Messinian rodents from Moncucco Torinese, NW Italy: palaeobiodiversity and biochronology

Simone COLOMBERO
Giulio PAVIA
Giorgio CARNEVALE
Dipartimento di Scienze della Terra, Università degli Studi di Torino,
Via Valperga Caluso 35, I-10125, Torino (Italia)
simone.colombero@unito.it
giulio.pavia@unito.it
giorgio.carnevale@unito.it

Colombero S., Pavia G. & Carnevale G. 2014. — Messinian rodents from Moncucco Torinese, NW Italy: palaeobiodiversity and biochronology. *Geodiversitas* 36 (3): 421-475. http://dx.doi.org/10.5252/g2014n3a4

ABSTRACT

The rodents from the Upper Messinian deposits of Moncucco Torinese (MCC) (Piedmont, NW Italy) are described. Stratigraphic considerations indicate that the fossiliferous deposits exposed at MCC date back to the post-evaporitic phase of the Messinian Salinity Crisis (5.40-5.33 Ma). Thirteen rodent taxa belonging to the families Cricetidae Fischer, 1817, Muridae Illiger, 1811, Gliridae Thomas, 1897 and Sciuridae Fischer, 1817 are recognized based on 1177 teeth. The occurrence of *Centralomys benericettii* (De Giuli, 1989), *Paraethomys meini* (Michaux, 1969) and *Apodemus gudrunae* van de Weerd, 1976 allows to compare MCC with other latest Messinian localities of northern Italy, such as Brisighella and Verduno. The rodent assemblages described herein and, more particularly, the taxa *A. gudrunae*, *Muscardinus vireti* Hugueney & Mein, 1965 and *Glirulus lissiensis* Hugueney & Mein, 1965, suggest that MCC can be referred to the Late Turolian (MN13). Moreover, the presence of taxa commonly found in Pliocene localities of western and central Europe (*Occitanomys brailloni* Michaux, 1969, *Micromys bendai* van de Weerd, 1979, *Neocricetodon magnus* (Fahlbusch, 1969) and *Sciurus warthae* Sulimski, 1964) indicates that some typical Ruscinian elements were already present at the end of the Miocene at least in southern-central Europe. The rodent assemblages of MCC also include *Apodemus atavus* Heller, 1936, *Eliomys* aff. *intermedius* Friant, 1953, *Glis minor* Kowalski, 1956, and *Pliopetaurista pliocaenica* (Depéret, 1897). Overall, the fossil assemblages documented in this paper remarkably expand our knowledge on the Late Miocene rodent communities of Italy, also providing useful data for the interpretation of biogeographic relationships between western and eastern Europe at the end of the Messinian.

KEY WORDS
Rodentia,
Turolian,
Late Messinian,
Italy.

RÉSUMÉ
Rongeurs messiniens de Moncucco Torinese, NW Italie: paléobiodiversité et biochronologie.
Les rongeurs des gisements du Messinien supérieur de Moncucco Torinese (MCC) (Piémont, NW Italie) sont décrits. Analyses biostratigraphiques indiquent que les gisements de MCC se corrèlent à la phase post-évaporitique de la Crise de salinité messinienne (5,40 à 5,33 Ma). Treize espèces des rongeurs appartenant aux familles de Cricetidae Fischer, 1817, Muridae Illiger, 1811, Gliridae Thomas, 1897 et Sciuridae Fischer, 1817 ont été reconnues sur la base de 1177 dents. L'apparition de *Centralomys benericettii* (De Giuli, 1989)*, Paraethomys meini* (Michaux, 1969) et *Apodemus gudrunae* van de Weerd, 1976 permet de comparer MCC avec d'autres localités du nord de l'Italie du Messinien terminal, comme Brisighella et Verduno. Les assemblages de rongeurs décrits et, plus particulièrement les taxons *A. gudrunae, Muscardinus vireti* Hugueney & Mein, 1965 et *Glirulus lissiensis* Hugueney & Mein, 1965*,* suggèrent que les gisements de MCC peuvent être attribués au Turolien supérieur, (MN13). Par ailleurs, la présence d'espèces communément trouvées dans les localités du Pliocène de l'Europe occidentale et centrale (*Occitanomys brailloni* Michaux, 1969*, Micromys bendai* van de Weerd, 1979*, Neocricetodon magnus* (Fahlbusch, 1969) and *Sciurus warthae* Sulimski, 1964) indique que certains éléments des faunes rusciniennes étaient déjà présents à la fin du Miocène au moins dans centre-sud de l'Europe. Les assemblages de rongeurs MCC comprennent aussi *Apodemus atavus* Heller, 1936, *Eliomys* aff. *intermedius* Friant, 1953, *Glis minor* Kowalski, 1956 et *Pliopetaurista pliocaenica* (Depéret, 1897). Globalement, ces assemblages élargissent remarquablement notre connaissance sur les communautés de rongeurs du Miocène supérieur de l'Italie, en fournissant également des données utiles pour l'interprétation des relations biogéographiques entre l'Europe occidentale et orientale à la fin du Messinien.

MOTS CLÉS
Rodentia,
Turolien,
Messinien supérieur,
Italie.

INTRODUCTION

The Miocene record of continental vertebrates of Italy includes a small number of localities, most of which are characterized by endemic assemblages resulted from evolutionary radiation in isolated contexts such as islands or archipelagos (Rook *et al.* 2006). Endemic faunas are well known from the Apulo-Abruzzo (Freudenthal 1971; Zafonte & Masini 1992; Rinaldi & Masini 2009; Patacca *et al.* 2013; Villier & Carnevale 2013; Villier *et al.* 2013) and Tusco-Sardinian paleobioprovinces (Engesser 1983; 1989; Kotsakis *et al.* 1997; Rook *et al.* 2011) whereas non-endemic faunas are actually extremely rare and sparse (Kotsakis 1986), primarily documented from central Italy (Marabini & Vai 1989; Ghetti *et al.* 2002; Abbazzi *et al.* 2008). The most conspicuous assemblages known to date are those of Baccinello V3 in Tuscany (Engesser 1983, 1989; Kotsakis *et al.* 1997; Rook *et al.* 1999; Rook *et al.* 2011) and Monticino quarry (Brisighella) in Romagna (De Giuli 1989; Kotsakis 1989; Torre 1989; Masini & Thomas 1989). More recently, two additional localities, Verduno (Colombero *et al.* 2013, 2014) and MCC (Angelone *et al.* 2011), have been discovered in the latest Messinian deposits of the Tertiary Piedmont Basin (TPB), NW Italy, thereby filling a broad gap in our knowledge of the fossil vertebrate faunas from this poorly known area. A cursory analysis of the vertebrate remains from MCC was recently carried out based on a small amount of fossils resulted from the first exploration of the productive site in summer 2008 (Angelone *et al.* 2011). Since then, new excavation campaigns led to the recovery of a large amount of material that allows us to better define the taxonomic composition of the fossil assemblages from different layers of MCC. The goals of this paper are therefore to describe the rich and diverse rodent assemblages from MCC and to determine the age of this locality.

Due to the pivotal position of the Italian territory in the Mediterranean context, the fossil rodent communities of north-western Italy certainly play a key role in the proper interpretation of the Late Turolian terrestrial biogeography of southern Europe. As a matter of fact, the Late Messinian vertebrate communities from western and south-eastern Europe have provided a large amount of data due to the abundant record from Spain (Mein *et al.* 1990; Martín-Suárez & Freudenthal 1998; Martín-Suárez *et al.* 2000; García-Alix *et al.* 2008a; Minwer-Barakat *et al.* 2012), France (Hugueney & Mein 1965; Aguilar *et al.* 1989, 1991) and Greece (van de Weerd 1979; Schmidt-Kittler *et al.* 1995; Hordijk & de Bruijn 2009). Some recent discoveries in Ukraine (Nesin & Nadachowski 2004) improved our knowledge of rodent faunas from the regions close to the boundaries with western Asia. On the contrary, Late Turolian localities are extremely scarce in central Europe, the most important being Polgardi in Hungary (Kretzoi 1952; Freudenthal & Kordos 1989). The localities from the Italian Peninsula provide reliable information about the possible biogeographic relationships between different European regions during the Late Miocene. The correlation of the localities from eastern and western Europe on the basis of consistent biochronological data is rather problematic due to the lack of record from central Europe. This absence of record aggravates the biases of large-scale biochronological correlations, including the great provincialism that characterized the rodent faunas during the Neogene (van Dam 2003; Gómez Cano *et al.* 2011), as well as the diachrony of mammal events (Sen 1997; van Dam 2003; van der Meulen *et al.* 2011). The rodent assemblages described herein therefore represent a useful tool for understanding the relationships between distant regions of Europe, also providing new intriguing data that allow to properly define the paleontological record of rodents at the end of the Miocene in Europe. Moreover, the high number of rodent taxa recognized appears to be extremely useful for biochronological correlations, not only with roughly coeval Italian localities, but also with those from western and eastern Europe.

GEOLOGICAL AND STRATIGRAPHIC SETTING

The TPB is an episutural basin, filled by a complex succession of Late Eocene to Messinian sediments that unconformably cover the contact between the Alpine and Apennine units. The TPB sediments are extensively exposed in the Torino Hill-Monferrato arch and in the Langhe, Alto Monferrato and Borbera-Grue domains (Mosca *et al.* 2010; Dela Pierre *et al.* 2011). The sedimentary evolution of the TPB was strongly influenced by the tectonic movements that involved the Alps-Apennine junction. The pre-Messinian succession is constituted by marine and, more rarely, continental sediments that until the Early Miocene were deposited in small fault-bounded basins. During the Burdigalian, the basin took the form of a larger and more uniform wedge-top basin delimited to the north by the Monferrato arch that in that period corresponded to a structurally-high area. During the Middle Miocene the southern sector of the TPB underwent through a progressive uplift and north-verging tilting. This process continued during the Late Miocene due to the regional N-S shortening caused by the north verging Apennine tectonics that affected also the Torino Hill area.

As in other sectors of the Mediterranean basin, at the end of the Miocene the sedimentary processes were strongly influenced by the Messinian Salinity Crisis (MSC) (CIESM 2008; Dela Pierre *et al.* 2007, 2011). The Lower Messinian deposits consist of the deep-water marine sediments of the Marne di Sant'Agata Fossili Marls Formation (SAF) primarily represented by hemipelagic marls and clays. These sediments are covered by the evaporitic deposits of the Primary Lower Gypsum Formation (PLG; formerly known as Vena del Gesso Formation), mainly consisting of different gypsum lithofacies alternated with euxinic shales. This unit corresponds to the evaporitic interval of the MSC and was deposited between 5.96 and 5.60 Ma (CIESM 2008). The cyclic deposition of gypsum and shale beds appears to be related to climatic changes linked to the Earth's precession (Krijgsman *et al.* 1999). The second stage of the MSC, also known as "MSC acme" (5.60-5.55 Ma, CIESM 2008), corresponds to a sea-level drop occurred at the Mediterranean scale, caused by the strong reduction in the Atlantic connections that in some areas led to the erosion of the PLG with the formation of the Messinian Erosional Surface (MES). In the TPB the MES is mainly recognizable in the marginal area of the basin (Dela Pierre *et al.* 2011). Nonetheless, in some sectors of the TPB, this phase caused the resedimentation of the erosive products, commonly reorganized in the chaotic or slumped deposits of the Valle Versa chaotic complex (VVC), which can be assigned to the Resedimented Lower Gypsum (RLG) units of other basinal areas of the Mediterranean (CIESM 2008; Dela Pierre *et al.* 2011). The uppermost portion of the Messinian succession of the TPB consists of the fresh-and brackish-water sediments (muddy and silty beds crossed by sandy and gravel layers) of the Conglomerati di Cassano Spinola Formation (CSC). This unit was deposited during the post-evaporitic phase of the MSC (5.55-5.33 Ka) (CIESM 2008; Dela Pierre *et al.* 2011), a time interval that recorded the so-called Lago Mare event (CIESM 2008). According to the traditional interpretation, the Mediterranean basin previously desiccated during the Salinity Crisis, would have been refilled with fresh and brackish water of Parathethyan origin (Cita *et al.* 1978; McCulloch & De Dekker 1989; Krijgsman *et al.* 1999) up to the normal marine conditions were restored at the beginning of the Pliocene with the Zanclean flooding. Nonetheless, the occurrence of marine stenohaline fishes (Carnevale *et al.* 2006a, b) and the geochemical data from fish otholiths and other fossils from some localities of central Italy (Carnevale *et al.* 2008) indicate that at least at the end of the Messinian the Mediterranean basin was already characterized by normal marine conditions. The Messinian deposits are therefore overlain by the Zanclean deposits of the Argille Azzurre Formation consisting of marine shales and marls (Dela Pierre *et al.* 2007; Mosca *et al.* 2010).

The productive site of MCC is located in a gypsum quarry in the northern sector of the TPB (Fig. 1), on the southern slope of the Torino Hill. The Messinian succession of this area is characterized by extensive sinsedimentary tectonic and diapiric processes, resulting in the *in-situ* dismemberment and consequent resedimentation of the pre-evaporitic (Marne di Sant'Agata Fossili Formation) and evaporitic (PLG) deposits during the successive phases. These processes led to the formation of the Valle Versa chaotic complex that was deposited during the "MSC acme" (5.60-5.55 Ma) and the initial parts of the post-evaporitic phase (Dela Pierre *et al.* 2007; CIESM 2008). This complex succession was then sealed, during the following post-evaporitic phases of the MSC (5.55-5.33 Ma) by the fresh and brackish water sediments of the Conglomerati di Cassano Spinola Formation that crop out in the upper portion of the quarry. The Conglomerati di Cassano Spinola are in turn overlain by the Zanclean marine marly clays of the Argille Azzurre Formation. The *Sphaeroidinellopsis* Banner & Blow, 1959 acme interval (5.30-5.21 Ma) was recognized slightly above an arenitic barren black level that marks the beginning of the Pliocene succession (Violanti *et al.* 2011).

Vertebrate fossils are extremely abundant in the Conglomerati di Cassano Spinola Formation together with fresh and brackish molluscs and ostracods (Angelone *et al.* 2011). During the excavation campaign, five fossiliferous levels were recognized in a three-meter thick succession (Fig. 2). The vertebrate fossil-bearing layers are named herein MCC3, MCC4, MCC5 and MCC7 (Angelone *et al.* 2011). The fossiliferous deposits mainly consist of silty and sandy clays including conglomeratic lenses. Vertebrate remains are not found in the basal layer MCC1, which instead contains brackish-water ostracods that

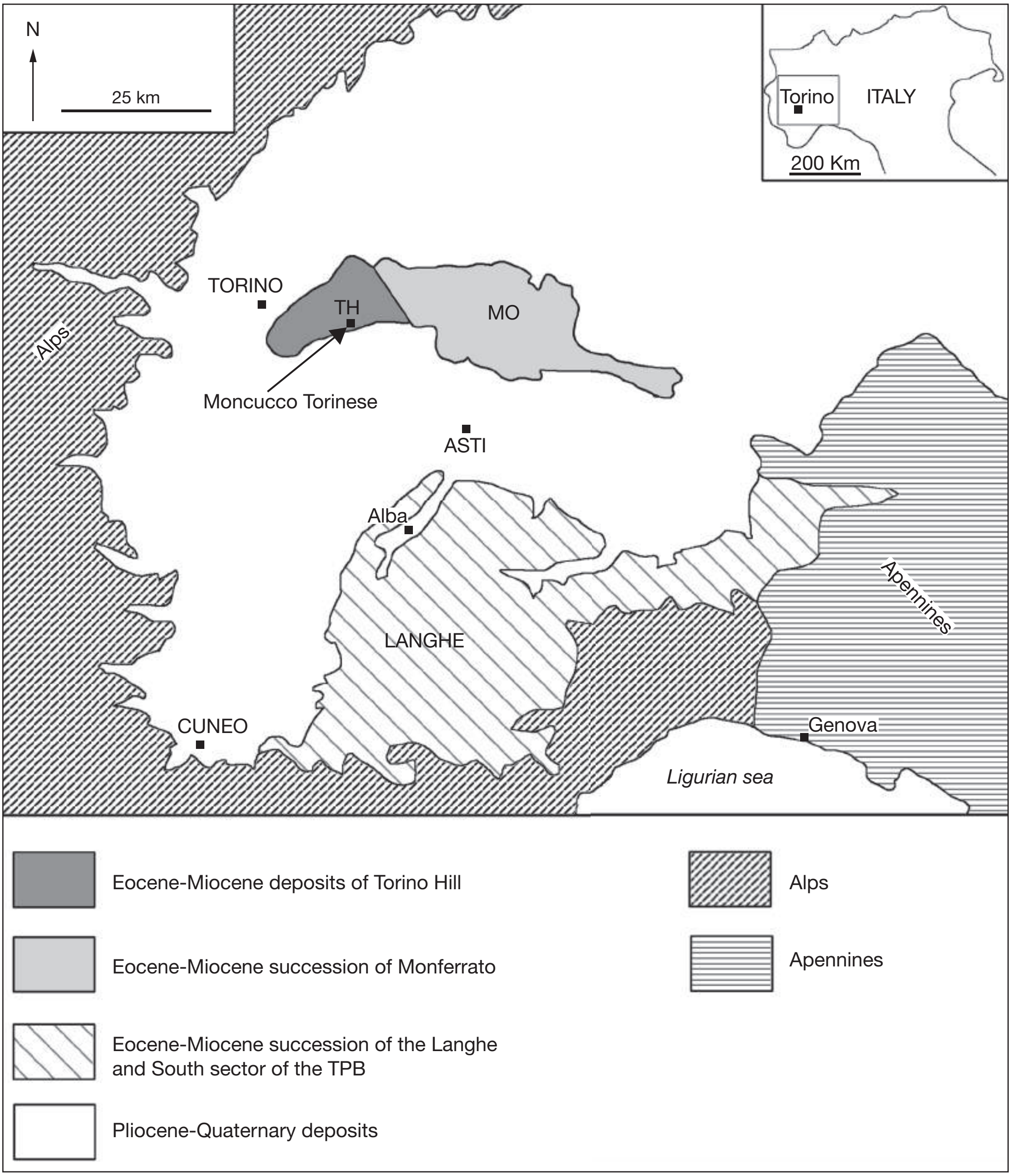

FIG. 1. — Geographic and stratigraphic setting of the Tertiary Piedmont Basin (**TPB**). The arrow indicates the position of Moncucco Torinese. Abbreviations: **TH**, Torino Hill; **MO**, Monferrato. Modified from Clari *et al.* (1994).

are correlatable with the *Loxocorniculina djafarovi* Schneider *in* Suzin, 1956 assemblage, suggesting an age that cannot be older than 5.40 Ma (Grossi *et al.* 2011), therefore correlatable with the so-called second post-evaporitic phase of the MSC (p-ev2) (CIESM 2008).

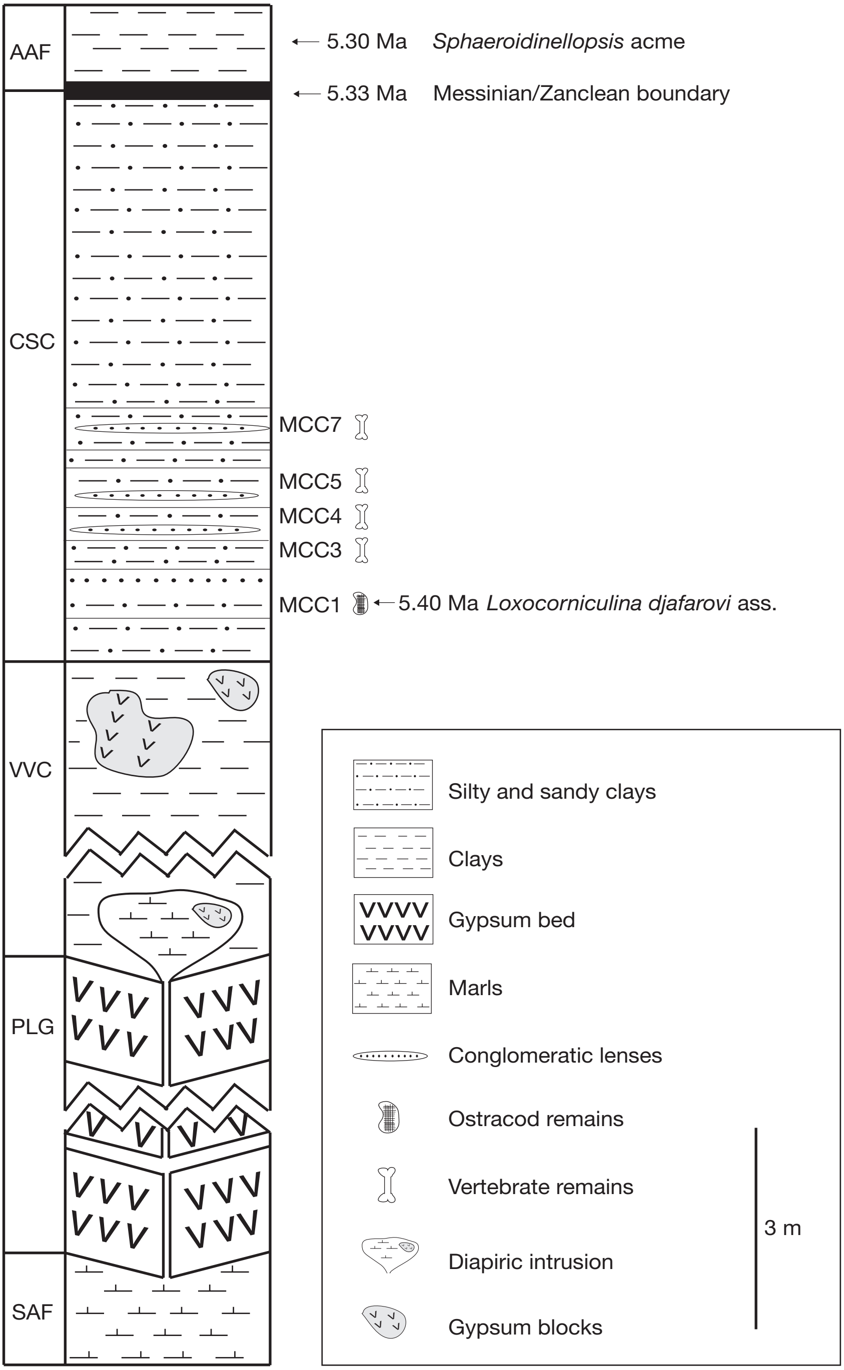

FIG. 2. — Stratigraphic scheme of the Moncucco Torinese section. Fossiliferous layers are indicated with the abbreviation **MCC**. Arrows indicate the main stratigraphic event recorded in the section. For further details see Dela Pierre *et al.* (2007) and Angelone *et al.* (2011). Abbreviations: **AAF**, Argille Azzurre Formation; **CSC**, Cassano Spinola Conglomerates; **VVC**, Valle Versa Chaotic complex; **PLG**, Primary Lower Gypsum; **SAF**, Sant'Agata Fossils marls.

MATERIAL AND METHODS

During the excavations at the MCC fossil site, two tons of sediments were collected from each fossiliferous layer (MCC3, MCC4, MCC5, MCC7). The sediment was successively screenwashed and sieved in order to obtain small vertebrate remains. The material is currently housed in the Museo di Geologia e Paleontologia, Università degli Studi di Torino (MGPT-PU). The number of rodent teeth recovered from each level consists in: 80 from MCC3, 195 from MCC4, 746 from MCC5, and 156 from MCC7. A complete list of the studied material is available in the Appendix 1.

Material from several Neogene European localities was used for comparative purposes (Appendix 2), which is stored in the following institutions: University of Lyon 1 (France), Instituut voor Aardwetenschappen Utrecht (The Netherlands), Netherlands Centre for Biodiversity-Naturalis of Leiden (The Netherlands), Dipartimento di Scienze della Terra, Università degli Studi di Firenze (Italy), Dipartimento di Studi Umanistici-sezione di Paleobiologia, Università degli Studi di Ferrara (Italy) and Dipartimento di Scienze della Terra, Università degli Studi di Torino (Italy).

Nomenclature and the measurements follow those of Freudenthal *et al.* (1994) and Cuenca-Bescós (2003) for the Cricetidae Fischer, 1817, van de Weerd (1976) for the teeth of Muridae Illiger, 1811, Daams (1981) and Engesser (1972) for the Gliridae Thomas, 1897, and Casanovas-Villar (2007) for the Sciuridae Fischer, 1817. Measures are given in mm. Upper teeth are indicated with capital letters (P4, M1, M2, M3); lower teeth are indicated by the lower case letters (p4, m1, m2, m3).

ABBREVIATIONS

Institutional abbreviations

MCC	Moncucco Torinese;
MGPT-PU	Museo di Geologia e Paleontologia-Collezione paleontologica dell'Università di Torino;
UNIFE	University of Ferrara;
UNIFI	University of Firenze;
UCBL	University of Lyon 1;
IVAU	Instituut voor Aardwetenschappen of Utrecht;
RMNH	Naturalis Biodiversity Center of Leiden.

Anatomical abbreviations

L	length;
W	width;
t1-t12	upper molar cusps of Muridae;
tma	anterocentral cuspid;
c1	accessory posterior cuspid.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family CRICETIDAE Fischer, 1817
Genus *Neocricetodon* Schaub, 1934

Neocricetodon magnus (Fahlbusch, 1969)
(Fig. 3A-F)

Kowalskia magna Fahlbusch, 1969: 112, pl. 9, fig. 6, pl. 10, figs 1, 2, pl.17, figs 1-6. — Pradel 1988: 252, pl. 9, figs 8-13.

Rotundomys (*Kowalskia*) *magna* – Janossy 1972: 34, pl. 2, figs 4, 5.

TYPE LOCALITY. — Podlesice, Poland.

REFERRED MATERIAL. — Two fragmented M1, two M3, four m1, seven m2, three m3. See further details in Appendix 1.

OCCURRENCE IN THE STUDIED LAYERS. — MCC4, MCC5, MCC7.

MEASUREMENTS. — Table 1.

DESCRIPTION

M1

The two available specimens are fragmented, lacking the posterior part. Anterocone split into two tubercles; the lingual anterolophule is present whereas the labial one is absent; in one specimen a low labial spur of the anterolophule develops in the anterosinus; anterior protoloph present; mesoloph partially preserved in one specimen in which is also visible a mesostyle.

M3

Labial anterolophule better developed than the lingual one; double protolophule; posterior part of the tooth strongly reduced: the posterior part is composed by a complex system of enamel crests and swellings in which hypocone and metacone are difficult to identify.

TABLE 1. — Dental measurements (in mm) of *Neocricetodon magnus* (Fahlbusch, 1969) from Moncucco Torinese. Abbreviations: **TNr**, total number of analyzed teeth for each dental element; **mNr**, number of measureable teeth for each dental element (length and width); **min**, minimum value; **mean**, mean value; **max**, maximum value; **σ**, standard deviation value.

	Layer		Length					Width				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
M3	MCC5	2	2	1.50	1.57	1.63	0.0919	2	1.37	1.43	1.48	0.0778
m1	MCC4	1	1	–	2.38	–	–	1	–	1.39	–	–
	MCC5	1	1	–	2.31	–	–	1	–	1.33	–	–
m2	MCC4	1	1	–	1.80	–	–	1	–	1.45	–	–
	MCC5	5	5	1.87	1.91	1.96	0.0336	5	1.43	1.55	1.62	0.0770
	MCC7	1	1	–	1.80	–	–	1	–	1.45	–	–
m3	MCC5	3	3	1.98	2.00	2.01	0.0173	3	1.54	1.55	1.57	0.0153

m1

A wide and stout anteroconid borders the entire anterior margin developing in sharp and flat ridges on the labial and lingual sides; in two specimens, a shallow incision in the distal side of the anteroconid wall is suggestive of an incomplete subdivision; anterolophulid double in three specimens and single and labial in one specimen; in two specimens the anterolophulids run parallel to each other whereas in the other one they are strongly divergent; mesolophid always present; well-developed and ending in a mesostylid.

m2

The lingual anterolophulid is strongly reduced; labial anterolophulid well-developed; well-developed mesolophid ending into a strong mesostylid.

m3

Large and triangular; anterolophulids well-developed both on the labial and lingual sides; well-developed mesolophid ending into a strong mesostylid.

REMARKS

The cricetine remains from MCC cannot be assigned to the genus *Apocricetus* Freudenthal, Mein & Martín-Suárez, 1998 because of the presence of strong mesolophs and mesolophids. The size of *Pseudocricetus polgardiensis* (Freudenthal & Kordos, 1989) from the Late Miocene of Polgardi (Hungary) is slightly smaller than that of *Neocricetodon magnus* from MCC even if the size ranges can partially overlap, while that of the sympatric *Pseudocricetus kormosi* (Schaub, 1930) is very similar (Freudenthal & Kordos 1989; Freudenthal *et al.* 1998). The material from MCC differs from *P. polgardiensis* in having more developed mesolophs and mesolophids especially in the m2 and m3, as well as in the undivided anteroconid. *P. kormosi* differs from the specimens from MCC in the strong reduction of mesolophs and mesolophids, which are nearly absent in this species, and in the strong subdivision of the anteroconid in the m1s.

The studied material is characterized by the presence of long and strong mesolophs and mesolophids and unified or slightly subdivided anteroconid wall in the m1s. These features are distinctive of the Eurasian Neogene genera *Neocricetodon* Schaub, 1934 and *Kowalskia* Fahlbusch, 1969 (Daxner-Höck 1995; Daxner-Höck *et al.* 1996; Freudenthal *et al.* 1998). The taxonomic status of these two genera has been the subject of a complex discussion. Some authors (Freudenthal *et al.* 1998) considered *Kowalskia* as a junior synonym of *Neocricetodon*, while others (Daxner-Höck *et al.* 1996) claimed that the material of the Late Miocene *Neocricetodon grangeri* (Young, 1927), the type species of the genus *Neocricetodon*, is rather scarce and does not provide substantial evidence about the possible separation of *Neocricetodon* and *Kowalskia*, thus preferring to use the better defined *Kowalskia*. More recently, de Bruijn *et al.* (2012) examined some pictures of unpublished material assigned to *N. grangeri* and after comparisons with *Kowalskia polonica* Fahlbusch,

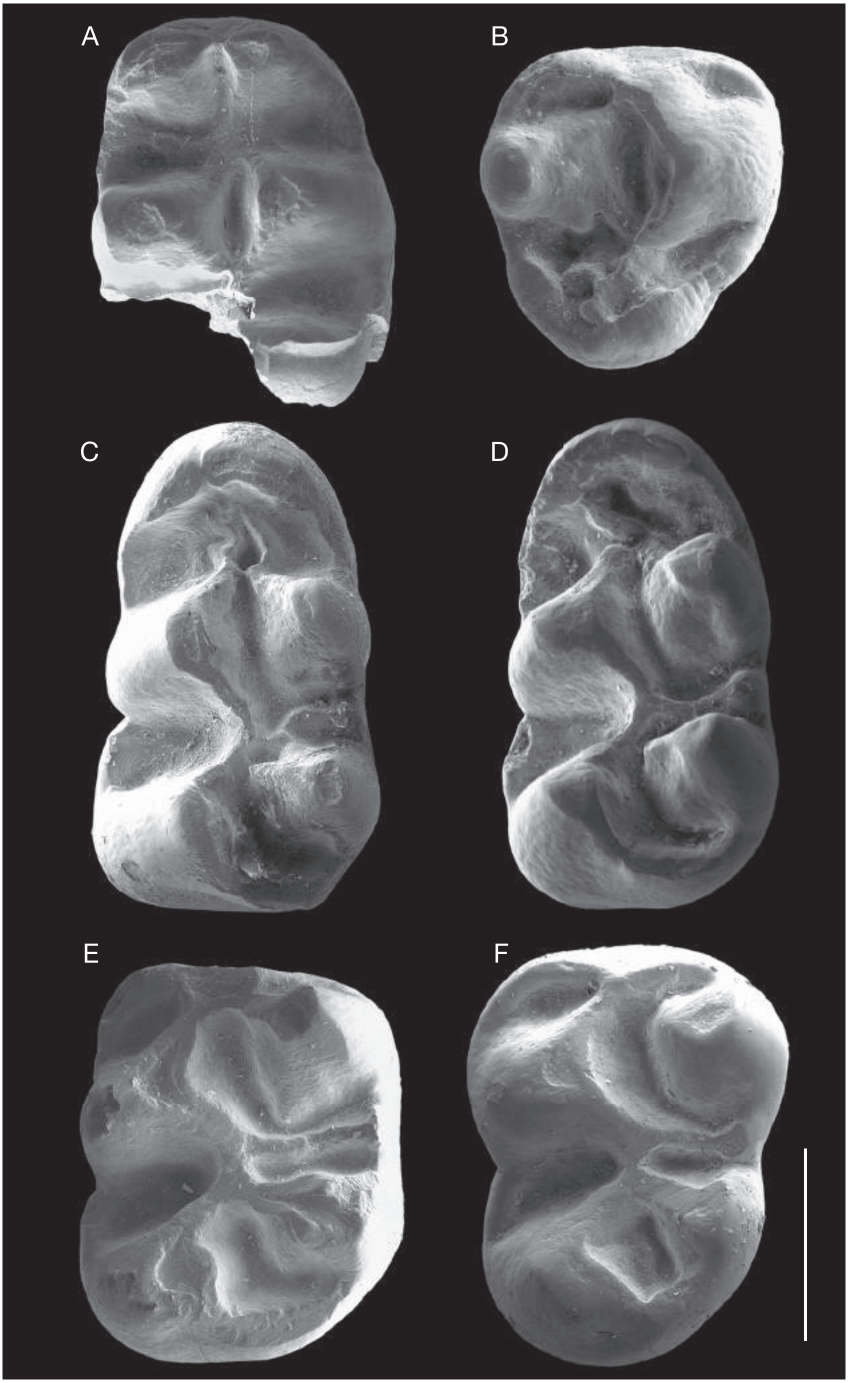

Fig. 3. — Isolated teeth of *Neocricetodon magnus* (Fahlbusch, 1969) from Moncucco Torinese. **A**, MGPT-PU127498, M1 dex (fragmented); **B**, MGPT-PU127500, M3 dex.; **C**, MGPT-PU127424, m1 sin.; **D**, MGPT-PU127932, m1 sin.; **E**, MGPT-PU127427, m2 sin.; **F**, MGPT-PU127423, m3 sin. Scale bar: 1 mm.

1969, the type species of *Kowalskia*, considered this latter genus as a junior synonym of *Neocricetodon* (in agreement with Freudenthal *et al.* 1998). Following this opinion, *Kowalskia* is considered herein a junior synonym of *Neocricetodon*.

Large-sized species of the genus *Neocricetodon*, as that recognized at MCC, are relatively uncommon in the Neogene of Europe. *Neocricetodon lavocati* (Hugueney & Mein, 1965) from the Late Miocene of Lissieu, *Neocricetodon browni* (Daxner-Höck, 1992) from Maramena (Miocene/Pliocene boundary of Greece) (Daxner-Höck 1992; 1995), the Late Miocene *Neocricetodon nestori* (Engesser, 1989) from Baccinello V3 and *Neocricetodon skofleki* (Kordos, 1987) from Tardosbanya display a smaller size. *Neocricetodon fahlbuschi* (Bachmayer & Wilson, 1970) from the Late Miocene of Austria (see also Freudenthal *et al.* 1998) is also smaller and only the size ranges of the M3 partially overlap with those of *Neocricetodon* from MCC. Direct comparisons with material referred to *N. lavocati* from Lissieu showed that it exhibits less developed mesolophids in the m3. From a morphological point of view, *N. browni* and *N. nestori* differ from the material of MCC in having a clearly subdivided anteroconid. *N. skofleki* differs from the material from MCC for a wider anterosinusid in the m2 and the presence of a double anteroloph in the M1. With respect to *N. fahlbuschi*, the studied material differs mainly in the strong reduction of the M3, less divided anterocones in M1 and the presence of a broader, stouter and almost undivided anteroconid in the m1s. Other slight differences include the presence of a double anterolophule, and the frequent absence of the anterior protoloph in the M1 of *N. fahlbuschi* and the overall better developed mesoloph(id)s of the molars from MCC in which they always reach the dental margins.

Neocricetodon seseae Aguilar, Calvet & Michaux, 1995 from the Late Miocene localities of Castelnou 1, Crevillente 14 and 22, Cucuron and Lissieu (see Freudenthal *et al.* 1998), even if slightly smaller, approaches the size of the cricetine material from MCC. However, this species shows some unique features, including the less developed mesolophids, the higher degree of subdivision of the anteroconid and the almost unreduced M3.

Neocricetodon polonicus (Fahlbusch, 1969) known from some Pliocene localities of Central Europe (Fahlbusch 1969; Pradel 1988) and *Neocricetodon intermedius* (Fejfar, 1970) from the Pliocene of Ivanovce and Vue-des-Alpes (Bolliger *et al.* 1993) have rather smaller molars, even though they display very similar morphological characters (e.g., long and strong mesolophids and mesolophs, and undivided, wide and stout anteroconid). The size of *Neocricetodon magnus* Fahlbusch, 1969 from the type locality of Podlesice (Fahlbusch 1969; Pradel 1988) and Osztramos 1 (Janossy 1972) fit very well with that of the specimens from MCC except for the length of M3, which is highly variable in the material from Podlesice. Moreover, the morphological features of *N. magnus* are consistent with those of the material from MCC, especially as far as concerns the long and strong mesolophids and mesolophs, the unified or slightly subdivided anteroconids in the m1s, and the reduction of the anterosinusids of the m2. Two M3 from Podlesice, MF/823/16 figured in Fahlbusch (1969: taf. XVI/5) and MF/1684 figured in Pradel (1988: pl. IX/10) display a strong reduction of the posterior part being remarkably similar to the M3 from MCC. However, some details are slightly different; one of four available m1 from MCC has a single anterolophulid, while a double anterolophulid generally occurs in *N. magnus* from Podlesice; the measurements of the M3 from Podlesice display a higher variability even if this is probably due to the scarce sample of MCC (two M3) These differences should not be regarded as significant considering the nearly unknown intraspecific variability of *N. magnus*. Moreover, a detailed morphological description of the dental elements was exclusively provided for the scarce material analyzed by Fahlbusch (1969), and very little is known about the morphological features of the Osztramos 1 assemblage.

In summary, the only known species of the genus *Neocricetodon* exhibiting a large size, well-developed mesolophids and mesolophs, broad, wall-like, undivided anteroconids, and reduction of the posterior portion of the M3 is *Neocricetodon magnus*. The few morphological differences, such as the presence of a single labial branch of the anterolophulid in one (of the four available) m1 can be related to the slightly older age of the material from MCC, even considering that this feature is more common in some Miocene species such as *N. fahlbuschi* (Bachmayer & Wilson 1970).

To date, *N. magnus* has been exclusively reported from the Pliocene deposits of Central Europe. The material from MCC indicates that this large cricetine was present at least at the end of the Messinian in southern Europe. This is the second record of the genus *Neocricetodon* in the Italian Peninsula, the first one being that of *N. nestori* in the slightly older locality of Baccinello V3 (Engesser 1989; Rook *et al.* 2011). The two species do not appear to be closely related (Engesser 1989).

According to Daxner-Höck (1995), *N. magnus* is in some ways related to *N. schaubi* (MN11), *N. skofleki* (MN11-MN12), *N. browni* (MN13), *N. polonicus* (MN14), and *N. intermedia* (MN15). However, as already pointed out by Fahlbusch (1969) and Fejfar (1970), the closest relatives of *N. magnus* should be *N. polonicus* and *N. intermedius* with which it shares a very similar morphology, mostly differing in its larger size.

Family MURIDAE Illiger, 1811
Genus *Paraethomys* Petter, 1968

Paraethomys meini (Michaux, 1969)
(Fig. 4A-F)

Anthracomys meini Michaux, 1969: 14, pl. 2, figs 6-9.

Occitanomys anomalus de Bruijn, Dawson & Mein, 1970: 548, pl. 2, figs 7-12.

Paraethomys miocaenicus Jaeger, Michaux & Thaler, 1975: 1674, pl. 1, figs 1-12.

Paraethomys anomalus – De Giuli 1989: 204, pl. 2, figs 3-14.

Paraethomys cf. *anomalus* – Cavallo *et al.* 1993: 15, fig. 7.

Paraethomys meini – Minwer-Barakat *et al.* 2009a: 98, fig. 2; 2009b: 860, fig. 7. (*cum syn.*). — Colombero *et al.* 2013: 116, fig. 4A-C, J-L.

TYPE LOCALITY. — Sète, France.

OCCURRENCE IN THE STUDIED LAYERS. — MCC3, MCC4, MCC5, MCC7.

REFERRED MATERIAL. — Nine maxillary fragments bearing M1 and M2; two maxillary fragments bearing M2 and M3; a single mandibular fragment bearing m2 and m3; 32 isolated M1; 26 isolated M2; 20 isolated M3; 30 isolated m1; 31 isolated m2; 13 isolated m3. See Appendix 1 for further details.

MEASUREMENTS. — Table 2.

DESCRIPTION.

M1

t1 and t3 exhibit a posterior spur directed to the t5; t3 smaller than t1; well developed t6 protruding from the labial margin; t4-t5-t6-t9-t8 form a partially developed stephanodont crest since t4 and t8 are not connected; t9 reduced; t12 very poorly developed.

M2

t5 and t8 very well developed; t3 much smaller than t1; t9 absent or strongly reduced; t12 absent.

M3

t3 absent or represented by a small bulge arising on the enamel; t8 usually isolated; a feeble connection with t4 can occasionally occur; three roots.

m1

tma present in 15% of specimens as a tiny cusplet formed by a slight swelling of the enamel; c1 always present; labial cingulum with one or two additional cusplets.

m2

Stout anterolabial cuspid; c1 always present; a second cusplet develops occasionally close to the protoconid.

m3

An accessory cusplet rarely occurs on the labial side; posterior complex isolated or labially connected to the anterior one.

REMARKS

The studied material can be assigned to the genus *Paraethomys* Petter, 1968 primarily due to the mod-

TABLE 2. — Dental measurements (in mm) of *Paraethomys meini* (Michaux, 1969) from Moncucco Torinese. Abbreviations: see Table 1.

	Layer		Length					Width				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
M1	MCC3	3	2	2.19	2.23	2.34	0.0283	2	1.40	1.46	1.51	0.0778
	MCC4	5	4	2.33	2.38	2.44	0.0512	4	1.56	1.59	1.64	0.0327
	MCC5	30	25	2.04	2.34	2.51	0.1101	26	1.40	1.60	1.71	0.0711
	MCC7	3	2	2.25	2.34	2.42	0.1202	2	1.62	1.66	1.69	0.0495
M2	MCC3	2	2	1.50	1.60	1.70	0.1414	2	1.38	1.46	1.54	0.1131
	MCC4	4	4	1.57	1.67	1.80	0.1044	4	1.49	1.55	1.59	0.0427
	MCC5	27	25	1.49	1.65	1.82	0.0823	24	1.42	1.56	1.65	0.0672
	MCC7	4	4	1.54	1.61	1.67	0.0548	4	1.45	1.55	1.60	0.0656
M3	MCC4	4	4	1.11	1.22	1.33	0.0900	4	1.10	1.26	1.33	0.1072
	MCC5	15	14	1.15	1.22	1.29	0.0380	15	1.12	1.22	1.31	0.0542
	MCC7	3	3	1.12	1.14	1.16	0.0200	3	1.18	1.21	1.26	0.0416
m1	MCC3	3	1	–	2.02	–	–	1	–	1.32	–	–
	MCC4	4	3	2.01	2.16	2.28	0.1365	3	1.41	1.46	1.51	0.0503
	MCC5	16	14	2.01	1.12	1.23	0.0721	14	1.24	1.33	1.44	0.0590
	MCC7	7	6	2.01	2.18	2.33	0.1330	7	1.30	1.39	1.46	0.0627
m2	MCC4	3	3	1.50	1.55	1.64	0.0757	3	1.42	1.47	1.49	0.0404
	MCC5	17	15	1.33	1.59	1.70	0.0915	17	1.27	1.44	1.51	0.0662
	MCC7	12	10	1.54	1.50	1.67	0.0407	8	1.42	1.48	1.56	0.0564
m3	MCC4	1	1	–	1.39	–	–	1	–	1.22	–	–
	MCC5	10	5	1.17	1.31	1.37	0.0942	8	1.18	1.24	1.30	0.0399
	MCC7	3	3	1.18	1.26	1.43	0.1443	2	1.04	1.15	1.25	0.1485

erately stephanodont molars and the absence or the presence of reduced t9 in M1 and M2. The size of the specimens of *Paraethomys* from MCC fits well with the range of *Paraethomys meini* (Michaux, 1969) from the type locality of Sète (Michaux 1969), being also consistent with those of many Late Turolian and Ruscinian European localities, including Purcal 4, 7, 13, Calicasas 3B, La Mina 4 from the Granada Basin (García-Alix *et al.* 2008b), Negratín-1 and Rambla de Chimeneas 3 (Minwer-Barakat *et al.* 2009a, 2009b), Mont-Hélène (Aguilar *et al.* 1991), Villalba Alta Río, Peralejos E, Orrios, Celadas 9 and La Gloria 4 from the Teruel Basin (Adrover *et al.* 1988, 1993a) and Verduno (Colombero *et al.* 2013). The morphology of the teeth of *P. meini* from MCC is very similar to that of the teeth from Sète, even if the posterior spurs of the available M1 are MCC usually slightly more developed. Moreover, material referred to *P. meini* from other localities, particularly La Dehesa 4A and 4B (García-Alix *et al.* 2008b), is extremely similar to that from MCC. Therefore, the material from MCC is referred herein to *Paraethomys meini.* Direct comparative analysis carried out on *Paraethomys* teeth from the localities of Amama 2 and Albacete housed in the UCBL collections and previously assigned to *Paraethomys miocaenicus* Jaeger, Michaux & Thaler, 1975 revealed only small differences, mostly related to the lesser development of the spurs on the t3, and the lower t6-t9 connections in the M1 from those localities. The material of *P. meini* from Brisighella (De Giuli 1989) and Maritsa (de Bruijn *et al.* 1970), formerly assigned to *Paraethomys anomalus* (de Bruijn, Dawson & Mein, 1970) shows remarkable affinities with the material from MCC, especially in the development of the spurs on the t3 of the M1, in the close position of the t1 with the t5, as well as in the number of cusplets on the labial cingulum (generally two) of the m1. Thus, there is no relevant argument to support a well-defined distinction between these assemblages and *P. meini*. Therefore, as already suggested by several authors (van de Weerd 1976; Montenat & de Bruijn 1976; García-Alix *et al.*

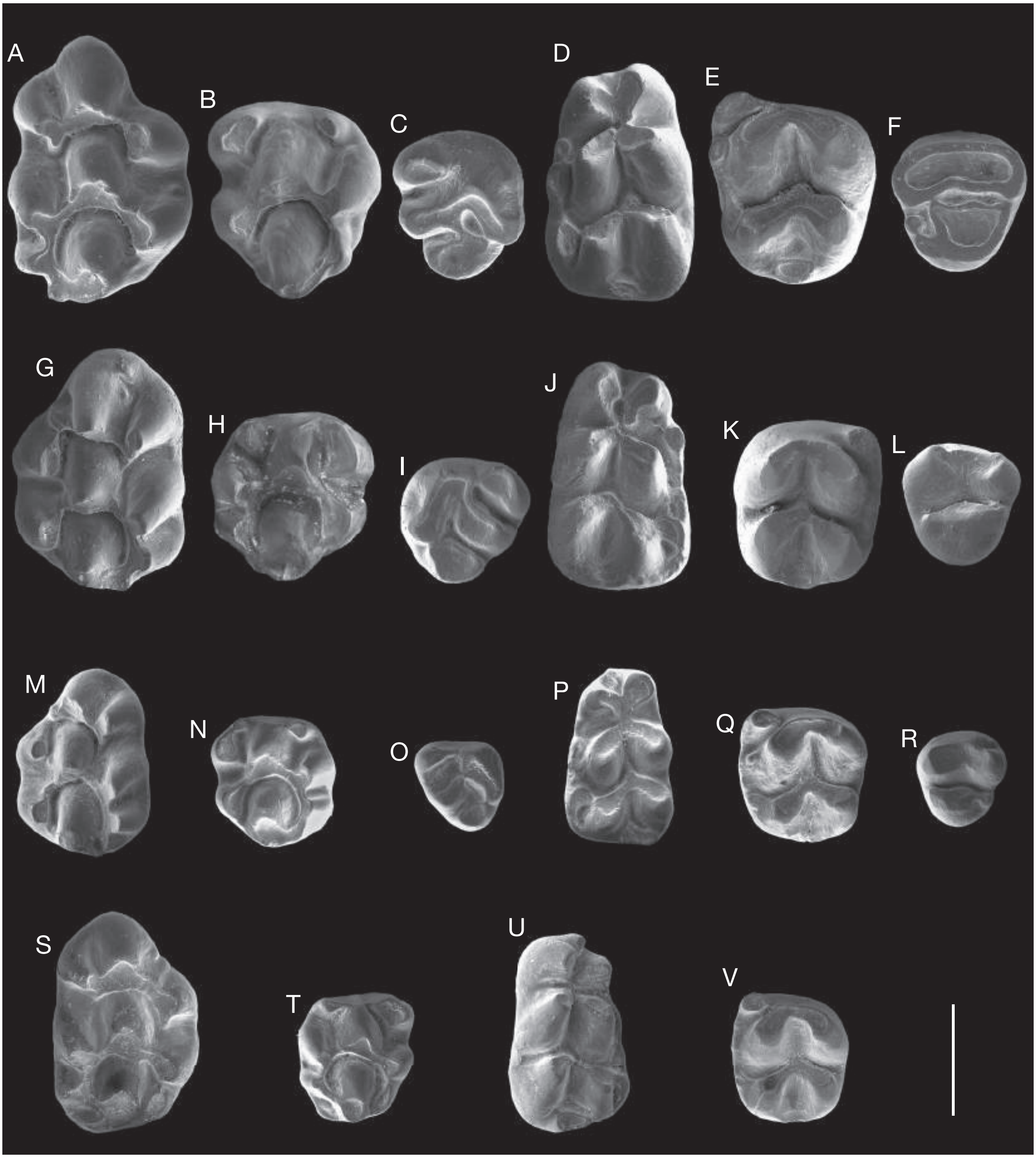

FIG. 4. — Isolated teeth of *Paraethomys* Petter, 1968, *Occitanomys* Michaux, 1969, *Centralomys* De Giuli, 1989 and *Micromys* Dehne, 1841 from Moncucco Torinese. **A**-**F**, *Paraethomys meini* (Michaux, 1969); **A**, MGPT-PU128032, M1 dex.; **B**, MGPT-PU128040, M2 sin.; **C**, MGPT-PU127602, M3 sin.; **D**, MGPT-PU127146, m1 sin.; **E**, MGPT-PU127302, m2 sin.; **F**, MGPT-PU127603, m3 sin.; **G**-**L**, *Occitanomys brailloni* Michaux, 1969; **G**, MGPT-PU127062, M1 sin.; **H**, MGPT-PU127447, M2 dex.; **I**, MGPT-PU127657, M3 dex.; **J**, MGPT- MGPTPU127166, m1 dex.; **K**, MGPT-PU127305, m2 dex.; **L**, MGPT-PU127658, m3 sin.; **M**-**R**, *Centralomys benericettii* (De Giuli, 1989); **M**, MGPT-PU128090, M1 sin.; **N**, MGPT-PU128278, M2 sin.; **O**, MGPT-PU128115, M3 sin.; **P**, MGPT-PU128272, m1 sin.; **Q**, MGPT-PU128321, m2 sin.; **R**, MGPT-PU128144, m3 dex.; **S**-**V**, *Micromys bendai* van de Weerd, 1979; **S**, MGPT-PU127434, M1 dex.; **T**, MGPT-PU127251, M2 dex.; **U**, MGPT-PU127600, m1 dex.; **V**, MGPT-PU127601, m2 sin. Scale bar: 1 mm.

2008b; Minwer-Barakat *et al.* 2009a, b), it is reasonable to conclude that *P. miocaenicus* and *P. anomalus* are junior synonyms of *P. meini*. On the contrary, a separate status is maintained for *Paraethomys abaiggari* Adrover, Mein & Moissenet, 1988, a Ruscinian species rarely reported from Spain, since it differs from *P. meini* in having a larger size and more developed spurs on the t3 of M1.

The earliest European record of *P. meini* is reported from Spain, thereby suggesting that this species entered Europe from North-Western Africa at the end of the Turolian (Agustí & Llenas 1996; van Dam *et al.* 2001; Agustí *et al.* 2006a). At the beginning of the Ruscinian, its geographical range broadened to the Eastern sector of the Mediterranean, as testified by the Maritsa record (de Bruijn *et al.* 1970).

Genus *Occitanomys* Michaux, 1969

Occitanomys brailloni Michaux, 1969
(Fig. 4G-L)

Occitanomys brailloni Michaux, 1969: 8, pl. 1, figs 6-11. — van de Weerd 1979: 132, pl. 1, figs 3-9. — de Bruijn 1989: 191. — Vasileiadou *et al.* 2003: 553, fig. 4I, J. — Minwer-Barakat *et al.* 2005: 434, fig. 3H. — Hordijk & de Bruijn 2009: 33, pl. 8, figs 1-7, pl. 9, figs 1-11.

Hansdebruijnia sp. – Angelone *et al.* 2011: 99, fig. 6 (11).

aff. *Huerzelerimys* – Angelone *et al.* 2011: 99, fig. 6 (13).

TYPE LOCALITY. — Layna, Spain.

OCCURRENCE IN THE STUDIED LAYERS. — MCC3, MCC4, MCC5, MCC7.

REFERRED MATERIAL. — Two maxillary fragments bearing M1 and M2; one maxillary fragment bearing M2 and M3; two mandibular fragments bearing m1, m2 and m3; two mandibular fragments bearing m1 and m2; 79 isolated M1; 79 isolated M2; 26 isolated M3; 64 isolated m1; 61 isolated m2; 31 isolated m3. See Appendix 1 for further details.

MEASUREMENTS. — Table 3.

DESCRIPTION

M1

t1bis present; t1 very close to t5; t3 exhibits a posterior spur that touches the base of the t5 or t5-t6 connection in 35% of the specimens; labial tubercles (t3-t6-t9) aligned, forming a straight labial margin; posterior tubercles (t4; t5; t6; t9; t8) connected in a stephanodont crest; t4-t8 connection low or absent; t12 weakly developed.

M2

Ovoid shape; t1 close to t5, t3 small; t1bis rarely present, posterior tubercles (t4; t5; t6; t9; t8) connected in a stephanodont crest; t12 absent or very poorly developed.

M3

t1 connected to t5; t3 generally absent even if a small swelling of the enamel occurs in few specimens; t8 isolated or weakly connected to t6.

m1

A low longitudinal spur develops from the entoconid-hypoconid complex, barely reaching the base of the protoconid-metaconid complex without constituting a complete crest (75% of the specimens) or remaining free (25%); the labial cingulum bears a c1 and an additional cusplet between protoconid and anteroconid.

m2

Well-developed anterolabial cuspid; a low longitudinal spur is present but it does not form a complete crest; labial cingulum departs from c1 and reaches a cusplet near the protoconid.

m3

The anterolabial cuspid is a small swelling of the enamel; posterior complex transversally elongated and isolated from the protoconid-metaconid complex.

REMARKS

The material described herein can be referred to the genus *Occitanomys* Michaux, 1969 because of its moderately developed longitudinal connections between the tubercles of lower and upper molars, a less pronounced stephanodonty than *Stephanomys* Schaub, 1938 and *Castillomys* Michaux, 1969 and the position of t1 close to t5 (Michaux 1969). In addition, *Stephanomys* usually displays higher-

TABLE 3. — Dental measurements (in mm) of *Occitanomys brailloni* Michaux, 1969 from Moncucco Torinese. Abbreviations: see Table 1.

	Layer		Length					Width				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
M1	MCC3	10	8	1.80	2.12	2.32	0.1531	5	1.44	1.50	1.60	0.0638
	MCC4	19	15	2.05	2.19	2.35	0.0895	15	1.41	1.50	1.56	0.0495
	MCC5	47	39	1.94	2.14	2.34	0.0988	39	1.43	1.51	1.64	0.0442
	MCC7	5	5	2.01	2.14	2.31	0.1272	5	1.50	1.54	1.62	0.0513
M2	MCC3	6	5	1.54	1.57	1.60	0.0283	5	1.35	1.47	1.56	0.0804
	MCC4	20	18	1.39	1.51	1.60	0.0657	17	1.34	1.44	1.54	0.0562
	MCC5	48	43	1.32	1.49	1.70	0.0782	45	1.25	1.43	1.56	0.0690
	MCC7	8	7	1.40	1.53	1.61	0.0739	7	1.30	1.44	1.52	0.0905
M3	MCC3	1	1	–	1.13	–	–	1	–	1.15	–	–
	MCC4	9	9	1.06	1.13	1.20	0.0500	9	1.07	1.14	1.17	0.0350
	MCC5	15	13	1.03	1.11	1.19	0.0556	13	1.00	1.12	1.20	0.0583
	MCC7	2	2	1.09	1.12	1.14	0.0354	2	1.11	1.12	1.12	0.0071
m1	MCC3	5	5	1.86	1.99	2.14	0.0945	4	1.24	1.30	1.36	0.0510
	MCC4	11	9	1.90	1.98	2.18	0.0797	9	1.26	1.29	1.36	0.0306
	MCC5	48	42	1.82	1.97	2.26	0.0834	42	1.17	1.28	1.52	0.0686
	MCC7	5	5	1.90	1.93	1.95	0.0182	5	1.25	1.32	1.36	0.0421
m2	MCC3	4	4	1.44	1.49	1.51	0.0332	4	1.27	1.39	1.47	0.0839
	MCC4	3	3	1.29	1.39	1.47	0.0907	3	1.21	1.29	1.36	0.0764
	MCC5	52	45	1.33	1.48	1.58	0.0577	45	1.18	1.36	1.45	0.0741
	MCC7	7	7	1.44	1.52	1.57	0.0550	6	1.34	1.41	1.46	0.0441
m3	MCC3	3	3	1.18	1.21	1.26	0.0416	3	1.08	1.15	1.23	0.0755
	MCC4	1	1	–	1.27	–	–	1	–	1.11	–	–
	MCC5	22	17	1.09	1.18	1.26	0.0495	17	1.01	1.08	1.16	0.0396
	MCC7	8	8	0.92	1.16	1.30	0.1263	8	0.91	1.09	1.26	0.1309

crowned teeth with better developed longitudinal connections, the tubercles of upper molars are more pointed than in *Occitanomys* in which, on the contrary, the tubercles are more rounded and the overall aspect is more bunodont. Moreover, in the M1 of *Stephanomys* the t6 is more voluminous, usually protruding over the labial outline of the tooth, whereas in the specimens from MCC the t6 is always well aligned with t3 and t9, forming a straight labial border. However, few upper molars of *Stephanomys ramblensis* van de Weerd, 1976 from some Messinian localities of the Teruel Basin (van de Weerd 1976; Adrover *et al.* 1993a) and the Granada Basin (García-Alix *et al.* 2008b) including Valdecebro 3, Villastar and Purcal 23 roughly resemble those from MCC in displaying less developed t3-t5 connections in some M1 and t1-t5 connections in some M2. Nonetheless the lower molars of this species clearly differ from the studied material in the significantly more developed longitudinal connections that are present even in the m3. Moreover, even if the size ranges partially overlap, the mean-size of the molars of *S. ramblensis* is slightly larger than that of *Occitanomys brailloni* from MCC.

The size of the molars of *Occitanomys* from MCC falls in the range of *Occitanomys brailloni* Michaux, 1969 from some Pliocene localities of western and eastern Europe including Layna, Nîmes (Michaux 1969), Kardia, Ptolemais 1 and 3 (van de Weerd 1979) and Tollo de Chiclana-1B (Minwer-Barakat *et al.* 2005). The measurements are also very similar to those of *O. brailloni* from Vorio 1 and Vorio 2 (Hordijk & de Bruijn 2009), even though the mean size of the M2 is slightly larger in MCC. However, the size variability of M2 is poorly known for this species. Comparisons with material referred to *O. brailloni* from Layna housed at the IVAU and from the UCBL collections revealed a very similar morphology of the molars that fall in the range of variation of the type assemblage. Slight differences can be found in the M1 since the specimens from MCC display less frequent longitudinal connections. In particular, in the examined M1 from Layna the t3-t5 connection is present in 60% of the specimens whereas this connection only appears in 35% of the specimens from MCC. In our opinion these differences are not significant and can be related to the older age of the assemblages from MCC since the longitudinal connections seem to become more frequent in younger assemblages such as that from Layna. Therefore, the material from MCC is referred herein to *Occitanomys brailloni*.

Teeth of *Occitanomys montheleni* Aguilar, Calvet & Michaux, 1986 reported in the Pliocene French localities of Mont Hélène and Serrat d'en Vaquer (Aguilar 1982; Aguilar *et al.* 1986) show a larger overall size; moreover, on the grounds of morphological comparisons with some specimens of *O. montheleni*, the posterior spurs of the t3 in the M1 of *O. brailloni* are more developed and the m1 shows a more developed labial cingulum.

Occitanomys adroveri (Thaler, 1966), a species occurring in Europe during the Late Miocene, differs from the studied material in displaying slender and less rounded cusps and much more developed t12 in M1 and M2. In addition, the connections in the upper teeth, especially t3-t5 connections in M1, are less developed than those occurring in the studied material. Moreover, the measures of the teeth of this species are usually smaller than those of the studied material. According to Michaux (1969), *O. adroveri* and *O. brailloni* belong to the same lineage that, from the Miocene to the Pliocene, should be characterized by a general size increase of the teeth in addition to a volume-increase of the cusps and a reduction of the t12. Moreover, as observed in the type assemblage of *O. brailloni* from Layna, the longitudinal connections of the upper molars are slightly more developed in the younger species. The earliest record of *O. brailloni* is that of Rema Marmara, a Greek locality dating back to the MN12 (de Bruijn 1989). This species is also reported in other Greek localities with an age close to the Mio-Pliocene boundary, such as Silata (Vasileiadou *et al.* 2003) and Kardia (van de Weerd 1979) and it appeared in France (Michaux 1969) and Spain (Michaux 1969; Minwer-Barakat *et al.* 2005) during the Pliocene. The record of MCC represents one of the oldest reports of this taxon documenting its presence in the central sectors of southern Europe at the end of the Miocene.

In a previous cursory analysis of the fossil assemblage from MCC (Angelone *et al.* 2011), a small sample of *Occitanomys brailloni* was tentatively assigned to *Hansdebruijna* sp. Nonetheless, *Hansdebruijna* Storch & Dahlmann, 1995 clearly differs in the more developed t12, poorly developed t1bis and a general smaller size. In the same paper, another very small sample of *O. brailloni* was tentatively attributed to aff. *Huerzelerimys* Mein, Martín-Suárez & Agustí, 1993. This genus can be distinguished from *Occitanomys* by its lesser degree of stephanodonty, more developed t6 and t12, and less developed t1 bis. In summary, all these specimens previously assigned to other taxa are now referred to *Occitanomys brailloni*.

Genus *Centralomys* De Giuli, 1989

Centralomys benericettii (De Giuli, 1989)
(Fig. 4M-R)

Castillomys (*Centralomys*) *benericettii* De Giuli, 1989: 204, pl. 3, figs 1-10.

Centralomys benericettii – Martín-Suárez & Mein 1991: 68, pl. 2, figs 12-17. — Abbazzi *et al.* 2008: 622, fig. 6E, F. — Colombero *et al.* 2013: 113, fig. 4D-F, M-O.

Castillomys sp. – Cavallo *et al.* 1993: 17, fig. 8A.

Centralomys cf. *benericettii* – Angelone *et al.* 2011: 98, fig. 14.

TYPE LOCALITY. — Brisighella 1, Italy.

OCCURRENCE IN THE STUDIED LAYERS. — MCC3, MCC4, MCC5, MCC7.

REFERRED MATERIAL. — One maxillary fragment bearing M1 and M2; one mandibular fragment bearing m1 and m2; 31 isolated M1; 26 isolated M2; four isolated M3; 35 isolated m1; 31 isolated m2; three isolated m3.

MEASUREMENTS. — Table 4.

TABLE 4. — Dental measurements (in mm) of *Centralomys benericettii* (De Giuli, 1989) from Moncucco. Abbreviations: see Table 1.

	Layer		Length					Width				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
M1	MCC3	3	2	1.63	1.71	1.78	0.1061	2	1.15	1.18	1.21	0.0424
	MCC4	6	6	1.68	1.74	1.81	0.0568	6	1.19	1.21	1.26	0.0250
	MCC5	14	11	1.56	1.68	1.89	0.0965	12	1.16	1.22	1.36	0.0710
	MCC7	9	7	1.54	1.71	1.86	0.1062	7	1.11	1.20	1.25	0.0454
M2	MCC3	2	2	1.09	1.16	1.22	0.0919	2	1.12	1.16	1.20	0.0566
	MCC4	7	7	1.10	1.20	1.29	0.0735	7	1.06	1.14	1.17	0.0404
	MCC5	13	13	1.09	1.18	1.28	0.0624	13	1.08	1.17	1.31	0.0705
	MCC7	5	5	1.12	1.22	1.26	0.0555	5	1.10	1.15	1.21	0.0488
M3	MCC5	3	3	0.74	0.82	0.86	0.0649	3	0.79	0.84	0.90	0.0530
	MCC7	1	1	–	0.87	–	–	1	–	0.94	–	–
m1	MCC3	3	2	1.75	1.81	1.87	0.0849	1	–	1.27	–	–
	MCC4	5	5	1.49	1.55	1.62	0.0546	4	0.97	1.03	1.05	0.0370
	MCC5	23	21	1.43	1.59	1.84	0.0980	19	0.93	1.04	1.14	0.0599
	MCC7	5	2	1.56	1.57	1.57	0.0071	4	0.96	1.01	1.08	0.0212
m2	MCC3	1	1	–	1.15	–	–	1	–	0.97	–	–
	MCC4	2	2	1.11	1.12	1.13	0.0141	2	0.94	1.00	1.05	0.0778
	MCC5	25	22	1.03	1.14	1.24	0.0566	23	0.94	1.04	1.17	0.0597
	MCC7	4	4	1.13	1.17	1.20	0.0299	4	1.03	1.11	1.17	0.0580
m3	MCC3	3	3	0.88	0.91	0.93	0.0265	3	0.81	0.82	0.83	0.0100

DESCRIPTION

M1

t3-t6-t9 are aligned forming a straight labial margin; t1 bis always present; t1 connected to t5; the t3 exhibits a posterior spur reaching the base of t5 in about 45% of the specimens; t4-t5-t6-t9-t8 form a stephanodont crest with low (or absent) t4-t8 connection; t12 strongly reduced.

M2

t1 bis always present, the t1 exhibits a posterior spur that reaches the base of t5 in 65% of the specimens; t3 smaller than t1; t4-t5-t6-t9-t8 form a stephanodont crest with low (or absent) t4-t8 connection; t12 absent or very reduced; three or four (10%) roots

M3

Large t1; t3 absent; t4-t8 connection low, t6-t8 connection rare and low.

m1

A tiny tma is present in 30% of the specimens, a longitudinal spur connects the hypoconid-entoconid complex and the protoconid-metaconid complex in 33% of the specimens; posterior heel poorly developed; the labial cingulum departs from the c1 and reaches the anteroconid without contacting the protoconid.

m2

A longitudinal spur connects the hypoconid-entoconid complex with the protoconid-metaconid complex in 35% of the specimens; c1 small; it can merge with the hypoconid; labial cingulum low without accessory cusplets.

m3

Anterolabial cuspid formed by a slight swelling of the enamel; the posterior complex exhibits a very compressed and transversely elongated shape; it is slightly shifted on the lingual side

REMARKS

The studied material belongs to a small stephanodont murid and is assigned to the genus *Centralomys*. As a matter of fact, the stephanodonty, the tendency to develop longitudinal connections between the tubercles of the molars (Schaub 1938), is not as well developed as in *Castillomys* Michaux, 1969, a genus that usually displays more developed longitudinal crests. Besides, the genus *Centralomys* differs also from *Occitanomys* Michaux, 1969, in which the longitudinal connections are less developed. Moreover, the presence of well-developed t1bis and t1-t5 connection in the M1 supports the ascription of the studied material to *Centralomys*. The measurements of *Centralomys* from MCC are nearly identical to those of *Centralomys benericettii* from the latest Miocene localities of Verduno (Colombero *et al.* 2013) and Brisighella 25 (Martín-Suárez & Mein 1991). Direct comparison of the material from MCC with that from Brisighella 1 (type locality), Brisighella 25 (De Giuli 1989), and Verduno (Colombero *et al.* 2013) revealed a very similar morphology especially in the t3-t5 connections in the upper molars (which are generally absent and, when present, are low) and in the poorly developed longitudinal spurs in the lower molars, thereby justifying the assignment to the species *Centralomys benericettii.* Moreover, the material from MCC is characterized by M2 always bearing a t1 bis and, like in the assemblages from Brisighella and Verduno, the 30% of the available m1 exhibit a tiny tma. However, it should be noted that specimens with slightly more pronounced stephanodonty are more frequent at Brisighella 25 and Verduno than in MCC (Colombero *et al.* 2013). As far as concerns Verduno and MCC, such differences might be related to different palaeoecological conditions (Colombero *et al.* 2013; Colombero & Pavia 2013).

According to some authors (García-Alix *et al.* 2008b; Hordijk & de Bruijn 2009), *C. benericettii* should be placed within the genus *Occitanomys.* In particular, García-Alix *et al.* (2008b) considered *C. benericettii* as a junior synonym of *Occitanomys alcalai* Adrover, Mein & Moissenet, 1988, a species present in the latest Miocene and Early Pliocene deposits of Spain, arguing that there is no morphological difference between these two forms. Actually, the measurements of *O. alcalai* are slightly larger than those of *C. benericettii* from Moncucco (Adrover *et al.* 1988; 1993a; García-Alix *et al.* 2008b; Minwer-Barakat *et al.* 2009a, b), as they only partially overlap. From a morphological point of view, in the M1 of *O. alcalai* the posterior spur of the t3 never reaches the t5 whereas in *C. benericettii* from MCC the contact is feeble but present in 45% of the M1. Other differences can be detected in the position of the t1 in the M1 that is more anteriorly placed in *O. alcalai*, in the less developed longitudinal spurs of the m1, in the lower frequency of the tma in the m1 and in the rarity of the t1bis in the M2 in *O. alcalai*. Moreover, in our opinion *Centralomys* cannot be considered a synonym of *Occitanomys* differing in particular in the presence of more developed longitudinal connections in both upper and lower molars.

Castillomys magnus Sen, 1977 from the Pliocene of Çalta (see Sen 1977) was ascribed to the genus *Centralomys* by Martín-Suárez & Mein (1991) mainly due to the presence of four roots (see Hordijk & de Bruijn 2009). In a successive paper, Sen (1998) confirmed the attribution of this species to the genus *Centralomys* pointing out the presence of four roots in the M2, weak longitudinal spurs in the lower molars and larger dimensions than *Castillomys*. *Centralomys magnus* differs from the studied material mainly in the larger average dimensions, even if the size ranges partially overlap, and in the presence of more developed longitudinal connections in the upper molars.

We compared the specimens of *C. benericettii* from MCC with *Castillomys gracilis* van de Weerd, 1976, known in Spain between the Late Miocene and the Pliocene. This species is smaller than *C. benericettii* (van de Weerd 1976; García-Alix *et al.* 2008b) except for the population from La Gloria 4 (Adrover *et al.* 1993a) whose range overlaps with that of MCC. Morphologically, *C. gracilis* mainly differs in the most developed stephanodont crest in the upper molars, and in the absence or very rare occurrence of the t1bis in the M2. In addition, the tma is usually absent in the m1 of *C. gracilis*, being only sketched in a single specimen from Calicasas-4b (García-Alix *et al.* 2008b), the longitudinal spurs are more developed and the labial cingula are weaker.

The record of *C. benericettii* is therefore restricted to the latest Messinian of Italy. Unfortunately, the very sparse record of continental vertebrates in the Italian Peninsula during the Miocene does not allow to define the evolutionary history of this taxon. Nonetheless, its occurrence in other localities such

TABLE 5. — Dental measurements (in mm) of *Micromys bendai* van de Weerd, 1979 from Moncucco Torinese. Abbreviations: See Table 1.

	Layer		Length					Width				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
M1	MCC3	1	1	–	1.83	–	–	1	–	1.20	–	–
	MCC4	3	3	1.73	1.90	1.99	0.1447	3	0.93	1.13	1.27	0.1795
	MCC5	5	4	1.86	1.88	1.91	0.0220	4	1.16	1.21	1.25	0.0426
	MCC7	4	3	1.67	1.68	1.71	0.0231	4	1.11	1.14	1.16	0.0222
M2	MCC5	4	3	1.14	1.16	1.19	0.0301	3	1.06	1.10	1.16	0.0509
	MCC7	1	1	–	1.10	–	–	1	–	0.95	–	–
M3	MCC5	1	1	–	0.75	–	–	1	–	0.80	–	–
m1	MCC3	2	2	1.74	1.87	2.00	0.1838	2	1.01	1.14	1.26	0.1768
	MCC4	1	1	–	1.56	–	–	1	–	0.93	–	–
	MCC5	7	7	1.58	1.66	1.71	0.0511	7	0.92	0.98	1.04	0.0457
	MCC7	3	1	–	1.96	–	–	2	0.93	0.95	0.97	0.0283
m2	MCC5	6	6	1.04	1.18	1.33	0.0966	6	0.98	1.07	1.21	0.0813
	MCC7	1	1	–	1.09	–	–	1	–	1.06	–	–

as Verduno (Colombero *et al.* 2013), Ciabót-Cagna (Cavallo *et al.* 1993), Borro Strolla (Abbazzi *et al.* 2008) and Brisighella (De Giuli 1989), indicates the existence of geographical connections between the northern and central parts of the Italian Peninsula, at least during the post-evaporitic phase of the MSC.

Genus *Micromys* Dehne, 1841

Micromys bendai van de Weerd, 1979
(Fig. 4S-V)

Micromys bendai van de Weerd, 1979: 144, pl. 3, figs 4, 5, 9, pl. 4, figs 6, 10. — Aguilar *et al.* 1989: 141, fig. 2. — Hordijk & de Bruijn 2009:41, pl. 12, figs 1-14.

OCCURRENCE IN THE STUDIED LAYERS. — MCC3, MCC4, MCC5, MCC7.

REFERRED MATERIAL. — Three mandibular fragments bearing m1 and m2; 13 isolated M1; five isolated M2; two isolated M3; ten isolated m1; four isolated m2.

MEASUREMENTS. — see Table 5.

DESCRIPTION

M1

t1 very close to or connected to t5;the t3 exhibits a short posterior spur; a small swelling of the enamel is present in most of the specimens on the anterior edge of the tooth between t1 and t2 or between t2 and t3;t3-t6-t9 are usually well aligned in an almost straight labial margin since the t6 can slightly protrude; t4-t5-t6-t7-t9-t8 are connected in a partially developed stephanodont crest since t7 is isolated from t4; t9 reduced; t12 moderately developed; five roots.

M2

t1 bis always present as an isolated cusplet or in a twinned complex formed by t1 and t1 bis t3 smaller than t1, usually connected to t5; t6 large, t9 reduced; t7 narrow or crest-like, isolated or weakly connected to t8; t12 present; four roots.

M3

t large; the t3 is a small swelling of the enamel; posterior complex connected to t6; t8 large and connected to the t6; three roots.

m1

Cuspids are pointed; small tma; longitudinal spur absent; a narrow labial cingulum departs from the c1 reaching the anteroconid without developing accessory cusplets; two main roots and one central rootlet.

m2

Anterolabial cuspid moderately or poorly developed; longitudinal spur absent; narrow labial cingulum departing from a rather small c1; posterior heel oval and poorly developed; two roots.

REMARKS

The average size of *Micromys* from MCC is slightly larger than that of *Micromys bendai* from Ptolemais 1 (type population, van de Weerd 1979) and Péage de Roussillon (Aguilar *et al.* 1989). However, it falls in the size range of other assemblages from Greece such as Tomea Eksi 1 and 2, Prosilion-Mercurion (Hordijk & de Bruijn 2009). Direct comparisons with molars of *M. bendai* from the type locality of Ptolemais 1did not reveal any relevant morphological difference suggesting that the material from MCC documented herein can be identified as *Micromys bendai*.

Micromys steffensi van de Weerd, 1979, from the Early Pliocene of Greece (Hordijk & de Bruijn 2009; Vasileiadou *et al.* 2012) displays larger dimensions even if the size range of m1 partially overlaps with that of *M. bendai* from MCC. Direct comparisons with specimens of *M. steffensi* from the type locality of Kardia, evidenced a great similarity with *M. bendai.* However, some small morphological differences can be detected, including the presence of a t1 bis in some M1 and the better development of the posterior spurs of t3 in M1 of *M. steffensi*.

The Late Miocene to Early Pliocene *Micromys paricioi* Mein*,* Moissenet & Adrover, 1983, known in Spain (Mein *et al.* 1983; Adrover *et al.* 1988; García-Alix *et al.* 2008b) and Greece (Vasileiadou *et al.* 2003), can be easily distinguished from *M. bendai* by its smaller size, less-developed t7 and less frequent t1 bis in M2.

Micromys cingulatus Storch & Dahlmann, 1995 from Maramena (Miocene/Pliocene boundary of Greece) is similar in size to *M. bendai* from MCC, but it exhibits less roots in M1 (three roots plus an extremely rare incipient fourth central rootlet), a reduced t7 and lacks the t1 bis in M2 (Storch & Dahlmann 1995).

The molars of *Micromys chalceus* Storch, 1987 from the Late Miocene of Mongolia are evidently smaller than the material from MCC (Storch 1987). Moreover, the M1 lacks a t7 and it usually displays a minor number of roots in M1 since a fifth rootlet is visible only in 11 out of 108 specimens (Storch 1987). The earliest Pliocene *Micromys kozaniensis* van de Weerd, 1979*,* from Ptolemais 3 (van de Weerd 1979) and the Mongolian locality of Bilike (Qiu & Storch 2000), differs from *M. bendai* in having narrower upper molars. From a morphological point of view, *M. kozaniensis* displays more posterior and slightly more developed t7 especially in the M2, more developed t12 and a deep inflexion in the outline of the M1 between t1 and t2 (van de Weerd 1979).

M. bendai is reported in the latest Miocene-to-Early Pliocene of Greece (de Bruijn 1989; Koufos 2006; Hordijk & de Bruijn 2009) and the Early Pliocene of France (Aguilar *et al.* 1989).

Micromys minutus (Pallas, 1771)*,* the Eurasian Harvest Mouse, is the only extant species of the genus *Micromys*. Towards the end of the Miocene and during the Pliocene this genus exhibited a greater diversity with a higher number of species whose phylogenetic relationships are still not resolved. As a matter of fact, even if some species such as *M. cingulatus* from Greece and *M. chalceus* from Asia exhibit less advanced morphological features (e.g., reduced number of roots, t7 absent or reduced), their presence in latest Miocene/earliest Pliocene localities of Europe and Asia indicates that they are contemporary to other species of this genus, namely *M. bendai*, *M. paricioi*, which, on the contrary, display more advanced morphological traits (e.g., higher number of roots and well developed t7) (Hordijk & de Bruijn 2009). In summary, as already evidenced by some authors (van de Wteerd 1979; Storch & Dahlmann 1995; Hordijk & de Bruijn 2009), it is extremely problematic to define a single lineage leading to the extant *M. minutus*. The evolutionary lineage *M. chalceus–M. cingulatus–M. paricioi* proposed by Storch & Dahlmann (1995) seems to be not valid because *M. paricioi* appeared in Spain almost contemporaneously to the appearance in Greece of *M. cingulatus* (García-Alix *et al.* 2008b). *Micromys steffensi* is reported from the Pliocene deposits of the Ptolemais basin (Hordijk & de Bruijn 2009) and shows a strong similarity with *M. bendai*, but it differs in its larger size and in some morphological details. In our opinion, *M. steffensi* probably should be regarded as an endemic form within the Ptolemais basin.

Some other species appeared subsequently, such as *Micromys caesaris* Minwer-Barakat, García-Alix, Martín-Suárez & Freudenthal, 2008, a form of small size reported in the Late Pliocene of the Guadix Basin, Spain (Minwer-Barakat *et al.* 2008) and *Micromys praeminutus*, known from some Pliocene localities of Europe (Michaux 1969; van de Weerd 1979).

Genus *Apodemus* Kaup, 1829

Apodemus gudrunae van de Weerd, 1976
(Fig. 5A-F)

Apodemus gudrunae van de Weerd, 1976: 84, pl. 3, figs 1-6. — Adrover *et al.* 1993a: 68, pl. 8, figs 4-9. — Sarica-Filoreau 2002: 19, figs 4, 5. — Minwer-Barakat *et al.* 2009b: 855, fig. 3. — Colombero *et al.* 2013: 118, fig. 4G, H, P, Q.

Apodemus cf. *gudrunae* – De Giuli 1989: 208, pl. 3, figs 13-20. — Abbazzi *et al.* 2008: 622, fig. 6D.

TYPE LOCALITY. — Valdecebro 3, Spain.

REFERRED MATERIAL. — Two maxillary fragments bearing M1 and M2; 68 isolated M1; 52 isolated M2; 20 isolated M3; 63 isolated m1; 35 isolated m2; 20 isolated m3. See Appendix 1 for further details.

OCCURRENCE IN THE STUDIED LAYERS. — MCC3, MCC4, MCC5, MCC7.

MEASUREMENTS. — see Table 6.

DESCRIPTION

M1

t1 smaller than t2; the t3 exhibits a short posterior spur not reaching the t5; t4-t7 connection generally low or rarely absent; t7 absent in two specimens, narrow or crest-like in 20% of specimens and well-developed in the others; t12 well developed.

M2

t6-t9 connection absent in 15% of specimens and low in the others; t7 generally narrow or crest-like; t4-t7 connection absent in 30% of the specimens and low in the others; t12 absent in 15% of specimens.

M3

t3 absent in 30% of specimens and very small in the rest; t8-t9 complex bilobed or elliptic, connected to the t6, and, more rarely, to the t4.

m1

tma always present and well developed; protoconid-metaconid complex connected with anteroconid complex through low connections mainly developed on the lingual side; hypoconid-entoconid complex isolated from the protoconid-metaconid complex; the c1 is well-developed; labial cingulum bearing two (50% of specimens); three (35% of specimens) or four (15% of specimens) cusplets.

m2

Anterolabial cuspid well developed; hypoconid-entoconid complex isolated from the protoconid-metaconid complexc1 well-developed; labial cingulum with one or two cusplets.

m3

Small anterolabaial cuspid formed by an enamel swelling; posterior complex rounded isolated; a small accessory cusplet can occur on the labial side.

REMARKS

The size of the large-sized species of *Apodemus* Kaup, 1829 from MCC are very similar to those of *Apodemus gudrunae* van de Weerd, 1976 from many Late Miocene localities of Europe such as the type locality Valdecebro 3 (van de Weerd 1976), Masada del Valle 7, La Fontana, Arquillo 1 (van de Weerd 1976; Adrover *et al.* 1993a), Negratín 1(Minwer-Barakat *et al.* 2009b), Verduno (Colombero *et al.* 2013), and Asmasya (southwestern Anatolia, Sarica-Filoreau 2002). The described material from MCC is somewhat larger than that referred to *A.* cf. *gudrunae* from Pino Mojón and Barranco de Cañuelas (Sesé 1989) and slightly smaller than that of *A.* cf. *gudrunae* from Castelnou 3 (Aguilar *et al.* 1991). From a morphological point of view, the assemblage of *A. gudrunae* from MCC is very similar to that of the type locality of Valdecebro 3 except for some M1 that display a slightly more developed t7.

With respect to *Apodemus gorafensis* Ruiz Bustos, Sesé, Dabrio, Peña & Padial, 1984, reported in Europe since the latest Miocene and widely distributed during the Pliocene, the size of the teeth from MCC is smaller. Nevertheless, the measurements of *A. gorafensis* from Tomea Eksi 1

TABLE 6. — Dental measurements (in mm) of *Apodemus gudrunae* van de Weerd, 1976 from Moncucco Torinese. Abbreviations: see Table 1.

	Layer		**Length**					**Width**				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
M1	MCC3	9	9	1.92	2.12	2.24	0.0960	7	1.25	1.35	1.47	0.0643
	MCC4	16	13	1.93	2.13	2.30	0.1127	15	1.25	1.34	1.45	0.0526
	MCC5	47	39	1.94	2.14	2.34	0.0988	39	1.43	1.51	1.64	0.0442
	MCC7	7	6	2.01	2.11	2.17	0.0539	6	1.31	1.34	1.36	0.0199
M2	MCC3	4	2	1.38	1.44	1.53	0.0634	2	1.31	1.33	1.34	0.0212
	MCC4	12	10	1.36	1.47	1.57	0.0634	9	1.25	1.34	1.42	0.0502
	MCC5	34	32	1.31	1.45	1.59	0.0721	32	1.13	1.33	1.48	0.0704
	MCC7	4	3	1.44	1.48	1.53	0.0458	3	1.41	1.44	1.47	0.0300
M3	MCC3	1	1	–	1.00	–	–	1	–	1.00	–	–
	MCC4	5	5	1.01	1.08	1.11	0.0415	4	0.97	1.08	1.20	0.0946
	MCC5	11	11	1.04	1.08	1.13	0.0301	11	1.01	1.09	1.19	0.0656
	MCC7	3	3	0.94	1.04	1.12	0.0917	3	0.93	1.04	1.12	0.0985
m1	MCC3	4	4	1.91	2.04	2.15	0.1118	4	1.13	1.25	1.36	0.0998
	MCC4	11	9	1.89	2.00	2.13	0.0835	8	1.11	1.17	1.26	0.0481
	MCC5	38	27	1.89	2.00	2.16	0.0788	28	1.11	1.21	1.37	0.0581
	MCC7	10	8	1.88	1.97	2.11	0.0758	8	1.15	1.20	1.25	0.0364
m2	MCC3	2	2	1.41	1.43	1.44	0.0212	2	1.24	1.27	1.29	0.0354
	MCC4	3	3	1.40	1.42	1.44	0.0200	2	1.22	1.27	1.31	0.0636
	MCC5	24	22	1.31	1.42	1.56	0.0575	20	1.16	1.26	1.41	0.0654
	MCC7	6	6	1.40	1.41	1.42	0.0103	6	1.25	1.30	1.37	0.0488
m3	MCC3	1	1	–	1.15	–	–	1	–	1.01	–	–
	MCC4	2	2	1.15	1.17	1.19	0.0283	2	1.00	1.01	1.02	0.0141
	MCC5	14	12	1.01	1.14	1.22	0.0665	12	0.93	1.02	1.12	0.0595
	MCC7	3	3	1.05	1.10	1.16	0.0557	3	0.99	1.01	1.03	0.0208

and 2 (Hordijk & de Bruijn 2009) largely overlap those of the material from MCC. According to Sarica-Filoreau (2002), the main morphological difference between *A. gudrunae* and *A. gorafensis* is the development of the t1 of the M1. This tubercle is larger and stout in *A. gorafensis* than in *A. gudrunae*. Moreover, the larger size of the t1 produces a deep inflexion between t1 and t2 on the lingual side of the M1 of *A. gorafensis*. The t1 of the specimens from MCC is rather small and the inflexion is shallow. Moreover, compared with *A. gorafensis* from the type locality of Gorafe A, the specimens of *Apodemus* from MCC exhibit a slightly smaller t7 and less developed posterior spurs on t3. For these reasons, the material from MCC is referred to as *A. gudrunae*.

The size of *Apodemus atavus* Heller, 1936, present in Europe since the latest Miocene and abundant in the Pliocene and the Pleistocene, is generally smaller than that of *A. gudrunae*. Moreover, in *A. atavus* the t7 is more frequently isolated and the t3 produces longer posterior spurs than in *A. gudrunae*. Some M1 of *A. gudrunae* from MCC exhibit an isolated t1. This morphological feature is relatively common among the species of the genus *Rhagapodemus* Kretzoi, 1959, widespread in Europe from the Late Miocene to the Pleistocene. Most of them, especially the Plio-Pleistocene species, namely *Rhagapodemus hautimagnensis* Mein & Michaux, 1970, *R. frequens* Kretzoi, 1959, *R. ballesioi* Mein & Michaux, 1970 and *R. vandeweerdi* de Bruijn & van der Meulen, 1975 can be easily differentiated by the higher-crowned teeth. Moreover, in the M1 of *Rhagapodemus*, the t1 is always isolated and the t3 is more anteriorly placed, being very close to the t2. However, some specimens of *Rhagapodemus primaevus* (Hugueney & Mein, 1965) from the Late Miocene of Lissieu are similar to *A. gudrunae* especially in the low-crowned teeth

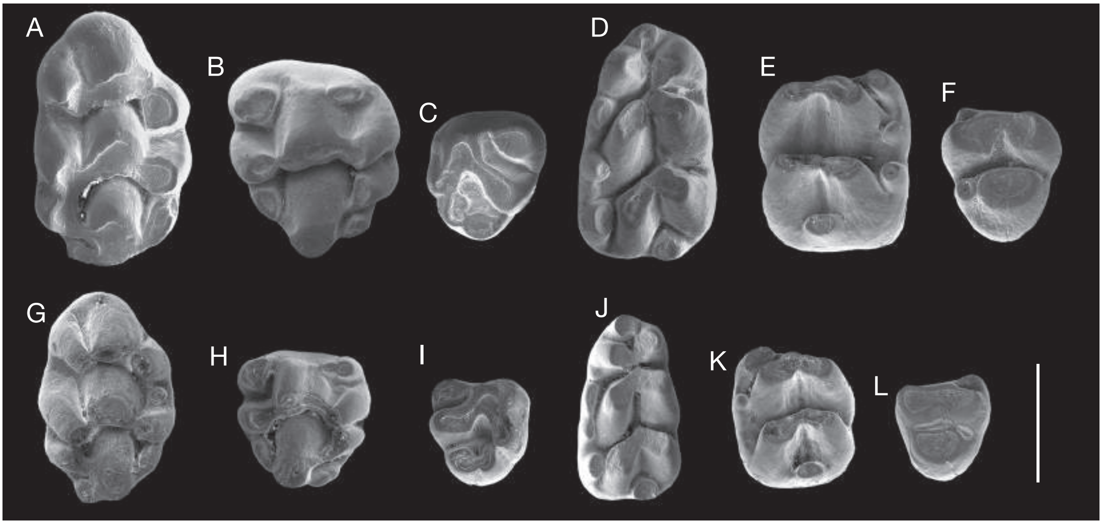

Fig. 5. — Isolated teeth of *Apodemus* Kaup, 1829 from Moncucco Torinese: **A**-**F**, *Apodemus gudrunae* van de Weerd, 1976; **A**, MGPT-PU127084, M1 dex.; **B**, MGPT-PU127731, M2 sin.; **C**, 127661, M3 dex.; **D**, MGPT-PU127974, m1 sin.; **E**, MGPT-PU127475, m2 dex.; **F**, MGPT-PU127665, m3 sin.; **G**-**L**, *Apodemus atavus* Heller, 1936 from Moncucco Torinese; **G**, MGPT-PU127659, M1 dex.; **H**, MGPT-PU127660, M2 sin.; **I**, MGPT-PU127661, M3 sin.; **J**, MGPT-PU127180, m1 sin.; **K**, MGPT-PU127662, m2 sin.; **L**, MGPT-PU127663, m3 dex. Scale bar: 1 mm.

and the shape and position of t3. Anyway, these two species exhibit some differences. In particular, the tubercles of the upper molars of *R. primaevus* are clearly vertical especially as regards the t1, whereas the tubercles of the lingual and labial sides of *A. gudrunae* are slightly inclined internally towards the longitudinal axis of the tooth.

A. gudrunae is a common member of the MN13 vertebrate assemblages of the Mediterranean area, being regularly reported in a number of latest Miocene localities of Spain, France, Italy, Greece and Turkey (see NOW Database, Fortelius 2012).

Apodemus atavus Heller, 1936
(Fig. 5G-L)

Apodemus atavus Heller, 1936: 126, pl. 10, fig. 2. — Rietschel & Storch 1974: 495, text figs 1-3, pls 1-4. — Fejfar & Storch 1990: 147, figs 39-50. — Bolliger *et al.* 1993: 1045, figs 9, 10. — Marchetti *et al.* 2000:98, figs 6, 17-40, 42-48. — Martín-Suárez & Mein 2004:116, fig. 1. — Minwer-Barakat *et al.* 2005: 432, fig. 3A-F. — García-Alix *et al.* 2008b: 192, fig. 3M-R. — Hordijk & de Bruijn 2009: 36, pl. 10, figs 5-12.

Apodemus dominans Kretzoi, 1959: 243. — van de Weerd 1976: 87, pl. 8, figs 6-10; 1979: 138, pl. 2, figs 1-9. — Sen 1977: 105, pl. 3, figs 7-10 (*cum syn.*). — Aguilar *et al.* 1986: 131; 1991: 159. — Adrover *et al.* 1988: 108, figs 3, 1-7. — Sesé 1989: 193. — Hordijk & de Bruijn 2009: 37, pl. 10, figs 1-4.

Apodemus cf. *dominans* – Adrover *et al.*1988: 107, figs 2, 9, 10; 1993a: 69, pl. 8, figs 10-13. — Storch & Dahlmann 1995: pl. 1, figs 8-14. — Mörs *et al.* 1998: 151, fig. 10. — Vasileiadou *et al.* 2012: 222, fig. 7d.

Sylvaemus dominans – Popov 2004: 26, figs 28, 29.

Apodemus cf. *etruscus* – Angelone *et al.* 2011: 99, figs 6, 12.

Type locality. — Gundersheim 4, Germany.

Occurrence in the studied layers. — MCC3; MCC4; MCC5; MCC7.

Referred material. — Twelve isolated M1; seven isolated M2; four isolated M3; 17 isolated m1; six isolated m2; three isolated m3.

Measurements. — see Table 7.

TABLE 7. — Dental measurements (in mm) of *Apodemus atavus* Heller, 1936 from Moncucco Torinese. Abbreviations: see Table 1.

	Layer		**Length**					**Width**				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
M1	MCC4	2	2	1.73	1.75	1.76	0.0247	2	1.14	1.15	1.16	0.0148
	MCC5	9	7	1.69	1.80	1.90	0.0820	8	1.08	1.13	1.18	0.0285
	MCC7	1	–	–	–	–	–	–	–	–	–	–
M2	MCC3	1	1	–	1.14	–	–	1	–	1.07	–	–
	MCC4	3	3	1.13	1.15	1.18	0.0251	3	1.07	1.11	1.14	0.0361
	MCC5	3	3	1.13	1.13	1.14	0.0050	2	1.03	1.07	1.11	0.0566
M3	MCC5	4	4	0.89	0.95	1.00	0.0519	4	0.82	0.97	1.04	0.1015
m1	MCC3	2	2	1.69	1.75	1.80	0.0778	2	1.02	1.07	1.11	0.0636
	MCC4	7	5	1.60	1.69	1.87	0.1080	6	0.94	0.99	1.11	0.0618
	MCC5	6	5	1.60	1.74	1.87	0.1074	4	0.98	1.09	1.24	0.1194
	MCC7	1	1	–	1.84	–	–	1	–	1.09	–	–
m2	MCC4	1	1	–	1.27	–	–	1	–	1.27	–	–
	MCC5	4	3	1.15	1.18	1.22	0.0852	3	0.95	1.03	1.11	0.0808
	MCC7	2	2	1.16	1.21	1.25	–	2	1	1.04	1.08	–
m3	MCC5	2	1	–	0.79	–	–	1	–	0.77	–	–
	MCC7	1	1	–	0.97	–	–	1	–	0.92	–	–

DESCRIPTION

M1

The t1 is close to but isolated from the t5; t1-t2 connection low; t3 small; 75% of the specimens exhibit a posterior spur on the t3 not connecting to t5, 25% of specimens with very reduced or absent posterior spur; t7 always present; t4-t7 connection absent in 50% of the specimens; t7-t8 connection absent in 20% of the specimen; t12 well-developed.

M2

t1 completely isolated; the t7 is always present and isolated from the t4; t7-t8 connection absent in 25% of the specimens and low and weak in the others; t9 and t12 well-developed.

M3

t1 strong; the posterior complex, formed by the t8 and t9, is bilobed and elliptic occasionally connected with the t6 but isolated from the t4.

m1

tma always present and well-developed; posterior heel ovoid or rounded; c1 isolated from hypoconid; labial cingulum composed by several cusplets, generally two or three in addition to the c1.

m2

Anterolabial cuspid well-developed and isolated; labial cingulum with two or three cusplets in addition to the c1.

m3

Anterolabial cuspid formed by a small swelling of the enamel; posterior complex rounded.

REMARKS

The medium-sized *Apodemus* present at MCC is smaller than *A. gudrunae*. From a morphological point of view *A. atavus* differs in the regular presence of a well-developed and frequently isolated t7 in both M1 and M2, more developed posterior spurs in the t3 of M1 and more developed t12.

In a previous cursory analysis of the vertebrate assemblage of MCC (Angelone *et al.* 2011), some of the specimens referred herein to as *A. atavus* were erroneously identified to as *Apodemus* cf. *etruscus* Engesser, 1989, a species reported only from the Late Miocene of Baccinello V3, central Italy. This species differs from *A. atavus* in having a poorly developed t7 in the upper molars and poorly developed spurs on the t3 of M1.

The measurements of the specimens of the medium-sized *Apodemus* from MCC fit well with those of *Apodemus atavus* from the Pliocene localities of Gundersheim (type locality) (Fejfar & Storch 1990), Saint Vallier (Martín-Suárez & Mein 2004), La Dehesa 1 (García-Alix *et al.* 2008b), Komanos 1 (low and high), Tomea Eksi 3, Vorio 3a and Notio 1 (Hordijk & de Bruijn 2009), and Willerhausen (Rietschel & Storch 1974). They are slightly smaller than *A. atavus* from the latest Miocene and Pliocene localities of Purcal 7, 13, Calicasas 3, 3B, 4B, Cerro del Águila 1C (García-Alix *et al.* 2008b), Vue-des-Alpes (Bolliger *et al.* 1993) and the Pleistocene locality of Monte La Mesa (Marchetti *et al.* 2000). The size ranges of the specimens belonging to *A. atavus* from the Pliocene localities of Tollo de Chiclana (Tollo de Chiclana 1, 1B, 3 and 13) (Minwer-Barakat *et al.* 2005) are very similar to those of MCC, even if the maximum values of M1 and m1 are slightly higher. The morphology of the studied material is perfectly consistent with that of *A. atavus* from Gundersheim, in particular as far as regards the development of t7 (which is isolated in half of the available M1), low t1-t2 connection, presence of spurs on t3 of M1, and well-developed tma in the m1.

The average size of *Apodemus dominans* Kretzoi, 1959, a species reported in Europe since the latest Miocene to the Pleistocene, from the type locality of Csarnota 2 (see van de Weerd 1976) is similar to that of MCC except for the M1 and m2 that are slightly larger than those from MCC. The size of *A. dominans* from the Pliocene localities of Escorihuela, Orrios (van de Weerd 1976), Castelnou 3 (Aguilar *et al.* 1991), Mont-Hélène (Aguilar *et al.* 1986, Concud Estación 3 and Concud Pueblo 3 (Adrover *et al.* 1988) is extremely similar to that of MCC, whereas that from Çalta (Sen 1977), Concud Estación 1 (Adrover *et al.* 1988), Hambach (Mörs *et al.* 1998), Muselievo (Popov 2004), Notio 1 (Hordijk & de Bruijn 2009), the latest Miocene locality of Bacochas 1 (Sesé,1989), the Late Miocene-Early Pliocene of Maramena (Storch & Dahlmann 1995); is only slightly larger. The lower molars of *A. dominans* from Celadas 9 and la Gloria 4 (Pliocene of Spain) (Adrover *et al.* 1993a) are slightly smaller than those from MCC. The separation between *A. atavus* and *A. dominans* based on morphology is highly problematic (Popov 2004; Hordijk & de Bruijn 2009; Vasileiadou *et al.* 2012). Fejfar & Storch (1990) suggested that putative distinctive characters of *A. dominans* such as the presence of a strong t12 in M1-2, three radiculated upper molars, and the presence of rearward c1 in m1-2 should be regarded as symplesiomorphies. The size differences between *A. dominans* from the type locality of Csarnota 2 (van de Weerd 1976) and *A. atavus* from the type locality of Gundersheim-4 (Fejfar & Storch 1990) are very slight; the mean values of M1 and m2 from Csarnota 2 are slightly larger than those from Gundersheim-4 but the size ranges partially overlap; the average sizes of M2, M3, m1, and m3 are very close and the size ranges are nearly identical. However, some authors (e.g., Storch & Dahlmann 1995; Mörs *et al.* 1998; Popov 2004; Hordijk & de Bruijn 2009; Vasileiadou *et al.* 2012) assigned some specimens from Maramena and Kessani (Miocene/Pliocene boundary of Greece), Hambach (Pliocene of Germany), Muselievo (Pliocene of Bulgaria), Notio 1 (Pliocene of Greece) to *A. dominans* and *A.* cf. *dominans* because of their slightly larger mean values with respect to those of *A. atavus* from Gundersheim-4. These slight size differences, however, should not be regarded as reliable criteria to discriminate between these two taxa. The size of other species of *Apodemus* such as *Apodemus sylvaticus* (Linnaeus, 1758) (see Cuenca Bescós *et al.* 1997; Renaud & Michaux 2003, 2007) and *Apodemus flavicollis* (Melchior, 1834) (see Michaux & Pasquier 1974; Capizzi & Filippucci 2008) is characterized by considerable variation through time and space due to the interrelationship of multiple factors involving climatic and/or latitudinal variations and interspecific competition (Renaud & Michaux 2007). Small differences in size between material from different regions and ages, as for example those reported for *A. atavus* and *A. dominans*, are to be expected and may be related to intraspecific variability. For these reasons, as already pointed out by several authors (Martín-Suárez & Mein 2004; Minwer-Barakat *et al.* 2005; García-Alix *et al.* 2008b), it is not possible to conclusively separate *A. atavus* and *A. dominans* from both a morphological and biometrical point of view and we follow the suggestions of these authors in considering *A. dominans* a junior synonym of *A. atavus*. As a consequence, the material from MCC is referred to *A. atavus*.

TABLE 8. — Dental measurements (in mm) of *Eliomys* aff. *intermedius* Friant, 1953 from Moncucco Torinese. Abbreviations: see Table 1.

	Layer		Length					Width				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
P4	MCC5	1	1	–	0.84	–	–	1	–	1.00	–	–
M1	MCC7	3	3	0.97	1.07	1.14	0.0873	3	1.37	1.38	1.40	0.0173
M2	MCC4	2	2	1.15	1.19	1.23	0.0566	2	1.42	1.44	1.45	0.0212
m1	MCC5	1	1	–	1.29	–	–	1	–	1.38	–	–
	MCC7	1	1	–	1.23	–	–	1	–	1.37	–	–
m2	MCC5	1	1	–	1.25	–	–	1	–	1.47	–	–

According to many authors (Rietschel & Storch 1974; Fejfar & Storch 1990; Martín-Suárez & Mein 1998), *A. atavus* should be considered as the ancestor of the extant species *A. sylvaticus.* This relationships might be corroborated by some remains of *A. atavus* from Willerhausen (Rietschel & Storch 1974), where the exceptional preservation of bones and soft tissues allowed the authors to note that the habitus and size of the two species are similar and that *A. atavus* solely differs for a few characters such as the shorter ulna and femur and the stronger t12 in M1 and M2.

Family GLIRIDAE Thomas, 1897
Genus *Eliomys* Wagner, 1840

Eliomys aff. ***intermedius*** Friant, 1953
(Fig. 6A-E)

Eliomys cf. *truci* – Angelone *et al.* 2011: 99, fig. 6 (17).

TYPE LOCALITY. — Sète, France.

OCCURRENCE IN THE STUDIED LAYERS. — MCC4; MCC5; MCC7.

REFERRED MATERIAL. — A single P4, three M1, two M2, two m1, and a single m2.

MEASUREMENTS. — Table 8.

DESCRIPTION

P4

Triangular outline; anteroloph short and connected to the paracone; the anterior centroloph extends to the midpoint of the tooth; posteroloph not fused with metacone.

M1-2

M1 and M2 display a very similar dental pattern; the M2 usually presents a less concave anteroloph; molars are shallow basined with trapezoidal outline, the lingual side being slightly shorter than the labial one; endoloph strong and continuous; paracone slightly stouter and higher than the metacone; the anterior centroloph reaches the midpoint of the molar; posterior centroloph always present; in both M2 and in one of three M1 the posterior centroloph fuses with the anterior centroloph forming a "Y-shaped" ridge that extends to the midpoint of the molar.

m1

Trapezoid in outline; the endolophid is discontinuous; anterolophid connected to protoconid in one of the two available specimens; metalophid connected to metaconid; centrolophid extending beyond the midpoint of the molar; well-developed posterior extra ridge; in both specimens, the connection between hypoconid and posterolophid marked by a slight narrowing of the ridge.

m2

Broader than long; the endolophid is discontinous; anterolophid not connected to the protoconid; metalophid not connected with the metaconid; centrolophid short; very reduced posterior extra ridge.

REMARKS

The presence of a continuous and strong endoloph in the upper molars excludes any possible assignment of the material from MCC to the genus

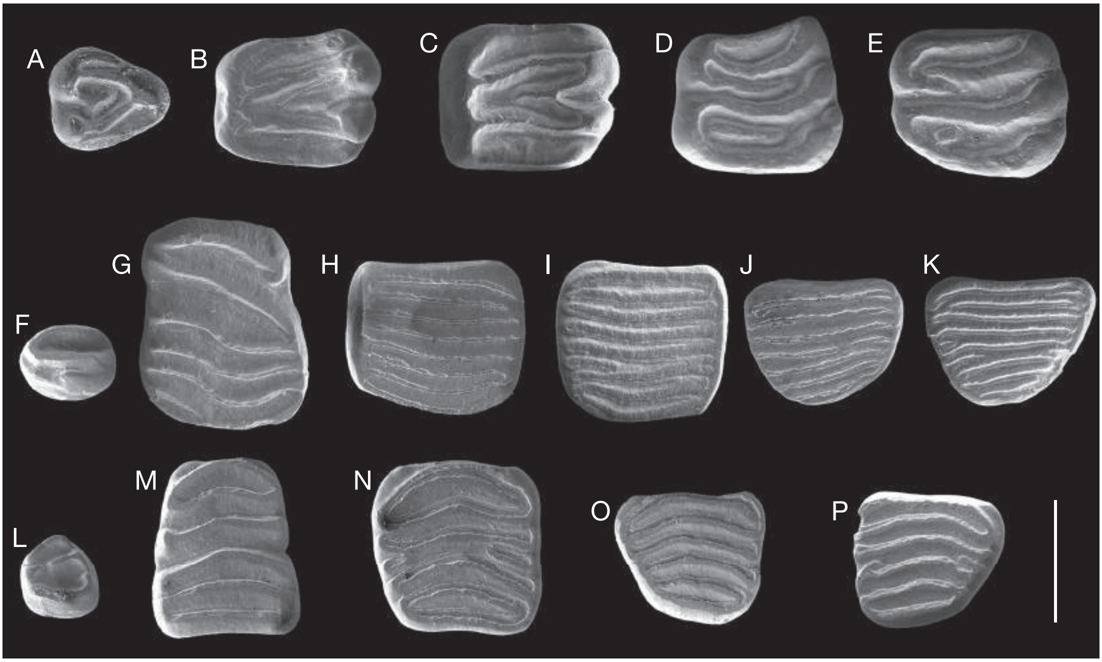

FIG. 6. — Isolated teeth of *Eliomys* Wagner, 1840 and *Muscardinus* Kaup, 1829 from Moncucco Torinese: **A**-**E**, *Eliomys* aff. *intermedius* Friant, 1953; **A**, MGPT-PU12128348, P4 dex.; **B**, MGPT-PU128270 M1 sin.; **C**, MGPT-PU127495, M2 sin.; **D**, MGPT-PU128269, m1 dex.; **E**, MGPT-PU127127368, m2 dex.; **F**-**P**, *Muscardinus vireti* Hugueney & Mein, 1965; **F**, MGPT-PU127604, P4 dex.; **G**, MGPT-PU12392, M1 dex.; **H**, MGPT-PU127606, M2 sin.; **I**, MGPT-PU128178, M2 dex.; **J**, MGPT-PU127607, M3 dex.; **K**, MGPT-PU128182, M3 dex.; **L**, MGPT-PU127608, p4 sin.; **M**, MGPT-PU127609, m1 dex.; **N**, MGPT-PU127610, m2 sin.; **O**, MGPT-PU127611, m3 sin.; **P**, MGPT-PU127513, m3 dex. Scale bar: 1 mm.

Myomimus Ognev, 1924. The presence of wider than long lower molars and continuous, strong endolophs in upper molars are characteristic of the genera *Dryomys* Thomas, 1906 and *Eliomys* Wagner, 1840. According to Freudenthal & Martín-Suárez (2006), the presence of an endolophid in the lower molars might be used to separate *Dryomys* from *Eliomys*. For this reason, we assign the specimens from MCC to the genus *Eliomys*.

Direct comparisons with *Eliomys truci* Mein & Michaux, 1970, a species distributed in Europe between the Late Miocene and the Late Pliocene, from the Early Ruscinian locality of Hautimagne, evidenced that the specimens from MCC mainly differ in the presence of a posterior centroloph in the upper molars, a shorter centrolophid in the m2 and in the strong reduction of the secondary accessory ridge in the m2. Moreover, in the m1-2 of *E. truci* from the Granada and Guadix basin, the metalophid-metaconid connection and the anterolophid-protoconid connection are rarer compared to the material from MCC (García-Alix *et al.* 2008a). The measurements of the teeth from MCC are slightly larger than those of *E. truci* from Hautimagne (Mein & Michaux 1970), Los Mansuetos, Concud 2 and 3 (van de Weerd 1976), Tollo de Chiclana 13 and 1B, Purcal 23 and 25a, La Dehesa 1 and 16, and Otura 1 and 4 (García-Alix *et al.* 2008a), especially as regards the width, whereas the length of the specimens of some other assemblages such as Masada del Valle 2 and 5, Concud Barranco de las Calaveras (van de Weerd 1976), and La Gloria 4 (Adrover *et al.* 1993a) is very close to that of MCC.

The measurements of *Eliomys intermedius* Friant, 1953, widespread in Europe between the Late Miocene and the Pleistocene, are usually larger than those of the sample from MCC (van de Weerd 1976; García-Alix *et al.* 2008a). Recent observations on

TABLE 9. — Dental measurements (in mm) of *Muscardinus vireti* Hugueney & Mein, 1965 from Moncucco Torinese. Abbreviations: see Table 1.

	Layer		Length					Width				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
P4	MCC5	2	1	–	0.60	–	–	1	–	0.88	–	–
M1	MCC3	2	1	–	1.70	–	–	1	–	1.33	–	–
	MCC4	1	1	–	1.59	–	–	1	–	1.32	–	–
	MCC5	14	14	1.59	1.71	1.80	0.0679	12	1.20	1.39	1.49	0.0796
	MCC7	3	3	1.58	1.65	1.71	0.0656	3	1.16	1.30	1.37	0.1185
M2	MCC3	1	1	–	1.40	–	–	–	–	–	–	–
	MCC4	2	2	1.34	1.36	1.37	0.0212	2	1.47	1.51	1.55	0.0566
	MCC5	11	11	1.24	1.35	1.46	0.0630	10	1.34	1.47	1.57	0.0929
	MCC7	2	1	–	1.48	–	–	1	–	1.45	–	–
M3	MCC5	3	3	1.06	1.09	1.11	0.0265	3	1.32	1.36	1.43	0.0586
p4	MCC5	1	1	–	0.63	–	–	1	–	0.65	–	–
m1	MCC3	2	2	1.50	1.59	1.67	0.1202	2	1.16	1.27	1.38	0.1556
	MCC4	4	4	1.59	1.67	1.80	0.0964	4	1.30	1.36	1.48	0.0826
	MCC5	14	14	1.44	1.59	1.68	0.0620	13	1.22	1.32	1.40	0.0593
	MCC7	2	2	1.59	1.62	1.64	0.0354	2	1.26	1.31	1.36	0.0707
m2	MCC3	1	1	–	1.37	–	–	1	–	1.41	–	–
	MCC4	4	3	1.40	1.45	1.50	0.0500	3	1.40	1.43	1.44	0.0231
	MCC5	17	16	1.31	1.45	1.59	0.0681	15	1.26	1.41	1.50	0.0591
	MCC7	2	2	1.47	1.49	1.50	0.0212	2	1.46	1.47	1.47	0.0071
m3	MCC4	3	3	1.10	1.18	1.30	0.1041	2	1.12	1.16	1.21	0.0458
	MCC5	6	6	1.12	1.16	1.21	0.0316	6	1.19	1.26	1.39	0.0708

some teeth from the type locality of Sète revealed that the remains of *Eliomys* from MCC share some morphological characteristics with this species, such as the presence of a posterior centroloph in the upper molars and the rounded outline of some dental elements, particularly the m2. Moreover, *E. intermedius* displays metalophid-metaconid and anterolophid-protoconid connections as observed in the small sample of MCC. The morphology of the lower molars from MCC is also similar to that of *E. intermedius* since the single m2 exhibits a strong reduction of the secondary posterior ridge even if in the latter species the reduction is stronger and frequently reported in the lower molars (García-Alix *et al.* 2008a). In a previous paper, Angelone *et al.* (2011) assigned a single left M1 from MCC (MGPT-PU 127) (erroneously identified as an M3) to *Eliomys* cf. *truci*; this molar is referred herein to as *Eliomys* aff. *intermedius* because its morphological features fit well with *E. intermedius*, even if the size is smaller and closer to that of *E. truci*. Some assemblages of *Eliomys* from Greek and Spanish localities of Late Miocene/Early Pliocene age are referred to *Eliomys* aff. *intermedius* (de Bruijn *et al.* 1970; Adrover *et al.* 1993a; García-Alix *et al.* 2008a), because they share an intermediate size between *E. truci* and *E. intermedius* and display morphological traits that fit better with *E. intermedius*, such as the presence of a posterior centroloph, more developed metalophid-metaconid and anterolophid-protoconid connections, and reduction of the posterior extra ridge. The assemblage of MCC exhibits some peculiar morphological features, such as the common occurrence of fused centrolophs developing into a Y-shaped ridge and a strong reduction of the posterior extra ridge in the m2. These assemblages are referred to *E.* aff. *intermedius* because the material is not rich enough to determine a clear attribution. Moreover even if the studied specimens display similar morphological features to those of *E. intermedius*, some reliable differences with the type locality assemblage, prevent us to securely refer the material from MCC to this species.

Genus *Muscardinus* Kaup, 1829

Muscardinus vireti Hugueney & Mein, 1965
(Fig. 6F-P)

Muscardinus vireti Hugueney & Mein, 1965: 118, figs 64-78.

Muscardinus aff. *vireti* – Engesser 1983: 776, fig. 6. — Colombero *et al.* 2013: 122, fig. 5E, F.

Muscardinus cf. *vireti* – Angelone *et al.* 2011: 99, fig. 6 (16).

TYPE LOCALITY. — Lissieu, France.

OCCURRENCE IN THE STUDIED LAYERS. — MCC3, MCC4, MCC5, MCC7.

REFERRED MATERIAL. — A single maxillary fragment bearing M1 and M2; two isolated P4; 18 isolated M1; 15 isolated M2; three isolated M3; a single isolated p4; 22 isolated m1; 25 isolated m2; 9 isolated m3.

MEASUREMENTS. — Table 9.

DESCRIPTION

P4
Ovoid in outline; three main ridges; first and second ridges connected on the lingual side.

M1
Six main ridges; first ridge convex and lingually bent forming a "crochet" (*sensu* Hugueney & Mein 1965); second ridge lingually inclined; all ridges but the first one connected by an elongate endoloph; a single specimen possesses small labial and lingual portions of an extra ridge situated between the third and fourth crests; four roots, three specimens with a supplementary anterolabial rootlet.

M2
Eight main low ridges; a complete endoloph connects all the ridges; half of the specimens exhibit a small labial portion of an extra ridge; usually arising as a bifurcation of the sixth ridge; three or four roots.

M3
Trapezoid or triangular in outline; eight main ridges connected by a complete endoloph; half of the specimens with a small labial portion of an extra ridge; usually as a bifurcation of the fifth or the sixth ridge; rare specimens with two labial portion of extra ridges; three roots.

p4
Ovoid in outline; three main ridges weakly connected on the labial side.

m1
Six main ridges; first and second ridges connected both on labial and lingual sides; third ridge convex or straight; forth, fifth and sixth ridges slightly convex; fifth and sixth ridges sometimes connected on the labial or lingual side; three roots.

m2
Six main ridges; lingual side of the molar slightly longer than labial one; a swelling of the enamel occasionally occurs on the anterolabial border of the molar; ridges frequently connected on the labial side, most notably between first and second and between fifth and sixth ridges; a lingual portion of an extra ridge regularly present between the third and fourth ridges; in half of the specimens a smaller labial portion of an extra ridge is present between the third and fourth ridges; four roots.

m3
Trapezoid in outline; lingual side longer than labial one; six main ridges; first and second ridges and fifth and sixth ridges occasionally connected on the labial and lingual side; 60% of specimens with a small lingual portion of an extra ridge between third and fourth ridges.

REMARKS

The flattened molars bearing a high number of roughly parallel ridges clearly support the attribution of the material documented herein to the genus *Muscardinus* Kaup, 1829.

The measurements of the studied material fit well with those of *Muscardinus helleri* Fejfar & Storch, 1990 from the Ruscinian locality of Gundersheim 4, even if the width of this latter species is generally larger. The morphology of the teeth from MCC is roughly similar to that of *M. helleri* primarily concerning the presence of six main ridges on the lower molars and M1, eight ridges on M2 and M3, as well as small lingual and labial extra ridges on the m2. However, some minor differences can be recognized, including the presence of a short endoloph in the M1 and M2 in *M. helleri* not reaching the last two ridges, the absence of extra ridges in the M2, and the presence in fewer specimens with a lingual "crochet" on the first ridge of M1.

The European Plio-Pleistocene *Muscardinus pliocaenicus* Kowalski, 1963 and the Late Miocene *Muscardinus pliocaenicus austriacus* Bachmayer & Wilson, 1970 from Austria (see also Daxner-Höck & Höck 2009) are slightly smaller than *M. vireti* from MCC. Moreover, these taxa are characterized by a minor number of ridges in the M1 and M2 and by the absence of extra ridges in the lower molars.

Muscardinus dacicus Kormos, 1930 from the Plio-Pleistocene of Europe shows a larger size and can be easily distinguished from the material of MCC by its simplified dental pattern without extra ridges on the m2 and with less developed ridges separated by larger valleys in the M1.

The Late Miocene species *Muscardinus davidi* Hugueney & Mein, 1965 from Lissieu is characterized by a size comparable to that of MCC from which it differs in having less seven ridges in the M2.

The measurements of *Muscardinus meridionalis* García-Alix, Minwer-Barakat, Martín-Suárez & Freudenthal, 2008 from the localities Purcal 24 (Late Turolian) and Purcal 4 (Early Ruscinian) in the Granada Basin (García-Alix *et al.* 2008c) are only slightly larger than those of the studied material from MCC. The general pattern of the molars is rather similar in displaying a similar number of main ridges in each dental element. However, in *M. meridionalis* extra ridges are not present on M2 and M3, the endoloph of upper molars seems to be weaker, the "crochet" on the first ridge of the M1 only rarely occurs and the extra ridges on the lower molars are extremely infrequent in the m2 and completely absent in the m3.

Compared with *Muscardinus vireti* Hugueney & Mein, 1965 from Lissieu, the specimens from MCC display slightly larger mean lengths and widths even if the size ranges partially overlap and also show a very similar morphology. In *M. vireti* the number of ridges is identical for each dental element (six in M1 and lower molars, eight in M2 and M3), the endoloph is well-developed and connects the last five ridges of M1, lingual and labial portions of extra ridges occur in many m2 and, finally, some M2 and M3 exhibit incomplete extra ridges very similar in shape to those observed in the specimens from MCC.

A few specimens assigned to *Muscardinus* aff. *vireti* were reported from Baccinello V3 (Engesser 1983). The measurements of that material are intermediate between those from MCC and Lissieu except for the m3 that are smaller. From the morphological point of view, the arrangement of the ridges of the molars is remarkably similar to that from MCC and no reliable differences can be detected.

The *Muscardinus* material from MCC is therefore assigned to *M. vireti*. The slight size differences with the material from Lissieu can be explained by the different age of the two localities, since Lissieu is probably slightly older than MCC (Gómez Cano *et al.* 2011). The intermediate size of the teeth from Baccinello V3 confirms that slight size differences are to be expected in assemblages of different age and geographic provenance.

According to García-Alix *et al.* (2008c), *M. vireti* should be considered the ancestor of *M. meridionalis*. This interpretation is followed herein, justified by several relevant morphological features that are shared by these two taxa, including the number of crests in upper and lower molars. Actually, *M. meridionalis* only differs in having a slightly modified dental pattern with very uncommon extra ridges, a much rarer occurrence of the "crochet" on the M1, and the weaker endoloph. García-Alix *et al.* (2008c) considered *M. helleri* as the descendant of *M. meridionalis*. Such hypothesis appears to be weak considering that *M. helleri* displays a slightly more complicated dental pattern than *M. meridionalis*, with more developed extra ridges in the m2. Therefore, the lineage *M. vireti*–*M. meridionalis*–*M. helleri* seems to be dubious since it would imply a simplification of the dental pattern (*M. vireti*–*M. meridionalis*) followed by a reversal of this trend (*M. meridionalis*–*M. helleri*). *Muscardinus meridionalis* possibly represents a taxon exclusive from southern Spain.

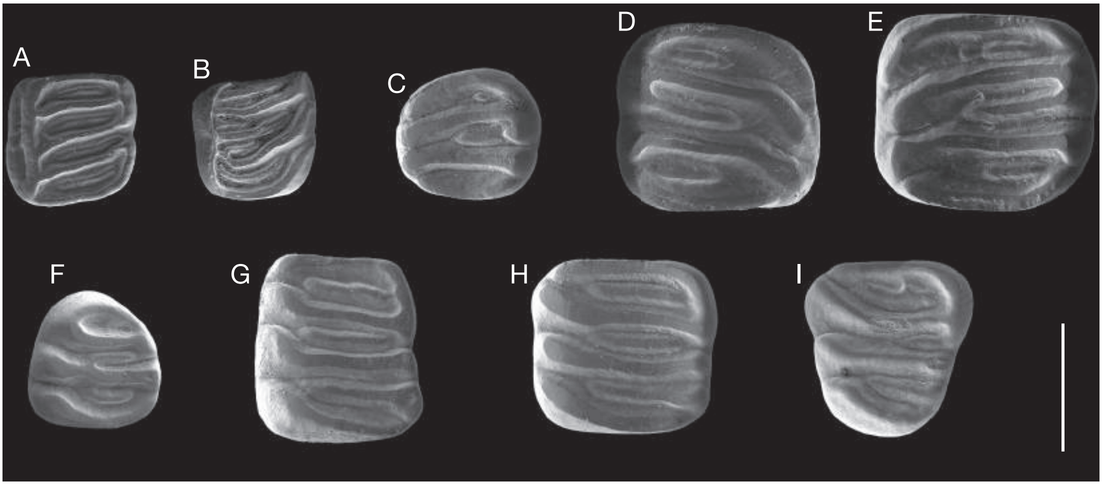

FIG. 7. — Isolated teeth of *Glirulus* Thomas, 1906 and *Glis* Brisson, 1762 from Moncucco Torinese: **A**, **B**, *Glirulus lissiensis* Hugueney & Mein, 1965; **A**, MGPT-PU127510, M2 sin.; **B**, MGPT-PU128351, m1 dex.; **C**-**I**, *Glis minor* Kowalski, 1956; **C**, MGPT-PU127494, P4 sin.; **D**, MGPT-PU127399, M1 dex.; **E**, MGPT-PU128208, M2 sin.; **F**, MGPT-PU127480, p4 dex.; **G**, MGPT-PU128207, m1 sin.; **H**, MGPT-PU127384, m2 sin.; **I**, MGPT-PU127387, m3 sin. Scale bar: 1 mm.

Genus *Glirulus* Thomas, 1906

Glirulus lissiensis Hugueney & Mein, 1965
(Fig. 7A, B)

Glirulus lissiensis Hugueney & Mein, 1965: 117, figs 57-63. — Daxner-Höck & Höck 2009: 419, fig. 17 (*cum syn.*).

TYPE LOCALITY. — Lissieu, France.

Occurrence in the studied layers. — MCC5; MCC7.

Referred material: — Two isolated M2; a single isolated m1.

Measurements. — M2: MGPT-PU 127496 (1.05 × 1.03); MGPT-PU 127510 (0.98 × 0.93); m1: MGPT-PU 128351 (0.96 × 0.95).

DESCRIPTION

M2

Five main and four accessory ridges; well-developed endoloph connected with all main ridges; slightly convex anteroloph; protoloph and anterior centroloph connected on the labial side; metaloph and posteroloph connected on the labial side; posterior centroloph elongate and weakly connected to the metaloph; three main roots plus a small rootlet partially fused with the antero-labial root.

m1

Five main and five accessory ridges; endolophid connected with all main ridges and narrowed between mesolophid and centrolophid; two accessory ridges between anterolophid and metalophid, the posterior one being very small; centrolophid not reaching the labial border; mesolophid long, strongly forward bent and weakly connected to the endolophid and to a small anterior accessory ridge on the lingual side; labial side of posterolophid strongly curved forward reaching the level of the lingual end of the mesolophid; two roots.

REMARKS

The small glirid recovered at MCC can be distinguished from the Miocene genus *Paraglirulus* Engesser, 1972 based on the absence of a free labial end on the anterior centroloph of the upper molars and of the presence of a complete endolophid in the m1 (van der Meulen & de Bruijn 1982). These features indicate that the material from MCC belongs to the genus *Glirulus* Thomas, 1906, distributed in Europe since the Early Miocene and currently represented by the small Japanese dormouse *Glirulus japonicus* (Schinz, 1845).

TABLE 10. — Dental measurements (in mm) of *Glis minor* Kowalski, 1956 from Moncucco Torinese. Abbreviations: See Table 1.

	Layer		Length					Width				
Element		TNr	mNr	min	mean	max	σ	mNr	min	mean	max	σ
P4	MCC3	1	1	–	1.24	–	–	1	–	1.41	–	–
	MCC4	1	1	–	1.16	–	–	1	–	1.32	–	–
	MCC5	1	1	–	1.19	–	–	1	–	1.30	–	–
M1	MCC3	1	1	–	1.55	–	–	1	–	1.64	–	–
	MCC5	3	3	1.48	1.54	1.65	0.0954	3	1.57	1.63	1.75	0.1039
M2	MCC3	1	1	–	1.47	–	–	1	–	1.71	–	–
	MCC4	1	1	–	1.52	–	–	1	–	1.82	–	–
	MCC5	3	3	1.47	1.49	1.51	0.0208	3	1.66	1.68	1.72	0.0321
	MCC7	1	1	–	1.57	–	–	1	–	1.63	–	–
p4	MCC5	4	4	1.03	1.07	1.15	0.0532	4	0.92	0.99	1.06	0.0640
m1	MCC4	1	1	–	1.74	–	–	1	–	1.53	–	–
	MCC5	3	2	1.65	1.71	1.77	0.0849	2	1.47	1.50	1.53	0.0424
m2	MCC4	1	1	–	1.62	–	–	1	–	1.68	–	–
	MCC5	1	–	–	–	–	–	1	–	1.73	–	–
m3	MCC5	1	1	–	1.47	–	–	1	–	1.41	–	–

The comparison with the material of *Glirulus lissiensis* Hugueney & Mein, 1965 from its type locality Lissieu did not reveal substantial morphological differences with the specimens from MCC. Moreover, the single m1 recognized in MCC is very similar to the holotype of *G. lissiensis* since both display a very similar structure of the endolophid that narrows between mesolophid and centrolophid, five accessory ridges, the first two lying between anterolophid and metalophid, and mesolophid and posterolophid strongly bent forward.

The size of the material from MCC is consistent with that of *G. lissiensis* from Lissieu (Hugueney & Mein 1965) and other Miocene European localities such as Oberdorf (de Bruijn 1998), Rudabanya (Daxner-Höck 2005), Eichkogels (Daxner-Höck & de Bruijn 1981), Belchatów (Kowalski 1997), Richaldholf, Schernham, and Kohfidish (Daxner-Höck & Höck 2009) except for one of the two available M2 (MPST-PU127496), which is slightly larger. The size of this latter specimen, however, fits well with those of *G.* aff. *lissiensis* from Saint Bauzile (Mein & Romaggi 1991). The material from MCC is also roughly similar in morphology and size to *Glirulus pusillus* (Heller, 1936) from some Pliocene and Pleistocene European localities (Kowalski 1963; Michaux 1970; Fejfar & Storch 1990; Daoud 1993; Mörs *et al.* 1998; Dahlmann 2001; van den Hoek Ostende 2003). According to Hugueney & Mein (1965), *G. lissiensis* differs from *G. pusillus* in having a less-developed endolophid, shorter labial branches of the main ridges in the lower molars and biradiculated lower molars. However, the number of roots in lower molars does not seem to be a reliable feature to distinguish these two species since lower molars of *G. pusillus* from Gundersheim 4 (Fejfar & Storch 1990) and many other localities (Daoud 1993; van den Hoek Ostende 2003) are biradiculated. The specimens of *Glirulus* from MCC are assigned to *G. lissiensis* since they are morphologically nearly indistinguishable from those of the type population from Lissieu. *G. lissiensis* is currently considered as the descendant of the Lower Miocene *Glirulus diremptus* (Mayr, 1979) (Daxner-Höck & de Bruijn 1981; van der Meulen & de Bruijn 1982; Nadachowski & Daoud 1994). According to Daxner-Höck & Höck (2009) its biochronological range extends from MN4 to MN13. The Plio-Pleistocene *G. pusillus* possibly derived from *G. lissiensis* (Daxner-Höck & de Bruijn 1981; van der Meulen & de Bruijn 1982; Nadachowski & Daoud 1994). The extant *G. japonicus,* a taxon endemic of the Japanese Archipelago, shows a dental pattern very similar to that of the extinct European species, also displaying slightly larger sizes and lower molars with three roots (van der Meulen & de Bruijn 1982; Mein & Romaggi 1991); this taxon has been classically interpreted as the descendant of Villanyan immigrant populations of *G. pusillus* from Europe (van der Meulen & de Bruijn 1982).

An exceptionally preserved specimen of *G.* aff. *lissiensis* was found at Saint-Bauzile (MN11) (Mein & Romaggi 1991). The extraordinary preservation of soft tissues revealed the presence of a patagium suggesting an adaptation to gliding, a locomotor behavior not observed in extant glirids.

Genus *Glis* Brisson, 1762

Glis minor Kowalski, 1956
(Fig. 7C-I)

Glis sackdillingensis minor Kowalski, 1956: 384, text fig. 2f, pl. 4, fig. 8.

Glis minor – Kowalski 1963: 545, text figs 8-10 (*cum syn.*). — Hordijk & de Bruijn 2009: 66, pl. 27, fig. 9. — Angelone *et al.* 2011: 99, fig. 6, 15. — Hellmund & Ziegler 2012: 84, pl. 4, figs 9-18.

Myoxus minor Daoud, 1993: 213.

Glis minor minor – Daxner-Höck & Höck 2009: 406, fig. 13 (*cum syn.*).

Type locality. — Podlesice, Poland.

Occurrence in the studied layers. — MCC3, MCC4, MCC5, MCC7.

Referred material. — Three P4; four M1; six M2; six p4; four m1; two m2; two m3. Further details in Appendix 1.

Measurements. — see Table 10.

Description

P4
Four main ridges; one to three accessory ridges; centroloph present and connected to protoloph in a single specimen; two roots.

M1-2
M1 and M2 display a very similar structure; M2 generally wider with less convex anteroloph; four main and three accessory ridges; main ridges slightly bent backward on the lingual side; centroloph labially connected to the protoloph in 40% of M1 and M2; three roots.

p4
Four main ridges free on their labial side; anterolophid and metalophid connected on the lingual side; two accessory ridges are present; a small ridge develops between anterolophid and metalophid in a single specimen; a single root.

m1-2
m1 morphologically similar to m2 but more elongated and anteriorly narrower. Anterolophid connected with metalophid on lingual side through an incomplete endolophid; first accessory ridge weakly connected to endolophid in half of the available m1 and isolated in all the m2; centrolophid weakly connected to metalophid in a single specimen; two roots.

m3
Trapezoid in outline; ridge arrangement identical to that of m1-2; centrolophid represented by a small swelling of the enamel in a single specimen; two roots.

Remarks

The morphological features and measurements of the material from MCC fit well with those of *Glis minor* Kowalski, 1956 from the type locality of Podlesice (Early Pliocene of Poland) (Kowalski 1956) and many other European Neogene localities such as Richardhof and Kohfidish (Daxner-Höck & Höck 2009), Węże 1 and Rebielece (Kowalski 1956, 1963; Daoud 1993), Notio 1 and Komanos 1 (Hordijk & de Bruijn 2009), Gundersheim 4 (Fejfar & Storch 1990), and Sondershausen (Hellmund & Ziegler 2012). The specimens from Rudabanya (Daxner-Höck 2005) are only slightly larger than those from MCC.

Glis sackdillingensis (Heller, 1930), a common Plio-Pleistocene European species, is slightly larger and has a larger number of accessory ridges in the M1-2 (Daoud 1993).

The dental pattern of the genus *Glis* is remarkably conservative, since that of the extant species *Glis glis* (Linnaeus, 1766) is hardly distinguishable from that of the extinct Miocene species (Daams & de Bruijn 1995). Therefore, it is extremely difficult to define the phylogenetic trajectories of this genus exclusively based on dental remains. Some authors (Daoud 1993; Nadachowski & Daoud 1994) hypothesized the reliability of the lineage *G. minor*–*G. sackdillingens*–*G. glis*.

Family Sciuridae Fischer, 1817
Genus *Sciurus* Linnaeus, 1758

Sciurus warthae Sulimski, 1964
(Fig. 8A, B)

Sciurus warthae Sulimski, 1964: 162, text fig. 3, pl. 3, figs 1-4. — Marchetti *et al.* 2000: 90, figs 3, 9-14. — Dahlmann 2001: 49, pl. 7, figs 20-27.

Sciurus cf. *warthae* – Black & Kowalski 1974: 465, pl. 12, figs 1, 2. — Siori & Sala 2007: 210, figs 2, 1-2.

TYPE LOCALITY. — Węże 1, Poland.

OCCURRENCE IN THE STUDIED LAYERS. — MCC5.

REFERRED MATERIAL. — A single isolated M3; a single isolated m1.

MEASUREMENTS. — M3: MGPT-PU 128219 (2.84 × 2.60); m1: MGPT-PU 128221 (2.28 × 2.42).

DESCRIPTION
M3

Triangular in outline; central basin deep and broad, moderately expanded posteriorly without evidence of crenulation; large and rounded protocone gradually rising from the endoloph; anteroloph lower than protoloph; paracone high and vertical; central basin bordered by a continuous rim interrupted just behind the paracone, where a cusplet occurs; three roots.

m1

Rhomboid in outline; molar basin without crenulation; the metaconid constitutes the higher cuspid followed by the hypoconid; protoconid less developed than hypoconid; well-developed and distinct entoconid resulting in an angular postero-lingual outline; anterolophid low; metalophid scarcely visible due to wear; mesostylid very poorly marked and represented by a weak enamel swelling; a notch is present anterior to the entoconid; mesoconid very low and separated from protoconid and hypoconid by two notches; roots not preserved.

REMARKS
The postero-lingual outline of the m1 is notably angular with a distinct entoconid, a feature present in tree squirrels and most of the flying squirrels (de Bruijn 1999). Among flying squirrels the morphology of the teeth of the genera *Hylopetes* Thomas, 1908 and *Neopetes* Daxner-Höck, 2004 is the most similar to the studied material. However, the dental morphology of the extant species of *Hylopetes* (see Bouwens & de Bruijn 1986 and Thorington *et al.* 1996, 2002), and comparison with some teeth of *Hylopetes lepidus* Horsfield, 1822 (IVAU and UCBL collections) evidenced the existence of some differences with the studied material. In particular, the m1-2 of extant *Hylopetes* are characterized by protoconid and hypoconid of roughly similar size and structure; both cuspids are high, distinctly vertical, remarkably protruding over the labial margin and from the postero-labial corner of the tooth; the protolophid can be easily distinguished from the hypoconid because it extends slightly posteriorly. In the single m1 from MCC the protoconid is less developed than the hypoconid; the hypoconid does not protrude over the postero-labial corner; the labial cuspids are not as distinct from the cingulids as in extant *Hylopetes*, the posterolophid constitutes a lingual extension of the hypoconid and does not extends posteriorly as in *Hylopetes*. In addition, in extant *Hylopetes* the anterolophid is well developed, always forming an evident anterosinusid and usually a distinct anteroconulid that is absent in the studied specimen; the mesostylid of extant *Hylopetes* is usually present and somewhat isolated whereas it is barely sketched in the single m1 from MCC. In the M3 of extant *Hylopetes* the protocone is well distinct from the endoloph, whereas in the specimen from MCC the protocone is broader and more rounded, gradually rising from the endoloph. Moreover, the enamel of the studied teeth is not sculptured as it

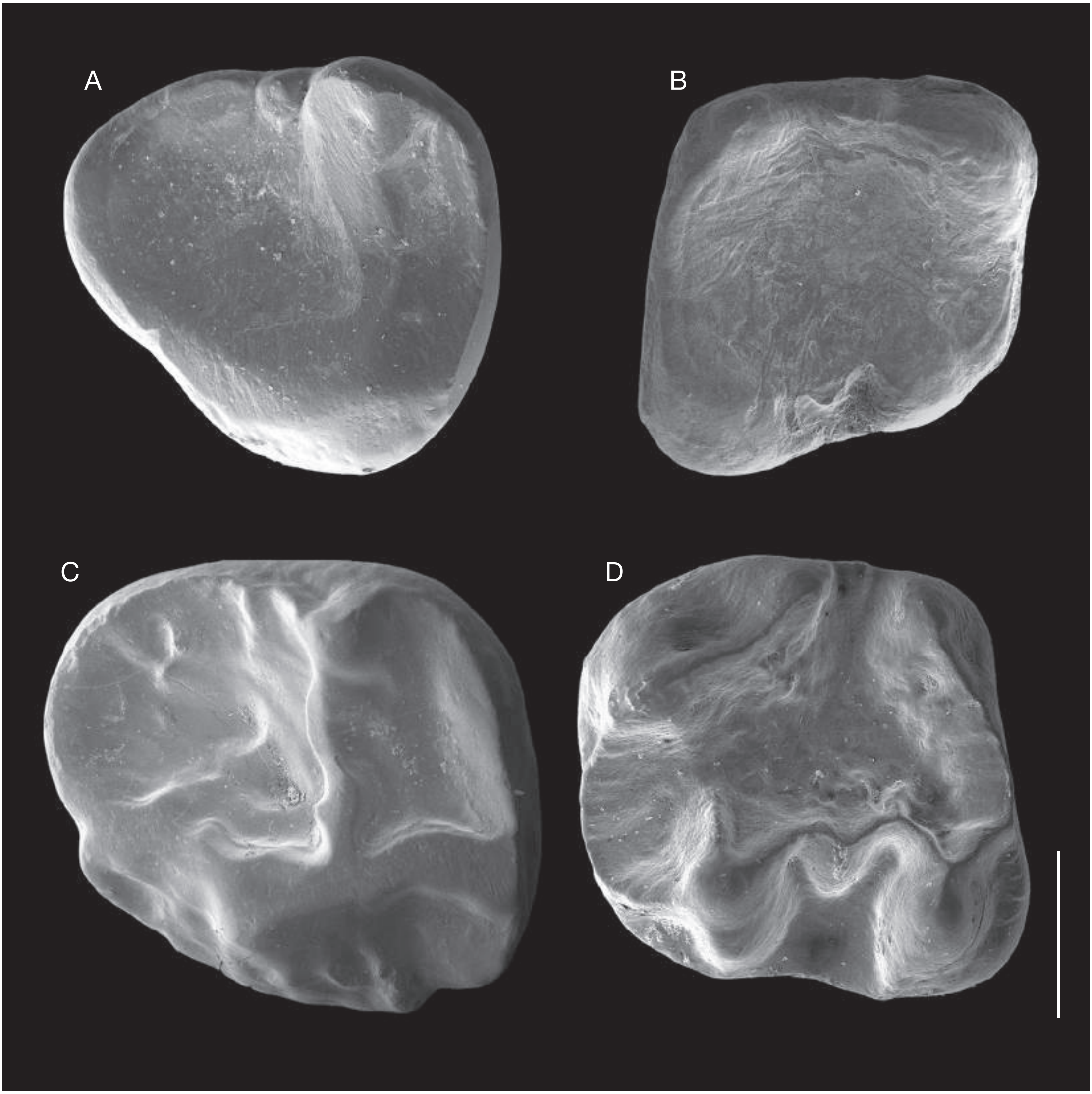

FIG. 8. — Isolated teeth of Sciuridae Fischer, 1817 from Moncucco Torinese: **A**, **B**, *Pliopetaurista pliocaenica* (Depéret, 1897); **A**, MGPT-PU 128220, M3 dex.; **B**, MGPT-PU 128221, m1 dex.; **C**, **D**, *Sciurus warthae* Sulimski, 1964; **C**, MGPT-PU 128347, M3 dex.; **D**, MGPT-PU 128218, m1 sin. Scale bar: 1 mm.

usually occurs in unworn teeth of *Hylopetes*. In summary, *Hylopetes* displays more isolated, distinct and higher tubercles, a pronounced anterosinusid and more sculptured and crenulated enamel with respect to the studied molars. Daxner-Höck (2004) included some Neogene species of sciurids previously assigned to the genus *Hylopetes*, such as *Hylopetes macedoniensis* Bouwens & de Bruijn, 1986 and *Hylopetes hoeckarum* de Bruijn, 1998, within the genus *Neopetes*. *Neopetes* differs from *Hylopetes* in having extremely low tooth-crowns and almost no sculptured enamel on unworn teeth; the lower teeth differ considerably by their rhomboid outline and by the presence of pronounced entoconids and mesostylids separated by a wide notch (Daxner-Höck 2004). Direct examination of material belonging to *Neopetes macedoniensis* (Bouwens & de Bruijn, 1986) from the latest Miocene of Maramena revealed that this species differs from the material of MCC also in the presence of better developed anterolophulids, commonly present anteroconulids and anterosinusids and more distinct labial cuspids in the lower molars. A very well-defined mesostylid is also present in *Neopetes hoeckarum* (de Bruijn, 1998) from Lower and Middle Miocene of Central Europe (see Daxner-Höck 2004). Therefore, the studied molars cannot be assigned to *Neopetes* especially because of the absence of mesostylid and anterosinusid and the presence of less distinct tubercles.

The morphology of the studied lower molars is remarkably similar to that of *Sciurus vulgaris* Linnaeus, 1758, type species of the genus *Sciurus* Linnaeus, 1758, with a well-developed metaconid and a distinct entoconid. Moreover, the lower teeth of *S. vulgaris* do not display strongly developed anterolophulids and they lack anterosinusids and anteroconulids. In addition, the m1 and m2 of *S. vulgaris* display a more quadrangular outline. The M3 from MCC is also very similar to that of *Sciurus vulgaris* in certain dental structures, including the large protocone, high paracone, very narrow basin between anteroloph and protoloph, and presence of a notch on the rim just behind the paracone. We therefore assign the studied specimen to the genus *Sciurus*.

The size of the teeth from MCC agrees very well with that of *Sciurus warthae* Sulimski, 1964 from Podlesice (Black & Kowalski 1974), being slightly smaller than those from younger localities as Węże 1 (type locality, Sulimski 1964), Zamkowa Dolna (Black & Kowalski 1974), Monte la Mesa (Marchetti *et al.* 2000), Wölfersheim (Dahlmann 2001), and Castagnone (Siori & Sala 2007). The material from MCC was compared with some teeth of *S. warthae* from Monte La Mesa where unfortunately no M3 was found; the morphology of the m1 from the two localities is strikingly similar, especially in the well-developed metaconid, in the poorly developed mesostylid and in the isolation of the low mesoconid. According to the original description of the type assemblage from Węże 1, *S. warthae* does not exhibit a mesostylid or it is very weak. The material from MCC is therefore assigned to *S. warthae* because of its remarkable similarity to the specimens from the type locality and from the other localities of Europe.

The material of MCC was compared with *Hylopetes magistri* van den Hoek Ostende & Reumer, 2011 from the Pleistocene of Tegelen (Reumer & van den Hoek Ostende 2003; van den Hoek Ostende & Reumer 2011). This species was originally identified as *Hylopetes debruijni* Reumer & van den Hoek Ostende, 2003 name already preoccupied by a different species, *Hylopetes debruijni* Mein & Ginsburg, 2002, and for this reason subsequently modified to *H. magistri* (see van den Hoek Ostende & Reumer 2011 for further details). The specimens from MCC differ from *H. magistri* in having a slightly smaller size and in the absence of enamel crenulation that barely affects two teeth from Tegelen. The overall morphological pattern of the lower molars is very similar since m1 and m2 display a well-developed entoconid, small and isolated mesoconid, absence of anterosinusid and anteroconulids, well-developed metaconid, absence or strong reduction of mesostylid in the lower molars. Moreover, the specimens of M3 from Tegelen are also very similar to those from MCC since they show a high paracone and a low and rather continuous rim from which a large protocone arises. In our opinion, the absence of well developed anterosinusids, anteroconulids and mesostylids as well as the occurrence of poorly isolated cuspids in the material from Tegelen do not support their assignment to *Hylopetes* or *Neopetes*. In addition, feeble crenulations as those affecting two teeth (upon 17 specimens) from the collection of Tegelen represent a weak diagnostic character for ascribing this material to *Hylopetes* or *Neopetes*. In fact, the presence of crenulations and ornamented enamel is not an exclusive feature of flying squirrels, but it can occur also in many genera of ground and tree squirrels (Thorington *et al.* 2005). The overall morphology of *H. magistri* fits better with that of the genus *Sciurus* Linnaeus, 1758. Moreover, pitted enamel can be observed in *Sciurus granatensis* and *Sciurus vulgaris* (Thorington *et al.* 2005: 954) thus suggesting that moderate enamel ornamentation could also rarely affect the teeth of *Sciurus*. Therefore, we tentatively assign *H. magistri* to the genus *Sciurus*. The new combination is therefore *Sciurus magistri* (van den Hoek Ostende & Reumer, 2011). The size and the morphological pattern of the teeth are very similar to *S. warthae* thus suggesting that *S. magistri* may be considered a junior synonym of *S. warthae*. Nonetheless, the presence of the slight enamel ornamentations, up to date unknown in *S. warthae*, prevents us to definitely synonymize these two taxa.

The record of *S. warthae* from MCC represents the oldest report of the genus *Sciurus* in Europe. *S. warthae* was previously known from the slightly younger fissure fillings of Podlesice (MN14) (Black & Kowalski 1974). To date *S. warthae* has been reported from some Pliocene and Pleistocene localities of Poland (Sulimski 1964; Black & Kowalski 1974), Germany (Dahlmann 2001) and Italy (Marchetti *et al.* 2000; Siori & Sala 2007). The few known specimens of this poorly documented taxon do not allow tracing its relationships within the genus *Sciurus* whose paleontological record is very scarce before the Pliocene (Emry *et al.* 2005). *Sciurus* sp. from the latest Miocene of Ertemte 2 (Qiu 1991) differs from *Sciurus warthae* in having a slightly better developed mesostylid, mesostyle in P4 absent and a weaker parastyle in the M1-2. The strong morphological affinities existing between *S. warthae* and *S. vulgaris* seem to indicate a close phylogenetic relationship between these two species. The earliest record of *S. vulgaris* is probably that from the Middle Pleistocene of Hórvölgy Cave, Hungary (Lurz *et al.* 2005). The first reliable records of the genus *Sciurus* are those of *Sciurus lii* Qiu & Yan, 2005 from the Early to Middle Miocene locality of Shanwang (China) (Qiu & Yan 2005) and *Sciurus olsoni* Emry, Kort & Bell, 2005 from the Clarendonian (early-Late Miocene) of Nevada (Emry *et al.* 2005). ?*Sciurus* sp. is reported in the Late Miocene of Anatolia (Bosma *et al.* 2013) thus suggesting that the genus *Sciurus* was already present in western Asia before the end of the Miocene. The record of MCC testifies that *Sciurus* entered Europe at least slightly before the beginning of the Pliocene.

Genus *Pliopetaurista* Kretzoi, 1962

Pliopetaurista pliocaenica (Depéret, 1897)
(Fig. 8C, D)

Sciuropterus pliocaenicus Depéret, 1897: 179, pl. 18, figs 34, 35.

Pliopetaurista pliocaenica – Mein 1970: 40, figs 66-71. — Adrover *et al.* 1993b: 98, pl. 6, figs 1-4. — Mörs *et al.* 1998: 137, figs 3, 1-3. — Dahlmann 2001:54, pl. 9, figs 1-21 (*cum syn.*). — García-Alix *et al.* 2007: 273, fig. 4A-E.

TYPE LOCALITY. — Perpignan, France.

OCCURRENCE IN THE STUDIED LAYERS. — MCC5.

REFERRED MATERIAL. — A single isolated M3; a single isolated m1.

MEASUREMENTS. — M3: MGPT-PU 128347 (2.84 × 2.64); m1: MGPT-PU 128218 (2.77 × 2.51).

DESCRIPTION

M3

The anteroloph is well developed and slightly lower than protoloph; protocone located slightly posteriorly with respect to the protoloph-endoloph contact; distal border of endoloph enlarged but not developed into a cusp.

m1

Rugose surface; protoconid and hypoconid connected by ectolophid on which a marked mesoconid is developed; anterolophid well-developed; metalophid interrupted without connection with metaconid; presence of a small hypoconulid on the posterolophid; hypolophid very short.

REMARKS

Large size, sinuous accessory ridges and labyrinthic appearance of the occlusal surface are diagnostic features of the Pteromyinae (García-Alix *et al.* 2007). Within this group, the absence of free mesostylids, presence of hypolophids and absence of metaloph in the M3 suggest that the material from MCC can be assigned to the genus *Pliopetaurista* Kretzoi, 1962. This genus was present in the Miocene of Europe with the species *Pliopetaurista kollmanni* Daxner-Höck, 2004, *Pliopetaurista bressana* Mein, 1970, *Pliopetaurista dehneli* (Sulimski, 1964), *Pliopetaurista pliocaenica* (Depéret, 1897), and was also present in Asia during the latest part of the Miocene represented by *Pliopetaurista rugosa* Qiu, 1991.

P. kollmanni from the Late Miocene of Austria differs from the material from MCC in the considerably smaller teeth, less pronounced loph(id)s (except for the metalophid that is more developed in *P. kollmanni*) and tubercles. The Middle to Late Miocene species *P. bressana* differs from the material of MCC in having a smaller size, less developed ridges and tubercles, a small anterosinusid and slightly more developed metalophids in the lower molars. *P. rugosa* from the latest Miocene locality of Ertemnte 2 (Qiu 1991) is larger than specimens from MCC. Moreover, the shape of the M3 is quite different in displaying a reduced basin and a thinner endoloph, not enlarged on the distal side. The size of the material from MCC is close to the higher values of *P. dehneli* from the type locality of Węże 1 (Sulimski 1964) and slightly larger than that from the latest Miocene/earliest Pliocene of Greece, Maramena, (de Bruijn 1995) and Kessani (Vasileiadou *et al.* 2012) and from the Early Pliocene of Hautimagne (Mein 1970). The material from MCC mainly differs from *P. dehneli* in having a less developed metalophid and in the presence of a small hypoconulid. Moreover, the presence of a distal enlargement of the endoloph in the M3 observed in the material from MCC is usually absent in the upper molars of *P. dehneli* (Mein 1970).

The size of the specimens from MCC agrees with the lower values of the size range of *P. pliocaenica* from the Pliocene localities of Wölfersheim (Mein 1970), Arquillo 3 (Adrover *et al.* 1993b), and Hambach (Mörs *et al.* 1998). The unique M3 assigned to *P. pliocaenica* from the latest Miocene of Purcal 24A (García-Alix *et al.* 2007) is larger than the specimen from MCC. *Pliopetaurista* cf. *pliocaenica* from the Early Pleistocene locality of Zamkowa Dolna (Black & Kowalski 1974) is larger than the material from MCC. The morphology of the specimens from MCC remarkably agrees with that of *P. pliocaenica*, primarily concerning the scarcely developed metalophid, the small hypoconulid in the single m1and the distal enlargement of the endoloph in the M3. Due to this similarity, the material from MCC is assigned to *P. pliocaenica*.

According to some authors (Mein 1970; Black & Kowalski 1974; de Bruijn 1995) the lineage *P. bressana–P. dehneli–P. pliocaenica*, characterized by a gradual increase in size, can be recognized within the genus *Pliopetaurista*. The recent findings of *P. pliocaenica* in some Upper Turolian localities of Spain (García-Alix *et al.* 2007), and thus contemporary or even slightly older than *P. dehneli* from eastern Europe (de Bruijn 1995; Vasileiadou *et al.* 2003, 2012), does not seem to support this view. According to García-Alix *et al.* (2007) the large-sized species *P. pliocaenica* evolved in the Iberian Peninsula and subsequently migrated to central and eastern Europe. The finding from MCC does not disagree with such hypothesis, even though it indicates that the expansion of the geographical range of this species may have occurred before the end of the Miocene, during or suddenly after the MSC.

BIOCHRONOLOGY

As discussed above, the absolute age of the deposits enclosing the rodent assemblages documented herein is well defined by cyclostratigraphic analyses and can be constrained in a time range of less than 70 Kyr, between 5.40 and 5.33 Ma.

In this section we discuss the biochronological implications of the rodent assemblages recovered from MCC. As a matter of fact, the diverse rodent assemblages recovered at MCC provide some useful data that notably enrich the scarce knowledge of the biochronological framework of Northern Italy at the end of the Miocene.

The lowermost layer of the investigated succession, MCC3, has yielded the less diverse rodent assemblage with eight species: *Glis minor*, *Muscardinus vireti*, *Apodemus gudrunae*, *Apodemus atavus*, *Micromys bendai*, *Paraethomys meini*, *Occitanomys brailloni* and *Centralomys benericettii*. Among them some species consent to define biochronological correlations on local and multiregional scale. The murid *Apodemus gudrunae* is very common in latest Turolian localities of the western sector of the Mediterranean (van de Weerd 1976; Aguilar *et al.*

1989, 1991; De Giuli 1989; Mein *et al.* 1990; Adrover *et al.* 1993a; Martín-Suárez & Freudenthal 1998; Martín-Suárez & Mein 1998; Mein 1999; Agustí *et al.* 2006b, 2011; Minwer-Barakat *et al.* 2012; Colombero *et al.* 2013). *Paraethomys meini* immigrated in Southern Spain from Northern Africa roughly around 6 Ma (Agustí *et al.* 2006a). Its presence is commonly reported from several Late Turolian localities of Western Europe and its co-occurrence with *A. gudrunae* defines the latest phase of the MN13 in the Guadix Basin (Minwer-Barakat *et al.* 2012). *Apodemus atavus* is reported in some latest Miocene localities of Spain, in the Granada Basin (García-Alix *et al.* 2008d), and Greece (de Bruijn 1989). Its records become more common at the Mio-Pliocene boundary when it is found in some localities of Greece (Hordijk & de Bruijn 2009; Vasileiadou *et al.* 2003, 2012) and France (Aguilar *et al.* 1989). *Micromys bendai* appears in Greece towards the end of the Messinian (de Bruijn 1989; Hordijk & de Bruijn 2009) where it is reported in some localities of the Ptolemais Basin. Among them, Tomea Eksi 1 and 2 are roughly coeval to MCC, being constrained between 5.43 and 5.30 Ma (Hordijk & de Bruijn 2009). *Occitanomys brailloni* was reported from the middle Turolian locality of Rema Marmara (de Bruijn 1989) and subsequently in other Greek localities close to the Mio-Pliocene boundary (van de Weerd 1979; Vasileiadou *et al.* 2003). *Centralomys benericettii* is exclusively found in Italy in deposits of Late Messinian age (De Giuli 1989; Cavallo *et al.* 1993; Colombero *et al.* 2013) or close to the Mio-Pliocene boundary (Abbazzi *et al.* 2008). *Muscardinus vireti* is a rather uncommon glirid, known in some MN13 localities of Europe such as Lissieu (Hugueney & Mein 1965), Can Vilella (Agustí *et al.* 2006b), Baccinello V3 (Engesser 1983), and Verduno (Colombero *et al.* 2013). Overall, the rodent assemblage of MCC3 can be assigned to the MN13 unit, mostly because of the co-occurrence of *A. gudrunae* and *P. meini*. The presence of *M. vireti* strongly supports the Late Turolian age of this assemblage, and the occurrence of *M. bendai* and *O. brailloni* indicates that it is very close to the boundary with the Ruscinian, when both these species became more widespread and abundant also in Western Europe. The assignment to the upper part of MN13 is also corroborated by the occurrence of other mammal taxa from the same layers such as *Prolagus sorbinii* and *Mesopithecus pentelicus* (Angelone *et al.* 2011). The latter species has not been found in any European Ruscinian locality (Alba *et al.* 2014).

The upper layers of the MCC succession, MCC4, MCC5 and MCC7, display more diverse rodent assemblages, including the same species recognized in MCC3 together with other taxa. *Eliomys* aff. *intermedius* is found in all the three uppermost layers of the sequence. As discussed above, the material from MCC is quite similar to that of *Eliomys* aff. *intermedius* found in some localities close to the Mio-Pliocene boundary such as Purcal 4 (García-Alix *et al.* 2008a) and Maritsa (de Bruijn *et al.* 1970). However, it is rather problematic to conclusively demonstrate their relationships. The uppermost layers of the MCC succession also contain the rare cricetid *Neocricetodon magnus*, representing the earliest record of this species reported up to now in some Pliocene localities of central Europe (Fahlbusch 1969; Janossy 1972; Pradel 1988). The material of MCC is characterized by archaic features that fit well with the slightly older age of this Italian locality. This species is considered to be of remarkable biochronological significance, since it marks the beginning of the Ruscinian in Poland (Nadachowski 1989). Nonetheless, it is worth noting that the rodent record from the central and central-eastern Europe during the Late Turolian (MN13) is inadequately known due to the very low number of localities (see e.g., Nadachowski 1989). The presence of *N. magnus* at MCC clearly indicates that this taxon was present in Europe slightly before the beginning of the Pliocene. Moreover, its co-occurrence with typical Turolian rodents such as *Apodemus gudrunae* and *Muscardinus vireti* actually implies that the appearance of this species in Europe slightly precedes the beginning of the Ruscinian. *Glirulus lissiensis* is represented by very few remains exclusively found in the layers MCC5 and MCC7. The biochronological range of this taxon extends from MN4 to MN13 (Daxner-Höck & Höck 2009), which is consistent with the Late Turolian age of these layers. The very sparse re-

TABLE 11. — Occurrence of the studied rodent species recovered at Moncucco Torinese for each productive layer.

	MCC3	**MCC4**	**MCC5**	**MCC7**
Neocricetodon magnus (Fahlbusch, 1969)		×	×	×
Paraethomys meini (Michaux, 1969)	×	×	×	×
Occitanomys brailloni Michaux, 1969	×	×	×	×
Centralomys benericettii (De Giuli, 1989)	×	×	×	×
Micromys bendai van de Weerd, 1979	×	×	×	×
Apodemus gudrunae van de Weerd, 1976	×	×	×	×
Apodemus atavus Heller, 1936	×	×	×	×
Eliomys aff. *intermedius* Friant, 1953		×	×	×
Muscardinus vireti Hugueney & Mein, 1965	×	×	×	×
Glirulus lissiensis Hugueney & Mein, 1965			×	×
Glis minor Kowalski, 1956	×	×	×	×
Sciurus warthae Sulimski, 1964			×	
Pliopetaurista pliocaenica (Depéret, 1897)			×	

mains of sciurids are exclusively reported in the layer MCC5. *Pliopetaurista pliocaenica* has been identified in other Late Turolian localities, such as Purcal 25 and 24A (García-Alix *et al.* 2007), both referred to the *Apocricetus alberti* zone and to the MN13 unit (García-Alix *et al.* 2008d). The record of *Sciurus warthae* in the layer MCC5 represents the earliest occurrence of the genus *Sciurus* in Europe. Up to date, the oldest known record of this genus was that from the earliest Pliocene of Podlesice, a locality correlated with the base of the Ruscinian. The occurrence of *Sciurus warthae* in the latest Messinian deposits of Northern Italy indicates that this genus appeared in Europe slightly before than previously known.

In summary, the rodent assemblages from the uppermost layers of the MCC succession, MCC4, MCC5 and MCC7, can be referred to the MN13 unit (Late Turolian). The attribution to the MN14 unit can be excluded due to the presence of typical Turolian taxa such as *Apodemus gudrunae*, *Muscardinus vireti* and *Glirulus lissiensis*. Anyway, the first occurrence of some taxa as *Neocricetodon magnus* and *Sciurus warthae* that became common during the Pliocene, might suggest a stratigraphic position very close to the boundary with the MN14 unit.

The subtle differences in the composition of the rodent assemblages from the various layers of the MCC succession might be correlated to the different number of specimens collected from each layer. The rare taxa are better represented in the largest samples of layers MCC4, MCC5 and MCC7, with the MCC5 layer also documenting the highest taxonomic diversity (Table 11). On the other hand, the rodent assemblage from MCC3 exhibits the lowest diversity and the absence of uncommon taxa. Considering that the entire succession originated within a maximum time span of less than 70 Kyr, the differences observed in the faunal composition cannot be related to actual biochronological discrepancies. The whole MCC succession probably recorded the very last evolutionary steps of the Turolian mammal assemblages in Northern Italy. The rodent assemblages of MCC can be easily correlated with those of other latest Messinian localities of Italy. In particular, the co-occurrence of *A. gudrunae* and *C. benericettii* provides evidence of the close age of MCC and Verduno (Piedmont, northern Italy) (Colombero *et al.* 2013), Brisighella (Romagna, central Italy) (De Giuli 1989) and Borro Strolla (Tuscany, central Italy) (Abbazzi *et al.* 2008) (Fig. 9). The rodent assemblage of the latest Miocene locality Ciabót-Cagna (Piedmont, northern Italy) can be also correlated to these sites due to the presence of *C. benericettii* (Cavallo *et al.* 1993). The faunal assemblage of Casino (Tuscany, central Italy) does not share any rodent species with MCC. Stratigaphical analyses suggest an age close to the fossiliferous layers of MCC (Rook 1999; Bossio *et al.* 2000; Abbazzi *et al.* 2008), but they cannot definitely exclude a slightly older age. The Mes-

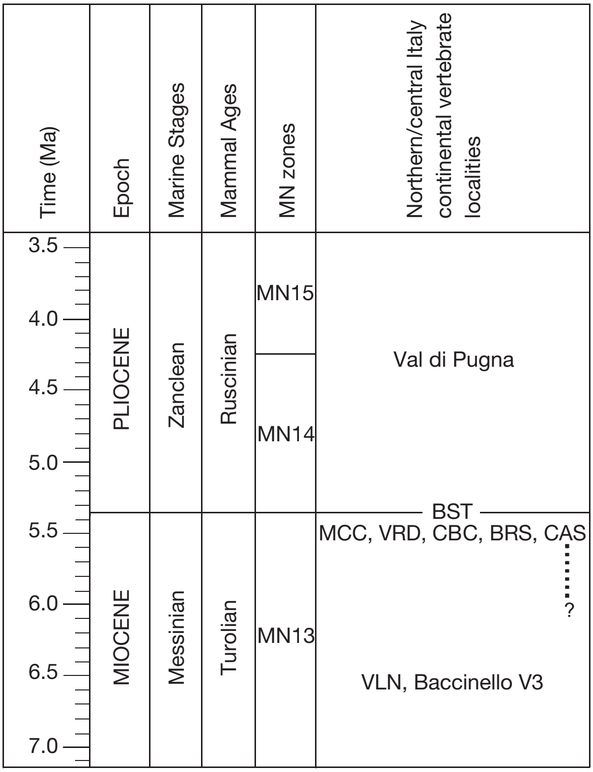

FIG. 9. — Correlation between some Late Miocene/Early Pliocene localities of Northern and Central Italy and chronostratigraphic, geochronologic and biochronologic scales. Abbreviations: **BST**, Borro Strolla; **MCC**, Moncucco Torinese; **VRD**, Verduno; **CBC**, Ciabòt Cagna; **BRS**, Brisighella; **CAS**, Casino; **VLN**, Velona. Data from: Engesser 1989; Cavallo *et al.* 1993; Kotsakis *et al.* 1997; Benvenuti *et al.* 2001; Bianucci *et al.* 2001; Ghetti *et al.* 2002; Palombo *et al.* 2003; Rook *et al.* 2006; 2011; Abbazzi *et al.* 2008; Colombero *et al.* 2013.

sinian localities of Tuscany (central Italy), Velona (Rook & Ghetti 1997; Ghetti *et al.* 2002) and Baccinello V3 (Engesser 1989; Kotsakis *et al.* 1997; Benvenuti *et al.* 2001; Rook *et al.* 2006, 2011) are older than the assemblage of MCC definitely preceding the onset of the MSC (Ghetti *et al.* 2002; Rook *et al.* 2011). The main compositional difference is the absence in these localities of *Centralomys benericettii*, a species that probably appeared only during the post-evaporitic phase of the MSC just before the end of the Messinian. The vertebrate locality of Gravitelli (Sicily) does not contain rodent remains but it is assigned to the MN13 unit (Palombo *et al.* 2003). The Early Pliocene locality of Val di Pugna is clearly younger, being assigned to the MN 14-15 (Bianucci *et al.* 2001). Compared to other European localities, the co-occurrence of *Apodemus gudrunae*, *Muscardinus vireti* and *Glirulus lissiensis* is only known at Lissieu (Hugueney & Mein 1965) and Can Vilella (Agustí *et al.* 2006b), both assigned to the MN13 unit. MCC can be also correlated with some Spanish localities assigned to the MN13 unit, such as Negratín-1 (Minwer-Barakat *et al.* 2009b), Almenara M (Agustí & Galobart 1986), and Crevillente 6 (Martín-Suárez & Freudenthal 1998), which are also characterized by the co-occurrence of *Apodemus gudrunae* and *Paraethomys meini*, even though all of these localities are slightly older, possibly preceding the onset of the MSC (Garcés *et al.* 1998; Gómez Cano *et al.* 2011). The coeval Spanish localities of the Granada basin La Dehesa 1, 16, and 14, as well as Cacín 5 and 11 (García-Alix *et al.* 2008d) are characterized by slightly different assemblages, with more advanced forms such as *Apodemus gorafensis* that replaces *Apodemus gudrunae*. The assemblage of MCC contains some taxa that appeared in Western Europe in the Pliocene such as *Occitanomys brailloni* and *Micromys bendai*. The co-occurrence of these two species has been previously reported in the Greek locality of Vorio 1 that is ciclostratigraphically dated at 5.04 Ma and assigned to the MN14 unit due to the presence of *Promimomys cor* Kretzoi, 1955 (Hordijk & de Bruijn 2009). Other Greek localities very close in age to MCC are certainly Tomea Eksi 1 and 2 (Hordijk & de Bruijn 2009) that were ciclostratigraphically dated between 5.43 and 5.30 Ma, and Maramena (Schmidt-Kittler *et al.* 1995), Silata (Vasileiadou *et al.* 2003) and Kessani (Vasileiadou *et al.* 2012), whose palentological record indicates an age close to the Mio/Pliocene boundary.

CONCLUSIONS

The study of the rodents from layers MCC3, MCC4, MCC5 and MCC7 of Moncucco Torinese indicates an age that is in agreement with that previously estimated for the sediments composing the section that were deposited in the latest Messinian during the p-ev2 of the MSC (5.40-5.33 Ma). Some of the recognized species of rodents, particularly *A. gudrunae*, *M. vireti* and *G. lissiensis,* suggest that the rodent assemblages should be assigned to the MN13 unit (Late Turolian). However, the occurrence of *M. bendai*, *O. brailloni*, *N. magnus* and *S. warthae* indicates that some elements that became more common in the Ruscinian were already present at least in eastern and central-southern Europe slightly before the beginning of the Pliocene. This mixture of Turolian and Ruscinian taxa is clearly related to the stratigraphic position of the fossiliferous deposits of Moncucco Torinese, close to Messinian-Zanclean boundary, as well as to its crucial geographical position, intermediate between eastern and western sectors of Europe. Due to the diachrony of migrations and dispersals at a continental scale, it is reasonable to hypothesize that certain taxa that migrated from Eastern Europe, as *M. bendai* and *O. brailloni,* arrived to Italy before than to western Europe. Moreover, the scarcity or absence of rodent record from vast portions of Central and Central-Eastern Europe does not allow to achieve a reliable knowledge of the distribution of some taxa during the latest Messinian, in particular of *N. magnus* and *S. warthae* for which that of Moncucco Torinese represents the earliest occurrence. The new data derived from the vertebrate assemblage of Moncucco Torinese indicate that, at least in the Italian Peninsula, the transition from the MN13 unit to the MN14 unit was not defined by a sharp faunal turnover, and that some typical Miocene mammals briefly co-existed with some Ruscinian elements slightly before the Mio/Pliocene boundary.

The data derived from other vertebrate groups, currently under study, will certainly provide additional information useful to define the faunal composition and to obtain a more precise interpretation of the biochronological significance of the locality of Moncucco Torinese.

Acknowledgements
This study was financially supported by grants PRIN 2009MSSS9L-002 (resp. G. Pavia, Torino). We are grateful to F. Biancofiore and F. Giudice for the improvement of the English. Dr S. Cavagna helped with the SEM. Special thanks to the referees Raef Minwer Barakat (Institut Català de Paleontologia, Barcelona) and Sevket Sen (Muséum national d'Histoire naturelle, Paris) for their valuable suggestions and the critical reading of the manuscript. Drs M. Hugueney, P. Mein and A. Prieur (University of Lyon 1, France), Drs W. Wessels and H. de Bruijn (IVAU, Utrecht, The Netherlands), Dr L. van den Hoek Ostende (Naturalis-Science Centre, Leiden, The Netherlands), Prof. L. Rook (Università degli Studi di Firenze), Dr C. Berto and Prof. B. Sala (University degli Studi di Ferrara), and Dr M. Pavia (Università degli Studi di Torino) for access to fossil material in their care and hospitality and kindness during our visits. Last but not least, our sincere thanks go to Piero Giuntelli for his precious help in the field and laboratory.

REFERENCES

Abbazzi L., Benvenuti M., Ceci M. E., Esu D., Faranda C., Rook L. & Tangocci F. 2008. — The end of the Lago-Mare time in the SE Valdelsa Basin (Central Italy): Interference between local tectonism and regional sea-level rise. *Geodiversitas* 30 (3): 611-639.

Adrover R., Mein P. & Moissenet E. 1988. — Contribucion al conocimiento de la fauna de roedores del Plioceno de la region de Teruel. *Teruel* 79: 91-151.

Adrover R., Mein P. & Moissenet E. 1993a. — Roedores de la transicion Mio-Plioceno de la region de Teruel. *Paleontologia i Evolució* 26-27: 47-84.

Adrover R., Mein P. & Moissenet E. 1993b. — Los Sciuridae del Turoliense superior, Rusciniense y Villanyense de la region de Teruel. *Paleontologia i Evolució* 26-27: 85-106.

Aguilar J.-P. 1982. — Biozonation du Miocène d'Europe occidentale à l'aide des Rongeurs et corrélations avec l'échelle stratigraphique marine. *Comptes Rendus de l'Académie des Sciences de Paris,* série II 294: 49-54.

Aguilar J.-P., Calvet M. & Michaux J. 1986. — Description des rongeurs pliocènes de la faune du Mont-Hélène (Pyrénèes orientales, France), nouveau jalon entre les faunes de Perpignan (Serrat-d'en-Vacquer) et de Sète. *Palaeovertebrata* 16: 127-144.

Aguilar J.-P., Clauzon G. & Michaux J. 1989. — La limite Mio-Pliocène dans le Sud de la France d'après les faunes de rongeurs : état de la question et remarques sur les datations à l'aide des rongeurs. *Bollettino della Società Paleontologica Italiana* 28: 137-145.

Aguilar J.-P., Michaux J., Bachelet B., Calvet M. & Faillat J. P. 1991. — Les nouvelles faunes de rongeurs proches de la limite Mio-Pliocéne en Roussillon. Implications biostratigraphiques et biogéographiques. *Palaeovertebrata* 20: 147-174.

Agustí J. & Galobart A. 1986. — La sucesión de micromamíferos en el complejo cárstico de Casablanca (Almenara, Castellón): problemática biogeográfica. *Paleontologia i Evolució* 20: 57-62.

Agustí J. & Llenas M. 1996. — The Late Turolian muroid rodent succession in eastern Spain. *Acta Zoologica Cracoviensa* 39: 47-56.

Agustí J., Garcés M. & Krijgsman W. 2006a. — Evidence for African-Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeogeography Palaeoclimatology Palaeoecology* 238: 5-14.

Agustí J., Oms O., Furió M., Pérez-Vila M.-J. & Roca E. 2006b. — The Messinian terrestrial record in the Pyrenees: The case of Can Vilella (Cerdanya Basin). *Palaeogeography, Palaeoclimatology, Palaeoecology* 238: 179-189.

Agustí J., Santos-Cubedo A., Furió M., De Marfa R., Blain H.-A., Oms O. & Sevilla P. 2011. — The Late Neogene-early Quaternary small vertebrate succession from the Almenara-Casablanca karst complex (Caste1lón, Eastern Spain): Chronologic and paleoclimatic context. *Quaternary International* 243: 183-191.

Alba D. M., Delson E., Carnevale G., Colombero S., Delfino M., Pavia M. & Pavia G. (2014). — First joint record of *Mesopithecus* and cf. *Macaca* in the Miocene of Europe. *Journal of Human Evolution* 67: 1-18. http://dx.doi.org/10.1016/j.jhevol.2013.11.001

Angelone C., Colombero S., Esu D., Giuntelli P., Marcolini F., Pavia M., Trenkwalder S., Van Den Hoek Ostende L. W., Zunino M. & Pavia G. 2011. — Moncucco Torinese, a new post-evaporitic Messinian fossiliferous site from Piedmont (NW Italy). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 259: 89-104.

Bachmayer W. & Wilson R. W. 1970. — Die Fauna der altpliozänen Höhlen und Spaltenfüllungen bei Köhfidisch, Burgenland Österreich). *Annalen des Naturhistorischen Museums in Wien* 74: 533-587.

Benvenuti M., Papini M. & Rook L. 2001. — Mammal biochronology, UBSU and paleoenvironmental evolution in a post-collisional basin: evidences from the Late Miocene Baccinello-Cinigiano Basin in southern Tuscany, Italy. *Bollettino della Società Paleontologica Italiana* 120: 97-118.

Bianucci G., Mazza P., Merola D., Sarti G. & Cascella A. 2001. — The Early Pliocene mammal assemblage of Val di Pugna (Tuscany, Italy) in the light of calcareous plankton biostratigraphical data and paleoeological observations. *Rivista Italiana di Paleontologia e Stratigrafia* 107: 425-438.

Black C. C. & Kowalski K. 1974. — The Pliocene and Pleistocene Sciuridae (Mammalia, Rodentia) from Poland. *Acta Zoologica Cracoviensa* 19: 461-486.

Bolliger T., Engesser B. & Weidman M. 1993. — Première découverte de mammifères pliocènes dans le Jura neuchâtelois. *Eclogae Geologicae Helvetiae* 86: 1031-1068.

Bosma A. A., De Bruijn H. & Wessels W. 2013. — Late Miocene Sciuridae (Mammalia, Rodentia) from Anatolia, Turkey. *Journal of Vertebrate Palaeontology* 33: 924-942.

Bossio A., Mazzei R., Salvatorini G. & Sandrelli F. 2000. — Geologia dell'area compresa tra Siena e Poggibonsi ("Bacino del Casino"). *Atti della Società Toscana di Scienze Naturali, Memorie, Serie A* 107: 69-85.

Bouwens P. & De Bruijn H. 1986. — The flying Squirrels *Hylopetes* and *Petinomys* and their fossil record. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 89: 113-123.

Capizzi D. & Filippucci M. G. 2008. — *Apodemus flavicollis* (Melchior, 1834). Descrizione morfologica, *in* Amori G., Contoli L. & Nappi A. (eds), *Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia.* Calderini, Milano: 594-598.

Carnevale G., Caputo D. & Landini W. 2006a. — Late Miocene fish otoliths from the Colombacci

Formation (Northern Apennines, Italy): implications for the Messinian 'Lago-mare' event. *Geological Journal* 41: 537-555.

Carnevale G., Landini W. & Sarti G. 2006b. — Mare versus Lago-mare: marine fishes and the Mediterranean environment at the end of the Messinian Salinity Crisis. *Journal of Geological Society* 163: 75-80.

Carnevale G., Longinelli A., Caputo D., Barbieri M. & Landini W. 2008. — Did the Mediterranean marine reflooding preceeded the Mio-Pliocene boundary? Paleontological and geochemical evidence from Upper Messinian sequences of Tuscany, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 257: 81-105.

Casanovas-Villar I. 2007. — *The Rodent Assemblage from the Late Aragonian and the Vallesian (Middle to Late Miocene) of the Vallès-Penedes Basin (Catalonia, Spain).* PhD thesis, Universitat Autònoma de Barcelona, Departement de Geologia, 282 p.

Cavallo O., Sen S., Rage J.-C. & Gaudant J. 1993. — Vertébrés messiniens du Faciès a Congéries de Ciabot-Cagna, Corneliano d'Alba (Piémont, Italie). *Rivista Piemontese di Storia Naturale* 14: 3-22.

CIESM 2008. — The Messinian Salinity Crisis from mega-deposits to microbiology, a consensus report. *CIESM Workshop Monographs* 33: 1-168.

Cita M. B., Wright R. C., Ryan W. B. F. & Longinelli A. 1978. — Messinian palaeoenvironments. *Initial Reports of the Deep Sea Drilling Project* 42: 1003-1035.

Clari P., Dela Pierre F., Novaretti A. & Timpanelli M. 1994. — La successione oligo-miocenica del Monferrato occidentale: confronti e relazioni con il Monferrato orientale e la Collina di Torino. *Atti ticinesi di Scienze della Terra* (*Serie Speciale*) 1: 191-203.

Colombero S. & Pavia G. 2013. — *Centralomys benericettii* (De Giuli, 1989) (Mammalia, Rodentia): a latest Messinian murid from northern and central Italy. New data from Piedmont. *Bollettino della Società Paleontologica Italiana* 52: 27-34.

Colombero S., Bonelli E., Kotsakis T., Pavia G., Pavia M. & Carnevale G. 2013. — Late Messinian rodents from Verduno (Piedmont, NW Italy): biochronological, paleoecological and paleobiogeographic implications. *Geobios* 46: 111-125.

Colombero S., Angelone A., Bonelli E., Carnevale G., Cavallo O., Delfino M., Giuntelli P., Mazza P., Pavia G., Pavia M. & Repetto G. 2014. — The upper Messinian assemblages of fossil vertebrate remains of Verduno (NW Italy): Another brick for a latest Miocene bridge across the Mediterranean. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 272: 287-324.

Cuenca Bescós G. 2003. — Analisis filogenético de *Allocricetus* del Pleistoceno (Cricetidae, Rodentia, Mammalia). *Coloquios de Paleontología* Vol. Ext. 1: 95-113

Cuenca Bescós G., Canudo J. I. & Arsuaga J. L. 1997. — Small mammals from Sima de los Huesos. *Journal of Human Evolution* 33: 175-190.

Daams R. 1981. — The dental pattern of the dormice *Dryomys*, *Myomimus*, *Microdyromys* and *Peridyromys*. *Utrecht Micropaleontological Bulletins Special Publication* 3: 1-115.

Daams R. & De Bruijn H. 1995. — A classification of the Gliridae (Rodentia) on the basis of dental morphology. *Hystrix* 6: 3-50.

Dahlmann T. 2001. — Die Kleinsäuger der unterpliozänen Fundstelle Wölfersheim in der Wetterau (Mammalia: Lipotyphla, Chiroptera, Rodentia). *Courier Forschungsinstitut Senckenberg* 227: 1-129.

Daoud A. 1993. — Evolution of Gliridae (Mammalia, Rodentia) in Pliocene and Quaternary of Poland. *Acta Zoologica Cracoviensa* 36: 199-231.

Daxner-Höck G. 1992. — Die Cricetinae aus dem Obermiozan von Maramena. *Paläontologische Zeitschrift* 66: 331-367.

Daxner-Höck G. 1995. — Some glirids and cricetids from Maramena and other Late Miocene localities in Northern Greece. *Münchner Geowissenschaftliche Abhandlungen* 28: 103-120.

Daxner-Höck G. 2004. — Flying Squirrels (Pteromyinae, Mammalia) from the Upper Miocene of Austria. *Annalen des Naturhistorischen Museums in Wien, Serie A* 106: 387-423.

Daxner-Höck G. 2005. — Eomyidae and Gliridae from Rudabánya. *Palaeontographica Italica* 90: 143-155.

Daxner-Höck G. & De Bruijn H. 1981. — Gliridae (Rodentia, Mammalia) des Eichkogels bei Mödling (Niederösterreich). *Paläontologische Zeitschrift* 55: 157-172.

Daxner-Höck G. & Höck E. 2009. — New data on Eomyidae and Gliridae (Rodentia, Mammalia) from the Late Miocene of Austria. *Annalen des Naturhistorischen Museums in Wien* 111 A: 375-444.

Daxner-Höck G., Fahlbusch V., Kordos L. & Wu W. 1996. — The Late Neogene cricetid rodent genera *Neocricetodon* and *Kowalskia*, *in* Bernor R. L., Fahlbusch V. & Mittmann H.-W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas.* Columbia University Press, New York: 220-226.

De Bruijn H. 1989. — Smaller mammals from the Upper Miocene and Lower Pliocene of the Strimon Basin, Greece. Part 1. Rodentia and Lagomorpha. *Bollettino della Società Paleontologica Italiana* 28: 189-195.

De Bruijn H. 1995. — Sciuridae, Petauristidae and Eomyidae, *in* Schmidt-Kittler N. (ed.), The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). *Münchner Geowissenschaftliche Abhandlungen A* 28: 87-102.

De Bruijn H. 1998. — Vertebrates from the early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria). *Annalen des Naturhistorischen Museums in Wien, Serie A* 99: 99-137.

De Bruijn H. 1999. — Superfamily Sciuroidea, *in* Rössner G. E. & Heissig K. (eds), *The Miocene Land Mammals of Europe*. Verlag Dr. Friederich Pfeil, München: 271-280.

De Bruijn H. & Van Der Meulen A. J. 1975. — The early Pleistocene rodents from Tourkobounia-1 (Athens, Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* B 78: 314-338.

De Bruijn H., Dawson M. R. & Mein P. 1970. — Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). I-III. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* B 73: 535-584.

De Bruijn H., Doukas C. S., Van Den Hoek Ostende L. W. & Zachariasse W. J. 2012. — New finds of rodents and insectivores from the Upper Miocene at Plakias (Crete, Greece). *Swiss Journal of Palaeontology* 131: 61-75.

De Giuli C. 1989. — The rodents of the Brisighella latest Miocene fauna. *Bollettino della Società Paleontologica Italiana* 28: 197-212.

Dela Pierre F., Festa A. & Irace A. 2007. — Interaction of tectonic, sedimentary, and diapiric processes in the origin of chaotic sediments: an example from the Messinian of Torino Hill (Tertiary Piedmont Basin, northwestern Italy). *Bulletin of the Geological Society of America* 119: 1107-1119.

Dela Pierre F., Bernardi E., Cavagna S., Clari P., Gennari R., Irace A., Lozar F., Lugli S., Manzi V., Natalicchio M., Roveri M. & Violanti D. 2011. — The record of the Messinian Salinity Crisis in the Tertiary Piedmont Basin (NW Italy): The Alba section revisited. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310: 238-255.

Emry R. J., Korth W. W. & Bell M. A. 2005. — A tree squirrel (Rodentia, Sciuridae, Sciurini) from the Late Miocene (Clarendonian) of Nevada. *Journal of Vertebrate Paleontology* 25: 228-235.

Engesser B. 1972. — Die obermiozäne Säugetierfauna von Anwil (Baselland). *Tätigkeitsberichte der Naturfoschenden Gesselschaft* 29: 37-363.

Engesser B. 1983. — Die jungtertiären Kleinsäuger des Gebietes der Maremma (Toskana, Italien). 1. Teil: Gliridae (Rodentia, Mammalia). *Eclogae Geologicae Helvetiae* 76: 763-780.

Engesser B. 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.

Fahlbusch V. 1969. — Pliozäne und Pleistozäne Cricetinae (Rodentia, Mammalia) aus Polen. *Acta Zoologica Cracoviensa* 14(5): 99-138.

Fejfar O. 1970. — Die Plio-Pleistozänen Wirbeltier faunen von Hajnacka und Ivanovce (Slowakei, CSSR), VI. Cricetidae (Rodentia, Mammalia). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 10: 227-296.

Fejfar O. & Storch G. 1990. — Eine Pliozäne (ober-Ruscinische) Kleinsäugerfauna aus Gundersheim, Rheinhessen-1. Nagetiere: Mammalia, Rodentia. *Senckenbergiana Lethaea* 71: 139-184.

Fortelius M. 2012. — New and Old Worlds Database of Fossil Mammals (NOW). University of Helsinki. http://www.helsinki.fi/science/now/

Freudenthal M. 1971.— Neogene vertebrates from the Gargano peninsula, Italy. *Scripta Geologica* 3: 1-10.

Freudenthal M. & Kordos L. 1989. — *Cricetus polgardiensis* sp. nov. and *Cricetus kormosi* Schaub, 1930 from the Late Miocene Polgardi localities (Hungary). *Scripta Geologica* 89: 71-100.

Freudenthal M. & Martín-Suárez E. 2006. — Gliridae (Rodentia, Mammalia) from the Late Miocene fissure filling Biancone 1 (Gargano, province of Foggia, Italy). *Palaeontologia Electronica* 9 (2): 1-23.

Freudenthal M., Hugueney M. & Moissenet E. 1994. — The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain). *Scripta Geologica* 104: 57-114.

Freudenthal M., Mein P. & Martín-Suárez E. 1998. — Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. *Treballs del Museu de Geologia de Barcelona* 7: 11-93.

Garcés M., Krijgsman W. & Agustí J. 1998. — Chronology of the Late Turolian deposits of the Fortuna Basin (SE Spain): implications for the Messinian evolution of the eastern Betics. *Earth and Planetary Science Letters* 163: 69-81.

García-Alix A., Minwer-Barakat R., Martín-Suárez E. & Freudenthal M. 2007. — New data on Mio-Pliocene Sciuridae (Rodentia, Mammalia) from southern Spain. *Comptes Rendus Palevol* 6: 269-279.

García-Alix A., Minwer-Barakat R., Martín-Suárez E. & Freudenthal M. 2008a. — Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. *Scripta Geologica* 136: 1-37.

García-Alix A., Minwer-Barakat R., Martín-Suárez E. & Freudenthal M. 2008b. — Muridae (Rodentia, Mammalia) from the Mio-Pliocene boundary in the Granada Basin (southern Spain). Biostratigraphic and phylogenetic implications. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 248: 183-215.

García-Alix A., Minwer-Barakat R., Martín-Suárez E. & Freudenthal M. 2008c. — *Muscardinus meridionalis* sp. nov., a new species of Gliridae (Rodentia, Mammalia) and its implications for the phylogeny of *Muscardinus*. *Journal of Vertebrate Paleontology* 28: 568-573.

García-Alix A., Minwer-Barakat R., Martín-Suárez E. & Freudenthal M. 2008d. — Biostratigraphy and sedimentary evolution of Late Miocene and Pliocene continental deposits of the Granada Basin (southern Spain). *Lethaia* 41: 431-446.

Ghetti P., Anadón P., Bertini A., Esu D., Gliozzi E., Rook L. & Soulié-Märsche I. 2002. — The early Messinian Velona Basin (Siena, central Italy): paleoenvironmental and paleobiogeographical reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 187: 1-33.

Gómez Cano A. R., Hernández Fernández M. & Álvarez-Sierra M. Á. 2011. — Biogeographic provincialism in rodent faunas from the Iberoccitanian Region (southwestern Europe) generates severe diachrony within the Mammalian Neogene (MN) biochronologic scale during the Late Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 307: 193-204.

Grossi F., Gliozzi E. & Cosentino D. 2011. — Paratethyan ostracod immigrants mark the biostratigraphy of the Messinian Salinity Crisis. *Joannea Geologie und Palaeontologie* 11: 66-68.

Hellmund M. & Ziegler R. 2012. — A Ruscinian mammalian microfauna from a fissure filling near Sondershausen (Thuringia, Central Germany). *Swiss Journal of Palaeontology* 131: 77-94.

Hordijk K. & de Bruijn H. 2009. —The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). *Hellenic Journal of Geosciences* 44: 21-103.

Hugueney M. & Mein P. 1965. — Lagomorphes et rongeurs du Néogène de Lissieu (Rhône). *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon Nouvelle Serie* 12: 109-123.

Janossy D. 1972. — Middle Pliocene microvertebrate fauna from the Osztramos Loc. 1.(Northern Hungary). *Annales Historico-Naturales Musei Naturali Hungarici* 64: 27-52.

Kotsakis T. 1986. — Problemi paleobiogeografici dei mammiferi fossili italiani: le faune mioceniche. *Geologica Romana* 23: 65-90.

Kotsakis T. 1989. — Turolian and Ruscinian castorids: some observations. *Bollettino della Società Paleontologica Italiana* 28: 271-276.

Kotsakis T., Barisone G. & Rook L. 1997. — Mammalian biochronology in an insular domain: the Italian Tertiary faunas. *Mémoires et Travaux de l'Institut de Montpellier de L'École Pratique des Hautes Études* 21: 431-441.

Koufos G. D. 2006. — The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. *Hellenic Journal of Geosciences* 41: 183-214.

Kowalski K. 1956. — Insectivores, bats and rodents from the early Pleistocene bone breccias of Podlesice near Kroczyce (Poland). *Acta Zoologica Cracoviensia* 1: 331-394.

Kowalski K. 1963. — The Pliocene and Pleistocene Gliridae (Mammalia, Rodentia) from Poland. *Acta Zoologica Cracoviensia* 8: 533-567.

Kowalski K. 1997. — Gliridae (Mammalia: Rodentia) from the Miocene of Belchatów in Poland. *Acta Zoologica Cracoviensia* 40: 173-198.

Kretzoi M. 1952. — Die Raubtiere der Hipparionfauna von Polgardi. *Annales Instituti Geologici Hungarici* 40 (3): 5-42.

Kretzoi M. 1959. — Insectivoren, Nagetiere und Lagomorphen der jüngstpliozänen Fauna von Csarnóta im Villányer Gebirge (Sudungarm). *Vertebrata hungarica* 1: 237-246.

Krijgsman W., Hilgen F. J., Raffi I., Sierro F. J. & Wilson D. S. 1999. — Chronology, causes and progression of the Messinian Salinity Crisis. *Nature* 400: 652-655.

Lurz P. W. W., Gurnell J. & Magris L. 2005. — *Sciurus vulgaris. Mammalian Species* 769: 1-10.

Marabini S. & Vai G. B. 1989. — Geology of the Monticino quarry, Brisighella, Italy. Stratigraphic implications of its Late Messinian mammal fauna. *Bollettino della Società Paleontologica Italiana* 28 (2-3): 369-382.

Marchetti M., Parolin K. & Sala B. 2000. — The Biharian fauna from Monte La Mesa. *Acta Zoologica Cracoviensia* 43: 79-105.

Martín-Suárez E. & Mein P. 1991. — Revision of the genus *Castillomys* (Muridae, Rodentia). *Scripta Geologica* 96: 47-81.

Martín-Suárez E. & Freudenthal M. 1998. — Biostratigraphy of the continental Upper Miocene of Crevillente (Alicante, SE Spain). *Geobios* 31: 839-847.

Martín-Suárez E. & Mein P. 1998. — Revision of the genera *Parapodemus*, *Apodemus, Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios* 31: 87-97.

Martín-Suárez E. & Mein P. 2004. — The Late Pliocene locality of Saint-Vallier (Drôme, France). 11. Micromammals. *Geobios* 37, Supplement 1: S115-S125.

Martín-Suárez E., Freudenthal M., Krijgsman W. & Fortuin A. R. 2000. — On the age of the continental deposits of the Zorreras Member (Sorbas Basin, SE Spain). *Geobios* 33 (4): 505-512.

Masini F. & Thomas H. 1989. — *Samotragus occidentalis* nov. sp. a new bovid from the Late Messinian of Italy. *Bollettino della Società Paleontologica Italiana* 28 (2-3): 307-316.

McCulloch M.T. & de Dekker P. 1989. — Sr isotope constraints on the Mediterranean environment at the end of the Messinian Salinity Crisis. *Nature* 342: 62-65.

Mein P. 1970. — Les Sciuroptères (Mammalia, Rodentia) neogènes d'Europe occidentale. *Geobios* 3: 7-77.

Mein P. 1999. — European Miocene Mammal Biochronology, *in* Rössner G. E. & Heissig K. (eds), *The Miocene Land Mammals of Europe*. Verlag Dr. Friederich Pfeil, München: 373-388.

Mein P. & Michaux J. 1970. — Un nouveau stade dans l'évolution des rongeurs pliocénes de l'Europe sud-occidentale. *Comptes rendus de l'Académie des Sciences D* 270: 2780-2783.

Mein P. & Romaggi J.-P. 1991. — Un Gliridé (Mammalia, Rodentia) planeur dans le Miocène supérieur de l'Ardèche: une adaptation non retrouvée dans la nature actuelle. *Geobios* 13: 45-50.

MEIN P. & GINSBURG L. 2002. — Sur l'âge relatif des differents depôts karstiques miocènes de La Grive-Saint-Alban (Isère). *Cahiers scientifiques du Muséum d'Histoire naturelle, Lyon* 2: 7-47.

MEIN P., MOISSENET E. & ADROVER R. 1983. — L'extension et l'âge des formations continentales pliocènes du fossé de Teruel (Espagne). *Comptes rendus des Séances de l'Académie des Sciences de Paris* 270: 2780-2783.

MEIN P., MOISSENET E. & ADROVER R. 1990. — Biostratigraphie du Nèogéne Supèrieur du bassin de Teruel. *Paleontologia i Evolució* 23: 121-139.

MICHAUX J. 1969. — Muridae (Rodentia) du Pliocène supérieur d'Espagne et du Midi de la France. *Palaeovertebrata* 3: 1-25.

MICHAUX J. 1970. — Les Rongeurs (Arvicolides, Murides et Glirides) de la localité Arondelli a Villafranca d'Asti (Italie). *Palaeontographia Italica* 66: 67-80.

MICHAUX J. & PASQUIER L. 1974. — Dynamique des populations de mulots (Rodentia, *Apodemus*) en Europe durant le Quaternaire. Premières données. *Bulletin de la Societe géologique de France* 16: 431-438.

MINWER-BARAKAT R., GARCÍA-ALIX A., MARTÍN-SUÁREZ E. & FREUDENTHAL M. 2005. — Muridae (Rodentia) from the Pliocene of Tollo de Chiclana (Granada, Southern Spain). *Journal of Vertebrate Paleontology* 25: 426-441.

MINWER-BARAKAT R., GARCÍA-ALIX A., MARTÍN-SUÁREZ E. & FREUDENTHAL M. 2008. — *Micromys caesaris*, a new murid (Rodentia, Mammalia) from the Late Pliocene of the Guadix Basin, Southeastern Spain. *Journal of Paleontology* 82: 436-441.

MINWER-BARAKAT R., GARCÍA-ALIX A., MARTÍN-SUÁREZ E. & FREUDENTHAL M. 2009a. — Late Turolian micromammals from Rambla de Chimeneas-3: considerations on the oldest continental faunas from the Guadix Basin (Southern Spain). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 83: 854-879.

MINWER-BARAKAT R., GARCÍA-ALIX A., AGUSTÍ J., MARTÍN-SUÁREZ E. & FREUDENTHAL M. 2009b. — The micromammal fauna from Negratín-1 (Guadix Basin, Southern Spain): new evidence of African-Iberian mammal exchanges during the Late Miocene. *Journal of Paleontology* 83: 854-879.

MINWER-BARAKAT R., GARCÍA-ALIX A., MARTÍN-SUÁREZ E., FREUDENTHAL M. & VISERAS C. 2012. — Micromammal biostratigraphy of the Upper Miocene to lowest Pleistocene continental deposits of the Guadix Basin, southern Spain. *Lethaia* 45: 594-614.

MONTENAT C. & DE BRUIJN H. 1976. — The Ruscinian rodent faunule from La Juliana (Murcia); its implication for the correlation of continental and marine biozones. *Proceedings Koninklijke Nederlandse Akademie Van Wetenschappen* B 79: 245-255.

MÖRS T., VON KOENIGSWALD W. & VON DER HOCHT F. 1998. — Rodents (Mammalia) from the Late Pliocene Reuver Clay of Hambach (Lower Rhine Embayment, Germany). *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO* 60: 135-160.

MOSCA P., POLINO R., ROGLEDI S. & ROSSI M. 2010. — New data for the kinematic interpretation of the Alps-Apennines junction (northwestern Italy). *International Journal of Earth Sciences* 99: 833-849.

NADACHOWSKI A. 1989. — Review of fossil Rodentia from Poland (Mammalia). *Senckenbergiana biologica* 70: 229-250.

NADACHOWSKI A. & DAOUD A. 1994. — Patterns of myoxid evolution in the Pliocene and Pleistocene of Europe. *Hystrix* 6: 141-149.

NESIN V. A. & NADACHOWSKI A. 2001. — Late Mioeene and Pliocene small mammal faunas (Insectivora, Lagomorpha, Rodentia) of southeastern Europe. *Acta zoologica cracoviensia* 44: 107-135.

PALOMBO M. R., AZANZA B. & ALBERDI M. T. 2003. — Italian mammal biochronology from latest Miocene to middle Pleistocene: a multivariate approach. *Geologica Romana* (2000-2002) 36: 335-368.

PATACCA E., SCANDONE P. & CARNEVALE G. 2013. — The Miocene vertebrate-bearing deposits of Scontrone (Abruzzo, Central Italy). Stratigraphic and paleoenvironmental analysis. *Geobios* 46: 5-23.

POPOV V. V. 2004. — Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria). *Geodiversitas* 26 (3): 403-491.

PRADEL A. 1988. — Fossil hamsters (Cricetinae, Rodentia) from the Pliocene and Quaternary of Poland. *Acta Zoologica Cracoviensa* 31: 235-296.

QIU Z. D. 1991. — The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. 8. Sciuridae (Rodentia). *Senckenbergiana Lethaea* 71: 223-255.

QIU Z.-D. & STORCH G. 2000. — The Early Pliocene micromammalian fauna of Bilike, Inner Mongolia, China (Mammalia: Lipotyphla, Chiroptera, Rodentia, Lagomorpha). *Senckenbergiana Lethaea* 80: 173-229.

QIU Z.-D. & YAN C.-L. 2005. — New sciurids from the Miocene Shanwang Formation, Linqu, Shandong. *Vertebrata PalAsiatica* 43: 194-207.

RENAUD S. & MICHAUX J. R. 2003. — Adaptive latitudinal trends in the mandible shape of *Apodemus* wood mice. *Journal of Biogeography* 30: 1617-1628.

RENAUD S. & MICHAUX J. R. 2007. — Mandibles and molars of the wood mouse, *Apodemus sylvaticus* (L.): integrated latitudinal pattern and mosaic insular evolution. *Journal of Biogeography* 34: 339-355.

REUMER J. W. F. & VAN DEN HOEK OSTENDE L.W. 2003. — Petauristidae and Sciuridae (Mammalia, Rodentia) from Tegelen, Zuurland, and the Maasvlakte (the Netherlands). *Deinsea* 10: 455-468.

Rietschel S. & Storch G. 1974. — Aussergewöhnlich erhaltene Waldmäuse (*Apodemus atavus* Heller, 1936) aus dem Ober-Pliozän von Willershausen am Harz. *Senckenbergiana Lethaea* 54: 491-519.

Rinaldi P. M. & Masini F. 2009. — New data on the taxonomy of the endemic Myomiminae (Gliridae, Rodentia) from the Late Miocene-Early Pliocene of Gargano (Southern Italy) with the description of the new species *Stertomys degiulii*. *Bollettino della Societa` Paleontologica Italiana* 48: 189-233.

Rook L. 1999. — Late Turolian *Mesopithecus* (Mammalia, Primates, Colobinae) from Italy. *Journal of Human Evolution* 36: 535-547.

Rook L. & Ghetti P. 1997. — Il bacino stratigrafico della Velona (Toscana, Italia): stratigrafia e primi ritrovamenti di vertebrati fossili. *Bollettino della Società Geologica Italiana* 116: 335-346.

Rook L., Abbazzi L. & Engesser B. 1999. — An overview on the Italian Miocene land mammal faunas, *in* Agustí J., Rook L. & Andrews P. (eds), *The Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge: 191-204.

Rook L., Gallai G. & Torre D. 2006. — Lands and endemic mammals in the Late Miocene of Italy: constrains for paleogeographic outlines of Tyrrhenian area. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238: 263-269.

Rook L., Oms O., Benvenuti M. G. & Paini M. 2011. — Magnetostratigraphy of the Late Miocene Baccinello-Cinigiano Basin (Tuscany, Italy) and the age of *Oreopithecus bambolii* faunal assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* 305: 286-294.

Sarica-Filoreau N. 2002. — *Faunes de rongeurs néogènes et quaternaires des grabens d'Anatolie occidentale. Systématique, biochronologie et implications tectoniques.* PhD thesis, Muséum national d'Histoire naturelle, Paris, 327 p.

Schaub S. 1938. — Tertiäre und quartäre Murinae. *Abhandlungen der Schweizerischen paläontologischen Gesellschaft* 69: 1-39.

Schmidt-Kittler N., de Bruijn H. & Doukas C. 1995. — 1. General introduction, *in* Schmidt-Kittler N. (ed.), The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). *Münchner Geowissenschaftliche Abhandlungen A* 28: 9-18.

Sen S. 1977. — La faune de rongeurs pliocènes de Çalta (Ankara, Turquie). *Bulletin du Muséum national d'Histoire naturelle, 3e série* 465: 89-172.

Sen S. 1997. — Magnetostratigraphic calibration of the European Neogene mammal chronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133: 181-204.

Sen S. 1998. — Pliocene vertebrate locality of Çalta, Ankara, Turkey. 4. Rodentia & Lagomorpha. *Geodiversitas* 20 (3): 359-378.

Sesé C. 1989. — Micromamíferos del Mioceno, Plioceno y Pleistoceno de la cuenca de Guadix-Baza (Granada), *in* Alberdi M. T., Bonadona F. P. (eds), *Geología y Paleontología de la Cuenca de Guadix-Baza.* Museo Nacional de Ciencas Naturales, CSIC, Madrid: 13-51

Siori M. S. & Sala B. 2007. — The mammal fauna from the late early Biharian site of Castagnone (Northern Monferrato, Piedmont, NW Italy). *Geobios* 40: 207-217.

Storch G. 1987. — The Neogene mammalian faunas of Ertemte and Harr Obo in inner Mongolia (Nei Mongol), China. 7. Muridae (Rodentia). *Senckenbergiana Lethaea* 67: 401-431.

Storch G. & Dahlmann T. 1995. — 10. Murinae (Rodentia, Mammalia), *in* Schmidt-Kittler N. (ed.), The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). *Münchner Geowissenschaftliche Abhandlungen* A 28: 121-132.

Sulimski A. 1964. — Pliocene Lagomorpha and Rodentia from Węże 1 (Poland). *Acta Paleontologica Polonica* 9: 149-240.

Thorington R. W. Jr., Musante A. L., Anderson C. G. & Darrow K. 1996. — Validity of three genera of flying squirrels: *Eoglaucomys*, *Glaucomys*, and *Hylopetes*. *Journal of Mammology* 7: 69-83.

Thorington R. W. Jr., Pitassy D. & Jansa S. A. 2002. — Phylogenies of flying squirrels (Pteromyinae). *Journal of Mammalian Evolution* 9: 99-135.

Thorington R. W. Jr., Schennum C. E., Lindsay A., Pappas L. A. & Pitassy D. 2005. — The difficulties of identifying flying squirrels (Sciuridae: Pteromyini) in the fossil record. *Journal of Vertebrate Paleontology* 25: 950-961.

Torre D. 1989. — *Plioviverrops faventinus* n. sp., a new carnivore of Late Messinian age. *Bollettino della Società Paleontologica Italiana* 28 (2-3): 323-327.

Van Dam J. A. 2003. — European Neogene mammal chronology: past, present and future. *Deinsea* 10: 85-95.

Van Dam J. A., Alcalà L., Zarza A. A., Calvo J. P., Garcés M. & Krijgsman W. 2001. — The Upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. *Journal of Vertebrate Paleontology* 21: 367-385.

Van de Weerd A. 1976. — Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins* 2: 1-217.

Van de Weerd A. 1979. — Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 82: 127-170.

Van den Hoek Ostende L. 2003. — Gliridae (Rodentia, Mammalia) from the Upper Pliocene of Tegelen (province of Limburg, The Netherlands). *Scripta Geologica* 126: 203-215.

Van den Hoek Ostende L. & Reumer J. W. F. 2011. — *Hylopetes magistri*, new name for *Hylopetes debruijni* Reumer & Van Den Hoek Ostende, 2003, preoccupied. *Journal of Vertebrate Paleontology* 31: 928-928.

Van der Meulen A. J. & de Bruijn H. 1982. — The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 2. The Gliridae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 85: 485-524.

Van der Meulen A. J., García-Paredes I., Álvarez-Sierra Á., van den Hoek Ostende L. W., Hordijk K., Oliver A., López-Guerrero P., Hernández-Ballarín V. & Peláez-Campomanes P. 2011. — Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe. *Geobios* 44 (2-3): 309-321.

Vasileiadou K. V., Koufos G. D. & Syrides G. E. 2003. — Silata, a new locality with micromammals from the Miocene/Pliocene boundary of the Chalkidiki peninsula,Macedonia, Greece. *Deinsea* 10: 549-562.

Vasileiadou K. V., Konidaris G. & Koufos G. D. 2012. — New data on the micromammlian locality of Kessani (Thrace, Greece) at the Mio-Pliocene boundary. *Palaeobiodiversity and Palaeoenvironments* 92: 211-237.

Villier B. & Carnevale G. 2013. — A new skeleton of the giant hedgehog *Deinogalerix* from the Miocene of Gargano, Southern Italy. *Journal of Vertebrate Paleontology* 33: 902-923.

Villier B., van den Hoek Ostende L. W., de Vos J. & Pavia M. 2013. — New discoveries on the giant hedgehog *Deinogalerix* from the Miocene of Gargano (Apulia, Italy). *Geobios* 46: 63-75.

Violanti D., Dela Pierre F., Trenkwalder S., Lozar F., Clari P., Irace A. & D'Atri A. 2011. — Biostratigraphic and palaeoenvironmental analyses of the Messinian/Zanclean boundary and Zanclean succession in the Moncucco quarry (Piedmont, northwestern Italy). *Bulletin de la Société géologique de France* 182: 149-162.

Zafonte F. & Masini F. 1992. — Enamel structure evolution in the first lower molar of the endemic murids of the genus *Microtia* (Pliocene, Gargano, Italy). *Bollettino della Societa` Paleontologica Italiana* 31: 349-355.

Submitted on 26 July 2013;
accepted on 8 January 2014;
published on 26 September 2014.

APPENDICES

APPENDIX 1. — List of the studied rodent material from Moncucco Torinese (NW Italy).

Neocricetodon magnus (Fahlbusch, 1969)

MCC 4
Two isolated m1: MGPT-PU 127932, 127845;
One isolated m2: MGPT-PU 127846.

MCC 5
Two isolated M1 (fragmented): MGPT-PU 127421, 127498;
Two isolated M3: MGPT-PU 127499, 127500;
One isolated m1: MGPT-PU 127424;
Five isolated m2: MGPT-PU 127420, 127425-127427, 127922;
Three isolated m3: MGPT-PU 127422, 127423, 127497.

MCC 7
One isolated m1: MGPT-PU 128268;
One isolated m2: MGPT-PU 128273.

Paraethomys meini (Michaux, 1969)

MCC 3
Three isolated M1: MGPT-PU 127439, 127440, 127765;
Two isolated M2: MGPT-PU 127766, 127767;
Three isolated m1: MGPT-PU 127461, 127768, 127769.

MCC 4
Five isolated M1: MGPT-PU 127120, 127126, 127829, 127830, 127831;
Four isolated M2: MGPT-PU 127233, 127832-127834;
Four isolated M3: MGPT-PU 127944, 127835-127837;
Four isolated m1: MGPT-PU 127186, 127190, 127945, 127946;
Three isolated m2: MGPT-PU 127238, 127947, 127838;
One isolated m3: MGPT-PU 127948.

MCC 5
Nine maxillary fragments bearing M1 and M2: MGPT-PU 127501, 127913, 127914, 128016-128021;
Two maxillary fragments bearing M2 and M3: MGPT-PU 128038, 128045;
One mandible bearing m2 and m3: MGPT-PU 127920;
21 isolated M1: MGPT-PU 127092, 127095, 127098, 127099, 127911, 127912, 128022-128036;
16 isolated M2: MGPT-PU 127204, 127205, 127212, 127915, 127916, 128037, 128039-128044, 128046-128049;
13 isolated M3: MGPT-PU 127345, 127353, 127356, 127602, 127886, 127917, 128050-128056;
16 isolated m1: MGPT-PU 127918, 127919, 128057-128070;
16 isolated m2: MGPT-PU 127268, 127272, 127280, 127283, 127302, 127921, 128071-128080;
Nine isolated m3: MGPT-PU 127603, MGPT-PU 128081-128087.

MCC 7
Three isolated M1: MGPT-PU 128242, 128243, 128336;
Four isolated M2: MGPT-PU 128275, 128277, 128286, 128288;
Three isolated M3: MGPT-PU 128291, 128293, 128297;
Seven isolated m1: MGPT-PU 128300, 127464, 127465, 128271, 128307, 128309, 128311;
12 isolated m2: MGPT-PU 127471-127474, 128312, 128317, 128322-128324, 128327-128329;
Three isolated m3: MGPT-PU 128342, 127865, 128337.

Occitanomys brailloni Michaux, 1969

MCC 3
One maxillary fragment bearing M1 and M2: MGPT-PU 127453;

Nine isolated M1: MGPT-PU 127435, 127436, 127438, 127451, 127452, 127454, 127455, 127745, 127746;
Five isolated M2: MGPT-PU 127442, 127444, 127446, 127447, 127781;
One isolated M3: MGPT-PU 127747;
Five isolated m1: MGPT-PU 127460, 127462, 127752-127754;
Four isolated m2: MGPT-PU 127748-127751;
Three isolated m3: MGPT-PU 127755-127757.

MCC 4
One maxillary fragment bearing M2 and M3: MGPT-PU 127789;
19 isolated M1: MGPT-PU 127116-127119, 127121-127125, 127127-127129, 127782-127787, 127926;
19 isolated M2: MGPT-PU 127230-127232, 127235-127237, 127239-127241, 127243, 127323, 127788, 127790-127794, 127927, 127928;
Eight isolated M3: MGPT-PU 127795-127800, 127929, 127930;
11 isolated m1: MGPT-PU 127187-127189, 127191, 127192, 127196, 127801-127804, 127931;
Three isolated m2: MGPT-PU 127805-127807;
One isolated m3: MGPT-PU 127808.

MCC 5
One maxillary fragment bearing M1 and M2: MGPT-PU 127868;
Two mandibular fragments bearing m1, m2 and m3: MGPT-PU 127507, 127508;
Two mandibular fragments bearing m1 and m2: MGPT-PU 127626, MGPT-PU 127872;
46 isolated M1: MGPT-PU 127088, 127090, 127091, 127093, 127094, 127096, 127097, 127100, 127103-127105, 127220, 127520-127552, MGPT-PU 127869;
47 isolated M2: MGPT-PU 127201-127203, 127206, 127208, 127211, 127216, 127218, 127219, 127225, 127226, 127229, 127553-127565, 127567-127586, 127874, 127875;
15 isolated M3: MGPT-PU 127350-127352, 127354, 127360, 127587-127594, 127657, 127876;
44 isolated m1: MGPT-PU 127154, 127156, 127158, 127160-127166, 127175, 127176, 127595-127599, 127605, 127612-127625, 127627-127636, 127870, 127873;
48 isolated m2: MGPT-PU 127269, 127271, 127273, 127274, 127277-127279, 127281, 127284, 127285, 127290, 127293, 127294, 127300, 127637-127656, 127666-127675, 127877-127880.
20 isolated m3: MGPT-PU 127658, 127676-127692, 127881, 127882.

MCC 7
One mandibular fragment bearing m1, m2 and m3: MGPT-PU 128302;
Five isolated M1: MGPT-PU 128244-128248;
Eight isolated M2: MGPT-PU 127853, 127854, 128227, 128274, 128281-128283, 128287;
Two isolated M3: MGPT-PU 128292, MGPT-PU 128296;
Four isolated m1: MGPT-PU 128303-128305, 127855;
Six isolated m2: MGPT-PU 128315, 128320, 128325, 128326, 127477, 127857;
Seven isolated m3: MGPT-PU 128334, 128338, 128339, 128343, 128345, 127858, 127859.

Centralomys benericettii (De Giuli, 1989)

MCC 3
One maxillary fragment bearing M1 and M2: MGPT-PU 127770;
Two isolated M1: MGPT-PU 127437, 127456;
One isolated M2: MGPT-PU 127771;
Three isolated m1: MGPT-PU 127459, 127772, 127773;
One isolated m2: MGPT-PU 127774.

MCC 4
Six isolated M1: MGPT-PU 127068, 127074, 127107, 127113-127115;
Seven isolated M2: MGPT-PU 127244-127246, 127839-127842;
Five isolated m1: MGPT-PU 127179, 127184, 127198, 127843, 127949;
Two isolated m2: MGPT-PU 127844, 127950.

MCC 5
14 isolated M1: MGPT-PU 127903, 128088-128100;
13 isolated M2: MGPT-PU 128101-128113;
Three isolated M3: MGPT-PU 127344, 128114, 128115;
23 isolated m1: MGPT-PU 127148-127150, 127152, 127153, 127155, 127157, 127174, 127871, 127904, 127905, 128116-128127;
25 isolated m2: MGPT-PU 127275, 127282, 127291, 127292, 127298, 127301, 127906-127908, 128128-128143;
Three isolated m3: MGPT-PU 127909, 128144, 128145.

MCC 7
One mandibular fragment bearing m1 and m2: MGPT-PU 128298;
Nine isolated M1: MGPT-PU 127468, 127866, 128249-128254, 128335;
Five isolated M2: MGPT-PU 127476, 128276, 128278, 128280, 128289;
One isolated M3: MGPT-PU 128294;
Four isolated m1: MGPT-PU 128272, 128299, 128308, 128310;
Three isolated m2: MGPT-PU 127867, 128321, 128330.

Micromys bendai van de Weerd, 1979

MCC 3
One isolated M1: MGPT-PU 127434;
Two isolated m1: MGPT-PU 127775, 127776.

MCC 4
Three isolated M1: MGPT-PU 127200, 127850, 127851;
One isolated m1: MGPT-PU 127852.

MCC 5
Three mandibular fragments bearing m1 and m2: MGPT-PU 127509, 128165, 128167;
Five isolated M1: MGPT-PU 127082, 127089, 128158-128160;
Four isolated M2: MGPT-PU 127224, 128161-128163;
One isolated M3: MGPT-PU 128164;
Four isolated m1: MGPT-PU 127147, 127151, 127600, 128166;
Three isolated m2: MGPT-PU 127601, 127910, 128168.

MCC 7
Four isolated M1: MGPT-PU 127467, 128257-128259;
One isolated M2: MGPT-PU 128279;
One isolated M3: MGPT-PU 128295;
Three isolated m1: MGPT-PU 128255, 128256, 128306;
One isolated m2: MGPT-PU 128314.

Apodemus gudrunae van de Weerd, 1976

MCC 3
One maxillary fragment bearing M1 and M2: MGPT-PU 127428;
Eight isolated M1: MGPT-PU 127429-127433, 127448-127450;
Three isolated M2: MGPT-PU 127445, 127758, 127759;
One isolated M3: MGPT-PU 127760;
Four isolated m1: MGPT-PU 127457, 127458, 127761, 127780;
Two isolated m2: MGPT-PU 127762, 127763;
One isolated m3: MGPT-PU 127760.

MCC 4
16 isolated M1: MGPT-PU 127106, 127108-127111, 127130, 127131, 127809-127814, 127933-127935;
12 isolated M2: MGPT-PU 127234, 127324-127326, 127815-127820, 127936, 127937;
Five isolated M3: MGPT-PU 127821-127823, 127938, 127939;
11 isolated m1: MGPT-PU 127182, 127183, 127185, 127193-127195, 127197, 127824-127826, 127940;
Three isolated m2: MGPT-PU 127827, 127941, 127942;
Two isolated m3: MGPT-PU 127828, 127943.

MCC 5
One maxillary fragment bearing M1 and M2: MGPT-PU 127699;
37 isolated M1: MGPT-PU 127083-127085, 127087, 127101, 127693-127698, 127700-127722, 127883-127885;
33 isolated M2: MGPT-PU 127207, 127209, 127210, 127213-127215, 127217, 127221, 127222, 127228, 127723-127744, 127897;
11 isolated M3: MGPT-PU 127664, 127358, 127955-127963;
38 isolated m1: MGPT-PU 127167-127173, 127887-127890, 127964-127990;
24 isolated m2: MGPT-PU 127505, 127270, 127276, 127286, 127288, 127295-127297, 127891, 127894, 127991-128004;
14 isolated m3: MGPT-PU 127665, 127892, 127893, 128005-128015.

MCC 7
Seven isolated M1: MGPT-PU 127469, 127470, 128222-128226;
Four isolated M2: MGPT-PU 128228-128230, 128285;
Three isolated M3: MGPT-PU 128231, 128232, 128290;
10 isolated m1: MGPT-PU 127466, 127860-127862, 128233-128238;
Six isolated m2: MGPT-PU 127475, 127863, 128313, 128318, 128319, 128333;
Three isolated m3: MGPT-PU 127864, 128340, 128341.

Apodemus atavus Heller, 1936

MCC 3
One isolated M2: MGPT-PU 127777;
Two isolated m1: MGPT-PU 127463, 127778.

MCC 4
Two isolated M1: MGPT-PU 127112, 127848;
Three isolated M2: MGPT-PU 127247, 127951, 127952;
Seven isolated m1: MGPT-PU 127177, 127178, 127180, 127181, 127199, 127849, 127953;
One isolated m2: MGPT-PU 127954.

MCC 5
Nine isolated M1: MGPT-PU 127502, 127503, 127086, 127659, 127895, 128146-128148, 128155;
Three isolated M2: MGPT-PU 127227, 127660, 128149;
Four isolated M3: MGPT-PU 127661, 127902, 128150, 128151;
Six isolated m1: MGPT-PU 127159, 127898, 127899, 128152-128154;
Four isolated m2: MGPT-PU 127504, 127662, 127900, 128156;
Two isolated m3: MGPT-PU 127663, 128157.

MCC 7
One isolated M1: MGPT-PU 128240;
One isolated m1: MGPT-PU 128241;
Two isolated m2: MGPT-PU 128316, 128332;
One isolated m3: MGPT-PU 128344.

Eliomys aff. *intermedius* Friant, 1953

MCC 4
Two isolated M2: MGPT-PU 127495, 128346.

MCC 5
One isolated P4: MGPT-PU 128348;
One isolated m1: MGPT-PU 128217;
One isolated m2: MGPT-PU 127368.

MCC 7
Three isolated M1: MGPT-PU 127048, 128270, 128349;
One isolated m1: MGPT-PU 128269.

Muscardinus vireti Hugueney & Mein, 1965

MCC 3
Two isolated M1: MGPT-PU 127415, 127487;
One isolated M2: MGPT-PU 127375;
Two isolated m1: MGPT-PU 127383, 127413;
One isolated m2: MGPT-PU 127417.

MCC 4
One isolated M1: MGPT-PU 127481;
Two isolated M2: MGPT-PU 127486, 127515;

Four isolated m1: MGPT-PU 127511, 127484, 127488, 127489;
Four isolated m2: MGPT-PU 127482, 127483, 127485, 127512;
Three isolated m3: MGPT-PU 127490, 127513, 127514.

MCC 5
One maxillary fragment bearing M1 and M2: MGPT-PU 128175;
Two isolated P4: MGPT-PU 127604, 128169;
13 isolated M1: MGPT-PU 127389, 127392, 127394, 127396, 127404, 127406, 127411, 128170-128174, 128176;
10 isolated M2: MGPT-PU 127391, 127403, 127409, 127410, 127606, 127923, 128177-128180;
Three isolated M3: MGPT-PU 127607, 128181, 128182;
One isolated p4: MGPT-PU 127608;
14 isolated m1: MGPT-PU 127388, 127393, 127402, 127412, 127609, 128190-128198;
17 isolated m2: MGPT-PU 127395, 127401, 127405, 127407, 127610, 127924, 128183-128185, 128199-128206;
Six isolated m3: MGPT-PU 127390, 127397, 127408, 127611, 128186, 128187.

MCC 7
Three isolated M1: MGPT-PU 127479, 128260, 128261;
Two isolated M2: MGPT-PU 128262, 128266;
Two isolated m1: MGPT-PU 128264, 128265;
Two isolated m2: MGPT-PU 128263, 128267.

Glirulus lissiensis Hugueney & Mein, 1965

MCC 5
Two isolated M2: MGPT-PU 127496, 127510.

MCC7
One isolated m1: MGPT-PU 128351.

Glis minor Kowalski, 1956

MCC 3
One isolated P4: MGPT-PU 127419;
One isolated M1: MGPT-PU 127418;
One isolated M2: MGPT-PU 127416;
One isolated m3: MGPT-PU 127414.

MCC 4
One isolated P4: MGPT-PU 127494;
One isolated M2: MGPT-PU 127491;
Two isolated p4: MGPT-PU 127480, 127516;
One isolated m1: MGPT-PU 127493;
One isolated m2: MGPT-PU 127492.

MCC 5
One isolated P4: MGPT-PU 127400;
Three isolated M1: MGPT-PU 128188, 128189, 127399;
Three isolated M2: MGPT-PU 128207bis, 128208, 128209;
Four isolated p4: MGPT-PU 127398, 127925, 128210, 128211;
Three isolated m1: MGPT-PU 128207, 128212, 128214;
One isolated m2: MGPT-PU 128213;
One isolated m3: MGPT-PU 127387.

MCC 7
One isolated M1: MGPT-PU 128239.

Sciurus warthae Sulimski, 1964

MCC 5
One isolated M3: MGPT-PU128219;
One isolated m1: MGPT-PU 128221.

Pliopetaurista pliocaenica (Depéret, 1897)

MCC 5
One isolated M3: MGPT-PU128347;
One isolated m1: MGPT-PU128218.

Appendix 2. — List of Neogene, Quaternary and extant rodent species from different localities of Eurasia analyzed for comparative purposes.

Apocricetus barrierei (Mein & Michaux, 1970) from Chabrier (UCBL).

Pseudocricetus kormosi (Schaub, 1930) from Polgardi (UCBL).

Neocricetodon lavocati Hugueney & Mein, 1965 from Lissieu (UCBL).

Neocricetodon browni (Daxner-Höck, 1992) from Maramena (IVAU).

Necricetodon seseae Aguilar, Calvet & Michaux, 1995 from Arquillo 1 (UCBL).

Neocricetodon fahlbuschi Bachmayer & Wilson, 1970 from Kohfidich (UCBL).

Paraethomys meini (Michaux, 1969) from Sète, Maritsa, Teruel, Caravaca (UCBL) and Brisighella (UNIFI).

Paraethomys abaigari Adrover, Mein & Moissenet, 1988 from Villalba Alta Río (UCBL).

Occitanomys adroveri (Thaler, 1966) from Los Mansuetos (UCBL).

Occitanomys brailloni Michaux, 1969 from Layna (UCBL) and Rema Marmara (IVAU).

Occitanomys montheleni Aguilar, Calvet & Michaux, 1986 from Mont Hélène and Serrat d'en Vaquer (UCBL).

Centralomys benericettii (De Giuli, 1989) from Brisighella 1 and 25 (UNIFI) and from Verduno (MGPT-PU).

Castillomys magnus Sen, 1977 from Çalta (UCBL).

Castillomys gracilis van de Weerd, 1976 from Caravaca (IVAU, UCBL).

Micromys bendai van de Weerd, 1979 from Kardia and Ptolemais 1 (IVAU).

Micromys steffensi van de Weerd, 1979 from Kardia (IVAU).

Apodemus gudrunae van de Weerd, 1976 from Orrios, Valdecebro 3 (IVAU), Arquillo 1, Villastar (UCBL), Brisighella (UNIFI), Verduno (MGPT-PU).

Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña & Padial, 1984 from Gorafe 4, Celadas 9 and Purcal 4 (UCBL).

Apodemus atavus Heller, 1936 from Gundersheim 4, Csarnota (IVAU), Concud Pueblo 3, Maramena, Mont Hélène, Perpignan (UCBL).

Rhagapodemus primaevus Hugueney & Mein, 1965from Lissieu (IVAU, UCBL) and Maramena (UCBL).

Rhagapodemus frequens Kretzoi, 1959 from Seynes, Layna and Sète (UCBL).

Rhagapodemus hautimagnensis Mein & Michaux, 1970 from Mont Hélène (UCBL).

Rhagapodemus ballesioi Mein & Michaux, 1970 from Mont Hélène and Perpignan (UCBL).

Rhagapodemus vandeweerdi de Bruijn & van der Meulen, 1975 from Maritsa (IVAU).

Eliomys truci Mein & Michaux, 1970 from Hautimagne (UCBL).

Eliomys intermedius Friant, 1953 from Sète (IVAU).

Muscardinus vireti Hugueney & Mein, 1965 from Lissieu (UCBL).

Muscardinus davidi Hugueney & Mein, 1965 from Lissieu (UCBL).

Glirulus lissiensis Hugueney & Mein, 1965 from Lissieu (UCBL).

Glis minor Kowalski, 1956 from Podlesice (IVAU).

Glis sackdillingensis (Heller, 1930) from Schernfeld (IVAU).

Sciurus vulgaris Linnaeus, 1758 from Torino (MGPT-PU).

Sciurus warthae Sulimski, 1964 from Monte la Mesa (UNIFE).

Sciurus magistri (van den Hoek Ostende & Reumer, 2011) from Tegelen (RMNH).

Hylopetes lepidus Horsfield, 1822 from Loang Speam (Cambodia) (UCBL) and from South-East Asia (IVAU).

Neopetes macedoniensis (Bouwens & de Bruijn, 1986) from Maramena (IVAU).

Pliopetaurista dehneli (Depéret, 1897) from Hautimagne (UCBL).