Ecomorphology of radii in Canidae: Application to fragmentary fossils from Plio-Pleistocene hominin assemblages

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Fragmentary long bone material from fossil Carnivora is rarely considered to support palaeoenvironmental reconstructions. Here, we use morphometry of the radius in extant carnivorans of the dog family (Canidae) to reconstruct the palaeobiology of extinct canids from Olduvai Gorge, Tanzania (Bed I and II) and Koobi Fora, Kenya. We use radius morphometrics to predict adaptation to prey size and introduce a new method for quantifying canid habitat adaptations based on the geographic distributions of the extant species sampled. Linear Discriminant Function Analyses (DFA) and cluster neighbour-joining algorithms are employed to investigate radial morphometrics as described by 29 linear measurements. Results of our analyses suggest that a phylogenetic signal is present in radial morphometrics, even if it does not allow us to accurately discriminate among genera. A binary prey size categorisation of "small-medium" versus "large" prey can be more accurately predicted than a habitat categorisation scheme (Open, Mixed, Closed). The East African fossil specimens examined show morphometric affinities with the golden jackal (*Canis aureus*) and coyote (*Canis latrans*) and are likely attributable to the genus *Canis*. Fragmentary fossil specimens from Olduvai Gorge are predicted as habitat generalists (Open for Bed I and Mixed for Bed II) adapted for hunting small-medium prey, whereas the specimen from Koobi Fora was predicted as inhabiting mixed habitats and adapted for killing large prey. This study supports the inclusion of fossil Canidae in palaeoecological analyses attempting to clarify the palaeoenvironment of early hominin fossil sites.

Key words: Mammalia, Canidae, *Canis*, habitat adaptation, palaeoenvironment, predation, Plio-Pleistocene, Kenya.

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Introduction

There is increasing evidence that, to some extent, morphological variability of long bones in mammalian carnivores reflects not only behavioural adaptations but also specialisation to different environments (Van Valkenburgh 1985, 1987; Harris and Steudel 1997; Lewis 1997; Meachen-Samuel and Van Valkenburgh 2009; Polly 2010; Meloro 2011b; Walmsley et al. 2012; Meloro et al. 2013). However, the latter intriguing relationship has rarely been explored because carnivorans tend to be secondary consumers, and their preferred habitats are assumed to be influenced directly by the distribution of their prey rather than by specific environmental conditions. Paradoxically, distinct evolutionary events in the history of the members of the order Carnivora are often interpreted in the light of climatic changes and concomitant reorganization of ecosystems (Turner 1990; Van Valkenburgh 1999; Louys 2014), and several palaeontologists have explained the spread of certain carnivoran taxa as a result of environmental changes. A classic example is the so-called "Wolf event" characterised by the spread of modern wolf-like taxa through Eurasia during the Late Pliocene-Early Pleistocene (Rook and Torre 1996). Specifically, Holarctic *Canis* spp. were all considered species adapted to "open" habitats, and their spread at 2.0 Ma was interpreted as being influenced by the expansion of *Artemisia* shrubs steppe environments in Eurasia during this time (Suc et al. 1995).

These studies suggest that a relationship exists between morphological variability and environmental conditions in the members of the order Carnivora. If so, understanding this relationship will provide new insights into the reconstruction of ancient ecosystems on the basis of ecomorphology, studies of which are currently heavily biased towards primary consumers (especially bovids, e.g., Kappelman

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1988; Kappelman et al. 1997; Kovarovic and Andrews 2007; Plummer et al. 2008; White et al. 2009; Bishop et al. 2011).

Recently, Klein et al. (2010), Davis and Calède (2012), and Davis and McHorse (2013) underlined an issue in ecomorphological studies which do not consider phylogenetic signal exhibited by bone morphometry. As such bovid and camelid postcranial morphometry can discriminate taxonomic categories better than ecological ones. In Carnivora, long bone morphology is generally informative of major differences among clades (Van Valkenburgh 1985, 1987; Bertram and Biewener 1990) even if Harris and Steudel (1997) suggested a strong association between hindlimb relative length and prey capture behaviour. For this reason, we restricted our analyses to members of the family Canidae, such that our results can be compared to previous studies that have focused on a single family (cf. Kappelman 1988; Kappelman et al. 1997; Bishop 1999; Elton 2001, 2002; Kovarovic and Andrews 2007; Plummer et al. 2008; Klein et al. 2010; Davis and McHorse 2013; Louys et al. 2013; Meloro et al. 2013). Furthermore, as there have been no attempts to explore radial morphometry in Carnivora to date, the restriction of our sample to Canidae is a reasonably conservative approach.

We present a series of morphometric analyses to interpret the ecological adaptations as well as phylogenetic affiliation of the Canidae, and use these to examine the taxonomy and palaeobiology of three fossil radii from Olduvai Bed I-II and Koobi Fora.

The aim of our study is twofold: (i) to explore if fragmentary fossil material of Carnivora can be considered for ecomorphological analyses; and (ii) to compare the use of morphometric analyses to predict phylogenetic affiliation versus ecological adaptations.

We also apply a new way of quantifying ecological adaptations related to environmental variables (Meloro et al. 2013). Previous authors have suggested the use of several habitat categories (4 or 3: Kappelman 1988; Bishop 1994, 1999; Kappelman et al. 1997; Elton 2001, 2002) in classifying the habitat adaptations of comparative extant species. These categorisations are certainly useful, but they can be subjective with regards to researcher interpretations of vegetation and habitats. Similar limitations have been identified explicitly for community-based palaeoecological reconstructions (Louys et al. 2009, 2011). We use a Geographic Information System (GIS) based methodology to simplify specimen ecological classification based on geographic distribution of species (cf. Meloro et al. 2013).

Institutional abbreviations.—KNM-ER, palaeontology collection, Kenya National Museum, Nairobi, Kenya; NHMUK, Natural History Museum, London, UK; OLD FLKI-II, FLKNI, palaeontology collection, Kenya National Museum, Nairobi, Kenya.

Other abbreviations.—DF, Discriminant Function; df, degrees of freedom; DFA, Linear Discriminant Function Analysis; p, probability value; WWF, World Wildlife Fund; GIS, Geographic Information System.

Material and methods

Sample.—Ninety-two radii belonging to 24 extant species of Canidae were examined (full specimen list available from the authors). The specimens are housed in The Natural History Museum, London and the Royal Museum for Central Africa, Tervuren. Twenty-nine linear measurements were collected by one of us (CM) to avoid inter-observer bias. The measurements describe radius length and robusticity together with distinctive features of the proximal and distal epiphyses. These measurements are generally informative of size and describe function related to muscle attachments (Fig. 1). A measurement error survey was also performed measuring the same bone three times at different temporal intervals (cf. DeGusta and Vrba 2003) to ensure that the selected measurements are repeatable (Table 1).

The twenty-nine linear measurements described in Table 1 were also collected from the fossils. The fossil canids are represented by one complete left specimen from Koobi Fora (KNM-ER 3741/ER75Fs765, from East Rudolf 116 Ph.1534 above Tulu Bor probably deposited between 2.6 and 2.0 Ma),

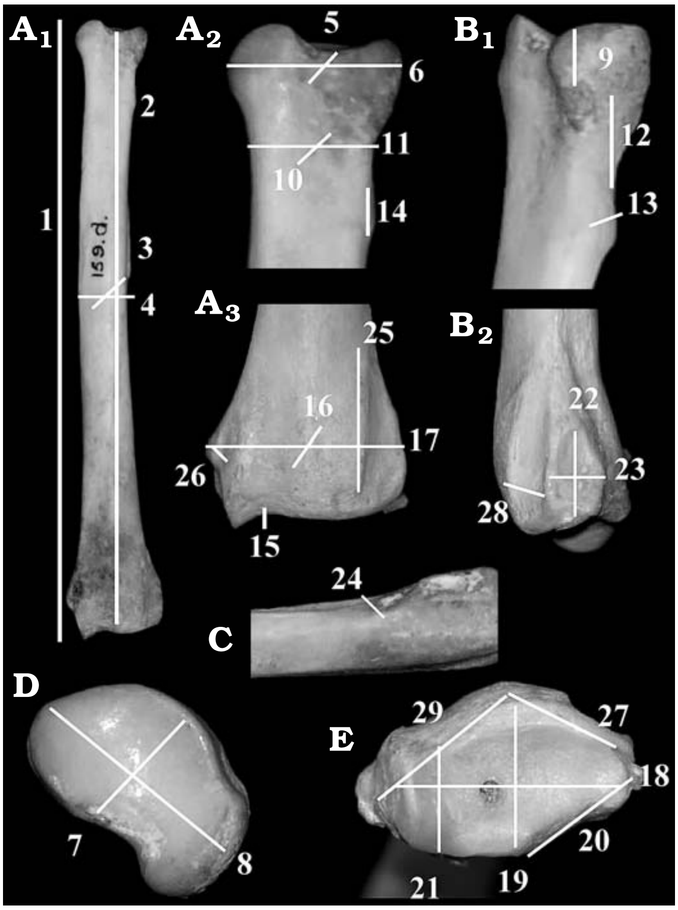

Fig. 1. Measurement scheme for the canid radius, illustrated using a left radius of *Cuon alpinus*, NHMUK M1888.2.5.22_159.d, in posterior view (A_1), proximal (A_2) and distal (A_3) end; lateral view proximal (B_1) and distal (B_2) end; distal view of radius lower extremity (C), proximal (D) and distal (E) views of radius epiphyses. Not to scale. Explanation of radial measurements 1–29 in Table 1.

Table 1. Radial measurements (partitioned into proximal 3–14 and distal 15–29), showing minimum, maximum, and average error in percentage after three replicas.

Id	Measurement	Description	Min	Max	Average
1	Length	maximum length	0.00	5.38	2.69
2	Ph_L	physiological length with spread calliper	0.18	6.06	3.06
3	Mds LL	midshaft medio-lateral	0.23	6.05	3.07
4	Mds AP	midshaft antero-posterior	0.27	7.18	3.63
5	Max H_mL	maximum medio-lateral head	2.21	7.31	4.09
6	Max_H_AP	maximum antero-posterior head	0.09	0.59	0.31
7	Min_H_AS_ml	minimum medio-lateral head at the articular surface	1.21	7.42	3.91
8	Min_H_AS_AP	minimum antero-posterior head at the articular surface	0.54	4.00	2.09
9	H_Neck	height of the neck	0.07	11.05	5.55
10	ML__Neck	mediolateral of neck	1.19	3.64	2.02
11	AP_Neck	antero-posterior of the neck	0.29	5.10	2.61
12	Max_Neck_L	distance between neck and bicipital tuberosity	0.42	3.85	2.00
13	Bcpt_W	bicipital tuberosity width	0.22	12.21	7.54
14	Bcpt_H	bicipital tuberosity height	0.97	12.70	6.53
15	Styloid_L	length of styloid	1.19	21.43	11.66
16	Dst_LL	distal maximum medio-lateral	0.39	4.69	2.41
17	Dst_Mx_AP	distal maximum antero-posterior	0.17	1.03	0.54
18	ScaphLun_AP	distal articular surface antero-posterior	0.26	2.13	1.24
19	ScaphLun_ML_max	maximum distal articular surface medio-lateral	1.65	6.46	3.61
20	ScaphLunPir_ML	distal articular surface medio-lateral oblique plane	1.14	10.01	5.20
21	Stiloyd_ML	medio-lateral of the styloid	0.35	3.67	1.93
22	Uln_arts_H	ulnar articular surface height	0.54	3.10	1.80
23	Uln_w	ulnar articular surface width	1.25	8.60	4.66
24	Pq_Gr_W	width of pronator quadratus scar	2.76	23.36	12.23
25	BrT_H	height of the extensor carpii tubercle	0.19	11.17	6.08
26	Pr_St_rad	height of the processus styloideus radialis	1.41	12.91	6.84
27	Max_Br_AP	maximum extensor carpi scar width	0.50	20.39	10.29
28	Min_Br_AP	extensor carpi scar width measured between the tubercles	0.76	19.11	9.73
29	Post_Br	antero-posterior measured from the extensor carpi tubercle	0.32	3.70	1.91

a proximal left fragment from Olduvai FLKNI-2, 1.75–1.749 Ma (cf. Fernández-Jalvo et al. 1998; OLD FLKI-II 1220), and a distal right fragment from Olduvai Bed II, 1.7–1.2 Ma (NHMUK M20235; Werdelin and Lewis 2005).

All measurements were collected with an electronic Sylvac 703 calliper with an accuracy of 0.05 mm. Multivariate analyses were performed on log transformed variables to normalise the data. Outliers were identified using box plot and removed, reducing our sample to 89 specimens (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app60-Meloro_Louys_SOM.pdf). A pilot survey performed on raw data measurements showed that the models—especially for discriminant analyses—were less accurate than when data were log transformed, thus confirming recent findings of Meloro et al. (2013) based on measurements of felid humeri. In that case the use of ratios or "size-free" measurements proved to be ineffective in comparison with log transformed variables.

Statistical analyses.—In this study, we restrict statistical analyses to Linear Discriminant Function Analysis (DFA) and cluster analyses. We follow Klein et al. (2010) and Davis and McHorse (2013) in order to predict possible taxonomic affiliation at the genus level from morphometric data.

Following DeGusta and Vrba (2003, 2005a, b) we considered our log transformed linear measurements as possible predictors of taxonomic categories (genera cf. Klein et al. 2010). Because the number of variables to be analysed was larger than the minimum number of specimens within a group, we conducted a stepwise procedure (Hair et al. 1998; Meloro 2011a; Kovarovic et al. 2011; Meloro et al. 2013) in order to select the fewest and most relevant measurements for classifying canid genera. Linear measurements can be redundant or autocorrelated, and the stepwise procedure is an automated algorithm that selects only the significant variables that improve the accuracy of the final model (Hair et al. 1998). An F probability threshold 0.05–0.10 was considered in order to add ($p < 0.05$) or exclude ($p > 0.10$) variables relevant to the DFA models (cf. Meloro 2011a; Meloro et al. 2013). We report percentage of correctly classified cases only after jack-knife procedures (Kovarovic et al. 2011). We excluded from the analyses several taxa for which only one or two specimens were available restricting the sample size for taxonomic DFA to 81 cases.

Phylogenetic affinities.—The DFA used to discriminate genera was attempted using a stepwise procedure for all the measurements, only proximal (N = 12), and only distal

(N = 14) measurements. These nested analyses allowed us to make taxonomic predictions on fragmentary or damaged fossil specimens. Cluster analysis using average measurements for each species was employed to confirm possible taxonomic similarity between fossil material and a selection of extant species (cf. Lewis 1997, 2008). Cluster analysis was chosen as it allows the detection of affinity between specimens based on morphometric Euclidean distances. Within the cluster analysis, the Neighbour-Joining algorithm was favoured because it provides better cophenetic correlation, more stable groupings, and is ideal for showing possible phylogenetic relationships based on morphometric distances (Klein et al. 2010)

Ecological categories.—We categorised each extant specimen according to species adaptations in hunting prey of different size range as well as habitat. The dietary classifications of Christiansen and Wroe (2007) were considered in order to identify the ability of each species for killing small or large prey. All the omnivore species (e.g., golden jackals, foxes) were categorised as adapted to killing small animals (including the specialist insectivore *Otocyon megalotis*) corresponding to the size of their favourite vertebrate prey (Sillero-Zubiri et al. 2004). Applying this classification scheme, hunters of large prey include the grey wolf (*Canis lupus*), the African hunting dog (*Lycaon pictus*), the dingo (*Canis dingo*), and the dhole (*Cuon alpinus*) whereas all the other species were classified as "small-medium prey" specialists.

In order to create an accurate system of habitat classification, we used maps of the extant species' geographic distribution superimposed on maps of biomes using Geographic Information system. Species-specific range size maps were extracted from Greneyer et al. (2006; shape file for Carnivora) whereas ecoregions were identified using the polygon extracted from WWF world ecoregion map (14 biomes in Olson et al. 2001). Maps of the species' geographic distributions were superimposed on maps of biomes using ESRI Arcview GIS and the percentage of each biome occupied by each species was calculated (cf. Meloro et al. 2013). These percentages were used to classify species into "Open" (when more than 60% of a species range occurred in "grassland" biomes), "Mixed" (when between 60% and 40% of a species' ranges occurred in "grassland" or "forest" biomes), and "Closed" (when more than 60% of a species' ranges occurred in "forest" biomes). We used a threshold of 60% to take into account, to a degree, the uncertainty regarding absolute range size. Indeed, an exact classification of 50% for closed or open biomes rarely occurred, and this may have underestimated the "Mixed" category. According to this classification scheme "Open" adapted taxa include foxes from arid ecosystems (*Vulpes pallida*, *V. rueppelli*, *V. zerda*, *Otocyon megalotis*, and *Alopex lagophus*), South American *Pseudalopex* spp. (*P. culpaeus* and *P. griseus*), jackals (*Canis mesomelas*, *C. aureus*, and *C. adustus*), the dingo (*Canis dingo*), the maned wolf (*Chrysocyon brachyurus*), and the African wild dog (*Lycaon pictus*). The "Mixed" category includes foxes (*Vulpes vulpes*, *V. bengalensis*, and *Urocyon cinereoargenteus*), the South American *Cerdocyon thous*, the grey wolf (*Canis lupus*), and the coyote (*Canis latrans*) whereas "Closed" species comprise the Asiatic dhole (*Cuon alpinus*), the raccoon dog (*Nyctereutes procyonoides*), and the South American *Pseudalopex fulvipes* and *Speothos venaticus*.

DFA was conducted with a stepwise procedure in order to predict the dichotomous category "small-medium prey" versus "large prey" as well as the habitat categories "Open", "Mixed", or "Closed" using linear measurements as predictors. We used DFA in order to obtain comparable results with taxonomic analyses.

Results

Complete sample.—Six discriminant functions (DFs) were extracted after the stepwise procedure selected 12 variables. The first two DFs together explained 88.5% of variance (Table 2). The first DF was highly loaded by physiological length, and on the second DF higher loadings were by distal measurements such as styloid medio-lateral length and maximum extensor carpii scar width, as well as medio-lateral midshaft and measurements related to the radius neck

Table 2. Basic statistics for the discriminant functions used to predict genera under different sample regimes. No Chrys, all species except *Chrysocyon*.

Sample	Function	Wilk's lambda	Chi-Square	df	p	Eigenvalue	% of variance
Overall sample	DF1	0.003	365.795	72	< 0.0001	12.645	69.4
	DF2	0.047	197.235	55	< 0.0001	3.479	19.1
All No Chrys	DF1	0.017	249.329	60	< 0.0001	5.242	60.4
	DF2	0.105	137.621	44	< 0.0001	1.938	22.4
Proximal	DF1	0.056	198.378	42	< 0.0001	3.233	62.8
	DF2	0.239	98.81	30	< 0.0001	1.192	23.1
Proximal No Chrys	DF1	0.105	148.517	30	< 0.0001	2.981	75
	DF2	0.419	57.336	20	< 0.0001	0.423	10.6
Distal	DF1	0.056	200.868	36	< 0.0001	4.338	73.9
	DF2	0.289	81.895	25	< 0.0001	0.874	14.9
Distal No Chrys	DF1	0.084	164.876	25	< 0.0001	3.61	74.9
	DF2	0.386	63.241	16	< 0.0001	0.836	17.4

Table 3. Correlation coefficient of the relationship between selected variables and extracted discriminant functions after different analyses based on the overall sample (N = 92), on a subsample inclusive of all species except *Chrysocyon* (No Chrys, N = 88), or on a subsample of large Canini only (Can, *Canis* spp. + *Lycaon*, N = 36). DF, Discriminant Function; ns, non-significant. For explanation of measurement abbreviations see Table 1.

Id	Measurement	Genera classification			Ecological classification			
		DF1	DF2	DF1 No Chrys	DF1	DF1	DF2	DF1 Can
					Prey size	Habitat		
1	Lenght	ns	ns	ns	0.438	ns	0.294	ns
2	Ph_L	0.457	0.399	0.669	0.424	ns	ns	ns
3	Mds_LL	0.357	0.437	ns	ns	ns	ns	ns
4	Mds_AP	ns	ns	0.571	ns	0.357	ns	ns
5	Max_H_mL	0.333	0.494	0.631	ns	ns	ns	0.535
7	Min_H_AS_ML	ns	ns	ns	0.580	ns	ns	ns
8	Min_H_AS_AP	ns	ns	ns	0.535	ns	ns	ns
10	ML__Neck	0.338	0.271	0.500	ns	ns	ns	ns
11	AP_Neck	0.302	0.402	0.540	ns	ns	ns	ns
12	Max_Neck_L	0.262	0.456	0.543	ns	ns	ns	ns
13	Bcpt_W	ns	ns	ns	ns	ns	ns	ns
14	Bcpt_H	0.24	0.446	0.489	ns	ns	ns	ns
15	Styloyd_ML	0.382	0.558	0.684	ns	ns	ns	ns
16	Dst_LL	ns	ns	ns	0.476	ns	ns	ns
17	Dst_Mx_AP	ns	ns	ns	ns	ns	ns	ns
19	ScaphLun_ML_max	ns	ns	ns	0.555	0.357	ns	ns
20	ScaphLunPir_ML	ns	ns	0.502	ns	ns	ns	0.014
21	Styloid_L	0.285	0.354	ns	ns	ns	ns	ns
23	Uln_w	ns	ns	ns	ns	ns	ns	ns
25	BrT_H	0.393	0.323	0.583	ns	0.019	ns	ns
27	Max_Br_AP	0.403	0.625	0.763	0.596	0.149	ns	ns
28	Min_Br_AP	ns	ns	ns	ns	ns	ns	ns
29	Post_Br	0.324	0.42	0.588	ns	ns	ns	ns

Table 4. Percentage of correctly classified cases after jack-knife analysis for Canidae genera as revealed by different samples. No Chrys, all species except *Chrysocyon.*

	Tribe	All Sample	All No Chrys	Proximal	Proximal No Chrys	Distal	Distal No Chrys
Canis	Canini	78.6	78.6	64.3	67.9	46.4	53.6
Chrysocyon	Canini	100.0	–	100.0	–	100.0	–
Lycaon	Canini	66.7	83.3	66.7	83.3	33.3	50.0
Alopex	Vulpini	80.0	90	70	70.0	80.0	80.0
Otocyon	Vulpini	0.0	25	50	25.0	0.0	25.0
Pseudalopex	Canini	55.6	44.4	55.6	33.3	77.8	66.7
Vulpes	Vulpini	65.0	65.0	45.0	55.0	45.0	40.0

(Table 3). The jack-knife predictions within Canidae were accurate for most of the Canini (*Canis*, *Lycaon*, *Chrysocyon*) and the Arctic fox *Alopex* (Table 4). Because of the unusual position of *Chrysocyon* in DF plots (Fig. 2), its exclusion improved the rate of classification for some large genera (Table 4). However, the model without *Chrysocyon* used the same variables as in the overall analysis and all but three variables loaded on the first DF (Table 3).

The plot of the first two DFs (Fig. 2) clearly shows the dichotomy between genera of the tribe Vulpini and genera of the tribe Canini, with South American *Pseudalopex* clustering with fox-like taxa. The centroid of *Canis* members is well defined within a morphospace region that also included the unknown fossil from Koobi Fora, which is classified within the genus *Canis* for both analyses.

The stepwise procedure selected seven variables (Table 3) as good predictors for the “small-medium prey” or “large” categories, and the discriminant function extracted is significant (Wilk’s lambda = 0.227, df = 7, Chi Square = 110.316, $p < 0.0001$). “Small-medium prey” adapted taxa had a jack-knifed classification rate of 95.7% and “large prey” had a rate of 85.0%. The fossil canid from Koobi Fora was predicted to be adapted to kill “small-medium prey”.

The DFA used to predict the three habitat categorisation schemes is significant even if it does not provide high predicting probabilities. The stepwise procedure selected five variables mostly correlated with DF1 (Table 3; Wilk’s lambda = 0.425, Chi-Square = 67.617, df = 10, $p < 0.0001$), with radius length being the only one associated with the second DF (Wilk’s lambda = 0.681, Chi-Square = 28.466,

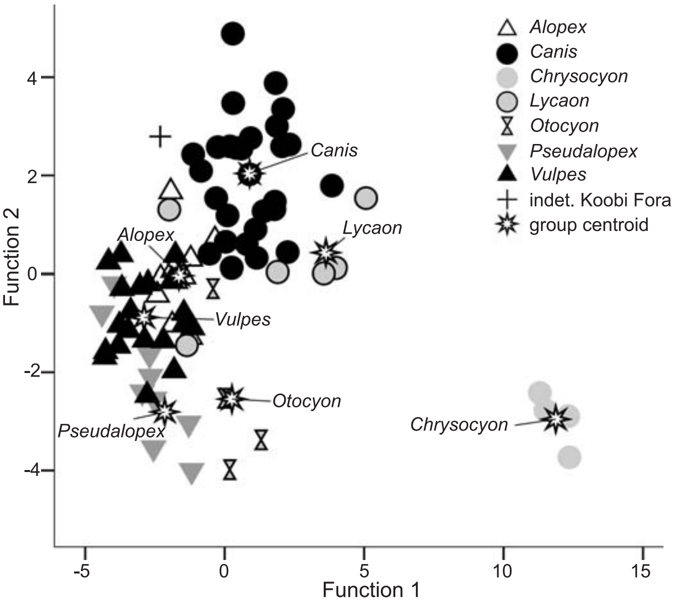

Fig. 2. Plot of the first two linear discriminant functions extracted from a combination of radial measurements used to classify genera within Canidae.

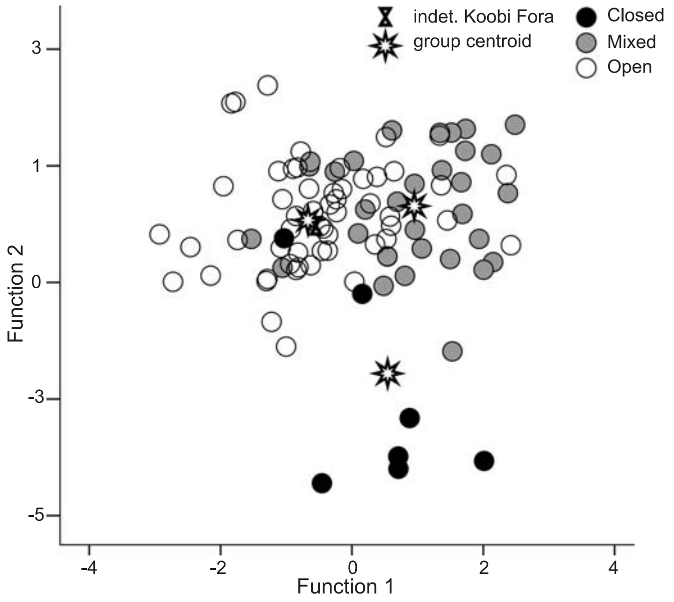

Fig. 3. Plot of the first two linear discriminant functions extracted from a combination of radial measurements used to classify habitat preferences within Canidae.

df = 2, p < 0.0001). Group centroids were well separated on the DF plots but overlap occurred among the categories (Fig. 3). The jack-knife analysis showed some degree of classification accuracy with “Open” correctly predicted 69.1% of the time, “Mixed” 71% correct and “Closed” 71.4% correct. The Koobi Fora specimen was classified as “Open”. In order to improve the accuracy of the habitat classification, we performed a second DFA on a nested set of specimens (only *Canis* spp. and *Lycaon*) that were more similar to the Koobi Fora fossil (cf. Meloro et al. 2013). Although the sample size was greatly reduced (N = 36) and we excluded the “Closed” category, the only DF extracted was significantly loaded by two variables (Wilk’s lambda = 0.323, Chi-Square = 32.81, df = 2, p < 0.0001; Table 3) and predicted “Open” and “Mixed” categories with a higher percentage (76.2% and 85.7% jack-knife prediction, respectively). In this analysis the Koobi Fora specimen was predicted as “Mixed”.

Proximal radius sample.—Seven variables were selected to predict genera based on measurements of the proximal radius. The first two of six significant discriminant functions accounted for 85.9% of variance (Table 2). The first DF was heavily loaded by midshaft measurements as well as maximum mediolateral length of the head (Table 5). Jack-knifed classification rate showed again the unusual morphology of *Chrysocyon* (100% correct classification) and a decrease for *Canis* and *Vulpes* (Table 4). A better percentage of correct classification was attained for *Lycaon* and *Canis* but not for *Pseudalopex* when *Chrysocyon* was excluded from the analysis (Table 4). Without *Chrysocyon* the first two significant DFs explained 85% of variance (Table 2) with DF1 being correlated with most of the same variables as for the complete sample except the substitution of mediolateral midshaft by bicipital tuberosity height (Table 5). The fossil specimen from Olduvai FLK NI was predicted as *Lycaon* in both these analyses whereas the canid from Koobi Fora was again within the range of *Canis*.

When using the “small-medium prey” versus “large prey” classification, correct classification percentages for proximal measurements were very similar to those of measurements from the complete radius. One significant DF was extracted (Wilk’s lambda = 0.41, df = 2, Chi-Square = 71.144, p < 0.0001), and it was dependent on two variables only (Table 5). “Small-medium prey” hunting canids were correctly predicted 88.4% of the cases and “large prey” 100%, with fossils KNM-ER 3741 and OLD FLKI-II 1220 predicted as “large prey”. Because of the discrepancy obtained with the previous analysis, we conducted another DFA on a subsample of large Canini (N = 36). Again one significant DF (Wilk’s lambda = 0.209, df = 2, Chi-Square = 47.719, p < 0.0001) showed correlation with only one variable (Table 4). Jack-knifed classification increased to 100% for both prey categories with the fossil from Olduvai FLKNI being predicted as “small-medium prey” hunter, whereas the specimen from Koobi Fora was classified again as a “large prey” hunter.

The classification of “Open”, “Mixed”, and “Closed” was achieved by one significant DF (Wilk’s lambda = 0.887, df = 2, Chi-Square = 10.087, p = 0.006) loaded by only one variable (Table 5). The jack-knife classification was low for all the three categories (21.8% for “Open”, 67.7% for “Mixed”, 57.1% for “Closed”), and both fossils were ascribed to the category that showed better prediction (“Mixed”). A nested analysis based on large Canini only (*Canis* spp. and *Lycaon*) resulted in one significant DF (Wilk’s lambda = 0.535, df = 2, Chi-Square = 18.781, p < 0.0001) loaded by two variables (Table 3). Prediction accuracy was much higher (85.7% for “Open” and 71.4% for “Mixed”) with the Olduvai specimen being categorised as “Open” and the Koobi Fora fossil as “Mixed”.

Table 5. Correlation coefficients of the relationship between selected variables and extracted discriminant functions for the proximal and distal measurements. Analyses are based based on the overall sample ($N = 92$), on a subsample inclusive of all species except *Chrysocyon* (No Chrys, $N = 88$), or on a subsample of large Canini only (Can = *Canis* spp. + *Lycaon*, $N = 36$). DF, Discriminant Function; ns, non-significant. For explanation of measurement abbreviations see Table 1.

Id	Measurement	Genera classification		Ecological classification			
		DF1	DF1 No Chrys	DF1	DF1 Can	DF1	DF1 Can
				prey size		habitat	
3	Mds_LL	0.881	ns	ns	ns	ns	ns
4	Mds_AP	0.813	0.779	ns	ns	ns	ns
5	Max_H_mL	0.863	0.814	0.922	1.00	ns	0.810
8	Min_H_AS_ml	ns	ns	ns	ns	ns	0.585
9	H_Neck	0.679	ns	0.582	ns	ns	ns
10	ML__Neck	0.725	0.658	ns	ns	ns	ns
11	AP_Neck	0.761	0.732	ns	ns	ns	ns
12	Max_Neck_L	0.741	0.733	ns	ns	ns	ns
14	Bcpt_H	ns	0.691	ns	ns	1.000	ns
15	Styloid_L	0.619	0.621	ns	ns	ns	ns
16	Dst_LL	ns	ns	0.723	ns	ns	ns
17	Dst_Mx_AP	ns	ns	ns	0.903	0.390	0.488
18	ScaphLun_AP	ns	ns	0.868	ns	ns	ns
19	ScaphLun_ML_max	ns	ns	ns	ns	0.418	ns
20	ScaphLunPir_ML	0.627	ns	ns	ns	ns	0.014
21	Styloid_ML	0.843	0.852	ns	ns	ns	0.553
23	Uln_W	ns	ns	ns	ns	ns	ns
25	BrT_H	0.736	0.687	ns	ns	ns	ns
27	Max_Br_AP	0.91	0.938	0.902	ns	0.173	ns
28	Min_Br_AP	ns	ns	ns	0.817	ns	ns
29	Post_Br	0.7	0.704	ns	ns	ns	ns

Distal sample.—In analyses with or without *Chrysocyon*, DFA extracted six significant vectors from the selection of six variables (Tables 2, 5). Both DFA models (Table 5) selected five of the six variables. The jack-knifed percentage of correctly classified cases for genus prediction was low for *Canis* and *Lycaon* as well as for *Otocyon*, but a good degree of accuracy occurred for *Alopex* (Table 3). However, the correct classification increased for both large genera (*Canis* and *Lycaon*) when *Chrysocyon* was excluded, but decreased for *Pseudalopex* and *Vulpes* (Table 3). In all the analyses, the distal fossil fragment from Olduvai Bed II was classified as *Canis*, as was the specimen from Koobi Fora.

Correct classifications for “small-medium prey” and “large prey” taxa were high when distal measurements were considered. With the overall sample, only three variables (Table 5) were selected by the first significant DF (Wilk’s lambda = 0.492, Chi-Square = 72.393, df = 3, $p < 0.0001$) and they provided a jack-knifed classification of 88.4% for “small-medium prey” and 85.0% for “large prey”. The fossils from Olduvai Bed II as well as the specimen from Koobi Fora were classified consistently as “small-medium prey”. The accuracy of prediction improved when only large Canini (*Canis* spp. and *Lycaon*) were considered (100% “small-medium prey”, 90.0% “large prey”), with the only significant DF axis being loaded by two variables (Table 5). Consistent with the previous analysis, both fossils were classified as “small-medium prey” predators.

The “Open”, “Mixed”, and “Closed” categories were predicted by two significant DFs (DF1: Wilk’s lambda = 0.585, df = 8, Chi-Square = 44.162, $p < 0.0001$; DF2: Wilk’s lambda = 0.843, df = 3, Chi-Square = 14.105, $p = 0.003$) but with low jack-knife classification accuracy (60.0% “Open”, 58.1% “Mixed”, 71.4% “Closed”). Three variables were significantly correlated with DF1 (Table 5) and only BrT_H (Height of the Extensor carpii tubercle) with DF2 ($r = 0.05$); both fossils were classified consistently into the “Open” category. DFA performed on the large Canini sample (*Canis* spp. and *Lycaon*) only extracted one DF (Wilk’s lambda = 0.336, df = 3, Chi-Square = 31.122, $p < 0.0001$) loaded on three variables (Table 5). Percentage of jack-knife classification accuracy was high (85.7% for “Open” and 92.9% for “Mixed”) and DF1 classified the Bed II specimen as ”Mixed” and the Koobi Fora as “Open”.

Cluster analyses.—Figures 4, 5, and 6 show neighbour-joining clusters performed on the species mean including the fossil canids from Olduvai and Koobi Fora. Bootstrap supports a robust grouping of the small Vulpini: *Vulpes rueppelli*, *V. pallida*, and the fennec (*V. zerda*). This cluster received strong support after 9999 randomizations with high associated p-values. Other small taxa like the arctic fox, *Urocyon*, and *Vulpes bengalensis* showed morphometric

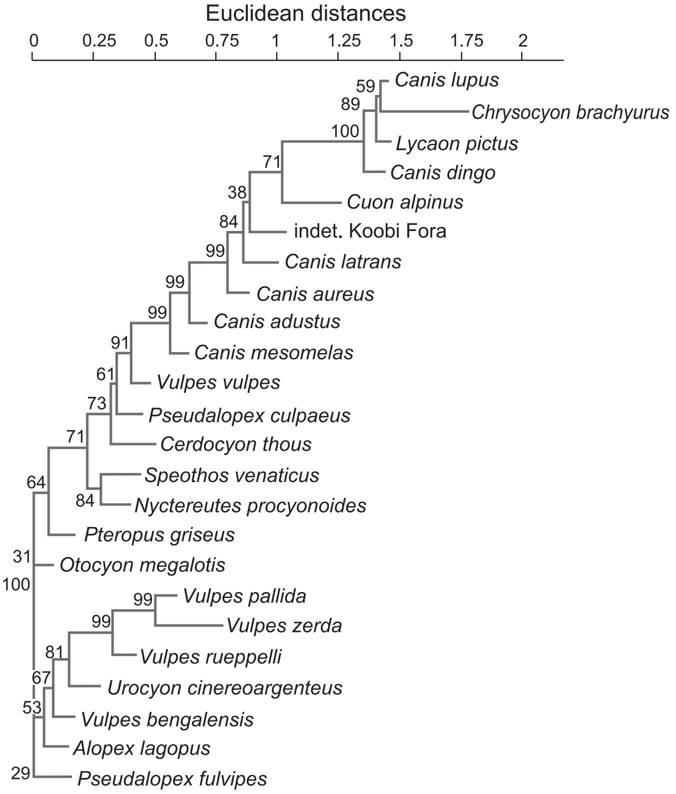

Fig. 4. Neighbour-joining cluster analysis performed using Euclidean distances extracted from all measurements. Bootstrap values show the support for each internal node.

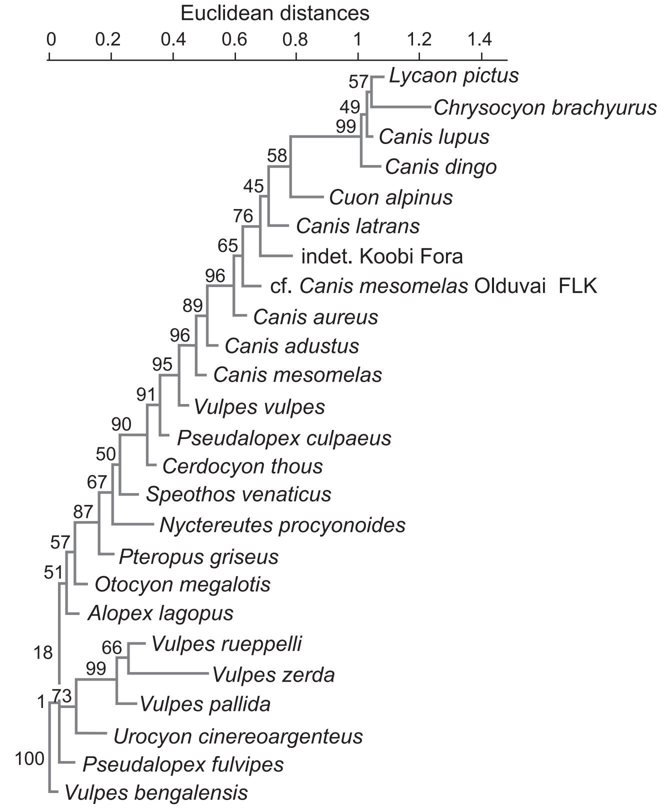

Fig. 5. Neighbour-joining cluster analysis performed using Euclidean distances extracted from proximal measurements. Bootstrap values show the support for each internal node.

affinities with this cluster, even if their grouping was not strongly supported. Another stable cluster emerged for the large wild canids including the dingo (*Canis dingo*), the grey wolf (*C. lupus*), the African wild dog (*Lycaon pictus*) and the maned wolf (*Chrysocyon brachyurus*). Clearly, the Asiatic dhole (*Cuon alpinus*) also shared some similarity with these taxa but its position is not strongly supported. Both the red fox (*V. vulpes*) and the culpeo (*P. culpaeus*) were at the base of all *Canis* spp. suggesting that morphometric convergence possibly applies for these taxa. The fossils clustered outside the black-backed jackal (*Canis mesomelas*) and the side-striped jackal (*Canis adustus*) which were very similar in radial morphometry; they all show closer similarities with the golden jackal (*Canis aureus*) and the coyote (*Canis latrans*). This conclusion was particularly accurate for the Koobi Fora specimen and the Olduvai FLKNI because of a strong p-value (0.999) that supported separation of the golden jackal from the other canids.

Discussion

Understanding the affinities of postcranial fossil material is always difficult, even if their anatomy closely resembles that of a comparative sample of extant species (Albrecht 1992; Meloro 2011a). All fossil specimens examined here are ascribed to Canidae even if their species identification is uncertain. The specimens from Olduvai FLK NI were originally identified as *Canis mesomelas*. Later, Lewis (1997), Werdelin and Lewis (2005) and Lewis and Werdelin (2007), questioned this identification suggesting that it could be a different *Canis* morphotype. The taxonomy of the specimens from Koobi Fora and Olduvai Bed II are even less certain. Their morphometry has never been analysed but attribution to *Canis* cf. *mesomelas* was suggested in the museum records (probably from the original collector or subsequently by the curator).

Our results show that it is possible to extract morphological signals from the complete, proximal, and distal radii of the Canidae such that taxonomy and ecological adaptations can be inferred for fossil specimens. Although biometry has traditionally been used to inform on taxonomy, the radii of the Canidae do not seem to be particularly robust in separating genera, even where a phylogenetic signal is detectable in the data. Our data show a clear morphometric distinction between the Vulpini and Canini, although small South American canids cluster with Vulpini. All previous phylogenetic analyses have supported the view that South American canids are a sister clade of Old World Canini (Tedford et al. 1995; Perini et al. 2010). Body size is the main driving force for any convergence observed, such that small-bodied *Pseudalopex* spp. resemble Old World foxes in radial proportions. Furthermore, we note that the long legged (large-bodied) *Chrysocyon brachyurus* shows affinities with both *Canis* and *Lycaon* even if its unique morphology emerges in all DFAs.

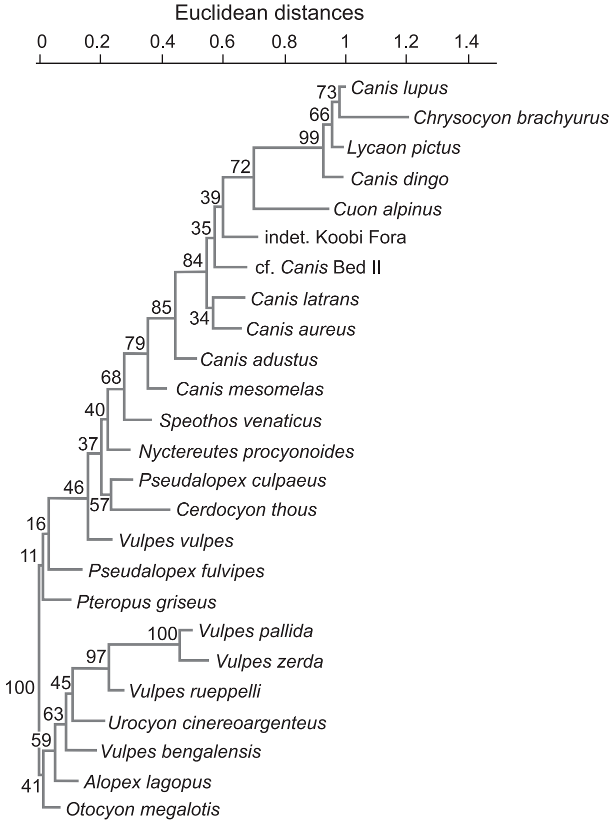

Fig. 6. Neighbour-joining cluster analysis performed using Euclidean distances extracted from distal measurements. Bootstrap values show the support for each internal node.

The best results in discriminating both genera and ecological categories were achieved by models using all bone measurements (when both proximal and distal were selected together with physiological length). Interestingly, physiological length is selected in both taxonomic and prey size DFA models suggesting that size partitioning clearly drives ecomorphological and taxonomic distinctions in Canidae. This is not unexpected based on recent ecomorphological analyses of Walmsley et al. (2012) and Meloro et al. (2013) that show how humerus size is important to discriminate locomotory and habitat adaptations in Felidae (see also Gittleman 1985 on body mass).

Some measurements selected by the stepwise DFA to discriminate genera were also those used for predicting ecological adaptations (Tables 3 and 5). For the proximal epiphysis, this included the maximum head medio-lateral length that is a robust indicator of the articulation size with the humerus trochlea. For the distal epiphysis, this included the maximum antero-posterior length of the extensor carpii muscle scar, highlighting its functional significance. Indeed, this muscle allows flexibility and movement to the metacarpal, which is used during stalking, jumping, and sprinting (Barone 1980). Canidae exhibit a broad range of locomotor abilities that are clearly related to their hunting strategies (Ewer 1973; Harris and Steudel 1997), and major differences seem to occur between the Canini (large members that tend to actively hunt their prey) and Vulpini (digging but also stalking followed by a pounce or chase). These behavioural differences suggest how both proximal and distal radial morphometry can be both taxonomically and ecologically informative to some degree.

The idea of using carnivorans in ecomorphological analyses was suggested by Lewis (1997) in an extensive survey of large-bodied species. Our results demonstrate that ecomorphology can be determined from not only complete material, but also fragments of radii using linear measurements, and not only "size-free" ratios (Meloro et al. 2013). Similar approaches were advocated by DeGusta and Vrba (2003, 2005a, b) based on metapodials of ungulates. These latter bone elements tend to be common in archaeological assemblages, and there is no reason to exclude the functional significance of other isolated long bones even if the material is fragmentary (cf. Davis and Calède 2012; Davis and McHorse 2013). In most of the analyses presented here, the fossil specimens emerged as belonging to the *Canis-Lycaon* lineage. Prey size classifications were consistent for all fossils except the Koobi Fora specimen whose proximal epiphysis indicates potential adaptation for killing large prey. Interestingly, both proximal and distal DFA models increase their statistical power when only large Old World Canini are analysed. This suggests that the ecological signal in the data is stronger when taxonomic diversity is reduced.

The biome-dependent habitat categorisation used in our study has given us the opportunity to explore a controversial topic regarding carnivoran habitat adaptations. Canidae are particularly opportunistic with respect to habitat selection and they have a global distribution. It is worth noting further that several carnivorans also select apparently unfavoured habitats to escape competition or due to other external factors (e.g., habitat reduction). A classic example is represented by the African wild dog (*L. pictus*). This species was historically associated with open plains—suggesting an exclusive adaptation to grassland biomes—but Creel and Creel (2002) clearly showed that current hunting success for *L. pictus* tend to be higher in woodlands, and furthermore that they favour woodier habitat in an effort to avoid competition with hyenas and lions (Creel and Creel 2002).

Using geographic species' ranges to refine habitat classification is perhaps not ideal due to the biases potentially introduced by historical factors (the geographic range of species today can be suboptimal), but its quantification using the method implemented here is less subjective than other methods. Varela et al. (2009, 2010) explored this issue when examining the geographic range of the spotted hyena. Their study suggested that the "environmental conditions of the localities with data on the presence of the species will not provide information on the whole spectrum of suitable environmental conditions" (Varela et al. 2009: 1652). However, our study represents the first time that this approach has been used on Canidae and, although it is an oversimplification of all the possible habitat adaptations of a species, it still produces good predictive accuracy and can be consistently extended to all kinds of mammals.

Our taxonomic results together with cluster analyses suggest that the fossil radii examined are difficult to ascribe to extant species. All the fossil specimens show affinity with medium sized *Canis*, but they cannot be ascribed robustly within the jackal lineage. We cannot exclude the hypothesis that all the specimens analysed belong to the same "East African *Canis* morphotype" (sensu Lewis 1997; Lewis and Werdelin 2007). Nevertheless, these fossils derive from distinct time intervals with the specimen from Koobi Fora being the oldest.

Our analyses suggest that similarities exist among the East African fossil specimens, the golden jackal (*C. aureus*), and the Holarctic coyote (*C. latrans*). Although these observations must be supported by cranio-dental material, they provide new hypotheses in the evolution of the jackal lineage as related to their monophyly (cf. Tedford et al. 2009). Indeed, the Plio-Pleistocene was characterised by the dispersal of medium sized Eurasian *Canis arnensis* whose taxonomic affinity with the North American *Canis lepophagus* and *Canis latrans* was supported by Kurtén (1974). The recent discovery of *Canis accitanus* in the Late Pliocene Fonelas P-1 site in Spain (Garrido and Arribas 2008) suggests a possible affinity of this other coyote-like taxon with African faunal elements (Arribas et al. 2009). Craniodental analyses might clarify this issue and possibly support the affinity between East African fossil canids and the golden jackal, which have no fossil record in Africa (Werdelin and Lewis 2005). Molecular and morphological phylogenies support a separation between the golden jackal and coyote from the black-backed and side-striped jackals (Lindblad-Toh et al. 2005; Tedford et al. 2009), supporting paraphyly in jackals. Our analyses suggest that a taxonomic revision is required to clarify the evolution of the jackals and their affinities with the coyote and other Plio-Pleistocene taxa.

This taxonomic issue also explains the discrepancy encountered in predicting prey size for the Koobi Fora specimen. Indeed, the extant radii misclassified by the DFA proximal models belong to the coyote and golden jackal. Both these species are opportunistic predators capable of killing large prey if vulnerable and this might apply equally to the Koobi Fora fossil. On the other hand, both fossils from Bed I and II show consistent adaptations for killing small-medium prey.

The habitat adaptation predictions for the fossil specimens from Koobi Fora and Olduvai are difficult to extrapolate to the level of landscape paleoecology in light of the few palaeoenvironmental reconstructions for this site. Plummer and Bishop (1994) and Plummer et al. (2008) showed that Bed I and lower Bed II were possibly associated with woodland environments with an increasing aridity at younger stratigraphic levels. For Koobi Fora, Bishop (1994), Reed (1997), and Kappelman et al. (1997) suggested a broader variety of woodland environments when compared to Olduvai Gorge. "Mixed" category is the most common prediction for the fossil canid of Koobi Fora (2 out of 3 "large Canini" DFA, the one with the highest accuracy) whereas the FLKNI specimen showed "Open" adaptations opposite to the Bed II predicted as "Mixed". This suggests that fossil canids were generalist species capable of occupying many different biomes and possessing a high potential of exploiting a variety of environmental conditions.

Conclusions

Our study demonstrates that it is possible to extract taxonomic and ecological signals from complete and fragmentary fossil material of mammalian carnivores. There is consistent evidence that long bones of carnivorans can be used to infer adaptation in killing different prey size classes and in habitat preference. Exploring this issue at broader taxonomic scales and for distinct appendicular long bones will provide a solid framework for interpreting the phylogenetic affinities and environmental preferences of fossil material, even when fragmentary. Expanding the application of ecomorphic studies will allow more fossil faunas to be categorised in consistent ecological—but also taxonomic—groups, improving inferences made about past environments.

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