

Large Mammal Guilds and Human Settlement in the Middle Pleistocene of Italy

Maria Rita PALOMBO
Dipartimento di Scienze della Terra
Università "La Sapienza", Roma

Margherita MUSSI
Dipartimento di Scienze dell'Antichità
Università "La Sapienza", Roma

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ABSTRACT – *In the Italian peninsula, the early Middle Pleistocene is characterised by a marked large mammal renewal which happens progressively in successive phases. Overall, richness increases, because new occurrences prevail over extinctions. A moderate community reconstruction characterizes the Galerian/Aurelian transition. Humans are among the new early Middle Pleistocene carnivore species. This ecologically flexible species adapts more successfully than many others to the environmental changes, taking advantage of the ongoing fragmentation of the habitat. After the extant evidence, this lead to a stable human settlement of Italy during the Middle Pleistocene.*

RIASSUNTO – [Associazioni a grandi mammiferi e primo popolamento umano nel Pleistocene medio dell'Italia] – *Un sensibile rinnovamento delle faune a grandi mammiferi caratterizza in Italia gli inizi del Pleistocene medio inferiore. Questo si completa in fasi successive che determinano, a causa del prevalere delle nuove comparse sulle estinzioni, un aumento di ricchezza. Una modesta ristrutturazione delle comunità diviene evidente al passaggio tra faune galeriane ed aureliane. Tra le nuove specie di predatori che fanno la loro comparsa con il Pleistocene medio figura anche l'uomo, specie ecologicamente flessibile che si adatta meglio di altre al mutare delle condizioni ambientali, traendo vantaggio anche dalla progressiva frammentazione degli habitat. Questo insieme dei fattori porta ad un popolamento continuativo della penisola italiana da parte dei gruppi umani.*

FOREWORD

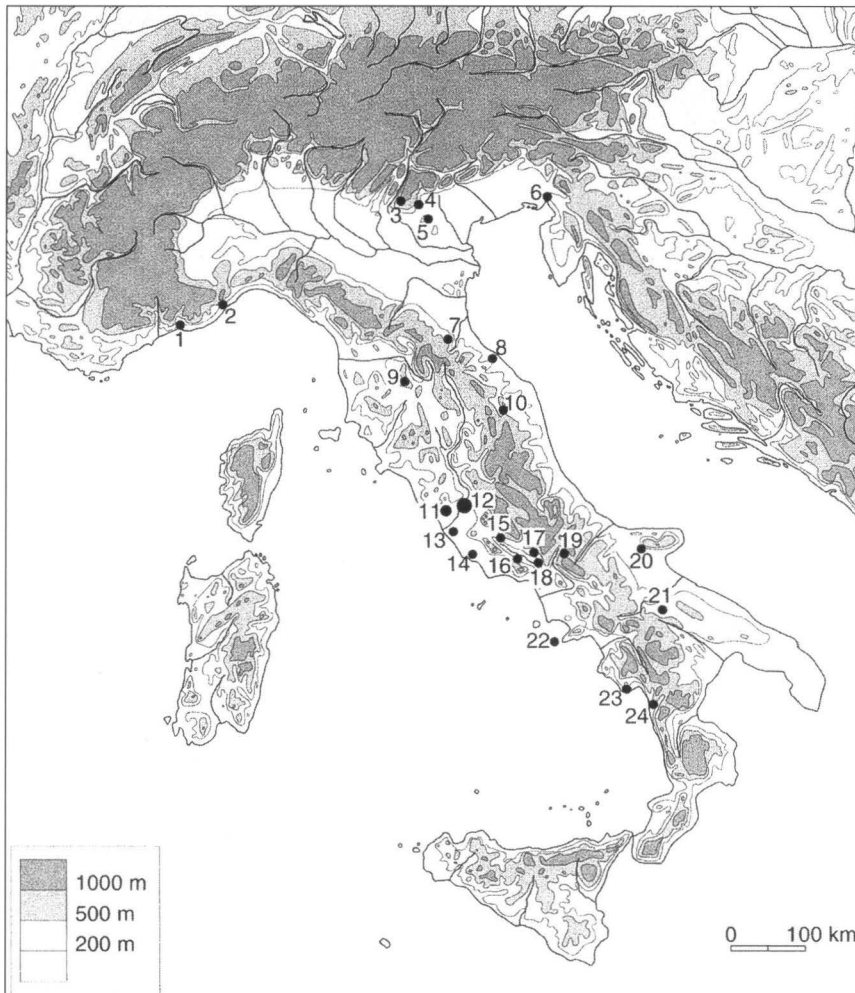
The large mammal renewal from typical late Villafranchian to relatively modern late Galerian faunas is a gradual process, which was completed in approximately 1 million years. The latest Early Pleistocene faunas (early Galerian *sensu* Gliozzi *et al.*, 1997) are quite similar to the Villafranchian faunal complexes, even if Galerian taxa are already well documented. The early Middle Pleistocene faunas (middle Galerian *sensu* Gliozzi *et al.*, 1997), vice versa, are quite similar to the later faunal complexes, even if some Villafranchian taxa survive. According to previous studies (Torre *et al.*, 1999; Sardella *et al.*, 1998; Caloi & Palombo, 1998, 1999) as well as to the result of multivariate analysis based both on similarity and on parsimony methods (Palombo *et al.*, in press), a substantial turnover only occurs during the climate worsening which follows the Early/Middle Pleistocene boundary (currently correlated with OIS 25: Cita & Castradori, 1994).

The arrival of *Homo* spp. is further evidence of this renewal. Aim of this paper is to characterise the faunal assemblages in which human presence is first firmly documented in Italy, and the main characteristics of the environment which allowed, from the early Galerian onwards, a continuous human peopling.

In the late 20th Century there was a general agreement that the earliest settlement of Europe (including Italy) by human groups had happened at least one

million years ago (Bonifay & Vandeermersch, 1991; Laboratoire de Préhistoire du Musée de l'Homme, 1981; Peretto, 1992). This assumption was questioned in the mid Nineties by Roebroeks & Van Kolfschoten (1994), who maintained that there was no such firm evidence before approximately 500 ka. The ensuing scientific debate, as well as new discoveries in the Iberian peninsula, both at Atapuerca and in the Orce basin, led to a re-assessment of this "short" chronology: an intermittent peopling of the Mediterranean perimeter of Europe before c. 500 ka was eventually suggested (Roebroeks & Van Kolfschoten, 1996). However, there is no evidence so far of human presence in continental Europe prior to 600-500ka, as also reaffirmed after a thorough revision of the archaeological evidence from Germany (Baales *et al.*, 2000).

In this perspective, the age of some Italian archaeological sites is critically important (Mussi, 1995; Mussi, in press; Villa, 2001) (Text-fig. 1). An age in the range of 1 Ma was put forward for Monte Poggiolo (Peretto, 1992), which, if confirmed, would fit into the model of intermittent early peopling of the revised "short" chronology, while an archaic-looking calvarium from Ceprano is so far only very loosely dated to a similar time-span (Ascenzi *et al.*, 1996). Only lithic artefacts are preserved at Monte Poggiolo. Better evidence turned out at Isernia and Notarchirico, both multi-layered sites of south-central Italy, with an outstanding preservation of lithics and faunal



Text-fig 1 - Location map. 1) Gr. del Principe; 2) Valdemino; 3) Cave di Quinzano; 4) Monte Tenda; 5) Gr. Maggiore di San Bernardino; 6) Slivia, Visogliano; 7) Monte Poggiolo; 8) Torrente Conca; 9) Bucine; 10) Colle Curti, Cesi; 11) Cerveteri, Torre in Pietra, Malagrotta, Castel di Guido, La Polledrara, GRA km 2; 12) Monte delle Gioie, Sedia del Diavolo, Prati Fiscali, Valchetta Cartoni, Cava Nera Molinaro, Redicicoli; 13) Vitinia; 14) Campo Verde; 15) Fontana Ranuccio; 16) Ceprano, Cava Pompei; 17) Carnello, Valle Radice; 18) Pontecorvo, Pignataro Interamna; 19) Isernia; 20) Gr. Paglicci; 21) Venosa-Loreto, Venosa-Notarchirico; 22) Capri-Quisisana; 23) Gr. del Poggio; 24) Rosaneto.

remains. A fragmented human bone, *i.e.* the diaphysis of a femur, was also found in level α , in the uppermost part of the sequence of Notarchirico.

While the different methods of dating have given some discrepant results (Rhodes & Grün, 1999), there is little doubt that Notarchirico is of early Middle Pleistocene age. A date of c. 640 ka was suggested for the beginning of the local archaeological sequence (Piperno, 1999). After a recent re-assessment, Isernia also has a quite similar age, as a sanidine crystal from a layer capping the deposit is dated to 605 ± 10 ka by Ar/Ar (Coltorti *et al.*, 2000).

Fontana Ranuccio is the next chronological landmark (Biddittu *et al.*, 1979). At this site, the only archaeological level was found to be 458 ± 5.7 ka old after K/Ar analysis. This date is bracketed by a determination of 366 ± 4.5 ka higher up in the stratigraphic sequence, and by 487 ± 7.5 ka at a lower level. Then, the many and extensive sites of the Aurelian Formation, which outcrops on the Tyrrhenian coast just north of Rome (Torre in Pietra, La Polledrara, Castel di Guido, Malagrotta) are correlated with OIS 9 (Caloi *et al.*, 1998).

Taking also into consideration the archaeological sites which are less firmly dated, or indirectly correlated with the previous ones, there is little doubt that human settlement was under way in Italy during the early Middle Pleistocene, possibly slightly before 600 ka (Mussi, 1995; Mussi, in press; Villa, 2001). This might be in accordance with the lack of any archaeological remains at sites of the Slivia FU as well as of the Ponte Galeria FU, as opposed to the "human signature" at most sites of the Isernia FU, and subsequent FUs (Tab. 1). Therefore, *Homo* spp. must be regarded as a component of the Galerian faunas and as part of the early Middle Pleistocene faunal turnover.

MATERIALS AND METHODS

During the Pleistocene, several important climatic events can be detected which affected physical and/or biotic environmental variations and are possibly reflected in concurrent bioevents in multiple lineages. Consequently, there are changes in the fauna and flora richness and diversity. The structure of mammal communities is sometimes affected.

MAMMAL AGES				GALERIAN					AURELIAN					
				EARLY	MIDDLE		LATE	EARLY	MIDDLE	LATE				
FAUNAL UNITS				Colle Curti	Slivia	Ponte Galeria	Isernia	Fontana Ranuccio	Torre in Pietra	Vitina				
OXYGEN ISOTOPE STAGES									OIS 5 OIS 4 OIS 3 OIS 2					
PRIMATES		HABITAT	DIET	WEIGHT										
<i>Homo</i> spp.	O-Wc	Om	I-IV	?										
<i>Macaca sylvanus</i>	Wc	Om	I-IV											
CARNIVORA														
<i>Vulpes vulpes</i>	Wc-O	sPr	II											
<i>Alopex lagopus</i>	O	sPr	II											
<i>Canis</i> sp. aff. <i>C. armenis</i> / <i>Canis</i> aff. <i>C. mosbachensis</i>	O-Wc	Pr	III											
<i>Canis lupus</i>	O-Wc	Pr	III											
<i>Canis alpinus</i>	W-Wc-O	Pr	III											
<i>Mustela putorius</i>	Wc-O	sPr	I											
<i>Mustela nivalis</i>	Wc-O	sPr	I											
<i>Mustela erminea</i>	Wc-O	sPr	I											
<i>Uro gulo</i>	W-Wc-O	Pr	III											
<i>Meles meles</i>	Wc-O	sPr	II											
<i>Martes foina</i>	O-Wc	sPr	I											
<i>Ursus deningeri</i>	Wc	Om	VI											
<i>Ursus spelaeus</i>	Wc-O	Om	VI											
<i>Ursus arctos</i>	Wc	Spr	IV											
<i>Hyaena prisca</i>	O	Sc (Pr)	III											
<i>Pachycrocuta brevirostris</i>	O-Wc	Sc (Spr)	IV											
<i>Crocuta crocuta</i>	O	Sc (Spr)	IV											
<i>Lynx</i> sp.	W-Wc	Pr	III											
<i>Lynx lynx</i>	W-Wc	Pr	III											
<i>Felis sylvestris</i>	W	sPr	II											
<i>Panthera</i> ex gr. <i>P. gombaszoegensis</i>	W	SPr	IV											
<i>Panthera (Leo) fossilis</i>	O	SPr	V											
<i>Panthera (Leo) spelaea</i>	O	SPr	V											
<i>Panthera pardus</i>	Wc-W-O	Pr	III											
<i>Homotherium</i> ex gr <i>H. latidens</i>	O	SPr	V											
PROBOSCIDEA														
<i>Mammuthus (Archidiskodon) meridionalis</i>	O	B-G	VII											
<i>Mammuthus (Mammuthus) trogontheri</i>	O	B-G	VII											
<i>Mammuthus (Mammuthus) ex gr. M. chosaricus - M. primigenius</i>	O	Gr	VII											
<i>Elephas (Palaeoloxodon)antiquus</i>	Wc-O	Br/Br-B-G	VII											
PERISSODACTYLA														
<i>Equus altidens</i> s.s.	O	Gr	VI											
<i>Equus</i> ex gr. <i>E. bressanus- E.suessenbornensis</i>	O	Gr	VI											
<i>Equus hydruntinus</i>	O	Gr	V											
<i>Equus ferus</i>	O	Gr	VI											
<i>Stephanorhinus hundsheimensis</i>	O	Br	VII											
<i>Stephanorhinus hemitoechus</i>	O	B-G	VII											
<i>Stephanorhinus richbergensis</i>	Wc-W	Br	VII											
<i>Coelodonta antiquitatis</i>	O	Gr	VII											
ARTIODACTYLA														
<i>Sus scrofa</i>	Wc	Om	IV											
<i>Hippopotamus</i> ex gr. <i>H. antiquus</i>	Aq-O	B-G	VII											
<i>Hippopotamus</i> ex gr. <i>H. amphibius</i>	Aq-O	Gr	VII											
<i>Capreolus capreolus</i>	Wc-W	Br	III											
<i>Pseudodama</i> sp.	O-Wc	B-G	IV											
<i>Dama clactoniana</i>	Wc-O	B-G	V											
<i>Dama dama</i>	O-Wc	B-G	IV											
<i>Cervus elaphus</i>	Wc	B-G	V											
<i>Alces alces</i>	Wc-W	Br	VI											
<i>Megacerini</i> gen spec indet			VI											
<i>Megaceroides verticornis</i>	O	B-G	VI											
<i>Megaceroides solilacus</i>	O	Br	VI											
<i>Megaloceros savini</i>	O?	Br	VI											
<i>Megaloceros giganteus</i>	O-Wc?	Br	VI											
<i>Bos galernianus</i>	O	Gr	VI											
<i>Bos primigenius</i>	O	Gr	VI											
<i>Bison schoetensacki</i>	O	Gr	VI											
<i>Bison priscus</i>	O	Gr	VI											
<i>Ovis ammon</i>	O	Gr	V											
<i>Hemitragus bonali</i>	O	Gr	IV											
<i>Capra ibex</i>	O	Gr	IV											
<i>Rupicapra</i> ssp.	O	Gr	III											

Tab. 1 - Biochronology of selected large mammal taxa of the Italian peninsula, dating from the latest Early Pleistocene to the Late Pleistocene. Habitat: W, closed woodland; O, grassland, steppe and tundra; Aq, aquatic. Diet: Om, omnivorous; sPr, small predator; Pr, predator; SPr, superpredator; Sc, scavenger; Gr, grazer; Br, browser; B-G, intermediate. Weight: class I, < 5 kg; class II, 5-15 kg; class III, 15-60 kg; class IV, 60-120 kg; class V, 120-350 kg; class VI, 350-850 kg; class VII, > 850 kg.

Multiple bioevents have been used in order to define the faunal biochronological setting. Through time several schemes have been put forward for the Italian local faunas of Middle Pliocene to Late Pleistocene age. A subdivision into mammal ages, further subdivided into Faunal Units (FUs) has been eventually proposed by Gliozzi *et al.* (1997).

This subdivision is based on faunal events which, at times, are related to just a few taxa which even happen to be of sub-specific rank. This is specially true for the Middle Pleistocene faunas. Therefore, the above-mentioned FUs have a local value, and should be seen in the perspective of the Italian peninsula only (Palombo *et al.*, in press). The Italian FUs, however, also are a biochronological time-scale, and conveniently more or less match the Middle Pleistocene interglacial/glacial cycles.

In this paper, the relevant Italian Middle Pleistocene record was accordingly split into a maximum number of suggested FUs, including Petronio & Sardella (1998) recent proposal. Our aim is to detect the compounded bio-events allowing a distinction between the Galerian faunas (with the earliest evidence of human colonization), and the Aurelian faunas (with more conspicuous evidence of human settlement). Because of the lack of well defined FUs, the late Aurelian faunal complexes were split following the oxygen isotope time scale (stages 5, 4, 3 and 2) (Tab. 1). In our analysis, the taxonomical composition of several local faunas have been revised. A selection of representative faunas is presented in table 2. Both rich assemblages and poorer ones, which nevertheless allow biochronological or ecological characterization, are included. Then, we selected for further analysis the taxa which were either commonly found at palaeontological sites, or had a peculiar biochronological or ecological significance. The biochronological range of the latter taxa was also fully reassessed (Tab. 1).

For each complex, we calculated the percentage of species in accordance to the preferred habitat: closed woodland (W), clear woodland (Wc), miscellaneous woodland (W-Wc), grassland, steppe and tundra (O). The percentage of more flexible species, which can live in forests as well as in the open, and at the fringe of both, was also calculated (Wc-O, O-Wc). In the end, three major ecological groups were retained: woodland (W, W-Wc, Wc), open (O) and intermediate (Wc-O, O-Wc). The herbivores were further split into grazers (Gr), browsers (Br), and intermediate (B-G), after their trophic specialization.

Average weight of fossil species was calculated using M1 length, M1 occlusal area and long bone dimension (Damuth & Mac Fadden, 1990), except for humans. In this case, we followed body-mass evaluation by Ruff *et al.* (1997). Sexual dimorphism of living species was also taken into account. Weights were eventually clustered in the following classes: < 5 kg (class I); 5-15 kg (class II); 15-60 kg (class III); 60-

120 kg (class IV); 120-350 kg (class V); 350-850 kg (class VI); > 850 kg (class VII).

As far as *Homo* spp. is concerned, we assume that, after mid-latitudes were colonised, the diet of this omnivorous primate, which had evolved in the tropical and sub-tropical belt, focussed at least seasonally on meat. This, because in an environment such as Europe's, there is a scarcity or lack of suitable vegetable resources during part of the year. Meat had to be consumed to allow for survival, especially in winter. At Atapuerca, possibly 1 Ma ago, the zooarchaeological study of the so-called "Aurora Stratum" is indicative of primary and early access to carcasses (Diéz *et al.*, 1999), while direct evidence of specialized hunting skills as early as 400-450 ka has been discovered at Schöningen: at this spectacular site of northern Germany, exceptional local conditions allowed for the preservation of sophisticated wooden spears, associated with the remains of butchered horses (Thieme, 1997). Accordingly, we take for granted that, because of the lack of specialized digestive enzymes, early humans could not assimilate rotten meat (see Mussi, 1999 for a discussion), and were competing as skilled group hunters, as well as for the access to freshly killed carcasses.

We also wish to underline that human presence was calculated not only when anthropological remains were retrieved, but also when specifically archaeological evidence was discovered, *i.e.* lithic industry and artificially modified bones.

The species richness is currently measured from the total number of taxa actually or potentially occurring in every interval. Nevertheless, the richness of a single time interval could be overestimated when first appearances have been considered to occur at the beginning of the interval, and last appearances at the end of it. In order to reduce this bias, we calculated standing richness value (Nsr) according to Harper's method (Harper, 1975) (see also Azanza *et al.*, 1999).

Different numbers of species in time intervals could reflect true richness changes or be due to sampling bias. Accordingly, we estimated the sampling quality by the proportion of range-through species (Nr) interval using two completeness indexes: CI and CIbda (Maas & Krause, 1994; Maas *et al.*, 1995; see explanations in Azanza *et al.*, 1999). After Maas *et al.* (1995) CIbda values <70 are likely to underestimate appearances, disappearances and taxonomic richness of intervals.

Finally, the faunal turnovers in unequal time intervals (FUs) were estimated following two different methods: 1) after the number of extinctions and new occurrences at the end of a biochron and at the beginning of the successive one; 2) from the appearances plus extinctions occurring during the same intervals. *In situ* speciations and immigrations have been both treated as 'first occurrences', and local extinctions as 'last occurrences'.

According to the first method, turnover indexes (TI = %FO + %LO/2) have been calculated using first

occurrence ($\%FO = FO/RM \times 100$) and last occurrence percentages ($\%LO = LO/RM \times 100$). This allows to normalise LO and FO from the number of species (n) at the transition between two successive biochronological units, using a running mean [$RM = n - (FO + LO / 2)$] (as in Torre *et al.*, 1999).

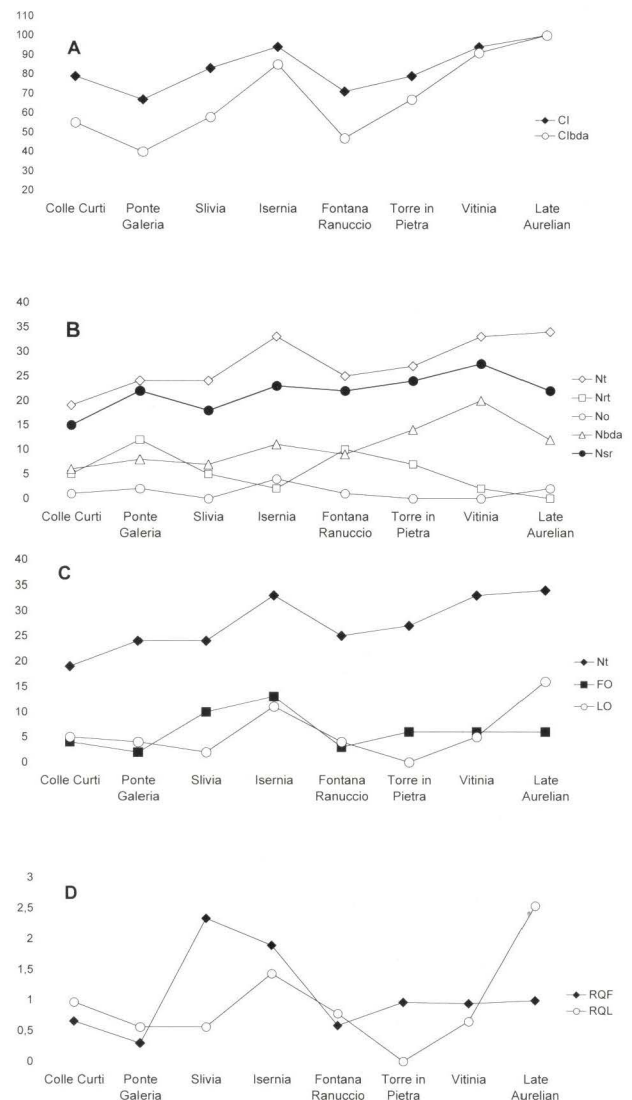
When faunal turnovers are established after total numbers of first and last occurrences in every interval, there are inherent biases such as difference in duration and number of taxa among time intervals. Rate quotient (RQ) is a method that aims at normalising such biases. The first appearances (RQF) and last appearances (RQL) rate quotients are calculated as the following ratio: observed number of first or last occurrences (Ro)/expected number of first or last appearances (Re). The expected rate is calculated using multiple regression of natural logarithm of observed number of first and last occurrence, on the natural logarithm of species richness, and the natural logarithm of the duration of the interval (Gingerich, 1987; Azanza *et al.*, 1999). A synthesis of our analysis is presented in tables 1-2 and in Text-figs. 2-6. The late Aurelian complexes of OIS 5 to 2 are included for comparative purposes.

RESULTS

The relative sampling quality is adequate in most intervals: only the more conservative Cibda index displays low values, especially so when calculated for the FUs of Ponte Galeria (which furthermore has a CI index close to 70) and Fontana Ranuccio. This is consistent with the relatively small number of species identified before, during and after both intervals (Text-fig. 2A).

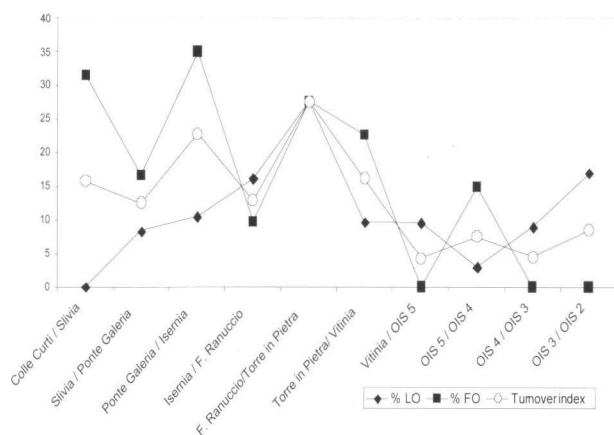
Standing richness progressively increases throughout the Middle Pleistocene (Text-fig. 2B). Isernia and Vitinia FUs display a maximum number of species, and the latter FU is also characterized by the highest diversity. The standardised richness markedly decreases in the final Aurelian, notwithstanding the great number of species. This is due to the many extinctions and, accordingly, to a smaller number of species before, during and after the interval.

After analyses based on FO and LO percentages at the transition between two successive FUs (Text-fig. 3), the early Pleistocene faunal renewal was a progressive one. Slivia and Isernia FUs are characterized by more new occurrences, and by an increasing rate of last occurrences, eventually reaching the highest value at the transition between Fontana Ranuccio and Torre in Pietra FUs. The highest turnover index is found at the Galerian/Aurelian transition, with a high value of both last and first occurrences. The latter also mark the next phase, i.e. the Vitinia FU, concluding the Middle Pleistocene faunal renewal. This is consistent with the high diversity of Vitinia FU. The turnover index, however, decreases, and the extinction of "Galerian" taxa is to some extent completed.



Text-fig 2 - Line charts: A) Mammal species completeness indexes; B) Standing richness (Nsr) calculated after the total number of species (Nt), the number of species of every faunal unit (No), the number of species before-during and after every faunal unit (Nbda), the number of species before and after but not in a given faunal unit (Nrt); C) Number of species (Nt) and number of first (FO) and last (LO) occurrences in each faunal unit; D) First (RQF) and last (RQL) occurrence rate quotients for every interval. Statistical elaboration from Azanza *et al.* (in prep.).

The analyses based on first and last occurrences indexes (RQF and RQL) (Text-fig. 2D) further emphasise that the early middle Galerian (Slivia FU) turnover was linked to new occurrences: the significantly high RQF is consistent with the observed increase in standing richness. Some faunal renewal is suggested during the Isernia FU by the relatively high value of both RQF and RQL.



Text-fig. 3 - Line chart of last (%LO) and first (%FO) occurrences percentages, and turnover indexes.

A turnover being related to extinctions, origination/immigration and local evolution that affect faunal richness does not always mean a reconstruction of the mammal communities. Changes in the community structure, however, can also be detected during the Middle Pleistocene. During the Galerian, the taxa suggesting open environments prevail, even if with decreasing percentages through time; among herbivores, however, there are less grazers than expected (Text-fig. 4). The structure changes at the Galerian/Aurelian transition: the percentage of herbivores taxa of open environments dwindle, while the species of mixed environments increase; browsers and taxa suggesting an intermediate diet are found in matching percentages. The many grazers of the Vitinia FU follow the cooling and aridity increase of early OIS 6.

The Galerian is also an age of large-sized taxa (Text-fig. 5), and of pachyderms as well as of middle-sized taxa, while small-sized taxa are subordinate. An opposite trend is evidenced at the Galerian/Aurelian transition: the middle-sized taxa, marginally more frequent in the Torre in Pietra FU, steadily increase in number during the Aurelian, just as the small-sized taxa. The pachyderms decline.

DISCUSSION

The transition from the Early Pleistocene to the early Middle Pleistocene, *i.e.* from early Galerian to middle Galerian Mammal Age *sensu* Gliozzi *et al.* (1997), was characterized by a considerable faunal renewal, at a time of significant climatic and paleoenvironmental changes. The arrival of immigrant species from Asia or central Europe, as well as the local evolution of pre-existing taxa, are both documented. Some Villafranchian large carnivores are still present, but the faunal complex now includes many taxa also found in more recent assemblages (Tab. 1).

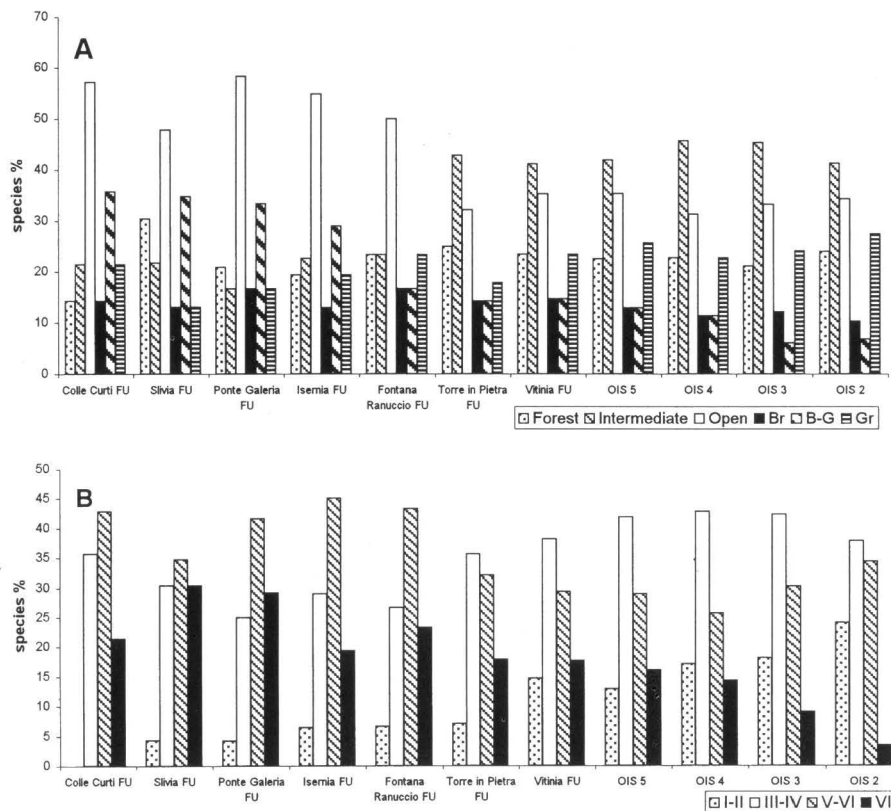
The renewal, after the successive phases corresponding to Slivia FU and to Ponte Galeria FU, reaches its maximum with Isernia FU. The resulting middle Galerian faunas, from a taxonomical point of view seem more closely related to the early and middle Aurelian, than to the early Galerian (Palombo *et al.*, in press). During the Middle and Late Pleistocene, however, the overall structure of the large mammal faunas progressively changes in taxonomical composition, in richness of species, in trophic structure, as well as in the percentage of forms inhabiting different environments (Tab. 2).

In the early Galerian (Colle Curti FU), the large mammal richness is at its lowest, according to a decreasing trend which started at the beginning of the early Villafranchian (Caloi & Palombo, 1998, 1999) (Text-fig. 3). Among both carnivores and herbivores, there is a marked prevalence of taxa of more or less open landscape. An intermediate dietary adaptation prevails among herbivores. The percentage of medium and large sized mammals is more or less equivalent, while the environment apparently does not support large numbers of pachyderms (Text-fig. 4). The scanty evidence provided by the mammal local faunas of the Colle Curti FU fits well into this general scheme (Tab. 1), as only large-sized herbivores and pachyderms were identified, which were grazers or had an intermediate dietary adaptation, and lived in open environments. They were accompanied exclusively by group hunting carnivores.

The middle and late Galerian large mammal assemblages are generally dominated by medium/large sized taxa, mainly herbivores, but the percentage of pachyderms, as well as the overall faunal richness, become markedly higher. Accordingly, the biomass was possibly steadily increasing, especially at the time of the Isernia FU assemblages. However, increasing biodiversity, and higher values of biomass, are not always directly linked to each other (Andrews *et al.*, 1979; Turner, 1992a). In our opinion, biodiversity is rather correlated with an optimization of resource exploitation, mostly taking place in a stable environment. A temperate to moderately cold climate, and a reduced range of oscillations, actually prevail from OIS 15 to 13/12 (cf. Baales *et al.*, 2000).

During the middle and late Galerian, at Ponte Galeria FU, the percentages of medium/large sized herbivores is at the highest, while the percentage of medium/large sized carnivores apparently is at the lowest (Text-fig. 5). The actual occurrence of carnivores (both surviving pre-existing taxa or immigrants from Central Europe) might well be underestimated. A small number of carnivores, however, would be consistent with changes in the carnivores guild documented around 600-500 ka in Central Europe (Turner, 1992b, 1994). At the transition from Slivia plus Ponte Galeria FUs to Isernia FU, the disappearance of two hyenas, and the first occurrence of a new large superpredator, the lion, marks a

Tab. 2 - Local large mammals faunas from selected Italian localities of latest Early Pleistocene (early Galerian) to Middle Pleistocene (middle Aurelian) age. References in (1) Palombo *et al.* (in press); in (2) Mussi (in press); in (3) Abbazzi *et al.* (2000).



Text-fig 4 - A) Bar chart of selected species, according to preferred environments and to trophic specialization; B) Bar chart of selected species, according to weight classes.

major change in the carnivore guild. In central European faunas the sabre-toothed tiger also becomes extinct at this point, while the leopard appears for the first time.

All things considered, the transition from Slivia to Ponte Galeria FU is less dramatic than the transition from the latter to Isernia FU (Text-fig. 2). The relatively archaic character of the Ponte Galeria local faunas, in comparison to the Isernia FU assemblages, is underlined by both new taxa appearance (including the human one) and by extinctions.

In the following Fontana Ranuccio FU, the main event is the occurrence of a new very large sized carnivore, the brown bear, whose hunting aptitude is well documented (Ewing, 1998). The number of very large cervid species is reduced.

During the early Middle Pleistocene, the percentage of taxa inhabiting different environments does not show any significant variation, except for the increase in forest taxa of the Slivia FU. A gradual change is displayed by the trophic structure of herbivores, mainly because of a progressive reduction of species with an intermediate dietary adaptation, while the percentage of grazers increases, especially among the taxa living in an open environment (Text-fig. 4A).

More differences, however, are evidenced by the analysis of local faunas. This is the case of Venosa-Notarchirico and Venosa-Loreto, both in the same

sedimentary basin, both displaying traces of human activity, and both of approximately the same age. At Notarchirico, vertebrate remains were discovered in seven different levels, level A and level α being the most extensively investigated (Cassoli *et al.*, 1999). This local fauna includes few species, most of them also identified in other late middle Pleistocene local faunas (Tab. 1). The taxonomical composition suggests a restricted chronological range. After different methods of relative and absolute dating, the age of the site should be in the range of 600 ka (Bonadonna *et al.*, 1998; Raynal *et al.*, 1998; Lefèvre *et al.*, 1999; Philleyre *et al.*, 1999; Rhodes & Grün, 1999).

At nearby Venosa-Loreto, after Bonadonna *et al.* (1998) the volcanoclastic levels interbedded with the archaeological levels point to a warm and wet period dating to c. 600 to 400 ka. The antler of *Megaceroides solhilacus* (Caloi & Palombo, 1979), found at Terranera, should be younger. The fauna from Venosa-Loreto includes typical early-middle Galerian taxa (*Equus altidens*, *Equus suessenbornensis*, *Stephanorhinus* aff. *S. hundsheimensis*, *Bison schoetensacki*, as well as *Elephas antiquus* and *Bos primigenius*) (Tab. 1). This is in contrast with the more modern character displayed by the assemblage of Venosa-Notarchirico, with a taxonomic composition transitional between Isernia and Fontana Ranuccio FUs. The structure is also quite different, because of the

lack of equids and the very high percentage of “intermediate” taxa at Notarchirico (Text-fig. 4).

Overall, the faunal assemblages of the two sites of Venosa are much less similar than expected, and further investigation is needed to fully apprehend this contradictory evidence.

With the end of Galerian and the transition to the Torre in Pietra FU, a significant faunal event occurs: most of the large-sized Galerian herbivores become extinct, while new little or medium sized carnivores appear (Tab. 2). The fauna progressively acquires modern characters. This renewal corresponds to important climatic modifications happening in the Mediterranean area around the OIS 11/OIS 10 transition, when the interstadial climate becomes progressively milder and the average rate of humidity increases (Vergnaud-Grazzini *et al.*, 1990). This event is marked by a peak in the turnover index, due both to new occurrences and to the above-mentioned extinction of Galerian taxa, mainly of open environments (Text-fig. 3).

The structure of the large mammal complexes changes, too, and the percentage of middle to large sized carnivores and herbivores becomes more balanced (Text-fig. 5): most Galerian large herbivores, such as *Equus altidens*, megacerini and *Bison schoetensacki* become extinct, while among the middle-sized carnivores only *Canis lupus* appears. Furthermore, following the expansion of wooded areas during OIS 9 and 7, the percentage of “open” taxa decreases while

the species of mixed environment gradually increase in number (Text-fig. 3).

Several local faunas are known, currently aggregated into two different FUs (Tabs. 1 and 2). Taxonomical, ecological and structural differences, however, are quite restricted (Text-figs. 2-5) (Caloi *et al.*, 1998; Palombo *et al.*, in press). Differences can only be detected at the level of approximately coeval local faunas of the same geographic area, as in the Campagna Romana of central Italy (Caloi *et al.*, 1998; Mussi & Palombo, in prep.).

A higher biodiversity apparently characterises the faunas of Vitinia FU, even if it is difficult to evaluate the actual diversity in mammal faunal complexes. Some new small and medium-sized taxa occur presumably at the beginning of OIS 6, when more severe and arid climatic oscillations allow, all over the peninsula, the spread of some “mountain” caprinae, and the dispersion of the “steppe horse” *Equus hydruntinus*.

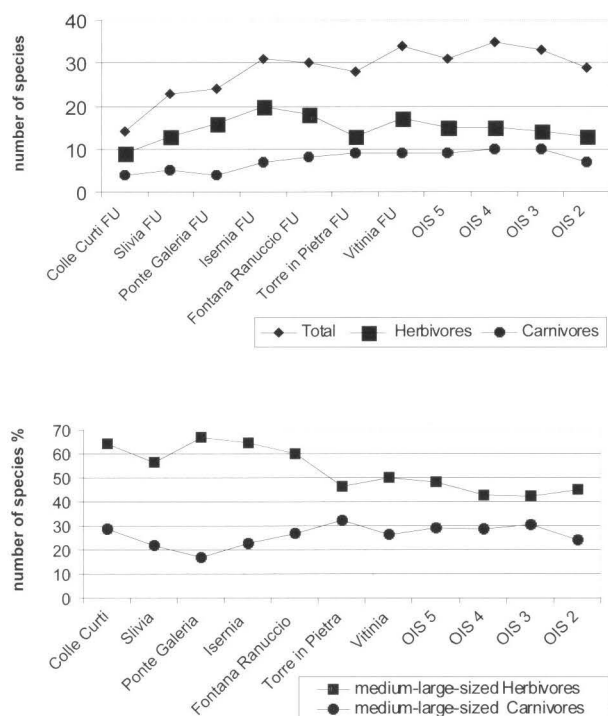
Many local large mammal faunas of Late Pleistocene age have been investigated, but a detailed biochronology is not yet available. In any case, the faunas of the Italian mainland were temperate-fresh even during the cold-arid peaks of the last glacial. Broad-leaved wooded areas always were in existence in refugia of the Tyrrhenian side of the peninsula, while the climate of the Adriatic side seems to have been drier.

The faunal complexes of the last interglacial/glacial cycle, which correspond to a rather fragmented environment, are characterized by a limited rate of renewal and by an increase of “intermediate” taxa (OIS 4 and 3), while the grazers are never as prevalent as they had been during the Galerian Mammal Age.

FINAL REMARKS

Different lines of analysis concurrently suggest increasing large mammal richness and diversity all over the Middle Pleistocene. They point, most notably, to large numbers of herbivores of open environments, both middle- and large-sized, including pachyderms. We have underlined a change in structure at the Galerian/Aurelian transition. The environment possibly also underwent transformations leading to the opening of new local niches.

A stable human colonization of Italy cannot have happened by chance just at a time of significant faunal renewal. This rather suggests that, during the early Middle Pleistocene, human behaviour, including the expansion into new environments, consistently adapted to the same processes as the other large mammals. Accordingly, the palaeontological approach to environmental changes can throw some light on human patterns of evolution. As said in the introduction, we believe that the impact of the new bipedal, middle-sized predator, entering the Italian scene, must be analysed in parallel with the evidence provided by other carnivores.



Text-fig 5 - Line chart of selected medium- and large-sized herbivores and carnivores.

As already underlined by Turner (1992b; 1994), a favourable ecological niche opened for humans around 600 ka, when the number of potentially competing carnivore species was at its lowest. Then, the moderate climatic oscillations of OIS 15 to OIS 13/12, which have been mentioned as a prerequisite for the earliest peopling of European middle latitudes (Baales *et al.*, 2000), also seem to have benefited human groups settling – on a more stable way – on the milder Mediterranean perimeter. After the evidence summarized in Text-figs. 4-5, they were taking advantage of an environment in which herds of herbivores were apparently steadily expanding. Most notably humans were almost inevitably around, when assemblages with *Elephas* (*Palaeoloxodon*) *antiquus*, *Cervus elaphus*, and *Bos primigenius* were deposited, suggesting that this was an adaptation to mixed environments. We have underlined elsewhere that, in comparison with more northern parts of Europe, the Italian “Lower Palaeolithic success” was linked to the richness and variety of environments over short distances, and to the fact that unspecialized hunter-gatherers were able to take advantage of this (Mussi, 1995, p. 41). Our current palaeontological analysis suggests that a growing number of middle-sized herbivore species must also be added to this varied picture, and that humans easily reacted to the ongoing changes evidenced by the high rate of turnovers of Text-fig. 3.

When more contrasted climatic oscillations occurred at the end of the Middle Pleistocene, human groups had already so successfully adapted to middle latitudes, that the speciation toward the typically European *Homo neanderthalensis* was already well under way.

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Maria Rita PALOMBO

Dipartimento di Scienze della Terra
Università degli Studi di Roma "La Sapienza"
P.le A. Moro 5, 00185 Roma, Italy
and
CNR, Centro di Studio per il
Quaternario e l'Evoluzione ambientale
e-mail: mariarita.palombo@uniroma1.it

Margherita MUSSI

Dipartimento di Scienze dell'Antichità
Università degli Studi di Roma "La Sapienza"
Via Palestro 63, 00185 Roma, Italy