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New data on Late Pleistocene and Holocene red squirrel, *Sciurus vulgaris* L., 1758, in Italy

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Abstract

The genus *Sciurus* is known since Late Miocene in the European fossil record, but it is quite rare. Fossil remains of squirrels occur in relatively few sites and generally with very few specimens, sometimes only one or two teeth. Recent finds of a *Sciurus vulgaris* mandible from Grotta Mora Cavorso (Latium), and the reanalysis of the red squirrel remains from the Caverna delle Arene Candide (Liguria), the Riparo Soman (Veneto) and the Grotta del Santuario della Madonna (Calabria) provide new data and insights on the change in size of the rodent and on its geographic and ecological distribution in the Pleistocene and Holocene of Italy.

The study of food preferences of the current red squirrel predators provides solid comparative data to measure the relative rarity of the bone remains found in the Late Pleistocene and Holocene paleontological deposits and archaeological contexts. Taphonomic analysis, particularly on the latest Pleistocene remains from the Caverna delle Arene Candide, sheds light on the alimentary and cultural use of the rodent made by prehistoric man, allowing to say that so far the human contribution to the accumulation of his bones has been underestimated.

Keywords

Late Pleistocene, Holocene, *Sciurus vulgaris*, Italy, Taphonomy, Palaeobiogeography, Palaeoecology, Human activity.

Riassunto

Nuovi dati sullo scoiattolo comune, *Sciurus vulgaris* L., 1758, nel Pleistocene Superiore e nell'Olocene in Italia. - Il genere *Sciurus* è conosciuto nel record fossile europeo fin dal Miocene Superiore, ma è piuttosto raro. Fossili di scoiattoli compaiono in relativamente pochi siti e generalmente con pochissimi resti, talvolta solo uno o due denti. Il recente rinvenimento di una mandibola di *Sciurus vulgaris* a Grotta Mora Cavorso (Lazio) ed il riesame dei resti di scoiattolo comune della Caverna delle Arene Candide (Liguria), del Riparo Soman (Veneto) e di Grotta del Santuario della Madonna (Calabria) forniscono nuovi dati e spunti di riflessione sulla variazione di taglia del roditore e sulla sua distribuzione geografica ed ecologica nel Pleistocene Superiore e nell'Olocene in Italia.

Lo studio delle preferenze alimentari degli attuali predatori dello scoiattolo fornisce solidi indizi per capire la relativa rarità dei resti rinvenuti nei giacimenti paleontologici e nei contesti archeologici pleistocenici e olocenici. L'analisi tafonomica, particolarmente dei resti tardopleistocenici della Caverna delle Arene Candide, getta luce sull'uso alimentare e culturale del roditore nella preistoria, permettendo di affermare che finora è stato sottovalutato il contributo umano all'accumulo dei suoi resti ossei.

Parole chiave

Pleistocene Superiore, Olocene, *Sciurus vulgaris*, Tafonomia, Paleobiogeografia, Paleoecologia, Attività umane.

1. INTRODUCTION

A mandible of red squirrel recently found at Grotta Mora Cavorso (Simbruini Mountains, Latium, Central Italy)

provided new data and insights on the geographical distribution and ecology of this species in the Late Pleistocene and Holocene in Italy. This find stimulated the reanalysis of the red squirrel remains from the

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Fig. 1: Location of the sites. AC: Caverna delle Arene Candide; So: Riparo Soman; MC: Grotta Mora Cavorso; SM: Grotta del Santuario della Madonna.

Caverna delle Arene Candide (west coast of Liguria, Northern Italy), the Riparo Soman (Lessini Mountains, Veneto, Northern Italy) and the Grotta del Santuario della Madonna (north Tyrrhenian coast of Calabria, Southern Italy) (Fig. 1).

The genus *Sciurus* Linnaeus, 1758 is currently divided into 28 species spread in the Palearctic, Nearctic and Neotropical regions (Thorington & Hoffmann, 2005). In Italy two species are currently present: the red squirrel, *Sciurus vulgaris* Linnaeus, 1758, and the gray squirrel, *Sciurus carolinensis* Gmelin, 1788; the latter is an allochthonous species native to North America that has been introduced in some localities of north-western Italy after the Second World War (Bertolino & Genovesi, 2008; Wauters & Martinoli, 2008). *S. vulgaris* is a medium-sized rodent that has a body length of about 198-250 mm with an additional 170-225 mm for the long and bushy tail; it is diurnal in habits, active throughout the whole year (it does not hibernate in winter), and it feeds mainly on seeds of trees; even though the vegetable food is predominant in its diet, it also eats grubs, insects, eggs and nestlings; predators of this species include mammalian carnivores, such as mustelids, wild and domestic cats, dogs and foxes, and birds of prey, such as Falconiformes and great-sized Strigiformes (Wauters & Martinoli, 2008 with references). *S. vulgaris* is an arboreal species that lives and nests in coniferous forests and deciduous woods, and also occurs in mixed forest, parks, gardens, and small conifer stands of Europe and

northern Asia, from the Iberian Peninsula and the Britain Isles, through continental Europe, Russia, Mongolia, and northwest and northeast China to the Pacific islands of Sakhalin (Russia) and Hokkaido (Japan) (Shar *et al.*, 2008). In Italy the species is spread both in the Alpine arc and in the peninsula, but it is not present in the islands (Wauters & Martinoli, 2008). Today it is also found in the areas surrounding the analyzed sites, Ligurian Alps (Borgna, 2014), Lessini Mountains (Chiesura Corona, 1995), Simbruini Mountains (Capizzi, 2009) and north-western Calabria (Rima *et al.*, 2008).

This paper describes the red squirrel remains from Caverna delle Arene Candide, Riparo Soman, Grotta Mora Cavorso and Grotta del Santuario della Madonna, and compares them with some fossil and extant squirrels. This work also aims to provide an overview on the occurrences of Late Pleistocene and Holocene fossil remains in Italy.

2. BRIEF HISTORY OF SQUIRRELS IN THE WESTERN PALEARCTIC

The fossil record of the genus *Sciurus* is not abundant and the relatively small number of faunal assemblages in which it occurs generally contains few specimens, sometimes only one or two molars. Few species of fossil *Sciurus* from Europe have been described. One of these, *Sciurus warthae* Sulimski, 1964 was described on the basis of a right lower jaw with incisor and alveoli of p4-m3, and a dozen of detached premolars and molars of both upper and lower jaws from the Late Pliocene locality of Węże 1, Działoszyn (Poland) (Sulimski, 1964). Specimens referred to this species (sometimes cf. or aff.) have been identified in some latest Miocene, Pliocene and Early Pleistocene localities of Poland (Kowalski, 1964; Black & Kowalski, 1974), Germany (Dahlmann, 2001), Hungary (Jánossy, 1972) and Italy (Marchetti *et al.*, 2000; Siori & Sala, 2007; Bellucci *et al.*, 2014; Colombero *et al.*, 2014). In the Pliocene of lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece), instead, *Sciurus anomalus* Gmelin, 1778 occurs (Hordijk & Bruijn, 2009); this is a species now widespread in extreme southeast Europe and southwest Asia, and that occurs also in the islands of Lesbos (Greece) and Gökçeada (Turkey) (Yigit *et al.*, 2008). This taxon was found (sometimes cf.) also in some Early Pleistocene sites of Greece (Meulen & Kolschoten, 1986; Meulen & Doukas, 2001, and references therein) and several Middle and Late Pleistocene sites from the Near East (e.g., Hooijer, 1961; Heller, 1970; Tchernov, 1988; Belmaker & Hovers, 2011; Marder *et al.*, 2011; Maul *et al.*, 2011).

Another species is *Sciurus whitei* Hinton, 1914, considered the direct ancestor of *S. vulgaris* by Jánossy (1962). This species was described on the basis of a single P4 from the Upper Freshwater-Bed at West

Runton, Norfolk (Britain). The author has commented on this P4: “It differs importantly from the P4 of *S. vulgaris*, and indicates a species which, when more fully known, will probably not be able to find a place within the genus *Sciurus* as restricted by modern mammalogists” (Hinton, 1914). For this reason, already Kurtén (1968) doubted the validity of this species and recently *S. whitei* was considered as a probable conspecific with *S. vulgaris* by Kowalski (2001) and an ill-defined species by Reumer & Hoek Ostende (2003). Nevertheless this name is sometimes used to indicate small-sized squirrel remains from the Early Pleistocene and early Middle Pleistocene, e.g. Tarkő-Felsnische and Újlaki-hegy (Hungary) (Jánossy, 1962; Jánossy & Topál, 1990), Untermassfeld (Germany) (Maul, 2001) and West Runton (Britain) (Maul & Parfitt, 2010). Moreover, have been attributed to *Sciurus* sp. several fossil remains referred to Late Pliocene, Early Pleistocene and early Middle Pleistocene of Spain (Cuenca-Bescós & García, 2007; Martínez *et al.*, 2010), France (Chaline, 1972), Britain (Stuart, 1982; Parfitt, 1999), Netherlands (Reumer & Hoek Ostende, 2003), Germany (Kofschoten & Turner, 1996), Poland (Kowalski, 1958; Bosák *et al.*, 1982), Hungary (Jánossy, 1972, 1978), Croatia (Paunovic & Rabeder, 1996), former Czechoslovakia, Austria, and Romania (Kowalski, 2001 with references), Slovenia (Aguilar *et al.*, 1998), Bulgaria (Popov, 2004), Greece (Kuss & Storch, 1978) and Italy (Kotsakis *et al.*, 2003 with references).

A single m2 from Hohensülzen, Worms (Germany), late Early Pleistocene, was ascribed to *S. vulgaris* by Storch *et al.* (1973). Another very old record attributed to modern red squirrel come from the lower layer (17/C) of the fissure filling 17 of Süttő Travertine Complex, Hegyháti quarry (Hungary), which is dated, mainly based on arvicolid, to the Early–Middle Pleistocene boundary (Pazonyi *et al.*, 2014).

In the Middle Pleistocene *S. vulgaris*, or *Sciurus cf. vulgaris*, occur at Hórvölgy Cave (Hungary) (Jánossy, 1986), Nyaravai 2 (Lithuania) (Kowalski, 2001 with references), Sîndomic-1, Valea Lupşa 10 and Părului (Romania) (Rădulescu & Samson, 1985, 1992), Petersbuch (Germany) (Kowalski, 2001 with references), Ostend, Cudmore Grove, Beihus Park and Itteringham (Britain) (Schreve, 1998), Caune de l’Arago and Baume Moula-Guercy (France) (Desclaux & Defleur, 1997; Hanquet, 2011) and Cova del Bolomor (Spain) (Guillem Calatayud, 2000). The fossil remains from the Cueva del Camino (Pinilla del Valle, Spain), preliminarily referred to the late Middle Pleistocene (Toni & Molero, 1990) were recently attributed to the Late Pleistocene, late Marine Isotope Stage 5 (=MIS 5), by Arsuaga *et al.* (2012).

The finds of red squirrel then become slightly more numerous in the first part of the Late Pleistocene (last Interglacial), from Spain (Guillem Calatayud, 2000; Arsuaga *et al.*, 2012), France (Schreuder, 1958; Chaline, 1972; Marquet, 1989; Desclaux & Defleur, 1997; Slimak

et al., 2010), Belgium (Bastin *et al.*, 1986), Hungary (Jánossy, 1964, 1986; Pazonyi & Kordos, 2004), Belarus (Kowalski, 2001 with references), Romania (Burgehele *et al.*, 1994) and Italy (see 7. *Sciurus vulgaris* in Italy).

Within the Last Glacial (Würm *Auctorum*), probably during more forested phases, red squirrel occur in several sites of Spain (Barandiarán, 1965; Viñas & Villalta, 1975; Guillem Calatayud, 2000), France (Chaline, 1972; Desclaux & Defleur, 1997), Belgium (Gautier & Heinzelin, 1980), Switzerland (Kowalski, 2001 with references), Germany (Brunner, 1952; Kowalski, 2001 with references; Münzel & Conrad, 2004), Poland (Kowalski, 2001 with references; Bieroński *et al.*, 2007), South Urals, Russia (Bachura & Kosintsev, 2007), Czech Republic (Diedrich & Žak, 2006), Hungary (Jánossy, 1964, 1986), Slovenia (Kryštufek, 1997), Croatia (Malez, 1963), Serbia (Dimitrijević, 1997), Romania (Paunescu, 2009), Greece (Roger & Darlas, 2008) and Italy (see 7. *Sciurus vulgaris* in Italy).

During the coldest periods of the Late Pleistocene and, namely, the Last Glacial Maximum (=LGM), the Iberian and Italian peninsulas, the Balkans and the former Soviet Union territory between Caucasus and southern Urals have played the role of main *glacial refugia* for many “temperate” or “warm” animal and plant species, which then repopulated the rest of Europe (Bilton *et al.*, 1998; Stewart & Lister, 2001; Sommer & Nadachowski, 2006). This phenomenon certainly involved also *S. vulgaris* (see Grill *et al.*, 2009; Gomes Rocha *et al.*, 2014). During the late-glacial and post-glacial times, coniferous forests and deciduous woods have progressively replaced the mammoth steppes and have taken hold even in many regions covered by ices in the LGM (Mangerud *et al.*, 1974; Ravazzi *et al.*, 2007; Magri, 2008). On the basis of fossil record, we can assume that in the Lateglacial red squirrel reached northern Portugal (Gabriel & Bearez, 2009), Venetian Prealps (see 8. Palaeobiogeography and Palaeoecology), Central Massif and Alpine valley of Haute Savoie (Chaline, 1972), the Hungarian side of Carpathian mountains (Jánossy & Kordos, 1976; Jánossy 1986) and Russia from south to north of the Urals (Bachura & Kosintsev, 2007; Teterina, 2009; Ponomarev *et al.*, 2012). In the early Holocene (Preboreal and Boreal chronozones), *S. vulgaris* quickly reached also the Cantabrian Mountains (Cuenca-Bescós *et al.*, 2008), the upper valleys of the southern Alps and of the Apennines (see 8. Palaeobiogeography and Palaeoecology), the Slovenian Karst (Toškan, 2009), the Jura Mountains and the northern side of the Alps (Koenigswald & Rähle, 1975; Chiquet, 2005; Kind, 2009), the northern Bohemian sandstone region and the Polish side of the Carpathian Mountains (Nadachowski *et al.*, 1989; Horáček, 2007), Britain (Price, 2003), Denmark and south-western Norway (Larsen & Mangerud, 1989; Noe-Nygaard, 1995), and Estonia and Finland (Kukk *et al.*, 2000; Ukkonen, 2001).

Remains of red squirrel dated to 4,480 ± 100 years BP

appear from landslip debris at Binnel Point in the Isle of Wight (English Channel, UK) (Preece, 1986), but whether this rodent was brought to the island by man is still unclear. However, it seems that squirrels were never introduced in any of the Mediterranean islands (Masseti, 2005).

3. STRATIGRAPHIC NOTES ON THE SITES

3.1. Caverna delle Arene Candide

The Caverna delle Arene Candide (Finale Ligure, Liguria; thereafter Arene Candide) is situated on the slopes of the Mount Caprazoppa, about 90 m above sea level (=a.s.l.) (Fig. 1). First research date back to the second half of the 19th century. More recent and accurate fieldwork campaigns, carried out by L. Cardini and L. Bernabò Brea around the half of the last century, adopted the stratigraphic method. This allowed to uncover a complex stratigraphic sequence, that included several phases of human occupation, divided in four horizons: the upper one, dated to the Holocene, held Neolithic to Byzantine pottery layers; the three lower horizons, with Upper Palaeolithic industry, are dated to the Late Pleistocene (Bietti & Molari, 1994 with references).

The lowest Late Pleistocene horizon (between $25,620 \pm 320$ and $23,450 \pm 220$ years BP) included 4 so-called "P" layers (P13-10) with rare Upper Palaeolithic industry (Bietti & Molari, 1994) and with scarce faunal remains (red deer, ibex, various carnivores, lagomorphs and large rodents) mainly accumulated by carnivores (Alhaique, 1994; Cassoli & Tagliacozzo, 1994). Layer P10 held the renowned burial of the "young prince" (Cardini, 1946; Alhaique & Molari, 2006). The upper "P" layers (P9-1, between $20,470 \pm 320$ and $18,560 \pm 210$ years BP) held Final Gravettian - Early Epigravettian industry and several ungulate remains (especially ibex, but also red deer, aurochs and wild boar), accumulated mainly by humans; there are also many remains of carnivores (particularly lynx and mustelids, but also bears, wolves and foxes) who continue to frequent the cave (Alhaique, 1994; Bietti & Molari, 1994; Cassoli & Tagliacozzo, 1994).

The 5 so-called "M" layers of the Late Pleistocene horizon, dated to between $11,750 \pm 95$ and $9,980 \pm 140$ years BP, held Final Epigravettian industry and several ungulate remains (especially red deer, roe deer and wild boar) accumulated mainly by humans; also most bone remains of carnivores (brown bear, wild cat, fox), lagomorphs and large rodents from this layers were accumulated mostly by humans (Alhaique, 1994; Bietti & Molari, 1994; Cassoli & Tagliacozzo, 1994). Those dates would indicate the last cold phase of the Dryas II, followed by the more temperate Allerød Interstadial and the early cold phases of the Dryas III (Bietti & Molari, 1994; Cassoli & Tagliacozzo, 1994; Salari, 2012). At the

base of the "M" horizon a vast necropolis was found, which held at least 15 burials; in some of these, numerous caudal vertebrae and other remains of red squirrel were recovered (Cardini, 1980; Alhaique & Molari, 2006).

The red squirrel remains analysed in this work, referred to 13 individuals (Cassoli & Tagliacozzo, 1994), come from the "P13" and the 5 "M" layers of the excavations conducted between 1940 and 1950 by the "Istituto Italiano di Paleontologia Umana" of Rome and directed by L. Cardini. All the squirrel remains from the "M" layers are most likely attributable to an anthropic introduction. This might not be the case for the only squirrel bone from the "P13" layer, where many bones were brought in by carnivores and there is little evidence of anthropic action compared to the later phases.

3.2. Riparo Soman

The Riparo Soman (Chiusa di Ceirano, Dolcè, Veneto) is located at the left bank of the Adige Valley at an altitude of about 100 m a.s.l. (Fig. 1). It was excavated in 1984-1988 by the University of Ferrara with the collaboration of the "Soprintendenza Archeologica del Veneto". The excavations have exposed a stratigraphic sequence which ranges from the late Upper Palaeolithic to the beginning of the Neolithic, and shows sporadic traces of human occupation also during the protohistory (Broglia & Lanzinger, 1986).

The Epigravettian levels, 30 cm thick, are divided into two occupation phases: Phase I has been dated to the Late Glacial Interstadial ($11,880 \pm 170$ years BP) and Phase II to the Younger Dryas (between $10,510 \pm 180$ and $10,370 \pm 110$ years BP) (Broglia & Improta, 1995). Mesolithic layers follow this sequence, with the earliest being referred to the Boreal and holding scarce Sauveterrian industry, and the most recent referred to the Atlantic, with rare Castelnovian industry (Broglia & Lanzinger, 1986). The fauna, mostly accumulated by humans, indicates a cold and dry climate with a preponderance of chamois and ibex on red deer in the Epigravettian levels, followed by a temperate and humid phase with a prevalence of red deer and wild boar on the caprines in the Mesolithic layers (Tagliacozzo & Cassoli, 1992).

The red squirrel ulna analysed in this work comes from the early Mesolithic layer. The relation of the squirrel remain with the human frequentation of the rockshelter is confirmed by its provenience. The bone was found in a combustion area along with other faunal remains which had been certainly brought in and used by humans. However, the hypothesis of an earlier introduction by a small carnivore or a bird of prey cannot be definitely ruled out.

3.3. Grotta Mora Cavorso

Grotta Mora Cavorso (thereinafter Mora Cavorso) is located 715 m a.s.l. near Jenne (Latium, Central Italy) and leans out on the right slope of the upper Aniene River valley, in the Simbruini Mountains Regional Natural Park (Fig. 1). Following the fortuitous discovery of human bones inside the cave, archaeological investigations started in 2006 by “Tor Vergata” University of Rome, in agreement with the “Soprintendenza per i Beni Archeologici” of Latium and with the collaboration of “Shaka Zulu” speleological group. The inner rooms held the remains of at least 21 individuals, i.e. the largest Neolithic human community in Latium and one of the largest in Europe (Rolfo *et al.*, 2012, 2016 with references). Several Holocene levels (Layers 1-3) with domestic mammal remains were identified in Room 1 (dated to the Neolithic, the Bronze Age and the historical period, Rolfo *et al.*, 2013, 2016 with references), along with a deep Late Pleistocene sequence which has not yet been fully investigated. Between 2007 and 2013, several vertebrate fossils were recovered in the three distinct horizons of this sequence: the most recent one (Layer 5), referred to the Lateglacial, held Upper Palaeolithic (Final Epigravettian) lithic artefacts and a mammal assemblage dominated by marmot, red deer and ibex; the remaining horizons did not hold human artefacts; of these, the first one (Layer 6) is correlated to the LGM and the second (Layer 7) is characterised by deeper sediments related to temperate oscillations of MIS 3 (Salari *et al.*, 2011, 2014; Rolfo *et al.*, 2016). In this investigated section of the Late Pleistocene sequence, *Microtus (Microtus) arvalis* is dominating the micromammal assemblage, followed by *Arvicola amphibius* and by rare rodents and insectivores of woodland or various habitats; conversely, the Neolithic layer is dominated by *Apodemus sylvaticus/flavicollis*, followed by *A. amphibius*, gliroids and *Microtus (Terricola) savii* (see Salari, 2014). The sediments between the latest Epigravettian evidence and the earliest Neolithic frequentations (Layer 4) are characterized by the presence of macro and micro mammal remains, such as *Glis glis*, *Eliomys quercinus*, *M. (M.) arvalis*, *A. amphibius* and *Sciurus vulgaris*. All these finds can be referred to the earliest phases of the Holocene (Preboreal and Boreal chronozones) and are probably correlated to the “red deer layer” of the inner rooms, radiometrically dated to between $8,805 \pm 45$ and $8,770 \pm 60$ years BP (Boreal chronozone) (see Salari *et al.*, 2011; Rolfo *et al.*, 2016). The mandible of *Sciurus vulgaris* here analysed shows traces of fire exposure (see 6. Bone Surface Modifications), which is consistent with the fragments of charcoal found in the layer. This could indicate the existence of hearths and would suggest a limited occurrence of human frequentation also in this phase. The lack of lithic artefacts, however, does not allow us to attribute this anthropic layer to a specific cultural facies. The integrity of this layer was significantly affected by

recent activities of soil removal carried out in Room 1, which erased the deposit of the more recent Holocene, especially in the area closest to the entrance.

3.4. Grotta del Santuario della Madonna

The cave (thereinafter Santuario della Madonna) is located on a high rock cliff, about 50 m a.s.l., south of Praia a Mare (North Calabria), in the Tyrrhenian side of the region (Fig. 1). The excavations carried out by the “Istituto Italiano di Paleontologia Umana” of Rome (1957-1970) have highlighted an impressive archaeological deposit, over 8 m thick, with several layers related to the human occupation of the cave, from the late phases of the Upper Palaeolithic to the Middle Ages. Earliest traces of human occupation are represented by several archaeological layers. The earliest one (Layer “L”, cuts 48-73) has been dated to the Upper Palaeolithic, with final Epigravettian industry, the second one (Layer “T”, cuts 42-47) to the Mesolithic and the remaining ones to a period ranging between the Middle Neolithic and the Roman period (Cardini, 1970; Tagliacozzo, 2000; Fiore *et al.*, 2004; Salari, 2009).

The red squirrel’s mandible was found in Layer L, cut 57, and is the only remain of this rodent, referred to the Palaeolithic-Mesolithic series. The fauna of these layers was almost fully accumulated by humans and shows the presence of mostly wild boar, red and roe deer on ibex and chamois; hare and edible dormouse are also common, as well as fox and wild cat with regard to the carnivores (Cardini, 1970; Fiore *et al.*, 2004). Cut 57 was radiometrically dated to $10,120 \pm 70$ years BP (Cardini, 1970), whereas cuts 51-58 of Layer L were correlated to Dryas III (Di Canzio, 2004). The archaeological documentation available does not provide any information on the taphonomical context of the remain, although an association between the human frequentation and the squirrel bone is suggested by the traces of combustion identified on the mandible (see 6. Bone Surface Modifications). This, however, does not allow us to exclude definitely that the find was introduced in the cave by small carnivores, birds of prey or other factors

4. MATERIALS AND METHODS

The mandible of red squirrel from Mora Cavorso is located in the Laboratory of Prehistory of the University of Rome “Tor Vergata”. The red squirrel remains from Arene Candide, Riparo Soman and Santuario della Madonna are stored in the Laboratory of Bioarchaeology of the National Museum of Prehistory and Ethnography “Luigi Pigorini” of Rome.

The finds described below are summarised in Table 1. Measurements of the mandible were taken as explained

Table 1: Skeletal elements of *Sciurus vulgaris* examined. 1A: Caverna delle Arene Candide (layer P13); 1B: Caverna delle Arene Candide (layers M5-1); 2: Riparo Soman; 3 Grotta Mora Cavorso; 4: Grotta del Santuario della Madonna.

	1 A	1 B	2	3	4
premaxillary		1			
maxilla		3			
mandible	1	10		1	1
isolated teeth		1			
scapula		4			
humerus		9			
radius		6			
ulna		7	1		
metacarpal bones		2			
pelvis		5			
femur		8			
tibia		9			
calcaneus		1			
talus		1			
metatarsal bones		11			
metapodial bones		19			
total NISP	1	97	1	1	1

in Fig. 2, those of the teeth were taken following Storch *et al.* (1973) (labial length, aboral width), long bones were measured following the methodology and the symbology introduced by Driesch (1976). Measurements were taken with a standard calliper and a 10X lens with a micrometer and expressed in mm.

Morphological features have been compared with the bones of extant red squirrel stored in the National Museum of Prehistory and Ethnography “Luigi Pigorini” of Rome. Morphometric data for comparisons with modern red squirrel have been taken from literature (Miller, 1912; Cavazza, 1913; Toschi, 1965; Chaline, 1966, 1972; Wiltafski, 1978). These comparisons have been restricted to the subspecies, or regional varieties (Thorington & Hoffmann, 2005), present in Italy: *S. vulgaris fuscoater* Altum, 1876, spread from France to Eastern Europe, in Northern Italy and part of the Balkans, *S. vulgaris italicus* Bonaparte, 1838, endemic of Central Italy, and *S. vulgaris meridionalis* Lucifero, 1907, endemic of Calabria (Toschi, 1965; Siderowicz, 1971; Wiltafski, 1978; Wauters & Martinoli, 2008). Both the Scandinavian red squirrels and those from the British Isles, of smaller size, were excluded from the comparative analysis, as well as those from the Iberian peninsula, as big as those from Calabria or even bigger (see Miller, 1912; Wiltafski, 1978; Mathias & Gurnell, 1998). Further morphometric comparisons were made with the red squirrel remains from the perialpine sites of Egozwil 3 (5th millennium BC, early Neolithic, Switzerland)

(Higham, 1967) and Mondsees (3th millennium BC, late Neolithic, Austria) (Wolff, 1977).

The age of death of the fossil specimens was estimated considering the age of eruption, change and wear of the teeth, according to the criteria reported in Shengkan & Mingshu (1979). Taphonomic analyses were carried out at both the macroscopic and microscopic level in the Laboratory of Bioarchaeology of the National Museum of Prehistory and Ethnography “Luigi Pigorini” of Rome. The analyses with the aid of stereomicroscopes (Nikon SMZ 1000, 8-80X) to identify and localize the bone surface alterations and the different types of traces, particularly by humans, as well as to reconstruct the different actions. Damage observed on red squirrel remains includes cut marks, fresh bone breakage, overextending and manual handling.

Manipulation of carcasses leaves very specific and peculiar traces during the skinning action of small preys (peeling, squashing, notches and *arrachement*). The process is to pull and twist the portion for dissecting and eating it. These actions can take place on carcasses that need to be cooked or are already cooked. These actions generate certain modifications (peeling and *arrachement*). Disarticulation by traction and rotation often produces a localized and oriented detachment of small portions of the bone surface (peeling = roughened surface with parallel grooves and fibrous texture) corresponding to important muscular and tendon insertions (White, 1992; Laroulandie, 2000, 2005). *Enfoncement* (or squashing) is caused by the pressure between two bones in the joint when they are flexed (perforations produced by forced extension of the humerus from the ulna) (Gourichon, 1994). *Arrachement* (or wrench) is the fracture and the loss of bone cortical tissue from a joint portion.

The incisions are striations with linear outlines of variable lengths, widths, and depths (Potts & Shipman, 1981; Dominguez-Rodrigo *et al.*, 2009, 2010; Juana *et al.*, 2010). Bone breakages were analyzed and classified following Villa & Mahieu (1991) and Steadman *et al.* (2002). Identified tooth marks were compared also with human marks (Haynes, 1983; Laroulandie, 2000; Landt, 2007). Thermal-modifications (Shipman *et al.*, 1984; Nicholson, 1993) were also identified. Traces of burning localised on a small part of bone was interpreted as a result of small portions that came into contact with fire; this determined the burning of the bony parts that were not protected by flesh (Cassoli & Tagliacozzo, 1997). The distribution of the anatomical elements provided important information about dismembering of the carcass before it was cooked (Vigne *et al.*, 1981; Vigne & Marinval-Vigne, 1983; Cassoli & Tagliacozzo, 1997; Henshilwood, 1997; Tagliacozzo & Fiore, 1998; Hockett & Ferreira Bicho, 2000; Laroulandie, 2001; Lloveras *et al.*, 2009; Medina *et al.*, 2012).

To test the past distribution of *S. vulgaris*, we carried out a literature search, identifying in the literature (after Second World War) the main vertebrate deposits and

archaeological contexts referred to the Late Pleistocene and the early and middle Holocene of Italy, and we took note of the presence of red squirrel remains.

5. DESCRIPTION AND COMPARISONS

5.1. Skull and upper teeth

We identified a premaxillary bone with an incisor and three maxillaries (Tab. 1), one with an almost complete cheekteeth row (only the very small P3 is missing) and two with M1 (Plate I, figs 1-2). All these remains come from the Arene Candide.

The incisor is robust, laterally compressed and has an elliptical section. The posterior premolar and the molars have two roots on the lingual side and one on the labial one; the crown is shallow and has a tubercle on the lingual edge (except for the third molar) and four tubercles on the labial edge, from which four transversal ridges take shape; the third molar has only one anterior transversal ridge and a wide posterior depression.

Teeth are little or no worn and are therefore attributable to the Group 4 - Adults I (see Shengkan & Mingshu, 1979). The length of the upper cheekteeth row (10.7 mm, see Tab. 2) of the specimen from the Arene Candide is greater of both that of the Neolithic red squirrels from Egozswil 3 (9.2-10.5 mm; Higham, 1967) and of the extant red squirrels (8.8-10.2 mm; Miller, 1912; Toschi, 1965; Chaline, 1966; Wiltafski, 1978).

5.2. Mandible and lower teeth

An intact hemimandible with incisor and p4 comes from the Santuario della Madonna (Plate I, fig. 9), while a mandible with part of the incisor and of the m1, but missing a part of the condyloid process comes from Mora Cavorso (Plate I, fig. 8); finally, 11 mandibles are from the Arene Candide (Tab. 1). Among these, one hemimandible with part of the incisor and of the p4 and without the ascending ramus was found in level P13, whereas the others were uncovered in levels M5-M1; one is intact with incisor, p4 and m2 (Plate I, fig. 4), one has incisor, p4 and m3 but lacks the ascending ramus, two do not have the coronoid process and any cheekteeth (Plate I, figs 3 and 5), two have the ascending ramus damaged and missing the cheekteeth (Plate I, fig. 6), two are intact

but lack jugal teeth (Plate I, fig. 7), one is fragmentary but has the m2 and, lastly, one is fragmentary and without jugal teeth.

The mandible is relatively robust and has a wide ascending ramus with a robust angular process and the apex leaning towards the outside of the labial side, extended condyle and a relatively short coronoid process; the mental foramen is located posteriorly to the p4. The incisor is similar to the upper one, but is more laterally compressed. The premolar is subtriangular and has an anterior and a posterior root, roughly squared molars, the first and second of which have four roots and the third three, two anterior and one posterior; the crown is shallow and has a wide depression, rimmed by a lateral ridge on the lingual side and by two bigger tubercles and one smaller in the middle on the labial side.

Among the mandibles that still had the jugal teeth, none belonged to immature or subadult individuals. One mandible from the Arene Candide (layer M2) has very worn p4 and m3, still not showing the dentin and therefore attributable to the Group 5 - Adult II; the remaining three mandibles from the Arene Candide, the one from Mora Cavorso and that from the Santuario della Madonna show little worn or unworn teeth and are therefore attributable to the Group 4 - Adult I (see Shengkan & Mingshu, 1979).

The average sizes of the mandibles of our sample are greater than the extant red squirrels, especially with regard to the length of the cheekteeth row. Maximum length of the mandibles from the Arene Candide (between 32.2 and 34.5 mm, the mean being of 33.1 mm, see Tab. 3) is similar to the maximum values of the extant red squirrels (between 29.1 and 34.8 mm; Miller, 1912; Cavazza, 1913; Toschi, 1965; Wiltafski, 1978), that of the Santuario della Madonna is greater (Tab. 3). The average length of the lower cheekteeth row of the whole sample (between 10.2 and 11.2 mm, the mean being of 10.7 mm; see Tab. 3) is greater than that of Mondsees (between 9.9 and 10.8 mm, the mean being of 10.3 mm; Wolff, 1977) and consistently greater of both the Neolithic ones of Egozswil 3 (9.4 mm; Higham, 1967) and those of the extant red squirrels (between 8.5 and 10.0 mm; Miller, 1912; Chaline, 1966; Wiltafski, 1978).

As for the single jugal teeth (Tab. 3), the second molar has the same length, but is slightly longer than the m2 from Hohensülzen (late Early Pleistocene, Germany), which is the oldest specimen of *S. vulgaris* known (Storch *et al.*, 1973).

Table 2: *Sciurus vulgaris*: upper cheek teeth measurements (mm). L.c.r.: length of upper cheekteeth row (alveolar); measurements of P4, M1, M2 and M3: length x width.

	L.c.r.	P4	M1	M2	M3
Arene Candide M1	10.7	2.0 x 2.3	2.2 x 2.5	2.3 x 2.8	2.7 x 2.8
Arene Candide M1			2.2 x 2.6		
Arene Candide M1			2.3 x 2.6		

Table 3: *Sciurus vulgaris*: mandible measurements (mm). 1: maximum length (condyle process - infradental); 2: length coronoid process - infradental; 3: length aboral border of m3 - aboral border of incisor; 4: length of lower cheekteeth row (alveolar); 5: height of ascending ramus; 6: height in front of m1; measurements of p4, m1, m2 and m3: length x width.

	1	2	3	4	5	6	p4	m1	m2	m3
Santuario della Madonna	35.4	30.1	18.4	10.8		9.2	2.0 x 2.1			
Mora Cavorso		25.6	17.2	10.6		9.1		2.2 x 2.4		
Arene Candide M1	32.2	27.1	18.1	10.4	17.8	8.3	2.2 x 2.4		2.4 x 2.6	
Arene Candide M1	34.5		18.6	10.7		9.0				
Arene Candide M1			17.8	10.5		8.8				
Arene Candide M2	32.6	27.8	18.3	11.2	18.1	8.8				
Arene Candide M2	33.8		17.4	11.2						
Arene Candide M2									2.3 x 2.6	
Arene Candide M2			18.4	10.4		8.7	2.2 x 2.2			2.8 x 2.6
Arene Candide M3	32.2	25.8	16.1	10.8	17.4	8.6				
Arene Candide M3			18.4	10.6		8.9				
Arene Candide M5						8.2				
Arene Candide P13				10.2	17.2	8.6	1.8 x 2.1			

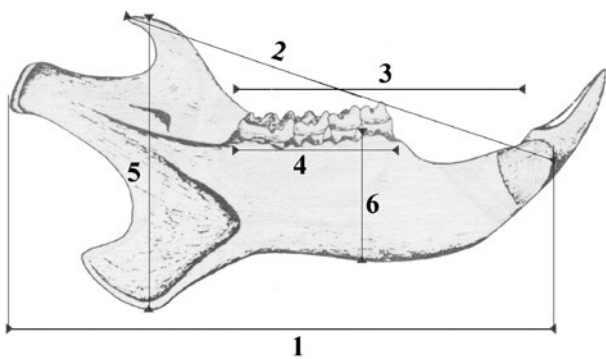


Fig. 2: Measurements of mandible: 1) maximum length (condyle process - infradental); 2) length coronoid process - infradental; 3) length of aboral border of m3 - aboral border of incisor; 4) length of the cheekteeth row (alveolar); 5) height of ascending ramus; 6) height in front of m1.

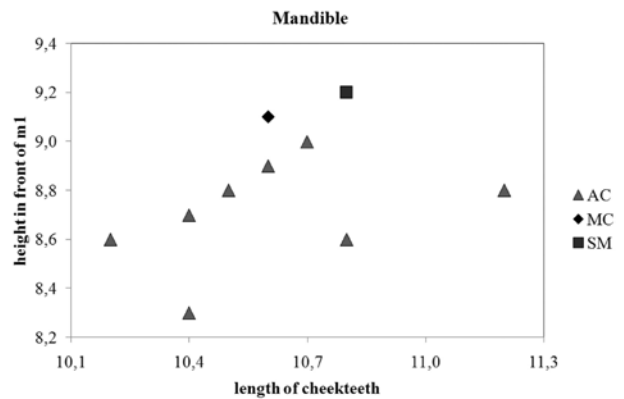


Fig. 3: Scattergram of mandible height in front of m1 versus length of lower cheekteeth (mm) of the specimens from Caverna delle Arene Candide (AC), Grotta Mora Cavorso (MC) and Grotta del Santuario della Madonna (SM).

Figure 3 shows the ratio between the lower cheekteeth row and the height of the horizontal ramus of the mandible in front of m1. It can be noticed that the mandibles from the Santuario della Madonna and Mora Cavorso are more robust than those from the Arene Candide, despite not necessarily having a longer cheekteeth row. Within the sample of the Arene Candide this scattergram shows two different alignments that identify two groups of mandibles, one more robust than the other. Considering that *S. vulgaris* has little or nothing about sexual dimorphism, this could be casual or be somehow connected to specific environmental conditions (see Wauters & Dhondt, 1989).

5.3. Post-cranial bones

Considering the high fragmentation rate of many remains of our sample and the scarcity of osteometric data from other sites, it is only possible to make some observation and a merely indicative comparison with the corresponding anatomic parts recovered in the perialpine sites of Egozswil 3 (Higham, 1967) and Mondsees (Wolff, 1977).

The long bones have the typical morphology of the Sciuridae, although with smaller sizes than those of the marmots and more slender than the European ground squirrel. According to Chaline (1966), the almost cylindrical diaphysis of the humerus in particular, as well as the very expanded apophysis of the third trochanter of the femur, observed on the sample from the Arene

Candide (Fig. 6), allow to easily attribute the remains to *Sciurus* rather than to *Spermophilus* Cuvier, 1925.

All the epiphyses of the long bones belong to adult individuals, except for a distal portion of a radius with the epiphysis and the diaphysis fused but with the fusion line still visible, and a femur with unfused distal epiphysis (layer M3). Differently from what could be inferred from the mandibles, there were some young and/or subadult individual at the Arene Candide. The age of fusion of the epiphyses of the femur is unknown, but the distal epiphysis of the radius fuses at around 7 months (see Degn, 1973). Given that the environmental conditions of reproduction during Lateglacial of Liguria might have been similar to the present Alpine ones, i.e. one litter per year (Wauters & Martinoli, 2008) between the end of February and May (Degn, 1973; Wauters & Martinoli, 2008), the subadult would have died between October and December.

The sizes of the post-cranial bones of our sample (essentially from the Arene Candide, see Tabs. 1 and 4), are usually greater of those from the Neolithic sites: the minimum width of the scapula neck (SLC between 5.1 and 5.4 mm, with a mean of 5.3 mm) is greater than that of Egozswil 3 (4.6 mm); the distal width of the humerus (Bd between 9.7 and 10.8 mm, with a mean of 10.2 mm) is greater than that of Egozswil 3 (9.4-9.5 mm); the proximal width of the radius (Bp between 3.9 and 4.2 mm, with a mean of 4.1 mm) is similar to that of Egozswil 3 (3.8-4.3 mm, with a mean of 4.1 mm); the size of the ulna from Riparo Soman fall within the variability range of those from the Arene Candide (Tab. 4), whilst the width of the coronoid processus of the ulna of the whole sample (BPC ~3.8 mm) is the same of those from Mondsees, but slightly smaller than that from Egozswil 3 (4.1 mm); the width of the coxal acetabulum (LA between 6.2 and 6.8 mm, with a mean of 6.4 mm) is greater of both Egozswil 3 (between 5.4 and 6.3 mm, with a mean of 5.8 mm) and Mondsees (5.5 mm); in the femur, both the

proximal (Bp between 9.7 and 10.4 mm, with a mean of 9.9 mm) and the distal width (Bd = 8.2 mm) are similar to the sizes of the sample of Mondsees (Bp between 9.6 and 10.5, with a mean of 10.1; Bd 8.1 mm), whereas the distal width is smaller than the specimens of Egozswil 3 (Bd between 8.4 and 8.7 mm, with a mean of 8.6 mm); the sizes of the tibiae (Bp ~9.4 mm; Bd between 5.8 and 6.2 mm, with a mean of 6.1 mm) are greater of both Mondsees (Bd = 5.3 mm) and Egozswil 3 (Bp between 8.8 and 9.3 mm, with a mean of 9.0 mm; Bd between 5.2 and 5.4 mm, with a mean of 5.3 mm).

Table 4: *Sciurus vulgaris*: measurements of post-cranial elements (mm). SLC: smallest length of collum scapulae; GLP: greatest length of glenoid process; LG: length of glenoid cavity; BG: breadth of glenoid cavity; GL: greatest length; Bp: breadth of proximal end; Btr: breadth of trochanter III region; Dp: depth of the proximal end; DC depth of *caput femoris*; SD: smallest breadth of the diaphysis; Bd: breadth of distal end; Dd: depth of the distal end; DPA: depth across the processus anconaeus; SDO: smallest depth of olecranon; BPC: breadth across the coronoid process; LA: length of the acetabulum.

scapula	SLC	GLP	LG	BG
Arene Candide M1	5.4	6.2	5.7	3.6
Arene Candide M1		6.1	5.4	3.3
Arene Candide M2	5.1	6.4	5.5	3.8
Arene Candide M3	5.4	6.2	5.6	3.6

humerus	GL	Dp	SD	Bd	
Arene Candide M1				9.9	
Arene Candide M1				9.7	
Arene Candide M2	43.9	7.5	3.4	10.8	
Arene Candide M2			3.0	10.5	
Arene Candide M2		6.9			
Arene Candide M3			3.4	10.5	
Arene Candide M3				10.1	
Arene Candide M4			3.3	10.4	
Arene Candide M4			2.8	9.9	
radius	Bp	SD	Bd		
Arene Candide M2	4.2				
Arene Candide M2	4.2				
Arene Candide M2		2.7	4.6		
Arene Candide M3	4.0				
Arene Candide M3	4.2				
Arene Candide M4	3.9				
ulna	DPA	SDO	BPC		
Riparo Soman	4.6	4.1	3.8		
Arene Candide M1	4.8	4.3	3.8		
Arene Candide M3	4.7		3.8		
Arene Candide M3	4.5	4.2	3.8		
Arene Candide M3			3.8		
pelvis	LA				
Arene Candide M1	6.8				
Arene Candide M2	6.4				
Arene Candide M2	6.2				
Arene Candide M4	6.3				
femur	Bp	Btr	DC	SD	Bd
Arene Candide M1	10.4	10.9	5.2		
Arene Candide M1		10.4			
Arene Candide M2	9.8	10.6	5.1		
Arene Candide M2		10.3	4.9		
Arene Candide M2					8.2
Arene Candide M4	9.7	10.2	4.7		
tibia	Bp	Dp	SD	Bd	Dd
Arene Candide M1			2.8	5.8	5.2
Arene Candide M1			2.9	6.0	5.3
Arene Candide M2			2.9	6.1	5.4
Arene Candide M2	9.4	7.8			
Arene Candide M3			3.1	6.2	5.5
Arene Candide M3			3.0	6.2	5.6
Arene Candide M3	9.4	8.0			

Table 5: *Sciurus vulgaris*: frequency of modifications in NISP. Key: CM = Cut mark; CM? = Cut mark?; O = Ochre traces; PL = Peeling; AR = *Arrachement*; PM = Percussion Mark; FBFr = Fresh Bone Fracture; B = Burned; LB = Localised Burn; S = Striae; HTM = Human Tooth Mark; CTM = Carnivore Tooth Mark; ER = Erosion. N.B.: a specimen can present one or more modifications that were separately accounted; the grey cells indicate uncertain attribution, possibly carnivores and/or humans, of the bites on the femur. Total NISP from Caverna delle Arene Candide with modification traces = 53.

specimen	total NISP	NISP modified	CM	CM?	Tools /Use	O.	PL	AR	PM	FBFr	B	LB	S	HTM	CTM	ER
premaxillary	1															
maxilla	3															
mandible	13	9	1			1	2			1	2	7				
isolated teeth	1															
scapula	4	2					1				1					
humerus	9	3									1	1		1		
radius	6	5								2	2	3				
ulna	8	6						1		1	1	3	1		1	
metacarpal bones	2															
pelvis	5	3					1	1		2						
femur	8	8			2		2	3	1	4	2	2		1?	1?	
tibia	9	7	1	1						2	4	2				
calcaneus	1															
talus	1															
metatarsal bones	11	} 13		1								12	1		1	1
metapodial bones	19															
Total	101	56	2	2	2	1	6	5	1	12	13	30	2	2?	3?	1

6. BONE SURFACE MODIFICATIONS

The analysis of the bone surfaces has been carried out on 101 red squirrel remains, mostly found at the Arene Candide (Number of Identified Specimens: 98 = 98 NISP); from each of the other sites (Riparo Soman, Mora Cavorso and Santuario della Madonna) comes only one find, adding up to 3 remains in total (Tabs 1 and 5).

The taphonomic analysis allowed to identify various modifications on over half of the finds (56 NISP). The traces that have been considered of anthropic nature (cut marks, tools/use wear, cut marks?, *arrachement*, peeling and ochre traces) were identified on 13 remains, with some bones showing more than one trace at the time. Combustion traces situated in specific places of 31 bones are particularly interesting, being the only traces found on 27 of these (Tab. 5). These modifications, too, are to be mostly ascribed to anthropic action, having been produced most likely during the cooking of small meat portions, formerly disarticulated.

Modifications are widely distributed on different portions of the skeleton, especially on the mandibles and the long bones of the limbs (Fig. 4). Cut marks produced by lithic tools on the red squirrel remains show the same features

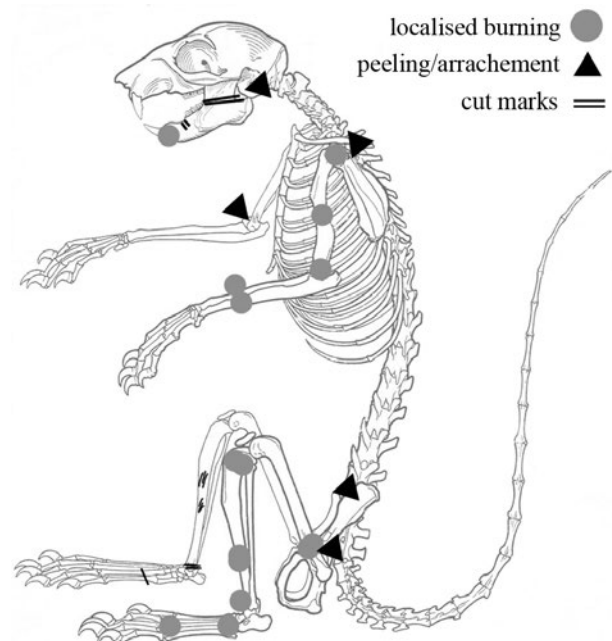


Fig. 4: *Sciurus vulgaris*: position of the main marks of anthropic nature.

of those found on the bones of other small animals, e.g. birds, big rodents, small carnivores (Alhaique, 1996; Cassoli & Tagliacozzo, 1997; Tagliacozzo & Fiore, 1998; Laroulandie, 2000; Fiore, 2003; Fiore *et al.*, 2004; Gala & Tagliacozzo, 2004, 2005): they are usually rare (given the small size of the animal it is not always necessary to use the tool to disarticulate the carcass in a repeated way, unlike what happens for the large-sized animals); striae are short, superficial and sometimes isolated (for the limited bone surface that the tools can touch). However, the micromorphology of the traces (inlet and outlet of the tool, presence of secondary striae), their localisation (functional to carcass processing) and their association to other anthropic traces (peeling, *arrachement*, combustion) allow to attribute them to intentional cuts.

Features of the main finds with anthropic modifications from the various sites are now described.

6.1. Arene Candide

Faunal remains of the Arene Candide have been already object of a general taphonomic analysis (Alhaique, 1994). The following analysis only addresses the red squirrel remains of this site that has provided the largest amount of finds, and which afford crucial data for the reconstruction of the anthropic exploitation of *S. vulgaris*.

Butchery marks made with lithic tools are rare and have been subdivided into certain ones, i.e. Cut Marks (NISP 2, mandible and tibia) (Fig. 5), and uncertain ones, i.e.

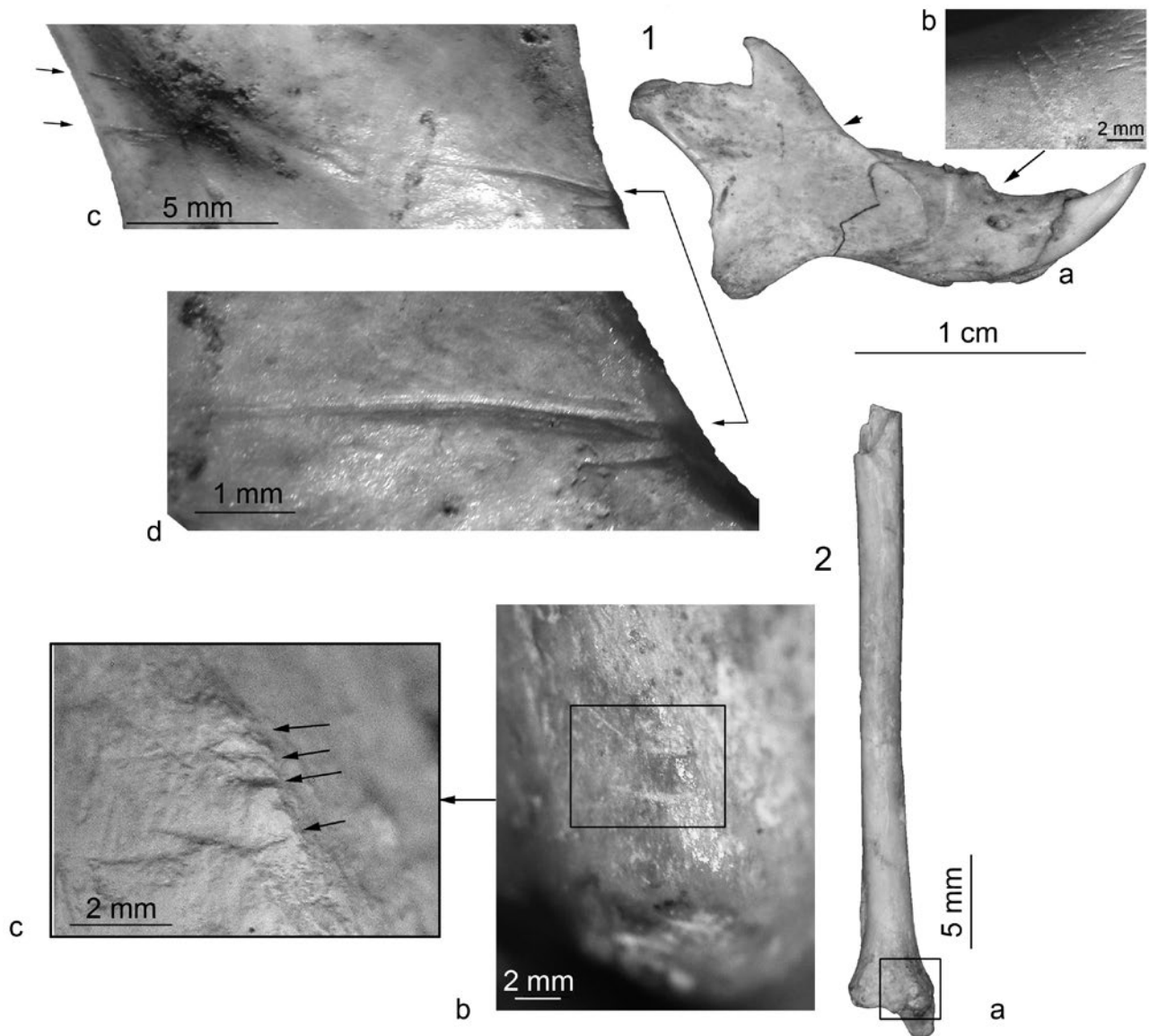


Fig. 5: Cut marks on the bones of *Sciurus vulgaris* from Caverna delle Arene Candide: 1a) hemimandible from layer M2 with peeling marks; 1b) detail of the localised cuts on the mandibular symphysis; 1c-d) details of the cuts on the branch; 2a) tibia from layer M1 with cuts on the distal articulation; 2b) details from the stereomicroscope; 2c) detail from an araldite replica.

Cut Marks? (NISP 2, tibia and metapodials). Other traces due to butchery and carcass processing are represented by *arrachement* (NISP 5, ulna, pelvis and 3 femurs), peeling (NISP 5, mandible, scapula, pelvis and 2 femurs) and by a probable impact (NISP 1, femur) (Fig. 6). Modifications have been also observed that could be related to the use of red squirrel bones as raw material to produce tools (NISP 2, femurs) (Fig. 7).

Fractures on fresh bones (BFBr) are relatively common (12 NISP, mandible, 2 radii, ulna, 2 pelvis, 4 femurs and 2 tibiae) and have been often found on bones with anthropic traces. Localised combustions, considered to be mostly related to cooking activities, are certainly more common (29 NISP, about 30% of the total) and in at least two cases are associated to other types of traces. The only find from older layers (P13), i.e. a fragment of hemimandible, shows fire traces on the incisors and

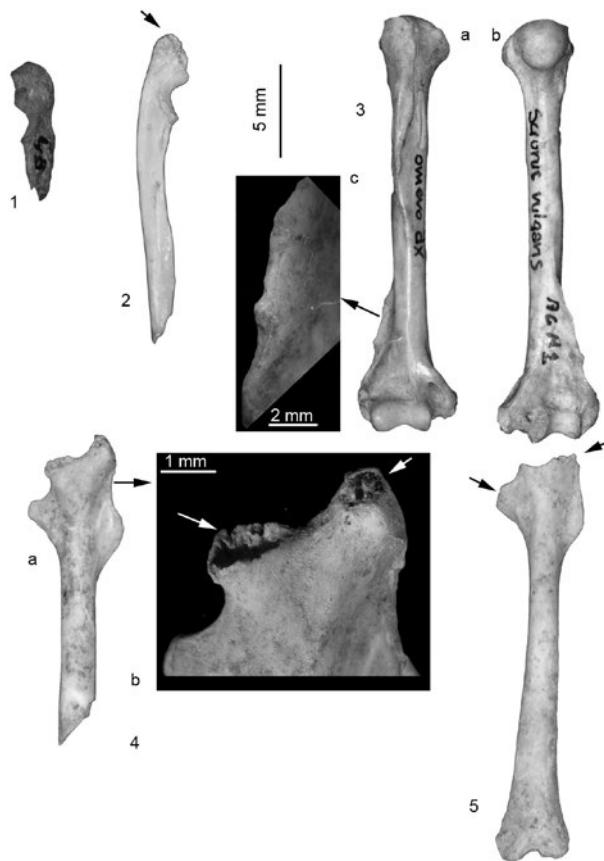


Fig. 6: Other anthropic traces on the bones of *Sciurus vulgaris*: Riparo Soman: 1) Burnt proximal ulna; Caverna delle Arene Candide: 2) proximal ulna from layer M2 with *arrachement* marks and traces of localised combustion; 3) intact humerus from layer M2, 3a) anterior view, 3b) posterior view; 3c) detail of the edge with small impacts/crushes due to gnawing; 4a) proximal femur from layer M1 with traces of *arrachement* and peeling, 4b) detail at the stereomicroscope; 5) intact femur with unfused distal epiphysis from layer M3 with traces of *arrachement* on the proximal end.

probably also laterally of the mandibular branch. Entirely or largely burnt remains might have been produced directly by human activity, although other accidental causes cannot be excluded, such as fire lighting next to the sediment that contained them.

Gnawing marks certainly due to small carnivores are rare, as they have been identified only on one ulna and one metapodial. Other gnawing marks, with specific shapes and micro-features of the grooves might perhaps be attributed to human chewing (see Landt, 2007). These are found on an intact humerus (Fig. 6a-c) and possibly on a femur.

Erosions of the bone surfaces are also rare and can be explained with alterations due to acid attacks of the sediment and/or the digestion. Some superficial striae, variously oriented, finally, are due to the action of sediments.

Many traces have been identified on an intact left hemimandible from layer M2 (see also Alhaique, 1994). The find shows a combination of several types of modifications, i.e. cut marks produced by lithic tools, peeling on the mandibular branch, burns in the incisor area and traces of ochre on the ventral side. At least two cuts have been identified, situated on the lateral side of the mandible branch, which are deep, sub-parallel and oblique to the bone axis. One of the cuts is long and goes through the whole mandible branch, with an interruption in the central part. This is probably due to the presence of the masseter muscle which has protected the bone from being notched by the tool; the second cut, short and shallow, is located on the edge of the branch (Fig. 5, 1a-d). These cuts are referred to the disarticulation of the mandible from the skull, carried out also manually through an action of torsion, as shown by the peeling traces. Two further cuts on the lateral side are located on the mandibular symphysis. These are short, shallow and transversal to the bone axis and can most likely be referred to peeling.

Disarticulation cuts (two short, parallel striae) have been identified on the distal articulation of a tibia from layer M1 (Fig. 5, 2a-c). Another cut mark, larger and deeper, is located on the lateral diaphysis, not far from the former ones. Interestingly, the distal extremity of the tibia shows also signs of combustion.

Striae on the diaphysis of one tibia (layer M3), i.e. two different groups referable to scraping, and on the diaphysis of a metapodial (layer M1), related to peeling, are not well preserved and are therefore only dubitatively attributed to anthropic action, although their morphology and position appears better explained by this interpretation rather than by that of the action of sediments.

The diaphysis of a right proximal femur (layer M1) shows a large fracture due to an impact, which can be observed on one edge; furthermore, the extremity of the bone appears to be sharpened (Fig. 7). Conversely, the edges appear rounded and the point shows a transversal fracture as well as a longitudinal detachment (Burin-

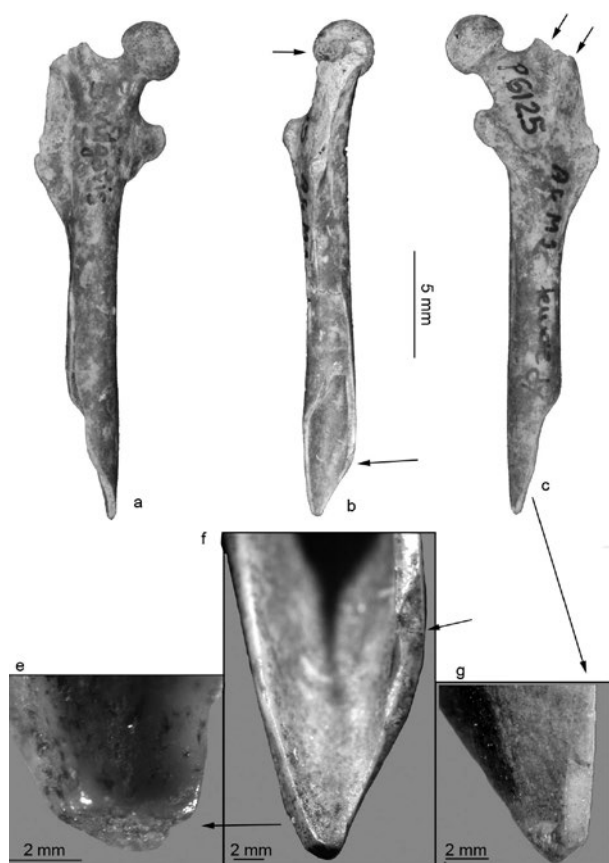


Fig. 7: Proximal femur of *Sciurus vulgaris* from Caverna delle Arene Candide, layer M1, probably used as an awl: a) anterior view, b) medial view, c) posterior view, d) zoom of the extremity of a fracture, with the impact point indicated, e) detail of the extremity of a straight fracture with rounded edges and polishing traces, f) detail of the extremity of a fracture with burin-type detachment.

like). This specimen, possibly used as an awl, might be considered as an expedient tool, i.e. a bone fragment that is object of limited modifications, focused on the active part, and that are only used for a short timespan.

The diaphysis of a distal femur (layer M2) shows a regular transversal fracture with rounded edges. Polishing is present (spotted at the microscope) in the shape of a longitudinal strip along the diaphysis. According to the shape and the rounding marks on the edges of the section, it cannot be excluded that this bone portion had been used (perhaps as a handle).

Overall, femurs show the largest amount of manipulation. Fractures of the head of the femur and of part of the greater trochanter, probably due to the torsion to disarticulate the bone from the acetabulum, often associated to both peeling, *arrachement* and localised burns (Fig. 6, 4-5).

Other traces of manipulation finalised to disarticulation are on a proximal ulna (*arrachement*) (Fig. 6, 2), on a scapula and a pelvis (peeling). The fact that these

modifications are not associated to other anthropic actions might indicate their derivation from other predators. However, traces that are only left by small carnivores or birds of prey, such as punctures and/or scoring, are absent. This suggests that the anthropic interpretation is the most reliable one.

Further evidence of human exploitation of *S. vulgaris* is provided by the fractures on fresh bones on most long bones of the limbs, which often show also localised burns (Fig. 4).

6.2. The other sites

The presence of combustion traces allows to hypothesize that humans exploited the red squirrel as a food supply also at Mora Cavorso and Santuario della Madonna (Plate I, figs 8 and 9). The anterior part of the hemimandible from Mora Cavorso shows dark brown burns on the incisor and on the bone surface around the alveolus. Even the hemimandible of Santuario della Madonna was also partly exposed to fire and presents light brown burns on the posterior part, between the condylus and the branch; the latter also shows a peeling-like edge of fracture caused by tissue ripping. It has to be mentioned that in the same Upper Palaeolithic levels of Santuario della Madonna where *S. vulgaris* was found, exploitation of another small mammal, i.e. the edible dormouse, is attested. This is mainly testified by the cooking methods and consumption inferred by the recurrence of fractures and the localisation of the combustion on the hemimandibles and the long bones (Fiore *et al.*, 2004).

The proximal ulna from Riparo Soman is fully burnt. It appears of a grey-brown colour, probably corroded by the permanence in the deposit (Fig. 6, 1). These alterations have been found of many macrofaunal remains (Tagliacozzo & Cassoli, 1992) and are thus not referable to the digestion of carnivores.

7. *SCIURUS VULGARIS* IN ITALY

7.1. Late Pleistocene

Tozzi (1969) recognised the presence of red squirrel remains, associated to a rich Pleistocene faunal assemblage, in the filling of the Grotta di Valdemino (Borgio Verezzi, Liguria). The reanalysis of these fossils, along with the study of new materials recovered in later excavations, allowed to identify two distinct chronological horizons, the earliest one being dated to the Middle Pleistocene and the latest to the beginning of the Late Pleistocene (Nocchi & Sala, 1997 with references). However, *S. vulgaris* does not appear in any of the published faunal lists from the two aforementioned horizons (see Nocchi & Sala, 1997; Kotsakis *et al.*, 2003; Masini & Sala, 2007, 2011; and references

therein). Pending a clarification on the stratigraphic and biochronological position of the squirrel from Grotta di Valdemino, the earliest remains attributed to *S. vulgaris* in Italy seem to be those from Grotta della Ciota Ciara (Borgosesia, Piedmont), referred to the earliest phase of the Late Pleistocene (MIS 5) (Arzarello *et al.*, 2012), followed by those from the Arma delle Manie (Finale Ligure, Liguria) attributed to the First Pleniglacial (MIS 4) (Abbassi, 1999).

The fossil remains found in Grotta di Torre Nave (Tortora, Calabria) (Bulgarelli, 1972) and in the Layer 11 of Cava Salnova (Saltrio, Lombardy) (Bona, 2011) are referred to the Interpleniglacial (MIS 3), whereas we are aware of more sites holding red squirrel remains for the Second Pleniglacial (MIS 2), especially for the latest part of it (Lateglacial) (Tab. 6).

The remains from the earliest part of the sequence of the Arene Candide (P13-10) was attributed to the Tursac Interstadial, which precedes the LGM, by Cassoli & Tagliacozzo (1994). Red squirrel remains from Layer V of Arma dello Stefanin (Val Pennavaira, Liguria) are following in time, along with those from the latest part of the Late Pleistocene sequence of the Arene Candide (layers "M"). These two faunal assemblages are respectively referred to the Dryas II (Barker *et al.*, 1990) and to the final cold phase of the Dryas II, followed by the more temperate Allerød Interstadial and by the early cold phase of the Dryas III (Bietti & Molari, 1994; Cassoli & Tagliacozzo, 1994; Salari, 2012).

We would like to mention that Liguria was a *glacial refugium* to several bat species: in the LGM this region was occupied, among the others, by *Barbastella barbastellus* and *Myotis mystacinus*. These species can be also found at present day in Central and Northern Europe, whilst being absent (or quite rare) during the LGM (Salari, 2012 with references). Although we lack fossil evidences in continental deposits of the LGM, both in Liguria and in the rest of the peninsula, it is likely that the coastal area of Liguria would have been a *glacial refugium* also to *S. vulgaris*, as this region had been hosting the rodent before and immediately after the LGM.

Further Lateglacial red squirrel remains come from the Venetian Prealps, namely from the Riparo Dalmeri (Altopiano di Asiago, Veneto), referred to the Allerød, from Layer 19 of Riparo Cogola (Altopiano di Folgaria, Trentino Südtirol), attributed to the Dryas III (Bartolomei, 2002, 2005), and from cut 57 of the Santuario della Madonna (North Tyrrhenian Calabria), referred to the Dryas III (Di Canzio, 2004).

In addition to the aforementioned Borgio Verezzi e Torre Nave, finally, Minieri *et al.* (1995) mention the Grotta dei Colombi (Liguria), Grotta del Broion (Veneto) and Grotta dei Tre Piani (Trentino Südtirol) as Late Pleistocene sites with red squirrel remains. However, according to our research, the dating of the Grotta dei Colombi's faunal assemblage is unclear and could either be attributed to Late Pleistocene and to Holocene (see Regalia, 1893).

Moreover, Grotta dei Tre Piani did not hold any fossil remains, but only modern micromammal bones, such as those of *S. vulgaris* (see Pasa, 1954). Finally, Grotta del Broion does not seem to have red squirrel remains at all (see Pasa, 1953; Bartolomei *et al.*, 1984 and references therein).

7.2. Holocene

Several sites dated to the earliest phases of the Holocene (Preboreal and Boreal chronozones) held red squirrel remains (Tab. 6), often associated to archaeological evidence of Mesolithic cultures, both in North-East, e.g. the rockshelters of Soman (Tagliacozzo & Cassoli, 1992 and this work), Pradstel (Bartolomei, 1974), Cogola (Bartolomei, 2005), Frea IV (Angelucci *et al.*, 1999) and Romagnano III (Bartolomei, 1974, 2005), and in Central-Southern Italy, i.e. Mora Cavorso (this work) and Latronico 3 (Dini *et al.*, 2008).

Sites of the middle Holocene (Atlantic and Subboreal chronozones) with red squirrel remains are slightly more numerous and widespread from the North-East to the Central Adriatic region and to Southern Italy (Tab. 6). These are mainly open-air sites, settlements and/or villages, e.g. Capo d'Acqua, Maddalena di Muccia and Ripabianca di Monterado (Wilkens, 2003a), S. Stefano di Ortucchio (Radi & Wilkens, 1989), Catignano (Wilkens, 2003a, b), Mulino Sant'Antonio (Albarella, 1988), but Neolithic to early Bronze Age caves and rockshelters are also known, e.g., Grotte di Castel Corno (Fontana *et al.*, 2009), Grotta Continenza (Wilkens, 1990), Grotta Sant'Angelo (Wilkens, 1996b, 2003a), Latronico 3 (Sorrentino, 1978).

8. PALAEOBIOGEOGRAPHY AND PALAEOECOLOGY

We can note from Table 6 that Italian sites with red squirrel remains are quite diverse, and that data collected are rather inhomogeneous: sometimes in the works consulted, only the presence of the species is recorded (e.g., Bulgarelli, 1972; Bartolomei, 1974). Even when the number of remains and/or of the individuals is indicated, however, data are hardly comparable. Therefore, we chose to mention here only the number of remains and their percentages. These were calculated either on the micromammals only (e.g., Bartolomei, 2002, 2005; Dini *et al.*, 2008; Bona, 2011), on the total of the macromammals only, (e.g., Barker *et al.*, 1990; Cassoli & Tagliacozzo, 1994), or on the total of micro and macromammals (e.g., Sorrentino, 1978; Wilkens, 1990, 1996b, 2003a, b). Consequently, these percentages might be somewhat misleading and thus have to be considered merely indicative. As in the vast majority of the sites in the rest of Europe, *S. vulgaris* is present in Italy with very

Table 6: List of Italian sites with *Sciurus vulgaris* remains, their age and geographic area. Alt. a.s.l.: altitude above sea level; MIS: Marine Isotope Stages; Radiometric dating (ka BP) are not calibrated; n.: number of red squirrel remains; %: percentage calculated on: a) large mammals only, b) small mammals only, c) micro and macromammals.

Site	Region	Alt. a.s.l.	Tipology	Age	MIS	Culture/ Industry	radiometric dating (ka)	n.	%	References
Ciota Ciara	Piedmont	670	cave	Late Pleistocene	5	Mousterian		1	0.14 ^a	Arzarello <i>et al.</i> , 2012
Arma delle Manie (layers VII-III)	Liguria	250	cave	Late Pleistocene	4	Mousterian		1	0.24 ^a	Abbassi, 1999
Torre Nave	Calabria	8	cave	Late Pleistocene	3	Mousterian		1	2.00 ^b	Bulgarelli, 1972
Cava Salnova (layer II)	Lombardy	775	cave	Late Pleistocene	3		35.1 - 34.2	1	2.00 ^b	Bona, 2011
Arene Candide (P13)	Liguria	90	cave	Late Pleistocene	2		25.6	1	0.24 ^a	Cassoli & Tagliacozzo, 1994; this work
Arma dello Stefanin (layer V)	Liguria	440	cave	Late Pleistocene	2	Epigravettian	<12.7	7	0.28 ^a	Barker <i>et al.</i> , 1990
Dalmeri	Trentino Südtirol	1240	shelter	Late Pleistocene	2	Epigravettian	11.3	1	1.02 ^b	Bartolomei, 2002, 2005
Cogola (US 19)	Trentino Südtirol	1075	shelter	Late Pleistocene	2	Epigravettian	10.6 - 10.4	4	40.00 ^b	Bartolomei, 2005
Arene Candide (M5-1)	Liguria	90	cave	Late Pleistocene	2	Epigravettian	11.7 - 9.9	97	1.92 ^a	Cassoli & Tagliacozzo, 1994; this work
Santuario della Madonna (L57)	Calabria	50	cave	Late Pleistocene	2	Epigravettian	10.1	1		Di Canzio, 2004; this work
Colombi	Liguria	30	cave	Late Pleistocene?				1		Mimieri <i>et al.</i> , 1995
Generosa (layer Cun. 0)	Lombardy	1450	cave	Pleist.-Holocene	2/1			1	0.4 ^b	Bona <i>et al.</i> , 2009
Edera	Friuli Venezia Giulia	210	cave	Holocene	1	Mesolithic		1		Boschian & Pitti, 1984
Pradstel	Trentino Südtirol	250	shelter	Holocene	1	Mesolithic		1		Bartolomei, 1974
Cogola (US 16-18)	Trentino Südtirol	1075	shelter	Holocene	1	Souveterrian	9.8	3	21.43 ^b	Bartolomei, 2005
Romagnano III (AC 6-9)	Trentino Südtirol	190	shelter	Holocene	1	Souveterrian		36	12.04 ^b	Bartolomei, 1974, 2005
Soman	Veneto	120	shelter	Holocene	1	Castelnovian		1	2.38 ^a	Tagliacozzo & Cassoli, 1992; this work
Frea IV	Trentino Südtirol	1930	shelter	Holocene	1	Castelnovian	9.6 - 9.4	5	2.51 ^b	Angelucci <i>et al.</i> , 1999
Romagnano III (ABI-2)	Trentino Südtirol	190	shelter	Holocene	1	Castelnovian		5	2.51 ^b	Bartolomei, 1974, 2005
Latronico 3 (cuts 26-40)	Basilicata	760	cave	Holocene	1	Castelnovian	<7.4	2	2.13 ^b	Dini <i>et al.</i> , 2008
Mora Cavorso	Latium	715	cave	Holocene	1			1		this work
Continenza	Abruzzi	710	cave	Holocene	1	Neolithic	6.6 - 6.2	3	1.64 ^c	Wilkins, 1990; Di Canzio, 2004
Santo Stefano di Ortucchio	Abruzzi	780	settlement	Holocene	1	Neolithic	6.6	1	0.31 ^c	Radi & Wilkens, 1989
Sant'Angelo Montagna dei Fiori	Abruzzi	600	cave	Holocene	1	Neolithic		1	0.27 ^c	Wilkins, 1996, 2003a
Capo d'Acqua	Abruzzi	370	settlement	Holocene	1	Neolithic		1	2.56 ^c	Wilkins, 2003a
Catignano	Abruzzi	205	settlement	Holocene	1	Neolithic	6.3 - 5.9	1	0.10 ^c	Wilkins, 2003a, 2003b
Latronico 3	Basilicata	760	cave	Holocene	1	Neolithic		1	0.16 ^c	Sorrentino, 1978
Mulino Sant'Antonio	Campania	300	settlement	Holocene	1	Neolithic		6	0.85 ^a	Albarella, 1988
Maddalena di Muccia	Marche	450	settlement	Holocene	1	Neolithic		1	0.16 ^c	Wilkins, 2003a
Ripabianca di Monterado	Marche	~160	settlement	Holocene	1	Neolithic	6.3 - 6.1	1	0.12 ^c	Wilkins, 2003a
Bressanone - Stufles	Trentino Südtirol	570	settlement	Holocene	1	Neolithic		2	0.46 ^a	Tecchiati & Zanetti, 2013
Castel Corno	Trentino Südtirol	846	cave	Holocene	1	Bronze		1		Fontana <i>et al.</i> , 2009

limited remains, with the partial exceptions of the Arene Candide and the Riparo di Romagnano III.

With regard to the typology of sites, the Late Pleistocene and the early Holocene ones consist exclusively of caves and rockshelters, distributed from the sea level to over 1900 m a.s.l. During the middle Holocene, open-air sites appear alongside the caves and rockshelters, and are distributed between the hills and the low mountain areas (at a maximum altitude of 850 m a.s.l.).

The sites are geographically distributed, although in inhomogeneous fashion, along the entire continental Italy. A concentration in the distribution appears in the North-East and in Adriatic side of Central Italy. This is not likely to reflect the real spread of *S. vulgaris* in the chronologies considered in this work, as it could result both by the type of the sites, in the vast majority anthropogenic, from a methodological bias in the study of the faunal remains, and especially from the historical lag in the study of micromammals in Central and Southern Italy (see Kotsakis *et al.*, 2003; Salari, 2014).

Considering all of the above, on the base of the data collected, we can hypothesize that *S. vulgaris* occurs in Italy at the beginning of the Late Pleistocene and that it soon spread in the entire continental Italy. Earlier than LGM it was probably widespread in Italy from Liguria (Arene Candide) and Lombardy (Cava Salnova) to Calabria (Grotta di Torre Nave). During the Lateglacial, red squirrel re-colonised the Venetian Prealps (Rockshelters Cogola and Dalmeri) and probably also the Lombardian Prealps (Caverna Generosa), spreading from its *glacial refugia* located in the Central and Southern part of the Peninsula and perhaps also in the coastal Liguria region, and following the glacier recession and the woodland expansions. Subsequently, in the early Holocene, it started to colonise the Upper Adige Valley (Rockshelters of Soman, Pradstel and Romagnano III), the eastern Alps (Riparo Frea IV) and the inner areas of the Apennines (Mora Cavorso).

With regard to the hypotheses on the accumulation agents of the red squirrel remains, Wilkens (1990, 2003a) hypothesized that some rodents such as vole, edible dormouse and red squirrel were consumed by man at Grotta Continenza, while Alhaique (1994), Cassoli & Tagliacozzo (1994) and our taphonomic analysis (see 6. Bone Surface Modifications) showed how red squirrel was at least in part brought in by humans at the Arene Candide, where it was even likely to be consumed. Outside of Italy, the finding of four sub-entire skeletons of red squirrel in the perialpine Swiss Neolithic site of Egolzwil 3 has suggested to Higham (1967) the exploitation of the rodent for fur, but even then taphonomic or archaeological evidences are not adduced. On the other hand, both Bartolomei (1974, 2002, 2005) and Di Canzio (2004) indicate generically the Strigiformes as responsible for the accumulation of micromammals from the Rockshelters Dalmeri, Cogola, Romagnano III and of Pradstel and from Santuario della

Madonna. For this last site, our new data (see 6. Bone Surface Modifications), combined with those already known regarding the edible dormouse (Fiore *et al.*, 2004), indicate that the red squirrel could be preyed and consumed by humans.

9. RAPTORS AND SQUIRRELS

From the excursus above it is clear that red squirrel fossils are quite rare, as they occur in relatively few sites, and almost always with very few remains. This scarcity in fossil deposits has been linked, on one hand, to its exclusive woodland habitat, which does not favour the fossilization processes of bones (Kurtén, 1968; Kotsakis, 2008); on the other hand, this rarity can be attributed to the difficulty of capture by birds of prey (Chaline, 1972; Kotsakis, 2008).

In this regard, it may be interesting to note that even today few red squirrel remains occur in the pellets of birds of prey. Table 7 shows the results of a search (certainly not exhaustive) on the diet of birds of prey in Europe. For several species that prey on red squirrels (*Aquila fasciata*, *A. heliaca*, *Circus aeruginosus*, *Falco cherrug* and *Milvus migrans*, among Falconiformes, *Aegolius funereus* and *Strix uralensis*, among Strigiformes, and *Corvus corax* among Passeriformes) we found only few works. In the majority of the over 300 papers consulted, the occurrence of red squirrel remains is not recorded, and it seems that the rodent is not preyed by *Tyto alba* and *Athene noctua*, Strigiformes, nor by *Falco tinnunculus* and *Accipiter nisus*, Falconiformes, whilst it falls only occasionally in the diet of *Strix aluco* and *Asio otus*, Strigiformes. Thus, the red squirrel is preyed mainly from Falconiformes, particularly *Accipiter gentilis*, *Aquila chrysaetos* and *Buteo buteo*, while among the Strigiformes only the predation by *Bubo bubo* seems to be relevant. This is also understandable considering the arboreal and diurnal habits of this rodent.

We can also note that the red squirrel is preyed mostly by those birds of prey which prefer hunting middle/small-sized mammals and/or birds, whereas it falls only occasionally in the diet of those that feed mainly on micromammals. For instance, in the pellets of *A. otus*, which feeds especially on micromammals, red squirrel remains appear only at one site (Rocca di Mezzo, Abruzzi: 3 finds out of 201) out of the 14 sites of Central and Northern Italy considered (Capizzi, 2000). Conversely, as it is known, among the Strigiformes *B. bubo* is the species that preys on other birds more frequently (Bergman, 1961; Frey & Walter, 1986; Roguin, 1988; Papageorgiou *et al.*, 1993; Tormen & Cibien, 1993; Förstel, 1995; Alivizatos *et al.*, 2005; Leditznig, 2005; Wassink & Bijlsma, 2006; Sándor & Ionescu, 2009; Bayle & Schauls, 2011; Mikkola & Tornberg, 2014). Regarding to the Falconiformes, the most frequent preys of *A. chrysaetos* are lagomorphs and young roe

deer, among the mammals, as well as corvids and tetraonids, among the birds (Bergman, 1961; Aldasoro, 1975; Austruy & Cugnasse, 1981; Pedrini & Sergio, 2001, 2002); *B. buteo* has a more varied diet, including amphibian (frogs), reptiles (colubrids and lacertids), birds (columbids, turdids and corvids), smaller-sized mammals (lagomorphs) and micromammals (mostly *Microtus* sp.) (Bergman, 1961; Mañosa & Cordero, 1992; Haberl, 1995; Sergio *et al.*, 2002; Zuberogoitia *et al.*, 2006; Šotnár & Obuch, 2009), whereas *A. gentilis* feeds almost exclusively on birds (columbids, tetraonids, corvids) (Bergman, 1961; Marquiss & Newton, 1982; Garrigues *et al.*, 1990; Penteriani, 1997; Ivanovsky, 1998; Padial *et al.*, 1998; Šotnár, 2000; Petty *et al.*, 2003; Rutz, 2004; Gylazov, 2005; Tornberg & Reif, 2007). Only in one case (not showed in Table 7), as an exception, *S. vulgaris* represented the most frequent prey: Bergman (1961) reports that amongst the food items of *A. gentilis*

examined at Sulkava (Finland) in 1955, the red squirrel reached 46% of the remains, whereas in previous years (1949-54) it did not exceed 6%. Finally, at least one case of *A. nisus*' egg predation by red squirrel is documented (Newton, 1991).

As it is known, the bone remains of non-volant micromammals in archaeological and paleontological caves are mainly originated by allochthonous sources, such as deposition after the ingestion and digestion from predators (Chaline *et al.*, 1974; Andrews & Nesbit-Evans, 1983; Andrews, 1990; Kowalski, 1990; Fernández-Jalvo & Andrews, 1992). The main micromammal predators are the birds of prey, diurnal (Falconiformes) and nocturnal (Strigiformes), and mammalian carnivores (mainly fox and mustelids). Falconiformes and mammalian carnivores produce greater destructive action on the bones, which can also affect the sample sizes and the recognisability of the specimens. Taphonomic analyses on fossil micromammal

Table 7: Birds that prey on squirrels; n. work: number of consulted works, in brackets the data related to Italian sites; *Sciurus*: number of works with predation of the squirrel, in brackets the data related to Italian sites; % *Sciurus*: percentages of the squirrel remains, provided by Korpimäki, 1988 (*Aegolius funereus*); Capizzi, 2000 (*Asio otus*); Bergman, 1961; Frey & Walter, 1986; Roguin, 1988; Papageorgiou *et al.*, 1993; Tormen & Cibien, 1993; Förstel, 1995; Alivizatos *et al.*, 2005; Leditznig 2005; Wassink & Bijlsma, 2006; Sándor & Ionescu, 2009; Bayle & Schauls, 2011; Mikkola & Tornberg, 2014 (*Bubo bubo*); Bergman, 1961; Sunde *et al.*, 2001; Gryz *et al.*, 2008; Roulin *et al.*, 2008 (*Strix aluco*); Kocijančič, 2013 (*Strix uralensis*); Bergman, 1961; Marquiss & Newton, 1982; Garrigues *et al.*, 1990; Penteriani, 1997; Ivanovsky, 1998; Padial *et al.*, 1998; Šotnár, 2000; Petty *et al.*, 2003; Rutz, 2004; Gylazov, 2005; Tornberg & Reif, 2007 (*Accipiter gentilis*); Bergman, 1961; Aldasoro, 1975; Austruy & Cugnasse, 1981; Pedrini & Sergio, 2001, 2002 (*Aquila chrysaetos*); Gil-Sánchez *et al.*, 2000 (*Aquila fasciata*); Horváth *et al.*, 2010 (*Aquila heliaca*); Bergman, 1961; Mañosa & Cordero, 1992; Haberl, 1995; Sergio *et al.*, 2002; Zuberogoitia *et al.*, 2006; Šotnár & Obuch, 2009 (*Buteo buteo*); Tornberg & Haapala, 2013 (*Circus aeruginosus*); Frey & Senn, 1980 (*Falco cherrug*); Bergman, 1961 (*Milvus migrans*); Laudet & Selva, 2004, 2005 (*Corvus corax*); +: presence only recorded.

common name	species	n. work		<i>Sciurus</i>		% <i>Sciurus</i>
boreal owl	<i>Aegolius funereus</i>	1	(0)	1	(0)	0.24
long-eared owl	<i>Asio otus</i>	36	(10)	1	(1)	1.49
little owl	<i>Athene noctua</i>	15	(8)	0	(0)	
Eurasian eagle-owl	<i>Bubo bubo</i>	52	(4)	12	(1)	0.13 - 3.76
tawny owl	<i>Strix aluco</i>	33	(12)	4	(0)	0.04 - 0.72
Ural owl	<i>Strix uralensis</i>	1	(0)	1	(0)	+
barn owl	<i>Tyto alba</i>	85	(50)	0	(0)	
northern goshawk	<i>Accipiter gentilis</i>	25	(1)	11	(1)	0.60 - 9.25
Eurasian sparrowhawk	<i>Accipiter nisus</i>	5	(0)	0	(0)	
golden eagle	<i>Aquila chrysaetos</i>	15	(2)	5	(2)	7.14 - 7.74
Bonelli's eagle	<i>Aquila fasciata</i>	6	(0)	1	(0)	+
eastern imperial eagle	<i>Aquila heliaca</i>	2	(0)	1	(0)	0.08
common buzzard	<i>Buteo buteo</i>	22	(4)	6	(1)	0.50 - 2.82
western marsh harrier	<i>Circus aeruginosus</i>	1	(0)	1	(0)	0.14
saker falcon	<i>Falco cherrug</i>	1	(0)	1	(0)	0.82
Eurasian hobby	<i>Falco subbuteo</i>	1	(0)	0	(0)	
Eurasian kestrel	<i>Falco tinnunculus</i>	3	(1)	0	(0)	
black kite	<i>Milvus migrans</i>	1	(0)	1	(0)	+
northern raven	<i>Corvus corax</i>	2	(0)	2	(0)	4.40

assemblages show that in most cases the agents that have brought small mammal remains into the paleontological and archaeological caves are Strigiformes, particularly *B. bubo*, *S. aluco* and *T. alba* (see Fernández-Jalvo & Andrews, 1992; Fernández-Jalvo, 2003; Belmaker & Hovers, 2011; Marder *et al.*, 2011; Desclaux *et al.*, 2011; Hanquet, 2011; Salari, 2014).

Considering the above, the relative rarity of fossils remains of red squirrel in paleontological and archaeological contexts can be related to multiple factors. In the open-air sites, this scarcity can be either attributed to the strictly forestry habitat of the rodent, which does not favour the processes of bone fossilization, or to the difficulty of catch by predators. On the other hand, red squirrel remains are hard to find also in cave sites both because of the difficulty of catch by the birds of prey and, even more importantly, because the Falconiformes, i.e. the main predators of red squirrel, go to caves less frequently than the Strigiformes.

Finally, with regards to the remains brought into the sites by humans, several factors come into play, such as food, economic and cultural choices (see below).

10. SQUIRRELS AND MEN IN THE PREHISTORY

As above mentioned, the presence of *S. vulgaris* remains in the Italian prehistoric sites is inhomogenous and often not quantified. It is also strongly affected by the methodology of research and by the studies conducted on the single deposits of the palaeontological or archaeological sites. However, excluding rare exceptions (i.e. Arene Candide and the Riparo di Romagnano III), red squirrel remains are usually very rare in the anthropic sites of the Late Pleistocene and of the early Holocene. The majority of studies used to indicate the Strigiformes or other birds of prey as the main agents responsible for the accumulation of the red squirrel remains (e.g., Bartolomei, 1974, 2002, 2005; Di Canzio, 2004).

Oldest presences of red squirrel remains in Italian sites with human frequentation are Grotta della Ciota Ciara, Arma delle Manie and Grotta di Torre Nave (Tab. 6), with Mousterian industries, thus produced by *Homo neanderthalensis*. In this sites, red squirrel and other small vertebrate remains have not been connected to anthropic action, although aimed taphonomic analyses do not seem to have been conducted.

Only occasionally humans are identified, at least partially,

as the agents responsible for the accumulation of red squirrel remains in archaeological deposits. Wilkens (1990, 2003a) hypothesized that red squirrel were consumed by man at Grotta Continenza, although neither taphonomic nor archaeological evidence is provided. In other Neolithic and early Bronze Age sites, however, the red squirrel remains were not considered evidences of human activity (e.g., Albarella, 1988; Wilkens, 2003b; Fontana *et al.*, 2009; Tecchiati & Zanetti, 2013).

Only in recent years detailed taphonomic analyses have highlighted that the small-game activity, i.e. the hunt to the small vertebrates (birds, small mammals, reptiles), should not be considered as one of the last skills acquired by anatomically modern man, linked especially to the use of the bow, as it was formerly believed, but this practice was already performed by Neanderthal man (Stiner, 1994; Thun Hohenstein *et al.*, 2001; Peresani *et al.*, 2011), and perhaps as old as the genus *Homo* (see Fernández Jalvo *et al.*, 1999). Apart from rare exceptions, Italian taphonomic studies on small mammal remains are relatively rare (e.g., Alhaique, 1996, 2003; Tagliacozzo & Fiore, 1998; Fiore, 2003; Fiore *et al.*, 2004; Mussi *et al.*, 2008; Romandini *et al.*, 2012) and those relating to the red squirrel still less (Alhaique, 1994; Cassoli & Tagliacozzo, 1994). Thus, we can talk about a relationship between humans and squirrels in the prehistory of Italy is nearly impossible and necessarily limited to the site of Arene Candide.

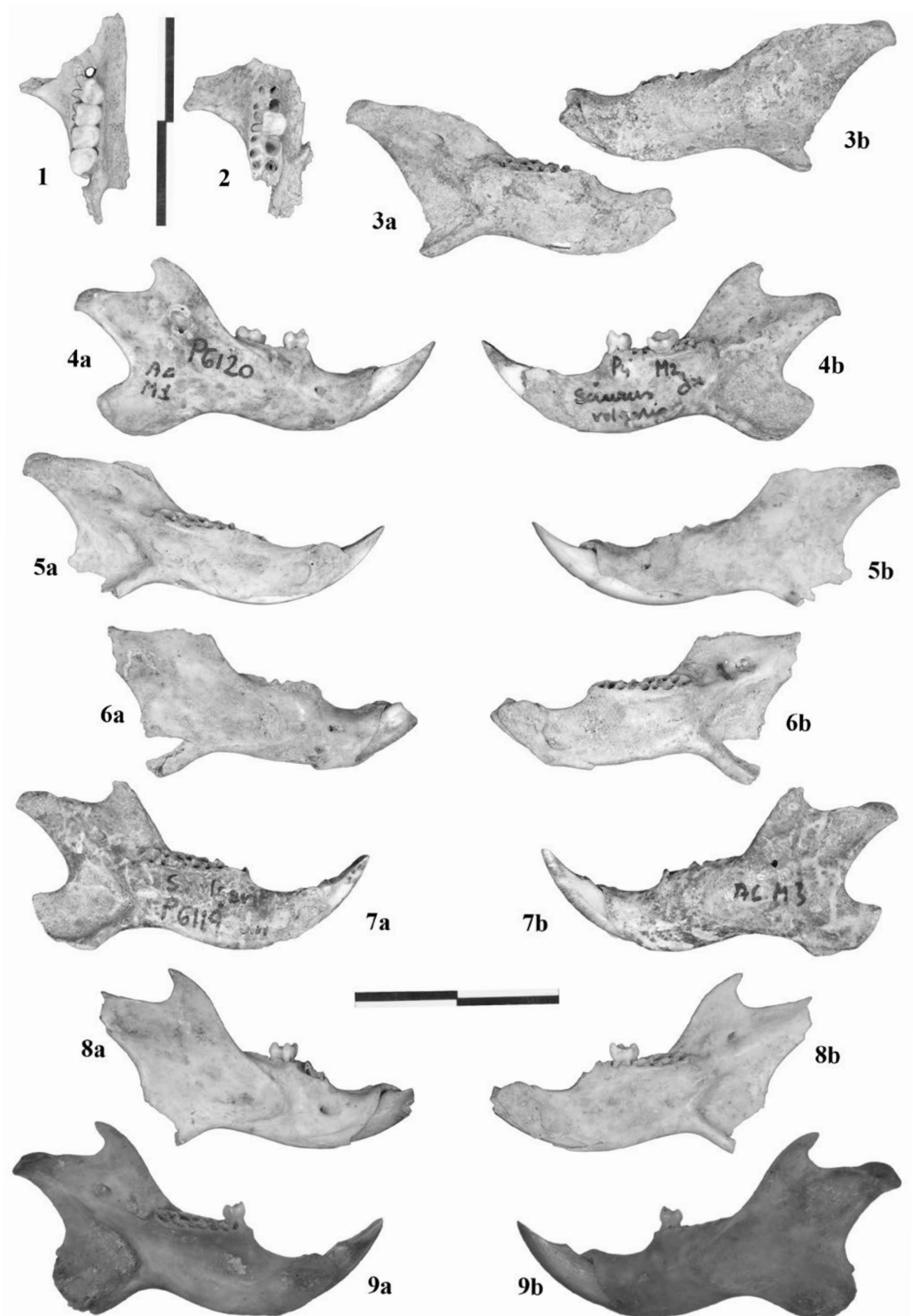
So far, the only certain evidence of the introduction of red squirrel in an anthropic site and of their consumption by humans were related to the final phase of the Upper Palaeolithic of the Arene Candide (Alhaique, 1994; Cassoli & Tagliacozzo, 1994). New taphonomic investigations confirm and expand our knowledge (see 6. Bone Surface Modifications). New evidences related to the Upper Palaeolithic layers of the Santuario della Madonna and of the early Holocene of Mora Cavorso, although based just on one hemimandible per site, add up to the old and new data from the Arene Candide.

Archaeological evidence and the new taphonomic analyses on the red squirrel remains of the Arene Candide provide key information about both their exploitation as food and their role in ritual practices.

Except for the right hemimandible from the bottom layers of the Pleistocene sequence (P13), all the other bones (NISP 97, referred to at least 12 individuals; Cassoli & Tagliacozzo, 1994) come from the final Epigravettian levels, especially from the upper layers M2 and M1, where they make between 2.5 and 4.5% of the

Plate I

Sciurus vulgaris, occlusal view of maxillary bones: 1) and 2) Caverna delle Arene Candide, layer M1; labial and lingual view of mandibles: Caverna delle Arene Candide: 3) and 4) from layer M1; 5) from layer M2; 6) and 7) from layer M3; 8) Grotta Mora Cavorso; 9) Grotta Santuario della Madonna. Scale bar: 2 cm.



faunal assemblage (Cassoli & Tagliacozzo, 1994). Most common skeletal portions are cranial bones, especially the mandibles, and metapodials (Tab. 1); bones of the forelimbs and hindlimbs are also present, except for the phalanges, whilst bones of the spine are absent.

New taphonomical data also allow to recognise several human uses of the squirrel at the Arene Candide during the final Palaeolithic. Several cut marks, peeling, *arrachement*, impact marks and fractures on the fresh bones validate the hypothesis of a carcass processing aimed at food consumption, starting from skinning (on the mandible and the metapodials), continuing with the disarticulation and the sectioning into smaller parts, and ending with the cooking directly on embers (localised burns) and with the consumption (bite marks).

It is also important to highlight the use of the small squirrel bones as active tools (awls) or as part of tools (handles), as shown by the carving and polishing marks identified on two femurs.

The abundance of red squirrel remains in layers M5-M1 is compliant with the grave goods of 6 burials (out of 15) of the Epigravettian necropolis in the site (burials VB, VIII, IX, X, XI and XV), which contained several skeletal elements of the limbs and the tails, mainly associated with young individuals' graves (Cardini, 1980; Alhaique & Molari, 2006). The limb bones were found in several graves: for example, grave X held some foot bones inside a shellfish valve (*Glycimerys* sp.); grave VIII held bones of 5 different limbs (Cardini, 1980; Alhaique & Molari, 2006).

Overall, more than 560 caudal vertebrae were found in the burials, 423 of which came from grave VIII. An estimate based on the number of vertebrae forming a red squirrel tail and on the biggest ossified vertebrae suggested to Cassoli & Tagliacozzo (1994) that over 60 red squirrel tails might have been used as personal ornaments or decorations for clothes, 10 of which in grave VB, 3 in grave XI, 4 in grave XV and at least 40 in grave VIII. Cardini (1980) and Alhaique & Molari (2006) further hypothesized that the red squirrel tails from grave VB were part of a "pectoral", whilst those from grave VIII, accurately disposed in rows, were part of a "cape". It is to be highlighted that vertebrae and limb bones are often impregnated by ochre (Cardini, 1980; Alhaique & Molari, 2006), which most likely covered the whole inumated. In this context, it has to be added that a mandible from layer M2, intentionally disarticulated from the skull, shows traces of ochre.

Further than suggesting that red squirrel tails were used as decorations, data from the Arene Candide indicate also the ritual value of this rodent (see the association of the tails with young individuals, the hindlimbs put in mollusk valves and the ochre coloration).

11. CONCLUSIONS

The finding of a mandible of *Sciurus vulgaris* at Mora Cavorso (Simbruini Mountains, Latium, Central Italy) and the reanalysis of the red squirrel remains from Arene Candide (western coast of Liguria, Northern Italy), Riparo Soman (Lessini Mountains, Veneto, Northern Italy) and Santuario della Madonna (northern Tyrrhenian coast of Calabria, Southern Italy) add fresh, crucial data to the knowledge of the size and of the palaeobiogeography and palaeoecology of this rodent in the Late Pleistocene and the less recent Holocene of Italy. Taphonomic analysis sheds light on the relationship between humans and red squirrels in the Italian prehistory.

Probably, the presence of *S. vulgaris* in Italy dates to the beginning of the Late Pleistocene (MIS 5). The rodent then, at least since MIS 3, spread throughout mainland Italy. Although we lack clear fossil records in deposits dated the LGM, probably during this cold phase of Latest Pleistocene some areas of Italy have been a *glacial refugium* for red squirrel, and they have played the role of source for northwards postglacial recolonization. But the Italian peninsula probably was also an area of endemism (Bilton *et al.*, 1998), at least at the subspecies level.

At present, three subspecies of *S. vulgaris* are known to live in Italy: *S. vulgaris fuscoater* is spread in Northern Italy, consistently with the other central-European populations of the same subspecies; *S. vulgaris italicus* lives in Central Italy and possibly in part of the South; finally, the presence of *S. vulgaris meridionalis* Lucifero, 1907, is limited to Calabria region and part of Basilicata (Massiccio del Pollino). The Calabrian subspecies shows more differences with the other Euroasiatic subspecies, both in the morphology (Cavazza, 1913; Toschi, 1965; Siderowicz, 1971) and the molecular biology (Grill *et al.*, 2009), to the point that Gippoliti (2013) proposed the rise to rank of the species (*Sciurus meridionalis*). Also Amori *et al.* (2014), after a modern statistical re-analysis of the historical data by Cavazza (1913), have recently shown that the Calabrian population is homogenous and distinct from the remaining Italian populations, especially looking at the different cranial measurements and the greater length of the mandible. Although other authors provide slightly different measurements (e.g. Miller, 1912 and Toschi, 1965 indicate a variability between 31.0 and 33.6 mm for *S. vulgaris italicus*, while Toschi, 1965 provides a measurement of 33.9 mm for *S. vulgaris meridionalis*), according to Cavazza (1913) and Amori *et al.* (2014) the mandible length of Italian populations of *S. vulgaris fuscoater* ranges between 27.3 and 31.0 mm, with a mean of 29.1 mm, whilst that of *S. vulgaris italicus* ranges between 28.9 and 31.2 mm, with a mean of 29.6 mm, and that of *S. vulgaris meridionalis* ranges between 31.8 and 34.1 mm, with a mean of 33.2 mm. It might not be a case that the biggest mandible in our sample is that from the Santuario della Madonna (Calabria) (Tab. 4), however it is not possible

to infer whether the Calabrian squirrels had already completed their differentiation process from the other Italian populations during the final phases of the Late Pleistocene by looking at just one specimen (*una rondine non fa primavera!*).

Considering the size of the mandible and of the long limb bones of *S. vulgaris* of the Italian peninsula and of the Alpine region, it emerges that the squirrels of the final Late Pleistocene and of the early Holocene were bigger than the extant ones. On the base of the available data, it can be inferred that the rodent would have gone through a progressive decreasing in size starting from the middle Holocene (Neolithic, V - III millennium BC) up to present day.

With regard to the hypotheses on the accumulation agents of *S. vulgaris* remains, our study has been able to answer some questions and to find more interesting research inputs. First of all, we showed how the human contribution to the accumulation of red squirrel remains had been undervalued.

The site of Arene Candide provides the most crucial information on the relationship between humans and squirrels, based both on the new taphonomical data and the discovery of the limb bones and of the tails in several burials of the necropolis. The tails might have been used as decorations for clothes or as proper furs, and they played a key role in the funerary ritual of the human deceased (especially the young ones), along with the limbs.

Anthropic marks found on the red squirrel bones of the human occupation layers (e.g., rare cut produced by lithic tool, peeling and *arrachement*, localised combustion) indicate the use of the red squirrel as food. This interpretation is strengthened in this context by the recovery of small mammal and bird remains also in the graves. These brand new analyses give an important contribution to the interpretation of marks that are often considered of non-anthropogenic nature, as lacking of the more obvious cut marks. Our study shows and confirms that the carcass of small vertebrates hardly keeps any sign of processing, except for some specific cases. The process can be still testified by other traces, such as ripping, torsion and impacts, which are harder to identify. Despite the limited amount of remains (one find per site), the new taphonomical evidences from the Upper Palaeolithic of the Santuario della Madonna and of the early Holocene of Mora Cavorso – and possibly, Riparo Soman – suggest that the food exploitation of small mammals such as the red squirrel was a very widespread practice in prehistoric times.

As for the role played by non-human predators in the accumulation of red squirrel remains, diurnal birds of prey (Falconiformes) appear more responsible for this phenomenon than the mammalian carnivores or the nocturnal birds of prey (Strigiformes). This may explain the relatively low number of *S. vulgaris* remains in paleontological and archaeological sites, especially in

caves, as the Falconiformes go to caves less frequently than the other predators of red squirrel, such as the Strigiformes.

NOTE

This work is the result of close collaboration among the authors, yet each one dealt with the drafting of specific chapters. Brief history of squirrels in the Western Palearctic and Description and comparisons: Salari; Bone surface modifications: Fiore; *Sciurus vulgaris* in Italy: Rolfo and Salari; Palaeobiogeography and palaeoecology and Raptors and squirrels: Silvestri and Salari; Squirrels and man in the Prehistory: Tagliacozzo; Introduction, Stratigraphic notes on the sites, Materials and methods and Conclusions: all the authors.

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