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1 A comparative study of the Early Pleistocene carnivore guild from Dmanisi (Georgia)

2
3 **Abstract**

4 The carnivore guild of the Early Pleistocene site of Dmanisi is among the most diverse of the Early
5 Pleistocene of the entire Old World. It includes 14 carnivoran taxa: *Homotherium latidens*,
6 *Megantereon whitei*, *Panthera onca georgica*, *Acinonyx pardinensis*, *Lynx issiodorensis*;
7 *Pachycrocuta brevirostris*; *Canis (Xenocyon) lycaonoides*, *Canis borjgali*, *Vulpes alopecoides*;
8 *Ursus etruscus*; *Lutra* sp., *Martes* sp., *Meles* sp. and *Pannonictis* sp. The analysis of this rich
9 carnivore guild was carried out under different methodological approaches in order to compare the
10 assemblage with other chronological coeval European, Asian and African sites from a
11 paleobiological perspective. To achieve the goal we used a permutational hierarchical method
12 called bootstrapping cluster analysis based on taxonomic absence/presence matrices (at both generic
13 and specific level) and on ecological matrices (considering dietary preferences/hunting strategies of
14 each carnivoran) and carried out Mantel tests assessing magnitude of time, space, ecology and
15 taxonomy as source of difference between guilds. Our results suggest a close similarity among the
16 Dmanisi carnivore assemblage and other guilds recorded from European late Villafranchian sites
17 such as Pirro Nord, Venta Micena and Apollonia 1 and, in a lesser extent, to European
18 Epivillafranchian sites as Vallonnet, Untermassfeld or the Vallparadís Section. Early to Middle
19 Pleistocene Asian carnivore assemblages display several similarities with the Dmanisi guild mainly
20 in the record and diversity of felid and the canid ecomorphotypes. Eastern African sites such as
21 Olduvai and Omo, as well as South African sites display a lower similarity with the studied sample,
22 basically for the most diverse hyenid taphocoenoses. To sum up, the present study suggests a close
23 similarity between the Dmanisi carnivore guild and other European late Early Pleistocene
24 assemblages without close parallels with African or Asian assemblages.

25
26 **Keywords:** Dmanisi; Carnivorans; Early Pleistocene; Quaternary; Eurasia; Africa

28

29 **1. Introduction**

30 The Georgian archeo-paleontological site of Dmanisi is located in the Mashavera river valley,
31 the Lesser Caucasus, 85 km southwest of Tbilisi, (44° 210E, and 41° 90N). The whole stratigraphic
32 sequence of the fossil assemblage is chronologically constrained to 1.85–1.76 Ma (Gabunia et al.,
33 2000; Vekua et al., 2002; Lordkipanidze et al., 2005, 2007; Ferring et al., 2011).

34 Dmanisi has one of the most extraordinary assemblage of fossil large mammals (including
35 hominins) of the late Early Pleistocene of Eurasia, coupled with an abundant record of Oldowan
36 tools (Lordkipanidze et al., 2005, 2007). This allows the study of potential interactions of the early
37 *Homo erectus* out of Africa in association with the other large mammal species, and to infer
38 paleoenvironmental details. The Dmanisi taphocoenosis is remarkably rich and diverse, with several
39 species that the hominins probably survived on. The favorable conditions recorded at Dmanisi, and
40 in general in the Pontocaspian region (Blain et al., 2104; Krijgsman et al., 2019) at the end
41 Gelasian–Calabrian transition, provided the optimal ecological conditions of the middle latitudes for
42 the faunal dispersal across Eurasia and Africa (Vekua, 1995; Lordkipanidze et al., 2007; Martínez-
43 Navarro, 2010; Espigares et al., 2013; Martínez-Navarro et al., 2014a; Capellini et al., 2019; Medin
44 et al., 2019; Bartolini-Lucenti et al., 2020).

45 The fossil record of Dmanisi includes 26 large mammal species, represented by a combination of
46 species evolved in Europe during the Villafranchian, including the elephant *Mammuthus*
47 *meridionalis*, or the large omnivorous carnivore *Ursus etruscus* (Medin et al., 2019) in association
48 with other taxa (mainly ungulates: bovids, cervids, equids, or rhinocerotids) that originated in Asia
49 (e.g., *Bison georgicus*, *Gallogoral meneghinii*, *Praemegaceros obscurus*), but also including
50 carnivorans, e.g. *Canis (Xenocyon) lycaonoides* or *Canis borjgali* (Bartolini-Lucenti et al., 2020;
51 2021). The Dmanisi fauna also includes taxa of African origin, e.g., *Megantereon whitei* which
52 dispersed into Europe at the beginning of the late Villafranchian (Vekua, 1995; Lordkipanidze et
53 al., 2007; Martínez-Navarro, 2010; Rook and Martínez-Navarro, 2010).

54 Fossil carnivore guilds, as all fossil associations, are affected by caveats of taphonomy (e.g.,
55 time-averaging, accumulation agent, direct or indirect selection, preferred fossilization; etc.) that
56 might limit their record as opposed to their original biocoenoses. Moreover, bias arising from
57 taxonomic attribution should not be ruled out. This considered, here we offer a comparative analysis
58 of the carnivore guild of Dmanisi with those from other Early Pleistocene localities across the Old
59 World in order to detect similarities and differences among them and to infer paleobiogeographic,
60 paleoecological and biochronological implications.

61

62 **2. Materials and methods**

63 To assess the degree of similarity among Dmanisi carnivore guild and other guilds of different
64 localities of the Old World, we performed a cluster analysis on the generic and specific composition
65 matrices of these assemblages (Table 1 and Supplementary Online Material [SOM] Table S1),
66 calculating the Jaccard's index (Jaccard, 1912) to further compare and estimate their similarity. The
67 thirty-seven localities selected to undertake the comparisons, are distributed across the Old World
68 (see Fig. 1) and span between the latest Pliocene and the beginning of the early Middle Pleistocene
69 (2.7–0.7 Ma). We tried to choose localities with accepted chronologies and with a consistent
70 number of carnivorans recorded. The compiled matrices of occurrences are based on published data
71 (Teilhard de Chardin, 1940; De Giuli and Masini, 1986; Arribas and Palmqvist, 1998; Sotnikova et
72 al., 2002; Palombo and Valli, 2003; Gaudzinski, 2004; Martinez-Navarro, 2004; Mazza et al., 2004;
73 Qiu et al., 2004; Delson et al., 2006; Lordkipanidze et al., 2007; O'Regan, 2007; Jin and Liu, 2009;
74 Martínez-Navarro et al., 2009; Sotnikova and Titov, 2009; Geraads et al., 2010; Rook and
75 Martínez-Navarro, 2010; Werdelin and Sanders, 2010; Geraads, 2011; 2016; Kahlke et al., 2011;
76 Petrucci et al., 2013; Rook et al., 2013; Wang et al., 2013; Madurell-Malapeira et al., 2010; 2012;
77 2014; Bartolini-Lucenti and Rook, 2016; 2018; Adams et al., 2016; Fourvel et al., 2017; Gkeme et
78 al., 2017; O'Regan and Steininger, 2017; Koufos, 2018; Sahnouni et al., 2018; Cohen et al., 2019;
79 Bartolini-Lucenti and Madurell-Malapeira, 2020; Bartolini-Lucenti et al., 2020; Jin et al., 2021) in

80 most cases revised and updated. The cluster analyses were carried out by applying a bootstrapping
81 cluster analysis (hereafter BCA). Bootstrapping cluster analysis is a partitioning methodology that
82 is useful to test the robustness of the clustering results. It was used in recent papers (Raia et al.,
83 2009 and Carotenuto et al., 2016) to statistically identify Pleistocene communities of Eurasian large
84 mammals. This method performs an initial clusterization of the dataset by means of the unweighted
85 pair group method with arithmetic mean (UPGMA) algorithm (Sokal, 1958). In this way the
86 analysis generates a reference clustering of the selected localities on the basis of their taxonomic
87 similarity which can putatively have biochronological, taphonomical and paleoecological
88 implications. This reference clustering is the used to assess probability of each branching in the
89 reference via a permutational approach. Subsequently, a sample of the original data is randomly
90 chosen and used to obtain a new UPGMA cluster analysis, which yield a new clustering. This
91 operation is repeated a number of times. The obtained new clusterization are compared with the
92 reference one. A similarity index (G^*) is computed between the reference and the sample clustering.
93 This index can range between 0 (if the two clusterizations are totally different) and 1 (if the
94 clusters generated with the original and sampled data coincides). The G^* is then compared with the
95 expected similarity value between reference and sample-based clustering (G°) under the null
96 hypothesis that the sampled dataset is a truly random sample of the original data. We repeated 1000
97 times the procedure of resampling the original dataset, performing as many the UPGMAs on
98 sampled data and computing similarity indices. In the end, if the probability that G^* is higher or
99 equal to G° is higher than the significant level ($P[G^\circ \leq G^*]; \alpha = 0.05$), the partitioning levels of the
100 reference cluster analysis are sharp (see Pillar, 1999 for a detailed explanation of the algorithm). We
101 performed BCA by using the R package ‘pvclust’ v. 2.2-0 (Suzuki et al., 2019).

102 We also compared ecological divisions in the analyzed guild grouping carnivorans according to
103 the classic diet categories: hypocarnivores (less than 50% vertebrate meat in the diet),
104 mesocarnivores (between 50–70% of vertebrate meat in the diet) and hypercarnivores (>70%
105 vertebrate meat in the diet; Crusafont-Pairó and Truyols-Santonja, 1956; Van Valkenburgh, 1989).

106 To these, we added an additional class of diet for insectivores (taxa specialized to insect feeding).
107 Finally, to better characterize hypercarnivorous spectrum of adaptations we included hunting
108 strategies (e.g., ambush or cursorial predation) and dietary habits (e.g., piscivorous or bone-cracking
109 carnivorans), following the ecological categories proposed in literature (e.g., Van Valkenburgh,
110 1989; Van Valkenburgh and Koepfli, 1993; Popowics, 2003; Werdelin and Peigné, 2010; Ester,
111 2012; Flower and Schreve, 2014; Medin et al., 2019). In this ecological analysis of the carnivore
112 guild of Dmanisi, we decided to ordinate the relative abundances of the diet classes of each locality
113 according to the order provided by a BCA on the ecological composition of each site.

114 Eventually, we tested whether the differences emerged from the previous analyses were
115 statistically related to temporal and/or geographical factors. To this aim, we performed a Mantel test
116 to asses any relationship between the taxonomical and the ecological distance matrices as used
117 before in comparison to the geographic and age distance matrices measured between all the fossil
118 localities here studied. More specifically, the kind of analysis we performed is able to test the
119 relationship between a response matrix and a predictor matrix while taking into account the effect
120 of other predictor matrices by means of permutations. Hence, we first analyzed the correlation
121 between taxonomic and ecological distance while taking into account time and geographic
122 distances. Then deepened the analysis taking into account taxonomy and ecological preference
123 singularly. We tested the relationship between the taxonomic distance and the geographic distance
124 by accounting for the effect of the temporal distance and, then, we repeated the same analyses, this
125 time by accounting for the effect of geographic distance on the relationship between taxonomic and
126 temporal distance matrices. We proceeded in the same way with the ecological distance matrix. In
127 addition, since we expected that the African sites would have accrued the contribution of geography
128 on determining taxonomical distances between fossil sites, we repeated the mantel tests this time by
129 using Eurasian fossil sites in order to test effect of both space and time in assessing the taxonomical
130 and ecological proximity of Dmanisi to the other Eurasian sites. We carried out the Mantel tests
131 using the R package 'ecodist' v. 2.0.1 (Goslee and Urban, 2007).

132

133 3. Results

134 Dmanisi carnivore guild is among the most diverse ones of the contemporary Old-World
135 assemblages analyzed in the present work (Table 1 and SOM Table S1). The carnivore guild from
136 Dmanisi is composed of five species of Felidae, i.e., *Homotherium latidens*, *Megantereon whitei*,
137 *Panthera onca georgica*, *Acinonyx pardinensis*, *Lynx issiodorensis*; one Hyaenidae (*Pachycrocuta*
138 *brevirostris*); three species of Canidae, i.e., *Canis (Xenocyon) lycaonoides*, *Canis borjgali*, *Vulpes*
139 *alopecooides*; one Ursidae (*Ursus etruscus*); and four Mustelidae, i.e., unstudied species of the
140 genera *Lutra*, *Martes*, *Meles* and *Pannonictis* (Fig. 2; Vekua, 1995; Lordkipanidze et al., 2007;
141 Hemmer et al., 2010; Medin et al., 2019; Bartolini-Lucenti and Madurell-Malapeira, 2020;
142 Bartolini-Lucenti et al., 2020, 2021). Compared to selected almost coeval localities from Africa and
143 East Asia (Fig. 2), the carnivoran association at Dmanisi is characterized by a lower diversity of
144 Hyaenidae (only a single species contrary to the two species of Olivola and Jinyuan Cave Lower
145 Fauna and the four of Kromdraai Member 2) but a considerably higher diversity of Mustelidae.
146 Felidae is instead the most abundant family in all the considered localities, with the exception of
147 Kromdraai Member 2, with the remarkable absence of the genus *Lynx* in Africa, a genus very
148 common in Eurasian localities. Additionally, homotherinii and smilodontinii felids are normally
149 recorded in Eurasian localities being metailurinii, the genus *Panthera* and *Acinonyx* more common
150 in African ones. Ursidae are very abundant in Eurasian localities and also present Northafrican
151 ones, but it is absent in subsaharian localities. Canidae diversity in Dmanisi is similar to those from
152 Asia and Europe, rather than to the African one. Peculiarity exclusive of the African site is the
153 presence of Hesperitidae and Viverridae in the assemblage, unlike the other localities. A more
154 extensive analysis of the guild composition of Dmanisi is here undertaken.

155

156 3.1. The Dmanisi carnivore guild structure: Comparison with European, Asian and African guilds

157 To assess the degree of similarity and/or differences between Old World localities we performed
158 a BCA on taxonomic matrices of absence/presence. The results of the BCA on the genera of the
159 carnivore guilds of numerous localities across the Old World are reported in the SOM S1 (SOM
160 Figures S1–S2, whereas that performed on the species are shown in Figures 3 and 4. The two
161 different analyses show similar patterns (i.e., distinction between African and Eurasian localities,
162 distinction between older and younger guilds, the position of Dmanisi). Of the two, the analysis on
163 the matrix of absence/presence based on species is, as expected, more resolved (Fig. 3), although its
164 Jaccard indices are in general lower than those of genera (see Fig. 4, SOM Fig. S2 and SOM Tables
165 S2–S3). Similarly to the genera-based analysis (SOM Fig. S1), the dendrogram of the BCA on the
166 species matrix shows two distinct groups: one composed only of African localities (hereafter the
167 ‘African cluster’; identified at node A1) and a second one is made up of the Eurasian ones
168 (hereafter the ‘Eurasian cluster’, sprouting from node B1). These two groups are well supported by
169 high values of percentage p -values (both 98%) and evidently separated also on the basis of Jaccard
170 similarity indices (Fig. 4). In the African cluster, the pattern of similarities yielded in the genera-
171 based hierarchical analysis (SOM Fig. S1) or in the respective Jaccard indices (SOM Fig. S2) are
172 more or less confirmed. For instance, the grouping of the South African and of the North African
173 sites, of the members of the Shungura Formation of Omo (Fig. 3). The Jaccard values of Omo
174 members are the highest of the African cluster (Fig. 4) and much higher in comparison to those of
175 SOM Figure S2, testifying to a considerably higher similarity when species are taken into
176 consideration (Fig. 4). In contrast to the genera-based hierarchical analysis, the site of Ahl al
177 Oughlam is rooted at the base of the African cluster and groups with the other North African site of
178 Tighennif. Both these sites have diverse and numerous peculiar taxa, supporting the distance in
179 comparison to other African sites. This is confirmed also by their Jaccard indices (Fig. 4). For
180 instance, in Tighennif there is the first record of Lyncodontini in the African continent (*Pannonictis*
181 *hoffstetteri*) whereas some taxa recorded in Ahl al Oughlam show affinity with Eurasian species like
182 the raccoon dog *Nyctereutes abdeslami*, the scimitar-toothed cat *Homotherium latidens*, *Lynx* gr.

183 *issiodorensis* and *Ursus etruscus*, although most of the species is African related. After Ahl al
184 Oughlam-Tighennif group, the following group to branch out (node A6) is that of the South African
185 localities. Of these four, Member 2 of Kromdraai is the first to separated from the others. This is
186 possibly due to the occurrence of taxa like *Aonyx capensis*, *Civettictis civetta*, *Mellivora capensis*,
187 *Propoecilogale bolti* and primitive wild of the *Canis (Xenocyon) falconeri* group, absent in the
188 other sites. The same can be said for Sterkfontein Member 4, which shares more affinity with
189 Drimolen and Coopers D, but also possess exclusive taxa absent in the latter sites, e.g.,
190 *Pachycrocuta* and *Canis brevirostris*. The support to node A8 is among the highest of the analysis
191 (percentage *p*-value = 98%). Despite their clear similarity and fairly numerous shared species (eight
192 taxa), Drimolen and Coopers possess several carnivorans that are present in one site but absent in
193 the other one. For instance, Drimolen lacks *Acinonyx jubatus*, *Herpestes ichneumon*, *Lupulella*
194 *mesomelas*, *Panthera leo*, but on the other side it records *Dinofelis barlowi*, *Lycaenops silberbergi*,
195 *Vulpes chama*. These differences are testified to also by the rather low Jaccard indices. The last
196 group in the African cluster is that composed of East African localites (node A3; Fig. 3). As
197 discussed before, the members of Shungura Formation of Omo form a well-supported and identified
198 subgroup (node A12). The Tanzanian Olduvai beds and Kenyan Koobi Fora members are arranged
199 together, apparently not strictly following a chronological order. They are joined by some elements
200 like the felids *Panthera leo* and *Panthera pardus* and the hyenid *Crocuta crocuta* and *Hyaena*
201 *hyaena* and the viverrid *Pseudocivetta ingens*, which are present in almost every site. Despite these
202 shared taxa, each site shows a number of species that differ from the other. This limited similarity is
203 reflected in the Jaccard values, which are high only for Olduvai Bed II and KBS member (that share
204 5 taxa out of eight, Olduvai Bed II, and of six, KBS, respectively).

205 The opposite group is entirely composed of Eurasian localities (Fig. 3). This Eurasian cluster is
206 further subdivided in two groups: one comprises all Chinese localities (node B2), whereas European
207 localities fall together (node B3). In turn, those groups, the Chinese and the European clusters, are
208 made up by two subclusters. The first of the two Chinese subclusters (node B4) is composed of

209 three localities close in age to one another, the upper levels of Jinyuan Cave, Zhoukoudian Loc. 1
210 and Gongwangling. The closer affinity between the latter two sites (node B5), is due to four shared
211 species although both record several taxa absent in the other (six of GWL absent in ZKD1 and five
212 of ZDK1 not present in GWL) as testified to by the fairly low percentage of the p -value (= 58%).
213 The second group of the Chinese cluster includes the oldest Asian localities on the analysis and it is
214 fairly well supported (percentage p -value = 92%). The first to branch out is Zhoukoudian Loc. 18.
215 The limited record of this site makes difficult to narrow down its affinity to other localities. The
216 latter are grouped in two small clusters, both well supported (node B12 = 95% and node B14 =
217 99%). Longguopo and and Renzidong form a group sharing almost all their carnivorans. The other
218 group is composed of three sites. Jinyuan Cave Lower Fauna lies at the base of the subcluster and is
219 distinguished from Longdan and Nihewan (Xiashagou), which cluster together (Fig. 3). The Jaccard
220 indices are high for the three sites (> 0.60 ; Fig. 4), testifying to their affinities. Of the last three
221 sites, Jinyuan Cave Lower Fauna is distinct from Longdan and Nihewan for the presence of *Martes*
222 *andressoni*. Moreover, there are some taxa shared by Jinyuan Cave Lower Fauna and Longdan and
223 others present only in Nihewan and Jinyuan Cave Lower Fauna. With Longdan, Jinyuan Cave
224 Lower Fauna shares *Panthera leo* and *Canis (Xenocyon) dubius*. With Nihewan these shared taxa
225 include *Nyctereutes sinensis* and *Ursus gr. etruscus*. Longdan and Nihewan share thirteen taxa and
226 have a high Jaccard similarity index (Fig. 4). The differences, in addition to those already discussed
227 above, Nihewan uniquely records *Acinonyx pardinensis*, *Canis (Xenocyon) gr. lycaonoides*, *Eucyon*
228 *minor*, *Lutra licenti* and *Ursus etruscus*, whereas Longdan records the presence of *Canis*
229 *(Xenocyon) dubius* and *Ursus gr. thibetanus*.

230 Opposite to this Chinese cluster, there is a large well-supported European cluster (node B3; Fig.
231 3), which is again divided in two subclusters (nodes B7 and B11). The smaller one (node B7), in
232 terms of number of sites included in it, is composed of six localities in two subgroups (nodes B9
233 and B10). This group includes localities dated between ca 2.5 and 1.7 Ma. The Casa Frata lies at the
234 base of the cluster composed of the Italian localities of Poggio Rosso and Olivola (Fig. 3), in a

235 group of geographically and spatially close localities. Jaccard similarity index for Casa Frata is
236 fairly higher of Olivola and Poggio Rosso (Fig. 4) because it lacks several elements of the latter
237 sites (e.g., *Canis etruscus*, *Chasmaporthetes lunensis*, and *Felis sylvestris*), while possessing other
238 taxa like *Canis (Xenocyon) falconeri* and *Vulpes alopecoides* absent in the latter sites. Poggio Rosso
239 and Olivola have high Jaccard indices (the highest of the group of node B7), thanks for the fourteen
240 shared taxa. The second small subgroup (node B9) shows Khapry Faunal Complex at the base of
241 the grouping of the French sites of St. Vallier and Senèze (node B13). Three sites share iconic
242 Gelasian species like derived *Nyctereutes gr. megamastoides* and *Pliocrocota perrieri*, as well as
243 others e.g., *Acinonyx pardinensis* and *Homotherium latidens*. The similarity between Senèze and St.
244 Vallier is undoubtful, although at a lower degree compared to the group of Olivola and Poggio
245 Rosso, as testified to by the Jaccard indices (Fig. 4). The second subcluster is the one that includes
246 also Dmanisi, together with all younger sites (node B11; Fig. 3). At its base stems ‘Ubeidiya. Its
247 guild shares with the other late Early Pleistocene sites the presence of some Eurasian elements like
248 *Canis mosbachensis*, *C. (Xenocyon) lycaonoides*, *V. alopecoides*, *Martellictis ardea* and *U.*
249 *etruscus*. On the other side, ‘Ubeidiya guild is characterized by the occurrence of African taxa like
250 *Crocota crocuta* and *Vormela peregusna*. Within the subcluster, there are two groups formed
251 respectively by late Villafranchian (node B19) and by Epivillafranchian sites (node B18).
252 Interestingly, these groups have the highest Jaccard index of all (Fig. 4). Within the late
253 Villafranchian cluster, Pirro Nord lies at the base. Pirro Nord is the most diverse guild of the late
254 Villafranchian group (with fourteen species). It shares almost all the taxa with the remaining sites
255 but has some exclusive taxa like: *Puma pardoides*, *Pannonictis nestii* and *Mustela palerminea*.
256 Dmanisi is closely associated with Venta Micena and Apollonia 1 (as it is visible from some of the
257 highest values of Jaccard similarity index, Fig. 4). Indeed, there are only few differences among the
258 guilds of the three sites, despite the difference in age: the badger of Venta Micena and Apollonia 1
259 belongs to the lineage of the extant *Meles meles*, whereas the specimens from Dmanisi are yet
260 unpublished and not studied in detail. Furthermore, no *Acinonyx* was found in the Spanish and

261 Greek sites, whereas *A. pardinensis* is present in Dmanisi. The Epivillafranchian sites are grouped
262 in couples with the two chronological groups of the Vallparadís Section grouped together (node
263 B21), whereas on the other side (node B20), Vallonnet is grouped with Untermassfeld for their
264 almost identical guild (Fig. 3). This is also confirmed by the indices of Fig. 4.

265 If we analyze in more detail the Jaccard similarity indices reported in Fig. 4, we see that the
266 African localities have very low indices (between 0.0 and 0.2; SOM Table S3) when compared to
267 Eurasian localities, justifying their clusterization in two different groups. Within the African group,
268 the East African sites of Olduvai Bed 2, KBS and Upper Burgi of Koobi Fora have fairly high
269 indices (0.20–0.56; SOM Table S3) when compared to other African localities, with the exception
270 of Drimolen which have particularly low indices, close to zero, as opposed to the East African sites.
271 Indeed, Drimolen is one of the most different of all African localities, possessing very low values
272 of Jaccard index, apart with Coopers D and Sterkfontein Member 4. Other guilds with fairly low
273 similarity indices are those of the North African Ahl al Oughlam and Tighennif (below 0.26).
274 Whereas, close to several East African guilds, e.g., Olduvai Bed 2, KBS and Upper Burgi, members
275 of Shungura Formation at Omo differ markedly in Jaccard indices from North and South African
276 ones (indices between 0.17 and 0.0). In comparison to the other guilds analyzed, Ahl al Oughlam
277 and Tighennif are the African localities with a limited similarity with Eurasian guild, as expected
278 considering the position and the connection between the Mediterranean Africa and the Levantine
279 corridor or the Iberian Peninsula. Indeed, the third highest Jaccard index of Tighennif is with
280 ‘Ubeidiya (still rather low: 0.22), whereas Ahl al Oughlam has a slightly high values (between
281 0.207 and 0.176) with St. Vallier and with 2.0 Ma-old localities of China (e.g., Nihewan,
282 Longgupo) and Europe (e.g., Olivola). The other African guilds, both East and South African, do
283 not show indices higher than 0.15 (SOM Table S3). The Eurasian group is characterized by sensibly
284 higher Jaccard indices (Fig. 4). As explained above this group is further subdivided into two
285 subclusters, a Chinese and a European one. The Jaccard indices confirm the pattern yielded by the
286 BCA, particularly showing that the cluster of Epivillafranchian localities, among which Dmanisi is

287 also included in spite of its older age (Fig. 4), has the highest Jaccard values of all the compared
288 guilds (above 0.56; SOM Table S3), with Venta Micena showing two greatest indices respectively
289 with Apollonia-1 (0.909) and with Dmanisi (0.818; SOM Table S3). Apart from the clear division
290 in two groups and the high values of the European Epivillafranchian guilds, Jaccard indices allow
291 additional comparisons. Of the Chinese group, the site younger in age (i.e., Gongwangling,
292 Zhoukoudian Loc. 1 and Jinyuan Cave Upper Fauna) are those with the lowest Jaccard values,
293 because of their taxonomic difference with the rest of the Chinese guilds. This is particularly
294 evident with Jinyuan Upper Cave (maximum Jaccard index with a Chinese locality = 0.27),
295 although this site shows similar values (0.214–0.231; SOM Table S3) with European sites, e.g.,
296 Venta Micena, EVT 10/12 and Dmanisi. A comparable degree of affinity with Western sites is
297 shown also by Xiashagou locality of Nihewan basin, which have modestly high values of Poggio
298 Rosso, Dmanisi and Olivola but also with the younger Apollonia-1. Within the European group, the
299 Jaccard indices are on average fairly high (average of the Jaccard indices = 0.373). The sites with
300 lowest Jaccard indices are Khapry FC and Senèze. The former has even an index of zero in
301 comparison to ‘Ubeidiya (Fig. 4; SOM Table S3). On the contrary, in comparison to Chinese
302 localities Khapry FC have modestly high values (between 0.150 and 0.238, SOM Table S3), apart
303 from Gongwangling, Zhoukoudian Loc. 1 and Loc. 18. Indeed, in respect to Chinese guilds, Senèze
304 is more different compared to Khapry FC and so is St. Vallier, whose Jaccard indices are below
305 0.125 (only Nihewan is above this value). The localities of Casa Frata, Olivola and Poggio Rosso
306 have intermediate values (roughly enclosed between 0.20 and 0.50) in comparison to the early
307 Gelasian and the later Calabrian localities of Western Europe. Apart from the high values of the late
308 Calabrian group that includes Dmanisi, ‘Ubeidiya interestingly possesses higher Jaccards with guilds
309 of Dmanisi, Venta Micena and Apollonia-1 than in comparison to other localities of Asia and
310 Europe (Fig.4; SOM Table S3). As privileged subject of this research, the Jaccard indices of
311 Dmanisi confirm its prominent affinity with younger sites (Figs. 3–4; SOM Table S3), but also a

312 certain affinity to the Italian sites of Olivola, slightly older, and Casa Frata, slightly younger of the
313 Georgian one.

314

315 3.2. *Ecological comparison between guild elements*

316 The comparison between the guild structures, in terms of ecological preferences is reported in
317 Figure 5. This figure shows the relative abundance of each preference in the locality but also a
318 clusterization of the site on the basis of their ecological composition. The BCA on these
319 parameters, because indirectly influenced by taxonomy, yields interesting results. The Asian
320 localities are separated from the others. Apart from Renzidong, which is completely separated from
321 all the other sites, the other localities are included in a group at the bottom of Figure 5, together
322 with the eastern European locality of Khapry FC. Despite this apparently large-scale geographic
323 clustering, the other sites, the European and African ones, are arranged in different clusters. Some
324 of the pattern seen in the BCA based on taxonomy are respected in Figure 5. Among these, the
325 relationship of Dmanisi with Pirro, Venta Micena and Apollonia 1. If analyzed in detail, the
326 carnivorans of the guild from Dmanisi spot out in their ecological preferences: although more than
327 70% of its taxa were plausibly hypercarnivorous, as meso- and hypocarnivorous species account for
328 30% of the guild, within this large group, different diet preferences and hunting strategies can be
329 observed. Of these hypercarnivorous taxa, surely the most abundant are the cursorial ones,
330 carnivores basing their hunting strategy on long pursuits such as the Eurasian hunting dog *C.*
331 (*Xenocyon*) *lycaonoides* and the cheetah *Acinonyx pardinensis*, evidencing the prevalence of open
332 environments at Dmanisi. These taxa comprise almost a third of the whole carnivore guild (Fig. 5).
333 The second most important component of the carnivore guild are the hypercarnivorous taxa that
334 ambush their prey (Fig. 5). In Dmanisi those are the felids *L. issiodorensis*, *M. whitei* and *P. onca*
335 *georgica*. Piscivorous and bone-cracker carnivores are limited to one taxon for each group in
336 Dmanisi, respectively *Lutra* and *Pachycrocuta*. The small-sized hypercarnivores are represented by
337 *Martes* sp. whilst mesocarnivorous and omnivorous species include respectively *V. alopecoides*,

338 and *Meles* and *Ursus*. In comparison to African guilds, Dmanisi lacks insectivorous taxa (Fig. 5),
339 e.g., of the families Herpestidae or even Canidae (as in the case of Olduvai Bed I). In turns, African
340 localities lack small-sized hypercarnivores common in Eurasian context (mainly represented by
341 mustelids of the genera *Martes* and *Mustela*; Fig. 5). In these two elements, Dmanisi is closer to
342 Eurasian sites. Moreover, generally African localities have a larger proportion of bone-cracking
343 Hyaeonidae in their guild compared to Dmanisi and Eurasian sites. Hypocarnivorous taxa with
344 adaptations to nearly herbivorous diet has only been recorded in Eurasia: *Ailuropoda* in eastern
345 Asian and *Ursus deningeri* in the late Villafranchian deposits of Europe. *Ursus etruscus* from
346 Dmanisi is related to the latter yet it does not show herbivorous-related adaptations in its
347 dentognathic features (Medin et al., 2019). As a whole, the most similar guilds are those from
348 Eurasia as the BCA of Figure 5 clearly shows. In terms of proportions between these ecological
349 divisions are 'Ubeidiya and Nihewan Basin, although the latter has fewer omnivorous species
350 compared to Dmanisi and in the former the percentage of ambush predators is larger compared to
351 the Georgian one.

352

353 3.3. Mantel test

354 The Mantel tests provided significant results when considering both the whole record and the
355 reduced sample of Eurasian sites. The first set of Mantel tests, at Old-World scale, yielded
356 significant relationships either between the taxonomic and ecological distance matrices, when
357 accounting for the effect of time and space ($r = 0.243$; $p_{(r<0)} = 0.002$; $p_{(r>0)} = 0.999$; $p_{(r=0)} = 0.002$).
358 When excluding ecology, the test yield significant result either between the taxonomic and the
359 temporal distance matrices when accounting of the effect of space ($r = 0.163$; $p_{(r<0)} = 0.008$; $p_{(r>0)} =$
360 0.993 ; $p_{(r=0)} = 0.008$) either between the taxonomic and geographic distance matrices when
361 accounting for time ($r = 0.551$; $p_{(r<0)} = 0.001$; $p_{(r>0)} = 1.000$; $p_{(r=0)} = 0.001$). If the ecology distance
362 matrix is used as response matrix in comparison to temporal (with space distance accounted for)
363 and then spatial (with time accounted for) are predictor matrices, we obtain interesting results.

364 When space is the main predictor matrix, we obtain significant correlation between it and ecology
365 distance ($r = 0.467$; $p_{(r<0)} = 0.001$; $p_{(r>0)} = 1.000$; $p_{(r=0)} = 0.001$), as in the case of the taxonomy
366 distance matrix. In the case of the ecology and age distance matrices accounting for the geographic
367 distance, the relationship is low and non-significant ($r = 0.088$; $p_{(r<0)} = 0.113$; $p_{(r>0)} = 0.888$; $p_{(r=0)} =$
368 0.240).

369 Comparable results are obtained when we performed by ruling out the African fossil sites. There is
370 significant relationships either between taxonomic and temporal distances when accounting for
371 geography ($r = 0.405$; $p_{(r<0)} = 0.001$; $p_{(r>0)} = 1.000$; $p_{(r=0)} = 0.001$); between taxonomic and spatial
372 distances when accounting for time ($r = 0.581$; $p_{(r<0)} = 0.001$; $p_{(r>0)} = 1.000$; $p_{(r=0)} = 0.001$); and
373 lastly, between ecological and geographic distance matrices when accounting for time ($r = 0.399$;
374 $p_{(r<0)} = 0.001$; $p_{(r>0)} = 1.000$; $p_{(r=0)} = 0.001$). When testing relationship between ecological and
375 temporal distances considering the effect of space differences, we find no significant relationship
376 between them ($r = 0.131$; $p_{(r<0)} = 0.066$; $p_{(r>0)} = 0.935$; $p_{(r=0)} = 0.104$).

377

378 **4. Discussion**

379 *4.1 Carnivore guild of Dmanisi in the framework of Old World carnivore guilds*

380 The association of carnivorans recovered from Dmanisi represent one of most diverse guilds of the
381 Old World, with fourteen taxa (ten recognized at a specific level and four only at a generic one) and
382 seven different ecological categories (the maximum among the studied guilds). While analyzing
383 similarities and differences between carnivore guilds, some issues must be kept in mind. A first idea
384 one might get dealing with large scale analyses of sites (as well as guilds) might be that their
385 clusterization was driven by biases in the taxonomic attributions made by authors describing those
386 associations or those carrying out the analyses. Undoubtedly, such biases arise for different reasons
387 (competency of the researcher; different interpretations, etc.) and are greater at a specific level,
388 rather than at a genus one. The correspondence between the patterns resulted from the analyses
389 genera and the species here carried out (Fig. 3; SOM Fig. S1) rules out the possibility that the

390 affinities yielded by the BCA could be explained by biases derived by questionable attributions of
391 taxa, especially at a specific level. Those similarities/differences are therefore related rather to
392 geography, age, taxonomic and ecological composition of the guild. More complex and
393 considerably difficult to assess, is the impact of taphonomic processes in the fossil assemblages, and
394 particularly for the carnivore guild. Indeed, taphonomy may affect greatly the interpretation derived
395 by comparisons between different guilds, both in terms of taxonomy and of ecology. For instance,
396 certain elements like carnivorans preying on small prey are generally small-sized themselves (e.g.,
397 herpestids, mustelids, viverrids) and could be underrepresented (or absent) in many sites due to a
398 selective biotic or abiotic agent of accumulation, unsuitable or unfavorable condition of burial
399 and/or fossilization, etc. Likewise, competition among large-sized carnivorans of similar ecology
400 might dwindle the chances of or even prevent the accumulation and the eventual fossilization of
401 some of them. Borne that in mind, the analyses of the considered guilds yielded interesting results.
402 Our study clearly points out the affinity of the carnivorans association of Dmanisi to the younger,
403 late Villafranchian ones of Western Europe in comparison to any other of the Old World. Among
404 these, particularly, Apollonia 1, Pirro Nord and Venta Micena, on the basis of both ecological
405 preferences of their carnivorans and their taxonomy (Figs. 3–5). Furthermore, the
406 similarities/differences resulted from the analyses sheds light on larger-scale patterns of dispersal
407 and affinity that took place during the Early Pleistocene. Although Eurasian sites shares circa one
408 thirds of the species with the African localities, this was not enough to homogenize the composition
409 carnivore guilds of the two continents, neither taxonomically nor ecologically, as explained by the
410 Mantel tests. This supports the importance of areas connecting different continent, e.g., the
411 Levantine corridor and the Pontocaspian region, in explaining association in the Old World. On the
412 one hand, it is an indirect proof that geographical corridors between the two continents acted as a
413 filter for many taxa and as ecological barriers limiting the dispersal of taxa in certain areas (e.g., the
414 presence of ursids in subsaharian Africa). On the other, many of the shared taxa are recorded in
415 these areas of contact. Although explained by geographic distance, the ecological differences are

416 poorly related to chronological difference, as visible from the Mantel test. The contribution of both
417 geography and time still explains the taxonomical differences when considering Eurasian sites only,
418 and likewise the ecological differences are still related to geographic distances rather than to
419 temporal ones.

420

421 4.2 *The Dmanisi carnivorans in the Old World context*

422 The carnivoran taxa that compose the diverse carnivore guild of Dmanisi can be ascribed to three
423 groups based on their paleogeographic origin.

424

425 Species previously recorded in European guilds Most of the species recorded in Dmanisi were
426 previously identified in the middle-late Villafranchian guilds of Europe as *H. latidens*, *A.*
427 *pardinensis*, *L. issiodorensis*, *U. etruscus* and *V. alopecoides* (Rook and Martínez-Navarro, 2010;
428 Madurell-Malapeira et al., 2010; Bartolini-Lucenti and Madurell-Malapeira, 2020 and references
429 therein). Within these typical Villafranchian species, *Homotherium latidens* was a pursuit predator
430 adapted to open environments with an estimated body mass of 150–250 kg (Hemmer, 2004). It is
431 recorded since the beginning of the Villafranchian (ca. 3.2 Ma) in localities like Perrier-Les
432 Etouaires, Saint Vallier, Senèze, Upper Valdarno or Incarcal complex (Viret, 1954; Ballesio, 1963;
433 Rook et al., 2013; Alba et al., 2016) being also widely recorded in Africa and Asia during the Plio-
434 Pleistocene (Werdelin and Peigné, 2010; Jin et al., 2021). Concerning the social behaviour of
435 *Homotherium*, or if this species hunts in packs as extant lions, a lot of literature is centered on the
436 sociality of sabertoothed cats, especially *Smilodon* (Carbone et al., 2009). Nowadays, no direct
437 evidence supports the sociality in *Homotherium*, however is reasonable to think that this species
438 displays a certain degree of social behavior (Antón, 2013).

439 The European record of the giant cheetah *A. pardinensis* is noticeably scarce. Although, it is
440 present in several European sites since the beginning of the Villafranchian as Montopoli, Saint
441 Vallier, Villarroya, Pantalla or Olivola, normally it is only recorded on the basis of partial or

442 fragmentary remains (Viret, 1954; Cherin et al., 2014a; Madurell-Malapeira and Vinuesa, 2016).
443 The record of a complete forelimb of this species in Dmanisi (Hemmer et al., 2011), show that *A.*
444 *pardinensis* is stoutly built solitary hunter (ca. 60–130 kg), which preferred open habitats and can
445 be a potential fresh meat supplier for other scavenger species, including hominins (Hemmer, 2004;
446 Hemmer et al., 2011). The genus is known to occur in Africa since 4 Ma (Werdelin and Peigné,
447 2010), whereas this species is also recorded in Asian Pleistocene taphocoenoses under different
448 taxonomical adscriptions (Qiu et al., 2004).

449 *Lynx*-like felids traditionally included in *Lynx issiodorensis* are recorded in Europe since the
450 beginning of the Pliocene in sites like Serrat d'en Vaquer or Cuevas de Alzamora (Werdelin, 1981;
451 Montoya et al., 2001). However, the taxonomic status of these early representatives of the *Lynx*
452 lineage remains controversial as a consequence of the scanty and poorly diagnostic record. Since
453 the beginning of the Villafranchian, true lynxes were recorded in several sites such as: Perrier-Les
454 Etouaires, Saint Vallier, Olivola and Pantalla (Viret, 1954; Ficcarelli and Torre, 1977; Kurtén,
455 1978; Cherin et al., 2013; Mecozzi et al., 2021). According to some authors *L. issiodorensis* was the
456 ancestor of both *Lynx lynx* and *Lynx pardinus* (Werdelin, 1981; Boscaini et al., 2015; 2016;
457 Mecozzi et al., 2021), with *L. pardinus* first recorded in eastern Iberian Peninsula at ca. 1.6 Ma
458 (Boscaini et al., 2015). The Dmanisi lynx together with the Upper Valdarno record probably
459 corresponds to the last representatives of this large species, larger than an extant boreal lynx and
460 with an estimated body mass of 23.5 Kg (Mecozzi et al., 2021) enabling it to hunt medium to large
461 species of ungulates.

462 In a recent work focused on the ursid remains from Dmanisi, Medin et al. (2019) provided some
463 inferences on the dietary behavior and evolutionary history of *U. etruscus*, recorded since the
464 Middle Villafranchian (ca. 2.6 Ma) in European localities like Saint Vallier, Upper Valdarno or
465 Kuruksay (Ristori 1897; Viret, 1954; Sotnikova, 1978). We favor the traditional point of view of
466 Kurtén (1958) who first hypothesized a phylogenetic line for cave bears started with the Early
467 Pleistocene *U. etruscus*, followed by the Middle Pleistocene *Ursus deningeri* and finally in the Late

468 Pleistocene for *Ursus spelaeus* s.l. Considering the profound effects of the Pleistocene climatic
469 shifts and their impact on the members of this lineage, it is possible that this pioneering hypothesis
470 of gradual evolution from the omnivorous etruscoid forms to the hyperherbivorous speleoid forms
471 needs to be improved. Especially considering the severity of climatic oscillations at the beginning
472 of the Early-Middle Pleistocene Transition (ca. 1.2 Ma), the sudden increase in size and the start of
473 cave dependence of these forms around that time, appears to fit more with rapid diversification rates
474 of the punctuated equilibria. However, the results of Medin et al. (2019) on the sample from
475 Dmanisi show the existence of a remarkable sexual dimorphism in the early forms of this lineage.
476 Moreover, the authors point evidence that *U. etruscus* inhabited mixed environments of woodlands
477 and/or wooded grasslands, where it fed on a broad variety of food items with a substantial intake of
478 meat and/or fish (Medin et al., 2017).

479 Regarding medium-to small sized carnivores, few remains of a small canid from Dmanisi can be
480 ascribed to *Vulpes alopecoides*. The taxonomy and phylogenetic relationships among European
481 Plio-Pleistocene foxes were a matter of considerable debate the last decades (Bartolini-Lucenti and
482 Madurell-Malapeira, 2020 and references therein). In paleontological literature, several different
483 species were described from Early Pleistocene deposits across Europe. These were *V. alopecoides*,
484 *Vulpes praeglacialis* and *Vulpes praecorsac*. One of the main criteria used to distinguish them was
485 size. In a recent revision of the Early Pleistocene fox record across Europe, Bartolini-Lucenti and
486 Madurell-Malapeira (2020) considered that the observed morphological and morphometric
487 variability of fossil foxes from this chronological time span can be accommodated in a single
488 species. Considering the priority of the name *V. alopecoides*, *V. praeglacialis* and *V. praecorsac*
489 should be junior subjective synonyms of *V. alopecoides*. Its origin seems to be related to the Near
490 Eastern forms of the late Early Pliocene (Bartolini-Lucenti and Madurell-Malapeira, 2021) and it is
491 plausibly related to the extant red fox, *Vulpes vulpes* (Bartolini-Lucenti and Madurell-Malapeira,
492 2020). The pan-European species *V. alopecoides* was most probably replaced at the beginning of

493 the Middle Pleistocene (ca. 0.6 Ma) by the red fox (Bonifay, 1971; Madurell-Malapeira et al.,
494 2021).

495 Although not yet studied in detail or fully characterized, the mustelids recovered from Dmanisi
496 confidently belong to some of the genera widespread in Eurasia during the Late Pliocene and Early
497 Pleistocene. For instance, *Pannonictis* spp. are known from the Earliest Pleistocene deposits of
498 Hungary (Ros-Montoya et al., 2021; Fig. 1). The most probable origin of the genus is the European
499 continent (Bartolini-Lucenti, 2018; Rook et al., 2018). Whereas *Meles* was recorded in other
500 European localities like Saint Vallier, Vatera and Lesvos islands (Viret, 1951; 1954; Madurell-
501 Malapeira et al., 2011; Koufos, 2014). The evolutionary history of *Lutra* is more complicated and
502 fragmentary (Cherin and Rook, 2014; Cherin, 2017). The earliest European record is that of *Lutra*
503 *bravardi* from Perrier-Les Etouaries yet the validity of this taxon was questioned by several
504 scholars as its type was lost (Willemsen, 1992; Cherin and Rook, 2014; Cherin, 2017). A certain
505 attribution is that of *Lutra fatimazohrae* from the Earliest Pleistocene of Morocco (Geraads, 1997).
506 Yet as the author of the original description asserts, this species cannot be regarded as the ancestor
507 of subsequent species (e.g., *Lutra simplicidens*) and so, for the moment an African origin for these
508 taxa could be excluded (Geraads, 1997). Although its origin is still clouded, *Lutra* and other similar
509 taxa (Cherin et al., 2016; Cherin, 2017), became widespread during the Late Villafranchian.

510

511 Species previously recorded in Asian guilds Although early, disputed, findings of *Canis* species are
512 recorded from 3 Ma deposits (Vialeto; Lacomat et al., 2006) of Western Europe, the center of
513 radiation and dispersion in the Old World is most certainly eastern Eurasia (Sotnikova and Rook,
514 2010). The subsequent records of *Canis* in Europe seem to testify these waves of dispersion of
515 different canid taxa from Asia. For instances, Coste San Giacomo, Fonelas P1, Gerakarou, Olivola,
516 Pantalla, Senèze and Upper Valdarno record the arrival of *C. etruscus* and *Canis senezensis* (Torre,
517 1967; Martin, 1973; Garrido and Arribas, 2008; Cherin et al., 2014b). *Canis arnensis* is slightly
518 younger and at present limited to Italy (Bartolini-Lucenti and Rook, 2016). The record in Dmanisi

519 of a new species of medium-sized canid, *Canis borjgali*, represents a novelty in the scenario of
520 Eurasian canids (Bartolini-Lucenti et al., 2020). As also noted by other scholars (e.g., Sotnikova and
521 Rook, 2010), the cranial features possessed by *C. borjgali* are more derived compared to the coeval
522 canids of Europe (i.e., *Canis etruscus*, *C. arnensis*) and Asia (e.g., *Canis chihliensis*; Bartolini-
523 Lucenti et al., 2020). Considering the similarity, *C. borjgali* can be regarded as the ancestor of the
524 *Canis mosbachensis* lineage, including *Canis orcensis* (Bartolini-Lucenti et al., 2017; 2020;
525 Martínez-Navarro et al., 2021) and, thus, strictly related to the wolf-crown group (i.e., *Canis lupus*,
526 *Canis latrans*, *Canis lupaster*, *Canis anthus*, *Canis aureus*; Sotnikova and Rook, 2010;
527 Gopalakrishnan et al., 2017; Bartolini-Lucenti et al., 2020). Moreover, the early record of this
528 derived form anticipates the turnover that can be called the ‘late Early Pleistocene canid revolution’,
529 when the diversity of medium- and large-sized Canidae dropped to two taxa (*C. mosbachensis* and
530 *Canis [Xenocyon] lycaonoides*) that replaced more primitive forms across Europe, probably
531 remaining in isolated refugia (Sotnikova, 2001; Rook and Martínez-Navarro, 2010; Sotnikova and
532 Rook, 2010; Petrucci et al., 2013; Bartolini-Lucenti et al., 2017).

533 Whereas other large-sized and hypercarnivorous species are known across Eurasia and Africa
534 during the Calabrian [e.g., *C. (Xenocyon) falconeri* and *C. (Xenocyon) africanus*; see Rook, 1994),
535 the specimen of *Canis (Xenocyon) lycaonoides* from Dmanisi is more derived compared to these
536 (Bartolini-Lucenti et al., 2021), clearly resembling the later forms from Venta Micena, Pirro Nord,
537 Vallparadís Estació and Untermassfeld (Sotnikova, 2001). Like in the case of *C. borjgali*, the
538 discovery a specimen of *C. (Xenocyon) lycaonoides* in Dmanisi confirms the relevancy of the
539 Georgian sites in the scenario of dispersion of Canidae, and other species across the entire Old
540 World. Unlike the medium-sized forms, *C. (Xenocyon) lycaonoides* also managed to disperse into
541 Africa (as testified by the record of Olduvai Bed II) and also to reach North America (Cripple Creek
542 Sump, Alaska; Tedford et al., 2009), becoming one of the extinct canids with the widest range of
543 distribution, larger than extant *C. lupus*.

544

545 Species previously recorded in African guilds Only three of the species identified in the Dmanisi
546 sample are putative possible African immigrants, namely: *M. whitei*, *Pa. brevirostris* and *P. onca*
547 *georgica*. Similarly to the genus *Homotherium*, the genus *Megantereon* was recorded in Europe
548 since the beginning of the Villafranchian (3.2 Ma; Rook and Martínez-Navarro, 2010).
549 *Megantereon* was clearly an ambush-predator with a powerful forelimb which might have preferred
550 closed and forested habitats. Its estimated body mass ranged between 80–150 Kg (Hemmer, 2004).
551 Some recent research in Asian taphocoenosis suggest *Megantereon* might not be well-adapted to
552 closed-humid forested environment but rather than more open-habitats (Zhu et al., in press). The
553 species diversity of the genus *Megantereon* have been highly debated in the past (Martínez-Navarro
554 and Palmqvist, 1995, 1996; Werdelin and Lewis, 2002; Palmqvist et al., 2007; Lewis and Werdelin,
555 2010;), from authors favoring the existence of only two main species in the Old World (Palmqvist
556 et al., 2007) while other support the existence of a higher diversity (Werdelin and Lewis, 2002).
557 Despite the debate, it seems to be widely accepted that in Europe in Early-Middle Villafranchian
558 times the most abundant species is *M. cultridens* and that, later on, *M. whitei* replaced this taxon.
559 *Megantereon whitei* was an African taxa that dispersed into Europe in the Calabrian, and Dmanisi is
560 indeed one of the first European records. This species was subsequently recorded in Venta Micena,
561 Pirro Nord, Argentario Apollonia 1, and lately at Untermassfeld and Vallparadís Section EVT12
562 (Martínez-Navarro and Palmqvist, 1996; Sardella et al., 2008; Petrucci et al., 2013; Hemmer, 2001;
563 Madurell-Malapeira et al., 2010, 2017). *Megantereon whitei* was an efficient hunter, which
564 probably used its powerful forelimbs to subdue its prey, in order to bite, suffocate and bleed out the
565 prey with a powerful bite with its sharp and long canines (around 10 cm length). Some authors have
566 pointed out that because of its canines and specialized check teeth, *M. whitei* was only able to eat
567 the soft parts of the prey, leaving a big part of the carcasses for scavengers, like the large-sized
568 hyena *Pa. brevirostris* and hominins (Martínez-Navarro and Palmqvist, 1995, 1996; Palmqvist et
569 al., 2007).

570 The origin and earliest records of the genus *Pachycrocuta* has also been strongly debated in the
571 last decades. Palmqvist et al. (2011) favored an African origin of this genus, while other authors
572 such as Werdelin (1999) and Liu et al. (2021) convincingly supported an Asian origin of this genus.
573 The latter scholars point out that the earliest records in Asia and Africa are practically simultaneous:
574 ca. 4.0–3.5 Ma (Turner and Antón, 1996). Moreover, these scholars argue that the earlier Asian
575 forms display more reliable morphological characters in comparison with the African ones
576 (Werdelin, 1999; Liu et al., 2021). In either case *Pa. brevirostris* dispersed into Eurasia around 2.0
577 Ma, where it became one of the most common elements in Eurasian faunas, often the primary agent
578 responsible for the accumulations. Its ubiquitous Eurasian presence lasted until the late Early
579 Pleistocene in Europe, until 0.86 Ma (Martínez-Navarro, 2004, 2010; Madurell-Malapeira et al.,
580 2010, 2017), and until the Middle Pleistocene in Asia, where it was extensively recorded at the
581 Zhoukoudian 1 site (Pei, 1934; Palmqvist et al., 2011; Espigares et al., 2013; Madurell-Malapeira et
582 al., 2017; Liu et al., 2021). The impact of this species in the European Pleistocene taphocoenosis
583 and their relationships of putative competition with early hominins raised also hotly debates the last
584 decades (see Espigares et al., 2013; Madurell-Malapeira et al., 2017).

585 Finally, the evolutionary story of Old-World jaguars is far from being resolved. Most of the
586 authors hypothesized an African origin of this species (Hemmer et al., 2010; Argant and Argant,
587 2011) linking their first appearance in Europe at ca. 1.8 Ma with the record of a large pantherine
588 form in the Late Pliocene of Laetoli Upper Beds (ca. 3.7 Ma) ascribed to Barry (1987) to *Panthera*
589 *leo* aff. *gombaszoegnesis*. Other authors on the contrary included the first pantherine material of
590 Laetoli to *Panthera leo* (Turner, 1990). Eventually, in a more parsimonious hypothesis, Werdelin
591 and Peigné (2010) pointed out that African pantherine specimens older than 2 Ma are not diagnostic
592 at species level. From 2 Ma onwards, all the African material can be ascribed to *P. leo* and *P.*
593 *pardus* (Werdelin and Peigné, 2010). We agree with the latter authors supporting the idea that there
594 is no a direct link among the African specimens and European *P. gombaszoegensis* s.l. Since 1.8 Ma
595 the early forms of *P. gombaszoegensis* (or *P. toscana* according to other authors) were common

596 elements of the Late Villafranchian faunas of Europe, as testified to by the records of Olivola,
597 Upper Valdarno, Tegelen, Pirro Nord, Untermassfeld and until the Middle Pleistocene of Chateau
598 (Hemmer, 2001; Argant and Argant, 2011; Hemmer et al., 2010; Jiangzuo and Liu, 2020). Hemmer
599 et al., (2010) analyzed the remains of jaguar from Dmanisi recently pointing several differences
600 with the European species *P. gombaszoegensis* and erecting a new sub-species *P. o. georgica* that in
601 the former authors opinion is the direct ancestor of the American species *P. o. augusta* (Hemmer et
602 al., 2010; Argant and Argant, 2011; Jiangzuo and Liu, 2020). In any case, Hemmer and coauthors
603 (2010) describe the jaguar from Dmanisi as an ambush-predator with an estimated body mass of ca.
604 100 kg, which preferred riparian landscapes in forested and open grassland areas.

605

606 *4.3. The role of humans in Dmanisi and the Early Pleistocene Old World carnivore context*

607 Dmanisi is characterized by the presence of an abundant lithic artifacts collection of the Oldowan
608 complex (Ferring et al., 2011) and, as it has been described in this study, by a relevant record of
609 fossil vertebrates and a high diversity of large carnivorans species. This abundance of carnivorans is
610 also similar to other Eurasian Early Pleistocene archeo-paleontological sites, such those from Orce,
611 Barranco León and Fuente Nueva 3 , dated 1.4 and 1.3 Ma, respectively (Martínez-Navarro et al.,
612 1997, 2010; Espigares et al., 2013, 2019; Toro et al., 2013; Tifton et al., 2021), Vallonnet in France,
613 (1.1 Ma; Moullè et al., 2006), or at the site of ‘Ubeidiya in Israel (1.6–1.2 Ma), where a very
614 primitive Acheulian lithic collection together with a rich carnivore assemblage was described
615 (Ballesio, 1986; Bar-Yosef and Goren-Inbar, 1993; Martínez-Navarro et al., 2009). Likewise,
616 carnivorans are well represented at the African sites older than 1.7–1.8 Ma, such as the South
617 African caves, i.e., the lower levels of Swartkrans or Sterkfontein Member 5 (Brian, 1980;
618 O’Regan, 2007; O’Regan and Steininger, 2017), or those from eastern Africa, such as Olduvai Bed
619 I, Lokalalei, or Shungura E–G, and in North Africa at Ain Hanech (see Sahnouni and van der Made,
620 2009, and references there in).

621 This scenario totally changes when the archeo-paleontological assemblages are dominated by the
622 presence of developed Acheulian tools. In this context, carnivorans are normally not recorded or, if
623 they are present, they are very scarce and their diversity is very reduced. This evidence is testified
624 to by African records younger than 1.7 Ma, as in the Eastern African sites of Melka Wakena
625 (Ethiopia, Hovers et al., 2021), Buia and Engel Ela-Ramud (Eritrea), dated close to 1.0 Ma
626 (Martinez-Navarro et al., 2004; Martínez-Navarro et al., 2016), or at the Middle Pleistocene site of
627 Asbole, (Ethiopia, ca 0.6 Ma; Geraads et al., 2004), and in North Africa at the site of Wadi Sarrat in
628 Tunisia (0.7 Ma; Martínez-Navarro et al., 2014b). An analogous pattern can be seen in sites out of
629 Africa characterized by developed Acheulian lithic industries and dated to the Early-Middle
630 Pleistocene transition, as those of Gesher Benot Ya'akob (Israel, 0.7–0.8 Ma; Martínez-Navarro and
631 Rabinovich, 2011), and in most of the Middle Pleistocene European Acheulian assemblages, such la
632 Solana del Zamborino in Spain, (0.4 Ma; Álvarez-Posada et al., 2017), or at Venosa Notarchirico in
633 Italy (ca. 0.5 Ma; Piperno, 2000). Nevertheless, an exception to this distribution may be found in
634 the Acheulian sites of Tighennif in Algeria (ca. 1.0 Ma; Geraads, 2016), where carnivores are well
635 represented (Geraads, 2016).

636 This evidence shows that when the lithic assemblages correspond to the Oldowan complex
637 carnivorans are abundant, whereas in Acheulian complexes carnivorans are less represented. How
638 may be interpreted this correlation? Martínez-Navarro (2018) suggested that this can be related to
639 the evolution of human behavior from scavenging to hunting. Humans with Oldowan tools probably
640 found challenging to compete with large carnivorans as active hunter and behaved more frequently
641 as opportunistic scavengers, trying to steal parts or the entire prey' s carrion hunted down by other
642 large carnivorans or simply found dead. This competition has been described especially with the
643 large hyenas (Epigares et al., 2013). In this scenario, humans were just another species with also
644 carnivore habits in the faunal assemblages of the Early Pleistocene, in strict ecological competition
645 with the large carnivore guild. On the contrary, the limited presence of large carnivorans in

646 Acheulian assemblages may indicate that a different and radical change in humans behavior have
647 taken place, from scavengers to active hunters.

648 Dmanisi fits with this interpretation, representing a typical Oldowan site with abundant large
649 carnivorans dominating the scenario.

650

651 **5. Conclusions**

652 We analyzed the composition of the Dmanisi carnivore guild under different perspectives. We
653 carried out a permutation cluster analysis (BCA; Fig. 3; SOM Fig. S1) on the generic and species
654 composition matrices comparing the studied sample with coeval European, Asian and African
655 Pleistocene sites. Later we tested the different ecomorphological diet categories present at Dmanisi
656 with the same key Old-World sites in order to decipher changes in the environment and carnivore
657 guild composition. Finally, we analyzed the origin and lineage history of the taxa of carnivorans
658 present at Dmanisi.

659 The results of the deep analyses of the Dmanisi carnivore assemblage show that it is consistently
660 most similar to the Late Villafranchian European sites of Pirro Nord, Venta Micena and Apollonia
661 1, and to a lesser extent with the Epivillafranchian localities of Le Vallonnet, Untermassfeld and
662 Vallparadís Section. All these localities, both Late Villafranchian and Epivillafranchian, are
663 characterized by a large diversity of felids, including species like *H. latidens*, *P. onca-*
664 *gombaszoegensis* and *M. whitei*, a reduced diversity of hyenids, with only *Pa. brevirostris* present,
665 and pursuit-predator canids as the medium-sized *C. borjgali-mosbachensis* and the large *C.*
666 (*Xenocyon*) *lycaonoides*. Such guild composition, characterized by new and more derived elements
667 like *M. whitei*, *C. gr. mosbachensis* and *C. (X.) lycaonoides*, which replaced the older and more
668 primitive taxa, respectively *M. cultridens*, *C. etruscus* and *C. (X.) falconeri*, has its First Appearance
669 Datum in Dmanisi. These results support evidence from other taxa (bovids, e.g., *Soergelia minor*
670 and *Bison georgicus*; equids, *Equus altidens*; Bernor et al., 2021) and fits also with the Eurasian
671 dispersion undertaken by the genus *Homo* at the end of the Gelasian-beginning of the Calabrian,

672 whose earliest western European record are the very same sites most closely affine to Dmanisi,
673 Pirro Nord and Orce Site complex.

674

675 **Author contribution**

676 SBL and JMM conceived the paper with the help of LR and BMN; D.L. and M.B. provided the
677 Dmanisi material; SBL created the dataset, performed the analyses and the comparisons; SBL and
678 JMM wrote the paper with the contributions from LR and BMN; OC, MB, DL, LP discussed the
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680

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691

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1096 **Figure Captions**

1097 **Figure 1.** Map of the Old World showing the considered localities in the present paper. Localities
1098 are grouped in chronological cluster: circles are localities dated 2.70–2.01 Ma; squares, sites
1099 between 2.00–1.20 Ma; triangles are localities between 1.19–0.70 Ma. Red star is the location of
1100 Dmanisi. Numbers are the same as in Table 1. Numbers: 1 = Dmanisi (Georgia); 2 = Ahl al
1101 Oughlam (Morocco); 3 = Tighennif (Algeria); 4 = Upper Burgi Member, Koobi Fora Formation

1102 (Kenya); 5 = KBS Member, Koobi Fora Formation (Kenya); 6 = Okote Member, Koobi Fora
1103 Formation (Kenya); 7 = Olduvai Bed I (Tanzania); 8 = Olduvai Bed II (Tanzania); 9 = Omo
1104 Members C–F, Shungura Formation (Ethiopia); 10 = Omo Members G–K, Shungura Formation
1105 (Ethiopia); 11 = Sterkfontein Member 4 (South Africa); 12 = Kromdraai Member 2 (South Africa);
1106 13 = Drimolen (South Africa); 14 = Coopers D (South Africa); 15 = Saint Vallier (France); 16 =
1107 Senèze (France); 17 = Olivola (Italy); 18 = Poggio Rosso (Italy); 19 = Casa Frata (Italy); 20 =
1108 Venta Micena (Spain); 21 = Pirro Nord (Italy); 22 = Apollonia 1 (Greece); 23 = Vallonnet (France);
1109 24 = EVT10/12, Vallparadís Estacio level 10–12 (Spain); 25 = EVT7/CGRD7, Vallparadís Estacio
1110 level 7/Cal Guardiola 7 (Spain); 26 = Untermassfeld (Germany); 27 = Ubeidiya (Israel); 28 =
1111 Khapry Faunal Complex (European Russia); 29 = Longdan locality (China); 30 = Zhoukoudian
1112 Locality 18 (China); 31 = Renzidong Cave (China); 32 = Xiashagou, Classic Nihewan (China); 33
1113 = Jinyuan Cave Lower fauna (China); 34 = Longgupo (China); 35 = Gongwangling (China); 36 =
1114 Jinyuan Cave Upper fauna (China); 37 = Zhoukoudian Locality 1 (China).

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1116 **Figure 2.** Pie charts of carnivore guild composition in Dmanisi and three roughly coeval localities
1117 of Europe (Olivola, Italy), Asia (Jinyuan Cave Lower Fauna; China) and Africa (Kromdraai
1118 Member 2; South Africa) with the relative percentage of the families there recorded.

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1122 **Figure 3.** Dendrogram resulting from the bootstrapping cluster analysis (BCA) based on the
1123 presence/absence species group matrix of 36 sites across the Old World (Table 1). Abbreviations:
1124 AaO = Ahl al Oughlam (Morocco); APL = Apollonia 1 (Greece); CF = Casa Frata (Italy); COOPD
1125 = Coopers D; DRIM = Drimolen (South Africa); EVT10/12 = Vallparadís Estacio level 10–12
1126 (Spain); EVT7/CGRD7 = Vallparadís Estacio level 7/Cal Guardiola 7 (Spain); GWC =
1127 Gongwangling (China); JYCLow = Jinyuan Cave Lower fauna (China); JYCUpp = Jinyuan Cave

1128 Upper fauna (China); KBS = KBS Member, Koobi Fora Formation (Kenya); KhFC = Khapry
 1129 Faunal Complex (European Russia); KRMD2 = Kromdraai Member 2 (South Africa); LGP =
 1130 Longgupo (China); Longdan = Longdan locality (China); Nihew = Xiashagou, Classic Nihewan
 1131 (China); Okot = Okote Member, Koobi Fora Formation (Kenya); Old 1 = Olduvai Bed I
 1132 (Tanzania); Old 2 = Olduvai Bed II (Tanzania); OLIV = Olivola (Italy); OMO C-F = Members C–
 1133 F, Shungura Formation (Ethiopia); OMO G-K = Members G–K, Shungura Formation (Ethiopia);
 1134 Pirro = Pirro Nord (Italy); PR = Poggio Rosso (Italy); RZD = Renzidong Cave (China); Sen =
 1135 Senéze (France); St.Val = St. Vallier (France); STK Mb4 = Sterkfontein Member 4 (South Africa);
 1136 TIGH = Tighennif (Algeria); U Burgi = Upper Burgi Member, Koobi Fora Formation (Kenya);
 1137 UBEI = ‘Ubeidiya (Israel); UMD = Untermassfeld (Germany); Vallt = Vallonnet (France); VM =
 1138 Venta Micena (Spain); ZKD1 = Zhoukoudian Locality 1 (China); ZKD18 = Zhoukoudian Locality
 1139 18 (China).

1140

1141 **Figure 4.** Heatmap of the Jaccard similarity index calculated on the presence/absence matrix of the
 1142 species of the thirty-six localities analyzed here (Table 1). Dendrograms are the same as in Figure
 1143 4. The color code is expressed by the legend on the top left corner of the graph. This color legend
 1144 also reports the number of each Jaccard index (light cyan histogram). Abbreviations: AaO = Ahl al
 1145 Oughlam (Morocco); APL = Apollonia 1 (Greece); CF = Casa Frata (Italy); COOPD = Coopers D;
 1146 DRIM = Drimolen (South Africa); EVT10/12 = Vallparadís Estacio level 10–12 (Spain);
 1147 EVT7/CGRD7 = Vallparadís Estacio level 7/Cal Guardiola 7 (Spain); GWC = Gongwangling
 1148 (China); JYCLow = Jinyuan Cave Lower fauna (China); JYCUpp = Jinyuan Cave Upper fauna
 1149 (China); KBS = KBS Member, Koobi Fora Formation (Kenya); KhFC = Khapry Faunal Complex
 1150 (European Russia); KRMD2 = Kromdraai Member 2 (South Africa); LGP = Longgupo (China);
 1151 Longdan = Longdan locality (China); Nihew = Xiashagou, Classic Nihewan (China); Okot = Okote
 1152 Member, Koobi Fora Formation (Kenya); Old 1 = Olduvai Bed I (Tanzania); Old 2 = Olduvai Bed
 1153 II (Tanzania); OLIV = Olivola (Italy); OMO C-F = Members C–F, Shungura Formation (Ethiopia);

1154 OMO G-K = Members G–K, Shungura Formation (Ethiopia); Pirro = Pirro Nord (Italy); PR =
1155 Poggio Rosso (Italy); RZD = Renzidong Cave (China); Sen = Senéze (France); St.Val = St. Vallier
1156 (France); STK Mb4 = Sterkfontein Member 4 (South Africa); TIGH = Tighennif (Algeria); U Burgi
1157 = Upper Burgi Member, Koobi Fora Formation (Kenya); UBEI = ‘Ubeidiya (Israel); UMD =
1158 Untermassfeld (Germany); Vallt = Vallonnet (France); VM = Venta Micena (Spain); ZKD1 =
1159 Zhoukoudian Locality 1 (China); ZKD18 = Zhoukoudian Locality 18 (China).

1160

1161

1162 **Figure 5.** Histograms of the relative proportions of the ecological preference of the carnivorans
1163 in the analyzed guilds of the Old World, arranged according to a BCA based on ecological matrix
1164 of the sites. Abbreviations: AMB = hypercarnivorous ambush predators; BoCr = hypercarnivorous
1165 species with bone-cracking adaptations; CURS = hypercarnivorous cursorial predators; HERB =
1166 hypocarnivorous adaptations towards herbivory; HSmp = small-sized hypercarnivorous species;
1167 INSE = insectivorous species; MESO = mesocarnivores; OMNI = omnivorous, hypocarnivorous
1168 and opportunistic feeders; PISC = hypercarnivores adapted to a piscivorous diet; AaO = Ahl al
1169 Oughlam (Morocco); APL = Apollonia 1 (Greece); CF = Casa Frata (Italy); COOPD = Coopers D;
1170 DRIM = Drimolen (South Africa); EVT10/12 = Vallparadís Estacio level 10–12 (Spain);
1171 EVT7/CGRD7 = Vallparadís Estacio level 7/Cal Guardiola 7 (Spain); GWC = Gongwangling
1172 (China); JYCLow = Jinyuan Cave Lower fauna (China); JYCUpp = Jinyuan Cave Upper fauna
1173 (China); KBS = KBS Member, Koobi Fora Formation (Kenya); KhFC = Khapry Faunal Complex
1174 (European Russia); KRMD2 = Kromdraai Member 2 (South Africa); LGP = Longgupo (China);
1175 Longdan = Longdan locality (China); Nihew = Xiashagou, Classic Nihewan (China); Okot = Okote
1176 Member, Koobi Fora Formation (Kenya); Old 1 = Olduvai Bed I (Tanzania); Old 2 = Olduvai Bed
1177 II (Tanzania); OLIV = Olivola (Italy); OMO C-F = Members C–F, Shungura Formation (Ethiopia);
1178 OMO G-K = Members G–K, Shungura Formation (Ethiopia); Pirro = Pirro Nord (Italy); PR =
1179 Poggio Rosso (Italy); RZD = Renzidong Cave (China); Sen = Senéze (France); St.Val = St. Vallier

1180 (France); STK Mb4 = Sterkfontein Member 4 (South Africa); TIGH = Tighennif (Algeria); U Burgi
1181 = Upper Burgi Member, Koobi Fora Formation (Kenya); UBEI = 'Ubeidiya (Israel); UMD =
1182 Untermassfeld (Germany); Vallt = Vallonnet (France); VM = Venta Micena (Spain); ZKD1 =
1183 Zhoukoudian Locality 1 (China); ZKD18 = Zhoukoudian Locality 18 (China).
1184

Table 1

Presence of species of carnivorans in selected European, Asian and African sites from the Early to Middle Pleistocene with their ecological characterization.

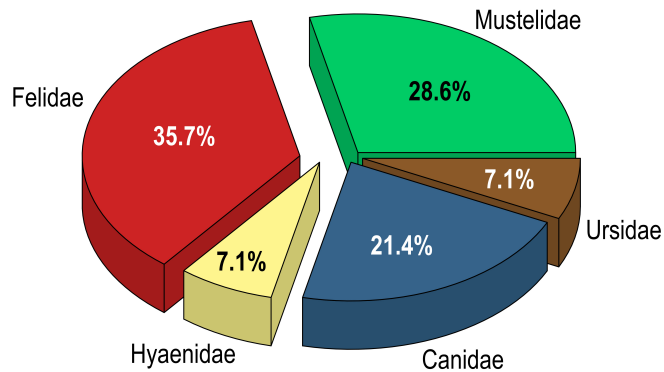
| Species | E. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | | |
|--------------------------------------|------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|--|
| <i>Crossarchus transvaalensis</i> | OMNI | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Galerella debilis</i> | MESO | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Helogale hirtula-kitafe</i> | MESO | | | | | | | | | X | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Herpestes gr. ichneumon</i> | MESO | | X | | | | | X | | | | | X | | X | | | | | | | | | | | | | | | | | X | | | | | | | | |
| <i>Ichneumia albicaudata</i> | INSE | | X | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Mungos minutus</i> | INSE | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Suricata suricatta</i> | INSE | | | | | | | | | | | X | | X | X | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Civettictis gr. civetta</i> | OMNI | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Cynictis penicillata</i> | INSE | | | | | | | | | | | | | X | X | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Genetta genetta</i> | MESO | | | | X | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Megaviverra gr. pleistocenica</i> | MESO | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | | X | | | | | |
| <i>Pseudocivetta ingens</i> | MESO | | | | X | X | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Viverra leakey</i> | MESO | | X | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Aonyx capensis</i> | HSmP | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Arctonyx minor</i> | OMNI | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | X | | | |
| <i>Arctonyx collaris</i> | OMNI | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | |
| <i>Baranogale helbingi</i> | HSmP | | | | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Eirictis gr. pachygnatha</i> | HSmP | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | X | X | | | | | | | | |
| <i>Lutra gr. simplicidens</i> | PISC | | X | | | | | X | X | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Lutra licenti</i> | PISC | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | |
| <i>Martellictis ardea</i> | MESO | | | | | | | | | | | | X | | X | | | | | | | | | | | | | X | | | | | | | | | | | | |
| <i>Martes crassa-andressoni</i> | HSmP | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | X | | |
| <i>Meles gr. thoralis-meles</i> | OMNI | | | | | | | | | | | | | | X | | | | | | X | X | X | X | X | X | X | | | | | | | | | | | | | |
| <i>Meles gr. chiai-teilhardi</i> | OMNI | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | X | X | X | X | X | X | X | | X | |
| <i>Mellivora gr capensis</i> | MESO | | X | X | X | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Mustela altaica</i> | HSmP | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | X | |

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|------|----|----|----|---|---|---|----|---|---|---|----|----|----|----|----|---|----|---|---|----|----|----|----|----|----|----|----|---|----|---|----|----|----|----|----|---|---|---|
| <i>Pachycrocuta brevirostris</i> | BoCr | X | | | | | | | | | X | | | | | | | | | | | | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | |
| <i>Parahyaena brunnea</i> | BoCr | | | | | | | | | | X | X | | | X | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Pliocrocuta perrieri</i> | BoCr | | X | | | | | | | | | | | X | X | X | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Proteles gr. cristatus</i> | INSE | | | | | | | | | | X | | X | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Canis amnensis</i> | MESO | | | | | | | | | | | | | | | X | X | | | | | | | | | | | | | | | | | | | | | | |
| <i>Canis brevirostris</i> | MESO | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Canis gr. chihliensis</i> | CURS | | | | | | | | | | | | X | | | | | | | | | | | X | X | | X | X | | | | | | | | | | | |
| <i>Canis gr. etruscus</i> | MESO | | | | | | | | | | | | | X | X | X | | | | | | | X | X | | | X | X | | | | | | | | | | | |
| <i>Canis gr. mosbachensis</i> | CURS | X | | | | | | | | | | | | | | | | | | | | | X | X | X | X | X | X | X | X | | | | | X | X | X | | |
| <i>Canis (Xenocyon) gr. dubius</i> | CURS | | | | | | | | | | | | | | | | | | | | | | X | X | | X | X | | | | | | | | | | | | |
| <i>Canis (Xenocyon) gr. falconeri</i> | CURS | | | | | | | | | | | X | | | | | | X | | | | | | | | | | | | | | | | | | | | | |
| <i>Canis (Xenocyon) gr. lycaonoides</i> | CURS | X | X | | | | X | | | | | | | | | | | | | | | | | X | X | X | X | X | X | X | X | X | | | | X | | | |
| <i>Cuon alpinus</i> | CURS | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | |
| <i>Eucyon minor</i> | HSmP | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | |
| <i>Lupulella gr. adustus</i> | OMNI | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Lupulella gr. mesomelas</i> | MESO | | X | | | X | X | | X | X | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Lycaon pictus</i> | CURS | | | | | | | | | | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | |
| <i>Nyctereutes gr. megamastoides</i> | OMNI | | X | | | | | | | | | | | | X | X | | | | | | | | | | X | | | X | X | X | X | | | X | | | | |
| <i>Protootocyon reckii</i> | INSE | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | | | | | | | | | | |
| <i>Vulpes alopecoides</i> | MESO | X | | | | | | | | | | | | X | X | | | X | X | X | X | X | X | X | X | X | X | X | | | | | | X | | | | | |
| <i>Vulpes chikushanensis</i> | OMNI | | | | | | | | | | | | | | | | | | | | | | | | X | X | | X | | | | | | | X | X | | | |
| <i>Vulpes gr. chama</i> | MESO | | | | | | | | | | | | X | X | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Vulpes gr. rueppelli</i> | OMNI | | X | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Ailuropoda gr. melanoleuca</i> | HERB | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | X | X | | | | |
| <i>Ursus gr. etruscus</i> | OMNI | X | X | | | | | | | | | | | X | X | X | X | X | X | X | X | X | X | | | X | | | X | X | | | X | X | | | | | |
| <i>Ursus deningeri</i> | HERB | | | | | | | | | | | | | | | | | | | | | | | X | X | X | X | | | | | | | | | | X | | |
| <i>Ursus gr. thibetanus</i> | OMNI | | | | | | | | | | | | | | | | | | | | | | | | X | | X | | | X | | | | X | | | | | X |
| Total number of species per site | | 10 | 21 | 11 | 9 | 6 | 7 | 15 | 8 | 7 | 4 | 12 | 15 | 11 | 16 | 14 | 9 | 11 | 8 | 8 | 10 | 14 | 11 | 13 | 10 | 11 | 11 | 11 | 7 | 16 | 8 | 14 | 19 | 14 | 13 | 10 | 6 | 9 | |

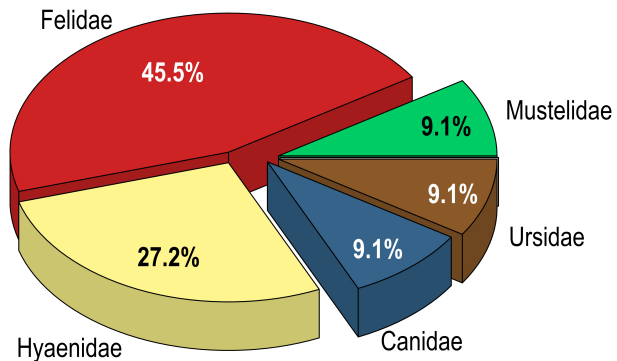
Abbreviations: E. = ecological preferences; AMB = hypercarnivorous ambush predators; BoCr = hypercarnivorous species with bone-cracking adaptations; CURS = hypercarnivorous cursorial predators; HERB = hypocarnivorous adaptations towards herbivory; HSMP = small-sized hypercarnivorous species; INSE = insectivorous species; MESO = mesocarnivores; OMNI = omnivorous, hypocarnivorous and opportunistic feeders; PISC = hypercarnivores adapted to a piscivorous diet; 1 = Dmanisi (Georgia; ca 1.8 Ma); 2 = Ahl al Oughlam (Morocco; ca 2.5 Ma); 3 = Tighennif (Algeria; ca 1.0 Ma); 4 = Upper Burgi Member, Koobi Fora Formation (Kenya; ca 2.0-1.9 Ma); 5 = KBS Member, Koobi Fora Formation (Kenya; ca 1.9-1.7 Ma); 6 = Okote Member, Koobi Fora Formation (Kenya; ca 1.5-1.3 Ma); 7 = Olduvai Bed I (Tanzania; ca 1.8 Ma); 8 = Olduvai Bed II (Tanzania; ca 1.2 Ma); 9 = Omo Members C–F, Shungura Formation (Ethiopia; ca 2.6-2.3 Ma); 10 = Omo Members G–K, Shungura Formation (Ethiopia; ca 2.0-1.5 Ma); 11 = Sterkfontein Member 4 (South Africa; ca 2.1 Ma); 12 = Kromdraai Member 2 (South Africa; ca 2.0 Ma); 13 = Drimolen (South Africa; ca 2.0-1.5 Ma); 14 = Coopers D (South Africa; ca 1.9 Ma); 15 = Saint Vallier (France; ca 2.4 Ma); 16 = Senèze (France; ca 2.2 Ma); 17 = Olivola (Italy; ca 2.0 Ma); 18 = Poggio Rosso (Italy; ca 1.9 Ma); 19 = Casa Frata (Italy; ca 1.7-1.6 Ma); 20 = Venta Micena (Spain; ca 1.5 Ma); 21 = Pirro Nord (Italy; ca 1.4 Ma); 22 = Apollonia 1 (Greece; ca 1.2-0.9 Ma); 23 = Vallonnet (France; ca 1.0 Ma); 24 = EVT10/12, Vallparadís Estacio level 10–12 (Spain; ca 1.1 Ma); 25 = EVT7/CGRD7, Vallparadís Estacio level 7/Cal Guardiola 7 (Spain; ca 0.9 Ma); 26 = Untermassfeld (Germany; ca 1.0 Ma); 27 = Ubeidiya (Israel; ca 1.4 Ma); 28 = Khapry Faunal Complex (European Russia; ca 2.5-2.0 Ma); 29 = Longdan locality (China; ca 2.4-2.2 Ma); 30 = Zhoukoudian Locality 18 (China; ca 2.2 Ma); 31 = Renzidong Cave (China; ca 2.0 Ma); 32 = Xiashagou, Classic Nihewan (China; ca 1.8-1.6 Ma); 33 = Jinyuan Cave Lower fauna (China; ca 2.0-1.8 Ma); 34 = Longguopo (China; ca 1.9 Ma); 35 = Gongwangling (China; ca 1.1 Ma); 36 = Jinyuan Cave Upper fauna (China; ca 1.1 Ma); 37 = Zhoukoudian Locality 1 (China; ca 1.0 Ma).



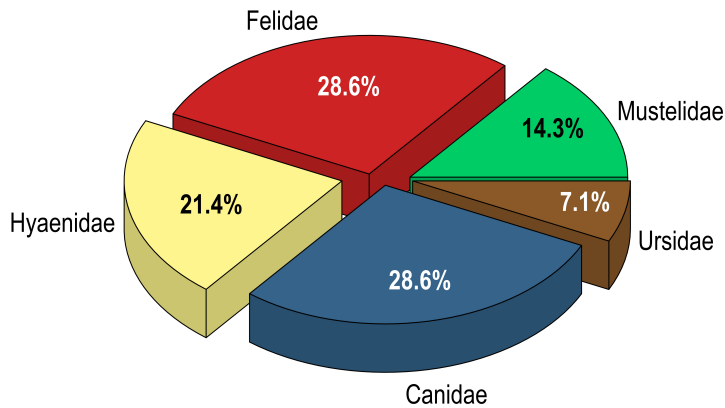
Dmanisi



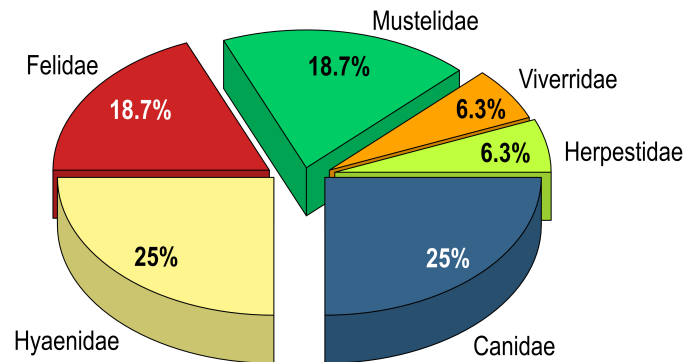
Olivola

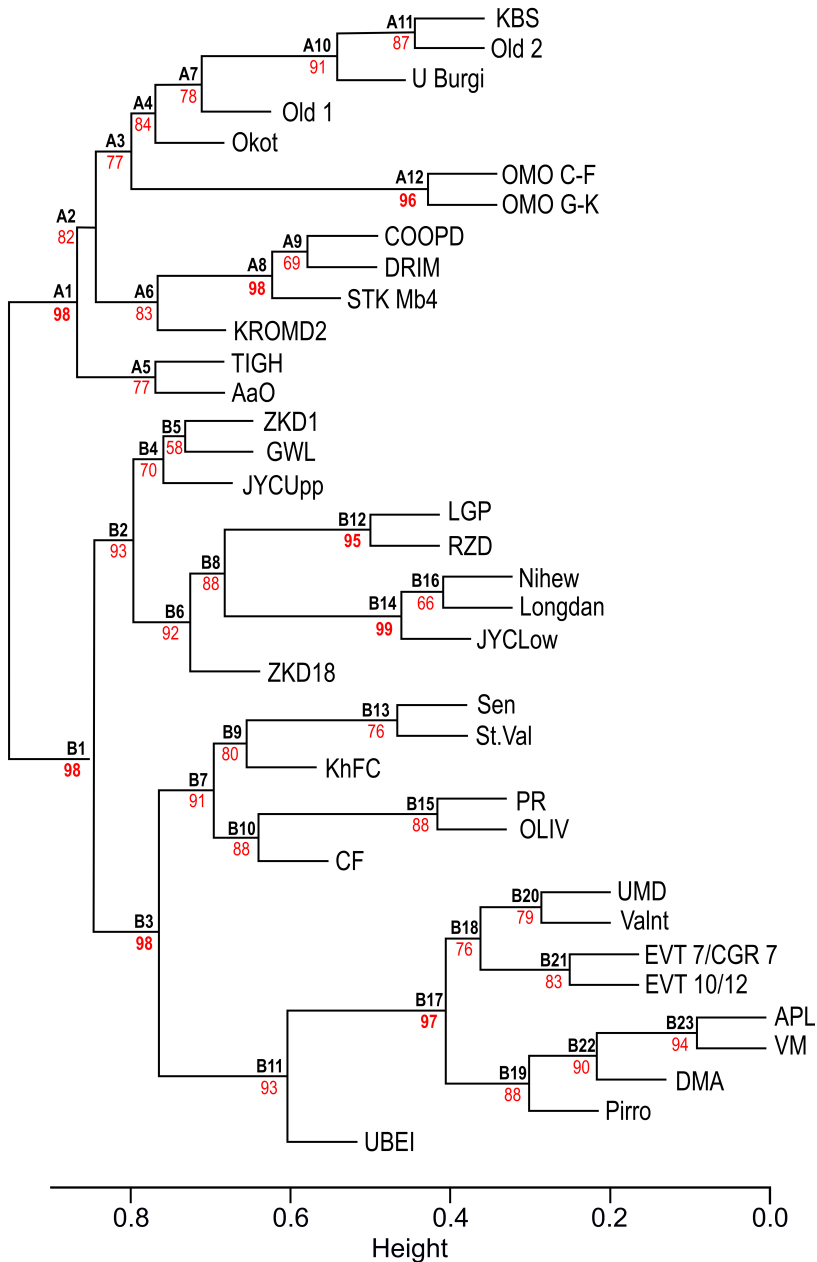


Jinyuan Cave Lower Fauna



Kromdraai Mb. 2





Color Key and Histogram

