

Large- and small-mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula

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Abstract

Over the last 50 years the studies on terrestrial mammals of the Italian peninsula have provided a large volume of data and a more detailed knowledge of faunal events during the Late Pliocene and Quaternary. Moreover geological, sedimentological, palynological and magnetostratigraphical investigations on the Pliocene–Pleistocene continental sedimentary basins have yielded the possibility of a detailed calibration of the faunal successions. Thus, palaeontologists have been able to reconstruct faunal sequences and to propose biochronological scales based on large and small mammals, respectively. In the present contribution an integration of the two biochronological scales is proposed, and the successions of bioevents are carefully compared. This integrated approach allows the constraint of the sequence of large- and small-mammal events in a more reliable way, and therefore it results in a more detailed and consistent chronological use of mammalian assemblages. Particular attention is paid to the faunal changes that correspond to the Middle–Late Pliocene (2.6 ma), Pliocene–Pleistocene (1.8 ma) and Early–Middle Pleistocene (Gauss–Matuyama transition) chronostratigraphical boundaries.

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1. Introduction

The Italian mammal chronology has been developed since the pioneering work of Azzaroli in the 1970s mainly on the basis of large-sized mammalian taxa. The Mammal Age (sensu Lindsay, 1990) names ‘Villafranchian’ and ‘Galerian’, although sometimes criticised, are widespread concepts used by the scientific community of continental stratigraphers in Southern Europe. In more recent years, thanks to the discovery of important new localities and the careful sieving of many fluviolacustrine deposits in Italy, small mammal stratigraphy is becoming of age. Italian micromammal students tend to refer to biochronological scales widely adopted in the European countries, instead of developing local units (Sala and Masini, 2004, 2006). The two biochronological sequences, apart from in some sporadic cases, are often treated as distinct. This is also

because the specialists in one group are often not very confident with knowledge from another.

The different body size that distinguishes the ‘large’ from the ‘small’ mammals also coincides with different clusters of taxonomic groups and has a two-fold influence. First, the two categories have a different taphonomy, which influences their distribution and recovery and the methods required during collection. Secondly, their size influences their evolutionary and dispersal behaviour and consequently the stratigraphical distribution of the two groups. Large mammals are less limited by local microclimatic and microenvironmental conditions; they are able to make more frequent and rapid dispersals, and therefore they apparently produce quicker turnover in the stratigraphical record. Small-sized mammals, on the other hand, are more strongly influenced by microenvironmental conditions, and, are in general more static in evolutionary terms and their turnover behaviour. During the Pliocene–Pleistocene, noticeable exceptions are the very dynamic sub-family Arvicolinae, and the shrews.

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Here, the authors present an integrated biochronological framework for large and small mammals to obtain a finer resolution and a more reliable control of the succession of faunal events. This framework has been integrated into a chronostratigraphical scheme by means of radiometric and magnetostratigraphical calibration and marine-continental correlations available from several sites (Fig. 1).

A consistent marine stratigraphical record occurs in the Neogene and Quaternary of Italy, so that several Global Stratotype Section and Point (GSSP) have been proposed from the peninsula (Rio et al., 2003). In the Miocene, the terrestrial mammalian record is predominantly insular and/or endemic: e.g. Scontrone (Molise), various localities in Maritime Tuscany (Tuscany), Sardinia (Mazza and Rusconi, 1996; Rook et al., 1999, 2000) (Fig. 2). Following the Messinian phase, documented by the localities of Gravitelli (Sicily), Brisighella (Emilia Romagna), Ciabot Cagna (Piedmont) (De Giuli and Vai, 1988; Cavallo et al., 1993) when no endemic faunas spread into the whole peninsula (Fig. 2), the Early Pliocene fossil mammal record becomes rather scant (Azzaroli et al., 1988). However, it is abundant and well known from the Middle Pliocene (Azzaroli et al.,

1988; Masini et al., 1995; Gliozzi et al., 1997; Kotsakis et al., 2003) (Fig. 2).

The aim of this paper is to present and discuss the faunal events that occurred close to three chronostratigraphic boundaries: Middle–Late Pliocene (Rio et al., 1994, 1998), Pliocene–Pleistocene (Aguirre and Pasini, 1985) and Early–Middle Pleistocene. The latter boundary is still under discussion by the scientific community. In the last years the proposal of Richmond (1996) to place the Early–Middle Pleistocene boundary at the Brunhes–Matuyama magnetic reversal epoch boundary has found consideration by Quaternary researchers (cf. Gibbard and van Kolfschoten, 2004), but also other proposals have been recently presented (e.g. Ciaranfi et al., 1997; Capraro et al., 2004; Ciaranfi et al., 2004; Ciaranfi and D’Alessandro, 2005). In this paper the proposal of Richmond (1996) is taken under consideration.

2. Middle Pliocene–Late Pliocene transition: Early–Middle Villafranchian, and the Early Villanyian

After the Messinian faunas of the MN13 zone, the record of fossil mammals becomes rather poor in the

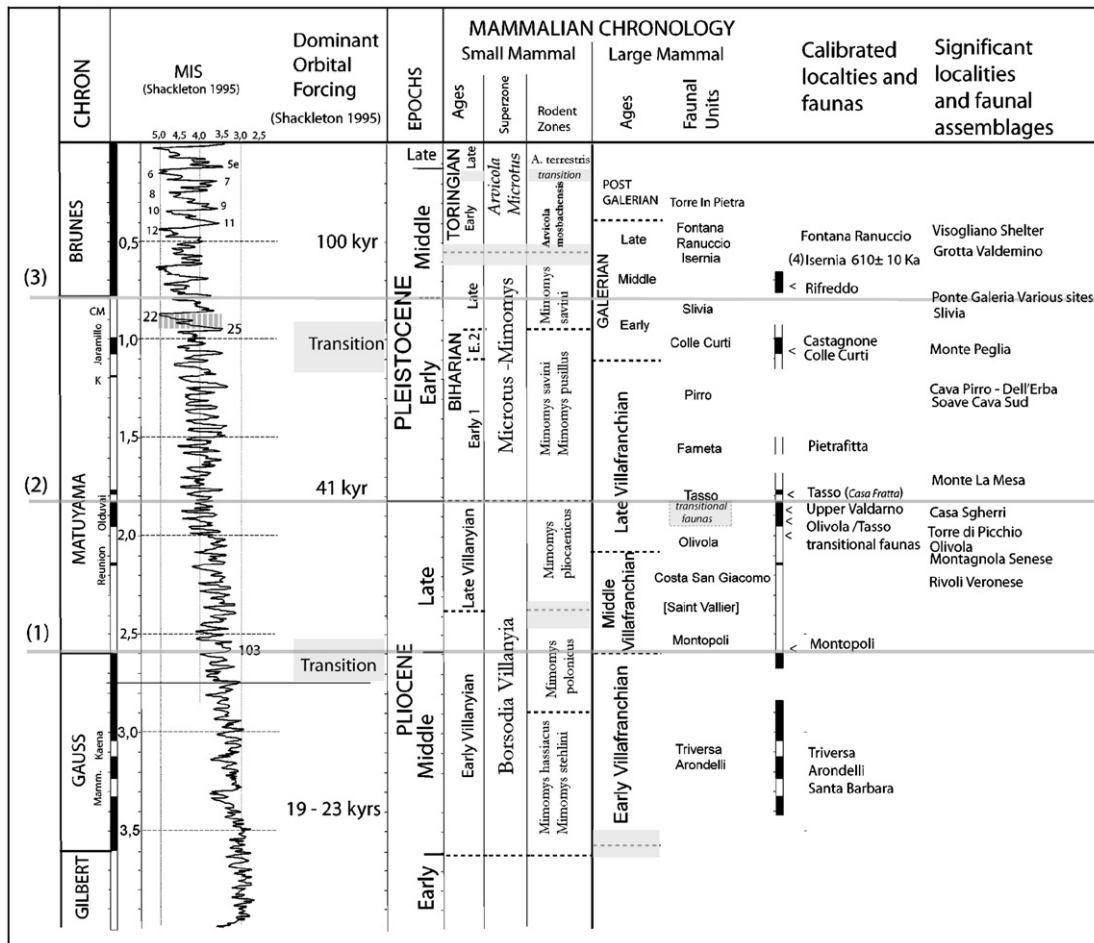


Fig. 1. Integrated stratigraphic scheme for the Middle Pliocene–Pleistocene large- and small-mammalian record of the Italian peninsula. The grey lines indicate the position of the chronostratigraphic boundaries discussed in the text: 1. Middle–Late Pliocene boundary (Rio et al., 1994, 1998). 2. Pliocene–Pleistocene boundary (Aguirre and Pasini, 1985). 3. Early–Middle Pleistocene boundary according to the proposal of Richmond (1996). 4. Isernia ⁴⁰Ar/³⁹Ar dating according to Coltorti et al. (2005).

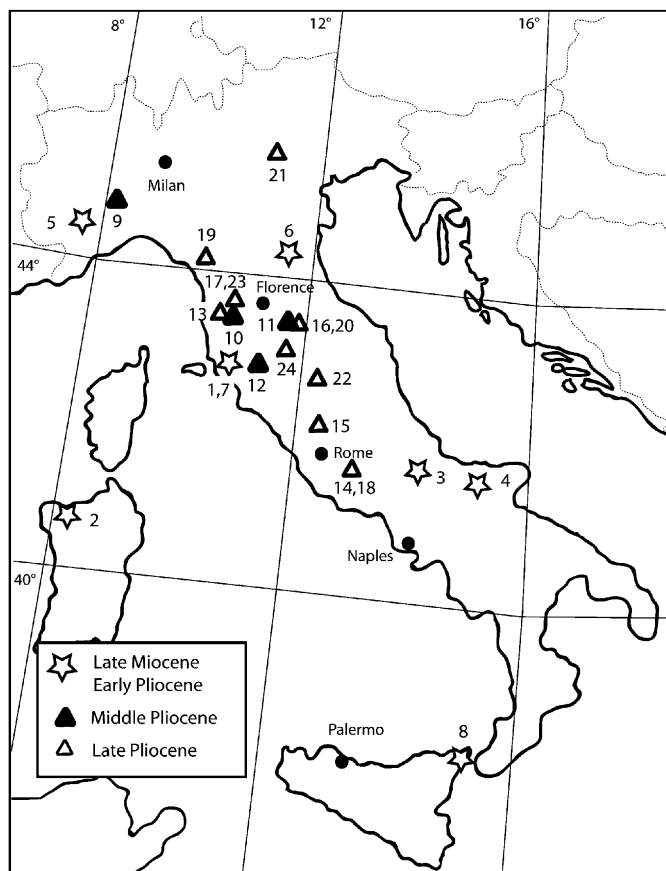


Fig. 2. Location map. 1–8: Late Miocene—Early Pliocene localities. 1. Maritime Tuscany (Grosseto, Tuscany), various sites, Late Miocene endemic fauna of the Tuscany–Sardinian palaeobioprovince (after Rook et al., 1999). 2. Fiume Santo (Sardinia), Late Miocene, endemic fauna of the Tuscany–Sardinian palaeobioprovince. 3. Scontrone (Abruzzi), Late Miocene endemic fauna of the Apulia–Abruzzi palaeobioprovince. 4. Gargano ‘terre rosse’ fissure fillings (Apricena, Apulia), Late Miocene (?)—Early Pliocene endemic fauna of the Apulia–Abruzzi palaeobioprovince. 5. Ciabot Cagna (Alba, Piedmont), Messinian continental fauna. 6. Cava Monticino (Brisighella, Faenza, Emilia Romagna), Late Messinian continental fauna. 7. Maritime Tuscany (Grosseto, Tuscany), various sites, Messinian, continental fauna. 8. Gravitelli (Messina, Sicily), Messinian continental fauna of African affinity (Rook et al., 1999, 2000). 9–12: Middle Pliocene localities. 9. Villafranca D’Asti (Asti, Piedmont): Triversa, Fornace RDB, Cascina Arondelli Quarry. 10. Lower Valdarno (Tuscany), several localities with Early Villafranchian–Early Villanyan faunas, among which San Giusto-type locality of *Mimomys stehlini*. 11. Upper Valdarno Basin (Arezzo, Tuscany), Lower Synthem: Castelnuovo dei Sabbioni, Santa Barbara and other localities. 12. Arcille (Grosseto, Tuscany). 13–24: Late Pliocene localities. 13. Montopoli (Lower Valdarno Basin, Pisa, Tuscany). 14. Colleparado (Anagni Basin, Frosinone, Latium). 15. Bocchignano (Rieti, Latium). 16. Upper Valdarno Basin (Arezzo, Tuscany), *Mimomys polonicus* find. 17. Vinci (Lower Valdarno Basin, Florence, Tuscany). 18. Costa San Giacomo (Anagni Basin, Frosinone, Latium). 19. Olivola (Aulla Basin, La Spezia, Tuscany). 20. Upper Valdarno Basin (Tuscany), several localities with Late Villafranchian large-mammal fauna (Olivola FU) and Castelfranco di Sopra (type locality of *Mimomys pliocaenicus*). 21. Rivoli Veronese (Verona). 22. Torre di Picchio (Tiberino Basin, Terni, Latium). 23. Casa Sgherri (Lower Valdarno Basin, Florence, Tuscany). 24. Montagnola Senese (Siena, Tuscany).

Italian peninsula. The first significant record after the Ruscinian gap is given by the Early Villafranchian faunas of the Triversa Faunal Unit (FU) and by the related Early Villanyan small mammals of *Mimomys hassiacus*–*Mimomys stehlini* zone, whose best record is at Cascina Arondelli (Piedmont) and at Arcille, near the town of Grosseto (Tuscany) (Berzi et al., 1967; Michaux, 1970; Azzaroli, 1977; Azzaroli et al., 1988; Fejfar, 2001) (Figs. 2–4).

These mammalian assemblages still retain the subtropical affinities, which were typical of the Ruscinian Mammal Age. They include many taxa with moist forest affinities (e.g. *Tapirus*, *Mammuth borsoni*, *Anancus arvernensis*, *Sus minor*, *Mesopithecus*, *Parailurus*, *Blarinoides*, flying squirrels) to which are associated new mammals, perhaps more linked to wooded parkland environment (e.g. the large-sized antelope *Leptobos stenometopon*, *Stephanorhinus elatus*, the medium-sized deer *Pseudodama lyra*). The occurrence of the sabre-tooth cat *Homotherium* and of the cheetah *Acinonyx pardinensis*, are also important (Fig. 3). The cooccurrence of two stratigraphic marker taxa, *Mammuth borsoni* and *Anancus arvernensis*, allow a fairly precise correlation with the European regions. These faunas occur in Piedmont, west of the town of Asti, along the western and southern side of Tuscany (Lower Valdarno basin, several localities) where they are superposed to marine sediments, and in the Lower Synthem of the Upper Valdarno Basin (Castelnuovo Synthem; Fig. 2). They are assigned to the Gauss Chron (Torre et al., 1996; Napoleone et al., 2003; Ghinassi et al., 2004).

The next significant large-mammal assemblage is that from Montopoli in the Lower Valdarno (Tuscany; Fig. 2), where it is stratigraphically superposed on faunas of Triversa unit and to shallow-water marine sediments of Middle Pliocene age (Benvenuti et al., 1995). This fauna, and the related faunal unit, occur at the Gauss–Matuyama transition (Lindsay et al., 1980) and provides an important signal of environmental change for the dispersals of the genus *Mammuthus* (with the primitive form *M. meridionalis gromovi*), the horse (*Equus* cf. *livenzovensis*), the ‘giant deer’ *Eucladoceros*, and of a *Gazella* (*G. borbonica*) (Fig. 3). The thar (*Hemitragus*) is also recorded for the first time in Italy at Colleparado (Anagni Basin, Frosinone; Fig. 2) a local fauna belonging to this unit, although it is perhaps slightly younger than the Montopoli fauna.

This faunal unit apparently corresponds to the upper part of the MN16b zone and was traditionally included in the Early Villafranchian (e.g. Azzaroli et al., 1988). Following the opinion of De Giuli et al. (1984) and Palombo et al. (2002), the authors are inclined here to consider it as the basal unit of the Middle Villafranchian, since the ‘open environment’ taxa, the dispersals of which are recorded at Montopoli, persist in the Middle Villafranchian faunas.

The Montopoli FU is correlated with the upper part of the *Mimomys polonicus* zone (Fig. 1). The documentation of this zone is very poor in Italy. A sporadic find

Large mammal Ages	EARLY VILLAGFRANCHIAN		MIDDLE VILLAGFRANCHIAN			L. VILLAGFR.
Faunal units	Triversa		Montopoli	St. Vallier	C.S.Giacomo	Olivola
Small mammal Ages	early VILLANYIAN			late VILLANYIAN		
Small mammal zones	<i>M. hassiacus</i> zone		<i>M. polonicus</i> zone	<i>M. pliocaenicus</i> zone		
TAXA	Triversa Faunal Unit several localities	Montopoli Faunal Unit several localities	Scattered Finds	Costa S.Giacomo Faunal Unit several localities	Olivola Faunal Unit several localities	
<i>Parailurus hungaricus</i>	cf.					
<i>Macaca</i> cf. <i>M. sylvanus</i> <i>priscus</i>	X					
<i>Mesopithecus monspessulanus</i>	X					
<i>Baranogale helbingii</i>	X					
<i>Megaviverra apennina</i>	X					
<i>Viverra prepraxi</i>	X					
<i>Ursus minimus</i>	X					
<i>Mammut borsoni</i>	X					
<i>Tapirus arvernensis</i>	X					
<i>Procapreolus cusanus</i>	X	X				
<i>Stephanorhinus elatus</i> (=jeanvireti)	X	X	cf.			
<i>Nyctereutes megamastoides</i>	X	X	X			
<i>Sus minor</i>	X	X	X			
<i>Plihyaena perrieri</i>	----	X		X		
<i>Anancus arvernensis</i>	X	X		X		
<i>Pseudodama lyra</i>	X	X		X		
<i>Chasmaportetes lunensis</i>	X	X		X	X	
<i>Leptobos stenom.-merlai-furtivus</i>	X	X	X	X	X	
<i>Acinonyx pardinensis</i>	X	X		?	X	
<i>Enhydriactis ardea</i>	X	X			X	
<i>Lynx issiodorensis</i>	X	X			X	
<i>Homotherium</i> ex gr. <i>H. crenatidens</i>	X	X			X	
<i>Megantereon cultridens</i> - <i>M. whitei</i>	?	X			X	
<i>Equus livenzovensis</i>		X				
<i>Eucladoceros falconeri</i>		X				
<i>Croizetoceros ramosus</i>		X				
<i>Hemitragus</i> cf. <i>H. orientalis</i>		X	?	?		
<i>Gazella borbonica</i>		X		X		
<i>Mammuthus meridionalis</i>		X		X	X	
<i>Equus stenonis</i>			?	X	X	
<i>Stephanorhinus etruscus</i>			?	X	X	
<i>Eucladoceros tegulensis</i>			?	X		
<i>Gallogoral meneghinii</i>			?	X	X	
<i>Gazellospira torticornis</i>			?	X	X	
<i>Macaca sylvanus florentinus</i>			?	X	X	
<i>Canis</i> ex gr. <i>C. etruscus</i>				X	X	
<i>Sus strozzi</i>				cf.	X	
<i>Vulpes</i> cf. <i>V. alopecoides</i>				X	X	
<i>Procamptoceras brivatense</i>				?	X	
<i>Leptobos etruscus</i>				?	X	
<i>Felis sylvestris lunensis</i>					X	
<i>Pseudodama nestii</i>					X	
<i>Eudadoceros dicranios-ctenoides</i>					X	
<i>Ursus etruscus</i>					X	
<i>Pachycrocuta brevirostris</i>					X	
<i>Panthera</i> ex gr. <i>gombaszoegensis</i>					X	
<i>Canis amensis</i>					?	

Fig. 3. Distribution pattern of large-mammalian faunal units and taxa of the Early and Middle Villafranchian in the Italian peninsula. The correlation with small-mammal biochronological units is also indicated. The Middle–Late Pliocene boundary is according to Rio et al. (1994, 1998). X, occurrence; —, rare occurrence;?, doubtful or questioned occurrence.

of *M. polonicus* comes from Bocchignano (Latium; Petronio et al., 2002, Kotsakis et al., 2003; Fig. 2), without correlation with large-mammal faunas. The recent find of an advanced *M. polonicus* in the Upper Valdarno Basin, in a succession correlated to early Matuyama (Ghinassi et al., 2004, 2005), corroborates that the *M. polonicus* zone includes also the Montopoli faunal zone in the Italian peninsula. This is also suggested by the occurrence of *Germanomys* sp. in the Vinci locality (Lower Valdarno; Fig. 2), in sediments referred to the Late Pliocene (Marcolini et al., 2000; Marcolini, 2003; Sardella et al., 2003) (Fig. 4). The *Germanomys* find is here tentatively correlated to the *M. polonicus* zone. However, a possible correlation of the Vinci locality with the younger Costa San Giacomo FU has been suggested by the previous authors, based on the occurrence of a single horse molar tentatively referred to *Equus senzensis* or to *Equus stenonis*.

The faunal renewal of the Middle–Villafranchian falls close to the Middle–Late Pliocene boundary (Gelasian Stage, GSSP at Monte san Nicola Section, Sicily; Rio et al., 1994; Gradstein et al., 2004). It correlates to the effects of the transition to a climate in which moderately increased glacial–interglacial fluctuations alternated, influenced by the 41 ka orbital cycle of the obliquity variation (Shackleton, 1995) (Fig. 1). This boundary is the starting point of a progressive global climate deterioration that affects the vegetational composition and consequently the fauna.

The St. Vallier FU, the second unit of the Middle Villafranchian is recorded in Italy by some sporadic finds, while a better record is given by the Costa San Giacomo FU (Anagni Basin, Latium). The faunal composition is very similar to that of the preceding unit, important first occurrences, however, are those of the rhinoceros *Stephanorhinus etruscus*, the horse *E. stenonis*, a large-sized boar *Sus* cf. *strozzi*, the rupicaprine *Gallogoral*, and the spiral

Large mammal Ages	EARLY VILLAGFRANCHIAN		MIDDLE VILLAGFRANCHIAN			L. VILLAGFR.
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Small mammal Ages	early VILLANYIAN			late VILLANYIAN		
Small mammal zones	<i>M. hassiacus</i> zone		<i>M. polonicus</i> zone	<i>M. pliocaenicus</i> zone		
TAXA	RDB-Quarry Arondelli Arcille S.Giusto Spoleto	Upper Valdarno Bocchignano Vinci		Rivoli V. Montagnola Senese Toppetti Q.	Castel - franco Casa Sgherri	
Hystrix sp.	X					
Sciuridae sp. I (Sciuroptera),	X					
Sciuridae sp. II	X					
Muridae gen. et sp. indet. I	X					
Muridae gen. et sp. indet. II	X					
Apodemus alsomyoides	X					
Mimomys (Cseria) stehlini	X					
Mimomys hassiacus	X					
Glirulus pusillus	X					
Muscardinus pliocaenicus	cf.					
Germanomys sp.	X		X			
Castor sp.	X			X		X
Mimomys polonicus			X			
Sciuroptera indet				X		
Apodemus mystacinus				X		
Ungaromys dehmi				X		
Villanyia cfr. V. exilis				X		
Dinaromys allegranzii				X		
Muscardinus sp.				X		X
Apodemus dominans				X		X
Mimomys pliocaenicus				X		X
Mimomys pitmyoides				X		X
Hystrix refossa				X		X
Sciurus warthae				X		
Glis minor				X		
Mimomys tigliensis - tornensis				X		
Glis sp.						X
Mimomys medasensis						X
Mimomys ostramosensis						X
Mimomys pusillus						X

Fig. 4. Distribution pattern of rodent taxa for the Villanyian Mammal Age of the Italian peninsula. The correlation with large-mammal biochronological units is also indicated. The Middle–Late Pliocene boundary is according to Rio et al. (1994, 1998). Explanations of symbols as in Fig. 3.

horned antelope *Gazellospira*. The mastodon *Anancus* and the genus *Gazella* are recorded for the last time. The sporadic occurrence of a relative of the modern wolf, *Canis* cf. *etruscus*, very common in the following units, is an important event among carnivores (Rook and Torre, 1996) (Fig. 3).

The first faunal unit of the Late Villafranchian, the Olivola FU, records a further change in faunal composition that yet it retains continuity. In this unit the gregarious ‘antelope’ *Leptobos etruscus* becomes the most widespread bovid, and derived forms of deer (*Eucladoceros dicranios-ctenoides*, *Pseudodama nestii*) appear. It is also worth mentioning the occurrence of the Caprinae *Procamptoceras*. The presence, among the carnivores, of the large, social, spotted hyaena *Pachycrocuta brevirostris* and the jaguar-like *Panthera gombaszoegensis* are also important.

Local faunas of the Olivola FU and faunas transitional to the next unit, the Tasso FU, are rather common in the Upper Valdarno Basin and represent the bulk of finds in older and more recent collections (Figs. 2 and 5). Magnetic investigations have allowed the correlation of these faunas to an interval that extends from the reverse polarity Matuyama Chron above the Reunion Event and the greater part of the Olduvai Subchron (Torre et al., 1993; Napoleone et al., 2003).

Considering the small mammal faunas, following the poorly represented *M. polonicus* zone, the Late Villanyian *Mimomys pliocaenicus* zone is fairly represented in Italy.

Rivoli Veronese (Venetia; Sala et al., 1994; Sala, 1996b; Sala and Masini, 2006) is the most important local fauna and, because it includes a rather primitive *M. pliocaenicus*, is considered the oldest record of this zone. Some other faunas are known in the Italian peninsula in which *M. pliocaenicus* or *Mimomys ostramosensis* are present (Figs. 2 and 4).

The occurrence of the type specimen of *M. pliocaenicus* (actually a derived morphotype) at locality Castelfranco di Sopra (Fig. 2) in the Upper Valdarno Basin is an element for correlation with the large-mammal succession. Here, sediments that have yielded large mammals of the Olivola FU or transitional to the Tasso FU are exposed (Masini and Torre, 1987; Mazza et al., 2004). *Mimomys medasensis* and *M. ostramosensis* have also been recently found in association with large mammals of the Olivola and Costa San Giacomo FU: Torre di Picchio, in the Tiberino Basin (Marcolini, 2002) and Casa Sgherri in Lower Valdarno (Marcolini et al., 2000; Girotti et al., 2003) (Fig. 2).

In short, the *M. pliocaenicus* zone is directly correlated with the Costa San Giacomo, Olivola and the transitional Olivola–Tasso Faunal Units (Fig. 1). The lack of small mammals finds from the localities of the older part of the Middle Villafranchian prevents a more accurate correlation. This gap in the record results in the small mammals of the *M. pliocaenicus* zone being markedly different in comparison to the Older Arondelli and coeval faunas (Fig. 4). Among the arvicolids, additional characteristic

taxa include *Mimomys tornensis* and *Mimomys pitymyoides*, which were widespread in the northern and central part of the peninsula. The survival of *Prolagus* into this unit is also significant. This Ochotonid was rather common in the central Italian basins, and the dominant taxa in the karstic deposit at Montagnola Senese. The unique occurrence of *Apodemus mystacinus*, the first occurrences of *Apodemus dominans* among the murids, of *Oryctolagus lacosti* within lagomorphs, and finally of *Crociodura* and *Sorex runtonensis* among insectivores are also noteworthy.

The Rivoli Veronese fauna (Sala et al., 1994) is especially important, since it includes the highest taxonomic diversity in the rodents and insectivores. This fauna yields the unique occurrences in Italy of *Ungaromys dehmi* and of the *Villanyia* genus and the first occurrence of the genus *Dinaromys*, with the primitive species *Dinaromys allegranzi* (Sala, 1996b). *D. allegranzi* is the oldest known species of this genus, which later spread mainly into the Balkan and the northern Italian regions.

3. Pliocene–Pleistocene boundary: the Olivola–Tasso and Villanyian–Biharian transitions

The transition from the Olivola to the subsequent Tasso FU is known from the Upper Valdarno Basin, where fossil-bearing sediments from the two stratigraphically superposed units are exposed (Torre, 1985; Masini and Torre, 1987; Azzaroli et al., 1988). This transition has been correlated magnetostratigraphically close to the top of the Olduvai Subchron (Napoleone et al., 2003), which is around the basal Pleistocene boundary (GSSP at La Vrica Section; Aguirre and Pasini, 1985; Albanelli et al., 2002, Gradstein et al., 2004) (Fig. 1). This boundary is placed within an interval of gradual climatic transition which mirrors the gradual change in faunal composition.

The Tasso FU includes some novel elements, such as the occurrence of *Praeovibos* (locality Casa Frata), of a primitive lycaon (*Lycaon falconeri*), of a derived form of medium-sized deer (*Pseudodama eurygonos-farnetensis*), of the small equid *Equus stehlini*, and of *Leptobos vallisarni*, a stouter relative of *L. etruscus*. This assemblage also includes the last occurrence on the Italian mainland of the genus *Prolagus* (Upper Valdarno; Rook and Masini, 1990), while the bovids *Gazellospira* and *Procamptoceras* are no longer present. The occurrence of *Hippopotamus* in this unit is doubtful, even though it is present at Carsoli (Anagni Basin, Latium), together with *Leptobos* aff. *furtivus* (Masini, 1989; Gentili and Masini, 2005) (Figs. 5, 6).

The finds of *Mimomys savini* in two localities of the Upper Valdarno (Le Strette al Tasso and Case Inferno; Fig. 5) in sediments which according to Torre (1985) and Masini and Torre (1987) are considered as the reference for the Tasso FU suggest that this unit can be correlated with the Early Biharian (Figs. 1 and 7). It is worth mentioning, however, that no remains of *Microtus (Allophaiomys)* have

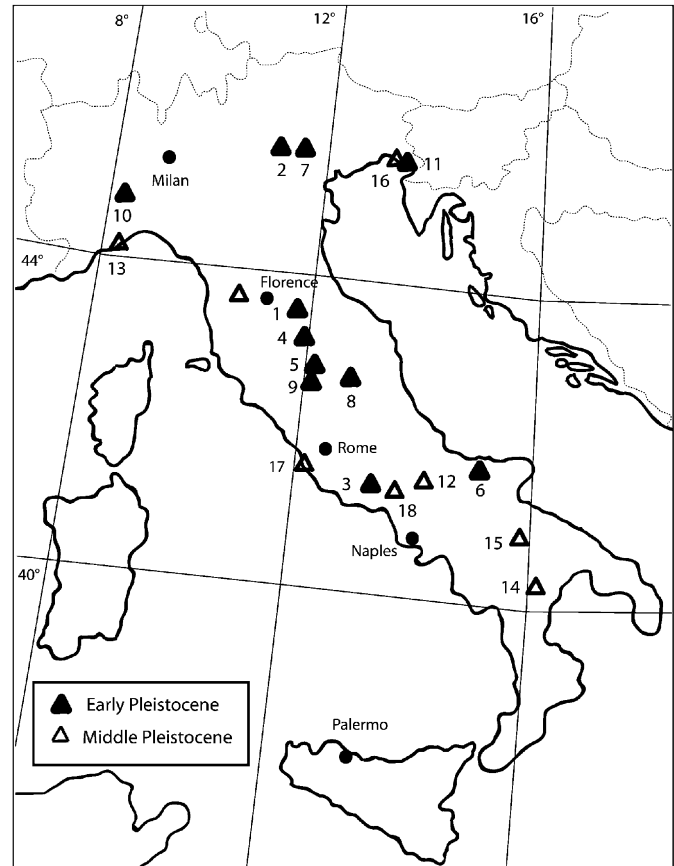


Fig. 5. Location map. Early Pleistocene–Middle Pleistocene (early part) localities. 1. Upper Valdarno Basin (Arezzo, Tuscany): Il Tasso, Casa Frata, Le Strette al Tasso, Case Inferno and other localities. 2. Monte La Mesa (Verona, Venetia). 3. Carsoli, (Anagni Basin, Frosinone, Latium). 4. Val di Chiana, (Arezzo, Tuscany): Farneta, Cava Liberatori, Selvella and other localities. 5. Pietrafitta, (Nestore Basin, Perugia, Umbria). 6. Cava Pirro (Gargano, Foggia, Apulia). 7. Soave Cava Sud (Verona, Venetia). 8. Colle Curti (Umbro Marchean Apennine). 9. Monte Peglia (Perugia, Umbria). 10. Castagnone (Alessandria, Piedmont). 11. Slivia (Trieste, Venetia Giulia). 12. Isernia La Pineta (Isernia, Molise). 13. Valdemino Cave (Savona, Liguria). 14. Rifreddo (Sant'Arcangelo Basin, Potenza, Basilicata). 15. Venosa Notarchirico (Potenza, Basilicata). 16. Visogliano Shelter (Trieste, Venetia Giulia). 17. Ponte Galeria (Rome, Latium); Fontignano, Ponte Galeria 2 and several other localities. 18. Fontana Ranuccio (Anagni Basin, Frosinone, Latium).

so far been found in the Late Villafranchian horizons of the Upper Valdarno Basin.

The most representative locality of the Early Biharian in Italy is Monte La Mesa (Venetia region), where a very rich and diverse small-mammal assemblage has been recovered (Marchetti et al., 2000). The occurrence of a typical *Microtus (Allophaiomys) pliocaenicus*, in association with *M. cf. ostramosensis* and *Mimomys pusillus*, allows it to be considered as the oldest Biharian assemblage in Italy. It is tentatively correlated to the Tasso unit. The Monte La Mesa assemblage records several significant occurrences: those of the genera *Allocricetus* and *Clethrionomys*, of *Pliomys episcopalism* among the rodents, of *Sorex minutus* and *Sorex prealpinus* among insectivores. *Mimomys* cf.

Large mammal Ages	M.VILL.		LATE VILLAFRANCHIAN			
	Faunal units	C.S.Giacomo	Olivola	Tasso	Farneta	Pirro
Small mammal Ages	late VILLANYIAN			BIHARIAN		
Small mammal zones	<i>M. pliocaenicus</i> zone			Early Biharian I		
TAXA	Costa S.Giacomo Faunal Unit several localities	Olivola Faunal Unit several localities	Tasso Faunal Unit several localities	Farneta Faunal Unit several localities	Pirro Faunal Unit several localities	
Hemitragus cf. H. orientalis	?					
Pliohyaena perrieri	X					
Anancus arvernensis	X					
Pseudodama lyra	X					
Gazella borbonica	X					
Eucladoceros tegulensis	X					
Chasmaportetes lunensis	X	X				
Gazellospira torticornis	X	X				
Gallogoral meneghini	X	X				
Procamptoceras brivatense	?	X	?			
Acinonyx pardinensis	?	X	X			
Leptobos sten.-merlai- furtivus	X	X	X			
Stephanorhinus etruscus	X	X	X			
Leptobos etruscus	?	X	X			
Enhydrictris ardea	X	X	X		
Equus stenonis	X	X	X	X		
Macaca sylvanus florentinus	X	X	X	X		
Canis ex gr. C. etruscus	X	X	X	X		
Sus strozzi	X	X	X	X	?	
Lynx issiodorensis		X	X	X	?	
Vulpes cf. V. alopecoides	X	X	X		X	
Megantereon cultridens - M. whitei		X	X		X	
Homotherium ex gr. H. crenatidens		X	X	X	X	
Mammuthus meridionalis	X	X	X	X	X	
Felis sylvestris lunensis		X				
Pseudodama nestii		X				
Eucladoceros dicranios- ctenoides		X	X			
Ursus etruscus		X	X	X	?	
Pachycrocuta brevirostris		X	X	X	X	
Pantera ex gr. P. gombaszoegensis		X	X	X	X	
Canis arvensis		?	X	X		
Martes sp.			X			
Praeovibos sp.			X			
Pannonictis nestii			X	X		
Lycaon falconeri			X	X		
Equus stehlini			X	X		
Leptobos ex gr. L. vallisarni			X	X		
Cervalces gallicus			X	X	?	
Pseudodama eurygonos- farnetensis			X	X	X	
Equus altidens			X	X	X	
Praemegaceros obscurus				X		
Stephanorhinus cf. S. hundsheimensis				X	X	
Megalovis sp. (= Ovibovini indet.)					X	
Canis aff. C. arvensis (advanced)					X	
Lycaon lycaonoides					X	
Bison (Eobison) degiulii					X	
Ursus sp.					?	
Hippopotamus ex gr. H. antiquus			?		X	
Equus gr.bressanus- sussenbornensis					X	

Fig. 6. Distribution pattern of large-mammalian faunal units and taxa of the Middle and Late Villafranchian Mammal Age in the Italian peninsula. The correlation with small-mammal biochronological units is also indicated. The Pliocene–Pleistocene boundary is according to Aguirre and Pasini (1985). Explanations of symbols as in Fig. 3.

malezi and *Dinaromys dalmatinus* indicate the affinity of the northern eastern Italian areas with the Balkan province (Fig. 7).

The faunal composition of the following Farneta FU (i.e. at the localities of Cava Liberatori and Pietrafitta; Fig. 5) is similar to that of Tasso, but it records two important new occurrences: that of the megalocerine group, with the species *Praemegaceros* (= *Megaceroidea*) *obscurus* (Abbazzi, 2004), and of the rhinocerotid *Stephanorhinus* cf. *hundsheimensis* (Alberdi et al., 1998; Zucchetta et al., 2003). At the same time many Villafranchian taxa are recorded for the last time in this unit. The occurrence of *Microtus (Allophaiomys) ex gr. ruffoi*, *Microtus (Allophaiomys) chalinei* and *M. pusillus* at Pietrafitta (Gentili et al., 1996) provide direct correlation of the unit with the Early Biharian (Figs. 1, 5–7).

The Cava Pirro assemblage indicates a further episode of faunal renewal and represents the last faunal unit of the Late Villafranchian, Pirro FU (De Giuli et al., 1987; Gliozzi et al., 1997) (Fig. 5). The most important find is the occurrence of a primitive bison (*Bison (Eobison) degiulii*), but also the occurrence of *Lycaon lycaonoides* (Martinez Navarro and Rook, 2003), and the spread of *Hippopotamus*, are worth mentioning (Fig. 6). Among the small mammals, the presence of *M. (Allophaiomys) ex gr. ruffoi*, with a more derived enamel differentiation pattern than that of Pietrafitta, is significant (Masini and Santini, 1991; Lippi et al., 1998). The Pirro FU also includes new insectivore taxa and the last find of the genus *Hypolaqus* in Italy. The assemblage from the Soave Cava Sud, the type locality of *Allophaiomys ruffoi* is included in this unit (Figs. 5–7).

Large mammal Ages	M.VILL.		LATE VILLAFRANCHIAN			
	Faunal units	C.S.Giacomo	Olivola	Tasso	Farneta	Pirro
Small mammal Ages	late VILLANYIAN			BIHARIAN		
Small mammal zones	<i>M. pliocaenicus</i> zone			Early Biharian I		
TAXA	Rivoli V. Montagnola S. Toppetti Quarry	Castelfranco Casa Sgherri	Tasso M. La Mesa	Petrafitta	Pirro Soave Cava sud	
Sciuroptera indet.	X					
Apodemus mystacinus	X					
Ungaromys dehmi	X					
Villanyia cfr. V. exilis	X					
Dinaromys allegranzi	X					
Castor sp	X	X				
Muscardinus sp	X	X				
Apodemus dominans	X	X				
Mimomys pliocaenicus	X	X				
Mimomys pitymyoides	X					
Hystrix refossa	X		X			
Sciurus warthae	X		X			
Mimomys tornensis	X		?			
Glis minor	X		?			
Glis sp.		X				
Mimomys medasensis		X				
Mimomys ostramosensis		X	cf.			
Mimomys pusillus - M.blanci		X	X	X		
Apodemus atavus			X			
Alloccitcus ehiki			X			
Mimomys malezi			X			
Muscardinus dacicus			cf.			
M. (Allophaiomys) pliocaenicus			X			
Glis sackdillingensis			X			X
Mimomys savini			X			X
Dinaromys dalmatinus			X			
Pliomys episcopalis			X			
Alloccitcus bursae			X			
Castor fiber			X			X
Clethrionomys sp			X			X
Microtus (Allophaiomys) chalinei				X		
M.(Allophaiomys) cfr. M. (A.) ruffoi				X		
M. (Allophaiomys) ruffoi						X
Eliomys sp						X
Apodemus flavicollis						X
Apodemus gr. A. sylvaticus - flavicollis						X
Muscardinus avellanarius						cf.

Fig. 7. Distribution pattern of rodent taxa of the Late Villanyian and Early Biharian Mammal Ages in the Italian peninsula. The correlation with large-mammal biochronological units is also indicated. The Pliocene–Pleistocene boundary is according to Aguirre and Pasini (1985). Explanations of symbols as in Fig. 3.

The Monte la Mesa, Pietrafitta (Farneta), Cava Pirro, and Soave Cava Sud faunas are characterised by primitive *Microtus (Allophaiomys)* species. They represent a Late Biharian succession that is distinct from the subsequent small mammal faunas, in which *Microtus (Allophaiomys)* species with more evolved features occur. This older part of the Early Biharian is shown as ‘Early Biharian I’ in Figs. 1, 6–9.

The Tasso, Farneta, and Pirro FU record the Pleistocene part of the Late Villafranchian, an interval during which the faunas were gradually and still not completely displaced by the large mammals that characterise the following Galerian Mammal Age.

4. The transition to glacial climates: Galerian, Late Biharian, and Early Toringian

The climatic deterioration that began in the Middle Pliocene progressively depleted the flora. The rapid climatic alternation (41 ka cycles) between moist and arid phases roughly corresponds to an alternation between vegetational assemblages of warm-temperate deciduous

forests and vegetational assemblages of steppe and/or conifer forest (Bertini, 2003). The onset of the 100 ka driven climatic fluctuations produced a more substantial variation, where xeric, cool to cold steppe vegetation alternates with deciduous forests (Bertini, 2003). A marked latitudinal cline, with predominant drier conditions in the southern part of the peninsula is also present, the regions east of the Apennines being drier than those on the western side (Sala, 2003).

The Colle Curti fauna (Central Apennine; Ficarelli and Silvestrini, 1991; Abbazzi et al., 1998; Martinez Navarro and Rook, 2003; Gentili and Masini, 2005) represents the first faunal unit of the Galerian Mammal Age (Fig. 5). This fauna, characterised by the dominant occurrence of *Hippopotamus*, records the first finds of the megalocerine *Praemegaceros (= Megaceroides) verticornis*, and of *Bison (Bison)*. Only two species of Arvicolid are present at Colle Curti, *Pliomys lenki*, which is its first occurrence in Italy, and *Microtus (Allophaiomys) sp.* The latter vole is characterised by a simple ACC morphology, fully comparable to *M. (Allophaiomys) pliocaenicus* and *M. (Allophaiomys) ruffoi*, together with an advanced,

microtine-differentiated enamel (cf. also Markova, 2004). This fauna has been assigned to the Jaramillo Subchron (Torre et al., 1996; Coltorti et al., 1998) (Figs. 1, 8, and 9).

The most important small-mammal locality correlated with Colle Curti is Monte Peglia (Umbria; Fig. 5) where *Microtus (Allophaiomys) burgondiae*, *Microtus (Allophaiomys) nutiensis*, *M. savini*, *Mimomys blanci* (a species strictly related to *M. pusillus*) and *Ungaromys nanus* occur (van der Meulen, 1973; Maul et al., 1998). The recent find of a small-mammal assemblage with a fully comparable

composition to that from Monte Peglia is the locality of Castagnone (Piedmont; Fig. 5). It is normally magnetised and is referred to the Jaramillo Subchron (Giraudi et al., 2003). Castagnone allows a stronger chronological correlation of the Monte Peglia fauna and confirms the correlation of the Colle Curti FU with the upper part of the Early Biharian (Figs. 1, 8, and 9).

The Colle Curti FU and the later part of Early Biharian, as defined above, correspond to the beginning of the most important faunal change of the Pleistocene. During this

Large mammal Ages	L. VILLAFR.		GALERIAN			
	Faunal units		Colle Curti	Slivia	Isernia	Fontana Ranuccio
Small mammal Ages	E. B. I		BIHARIAN		TORINGIAN	
Small mammal zones	<i>M. savini</i> - <i>M. pusillus</i>		E. B. II	Late Biharian	Early Toringian	
	<i>M. savini</i> - <i>M. pusillus</i>		<i>M. savini</i>		<i>A. mosbachensis</i>	
TAXA	Pirro F.U. several localities	Colle Curti F.U. several localities	Slivia F.U. several localities	Isernia F.U. several localities	Fontana Ranuccio F.U. several localities	
<i>Cervalces gallicus</i>	?					
<i>Lynx issiodorensis</i>	X					
<i>Megantereon cultridens</i> - <i>M. whitei</i>	X					
<i>Vulpes</i> cf. <i>V. alopecoides</i>	X					
<i>Megalovis</i> sp. (= <i>Ovibovini</i> indet.)	X					
<i>Homotherium</i> ex gr. <i>H. crenatidens</i>	X	X				
<i>Canis</i> aff. <i>C. arnensis</i> (advanced form)	X	X				
<i>Lycyon lycaonoides</i>	X	sp				
<i>Bison</i> (<i>Eobison</i>) <i>degiulii</i>	X	X				
<i>Ursus</i> sp.	?	X				
<i>Stephanorhinus</i> cf. <i>S. hunsheimensis</i>	X	X				
<i>Mammuthus meridionalis</i>	X	X				
<i>Pachycrocuta brevirostris</i>	X		X			
<i>Pantera</i> ex gr. <i>P. gombaszoegensis</i>	X	X	X			
<i>Pseudodama farnetensis</i>	X	X	X	?		
<i>Equus altidens</i>	X	X	X	X	X	
<i>Equus</i> ex gr. <i>bressanus</i> - <i>sussenbornensis</i>	X	X	X	X	X	
<i>Hippopotamus</i> ex gr. <i>H. antiquus</i>	X	X	X	X	?	
<i>Bison</i> aff. <i>B. schoetensacki</i>		X				
<i>Praemegaceros verticornis</i>		X	X			
<i>Megacerini</i> gen et sp. indet		X	X	X	?	
"Hemibos" <i>galerianus</i>			X			
<i>Megaloceros savinii</i>			X			
<i>Homotherium</i> ex gr <i>H. latidens</i>			X	X		
<i>Ursus deningeri</i>			X	X		
<i>Mammuthus trogontherii</i>			X	X		
<i>Bison schoetensacki</i>			X	X	X	
<i>Stephanorhinus hundsheimensis</i>			X	X	X	
<i>Elephas antiquus</i>			X	X	X	
<i>Stephanorhinus hemithoechus</i>			X	X	X	
<i>Canis arnensis</i> / aff. <i>mosbachensis</i>			X	X	X	
<i>Sus scrofa</i>			X	X	X	
<i>Cervus elaphus</i>			X	X	X	
<i>Stephanorhinus kirchbergensis</i>			cf.	cf.	X	
<i>Meles meles</i>			cf.		X	
<i>Dama clactoniana</i>			?	X	X	
<i>Praemegaceros solhilacus</i>			?	X	X	
<i>Lynx</i> sp.			?	X	X	
<i>Capreolus</i> sp				X		
" <i>Hyaena prisca</i> "				X		
<i>Ovis ammon</i>				X		
<i>Hemitragus bonali</i>				X		
<i>Panthera leo fossilis</i>				X	X	
<i>Macaca sylvanus sylvanus</i>				X	X	
<i>Panthera pardus</i>				X	X	
<i>Crocuta crocuta</i>				X	X	
<i>Bos primigenus</i>				X	X	
<i>Equus ferus</i>				?	X	
<i>Hippopotamus</i> ex gr. <i>H. amphibius</i>					X	
<i>Martes martes</i>					X	
<i>Vulpes vulpes</i>					X	
<i>Felis silvestris silvestris</i>					X	
<i>Capreolus capreolus</i>					X	
<i>Ursus arctos</i>					?	

Early - Middle Pleistocene Boundary →

Fig. 8. Distribution pattern of large-mammalian faunal units and taxa of the late part of the Late Villafranchian and the Galerian Mammal Ages in the Italian peninsula. The correlation with small-mammal biochronological units is also indicated. Early–Middle Pleistocene boundary according to Richmond (1996). Explanations of symbols as in Fig. 3.

Large mammal Ages	L. VILLAGR.		GALERIAN		
	Pirro	Colle Curti	Slivia	Isernia	Fontana Ranuccio
Faunal units					
Small mammal Ages	BIHARIAN		TORINGIAN		
Small mammal zones	E.B. I	E. B. II	Late Biharian	Early Toringian	
	<i>M.savini</i> - <i>M.pusillus</i>		<i>M.savini</i>	<i>A. mosbachensis</i>	
TAXA	Pirro Soave Cava sud	Colle Curti Monte Peglia Castagnone	Slivia Rifreddo Fontignano	Isernia Venosa	Valdemino Visogliano
<i>Glis sackdillingensis</i>	x				
<i>Microtus (Allophaiomys) ruffoi</i>	x				
<i>Eliomys</i> sp.	x				
<i>Mimomys pusillus</i> - <i>M.blanci</i>	x	x			
<i>Mimomys savini</i>	x	x	x		
<i>Dinaromys dalmatinus</i>					cf
<i>Pliomys episcopalis</i>		x	x		x
<i>Allocricetus bursae</i>			x		x
<i>Castor fiber</i>			x		x
<i>Clethrionomys</i> sp.	x				x
<i>Apodemus flavicollis</i>	x				
<i>Apodemus</i> gr. <i>A. sylvaticus</i> – <i>A. flavicollis</i>	x				x
<i>Muscardinus avellanarius</i>	cf				x
<i>Sciurus</i> sp.		x			
<i>Apodemus</i> cfr. <i>A. maastrichtensis</i>		x			
<i>Ungaromys nanus</i>		x			
<i>Microtus (Allophaiomys) nutiensis</i>		x			
<i>Microtus (Allophaiomys) burgondiae</i>		x			
<i>Microtus (Allophaiomys) sp.</i>		x			
<i>Glirulus</i> sp.		x			
<i>Apodemus</i> sp.		x			x
<i>Apodemus sylvaticus</i>		cf			x
<i>Pliomys lenki</i>		x			x
<i>Prolagus pannonicus</i>			x		
<i>Predicrostonyx</i> sp.			x		
<i>Dinaromys</i> sp.			x		
<i>Microtus (Neodon) gregaloides</i>			x		
<i>Microtus (Microtus) sp.</i>			x		
<i>M. (Iberomys) ex gr. huescarensis brecciensis</i>			x		
<i>Microtus (Terricola) arvalidens</i>			x		x
<i>Terricola</i> sp.			x		x
<i>Spermophilus</i> sp.					x
<i>Apodemus microps</i>					cf.
<i>Terricola thomasi</i>					aff
<i>Microtus arvalinus</i>					x
<i>Arvicola mosbachensis</i>					x
<i>Cricetus cricetus</i>					x
<i>Clethrionomys glareolus</i>					x
<i>Dinaromys</i> cf. <i>bogdanovi</i>					x
<i>Chionomys nivalis</i>					x
<i>Terricola</i> gr. <i>T. multiplex</i> – <i>T. subterraneus</i>					x
<i>Terricola</i> ex gr. <i>savii</i>					x
<i>Microtus (Iberomys) brecciensis</i>					x
<i>Microtus</i> ex gr. <i>arvalis-agrestis</i>					x
<i>Microtus (Stenocranius) gregalis</i>					x
<i>Glis glis</i>					cf

Fig. 9. Distribution pattern of rodent taxa of the Early to Late Biharian and Early Torinigan Mammal Ages in the Italian peninsula. The correlation with large-mammal biochronological units is also indicated. Early–Middle Pleistocene boundary according to Richmond (1996). Explanations of symbols as in Fig. 3.

renewal, the Villafranchian taxa became extinct, or in some cases gave rise to new species more adapted to arid, cold climates. Here, the Galerian forms appear together with some of the direct ancestors of the ‘modern’ faunal elements through a sequence of dispersal events (Figs. 8 and 9).

Colle Curti and the subsequent Slivia FU (Ambrosetti et al., 1979; Gliozzi et al., 1997) occur within the interval that apparently corresponds to the long transition between climates forced by the 41 ka cycles and the later ‘glacial’ climate characterised by the alternation of pronounced glacial–interglacial periods modulated by the 100 ka periodicity (Shackleton, 1995) (Fig. 1).

The strong fluctuations observed in the North Atlantic marine isotope record between Marine Isotope Stage (MIS) 25 and MIS 22 possibly represents a type of critical

transition zone between the two climatic systems. The repeated climate oscillations changed the structure of the vegetational composition, and consequently also modified the structure of the faunal assemblages. Since this time, the faunal renewal apparently became more rapid with the dispersals of taxa with warm-humid and cold-steppe affinities during interglacial and glacial events, respectively. This process established a new assemblage of resident taxa, many of which disappeared during the extinction phase of the last glacial cycle (Weichselian, Würmian) or persist into the Holocene.

At the same time, the peninsula starts to play a more important role as a refuge area for temperate taxa during stadial phases, resulting in an increased faunal diversity. Finally, the climatic subdivision into two main zones, the Western Ligurian–Tyrrhenian and the Eastern Adriatic

becomes more apparent. The southern peninsula possibly formed a third zone but it is still poorly defined.

Within the Slivia and the following Isernia faunal units the most important large-mammals events are: the spread of slender bison, *Bison schoetensacki*, of archaic forms of several recent species, such as the roe deer (*Capreolus* sp.), red deer (*Cervus elaphus acoronatus*), spotted hyaena (*Crocuta crocuta*, Ponte Galeria 2; Milli and Palombo, 2005), lion (*Panthera leo fossilis*), leopard *Panthera pardus* (Valdemino Cave, Liguria; Sala, 1992) and fallow deer (*Dama clactoniana*); and eventually of extinct species such as a primitive water buffalo (*Hemibos galerianus*; in Martinez Navarro and Palombo, 2004), the giant deer *Praemegaceros solihachus* (Abbazzi, 2004), the steppe elephant (*Mammuthus trogontherii*), the straight-tusked elephant (*Elephas antiquus*) the Merk's rhinoceros (*Stephanorhinus kirchbergensis*), and Deninger's bear (*Ursus deningeri*) (Figs. 8 and 9).

The Slivia FU correlates directly with the Late Biharian based on the occurrence of *Microtus* (*Stenocranius*) and *Microtus* (*Terricola*), associated with *M. savini*. The Rifreddo locality in the San Lorenzo succession (Sant'Arcangelo Basin, Basilicata; Masini et al., 2005; Sabato et al., 2005; Fig. 5) has yielded a slightly younger small-mammal fauna, equated to the early part of Brunhes Chron (Sabato et al., 2005), which records the first occurrence of *Microtus* (*Iberomys*), a taxon that persisted into the Late Middle Pleistocene in Southern Italy, and of *Microtus* (*Terricola*) *arvalidens* (Fig. 9).

The archaeological site Isernia La Pineta (Molise; Fig. 5), which is the type locality of the Isernia FU, has yielded the Oldest Toringian fauna in Italy, in which, however, the 'marker' vole *Arvicola mosbachensis* still retains a small percentage of molars with incipient roots. Important large-mammal taxa present include *Praemegaceros* (= *Megacerooides*) *solihachus*, the thar *Hemitragus bonali*, *D. clactoniana* and *Capreolus* sp., while significant small-mammal taxa include: *Pliomys episcopalis*, *Pliomys lenki*, *Microtus* aff. *arvalis*, *Microtus* (*Iberomys*) *brecciensis* and *M. (Terricola)* ex gr. *multiplex-subterraneus* (Sala, 1996a; Koenigswald and van Kolfschoten, 1996). The Grotta Valdemino fauna (Liguria; Fig. 5) is a good example of a 'warm assemblage' of the Early Toringian in which a dominant small-sized *M. (Iberomys)* *brecciensis* is associated to *Microtus* (*Terricola*) sp. (Sala, 1992; Nocchi and Sala, 1997). The thick archaeological sequence of Visogliano Shelter (Carso Triestino, Friuli Venezia Giulia; Fig. 5) in which a warm to cool climatic fluctuation is recorded, has yielded a typical *A. mosbachensis* and represents a Middle–Late Galerian assemblage. In this site skeletal remains referred to 'archaic' *Homo sapiens* have also been recovered (Abbazzi et al., 2000). Here, the whole stratigraphical sequence is dominated by *Microtus* cf. *arvalinus*, the endemic vole *Dinaromys* cf. *bogdanovi* and the red deer *C. elaphus acoronatus*. *Crociodura*, *M. (Terricola)* cf. *arvalidens*, *Macaca*, and fairly abundant Clacton fallow deer *D. clactoniana* occur in the temperate

climate lower levels (Abbazzi et al., 2000). Significant occurrences within the upper cooler climate levels are those of the tundra vole *Microtus* (*Stenocranius*) *gregalis*, the pika *Ochotona* sp., the suslik *Spermophilus* sp., and the argali *Ovis ammon* (Figs. 8 and 9).

During the interval spanning from Colle Curti-Monte Peglia to Isernia, the evolutionary radiation of genus *Microtus* (*sensu lato*) became evident in the fossil record. Starting with diversified *Microtus* (*Allophahiomys*) species, this genus, with his sub-generic branches, became dominant among voles in the Italian faunal assemblages. Meanwhile, the rooted arvicolids become rare and progressively disappear except for *Clethrionomys* and *Dinaromys*; the latter still surviving in a restricted area of the Balkans. The last extinction event is that of *P. lenki* at the beginning of the Late Pleistocene (MIS 5e; see Gibbard and van Kolfschoten, 2004, for a discussion on this chronostratigraphical boundary).

The greatest number of new occurrences of large mammals is reported at Slivia FU (Fig. 8), while the greater renewal impulse for small mammals corresponds to the Isernia FU (Fig. 9). This shift in first occurrences could be due to the limited representation (only two significant localities, Slivia and Rifreddo) of Late Biharian small-mammal faunas, while the Slivia FU includes several finds of large mammals from Ponte Galeria (Ponte Galeria 2; Petronio and Sardella, 1999; Milli et al., 2004; Milli and Palombo, 2005).

Concerning the Early–Middle Pleistocene boundary, during the last years several proposals have been presented (i.e. Ruggieri et al., 1984; Cita and Castradori, 1994; Capraro et al., 2004; Ciaranfi and D'Alessandro, 2005). Nowadays, as mentioned in the Introduction, the proposal of Richmond (1996) has acquired more approval.

From what has been previously reported on the biochronological patterns of small and large mammals in Italy, the Early Middle Pleistocene boundary is placed within the Late Biharian for small mammals, and within the Slivia FU for large mammals (Figs. 1, 8 and 9). However, a boundary placed close to MIS 25 would be more precisely approximated by faunal patterns, since it would roughly coincide with the transitions from the Early to the Late Biharian and from the Colle Curti to the Slivia faunal units, for small and large mammals, respectively.

5. Post-Galerian

At the end of the Galerian, possibly c. 0.4–0.3 ma, many taxa that characterise this Mammal Age disappear and the recent mammalian assemblage begins. The Post-Galerian (Aurelian; in Gliozzi et al., 1997) represents the later part of the Middle Pleistocene and the Late Pleistocene during which the strongest climatic fluctuations occurred, probably corresponding to MIS 10–MIS 2 (Fig. 1). The Post-Galerian fauna, however, is depleted by several terminal extinction events of very large taxa (the woolly mammoth, the woolly rhinoceros, the giant deer, several large

carnivores). These extinctions occurred mainly during the Würmian Stage, as a response to climatic effects and, according to some authors, human action. During the Holocene, the spread of human cultures in the Mediterranean regions from the Neolithic Period onwards caused modifications of the environment, influenced the dispersal patterns and greatly changed the natural assemblages by the introduction of exotic species.

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