Plio-Pleistocene biogeography of Italian mainland micromammals

INTRODUCTION

Many Italian fossil mammals of Plio-Pleistocene age are known and several localities of the Italian peninsula are famous among vertebrate paleontologists. However, till the Second World War the number of fossil remains of small mammals was very low. A few paleontologists (C.I. Forsyth Major, A. De Gregorio, C. Bosco, R. Fabiani & D.M.A. Bate) illustrated remains of rodents and insectivores (especially from the islands) but only large-sized ‘micromammals’ such as Marmota, Castor, Hystrix and lagomorphs, easier to discover during excavations, have been carefully studied. After the World War 2, the works of A. Pasa and G. Bartolomei illustrated for the first time the rich micromammalian Quaternary faunas of north-eastern Italy. During the last decades of the 20th century an increasing number of researchers followed the first pioneers.

Italian micromammalian assemblages are...
mainly found in Pleistocene deposits. Nevertheless, Neogene remains are very important for paleobiogeographical reconstruction of Italian bioprovinces. During Late Miocene, mammalian evidences point out the presence of three different sub-provinces: the Apulia-Abruzzi, the Sardinia-Tuscany (both with strong endemic character) and the Calabrian-Sicilian subprovince (with evident African affinities; Torre et al. 2000). Only since the latest Miocene Italy has firm contacts with the rest of Europe, as testified by the presence of several immigrated taxa (most of them from eastern Europe, and a few elements from western Europe; Kotsakis et al. 1997).

Italian Pliocene micromammalian fossil assemblages are very few and very unbalanced from a geochronological point of view. Remains of Ruscinian age are almost unknown from the Italian mainland (this also applies to macromammals), whilst fossils of Villányian age (Fig. 1) are relatively few, but sufficient for a paleobiogeographical analysis. The number of Biharian fossiliferous sites bearing small mammals is quite low too and only Toringian assemblages are abundant, even if not well distributed in the Peninsula (Fig. 2).

In the present paper we examine micromammalian assemblages of the Italian mainland, excluding endemic assemblages from Sicily, Sardinia, smaller islands and paleoislands of the Gargano Archipelago because of their peculiar problems. Among fossil assemblages we chose to examine just the recently described or re-examined ones and chose to ignore isolated remains (if not important for paleobiogeography). Fossiliferous sites are correlated with MN unites (Mein 1990) for the Villányian, with zones of Fejfar & Heinrich (1990) and also with the Faunal Units (F.U.) succession system proposed by Azzaroli (1977) and emended by Gliozzi et al. (1997), a system accepted by all the Italian paleontologists working on continental Plio-Pleistocene fossil animals, both vertebrates and invertebrates. The locality list, containing faunal lists of small mammals and the bibliographical references are reported in chronological order in the Appendix. A systematic revision or a study of biochronological succession of several groups of Italian fossil micromammals is a topic of some general papers followed in this publication: Chaline (1977), Bartolomei (1980), Masini & Torre (1987), Kotsakis (1988), Bon et al. (1991), Brunet-Lecomte et al. (1994), Zanalda (1994a), Masini et al. (1996, 1998), Maul et al. (1998), Argenti (1999), Argenti & Kotsakis (1999), Fanfani (2000), Marcolini (2002). In the biochronological charts the position of some localities is approximate and their chronological attribution is not certain.

**RUSCINIAN**

Only a single rodent tooth (M/1), collected in an ?early Middle Pliocene (Lina Barbera pers. comm.), brackish-marine deposit near Ariano Irpino (Campania, southern Italy) has been found. This molar has been attributed to a murid, *Centralomys* sp. (T. Kotsakis & P. Argenti unpublished data). The genus is known from the late Turolian site of Brisighella (Emilia-Romagna, northern Italy) with the type species *Centralomys benericettii* (De Giuli) (De Giuli 1989). The age of the brackish-marine sediments of Ariano Irpino ought to correspond to the uppermost part of MN 15 unit. The more advanced faunas from the Gargano Archipelago (Apulia, southern Italy) fossil islands (where many micromammalian endemic lineages evolved) have been assigned to the latest phases of Miocene and/or to the earliest phases of Pliocene (Abbazzi et al. 1998). A discussion of the affinities of these endemic faunas is not a topic of the present work.

A migration from the European mainland to Sardinia near the Zanclean-Piacenzian boundary, corresponding to the uppermost part of MN 15 unit (Angelone & Kotsakis 2000, 2001), is suggested in recent works. Such a migration very probably followed an Italian-Corsican route but no fossil evidence of the ancestors of Sardinian *Prolagus* and *Rhaga-
podemus (known in southern France) has been found in Italy till now.

**EARLY VILLÁNYIAN (Fig. 3)**

Cascina Arondelli in the Triversa Valley (Piedmont, north-western Italy) is a famous Italian site of Early Villányian age. An assemblage of insectivores, lagomorphs and rodents has been described from this site. This fauna, assigned to MN 16a by Mein (1990) or to the *Mimomys hassiacus* (= *Mimomys hajnackensis* see Mörs et al. 1998) + *Mimomys stehlini* zone by Fejfar & Heinrich (1990) and Fejfar *et al.* (1998), has been collected in a sequence of mudstones, clays and fine-grained sandstones. The two rodent species collected in the fluvio-lacustrine sediments of Fornace RDB (Piedmont, north-western Italy) belong to taxa also present at Arondelli. Azzaroli (1977) formalised the Triversa F.U. as a unique fossil assemblage of small mammals (collected in Cascina...
Arondelli) and large mammals (collected in Fornace RDB). After Lindsay et al. (1997) the age of macromammals from Fornace RDB is older than that of the micromammals from Arondelli. For this reason they assigned the large mammals of Fornace RDB (the classical Villafranchian fauna) to MN 15. For the moment there is no paleontological support to the opinion of Lindsay et al. (1997).

Micrommamals of these assemblages belong to species of large European distribution. Similar taxa of insectivores and also rodents are present at Arcille (small sequence of clays and lignite) and San Giusto (marine-brackish

![Figure 2. Biochronology of Biharian and selected Toringian sites of Italy with micromammals. In bold character recently studied localities with relevant micromammalian remains. The chronological position of some localities is approximate.](image-url)
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Figure 3  Distribution of micromammals in Italy during Early Villányian. Arondelli - a) Apodemus alsomyoides; b) Mimomys stehlini; c) Mimomys hassiacus. S. Giusto - d) Mimomys stehlini. Arcille - e) Prologus sp.

Figure 4  Distribution of micromammals in Italy during Late Villányian. Rivoli Veronese - a) Dinomys allegranzii; b) cf. Ellobius sp.; c) Mimomys pitymyoides. Montagnola Senese - d) Mimomys pitymyoides; e) Apodemus mystacinus. Torre di Picchio - f) Prologus sp.; g) Mimomys medasensis.

sediments) (type-locality of Mimomys (Cseria) stehlini), both in Tuscany (central Italy). The age of the two localities is the same as Arondelli. The limited evidences support the existence of a common fauna in the western part of the Peninsula. A large vole, probably belonging to Mimomys polonicus was collected many years ago in the clays of Bocchignano (Latium, central Italy). The same species of arvicolid has been discovered in Upper Valdarno (Tuscany, central Italy) (Abbazzi, unpublished data). No other discoveries of small mammals corresponding to the Montopoli F.U. have been made. Unfortunately the extremely scanty remains of micromammals belonging to MN 16b or the Mimomys polonicus zone of Fejfar & Heinrich (1990) make impossible any paleobiogeographical consideration.

LATE VILLÁNYIAN (Fig. 4)

Three successive F.U.’s have been assigned to the Late Villányian (Azzaroli 1977, Gliozzi et al. 1997): Saint Villard F.U., Costa San Giacomo F.U. and Olivola F.U. Small mammals belonging to Saint Villard F.U. have not been found in Italy yet. A rich micromammalian fauna has been collected in a karst fissure near Rivoli Veronese (Veneto, north-eastern Italy). This assemblage is Late Villányian in age, and must be assigned to MN 17, to the Mimomys plioacaenicus zone of Fejfar & Heinrich (1990), or to Costa San Giacomo F.U. following Gliozzi et al. (1997). Many insectivores or rodents have a large European distribution (many of them have been described for the first time from Polish or Hungarian sites) but two elements are of particular interest: Dinomys allegranzii and cf. Ellobius sp. (on the systematic position of
the last species see contrasting opinions in Sala et al. 1994 and Tesakov 1998). The first arvicolid is the older species of the genus, living today in the Dalmatian area. Its past distribution ranged from eastern Europe (Ukraine) to northern Italy through the Balkan peninsula (Sala 1996a). The second arvicolid genus is now present from Ukraine and eastern Turkey to Pakistan and Mongolia. Its presence in Europe must be assigned after Tesakov (1998) to the latest part of the Late Pliocene. At the beginning of Middle Pleistocene it reached the Maghreb (Jaeger 1988). The presence of two oriental elements at Rivoli demonstrates affinities of northeastern Italy with eastern Europe and Balkans during the Late Villányian. Some isolated remains of the same age (Costa San Giacomo F.U.) are known from a few sites of central Italy but they belong to taxa with very large distribution.

The last F.U. of the Villányian is Olivola F.U.; some assemblages with large mammals have been assigned to it, but small mammals are very rare. Among the sites ascribed to the same F.U. (all from Tuscany and Umbria, central Italy) should be mentioned Castelfranco di Sopra (lacustrine clays and sands; Upper Valdarno), type locality of Mimomys pliocaeicus.

Fossil assemblages coming from three central Italian localities, the karstic fissure of Montagnola Senese (Tuscany), the fluvial deposit of Casa Sgherri (Tuscany) and the fluvio-lacustrine clays and sands of Torre di Picchio (Umbria) have been assigned to the Late Villányian, to a more recent phase than Costa San Giacomo F.U. The soricid Crocidura appears in Italy for the first time. This African genus reaches Europe through the Levant-Anatolian-Balkan area (Fanfani 2000). The murid Apodemus mystacinus, a species of Mediterranean distribution, now living in part of the Balkan peninsula, Anatolia and Levant is also present at Montagnola Senese. The origin of this taxon has been claimed from both Iberian and Balkan peninsulas. An oriental origin is possible but for the moment the most ancient records of the species are located in Iberian and Italian peninsulas and southern France (latest Villányian). The reduction of its distribution area is very probably due to the strong Middle Pleistocene climatic changes (Argenti et al. 2000). An Iberian element (sensu Michaux 1982), Mimomys medasensis, is present at Torre di Picchio. This arvicolid is known from late Villányian sites of the Iberian peninsula (Agustí 1990). The presence of Prolagus sp. in two of these sites (Montagnola Senese and Torre di Picchio) is also interesting. The genus has a large European distribution during the Miocene, but during the Pliocene its distribution is more restricted; at the end of the Pliocene it is reduced to western Europe with relict populations farther east. A molossid bat of the genus Tadarida very close to the living species Tadarida teniotis is present at Montagnola Senese. This typical Mediterranean species of African origin is known in the northern board of the Mediterranean till the late Turolian (Legendre 1985).

**EARLY BIHARIAN (Figs. 5, 6)**

There is a good number of Early Biharian micromammalian fossiliferous sites, but very few of them yield species-rich assemblages. Usually only one or two species of small mammals are present. Four F.U.’s correspond to the Early Biharian: Tasso F.U., Farneta F.U., Pirro F.U. and Colle Curti F.U.

The oldest Biharian assemblage, belonging to Mimomys pusillus + Mimomys savini zone of Fejfar & Heinrich (1990), comes from Monte La Mesa (Veneto, north-eastern Italy). A very rich assemblage of small mammals has been collected in this karstic site (Marchetti et al. 2000). The greatest part of the species has a large European distribution but some of them are more common in central-eastern Europe. In this site Microtus (Allophaiomys) makes its first occurrence in Italy. This arvicolid first appeared in localities of central-eastern Europe of slightly older
age (Microtus (Allophaiomys) deucalion in Villány 5, Janossy 1986). The genus Dinaromys is present with the species Dinaromys dalmatinus known from the Dalmatian area and north-eastern Italy. The murid Apodemus atavus is known from a few sites of central Europe and from Anatolia (Argenti 1999). All these elements indicate marked affinities between this area, the Balkans and central-oriental Europe.

Many faunas collected in central Italy (Tuscany, Umbria and Latium) are assigned to Early Biharian (Tasso F.U.) but they contain a few small mammals and all but one, rather big elements (Castor, Hystrix and lagomorphs). No elements in common with Monte La Mesa are present in these sites. This fact is probably due to ecological rather than biogeographical differences. In fact the fossils found in localities of central Italy have been collected in fluvio-lacustrine deposits whilst the assemblage of Monte La Mesa comes from a karstic fissure. Among lagomorphs the genus Prolagus is present for the last time in Italian mainland (cf. Rook & Masini 1990). The assemblage collected in the succession of clays and lignite of Pietrafitta (Umbria, central Italy) belongs to the Farneta F.U. Among the small mammals of this locality (Gentili et al. 1996) the iberooccitanian arvicolid Microtus (Allophaiomys) chalinei is present. This species is also present in many sites of the same age of the Iberian peninsula (Agustí 1992). In the same assemblage Microtus (Allophaiomys) gr. M. (A.) ruffoi is present for the first time.
In the local fauna of Pirro Nord (typical fauna for the Pirro F.U.) and in the neighbouring local fauna of Cava dell’Erba, both collected in fissure fillings of Gargano promontory (Apulia, southern Italy), a good number of small mammals has been collected. They belong to species with large distribution. The soricid Asoriculus aff. A. theni is very similar to the typical form described on material discovered in Croatia but it is also present in some sites of western Europe (Fanfani 2000). A bat of the family Rhinolophidae, Rhinolophus birzebuggensis, known only from the older deposits of Ghar Dalam cave at Malta is also present. The small fauna collected in a breccia near Palena (Abruzzi, central Italy) (Kotsakis, unpublished data) is very similar to that of Pirro Nord. A third assemblage of the same age, also collected in a site of karstic origin, is that of Cava Sud (Veneto, north-eastern Italy). Microtus (Allophaiomys) ruffoi is a common element of the three localities; the other arvicolid species present in Cava Sud are absent from the southern localities. This fact reflects ecological rather than biogeographical differences. On the contrary the presence of a big species of the genus Crocidura, C. zorzii at Cava Sud and its absence from Pirro Nord, where two other species of the genus are present, is of greatest importance. C. zorzii is present for a long time-span in north-eastern Italy but it is only occasionally found in other Italian regions (Fanfani 2000).

In the small fossil assemblage collected in the clayey beds of a lacustrine deposit at Colle Curti (Marche, central Italy) (Abbazzi et al. 1998) the first Italian occurrence of the rhizodont arvicolid Pliomys lenki is reported. This assemblage is also characterized by the presence of a member of the subgenus Microtus (Allophaiomys) close to the beginning of the lineage leading to Microtus (Pallasinus) ratticepoides - M. (P.) oeconomus. The second site assigned to the Colle Curti F.U. is the very well known karstic deposit of Monte Peglia (Umbria, central Italy). Two different faunas have been collected in this site but they are chronologically very close (Van der Meulen 1973). The most advanced species of Microtus (Allophaiomys) are known from western Europe (Chaline 1972; Agustí 1992; Laplana et al. 2000), but also from Russia (Markova 1990). Mimomys blanci is known from western European sites of older age (Agustí 1992; but the records of the species from north-western Europe have been rejected by Tesakov 1998) whilst the genus Ungaromys is an element of central and eastern Europe (Rabeder 1981). Another element of western affinities is Apodemus cf. A. maastrichtiensis (cf. Argenti 1999).

In the ‘Helicella’ bearing clays of Fontignano (Ponte Galeria, Rome) two species of rodents have been collected. Surprisingly they belong to eastern species (Prolagurus pannonicus, and Predicrostonyx sp.) of cold ‘steppe’ environment not known from the sites of north-eastern Italy where the elements of oriental distribution are relatively common. Probably they testify a very short cold interval. The locality could be assigned to the upper part of the Early Biitarian or to the lower part of the Late Biitarian (Kotsakis et al. 1992; Barisone & Kotsakis 2001). Predicrostonyx is an arvicolid of north-eastern Asia and Alaska known also in eastern Europe (Nadachowski 1992). A similar form, Predicrostonyx antiquitatis is known from Les Valerots (France) (Chaline 1972).

**LATE BIHARIAN (Fig. 7)**

The faunas assigned to the Late Biitarian, corresponding to the Mimomys savini - Neodon gregaloides zone of Fejfar & Heinrich (1990) or to the Slivia F.U., are very few. In Slivia (Venezia Giulia, north-eastern Italy), in a fossiliferous breccia, both the characteristic species of the zone are present, as the Balkan element Dinaromys sp. Gliozi et al. (1997) assigned the Monte Tenda (Veneto, north-eastern Italy) assemblage, collected in a karstic deposit, to the same time interval. The first member of the subgenus Microtus (Microtus) appears in this site. Other assemblages collected in fissure-fil-
lings in the Soave region, Cengelle and Viatelle (Veneto, north-eastern Italy) and illustrated by Pasa (1947) and Bartolomei (1980) very probably belong to the same age, but these faunas are not homogeneous and include elements of different age.

The fauna collected in the clays and sands of Sant’Arcangelo (Lucania, southern Italy) must be assigned to the same period but to a slightly later stage. Perhaps this fauna corresponds to Ponte Galeria F.U., a new F.U. introduced by Petronio & Sardella (1999) between Slivia F.U. and Isernia F.U. In the Sant’Arcangelo assemblage a primitive member of the genus Terricola, Terricola cf. T. arvalidens is present. Another very remarkable element is Microtus (Iberomys) cf. M. (I.) brecciensis, of Iberian origin. This is the third appearance of an Iberocccitan rodent in Italy since the beginning of the Pliocene. The subgenus made its first appearance in the Iberian Peninsula a short time before (Cuenca Bescos et al. 1999). In this site the soricid Macronemys and Talpa cf. T. romana, a talpid very similar to the living endemic Italian species, appear for the first time (Fanfani 2000).

**EARLY TORINGIAN (Figs. 8, 9)**

Early Toringian faunas have been assigned to Arvicola cantianus zone by Heinrich & Fejfar (1990) and to Isernia F.U. and Fontana Ranuccio F.U. by Gliozzi et al. (1997). To the first F.U. have been assigned the assemblages collected in a paleosol in the type locality of Isernia (Molise, southern Italy) and in a cave in Borgo Verezzi (Valdemino, Liguria, north-
western Italy). At Isernia Arvicola cantianus first appears in Italy. After recent radiometric data the age of this site is younger than the one previously estimated (Coltorti et al. 1982, 2000). In both localities the Ibero-occitanian element Microtus (Iberomys) breccien-sis is present. The other elements have a large European distribution except for the leporid Oryctolagus burgi, only known from Borgio Verezzi (Nocchi & Sala 1997a, 1997b).

The assemblages from Riparo A of Visogliano (Venezia Giulia, north-eastern Italy) belong to a more recent phase of Early Toringian, between Isernia F.U. and Fontana Ranuccio F.U. The micromammals have been collected from strata of slightly different age. In this site many ‘cold’ and ‘cool’ elements such as the ochotonid Ochotona sp., the sciurid Citellus sp., the cricetid Crictetus cricetus and the arvicolids Microtus (Stenocranius) gregalis and Chionomys nivalis make their first occurrence in Italy. A Balkan element, Dinaromys bogdanovi, and the Italian endemic talpid Talpa romana, now living in central and southern Italy only, are also present. The ‘cold’ and ‘cool’ elements clearly arrived in the area from the east/north-east. All these species, except for Chionomys nivalis, lack from the assemblage of the same age collected in a fluvio-lacustrine basin at Venosa – Notarchirico (Lucania, southern Italy).

Many assemblages assigned to Fontana Ranuccio F.U. come from the same area: Boscochiesanuova (Veneto), San Giovanni di Duino (Venezia Giulia), Spessa II (Veneto) and San Vito di Leguzzano 2 (Veneto) are all karstic deposits located in north-eastern Italy. The big soricid Macronemys sp. and the Balkan arvicolid Dinaromys are characteristic elements of these faunas. At least for this period the presence of Dinaromys is testified in western Lombardy (north-western Italy) in the caves of Campo dei Fiori and Fontana Marella (lower levels). At Spessa II, the presence of Apodemus cf. A. microps is worth to be mentioned. This is a living form whose distribution is limited to central Europe; fossil remains have been reported from Germany and (very probably) Hungary in coeval sites (Koenigswald 1972; Argenti 1999).

In two different sites of central Italy, Cava Campani (paleosol - Tuscany) and Case Picconetto (paleosol - Abruzzi), radiometrically related with Fontana Ranuccio F.U., a primitive form of the lineage of the endemic Italian arvicolid Terricola savii makes its first appearance (Marcolini 2002). This ‘Mediterranean’ species is also present at San Giovanni di Duino. In Cava Campani another remarkable arvicolid is present: a big Terricola very similar to the living T. thomasi, an endemic species of western Balkan area. For the moment it is impossible to decide if the remains from Tuscany belong to an ancestral form of this species or to another lineage. In this latter case the similarity
would be due to convergence phenomena.

Monte del Cros (Piedmont), another north-western Italian assemblage, is of more difficult chronological attribution. The contemporaneous presence of *Pliomys episcopalis* and *Pliomys lenki* is characteristic of some Early Toringian assemblages but a Late Biharian age cannot be excluded. The paleobiogeographical interest of this site is due to the presence of a species of *Hystrix* that is smaller than the Villányian and Early Biharian *Hystrix refossa* (or *Hystrix etrusca* after other authors, see Azzaroli 1998). These remains very probably belong to the small eastern (and central) European species *Hystrix vinogradovi*.

The faunas belonging to Torre in Pietra F.U. such as those of the karstic sites of Loara (Veneto, north-eastern Italy) and Sant’Agostino (Veneto, north-eastern Italy) (Gliozzi et al. 1997) must be assigned to a later phase of the Early Toringian. *Dinaromys bogdanovi* is present at Loara; in both assemblages the presence of *Clethrionomys* cf. *C. rufocanus* is signaled, even if a revision of the material assigned to the Sundevall’s vole is necessary. Beyond north-eastern Italy only remains of species with very large distribution have been found (Torre in Pietra lower levels, Latium, central Italy).

An endemic arvicolid of the genus *Terricola*, *Terricola tarentina*, has been collected in a locality of southern Italy (Cava di Villa Castelli, Apulia) but the associated fauna is unknown. The age of this species (corresponding to the late Early Toringian) has been inferred by Brunet-Lecomte & Chaline (1991, 1992) on the ground of the supposed first appearance datum of *Terricola savii* in Italy (Brunet-Lecomte 1988).

**LATE TORINGIAN (Figs. 10, 11, 12)**

Late Toringian corresponds to the *Arvicola terrestris* zone of Fejfar & Heinrich (1990). In the present paper the faunas where *Arvicola* that is transitional between *A. cantianus* and *A. terrestris* is collected (e.g. Torrente Conca, Marche, central Italy, Conti et al. 1982) have been assigned to this age. To Vitinia F.U. belong the assemblages from the karstic deposits of Grotta Maggiore di San Bernardino (Veneto, north-eastern Italy) and Grotta di San Leonardo (Venezia Giulia, north-eastern Italy). In both faunas *Dinaromys bogdanovi* and *Marmota marmota* are present. It is the first occurrence of the alpine marmot, a sciurid of eastern origin, in Italy. An arvicolid of boreal distribution, *Microtus oeconomus* is reported from Grotta di San Leonardo. Very probably of the same age are the assemblages collected in Torrente Conca (Marche, central Italy), in Grotta del Vento (Marche, central Italy) where the boreal vesperilionid bat *Myotis dasycneme* is present, and those of Torre in Pietra upper levels (Latium, central Italy) and Grotta Paglicci (outer levels 4-3) (Apulia, southern Italy). In the latter, the Iberocastilian element *M. (I.) brecciensis* and *Hystrix* sp. are present. Another locality where remains of *Marmota marmota* associated with a not very advanced *Arvicola* have been found is Montignoso (Tuscany, central Italy). In this assemblage an *Hystrix* dimensionally comparable with *Hystrix vinogradovi* has been found (Rustioni et al. 1999). Unfortunately, we cannot state with certainty that all the faunal elements have the same age, due to the fact that the fauna comes from old collections.

Assemblages dating back to last interglacial have been collected in the karstic deposits of Montorio (Veneto, north-eastern Italy), San Sidero 3 (Apulia, southern Italy) and Grotta Grande di Scario (Campania, southern Italy) among others. The survival of *Crocidura zorzi* in north-eastern and southern Italy is remarkable. The rest of the faunal elements shows a distribution similar to the present-day one, except for the presence in southern Italy of some northern-Italian elements even if in very low percentages (*Microtus* cf. *M. agrestis* at San Sidero 3 and *Terricola subterraneus* at Scario).

Many faunas date back to the last glacial. For each Isotopic Stage (4, 3 and 2) it is pos-
possible to make detailed observations about the composition of the assemblages, but our target is to provide a general framework. Thus, associations will not be ordered and divided on the basis of their age within the last glacial. The assemblages collected in the following sites have been considered: Grotta del Broion (Veneto, north-eastern Italy), Grotta A di Veja (Veneto, north-eastern Italy), Riparo Mezzena (Veneto, north-eastern Italy), Riparo della Ghiacciaia (Veneto, north-eastern Italy), Riparo Tagliente lower levels (Veneto, north-eastern Italy), Riparo Tagliente upper levels (Veneto, north-eastern Italy), Moncucco Torinese (Piedmont, north-western Italy), Grotta della Ferrovia (Marche, central Italy), Grotta Breuil (Liatum, central Italy), Grotta di Sant’Agostino (Liatum, central Italy), Grotta Cala (Campania, southern Italy), Grotta di Castelcivita (Campania, southern Italy), Grotta della Serratura (Campania, southern Italy), Praia a Mare (Calabria, southern Italy) and Grotta Paglicci inner levels (Apulia, southern Italy).

A general characteristic of these faunas is the appearance in north-eastern Italy of ‘cold’ or ‘cool’ elements from northern or north-eastern Europe not present in present-day Italian faunas, such as *Sicista betulina*, *Microtus (Iberomys) brecciensis*, *Dinaromys bogdanovi*, *Microtus (Stenocranius) gregalis*, *Ochotona pusilla*. Some of them reach central Italy in its Adriatic side (*S. betulina* and *M. oeconomus*). In the central and southern portion of the Peninsula species now living in the northern part of Italy are very common: *Marmota marmota*, *Cricetus cricetus*, *Terricola multiplex*, *Microtus cf. M. arvalis*, *Scario* - *Crocidura zorzii*. 

Figure 10  Distribution of micromammals in Italy during Late Tortonian (early phases). Grotta S. Bernardino - a) Marmota marmota (not in scale); b) Cricetus cricetus. Several localities of Veneto - c) Dinaromys bogdanovi. Grotta Paglicci, outer levels - d) *Microtus (Iberomyys) brecciensis*. Torre in Pietra (upper levels) - e) *Microtus arvalis*.
Chionomys nivalis (relict populations of this species still live in some upland zones of central Apennines), Microtus arvalis-agrestis, Terricola gr. T. multiplex – T. subterraneus, and Cricetus cricetus (now absent from the Italian faunas). In the southern part of the Peninsula a greater percentage of ‘cold’ elements on the Adriatic side is evident in comparison to the Tyrrhenian side (Capasso Barbato & Gliozzi 2001). On the contrary, ‘Mediterranean’ elements (Talpa romana, Terricola savii) are present in relatively small percentages during the coldest climatic oscillations in southern Italian fossiliferous sites and totally absent from northern ones; during warmer oscillations they dominate the faunal associations in southern Italy.

Repetitive variations and fluctuations of the areal distribution boundaries of the various species left some relict populations, such as the glirid Dryomys nitedula in Calabria, quite far from the present-day main distribution of the species (no further than north-eastern Italy). Fossil remains found in Latium (Kotsakis 1991) confirm its past wider distribution and the fact that the Calabrian population is the result of a past widening of its distribution area, and not of an anthropic deed.

More complex is the case of Hystrix. Its presence is signaled in a few Late Pleistocene sites both in northern and southern Italy (Anelli 1967; Broglio & Cremaschi 1992) but there is no evidence to classify them as fossils or subfossils. Till very recent times the Balkan species Dinaromys bogdanovi was present in north-eastern Italy. In north-western Italy a western European element Arvicola sapidus MILLER (Arma delle Manie, Liguria), makes its appearance, together with Terricola multiplex (cf. Abassi & Desclaux 1996; Abassi & Brunet-Lecomte 1997; Abassi et al. 1998).

HOLOCENE

Beyond Hystrix, introduced by man in Roman times but perhaps already present in the Peninsula (see above), during the Holocene the following species appear in Italy: Suncus etruscus, Apodemus agrarius, Micromys minutus, Mus domesticus, Rattus rattus and Rattus norvegicus (Amori 1993). Cricetulus migratorius not present in Italy at the present day, is signaled by Bartolomei (1982) in early Holocene sediments of Grotta degli Zingari (Venezia Giulia, north-eastern Italy). Many species of bats now living in Italy are not present in the fossil record of Plio-Pleistocene mammals of the Peninsula because studies about fossil bats are very few.

Some living terrestrial mammalian species of Italian mainland are absent from the fossil record: Neomys anomalus, Terricola liechtensteini, Apodemus alpicola and the endemic Italian species Sorex samniticus, Sorex aurun-
chi, Terricola brachycercus, Lepus corsicanus (Nappi 2001). Some of these species have been erected or accepted as valid taxa in recent times: thus, future revisions of fossil material collected in Italy could evidence their presence in the fossil record.

**CONCLUSIONS**

Our observations about the distribution of small mammals in the Italian peninsula during Plio-Pleistocene may be summarised as follows:

(a) During the Ruscinian only a single tooth belonging to Centralomys sp. has been collected in Italy.

(b) During the Early Villányian (Triversa F.U.) the few micromammal faunas of the Italian peninsula are composed by elements with large European distribution.

(c) In the Late Villányian (Costa San Giacomo F.U. and Olivola F.U.) north-eastern Italy is populated by species with a large European distribution and also by some typically eastern elements never collected more westward (Dinaromys, cf. Ellobius sp.). In central Italy an Iberian element (Mimomys medasensis) is present; for the first time in Italy Crocidura, a genus of African origin (arrived from the east through Near East - Balkans) and Apodemus mystacinus a typically Mediterranean murid also occur. The ocho-tonid Prolagus persists.

(d) In the earliest phases of the Early Biharian (Tasso F.U. and Farneta F.U.) a lot of new elements with large European distribution arrive in Italy from the north-east. The assemblages of north-eastern Italy are characterised by the presence of central-eastern European or Balkan elements like Dinaromys and Apodemus atavus whilst in central Italy another Iberocccitan element (Microtus (Allophaiomys) chalinei) is present.

(e) In the later phases of the Early Biharian (Pirro F.U. and Colle Curti F.U.) the differences between north-eastern Italy and the other parts of the Peninsula are not very marked (only the soricids of the genus Crocidura are different in the two areas) but our knowledge of the assemblages of north-eastern Italy is limited. Advanced members of the subgenus Microtus (Allophaiomys) are characteristic elements of this time-span. A possible Iberocccitan element (Mimomys blanci) is present in central Italy. An element of central-eastern European distribution (Ungaromys) also reaches central Italy.

(f) In the Late Biharian (Slivia F.U. and Ponte Galeria F.U.), north-eastern Italy is well characterised by elements as Dinaromys and Neodon gregaloides and by the first member of the subgenus Microtus (Microtus), whilst in a slightly earlier moment oriental immigrants like Prolagurus and Predicrostonyx reach central Italy. In southern Italy some characteristic ‘Mediterranean’ elements (Talpa cf. T. romana and Terricola arvalidens) and another Iberocccitan species (Microtus (Iberomys) cf. M. (I.) brecciensis) are present.

(g) During the early phases of the Early Toringian (Isernia F.U.) the assemblages of north-western and central Italy are characterised by the presence of M. (I.) brecciensis and by the appearance of Arvicola cantianus whilst in a slightly later moment, in north-eastern Italy we observe the arrival of many new elements of north-eastern origin (Citellus, Cricetus cricetus, Microtus (Stenocranius) gregalis, Chionomys nivalis, Ochotona) and the persistence of the genus Dinaromys. C. nivalis is the only species of the newcomers that penetrates during this period in southern Italy.

(h) In the later part of the Early Toringian (Fontana Ranuccio F.U.), north-eastern Italy is characterised by the persistence of the genus Dinaromys. During this timespan this arvicolid expands its range westward to north-western Italy. A central European spe-
cies, *Apodemus* cf. *A. microps* is present in an assemblage of north-eastern Italy. In central Italy we observe the first appearance of a possible ancestral form of *Terricola savii* and, a little later, its migration towards the north-east. In north-western Italy an oriental element, *Hystrix vinogradovi*, is present, but the age of this fossil is not very precise.

(i) The latest phase of the Early Toringian (Torre in Pietra F.U.) is characterised by the presence of *Dinaromys* in north-eastern Italy and the arrival of *Clethrionomys* cf. *C. rufocanus* from the north-east (but the systematic attribution of this last arvicolid is not certain).

(j) At the beginning of the Late Toringian (Vitinia F.U.) the assemblages are characterized by the presence of an *Arvicola* with S.D.Q. between *A. cantianus* and *A. terrestris*. In north-eastern Italy *Dinaromys* is always present, whilst *Marmota marmota* and *Microtus oeconomus* make their first appearance in this area. In southern Italy we observe the last occurrences of *Allocricetus bursae* and *Microtus (I.) brecciensis* and the presence of the genus *Hystrix*.

(k) During the last interglacial the distribution of micromammals is very similar to the present-day situation, but *Crocidura zorzii* is present both in the north-east and in the south while in southern Italy some species new limited to the northern part of the Peninsula are present, even if with very scanty remains (*Microtus agrestis, Terricola subterraneus*).

(l) The assemblages assigned to the last Glacial are very abundant. Many ‘cold’ elements penetrate in north-eastern Italy (*Sicista, M. (S.) gregalis, M. oeconomus, Ochotona pusilla*) and some of them (*Sicista, M. oeconomus*) reach the Adriatic side of central Italy. *Dinaromys* is always present in north-eastern Italy. On the Tyrrenhian side of the Peninsula and in central and southern Italy many elements now absent are very abundant (*Marmota marmota, Cricetus, Microtus (Microtus), Chionomys nivalis*), whilst the ‘Mediterranean’ elements are always present even if in low percentages. In north-western Italy some western elements as *Arvicola sapidus* are observed during this period.

(m) In the assemblages of Holocene age ‘cold’ species disappear, whilst new elements (*Suncus, Micromys, Mus, Rattus*) arrive as result of human activity.

Quite a large number of micromammals have a limited range of geographical distribution; this makes them very useful for biogeographical analyses, both present-day and past ones. On the other hand, even though the big mobility of macromammals allows large-scale biochronological correlations, it does not allow a paleobiogeographical characterization at the bioprovince or sub-bioprovince level of areas with a limited geographical extension (unless we talk about islands) such as the Italian Peninsula. The only comparison we can make between large and small mammals concerns, then, the possible synchronicity of dispersal events.

The study of fossil amphibians and reptiles (in which classes we find very useful taxa for biogeographical reconstructions) does not allow observations or comparisons so far. Studies in progress, though (cf. Delfino 2002) will certainly bring very useful data. The only other group of continental animals with a considerable fossil documentation is that of non-marine molluscs. They show a particular biogeographical distribution, especially aquatic ones, for which the extension of endorheic basins and the possibilities of communication between the different hydric systems have a major importance. The non-marine mollusc faunas (especially the fresh-water ones) collected in Fornace RDB and other localities of Piedmont are characterized by a good number of endemic species and indicate strong affinities with the Rhône (France) and Rhine (Germany) valleys coeval assemblages. The
presence of assemblages dominated by endemic primitive fluvio-lacustrine prosobranchs characterize the faunas of Tuscany, Umbria and Northern Latium during the Villafranchian (corresponding to Villányian and Early Biharian) (Esu et al. 1993; Ciangherotti et al. 1998). No micromammal species, even those closely related to continental waters environments, show a similar geographical distribution.

The analytical study of macromammalian faunas evidenced several turnovers, some of which are very evident (Triversa – Montopoli, Costa San Giacomo – Olivola, Olivola – Tasso, Colle Curti – Slivia and Last Pleniglacial - Holocene) (Sardella et al. 1998). Other studies concerning Dispersal Events displayed at least three big events: the ‘Elephas – Equus’ event, the ‘Wolf’ event and the ‘End-Villafranchian’ event (Azzaroli et al. 1988; Torre et al., 1992) in addition to the migration of single species (Torre et al., 1992; Sala et al. 1992). The lack of data concerning micromammals does not allow comparisons between small and large mammals with regard to the first event. For the second one data are scanty too. Some changes in the composition of micromammal assemblages may be observed in north-eastern Italy comparing the faunas of Rivoli Veronese and Monte La Mesa. A major change within faunas seems to take place in coincidence with the passage between Colle Curti F.U. and Slivia F.U. It corresponds, then, to the ‘End-Villafranchian’ event sensu lato, whose existence has been doubted by Agustí & Moyá-Solà (1998). Anyway, an even more marked event seems to take place within micromammals, at least in north-eastern Italy, in Visogliano, comprised between Slivia F.U. and Isernia F.U.

In general, there does not seem to be a coincidence between large mammal and small mammal dispersal events. Moreover, the appearance of many small mammals in Italy seems to be the result of single species migration (cf. Koenigswald 1992) and not whole faunas dispersal events. Some ‘cold’ or ‘cool’ species modify their distribution area with long-timespan fluctuations due to climatic (and consequently environmental) changes; for this reason they appear more than once in north-eastern Italy, while other species living in the same area at the present day, during those time spans expand their geographical range toward the south. On the contrary ‘Mediterranean’ elements during warmer periods expand their distribution area towards the north, even if in a less marked way.

Kowalski (1992) distinguished the presence of a Western Mediterranean area (northern border of the western Mediterranean), which is characterized by a limited number of rodent taxa during the whole Pleistocene. In the Italian Peninsula those taxa are certainly present, even in a limited number if compared with the Iberian Peninsula (Agustí & Moyá 1992). The Plio-Pleistocene micromammal assemblages of Italian mainland are indeed paleobiogeographically characterized by the presence, during certain moments, of some typical elements of the Mediterranean area, such as some species of the genus Terricola, Talpa romana and some Iberocccitan species (Mimomys medasensis, Microtus (Allophaiomys) chalinei, Microtus (Iberomys) brecciensis, and, perhaps, Mimomys blanci).

The renewal of Italian micromammal faunas in the great part of its elements, takes place through the north-eastern area, which first constituted the northern border of the Padanian Gulf and later on, during the maximum extension of glaciers, comprised also the area nowadays occupied by the northern Adriatic Sea. Central - Eastern Europe species expand on the whole peninsular territory, while other taxa, linked to colder climates, reach north-eastern Italy during the climatic deterioration maximums. Some of them reach central Italy, while others stop in the north-eastern area that seems to constitute a transitional area between the Mediterranean and central Europe. In north-eastern Italy the presence of a Balkan element such as
Dinaromys is almost constant. Even a few rare African elements (Crocidura) or Anatolian-Balkan elements (Apodemus mystacinus, if its origin is really in the same area where it is nowadays widespread) reach Italian Peninsula from the north-east.

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APPENDIX

List of Italian mainland Plio-Pleistocene localities, with taxa and references updated to May 2001.

EARLY VILLÁNYIAN LOCALITIES

?BARGA (TUSCANY, CENTRAL ITALY) (Kotsakis 1986)
Hystrix sp.

RDB QUARRY (PIEDMONT, NORTH-WESTERN ITALY) (Argenti 1999)
Castor sp., Apodemus alsomyoides

CASCINA ARONDELLI (PIEDMONT, NORTH-WESTERN ITALY) (Berzi 1967; Berzi et al. 1967; Michaux 1970; Masini & Torre 1987; Fejfar 2001)

ARCILLE (TUSCANY, CENTRAL ITALY) (Hürzeler & Engesser 1976; Masini & Torre 1987; Engesser 1989; Fanfani 2000)

S. GIUSTO (TUSCANY, CENTRAL ITALY) (Kormos 1931; Masini & Torre 1987)
Mimomys (Cseria) stehlini

SPOLETO (UMBRIA, CENTRAL ITALY) (Clerici 1894; Barisone et al. in press)
Castor sp.

LATE VILLÁNYIAN LOCALITIES

UPPER VALDARNO (TUSCANY, CENTRAL ITALY) (Abbazzi unpublished data)
Mimomys polonicus

BOCCHIGNANO (LATIUM, CENTRAL ITALY) (Tuccimei 1893; Kotsakis 1988)
Mimomys cf. M. polonicus

VINCI (TUSCANY, CENTRAL ITALY) (Marcolini 2002)
Germanomys sp.

TOPPETTI QUARRY (UMBRIA, CENTRAL ITALY)

(Rivoli Veronese (VENETO, NORTH-EASTERN ITALY) (Sala et al. 1994; Sala 1996a; Fanfani & Masini, 1997)

VALLE CATENACCIO (LATIUM, CENTRAL ITALY) (Masini et al. 1996)
Castor sp.

COSTA S. GIACOMO (LATIUM, CENTRAL ITALY) (Masini et al. 1996)
Hystrix cf. H. refossa

OLIVOLA (TUSCANY, CENTRAL ITALY) (Bosco, 1898; Azzaroli 1998)
Hystrix cf. H. refossa

CASTELFRANCO DI SOPRA (TUSCANY, CENTRAL ITALY) (Major 1902)
Mimomys plicaenicus

UPPER VALDARNO, SEVERAL SITES OF OLIVOLA F.U. (TUSCANY, CENTRAL ITALY) (Bosco 1898; Rook & Masini, 1990; Torre et al. 1996; Azzaroli 1998; Fanfani, 2000)
?Erinaceus praegracilis, Hystrix refossa, Prolagus sp., Oryctolagus lacosti (the fossils classified as Lepus etruscus and Lepus valdarncensis, cf. Forteleoni 1971, have been classified as Oryctolagus lacosti by Lopez 1977)

PANTALLA (UMBRIA, CENTRAL ITALY) (Gentili et al. 1997)
Apodemus dominans
CASASGHERRI (TUSCANY, CENTRAL ITALY)
(Marcolini et al. 2000; Marcolini 2002)
Castor sp., Mimomys pitymyoides, Mimomys pusillus,
Mimomys ostramosensis, Apodemus dominans, Glis sp.,
Hystrix refossa, Oryctolagus cf. O. lacosti
TORRE DI PICCHIO (UMBRIA, CENTRAL ITALY)
(Girotti et al. 2003)
Mimomys medasensis, Prolagus sp., Oryctolagus cf. O. lacosti

EARLY BIHARIAN LOCALITIES

MONTE LA MESA (VENETO, NORTH-EASTERN ITALY)
(Argenti 1999; Marchetti et al. 2000)
Erinaceus sp., Crocidura sp., Beremedia fassidens,
Petenyia hungarica, Asoriculus gibberodon, Sorex bor,
Sorex minutus, Sorex praealpinus, Sorex (Drepanosorex)
praearaneus, Soricidae indet. I, Soricidae indet. II, Talpa
minor, Scirius warthae, Sciriciidae indet., Allocricetus
bureaui, Allocricetus ehiki, Pliomys episcopalis,
Dinaromys dalmatinus, Mimomys tornensis, Mimomys
pusillus, Mimomys cf. M. ostramosensis, Clethrionomyss
sp., Microtus (Allophaiomys) gr. M. (A.) pliocaenicus,
Apodemus dominans, Pliomys episcopalis, Cautus (Allophaiomys)
Sorex bor, Petenyia hungarica, Asoriculus aff. A.
theni, Talpa gr. T. minor – T. caeca, Rhinolophus ferru-
mequinum, Rhinolophus birzebbugensis, Rhinolophus
euryale, Myotis cf. blythi, Myotis sp., Miñoiterus
schreiberi, Miñoiterus n. sp., Microtus (Allophaiomys)
cf. M. (A.) ruffoi, Apodemus flavicollis, M. (A.) ruffoi,
M. (A.) ruffoi

UPPER VALDARNO, SEVERAL SITES OF TASSO
F. U. (TUSCANY, CENTRAL ITALY) (Bosco 1898,
1899; Torre 1985; Rook & Masini 1990; Rook &
Kotsakis 1994; Torre et al. 1996; Azzaroli 1998)
Castor fiber, Mimomys savini, Hystrix refossa, Prolagus
gr. P. michaui – P. calpensis, Oryctolagus lacosti

TIBERINO BASIN, SOME LOCALITIES OF TASSO
F. U. (UMBRIA, CENTRAL ITALY) (Sardella et al.
1995)
Castor fiber

CASTEL SAN PIETRO (LATIUM, CENTRAL ITALY)
(Tucciemei 1891; Barisone et al. in press)

SAVIGNANO SUL PANARO (EMILIA, NORTHERN ITALY)
(Cremaschi & Sala 1982)

STEGGIO BASIN (VENETO, NORTH-EASTERN ITALY)
(Paronuzzi 1994)
Pliomys episcopalis, Mimomys sp., Glis minor

PIETRAFITTA (UMBRIA, CENTRAL ITALY) (Gentili
et al. 1996; Argenti 1999; Barisone et al. in press;
Argenti & Kotsakis in press)

Sorex cf. S. minutus, Castor fiber, Borsodius sp., Mimomys
pusillus, Microtus (Allophaiomys) chalini, Microtus
(Allophaiomys) cf. M. (A.) ruffoi, Oryctolagus lacosti

SCOPPITO (ABRUZZI, CENTRAL ITALY)
(Masini et al. 1996)
Mimomys savini

LEFFE (LOMBARDY, NORTH-WESTERN ITALY)
(Stehlin 1930; Masini et al. 1996)
Castor fiber, Mimomys cf. M. savini

PIRRO NORD (APULIA, SOUTHERN ITALY)
(De Giuli & Torre 1984; De Giuli et al. 1987; Masini &
Santini 1991; Masini et al. 1996; Fanfani 2000)
Erinaceus praegalcialis, Crocidura kornfeldi,
Crocidura sp., Sorex bor, Petenyia hungarica,
Asoriculus aff. A. theni, Talpa gr. T. minor – T. caeca,
Rhinolophus ferrumequinum, Rhinolophus birzebbugensis,
Rhinolophus euryale, Myotis cf. blythi, Myotis sp.,
Miñoiterus schreiberi, Miñoiterus n. sp., Microtus
(Allophaiomys) cf. M. (A.) ruffoi, Apodemus flavicollis,
M. (A.) ruffoi, M. (A.) ruffoi

SOAVE CAVA SUD (VENETO, NORTH-EASTERN
ITALY) (Pasa 1947; Bartolomei 1980; Masini & Santini
1991; Fanfani 2000)
Crocidura zorzi, Asoriculus castellarini, Neomys aff. N.
newtoni, Sorex (Drepanosorex) praearaneus, Sorex bor,
Beremedia fassidens, Petenyia hungarica, Talpa gr. T.
minor – T. caeca, Pliomys episcopalis, Mimomys cf. M.
savini, ?Mimomys reich, Microtus (Allophaiomys)
ruffoi, Apodemus gr. A. sylvaticus – A. flavicollis

COLLARMELE (ABRUZZI, CENTRAL ITALY)
(Esu et al. 1991)
Microtus (Allophaiomys) sp.

COLLE CURTI (MARCHE, CENTRAL ITALY)
(Ficcarelli et al. 1990; Torre et al. 1996; Abbazzi et al.
1998; Masini et al. 1998)
Pliomys lenki, Microtus (Allophaiomys) sp.

MONTE PEGLIA (UMBRIA, CENTRAL ITALY)
(Van der Meulen 1973, 1999; Argenti 1999)
Sorex runtonensis, Beremedia fassidens, Asoriculus cf.
A. castellarini, Neomys cf. N. newtoni, Talpa cf. T.
fossilis, Ungaromys nana (= Ungaromys meuli after
Rabeder 1981), Pliomys episcopalis, Mimomys savini,
Mimomys blanci, Microtus (Allophaiomys) nutiensis,

FON'TIGNANO (ROME, LATIUM, CENTRAL ITALY) (Kotsakis et al. 1992; Barisone & Kotsakis, 2001)
Prolagus pannonicus, Predicrostonyx sp.

LATE BIHARIAN LOCALITIES

SLIVIA (VENEZIA GIULIA, NORTH-EASTERN ITALY) (Ambrosetti et al. 1979; Bon et al. 1991; Gliozzi et al. 1997)
Rhinofossus ferrumequinum, Miopineura sciuroides, Chiroptera ined., Castor fiber, Allocricetus bursae, Mimomys savini, Dinaromys sp., Neodon gregaloides, Lepus sp.

MONTE TENDA (VENETO, NORTH-EASTERN ITALY) (Bon et al. 1991; Masini et al. 1996)
Pliomys episcopalis, Mimomys savini, Microtus (Microtus) sp., Terricola sp.

SANT'ARCANGELO (LUCANIA, SOUTHERN ITALY) (Fanfani 2000; Masini et al. 2000)

EARLY TORKINGIAN LOCALITIES

ISERNIA (MOLISE, SOUTHERN ITALY) (Coltorti et al. 1982; Sala 1983, 1996b; Coltorti et al. 2000)

BORGIO VEREZZI (VALDEMINO, LIGURIA, NORTH-WESTERN ITALY) (Nocchi & Sala 1997a, 1997b; Fanfani 2000)

PONTE GALGIA, UPPER LEVELS (LATIUM, CENTRAL ITALY) (Unpublished data)
Allocricetus bursae, Terricola sp.

TRE FOSSI (APULIA, SOUTHERN ITALY) (Fanfani 2000 and unpublished data)
Erinaceus praelagalis, Crocidura kornfeldi, Allocricetus bursae

VISOGLIANO, SHELTER A (VENEZIA GIULIA, NORTH-EASTERN ITALY) (Bartolomei et al. 1976b; Bartolomei & Tozzi, 1978; Catani et al. 1991; Fanfani 1998, 2000)

VENOSA – NOTARCHIRICO (LUCANIA, SOUTHERN ITALY) (Sala 1989, 1999)
Sorex cf. S. runtonensis, Talpa sp., Pliomys episcopalis, Microtus afr., M. arvalis, Terricola sp., Chionomys nivalis, Arvicola cantianus, Apodemus sp.

POGGITAZZI (TUSCANY, CENTRAL ITALY) (Torre 1985)
Arvicola cantianus

MONTE DEL CROS (PIEDMONT, NORTH-WESTERN ITALY) (Giacobini et al. 1980)
Sorex runtonensis, Talpa minor, Pliomys episcopalis, Pliomys lenki, Glis sp., Hystrix sp. (= ? Hystrix vinagra-dovi)

FONTANA RANUCCIO (LATIUM, CENTRAL ITALY) (Masini et al. 1996)
Lepus sp., Castor fiber

CAMPANI QUARRY (TUSCANY CENTRAL ITALY) (Marcolini et al. 2000; Marcolini 2002)

CASE PICCONETTO (ABRUZZI, CENTRAL ITALY) (Marcolini et al. 2000)
Crocidaura sp., Terricola gr. T. savii, Apodemus gr. A. syl-vaticus – A. flavicollis

BOSCOCHIESANUOVA (VENETO, NORTH-EASTERN ITALY) (Bartolomei & Pasa 1969; Bon et al. 1991; Fanfani 2000)
Crocidaura zorzi, Sorex gr. S. subaraneus – S. runtonen-

SAN GIOVANNI DI DUINO (VENEZIA GIULIA, NORTH-EASTERN ITALY) (Bartolomei 1976; Bon et al. 1991; Fanfani 2000)


SPESSA II (VENETO, NORTH-EASTERN ITALY) (Bartolomei 1964, 1969; Bon et al. 1991; Argenti & Kotsakis 1999)


FONTANA MARELLA, LOWER LEVELS (LOMBARDY, NORTH-WESTERN ITALY) (Tintori et al. 1995)
Pliomys episcopalís, Dinaromys bogdanoví

CAMPO DEI FIORI (LOMBARDY, NORTH-WESTERN ITALY) (Zanadlal, 1994b)

Chiroptera indet., Dinaromys bogdanoví, Clethrionomys sp., Chionomys nivalís, Glis glis

BISTIE I (VENEZIA GIULIA, NORTH-EASTERN ITALY) (Lugi & Sala, 2000)

Dinaromys gr. D. bogdanoví, Lepus europaeus

TORRE IN PIETRA, LOWER LEVELS (LATIUM, CENTRAL ITALY) (Caloi & Palombo 1978)

Castor fiber, Glis glis, Lepus sp., Oryctolagus cuniculús

LOARA (VENETO, NORTH-EASTERN ITALY) (Bartolomei 1966a, 1969; Bon et al. 1991)


SANT’AGOSTINO (VENETO, NORTH-EASTERN ITALY) (Bartolomei 1966a, 1969; Bon et al. 1991)


LATE TORGIANING LOCALITIES

TORRENTE CONCA (MARCHE, CENTRAL ITALY) (Conti et al. 1982)


GROTTE MAGGIORE DI SAN BERNARDINO (VENETO, NORTH-EASTERN ITALY) (Bartolomei 1960, 1969; Bon et al. 1991)

Talpa europaea, Marmota marmota, Crictetus cricetus, Dinaromys bogdanoví, Clethrionomys sp., Microtus agrestis, Arvicola sp., Glis glis, Dryomys nitedula, Lepus sp.

GROTTE DI SAN LEONARDO (VENEZIA GIULIA, NORTH-EASTERN ITALY) (Bartolomei 1982; Bon et al. 1991)

Crocidura sp., Marmota marmota, Crictetus cricetus, Pliomys lenki, Dinaromys bogdanoví, Microtus arvalis, Microtus oceconomus, Chionomys nivalís, Apodemus sylvaticus, Glis glis

GROTTE DEL VENTO (MARCHE, CENTRAL ITALY) (Esu et al. 1990)

Sorex araneus, Sorex minutus, Rhinolophus ferrumequinum, Myotis dasybrachy, Pliomys lenki, Microtus arvalis, Chionomys nivalís, Apodemus cf. A. sylvaticus

TORRE IN PIETRA, UPPER LEVELS (LATIUM, CENTRAL ITALY) (Caloi & Palombo 1978)


GROTTE DEL PRINCIPE, LOWER LEVELS (LIGURIA, NORTH-WESTERN ITALY) (Barral & Simone 1971)

Microtus arvalis, Arvicola terrestrís, Apodemus sylvaticus, Glis glis, Eliomys quercinus, Oryctolagus cuniculus

GROTTE PAGLICCI, OUTER LEVELS (APULIA SOUTHERN ITALY) (Bartolomei 1980; Calabret 1984)
Allocricetus bursae, Microtus brecciensis, Microtus arvalis, Terricola savii, Arvicola sp., Apodemus sp., Eliomys sp., Hystricops, Oryctolagus sp.


Pianico Sellere (Lombardy, North-Western Italy) (Lona & Venzo 1957) Dryomys nitedula

San Sidero 3 (Apulia, Southern Italy) (De Giuli 1983) Microtus cf. M. agrestis, Terricola savii, Apodemus sylvaticus, Eliomys quercinus, Oryctolagus cuniculus


Grotta di Sant'Agostino (Latium, Central Italy) (Tozzi, 1970) Erinaceus europeaus, Talpa romana, Rhinolophus ferrumequinum, Myotis blythi, Marmota marmota, Cricetus cricetus, Microtus arvalis, Terricola terrestris, Apodemus sylvaticus, Glis glis, Eliomys cf. E. quercinus, Lepus europaeus, Oryctolagus cuniculus

Grotta del Broion (Veneto, North-Eastern Italy) (Pasa 1953; Sala 1980, 1990; Zanalda 1994a) Sorex araneus, Marmota marmota, Sicista sp., Cricetus cricetus, Clethrionomys glareolus, Dinaromys gr. D. bogdanovi, Microtus agrestis, Microtus arvalis, Chionomys nivalis, Terricola sp., Arvicolata terrestris, Apodemus sylvaticus, Glis glis, Muscardinus avellanarius, Dryomys nitedula, Lepus europaeus


Tagliente Shelter, Lower Levels (Veneto, North-Eastern Italy) (Bartolomei et al. 1982; Sala 1990; Bon et al. 1991) Crocidura sp., Sorex araneus, Sicista sp., Cricetus cricetus, Clethrionomys sp., Dinaromys gr. D. bogdanovoi, Microtus agrestis, Microtus arvalis, Microtus (Stenorcanthus) gregalis, Microtus oeconomus, Chionomys nivalis, Arvicolata sp., Apodemus sylvaticus, Glis glis, Eliomys quercinus, Dryomys nitedula, Ochotonata cf. O. pusilla


Grotta Cala (Campania, Southern Italy) (Bartolomei et al. 1976a, 1977) Sorex araneus, Sorex minutus, Talpa cecca, Talpa roma-
na, Clethrionomys glareolus, Microtus arvalis, Microtus agrestis, Terricola savii, Arvicola sp., Apodemus sp., Glis glis, Eliomys quercinus, Muscardinus avellanarius

**Grotta di Castelcivita** (Campania, Southern Italy) (Cioni et al. 1979; Masini & Abbazzi 1997; Fanfani 2000)

**Moncucco Torinese** (Piedmont, North-Western Italy) (Alessio et al. 1982)
Sorex araneus, Talpa europaea, Clethrionomys cf. C. glareolus, Microtus arvalis, Microtus agrestis, Terricola cf. T. savi, Arvicola cf. A. terrestris, Apodemus sylvaticus, Glis glis

**Grotta Breuil** (Latium, Central Italy) (Kotsakis, 1991)
Crocidura suaveolens, Rhinolophus ferrumequinum, Miniopterus schreibersi, Myotis myotis, Nyctalus noctula, Tadarida teniotis, Terricola cf. T. savi, Arvicola terrestris, Apodemus sylvaticus, Glis glis, Eliomys quercinus, Dryomys nitedula

**Praia a Mare** (Calabria, Southern Italy) (Capasso Barbato & Gliozzi 2001)
Sorex araneus, Sorex minutus, Clethrionomys glareolus, Microtus arvalis, Microtus agrestis, Terricola savii, Arvicola terrestris, Apodemus sylvaticus, Glis glis, Eliomys quercinus, Muscardinus avellanarius, Lepus europaeus

**Grotta Poglizzi, Inner Levels** (Apulia, Southern Italy) (Bartolomei 1975; Bartolomei et al. 1977)
Sorex araneus, Sorex minutus, Talpa romana, Clethrionomys glareolus, Microtus gr. M. arvalis, Microtus agrestis, Chionomys nivalis, Terricola savii, Arvicola sp., Apodemus sylvaticus, Glis glis, Eliomys quercinus, Muscardinus avellanarius, Lepus sp.

**Tagliente Shelter, Upper Levels** (Veneto, North-Eastern Italy) (Capuzzi & Sala 1980; Sala 1990; Bon et al. 1991)

**Grotta della Serratura** (Campania, Southern Italy) (Bertolini et al. 1996)
Erinaceus europaeus, Crocidura suaveolens, Sorex sp., Talpa romana, Talpa caeca, Clethrionomys glareolus, Microtus arvalis, Microtus agrestis, Terricola savii, Chionomys nivalis, Arvicola terrestris, Apodemus gr. A. sylvaticus – A. flavicolis, Glis glis, Eliomys quercinus, Muscardinus avellanarius

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