Evidence of late Gelasian dispersal of African fauna at Coste San Giacomo (Anagni Basin, central Italy): Early Pleistocene environments and the background of early human occupation in Europe

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ARTICLE INFO

ABSTRACT

Since the late 70s, the Early Pleistocene (Gelasian) site of Coste San Giacomo (Anagni Basin, central Italy) has been known amongst palaeontologists for its diverse vertebrate fauna. During the last 5 years, new excavations and the drilling of a 46-m-deep core have provided novel pieces of information. Palaeomagnetic data, pollen and small vertebrates analyses are presented here for the first time and combined with the updated list of the large vertebrates and ostracod analysis in a multidisciplinary perspective. Large and small mammals, pollen and ostracod analyses have allowed an integrated palaeoenvironmental reconstruction of the sedimentary sequence, depicting the evolution of the alluvial plain in the surrounding landscape. Moreover, magnetostratigraphy, pollen and small mammal biochronological data have confirmed the position of the Coste San Giacomo Faunal Unit, focusing the possible age of the mammal assemblage around 2.1 Ma, in a reversed phase before the base of the Olduvai chron. In particular, the occurrence of the large vole *Mimomys pliocaenicus* has important biochronological significance. The Coste San Giacomo site offers a unique opportunity to investigate the faunal and environmental changes that occurred in Mediterranean Europe during the Early Pleistocene, coinciding with major climatic changes at a global scale. The occurrence of taxa such as *Hippopotamus* sp. in the assemblage provides evidence of early dispersal events of African taxa prior to the early *Homo* diffusion into Europe.

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1. Introduction

The Anagni Basin (central Italy) is a Plio-Pleistocene intermontane basin in the Italian peninsula, which developed largely between the Late Pliocene and the early part of the Middle Pleistocene (Carrara et al., 1995; Galadini and Messina, 2004). The sequence includes lacustrine-alluvial sediments covered by travertine (Segre and Ascenzi, 1984) and by Middle Pleistocene pyroclastics, dated at the site of Fontana Ranuccio to between 0.528 Ma and 0.366 Ma (K–Ar dating; Biddittu et al., 1979) and attributed to the Alban Hills magmatic district (∼0.7–0.02 Ma; Peccerillo, 2005). In the Anagni Basin, the Coste San Giacomo (CSG) (Fig. 1) and Fontana Ranuccio

sites have yielded important large mammal assemblages from the earliest and the middle Pleistocene respectively (Segre Naldini et al., 2009; Bellucci et al., 2012 and references therein).

Given the position of the Italian peninsula at the crossroads of Africa and Eurasia and the occurrence of African taxa such as *Hippopotamus* sp. in the assemblage, the CSG site provides information regarding early dispersal events of African fauna. It is a matter of debate as to whether the presence of African species is linked to hominin dispersal or whether there was an African faunal background preceding that dispersal (O'Regan et al., 2011 and references therein). In this context, the Italian earliest Pleistocene (Gelasian) site of CSG assumes exceptional significance due to its faunal diversity and chronological position prior to the early *Homo* dispersal in Europe.

In this work, we present a comprehensive study of the CSG site by integrating different proxies such as palaeomagnetism, pollen,

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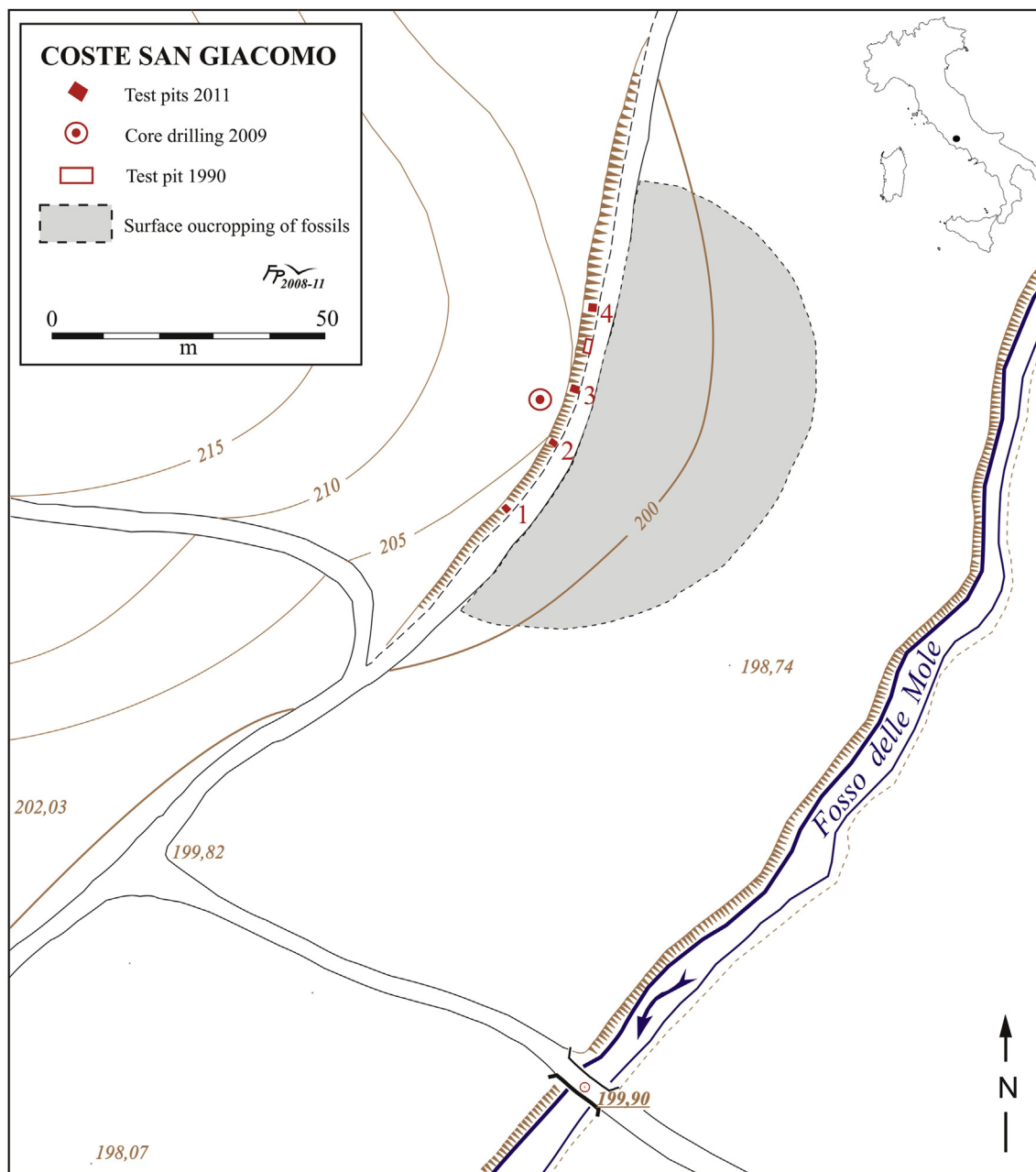 E-mail address: lbellucci78@gmail.com (L. Bellucci).

Fig. 1. Topographic map of CSG site.

and ostracod analyses. Moreover, the co-occurrence of diverse small and large vertebrate assemblages allows a comparison between the respective established biochronological scales.

2. Materials and methods

In 2009, a joint IsIPU (Italian Institute of Human Palaeontology) and Sapienza – University of Rome team conducted by F. Parenti and R. Sardella began re-prospecting and re-excavating the CSG site. This process has led to new palaeontological and magneto-stratigraphical data being recovered. The first fossil remains from CSG were reported in 1978. After their discovery and following several field seasons in the ensuing years, an exploratory trench was dug in August 1990 (Bellucci et al., 2012). 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 46m-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 whole area has been surveyed in detail with a transit and alidade at 1:1000 scale (in 2008, 2009 and 2011). As a datum reference, the elevation point at 199.9 m a.s.l. from the 1:10000 regional map (sheet 389020) on the top of the bridge on Fosso delle Mole has was chosen (Fig. 1). Planimetric and altimetric tolerances are ±20 cm and ±5 cm, respectively.

The four test pits, numbered S1–4 from S to N (Fig. 1) have a minimum surface area of 1 m^2 and a maximum depth of 1.5 m from the road level. For small vertebrate analyses, at least four sediment samples of 15 kg each were collected from each pit; preliminary dry-sieving with 1 mm mesh confirmed the occurrence of a rich

and diverse small vertebrate assemblage. In all test pits, the succession consists of laminated medium-to fine-grained yellowish sands with Fe—Mn coatings, passing upward into massive fines with $CaCO_3$ nodules (Fig. 2).

Large vertebrate remains have been recovered from pits S2, S3 and S4 (area delimited in Fig. 2), mainly consisting of diaphyses, teeth, metapodial bones and antlers, with different surface preservation colors (mainly blackish), mineralization stages, and abrasion traces. No articulated skeletal parts have been observed but the bones are generally well preserved. The occurrence of large bone remains, taking the average of the three test pits S2, S3, and S4, reached a maximum of $1000/m^3$, about 10% of which are potentially determinable.

Small mammal analyses were performed on a total of ca 200 kg of sediment from test pits S2 and S3. The sediment was sieved in the field with a set of 4, 2 and 1 mm sieves. In the laboratory, the sediment was screened under a stereomicroscope. The large and small vertebrate material is housed in the collection of the IsIPU laboratory (Anagni, Italy). The revised vertebrate faunal assemblage is presented in Table 1.

Palaeomagnetic analyses were performed on 64 cubic samples ($\sim 8\ cm^3$) from the CSG1 core (Fig. 3) and on 18 oriented cylindric samples ($\sim 10\ cm^3$) from the fine sediments representing fluvial abandonment in test pits S2 and S4 (Figs. 2 and 4). Samples were stepwise demagnetized by thermal treatment and one core specimen every other stratigraphically-superimposed sample was demagnetized by alternating field (AF). The intensity of natural remanent magnetization (NRM) was measured with a 2G-Enterprises DC SQUIDs cryogenic magnetometer at the Alpine Laboratory of Palaeomagnetism (Peveragno, Italy).

The CSG1 core was also sampled for pollen. A total of 32 samples were collected in the 8—35 m depth interval, but only 15 samples

Table 1
CSG faunal list.

Small Mammals	
Arvicolidae	*Mimomys pliocaenicus*
Muridae	*Apodemus* sp.
Gliridae	*Sciurus* cf. *S. warthae*
Castoridae	*Castor fiber*
Hystricidae	*Hystrix refossa*
Soricidae	*Beremendia fissidens*
Talpidae	*Talpa* sp.
	Galemys sp.
Large Mammals	
Mastodontidae	*Anancus arvernensis*
Elephantidae	*Mammuthus meridionalis*
Rhinocerotidae	*Stephanorhinus* sp.
Equidae	*Equus stenonis*
Cervidae	*Eucladoceros* sp.
	Axis cf. *lyra*
	Croizetoceros cf. *ramosus*
Bovidae	*Leptobos* sp.
	Gallogoral meneghini
	Gazellospira torticornis
	Gazella borbonica
Suidae	*Sus strozzii*
Hippopotamidae	*Hippopotamus* sp.
Hyanidae	? *Pliocrocuta perrieri*
Ursidae	*Ursus* cf. *etruscus*
Canidae	*Canis* sp.
	Vulpes cf. *alopecoides*
Felidae	*Homotherium* sp.
Cercopithecidae	*Macaca sylvanus*

from 20 to 35 m yielded enough pollen to be represented on diagrams. For each sample, a known amount of dry sediment (approximately 1 g) was chemically processed as follows: removal of calcium carbonate (HCl 37%), silica (cold HF 40% for 12 h) and humic acids (boiling
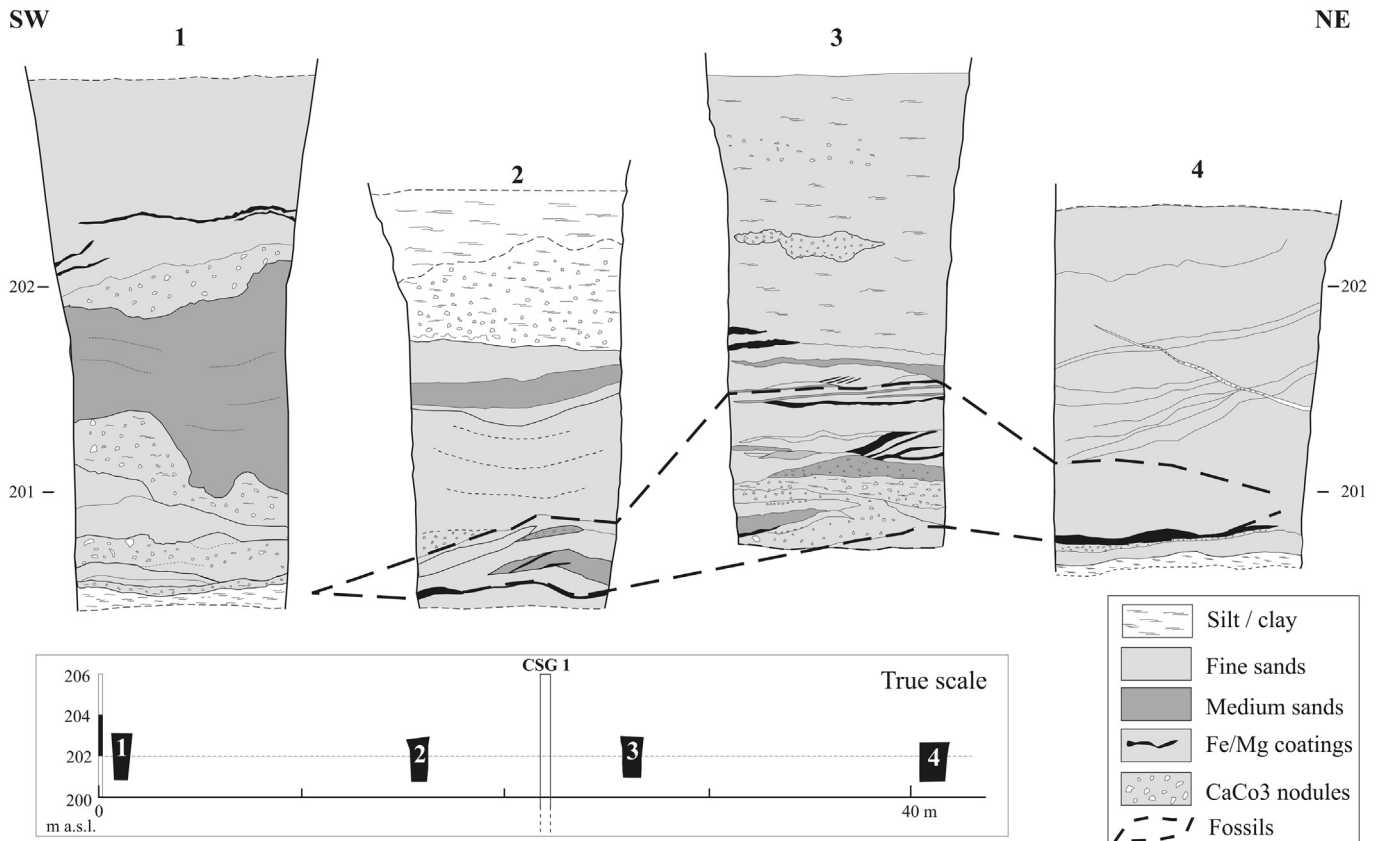

Fig. 2. Stratigraphic logs of the CSG test pits S1—4. The position of the CSG1 core between S2 and S3 is shown.
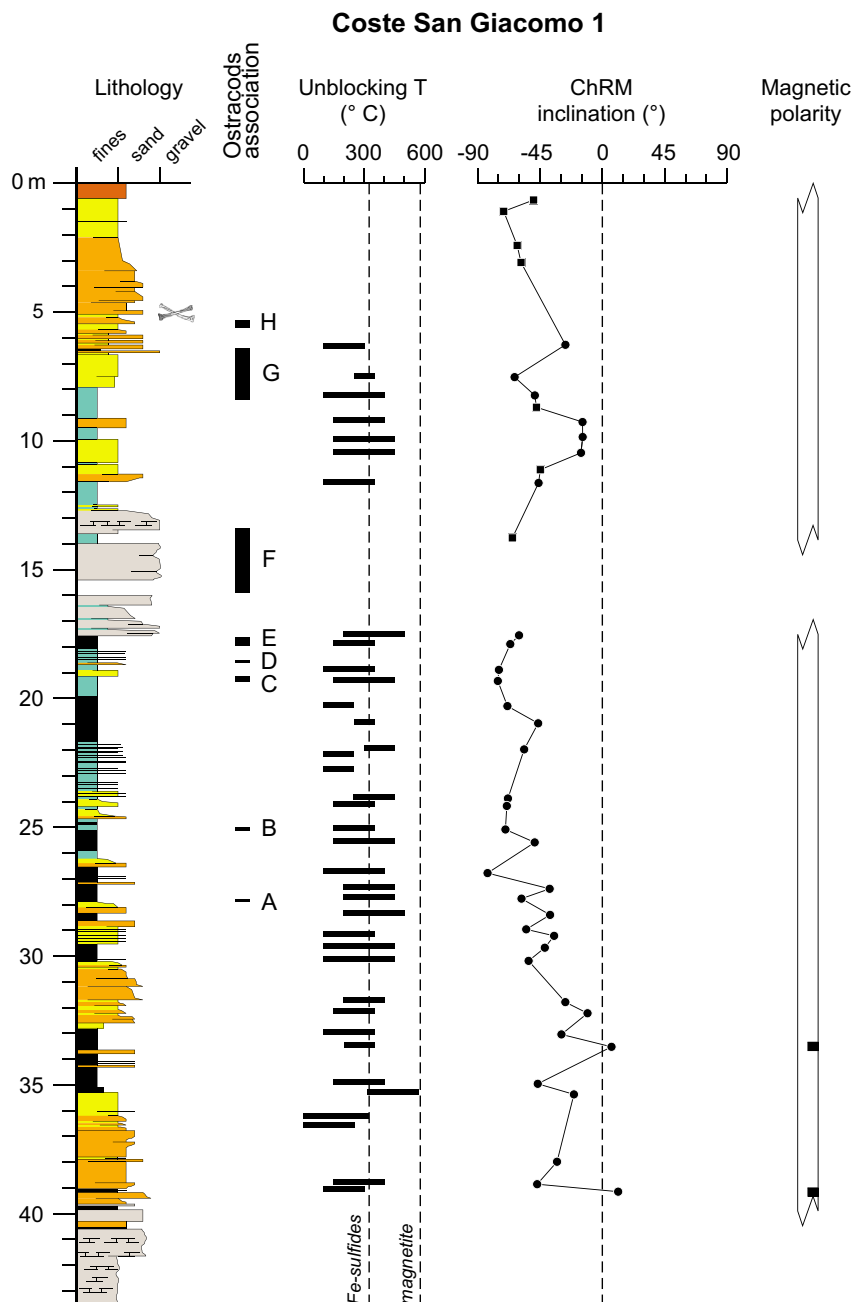
Fig. 3. Lithology, ostracod association, unblocking temperatures, and inclination values of the characteristic remanent magnetization (ChRM) of the Coste San Giacomo 1 core. The maximum unblocking temperatures of the Fe-sulfides and magnetite are shown. ChRM values displayed by squares have been calculated with the McFadden and McElhinny (1988) method (see text for discussion). The magnetic polarity stratigraphy was retrieved from the inclination of the characteristic component vectors expressed in degrees from horizontal. White is reverse polarity, black is normal polarity. The position of the fossiliferous bed at ca 5 m is also shown.

in NaOH 10%), and mounting in glycerine. A known amount of *Lycopodium* spores was added to obtain estimates of pollen concentration/g of dry sediment. Pollen grains were identified according to Reille (1992, 1995, 1998), Beug (2004), and the reference collection at the Laboratory of Palaeobotany and Palynology of Sapienza University of Rome. *Cathaya* type has been identified following the criteria of Sivak (1976), Liu and Basinger (2000) and Zanni and Ravazzi (2007). Pollen of *Taxodium* type may include *Taxodium* and *Glyptostrobus*, similarly to several Italian records (Bertini, 2010).

An average of 149 pollen grains was counted in the 15 samples represented in the diagram (Fig. 5). The total pollen concentration is on average 12700 grains/g, the lowest value being 1400 grain/g at

29.50 m and the highest value 51900 at 21.90 m. A total of 31 pollen types and 3 spore types were identified. The computer program Psimpoll 4.25 (Bennett, 2009) was used to plot the diagram of Fig. 5.

The Mutual Ostracod Temperature Range (MOTR: Horne, 2007; Horne and Mezquita, 2008; Horne et al., 2012) method was applied to the ostracod assemblage from the CSG sediment core, already presented in Bellucci et al. (2012). This new technique uses the occurrence of freshwater ostracods to derive past air temperatures by combining the modern distribution of ostracod species with modern climate data. The MOTR derives its data from the Non-marine Ostracod Distribution in Europe (NODE) database (Horne and Mezquita, 2008). A mean air temperature range is assigned
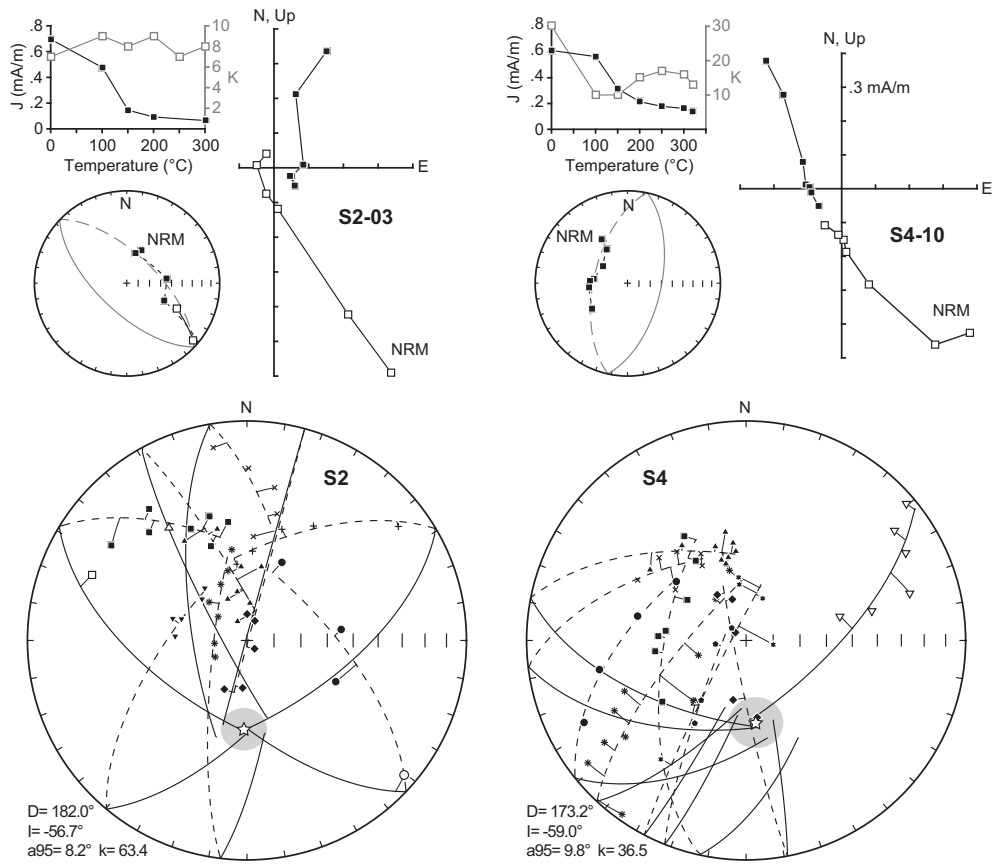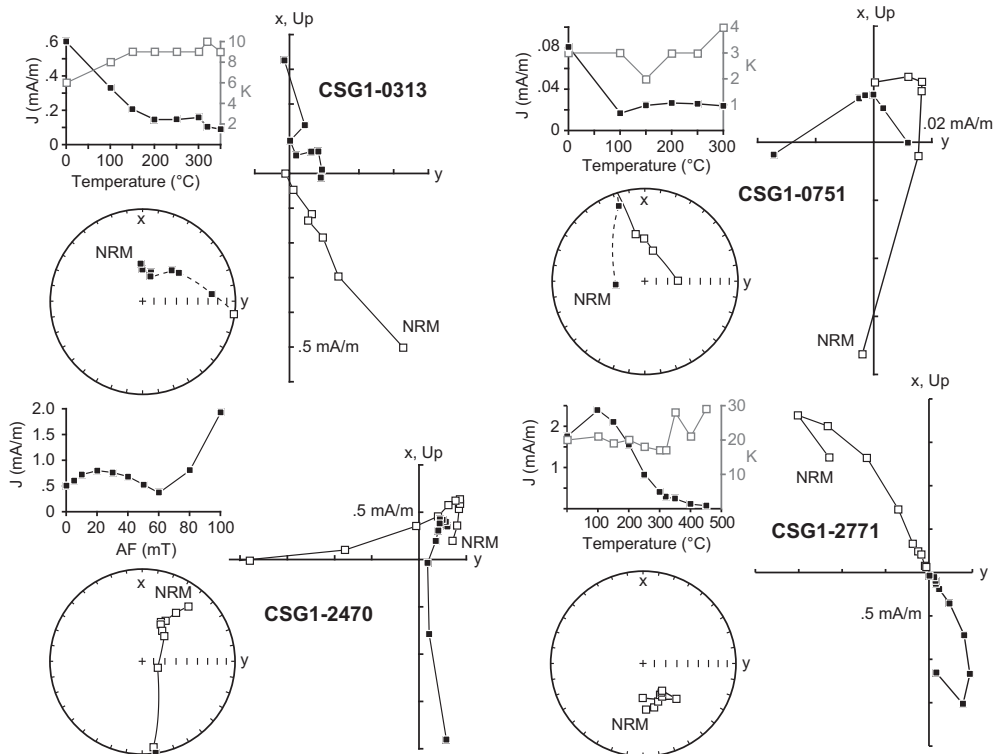
Fig. 4. Demagnetization plots of representative samples from the test pits and the CSG1 core. K is magnetic susceptibility. Orthogonal vector diagrams: open and closed symbols represent projections onto vertical and horizontal plane, respectively. Equal-area projection: open and closed symbols represent projections onto upper and lower hemisphere, respectively. Star is the site mean value calculated according to McFadden and McElhinny (1988).
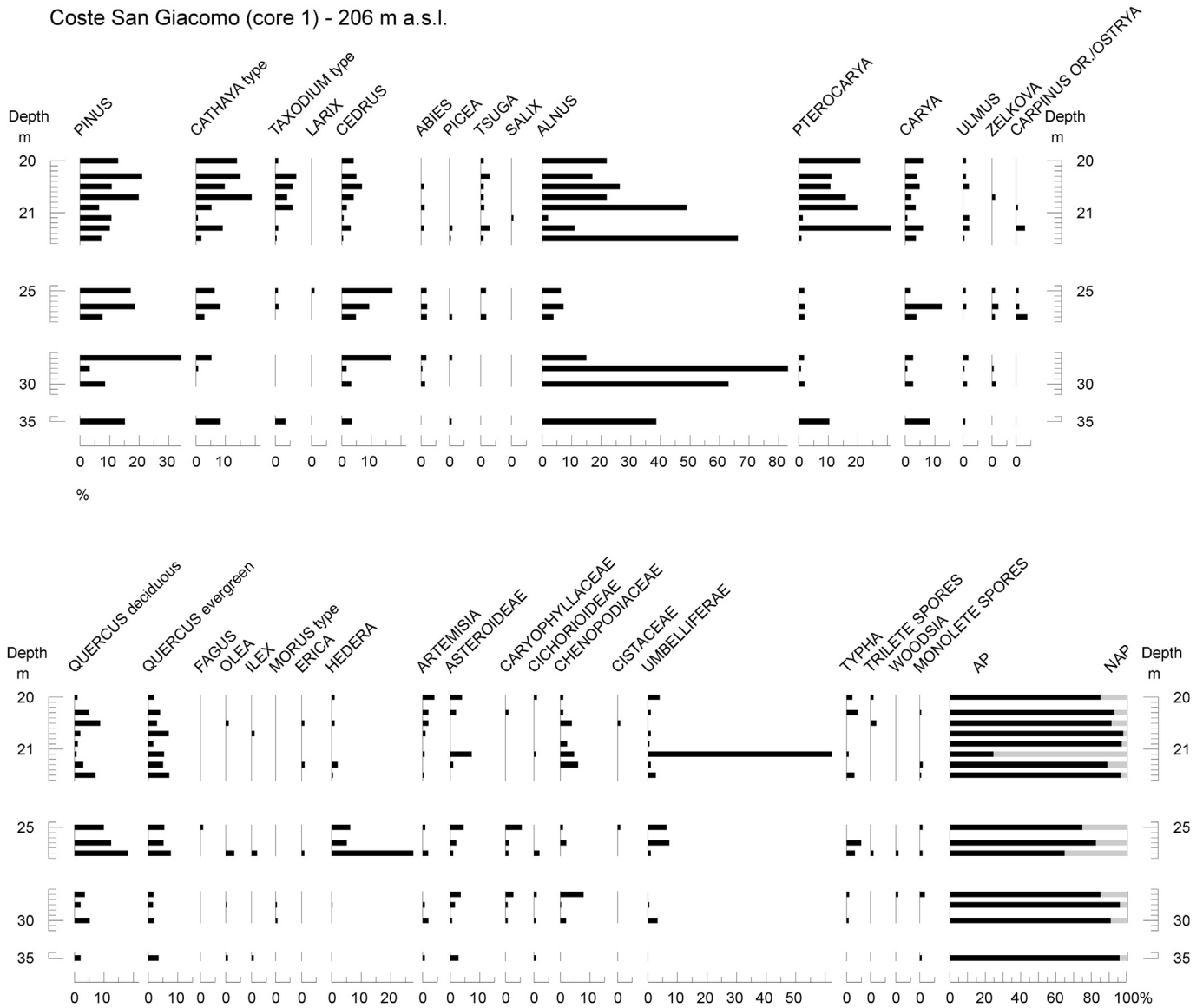
Coste San Giacomo (core 1) - 206 m a.s.l.

Fig. 5. Pollen percentage diagram from Coste San Giacomo.

to each ostracod species (for example for January and July) and the overlapping ranges of the fossil species can be used to estimate the mutual temperature range in which the assemblage could live. This method utilizes all the ostracod species in an assemblage that can be calibrated in terms of their modern distribution. Such a distribution is then related to the modern climate space, i.e. the modern mean January and July temperatures of their distribution areas (Horne et al., 2012). The accuracy of the method is limited by two main factors: the calibration gives the same weight to all the species forming the assemblage, not considering their frequency in the fossil samples, and some taxa are still poorly represented in the NODE database, giving partial information to their distribution.

3. Results

3.1. CSG mammals

The large mammal assemblage of CSG includes 19 species of carnivores, artiodactyls, perissodactyls and proboscideans (Table 1). The most abundant material is that of medium-sized herbivores such as *Equus stenonis*, *Axis* cf. *lyra* and *Eucladoceros*

sp. Large-sized herbivores such as *Hippopotamus* and *Stephano-rhinus* are poorly represented.

The occurrence of the proboscideans *Mammuthus meridionalis* and *Anancus arvernensis* is attested to by several tusk portions and molar tooth fragments. In particular, a worn left upper second molar is referable to the latter species. The equid *E. stenonis* is the most abundant taxon among the large mammals, represented by several isolated cheek teeth and postcranial bones. Three species of cervids have been identified: the small-sized *Croizetoceros* cf. *ramosus*, the medium-sized *Axis* cf. *lyra* and the large-sized *Eucla-doceros* sp. The systematic attributions have been based on dental morphology due to the scarcity and the fragmentation of the antlers present. Two species of the tribe Antilopini have been found in the CSG assemblage, *Gazella borbonica* and *Gazellospira torticornis*. *G. borbonica* is represented in particular by seven horn cores referable to adult individuals and one horn core of a young female. Only one horn core belongs to *G. torticornis*. Isolated teeth and postcranial bones can be also referred to these two taxa. The caprine *Gallogoral meneghinii* is represented by two upper molars. The other taxa are represented by few remains only, including isolated teeth and postcranial bones.

The scavenging activity of hyaenids is documented extensively by 108 coprolites, as well as by many fossil bones showing gnaw-marks and impact fractures from bites. The carnivore guild at CSG consists of a machairodontine cat of the genus *Homotherium*, hyaenids (intermediate in size between *Pliocrocuta perrieri* and *Pachycrocuta brevirostris*; the presence of the cursorial *Chasmaportetes* cannot be confirmed due to the fragmentary nature of the fossils), two species of canids, *Canis* sp. and *Vulpes* cf. *alopecoides*, and a bear *Ursus* cf. *etruscus*. A single lower molar can be ascribed to *Macaca sylvanus*.

The CSG small mammal fauna is represented by limited remains, including *Mimomys pliocaenicus*, *Apodemus* sp., *Sciurus* cf. *warthae*, *Beremendia fissidens*, *Talpa* sp., *Castor fiber* and *Hystrix refossa* (Fig. 6).

3.2. Pollen analysis

The samples between 8 m and 19.53 m are not represented on the pollen diagram, as they are very poor in pollen, probably because of the coarse grain size of the sediment. In the interval between 20 m and 35 m, shown in Fig. 5, there is no stratigraphic continuity between the samples containing pollen grains so it is not possible to define any pollen zone.

Arboreal taxa are dominant in all samples except at 21.10 m, where, possibly because of a temporary drying-out of the environment, a massive presence of Apiaceae causes a reduction of arboreal pollen. High frequencies of *Alnus* in the samples at 21.10 m and 29.70—35 m may be ascribed to local swampy conditions, similar to those observed in the Fontana Ranuccio sediment core (Corrado and Magri, 2011). Among the arboreal taxa, *Pinus*, *Cathaya* type, *Alnus*, *Cedrus*, *Carya* and *Pterocarya* attain percentages ≥10%, while *Tsuga*, *Zelkova*, *Carpinus orientalis* type, *Quercus* deciduous and *Quercus* evergreen show values ≤10%. Only rare occurrences of *Larix* and *Fagus* were found. The herbaceous plants are represented by *Artemisia*, Asteroideae, Cichorioideae, Chenopodiaceae, Caryophyllaceae and Apiaceae, the last being the most abundant taxon. Among aquatic plants, only *Typha* is present. Spores of *Pteris*, *Woodsia* and trilete spores are present in low percentages.

On the whole, the pollen record between 35 m and 20 m represents a forested landscape, suggesting a temperate climate typical of an interglacial phase. The discontinuous nature of the record does not, however, allow assessment of whether it corresponds to a single forest phase or to multiple expansions of trees.

3.3. Air-temperature reconstruction

Air-temperature reconstruction was made by applying the MOTR method (Horne and Mezquita, 2008) to the most common species determined in the CSG core (*Candona candida*, *Candonopsis kingslei*, *Herpetocypris reptans*, *Potamocypris zschokkei*, *Pseudocandona marchica* (*P. eremita* in Bellucci et al., 2012), *Pseudocandona rostrata* and *Cyclocypris ovum*). Although the ostracods occur in 8 different assemblages along the sediment core from 5 m to 28 m, for the purposes of the MOTR analysis, they have been considered a single assemblage.

The analysis provided estimates of mean July air temperatures of between 15 °C and 22 °C and mean January air temperatures of between −5 °C and 5.2 °C (Fig. 7). Both ranges are just slightly inferior to the respective modern mean July (22.8 °C) and January (5.3 °C) air temperature values instrumentally measured for the last 10 years at the nearby Colleferro (2003—2012, Hydrological Annals). The ostracod assemblages suggest the occurrence of mild climatic conditions in an alluvial environment with clear, running waters, sensitive to the precipitation regime. The environment was rich in aquatic vegetation (abundance of phytophilic species) and algae (occurrence of Characeae). The CSG climate may have had similar winter temperatures to today although somewhat shifted toward colder values, but the seasonal range was less enhanced and summer temperature could have been lower.

3.4. Palaeomagnetic analysis

The NRM of analyzed samples is in the 10^{-5}—10^{-3} A/m range. Orthogonal projections of demagnetization data (Zijderveld, 1967) for the CSG1 core indicate a clear two-component magnetization with a present field component removed at the first demagnetization steps (<250 °C) superimposed on a stable component (Fig. 4, sample CSG1-2771), regarded as the characteristic remanent magnetization (ChRM). The maximum unblocking-temperatures, usually in the 350—450 °C range, suggest (titano-)magnetite as the
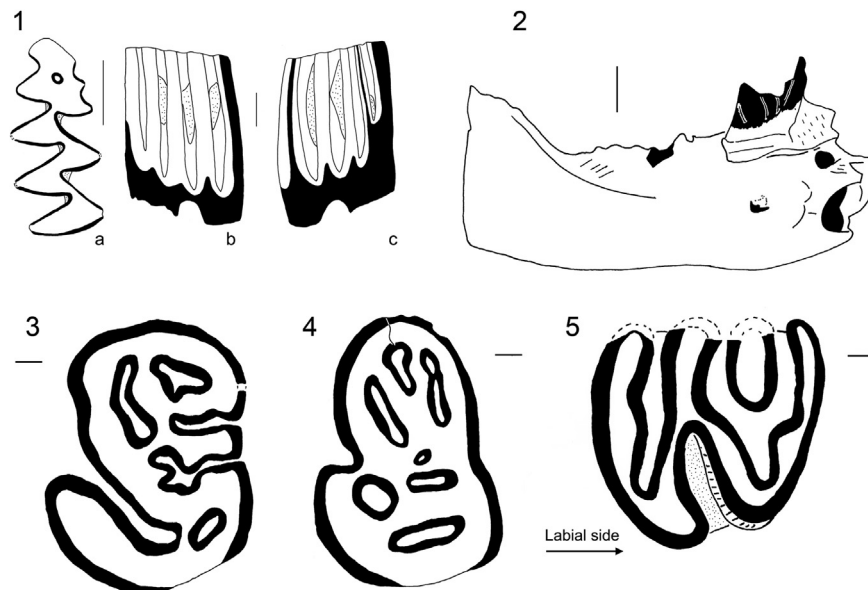

Fig. 6. CSG selected small mammals 1 *Mimomys pliocaenicus*: right M1, a-occlusal view, b-lingual view, c-buccal view; 2 *Beremendia fissidens*: right hemimandible with fragmented m1; 3 *Hystrix refossa*: left p4; 4 *Hystrix refossa*: dp4; 5 *Castor fiber*: right m1—2. Scale bar 1 mm.
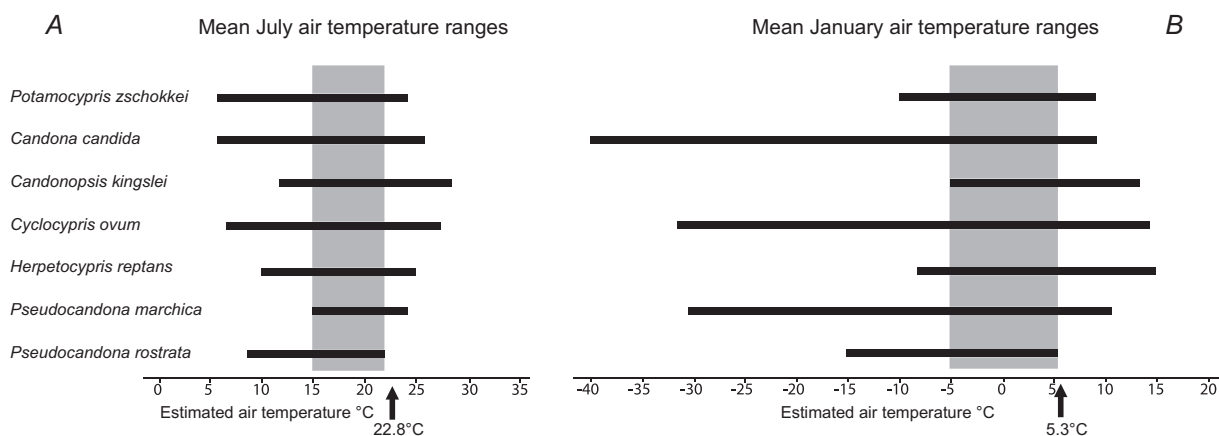
Fig. 7. Mean July (A) and January (B) air temperature ranges, for the occurrences of ostracod taxa found in between 25 m and 5 m of the CSG sediment core using the MOTR method. In both figures, the black arrow indicates the present-day instrumental mean temperatures from Colleferro.

dominant remanence carrier. Some samples in the 18–34 m core interval show acquisition of a spurious gyromagnetic remanent magnetization (GRM) at AF higher than 50–60 mT, suggesting the occurrence of greigite (Sagnotti and Winkler, 1999; Hu et al., 2002; Roberts et al., 2011; Fig. 4, sample CSG1-2470). Magnetization components were resolved from the demagnetization data using the standard least squares method (Kirschvink, 1980). The CSG1 core bears dominant negative inclination values of the ChRM, except for the uppermost meters (the palaeontological horizon), where positive magnetic inclinations are observed. However, stereonet projections show that samples from the uppermost interval have directions from each demagnetization step lying along an arc of a great circle, interpreted as circle of remagnetization (Fig. 4, samples CSG1-0313 and CSG1-0751), thus suggesting that the positive inclinations measured are not primary. This is better seen in the samples collected from the test pits S2 and S4 of the palaeontological horizon (Fig. 4, samples S2–03 and S4–10). As the samples could be oriented with respect to the north, we observe that the great circles defined by demagnetization data are converging to a remanence direction of Dec = 182° Inc = −57° and Dec = 173° Inc = −59°, defined with the method of McFadden and McElhinny (1988) for the sites S2 and S4, respectively. Based on the evidence from the exposed sections, we estimated the ChRM inclinations for each sample in the uppermost interval of the CSG1 core. This was done by retrieving the azimuth of the core's samples from their secondary component, assuming that it is a viscous overprint produced by the recent Earth's geomagnetic field, and then combining the fitted great circle from the CSG1 samples with a fixed direction obtained from the average of the S2 and S4 sites values (Fig. 3) (following McFadden and McElhinny, 1988). In summary, the palaeomagnetic data allowed a reversed palaeomagnetization for the CSG palaeontological horizon to be identified.

4. Discussion

4.1. Vertebrates and palaeoenvironments

Fragmented teeth testify the coexistence of the newly-arrived southern mammoth (Fig. 8) with the mastodon *Anancus arvernensis*. The coexistence of these two taxa occurs equally in the French site of St. Vallier (Guérin et al., 2004; Nomade et al., 2013), testifying the gradual replacement of the mastodons by the early species of *Mammuthus*. The coexistence of these two proboscideans has a significant palaeoenvironmental implication, since the arrival in Italy of *Mammuthus meridionalis* corresponds with an opening-up

of the vegetation during the earliest Pleistocene. Equally, the prevalence of stenonid equids over deer could suggest drier and more open landscapes.

The ungulates recovered at CSG indicate a rich and diverse environment consisting of both forested and open areas. According to Rivals and Athanassiou (2008), the small-sized *Croizetoceros* had the same habits as the extant *Dama dama* and *Capreolus capreolus*, which are mixed feeders living in both wooded and more open environments. On the other hand, the larger browsers *Axis* and *Eucladoceros* were adapted to live in more closed environments. Valli and Palombo (2005) indicated that *Eucladoceros* from Saint Vallier was a leaf-eater, similar to modern wapiti with a major intake of leaves and bark.

With respect to the Antilopini in the CSG assemblage, according to several authors (Heintz, 1971; Helmer and Rocheteau, 1994; Crégut Bonnoure and Valli, 2004), *G. borbonica* compares most closely with the present-day *G. dorcas* and was adapted to open environments characterized by a sandy/rocky substratum. In contrast, *G. torticornis* (with its anti-clockwise spiraling horns) had a more generalist habit (Guérin, 1965) and preferred environments with low cover and bushes. The large size bovine *Leptobos* sp. has a more gracile morphology when compared with modern *Bos* and *Bison* and according to Alcalde (2013), *Leptobos* from St. Vallier and Villarroya sites was adapted to grassy plains with some patches of shrubs. According to Guérin (1965), the caprine *Gallogoral meneghinii* is similar to the Asiatic gorals (*Naemorhedus*) and serows (*Capricornis*) living at present day in steep terrain associated with wooded plains and scrub.

The high diversity of bovids underlines the importance of grazers in the faunal assemblages of CSG. The significant quantity of stenonid horses indicates that these animals probably lived in herds, at least during certain times of the year. These herds of grazers most probably migrated away from harsh environmental conditions (Mazza, 2006), as wildebeest and zebra do today: *Leptobos* and *E. stenonis* can be considered their ecological equivalents. Browsers roaming in the remaining forests included the cervids *Eucladoceros* and *Axis*.

Finally, the presence of hippos is consistent with flowing and/or clear waters on the floodplain. *Hippopotamus antiquus* has generally been associated with wet climates but the living African hippo cannot be considered itself an indicator of warm climate conditions (Russo Ermolli et al., 2010). Despite differences in feeding and living habits, it is possible that similar habits could be inferred for *H. antiquus*.

Cercopithecids of the genus *Macaca* were commonly found in Early Villafranchian woodlands and are associated with humid
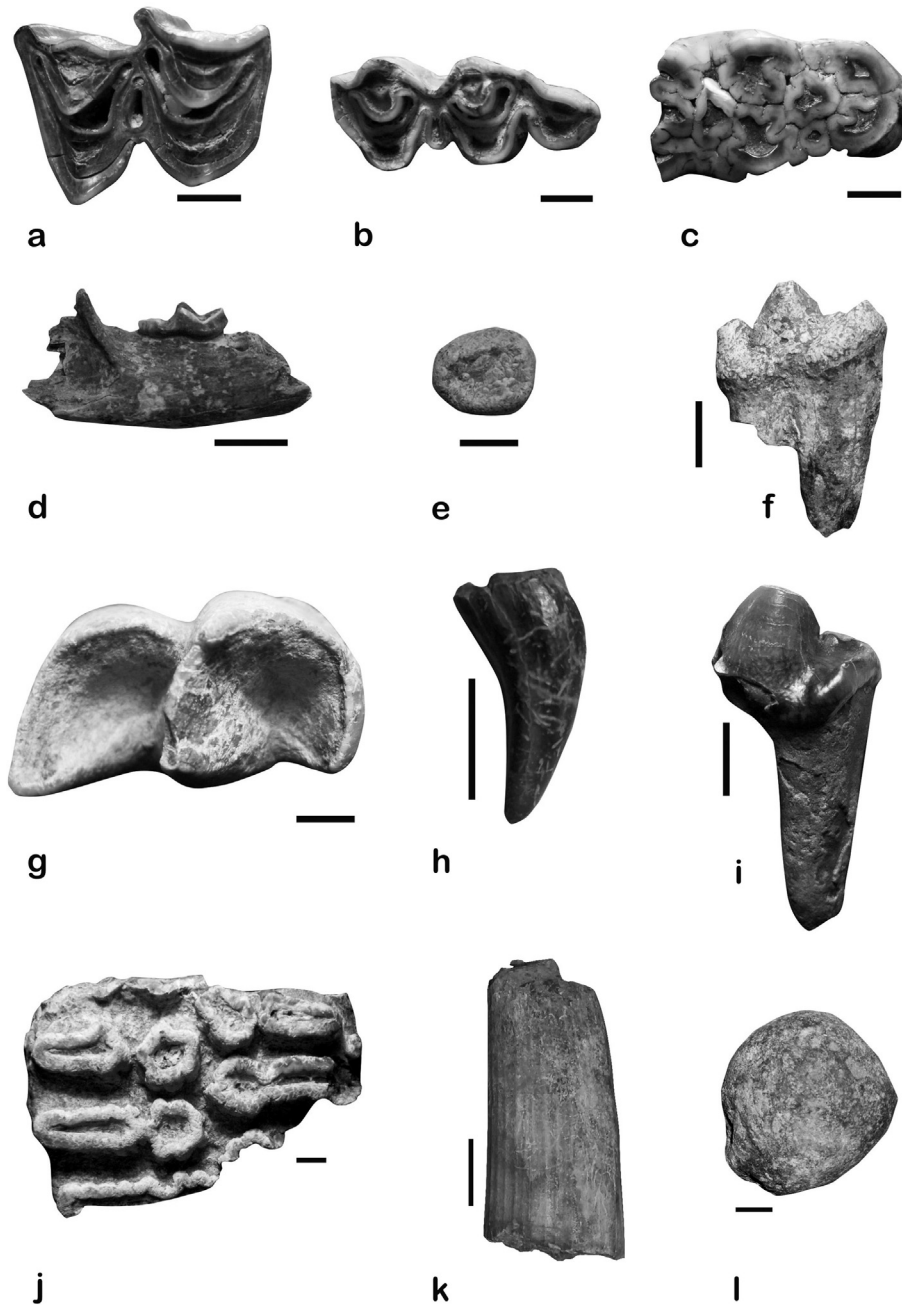
Fig. 8. CSG selected large mammals a: *Gallogoral meneghinii*, left m2; b: *Leptobos* sp., left m3; c: *Sus strozzii*, left m3; d: *Vulpes* cf. *alopecoides*, right hemimandible with m1; e: *Ursus* cf. *etruscus*, left m3; f: *Homotherium* sp., right p4; g: *Stephanorhinus* sp., lower tooth; h: *Canis* sp., c; i: ? *Pliocrocuta perrieri*, right p4; j: *Mammuthus meridionalis*, fragmented lower left molar; k: *Hippopotamus* sp. I; l: coprolite (hyaenid ?). Scale bar 10 mm.

areas, although since the MN17 mammal zone (early Gelasian), they inhabited a wide range of environments (Eronen and Rook, 2004).

Canids, and in particular the genus *Canis*, enjoyed an extraordinary development during this period, particularly taking advantage of the development of open habitats. The spread of this pack hunter marks the beginning of the so-called "wolf event" (Azzaroli, 1983).

4.2. Palaeoenvironmental reconstruction

The CSG site provides an in-depth snapshot of Early Pleistocene (Gelasian) palaeoenvironments in the Mediterranean region.

Although all the analyzed proxies have provided detailed palaeoenvironmental data, they unfortunately never co-occur in the core. The lower part of the core (35-20 m) has provided a relatively rich pollen assemblage, the middle part of the core has yielded a rich ostracod fauna (20-5 m) and at 5 m of depth the bone bed level occurs.

The pollen assemblage depicts a forested phase, probably during an interglacial, characterized by swampy episodes as suggested by the abundance of *Alnus*, in agreement with sedimentological and ostracod data (Bellucci et al., 2012). The occurrence of humid conditions is confirmed by the presence of *Typha* and Chenopodiaceae. The water body, as indicated by the ostracod fauna, was characterized by slow-running clear waters, rich in vegetation and

locally fed by springs (Bellucci et al., 2012). The palaeotemperature reconstruction provides evidence of summer and winter temperatures slightly lower than those of the region today. Mutual temperature range estimates from ostracods indicate that the mean summer temperatures were similar to or possibly slightly colder than those registered today in the area and mean winter temperatures were similar to the actual conditions.

At 5 m depth, the abundance of vertebrate remains, confirmed in the three of the four test-pits, points to the occurrence of river channels. The high palaeobiodiversity together with the presence of gnawed bones and an abundance of coprolites is consistent with the hypothesis of the presence of hyaena dens, as already observed at Poggio Rosso (Mazza, 2006). The detailed analysis of the CSG assemblage has allowed the identification of vertebrates indicating different palaeoenvironments. *Galemys*, *Castor* and *Hippopotamus* are consistent with the existence of a fluvial environment. The desman *Galemys* represents the first occurrence of this insectivorous species ever found in the Italian peninsula. *Anancus arvernensis*, large cervids, rhinos and squirrels indicate a forested environment. *Mammuthus meridionalis*, stenonid equids, gazelles, canids and hyaenids confirm the occurrence of open environments. The combination of these forms indicates that the landscape of CSG featured both savannah and woodland. Species of broad environmental adaptations, such as felids, bears and wild boar are also present. Cooperative predators as canids and hyaenids hunted herds of large-sized ungulates such as stenonid horses, bovines and cursorial antelopes, whereas large deer, rhinos and proboscideans are inferred to have been the preferred prey of the sabertooth cat *Homotherium*.

4.3. Bio − magnetochronological framework

The age of the CSG bone bed is constrained by a combination of palaeomagnetic, biostratigraphic and palaeoclimatic data. The large mammals recovered at CSG have a clearly Middle Villafranchian character, shedding light on the biochronology and palaeobiogeography of the Neogene−Quaternary transition in Eurasia. Most of the taxa are recorded in other Early Pleistocene (Middle Villafranchian assemblages) localities throughout Europe, including Sesklo, Dafnero, Vatera and Volakas (Greece), Saint Vallier (France) and Fonelas P-1 (Spain) (the last referred to the Olivola Faunal Unit [FU]) (Rook and Martinez Navarro, 2010). The most important biochronological event registered at CSG is the FAD (First Appearance Datum) of *Hippopotamus* sp. in Europe and the FAD of genus *Canis* in the Italian peninsula. The LAD (Last Appearance Datum) of *G. borbonica* and the small cervid *Croizetoceros* is also recorded at CSG.

Concerning the small mammals, biochronological considerations it is possible to compare the remains of the large vole *Mimomys pliocaenicus* with those from other Italian and European sites using the morphology of the lower first molar. The large *Mimomys* of CSG shows greater hypsodonty than the archaic species *Mimomys hajnackensis* and *Mimomys polonicus* (Sabol et al., 2006; Mayhew et al., 2008). At the same time, it appears to be more brachyodont and was therefore considered less advanced than the type specimen of *M. pliocaenicus* from Castelfranco di Sopra (Upper Valdarno, Tuscany) referred to the Olivola FU (Gliozzi et al., 1997). According to Masini and Torre (1990), the type of *M. pliocaenicus* is comparable in size and degree of hypsodonty to *Mimomys ostramosensis* from Osztramos 3 (for discussion see Sala et al., 1994). The *Mimomys pliocaenicus* of CSG can also be compared with *Mimomys* cf. *pliocaenicus* of Rivoli Veronese (Sala et al., 1994) and the specimens of Tegelen (Tesakov, 1998), attributed to the Middle Villafranchian/end of Villanyian Small Mammal Age (Fejfar and Heinrich, 1990). Compared with the minor degree of

hypsodonty seen in *Mimomys* of Castelfranco di Sopra, the *M. pliocaenicus* of CSG can therefore be considered older than the Olivola FU. The absence of eastern European small mammal taxa testifies to a phase prior to the expansion of eastern taxa into western Europe, as seen in the Rivoli assemblage (Sala et al., 1994), or alternatively to the persistence in central Italy of environmental conditions that retarded the distribution of these taxa.

The comparison of both small and large mammalian assemblages is thus of great biochronological importance and confirms the correlation of CSG to the end of the Middle Villafranchian and the end of Villanyan (Masini and Sala, 2007).

The stratigraphical framework of the pollen record is mainly based on the presence and abundance of tree taxa that are currently absent from Italy, including *Cathaya* type, *Taxodium* type, *Cedrus*, *Tsuga*, *Carya* and *Pterocarya*. The percentages of these taxa have been compared with Early Pleistocene (late Gelasian to early Calabrian) pollen records from the Italian Peninsula between 40° and 44° lat. N, namely Fosso Bianco, Poggio Rosso and Camerota (Fig. 9).

The Fosso Bianco section, located about 70 km south of Perugia, has been attributed to the Gelasian stage after integrated palynological and stratigraphical analyses (Pontini and Bertini, 2000; Bertini, 2010). The pollen record covers a period of ca 400 ka, between MIS 100 and MIS 82 (approximately 2.55 to 2.15 Ma), corresponding to a time interval with reversed magnetic polarity (Pontini and Bertini, 2000). It was divided into four pollen zones. *Taxodium* type is present throughout the record with percentages around 10% in the bottom zone, 20% in the intermediate zone, and 5% in the top zone. These frequencies are clearly higher than in core CSG1. The percentages of *Cedrus* (5–10%), *Cathaya* type and *Pinus haploxylon* (5–10%), and *Tsuga* (≤5%) are comparable with CSG1. The presence of *Engelhardia* and *Liquidambar*, absent from CSG1, and the high percentages of *Taxodium* type clearly indicate that the section of Fosso Bianco is older than Coste San Giacomo. Poggio Rosso is located about 25 km south−east of Florence, in Tuscany, and is one the best exposed successions of the middle−upper part of the Montevarchi Synthem, most likely corresponding to MIS 68 to 67 (between 1.8 and 1.9 Ma), within the Olduvai chron. Two major pollen zones have been documented (Bertini et al., 2010). *Taxodium* type, *Cathaya* type and *Pinus haploxylon* are restricted to the oldest pollen zone (Phase I). In the CSG1 core, these taxa are present in all the analyzed samples. *Cedrus*, present in Phase I of Poggio Rosso, with percentages around 10%, is always present in CSG1 with maximum values of about 17% (at 25.00 m and 29.50 m). Similarly, *Tsuga*, present only in Phase I of Poggio Rosso, is found in all the samples of CSG1. On the basis of these elements, Phase I of Poggio Rosso and CSG1 appear very similar. However, Phase II of Poggio Rosso shows a decrease of conifers and an increase of deciduous elements (*Ulmus-Zelkova*, *Carpinus*, *Carya* and *Juglans*), which do not match well Coste San Giacomo.

At Camerota, in the Campania region, two sections were studied from a lacustrine basin (Brenac, 1984). From a stratigraphical point of view, this site has been correlated with the early Calabrian, as it contains a palaeomagnetic reversal interpreted as Gilsa (1.68 Ma) (Suc and Popescu, 2005; Bertini, 2010). The pollen diagram shows *Cedrus* and *Carya* throughout the entire record, whereas *Tsuga* and *Pterocarya* are discontinuously present. Taxodiaceae were found only in a sample in the upper part of the section, while *Cathaya* is absent. An interesting feature is the presence, although sporadic, of *Liquidambar* and *Engelhardia*. The occasional presence of Taxodiaceae, together with the absence of *Cathaya*, therefore imply a more recent age for Camerota than Coste San Giacomo.

On the basis of the above considerations, we suggest for the Coste San Giacomo pollen record an age that is certainly younger than Fosso Bianco, which is characterized by high proportions of
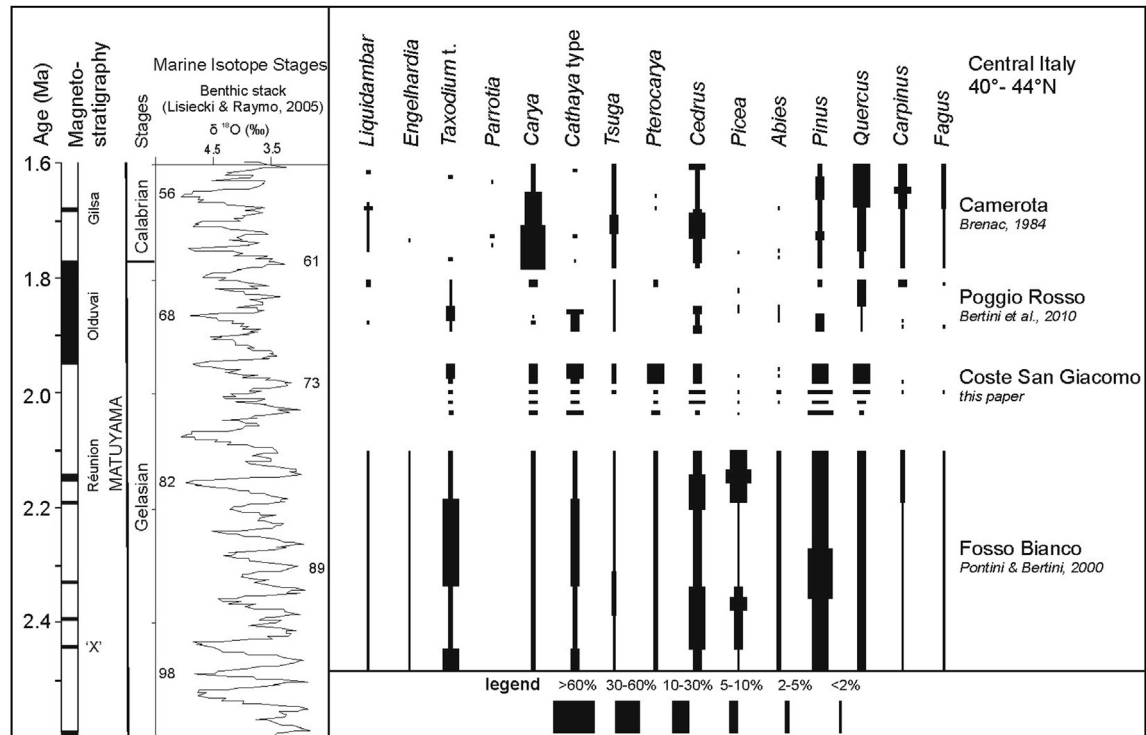
Fig. 9. Stratigraphical setting of selected Early Pleistocene Italian pollen records and schematic pollen biostratigraphy of selected pollen taxa at the latitude 40–44°N.

Taxodium type and by the presence of *Engelhardia* and *Liquidambar*, and is further considered to be older than 2.1 Ma. In addition, the section CSG1 appears older than Camerota (of early Calabrian age), where *Cathaya* is absent and Taxodiaceae are sporadic. The most comparable pollen record is that from Poggio Rosso, especially Phase I, which shows substantial affinities with that from Coste San Giacomo and thereby suggests temporal equivalence.

In summary, it is therefore possible to suggest an age between 2.2 and 1.95 Ma for the forest phase recorded at Coste San Giacomo (Fig. 9), a result that contributes an important new stone in the mosaic of Quaternary vegetation development in Italy.

The age of the CSG faunal assemblage can also be better defined thanks to a multidisciplinary approach. The palaeomagnetic analysis has indicated an interval of reversed polarity, which could be related to the Matuyama Chron (2.58–0.78 Ma; Lourens et al., 2005). The two biochronological scales (both large and small mammals) suggest an age older than the Olivola FU and the Poggio Rosso Local Fauna, both assigned to the Olduvai Chron. Thus, the CSG faunal assemblage is apparently older than the base of the Olduvai Chron at 1.95 Ma. Taking into account the age span determined by the pollen analyses, it is reasonable to suggest an age for the CSG faunal assemblage around 2.1 Ma (Fig. 10).

5. Conclusions

This study provides a general framework for the palaeoenvironmental changes that occurred during the earliest Pleistocene (Gelasian) in the Anagni basin and enhances, once again, the critical importance of the CSG site (Bellucci et al., 2012).

Palaeoenvironmental analysis of the CSG1 core allows the recognition of at least three distinct phases, all within the pre-Olduvai Matuyama chron. From the base upwards, these are:

- 35 m–20 m: the pollen record is consistent with the presence of a forested landscape, corresponding to a temperate climate

typical of an interglacial phase. No pollen zones can be defined because of the absence of stratigraphical continuity between the samples.
- from 20 to 5 m: mutual temperature range estimates from ostracods suggest the occurrence of mild climatic conditions in an alluvial environment with clear, running waters, sensitive to the precipitation regime. Inferred temperatures are slightly lower than the present day ones. The aquatic environment was rich in aquatic vegetation.
- from 5 m to 0.6 m: bone accumulation (partially due to hyaena activity), possibly deposited in an abandoned fluvial channel.

The study of the four test pits has confirmed the occurrence of a bone bed, rich in well-preserved remains of both small and large vertebrates. Notwithstanding the lack of a systematic excavation, 5000 bone fragments have already been recovered from the site, of which approximately 10% can be taxonomically determined. The assemblage is characterized by high species diversity, as well as taphonomic features such as gnaw-marks and the abundance of coprolites, which point to the active role of hyaenas in the fossil accumulation. The multidisciplinary approach has allowed an integrated palaeoenvironmental reconstruction of the sedimentary sequence to be developed, depicting the evolution of the alluvial plain and surrounding landscapes. Moreover, such a multiproxy approach has successfully constrained the biochronological position of the CSG FU, placing it around 2.1 Ma, in a phase of reversed polarity before the base of the Olduvai chron, slightly younger than indicated by previous researchers (Gliozzi et al., 1997; Rook and Martinez Navarro, 2010 and references therein).

The CSG faunal assemblage is characterized by the occurrence of an African newcomer (*Hippopotamus* sp.) and by the earliest occurrence of *Canis* in Italy. In addition the presence of *G. borbonica*, which is relatively well represented in the fossil sample, may be considered the LAD of this species, known from Middle Villafranchian faunal assemblages in South-Western Europe (Rook and
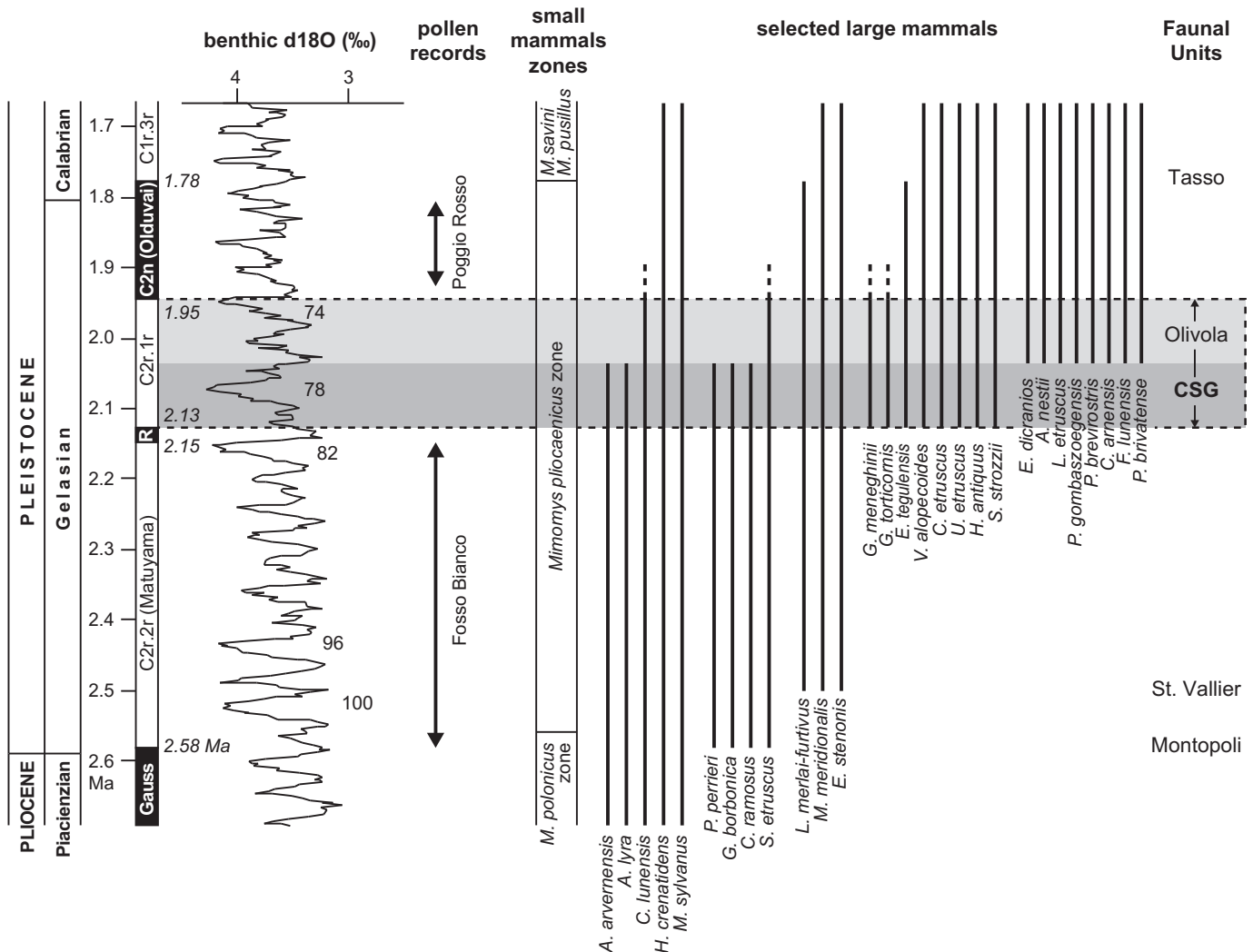
Fig. 10. CSG biochronological framework.

Martinez Navarro, 2010 and references therein). Moreover, at CSG the last occurrence of *Anancus* and *Croizetoceros* is documented. Finally the occurrence and evolutionary degree of *Mimomys plio-caenicus* provides a valuable biostratigraphical constraint and enables correlation between the large and small mammal biochronological scales.

The abundance of coprolites and evidence of gnawing on some large bones suggests an active role for hyaenas in the accumulation of the bones. Up to now, only fragmentary and isolated hyaena teeth have been recorded and the taxonomic identity of these animas cannot be clearly established as either *Pliocrocuta perrieri* and *Pachycrocuta brevirostris*. The latter, a giant short-faced hyaena, characterized the Late Villafranchian and earliest Galerian faunal assemblages (Olivola, Poggio Rosso, Venta Micena, Pirro Nord among the others), whereas *Pliocrocuta perrieri* is documented in the Middle Villafranchian assemblages (Montopoli, Saint Vallier). At Fonelas P1 (Spain), both species allegedly co-occur together with *Parahyaena brunnea* (the living brown hyaena) in a large mammal assemblage referred to the Olivola FU (Viseras et al., 2006; Rook and Martinez Navarro, 2010 and references therein). In contrast, Arribas et al. (2009) reported the co-occurrence at the same site of *Chas-maporthetes lunensis*, *Hyaena brunnea* and *Pachycrocuta brevirostris*, but not *Pliocrocuta perrieri*. The faunal lists from Fonelas P1 are

therefore incongruous and it is clear that revision of the hyaenid material is required.

Napoleone et al. (2003) proposed reversed polarity for the sediments at the site of Olivola and suggested an age of 2.1 Ma for the vertebrate assemblage. Following Azzaroli (1983) and Gliozzi et al. (1997), Napoleone et al. (2003) thus considered the Olivola faunal assemblage to be younger than that from CSG. However, analysis of the sedimentary sequence from CSG suggests an even younger age for the Olivola fauna, possibly very near the top of the reverse magnetochron at 1.95 Ma.

In summary, the CSG site records a transitional phase in the terrestrial ecosystems of the Italian peninsula during the Early Pleistocene, prior to the Late Villafranchian turnover characterized by the extinction of *Anancus*, *Croizetoceros* and *G. borbonica*, the dispersal of *Panthera gombaszoegensis* and *Pachycrocuta brevirostris*, the diffusion of different canids (*Canis etruscus*, *Canis arnensis* and *Xenocyon lycanoides*) and ovibovines (*Praeovibos*, *Soergelia*). Climatic deterioration led to the spread of savannah-like conditions that can be clearly related to the dispersal events of the Early Pleistocene, with the diffusion into the Mediterranean region of species of Asian and African origin.

Many authors have debated the "Out of Africa" and "Out of Asia" models, where hominins are viewed in the context of a (single)

wave of large mammal dispersals during the Early Pleistocene (O'Regan et al., 2011 and references therein). The occurrence of *Hippopotamus* at CSG, however, indicates that these animals dispersed into Europe earlier than previously supposed, at the same time as the diffusion into Europe from the east of *Canis* (the aforementioned "wolf event"). The CSG evidence may therefore represent an early bioevent through the Levantine corridor into south-western Europe during the Early Pleistocene, possibly preceding the dispersal of *Pachycrocuta brevirostris*, *P. gombaszoegensis*, *Megantereon whitei*, *Theropithecus* and *Homo* (Martínez-Navarro, 2010).

The study of the CSG site has therefore shed light on the background of environmental changes associated with the very earliest hominin occupation in Europe. Future investigations from 2013 onwards will concentrate on the collections of new data, especially the recovery of complete vertebrate material in order to understand better the taxonomic position of the CSG taxa and their taphonomy.

Acknowledgments

References

Alcalde, G.M., 2013. Caracterización ecomorfológica del esqueleto postcraneal en rumiantes (Artiodactyla, Mammalia): aplicación en la inferencia de las adaptaciones ecológicas de los rumiantes del plio-pleistoceno de España (PhD thesis). Universidad Complutense de Madrid, Facultad de Ciencias Geológicas, Departamento de Paleontología, Madrid, Spain.

Arribas, A., Garrido, G., Viseras, C., Soria, J.M., Pla, S., Solano, J.G., Garcés, M., Beamud, E., Carrión, J.S., 2009. A mammalian lost world in southwest Europe during the late Pliocene. PLoS ONE 4 (9), e7127. http://dx.doi.org/10.1371/journal.pone.0007127.

Azzaroli, A., 1983. Quaternary mammals and the "end-Villafranchian" dispersal event — a turning point in the history of Eurasia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 44, 117–139.

Bellucci, L., Mazzini, I., Scardia, G., Bruni, L., Parenti, F., Segre, A.G., Segre Naldini, E., Sardella, R., 2012. The site of Coste San Giacomo (Early Pleistocene, central Italy): palaeoenvironmental analysis and biochronological overview. Quat. Int. 267, 30–39.

Bennett, K.D., 2009. Psimpoll 4.27: C Program for Plotting Pollen Diagrams and Analyzing Pollen Data. Available online from: Queen's University of Belfast, Department of Archaeology and Palaeoecology.

Bertini, A., 2010. Pliocene to Pleistocene palynoflora and vegetation in Italy: state of the art. Quat. Int. 225, 5–24.

Bertini, A., Magi, M., Mazza, P.P.A., Fauquette, S., 2010. Impact of short-term climatic events on latest Pliocene land settings and communities in Central Italy (Upper Valdarno basin). Quat. Int. 225, 92–105.

Beug, H.J., 2004. Leitfaden der Pollenbestimmung fur Mitteleuropa und angrenzende Gebiete. Verlag Friedrich Pfeil, Munich.

Biddittu, I., Cassoli, P.F., Radicati di Brozolo, F., Segre, A.G., Segre Naldini, E., Villa, I., 1979. Anagni, a K–Ar dated Lower and Middle Pleistocene site, central Italy: preliminary report. Quaternaria 21, 53–71.

Brenac, P., 1984. Végétation et climat de la campanie du Sud (Italie) au pliocène final d'après l'analyse pollinique des dépôts de Camerota. Ecol. Mediterr. 10, 207–216.

Carrara, C., Frezzotti, M., Giraudi, C., 1995. Stratigrafia plio-quaternaria. In: Carrara, C. (Ed.), Lazio Meridionale, Sintesi Delle Ricerche Geologiche Multi-disciplinari. ENEA, Roma, pp. 62–85.

Corrado, P., Magri, D., 2011. A late Early Pleistocene pollen record from Fontana Ranuccio (central Italy). J. Quat. Sci. 26, 335–344.

Crégut Bonnoure, E., Valli, A.M.F., 2004. Les Bovidés du gisement pliocène supérieur (Villafranchien moyen) de Saint-Vallier (Drôme, France). Geobios 37 (S1), 233–258.

Eronen, J.T., Rook, L., 2004. The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. J. Hum. Evol. 47, 323–341.

Fejfar, O., Heinrich, W.-D., 1990. Muroid rodent biochronology of the Neogene and Quaternary of Europe. In: Lindsay, E.H., et al. (Eds.), European Neogene Mammal Chronology. Plenum Press, New York, pp. 91–117.

Galadini, F., Messina, P., 2004. Early-Middle Pleistocene eastward migration of the Abruzzi Apennine (central Italy) extensional domain. J. Geodyn. 37, 57–81.

Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficcarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E., Torre, D., 1997. Biochronology of selected mammals, molluscs and ostracods from the middle Pliocene to the late Pleistocene in Italy. Riv. Ital. Paleontol. S. 103, 369–388.

Guérin, C., 1965. *Gallogoral* (nov. gen.) *meneghinii* (Rütimeyer, 1878) un rupicapriné du Villafranchien d'Europe occidentale. In: Documents des Laboratoires de Géologie de la Faculte des Sciences de Lyon, pp. 11–353.

Guérin, C., Faure, M., Argant, A., Argant, J., Crégut-Bonnoure, E., Debard, E., Delson, E., Eisenmann, V., Hugueney, M., Limondin-Lozouet, N., Martín-Suárez, E., Mein, P., Mourer-Chauviré, C., Parenti, F., Pastre, J.F., Sen, S., Valli, A., 2004. Le gisement pliocène supérieur de Saint-Vallier (Drôme, France): synthèse biostratigraphique et paléoécologique. Geobios 37 (Suppl. 1), 349–360.

Heintz, E., 1971. *Gazella deperdita* (Gervais), 1847 (Bovidae, Artiodactyla, Mammalia) du Pontien du Mont Lubéron, Vaucluse, France. Ann. Paléontol. 2, 209–229.

Helmer, D., Rocheteau, M., 1994. Atlas du squelette appendiculaire des principaux genres holocènes de petits ruminants du nord et la Méditerranée et du Proche-Orient (*Capra, Ovis, Rupicapra, Capreolus, Gazella*). In: Desse, J., Desse-Berset, N. (Eds.), Fiches d'Ostéologie animale pour l'Archéozoologie, Série B: Mammiféres. APDCA éditeur, pp. 1–21.

Horne, D.J., 2007. A Mutual Temperature Range method for Quaternary palaeoclimatic analysis using European non marine Ostracoda. Quat. Sci. Rev. 26, 1398–1415.

Horne, D.J., Mezquita, F., 2008. Palaeoclimatic applications of large databases: developing and testing methods of palaeotemperature reconstruction using non-marine ostracods. Senck. Lethaea 88, 93–112.

Horne, D.J., Curry, B.B., Mesquita-Joanes, F., 2012. Mutual climatic range methods for Quaternary ostracods. In: Horne, David J., Holmes, Jonathan A., Rodriguez-Lazaro, Julio, Viehberg, Finn A. (Eds.), Developments in Quaternary Sciences, 17. Elsevier, pp. 65–84.

Hu, S., Stephenson, A., Appel, E., 2002. A study of gyroremanent magnetisation (GRM) and rotational remanent magnetisation (RRM) carried by greigite from lake sediments. Geophys. J. Int. 151 (2), 469–474.

Kirschvink, J., 1980. The least-squares line and plane and the analysis of palaeomagnetic data. Geophys. J. R. Astron. Soc. 62 (3), 699–718.

Liu, Y.S., Basinger, J.F., 2000. Fossil *Cathaya* (Pinaceae) pollen from the Canadian high Arctic. Int. J. Plant Sci. 161, 829–847.

Lourens, L.J., Hilgen, F.J., Laskar, J., Shackleton, N.J., Wilson, D.S., 2005. The Neogene period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), A Geologic Time Scale 2004. Cambridge University Press, pp. 409–440.

Martínez-Navarro, B., 2010. Early Pleistocene faunas of Eurasia and hominid dispersals. In: Fleagle, J.G., Shea, J.J., Grine, F.E., Baden, A.L., Leakey, R.E. (Eds.), The First Hominin Colonization of Eurasia, Contributions from the Second Stony Brook Human Evolution Symposium and Workshop, September 27–30, 2005. Springer, pp. 207–224 (Chapter 13).

Masini, F., Sala, B., 2007. Large- and small-mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula. Quat. Int. 160, 43–56.

Masini, F., Torre, D., 1990. Review of the Villafranchian arvicolids of Italy. Geol. Rom. 26, 127–133.

Mayhew, D.F., Dieleman, F.E., Boele, J., Verhaard, L., van den Hoek Ostende, L.W., 2008. *Mimomys hajnackensis* from the Pliocene of the Netherlands. Neth. J. Geosci. 87 (2), 181–188.

Mazza, P., 2006. Poggio Rosso (Upper Valdarno, central Italy), a window on latest Pliocene wildlife. Palaios 21, 493–498.

McFadden, P.L., McElhinny, M.,W., 1988. The combined analysis of remagnetization circles and direct observations in paleomagnetism. Earth Planet. Sci. Lett. 87 (1–2), 161–172.

Napoleone, G., Albianelli, A., Azzaroli, A., Bertini, A., Magi, M., Mazzini, M., 2003. Calibration of the Upper Valdarno basin to the Plio-Pleistocene for correlating the Apennine continental sequences. Il Quaternario (It. J. Quat. Sci.) 16 (1 bis), 131–166.

Nomade, S., Pastre, J.F., Guillou, H., Faure, M., Guérin, C., Delson, E., Debard, E., Voinchet, P., Messager, E., 2013. ^{40}Ar/^{39}Ar constraints on some French landmark Late Pliocene to Early Pleistocene large mammalian paleofaunas: paleoenvironmental and paleoecological implications. Quat. Geochronol. Available online 9 January 2013, ISSN 1871-1014, http://dx.doi.org/10.1016/j.quageo.2012.12.006.

O'Regan, H.J., Turner, A., Bishop, L.C., Elton, S., Lamb, A.L., 2011. Hominins without fellow travellers? First appearances and inferred dispersals of Afro-Eurasian large-mammals in the Plio-pleistocene. Quat. Sci. Rev. 30 (11–12), 1343–1352.

Peccerillo, A., 2005. Plio-Quaternary Volcanism in Italy. Springer, Berlin.

Pontini, M.R., Bertini, A., 2000. Late Pliocene vegetation and climate in central Italy: high resolution pollen analysis from the Fosso Bianco section (Tiberino Basin). Geobios, 519–526.

Reille, M., 1992. Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, URA CNRS 1152, Marseille.

Reille, M., 1995 (Suppl. 1). Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, URA CNRS 1152, Marseille.

Reille, M., 1998 (Suppl. 2). Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, URA CNRS 1152, Marseille.

Rivals, F., Athanassiou, A., 2008. Dietary adaptations in an ungulate community from the late Pliocene of Greece. Palaeogeogr. Palaeoclimatol. Palaeoecol. 265, 134–139.

Roberts, A.P., Chang, L., Rowan, C.J., Horng, C.-S., Florindo, F., 2011. Magnetic properties of sedimentary greigite (Fe$_3$S$_4$): an update. Rev. Geophys. Space Phys. 49, RG1002. http://dx.doi.org/10.1029/2010RG000336.

Rook, L., Martinez Navarro, B., 2010. Villafranchian: the long story of a Plio- Pleistocene European large mammal biochronologic unit. Quat. Int. 219, 134–144.

Russo Ermolli, E., Sardella, R., Di Maio, G., Petronio, C., Santangelo, N., 2010. Pollen and mammals from the late Early Pleistocene site of Saticula (Sant'Agata de' Goti, Benevento, Italy). Quat. Int. 225, 128–137.

Sabol, M., Konecny, V., Vass, D., Kovácová, M., Duritová, A., Túnyi, I., 2006. Early late Pliocene site of Hajnáčka I (Southern Slovakia) – geology, palaeovolcanic evolution, fossil assemblages and palaeoenvironments. Cour. For. Senckenberg 256, 261–274.

Sagnotti, L., Winkler, A., 1999. Rock magnetism and palaeomagnetism of greigite-bearing mudstones in the Italian peninsula. Earth Planet. Sci. Lett. 165 (1), 67–80.

Sala, B., Masini, F., Torre, D., 1994. Villanyian arvicolids from Rivoli Veronese, a karst fissure in the Adige Valley, Northeastern Italy. Boll. Soc. Paleontol. I. 33 (1), 3–11.

Segre, A.G., Ascenzi, A., 1984. Fontana Ranuccio: Italy's earliest Middle Pleistocene hominid site. Curr. Anthropol. 25, 230–233.

Segre Naldini, E., Muttoni, G., Parenti, F., Scardia, G., Segre, A.G., 2009. Nouvelles recherches dans le bassin Plio-Pléistocène d'Anagni (Latium méridional, Italie). L'Anthropologie 113, 66–77.

Sivak, J., 1976. Nouvelles especes du genre *Cathaya* d'apres leurs grains de pollen dans le Tertiaire du Sud de la France. Pollen Spores 18, 243–288.

Suc, J.P., Popescu, S.M., 2005. Pollen records and climatic cycles in the North Mediterranean region since 2.7 Ma. In: Head, M.J., Gibbard, P.L. (Eds.), Early-Middle Pleistocene Transitions: the Land-Ocean Evidence, Geological Society of London, vol. 247, pp. 147–157 (Special Publication).

Tesakov, A.S., 1998. Voles of Tegelen fauna. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO 60, 71–134.

Valli, A.M.F., Palombo, M.R., 2005. Le régime alimentaire du Cervidae (Mammalia) *Eucladoceros ctenoides* (NESTI 1841) reconstitué par la morphologie du crâne et par l'usure dentaire. Eclogae Geol. Helv. 98, 133–143.

Viseras, C., Soria, J.M., Durán, J.J., Pla, S., Garrido, G., García-García, F., Arribas, A., 2006. A large-mammal site in a meandering fluvial context (Fonelas P-1, Late Pliocene, Guadix Basin, Spain): sedimentological keys for its paleoenvironmental reconstruction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 242, 139–168.

Zanni, M., Ravazzi, C., 2007. Description and differentiation of *Pseudolarix amabilis* pollen: palaeoecological implications and new identification key to fresh bisaccate pollen. Rev. Palaeobot. Palynol. 145, 35–75.

Zijderveld, J., 1967. AC Demagnetization of Rocks: Analysis of Results. In: Collinson, D.W., Creer, K.M., Runcorn, S.K. (Eds.), Methods in Palaeomagnetism, vol. 3. Elsevier, pp. 254–268.