

Fossil glirids of Italy: the state of the art

Glíridos fósiles de Italia: situación actual

por

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Abstract: In this paper the fossil glirids of Italy are reviewed. Non-endemic species of the family are known from sites of Turolian, Villanyian and Biharian age but their remains are rare. In Toringian, mammal assemblages are more common and micromammalian associations of this period are better known. The peculiar endemic glirids characterising mammalian assemblages of low biodiversity in insular environment are more interesting. Endemic species are present in the Early Miocene of Oschiri (Sardinia), in the Late Miocene of the Tusco-Sardinian palaeobioprovince and of the Abruzzi-Apulian palaeobioprovince, in the Plio-Pleistocene of Sardinia and of Sicily and in the late Pleistocene of Capri Island.

Key words: Gliridae (Rodentia), Neogene, Quaternary, Italy.

Resumen: En este artículo se revisan los glíridos fósiles de Italia. Especies no endémicas de la familia son conocidas en yacimientos del Turoliense, del Villaniense y del Bihariense, aunque sus restos sean raros. En el Toringiano las asociaciones fósiles de mamíferos son más numerosas y las asociaciones de micromamíferos son mejor conocidas. Los peculiares glíridos endémicos que caracterizan las asociaciones oligotípicas de medios insulares son más interesantes. Se han hallado especies endémicas en el Mioceno inferior de Oschiri (Cerdeña), en el Mioceno superior de la paleobioprovincia Tosco-Sarda y de la paleobioprovincia de Abruzzi-Apulia, en el Plio-Pleistoceno de Cerdeña y Sicilia y en el Pleistoceno de la isla de Capri.

Palabras clave: Gliridae (Rodentia), Neógeno, Cuaternario, Italia.

INTRODUCTION

Fossil rodents are rare in the Tertiary mammal bearing deposits of Italy. The few Paleogene sites did not yield any rodent remains and only one among the Neogene micromammalian assemblages is older than Late Miocene (KOTSAKIS *et alii*, 1997). Abundant rodent faunas are known from the Middle Pleistocene and younger deposits. Our knowledge of the Gliridae follows more or less the same pattern.

EARLY MIOCENE OF SARDINIA

The oldest glirids of Italy are known from the Early Miocene lacustrine deposits of the Oschiri basin (N Sardinia) where they occur associated with ctenodactylids and insectivores (DE BRUIJN & RÜMKE, 1974). The species poverty of the association, the endemic character of its components and

the gigantism of some ctenodactylids and of *Glis* indicate insular conditions. The different biogeographical origin of the taxa, ctenodactylids probably from Asia through a Mesogean way (like that hypothesized by GINSBURG & ANTUNES (1979) for a more recent moment of the Miocene) and the remaining fauna from Europe, suggests that the respective ancestors arrived at different times (ESU & KOTSAKIS, 1985). The glirids are represented by three endemic species (DE BRUIJN & RÜMKE, 1974; DAAMS, 1981): *Peridyromys* aff. *P. murinus* (POMEL, 1853), *Microdyromys* aff. *M. koenigswaldi* DE BRUIJN, 1966 and *Glis major* DE BRUIJN, 1974. The first two species are morphologically similar but somewhat larger than their respective relatives from the European mainland. All three above mentioned genera are known from Early Miocene deposits of Western and Central Europe, which is supposed to be the area of origin of the endemic Sardinian species (DAAMS & DE BRUIJN, 1995).

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LATE MIOCENE

In Italy four different biogeographical areas are recognized in the Late Miocene for the continental vertebrate faunas (KOTSAKIS *et alii*, 1997; TORRE *et alii*, 2000):

- 1) Romagna - Piedmont
- 2) Southern Tuscany - Sardinia
- 3) Abruzzo - Gargano
- 4) Sicily - Calabria

The late Turolian lacustrine deposits of Gravitelli in North-eastern Sicily yielded large mammals only, and will therefore not be discussed here. The mammalian fauna collected in the marine *Clypeaster*-bearing sands of Cessaniti (Calabria) also contains large mammals only. TORRE *et alii* (2000) suggest an African origin for both faunas.

The Late Turolian (late MN 13) fissure fillings of Brisighella in Romagna contain numerous rodents, but only one glirid, *Myomimus* sp. (DE GIULI, 1989). Another glirid of the same age (MN 13), *Muscardinus* sp., is reported from Ciabòt Cagna (Piedmont), collected with some other species of microvertebrates in oligohaline Messinian deposits (CAVALLO *et alii*, 1994).

In South Tuscany (Baccinello, Casteani, Montebamboli etc. from the Maremma area) the fossil remains come from four different fluvio-lacustrine levels (V_0 , V_1 , V_2 and V_3). The first three levels contain mainly endemic mammals. The presumed African origin of some large mammals of these levels are questioned by TORRE *et alii* (2000) but for the micromammals there is a general agreement about their European origin. ENGESSER (1989) suggests an Early Turolian age (MN 11) for level V_0 , a Middle Turolian (MN 12) for V_1 and a Late Turolian one (MN 13) for level V_2 . Two endemic glirids are present in level V_1 (ENGESSER, 1983): *Anthracoglis marinoi*, ENGESSER, 1983 and a giant unnamed form, which is represented by one tooth only. *A. marinoi* is also present in level V_2 of Baccinello, and a new, unnamed species of *Anthracoglis* is present in level V_2 of Montebamboli. ENGESSER (1983) suggests that the ancestors of *Anthracoglis* and of the unnamed giant form are *Microdryomys* and *Peridyromys* respectively. DAAMS & DE BRUIJN (1995) indicate *Dryomys* as a possible ancestor of *Anthracoglis*. The possibility of phylogenetic relationships between *Peridyromys* and the giant unnamed form of Baccinello V_1 is rather difficult to accept because *Peridy-*

romys last occurrence is reported in the MN 4 zone whilst the arrival of the ancestors of the endemic forms of Baccinello is supposed to be more recent. ENGESSER (1989) supposes that the immigration(s) of the ancestors of the two glirids took place during the Late Aragonian (MN 7/8, Middle Miocene) or earlier (for the bigger one). BENVENUTI *et alii* (2001) indicate the Early Tortonian as a possible moment of the colonisation of the area (or areas) of the Tusco-Sardinian palaeobioprovince by the ancestors of the older wave of immigrants. A similar fauna, correlated with that of V_2 level of Baccinello, has been signalled in Fiume Santo (Sardinia) by CORDY *et al.* (1996). These authors identify a glirid of big size among the fossils collected in the sands and clays of this locality.

The fauna of level V_3 of Baccinello shows continental European affinities and is thus completely different from the endemic faunas of the older levels and much more similar to that of N Italy. ROOK & TORRE (1995) assign a Late Turolian age to this assemblage. *Muscardinus* aff. *M. vireti* HUGUENY & MEIN, 1965 is the only dormouse species present (ENGESSER, 1989).

The Gargano promontory in Apulia yielded numerous faunas from fissure fillings. These faunas contain abundant remains of giant erinaceids, lagomorphs, glirids, cricetidids and murids and dwarf artiodactyls, typical for an insular environment. Phylogenetical reconstructions of erinaceids, cricetidids, murids and ochotonids allow placing the fauna of each fissure filling in a chronological succession. There is no agreement on the age of the faunal complex. FREUDENTHAL (1985) suggests a Late Miocene age, and DE GIULI *et alii* (1987b) propose an Early Pliocene age, modified in Late Miocene and/or Late Pliocene in ABBAZZI *et alii* (1996). The attribution of the *Apodemus* from the Gargano fissures to *Apodemus gorafensis* RUIZ BUSTOS, SESÉ, DABRIO, PEÑA & PADIAL, 1984 (FREUDENTHAL *et alii*, 2001), a typical Ruscinian species (MARTIN SUAREZ & MEIN, 1998), supports the hypothesis of ABBAZZI *et alii* (1996). An Late Miocene – Pliocene age is proposed also by PARRA *et alii* (1999). The affinities of the different mammal species suggest that the Gargano archipelago has been colonized in different moments and from different geographical areas. Hitherto only one glirid has been described, the giant *Stertomys laticrestatus* DAAMS & FREUDENTHAL, 1985 which the authors (DAAMS & FREUDENTHAL, 1985) consider to be a descendant of *Glis*. Other glirids are still under study,

but several of them are provisionally assigned to *Eliomys* (similar to its relatives from the mainland, and scarcely represented in the faunas) and *Peridyromys* (DE GIULI *et alii*, 1990). The presence of *Peridyromys* in these faunas is improbable because the genus became extinct in Early Aragonian (MN 4B) (DAAMS, 1981; DAAMS & DE BRUIJN, 1995). Affinities of these glirids from Gargano with *Myomimus* seems more probable.

PLIOCENE AND PLEISTOCENE OF THE ITALIAN MAINLAND

The Plio-Pleistocene fossiliferous sites of mainland Italy are assigned to several Faunal Units (F.U.) as defined in GLOZZI *et alii* (1997). Some assemblages are transferred in this paper to a different F.U. or even to a different Mammal Age (for a discussion of some problems of this type and for the composition of the assemblages see KOTSAKIS *et alii*, in press).

Hitherto glirids have not been found in the very few Ruscinian (Early Pliocene) faunas of the Italian mainland.

In the Early Villanyian (Middle Pliocene, MN 16) lacustrine deposits of Triversa (Villafranca d'Asti, Piedmont – Triversa F.U.) two glirids are present: *Glirulus pusillus* (HELLER, 1936) and *Muscardinus* sp., of which the latter one is different from the extant *M. avellanarius* according to MICHAUX (1970).

Undescribed glirid species from the Late Villanyian (Late Pliocene) karst fauna of Rivoli Veronese (Veneto – Costa San Giacomo F.U.) (SALA *et alii*, 1994; SALA, 1996) are provisionally determined as *Muscardinus pliocaenicus* KOWALSKI, 1963, *Glis minor* KOWALSKI, 1956 and *Eliomys* sp. (an extinct species). *Muscardinus* sp. is mentioned from the fissure filling of Montagnola Senese (Tuscany) which age is presumably Late Villanyian (FONDI, 1972). *Glis* sp. from Casa Sgherri (Tuscany) is of Late Villanyian age also (MARCOLINI *et alii*, 2000).

In the fauna of earliest Biharian age collected in a fissure filling of Monte La Mesa (Veneto), two species of glirids have been described (MARCHETTI *et alii*, 2000): *Muscardinus* cf. *M. dacicus* KORMOS, 1930 and *Glis sackdillingensis* (HELLER 1930). In a site of approximately the same age, the lacustrine deposit of Steggio (Veneto), another glirid, *Glis minor*, is reported in an abstract (PARONUZZI, 1994). This last attribution should be checked (see DAUD,

1993 for the chronological distribution of some Plio-Pleistocene glirids and the phylogenetical relationships of *G. minor* – *G. sackdillingensis*).

The Early Biharian (Early Pleistocene, Pirro F.U.) fauna of Palena (Abruzzi) yielded one tooth of *Glis* cf. *G. sackdillingensis* (KOTSAKIS *et alii*, 1992). From another fauna of the same age, Pirro Nord 24 (Apulia) *Muscardinus avellanarius* and *Eliomys* sp. are reported (DE GIULI *et alii*, 1987a). In the rich fauna of late Early Biharian (latest Early Pleistocene) age collected at Monte Peglia (Umbria) (VAN DER MEULEN, 1973) only one tooth belonging to a small

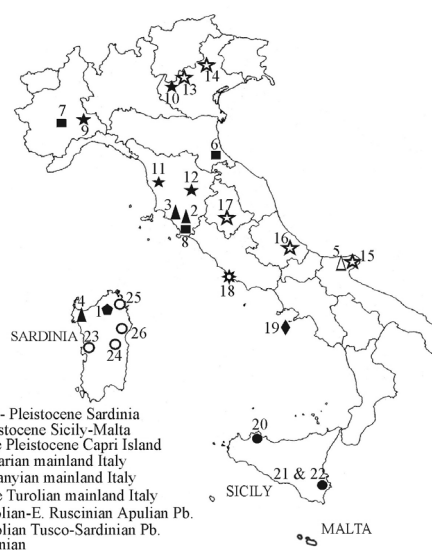


Fig. 1.- Fossiliferous localities of Italy with glirid remains. 1. Oschiri; 2. Baccinello V1 and V2; 3. Montebamboli; 4. Fiume Santo; 5. Gargano fissures; 6. Brisighella; 7. Ciabot Cagna; 8. Baccinello V3; 9. Arondelli (Triversa); 10. Rivoli Veronese; 11. Casa Sgherri; 12. Montagnola Senese; 13. Monte La Mesa; 14. Steggio; 15. Pirro Nord; 16. Palena; 17. Monte Peglia; 18. Grotta Breuil; 19. Capri Island; 20. Monte Pellegrino; 21. Spinagallo; 22. Contrada Fusco; 23. Mandriola; 24. Nuraghe Su Casteddu; 25. Capo Figari; 26. Monte Tuttavista. The localities of Toringian age with glirids belonging to living species are omitted (with the exception of Grotta Breuil where *D. nitedula* is collected well outside its present distribution area).

Fig. 1.- Yacimientos fosilíferos de Italia en que se han hallado restos de gliridos. No se han mencionado los yacimientos del Toringiense en que se hayan hallado restos de gliridos de especies actuales (la única excepción es el yacimiento de Grotta Breuil, por el hecho de que, en este caso, *D. nitedula* ha sido hallado en un área muy lejana respecto a su distribución actual).

Glirulus sp. is signalled. All these assemblages are collected from karstic deposits.

In Toringian faunas (middle and late Middle Pleistocene and Late Pleistocene) *Glis glis* (LINNAEUS, 1766), *Muscardinus avellanarius* (LINNAEUS, 1758) and *Eliomys quercinus* (LINNAEUS, 1766) are present (KOTSAKIS *et alii*, in press). All three species still live on the Italian peninsula.

The first fossil evidence of *Dryomys nitedula* (PALLAS, 1778), the fourth living Italian dormouse species, is from Late Toringian (Late Pleistocene) deposits of N Italy (BON *et alii*, 1991). In Peninsular Italy this species (now living only in Calabria with a disjunct population, *D. n. aspromontis* von LEHMANN, 1964; see STORCH, 1978) was found in deposits of the Grotta Breuil (Monte Circeo, Latium), which are assigned to Late Toringian (Late Pleistocene - Isotopic Stage 3) (KOTSAKIS, 1991).

CAPRI ISLAND

In the Late Pleistocene fauna of the Grotta "Vascio 'o Funno" at the island of Capri (Campania) two species of rodents have been collected, a murid and a glirid. The dormouse, a giant form, *Muscardinus malatestai* GLIOZZI, 1995, is considered to be a descendant of *Muscardinus avellanarius* (CINQUE *et alii*, 1985; GLIOZZI, 1995).

PLIOCENE / PLEISTOCENE OF SARDINIA

During the Messinian "Salinity Crisis" (Late Miocene) Sardinia and Corse were colonised by vertebrates from the European mainland, before the establishment of insular conditions (ESU & KOTSAKIS, 1985). Another colonisation of Sardinia (and Corsica) took place during the latest Ruscinian (late MN 15) (ANGELONE & KOTSAKIS, 2001). Among the invaders (for the glirids is impossible to distinguish if they arrived during the first or the second colonisation), *Eliomys* is considered to be the ancestor of the endemic *Tyrrhenoglis*. The type locality Capo Figari I (NE Sardinia) of *Tyrrhenoglis figariensis* (ZAMMIT MAEMPEL & DE BRUIJN, 1982) may be of Pleistocene age but *T. aff. T. figariensis* is mentioned from the latest Ruscinian (basal Middle Pliocene) lagoon deposit of Mandriola (W Sardinia) (PECORINI *et alii*, 1974; ZAMMIT MAEMPEL & DE BRUIJN, 1982). Another fis-

sure filling at Capo Figari yielded *Tyrrhenoglis majori* ENGESSER, 1976, the type-species of the genus, which is larger in size than *T. figariensis* (cfr. ENGESSER, 1976). The age of both fissure fillings of Capo Figari is not known. In the Early Villanyian (Middle Pliocene) faunule collected in lacustrine clays of Nuraghe Su Casteddu (E Sardinia), a large-sized dormouse is present whose systematic position is not clear. It shows affinities to the endemic *Hypnomys* from the Plio-Pleistocene of the Balearic islands (ESU & KOTSAKIS, 1980, 1985; MEIN, 1983) but an attribution to the genus *Tyrrhenoglis* seems more probable. Many fossil assemblages have been collected from fissure fillings of Plio-Pleistocene age of Monte Tuttavista (Orosei, E Sardinia). In a few of them remains of a glirid have been reported (CORDY, 1997). Very probably they belong to a member of the genus *Tyrrhenoglis*.

During the Pleistocene some new European elements (the ancestors of the arvicolid *Tyrrhenicola* and some large mammals) arrived in Sardinia. Several of the endemic species survived this new wave until Neolithic times, but others such as *Tyrrhenoglis* became extinct (KOTSAKIS, 1981; ESU & KOTSAKIS, 1983).

Glis glis is reported in the layer 1 of the Corbeddu cave near Oliena (E Sardinia) associated with endemic and non endemic micromammals and remains of a Neolithic culture (Sondaar *et alii*, 1984).

PLEISTOCENE OF SICILY AND MALTA

Two endemic lineages of glirids evolved in Sicily and Malta during the (?)Pliocene and Pleistocene. The first lineage is that of *Maltamys* whose ancestor is supposed to be *Eliomys* according to ZAMMIT MAEMPEL & DE BRUIJN (1982). (*Maltamys* is considered as subgenus of *Eliomys* by ZAMMIT MAEMPEL & DE BRUIJN (1982) like the other insular Plio-Pleistocene endemic glirids of Western Mediterranean, *Hypnomys* and *Tyrrhenoglis*, but they have been assigned to separate genera by AGUSTI, 1986 and DAAMS & DE BRUIJN, 1995). The most primitive form of this lineage is present both in the ossiferous breccias of Monte Pellegrino (Palermo, Sicily) (*Leithia* n.sp. in THALER, 1972) and in Malta (*Maltamys* cf. *M. gollcheri* in ZAMMIT MAEMPEL & DE BRUIJN, 1982). The age of the endemic fauna of Monte Pellegrino is presumably Early Pleistocene but the age of Maltese

faunas cannot be given with more precision than Pleistocene. Two more evolved species are present in Malta: *Maltamys gollcheri* (BRUIJN, 1966) from Mnaidra Gap and *Malatamys wiedincitensis* (ZAMMIT

MAEMPEL & DE BRUIJN, 1982) from Wiedincita. Both species, are also present in Sicily in Middle Pleistocene or early Late Pleistocene deposits (KOTSAKIS, 1996; BONFIGLIO *et alii*, 2001).

| GEOCHRONOLOGY | MAMMAL AGES | MN ZONES | ITALIAN FAUNAL UNITS | FOSSILIFEROUS LOCALITIES WITH GLIRIDS | | |
|--------------------|-------------|----------------|---|--|--|---|
| | | | | MAINLAND ITALY | SARDINIA | SICILY |
| HOLOCENE | | | | | | |
| PLEISTOCENE | TORINGIAN | Late | Torre in Pietra F. Ranuccio Isernia | Grotta Breuil Capri Is. | | Contrada Fusco (<i>Elephas mnaidriensis</i> faunal complex) Spinagallo (<i>Elephas falconeri</i> faunal complex) |
| | Early | | | Several localities | | |
| | BIHARIAN | Late | Ponte Galeria Slivia Colle Curti Pirro Farneta Tasso | Monte Peglia Pirro Nord, Palena Monte La Mesa, Steggio | Capo Figari I (?) | Monte Pellegrino (M. Pellegrino faunal complex) |
| | Early | | | | | |
| PLIOCENE | VILLANYAN | Late | Olivola Costa San Giacomo S. Vallier Montopoli Triversa | Casa Sgheri, Montagnola Senese Rivoli Veronese | | |
| | Early | MN 17 MN 16 | | Aronelli (Triversa) | Nuraghe Su Casteddu | |
| | RUSCINIAN | Late | | | Mandriola | |
| | Early | MN 15 MN 14 | | | | |
| MIOCENE | TUROLIAN | Late | | Brisighella, Ciabot C., Baccinello V3 Baccinello V2, Montebamboli | Gargano fissures (<i>Microtia - Hoplitomyx</i> fauna) | Fiume Santo ? |
| | Middle | MN 13 MN 12 | | Baccinello V1 Baccinello V0 | | |
| | AGENIAN | Late | | | | |
| | Early | MN 2 MN 1 | | | Oschiri | |

Table 1.- Biochronological distribution of fossiliferous localities mentioned in the text. In dark gray localities of the Tusco-Sardinian palaeobioprovince. In pale gray localities of Apulian palaeobioprovince.

Tabla 1.- Distribución biocronológica de las localidades fosilíferas mencionadas en el texto. En gris obscuro, las localidades de la provincia Tosco-Sarda. En gris claro, las localidades de la paleobioprovincia de Apulia.

| | <i>Glis major</i> * | <i>Glis minor</i> | <i>Glis sackdillingensis</i> | <i>Glis glis</i> | <i>Glis sp.</i> | <i>Muscardinus vireli</i> | <i>Muscardinus plocaenicus</i> | <i>Muscardinus dacicus</i> | <i>Muscardinus avellamaris</i> | <i>Muscardinus malatestai</i> * | <i>Muscardinus sp.</i> | <i>Stertomys laitrestatus</i> * | <i>Dryomys nitidula</i> | <i>Eliomys quercinus</i> | <i>Eliomys sp.</i> | <i>Leithia melitensis</i> * | <i>Leithia cartei</i> * | <i>Glirulus pusillus</i> | <i>Glirulus sp.</i> | <i>Microdryomys koenigswaldi</i> | <i>Tyrhenoglis majori</i> * | <i>Tyrhenoglis figatensis</i> * | <i>Tyrhenoglis sp.</i> | <i>Maltamys gollcheri</i> * | <i>Maltamys wiednichtensis</i> * | <i>Anthracoaglis marinol</i> * | <i>Anthracoaglis sp.</i> * | <i>Myomimus sp.</i> | <i>Peridromys murinus</i> | Gliridae indet. (giant form) * | Gliridae indet. * | | | |
|--|---------------------|-------------------|------------------------------|------------------|-----------------|---------------------------|--------------------------------|----------------------------|--------------------------------|---------------------------------|------------------------|---------------------------------|-------------------------|--------------------------|--------------------|-----------------------------|-------------------------|--------------------------|---------------------|----------------------------------|-----------------------------|---------------------------------|------------------------|-----------------------------|----------------------------------|--------------------------------|----------------------------|---------------------|---------------------------|--------------------------------|-------------------|------|------|-----|
| AGENIAN / SARDINIA | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Oschiri | X | | | | | | | | | | | | | | | | | | | | aff. | | | | | | | | | | | aff. | | |
| TUROLIAN / TUSCO-SARDINIAN PB | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Baccinello V1 | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | X | | |
| Baccinello V2 | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | | |
| Montebamboli | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | | |
| Fiume Santo | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | |
| TUROLIAN- E. RUSCINIAN / APULIAN PB | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Gargano fissures | | | | | | | | | | | | X | | X | | | | | | | | | | | | | | | | | ssp | | | |
| LATE TUROLIAN / MAINLAND ITALY | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Brisighella | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | |
| Ciobot Cagna | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | |
| Baccinello V3 | | | | | | | aff. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| VILLANYAN / MAINLAND ITALY | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Aronelli (Triversa) | | | | | | | | | | | X | | | | | | | | X | | | | | | | | | | | | | | | |
| Rivoli Veronese | | X | | | | | X | | | | | | | X | | | | | | | | | | | | | | | | | | | | |
| Casa Sgherri | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Montagnola Senese | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | |
| BIHARIAN / MAINLAND ITALY | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Monte La Mesa | | X | | | | | | cf. | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Sleggio | | ? | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pirro Nord | | | | | | | | X | | | | | | X | | | | | | | | | | | | | | | | | | | | |
| Palena | | | | | cf. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Monte Peglia | | | | | | | | | | | | | | | | | | | | | X | | | | | | | | | | | | | |
| EARLY TORINGIAN / MAINLAND ITALY | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Campani Quarry | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Boscochiesanuova | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| San Giovanni di Duino | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Spessa II | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Campo dei Fiori | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| LATE TORINGIAN / MAINLAND ITALY | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Grotta Maggiore di S. Bernardino | | | | X | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | |
| Grotta San Leonardo | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Torre in Pietra, upper levels | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Grotta del Principe, lower levels | | | | X | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | |
| Montorio | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| San Sidero 3 | | | | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | |
| Grotta di Scario, level A | | | | X | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | |
| Grotta San Agostino | | | | X | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | |
| Grotta del Broion | | | | X | | | | X | | | | X | | | | | | | | | | | | | | | | | | | | | | |
| Mezzena Shelter | | | | X | | | | X | | | | | | X | | | | | | | | | | | | | | | | | | | | |
| Tagliente Shelter, lower levels. | | | | X | | | | | | | | | X | X | | | | | | | | | | | | | | | | | | | | |
| Grotta Cala | | | | X | | | | X | | | | | | X | | | | | | | | | | | | | | | | | | | | |
| Grotta di Castelcivita | | | | X | | | | X | | | | | | X | | | | | | | | | | | | | | | | | | | | |
| Moncuoco Torinese | | | | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Grotta Breuil | | | | X | | | | | | | | | | X | X | | | | | | | | | | | | | | | | | | | |
| Praia a Mare | | | | X | | | | X | | | | | | X | X | | | | | | | | | | | | | | | | | | | |
| Grotta Paglicci, inner levels | | | | X | | | | X | | | | | | X | X | | | | | | | | | | | | | | | | | | | |
| Tagliente Shelter, upper levels | | | | X | | | | | | | | | | X | X | | | | | | | | | | | | | | | | | | | |
| Grotta della Serratura | | | | X | | | | X | | | | | | X | X | | | | | | | | | | | | | | | | | | | |
| LATE TORINGIAN / CAPRI ISLAND | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Capri Island | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | |
| PLEISTOCENE / SICILY-MALTA | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Monte Pellegrino | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Spinagallo | | | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | aff. | |
| Some localities with <i>E. falconeri</i> f.c. | | | | | | | | | | | | | | X | X | | | | | | | | | | | | | | | | | | cf. | |
| Contrada Fusco | | | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | X | |
| Many Localities with <i>E. mnaidriensis</i> f.c. | | | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | | | X | |
| PLIO-PLEISTOCENE / SARDINIA | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Mandriola | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | aff. | |
| Nuraghe Su Casteddu | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | |
| Capo Figari I | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X |
| Capo Figari (old collections) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X |
| Monte Tuttavista | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | ssp |

Table 2. Distribution of fossil glirid taxa of Italy. The endemic taxa are marked with an asterisk.

Tabla 2. Distribución de los taxones de gliridos fósiles de Italia. Los taxones endémicos están marcados por un asterisco.

The second lineage, that of *Leithia*, a genus whose origin and affinities are not known includes species of both medium and large size. The large-sized *Leithia melitensis* (ADAMS, 1863) is known from many cave deposits from both Sicily and Malta (RICHARD, 1954; BRUIJN, 1966; PETRONIO, 1971; ZAMMIT MAEMPEL & DE BRUIJN, 1982; ESU *et alii*, 1986; BONFIGLIO *et alii*, 1997) and has been discovered also in limnic or coastal deposits in E Sicily (BONFIGLIO & INSACCO, 1992; KOTSAKIS, 1996). A form slightly different (*Leithia* aff. *L. melitensis*) is reported from Wiedincita by ZAMMIT MAEMPEL & DE BRUIJN (1982). A medium-sized species of the genus *Leithia*, *L. cartei* (ADAMS, 1863) from Malta, is also present in Sicily (Petruso, pers. com.).

The Plio(?)–Pleistocene Sicilian mammalian (and also other vertebrate) faunas have been grouped in five Faunal Complexes (KOTSAKIS, 1979; BONFIGLIO *et alii*, 2001). Fossil endemic glirids are present in the first three Faunal Complexes: in the “Monte Pellegrino F. C.” (*Maltamys* aff. *M. gollcheri*), in the “*Elephas falconeri* F. C.” (*Maltamys gollcheri*, *Leithia melitensis* and *Leithia cartei*) and in the “*Elephas mnaideriensis* F. C.” (*Maltamys* cf. *M. wiedincitensis*, *Leithia* cf. *L. melitensis*) (BONFIGLIO *et alii*, 2001). *Glis glis* make his first appearance in Sicily during the Neolithic (PETRUSO, 2000).

The fossil dormice of Sicily exhibit a greater variety in tooth size than those of Malta in both lineages and also some morphological differences (PETRUSO & MASINI, 2001). A Ph.D. thesis on the fossil glirids of Sicily (Daria Petruso) is in progress.

CONCLUSIONS

The Italian fossil mammalian assemblages reflect the palaeogeographical situations of the area and are characterised by the presence of peculiar endemic faunas testifying insular conditions.

The glirids are rather common in these endemic faunas: three genera (*Peridyromys*, *Microdyromys* and *Glis*), each with one endemic species, are present in the Early Miocene fauna of Oschiri. At least two endemic genera (*Anthracoqlis* and a giant unnamed form) and three species characterise the Late Miocene endemic associations of Tusco-Sardinian palaeobioprovince; at least three genera (*Stertomyx* (endemic), *Eliomys* and (?)*Myomimus*) with many species (only one described till now) are present in

the endemic insular assemblages of Late Miocene Abruzzi-Apulian palaeobioprovince.

The Plio-Pleistocene faunas of Sardinia are characterised by an endemic genus of glirid (*Tyrrhenoglis*) with at least two species whilst in Sicily (and Malta) two endemic genera (*Maltamys* and *Leithia*) with many species (four are officially erected) characterise the Pleistocene endemic faunas. An endemic species of the genus *Muscardinus* is present in an assemblage of very low biodiversity of late Pleistocene age in the island of Capri.

Non-endemic glirids with normal continental distribution are rare in the fossil mammalian assemblages of Italy. Two genera (*Muscardinus* and *Myomimus*) are reported from Late Turolian sites of north and central Italy. *Muscardinus*, *Glis*, *Eliomys* and *Glirulus* are present in Villanyian and Biharian associations of mainland Italy with a rather low number of extinct species, whilst in Toringian the first three genera are present in the same area each with the single living species. During this period *Glirulus* disappears and *Dryomys* makes its first appearance. During Holocene *Glis* and *Eliomys* arrive in Sardinia and Sicily; the last island is also reached by *Muscardinus*. The Holocene colonisations are the result of passive transport by man.

BIBLIOGRAPHY

- ABBAZZI L., BENVENUTI, M., BOSCHIAN, G., DOMINICI, S., MASINI, F., MEZZABOTTA, C., PICCINI, L., ROOK, L., VALERI, G. & TORRE, D. 1996. Revision of the Neogene and Pleistocene of the Gargano region (Apulia, Italy). The marine and continental successions and the mammal faunal assemblages in an area between Apricena and Poggio Imperiale (Foggia). *Memorie della Società Geologica Italiana*, **51**: 383-402.
- AGUSTÍ, J. 1986. Dental evolution in the endemic glirids of the western Mediterranean islands. *Mémoires du Muséum National d'Histoire Naturelle de Paris*, **C**, **53**: 227-232.
- ANGELONE, C. & KOTSAKIS, T. 2001. *Rhagapodemus azzarolii* n.sp. (Muridae, Rodentia) from the Pliocene of Mandriola (Western Sardinia – Italy). *Bollettino della Società Paleontologica Italiana*, **40**: 127-132.
- BENVENUTI, M., PAPINI, M. & ROOK, L. 2001. Mammal biochronology, UBSU and paleoenvironmental evolution in a post-collisional basin: evidence from the Late Miocene Baccinello-Cinigiano basin in southern Tuscany, Italy. *Bollettino della Società Geologica Italiana*, **120**: 97-118.
- BON, M., PICCOLI, G. & SALA, B. 1981. I giacimenti quaternari di vertebrati fossili nell'Italia nord-occidentale. *Memorie di Scienze Geologiche*, **43**: 185-231.

- BONFIGLIO, L. & INSACCO, G. 1992. Palaeoenvironmental, palaeontological and stratigraphical significance of vertebrate remains in Pleistocene limnic and alluvial deposits from South Eastern Sicily. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **95**: 195-208.
- INSACCO, G., MARRA, A.C. & MASINI, F. 1997. Large and small mammals, amphibians and reptiles from a new late Pleistocene fissure filling deposit of the Hyblean Plateau (South Eastern Sicily). *Bollettino della Società Paleontologica Italiana*, **36**: 97-122.
- MANGANO, G., MARRA, A.C. & MASINI, F. 2001. A new late Pleistocene vertebrate faunal complex from Sicily (S. Teodoro cave, North-eastern Sicily, Italy). *Bollettino della Società Paleontologica Italiana*, **40**: 149-158.
- BRUIJN, H. DE 1966. On the Pleistocene Gliridae (Mammalia, Rodentia) from Malta and Mallorca. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, B, **69**: 481-496.
- & RÜMKE, C.G. 1974. On a peculiar association from the Miocene of Oschiri (Sardinia). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, B, **77**: 45-79.
- CAVALLO, O., SEN, S., RAGE, J.-C. & GAUDANT, J. 1994. Vertébrés messiniens du faciès à congéries de Ciabòt Cagna, Cornelianò d'Alba (Piémont, Italie). *Rivista Piemontese di Storia Naturale*, **14**: 3-22.
- CINQUE, A., GLIOZZI, E. & ESU, D. 1986. Il riempimento della grotta "Vascio 'o Funno" a Capri. Primi risultati dello studio geomorfologico e paleontologico. *Pubblicazioni del Dipartimento di Scienze della Terra dell'Università di Napoli*, **33**: 105-119.
- CORDY, J.M. 1997. I karst fossiliferi di Orosei. In: *Il Monte Tuttavista Orosei*. S. GINESU & J.-M. CORDY, Eds. pag. 34-45. Gallati, Edizioni Poddighe, Sassari.
- GINESU, S., OZER, A. & SIAS, S. 1996. Geomorphological and palaeogeographical characteristics of the *Oreopithecus* site of Fiume Santo (Sassari, Northern Sardinia, Italy). *Geografia Fisica e Dinamica Quaternaria*, **18**: 7-16.
- DAAMS, R. 1981. The dental pattern of the dormice *Dryomys*, *Myomimus*, *Microdryomys* and *Peridyromys*. *Utrecht Micropaleontological Bulletin, Sp. Publ.*, **3**: 1-115.
- 1999. Family Gliridae. In: *The Miocene Land Mammals of Europe*. E. RÖSSNER & K. HEISSIG, Eds. pag. 301-318. Verlag Dr. Friedrich Pfeil. München.
- & BRUIJN, H. DE 1995. A classification of the Gliridae (Rodentia) on the basis of dental morphology. *Hystrix*, n.s., **6**(1994): 3-50.
- & FREUDENTHAL, M. 1985. *Stertomys laticrestatus*, a new glirid (dormice, Rodentia) from the insular fauna of Gargano (Prov. of Foggia, Italy). *Scripta Geologica*, **77**: 21-27.
- DAUD, A. 1993. Evolution of Gliridae (Rodentia, Mammalia) in the Pliocene and Quaternary of Poland. *Acta Zoologica Cracoviensis*, **36**: 199-231.
- DE GIULI, C. 1989. The rodents of the Brisighella latest Miocene fauna. *Bollettino della Società Paleontologica Italiana*, **28**: 197-212.
- MASINI, F. & TORRE, D. 1987a. The latest Villafranchian faunas in Italy: the Pirro Nord fauna (Apricena, Gargano). *Palaeontographia Italica*, **74**(1986): 51-62.
- MASINI, F. & TORRE, D. (1990) - Island endemism in the Eastern Mediterranean mammalian paleofaunas: radiation patterns in the Gargano paleo-archipelago. *Atti dei Convegni Lincei*, **85**: 247-262.
- MASINI, F. & VALERI, G. 1987b. Paleogeographic evolution of the Adriatic area since Oligocene to the Pleistocene. *Rivista Italiana di Paleontologia e Stratigrafia*, **93**: 109-126.
- ENGESSER, B. 1976. *Tyrhenoglis majori*, ein neuer fossiler Gliridae (Rodentia, Mammalia) aus Sardinien. *Eclogae Geologicae Helvetiae*, **69**: 783-793.
- 1983. Die jungtertiären Kleinsäuger des Gebietes der Maremma (Toskana, Italien). 1. Teil: Gliridae (Rodentia, Mammalia). *Eclogae Geologicae Helvetiae*, **76**: 763-780.
- 1989. The Late Tertiary small mammals of the Maremma region (Tuscany, Italy). 2nd part: Muridae and Cricetidae (Rodentia, Mammalia). *Bollettino della Società Paleontologica Italiana*, **28**: 227-252.
- ESU, D. & KOTSAKIS, T. 1980. Presenza di *Hypnomys* Bate (Gliridae, Rodentia) nel Villafranchiano di Nuraghe Su Casteddu (Nuoro, Sardegna). *Rendiconti dell'Accademia Nazionale dei Lincei*, **8**, **68**: 123-127.
- & KOTSAKIS, T. 1983. Paleobiogeografia dei vertebrati e dei molluschi continentali del Terziario e del Quaternario della Sardegna. *Lavori della Società Italiana di Biogeografia*, n.s., **8**: 53-82.
- & KOTSAKIS, T. 1985. Les vertébrés et les mollusques continentaux de la Sardaigne: paléobiogéographie et biostratigraphie. *Geologica Romana*, **22**(1983): 177-206.
- KOTSAKIS, T. & BURGIO, E. 1986. I vertebrati e i molluschi continentali pleistocenici di Poggio Schinaldo (Palermo, Sicilia). *Bollettino della Società Geologica Italiana*, **105**: 233-241.
- FILIPPUCI, M.G. & KOTSAKIS, T. 1995. Biochemical systematics and evolution of Myoxidae. *Hystrix*, n.s., **6**(1994): 77-97.
- FONDI, R. 1972. Fauna cromeriana della Montagnola senese. *Palaeontographia Italica*, **68**: 1-27.
- FREUDENTHAL, M. 1985. Zonation of the Neogene mammal faunas from Gargano (Italy). *Abstracts of the VIII RCMNS Congress*, pag. 221-223, Budapest.
- MARTIN-SUAREZ, E. & BENDALA, N. 2002. Molar wear as an age indicator in *Apodemus* (Rodentia, Mammalia). *Abstracts of the International Conference in Honor of H. De Bruijn "Distribution and Migration of Tertiary Mammals in Eurasia"*, pag. 18-20, Utrecht.
- GINSBURG L. & ANTUNES, M.T. 1979. Les Rhinocerotidés du Miocène inférieur et moyen de Lisbonne (Portugal). Succession stratigraphique et incidences paléogéographiques. *Comptes Rendues de l'Académie de Sciences de Paris*, D, **288** : 493-495.
- GLIOZZI, E. 1995. Un nouveau muscardin (Gliridae, Rodentia) endémique du Pléistocène supérieur de l'île de Capri (Italie). *Il Quaternario*, **8**: 257-262.
- ABBAZZI, L., ARGENTI, P., AZZAROLI, A., CALOI, L., CAPASSO BARBATO, L., DI STEFANO, G., ESU, D., FICCARELLI, G., GIROTTI, O., KOTSAKIS T., MASINI, F., MAZZA, P., MEZZABOTTA, C., PALOMBO, M. R., PETRONIO, C., ROOK, L., SALA, B., SARDELLA, R., ZANALDA, E. & TORRE, D. 1997. Biochronology of

- selected mammals, molluscs and ostracods from the middle Pliocene to the late Pleistocene in Italy. The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia*, **103**: 369-388.
- KOTSAKIS, T. 1979. Sulle mammalofaune quaternarie siciliane. *Bollettino del Servizio Geologico d'Italia*, **99**(1978): 263-276.
- 1981. Osservazioni sui vertebrati quaternari della Sardegna. *Bollettino della Società Geologica Italiana*, **99**(1980): 151-165.
- 1991. Late Pleistocene fossil microvertebrates of Grotta Breuil (Monte Circeo, Central Italy). *Quaternaria Nova*, **1**: 325-332.
- 1996. I micromammiferi. In: *Siracusa. Le ossa dei giganti. Lo scavo paleontologico di Contrada Fusco*. B. Basile & S. Chirlardi, Eds. pag. 68-71. Arnaldo Lombardi, Siracusa-Palermo.
- ABBAZZI, L., ANGELONE, C., ARGENTI, P., BARISONE, G., FANFANI, F., MARCOLINI, F. & MASINI, F. in press. Plio-Pleistocene biogeography of Italian mainland micromammals. *Deinsea*, Rotterdam.
- BARISONE, G. & ROOK, L. 1997. Mammalian biochronology in an insular domain: the Italian Tertiary faunas. *Actes du Congrès Biochrom'97, Mémoires et Travaux de l'E.P.H.E. Institut de Montpellier*, **21**: 431-441.
- ESU, D. & GIROTTI, O. 1992. A post-Villafranchian cold event in Central Italy testified by continental molluscs and rodents. *Bollettino della Società Geologica Italiana*, **111**: 335-340.
- MARCHETTI, M., PAROLIN, K. & SALA, B. 2000. The Biharian fauna from Monte La Mesa (Verona, northeastern Italy). *Acta Zoologica Cracoviensia*, **43**: 79-105.
- MARCOLINI, F., BONADONNA, F.P., KOTSAKIS, T., MAZZA, P. & ZANCHETTA, G. 2000. Preliminary data on the micro- and macromammal remains from Casa Sgherri, Lower Valdarno (Tuscany, Italy). *Bollettino della Società Paleontologica Italiana*, **39**: 243-252.
- MARTIN-SUAREZ, E. & MEIN, P. 1998. Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios*, **31**: 87-97.
- MEIN, P. 1983. Particularités de l'évolution insulaire chez les petits mammifères. *Colloque International du C.N.R.S.*, **330**: 189-193.
- MEULEN, A.J. VAN DER 1973. Middle Pleistocene smaller mammals from Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). *Quaternaria*, **17**: 1-144.
- MICHAUX, J. 1970. Les rongeurs (Arvicolidés, Muridés et Gliridés) de la localité Arondelli à Villafranca d'Asti (Italie). *Palaeontographia Italica*, **66**: 69-80.
- PARONUZZI, P. 1994. Facies and depositional architecture of the Upper Villafranchian in the Steggio Basin, North-eastern Alps (Treviso, Italy). *Abstracts of AIQUA Congress «Il significato del Villafranchiano nella stratigrafia del Plio-Pleistocene»*, 2 pag., Peveragno.
- PARRA, V., JAEGER, J.-J. & BOCHERENS, H. 1999. The skull of *Microtia*, an extinct burrowing murine rodent of the Late Neogene of Gargano palaeoisland. *Lethaia*, **32**: 89-100.
- PECORINI, G., RAGE, J.C. & THALER, L. 1974. La formation continentale de Capo Mannu, sa faune de vertébrés pliocènes et la question du Messinien en Sardaigne. *Rendiconti del Seminario della Facoltà di Scienze dell'Università di Cagliari*, vol. sp. Paleogeografia del Terziario Sardo, pag. 306-319.
- PETRONIO, C. 1971. I roditori pleistocenici della Grotta di Spinalgato (Siracusa). *Geologica Romana*, **9**(1970): 149-194.
- PETRUSO, D. 2000. I ghiri della Sicilia antica. In: *I ghiri in Sicilia*. M. Sarà, Ed. pag. 27-41, Doramarkus, Palermo.
- & MASINI, F. 2001. Dormice (Mammalia: Gliridae) records from the Pleistocene of Sicily. *Abstracts of the 6th European Workshop on Vertebrate Palaeontology*, pag. 48, Florence and Montevarchi.
- RICHARD, C. 1954. Il ghiri gigante del Pleistocene di Sicilia ("Leithia melittensis Leith Adams"). *Palaeontographia Italica*, **44**(1947-51): 1-52.
- ROOK, L. & TORRE, D. 1995. *Celadensia grossetana* nov. sp. (Cricetidae, Rodentia) from the Late Turolian of Baccinello – Cinigiano basin (Italy). *Geobios*, **28**: 379-382.
- SALA, B. 1996. *Dinaromys allegranzi* n. sp. (Mammalia, Rodentia) from Rivoli Veronese (north-eastern Italy) in a Villanyian association. *Acta Zoologica Cracoviensia*, **39**: 469-472.
- MASINI, F. & TORRE, D. 1994. Villanian arvicolids from Rivoli Veronese, a karst fissure in the Adige Valley, Northeastern Italy. *Bollettino della Società Paleontologica Italiana*, **33**: 3-11.
- SONDAAR, P.Y., BOER, P.L. DE, SANGES, M., KOTSAKIS, T. & ESU, D. 1984. First report on a paleolithic culture in Sardinia. *British Archaeological Reports International Series*, **229**: 29-47.
- STORCH, G. 1978. Familie Gliridae. In: *Handbuch der Säugethiere Europas*. J. NIETHAMMER & F. KRAPP (Eds.), vol. 1, pag. 201-280. Akademische Verlagsgesellschaft. Wiesbaden.
- THALER, L. 1972. Les rongeurs (Rodentia et Lagomorpha) du Monte Pellegrino et la question des anciens isthmes de la Sicile. *Comptes Rendues de l'Académie de Sciences de Paris*, **D, 274**: 188-190.
- TORRE, D., ABBAZZI, L., DELFINO, M., FANFANI, F., FERRETTI, M., FICCARELLI, G., MAZZA, P., RUSTIONI, M. & ROOK, L. 2000. Mammal paleobioprovinces in the Italian Late Miocene. *Abstracts of the XI RSMNS. Congress*, pag. 42, Fez.
- ZAMMII MAEMPEL, G. & BRUIJN, H. DE 1982. The Plio/Pleistocene Gliridae from the Mediterranean Islands reconsidered. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **B, 85**: 113-128.

