

Palaeoecological significance of the “wolf event” as revealed by skull ecometrics of the canid guilds

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ABSTRACT

Members of the mammalian order Carnivora are rarely considered as proxies for palaeoecological reconstructions due to their broad phenotypic plasticity and high climatic tolerance. However, palaeontologists have traditionally interpreted the appearance of some particular carnivoran species in relation to major climatic events. The ‘wolf event’ characterised the inset of climatic deterioration for continental Eurasian fauna, ca 2.0 million years ago. It was defined as the dispersal of cursorial wild canids from East Asia to Europe consequently to the spread of the steppe environment. Anecdotal interpretations were never supported by rigorous testing about the palaeoecological significance of these canid taxa. Here, we employ two dimensional geometric morphometrics of canid skulls to characterise and interpret the structure of extant guilds and its relationship with climate and provide

inferences on the early Pleistocene Valdarno community. Averaged skull size and shape of canid guilds are currently associated with climatic parameters that reflect annual mean temperature, seasonality and precipitation. The canid guild from Valdarno showed a clustered phylogenetic structure and its average shape resembles those of communities characterised by relatively high seasonal environments. This study supports the use of canid community structure for palaeoclimatic reconstructions and validate the early Pleistocene as a period of climatic deterioration for Eurasian large mammal fauna.

Keywords: Canidae, geometric morphometrics, skull, guild, Quaternary, Plio-Pleistocene, wolf event, ecometrics, functional richness, paleoecology

1. Introduction

Faunal responses to environmental changes are well documented across many mammalian groups (Blois and Hadly, 2009). Primary consumers such as ungulates or rodents are expected to be directly influenced by vegetation showing individualistic (Jernvall et al., 1996; Eronen et al., 2010; Damuth and Janis, 2011) and group response to major climatic events (Fortelius et al., 2002; Mhlaher et al., 2011; Schap et al., 2021). In turn, secondary consumers such as members of the order Carnivora (=carnivorans) have a comparatively good record of biological trait changes (i.e., body size) in relation to climate (Klein and Scott, 1989; Meiri et al., 2004, 2009; Clauss et al., 2013), but variation at the community level through space and time is not well understood. Recently, the employment of ecometrics (Polly et al., 2011) has provided an explicit tool to test for the response of averaged biological traits across animal communities through space and time. Polly (2010) and Polly et al. (2017)

demonstrated that calcaneal gear ratio in Carnivora is a good proxy for locomotor behaviour as its changes at community level can be tracked in relation to climate on a continental scale. The same holds for the temporal scale where changes in calcaneal gear ratio have been identified within fossil cat communities from North America across the Neogene (Polly, 2020).

Other aspects of carnivorans postcranial morphology have been equally investigated to identify habitat and climatic adaptations in extant and fossil species (Lewis, 1997; Meloro, 2011a; Meloro et al., 2013; Meloro and Louys, 2015; Meachen et al., 2016; Meloro and de Oliveira, 2019; Tomya and Meachen, 2018) together with cranial and dental metrics. The latter elements traditionally received much more attention due to their diagnostic taxonomic significance. In this regard, the seminal work of Van Valkenburgh and many others (Van Valkenburgh, 1985, 1988, 2007; Turner, 1990; Wesley-Hunt, 2005; Meloro, 2011b) supported ecomorphological stasis of the carnivoran feeding morphologies across time. Terrestrial carnivores evolved distinct feeding adaptations very early in their evolutionary history (Meloro and Raia 2010; Slater and Friscia, 2019; Meloro and Tamagnini, 2021) thus showing little variation at community level through space and time (Meloro, 2011a). On the other hand, Dalerum et al. (2009) and Dalerum (2013) noted that modern carnivore guilds are functionally depleted in several continents and their functional diversity and taxonomic richness changes at large continental scale. This suggests that trophic morphology can be confidently used as a proxy to detect subtle changes in carnivore community structures linked to complex evolutionary processes (Dalerum, 2013).

The end of Pliocene/beginning of Pleistocene was traditionally identified as an important benchmark for the Eurasian continental fauna due to the renewal of the carnivoran guilds (defined as a group of species that exploit the same class of environmental resources in a similar way, Simberloff and Dayan, 1991) concomitant with dramatic climatic changes.

Azzaroli (1983) proposed the term “wolf event” to characterise the dispersal of large cursorial canids, i.e., *Canis etruscus*, *Canis arnensis*, and *Lycaon falconeri*, (Rook and Torre, 1996; Rook and Martinez-Navarro, 2010), from Asia to Western Europe and the Mediterranean region occurring ca 2.0 Ma (Azzaroli et al., 1988; Masini and Torre, 1990; Napoleone et al., 2001; Augusti and Antòn, 2002). Re-evaluation of the canid fossil record supported members of the genus *Canis* to sporadically appear much earlier than 2.0 Ma in the Chinese and European fossil record (Sotnikova and Rook, 2010; Jangzuo, 2021) and the “wolf event” has now been substituted by the “*Pachycrocuta brevirostris* event” of 1.8 Ma, due to the over-abundance of the giant hyena species in fossil sites (Martínez-Navarro, 2010; Rook and Martínez-Navarro, 2010). The Miocene rise of canid diversity has been equally linked to environmental changes in North America (Figueirido et al., 2015) due to the evolution of highly cursorial forms concomitant with the spread of the grassland ecosystem. Emergence of this pattern left open the question about association between canid morphological diversity and climate. Several authors provided insights into the ecomorphological characterisation of the Plio-Pleistocene dogs (Brugal and Boudadi-Maligne, 2010; Meloro, 2011c; Cherin et al., 2013, 2014; Flower and Schreve, 2014; Bartolini Lucenti and Rook, 2016; Jiangzuo et al., 2018; Koufos, 2018; Bartolini Lucenti et al., 2021, 2020, 2017; Bartolini Lucenti and Spassov, 2022), but still a re-evaluation of their palaeoecological significance for palaeoclimatic reconstruction is needed.

Here, we employ 2D geometric morphometrics (gmm) in conjunction with comparative methods to test for association between canid morphological diversity and climate in modern ecosystems. Recent work already highlighted for South American canids a significant association between cranial morphology and climatic adaptation at species (Zurano et al. 2017) and community level (Bubadué et al., 2016). Such a test based on worldwide canid guilds will allow us predicting climatic adaptations of Plio-Pleistocene canid community that

characterised the “wolf event”. Meloro et al. (2015) already demonstrated that gmm of the ventral cranium successfully characterise feeding ecology of extant and fossil canids and this will be equally employed here to investigate trophic diversity at guild level.

2. Material and methods

2.1 Sample

We collected data for 105 skulls of extant canid species (see Meloro et al. 2017 for specimen details) and four complete fossil skulls belonging to three species of the Early Pleistocene (= Upper Villafranchian) Valdarno faunal community mainly housed in Natural History Museum, Geology and Paleontology section, University of Florence (Italy): *Canis etruscus* (IGF 12867), *Canis arnensis* (two specimens, IGF 601 and IGF 867) and *Lycaon falconeri* (AMNH 97052 in Rook 1994 [Plate 1, page 73]). Although this specimen is referred to *Canis (Xenocyon) antonii* it represents the only complete skull representative of *Lycaon falconeri* (sensu Martínez-Navarro and Rook, 2003; but see Palmqvist et al. 1999 for a deformed specimen from Venta Micena) and it compares well with fragmentary Valdarno specimens so that Tedford et al. (2009) placed this specimen directly basal to the Valdarno taxon. The extant canid dataset was categorised into 33 OTUs (= Operational Taxonomic Unit) representative of 24 extant canid species. Multiple OTUs were selected when specimen geographic location was available for the species with particularly large range size (e.g., the red fox, *Vulpes vulpes* or the grey wolf, *Canis lupus*). In these cases, specimens were averaged per geographic area (e.g., all the red foxes from North America vs the ones from Eurasia) and treated as separate OTUs. This procedure allowed to account for (when possible) intraspecific phenotypic variation related to geography.

To characterise worldwide morphological variation of canid communities, we selected from the MAB database (<http://www.ice.ucdavis.edu/bioinventory/bioinventory.html>) 13 national parks representative of distinct climatic regions (a minimum of 3 canid species / site was allowed, see Meloro, 2011a). These included: Lake Torne Area (Sweden, N = 3), Daweishan Nature Reserve (China, N = 3), Kanha Tiger Reserve (India, N = 4), Azraq Wetland Reserve (Israel, N = 3), Radom National Park (Sudan, N = 3), Dana Biosphere Reserve (Jordan, N = 4), Amboseli (Kenya, N = 5), Yellowstone (Montana, N = 3), El Morro National Monument (New Mexico, N = 4), Reserva de biosphere de Cerrado (Brazil, N = 3), Iguazu National Park (Brazil/Argentina, N = 3), Estacion Biologica Beni (Ecuador, N = 4), and Reserva Provincial San Guilllermo (Argentina, N = 3). These geographic locations were representative of the extant worldwide canid guild variation, and they were used as a comparative sample to characterise the fossil community from the Valdarno basin (ca 1.9 – 1.83 Ma).

2.2 Phylogeny

A molecular phylogeny inclusive of 33 living OTUs was constructed using the 10k tree project database (Arnold et al., 2010). We selected both species and subspecies of canids for which genetic data were available. When subspecies genetic data were not present (e.g., for the red fox, while for the grey wolf we included the Himalayan and Indian subspecies) polytomies were constructed at the basis of the species node. Time of divergences for polytomies were estimated to a minimum of 1.0 Ma, based on dates obtained for other subspecies with molecular record. After generating the topology with branch lengths as time of divergence for extant species, we added the position of the fossil taxa (OTU = 3) from 2.0 Ma following Tedford et al. (2009). Branch lengths for these taxa were based on their first and last occurrence (as in Raia et al., 2013). The final tree resulted in a non-ultrametric

phylogeny inclusive of 36 OTUs of which three were fossils (see Supplementary Material,
<https://data.mendeley.com/datasets/42zgw9pkz2/draft?a=788baf9c-8415-40f5-b279-1d2f551289ef>).

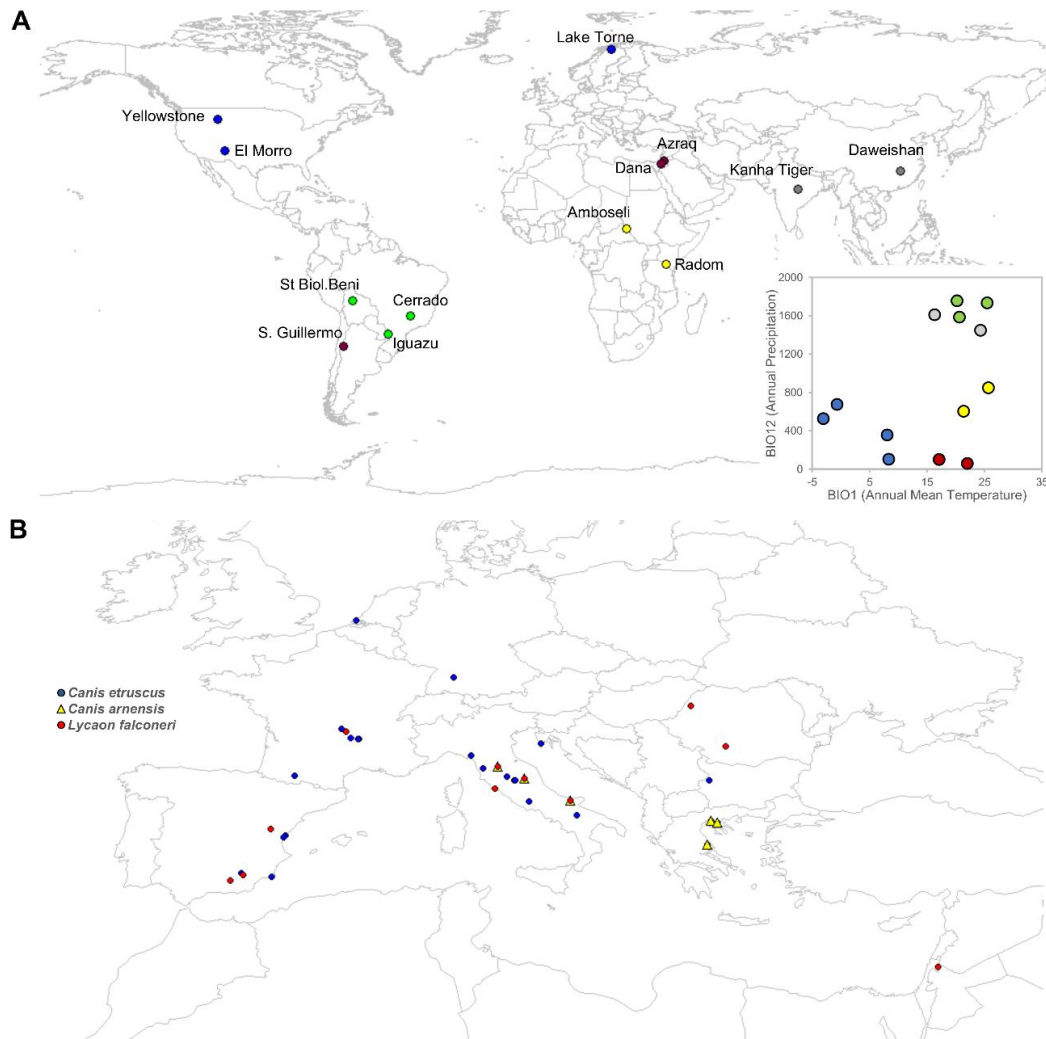


Fig. 1. Map showing the geographic locations of the 13 national parks selected to represent variation in canid guild composition worldwide (A). Locations are colour coded according to their climatic similarity. A plot of BIO1 (Annual Mean Precipitation) vs BIO2 (Annual Precipitation) indicates the general climatic cluster for the selected locations. In B the distribution of fossil sites that recorded presence of the three Pleistocene canids (*Canis etruscus*, *Canis arnensis* and *Lycaon falconeri*) based on the paleobiology database (<https://paleobiodb.org/#/>). Note that overlap among the three species occurs only in the Val d'Arno province (Tuscany, central Italy) and to lesser extent in the Apulia region.

2.3 Geometric morphometrics

The skulls were photographed in ventral view at 1 meter distance using a Nikon D40 attached to a Manfrotto tripod. They were placed on the floor and a spirit level was positioned on the palate to ensure parallelism between the palatal plane, the floor, and the camera plane (Meloro et al., 2015). The software tpsDig2 (Rohlf, 2015) was employed to digitize 23 anatomical landmarks (Fig. 2) to cover palatal, dental, zygomatic and occipital region. A similar configuration was employed by Bubadu  et al. (2016) to investigate South American canid guilds. Landmarks were digitized only by one user (CM) and a subsample of three skulls was digitized three times over three different days to test for digitalisation error (in all cases no differences occurred in the size and shape variables between replicas, Procrustes ANOVA $p = 0.99$).

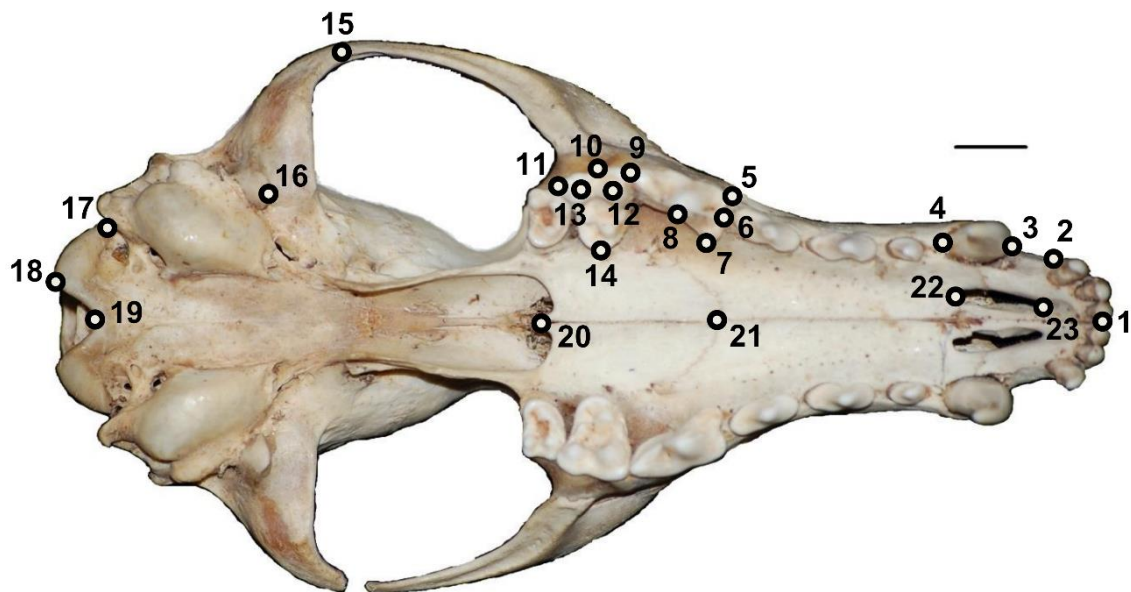


Fig. 2. Skull of *Vulpes vulpes* showing the landmark configurations employed to describe skull size and shape in Canidae. (1) tip of the snout defined by middle point between the first two frontal incisors, (2) posterior tip of the third incisor, (3) anterior tip of canine, (4) posterior tip of canine, (5, 6, 7, 8, 9) outline of carnassial tooth (P4), (10-11) central and posterior labial edges of molar one, (12, 13) cusps of molar one, (14) anterior tip of molar

one, (15) (17, 18, 19) outline of the occipital condyle; (20) junction of the stiff and hard palate, (21) palatine-maxilla suture, (22) posterior and (21) anterior tip of the incisive foramen. Scale bar equals 1 cm.

A Generalized Procrustes analysis (GPA) (Rohlf and Slice, 1990) was used to rotate, translate, and scale landmark configurations to unit centroid size (CS = the square root of the sum of squared distances of the landmarks from their centroid; Bookstein, 1989). To visualize the multivariate ordination of the aligned specimens in relation to their relative reconstructed ancestral nodes, we generated a phylomorphospace (Sydlauskas, 2008; Sakamoto and Ruta, 2012) as a principal component analysis (PCA) of the procrustes shape coordinates. Additionally, phylogenetic signal for size and shape data was tested using the R function ‘physignal’ (Adams, 2014). Allometry defined as the influence of size on shape variation (Klingenberg, 2016) was tested in our 36 OTUs sample using the function ‘procD.lm’ and ‘procD.pgls’ included in the R package “geomorph” (Adams and Otárola-Castillo, 2013) to account for the phylogenetic covariance matrix (Adams and Collyer, 2018).

Due to some species phenotype being present in multiple guilds (e.g., *Chrysocyon brachyurus* is found in Reserva de biosphere de Cerrado, Iguazu and Estacion Biologica Beni) a ‘guild’ morphospace (n-taxa = 48) was generated using replicas of PC scores from the 36 OTU morphospace. This allowed testing size and shape differences due to guild membership using non-parametric Kruskal-Wallis (for size) and non-parametric MANOVA with 9,999 permutations. To test multivariate dispersion of shape data around their centroid, we computed per-group (guilds) morphological disparity (=MD) as the average Euclidean distance from group centroid, and then we performed a permutation test using ‘betadisper’ and ‘permutest’ functions available in the R package ‘vegan’ (Oksanen et al., 2013) to assess the significance in disparity differences between guilds. The same procedure was applied to test the dispersion of size data around their centroid.

2.4 *Phylogenetic structure and environmental variables*

We characterized each canid guild using metrics of phylogenetic distances between the taxa (PD), net relatedness index (NRI) and nearest taxon index (NTI) (Webb et al., 2002). These metrics are descriptors of community composition based on phylogenetic relationships observed for each canid assemblage. They have been used extensively in community ecology of extant and fossil mammals and they are better descriptors of community structure than species richness (Raia, 2010; Kamilar et al., 2015). We employed the package *picante* that computes PD, $mn\text{pd}$ (= mean nearest taxon phylogenetic distance, $\text{NRI} = mn\text{pd} * -1$) and $mn\text{ptd}$ (= mean nearest taxon phylogenetic distance, $\text{NTI} = mn\text{ptd} * -1$) and compares their distribution with random models generated after 9,999 permutations.

Additionally, the climate theoretically experienced by each of the 13 extant canid guilds was described using nineteen bioclimatic variables as defined in Hijmans et al. (2005). Geographic location for the centroid of each national park selected was assumed to be a good spatial proxy for their climatic condition (see Meloro, 2011b). The nineteen bioclimatic variables were extracted from the centroid of each national park using the WorldClim Database (Hijmans et al., 2005) with a 2.5 arc spatial resolution.

2.5 *Ecometric association and climate prediction*

Each of the 14 canid guilds (13 extant plus one fossil) analysed can be phenotypically described using ecometrics (Polly et al., 2011). Morphological disparity (=MD, the morphospace volume occupied by each community) of shape and size represents a potential ecometric that we tested for association with phylogenetic community structure and climate using non-parametric correlations (see also Meloro, 2011a). Work by Polly (2010, 2020) and Polly et al. (2017) also highlighted the potential of using averaged traits as ecometrics, so we opted to characterize each canid guild using skull shape consensus configuration. In our case,

the ecometric trait was multivariate ($n = 46$ procrustes coordinates) and we employed different strategies to test for association with phylogenetic structure and climate.

Firstly, we applied the clustering UPGMA (=unweighted pair group method with arithmetic mean) method based on the procrustes distances between averaged skull shape of canid guilds. This allowed to graphically identify similarities between canid guilds based on their averaged skull shape. Same procedure was applied to generate cophenetic trees based on the Euclidean distance matrices of phylogenetic community descriptors (PD, NRI and NTI) and selected bioclimatic variables that were associated with averaged skull shape. Each bioclimatic variable was tested for association with averaged skull shape using multivariate regression with permutation and retained for further analyses, all the others were discarded. Mantel test was employed to verify association between procrustes and phylogenetic and/or bioclimatic distance matrices. When climatic variables were concerned, the fossil community was not included in the analyses.

Secondly, two-blocks Partial Least Squares (Rohlf and Corti, 2000) was applied to test association between averaged skull shape and the previously selected bioclimatic variables. This analysis is based on a singular value decomposition of the matrix of covariances between two sets of variables that in our case are the block “climate” (the selected bioclimatic variables per guild, appropriately standardised) and the block “averaged guild shape” (the consensus configuration obtained for each guild).

We employed robust regression models to reconstruct bioclimatic variables for Valdarno fossil community when univariate ecometric traits (MD of size and shape) and phylogenetic community descriptors were used as independent variables. A projection of the Valdarno community into the PLS climate-shape morphospace was also employed and based on predicted PLS1 climatic scores, bioclimatic variables were extrapolated. To obtain Valdarno climatic score in PLS space we opted to use linear model and robust regression.

Both methods were considered to explore their suitability for climatic predictions. Robust regression is generally less dependent on assumptions concerning data distribution and it is much less sensitive to outlier, which can be common in palaeocological studies (Gebregiorgis et al. 2020). The most likely climatic variables were identified subsequently based on the accuracy of each univariate or multivariate predictor.

3. Results

3.1 Shape and size analysis

Phylomorphospace identified a clear distinction between the members of Old World Canini tribes and Vulpini and New World Canini. Significant overlap occurred between Old and New World foxes (Fig. 3). PC1 describes shape changes in the skull related to the relative proportion of the palate. On the negative scores, *Otocyon*, *Nyctereutes* and South American genera are characterised by very short muzzle and upper dentition, while on positive PC1 wolves and fossil *Lycaon falconeri* show a broader and wider palate and upper dentition. On PC2 taxa are partitioned based on the relative position of the zygomatic arch with hypercarnivorous species (e.g., the arctic wolf *Canis lupus arctos*, *Lycaon* and *Cuon*) exhibiting negative scores, while hypocarnivores have positive scores (Fig. 3).

Although low, phylogenetic signal was significant in this canid shape sample (K_{multiv} 0.2042, P-value: 0.001). When size was analysed, a stronger and still significant signal was identified (K : 0.5023, P-value: 0.001). There was a significant impact of size on skull shape in the sample of 36 OTUs (33 living + 3 fossils), however this pattern was not valid when accounting for phylogeny (Table 1).

Table 1. Procrustes ANOVA without (OLS) and with (PGLS) phylogenetic correction to test for the impact of size on shape variation in 36 canid OTUs. Significant p values are highlighted in bold. The test was implemented with 9,999 permutations.

			Df	SS	MS	Rsq	F	Z	Pr(>F)
Allometry	OLS	Centroid Size	1	0.020	0.020	0.159	6.435	4.702	0.001
		Residuals	34	0.106	0.003				
		Total	35	0.126					
	PGLS	Centroid Size	1	0.001	0.001	0.046	1.640	0.886	0.339
		Residuals	34	0.026	0.001				
		Total	35	0.028					

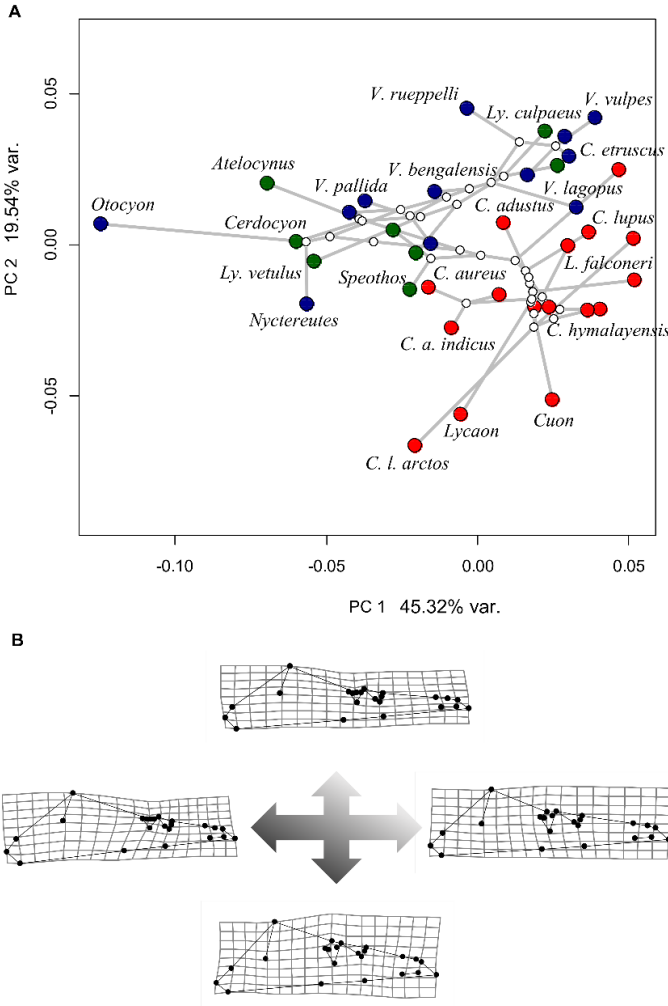


Fig. 3. A, Phylomorphospace for skulls of 33 canid taxa (OTUs). B, Thin plate spline showing skull shape deformation from the most extreme negative to the positive scores along PC1 (horizontal) and PC2 (vertical).

The 14 guilds (13 extant plus 1 fossil) did not show any difference in average skull size ($K-W = 10.57$, $p=0.647$) as well as shape (Tot SS = 0.164, Within-group SS = 0.107, $F = 1.39$, $p = 0.068$). Similarly, the betadisper analysis returned a non-significant result when performed on both size and shape variables ($p\text{-value} = 0.901$ and $p\text{-value} = 0.246$ respectively) showing that variances were homogeneously distributed between canid guilds (Table 2).

Table 2. Species richness, morphological disparity for shape and size, phylogenetic distance (PD), net relatedness index (NRI) and nearest taxon index (NTI) computed for each extant canid guild and the fossil one from Valdarno. In bold the guild NRI and NTI values significantly different from random expectation.

Guild	# Species	MD _{shape}	MD _{size}	PD	NRI	NTI
St Biol Beni	4	0.0030	0.0526	70.2970	1.7201	1.4311
Lake Torne	3	0.0040	0.0847	87.9814	-0.4364	-0.0186
Iguazu	3	0.0029	0.0681	64.0416	1.2882	1.0657
Cerrado	3	0.0041	0.0658	62.0618	1.3452	1.2552
Daweishan	3	0.0026	0.0793	110.1744	-1.2361	-2.0509
Kanha Tiger	4	0.0022	0.0800	93.2464	0.2288	0.0271
Azraq	3	0.0028	0.0811	85.1021	-0.3341	0.2489
Dana	4	0.0045	0.0822	94.6436	0.1510	0.0158
Amboseli	5	0.0056	0.0808	110.1736	0.4570	-0.7491
Yellowstone	3	0.0030	0.0820	84.5699	-0.3280	0.2968
El Morro	4	0.0018	0.0749	100.0086	-0.7041	0.9462
San Guillermo	3	0.0020	0.0677	42.8479	2.5570	2.3372
Radom	3	0.0019	0.0779	91.6090	-0.5789	-0.3578
Valdarno	3	0.0047	0.0763	61.6456	1.4894	0.9919

3.2 Phylogenetic community composition and climate

Table 2 reports PDI, NRI and NTI for each canid guild. Only the Patagonian canid community of San Guillermo showed a significant phylogenetic clustering due to the presence of three foxes all belonging to the same genus *Lycalopex*. The canid guild from

Sweden (arctic ecosystem) showed the lowest NRI and NTI values but was not significantly over-dispersed.

Spearman non-parametric rank correlation was employed to explore association between univariate ecometrics, phylogenetic descriptors and climate. Averaged skull size of canid communities was significantly associated with several bioclimatic variables (BIO1, BIO3, BIO4, BIO7, BIO15, BIO19) while morphological shape disparity correlated with PD and NTI (Table 3). Among the other parameters, also NRI exhibited a significant relationship with bioclimatic variables 3, 4 and 7 (Table 3).

Multivariate regressions allowed the selection of 10 bioclimatic variables that were significantly ($P < 0.001$) associated with averaged skull shape. These included BIO1 (Annual Mean Temperature) that explained 26.34% of shape variance, BIO3 (Isothermality, 31.95% var.), BIO4 (Temperature Seasonality, 40.44% var.), BIO6 (Min Temperature of Coldest Month, 36.32% var.), BIO7 (Temperature Annual Range , 45.86%), BIO8 (Mean Temperature of Wettest Quarter, 38.67%), BIO11 (Mean Temperature of Coldest Quarter, 33.65% var.), BIO12 (Annual Precipitation, 32.79% var.), BIO16 (Precipitation of Wettest Quarter, Precipitation of Warmest Quarter, 22.64% var.) and BIO18 (39.53% var.). All the other bioclimate variables were discarded from further analyses.

Table 3. Spearman correlation coefficient (below diagonal) and their respective P values (above) to test degree of univariate association between bioclimatic parameters and ecometrics of canid guilds. Only three bioclimatic indices were significantly associated with NRI. All the other associations were non-significant. BIO1 Annual Mean Temperature, BIO3 Isothermality, BIO4 Temperature Seasonality, BIO7 Temperature Annual Range, BIO15 Precipitation Seasonality, BIO19 Precipitation of Coldest Quarter. Significance is highlighted in bold.

	Ln CS	MD Shape	MD Size	PD	NRI	NTI	BIO1	BIO3	BIO4	BIO7	BIO15	BIO19
Ln CS	—	0.721	0.901	0.775	0.112	0.721	0.027	0.025	0.024	0.035	0.049	0.010
MD Shape	-0.110	—	0.803	0.021	0.144	0.009	0.482	0.831	0.817	0.802	0.748	0.364
MD Size	0.038	0.077	—	0.448	0.094	0.603	0.668	0.471	0.181	0.296	0.529	0.394
PD	0.088	0.632	0.231	—	0.008	0.001	0.803	0.374	0.316	0.157	0.517	0.642
NRI	-0.462	-0.429	-0.484	-0.698	—	0.010	0.344	0.033	0.010	0.004	0.831	0.694
NTI	-0.110	-0.692	-0.159	-0.824	0.687	—	0.775	0.255	0.364	0.425	0.494	0.517
BIO1	-0.610	0.214	-0.132	0.077	0.286	-0.088	—	0.046	0.007	0.077	0.008	0.128
BIO3	-0.615	0.066	-0.220	-0.269	0.593	0.341	0.560	—	0.000	0.001	0.297	0.133
BIO4	0.621	-0.071	0.396	0.302	-0.687	-0.275	-0.703	-0.923	—	0.000	0.162	0.128
BIO7	0.587	-0.077	0.314	0.416	-0.741	-0.242	-0.507	-0.799	0.893	—	0.522	0.343
BIO15	-0.555	0.099	-0.192	0.198	0.066	-0.209	0.698	0.313	-0.412	-0.196	—	0.001
BIO19	0.681	-0.275	0.258	-0.143	-0.121	0.198	-0.445	-0.440	0.445	0.287	-0.808	—

UPGMA trees showed distinct community associations depending on the use of average skull shape, phylogenetic descriptors or climate (Fig. 4).

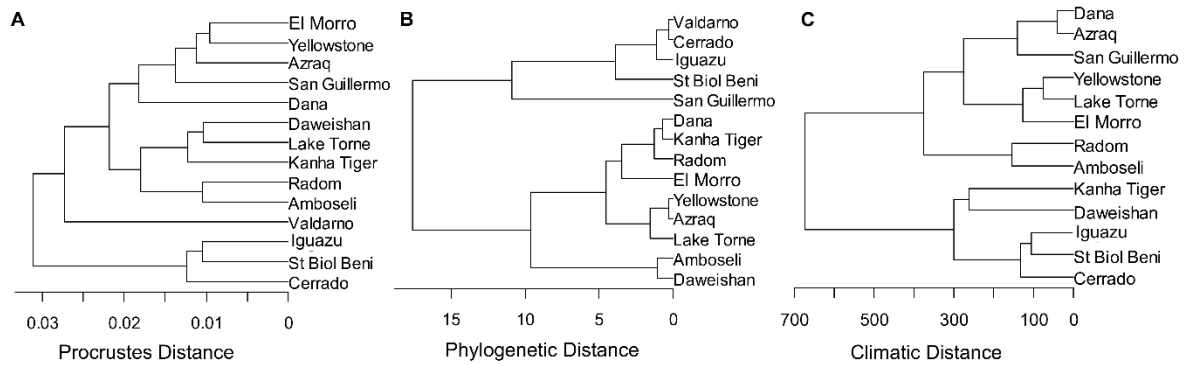


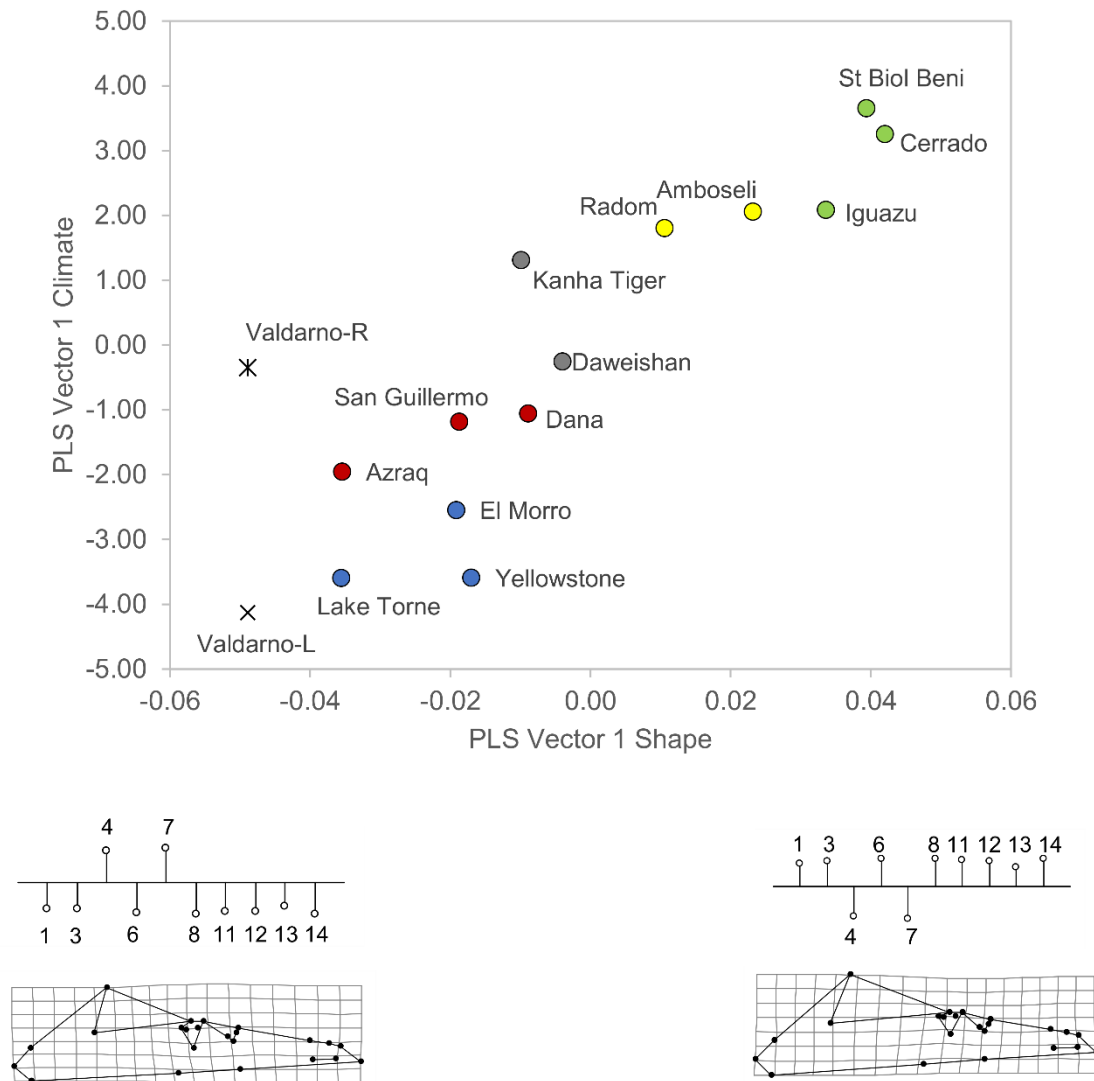
Fig. 4. UPGMA trees based on procrustes distance metrics (A), phylocom distance matrix (B) and Euclidean distances obtained from 19 bioclimatic variables (C). In C the fossil Valdarno community was not included due to the lack of climatic data.

Based on shape, the fossil community Valdarno is basal to a cluster that separates all canid communities of Old World from those of New World (Fig. 4A). If phylocom is considered, Valdarno clusters with South American communities since it includes all members belonging to the same genus (Fig. 4B) while when bioclimatic variables are concerned, two clusters showed differences between more seasonal (mostly Old World canid communities except Chinese and Indian) and less seasonal areas (Fig. 4C).

Mantel test was significant only when average cranial shape distance matrix was contrasted with climate distance matrix between the guilds ($z = 3692.987$; $p = 0.005$). The morphological distances between guilds were not associated with phylocom distances ($z = 83.26294$; $p = 0.283$) and the latter was equally not related to climatic distances ($z = 1781194$; $p = 0.231$).

3.3 Two blocks PLS and Valdarno reconstruction

Two blocks PLS returned a significant result when contrasting the averaged skull shape variables against the pre-selected ten bioclimatic variables with the first pair of vectors showing strong positive correlation ($p\text{-value} = 0.002$; $r\text{-PLS1} = 0.91$; see Fig. 5).



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Figure 5. Scatterplot showing the first pair of Partial Least Squares vectors obtained from testing association between averaged skull shape vs selected bioclimatic variables for each extant guild. Deformation grids show shape changes in correspondence of the extremes of the first PLS vector, while variable profiles give the estimate of the standardized scores of each bioclimatic variable (including BIO1, 3, 4, 7, 8, 11, 12, 13, 14) as vertical lines extending from a horizontal axis corresponding to the mean. Valdarno-L = projected score of fossil guild based on linear regression; Valdarno-R=project score of fossil guild based on robust regression.

On the negative PLS1 scores, canid communities are characterised by relatively longer muzzle and wider teeth, traits associated with high temperature seasonality (BIO4) and temperature annual range (BIO7) but lower temperature parameters (BIO1, 3, 6, 8 11) and precipitation (BIO12, 13, 14). On the PLS1 positive scores, neotropical communities from South America clusters in relation to their higher temperature and precipitation parameters. The average shape of these communities shows a relatively shorter muzzle and wider zygomatic arch. A projection of Valdarno into PLS morphospace based on linear regression function (Valdarno-L, Fig. 5) clusters this community at the basis of the most seasonal extant guild (Lake Torne). If robust regression is applied to predict PLS climatic score, the Valdarno community show a much higher value in climate vector compatible with that of Daweishan Reserve (China, Fig. 5).

The PLS1 climatic scores of Valdarno have a strong impact on the predictions of bioclimatic variables depending on if linear or robust model is assumed to be correct (Table 4).

Table 4. Climatic parameters reconstructed for Valdarno canid guild based on multiple methods (PLS = projection of Partial Least Square scores on first PLS climate vector, NRI = net relatedness index).

	PLS-L	PLS-R	NRI
BIO1 Annual Mean Temperature	0.722	12.539	-
BIO3 Isothermality	36.575	51.823	64.369
BIO4 Temperature Seasonality	899.962	542.734	221.9
BIO6 Minimum Temp. Coldest Month	-19.941	0.4508	-
BIO7 Temperature annual range	39.662	28.965	25.301
BIO8 Mean Temperature of wettest quarter	4.592	15.213	-
BIO11 Minimum Temp. Coldest Quarter	-12.201	5.7216	-
BIO12 Annual Precipitation	473.500	1143.41	-
BIO16 Precipitation of Wettest Quarter	56.780	396.036	
BIO18 Precipitation of Warmest Quarter	130.425	91.277	-

Reconstructions based on lower score of linear model support Valdarno canid community to be adapted to very cold and harsh conditions with average annual temperature of 0.72 degrees Celsius, high temperature seasonality (BIO4) and relatively low precipitations (BIO12, 16, 18). The use of score obtained from robust regression model provides for Valdarno a relatively higher annual temperature (12.53 degrees Celsius) although lower than those experienced by extant canid communities in East Asia, and a seasonality and precipitation parameter compatible (but still lower) with the Indian ecosystem of Kanha Tiger reserve.

NRI is also a univariate trait that allows predictions for BIO3, 4 and 7 with parameters generally similar to that of PLS climatic robust score. Although the centroid size averaged by community correlated with many bioclimatic parameters (Table 3), no linear model turned to be significant so no predictions could be made based on this metric.

4. DISCUSSION

Palaeoenvironmental reconstruction is a challenging task that requires a multidisciplinary approach. So far, mammalian community structures have been used to predict palaeoenvironments (Reed, 1998; Fernández and Paláes-Campomanes, 2003; Fernández and Vrba, 2006; Rodriguez et al., 2006; Louys et al., 2011, 2015; Kovarovic et al., 2018) however, there is a multitude of traits and categories that investigators can employ. We demonstrate that average skull shape is a reasonably good ecometric trait to characterise extant canid guilds, hence this approach could also be applied to other mammalian groups to improve palaeoenvironmental reconstruction.

4.1 Palaeoecology of Valdarno canids based on skull morphology

Most of extant canids are secondary consumers with a catholic diet that allowed them to adapt to a multitude of environments (Sillero-Zubiri et al., 2004). Biogeographical events (e.g., the canid invasion of South America) generated unique signatures in canid community composition whose structural changes might reflect evolutionary history as well as adaptations to local conditions (Bubadu   et al., 2016). In keeping with Meloro et al. (2017), the canid skull shape data exhibit a significant phylogenetic signal in both size and shape in spite being indicative of dietary adaptations and bite force capabilities (Damasceno et al., 2013; Meloro et al., 2015). This result did not change even if we considered subspecies as separate OTUs suggesting that geographical variation, to a certain extent, could be taken into account also in the analyses of guild ecometrics. Polly et al. (2017) demonstrated that the American red fox varies considerably in calcaneal/gear ratio across latitudes as it might be expected for mammalian body size following Bergmann's rule (Clauss et al., 2013). Although this variation might not impact strongly interspecific data analyses, we noted that, especially for shape, it might be relevant when genetic data support subspecies segregation for taxa with a particularly broad geographical range size.

In our data set the grey wolf represents a good example since, based on phylomorphospace occupation, the arctic subspecies (*C. lupus arctos*) separates from the rest of large canids being characterised by the extreme development of hypercarnivorous traits (short muzzle, wide upper carnassial, broad zygomatic arch, Fig. 3). Such genetic/phenotypic resolution was not available in many other cases from our sample but the inclusion of few established subtaxa appears to make a difference when interpreting phylogenetic signal in the data. This trait does not hinder the identification of an adaptive signal. Indeed, our sample clearly showed consistent clustering of hypercarnivorous large dogs (including the fossil *Lycaon falconeri*, Rook, 1994) vs other more generalist taxa, further supporting the presence of a

pattern of convergence in the feeding apparatus driven by the adaptation to kill relatively large prey (Van Valkenburgh, 2007; Slater et al., 2009). Coherently with this pattern, the fossils *Canis etruscus* and *Canis arnensis* occupy positive PC1 scores as the rest of modern *Canis* spp. (Fig. 3), although *C. etruscus* clusters closely with the red fox based on PC2 score, while *C. arnensis* with *C. lupus*. Cherin et al. (2014) already noted that in several cranial traits the Etruscan wolf is lesser similar to the extant grey wolf than *Canis arnensis*, thus supporting patterns observed in the phylomorphospace. A unique combination of cranial traits made *Canis etruscus* a flexible species that possibly altered its ecological adaptations in relation to the presence of other canid competitors (see Garcia and Virgos, 2007). The ecological flexibility of *C. etruscus* is equally reflected in its relative abundance across Eurasia that is much higher when compared to *C. arnensis* whose distribution remains limited to the Mediterranean area (Fig. 1B; Bartolini Lucenti and Rook, 2016; <https://paleobiodb.org/#/>).

4.2 Variation between extant and fossil canid guilds

No significant difference in averaged or variance skull morphometric traits was detectable in the canid sample. This reinforces previous generalisations on the resilience of carnivoran evolution to change in functional community structure through time. Such a lack of difference (as previously identified by Van Valkenburgh, 1985, 1988; Meloro, 2011b) does not prevent to detect subtle changes that can be linked with climatic adaptations (see Belmaker, 2018; Koufos, 2014). This was achieved by using averaged phenotypic traits (as in Polly et al., 2017), that are significantly associated with bioclimatic variables. The different approaches we employed converged towards this conclusion. PLS appeared to be the method suitable to maximise the degree of covariation between average skull shape and climatic differences. The use of distance matrices equally confirmed a genuine association between

guild morphological distances and climatic distances. Interestingly, no strong pattern was identified when phylogenetic distance metrics were used to test their association with climatic data. The work of Kamilar et al. (2015) suggested that phylogenetic community metrics can be indicative of environmental changes however, as for large scale clade sorting, such a result applies to larger communities (e.g., the whole Carnivora) at larger spatial scale. On the one hand, we opted to avoid pseudoreplications by analysing only selected/representative canid guilds, although large spatial scale analyses might provide a stronger pattern of ecometrics variation (Barr, 2017; Schap et al. 2021). On the other hand, we argue that large spatial patterns in ecometrics requires spatial bias to be accounted for, since our phylomorphospace clearly showed the impact of taxonomic distinctiveness. In summary, we believe that large spatial scale approaches require more caution when intraspecific variation is concerned.

4.3 Reconstruction of Valdarno palaeoenvironments

Because Valdarno canid (and not only) community appears to have little in common with modern analogues (see cluster analysis, Fig. 4A), it is particularly difficult to provide accurate predictions for many environmental parameters. By reducing the number of bioclimatic variables, we were able to reduce statistical noise in our data and provided realistic parameters although quite distinct depending on the use of linear or robust regression. If fossil data are projected within the PLS morphospace using linear approach, the Valdarno canid guild predicts a harsh, highly seasonal environment characterised by very low average annual temperature and low precipitation. In this respect, the Valdarno guild appears to resemble guilds sampled in the Northern Hemisphere such as Lake Torne characterised by extreme arctic conditions. This similarity is partially due to the predominance of carnivorous adaptations in the morphologies of the extant Arctic wolf (*C. lupus arctos*) that resembles *L.*

falconeri from Valdarno, while the red and the Arctic fox (*V. vulpes*, and *V. alopex*) equally share positive PC2 scores of shape space as for *C. etruscus* (Fig. 3).

Alternatively, the robust regression provides an average annual temperature strongly compatible with that already predicted by Bertini et al. (2010) based on the pollen record of Poggio Rosso (12.5-14 degrees Celsius). Poggio Rosso (1.87-1.83 MA) is slightly younger than the Tasso Faunal Unit (1.9 Ma, where all Valdarno canids co-occur) and register the co-occurrence of *C. etruscus* and *C. arnensis* but no presence of *Lycaon falconeri*. Still, its fauna is highly compatible with Tasso FU (Mazza et al., 2004) and predicted precipitation parameters for interglacial phases (750-1200 mm) are within the range of that predicted by our Valdarno data (Table 3, 1159 mm).

Other climatic projections for Tasso FU were obtained using cenograms by Montuire and Marcolini (2002) that for ‘il Tasso’ locality suggested an average annual temperature of 17.36 degrees Celsius while for ‘Pietrafitta’ (another Early Pleistocene site with typical Valdarno faunal assemblage) 11.9 degrees.

All these predictions converge in supporting previous inferences on the inset of a strong glacial event that around 2.0 Ma altered flora and fauna of continental Western Europe. The concomitant co-occurrence of the Val d’Arno canids in the Mediterranean region (Fig. 1B) supports stability of this climatic condition in the area during this time, while more advanced species (e.g., *C. mosbachensis*, *L. lycaonoides*) were spreading from China to Europe towards Dmanisi, a site coeval with Tasso FU (Qui et al., 2004; Jangzuo et al., 2018; Jangzuo, 2021; Bartolini-Lucenti et al. 2020, 2021). Interestingly, Azzaroli (1983) proposed another faunal event at 2.6 Ma characterised by the spreading of large grazing genera like *Mammuthus* and *Equus*. Since the temporal distribution of the canid Euroasiatic record has been updated multiple times with the occurrence of *Canis etruscus* earlier than expected by the ‘Wolf event’, it is likely that the spreading of steppe environments already favoured dispersal of

cursorial and potentially pack-hunter large dogs (Sotnikova and Rook, 2010; Cherin et al., 2013).

Credit author statement

Carlo Meloro: Conceptualization, Data collection, Methodology, Formal analysis, Investigation, Writing, Visualisation, Funding acquisition.

Gabriele Sansalone: Conceptualization, Methodology, Formal analysis, Writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Supplementary data to this article can be found in the Mendeley archive:

<https://data.mendeley.com/datasets/42zgw9pkz2/draft?a=788baf9c-8415-40f5-b279-1d2f551289ef>

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