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Plio-Pleistocene large carnivores from the Italian peninsula: functional morphology and macroecology

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To my family & Adele

Abstract

The evolutionary history of large carnivorous mammals through the Ice Age have been investigated for the Italian peninsula. No endemisms are recorded in the mainland of Italy and large carnivore species composition reflected the similar fauna of European continent.

Morpho-ecological adaptation of extinct Plio-Pleistocene species have been investigated throughout temporal PaleoCommunities (9 PCOMs – spanning 3.2 to 0.3 Ma) with statistical accuracy. Trophic apparatus of extant and extinct species was investigated with a geometric morphometric analysis of mandible shape while locomotory habits were assessed using long bone indices.

The mandible shape analysis performed on extant Carnivora taxa confirms their morphological differences due principally to taxonomic affiliation (family). Although, when phylogenetic history is controlled with comparative methods, significant differences still to occur among taxa with different diets and between small and large forms (threshold posed at 7 kilograms). Interestingly, both mandibular regions (corpus and ascending ramus) are informative of Carnivora ecological adaptations and they result integrated at a macroevolutionary scale.

This survey allows to consider geometric morphometric as a reliable technique to apply on fossil mandibles. Feeding habits have been predicted with a good degree of accuracy in several Plio-Pleistocene large carnivores on the basis of mandible shape data. The latter data –selecting only the corpus region- have been considered also to perform a morphospace comparison between large carnivore guilds of Italian PCOMs and extant guilds representative of five mainland ecosystems worldwide. Disparity values computed for mandibular corpus shape of Plio-Pleistocene guilds did not differ significantly from extant guilds. Morphological variability in mandible shape is negatively influenced by number of species in each guild as well as number of prey confirming that ecomorph specialization does not occur at the extreme region of morphospace.

Long bone proportions of Plio-Pleistocene large carnivores are grouped in the variability of extant species. Although some phenomena of morphological convergences occur among extinct and extant taxa because of similar locomotor adaptation (e.g. cursorial) and same body size constraint. These morphoecological data were also used to predict the relative adaptability of Plio-Pleistocene species to certain habitats (grassland and tropical).

The macroecological analysis of presence/absence data confirms the striking relationship between the abundances of both predators and their prey thought Ice Age. On the other hand no morpho-ecological coordinate changes occurs between predators and their prey. It is noteworthy that large carnivores are overrepresented in the Italian fossil record and became rarer from Galerian to the Aurelian (also because of a possible interaction with human activities).

A GIS model was then computed to compare large mammal communities toward Plio-Pleistocene in Italy. Structural changes occurred in large herbivore communities from Villafranchian through the Aurelian because of climate changes. On the other hand, the spatial structure of large carnivore communities was more affected by their prey during the Villafranchian, while in the Galerian and Aurelian there was a greater influence of uncontrolled factors like climate and human activity as well.

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Index

Preface

“Why am I a human being in the XXI century?
I am surrounded by screens, information, and screens again.
I wanted to be a human being in the Ice Age
Surrounded by mammoths, sabertooths, hyenas
Companions of an endless fear”
(Colamarco A., 2007)

There is an increasing evidence of the intimate relationship between large mammal communities and the environment they occupy through space and time. Among the taxonomic groups, the order Carnivora is certainly the most peculiar to analyse because most of the large members of this group are apex predators and are more influenced by their vertebrate prey.

On the other hand, large carnivores always fascinated and stimulated human culture because they are represented by charismatic species (Gittleman et al. 2004). There is a huge amount of data on the ecology and behaviour of extant species and a similar knowledge has been achieved on extinct species.

Van Valkenburgh (1999, 2007) reviewed the evolutionary history of Carnivora worldwide but the effect of environmental factors (e.g. climate) on carnivore diversity (both morphological and numerical) still to be enigmatic (cfr. Werdelin 1996, Wesley-Hunt 2005).

This issue is a special question to clarify not only theoretically but also on the light of the recent practical conservation biology (e.g. re-wilding North America in Donland et al. 2006). Basically, the world of biological conservation have been stimulated by the idea that large mammals once roaming North America could come back (Donland 2007). Among the others, the cheetah (*Acinonyx jubatus*) and the lion (*Panthera leo*) have been considered as possible candidate for this conservation experiment considering their critical status in Africa and their relatively high abundance in captivity. As a “carnivore obsessed” individual this idea fascinated me and I felt a mix of curiosity and uncertainty to imagine grey wolves and lions fighting (again). But I must admit that this proposal underlines a current change in science and I am convinced that palaeontology needs to be part of this change. What is stimulating is the fact that this idea comes from the world of Conservation Biology. The formalization of this discipline is relatively recent (if compared to palaeontology) and I always remember one of the earliest paradigm: Conservation Biology is a “crisis discipline” and needs to consider multiple approaches (Natural Sciences and Social Sciences) (Meffe, Carroll et al. 1997).

The evolutionary history of mammals is usually included as background for conservation of organisms but I was always disappointed by the poor integration among disciplines. That is results coming from studies that consider fossils as backbone data are rarely integrated in conservation programs. Especially if we consider studies of large mammal communities, palaeontologists and conservation biologists used to run on two parallel binaries. But this approach is changing especially on the light of the new application and open sources database on mammal fossil record (e.g. FAUNMAP 1996; NOW database 2003). There is an increasing application of new techniques to palaeontological data and this result in more accurate outputs that could be useful also to practical issue.

In the course of my research I tried to be in line with this "wind of change" and the application of several new statistical techniques to the Italian Plio-Pleistocene fossil record reveal at least to gave reliable results. The topic of the present thesis born from my personal background and reflects my interests but I tried to focus on several questions which are not only "evolutionary attractive" but also useful for a potential practical issue.

The period analysed is of particular interest because Plio-Pleistocene have seen the spread of humans but also the striking change in climate. I am indebted to the seminal job of European systematic palaeontologists (the list could be endless) which furnished the backbone to re-evaluate critically the Italian fossil record.

The question I tried to answer is simple: "what factors influenced the evolution of large carnivores mammals during Plio-Pleistocene in the Italian peninsula?". But in its simplicity there are multiple effect to consider and to control: changes in climate, changes in herbivore communities, inter-specific interactions, interaction with human. The practical issue is simple: we could learn from the past to predict the future. Italy is quite enigmatic for conservation biology because it is relatively a little region but surrounded by a great number of ecosystems. A great history of co-existence let several large species survive: the grey wolf (*Canis lupus*), the brown bear (*Ursus arctos*) with an endemic subspecies (*U. arctos marsicanus*), the european lynx (*Lynx lynx*).

In spite of the promising results of the great conservation effort (Boitani 2000; Ensenrink et al. 2006) the population of brown bear and lynx still to be endangered especially in the Apennine region. Interestingly, the golden jackal (*Canis aureus*) started a process of re-colonization from the the eastern Alps. Should we focus on these species to manage healthy ecosystems or are there enough carnivores in Italy?

I think it could be possible to learn from the past. And palaeontological investigations can be an accurate instrument of analysis of past ecosystems.

Chapter 1

Introduction

1.1 The order Carnivora: a synopsis

The order Carnivora is represented by 271 living species belonging to 129 genera distributed across 12 families (Nowak 1999; Bininda-Emonds et al. 1999). This group of mammals received considerable attention by scientists because its members encompass most of the possible ecological and morphological adaptations to the life on terrestrial or aquatic environments (Gittleman 1985; Nowak 1999). Although their variability is remarkable, carnivores are not unusual in terms of species taxonomic diversity if compared with other groups such as rodents or bats (Nowak 1999).

But ecologically, carnivores are unique in their adaptability. They occupy every habitat from the desert to the arctic tundra and the rivers and oceans. In spite of the literal name, carnivores exhibit a range of feeding adaptations from specialized insectivory to meat-eating to total herbivory.

Such pattern of variation, is, usually, explained by the range of species body size which spans from the 100 g least weasel to the c.ca 800 kg polar bear (*Ursus maritimus*) (Gittleman 1985). Body size distribution also reflects taxonomic differences at a macroevolutionary scale: Mustelidae, Viverridae, and Herpestidae are generally represented by small species (mean body weight range: 1 kg – 10 kg) while Ursidae comprise the largest species (Gittleman 1985).

Members belonging to the same family, possibly, share also feeding ecology and morphology but there are several exceptions: among the meat eaters hyaenids, the aardwolf (*Proteles cristatus*) specializes on termites like the bat-eared fox (*Otocyon megalotis*) a member of family Canidae. Most of the extant bears possess adaptation to herbivory or insectivory habits with the exception of the highly carnivorous polar bear (Sacco and Van Valkenburgh 2004). The Felidae is , probably, the most homogeneous family including just species adapted (behaviourally, physiologically and morphologically) to strict carnivory except for some omnivorous tropical small cats.

These examples are indicative of a complex evolutionary history, which allows modern carnivores to colonize different ecological niches. Such a large range of adaptability, is of course reflected in carnivore morphology. Among traits amenable to morphological adaptation, the dentition is the most peculiar character of the carnivore "evolutionary success" (Werdelin 1987; Van Valkenburgh 1999, 2007): the upper fourth premolar and the lower first molar are the "carnassial" teeth modified in order to obtain a high functionality in meat slicing (Fig. 1.1a, b). In the lower first molar, two areas play an important rule in feeding adaptations: the trigonid which includes the sharp paraconid and protoconid cusps, and the talonid region, which is usually elongated to allow crushing of food particles. The ratio of these two regions reflects distinct feeding adaptations: in the extreme hypercarnivores the talonid is absent (Fig. 1.1b) while in omnivores the latter region is more developed (Fig. 1.1a) (Crusafont Pairó and Truyols Santonja 1956, 1957, 1958; Van Valkenburgh 1988, 1989, 1996, 2007). The dental formula of Carnivora is I3 - i3; C1 – c1; P4 – p4; M3 - m3 and it allows further specialization by reducing (hypercarnivores Fig. 1.1b) or retaining (hypocarnivorous Fig. 1.1a) premolars and molars.

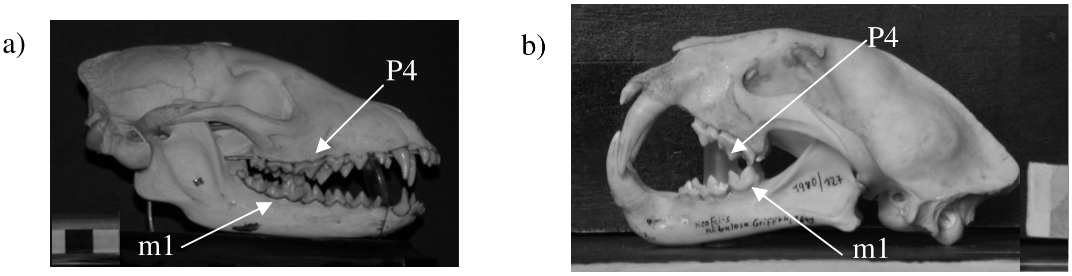


Figure 1.1: Skulls of the hypocarnivorous South American fox *Pseudalopex microtis* (a specimen C1518 Museum "La Specola" Florence, Italy) and the hypercarnivore clouded leopard *Neofelis nebulosa* (b specimen 1980/157 Zoologische Staatssammlung München, Munich, Germany). White square length = 1cm.

This kind of morphology developed since the early radiation of Carnivoramorpha with the small insectivores members of Miacoidea that evolved 65-60 Ma (Werdelin 1996). Carnivoramorpha is, actually, considered a broad taxonomic group including both Carnivora and extinct Miacoidea, the latter represented by the monophyletic Viverravidae and polyphyletic Miacidae (Wesley-Hunt and Flynn 2005).

In modern Carnivora, the taxonomic relationships among families have been clarified and confirmed by similar results obtained from several tree topologies (Bininda-Emonds et al. 1999; Flynn et al. 2005). According with Bryant's (1996) terminology different sub-taxonomic groups can be identified: Caniformia includes Canidae (wild dogs, jackals, foxes) and Actoidea (Ursidae –all bears and the giant panda; pinnipedia such as seals and walrus; *Ailurus fulgens* the red panda; Procyonidae –racoons, coatis, olingos; Mustelidae – wolverine, weasels, badger, otters) (Fig. 1.2). Instead the Feliformia are represented by members of family Felidae (cats, lynxes, panthers), Hyaenidae (represented by three extant hyenas and the aardwolf), the Herpestidae (mongooses) and the Viverridae (civets, genets) (Fig. 1.2). In such classification several taxa form distinctive groups (morphologically and genetically) like the red panda or the mephitinae tribe (skunks) among Caniformia and malagasy carnivores (the fossa) and *Nandinia binotata* among feliforms (cfr. Flynn et al. 2005).

But what we observe today, is only a small fraction of c.ca 58 million years of evolution. The fossil record of Carnivora defines numerous adaptive radiations occurred in the group: the estimated number of fossil genera is 352 (McKenna and Bell 1997) and at least two other families (the enigmatic Nimravidae and the "bear-dog" Amphicyonidae) appeared and went extinct in the geological time. The third family, Percrocutidae, has not been considered in phylogenetic analysis, so far (Wyss and Flynn 1993; Wesley-Hunt and Flynn 2005 but see Howell and Petter 1985; Werdelin and Solounias 1991).

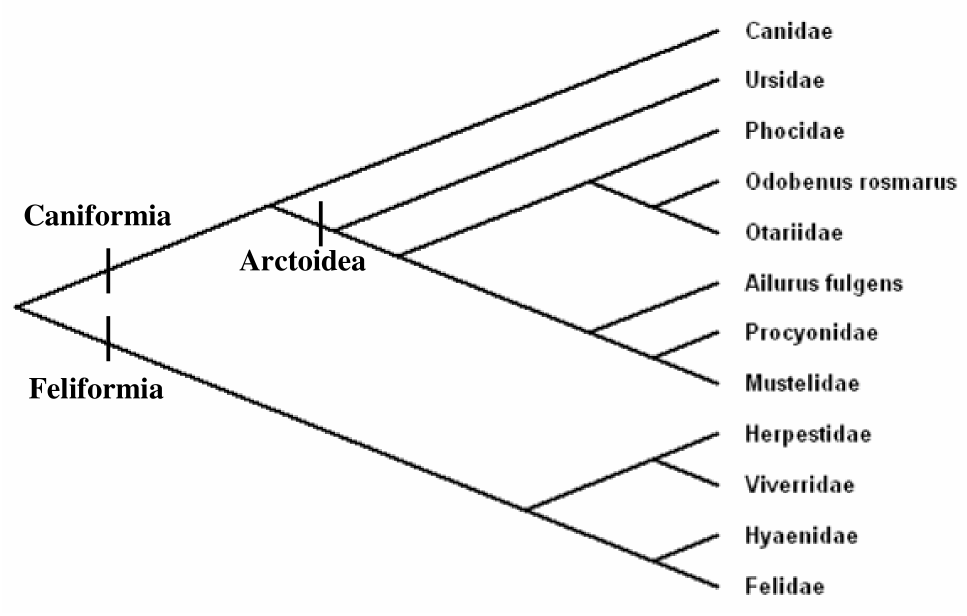


Figure 1.2: Tree topology of extant Carnivora (data source: Bininda-Emonds et al. 1999).

The systematic position of most extinct forms was evaluated in several analyses although the fossil material is scattered and does not allow to obtain enough data for some taxa. Among the other studies, good examples of robust phylogenies for extinct species can be seen in Werdelin and Solounias (1991) for family Hyaenidae, or Wang (1994) and Wang et al. (1999) for the extinct canid tribes Hesperocyoninae and Borophaginae. Phylogenetic relationships of fossil taxa among the other groups are scattered in the literature and specific to some forms restricted to a geographic area (e.g: the European Amphicyonidae in Viranta 1996); or taxonomic higher status (e.g: the genus level phylogeny of Ursidae in Ginsburg and Morales 1998). Different opinions exist for the systematic position of extinct families such as Nimravidae (probably a sister group of all the other Feliformia Wesley-Hunt and Flynn 2005; Wyss and Flynn 1993 but see also Werdelin 1996 or Flynn and Galiano 1982) and the bear dog Amphicyonidae (sister group of the Caniformia in Wesley-Hunt and Flynn 2005 or of the family Ursidae in Wyss and Flynn 1993).

Even if the taxonomic position of extinct forms is somewhat enigmatic, the morphological evolution of Carnivora has been well investigated since early nineties. The evolution of carnassial and mandibular morphology was clarified by Crusafont Pairó and Truyols Santonja (1956, 1957, 1958) in most fissiped (all terrestrial taxa excluding pinnipeds) that identified a "mean" plesiomorphic morphology in the genus *Cynodictis*. They evidenced also a macroevolutionary differentiation in hypocarnivorous (represented by amphicyonids, canids, mustelids, ursids, herpestids, viverrids) and hypercarnivores (felids, nimravids, hyaenids) taxa through geological time (from Eocene to the late Quaternary). Radinsky (1981a, b; 1982) investigated skull morphology at family level underlining a net differentiation related with the hunting techniques (e.g: felids and mustelids kill prey with a strong neck biting and have a shorter snout relative to the skull length). Greaves (1983, 1985, 1995) identified the biomechanics of mastication (in Carnivora but also other groups as well) and demonstrated how cheek teeth are optimally positioned in order to sustain large stress in the mastication. Martin (1989) reviewed the evolutionary history of Carnivora and introduced the ecomorphological concept of "dog-like" or "cat-like" phenotypes. Basically these species descriptors assume no overlap in morphology or ecology of Caniformia and Feliformia. But Werdelin (1996) demonstrated, later, how phylogeny can be a confounding factor in defining carnivore ecomorphology and, for this reason, introduced a taxon-free descriptor based on general morphology (e.g: scansorial/cursorial; bone-cracker/meat slicer/omnivore).

Specific studies on the evolution of locomotory adaptations rarely cover the entire Carnivora variability even if good examples are available in the recent literature (e.g: Taylor 1989; Christiansen 2002; Polly 2007 for extant species; Andersson and Werdelin 2003). Basically, locomotor adaptations reflects phylogenetic differences and constraint imposed by body weight: cursoriality is achieved by canids, the cheetah *Acinonyx* spp. (plus some extinct forms) and the large Caniformia (mustelids and ursids) of the Oligocene and Miocene while felids and nimravids have a high degree of supinatory ability. Modern taxa heavier than 100 kg (bears) are usually plantigrade and reduce both supinatory and cursorial abilities.

Hunt (1996) reviewed zoogeographical history in the all carnivore clades concluding that most of these groups started their radiation in the Eocene-Oligocene from Holartic region and then some migrated to Africa in the early Miocene while this continent was still dominated by creodonts. The Miocene was a period of rapid radiation for all carnivores but the highest peak in diversity is during Plio-Pleistocene. In such a period most of Artoid carnivorans migrate to South America where the earliest carnivore appearance in the fossil record is 7 Ma (Hunt 1996).

The patterns observed in the evolution of Carnivora converge in the fact that this group evolved within a complex interplay of factors basically driven by the dichotomy of phylogenetic constraint and environmental adaptation (Werdelin 1996; Van Valkenburgh 2007). Such a dichotomy moulds morphology and ecology of species and in several carnivore sub groups it was possible to demonstrate broad evolutionary phenomena across time such as iterative evolution (e.g: hypercarnivory in canids Van Valkenburgh 1991); Cope's rule (Van Valkenburgh et al. 2004) or adaptive convergence (e.g: bone cracking morphology in Borophagine canids and hyenas Werdelin 1989). Even across mammalian orders the adaptation to the carnivore life style produced famous examples of convergence like sabertooth morphology in extinct felids, nimravids and in the marsupial *Thylacosmilus atrox* or wolf like morphology in the thylacine Tasmanian wolf. Another extinct group, the Creodonta shows morphological convergence with Carnivora.

1.2 Aim of the thesis

The complex mosaic of knowledge on the evolutionary history of Carnivora is the results of specific investigations on taxonomic groups or particular morphotypes. The aim of this thesis is to add another panel in the mosaic of Carnivora studies by investigating a particular class of carnivores (large species) of a particular period (Plio-Pleistocene) in a specific geographic area (Italy). Such a strict objective allows to take into account the scatter nature of the fossil record and the complexity of questions derived from patterns of speciation and extinction in a relatively (from a geological point of view) short period of time. The period under investigation allows to consider simultaneously the effect of dramatic climate changes together with the spread of modern human being. There is a complex debate on the effect people had on large carnivores distribution and survival.

1.3 Why large carnivores?

Categories always allow to investigate complex problems under a factor of control. In the order Carnivora it is possible to distinguish several categories on the basis of taxonomy, morphology, and ecology: every kind of factor defines groups constrained by adaptive responses. Body size can be such a factor and it closes carnivores in several functional “boxes”. One way to define boxes is to think about “small” and “large” carnivores. The roots of this terminology has a human dimension but scientists defined also thresholds on the basis of important –field- observations.

In particular, the human dimension can still to be seen in every book on a charismatic species of carnivore: the wolf (Mech 1980, the Serengeti lion (Schaller 1972), the spotted hyena (Kruuk 1972) are only some examples of the most cited books in carnivore scientific literature and all of them concern a “large” species. Such dimension covers all the fields of human cultural modern life: television documentaries, cartoons for children, movies and so on and its root needs to be traced back to our ancestry. Large carnivores represent the fierce beasts and their relationship with human being are well documented and supported also by one of the first recognized case of domestication: the dog (*Canis familiaris*) (Massetti 2002). Medieval negative symbolism accrues to large carnivores (the wolf as beast of luxury and devastation) testifying a *continuum* in the relationship between human culture and large carnivorous mammals. Cases of attacks on humans by large carnivores are still actual (Løe 2002) and the competition between large carnivores and human activity is a common ground of conflict everywhere on earth. For these reasons it seems obvious that humans concentrated their attentions on large carnivores: most of the conservation programs use the charismatic species to recover entire ecosystems (e.g: the reintroduction of grey wolf *Canis lupus* in Yellowstone). From a strictly ecological point of view, there is compelling evidence that large carnivores have an important impact on terrestrial and aquatic ecosystems (for several examples see Ray et al. 2005).

What is not clear is how to interpret the terms “large” or “small”. A strict definition is impossible if we consider the relative meaning of the words but important suggestions come from the branch of palaeontology. Van Valkenburgh (1985, 1988, 1989) formalized in a series of papers the size threshold of large terrestrial carnivores -7 kilograms- on the basis of higher reported competition within the resulting categories in extant species and better representation in the fossil record. Unfortunately, body size is a characteristic that can only be approximated by looking at skeletal elements (Damuth and MacFadden 1990; Calder 1996). Such approximation may result in errors whose reduction requires applying appropriate regression equations with the minimum Standard Error (SE). For such a purpose, Van Valkenburgh (1990) conducted a survey on skeletal material of extant carnivores. The best predictor of body size she found is represented by head-tail length; skull length and lower carnassial (m1) length. Long bones elements allometrically scales with body mass and Egi (2001) proposed several equations. Recently, Andersson (2004) proposed the use of humerus elbow joint shape data as the best predictor of body mass in carnivorous mammals. All these observations converge on the fact that body mass can be predicted with a good level of accuracy in mammalian extinct carnivores, allowing to treat large (or small carnivores) as separate categories.

In this regard, the evolutionary history of large carnivores has been clarified (Van Valkenburgh 1999). Seven turnover events were identified since 46 million years ago in North America and Eurasia and competition represents the most important factor that drive the “rise” and “fall” of large carnivores through time (Van Valkenburgh 1999).

Another important aspect of the evolution of large carnivorous mammals is represented by the unchanged morphological variability in feeding apparatuses through time (Van Valkenburgh 1988, 1989) as well as locomotory traits (Van Valkenburgh 1985). This pattern of constant (occupied) morphospace through time was recently demonstrated for the entire Carnivoramorpha during the Cenozoic of North America (Wesley-Hunt 2005): morphological disparity change as a function of taxonomic diversity and the maximum morphological disparity was achieved early in the radiation of the group.

These studies suggest that large carnivores changed little through their evolutionary history. Unfortunately, there are no related studies for European fossil record and, here, I cover the gap at least for the Italian Plio-Pleistocene. Before analysing large carnivores as a separate "functional" box, I demonstrate if 7 kilogram is an appropriate size threshold (among the others possible ecological categorizations) related to the morphological traits analysed (mandible shape and long bones anatomy) by using extant species samples (chapters 3-5).

1.4 The Plio-Pleistocene of Italy: geological framework and large mammal fauna

The continental fossil record has several limitations and the relatively short geological life of Italian landscape results in an incomplete Tertiary large mammal fossil record (Kotsakis 1986). Plio-Pleistocene (or Plio-Quaternary) is the period better represented in the Italian fossil record with a rich continental fauna reviewed in several papers (Caloi et al. 1986; Azzaroli et al. 1988; Gliozzi et al. 1997; Palombo et al. 2003). Such a period is particularly important to understand the complex interaction between biotic and non-biotic world.

At a global scale, Plio-Pleistocene is well-known because it was affected by dramatic climate changes. In Europe such changes began some 3.2 Ma (middle Pliocene) with a glaciation that was followed by another cold event 2.6 Ma (Late Pliocene) (Agustì and Antón 2002; Casati 1996; Malatesta 1985). The Pleistocene was, then, characterized by the big glaciations once classified according to alpine sediments in Donau, Günz, Mindel, Riss and Würm (Smiraglia 1992). This classification was used by Kurtén (1968) to introduce chronological elements for European continental fossil record: Günz covers c.ca 500 ka (from 1.0 Ma to 0.5 Ma) and is represented by two cold stadials; the Mindel begins < 400 ka until the interglacial D-Holstein (230 ka); Riss is divided in two stadials until the F-Eem interstadial (70 ka – 40 ka) which represents also the beginning of the Late Pleistocene characterized by the coldest periods of Würm with two stadials until 10 ka (the Last Glacial Maximum – LGM).

The cycles of cold and warm periods (glacial-interglacial) are also characterized by changes in the oxygen isotopic values which allow obtaining a better chronology of climate changes, although based on marine sediments. Kroon et al. (1998) identified cycles in oxygen 18 record of Eastern Mediterranean directly related with the 40 ka cycles of climate changes from 3.2 - 2.1 Ma and 1.9 to 1.0 Ma. Williams et al. (1988) describe the later four climate cycles: 0 to 0.47 Ma, 0.47 - 0.91 Ma, 0.91 - 1.30 Ma and from 1.30 since 1.88 Ma.. Glacial cycles of 500 ka are uniformly represented by the oxygen stadium 65 - 25 (period 1.9 – 0.85 ma) and the stadium 21 - 27 (76 ka – 64 ka). The stadium 22 (79 ka) records a high level of glacial ice sheet covering across the Northern hemisphere while the stadium 16 (60 ka) represents the coldest period in Europe (Williams et al. 1988).

In this context, the Italian peninsula evolved its geological history with some tectonic events which cover all the Plio-Pleistocene. Tectonic activities are related with the raising of the Alps and the Appennines (Casati 1996; Malatesta 1985). The latter activity generated several volcanic eruptions especially in the Thyrrenian region. The Tolfa complex (central Italy) was active in the late Pliocene, and the Cimino between 1.4 – 0.9 Ma. In the south, the Pontian islands were active during most of the Pleistocene while the Roccamonfina complex is another important eruptive centre (active some 1.2 Ma) (Malatesta 1985; Casati 1996).

Another important source of change in the Italian landscape is represented by the changes in the sea level. Such phenomenon creates land bridges between the peninsula and some islands during cold periods –with low sea stands- and isolated the island during the interglacials. Most of Italian islands gave rise to special dwarf fauna (e.g: dwarf deer *Cervus thirrenicus* of Capri; or the dwarf elephant *Elephas falconeri* of Sicily) but these elements will not be considered in this thesis. It is worth mentioning that in some islands like Capri, a continental fauna was recorded for the early Late Pleistocene and therefore considered.

Such remarkable geological changes are generally recorded in the fossil record of the fauna and flora. The marine fossil record best characterizes climatic cycles but the continental chronology defines several important climatic events. For the continental Eurasiatic fossil record Azzaroli (1983) and Azzaroli et al. (1988) proposed the faunal "events" in coincidence with climate shifts and evolutionary changes in large mammal fauna. The faunal events represent the spread of several taxa all over the Eurasiatic continent and then are defined by the First Occurrence of some particular taxa (Tchernov 1992).

During the early Pliocene European landscapes were dominated by "temperate" forests with the diffusion of the arboreal forms *Taxodium*, *Cedrus*, *Tsuga*, *Abies*, *Picea* and *Sequoia* (Suc et al. 1995) and such homogenous climatic conditions are also reflected in the recorded mammalian species: *Mammut borsoni*, *Tapirus arvernensis*, *Sus minor*, ancestor of the modern suids, and *Ursus minimus* (Thibetan bear like). This forms characterize the end of the Ruscininan mammal age and the beginning of the Early Villafranchian and are important because their extinction defines the beginning of the rise and fall of cold and warm climate of Plio-Pleistocene. 2.6 Ma begins the spread in all Eurasia of the genus *Artemisia* (a member of steppe vegetation) which relates with the *Equus-Mammuthus* event (Suc et al. 1995; Azzaroli 1983; Augustì and Antòn 2002). Another important dispersal event is recorded at 2.0 Ma with the spread of modern *Canis* spp. that defines the upper Villafranchian association (*Wolf* event) (Azzaroli 1983; Azzaroli et al. 1988; Torre et al. 1992; Napoleone et al. 2001; Augustì & Antòn 2002).

From the end of early Pleistocene, the Villafranchian mammal age is substituted by the Galerian (c.ca 1.0 Ma covering also part of the Middle Pleistocene) defined by the fauna of Ponte Galeria site with some transitional taxa and new *Megacerine* deers (Ambrosetti et al. 1972; Azzaroli et al. 1988; Sala et al. 1992), and then the Aurelian (Middle-Late Pleistocene c.ca 400 ka) mammal age characterized by modern incomers well adapted to cold climate: the wolf *Canis lupus*; ibex *Capra ibex*; straight-tusked elephant *Elephas antiquus* (Gliozzi et al. 1997).

In this context the Italian fossil record is well represented all over the mammal ages of Plio-Pleistocene. The biochronology of the Italian fossil record (related to the major faunal events) has been discussed and several approaches proposed and still debated (Gliozzi et al. 1997; Palombo et al. 2003; Raia et al. 2005; 2006a; Masini and Sala 2006; Sardella and Palombo 2007).

Basically, the richest and the most representative fossil sites (Faunal Units, FUs) have been related with mammal age in order to obtain a better resolution of the Italian large mammal bio-stratigraphy (Table 1.1). The FUs are operationally useful and relate well with the biochrones as defined by the small mammal fossil record (Masini and Sala 2006) as well as land invertebrates (molluscs and ostracods) (Gliozzi et al. 1997).

Another approach is instead represented by the PaleoCommunities (PCOMs) (Raia et al. 2005, 2006a). This concept is based on bootstrap cluster analysis performed on presence-absence data matrix for 73 Italian local assemblages spanning 3.2 – 0.3 Ma. Then, nine PCOMs can be defined on the basis of species composition and it has been demonstrated that they relates with the classic Faunal Units (Raia et al. 2005; Table 1.1). It is worth noting that these biochronological units allow also to obtain macroecological data on species abundance which reflects similar trends observed in extant communities (Raia et al. 2006b, 2007; Meloro et al. 2007).

For the purpose of this thesis, the PCOM units will be considered in order to obtain a better resolution on large carnivores' distribution and abundance (see Chapters 4, 6).

Mammal Age	Faunal Unit	PCOM	Mya
Early Villafranchian	Triversa	Triversa	3.2
Middle Villafranchian	Montopoli Costa S. Giacomo	Montopoli	2.4
Late Villafranchian	Olivola Tasso	Upper Valdarno	1.9
	Farneta	Val di Chiana	1.5
	Pirro	Pirro	1.1
Early Galerian	Colle Curti		
	Slivia	Galerian 1	0.8
Middle Galerian	Isernia	Galerian 2	0.6
Late Galerian	Fontana Ranuccio	Galerian 3	0.45
Aurelian	Torre in Pietra Vitinia	Aurelian	0.3

Table 1.1: Mammal age, Italian Faunal Units and PCOMs (from Palombo et al. 2003; Masini and Sala 2006; Raia et al. 2005, 2006a). Time in million of years is represented only for PCOM chronology.

1.5 Plio-Pleistocene large carnivores: species accounts

Defining Plio-Pleistocene large carnivores of Italian peninsula is, operationally, a difficult task that is highly dependent on the size threshold used as well as the body mass species reconstruction. The 7 kilograms threshold defined by Van Valkenburgh (1985, 1988, 1989) is, here, applied according to the morphological traits analysed in this thesis (mandible shape Chapters 1-4.; long bones Chapter 5). Such threshold allows to exclude *a priori* rare fossil forms like the small mustelids *Baranogale* spp. of Triversa and Torre di Picchio localities (Palombo et al. 2003) and the viverrid *Viverra prepaxi* of Triversa together with the Late Pleistocene weasels *Mustela* spp. and the martens *Martes martes* and *Martes foina*. During the Villafranchian some aquatic mustelids are present in the Italian record: *Enhydrictis ardea* and *Pannonictis nestii* both of them small in size and, then, certainly well below the 7 kilograms threshold (Rook 1995). Palombo et al. (2003) and Raia et al. (2006a) do not report Eurasiatic otter (*Lutra lutra*) in Italian Plio-Pleistocene record then this species, even if large in size (mean body weight c.ca 10 kilograms in Meiri et al. 2005), will not be considered also because of its exclusive semi-aquatic life style. The wolverine (*Gulo gulo*) is another large mustelid whose range distribution achieves also the Italian peninsula during the Late Pleistocene (Sardella 2000). Although Palombo et al. (2003) and Raia et al. (2005, 2006a) do not report this species in their taxonomic lists and for this reason it was excluded from the analysis. Sardella (2000) reported several Italian deposits were the wolverine is present but all represents the latest part of late Pleistocene (not included in the PCOM Aurelian).

Among felids, *Felis lunensis* of Upper Villafranchian (Ficcarelli and Torre 1974) and the European wild cat (*Felis silvestris*) recorded in the Upper Pleistocene deposits (Palombo et al. 2003) are excluded as well for their mean body weight equal to 5 kilograms. The body weight reconstruction of *Felis lunensis* is based on the fact that such form is similar in size and morphology to modern wild cat and, probably, does not represent a distinct species (Ficcarelli and Torre 1974).

Megaviverra appenninica is a large species (family Viverravidae) recorded at Triversa (Palombo et al. 2003) but was excluded from all the analyses because of the incompleteness of fossil material. It is present only in the fossil locality of Triversa.

The red fox (*Vulpes vulpes*) of Late Pleistocene and its Villafranchian counterpart (*Vulpes alopecoides*) were excluded from the analyses for their body weight. Actually, the body mass range of a red fox can be higher than seven kilograms, but the mean body weight is usually above 5.5 kilograms (Gittleman et al. 2004). It is certainly true that the Pleistocene red fox was larger in size of its modern counterpart, but this fact does not directly indicate that it could have had strong competitive interactions with larger carnivores. Such variation in body mass is simply an effect of the Bergmann's rule as already evidenced by Kurtén (1968). From a morphological point of view, Italian Pleistocene specimens of red fox do not show significant differences from their extant counterpart (except for the relative size).

Kurtén (1968) described the alopecoid fox (*Vulpes alopecoides*) as an animal of "about the same size as the living arctic fox". A body weight reconstruction based on the lower m1 of the complete mandible specimen 458 M (Villaroya - Spain) gave a value of 6.4 kilograms (applying equation for canids only in Van Valkenburgh 1990). It is worth noting, that in the sample of extant large carnivores (Chapter 1) the red fox is considered an animal whose mean body mass is below 7 kilograms and than not included in large carnivores.

The species *Cuon alpinus* is the last large form that has been excluded from this investigation. In the Italian Plio-Pleistocene fossil record there is only one occurrence in Fontana Ranuccio FU of the middle Galerian (Palombo et al. 2003). This record was not considered in Raia et al. (2006a) because it is based only on a tooth fragment with uncertain attribution. In keeping with Raia et al. (2006a) I exclude this taxon from the Galerian – Aurelian large carnivores because it is not well represented by the fossil record (just one fossil site) and further investigations are needed to support its presence in Italy. Del Campana (1947) described fossil material from Grotta degli Equi of *Cuon alpinus* but such site is not considered in the PCOMs.

In conclusion, the taxonomic list of large carnivores analysed in this thesis comprises 25 species: five are Canidae, ten belong to Felidae, four are hyaenids, one Mustelidae and five Ursidae (Table 1.2). The species selected from the Italian fossil record compare well with the other forms founds in continental Europe. The only recorded endemisms are represented by the insular species

Cynotherium sardous (Malatesta 1962) and *Chasmaporthetes melei* but they will not be considered in this thesis.

There is a strong taxonomic bias in favour of the members of family Felidae. This fact partially reflects the better taxonomic resolution on this latter group, but it could also be related to ecological arguments. For Canidae, there are several opinions on the taxonomic attribution of Galerian forms and this will be discussed in detail, although a non-conservative approach can elongate the number of species to seven. Mustelidae are overrepresented but this fact reflects simply the low number of "large" species evolved in Europe. Hyaenidae and Ursidae are better described and their taxonomic validity is well supported (Werdelin and Solounias 1991; Mazza and Rustioni 1994).

Species	**Family**	**Description**	**Period**
Acinonyx pardinensis	Felidae	giant cheetah	mid-Up Villafranchian
Chasmaporthetes lunensis	Hyaenidae	running hyena	mid-Up Villafranchian
Homotherium crenatidens	Felidae	sabre-tooth cat	mid-Up Villafranchian
Megantereon cultridens	Felidae	dirk-tooth cat	mid-Up Villafranchian
Pliocrocuta perrieri	Hyaenidae	Perrier hyena	mid Villafranchian
Ursus minimus	Ursidae	Tibetan bear ancestor	mid Villafranchian
Nyctereutes megamastoides	Canidae	racoon dog ancestor	mid-Villafranchian
Canis arnensis	Canidae	coyote like	Up Villafranchian-Aurelian
Canis etruscus	Canidae	wolf ancestor	Up Villafranchian
Lycaon falconeri	Canidae	European wild dog	Up Villafranchian
Lynx issiodorensis	Felidae	Etouaires lynx	Up Villafranchian
Pachycrocuta brevirostris	Hyaenidae	short faced hyena	Up Villafranchian
Panthera gombaszoegensis	Felidae	European jaguar	Up Villafranchian
Ursus etruscus	Ursidae	Etruscan bear	Up Villafranchian
Homotherium latidens	Felidae	sabre-tooth cat	Galerian
Megantereon whitei	Felidae	dirk-tooth cat	Galerian
Canis lupus	Canidae	grey wolf	Galerian-Aurelian
Meles meles	Mustelidae	European badger	Galerian-Aurelian
Crocuta crocuta	Hyaenidae	spotted hyena	Galerian-Aurelian
Lynx spelaeus	Felidae	cave lynx	Galerian-Aurelian
Panthera leo	Felidae	lion	Galerian-Aurelian
Panthera pardus	Felidae	leopard	Galerian-Aurelian
Ursus arctos	Ursidae	brown bear	Galerian-Aurelian
Ursus deningeri	Ursidae	Deninger bear	Galerian-Aurelian
Ursus spelaeus	Ursidae	cave bear	Galerian-Aurelian

Table 1.2: List of species analysed in this thesis.

The choice of some taxonomic names is conservative even if several alternatives exist for some taxa. Here, I consider a valid species status only the names that have been formalized in papers where also species diagnosis is available. In the species account, the taxonomic choice is discussed in detail. It is worth noting, that such taxonomic list agrees with Raia et al. (2005; 2006a; 2006b;

2007) and Meloro et al. (2007). Only the European badger is not mentioned in Raia et al (2006a) but its distribution in the Italian fossil record follows Palombo et al. (2003).

CANIDAE (Gray, 1821)

Italian fossil record is mainly important for the history of European Plio-Pleistocene canids. In fact, Costa San Giacomo FU records the first European occurrence of *Canis etruscus* which fixes the beginning of the *Wolf event* (Rook 1993; Torre et al. 1992; Rook and Torre 1996a), and the most important descriptions of Villafranchian dogs come from fossil material of the Valdarno basin (Del Campana 1913). The taxonomic status of several species changed recently even if the evolution of several enigmatic forms still to be clarified. In particular, the Italian fossil material of a medium size canid from several Galerian localities still to represent a matter of controversy. Rook (1993) proposed a separate taxonomic status for the “middle Pleistocene small wolf” which should represent an advanced form of the Villafranchian *Canis arnensis* but there is not a complete consensus. A possible robust approach will be applied in order to clarify the taxonomy of some fossil specimens from different Italian localities.

Nyctereutes megamastoides (Pomel, 1842)

This racoon dog is poorly represented in the Italian Plio-Pleistocene and appears only in the PCOM Montopoli (localities Montopoli and Colle Pardo). This species is probably replaced by the arrival of wolf like Villafranchian canids all over Europe and it characterizes the fauna of middle Villafranchian. Thorough anatomical descriptions of the European forms of this species are in Viret (1954): the skull is characterized by strong sagittal and nucal crests, the anterior part of the palate is narrow and slender and becomes elongated posteriorly; the mandible presents a typical subangular lobe (Fig. 1.3); dentition is fox-like with short canines and an elongated carnassials even if some traits are discriminant (e.g: size of M2 relative to P4) and clearly separate the genus *Nyctereutes* from *Vulpes* (Koufos 1993).

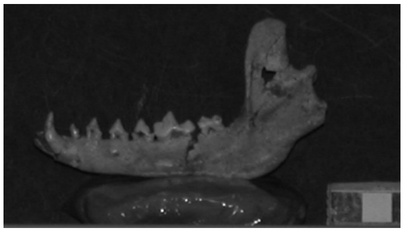


Figure 1.3: Left hemi-mandible fragment of *Nyctereutes megamastoides* I739M from Villaroja Spain, Museo Geologico y Minero. Black square length: 1 cm.

A recent description of long bones morphology is known from the material of Saint Vallier: generally it resembles the proportion of the genus *Vulpes* even if some bones are wider on the articular surface (e.g. the humerus and radius), the tibia presents a typical morphology in the crest (Argant 2004). Generally, the morphology of Villafranchian raccon dog resembles that of its modern counterpart. On the basis of this observation Kurtén (1968) suggested an adaptation to omnivory feeding habits dominated by vegetables and sometimes meat.

As the Italian fossil material is fragmented I used for morphometric analysis several complete mandible samples from IGME (Istituto Geológico y Minero de España. Museo Geominero. Madrid, Spain.) and NMB (Naturhistorisches Museum Basel, Switzerland). The estimated body mass should be usually larger than that of modern racoon dogs (*Nyctereutes procyonoides*) (Kurtén 1968). On the basis of several lower carnassial measurements is 7.7 kilograms but a complete skull from Saint Vallier (Argant 2004) gave a better estimated body mass of 11 kilograms that will be considered valid and more accurate for this thesis.

Canis etruscus (Forsyth Major, 1877)

The Etruscan wolf is the most abundant member of family Canidae towards Upper Villafranchian all over Europe. Italian specimens from Valdarno were, firstly, described by Del Campana (1913), then Torre (1967) and Rook (1993) who gave accurate statistical analyses on dentition together with species diagnosis. The skull of *Canis etruscus* resembles that of the modern grey wolf: nasals are elongated, a strong sagittal crest is present, the tympanic bullae are less developed than in jackals, the palate proportions are similar to the wolf. The dentition of *Canis etruscus* is probably more jackal-like and does differ from that of the wolf especially in the lower carnassial (m1) whose paraconid cusp is not higher than p4 (the contrary can be observed in the wolf) (Fig. 1.4a). Relative proportion of the upper teeth are similar to the wolf. The only differences in the upper dentition is represented by the presence of a more developed deuterocone in the P4 of *Canis etruscus* (Fig. 1.4b).

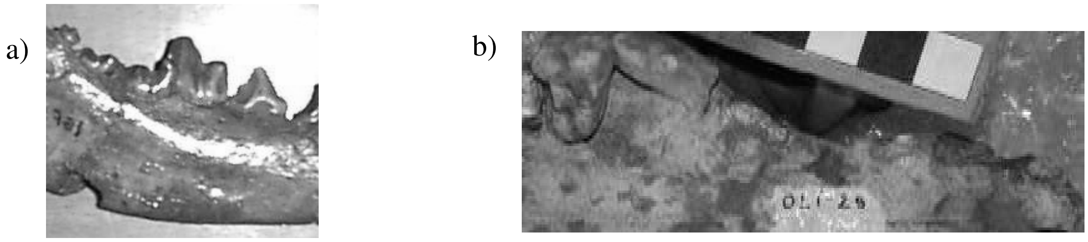


Figure 1.4: Particular of lingual side of left hemi-mandible (a, IGF 187) and palate (b, cast Oli-29 in MNCN) of *Canis etruscus*.

The post cranial skeleton morphology is similar to that of *C. lupus* with size proportion resembling small wolves.

Generally, *Canis etruscus* is like a shepherd dog in size (Kurtén 1968) while palaeoecological reconstructions have been performed on the basis of Venta Micena (Spain) specimens (Palmqvist et al. 1999; 2002). The Spanish fossil material belong to a much smaller form than Italian and Rook (1993) proposed that it belong to *Canis* aff. *arnensis*. For this reason, here, I use a body mass reconstructed only from Italian fossil specimens. According with Meloro et al. (2007, Appendix data) the estimated body mass of *C. etruscus* is 21 kilograms. Palmqvist et al. (1999, 2003) suggested an omnivorous diet but there are no evidence from Italian specimens. Usually *Canis etruscus* is considered a pack hunter but there is no formal evidence or palaeoecological reconstruction of such a behaviour. It is worth mentioning that *C. etruscus* is one of the most abundant canids in Italy (Raia et al. 2006b) and, probably, Europe as well.

Palaeoecology of the Etruscan wolf will be clarified in several morpho-ecological analyses based on the mandible and long bones measurements (see Chapters 3 – 5). The stratigraphic range of this species is restricted to Upper Villafranchian. In Italy, *C. etruscus* is present in successive Montopoli, Upper Valdarno and ValdiChiana PCOMs.

Canis arnensis (Del Campana, 1913)

The taxonomic history of this species is complex and it is necessary to elucidate several points to clarify the position adopted in this thesis. The description of this species comes from the abundant material of Valdarno (Del Campana 1913) and it was successively analysed by Torre (1967) and Rook (1993). Rook (1993) proposed a new species similar in morphology to *C. arnensis* but more advanced in the dentition. This new species is interpreted as *Canis* aff. *arnensis* and its stratigraphic range is limited to the middle Pleistocene (Galerian) of the Mediterranean region (Rook and Torre 1996b). The authors argue for caution of this interpretation because a comparison with the material of Galerian dogs of Central - North Europe was not performed. Conservatively, here I considered all the uncertain nomenclature as *Canis arnesis* = *Canis* cfr. *arnensis* = *Canis* aff. *arnensis* in keeping with Raia et al. (2005; 2006a; 2006b) as belonging to *C. arnensis*.

Generally, *Canis arnensis* resembles jackals in skull morphology with a short muzzle (compared to *C. etruscus*), poorly developed nasals and frontal sinus and a weak sagittal crest (Torre 1967). The teeth ratio were interpreted as jackal-like but Kurtén (1974) points out a stronger affinity with coyotes in M1/P4, p4/m1 and m1 length/m1 breadth ratios. *Canis* aff. *arnensis* has a broader upper M1 and a shorter trigonid in m1 compared with *C. arnensis* (Rook 1993), but the taxonomic relevance of such features is unclear.

Post-cranial fossil material of *Canis arnensis* is scanty and fragmented but Torre (1967) stressed how the remains of Valdarno resemble modern jackals in proportion and morphology.

The palaeoecology of this canid was never clarified, although Kurtén (1974) suggested a close affinity with the North American coyote ancestor *Canis priscolatrans* indicating that *C. arnensis* could be a possible geographic variant of a large coyote holartic population. Body mass estimates is reported in Meloro et al. (2007) as 16 kilograms and will be used for this thesis. Its stratigraphic range is the largest (especially in virtue of the uncertain taxonomic validity of Galerian forms). Its presence in PCOMs units span from Upper Valdarno (Upper Villafranchian) to Aurelian with some advanced forms recorded at Capri (Quisisana), Contrada Monticelli, Grotta Romanelli (lower beds of "terre rosse") and Campo Verde (Raia et al. 2006a).

Lycaon falconeri ((Forsyth Major) 1877)

The distribution of *Canis* (*Xenocyon*) *falconeri* in the Italian Plio-Pleistocene was clarified by Rook (1993, 1994) who proposed a large taxonomic group *Canis* (*Xenocyon*) gr. *falconeri* to include also Asiatic and African forms, usually, with a different specific name but similar in morphology.

This canid is similar in size to a large North American grey wolf but it resembles the African wild dog (*Lycaon pictus*) in the morphology of teeth and metacarpals. The neural region of the skull is short and in the dentition occurs some hypercarnivore features such as the reduction of metaconid in the lower carnassial; accessory cusps are present in upper premolars and the upper carnassial tend to brachiodonty (Fig. 1.5).

Figure 1.5: Type specimen of *Lycaon falconeri* from Valdarno IGF 883.

In metacarpals there is the lack of articular facet between the second and the first that was, therefore, interpreted as lost like in the African wild dog. Such feature is considered an adaptation to cursoriality and is unique to *Lycaon.* This observation together with the tendency to hypercarnivory allowed, recently, Martínez-Navarro and Rook (2003) to reassign *falconeri* material to *Lycaon*, with the species *L. falconeri* and *L. lycaonoides*, the latter being latest Villafranchian to Middle Pleistocene in age. I maintain the attribution to *Lycaon.*

From a palaeoecological perspective, *L. falconeri* is well known (Palmqvist et al. 1999; 2003). A complete skull from Venta Micena has anomalies that could have severely affected the survival of the individual it belongs to. This fact, together with further anatomical analyses, suggests a behavioural and morpho-ecological similarity between *L. falconeri* with the modern African wild dog. Probably this highly-cursorial, pack hunting species was capable to kill horses (e.g. *Equus stenosis*) and ungulates adapted to open terrains (Palmqvist et al. 2003). The estimated body mass should be 28 kilograms (Palmqvist et al. 1999) but Meloro et al. (2007) reported 26 kilograms on the basis of Italian fossil material in Rook (1994). The latter value (that is not so different from Palmqvist et al. 1999) will be considered valid.

Lycaon falconeri is present in Upper Valdarno and Pirro Nord PCOMs. Its absence from ValdiChiana PCOM suggests rarity in this species for a short period of the Italian fossil record.

Canis lupus (Linnaeus, 1758)

The grey wolf is well represented in the Aurelian sites of Italy. This species still to be present in the Italian Apennines and recently colonized the Alps (Boitani 2000). Together with the bush dog (*Speothos venaticus*), dhole (*Cuon alpinus*) and African wild dog (*Lycaon pictus*) the grey wolf is the only extant canid showing hypercarnivorus dentition (Van Valkenburgh 1991). Such a feature results from a trenchant-heel condition of the lower carnassial which exhibits a single hypoconid cusp in the talonid region. The skull of the wolf is characterized by a strong sagittal and nucal crest and large strong concave tympanic bullae, the mandible is well adapted to crack bones in the molar area, the post cranial anatomy is adapted to cursoriality although it does not achieve the extreme adaptation of *Lycaon* (Mech 1980). The ecology of the extant wolf has been clarified and it is clear its high adaptability to holartic environments (woodland forest but also tropical areas in India or deserts). The mean body mass of this species is c.ca 38 kilograms but it varies greatly according to the climate of the region. In this regard it follows the Bergmann's rule and exhibits changes in size also in prehistoric forms. Especially in the Riss, the wolf achieve small size while in the late part of Pleistocene European forms becomes bigger as the extant Siberian wolves (Kurtén 1968). The wolf is an elastic predator of medium-large ungulates and it lives in social familiar nuclei (the number of individuals in a pack may vary from 3 until 36 the maximum recorded in Mech 1980).

In Italian Aurelian sites, the wolf early occurs in localities near Rome with fragmentary fossil material whose morphology does not differ from the extant forms except the size that is usually smaller (Capasso Barbato and Minieri 1987). What is not clear is the co-occurrence of the grey wolf with the little coyote of the middle Pleistocene (*Canis* aff. *arnensis*). Palombo et al. (2003) reports only one locality, Casal de' Pazzi, where *Canis* cfr. aff, *arnensis* would co-occur with the wolf, but the uncertainty in identification makes the presence uncertain (as in Raia et al. 2006a). Anyway, the biochronological scale used (PCOM), let me considering the co-occurrence as real but conservatively I opted to consider in morpho-ecological data only fossil material from Grotta Romanelli (cfr. *Canis lupus*) as representative of early Aurelian wolf.

MUSTELIDAE (Swainson, 1835)

Large members of family Mustelidae are represented in the Italian Plio-Pleistocene by few forms. Here, I consider only the European badger (*Meles meles*) that is a member of large carnivore guild also in extant ecosystems.

Meles meles (Linnaeus, 1758)

This form has a unique omnivore morphology and it has been recorded in few but significant sites of the Italian Paleo-Communities: in the locality G.R.A of the Galerian 2 (Caloi and Palombo 1986) Visogliano of Galerian 3 and Torre in Pietra of the Aurelian (Data source Palombo et al. 2003).

In Slivia of Galerian 1 Palombo et al. (2003) report cf. *Meles meles* but this record, which should be the oldest for the Italian peninsula, has not been considered because it is doubtful.

Even if it is rare, the badger is present continuously from the Galerian to Aurelian. It is a typical member of modern Holarctic fauna and Kurtén (1968) reported first occurrences of the species all over European localities from the middle Pleistocene.

The skull is massive with a strong sagittal crest, the rostrum is short relative to the braincase as it is common in mustelids; the lower carnassial has an elongated talonid region relative to the trigonid and with some accessory cusps. The post cranial morphology is typical as in burrowing animals with short legs and large carpals and tarsals.

The considered Italian fossil material is represented by few fragments and for morphometric analyses I used fossil material of the Italian Late Pleistocene from Monte Rufeno (Viterbo, Italy) preserved in the Pigorini Museum (Rome). In the described material from G.R.A. there are no significant differences in size and morphology from extant badgers (Caloi and Palombo 1986) and for this reason a body mass of 12 kilograms (cf. Gittleman 1985) was assumed.

URSIDAE (Gray, 1825)

Plio-Pleistocene bears are equally represented in the Italian fossil record by several forms that are generally common all over Europe and are limited to certain stratigraphic range. *Ursus minimus* is usually present in the Middle Villafranchian, the Etruscan bear characterizes the Late Villafranchian fauna, *Ursus deningeri* occurs in the Galerian while the brown bear *Ursus arctos* and the cave bear

Ursus spelaeus co-occur in the Galerian and Aurelian. Generally, this time partition observed in various species reflects some evolutionary changes as reported by Ficcarelli (1979a) who observed a decrease in p4 length of the *Ursus* lineages such as a continuous adaptation towards omnivory. No endemism was recorded in the Italian fossil record although Raia et al. (2006a) reported several occurrence of *Ursus* sp. whose taxonomic status has not been clarified and, conservatively, will not be considered here.

Ursus minimus (Devèze and Bouillet, 1827)

The most important Italian remains of *Ursus minimus* came from Gaville Valdarno and were reviewed by Berzi (1966). She pointed out close similarities of *U. minimus* with modern black bear (*U. thibethanus*) and such opinion has been validated in Mazza and Rustioni (1994) who grouped *U. minimus* and *U. thibetanus*. In the skull, the neurocranium appears more elongated than the rostrum, the upper premolars 1-3 are small and spaced like the lower premolars 1-3, the lower carnassial exhibits a zig-zag morphology defined by the lingual and buccal cusps similar to that of modern black bears. The dentition does not show a strict trend in the p4 size reduction because in *U. minimus* this tooth is smaller than in *U. etruscus* (Ficcarelli 1979a; Fig. 1.6a, b) but it has been clarified that *U. minimus* represents a primitive stock for the evolution of both European and Asiatic bears (Mazza and Rustioni 1994; Petronio et al. 2003). In the post-cranial elements Berzi (1966) reconstructed the correct physiological position of metapodials and metatarsals which should have allowed the species to climb the trees.

Figure 1.6: Right hemi-mandible of *U.minimus* from Gaville IGF 11 568 (a) and skull (b) of *U.etruscus* IGF 906.

Among Italian PCOMs, *U. minimus* is recorded only at Triversa with a very limited fossil record (only two local occurrences). Palaeoecology of this form was never clarified and a body mass of 104 kilograms has been reconstructed by using skull-length (in Meloro et al. 2007).

Ursus etruscus (Cuvier, 1823)

Mazza and Rustioni (1992) furnished a comprehensive overview of *Ursus etruscus* morphology as well as occurrence in Plio-Pleistocene Italian sites. This bear is restricted to the Upper Villafranchian and it occurs continuosly in PCOMs Upper Valdarno, Val di Chiana and Pirro.

The morphology is peculiar and it confirms that premolar reduction in bears does not begin with the cave bears but earlier. The skull is elongated and flatted, premolars (upper and lower) are reduced (Fig. 1.6b), the lower carnassial and the upper M1 exhibits a lateral compression. Such features suggests an early adaptation to omnivory but a thorough palaeoecological reconstruction has never been performed. Long bones are generally more elongated than in *U. minimus* with plantigrady adaptations such as in brown bear.

A body mass reconstruction based on the Italian fossil specimens gave a value of 160 kilograms (in Meloro et al. 2007).

Ursus deningeri (Reichnau, 1906)

The earliest Italian founding of this cave bear of the middle Plestocene is Isernia La Pineta (PCOM Galerian 2), then it is reported in other two localities of Galerian 3 before its extinction. The stratigraphic range of this form is restricted to the middle Pleistocene and this represents the most peculiar feature that allow to distinguish it from *Ursus spelaeus*. Both of these forms are phylogenetically correlated and probably, *Ursus etruscus* is their ancestor (Mazza and Rustioni 1994; Petronio et al. 2003). Morphologic features are so similar that Mazza and Rustioni grouped *U. deningeri* and *U. spelaeus* together for the reduction of premolars (upper and lower) and the skull shape with a dorsal profile usually interrupted in the orbital region and a more elongated facial skeleton. The mandible also has some diagnostic traits such as the position of condyles and angular process (uplift) and the massive horizontal rami. But Kurtén (1968) suggests that *U. deningeri* did not achieve the same specialization of *U. spelaeus* in locomotor apparatus. The size of *U. deningeri* is probably similar to that of cave bear and here I use a similar body mass reconstruction for both: 275 kilograms as in Meloro et al. (2007).

An accurate palaeoecological reconstruction was performed by Stiner et al. (1998) which use both morphological features and isotopic data (taken form the dentine) to demonstrate the diet of *U. deningeri* was dominated by tough food especially vegetables like nuts or roots. An hibernation behaviour to survive in the colder season is also likely for this species.

Ursus spelaeus (Rosenmüller and Heinroth, 1784)

This is the most peculiar species of the Pleistocene: it represents a European endemism and the most important Italian findings came from the Alps (Kurtén 1968). Reynolds (1906) furnished a comprehensive description of the material from Great Britain furnishing several diagnostic features to discriminate the cave bear from the brown bear (*U. arctos*) that usually co-exist in the same period and can be found in the same site (for Italy see Perego et al. 2001 as an example).

Even if it is common in the deposit of the late Pleistocene, the cave bear is recorded only in two Aurelian localities: Torre in Pietra and Quisisana of Capri (Palombo et al. 2003; Raia et al. 2006a).

Skull and lower jaw morphology is similar to that of *U. deningeri,* and *U. spelaeus* can be discriminated from *U. arctos* by the skull morphology (Capasso Barbato et al. 1993) and biometry of the fourth lower premolar together with the second upper molar (Capasso Barbato et al. 1990). Recently, Petronio et al. (2003) reviewed also long bones features which can overlap in size but the cave bear bones are generally more massive and their breadth is larger than in the brown bear.

Palaeoecology of cave bear resembles that of *U. deningeri* and the hibernation behaviour is really likely because most juvenile individuals have been reported in cave fossil material (Stiner et al. 1998). The body size of the cave bear could achieve 300 kilograms or more and here I opted to use a conservative estimate of 275 kilograms (in Meloro et al. 2007).

Figure 1.7: Cave bear skull from Grotta delle Fate housed in Hunterian Museum of Glasgow. Scale bar length: 10 cm (1 cm for each square).

Ursus arctos (Linnaeus, 1758)

The brown bear characterizes several assemblages of late Pleistocene in Italy. Its commonness in the Aurelian is low (with just two occurrences) and the earliest certain record is from Spessa 2 (PCOM Galerian 3). This species exhibits a large body size and, actually, it is spread all over continental Europe and North America with several sub-species. In Italy, brown bear persists with a small population in the central Appennine but it is recolonizing the Alps thanks to several reintroduction programs.

The most significant Italian remains were described by Capasso Babato et al. (1982) belonging to the Upper Pleistocene site of Monte Cucco (not included in Aurelian fossil localities). Generally, the Pleistocene brown bear becomes larger in size than the actual forms but their morphology does

not change so much. Its dentition is entirely adapted to an omnivorous feeding habit and this fact allows to consume meat as well (with no extreme reduction as in *U. deningeri-spelaeus* group).
The skull is less prominent than in cave bears and long bone morphology is generally more slender. As this species is extant, there are few palaeoecological reconstructions about some peculiar behaviours or more accentuated meat consumption in the diet of Pleistocene bears. Stiner et al. (1998) reported a high degree of overlap in the diet of *U. deningeri* and brown bear. Actually, the brown bear occupies forest habitat but also mountain high plains with shrub vegetation. Its diet is based on vegetables and insects but meat is consumed to some extent. The body mass range is really high and it depends on the regions: here I use an estimate of 167 kilograms based on the maximum skull length of specimens figured in Capasso Barbato et al. (1993) in Meloro et al. (2007).

HYAENIDAE (Gray, 1869)

The Italian peninsula represents an important scenario in the taxonomic history of Plio-Pleistocene hyaenids. In fact, the type specimen of the running hyena *Chasmaporthetes lunensis* was described by Del Campana (1914) on the basis of a palate fragment from Olivola. Short -faced hyenas *Pachycrocuta brevirostris* and *Pliocrocuta perrieri* have a good fossil record in Italy with the latter being rarer than the former. As suggested by Turner (1990), the European stratigraphic range of *Pliocrocuta perrieri* is not restricted to the middle-late Villafranchian. This form reappears in the Middle Pleistocene in several localities (L'Escale, Lunel Viel, Mosbach) and also in Italy one record is described by Caloi and Palombo (1986) at GRA site near Rome. These records are considered by several authors as a distinct species: *Hyaena prisca* but later, Werdelin and Solounias (1991) synonimised such a species with *P. perrieri*. Raia et al. (2006a) consider the only Italian Galerian record from Rome as *Hyaena prisca* but here I maintain the synonymy of Turner (1990) and Werdelin and Solounias (1991). The last hyaenid of Plio-Pleistocene is the spotted hyena and its occurrence in Italy is well characterised by several Aurelian localities although such form will be much more common in the last part of the Late Pleistocene.

Chasmaporthetes lunensis (Del Campana, 1914)

The running hyena is a typical Villafranchian form and its earliest occurrence in Italy is at Triversa. Del Campana (1914) described the morphology of the palate but he identified the fossil material as belonging to the genus *Lycyaena.* Later, Viret and De Beaumont (in Werdelin and Solounias 1991) re-interpreted this species as *Euryboas lunensis*. Kurtén and Werdelin (1988) reviewed the genus *Chasmaporthetes* clarifying the relevance of several dental features which allow to distinguish *Euryboas* spp. from *Chasmaporthetes lunensis*. The latter is characterised by the absence of p1 and m2 in the lower jaw which is slender and elongate (Fig. 1.8a); the skull is *Hyaena*-like with a strong sagittal crest a broad rostrum but also a well-developed braincase; the upper premolars are slender and elongate with the P4 carnassial possessing a prominent protocone and a long parastyle (Fig. 1.8b). In the m1 proto and paraconid are subequal in size and the talonid exhibits a well developed hypoconid with a blade function. Post cranial material is well represented only in the North American form *C. ossifragus* (Berta 1981) which is characterised by typical cursorial limb proportion. On the basis of material from Mt. Perrier Kurtén and Werdelin (1988) observed that the European *C. lunensis* possesses a radius longer than the tibia. There is a complete metacarpal from Layna in Spain while the other long bones are poorly known.

On the basis of some aspects of functional morphology Kurtén and Werdelin (1988) propose that *C. lunensis* was an active predator with some adaptations to bone cracking as well. Ferretti (1999, 2007) confirms the presence of a typical zig zag structures in tooth enamel but in a more primitive (as compared to other hyenas) condition and, consequently, minor bone cracking specialization. The ecological rule of *C. lunensis* was probably similar to that of modern spotted hyena in the African savannah. The body weight of this animal (75 kilograms in Meloro et al. 2007) partially resembles that of a very large modern spotted hyena (Kruuk 1972).

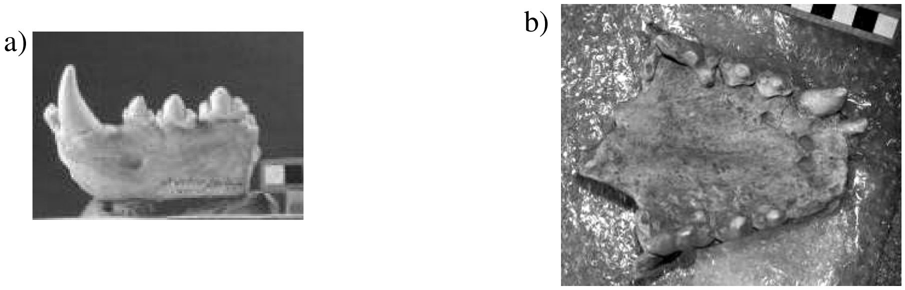


Figure 1.8: *Chasmaporthetes lunensis* left hemi-mandible QSV53 (a) and palate QSV52 (b) from Saint Vallier housed at MNHN of Paris. White square length = 1 cm.

Pliocrocuta perrieri (Croizet and Jobert, 1828)

This species spread its range two times all over Europe: during the middle Villafranchian and in the Galerian (Turner 1990). In Italy it occurs in two localities of PCOM Montopoli, than it disappeared in Upper Valdarno until a single occurrence of a fragmented upper carnassial in Rome during the Galerian 2 (Palombo et al. 2003; Caloi and Palombo 1986). Morphological features have been well described by Howell and Petter (1980): the skull has a relatively long muzzle, a short braincase with a well developed sagittal crest, the upper carnassial has a strong protocone while in the lower premolars there is an increasing size of premolars. The carnassial m1 is diagnostic: it possesses a thick trigonid and a little-developed hypo-entoconid; the metaconid is not present or poorly developed. This latter feature allows to distinguish *P. perrieri* with the modern brown hyena (*Parahyaena brunnea*) with which there is a remarkable morphological similarity (Kurtén 1968). Post-cranial material is unknown except for humerus fragments from Montopoli and St. Vallier that resembles modern *Crocuta* and *Hyaena* in its morphology (Argant 2004). The close similarity with modern brown hyena suggests a scavenging adaptation although there are no other evidences on behavioural preference to hunting or scavenging. Body mass reconstruction is based on m1 length from Italian specimens (Bebi 1998) and it gives a value of 80 kilograms (Meloro et al. 2007).

Pachycrocuta brevirostris (Aymard, 1846)

Kurtén (1968) described *Pachycrocuta brevirostris* as a short faced hyena characterised by the large size (lion like). This species is biochronologically indicative of the European Upper Villafranchian (Torre et al. 1992). Its first appearance in Europe is at Olivola and is represented in the fossil localities of Upper Valdarno but also Pirro and Galerian 1 with one occurrence at Slivia. The skull of this species is massive and canines are robust, upper dentition resembles modern *Hyaena* condition even if the P4 is more elongated and M1 is large. In the lower dentition premolars are very broad, typically adapted to bone cracking, and the cheek tooth m1 exhibits a long talonid with two cusps and also the trigonid is well developed but the metaconid is not present (Fig. 1.9) (Howell and Petter 1980).

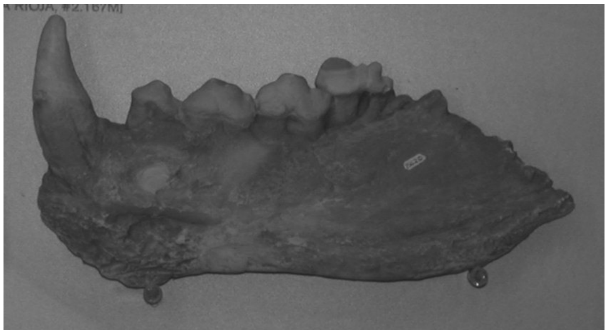


Figure 1.9: Lingual side of *P.brevirostris* right hemimandible from Venta Micena exposed in Museo Geologico y Minero.

Post cranial material is described from several European localities and Turner and Antón (1996) furnished important observations on the functional morphology of limb proportion. The tibia of *P. brevirostris* is shorter than in extant hyenas suggesting less cursoriality but also great powerful hind limb that together with a an elongated radius represents an adaptation for carrying pieces (especially long bones) of ungulate carcasses. Such a behaviour has been extensively demonstrated by the taphonomy of Venta Micena where *P. brevirostris* is the principal agent of transport of other large mammals' remains (Palmqvist et al. 1996; Arribas and Palmqvist 1998). Recently, Mazza et al. (2004) and Mazza (2006) reported a similar behaviour for *P. brevirostris* at the site Poggio Rosso where several complete skulls of carnivores together with gnawed ungulates long bones indicate that such site was probably used as den by a short faced hyenas clan. Palmqvist et al. (2003, 1996) indicates that the short faced hyena was broadly adapted for scavenging and used to select carcasses of large ungulates. Its life style should be similar to that of spotted hyena and it seems likely that such a large hyena was also a social animal (Turner and Antón 1996). The body mass of *P. brevirostris* was similar to that of a modern female lion: 127 kilograms in Meloro et al. (2007).

Crocuta crocuta (Erxleben, 1777)

The spotted hyena represents one of the most representative large mammal of European Ice Age. Several authors suggest that the Pleistocene form is represented by the subspecies *C. crocuta spelea* (Goldfuss, 1832) but this issue will not be considered here. It is noteworthy that modern molecular analysis do not support such a taxonomic separation (Rohland et al. 2005). What is certainly clear, is the morphological differences between modern spotted hyena (whose range is restricted to Africa continent) and the extinct European forms. Kurtén (1968) showed a clear cline distribution in the length of the lower carnassial of *Crocuta crocuta* with the smallest dimension in the populations from the equator latitude and an increasing in the population of South Africa and northern Europe.

In the Italian peninsula, the spotted hyena is recorded continuously in Galerian 3 PCOM and Aurelian. Italian fossil material has been abundantly described (especially for Upper Pleistocene specimens) but there are no systematic studies on the morphology of Italian *Crocuta*. The best known European fossil material comes from Kent's Cavern (UK) where it is evident a larger relative size (if compared with the actual hyenas) (Kurtén 1968). The morphology of spotted hyena is characterised by its extreme adaptation to bone cracking, determining an elongated metacone in the upper carnassial and in the lower p4 together with broad premolars (P3 – p3), a deep mandible curved under p3 – m1 region and a strong sagittal crest (Kruuk 1972; Werdelin 1989; Biknevicius and Van Valkenburgh 1996).

Even if morphological adaptation to bone cracking is remarkable, the spotted hyena is an active predator usually more than the lion (*Panthera leo*) (Kruuk 1972; Schaller 1972). Its postcranial anatomy together with well developed stamina muscle cells provide high resistance in long-distance chase of prey that hyenas use to tackle in large pack. Pack hunting strategy reflects a complex sociality (females are dominant and larger than males and they live together in a clan) and represents also a defensive response from lion attacks at killing sites (Kruuk 1972). Prey selection is biased toward most vulnerable individuals of large sized ungulates (in Africa represented by wildbeest *Connochaetes taurinus*, and zebra *Equus burchelli*) and medium sized gazelle such as Thomson gazelle (*Gazella thomsonii*).

Another peculiar behaviour is the choice of natural caves as denning sites that is also the cause of rich Pleistocene assemblages (Kurtén 1968; Kruuk 1972). From Pleistocene cave deposits Diedrich and Žák (2006) identified the horse *Equus ferus* and the rhinoceros *Coelodonta antiquitatis* as the commonest prey in the Bohemian Karst and Prague region (Czech Republic) together with *Bison priscus*, the red deer *Cervus elaphus* and other middle sized ungulates. Heavy predation on red deer (but also on Aurochs *Bos primigenius*) was also reported by Stiner (1992) on the basis of several Upper Pleistocene caves in west-central Italy. Scavenging is instead reported also on other large carnivores such as wolves and cave bear carcasses (Diedrich and Žák 2006).

Considering the larger body size of Pleistocene spotted hyenas, I used a mean estimate of 102 kilograms (Meloro et al. 2007).

FELIDAE (Gray, 1821)

Large cats are present in the Italian peninsula with a variety of forms during Plio-Pleistocene. The most peculiar representatives are the sabre tooth cats *Homotherium* spp. and the dirk tooth *Megantereon* spp.. Italian specimens were described by the seminal work of Fabrini (1890) although the most complete fossil specimens belong to French localities (e.g. Senèze) (Kurtén 1968; Turner and Antón 1997). These large cats persist from the Villafranchian since Galerian with several species: the Villafranchian *Homotherium crenatidens* is replaced by *H. latidens* while *Megantereon cultridens* by the more advanced form *M. whitei*. *Homotherium latidens* is discriminated by few morphological traits (Ficcarelli 1979b; Kurtén 1968) while the differences in the two forms of *Megantereon* have been a long matter of debate. But recently, Palmqvist et al. (2007) demonstrated that *M. cultridens* and *M. whitei* are two different species.

Other Villafranchian felids are the giant cheetah (*Acinonyx pardinensis*), the Etouaires lynx (*Lynx issiodorensis*) and the jaguar like *Panthera gombaszoegensis.* For this latter species, it is worth mentioning that Del Campana (1916) described the Valdarno fossil remains as a distinct form (*Panthera toscana*) but it is currently accepted the synonymy with *P. gombaszoegensis* (O' Regan and Turner 2004). The Villafranchian cheetah is represented by several long bones remains and skull fragments and it does not show any significant difference from the other European fossils. For the Etouaires lynx, Werdelin (1981) suggested a sub species rank for the fossil material of Valdarno (*Lynx issiodorensis valdernensis*) but I prefer, conservatively, to leave (also for Italian forms) only the specific name. Interestingly, Morales et al. (2003) propose the genus *Caracal* for the Etouaires lynx but they did not furnished a clear species diagnoses on the basis of all the European material but just the Layna (Spain) fossil samples. The evolutionary lineage of lynx is represented in the Middle Pleistocene by the small *Lynx pardinus* like. The species name of such form has been proposed according with its similarity to the extant Spanish endemic lynx, and Raia et al. (2006b) consider the only Italian record as *L. pardina spelaeus*. Recently, Testu (2006) argues that such specific name is not valid while the correct nomenclature to describe middle Pleistocene forms is *Lynx spelaeus* and this will be also applied here.

During the middle Pleistocene the Villafranchian forms are replaced by modern pantherine cats which spread all over Eurasia: *Panthera leo* and *Panthera pardus*. These forms will be much more common in Italian Upper Pleistocene deposits achieving high abundance (e.g: in the Equi cave Del Campana 1947). The Pleistocene leopard does not represent a distinct extinct species while for the lion several specific or sub-specific names have been proposed. Here, conservatively, I use the old Kurtén (1968) proposal about the fact that the Pleistocene lion were remarkably larger than extant one because of different climate but such feature is not enough to support a different species. The Italian lion from Isernia probably represent one of the oldest European specimen, even if, unfortunately, it is represented only by one tooth (Sala 1990).

Acinonyx pardinensis (Croizet and Jobert, 1828)

The giant cheetah is well represented in the Villafranchian fossil record from Italy. This species occurs at Triversa, in two localities (Montopoli and Costa S.Giacomo) of Montopoli PCOM, at Olivola, Casa Frata and Pirro. Its geographic range covers all Europe since Asiatic localities as well (Kurtén 1968). Morphologically, *Acinonyx pardinensis* resembles its modern African counterpart *A. jubatus* and only size represents an evident trait of discrimination (Ficcarelli 1984; Turner and Antón 1997; Argant 2004). The skull possesses a distinct shape with high and enlarged nasals, high and well developed orbits, a broad rostrum in the posterior region. The upper dentition is characterised by short canines, a P3 with a reduced anterior lateral cusp which is larger in *A. jubatus* and an upper carnassial with a more reduced paracone.

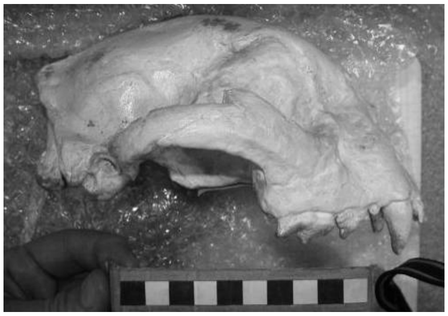


Figure 1.10: Skull in lateral view of *Acinonyx pardinensis* QSV112 from St. Vallier (housed at MNHN of Paris). Scale bar length 10 cm (1 cm per square).

The lower jaw of *A. pardinensis* is similar to that of *A. jubatus* and only the morphology of p3 is distinctive. Post cranial material is well known from the specimens (hind limb bones) collected at Olivola and several fore limb elements from St. Vallier. Their morphology is similar to that of modern cheetah and this fact suggests a similar adaptation (probably more advanced) to high-speed chasing. All the morphological traits lead considering the giant cheetah as similar in ecology to the modern forms (Turner and Antón 1997). The body weight estimates should resemble a lion-sized animal of c.ca 90 kilograms in keeping with Argant (2004). For this thesis I will use a conservative estimate of 67 kilograms based on lower carnassial length (Meloro et al. 2007).

Homotherium crenatidens (Fabrini, 1890)

The type specimen of this remarkable sabre tooth cat is represented by Valdarno material. This form is present in each Villafranchian Italian PCOM and its last occurrence is at Pirro.

Long canines are the most important morphological feature of *H. crenatidens.* Their morphology differs from that of the dirk-tooth *Megantereon* spp. for having distinctive crenulations. Such feature is present also in all teeth of juvenile individuals of *H. crenatidens* (Ficcarelli 1979b). The sabres are curve, flatter and shorter than in *Megantereon* and they are accompanied by a not so reduced lower canines. Among the incisive, the third is more developed than the others. The skull is elongated, with the rostrum longer than the brain case (Fig. 1.11a, b). A diastema separates the sabres from premolars. The second upper premolar is not present while the carnassial P4 exhibits a developed deuterocone and a long metastyle relative to the parastyle. Such feature is accompanied by a sharp lower m1 demonstrating a clear adaptation in meat slicing.

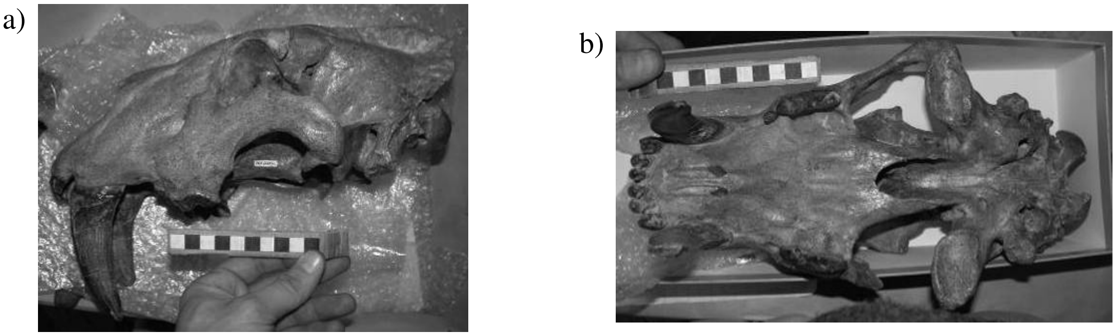


Figure 1.11: Skull in lateral and ventral view of *Homotherium crenatidens* from Perrier (PER 2000) housed in MNHN of Paris. Scale bar length 10 cm (1 cm per square).

The post cranial material is unique as well with fore limb longer than hind limb resembling a typical hyena like posture. *Homotherium* exhibits also a short tail. Palaeoecology of this species has been little investigated because the greatest number of studies were conducted on *Homotherium latidens* (see below). A peculiar pathology has been recorded on humeri from French localities (St. Vallier and Senèze) and probably this demonstrates how the fore limbs were overloaded during the chasing of prey (Turner and Antón 1997; Argant 2004).

This cat was remarkable heavy and probably its body weight was greater then that of a large lion. Here, I use an estimate of 231 kilograms (Meloro et al. 2007).

Homotherium latidens (Owen, 1846)

The late *Homotherium* is represented in three Galerian localities of the Italian fossil record (Palombo et al. 2003; Raia et al. 2006b). This species usually resembles *H. crenatidens* in skull morphology as well as post cranial elements even if the canines are shorter and differ in shape (Ficcarelli 1979b). The functional morphology of this species has been broadly investigated especially in the light of the long debate concerning its hunting behaviour (Antón and Galobart 1999; Antón et al. 2004, 2005). Basically, there are two theories: the "stabbing" suggests that sabre tooth cats use their sabres for a lacerating function (the attack to the prey should be at belly or other soft parts) and this implies a rotation along the thoracico-cervical joint; the "canine shear bite" implies a much more precision in the movement of the neck whose strong musculature allows to perform a precise jugular bite (while the strong fore limbs stop the potential prey movements). The studies of Spanish palaeontologists agrees with this latter theory and widely demonstrate its validity on the basis of the well developed mastoid region together with cervical vertebrae morphology and lower jaw and dental features. Antón et al. (2005) demonstrated also that *Homoterium latidens* was broadly adapted to cursoriality and its fore limb is not so strong to allow a single individual in bringing down large ungulates. This fact suggests that *H. latidens* was constrained to hunt in group like modern lions do even if its hunting technique differs in immobilising prey as well as in the canine shearing biting. On the basis of Texas cave remains belonging to *Homotherium serum*, it has been suggested that also *Homotherium latidens* specialized its target prey on juvenile of mammoths (Turner and Antón 1997). Palmqvist et al. (1996) evidenced for *H. latidens* a prey class selection similar to the extant lion. Later Palmqvist et al. (2003) also demonstrated that isotopic values (carbon, nitrogen and oxygen) of the sabre tooth cat at Venta Micena is similar to that of large grazer ungulates and most interestingly to juvenile mammoths. There are no doubt that *H. latidens* was a cursorial predator and then specialised on grazer ungulates. The specialization on juvenile mammoths still to be debated especially on the basis of long bone morphology that does not support completely such a behaviour (Antón et al. 2005).

The body mass of *Homotherium latidens* is higher than that of the Villafranchian *H. crenatidens* (274 kilograms). It is noteworthy that this reconstruction is based on lower carnassial length and it is only indicative but not accurate especially for felids whose body mass greatly varies intraspecifically.

Megantereon cultridens (Cuvier, 1824)

The dirk tooth cat is another characteristic member of the Italian Villafranchian. Turner (1987) furnished an accurate diagnosis of *M. cultridens* but he considered *M. whitei* in synonymy with the latter justified by the potential high sexual size dimorphism. Sardella (1998) reviewed the taxonomy of *Megantereon* spp. and grouped in *M. cultridens* also the Italian specimens from Pirro and Farneta. In Raia et al. (2006b) *M. cultridens* is present only in Montopoli and Upper Valdarno PCOMs but not Pirro. According with Palmqvist et al. (2007) I consider valid such strict stratigraphic range to *M. cultridens* present only in Valdarno FU (=Upper Valdarno PCOM).

Megantereon cultridens can be easily distinguished from *Homotherium* spp. for its smaller size and its longer non-crenulated canines. The canines are unserrated, more curved and laterally compressed. The brain case of *M. cultridens* is long while the rostrum is shorter and broad posteriorly. There is a short diastema between the incisors and the upper canine that in *Homotherium* is less developed. Both second premolars (upper and lower) are not present. The ratio between P4 and P3 is highly variable and in the P4 the deuterocone is usually prominent.

In the lower jaw, the canine is very reduced as well as p3. The presence of a developed mandibular flange is a distinctive trait (Fig. 1.12). The neck is long and the limbs are short and robust.

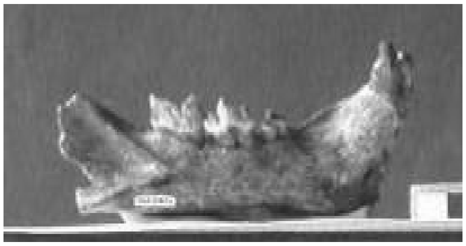


Figure 1.12: Right hemimandible of *Megantereon cultridens* from Perrier (PER 2001) housed at MNHN of Paris. White square length: 1 cm.

Such features explains the peculiar hunting behaviour that should conform to canine shearing bite. In *Megantereon* the limb bones are stronger than in *Homotherium* and this feature allows the species to ambush its prey alone (Turner and Antón 1997). It is worth mentioning that post cranial material of *M. cultridens* is scanty (Argant 2004 describes several metapodials) and most of long bone morphology is better known for *M. whitei*. The size of *M. cultridens* is much smaller (63 kilograms in Meloro et al. 2007) than *H. crenatidens* but its morphology probably is indicative of a solitary hunting style. The target prey of *Megantereon* were represented by medium size ungulates but also large deer of the genus *Eucladoceros* (Turner and Antón 1997). Much more palaeoecological reconstructions have been proposed for *Meganteron whitei* of Venta Micena.

Megantereon whitei (Broom, 1937).

This advanced form of *Megantereon* is recorded only at Pirro site in Italy (Raia et al. 2006b) and other European localities Galerian in age like Untermassfield (Germany) and Venta Micena (Spain) (Palmqvist et al. 2007). Martínez-Navarro and Palmqvist (1996) underline the importance of this species in understanding the routes of *Homo* dispersal from Africa to Europe and Asia. Probably this hypercarnivorous species provide carcass for scavenging by early *Homo* members.

Morphologically, *M. whitei* is similar to *M. cultridens* and can be distinguished on the basis of several features: upper canine length and breadth; P4, m1 and p4 length and breadth. The dirk canines are much more developed than in *M. cultridens* while the carnassials are smaller in size.

Interestingly, also the mandible shape differs among the two species with *M. cultridens* having a different biomechanical efficiency than *M. whitei* that maximized the bite force at the m1.

Post cranial anatomy should resemble the extant jaguar (*Panthera onca*) according with the studies based on African *Megantereon* (Lewis 1997). Fore limbs are stronger and massive. Such trait are characteristic of an ambush predator and Palmqvist et al. (2003) confirms that *M. whitei* prefers habitat with cover vegetation and as consequence also browser ungulates. Although, the morphology of *M. whitei* is well equipped in killing prey much more larger that the predator itself. Limb morphology suggests also a slight adaptation in tree climbing but such behaviour is implausible considering the long canines. Body weight reconstruction of this species differs a lot when using several traits. A body mass of 55 kilograms is estimated when using m1 length or 100 kilograms when using humerus cross sectional diaphysis (Martínez-Navarro and Palmqvist 1996). Although the authors suggest a body mass of 100 kilograms is probably much more accurate I consider valid a body weight of 55 kilograms that is much more similar to that of *M. cultridens* for which a reconstruction based on skull length (PER 2001a) achieves a 60 kilograms value.

Lynx issiodorensis (Croizet and Jobert, 1862)

The Etouaires lynx is another typical Villafranchian element that spread all over Europe. In Italy it is present continuously in Upper Valdarno, ValdiChiana and Pirro PCOMs (Raia et al. 2006b). The Valdarno fossil material was described in detail by Fabrini (1896) who furnished accurate description of both cranial and post cranial elements. But Kurtén (1978) furnished an accurate comparative analysis of *L. issiodorensis* with modern linxes. The skull is very large with narrow zygomatic arches and wider and longer rostrum (compared with the skull length) (Fig. 1.13). The nucal crest is well developed and also lower jaw morphology suggests a strong biting force: mandible possess a large dentition and a deep masseteric fossa.

On the upper dentition, the P2 is not present, P3 is slender and more elongated than in modern *Lynx* and in the upper carnassial a small ectoparastyle is prominent (Fig. 1.13).

In the mandible there is a long diastema, p3 and p4 can be separated by a gap and m1 is very short lacking the metaconid and talonid complex.

Figure 1.13: Type skull in ventral view of *Lynx issiodorensis* (MNHN 1964-12) from Perrier Etouaires. White square length 1 cm.

L. issiodorensis exhibits a long neck as well as long lumbar region while the hind limb region is less developed than in modern lynx. Generally Kurtén (1978) noted that from the 4th lumbar vertebra to the anterior part of the body the Etouaires lynx is larger than the extant lynx while from the 5th lumbar vertebrae it is shorter.

Limb bones proportion resembles the American puma (*Puma concolor*) being more robust than in lynx. In Europe Werdelin (1981) suggests an evolutionary trend in *L. issiodorensis* from early Villafranchian members that are larger in size to the late representatives of the species that are smaller but possess a longer m1.

Palaeoecological reconstruction of *L. issiodorensis* were deduced from its morphological similarity with modern lynx: probably the Etouaires lynx specialized on small rabbits (e.g: *Oryctolagus* spp.) but was also capable of killing medium size ungulates (like the modern European lynx kills roe deer) (Kurtén 1978). A body mass reconstruction of 22 kilograms is here applied on the basis of m1 length as well as skull length (Meloro et al. 2007).

Lynx spelaeus (Boule, 1906)

The cave lynx is an enigmatic form that in the Italian middle Pleistocene is represented by the remains of Valdemino (Sala et al. 1992). What is not clear, is the evolution of such form and its relationship with the actual lynxes. Ficcarelli and Torre (1977) proposed that *L. issiodorensis* is ancestral to the modern Spanish lynx (*Lynx pardinus*) and suggested for Pleistocene specimens a sub-specific rank (*L. pardina spelea*) for which an Asian immigrations seems likely. Recently, Testu (2006) described specimens of *L. spelaeus* from French localities (Caune de L'Arago; L'Obervatoire). These forms differ slightly in morphology from *L. pardinus* as well as *L. lynx*: the upper carnassial is larger while P3 is more elongated than larger; in the lower dentition the m1 morphology is quite distinctive with the relative presence of metaconid-talonid complex in *L. spelaeus* while this feature lack in *L. pardinus*. Long bones morphology is generally robust and less elongated than in modern lynx. The dentition traits of *L. spelaeus* sometimes exhibit overlap with *L. issiodorensis* or *L. lynx* and this fact suggests that a gradual evolution occurred in Eurasiatic lynx starting from the Villafranchian Etouaires lynx, to an intermediate cave forms which splits in European lynx (*L. lynx*) and endemic Spanish form (*L. pardinus*) (cf. Testu 2006). The European lynx will be common in the Late Pleistocene all over Italian fossil record (Rustioni et al. 1995).

The palaeoecology of cave lynx is unknown but its morphological features suggest a similar behaviour to modern lynx. Body mass reconstruction based on m1 length from Valdemino gives a value of 23 kilograms only slightly large than Etouaires lynx (Meloro et al. 2007).

Panthera gombaszoegensis (Kretzoi, 1938)

This large cat is the oldest pantherine of Europe. The Italian fossil material is one the richest (among the other Villafranchian European localities) and it has been described by Del Campana (1916) and later by Ficcarelli and Torre (1979b). Compared with the saber toothed cats, *P. gombaszoegensis* is characterized by less developed upper canine that are larger; the dentition is generally not extremely reduced. Skull exhibits a frontal bone tiger like while the sagittal crest is strong as in the jaguar (*Panthera onca*). Nasal process extends to the extreme of nasal bone (Fig. 1.14) like in leopard (*P. pardus*) and jaguar. In the upper dentition the P3 (even if with little diagnostic value) shows anterior and posterior accessory cusps, P4 has a distinctive cingulum, the canine is robust and incisor battery are arranged in a straight line with the third being larger (O'Regan and Turner 2004). In the mandible the lower canine is large and conical, the p4 has a large protocone together with anterior and posterior cusps, the lower carnassial is much distinctive with protoconid longer than paraconid and with rudimentary metaconid present.

Long bones anatomy resembles some traits typical of the jaguar: the tibia is robust and the digital cavity of femur is similar to *P. onca* even if the neck of the femur is much more developed than in *P. pardus* and jaguar. In the fore limb the humerus shows several traits common to the lion *P. leo* (e.g condyle) while the trochlea is similar in size to the jaguar. Instead, the radius is much more similar to the tiger (*P. tigris*). The oleocran region of the ulna is more developed than in the leopard. Metapodials are generally robust and jaguar like (Del Campana 1916).

Figure 1.14: A deformed skull of *P. gombaszoegenis* (I.G.F. 4376) from Olivola (Tuscany).

All such features converge so strongly with the fact that *P. gombaszoegensis* resembles the jaguar that Hemmer et al. (2001) considers the specimens from Dmanisi (Georgia) as a subspecies of *P. onca*. These authors propose a body mass reconstruction between 90 and 210 kilograms even if the Akhalakari specimen (Dmanisi) is larger then the early Villafranchian *P. gombaszoegensis*. Palaeoecological reconstruction were rarely proposed and only Hemmer (2001) suggested that at Untermassfield "*P. onca gombaszoegensis*" specialises on medium size ungulates like *Eucladoceros* and *Sus*.

On the basis of Italian specimens, I consider valid a body mass of 90 kilograms (Meloro et al. 2007).

Panthera leo (Linnaeus, 1758)

The lion is an extant species whose geographic range is today restricted to Africa and the Indian forest of Gir (Barnett et al. 2006). Its occurrence in European fossil record begins in Galerian localities (Kurtén 1968). The oldest record is for Isernia La Pineta (Sala 1990) that recently has been re-dated at 600-500 ka (Coltorti et al. 2005). In PCOM Galerian 3, the lion is recorded at Fontana Ranuccio and in the Aurelian this species still to be rare at Torre in Pietra and Castel di Guido (Capasso Barbato and Minieri 1987; Palombo et al. 2003; Raia et al. 2006b).

The Pleistocene lion is generally subdivided in two sub species: the ancient form *P. leo fossilis* of Middle Pleistocene and the Upper Pleistocene *P. leo spelaea* that is less massive and achieve similar upper size limits of extant lions (Kurtén 1968). Recently, Sotnikova and Nikolskiy (2006) proposed a specific rank for the Upper Pleistocene form (*P. spelaea*) on the basis of several skull and upper carnassial traits. Although this hypothesis cannot be excluded, I prefer to use a conservative approach by excluding sub-specific or new specificic denomination for Pleistocene lion. In keeping with Testu (2006) it is possible to consider the form *fossilis* and *spelaea* as chronomorphotypes whose morphological variability is the reflection of different climate. In such perspective the Italian specimens of middle Pleistocene lion are representative of the *P. leo fossilis* morphotype.

This form is characterised by being larger and more robust than Upper Pleistocene and extant lion. Teeth are massive and less compressed. A shorter metacone can be discriminated in the upper cheek tooth. In m1 protoconid is higher than paraconid, talonid is marked and a neat metaconid developed. The lower carnassial is generally more elongated than actual lion but less than in Upper Pleistocene lion. For middle Pleistocene there are non-complete skulls (on the basis of Italian fossil record) but Sotnikova and Nikolskiy (2006) describes features belonging to specimens from Azé (French): the skull shares similar features with extant lion and Upper Pleistocene lion in being very large and with developed nuchal crest, the incisors are relatively smaller than in other lions, the orbits are small as well while the nuchal surface is broader.

In the postcranial elements the humerus is massive with a medial epicondyle well developed on the supracondylar foramen (present in felids and mustelids), metacarpal is massive with an elevated distal portion (typical for felids).

The femur is elongated and massive and the hindlimb is longer or similar in proportion to fore limb.

The general morphological modification of Pleistocene lions appears to be a by product of their larger size hence a consequence of different environmental conditions. The palaeoecology of Pleistocene lion is generally based on several generalization that can be done by looking at the ecology of extant lion (Schaller 1972). The lion is a remarkable, highly dimorphic, opportunistic predator: its social behaviour is unique among felids (usually lives in a pride familiar nucleus with multiple females and a dominant male) and its prey preference is represented by medium-large ungulates (in Serengeti the buffalo *Syncerus caffer*, the wildebeest, zebra). Such a preference causes overlap with several predators like spotted hyenas, African wild dogs but also cheetah. The latter two species evolved distinct hunting behaviour in order to avoid lion that is generally dominant by virtue of its larger size. Sometimes lion is capable to kill also very large ungulates like rhinoceros or juvenile of elephants but they never constitute an important proportion in the diet (Schaller 1972).

It has been suggested that the steppe bison was, probably, an important prey for the Pleistocene lion but such observation is valid on the basis of the bison “Blue babe” from a cave in Alaska (Turner and Antón 1992). For European lion there are no evidence of particular prey selection even if at Isernia La Pineta, for instance, the steppe bison (*Bison schoetensacki*) bones are really high in number but there are sign of human activity on them (Anconetani and Peretto 1996). It is not excluded that auroch (*Bos primigenius*), wild boar (*Sus scropha*) and red deer (*Cervus elaphus*) could have been important for the middle Pleistocene European lion like gaur (*Bos gaurus*), wild boar and Sambar deer (*Cervus unicolor*) are important for the tiger (*P. tigris*) (Sunquist and Sunqist 1989; Kawanishi 2002). It is noteworthy that some authors suggest several morphological similarities between Pleistocene lion and the tiger such that it can be considered more related to the latter. Recently, Yamaguchi et al. (2004) evidenced that the Pleistocene lion already lived in group but the typical mane (now present in males as a secondary sexual trait) was not present. For body mass I use an estimate of 183 kilograms as mean between males and females (Meloro et al. 2007).

Panthera pardus (Linnaeus, 1758)

The leopard is a rare species in the Italian fossil record. Kotsakis and Palombo (1979) reviewed its distribution in the Italian fossil record. For the middle Pleistocene the earliest record is Valdemino (Galerian 2), than in the Aurelian the leopard is recorded at Capri and Prati Fiscali (Palombo et al. 2003; Raia et al. 2006b). Its distribution will be broader in the Upper Pleistocene, and in some localities leopard remains were high in number (100 individuals in Caverna degli Equi Del Campana 1947). The skull of this predator exhibits a short muzzle with a more developed postorbital region than in the jaguar (Fig. 1.15); there are two typical inflations (frontal and parietal region) and one is below the alveolus of the upper canine; the orbits are circular and the bullae are elongated. Upper premolars are variable in number and the P1 can be supported by supranumerary aleveolus; upper canines are flat in lingual side and the cheek tooth P4 is compressed.

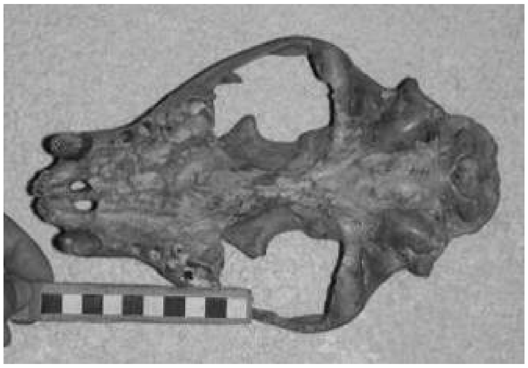


Figure 1.15: Skull in ventral view of *P. pardus* from Monte Sacro (figured in Kotsakis and Palombo 1979).

In the mandible, the profile is generally not curved with a long diastema between canine and p3 and also a short diastema can be present between p3 and p4. The massetteric fossa is well developed and can achieve in length the posterior extremity of m1 suggesting a strong masticatory power. The premolars do not exhibit significant morphologies (in p3 the anterior cusp can disappear while p4 show tri-cusps), the m1 is typical in its hypercarnivore morphology without metaconid and the protoconid is generally higher than paraconid (cf. Testu 2006).

On the basis of Upper Pleistocene fossils, Del Campana (1947) demonstrated that no significant differences can be found in the morphology of the post-cranial anatomy of Pleistocene leopard and the extant one even if the Equi specimens exhibited a high proportion of arthritis in humerus. The hind limb is proportionally longer than the forelimb (Lewis 1997) and this confers a high adaptability in tree climbing. The leopard is considered one of the most peculiar biotic agents in the taphonomy of several caves especially in Africa because of its capacity to drag carcasses on trees or near caves: among the other prey also hominid were founds in Swartkans (Turner and Antón 1997). The extant leopard is sexually dimorphic and can achieve 70 kilograms (males): for the Pleisotcene form I use an estimate of 60 kilograms (Meloro et al. 2007).

Chapter 2

What is a large carnivore? Evidence from mandible shape

2.1 Introduction

The relationship between morphology and ecology is a well established pattern in extant mammals. This link is particularly evident in members of order Carnivora. In spite of the literal meaning, mammalian carnivores occupy a wide variety of ecological niches (Nowak 1991; Gittleman 1985) and their high adaptability is reflected in a large range of distinctive morphologies. In particular, teeth are the most significant ecomorphological traits: modified carnassials and large canines are features common to all carnivores even if cusp sharpness as well as proportion of slicing and crushing areas in lower molars represent adaptation to different feeding habits (Crusafont-Pairó and Truyols-Santonja 1956, 1957, 1958; Biknevicius and Van Valkenburgh 1996).

These broad generalizations allow to investigate carnivore species packing among communities (in space and time) by using tooth related features as representative of feeding niche (Van Valkenburgh 1985, 1988, 1989; Van Valkenburgh and Wayne 1994; Dayan and Simberloff 1996 and references therein; Farlow and Pianka 2002). Results of these studies suggest a competition-driven pattern in carnivore assemblages even if the "pack" of species can change.

The definition of carnivore community is subjective and, usually, the guild concept helps to select species. This term –guild- occurs under different interpretations since Root's definition as a group of "species that exploit the same class of environmental resources in similar way" (in Blondel 2003). Under this perspective, the guild concept allows to include mammalian carnivores in distinctive groups according to their body size and/or hunting style. Simberloff and Dayan (1991) reviewed the guild concept in ecological literature and pointed out that it has "too many connotations" and should be robustly defined in order to avoid misinterpretations. Under this perspective, the guild concept allows to include mammalian carnivores in distinctive groups according to their body size and/or hunting style.

A body weight threshold of seven kilogram was operationally defined by Van Valkenburgh (1985, 1988, 1989) in order to separate "large" from "small" carnivore guild.

Carnivore guild membership can be also defined according to distinctive morphologies related with locomotion. In turn, this fact is reflected in high-clade groups (e.g: family) that are also morpho-ecologically distinctive (Dayan and Simberloff 1996).

On the other hand, Jaksić (1981) proposed objectives methodologies to define a guild. He re-defined the guild of predatory vertebrates as representative of all predaceous species including raptors, carnivorous reptiles and mammals (Jaksić et al. 1981, Jaksić and Delibes 1987).

Although Jaksić's studies have a merit, their interpretations of guild give less emphasis to the way resources are exploited (e.g: hawks are flying predators while coyote is terrestrial).

In order to furnish a clear classification of different ecological species grouping, Blondel (2003) proposed two terms: the guild and the functional groups. The first concept considers the species in the light of their competitive relationship, the second explains the effect of species on the ecosystem.

It is clear that all defined Carnivora-pack of species represent guilds sensu Root (1967) other than functional groups. Furthermore, the Rootian guild concept can be grouped in the α guild (sensu Wilson 1999) that includes "subjective a priori" (α1, when the guild is identified without testing its validity), "tested a priori" (α2, when a previously identified guild is supported with a posteriori tests), "objective character" (α 3, guilds formed with objective methodology) and "intrinsic" guilds (α4, guild identified by species that do not tend to co-occur). The α category is alternative to the β guild that considers species as occupiers of similar environments. Literature on carnivore guild considers all the guilds as α1 because they have been always previously identified by the investigator.

Here, I test the validity of different α1 carnivore guild concepts by investigating at a macroevolutionary scale the variability of a morphological trait relevant in feeding ecology: the mandible. Mandible is a mobile head structure entirely functional for the mastication (Barone 1980). It is attached with the skull through the masseter, temporalis and pterigoid muscles that insert into the *ramus mandibulae*. On the other hand, the *corpus mandibulae* supports the teeth that mould its shape during the development (Atchley et al. 1985).

Greaves (1983, 1985, 1995) demonstrated how mandible is optimized for chewing in carnivores and other mammals. Its morphology in Carnivora is widely driven by phylogenetic constraints (Radinsky 1981a, b, 1982; Werdelin 1989) as well as feeding habits and hunting behaviour (Biknevicius and Van Valkenburgh 1996; Therrien 2005a, b).

Recently, Christiansen and Adolfssen (2005) confirm the co-variation between mandible and skull length even after phylogenetic control. Although mandible morphology weakly co-varies with moment arms of the masseter and temporalis muscles. On the other hand, Christiansen and Wroe (2007) demonstrate how bite forces (estimated by skull biometry) differ among feeding categories irrespective of differences in body size and in phylogenetic relationship.

These studies support the fact that mandible can be more ecologically informative if compared to the teeth because its shape is influenced also by muscles' attachments that allow the process of mastication (Weijs 1994).

The limitation of mandible as a feeding-relevant morphological trait is represented by its complex shape, difficult to quantify with univariate morphometrics. Great advance in morphometric methodologies allow to quantify and visualize the shape of objects by using a subset of homologous landmarks (Adams et al. 2004). This technique, namely geometric morphometrics (GM), is strictly related with the definition of shape as a comparison metric among different objects after removing the effect of size, orientation and translation (Bookstein 1993; Marcus and Corti 1996; Dryden and Mardia 1998; Zelditch et al. 2004). Through a procedure of superimposition, it is possible to visualize and quantify shape differences by using D'Arcy Thompson (1917) idea of deformation grids. A great variety of GM studies were conducted on shape variability in mandible especially of small mammals (De Moraes et al. 2000; Cardini 2003; Klingenberg et al. 2004; Zelditch et al. 2004; Caumul and Polly 2005; Monteiro and Reis 2005). Marcus et al. (2000) performed a 3D skull and mandible survey on a large variety of mammalian orders, although only Raia (2004) furnished a comprehensive 2D morphometric survey of extant and extinct large mammalian carnivores.

The aim of the present investigation is to validate carnivore-guild membership by looking at morphological discontinuities in mandible shape of the most representative species of Carnivora. If competition is a driving force separating carnivore-guilds at temporal and geographical scale, it is theoretically expected that all the members belonging to similar guilds should be morphologically similar. Shape data of mandibles are considered to test if morphological differences occur among ecological or guild categories. Phylogenetic relatedness is taken into account as well in order to verify or falsify differences revealed by tip data.

Recently numerous comparative methods emerged (for review Miles and Durham 1993) and in most of Carnivora-related studies independent contrasts (Felsenstein 1985) have been applied to test for differences or co-variation patterns revealed by morphological traits (Garland et al. 1992, 1993; Polly 1998, 2001, 2002; Andersson 2004; Christiansen and Adolfssen 2005; Chrisitansen and Wroe 2007). With shape multivariate dataset, MacLeod (2001, 2002) proposed the application of autocorrelograms (Gittleman and Kot 1990) even if Rohlf (2001) identified a better statistical power in Phylogenetic Generalized Least Square (Martins and Hansen 1997). The latter methodology is here applied to verify differences after taking into account phylogeny.

These tests allow to verify previous identified categories coherently with the α2 guild concept. Procustes distances among species are explored as well in order to define objectively (α3) potential guild members.

2.2 Materials and Methods

2.2.1 Sample size

A subset of ninety seven terrestrial species of order Carnivora (Appendix 1) was chosen as representative of the most relevant ecosystem of the world: Kruger (South Africa), Gunung (Indonesia; Asia), La Amistad (Panama; Central America), Krknose (Czech Republic; Europe), Yasuni (Ecuador; South America); Yellowstone (USA). Species lists were drawn from BioInventory Builder (2004). Each species is represented by one adult mandible from specimens collected in the wild. It is assumed that the collected specimens are representative of every single species.

The species belong to eight families of fissiped carnivores (Table 2.1) and their number is homogeneously proportional to the total number of recorded fissiped forms (in Bininda Emonds et al. 1999). Only members of family Felidae are overrepresented with 58% of known species present in the mandible sample (Table 2.1). The aardwolf (*Proteles cristatus*) was excluded from the mandible sample because its teeth morphology does not allow to record landmarks data.

	Sample	**Tot Species**	**% Species**
Canidae	12	34	35%
Felidae	21	36	58%
Herpestidae	10	37	27%
Hyaenidae	2	4	50%
Mustelidae	30	65	46%
Procyonidae	7	18	39%
Ursidae	3	8	38%
Viverridae	12	34	35%
Tot	97	236	41%

Table 2.1: Number of species sampled respect to the total number of species.

2.2.2 Geometric morphometrics

Mandibles were photographed in lateral view at two meter distance with a Nikon 995 digital camera. This procedure standardizes the sample of digital images and allows to avoid deformation due to the parallax effect (cfr. Raia 2004). On each mandible picture a subset of fourteen landmarks was digitized with the software TpsDig 2.09 (Rohlf 2006a). Landmarks from 1 to 6 and 12 to 14 describes the *corpus mandibulae*, instead landmarks 7 to 12 are representative of the *ramus mandibulae* (Fig.2.1).

The landmarks 1, 2, 3, 4 and 6 were recorded at the tip of the teeth alveoli. In particular 1-2 represent the length of the canine, 3-4 the premolar row, instead 4-6 the molar row. The landmark 5 is functionally defined and it represents 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 it is defined as the projection of the protocone cusp on the m1 baseline. In some cases, when there is no crushing area in the molar row, it overlaps with landmark number 6. Landmarks 12 to 14 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. The distances 2-14, 4-13 and 6-12 represent the thickness of mandibular corpus under the canine and the molar row, respectively.

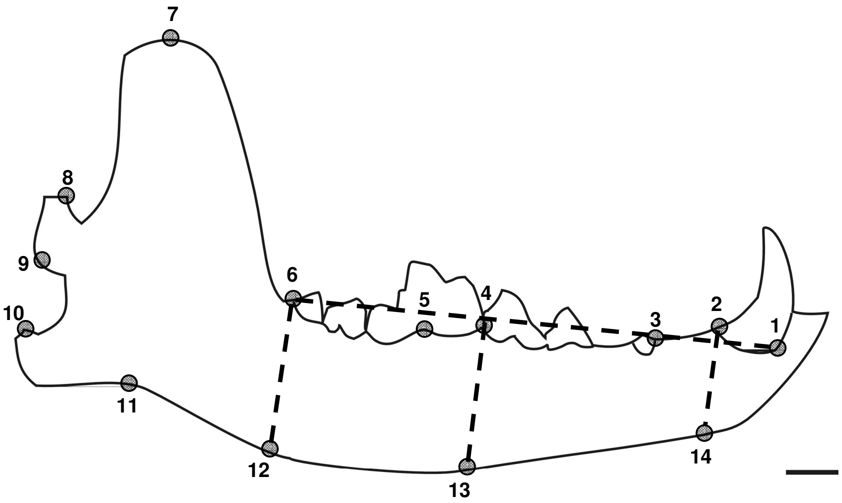


Figure 2.1: The position of landmarks on a mandible outline of *Canis lupus* NHM 34.6.28.47. Scale bar: 1.0 cm.

Landmark 7 is the tip of the coronoid process and was recorded at highest tangent point of the line parallel to 1-6. Landmarks 8 and 9 record the maximum depth of the condylar process (*Processus condylaris*) and the thresholds of the articular surface (*Caput mandibulae*) were chosen as reference. Landmarks 10 and 11 are representative of the angular process (*Processus angularis*). Landmark 10 records the lateral extreme of angular process while the landmark 11 records the ventral extreme. The muscle scar on the bone surface was used to place landmark 11 on the edge between angular process and the ramus. Most of the recognized landmarks are type 2 (1-6; 8-11) or type 3 (7, 12-14) (sensu Bookstein 1991), because they record tips of bone structures or are geometrically determined.

A Generalized Procustes Analysis (GPA) was performed on 2 dimensional landmark coordinates in order to translate, rotate and scale at unit centroid size the landmark configuration (Rohlf and Slice 1990; Adams et al. 2004). Procrustes are distances among landmark configurations projected onto Kendall shape space (Rohlf 1996, 1999, 2000a, b). The software tpsSmall 1.20 (Rohlf 2003) was used to check for distortion introduced by projecting procustes distances of landmark configurations onto Kendall tangent euclidean space.

Non-affine components of shape variation, called Partial Warps (PWs), provide an alternative to Procrustes coordinates to quantify shape variability (Bookstein 1996a; Zelditch et al. 2004). The mean shape configuration, namely consensus, can be considered as lying on a surface of an infinite thin metal plate. The landmark configuration for each specimen is obtained from the mean configuration by bending the thin metal plane. In this way it is possible to produce a bending energy matrix whose eigenvectors are the Partial Warps. Partial Warps are, in essence, crude shape variables that explain regional landmark variations along x and y axes (Zelditch et al. 2004). Partial Warp scores have been computed for the landmarks configurations of mandible dataset using the tpsRelw 1.44 software (Rohlf 2006b). Uniform shape components, which represent shape transformations requiring no bending energy (Bookstein 1996b), i.e. corresponding to linear transformations of the plane (stretching and shrinking), were obtained with the same software.As the exploration of evolutionary processes underlying shape variation is the principal topic of the present survey, a principal component analysis was performed on the non-affine components of shape variation (Relative Warp Analysis) in order to check for covariation across components. For the relative warp (RW) analysis the alpha parameter (an index of exponential weight) was set to zero (Rohlf 1993; Bookstein 1996a). In this way, the partial warps have equal weights at all spatial scales meaning that large and small variations in shape have the same importance. Relative warps were used to look, eventually, at differences across families and ecological groups.

2.2.3 Ecological categories

In order to explore shape variability from an ecological perspective, each species was assigned to an ecological membership (Appendix 1) according to literature hypotheses about guilds. The first category is represented by family membership consistently with Dayan and Simberloff (1996) guild concept.

Feeding categories were explored as well. Mandible shape should differ among feeding groups, although the latter can be subjectively defined. Here, I used three distinct published feeding categories according to Gittleman (1985), Meiri et al. (2005), Christiansen and Wroe (2007). Gittleman (1985) defined five categories: carnivorous (=M), omnivorous (=O), insectivorous (=I), folivorous and frugivore (=V) and piscivore (=F). Meiri et al. (2005) considered five categories as well, according to the percentage of food consumed: vertebrates, invertebrates, fruit, fish and crabs.

Christiansen and Wroe (2007) defined seven categories comprehensive also of the size of the common prey among vertebrate meat eaters: 1, herbivores (including frugivores); 2, omnivores; 3, piscivores; 4, carnivores, small prey; 5, carnivores, medium-sized prey; 6, carnivores, large prey; 7, insectivores. In the present dataset only *Potos flavus* is considered as "herbivore" and, for this reason, this category was omitted. *P. flavus* is considered omnivorous.

It is evident that feeding categories overlap in some cases even if Gittleman (1985) and Christiansen and Wroe (2007) did not consider crab eating as a specialization. The omnivorous category is ascribed to bears by Meiri et al. (2005) as well by Christiansen and Wroe (2007) while Gittleman (1985) ideated the Folivores category for most of the ursids. When data in Gittleman (1985) or in Christiansen and Wroe (2007) were not available, I used Meiri et al. (2005) data to ascribe feeding category according to Gittlleman (1985) criteria (happened for nine species) or Christiansen and Wore (2007) criteria (for ten species).

Size of prey, alone, defined in Very small (V), Small (S), Medium (M) and Large (L) (Gittleman 1985), was considered an ecological category relevant in guild membership as well. When the category of size of prey was not specified, than a neutral category was assigned as indicative of species that use not to hunt.

Finally species were categorized according to their mean body weight into small and large categories. Van Valkenburgh (1985, 1988, 1989) defined 7 kilogram as a size threshold: all small carnivores have mean body weight < 7 kg. Large carnivores are defined as species whose mean body weight is major to 7 kg. Where species body weight was recorded on the collected specimen that value was used and it was compared with published mean body weight (Gittleman 1985; Meiri et al. 2005) in order to ascribe correctly guild membership. For instance, the specimen of Eurasian otter (*Lutra lutra*) has a recorded body weight of 7 kilogram; Gittleman (1985) and Meiri et al. (2005) reported a mean body weight of 8.8 kg for Eurasian otter than it is ascribed to large carnivore group. Although Van Valkenburgh did not consider aquatic fissiped carnivores as members of large carnivore guilds there are evidence of interspecific killing between terrestrial and aquatic forms (Palomares and Caro 1999) and also of competition (e.g: with *Mustela vison* cfr. Bonesi et al. 2004). For this reason, aquatic fissiped forms were not excluded for testing differences between small and large species.

Another size threshold has been defined in Carbone et al. (1999) on the basis of metabolic arguments. That study suggests a constrain in eating large prey when carnivores' body weight is higher than 21.5–25 kilogram. In our sample only the giant otter (*Pteronura brasiliensis*) approach 24 kilogram without hunting large prey. For this reason the upper limit of 25 kg is considered as another possible relevant threshold to separate small (< 25 kg) from large (> 25 kg) carnivores.

2.2.4 Testing morphological discontinuity

GM data represented by affine and non-affine components of shape are explored in order to check for morphological differences among ecological or potential guild categories by using MANOVA. The same test is performed with Phylogenetic Generalized Least Square model in order to take into account phylogenetic species relatedness.PGLS is a generalized least square regression model where the OTU (Operational Taxonomic Units) matrix is the covariate.

The latter matrix represents the variance and covariance among species expected under a Brownian Motion model of evolution (Martins and Hansen 1997; Rohlf 2006c). The SuperTree proposed by Bininda Emonds et al. (1999) is the topology used for the present investigation. Branch lengths are time of divergence among species as presented in Bininda Emonds et al. (1999).

An UPGMA clustering is applied to the Procustes Distances matrix extracted with TpsSmall. This technique allows to evidence morphological similarities among taxa as revealed by shape data. Eventually, Procustes distances matrix was also used to explore the relationship between shape similarities and time of divergence among taxa. An Ultrametric distance matrix was obtained from Bininda-Emonds et al. (1999) SuperTree and Mantel test (Mantel 1967) was performed in order to validate its relationship with Procustes distance matrix. All the analysis were performed with NTSYS vr 2.2 (Rohlf 2006d).

2.3 Results

2.3.1 Shape differences

The tangent shape space is a good approximation of the Kendall shape space as revealed by its strong linear relationship with the latter (r^2=0.999). Twenty four relative warps are extracted and the first nine share altogether 95% of the total variance: RW1 accounts for 33.64%, RW2 for 22.98% and RW3 explains 15.53%. These three axes are the most morphologically informative and their combinations allow to discriminate families (Fig. 2.2) as well as diet categories (Fig. 2.3).

On the first relative warp, most of the shape variability is represented by changes in the length of the premolar row relative to the molar row, and by correlated change of the crushing molar region relative to the slicing carnassial region. Landmarks 1 and 2 also changes their relative position defining a larger (on negative scores) or shorter canine. The thickness of the mandibular corpus region varies as well along the RW1 axis. Changes in the ramus region are related to the position of the tip of the coronoid process and with the lengthening (or shortening) of the angular process. On the second relative warp, most of the shape variability is driven by the changes of molar crushing area relative to the other regions.

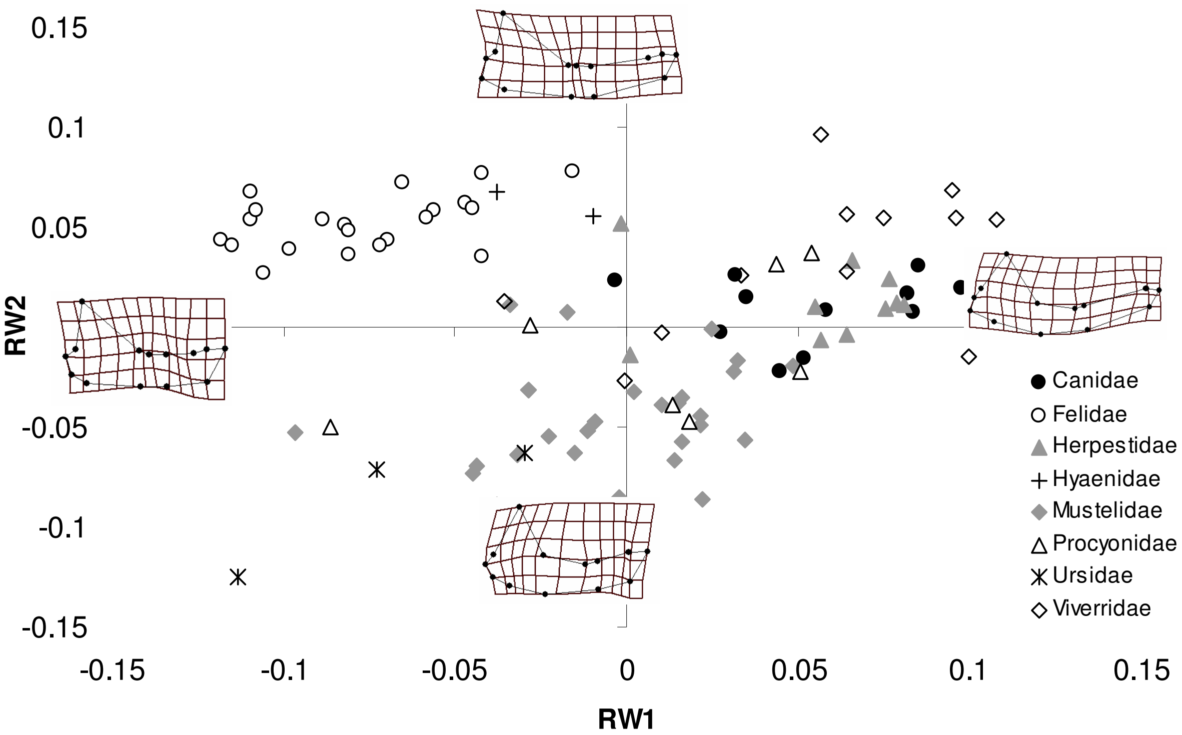


Figure 2.2: Scatter plot of RW1 and RW2. Deformation grids represent shape deformation at the positive or negative extreme of every single RW axis. Symbols are on the agenda (bottom left).

This fact determines great differences in the relative position of landmark 7 as the tip of coronoid region. Altogether, the first and the second relative warp define distinctive mandible morphologies among families. Felids and hyaenids exhibit a short (usually non-existent) crushing area, a long premolar row and a large muscle attachment in the *ramus mandibulae*. Members of Canidae overlap with Herpestidae, some Procyonidae and share with Viverridae a long premolar row. Ursidae and Mustelidae have a longer molar crushing area and a short cutting blade, premolar row is not long as in Canidae and the depth of mandibular corpus is larger under the crushing area. *Potos flavus* share similar morphology and is a clear outlier among Procyonidae.

On the third axis, changes in mandible shape are associated with the proportion between the slicing and the crushing sections of the carnassial. Large crushing sections in m1 associate to the lower ramus, while higher ramii associate to carnassials dominated by the slicing fraction. This happens to define a strong variation in the attachment surface of the temporalis reflecting, in turn, shape variability related to different feeding habits (as in Meiri et al. 2005). Some overlap occurs between fish and vertebrates eaters. *Cynogale benetti* is a crab eater outlier relative to *Aonyx capensis* and *Amblonyx cynereus* that are near the consensus and the other fish eater otters (e.g: *Lutra*, *Pteronura*). Overlap occurs between invertebrates eaters and frugivores as well. The extreme mandible morphology of the Malaysian sun bear (*Helarctos malayanus*) overlaps in the RW1 and RW3 with the cheetah (*Acinonyx jubatus*) and this fact reflects similarity in mandible curvature and corpus depth. These species are clearly at opposite ends along RW2 (because of differences in crushing and slicing area) although same position in RW1.

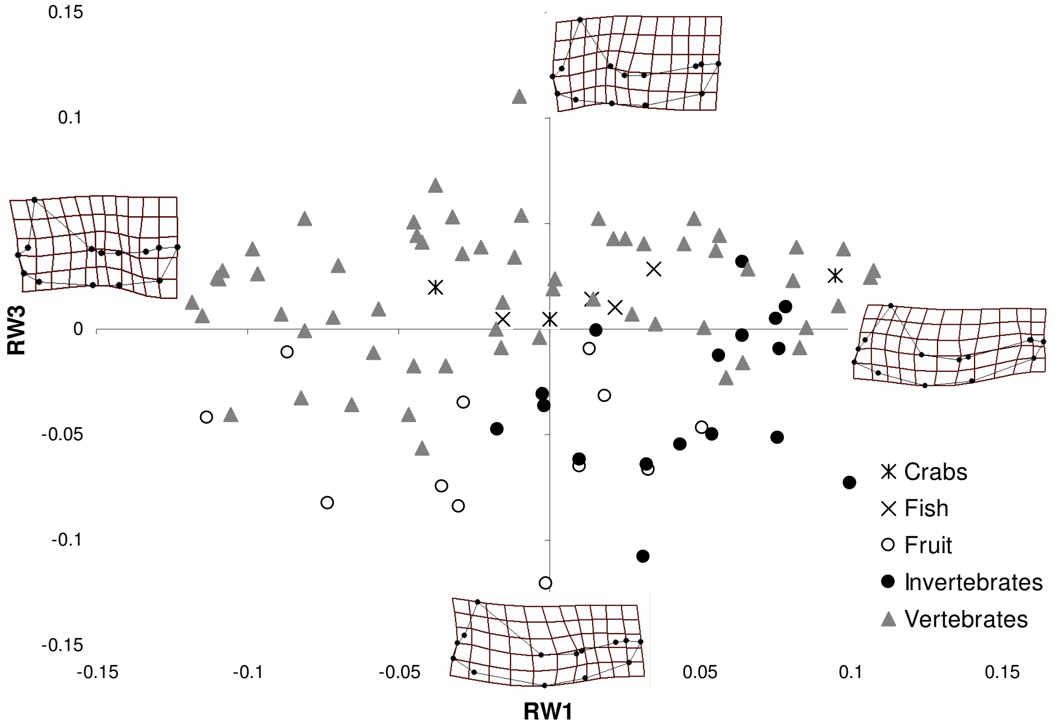


Figure 2.3: Scatter plot of RW1 and RW3. Deformation grids represent shape deformation at the positive or negative extreme of every single RW axis. Symbols are on the agenda (bottom left).

When Gittleman (1985) or Christiansen and Wroe (2007) categories are used, there is no evident diet discrimination in the plot of the first and the third relative warps. Several combination of relative warp axes do not give a clear diet signal in shape data if compared with Meiri et al. (2005) whose categories seem more morphologically homogeneous.

2.3.2 Ecological differences

MANOVA reveals significant differences in mandible shape among families (Wilk's lambda = 0.00026, Fs = 6.496; df1 = 168, df2 = 456.7, p = 3.30E-57, explained variance = 52.91%), diet categories according to Meiri et al. (2005) (Wilks' Lambda = 0.05840971; Fs = 3.012; df = 96, 275.9; p= 7.916E-013; explained variance = 18.53%) as well as Gittleman (1985) (Wilks' Lambda = 0.06159633; Fs = 2.934; df = 96, 275.9; p = 2.770E-012; explained variance = 19.19%) and

Christiansen and Wroe (2007) (Wilks' Lambda = 0.04097248; Fs = 2.587; df = 120, 339.1; p = 7.744E-012, explained variance = 20.43%). Prey size categories also differ significantly in mandible shape (Wilks' Lambda = 0.07190214; Fs = 2.711; df = 96, 275.9; p = 9.703E-011; explained variance = 15.76%).

When in the full factorial model the interaction between family and ecological categories is included MANOVA reveals no significant interaction between Family and diet categories as in Meiri et al. (2005) (Wilks' lambda = 0.13108; Fs = 1.216; df = 120, 285.03; p = 0.096) and in Gittleman (1985) (Wilks' lambda = 0.05162; Fs = 1.057; df = 192, 426.893; p = 0.319). On the other hand, a significant interaction occurs between Family and diet categories as in Christiansen and Wroe (2007) (Wilks' lambda = 0.00161; Fs = 1.595; df = 288, 562.457; p = 1.55E-006) and between Family and Size of prey category (Wilks' lambda = 0.001367; Fs = 1.349; df = 336, 627.649; p = 0.00073). Interestingly, interaction occurs between diet and size of prey (Gittleman 1985) (Wilks' lambda = 0.09136; Fs = 1.181; df = 240, 534.167; p = 0.06133) but when a complex model include also Family the three factors (Family, diet and size of prey) do not interact (Wilks' lambda = 1.7248E-006; Fs = 1.122; df = 648, 665.471; p = 0.070).

Differences in guild categories are evidenced by Hotelling t square whose p value resembles the Hotelling-Lawley trace or Wilk's lambda that are both presented here. Differences are significant in both cases when size threshold is represented by seven kilograms (Hotelling-Lawley trace = 0.84526257; Wilks' Lambda = 0.5419283; Fs =2.595; df = 24, 72.0; p = 0.0013, explained variance 5.11%) or 25 kilograms (Hotelling-Lawley trace = 1.28403334; Wilks' Lambda = 0.43782198; Fs = 3.852; df = 24, 72.0; p = 4.859E-006, explained variance 7.33%).

Interaction occurs between Family and the 7 kilogram category (Hotelling-Lawley trace = 1.963; Wilks' lambda = 0.228; Fs = 72; 186.148; p = 0.004) but not between Family and 25 kilogram (Hotelling-Lawley trace = 0.305; Wilks' lambda = 0.766; Fs = 24; 64; p = 0.706).

2.3.3 PGLS

The same MANOVA analyses performed under PGLS model on shape data show significant differences only among some of the ecological categories. Mandible shape does not differ among diet categories of Meiri et al (2005) (Wilks' Lambda = 0.34612572; Fs= 0.691; df = 120, 344.0; p = 0.9910) but differences are significant among diet categories as in Gittleman (1985) (Wilks' Lambda = 0.11250841; Fs = 1.605; df = 120, 344.0; p = 5.080E-004) and in Christiansen and Wroe (2007) (Wilks' Lambda = 0.02067327; Fs = 2.651; df = 144, 405.3; p = 1.790E-014).

Significant differences apply also to size of prey categories (Wilks' Lambda = 0.07545794; Fs = 1.983; df = 120, 344.0; p = 7.552E-007).

Shape data of small and large carnivores differ only when 7 kilogram is considered as a body weight threshold (Hotelling-Lawley trace = 3.01753342; Fs = 4.463; df = 48, 142.0; p = 2.264E-012- Wilks' Lambda = 0.24890894; Fs = 3.013; df = 48, 144.0; p = 2.133E-007) and not for 25 kilograms (Hotelling-Lawley trace = 0.70945222; Fs = 1.049; df = 48, 142.0; p = 0.4038 - Wilks' Lambda = 0.58498272; Fs = 0.922; df = 48, 144.0; p = 0.6179).

These results show that phylogenetic relatedness drive shape differences in diet categories as in Meiri et al. (2005) and small (<25 kg) and large (>25 kg) carnivores.

2.3.4 Clustering

Finally UPGMA reveals strong shape similarities in members of Ursidae, Felidae and Hyaenidae families (Fig. 2.4). Aquatic fissiped carnivores are generally identified as morpho-ecologically similar cluster (*Amblonyx cynereus*, *Lutra* spp. and *Pteronura brasiliensis*) even if *Aonyx capensis* is grouped with *Mustela* spp. Outliers occur especially among canids: the African wild dog (*Lycaon pictus*) is similar in mandible shape to small *Martes* spp. while the bat eared fox (*Otocyon megalotis*) is grouped with frugivorous viverrids. Among Procyonidae, both *Nasua* spp. define a clear cluster while *Procyon* spp. and the other genus are usually grouped within most of invertebrates eaters mustelids. Several members of family Viverridae are grouped together but their position is within Caniformia and the same applies to Herpestidae. The only species grouped within Feloid are the marsh (*Atilax paludinosus*) and dwarf (*Helogale parvula*) mongooses together with the binturong (*Arctictis binturong*) that are grouped within the variability of the small felid *Prionailurus* spp.. In this group some outliers are represented by the hypercarnivore bush dog (*Speotohs venaticus*) and the mustelid *Mellivora capensis*.

Interestingly, the procustes distance matrix does not correlate with the ultrametric distance matrix extracted from Bininda-Emonds et al. (1999) phylogeny (r=0.423, Mantel t-test =23.1814, Prob random Z < obs. Z = 1.000). This means that there is a weak relationship between shape morphological distances among species, and their time of divergences.

In conclusion there is no clear ecological or phylogenetic signal in mandible shape data even if aquatic fissiped, felids, hyaenids and ursids are more morphologically distinct in mandible shape.

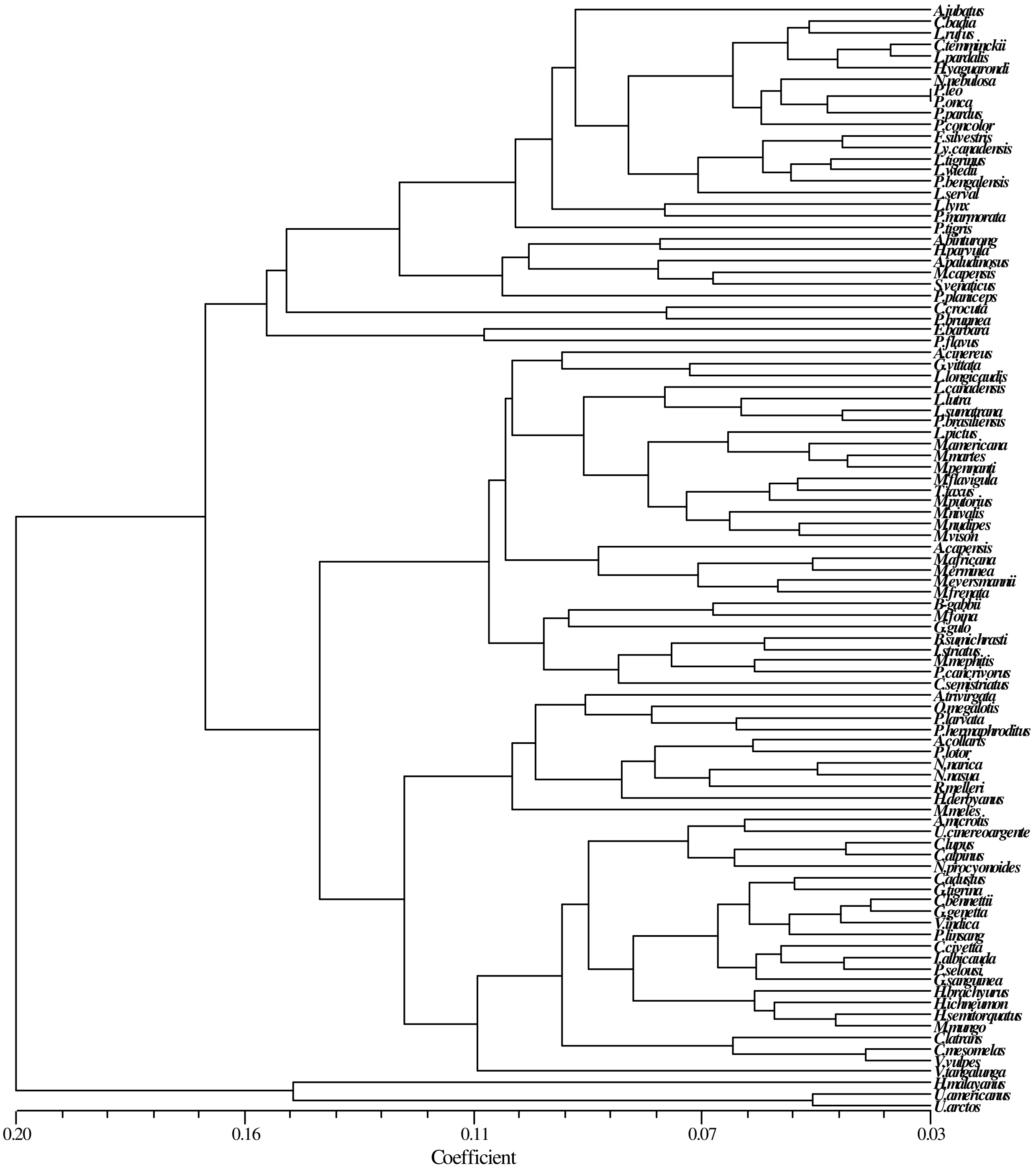


Figure 2.4: UPGMA cluster analysis performed on Procustes distances of 97 species of carnivores.

2.4 Discussion

Members of the order Carnivora are well characterized in mandible shape morphology. Shape variability in the chosen landmark configuration confirms patterns observed in the past (cfr. Crusafont Pairó and Truyols Santonja 1957; Radinsky 1981a, b, 1982, Biknevicius and Van Valkenburgh, 1996; Therrien 2005a, b). Among Feliformia, felids are characterized by a strong high ramus with a caudal projection of the tip of coronoid and condylar process, a poorly developed angular process, a large canine area, and a well developed slicing area in the carnassial. Hyaenids are similar to felids, while members of Viverridae and Herpestidae possess a generalized mandible shape with long premolar row and a similar proportion in the slicing and crushing area of the molar row (see Figure 2.2). This fact generates overlap between these two groups and the caniforms Mustelidae, Canidae and Procyonidae (Figs. 2.2, 2.4). In general, caniforms possess a thin and more elongated mandibular corpus with a long premolar row and a long crushing molar area; the ramus region is projected rostrally, the condyl is large and develops vertically, the angular process is stronger and more elongated than in feliforms. Members of Canidae match these characteristics while mustelids have a thicker *corpus mandibulae* and a stronger lower canine. Along this shape variability procyonids are in the middle between Canidae and Mustelidae while ursids have a thicker corpus under the crushing area and a strong ramus for muscle attachments (Fig. 2.2).

These anatomical features reflect high morpho-ecological specialization achieved by members of each carnivore family and confirm that broad-scale taxonomy can be useful to define members of the same guild (Dayan and Simberloff 1996). Compared with the other pre-assigned groups, family explains the greatest portion of shape variability in mandible (Fig. 2.5).

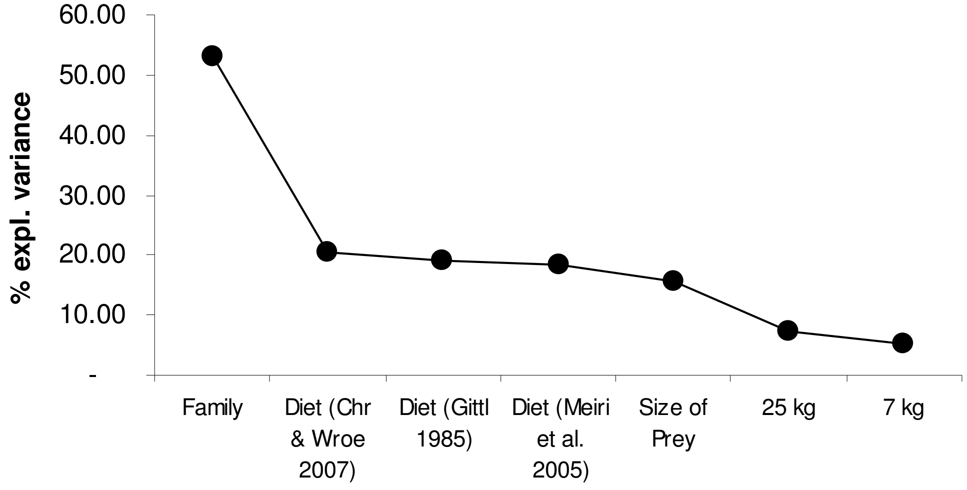


Figure 2.5: Percentage of variance explained by each categories before and after PGLS model. Symbols are on the agenda (top left).

On the one hand, broad-scale taxonomic differences are informative of the different developmental programs which allow to discriminate species, since early developmental stage, on the basis of mandible morphology (see Biknevicius and Leigh 1997 as case study in puma and spotted hyena).

From a macroevolutionary perspective, it is plausible that developmental constraint could have affected morphological variability at family level in such a way that few overlaps occur among families in mandible shape of carnivores. Although remarkable examples of convergence appear iteratively in the evolutionary history of the Carnivora (Van Valkenburgh 1999, 2007), there are other evidences on the limited variability of morphological overlap in Carnivora explained by phylogenetic constraint (Werdelin 1989, 1996). As suggested by Gould (2002), constraint does not need to be interpreted in a negative way. In particular for Carnivora, the phylogenetic constraint is, probably, at basis of their phenotypic plasticity in jaw geometry and dental morphology, such that this order has "*greater evolutionary success"* than marsupial carnivores (Werdelin 1987) or, probably, creodonts (Van Valkenburgh 1999; Wesley-Hunt 2005).

Biomechanics drive shape differences among families as well. This pattern is highly visible if we consider the ramus region where most of masticatory muscles attach: coronoid, condyle and angular process changes their position in most of the families as a result of distinct skull and muscle attachments. In the *corpus mandibulae* biomechanics drive shape differences as well even if similarity in crushing/slicing area proportion determines overlap among small feliforms and caniforms.

On the other hand, there is also an ecological explanation on mandible shape differences among families. Interspecific competition is usually high among members of the same families. For instance, Donadio and Buskirk (2006) recently demonstrated that interspecific killing occurs with great extent among members of the same families. In Palomares and Caro dataset (1999) c.ca 24% of interspecific killing cases occur among members of the same families with similar percentage distributed among families (Table 2.2).

Families	**% kill inter**
Felidae	23.40%
Canidae	27.03%
Ursidae	20.00%
Hyaenidae	20.00%
Mustelidae	8.00%
All	23.71%

Table 2.2: Percentage of interspecific killing cases that occur among members of the same families (Data from Palomares and Caro 1999).

This phenomenon is part of the Intra Guild Predation (IGP) and it is likely to affect not only the demography of species involved, but also species' evolution (Polis et al. 1989). In this regard, mandible shape similarities can reflect also high competitive interactions in members of the same families. Of course, the role of species in a community is not defined just on its taxonomic status even if it seems to influence the structure of carnivore morpho-ecological variability.

The rule of other factors in generating mandible shape dissimilarities of carnivores, is less important although relevant at different scale. Firstly, diet categories share another important source in mandible shape variance. Diet needs to be considered carefully because its quantification is not universal and can have different meaning. For instance, diet as quantified recently by Meiri et al. (2005), explains differences in mandible shape only when phylogenetic relatedness is not considered. This means that broad feeding categories are not enough to define adaptive differences in mandible shape morphology. On the other hand, at finer diet scale, phylogeny has not a relevant effect. The diet categories of Christiansen and Wroe (2007) have the best discrimination power in mandible shape (Fig. 2.5) also because they incorporate size of prey, an important feature in moulding Carnivora body mass differences as well as morphology (Gittleman 1985, for mandible see Therrien 2005 a, b). The functional relationship between mandible shape and diet (or prey size) categories is here validated even if it is dependent on the way of defining diet categories. This pattern is moulded by the well-known link between mandible shape and feeding habits in all mammals (for a review Weijs 1994). There are no doubts that mandible is functional to the mastication and the physical stress in crushing similar food items affects its morphology. The question of defining food properties is an issue here (Weijs 1994) and it is possible to overcome practical difficulties by combining informative features in diet categories.

In studies of mandible shape, guild can be also defined as a group of carnivores sharing similar feeding habits (sensu Christiansen and Wroe 2007 or Gittleman 1985). The morphological similarities in such groups is expected especially on the light of field studies that usually support high overlap in diet in different carnivore species assemblages (e.g: Schaller 1972; Van Valkenburgh 1996; Ray and Sunquist 2000; Creel and Creel 2002; Woodroffe and Ginsberg 2005).

Body size threshold, is the last effect that is validated completely only in the case of the 7 kilograms threshold. Mandible shape differences in little and small carnivores are truly adaptive and do not reflect phylogenetic relatedness when we use 7 kilograms as a size threshold. Although, 25 kilograms threshold explains more shape variance, it reflects phylogenetic affinities among taxa. This result has important implication for paleobiological studies as well as conservation practice. Intense competition drives mandible shape similarities in small and large carnivores that can be considered operationally valid if defined as in Van Valkenburgh (1985, 1988, 1989). In this case, studies on predator/prey relationship in the past ecosystems are relevant when only large predators are considered (Van Valkenburgh and Janis 1993, Raia et al. 2007, Meloro et al. 2007). Radloff and DuToit (2004) consider in African savannah large carnivores only the species larger than 24 kilograms: this observation is partially true and allows to obtain more precise pattern of predator/prey size relationship (Carbone et al. 1999) but in terms of morpho-ecological studies it resembles too much phylogenetic information.

Here, I suggest the validity of small and large carnivore separation with 7 kilograms threshold in morpho-ecological studies. The rule of such threshold has important implications for conservation strategies as well. Carnivores receive a lot of attention by conservationists and in the past most of the conservation programs were based on a single species approach. With a great advance in knowledge of species ecology and behaviour, new patterns emerged such that for some species, the interaction with members of the same guild is crucial for their survival (e.g: the cheetah, Durant 1998, 2000; the African wild dog Creel and Creel 2002). Conservation studies should treat large (or small) carnivore guild as a group of species whose complex interaction mould their morphological differentiation and, in turn, can have strong impact on the ecosystems. Multi-species conservation is difficult especially for carnivores because of their conflict with human being but there are good successful examples (e.g: large carnivores in Europe; Enserhinck and Vogel 2006).

What still not to be clear is the "morpho-ecological" redundancy of some species in carnivore guild assemblage, although it is clear that large carnivore guild has great impact on the ecosystem (Woodroffe and Ginsberg 2005).

In terms of morpho-ecological patterns, the clustering technique allows to identify some similarities in mandible shape that reflects same morpho-ecology. This approach is less methodologically constrained in the groups identification (cfr. α 3 Wilson 1999) but it allows to identify some clear clusters: felids and hyaenids, ursids and acquatic carnivores. The first cluster –from which all the other groups belongs- is that one of bears (see Fig. 2.4) whose mandible shape morphology is distinctive among the others. This suggests that bears can also be treated as a separate carnivore guild because of their unique biological traits (e.g: the capacity to be in torpor, the plantigrade posture, the huge body-mass Gittleman 1999) that is reflected in their high vulnerability and few multispecies co-existence cases (usually no more than two different bears co-exist in the same ecosystem).

The cluster of felids and hyaenids is in agreement with their high specialization in meat consumption (with few cases of omnivores or insectivores species): large forms (members of *Panthera* spp., puma and the clouded leopard *Neofelis nebulosa*) can be separated from the smallest cats and lynxes; among hyaenidae both the spotted and brow hyena cluster together according with their special mandible adaptation in cracking bones (Kruuk 1972; Werdelin and Solounias 1991).

Aquatic carnivores are distinctive among mustelids and other small carnivores as well. This fact reflects physical constraint that has been already underlined by Bininda-Emonds et al. (1999) in the flat and more elongated skull as compared with the other carnivores. Scapino (1976) founds heavier digastric (that attaches in the both labio and lingual sides of the mandibular corpus) in otters and explained this fact as the result of physical resistance in opening mouth under water. This explanation is plausible and such muscle morphology could have affected also the distinctiveness of felids which are able to obtain high bite gape compared with caniforms. For this reason, the distinctive mandible shape of otters can be safely explained by biomechanics even if this argument is plausible only for some traits (Bininda Emonds et al. 1999). In particular, it is not clear to what degree otters can be separated from the other fissiped carnivores. For instance, overlap in feeding niche occurs between Eurasian otter and the American mink (*Mustela vison*) but in otter there is always a greater consumption of fish. Mcdonald (2002) demonstrated that morphological variability in british mustelid guild is not driven by resource partitioning but more by interspecific competition. In that analysis otters were always distinctive for their feeding habits and niche space. The cluster analysis made on mandible shape support this argument and otters can be considered separate guild exhibiting small degree of overlap in morphology with the other terrestrial carnivores. Generally, crab-eating does affect in a limited way the mandible shape variability of otters as suggested also by the results achieved on diet categorization of Meiri et al. (2005) which are phylogeny-dependent.

The clusters observed among other caniforms, usually, reflect expected patterns (cluster at genus level in *Mustela* spp. *Martes* spp., *Nasua* spp., *Herpestes* spp., see Figure 2.4 and results section) but there are a lot of outliers that I can explain like examples of "*apparent shape convergence"*. In most gmm studies the PD clusters are not always congruent with shape similarity expected. This is because Procustes distance is a pure shape metric and it does not allow to consider size at the same time. Shape similarities in structures with great size differences is usually rare and it could represent more a methodological by-product other than a pure biological example of convergence. Here I present the same PD clusters but in two groups of small (< 7kg) and large (> 7 kg) carnivores.

When only small carnivores are considered, UPGMA cluster (Fig. 2.6) is more informative when compared with the general analysis in Figure 2.4.

The distinctive morphology of the procyonid *Potos flavus* -an outlier among its family- groups this form with the mustelid *Eira barbara*. The *Mustela* and *Martes* groups are better defined and small felids are well characterized in mandible shape morphology. All the Herpestidae and most members of Viverridae are clustered together like small canids as well.

The cluster obtained on large carnivores support similarities in all analysed members with really precise results (Fig. 2.7) as in the clusters of bears, *Panthera* forms (among felids) or the aquatic and terrestrial mustelids with some outliers as *Mellivora capensis* or the American badger which is grouped within otters. Among large canids –all grouped together- it is interesting to note the cluster of hypercarnivores wild dogs: *Lycaon pictus*, *Cuon alpinus* and *Canis lupus* considered with the bush dog, part of the subfamily Symocyoninae (Van Valkenburgh 1991).

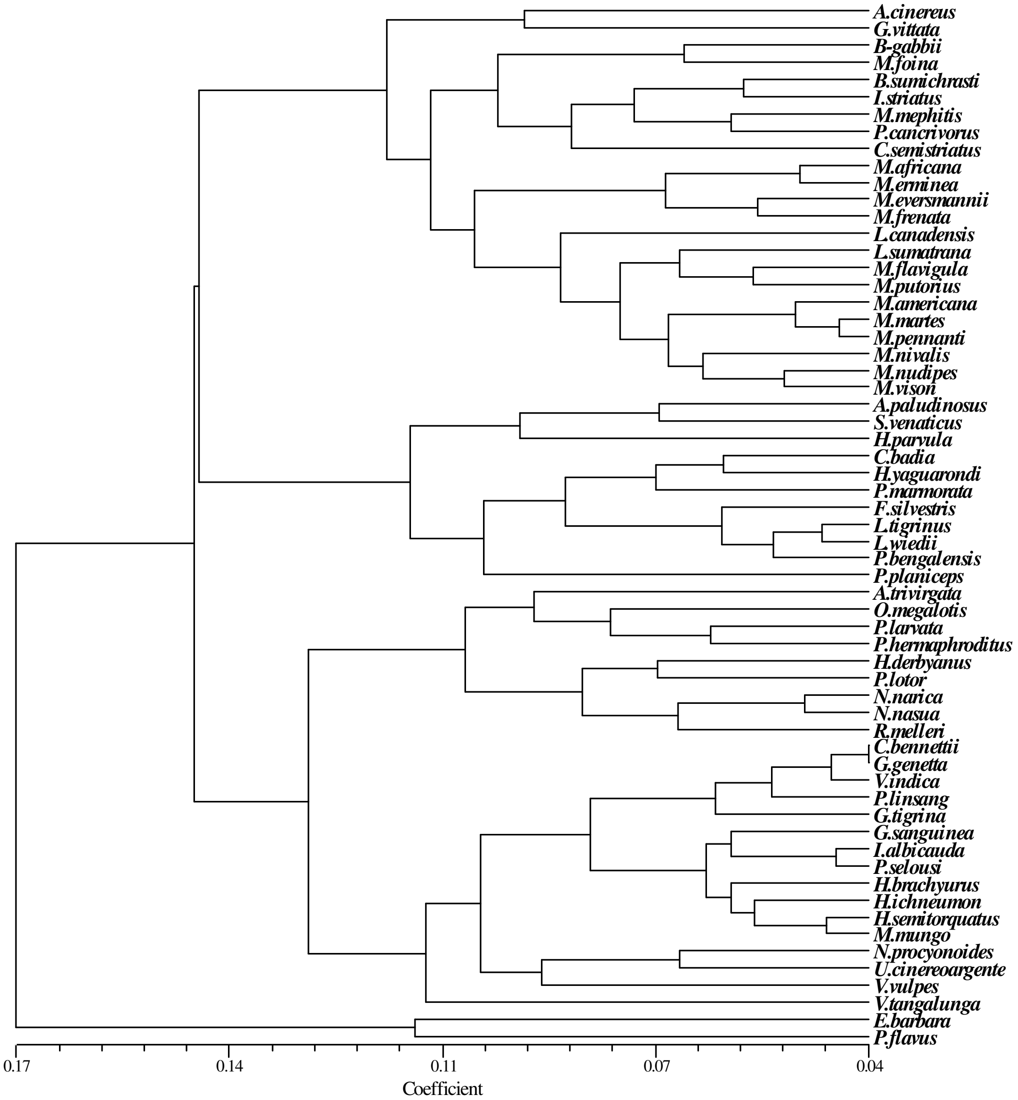


Figure 2.6: UPGMA cluster dendogram performed on PD obtained from a subset of small (<7 kg) carnivores).

This nested clustering shows precise similarities in mandible shape that is mostly driven by phylogenetic relatedness as well (cfr. PGLS results).

It confirms also that shape similarities observed in general analysis (Fig. 2.4) are the results of pure mechanical shape constraints and can be interpreted as "*apparent shape convergence*": species with large size differences may achieve similar shape in mandibles as the results of different physical constraints. In this regard, clustering technique on PD is informative but should be interpreted with caution in inter-specific studies where great dissimilarities in size of structures occur among species analysed.

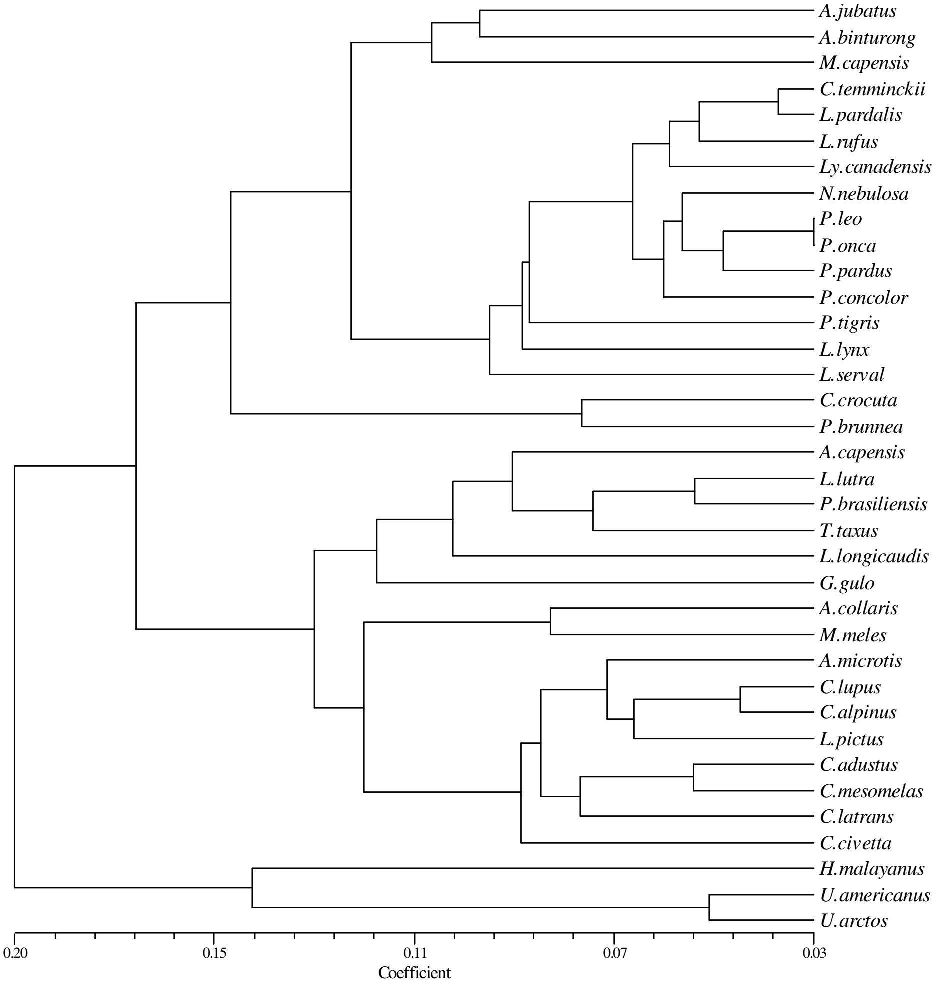


Figure 2.7: UPGMA cluster dendogram performed on PD obtained from a subset of small (>7 kg) carnivores).

Chapter 3

Integration in mandible of carnivorous mammals: a macroevolutionary test

3.1 Modules of mammalian mandible

The mammalian mandible is a complex osteological structure whose definitive shape represents the result of distinct developmental processes. It is the only skull mobile bone (except hyoid) (Barone 1980) and consists of two symmetrical halves (hemi-mandibles) that are fully integrated with the remaining skull structures. Each hemi-mandible is formed by the dentary bone (common to all vertebrates) which is identified by different regions functionally distinct. Basically, the *corpus mandibulae* is elongated and it holds the teeth with few muscles inserted lingually (e.g: the *digastric* and *milo-ioideus*) while the ascending ramus holds the articular surface for the skull (condyle) and a vertically developed bone tissue which allows the insertion of the principal chewing muscles: *masseter*, *temporalis* and *pterigoid*.

Atchley and Hall (1991) underlined the fact that each mandibular region can be considered a single morphogenetic component that is embriologically controlled by the differentiation of the mesenchymal cells. Specifically, Atchley and Hall (1991 and see also Atchley et al. 1985) emphasize a distinct genetic control on six functional mandibular regions (alveolar, body, chin, coronoid, angular, condylar process) that can be easily recognised in the mouse mandible. Genetically, the definitive mandible form is controlled by a cascaded process of the activation of several Hox genes implicated in the development and integration also of the cells responsible for the teeth formation. Recently, Klingenberg et al. (2004) identified for the mouse mandible 33 Quantitative Trait Loci which represent traits under polygenetic control exhibiting continuous variation among populations (Erickson et al. 2004).

Several studies were performed in order to validate the nature of regional integration in mammalian mandible (Cardini 2003; Klingenberg and Leamy 2001; Klingenberg et al. 2003; Monteiro et al. 2005) but there is not a definitive consensus for a general theory. The six regions identified by Atcheley and Hall (1991) exhibit distinct shape correlation at intraspecific, interspecific and family level in spiny rodents (Monteiro et al. 2005) while Klingenberg et al. (2003) confirm the possible partitioning of the mouse mandible in two integrated modules: the alveolar region and the ascending ramus.

Such studies benefit of the higher environmental and genetic control of small mammal populations (easy to manage in laboratory) as well as on the well defined morphogenetic regions in the rodent mandible. For this reason, in spite of the great morpho-ecological variability exhibited by the mammalian order of Carnivora (Nowak 1991), few investigations have been performed in this group to explore the possible integration of mandible regions.

Goswami (2006) analysed 3D skull integration (except mandible) in mammalian carnivores evidencing a strong influence of phylogeny as well as dietary habits. A similar pattern of integration is expected for the mandible as well. Meiri et al. (2005) evidenced differences in variability and correlations of crania and dentition of carnivores driven by phylogeny and dietary specialization although it is not clear to what degree mandibular regions can be affected by these two factors. The implication of testing such hypothesis is especially influent for application in palaeobiological studies. The mandible, in fossil carnivores, is usually a well preserved structure and its shape can be explored (together with teeth morphology) for palaeoecological reconstruction (diet prediction, hunting habits and prey preference). Unfortunately, the generalised carnivore mandible cannot be precisely two dimensionally distinguished in the six regions as identified for the rodent.

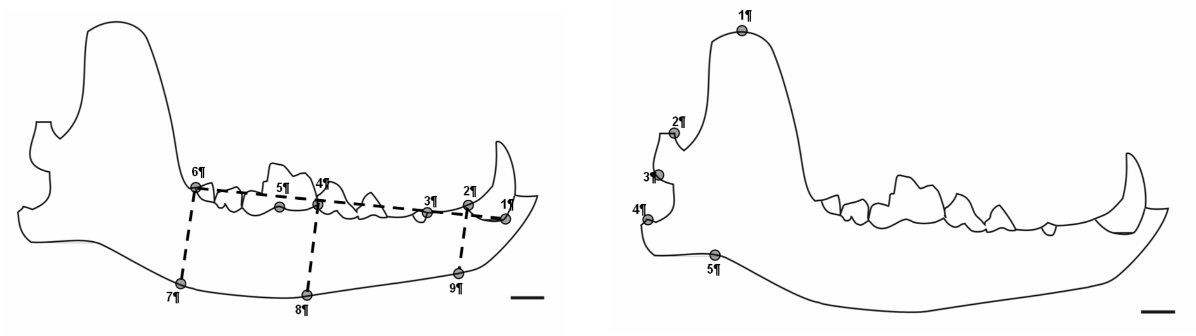
Here, I explore the possible pattern of covariation between the alveolar (mandibular corpus) and the ascending ramus in extant mammalian carnivores at macroevolutionary scale. Such division is at least conservative and allows to consider separately two regions with a different rates of fossilisation in carnivores as well as different functions. For instance, on a subset of 277 fossil mandibles belonging to carnivores from Paleocene until Pleistocene (Synthesys Meloro dataset, unpublished) the 75% is constituted by specimens without a complete ramus. The same proportion (c.ca 70% incomplete) applies for a subset of 104 specimens of Plio-Pleistocene carnivores.

Concerning the function, the *corpus mandibulae* holds teeth and its morphometric variability has been considered in carnivores to be important in discriminating families as well as to identify adaptation to distinct feeding habits (Crusafont Pairó and Truyols Santonja 1957; Biknevicius and Van Valkenburgh 1996; Therrien 2005a, b). On the other hand, the ascending ramus is much more influenced by the powerful masticatory muscles and its morphology is usually considered for the estimation of bite force. The latter feature is influenced by body mass and feeding habit in mammalian carnivores (Wroe et al. 2005a). For these reasons, the dietary predictive power of both mandibular regions will be tested independently in order to clarify what mandibular region can be used for palaeoecological purposes.

3.2 Materials and Methods

97 mandible specimens belonging to adult individuals of 97 species (same sample as in Chapter 1) were explored through geometric morphometrics. The landmark configuration resembles the one used to cover the entire lower jaw (Chapt. 1) with the exception that the landmarks sample was split in two sub-samples in order to represent the two distinct mandibular modules.

For the *corpus mandibulae* region 9 landmarks were defined according to the previous landmark configuration (Chapt 1) while the ascending ramus is here represented by 5 landmarks (Fig. 3.1). Although the ascending ramus can be covered also by the landmark number five (which defines the end of crushing molar area) I prefer to avoid this landmark from the configuration in order to decrease the probability of obtaining spurious correlation between the corpus and the ramus region that in this way do not share any landmark. It is worth noting that a similar landmarks distribution of two mandibular regions was chosen and validated by Klingernberg et al (2003) in the mouse mandible.



6 **Figure 3.1:** Landmark configurations which cover the corpus (left) and ramus mandibulae (right).

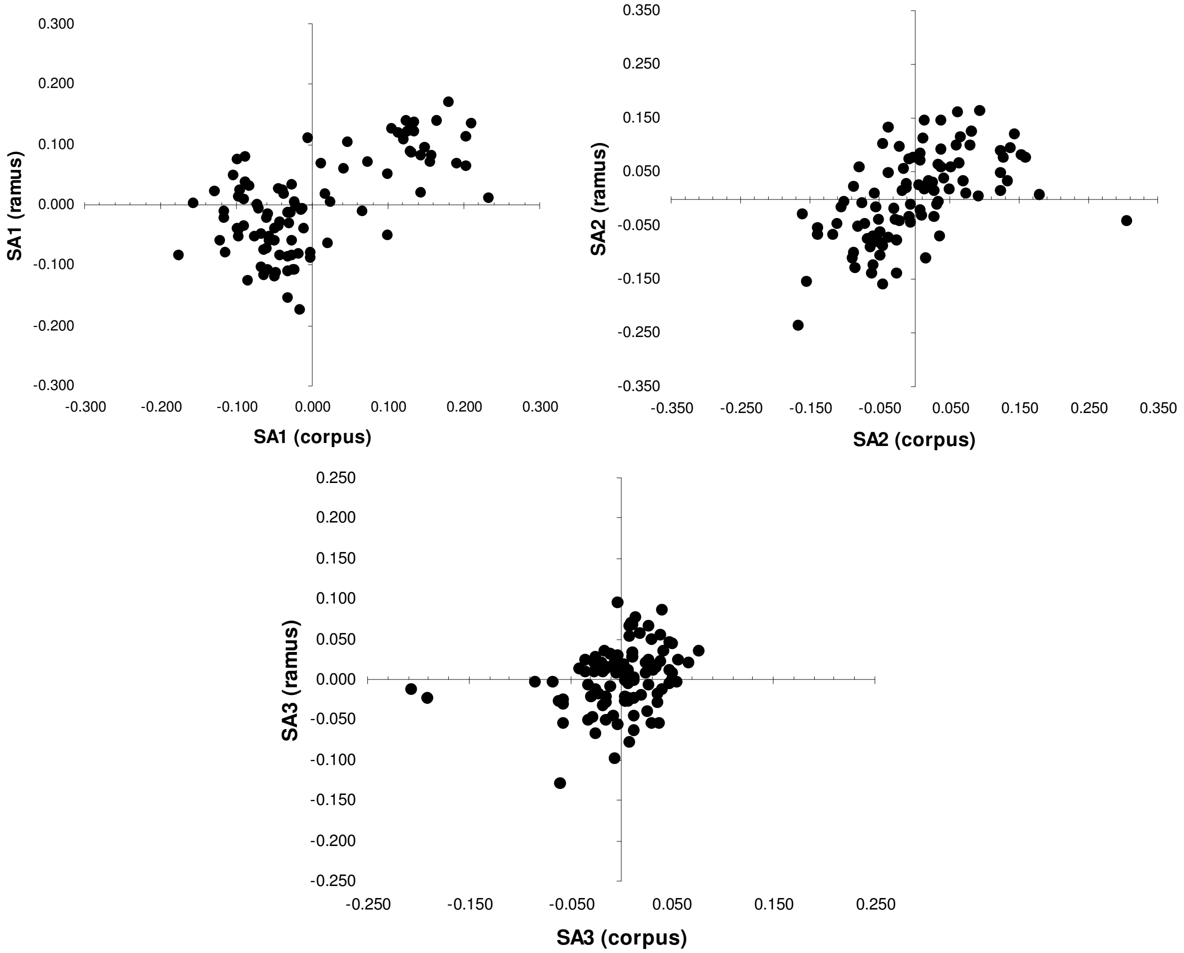
A GPA procedure was performed to extract shape variables, independently, for both corpus and ramus area. The correlation between the shape of both mandibular regions was then tested through a two-blocks Partial Least Squares (PLS) (Rohlf and Corti 2000). The PLS is particularly useful especially with landmark based data because it does not assume variables as dependent and independent (e.g: regression) but as separate blocks. PLS extracts pairs of orthogonal vectors (Singular Axis, SA) of variation for each block of variables (that in our cases are represented by shape data for each landmark configuration). Through a Singular Value Decomposition (SVD) each pair of Singular Axis is associated with a Singular Value (SV) which is a relative measure of the covariance explained by the paired axes (Zelditch et al. 2004). This procedure allows to consider the covariation of two or more blocks of variables even if the blocks are constituted by a different number of variables such as the case when the number of landmarks differs between two or more configurations.

In order to identify factors implicated in shape correlation of both corpus and ramus region a series of nested non parametric correlations were performed on the scores obtained for each significant pair of SA. Family categories as well as feeding categories (in Christiansen and Wroe 2007), size of prey (Gittleman 1985) and the 7 kilogram groups were chosen as grouping categorical variables. This choice is justified by the previous MANOVA PGLS analyses (Chapter 1) which evidenced no significant effect of OTU covariance matrix on the discrimination of mandible shape among such ecological groups.In order to better recognise the relative statistical predictive power of the corpus and the ramus region separately, the same MANOVA and PGLS analyses already performed for the entire set of shape variables of the lower jaw are reassessed. Again, family categories as well as feeding categories (in Christiansen and Wroe 2007), size of prey (Gittleman 1985) and the 7 kilogram groups were chosen as grouping categorical variables

3.3 Results

3.3.1 Correlation between the corpus and the ramus region

After GPA were performed on the corpus and the ramus landmark configurations, two blocks PLS extracts six dimensions (SV) and among them the first three are significantly correlated (percentage of correlations expected by chance > observed correlations after 999 random permutations: 1% for SV1; 1% for SV2; 2% for SV3). The first and the second Singular Values explain a considerable part of the total variance (61.98% and 37.13% respectively) while the third SV only the 0.62%.



Fgure 3.2: Scores of the first three significant Singular Axis of the corpus and the ramus region.

The highest correlation occurs between the first two Singular Axes (r = 0.6313) (Fig.3.2a), followed by the second SAs (r = 0.5568) (Fig. 3.2b)and the third (r = 0.2837) (Fig. 3.2c).

The relationship between the corpus and the ramus region can be visualized by looking at the deformation grids originated on Singular Axis scores. On the SA1 the relative thickness of the corpus and the diastema length as well as the proportion between the slicing and the grinding area are associated with changes in the position of the coronoid process relative to the condyle and changes of the condyle relative to the angular process (whose shortening increase from negative to positive scores) (Fig. 3.3).

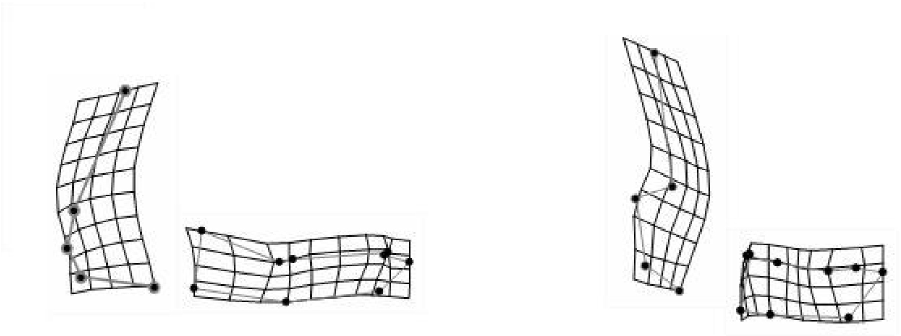


Figure 3.3: Shape deformation of the corpus and the ramus region on the first Singular Axis from negative (left) to positive (right) scores.

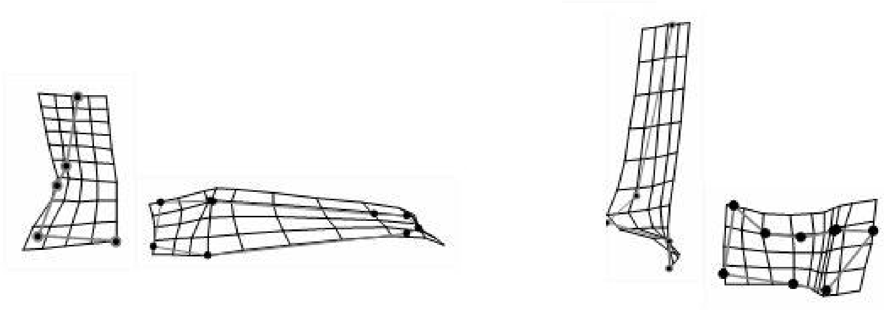


Figure 3.4: Shape deformation of the corpus and the ramus region on the second Singular Axis from negative (left) to positive (right) scores.

On the second SA shape changes of the corpus are more related with the relative length of the premolar row (together also with the other parameters) which correlates with the relative length of the condyle (Fig. 3.4).

The shape changes along the third SA imply shortening of the diastema (from negative to positive scores) and changes in the position of crushing relative to the slicing area of the m1 which relates with the shortening of condylar and angular region (Fig. 3.5).

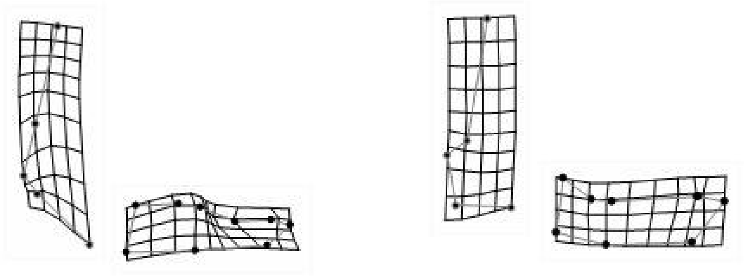


Figure 3.5: Shape deformation of the corpus and the ramus region on the third Singular Axis from negative (left) to positive (right) scores.

The correlation between the corpus and ramus region can be driven by several factors and one source of variability could be represented by the species taxonomy or ecology. Although the scatter plot of the first SA evidences a separation between Felidae and Hyaenidae from the other families (Fig. 3.6) nested non parametric correlations (between SA1 corpus vs SA1 ramus; SA2 corpus vs SA2 ramus and SA3 corpus vs SA3 ramus) at family level are never significant.

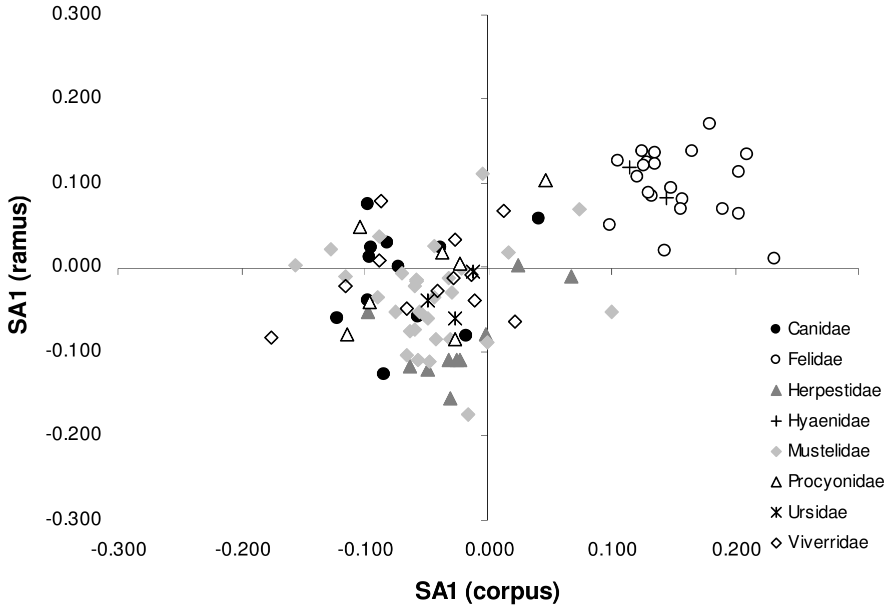


Figure 3.6: Scatter plot of the first Singular Axis with family categories.

Interestingly, correlations between the extracted Singular dimensions are significant for several ecological categories (Fig. 3.7; Table 3.1). For groups of the same diet the first and the second SAs are simultaneously correlated in the consumers of Small and Large prey (Fig. 3.7 only for SA1) while the third SAs of corpus and ramus are correlated only in Insectivores. The prey categories exhibit the strongest relationship which applies for all three significant Singular Axes in the Very

Small category. In keeping with such observation the relationship among singular axis is more represented by all the significant dimensions (1, 2, 3) in carnivores < 7 kilograms while in large carnivores the first dimension exhibits the stronger relationship.

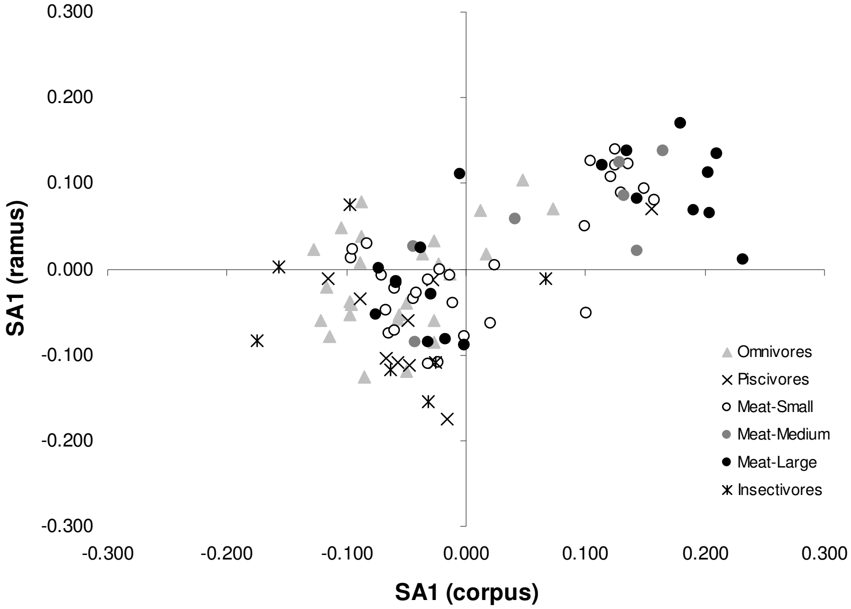


Figure 3.7: Scatter plot of the first Singular Axis with family categories.

A	Dim 1	Dim 2	Dim 3
Omnivores	0.402*	ns	ns
Piscivores	ns	0.775*	ns
Meat Small prey	0.706**	0.708**	ns
Meat Medium prey	ns	0.903**	ns
Meat Large prey	0.694**	0.645**	ns
Insectivores	ns	ns	0.776**

B	Dim 1	Dim 2	Dim 3
No prey	ns	ns	ns
Very small	0.454**	0.732**	0.450**
Small	0.793**	0.490*	ns
Medium	0.799**	ns	ns
Large	ns	ns	ns

C	Dim 1	Dim 2	Dim 3
< 7kg	0.508**	0.678**	0.468**
> 7kg	0.677**	ns	ns

Table 3.1: Pearson's correlation index between SA nested in ecological categories (A, B, C). One star $p < 0.05$; two stars $p < 0.001$.

3.3.2 Shape of the corpus mandibulae

When GPA is applied only to the mandibular corpus landmark configuration fourteen shape variables were extracted and reduced through relative warps. Of 14 RWs the first four explain altogether c.ca 95% of the variance (Table 3.2). The most evident discrimination in the relative warp plot is between the families (Fig. 3.8). Along the first RW shape deformations are associated with changes in diastema length as well crushing-slicing area of the molars while in the second RW deformation occurs in canine depth, premolar row length and general corpus thickness (Fig. 3.8).

MANOVA performed on 14 shape variables (12 PWs and 2 Uniform components) evidences significant differences among families (Wilks' Lambda = 0.00244270; Fs = 7.935; df = 98, 489.6, p = 2.009E-056), diet categories (Wilks' Lambda = 0.16395858; Fs = 2.478, df = 70, 375.4; p = 2.312E-008), size of prey categories (Wilks' Lambda = 0.18844663; Fs = 2.961; df = 56, 309.5, p = 1.176E-009) and small (< 7 kg) and large (> 7 kg) carnivores (Hotelling-Lawley trace = 0.58639064; Wilks' Lambda = 0.63036176; Fs = 3.435; df = 14, 82, p =.0 2.162E-004).

Families explain 64.25% of the shape variance, diet 19.14%, size of prey 18.60% and the 7 kg categories 7.42%.

	SV	%	Cum %
RW1	0.95995	45.33%	45.33%
RW2	0.8568	36.11%	81.45%
RW3	0.40146	7.93%	89.38%
RW4	0.31066	4.75%	94.12%
RW5	0.19607	1.89%	96.02%
RW6	0.16239	1.30%	97.31%
RW7	0.13983	0.96%	98.27%
RW8	0.11302	0.63%	98.90%
RW9	0.09527	0.45%	99.35%
RW10	0.07383	0.27%	99.62%
RW11	0.0636	0.20%	99.82%
RW12	0.05776	0.16%	99.98%
RW13	0.01567	0.01%	99.99%
RW14	0.01221	0.01%	100.00%

Table 3.2: Percentage of variance explained by each RW on corpus region.

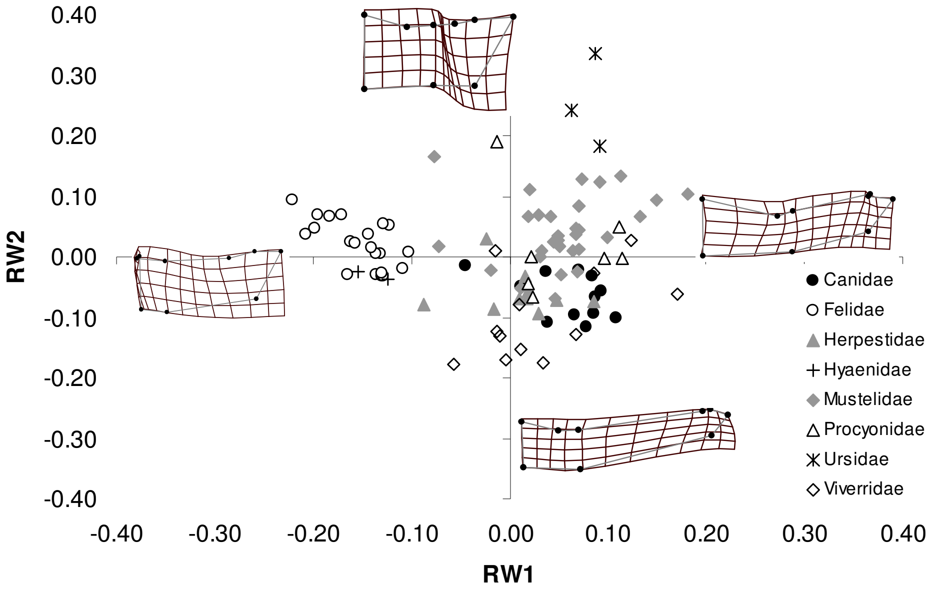


Figure 3.8: Scatter plot of RW1 and RW2. Deformation grids represent shape deformation at the positive or negative extreme of every single RW axis. Symbols are on the agenda (bottom left).

A PGLS MANOVA performed with OTU covariance matrix shows that differences among diet categories still to be significant (Wilks' Lambda = 0.12612799; Fs = 2.362, df = 84, 441.1, p= 9.163E-009) as well as size of prey (Wilks' Lambda = 0.20548665; Fs = 2.141; df = 70, 380.2, p = 2.881E-006) and 7 kilogram categories (Hotelling-Lawley trace = 1.24181367; Fs = 3.592; df = 28, 162.0; p = 1.566E-007; Wilks' Lambda = 0.44606740; Fs = 2.913; df = 28, 162.0; p = 1.265E-005).

3.3.3 Shape of the ascending ramus

The ramus region is here represented only by 5 landmarks which are informative of the position of the coronoid, condyle and angular process. GPA extracts 4 Partial Warps and two Uniform Components which are reduced in Relative Warp analysis in six RWs. The first four RW explain c.ca 93% of the variance (Table 3.3) with the combination of the first two being more informative to discriminate family categories (Fig. 3.9).

	SV	**%**	**Cum %**
RW1	0.83043	41.43%	41.43%
RW2	0.78293	36.83%	78.26%
RW3	0.37724	8.55%	86.81%
RW4	0.30912	5.74%	92.55%
RW5	0.2903	5.06%	97.62%
RW6	0.19914	2.38%	100.00%

Table 3.3: Percentage of variance explained by each RW on ramus region.

On the first axis deformation grids evidence a change in the relative position of the condyle and the angular process (which is more elongated on positive scores), on the second RW the condyle changes its position relative to the coronoid region and greatest shape changes are associated with the depth of the angular process. The combination of the first two RWs as well as others does not allow to discriminate diet categories or Size of prey categories.

The differences in ramus shape are significant among families (Wilks' Lambda = 0.05814389; Fs = 9.408; df = 36, 371.6; p = 4.660E-034), diet (Wilks' Lambda = 0.43461152; Fs = 2.671; df = 30, 346.0; p = 1.032E-005), size of prey (Wilks' Lambda = 0.49682011; Fs = 2.819; df = 24, 304.7; p = 2.186E-005) but not in 7 kilograms categories (Hotelling-Lawley trace = 0.14321602; Wilks' Lambda = 0.87472532; Fs = 2.148; df = 6, 90.0; p = 0.0554) even if the significance of the test approach but is higher of 0.05 level.

Again, families explain a great part of shape variance (47.42%) while diet categories 13.80%, size of prey 12.83% and 7 kilograms categories 3.67% although only slightly significant at 0.05 level.

When OTU covariance matrix is taken into account differences in shape among diet categories still to be significant (Wilks' Lambda = 0.40637676; Fs = 2.405; df = 36, 380.4; p = 2.285E-005) as well as size of prey (Wilks' Lambda = 0.40290994; Fs = 2.977; df = 30, 350.0; p = 8.189E-007) and 7 kilogram threshold (Wilks' Lambda = 0.53075928; Fs = 5.589; df = 12, 180.0; p = 4.157E-008; Hotelling-Lawley trace = 0.88409329; Fs = 6.557, df = 12, 178.0; p = 1.201E-009).

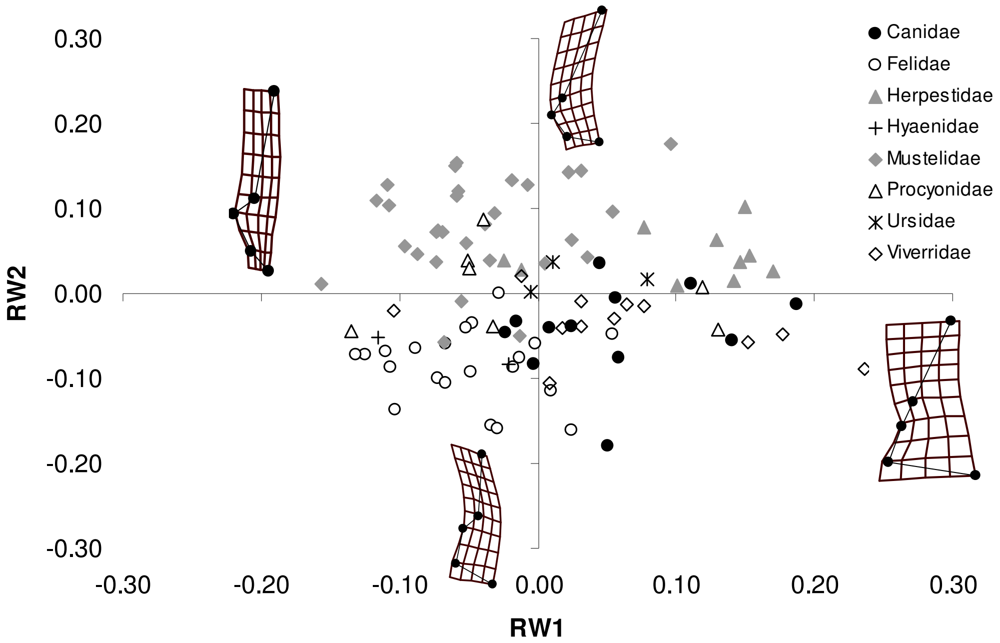


Figure 3.9: Scatter plot of RW1 and RW2. Deformation grids represent shape deformation at thepositive or negative extreme of every single RW axis. Symbols are on the agenda (top left).

3.4 Discussion

Shapes of the corpus and the ascending ramus region co-vary in mammalian carnivores. This result is not unexpected because both these regions are part of the same osteological structure which is basically designed for chewing and prey holding. Interestingly, the corpus region develops horizontally while the ascending ramus vertically but the strongest correlation does not occur for such directions. In fact, on the first singular axis changes in premolar row and crushing area length are associated with lateral changes in the ascending ramus (see Figure 3.3) suggesting different biomechanics of masticatory process in hypo and hyper carnivores. Carnivores with an elongated molar crushing area possess generally a longer dental row which in turn allow a greater dissipation of vertical forces in chewing activity. This fact influences the shape of the ascending ramus because of the stronger importance of forces applied posteriorly (see Figure 3.3). On the other hand, opposite trend occurs in hypercarnivores because the crushing area is shorter (or non existent) then chewing activity is concentrated in a short dental region. As a result, the ascending ramus is projected anteriorly.

The covaration pattern between corpus and ascending ramus is weakly supported at family level. Independently, the shape of both corpus and ramus regions are informative and broadly affected by taxonomic affiliation while their integration is not. This fact is partly expected if we consider the general morphological variability of carnivores (Crusafont Pairó and Truyols Santonja 1956, 1957, 1958; Nowak 1991): the variability of corpus and ascending ramus is small at family level (if compared with that of the overall Order) thus obscuring the possible covariation (hence integration) between both regions of the mandible.

On the other hand, the nested analyses are indicative of a stronger relationship between the ramus and the corpus region among ecological categories. Small and large predatory carnivores exhibits the highest integration pattern suggesting a stronger functional constrain on species that consume meat (independently of their taxonomic affiliation) and than need to sustain higher stress in both regions of the mandible due also to the different hunting techniques (cfr. Biknevicius and Van Valkenburgh 1996; Therrien 2005a, b). Most of the other feeding categories exhibit a positive relationship in the Dimension 2 which is broadly affected by the length of both corpus and ramus region: when the corpus is more elongated the ramus is proportionally shorter (or the opposite). The third dimension explains only a small portion of the total variance and its singular axes are positively correlated only in Insectivores and in predators of very small prey. Taken overall, these results are clearly indicative of a purely adaptive response of mandible to the stress induced by the mastication.

Food processing is physically constrained by the movements that the lower jaw is able to do (Herring 1993). For this reason, development of the lower dentition (and its general shape and position on the mandible) needs to be integrated with the upper jaw dentition. On the other hand, the condylar region should allow the articulation between lower jaw and the skull and, as a consequence, its shape needs to be integrated as well. Most importantly, the spatial arrangement of both lower dentition and condyle avoids dislocation during the mastication (Greaves 1983; Dressem and Druzinsky 1992). The angular process (that here is not considered a distinctive region but part of the ascending ramus) represents another well-integrated region of the lower jaw complex. In carnivore it is usually reduced in order to obtain large gapes for a contracting masseter muscle (Herring and Herring 1974).

These mechanical arguments support the relationship between the ramus and the corpus regions in mammalian carnivores also at an inter-specific level (macroevolutionary *sensu* Levinton 1983).

Another possible mechanism driving shape covariance of the two separate lower jaw regions is the integrated activity of several muscles implicated in the mastication.

The activity pattern of the principal masticatory muscles (masseter, temporalis) which attach to ascending ramus has been well investigated in several species of Carnivora and some generalizations emerge. Temporalis, masseter and zygomatico-mandibularis are involved in vertical and sub-horizontal movements of the mandible during mastication; temporalis has usually a greater activity than masseter; muscle activity is linearly related with bite force which in turn generally increase with the hardness of food (Gorniak and Gans 1980, Gans et al. 1990: *Felis catus*; Gorniak 1986: *Procyon lotor*; Dessem 1989: *Canis familiaris*; Dessem and Druzisky 1992, He and Kiliaridis 2003: *Mustela putorius*). The digastric (which attaches to the *corpus mandibulae*) is involved in jaw opening and its relative position on the mandible is generally related with the degree of jaw opening. As a result, specialised killers like most of felids and mustelids possess a less elongated mandible which allows the digastric to be positioned forward as compared to other carnivores (Scapino 1976).

It is worth noting that the muscle activity moulds the growth of jaw and skull shape during ontogeny (Herring 1993) but the cited multiple evidences from different species support a generalisation at the interspecific level: food processing influences muscles activity which in turn moulds simultaneously and with an integrated fashion the corpus and the ascending ramus regions.

Coherently, high level of shape correlation occur at ecological hierarchy which reflects diet, hunting specialisation, or allometric scaling.

This result is not unexpected because Klingenberg et al. (2003) and Monteiro et al (2005) suggest a similar explanation for the integration of these two mandibular modules even if their analysis were based on a much more complete dataset of a single species or single family. It is worth noting that micro and macroevolutionary processes are linked (Elderidge 1984, Jablonski 2000, 2007, Gould 2002, Grantham 2007) hence the survey presented here simply explains morphological variability in an evolutionary context, other than developmental.

Another interesting result is represented by the separated shape analyses of the corpus and the ascending ramus region. The percentage of variance explained by the shape of each module among categories is broadly similar to that of the entire lower jaw and it follows the same pattern of variability (Fig. 3.10). Taxonomic affiliation is always the most important category which explains the shape variability with the corpus exhibiting the highest value. As already observed by Crusafont Pairó and Truyols Santonja (1957) the corpus region holds teeth and it is indicative of the pure tricotomy between form, function and phylogeny in carnivorous mammals. This result argue for caution on the use of mandibular corpus shape data in predicting ecological categories because of its strong phylogenetic signal. Although the corpus shape is more informative of the size of prey categories and this fact support the recent observations of Therrien (2005a, b).

Also in the discrimination between small (< 7 kg) and large (> 7 kg) carnivores the corpus shape data exhibit a better predictive power.

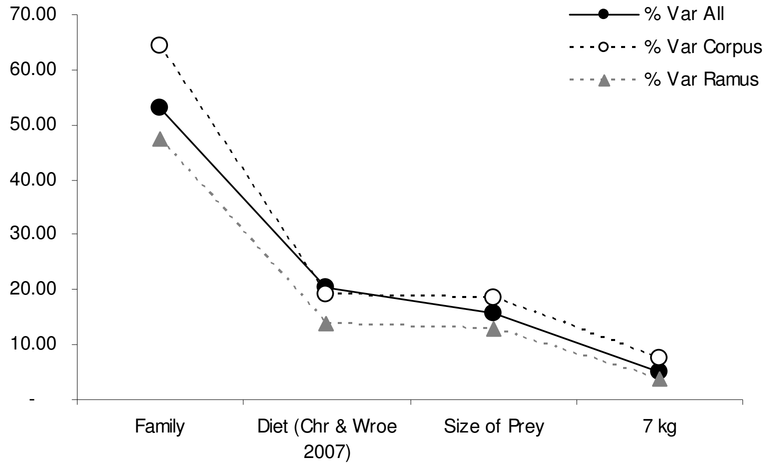


Figure 3.10: Percentage of shape variance explained by each categories after MANOVA on all mandible shape (black circle), corpus shape (white circle) and the ramus (grey triangles).

On the other hand, the ascending ramus perform poorly in predicting all of taxonomic and ecological categories. It is worth noting that this region is more influenced by muscle activity and probably its variability at macroevolutionary scale is less informative other than at intra-specific level. Interestingly, PGLS analyses confirm that shape differences (for both corpus and ramus) are truly affected by species ecology, and this pattern is not an artefact of phylogenetic relatedness.

Such results have important implication for palaeoecological studies. First of all, the lower jaw shape data are informative of both species taxonomy and ecology. Secondly, mandibular regions can be analysed separately with the corpus being more informative than ascending ramus.

Thirdly, the morphological (and ecological) separation between small and large carnivores still to apply in the analysis of single mandibular modules. The validation of such difference is important for the large carnivore guild analysis through time that can benefit also of incomplete data from the fossil record (Van Valkenburgh 1985, 1988, 1989). Most importantly, palaeo-ecological studies of large carnivorous mammals can apply geometric morphometrics in order to obtain and visualise shape data of lower jaw complex (or part of it) as recently demonstrated for other singular anatomical structures (cfr. Andersson 2003; Schutz and Guralnick 2007).

Chapter 4

Reconstructing feeding habits of Plio-Pleistocene large carnivores: a geometric morphometrics approach

4.1 Feeding habits and jaw morphology in Carnivora

The reconstruction of feeding habits in extinct Old World Plio-Pleistocene carnivores could be a special achievement in the light of the interaction of such beasts with early humans, who are simultaneously considered the “hunters” and the “hunted” of the Late Pliocene landscapes in the Old World. Different approaches have been applied according to the evidence drawn from fossil material, but it is difficult to obtain complete robust ecological data on extinct species. This happens to be the case because feeding habit (as a synonymous of diet) is a difficult variable to quantify even in extant carnivores where the intra-specific variability of dietary preference can be high. While in extant species it is possible to obtain feeding habits data usually from direct field observation or indirect methods as the analysis of postingestion samples (Litvaitis 2000) for extinct species only indirect methodologies are available. Analyses of faecal samples, may be representative of these latter category, but they rarely pertain to analyses of extinct carnivores diet (Dalquest 1969). This is because they are hardly distinguishable within the same phylogenetic group and their preservation is usually non-optimal. An alternative approach is the complete taphonomic analysis of the fossil material. The evidence of tooth marks on bones of large ungulates allowed to reconstruct the prey preferences of several European Ice Age predators (e.g. Palmqvist et al. 1996; Arribas and Palmqvist 1998; Echassoux 2004). Although such approach gives remarkable results, it does not consider the dietary preference of omnivorous or even herbivorous species. A more complete approach is recently represented by the isotopic analysis: Stiner et al. (1998) confirmed the high herbivory adaptation of cave bears while Palmqvist et al. (2003) shed light on dietary preference of the Upper Villafranchian mammalian community (both carnivores and herbivores) of the Orce basin. It is worth noting that such approach (like the taphonomic one) is site specific and it can confirm or neglect much simpler palaeoecological observations.

The comparative method (Munthe 1989) is one of the methodology which allows to obtain simple information the ecology of extinct carnivores. In particular for feeding habits, such approach refers to biological structures related to mastication. Teeth are the most obvious structures involved in feeding; not surprisingly their morphology was a primer for understanding dietary adaptations in both extant and extinct carnivores (Crusafont Pairó and Truyols Santonja 1956, 1957, 1958; Van Valkenburgh 1986, 1988, 1991, 1996, 2007; Werdelin 1996a, b). Shape, dimension and even the number of teeth are clearly representative of different feeding strategies irrespective of evolutionary processes (Van Valkenburgh 1991, 2007).

Mandible is another osteological structure particularly relevant to the mastication in mammals (Herring 1980, 1993). It is implicated in chewing and assumes a great importance in carnivore predators for prey holding (Biknevicius and Van Valkenburgh 1996, Therrien 2005a, b). Different levels of biomechanical stress together with temporal muscle size and orientation mould mandible structure. As a consequence, canids or hyaenids have longer mandibles than felids and mustelids (Radinsky 1981a, b, 1982). Bone consumption (for feeding on marrow) is another factor that greatly influences mandible's shape as it affects the growth of bone tissue (Biknevicius and Van Valkenburgh, 1996). Bone-splitting mandibles have to withstand sizeable bending stresses during mastication, hence their great deepening just below the tooth row. Such extreme adaptation is quite visible in the spotted hyena (*Crocuta crocuta*) (Kruuk 1972; Biknevicius and Van Valkenburgh 1996; Therrien 2005a). In sharp contrast felids, which are homogenously adapted to meat slicing, exhibit slender mandibles and teeth number reduction (Turner and Antón 1997; Van Valkenburgh 1996; Biknevicius and Van Valkenburgh 1996; Therrien 2005b). Interestingly, Biknevicius and Leigh (1997) demonstrated that differences in the *corpus mandibulae* between the spotted hyena and the puma (*Puma concolor*) occur since early stage of development suggesting a sort of morphological pre-adaptation to certain feeding habits.

In spite of being potentially highly indicative, few studies on Plio-Pleistocene carnivores include the mandible in the analysis of the dietary adaptation (Ficcarelli, 1979a; Palmqvist et al. 1999, 2007). This probably depends on the scarcity of intact specimens in the fossil record and an objective difficulty in quantifying its shape and size with conventional statistical methods.

Recently, there is an increasing evidence of the fact that cranial (including mandible) morphological variability can be used in both small (Friscia et al. 2006) and large carnivores (e.g. bears Sacco and Van Valkenburgh 2004) to infer on feeding habits of extinct species.

It is worth mentioning that a great number of studies benefit of multiple cranial measurement in order to obtain relevant morpho-ecological data.

Being geometric morphometrics intended to study shape variation among objects (Rohlf 2000), it offers the possibility of analyzing mandible shape and how it correlates with diet (Raia 2004). Most interestingly, such technique allows also to visualize spatial variation in shape of structures. For carnivores mandibles, Raia (2004) found out that 2D shape could be successfully used to infer feeding habits in living and few extinct 'test' species.

On the light of the results obtained by performing an extensive survey of mandible shape in extant Carnivora (chapters 1, 2), here I propose a mandible shape analysis on a selected subset of both extant and extinct species in order to infer feeding habit in extinct Plio-Pleistocene form with a degree of statistical probability. The multivariate shape data are also used to reconstruct possible mandible shape similarities between both extant and Plio-Pleistocene species.

4.2 Materials and Methods

A two-level analysis was conducted on distinct datasets of lower jaw in order to take into account the incompleteness of fossil material. The first approach is applied to complete mandible specimens of both extant and Plio-Pleistocene species. 155 2D pictures of mandible specimens belonging to 53 species (Appendix 2) were explored through geometric morphometrics (Table 4.1).

	N.Species	**N. Specimens**
Ursidae	12	26
Canidae	18	53
Hyaenidae	4	15
Felidae	19	61
Tot	53	155

Table 4.1: Sample size of complete mandibole shape dataset for both extant and extinct specimens.

Of the 53 species 10 are extinct Plio-Pleistocene carnivores for which mandibles were complete enough: among canids *Canis arnensis*, *Lycaon falconeri*, *Canis etruscus* are represented; for Ursidae *Ursus etruscus*, *Ursus minimum*, *Ursus spelaeus*, *Ursus deningeri*; and among Felidae the two sabertooth cats *Megantereon cultridens* and *Homotherium crenatidens*, *Lynx issiodorensis* and the Pleistocene lion *Panthera leo*. Only European mandible specimens of extinct form were analysed and when possible fossil specimens from Italian localities included (Appendix 2).

Also two specimens of *Canis dingo* probably belonging to Pleistocene fossil record were included. The badger (*Meles meles*) was excluded from such analysis because it is the only large mustelid included in Italian Upper Pleistocene guild and its morphology is quite distinctive: mandible and tooth morphology do not show any significant difference from extant specimens.

The same landmark configuration as in Chapter 1 was applied and then analysed with a GPA procedure in order to extract shape data. Principal component analysis was performed to explore the shape space while shape data were successively analysed with a Discriminant (or Canonical Variate) analysis.

For each extant species a feeding category was taken from the literature (Christiansen and Wroe 2007 as evidenced in Chapter 1) while for extinct form no feeding categories were assigned.

Discriminant analysis allows to obtain from multivariate data some vectors (Discriminant Functions) that maximize the differences among pre-determined groups (Zelditch et al. 2004). In such case the multivariate data are represented by PWs and Uniform components of mandible landmark configuration while the groups are defined by feeding categories. A leave-one-out procedure was then applied to validate the predictive power of discriminate functions and to predict dietary categories of extinct specimens.

In order to include more fossil specimens in mandible shape analysis (Appendix 2), a second survey was conducted at family level by using a landmark configuration which describes only the mandibular corpus region (in Chapter 2). For each family a separate shape analysis was performed in order to explore shape space and eventually perform Discriminant analysis to reconstruct feeding habits in fossil specimens from corpus shape data. Procustes distance matrix among specimens was also explored with a UPGMA cluster analysis in order to visualize the degree of shape similarities between extant and extinct species. As in such analyses each species is usually represented by more than one specimens, a mean consensus configuration was applied and then used as species mean shape in UPGMA procedure.

4.3 Complete mandibles analyses

GPA procedure applied to a sample of 155 lower jaws extracts 24 shape data (22 Partial Warps and 2 Uniform components) from the 14 landmark configuration. Of the 24 RWs the first eight explains 95% of the total shape variance (Table 4.2).

	SV	%	Cum %
RW1	0.90166	37.36%	37.36%
RW2	0.78994	28.68%	66.04%
RW3	0.4417	8.97%	75.01%
RW4	0.39723	7.25%	82.26%
RW5	0.35387	5.75%	88.01%
RW6	0.25303	2.94%	90.96%
RW7	0.22688	2.37%	93.32%
RW8	0.19634	1.77%	95.09%
RW9	0.15036	1.04%	96.13%
RW10	0.12821	0.76%	96.89%
RW11	0.11464	0.60%	97.49%
RW12	0.11046	0.56%	98.05%
RW13	0.09741	0.44%	98.49%
RW14	0.08213	0.31%	98.80%
RW15	0.07968	0.29%	99.09%
RW16	0.0727	0.24%	99.33%
RW17	0.06334	0.18%	99.52%
RW18	0.05944	0.16%	99.68%
RW19	0.04848	0.11%	99.79%
RW20	0.04359	0.09%	99.87%
RW21	0.03792	0.07%	99.94%
RW22	0.03213	0.05%	99.99%
RW23	0.01435	0.01%	100.00%
RW24	0.00802	0.00%	100.00%

Table 4.2: Variance explained by each RW on sample of 155 mandible with 14 landmarks.

By looking at the first two Relative Warps it is evident the discrimination among families (Fig. 4.1). The first RW is associated with changes in relative canine length, diastema, premolar row, and grinding area length relative to the slicing area. There is an evident association of RW1 with mandibular corpus thickness as well. The coronoid process changes its position relative to the corpus area by being projected more anteriorly in canids (negative scores of RW1) other than posteriorly (in felids positive scores of RW1). The landmarks of condyle change as well being more vertically projected in canids while the depth of the angular process is unchanged.

On the second axis, changes in mandible shape are driven by changes of the grinding area relative to slicing one and condylar region (Fig. 4.1).

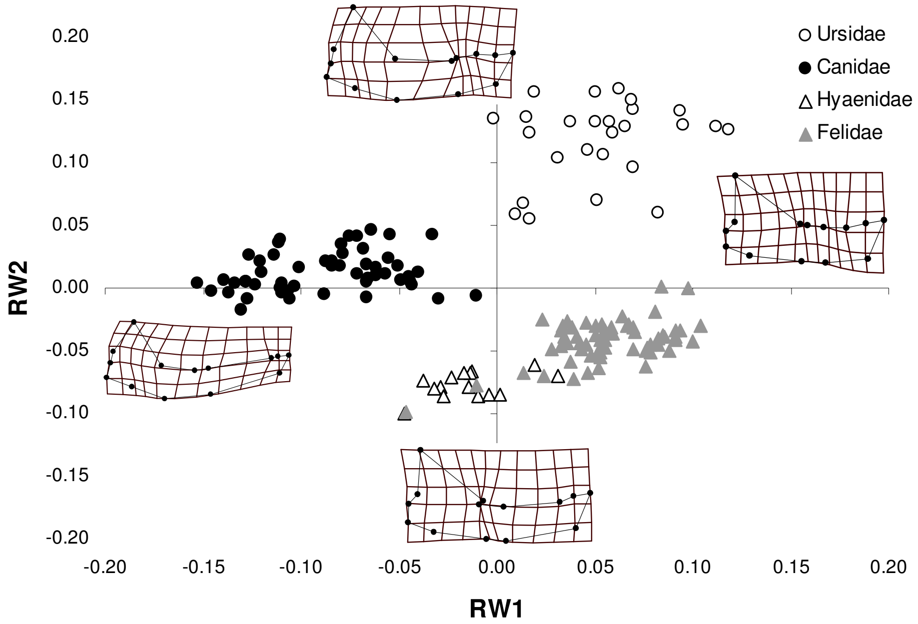


Figure 4.1: Plot of the first and second RW in a subset of 155 scomplete mandible of large carnivores.

The only overlap in the plot of RW1-2 occurs between some felids and members of family Hyaenidae. The felids specimens are represented by two mandibles of *H. crenatidens* and one of *M. cultridrens* together with one specimen of *Neofelis nebulosa* that is at threshold between felids and hyaenids. This fact suggests what a unique morphology characterises the sabertooths and dirk-toothed cats.

Such a uniqueness appears also in the plot of the RW1-3 (Fig. 4.2). The RW3 axis is associated with changes in the height of the condylar process relative to the corpus mandibulae and the changes of angular process relative to the corpus region. Changes in the diastema region are also represented by this third axis as well as changes in the corpus thickness under this region.

On the first and the third axis little grouping occurs among diet categories (as in Christiansen and Wroe 2007). The variability of meat eaters is high even if generally the predators of large prey do not occupy extreme RW1 negative scores (that instead can be occupied by meat eaters of small prey). Negative scores of RW3 discriminates Meat eaters of medium prey.

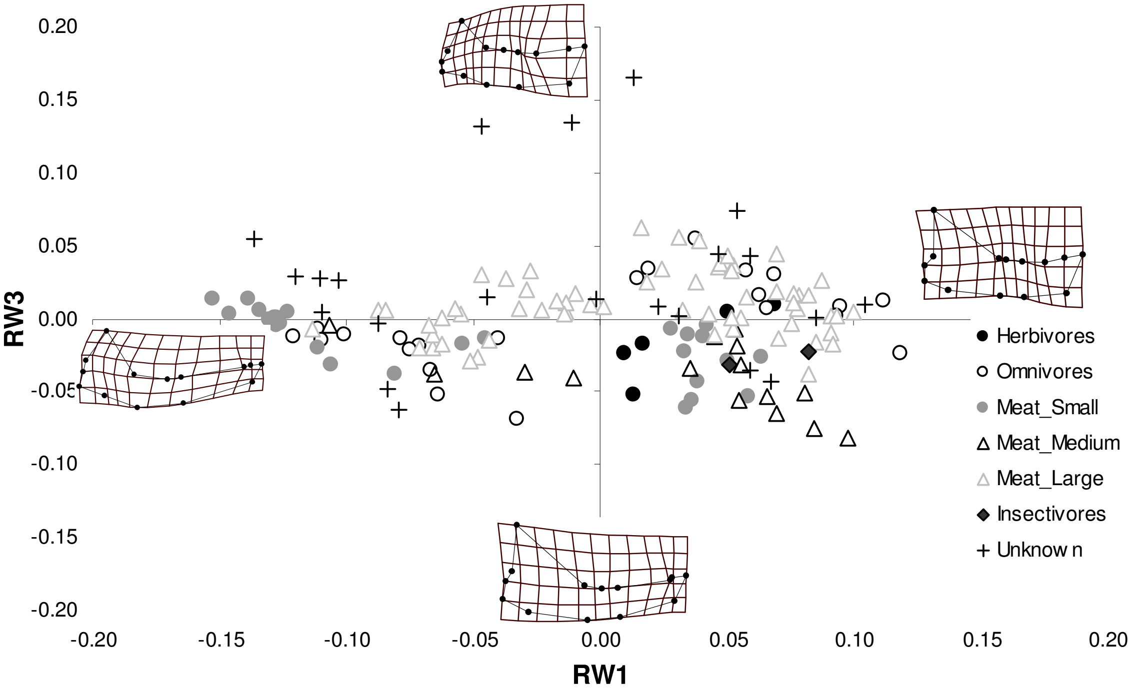


Figure 4.2: Plot of the first and third RW in a subset of 155 scomplete mandible of large carnivores.

Herbivorous bears (black dots) are well separated (except two specimens of *Tremarctos ornatus*) while omnivores occupy all the morphospace defined by RW1-3 in a continuum axis stretching from the shape of jackals to bears. The insectivorous *Melursus ursinus* does not exhibit a distinctive morphology. For extinct Plio-Pleistocene carnivores the diet has not been previously defined in order to make prediction with CVA.

A MANOVA model performed with shape variables as dependent variables and diet (with extinct species excluded) and family as fixed factors evidences that there is a significant difference in mandible shape among families (Wilk's lambda = 0.0003; F = 51.922; df = 72, 293.733; $p < 0.0001$) and diet categories (Wilk's lambda = 0.017; F = 5.288; df = 120, 486.533; $p < 0.0001$) and the interaction between both of these factors is significant as well (Wilk's lambda = 0.135; F = 3.886; df = 72, 293.733; $p < 0.0001$).

This analysis demonstrates how complex is the relationship between family, feeding categories and mandible shape. Phylogenetic hierarchy and feeding ecology interacts and suggesting that a nested approach is necessary in order to eventually remove the great share of variance explained by phylogeny.

In order to perform diet prediction on extinct species this complete landmark configuration is used for a Discriminant analysis. Five discriminant functions are extracted and all of them are significant (Table 4.3).

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 5	0.015	494.505	120	< 0.001
2 through 5	0.072	308.205	92	< 0.001
3 through 5	0.206	185.078	66	< 0.001
4 through 5	0.436	97.251	42	< 0.001
5	0.720	38.508	20	0.008

Table 4.3: Statistics of the discrimnant function extracted on mandible shape data.

A plot of the first and the second discriminant function (Fig. 4.3) demonstrates that all group centroids are separated although some overlap occur between Meat eaters categories.

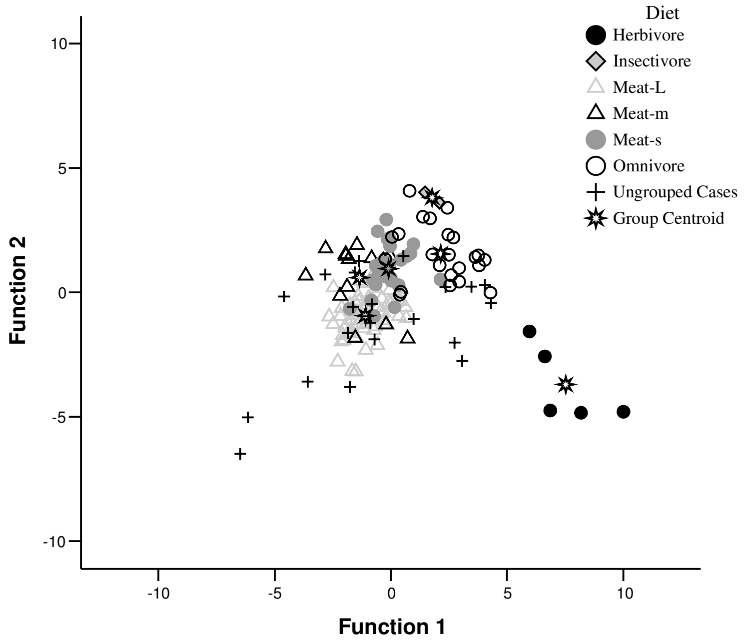


Figure 4.3: Plot of the first and second Discriminant Functions in a subset of 155 scomplete mandible of large carnivores.

Original classification demonstrates that all groups are well classified and such result still to apply in a cross validated categorization (Table 4.4). Among the meat eaters, species which hunt small or medium sized prey (as compared to their own size) are less predictable on the basis of their mandible shape while hunters of large prey exhibit more than 75% of correctly classified cases. Insectivores are 100% correctly classified but they are represented only by two specimens of *Melursus ursinus*. Interestingly, among the bears, the polar bear (*Ursus maritimus*) is misclassified in cross validated analysis in Omnivore group thus meaning that its mandible shape is not different enough from the other more generalized bears.

	Diet	Predicted Group Membership						Total
		Herbivore	Insectivore	Meat-L	Meat-m	Meat-s	Omnivore	
Count	Herbivore	5	0	0	0	0	0	5
	Insectivore	0	2	0	0	0	0	2
	Meat-L	0	0	57	1	4	0	62
	Meat-m	0	0	1	12	2	0	15
	Meat-s	0	0	3	2	21	0	26
	Omnivore	0	0	0	0	4	19	23
	Ungrouped	1	0	11	4	1	5	22
%	Herbivore	100.00	0.00	0.00	0.00	0.00	0.00	100.00
	Insectivore	0.00	100.00	0.00	0.00	0.00	0.00	100.00
	Meat-L	0.00	0.00	91.94	1.61	6.45	0.00	100.00
	Meat-m	0.00	0.00	6.67	80.00	13.33	0.00	100.00
	Meat-s	0.00	0.00	11.54	7.69	80.77	0.00	100.00
	Omnivore	0.00	0.00	0.00	0.00	17.39	82.61	100.00
	Ungrouped	4.55	0.00	50.00	18.18	4.55	22.73	100.00
Count	Herbivore	3	0	0	0	0	2	5
	Insectivore	0	2	0	0	0	0	2
	Meat-L	0	0	48	5	7	2	62
	Meat-m	0	0	3	9	3	0	15
	Meat-s	0	0	3	4	15	4	26
	Omnivore	0	2	0	0	7	14	23
%	Herbivore	60.00	0.00	0.00	0.00	0.00	40.00	100.00
	Insectivore	0.00	100.00	0.00	0.00	0.00	0.00	100.00
	Meat-L	0.00	0.00	77.42	8.06	11.29	3.23	100.00
	Meat-m	0.00	0.00	20.00	60.00	20.00	0.00	100.00
	Meat-s	0.00	0.00	11.54	15.38	57.69	15.38	100.00
	Omnivore	0.00	8.70	0.00	0.00	30.43	60.87	100.00

Table 4.4: Count and percentage of correctly classified cases before (up) and after (down) leave one out cross validation performed on DF extracted from 24 shape variables of large carnivore lower jaw.

For extinct species, really good results were obtained: the cave bear *U. spelaeus* is classified as herbivore and this fact currently agrees with previous palaeoecological investigation. The Deninger bear is instead considered omnivore as the other modern *Ursus* spp. This result partly suggests that *U. spelaeus* is more herbivorous because also of its co-existence with the brown bear (*U. arctos*): a highly specialised diet allowed cave bear to occupy a different eco-morphological niche.

The Etruscan bear (*U. etruscus*) as well as *U. minimus* are both classified as omnivores. Their mandible shape were already specialised for an opportunistic feeding. Although a nested analysis might clarify some eco-morphological specialisation.

Among canids, both specimens of *Canis etruscus* are classified as meat-eater of large prey. This means that such dog, in Italian peninsula, was probably already a pack hunter and its morphological similarity with the extant wolf is definitely striking. Fossil dingo is well classified as its extant counter-part even if one specimens is misclassified from Meat-m group to Meat-L group.

For the Arno dog *C. arnensis* results are more enigmatic: one specimen is considered Meat eater of small prey while another as Meat eater of large prey. Only a nested analysis can clarify its feeding ecology although such result suggests that this dog was less specialized than *C. etruscus* and probably more specialised on rodents and lagomorphs, much alike extant coyote.

Discriminant analysis confirms the hypercarnivory habit of *Lycaon falconeri* which is classified as meat eater of large prey. *Nyctereutes megamastoides* exhibits a distinctive mandible morphology and both specimens are classified as omnivore, alike its modern counterpart *N. procyonoides*.

Among hyenas, *Pliocrocuta perrieri* is classified as hunter of large prey (as expected). Unfortunately, the used feeding categories do not consider bone cracking and scavenging as a special "adaptation" although such feature will be considered in a nested analysis.

Among felids, the giant cheetah (*Acinonyx pardinensis*) is classified as meat-eater of medium prey like the extant cheetah. It's likely that, in spite of its larger size, the giant cheetah happened to hunt in the same way of the extant form and such specialization for high-speed chasing (together with a probably solitary behaviour) does not allow this form to hunt larger ungulates.

All the specimens of the sabercat *Homotherium crenatidens* are classified as Meat-L like the dirk toothed *Megantereon cultridens*. Overlap in prey choice is likely in these two extinct cats even if their locomotory habit suggests some eco-morphological differentiation.

For the extinct lynx, *Lynx issiodorensis* one specimen is classified in group Meat-s and the other in Meat-m. This form, was probably less capable of hunting ungulates while does specialise on lagomorphs, much alike the bobcat (*Lynx rufus*). The extinct lion is considered a predator of large prey according to the expected hypothesis.

These results demonstrate how powerful is mandible shape analysis for feeding habit prediction in spite of the interaction between this factor and family categories. It is worth noting that this analysis benefits of a complete landmark configuration which generally is not possible to apply to most fossil specimens.

In order to include more fossils, a nested survey at family level was performed. The landmark configuration include only the mandibular corpus region (see Chapter 2).

4.4 Nested analyses of corpus shape

4.4.1 Ursidae

36 mandibles were included and a nine landmark configuration was used to extract shape variables (14) from only the mandibular corpus region. Relative warp analysis reduced the variables such that the first 4 axes explain c.ca 95% of the total shape variance (Table 4.5).

By following Sacco and Van Valkenburgh (2004) feeding categories, it is possible to discriminate more carnivorous bears (brown bear and polar bear) from the other insectivores (*M.ursinus*), omnivores (*U.americanus*; *U.thibetanus*, *H.malayanus*) and herbivores (*A.melanoleuca*; *T.ornatus*) by plotting scores of the first and the second RW (Fig. 4.4).

	SV	%	Cum %
RW1	0.51173	46.83%	46.83%
RW2	0.39807	28.34%	75.17%
RW3	0.30504	16.64%	91.81%
RW4	0.12629	2.85%	94.66%
RW5	0.12051	2.60%	97.25%
RW6	0.07282	0.95%	98.20%
RW7	0.05526	0.55%	98.75%
RW8	0.05244	0.49%	99.24%
RW9	0.04888	0.43%	99.67%
RW10	0.03251	0.19%	99.86%
RW11	0.0207	0.08%	99.93%
RW12	0.01757	0.06%	99.99%
RW13	0.00586	0.01%	100.00%
RW14	0.00513	0.00%	100.00%

Table 4.5: Variance explained by each RW on sample of 36 mandibles with 9 landmarks belonging to ursids.

On the first axis the corpus shape changes are associated with changes in the diastema length while on the second RW changes occur in the relative length of the premolar row (Fig. 4.4).

The same degree of discrimination occurs also in the plot of RW1 vs RW3 (Fig. 4.5). Such a pattern can be explained by the highly adaptive shape association of the third RW which reflects ratio in crushing vs slicing area of the molar region.

The shape of extinct species is quite distinctive even if it follows the variability of modern bears. Two Pleistocene specimens of *U. arctos* cluster within the range of extant specimens. For cave bears, their similarity with *U. arctos* reflects phylogenetic history and it is mostly driven by the shape of elongated diastema (as consequence of reduced premolar development) explained on the first vector. The Etruscan bear has a corpus shape similar to brown bear and the other omnivores modern Ursinae. Interestingly, *U. minimus* forms a distinctive cluster between herbivores, insectivores and omnivores. In the first and third RWs *U. minimus* is in the same cluster of herbivores.

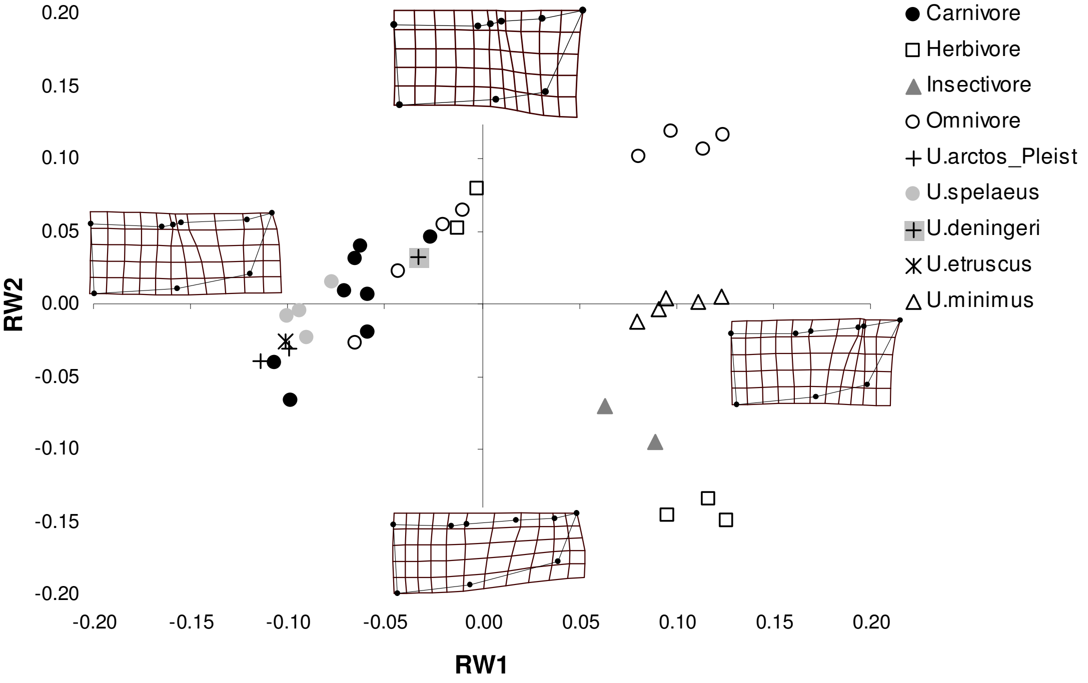


Figure 4.4: Plot of the first and second RW in a subset of 36 specimens of ursids.

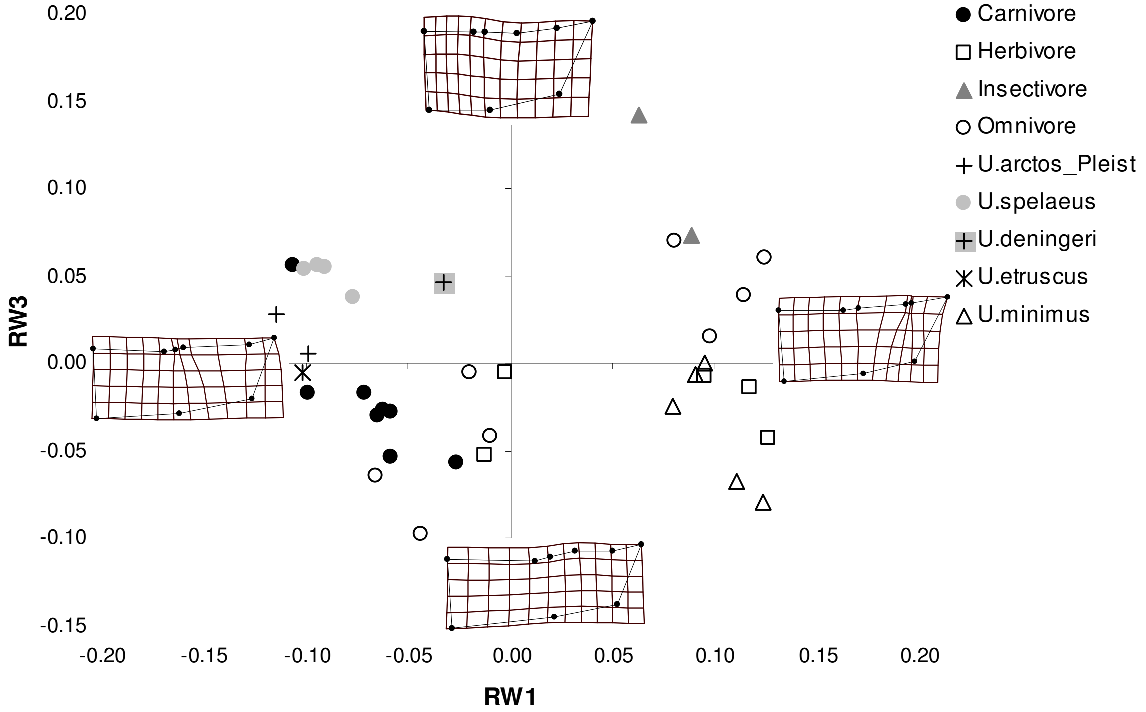


Figure 4.5: Plot of the first and second RW in a subset of 36 specimens of ursids.

An UPGMA analysis was then performed on mean shape computed for each species after GPA procedure. The tree (Fig. 4.6) demonstrates how strong is the phylogenetic signal in corpus shape especially for brown bear lineage. The cave bears cluster together and in between two omnivores species. This suggests that their corpus shape is not so specialised for herbivory (but that adaptation on the entire lower jaw is evident). Interestingly *U. etruscus* is sister group of both brown and polar bear confirming previous phylogenetic hypothesis and also that it was adapted to an opportunistic generalised feeding habit. The similarity between *U. minimus* and *H. malayanus* reflects basic ecological adaptation of both species to tropical habitat and then to a diet rich of insects but also fruits and vegetables.

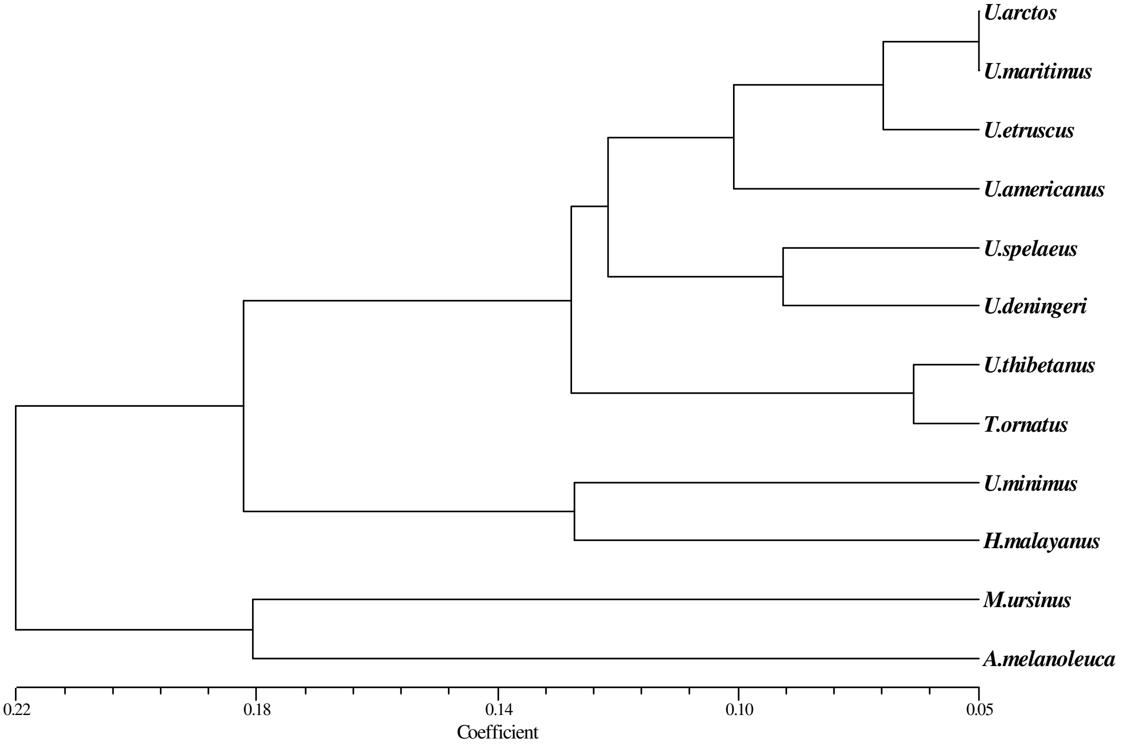


Figure 4.6: UPGMA tree from Procustes distance matrix of corpus shape data in Ursidae.

4.4.2 Canidae

GPA was repeated on a subset of 62 mandible specimens (for 20 species) with 9 landmark of family Canidae. A principal component performed on shape variables evidences that the at least six RW axes are necessary to explain 95% of the variance (Table 4.6).

The first two relative warps are useful to discriminate diet categories as in Christiansen and Wroe (2007). On the RW1 corpus shape changes are associated with general thickness of the mandible with most hypercarnivores exhibiting negative scores (bush dog *S. venaticus* is at the negative extreme of Meat-m group), while on the RW2 the diastema become more or less elongated together with a changes in the crushing region which is usually more developed on negative RW2 scores (Fig. 4.7).

	SV	%	Cum %
RW1	0.33927	43.39%	43.39%
RW2	0.25494	24.50%	67.89%
RW3	0.18173	12.45%	80.34%
RW4	0.13839	7.22%	87.56%
RW5	0.1009	3.84%	91.39%
RW6	0.08971	3.03%	94.43%
RW7	0.06703	1.69%	96.12%
RW8	0.05628	1.19%	97.32%
RW9	0.04773	0.86%	98.17%
RW10	0.04378	0.72%	98.90%
RW11	0.04196	0.66%	99.56%
RW12	0.03066	0.35%	99.92%
RW13	0.01301	0.06%	99.98%
RW14	0.00746	0.02%	100.00%

Table 4.6: Variance explained by each RW on sample of 62 mandibles with 9 landmarks belonging to Canidae.

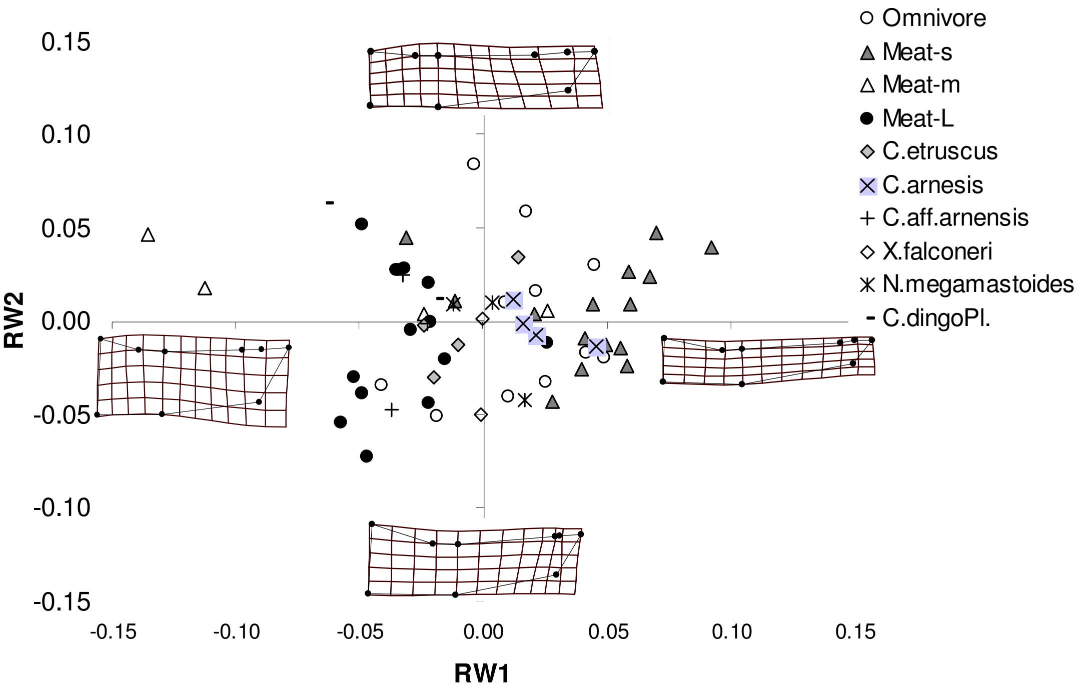


Figure 4.7: Plot of the first and second RW in a subset of 62 specimens of canids.

Interestingly also the plot RW1 vs RW3 shows a matter of discrimination (Fig. 4.8). The meat eaters of small prey are generally well discriminated in the plot RW1 vs RW3 (with this latter axis associated to changes in relative premolar row length and diastema) like omnivores as well.

Among extinct canids *C. etruscus* clearly clusters with Meat-L while *C. arnensis* specimens are usually between Omnivores and Meat-s. The enigmatic form interpreted as *C.* aff. *arnensis* from Grotta Romanelli is always associated at the opposite side of *C. arnensis* between Meat-L. This suggests that probably these specimens could belong to a wolf. *L. falconeri* is not generally in Meat-L while it cluster with omnivores. Such result disagree with the analysis from complete mandible and it indicates that corpus shape does not allow to verify the hypercarnivory habit of this extinct canid. *N. megamastoides* usually is grouped with Omnivores while, the fossil dingo is grouped with Meat-L and does not confirm adaptation of *C. dingo* to Meat-m in the past.

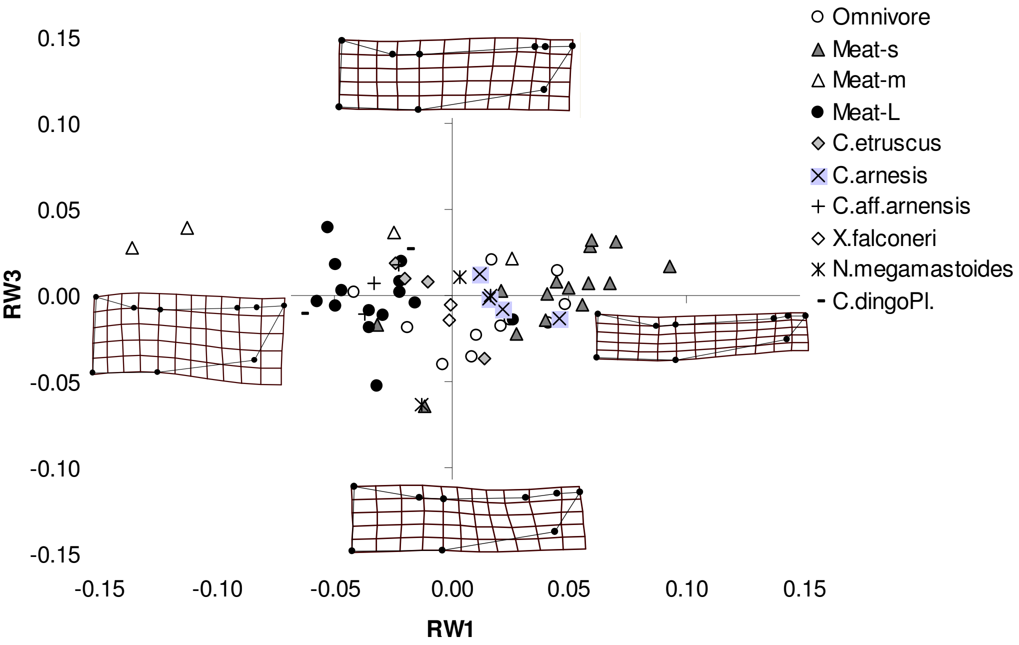


Figure 4.8: Plot of the first and third RW in a subset of 62 specimens of canids.

Discriminant analysis has been applied to canid corpus shape data as well in order to classify with some degree of probability the feeding habit of extinct analysed canids.

Three discriminant functions were extracted and two of them are significant (Tab. 4.7).

A plot of the first two functions (Fig. 4.9) clearly demonstrates that no overlap occurs among diet categories except to a certain extent between Omnivores and Meat-s dogs. Such overlap is evidenced also in the predicted membership of Omnivore categories that in a cross validated analysis is really poor (36.6%) with most of the misclassified cases in the Meat-s category (Table 4.8).

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 3	.037	111.857	42	.000
2 through 3	.258	46.036	26	.009
3	.576	18.772	12	.094

Table 4.7: Statistics of discriminate analysis applied to a subset of 62 mandible of canids.

Predictions validate some previous observations made on the entire lower jaw: all *C. etruscus* are classified in Meat-L categories except 1 (on 4 specimens) classified as Meat-s; *C. arnensis* specimens are half considered Meat-s and half as Meat-L; the *Canis* specimens from Grotta Romanelli are classified as Meat-L; all specimens of *N. megamastoides* are classified as omnivores except one (as Meat-m) and surprisingly both *L. falconeri* are misclassified (one case as Meat-m and the other as Omnivore).

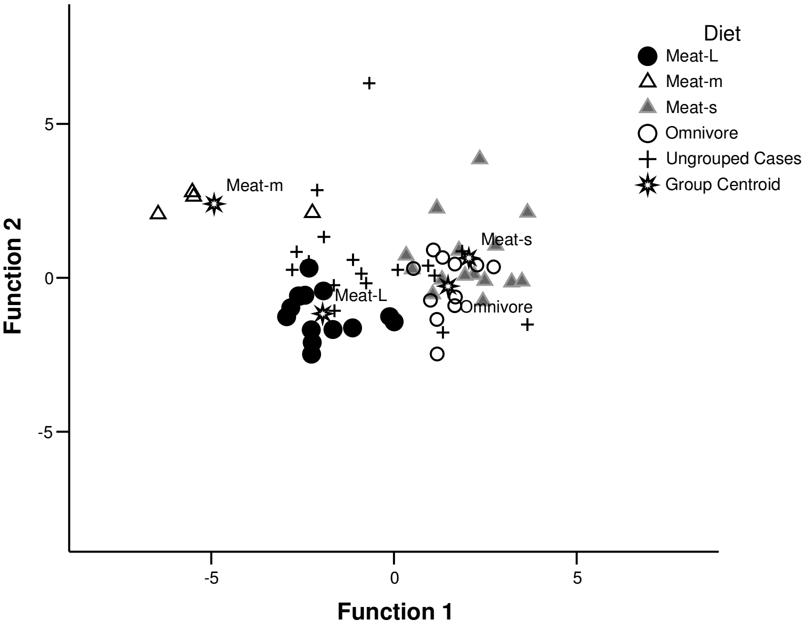


Figure 4.9: Plot of the first and second Discriminant Functions in a subset of 62 mandible of large canids.

This analysis confirms that corpus shape alone cannot be used to obtain certain dietary prediction on extinct canids although it can be informative with certain caution. For the case of the Arno dog it still to validate a meat-eating feeding strategy (not omnivore) but probably less specialised than the *C. etruscus*. Some misclassification occurs also because the grinding area proportion is generally affected by the development of the third small molar that on the same species can be present or absent (e.g. *Cuon alpinus*).

The results for *L. falconeri* are quite misleading and suggest that the mandibular corpus of this species was not so specialised as in extant African wild dog which is capable also of bone crushing (an adaptation that probably occur to lesser extent in *L. falconeri*). Interestingly, the classification of Romanelli dog as Meat-L is informative of the fact that, if these specimens represent an advanced form of *C. arnensis*, than this species becomes more specialised in hunting and a pre-adaptation in mandibles of Villafranchian form for such habit is validated. This character release can be explained by the fact that during Galerian *C.* aff. *arnensis* was the only large dog in canid guild of Italy and will be replaced by the grey wolf. On the other hand, it seems likely that such specimens belong to *Canis lupus* (Tagliacozzo, personal communication).

An UPGMA analysis performed on consensus configurations for each species demonstrates that the shape data of mandibular corpus are quite informative for certain species but in several cases it poorly fits with phylogenetic or functional relationship among species (Fig. 4.10).

	Diet	**Predicted Group Membership**				**Total**
		Meat-L	Meat-m	Meat-s	Omnivore	
Count	Meat-L	13	0	0	1	14
	Meat-m	0	4	0	0	4
	Meat-s	0	0	13	2	15
	Omnivore	0	0	1	10	11
	Ungrouped	10	2	3	3	18
%	Meat-L	92.86	0.00	0.00	7.14	100.00
	Meat-m	0.00	100.00	0.00	0.00	100.00
	Meat-s	0.00	0.00	86.67	13.33	100.00
	Omnivore	0.00	0.00	9.09	90.91	100.00
	Ungrouped	55.56	11.11	16.67	16.67	100.00
Count	Meat-L	12	0	1	1	14
	Meat-m	1	3	0	0	4
	Meat-s	1	0	11	3	15
	Omnivore	2	0	5	4	11
%	Meat-L	85.71	0.00	7.14	7.14	100.00
	Meat-m	25.00	75.00	0.00	0.00	100.00
	Meat-s	6.67	0.00	73.33	20.00	100.00
	Omnivore	18.18	0.00	45.45	36.36	100.00

Table 4.8: Count and percentage of correctly classified cases before (up) and after (down) leave one out cross validation.

L. falconeri is grouped with omnivores species thus confirming that its mandibular corpus does not achieve adaptations in bone crushing as with the hypercarnivores *Lycaon pictus* and the bush dog. The extinct *Nyctereutes megamastoides* cluster with its extant counterpart confirming its unique mandibular corpus morphology. In the *Canis* spp. group there is an interesting phylogenetic signal (except for the cluster grey wolf-dhole which is probably a case of functional convergence). *C. arnensis* is the outgroup of most "rodent-generalist" dogs and cluster with dingo (confirming its ambiguous adaptation to both Meat-s and Meat-L). The Pleistocene specimens of *C. dingo* cluster with wolf-*C. etruscus*-golden jackal (*C. aureus*) group suggesting that during Pleistocene the morphology of dingo was probably different than that of modern forms. The dog from Romanelli is grouped with wolf. The only outlier among *Canis* spp. is the Simien wolf whose thin mandible is probably too generalised to allow clustering according to its phylogenetic relationship with grey wolf.

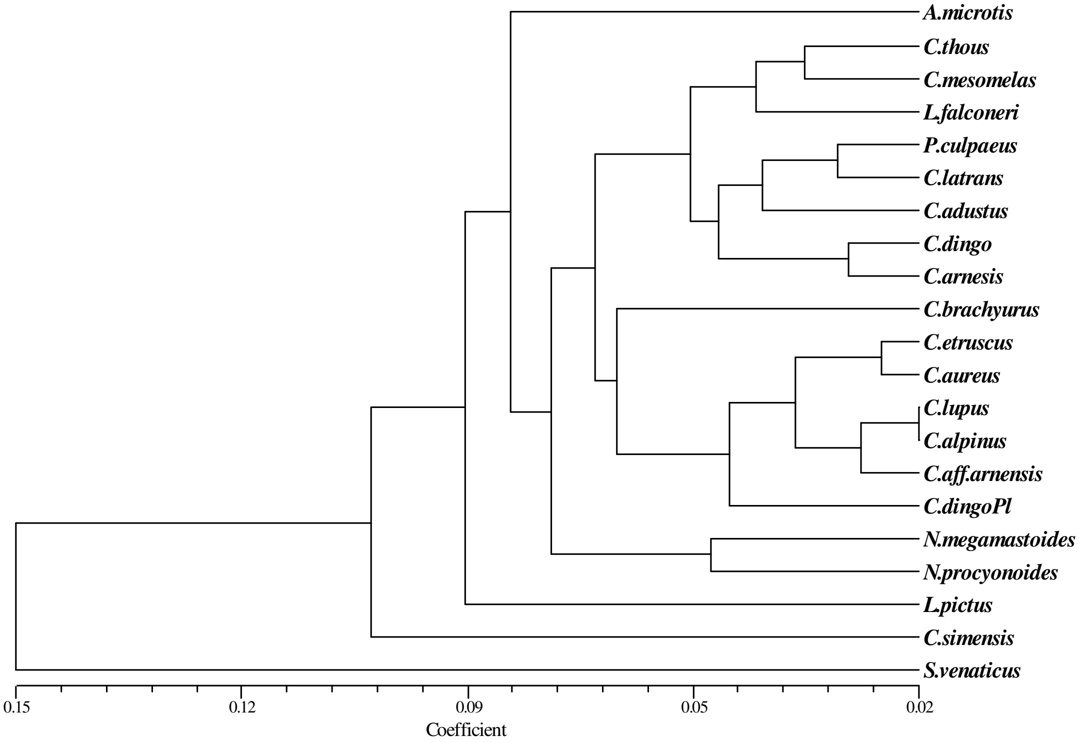


Figure 4.10: UPGMA tree from Procustes distance matrix of corpus shape data in Canidae.

4.4.3 Hyaenidae

GPA was performed on 27 specimens belonging to 7 species. The Pleistocene specimens of spotted hyena (*Crocuta crocuta*) were considered as separate group in order to eventually evidence differences with extant hyenas. Relative Warp analysis extracts 14 axes and of them, the first six explain 95% of the total shape variability.

Interestingly the plot RW1 vs RW2 (Fig. 4.11) allows to discriminate several groups according to taxonomy and functional requirements. Along these two axes it is evident a discrimination between extant hyenas and all of Plio-Pleistocene hyenas (including *C. crocuta* specimens) except *Chasmaporthetes lunensis*.

This fact is mainly the result of the shape variability explained by the first axis which is related with general corpus thickness. It represents also a functional axis because mandible thickness in hyenas can be generally associated with larger body mass and a better adaptation in bone crushing. There are no doubt that *P. brevirotris* and *P. perrieri* were adapted in bone crushing but this analysis demonstrated that they were better equipped than extant hyenas in doing so. Pleistocene specimen of modern spotted hyena were larger as well and, as consequence, its corpus shape changes accordingly.

	SV	%	Cum %
RW1	0.21017	48.85%	48.85%
RW2	0.13385	19.81%	68.66%
RW3	0.10031	11.13%	79.79%
RW4	0.08318	7.65%	87.44%
RW5	0.06044	4.04%	91.48%
RW6	0.05666	3.55%	95.03%
RW7	0.04262	2.01%	97.04%
RW8	0.03736	1.54%	98.58%
RW9	0.0237	0.62%	99.20%
RW10	0.02117	0.50%	99.70%
RW11	0.01436	0.23%	99.92%
RW12	0.00596	0.04%	99.96%
RW13	0.00439	0.02%	99.99%
RW14	0.00367	0.01%	100.00%

Table 4.9: Variance explained by each RW on sample of 27 mandibles with 9 landmarks belonging to Hyaenidae.

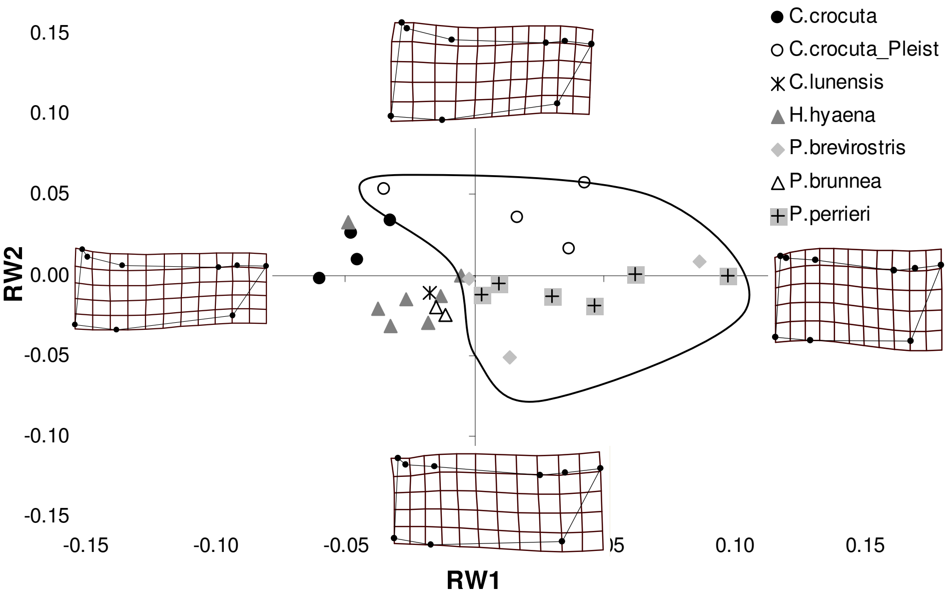


Figure 4.11: Plot of the first and second RW in a subset of 27 specimens of hyaenids.

This relationship is also validated in linear regression model with Ln Centroid Size (CS) –with CS being the square root of the mean squared distance from each landmark to the centroid of the landmark configuration (Bookstein 1989)- as an explanatory variable) and RW1 scores as dependent (Fig. 4.12). Although the slope of such relationship is low (b = 0.0523) it is significant ($R^2 = 0.176$; p = 0.028).

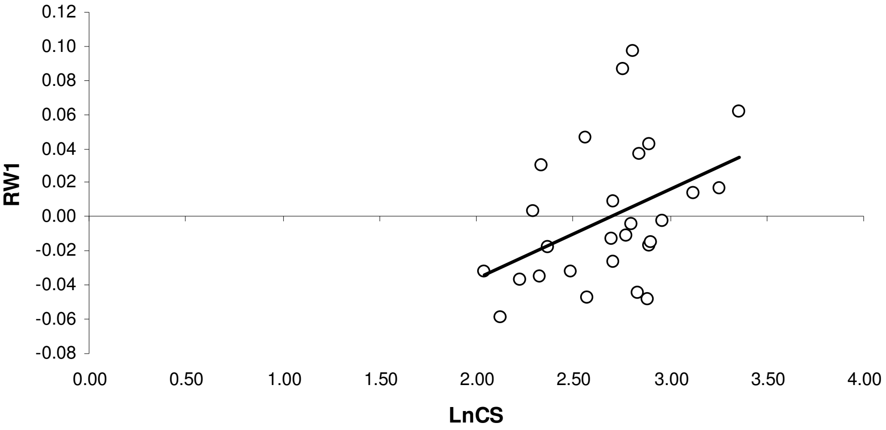


Figure 4.12: Scatter plot of LnCS and RW1 in a subset of 27 hyenids. The slope of the regression line is positive.

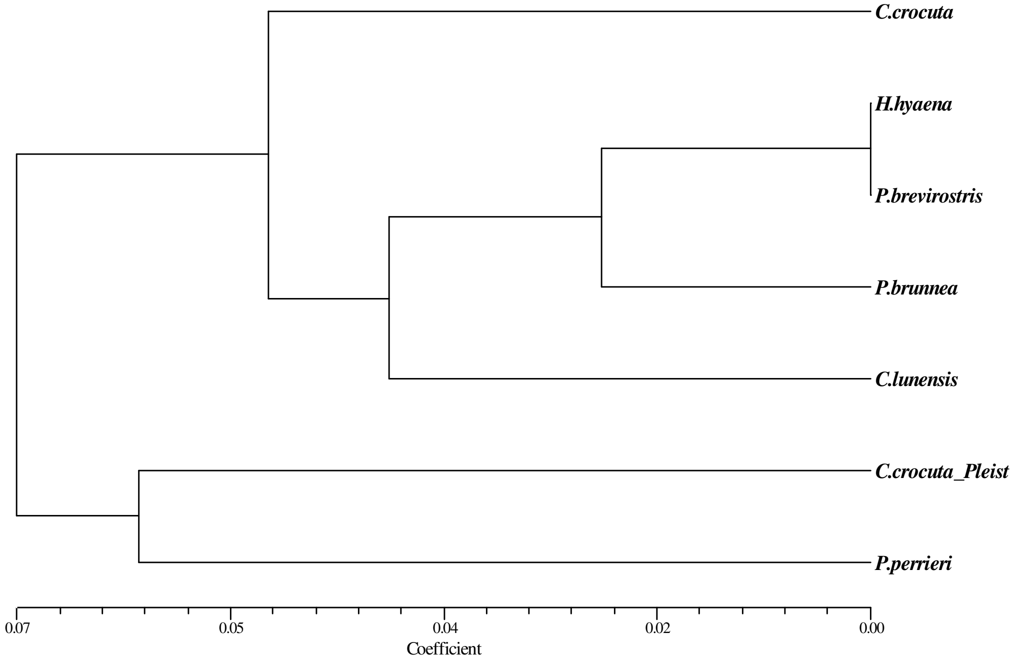


Figure 4.13: UPGMA cluster tree on huaenids corpus shape data.

An UPGMA performed on consensus configuration for each species (Fig. 4.13) is not indicative of some particular phylogenetic relationship (*P.brevirostris* is unusually related with the striped hyena) even if it is clear that fossil *C. crocuta* and *P. perrieri* share a similar corpus shape as a functional response to increasing bone crushing. Interestingly, the running hyena *C. lunensis* usually cluster with extant spotted hyenas confirming its hunting attitude but also its capability of bone crushing less specialised than in *P. brevirostris* and *P. perrieri*.

4.4.4 Felidae

GPA was performed on 81 specimens of felids (24 of them fossils). Pleistocene specimens of lion, lynx and leopard were treated as separate groups.

The performed relative warp analysis extracts 14 axes and six of them explain c.ca 95% of the variance (Table 4.10).

	SV	**%**	**Cum %**
RW1	0.4321	47.15%	47.15%
RW2	0.32813	27.19%	74.34%
RW3	0.18126	8.30%	82.64%
RW4	0.145	5.31%	87.95%
RW5	0.12975	4.25%	92.20%
RW6	0.10487	2.78%	94.98%
RW7	0.07796	1.53%	96.51%
RW8	0.0743	1.39%	97.91%
RW9	0.06422	1.04%	98.95%
RW10	0.0508	0.65%	99.60%
RW11	0.03293	0.27%	99.87%
RW12	0.01487	0.06%	99.93%
RW13	0.01308	0.04%	99.97%
RW14	0.01024	0.03%	100.00%

Table 4.10: Variance explained by each RW on sample of 81 mandibles with 9 landmarks belonging to Felidae.

The first two are broadly indicative of corpus shape differences related with prey size (Fig. 4.14). On the first axis there is a high variability in relative corpus thickness and length associated with canine depth and a shorter premolar region relative to the molar slicing and grinding area (which is usually absent or very reduced). On the second RW corpus changes are relative to diastema region, premolar row and slicing/grinding area (Fig. 4.14).

Interestingly, on RW1-2 plot extinct species are grouped as predicted: *H. crenatidens* and *M. cultridens* occupy the extreme threshold of Meat-L felids together with one outlier (isolated black dot on negative scores of RW1) of *N. nebulosa*, Pleistocene lion is at the extreme threshold as well, thus suggesting a different corpus shape from its extant relative while such difference does not occur for the leopard; one specimens of Pleistocene lynx (probably *Lynx lynx*) is grouped in Meat-L as well like modern eurasiatic form while *L. issiodorensis* is in the threshold area were thrre prey categories sometimes overlap; *P. gombaszoegensis* is definitely a Meat-L and *A. pardinensis* a Meat-m as the extant cheetah.

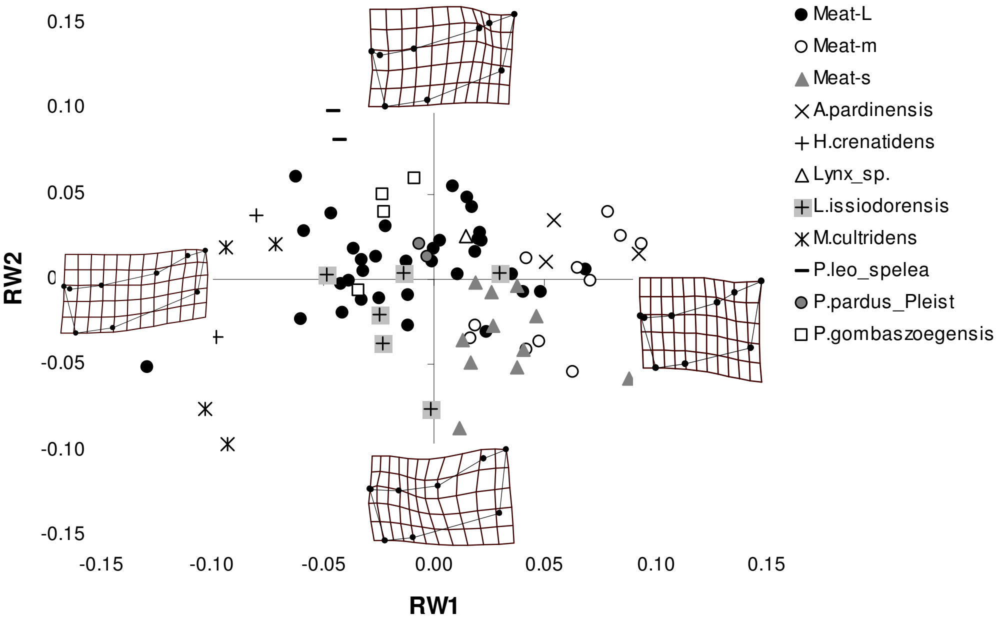


Figure 4.14: Plot of the first and second RW in a subset of 81 specimens of felids.

A discriminant analysis was performed on all felid corpus shape data. Two significant functions are extracted and both of theme are significant (Table 4.11).

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 2	.112	104.162	28	<.0001
2	.521	30.940	13	.003

Table 4.11: Statics of two discriminant function extracted from felid corpus shape data.

On both functions centroids of groups are well separated even if some overlap occurs in all the categories (Fig. 4.15). The category of Meat-L is predicted with a high percentage of correct classifications also in a cross-validated analysis while Meat-s is correctly classified in half cases. Predicted groups agree with previous palaeoecological investigation especially for large cats: *M. cultridens*, *P. gombaszoegensis* and both Pleistocene lion and leopard are classified as Meat-L.

Both fossils of *H. crenatidens* are classified as Meat-m but they represent clear outliers (two crosses on negative scores of Function 2 in Fig. 4.15) in this analysis. Two specimens of *A. pardinensis* are considered Meat-m while one is misclassified as Meat-s. The Pleistocene *Lynx* sp. is classified as Meat-m while the majority of *L. issiodorensis* are classified as Meat-L even if one is considered Meat-m and another Meat-s.

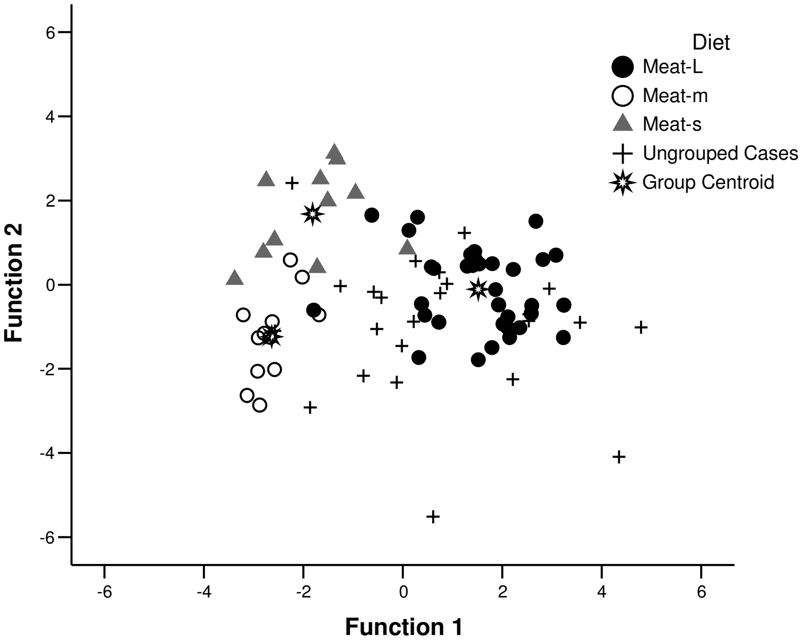


Figure 4.15: Plot of the first and second Discriminant Functions in a subset of 81 mandible of large felids.

	Diet	**Predicted Group Membership**			**Total**
		Meat-L	Meat-m	Meat-s	
Count	Meat-L	32	1	1	34
	Meat-m	0	10	2	12
	Meat-s	1	1	9	11
	Ungrouped cases	16	6	2	24
%	Meat-L	94.12	2.94	2.94	100.00
	Meat-m	0.00	83.33	16.67	100.00
	Meat-s	9.09	9.09	81.82	100.00
	Ungrouped	66.67	25.00	8.33	100.00
Count	Meat-L	29	2	3	34
	Meat-m	0	8	4	12
	Meat-s	1	4	6	11
%	Meat-L	85.29	5.88	8.82	100.00
	Meat-m	0.00	66.67	33.33	100.00
	Meat-s	9.09	36.36	54.55	100.00

Table 4.12: Count and percentage of correctly classified cases before (up) and after (down) leave one out cross validation.

An UPGMA analysis performed on species consensus agrees with several phylogenetic and palaeoecological hypotheses (Fig. 4.16). The large cats are well characterised with both extinct saber and dirk toothed cats clustering together. The Pleistocene lion is quite distinctive while *P. gombaszoegensis* cluster with the jaguar as expected. *A. pardinensis* and the extant cheetah share a distinctive corpus morphology as well.

The group of extant lynx form a separate cluster but unexpectedly the Pleistocene specimens is grouped with Pleistocene leopard-puma group like *L. issiodorensis* which clusters with the leopard.

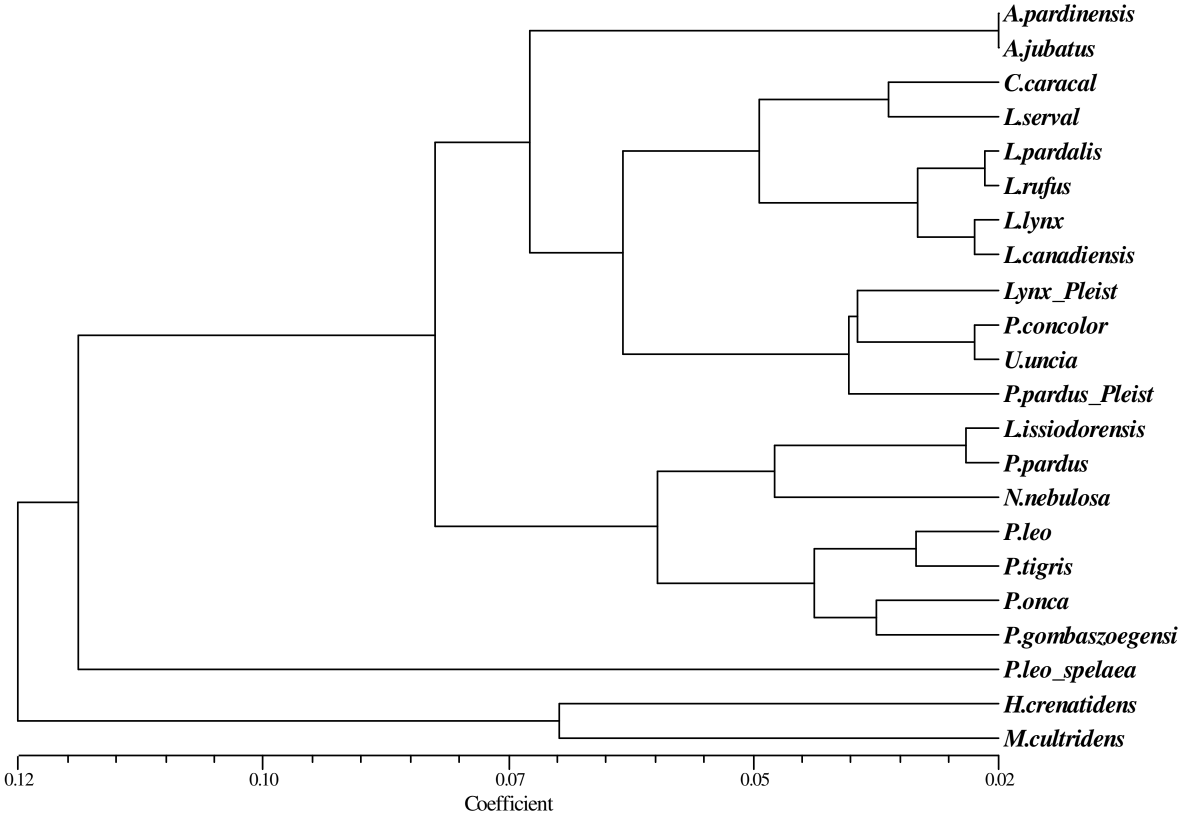


Figure 4.16: UPGMA cluster tree on felids corpus shape data.

4.5 Discussion

Mandible shape data appear to be useful in defining feeding adaptation in extant carnivores and predicting feeding habits of Plio-Pleistocene forms. The statistical analyses define always significant differences among dietary categories of extant large carnivores even if some predictions are misleading especially when applied to multiple specimens of the same extinct species. This fact urges some caution in the interpretation of mandible shape data in extinct forms but several generalisation can be extrapolated.

Firstly, the mandible shape analysis is highly informative when most of the mandible is included in the landmark configuration. The predictive power of the obtained discriminant functions is higher and the results for Plio-Pleistocene species are reliable. This fact has been already tested in Chapter 2 with a different sample of extant carnivores and it applies also when only large (> 7 kg) species are investigated. It is worth noting that complete mandible shape analysis allows also to define several unique morphologies (e.g. saber-tooth cats) by exploring the combination of different RWs axes (see Figures 4.1-2). Most interestingly, such unique forms are predicted in reliable feeding categories as expected by previous observations. In this regard, both the saber and dirk toothed cats are considered Meat eaters specialised on large prey (Tuner and Antón 1997; Palmqvist et al. 2007). Unfortunately, the used diet categories do not include scavenging (or bone crushing) as a particular specialisation and, as a consequence, the highly specialised *Pliocrocuta perrieri* (for which complete mandible was available) is considered as a member of Meat-L category. Although such category is misleading, it allows at least to define the prey mass range of extinct predators.

The omnivore or herbivore specialisation is well defined in early members of Ursinae as well as in highly specialised cave bear. The polar bear is misclassified (from Meat-L to Omnivore) and this fact does not allow to define with precision adaptation to carnivory from complete mandible shape of bears. Sacco and Van Valkenburgh (2004) mentioned several ecomorphological traits of carnivorous bears that are quite unexpected (e.g. the short carnassial blade) while Christiansen (2007) recently suggests that the bite force of the polar bear is similar to that one of omnivore forms because of its short-lived differentiation. This fact suggests that it is difficult to extrapolate appropriate adaptation to carnivory from skull morphology in modern Ursinae and as consequence lower jaw shape data can only validate extreme herbivory (as in the giant panda).

Complete mandible data appears informative for most of canids as well: *C. etruscus* specialised on Meat of large prey, like *Lycaon falconeri* while *N. megamastoides* has been identified as omnivore. All these results agree with general palaeoecological estimation but how can we interpret the misclassification of *Canis arnensis* or *Lynx issiodorensis*?

It seems likely that multiple specimens of the same species incorporate a high morphological variability that in some Plio-Pleistocene carnivores can be interpreted as an adaptation to a generalised diet. The classification functions are good predictors but it is worth noting that a unique shape combination in the mandible of large carnivores is plausible during the evolutionary history of some species. Consequently, forms like the giant cheetah (*Acinonyx pardinensis*) are easily interpreted because of their striking shape similarities in morphology with its extant counterpart (*A. jubatus*). On the other hand *C. arnensis* has an enigmatic evolutionary history -it is considered a coyote like dog but also the possible ancestor of wolf in the Mediterranean area (Kurtén 1974; Rook

1993)- and *L. issiodorensis* has a unique morphological combination in the mandible with a stronger lower jaw morphology than that observed in extant lynxes (Kurtén 1978).

For this reason it is plausible that *C. arnensis* possessed in lower jaw shape a pre-adaptation for feeding on large prey while *L. issiodorensis* was really capable to include larger prey in its diet (compared with the other extant lynx).

The nested analysis on corpus landmark data was performed with the objective of clarifying general misleading obtained for complete lower jaw data. As expected, the corpus shape data perform poorly (compared with complete lower jaw) in identifying appropriate feeding categories for both extant and Plio-Pleistocene large carnivores, even if the scale of the analyses was more accurate (at family level). But several results are informative of particular adaptation of Plio-Pleistocene large carnivores compared with extant form.

For instance, it is evident that the corpus shape of Ursinae (both extant and extinct forms) do highly reflect phylogenetic relatedness. The corpus shape similarity of brown bear and cave bear lineages (Fig. 4.6) is exactly the same expected under a phylogenetic history of the group (see Mazza and Rustioni 1994). Similar striking similarities occur among some felids like *Panthera gombaszoegensis* or *Acinonyx pardinensis* whose corpus shape is highly similar to that of their expected ancestor -the jaguar and the cheetah, respectively (Turner and Antón 1997).

For Canidae and Hyaenidae results of corpus shape data are more enigmatic. In the latter family there is a plausible evolutionary explanation for the unique corpus morphology of Plio-Pleistocene species from the extant form (Figs. 4.11-13). Werdelin and Solounias (1991) and Massetti (2007) already underlined an increasing in bone cracking ability through time with the higher specialization achieved by both genus *Pliocrocuta* and *Pachycrocuta* together with the extant hyenas (except the aardwolf). The positive relationship between mandibular corpus thickness and size of the structure support such mechanism of increasing bone-cracking as a by-product of increasing size (Fig. 4.12). The running hyena *Chasmaporthetes* was probably less specialised in bone-cracking but already exhibits such adaptation (Kurtén and Werdelin 1988; Ferretti 2007).

In Canidae, the corpus shape similarities are quite misleading for large dogs and several diet classification of extinct specimens (e.g. *Lycaon falconeri*) are not congruent with the expected pattern. There are various reasons to explain such imprecise results of corpus shape data and most of these arguments are applicable also for other cases. Firstly, the “apparent shape convergence” (see Chapter 1) can be considered for some misleading similarities. For instance, the similarity of corpus shape of *L. falconeri* with the omnivore smaller dogs (the South American *Cerdocyon thous* and the black backed jackal) may represent a case of similar adaptation to different kind of food (the meat in extinct *Lycaon* and hard food in smaller dogs). In such interpretation there is also an evolutionary argument concerning the fact that probably *L. falconeri* did not developed a powerful mandibular corpus like modern African wild dog and, as consequence, was not so specialised in meat eating and bone crushing with lower molars. Most interestingly, the landmark configuration can be misleading itself especially in Caniforms (and such argument is plausible also for large bears too). The premolar-molar rows are useful traits to discriminate families (Fig. 4.1 cfr. Crusafont-Pairó and Truyols Santonja 1957) but they are also effected by some developmental process. In particular, canids may develop (or not) the third lower molar. In the case of modern *Lycaon pictus* the third molar develops in the curved threshold between corpus and ascending ramus as the result of withstanding high stress in the mastication. The specimens of *L. falconeri* analysed possess the m3 but this tooth develops more anteriorly and in a less curved portion of the mandibular corpus.

This same argument can be applied for bears whose premolar row is, in some istances, difficult to identify because of the presence of a vestigial p1 followed by a large diastema since p4. Such trait is probably a characteristic of modern Ursinae and appeared iteratively in the evolution of *Ursus* spp. since *U. etruscus.*

Anyway, in spite of some imprecise results most of palaeoecological data have been confirmed and new results emerged from all lower jaw shape analyses. For each family there is a statistical bias that can be controlled and interpreted if we consider the biological meaning of the applied landmark configuration together with several shape phenomena which occurred also in previous controlled surveys (e.g. Chapter 1).

In family Ursidae the mandible shape is indicative of an extreme herbivory adaptation of *U. spelaeus* (cfr. Stiner et al. 1998) and a close similarity of such form with the Galerian Deninger's bear. The Pleistocene brown bear does not differ significantly in mandible shape from extant forms while new results were obtained for the Villafranchian *U. minimus* and *U. etruscus.* The first is more adapted to a tropical environment with an omnivorous diet, while the second achieves mandible shape similar to the brown-polar bears being generalist feeder (probably omnivore with some preference to meat).

Among Canidae, the extinct *Canis etruscus* can be considered a dog adapted in meat eating with preference for large prey. Such result contrast with previous observations made on Spanish fossil material (Palmqvist et al. 1999, 2003) but it confirms the close morphological similarities between this form and the modern grey wolf (Torre 1967, Rook 1993). *Lycaon falconeri* is a specialised meat eater of large prey (cfr Palmqvist et al. 1999, 2003) even if its corpus shape suggests that its morphological differentiation was not high (hence less specialised in bone crushing) as in the extant African wild dog to which it is phylogenetically related (Martínez Navarro and Rook 2003).

The Arno dog *C. arnensis* possesses a lower jaw primarily adapted for chewing meat of small-medium sized prey. It is plausible that this dog was an opportunistic feeder like most medium sized canids (e.g. coyote). The enigmatic fossils from Grotta Romanelli probably belong to Aurelian grey wolf and (even if it could be plausible that they belong to an advanced form of *C. arnensis*) they belong to a meat eater of large ungulates.

In family Hyaenidae, it has been confirmed an high adaptation to bone cracking of extinct Plio-Pleistocene hyenas with the exception of *C. lunensis*. The extinct European spotted hyena could achieve stronger specialisation in bone cracking by virtue of its larger body mass as it is likely for *P. perrieri* and *P. brevirostris.*

For felids, it has been confirmed the strong morpho-ecological similarity of the specialised speeder *Acinonyx pardinensis* with the extant cheetah adapted in eating medium sized prey (Turner and Antón 1997), like also the affinity of *P. gombaszoegensis* with *P. onca*. Both *Homotherium crenatidens* and *Meganteron cultridens* have a unique mandible shape that allow them to feed on large ungulates. The Etouaire lynx (*L. issiodorensis*) was probably specialised in hunting small-medium sized prey although its lower jaw is stronger than modern lynxes suggesting an adaptation in the mastication to bone crushing of small lagomorphs and rodent bones. It is likely that such lynx was also capable to kill occasionally medium sized ungulates. The Pleistocene mandible specimen of *Lynx* sp. does not cluster with extant European lynx suggesting stronger adaptation in mastication. It is likely that such specimen belongs to a large individual of *Lynx spelea*.

The European Pleistocene leopard and lion are both considered predators of large ungulates on the basis of their lower jaw shape like their modern counterpart although their corpus shape is slightly different being probably an artefact of their different size.

It is worth noting that the mandible shape variability of Plio-Pleistocene carnivores (excluding the extinct saber and dirk toothed cats) is similar to that observed in extant forms. This suggests that Plio-Pleistocene represents a period of morphological innovation toward the modern fauna variability. Such question is discussed in detail in the next section.

Chapter 5

Mandible shape disparity in Plio-Pleistocene large carnivore guilds

5.1 Introduction

The structure of morphological variability in organisms through space and time received particular attention especially on the light of its potential relationship with taxonomic diversity (Foote 1997).

Large carnivorous mammals have been intensively studied in such aspect 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 trophic apparatus (as defined by cranio-dental features) has been intensively investigated and it is clear that such a structure 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 generalisation is probably applicable to different contexts other than the American fossil record and all 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 of years. But, in the history of carnivores and mammalian communities in general, there are interesting taxonomic changes which occurred in relation to much severe geological changes over shorter time periods. The Plio-Pleistocene can be certainly considered such a period. Evidence points to unprecedented climate changes occurring worldwide (Zachos et al. 2001) and a remarkable mammalian fauna seems to be influenced by such changes (Kurtén 1968; Augustì and Antón 2002; Lister 2004). The most important experiment that occurred in the last part of Plio-Pleistocene is also represented by the invasion of mammalian community of a biped hunter –man- whose rule in the extinction of some species still to be enigmatic (Alroy 2001; Cardillo and Lister 2002; Barnosky et al. 2004; Wroe et al. 2005b).

Large carnivores were certainly 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 partly related with the disappearance of large ungulates (Turner and Antón 1997) but it is not clear to what extent such 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 taxonomical diversity of large carnivores.

The European fossil record is of particular interest especially for the Plio-Pleistocene because there is a very good mammalian bio-chronology (Azzaroli et al. 1983; 1988) and also because some large carnivores defined particular faunal "events" which represent significant changes in faunal composition. Among the others, the *Wolf event* (c.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 considered more adapted to open environments (Rook and Torre 1996). Because of such 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 Plio-Pleistocene.

A significant effect was already determined on the entire large mammal community from Italy where climate change during Plio-Pleistocene affects the turnover rates of species: that is a taxonomic evolutionary process (Raia et al. 2005). But on the same fossil record Meloro (2004) found a non-significant change of species diversity toward Plio-Pleistocene. The number of species in each period of all groups of large mammals (including carnivores) are more affected by sample bias other than truly environmental changes.

It is worth noting that Italian peninsula represents a special biogeographic case as compared with other European Plio-Pleistocene regions. The rate of large mammal endemisms is particularly low (excluding islands, Kotsakis et al. 2002) and for several carnivores Italy could probably represent an Ice Age refugium (e.g. *Panthera gombaszoegensis* O'Regan et al. 2002). The rule of humans is also enigmatic in Italy because, recently, there is evidence of early occupation since Pirro FU (1.5 – 1.1 Ma) (Arzarello et al. 2007) even if the evident impact of *Homo* on local fauna is recorded only at Isernia - 600/500 ka - (Anconetani and Peretto 1996; Coltorti et al. 2005).

Application of geometric morphometrics to the fossil lower jaw representative of the Italian large carnivore fauna (see Chapter 3) represents an opportunity to explore the evolution of morphological variability through Plio-Pleistocene. It is also possible to delight mechanisms that drove guild compositional changes by comparing Plio-Pleistocene with extant carnivore guilds (cfr. Van Valkenburgh 1988). The metric of comparison is, here, represented by morphological disparity (Foote 1992). Such metric is ideal to quantify the morphological variability –variance, max and min range- especially with a multivariate dataset. Usually, disparity is applied to principal components scores with several formula (Ciampaglio et al. 2001) that allow to compute the amount of morpho-space occupied by the sample of interest in a broad context. Most of the literature is concentrated on macroevolutionary studies in the context of interspecific (or higher taxonomic units) variability within an order (Foote 1992, 1993; Wills et al. 1994; Foote 1997 for review) even if Van

Valkenburgh (1988, 1989) already performed several analyses on carnivore guild variability through space and time.

This study has the same spirit as Van Valkenburgh's surveys (1988, 1989) but here I will look at lower jaw shape variability through geometric morphometrics and the Procustes Distances (PD) metric will be used to compute disparity (Zelditch et al. 2004). Such approach allows to obtain conservative estimates of the shape disparity which can be used for comparison among guilds.

5.2 Materials and Methods

5.2.1 Samples

Geometric morphometrics is here applied to a subset of 2D pictures of lower jaws of both extant and extinct large carnivorous mammals (Appendix 3). In order to take into account the incompleteness of the fossil record shape data were extracted on a sample of both extant and extinct mandibles only from the mandibular corpus. Although such region is less informative of feeding habits than the entire lower jaw (see Chapter 2) it allows to include more fossil specimens that for some species are the only available (e.g. *Chasmaporthetes lunensis*).

For each species I have used one specimen assuming that intraspecific variability is not a determinant factor in the interspecific morphospace comparison. A subset of 34 species of extant carnivores was chosen according to the taxonomic list (source MAB database) of the most representative large carnivore guilds in the world (for Europe 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 (cfr. Van Valkenburgh 1988). Amphibious and aquatic carnivores were excluded from the analysis. For the Plio-Pleistocene guilds a total of 23 species of large carnivores were chosen as representatives of nine Italian Paleo-Communities (PCOMs): Triversa, Montopoli, Up Valdarno, ValdiChiana, Pirro, Galerian 1, 2, 3 and Aurelian (as in Raia et al. 2005; 2006a).

Each species was represented in the overall sample by one mandible even if the species belong to several guilds. For the extant guilds only the Puma (*Puma concolor*) is represented in two guilds (USA and Peru) as well as the grey wolf and the brown bear (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 a high degree of overlap among specimens that 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* present continuously from PCOMs Triversa to Pirro). Unfortunately, it was not possible to collect significant specimens for the same species in each PCOM. It is worth mentioning that even in considering only the corpus region, the lower jaws of large carnivores are usually rare, especially for Villafranchian species.

When available Italian fossil specimens were chosen as representatives of Plio-Pleistocene species. For Pleistocene species I chose fossil specimens even if the species could be present in extant ecosystem according with previous observations on corpus shape (e.g. Pleistocene lion see Chapter 3). Because of the availability of the fossil record some species were replaced by other similar morphotypes of the same lineage, assuming that no significant differences may occur for an inter-specific analysis. This happens for both Pleistocene saber-tooth and dirk toothed cats. It was not possible to obtain 2D pictures of *H. latidens* and the form *M. whitei* that were substituted by their ancestors (*H. crenatidens* and *M. cultridens*) for which mandibles were available. There are no significant fossil of *Chasmaporthetes lunensis* for the lower jaw that was substituted by an incomplete mandible of *Chasmaporthetes kani*. The little Pleistocene wolf of the Galerian (*Canis* aff. *arnensis*) is represented by a specimen of the Valdarno basin because of the lack of mandibles complete enough for gmm analysis. Aurelian canids are, here, represented only by the *Canis* sp. from Grotta Romanelli which probably belong to the grey wolf and 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 (see Introduction) the fossil record is scanty for such forms and at list the specimens from Grotta Romanelli were complete enough to perform the analyses.

5.2.2 Morphospace comparisons

Nine landmark were chosen as representative of the mandibular corpus shape (see Chapter 2).

GPA was performed on the total sample of 57 large carnivores (both extant and extinct together) according to the previously presented procedures (see procedure in Chapter 1). The morphospace of the overall sample was explored through a Principal Component analysis while morphospace comparison for each guild was assessed by computing disparity values (Foote 1992, 1993). Basically, disparity is a measure of morphological variability.

The formula of Foote (1993) for disparity is:

$$D = \Sigma (d_i^2)/(N-1)$$

where d_i represents the distance of the ith individual (specimen) to the group centroid while N is the number of individuals in the group considered. Zelditch et al. (2004) readapted this formula to gmm data, where the individual distances are represented by the squared Procustes distance of each specimen to the group consensus (centroid). Then d_i is substituted by PW_j the Partial Warp scores. The application of a bootstrap procedure (in Zelditch et al. 2004) allows also to obtain 95%

confidence intervals around disparity values which can be used to perform comparisons among groups.

In this case, groups are firstly defined in order to compare extant and Plio-Pleistocene carnivores. Consequently, disparity values were computed separately for extant (34 species) and fossil specimens (23). For a finer scale analysis groups are defined as each guild (in space and time). 14 guilds (9 from Plio-Pleistocene PCOMs and 5 from extant ecosystems) are defined.

Patterns of potential covariation between disparity values and other variables were explored by using non parametric spearman correlation. The number of carnivores composing each guild (sample size bias), the number of prey were considered as potential mechanisms which affects disparity variability through space and time. The absolute values were log transformed (cfr. Wesley Hunt 2005).

A nearest neighbour analysis was performed as well on each defined group in order to test hypothesis about clustering or overdispersion of species lower jaw shape distribution in the morphospace (Zelditch et al. 2004). The morphospace occupied by each group is compared with all the possible morphospaces generated under a random simulation. The random simulation (with a Monte Carlo procedure) was performed by taking into account the Uniform model which consider equal the probability of being in any location of the morphospace. The P_i metric ideated by Foote was used to perform such comparison 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-neighboor 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 than 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 overdispersed. A range of 95% of confidence intervals was computed around P_i by simulating Monte Carlo 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). Such procedure allows to compute the "true" minimum and maximum values of the neighrest-neighboor normal distribution. All the analyses were performed with and without such correction in order to evidences some discrepancies (Zelditch et al. 2004).

5.3 Results

Fourteen shape variables were extracted under a GPA model and then reduced with a Relative Warp analysis. The first four RWs explains more than 95% of the shape variability (Table 5.1).

	SV	%	Cum %
RW1	0.89606	45.72%	45.72%
RW2	0.82243	38.52%	84.24%
RW3	0.40577	9.38%	93.62%
RW4	0.18812	2.02%	95.63%
RW5	0.16832	1.61%	97.24%
RW6	0.13929	1.10%	98.35%
RW7	0.1004	0.57%	98.92%
RW8	0.08213	0.38%	99.31%
RW9	0.07191	0.29%	99.60%
RW10	0.06423	0.23%	99.84%
RW11	0.04956	0.14%	99.98%
RW12	0.01552	0.01%	99.99%
RW13	0.00928	0.00%	100.00%
RW14	0.00867	0.00%	100.00%

Table 5.1: Variance explained by each RW on sample of 57 mandibles with 9 landmarks.

According to previous observations (see Chapter 1-3) the first two RW axes allow to discriminate specimens on the basis of their familial affiliation (Fig. 5.1). The RW1 is here related with shape changes in molar crushing area lengthening relative to slicing. On the second RW shape changes are driven by the relative corpus thickness as well as diastema and premolar length proportion. Some overlap occurs between Felidae and Hyaenidae because their short or non-existent crushing molar area (see Chapter 3). All the Caniforms (Canidae, Ursidae and Mustelidae) occupy the first and the second quadrants except *Mellivora capensis* which is an outlier among the mustelids because the specimen available had only one molar (hence the proportion slicing/crushing area is shorter compared with the others).

Interestingly, the variability of extant large carnivores is similar to that of Plio-Pleistocene species (Fig. 5.2). Among Feliforms, the fossil forms appear to achieve more extreme morphologies (IV quadrant with negative RW1 scores) and this is justified by the presence of saber-tooth cats as well as extinct specialised hyenas. Among Caniforms the extinct bears appears instead less specialised in corpus shape than extant forms (quadrant I with positive scores of RW1 and 2).

The third RW is associated with changes of canine-premolar row (length of the diastema) and its combination with the first or the second is not significantly informative on phylogenetic or ecological grouping (Fig. 5.3).

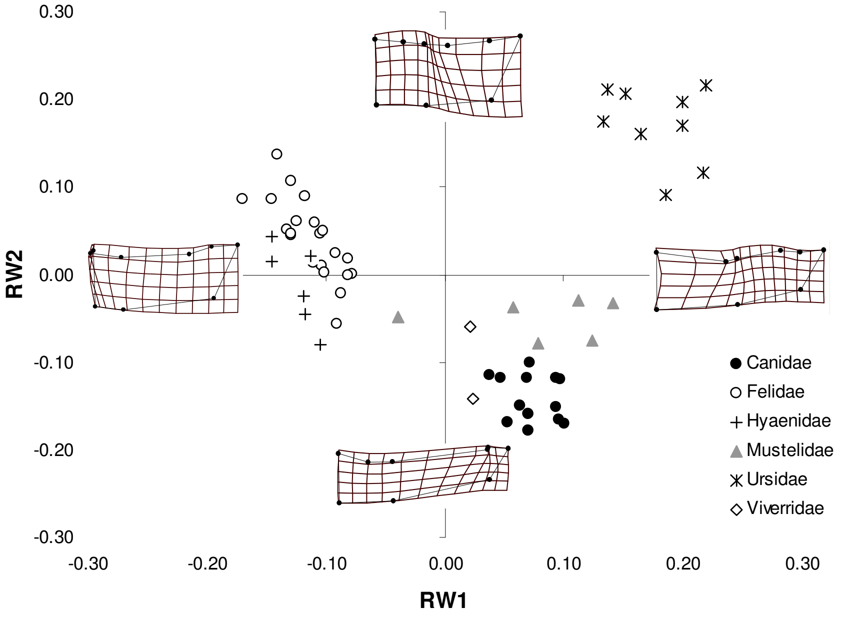


Figure 5.1: Plot of the first and second RW in a subset of 57 mandibular corpus data of large carnivores.

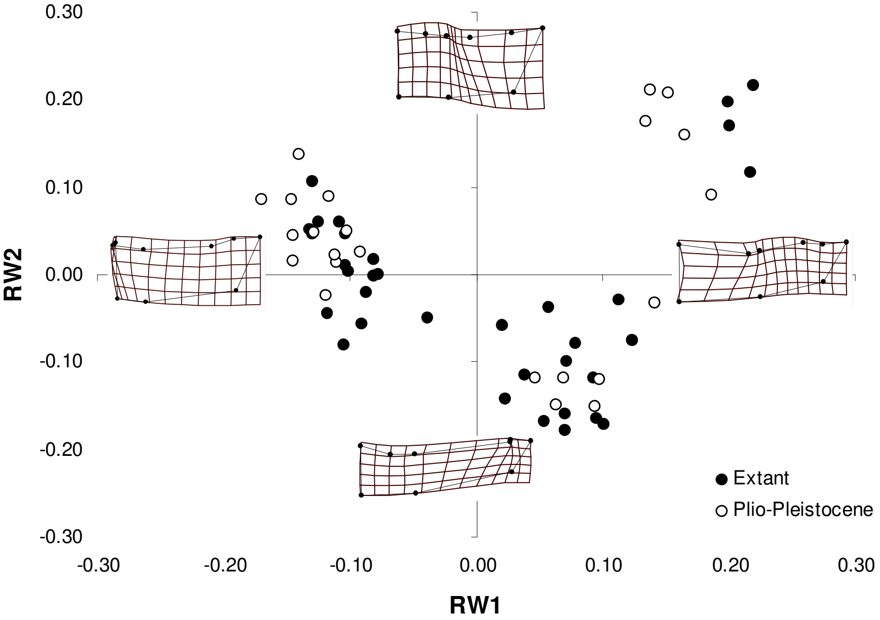


Figure 5.2: Same plot of fig. 1 evidencing differences in morphospace of extant and extinct carnivores.

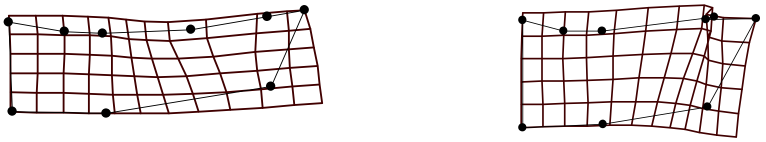


Figure 5.3: Corpus shape deformations associated with negative (left) and positive (right) scores of RW3.

When all grouping of large carnivore guilds are considered in the representation of the morphospace defined by RW1 and 2 several overlaps occur among extant guilds even if the morphospace of African large carnivore guild is quite distinctive (Fig. 5.4). This ecosystem in fact lacks any bear-like morphotype (which occupies the I quadrant) but such phenomenon is compensated by a greater number of other caniforms and feliforms. Plio-Pleistocene guilds overlap as well and similar patterns of morphospace occupation emerge graphically (Fig. 5.5).

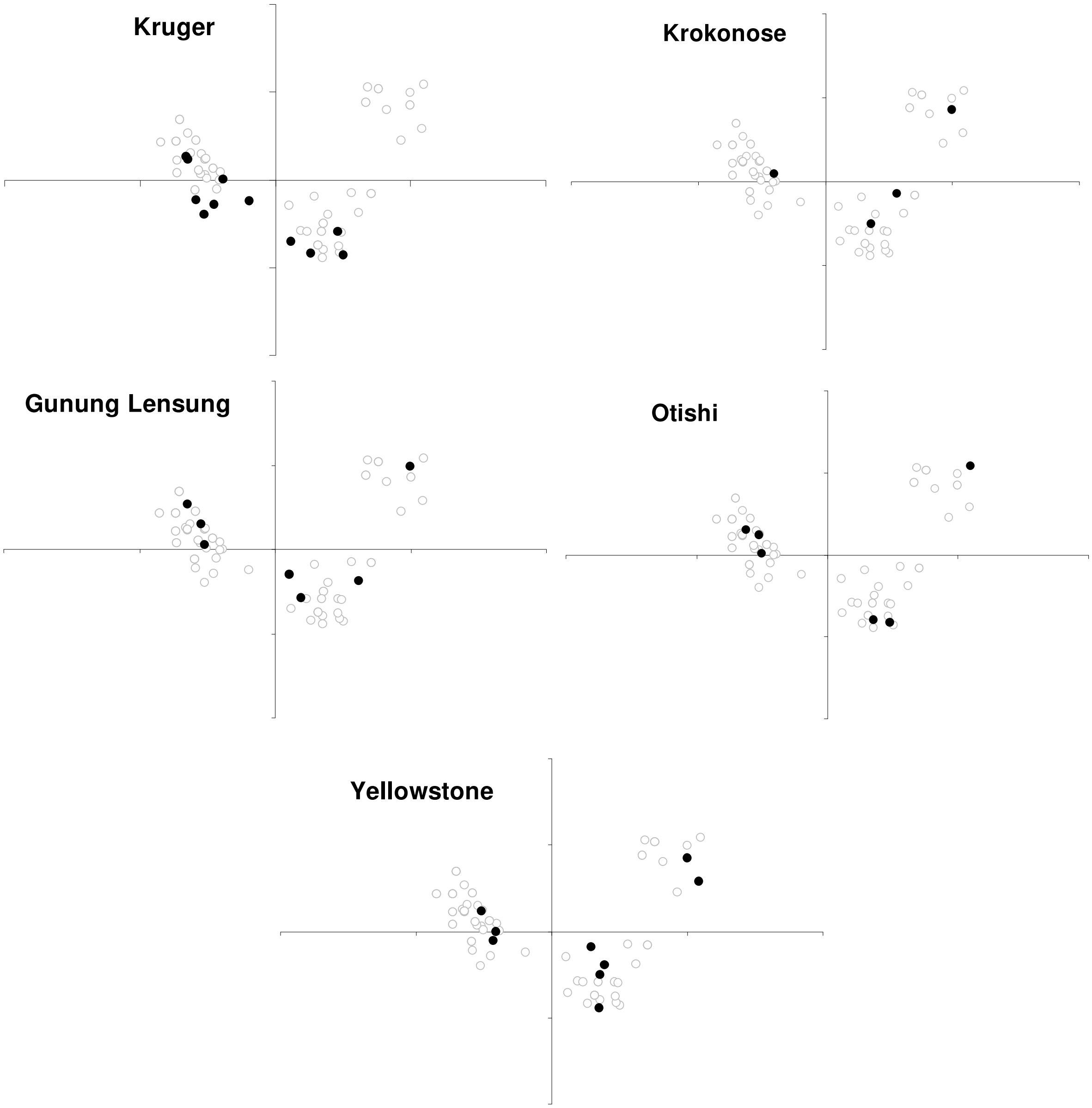
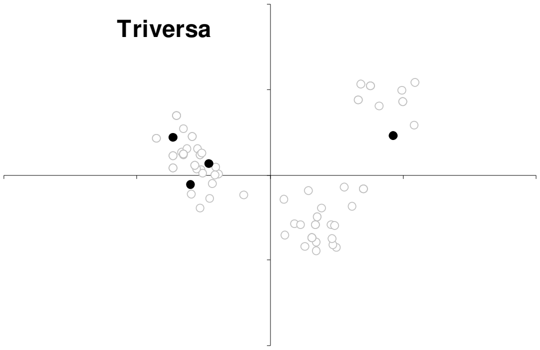
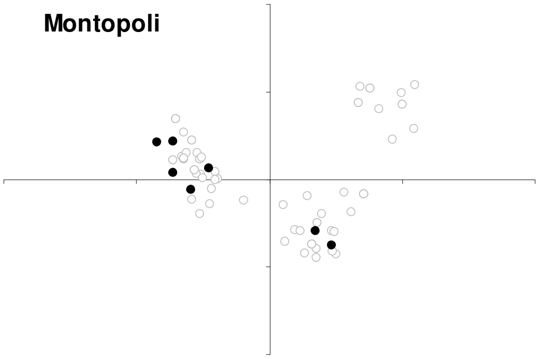
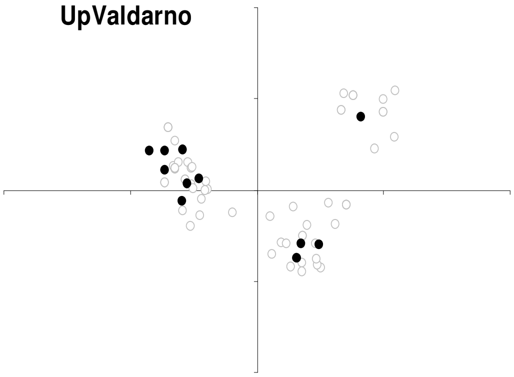
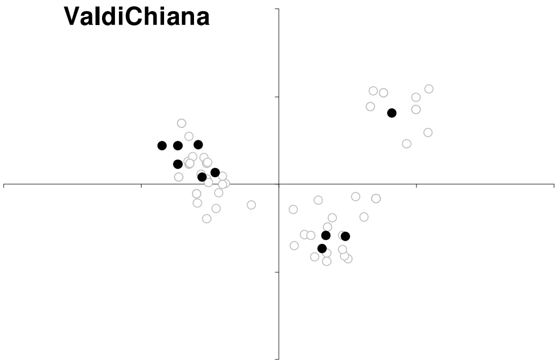


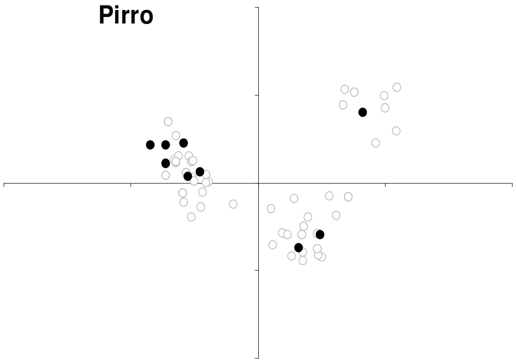
Figure 5.4: Morphospace of each extant large carnivore guild. X axis RW1 (scale -0.40 / +0.40). Y axis RW2 (scale -0.40 / +0.40).

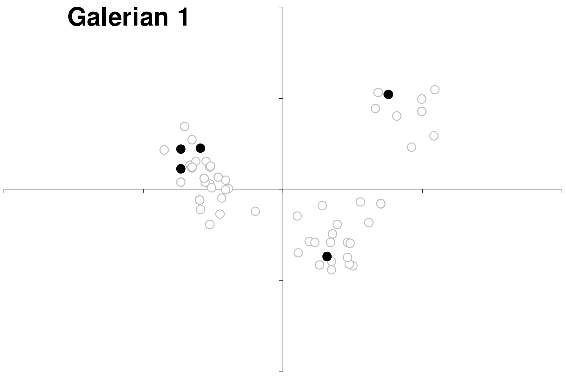

Triversa

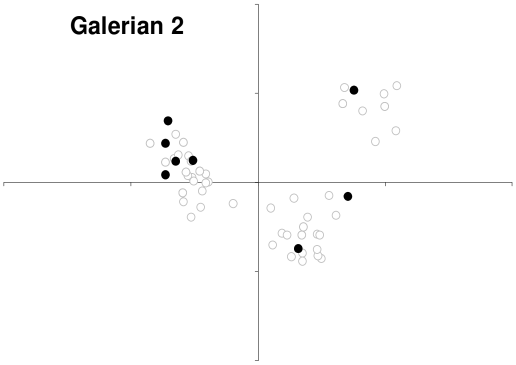

Montopoli

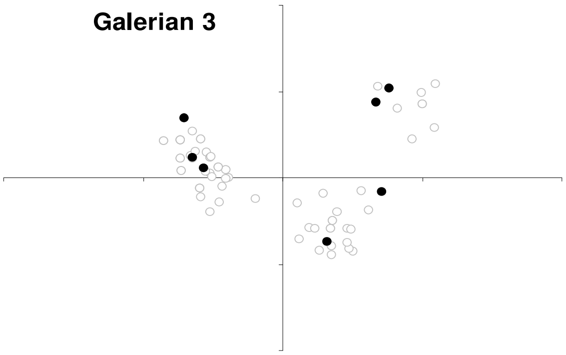

UpValdarno


ValdiChiana


Pirro


Galerian 1


Galerian 2


Galerian 3

continue ⟶

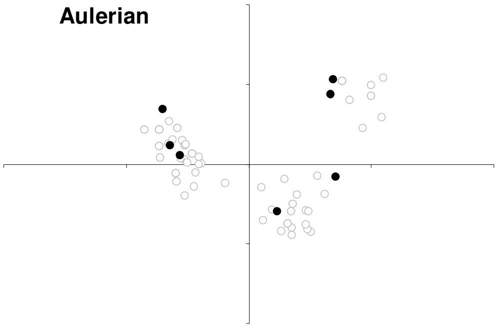


Figure 5.5: Morphospace of each Plio-Pleistocene large carnivore guild. X axis RW1 (scale -0.40 / +0.40). Y axis RW2 (scale -0.40 / +0.40).

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 such trend is not significant because 95% confidence intervals overlap (Fig. 5.6).

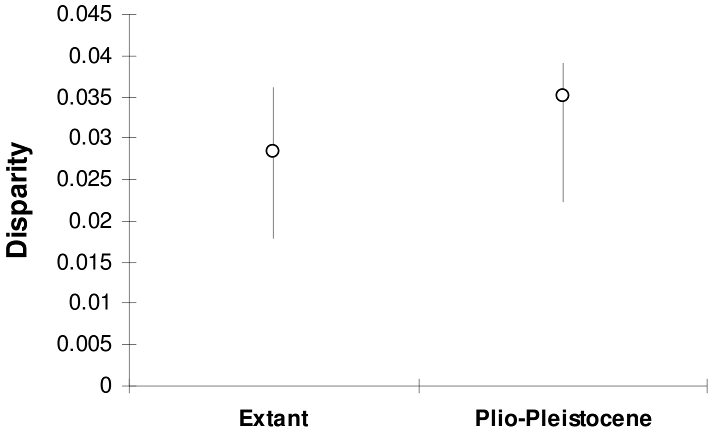


Figure 5.6: Disparity values computed for morphospace of extant (n = 34) and Plio-Pleistocene large carnivores (n = 22). Lines define 95% confidence interval under 999 randomizations.

When disparity values are computed for each large carnivore guild the overlap in morphospace variability still occurs (Fig. 5.7). Such pattern clearly demonstrates that in spite of the presence of unique morphotypes in extinct large carnivores, the morphospace occupation is similar to that of extant species. Interestingly, no significant differences occur among extant guilds as well hence biogeographical phenomena seem not to have affected morphological variability (at least in corpus shape) of large carnivorous mammals.

A pairwise distance matrix of absolute values of differences in disparity evidences morphospace similarities performing an UPGMA clustering tree (Fig. 5.8). Again, the African large carnivore guild is more dissimilar from the other guilds because of its low disparity value. This result supports previous empirical observation that African large carnivores occupy less morphospace (yet not significantly different) than other ecosystems.

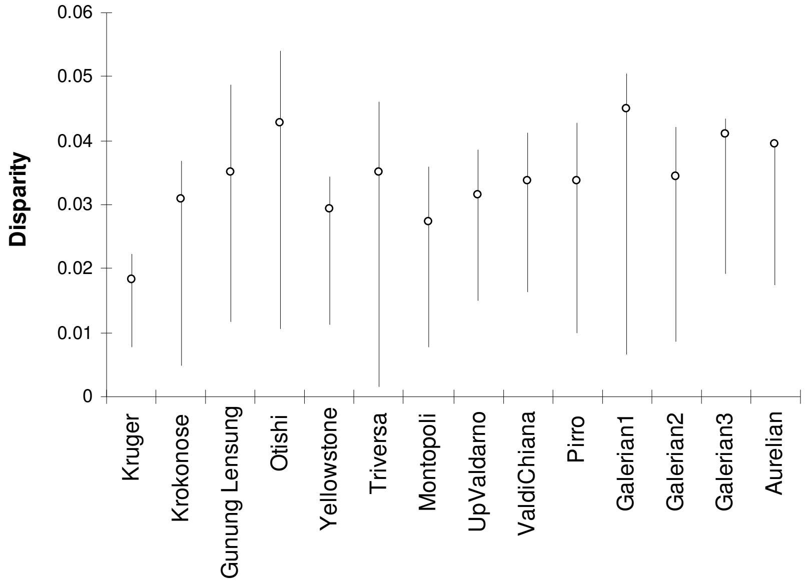


Figure 5.7: Disparity values computed for morphospace of each extant and Pli-Pleistocene large carnivore guild. Lines define 95% confidence interval under 999 randomizations.

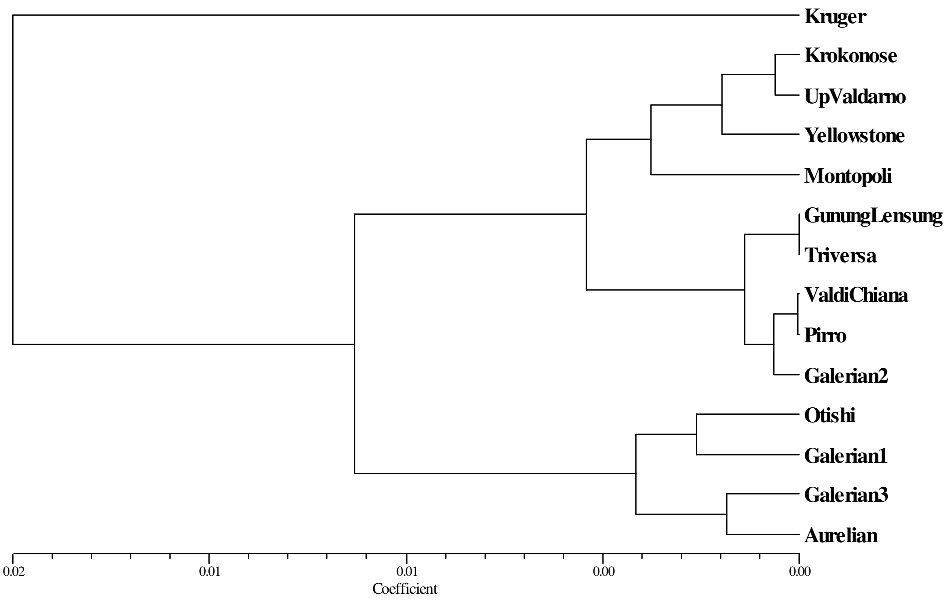


Figure 5.8: UPGMA cluster performed on absolute values of disparity pairwise differences among guilds.

Interestingly, the Triversa large carnivore guild exhibits similar corpus shape variability of an Asiatic ecosystem which is representative of a tropical warm environment.

Galerian 2 (a period of cold-warm glacial alternation) cluster with Pirro and ValdiChiana. Such result is unexpected because ValdiChina and Pirro represent relict faunas of the end of Villafranchian and should cluster with UpValdarno. But in a certain way this similarity reflects intermediate period of faunal changes. In fact, Galerian 2 is a Palaeo Community that represents a transitional phase of a changing fauna: large herbivores change completely (as compared to Villafranchian forms) while in carnivores some Villafranchian species still survive (like the saber-cat *Homotherium latidens*).

The cluster of the other Galerian PCOMs and the Aurelian together with the Peru carnivore guild is unexpected as this latter guild is representative of a complex mixed mountain ecosystem with several habitats (mountain forests to tropical wet forest). It is clear that in this case the morphospace occupation is not related with changes in habitat and environment. But it is interesting to note that the last Italian Ice Age carnivores were quite different in corpus shape variability from the present temperate ecosystems.

On the other hand, the Villafranchian guilds of Montopoli and Upper Valdarno exhibit disparity values similar to the temperate European and North American guild. This basically means that shape differentiation of extant carnivores was already achieved during Plio-Pleistocene.

Such pattern is not unexpected because Van Valkenburgh (1988) already achieves similar results by analysing morphological differentiation of large carnivore guild all over the Cenozoic. By the way, it is not clear what could drive disparity values which still to exhibit small changes. Such small changes in disparity values may be related with sample size but non parametric correlation between Log n species/ guild and disparity values is not significant (N = 12; p = 0.101) even if a negative trend is likely (Fig. 5.9).

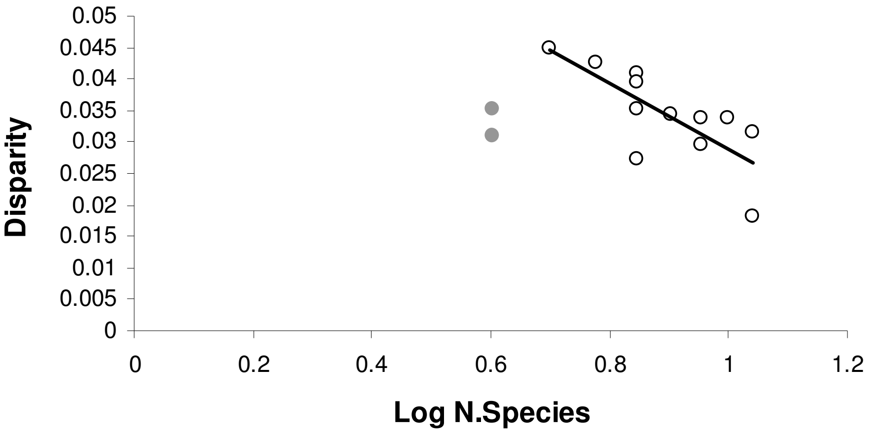


Figure 5.9: Scatter plot of Log. N of large carnivores vs disparity values computed by their guild.

Such trend become significant when two outliers (the guilds from Europe and Triversa PCOM with only 4 species) are excluded ($r_s = -0.761$; $p = 0.004$, Fig. 9). This means that corpus shape disparity can be driven by the number of species represented in a guild. This counterintuitive effect could be driven by the resources that large carnivores exploit. As suggested by Van Valkenburgh (1988) morphological variability should be driven by number of prey present in ecosystem but correlation is not significant when both number of artiodactyls and perissodactyls are considered as potential prey in each ecosystem (using log transformed values of n. species Fig. 5.10).

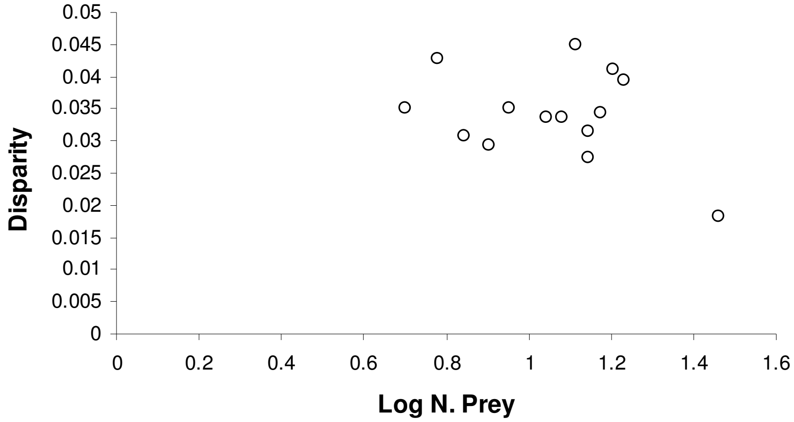


Figure 5.10: Scatter plot of Log. N of prey (=n artiodactyls + n perissodactyls) vs large carnivores disparity values.

But scatter plot suggest a negative trend that , in fact, is significant when only artiodactyls are considered (N = 14; rs = -0.546; p = 0.043; Fig. 5.11).

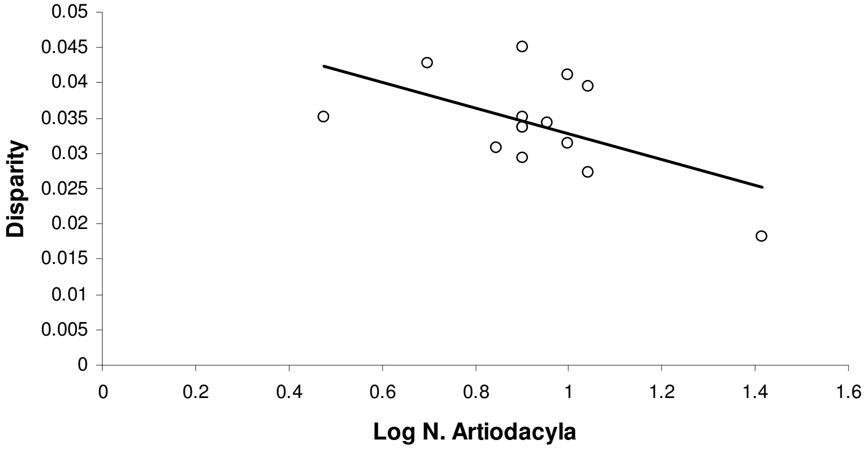


Figure 5.11: Scatter plot of Log. N of artiodactyls vs large carnivore disparity values.

Interesting patterns emerge in the comparison between observed morphospace variability and that expected for a random model.

The morphospace defined by extant carnivores is clustered (Pmean = -0.5895 with range -0.6378 to -0.5340 that is smaller than zero) like that one of Plio-Pleistocene forms (Pmean was -0.4944 with range -0.5507 to -0.4347).

Africa is clustered (Pmean = -0.3307 with range -0.4089 to -0.2310). Europe is overdispersed (Pmean = 0.2650 with range 0.0188 to 0.5436). Indonesia is clustered (Pmean = -0.3391 with range -0.4404 to -0.2219) like Peru (Pmean = -0.4531 with range -0.5248 to -0.3164) and USA as well (Pmean = -0.4661 with range -0.5452 to -0.3777).

For extinct PCOMs Triversa does not differ from random expectation (Pmean = -0.0474 with range -0.1751 to 0.2070); Montopoli is clustered (Pmean = -0.4168 with range -0.4920 to -0.3090) like UpValdarno (Pmean = -0.4114 with range -0.4824 to -0.3316), ValdiChiana (Pmean = -0.3882 with range -0.4600 to -0.2706) and Pirro (Pmean = -0.3685 with range -0.4451 to -0.2601). Galerian 1 is overdispersed (Pmean = 0.1439 with range 0.0190 to 0.3144) but not Galerian 2 that is clustered (Pmean = -0.2203 with range -0.3000 to -0.1020) like Galerian 3 (Pmean = -0.1703 with range -0.2679 to -0.0222). Aurelian is clustered as well (Pmean = -0.2227 with range -0.3311 to -0.0629).

Such results demonstrate that most large carnivore guilds can be considered saturated of morphotypes: they occupy less morphospace than expected by chance. It is worth noting that such results are extracted by using a Sadler-Style range and they are validated when such correction is not considered. Only in the case of overdispersed guilds there are different result that suggest only a morphospace distribution similar to the expected random model (for Europe Pmean = 0.1675 with range -0.0330 to 0.4376; and for Galerian 1 Pmean = 0.0830 with range -0.0540 to 0.2254).

On the other hand some large carnivore guilds are overdispersed or random morphotype assemblages thus meaning that their community structure is –in a certain way- incomplete because of external factors. For instance European large carnivore community is overdispersed if we consider the lack of several large carnivores that at the same latitudes can be present (e.g.: Yellowstone with 9 large carnivores living together). Galerian 1 PalaeoCommunity is overdispersed as well indicating a period of a transitional change in carnivore communities with some elements of the Villafranchian and new incomers of the Galerian (e.g. *U. deningeri*). Triversa PCOM guild exhibits a random morphospace occupation as the result of a guild lacking several typical late Villafranchian elements.

5.4 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 trophic apparatus of large carnivorous mammals was already achieved more than 30 million years ago and it remains constant probably because of competition (as 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 unchanged).

Yet, the small variability of shape disparity exhibits several counterintuitive relationships in need of further explanations. Firstly, it seems that corpus shape disparity is negatively affected by the number of large carnivores in each guild. This sample size effect does not confirm a general pattern already observed in carnivores with different dataset: Wesley-Hunt (2005) found a positive relationship between morphological disparity of skull traits and number of species through the entire Cenozoic.

Interestingly, a difference in time scale does occur between the results presented here and those of Wesley-Hunt (2005). Moreover, the corpus shape analyses mix both temporal and spatial scales (cfr. Van Valkenburgh 1988). When such scales are analysed separately, the negative effect of sample size on corpus disparity is more evident in extant carnivore guilds (Fig. 5.12).

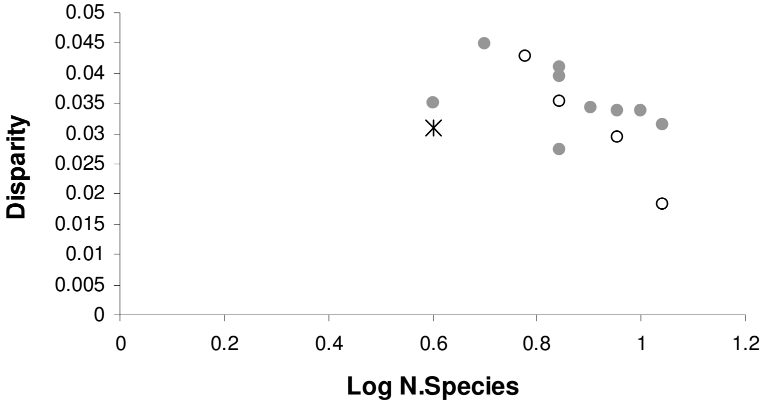


Figure 5.12: Scatter plot of Log. N of large carnivores vs disparity values computed by their guild. White circles extant ecosystems, grey circles Plio-Pleistocene guilds, asterisk Krokonose guild.

The South African carnivore guild comprises the greatest number of species but also the smallest corpus shape disparity while Krokonose European guild is clearly an outlier (cfr. Figs. 5.9, 5.12) exhibiting a small number of species and a small disparity value. The Plio-Pleistocene guilds do not show any trend due to sample size effect (Fig. 5.12) hence meaning that the observed phenomenon cannot be generalised.

Extant guilds are representative of diverse ecosystems whose spatial separation results in different evolutionary history at greater scale than ice age climatic oscillations. Hence the sample size effect is likely to occur as the result of different evolutionary and zoogeographical histories even if most of the disparity studies predict a positive and not negative correlation between disparity and diversity (Foote 1997).

As pointed out by Van Valkenburgh (1988) change in disparity among large carnivore guilds can be related with the number of prey as well. Again the mix of scales (temporal and spatial) can be considered as a possible mechanism for the observed pattern (cfr. 5.11, 5.13).

But again the negative effect of number of artiodactyls is more evident on extant carnivore guilds while Plio-Pleistocene guilds exhibit no trend (Fig. 5.13).

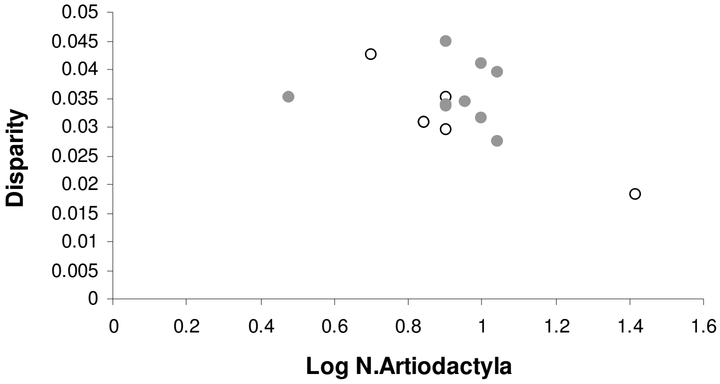


Figure 13: Scatter plot of Log. N of Artiodactyla vs disparity values computed by their guild. White circles extant ecosystems, grey circles Plio-Pleistocene guilds.

Van Valkenburgh (1988) explained the greater morphological richness of tropical carnivore guild as a consequence of a greater productivity of such ecosystems (measured as number of prey) but how the observed inverse trend can be explanained? It is worth mentioning that Van Valkenburgh (1988) didn't test the latter hypothesis only on mandible shape data and she pointed out that the most productive ecosystems (Serengeti and Indonesia cfr. Kruger and Gunung Lensung in the present analysis) have the same number of hypercarnivore predators and are really similar if we exclude the presence or absence of bearlike morphotype. And this latter point is central to explain corpus shape disparity in carnivores.

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 number of large carnivores (respectively 4, 4 and 5) and all of them have an ursid in the faunal composition. The relative warp plots (Fig. 5.4 and 5.5) help to identify a common unbalanced morphospace occupation in such ecosystems (more than one ecomorph present only in a particular region of morphospace e.g. the II quadrant with RW1+ and RW2- scores in Krokonose or the IV quadrant in Galerian 1 with three catlike morphotypes).

Such phenomenon goes someway to explain the negative relationship between disparity and other guild parameters: ecosystems with small number in large carnivores still preserve extreme ecomorph which inevitably affect corpus shape disparity values. This in turn reflects the general negative relationship with productivity values (number of artiodactyls) because extreme omnivore "ecomorphs" can occupy ecosystems with low number of ungulates.

Another possible mechanism which explains the observed pattern in the evolution of corpus shape disparity of large carnivores through Ice Ages is the evolution of size-related traits.

As pointed out by Shepherd (1998) morphological diversity of mammalian communities can be inversely related with their size diversity: mammals in tropical regions are less size diverse and more shape diverse while the opposite occur at polar sites. According to Zelditch et al. (2004) disparity values can be computed also for centroid size or other traits other than shape variables by applying the same formula (see Materials and Methods).

No trend occurs between shape disparity and centroid size disparity values (Fig. 5.14), hence meaning that shape variability is not an artefact of size variability in the mandibular corpus.

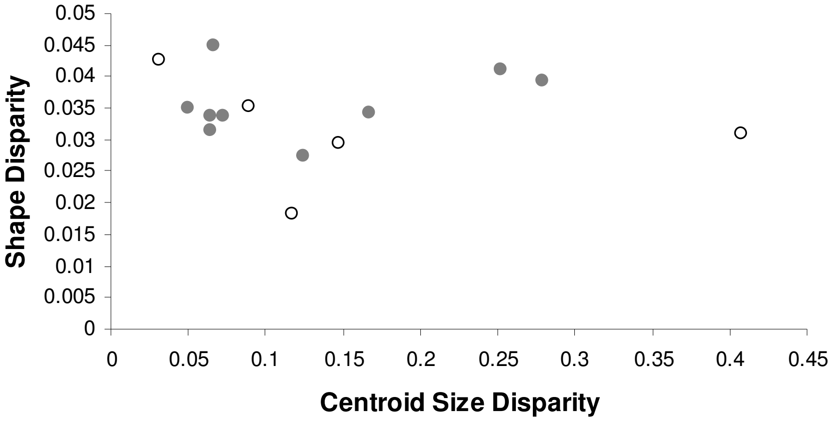


Figure 5.14: Scatter plot of centroid size disparity vs shape disparity. White circles extant ecosystems, grey circles Plio-Pleistocene guilds.

On the other hand, body mass value of extant carnivores and that reconstructed for extinct forms (see introduction) can be used to consider size-disparity among guilds.

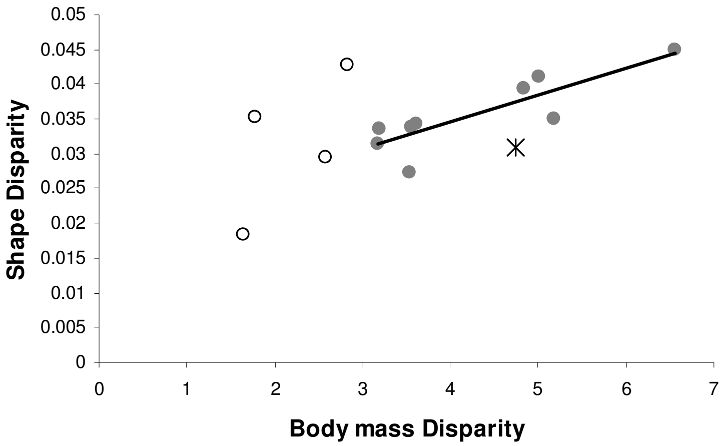


Figure 5.15: Scatter plot of body mass disparity vs shape disparity. White circles extant ecosystems, grey circles Plio-Pleistocene guilds, asterisk is Krokonose guild.

A general positive relationship occurs between body mass and shape disparities ($r_s = 0.612$, $p = 0.020$) even if a stronger positive trend occurs when only Plio-Pleistocene guilds are considered ($r_s = 0.849$, $p = 0.004$, Fig. 5.15). This means that the small variation in mandible shape disparity of Ice Age carnivores is a biological artefact of variation in body mass of large carnivore communities. It is worth mentioning that Italian Plio-Pleistocene large carnivore guilds did not exhibit a significant change in mean body mass through time (cfr. Raia et al. 2007). Interestingly, the body mass/shape disparity value of the Krokonose guild occupy the same variability of the Plio-Pleistocene guilds (Fig. 5.15) meaning that such relationship is also driven within a zoogeograpical area (Krokonose carnivore list is the same of the Italian one as for extant carnivore).

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 variation that are not intimately affected by climate changes. On the other hand, there is an 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; Raia et al. 2005, 2007). Mendoza et al. (2005) underlined that ecological assembly of mammalian communities is an intrinsic property of that systems which reflects habitat complexity. It is worth noting that such evidences come from quantitative models where all mammals are considered. In this case, the inclusion of ungulate community have a key rule as they are intimately related with the physical environment (Janis 1984; Janis et al. 2000, 2004; Owen Smith 1990; Fortelius et al. 2002). Hence the rule of carnivore community structure is only marginal to define changes in physical environment and this fact can be explained biologically. Recently, Hernández Fernández and Vrba (2005) reported for African mammal fauna a larger proportion of eurybiomic carnivores compared with herbivores. This means that generally carnivores 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 to this contention, O'Regan et al. (2002) consider Italian peninsula a possible Ice Age refugium for a large carnivore like *Panthera gombaszoegensis*. Then, it is likely that large carnivore communities of Italy where less affected by climate other than Northern European assemblages.

In conclusion corpus shape disparity of carnivore guilds didn't change significantly through space and time. In extant ecosystems, corpus shape disparity is negatively affected by the number of species and the number of artiodactyls present in each guild because of broad evolutionary, zoogeographical differences. Interestingly, large carnivores tend to saturate some morphospace regions confirming (for both extant and extinct ecosystems) that ecomorph specialization does not occur in extreme region of morphospace (Van Valkenburgh 1995).

On the other hand, shape disparity in Plio-Pleistocene ecosystems is affected by body mass disparity as a biological artefact. Interestingly, some large carnivore guilds (Triversa, Galerian 1 and Krokonose) are clearly outlier in morphospace occupation exhibiting an ecomorph random distribution (or possibly overdispersed) and unusual disparity values for their number of species.

They indicate periods with a poor carnivore diversity (as number of species) allowing occupation of several niches through time. Triversa is a PCOM representative of the last Pliocene "warm green house" fauna precluding the structural faunal change of the Middle/Upper Villafranchian *Wolf Event* (Raia et al. 2006; Gliozzi et al. 1997). Galerian 1 represent a *fuzzy subgroup* (in Raia et al. 2006) which, especially for carnivore species list, still to include several Villafranchian relict elements. The extant European guild lack some elements that can occur in other localities. For instance, in Italy the golden jackal (*Canis aureus*) is recently adding to the faunal list of large carnivores as this species normally occur in Slovenia (MAB 2004). In Northern Europe also the wolverine can be an important element of large carnivore guild that here was not included to avoid redundancy with the USA faunal composition.

Chapter 6

Locomotor adaptations in large Plio-Pleistocene carnivores: Palaeoecological Implications

6.1 Introduction

Although members of Carnivora are literally defined by virtue of what they eat, they exhibit a great variability also in locomotor adaptations (Taylor 1989). All the elements of the appendicular skeleton of carnivores are usually modified in order to maximise locomotor performance which can be remarkable if compared with that exhibited by other mammals (e.g. the cheetah *Acinonyx jubatus* can achieve the highest speed ever recorded among extant terrestrial mammals).

Such intuitive relationship between bones and performance is reflected in the external morphology of the pelvis, of long bones and other appendicular elements like scapula. It is also useful to infer locomotor behaviour in extinct species (Taylor 1989, Viverridae, Munthe 1989; Ginsburg 1999; Argant 2004; Antón et al. 2005). Accordingly, Taylor (1989) categorised carnivores for their ability in running or climbing or digging. These categories are reflected also in long bone shape and dimension. The latter observation allows quantitative analyses which, for carnivores, were firstly performed by Van Valkenburgh (1985) in her survey of extant and extinct large carnivore guilds. Her study reveals a complex relationship between the morphological variability of long bones shape and the environment occupied by both extant and extinct species.

Interestingly, several long bone length ratios of carnivores appears to be related with the running performance (e.g. maximum speed). In particular, metatarsal/femur length ratio has been intensively investigated because it can be applied also to the scatter record of extinct carnivores and their prey (Janis and Wilhem 1993). Garland and Janis (1993) revealed that the relationship of such ratio with speed (in large mammals) is not an artefact of phylogenetic relatedness although it cannot be described by a straightforward line. Christiansen (1999) confirms that in both carnivores and ungulates mt/f co varies with speed but other long bone ratios can also be considered as even better descriptor of running performance (e.g. Olecranon/Radius length).

It is worth noting that relationship between long bones shape and running performance is not only complicated by the fact that carnivores (and mammals in general) do not use to run at their fastest possibility, but also by the complex constraint of allometric scaling (Calder 1996).

Iriarte-Diaz (2002) demonstrated that locomotor performance scale differently in small (< 30 kg) and large (> 30 kg) mammals. The issue of how to define small and large species is particularly important here because it defines also a biological (other than ecological) threshold.

Christiansen (1999) defined small and large mammal at < 50 kg and > 100 kg values and evidenced differences in long bone scaling (as already revealed by Bertram and Biewener 1990).

These categories are not consonant with the large carnivore guild concept which –on the basis of feeding morphology and ecology (see.Chapter 1)- puts a threshold at 7 kg.

Interestingly, the cited studies were looking for a general theory on the allometric scaling of appendicular skeleton in mammals but just few concentrated only on Carnivora. Bertram and Biewener (1990) focused their survey on Carnivora as an order and identified allometric differences as driven by intrafamilial differences.

If the problem of differences of allometric scaling in long bones of carnivores is an open question, the functional constraint in locomotion of small and large carnivores has been recently clarified by Andersson (2004; see also Andersson and Werdelin 2003) by investigating the shape variability of the elbow joint. This structure is of particular interest because it allows the articulation between humerus and the radius/ulna complex and, as a consequence, is indicative of grappling in some carnivore as opposed to cursorial forms.

Andersson (2003) pointed out that a functionally relevant limit occurs at some 20 kg (a value similar to the physiological 21.5 kg in Carbone et al. 1996) because all carnivores larger than this mass adapt their elbow joint shape, in a mutually exclusive way, either to a cursorial life style (which generally accompanies a fair increase of size) or to retain supinatory ability (an adaptation that persists also in very large forms) (Andersson and Werdelin 2003). Even if this observation switches the concept of small and large carnivores in another body weight direction, Andersson (2005) observed also a low and uniform variation of elbow joint shape in species below 10 kilograms while an increase of shape variation with size occurs between 10-30 kg.

This fact convincingly supports the use of large carnivore 7 kilogram threshold also in study of locomotor adaptation and its extension to extinct species (cfr. Van Valkenburgh 1985).

Although Andersson utilised elbow joint as a shape descriptor, the validity of long bone indexes is indisputable especially on the light of their application to the fossils.

In particular, Lewis (1997) extended the analysis of long bones index to clarify locomotor adaptation of African Plio-Pleistocene carnivores. She evidenced a difference in eco-morphology between extant African carnivores and Plio-Pleistocene species. The extinct sabertooth cats (*Homotherium*, *Megantereon* and *Dinofelis*) were prey grappler. The African Plio-Pleistocene *Canis* spp. were more adapted to omnivory and to cursoriality.

Here, I present a similar survey of long bone indices in extinct Italian Plio-Pleistocene large carnivores. I focus on the implication of reconstructing locomotor behaviour for palaecological reconstructions and, in particular, environmental ones. As Lewis (1997) pointed out, some indices like the brachial (radius/humerus length), can be useful to describe the adaptation of a large carnivore for special habitats (closed, mixed, open savannah). This relationship will be empirically tested in order to define for each extinct carnivore analysed a particular preference for an habitat.

On the other hand, the locomotor categories will be avoided. According to Carrano (1999) morphometric variability of long bones is enough to describe quantitatively locomotor adaptations that are interpreted as a continuous traits and not categorical that is too reductive.

6.2 Materials and Methods

6.2.1 Long bones indices

22 extant species of large carnivores belonging to families Canidae, Felidae, Hyaenidae and Ursidae (see Appendix 4.1) were considered in order to reconstruct locomotor behaviour in extinct Italian Plio-Pleistocene large carnivores (all except the badger whose digging behaviour is peculiar, in modern and in Pleistocene specimens as well, Kurtén 1968). For each extant species humerus and radius length (L in cm) measurements were directly extracted from the literature (Bertram and Biewener 1990) and combined into the brachial index (BI = radius/humerus length cfr. Lewis 1997). The same data source was used to extract long bones length computed without considering metapodials appendices (Forelimb L = (radius L) + (humerus L); Hindlimb L = (femur L) + (tibia L) cfr. Lewis 1997; Christiansen 2002). The long bone lengths were log-transformed in order to make them comparable with long bone indexes which are dimensionless (cfr. Lewis 1997).

Data in Janis and Wilhem (1993) and Christiansen (2002) were reviewed to extract for each species the metatarsal/femur ratio.

Taken overall, four variables were considered for each extant large carnivore: BI, Log Forelimb L; Log Hindlimb L, mt/f. These are relevant to understand locomotor behaviour and the relationship of each species with the environment (cfr. Lewis 1997).

6.2.2 Fossil sample

For extinct Plio-Pleistocene forms, the latter variables were computed combining measurements directly taken from museum collections or after an extensive review of the Italian and European literature on each large carnivore (see Appendix 4.2). As the fossils are usually incomplete and scattered in space, several long bone indexes were obtained combining long bone lengths from different localities. When possible, multiple long bone measurements from the same locality were combined by computing their mean as representative of the species mean value. In most cases, it was possible to use linear measurements of specimens from Italian localities. Among Caniforms only Italian specimens were used to estimate indices in: *Canis etruscus*, *Canis arnensis*, *Lycaon falconeri*, *Ursus spelaeus* and *Ursus arctos* while for Feliforms only in *Lynx issiodorensis* and in the Pleistocene European lynx (*Lynx lynx*).

Among extinct species I included also European Galerian canids like *C. mosbachensis* and *C.* aff *arnensis* from L'Escale for which linear measurements were available. It was not possible to obtain linear measurement of *Pliocrocuta perrieri* and the Pleistocene leopard (*Panthera pardus*) for which Del Campana (1947) reported the same variability as in extant leopards.

It is worth mentioning that for most Plio-Pleistocene species only fragments of some long bones exist. In this case, the maximum length was estimated from medio-lateral or antero-posterior diameter by using regression equations (at family level) with the highest R value reported in Bertram and Biewener (1990). Although this approach is not ideal, it allows to reconstruct long bones length for several species: *C. arnensis*, *L. falconeri*, *A. pardinensis*, *L. spelaeus*, *M. cultridens* and *P. gombaszoegensis* (see Appendix). When no diameter was available, long bone length was estimated by applying regression equations relative to another element (of the same limb anterior or posterior) for which allometric scaling can be evidenced at family level (data Bertram and Biewener 1990, Appendix). This was the only way to estimate the radius length in *A. pardinensis* (from humerus length), the femur length in *L. falconeri*, *Lynx spelaeus*, *Chasmaporthetes lunensis*, the tibia in *C. arnensis* and the III metacarpus length (from humerus L) in *Pachycrocuta brevirostris*.

Taken overall on 20 extinct species analysed, 35% have at least one length's element reconstructed from another element of the same limb.

For *Chasmaporthetes lunensis* long bone linear measurements were available only for the tibia (from Mt. Perrier) and the III metacarpal (from Layna) (in Kurtén and Werdelin 1988). The length of other elements were estimated by considering long bone measurements of both *Chasmaporthetes borissiaki* and *Chasmaporthetes ossifragus* (in Berta 1981). Although Kurtén and Werdelin (1988) reported some differences in length proportions of *Chasmaporhetes* spp. it is, here, assumed that such differences are not relevant at comparison to other large carnivores analysed.

This is not a robust approach but it allows to obtain estimates of four long bone indices which are useful to describe the locomotor behaviour of extinct taxa. Each case will be considered with caution in the interpretation of the results bearing in mind that for some species several long bone estimates could be unreliable.

6.2.3 Multivariate analyses

Lewis (1997) consistently demonstrated that each of the four long bone indexes considered, can be interpreted singularly in order to infer locomotor behaviour in extinct taxa. Accordingly, a species can be analysed also in a multivariate morpho-ecological space (cfr. Van Valkenburgh 1985; Lewis 1997) in order to obtain better information on its general long bone proportion.

For the latter reason, a Principal Component Analysis (PCA, Blackith and Reyment 1971) is, here, applied to reduce the four long bone indexes in a sample of 22 extant and 20 extinct large carnivores. The Principal Component vectors were extracted using a correlation matrix which allow to maximise the variance of both indexes BI and mt/f and log transformed fore and hind limb length (variables exhibiting different scale). The morphospace defined by the first two PCs (which explain the highest percentage of explained variance) was interpreted in order to infer locomotor behaviour of extinct Plio-Pleistocene carnivores. An UPGMA clustering was also applied to the Euclidean dissimilarity matrix extracted by considering the four indices simultaneously.

6.2.4 Habitat and climate variables

In order to validate the possible relationship between locomotor behaviour and habitat, each extant large carnivore ($n = 22$) was assigned to an habitat value according with Janis and Wilhem (1993) and Ortolani and Caro (1996). Note that Janis and Wilhem habitat values are mutually exclusive (Open/Closed environment) and are here quantified as 0 = Open or 1 = Closed.

For the variables in Ortolani and Caro (1996) such condition is not present (e.g. the grey wolf is considered adapted to Arctic, Temperate forest, Grassland and Desert as well). Consequently, for each habitat category (e.g. Arctic) I scored 0 as indicative of “not adapted” and 1 as “adapted” to a particularly habitat.

A series of logistic regressions (with forward Wald option) were performed by considering all studied indices (BI, mt/f, Log Fore limb L; Log Hind limb L) as covariates of the independent variable (0, 1) chosen from habitat classification. The Wald option allows to consider a stepwise approach where covariates are singularly added to the model step by step if the Wald statistic corresponds to a $p < 0.005$, while if Wald probability > 0.005 variables are not included in the model (Hair et al. 1998).

These models, after validation on extant carnivore data, allow to predict habitat adaptations in extinct Plio-Pleistocene carnivores by their long bone proportions.

The latter palaeoecological reconstruction of large carnivores adaptation to a particular habitat will be discussed on the light of the climate changes raised by Italian Plio-Pleistocene PaleoCommunities (PCOMs). Firstly, each PCOM is characterised by a proportion of large carnivores adapted to particular habitats (e.g. 50% of tropic adapted and 50% of Grassland adapted). For Pleistocene leopard and badger I used the same habitat preferences as in Ortolani and Caro (1996). These relative proportions are compared with the proportions observed in extant large carnivore guilds (selected as in Chapter 4). An UPGMA clustering is applied to the Euclidean dissimilarity matrix obtained with guild as raw data and proportion of carnivores adapted to particular habitat as column. In this way it is possible to cluster extant and extinct large carnivore guilds accordingly with the proportion of carnivores adapted to habitat categories.

Another quantitative approach is applied by quantifying climate for each PCOM with the Oxygen 18 Isotopic values drawn from Kroon et al. (1998), site 967 which exhibited a continuous record from 3.2 Ma (cfr. Raia et al. 2005). A total of 441 records were considered spanning 3.2 – 0.8 Ma. For each time bin of each PCOM I computed mean of Oxygen 18 values. The latter value is indicative of major climate shifts from warm to cold conditions which could be correlated with the relative proportion of carnivores adapted to particular habitats.

6.3 Results

6.3.1 Locomotor behaviour

Four Principal Component axes were extracted on a sample of 22 extant large carnivores and 20 extinct forms. The first two axes explain together c.ca 88% of the total variance (Table 6.1). They are informative of the intra family variation of locomotory features (Figure 6.1) with which they are strongly associated: the first axis is positively associated with the log length of both fore and hind limb while the second is strongly influenced by the brachial index (Table 6.2.).

	Eigenvalue	% Variance	Cum. %
PC1	2.507	62.685	62.685
PC2	1.021	25.531	88.217
PC3	.393	9.833	98.049
PC4	.078	1.951	100.000

Table 6.1: Eigenvalues and % of explained variance for each Principal Components.

	PC1	PC2	PC3	PC4
Log_Fore	.929	.283	.119	.206
Log_Hind	.899	.328	.223	-.187
BI	-.398	.877	-.268	-.005
Mt_F	-.823	.253	.507	.031

Table 6.2: Correlation coefficients for each Principal Component.

Graphically, it is possible to note a neat separation between families even if some region of overlap occurs between cursorial canids e.g. grey wolf, and the spotted hyena together with the sprinter *A. jubatus* (Fig. 6.1), suggesting also a functional meaning. Interestingly the long legged canid

Chrysocyon brachyurus is near the "long legged hyena" *Chasmaporthetes lunensis*. The sabre tooth *Homotherium crenatidens* clusters at the extreme positive scores of Felidae together with the European Ice Age lion while the extinct *Megantereon cultridens* is similar to puma and jaguar (more adapted to hunt in closed environments). *Panthera gombaszoegensis* overlaps with the extant lion near the extinct hyenas (*Pachycrocuta brevirostris* and the Pleistocene *Crocuta*) and together with the extinct *Acinonyx pardinensis* (white circle below *P. gombaszoegensis* Fig. 6.1). The extinct lynx *Lynx issiodorensis* is different from the extant forms while the position of *L. spelaeus* is similar to that of the European lynx (near canids). Among canids, most Plio-Pleistocene forms are grouped within the variability of modern species defined by the golden jackal, the coyote, the African wild dog and the grey wolf. Interestingly, the Pleistocene grey wolf (black dot below *A. jubatus*) is near the extant form (Fig. 6.1). *Lycaon falconeri* is a clear outlier even if it still represents canids variability like the omnivorous and peculiar crab eating fox (*Cerdocyon thous*) and the racoon dog (*Nyctereutes procyonoides*). The extinct bears exhibit the same variability of modern ones with *Ursus minimus* and *U. etruscus* near the brown bear while cave bear cluster with the polar bear (*U. maritimus*).

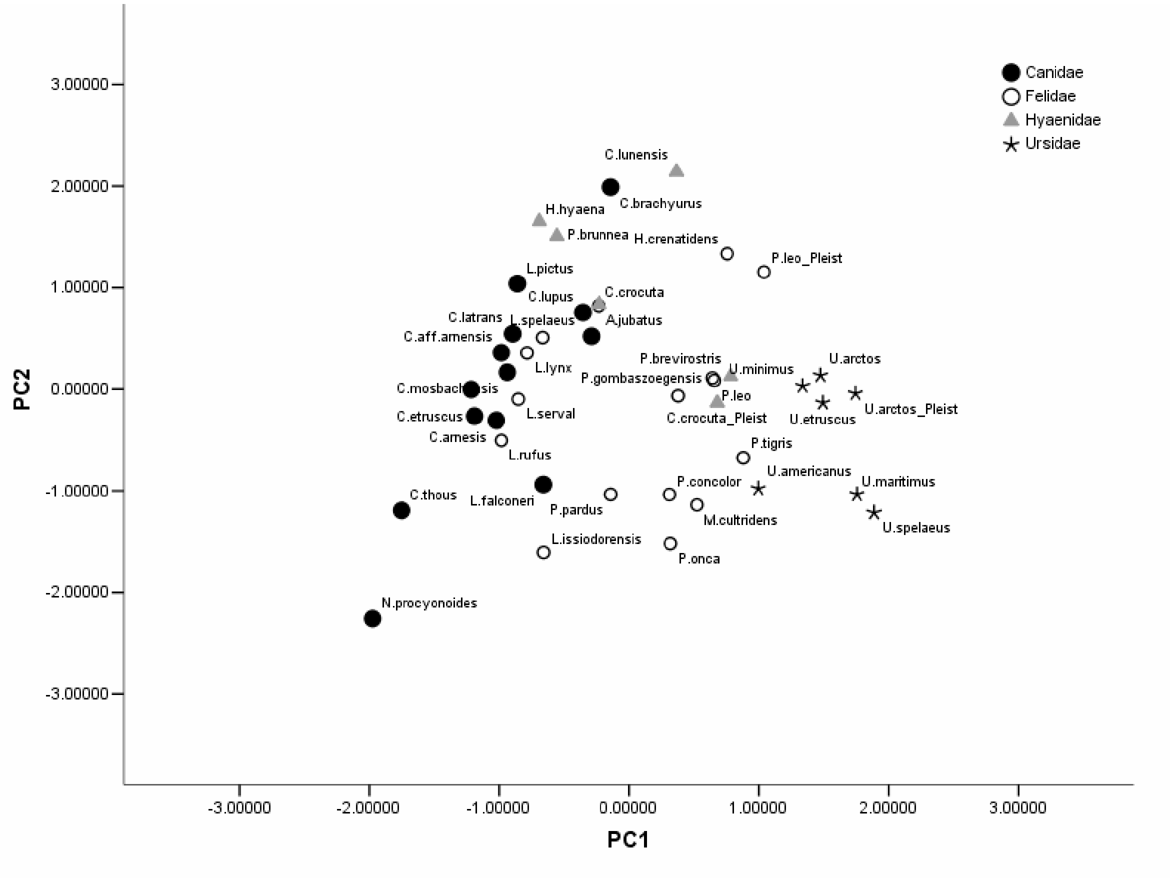


Figure 6.1: Scatter plot of the first vs the second Principal Component axes.

If PCA scatter plot is informative of both phylogenetic and functional influences on long bone indices variability, UPGMA confirms this observation and evidences groups according to a body mass constraint (Fig. 6.2). Three major clusters can be identified.

The first is characterised by the two peculiar small omnivorous dogs which differ functionally from all the other large carnivores because they are not active predators. The second cluster grouped large bears, most of large felids (Body Weight between 50 and more than 100 kg) and the extinct giant hyenas (more than 100 kg of estimated mass) together with two long legged species: the maned wolf and *Chasmaporthetes*. On the other cluster, we found lynxes (c.ca 20 kg in mean BW) with extant and extinct canids whose body mass generally vary between 10 - 20 kilograms. Larger cursorial forms like grey wolf and extant hyenas are grouped in this latter cluster as well (between 30-60 kg) together with *Lycaon falconeri* and *Lynx issiodorensis* unusual forms (the first is a typical canid cursorial while the second is lynx ancestor) but being in mass between 20 and 30 kg.

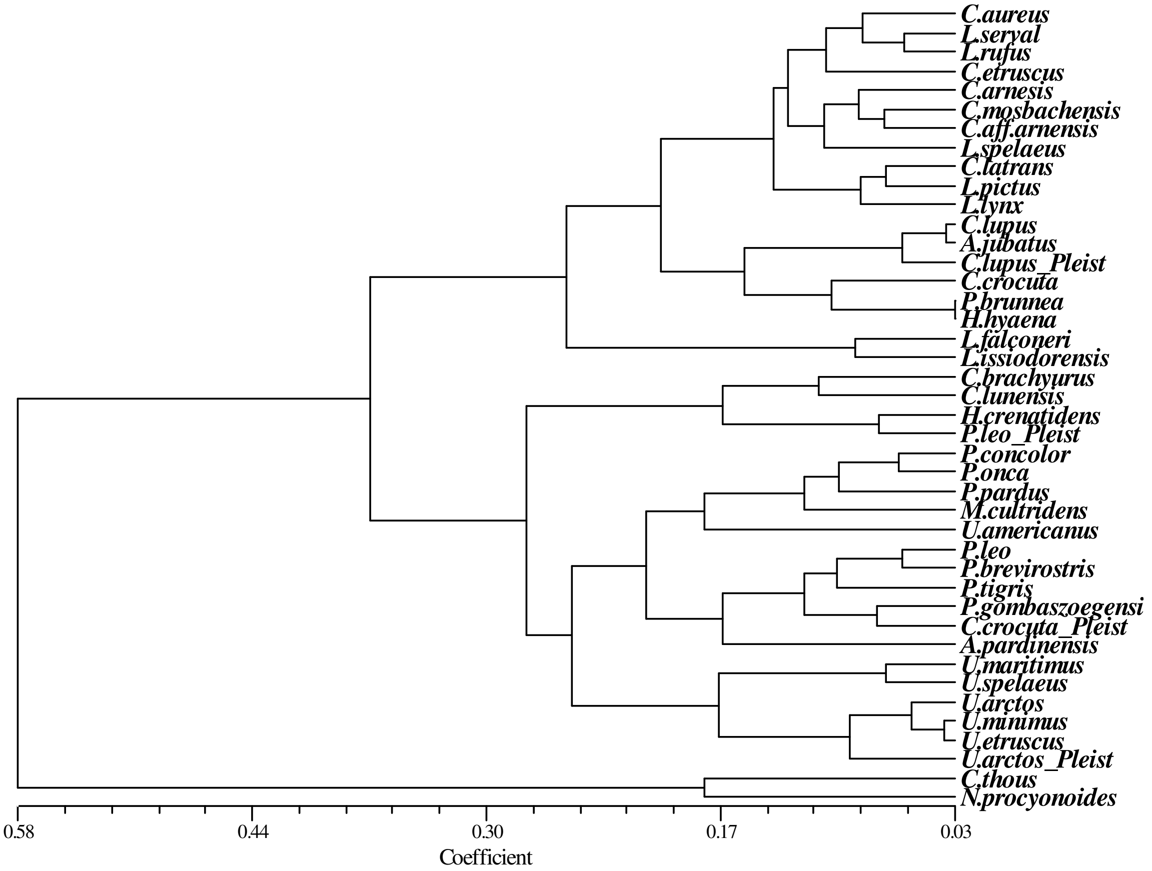


Figure 6.2: UPGMA tree obtained from Euclidean distance matrix extracted on the basis of four locomotor indices computed for each species.

6.3.2 Locomotion, habitat and climate

Several logistic models were considered to predict habitat preference in extinct species from long bone indexes. A first logistic model was assessed with the generalised category open/close habitat (in Janis and Wilhem 1993) as the dependent. Hosmer and Lemeshow test for godness of fit (χ^2 = 8.565, df = 8; p = 0.380) validates the model at the first step when only the BI enters as a good predictor of species adapted to open or closed habitat (Table 6.3). The 75% of extant species adapted to open habitat were rightly predicted with 70% of correct classification for species adapted to closed environment.

		B	**S.E.**	**Wald**	**df**	**Sig.**
Step 1	*BI*	-11.251	5.374	4.383	1	.036
	Constant	10.428	5.073	4.226	1	.040

Table 6.3: Logistic model with Open/Closed variable as dependent.

The presence/absence of large carnivores in temperate habitats cannot be predicted because no long bone indexes enter in a logistic regression model.

On the other hand, BI is also the only variable in a model computed to predict adaptation for tropical environments (Hosmer and Lemeshow at first step: χ^2 = 0.885, df = 8; p = 0.999) (Table 6.4). In this case 95% of species not present in tropics are well predicted while 75% of tropic carnivores are classified correctly.

		B	**S.E.**	**Wald**	**df**	**Sig.**
Step 1	*BI*	-28.509	14.747	3.737	1	.053
	Constant	23.535	12.456	3.570	1	.059

Table 6.4: Logistic model with tropic (adapted/not adapted) variable as dependent.

For grassland environments a complex model allows to include two variables: mt/f ratio at the first Wald step, and Log Fore limb length at the second step (Table 6.5, 6.6) with 100% of correct classification when step 2 is achieved.

	χ^2	**df**	**Sig.**
Step 1	5.660	8	.685
Step 2	.000	2	1.000

Table 6.5: Hosmer and Lemeshow test in a model with grassland (adapted/not adapted) variable as dependent.

The other environmental variables of Ortolani and Caro (1996) do not allow to obtain significant logistic regression models hence long bone indices of large carnivores cannot be used to predict their presence or absence in extreme environments like the artic or desert but even in riparian ones.

		B	**S.E.**	**Wald**	**df**	**Sig.**
Step 1	*mt/f*	34.723	16.218	4.584	1	.032
	Constant	-10.254	5.350	3.674	1	.055
Step 2	*Log_Forelimb*	285.434	33690.521	.000	1	.993
	Mt_F	1463.77	163202.668	.000	1	.993
	Constant	1205.429	138335.611	.000	1	.993

Table 6.6: Logistic model with grassland (adapted/not adapted) variable as dependent.

The significant logistic models allows to make some prediction on extinct Plio-Pleistocene forms. Some are reliable while others need to be considered with caution (Table 6.7).

Species	**Open/Closed**	**Tropical**	**Grassland**
Canis etruscus	0	0	1
Canis arnesis	0	0	1
Lycaon falconeri	1	1	1
Canis mosbachensis	0	0	1
C. aff.*arnensis* (L'Escale)	0	0	1
Canis lupus Pleist.	0	0	1
Homotherium crenatidens	0	0	1
Megantereon cultridens	1	1	1
Acinonyx pardinensis	1	0	1
Lynx issiodorensis	1	1	1
Lynx spelaeus	0	0	1
Panthera leo Pleist	0	0	1
Panthera gombaszoegensis	1	0	1
Pachycrocuta brevirostris	1	0	1
Crocuta crocuta Pleist	1	0	1
Chasmaporthetes lunensis	0	0	1
Ursus minimus	1	0	0
Ursus etruscus	1	0	0
Ursus spelaeus	1	1	0
Ursus arctos Pleist	1	0	0

Table 6.7. Predicted habitat preference for Plio-Pleistocene large carnivores. 0 = "open" and "non-adapted" for columns tropical and grassland ; 1 = "closed" and "adapted" for columns tropical and grassland.

For instance, most of the canids are predicted as grassland specialist even if the result for *L. falconeri* is enigmatic also because most of long bone indexes are estimates for this species. Generally, the multiple estimates for habitat adaptability are not contrasting values even if the variable Open/Closed is usually too enigmatic and too broad to be considered. There are few Pleistocene species adapted for tropical environment and among them the extinct *Megantereon* *cultridens* is certainly a reliable estimate (cfr. Turner and Antón 1997) while the estimate for the cave bear is probably driven by its peculiar long bone proportion interpreted as a special adaptation to hibernate in caves (Kurtén 1968). As for *Nyctereutes megamastoides* and *Pliocrocuta perrieri*, no long bones were available, I've assumed that their locomotor adaptation could have been similar to that of their extant counterpart *Nyctereutes procyonoides* and *Parahyena brunnea* (Kurtén 1968), respectively. Consequently, the habitat preference was scored accordingly with the data available for the latter extant species in Ortolani and Caro (1996).

In order to avoid the misleading interpretation of the variable "Open/Closed" UPGMA clustering was applied by considering for each guild only the proportion of "tropic adapted" and "grassland adapted" carnivores.

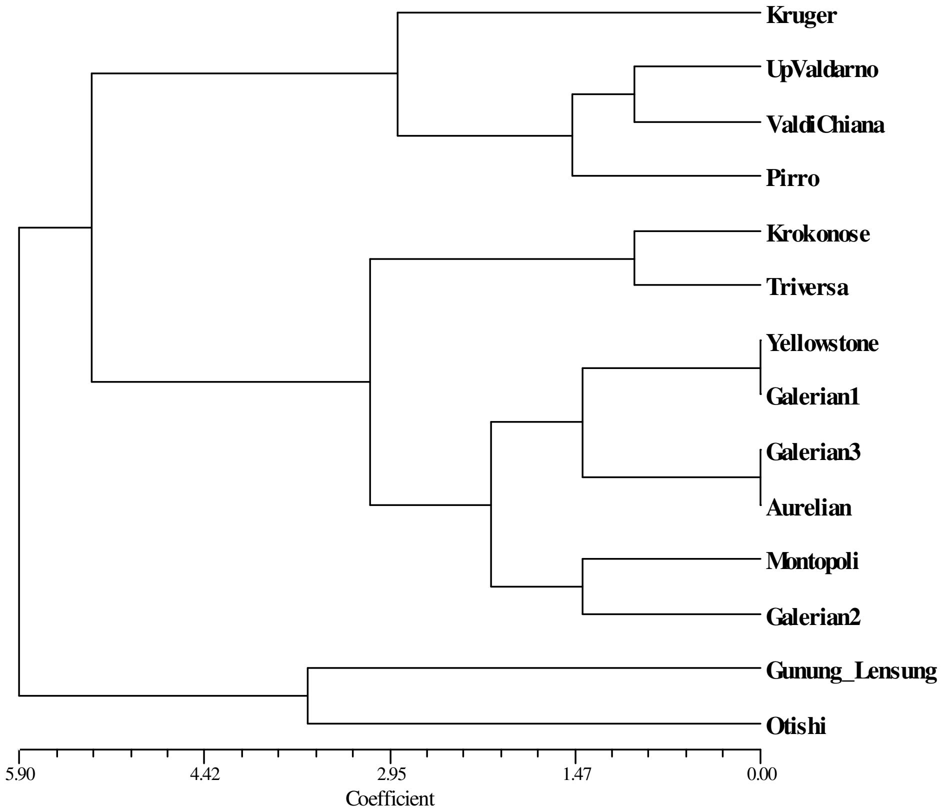


Figure 6.3: UPGMA tree based on Euclidean distance matrix indicative of the relative proportion of large carnivores adapted to "tropical" or "grassland".

The obtained tree is completely different from the tree reconstructed on the basis of mandibular corpus shape data (cfr. Figure 5.8, Chapter 5). Generally, Upper Villafranchian PCOMs cluster with the South African guild suggesting a similar environmental matrix represented by a preponderance of grassland adapted carnivores. The lower/middle Villafranchian Triversa is grouped with the European guild of Czech Republic while the cluster of Galerian and Aurelian PCOMs with the Yellowstone ecosystem is a reliable analogy of "temperate" carnivore guild. The structure of

Indonesian and Peruvian guild appears to be similar on the basis of habitat preference of carnivores and such analogy is supported by a high proportion of tropical adapted carnivores.

The rule of the proportion of grassland/tropical carnivores for climatic reconstruction is validated by a significant correlation exhibited between such variables (expressed as ratios –from 0 to 1- and not percentage) and the mean δ^{18} O computed for each PCOM. Interestingly and counter intuitively a positive correlation occurs between mean δ^{18} O and the proportion of tropic adapted taxa while the same relationship is negative when grassland taxa are considered (Table 6.8; Fig. 6.4). That is cold PCOMs (Galerian, Aurelian) have higher proportion of "tropical adapted" carnivores and lower proportion of "grassland adapted" carnivores. No correlation occurs with the variance of δ^{18} O computed for each PCOM and also the proportion of open/closed adapted carnivores that in turn are correlated with tropical/grassland proportions.

Pearson r \ *p*	tropical	grassland	Open/Closed	mean δ18 O	Var δ18 O
tropical	-	0.000	***0.079***	***0.004***	*0.171*
grassland	-1.000	-	***0.079***	***0.004***	*0.171*
Open/Closed	**-0.614**	**0.614**	-	*0.166*	*0.812*
mean δ18 O	**0.848**	**-0.848**	-0.505	-	***0.035***
Var δ18 O	0.500	-0.500	0.093	**0.703**	-

Table 6.8: Pearson correlation coefficients and associated p values for proportion of carnivores and isotopic values computed for each PCOM (n = 9). Fold values are significant at $p < 0.005$.

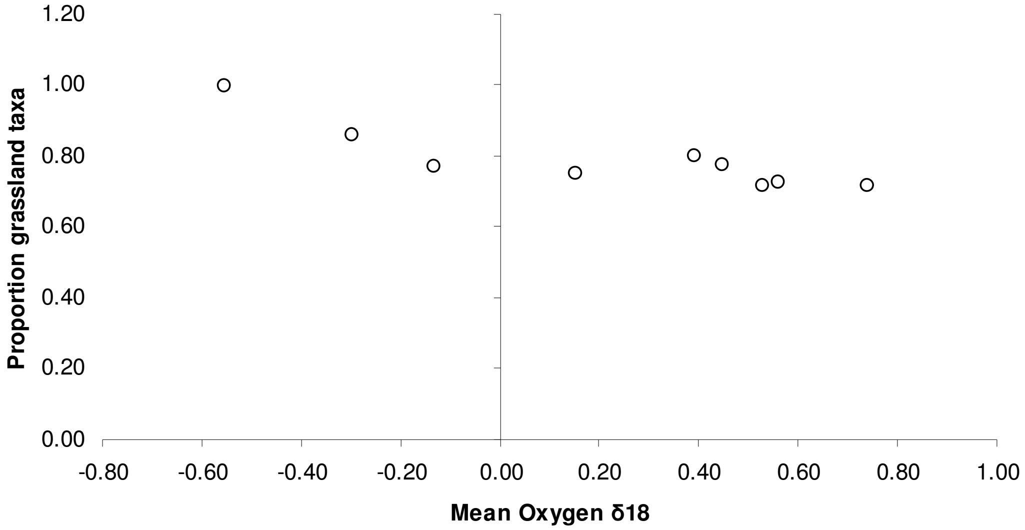


Figure 6.4: Scatter plot of mean δ^{18} O vs proportion of grassland carnivores.

6.4 Discussion

Like feeding apparatus, also locomotor appendices of large carnivores describe the dichotomy between functional morphology and phylogenetic constraint. The survey performed on long bone indices variability of both Plio-Pleistocene and extant carnivores is clearly indicative of the fact that morphological convergence is a rare (but possible) event in the recent evolutionary history of the group (cfr. Van Valkenburgh 1985, 1999, 2007). Such convergence is showed in the similarity of long bone proportion between grey wolf with cursorial hyenas or long legged *Chasmaporthetes* with the maned wolf. The long bone indices are, here, considered to describe functional adaptation but phylogenetic patterns still to be revealed in the morphospace variability (cfr. Fig. 6.1). This pattern is consistent with previous observations as in Jones (2003). She analysed several long bone ratios in both placental and marsupial carnivores evidencing similarities more at family level than by virtue of locomotor adaptation.

Interestingly, the functional constraint, in my dataset, still apply at intrafamily level meaning that it is important as well. Body mass is the principal determinant of such functional constraint (cfr. Fig. 6.2) and it is plainly expected considering the theoretical evidence of the general allometric scaling in vertebrate long bones (for review Garcia and da Silva 2006). Carnivores of the same body size need to sustain similar bending loading during locomotion and, consequently, their long bone proportions are constrained to vary to a restricted degree. But, as it is the case for feeding apparatus (cfr. Chapter 1), this is not a maladaptive factor.

On the basis of this general theory, the results obtained for Plio-Pleistocene carnivores needs to be interpreted casewise.

Among canids, most of the analysed extinct species possess only few complete long bone specimens. In spite of the approximation in computing several indexes, the long bone shape variability of extinct species is concordant with that exhibited by extant dogs. It is not useful to define if one species was faster than another one by virtue of its long bone proportion but what emerged is the relatively lack of peculiar morphologies among Plio-Pleistocene dogs. *Canis etruscus* and *Canis arnensis* cluster with the extant golden jackal (*Canis aureus*) and this result consistently confirms the earliest observation of Del Campana (1913) and Torre (1967). Interestingly, the Galerian dogs from L'Escale and Untermassfield are similar to the Villafranchian Arno dog but not to the wolf, as with locomotory habitus. The peculiarity of these Plio-Pleistocene forms, probably, consists in the fact that their feeding apparatus was already adapted in chewing meat of relatively large ungulates, but their legs were not extremely adapted in running like the grey wolf or the African wild dog.

The lack of an expected similarity between *Lycaon falconeri* and its extant counterpart *Lycaon pictus* leaves an open question about the running adaptation of the latter extinct dog. The lack of the first metacarpal digit supports the adaptation of *Lycaon falconeri* to a cursorial lifestyle (Rook 1994), but more long bone data are necessary to validate such observation. In fact, it could also be possible that the latter morphological character is not a case of functional convergence but it is due to its parental relationship with the extant *Lycaon pictus* (Martínez-Navarro and Rook 2003).

Anyway, it is clear that all Plio-Pleistocene dogs were more cursorial than extant and extinct large cats or bears. Within this cursorial group, it is possible to include (as expected) also the extant hyenas together with *Chasmaporthetes*. The indices obtained for the latter species are estimates but they are based on *C. borrissiaki* and *C. ossifragus* which should be less long legged than European *C. lunensis* (Kurtén and Werdelin 1988). It is worth noting, that *C. lunensis* appears to be similar to *Chrysocyon brachyurus* whose long legs are not considered an adaptation for running faster, but probably for foraging in tall grass (Janis and Wilhem 1993; Rodden et al. 2004). If this similarity is confirmed by new fossil remains, the adaptation to fast running of *Chasmaporthetes lunensis* should be re-considered with caution.

On the other hand, the giant *Pachycrocuta brevirostris* appears to be similar to the extant lion in long bone proportion. This fact is partially confirmed by palaeoecological description of Turner and Antón (1996). Accordingly, the tibia of *P. brevirostris* is shorter than that of extant and other Plio-Pleistocene hyenas suggesting a powerful hindlimb. Relative shortening is exhibited also by the radius. This suggests that the similarity between *P. brevirostris* and lion is reliable especially because driven by their similarity in mean body mass (127 kg and 156 kg respectively).

Different observations emerge in the long bone proportions of extinct and modern large cats. It is remarkable the similarity of Pleistocene lion from Equi (measurements taken in Del Campana 1947) and the sabre tooth *Homotherium crenatidens*. This fact probably reflects similarity in body mass but also peculiar functional convergence imposed by the emphasized cursoriality in *H. crenatidens* as compared to the other modern felids (see Turner and Antón 1997; Antón et al. 2005). On the other hand, the relatively long legs of Pleistocene lion could be an adaptation to hunt in the severe snow conditions of the coldest glacial periods, but this is inferential at best. There are also implication for the hunting behaviour of both species: *H. crenatidens* was adapted to hunt very large prey (Lewis 1997; Turner and Antón 1997; Antón et al. 2005), and probably such adaptation was achieved also by the Pleistocene lion, that in Europe could have hunted species heavier than modern African ungulates.

The results obtained for the dirk tooth *Megantereon* confirm its adaptation as a stalker hunter of close forests (Turner and Antón 1997) like the modern puma or jaguar. The fact that it clusters together with black bear as well (see Figure 6.2) suggests a peculiar proportion due by virtue of its size.

Panthera gombaszoegensis is, here, considered more cursorial than expected for a jaguar-like large cat (cfr. Figs. 6.1-2) but this result needs be considered with caution because complete long bones are scanty in the fossil record. On the other hand, the similarity of *Acinonyx pardinensis* with cursorial extant lion and Pleistocene *Crocuta* is plausible if we consider its body mass but also its relative convergence with the extant sprinter: the cheetah (which cluster with canids and hyenas as well cfr. Figs. 6.1, 2). It is difficult to deduce if *A. pardinensis* was faster than the extant cheetah but this analysis does not support such hypothesis: it is plausible that *A. pardinensis* was a sprinter (Turner and Antón 1997) but, because of its large body mass, its agility and speed was probably not as extreme as in *A. jubatus*.

Lynxes are not so enigmatic in clustering with medium-sized canids, but what it is possible to note is the relatively shorter and more robust limbs of *Lynx issiodorensis* from Olivola if compared with extant lynxes and the serval (Figs. 6.1-2). This fact confirms the observation of Kurtén (1981) and such feature could be the consequence of two different factors. Firstly, *Lynx issiodorensis* was less specialised than extant lynxes in hunting in different conditions (from the American deserts to the snowy mountains of Carpathians) and as a typical Villafranchian element, was probably specialised in woody habitats (to escape competition with cursorial canids). Secondly, it is also probable that *Lynx issiodorensis* was more adapted to hunt on medium-sized ungulates other than lagomorphs. Medium-sized ungulates generally represent an important source of food for extant lynxes (Tumlison 1987; Nowell and Jackson 1996) and it is considered a “misconcept” the fact that lynxes are lagomorph specialists (Nowell and Jackson 1996). As a consequence, it is likely that the Plio-Pleistocene lynxes in general where well adapted in hunting small ungulates, with *Lynx issiodorensis* being more specialised in larger prey (see also Chapter 3).

In extinct bears, we note again a pattern of long bone variability specially driven by phylogenetic relationships (cfr. Chapter 3). The lineage of brown bear is defined by *U. minimus* - *U.etruscus* group which are similar in long bone proportions, as well. On the other hand, *U. spelaeus* is similar to the polar bear, suggesting that its limb proportions reflected a particular adaptation to very cold climates.

This species by species approach revealed useful in defining locomotor behaviour of extinct large carnivores but, most interestingly, long bone indices are also indicative to define general patterns of association between carnivores and habitat. Lewis (1997) already mentioned and utilised the brachial index as an indicator of adaptability to open or mixed or closed habitats. But it is important to note that the logistic regression models presented here are statistically more robust and they allow to include more than one long bone indices in defining morphology/habitat relationship.

Such relationship is complex especially because carnivores are not habitat specialists like ungulates or rodents. Generally, large carnivores have large home range and their habitat selection depends on prey availability but also densities of other competitors (Gittleman 1985; Carbone and Gittleman 2002; Woodroffe and Ginsberg 2005). As a consequence, several species morphologically well-adapted to particular habitats may select sub-optimal habitats by virtue of external environmental factors. For instance, the African wild dog is a large carnivore adapted to cursoriality and it is supposed to be a grassland species (as in Ortolani and Caro 1996). But recent studies demonstrated that *Lycaon pictus* selects deciduous woodlands more than expected (Creel and Creel 2002). This is just one case that is considered to have ecological explanations (avoiding competition with lions and hyenas) but most other large carnivores are usually constrained in sub-optimal habitat because of habitat fragmentation due to human activity.

As a consequence, the habitat preferences used here for extant carnivores need to be interpreted with caution. On the other hand, the results obtained for extinct carnivores appears to be plausible at least if we consider valid the variable “grassland”. The preference of *Lycaon falconeri*, *Megantereon cultridens*, *Lynx issiodorensis* and *Ursus spelaeus* to potential “tropical” environments needs to be interpreted as preference to more forested areas. In fact, the variable tropical is negatively correlated with the mutually exclusive variable “Open/Closed” (Table 7). Furthermore, several species are predicted in neither tropical or grassland categories suggesting that they should be more adapted to other unpredictable categories (e.g. temperate forest) as is the case for the extant (see Ortolani and Caro 1996) and extinct bears.

This survey demonstrates only that long bone indices can be used to predict habitat preference at least for the non-mutually exclusive variables “grassland” and “tropical”. The other habitat categories can be probably predicted by morphological features when more taxa are included without any body mass threshold.

Interestingly, the proportion of “grassland” or “tropical” large carnivores in each Plio-Pleistocene ecosystem gives plausible similarity with extant ecosystems (Fig. 6.3), at least, in terms of potential environmental matrix. As expected the Villafranchian ecosystems are similar to the South African ecosystem with a great number of large cursorial carnivores. On the other hand, Galerian and Aurelian environments could have supported temperate forest like Yellowstone which experienced severe winter condition and temperate summer. Although these similarities are attractive and makes sense, Janis et al. (1994) and Guthrie (2001) cautioned avoiding direct comparison of apparently similar past habitats with modern ones. But there is a compelling evidence that large mammal fauna composition is particularly indicative to determine biome structure (Hernández Fernández and Campomanes 2003, 2005; Rodríguez 2004; Raia et al. 2005, 2007) and this survey demonstrates that also large carnivores are important components to predict extinct biomes.

The last result (Fig. 6.4) supports such statement validating the potential relationship between climate change and large carnivore species composition. Basically as the climate became colder in the Mediterranean region the proportion of “grassland specialised” carnivores diminished. If we consider biome changes, this is plausible because several vegetation analyses support the arid conditions of Villafranchian ecosystems characterised by abundance of *Artemisia* shrub lands (Suc et al. 1995; Fauquette et al. 1999; Ghinassi et al. 2004) that, as a consequence, support more “grassland” carnivores. Instead, Galerian and Aurelian are characterised by the alternation of colder/ temperate phases which result in the spread of montane-subalpine forests (Malatesta 1985).

Torre et al. (2001) already mentioned a structural change in Plio-Pleistocene large mammal fauna of Italian peninsula directly related with climate oscillations. My results validate previous observations on the spread of large carnivores in Italy with cursorial “grassland” canids being favoured during Villafranchian (which characterises also the *Wolf event*) while pantherine cats and modern elements of temperate habitat (e.g. wolf, brown bear) spread in the colder Pleistocene phases.

Chapter 7

On abundance, predation and competition in Italian Plio-Pleistocene large mammal communities

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7.1 Introduction

Although morpho-ecological analyses allow evidencing the evolutionary changes of Italian Plio-Pleistocene large carnivores, the fossil record offers the opportunity to analyse relative changes in their abundance and their consequences. The first attempt to reconstruct species abundance in fossil mammals comes from Damuth's (1982) observations. The minimum number of individuals (MNI) that occurs in each fossil site is indicative of a taphonomic bias induced by differences in probability of fossilization due to body mass. As a consequence, it is possible to reconstruct species relative abundance correcting the MNI for the abundance expected by virtue of species body mass. This approach is particularly useful when accurate data on fossil assemblages are on hand. Yet for most of Italian Plio-Pleistocene localities there is an historical bias induced by the fact that several sites have been excavated in different time step (but see Mazza et al. 2004 for an accurate example on Poggio Rosso fauna).

On the other hand, Raia et al. (2006a, b) and Meloro et al. (2007) consistently demonstrated that macroecological theories (Gaston and Blackburn 2000) can be successfully applied to Italian fossil record presence/absence data in order to extract relative abundance data. This approach derives from the basic principle that, at the regional scale, species occurrence is directly related to local species abundance. Alroy (1996, 2000) applied such a principle to North American fossil record of Cenozoic mammals and ideated species occupancy metric which represents the relative number of localities occupied by a species in a specific time range. Jernvall and Fortelius (2004) used the same principle to define locality coverage in a sub-set of European Cenozoic mammals.

On the basis of Italian fossil record data matrix (presence/absence data for each Plio-Pleistocene large mammal, in Palombo et al. 2003) it was possible to extract occupancy data which represent the number of localities where each species is present/ total number of localities for a specific time interval. Interestingly, the subdivision in PalaeoCommunities (PCOMs, Raia et al. 2005; 2006a) allowed to use these time intervals that, even if uneven, have a significant palaecological meaning. For instance, *Canis etruscus* is present in nine localities of Upper Valdarno PCOM. This PCOM grouped together 14 local assemblages. As a consequence, *C. etruscus* occupancy in Upper Valdarno PCOM is equal to 9/14 = 0.643.

Several general principles were validated from the analysis of Italian species occupancy through Plio-Pleistocene:

- the distributional properties of species occupancy in each PCOM resemble that observed for the species abundance in extant ecosystems (that is: occupancy is reliable estimate);
- species tend to change their occupancy in time exhibiting a peaked trajectory (that is: species are less abundant when they invade a community and before their extinction);
- species with higher occupancies survive longer.

Meloro et al. (2007) utilise species occupancy to determine predator-prey relationship in Italian communities at macro-palaeo ecological scale. Basically, Meloro et al. (2007) corrected species occupancy according to the expected n. individuals/ Km^2 from species body mass (Silva and Downing 1995). This correcting factor is formalised as the ADI (Abundance Disparity Index) metric: when ADI is equal to 0 than abundance extracted from fossil record occupancy data is the same as expected for species body mass; ADI < 0 indicates that a species is rare in the fossil record while the opposite indicates that a species is more abundant than expected for its body mass.

As expected from recent theory on mammalian herbivores abundance (Owen-Smith 1980; Sinclair et al. 2003), such index was negatively correlated with the intensity of predation computed for each Plio-Pleistocene large herbivore (considered as potential prey species): that is abundant herbivores were less affected by predation and survived longer. Most interestingly, key Plio-Pleistocene prey were identified according to previous taphonomic observations.

At the same time, Raia et al. (2007) evidenced a significantly higher proportion of mammalian predators relative to their prey during Upper Villafranchian. This high rate is explained in terms of ecosystem functioning: herbivore richness was controlled by predators during Late Villafranchian while, from Galerian ungulates became heavier (thus some of them were even able to escape predation) and were more controlled by resources (e.g. low quality "steppe grass").

These recent studies clarified most aspects of ecosystem functioning during Plio-Pleistocene in Italian mammal communities. But other aspects remain obscure. Here, I will cover different topics particularly related with evolutionary ecology of large carnivores.

Does carnivores occupancies change through time? What factors influenced carnivore abundance during Plio-Pleistocene? Does predation alter morphological evolution of prey?

These questions look simple but they cover several topics of carnivores biology. Firstly, most large carnivores are rare species and the influence of prey biomass on their abundance is usually significant (Schaller 1972; Mech 1980; Carbone and Gittleman 2002). Secondly, large carnivores are very competitive species and interspecific interactions alter both species behaviour and relative abundances (Schaller 1972; Kruuk 1972; Durant 1998, 2000; Palomares and Caro 1999; Linnel and Strand 2000; Creel and Creel 2002; Woodroffe and Ginsberg 2005).

Consequently, several possible causes and effect will be analysed separately in order to extrapolate an organic theory valid for Plio-Pleistocene large carnivores.

7.2 Species occupancy in Plio-Pleistocene large carnivores

25 Plio-Pleistocene large carnivores (see Introduction) are here considered and occupancy values as well as ADI are extracted from the Italian fossil record (n = 64; data as in Raia et al. 2006a; Meloro et al. 2007). As occupancy changes through time species by species (Raia et al. 2006a) it could be possible that such change could occur on carnivore guild taken as a whole. In this case Jonckheere-Terpstra test allows to consider successive PCOMs as time series and to evidence if changes in species occupancy or ADI occur in time (see also Raia 2003). The test is not significant for both variables (Table 7.1).

	occupancy	**ADI**
N. of Levels in PCOMs	8	8
N	64	64
Observed J-T Statistic	749.500	891.000
Mean J-T Statistic	889.500	889.500
Std. Deviation of J-T Statistic	84.793	85.433
Std. J-T Statistic	-1.651	.018
Asymp. Sig. (2-tailed)	.099	.986

Table 7.1: Jonckheere-Terpstra statistic on occupancy and ADI values of 23 large carnivores distributed in 8 PCOMs.

Interestingly, box plots evidenced several outliers (Figs. 7.1, 7. 2). In the case of species occupancy, canids are usually outliers in having higher occupancy than the other carnivores. And when these outliers are excluded Jonckheere-Terpstra evidenced significant differences of large carnivore occupancy through time (Observed J-T = 497.000; Mean J-T = 633.500; Std Deviation of J-T = 65.667; Std. J-T = -2.079; p (2 tailed) = 0.038). In particular, it is possible to note a significant decrease in carnivore occupancies from Up Valdarno to ValdiChiana and from Galerian 1 to Aurelian.

On the other hand, ADI values are indicative of the relative abundance or rarity of large carnivores through PCOMs. It is important to note that ADI values are usually higher than 0 (see Fig. 7.2). This means that large carnivores abundance is generally overrepresented in the Italian fossil record. That is: taphonomy includes a significant biases allowing a high rate of fossilisation for large carnivores in spite of their rarity expected from their body mass in natural ecosystems.

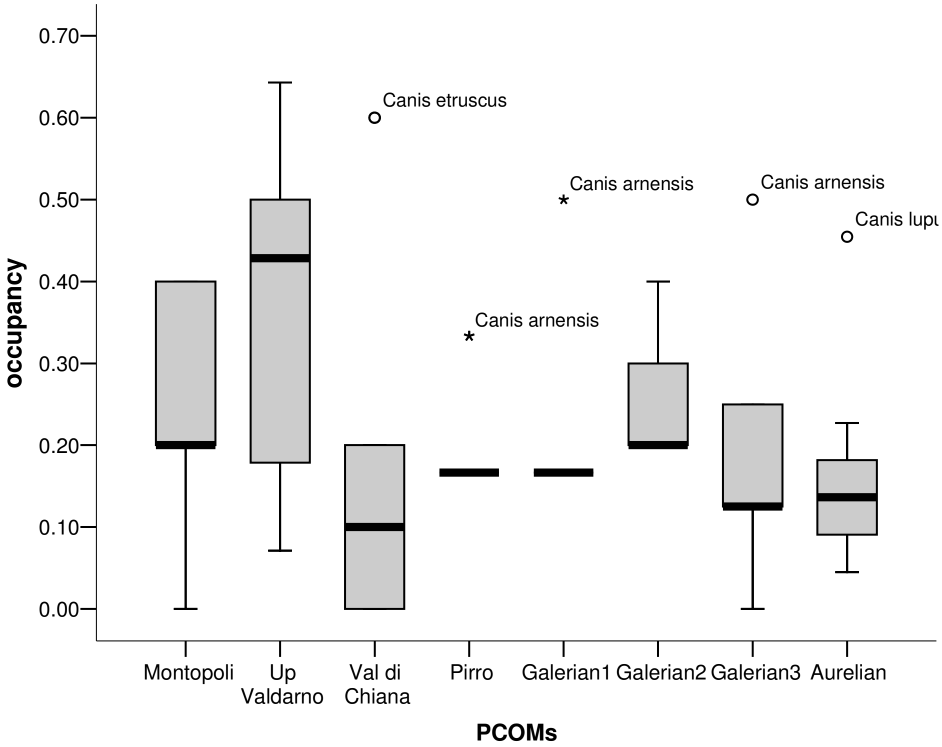


Figure 7.1: Box plot of large carnivore occupancies through PCOMs. Black band is the median while grey box length represents the interquartile range of occupancy distribution. White circles and stars: outliers.

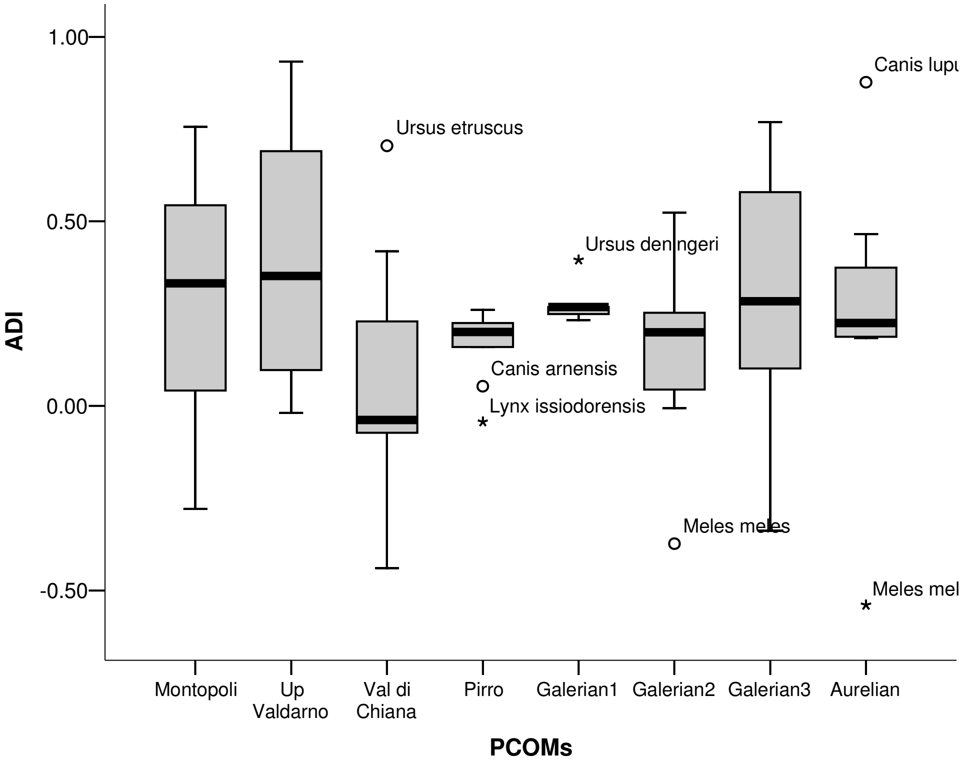


Figure 7.2: Box plot of large carnivore ADI through PCOMs. Black band is the median while grey box length represents the interquartile range of ADI distribution. White circles and stars: outliers.

It is worth mentioning that species occupancy obtained for large carnivores is not correlated with species body mass –log transformed- ($n = 64$; $r_s = -0.146$; $p = 0.251$) but ADI does exhibit a strong positive relationship ($n = 64$; $r_s = 0.423$; $p < 0.0001$).

Possible source of variability in large carnivore species abundance could be evidenced by looking at the mean, the geometric mean, the maximum and the minimum value of species occupancy and ADI for each large carnivore. In this case, time is not considered as categorical variable but other factors are explored like taxonomic affiliation, body mass categories or dietary adaptation. This analysis allows to determine if some families or ecological adaptations were more favoured than others in exhibiting higher relative abundance in the fossil record.

In general, Kruskall Wallis does not evidence any significant difference in occupancy values among taxonomic, body mass and diet categories (Table 7.2).

		Mean_adi	**max_adi**	**min_adi**	**mean_occ**	**max_occ**	**min_occ**
Family	Chi-Square	9.089	5.611	9.704	6.132	4.139	2.578
	df	4	4	4	4	4	4
	Asymp. Sig.	0.059	0.230	0.046	0.19	0.388	0.631
Diet	Chi-Square	1.855	3.506	3.419	0.131	1.677	2.235
	df	2	2	2	2	2	2
	Asymp. Sig.	0.396	0.173	0.181	0.937	0.432	0.327
BW_cat.	Chi-Square	7.843	1.718	7.326	4.497	4.082	2.003
	df	4	4	4	4	4	4
	Asymp. Sig.	0.097	0.787	0.120	0.343	0.395	0.735

Table 7.2. Kruskall Wallis statistics performed on mean, maximum and minimum values of both ADI and species occupancy among taxonomic and ecological categores (N = 25).

Minimum values of ADI is the only variable which is significantly different among families (Fig. 7.3). As ADI reflects the relative abundance or rarity related to body mass, this means that most canids, when rare, tend to be underrepresented respect to their body size. Felidae are overrepresented if compared to both Hyaenidae and Ursidae. Such effect reflects just a taphonomic bias and not a clear ecological phenomenon.

On the other hand, if we look at the variability in mean occupancies (Fig. 7.4), there is a slight signal that canids have the highest values although it is not significant.

But in general these results demonstrate that no significant changes occur in the relative abundances of large carnivores through taxonomic groups and ecological categories. A significant decrease in relative abundance occurs by the end of Villafranchian and continuously from Galerian through Aurelian. It is worth mentioning, that carnivores are usually more abundant in the Italian fossil record than expected by their body mass. This reflects a taphonomic bias that can generally be produced by the behaviour of most large carnivore species (hyenas, leopards) which used sites as den or shelter accumulating bones of other mammals (see Palmqvist et al. 1996; Mazza et al. 2004).

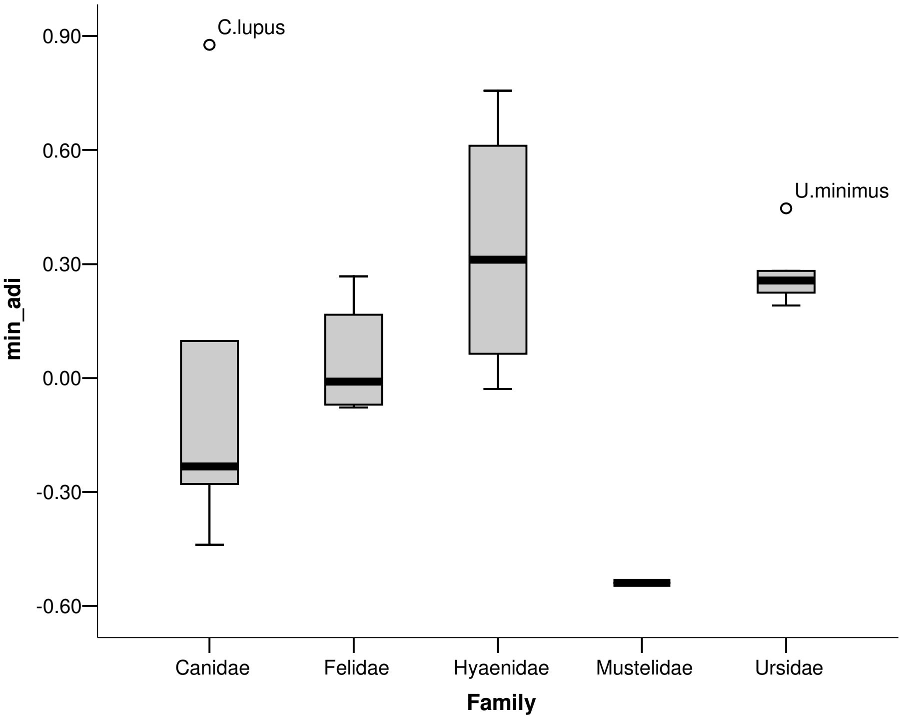


Figure 7.3: Box plot of large carnivore min ADI through PCOMs. Black band is the median while grey box length represents the interquartile range of min ADI distribution. White circles: outliers.

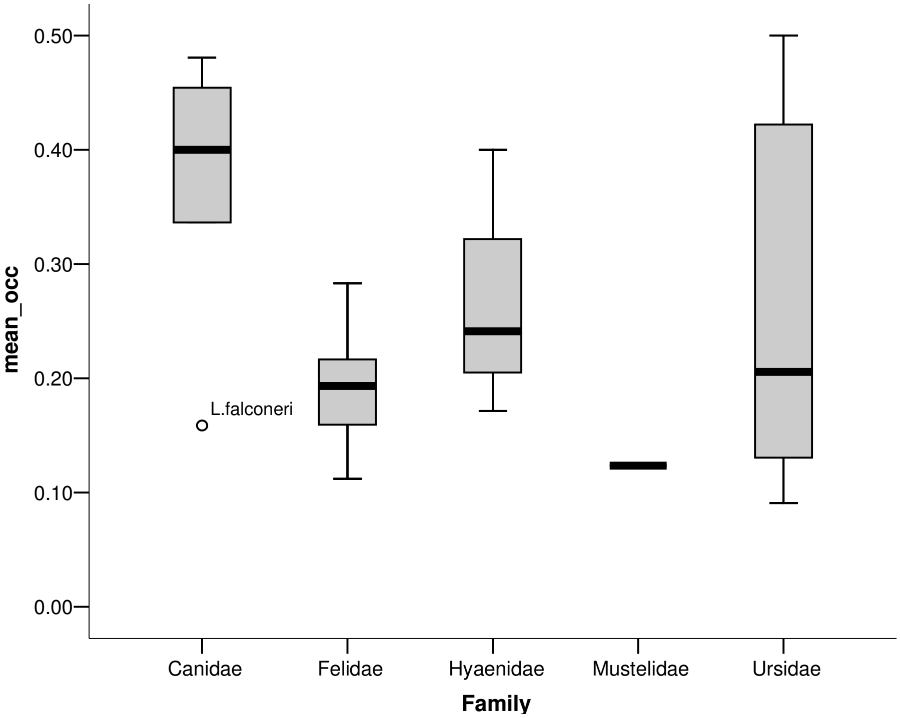


Figure 7.4: Box plot of large carnivore mean occupancy through PCOMs. Black band is the median while grey box length represents the interquartile range of mean occupancy distribution. White circles: outliers.

7.3 Predator-prey abundances

As most of Italian Plio-Pleistocene large carnivores were active predators it is likely that their abundance could have been influenced by the abundance of large mammalian herbivores. In order to test such hypothesis, I firstly explore herbivore occupancy and ADI values through time.

Herbivore data belong to 56 species recorded in the Italian Plio-Pleistocene fossil record (as in Raia et al. 2006a; Meloro et al. 2007). All members of Artiodactyla, Perissodactyla and Proboscidea were included. Jonckheere-Terpstra test evidences significant changes of herbivores occupancies through time but not of ADI (Table 7.3). This trend still to be significant (N = 92; Observed J-T = 1545.500; Mean J-T = 1847.000; Std Deviation of J-T = 146.530; Std. J-T = -2.058; p (2 tailed) = 0.040) if we exclude Plio-Pleistocene megaherbivores (species > 2000 kg)

	occupancy	ADI
N. of Levels in PCOMs	8	8
N	117	117
Observed J-T Statistic	2528.000	3043.000
Mean J-T Statistic	2987.000	2987.000
Std. Deviation of J-T Statistic	209.846	210.365
Std. J-T Statistic	-2.187	0.266
Asymp. Sig. (2-tailed)	0.029	0.790

Table 3: Jonckheere-Terpstra statistic on occupancy and ADI values of 56 herbivores distributed in 8 PCOMs.

An interesting pattern is evidenced by graphically comparing changes in occupancies between predators (all excluding badger, cave bears and *Nyctereutes megamastoides*) and large herbivores (including megaherbivores) (Fig. 7.5). A decrease in occupancy occurs among herbivores during Late Villafranchian from Upper Valdarno to Pirro. Between Pirro and Galerian 2 there is sharp increase in herbivore occupancies but a decrease occurs again continuously since Aulerian. This fact confirms the previous observations for large carnivores (significant when outliers are excluded) suggesting a real ecological phenomenon in the reduction of large mammal abundance occured from Up Villafranchian to Pirro and Galerian 2 until Aulerian.

In order to validate the eventual inter-independence between predator and prey abundance, I computed the theoretical biomass of both predators and herbivores for each PCOM. The relative abundance expected for each species in the PCOM was computed directly using occupancy raw data. The transformation factor (TF see Meloro et al. 2007) allows to change occupancy dimensionless data in n. of individuals/km^2. It is worth mentioning that these values are not biologically reliable because they reflect the proportion of species occupancy in the fossil record but they can represent a proxy for relative abundance.

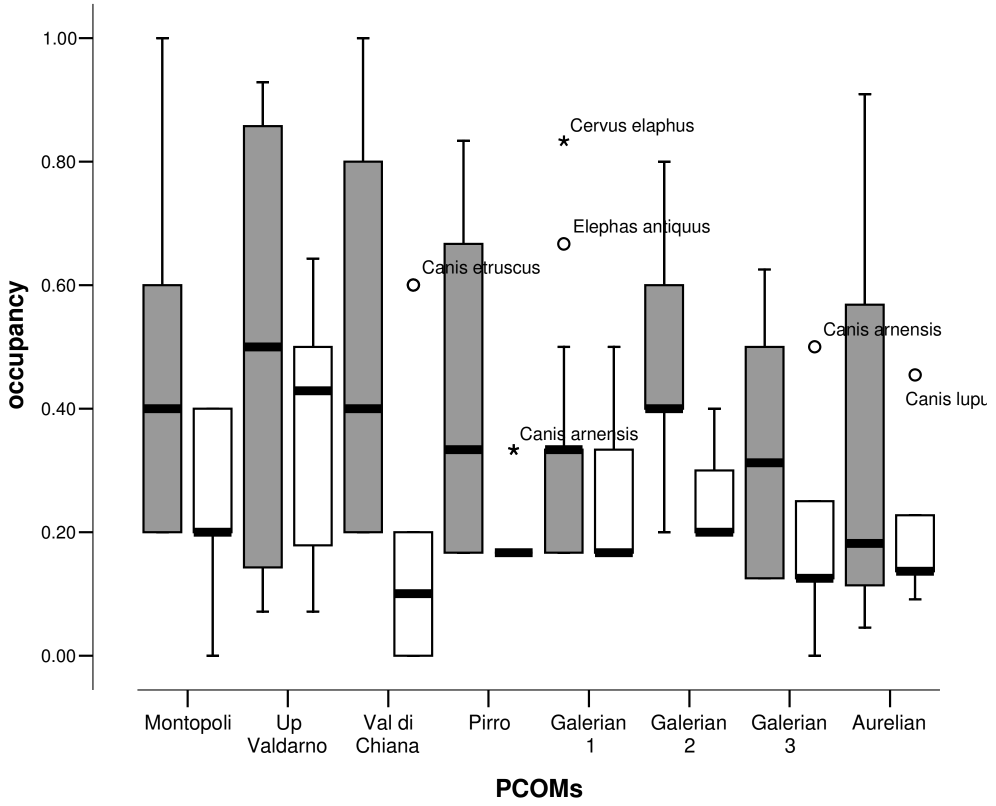


Figure 5: Box plot of large carnivore and herbivores mean occupancy through PCOMs. White box: carnivores, grey box: herbivores. Black band is the median while box length represents the interquartile range of mean occupancy distribution. White circles and stars: outliers.

For instance, the species *Mammuthus meridionalis* occurs in 5/5 local assemblages of PCOM Val di Chiana. Its occupancy is equal to 1.00 and as the TF for Val di Chiana is 1.21 its relative abundance (n ind/km^2) is: 1.00 * 1.21 = 1.21. This value represents the abundance observed in the fossil record that is quite different from the abundance expected by virtue of *M. meridionalis* body size (0.22 ind./ km^2).

The observed abundance was computed for both predators and herbivores in each PCOM and then summed in order to have a metric comparable with the total biomass of both predators and herbivores for each PCOM (cfr. Schaller 1972 for extant ecosystems).

From the scatter plot, it is possible to evidence that among Villafranchian PCOMs the biomass of large predators of Up Valdarno is too high if compared with that of herbivores (Fig. 7.6). This result is expected especially on the light of the significantly high predator/prey ratio (Raia et al. 2007). A non-significant relationship occurs between total observed biomass of predators and prey (n = 8; r_s

= 0.470, p = 0.240), but the exclusion of Upper Valdarno outlier reveals an expected positive trend (n = 7; r_s = 0.826; p = 0.022; Fig. 7.6).

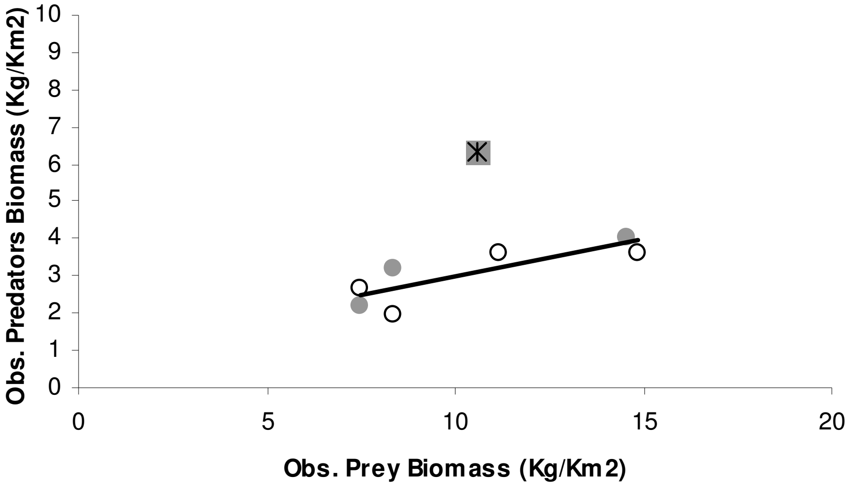


Figure 7.6: Scatter plot of Observed Predator vs Prey Biomass. Grey circles are Villafranchian PCOMs; white circles are Galerian and Aurelian PCOMs. Square with cross is Up Valdarno.

Again, this result validates previous observations on predator prey relationship in large mammals of Italian peninsula during Ice Ages (Raia et al. 2007; Meloro et al. 2007). Interestingly, occupancies estimates change synchronously through time in both predators and prey. Although such values are not biologically reliable, they can be used to validate macroevolutionary trends expected under predator-prey theories. In particular, the observed total predator biomass in each PCOM is positively influenced by prey biomass as it happens in extant mammalian communities (see Schaller 1972; Prins and Reitsma 1989; Kawanishi 2002; Mills 2005; Jędrzejewska and Jędrzejewski 2005; Boutin 2005).

7.4 Running wolves, running deer

The effect of prey abundance on large carnivores abundance is a common rule in macroecological literature, but Italian Plio-Pleistocene fossil record offers another important opportunity to test the hypothesis of "arm race" that is: if changes in long bone morphology occurs in large predator guild through time we expect a significant change also in their prey.

Janis and Wilhem (1993) already tested this hypothesis on North American Cenozoic large mammals founding no coordinated changes in mt/f ratio between predators and their prey. Significant changes occurred only in very dramatic climatic events which generated a significant turnover in both carnivores and ungulates. But, Janis and Wilhem (1993) underlined also the fact that few Plio-Pleistocene specimens were included in the study. The cyclical change in climate could have affected simultaneously predators and prey. Here, I present a similar test by considering the Italian Plio-Pleistocene faunal lists. PCOMs are considered as the time units to analyse mt/f ratio changes in mammalian communities. Triversa was excluded because few data on mt/f were available for herbivores.

In keeping with Janis and Wilhem (1993) the mt/f ratio of large carnivores (see Chapt. 5 for its computation) was considered only for large digitigrade predators. For this reason, I excluded all Italian Plio-Pleistocene Ursidae together with the omnivores *Nyctereutes* and *Meles*.

Among prey, I included all large herbivores except proboscideans and hippos. A review of European literature allowed to obtain reliable mt/f estimates on 26 species (belonging to family Bovidae, Cervidae, Suidae, Equidae and Rhinocerotidae) (Appendix 5). When possible metatarsals and femur length were obtained for each species from Italian fossil sites. Multiple measurements for one long bone element were combined and arithmetic mean was used (same procedure in Chapt. 6).

For eight species it was possible to combine reliable measurement of mt length (taken from the literature) with estimated length of femur by using allometric equations based on body mass or tibia length (3 cases) as the explanatory variable (data in Christiansen 2002). It is worth noting that the body mass of extinct ungulates was predicted by using craniodental features (see Meloro et al. 2007) hence estimates of femur length can be reliable.

The course of mt/f ratio through 8 successive PCOMs in both predators and prey was analysed with Jonckheere-Terpstra test. No significant changes occur for both predators and prey in mt/f (Table 7.4).

	Pred.mt/f	**Prey mt/f**
Number of Levels in PCOM	8	8
N	51	78
Observed J-T Statistic	461.000	1404.500
Mean J-T Statistic	559.000	1321.000
Std. Deviation of J-T Statistic	60.601	114.603
Std. J-T Statistic	-1.617	.729
Asymp. Sig. (2-tailed)	.106	.466

Table 7.4: Jonckheere-Terpstra statistic on both predators and prey distributed in 8 PCOMs.

The stability of mt/f ratio through time can be evidenced by looking at box plot computed for both predators and large herbivores (Fig. 7.7). No outliers occur among carnivores while for herbivores *Eucladoceros dicranios* and *Sus strozzii* exhibit the highest and the lowest value, respectively for Upper Villafranchian herbivore community.

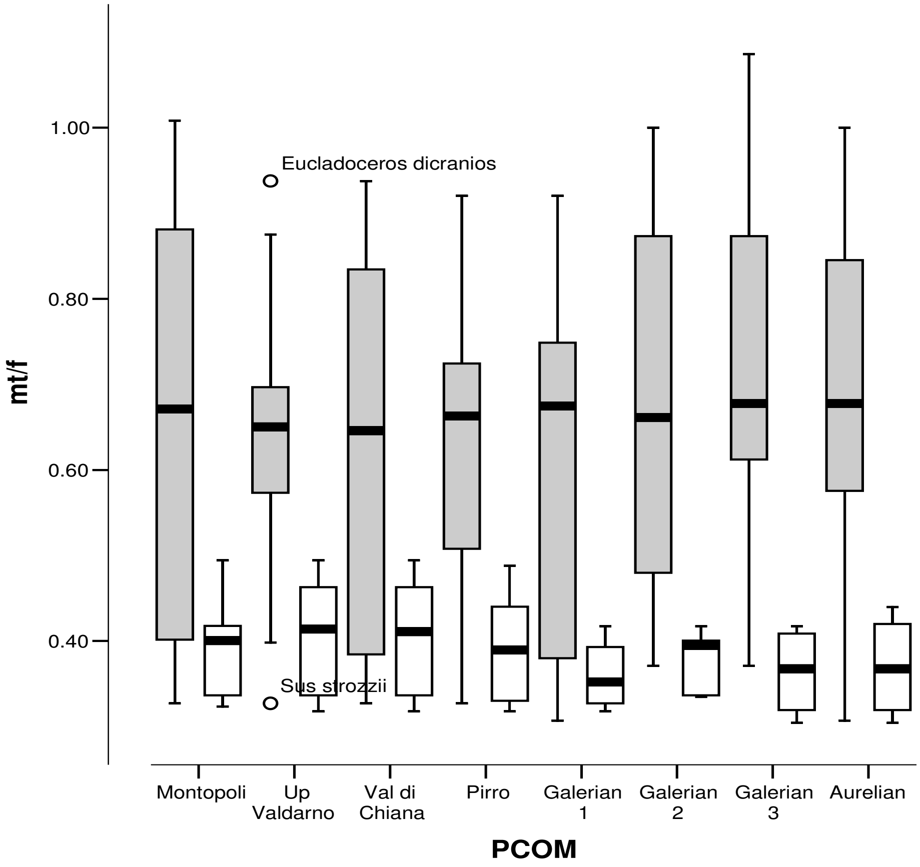


Figure 7.7: Box plot of large carnivore and herbivores mt/f through PCOMs. White box: carnivores, grey box: herbivores. Black band is the median while box length represents the interquartile range of mean occupancy distribution. White circles and stars: outliers.

A possible trend in carnivores is exhibited by the transition Pirro/Galerian 1 suggesting that larger time series could be used as categories. But even dividing time series in Villafranchian, Galerian and Aurelian, no significant changes occur in mt/f for both carnivores and ungulates (Table 5).

	Pred.mt/f	**Prey mt/f**	**Prey < 200 kg mt/f**
Number of Levels in Villafr., Galer., Aur.	3	3	3
N	24	48	20
Observed J-T Statistic	64.5	371	58.5
Mean J-T Statistic	89.5	377.5	66.5
Std. Deviation of J-T Statistic	18.35884	52.46133	14.34873
Std. J-T Statistic	-1.36174	-0.1239	-0.55754
Asymp. Sig. (2-tailed)	0.173279	0.901394	0.577158

Table 7.5: Jonckheere-Terpstra statistic on both predators and prey distributed in 3 successive time series.

Another possible test can be performed by excluding large herbivores > 200 kg. In fact, according to Janis and Wilhem (1993) these forms scale differently resulting in an unexpected lower mt/f value.

But this criteria do not allow to consider PCOMs as a significant time scale because of the lack of data for some PCOMs. Hence the test was repeated only for Villafranchian-Galerian-Aurelian time scale but it is, again, non-significant (Table 7.5).

According to previous theories and observations on morphological changes in carnivores (see Chapt. 4, 5) the results obtained are expected. It is worth noting that most PCOMs lack data for several ungulates but the principal species were included with reliable estimates supporting that the trend less pattern in mt/f is genuine. In spite of the high diversity (compared with that of European extant fauna) in both carnivores and herbivores, Plio-Pleistocene species exhibited already morpho-ecological variability similar to extant forms. The climate changes determine only the taxonomic replacement and the abundance of species without altering morphological variability.

This fact confirms also the previous findings on feeding apparatuses in carnivores (see Chapter 4) and most interestingly detect similar pattern for herbivores whose although body mass change significantly in time (see Raia et al. 2007) were not affected on long bone morphology.

7.5 Interspecific competition in Plio-Pleistocene large carnivores

Large carnivore populations are usually regulated by multiple factors. Although their relationship with abundance of prey is usually striking, another important feature needs to be considered: the interspecific interaction. This factor has an increasing importance in ecological literature especially because it can act as a demographic regulator modifying also species distribution (Palomares and Caro 1999; Linnell and Strand 2000). Several examples on extant species demonstrates this issue: the population of coyotes in Yellowstone had a rapid expansion after the historical extinction of wolves; the distribution of African wild dog and cheetah is widely affected by abundance of lions and hyenas (Durant 1999, 2000; Creel and Creel 2003; Mills 2005).

This fact is theoretically expected because large carnivores are species with a high degree of interaction whose extreme case result in the interspecific killing or the so called phenomenon of Intra Guild Predation (IGP, see Daugherty et al. 2007 for recent review of the literature). Palomares and Caro (1999) reviewed this phenomenon in Carnivora and general rules were extrapolated:

- larger carnivores kill smaller;
- interspecific killing is likely to occur in members of the same family;
- canids and felids are the families with the highest level of interspecific killing.

Recently, Donadio and Burskirk (2006) confirm these patterns and observe a high level of interaction due to diet overlap among species whose body mass is more similar.

The increasing evidence that species interaction is an important factor in moulding large carnivore species composition as well as abundance came also from studies of morphological variability. Davies et al. (2007) consistently demonstrated that co-occurring carnivores are morphologically dissimilar (especially on the basis of carnassial length) in agreement with the theory of character displacement (Dayan and Simberloff 2005 for a recent review). It is likely that interspeficic competition regulate carnivores species composition and affect zoogeographical species distribution. This observation has been validated also on Plio-Pleistocene large carnivores (only canids and felids) (García and Virgós 2007). But, because of the bias introduced by the fossil record, character displacement in canids was only observed in Valdarno site but not in other Pleistocene European sites. For felids, character displacement was observed on both Villafranchian and Pleistocene sites.

On the light of this theoretical evidence, the Italian fossil record and the occupancy metric offer a unique opportunity to test if interspefic competition could have affected the abundance of Italian large carnivores during Plio-Pleistocene.

As fossils rarely offer the opportunity to understand what degree of species interaction occurred in the past, I apply general rules of interspecific killing. According to species composition in each PCOM it is possible to describe an index of species interaction by taking into account the relative body mass (in Meloro et al. 2007). Basically, the smallest species in each large carnivore guild should exhibit the highest value of species interaction (it is likely that it can be killed by more carnivores) other than the largest form that is vulnerable only before becoming adult.

Unfortunately, few Italian sites allow to obtain age class of each carnivore species. As a consequence, I introduced the ISKI: Index of InterSpecific Killing which simply considers the mass of each carnivore present in each PCOM. If *n* is the number of large carnivores, and the body mass (BW) of species *j* is equal to *x*, then its ISKI is:

$$\Pi\ n - 1_{(BW> x)} / n - 1$$

For instance the European badger is the smallest of large carnivore guild of Aurelian (n =7) and its ISKI = 6/6 = 1. On the other hand, the cave bear is the largest species and its ISKI = 0.

It is worth mentioning that this index is a crude but useful metric because it is based on body mass difference (the most important factor in carnivores) without considering other factors like the number of species in the same family or other possible morphological attributes that allow species to avoid competition.

It could be possible to test if this index is relevant in predicting species relative abundance quantified by occupancy and ADI. A simple linear regression model was performed on a general sample of 64 species records available from the Italian fossil record. The model results in a non significant relationship between ISKI (independent) and species occupancy (b = 0.056, $R^2 = 0.012$; p = 0.385) but, interestingly, a significant negative relationship is evidenced when ADI is considered the predicted variable (Fig. 7.8; b = -0.402; $R^2 = 0.176$; p = 0.001).

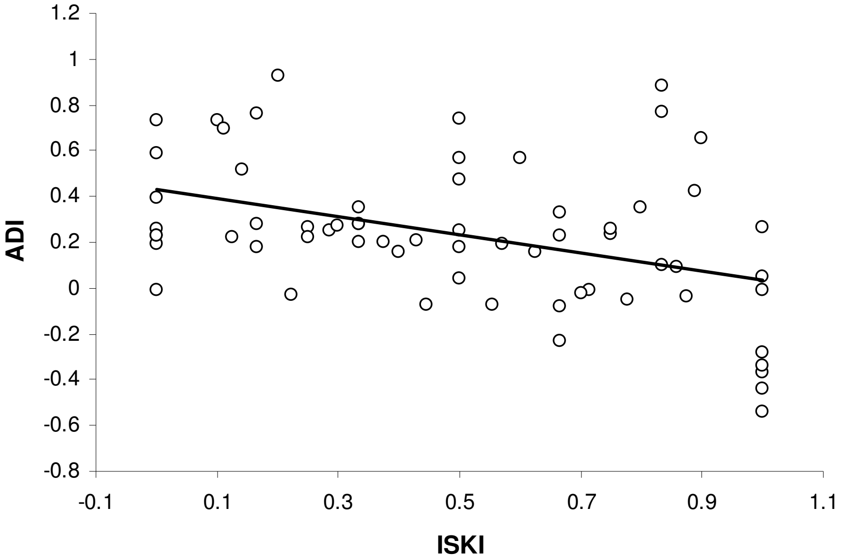


Figure 7.8: Linear regression calculated for ADI on ISKI.

That is: species more likely to be killed are also usually rare in the fossil record.

When each PCOM is considered separately a significant negative relationship is evidenced between ADI and ISKI only at Galerian 2 (Table 7.6). It is worth mentioning that there is a general tendency to a negative relation except for Aurelian.

	N	Rs	P
Montopoli	7	-0.429	0.337
Up Valdarno	11	-0.582	0.06
ValdiChiana	10	-0.552	0.098
Pirro	9	-0.663	0.067
Galerian 1	5	-0.4	0.505
Galerian 2	8	-0.952	<0.001
Galerian 3	7	-0.357	0.432
Aurelian	7	0.107	0.819

Table 7.6: Spearman correlation between ISKI and ADI in each PCOM.

Taken as overall, we can certainly consider interspecific competition as a general phenomenon which affected species abundance also in Plio-Pleistocene communities. But this factor is not of primary concern especially if we consider the fact that taphonomic bias occur in several PCOMs like Montopoli, ValdiChiana and Galerian 2. Meloro et al. (2007) evidenced that the mammalian record of these PCOMs resulted in a nested matrix of presence absence data which reveal potential taphonomic agents. Significant evidence on the possible taphonomic bias occurring in the record of Italian Plio-Pleistocene large carnivores are represented by the previous observation that ADI is usually > 0 hence carnivores are overrepresented at macroecological scale.

Mazza et al. (2004) also observe a significant bias in the fossil record of Poggio Rosso. Their data on carnivores reveals a strong bias in favour of one of the smallest canid present at the site *Canis arnensis* with a minimum estimate of 8 individuals (Fig. 7.9).

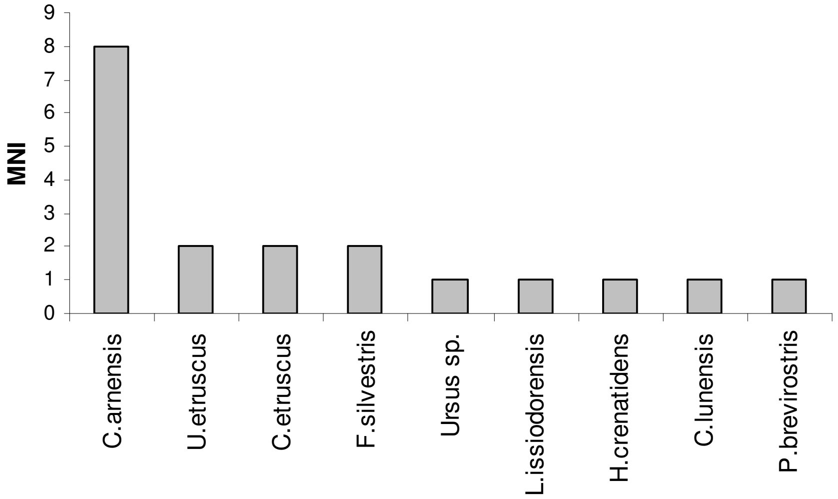


Figure 7.9: Frequency of Minimum Number of Individuals (MNI) estimated in Poggio Rosso (data in Mazza et al. 2004).

It is likely that complex interplay of factors determine large carnivore abundance in the fossil record. This fact does not necessarily limit the use of macroecological data to test hypothesis about species interaction in the past (cfr. Meloro et al. 2007) but such data are limited to broad scale. As a consequence, species alike large carnivores appear to be affected at broad scale by interspecific competition as well as abundance of large herbivores; but a site by site approach should be integrated in order to give a clear answer on which factor had determined relative abundances in the fossil record.

Chapter 8

Mapping Plio-Pleistocene large carnivores of the Italian peninsula

8.1 Introduction

Since the formulation of earliest theories on the history of the Earth, palaeontology had a key role in identifying spatial distribution of extinct organisms and its relationship with geological phenomena (Allasinaz 1983). Under this perspective, the distribution of Plio-Pleistocene large mammals was certainly important to understand the dramatic climatic changes of the last 3 million years ago. As a consequence, species like the mammoth *Mammuthus primigenius* or the cave bear (*Ursus spelaeus*) are generally associated to one of the coldest climatic phase of Europe (Kurtén 1978) even if species evolution was not necessarily related with Milankovich cycles (Lister 2004). Other key Quaternary species are represented by forms still living today in the strict arctic biome like the Artic fox (*Alopex lagopus*) or the reindeer (*Rangifer tarandus*) that in the past extended their range to much lower latitudes.

There are no doubts that such observations evidence a strict link between mammal fauna and Ice Age but how can we quantitatively test such relationship? The mapping procedure is certainly the first instrument which allows visualising extant and extinct species distributions like points in the space. Interestingly, Geographic Information System (GIS) helps in this procedure allowing to integrate spatial information with other kind of data (Aronoff 1989). GIS is a recent methodology defined as any manual or computer based set of procedure which allows to store and manipulates geographical data (Aronoff . These data are resumed in three simple categories: points, polygons and areas which are spatially contextualised in a system of coordinates: latitude and longitudes. With this basic structure GIS allows to map the distribution of rivers on Earth or other objects of interest like altitude data, but also the presence or absence of certain species. In the zoological research, this instrument revolutionizes spatial data analysis because by using GIS it is possible to contextualise the distribution of species graphically with other features like mean temperatures, altitude, vegetation structure. Under this perspective, wildlife management and zoogeography widely applied such methodology to understand what factors affect spatial distribution of extant species (Meffe, Carroll et al. 1997; Corsi et al. 2000).

On the other hand, only recently palaeontologists consider the opportunity of GIS spatial analysis to test relevant hypothesis on species distribution in the palaeontological record.

FAUNMAP (1994) is the most important example concerning Quaternary fauna distribution in North America. On the other hand, Fortelius et al. (2002) applied GIS to visualise the relative distribution of hypsodonty index in Euroasiatic Neogene fossil localities. With this approach, Fortelius et al. (2002) basically assigned to each point (that is a fossil locality) a feature represented by the mean value of hypsodonty which is indicative of relative proportion of grass eaters or browsers recorded in a certain locality. The association of colours to each hypsodonty index shows a marked difference in the distribution of arid areas throughout Eurasia relative to that observed today.

Increasing evidence on the GIS application to palaeontological data came from Sommer and Benecke (2004a, b, 2005) who furnish a spatial data base of several European carnivores in late Pleistocene-early Holocene with particular emphasis on Canidae, Ursidae and Mustelidae.

Interestingly, Martinez-Mayer et al. (2004) modelled potential Quaternary distribution of several North American mammals according to their niche requirements evidencing a striking effect of climate change on species distribution. Eronen and Rook (2004) identified geographically the rule of climate on Neogene primate distributions while Eronen and Rössner (2007) equally applied GIS modelling on the Miocene herbivore fossil record of Germany.

An obvious limiting factor in the spatial analysis of fossil communities is the relative distribution of mainland on the Earth (which changed consistently on million years scale). But it is noteworthy, that such feature can be considered of little relevance for recent geological periods like Plio-Pleistocene.

Physical parameters (mean temperature, precipitation) are difficult to consider as well but several approximations allow to use mammal fauna as good climate indicators. Fortelius et al. (2002) consistently demonstrated that mean hypsodonty index is associated with mean annual rainfall (cfr. Damuth and Fortelius 2001). The relative percentage of brachydont mammals among ungulates is equally informative (Eronen and Rössner 2007) to approximate climate in past communities.

These evidences offer a unique opportunity to analyse spatially the relative influence of climate indices on extinct mammalian communities. Analyses performed on extant mammal fauna do support such statement and most of the causal factors are searched in the Plio-Pleistocene glaciations. In particular, the extant European mammal fauna have been investigated at several scales: Heihikinheimo et al (2007) demonstrate that mammal species composition is biogeographically informative (with small species being more indicative of zoogeographic regions) and Rodriguéz et al. (2006) support the Bergmann rule at macroecological scale of European mammal communities. The ice spread of Pleistocene is considered as a causal factor in European mammal body mass decrease southwards.

Within this increasing amount of GIS application to palaeoecological studies, here I present an example of GIS application to the Plio-Pleistocene mammalian fossil record of Italian peninsula with the particular evidence on large carnivores.

Firstly, the relative distribution of fossil localities will be considered to evidence potential biases in the distribution of fossil record. Than, each local assemblage will be characterised according to its fauna composition. A general model is applied to both large herbivores and carnivores in order to obtain significant palaeobioclimatic data.

8.2 Materials and Methods

Large mammal fossil sites of Italy spanning 3.2 to 0.8 Ma are here considered according to Raia et al. (2005; 2006a, b, 2007) and Meloro et al. (2007). Latitude and longitude data of 69 fossil sites (Local Assemblages) were extracted from literature (data source in Palombo et al. 2003). For most sites, it was not possible to obtain accuracy at level of the second and for this reason latitude and longitudes are recorded only in degrees and minutes.

This spatial data were elaborated through the free software DIVA GIS (Hijmans et al. 2001, Hijmans and Spooner 2001). Basically this software was presented to analyse each kind of geographical data with particular emphasis on species distribution. It allows to apply each option commonly available under GIS ArcView which is the commonest system for spatial analysis (ESRI 1999).

Latitude and longitude data were projected into a simple administrative world map obtained by geographic projection in a unit of decimal degrees.

In order to avoid the effect of small sample size for spatial analysis, localities were clustered according to the mammal age they represent other than PalaeoCommunity (PCOMs *sensu* Raia et al. 2006a). In this way three time series are considered: Villafranchian (from 3.2 to 1.1); Galerian (1.1 – 0.45) and Aurelian (0.45 – 0.3). Although the time bins of these mammal ages are not homogenous they significantly remark changes in the continental mammal fauna (Abbazzi et al. 1997) and allow to compare periods covered by similar number of local assemblages (30 LAs for Villafranchian; 18 for Galerian and 21 for Aurelian).

Several ecological and numerical data have been recorded for each LA according to the faunal list.

The raw number of species was recorded for taxonomic groups: Carnivora, Artiodactyla and Perissodactyla together with the total number of large herbivores (including Proboscidea, *sensu* prey Meloro et al. 2007).

Ecological variables were recorded as well according to the palaeoecology of each large mammal present in a LA. Large herbivores were classified in brachydont, mesodont and hypsodont according to Fortelius et al. (2002). The NOW database together with specific references for extant species were consulted. These categories were scored as 1 (brachydont), 2 (mesodont) and 3 (hypsodont) and a mean hypsodonty index was computed for each locality.

The relative percentage of brachydont and hypsodont ungulate was considered as well.

Large carnivores were classified according to their habitat preference as in Chapter 5, and the relative percentage of grassland adapted carnivores was considered in order to validate potential relationship with ungulate ecological data. If large carnivores tracked the habitat it is likely that the percentage of grassland adapted species is related with local aridity or humidity indices.

Another important ecological data are represented by the mean body mass (in kilograms) calculated for each taxonomic category (Artiodactyla, Perissodactyla and Carnivora) but also for general categories of predators (all Carnivora except omnivorous species e.g. bears, badger, as in Meloro et al. 2007) and their prey (all large ungulate including megaherbivores proboscideans, hippos and rhinos) recorded in each Local Assemblage.

All of these palaeoecological data were spatially analysed by computing thematic grids according to each ecological variable. Grids allow to divide Italian peninsula in several cells that describe, through colours, quantitative data assigned to each point. When in the same cell two fossil localities occurred, the quantitative datum is assumed to correspond to the mean of both data.

The grids were automatically assessed for each mammal age with the software DIVA GIS. Each grid is composed by cells of 50 x 50 km. This parameter was chosen because the spatial resolution of Local Assemblages is not particularly precise and fossil sites usually describe an area other than a specific point in the space. In order to take into account this bias, the grids were computed with a simple procedure without assessing a circular neighbourhood approximation that is usually applied when latitude and longitude are particularly precise (cfr. Hijmans et al. 2001; Hijmans and Spooner 2001).

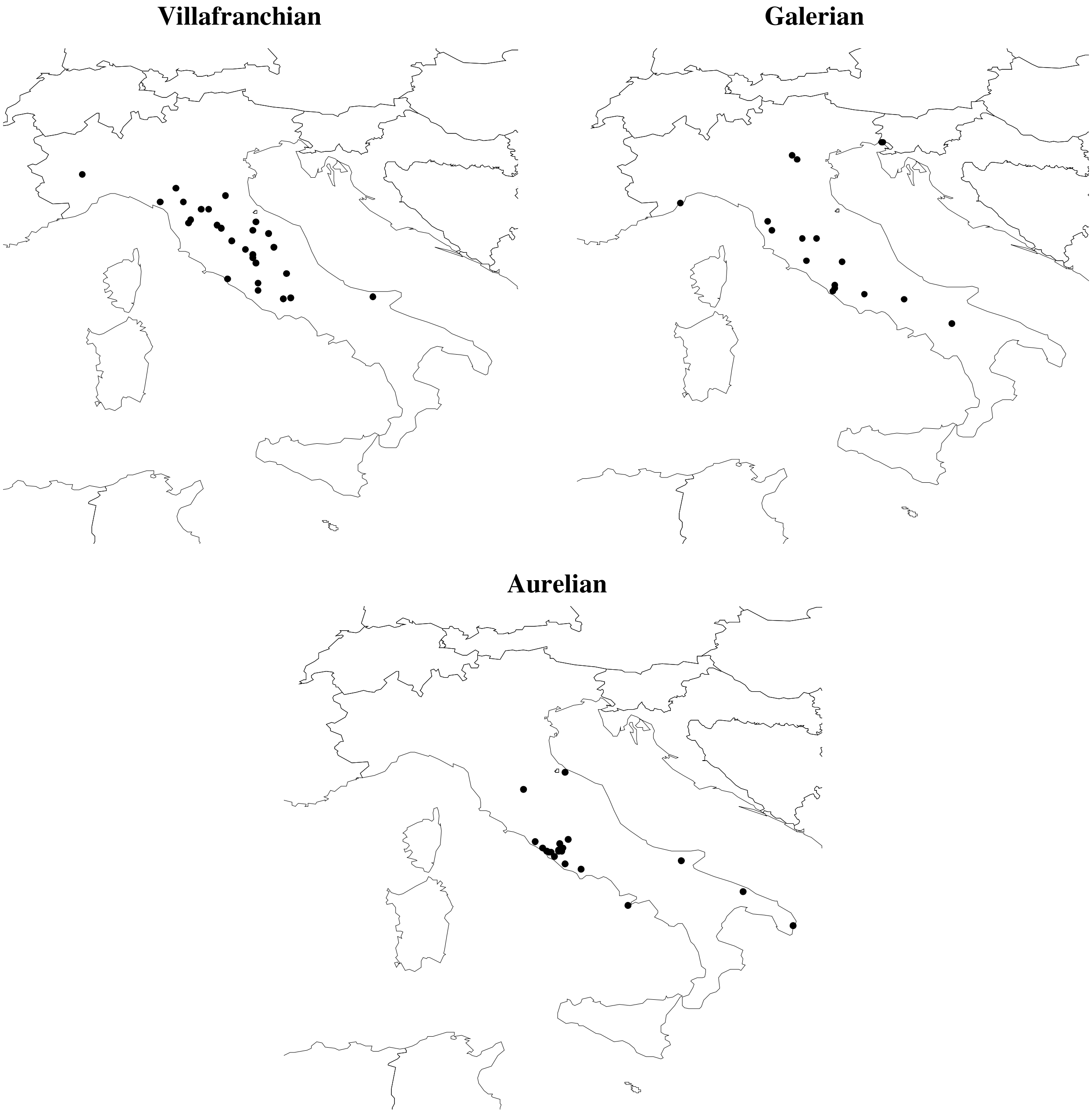
Raw data obtained for each locality were than analysed through non parametric correlations (Spearman rank) in order to validate the potential effect of latitude (or longitude) on palaeoecological data. The correlations were separately computed within each mammal age.

The same procedure was computed to validate the potential relationships between palaeoecological data obtained for each cell within each mammal age.

Although, raw data allow to obtain a local resolution of fossil assemblages, the cell grid data are more useful to realize if the observed spatial trends are realistic at a larger scale (50 x 50 km) not restricted to a single point in the space.

8.3 Results

The spatial distribution of Italian Plio-Pleistocene Local Assemblages is partially homogeneous even if most of the Villafranchian localities come from central-north Apennine while the Aurelian localities are more concentrated in central-southern Italy (Fig. 8.1).



Villafranchian

Galerian

Aurelian

Figure 8.1: Spatial distribution of Local Assemblages for each Mammal Age.

When each mammal age is considered, latitude data are never related with any palaeoecological data associated to each LA. On the other hand, longitude is positively correlated with mean body weight (BW) computed for predator carnivores of Galerian ($N = 18$; $R_s = 0.489$; $p = 0.039$) but negatively associated with mean BW of Aurelian predators ($N = 21$; $R_s = -0.483$; $p = 0.026$). That is: in the Galerian predators tend to be larger at eastern localities while the opposite occur in the Aurelian.

The computed grids are composed of 572, 572 and 468 cells for Villafranchian, Galerian and Aurelian respectively. Most singular cells are empty because of the lack of data and because they cover the sea as well. For Villafranchian 19 cells cover all the LAs, Galerian is covered by 12 cells and Aurelian by 11.

The grid values obtained for both mean hypsodonty and % of brachydont taxa are indicative of changes in climate and for the latter category a significant decrease is observed (3 levels; N = 42; Obs. J-T = 129; Mean J-T = 284.5; Std. Deviation of J-T = 42.604; Std. J-T = -3.65; $p < 0.0001$).

It is important to note that the non significant increase in mean hypsodonty through mammal age (3 levels Jonckheere-Terpstra: $p = 0.070$) is driven by the presence of one outlier grid in the Galerian (Fig. 8.2). When this cell value is excluded the increasing trend is statistically significant (3 levels; N = 41; Obs. J-T = 351; Mean J-T = 269.5; Std. Deviation of J-T = 41.098; Std. J-T = 1.983; $p = 0.047$).

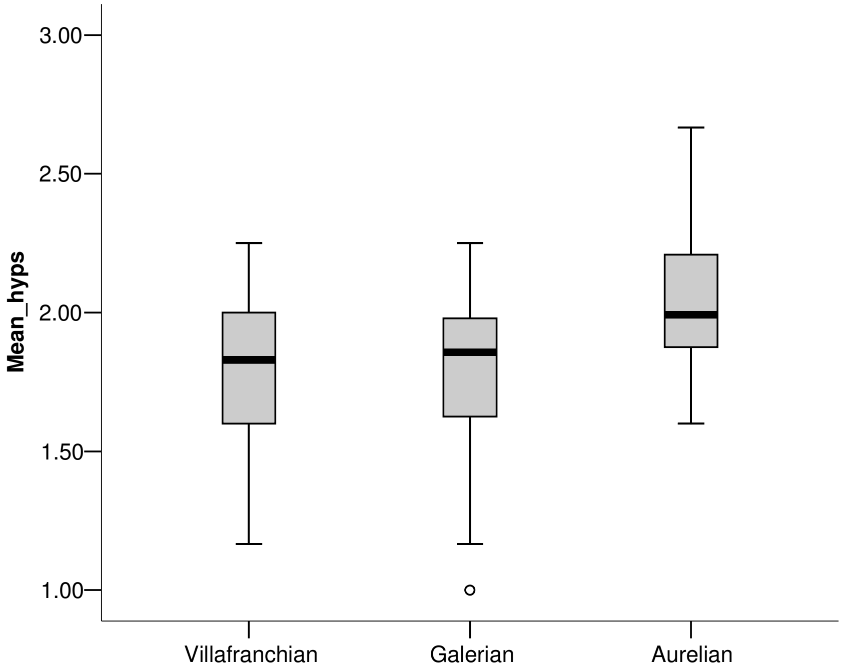


Figure 8.2: Box plot of percentage of mean hypsodonty index per cell. Black band is the median while box length represents the interquartile range of mean % brachydont distribution. White circle: outliers.

It is noteworthy that no other palaeoecological data change significantly through time when cell values are considered. On the other hand, the raw data of LAs allow to evidence differences through time in mean hypsodonty, % of brachydont, number of carnivores and mean body weight of large ungulates (Table 8.1).

In particular, both mean hypsodonty and mean prey body mass increase from Villafranchian to Aurelian while number of carnivores and % of brachydont decrease (Table 8.1).

	Mean_hyps	%Brachy	Carnivores	BW_Prey
N. Levels Mammal_Age	3	3	3	3
N	69	69	69	69
Observed J-T Statistic	1074	303	561	966
Mean J-T Statistic	774	774	774	774
Std. Deviation of J-T Statistic	89.447	89.424	87.704	89.916
Std. J-T Statistic	3.354	-5.267	-2.429	2.135
Asymp. Sig. (2-tailed)	0.001	< 0.0001	0.015	0.033

Table 8.1: Jonckheere-Terpstra statistics on palaeoecological data distributed per LAs in 3 successive Mammal Ages.

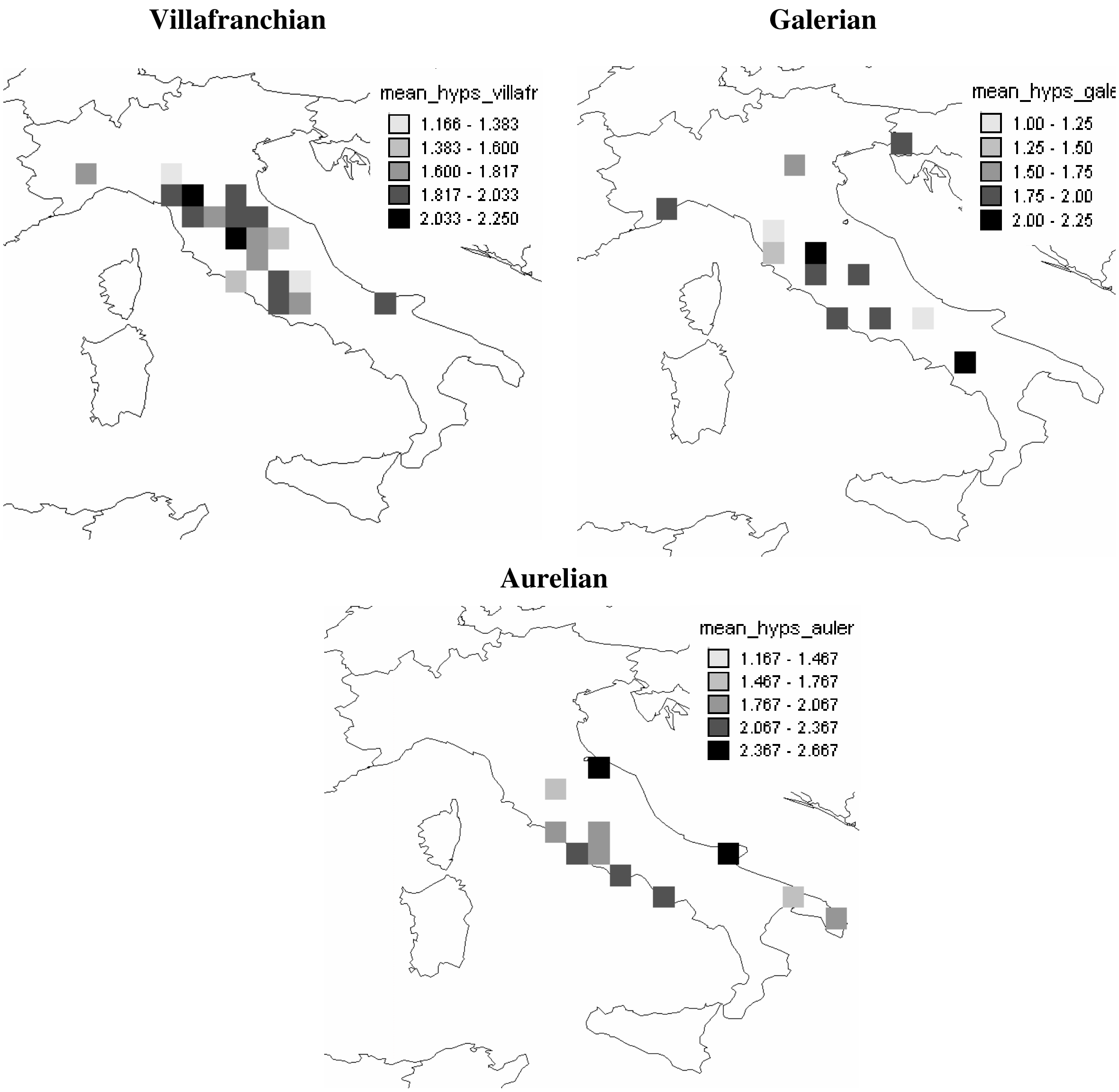


Figure 8.3: Maps of mean hypsodonty index through Mammal Age. Cell size: 50 x 50 km.

The maps of mean hypsodonty identify the distribution of aridity and of mean annual precipitation in each mammal age (Fig. 8.3). During Villafranchian high aridity is recorded in the central-north

Apennine. In the Galerian there is a mix of both arid and humid weather with the highest hypsodonty values recorded in the centre and in the south Apennine. For the Aurelian the highest aridity is on the Adriatic coast even if the southern part of Apulia region was humid. On the Tyrrhenian coast the central Italy has the highest hypsodonty values.

Generally, similar climatic signal can be obtained by looking at the maps generated considering the general percentage of brachydont herbivores (Fig. 8.4).

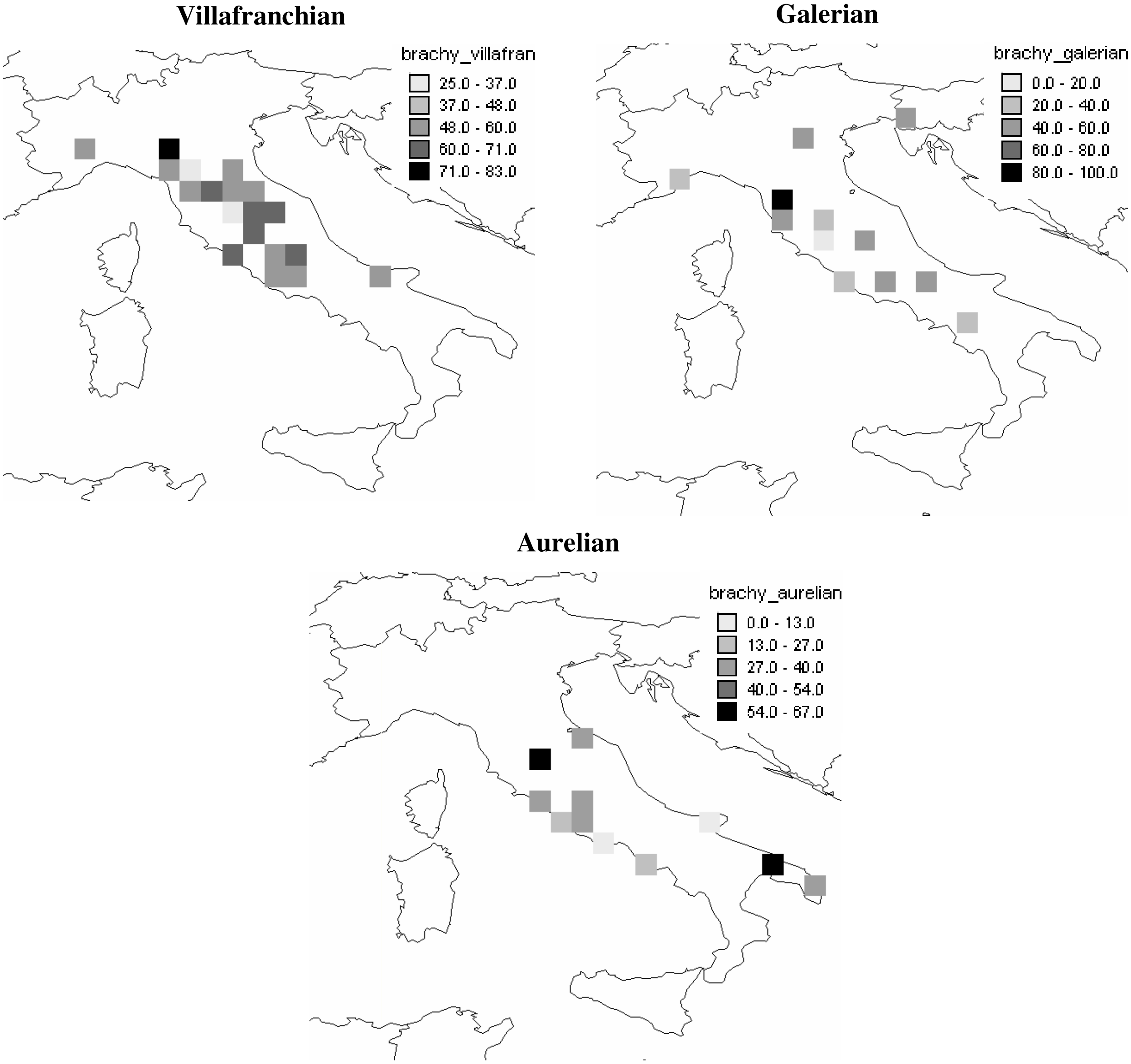


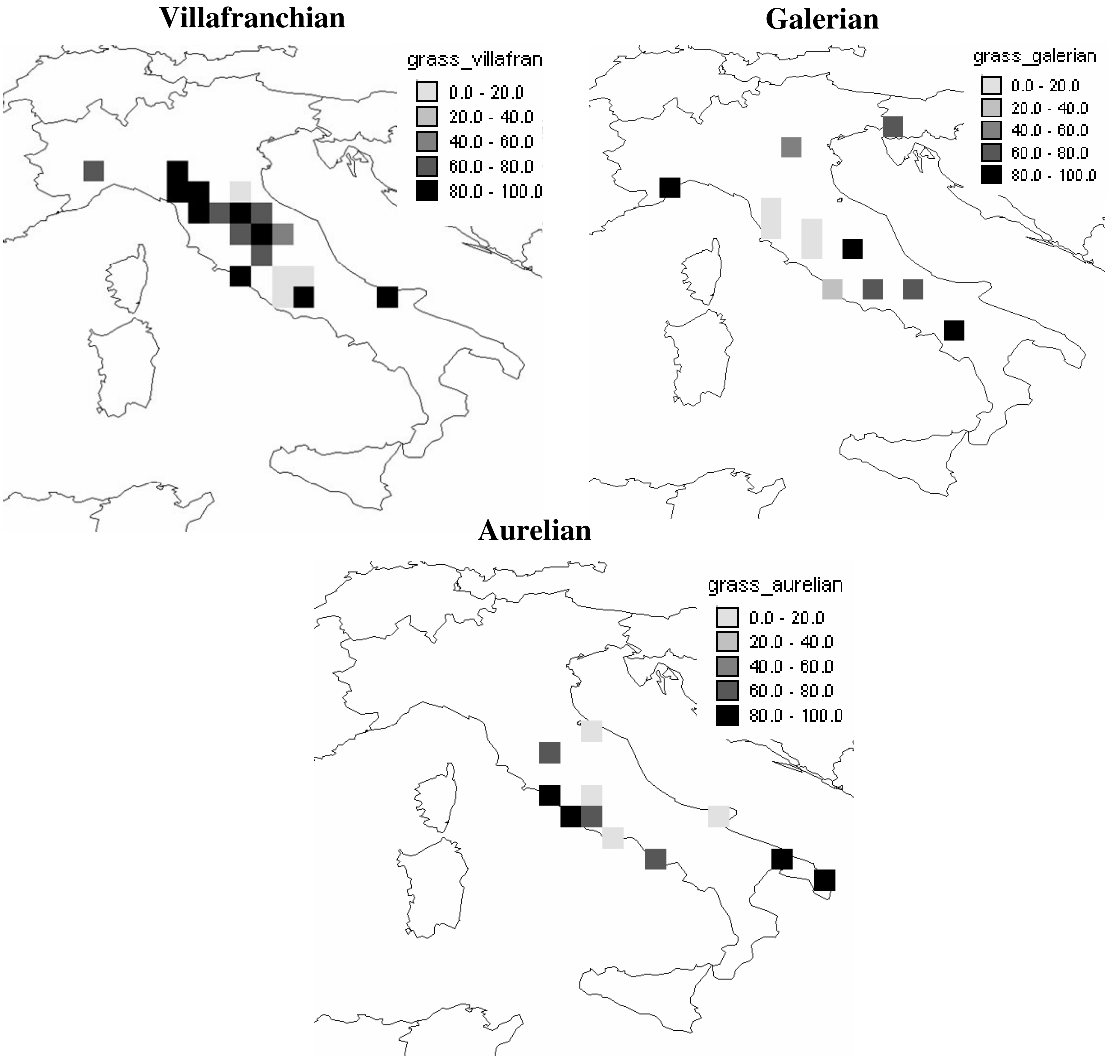
Figure 8.4: Maps of relative percentage of brachydont through Mammal Age. Cell size: 50 x 50 km.

The strict relationship between mean hypsodonty cell values and percentage of brachydont is validated statistically for each mammal age. A negative correlation is always present in all periods:

Villafranchian (N = 19; $R_s = -0.933$; $p < 0.0001$), Galerian (N = 12; $R_s = -0.90$; $p < 0.0001$) and Aurelian (N = 11; $R_s = -0.82$; $p = 0.0018$).

For Villafranchian, mean hypsodonty index is particularly indicative of a negative association with mean body weight of perissodactyls (N = 19; $R_s = -0.66$; $p = 0.0021$). This pattern is validated also when raw data are considered (N = 30; $R_s = -0.52$; $p = 0.003$).

In the Galerian climate indices (both mean hypsodonty index and % of brachydont) are not associated with any palaeoecological data. But it is worth mentioning that in this mammal age % of hypsodont taxa is positively associated with number of carnivores (N = 12; $R_s = 0.62$; $p = 0.0304$) and % of grassland carnivores (N = 12; $R_s = 0.76$; $p = 0.004$) (Fig. 8.5). Raw data validate this latter trend (N = 18; $R_s = 0.73$; $p = 0.001$) even if no significant correlation occur between % of hypsodont taxa and number of carnivores.


Villafranchian

Galerian

Aurelian

Figure 8.5: Maps of relative percent. of grassland carnivores through Mammal Age. Cell size: 50 x 50 km.

During the Aurelian, climate hypsodonty index affects the percentage of grassland carnivorous taxa but with a negative relationship (N = 11; R_s = 0.67; p = 0.023; cfr. Fig. 8.3-5). This relationship needs to be considered with caution because it is driven by the lack of carnivore taxa in three of eleven cells (Fig. 6) reflecting a potential taphonomic bias for certain areas. Raw data evidence the negative trend observed for the cell values but it is not significant (N = 21; R_s = - 0.27; p = 0.234). Interestingly, a positive association occurs between % of brachydont and % of grassland (N = 21; R_s = 0.44; p = 0.046).

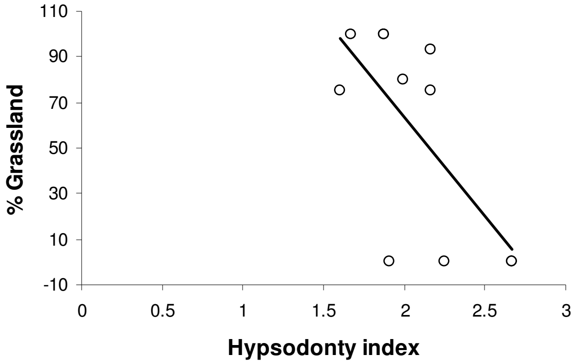


Figure 8.6: Scatter plot of hypsodonty index on percent. of grassland carnivores observed in cell values of the Aurelian.

Diversity trends observed in cell data generally reflect genuine ecological relationships but also taphonomy. In both Villafranchian and Galerian the number of Carnivora is positively associated with both number of Artiodactyla (for Vill.: N = 19; R_s = 0.60; p = 0.006; for Gal.: N = 12; R_s = 0.76; p = 0.004) and number of prey (all large herbivores) (for Vill.: N = 19; R_s = 0.63; p = 0.0036; for Gal.: N = 12; R_s = 0.77; p = 0.0031).

On the other hand, no trend is evidenced in the Aurelian even considering raw data: that is number of carnivores is not associated with prey diversity.

The mean body weight of Carnivora is always positively correlated with the mean body weight of predators (R_s > 0.90 p < 0.0001 for both Villafranchian and Galerian while Aurelian N = 21; R_s = 0.60; p = 0.049). Interestingly, mean body weight of Villafranchian predators is negatively associated with mean body mass of artiodacyls (N = 19; R_s = - 0.66; p = 0.002, Fig. 8.7).

In the Galerian a positive relationship occurs between mean BW of predators (but also of carnivores in general) and mean BW of perissodactyls (N = 12; R_s = 0.78; p = 0.003, Fig. 8). A positive association is evidenced also between mean BW of either carnivores or predators and number of artiodactyls, perissodactyls, prey and carnivores as well (R_s > 0.75, p < 0.005).

For the Aurelian the mean BW of either carnivores or predators is never associated with any parameter of herbivores.

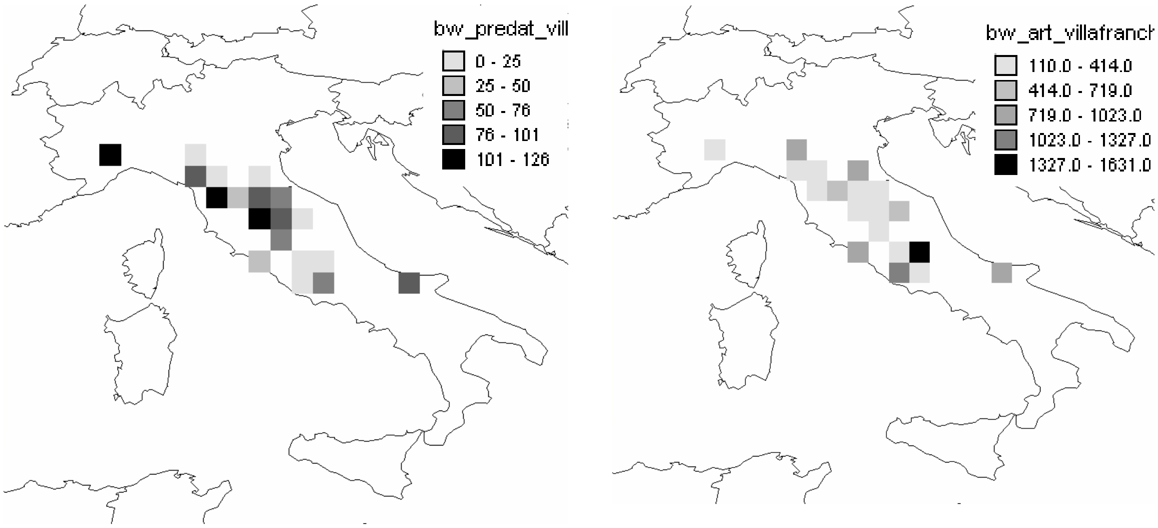


Figure 8.7: Maps of mean body weight of Villafranchian predators and artiodactyls. Cell size: 50 x 50 km.

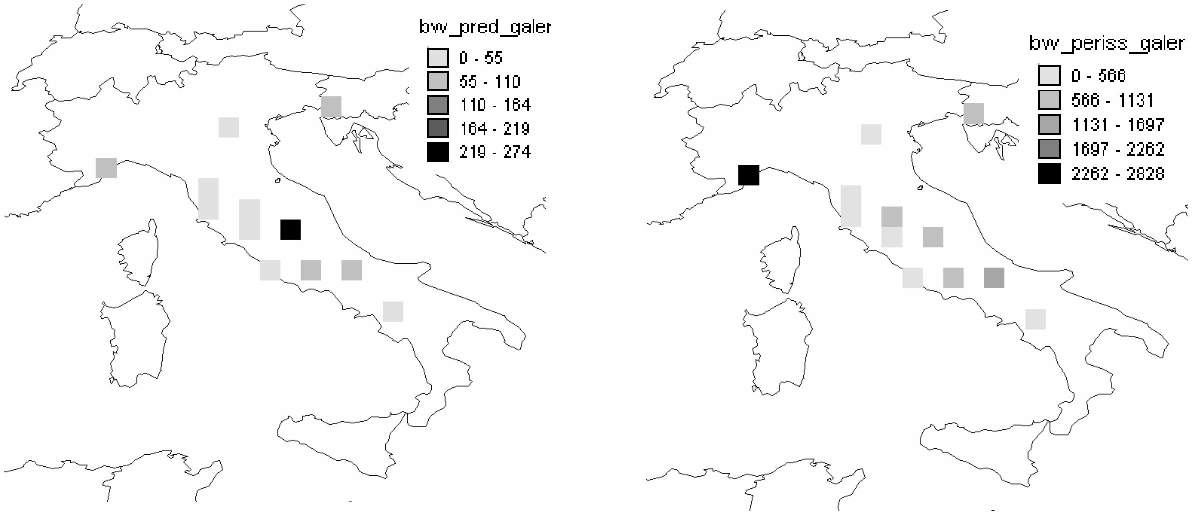


Figure 8.8: Maps of mean body weight of Villafranchian predators and perissodactyls. Cell size: 50 x 50 km.

8.4 Discussion

Mapping procedures visualise relative palaeoclimatic trends towards Plio-Pleistocene in Italian peninsula. Generally indices derived from large ungulate fauna composition validate previous observations on Villafranchian Mammal Age that is characterised by high aridity (especially in north-central Apennine) while in the Galerian and the Aurelian there is a mix of both humid and arid conditions in Italy due to the high frequency of cold and warm cycles (cfr. Suc et al. 1995; Kroon et al. 1998; Zachos et al. 2001; Ghinassi et al. 2004). This observation is clearly expressed in the relative decrease of brachydont ungulates through time. It is plausible that such ungulate category was more affected by Plio-Pleistocene climate changes at local scale other than the mean hypsodonty index which is more useful to track changes at larger temporal and geographical scale. In fact, Fortelius et al. (2002) excluded Pleistocene from their 20 million year analysis because mean hypsodonty distribution in Pliocene was already similar in Eurasia to that to be observed in extant data. As a consequence, we never observe in the Italian Plio-Pleistocene fossil record mean hypsodonty values higher than 2.25 (except Aurelian = 2.66) justifying non striking changes in variability through time (cfr. Figs. 8.2-3). But it is noteworthy that in spite of the paucity of grid values they give very precise spatial resolution whose interpretation needs to consider also external factors that mould ungulate community.

In fact, some changes in climatic indices are spatially associated to ecological parameters of mammalian communities. The Villafranchian mammal age is characterised by a negative relationship between mean hypsodonty index and mean body mass of perissodactyls that is: increasing aridity are associated with decreasing in body mass of horses and rhinos. It is important to note that this trend is counterintuitive but it is explained by the low ecological diversity of Villafranchian rhinos (all brachydont species) that were lighter than their Pleistocene counterpart.

Also taphonomy needs to be considered in this interpretation because Villafranchian mammal age spans more than 1.0 million of years (with Triversa PCOM covering 3.5 – 1.1 Ma) and it is likely that the spatial arrangement of Local Assemblages is much more affected by evolutionary processes of local extinction (e.g. the tapir of 3.5 Ma *Tapirus arvernensis*) and dispersal events.

On the other hand, the Galerian is a transitory period and climate indicators do not affect local fauna. But the positive association between the percentage of grassland carnivores and percentage of hypsodont taxa gives a partial signal on the effect of local climate on mammal fauna.

The trend observed for Aurelian partially explains the similar relationship observed for the negative association between percentage of grassland carnivores and oxygen isotopic values towards Plio-Pleistocene (Chapter 5). In the Aurelian we observe a similar trend with increasing humidity characterised by a greater proportion of grassland-adapted large carnivores. The latter ecological category needs to be considered with caution especially in the analysis of late Pleistocene large carnivores whose habitat choice is not only driven by their morpho-ecological adaptations.

In fact, it is necessary to take into account the spread of humans, which happens to be a significant disturbing factor also on large mammal species composition. This point let us switch the geographical climatic argument on Italian Plio-Pleistocene mammal community to ecological arguments that are more important especially in describing fauna composition. In particular, it is important to note that the number of carnivores is usually associated with diversity of their prey in the Italian peninsula (cfr. Meloro 2004) but no significant trend is evidenced in Aurelian localities.

Mean body mass parameter of both predators and their prey (that is a crude ecological descriptor of mammal fauna) are locally associated in both Villafranchian (with a negative association) and Galerian (with positive association) but not in the Aurelian.

This observation supports an unusual geographical distribution of mammal fauna in the latter part of the Italian Pleistocene when changes in climate become more frequent but were also accompanied by a significant impact of human being activities.

The oldest evidence of such disturbing factor in Italy is represented by Isernia faunal unit (Galerian 2 PCOM) and it characterises also a transitional phase in ecosystem functioning of Italian peninsula. In fact, Raia et al. (2007) stressed that the high predator/prey ratio observed in Villafranchian was the result of a "predation guided" ecosystem while from the Galerian megaherbivores monopolise resources. Similarly, Meloro et al. (2007) demonstrate that a direct link is evident between Villafranchian predators and small-medium sized ungulates. That is since the Galerian predation was less effective on the entire ecosystem.

In this context the rule of human being is yet ambiguous because trends in ecosystem functioning appear to be a mere product of climate changes. But we need to consider also the macroecological trends in the abundance of large carnivores and ungulates (see Chapter 6). It is not a case that large carnivores become significantly rarer in the Italian fossil record since Galerain 2 PCOM (cfr. Fig. 1 Chapter 6). This observation opens a window to a general theory on the evolution of mammalian communities in Italy towards Ice Ages.

It is clear that herbivore fauna composition is affected by climate condition. Both hypsodonty index and percentage of brachydont taxa change significantly trough mammal ages. But local mammalian assemblages are also moulded by ecological factors that are: predator-prey interaction and interaction with human being activities.

The rule of predation is locally more important during Villafranchian and Galerian as well. On the other hand, there is a trend less pattern in the Aurelian due to the disturbance of human being activity. This partially can be an artefact of taphonomy but it is also a genuine trend. In fact, if taphonomy was an issue we expect nestedness in the Aurelian PCOM but this is not the case (except for Galerian 2) (cfr. Meloro et al. 2007). There is an effective rarity of large carnivores during Aurelian that in turn do not have a significant impact on LA fauna composition.

Conclusions

There are no doubts that Italy is a peculiar European zoogeographic region. As a peninsula in the middle of the Mediterranean sea, its climatic conditions are both affected by the sea and the mainland. Such conditions together with a complex topography are probably relatively unchanged from the latest Pliocene.

It is clear that the striking climatic changes of the beginning of 3.5 Ma moulded the old landscape and affected significantly the local Italian fauna as well. In line with other European regions, mainland mammalian fauna changed according to major climatic events of Plio-Pleistocene (Azzaroli 1983; Torre et al. 2001; Raia et al. 2005) and the large carnivores are part of this process.

As most carnivores are apex predators, this group of mammals is of particular interest because its relationship with environmental changes cannot be represented by a straight line.

All mainland Italian carnivores are not endemic forms and it is likely that in the coldest period of Ice Age, some species consider this peninsula as a refugia (O'Regan et al. 2002). In this regard, several genus are recorded in the Italian Plio-Pleistocene fossil record continuously from c.ca 2.0 Ma since nowadays (e.g. *Canis*) but other peculiar forms disappear probably forever (e.g. the sabertooth *Homotherium* and the dirk tooth *Megantereon*).

It is worth mentioning that several extinct carnivores survived for more than 1.0 Ma not being a significant outlier in time span among the other modern forms. For this reason, I focused most of the analyses on the possible changes that can occur at community level. As a group of interacting species, large carnivores can be consistently considered as a whole and this evidence applies to both extant and extinct forms (cfr. Van Valkenburgh 1985, 1988, 1989, 1995, 1999 and see also Chapter 1). Fossils represented the major source of data to test hypotheses of changes in large carnivores communities but it was surprising how the application of modern techniques can be particularly precise and accurate.

In this regard geometric morphometrics of complex osteological structures reveals to be useful as a modern statistical synthesis of shape analysis (Adams et al. 1990). The mandible geometry of large carnivores was of main concern because it simply represents the complex dichotomy of form and function. Mandible shape structure identifies significantly morphoecology of both extant and extinct species irrespective of species taxonomic affiliation. Consistently mandible shape validate the previous discrimination of small/large carnivores whose body mass threshold is 7 kg. And its variability among species through time and space reveals to be unchanged.

The results obtained on the basis of Italian Plio-Pleistocene large carnivores do not evidence any structural change in morpho-ecology through time. Although expected (cfr. Van Valkenburgh 1988, 1989, 1995, Wesley-Hunt 2005), the lower jaw shape variability was also negatively associated to number of carnivores present in an ecosystem as well as number of prey.

The results obtained for Italian Plio-Pleistocene forms reflect intrinsic properties of large carnivore communities. Most of large carnivores are predators whose morphological variability depends on what they eat. Morphological differentiation is usually established also in carnivore communities small in number where at least extreme ecomorphs are present (e.g. bearlike, doglike, catlike sensu Martin 1989). When number of carnivores (or number of prey) is high the same morphospace – defined by extreme ecomorphs- is filled by interacting and competitive forms resulting clustered.

In line with this principle, Italian Plio-Pleistocene large carnivore communities are not unusual and they obey to the same rules that govern extant communities. Consequently, the presence of saber tooth cats or short faced hyena did not affect large carnivore community in their structure.

Similar signal come from the analysis of long bones. Although this fossil material was fragmentary it reveals to be useful also in determining carnivores adaptability to certain habitat rather than locomotory habits. Interestingly, several phenomena of evolutionary convergence seem to occur between Plio-Pleistocene species and extant forms. This mechanism is driven by a body mass constraint that allow species to have similar long bone proportion.

On the other hand, presence/absence data of species in Italian fossil record confirm the strict dependence (in terms of ecological abundance) between large carnivores and their prey (Raia et al. 2007; Meloro et al. 2007). Interestingly, large carnivores are usually overrepresented in the Italian fossil record and their abundance became significantly lower from the Galerian to the Aurelian (a period accompanied also by the significant spread of modern humans).

The morphoecological data obtained on both Plio-Pleistocene large carnivores and their prey were also mapped and this result in an important step forward to a modern synthesis on the evolution of large mammal community. There are not striking geographic differences in local mammal communities of Italian Plio-Pleistocene but structural change in herbivore communities occur from Villafranchian through Aurelian because of increasing in climate change frequency.

Large carnivores are more controlled by their prey during the Villafranchian while in the Galerian and Aurelian there is a major interference of different climatic conditions as well as human activity.

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Appendix 1

Mandible specimens from Natural History Museum of London, London, UK (NHM). *Panthera leo* is from Zoologische Staatssammlung München, Munich, Germany (ZSM) and *Panthera tigris* is from Royal Museum of Scotland, Edinburgh, UK (RMS).

Species	Family	Catalogue	BW	D 1	D 2	D 3	S_P	Guild
Atelocynus microtis	Canidae	26.15.5	10.00	O	Vert	4	S	Yasuni
Canis adustus	Canidae	34.11.1.6	8.30	O	Vert	2	S	Kruger
Canis latrans	Canidae	2.3.7.4	11.60	M	Vert	4	S	Yellowstone
Canis lupus	Canidae	34.6.28.47	45.00	M	Vert	6	M	Yellowstone Krokonose
Canis mesomelas	Canidae	27.8.14.2	7.40	O	Vert	2	S	Kruger
Cuon alpinus	Canidae	44.11.9.3	17.50	M	Vert	6	M	Gunung
Lycaon pictus	Canidae	99.6.29.1	28.00	M	Vert	6	M	Kruger
Nyctereutes procyonoides	Canidae	54.32	4.50	O	Vert	2	V	Krokonose
Otocyon megalotis	Canidae	26.12.7.336	4.00	I	Inv	7	V	Kruger
Speothos venaticus	Canidae	52.1086	6.50	M	Vert	5	M	Yasuni
Urocyon cinereoargenteus	Canidae	88.11.25.3	3.30	I	Vert	2	V	La Amistad
Vulpes vulpes	Canidae	8.7.7.13	5.30	M	Vert	4	V	Yellowstone Krokonose
Acinonyx jubatus	Felidae	1927.2.11.16	38.00	M	Vert	5	M	Kruger
Catopuma badia	Felidae	88.8.13.1	3.50	M	Vert	5	S	Gunung
Catopuma temminckii	Felidae	23.1.7.7	11.70	M	Vert	5	M	Gunung
Felis silvestris	Felidae	87.770	5.00	M	Vert	4	V	Krokonose
Herpailurus yaguarondi	Felidae	34.9.2.33	5.90	O	Vert	4	V	La Amistad Yasuni
Leopardus pardalis	Felidae	1910.9.29.12	11.50	M	Vert	4	S	La Amistad Yasuni
Leopardus tigrinus	Felidae	63.1211	2.20	O	Vert	4	V	Yasuni
Leopardus wiedii	Felidae	13.12.18.2	3.20	O	Vert	4	V	La Amistad Yasuni
Leptailurus serval	Felidae	70.679	12.00	M	Vert	4	S	Kruger
Lynx canadensis	Felidae	92.4.19.1	9.80	M	Vert	4	S	Yellowstone
Lynx lynx	Felidae	69.10.19.16	11.30	M	Vert	6	S	Krokonose
Lynx rufus	Felidae	19.4.2.1	9.30	M	Vert	5	S	Yellowstone
Neofelis nebulosa	Felidae	58.6.24.49	15.50	M	Vert	6	M	Gunung
Panthera leo	Felidae	ZSM 1952/174	181.00	M	Vert	6	L	Kruger
Panthera onca	Felidae	1987.236	57.00	M	Vert	6	L	La Amistad Yasuni
Panthera pardus	Felidae	35.10.22.71	30.00	M	Vert	6	M	Kruger
Panthera tigris	Felidae	RMS 2002.186	130.00	M	Vert	6	L	Gunung
Pardofelis marmorata	Felidae	46.6.15.8	2.77	M	Vert	4	S	Gunung

Species	Family	Catalogue	BW	D 1	D 2	D 3	S_P	Guild
Prionailurus bengalensis	Felidae	1938.11.30.26	4.20	M	Vert	4	S	Gunung
Prionailurus planiceps	Felidae	79.11.21.627	1.86	F	Vert	3	S	Gunung
Puma concolor	Felidae	1901.11.14.1	62.50	M	Vert	6	L	La Amistad Yasuni Yellowstone
Atilax paludinosus	Herpestidae	33.3.11.16	3.71	O	Vert	4	V	Kruger
Galerella sanguinea	Herpestidae	61.1091	0.65	O	Vert	4	V	Kruger
Helogale parvula	Herpestidae	36.10.22.4	0.27	I	Inv#	7	V	Kruger
Herpestes brachyurus	Herpestidae	8.7.17.11	2.51	O	Vert	7	O	Gunung
Ichneumia albicauda	Herpestidae	37.9.26.93	3.63	I	Inv	2	V	Kruger
Herpestes ichneumon	Herpestidae	0.6.21.7	3.10	O	Vert	4	V	Kruger
Herpestes semitorquatus	Herpestidae	92.2.7.2	3.16	O	Vert	4	V	Gunung
Mungos mungo	Herpestidae	14.7.10.65	1.26	I	Inv	7	V	Kruger
Paracynictis selousi	Herpestidae	68.1078	1.70	I	Inv	7	V	Kruger
Rhynchogale melleri	Herpestidae	94.1.28.9	2.40	I	Inv#	2	O	Kruger
Crocuta crocuta	Hyaenidae	28.9.11.183	55.00	M	Vert	6	L	Kruger
Parahyaena brunnea	Hyaenidae	35.9.1.288	40.00	O	Vert	6	M	Kruger
Amblonyx cinereus	Mustelidae	9.4.1.121	3.10	O	Crab	3	V	Gunung
Aonyx capensis	Mustelidae	36.2.28.25	20.00	O	Crab	3	V	Kruger
Arctonyx collaris	Mustelidae	38.10.10.1	10.47	O	Inv	2	V	Gunung
Conepatus semistriatus	Mustelidae	52.61	2.45	O	Inv§	7	S	La Amistad
Eira barbara	Mustelidae	14.4.24.16	3.62	O	Vert	4	V	La Amistad, Yasuni
Galictis vittata	Mustelidae	34.9.2.54	2.34	O	Vert*	4	S	La Amistad, Yasuni
Gulo gulo	Mustelidae	14.5.1.1	11.80	M	Vert	6	L	Yellowstone
Ictonyx striatus	Mustelidae	6.11.8.55	1.00	O	Inv*	4	V	Kruger
Lontra canadensis	Mustelidae	89.10.20.1	4.30	F	Fish	3	V	Yellowstone
Lontra longicaudis	Mustelidae	1844.5.29.1	10.00	F	Fish	3	V	La Amistad
Lutra lutra	Mustelidae	59.9.6.62	7.00	F	Fish	3	V	Gunung Krokonose
Lutra sumatrana	Mustelidae	79.11.21.266	5.50	F	Fish	3	V	Gunung
Martes americana	Mustelidae	92.4.19.2	0.83	M	Vert	4	V	Yellowstone
Martes flavigula	Mustelidae	50.553	2.50	M	Vert	4	S	Gunung
Martes foina	Mustelidae	1987.404	1.26	O	Vert	2	S	Krokonose
Martes martes	Mustelidae	19.7.7.3351	1.52	M	Vert	4	S	Krokonose
Martes pennanti	Mustelidae	92.4.19.3	3.50	M	Vert	4	S	Yellowstone
Meles meles	Mustelidae	11.6.3.13	10.10	I	Inv	2	V	Krokonose
Mellivora capensis	Mustelidae	86.9.4.08	8.08	I	Vert	2	V	Kruger
Mephitis mephitis	Mustelidae	7.7.7.3944	2.41	I	Inv	2	V	Yellowstone
Mustela africana	Mustelidae	5.1.25.1	2.73	M	Vert	6	V	Yasuni
Mustela erminea	Mustelidae	1938.11.11.9	0.32	M	Vert	6	V	Yellowstone Krokonose
Mustela eversmannii	Mustelidae	41.1.17.4	1.70	M	Vert	6	V	Krokonose
Mustela frenata	Mustelidae	1984.1	0.23	M	Vert	6	V	La Amistad Yellowstone

Species	Family	Catalogue	BW	D 1	D 2	D 3	S_P	Guild
Mustela nivalis	Mustelidae	3.2.2.17	0.12	M	Vert	6	V	Krokonose
Mustela nudipes	Mustelidae	55.740	1.29	M	Vert	6	V	Gunung
Mustela putorius	Mustelidae	1952.56.8	0.69	M	Vert	5	V	Krokonose
Mustela vison	Mustelidae	60.2.20.2	0.88	O	Vert	5	V	Yellowstone Krokonose
Pteronura brasiliensis	Mustelidae	8.6.30.1	24.00	F	Fish**	3	V	Yasuni
Taxidea taxus	Mustelidae	1856.4.11.3	8.22	M	Vert#	4	S	Yellowstone
Bassaricyon gabbii	Procyonidae	5.5.4.5	0.79	V	Fruit	2	O	La Amistad
Bassariscus sumichrasti	Procyonidae	75.2.27.8	1.10	O	Fruit	2	O	La Amistad
Nasua narica	Procyonidae	98.3231	5.00	O	Inv	2	O	La Amistad
Nasua nasua	Procyonidae	3.3.3.26	3.31	O	Inv	2	O	Yasuni
Potos flavus	Procyonidae	8.6.17.15	2.05	O	Fruit	2	O	La Amistad Yasuni
Procyon cancrivorus	Procyonidae	0.7.24.1	5.01	O	Fruit	2	O	Yasuni
Procyon lotor	Procyonidae	1860.11.19.13	6.40	O	Fruit	2	V	La Amistad Yellowstone
Helarctos malayanus	Ursidae	1938.11.30.70	45.60	V	Fruit	2	O	Gunung
Ursus americanus	Ursidae	61.1282	55.00	V	Fruit	2	O	Yellowstone
Ursus arctos	Ursidae	88.2.20.3	320.00	V	Fruit	2	O	Yellowstone Krokonose
Arctictis binturong	Viverridae	84.5.19.8	12.90	V	Fruit	2	O	Gunung
Arctogalidia trivirgata	Viverridae	55.1632	2.30	O	Fruit	2	O	Gunung
Civettictis civetta	Viverridae	66.778	12.10	O	Inv	2	V	Kruger
Cynogale bennettii	Viverridae	50.10.24.16	3.60	O	Crab	3	V	Gunung
Genetta genetta	Viverridae	70.63	1.90	O	Vert	4	V	Kruger
Genetta tigrina	Viverridae	65.2573	2.10	O	Vert#	4	V	Kruger
Hemigalus derbyanus	Viverridae	85.8.1.29	0.83	I	Inv	7	V	Gunung
Paguma larvata	Viverridae	8.11.14.5	2.75	O	Fruit	2	O	Gunung
Paradoxurus hermaphroditus	Viverridae	14.8.22.15	3.00	V	Fruit	2	O	Gunung
Prionodon linsang	Viverridae	42.4.12.11	0.67	O	Vert	4	V	Gunung
Viverra tangalunga	Viverridae	1992. 010. 025	3.38	O	Inv	4	V	Gunung
Viverricula indica	Viverridae	1924. 139. 1a	2.19	O	Inv	4	O	Gunung

BW = Body Weight in kilograms; **D 1** = Diet as in Gittleman (1985): carnivorous (=M), omnivorous (=O), insectivorous (=I), folivorous and frugivore (=V) and piscivore (=F);

D 2 = Diet as in Meiri et al. (2005): Vert = vertebrates, Inv = invertebrates, fruit, fish and crabs.

D 3 = Diet as in Christiansen and Wroe (2007): 1, herbivores (including frugivores); 2, omnivores; 3, piscivores; 4, carnivores, small prey; 5, carnivores, medium-sized prey; 6, carnivores, large prey; 7, insectivores; **S_P** = Size of prey as in Gittleman (1985): V = very small; S = small; M = medium; L = large; O = no prey.

Ecological data:

Atelocynus microtis = from Piman and William (2004)

Speothos venaticus = size of prey from Zuecher et al. (2004)

Neofelis nebulosa = from Nowell and Jackson (1996).

Catopuma temmincki = from Nowell and Jackson (1996).

Prionailurus planiceps = from Nowell and Jackson (1996).

Prionailurus bengalensis = from Nowell and Jackson (1996).

Panthera onca = size of prey from Nowell and Jackson (1996).

Leopardus wiedi = from Nowell and Jackson (1996).

Lynx canadensis = from Nowell and Jackson (1996).

Leopardus pardalis = from Nowell and Jackson (1996).

Amblonyx cinereus = Diet is mainly on crabs from Larivière (2003)

Eira barbara = from Prestley (2000)

Galictis vittata = from Yensen and Tarifa (2003)

Gulo gulo = from Pasitschniack-Arts and S.Larivière (1995)

Lontra canadensis =from Larivière and Walton (1998)

Lutra longicaudis = from Larivière (1999)

Martes pennanti=from Powell (1981)

Mustela vison =from Larivère (1999)

Viverra tangalunga = from Colòn (1999)

Pteronura brasiliensis = info from http://www.arkive.org

Martes foina = diet from Rodel and Stubbel (2006).

Arctonyx collaris = from http://animaldiversity.ummz.umich.edu

Conepatus semistriatus = from http://animaldiversity.ummz.umich.edu

Galerella sanguinea = from http://animaldiversity.ummz.umich.edu

Bassaricyon gabbii = from http://animaldiversity.ummz.umich.edu

Bassaricyon sumichristi = from http://animaldiversity.ummz.umich.edu

Procyon cancrivorous = from http://www.lioncrusher.com

Cynogale bennetti = from http://animaldiversity.ummz.umich.edu

Paguma larvata = diet from http://animaldiversity.ummz.umich.edu

Paradoxorus hermaphroditus = diet from http://animaldiversity.ummz.umich.edu

Prionodon linsang = diet from http://animaldiversity.ummz.umich.edu

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Appendix 2

Complete mandible specimens considered for geometric morphometrics analysis on both extinct and extant carnivores. Diet category for extant species from Christiansen and Wroe (2007).

Museum abbreviations:

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
MZLS: Museo Zoologico 'La Specola' Firenze, Italy
CE: Museo Civico di Storia Naturale "G. Doria" Genova, Italy
MCZR: Museo Civico di Zoologia. Roma, Italy
MGPD: Museo di Paleontologia Università di Padova, Padova, Italy
MVNA: Museo di Anatomia Veterinaria, Università degli Studi di Napoli "Federico II"
MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN: Muséum National d'Histoire Naturelle, Paris, France

NHM: Natural History Museum of London, UK
NMB: Naturhistorisches Museum Basel, Switzerland
RMS: Royal Museum of Scotland. Edinburgh, Scotland, UK
ZSM: Zoologische Staatssammlung München, Munich, Germany

Species	Family	Catalogue	Diet_CW
Ursus arctos	Ursidae	F C11883	2
Ursus arctos horribilis	Ursidae	NHM 18.4.6.1	2
Ursus arctos marsicanus	Ursidae	C 3584	2
Ursus arctos marsicanus	Ursidae	C 3583	2
Ursus maritimus	Ursidae	NHM 1938.11.11.8	6
Ursus maritimus	Ursidae	Mc 440	6
Ursus maritimus	Ursidae	NHM 90.8.4.1	6
Ursus spelaeus	Ursidae	Hu V5226	
Ursus deningeri	Ursidae	NHM - M6186	
Ursus thibetanus	Ursidae	NHM 219	2
Ursus thibetanus	Ursidae	MCZR 6669	2
Ursus americanus	Ursidae	MCZR 444	2
Ursus americanus	Ursidae	NHM 61.1282	2
Ursus etruscus	Ursidae	NHMP 1880-1	
Ursus minimus	Ursidae	MNHN No Cat	
Helarctos malayanus	Ursidae	NHM 1938.11	2
Helarctos malayanus	Ursidae	HM V5648	2
Helarctos malayanus	Ursidae	HM NoCat	2
Helarctos malayanus	Ursidae	MCZR 7951	2
Melursus ursinus	Ursidae	NHM 34.8.12.9	7

Species	Family	Catalogue	Diet_CW
Melursus ursinus	Ursidae	NHM 35.1.1.5	7
Tremarctos ornatus	Ursidae	NHM 27.11.1.7	1
Tremarctos ornatus	Ursidae	NHM 9.7.26.1	1
Ailuropoda melanoleuca	Ursidae	RMS 1938.71	1
Ailuropoda melanoleuca	Ursidae	NHM 39.3808	1
Ailuropoda melanoleuca	Ursidae	NHM 55.587	1
Atelocynus microtis	Canidae	NHM 26.15.5	4
Cerdocyon thous	Canidae	MZLS - C4125	4
Cerdocyon thous	Canidae	NHM 21.15.30	4
Pseudalopex culpaeus	Canidae	NHM 1903.7.9.3	4
Pseudalopex culpaeus	Canidae	NHM 21.6.21.2	4
Chrysocyon brachyurus	Canidae	RMS 1.993.049	2
Chrysocyon brachyurus	Canidae	NHM 48.401	2
Chrysocyon brachyurus	Canidae	NHM 94.3.6.6	2
Speothos venaticus	Canidae	NHM 3.7.7.43	5
Speothos venaticus	Canidae	NHM 52.10.86	5
Canis etruscus	Canidae	IGF11791	
Canis etruscus	Canidae	NMB - VA2749	
Canis simensis	Canidae	NHM 24.8.7.11	4
Canis simensis	Canidae	NHM 24.8.7.12	4
Canis simensis	Canidae	CE 818	4
Canis lupus	Canidae	MVNA 99.21	6
Canis lupus	Canidae	NHM 34.6.28.47	6
Canis lupus	Canidae	NHM 47.1121	6
Canis lupus	Canidae	HM - an4560 – 323	6
Canis lupus signatus	Canidae	MNCN 16324	6
Canis lupus signatus	Canidae	MNCN 16325	6
Canis dingo	Canidae	MZLS - C1454	5
Canis dingo	Canidae	NHM 6.11.9.3	5
Canis dingo Pleist	Canidae	HM - S98.99.100	
Canis dingo Pleist	Canidae	HM - S98.99.101	
Canis aureus	Canidae	NHM 64.2181	4
Canis aureus	Canidae	HM - an5007	4
Canis arnesis	Canidae	IGF 868	
Canis arnesis	Canidae	IGF_exposed	
Canis latrans	Canidae	MZLS - MSC418	4
Canis latrans	Canidae	NHM 2.3.7.3	4
Canis latrans	Canidae	RMS - 2003.130.002	4
Canis latrans	Canidae	RMS - 2003.130.003	4
Canis latrans	Canidae	RMS - 2003.130.008	4
Cuon alpinus javanicus	Canidae	NHM 44.11.9.3	6
Cuon alpinus	Canidae	MCZR 270	6
Cuon alpinus javanicus	Canidae	NHM 7.11.14.7	6
Cuon alpinus dukhnensis	Canidae	RMS_NoCat	6
Lycaon pictus	Canidae	NHM 2.1.6.34	6
Lycaon pictus	Canidae	NHM 99.6.29.1	6
Lycaon pictus	Canidae	MCZR 451	6
Lycaon pictus	Canidae	RMS - Z1908 078	6
Lycaon falconeri	Canidae	IGF865	
Canis mesomelas	Canidae	MVNA 79.1	2
Canis mesomelas	Canidae	MCZR 61	2
Canis mesomelas	Canidae	NHM 69.10.24.7	2

Species	Family	Catalogue	Diet_CW
Canis adustus	Canidae	NHM 26.6.11.5	2
Canis adustus	Canidae	NHM 34.1.1.6	2
Nyctereutes megamastoides	Canidae	NMB - StV766	
Nyctereutes megamastoides	Canidae	IGME - s I739M	
Nyctereutes procyonoides	Canidae	NHM 26.10.21	2
Nyctereutes procyonoides	Canidae	NHM 54.32	2
Nyctereutes procyonoides	Canidae	MZLS - C429	2
Crocuta crocuta	Hyaenidae	MCZR 223	6
Crocuta crocuta	Hyaenidae	MNHN1911-8	6
Crocuta crocuta	Hyaenidae	RMS NoCat	6
Crocuta crocuta	Hyaenidae	NHM 28.9.11.183	6
Crocuta crocuta	Hyaenidae	NHM 59.272	6
Pliocrocuta perrieri	Hyaenidae	IGF 5504V	
Hyaena hyaena	Hyaenidae	MCZR 3a	6
Hyaena hyaena	Hyaenidae	MCZR 337	6
Hyaena hyaena	Hyaenidae	MCZR 3933	6
Hyaena hyaena	Hyaenidae	MZLS - C12413	6
Hyaena hyaena	Hyaenidae	HM no catalogue	6
Hyaena hyaena	Hyaenidae	MZLS - C2137	6
Hyaena hyaena	Hyaenidae	MZLS 6667	6
Parahyaena brunnea	Hyaenidae	RMS 1993.030	6
Parahyaena brunnea	Hyaenidae	NHM 35.9.1.288	6
Acinonyx pardinensis	Felidae	MNHNL20-161819	
Acinonyx jubatus	Felidae	ZSM 1911-739	5
Acinonyx jubatus	Felidae	ZSM 1949-1028	5
Acinonyx jubatus	Felidae	ZSM 1952-274	5
Acinonyx jubatus	Felidae	NHM 1927.2.11.16	5
Caracal caracal	Felidae	ZSM 1902-200	5
Caracal caracal	Felidae	ZSM 1914-901	5
Caracal caracal	Felidae	ZSM 1951-246	5
Caracal caracal	Felidae	ZSM 1969-624	5
Homotherium crenatidens	Felidae	MNHN PER2000	
Homotherium crenatidens	Felidae	MNCN no catalogue	
Megantereon sp.	Felidae	MNHN cast from Seneze	
Leptailurus serval	Felidae	ZSM 1913-14	4
Leptailurus serval	Felidae	ZSM1915-28	4
Leptailurus serval	Felidae	ZSM1915-152	4
Leptailurus serval	Felidae	ZSM1964-150	4
Leopardus pardalis	Felidae	ZSM 1910-3000	4
Leopardus pardalis	Felidae	ZSM 1925-373	4
Leopardus pardalis	Felidae	NHM 1910.9.29.12	4
Lynx lynx	Felidae	NHM 69.10.19.16	6
Lynx lynx	Felidae	P S17	6
Lynx pardellus	Felidae	P73	
Lynx issiodorensis	Felidae	IGF 15072	
Lynx issiodorensis	Felidae	MNCN nocatalogue	
Lynx canadiensis	Felidae	NHM 92.4.19.1	4
Lynx canadiensis	Felidae	ZSM 1965-88	4
Lynx canadiensis	Felidae	ZSM 1966-1	4
Lynx canadiensis	Felidae	ZSM 1966-2	4
Lynx rufus	Felidae	NHM 19.4.2.1	5
Lynx rufus	Felidae	ZSM 1949-689	5

Species	**Family**	**Catalogue**	**Diet_CW**
Lynx rufus	Felidae	ZSM AM704	5
Neofelis nebulosa	Felidae	ZSM 1905-1111	6
Neofelis nebulosa	Felidae	ZSM 1973-269	6
Neofelis nebulosa	Felidae	ZSM AM712	6
Panthera leo	Felidae	RMS 2001.118.2	6
Panthera leo massaica	Felidae	ZSM 1952-178	6
Panthera leo massaica	Felidae	ZSM 1952-174	6
Panthera leo massaica	Felidae	ZSM 1952-17	6
Panthera leo spelea	Felidae	MGPD25264	
Panthera tigris	Felidae	MNHN 1992-3	6
Panthera tigris	Felidae	MNHN MAT412	6
Panthera tigris	Felidae	RMS V5720	6
Panthera tigris sondaica	Felidae	RMS 1995.29.002	6
Panthera tigris sondaica	Felidae	RMS 1995.291.001	6
Panthera pardus	Felidae	HM 5811Rm215	6
Panthera pardus	Felidae	NHM 35.10.22.71	6
Panthera pardus	Felidae	ZSM AM722	6
Panthera pardus	Felidae	ZSM 1971-650	6
Panthera onca	Felidae	NHM 1987.236	6
Panthera onca	Felidae	ZSM 1949-583	6
Panthera onca	Felidae	ZSM AM706	6
Panthera onca	Felidae	ZSM 1949-585	6
Puma concolor	Felidae	ZSM 1910-184	6
Puma concolor	Felidae	NHM 1901.11.14.4	6
Puma concolor	Felidae	ZSM 1925-572	6
Puma concolor	Felidae	ZSM 1928-279	6
Uncia uncia	Felidae	ZSM 1906-1295	6
Uncia uncia	Felidae	ZSM 1992-23	6
Uncia uncia	Felidae	NHM 32.8.21.2	6
Uncia uncia	Felidae	ZSM 1906-1275	6

Fragmentary specimens added in geometric morphometric analyses on mandibular corpus shape.

Species	**Family**	**Catalogue**
Ursus arctos marsicanus	Ursidae	C3586
Ursus arctos	Ursidae	P 32
Ursus arctos	Ursidae	from Petina no Cat
Ursus spelaeus	Ursidae	HM No cat.
Ursus spelaeus	Ursidae	HM V5226
Ursus spelaeus	Ursidae	NMB UP847
Ursus minimus	Ursidae	MNCN 32680
Ursus minimus	Ursidae	MNCN 5751
Ursus minimus	Ursidae	IGF 11569
Ursus ruscinensis	Ursidae	MNHN no cat
Canis etruscus	Canidae	IGF 856
Canis etruscus	Canidae	IGF 874
Canis arnensis	Canidae	IGF869

Species	**Family**	**Catalogue**
Canis arnensis	Canidae	IGF 2
Canis sp.	Canidae	P3591
Canis sp.	Canidae	P3589
Canis sp.	Canidae	P3590
Lycaon falconeri	Canidae	IGF683V
Nyctereutes megamastoides	Canidae	NMB - Se1780
Crocuta prespelea	Hyaenidae	MNHN PEC-6
Crocuta crocuta	Hyaenidae	IGF4727
Crocuta crocuta	Hyaenidae	P_F4
Pachycrocuta brevirostris	Hyaenidae	RMS 1884.005.11
Pachycrocuta brevirostris	Hyaenidae	IGME exposed
Pachycrocuta brevirostris	Hyaenidae	IGF835
Pliocrocuta perrieri	Hyaenidae	MNHN M4024
Pliocrocuta perrieri	Hyaenidae	NMB Se313
Pliocrocuta perrieri	Hyaenidae	NMB Va1719
Pliocrocuta perrieri	Hyaenidae	IGF 4854
Pliocrocuta perrieri	Hyaenidae	IGME I764M
Chasmaporthetes kani	Hyaenidae	MNHN F-AM99789
Acinonyx pardinensis	Felidae	MNHN coll. Croizet
Acinonyx pardinensis	Felidae	MNCN47141
Acinonyx pardinensis	Felidae	MNHNL20-161820
Lynx sp.	Felidae	P26
Lynx issiodorensis	Felidae	IGF891.M.169
Lynx issiodorensis	Felidae	Holotype in MNHN
Lynx issiodorensis	Felidae	MNHN no catalogue
Lynx issiodorensis	Felidae	IGF4397
Megantereon cultridens	Felidae	MNHN PER2002
Megantereon cultridens	Felidae	MNHN coll. Croizet
Megantereon cultridens	Felidae	IGF1390V
Neofelis nebulosa	Felidae	ZSM 1980-128
Panthera leo spelea	Felidae	MGPD25265
Panthera pardus	Felidae	IGF10038
Panthera pardus	Felidae	IGF6103V
Panthera gombaszoegensis	Felidae	IGF851V
Panthera gombaszoegensis	Felidae	IGF851
Panthera gombaszoegensis	Felidae	IGF4375
Panthera gombaszoegensis	Felidae	IGF853
Puma concolor	Felidae	ZSM 1907-100

Appendix 3

Mandible specimens used for geometric morphometric guild comparison.

Museum abbreviations as in Appendix 2.

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 “and” (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	N. Catalogue	Guild
Acinonyx jubatus	Felidae	NHM 1927.2.11.16	Kruger
Arctictis binturong	Viverridae	NHM 84.5.19.8	Gunung
Arctonyx collaris	Mustelidae	NHM 38.10.10.1	Gunung
Atelocynus microtis	Canidae	NHM 26.15.5	Otishi
Canis adustus	Canidae	NHM 34.11.1.6	Kruger
Canis latrans	Canidae	NHM 2.3.7.4	Yellowstone
Canis lupus	Canidae	NHM 34.6.28.47	Yellowstone Krokonose
Canis mesomelas	Canidae	NHM 27.8.14.2	Kruger
Catopuma temminckii	Felidae	NHM 23.1.7.7	Gunung
Civettictis civetta	Viverridae	NHM 66.778	Kruger
Crocuta crocuta	Hyaenidae	NHM 28.9.11.183	Kruger
Cuon alpinus	Canidae	NHM 44.11.9.3	Gunung
Gulo gulo	Mustelidae	NHM 14.5.1.1	Yellowstone
Helarctos malayanus	Ursidae	NHM 1938.11.30.70	Gunung
Leopardus pardalis	Felidae	NHM 1910.9.29.12	Otishi
Leptailurus serval	Felidae	NHM 70.679	Kruger
Lycaon pictus	Canidae	NHM 99.6.29.1	Kruger
Lynx canadensis	Felidae	NHM 92.4.19.1	Yellowstone
Lynx lynx	Felidae	NHM 69.10.19.16	Krokonose
Lynx rufus	Felidae	NHM 19.4.2.1	Yellowstone
Meles meles	Mustelidae	NHM 11.6.3.13	Krokonose
Mellivora capensis	Mustelidae	NHM 86.9.4.08	Kruger
Neofelis nebulosa	Felidae	NHM 58.6.24.49	Gunung
Panthera leo	Felidae	ZSM 1952/174	Kruger
Panthera onca	Felidae	NHM 1987.236	Otishi
Panthera pardus	Felidae	NHM 35.10.22.71	Kruger
Panthera tigris	Felidae	MCZR 2002. 186	Gunung
Parahyaena brunnea	Hyaenidae	NHM 35.9.1.288	Kruger
Pseudalopex culpaeus	Canidae	NHM 1903.7.9.3	Otishi
Puma concolor	Felidae	NHM 1901.11.14.1	Otishi Yellowstone
Taxidea taxus	Mustelidae	NHM 1856.4.11.3	Yellowstone
Tremarctos ornatus	Ursidae	NHM 27.11.1.7	Gunung
Ursus americanus	Ursidae	NHM 61.1282	Yellowstone
Ursus arctos	Ursidae	NHM 88.2.20.3	Yellowstone Krokonose
Ursus minimus	Ursidae	IGF 11568	Triversa
Nyctereutes megamastoides	Canidae	IGME - s I739M	Triversa
Acinonyx pardinensis	Felidae	MNCN47141	Triversa-Pirro

Species	**Family**	**N. Catalogue**	**Guild**
Canis arnesis	Canidae	IGF 868	Up Valdarno-Galerian 3
Canis etruscus	Canidae	IGF 856	Montopoli-ValdiChiana
Lycaon falconeri	Canidae	IGF 683V	Up Valdarno-Pirro
Chasmaporthetes kani	Hyaenidae	MNHN F:AM99788	Triversa-ValdiChiana
Homotherium crenatidens	Felidae	PER2000	Triversa-Galerian 2
Lynx issiodorensis	Felidae	MNHN no cat.	UpValdarno-Pirro
Megantereon megantereon	Felidae	MNHN coll. Croizet	Up Valdarno-Pirro
Pachycrocuta brevirostris	Hyaenidae	MNCN no cat	Up Valdarno-Galerian 1
Panthera gombaszoegensis	Felidae	IGF4375	Up Valdarno-Galerian 1
Ursus etruscus	Ursidae	MNHN IGF1880-1	Up Valdarno-Pirro
Pliocrocuta perrieri	Hyaenidae	IGF 5504V	Montopoli and Galerian 2
Lynx sp.	Felidae	P25	Galerian 2
Panthera leo spelea	Felidae	MGPD25264	Galerian 2-Aurelian
Panthera pardus	Felidae	IGF10037	Galerian 2-Aurelian
Meles meles	Mustelidae	P2404	Galerian 2-Aurelian
Ursus deningeri	Ursidae	NHM - M6186	Galerian 1-3
Ursus arctos	Ursidae	P 32	Galerian 3-Aurelian
Canis sp.	Canidae	P3589	Aurelian
Crocuta crocuta	Hyaenidae	P F3	Galerian 3-Aurelian
Ursus spelaeus	Ursidae	HM V5226	Aurelian

Appendix 4

4.1

Long bone indices computed for extant large carnivores. **Log Fore** = Log Fore limb length (in cm); **Log Hind** = Log Hind limb length (in cm); **BI** = Brachial Index; **Mt/F** = metatarsus-femur ratio.

Data source Bertram and Biewener (1990); Janis and Wilhem 1993, Christiansen (2002).

The habitat score (Hab) is from Janis and Wilhem (1993): 0 = Open; 1 = Closed.

Adaptations to tropical or grassland environments as in Ortolani and Caro (1996): 0 = Non adapted; 1 = adapted.

Species	Family	Hab	Tropic	Grasslan	Log Fore	Log Hind	BI	Mt/F
Canis aureus	Canidae	0	0	1	2.487	2.435	1.006	0.420
Canis latrans	Canidae	1	0	1	2.565	2.519	1.029	0.430
Canis lupus	Canidae	0	0	1	2.673	2.629	0.999	0.440
Cerdocyon thous	Canidae	1	0	1	2.368	2.296	0.924	0.430
Lycaon pictus	Canidae	0	0	1	2.604	2.560	1.058	0.460
Nyctereutes procyonoides	Canidae	0	0	0	2.266	2.178	0.871	0.370
Chrysocyon brachyurus	Canidae	0	0	1	2.765	2.729	1.088	0.470
Acinonyx jubatus	Felidae	0	0	1	2.703	2.647	0.996	0.440
Puma concolor	Felidae	1	1	1	2.688	2.582	0.841	0.310
Leptailurus serval	Felidae	0	0	1	2.547	2.486	0.972	0.410
Lynx lynx	Felidae	1	0	1	2.625	2.518	0.984	0.460
Lynx rufus	Felidae	1	0	1	2.525	2.446	0.936	0.420
Panthera leo	Felidae	0	0	1	2.780	2.735	0.901	0.350
Panthera onca	Felidae	1	1	1	2.665	2.588	0.785	0.320
Panthera pardus	Felidae	1	1	1	2.650	2.563	0.825	0.400
Panthera tigris	Felidae	1	1	1	2.809	2.734	0.806	0.350
Crocuta crocuta	Hyaenidae	0	0	1	2.639	2.621	1.045	0.360
Parahyaena brunnea	Hyaenidae	0	0	1	2.609	2.615	1.121	0.390
Hyaena hyaena	Hyaenidae	0	0	1	2.599	2.598	1.141	0.400
Ursus americanus	Ursidae	1	0	0	2.717	2.676	0.855	0.200
Ursus arctos	Ursidae	1	0	0	2.857	2.802	0.917	0.220
Ursus maritimus	Ursidae	0	0	0	2.890	2.825	0.757	0.249

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4.2

Long bone indices computed for Plio-Pleistocene large carnivores.

Abbreviations: Humerus = H; Femur = F; Radius = R; Mt = III Metatarsus

Species	Family	Fore	Hind	BI	Mt/Femur	Localities	References
Canis etruscus	Canidae	2.507	2.494	0.932	0.494	Olivola	Meloro 2003
Canis arnesis	Canidae	2.447	2.525	0.958	0.417	Tasso but F is estimated	Meloro 2003
Lycaon falconeri	Canidae	2.543	2.597	0.822	0.488	Pirro but H, F, R estimated	Meloro 2003
Canis mosbachensis	Canidae	2.525	2.553	0.976	0.457	UntermaBfeld	Sotnikova 2003
Canis aff. *arnensis*	Canidae	2.490	2.540	1.022	0.419	L'Escale	Sotnikova 2003
Canis lupus	Canidae	2.646	2.665	0.969	0.440	G. Jaurens and F estimated	Ballesio 1979
Homotherium crenatidens	Felidae	2.797	2.822	1.026	0.337	Pirro and Senéze	Sardella 1994
Megantereon cultridens	Felidae	2.675	2.683	0.803	0.324	Pirro, Argentario, St.Vallier, Valdarno	Sardella 1994
Acinonyx pardinensis	Felidae	2.655	2.827	0.869	0.411	Olivola, Casa Frata posterior bones; St Vallier anterior	Ficcarellli 1984, Argant 2004
Lynx issiodorensis	Felidae	2.479	2.591	0.768	0.463	Tasso	Meloro 2003
Lynx spelaeus	Felidae	2.516	2.619	1.021	0.401	Observatoire	Testu 2006
Panthera leo	Felidae	2.848	2.857	0.986	0.335	Equi	Del Campana 1947
Panthera gombaszoegensis	Felidae	2.696	2.782	0.922	0.318	Valdarno and H of UntermasBfield	Del Campana 1916, Hemmer 2001
Pachycrocuta brevirostris	Hyaenidae	2.798	2.787	0.884	0.368	China but Mt is from Valdarno	Turner and Antón 1996; Meloro 2003
Crocuta crocuta	Hyaenidae	2.735	2.722	0.904	0.304	G. Jaurens	Ballesio 1979
Chasmaporthetes lunensis	Hyaenidae	2.817	2.809	1.092	0.418	as in *C. ossifragus*	Berta 1981
Ursus minimus	Ursidae	2.799	2.787	0.927	0.203	Gaville	Berzi 1966
Ursus etruscus	Ursidae	2.822	2.796	0.903	0.193	St. Vallier but Mt from Valdarno	Argant 2004, Meloro 2003
Ursus spelaeus	Ursidae	2.847	2.848	0.757	0.199	Equi but Mt from Potočka zijalka	Fracassi 1920 Withalm 2004
Ursus arctos	Ursidae	2.852	2.873	0.886	0.202	Malaspino	Koby 1945

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Appendix 5

Metatarsal-Femur ratio computed for Plio-Pleistocene large herbivores.

Estimation of femur length is based on regression equations whose R^2 is always > 0.90 (derived from data in Christiansen 2002). For *Bison schoetensacki*, *Gallogoral meneghini*, *Gazella borbonica*, *Gazzelospira torticornis*, , *Pseudodama* cf. *lyra*, *Equus suessenbornensis* femur length is based on body mass (in Meloro et al. 2007). For *Croizetoceros ramosus*, *Eucladoceros dicranios* the femur length is estimated from tibia length.

Species	Order	Family	Mt/F	Locality	References
Bison degiulii	Artiodactyla	Bovidae	0.700	Pirro Nord	Masini 1988
Bison priscus	Artiodactyla	Bovidae	0.572	Cava Filo	Sala 1986
Bison schoetensacki	Artiodactyla	Bovidae	0.645	Sussenborn	Sala 1986 but F estimated
Bos primigenius	Artiodactyla	Bovidae	0.579	Ilford, Rhine Gravels, Grayls	Reynolds 1939; Sher 1992
Capra ibex	Artiodactyla	Bovidae	0.585	Monte Cucco	Capasso Barbato et al. 1982
Gallogoral meneghini	Artiodactyla	Bovidae	0.573	La Puebla del Verde, Senéze, Olivola	Duvernois and Guérin 1989 but F estimated
Gazella borbonica	Artiodactyla	Bovidae	0.890	La Puebla del Verde	Sher 1999 but F estimated
Gazzelospira	Artiodactyla	Bovidae	0.693	Senéze, Roccaneyra, Pardines, Villany	Duvernois and Guérin 1990 but F estimated
Leptobos etruscus	Artiodactyla	Bovidae	0.640	Olivola	Merla 1949
Leptobos furtivus	Artiodactyla	Bovidae	0.697	Senéze	Masini 1988
Leptobos vallisarni	Artiodactyla	Bovidae	0.651	unknown	Merla 1949
Ovis ammon	Artiodactyla	Bovidae	1.086	extant, unknown	Christiansen 2002
Rupicapra rupicapra	Artiodactyla	Bovidae	0.820	Monte Cucco	Capasso Barbato et al. 1982
Cervus elaphus	Artiodactyla	Cervidae	0.870	Riano	Leonardi and Petronio 1974
Cervus philisi	Artiodactyla	Cervidae	0.978	Senéze	Petronio 1979
Croizetoceros ramosus	Artiodactyla	Cervidae	1.008	St. Vallier	Valli 2004 but F estimated
Dama dama	Artiodactyla	Cervidae	0.975	Salento	De Giuli 1987
Dama dama clactoniana	Artiodactyla	Cervidae	0.876	Riano	Leonardi and Petronio 1976
Eucladoceros dicranios	Artiodactyla	Cervidae	0.938	Up Valdarno	Azzaroli and Mazza 1992 but F estimated
Megaloceros giganteus	Artiodactyla	Cervidae	0.773	Enniscorthy (UK)	Reynolds 1929
Pseudodama cf. lyra	Artiodactyla	Cervidae	0.881	Montopoli	Azzaroli 1992 but F estimated

Species	Order	Family	Mt/F	Locality	References
Pseudodama cfr. nestii	Artiodactyla	Cervidae	0.875	Selvella	Azzaroli 1992
Pseudodama nestii eurygonos	Artiodactyla	Cervidae	0.920	Capena	Petronio 1979
Equus cf. altidens	Perissodactyla	Equidae	0.749	Pirro Nord	De Giuli et al. 1986
Equus ferus	Perissodactyla	Equidae	0.678	Castro (Arezzo)	Azzaroli 1999
Equus hydruntinus	Perissodactyla	Equidae	0.819	Salento	De Giuli 1987
Equus stenonis vireti	Perissodactyla	Equidae	0.650	St. Vallier	Eisenmann 2004
Equus suessenbornensis	Perissodactyla	Equidae	0.675	Akhalkalaki	Vekua 1986
Stephanorhinus cfr. hundsheimensis	Perissodactyla	Rhinocerotidae	0.371	Pietrafitta	Mazza et al. 1993
Stephanorhinus etruscus	Perissodactyla	Rhinocerotidae	0.398	various localities	Fortelius et al. 1993
Stephanorhinus hemitoechus	Perissodactyla	Rhinocerotidae	0.307	unknown	Fortelius et al. 1993
Stephanorhinus hundsheimensis	Perissodactyla	Rhinocerotidae	0.347	unknown	Fortelius et al. 1993
Stephanorhinus jeanvireti	Perissodactyla	Rhinocerotidae	0.402	various localities	Guerin 1980
Sus scropha	Artiodactyla	Suidae	0.380	Unknown	Housed in MVNA
Sus strozzii	Artiodactyla	Suidae	0.327	Seneze	Azzaroli 1964

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