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Before and after the earliest *Homo* dispersal in Europe: Evidence from the early Pleistocene sites of the Italian Peninsula

L'avant et l'après de la dispersion en Europe du premier Homo *: les preuves à partir de sites du Pléistocène inférieur de la péninsule Italienne*

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ABSTRACT

Fossil mammal assemblages found in various localities of the Italian Peninsula provide significant information to create a detailed biochronological framework for the middle–late Villafranchian and Epivillafranchian of Europe and to reconstruct the evolution of early Pleistocene terrestrial ecosystems, when the earliest dispersal of *Homo* in Europe occurred. Here, we provide an updated critical overview on three Italian sites that in the last few years have provided the most interesting information on this crucial time interval: Coste San Giacomo (Latium; about 2.1 million years, Ma), Pantalla (Umbria; about 1.9–1.7 Ma), and Pirro Nord (Apulia; about 1.6–1.3 Ma).

RÉSUMÉ

Les assemblages de mammifères fossiles trouvés dans différentes localités de la péninsule Italienne fournissent des informations significatives permettant de créer un cadre biochronologique détaillé pour la période du Villafranchien moyen–supérieur et de l'Épivillafranchien d'Europe, ainsi que de reconstituer l'évolution des écosystèmes terrestres au Pléistocène inférieur, lors de la dispersion la plus précoce de l'*Homo* en Europe. Nous apportons ici une vue d'ensemble critique à jour sur trois sites italiens qui, ces dernières années, ont fourni les informations les plus intéressantes sur cet intervalle de temps crucial : Coste San Giacomo (Latium, environ 2, 1 Ma), Pantalla (Ombrie, environ 1,9–1,7 Ma) et Pirro Nord (Apulie, environ 1,6–1,3 Ma).

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1. Introduction

Since 1991, when direct evidence of the presence of *Homo* was discovered in the Caucasus, at Dmanisi (Georgia) (Dzaparidze et al., 1989), the timing and pattern of *Homo* dispersal and earliest occupation of Europe is the focus of an ongoing scientific debate. Recent discoveries in Italy, France and Spain, and the consequent increase of available evidence suggest that humans dispersed into western Europe during the early Pleistocene. The Italian fossil record is of special interest for the reconstruction of terrestrial ecosystems during this time span and also for providing a detailed biochronological framework in which the dispersal events of *Homo* and of other taxa can be placed.

The study of the Italian Plio-Pleistocene mammal faunas was one of the important scientific focal points of the internationally renowned palaeontologist Augusto Azzaroli (1920–2015).

The record from the Upper Valdarno Basin (Tuscany, central Italy) (Fig. 1) is the basis for the taxonomic definition of many Plio-Pleistocene (early to late Villafranchian) species and genera, as well as for the definition of biochronological subdivisions of the continental biochronological scale that formed the bulk of Azzaroli's research (Azzaroli, 1977; Azzaroli et al., 1982; Azzaroli et al., 1988). The vertebrate record from the Upper Valdarno is unique, both in terms of amount of the fossil remains, as well in terms of historical significance for the impressive number of collections, built up along the last 500 years (Rook et al., 2013). Besides the historical collections, the fossil documentation from the Upper Valdarno Basin considerably increased in the last decades with the discovery of important faunal assemblages, like those of Casa Frata in the early 1980s and Poggio Rosso in the 1990s (Borselli et al., 1980; De Giuli and Masini, 1983; De Giuli and Masini, 1986; Napoleone et al., 2003). Although the Upper Valdarno Basin stratigraphic sequence also yielded small local faunal assemblages referable to the early and middle Villafranchian (Gaville–Santa Barbara and Montecarlo, respectively), the bulk of the collections is referred to the early late Villafranchian, i.e. Olivola and Tasso Faunal Units (FUs). As a matter of fact, the type locality of the Tasso FU itself is located in the Upper Valdarno Basin ("Il Tasso", near San Giovanni Valdarno) (Rook et al., 2013).

Recently, new data from early Pleistocene sites of the Italian Peninsula (Fig. 1) became available thanks to the revision of historical collections and new excavations and field surveys. Although an early occurrence of humans has been suggested for the karst filling deposit of Monte Peglia (Umbria, central Italy), where an Epivillafranchian local fauna was recorded together with a few and debatable Mode 1 lithic tools (one chopper and four flints) (Piperno, 1972; Piperno et al., 1984), the absence of a clear stratigraphic position of the artefacts and the uncertainty of their attribution did not provide a clear evidence for the scientific community. These artefacts and the fossil bones were considered as coeval based on the occurrence of a ferromanganese patina on both of them (Piperno, 1972; Piperno et al., 1984).

The faunal assemblage found at Monte Peglia is referred to the Colle Curti FU (early Biharian–Epivillafranchian), because of the occurrence of *Microtus* (*Allophaiomys*) *nutiensis* and *Microtus* (*Allophaiomys*) *burgondiae* (Gliozzi et al., 1997; Sala and Masini, 2007; Van der Meulen, 1973). Piperno et al. (1984) provide the following faunal list: *Macaca florentinus*, *Felis* cf. *lunensis*, *Panthera* cf. *toscana*, *Homotherium crenatidens, Canis* cf. *etruscus*, *Canis* cf. *arnensis*, *Ursus* cf. *etruscus*, *Lepus terrarubrae, Leptobos* sp., *Cervus* cf. *perrieri*, and *Hemitragus* sp. among the mammals and *Falco antiquus, Corvus pliocaenus*, and *Perdix palaeoperdix* among the birds. The vertebrate remains from Monte Peglia need to be revised in detail; only the sabertooth cat *Homotherium latidens* has been recently described and discussed (Sardella and Iurino, 2012).

The earliest clear occurrence of humans in Italy is documented at Pirro Nord (Apulia, South Italy), where lithic artefacts have been found together with a diversified late Villafranchian vertebrate assemblage dated around 1.6–1.3 Ma. The Pirro Nord assemblage shares similarities in age and composition with those from Monte Argentario (Tuscany) and Pietrafitta (Umbria), referred to the Farneta FU, where no evidence of human presence has been documented up to now. Older faunal assemblages (approximately between 2.1 and 1.6 Ma) from Italy have been investigated in recent years. An increasing number of data became available from new excavations in central Italy at Coste San Giacomo (Latium) and Pantalla (Umbria), where diversified and well-preserved vertebrate faunas have been found.

2. Before *Homo*

2.1. Coste San Giacomo (Anagni Basin, central Italy)

The site of Coste San Giacomo (CSG) was discovered in 1978 by the archaeologist Italo Biddittu during a survey in the Anagni Basin (Fig. 1). After the discovery and following several field seasons led by the Italian Institute of Human Palaeontology (IsIPU) in the ensuing years, an exploratory trench was dug in August 1990 (Bellucci et al., 2012). A new research phase on CSG started in 2009 with a scientific collaboration between IsIPU and the Earth Science Department of Sapienza University of Rome. For a better understanding of the stratigraphy and to establish the lateral extension of the fossiliferous beds, four test pits were dug in the same position as the previous trench. In addition, a 46 m-deep core was drilled in 2009, a few meters from the 1990 exploratory trench (Bellucci et al., 2012). The fossiliferous horizon was detected in the core at about 5 m below the ground surface. The new sedimentological and palaeoecological data allowed to define a palaeoenvironment mainly ascribable to an alluvial plain, characterized by a marsh evolving into a floodplain with overbank deposits and a sand-bed fluvial channel. A multidisciplinary research was carried out combining palaeomagnetic data, pollen, and small vertebrate analyses with the updated list of the large vertebrates (*Anancus arvernensis, Mammuthus meridionalis, Stephanorhinus* sp., *Equus* aff. *senezensis stelini, Eucladoceros* sp., *Pseudodama* cf. *lyra, Croizetoceros* cf. *ramosus, Leptobos* sp., *Gallogoral*

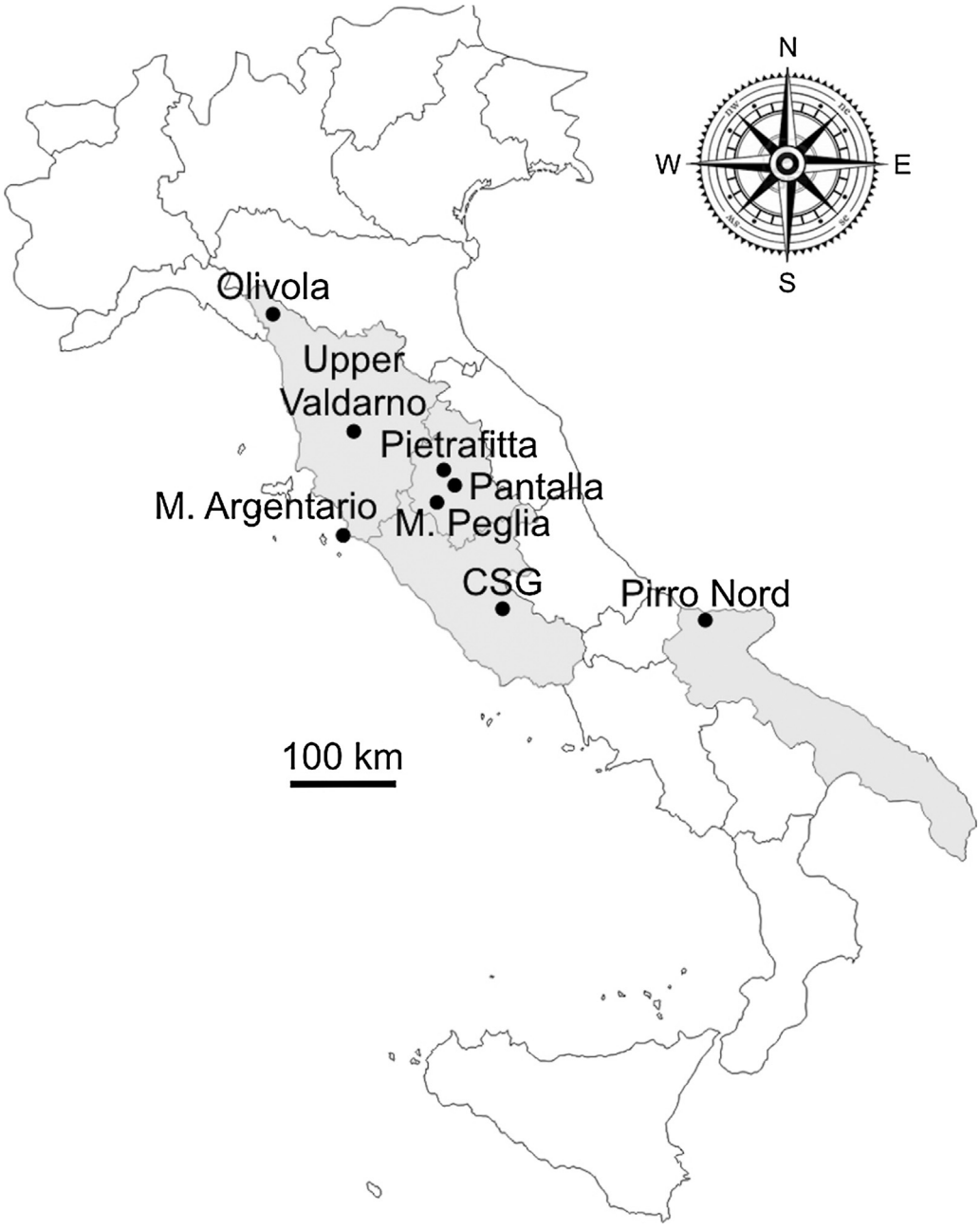

Fig. 1. Geographic distribution of selected early Pleistocene sites of Italy.
Fig. 1. Répartition géographique des sites du Pléistocène inférieur d'Italie sélectionnés.

meneghini, *Gazellospira torticornis*, *Gazella borbonica*, *Sus strozzii, Hippopotamus* sp., *Pliocrocuta perrieri*, *Ursus* cf. *etruscus*, *Canis* sp., *Vulpes* cf. *alopecoides*, *Homotherium* sp., *Macaca sylvanus*) (Fig. 2) and ostracod analysis to better depict the evolution of the alluvial plain in the surrounding landscape (Bellucci et al., 2014; Palombo et al., 2017; Strani et al., 2015). Magnetostratigraphy, pollen, and small mammal biochronological data have confirmed the position of the Coste San Giacomo FU in a reversed phase before the base of the Olduvai Subchron, suggesting a possible age of the mammal assemblage around 2.1 Ma. The diversified CSG small mammal assemblage has been studied in detail (Bona et al., 2015) and the following taxa have been identified and described: *Mimomys pliocaenicus*, *Mimomys* gr. *tigliensis–tornensis, Apodemus* sp., *Sciurus* cf. *warthae*, *Castor fiber*, *Hystrix refossa, Prolagus italicus*, *Sorex* cf. *minutus, Talpa minor, Talpa* sp. and *Galemys kormosi*. The occurrence of the large vole *M. pliocaenicus* has important biochronological significance. The CSG small mammal assemblage has provided the largest collection in Europe of *M. pliocaenicus* and, for this reason, it can be considered as a reference. Moreover, the occurrence of

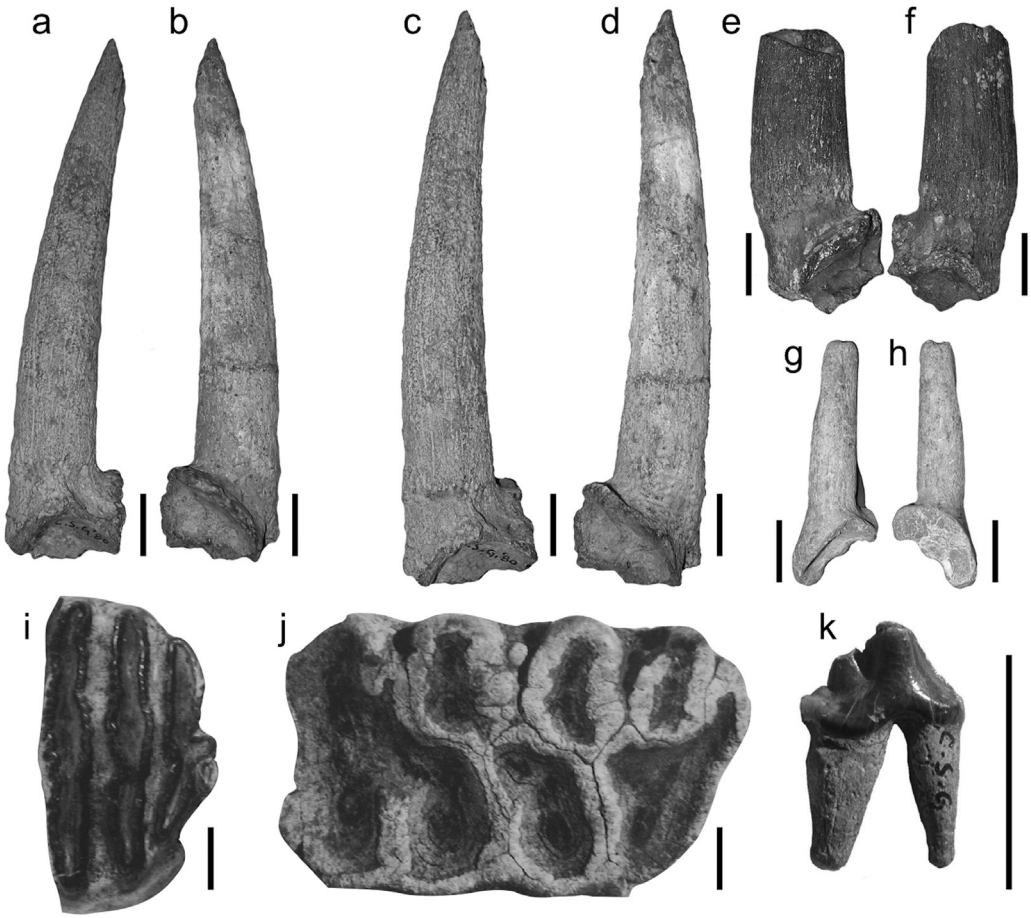

Fig. 2. Selection of vertebrate remains from Coste San Giacomo. a–h: *Gazella borbonica* 56692 in lateral (a) and mesial (b) views, CSG80 in lateral (c) and mesial (d) views, CSG11-44 in lateral (e) and mesial (f) views, 981127 in lateral (g) and mesial (h) views; i–j: *Mammuths meridionalis* 56642 in occlusal view; k: *Canis* cf. *C. etruscus* 931153 in buccal view. Scale bars: 2 cm.
Fig. 2. Sélection de restes de vertébrés en provenance de Coste San Giacomo. a–h : *Gazella borbonica* ; 56692 en vues latérale (a), mésiale (b) CSG80 en vues latérale (c) et mésiale (d), CSG11-44 en vues latérale (e) et mésiale (f), 981127 en vues latérale (g) et mésiale (h) ; i–j : *Mammuths meridionalis* en vue occlusale ; k : *Canis* cf. *etruscus* 931153 en vue buccale. Barres d'échelle : 2 cm.

the subfamily Desmaninae is reported for the first time in Italy.

Analyses of tooth wear patterns of ungulates from CSG have been recently carried out (Strani et al., 2015, 2017) in order to obtain additional palaeoenvironmental data. The results show that the CSG area was composed by a mosaic of steppe and woodland/wetland biomes. Evidence of such heterogeneity is provided by the wide spectrum of feeding behaviours found among the numerous ungulate herbivores, with cervids (*Pseudodama* cf. *lyra, Croizetoceros* cf. *ramosus*, and *Eucladoceros* sp.) exhibiting browsing-based diets, most of the bovids (*Gazella borbonica, Leptobos* sp., and *Gallogoral meneghinii*) being intermediate feeders, and the equid *Equus* aff. *senezensis stehlini* (following Palombo et al., 2017) showing a strict grazing behaviour. Further taxonomical and palaeoecological analyses on CSG and Olivola ungulates are in progress. Despite the two assemblages share many similarities in faunal composition, differences in taxonomy (e.g., stenonoid equids, with *Equus* aff. *senezensis stehlini* at CSG and a large *Equus stenonis* at Olivola) (Palombo and Alberdi, 2017; Palombo et al., 2017) and in palaeocology (mesowear and microwear analyses, Strani personal communication) suggest that they should be referred to distinct time intervals and environmental conditions.

The studies on CSG support the hypothesis that Europe was strongly affected by climatic deterioration during the early Pleistocene; the substitution of browser and mixed feeder species by open habitat grazers, was probably a gradual process. The palaeoenvironments of central Italy during the early Pleistocene (Gelasian) show similarities in climate with localities from the fossil record of France (as Saint-Vallier) and were characterized by more wooded areas and more humid climatic conditions than those of coeval eastern Mediterranean assemblages (as Sesklo in Greece) (Strani et al., 2015).

Moreover, the discovery of a single *Hippopotamus* sp. fragmentary incisor coming from the 1980s field collections at CSG pre-dates to the middle Villafranchian the arrival of this large ungulate in Europe, suggesting that this would be only one of multiple dispersal events that occurred during the Pleistocene from Africa into Europe.

The incisor from CSG was not collected during a systematic excavation but it comes, together with many others isolated teeth and fragments of equids and antelopes, from the exposed deposit bearing all the fossils of the 1970–2000 campaigns. In Europe, the occurrence of *Hippopotamus* in early Pleistocene (Gelasian) sites has been debated in literature (Mazza and Bertini, 2013) and previous discoveries of hippo remains at Senéze (France) (Mazza and Rustoni, 1994) and at Ellis (Greece) (Athanassiou and Bouzas, 2010; Reimann and Strauch, 2008; Thenius, 1955) were considered with great caution because of their unclear stratigraphic position. Recently, Pandolfi and Petronio (2015) briefly described mandibles of hippos coming from the Chiusi Basin (Tuscany, central Italy) (Cuscani Politi, 1966). The faunal assemblage of the Chiusi Basin has not been studied in detail yet, but the presence of cervids and *Gazella* sp. suggests a possible attribution to the Coste San Giacomo or Olivola FUs. Further studies will clarify the taxonomic and chronological position of the Chiusi Basin faunal assemblage. The available data suggest that hippo fossils are very rare in deposits around 2.0 Ma, while it becomes a relatively common taxon in the European late Villafranchian (Rook and Martínez-Navarro, 2010).

2.2. Pantalla (Umbria, Tiber Basin, central Italy)

The site of Pantalla was discovered in 1994 and two palaeontological excavations were carried out in 1995 by the "Soprintendenza per i Beni Archeologici dell'Umbria" (SBAU), with the scientific supervision of the University of Perugia. These excavations allowed recovering about eighty mammal fossils in excellent state of preservation, including almost complete crania and mandibles of carnivorans (Fig. 3) and artiodactyls.

The site is located about 30 km south of Perugia (Fig. 1), in the southwestern branch of the Tiber Basin, a wide extensional intermontane basin that was filled mainly by clastic (lacustrine, palustrine, and fluvial) deposits since the late Pliocene (Basilici, 1997). The basin encompasses approximately 1800 km^2 and extends from Sansepolcro to Terni and Spoleto describing an "upside-down Y" shape, splitting in a southeastern and a southwestern branch south of Perugia. The Pantalla mammal fauna was recovered from a 15-m-thick stratigraphic succession referred to the early Pleistocene Santa Maria di Ciciliano subsyntheme. Mammal remains occurred within two different levels (Gentili et al., 1997). The first is a silty sand level interpreted as a crevasse-splay deposit located in the middle part of the succession. Several carnivore (Fig. 3) and herbivore remains–especially skulls–were recovered from this level, mainly concentrated in a very small area of about 2 m^2. The taphonomic features of this assemblage suggest that bones were winnowed and accumulated by fluvial transport. The second mammal-bearing level (about 2 m above the previous one) is a drained palaeosol where plant remains (roots, leaves, and charcoal), terrestrial gastropods, and scanty fragmented postcranial bones of herbivore mammals were found. The absence of fluvial transport is evident and the "mosaic" pattern of the cracks on the bone surface suggests a pedogenetic origin of the accumulation.

The following mammal species are identified at Pantalla (fossils from the two stratigraphic levels have been considered as belonging to the same faunal assemblage): *Apodemus* cf. *dominans*, *Canis etruscus*, *Vulpes* sp., *Lynx issiodorensis valdarnensis*, *Acinonyx pardinensis*, *Sus strozzii*, *Pseudodama nestii*, *Leptobos merlai, Equus* sp., *Mammuthus* cf. *meridionalis* (Cherin et al., 2013a; Cherin et al., 2014a; Cherin et al., 2014b; Cherin et al., in press). Of particular relevance is the occurrence of a large-sized otter referred to *Lutraeximia umbra* (Cherin et al., 2016), the type material of which represents the only early Pleistocene Lutrinae cranium in the Mediterranean area. The above faunal composition allows referring the Pantalla assemblage to the Olivola/Tasso FUs (Gentili et al., 1997).

The taphonomic and ecological features of the site are still under investigation. Cherin et al. (2013b) emphasized that despite the excellent preservation and richness of fossils discovered, the assemblage seems to lack some important elements of the late Villafranchian carnivore palaeoguild such as hyaenids, possibly reflecting a reduced prey biomass and/or diversity in respect to other Italian sites. Surprisingly, some preliminary analyses of bite marks identified on three crania of medium-sized carnivores (*Canis* and *Lynx*) seem to be due to *Acinonyx pardinensis*, thus highlighting a very interesting case of carnivore intraguild predation (Cherin and Iurino, 2014), which is still under study.

3. *Homo* arrival in Europe: Pirro Nord (Gargano, southern Italy)

The fossiliferous site of Pirro Nord is located in the municipality of Apricena (Foggia, Apulia, southern Italy) (Fig. 1) on the northwest of the Gargano Promontory and, in the literature of the 1980s and 1990s, is known also as Cava Pirro or Cava Dell'Erba. The site is part of a complex interconnected karst system which includes palaeontological and archaeological deposits (Pirro 13) exposed in huge quarries exploiting limestones of the Mesozoic Calcari di Bari Formation (Arzarello et al., 2007, 2012; Pavia et al., 2012). A marine succession, composed of carbonate to siliciclastic sediments (ramp to shelf sediments spanning from the latest early Pliocene to the early Pleistocene) lies in unconformity on the Mesozoic limestones. The marine succession is comprised between two karst cycles that are represented, at the base, by the residual Terre Rosse with the well-known late Miocene to early Pliocene "*Mikrotia* fauna" and, at the top, by the sandy-clayey fossiliferous deposits of the early Pleistocene Pirro FU (Pavia et al., 2012). The early Pleistocene vertebrate assemblage comes from the siliciclastic sedimentary filling of the karst fissure network and fossils have been collected since the late 1960s (Pieri collection, University of Bari) and reported in scientific papers since the 1970s/1980s (Abbazzi et al., 1996; Arzarello et al., 2007, 2009; De Beaumont, 1976; De Giuli and Torre, 1984; De Giuli et al., 1986; Freudenthal, 1971; Pavia et al., 2012). The fossil assemblage includes more than one hundred vertebrate species.

The late Villafranchian elements of the mammal fauna indicate an early Pleistocene age. The geomagnetic polarity of the sediments (Napoleone et al., 2003; Pavia et al., 2012)

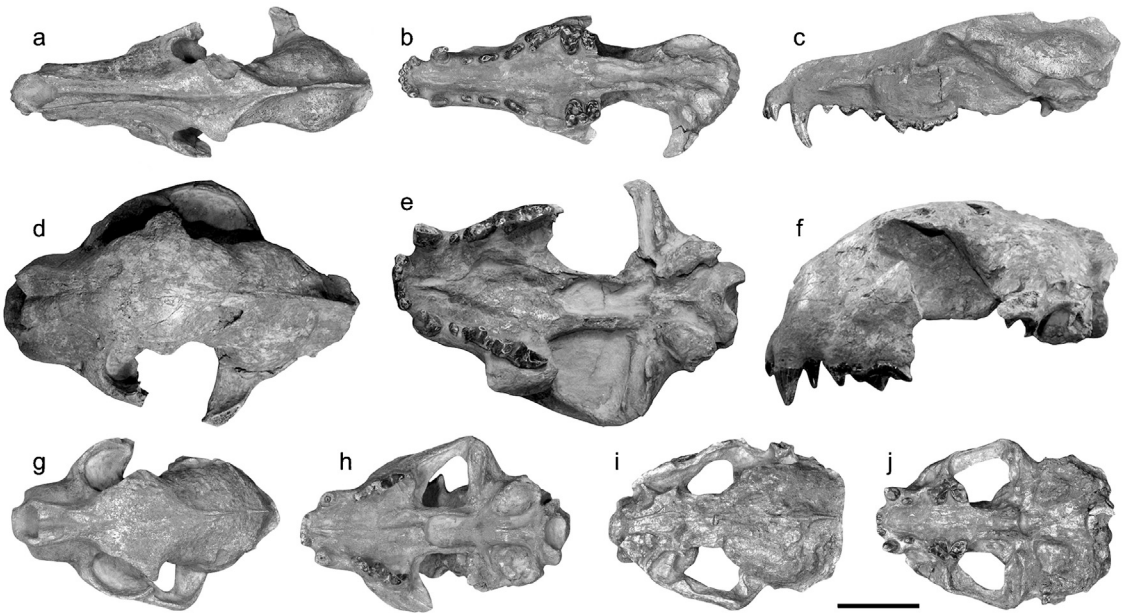

Fig. 3. Selection of carnivoran crania from Pantalla. a–c: *Canis etruscus* SBAU337646 in dorsal (a), ventral (b), and lateral (c) views; d–f, *Acinonyx pardinensis* SBAU337624 in dorsal (d), ventral (e), and lateral (f) views; g–h, *Lynx issiodorensis valdarnensis* SBAU337653 in dorsal (g) and ventral (h) views; i–j : *Lutraeximia umbra* SBAU337654 in dorsal (i) and ventral (j) views. Scale bar: 5 cm.
Fig. 3. Sélection de crânes de carnivore en provenance de Pantalla. a–c : *Canis etruscus* SBAU337646 en vues dorsale (a), ventrale (b) et latérale (c) ; d–f, *Acinonyx pardinensis* SBAU337624, en vues dorsale (d), ventrale (e) et latérale (f) ; g–h, *Lynx issiodorensis valdarnensis* SBAU337653, en vues dorsale (g) et ventrale (h) ; i–j : *Lutraeximia umbra* SBAU337654 en vues dorsale (i) et ventrale (j). Barre d'échelle : 5 cm.

further suggests a chronology preceding the Jaramillo Subchron.

The assemblage is characterized by the occurrence of the vole *Allophaiomys* gr. *ruffoi* (López-García et al., 2015; Masini et al., 1998), a species that is indicative of the early Biharian (micro-) Mammal Age (Sala and Masini, 2007). The fossil assemblage is considered one of the latest Italian Villafranchian faunas, and Cava Pirro has been designated as the type locality of the Pirro FU (Gliozzi et al., 1997; Rook and Martínez-Navarro, 2010; Torre et al., 2001).

The most important bioevents characterizing the Pirro FU are the first occurrence of *Equus altidens*, *Bison* (*Eobison*) *degiulii* and, among carnivorans, of the wild dog *Xenocyon lycaonoides*, the badger *Meles meles*, and the weasel *Mustela palaerminea*. Moreover, the Pirro FU represents the last occurrence in Italy for some taxa of earlier origin, such as the dirktooth cat *Megantereon whitei*, the giant cheetah *Acinonyx pardinensis*, and the porcupine *Hystrix refossa*. Pirro Nord is peculiar also for the abundance of carnivorans, both in taxon diversity and specimen number (from the Pirro 10 site, 14 carnivoran taxa have been found) (Pavia et al., 2012; Petrucci et al., 2013). The sabertooth cat *Homotherium latidens* can be considered the best represented carnivoran at Pirro Nord, followed by the canid *Canis mosbachensis* and the giant hyena *Pachycrocuta brevirostris*.

The Pirro 13 karst fissure (Cava dell'Erba) shows a significant vertebrate assemblage (Fig. 4) associated with lithic artefacts attributable to Mode 1. The Pirro 13 fissure was excavated in 2007 and 2008 by an interdisciplinary team composed by researchers from the Universities of Ferrara, Torino and Sapienza of Rome. Since 2012, the excavations are carried out by a team of archaeologists of the University of Ferrara and the analysis of the lithic tools is in progress (Arzarello et al., 2012; Arzarello et al., 2014). The lithic assemblage is characterized by a high degree of opportunism and by the exclusive presence of debitage reduction sequences.

The Pirro Nord vertebrate assemblage shares similarities with other early Pleistocene Italian sites such as Pietrafitta (Umbria) and Monte Argentario (Tuscany), referred to the Farneta FU. In particular, the analysis of the micromammal remains suggests that the Pirro Nord and Monte Argentario sites could be very close in their biochronology and, in general, that the differences between the Farneta and Pirro FUs could be due more to geographical and ecological factors than to chronological changes (Siori et al., 2014).

4. Concluding remarks

The early Pleistocene vertebrate assemblages from Italy (Fig. 5) have a historical importance for the definition of a biochronological framework for the Mediterranean region, as well as for other Eurasian areas. Terms like Villafranchian and Galerian come from Italian sites and are still widely used by vertebrate palaeontologists interested in the Old World terrestrial faunas. The Italian territory thanks to its geographical position, has represented, at least from the Plio-Pleistocene transition, a crossroad between Europe and Africa, East and West. Therefore, the Italian fossil record can be considered of special interest for the study of the Plio-Pleistocene terrestrial ecosystems, in particular at the time of the earliest dispersal of humans from

Fig. 4. Selection of vertebrate remains from Pirro Nord. a: *Homotherium latidens* in lateral view; b–c: *Stephanorhinus* cf. *hundsheimensis* in occlusal (b) and lateral (c) views; d–e: *Pachycrocuta brevirostris* G106 in right lateral (d) and left lateral (e) views; f: *Praemegaceros obscurus* PU 106772 in occlusal view. Scale bar: 5 cm.

Fig. 4. Sélection de restes de vertébrés en provenance de Pirro Nord. a, *Homotherium latidens* en vue latérale ; b–c : *Stephanorhinus* cf. *hundsheimensis* en vues occlusale (b) et latérale (c) ; d–e : *Pachycrocuta brevirostris* G106 en vue latérale droite (d) et latérale gauche (e) ; f, *Praemegaceros obscurus* PU106772 en vue occlusale. Barre d'échelle : 5 cm.

Africa to Eurasia. Evidence of the early Pleistocene occurrence of humans in Italy has been found at Pirro Nord, and in recent years an increasing number of coeval sites from the Mediterranean region and western Europe have been discovered. In addition, the study of new sites and the reappraisal of pre-existent collections provide further data about the terrestrial ecosystems before and after the earliest dispersal of *Homo* in Europe.

The occurrence at CSG of a single hippo tooth could be related to an early dispersal event of large mammals from Africa around 2 Ma ago. Moreover, the rich fossil record discovered at Pantalla is providing valuable information on the taxonomy and ecology of many different species (carnivorans in particular). The transition before and after the dispersal of *Homo* into Europe is well represented in Italy by the ungulate guild, with the middle and early late Villafranchian antelopes-*Eucladoceros*–*Leptobos* being replaced by the late late Villafranchian-Epivillafranchian ovibovines-*Praemegaceros*–*Bison* assemblages. The environmental context at CSG, as stated by Strani et al. (2015) (a mosaic environment with steppe and woodland/wetland areas) is different from that reported for other similarly-aged eastern Mediterranean localities (as Sesklo in Greece), and seems to be more similar to that testified by the French fossil record (as Saint-Vallier) in this time period. The hipsodonty and mesowear analyses on ungulate teeth from Olivola suggest clear differences both in chronology and in feeding behaviours with the CSG sample (Strani personal communication). At Olivola, the first occurrence of *Pachycrocuta brevirostris*, a very significant bioevent (Sardella and Palombo, 2007), is documented together with the last occurrence of *Anancus* and antelopes (Bellucci and Sardella, 2015; Sardella and Palombo, 2007). Among ungulates, during the Olivola-Tasso transition, antelopes became extinct and ovibovines spread, despite their remains are relatively scanty in the Italian fossil record. In western Europe, Antilopini were replaced by Ovibovini, such as *Praeovibos* and the rare brachyodont *Soergelia*, better adapted to the harshening of environmental conditions that became evident during both cooler and warmer phases. In the Italian Peninsula, the first record of Ovibovini is documented in the site of Casa Frata (Upper Valdarno) in the Tasso FU (around 1.7 Ma), where De Giuli and Masini (1983) described postcranial remains attributable to cf. *Praeovibos* and *Soergelia* can be considered an important biochronological marker for the second half of the early Pleistocene in Europe. *Soergelia minor* is documented at Dmanisi (Georgia) and Venta Micena (Spain), and *Soergelia brigittae* at Apollonia (Greece) (Martínez-Navarro et al., 2012, with references therein). The occurrence of *Soergelia* at Monte Argentario (Tuscany) testifies the dispersal in Italy.

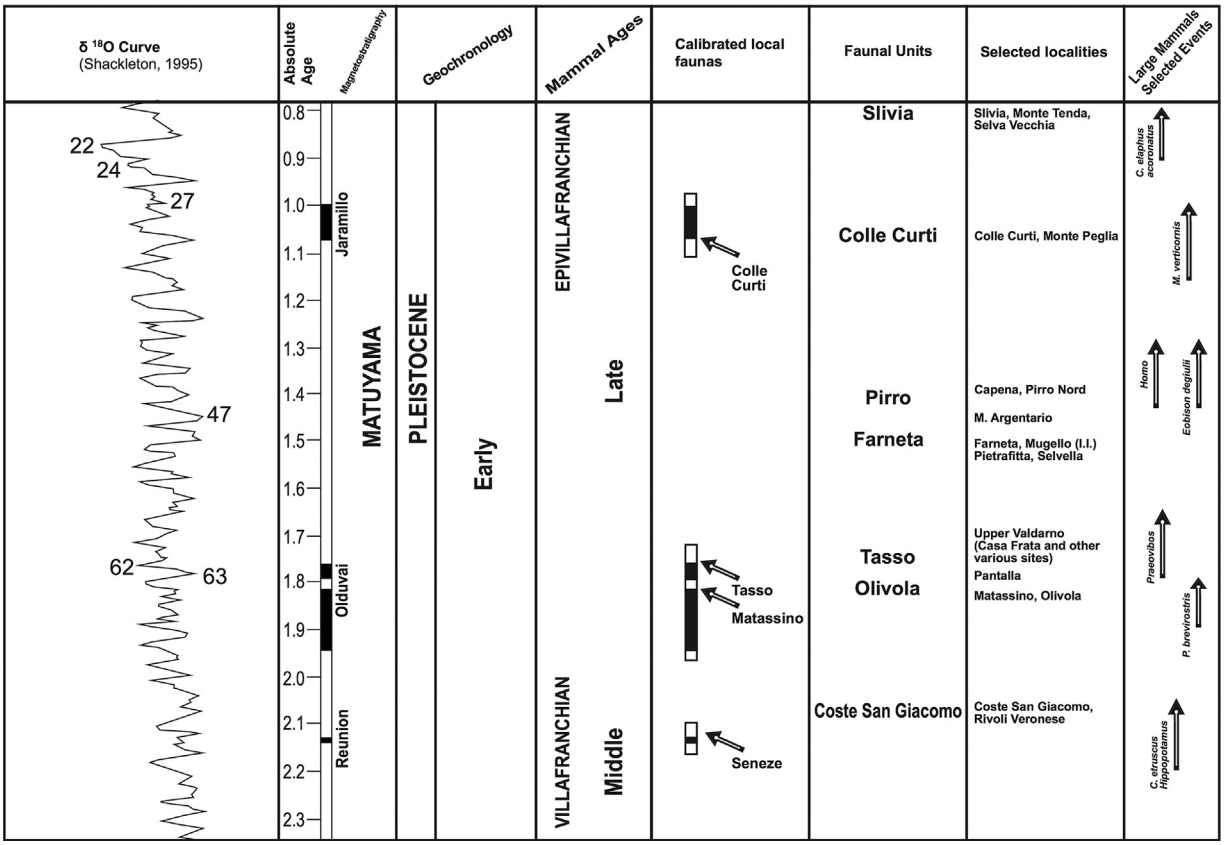

Fig. 5. Biochronological framework of the Italian selected localities.
Fig. 5. Cadre biochronologique des localités italiennes sélectionnées.

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