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The Early Pleistocene Carnivoran of Coste San Giacomo (Anagni, Central Italy): Biochronological Implications

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Abstract: Coste San Giacomo (CSG) represents a significant paleontological site to investigate the faunal and environmental changes that occurred in Mediterranean Europe during the Early Pleistocene. In this work, we described for the first time the Carnivoran assemblage. We ascribed the fossil remains to the following taxa: *Ursus* sp., *Homotherium latidens*, *Canis etruscus*, *Pliocrocuta perrieri*, *Martellictis ardea* and *Vulpes alopecoides*. Considering the value of the carnivoran taxa here identified, we discuss their particular biochronological significance, since the CSG site records the last occurrence of *P. perrieri* and the first occurrences of *H. latidens*, *C. etruscus*, *M. ardea* and *V. alopecoides* for the Italian Peninsula. These results will allow us to improve the data of the biochronological scheme of the Villafranchian European Land Mammal Age, recognizing the earliest dispersals and latest occurrences across Europe.

Keywords: Carnivora; Pleistocene; Villafranchian; *Homotherium*; *Pliocrocuta*; *Canis*; *Vulpes*; *Pannonictis*

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1. Introduction

The Coste San Giacomo site (hereinafter CSG), recently dated around 2.2 Ma [1], represents a key palaeontological site to investigate the environmental and faunal changes that occurred in the European Mediterranean region during the Gelasian (Early Pleistocene) as a result of major climatic changes at a global scale [2,3]. Forest diversity decreased because of a progressive decline in, and loss of, subtropical taxa during the Early and Middle Pleistocene [4].

The CSG site was discovered by Italo Biddittu, archaeologist of the Istituto Italiano di Paleontologia Umana (hereinafter IsIPU) during a survey carried out in September 1978. Intense fieldwork and scientific activities were performed by IsIPU researchers and, in the last fifteen years, in collaboration with the Dipartimento di Scienze della Terra of the Sapienza Università di Roma ([5–11] and references therein).

The CSG site is located 70 km southeast of Rome (central Italy), in the Anagni basin (Figure 1). This deeply faulted and extensional depression covers an area of around 20 km^2 and was produced during the initial phases of the neotectonic evolution of the Apennines Chain. This basin developed largely between the Late Pliocene and the early part of the Middle Pleistocene [1,12] and, in addition to CSG, other palaeontological sites such as Fontana Acetosa (FA), Colle Marino (CM) and Fontana Ranuccio (FR) have yielded important mammal records spanning from the earliest (CSG and FA) to the Middle (CM and FR) Pleistocene [5].

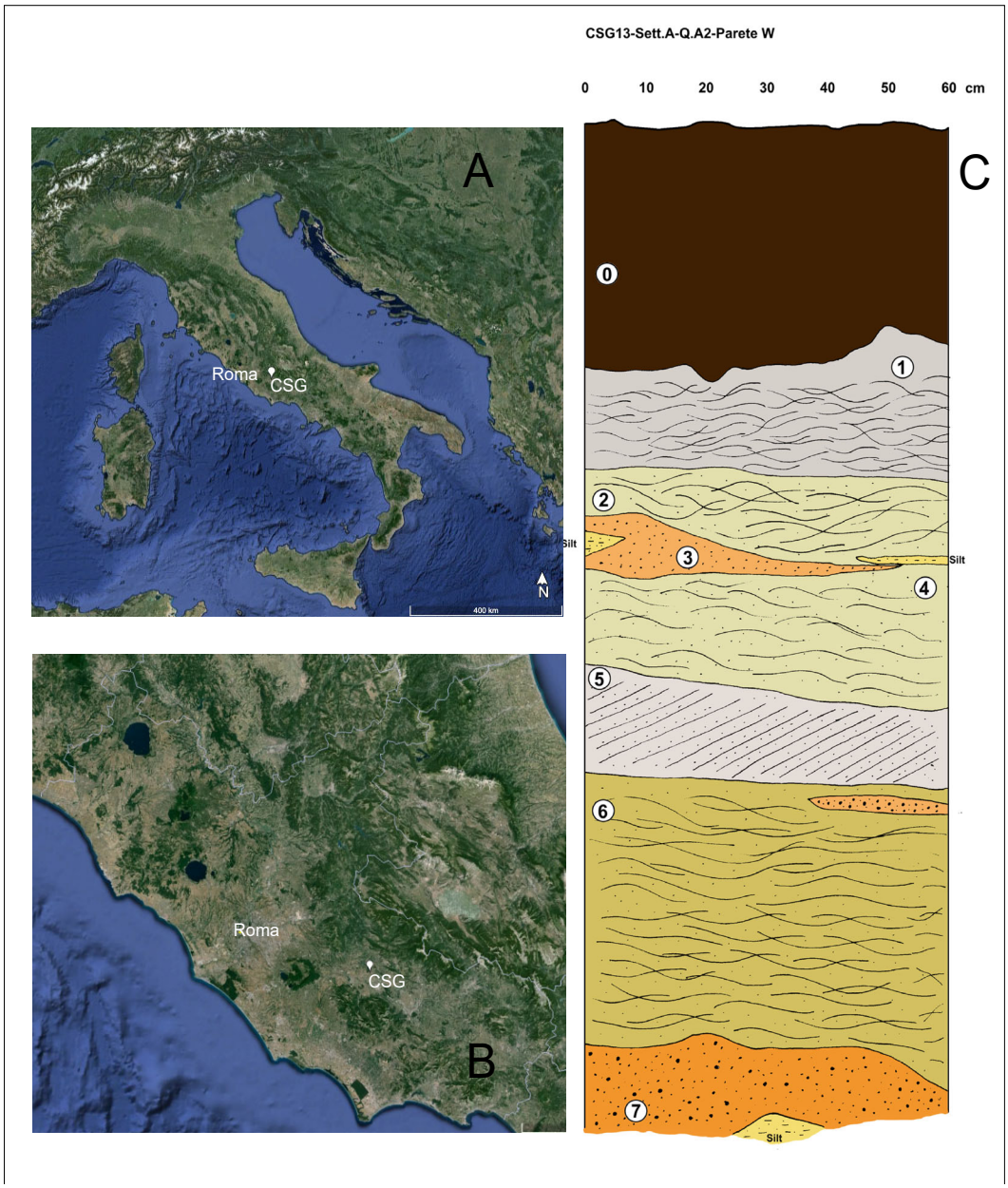

Figure 1. (**A**) CSG geographical position within the Italian Peninsula. (**B**) CSG geographical position within the Latium Region. (**C**) Stratigraphical scheme of the CSG section excavated in 2013: (0) The first 50 cm below the surface have been subject to the action of a plough. (1) Compact silt partly cemented by calcium carbonate recognised by the presence of whitish lineations shows an oblique trend in relationship to the sedimentation. The precipitation of the mineral is probably catalysed by the presence of the root systems of plants. (2, 3, 4) Fine festooned sand with scant traces of iron and manganese oxides. (5) Laminated sands with strong inclination of approximately 28°. (6, 7) Coarse sands with gravelly lenses; the gravels are mostly composed of travertine fragments. The upper portion is characterised by slightly undulating sands and gravelly lenses (20–30 cm high). Towards the bottom, the gravelly component increases, with abundant presence of iron and manganese oxides probably due to a braided river course.

Owing to the extensive large and small mammal sample, CSG has been regarded as representative of the Middle Villafranchian Large Mammal Age and of the Late Villanyan Small Mammal Age, respectively (Coste San Giacomo Faunal Unit) [13,14]. It is worth recalling the following significant biochronological occurrences recorded in the CSG site: the

coexistence of both the European mastodon *Anancus arvernensis* and the newcomer southern mammoth *Mammuthus meridionalis*; the occurrence of *Hippopotamus,* providing clear evidence of early dispersal events of African taxa prior to the early *Homo* radiation into Europe (Hippo event *sensu* Iannucci et al. [15]); the occurrence of the vole *Mimomys pliocaenicus*—the CSG specimens represent the largest collection in Europe—and the occurrence of the water mole *Galemys kormosi*, the first Desmaninae reported in the Italian Peninsula.

In this paper, the carnivoran palaeoguild from CSG is studied for the first time, providing the first formal description of the fossil specimens. Our results will improve the data of the biochronological scheme of the European Land Mammal Age, considering the value of the carnivoran taxa identified here for recognizing earliest dispersals and latest occurrences across the continent.

2. Geological and Paleontological Setting

The site of Coste San Giacomo was discovered by Italo Biddittu during a survey carried out in September 1978 and is located near Anagni (Frosinone), at approximately 50 km southeast of Rome (Latium, central Italy) (41°45′21.7″ N; 13°05′49.4″ E).

After its discovery, trenches were excavated in 1985, 1989 and 1990, identifying traceable levels with fossil vertebrates in the yellow sands [6]. In September 2009, a 46 m deep core was drilled, which allowed researchers to obtain new magnetostratigraphical, pollen and small mammal data and confirmed the possible age of the mammal assemblage to be around 2.1 Ma, in a reversed phase before the base of the Olduvai chron [7]. In order to better investigate the chronostratigraphic setting of the site, four pits were excavated in 2011, and three of these yielded vertebrate remains [7]. The last fieldwork activities were performed in 2013, coordinated by Fabio Parenti (IsIPU) and Raffaele Sardella (Sapienza Università di Roma) and authorised by the Soprintendenza per i Beni Archeologici del Lazio. During these excavations, vertebrate bones were collected in a single fossiliferous level.

The age of the faunal assemblage of CSG was recently refined by Florindo et al. [1] at 2.233 ± 0.032 Ma.

The stratigraphic series of CSG here described is based on the 2013 field excavation. This is characterised by the presence of five main sedimentary bodies (Figure 1):

- Starting from the surface, about 50 cm of deposit have been subjected to the action of the plough (0).
- Compact silt partly cemented by calcium carbonate, which can be recognised by the presence of whitish lineations that have an oblique trend with respect to the sedimentation, and the precipitation of the mineral is probably catalysed by the presence of the root systems of plants (1).
- Fine festooned sand with scant traces of iron and manganese oxides (2, 3, 4).
- Sand laminate with strong inclination (approximately 28°) (5).
- Coarse sand with gravelly lenses (the gravels are mostly composed of fragments of travertine). The upper portion of this last sedimentary body is characterised by slightly undulating sands and gravelly lenses (20–30 cm of development); towards the bottom, the gravelly component increases, with an abundant presence of iron and manganese oxides (probable braided river course) (6, 7).

Most of the fossil finds, and the best-preserved ones, come from the gravelly basal bodies (units 6–7; Figure 1). The accumulation of bone was possibly related to the presence of river channels in a fluviolacustrine environment.

The updated fauna list of the CSG large-mammal assemblage, excluding the carnivorans that are the focus of this work, is *Anancus arvernensis*, *Mammuthus meridionalis*, *Stephanorhinus* sp., *E. senezensis* aff. *E. sen. stehlini*, *Eucladoceros* sp., *Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus*, *Leptobos* sp., *Gallogoral meneghini*, *Gazellospira torticornis*, *Gazella borbonica*, *Sus strozzii*, *Hippopotamus* sp. and *Macaca sylvanus*. Small mammals were described by Bona et al. [9]: *Mimomys pliocaenicus*, *Mimomys* gr. *tigliensis/tornensis*, *Apodemus* sp., *Sciurus* cf.

S. warthae, *Castor fiber*, *Hystrix refossa*, *Prolagus italicus, Soricinae indet*., *Beremendia fissidens*, *Sorex* cf. *S. minutus*, *Talpa minor*, *Talpa* sp. and *Galemys kormosi*.

Finally, Villa et al. [16]) identified Amphibia (Bufonidae indet., *Pelophylax* sp., *Rana* sp., Ranidae indet., Anura indet.) and Reptilia remains (Lacertidae indet., *Pseudopus* sp., *Natrix* sp., Serpentes indet., Reptilia indet.). This assemblage comprises taxa that are common in the Italian Quaternary, but also presents the first occurrence of the large anguid *Pseudopus* from the Apennine Peninsula in this period.

The dietary analyses of the ungulate community revealed the presence of a mosaic of habitats, from woodlands to open landscapes [8,11,17]. However, the presence of humid environments was probably limited to the surroundings of the watercourse, as documented by fossils of *Hippopotamus*, *Castor fiber*, *Mimomys pliocaenicus* and *Galemys kormosi* and by the herpetofauna.

3. Materials and Methods

The carnivoran specimens from Coste San Giacomo were discovered in 1985, 1989 and 1990 in the yellow sands that were exposed when trenches were excavated at the base of a terrace during the IsIPU field activities. Others were collected from the ground surface where the fossil-bearing yellow sands are ploughed for agriculture. Finally, some specimens were excavated during the 2011 and 2013 campaigns, and, consequently, labelled "CSG 11-. . ." or "CSG 13-. . .".

These specimens are currently housed at the IsIPU depository and in the Museo Archeologico Ernico, both in Anagni (Frosinone, Italy). The determination of the palaeontological specimens is based on the anatomical feature descriptions and morphometric comparative analyses. Morphological and morphometric data used for comparison are from the cited literature. All measurements are taken with a digital calliper to the nearest 0.1 mm.

4. Systematic Palaeontology

4.1. Class Mammalia LINNAEUS, 1758

Order Carnivora BOWDICH, 1821
Family Ursidae FISCHER DE WALDHEIM, 1817
Genus *Ursus* LINNAEUS, 1758

4.1.1. Referred Material

CSG 981147: upper canine; CSG 82-5: lower canine; CSG 981149: lower fourth premolar; CSG 13-272: lower fourth premolar; CSG sd-76: lower third molar (Figure 2, *Ursus*).

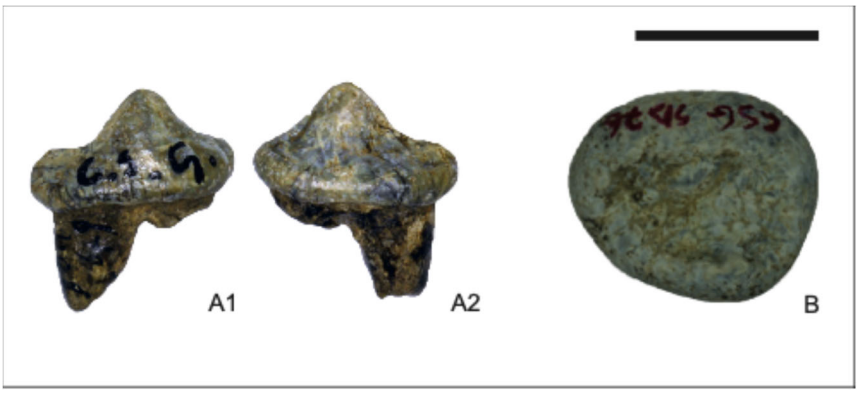

Figure 2. CSG *Ursus* specimens. CSG 981149: fourth premolar, A1 labial view, A2 buccal view; CSG sd-76: right lower third molar, B occlusal view. Scale bar 10 mm.

4.1.2. Description

The upper left canine CSG 981147 shows an elongated and narrow profile mainly consisting of only the root; the crown is broken almost at the height of the collar, probably

due to post-mortem damage. The lower left canine CSG 82-5 is poorly preserved; the tip is missing and it lacks the root. The enamel profile of the crown is jagged rather than worn. The right lower fourth premolars CSG 981149 and CSG 13-272 show a narrow occlusal surface with an ellipsoid profile; a thin crest joins a barely developed metaconid and paraconid, passing through a pronounced protoconid that occupies a large part of the chewing surface. There are no tubercles or accessory cusps; the root is double and divided, even if CSG 981149 lacks the anterior branch and CSG 13-272 lacks the posterior one. There are no signs of wear on the occlusal surface; thus, they probably belonged to young individuals. The third right lower molar CSG sd-76 shows an ellipsoid morphology with a rounded proximal margin. On the chewing surface, there are several ridges and accessory cusps, but it is still possible to recognise the mesoconid, the entoconid and the hypoconid, which is less visible, whereas the protoconid is the only cuspid well developed. This tooth does not present any sign of wear on the occlusal surface; juvenile status is also confirmed by the absence of the root and any sign of its fusion with the crown.

4.1.3. Discussion

The *Ursus* material from CSG is composed of only isolated teeth that do not allow a specific determination, since an extremely high morphological variability of the teeth is observed in different Plio-Pleistocene bear species [18]. The CSG specimens have been morphometrically compared with fossil remains reported in Europe during the Early Pleistocene belonging to the *U.* cf. ex. group *etruscus* and *U. thibetanus-minimus*. These two species are mainly distinguished by the size and morphology of the carnassial teeth, the upper fourth premolar and the first lower molar, respectively, that represent the most taxonomically significant teeth according to Wagner et al. [18] and by the general latero-medial compression of the teeth in *U. minimus* [19]. The lower fourth premolar and the third molar teeth were compared with other specimens from different Italian and European localities (Figures 3 and 4) (Table S1). These morphometric analyses identify the main size groups, the larger *U. etruscus* and the smaller *U. minimus*. The CSG teeth occupy the central part of the graphs, lacking distinct identification with either of these groups. Considering the morphological variability observed in Pleistocene bears and the intermediate size of the CSG specimens, the material is here ascribed to *Ursus* sp.

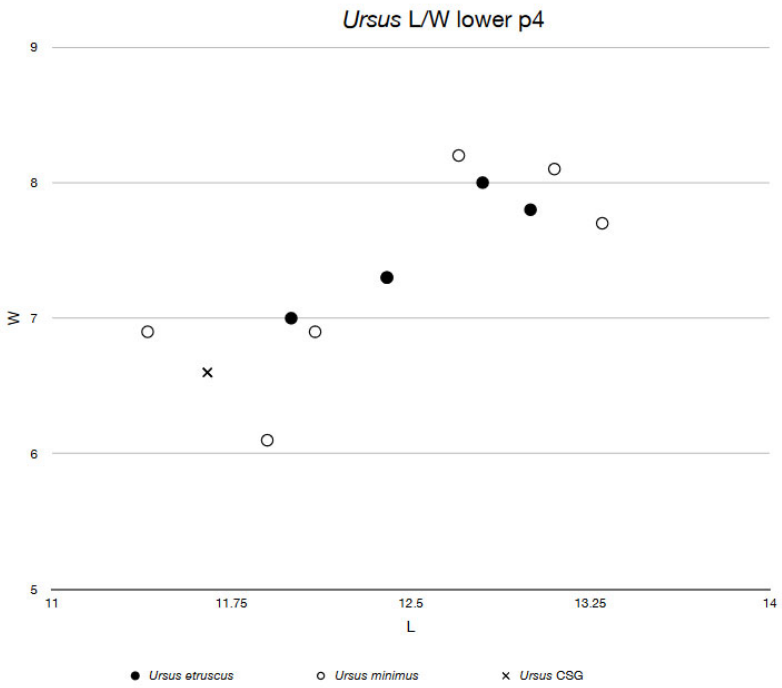

Figure 3. Scatter plot of the length/width of the *Ursus* lower p4.

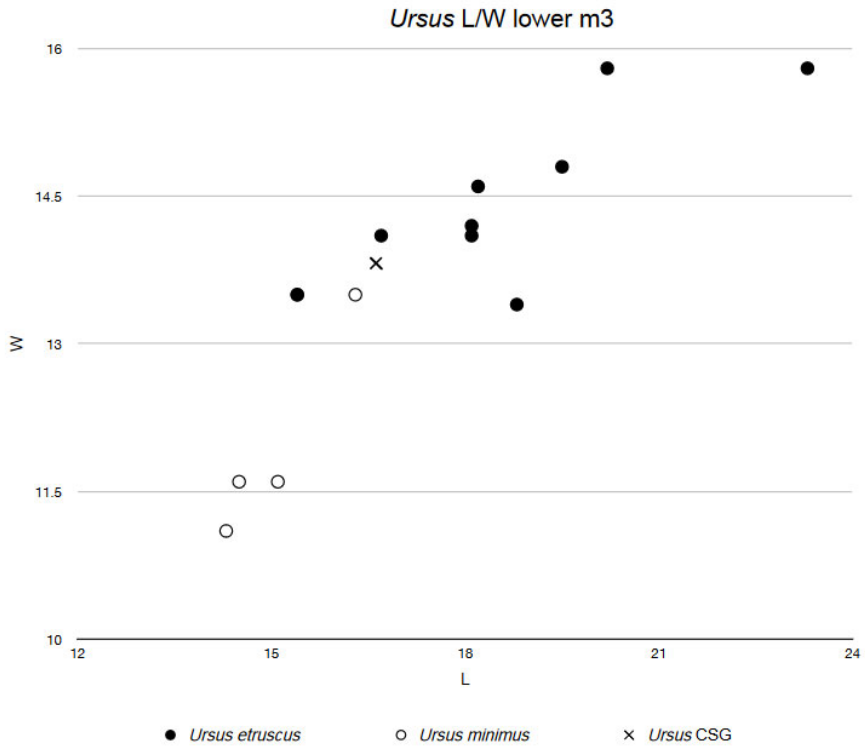

Figure 4. Scatter plot of the length/width of the *Ursus* lower m3.

4.2. Family Felidae GRAY, 1821

Genus *Homotherium* FABRINI, 1890
Homotherium latidens OWEN, 1846

4.2.1. Referred Material

CSG 11-172: a fragment of an upper canine; CSG 13-464: an upper fourth premolar; CSG 13-469: a lower canine; CSG 90-13: a lower third premolar; CSG sd-61 a fourth premolar (Figure 5).

4.2.2. Description

The scimitar-toothed cat *Homotherium* is represented by only isolated teeth. The small portion (28 mm long) of the upper canine is serrate (22 in 10 mm). In the anterior edge of the upper fourth premolar, the presence of a preparastyle is not observed. The morphology of the parastyle displays a vertical anterior side. The wear degree suggests an aged specimen. The lower third premolar is quite reduced in comparison with the fourth premolar; it is a single-rooted and unicuspid tooth with crenulations in both the distal and mesial margins. A marked cingulum is also present. The lower fourth premolar is not well preserved; it displays a high main cuspid and two mesial and distal cuspids, the last one buccolingually wider. These cuspids are mesially oriented.

4.2.3. Discussion

The length/width ratio of the upper fourth premolar from CSG has been compared with specimens from selected European Early to Middle Pleistocene localities, as listed in Table S2. The morphometric analysis confirms the attribution of the CSG specimen to *Homotherium latidens* (Figure 6). As many studies have stated, the Eurasian homotheres show a high degree of variation in the overall size and craniodental morphology and proportions. In this context, the extensive sample collected at Incarcal (Spain) shows a high morphological polymorphism, embracing nearly all the variation in the *Homotherium* record from Eurasia [20]. Following this, Turner and Antón [20] proposed attributing all the

Plio-Pleistocene Eurasian fossils to *Homotherium latidens*. In a splitter perspective, the latest Pliocene to earliest Pleistocene Eurasian homotheres, which have relatively longer upper canines and a more robust and convex mental area in the mandibula, could be referred, respectively, to *Homotherium nestianus* (western Europe) and to *Homotherium davitasvili* (Caucasus region) [21]. Although the isolated teeth from CSG cannot be useful clues to solve such a taxonomical dilemma, the hypothesis to consider only one polymorphic species, *Homotherium latidens*, for the Plio-Pleistocene Eurasian material seems to be the most conservative approach.

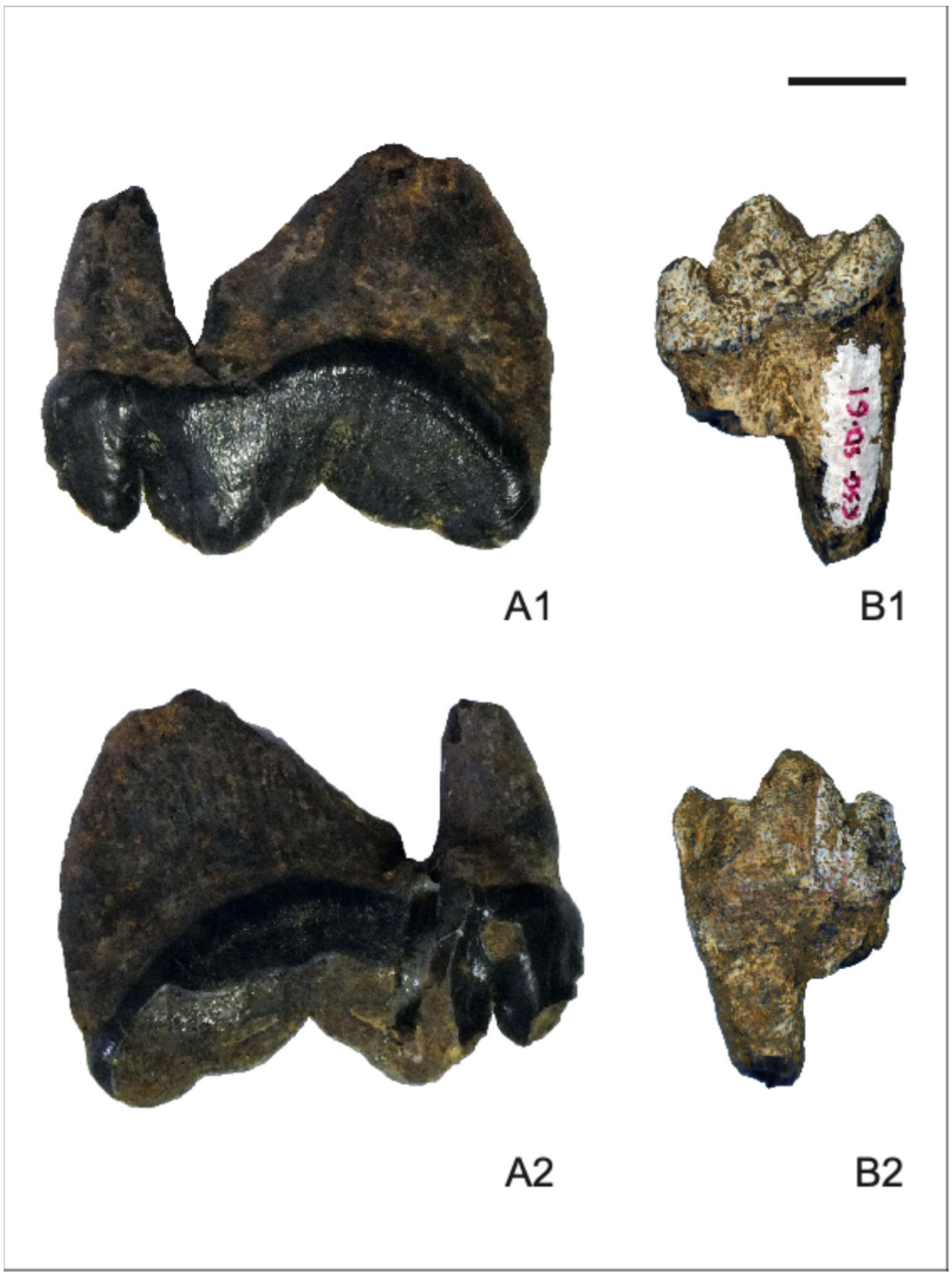

Figure 5. CSG *Homotherium* specimens. CSG 13-464: right upper fourth premolar, A1 buccal view, A2 lingual view; CSG sd-61: right lower fourth premolar, B1 buccal view, B2 lingual view. Scale bar 10 mm.

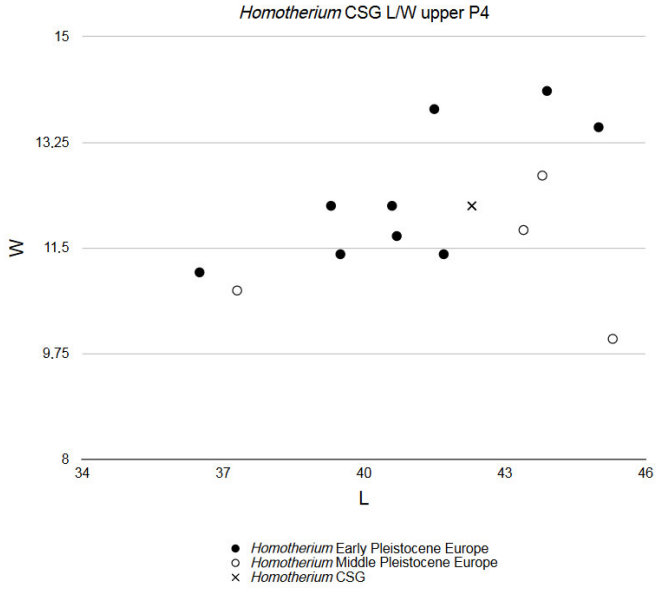

Figure 6. Scatter plot of the length/width of the *Homotherium* upper p4.

4.3. Family Hyaenidae GRAY, 1821

Genus *Pliocrocuta* Kretzoi, 1938
Pliocrocuta perrieri (Croizet and Jobert, 1828)

4.3.1. Referred Material

CSG 11-48: an upper third incisor; CSG 11-99: an upper juvenile third deciduous tooth; CSG sd-59: an incomplete upper fourth premolar; CSG 11-87: a lower third premolar; CSG 981146 and CSG 11-80: two lower broken fourth premolars; CSG 56700: three coprolites (another 54 without any inventory number) (Figure 7).

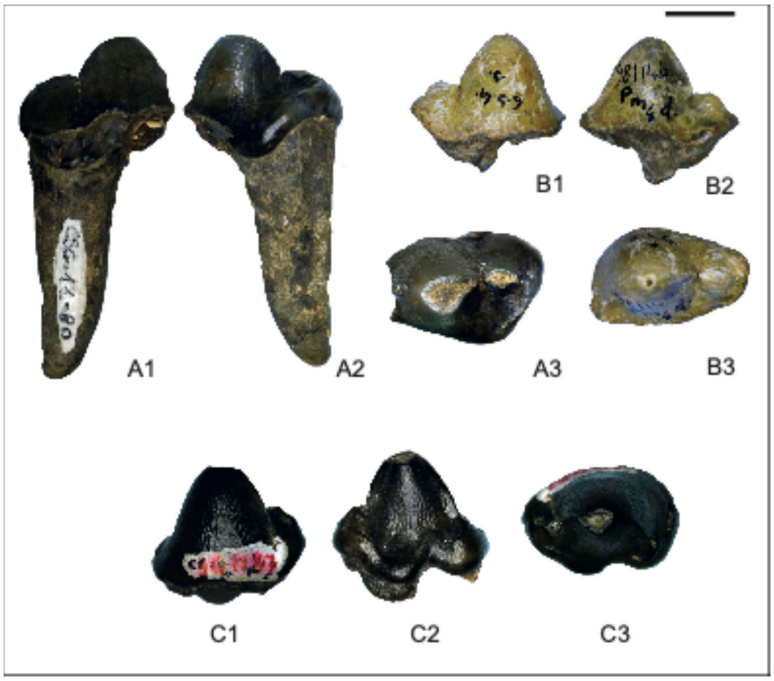

Figure 7. CSG *Pliocrocuta* specimens. CSG 11-80: right lower fourth premolar, A1 buccal view, A2 lingual view, A3 occlusal view; CSG 981146: right lower fourth premolar, B1 buccal view, B2 lingual view, B3 occlusal view; CSG 11-87: right lower third premolar, C1 buccal view, C2 lingual view, C3 occlusal view. Scale bar 10 mm.

4.3.2. Description

The upper fourth premolar CSG sd-59 is broken, and only the parastyle is preserved. The lower premolars display a rectangular occlusal outline. The lower third premolar CSG 11-87 is formed by a well-developed protoconid and a defined distal accessory cuspid and is lacking the mesial accessory cuspid. The upper deciduous carnassial (CSG 11-99) has a sub-rectangular outline; the parastyle is well-defined and labially set and the paracone and the metastyle blade are aligned. Both the lower fourth premolars, CSG 981146 and CSG 11-80, are broken, and the mesial cuspids are not preserved. The protoconid is well-developed, as in the living bone-cracking hyaenas. The distal accessory cuspid is also well-defined and is labially placed behind the protocone.

4.3.3. Discussion

The morphology of these teeth strongly resembles the specimens described by Viret ([22], pp. 46–52, Planches 5: Figures 1 and 2; Planches 6: Figures 1–8; Planches 7: Figures 1–5; Planches 8: Figures 1 and 2) as "*Crocuta* (*Plesiocrocuta*) *perrieri* subgen. nov.", in particular in the reduction stage of the accessory cuspids in the lower premolars [23]. Only the lower third premolar CSG 11-87 was morphometrically compared with *Pachycrocuta brevirostris* and *Pliocrocuta perrieri* specimens from different selected sites (Table S3), since the other teeth are incomplete. As shown in Figure 8, the CSG specimen fits in the *Pliocrocuta perrieri* variability. For these reasons, the CSG remains are here ascribed to the bone-cracking *Pliocrocuta perrieri*.

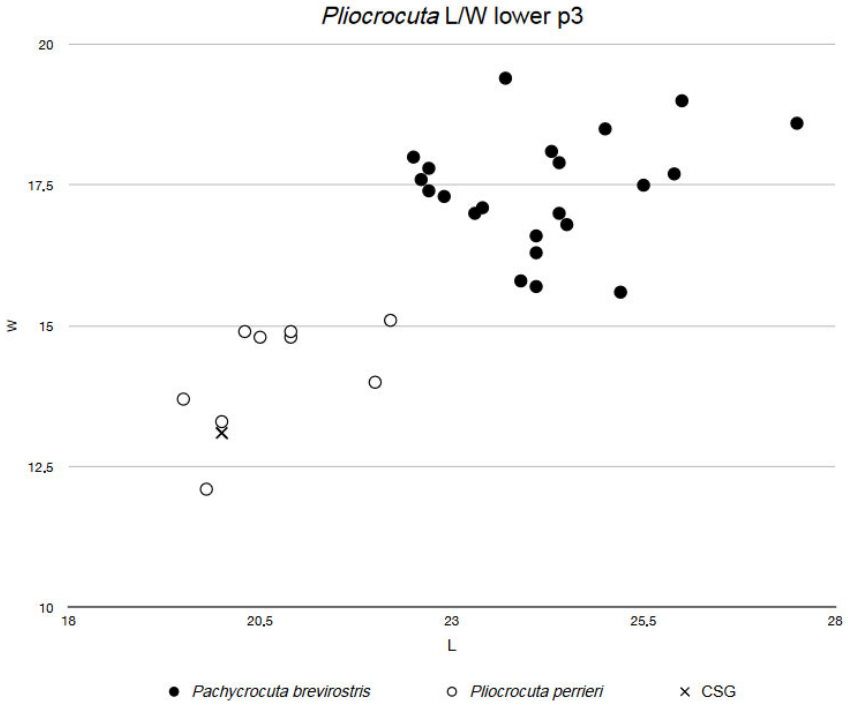

Figure 8. Scatter plot of the length/width of the *Pliocrocuta* lower p3.

4.4. Family Canidae GRAY, 1821

Genus *Canis* LINNAEUS, 1758
Canis etruscus FORSYTH MAJOR, 1877

4.4.1. Referred Material

CSG sd-81: upper canine; CSG sd-74: portion of an upper canine; CSG sd-63: portion of a lower canine; CSG sd-75: portion of a canine; CSG 78-40: portion of a canine; CSG 56699, CSG 581152: lower fourth premolars; CSG sd-62: lower fourth premolar; CSG 961159: fragmented fourth premolar; CSG 56690, CSG 13-233: two lower first molars; CSG 13-439: lower second molar; CSG sd-60: coprolite (Figure 9).

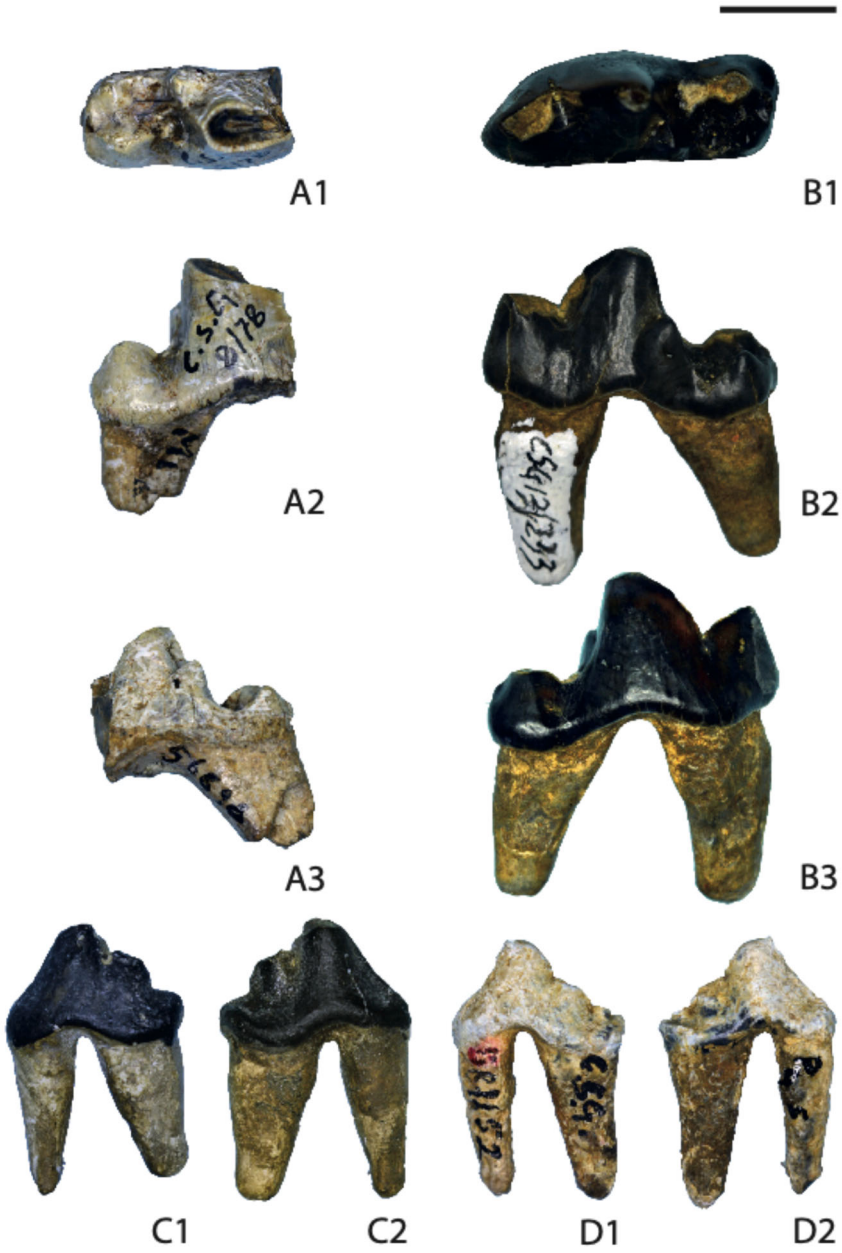

Figure 9. CSG *Canis* specimens. CSG 56690: left lower first molar, A1 occlusal view, A2 lingual view, A3 buccal view; CSG 13-233: right lower first molar, B1 occlusal view, B2 lingual view, B3 buccal view; CSG 56699: left lower fourth premolar, C1 buccal view, C2 lingual view; CSG 581152: left lower fourth premolar, D1 buccal view, D2 lingual view. Scale bar 10 mm.

4.4.2. Description

This species is the most represented amongst the CSG carnivoran specimens. The canines, both upper and lower, have curved crowns and are mesiodistally elongated. The fourth lower premolars are also mesiodistally elongated and show a symmetric protoconid and two distal accessory cuspids; the first is well developed, whereas the second is smaller and set on the distal cingulum. Only one lower first molar is complete (CSG 13-233). Its paraconid is less developed than the protoconid, which represents the main cusp of the tooth. The metaconid is well developed and is distinguished from the protoconid. The talonid basin is deep and surrounded by three cuspids. The hypoconid, labially set, is the largest cuspid of the talonid, whereas the entoconid, lingually placed, is less developed. The other cuspids generally present in the Pleistocene canids are reduced (mesoconid) or absent (entoconulid). The lower second molar is mesiodistally elongated, appearing rectangular

in the occlusal view. It displays three main cuspids; the protoconid and hypoconid are lingually set, whereas the metaconid is labial. The protoconid is the largest, and is mesially located, whereas the hypoconid is quite reduced and is set on the distal cingulum. The metaconid is quite large and is developed along the mesiolabial cingulum. The entoconid is present and is distally set in relationship to the metaconid.

4.4.3. Discussion

The morphological characteristics useful to distinguish the two *Canis* species recorded in the Italian Peninsula during the Early Pleistocene, *Canis etruscus* and *Canis arnensis*, are that the Etruscan wolf possesses some wolf-like dental features which cannot be found in *C. arnensis.* These are detected, for example, in the lower molars, with the first molar hypoconid being stronger than the entoconid, and a larger protoconid compared with the metaconid on the second molar [24]. These features are observed in the CSG first and second molars. Moreover, the lower M_1 CSG 13-233 has been morphometrically compared with selected *Canis etruscus* and *C. arnensis* specimens from the Italian Peninsula (Table S4), strengthening the attribution of the CSG canids to the Etruscan wolf (Figure 10). In fact, the Etruscan wolf is considerably larger in general terms compared with *C. arnensis* [24].

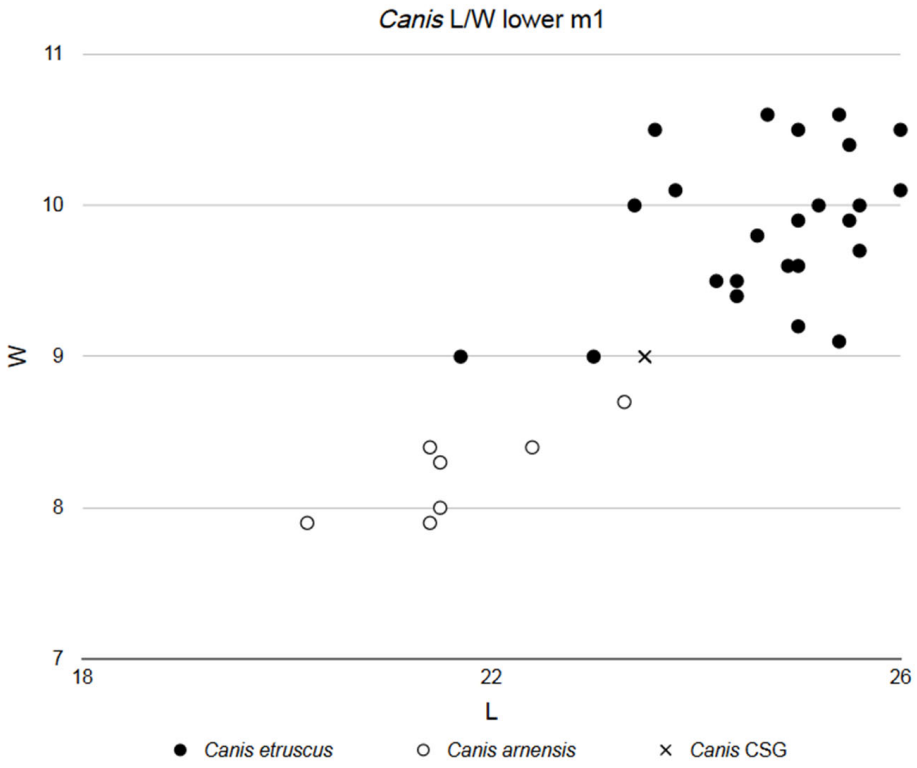

Figure 10. Scatter plot of the length/width of the *Canis* lower m1.

4.5. Genus Vulpes FRISCH, 1775

Vulpes alopecoides (DEL CAMPANA, 1913) pro parte

4.5.1. Referred Material

CSG 981154: upper fourth premolars; CSG sd-80: lower fourth premolar; CSG 11-173, CSG sd-79: lower first molars (Figure 11).

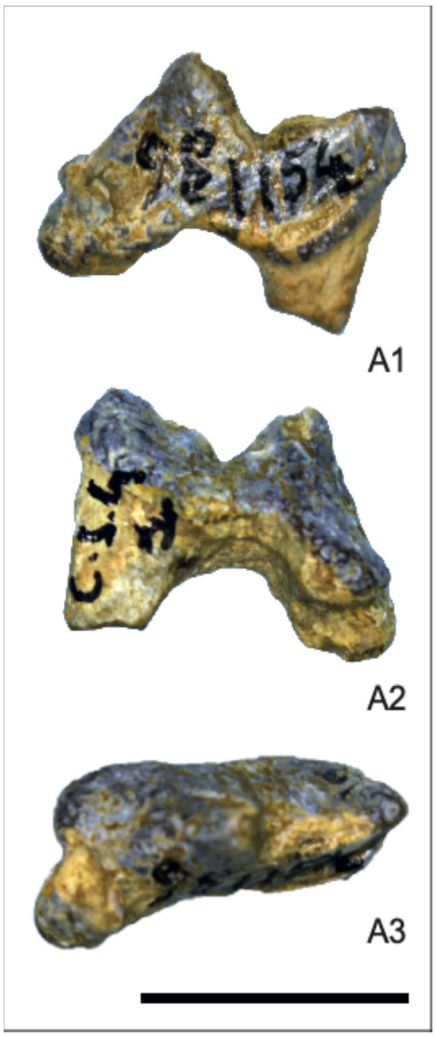

Figure 11. CSG *Vulpes* specimen. CSG 981154: left upper fourth premolar, A1 lingual view, A2 buccal view, A3 occlusal view. Scale bar 10 mm.

4.5.2. Description

The upper fourth premolar is mesiodistally elongated and shows a well-developed protocone, which is anteriorly projected in the occlusal view. The mesiolabial cingulum is quite marked, as is the distal cingulum. The parastyle is absent. The paracone is the largest and highest cuspid. The metastyle is quite elongated, with an incipient cuspid on the distal part which is connected to the distolabial cingulum. The lower fourth premolar preserves only the distal portion, with a marked distal cuspid and cingulum. The two lower first molars are both fragmentary. The lower carnassial is relatively mesiodistally elongated; the paraconid is large, but it is, however, less developed and lower than the protoconid, being the largest cuspids of the tooth. The metaconid is set on the lingual margin, just distally to the protoconid, and is reduced compared with the other trigonid cuspids, but is larger than the other talonid cuspids. Four cuspids are on the talonid, which is delimited by a round and deep talonid basin. On the labial margin, two cuspids occur; the larger entoconid is distally located, and the incipient entoconulid is set between the metaconid and the entoconid. The cristid-like cingulid is distally placed in relationship to the entoconid and to the hypoconid, just along the distal margin of the tooth. The hypoconid is stout and as high as the entoconid, and it is well separated from the protoconid. The mesoconid is absent.

4.5.3. Discussion

The CSG *Vulpes* teeth specimens can be ascribed to *V. alopecoides*, according to the diagnosis reported in Bartolini Lucenti and Madurell-Malapeira [25]. In particular, the upper fourth premolar is mesiodistally elongated, with a large paracone and a pointed and large protocone, while the parastyle is absent.

The presence of fox fossils in the Plio-Pleistocene Eurasian record is quite scarce, leading to the identification of different species and several hypotheses of their relative taxonomic relationships. A large review of *Vulpes* fossil material was published by Bartolini Lucenti and Madurell-Malapeira [25] that attributed all Early Pleistocene European fossils to the single, polymorphic species *Vulpes alopecoides*. According to the chronological setting of the site, the CSG record represents one of the oldest attested occurrences in western Europe.

4.6. Family Mustelidae FISCHER, 1817

Genus *Martellictis* BARTOLINI LUCENTI, 2018
Martellictis ardea (GERVAIS, 1848-1852)
Referred material
CSG sd-78: hemimandible

4.6.1. Description

This specimen (Figure 12) consists of an incomplete hemimandible, which preserves only the lower first molar. The corpus is quite gracile and low; the opening of the masseteric fossa is distally placed close to the margin of the lower first molar. The lower carnassial is mesiodistally elongated and is quite slender. The paraconid is well extended, and it is less high than the protoconid. Even though the tooth shows advanced wear of the cuspids, the metaconid seems to be located posteriorly to the protoconid. In addition, the metaconid is as high as the paraconid. The talonid is short; only the hypoconid is recognizable. Considering the wear stage, the presence of other cuspids cannot be excluded.

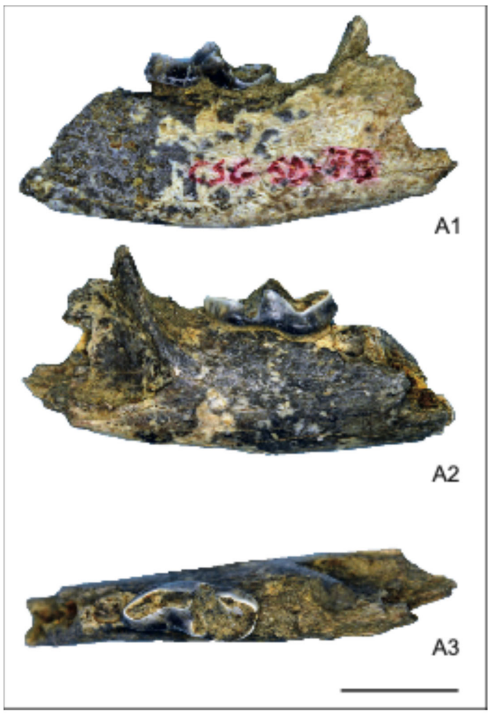

Figure 12. CSG sd-78: *Martellictis ardea* hemimandible, A1 buccal view, A2 lingual view, A3 occlusal view. Scale bar 10 mm.

4.6.2. Discussion

Lyncodontini remains are relatively scarce in the European fossil record, complicating the reconstruction of the evolutionary history of this group. Recently, Bartolini Lucenti [26] introduced a new genus, *Martellictis*, based on the samples from the Late Pliocene to the Early Pleistocene of Europe, Olivola (Italy), Perrier-Les Étouaires (France) and Saint Vallier (France), recognizing only the species *Martellictis ardea*.

Morphologically, there is no clear separation between *Pannonictis* and *Martellictis* based on the lower first molar. The only feature observable in the CSG fossil is the development of the mandible corpus, which appears to be relatively gracile (even if incomplete), resembling *Martellictis* [26]. The height (11.6 mm) and the breadth (5.6 mm) of the CSG hemimandible at m1 falls in the *Martellictis* variability, according to the data reported in Ros-Montoya et al. [27], strengthening the attribution to this taxon.

5. Discussion

5.1. Biochronological Implications

The CSG carnivoran assemblage includes *Ursus* spp.; the scimitar-toothed cat, *Homotherium latidens*; the bone-cracking hyena, *Pliocrocuta perrieri*; the Etruscan wolf, *Canis etruscus*; *Vulpes alopecoides* and the mustelid *Martellictis ardea*. These remains represent a key sample to investigate carnivoran diversity and, consequently, its biochronological and palaeogeographical implications during the Gelasian (Early Pleistocene) in Mediterranean Europe.

A "historic" major faunal turnover that affected the Carnivoran palaeoguild in western Europe during the Gelasian was the so-called "Wolf event", initially dated to ca. 2.0–1.7 Ma [28,29], best represented by the First Appearance Datum of *Canis* spp. However, findings of *C. etruscus* and other species traditionally considered to be involved in the "Wolf event" are today known from several European sites [15]. These fossil remains, in fact, backdated the "Wolf event" as defined by Azzaroli [28], pointing out also its diachronous nature [30], and thus, questioning its biochronological significance [31]. A recent, extensive review of this significant biochronological event is discussed in Iannucci et al. [15], where it is reported that the arrival of wolf-like canids in Europe is at least as early as the Coste San Giacomo FU (middle Villafranchian), even if putative evidence could suggest an even older age. Moreover, there has been a conceptual shift from considering the "Wolf event" from the earliest appearance of *Canis* in the fossil record to an abundance increase, i.e., the late Villafranchian "massive expansion", as it has been called by Azzaroli et al. [29], and is generally agreed in subsequent research [15]. At the present time, *Canis etruscus* remains from CSG are the clear, earliest evidence of wolf-like canid occurrence from the Early Pleistocene in the Italian Peninsula, concurrently with those of Pantalla, now also dated to ca. 2.2 Ma [32], and maybe in Europe as a whole, pending the taxonomical attribution and the chronology of other Gelasian specimens. In Italy, for instance, several findings of *Canis* sp. are known from localities placed within the CSG Faunal Unit, namely, Fontana Acetosa [33], Montagnola Senese [34], Quercia [35], Torre Picchio [36] and Vigna Nuova [37]. The CSG specimens slightly pre-date the Italian findings from the Olivola (Val di Magra, Tuscany, ca. 2 Ma; Rook and Martínez-Navarro [38]) and Poggio Rosso (Upper Valdarno, Tuscany; ca. 1.9–1.8 Ma; Napoleone et al., 2001 [39,40]; Bartolini Lucenti and Rook [24]) sites, where three different species of canids, the wolf-like *C. arnensis* and *C. etruscus* and the Lycaon-like *Xenocyon falconeri*, occur [28,41,42].

Another important biochronological signal recorded in the CSG large-mammal assemblage is the last occurrence in the Italian Peninsula of the medium-sized hyaenid *Pliocrocuta perrieri*. This taxon also occurred in the Montopoli site (Tuscany; ~2,6 Ma, Gelasian, Montopoli FU) [43], thus, well characterising the Italian middle Villafranchian assemblages. *Pliocrocuta perrieri* (= *Pachycrocuta perrieri*) was also reported in the Valle Catenaccio site (Latium; Gelasian, Coste San Giacomo FU?) by Cassoli and Segre Naldini [33]; Segre Naldini and Valli [44] verbatim indicated "*Pachicrocuta* sp.". This hyaenid tooth (V.C. 981247), housed at the IsIPU depository (Anagni, Frosinone), is a worn lower premolar and does not provide here any specific determination. Recently, Iannucci et al. [45] redescribed and revised the taxonomic attribution of a hyena hemimandible recovered from Paciano (Um-

bria, Italy), originally reported in the early 1900s and attributed to *Hyaena striata* (= *Hyaena hyaena*) and subsequently listed as a record of the giant hyena *Pachycrocuta brevirostris*, but now assigned to *Pliocrocuta perrieri*. Unfortunately, the exact provenance of the hyena from Paciano is unknown, as is its dating [45]. The last occurrences in Mediterranean Europe of *P. perrieri* are recorded in the Iberian Peninsula, where it is documented at the site of Fonelas P-1 and dated around ~2.1–1.9 Ma [46], and in Greece, at the site of Gerakarou 1 (= *Pliohyaena perrieri*; Koufos [47]), biochronologically referred to the late Villafranchian, and in particular, to the Olivola Faunal Unit [48]. In Georgia, it is recorded at Dmanisi and dated around 1.8 Ma [49]. It is worth noting that in these last sites, *P. perrieri* is recorded together with *Pachycrocuta brevirostris* [46]. The short-faced giant hyaena *Pachycrocuta brevirostris*, sister-taxon of *Pliocrocuta* [50,51] or even its direct descendant [23,50–52], in fact gradually replaced *Pliocrocuta,* becoming one of the most widespread carnivoran species in Eurasia during the second half of the Early Pleistocene. Moreover, the dispersal across Eurasia of *Pachycrocuta brevirostris* has been regarded as a major event during the Early Pleistocene (e.g., the "large canids and *Pachycrocuta*" events in Sardella and Palombo [31]; the "*Pachycrocuta brevirostris* event" in Martínez-Navarro et al. [53]. According to Vinuesa et al. [54], *Pliocrocuta* probably displayed a less-complex social behaviour than extant bone-cracking hyenas, especially compared with the spotted hyaena, *Crocuta*. These scholars, on the basis on the relative size of the anterior cerebrum, have hypothesised that *Pliocrocuta* is more comparable in its home range and forelimb usage to the living genera *Hyaena* and *Parahyaena* and is probably also lacking the complex pack-hunting and territorial behaviours of *Crocuta*. The spotted hyaena is, in fact, an active pack hunter [55,56], whereas both *Hyaena* and *Parahyaena* are basically scavengers, although they can also chase small prey alone [55,57,58]. In conclusion, *P. perrieri* went extinct in Mediterranean Europe around 2–1.8 Ma, suffering from ecological competition with both the larger, bone-cracking hyaena *P. brevirostris* in accessing carcasses, and with the several other carnivoran species present at the time, especially the hypercarnivorous and ambush-hunting felids, which limited its possibilities to deviate towards a different feeding behaviour [28,59–61]. Finally, several coprolites have been found in the CSG site, thus questioning the active role in the massing of carcass parts played by the hyaenas as in the Italian site of Poggio Rosso [62]. Taphonomic studies could clarify this hypothesis.

The lion-sized sabre-toothed cat *Homotherium latidens* was the dominant predator in the CSG large-mammal assemblage. *Homotherium* spread into Europe around 3 Ma, probably when the climate became cooler and drier and vegetation cover decreased, becoming an important faunal taxon in the Plio-Pleistocene Eurasian carnivore guild. According to [63], the First Appearance Datum of *Homotherium* in Europe is recorded in the fauna of the Odessa Catacombs (end of MN15). Nowadays, *H. latidens* is recognised as a single variable species in the Plio-Pleistocene of Eurasia (see, e.g., Sardella and Iurino [21]; Antón et al. [64] and references therein). The first occurrence of this taxon in the Italian Peninsula is not clear. Two upper canines of a Machairodontinae specimen were collected at the site of "Fornaci al Ponte di Castiglione" (= "Fornaci di Pievefosciana" or "Pievefosciana" or "Pieve Fosciana") in the Garfagnana area (Tuscany) by De Stefani in 1882. These fossils, IGF 53V and IGF 112V, were originally labelled as "*Megantherеon Nestianus*" (IGF 53V) and *Megantherеon (Machairodus) Nestianus* (IGF 112V) and are housed at the Museo di Geologia e Paleontologia of the Università di Firenze. Azzaroli [65] reported from the site of Pieve Fosciana the following taxa: *Anancus arvernensis*, *Tapirus arvernensis*, *Sus minor*, *Megantherеon megantherеon* and *Cervus* sp. Later, Azzaroli [66] referred, with question, this fauna to the Triversa FU (Early Villafranchian). Subsequently, Ficcarelli [67] ascribed these two upper canines to *Homotherium crenatidens*. Finally, Rustioni [68] revised the Pievefosciana mammal association indicating the occurrence of these taxa: *Anancus arvernensis*, *Stephanorhinus* sp., *Tapirus arvernensis*, *Cervus* sp., *Sus minor* (now recognised as a junior synonym of *Sus arvernensis*) [69], *Lynx issiodorensis*, *Megantherеon cultridens*, *Vulpes alopecoides* and an undetermined Carnivora without any evidence of *Homotherium* remains. Since it is not possible at the present time to provide for the remains of "Fornaci al Ponte di Castiglione",

any accurate taxonomical attribution of the *Homotherium* remains from CSG currently represents the First (clear) Appearance Datum in the Italian Peninsula.

Although different extinct fox species and several hypotheses of their relative taxonomic relationships have been proposed in the literature, the Early Pleistocene European sample was recently referred to as a single and polymorphic taxon, *Vulpes alopecoides* [25]. In western Europe, the oldest fossils of this taxon come from the Iberian Peninsula, in particular from Fonelas P-1 (dated around ~2.1–1.9 Ma; Arribas et al. [70]), La Puebla de Valverde (calibrated between the Reunion and Olduvai subchrons at ~2.12–1.92 Ma; Sinusía et al. [71] and Cuccu et al. [72]) and Villaroya (calibrated to the Reunion chron at ~2.14–2.11 Ma; Pueyo et al. [73]). The CSG record thus represents one of the oldest attested occurrences of *Vulpes alopecoides* in western Europe.

Finally, the *Martellictis ardea* at CSG is one of a few occurrences of this species in Europe during the middle Villafranchian. Ros-Montoya et al. [27] recently reported the presence of this small Lyncodontini in the Spanish localities of Barranco León and Fuente Nueva-3, dated approximately between 1.4 and 1.3 Ma, suggesting its survival during the late Villafranchian.

5.2. Paleoenvironmental Implications

The CSG paleoenvironment was mainly a braided stream surrounded by a watercourse, with the presence of mainly grasslands, as testified by the abundant presence of large arvicolids such as *Mimomys pliocaenicus* [7]. The very poorly represented Eulipotyphla and Muridae could be a clue to reduced and unstructured covered areas. The humid environment was limited to the surroundings of the watercourse, and it was the habitat of hippopotamuses, beavers, arvicolids and the water mole *Galemys kormosi* [9].

This paleoenvironmental reconstruction is also strengthened by the coexistence of two proboscideans, which clearly testifies to the gradual replacement of the European mastodons by early species of *Mammuthus*, since the arrival of the Southern Mammoth in the Italian Peninsula corresponds with an opening up of the vegetation during the Early Pleistocene. Forest diversity decreased, in fact, as a result of a progressive decline in and loss of subtropical taxa during the Early and Middle Pleistocene [4].

Studies carried out by Strani et al. [8,11,17] on the dietary adaptations of the CSG fossil herbivorous ungulates allowed them to obtain information on the palaeoenvironmental context that characterised the area during the Early Pleistocene. A wide range of feeding behaviours has been recorded, suggesting that herbivores had access to a variety of plant resources in a mosaic of biomes that spanned wetlands to woodlands to grasslands. The abundant remains of the stenonid equid *E. senezensis* aff. *E. s. stehlini* (one of the best-represented taxa at CSG), which display mesowear patterns and an isotopic signal compatible with a grazing behaviour in open habitats [11], indicate that grasslands were widespread in the area, which is in accordance with vegetation data reported from other localities on the Italian Peninsula [74].

In this palaeoenvironmental scenario, the Etruscan wolf operated as a pack-hunting animal able to harry rodents and lagomorphs, which are assumed be the main meat resources. However, sporadic ungulate hunting in the 10–45 kg size category is also considered feasible according to Rodríguez et al. (2012), as, for example, the cervids *Axis* cf. *lyra* and *Croizetoceros* cf. *ramosus* and the bovid *Gazella borbonica*. Carrion would be eaten when available.

The killing behaviour and prey preferences of *Homotherium* is a controversial topic (see Rodríguez et al. [75] and references therein). Anatomical and morphofunctional analyses suggest that *Homotherium* killed large prey, the size of a horse or a large bovid; probably, its postcranial skeleton was better adapted to long-distance travel than that of the pantherines, but their jumping abilities were less developed [76]. These characteristics suggest an adaptation to open environments, as reconstructed in the CSG site, and a large home range. According to Palmqvist et al. [77], juvenile *Mammuthus* were an important part of the diet of *Homotherium* at Venta Micena (Spain), together with *Bison* sp. (52%) and *Equus altidens*

(38%) [78]. *Homotherium* was a top predator and likely a pack hunter, with a preferred prey size in the 90–360 kg range; it could also kill prey in the 10 to 1000 kg range, depending on their availability. Juveniles of species weighing more than one ton are also considered vulnerable to *Homotherium* attack according to Rodríguez et al. [75]. However, *Homotherium* was itself vulnerable to hyaenid *Pliocrocuta perrieri* ambush. *Pliocrocuta perrieri* was, in fact, a medium-sized hyaenid that Turner et al. [51] classifies in their Ecomorph Group 6, "fully developed bone crackers".

In consideration of all the above, the CSG assemblages described testify to a high Carnivoran richness, apporting new data for studies that will address the predator/prey relationships at the regional and/or local community fauna scales during the Early Pleistocene in Mediterranean Europe.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/quat7040057/s1, Table S1: *Ursus* teeth measurements [18,19,79,80]; Table S2: *Homotherium* teeth measurements [21,67,81,82]; Table S3: *Pliocrocuta* teeth measurements [45,48,70,79,83–93]; Table S4: *Canis* teeth measurements [94].

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