Human/carnivore interaction in the Middle Pleistocene of Latium (Central Italy): an open question

M. Mussi¹, M.R. Palombo²

¹Dipartimento di Scienze dell'Antichità, Università degli Studi di Roma "La Sapienza", Roma, Italy - margherita.mussi@uniroma1.it

²Dipartimento di Scienze della Terra, Università degli Studi di Roma "La Sapienza", CNR Centro di Studio per il Quaternario e l'Evoluzione Ambientale, Roma, Italy mariarita.palombo@uniroma1.it

SUMMARY: Current views on the earliest peopling of Europe, and on interaction between carnivore and primitive hominids, are tested against the complex palaeontological and archaeological record of Latium. While the available evidence does not allow for a full evaluation of late Pliocene or early Pleistocene peopling, there is ample evidence of human colonisation of the area after 500 ka. During the middle Pleistocene, human groups successfully competed in Latium with modern carnivores, possibly occupying a niche that only partially overlapped with that of other predators.

1. CURRENT VIEWS ON THE EARLIEST PEOPLING OF EUROPE

The chronology of the first colonisation of Europe by hominids is still a hotly debated question. In the last fifty years or so, "long chronologies" of 1 to 2 Ma have been again and again opposed to "short chronologies" of approximately 500 ka. In recent years a compromise of a kind was reached by Dennel & Roebroeks (1996), whose "revised short chronology" suggests an intermittent peopling of the Mediterranean perimeter of Europe around 1 Ma, and a stable colonisation starting around 600 to 500 ka. An even greater antiquity is actually claimed for some European sites, but the dates are still controversial (see Palmqvist & Arribas 2001; Peretto 2001 for an update of the debate).

Whatever the exact date of the earliest peopling, given the very limited technological complexity at the time, any dispersal of human groups out of Africa and into the middle latitudes of Eurasia is better seen in the context of similar events involving other species: human behaviour, including the expansion into new environments, underwent the same processes as other large mammals. Humans, furthermore, were both adapted to meat consumption (Henneberg *et al.* 1998) and in need of eating it, at least seasonally, in order to colonise areas in which vegetation growth was limited for several months (Mussi 1999). Accordingly, human/carnivore interaction at the Plio-Pleistocene boundary must be investigated, and the available resources evaluated.

After Palmqvist et al. the sabre-tooth felid Megantereon played a significant role in Late Villafranchian Eurasia, as this hypercarnivore supposedly produced large numbers of carcasses. Furthermore, the dental characteristics of Machairodontinae, and most notably the peculiar development of both the enlarged upper incisors and the upper carnassials, would not have allowed for carcasses to be fully stripped of their flesh. Subsequently Megantereon activity would have opened a niche for scavengers, including both Homo and Pachycrocuta, allowing for late Pliocene human colonisation of Europe. (Palmqvist & Arribas 2001; Palmqvist et al. 1996; Martínez-Navarro & Palmqvist 1996).

P. brevirostris was a large, short-faced hyena, well adapted to the destruction of carcasses and bone consumption, as implied by its short distal limb segments which gave it greater power and more stability for dismembering and carrying (Palmqvist et al. 1996b; Arribas & Palmqvist 1998; Turner & Antón 1996). Turner (1990, 1992, 1994), accordingly, had previously argued that humans could not have easily won the competition with this large hyena for access to Megantereon leftovers, making it difficult for hominids to develop an adaptive scavenging pattern. Consequently, a stable, suitable and productive niche for hominids only opened in Europe around 500 ka, when sabre-toothed felids and giant hyenas were replaced by modern African carnivores such as the lion, the leopard and the spotted hyena.

Meanwhile, new evidence on human behaviour came to light on two archaeological sites: the zooarchaeological analysis of the so-called "Aurora Stratum" of Atapuerca, pointed to primary and early access to carcasses possibly as early as 1 Ma ago (Diéz *et al.* 1999); while at the 400-450 ka year old site of Schöningen, in northern Germany, exceptional local conditions allowed for the preservation of sophisticated wooden spears, associated with the remains of butchered horses (Thieme 1997), giving positive evidence of hunting capacities.

2. THE ITALIAN RECORD

As far as Italy is concerned, there is little doubt that human settlement was well underway during the early Middle Pleistocene, possibly some time before 600 ka after the recent dates of Notarchirico and Isernia (Coltorti *et al.* 2000: Piperno 1999). An earlier age has also been suggested on a few more sites (for a discussion: Mussi 1995; Mussi in press; Villa 2001; see also Palombo *et al.* 2001).

Overall, the Middle Pleistocene was a time of substantial faunal turnover, occurring in Italy during the worsening climate which followed the Early/Middle Pleistocene boundary, correlated with OIS 25 by Cita & Castradori (1994) (Palombo & Mussi 2001 and references there in). The main climatic fluctuations of the Pleistocene affected physical and/or biotic environmental variations and are possibly reflected in concurrent bioevents in multiple lineages. There are changes in the richness and diversity of the fauna and flora, and the structure of mammal communities is sometimes affected. Different lines of analysis actually suggest an increase in the richness and diversity of large mammals. They point, most notably, to great numbers of both medium and large herbivores of open environments, including pachyderms, and to a progressively changing carnivore guild.

The final Lower Pleistocene (Early Galerian, Colle Curti FU, *sensu* Gliozzi *et al.* 1997) carnivore guild is dominated by large, flesh eating and bone consuming species (Tab. 1).

Canis etruscus, with a cranial morphology similar to that of modern omnivorous species, disappears in the late Villafranchian, before the Pirro FU. The same happens to *Canis* (*Xenocyon*) falconeri in the early Galerian. This very large canid has a craniodental morphology similar to that shown by extant hypercarnivorous canids, more than 70% of whose diet includes vertebrate meat. According to morphofunctional skeletal features, the species may have developed a cooperative behaviour similar to that of modern African wild dogs, who are savannah hunters also active by day (Palmquist *et al.* 1999).

More large carnivores become extinct in the Late Villafranchian, including *Megantereon* "cultridens"¹ and the large cheetah Acinonyx pardinensis (even if a small Acinonyx possibly survives until later in Mediterranean environments: Moullé 1997). Throughout the Galerian, however, another sabre-tooth cat is active: this is *Homotherium latidens*, possibly living in small prides, adapted to pursuit hunting and able to attack large prey, such as young elephants. Accordingly, it was also producing carcasses rich in flesh.

Pachycrocuta brevirostris, the large and effective carcass destroyer, disappears later than other species, and is still well represented for part of the middle Galerian.

More large carnivores enter the Italian scene during the Galerian. *Panthera (Leo) fossilis*,

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	VILLAFRANCHIAN			GALERIAN				AURELIAN	
MAMMAL AGES	LATE	EARLY		MIDDLE		LATE	EARLY	MIDDLE	LATE
FAUNAL UNITS	Pirro	Colle Curti	Slivia	Ponte Galeria	Isernia	Fontana Ranuccio	Torre in Pietra	Vitinia	
MIDDLE to LARGE SIZED CARNIVORA									
Canis (Xemicyon) falconeri									
Canis aff. C. arnensis (advanced form)									
Canis sp. aff. C. arnensis/Canis aff. C. mosbachensis									
Canis lupus									
Cuon alpinus					I				
Gulo gulo									
Ursus etruscus									
Ursus deningeri		I			ĺ				
Ursus spelaeus									
Ursus arctos					i				
Hyaena prisca				 ب					
Pachycrocuta brevirostris									
Crocuta crocuta		1							
Lynx issiodorensis									
Lynx sp.									
Lynx lynx							1		
Acinonyx pardinensis									
Panthera ex gr. P. gombaszoegensis									
Panthera (Leo) fossilis									
Panthera (Leo) spelaea									
Panthera pardus						<u>~</u>			
Megantereon cultridens (advanced form)									
Homotherium crenatidens									
Homotherium ex gr H. latidens	·								

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Tab.2 – Local large mammal faunas from selected Italian localities from the latest Early Pleistocene (latest Villafranchian) to the Middle Pleistocene (middle Aurelian).

(1) references in Palombo et al. (in press), (2) references in Mussi (2001).

MAMMAL AGE	GALERIAN EARLY MIDDLE						LATE EARLY																				
	-			MIDDLE				LATE Fontar								MIDDLE											
FAUNAL UNIT	C.0	Curti	P. G.		Isernia	3	F	Ranuco	io			Torre i	n Pietr	a							Vitinia						
Selected Taxa Selected Localities	Calle Curti (1)	Redicicali (1)	Ponte Galería (various sites) (1)	sernia-La Pineta (1)	Cesi (1)	G.R.A. (Roma) (1)	Fontana Ranuccio (1)	Cava Pompi (2)	Cava nera Molinario (1)	X La Polledrara di Cecanibbio (1)	Torre in Pietra (lower) (1)	Castel di Guido (1)	Malagrotta (1)	X Pontecorvo (1)	X Pignataro	Bucine (1)	Campo Verde (1)	Torre in Pietra (upper) (1)	Vitinia (upper beds) (1)	Cerveteri (1)	Casal de' Pazzi (1)	Sedia del Diavolo (1)	X Monte delle Gioie (1)	Prati Fiscali (1)	Carnello (2)	Valle Radice (2)	
Human impact		-	-	×	•	•	X	X	•	X	X	X	X	X	X	X	X	X	X	•	X	X	X	•	X	X	
Macaca sylvanus	-	-	-		-	-	?	x	-	-			-	-	-	-		x	-	-	-		-	-			
Hyaenidae gen. spec. indet.	x	x	-	-	-	x	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Crocuta crocuta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	х	x	x	-	-	х	-	-	-	х	x	
Canis (Xenocyon) ex gr. C. falconerii	X	-	-	•	-	-	-	-	-	-	•	•	-	-	-	-	-	-	-	-	-	•	-	-	-	-	
Canis sp. aff. C. amenesis	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	х	-	-	-	?	-	-	-	-	-	
Canis sp. aff. C. "mosbachensis"	-	-	-	-	-	-	-	-	-	-	•	X	-	-	-	-	-	-	-	-	-	-	-	•	-	-	
Canis lupus	-	-	-	-	-	-	-	-	-	X	х	X	cf.	-	-	х	-	X	X	-	х	X	-	-	-	-	
Cuon alpinus	-	-	-	-	-	-	х	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	
Ursus spelaeus	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	х	X	
Ursus deningeri	-	-	-	X	-	-	х	-	-	-	•	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ursus arctos	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-		-	-	-	-	-	-	-	-	
Ursus sp.	x	-	-	-		-	-	-	-	-	-	-	-	-	-	-	х	x	-	-	-	-	-	-	-	-	
Homotherium ex gr. H. latidens	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Lynx</i> sp.	-	-	-	:	-	-	-	-	-	-	•	-	•	-	-	-	-	-	-	-	-	-	-	-	X	X	
Panthera (Leo) fossilis	-	-	-	x	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	
Panthera (Leo) spelaea	-	-	-	-	-	-	-	1	-	-	x	x	•	-	-	-	-	-	-	-	-	-	-	-	x	X	
Panthera (Leo) sp.	-	-	-	-	-	-	x		-	-	-	-	-	-		-	-	-	-	-	-	-	-	- 7	· x	x	
Panthera pardus	-	-	-	1	-			1				1	:		-	-		1	-		-	1	-	ŕ		^	
Elephantinae gen. Spec. Indet.	x	x	- ?		х				1																		
Mammuthus meridionalis	^	<u>^</u>	x																				1				
Mammuthus trogontherii M. ex gr. M. chosaricus-M. primigenius			^													x	x							1			
Equus altidens		x	x							-						î.	î.										
Equus suessenbornensis		î.								-				-	-	aff.			-								
Equus hydruntinus	-		-		-	-	-			-				-		-			-	-	-	x		-	x		
Equus forus	-	-	?	-	cf.	-	x		-	x	x	x	x	x	-	-	x	x	-	x	x	x	-	x	x		
Stephanorhinus sp.	-	-			-	-			-	x				x	х	х	x		x	x	x		-	•	x	x	
Stephanorhinus hundsheimensis	-	x	x	x	x	-	cf.	- I	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
S. sp. aff. S. hundsheimensis	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	cf.	-	-	-	-	-	-	-	-	-	
Stephanorhinus hemitoechus	-	-	-	-	-	-	-	-	-	-	x	-	cf.	-	-	-	cf.	x	-	-	-	х	х	х	-	-	
Sus scrofa	-	-	-	х	-	-	х	-	-	-	х	-	х	?	-	х	x	х	-	-	х	х	-	-	-	-	
Hippopotamus ex gr. H. antiquus	X	X	x	X	cf.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Hippopotamus ex gr. H. amphibius	-	-	-	-	-	-	X	-	X	-	-	X	х	х	х	-	X	X	-	-	х	X	Х	-	-	-	
Capreolus capreolus	-	-	-	X	-	-	-	-	-	-	-	-	х	-	-	х	х	X	-	-	Х	-	-	-	-	-	
Pseudodama sp	X	X	X	•	-	-	-	-	-	-	•	-	•	-	-	-	-	-	-	-	-	•	•	•	-	-	
Dama clactoniana	-	-	-	X	X	cf.	Х	-	-	-	-	-	cf.	-	-	-	-	-	-	?	-	X	-	-	-	-	
Dama dama	-	-	-	•	-	-	-	-	-	-	•	-	-	-	-	-	X	X	X	х	х	X	X	х	-	-	
Dama sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	
Cervus elaphus		-	X	x	x	-	x	-	x	x	x	x	х	х	х	x	х	x	x	х	х	x	x	х	-	•	
Megaceroides verticornis	X	-	x	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Megaceroides solhilacus	-	-	-	x	x	-	-	cf.	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	•	
Megaloceros savini	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Megaloceros giganteus	-	-	-	-	-	-	-	-	-	-	x	-	•	x	-	cf.	x	-	-	-	-	-	-	-	-	· ·	
Megacerini indet.	-	-	-	1	-	-	x	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	
Bos galerianus		-	X ?		1	x	- x	x	1	×	x	x	x	-	×	- ?	×	x	×	x	×	x	x	×	1	1	
Bos primigenius	1	x		1		×		×		×				-	×		×		×	×	×	×	×	×		-	
Bison sp. cf B. (Eobison) degiuli		X	1		1	1	1	1	1	1		1	1	1	1	-	-	1	1	-	-		1	1	:	· ·	
Bison sp. aff. B. schoetensacki				x	x	-								-						-							
Bison schoetensacki				^	^							1		1	-	?											
Bison priscus Homitrague boneli	-			x	-		-																				
Hemitragus bonali	1	1	1	^		1	1		1	1		1		1	-		x						1	1			
Caprinae gen. Spec. Indet.	L -	1 -	1 -		-	-	-	1	1 -	1 -	-	- T	-	- T	-	-	^	- T	-	-	-	-	-	· -	-	x	

the primitive lion, markedly larger than modern lions, disperses into the Old World at about 600 ka, when open savannah or steppe-like environments develop. It is then substituted during the late Middle Pleistocene by the more advanced cave lion, *Panthera (Leo) spelaea*. Both taxa, just like modern lions, were most probably able to hunt large prey, often in groups. Other carnivores (including humans) were not allowed to gain access to the carcasses, and lions could displace other predators in order to scavenge (Ewer 1998).

Crocuta crocuta, the spotted hyena, is another open environment group hunter, and a marginal scavenger as well. It is also present in Italy at the beginning of the Middle Pleistocene (middle Galerian, Slivia FU, sensu Gliozzi et al. 1997). There is no further evidence of the spotted hyena in the late Galerian and lower Aurelian, but then there are more and more occurrences during the middle and late Aurelian. Hyaena prisca, of possibly similar habits, is only documented at G.R.A., a site on the outskirts of Rome. Ursus deningeri, the brown bear, whose hunting aptitude is well documented in modern populations (Ewing 1998), is similarly first documented in middle Galerian assemblages.

3. THE CASE OF MIDDLE PLEISTOCENE LATIUM

Many archaeological and palaeontological sites have been discovered in the area surrounding Rome, the *Campagna Romana*, and more are located in the rest of Latium. In the discussion below, we will focus on the evidence from Latium itself, but the 26 assemblages of our sample also include a few sites, such as Isernia, outside the regional border, even if not far away from it (Tab. 2). The latitude ranges between 41° and 43° N.

The earliest part of the record is not that rich, however. Early and middle Galerian faunas were discovered at Redicicoli and Ponte Galeria, both in the Campagna Romana (Colle Curti and Ponte Galeria FUs²). The remains are not abundant, and carnivores, most notably, are probably under represented. There is no evidence, so far, of any human presence. Middle Galerian faunas are even scarcer and one must turn to Isernia as a reference site, with the earliest evidence of the dispersal in Italy of the lion as well as *Ursus deningeri*.

This large-bodied brown bear is first documented in Latium at Fontana Ranuccio (Fontana Ranuccio FU).

At this site, which K/Ar dating puts at c. 450 ka old, the much more diversified mammal assemblage also includes *Cuon alpinus*, while very large cervid species are reduced in number (Tab. 2). There is also ample evidence of human presence, such as some teeth, and Acheulean assemblages with both lithic and bone handaxes. More archaeological evidence turned up on sites of the same age, such as Cava Pompi and Valchetta Cartoni, which are less endowed with faunal remains.

There is no reason why the Latium inhabitants of the time should have been less skilled hunters than the "contemporary" ones of Schöningen, who killed horses with sophisticated wooden spears. If this hypothesis is correct, then they would have been competing for the same class of prey as lions and brown bears.

Outstanding palaeontological evidence from the Campagna Romana only comes later, when a combination of Late Quaternary volcanism and exogenous agents led to widespread site preservation and to a good chance of archaeological recovery (Arnoldus-Huyzendveld et al. 2001; Caputo et al. 2001). This is better seen on the many archaeological sites of the Aurelian Formation as well as on those of the subsequent Vitinian Formation (Tab. 2). With the end of Galerian and the transition to the Torre in Pietra FU there is evidence of a significant change as the fauna progressively acquires a modern character. The relevant sites, namely those of the Aurelian Formation, are dated to OIS 9, but the renewal might have started earlier, around the OIS 11/OIS 10 transition, when in the Mediterranean area the interstadial climate had become progressively milder and the average rate of humidity had increased (Vergnoux-Grazzini et al. 1990). Most of the large Galerian herbivores, such as Equus altidens, megacerini and Bison schoetensacki become extinct, while new carnivores appear. These are small species, however, except for the medium sized *Canis lupus*. The pachyderms decline. Overall, during the Aurelian, the percentage of medium to large carnivores and herbivores becomes more balanced (Fig. 1).

A smaller number of large bodied animal species cannot have been detrimental to humans. Even more so, at a time of increased faunal richness and diversity, when new occurrences prevail over extinctions, as happens in the transition between Torre in Pietra and Vitinia FUs. The spectacular record from the Aurelian Formation sites, such as La Polledrara, possibly points to the fact that a more limited number of pachyderm species was amply compensated by the higher frequency of the extant taxa. If, as Anzidei et al. (1988) suggest, killing weak animals trapped in the mud and scavenging carcasses of dead animals were two possible options at spots where herds of elephants seasonally congregated, human group organisation would have been adequate to keep at bay, at least for a while, an array of powerful competitors, including both lone hunters, such as the brown bear, and group hunters, such as lions, spotted hyenas and wolves. Evidence of artificial bone modification (Anzidei & Cerilli 2001) is further evidence of some control over the carcasses.

4. FINAL REMARKS

The Italian record does not allow for fully testing the theory of Palmqvist *et al.* (1996, 1999) as to the relevance of sabre-tooth cats in the production of fleshy carcasses for human consumption. The scarcity of archaeological sites during the early Galerian, however, rather points in the opposite direction. The evidence from Latium rather conforms to Turner's anticipations (1992a; 1992b; 1994), in that there is good evidence of human peopling after 500 ka, when the fauna – including carnivores – acquires a modern character. The many sites of OIS 9 suggest that humans at the time, on top of a possible ability to kill medium sized herbivores, were also able to take advantage of

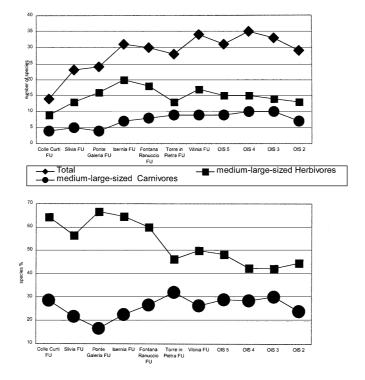


Fig.1 - Line chart of selected medium and large herbivores and carnivores.

pachyderms and other animals dying naturally. This means that they were also able to win in an aggressive confrontation with other carnivores similarly interested in carcasses.

This also points to the fact that, just like any other predator, they included meat in their diet in an opportunistic way, hunting, searching for dead animals, scavenging leftovers, maybe even displacing other carnivores and stealing their prey. A limited running capacity and moderate strength was supplemented by cultural means, such as the ability to shape weapons - possibly wooden ones - and to fully co-operate in the hunt. Language development can only be guessed at, but would have helped greatly in planning ambushes, while flying vultures and crows - all of them amply documented in middle Pleistocene inventories (M. Pavia 2001 personal communication) would have made it easier to find carcasses.

Being omnivorous, however, and because of their strictly diurnal activity, humans differ from other predators. Overall, there are grounds to believe that this ecologically flexible and adaptable species took advantage of a niche only partially overlapping that of other carnivores.

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The World of Elephants - International Congress, Rome 2001

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Human/carnivore interaction in the middle Pleistocene of Latium (central Italy): an open question

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6. Notes

¹ The taxon has been identified as *M. whitei* by Martínez-Navarro & Palmqvist (1995), in whose opinion in Western and Central Europe *M. cultridens* gave rise to *M. white*i at the Plio/Pleistocene boundary.

² For Slivia FU, an age older than the other middle Galerian FUs, is generally accepted on the basis of the occurrence of *Mimomys savini* and the survival of some Villafranchian carnivores (Gliozzi *et al.* 1997). We do not rule out, however, that both the Slivia and the Ponte Galeria assemblages actually belong to the same FU. In fact, the identification of most herbivores of the Slivia local fauna is doubtful, and not much is known of the carnivores and micromammals belonging to Ponte Galeria FU. Accordingly, the differences between the two faunas might well be overestimated.