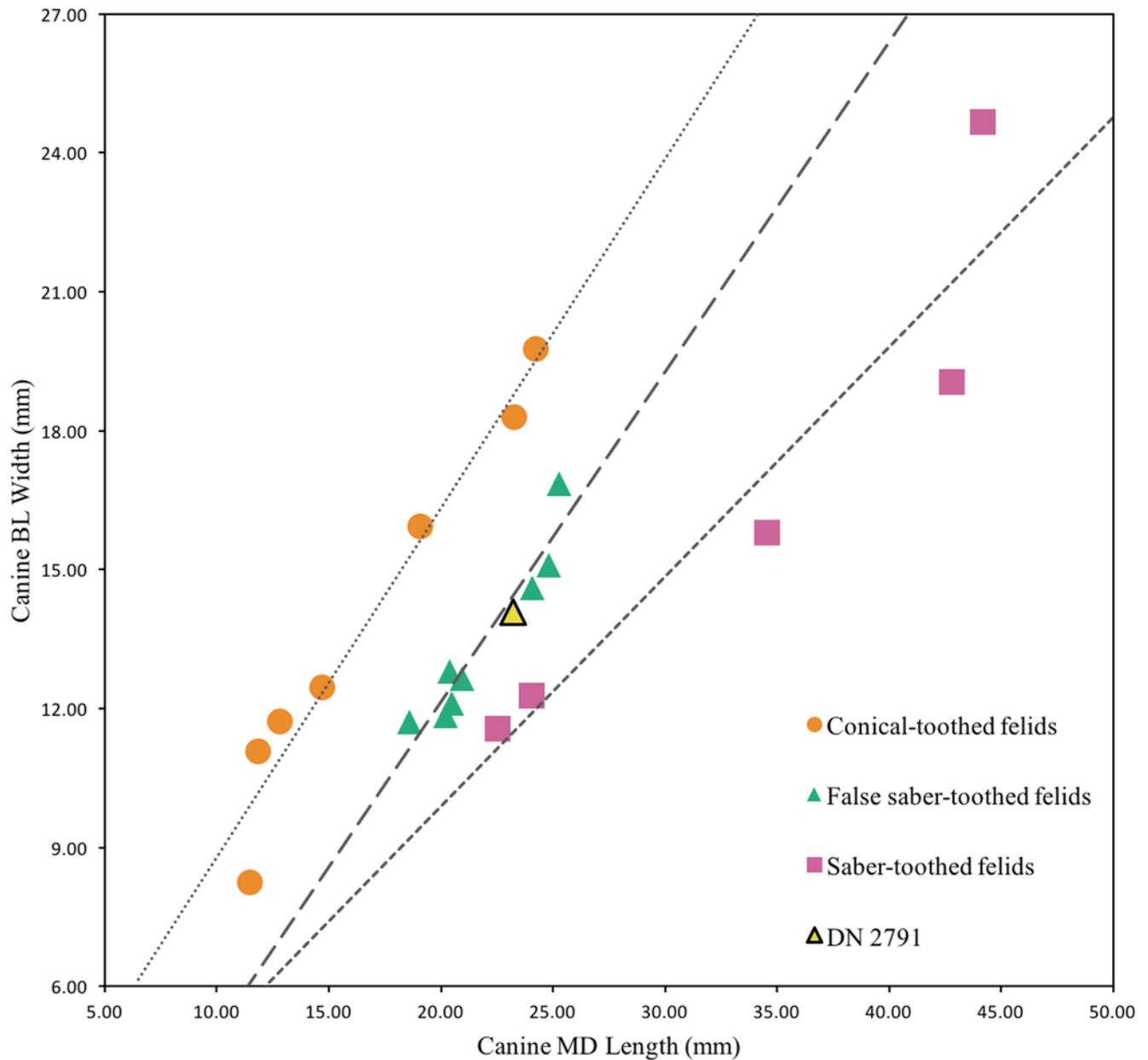
Order Carnivora specimens attributed to the Family Felidae from the Drimolen Main Quarry.

A, DN 2791 *Dinofelis* cf. *barlowi* right maxillary canine, buccal (left) and distal (right) views. B, DN 976 *Megantereon whitei* left P4, buccal (left) and lingual (right) views. C, DN 3254 *Megantereon whitei* left mandibular corpus, lateral (left) and anterior oblique (right) view of surface scan to highlight sharp diastema margin and mandibular flange. Scale bars equal 1cm.



## 4

Bivariate plot of select Felidae maxillary canine MD length on BL width (mm), including DN 2791 *Dinofelis* cf. *barlowi*. Metrics and regression equations presented in Table 3.



## 5

Order Carnivora specimens attributed to the Family Felidae and Hyaenidae from the Drimolen Main Quarry.

A, DN 4300 Felidae gen. et sp. indet. right P4, buccal view. B, DN 974 *Lycyaenops silberbergi* right P3, occlusal (top), lingual (left) and buccal (right) views. Scale bars equal 1cm.

A



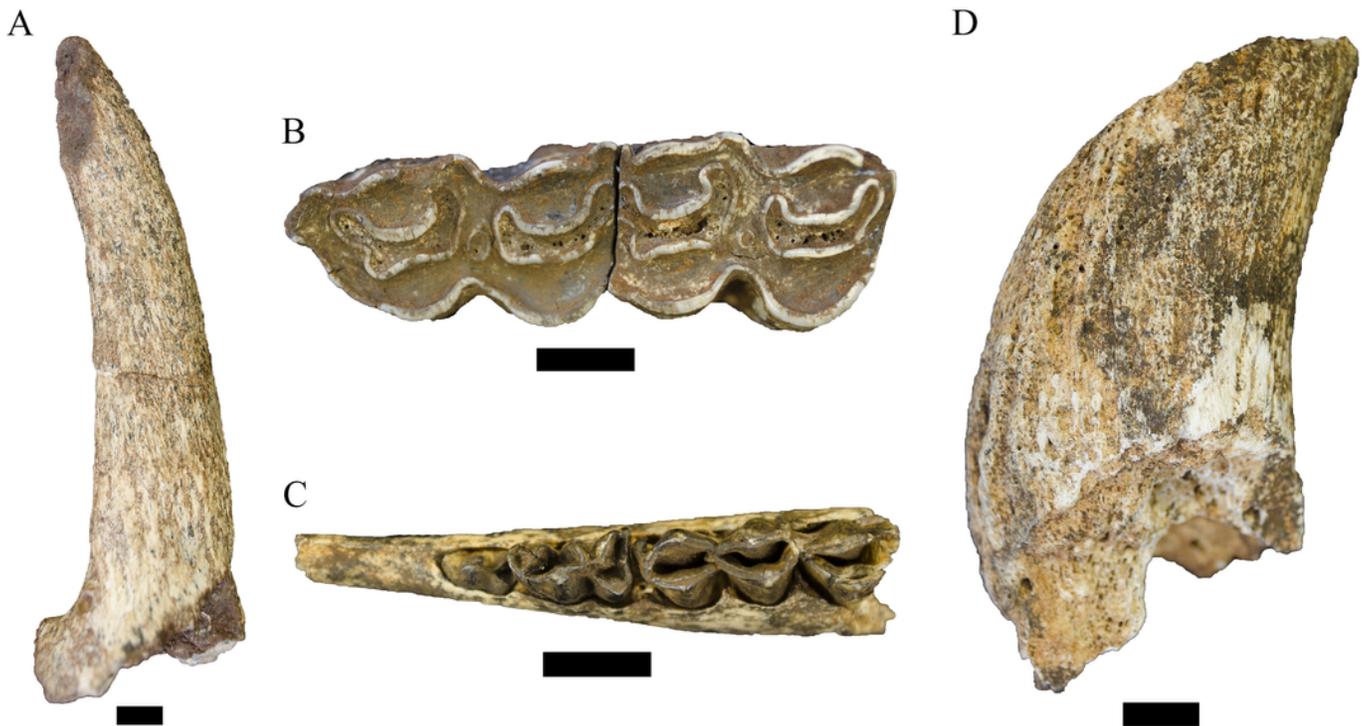
B



## 6

Order Cetartiodactyla specimens attributed to the Family Bovidae from the Drimolen Main Quarry.

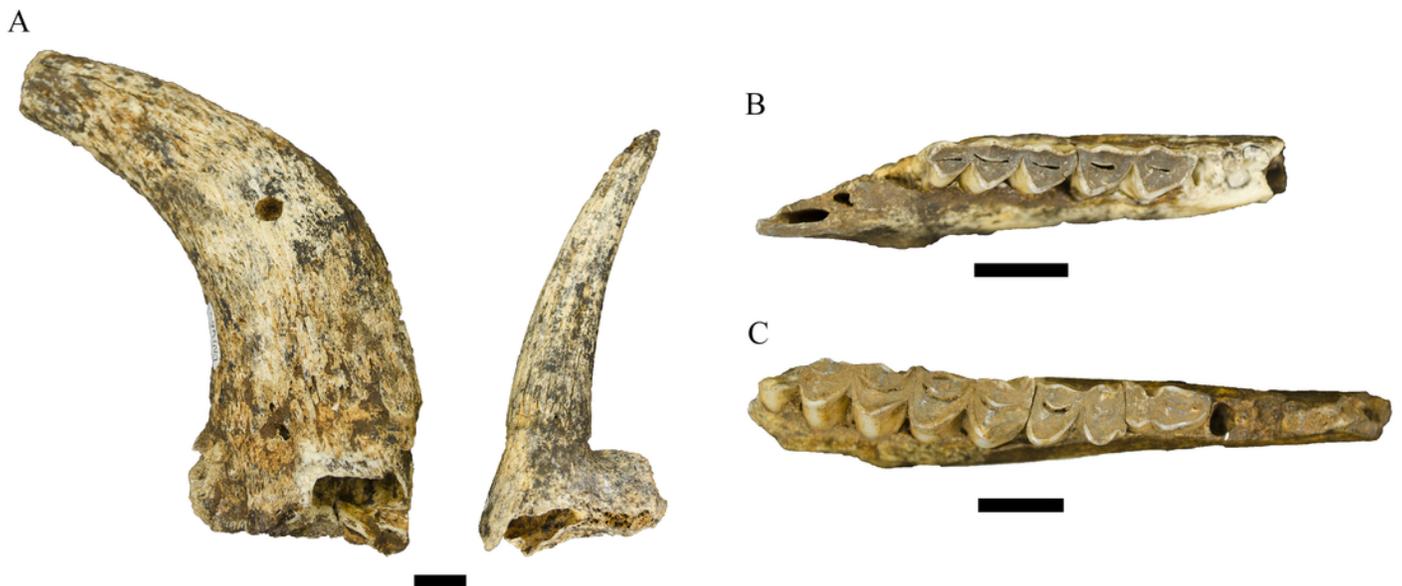
A, DN 2790, *Damaliscus* sp. right horn core, medial view. B, DN 748a and 748b, *Megalotragus* sp. right M2 and M3, occlusal view. C, DN 1015, Alcelaphini gen. et sp. indet. left mandible, occlusal view. D, DN 1013 Alcelaphini gen. et sp. indet. right horn core, anterior (probable) view. Scale bars equal 1cm.



## 7

Order Cetartiodactyla specimens attributed to the Family Bovidae from the Drimolen Main Quarry.

A, DN 1060, *Antidorcas recki* right male horn core, medial view (left); DN 995, *Antidorcas recki* left female horn core, medial view (right). B, DN 438, *Oreotragus* sp. right mandible, occlusal view. C, DN 120, *Tragelaphus* sp. right mandible, occlusal view. Scale bars equal 1cm.



## 8

Order Cetartiodactyla specimens attributed to the Families Giraffidae and Suidae from the Drimolen Main Quarry.

A, DN 1097, Giraffidae gen. et sp. indet. right humerus, anterior (left) and posterior (right) views. B, DN 2850, Suidae gen. et sp. indet. right third metatarsal, medial (left) and lateral (right) views. Scale bars equal 1cm.

A



B



## 9

Specimens attributed to the Orders Proboscidea, Rodentia, and Tubulidentata from the Drimolen Main Quarry.

A, DN 4335, Elephantidae gen. et sp. indet., maxillary tusk fragment, internal view. B, DN 2760 *Hystrix* sp. left maxillary molar, occlusal view. C, DN 1062 *Orycteropus* cf. *affer* right proximal radius, posteromedial view. Scale bars equal 1cm.

A



B



C

