Canis etruscus (Canidae, Mammalia) and its role in the faunal assemblage from Pantalla (Perugia, central Italy): comparison with the Late Villafranchian large carnivore guild of Italy

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ABSTRACT - A very rich faunal assemblage referred to the early Late Villafranchian (Olivola/Tasso Faunal Unit) has been found at the Early Pleistocene site of Pantalla (Perugia, central Italy). The assemblage contains a number of carnivores, including several specimens of the Etruscan wolf Canis etruscus *Forsyth Major, 1877.*

Canis etruscus *appeared in Europe about 2 Ma. This species is regarded as an important taxon for biochronology: its first occurrence (the so-called "wolf event") has been used to define one of the Villafranchian faunal turnovers.*

The Late Villafranchian assemblage from Pantalla provides valuable information about the Early Pleistocene carnivore guild in Italy. Together with the Etruscan wolf (probably a cooperative species hunting in packs) and Vulpes *sp., the Pantalla faunal assemblage also records the occurrence of two felids,* Lynx issiodorensis *(Croizet & Jobert, 1828) and the giant cheetah* Acinonyx pardinensis *(Croizet & Jobert, 1828). Despite the excellent preservation and richness of fossils discovered, the Pantalla fauna seems to lack some important elements of the Late Villafranchian carnivore paleoguild, possibly reflecting a reduced biomass and/or diversity of preys in respect to other Italian sites.*

RIASSUNTO - [Il Canis etruscus *(Canidae, Mammalia) di Pantalla (Perugia, Italia centrale): un tipico elemento delle associazioni a carnivori del Villafranchiano Superiore italiano] - Il sito del Pleistocene Inferiore di Pantalla (circa 30 km a Sud di Perugia, Italia centrale) ha restituito abbondanti resti di mammiferi continentali in eccellente stato di conservazione. Allo stato dell'arte, l'associazione di Pantalla è stata riferita alla parte iniziale del Villafranchiano Superiore (U.F. Olivola/Tasso). Il campione di Pantalla include alcuni carnivori, tra i quali spicca il canide* Canis etruscus, *documentato da quattro crani praticamente completi.*

Canis etruscus *Forsyth Major, 1877 compare in Europa circa 2 milioni di anni fa ed è considerato una specie molto importante dal punto di vista biocronologico, visto che la sua "prima comparsa" viene convenzionalmente utilizzata per marcare uno dei principali turnover faunistici del Villafranchiano, il cosiddetto "wolf event".*

L'associazione del Villafranchiano Superiore di Pantalla ci ha fornito lo spunto per un confronto della struttura delle associazioni a carnivori del Pleistocene Inferiore. Infatti, nel sito di Pantalla, accanto a C. etruscus *(verosimilmente una specie con comportamento gregario che cacciava in branco) e a* Vulpes *sp., sono stati rinvenuti anche due felidi, la lince* Lynx issiodorensis *(Croizet & Jobert, 1828) e il ghepardo gigante* Acinonyx pardinensis *(Croizet & Jobert, 1828). Nonostante l'eccellente stato di conservazione e la ricchezza dei fossili rinvenuti, la fauna di Pantalla sembra mancare di alcuni importanti elementi delle associazioni a carnivori del Villafranchiano Superiore, riflettendo forse una minore biomassa e/o diversità di prede rispetto ad altri siti fossiliferi italiani.*

INTRODUCTION

The site of Pantalla (Fig. 1) was discovered in 1994 and two paleontological excavations were carried out in 1995 by the Soprintendenza per i Beni Archeologici dell'Umbria (SBAU), with the scientific and technical support of the Dipartimento di Scienze della Terra, Perugia University. These excavations allowed recovering about eighty mammal fossils in excellent state of preservation, including eight carnivore and three herbivore almost complete crania, together with several isolated mandibles.

The site is located about 30 km south of Perugia, in the southwestern branch of the Tiber Basin, a wide extensional continental basin that was filled mainly by clastic (lacustrine, palustrine and fluvial) deposits since the early Late Pliocene (Basilici, 1997). The basin is approximately 1800 km² wide, and extends from Sansepolcro to Terni and Spoleto describing an "upside-down Y" shape and

splitting in a southeastern and a southwestern branch south of Perugia (Fig. 1). Basilici (1997) has demonstrated that at least the southwestern branch of the Tiber Basin has been characterized by a quite uniform depositional history, identifying four lithostratigraphic units, vertically exposed for about 450 m: 1) the Fosso Bianco Formation is mainly constituted by silty clays deposited in a large lake system; 2) the Ponte Naja Unit is probably partially heteropic with the uppermost part of the Fosso Bianco Unit, and is the result of the depositional activity of an alluvial fan on the lake margin; 3) the Santa Maria di Ciciliano Unit is made up of silty clays and clayey silts deposited in alluvial plain environments, and sand bodies deposited in meandering fluvial channels; 4) the Acquasparta Unit is constituted by continental carbonates (travertines sensu lato) deposited within shallow-lake and wetland environments. The Pantalla mammal fauna was recovered from a 15 m thick stratigraphic succession
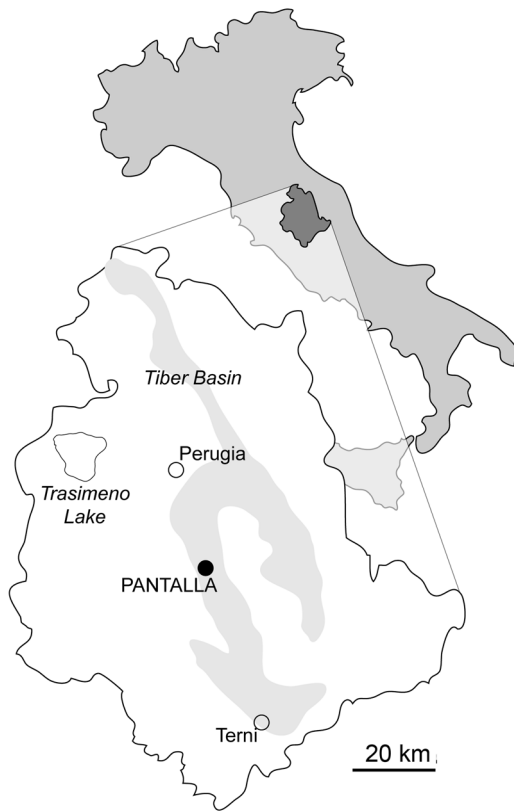
Fig. 1 - Location of the paleontological site of Pantalla (Umbria, central Italy). The "upside-down Y"-shaped Tiber Basin is highlighted in light grey along the middle part of Umbria.

referred to the Early Pleistocene Santa Maria di Ciciliano Unit. Mammal remains occurred within two different levels (Gentili et al., 1997): 1) a silty sand level interpreted as a crevasse-splay deposit located in the middle part of the succession. Several carnivore and herbivore remains - especially skulls - were recovered from this level, and they were particularly concentrated in a very small area of about 2 m². The taphonomic features of this assemblage suggest that bones were winnowed and accumulated by fluvial transport. 2) The second mammal-bearing level (about 2 m above the previous one) is represented by a drained paleosol where vegetal remains (roots, leafs, and charcoal), terrestrial gastropods, and scanty fragmented postcranial bones of herbivore mammals were found. The absence of fluvial transport evidences and the "mosaic" pattern of the surface bone-cracking suggest a pedogenetic origin of the accumulation.

The following mammal species have been identified at Pantalla (fossils from the two stratigraphic levels have been considered as belonging to the same faunal assemblage): *Apodemus* sp. cf. *A. dominans* Kretzoi, 1959, *Canis etruscus* Forsyth Major, 1877, *Vulpes* sp., *Lynx issiodorensis* (Croizet & Jobert, 1828), *Acinonyx pardinensis* (Croizet & Jobert, 1828), *Lutra* sp., *Sus* sp. cf. *S. strozzii* Forsyth Major, 1881, *Axis nestii* (Azzaroli, 1947), Cervidae indet. (large form), *Leptobos* sp. aff. *L. furtivus* Duvernois & Guérin, 1989, *Equus* sp., *Mammuthus* sp. cf. *M. meridionalis* (Nesti, 1825). The faunal list is derived from the preliminary study by Gentili

et al. (1997) and updated by first author, who has carried out a PhD thesis on the vertebrate paleontology of the Pantalla fauna (Cherin, 2013).

From a biochronological point of view, the assemblage has been referred to the Olivola/Tasso Faunal Unit (Gentili et al., 1997), thus having an age near to the so-called "wolf event" (Azzaroli, 1983; Azzaroli et al., 1988; Torre et al., 1992, 2001; Rook & Torre, 1996; Wang et al., 2006; Sardella & Palombo, 2007; Rook & Martínez-Navarro, 2010; Sotnikova & Rook, 2010; Rook et al., 2013). This event consists in the first occurrence in Europe of *Canis* sensu stricto (with the species *C. etruscus*), and marks the important faunal turnover that involved large mammal communities at the Middle to Late Villafranchian transition.

THE SIGNIFICANCE OF THE ETRUSCAN WOLF SAMPLE FROM PANTALLA

Several species of Caninae have been described in the Pleistocene of the Old World, but most of their systematic and phylogenetic relationships are still unresolved, mainly due to the difficult interspecific distinction related to a great morphologic homogeneity. Species belonging to the genus *Canis* are usually opportunistic and generalist. Such great ecological adaptability let them occupy wide geographical areas and is also responsible for the emergence of geographical clines (cfr. Brugal & Boudadi-Maligne, 2011).

Recently, Brugal & Boudadi-Maligne (2011) have recognized only two species in the Early Pleistocene of Europe: *C. arnensis* Del Campana, 1913 and *C. etruscus*. As a matter of fact, however, the relationships between *C. etruscus* and the coeval *C. arnensis* are not yet clear or widely agreed. Kurtén (1974) considered *C. arnensis* as clearly different from *C. lupus* Linnaeus, 1758. Although similar to jackals because of the relative length of M_1 and M_2 (Torre, 1967), in Kurtén (1974) opinion *C. arnensis* is more related to *C. priscolatrans* Cope, 1899, thus included in the coyote lineage. On the other hand, the phylogenetic descent of the extant wolf *C. lupus* from *C. etruscus* through *C. mosbachensis* Soergel, 1928 is widely accepted (Torre, 1967, 1974, 1979; Kurtèn, 1968; Martin, 1973; Sotnikova, 1989, 2001; Sotnikova & Rook, 2010).

Forsyth Major (1877) has been the first to study the rich collections of fossil dogs from Tuscany, describing two new species: the larger "*Canis" falconeri* and the smaller *Canis etruscus*. Nevertheless, Forsyth Major (1877) did not provide a formal diagnosis for *C. etruscus*, nor a diagnosis has been published by the authors that in later times studied the fossil dogs from Tuscany (Del Campana, 1913, 1924; Torre, 1967). The discovery at Pantalla of a sample consisting of four almost complete crania of *C. etruscus* (Fig. 2) prompted us to provide a re-definition of this species (Cherin et al., 2013). Since early studies (cfr. Del Campana, 1913), the distinction between *C. etruscus* and the coeval *C. arnensis* is normally based mainly on mandibular traits. In particular, past works have identified six characters separating these two very similar species, and only two of them concern the cranium: 1) nasal bones extending beyond the maxillofrontal suture in *C. etruscus* and shorter in *C. arnensis*, and 2) paracone
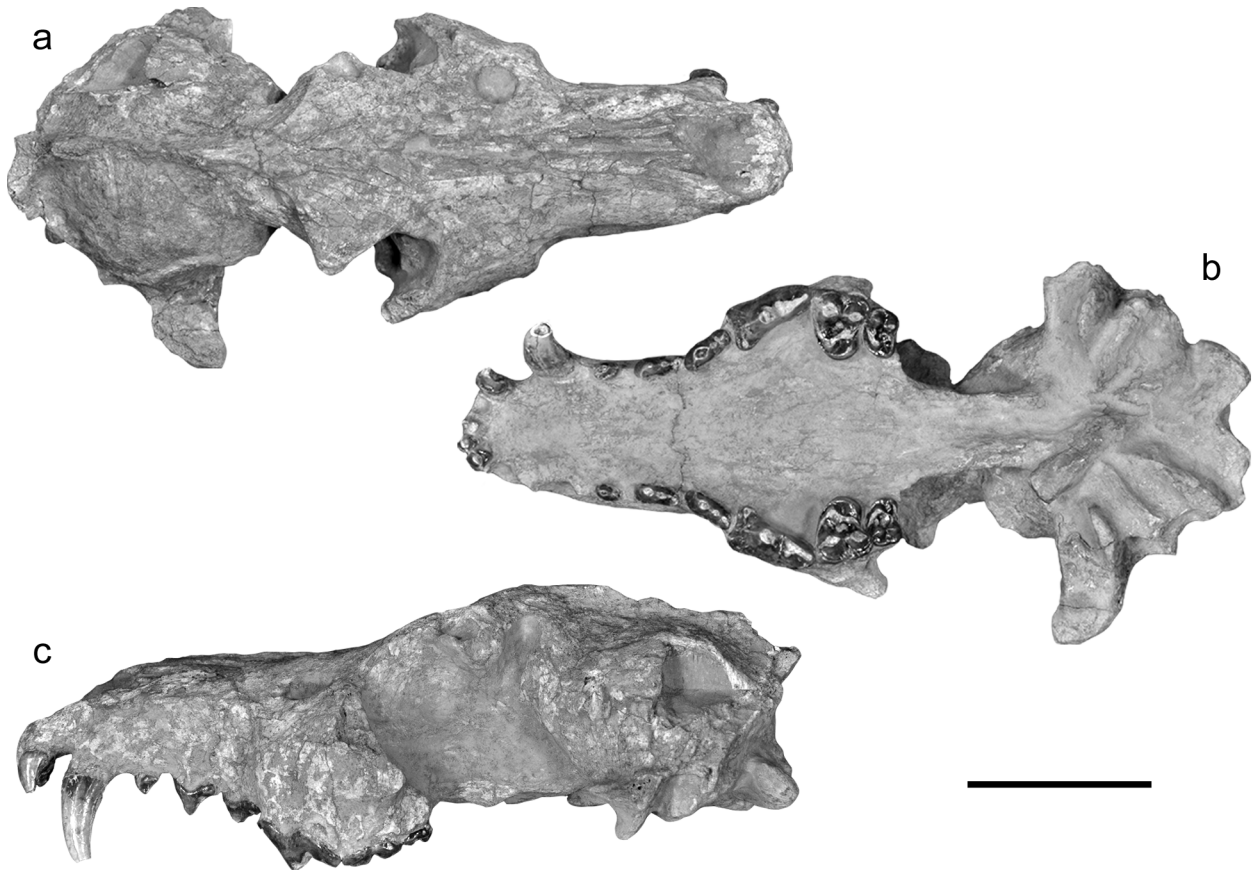
Fig. 2 - *Canis etruscus* Forsyth Major, 1877 (SBAU 337628) from Pantalla (Umbria, central Italy) in a) dorsal, b) ventral, and c) left lateral view. Scale bar represents 50 mm.

of M^1 more developed than metacone in *C. etruscus* and cusps of similar size in *C. arnensis* (Del Campana, 1913; Torre, 1967; Martínez-Navarro, 2002; Tedford et al., 2009). The morphologic and morphometric analysis of the Pantalla *C. etruscus* allowed the recognition of a number of additional significant differences with *C. arnensis*: 1) the contact area between M^1 and M^2 is reduced in *C. etruscus* and quite broad in *C. arnensis*, which is characterized by a "bean-shaped" M^2; 2) the length of the molar row is higher in *C. etruscus* than in *C. arnensis*; 3) *C. etruscus* shows a relatively more enlarged occipital region (Cherin et al., 2013). In a comparative study that included four extant Canini species (*C. lupus*, *C. aureus* Linnaeus, 1758, *C. lupaster* Hemprich & Ehrenberg, 1833, *C. mesomelas* Schreber, 1778) and the Italian fossil *Canis* species (*C. etruscus*, *C. arnensis*), most of the craniodental morphometric characters proved to be strongly conservative among the studied samples, confirming the great anatomical homogeneity within the Canini tribe (Cherin et al., 2013).

Besides the role taken by the Etruscan wolf in the paleoecology of Late Villafranchian terrestrial vertebrate communities (a matter that will be touched in the next chapter), this species represents a key taxon for mammal biochronology. In a seminal paper in 1983 Azzaroli defined as "wolf-event" one of the faunal turnovers characterizing the beginning of the Late Villafranchian.

The term "wolf-event" is still in use although details of the Late Villafranchian canid biochronological distribution is still unclear for Western Europe sites, and only a general framework can be depicted due to different taxonomical interpretations based on incomplete fossil samples. *Canis etruscus*, the oldest "true" representative of the genus *Canis* in Europe, characterized the early Olivola and Tasso Faunal Units, whilst in the late Farneta and Pirro Faunal Units the primitive wolf *Canis mosbachensis* occurs (Martínez-Navarro et al., 2009; Rook & Martínez-Navarro, 2010; Petrucci et al., 2013).

THE LATE VILLAFRANCHIAN CARNIVORE GUILD

The use of the term "guild" (and "paleoguild") referring to large carnivore assemblages is relatively common in paleontological literature since early 1980's (Walker, 1984; Van Valkenburgh, 1985, 1988, 1989; Turner, 1990, 1995; O'Regan & Reynolds, 2009; Meloro, 2011). The term "guild" was originally used by Root (1967) to describe a group of species that exploits a resource in a similar way. In the context of large carnivores, this common trait is the food resource (meat, bones, but also invertebrates or other sources) as represented by preys (or other food items), and the diversity of the different way of predation and exploitation of prey/food resources.

MEAT/NON-VERTEBRATE	MEAT/BONE	MEAT		FLESH EATERS	CARCASSE DESTROYERS	BONE EATERS
			PANTALLA			
		X	*Canis etruscus*			X
X			*Vulpes* sp.	X		
		X	*Lynx issiodorensis*	X		
		X	*Acinonyx pardinensis*	X		
			PIRRO NORD			
X			*Ursus etruscus*	X		
		X	*Lycaon lycaonoides*			X
		X	*Canis mosbachensis*			X
X			*Vulpes alopecoides*	X		
		X	*Lynx issiodorensis*	X		
		X	*Acinonyx pardinensis*	X		
		X	*Megantereon whitei*	X		
		X	*Homotherium latidens*	X		
		X	*Panthera toscana-gomb.*	X		
		X	*Puma pardoides*	X		
	X		*Pachycrocuta brevirostris*		X	
X			*Pannonictis nestii*	X		
			TASSO			
X			*Ursus etruscus*	X		
		X	*Lycaon falconeri*			X
		X	*Canis etruscus*			X
		X	*Canis arnensis*			X
X			*Vulpes alopecoides*	X		
		X	*Lynx issiodorensis*	X		
		X	*Acinonyx pardinensis*	X		
		X	*Megantereon whitei*	X		
		X	*Homotherium latidens*	X		
		X	*Panthera toscana-gomb.*	X		
	X		*Pachycrocuta brevirostris*		X	
	X		*Chasmaporthetes lunensis*		X	
X			*Pannonictis nestii*	X		

Tab. 1 - Classification of fossil carnivore assemblages discussed in the text according to different dietary categories. On the left side Van Valkenburgh (1985, 1988) dietary categories (the Van Valkenburgh's "Non-Vertebrate/Meat" category has not been considered, as specified in the text), on the right side Turner (1995) dietary categories (see text for discussion).

Details of carnivore paleoecology are difficult to interpret due to the biases of preservation typical of the fossil record and, very often, because of the fragmentary status of the carnivore fossil record (Damuth, 1982; Palmqvist et al., 2003). In order to explore carnivore guild structure and carnivore ecology within the fossil record, features most frequently used by paleontologist are: 1) locomotor style, 2) body mass distribution, and 3) feeding habits.

In the analysis here reported, we focus only on the third one, the feeding habits. In terms of diet, carnivores utilize a wide range of food sources, and this is reflected in their dentitions. As a basic principle, molars are used for grinding and premolars for cutting and crushing. The lower carnassial (M_1) is an exception, being designed (at different extent according to dietary specialization) for both cutting and grinding. On the contrary, the upper carnassial (the fourth upper premolar) never has been molarized during the entire history of the order Carnivora, and strictly maintains its cutting function (Butler, 1946). The relationship in the dentition between cutting and grinding areas changes as an adaptation to feeding habit, which in carnivores varies in a wide range of adaptations, from hypercarnivorous species (where the cutting features prevails) to omnivorous or even invertebrate/herbivores (where the dentitions reveals a dominancy of crushing/grinding abilities). For this reason, the proportion of slicing (trigonid) length/grinding (talonid) length in the lower carnassials is the dental index to determine the relative importance of meat vs. non-vertebrate foods in the carnivore diet (Van Valkenburgh, 1989).

Since competition for food is an important patterning force in the guilds structure of large terrestrial carnivores (Van Valkenburgh, 1988, 1989), we regarded of some interest comparing the Pantalla assemblage with other Late Villafranchian assemblages from Italy (Tasso and Pirro Nord) and to extant East African guild (Serengeti; data from Van Valkenburgh, 1988).

For this purpose we have classified the carnivore assemblages according to different dietary categories, matching two different approaches. The first one follows Van Valkenburgh (1985, 1988), whose dietary categories, basing on a broader spectrum of predatory mammals, are slightly different from those utilized in Turner (1995), who focuses more specifically on large carnivores. In order to provide a wider comparative basis, we utilized both categorization systems, and given that each of the two reveals interesting clues, we compare here the two different summarizing graphs (Tab. 1; Fig. 3).

Van Valkenburgh (1985, 1988) dietary categories are: 1) Meat: diet greater than 70% in meat; 2) Meat/Bone: greater than 70% in meat with addition of large bones; 3) Meat/Non-Vertebrate: 50-70% in meat with the balance of fruit and/or insects; 4) Non-Vertebrate/Meat: less than 50% meat with fruit and/or insects predominating (the latter category does not appear in our graph). On the other hand, the dietary categories according to Turner (1995) refer to: 1) the necessary concentration of meat (Flesh eaters); 2) the ability to eat bones and destroy carcasses of medium size ungulates (Carcasse destroyers); and 3) those species able to eat bones to a moderate extent (Bone eaters).

In both graphs (Fig. 3) the carnivore guild from Pantalla reveals its peculiarity of having under-represented (or non-represented), among large carnivores, the Hyaenidae, the typical taxon occupying the "Meat/Bone" (Fig. 3a) or the "Carcasses destroyers" (Fig. 3b) feeding categories.

In Fig. 3a (Van Valkenburgh categories), the two Late Villafranchian Italian sites (Tasso and Pirro Nord) closely
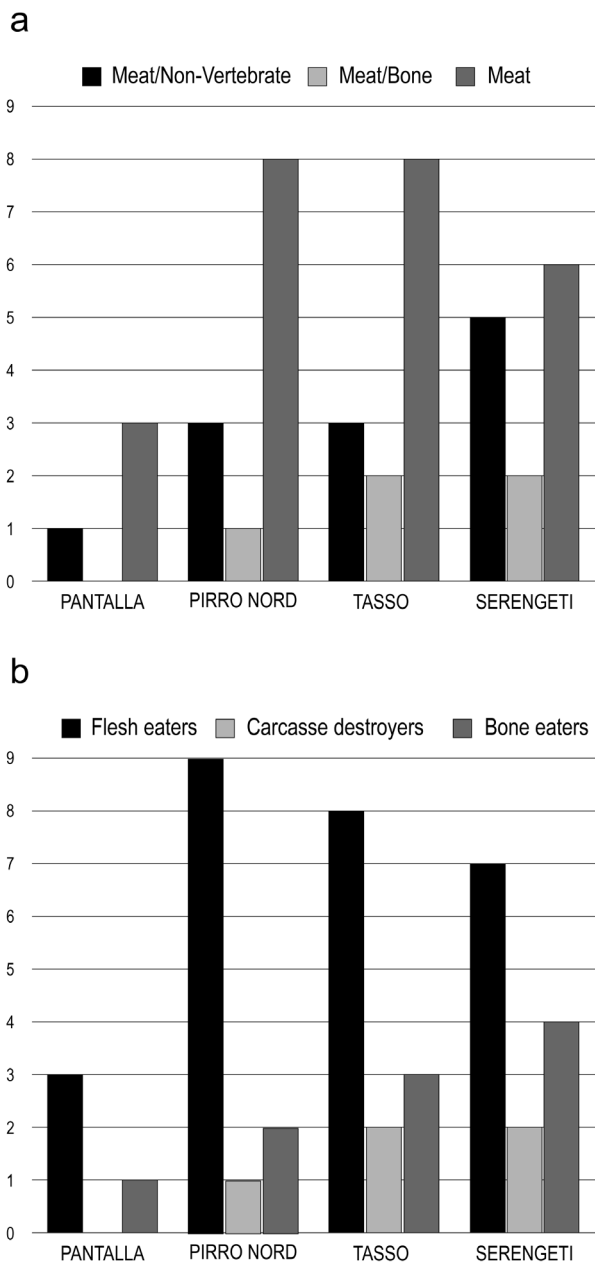
a

b

Fig. 3 - Structure of Pantalla carnivore guild, compared to selected Late Villafranchian Italian Local Faunas (Pirro Nord, Tasso; Tab. 1) and extant East African guild (Serengeti; data from Van Valkenburgh, 1988). In 3a, feeding categories are as specified in Van Valkenburgh (1985, 1988) (the Van Valkenburgh's "Non-Vertebrate/Meat" category has not been considered, as specified in the text), while in 3b taxa are grouped according to feeding categories as defined by Turner (1995). The vertical axis represents the number of recorded species.

the same value in Tasso and Serengeti, because of the occurrence in the Tasso assemblage of the hunting hyaena *Chasmaporthetes lunensis* (Del Campana, 1914). This peculiar hyaenid was, in fact, characterized by a dental specialization to bone consumption lesser developed than in the "hyper-scavenger" *Pachycrocuta*, or in the extant bone-crackers *Hyaena* and *Crocuta* (Ferretti, 1999, 2007; Rook et al., 2004). The same reasoning can be addressed concerning the category "Carcasse destroyers" of Fig. 3b.

In Fig. 3b, the difference in "Bone eaters" (i.e., those species able to eat bones to a moderate extent, actually mid- to large-sized Canidae) among extant East African guild and our fossil localities is given by the fact that East Africa guild is characterized by the co-occurrence of four medium to large-sized canids (*Lycaon* and three jackal species), while Tasso records three dogs (*Lycaon* and two *Canis* species), and in Pirro Nord only two species occur (*Lycaon* and *Canis mosbachensis*).

During the Early Pleistocene the large carnivore guild was characterized by a great biodiversity, being composed by a high number of species. In particular, around 2 Ma the giant hyaena *Pachycrocuta brevirostris* (Aymard, 1846) spread into Western Europe, together with the Eurasian jaguar *Panthera gombaszoegensis* (Kretzoi, 1938). Therefore, large felid diversity increased with the machairodontine cats *Homotherium* and *Megantereon*, besides the pantherine cat *Puma pardoides* (Owen, 1846) and the giant cheetah *Acinonyx pardinensis*. At the same time, *Lynx issiodorensis* continues to be recorded in several European sites. Finally, even if the arrival of the first *Canis* sensu stricto in Western Europe probably occurred slightly before 3 Ma (Lacombat et al., 2008; Sotnikova & Rook, 2010), the wide diffusion of these wolf-sized dogs is registered around the Middle to Late Villafranchian transition (~2 Ma), with the so-called "wolf event" (Azzaroli, 1983). The second half of the Early Pleistocene (after the Olduvai magnetic chron) is characterized by the contemporary presence of the three canid species (*C. etruscus*, *C. arnensis*, and *Lycaon falconeri*), enriching the complex framework of the carnivore guild. The coexistence of several species of top terrestrial predators (Hyaenidae, Felidae, and Canidae) during the Early Pleistocene in Western Europe finds, in some way, its Present-day equivalent in East Africa, where - as far as canids - three jackal species (*C. aureus*, *C. mesomelas*, and *C. adustus* Sundevall, 1847) and the African wild dog *Lycaon pictus* (Temminck, 1820) share the same territory, occupying different ecological niches (Macdonald & Sillero-Zubiri, 2004). The canid species richness in the Late Villafranchian carnivore assemblages is expressed in the "Bone eaters" diversity (Fig. 3b), reaching values similar to what observed in extant East African guilds.

A comparative look at the Late Villafranchian Pantalla assemblage provides some clues about the Early Pleistocene carnivore guild in Italy. Together with the Etruscan wolf (a cooperative carnivore hunting in packs), solitary predators such as *A. pardinensis* and *L. issiodorensis* have been also recorded. The paleoecological study of this site could provide new data concerning the patterning of the large carnivore guild and the strategies in which Pleistocene large felids and canids competed to reach and exploit food resources (i.e., prey). These

match the Serengeti structure: in all three the "Meat" eaters consist of six species (excluding the two saber-toothed felids *Homotherium* and *Megantereon* from the two Late Villafranchian sites). This aspect is evidenced in Fig. 3b by the higher values of "Flesh eaters" in both Pirro Nord and Tasso Local Faunas.

Back to Fig. 3a, in Italian fossil localities the "Meat/Non-Vertebrate" eaters are underrepresented in respect to East African guild, while the "Meat/Bone" eaters reach

two groups of predators are characterized by different hunting behaviors: cats normally prey with a short chase and a quick kill through a combination of speed, agility, and power; on the contrary, dogs (that lack as powerful weapons as felid's canines or retractile claws) normally rely more on social hunting, aiming on exhausting the prey. Assuming that *C. etruscus* was a social dog, it probably could prey large ungulates such as bovids and cervids, thus entering in competition with both the cheetah *A. pardinensis* (that was considerably larger that the Present-day *A. jubatus* [Schreber, 1778]) and with the lynx *L. issiodorensis* (the extant *L. lynx* [Linnaeus, 1758] can kill up to 220 kg adult male deers; Macdonald et al., 2010). In such a situation of interspecific competition, probably scavenging could have been an advantageous strategy for Late Villafranchian canids, as it often occurs in Present-day forms (Macdonald et al., 2004). Moreover, taking in mind the behavior of extant sympatric large carnivores, intra-guild predation has to be taken in consideration too. For example, in North America between 12% and 62% of bobcats (*Lynx rufus* [Schreber, 1778]) are killed by coyotes (*Canis latrans* Say, 1823) and pumas (*Puma concolor* [Linnaeus, 1771]) (Macdonald et al., 2010).

CONCLUSIVE REMARKS

As already demonstrated since early studies approaching the paleoecology of mammal assemblages and environmental reconstructions (Azzaroli, 1983), the carnivore guild structure of the Late Villafranchian faunas reveals a strong affinity with the extant East African large carnivores guild. Albeit outstanding in the state of preservation and number of fossils recovered, the Pantalla carnivore assemblage is still missing an important part of its paleoguild. It is in fact known that, in general, species richness within predator guilds, especial for "Bone/Meat" and "Meat" or "Flesh eaters" and "Bone eaters" (according to the dietary characterization preferred), is greater in environments where biomass and species richness of prey are greater.

In the transition from Olivola FU to Tasso FU *C. etruscus* habitats face the invasion of two other canids: *Canis arnensis* and *Lycaon falconeri*. The co-occurrence of three canids in the same habitat is a particular condition that nowadays occurs just in Eastern Africa. *L. falconeri* probably occupied the niche vacant since the extinction of the cursorial hyaenid *Chasmaportetes lunensis*, while *C. arnensis* was possibly more omnivorous than *C. etruscus*.

The number of carnivores supported by a bioma is strongly dependent from the predator/prey ratio. Thus, the richness and diversity of the predator guild is an index of abundant prey biomass.

The Villafranchian faunas are characterized by high biodiversity levels and our knowledge of the Italian and European Late Villafranchian fossil record reveals that the carnivore diversity can exceed the number of fifteen species. Further recoveries will hopefully allow the carnivore species documented at Pantalla to be increased.

ACKNOWLEDGEMENTS

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