Large mammal associations from the Early Pleistocene: Italy and Spain

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Abstract

The palaeoecological character of the main large mammal associations grouped into the faunal units of the Early Pleistocene of Italy and Spain are examined here for the definition of possible environmental differences between the two areas. The comparative analysis shows a dominance of open environments both in Spain and Italy, while the dietary type of herbivores shows some differences. The palaeoenvironmental indications derived from the large mammal assemblages are in agreement with those of the climate, especially with the climatic cooling that occurred around 2.5 and 0.9 Ma. With respect to the herbivorous diet, there is a dominance of browsers in the Montopoli Faunal Unit, grazers in the Tasso and Farneta Faunal Units, and intermediate feeders in the remaining ones, especially from the later part of the Late Villafranchian to the Early Galerian.

Introduction

Large mammal faunas from Early Pleistocene have been classically divided in three faunal units (FU): Olivola, Tasso and Farneta (Azzaroli, 1977), based on bio-events that characterized mammal faunas. These subdivisions have been in general use for many years in Italy, while in Spain a subdivision into biozones, based on the biochronology of micromammals (Agustí et al., 1987; Aguirre & Morales, 1990) has been correlated with large mammal first occurrences (FO) and last occurrences (LO).

The acquisition of new data, the discovery of new fossil sites and a review of the collections have shown how the biochronological succession of large mammal faunas is due to a sequence of bio-events, each one more or less distinct and isolated in time. In this sequence, a progressive appearance of new forms takes place that makes up the typical elements of the successive FUs. These progressive appearances are particularly evident at the passage between Middle Villafranchian and Late Villafranchian mammal faunas and even more so between Late Villafranchian and Galerian ones. Recently, Torre et al. (1992) proposed that the Senèze FU should be placed in the latter part of the Middle Villafranchian (including Chilhac, Le Coupet, Costa San Giacomo, Senèze, Tegelen); while Caloi & Palombo (1995, 1996) proposed a new Mammal age (Protogalerian, including Farneta, Pirro and Colle Curti FUs) for the latest Villafranchian faunal complex where taxa, which were later to characterize the typical Galerian fauna, had progressively appeared.

At the last INQUA congress (Gliozzi et al., 1995) a division of the large mammal fauna from the Italian Plio-Pleistocene into three Mammal ages was proposed: Villafranchian, Galerian (the beginning was correlated with the *Megaceroides verticornis* FO in the Colle Curti FU assemblage, calibrated with the base of the Jaramillo Event and the Aurelian (correlated with the Stages 10-2 of the Oxygen Isotope sequence). In this framework, the Late Villafranchian is divided into Olivola, Tasso, Farneta and Pirro FUs (Table 1).

The progressive change of the faunas has usually been related to climatic variations, during the Early Pleistocene these cycles show a progressive displacement of the climatic curve toward lower temperatures with cycles around 50 Ka long (Williams et al., 1988), and the alternation of mostly humid forest phases during 'warm' climate periods with arid phases during the 'cool' periods.

Here the authors have attempted to determine whether the changes between the different FUs are more or less correspond with the climatic and palaeoenvironmental data and, where possible, to analyze the similarities or differences between Spanish and Italian localities. This study has been carried out based on the species present in each faunal unit and not on each locality, because the individual sites are often not sufficiently species rich. In order to better test the Early Pleistocene FUs we have also included the next earlier and the subsequent FUs in our analysis.

Material and Method

The comparative analysis is based on 13 localities grouped into 9 FUs for Italy (Table 2) and 9 localities grouped into 4 FUs for Spain (Table 3) from the Early Pleistocene. The FUs defined by Gliozzi et al. (1995) have been used. The faunal associations from Italy and Spain have been correlated by means of bar chart histograms that permit the differences and similarities between the predominant habitats and diet types in Italy and in Spain to be more clearly displayed and to facilitate inter-comparison.

In Table 2 (Italy) the taxonomic level reached subspecific level in many cases, while in Table 3 (Spain) only the species are reported.

These bar chart histograms have been developed using the number of species in each FU, from different habitats and diet types and also their respective frequencies are considered (Figures 1 to 7).

To emphasise the habitat changes of the Early Pleistocene

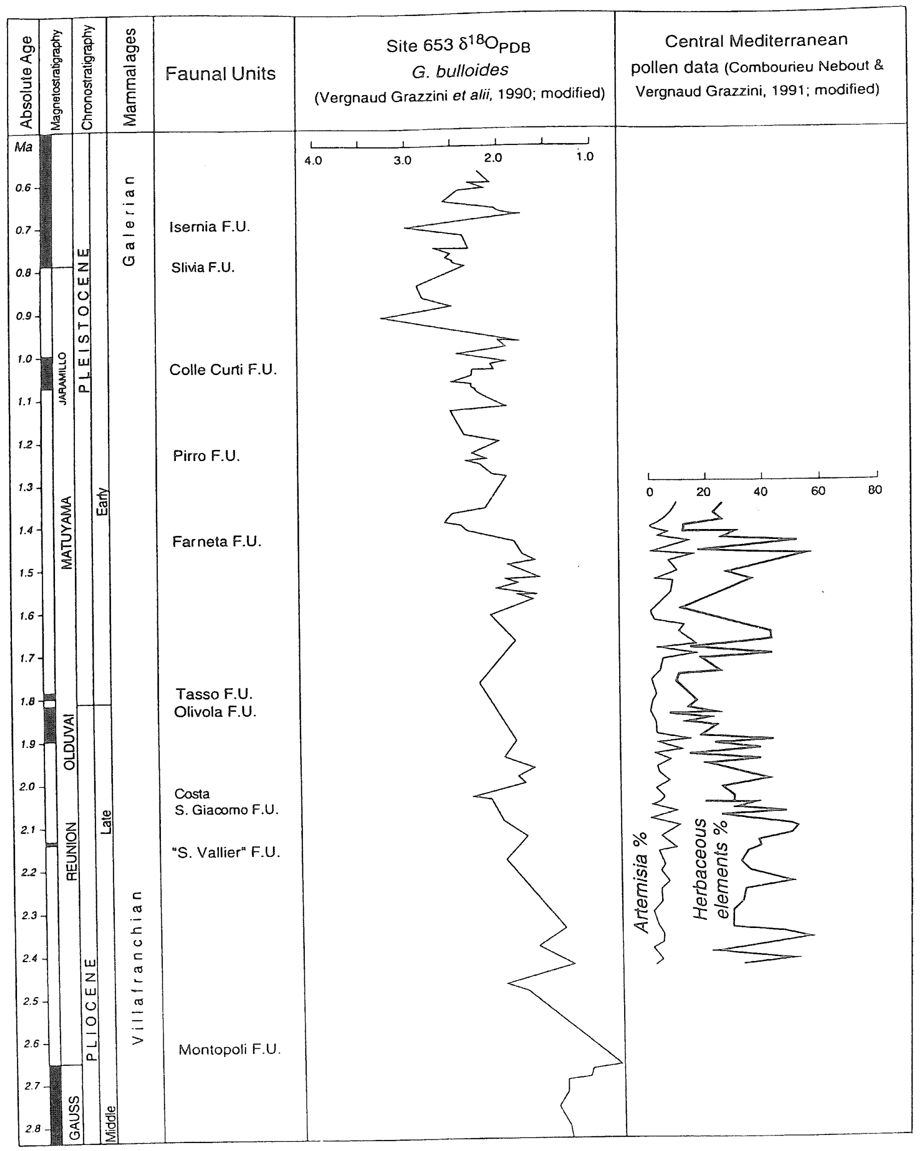


Table 1
Biochronology of Faunal Units (FU), after Gliozzi et al. (1995), and their correlation with the δ¹⁸O curve (modified from Vergnaud Grazzini et al., 1990) and Central Mediterranean pollen sequence (modified from Combourieu Nebout & Vergnaud Grazzini, 1991).

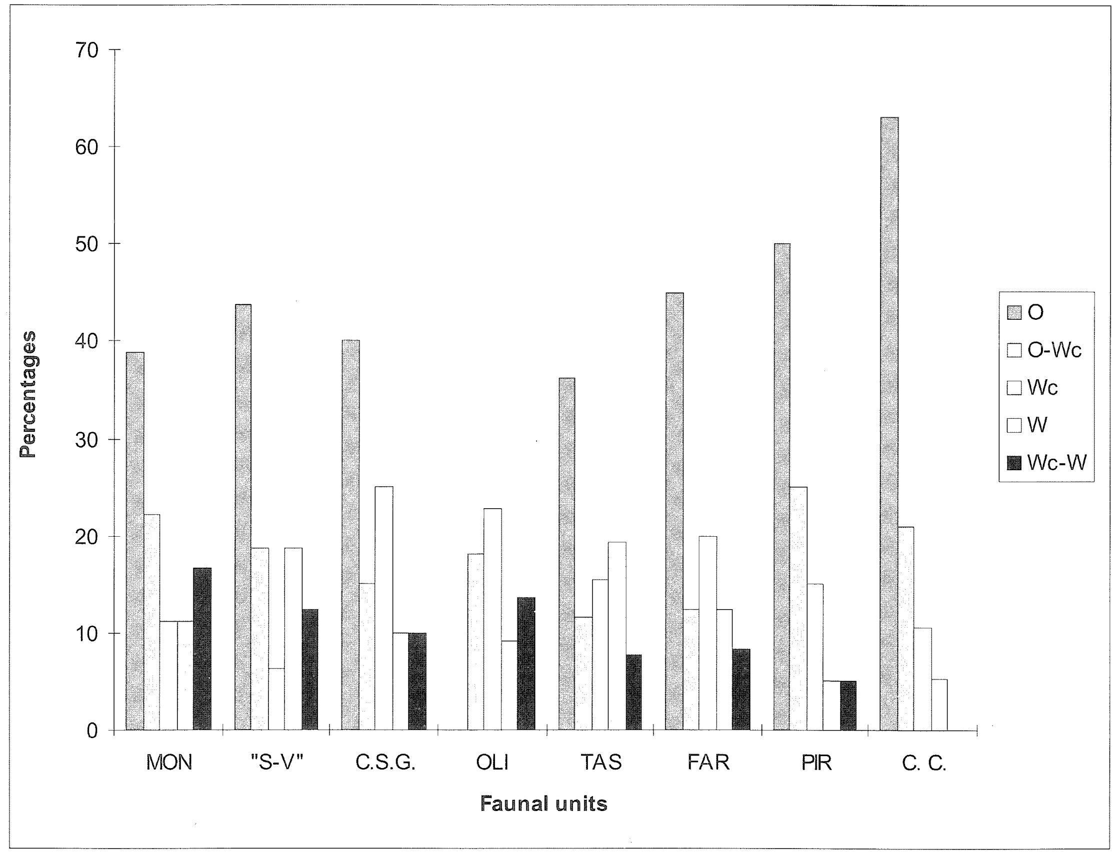


Figure 1
Histogram of the Italian FUs habitats percentages. O = Open; Wc = woodland clear; W = woodland. MON = Montopoli FU; "S-V" = "Saint-Vallier" FU; CSG = Costa San Giacomo; OLI = Olivola FU; TAS = Tasso FU; FAR = Farneta FU; PIR = Pirro FU; C.C. = Cole Curti FU.

Habitat	MON	"S-V"	C.S.G.	OLI	TAS	FAR	PIR	C.C.
O	38,89	43,75	40	36,36	36,15	45,03	50	63,16
O-Wc	22,22	18,75	15	18,1	11,54	12,5	25	21,05
Wc	11,11	6,25	25	22,73	15,5	20,03	15	10,53
W	11,11	18,75	10	9,09	19,23	12,5	5	5,26
Wc-W	16,67	12,5	10	13,64	7,69	8,33	5	0

large mammals from Spain and Italy, the species have been characterized according to their presumed environmental preferences. The following habitats are assumed: O (from open plains; prairie, savannah, steppes), Wc (from clear woodland; with broad leaf and/or coniferous trees), and W (from dense forest). The more ecologically adaptable species have been subdivided into two categories: those that live in open areas with limited tree cover (including the 'Mediterranean bush vegetation') and those that inhabit forested environments of different kinds (column H in Table 2 for Italy, and in Table 3 for Spain). The herbivorous species have been classified according to diet types: Br (browsers), Gr (grazers), and B-G (intermediate feeders) (column DT in Table 2 and in Table 3 respectively).

Results and Discussion

In Italy, in the Montopoli and Saint-Vallier FUs some species indicate the existence of different kinds of environments, but species that inhabit open spaces are predominant and this trend is more accentuated in the Saint Vallier FU (Figure 1). This might be confirmed in the type of herbivorous diet: in the Montopoli FU the Br forms dominate, while in the Saint Vallier FU the dominant type is B-G (Figure 2). The latter can possibly be correlated with the beginning of climatic cooling that was more pronounced around 2.6-2.5 Ma and led to a reduction of the European forest, with a spread of the tundra-like vegetation in the North, and more or less steppe arid, in the South (Suc, 1984; Zagwijn, 1992a,1992b; Combourieu Nebout & Vergnaud Grazzini, 1991). During the subsequent phases in Italy, the climate changes to a relatively warm period were linked to the spread of the grassland in Valdarno (Albianelli et al., 1995) and of the steppe-like elements in South Italy (Coumbourieu Nebout & Vergnaud Grazzini, 1991; Coumbourieu Nebout, 1993).

In the Costa San Giacomo FU there is a slight decrease in the mammal species adapted to grassland and open/wooded environments (Figure 1). At the Olivola FU the former diminished while there was an increase in the latter. In both FUs, the number of species of the wooded environment reached the highest value among the Early Pleistocene FUs. In the Costa San Giacomo and Olivola FUs, intermediate feeders were predominant, a fact that supports the hypothesis that there was a denser forest cover than during the two preceding faunal units. Note, however, that the open forms were well represented at the Costa San Giacomo FU. In southern Italy, between the end of the Pliocene and the beginning of the Pleistocene, a mesothermic and relatively moist forest phase occurs interrupted by very short more arid episodes (Coumbourieu Nebout & Vergnaud Grazzini, 1991). The Costa San Giacomo FU might correspond to the beginning of this woodland phase at a time when the vegetation was still predominantly herbaceous. The Olivola FU is correlated with Oxygen Isotopic Stage (IOS) 62 which corresponds

Table 2
Selected large mammals of Italy.
I occurrence;
¡ conformis or affinis form (in relation to the localities);
? doubtful occurrence;
- certain occurrence (in relation to faunal units);
- doubtful presence (in relation to faunal units).
DT = Dietary type;
sPr = small predators;
sPr = super predator;
Pr = predators;
Sc = Scavenger;
Om = omnivorous;
Gr = Grazer; Br = Browser;
G-B = intermediate.
l = large sized;
m = middle sized;
p = pachyderm.
H = habitats; O = Open;
O-Wc = intermediate;
Wc = Woodland clear;
W = Woodland;
Wc-W = intermediate.

Mammal Ages			Middle Villafranchian			Late Villafranchian							Galerian	
Mammal Faunal Units			*Montopoli*	*"Saint-Valier"*	*S. Giacomo*	*Olivola F.U.*		*Tasso F.U.*	*Farneta F.U.*			*Pirro F.U.*	*Colle Curti F.U.*	
Selected localities of Italian Peninsula			Montopoli	Colegordo	Costa S. Giacomo	Olivola	Matassino	Casa Frata	Selvella	Pietrafita	Cava Liberatori	Pirro	Colle Curti	Redicicoli
Selected Taxa	DT	H												
Enhydrictis ardea	sPr	W				x								
Chasmaportetes lunensis	Pr	O			x	x								
Pachycrocuta perrieri	Sc	O-Wc	x											
Nyctereutes megamastoides	Om	W	x	x										
Homotherium crenatidens- H. ex gr. latidens	SPr	O-Wc				x	?	x				x		
Megantereon cultridens	SPr	Wc-W		x		x	?					x		
Acinonyx pardinensis	Pr	O	x			?		?						
Lynx issiodorensis	Pr	O-Wc				x	x	x	x			x		
Anancus arvernensis	pBr	O	x		x		?							
Mammuthus meridionalis gromovi	pB-G	O	x											
Stephanorhinus jeanvireti	pBr	Wc-O	x	?										
Stephanorhinus etruscus	pBr	O			x	x	x	x						
Equus livenzovensis	lGr	O	x											
Eucladoceros falconeri	lBr	Wc	x											
Croizetoceros ramosus	mBr	Wc-W	x											
Pseudodama lyra	mB-G	Wc-O	x	x	x									
Leptobos stenometopon	LGr	O	x											
Gazella borbonica	mB-G	O	x		x									
Mammuthus meridionalis meridionales	pB-G	O			x	x	x	x						
Equus stenonis	lGr	O			x	x	x				?			
Sus sp. (small form)	Om	W		x										
Leptobos ex gr. L. merlai-L. furtivos	lGr	O			x	x								
? Hemitragus cf. H. stehlini	mB-G	R?		?										
Macaca sylvana florentina	Om	Ar			x					x				
Canis etruscus	Pr	O-Wc			z	x	x	x	x					
Sus strozzii	Om	Wc			z	x	x	x				?		
Gallogoral meneghinii	mB-G	O			?	x								
Gazellospira torticornis	mB-G	O			x									
Eucladoceros teguliensis	lBr	Wc			x									
Ursus etruscus	Om	W-Wc				x	?	x		x				
Pachycrocuta brevirostris	Sc	O-Wc				x		x				x		
Panthera ex gr. P. gombaszoegensis	Spr	W				x				x				
Eucladoceros dicranios olivolanus	lBr	Wc				x	z							
Pseudodama nestii	mB-G	Wc				x	x	x						
Leptobos etruscus	lGr	O				x	x							
Procamptoceras brivatense	mB-G	O				x								
Pannonictes nestii	sPr	W?								x				
Canis arnensis	Pr	O												
Canis falconeri	Pr	O						x				z	x	
Equus stehlini	lGr	O						x						
Hippopotamus ex gr. H. antiquus	pB-G	Aq-O									z	z	z	x
Eucladoceros dicranios dicranios	lBr	Wc						?						
Eucladoceros ctenoides	lBr	Wc						?						
Leptobos ex gr. L. vallisarni	lGr	O						x	z	x	x			
Praeovibos sp.	lGr	O						x						
Mammuthus meridionalis vestinus	pB-G	O							x	x	x	x	z	x
Stephanorhinus sp. aff. S. hundsheimensis	pBr	O								x	z	x	x	
Equus altidens (1)	lGr	O							z	z		x		z
Equus ex gr. E. bressanus-E. sussenbornensis	lGr	O										x		
Pseudodama farnetensis	mB-G	O-Wc							x	x	x			
Megaceroides obscurus	lB-G	Wc							z	x	x			
Ursus sp.	Om	Wc										x	x	
Canis aff. C. arnensis and "C. mosbachensis" (2)	Pr	O-Wc										x	x	x
Megaceroides sp. aff. M. solilhacus	lB-G	O										x	x	x
Pseudodama sp. (advanced form)	mB-G	O-Wc										x		z
Bison (Eobison) degiulii	lGr	O										x		
Ovibovini gen. spec. indet.	lGr	O										x		
Stephanorhinus hundsheimensis	pBr	O												x
Megaceroides verticornis	lB-G	O											x	
Bison sp. (primitive form) and B. schoetensacki	lGr	O											x	x
Meles meles	sPr	Wc-O												
Ursus deningeri	Om	Wc												
Crocuta crocuta	Sc	O												
Mammuthus trogontherii	pB-G	O												
Elephas antiquus	pBr	Wc-O												
Stephanorhinus kirchbergensis	pBr	Wc-W												
Stephanorhinus hemitoechus	pB-G	O												
Sus scrofa	Om	Wc												
Capreolus capreolus	mBr	Wc-W												
Cervus elaphus acoronatus	mB-G	Wc												

with a spread of herbaceous elements, including *Artemisia*, in southern Italy. The Olivola FU might include the last spread of the mesothermic wooded elements and *Cathaya*. During this time in the Valdarno, a relatively dry phase occurred with an increase of herbaceous and a decrease of thermophilic species. This phase is correlated with the beginning of the Eburonian Stage in the Netherlands, followed by an even cooler, but relatively moist, phase with a strong increase of herbaceous elements (Albianelli et al., 1995).

Beginning with the Tasso FU, the dominant species were those that characterise open environments, as indicated by the spread of *Canis arnensis, C. (Xenocyon) falconeri*, the diversification of the equids and also the sporadic appearance of some peculiar bovids. Nevertheless, both in Tasso FU and in Farneta FU, the forms which lived in the forest have a relatively high frequency value while the number of forms which lived in open environments with some woodland only reached low values (Figure 1).

The number of Gr species in the Tasso and Farneta FUs achieves the maximum percentage values, while the number of Brs remain is low, especially in the Farneta FU (Figure 2). Consequently, the existence of an environment with relatively contrasting characters seems to be indicated. The Farneta FU seems to be characterized by an association that indicates the presence of different environments, as well as in a restricted area, as has been shown from the comparison between the Selvela (De Giuli, 1987) and Pietrafitta (Ambrosetti et al., in press) faunal assemblages. In fact, in the first, the forms adapted to more or less open areas occur in large numbers, while in the second, forest species are almost equal in number to the open area taxa.

During a period, *'grosso modo'* generally correlatable with the Tasso and Farneta FUs in southern Italy, successive and rapid spreads of Gr elements took place interspersed with short phases of partial reforestation. The different types of large mammal assemblages may correspond to more or less arid or forested phases. Ravazzi & Moscariello (1998) argue that in the Tasso and Farneta FU environments forest-like assemblages occurred.

In the Pirro FU, and especially in the Colle Curti FU, the species adapted to open environments reach their maximum values, although some forms that inhabit environments with a more dense woodland are still present (Figure 1). In both FUs, B-G species predominate and the Gr forms are not very frequent (Figure 2). This fact suggests a spread of grassland and/or steppe, possibly equivalent to a climatic cooling, which corresponds to the Menapian Stage in northern Europe. The effect of these cool oscillations was felt before the Jaramillo Event (Zagwijn, 1992a, 1992b).

The Slivia FU is characterized in general by an increase in numbers of the species that lived in partially wooded areas, and especially by increases of forms which lived both in open and in partially wooded environments (Figure 1). The percentages of these species provides the highest values among the FUs considered in this study.

These data are confirmed by the herbivorous dietary types: small numbers of Grs, a higher number of B-Gs, and a limited number of Brs. It is important to note that in the interval corresponding to the time in which the Slivia faunal complex formed, the periodicity cycle of the $\delta^{18}O$ curve passes from that of about 41 Ka (orbital obliquity) to about 100 Ka (orbital eccentricity), together with a significant increase of the oscillation amplitude. The climatic variations, and the seasonality and the aridity increase, influenced the vegetation leading to the disappearance of species of warm-humid Neogene origin.

Concerning Spanish large mammal association faunas, it is important to note that fewer localities and FUs are represented than in Italy (Table 3). There are some marked diversifications among species (in the Montopoli and Saint Vallier FUs) that suggest different environments, with most species adapted to open areas, more clearly so in the Saint Vallier FU than in the Montopoli FU (Figure 3). There is no difference among herbivorous dietary types in the Montopoli FU (El Rincón and Huélago localities): all show the same percentage representations, possibly resulting from the low numbers of species (Figure 4). Nevertheless, in the Saint Vallier FU (La Puebla de Valverde locality), as in Italy, the B-G prevailed as well as in the Pirro and Colle Curti FUs (Figure 4). In Spain, there are no localities assigned to the Tasso and Farneta FUs and it cannot be confirmed whether the Brs were predominant during this time. In spite of the low representation in the number of localities and FUs in Spain, it is important to note that the dietary type patterns in relation to FUs in Italy and Spain are similar (Figure 5).

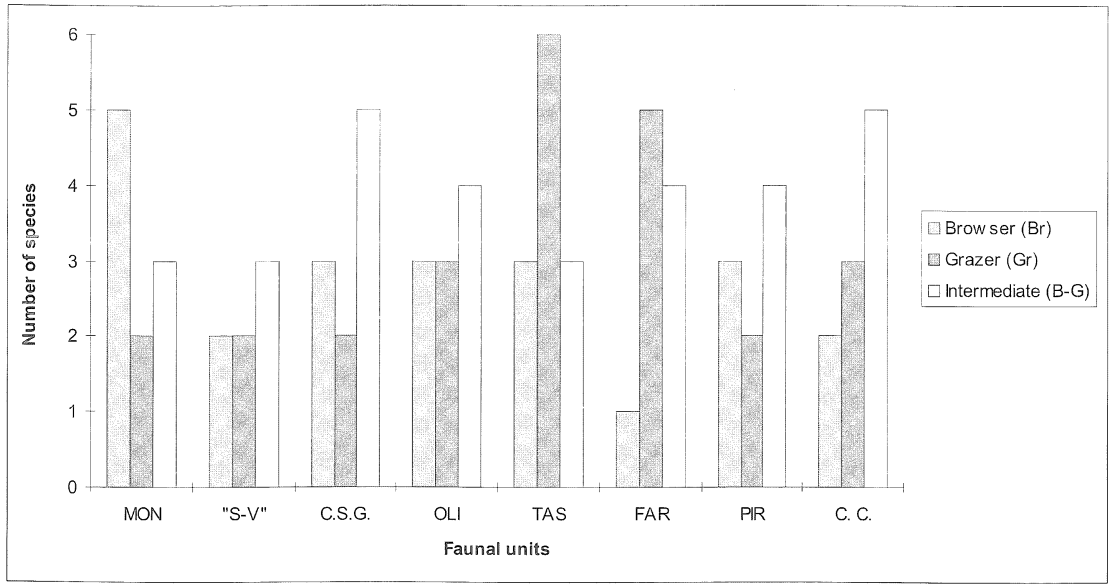
Concerning the environment, the patterns in Spain are similar to those in Italy, with a marked predominance of species adapted to open areas (Figures 6 and 7). These patterns can be correlated with the global climatic changes during this time. In this sense, these changes can possibly be correlated with the climatic cooling that was more pronounced initially around 2.6-2.5 Ma, and consequently led to the reduction of forest in Europe, to the spread of tundra in the north and of the steppe, more or less arid, in the south.

Conclusions

Based on our analysis of the Italian and Spanish faunal complexes, it can be seen that the resulting data agree with the existing palaeoclimatic and palaeoenvironmental data. The Pliocene FU species (from Montopoli to Costa San Giacomo FUs) show a certain environmental uniformity that seems to persist to the beginning of the Pleistocene (Olivola FU). In contrast, the taxonomic analysis shows a more significant environmental change in the passage from the Olivola FU to the Tasso FU, than from the Pirro FU to the Colle Curti FU, and above all from the latter to the Slivia

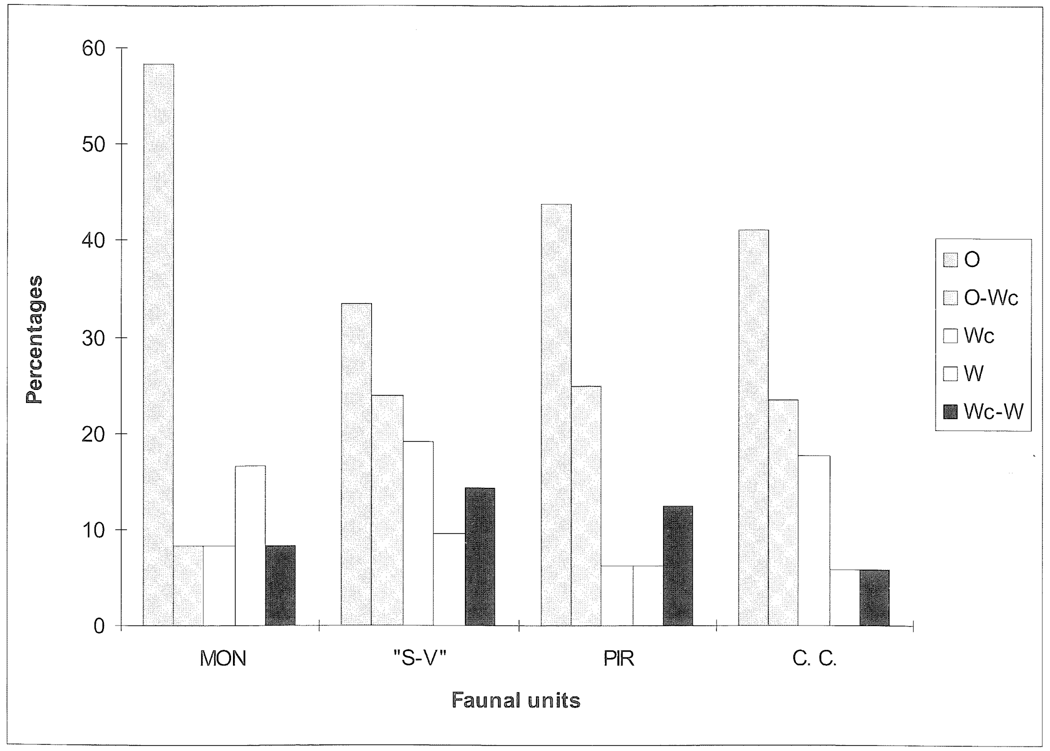
Mammal Ages			Middle Villafranchian		Upper Villafranchian			Galerian		
Mammal Faunal Units			*Montopoli FU*		*"Saint-Vallier"*	*Tasso-Farneta FUs*		*Colle-CurtiFU*		
Selected localities of Spanish Peninsula			El Rincón	Huélago	La Puebla de Valverde	Venta Micena	Lachar and Fuensanta	29 Huéscar	Cúllar 1	Cúllar 2
Selected Taxa	DT	H								
Viretailurus schaubi	Spr	W	x		x					
Equus livenzovensis	lGr	O	x	x						
Leptobos elatus	lGr	O		x						
Hesperidoceras merlai	lGr	O		x						
Croizetoceros ramosus	mBr	Wc-W		x	x					
Gazella borbonica	mB-G	O	x	x	x					
Mammuthus meridionalis	pB-G	O		x	x	x	x			
Gazellospira torticornis	mB-G	O		x	x					
Eucladoceros teguliensis (= senezensis)	lBr	Wc	x	x	x					
Nyctereutes megamastoides	Om	W	x	x	x					
Felis issiodorensis	Pr	O-Wc	x		x					
Stephanorhinus etruscus	pBr	O	x	x	x	x	x	x	x	x
Vulpes alopecoides	Pr	O-Wc			x					
Homotherium crenatidens	SPr	O-Wc			x					
Acinonyx pardinensis	Pr	O			x					
Chasmaportetes lunensis	Pr	O			x					
Pachycrocuta perrieri	Sc	O-Wc			x					
Pseudodama rhenanus (=philisi)	mB-G	Wc			x					
Vulpes (Xenocyon) falconeri	Pr	O-Wc			x	x				
Gallogoral meneghinii	mB-G	Wc?			x					
Paradolichopithecus sp.1	LBr	Wc			x					
Equus stenonis vireti	lGr	O			x					
Megantereon megantereon	Spr	Wc-W			x					
Ursus etruscus	Om	W-Wc			x	x				
Vulpes praeglaciaris	Om	W-Wc				x				
Pachycrocuta brevirostris	Sc	O-Wc				x				
Canis etruscus	Pr	O-Wc				x		x	x	x
"Cervus" aff. elaphoides/nov.sp.	mB-G	Wc					x			
Leptobos etruscus	LGr	O				x				
Bubalus sp.	LGr	O				x				
Soergelia minor	lB-G	O-Wc				x				
Capra alba	lB-G	O				x				
Equus stenonis granatensis	lGr	O				x	x			
Hippopotamus antiquus (= major)	pB-G	Aq-O				x		x		
Elephas (Paleoxodon) antiquus	pBr	Wc-O						x		
Panthera gr. toscana-gombaszoegensis	Spr	W						x		x
Equus altidens	lGr	O						x	x	?
Equus sussenbornensis	lGr	O						x	x	?
Praemegaceros solilhacus	lB-G	O				?		x		
Dolichodoryceros savini	lB-G	O							x	
Sus scrofa	Om	Wc							x	
Dama sp.	mB-G	O-Wc								x
Bison schoetensacki	lGr	O								x
Mammuthus trogontherii	pB-G	O							x	
Crocuta crocuta	Sc	O-Wc							x	x
Ursus praearctos	Om	W-Wc								x
Cervus sp.	mB-G	Wc								x
Cervus elaphus	mB-G	Wc								

Table 3
Selected large mammals of Spain. Symbols and abbreviations as in Table 2.



Dietary Type	MON	"S-V"	C.S.G.	OLI	TAS	FAR	PIR	C. C.
Browser (Br)	5	2	3	3	3	1	3	2
Grazer (Gr)	2	2	2	3	6	5	2	3
Intermediate (B-G)	3	3	5	4	3	4	4	5

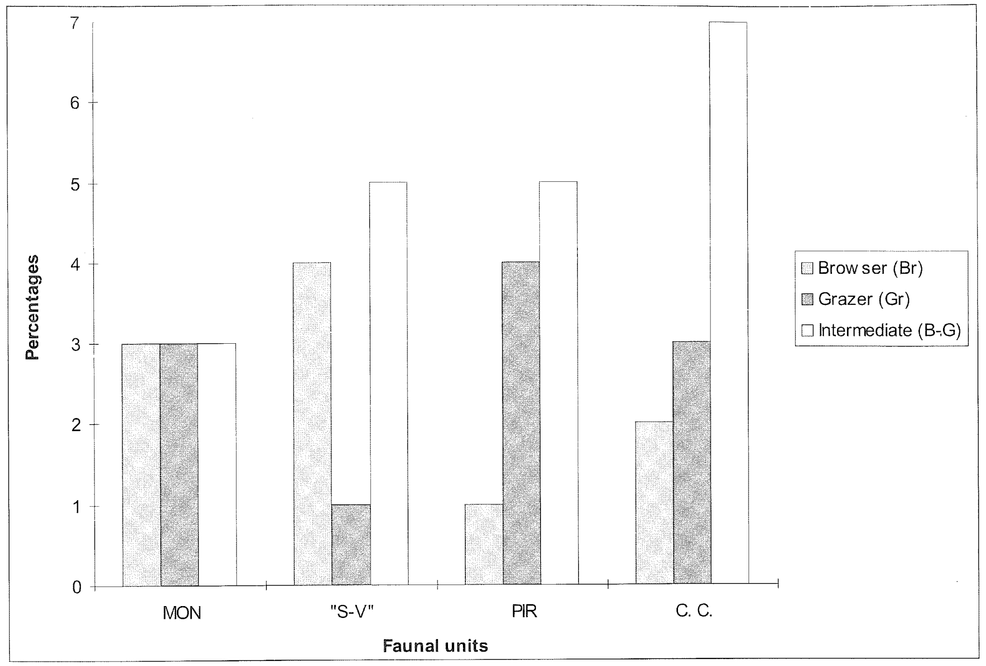
Figure 2
Histogram of the Italian FUs per number species of dietary types. Abbreviations as in Figure 1.



Habitat	MON	"S-V"	PIR	C.C.
O	58,33	33,33	43,75	41,18
O-Wc	8,33	23,81	25	23,53
Wc	8,33	19,05	6,25	17,65
W	16,67	9,52	6,25	5,88
Wc-W	8,33	14,28	12,5	5,88

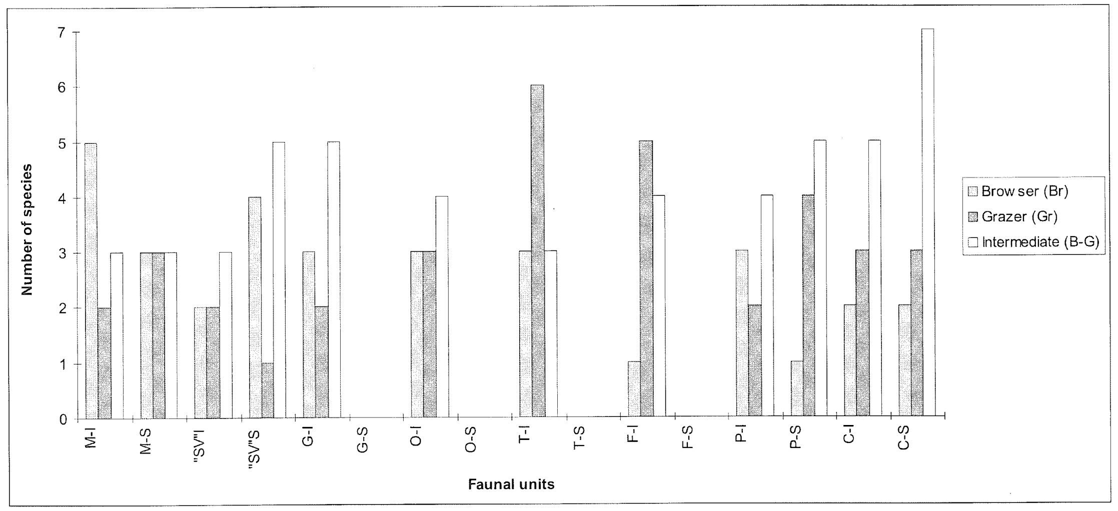
Figure 3
Histogram of the Spanish FU habitats percentages. Abbreviations as in Figure 1.

Figure 4
Bar chart histogram of the Spanish FUs per number species of dietary types. Abbreviations as in Figure 1.



Dietary Type	MON	"S-V"	PIR	C.C.
Browser (Br)	3	4	1	2
Grazer (Gr)	3	1	4	3
Intermediate (B-G)	3	5	5	7

Figure 5
Comparative histogram of the Italian and Spanish FUs per number species of dietary types. M-I= Montopoli FU Italy; M-S = Montopoli FU Spain; "SV"I = "Saint-Vallier" FU Italy; "SV"S = "Saint-Vallier" FU Spain; G-I = Costa San Giacomo FU Italy; G-S = Costa San Giacomo FU Spain; O-I = Olivola FU Italy; O-S = Olivola FU Spain; T-I = Tasso FU Italy; T-S = Tasso FU Spain; F-I = Farneta FU Italy; F-S = Farneta FU Spain; P-I = Pirro FU Italy; P-S = Pirro FU Spain; C-I = Colle Curti FU Italy; C-S = Colle Curti FU Spain.



Dietary Type	M-I	M-S	"SV"I	"SV"S	G-I	G-S	O-I	O-S	T-I	T-S	F-I	F-S	P-I	P-S	C-I	C-S
Browser (Br)	5	3	2	4	3	0	3	0	3	0	1	0	3	1	2	2
Grazer (Gr)	2	3	2	1	2	0	3	0	6	0	5	0	2	4	3	3
Intermediate (B-G)	3	3	3	5	5	0	4	0	3	0	4	0	4	5	5	7

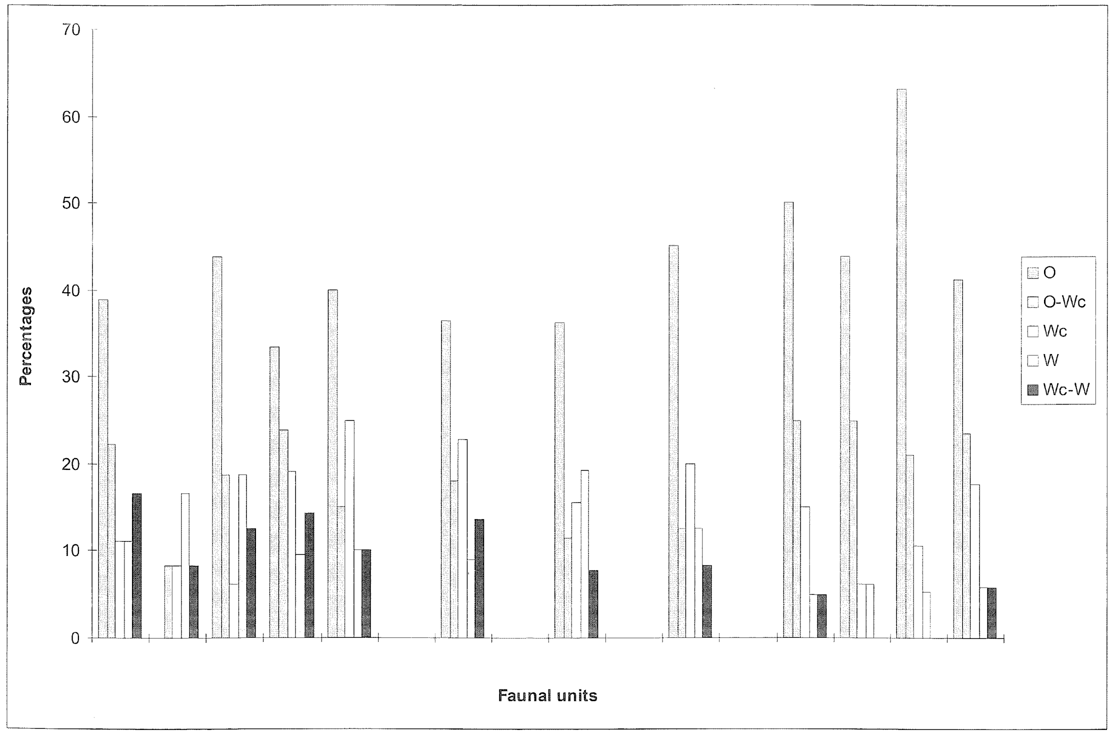


Figure 6
Comparative bar chart histogram of the Italian and Spanish FUs habitats percentages. Abbreviations as in Figure 5.

Habitat	M-I	M-S	"SV"I	"SV"S	G-I	G-S	O-I	O-S	T-I	T-S	F-I	F-S	P-I	P-S	C-I	C-S
O	38,89	58,33	43,75	33,33	40	0	36,36	0	36,15	0	45,03	0	50	43,75	63,16	41,18
O-Wc	22,22	8,33	18,75	23,81	15	0	18,1	0	11,54	0	12,5	0	25	25	21,05	23,53
Wc	11,11	8,33	6,25	19,05	25	0	22,73	0	15,5	0	20,03	0	15	6,25	10,53	17,65
W	11,11	16,67	18,75	9,52	10	0	9,09	0	19,23	0	12,5	0	5	6,25	5,26	5,88
Wc-W	16,67	8,33	12,5	14,28	10	0	13,64	0	7,69	0	8,33	0	5	12,50	0	5,88

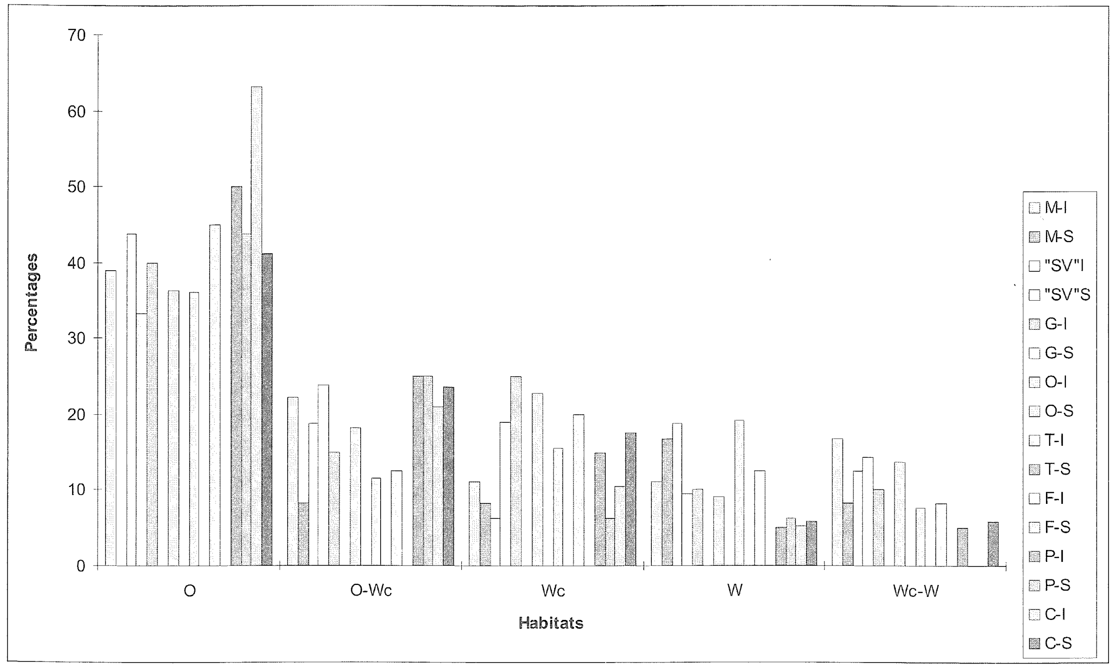


Figure 7
Comparative bar chart histogram of the habitat percentages and FUs from Italy and Spain. Abbreviations as in Figures 1 and 5.

Habitat	M-I	M-S	"SV"I	"SV"S	G-I	G-S	O-I	O-S	T-I	T-S	F-I	F-S	P-I	P-S	C-I	C-S
O	38,89	58,33	43,75	33,33	40	0	36,36	0	36,15	0	45,03	0	50	43,75	63,16	41,18
O-Wc	22,22	8,33	18,75	23,81	15	0	18,1	0	11,54	0	12,5	0	25	25	21,05	23,53
Wc	11,11	8,33	6,25	19,05	25	0	22,73	0	15,5	0	20,03	0	15	6,25	10,53	17,65
W	11,11	16,67	18,75	9,52	10	0	9,09	0	19,23	0	12,5	0	5	6,25	5,26	5,88
Wc-W	16,67	8,33	12,5	14,28	10	0	13,64	0	7,69	0	8,33	0	5	12,50	0	5,88

FU. This corresponds with the Olivola/Tasso FUs, Colle Curti FU/Slivia FUs or more marked with the Pirro/Colle Curti FUs, than species turnovers (Sardella et al., 1998). Differences between the Early Galerian (Colle Curti FU) and the Middle Galerian (Slivia FU) palaeoenviroments should be the most significant of those analyzed here.

It must be emphasised that the data used in this analysis have been influenced by the species richness of each site; the number of sites ascribed to a single FU; the geographical position of each site; local microclimatic factors; the time duration of each FU and consequently the possible heterochrony between sites. This heterochrony may not be appreciated on the basis of association composition of a given FU, but can affect the number of species or the percentage of forms adapted to the different environments. In some cases, the intensity or amplitude of the climatic variations are such that they partially modify the vegetation without the determining faunal turnover.

In addition, it can be seen that during a long period, in general, between Montopoli FU and Pirro FU, many herbivorous species are characterized by a relative slenderness in the leg bones. This indicates an adaptation to rather cool, arid environments (Eisenmann & Guérin, 1984). In Colle Curti FU heavier and larger forms had already appeared; in Slivia FU other species of greater size and stockier legs arrived, possibly adapted to colder climates and somewhat more relatively moist environments. The indications of a notable aridity suggested by assemblages of Pirro FU and Colle Curti FU could, in part, result from the differing geographical position of these two Italian sites, on the Adriatic side of the peninsula.

With regard to dietary type, some differences occur between Italy and Spain, even in situations where the palaeoenvironmental signals are quite similar. For example, in the Montopoli FU, the Brs prevail in Italy, while in Spain, Brs, Grs and B-Gs occur at about the same frequency (Figures 2, 4 and 5). In the Pirro FU, the Brs are poorly represented in Spain, while in Italy, Brs and Grs species are present in equal numbers. Finally, in the Colle Curti FU the large number of B-Gs is still more pronounced in Spain (Figure 4). Therefore, it seems possible to hypothesise that in Spain the environments were relatively more arid than those in Italy.

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Updating the Neogene Rodent biochronology in Europe

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Abstract

An updated rodent biochronology of the European Neogene and Quaternary is given. The biochronological framework covering the time span from the Vallesian to the Toringian (about 11 Ma) is based on muroid rodents. The correlation of the European late Cenozoic rodent biochronology with the geomagnetic polarity time scale is discussed and graphically summarized in a correlation chart.