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Review of the first occurrences of some selected Late Pleistocene Italian mammals

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ABSTRACT

*The Late Pleistocene certainly represents a crucial period for faunal renewal, especially in the Italian area, characterised by diverse climatic and environmental conditions. The critical reappraisal of data on several taxa of mammals that occur for the first time in Italy during the Late Pleistocene (particularly *Crocidura gr. suaveolens*, *Lepus timidus*, *Sicista spp.*, *Cricetulus migratorius*, *Arvicola gr. amphibius-italicus*, *Microtus (Terricola) gr. savii-brachycercus*, *Mammuthus primigenius*, *Mustela erminea*, *Lynx lynx*, *Coelodonta antiquitatis*, *Alces alces*, *Rangifer tarandus*, *Cervus elaphus* and *Dama dama*) has made it possible to verify their real biochronological limits, on the basis of fully recognisable morphological features. This review also provides an opportunity to highlight the difficulties involved in establishing the elements that could enable the identification of Faunal Units valid for Italian territory as a whole. Moreover, previous attempts to identify Faunal Units corresponding to the two most important phases of the Late Pleistocene (last interglacial and last glacial) have been re-examined. The two Apulian local faunas previously identified as type of the Late Pleistocene Faunal Units do not have biochronological features that could justify their validity for the whole of mainland Italy, but can only be considered valid locally, in a more limited geographical context.*

Key words: Late Pleistocene, Italy, mammals, Biochronology.

RIASSUNTO

Il Pleistocene superiore rappresenta certamente un periodo cruciale per il rinnovamento faunistico, soprattutto nell'area italiana, caratterizzata da diverse condizioni climatiche e ambientali. La revisione critica dei dati di numerosi taxa dei mammiferi che compaiono per la prima volta in Italia durante il Pleistocene superiore (in particolare *Crocidura gr. suaveolens*, *Lepus timidus*, *Sicista spp.*, *Cricetulus migratorius*, *Arvicola gr. amphibius-italicus*, *Microtus (Terricola) gr. savii-brachycercus*, *Mammuthus primigenius*, *Mustela erminea*, *Lynx lynx*, *Coelodonta antiquitatis*, *Alces alces*, *Rangifer tarandus*, *Cervus elaphus* e *Dama dama*) ha permesso di verificarne i reali limiti biocronologici, sulla base di caratteri morfologici pienamente riconoscibili. Questa revisione offre anche l'occasione per mettere in luce le difficoltà di stabilire gli elementi che potrebbero consentire l'individuazione di Unità Faunistiche valide per l'intero territorio italiano. Sono stati, inoltre, riesaminati i precedenti tentativi di identificare Unità Faunistiche corrispondenti alle due fasi più importanti del Pleistocene superiore (ultimo interglaciale e ultimo glaciale). Le due associazioni faunistiche pugliesi precedentemente identificate come tipo delle Unità Faunistiche del Pleistocene superiore non presentano caratteri biocronologici che ne giustificano la validità per l'intero territorio dell'Italia continentale, ma possono ritenersi valide solo localmente, in un contesto geografico più ristretto.

Parole chiave: Pleistocene superiore, Italia, mammiferi, Biocronologia.

INTRODUCTION

A large number of open-air or cave-based fossiliferous deposits relating to the late Middle Pleistocene and, above all, to the Late Pleistocene have been identified in mainland Italy. These deposits, corresponding to the late Aurelian Mammal Age, are rich in mammal remains, characterised especially by perissodactyls (such as *Equus ferus* and *E. hydruntinus*) and artiodactyls (*Bos primigenius*, *Bison priscus*, *Cervus elaphus* and *Dama dama*).

An updated reappraisal of these Late Pleistocene deposits, which often also yield small mammal species represented primarily by arvicolid remains, makes it possible to establish and/or to verify the biochronology of this time span, corresponding to the last interglacial and the last glacial periods, from Marine Isotope Stage (MIS) 5e to MIS 2.

Biochronological analysis using Faunal Units (FUs), based on the first occurrence (FO) and last occurrence (LO) of one or more taxa in a faunal association, is an increasingly effective tool the more it is based on species that are particularly sensitive to environmental and climatic variations: these variations in fact produce continuous faunal changes that are often well dated.

Gliozzi *et al.* (1997) used the data available at that time (including those concerning small mammals) to establish a biochronological scale valid for the Italian Peninsula, shared by all researchers (including malacologists and ostracologists) who worked on the Plio-Pleistocene continental deposits. The proposed biochronological scheme received general approval and has been used by all Italian scholars. Over the past twenty-five years, new geological research, geochemical methods, radiometric dating, fossil discoveries, and systematic reviews of material collected has led to a large amount of new data. As a result, there have been a series of proposals for modification or integration of the biochronological chart (for the entire period of time or for a part of it) with the unification of various FUs, introduction of further FUs, and establishment of a new Mammal Age (e.g., Petronio and Sardella, 1999; Palombo *et al.*, 2004; Palombo, 2007, 2009, 2018; Palombo and Sardella, 2007; Masini and Sala, 2007, 2011; Petronio *et al.*, 2007, 2011; Sardella and Palombo, 2007; Bellucci *et al.*, 2015). In the same period, works based on small mammals were also published (Kotsakis *et al.*, 2003; Sala and Masini, 2007). Finally, scales have been proposed,

based on the concept of «palaeocommunity» (Raia *et al.*, 2006) as a non-alternative but integrative method of the biochronological scale based on FO / LO of taxa, or on the concept of Faunal Complexes (Palombo, 2014).

Since the scheme of Gliozzi *et al.* (1997) continues to be a point of reference for many researchers and because it has been used for comparisons with the faunas of various European countries (e.g., Alberdi *et al.*, 1998, Barishnikov, 2002, Palombo and Valli, 2004, Palombo *et al.*, 2006; Kostopoulos *et al.*, 2007; Nomade *et al.*, 2014), it will be used provisionally in this work, waiting for a new collective effort to update/modify/change it using all new data.

As for the Late Pleistocene, Gliozzi *et al.* (1997) did not propose any FU, in particular because no FU could be considered representative for Italian territory as a whole over this specific period, due to the microclimatic and environmental conditions. Subsequently, Petronio *et al.* (2007) proposed the Melpignano and Ingarano FUs for this time period, as representatives of “warm” and “cold” Late Pleistocene faunal assemblages, respectively, pointing out the FOs of the modern *C. elaphus* and *D. dama* (MIS 5e), and *Coelodonta antiquitatis* and *Mammuthus primigenius* (MIS 4/3) as the most significant bioevents. The type localities for these FUs were Cava Nuzzo, in the municipality of Melpignano in Salento, Apulia (Bologna *et al.*, 1994), and Ingarano on the Gargano promontory, Apulia (Capasso Barbato *et al.*, 1992; Petronio *et al.*, 1995; Petronio and Sardella, 1998).

It is worth noting that on the Italian peninsula, which landscape is very complex orographically, habitats with temperate-fresh or temperate-warm climates are almost complementary and occur more or less together on the Tyrrhenian and Adriatic sides of the landmass, both in the glacial and interglacial periods. This characteristic is more evident in the last 200,000 years, when the effects produced by neotectonic volcanism in the central-southern area and the most significant climatic variations since the late Middle Pleistocene can be appreciated (Marra *et al.*, 2014, 2017, 2018a).

The biochronology of several taxa relating to the Late Pleistocene and probably more sensitive to these environmental and climatic stresses is studied in this paper, which discusses their FOs during the time period considered.

METHOD

To test the FOs of mammals that occur in the Late Pleistocene of Italy a literature search was conducted, updating the data published by Gliozzi *et al.* (1997), Kotsakis *et al.* (2003), Sala and Masini (2007), Petronio *et al.* (2007, 2011) and Masini and Sala (2011), relating to the late Middle Pleistocene up to the Holocene.

In the light of the above research, two tables have been realized, for small and middle and large mammals respectively, with the chronological distribution of the taxa occurring in Italy from the late Middle Pleistocene to the present day. Among these taxa, according the recent literature, those occurring for the first time in Italy in the Late Pleistocene were selected. Therefore, their biochronology is discussed, to verify their validity and any biochronological limits, on the basis of fully recognizable morphological features, clear stratigraphic positions and, where possible, radiometric dating.

RESULTS

Small Mammals

The small mammals (Eulipotyphla, Lagomorpha and Rodentia) of the Italian mainland during the Late Pleistocene (late Toringian in terms of the biochronological scale of European small mammals; Fejfar and Heinrich, 1983) belong to two different biogeographical areas (Berto *et al.*, 2019a). Consequently, the FOs of some taxa during this period are limited in their respective areas, roughly divided by a line that joins central-southern Tuscany and central-southern Marche. Species that appeared in central-northern Italy during the Late Pleistocene are *Cricetulus migratorius* (Pallas, 1773), *Sicista betulina* (Pallas, 1779) and *Sicista* cf. *subtilis*. *Microtus (Terri-cola)* gr. *savii-brachycercus* spreads only in the central-southern part of the country. *Crocidura* gr. *suaveolens* and *Arvicola* gr. *amphibi-us-italicus* are present in both areas.

The presence of two other species in central-northern Italy is doubtful. *Mesocricetus newtoni* Nehring 1898 was reported by Berto (2013) and Berto and Rubinato (2013) at the Caverna degli Orsi (Friuli-Venezia Giulia) but is missing as a characteristic element of the central-northern area in Berto *et al.* (2019a). *Arvicola sapidus* Miller, 1908 was reported in Arma delle Manie (Liguria) (Abbassi and Desclaux,

1996) and in Riparo Mochi (Liguria) (Desclaux *et al.*, 2000). A study of further material from Riparo Mochi led Berto *et al.* (2019b) to classify the voles at this site as *A. amphibi-us*. For that reason, we believe that the material previously collected at the two Ligurian sites, and assigned to *A. sapidus*, should be re-examined.

Order Eulipotyphla Waddell, Okada
and Hasegawa, 1999

Family Soricidae Fisher, 1817

Genus *Crocidura* Wagler, 1832

Crocidura gr. *suaveolens* (Pallas, 1811)

In a recent phylogeographic study, Castiglia *et al.* (2017) indicate a time span of between 60 and 149 ka as a cloning period for *Crocidura suaveolens* populations on the Italian peninsula. However, while Castiglia *et al.* (2017) underline an affinity of Italian populations with Balkan ones, Burgin and He (2018) believe that the affinities of small Italian *Crocidura* lie with the populations in Western Europe, which would constitute a different species, *Crocidura gueldenstaedtii* (Pallas, 1811). However, the fossil remains of small *Crocidura* collected in Italy and definitely attributed to *C. suaveolens* (regardless of the species they belong to) are known, in any case, from fossiliferous sites from the Late Pleistocene age (Fanfani, 2000; Kotsakis *et al.*, 2003; 2020) (*C.* gr. *suaveolens* in Fig. 1.a). The species is common at sites in central-southern Italy while its presence is rare in central-northern Italy.

Order Lagomorpha Brandt, 1855

Family Leporidae Fischer, 1817

Genus *Lepus* Linnaeus, 1758

Lepus timidus, Linnaeus, 1758

The mountain hare, *Lepus timidus*, has been reported exclusively from sites of Late Pleistocene age (Sala, 1980, 1990; Bartolomei *et al.*, 1982; Bon *et al.*, 1991; Berto and Rubinato, 2013). However, many hare remains collected from late Middle Pleistocene (Early Toringian) sites are assigned to *Lepus* sp. (Kotsakis, 2008). Consequently, the presence of *L. timidus* among these remains cannot be excluded (Angelone *et al.*, 2020).

Order Rodentia Bowdich, 1821

Family Dipodidae Fischer, 1817

Genus *Sicista* Gray 1827

Sicista spp.

Species of the dipodid *Sicista* are present in northern Italy but with geographically more extensive findings. The presence of *S. betulina* has been reported in Veneto, Friuli-Venezia Giulia, Marche and possibly Liguria (Berto, 2013; Berto and Rubinato, 2013; Bona

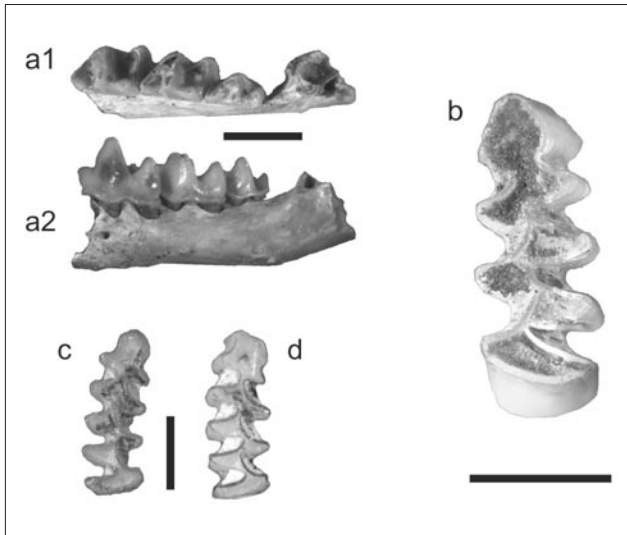


Fig. 1 – Micromammals from Avetrana karst filling (southern Italy) (T. Kotsakis photo archive): *Crocidura* gr. *suaveolens*: mandible fragment a1) in occlusal view, a2) in labial view (scale bar 1 mm); *Arvicola italicus*: b) first lower molar in occlusal view (scale bar 2 mm); *Microtus (Terricola)* gr. *savii-brachycercus*: c) and d) first lower molar in occlusal view (scale bar 1 mm)

and Savoldi, 2016). *Sicista betulina* first appears in Italy during the early Late Pleistocene, but is (relatively) more common during MIS 3. The species, which is currently widespread from Baikal to central and northern Europe, is known as a fossil in Europe at fossiliferous Middle and Late Pleistocene sites. *Sicista betulina* is a forest dweller (Rofes *et al.*, 2012). Bona and Savoldi (2016) reported the presence in Caverna Generosa (Lombardy) of a second species of the genus, larger than the previous one, classified as *Sicista* cf. *subtilis*. The age of the assemblage to which this species belongs is assigned to late MIS 3 or early MIS 2 (Bona and Savoldi, 2016). These authors hypothesised a possible arrival in Italy from the West. The presence of *Sicista subtilis* (Pallas, 1773), which currently lives in an area ranging from southern European Russia to Mongolia, has certainly been reported in Europe from the Middle Pleistocene and, unlike the previous species, testifies to the existence of arid environments (Rofes *et al.*, 2012).

Family Cricetidae Fischer, 1817

Genus *Cricetulus* Milne-Edwards, 1867

Cricetulus migratorius (Pallas, 1773)

In the northern area, a cricetid, *C. migratorius*, made its appearance during the Late Pleistocene.

This species reached the extreme north-east of the peninsula during MIS 4 and survived until the (?early) Holocene (Bartolomei, 1982; Bon *et al.*, 1991; Berto, 2013; Berto and Rubinato, 2013). *Cricetulus migratorius*, which currently lives in a large part of Asia and Eastern Europe, has been found as a fossil at several Pleistocene sites in Eastern Europe including the Balkan Peninsula and is characterised of open and arid environments (for the distinction between the genera *Cricetulus* and *Allocricetus*, see the discussion in Berto, 2013 and Filek and Joniak, 2020).

Genus *Arvicola* Lacépède, 1799

Arvicola gr. *amphibius* (Linnaeus, 1758) –

italicus (Savi, 1838)

This group includes two species: *Arvicola amphibius* and *Arvicola italicus*. Recent studies concerning the species of the genus *Arvicola* have modified many points of the systematic hypothesis valid until a few years ago. This hypothesis indicated, for almost all of Europe, a species that characterised the early Toringian (upper part of the Middle Pleistocene), *Arvicola mosbachensis* (Schmidtgen, 1911) (= *Arvicola cantianus* (Hinton, 1910)). This species would have given rise to *A. amphibius* (= *Arvicola terrestris* (Linnaeus, 1758)), characterising the late Toringian (Late Pleistocene) (Fejfar and Heinrich, 1990; for Italy see Kotsakis *et al.*, 2003; Sala and Masini, 2007) and still extant across almost all of the European continent. *Arvicola mosbachensis* and *A. amphibius* have been found in overlapping layers (attributed to MIS 7 and MIS 5d respectively) of the same fossiliferous site (Grotta Maggiore di San Bernardino, Veneto, Italy; López-García *et al.*, 2017). The possibility that the *Arvicola* specimens from the Italian peninsula belonged to a different species had already been foreseen in the past in palaeontological terms (see Masini *et al.*, 2020 with references) and was confirmed for the extant population on a biomolecular basis by Castiglia *et al.* (2016), who proposed the name *A. italicus* for the Italian species. Further studies (Mahmoudi *et al.*, 2019) have confirmed the validity of this species. From a chronological point of view, while the populations from the Late Pleistocene in central-southern Italy can be attributed to *A. italicus* (Fig. 1.b), at least one population from the Grotta Grande di Scario (Campania, Italy), collected in a layer attributed to MIS 6, shows intermediate characteristics between *A. mosbachensis* and *A. italicus* and is classified as *Arvicola* gr. *amphibius* (see Masini *et al.*, 2020). In central-northern Italy, the possibility of the presence of both *A. amphibius* and *A. italicus* dur-

ing the Late Pleistocene (obviously at different sites) cannot be excluded.

Genus *Microtus* Schrank, 1798

Subgenus *Terricola* De Selys-Longchamps, 1838

Microtus (Terricola) gr. *savii* (De Selys-Longchamps, 1838) - *brachycercus* (von Lehmann, 1961)

This group includes two very similar species, *Microtus (Terricola) savii* and *Microtus (Terricola) brachycercus*. Until a few years ago, *M. (T.) savii* was considered a quasi-endemic species of the Italian peninsula and Sicily (Capizzi and Santini, 2002; Contoli, 2008). Some geographically limited populations from Calabria (southern Italy) were attributed to the second species, *M. (T.) brachycercus* (see Contoli, 2008). Currently the populations in central-northern Italy are attributed to *M. (T.) savii* while those in central-southern Italy are attributed to *M. (T.) brachycercus* and those in Sicily to *Microtus (Terricola) nebrodensis* (Minà-Palumbo, 1868) (Bezzerra *et al.*, 2016; Amori and Castiglia, 2018; Spina *et al.*, 2021). The morphology and morphometry of first lower molar (m1) of the different populations in the *M. (T.) savii* group has been the subject of study in numerous papers (Curcio *et al.*, 2005; Nappi *et al.*, 2005, 2006, 2019; Piras *et al.*, 2009, 2010; Petruso *et al.*, 2011), although the conclusions are still open to debate. For that reason, we prefer to use the term *Microtus (Terricola)* gr. *savii-brachycercus* to indicate the species *M. (T.) savii* and *M. (T.) brachycercus*. In biochronological terms, the most ancient remains classified as *Terricola* cf. *savii* (again based on the morphology of m1) date to MIS 6 and were found in Grotta Grande di Scario, in sector C (Petruso *et al.*, 2009). Fossil specimens with m1 identical to that of extant populations are present from the MIS 5e (Kotsakis *et al.*, 2003, 2020; Petruso *et al.*, 2011; Ceruleo *et al.*, 2023). Piras *et al.* (2009) have highlighted that, during the Late Pleistocene, the morphology of m1 in *M. (T.)* gr. *savii* (including the fossil populations from Melpignano Cava Nuzzo, Avetrana and Ingarano), apart from some adaptations to local climatic conditions, is evidence of evolutionary stasis. These populations show the typical “savimorph” m1 (Ronchitelli *et al.*, 2011; Kotsakis *et al.*, 2020) (Fig. 1.c-d). This group of arvicolins is almost always present at the fossiliferous sites in central-southern Italy from the Late Pleistocene, while in central-northern Italy it is absent. Some previous reports of *M. (T.) savii* in the north have been reported as *Microtus (Terricola)* gr. *multiplex-subterraneus* (see Paunescu *et al.*, 2010; Berto *et al.*, 2019b).

Middle and large Mammals

Middle and large mammals (Proboscidea, Carnivora, Perissodactyla and Artiodactyla) usually show a greater ability to adapt to different climatic variations than small mammals: this means that it is not easy to separate clearly the areas of the peninsula where some taxa occur rather than others and, therefore, it is difficult to identify biogeographical areas in biochronological terms. However, we must bear in mind that in the short time span from the latest Middle Pleistocene to the Late Pleistocene, occurrences of new species are significantly more limited than extinctions (total or local). Therefore, we focused on the taxa with a biochronological interval limited to the Late Pleistocene or just prior to the period, occurring in large areas.

Order Proboscidea Illiger, 1811

Family Elephantidae Gray, 1821

Genus *Mammuthus* Brookes, 1828

Mammuthus primigenius (Blumenbach, 1799)

The classification of *M. primigenius* is often problematic because the attribution of its fossil remains is based mainly on dental structures that have considerable variability in terms of frequency and lamellar thickness. It is not therefore possible to separate *M. primigenius* easily from the more archaic transitional forms (*Mammuthus “chosaricus”*, Dubrovo, 1964; Kotsakis *et al.*, 1978; Palombo, 1994; Lister, 1996b; Palombo and Ferretti, 2005) occurring in the late Middle Pleistocene and the early Late Pleistocene (Table 2). *Mammuthus primigenius* remains are always more frequent (Palombo and Ferretti, 2005) from the middle Late Pleistocene (MIS 5a /4) in many fossiliferous areas of Italy (Pianura Pontina, Latina, Montecatini, Bucine, Arezzo; the Po Valley, Liguria, Veneto) but probably the best-known remains are those from Cardamone (Lecce) (Rustioni *et al.*, 2003). Uncertainty about the systematic, phylogenetic and biochronological data relating to *M. primigenius* seems to characterise all the findings on the Italian peninsula and, therefore, this taxon cannot be used with enough certainty for biochronological purposes.

Order Carnivora Bowdich, 1821

Family Mustelidae Fischer, 1817

Genus *Mustela* Linnaeus 1758

Mustela erminea Linnaeus 1758

The ermine, *Mustela erminea*, is known in Italy only from sites from the Late Pleistocene age (Cassoli and Tagliacozzo, 1991, 1994; Alhaique, 2003) but could also be present in Middle Pleistocene sites (Cassoli and Tagliacozzo, 1991; Tagliacozzo *et al.*, 2013).

Family Felidae Fischer von Waldheim, 1817

Genus *Lynx* Kerr, 1792

Lynx lynx (Linnaeus, 1758)

Rodríguez-Varela *et al.* (2015) attributed several Western Europe lynx remains previously ascribed to the Eurasian lynx, *Lynx lynx*, to the Iberian lynx, *L. pardinus* (Temminck, 1827), a species at present day restricted to small populations living in southern Iberian Peninsula, but widespread in Europe since the Middle Pleistocene. Recently, also Mecozzi *et al.* (2021c) referred the lynx remains from Ingarano (Apulia) to *L. pardinus*. According these Authors, *L. lynx* spreads in Western Europe at the beginning of the Late Pleistocene and it is recorded together with *L. pardinus* in some Mediterranean localities. Therefore, all the lynx remains should be revised and this taxon cannot be useful as a biochronological indicator for this period.

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Gray, 1820

Genus *Coelodonta* Bronn, 1821

Coelodonta antiquitatis (Blumenbach, 1799)

The woolly rhino has been found in Europe since the Middle Pleistocene (MIS 12) (Kahlke and Lacombat, 2008). In Italy the fossil remains of *Coelodonta antiquitatis* have been collected from MIS 4-3 in a few areas, including Ingarano (Gargano promontory) (Petronio *et al.*, 1995; Petronio and Sardella, 1998), Grotta Romanelli and Cardamone (Salento, southern Apulia) (Rustioni *et al.*, 2003; Pandolfi and Tagliacozzo, 2013), and Monte Circeo (Latium) (Palmarelli and Palombo, 1981), and at some sites in north-eastern Italy, such as Opicina, Fadalto, Riparo di Fumane and Settepolesini di Bondeno (Leonardi, 1947, 1948; Gallini and Sala, 2001; Cremaschi *et al.*, 2005). Most of these localities have been linked to the cold phases of the Late Pleistocene and, therefore, the occurrence of the woolly rhino suggested to Petronio *et al.* (2007) the paleoclimatic and biochronological data that enabled the institution of the Ingarano FU. In this last locality the woolly rhino has also been found with *Palaeoloxodon antiquus* and *Stephanorhinus bemitoechus*, which would indicate a slightly more temperate phase during MIS 4-MIS 3.

Coelodonta antiquitatis also occurs in Apulia at Cardamone (Salento, Lecce) (Rustioni *et al.*, 2003), associated with mammal remains characteristic of relatively open landscapes in rather cold climatic conditions, although there is no shortage of taxa already present in many areas on the Italian peninsula, some of which characterise temperate climates.

The biochronological data on *C. antiquitatis* are much more complicated, because of its occurrence at Grotta Romanelli (Level XI) (Pandolfi and Tagliacozzo, 2013), dated between 80 and 69 ka and, therefore, much earlier than the 30-40 ka at Ingarano (Petronio and Sardella, 1998). If we also consider the stratigraphically uncertain occurrence of a woolly rhino skull from slope breccias on the Circeo promontory (Palmarelli and Palombo, 1981) and the numerous reports from Polesine and Veneto (Cremaschi *et al.*, 2005), we can conclude that this species can be considered with caution a biochronological indicator for the time span corresponding to MIS 4/3.

Order Artiodactyla Owen, 1848

Family Cervidae Goldfuss, 1820

Genus *Alces* Gray, 1821

Alces alces (Linnaeus, 1758)

This large cervid is characteristic of Northern Europe and occurred in the cold stages of the Late Pleistocene (MIS 4?) in north-eastern Italy (Breda, 2001), but also in Piedmont, Lombardy, Emilia Romagna (Gallini and Sala, 2000; Breda, 2002) and, finally, in Liguria (Arene Candide: Cassoli and Tagliacozzo, 1994; Balzi Rossi: Boule, 1910; Arellano, 2009). *Alces alces* does not seem to spread beyond the Apennines and only occurs in the north-western and north-eastern Italy. Unfortunately, except for some sites (e.g., Arene Candide and Riparo Soman; late MIS 2), precise stratigraphical data are lacking in most of the localities where it was collected, both open-air and karst deposits, and this means it is not possible to establish the FO and LO of this moose species in Italy with certainty.

Genus *Rangifer* Smith, 1827

Rangifer tarandus (Linnaeus, 1758)

Reindeer remains have been collected along with other abundant faunal remains from the Grimaldi Cave (Arellano *et al.*, 2009) and are potentially dated to MIS 6 and more certainly to MIS 4/3.

Rangifer tarandus has been identified in Italy from Grotta dei Fanciulli (Imperia, Liguria) (Boule, 1910; Palma di Cesnola, 1983), from Caverna degli Zerbi (Savona, Liguria) (Bona and Savoldi, 2016) and doubtfully from Grotta Pocala in the Trieste Karst (Friuli-Venezia Giulia) (Esu and Kotsakis, 1987). All these localities are generically referred to as “Wurmian” or Last Glacial Maximum and, therefore, lacking precise biostratigraphical and biochronological boundaries, reindeer is not useful for any biochronological use in Italy.

Genus *Cervus* Linnaeus, 1758

Cervus elaphus Linnaeus, 1758

Cervus elaphus spread widely in Italy during the Middle and Late Pleistocene, from the Slivia FU (Bon *et al.*, 1992) and is characterised by significant phenotypic variability that allows this species to colonise almost all the environments of the peninsula (Di Stefano and Petronio, 2021). Some cronosubspecies, such as *C. elaphus acoronatus* (Beninde, 1937) occurring until the Isernia FU and *C. elaphus eostephanoceros* (Di Stefano and Petronio, 1993) typical of the Fontana Ranuccio FU, have an important role in the biochronological picture of the European Middle Pleistocene (Di Stefano and Petronio, 1992, 1993, 2002, 2021; Geist, 1998; Gliozzi *et al.*, 1997; Marra *et al.*, 2014, 2016; Petronio *et al.*, 2019). However, it is not possible to recognise fossil red deer populations during the late Middle and Late Pleistocene with significant biochronological value (Table 2), although some trends in certain areas of the peninsula can be observed (Di Stefano *et al.*, 2015; Di Stefano and Petronio, 2021). In this picture the abundance of red deer remains compared to those of fallow deer has significant paleoecological and paleoenvironmental value and is characteristic of the colder phases of the Late Pleistocene.

More specifically, the red deer is more abundant in temperate-fresh climatic conditions while the fallow deer is more common in warmer climates and occurs above all in central-southern Italy. This observation, however, is of little use for biochronological purposes. Finally, the possible spread from Eastern Europe of deer populations classifiable as *C. canadensis* during the coldest phases of the latest Pleistocene should be considered (Croitor, 2018; Di Stefano and Petronio, 2021).

Genus *Dama* Frisch, 1775

Dama dama (Linnaeus, 1758)

The modern fallow deer is a faunal element occurring in Italy from the latest Middle Pleistocene (MIS 8.5). From an evolutionary point of view, *Dama dama* derives from *Dama clactoniana* (Falconer, 1868) (Leonardi and Petronio, 1976; Di Stefano and Petronio, 2002), which is preceded by the archaic form *Dama roberti* Breda and Lister, 2013, occurring until the Isernia FU (Breda and Lister, 2013).

The FO of a primitive form of the extant fallow deer, *Dama dama tiberina* Di Stefano and Petronio, 1997, has been identified from numerous localities in central and southern Italy (Di Stefano and Petronio, 1997; Abbazzi *et al.*, 2001; Petronio *et al.*,

2011, 2019). This form, characterised by antlers with terminal tines facing in a posterior direction like the living species, and other well recognizing features (Di Stefano and Petronio, 1997), has been collected only from sediments chronostratigraphically constrained to MIS 8.5-7 but never before or after (Di Stefano *et al.*, 1998; Di Stefano and Di Canzio, 2003; Marra *et al.*, 2014, 2017, 2018a, 2018b; Petronio *et al.*, 2007, 2011, 2019; Salari *et al.*, 2019b), therefore, it indicates the Vitinia FU. In this context, the hypothesis put forward by Mecozzi *et al.* (2021b) for which the subspecies *D. dama tiberina* is not to be considered valid is not corroborated by any objective evidence.

The FO of *D. dama dama* dates to the temperate-warm phases of the Late Pleistocene. This fallow deer has been found in many cave deposits (Grotta Romanelli, Grotta del Cavallo, Grotta delle Striare, Grotta del Sarcofago, Grotta dei Giganti, etc.) or open-air deposits (S. Sidero 3, Fondo Cattiè, Cava Nuzzo, Avertrana etc) in Apulia (De Giuli, 1983; Bologna *et al.*, 1994; Corridi, 1987; Di Stefano *et al.*, 1992; Petronio *et al.*, 2007; Ceruleo *et al.*, 2023, and references therein). Furthermore, *D. dama dama* also occurs in fossiliferous deposits at Pianura Pontina and in the upper levels of Campoverde (Marra *et al.*, 2018b), certainly referable to the Late Pleistocene, and in other localities of central Italy, such as Fosso del Cupo (Rome), testifying to the presence of the extant subspecies from sediments chronostratigraphically constrained to MIS 5 (Ceruleo *et al.*, 2016; Marra *et al.*, 2018a; Petronio *et al.*, 2019). Finally, *D. dama* has also been identified at several Late Pleistocene sites in Tuscany (Farina, 2011; Petronio *et al.*, 2014) and north-eastern Italy (Bon *et al.*, 1991).

In this context, the attribution of fallow deer remains from some Apulian sites in the Melpignano-Maglie-Corigliano d'Otranto area (e.g., Cava Nuzzo, Cava della Terra, Cava Bianco) and S. Sidero (San Sidero 3) to *D. clactoniana* (e.g., Stefanelli and Mecozzi, 2020; Mecozzi *et al.*, 2021a), mainly on the basis of the larger size compared to the extant *D. dama dama* and some presumed morphological characteristics of the antlers, molars and postcranial skeleton, has to be considered unfounded. In fact, the antler remains described by Mecozzi *et al.* (2021a - fig. 8), particularly the specimen MPSD296 from Cava Bianco, clearly show the same characteristics as the extant fallow deer (e.g., the posterior tine at the same height of the second anterior tine and not at the same height of the third anterior tine, as *D. clactoniana*) and the presumed resemblance with a

specimen from Swanscombe contrasts with the large number of more complete remains from the “classic” sites (i.e. Swanscombe, Clacton, Riano) (Fig. 2), where the morphological features can be easily observed (Leonardi and Petronio, 1976, Lister 1986; Di Stefano and Petronio, 1997).

Similarly, the other distinguishing features listed by Mecozzi *et al.* (2021a) are also generic or unfounded. For example, as regards teeth, the lack of separation between paraconid and parastylid in p3 is fairly frequent in living fallow deer. The presence of a lingual wall made up of metaconid and paraconid in p4, again, is common to all the representatives of the genus *Dama* and is more or less evident depending on the level of wear of the teeth (Di Stefano, 1994, 1995; Lister, 1996a). On the basis of the observations of thousands of fallow deer tooth remains (see in particular Di Stefano, 1994), it is clearly evident that *D. clactoniana* almost always shows well developed ectostylids in the lower molars

(between protoconid and ipoconid) often reaching the chewing level, depending on wear. This characteristic is almost always accompanied by the presence of anterior cingula and, less frequently, by posterior ones. Both these features are typical of the lower teeth of *D. clactoniana* but tend to disappear in *D. dama*, lack in the extant fallow deer and in the fallow deer remains from the cited quarries near Melpignano.

Finally, as regards the postcranial skeleton, Mecozzi *et al.* (2021a) cited some characteristics that were “generally observed” in *D. clactoniana*. However, according to the same authors, most of these characteristics (development of the radial fossa and coracoid in the humerus, articular surface in the posterior edge of the metatarsus) are “variable”, which means they cannot be defined as relevant morphological features for recognising the species (Leonardi and Petronio, 1976; Di Stefano, 1994, 1995; Lister, 1996a).

DISCUSSION

Notwithstanding many radiometric dating and, particularly in deposits of caves frequented by human, pollen, micromammal and lithic industry successions allow detailed stratigraphic information, often with a better chronological resolution than the one offered by biochronology, it is nevertheless useful to underline and discuss the bioevents, particularly the FO of species, which characterize the Late Pleistocene.

Arvicola gr. *amphibi*-*italicus* occurs widely on the Italian peninsula only from the Late Pleistocene (Table 1) and its discovery therefore provides sufficient certainty as to the age of the sediments in which it is found (Kotsakis *et al.*, 2003, 2020; López-García *et al.*, 2017). The same biochronological span is characterised by the presence (less frequent) of *Crocidura* gr. *suaveolens* and the more advanced forms of *Microtus* (*Terricola*) gr. *savii-brachycercus* (see Fanfani, 2000; Kotsakis *et al.*, 2003, 2020; Petruso *et al.*, 2011) collected from different Apulian sites such as Cava Donno (Pandolfi *et al.*, 2017) and other sites in the Melpignano-Maglie-Corigliano d’Otranto area, such as Cava Nuzzo (Bologna *et al.*, 1994) and S. Sidero 3 (De Giuli, 1983), and finally from the Avetrana site (Salari *et al.*, 2019c; Kotsakis *et al.*, 2020; Ceruleo *et al.*, 2023).

As already mentioned, a more detailed time sequence is offered by the genus *Dama*, which occurs from MIS 5e with the extant form *D. dama dama*



Fig. 2 – Antler fossils of fallow deer at the same scale (G. Di Stefano photo archive): a) right and b) left antlers of *Dama clactoniana* from Swanscombe (UK), c) left antler of *Dama dama dama* from Cava Nuzzo (Melpignano, Apulia, Italy)

Taxa	M.P.	MIS 5	MIS 4	MIS 3	MIS 2	Holoc.	Recent
<i>Erinaceus europaeus</i>	X	X	X	X	X	X	X
<i>Erinaceus roumanicus</i>						X	X
<i>Talpa europaea</i>	X	X	X	X	X	X	X
<i>Talpa caeca</i>	X	X	X	X	X	X	X
<i>Talpa romana</i>	X	X	X	X	X	X	X
<i>Crocidura zorzii</i>	X	?					
<i>Crocidura leucodon</i>	X	X	X	X	X	X	X
<i>Crocidura suaveolens</i>	?	X	X	X	X	X	X
<i>Crocidura russula</i>	?	?	?	?	?	?	X
<i>Suncus etruscus</i>						X	X
<i>Neomys fodiens</i>	X	X	X	X	X	X	X
<i>Neomys</i> gr. <i>anomalus/milleri</i>	?	X	X	X	X	X	X
<i>Sorex</i> gr. <i>antinorii/araneus</i>	X	X	X	X	X	X	X
<i>Sorex minutus</i>	X	X	X	X	X	X	X
<i>Sorex alpinus</i>	X	X	X	X	X	X	X
<i>Sorex samniticus</i>	?	?	X	X	X	X	X
<i>Sciurus vulgaris</i>	X	X	X	X	X	X	X
<i>Sciurus meridionalis</i>	?	?	?	?	?	?	X
<i>Marmota marmota</i>	?	X	X	X	X	X	X
<i>Marmota primigenia</i>		?	?	?	?		
<i>Castor fiber</i>	X	X	X	X	X	X	
<i>Sicista betulina</i>	?	X	X	X	?		
<i>Sicista</i> cf. <i>subtilis</i>				X			
<i>Cricetus cricetus</i>	X	X	X	X	X		
<i>Cricetulus migratorius</i>			X	X	X	X	
<i>Mesocricetus</i> cf. <i>newtoni</i>			?			?	
<i>Pliomys coronensis</i>	X	X	X	X			
<i>Dinaromys bogdanovi</i>	X	?	X	X	X	?	
<i>Clethrionomys glareolus</i>	X	X	X	X	X	X	X
<i>Arvicola mosbachensis</i>	X						
<i>Arvicola</i> gr. <i>amphibius/italicus</i>		X	X	X	X	X	X
<i>Arvicola sapidus</i>			X				
<i>Chionomys nivalis</i>	X	X	X	X	X	X	X
<i>Iberomys brecciensis</i>	X	?				X	
<i>Microtus arvalis</i>	X	X	X	X	X	X	X
<i>Microtus</i> gr. <i>agrestis/leverendii</i>	X	X	X	X	X	X	X
<i>Microtus oeconomus</i>	X		X	X	X		
<i>Lasiopodomys gregalis</i>	X	?	?	?	?		
<i>M. (Terricola)</i> gr. <i>savii/brachycercus</i>		X	X	X	X	X	X
<i>M. (Terricola)</i> gr. <i>multiplex/subterraneus</i>	X	X	X	X	X	X	X
<i>M. (Terricola)</i> <i>liechtensteini</i>	?	?	?	?	?	?	X
<i>Apodemus agrarius</i>						X	X
<i>Apodemus sylvaticus</i>	X	X	X	X	X	X	X
<i>Apodemus flavicollis</i>	X	X	X	X	X	X	X
<i>Apodemus alpicola</i>	?	?	?	?	?	?	X
<i>Mus domesticus</i>						X	X
<i>Rattus rattus</i>						X	X
<i>Rattus norvegicus</i>							X
<i>Micromys minutus</i>						X	X
<i>Glis glis</i>	X	X	X	X	X	X	X
<i>Eliomys quercinus</i>	X	X	X	X	X	X	X
<i>Muscardinus avellanarius</i>	X	X	X	X	X	X	X

Taxa	M.P.	MIS 5	MIS 4	MIS 3	MIS 2	Holoc.	Recent
<i>Dryomys nitedula</i>	X	X	X	X	X	X	X
<i>Dryomys aspromontis</i>	?	?	?	?	?	?	X
<i>Hystrix vinogradovi</i>	X	X	X	X			
<i>Hystrix cristata</i>							X
<i>Ochotona pusilla</i>	X		X				
<i>Oryctolagus cuniculus</i>	X	X	X	X	X	X	X
<i>Lepus corsicanus</i>	X	X	X	X	X	X	X
<i>Lepus europaeus</i>	X	X	X	X	X	X	X
<i>Lepus timidus</i>	?	X	X	X	X	X	X

Tab. 1 – Distribution of Pleistocene, Holocene and Extant small mammals (excluding Chiroptera) of mainland Italy. M.P.: Middle Pleistocene; MIS: Marine Isotope Stage; Holoc.: Holocene.

For the preparation of this table, data on extant species were taken from the list reported by Loy *et al.* (2019) with the addition of *Crocidura russula* (Mori *et al.*, 2020) and *Sorex araneus* (Ladurner *et al.*, 2021). Species introduced after 1950 are not considered. Many publications are used for the distribution of fossil species, including: Abbassi and Desclaux (1996); Fanfani (2000); Kotsakis *et al.* (2003 with references, 2011, 2020); Bona *et al.* (2007, 2009); Curcio *et al.* (2007); Kotsakis (2008); Zhuowei and Kotsakis (2008); Petruso *et al.* (2009, 2011); Salari and Sardella (2009); Paunesco *et al.* (2010); Bona (2011); Ronchitelli *et al.* (2011); Berto (2013); Berto and Rubinato (2013); Lopez-García *et al.* (2014, 2015a, b, 2017, 2018, 2019); Berto *et al.* (2016, 2017, 2018, 2019a, b); Bona and Savoldi (2016); Rolfo *et al.* (2016); Tagliacozzo *et al.* (2016); Angelone *et al.* (2019, 2020); Gatta *et al.* (2019); Luzi *et al.* (2019, 2022a, b); Moroni *et al.* (2019); and Salari *et al.* (2019a, b, c)

(Table 2) in many areas of central and southern Italy and especially in the Apulian area (e.g., Bologna *et al.*, 1994; Petronio *et al.*, 1995; Di Stefano and Petronio, 1997, 2002; Petronio *et al.*, 2007; Pandolfi and Petronio, 2011; Pandolfi *et al.*, 2013, 2017; Ceruleo *et al.*, 2016, 2023; Marra *et al.*, 2018b; Salari *et al.*, 2019c). In fact, in the southern area of Apulia (Salento), many fossiliferous sites (Fondo Cattie, S. Sidero 3, Cava Nuzzo, Cava Donno, Grotta delle Striare, Grotta Romanelli, Grotta del Cavallo, Grotta del Sarcofago, Avetrana, etc.) contain abundant remains of fallow deer, often with particularly advanced forms of *M. (T.) gr. savii-brachycercus* typical of the Late Pleistocene (Kotsakis *et al.*, 2003, 2020; Petruso *et al.*, 2011, and references therein). In particular, the recent dating (about 120 ka) of a volcanoclastic layer in the highest part of the stratigraphic succession from Avetrana (Ceruleo *et al.*, 2023), allows us to confirm that some taxa, such as *C. gr. suaveolens*, *A. gr. amphibius-italicus*, the evolved form of *M. (T.) gr. savii-brachycercus*, and the modern form of *D. dama*, occur for first time in Italy at the beginning of Late Pleistocene.

The occurrence of *D. dama dama* in Cava Nuzzo (Bologna *et al.*, 1994) and in many other sites in Salento and in the Tyrrhenian area (Ceruleo *et al.*, 2016; Marra *et al.*, 2018b), and, as already mentioned, the contemporary occurring of the advanced form *M. (T.) gr. savii-brachycercus* and/or *A. gr. amphibius-*

italicus, are biochronological data that contrast with the aim stated by Mecozzi *et al.* (2021a) of dating many sites of Salento back to MIS 9 and to the late Middle Pleistocene. The possible discovery of late Middle Pleistocene mammal remains in the Melpignano-Maglie-Corigliano d'Otranto area means it is not possible to attribute all the faunal assemblages of all the “ventarole” in the quarries in the area to the late Middle Pleistocene, just as it was a mistake in the past to attribute all of these to MIS 5, as shown by Pandolfi *et al.* (2017), above all in an area where karst phenomena have been activated several times in the past (Marsico *et al.*, 2003; Selleri *et al.*, 2003; Leucci *et al.*, 2005), especially during the optimum climatic periods (Pandolfi *et al.*, 2017).

The presence of other large mammal taxa, more specifically *Mammuthus primigenius* and modern populations of *Cervus elaphus*, which are considered representative of the Late Pleistocene in previous works (such as Petronio *et al.*, 2007), makes only a limited contribution on the basis of the considerations above.

The altitudinal and/or latitudinal diffusion outside of its distribution area of some species, such as *Bison priscus*, *Capra ibex*, *Rupicapra rupicapra*, *R. pyrenaica*, *Megaloceros giganteus* and *Marmota marmota*, present in Italy since the late Middle Pleistocene can also be useful for palaeoenvironmental and palaeoclimatic purposes.

Taxa	M.P.	MIS 5	MIS 4	MIS 3	MIS 2	Holoc.	Recent
<i>Palaeoloxodon antiquus</i>	X	X	X	X			
<i>Mammuthus primigenius</i>	?	?	X	X	?		
<i>Canis lupus</i>	X	X	X	X	X	X	X
<i>Canis aureus</i>							X
<i>Vulpes vulpes</i>	X	X	X	X	X	X	X
<i>Cuon alpinus</i>	?	X	X	X	?		
<i>Ursus spelaeus</i>	X	X	X	X	X		
<i>Ursus arctos</i>	X	X	X	X	X	X	X
<i>Martes martes</i>	X	X	X	X	X	X	X
<i>Martes foina</i>					?	X	X
<i>Mustela putorius</i>	X	X	X	X	X	X	X
<i>Mustela erminea</i>	?	?	X	X	X	X	X
<i>Mustela nivalis</i>	X	X	X	X	X	X	X
<i>Meles meles</i>	X	X	X	X	X	X	X
<i>Gulo gulo</i>	X	X	X	X	X		
<i>Felis silvestris</i>	X	X	X	X	X	X	X
<i>Lynx lynx</i>		?	X	X	X	X	X
<i>Lynx pardinus</i>	X	X	X	X	X		
<i>Panthera spelaea</i>	X	X	X	X	X	X	
<i>Panthera pardus</i>	X	X	X	X	X		
<i>Crocuta crocuta</i>	X	X	X	X	X		
<i>Coelodonta antiquitatis</i>		X	X	X	?		
<i>Stephanorhinus hemitoechus</i>	X	X	X	X			
<i>Equus ferus</i>	X	X	X	X	X	X	
<i>Equus hydruntinus</i>	X	X	X	X	X	X	
<i>Hippopotamus amphibius</i>	X	X	X	X			
<i>Sus scrofa</i>	X	X	X	X	X	X	X
<i>Megaloceros giganteus</i>	X	X	X	X	X		
<i>Dama dama tiberina</i>	X						
<i>Dama dama dama</i>		X	X	X	?	?	X
<i>Cervus elaphus</i>	X	X	X	X	X	X	X
<i>Capreolus capreolus</i>	X	X	X	X	X	X	X
<i>Alces alces</i>	?	?	X	X	X	?	
<i>Rangifer tarandus</i>	?		X	X	X		
<i>Bos primigenius</i>	X	X	X	X	X	X	
<i>Bison priscus</i>	X	X	X	X	X		
<i>Capra hibex</i>	X	X	X	X	X	X	X
<i>Rupicapra rupicapra</i>	X	X	X	X	X	X	X
<i>Rupicapra pyrenaica</i>	X	X	X	X	X	X	X

Tab. 2 – Biochronological picture of middle and large mammals in the late Pleistocene of Italy. M.P.: Middle Pleistocene; MIS: Marine Isotope Stage; Holoc.: Holocene. Data from Gliozzi *et al.* (1997), Breda (2001, 2002), Boitani *et al.* (2003), Sala (2005), Petronio *et al.* (2005, 2007, 2011, 2019), Masini and Sala (2007), Ghezzi and Rook (2014), Mecozzi *et al.* (2021c)

CONCLUSIONS

A careful biochronological review of all the taxa occurring in the period between the late Middle Pleistocene and the present day (Tables 1 and 2) reveals that the major faunal changes of the Early and

Middle Pleistocene, which made it possible for palaeontologists to introduce and justify numerous FUs valid for the entire Italian peninsula for the Villafranchian and Galerian Mammal Ages (Gliozzi *et al.*, 1997), are clearly mitigated in the last 130 ka during the late Aurelian (Late Pleistocene). In this time

period the LOs predominate sharply over the FOs and there are no significant faunal variations valid for all of Italy.

In fact, analysis of the biochronological data on the taxa present in Italy during the Late Pleistocene admits an observation concerning the clear separation, which is quite evident even now, especially in small mammals, between the more continental area and the peninsular one, in the last phase of the Late Pleistocene. The occurrence of *Alces alces*, *Mustela erminea*, *Bison priscus*, *Rupicapra rupicapra* and (geographically marginal) *Rangifer tarandus* in northern or central-northern Italy allows us to distinguish this area from central-southern Italy, which is characterised by the presence of *Rupicapra pyrenaica* (see Masini and Lovari, 1988; Masseti and Salari, 2017) and *Dama dama* and by the abundance of *Bos primigenius*. As regards small mammals, in the first phases of the Late Pleistocene in central-southern Italy the dominant species among small mammals are the arvicolins of the *Microtus (Terricola)* gr. *savii-brachycercus*, while in central-northern Italy the arvicolins of *Microtus* gr. *agrestis-leverendi* and *Microtus arvalis* are the most abundant species. With the fall in temperatures, *M.* gr. *agrestis-leverendi* and *M. arvalis* also become abundant in central and southern Italy and some of these central-southern areas are also colonised by *Marmota marmota*. During the same period the genera *Sicista* and *Cricetulus* make their first appearance in the central-northern Italy and the arvicolin *M. (Alexandromys) oeconomus* and the ochotonid *Ochotona* cf. *pusilla* reappear (Bartolomei *et al.*, 1982; Sala, 1990; Berto and Rubinato, 2013; Angelone *et al.*, 2020).

Therefore, the formal conditions that allowed Petronio *et al.* (2007) the institution of the two Late Pleistocene FUs, Melpignano and Ingarano, are lacking for the whole mainland Italy.

More specifically, only the FO of the extant fallow deer subspecies (*D. dama dama*) in southern Italy and accompanied by *Crocidura* gr. *suaveolens*, *Arvicola* gr. *amphibiis-italicus* and the advanced forms of *M. (T.)* gr. *savii-brachycercus*, as described by Kotsakis *et al.* (2020) for the Apulian site of Avetrana, is not a biochronological feature that can justify the validity of the Melpignano FU and cannot be easily extended to other Italian areas. A careful study of the numerous Late Pleistocene sites undermines this validity.

The Ingarano FU (MIS 4-3) is characterised by the occurrence of the woolly rhino among the numerous remains from the type locality (Ingarano, northern

Apulia) dated to about 38/40 ka. However, as previously mentioned, *C. antiquitatis* is a species relatively rare in Italy and it occurs at Grotta Romanelli (Level XI) dated between 80 and 69 ka, therefore this FU lacks any clear, universal biochronological indicators.

In conclusion, the two Apulian local faunas previously identified as type of the Late Pleistocene FUs do not have biochronological features that could justify their validity for the whole mainland Italy, but can be considered representative of a warmer phase at the beginning of the Late Pleistocene (Melpignano) and of a subsequent colder phase (Ingarano) limited only to the southern Adriatic zones of the Italian Peninsula.

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