



ELSEVIER

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution (Invertebrate Palaeontology)

Late Miocene (Turolian, MN13) squirrels from Moncucco Torinese, NW Italy

*Écureuils du Miocène supérieur (Turolien, MN13) de Moncucco Torinese, Nord-Ouest de l'Italie*

Simone Colombero*, Giorgio Carnevale

Dipartimento di Scienze della Terra di Torino, Via Valperga Caluso 35, 10125 Torino, Italy

ARTICLE INFO

Article history:

Received 24 July 2015

Accepted after revision 30 November 2015

Available online 22 March 2016

Handled by Annalisa Ferretti

Keywords:

Rodentia

Sciuridae

Messinian

Italy

Paleoecology

Mots clés :

Rodentia

Sciuridae

Messinien

Italie

Paléoécologie

ABSTRACT

Squirrel remains are rare in the fossil record, which hampers a properly documented interpretation of their evolutionary history. The Late Miocene sciurids from Moncucco Torinese (NW Italy) are described based on a diverse tooth assemblage. The data presented herein confirm the presence of *Sciurus warthae* and *Pliopetaurista pliocaenica*, and also include the first unquestionable occurrence of *Hylometes hungaricus* plus an indeterminate Sciurinae. The report of *Sciurus warthae* from Moncucco Torinese represents the earliest record of the genus *Sciurus* in Europe. Moreover, Moncucco Torinese is the first European locality recording the co-occurrence of Sciurini and Pteromyini in the Late Miocene. Comparative analyses support a close relationship between *S. warthae* and *Sciurus vulgaris* corroborating the hypothesis of an earliest divergence of the “*Sciurus vulgaris* clade” in the Late Miocene. Biochronological, paleobiogeographical and paleoecological implications are also discussed.

© 2016 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Les fossiles d'écureuil sont rares dans le registre fossile, avec des conséquences négatives pour une interprétation bien documentée de leur histoire évolutive. Les sciuridés du Miocène supérieur de Moncucco Torinese, Italie du Nord-Ouest, sont décrits ici sur la base de restes dentaires plutôt diversifiés. Les données présentées ici confirment la présence de *Sciurus warthae* et *Pliopetaurista pliocaenica*, et incluent aussi la première occurrence de *Hylometes hungaricus* en Italie, plus un taxon indéterminé. La présence de *Sciurus warthae* à Moncucco Torinese représente la documentation la plus ancienne du genre *Sciurus* en Europe. En outre, Moncucco Torinese est la première localité européenne qui enregistre l'occurrence simultanée de Sciurini et de Pteromyini dans le Miocène supérieur. Les analyses comparatives sont en faveur d'une relation étroite entre *S. warthae* et *Sciurus vulgaris*, corroborant l'hypothèse d'une première divergence du clade « *Sciurus vulgaris* » au Miocène supérieur. Les implications biochronologiques, paléobiogéographiques et paléoécologiques sont également discutées.

© 2016 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

* Corresponding author.

E-mail addresses: simone.colombero@unito.it (S. Colombero), giorgio.carnevale@unito.it (G. Carnevale).

1. Introduction

In the past decade, new fossiliferous localities characterized by abundant continental vertebrate remains have been discovered in the Upper Miocene deposits of northern and central Italy (Abbazzi et al., 2008; Angelone et al., 2011; Colombero et al., 2013, 2014a, 2014b, 2015; Rook et al., 2006). Overall, the recovered fossil assemblages provided a large amount of data regarding the terrestrial vertebrate paleobiodiversity of Italy, and more generally of southern Europe, slightly before the Mio/Pliocene boundary. In this paper, we will focus on the fossil squirrels collected in the upper Messinian sediments exposed in the surroundings of Moncucco Torinese, NW Italy, a small village that gives the name to the fossiliferous locality in which the studied material has been found. A cursory analysis of the vertebrate remains from this locality revealed an extraordinary rich assemblage that includes fishes, amphibians, reptiles, birds and mammals (Angelone et al., 2011). Mammal remains are dominated by far by rodents that are particularly abundant and diverse, represented by at least five families: Cricetidae, Gliridae, Hystricidae, Muridae, and Sciuridae (Colombero et al., 2014b, 2015). Despite their scarcity, members of family Sciuridae are rather diverse and provide relevant data about the evolution and paleobiogeography of squirrels, as well as concerning the paleoecology and biochronology of Moncucco Torinese.

The study of the evolutionary history of sciurids is somewhat problematic due to the poor and scattered fossil record, mostly represented by teeth (Emry and Thorington, 1982), often displaying elusive diagnostic characters (Thorington et al., 2002, 2005). In their

extensive analyses of the fossil rodents from Moncucco Torinese, Colombero et al. (2014b) preliminarily referred a few sciurid teeth to the sciurine *Sciurus warthae* and the pteromyine *Pliopetaurista pliocaenica*. Subsequent field-work yielded additional material allowing more detailed analyses of *S. warthae* and leading to the identification of further taxa of Sciurinae. Pteromyini and Sciurini are sister taxa within the subfamily Sciurinae (Mercer and Roth, 2003; Steppan et al., 2004). Among sciurins, the genus *Sciurus* is currently the most diverse with at least 28 species widespread in Eurasia and Americas, including the Eurasian red squirrels *Sciurus vulgaris* (Thorington et al., 2012). According to recent molecular analyses, *Sciurus* diverged from other sciurins between late Middle and early Late Miocene (Mercer and Roth, 2003; Pečnerová and Martínková, 2012). However, the pre-Pliocene record that can be reliably assigned to this genus solely consists of very few reports from the Late Miocene of North America and Eurasia (Fig. 1) (Bosma et al., 2013; Emry et al., 2005; Qiu, 1991; Qiu et al., 2008). Therefore, the teeth of *Sciurus* from Moncucco Torinese documented herein are highly significant for the interpretation of the early evolutionary and paleobiogeographic history of this genus. The primary goal of this paper is therefore the description of the sciurid material recovered from Moncucco Torinese. In addition, evolutionary and paleoenvironmental implications are also discussed.

2. Locality

The site of Moncucco Torinese is located in the Torino Hill, at the top of a gypsum quarry (Fig. 2). A detailed



Fig. 1. Late Miocene records of the genus *Sciurus*. 1: *Sciurus olsoni*, Late Miocene (Clarendonian): Hazen, Lyon County, Nevada, USA (Emry et al., 2005); 2: *Sciurus* sp., Late Miocene (Early Baodean): Loc. 36, Lantian County, Shaanxi, China (Qiu et al., 2008); 3: ?*Sciurus* sp., Late Miocene (Late Vallesian/Early Turolian): Hayranlı 1, central Anatolia, Turkey (Bosma et al., 2013); 4: *Sciurus* sp., Late Miocene (late Turolian): Ertemte 2, Huade County, Inner Mongolia, China (Qiu, 1991); 5: *Sciurus warthae*, Late Miocene (Late Turolian): Moncucco Torinese, NW Italy (Colombero et al., 2014b; this work).

Fig. 1. Fossiles du genre *Sciurus* du Miocène supérieur. 1 : *Sciurus olsoni*, Miocène supérieur (Clarendonien) : Hazen, Comté de Lyon, Nevada, États-Unis (Emry et al., 2005) ; 2 : *Sciurus* sp., Miocène supérieur (Baodéen inférieur) : Loc. 36, Comté de Lantian, Shaanxi, Chine (Qiu et al., 2008) ; 3 : ?*Sciurus*, Miocène supérieur (Vallésien/Turolien) : Hayranlı 1, Anatolie centrale, Turquie ; (Bosma et al., 2013) ; 4 : *Sciurus* sp., Miocène supérieur (Turolien) : Ertemte 2, Huade, Mongolie, Chine (Qiu, 1991) ; 5 : *Sciurus warthae*, Miocène supérieur (Turolien) : Moncucco Torinese, Nord-Ouest de l'Italie (Colombero et al., 2014b ; ce travail).



Fig. 2. Geographic and stratigraphic setting of the Tertiary Piedmont Basin (TPB). White area: Pliocene to recent deposits; dark grey area: Messinian deposits; dotted area: Eocene to Tortonian deposits; dashed area: Alpine sectors; light grey: Ligurian Sea. The arrow indicates the geographic position of the fossiliferous site Moncucco Torinese (MCC). TH: Torino Hills; MO: Monferrato Hills; AM: Alto Monferrato.

Fig. 2. Géographie et stratigraphie du bassin tertiaire du Piémont (TPB). Zone blanche : dépôts Pliocène à Récents ; zone gris foncé : Messinien ; zone en pointillés : dépôts Éocène à Tortonien ; zone hachurée : secteurs alpins ; gris clair : mer Ligure. La flèche indique la position géographique du site fossilifère du Moncucco Torinese (MCC). TH : Torino Hills ; MO : Monferrato Hills ; AM : Alto Monferrato.

Modified from Lozar et al. (2014).

description of the geological setting and stratigraphy of the area and fossil site was provided by Dela Pierre et al. (2007) and Colombero et al. (2014b). The fossiliferous deposits belong to the Cassano Spinola Conglomerates Formation, the uppermost lithostratigraphic unit of the Messinian succession of the Tertiary Piedmont Basin (Fig. 3). Moreover, micropaleontological data indicate that the fossiliferous layers can be correlated to phase 3.2 (*sensu* Roveri et al., 2014) of the Messinian Salinity Crisis, chronologically constrained between 5.42 and 5.33 Ma (see Alba et al., 2014; Colombero et al., 2014b).

3. Material and methods

The studied material consists of nine sciurid teeth including premolars and molars, selected from 2800 rodent teeth derived from the processing of 18 tons of sediment. Fossils are currently housed in the Museo di Geologia and Paleontologia, Università degli Studi di Torino. Nomenclature and measurement follow Casanovas-Vilar et al. (2015) except the definition of the mesoloph. Following Marivaux et al. (2004), the mesoloph is the short crest developing from the mesostyle, whereas the crest departing from

the protocone between the protoloph and the metaloph is the protolophule. The tiny crest developing between anteroloph and protoloph is an anterior accessory ridge. Measurements are given in mm. All measurements provided herein and the pictures of *Sciurus vulgaris* have been taken with the Leica Application Suite V. 3.3 of a stereomicroscope Leica M205C, whereas dental remains from Moncucco Torinese were photographed with the Scanning Electron Microscope Cambridge S-360 of the Dipartimento di Scienze della Terra di Torino. Dental material of *Sciurus warthae* from the Early Pleistocene of Monte La Mesa (STUM), as well as of the extant *Sciurus vulgaris* (MCCI, DBIOS) and *Sciurus carolinensis* (MCCI) from Italy was examined for comparative purposes. As regards the taxonomic classification of Scuridae, we follow Steppan et al. (2004), thereby implying that we consider Pteromyini and Sciurini as two closely related tribes within the subfamily Sciurinae. Fig. 4C and D (M3 and m1 of *Sciurus warthae*) and Fig. 4G and H (M3 and m1 of *Pliopetaurista pliocaenica*) were originally presented in Colombero et al. (2014b) with erroneously inverted captions; such a mistake is corrected herein.

Institutional abbreviations: DBIOS: Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università degli Studi di Torino, Italy; MCCI: Museo Civico di Storia Naturale di Carmagnola, Carmagnola, Italy; MGPT-PU: Museo di Geologia e Paleontologia, Università degli Studi di Torino, Italy; STUM: Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, Italy.

4. Systematic paleontology

Order Rodentia Bowdich, 1821
 Family Sciuridae Fischer, 1817
 Subfamily Sciurinae Fischer, 1817
 Tribe Sciurini Fischer, 1817
 Genus *Sciurus* Linnaeus, 1758
Sciurus warthae Sulimski, 1964

Referred material and measurements: a right dP4 (MGPT-PU136604, L: ? -W: 1.77), a left P4 (MGPT-PU136591, L: 2.13-W: 2.30), a right M3 (MGPT-PU128219, L: 2.84-W: 2.60), a right m1 (MGPT-PU 128221, L: 2.28-W: 2.42), a left m2 (MGPT-PU 136592, L: 2.35-W: 2.66).

Description

dP4 – (Fig. 4A). Completely unworn tooth, parastyle not preserved. Distinct paracone and metacone, well-developed protocone; hypocone tiny but distinct; anteroloph partially preserved and low; protoloph short and interrupted at its midlength by a deep notch; metaloph uninterrupted bearing a small metaconule; tiny mesostyle present; roots not preserved.

P4 – (Fig. 4B). Worn tooth with exposed dentine in some portions of the occlusal surface. Roughly triangular outline; large protocone; parastyle slightly more lingually positioned than paracone and metacone; paracone and metacone worn but evident; a trace of a small mesostyle is observable; anteroloph and posteroloph completely worn, metaloph and protoloph visible. Due to the poor preservation of this specimen, the presence of protoconule and metaconule cannot be observed; three roots.

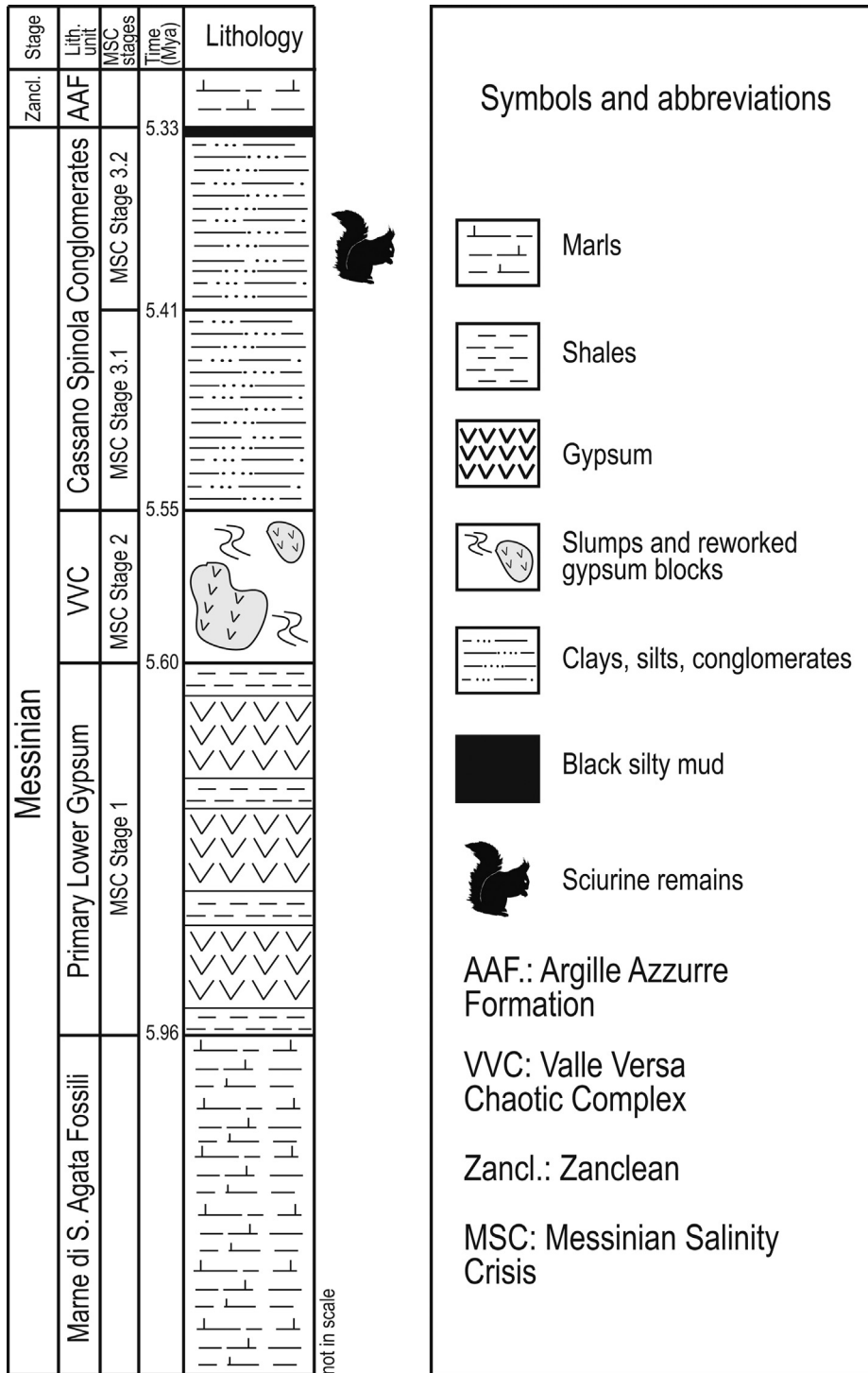


Fig. 3. Synthetic stratigraphic scheme of the Messinian and basal Pliocene succession of the Tertiary Piedmont Basin (TPB). The column represents the succession of the lithostratigraphic units correlated with the different phases of the Messinian Salinity Crisis (MSC) according to [Dela Pierre et al. \(2007, 2011\)](#), [Colombero et al. \(2014b\)](#) and [Roveri et al. \(2014\)](#).

Fig. 3. Schéma stratigraphique synthétique de la succession sédimentaire du Messinien et du Pliocène basal du bassin tertiaire du Piémont (TPB). La colonne représente la succession des unités lithostratigraphiques en corrélation avec les différentes phases de la crise de salinité messinienne (MSC), selon [Dela Pierre et al. \(2007, 2011\)](#), [Colombero et al. \(2014b\)](#) et [Roveri et al. \(2014\)](#).

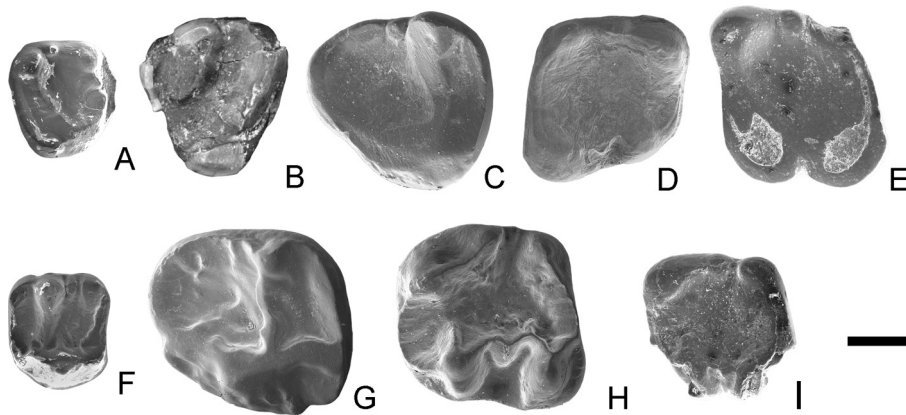


Fig. 4. Dental remains of Sciuridae from Moncucco Torinese. *Sciurus warthae*: A: MGPT-PU136604, right dP4; B: MGPT-PU136591, left P4; C: MGPT-PU128219, right M3; D: MGPT-PU 128221, right m1; E: MGPT-PU136592, left m2. *Hylopetes hungaricus*: F: MGPT-PU136589, left M1. *Pliopetaurista pliocaenica*: G: MGPT-PU 128347, right M3; H: MGPT-PU 128218, left m1. Sciurinae indet.: I: MGPT-PU136590, left m1-2. Bar scale: 1 mm.

Fig. 4. Restes dentaires de Sciuridae de Moncucco Torinese. *Sciurus warthae* : A : MGPT-PU136604, dP4 droite ; B : MGPT-PU136591, P4 gauche ; C : MGPT-PU128219, M3 droite ; D : MGPT-PU 128221, m1 droite ; E : MGPT-PU136592, m2 gauche. *Hylopetes hungaricus* : F : MGPT-PU136589, M1 gauche. *Pliopetaurista pliocaenica* : G : MGPT-PU 128347, M3 droite ; H : MGPT-PU 128218, m1 gauche. Sciurinae indet. : I : MGPT-PU136590, m1-2 gauche. Barre d'échelle : 1 mm.

M3 – (Fig. 4C). Triangular outline with expanded posterior basin; protocone large; paracone high and distinct; mesostyle small and distinct; continuous posterior rim enclosing the posterior basin; worn protoloph connecting protocone to paracone; metaloph absent; anteroloph low; three roots.

m1 – (Fig. 4D). Subtrapezoidal outline; high metaconid and hypoconid; protoconid smaller than hypoconid; evident entoconid; mesoconid small; metastylid partially merged with the metaconid and separated from the entoconid by a notch; metalophid partially observable due to wear, anterolophid low and connected to the anterolingual part of the protoconid; reduced trigonid basin; posterolophid continuous and not posteriorly projected; roots not preserved.

m2 – (Fig. 4E). Sub-rectangular outline; worn tooth especially along the labial margin; postero-lingual corner partially abraded, lacking the enamel; metaconid high; hypoconid and protoconid strongly worn; entoconid partially damaged but suggesting the presence of an angular postero-lingual corner; mesoconid not visible due to wear, metastylid well-developed and only partially connected to the metaconid; metalophid very low due to wear; anterosinusid absent; posterolophid low and lingually connected to hypoconid; four roots.

Remarks. The occurrence of an evident entoconid defining an angular postero-lingual corner in the lower molars is a typical feature of most of the squirrels within the subfamily Sciurinae. In particular, the simple pattern of the lower molars, devoid of marked enamel ornamentation and of evident anterosinusids, is strongly similar to that of extant Sciurini and more specifically, to that of the genus *Sciurus*. The dental remains from Moncucco Torinese are closed in size and morphology to the cheek teeth of the extant Eurasian Red Squirrel *Sciurus vulgaris*. In particular, the dimensions of the studied sample from MCC fall within the size range of *S. vulgaris* from northern Spain (Colección J.M. Rey, Universidad de Santiago de Compostela)

(Cuenca-Bescós, 1988) and are also very similar to those of the studied collection of *S. vulgaris* from northern and central Italy (DBIOS collection) to which differ mainly for the slightly longer M3 (Fig. 5). The morphology of the teeth is strikingly similar and the sample from MCC differs from *S. vulgaris* only in the slightly less pronounced hypoconids of m1, in the more developed and isolated metastylid of m2, and in the slightly narrower M3 that displays a more elongated posterior basin. The evident morphological affinities with extant *Sciurus* support the attribution of the material from Moncucco Torinese to this genus. The Miocene record of the genus *Sciurus* is rather poor. In Asia, very scarce and poor samples of dental remains assigned to undetermined species of *Sciurus* have been found in the Late Miocene of China and Turkey (Bosma et al., 2013; Qiu et al., 2008). In North America, *Sciurus olsoni* from the Late Miocene of Nevada is considered by many authors the oldest species of this genus (Oshida et al., 2009; Pečnerová and Martínková, 2012), representing the earliest reliable record of *Sciurus* in the New World (Emry et al., 2005). The dental remains of this American species are considerably smaller but morphologically roughly similar to those of Moncucco Torinese. The described teeth from Moncucco Torinese represent the only European record of the genus *Sciurus* before the Pliocene. Among the Pliocene and Pleistocene Eurasian species, *Sciurus maltei* from the Early Pliocene of Wölferheim (Germany) and *Sciurus whitei* from the Middle Pleistocene of Norfolk (UK) and Tarkö (Hungary) differ from the material from Moncucco Torinese in their notably smaller size (Dahlmann, 2001). The morphology of the teeth of *Sciurus* described herein fits well with *Sciurus warthae*, a species documented by sparse remains found in the Early Pliocene of Poland (Sulimski, 1964), Germany (Dahlmann, 2001) and in the Pleistocene of Monte La Mesa (Marchetti et al., 2000). *Sciurus* cf. *warthae* has been recorded in other Polish Pliocene localities (Black and Kowalski, 1974), as well as in the Pleistocene of northern Italy (Siori and Sala, 2007). The material from Monte la Mesa is nearly identical

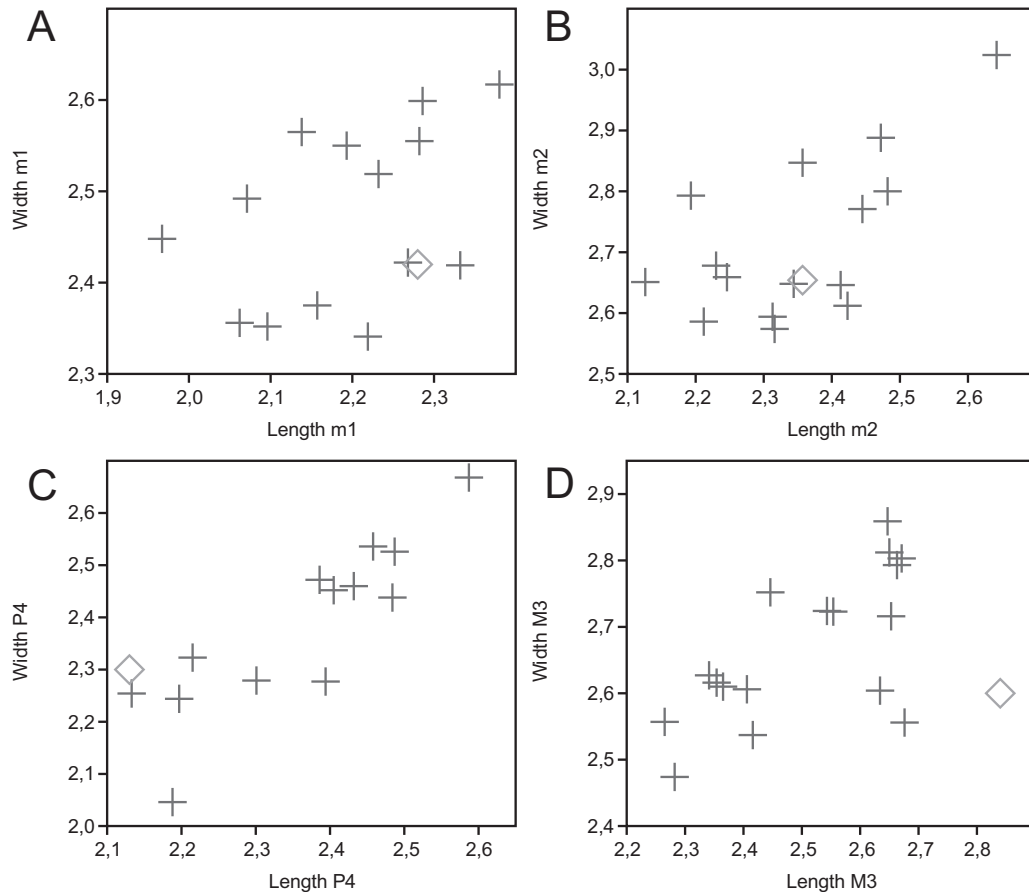


Fig. 5. Scatter diagrams of Width/Length ratio of some dental elements of extant *Sciurus vulgaris* (crosses) from northern and central Italy (DBIOS collection) and *Sciurus warthae* (diamonds) from MCC. A: W/L of m1; B: W/L of m2; C: W/L of P4; D: W/L of M3.

Fig. 5. Diagrammes de dispersion du rapport largeur/longueur de quelques éléments dentaires de *Sciurus vulgaris* (croix) de l'Italie septentrionale et centrale (collection DBIOS) et *Sciurus warthae* (diamants) du MCC. A : W/L de m1 ; B : W/L de m2 ; C : W/L de P4 ; D : W/L de M3.

to that from Moncucco Torinese. The overall size of the specimens from Moncucco Torinese is very similar to or slightly smaller than that of *S. warthae* from its type population of Weże 1, Poland, and other localities (Dahlmann, 2001; Marchetti et al., 2000; Sulimski, 1964).

Sciurus warthae from Moncucco Torinese represents the earliest European record of *Sciurus*. Sulimski (1964) indicated that *S. warthae* differs from *S. vulgaris* for the presence of four roots in the m3, remarkably shorter diastema, large and solid cusps, and greater overall dimensions. However, the dimensions of *S. vulgaris* are very similar to those reported for the known specimens of *S. warthae* (see Fig. 5 and data in Sulimski, 1964; Black and Kowalski, 1974; Cuenca-Bescós, 1988; Dahlmann, 2001; Marchetti et al., 2000) and the cusps of *S. vulgaris* are as large and solid as in *S. warthae*. Our comparative observations revealed that this species is very close to *S. vulgaris*, suggesting that it pertains to the same evolutionary lineage. In particular, lower molars of *S. warthae* are remarkably similar to those of *S. vulgaris*, even if they differ in having a less labially extended hypoconid in the m1 and slightly more distinct metastylid in the m2. The P4 presents a triangular outline and a parastyle slightly more lingually placed

than paracone and metacone, a morphological pattern that is can be also found in *S. vulgaris*. Moreover, the mesostyle present in the single M3 from Moncucco Torinese is also observed in some specimens of *S. vulgaris*. Finally, in many unworn upper cheek teeth of *S. vulgaris*, the lingual wall of the protocone displays a peculiar slight enamel ornamentation consisting of shallow but dense small pits associated to a rugose surface (Fig. 6A), that are also documented in unworn specimens of *S. warthae* (e.g., Dahlmann, 2001).

As far as concerns the phylogenetic history of extant species of *Sciurus*, Mercer and Roth (2003) demonstrated that the earliest divergence within this genus occurred 8.6 ± 1.3 Ma, giving rise to the Eurasian lineage including *S. vulgaris*. More recent molecular analyses based on some extant species of Sciurini (Oshida et al., 2009; Pečnerová and Martínková, 2012; Villalobos and Gutierrez-Espeleta, 2014) suggested a basal divergence of the “*S. vulgaris* clade”, followed by a colonization of the New World that led to the origin of the extant North American and Neotropical lineages whose speciation took place during the Pliocene-Pleistocene (Oshida et al., 2009). The close relationship between *S. vulgaris* and *S. warthae* interpreted on the basis of some shared morphological features, and

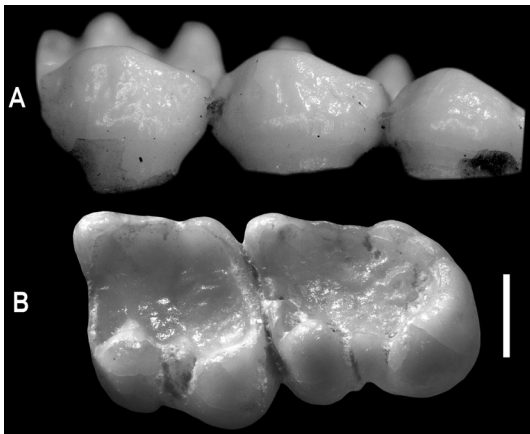


Fig. 6. Enamel ornamentation in molars of *Sciurus vulgaris*. A: lingual view of the left upper molar row. Rugose enamel associated to small and dense pits can be observed on the protocone walls of M1, M2 and M3 (specimen DBIOS 4995 AC from Piedmont, northern Italy). B: occlusal view of unworn left m2 and m3. Wrinkles, moderately developed crevules and rugosity can be observed on the enamel surface (specimen DBIOS 4986 AC, Veneto, northern Italy). Bar scale: 1 mm.

Fig. 6. Ornementations d'émail de dents de *Sciurus vulgaris*. A : Vue linguale de la rangée des molaires supérieures gauches. De l'émail rugueux, associé à des cavités petites et denses, peut être observé sur le bord linguale de protocône de M1, M2 et M3 (spécimen DBIOS 4995 AC, Piémont, Nord de l'Italie). B : vue occlusale de m2 et m3 gauches non usées. Des ondulations, des crénelures moyennement développés et une certaine rugosité peuvent être observées à la surface de l'émail (spécimen DBIOS 4986 AC, Vénétie, Nord de l'Italie). Barre d'échelle : 1 mm.

the Messinian report of *S. warthae* at Moncucco Torinese strongly support the hypothesis of a Late Miocene divergence of the “*S. vulgaris* clade”. However, the occurrence of *S. olsoni* in the early Late Miocene of North America (Clarendonian, approximately 9.8 Ma) (Emry et al., 2005) and some sparse remains assigned to the genus *Sciurus* in the Miocene of Asia (Bosma et al., 2013; Qiu et al., 2008) concur to indicate that the early evolutionary history of tree squirrels is rather complicated, and a North American origin of *Sciurus* cannot be definitely excluded.

Tribe Pteromyini Brandt, 1855

Genus *Hylopetes* Thomas, 1908

Hylopetes hungaricus (Kretzoi, 1959)

Referred material and measurements: a left M1 (MGPT-PU 136589, L: 1.49–W: 1.68)

Description

M1 – (Fig. 4F). Moderately worn tooth, subquadratic in outline; evident rugose enamel absent; slight wrinkles and deep short valleys developed on the walls of the lobes; distinct mesostyle, strongly developed parastyle; a short anterior accessory loph develops between anteroloph and protoloph; protolophule moderately developed; mesoloph weak; contacts of protoloph and metaloph with protocone characterized by marked constrictions; anteroloph and protoloph parallel to each other and orthogonal to endoloph; metaloph slightly oblique due to the posterior position of the metacone with respect to the protocone; sinuous endoloph with distinct constriction in front of the quite well-developed anteroconule; protocone massive

and high; endoloph posteriorly thickened indicative of a small hypocone; paracone very robust; metacone slightly smaller than paracone; posteroloph worn and low. A single root preserved.

Remarks. The single upper molar described above pertains to a small sciurid characterized by short accessory lobes and very slight wrinkles associated to a rather distinct mesostyle, well-developed parastyle, quadratic outline and presence of constrictions on protoloph and metaloph. These features are indicative of *Hylopetes*, a genus of flying squirrel today widespread in South-East Asia with nine species (Thorington et al., 2012). As far as concerns the Late Miocene European pteromyin squirrels of Europe, *Pliopetaurista*, *Miopetaurista* and *Albanensia* clearly differ from the tooth from Moncucco Torinese due to their peculiar labyrinthic aspect, and larger size (Daxner-Höck and Mein, 1975; De Bruijn, 1995; Mein, 1970), *Forsythia* lacks a mesostyle (Mein, 1970), and *Blackia* lacks accessory lobes and protolophule, a well-developed mesostyle, constrictions on protoloph and metaloph, and exhibits a less antero-posteriorly extended lingual margin (Daxner-Höck, 1975, 2004; Mein, 1970). Some small-to-medium sized species of sciurids from the Neogene of Europe have been assigned to the flying squirrel *Neopetes* or *Hylopetes*, including *Neopetes hoeckarum*, *Hylopetes debruijini*, *Hylopetes macedoniensis*, *Hylopetes magistri* and *Hylopetes hungaricus*. *Neopetes hoeckarum* represents the earliest record of this group in Eurasia and its biochronological range extends from MN4 (late Early Miocene) to MN11 (Late Miocene) (De Bruijn, 1998; Daxner-Höck, 2004). This taxon differs from *Hylopetes* by lacking the accessory lobes and protolophule and having less distinct and lower cusp(id)s. *Hylopetes debruijini* is known from the Middle Miocene of France (?MN6–MN7) (Mein and Ginsbourg, 2002). This primitive species exhibits a large size, anterior accessory loph absent, protolophule absent or poorly developed and constrictions on protoloph and metaloph absent. *Hylopetes macedoniensis* is known from the Late Miocene of the Eastern Mediterranean in Greece (Maramena, MN13) and Turkey (Düzayla, MN10–12) (Bosma et al., 2013; Bouwens and De Bruijn, 1986; De Bruijn, 1995). The upper teeth of *H. macedoniensis* differ from the single tooth of Moncucco Torinese in the slightly larger size, less developed protolophule, smaller parastyle, and in lacking anterior accessory lobes between anteroloph and protoloph. *Hylopetes magistri*, originally described as *Hylopetes debruijini* (see Reumer and Van den Hoek Ostende, 2003 and Van den Hoek Ostende and Reumer, 2011) is a sciurine recovered in the Pleistocene of Tegelen, The Netherlands. Colombero et al. (2014b) proposed that this species does not pertain to the genus *Hylopetes* and should be assigned to the genus *Sciurus*. They observed that the lower molars of this taxon are devoid of the typical morphological features of *Hylopetes* such as deep anterosinusids, distinct anteroconulids, posteriorly projected posterolophids and high and distinct labial cuspids (see Chaimanee, 1998; Ellerman, 1940). Moreover, the upper molars from Tegelen lack the accessory lobes and the protolophules that can be observed in *Hylopetes* and the constrictions that are always present in metalophes and common in protolophes of *Hylopetes*. The presence

of rare and barely observable enamel wrinklings as those described by Reumer and Van den Hoek Ostende (2003) in *H. magistri* is not a valid criterion to distinguish flying and tree squirrels (Thorington et al., 2005). As a matter of fact, even if enamel ornamentations are usually more common and developed among pteromyins, they can be also observed in sciurins, for example in the genus *Sciurus* where pits and enamel crenulations can be observed in unworn lower molars and in the lingual wall of the protocones of *Sciurus vulgaris* (Fig. 6). Thorington et al. (2005) noted the presence of pitted enamel in *Sciurus granatensis* and *S. vulgaris*. Finally, it is worth noting that enamel ornamentations is a plesiomorphy, occurring in some early (Eocene to Oligocene) sciurid taxa (Cuenca-Bescós and Canudo, 1992; De Bruijn and Ünay, 1989; Emry and Korth, 2007). Pteromyini and Sciurini are closely related to each other and grouped within the subfamily Sciurinae; they probably diverged in the Early Miocene (Mercer and Roth, 2003), thereby suggesting that the enamel ornamentations cannot be regarded as an apomorphy of Pteromyini. Since the morphological features of *H. magistri* are remarkably close to those of *Sciurus* (see Colombero et al., 2014b) we tentatively assign this species to *Sciurus*. *Hylopetes hungaricus* is a very rare species known only from sparse remains from the Pliocene (MN14–MN15) of central Europe (Black and Kowalski, 1974; Kretzoi, 1959, 1962; Mörs et al., 1998; Sulimski, 1964). *Hylopetes* cf. *hungaricus* has been also reported in the early Late Miocene (MN10–MN11) of Austria (Daxner-Höck, 1975, 2004), Late Miocene (MN13) of Greece (Bosma et al., 2013), and in the Pliocene (MN15) of Germany (Dahlmann, 2001). The morphology and the size of the tooth from Moncucco Torinese described herein fit well with those of the M1-2 of *H. hungaricus* from the Pliocene of Poland (Black and Kowalski, 1974), and Germany (Mörs et al., 1998) and also with those of *H. cf. hungaricus* from the Pliocene of Wölfersheim, Germany (Dahlmann, 2001). In particular, the short anterior accessory loph is characteristic of the upper molars of these taxa. The size and the morphology of the tooth from Moncucco Torinese are also similar to those of the early Late Miocene (MN10–MN11) specimens from Schernham and Kohfidisch identified as *H. cf. hungaricus* (Daxner-Höck, 1975, 2004) that solely differ in lacking the anterior accessory lophes. Therefore, morphological and biometrical evidences indicate that the single M1 from Moncucco Torinese described herein can be assigned to *H. hungaricus*. A single m1 from the locality of Brisighella 6 (Latest Miocene, Monticino Quarry, central Italy) was identified as *Hylopetes* sp. by De Giuli (1989). This tooth can be tentatively assigned to *H. hungaricus* based on its morphology and the small size that clearly differentiate it from the coeval *H. macedoniensis*. *Hylopetes hungaricus* was originally described as *Pliopetes hungaricus* and successively transferred to *Hylopetes* by Van de Weerd (1979). Such a generic assignment is justified by the morphological features of the upper teeth that are characteristic of the genus *Hylopetes*. Moreover, the lower molars of *H. hungaricus* display marked anterosinusids (Kretzoi, 1962) that are also usually well-developed in extant *Hylopetes* (Chaimanee, 1998; Colombero et al., 2014b; Ellerman, 1940). The morphology and dimensions of *H.*

hungaricus are notably similar to those of the Pleistocene record of the extant Red-checked flying squirrel *Hylopetes spadicus* from Thailand, a species currently widespread in south-east Asia (Chaimanee, 1998). The fossil record of *H. spadicus* dates back to the Late Pliocene (Chaimanee, 1998), suggesting that a close relationship between these two species cannot be excluded.

Genus *Pliopetaurista* Kretzoi, 1962

Pliopetaurista pliocaenica (Depéret, 1897)

Referred material and measurements: a right M3 (MGPT-PU 128347, L: 2.84–W: 2.64); a left m1 (MGPT-PU 128218, L: 2.77–W: 2.51)

Description

M3 – (Fig. 4G). Subovoid outline with lophes and wrinkles providing a labyrinthic aspect to the occlusal surface; protocone rather posterior with respect to protoloph; distinct paracone connected to endoloph by a well-developed protoloph; anteroloph lower than protoloph; anteroconule slightly worn but large, hypocone slightly worn and represented by a marked enlargement of the endoloph; metacone represented by a slight and barely observable enlargement of the posteroloph; metaloph and metaconule absent.

m1 – (Fig. 4H). Subquadratic outline with lophids and wrinkles providing a labyrinthic aspect to the occlusal surface; protoconid and hypoconid well-developed, metaconid high, entoconid small but distinct; well-developed anterolophid connecting protoconid and metaconid; metalophid very short and interrupted, trigonid basin large, long posterior arm of the metaconid ending in a small metastylid; deep notch between the metastylid and the entoconid; posterolophid feebly enlarged near the hypoconid, suggesting the occurrence of a minuscule hypoconulid; distinct mesoconid.

Remarks. The teeth documented herein can be assigned to *Pliopetaurista* due to the typical labyrinthic morphology of the occlusal surface associated to a short hypolophid in the lower molar and the absence of metaloph in the M3. Size and morphological patterns of the molars from Moncucco Torinese are indicative of *Pliopetaurista pliocaenica*. In particular, the presence of a hypocone in the M3 and a very reduced metalophid are indicative of this taxon. As a matter of fact, the very similar *Pliopetaurista dehneli* displays less developed or absent hypocones in upper molars and slightly more developed metalophids (Mein, 1970). The size of the specimens from Moncucco Torinese is intermediate between the mean values of *Pliopetaurista dehneli* and *P. pliocaenica*. The former species is common in the Early Pliocene of central and eastern Europe (Mein, 1970; Sulimski, 1964), and has also been reported close to the Mio-Pliocene boundary at Maramena and Kessani (De Bruijn, 1995; Vasileiadou et al., 2012); *P. pliocaenica* ranges chronologically from the Latest Miocene (in Spain; García-Alix et al., 2007) to the Plio-Pleistocene (in western and central Europe; Adrover et al., 1993; Black and Kowalski, 1974; Mein, 1970; Minwer-Barakat et al., 2012; Mörs et al., 1998). *Pliopetaurista kollmanni* (Late Miocene) and *Pliopetaurista bressana* (Middle to Late Miocene) from central Europe are smaller with less pronounced

ridges and tubercles (Daxner-Höck, 2004; Mein, 1970). *Pliopetaurista rugosa* from the Latest Miocene of Eastern Asia does not have a hypocone also displaying a thinner endoloph (Qiu, 1991).

Sciurinae indet.

Referred material and measures: a fragmented left m1–2 (MGPT-PU 136590, L: 2.02-W:?)

Description

m1–2 – (Fig. 4I). Fragmented lower molar; protoconid and hypoconid completely abraded; small mesoconid preserved; prominent metaconid; large and cylindrical entoconid; metastylid partially merged with the metaconid and separated from the entoconid by a notch; a shallow flexus corresponding to this interruption can be observed in the lingual outline of the molar; posterolophid continuous; metalophid interrupted before reaching the metaconid; trigonid partially preserved. Roots not preserved.

Remarks. This poorly preserved specimen displays a distinct entoconid defining an angular postero-lingual corner and a rather small mesoconid. A short metalophid, connected with the anterolophid, has been previously reported in the Early Pliocene species *Sciurus maltei* from Wölfersheim (Dahlmann, 2001), while an interrupted metalophid has been observed in the single m1 of *Sciurus anomalus*, the extant Persian Squirrel, from the Greek locality of Notio 1 (Hordijk and De Bruijn, 2009). However, the size of the tooth documented herein is slightly larger than that of *S. maltei* and smaller than *S. anomalus* and *S. warthae* preventing any possible attribution to these taxa. Moreover, this tooth does not belong to *Hylopetes hungaricus*, previously described in this paper, due to the much smaller size of this species. The dimensions of m1–2 of *Hylopetes macedoniensis* from the Late Miocene of Greece (Bouwens and De Bruijn, 1986; De Bruijn, 1995) and Turkey (Bosma et al., 2013) are usually only slightly smaller than those of the specimen from Moncucco Torinese. Conversely, the morphology of the preserved portion of this molar is consistent with that characteristic of *Hylopetes* in some traits such as the distinct entoconid, prominent metaconid, and well-developed metastylid. However, the poorly developed mesoconid is an uncommon feature for *H. macedoniensis*. The described morphological features alone are not fully adequate to conclusively discriminate between *Sciurus* and *Hylopetes*. As a matter of fact, deep anterosinusids associated to variably developed anteroconulids and a posteriorly projected posterolophid are the main distinctive morphological traits of *Hylopetes*. Unfortunately, these features are not preserved in the studied specimen thereby preventing any conclusive and more detailed taxonomic attribution. Due to the morphological and biometrical differences with the sciurid species from MCC described above, this tooth represents an additional indeterminate taxon that is referred to as Sciurinae indet.

5. Discussion

The fossil squirrels described herein provide useful information that improves our knowledge of the rodent

bioevents at the end of the Messinian and, more generally, of the Neogene mammal biochronology of Europe. As previously evidenced by the analysis of fossil mammals from Moncucco Torinese, this locality can be referred to the Late Turolian (MN13) (Alba et al., 2014; Colombero et al., 2014b). As far as the sciurids are concerned, the presence of *H. hungaricus* at Moncucco Torinese is consistent with the broad chronological range of this taxon and *H. cf. hungaricus* that spans from the late Vallesian to the Early Villanyian of central and south-eastern Europe (Daxner-Höck, 2004; Kretzoi, 1962; Mörs et al., 1998). *Pliopetaurista pliocaenica* appeared in south-western Europe during the Late Turolian (MN13), in the Spanish localities of Purcal 25 and 24A (García-Alix et al., 2007, 2008) and it has been successively found in some Ruscinian, Villanyian and Biharian localities of western and central Europe (e.g., Adrover et al., 1993; Black and Kowalski, 1974; García-Alix et al., 2007; Mein, 1970; Minwer-Barakat et al., 2012; Mörs et al., 1998). The occurrence of these taxa at Moncucco Torinese fits well with their known biochronological ranges. The occurrence of *S. warthae*, represents the earliest documented report of the genus *Sciurus* in Europe. This species and *S. cf. warthae* have been also found in some Ruscinian, Villanyian and Biharian localities of Poland, Germany, and Italy (Black and Kowalski, 1974; Dahlmann, 2001; Siori and Sala, 2007; Sulimski, 1964). Tree squirrels of the genus *Sciurus* are extremely rare in the fossil record. High humidity in soil can lead to the corrosion and the breakage of the bones of small mammals (Andrews, 1990). Thus, densely forested areas, the typical habitat of tree squirrels, can be scarcely conducive to the preservation of fossil remains. Tree squirrels were probably less abundant than other rodents in the original biocenoses of Moncucco Torinese, probably representing rare elements of the original mammal communities as similarly hypothesized for other assemblages of fossil rodents (Emry et al., 2005). Moreover, considering the strong importance of nocturnal birds of prey as small mammal bone accumulators (Andrews, 1990) compared to other diurnal predators, the diurnal lifestyle of sciurids of the tribe Sciurini (see Thorington et al., 2012) may represent another factor that contributes to underestimate the abundance of tree squirrel within original rodent communities. As a matter of fact, diurnal predators, including both mammalian and avian taxa, have high corrosive digestive processes that do not favor the conservation of the bones in pellets and scats. On the contrary, in many species of nocturnal birds of prey, the digestion does not or can only partially affect mineralized components such as bones and teeth (Andrews, 1990). Since predation is one of the main cause of death for small mammals and probably the most important single factor that preside over the accumulation of small mammal bones (Andrews, 1989), the digestive processes of predators are among the most important biostratigraphic events that affect the earliest taphonomic phases of the fossilization of the small mammal bones. Moreover, experimental evidences indicate that bones included in pellets and scats of predators are protected from weathering also for a long time (Andrews, 1990), thus increasing the potential of their successful fossilization. However, rather diverse sciurid assemblages, have been found within large rodent samples in fluvial

deposits (Cuenca-Bescós and Canudo, 1992), thus suggesting that inadequate sampling is probably one of the main biases in detecting rare taxa such as tree squirrels. As a matter of fact, the material of *S. warthae* collected at Moncucco Torinese consists of five teeth out of 2800 rodent teeth collected after washing and sieving more than 18 tons of sediments. Therefore, it appears that our knowledge about the evolutionary history of the genus *Sciurus* is negatively affected by paleoecological and taphonomical factors that, together with inadequate sampling, concur to compromise the reconstruction of the evolutionary events of this genus, including diversification and dispersal. Our data clearly indicate that *Sciurus* was already present in Europe in the Messinian, even though an earlier appearance cannot be excluded. The sciurids from the Late Turolian of Moncucco Torinese include some taxa that are also present in the Ruscinian of Europe such as *S. warthae* and *P. pliocaenica*, thereby suggesting that the sciurid communities of central Europe were not affected by any abrupt turnover at the transition between Turolian and Ruscinian. Similar conclusions are also drawn for other rodent taxa such as hystricids, murids, glirids and cricetids since several taxa common in the Early Ruscinian of Europe were already present at the end of the Turolian in NW Italy (Colombero et al., 2013, 2014b).

The scarcity of sciurid fossil remains prevent an accurate analysis of the paleobiogeographic history of this group. *H. hungaricus* (and/or *H. cf. hungaricus*) have been previously found in central, eastern and south-eastern Europe (Dahlmann, 2001; Daxner-Höck, 2004; Kretzoi, 1962; Mörs et al., 1998). The report from Moncucco Torinese and its occurrence at Brisighella expand its paleogeographical range with the inclusion of north-western and central Italy. The occurrence of *P. pliocaenica* at the end of the Messinian in Italy confirms the expansion of this taxon from the Iberian Peninsula to the central-southern regions of Europe, slightly before the Mio/Pliocene boundary (see, e.g., Colombero et al., 2014b; García-Alix et al., 2007, 2008). Finally, the occurrence of *S. warthae* at Moncucco Torinese suggests that the European distribution of this genus expanded at least during the latest part of the Miocene.

Flying squirrels of the genus *Hylapetes* are currently widely distributed in South-East Asia, inhabiting a variety of forested habitats. The morphology of the teeth of *H. hungaricus* seems to indicate a close relationship with *H. spadicus*. This extant species inhabits a variety of closed biotopes including primary forests, as well as degraded and cultivated forests, thereby suggesting a certain degree of environmental tolerance (Thorington et al., 2012). Similar environmental requirements might be hypothesized for *H. hungaricus*. Although *Pliopetaurista* does not have a clearly defined extant relative, it belongs to the tribe Pteromyini, suggesting the presence of some kind of forested areas in the original paleobiotope. *Sciurus warthae* displays a dental morphology strongly reminiscent to that of *S. vulgaris*, the extant Eurasian Red squirrel to which is closely related. *Sciurus vulgaris* is an arboreal species that requires extended forested territories, decreasing in number or even disappearing in highly fragmented habitats. *Sciurus lis*, the Japanese Squirrel and the extant closest relative of *S. vulgaris* is also linked to the presence of primary and secondary

forest. Similar environmental requirements can be confidently assumed also for *S. warthae*.

Remains of flying and tree squirrels are extremely rare in the Upper Miocene deposits of Moncucco Torinese (nine specimens out of more than 2000 dental remains), representing less than 5% of the total amount of recovered rodent teeth. However, they suggest that closed habitats or at least connected forested areas were present at that time in the north-western sectors of Italy. These conclusions are also supported by the occurrence of other arboreal rodents such as glirids, which are rather common at Moncucco Torinese, where are represented by four species (*Eliomys aff. intermedius*, *Glirulus lissiensis*, *Glis minor* and *Muscardinus vireti*) (Colombero et al., 2014b). Strongly humid conditions, however, were not postulated based on the composition of terrestrial gastropods assemblages (Harzhauser et al., 2015) that indicated mostly dry conditions and presence of rocky outcrops associated to rare moist habitats in the original paleobiotope. This view is perfectly consistent with the paleobotanical data that hypothesized the presence of extensive “sub-humid” forests in NW Italy during the latest part of the Messinian (Bertini and Martinetto, 2011).

6. Conclusions

The data reported herein expand our knowledge about the evolutionary history of the genus *Sciurus* supporting the hypothesis that the “*S. vulgaris* clade” arose during the Late Miocene (Mercer and Roth, 2003; Oshida et al., 2009; Pečnerová and Martínková, 2012; Villalobos and Gutierrez-Espeleta, 2014). The material from Moncucco Torinese indicates that the genus *Hylapetes* was widespread in the emerging Italian Peninsula at the end of the Messinian, and that other pteromyine squirrels, such as *P. pliocaenica*, were present in NW Italy slightly before the Pliocene. The squirrel material from Moncucco Torinese documents the first reliable co-occurrence of Sciurini and Pteromyini (*sensu* Steppan et al., 2004) in the Late Miocene of Europe.

Squirrels are extremely fine proxies for paleoecological analyses due to their strict ecological requirements. As demonstrated herein, adequate sampling provided higher probability of detecting the rarest taxa allowing to refine the original paleobiodiversity spectrum, with the inclusion of uncommon and highly informative taxa such as the tree squirrels. As a final note, it is interesting to evidence that the occurrence of tree and flying squirrels in NW Italy strongly supports geochemical and paleontological evidence suggesting that increased humid conditions took place during the Lago-Mare phase at the end of the Messinian Salinity Crisis (Bertini, 2006; Bertini and Martinetto, 2011; Carnevale et al., 2006; Roveri et al., 2014).

Acknowledgments

Fassa Bortolo factory (owner of the gypsum quarry of Moncucco Torinese) and ing. Igor Muller gave substantial support during excavations at Moncucco Torinese. We are grateful to Benedetto Sala (STUM), Claudio Berto (STUM), Maria Stella Siori (DBIOS) and Giovanni Boano (MCCI) for access to fossil and recent material in their care and

hospitality and kindness during our visits. Simona Cavagna (Dipartimento di Scienze della Terra, Torino) helped operating the SEM. Finally, the authors are indebted with Giulio Pavia who organized and led the excavation at Moncucco Torinese, to Giorgia Palaia and Mara Bruno who washed and sorted part of the Moncucco Torinese sediment and to Piero Giuntelli, Marco Pavia and all the others who participated to the excavation campaigns at Moncucco Torinese and Verduno.

The suggestions of the reviewers Raef Minwer-Barakat, Francisco Javier Ruiz-Sanchez and Gloria Cuenca-Bescós and the editorial notes of Lars Van Den Hoek Ostende notably improved our manuscript.

This work was supported by grants MIUR (PRIN 2009MSS9L.002) and grants ex-60% 2014 of the Università degli Studi di Torino.

Appendix 1. List of specimens of Quaternary and extant *Sciurus* species analyzed for comparative purposes

Sciurus vulgaris Linnaeus, 1758

Host Institution: MCCI

Specimens: MCCI 886; MCCI 480

Host Institution: DBIOS

Specimens: Rod 2244; 4995 AC; 4988 AC; 4990 AC; 4985 AC; 4987 AC; 4994 AC; Rod 2243; 507; 4990 AC; 2721 AC; 5917; 4992 AC; 4986 AC; Rod 2245; 10295 DBAU; 2755 CG.

Sciurus carolinensis Gmelin, 1788

Host Institution: MCCI

Specimens: MCCI 755; MCCI 943

Sciurus warthae Sulimski, 1964

Host Institution: STUM

Specimens: MLM0151–MLM0160; MLM1401; MLM1402.

References

- Abbazzi, L., Benvenuti, M., Ceci, E., Esu, D., Faranda, C., Rook, L., Tangocci, F., 2008. The end of the Lago-Mare time in the SE Val d'Aosta Basin (Central Italy): interference between local tectonism and regional sea-level rise. *Geodiversitas* 30, 611–639.
- Adrover, R., Mein, P., Moissenet, E., 1993. Los Sciuridae del Turoliense superior, Rusciniense y Villanyense de la region de Teruel. *Paleontologia i evolució* 26–7, 85–106.
- Alba, D.M., Delson, E., Carnevale, G., Colombero, S., Delfino, M., Giuntelli, P., Pavia, M., Pavia, G., 2014. First joint record of *Mesopithecus* and cf. *Macaca* in the Miocene of Europe. *J. Hum. Evol.* 67, 1–18.
- Andrews, P., 1989. Small mammal taphonomy. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), *European Neogene Mammal Chronology*. NATO ASI Ser. A 180, pp. 487–494.
- Andrews, P., 1990. Owls, caves and fossils: predation, preservation and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-sub-Mendip, Somerset, UK, 1st edition. The Natural History Museum, London.
- Angelone, C., Colombero, S., Esu, D., Giuntelli, P., Marcolini, F., Pavia, M., Trenkwalder, S., Van den Hoek Ostende, L., Zunino, M., Pavia, G., 2011. Moncucco Torinese, a new post-evaporitic Messinian fossiliferous site from Piedmont (NW Italy). *Neues Jahrb. Geol. Paläontol.- Abh* 259, 89–104.
- Bertini, A., 2006. The Northern Apennines palynological record as a contribute for the reconstruction of the Messinian palaeoenvironments. *Sediment. Geol.* 188, 235–258.
- Bertini, A., Martinetto, E., 2011. Reconstruction of vegetation transects for the Messinian-Piacenzian of Italy by means of comparative analysis of pollen, leaf and carpological records. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 304 (3), 230–246.
- Black, C.C., Kowalski, K., 1974. The Pliocene and Pleistocene Sciuridae (Mammalia, Rodentia) from Poland. *Acta Zool. Crac.* 19, 461–486.
- Bosma, A.A., De Bruijn, H., Wessels, W., 2013. Late Miocene Sciuridae (Mammalia, Rodentia) from Anatolia, Turkey. *J. Vert. Palaeontol.* 33, 924–942.
- Bouwens, P., De Bruijn, H., 1986. The flying Squirrels *Hylopetes* and *Petinomys* and their fossil record. *Proc. K. Ned. Akad. van Wet.* B 89, 113–123.
- Bowdich, T.E., 1821. An analysis of the natural classification of mammals-for the use of students and travelers. J. Smith, Paris.
- Brandt, J.F., 1855. Beiträge zur nähern Kenntniss der Säugethiere Russlands. *Kaiserlich. Akad. Wiss. Mem. Math. Phys. Nat.* 7, 1–365.
- Carnevale, G., Caputo, D., Landini, W., 2006. Late Miocene fish otoliths from the Colombacci Formation (Northern Apennines, Italy): Implications for the Messinian 'Lago-mare' event. *Geol. J.* 41, 537–555.
- Casanovas-Vilar, I., Almécija, S., Alba, D.M., 2015. Late Miocene flying squirrels from Can Llobateres 1 (Vallès-Penedès Basin, Catalonia): systematics and palaeobiogeography. *Palaeobiodivers. Palaeoenviro.* 95 (3), 353–372.
- Chaimanee, Y., 1998. Plio-Pleistocene rodents of Thailand. *Thai Stud. Biodivers.* 3, 1–303.
- Colombero, S., Bonelli, E., Kotsakis, T., Pavia, G., Pavia, M., Carnevale, G., 2013. Late Messinian rodents from Verduno (Piedmont, NW Italy): biochronological, palaeoecological and palaeobiogeographic implications. *Geobios* 46, 111–125.
- Colombero, S., Angelone, C., Bonelli, E., Carnevale, G., Cavallo, O., Delfino, M., Giuntelli, P., Mazza, P., Pavia, G., Pavia, M., Repetto, G., 2014a. The Upper Messinian assemblages of fossil vertebrate remains of Verduno (NW Italy): Another brick for a Latest Miocene bridge across the Mediterranean. *Neues Jahrb. Geol. Paläontol.-A.* 272, 287–324.
- Colombero, S., Pavia, G., Carnevale, G., 2014b. Messinian rodents from Moncucco Torinese, NW Italy: palaeobiodiversity and biochronology. *Geodiversitas* 36, 421–475.
- Colombero, S., Pavia, M., Carnevale, G., 2015. Old World porcupine (Rodentia, Hystricidae) remains from the Late Messinian of Piedmont, NW Italy. *Riv. Ital. Paleontol. Stratigrafia* 2, 243–253.
- Cuenca-Bescós, G., 1988. Revision de los Sciuridae del Arago-niense y del Ramblense en la fosa de Calatayud-Montalbán. *Scripta Geol.* 87, 1–116.
- Cuenca-Bescós, G., Canudo, J.L., 1992. Los Sciuridae (Rodentia, Mammalia) del Oligoceno inferior de Montalbán y Olalla (Teruel, España). *Discusión sobre el origen de los esciúridos*. *Bol. R. Soc. Esp. Hist. Nat. (Sec. Geol.)* 87, 155–169.
- Dahlmann, T., 2001. Die Kleinsäuger der unter-pliozänen Fundstelle Wölfersheim in der Wetterau (Mammalia: Lipotyphla, Chiroptera, Rodentia). *Cour. Forsch. Inst. Senckenberg.* 227, 1–129.
- Daxner-Höck, G., 1975. Sciuridae aus dem Jungtertiär von Österreich. *Paläontol. Z.* 49, 56–74.
- Daxner-Höck, G., 2004. Flying Squirrels (Pteromyinae, Mammalia) from the Upper Miocene of Austria. *Ann. Naturhist. Mus. Wien* A 106, 387–423.
- Daxner-Höck, G., Mein, P., 1975. Taxonomische Probleme um das Genus *Miopetaurista* Kretzoi, 1962 (Fam. Sciuridae). *Paläontol. Z.* 49, 75–77.
- De Bruijn, H., 1995. 8– Sciuridae, Petauristidae and Eomyidae. in Schmidt-Kittler, N. (Ed.) *The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Rusciniian boundary (Neogene)*. *Münch. Geowiss. Abh.* A. 28, 87–102.
- De Bruijn, H., 1998. Vertebrates from the Early Miocene lignite deposits of the open-cast mine Oberdorf (western Styrian Basin, Austria): 6. Rodentia I (Mammalia). *Ann. Naturhist. Mus. Wien* A 99, 99–137.
- De Bruijn, H., Ünay, E., 1989. Petauristinae (Mammalia, Rodentia) from the Oligocene of Spain, Belgium, and Turkish Thrace. *Ser. Nat. Hist. Mus. Los Angel. Cty* 33, 139–145.
- De Giuli, C., 1989. The Rodents of the Brisighella Latest Miocene fauna. *Boll. Soc. Paleontol. Ital.* 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 the Torino Hills (Tertiary Piedmont Basin, northwestern Italy). *Bull. Geol. Soc. Am.* 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. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310, 238–255.
- Depéret, C., 1897. Les animaux pliocènes du Rousillon. *Mem. Soc. Geol. France Paleontol.* 3, 1–198.
- Ellerman, J.R., 1940. The Families and Genera of Living Rodents, vol. 1. Rodents other than Muridae. British Museum of Natural History, London.

- Emry, R.J., Thorington, R.W., 1982. Descriptive and comparative osteology of the oldest fossil squirrel, *Protosciurus* (Rodentia: Sciuridae). *Smithson. Contrib. Paleobiol.* 47, 1–35.
- Emry, R.J., Korth, W.W., 2007. A new genus of squirrel (Rodentia, Sciuridae) from the mid-Cenozoic of North America. *J. Vert. Paleontol.* 27, 693–698.
- Emry, R.J., Korth, W.W., Bell, M.A., 2005. A tree squirrel (Rodentia, Sciuridae, Sciurini) from the Late Miocene (Clarendonian) of Nevada. *J. Vert. Paleontol.* 25, 228–235.
- Fischer, G., 1817. *Adversaria Zoologica. Mémoires de la Société Impériale des Naturalistes de Moscou.*
- García-Alix, A., Minwer-Barakat, R., Martín Suárez, E., Freudenthal, M., 2007. New data on Mio-Pliocene Sciuridae (Rodentia, Mammalia) from southern Spain. *C. R. Palevol* 6, 269–279.
- García-Alix, A., Minwer-Barakat, R., Martín, J.M., Martín Suárez, E., Freudenthal, M., 2008. Biostratigraphy and sedimentary evolution of Late Miocene and Pliocene continental deposits of the Granada Basin (southern Spain). *Lethaia* 41, 431–446.
- Gmelin, J.F., 1788. *Caroli a Linné systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima tertia, aucta, reformata. G. E. Beer, Lipsiae.*
- Harzhauser, M., Neubauer, T.A., Georgopoulou, E., Esu, D., D'Amico, C., Pavia, G., Giuntelli, P., Carnevale, G., 2015. Late Messinian continental and Lago-Mare gastropods from the Tertiary Piedmont Basin (NW Italy). *Boll. Soc. Paleontol. Ital.* 54, 1–53.
- Hordijk, K., De Bruijn, H., 2009. The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). *Hell. J. Geosci.* 44, 21–103.
- Kretzoi, M., 1959. Insectivoren, Nagetiere und Lagomorphen der jüngstpliozänen Fauna von Csarnóta im Villányer Gebirge (Sudungarm). *Vertebr. Hung.* 1, 237–246.
- Kretzoi, M., 1962. Fauna und faunenhorizont von Csarnóta. *Jahresber. Ung. Geol. Anst.* 1959, 297–396.
- Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentius Salvius, Stockholm.*
- Lozar, F., Clari, P., Dela Pierre, F.D., Natalicchio, M., Bernardi, E., Violanti, D., Costa, E., Giardino, M., 2014. Virtual Tour of Past Environmental and Climate Change: the Messinian Succession of the Tertiary Piedmont Basin (Italy). *Geoheritage* 7, 47–56.
- Marchetti, M., Parolin, K., Sala, B., 2000. The Biharian fauna from Monte La Mesa. *Acta Zool. Crac.* 43, 79–105.
- Marivaux, L., Vianey-Liaud, M., Jaeger, J.J., 2004. High-level phylogeny of Early Tertiary rodents: dental evidence. *Zool. J. Linn. Soc.* 142, 105–134.
- Mein, P., 1970. Les Sciuroptères (Mammalia, Rodentia) néogènes d'Europe occidentale. *Geobios* 3, 7–77.
- Mein, P., Ginsbourg, L., 2002. Sur l'âge relatif des différents dépôts karstiques miocènes de La Grive-Saint-Alban (Isère). *Cah. Sci. Mus. Hist. Nat. Lyon* 2, 7–47.
- Mercer, J.M., Roth, V.L., 2003. The effects of Cenozoic global change on squirrel phylogeny. *Science* 299, 1568–1572.
- 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.
- Mörs, T., von Koenigswald, W., von der Hocht, F., 1998. Rodents (Mammalia) from the Late Pliocene Reuver Clay of Hambach (Lower Rhine Embayment, Germany). *Meded. Ned. Inst. Toegep. Geowet. TNO* 60, 135–160.
- Oshida, T., Arslan, A., Noda, M., 2009. Phylogenetic relationships among the Old World *Sciurus* squirrels. *Folia Zool.* 58, 14–25.
- Pečnerová, P., Martínková, N., 2012. Evolutionary history of tree squirrels (Rodentia, Sciurini) based on multilocus phylogeny reconstruction. *Zool. Scr.* 41, 211–219.
- Qiu, Z.D., 1991. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. 8. *Sciuridae* (Rodentia). *Senckenberg. Lethaia* 71, 223–255.
- Qiu, Z.D., Zheng, S.H., Zhang, Z.Q., 2008. Sciurids and zapodids from the Late Miocene Bahe Formation, Lantian, Shaanxi. *Vert. Palasiatica* 46, 111–123.
- Reumer, J.W.F., Van den Hoek Ostende, L.W., 2003. *Petauristidae* and *Sciuridae* (Mammalia, Rodentia) from Tegelen, Zuurland, and the Maasvlakte (the Netherlands). In: Reumer, J.W.F., Wessels, W. (Eds.), *Migration and distribution of Neogene mammals in Eurasia, a volume in honour of Hans De Bruijn, 10. Deinsea*, pp. 455–467.
- Rook, L., Gallai, G., Torre, D., 2006. Lands and endemic mammals in the Late Miocene of Italy: constraints for paleogeographic outlines of Tyrrhenian area. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 263–269.
- Roveri, M., Lugli, S., Manzi, V., Gennari, R., Schreiber, B.C., 2014. High-resolution strontium isotope stratigraphy of the Messinian deep Mediterranean basins: Implications for marginal to central basins correlation. *Mar. Geol.* 349, 113–125.
- 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.
- Steppan, S.J., Adkins, R.M., Anderson, J., 2004. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. *Mol. Phylog. Evol.* 53, 533–553.
- Sulimski, A., 1964. Pliocene lagomorpha and Rodentia from Weże 1 I (Poland). *Acta Paleontol. Pol.* 9, 149–240.
- Thomas, O., 1908. The genera and subgenera of the *Sciuropterus* group with description of three new species. *Ann. Mag. Nat. Hist.* 8, 1–8.
- Thorington Jr., R.W., Pitassy, D., Jansa, S.A., 2002. Phylogenies of flying squirrels (Pteromyiinae). *J. Mammal. Evol.* 9, 99–135.
- Thorington Jr., R.W., Schennum, C.E., Pappas, L.A., Pitassy, D., 2005. The difficulties of identifying flying squirrels (Sciuridae: Pteromyini) in the fossil record. *J. Vert. Paleontol.* 25, 950–961.
- Thorington Jr., R.W., Koprowski, J.L., Steele, M.A., Whetton, J.F., 2012. *Squirrels of the World*. Johns Baltimore, Maryland, Hopkins University Press.
- Van de Weerd, A., 1979. Early Ruscian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proc. K. Ned. Akad. Wet.* B 82, 127–170.
- Van den Hoek Ostende, L.W., Reumer, J.W.F., 2011. *Hylopetes magistri*, new name for *Hylopetes debruijni* Reumer & Van den Hoek Ostende, 2003, preoccupied. *J. Vert. Paleontol.* 31, 928.
- Vasileiadou, K.V., Konidaris, G., Koufos, G.D., 2012. New data on the micromammalian locality of Kessani (Thrace, Greece) at the Mio-Pliocene boundary. *Palaeobiodivers. Palaeoenviron.* 92, 211–237.
- Villalobos, F., Gutierrez-Espeleta, G., 2014. Evolución de las ardillas arborícolas mesoamericanas (Rodentia: Sciuridae): un análisis filogenético molecular. *Rev. Biol. Trop.* 62, 649–657.