

## THE VILLAGRANCHIAN LARGE CARNIVORE GUILD: GEOGRAPHIC DISTRIBUTION AND STRUCTURAL EVOLUTION\*

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**RIASSUNTO** - Il gruppo dei grandi carnivori villafranchiani: distribuzione geografica ed evoluzione strutturale - Il Quaternario *Italian Journal of Quaternary Sciences*, 8(2), 1995, 349-356 - L'evoluzione del gruppo dei grandi carnivori è una caratteristica precipua dell'evento faunistico villafranchiano. L'estinzione di forme arcaiche e la comparsa di taxa con aspetto più moderno portò come risultato finale ad avere nel Pleistocene medio un insieme simile per specie presenti e praticamente identico per composizione all'insieme attualmente vivente in Africa orientale. Tuttavia, l'estinzione e la comparsa di elementi del gruppo non sono da considerare come l'effetto di un unico mutamento poiché i momenti dei vari eventi sono sia cronologicamente sia geograficamente molto più complessi. A circa 1.6 Ma in alcune regioni si estinse l'iena *Chasmaporthetes lunensis* che fu rimpiazzata da *Pachycrocuta brevirostris*, *Panthera gombaszoegensis* e diverse specie di *Canis*. All'incirca nello stesso periodo sembra che si sia estinta anche la *Pliocrocuta perrieri*, di grandi dimensioni, anche se il periodo esatto di tale evento non è molto chiaro. A Untermassfeld, il *Megantereon cultridens* dai denti a sciabola riuscì a sopravvivere sino al tardo Pleistocene inferiore, quando *Panthera leo*, *Panthera pardus* e forse anche *Crocuta crocuta* si diffusero in Europa. Tale comparsa fu seguita dalla ricomparsa, all'inizi del Pleistocene medio, della *Pliocrocuta perrieri*. Verso la fine del Villafranchiano e fino nell'ambito del Pleistocene medio, il gruppo dei grandi carnivori raggiunse il massimo livello di complessità e di taglia con taxa arcaici — quali *Homotherium latidens*, *Acinonyx pardinensis*, *Panthera gombaszoegensis*, *Pachycrocuta brevirostris* e *Canis (Xenocyon) lycaonoides* — che convivevano con specie moderne quali *Panthera leo*, *Panthera pardus*, *Crocuta crocuta* e il piccolo *Canis mosbachensis*. Solo dopo gli 0.5 Ma l'associazione subì una riduzione di taglia e la contemporanea scomparsa delle specie arcaiche. La variabilità geografica è sottolineata dalla precoce scomparsa di *Pachycrocuta brevirostris* dalla Penisola Iberica e dalla apparente assenza di *Acinonyx pardinensis* che è segnalata per l'ultima volta a Puebla de Valverde. Si sa che questa specie raggiunse la Britannia, come sembra dimostrare un campione di dente rinvenuto nei depositi della *Norwich Crag Formation* a Easton Bavents. La ricomparsa di *Pliocrocuta perrieri* nel Pleistocene medio non sembra interessare l'Italia, la Penisola Iberica e la Britannia, sebbene queste due ultime regioni potrebbero aver visto le ultime apparizioni di *Panthera gombaszoegensis*. Malgrado queste informazioni, è evidente che rimangono da chiarire per il gruppo dei grandi carnivori molti dettagli del loro assetto biogeografico.

**ABSTRACT** - *The Villafranchian large carnivore guild: geographic distribution and structural evolution* - Il Quaternario *Italian Journal of Quaternary Sciences*, 8(2), 1995, 349-356 - Evolution in the guild of larger carnivores is a marked feature of the Villafranchian faunal span. The eventual extinction of archaic forms and the incursion of taxa of more modern aspect finally produced a Middle Pleistocene guild similar in actual species, and almost identical in structure, to that of modern-day eastern Africa. However, the extinctions and appearances of members of the guild cannot be seen as a single turn-over, since the timing of the various events is both chronologically and geographically more complex. At around 1.6 Ma the hyaena *Chasmaporthetes lunensis* became locally extinct and was replaced by *Pachycrocuta brevirostris*, *Panthera gombaszoegensis* and several species of *Canis*. The large *Pliocrocuta perrieri* may also have become extinct around this period, although the timing is not clear. The dirk-toothed *Megantereon cultridens* managed to continue until the latest Lower Pleistocene at Untermassfeld, a time when *Panthera leo*, *Panthera pardus* and perhaps *Crocuta crocuta* dispersed into Europe. This incursion was followed during the earliest Middle Pleistocene by the re-appearance of *Pliocrocuta perrieri*. Towards the end of the Villafranchian, and until well into the Middle Pleistocene, the guild reached its greatest size and structural complexity with archaic taxa such as *Homotherium latidens*, *Acinonyx pardinensis*, *Panthera gombaszoegensis*, *Pachycrocuta brevirostris* and *Canis (Xenocyon) lycaonoides* coexisting with modern species such as *Panthera leo*, *Panthera pardus*, *Crocuta crocuta* and the small *Canis mosbachensis*. Only after 0.5 Ma did the guild reduce in size with the disappearance of the archaic species. Geographic variability is marked by an early disappearance of *Pachycrocuta brevirostris* from Iberia and by the apparent absence of *Acinonyx pardinensis* after its last appearance at Puebla de Valverde. The latter species is now known to have reached Britain, based on a dental specimen from Norwich Crag Formation deposits at Easton Bavents. The reappearance of *Pliocrocuta perrieri* during the Middle Pleistocene did not apparently include Italy, Iberia or Britain, although both of the latter regions may have witnessed the latest appearances of *Panthera gombaszoegensis*. However, it is clear that many details of the biogeographic pattern of the guild remain to be established.

Keywords: Large carnivores, structural evolution, geographic distribution, Villafranchian

Parole chiave: Grandi carnivori, evoluzione strutturale, distribuzione geografica, Villafranchiano

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## 1. INTRODUCTION

The chronological significance of the term Villafranchian has unquestionably changed over the years since Pareto (1865) first introduced it, and even since it was used more recently by Kurtén (1963; 1968) in some of his major syntheses. It is therefore entirely appropriate that the use of the term be subject to scrutiny, and the AIQUA<sup>(1)</sup> meeting provided a useful forum for such discussion. My use of the term is based on the view that it satisfactorily demarcates the large-mammal faunistic complex of western Europe that lasts from approximately 3.2 Ma to approximately 1.0 Ma. This view has been succinctly expressed most conveniently by Masini & Torre (1990, figure 1), although Azzaroli (1992) and Azzaroli *et al.* (1988) have laid stress on the need for qualified application.

A major feature of the evolution of the European Villafranchian mammalian fauna lies in the changing composition of the 'guild' of larger carnivores (Turner, 1992a, b)<sup>(2)</sup>. That changing composition reflects an alteration not only in taxa (Fig. 1), with archaic species becoming extinct and modern and eventually extant forms taking their place, but also in what may be termed the structure of the guild. By structure I mean the combination of, on the one hand, primarily flesh-eating animals such as the cats and on the other the facultative carcass-destroying animals such as the dogs and, in particular, the hyaenas.

For the earlier part of the Villafranchian faunal span, until around 1.6 Ma and the beginning of the Pleistocene, the flesh-eating component of the guild consisted of the machairodont cats *Homotherium latidens* and *Megantereon cultridens*, animals with little bone-destroying ability. That role was probably shared for much of the time by the gracile hunting hyaena, *Chasmaporthetes lunensis*, and certainly by the cheetah, *Acinonyx pardinensis*, and, to an unknown extent, by the smaller and poorly known *Viretailurus schaubi*. The bone-destroying role until that time, in the absence of any significant canids, was held by the large hyaenid *Pliocrocuta perrieri*.

The change at 1.6 Ma witnessed the local extinction of *Chasmaporthetes lunensis* and *Pliocrocuta perrieri* and several important first appearances that appear to mark immigrations. The European jaguar, *Panthera gombaszoegensis*, became a major addition to the felid component of the flesh eaters, while the gigantic hyaenid *Pachycrocuta brevirostris* replaced *P. perrieri*. The small *Nyctereutes megamastoides* became extinct and the canids were for the first time represented by larger taxa in the form of *Canis arnensis* and *C. etruscus* (or *C. mosba-*

*chensis* if the latter is, as I suspect, synonymous with *C. etruscus*) and by *Canis (Xenocyon) falconeri*. This initial change was reinforced by around 0.9 Ma by the first European appearances of the living species *Panthera leo*, *Panthera pardus* and *Crocuta crocuta*, incursions that were part of the changes in the fauna that characterised the 'end-Villafranchian event' of Azzaroli (1983).

## 2. GEOGRAPHIC AND CHRONOLOGICAL PATTERNS

As in all aspects of palaeontology, chance no doubt plays some part in the patterns of distribution in time and space that we see in the Carnivora, so that the next assemblage examined may always extend the known range of a taxon. Nevertheless we can see some broad features of the geography of the guild as we can for the fauna as a whole (Azzaroli *et al.*, 1988).

### 2.1 Hyaenidae

*Chasmaporthetes lunensis* appears to have been widespread throughout the earlier part of the Villafranchian (Werdelin & Solounias, 1991), although it has not been recorded from Britain. Its last European appearance after Olivola is seemingly at the German Lower Pleistocene site of Schernfeld (Dehm, 1962; Turner, 1992b) where it was accompanied by *Megantereon*.

*Pachycrocuta brevirostris* seems to have disappeared from Iberia earlier than in many other parts of western Europe, following its restricted appearance at sites such as Cueva Victoria, Venta Micena, Almenara, Ponton de l'Olivola and Incarcial, and it is not recorded there in the Middle Pleistocene (Turner, in press-e). The species is abundant at Untermassfeld in Germany in latest Lower Pleistocene deposits (Turner, in press-b), where its bone-consuming abilities are very much in evidence, and is also seen at the contemporary site of Vallonnet (de Lumley *et al.*, 1988). Middle Pleistocene occurrences at sites such as Gombaszög, Süssenbom and Verteszollos attest to its continued presence as an important member of the larger mammal fauna (Turner, 1992b, in press-b), and it has been recorded from the Italian early Middle Pleistocene site of Slivia (Bon *et al.*, 1992). In Britain it is known from deposits of the Cromer Forest-Bed Formation, although it is not recorded in the Freshwater Bed of the type Cromerian (Turner, in press-c).

*Pliocrocuta perrieri* is last recorded in Iberia at Puebla de Valverde, earlier than elsewhere in Europe where it seems to have become locally extinct after appearances at Chilhac, Senèze and Tegelen (Turner, 1992a, b). In Britain it is recorded from a number of localities in the Red Crag deposits of Suffolk (Turner, in press-c). Stuart (1982) suggests that Red Crag material may be placed within the pre-Ludhamian of the British sequence, equating with the late Pliocene Praetiglian of the Netherlands (Gibbard *et al.*, 1991). Former records of the species in

(1) Associazione Italiana per lo Studio del Quaternario.

(2) For the purpose of this discussion I shall omit consideration of the Ursidae and confine attention to the Felidae, Hyaenidae and Canidae.

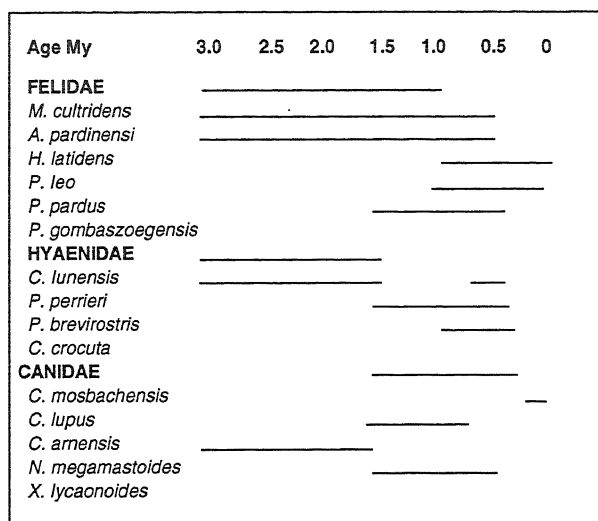


Fig. 1 - Chronological distribution of European Felidae, Hyaeonida and Canidae, Villafranchian and later.

*Distribuzione cronologica (dal Villafranchiano in poi) dei Felini, Hyaeonidi e Canidi europei.*

deposits of the Olivola Unit (Azzaroli, 1983) are now regarded as incorrect (Torre, *in lit.*), and although there are specimens in Firenze that are listed as "*Valdarno superiore*" it is clear that such allocations are not stratigraphically secure (Torre, pers. comm.). The species reappears in Europe in the Middle Pleistocene, but does not seem to have re-entered Spain, Italy or Britain at that time although it is clearly represented in France (Lunel Viel, l'Escale), Germany (Mosbach, Mauer), Austria (Hundsheim) and Greece (Petralona) (Kurtén & Poulianos, 1977, 1981; Turner, 1990, 1992b).

*Crocota crocuta* is reported from the lower unit TD 3 of the Spanish site of Atapuerca, just above what appears to be the Brunhes/Matuyama boundary (Aguirre *et al.*, 1990; Aguirre & Morales, 1990). This may well be the earliest record of the species in Europe, although it is also found in latest Villafranchian assemblages from the karst fissures at Selva Vecchia in Italy (Azzaroli, 1983; Torre, *in lit.*). Aguirre (pers. comm.) has mentioned the presence of probable hyaena coprolites in the latest Lower Pleistocene deposits at Lachar (Granada), but the species responsible is not clear (Turner, in press-e). In Britain it first appears in the Freshwater Bed deposits of the Cromerian type locality at West Runton and, perhaps slightly later, at Westbury-sub-Mendip (Turner, in press-a). Such an early appearance in Iberia implies equally early presence at least in the central part of Europe. However, Agustí & Moya-Sola (1992) point to the general scarcity of hyaenas in Middle Pleistocene deposits of Iberia, and it is clear that the large, hyaena-accumulated assemblages containing copious quantities of *Crocota crocuta* itself that are known from many sites in other parts of western Europe do not seem to occur there.

## 2.2 Felidae

Among the members of the guild, *Megantereon cultridens* has probably the most restricted geographical distribution. Some years ago Kurtén (1968) suggested that it was largely confined to circum-Mediterranean localities, although of course it has long been known from the Massive Central of France. Until recently the latest European occurrences appeared to be at Cueva Victoria and Venta Micena in Spain (Martinez, 1991; Turner, in press-e), at Pirro Nord in Italy (De Giuli *et al.*, 1986) and at Schemfeld in Bavaria (Dehm, 1962; Turner, 1992b). However, recent discoveries of a specimen at the Jaramillo-age site of Untermassfeld in Thuringia have extended its range in both time and space (Turner, unpublished data), although it remains unknown from Britain.

The larger machairodont *Homotherium latidens* is known in Europe throughout the Villafranchian and into the Middle Pleistocene, where it continues to appear widely until what may be its last records in Mosbach 2 and in the upper levels at Westbury-sub-Mendip (Turner, in press-a). If the later Villafranchian *H. latidens* is indeed conspecific with the early Villafranchian *H. crenatidens*, as seems increasingly likely (Martinez, 1991; Turner, in press-a), then this animal is one of the longest-lived of all the larger Villafranchian species. In Iberia it is recorded at Villarroya by Alcalá *et al.* (1990), but the only other reference to that presence that I can find is made by Viret (1954) in his unnumbered table where he lists a proximal radius figured by De Villalta (1952, plate XIV) as *Homotherium*. De Villalta had referred the specimen to *Megantereon*, and on the basis of his illustration it does look rather small for *Homotherium*. Alcalá *et al.* (1990) also list *Homotherium* at Puebla de Valverde. This species was not mentioned by Kurtén & Crusafont Pairo (1977) in their treatment of material from the locality, but in this case I can confirm the record based on an un-mistakable fragment of an upper canine in the collections of the Palaeontological Institute in Sabadell (Turner, unpublished data). The species is therefore less restricted in its Iberian distribution than previously suggested (Turner, in press-e), although its main appearances are at Incarcàl, Venta Micena and Cueva Victoria (Martinez, 1991), and it is last recorded in Huescar-I deposits (Alcalá & Morales, 1989).

The medium-sized *Viretailurus schaubi*, as Hemmer (1964) named it, is only really known from St Vallier (Viret, 1954), although its presence has been tentatively claimed at Villarroya (Alcalá *et al.*, 1990), Puebla de Valverde (Kurtén & Crusafont Pairo, 1977) and Cueva Victoria (Carbonell *et al.*, 1981). However, one should note that both latter identifications were essentially made by default, rather than by positive matching with known characters of the material from St Vallier.

*Panthera gombaszoegensis* is first recorded at Olivola and in what appear to have been upper levels at Tegelen in the Netherlands (Turner, 1992b). Its known overall distribution is now considerable. It may have lin-

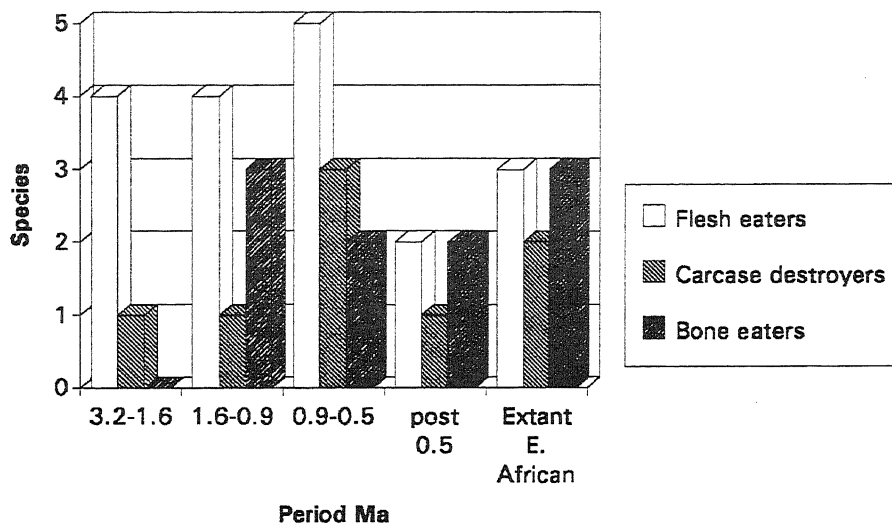


Fig. 2 - Structure of the European Villafranchian-Upper Pleistocene large carnivore guild compared with the extant east African guild.

*Composizione del gruppo dei grandi carnivori europei nel Villafranchiano-Pleistocene superiore in paragone a quella del gruppo attualmente presente in Africa orientale.*

gered in the Iberian Peninsula longer than in many other parts of Europe in view of its discovery in upper levels at Atapuerca (Aguirre *et al.*, 1990), although it is now known from Britain in uppermost deposits at Westbury-sub-Mendip, perhaps from the Cromerian type deposits at West Runton and possibly also from Swanscombe (Turner, in press-a, c).

*Acinonyx pardinensis*, together with *Homotherium latidens*, is one of the longest-lived of the Villafranchian taxa. In Spain it is known from Villarroya and at Puebla de Valverde, the latter a deposit contemporary with the French site of St Vallier where it is perhaps best represented. But it is not recorded in the peninsula after its appearance at Puebla de Valverde. The subsequent record of the species until what may be its last record in Europe at Mosbach (Turner, 1992b) is extremely patchy, rendering a true appreciation of its distribution very difficult. Just how imprecise our knowledge may be is implied by the recent identification of a broken P3 from pre-Cromer Forest-bed deposits at Easton Bavents in Suffolk held in the Natural History Museum and previously identified as *Felis pardoides* (Turner, in press c). Sala *et al.* (1992) point out that it is not currently known in Italian post-Villafranchian faunas.

The earliest European appearance of *Panthera leo* is at Vallonnet (de Lumley *et al.*, 1988; Turner, 1992b), and it has now been recorded at the Italian site of Isernia la Pineta at the very end of the Lower Pleistocene (Sala, 1990). In Britain, the earliest record is at Westbury-sub-Mendip (Turner, in press-a, c), while in Spain the earliest records of this cat are in deposits at Atapuerca and Solana de Zamborino (Turner, in press-e). Once established in Europe, it became an extremely widely-dispersed member of the fauna.

The first European record of *Panthera pardus* is cur-

rently also at Vallonnet (de Lumley *et al.*, 1988, Turner, 1992b). It is never a common member of fossil assemblages, except perhaps at the Italian Upper Pleistocene locality of Equi Cave (Del Campana, 1954), although its known range in Europe is now extensive. In Iberia it is rare, although specimens are known from the Upper Pleistocene deposits of the Genista Cave in Gibraltar (Busk, 1879).

### 2.3 Canidae

The genus *Canis* dispersed into Europe at the end of the Pliocene and rose to prominence in the

earliest Pleistocene with the immigration of *Canis arnensis*, and *Canis mosbachensis* (Torre *et al.*, 1992; Turner, 1992b). The latter species in particular had a wide distribution, and is found in Spain at Venta Micena and in the earlier Olivola and Tasso Faunal Units of Italy. *Canis (Xenocyon) falconeri* is first recorded in the Tasso Unit and is also present at Venta Micena. By the Middle Pleistocene some differentiation and fragmentation of ranges is apparent, with *Canis mosbachensis* almost ubiquitous while *C. (X.) falconeri* [or its apparent descendant *C. (X.) lycaonoides*] is found in Germany, Hungary and Britain but not recorded in Spain or Italy (Turner, 1992b, in press-a, e). The Thuringian site of Untermassfeld has produced several specimens of what appear to be *C. (X.) lycaonoides* in deposits of Jaramillo age.

At some time during the Middle Pleistocene the dhole, *Cuon alpinus*, also entered Europe from the east, and is perhaps best recorded at Mosbach (Schütt, 1973) and Lunel-Viel (Bonifay, 1971).

### 3. GUILD STRUCTURE

Most large carnivores will scavenge if given the opportunity, and even lions may obtain the major portion of their food in that way if their numbers are sufficient to overcome smaller species of pack-hunting animals such as hyaenas (Kruuk, 1972). The overall structure of the Villafranchian guild of larger carnivores at any point in time would therefore have had a major impact upon its constituent species, since it would have conditioned both the availability of and access to ungulate carcasses just as it does in present ecosystems (Turner, 1988).

Table 1 gives the overall structure of the guild at various times during and after the Villafranchian faunal

Table 1 - Generalised European Villafranchian and post-Villafranchian large carnivore guild in various time segments with living eastern African guild for comparison. The categories refer to necessary concentration on meat (Flesh Eaters), ability to eat bone and destroy carcasses of medium-sized ungulates (Carcase Destroyers) and those species able to eat bone (Bone Eaters) to a moderate extent.

*I grandi carnivori villafranchiani e post-villafranchiani europei suddivisi per intervalli di tempo e quelli attualmente viventi in Africa orientale per confronto. Le tre categorie si riferiscono a necessario ricorso alla carne (mangiatori di carne, flesh eaters), abilità di mangiare ossa e distruggere carcasse di ungulati di taglia media (distruttori di carcasse, carcasse destroyers) e capacità limitata di mangiare ossa (mangiatori di ossa, bone eaters)*

Flesh Eaters	Carcase Destroyers	Bone Eaters
<b>EUROPE</b>		
<b>3.2 - 1.6 Ma</b>		
<i>Homoherium latidens</i>	<i>Pliocrocota perrieri</i>	
<i>Megantereon cultridens</i>		
<i>Acinonyx pardinensis</i>		
<i>Chasmaporthetes lunensis</i>		
<b>1.6 - 0.9 Ma</b>		
<i>Homoherium latidens</i>	<i>Pachycrocota brevisrostris</i>	<i>Canis mosbachensis</i>
<i>Megantereon cultridens</i>		<i>Canis arnensis</i>
<i>Acinonyx pardinensis</i>		<i>C. (X.) falconeri.</i>
<i>Panthera gombaszoegensis</i>		
<b>0.9 - 0.5 Ma</b>		
<i>Homoherium latidens</i>	<i>Pachycrocota brewrosms</i>	<i>Canis mosbachensis</i>
<i>Acinonyx pardinensis</i>	<i>Crocota crocuta</i>	<i>C. (X.) lycanoides</i>
<i>Panthera gombaszoegensis</i>	<i>Pliocrocota perrieri</i> **	
<i>Panther leo</i>		
<i>Panthera pardus</i>		
<b>After 0.5 Ma</b>		
<i>Panthera leo</i>	<i>Crocota crocuta</i>	<i>Canis mosbachensis</i> †
<i>Panthera pardus</i>		<i>Cuon alpinus</i>
<b>EXTANT EAST AFRICA</b>		
<i>Panthera leo</i>	<i>Crocota crocuta</i>	<i>Lycan pictus</i>
<i>Panthera pardus</i>	<i>Hyaena hyaena</i>	<i>Canis mesomelas</i>
<i>Acinonyx jubatus</i>		<i>Canis adustus</i>
** for only part of the time		
† <i>Canis lupus</i> in the Upper Pleistocene		

span. Several features of the distribution in time stand out. First is the overwhelming importance of the flesh-eating component of the guild for most of the Villafranchian, with *Chasmaporthetes* taking its place among the cats on the basis of its dentition and only *Pliocrocota perrieri* with the potential to act as a carcass-destroying scavenger. The second is the massive increase in overall taxon numbers at the end of Lower Pleistocene and during the early half of the Middle Pleistocene. All three families underwent significant change at that time, resulting in a shift from the dominance of the flesh-eating felids of the later Pliocene to the taxonomic parity between cats on the one hand and hyaenas and dogs on the other. This change was clearly underway during the Lower Pleistocene, with *P. brevisrostris* replacing *P. perrieri* and with the incursions of the medium- and large-sized canids. The appearance of *Canis (Xenocyon) falconeri* in particular is likely to have had a significant impact, as an animal around the size of the largest of living representatives of the true wolf, *Canis lupus* (Rook, in press).

However, the change is notable for more than simply an increase in taxon numbers and the shift in the balance of consumption abilities. One of the most notable features of the guild after 0.9 Ma is the co-occurrence of the modern taxa, such as *Panthera leo*, *P. pardus* and *Crocota crocuta*, and many of the older, Villafranchian species. That situation came to an end at around 0.5 Ma with the final demise of the archaic members of the guild, leaving a European community broadly similar in membership and structure to that of East Africa today (Table 1). A similar pattern of overlap and eventual replacement had already taken place in Africa, but with a different time scale. In Africa, most of the modern large carnivore species were present by 3.0 - 3.5 Ma, whereas the archaic elements of the guild such as *Homoherium*, *Megantereon* and *Chasmaporthetes* became extinct there around 1.5 Ma (Turner, 1990).

There can be little doubt that some of the features seen in the evolution of the large carnivore guild in Europe reflect changes in the ungulate fauna that formed the prey of its members. But those changes in the ungulates were themselves under the ultimate influence of changes in climate (De Jong, 1988; Zagwijn, 1985, 1992; Zagwijn & Suc, 1984),

and part of larger-scale pattern of Plio-Pleistocene dispersals many of which originated in Asia (Sher, 1986, 1992). The effect of climatic influences on the Plio-Pleistocene large mammal fauna of Africa has recently been examined in some detail for the period around 2.5 Ma, when evidence from a diversity of sources points to cooling and an increase of aridity (Turner & Wood, 1993; Turner, in press-d). However, neither in Africa nor Europe is there clear evidence of a direct and rapid association between climatic events and changes in the carnivore guild (Turner, 1990, 1992b). The very fact that many large predators are now and have been in the past so widely dispersed suggests that constraints on their distribution are relatively few provided that a sufficiency of food is available. But of course change in food availability could very easily result from shifts in the structure of the prey community, such as the increased importance of open country, cursorial species that occurred in Africa after 2.5 Ma. Long term effects of such changes have been suggested as a significant agent of extinction in some of the archaic elements of the African guild (Turner,

TIME PERIOD	1	2	3	4	5	6
<i>Pseudodama pardinensis</i>	S-M					
<i>Pseudodama rhenanus</i>		S-M	S-M			
<i>Pseudodama perolensis</i>				S-M		
<i>Pseudodama lyra</i>	S-M	S-M				
<i>Pseudodama nestii</i>			S-M			
<i>Pseudodama farnetensis</i>				S-M		
<i>Croizetoceros ramosus</i>	S-M	S-M	S-M			
<i>Cervus perrieri</i>	M					
<i>Arvernoceros ardei</i>	M					
<i>Procapreolus cusanus</i>	S					
<i>Eucladoceros falconeri</i>		M				
<i>Eucladoceros teguliensis</i>			L			
<i>Eucladoceros dicranios</i>				M-L		
<i>Eucladoceros tetraceros</i>			M-L	M		
<i>Megaceroides boldrini</i>				L		
<i>Megaceroides verticornis</i>					L	
<i>Megaceroides solilhacus</i>					L	
<i>Megaloceros savini</i>					M-L	
<i>Megaloceros giganteus</i>						L
<i>Alces gallicus</i>				M		
<i>Alces latifrons</i>					L	
<i>Alces alces</i> †						L
<i>Dama dama</i> †					M	M
<i>Cervus elaphus</i> †						M-L
<i>Capreolus capreolus</i> †					S	S
<i>Rangifer tarandus</i> †						M
† living species						
<b>Time periods:</b> 1, 3.0±2.5 Ma; 2, 2.5±2.0 Ma; 3, 2.0±1.5 Ma; 4, 1.5±1.0 Ma; 5, 1.0±0.5 Ma; 6, 0.5 Ma+present.						
<b>Size classes:</b> S = small, M = medium, L = large, based on living European <i>Capreolus</i> , <i>Cervus</i> and <i>Alces</i> (Lister, 1988).						
<b>Taxonomy:</b> after Lister (1988), Azzaroli (1992) and Azzaroli & Mazza (1992, 1993).						

1990), while the appearance of larger bodied cervids and bovids in Europe towards the end of the Villafranchian may have acted to the detriment of the machairodont cats (Turner, 1992b). This latter point is briefly illustrated here in Table 2, where size distributions of European cervids over time are summarised and where the increased incidence of larger taxa in the period after 1.0 Ma is readily apparent.

One other feature that the African and European large carnivore guilds share is the fact that the incursion of *Canis* in both regions changed the balance in favour of potentially co-operative, pack-hunting behaviour. I suspect that we may see a clue to the extinction of archaic guild members in Africa and Europe in that arrival of the dogs, which in the longer term perspective of the Miocene-Recent evolution of the guild seem to have taken over the ecological role formerly performed by the hyaenas (Werdelin & Turner, in press). In Africa, the canids plus the modern predators may have been too much for the archaic, machairodont cats, who were unable to retain control of carcasses for long enough to obtain flesh. In Europe the arrival of the dogs, together with *Pachycrocuta brevirostris* and *Panthera gombaszoegensis*, was at first containable to some extent, with *Homotherium latidens* and *Megantereon cultridens* surviving although *Chasmaporthetes lunensis* went extinct and *Pliocrocuta perrieri* disappeared locally. In this sce-

Table 2 - European Cervidae, Upper Pliocene to Recent. Time periods are shown as 500,000 yr intervals.

*Cervidi europei, dal Pliocene superiore al Presente. Gli intervalli di tempo sono di 500.000 anni.*

nario the end-Villafranchian arrival of *Panthera leo*, *Panthera pardus* and *Crocuta crocuta*, together with the return of *Pliocrocuta perrieri*, may then have operated in concert with the activities of the dogs to tilt the balance against long-term survival of the machairodonts with first *Megantereon* and then *Homotherium* disappearing. However, such a scenario must be seen as a crude first approximation to reality, since it is apparent that the true pattern of change in the large carnivore guild is rather more complicated. The extinctions of at least three other major taxa, *Panthera gombaszoegensis*, *Acinonyx pardinensis* and *Canis (Xenocyon) lycaonoides* (the latter itself a canid) have to be accommodated. It is possible that *Canis (Xenocyon)* was more solitary in its habits and therefore less equipped than living dogs for the conditions of the later Middle Pleistocene, although it is not clear that all of the extinctions in the larger predator guild can be accounted for simply in terms of the incursion

of the modern taxa acting in concert with the activities of packs of dogs. We have some way to go in seeking to understand these changes, but we can now see that many of the most significant alterations in the guild occur in Europe during the span of the Villafranchian large-mammal age.

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