Morphological disparity in Plio-Pleistocene large carnivore guilds from Italian peninsula

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Communities of large mammals exhibit changes in morphological diversity through space and time; changes that are possibly correlated to distinct aspects of the physical environment. Here, I explore shape changes in the trophic apparatus of large carnivore guilds, comparing extant communities with Quaternary ones, from peninsular Italy. Mandibular shape is quantified through geometric morphometrics and its disparity is computed for each carnivore guild. Patterns of morphospace occupation through space and time reveal that extant carnivore guilds are negatively influenced by number of artiodactyls. Very productive ecosystems show low values of morphological disparity because species tend to occupy central regions of the morphospace rather than extreme areas. Disparity of mandibular corpus shape remains relatively stable throughout the Quaternary in the large carnivore communities of the Italian peninsula. They exhibit similar values to extant guilds because the trophic apparatus did not evolved important morphological novelties. Interestingly, carnivore guilds of the late Pliocene (3.5 Ma) and early Pleistocene (0.8 Ma) show over-dispersed or random morphospace occupation because of a depleted fauna, precluding successive structural changes. The same applies for the extant European carnivore guild as a result of recent extinctions without replacement.

Key words: Carnivora, geometric morphometrics, mandible shape, Quaternary, Italian Peninsula, Italy.

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Introduction

The structure of morphological variability in organisms through space and time has received particular attention especially in the light of its potential relationship with taxonomic diversity (Foote 1997). Large carnivorous mammals have been intensively studied in this respect because of the great morphological and ecological variability exhibited by extant, and even more by extinct, species (Nowak 1991; Van Valkenburgh 1989, 1999, 2007). In this group, the trophic apparatus (as defined by cranio-dental features) has been investigated and it is clear that this system combines traits that evolved early in the history of the order, remaining relatively unchanged through time (Van Valkenburgh 1988, 1995, 1999, 2007; Werdelin 1996; Holliday and Steppan 2004; Wesley-Hunt 2005). Such generalization is probably applicable to different contexts other than the American fossil record and the entirely of the Cenozoic, from which most of the hypotheses have been tested, but no comparative approaches have been performed for a shorter geological period or a different geographical area so far.

Van Valkenburgh (1988) computed a large carnivore guild comparison between several extant representative ecosystems and few extinct assemblages spanning 30 million years. But, in the history of carnivores and mammalian communities in general, there are interesting taxonomic changes which occurred in relation to more severe geological changes over shorter time periods. The Plio-Pleistocene can certainly be considered such a period. Evidence points to strong climate changes occurring worldwide (Zachos et al. 2001) and the mammalian fauna seems to have been influenced by such changes (Kurtén 1968; Augustě and Antón 2002; Lister 2004; Barnosky et al. 2004; Barnosky 2005; Barnosky and Kraatz 2007). An important experiment occurred in the last part of the Plio-Pleistocene: modern humans invaded the mammalian community causing dramatic changes in faunal composition (Alroy 2001; Cardillo and Lister 2002; Wroe et al. 2005; Koch and Barnosky 2006). Large carnivores were possibly affected by these processes. Some remarkable Ice Age predators disappeared completely (e.g., saber-tooth cats) without leaving any descendent or similar eco-morphological type of species. This fact may be related to the disappearance of large ungulates (Turner and Antón 1997) but it is not clear how such a phenomenon affected the extinction of certain large carnivores and the survival of others. Further investigations are needed in order to understand the effect of climate change on morphological and taxonomic diversity of large carnivores.

The European fossil record is of particular interest for the Plio-Pleistocene because there is a very good mammalian bio-chronology (Azzaroli 1983; Azzaroli et al. 1988; Raia et al. 2009) and also because some large carnivores defined particular faunal "events" which represent significant changes in

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faunal composition. Among the others, the Wolf event (ca. 2.0 Ma) is considered a period of important changes determined by a striking change in climate accompanied by the dispersal all over Eurasia of large canids that are considered to have been more adapted to open environments (Azzaroli 1983; Rook and Torre 1996). Because of this apparently intimate link between carnivore faunal composition and climate changes we expect possible trends to have emerged in the evolution of taxonomic and morphological diversity of large carnivores during the Plio-Pleistocene.

A significant effect of climate was already determined on the entire large mammal community from Italy because of the strong influence on the turnover rates of species: that is a taxonomic evolutionary process (Raia et al. 2005). Based on the same fossil record, Meloro et al. (2008a) found a non-significant change of species diversity toward the Plio-Pleistocene. The number of species of all groups of large mammals (including carnivores) in each period is more affected by sample bias other than environmental changes. It is worth noting that the Italian peninsula represents a special biogeographic case as compared with other European Plio-Pleistocene regions. The rate of large mammal endemism is particularly low (excluding islands, Kotsakis et al. 2002) and for several carnivores Italy was probably an Ice Age refugium (e.g., *Panthera gombaszoegensis*, O'Regan et al. 2002). The role of humans is also enigmatic in Italy because, recently, there is evidence of early occupation since Pirro Faunal Unit (1.5–1.1 Ma) (Arzarello et al. 2007), even if the evident impact of *Homo* on the local fauna is recorded only at Isernia, dated at 600/500 ka (Anconetani and Peretto 1996; Coltorti et al. 2005).

Application of geometric morphometrics to the Italian large carnivore fauna represents an opportunity to explore the evolution of morphological variability through the Plio-Pleistocene. It is also possible to illuminate mechanisms that drove compositional changes of guilds by comparing Plio-Pleistocene with extant carnivore guilds (cf. Van Valkenburgh 1988). The metric of comparison is, here, represented by morphological disparity (Foote 1992). Such a metric is ideal to quantify morphological variability with a multivariate dataset. Usually, disparity is applied to principal components scores with several formulae (Ciampaglio et al. 2001) that allow computing the amount of morphospace occupied by the sample of interest in a broad context. Previous studies focused on understanding morphospace occupation of distinct clades at large time scale (Foote 1992, 1993, 1997; Wills et al. 1994; Holliday and Steppan 2004; Wesley-Hunt 2005). Van Valkenburgh (1988, 1989) already performed several analyses to explore morphospace occupation of large carnivore guilds through space and time, finding few significant differences at large scale. This study has the same spirit as Van Valkenburgh's surveys (1988, 1989) but I will look at lower jaw shape variability through geometric morphometrics and the Procustes Distances (PD) will be the metric used to compute disparity (Zelditch et al. 2003, 2004). This approach permits the obtaining of conservative estimates of the shape disparity in order to compare guilds through space and time.

Institutional abbreviations.—BMNH, The Natural History Museum (formerly British Museum of Natural History) London, UK; HM, Huntherian Museum and Art Gallery, University of Glasgow, Glasgow, Scotland, UK; IGF, Museo di Geologia e Paleontologia dell'Università di Firenze, Firenze, Italy; IGME, Istituto Geológico y Minero de España, Museo Geominero, Madrid, Spain; MCZR, Museo Civico di Zoologia, Roma, Italy; MGPD, Museo di Paleontologia Università di Padova, Padova, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNPE, Museo Nazionale Preistorico Etnografico "Luigi Pigorini", Roma, Italy; MZLS, Museo Zoologico "La Specola", Firenze, Italy; NMB, Naturhistorisches Museum Basel, Switzerland; ZSM, Zoologische Staatssammlung München, Munich, Germany.

Other abbreviations.—GPA; Generalised Procustes Analysis; MD, Morphological Disparity; PCOM, Paleo-Communities; RW, Relative Warps.

Material and methods

Sample size.—A subset of 57 large mammals of the order Carnivora was considered in order to explore morphological variability of the mandible through space and time. Each species is represented by one adult specimen, either modern, collected from the wild, or fossil (Appendix 1). In this way, both extant and extinct species exhibit similar random bias due to sampling. Indeed, fossil mandibles are unsexed and in this study intraspecific morphological variability is assumed to be negligible (cf. Van Valkenburgh 1985, 1988, 1989; Raia 2004; Christiansen and Adolfssen 2005; Evans et al. 2007; Polly and MacLeod 2008). Thirty-four species of extant carnivores were chosen according to the taxonomic list (source: Biological Inventory 2004, http://www.ice.ucdavis.edu/bioinventory/bioinventory.html) of the most representative large carnivore guilds in the world (for Europe, Czech Republic, Krokonose; USA, Yellowstone; Indonesia, Gunung Lensung; Africa, Kruger National Park; and Peru, Otishi National Park). Large carnivores are defined as species whose mean body mass is larger than 7 kilograms (Van Valkenburgh 1988). Amphibious and aquatic carnivores were excluded from the analysis because they rarely compete directly with large terrestrial taxa (Van Valkenburgh 1985, 1988). For the Plio-Pleistocene guilds, a total of 23 species of large carnivores were chosen as representatives of nine Italian Paleo-Communities (PCOMs): Triversa, 3.2 Ma; Montopoli, 2.6 Ma; Up Valdarno, 1.9 Ma; ValdiChiana, 1.5 Ma; Pirro, 1.1 Ma; Galerian 1, 0.8 Ma; Galerian 2, 0.6 Ma; Galerian 3, 0.45 Ma; and Aurelian, 0.3 Ma (as in Raia et al. 2005, 2006; Meloro et al. 2007, 2008a).

Each species is represented in the overall sample by one mandible even if it belongs to several guilds. For the extant guilds the puma (*Puma concolor*) is represented in two areas (USA and Peru), as is the grey wolf (*Canis lupus*) and the brown bear (*Ursus arctos*) (USA and Europe). A pilot survey performed with the sample of both North American and South American specimens of puma together with North American and European specimens of wolf showed that a high degree of overlap among specimens did not affect the accuracy of analyses performed by using one specimen/species. For Plio-Pleistocene guilds, multiple appearances are much more common (e.g., *Acinonyx pardinensis* is present continuously from PCOMs Triversa to Pirro). Unfortunately, it was not possible to collect sufficiently complete specimens for the same species in each PCOM. Fossil lower jaws of large carnivores are usually rare, especially for Villafranchian forms.

When available, Italian fossil specimens were considered as representatives of Plio-Pleistocene species. For Pleistocene species, I chose fossil specimens, even if the species could be present in the extant ecosystem, because their morphology could have been substantially different. In a few cases, fossil species were replaced by other similar morphotypes. It was not possible to include *Homotherium latidens* and *Megantereon whitei*; they were substituted by their ancestors (*H. crenatidens* and *M. cultridens*), for which mandibles were available. There are no significant fossils of *Chasmaporthetes lunensis*; the lower jaw was substituted by an incomplete mandible of *Chasmaporthetes kani*. The little Pleistocene wolf of the Galerian fauna (*Canis* aff. *arnensis*) is represented by a specimen from the Valdarno basin because of the lack of mandibles complete enough for the analysis. Aurelian canids are, here, represented only by *Canis* sp. from Grotta Romanelli. This specimen probably belongs to the grey wolf or to an advanced form of *C. arnensis*. Although it is plausible that both *C.* aff. *arnensis* and *C. lupus* were simultaneously present during the Aurelian in Italy, the fossil record is scanty for such forms and more robust taxonomic revision is needed.

Geometric morphometrics.—Mandibles were photographed in lateral view at two metres using a Nikon 995 digital camera. This procedure standardises the sample of digital images and minimises parallax (Raia 2004; Meloro et al. 2008b). Nine landmarks were digitised with the software tpsDig 2 (Rohlf 2006a) to describe the mandibular corpus shape (Fig. 1). This region allows the inclusion of fragmentary fossil specimens; as well, previous studies have demonstrated that it is informative to the study of trophic morphology in Carnivora (Crusafont-Pairó and Truyols-Santoja 1956, 1957, 1958; Van Valkenburgh 1988, 1989; Meloro et al. 2008b).

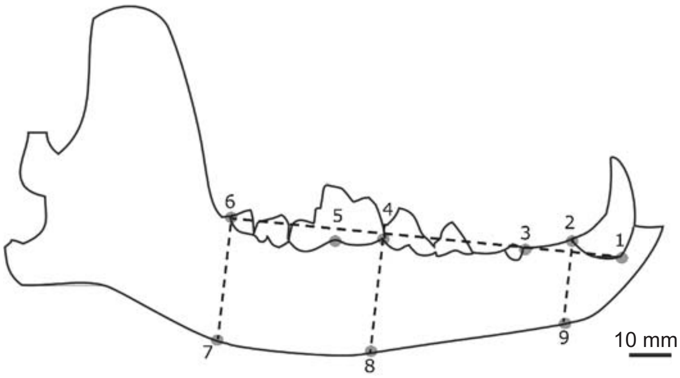

Fig. 1. Landmark configuration on a mandible of *Canis lupus*, BMNH 34.6.28.47.

Meloro et al. (2008b) applied a landmark configuration that describes the relative position of p4 and m1 in the mandible of Carnivora. Here, I chose a different configuration which is more informative because includes the entire premolar row and the relative position of slicing versus crushing area. Landmarks 1, 2, 3, 4 and 6 were recorded at the tip of the teeth alveoli. In particular, 1–2 records the length of the canine, 3–4 the premolar row, and 4 and 6 the molar row (Fig. 1). Landmark 5 is functionally defined as the slicing portion of the lower carnassial in lateral view (Crusafont-Pairó and Truyols-Santoja 1956, 1957, 1958; Van Valkenburgh 1988, 1989). It is recorded on the tooth edge and positioned as the projection of the protocone cusp on the m1 baseline (Fig. 1). In some cases, when there is no crushing area in the molar row, it overlaps with landmark number 6. Landmarks 7 to 9 are the projections on the ventral edge of the corpus of landmarks 6, 4, and 2 perpendicular to the curve joining the line 1–6. Distances 2–9, 4–8, and 6–7 record the thickness of the mandibular corpus under the canine and the mesial and distal ends of the molar row, respectively (Fig. 1).

A Generalised Procustes Analysis (GPA) was performed on 2-dimensional landmark coordinates in order to translate, rotate and scale at unit centroid size (i.e., the square root of the mean squared distance from each landmark to the centroid of each configuration, Bookstein 1989) the landmark configurations (Rohlf and Slice 1990; Adams et al. 2004).

GPA generates a new set of coordinates (Procustes) that represent shape variables. The latter can also be decomposed into affine (Uniform) and non-affine components (Partial Warps), which are eigenvectors of the bending energy matrix (Bookstein 1996; Zelditch et al. 2004).

A Principal Component Analysis of the Partial Warps and Uniform components allows obtaining vectors of maximum variation (Relative Warps or RW) that describe major shape changes of each specimen relative to the mean (consensus) configuration. Shape changes along RW axes are graphically described by Thin Plate Spline deformations (Bookstein 1996). The software tpsRelw vs. 1.44 (Rohlf 2006b) was used to compute PCA and deformation grids.

Morphospace disparity.—Morphospace comparison for each guild (extant and extinct) was assessed by computing Morphological Disparity (MD) (Foote 1992, 1993). Disparity is a measure of morphological variability. The formula of Foote (1993) for morphological disparity is:

$$MD = \frac{\sum_{i=1}^{N} d_i^2}{(N-1)}$$

where d_i represents the distance of the ^{ith}specimen to the group centroid while N is the number of specimens in the group considered. In the geometric morphometric case d_i is the Procustes distance between the average shape of each group i and the grand mean shape, N is the number of groups (Zelditch et al. 2003, 2004). For this study, MD was computed after applying a bootstrap procedure (999 random models) to obtain 95% confidence intervals around the original values. This procedure allows taking into account the uncertainty in the computation of the mean shape in the hyperspherical morphospace (Zelditch et al. 2003, 2004).

Groups are defined in order to compare extant and Plio-Pleistocene carnivores. Disparity values were computed for extant (34 species) and fossil specimens (23 species), separately. For a detailed analysis, groups are defined as each separate guild (in space and time). Fourteen guilds (9 for Plio-Pleistocene PCOMs and 5 for extant ecosystems) are considered. Patterns of potential relationship between disparity values and other variables were explored by using a linear correlation coefficient. The number of carnivores composing each guild (sample size bias) and the number of prey species (= number of total herbivores, number of perissodactyls or number of artiodactyls, α diversity in Meloro et al. 2008a) were considered as potential mechanisms which affect disparity variability through space and time. Absolute values for such variables were all log transformed (Foote 1992).

A nearest-neighbour analysis was performed on each defined group in order to test hypotheses about clustering or over-dispersion of species lower jaw shape distribution in the morphospace (Zelditch et al. 2004). The morphospace occupied by each group is compared to all the possible morphospaces generated under a Monte Carlo bootstrap random simulation. The random sample (999 datasets) simulates data based on the observed sample that are assumed to follow a Uniform null model. The Uniform model considers equal the probability of being in any location of the morphospace and it is ideal for comparison among species (Zelditch et al. 2004). The P_i metric given by Foote (1990) was used to perform such comparisons between each group morphospace and the simulated random models. This is Foote's formula:

$$P_i = \frac{D_i - R_i}{R_i}$$

where D_i is the nearest-neighbor distance for each i of the N sample and R_i is the distance between an observed specimen and the nearest Monte Carlo simulated specimen. As the result of a difference between the observed and the random expected model, if P_i mean is equal to zero then non-significant difference occurs between the observed and the expected morphospace. If P_i is a negative value, the observed morphospace is clustered, while if it is positive the morphospace is over-dispersed. A range of 95% confidence intervals was computed around P_i by Monte Carlo simulation of the dataset many times (Zelditch et al. 2004). A Strauss and Sadler correction was applied in order to take into account the non-normality of morphospace distribution when sample size is small (Zelditch et al. 2004). "True" minimum and maximum values of the nearest-neighbour normal distribution are computed. All the analyses were performed with and without such correction, in order to make apparent any discrepancies (Zelditch et al. 2004). All the statistical analyses on disparity were computed with the IMP package Disparity box.

Results

Fourteen shape variables were extracted after GPA and then reduced with a RW analysis. The first four RWs explain more than 95% of the shape variability, with RW1 and 2 being the most informative (45.72% and 38.52% of the variance, respectively). On the other hand, RW3 and 4 explain less than 15% of the variance (9.38% and 2.02%, respectively).

The first three RW axes discriminate specimens on the basis of their familial affiliation (Fig. 2). RW1 describes shape changes in molar crushing area relative to slicing. On the second RW, shape changes occur in the relative corpus thickness as well as diastema and premolar length proportion. Some overlap occurs between Felidae and Hyaenidae because of their short or non-existent molar crushing area. All the caniforms (Canidae, Ursidae, and Mustelidae) have the positive scores for RW1 and negative scores for RW2 except *Mellivora capensis*, which is an outlier among the mustelids and cluster with feliforms (see white dot among triangles, Fig. 2). Interestingly, large viverrids from Africa occupy same region as small caniforms suggesting convergence in mandibular corpus shape. The third RW is associated with changes of canine-premolar row (length of the diastema) and its combination with the first and the second RWs underline the differences between Ursidae and remaining carnivores (Fig. 2).

A graphic display of morphospace regions occupied by each guild on RW1-2 is particularly informative for both extant and extinct ecosystems (Figs. 3, 4). All extant carnivore guilds tend to occupy the same morphospace regions except

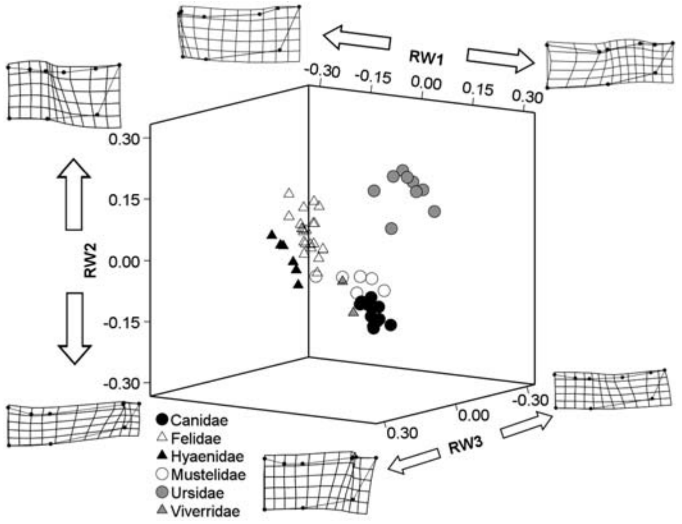

Fig. 2. Plot of the first three RWs in a subset of 57 mandibular corpus data of large carnivores.

the Kruger guild, where no bear morphotype is present (no specimens occupy the I quadrant). But the Kruger guild shows a greater number of other caniforms and feliforms. Plio-Pleistocene guilds overlap with each other and similar patterns of morphospace occupation emerge graphically (Fig. 4).

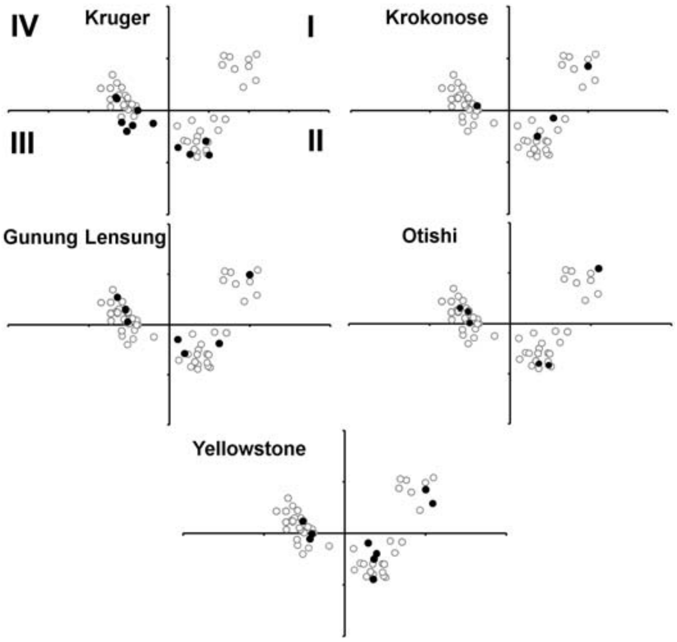

Fig. 3. Scatter plots of RW1 (X axis, scale -0.40 / +0.40) versus RW2 (Y axis, scale -0.40 / +0.40). Each extant large carnivore guild is highlighted by closed circles. The Kruger, Africa guild represents Africa, Krokonose is for Czech Republic, Gunung Lensung, Indonesia Lensung for Indonesia, Otishi for South America and Yellowstone for North America.

The degree of overlap between extant and extinct Plio-Pleistocene large carnivore guilds is more evident considering disparity values. The value computed for the morphospace defined by all extinct Plio-Pleistocene carnivores is slightly higher than that defined for extant large carnivores, but this difference is not significant because of large 95% confidence intervals (Fig. 5).

When disparity values are computed for each large carnivore guild, the overlap in morphospace variability still applies (Fig. 5). No significant differences occur between extant guilds; hence biogeographic phenomena seem not to have affected morphological variability (at least in corpus shape) of large carnivorous mammals. Disparity throughout the Plio-Pleistocene slightly increases after PCOM Triversa (3.5 Ma) and a very high peak is exhibited by the carnivore guild of 0.8 Ma (Galerian 1). Then disparity drops (Galerian 2) and increases again (Galerian 3). All the values are very similar to the one of extant guilds and no significant differences occur.

Morphological Disparity values are probably not influenced by sample size or number of prey in each guild ($p > 0.10$). This lack of correlation appears also when analysing extant ($N = 5$) and fossil ($N = 9$) guilds separately. A different signal occurs when considering number of artiodactyls. A scatter plot suggests a negative trend that is significant when all guilds are considered together ($N = 14$; $r = -0.546$; $p = 0.043$, Fig. 6) or in extant guilds ($N = 5$, $r = -0.94$, $p = 0.0023$), while fossil ecosystems exhibit no trend when analysed separately ($N = 9$, $r = -0.04$, $p = 0.90$).

The comparison between observed morphospace variability and that expected from the Monte Carlo bootstrapped uniform model allows understanding whether carnivore guilds were saturated by morphotypes (Table 1). All the carnivore guilds tend to be clustered (negative P_i values), even if Krokonose (European carnivores) and Galerian 1 are over-dispersed. Triversa has a morphospace distribution that is not different from random expectation. Such results demonstrate that most large carnivore guilds can be considered saturated by morphotypes: they occupy less morphospace than expected by chance. It is worth noting that these results were extracted by

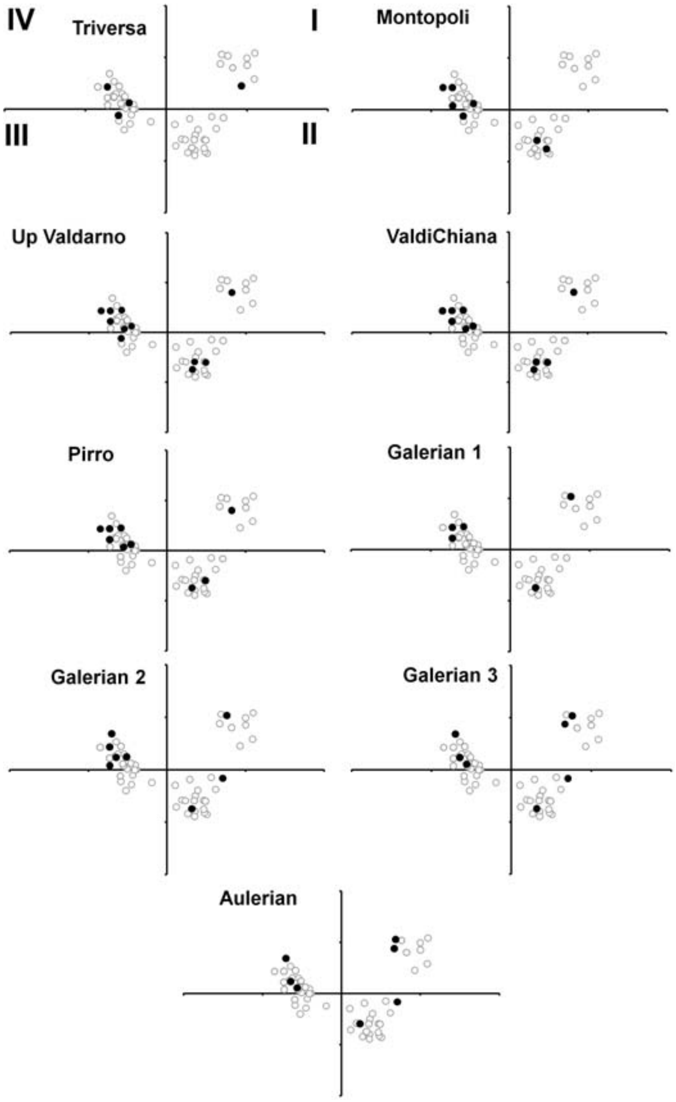

Fig. 4. Scatter plots of RW1 (X axis, scale -0.40 / +0.40) versus RW2 (Y axis, scale -0.40 / +0.40). Each Plio-Pleistocene carnivore guild is highlighted by closed circles. Guild are representative of distinct Paleo-Communities trough time: Triversa, 3.2 Ma; Montopoli, 2.6 Ma; Up Valdarno, 1.9 Ma; ValdiChiana, 1.5 Ma; Pirro, 1.1 Ma; Galerian 1, 0.8 Ma; Galerian 2, 0.6 Ma; Galerian 3, 0.45 Ma; and Aurelian, 0.3 Ma.

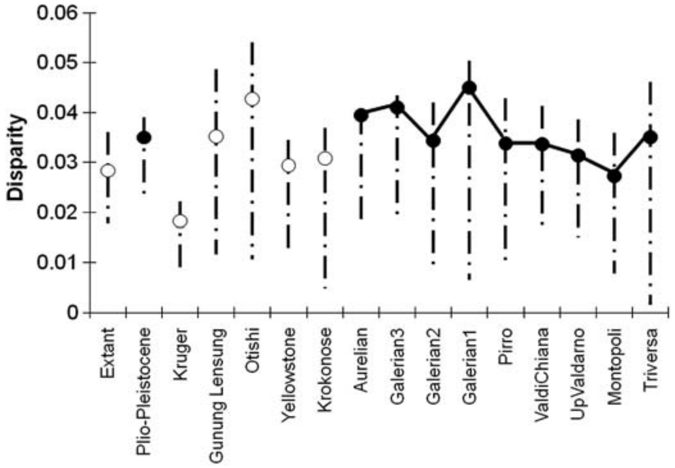

Fig. 5. Disparity values computed for morphospace of each extant and Plio-Pleistocene large carnivore guild. Lines define 95% confidence interval under 999 randomizations. Extant is for all living taxa (N = 34) while Plio-Pleistocene stand for all fossil taxa (N = 23). Kruger, Africa is for Africa, Gunung Lensung, Indonesia for Indonesia, Otishi for South America, , Yellowstone for North America, Krokonose for Czech Republic. Fossil communities are ordered from the youngest to the oldest: Aurelian, 0.3 Ma; Galerian 3, 0.45 Ma; Galerian 2, 0.6 Ma; Galerian 1, 0.8 Ma; Pirro, 1.1 Ma; ValdiChiana, 1.5 Ma; Up Valdarno, 1.9 Ma; Montopoli, 2.6 Ma; Triversa, 3.2 Ma.

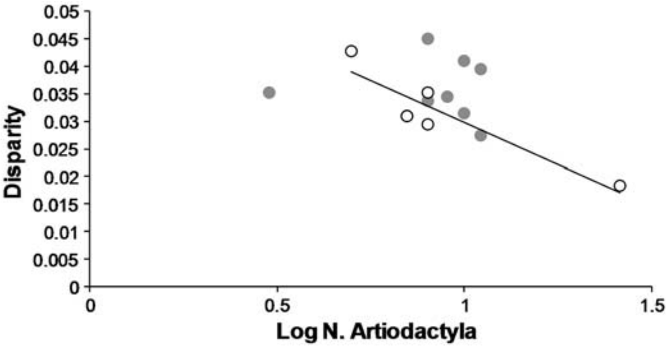

Fig. 6. Scatter plot of log number of artiodactyls vs. large carnivore disparity values. Open circles, extant ecosystems; closed, fossil ecosystems. A linear trendline is placed on extant data points. Open circles represent extant ecosystem including Kruger, Africa, Africa; Gunung Lensung, Indonesia Lensung, Indonesia; Otishi, South America; Yellowstone, North America; Krokonose, Czech Republic. Closed circles are fossil communities: Triversa, 3.2 Ma; Montopoli, 2.6 Ma; Up Valdarno, 1.9 Ma; ValdiChiana, 1.5 Ma; Pirro, 1.1 Ma; Galerian 1, 0.8 Ma; Galerian 2, 0.6 Ma; Galerian 3, 0.45 Ma; and Aurelian, 0.3 Ma.

using a Strauss and Sadler range, and they are validated when this correction is not applied. Only in the case of over-dispersed guilds are there different results that suggest a morphospace distribution similar to the expected random model (for Krokonose P_{mean} = 0.1675 with range -0.0330 to 0.4376; and for Galerian 1 P_{mean} = 0.0830 with range -0.0540 to 0.2254).

Discussion

The lack of differences in mandibular corpus shape disparity among large carnivore guilds through space and time is not an unexpected trend. As suggested by Van Valkenburgh (1988, 1995), morphological diversity in the trophic apparatus of carnivores was already achieved more than 30 million years ago and it remains constant probably because of competition (as a strong driving force in moulding carnivore diversity) as well as unchanged pattern in the nature of consumed resources (skin and bone structure of prey remain basically the same). The morphospace identified by mandibular corpus shape is informative from a taxonomic perspective and it shows that the landmark configuration chosen discriminates hypercarnivorous taxa from more generalist one (Fig. 2). Interestingly, this dichotomy is not entirely "phylogenetic" if we consider the suborder level (Caniformia–Feliformia, Bryant 1996). Extant viverrids overlap with both canids and mustelids, suggesting that convergence occurs in these clades. Ewer (1973) identified common features between Caniformia and Viverridae which are possibly the result of parallel evolution, while Friscia et al. (2007) noted functional convergence due to similar dietary adaptations. Morphospace regions also show an ecological signal even if hypercarnivorous canids (grey wolf *Canis lupus*, African wild dog *Lycaon pictus*, dhole *Cuon alpinus*; sensu Van Valkenburgh 1991) are not grouped with the specialist predators such as felids and hyaenids. Meloro et al. (2008b) already explained this lack of overlap in corpus shape because of the extremely reduced dentition of hypercarnivore feliforms. This pattern is even more evident because of the different landmark configuration used in this study.

In general, the I and the II quadrants of RW1-2 morphospace are occupied by caniforms and feliforms with a generalist dentition and more elastic feeding behaviour (primarily omnivores). Members of Ursidae are the most distinctive because they are characterised by an elongated molar crushing

Table 1. P_i values exhibited by each guild morphospace. Range values are computed after 999 random permutations following the Strauss and Sandler distribution.

Guild	P_{mean}	Range	
Extant	-0.5895	-0.6378	-0.534
Plio-Pleistocene	-0.4944	-0.5507	-0.4347
Kruger	-0.3307	-0.4089	-0.231
Gunung Lensung	-0.3391	-0.4404	-0.2219
Otishi	-0.4531	-0.5248	-0.3164
Yellowstone	-0.4661	-0.5452	-0.3777
Krokonose	0.265	0.0188	0.5436
Triversa	-0.0474	-0.1751	0.207
Montopoli	-0.4168	-0.492	-0.309
Up Valdarno	-0.4114	-0.4824	-0.3316
ValdiChiana	-0.3882	-0.46	-0.2706
Pirro	-0.3685	-0.4451	-0.2601
Galerian 1	0.1439	0.019	0.3144
Galerian 2	-0.2203	-0.3	-0.102
Galerian 3	-0.1703	-0.2679	-0.0222
Aurelian	-0.2227	-0.3311	-0.0629

area, a very thick corpus, and an extremely reduced premolar row. These features evolved since the Pliocene, an important time period for the evolution of the subfamily Ursinae (Kurtén 1968; Mazza and Rustioni 1994). The phylogenetic pattern in morphospace occupation (Fig. 2) preludes a lack of differentiation between extant and Plio-Pleistocene fossil carnivore guilds. The presence of slash and ambush stalkers (long canine cat morphotype, sensu Werdelin 1996) as well as of specialised bone crackers (hyenas of the genus *Pachycrocuta* and *Pliocrocuta*) do not alter morphospace occupation; and even distinct taxa, such as *Chasmaporthetes,* clearly cluster according to their family affiliation (Hyaenidae, Figs. 2, 4). Plio-Pleistocene canids that characterise the Wolf event are all part of modern Canini radiation (Rook and Torre 1996; Wang and Tedford 2008) and they share with them similar mandibular corpus morphology (Fig. 2 but see also II quadrant from Montopoli until Pirro, Fig. 4). The racoon-dog like ancestor (*Nyctereutes megamastoides*) is present only in Montopoli, occupying the second quadrant.

Galerian 1 (0.8 Ma) possibly represents a period when important changes occurred in the large carnivore guild. Several Villafranchian taxa persisted among feliforms (*Homotherium*, *Pachycrocuta* and *P. gombaszoegensis*), while one species of dog (*C. arnensis*) and the newcomer cave bear (*Ursus deningeri*) are the only Caniformia. This large carnivore guild was soon filled in Galerian 2 by pantherine cats, cave lynx, the reappearance of *Pliocrocuta perrieri* (according to Turner 1995), the large mustelid *Meles meles*, and the brown bear *Ursus arctos*. In Galerian 3 *Homotherium* disappears even if the feliform region is overfilled by lion (*Panthera leo*), leopard (*Panthera pardus*), and spotted hyena (*Crocuta crocuta*), that persist in the Aurelian.

Clearly, the disappearance of archaic “ecomorphs” (e.g., long-canine cats, giant hyenas) does not affect morphospace occupation because they were soon replaced by newcomers. This result is also supported by the analyses of species diversity as presented in Meloro et al. (2008a), where number of species of large carnivores remained relatively unchanged throughout the Plio-Pleistocene.

The geometric morphometric approach to the quantification of morphological disparity appears to be robust and insensitive to sample size variation. As confidence intervals are very large, it is necessary to interpret Morphological Disparity values with caution. Yet, the small variability of shape disparity exhibits several counterintuitive relationships in need of further explanation. Van Valkenburgh (1988) pointed out that changes in disparity among large carnivore guilds could be related with the number of prey. Here, the absolute number of prey does not affect morphological disparity, even if number of Artiodactyla does in a negative way. It is likely that the latter parameter is more informative because artiodactyls do not include megaherbivores (species > 1000 kg), which are rarely preyed by large carnivores in both extant and possibly ancient ecosystems (Owen-Smith 1988; Meloro et al. 2007). Nevertheless, the mix of scales (temporal and spatial) clearly suggests that number of artiodactyls influence only MD of extant carnivore guilds.

Extant large carnivores are represented by very different ecosystems whose zoogeographical evolutionary history could be possibly traced back before the Plio-Pleistocene. On the other hand, carnivore communities of the Plio-Pleistocene that were analysed belong to a very restricted time period —3.5 Ma/0.3 Ma—where the dramatic climate changes affected only partially the local fauna of large mammals (Raia et al. 2005; Meloro et al. 2008a; Blois and Hadly 2009). Because of this, MD changes are not particularly informative when comparing community assemblages that are too similar.

For extant ecosystems, Van Valkenburgh (1988) already explained the greater morphological richness of tropical carnivore guild as a consequence of a greater productivity of such ecosystems (measured as number of prey). Interestingly, she pointed out that the most productive ecosystems (Serengeti and Indonesia, cf. Kruger and Gunung Lensung in the present analysis) have the same number of hypercarnivore predators and are strikingly similar if we exclude the presence or absence of a bearlike morphotype. This latter point is central to explaining corpus shape disparity in modern carnivore community. Indeed, the European carnivore guild shows a random to over-dispersed morphospace occupation as the result of high morphological differentiation among species. Counter intuitively, this is due to the small diversity in prey. A low number of ungulate species affects guilds of mammalian carnivores because it can support very few specialist meat-eaters. On the other hand, omnivore Carnivora morphotypes have little competition for resources and can grow in number. The latter occupy extreme regions of morphospace (e.g., bears, canids, mustelids), increasing the relative volume.

Changes of MD through time are possibly better interpreted on the light of theories on morphospace occupation. Van Valkenburgh (1995) described in carnivores a phenomenon of morphospace occupation in time that does not conform to general theory: “ecomorphs” tend to invade central and not extreme positions in morphospace through time. All the analysed guilds are clustered in the morphospace except Krokonose, Triversa, and Galerian 1. They have the smallest numbers of large carnivores (respectively 4, 4, and 5) and all of them have an ursid in the faunal composition. The relative warp plots (Fig. 3, 4) help identify a common unbalanced morphospace occupation in such ecosystems (more than one ecomorph present only in a particular region of morphospace e.g., II quadrant with RW1+ and RW2- scores in Krokonose; or IV quadrant in Galerian 1, with three catlike morphotypes).

This phenomenon also validates the negative relationship between disparity and productivity values (number of artiodactyls), because extreme omnivore “ecomorphs” can occupy ecosystems with low numbers of ungulates. Moreover, Dalerum et al. (2009) demonstrated that the extant European large carnivore guild exhibits a depleted fauna, possibly the result of extinction without replacement. This explanation applies also to Triversa and Galerian 1, periods of important structural changes for the Italian mammal fauna (Meloro et al. 2008a).

It is likely that corpus shape disparity of Italian Plio-Pleistocene carnivores can be considered a comparative metric to explore some biological reason for small variations that are not intimately affected by climate changes. There is increasing evidence that the structure of European Plio-Pleistocene large mammalian communities should reflect accurately changes in climate (Hernández Fernández and Peláez-Campomanes 2003, 2005; Rodriguéz et al. 2004; Raia et al. 2005, 2009; Meloro et al. 2008a). Mendoza et al. (2005) underlined that ecological assembly of mammalian communities is an intrinsic property of the ecosystems, which reflects habitat complexity. Such evidence comes from quantitative models where all mammals are considered. In this case, the inclusion of the ungulate community has a key role because herbivores are intimately related to the physical environment (Janis 1984; Janis et al. 2000, 2004; Owen-Smith 1988; Fortelius et al. 2002). Hence the role of carnivore community structure is only marginal to define changes in physical environment, and this fact can be explained biologically. Hernández Fernández and Vrba (2005) reported for the African mammal fauna a large proportion of eurybiomic carnivores compared to herbivores. This means that carnivores generally tend to occupy more biomes than other species in lower trophic levels. As a consequence, it is likely that such generalisation is also valid for Ice Age European carnivores—hence morphological variability of such group does not reflect climatic oscillations. In support of this contention, O'Regan et al. (2002) consider the Italian peninsula a possible Ice Age refugium for a large carnivore like *Panthera gombaszoegensis*. It is likely that large carnivore communities of Italy were less affected by climate than assemblages of Northern Europe.

Conclusion

Corpus shape disparity of large carnivore guilds did not change significantly through space and time. In extant ecosystems, corpus shape disparity is negatively affected by the number of artiodactyls because of broad evolutionary, zoogeographical differences.

Large carnivores tend to saturate central morphospace areas, confirming (for both extant and extinct ecosystems) that ecomorph specialisation does not occur in extreme regions of morphospace (Van Valkenburgh 1995). Shape disparity of large carnivore guilds in Plio-Pleistocene ecosystems is possibly influenced by species turnover. Interestingly, some large carnivore guilds (Triversa, Galerian 1, and Krokonose) are outliers in morphospace occupation, exhibiting an ecomorph-random distribution (or over-dispersed) and unusual disparity values for their numbers of species. They indicate periods—or areas—characterised by low carnivore diversity (reflected by number of species) with a high morphological variability.

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Appendix 1

List of mandible specimens photographed with family affiliation and guild membership.

Guild membership is ascribed accordingly to the presence of a species in a geographic or temporal area. When species are present continuously from one PCOM to another I used the score "–" (e.g., *Meles meles* is present from PCOM Galerian 2 to Aurelian), but when their presence is validated only for certain periods I used the suffix "&" (e.g., *Pliocrocuta perrieri* is present in Montopoli and Galerian 2 but not in the other PCOMs, that is no range through is applied).

Species	Family	Catalogue N.	Guild
Acinonyx jubatus	Felidae	BMNH 1927.2.11.16	Kruger, Africa
Arctictis binturong	Viverridae	BMNH 84.5.19.8	Gunung Lensung, Indonesia
Arctonyx collaris	Mustelidae	BMNH 38.10.10.1	Gunung Lensung, Indonesia
Atelocynus microtis	Canidae	BMNH 26.15.5	Otishi, South America
Canis adustus	Canidae	BMNH 34.11.1.6	Kruger, Africa
Canis latrans	Canidae	BMNH 2.3.7.4	Yellowstone, USA
Canis lupus	Canidae	BMNH 34.6.28.47	Yellowstone, USA; Krokonose, Czech Republic
Canis mesomelas	Canidae	BMNH 27.8.14.2	Kruger, Africa
Catopuma temminckii	Felidae	BMNH 23.1.7.7	Gunung Lensung, Indonesia
Civettictis civetta	Viverridae	BMNH 66.778	Kruger, Africa
Crocuta crocuta	Hyaenidae	BMNH 28.9.11.183	Kruger, Africa
Cuon alpinus	Canidae	BMNH 44.11.9.3	Gunung Lensung, Indonesia
Gulo gulo	Mustelidae	BMNH 14.5.1.1	Yellowstone, USA
Helarctos malayanus	Ursidae	BMNH 1938.11.30.70	Gunung Lensung, Indonesia
Leopardus pardalis	Felidae	BMNH 1910.9.29.12	Otishi, South America
Leptailurus serval	Felidae	BMNH 70.679	Kruger, Africa
Lycaon pictus	Canidae	BMNH 99.6.29.1	Kruger, Africa
Lynx canadensis	Felidae	BMNH 92.4.19.1	Yellowstone, USA
Lynx lynx	Felidae	BMNH 69.10.19.16	Krokonose, Czech Republic
Lynx rufus	Felidae	BMNH 19.4.2.1	Yellowstone, USA
Meles meles	Mustelidae	BMNH 11.6.3.13	Krokonose, Czech Republic
Mellivora capensis	Mustelidae	BMNH 86.9.4.08	Kruger, Africa
Neofelis nebulosa	Felidae	BMNH 58.6.24.49	Gunung Lensung, Indonesia
Panthera leo	Felidae	ZSM 1952/174	Kruger, Africa
Panthera onca	Felidae	BMNH 1987.236	Otishi, South America
Panthera pardus	Felidae	BMNH 35.10.22.71	Kruger, Africa
Panthera tigris	Felidae	MCZR 2002.186	Gunung Lensung, Indonesia
Parahyaena brunnea	Hyaenidae	BMNH 35.9.1.288	Kruger, Africa
Pseudalopex culpaeus	Canidae	BMNH 1903.7.9.3	Otishi, South America
Puma concolor	Felidae	BMNH 1901.11.14.1	Otishi and Yellowstone
Taxidea taxus	Mustelidae	BMNH 1856.4.11.3	Yellowstone, USA
Tremarctos ornatus	Ursidae	BMNH 27.11.1.7	Otishi, South America
Ursus americanus	Ursidae	BMNH 61.1282	Yellowstone, USA
Ursus arctos	Ursidae	BMNH 88.2.20.3	Yellowstone, USA; Krokonose, Czech Republic
Ursus minimus	Ursidae	IGF11568	Triversa (3.2 Ma)
Nyctereutes megamastoides	Canidae	IGME-s-I739M	Triversa (3.2 Ma)
Acinonyx pardinensis	Felidae	MNCN47141	Triversa (3.2 Ma) – Pirro (1.1 Ma)
Canis arnesis	Canidae	IGF 868	Up Valdarno (1.9 Ma) – Galerian 3 (0.45 Ma)
Canis etruscus	Canidae	IGF 856	Montopoli (2.6 Ma) – ValdiChiana (1.5 Ma)
Lycaon falconeri	Canidae	IGF 683V	Up Valdarno (1.9 Ma) – Pirro (1.1 Ma)
Chasmaporthetes kani	Hyaenidae	Cast MNHN-F:AM99788	Triversa (3.2 Ma) – ValdiChiana (1.5 Ma)
Homotherium crenatidens	Felidae	Cast MNHN PER2000	Triversa (3.2 Ma) – Galerian 2 (0.6 Ma)

Species	Family	Catalogue N.	Guild
Lynx issiodorensis	Felidae	MNHN no cat	Up Valdarno (1.9 Ma) – Pirro (1.1 Ma)
Megantereon cultridens	Felidae	MNHN coll. Croizet	Up Valdarno (1.9 Ma) – Pirro (1.1 Ma)
Pachycrocuta brevirostris	Hyaenidae	MNCN no cat.	Up Valdarno (1.9 Ma) – Galerian 1 (0.8 Ma)
Panthera gombaszoegensis	Felidae	IGF4375	Up Valdarno (1.9 Ma) – Galerian 1 (0.8 Ma)
Ursus etruscus	Ursidae	Cast MNHN IGF1880-1	Up Valdarno (1.9 Ma) – Pirro (1.1 Ma)
Pliocrocuta perrieri	Hyaenidae	IGF 5504V	Montopoli (2.6 Ma) & Galerian 2 (0.6 Ma)
Lynx sp.	Felidae	MNPE 25	Galerian 2 (0.6 Ma)
Panthera leo	spelea	MGPD 25264	Galerian 2 (0.6 Ma) – Aurelian (0.3 Ma)
Panthera pardus	Felidae	IGF 10034	Galerian 2 (0.6 Ma) – Aurelian (0.3 Ma)
Meles meles	Mustelidae	MNPE 2404	Galerian 2 (0.6 Ma) – Aurelian (0.3 Ma)
Ursus deningeri	Ursidae	BMNH M6186	Galerian 1 (0.8 Ma) – 3 (0.45 Ma)
Ursus arctos	Ursidae	MNPE 32	Galerian 3 (0.45 Ma) – Aurelian (0.3 Ma)
Canis sp.	Canidae	MNPE 3589	Aurelian (0.3 Ma)
Crocuta crocuta	Hyaenidae	MNPE F3	Galerian 3 (0.45 Ma) – Aurelian (0.3 Ma)
Ursus spelaeus	Ursidae	HM V5226	Aurelian (0.3 Ma)