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**Feeding habits of extant and fossil canids as determined by
their skull geometry**

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3 **1 Feeding habits of extant and fossil canids as determined**
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6 **2 by their skull geometry**
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51 **17 Short title:** Canidae skull shape
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3 **Abstract**
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20 **Abstract**

21 The canids belong to one of the most prominent families of mammalian carnivores. Feeding
22 adaptations of extant species is well documented by field observations; however we are still
23 missing palaeoecological insights for many enigmatic fossil specimens. We employ
24 geometric morphometrics to quantify skull size and shape in extant and fossil members of the
25 Canini tribe, inclusive of jackals and wolf-like taxa. Skull data are tested to identify correlates
26 of dietary adaptations in extant species for predicting adaptations in fossils. Main vectors of
27 shape variation correlate with the relative skull-palatal length, the position of the upper
28 carnassial tooth and the anterior tip of the secondary palate. Allometry occurs in the palatal
29 shape but size explains only a small fraction (about 4%) of shape variance.

30 Although we quantified only palatal and tooth shape for the inclusion of fragmentary fossils,
31 discriminant function analysis successfully classify extant Canini in dietary groups (small,
32 medium and large prey specialist) with 89% of accuracy. The discriminant functions provide
33 insights into many enigmatic specimens such as *Eucyon adoxus* (= small prey), fossil jackal-
34 like from Koobi Fora formation (= small prey) and the Plio-Pleistocene Old World canid
35 guild (*Canis etruscus*, *C. arnensis* and *Lycaon falconeri*). Clearly both skull size and shape
36 are excellent predictors of feeding habits in Canini thus also provide information about fossil
37 taxonomic affinities.

38 **Keywords:** *Canidae*, *geometric morphometrics*, *skull shape*, *diet*, *hypercarnivore*

43 Introduction

44 Members of the family Canidae have successfully invaded every continent, except
45 Antarctica, occupying a multitude of ecological niches, which is a testament to their
46 adaptability in the present and in the past (Sillero-Zubiri *et al.*, 2004). The most updated
47 molecular phylogeny (Lindbald-Toh *et al.*, 2005) identified distinct clades within the
48 Canidae: i) the redfox-like clade, the South American clade, the wolf-like clade and the grey
49 and island fox clade. This study will focus on the wolf-like clade (tribe Canini), which exhibit
50 one of the most complete fossil record in the Old World (Tedford *et al.*, 1995, 2009). Tedford
51 *et al.* (2009) recently provided a morphological phylogeny merging both extant and fossil
52 species although functional morphology of many enigmatic fossil specimens is still obscure
53 and difficult to characterise (e.g. the genus *Eucyon*, or the wolf-like *Canis etruscus*; Cherin *et*
54 *al.*, 2014).

55 The wolf-like clade had an explosion of forms during the Plio-Pleistocene so that
56 biochronology considers such a proliferation of species in the Old World into a separate
57 faunal event (the wolf event, c.ca 2.0 Ma; Azzaroli, 1983; Azzaroli *et al.*, 1988; Torre *et al.*,
58 1992, 2001; Rook & Torre, 1996a; Sardella & Palombo, 2007; Rook & Martínez-Navarro,
59 2010; Sotnikova & Rook, 2010). Palaeoecology of many of these canids represented by a
60 coyote-like (*Canis arnensis*), a small wolf-like (*Canis etruscus*) and an African hunting dog-
61 like (*Lycaon falconeri* group; Rook, 1994; Martínez-Navarro & Rook, 2003) was pioneered
62 by Kurtén (1974) and Palmqvist *et al.* (1999) and later reconsidered by Meloro (2011) in a
63 study on mandible shape. Here we aim to investigate skull shape that is expected to provide
64 better insights into feeding ecology of extant, hence fossil Canini.

65 There have been numerous studies on the relationship between diet and craniodental
66 form in Carnivora and canids in particular (Biknevicius & Ruff, 1992; Van Valkenburgh *et*

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3 67 *al.*, 2003; Sacco & Van Valkenburgh, 2004; Christiansen & Adolfssen, 2005; Christiansen &
4
5 68 Wroe, 2007). Within canids, a shorter snout indicates larger moment arms for the temporalis
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7 69 and masseter muscles (Damasceno *et al.*, 2013) and the canines are closer to the fulcrum,
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9
10 70 both creating a more powerful bite force (Christiansen & Adolfssen, 2005; Christiansen &
11
12 71 Wroe, 2007). This is interpreted as an adaptation to kill large prey and can be detected in
13
14 72 living and extinct canid tribes (Valkenburgh & Koepfli, 1993; Andersson, 2005; Van
15
16 73 Valkenburgh *et al.*, 2003; Slater *et al.*, 2009).

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19 74 Early morphometric attempts on Canidae general morphology already elucidated
20
21 75 cophenetic similarities in relation to their taxonomy and ecology (Clutton-Brock *et al.*, 1976).
22
23 76 By focusing on palatal and upper teeth morphology with geometric morphometric techniques
24
25 77 we intend to capture both size and shape aspects relevant to interpret fossil species.
26
27 78 Geometric morphometrics has the advantage of allowing clear data visualisation in
28
29 79 multivariate shape space (Adams *et al.*, 2004, 2013; Lawing & Polly, 2009). In addition,
30
31 80 shape distances can be employed to infer morphological similarities: this is a straightforward
32
33 81 way to compare data between living and fossil specimens (Caumul & Polly, 2005; Meloro *et*
34
35 82 *al.*, 2008; Meloro, 2011). Due to the tendency in canids of increasing body mass towards
36
37 83 their evolution in relation to ecological feeding specialisation (Van Valkenburgh *et al.*, 2004)
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39 84 we will also explore skull size as possible proxy for predicting diet in extant and fossil
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41 85 species.
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49 87 **Materials and Methods**

50 51 52 53 88 **Sample Size** 54 55 56 57 58 59 60

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3 89 Skulls belonging to 102 specimens (85 extant and 17 fossils) were included in this study
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5 90 (Appendix 1). Our sample is representative of the broad diversity within the *Canis* clade
6
7 91 including jackals and wolf-like ecomorphs (9 extant and 10 fossil species, Table 1). All
8
9
10 92 extant specimens belong to wild captured individuals. Both male and female skulls were used
11
12 93 indistinctively because sexual dimorphism is considered a negligible source of variance to
13
14 94 infer dietary adaptations from the skulls. Indeed, sexual dimorphism within canids is
15
16 95 generally small (Van Valkenburgh & Gittleman, 1997) and the gender is unknown for many
17
18 96 fossil specimens.

20
21
22 97 For fossil species we used the nomenclature finalised by Tedford *et al.* (2009). The
23
24 98 small genera *Eucyon* and *Cynotherium* (with the species *Eucyon adoxus* and *Cynotherium*
25
26 99 *sardous*) were also considered for their unequivocal affinities with extant *Canis*-like species
27
28 100 (Rook, 2009; Lyras *et al.*, 2006).
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34 102 **Data Capture**

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37 103 Digital photographs were collected on skulls positioned in ventral view by Meloro C. using a
38
39 104 Nikon 995 at a 1 metre distance. A spirit level was positioned on the palate of the skull to
40
41 105 ensure parallelism between camera optical plan and the flattest region of the skull. On each
42
43 106 skull, 15 landmarks were recorded by one of us (Hudson A.) in the palate region to capture
44
45 107 details of tooth and cusp positioning using the software tpsDig2 ver. 2.17 (Rohlf, 2013a) (Fig.
46
47 108 1). Landmarks 1-2 record the width of the incisor arch, 3-4 the relative size of canine,
48
49 109 landmark 5 is at the anterior tip of P3, 6 to 10 relative size of the upper carnassial (P4)
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51 110 together with the positioning of the main cusps, 10-14 covers the M1 morphology and
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53 111 landmark 15 is the most posterior point delimiting the end of the palate.
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3 112 Cusp positions were recorded on P4 and M1 as good proxy for dietary adaptations but also to
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5 113 understand possible phylogenetic affinities between extant and fossil taxa (cf. Rook & Torre,
6
7 114 1996; Brugal & Boudadi-Maligne, 2010). The posterior part of the skull and the zygomatic
8
9 115 arch were not covered by landmarks because they were not present in many of the analysed
10
11 116 fossils.

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15 117 Intra-individual error in landmarking was assessed using three landmarked replicas for three
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17 118 specimens. There were no differences in the variance of coordinates values between replicas
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19 119 (ANOVA and MANOVA $p > 0.9$).

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23 24 25 121 **Geometric Morphometrics**

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28 122 Landmark coordinates were aligned using Generalised Procrustes superimposition (Rohlf &
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30 123 Slice, 1990) with the software tpsRelw ver. 1.53 (Rohlf, 2013b). The software performed
31
32 124 three operations: translation, rotation and scaling to transform the original 2D coordinates of
33
34 125 landmarks into shape coordinates. A Principal Component analysis of the covariance matrix
35
36 126 of the shape coordinates was then computed. Shape variation along each principal component
37
38 127 axis was visualised using a thin-plate spline (Bookstein, 1991). Thin plate splines visualize
39
40 128 shape variation assuming that the average consensus configuration has no deformation and
41
42 129 line on an infinite metal plane whose bending describe shape changes (Zelditch *et al.*, 2004).

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47 130 The size of landmark configuration was extrapolated from the raw coordinates via centroid
48
49 131 size (=the square root of the mean squared distance from each landmark to centroid of the
50
51 132 landmark configuration Bookstein, 1989). In order to scale centroid size to the mean, natural
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53 133 log transformation was used (cf. Meloro *et al.*, 2008).

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135 **Feeding Categories**

136 For each extant species, a feeding category was assigned following multiple references. Van
137 Valkenburgh (1989) grouped extant carnivores into three dietary categories: hypercarnivores,
138 mesocarnivores and hypocarnivores. However, because there are no hypocarnivores in the
139 sample for this study, Palmqvist *et al.*'s (1999) grouping of canids was also considered.
140 Using both categorisations as a template, diet categories were assigned as small prey
141 (mesocarnivore, mostly feeding on rodents and lagomorphs), medium prey (mesocarnivore
142 that can include a wider range of prey sizes) and large prey (hypercarnivore, mostly preying
143 on large ungulates). Extant jackals and the Ethiopian wolf belong to the category "small
144 prey", while the grey wolf, the African wild dog and the dhole are categorised as "large prey"
145 (cf. Slater *et al.*, 2009). The coyote and the dingo were categorised as "medium prey"
146 because of their broad adaptability in also hunting large prey in group (Gese *et al.*, 1988;
147 Lingle, 2002; Sillero-Zubiri *et al.*, 2004; Christiansen & Wroe 2007; Letnic *et al.*, 2012).

149 **Data Analyses**

150 Differences in skull size and shape due to diet were preliminary tested using ANOVA and
151 parametric and non-parametric MANOVA. Due to the large number of independent shape
152 variables a selection of Principal Components (the one explaining at least 95% of variance)
153 was employed to validate MANOVA models based on the full set of shapes (cf. Meloro &
154 O'Higgins, 2011).

155 Additionally, allometry was tested in order to identify the possible influence of size on shape
156 data (Mitteroecker *et al.*, 2013). A multivariate regression was employed to identify and
157 visualise allometric signal in the whole sample of 102 skulls using thin plate spline.

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3 158 Discriminant Function Analysis was employed to provide prediction for fossil species
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5 159 using diet categories as factor and shape coordinates and natural log centroid size as
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7 160 independent variables. To considerably reduce the number of independent dietary predictors a
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9 161 stepwise procedure was applied: a variable was entered into the model if the probability of its
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11 162 F value was bigger than 0.05 and was removed if the probability was less than 0.10. Meloro
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13 163 (2011) consistently demonstrated the importance of including mandibular size as a predictor
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15 164 of feeding adaptation in Carnivora. We expect this to also hold for skull size in canids.
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19 165 An UPGMA cluster analysis was employed to identify cophenetic similarities
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21 166 between fossil and extant specimens. Averaged shape coordinates were first computed for
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23 167 each extant and fossil species, then Procrustes distances calculated to construct the clustering
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25 168 UPGMA tree (cf. Meloro, 2011).
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32 170 **Results**

33 34 35 171 **Skull shape**

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38 172 Variability in skull shape is significantly reduced by using Principal Component analysis,
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40 173 with the first 12 PC axes explaining 95.26% of total shape variance. PC1 and PC2 explain
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42 174 45.76% and 15.60% of total variance respectively and their combination show substantial
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44 175 differences between small jackal-like and large wolf-like species (Fig. 2). At the extreme
45
46 176 negative of PC1 *Canis simensis* is represented by a thin and slender palate with relatively
47
48 177 short incisor row and canine but long snout, on the opposite of PC1 *Lycaon pictus* together
49
50 178 with *Cuon* share a much larger palate with relatively larger upper carnassial and M1. PC2 is
51
52 179 highly influenced by position of landmark 15 and separates jackals and hypercarnivore
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54 180 *Lycaon-Cuon* from grey wolf and coyote. Fossil canids are evenly spaced in different areas of
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3 181 the morphospace and tend generally to occupy less extreme scores with the exception of
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5 182 *Lycaon falconeri* (at the extreme positive PC1 and negative PC2).
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8 183 MANOVA shows significant differences between diet in skull shape (represented by the first
9
10 184 12 PCs) (Wilk's lambda = 0.164, F = 8.677, df = 24, 142, p < 0.0001). Same applies when
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12 185 non-parametric MANOVA is computed after permuting Euclidean distances between dietary
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14 186 groups 9,999 times (F = 16.74, p < 0.0001).
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18 187 Skull shape differs significantly also between dietary categories (Wilk's lambda = 0.050, F =
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20 188 3.88, df = 52, 58, p < 0.0001).
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26 190 **Skull size and allometry**

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29 191 Skull size (here represented by ln centroid size of the landmark configuration) was normally
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31 192 distributed across dietary categories (P values after Kolgomorov-Smirnoff always > 0.06).
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34 193 This allowed us to perform an ANOVA test that shows significant differences between small,
35
36 194 medium and large prey consumers (F = 22.963, df = 2, 82, p < 0.0001; Fig. 3a). Due to
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38 195 significant differences in homogeneity of variance test (Levene statistic 5.702, df = 2, 82, p =
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40 196 0.005), Dunnett's T3 was employed. This test shows significant differences in size between
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42 197 all the diet categories (p < 0.025 in all pairwise comparisons).
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45 198 A significant allometric component was also detected even if ln centroid size explains only a
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47 199 very small fraction of total shape variance (Wilks' Lambda = 0.343, F = 5.531, df = 26, 75, p
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49 200 < 0.0001; 4.11% of variance). Indeed, deformation grids depicted only a small deformation
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51 201 occurring mostly in the canine and upper carnassial (P4) areas (Fig. 3b). A closer inspection
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53 202 of allometry shows significant negative correlation only between ln CS and PC3 (10.12% of
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3 203 variance, $r = -0.541$), PC8 (1.85% of variance, $r = -0.281$) and PC10 (1.20 % of variance,
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5 204 Spearman $r = -0.119$).

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11 206 **Dietary discrimination**

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14 207 After stepwise only five out of 30 shape coordinates and ln Centroid Size were selected by
15
16 208 the Discriminant Function analysis. Two significant DF were extracted to differentiate dietary
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18 209 groups (DF1: 93.8% variance, Wilk's lambda = 0.113, $\chi^2 = 173.66$, $df = 12$, $p < 0.0001$; DF2:
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20 210 6.2% variance, Wilk's lambda = 0.733, $\chi^2 = 24.691$, $df = 5$, $p < 0.0001$).

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24 211 Percentage of correctly classified cases after cross-validation is high (Small = 86.5%;
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26 212 Medium = 86.7% and Large = 93.9%).

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29 213 DF1 was positively and significantly loaded on ln CS ($r = 0.314$), procustes coordinate X of
30
31 214 the landmark 6 (the anterior tip of P4, $r = 0.251$), and negatively on coordinate Y for
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33 215 landmark 1 (tip of the snout, $r = -0.586$). DF2 correlated positively with coordinate Y of
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35 216 landmark 3 (anterior tip of the canine, $r = 0.841$) and negatively on coordinate X of landmark
36
37 217 11 (M1 paracone, $r = 0.478$), Y for landmark 13 (anterior tip of M1, $r = 0.398$).

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41 218 The deformation grids were obtained after regressing discriminant function scores vs shape
42
43 219 coordinates. They show how species adapted to kill large prey at the positive DF1 are
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45 220 characterised by a shorter and thicker muzzle opposite to species adapted in killing small prey
46
47 221 (Fig. 4). Medium prey specialists exhibit intermediate DF1 scores and negative DF2 scores.
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49 222 They are discriminated by "small prey" due to a thin and long muzzle with relatively bigger
50
51 223 carnassial (P4) and M1 (Fig. 4).

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55 224 Fossil specimens are predicted to cover the whole range of dietary adaptations of extant
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57 225 Canini (Table 2). Species represented by multiple specimens are sometimes predicted into
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3 226 more than one category with the exception of the dire wolf for which both specimens are
4
5 227 consistently categorised as predators of large prey. *Eucyon adoxus*, *Cynotherium sardous*, *C.*
6
7 228 *cf. mesomelas* and one specimen of *C. arnensis* and *C. etruscus* follow within the “small
8
9 229 prey” category, while *C. lupus* from Romanelli, one specimen of *C. arnensis* and one of *C.*
10
11 230 *chihliensis* follow within category “medium prey”. All large fossil hypercarnivores are
12
13
14 231 classified as “Large” (Table 2).
15
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20 233 **Clustering**

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23 234 The UPGMA based on procustes distances yields a cophenetic cluster with a high cophenetic
24
25 235 correlation ($r = 0.882$). There is a mix of ecological and taxonomic signal with some fossil
26
27 236 taxa clustering together due to their unique affinities (e.g., *E. adoxus* with *C. cf. mesomelas*
28
29 237 from Olduvai Gorge). The fossil hunting dog *L. falconeri* is clearly an outgroup that allows
30
31 238 identifying three main groups: 1. a cluster showing the affinity of the extant Ethiopian wolf
32
33 239 (*C. simensis*) with the prehistoric *C. arnensis*; 2. a cluster that separates extant jackal-like
34
35 240 forms (inclusive of the fossil hypercarnivore *C. antonii* and wolf-like *C. etruscus* and *C.*
36
37 241 *mosbachensis*) from grey wolf cluster inclusive of the dingo and the dire wolf; 3.
38
39 242 hypercarnivore cluster inclusive of fossil *C. africanus*, extant *Lycaon* and *Cuon* and a fossil
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41 243 grey wolf from Spain.
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49 245 **Discussion**

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52 246 With no doubt, skull size and shape of extant Canini can strongly be linked to their feeding
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54 247 habits (Van Valkenburgh & Koepfli, 1993; Van Valkenburgh *et al.*, 2003; Andersson, 2005;
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56 248 Slater *et al.*, 2009; Damasceno *et al.*, 2013). By investigating only the palate, we critically
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3 249 limited the amount of size and shape information, but demonstrate that this area is
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5 250 ecologically and taxonomically informative. Indeed, MANOVA and ANOVA show
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7 251 significant differences between feeding categories re-defined to fit the broad dietary variation
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10 252 observed in the Canini tribe (Sillero-Zubiri *et al.*, 2004).

11
12 253 The palate of species adapted to hunt small prey is thin, longer and characterised by
13
14 254 relatively shorter P4 and M1. All these adaptations can be observed in extant jackals and
15
16
17 255 especially in the Ethiopian wolf (*C. simensis*) that occupy the extreme morphological
18
19 256 variation on the first RW (Fig. 2). This confirms early morphometric observation by Rook &
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21 257 Azzaroli Puccetti (1996) and functional morphology by Slater *et al.* (2009). In contrast, the
22
23 258 grey wolf, African hunting dog and the dhole cluster together in the morphospace (Fig. 2) for
24
25 259 their typical hypercarnivorous traits (Van Valkenburgh, 1991): a short and broad muzzle with
26
27
28 260 larger incisors and canine (cf. Andersson, 2005) and relatively larger upper carnassial. All
29
30 261 these features correlate with higher bite forces (Christiansen & Wroe, 2007; Damasceno *et*
31
32 262 *al.*, 2013) hence the ability to kill prey much larger than themselves. Not surprisingly, these
33
34 263 morphologies are well separated from the other feeding groups, supporting the highest
35
36 264 classification rate in the Discriminant Function analysis.

37
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39
40 265 In agreement with previous findings on the mandible, it is not only palatal shape that
41
42 266 is a good discriminator of diet in extant Canini but also its size (cf. Meloro, 2011). The
43
44 267 ecological continuum observed in Canini diet is reflected into skull morphology so that
45
46
47 268 intermediate sized dogs (the coyote and the dingo) show intermediate skull shapes allowing
48
49 269 them to expand feeding niches under different circumstances. Indeed, the medium size canid
50
51 270 hunters possess relatively larger upper carnassial and M1 but retain a longer and thin snout
52
53 271 (in the case of the coyote) or have a broad palate but not so extreme as in *Cuon* or *Lycaon*
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55 272 (the dingo in Fig. 2).
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3 273 It is important to note that although an allometric component was detected in our data,
4
5 274 it accounts only for a small percentage of shape variance. When size generally explains large
6
7 275 portion of shape variance it is common practice to use “size-free” shape residuals, although
8
9 276 this correction generally does not provide additional insights (cf. Meloro *et al.*, 2014).
10
11 277 Mitteroecker *et al.* (2013) recently argued the necessity to take size into account by actually
12
13 278 adding, and not removing this variable from subsequent analyses. Our results confirm such
14
15 279 assertion thus supporting the combined interpretation of palatal size and shape to infer
16
17 280 palaeoecology of fossil species.
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20
21 281 Fossil genera *Eucyon* and *Cynotherium* cluster well within the morphological
22
23 282 variation of extant Canini confirming previous taxonomic observations on their affinities
24
25 283 (Rook, 2009; Lyras *et al.*, 2010). The Principal Component plot shows similar scores
26
27 284 between these taxa and the extant jackals, both clustering within the range of the side-striped
28
29 285 jackal (Fig. 2). Consequently, the dietary reconstruction as specialist hunter of small prey fits
30
31 286 well with previous attempts for the *Cynotherium* (cf. Abbazzi *et al.*, 2005; Lyras *et al.*, 2006)
32
33 287 and underlines the strong affinity of *Eucyon* (at least for the species *E. adoxus*) with jackals.
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38 288 Dietary reconstruction for Plio-Pleistocene dogs confirms the puzzling evolution of
39
40 289 the Etruscan wolf (*Canis etruscus*) and the coyote-like *Canis arnensis* while supporting the
41
42 290 hypercarnivorous traits of *Lycaon falconeri*, *C. antonii* and *C. africanus* (cf. Rook, 1994;
43
44 291 Tedford *et al.*, 2009). Both *C. etruscus* and *C. arnensis* specimens occupy more than one
45
46 292 dietary classification in agreement with previous studies (Cherin *et al.*, 2014; Flower &
47
48 293 Shreve, 2014; Meloro, 2011). However, there is a clear size partitioning with the Arno dog
49
50 294 being classified as small-medium, while only one *C. etruscus* is predicted as small prey with
51
52 295 the others grouped into large prey category. Due to ecological character displacement, it is
53
54 296 possible that morphological variation in these taxa was broad and influenced by presence or
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56 297 absence of larger competitors (García & Virgós, 2007).
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3 298 Diet of the large American dire wolf fits consistently with previous palaeoecological
4
5 299 reconstructions (Anyonge & Baker 2006; Meloro, 2011, 2012), while new insights emerge
6
7 300 for *Canis chihliensis* from the lower Pleistocene of China. Tong *et al.* (2012) identified a
8
9 301 mosaic of features combining hypercarnivorous dentition with a relatively small size
10
11 302 compared to the grey wolf. Consequently, the size constraint on hunting behaviour supports
12
13 303 our prediction of *C. chihliensis* as an adaptable hunter within the medium category (cf. dingo,
14
15 304 see also Fig. 2). For the middle Pleistocene *C. mosbachensis* a large size categorisation also
16
17 305 seems likely based on its morphofunctional similarity to the grey wolf (cf. Flower & Shreve,
18
19 306 2014). Diet prediction for the wolf of Romanelli cave also fits within the category “Medium”.
20
21 307 Although Sardella *et al.* (2014) confirmed its taxonomic affinity to the grey wolf, they also
22
23 308 pointed out how its smaller size confounded previous taxonomic attempts of this species into
24
25 309 golden jackal or *C. mosbachensis*. The grey wolf is highly flexible in size and ecology
26
27 310 (Sillero-Zubiri *et al.*, 2004). Such flexibility has been observed in prehistoric specimens
28
29 311 (Flower & Shreve, 2014) as well as ancestral forms supporting possible ecogeographical
30
31 312 differentiation in the past. Comfortably the fossil grey wolf from Spain is predicted as large
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33 313 prey specialist.

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39 314 The enigmatic *Canis cf. mesomelas* from Koobi Fora deserves a separate note.
40
41 315 Werdelin & Lewis (2005) and Werdelin & Peigné (2010) reviewed the rich Plio-Pleistocene
42
43 316 East African carnivore fauna. Taxonomy of jackals is not clear yet and there seems to be
44
45 317 evidence for different ecomorphotypes in hominin fossil sites. Our analysis suggests the
46
47 318 Koobi Fora specimen being adapted for hunting small-sized prey. Interestingly, the UPGMA
48
49 319 analysis (Fig. 5) supports shape similarity not with extant jackals, but with the Mio-Pliocene
50
51 320 genus *Eucyon* suggesting that it was a distinct (but ecologically equivalent to the extant
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53 321 jackal) morphotype.
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3 322 For the other taxa, the UPGMA cluster analysis shows a mixed signal based on shape
4
5 323 data. P4 and M1 morphology are phylogenetic characters in Canini (Tedford *et al.*, 2009)
6
7 324 although the presented UPGMA (Fig. 5) cannot disentangle the ecological from the
8
9 325 phylogenetic signal (cf. Meloro, 2011). The clustering of *C. africanus* within *Lycaon-Cuon*
10
11 326 confirms the grouping proposed by Rook (1994). However, the palate of *Lycaon falconeri*
12
13 327 from Valdarno and that of *C. antonii* are highly distinct from *C. africanus*. Ecogeographical
14
15 328 and temporal variation could explain such a pattern even if larger and more complete sample
16
17 329 is needed to prove this assertion. The grouping of *E. adoxus* with the jackal from Koobi Fora
18
19 330 suggests how distinct the morphology is from these Plio-Pleistocene forms with no extant
20
21 331 relatives, even if their smaller size supports ecological similarities with jackals and coyotes.
22
23 332 *Cynotherium* is also enigmatically positioned (although outside of the wolf cluster) while the
24
25 333 cluster of *C. etruscus* with *C. adustus* also does not support the wolf phylogenetic hypothesis
26
27 334 (cf. Tedford *et al.*, 2009). Interestingly, recent research on African jackals supports the
28
29 335 identification of a wolf North African subspecies (*Canis lupus lupaster*) that was
30
31 336 morphologically ascribed to the golden jackal (Gaubert *et al.*, 2013) suggesting how puzzling
32
33 337 morphological characters can be not only in fossil but also in extant species. The Romanelli
34
35 338 grey wolf is an outgroup within the wolf cluster while the dire wolf is grouped with the dingo
36
37 339 and grey wolf. Extant *Lycaon* and *Cuon* clusters together consistently with their
38
39 340 hypercarnivorous feeding habits.
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46 341 Members of Canini clearly occupied a broad range of ecological niches since the
47
48 342 Pliocene then differentiating during Early Pleistocene with the evolution of modern taxa
49
50 343 (Sotnikova & Rook, 2010). Such a rapid differentiation resulted in a high flexibility of
51
52 344 ecomorphological skull traits whose combination provide robust palaeoecological insights.
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3 524**Figures Legend**4
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6 525 **Figure 1** Skull of *Canis adustus* showing the landmark locations placed on each specimen.7
8 526 (1) tip of the snout defined by middle point between the first two frontal incisors, 2) posterior9
10 527 tip of 3rd incisor, 3) anterior tip of canine, 4) posterior tip of canine, (5) anterior tip of the11
12 528 third premolar, (6, 7, 8, 9, 10) outline of carnassial tooth, (11, 12) cusps of molar, (13)13
14 529 anterior tip of molar, (14) posterior tip of molar, (15) junction of the stiff and hard palate. The15
16 530 distance between 3 and 4 describe canine length. The distance between 8 and 10 describe17
18 531 carnassial tooth length. The distance between 1 and 15 describes snout length. Deviation of19
20 532 the specimens analysed from the consensus configuration of landmarks are shown below the21
22 533 skull. Scale bar equals 1cm.23
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30 535 **Figure 2** Plot of the first and second principal components. Thin-plate spline diagrams31
32 536 illustrate patterns of landmark displacements along each warp. Triangles indicate canids in33
34 537 the large dietary category, ellipsoid indicate canids in the medium dietary category and35
36 538 circles indicate canids in the small dietary category. Crosses and stars indicate fossil37
38 539 specimens with an unknown diet category. Below deformation grids from positive to negative39
40 540 RW scores.41
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46 542 **Figure 3** (a) Box plot showing differences in natural log transformed centroid size between47
48 543 diet categories of extant specimens of canid skull (the outlier in the “Medium Prey” category49
50 544 is a specimen of *C. latrans*); (b) skull shape deformation related to size from the smallest (*C.*51
52 545 *mesomelas*) to the largest (*C. dirus*) canid species. Values in parentheses are ln centroid size.53
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3 547 **Figure 4** Plot of the first two discriminant functions (DF) extracted from a combination of
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5 548 shape and size variables. Extant specimens are labelled according to their diet categorisation.
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7 549 Fossil specimens are labelled individually. Below deformation grids from positive to negative
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9 DF scores.
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14 552 **Figure 5** UPGMA Cluster analysis obtained on procrustes distances of averaged sample for
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16 553 23 canid species.
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3 568**Tables Legend**4
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9 **Table 1** Skull sample sizes of extant and fossil canid species together with assigned dietary
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11 grouping. *Includes subspecies (*Canis lupus gigas* and *Canis lupus pambasileus*); **
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13 includes subspecies (*Cuon alpinus dukhnensis* and *Cuon alpinus javanicus*). Small =
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15 mesocarnivore feeding on small prey, medium = mesocarnivore feeding on medium prey,
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17 large = hypercarnivore feeding on large prey.
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27 **Table 2** Dietary classification provided for fossil specimens using discriminant function
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29 analysis. $P(D | G)$ is the probability of membership in a group given the discriminant
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31 function score. $P(G | D)$ is the posterior probability based on the sample employed to
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33 generate the discriminant functions.
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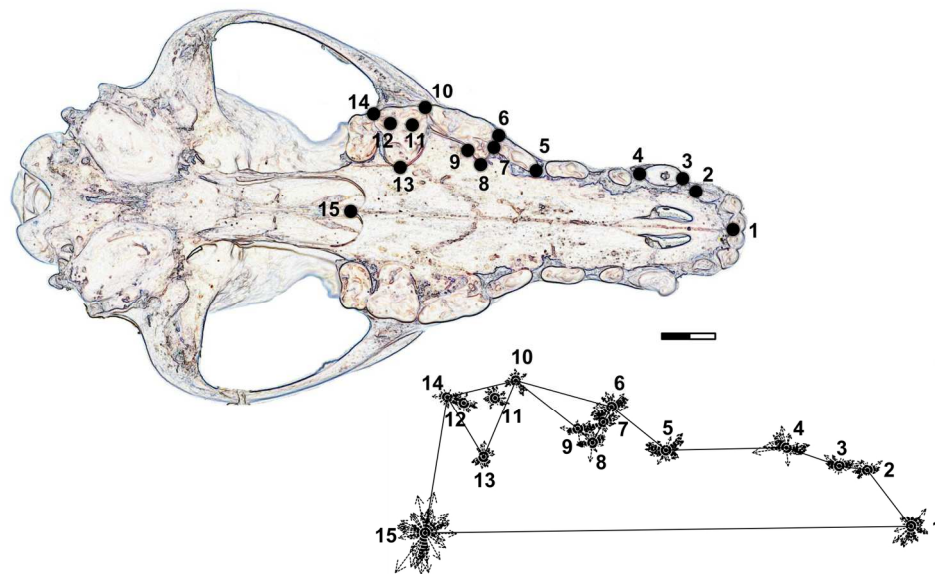


Figure 1 Skull of *Canis adustus* showing the landmark locations placed on each specimen. (1) tip of the snout defined by middle point between the first two frontal incisors, 2) posterior tip of 3rd incisor, 3) anterior tip of canine, 4) posterior tip of canine, (5) anterior tip of the third premolar, (6, 7, 8, 9, 10) outline of carnassial tooth, (11, 12) cusps of molar, (13) anterior tip of molar, (14) posterior tip of molar, (15) junction of the stiff and hard palate. The distance between 3 and 4 describe canine length. The distance between 8 and 10 describe carnassial tooth length. The distance between 1 and 15 describes snout length. Deviation of the specimens analysed from the consensus configuration of landmarks are shown below the skull. Scale bar equals 1cm.
157x100mm (300 x 300 DPI)

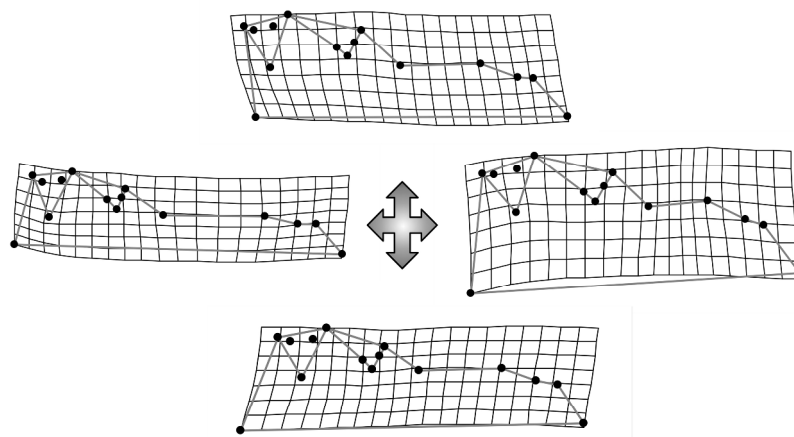
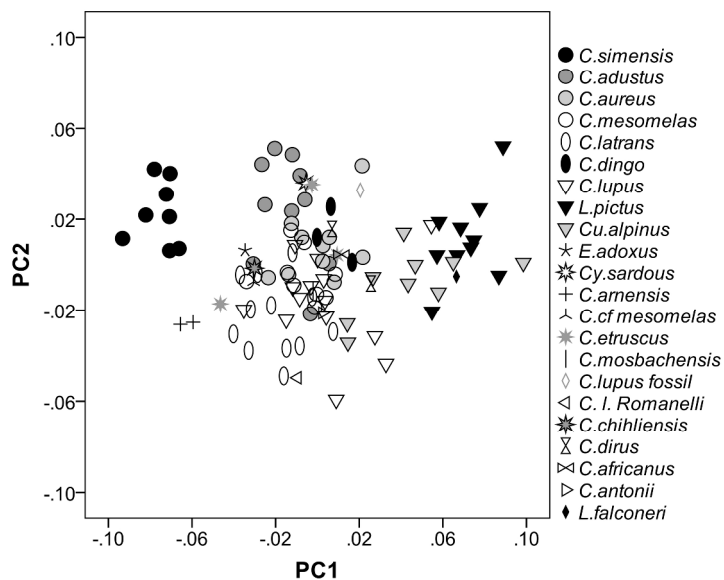


Figure 2 Plot of the first and second principal components. Thin-plate spline diagrams illustrate patterns of landmark displacements along each warp. (Triangles indicate canids in the large dietary category, ellipsoid indicate canids in the medium dietary category and circles indicate canids in the small dietary category. Crosses and stars indicate fossil specimens with an unknown diet category). Below deformation grids from positive to negative RW scores.
259x350mm (300 x 300 DPI)

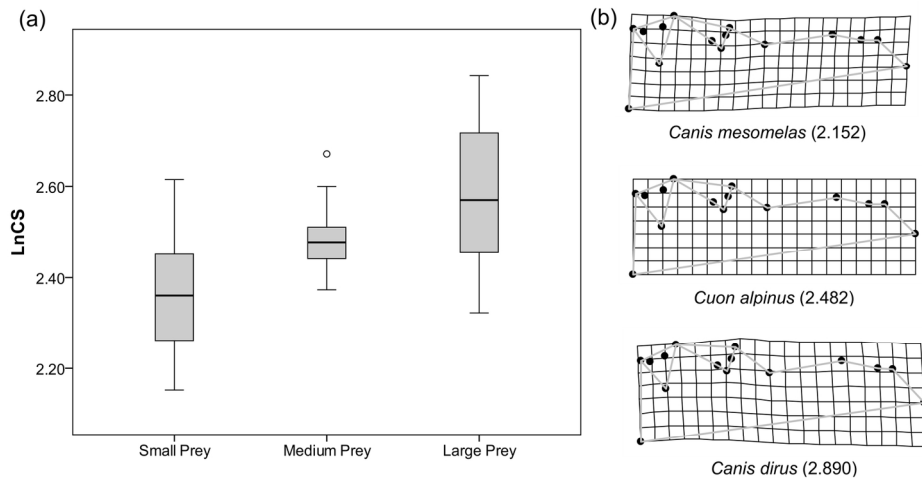


Figure 3 (a) Box plot showing differences in natural log transformed centroid size between diet categories of extant specimens of canid skull (the outlier in the "Medium Prey" category is a specimen of *C. latrans*); (b) skull shape deformation related to size from the smallest (*C. mesomelas*) to the largest (*C. dirus*) canid species. Values in parentheses are Ln centroid size.
159x88mm (300 x 300 DPI)

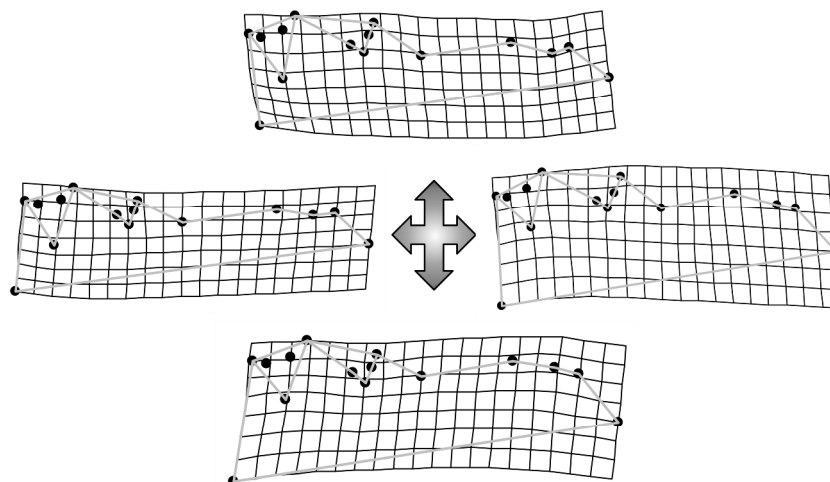
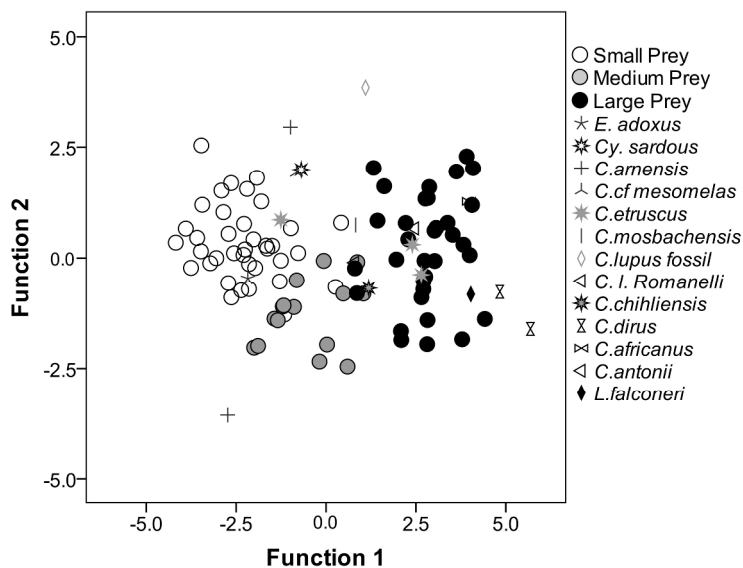


Figure 4 Plot of the first two discriminant functions (DF) extracted from a combination of shape and size variables. Extant specimens are labelled according to their diet categorisation. Fossil specimens are labelled individually. Below deformation grids from positive to negative DF scores.
249x321mm (300 x 300 DPI)

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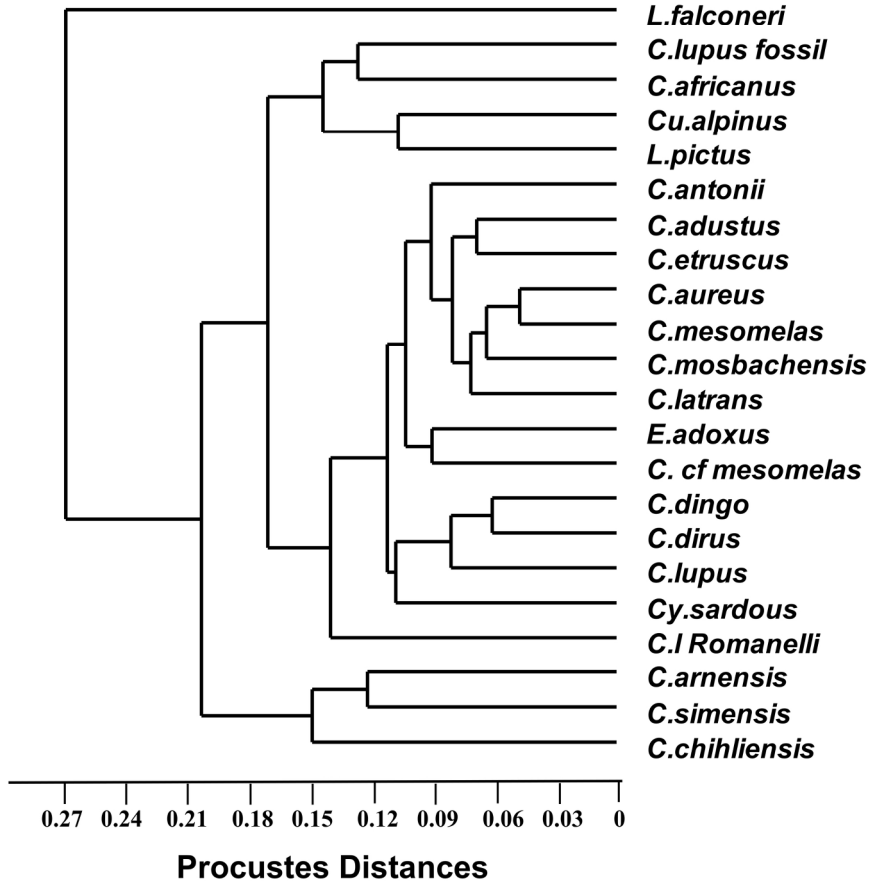


Figure 5 UPGMA Cluster analysis obtained on procustes distances of averaged sample for 23 canid species.
189x202mm (300 x 300 DPI)

TABLE 1

Species	Status	# Specimens	Diet
<i>Canis lupus</i> *	Extant	14	Large
<i>Canis dingo</i>	Extant	3	Medium
<i>Canis latrans</i>	Extant	12	Medium
<i>Canis aureus</i>	Extant	10	Small
<i>Canis adustus</i>	Extant	10	Small
<i>Canis mesomelas</i>	Extant	9	Small
<i>Canis simensis</i>	Extant	8	Small
<i>Cuon alpinus</i> **	Extant	9	Large
<i>Lycaon pictus</i>	Extant	10	Large
<i>Eucyon adoxus</i>	Fossil	1	
<i>Cynotherium sardous</i>	Fossil	1	
<i>Canis africanus</i>	Fossil	1	
<i>Canis antonii</i>	Fossil	1	
<i>Canis arnensis</i>	Fossil	2	
<i>Canis chiliensis</i>	Fossil	1	
<i>Canis dirus</i>	Fossil	2	
<i>Canis etruscus</i>	Fossil	3	
<i>Canis cf. mesomelas</i>	Fossil	1	
<i>Canis mosbachensis</i>	Fossil	1	
<i>Canis lupus</i> (Grotta Romanelli)	Fossil	1	
<i>Canis lupus</i> (Spain)	Fossil	1	

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Lycaon falconeri

Fossil

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TABLE 2

	Most likely group	P(D G)	P(G D)	Second most likely group
<i>Eucyon adoxus</i>	Small	0.726	0.796	Medium
<i>Canis africanus</i>	Large	0.280	1.000	Medium
<i>Canis antonii</i>	Large	0.852	0.998	Medium
<i>Canis arnensis</i> IGF 601V	Small	0.015	0.991	Medium
<i>Canis arnensis</i> IGF 867	Medium	0.006	0.935	Small
<i>Canis chiliensis</i>	Medium	0.192	0.503	Large
<i>Canis dirus</i> cast M11960	Large	0.003	1.000	Medium
<i>Canis dirus</i> cast unknown	Large	0.078	1.000	Medium
<i>Canis etruscus</i> cast MNCN an5006	Small	0.522	0.867	Medium
<i>Canis etruscus</i> SBAU337628	Large	0.839	0.995	Medium
<i>Canis etruscus</i> SBAU398989	Large	0.922	0.996	Medium
<i>Canis. cf. mesomelas</i>	Small	0.101	0.941	Medium
<i>Canis mosbachensis</i>	Large	0.126	0.677	Medium
<i>Canis lupus</i> (Romanelli)	Medium	0.208	0.599	Large
<i>Canis lupus</i> (Spain)	Large	0.000	0.975	Small
<i>Cynotherium sardous</i>	Small	0.073	0.932	Medium
<i>Lycaon falconeri</i>	Large	0.276	1.000	Medium

Appendix 1

List of extant and fossil skull specimens of Canidae.

RMS = Royal Museum of Scotland, Edinburgh UK

NHM = Natural History Museum, London UK

MNCN = Museo Nacional de Ciencias Naturales, Madrid Spain

RMCA = Royal Museum of Central Africa, Tervuren Belgium

ZMF = Zoological Museum Florence University / CE = Museo Doeria, Genoa Italy

Species	Catalogue	Locality	Museum	Period
<i>Canis adustus</i>	66.26	Sakala Ethiopia	NHM, London	Extant
<i>Canis adustus</i>	70.23.27	Kukawa Borno Niger	NHM, London	Extant
<i>Canis adustus</i>	35.9.1.292	Grootefontein	NHM, London	Extant
<i>Canis adustus</i>	70.661	Ethiopia	NHM, London	Extant
<i>Canis adustus</i>	23.1.4.1	Angola	NHM, London	Extant
<i>Canis adustus</i>	26.6.11	Nyasaland	NHM, London	Extant
<i>Canis adustus</i>	RMCA 3921	Zaire	RMCA, Tervuren	Extant
<i>Canis adustus</i>	RMCA 9329	Rwanda	RMCA, Tervuren	Extant
<i>Canis adustus</i>	RMCA 9330	Rwanda	RMCA, Tervuren	Extant
<i>Canis adustus</i>	RMCA 17190	Rwanda	RMCA, Tervuren	Extant
<i>Canis aureus</i>	an 5007	Unknown	Glasgow	Extant
<i>Canis aureus</i>	1937.2.24.49	Dangila Abyssinia	NHM, London	Extant
<i>Canis aureus</i>	23.3.26.14	Laketsana Abyssinia	NHM, London	Extant
<i>Canis aureus</i>	64.21.81	Pircolo Abbai Ethiopia	NHM, London	Extant
<i>Canis aureus</i>	70.66	Ethiopia 2500m	NHM, London	Extant
<i>Canis aureus</i>	36.5.20.6	Goulse Bale Abyssinia	NHM, London	Extant
<i>Canis aureus</i>	36.5.20.4	Arussi Abyssinia	NHM, London	Extant
<i>Canis aureus</i>	75.2312	Assam	NHM, London	Extant
<i>Canis aureus</i>	67.69	Sri Lanka	NHM, London	Extant
<i>Canis aureus</i>	1892.7.16.1	Luxor, Egypt	NHM, London	Extant
<i>Canis dingo</i>	an5007	Unknown	Glasgow	Extant
<i>Canis dingo</i>	140c	Unknown	Glasgow	Extant
<i>Canis dingo</i>	1952.4.1.2	Australia	NHM, London	Extant
<i>Canis latrans</i>	2003.130.02	Unknown	RMS, Edinburgh	Extant
<i>Canis latrans</i>	2003.130.03	Unknown	RMS, Edinburgh	Extant
<i>Canis latrans</i>	2003.130.64	Unknown	RMS, Edinburgh	Extant

Species	Catalogue	Locality	Museum	Period
<i>Canis latrans</i>	2003.130.05	Unknown	RMS, Edinburgh	Extant
<i>Canis latrans</i>	2003.130.07	Unknown	RMS, Edinburgh	Extant
<i>Canis latrans</i>	2003.130.08	Unknown	RMS, Edinburgh	Extant
<i>Canis latrans</i>	2.3.7.4	Penington British Columbia	NHM, London	Extant
<i>Canis latrans</i>	94.5.9.4	Chapham New Mexico	NHM, London	Extant
<i>Canis latrans</i>	98.12.21.1	Chihout Mt. British Columbia	NHM, London	Extant
<i>Canis latrans</i>	40.82.1	San Quintin Lower California Mexico	NHM, London	Extant
<i>Canis latrans</i>	2.82.2	Jouchood Hillo Asauriboia New Mexico	NHM, London	Extant
<i>Canis latrans</i>	10909	Hansoon Lagoon L.C. Mexico	NHM, London	Extant
<i>Canis lupus</i>	an4560	Unknown	Glasgow	Extant
<i>Canis lupus pambasilens</i>	19.7.15.4	McMillan River Youkon Territories	NHM, London	Extant
<i>Canis lupus gigas</i>	63.2.24.51	Fort Langley New Wesminster British Columbia	NHM, London	Extant
<i>Canis lupus gigas</i>	63.2.24.31	British Columbia	NHM, London	Extant
<i>Canis lupus pambasilens</i>	19.7.15.5	McMillan River Youkon Territories	NHM, London	Extant
<i>Canis lupus</i>	1852.3.24.4_168.c.	Azraq, Jordan	NHM, London	Extant
<i>Canis lupus arabs</i>	84.1312	Unknown	NHM, London	Extant
<i>Canis lupus arctos</i>	86.1595	Ellesmere island, Canada	NHM, London	Extant
<i>Canis lupus occidentalis</i>	1855.5.14.11	"Arctic" America, Canada	NHM, London	Extant
<i>Canis lupus pallipes</i>	1863.12.28.14	India	NHM, London	Extant
<i>Canis lupus chanco</i>	1875.4.10.1_1670.a.	Near Tshommeriri lake, Tibet	NHM, London	Extant
<i>Canis lupus</i>	1935.8.5.1	Bosnia, Yugoslavia	NHM, London	Extant
<i>Canis lupus</i>	1937.2.10.2	Abrantos, S. of Taqus, Portugal	NHM, London	Extant

Species	Catalogue	Locality	Museum	Period
<i>Canis lupus chanco</i>	1961.9.21.2	Khumbu, East Nepal	NHM, London	Extant
<i>Canis mesomelas</i>	24.1.1.91	Samumba Singida	NHM, London	Extant
<i>Canis mesomelas</i>	29.8.14.2	Somaliland	NHM, London	Extant
<i>Canis mesomelas</i>	23.3.4.23	Mlawa Mkalam	NHM, London	Extant
<i>Canis mesomelas</i>	69.10.24.7	Anseba	NHM, London	Extant
<i>Canis mesomelas</i>	25.1.2.210	Unknown	NHM, London	Extant
<i>Canis mesomelas</i>	28.9.11.138	Unknown	NHM, London	Extant
<i>Canis mesomelas</i>	1991.586	Zimbabwe	NHM, London	Extant
<i>Canis mesomelas</i>	RMCA 2145	Ziwani, Brit East A	RMCA, Tervuren	Extant
<i>Canis mesomelas</i>	RMCA 2164	Ziwani, Brit East A	RMCA, Tervuren	Extant
<i>Canis simensis</i>	23.10.10.1	Arusi 1300 m	NHM, London	Extant
<i>Canis simensis</i>	24.8.7.11	Chilalo Arussi Galla	NHM, London	Extant
<i>Canis simensis</i>	36.5.20.4	Chilalo W.Arussi Abyssinia	NHM, London	Extant
<i>Canis simensis</i>	24.8.9.10	Gojam Abyssinia	NHM, London	Extant
<i>Canis simensis</i>	24.8.7.12	Simien	NHM, London	Extant
<i>Canis simensis</i>	2.4.00	Abyssinia	NHM, London	Extant
<i>Canis simensis</i>	ZMF 13718	Senneti Platue	ZMF, Florence	Extant
<i>Canis simensis</i>	CE 818	Arussi Abyssinia	Museum Doria, Genoa	Extant
<i>Cuon alpinus</i>	34.10.4.4	Ramnagar Kumaon	NHM, London	Extant
<i>Cuon alpinus dukhnensis</i>	No catalogue	Unknown	RMS, Edinburgh	Extant
<i>Cuon alpinus javanicus</i>	35.3.22.1	Chamrajnagar S.Mysore	NHM, London	Extant
<i>Cuon alpinus javanicus</i>	1939.1.10.24	Masangaudi Bilgiris S.India	NHM, London	Extant
<i>Cuon alpinus javanicus</i>	1937.12.3.31	Shan States Upper Burma	NHM, London	Extant
<i>Cuon alpinus javanicus</i>	34.9.18.2	Tian Shan (Central Asia)	NHM, London	Extant
<i>Cuon alpinus javanicus</i>	5.11.19.1	Ussuri River Manchuria	NHM, London	Extant

Species	Catalogue	Locality	Museum	Period
<i>Cuon alpinus javanicus</i>	88.2.5.22_15 9.d.	Anamalai Hills, Coimbatore, S.India	NHM, London	Extant
<i>Cuon alpinus dukhnensis</i>	1936.4.8.1	India	NHM, London	Extant
<i>Lycaon pictus</i>	61.976	Kabompo Dist. (Rhodesia)	NHM, London	Extant
<i>Lycaon pictus</i>	10.10.3.2	Linyanti R.N.Banr. Rhodesia	NHM, London	Extant
<i>Lycaon pictus</i>	1.4.26.3	Rift Valley	NHM, London	Extant
<i>Lycaon pictus</i>	49.122	Mont Kenya	NHM, London	Extant
<i>Lycaon pictus</i>	Z1908 077c	Unknown	RMS, Edinburgh	Extant
<i>Lycaon pictus</i>	1963.9.30.1	(P) Zool. Soc. London, Africa	NHM, London	Extant
<i>Lycaon pictus</i>	1969	(P) Zool. Soc. London, Africa	NHM, London	Extant
<i>Lycaon pictus</i>	RCMA 15896	buta, Zaire	RMCA, Tervuren	Extant
<i>Lycaon pictus</i>	RCMA 1096	buta, Zaire	RMCA, Tervuren	Extant
<i>Lycaon pictus</i>	RCMA 2144	camp simba ziwani, Brit East A	RMCA, Tervuren	Extant
<i>Cynotherium sardous</i>	CB 848022	Corbeddu, Sardinia	In: Lyras et al. (2006) JVP 26:735-745	Pleistocene
<i>Canis dirus</i>	M11960	Cast from Rancho La Brea	NHM, London	Late Pleistocene
<i>Canis dirus</i>	unknown	Cast from Rancho La Brea	NHM, London	Late Pleistocene
<i>Canis lupus</i> (fossil)	P3580	Grotta Romanelli, Puglia	Pigorini, Rome	Middle Pleistocene
<i>Canis lupus</i> (fossil)	MNCN 31649A	Unknown	MNCN, Madrid	Upper Pleistocene
<i>Canis mosbachensis</i>	Unknown	Untermmassfield	from: Sotnikova (1998)	Middle Pleistocene
<i>Canis chihliensis</i>	IVPP V 18333.1	Nihewan	From Tong et al., (2012)	Pleistocene, ca. 1.3 Ma - 1.8 Ma
<i>Eucyon adoxus</i>	RSS45	Perpignan, France	cast_MNCN Madrid	Pliocene
<i>Canis antonii</i>	Cast of F:AM 97052	Nihewanian, Shanxi Province, China	Florence	Pliocene (3.5 Ma)
<i>Canis cf. mesomelas</i>	KNM- ER3667	Koobi Fora, East Africa	Kenya National Museum	Plio- Pleistocene

Species	Catalogue	Locality	Museum	Period
<i>Canis africanus</i>	OLD74	Olduvai Bed I	Kenya National Museum	Plio-Pleistocene (c.ca 1.9 Ma)
<i>Canis arnensis</i>	IGF 601V	Valdarno (Italy)	Florence	Plio-Pleistocene (c.ca 1.9 Ma)
<i>Canis arnensis</i>	IGF867	Valdarno (Italy)	Florence	Plio-Pleistocene (c.ca 1.9 Ma)
<i>Canis etruscus</i>	an5006c	Olivola	cast_MNCN Madrid	Plio-Pleistocene (c.ca 1.9 Ma)
<i>Canis etruscus</i>	SBAU33762 8	Pantalla, Italy	from Cherin et al. (2014)	Plio-Pleistocene (c.ca 1.9 Ma)
<i>Canis etruscus</i>	SBAU39898 9	Pantalla, Italy	from Cherin et al. (2014)	Plio-Pleistocene (c.ca 1.9 Ma)
<i>Lycaon falconeri</i>	IGF 865	Valdarno (Italy)	Florence	Plio-Pleistocene (c.ca 1.9 Ma)