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



 Feeding habits of extant and fossil canids as determined by their skull geometry Carlo Meloro¹, Angela Hudson¹, Lorenzo Rook² ¹ Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, United Kingdom ² Dipartimento di Scienze della Terra, Università di Firenze, via G. La Pira, I-50121 Firer (Italy) Correspondence Carlo Meloro, Research Centre in Evolutionary Anthropology and Palaeoecology, School Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, United Kingdom e-mail: C.Meloro@ljmu.ac.uk 	of 39	JZO: For review purposes only - please do not distribute
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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

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

The wolf-like clade had an explosion of forms during the Plio-Pleistocene so that biochronology considers such a proliferation of species in the Old World into a separate faunal event (the wolf event, c.ca 2.0 Ma; Azzaroli, 1983; Azzaroli et al., 1988; Torre et al., 1992, 2001; Rook & Torre, 1996a; Sardella & Palombo, 2007; Rook & Martínez-Navarro, 2010; Sotnikova & Rook, 2010). Palaeoecology of many of these canids represented by a coyote-like (Canis arnensis), a small wolf-like (Canis etruscus) and an African hunting dog-like (Lycaon falconeri group; Rook, 1994; Martinez-Navarro & Rook, 2003) was pioneered by Kurtén (1974) and Palmqvist et al. (1999) and later reconsidered by Meloro (2011) in a study on mandible shape. Here we aim to investigate skull shape that is expected to provide 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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al., 2003; Sacco & Van Valkenburgh, 2004; Christiansen & Adolfssen, 2005; Christiansen &
Wroe, 2007). Within canids, a shorter snout indicates larger moment arms for the temporalis
and masseter muscles (Damasceno *et al.*, 2013) and the canines are closer to the fulcrum,
both creating a more powerful bite force (Christiansen & Adolfssen, 2005; Christiansen &
Wroe, 2007). This is interpreted as an adaptation to kill large prey and can be detected in
living and extinct canid tribes (Valkenburgh & Koepfli, 1993; Andersson, 2005; Van
Valkenburgh *et al.*, 2003; Slater *et al.*, 2009).

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

86

87 Materials and Methods

88 Sample Size

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

For fossil species we used the nomenclature finalised by Tedford *et al.* (2009). The
small genera *Eucyon* and *Cynotherium* (with the species *Eucyon adoxus* and *Cynotherium sardous*) were also considered for their unequivocal affinities with extant *Canis*-like species
(Rook, 2009; Lyras *et al.*, 2006).

102 Data Capture

Digital photographs were collected on skulls positioned in ventral view by Meloro C. using a Nikon 995 at a 1 metre distance. A spirit level was positioned on the palate of the skull to ensure parallelism between camera optical plan and the flattest region of the skull. On each skull, 15 landmarks were recorded by one of us (Hudson A.) in the palate region to capture details of tooth and cusp positioning using the software tpsDig2 ver. 2.17 (Rohlf, 2013a) (Fig. 1). Landmarks 1-2 record the width of the incisor arch, 3-4 the relative size of canine, landmark 5 is at the anterior tip of P3, 6 to 10 relative size of the upper carnassial (P4) together with the positioning of the main cusps, 10-14 covers the M1 morphology and landmark 15 is the most posterior point delimiting the end of the palate.

> Cusp positions were recorded on P4 and M1 as good proxy for dietary adaptations but also to understand possible phylogenetic affinities between extant and fossil taxa (cf. Rook & Torre, 1996; Brugal & Boudadi-Maligne, 2010). The posterior part of the skull and the zygomatic arch were not covered by landmarks because they were not present in many of the analysed fossils.

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

Geometric Morphometrics

Landmark coordinates were aligned using Generalised Procustes superimposition (Rohlf & Slice, 1990) with the software tpsRelw ver. 1.53 (Rohlf, 2013b). The software performed three operations: translation, rotation and scaling to transform the original 2D coordinates of landmarks into shape coordinates. A Principal Component analysis of the covariance matrix of the shape coordinates was then computed. Shape variation along each principal component axis was visualised using a thin-plate spline (Bookstein, 1991). Thin plate splines visualize shape variation assuming that the average consensus configuration has no deformation and line on an infinite metal plane whose bending describe shape changes (Zelditch *et al.*, 2004). The size of landmark configuration was extrapolated from the raw coordinates via centroid size (=the square root of the mean squared distance from each landmark to centroid of the landmark configuration Bookstein, 1989). In order to scale centroid size to the mean, natural log transformation was used (cf. Meloro et al., 2008).

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135 Feeding Categories

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

149 Data Analyses

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

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

158	Discriminant Function Analysis was employed to provide prediction for fossil species
159	using diet categories as factor and shape coordinates and natural log centroid size as
160	independent variables. To considerably reduce the number of independent dietary predictors a
161	stepwise procedure was applied: a variable was entered into the model if the probability of its
162	F value was bigger than 0.05 and was removed if the probability was less than 0.10. Meloro
163	(2011) consistently demonstrated the importance of including mandibular size as a predictor
164	of feeding adaptation in Carnivora. We expect this to also hold for skull size in canids.
165	An UPGMA cluster analysis was employed to identify cophenetic similarities
166	between fossil and extant specimens. Averaged shape coordinates were first computed for
167	each extant and fossil species, then procustes distances calculated to construct the clustering
168	UPGMA tree (cf. Meloro, 2011).
169	
170	Results
171	Skull shape
172	Variability in skull shape is significantly reduced by using Principal Component analysis,
173	with the first 12 PC axes explaining 95.26% of total shape variance. PC1 and PC2 explain
174	45.76% and 15.60% of total variance respectively and their combination show substantial
175	differences between small jackal-like and large wolf-like species (Fig. 2). At the extreme
176	negative of PC1 Canis simensis is represented by a thin and slender palate with relatively
177	short incisor row and canine but long snout, on the opposite of PC1 Lycaon pictus together

- 178 with *Cuon* share a much larger palate with relatively larger upper carnassial and M1. PC2 is
 - 179 highly influenced by position of landmark 15 and separates jackals and hypercarnivore
- *Lycaon-Cuon* from grey wolf and coyote. Fossil canids are evenly spaced in different areas of

the morphospace and tend generally to occupy less extreme scores with the exception of Lycaon falconeri (at the extreme positive PC1 and negative PC2). MANOVA shows significant differences between diet in skull shape (represented by the first 12 PCs) (Wilk's lambda = 0.164, F = 8.677, df = 24, 142, p < 0.0001). Same applies when non-parametric MANOVA is computed after permuting Euclidean distances between dietary groups 9,999 times (F = 16.74, p < 0.0001). Skull shape differs significantly also between dietary categories (Wilk's lambda = 0.050, F = 3.88, df = 52, 58, p < 0.0001). **Skull size and allometry** Skull size (here represented by ln centroid size of the landmark configuration) was normally distributed across dietary categories (P values after Kolgomorov-Smirnoff always > 0.06). This allowed us to perform an ANOVA test that shows significant differences between small, medium and large prey consumers (F = 22.963, df = 2, 82, p < 0.0001; Fig. 3a). Due to significant differences in homogeneity of variance test (Levene statistic 5.702, df = 2, 82, p =0.005), Dunnett's T3 was employed. This test shows significant differences in size between all the diet categories (p < 0.025 in all pairwise comparisons).

A significant allometric component was also detected even if ln centroid size explains only a very small fraction of total shape variance (Wilks' Lambda = 0.343, F = 5.531, df = 26, 75, p < 0.0001; 4.11% of variance). Indeed, deformation grids depicted only a small deformation occurring mostly in the canine and upper carnassial (P4) areas (Fig. 3b). A closer inspection of allometry shows significant negative correlation only between ln CS and PC3 (10.12% of variance, r = -0.541), PC8 (1.85% of variance, r = -0.281) and PC10 (1.20% of variance,
Spearman r = -0.119).

206 Dietary discrimination

207 After stepwise only five out of 30 shape coordinates and ln Centroid Size were selected by

208 the Discriminant Function analysis. Two significant DF were extracted to differentiate dietary

209 groups (DF1: 93.8% variance, Wilk's lambda = 0.113, χ^2 = 173.66, df = 12, p < 0.0001; DF2:

210 6.2% variance, Wilk's lambda = 0.733, χ^2 = 24.691, df = 5, p < 0.0001).

211 Percentage of correctly classified cases after cross-validation is high (Small = 86.5%;

212 Medium = 86.7% and Large = 93.9%).

213 DF1 was positively and significantly loaded on $\ln CS$ (r = 0.314), procustes coordinate X of

the landmark 6 (the anterior tip of P4, r = 0.251), and negatively on coordinate Y for

215 landmark 1 (tip of the snout, r = -0.586). DF2 correlated positively with coordinate Y of

216 landmark 3 (anterior tip of the canine, r = 0.841) and negatively on coordinate X of landmark

217 11 (M1 paracone, r = 0.478), Y for landmark 13 (anterior tip of M1, r = 0.398).

218 The deformation grids were obtained after regressing discriminant function scores vs shape

219 coordinates. They show how species adapted to kill large prey at the positive DF1 are

220 characterised by a shorter and thicker muzzle opposite to species adapted in killing small prey

221 (Fig. 4). Medium prey specialists exhibit intermediate DF1 scores and negative DF2 scores.

222 They are discriminated by "small prey" due to a thin and long muzzle with relatively bigger

carnassial (P4) and M1 (Fig. 4).

224 Fossil specimens are predicted to cover the whole range of dietary adaptations of extant

225 Canini (Table 2). Species represented by multiple specimens are sometimes predicted into

more than one category with the exception of the dire wolf for which both specimens are
consistently categorised as predators of large prey. *Eucyon adoxus, Cynotherium sardous, C.*cf. *mesomelas* and one specimen of *C. arnensis* and *C. etruscus* follow within the "small
prey" category, while *C. lupus* from Romanelli, one specimen of *C. arnensis* and one of *C. chihliensis* follow within category "medium prey". All large fossil hypercarnivores are
classified as "Large" (Table 2).

233 Clustering

The UPGMA based on procustes distances yields a cophenetic cluster with a high cophenetic correlation (r = 0.882). There is a mix of ecological and taxonomic signal with some fossil taxa clustering together due to their unique affinities (e.g., E. adoxus with C. cf. mesomelas from Olduvai Gorge). The fossil hunting dog L. falconeri is clearly an outgroup that allows identifying three main groups: 1. a cluster showing the affinity of the extant Ethiopian wolf (C. simensis) with the prehistoric C. arnensis; 2. a cluster that separates extant jackal-like forms (inclusive of the fossil hypercarnivore C. antonii and wolf-like C. etruscus and C. *mosbachensis*) from grey wolf cluster inclusive of the dingo and the dire wolf; 3. hypercarnivore cluster inclusive of fossil C. africanus, extant Lycaon and Cuon and a fossil grey wolf from Spain.

Discussion

With no doubt, skull size and shape of extant Canini can strongly be linked to their feeding
habits (Van Valkenburgh & Koepfli, 1993; Van Valkenburgh *et al.*, 2003; Andersson, 2005;
Slater *et al.*, 2009; Damasceno *et al.*, 2013). By investigating only the palate, we critically

limited the amount of size and shape information, but demonstrate that this area is ecologically and taxonomically informative. Indeed, MANOVA and ANOVA show significant differences between feeding categories re-defined to fit the broad dietary variation observed in the Canini tribe (Sillero-Zubiri et al., 2004). The palate of species adapted to hunt small prey is thin, longer and characterised by relatively shorter P4 and M1. All these adaptations can be observed in extant jackals and especially in the Ethiopian wolf (C. simensis) that occupy the extreme morphological variation on the first RW (Fig. 2). This confirms early morphometric observation by Rook & Azzaroli Puccetti (1996) and functional morphology by Slater et al. (2009). In contrast, the grey wolf, African hunting dog and the dhole cluster together in the morphospace (Fig. 2) for their typical hypercarnivorous traits (Van Valkenburgh, 1991): a short and broad muzzle with larger incisors and canine (cf. Andersson, 2005) and relatively larger upper carnassial. All these features correlate with higher bite forces (Christiansen & Wroe, 2007; Damasceno et al., 2013) hence the ability to kill prev much larger than themselves. Not surprisingly, these morphologies are well separated from the other feeding groups, supporting the highest classification rate in the Discriminant Function analysis. In agreement with previous findings on the mandible, it is not only palatal shape that is a good discriminator of diet in extant Canini but also its size (cf. Meloro, 2011). The

ecological continuum observed in Canini diet is reflected into skull morphology so that
intermediate sized dogs (the coyote and the dingo) show intermediate skull shapes allowing
them to expand feeding niches under different circumstances. Indeed, the medium size canid
hunters possess relatively larger upper carnassial and M1 but retain a longer and thin snout
(in the case of the coyote) or have a broad palate but not so extreme as in *Cuon* or *Lycaon*

272 (the dingo in Fig. 2).

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273 It is important to note that although an allometric component was detected in our data, 274 it accounts only for a small percentage of shape variance. When size generally explains large 275 portion of shape variance it is common practice to use "size-free" shape residuals, although 276 this correction generally does not provide additional insights (cf. Meloro *et al.*, 2014). 277 Mitteroecker et al. (2013) recently argued the necessity to take size into account by actually 278 adding, and not removing this variable from subsequent analyses. Our results confirm such 279 assertion thus supporting the combined interpretation of palatal size and shape to infer 280 palaeoecology of fossil species.

Fossil genera *Eucyon* and *Cynotherium* cluster well within the morphological
variation of extant Canini confirming previous taxonomic observations on their affinities
(Rook, 2009; Lyras *et al.*, 2010). The Principal Component plot shows similar scores
between these taxa and the extant jackals, both clustering within the range of the side-striped
jackal (Fig. 2). Consequently, the dietary reconstruction as specialist hunter of small prey fits
well with previous attempts for the *Cynotherium* (cf. Abbazzi *et al.*, 2005; Lyras *et al.*, 2006)
and underlines the strong affinity of *Eucyon* (at least for the species *E. adoxus*) with jackals.

288 Dietary reconstruction for Plio-Pleistocene dogs confirms the puzzling evolution of 289 the Etruscan wolf (Canis etruscus) and the coyote-like Canis arnensis while supporting the 290 hypercarnivorous traits of Lycaon falconeri, C. antonii and C. africanus (cf. Rook, 1994; 291 Tedford et al., 2009). Both C. etruscus and C. arnensis specimens occupy more than one 292 dietary classification in agreement with previous studies (Cherin *et al.*, 2014; Flower & 293 Shreve, 2014; Meloro, 2011). However, there is a clear size partitioning with the Arno dog 294 being classified as small-medium, while only one C. etruscus is predicted as small prey with 295 the others grouped into large prey category. Due to ecological character displacement, it is 296 possible that morphological variation in these taxa was broad and influenced by presence or 297 absence of larger competitors (García & Virgós, 2007).

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298	Diet of the large American dire wolf fits consistently with previous palaeoecological
299	reconstructions (Anyonge & Baker 2006; Meloro, 2011, 2012), while new insights emerge
300	for Canis chihliensis from the lower Pleistocene of China. Tong et al. (2012) identified a
301	mosaic of features combining hypercarnivorous dentition with a relatively small size
302	compared to the grey wolf. Consequently, the size constraint on hunting behaviour supports
303	our prediction of C. chihliensis as an adaptable hunter within the medium category (cf. dingo,
304	see also Fig. 2). For the middle Pleistocene C. mosbachensis a large size categorisation also
305	seems likely based on its morphofunctional similarity to the grey wolf (cf. Flower & Shreve,
306	2014). Diet prediction for the wolf of Romanelli cave also fits within the category "Medium".
307	Although Sardella et al. (2014) confirmed its taxonomic affinity to the grey wolf, they also
308	pointed out how its smaller size confounded previous taxonomic attempts of this species into
309	golden jackal or C. mosbachensis. The grey wolf is highly flexible in size and ecology
310	(Sillero-Zubiri et al., 2004). Such flexibility has been observed in prehistoric specimens
311	(Flower & Shreve, 2014) as well as ancestral forms supporting possible ecogeographical
312	differentiation in the past. Comfortably the fossil grey wolf from Spain is predicted as large
313	prey specialist.

The enigmatic *Canis* cf. *mesomelas* from Koobi Fora deserves a separate note. Werdelin & Lewis (2005) and Werdelin & Peigné (2010) reviewed the rich Plio-Pleistocene East African carnivore fauna. Taxonomy of jackals is not clear yet and there seems to be evidence for different ecomorphotypes in hominin fossil sites. Our analysis suggests the Koobi Fora specimen being adapted for hunting small-sized prey. Interestingly, the UPGMA analysis (Fig. 5) supports shape similarity not with extant jackals, but with the Mio-Pliocene genus Eucyon suggesting that it was a distinct (but ecologically equivalent to the extant jackal) morphotype.

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3	322	For the other taxa, the UPGMA cluster analysis shows a mixed signal based on shape
5	323	data. P4 and M1 morphology are phylogenetic characters in Canini (Tedford et al., 2009)
7 8	324	although the presented UPGMA (Fig. 5) cannot disentangle the ecological from the
9 10	325	phylogenetic signal (cf. Meloro, 2011). The clustering of C. africanus within Lycaon-Cuon
11 12 13	326	confirms the grouping proposed by Rook (1994). However, the palate of Lycaon falconeri
14 15	327	from Valdarno and that of C. antonii are highly distinct from C. africanus. Ecogeographical
16 17	328	and temporal variation could explain such a pattern even if larger and more complete sample
18 19	329	is needed to prove this assertion. The grouping of <i>E. adoxus</i> with the jackal from Koobi Fora
20 21	330	suggests how distinct the morphology is from these Plio-Pleistocene forms with no extant
22 23 24	331	relatives, even if their smaller size supports ecological similarities with jackals and coyotes.
25 26	332	Cynotherium is also enigmatically positioned (although outside of the wolf cluster) while the
27 28	333	cluster of C. etruscus with C. adustus also does not support the wolf phylogenetic hypothesis
29 30	334	(cf. Tedford et al., 2009). Interestingly, recent research on African jackals supports the
31 32 33	335	identification of a wolf North African subspecies (Canis lupus lupaster) that was
34 35	336	morphologically ascribed to the golden jackal (Gaubert et al., 2013) suggesting how puzzling
36 37	337	morphological characters can be not only in fossil but also in extant species. The Romanelli
38 39	338	grey wolf is an outgroup within the wolf cluster while the dire wolf is grouped with the dingo
40 41 42	339	and grey wolf. Extant Lycaon and Cuon clusters together consistently with their
42 43 44	340	hypercarnivorous feeding habits.
45 46 47	341	Members of Canini clearly occupied a broad range of ecological niches since the
48 49	342	Pliocene then differentiating during Early Pleistocene with the evolution of modern taxa
50 51	343	(Sotnikova & Rook, 2010). Such a rapid differentiation resulted in a high flexibility of
52 53 54	344	ecomorphological skull traits whose combination provide robust palaeoecological insights.
55 56	345	

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References

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52 52	
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55	
56	
57	
58	
59	
60	

368	Abbazzi, L., Arca, M., Tuveri, C., Rook L. & (2005). The endemic canid Cynotherium
369	(Mammalia, Carnivora) from the Pleistocene deposits of Monte Tuttavista (Nuoro,
370	Eastern Sardinia). Riv. Ital. Paleontol. S. 111, 493-507.
371	Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: Ten years of
372	progress following the 'revolution'. Ital. J. Zool. 71, 5–16.
373	Adams, D. C., Rohlf, F. J., & Slice, D. E. (2013). A field comes of age: geometric
374	morphometrics in the 21st century. Hystryx, the Italian Journal of Mammalogy
375	24, 7–14.
376	Andersson, K. (2005). Were there pack-hunting canids in the Tertiary, and how can we
377	know? <i>Paleobiology</i> 31 , 56–72.
378	Anyonge, W., & Baker, A. (2006). Craniofacial morphology and feeding behavior in Canis
379	dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316.
379 380	dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a
379 380 381	 dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. Palaeogeogr., Palaeoclimatol., Palaeoecol. 44, 117–
379 380 381 382	dirus, the extinct Pleistocene dire wolf. <i>J. Zool.</i> 269 , 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. <i>Palaeogeogr., Palaeoclimatol., Palaeoecol.</i> 44 , 117–139.
379 380 381 382 383	 dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. Palaeogeogr., Palaeoclimatol., Palaeoecol. 44, 117–139. Azzaroli, A., De Giuli, C., Ficcarelli, G., & Torre, D. (1988). Late Pliocene to early mid-
379 380 381 382 383 383	 dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. Palaeogeogr., Palaeoclimatol., Palaeoecol. 44, 117–139. Azzaroli, A., De Giuli, C., Ficcarelli, G., & Torre, D. (1988). Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. Palaeogeogr.,
379 380 381 382 383 384 385	 dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. Palaeogeogr., Palaeoclimatol., Palaeoecol. 44, 117–139. Azzaroli, A., De Giuli, C., Ficcarelli, G., & Torre, D. (1988). Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeoecol. 66, 77–100.
379 380 381 382 383 384 385 386	 dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. Palaeogeogr., Palaeoclimatol., Palaeoecol. 44, 117–139. Azzaroli, A., De Giuli, C., Ficcarelli, G., & Torre, D. (1988). Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeogeogr., Biknevicius, A. R. and Ruff, C. B. 1992. The structure of the mandibular corpus and its
 379 380 381 382 383 384 385 386 387 	 dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. Palaeogeogr., Palaeoclimatol., Palaeoecol. 44, 117–139. Azzaroli, A., De Giuli, C., Ficcarelli, G., & Torre, D. (1988). Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeoecol. 66, 77–100. Biknevicius, A. R. and Ruff, C. B. 1992. The structure of the mandibular corpus and its relationship to feeding behaviors in extant carnivorans. J. Zool. 228, 479–507.
 379 380 381 382 383 384 385 386 387 388 	 dirus, the extinct Pleistocene dire wolf. J. Zool. 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. Palaeogeogr., Palaeoclimatol., Palaeoecol. 44, 117–139. Azzaroli, A., De Giuli, C., Ficcarelli, G., & Torre, D. (1988). Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. Palaeogeogr., Palaeoclimatol., Palaeoecol. 66, 77–100. Biknevicius, A. R. and Ruff, C. B. 1992. The structure of the mandibular corpus and its relationship to feeding behaviors in extant carnivorans. J. Zool. 228, 479–507. Bookstein, F. L. 1989. 'Size and Shape': a comment on semantics. Syst. Zool. 38,173–180.
 379 380 381 382 383 384 385 386 387 388 389 	 dirus, the extinct Pleistocene dire wolf. <i>J. Zool.</i> 269, 309–316. Azzaroli, A. (1983). Quaternary Mammals and the End-Villafranchian Dispersal event - a turning point in the history of Eurasia. <i>Palaeogeogr., Palaeoclimatol., Palaeoecol.</i> 44, 117–139. Azzaroli, A., De Giuli, C., Ficcarelli, G., & Torre, D. (1988). Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. <i>Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeogeogr., Palaeoclimatol., Palaeoecol.</i> 66, 77–100. Biknevicius, A. R. and Ruff, C. B. 1992. The structure of the mandibular corpus and its relationship to feeding behaviors in extant carnivorans. <i>J. Zool.</i> 228, 479–507. Bookstein, F. L. 1989. 'Size and Shape': a comment on semantics. <i>Syst. Zool.</i> 38,173–180. Bookstein, F. L. 1991. Morphometric tools for landmark data. Geometry and Biology.

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30	
57	
58	
59	
60	

391	Brugal, J.P., & Boudadi-Maligne, M. (2010). Quaternary small to large canids in Europe:
392	taxonomic status and biochronological contribution. Quat. Int. 243, 171-182
393	Caumul, R., & Polly, P.D. (2005). Phylogenetic and environmental components of
394	morphological variation: skull, mandible and molar shape in marmots (Marmota,
395	Rodentia). Evolution 59, 2460–2472.
396	Cherin, M., Bertè, D.F., Rook, L., & Sardella, R. (2014). Re-defining Canis etruscus
397	(Canidae, Mammalia): a new look into the evolutionary history of Early Pleistocene dogs
398	supported by the outstanding fossil record from Pantalla (Perugia, central Italy). J.
399	Mamm. Evol. 21 , 95–110.
400	Christiansen, P., & Adolfssen, J.S. (2005). Bite forces, canine strength and skull allometry in
401	carnivores (Mammalia, Carnivora). J. Zool. 266, 133–151.
402	Christiansen, P., &Wroe, S. (2007). Bite forces and evolutionary adaptations to feeding
403	ecology in carnivores. <i>Ecology</i> 88 , 347–358.
404	Clutton-Brock, J., Corbet, G.B., & Hills, M. (1976). A review of the family Canidae, with a
405	classification by numerical methods. Bulletin of the British Museum (Natural History),
406	Zoology 29 ,119–199.
407	Damasceno, E. M. Hignst-Zaher, E., & Astúa, D. (2013). Bite force and encephalization in
408	the Canidae (Mammalia: Carnivora). J. Zool. 290, 246–254.
409	Flower, L.O.H., & Shcreve, D.C. (2014). An investigation of palaeodietary variability in
410	European Pleistocene canids. Quat. Sci. Rev. in press.
411	García, N., & Virgós, E. (2007). Evolution of community composition in several carnivore
412	paleoguilds from the European Pleistocene: the role of interspecific competition. Lethaia
413	40 , 33–44.

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16
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47
48
49
50
50
51
52
53
54
54
55
56
57
58
50
59
60

414	Gaubert, P., Bloch, C., Benyacoub, S., Abdelhamid, A., Pagani, P. et al. (2012). Reviving the
415	African wolf Canis lupus lupaster in North and West Africa: a mitochondrial lineage
416	ranging more than 6,000 km wide. <i>PLoS ONE</i> 7(8) , e42740.
417	Gese, E.M., Rongstad O.J., & Mytton W.R. (1988). Relationship between coyote group size
418	and diet in Southeastern Colorado. J. Wildl. Manage. 52, 647-653.
419	Gittleman, J. L., & Van Valkenburgh, B. (1997). Sexual size dimorphism in the canines and
420	skulls of carnivores: effects of size, phylogeny, and behavioural ecology. J. Zool., Lond.
421	242 , 97–117.
422	Kurtén, B. (1974). A history of coyote-like dogs (Canidae, Mammalia). Acta Zool. Fenn. 140,
423	1-38.
424	Letnic, M., Ritchie, E.C., & Dickman, C.R. (2012). Top predators as biodiversity regulators:
425	the dingo Canis lupus dingo as a case study. Biol. Rev. 87, 390-413.
426	Lindbald-Toh K., et al. (2005). Genome sequence, comparative analysis and haplotype
427	structure of the domestic dog. <i>Nature</i> 438 , 803–819.
428	Lingle, S. (2002). Coyote predation and habitat segregation of white-tailed deer and mule
429	deer. Ecology 83 , 2037–2048.
430	Lawing, A. M., & Polly, P.D. (2009). Geometric morphometrics: recent applications to the
431	study of evolution and development. J. Zool. 280, 1–7.
432	Lyras, G.A., van der Geer, A.A.E., Dermitzakis, M., & De Vos, J. (2006). Cynotherium
433	sardous, an insular canid (Mammalia: Carnivora) from the Pleistocene of Sardinia (Italy),
434	and its origin. J. Vert. Paleontol. 26, 735–745.

1		
2 3	435	Lyras, G., van Der Geer, A.A.E., Rook, L. 2010. Body size of insular carnivores: evidence
4 5 6	436	from the fossil record. J. Biogeogr. 37, 1007–1021.
7 8	437	Martínez-Navarro, B., & Rook, L. (2003). Gradual evolution in the African hunting dog
9 10 11	438	lineage systematic implications. C.R. Palevol 2, 695–702.
12 13 14	439	Meloro, C. (2011). Feeding habits of Plio-Pleistocene large carnivores as revealed by the
15 16	440	mandibular geometry. J. Vert. Paleontol. 31, 428-446.
17 18 19	441	Meloro, C. (2012). Mandibular shape correlates of tooth fracture in extant Carnivora:
20 21	442	implications to inferring feeding behaviour of Pleistocene predators. Biol. J. Linn. Soc.,
22 23 24	443	106, 70–80.
25 26 27	444	Meloro, C., Raia, P., Piras, P., Barbera, C., & O'Higgins. P. (2008). The shape of the
28 29	445	mandibular corpus in large fissiped carnivores: allometry, function and phylogeny. Zool.
30 31 32	446	J. Linn. Soc. 154, 832–845.
33 34	447	Meloro, C., & O'Higgins, P. (2011). Ecological Adaptations of mandibular form in fissiped
35 36 37	448	carnivore. J. Mammal. Evol. 18, 185–200.
38 39 40	449	Meloro, C., Cáceres, N., Carotenuto, F., Sponchiado J, Melo GL. Passaro, F. & Raia, P.
40 41 42	450	(2014). In and out the Amazonia: evolutionary ecomorphology in howler and capuchin
43 44 45	451	monkeys. Evolutionary Biology 41, 38–51.
46 47	452	Mitteroecker, P., Gunz, P., Windhager, S., & Schaefer K. (2013). A brief review of shape,
48 49 50	453	form, and allometry in geometric morphometrics, with applications to human facial
51 52	454	morphology. Hystrix - Italian Journal of Mammalogy 24, 59-66.
53 54 55	455	Palmqvist, P. Arribas, A., & Martinez-Navarro, B. (1999). Ecomorphological study of large
56 57 58 59 60	456	canids from the lower Pleistocene of southeastern Spain. <i>Lethaia</i> , 32 , 75–88.

45	Rohlf, F. J. 2013a. tpsDig2 ver.2.16. Ecology & Evolution, SUNY at Stony Brook.
45	Rohlf, F. J. 2013b. tpsRelw ver.1.53. Ecology & Evolution, SUNY at Stony Brook.
45	Rohlf, F.J., & Slice, D.E. (1990). Extensions of the Procrustes method for the optimal
46	superimposition of landmarks. <i>Syst. Zool.</i> 39 , 40–59.
46	Rook, L. (1992). "Canis" monticinensis sp. nov., a new Canidae (Carnivora, Mammalia)
46	from the late Messinian of Italy. <i>Boll. Soc. Paleontol. I.</i> 31 , 151–156.
46	Rook, L. (1994). The Plio-Pleistocene Old World Canis (Xenocyon) ex. gr. falconeri, Boll.
46	4 Soc. Paleontol. I. 33 , 71–82.
46	5 Rook, L. (2009). The wide ranging genus <i>Eucyon</i> Tedford & Qiu, 1996 (Mammalia,
46	6 Carnivora, Canidae) in Mio-Pliocene of the Old World. <i>Geodiversitas</i> 31 , 723–743.
46	7 Rook, L., & Azzaroli Puccetti, M.L. (1996). Remarks on the skull morphology of the
46	8 endangered Ethiopian jackal, <i>Canis simensis</i> Rüppel, 1838. <i>Memorie Fisiche della</i>
46	9 Accademia Nazionale dei Lincei, ser. 9 (7), 277–302.
47	Rook, L., & Torre, D. (1996). The wolf event in western Europe and the beginning of the
47	1 Late Villafranchian. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 8, 495–
47	2 501.
47	Rook, L., & Martínez-Navarro, B. (2010). Villafranchian: The long story of a Plio-
47	Pleistocene European large mammal biochronologic unit. <i>Quat. Int.</i> 219 , 134–144.
47	5 Rueness, E.K., Asmyhr, M.G., Sillero-Zubiri, C., Macdonald, D.W., Bekele, A., et al. (2011).
47	5 The cryptic African wolf: <i>Canis aureus lupaster</i> is not a golden jackal and is not
47	endemic to Egypt. <i>PLoS ONE</i> 6 (1), e16385.Sacco, T. and Van Valkenburgh, B. 2004.
47	Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). J.
47	9 Zool. 263 , 41–54.

2
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3
4
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45
46
40
47
48
49
50
51
52
52
23
54
55
50
90
57
58
50
59
60

480	Sardella, R., & Palombo, M.R. (2007). The Plio-Pleistocene boundary: which significant for
481	the so-called "wolf-event"? Evidence from Western Europe. Quaternaire 18, 65–71.
482	Sardella, R., Bertè, D., Lurino, D.A., Cherin, M., & Tagliacozzo, M. (2014). The wolf from
483	Grotta Romanelli (Apulia, Italy) and its implications in the evolutionary history of Canis
484	lupus in the Late Pleistocene of Southern Italy. Quat. Int. 328-329, 179-195.
485	Sillero-Zubiri, C. Hoffmann, M. & Macdonald, D.W. (2004). Canids: Foxes, Wolves, Jackals
486	and Dogs. Status Survey and Conservation Action Plan. IUCN/SSC Canid Specialist
487	Group.
488	Slater, G., Dumont, E. R., & Van Valkenburgh, B. (2009). Implications of predatory
489	specialization for cranial form and function in canids. J. Zool. 278, 181–188.
490	Sotnikova, M.V., Rook, L. 2010. Dispersal of the Canini (Mammalia, Canidae: Caninae)
491	across Eurasia during the Late Miocene to Early Pleistocene. Quat. Int. 212, 86–97.
492	Tedford, R. H., Taylor, B. E., & Wang X. (1995). Phylogeny of the Canidae (Carnivora:
493	Canidae): the living taxa. Am. Mus. Novit. 3146, 1–37.
494	Tedford, R. H., Wang, X., & Taylor, B. E. (2009). Phylogenetic systematics of the North
495	American fossil Caninae (Carnivora: Canidae). B. Am. Mus. Nat. Hist. 325, 1–218.
496	Tong, H., Hu, N., & Wang, X. (2012). New remains of Canis chihliensis from
497	Shianshenmiazoui, a lower Pleistocene site in Yanguai, Hebei. Vertebrat. Palasiatic. 50,
498	335–360.
499	Torre, D., Ficcarelli, G., Masini, F., Rook, L., & Sala, B. (1992). Mammal dispersal events in
500	the Early Pleistocene of Western Europe. Courier Forschungs-Institut Senckenberg 153,
501	51–58.

502	Torre, D., Abbazzi, L., Bertini, A., Fanfani, F., Ficcarelli, G., Masini, F., Mazza, P., & Rook,
503	L. (2001). Structural changes in Italian Late Pliocene - Pleistocene large mammal
504	assemblages. Boll. Soc. Paleontol. I. 40, 303–306.
505	Van Valkenburgh, B. (1991). Iterative evolution of hypercarnivory in canids (Mammalia:
506	Carnivora): evolutionary interactions among sympatric predators. Paleobiology 17, 340-
507	362.
508	Van Valkenburgh, B. (1989). Carnivore dental adaptations and diet: a study of trophic
509	diversity within guilds. In Carnivore Behavior, Ecology, and Evolution, Volume 1: 410-
510	436. Gittleman, J.L. (Ed.), Cornell University Press, Ithaca, New York.
511	Van Valkenburgh, B., & Koepfli, K. (1993). Cranial and dental adaptations for predation in
512	canids. Symposia of the Zoological Society of London 65, 15–37.
513	Van Valkenburgh, B. V. Sacco, T., & Wang, X. (2003). Pack hunting in Miocene
514	borophagine dogs; evidence from craniodental morphology and body size. B. Am. Mus.
515	Nat. Hist. 279, 147–162.
516	Van Valkenburgh, B., Wang, X., Damuth, J. (2004). Cope's rule, hypercarnivory, and
517	extinction in North American canids. Science 306 , 101–104.
518	Werdelin, L. & Lewis, M.E. (2005). Plio-Pleistocene Carnivora of eastern Africa: species
519	richness and turnover patterns. Zool. J. Linn. Soc. 144, 121-144.
520	Werdelin, L. & Peigné, S. (2010). Carnivora, Chapter: 32. In Cenozoic mammals of Africa:
521	603-657. Werdelin, L., & Sanders, W.J. (Eds.), University of California Press.
522	Zelditch, M. L. Swiderski, D. L., & Sheets, H. D. (2004). Geometric Morphometrics for
523	Biologists: A Primer. Second Edition. Elsevier.

2 3 4	524	Figures Legend
5 6 7	525	Figure 1 Skull of <i>Canis adustus</i> showing the landmark locations placed on each specimen.
8 9	526	(1) tip of the snout defined by middle point between the first two frontal incisors, 2) posterior
10 11	527	tip of 3rd incisor, 3) anterior tip of canine, 4) posterior tip of canine, (5) anterior tip of the
12 13 14	528	third premolar, (6, 7, 8, 9, 10) outline of carnassial tooth, (11, 12) cusps of molar, (13)
15 16	529	anterior tip of molar, (14) posterior tip of molar, (15) junction of the stiff and hard palate. The
17 18	530	distance between 3 and 4 describe canine length. The distance between 8 and 10 describe
19 20	531	carnassial tooth length. The distance between 1 and 15 describes snout length. Deviation of
21 22 23	532	the specimens analysed from the consensus configuration of landmarks are shown below the
24 25	533	skull. Scale bar equals 1cm.
26 27 28	534	
29 30 31	535	Figure 2 Plot of the first and second principal components. Thin-plate spline diagrams
32 33	536	illustrate patterns of landmark displacements along each warp. Triangles indicate canids in
34 35	537	the large dietary category, ellipsoid indicate canids in the medium dietary category and
36 37 28	538	circles indicate canids in the small dietary category. Crosses and stars indicate fossil
39 40	539	specimens with an unknown diet category. Below deformation grids from positive to negative
41 42 43	540	RW scores.
44 45 46	541	
47 48	542	Figure 3 (a) Box plot showing differences in natural log transformed centroid size between
49 50	543	diet categories of extant specimens of canid skull (the outlier in the "Medium Prey" category
51 52 53	544	is a specimen of <i>C. latrans</i>); (b) skull shape deformation related to size from the smallest (<i>C.</i>
53 54 55	545	mesomelas) to the largest (C. dirus) canid species. Values in parentheses are ln centroid size.
56 57 58	546	

Figures Legend

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2 3 4	547	Figure 4 Plot of the first two discriminant functions (DF) extracted from a combination of
5 6	548	shape and size variables. Extant specimens are labelled according to their diet categorisation.
7 8	549	Fossil specimens are labelled individually. Below deformation grids from positive to negative
9 10	550	DF scores.
12 13	551	
14 15	552	Figure 5 UPGMA Cluster analysis obtained on procustes distances of averaged sample for
16 17	553	23 canid species.
18 19 20	554	
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50 51 52	565	
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568	Tables Legend
569	
570	Table 1 Skull sample sizes of extant and fossil canid species together with assigned dietary
571	grouping. *Includes subspecies (Canis lupus gigas and Canis lupus pambasileus); **
572	includes subspecies (<i>Cuon alpinus dukhnensis</i> and <i>Cuon alpinus javanicus</i>). Small =
573	mesocarnivore feeding on small prey, medium = mesocarnivore feeding on medium prey,
574	large = hypercarnivore feeding on large prey.
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577	Table 2 Dietary classification provided for fossil specimens using discriminant function
578	analysis. P (D G) is the probability of membership in a group given the discriminant
579	function score. P (G D) is the posterior probability based on the sample employed to
580	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)

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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)



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

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

1 2 3 4 5	Lycaon falconeri	Fossil	1
4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 21 22 23 24 25 26 27 28 29 30 31 32 33			
34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60		JZO submitt	ed manuscript

TABLE 2

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

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

Species	Catalogue	Locality	Museum	Period
Canis latrans	2003.130.05	Unknown	RMS, Edinburgh	Extant
Canis latrans	2003.130.07	Unknown	RMS, Edinburgh	Extant
Canis latrans	2003.130.08	Unknown	RMS, Edinburgh	Extant
Canis latrans	2.3.7.4	Penington British Columbia	NHM, London	Extant
Canis latrans	94.5.9.4	Chapham New Mexico	NHM, London	Extant
Canis latrans	98.12.21.1	Chihout Mt. British Columbia	NHM, London	Extant
Canis latrans	40.82.1	San Quintin Lower California Mexico	NHM, London	Extant
Canis latrans	2.82.2	Jouchood Hillo Asauriboia New Mexico	NHM, London	Extant
Canis latrans	10909	Hansoon Lagoon L.C. Mexico	NHM, London	Extant
Canis lupus	an4560	Unknown	Glasgow	Extant
Canis lupus pambasilens	19.7.15.4	McMillan River Youkon Territories	NHM, London	Extant
Canis lupus gigas	63.2.24.51	Fort Langley New Wesminster British Columbia	NHM, London	Extant
Canis lupus gigas	63.2.24.31	British Columbia	NHM, London	Extant
Canis lupus pambasilens	19.7.15.5	McMillan River Youkon Territories	NHM, London	Extant
Canis lupus	1852.3.24.4_ 168.c.	Azraq, Jordan	NHM, London	Extant
Canis lupus arabs	84.1312	Unknown	NHM, London	Extant
Canis lupus arctos	86.1595	Ellesmere island, Canada	NHM, London	Extant
Canis lupus occidentalis	1855.5.14.11	"Arctic" America, Canada	NHM, London	Extant
Canis lupus pallipes	1863.12.28.1 4	India	NHM, London	Extant
Canis lupus chanco	1875.4.10.1_ 1670.a.	Near Tshommeriri lake, Tibet	NHM, London	Extant
Canis lupus	1935.8.5.1	Bosnia, Yugoslavia	NHM, London	Extant
Canis lupus	1937.2.10.2	Abrantos, S. of Taqus, Portugal	NHM, London	Extant

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

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

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

