Paleoenvironments and climatic changes in the Italian Peninsula during the Early Pleistocene: evidence from dental wear patterns of the ungulate community of Coste San Giacomo

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A B S T R A C T

Quaternary glacial/interglacial alternations, influenced by orbital obliquity cycles with a 41-ka long periodicity, started in the northern hemisphere around 2.6 Ma ago. Such alternations affected the terrestrial ecosystems, especially those of the Mediterranean region, with changes in the floristic communities and the dispersal and radiation of a number of large mammal open dwellers. Analyses of tooth wear patterns of ungulates from the Early Pleistocene site of Coste San Giacomo allow for a more objective reconstruction on the paleoenvironments and the climate in the Italian Peninsula during this epoch. Our results show that this area was composed by a mosaic of biomes, in particular by steppe and woodlands/wetlands. Evidence of such heterogeneity is provided by the wide spectrum of feeding behaviours found among the numerous ungulate herbivores here recorded, with cervids (*Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus* and *Eucladoceros* sp.) exhibiting browser diets, most of the bovids (*Gazella borbonica* and *Leptobos* sp. and *Gallogoral meneghinii*) being intermediate feeders and the equid *Equus stenonis* showing a strict grazer behaviour. These results provide new insights for a timing of changing ecosystems in Southern Europe and reveal the environmental legacy of this global climatic shift, which is essential for understanding the early occupation of *Homo* in Europe. Thus, our data provide new evidence that such an environmental heterogeneity and a wide spectrum of available food resources could have been the main factors favouring the settlement of early species of *Homo* in this area.

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1. Introduction

The setting of 40 Ka obliquity-forced thermal glacial/interglacial (G/I) cycles (~2.6 Ma) (Bertini, 2010) had strong effects on seasonality, with the first record of cool winters and dryer climates as testified by the diffusion of herbaceous steppe vegetation (Fortelius et al., 2006; Kahlke et al., 2011). Thus, from the Late Pliocene/Early Pleistocene transition the climate was characterized by rapid alternations between xeric, cool temperate (glacials) and humid warm (interglacials) phases (Bertini, 2010). In the Italian Peninsula, "warm" steppes or coniferous forests alternated with subtropical to warm-temperate deciduous forests. All these events had severe consequences on the evolution of terrestrial mammalian faunas.

More specifically, the Early Pleistocene is characterized by a succession of extinctions and faunal dispersals recorded in the European large mammal assemblages (Palombo, 2014 and references therein), with herbivores being the group most significantly affected, since they are highly susceptible to changes in vegetation. The increasing of herbaceous plants and more open environments is clearly reflected by a higher abundance of grazer taxa (i.e., animals subsisting primarily on grasses, rushes and sedges), and a decrease of the presence of browser species (i.e., animals feeding primarily on herbaceous and woody material, such as forbs, leaves and fruits).

The mammal assemblage of Coste San Giacomo (CSG), in works prior to Bellucci et al. (2012) referred as Costa San Giacomo (Palombo et al., 2008; Kahlke et al., 2011), has been recently dated around 2.1 Ma (middle Villafranchian, MN 17 biozone) (Bellucci et al., 2014). This site is therefore crucial to investigate the environmental and faunal changes that occurred in the Mediterranean

region during the Gelasian, which were a result of major climatic changes at a global scale. The occurrence of taxa such as *Hippopotamus* in the CSG assemblage provides evidence of early dispersal events of African taxa prior to the early *Homo* radiation into Europe.

In the CSG large mammal assemblage the newcomer Southern mammoth *Mammuthus meridionalis* is recorded together with the mastodon *Anancus arvernensis* (Bellucci et al., 2012). The coexistence of these two taxa clearly testifies the gradual replacement of the mastodons by early species of *Mammuthus* with a significant palaeoenvironmental implication, since the arrival of *M. meridionalis* at the Italian Peninsula corresponds with an opening-up of the vegetation during the earliest Pleistocene. Similarly, the prevalence of stenonid equids instead of deer seems to suggest drier and more open landscapes.

Given the unusual abundance of plant-eating taxa such as artiodactyls (mostly cervids and bovids) and perissodactyls (equids) in CSG, and because palaeontologists often refer to the guild of these herbivores mammals to infer paleoenvironments and paleoclimate (as their feeding preferences mirror the availability of vegetal resources, and these latter are a direct consequence of particular ecological factors; DeMiguel et al., 2010, 2011), we consider this site as an extraordinary example for gaining an updated knowledge and better understanding on the effects of climate in Central Italy during the 2.6−1.8 Ma time span. Because competition is of overriding importance in shaping the composition and structure of animal communities and is commonly climate-dependent (Dunson and Travis, 1991), it is implied as an objective to explore whether and how ungulate species partitioned the available food resources in CSG.

2. Materials and methods

The studied fossil material belongs to the Early Pleistocene locality of CSG, in Central Italy (Anagni, Frosinone) (Fig. 1). Extensive fieldwork has been carried out since 1978 by researchers of the Italian Institute of Human Palaeontology (IsIPU) (Segre Naldini et al., 2009; Bellucci et al., 2014 and references therein). The material is currently housed at the IsIPU laboratory in Anagni (Frosinone, Central Italy).

The updated faunal list of CSG (Bellucci et al., 2014) comprises 19 large and 7 micromammal taxa. Among them, the most important are: *Anancus arvernensis, Mammuthus meridionalis, Stephanorhinus sp., Equus stenonis, Eucladoceros* sp., *Axis* cf. *lyra* (="*Metacervoceros*" *rhenanus, Cervus phillisi*), *Croizetoceros* cf. *ramosus, Leptobos* sp., *Gallogoral meneghini, Gazellospira torticornis, Gazella borbonica, Sus strozzii, Hippopotamus* sp., ?*Pliocrocuta perrieri, Ursus* cf. *etruscus, Canis* sp., *Vulpes* cf. *alopecoides, Homotherium* sp., *Macaca sylvanus, Mimomys pliocaenicus, Apodemus* sp., *Sciurus* cf. *S. warthae, Castor fiber, Hystrix refossa, Beremendia fissidens* and *Talpa* sp. As can be observed, there is an exceptional record of artiodactyls (with several species of deer and bovids) and perissodactyls. Together with previous results for other similar Pleistocene localities (from both a temporal and faunal point of view) from elsewhere in Greece and France (Rivals and Athanassiou, 2008; Valli and Palombo, 2008), our results allow us to investigate the environmental and climatic effects of this epoch in the Mediterranean Europe.

The fossil material here studied consists of dental (molar) specimens of the following ungulate taxa: *Axis* cf. *lyra* (n = 26), *Croizetoceros* cf. *ramosus* (n = 5), *Eucladoceros* sp. (n = 26), *Gazella borbonica* (n = 8), *Gazellospira torticornis* (n = 8), *Gallogoral meneghinii* (n = 2), *Leptobos* sp. (n = 2) and *Equus stenonis* (n = 21). As a limiting factor in this study, we recognize the low number of dental specimens available for some artiodactyl samples (5 > n). As such, it was decided to stay with generalities in the dietary discussions that apply to these samples (in particular to *C.* cf. *ramosus, G. meneghinii*

and *Leptobos* sp.). To investigate the environmental conditions and changes in climate, we focused on the following techniques of dietary assessment in the ungulate community of CSG.

2.1. Hypsodonty inference

Since molar crown height (or hypsodonty) yields some information about feeding ecology (Janis, 1988; Rivals and Semprebon, 2006; DeMiguel et al., 2008) and habitat openness (especially aridity degree) (Janis, 1988), we measured crown height in the fossil taxa according to the index defined by Janis (1988). Because hypsodonty summarizes the history of adaptation of an animal, it also carries with phylogenetic effects (Janis, 1988). Hypsodonty Index (HI) for unworn lower third molars (n = 21) was determined as m3 height divided by m3 width, and teeth classified as "brachydont" (HIm3 < 1.5), "mesodont" (1.5 < HIm3 < 2.5) and "hypsodont" (HIm3 > 2.5). We calculated an average HI (Average HI) for each taxon. Due to the lack of unworn lower third molars of *G. meneghinii*, this species was excluded from those analyses where HI was required. For this reason, any conclusion regarding this species should be considered as tentative (and qualitative) in terms of dental crown height.

2.2. Dental mesowear

Mesowear is considered a good dietary indicator in herbivore species, as it represents the cumulative effects of the items ingested (both foods and exogenous particles such as dust and grit) on the dental morphology that are produced in a long period of time compared to the lifespan of the animal (Fortelius and Solounias, 2000). Importantly, mesowear is, in contrast to hypsodonty, a direct (i.e., not related to phylogeny) signal of the species' diet. The method is based on the relief of the worn occlusal surface and on the shape of the cusps. These factors are heavily influenced by the attrition (tooth-to-tooth contact) and the abrasion (tooth-to-food contact). High levels of attrition produce sharper cusps and higher tooth relief whereas high levels of abrasion produce blunter cusps and lower tooth relief (Fortelius and Solounias, 2000; Merceron et al., 2005; DeMiguel et al., 2008; Rivals and Athanassiou, 2008; Valli and Palombo, 2008). Mesowear analysis, originally limited to the second upper molar (M2), was here extended to upper (M1−M3) (according to Kaiser and Solounias, 2003) and lower (m1−m3) molars (following DeMiguel et al., 2010, 2012) to obtain a reasonably accurate classification of samples. Although some studies (Franz-Odendaal and Kaiser, 2003; Fraser et al., 2014) have shown that mesowear scores differ between upper and lower molars, some others instead have tested that there are no significant differences in the mesowear signal between tooth types (DeMiguel et al., 2010, 2012; Hernesniemi et al., 2011). Furthermore, the results that we obtained in preliminary statistical tests for our sample case indicate that lower teeth are well suited for estimating mesowear scores, and therefore the abrasiveness of the diet of species. Occlusal relief (high or low) and cusp shape (sharp, rounded or blunt) of the apex of the paracone and metacone of the M1−M3 and the metaconid and entoconid of the m1−m3 were examined in a total of 96 dental specimens by either the naked eye or using a 6× magnifying portable glass and qualitatively scored. Then, variables were converted to a single score (mesowear score) according to Rivals et al. (2009). Thus, a score 0 is given to teeth showing a combination of high relief and sharp cusps; 1 to the teeth with high relief and rounded cusps; 2 to teeth with low relief and rounded cusps; 2.5 to teeth with low relief and sharp cusps; and 3 to teeth with low relief and blunt cusps.

A comparative database composed of 54 extant ungulates with well-known diets was used as a reference, and both the
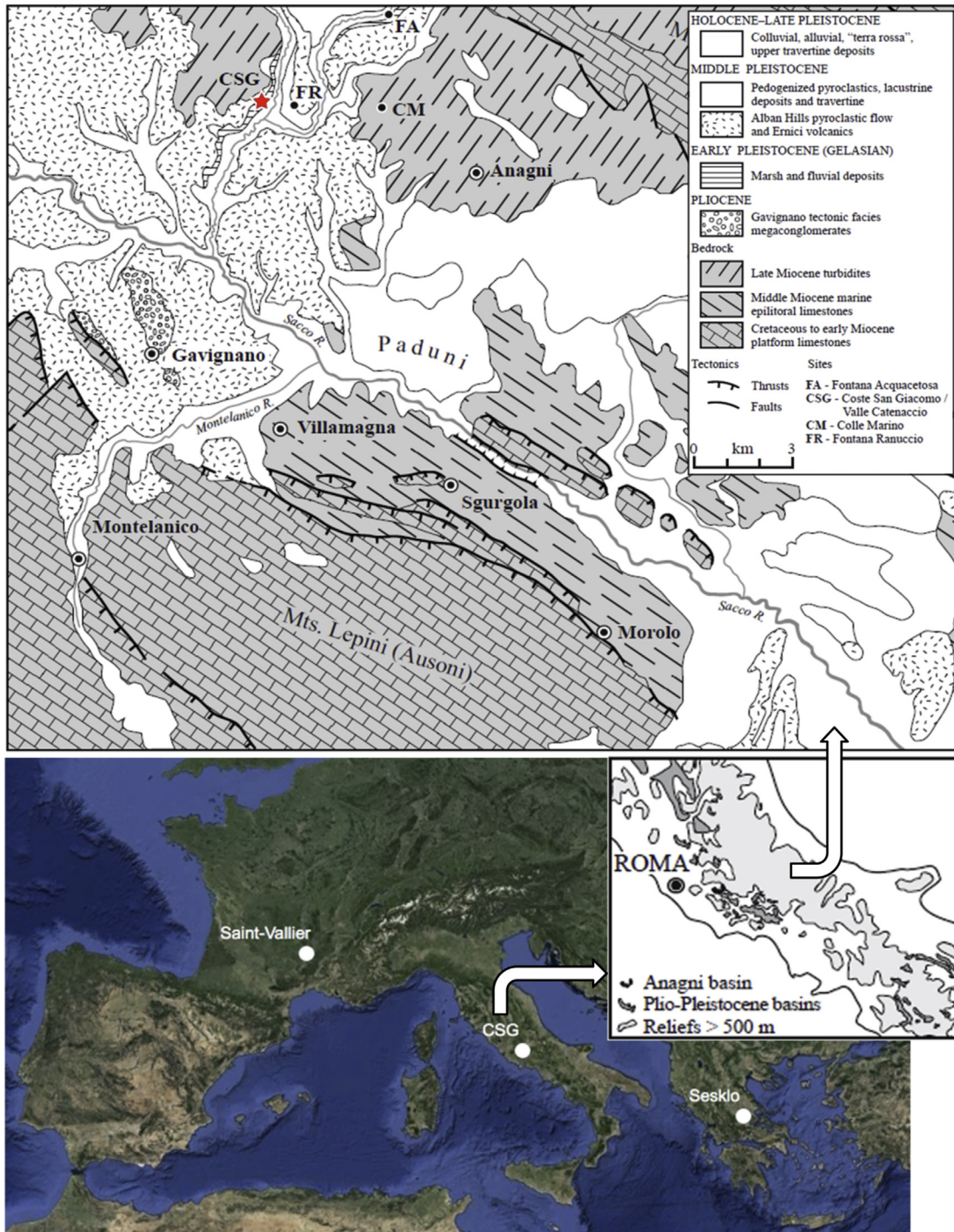
Fig. 1. Geographical location of the Pleistocene sites of Coste San Giacomo (and geological context), Saint-Vallier (France) and Séyklo (Greece).

conservative and the radical dietary classifications were employed according to Fortelius and Solounias (2000). The set of extant species was partitioned into conservative fruit (n = 5) and leaf-browsers (n = 12), conservative mixed feeders (n = 26) and conservative grazers (n = 11).

We also analysed our hypsodonty and mesowear results together with those previously published for other contemporaneous European artiodactyls and perissodactyls, including: "*Metacervoceros*" *rhenanus* and *Croizetoceros ramosus* from Saint-Vallier, France (Valli and Palombo, 2008); and *cf. Croizetoceros ramosus*,

Gazella sp., *Gazella bouvrainae*, *Gazellospira torticornis*, *Euthyceros thessalicus* and *E. stenonis* from Séyklo, Greece (Rivals and Athanassiou, 2008).

To offer insights into the abrasiveness of the items eaten and to characterize dietary traits of species, discriminant Canonical Variate Analyses (CVA) were performed to analyse the extant and fossil data sets following DeMiguel et al. (2008, 2010). These studies were developed using the combination of rounded and blunt cusps, and high relief as criterion variables. CVA was intended to evaluate the reliability of these mesowear variables for distinguishing

between the various dietary categories defined for extant taxa, as well as to classify fossils to these categories. Extant ungulates were thus included a priori in one of the four dietary categories described above, whereas the extinct taxa were left unclassified and classified a posteriori on the basis of the classification probabilities derived by the analysis from Mahalanobis squared distances to extant group centroids. Both dietary classifications (conservative and radical) were used alternately as a grouping variable, which allowed us to recognize fossil taxa that, although being adapted to feed on a mixed diet, were shifted toward the browse-dominated or the grass-dominated end of the mixed feeder continuum. Only extinct data from Valli and Palombo (2008) were used in the CVA with comparative purposes, as Rivals and Athanassiou (2008) do not provide values of cusp shape and high relief (only mesowear score data) which are required for this analysis in order to use more than one independent discriminant variable. All statistical analyses were performed using the SPSS Statistics v. 19 statistical package.

3. Results

3.1. Hypsodonty inference

All the cervid species are brachydont according to their HI, with *C.* cf. *ramosus* displaying the lowest value (HI = 1). There is, however, a somewhat differentiation in degree of hypsodonty among the bovids, with both *G. torticornis* and *Leptobos* sp. being mesodont species, and *G. borbonica* a hypsodont one. Finally, *E. stenonis* exhibits the highest HI, as expected for an equid, thus being a hypsodont species. Despite that hypsodonty entails a certain degree of phylogenetic signal, as above mentioned, it is generally accepted, though there are some inconsistencies in this respect (Damuth and Janis, 2011; DeMiguel et al., in press), that low hypsodonty indices (i.e., usually brachydont) are related with ungulates with low dietary abrasion (i.e., leaf-dominated browsers) in relatively dust-free habitats, while higher hypsodonty indices (i.e., usually hypsodont taxa) usually indicate higher dietary abrasion (i.e., grass-dominated feeders) and more open and arid environments (Janis, 1988; Eronen et al., 2010; Semprebon and Rivals, 2010). According to this, it is apparent that the fauna from CSG represents a wide spectrum of feeding styles and abrasiveness of the items ingested, with the cervids being related with the lowest dietary abrasion and the more close and less dry areas, *G. borbonica* and *E. stenonis* representing an increased dominance of dietary abrasion and, at least for the latter, more open and arid areas, and the remaining taxa (all the bovids but *G. borbonica*) being intermediate in both dietary behaviour and degree of abrasiveness of the foods ingested (i.e., subsisting on both soft-browse and abrasive grass). Hypsodonty values are reported in Table 1.

3.2. Dental mesowear

The predominant mesowear pattern among the fossil deer is to display sharp cusps and high occlusal relief. None of deer population show incidence of blunt cusps (Table 1). All these facts indicate non-abrasive diets, probably equalling those of extant browsers such as the white-tailed deer *Odocoileus virginianus*. Among the bovids, *G. borbonica* and *G. meneghinii* show a combination of sharp and rounded apices, and high occlusal relief (Table 1), which is indicative of intermediate levels of abrasion and diets similar to that of the extant mixed feeder *Gazella granti*. The mesowear of *Leptobos* sp. is however characterized by the predominance of rounded cusps and high relief (Table 1), which suggests more abrasives in diet and a feeding behaviour similar to that of the mixed feeder *Boselaphus tragocamelus*. In contrast, *G. torticornis* exhibits a mesowear mostly comprised of sharp cusps and high relief (Table 1), and essentially suggests less abrasives in its diet and a browser feeding behaviour. Finally, *E. stenonis* is the only species with teeth showing presence of blunt cusps, and very high percentages of low occlusal relief (Table 1), which is indicative of highly abrasive diets, similar to those exhibited today by extant grazers such as *Equus quagga* or *E. grevyi*.

When the rate of cusp shape and the HI is compared, the three species of cervids and the spiral horned antelope *G. torticornis* fall into the browser group (Fig. 2A–C). The leptobovine *Leptobos* sp. and the small gazelle *G. borbonica* belong instead to the mixed feeder group (Fig. 2D–F). The equid *E. stenonis* fits into the grazer group (Fig. 2G–I).

According to the bivariate plot of HI and the mesowear score of both extant taxa and CSG ungulates species (Fig. 3) the deer *A.* cf. *lyra*, *E.* cf. *E. tegulensis*, and *C.* cf. *ramosus*, and the bovid *G. torticornis* fall again into the leaf-browser domain. On the other hand, *Leptobos* sp. and *G. borbonica* fall clearly into the mixed feeder group, and *E. stenonis* is the only species plotted among the modern grazers. When compared with European ungulates from other contemporaneous fossil sites, both "M." *rhenanus* and *C. ramosus* from Saint-Vallier (France) fall into the leaf-browser group. It is worth mentioning that the latter plots particularly close to *A.* cf. *lyra*, *E.* cf. *E. tegulensis*, and *C.* cf. *ramosus* from CSG. *E. stenonis* and cf. *C. ramosus* from Sésklo (Greece) fall into the grazer and leaf-browser domain, respectively, as occur in CSG. The emplacement of *G. torticornis* differs instead from that of its Italian relative, since the Greek species is placed into the mixed feeder group instead into the browser, as observed for the species from CSG. This fact seems to suggest a certain degree of variability in the diet of this fossil bovid.

The bivariate diagrams (Fig. 4) confirm that the investigated variables provide a satisfactory dietary discrimination, in particular
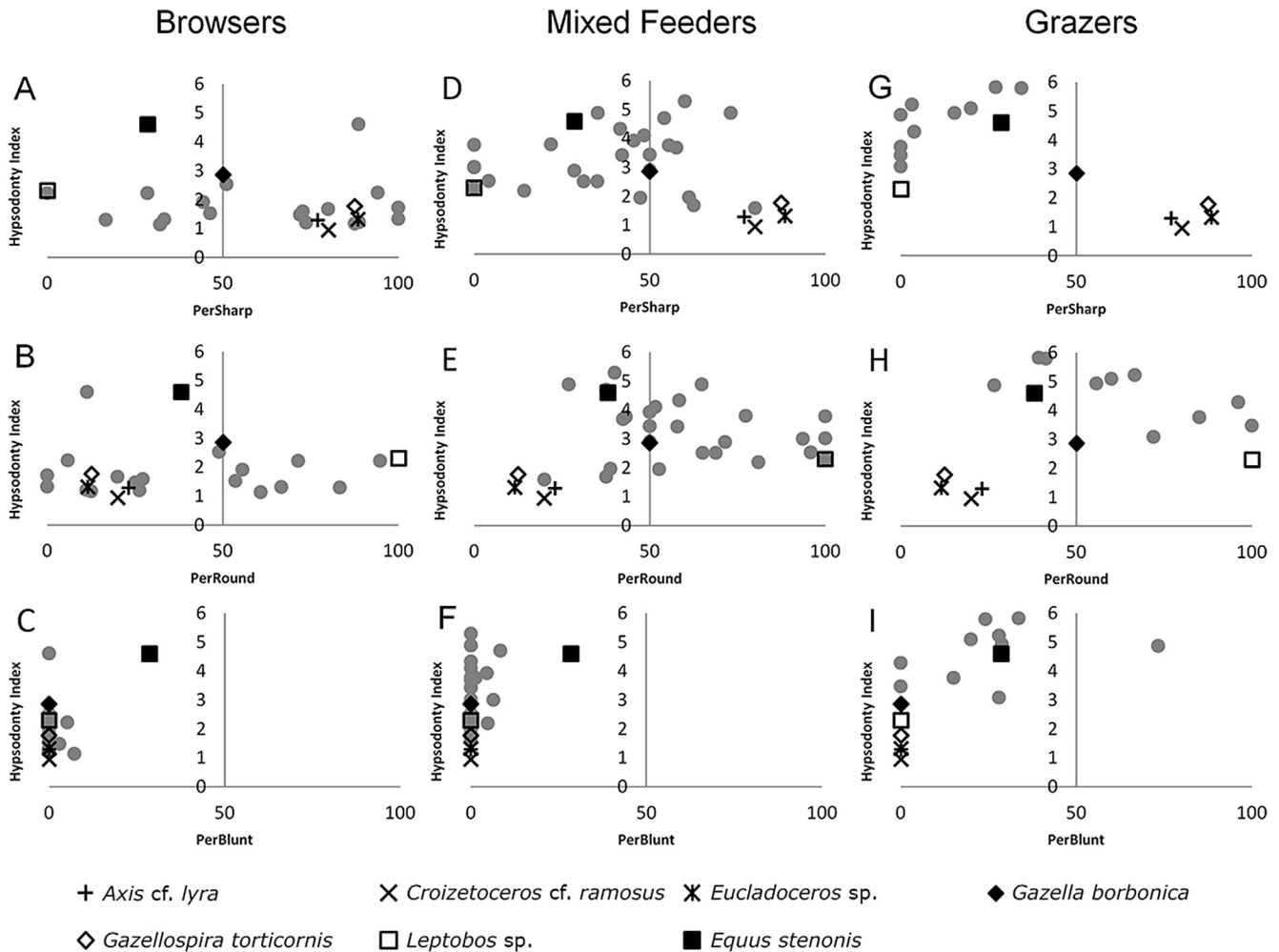
Table 1

Summary of hypsodonty and dental mesowear results. Number of specimens measured (N); hypsodonty index calculated as in Janis (1988) (HI); number of specimens with high (#High) and (#Low) occlusal relief; percentage of specimens with high (PerHigh) and low (PerLow) occlusal relief; number of specimens with sharp (#Sharp), rounded (#Rounded) and blunt (#Blunt) cusps; percentage of specimens with sharp (PerSharp), rounded (PerRounded) and blunt (PerBlunt); and mesowear score calculated as in Rivals and Semprebon (2006) (MWS).

Species	Hypsodonty		Dental mesowear											
	N	HI	N	#High	#Low	PerHigh	PerLow	#Sharp	#Rounded	#Blunt	PerSharp	PerRound	PerBlunt	MWS
Axis cf. *lyra*	8	1.3	26	26	0	100	0.0	20	6	0	76.9	23.1	0.0	0.19
Croizetoceros cf. *ramosus*	1	1.0	5	5	0	100	0	4	1	0	80.0	20.0	0.0	0.20
Eucladoceros sp.	5	1.3	26	26	0	100	0.0	23	3	0	88.5	11.5	0.0	0.12
Gazella borbonica	3	2.9	8	7	1	87.5	12.5	4	4	0	50.0	50.0	0.0	0.63
Gazellospira torticornis	2	1.8	8	8	0	100	0.0	7	1	0	87.5	12.5	0.0	0.13
Gallogoral meneghinii	–	–	2	2	0	100	0.0	1	1	0	50.0	50.0	0.0	0.50
Leptobos sp.	1	2.3	2	2	0	100	0.0	0	2	0	0.0	100	0.0	1.0
Equus stenonis	1	4.6	21	1	20	4.8	95.2	6	8	7	28.6	38.1	33.3	2.33

Fig. 2. Percentage of cusps shape (x-axis) plotted against hypsodonty index in extant and fossil taxa. Different symbols are employed to distinguish fossil species. Grey filled circles representing extant taxa (data taken from Fortelius and Solounias, 2000).

that 80.0% of extant taxa (75.6% cross-validation) are correctly classified according to the conservative classification (Figs. 4A) and 75.6% (75.6% cross-validation) according to the radical one (Fig. 4B). Results show a wide spectrum of dietary assignments among the taxa, thus corroborating a significant heterogeneity in the environments of CSG and in the relative abrasive nature of the diets, with all the cervids (*A.* cf. *lyra*, *C.* cf. *ramosus* and *Eucladoceros* sp.) being classified as browsers, the bovids (*G. borbonica*, *G. meneghinii* and *Leptobos* sp.) as mixed feeders (except *G. torticornis* which is classified as a browser), and *E. stenonis* exhibiting grazing habits. The same assignments were obtained using the radical classification, with the exception of *Leptobos* sp. that now bears more resemblance to a grazer, thereby suggesting a strong leaning towards grazing for the bovid, probably as a grass-dominated mixed feeder. With regard to the species from Saint-Vallier, "*M.*" *rhenanus* and *C. ramosus* are classified as browsers according to both the conservative and radical classifications, hereby corroborating similarity with their relative cervids from CSG.

4. Discussion

Results here obtained from both dental mesowear and hypsodonty analyses allow us to significantly improve our knowledge on the palaeoecology and environmental setting of CSG, which is of outmost relevance since previous reconstructions of the site were only based

on its faunal composition (Bellucci et al., 2012, 2014). Overall, the results suggest the occurrence of a highly heterogeneous paleoenvironment, and points to a mosaic of biomes, with presence of both open and woodland forested areas around the site, potentially offering both ligneous (bushes, leaves, fruits, etc.) and graminoid (grass) food resources and accommodating a plethora of feeding styles. Our results are in strong accordance with the palaeoenvironmental reconstruction recently proposed by Bellucci et al. (2014).

The three species of cervids (*A.* cf. *lyra*, *C.* cf. *ramosus* and *Eucladoceros* sp.) show a clear browsing feeding behaviour, and could have partitioned the available vegetation through body size differences (in terms of height above ground level) and use of different habitats. In this regard, *C.* cf. *ramosus* was a medium/small-sized deer similar to the extant fallow deer *Dama dama*. As this extant species, it could feed on leaves and buds in both open and forested areas (Rivals and Athanassiou, 2008). The medium/small sized *A.* cf. *lyra* shows postcranial bones (metacarpal III–IV) with adaptations similar to typical extant deer living in humid habitats, such as the Eurasian elk *Alces alces* and the barasingha *Rucervus duvaucelii* (Alcalde, 2013). *Eucladoceros* sp. is a large cervid (Kaiser and Croitor, 2004; Valli and Palombo, 2008; Baygusheva and Titov, 2013) and the largest species of those recorded in the CSG mammal assemblage. Given that its mesowear is similar to that found in *O. virginianus*, it could feed mostly on shrubs in the wooded areas of CSG (Ramirez et al., 1996).
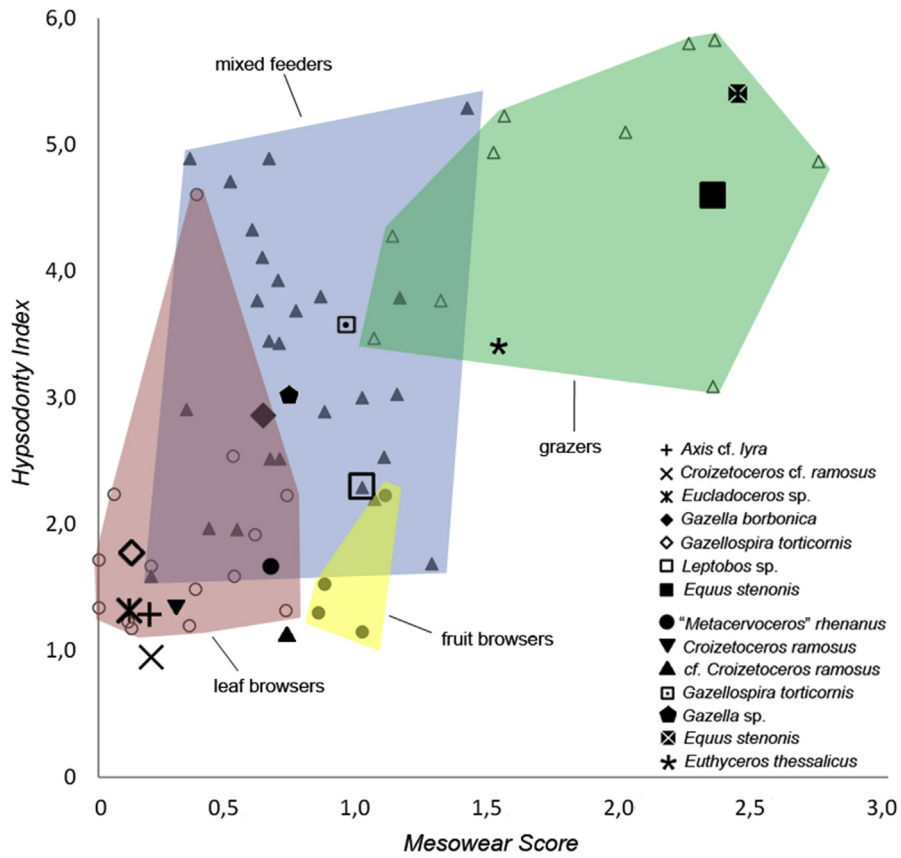
Fig. 3. Bivariate plot of mesowear score against hypsodonty index. Mesowear scores on extant species obtained from Fortelius and Solounias (2000). Data of species from the sites of Saint Vallier and Sésklo taken, respectively, from Valli and Palombo (2008) and Rivals and Athanassiou (2008).
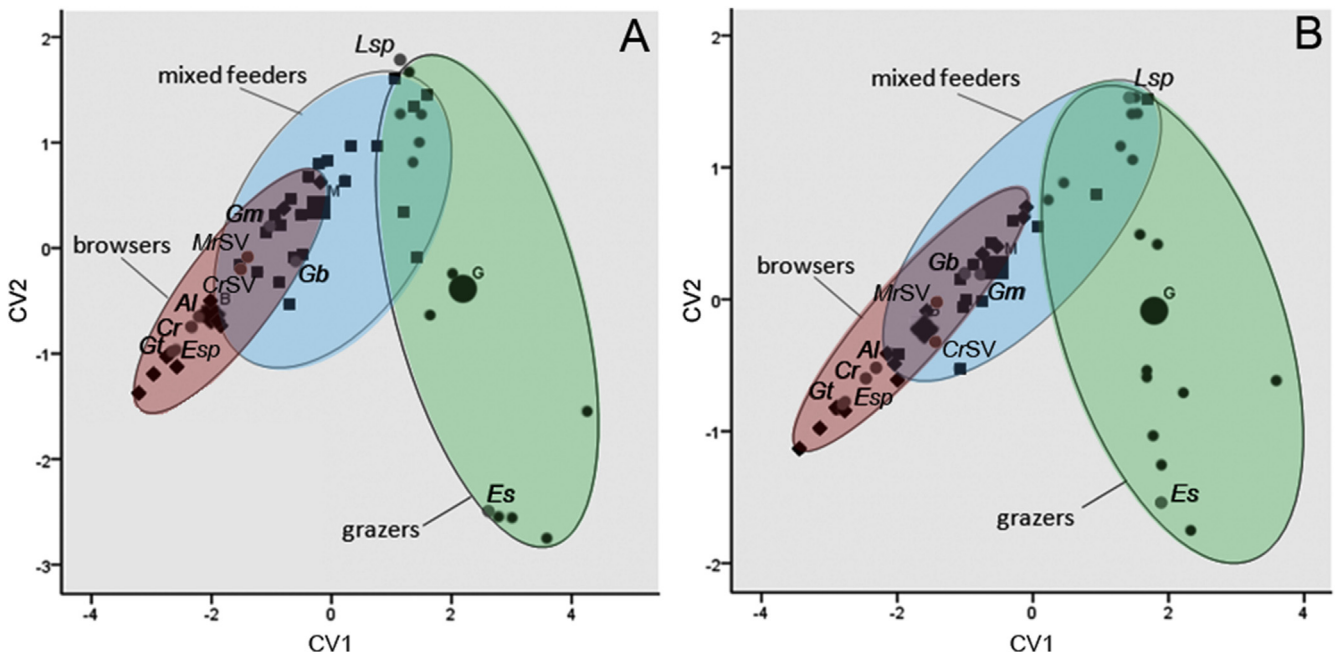

Fig. 4. Bivariate diagrams based on discriminant analysis. Ellipses denote the morphospace defined by each extant group, black symbols extant taxa (group centroids by larger black symbols). Symbols' shapes represent browser taxa (diamonds), mixed feeder taxa (triangles) and grazer taxa (circles). Fossil taxa abbreviations: Al, Axis cf. lyra; Cr, Croizetoceros ramosus; Esp, Eucladoceros sp.; Gb, Gazella borbonica; Gt, Gazellospira torticornis; Gm, Gallogoral meneghini; Lsp, Leptobos sp.; Es, Equus stenonis; MrSV, "Metacervoceros" rhenanus from Saint Vallier; and CrSV, Croizetoceros ramosus from Saint Vallier. Extant data from Fortelius and Solounias (2000). Extinct data of species from Saint Vallier from Valli and Palombo (2008).

The presence of pure grazing signatures (as that obtained for the equid *E. stenonis*), as well as the existence of species that grazed periodically or occasionally, indicates a consume of abrasive items (such as grasses and exogenous dust and grit) in CSG, hereby corroborating the presence of grass/dusty-dominated open environments inhabited also by *E. stenonis* and mixed feeders such as *Leptobos* sp. and *G. borbonica*. In contrast, *G. meneghinii* seems to have exhibited mixed diets in rocky and steep areas, probably in the mountains surrounding the Anagni basin, as indicated by its considerably variation in the proportion of rounded/sharp cusps and the morphology of the postcranial bones of the species (Alcalde, 2013). *G. torticornis* probably inhabited closed areas as suggested by its mainly browsing behaviour, though it can be also typical of more open and low covered lands (Guérin, 1965). Such a specialized feeding in CSG could have been developed to elude competition with the other species similar in size living in open environments.

There are other two European sites comparable in both age and faunal composition to CSG that serve as reference localities, for which dental wear analyses have been also performed on the ungulates: the Greek site of Sésklo (Rivals and Athanassiou, 2008) and the French site of Saint-Vallier (Valli and Palombo, 2008). Sésklo is dated in the MN17 biozone and has a faunal composition with the predominance of grazer species and grass-dominated mixed feeders such as the equid *E. stenonis* and the large bovid *Euthyceros thessalicus*. This indicates more open grasslands and drier conditions than those inferred for CSG. The cervid *Croizetoceros ramosus* occurs in Sésklo with a browsing feeding behaviour similar to that exhibited in CSG. *Gazellospira torticornis* is considered to be a mixed feeder whereas the specimens from CSG are more consistent with a browsing habit. A possible explanation to this discrepancy is the different climatic conditions of the Italian and Greek peninsulas during the Early Pleistocene, as this latter was characterized by more arid and savannah-like environments (Rivals and Athanassiou, 2008; Kahlke et al., 2011). Thus, such a difference in the diet may indicate that *G. torticornis* was a generalist species, exhibiting a more specialized dietary behaviour or a more flexible diet depending on the specific environmental conditions and resources partitioning.

The ungulate composition of the Middle Villafranchian site of Saint-Vallier (MN17 biozone) is similar to that of CSG, with the presence of the cervids *Eucladoceros*, *Croizetoceros* and *Axis*, the leptobovine *Leptobos*, the bovids *Gallogoral*, *Gazella* and *Gazellospira* and the equid *E. stenonis* (Guérin et al., 2004). Their dental wear analyses (Valli and Palombo, 2008) indicate that *A. lyra* and *C. ramosus* had a mainly browsing behaviour but with a significant feeding flexibility, probably to reduce the overlap of their ecological niches. This suggests a certain development of wooded areas and tree vegetation in Saint-Vallier (as indicated also by the presence of *Macaca*).

These facts indicate that the paleoenvironments of Central Italy during the Early Pleistocene were characterized by more wooded areas and more humid climatic conditions than those of similarly-aged Eastern Mediterranean localities (as Sésklo in Greece), while show larger similarities in climate with localities from the fossil record of France (as Saint-Vallier). This would entail that the replacement of forests by grasslands, and the substitution of browser and mixed feeder species by open habitat grazers, was a gradual process. Moreover, our study confirms the hypothesis that Europe was strongly affected by climatic deterioration during the Early Pleistocene. In Eastern and South-Eastern Europe cooling and aridification started earlier than in Central, Western and Southern Europe (Kahlke et al., 2011). This hypothesis is also supported by palynological data (Bertini, 2003, 2010; Kahlke et al., 2011). In the Northern Italian Peninsula, colder phases during the Early Pleistocene were characterized by moist conditions that favoured high-altitude vegetation dominated by the genus *Picea*; the Central and Southern Italian Peninsula was instead characterized by the diffusion of steppe-like open vegetation dominated by the genus *Artemisia* in response to a long and warmer interval. Subtropical forests were replaced by warm-temperate vegetation dominated by deciduous tree taxa like *Quercus*, *Carya*, *Ulmus*, *Carpinus*, and the now relict taxon *Zelkova* (Bertini, 2003, 2010; Kahlke et al., 2011).

In the Italian Peninsula, the climatic and ecological shift towards dryer conditions favoured the expansion of grasslands and the dispersal of new herbivore taxa with grazing feeding behaviours (as *E. stenonis* and *Mammuthus meridionalis*; Kahlke et al., 2011) and pack-hunting carnivores belonging to the genus *Canis*.

Importantly, our new data from CSG provide a clear evidence on the changes in the ecosystems in the Mediterranean Europe around 2 Ma. In particular, a mosaic of biomes seems to have been the necessary precondition for the first hominin dispersal from Africa to Eurasia. The climatic deterioration that occurred during the Early Pleistocene resulted in the fragmentation of habitats, with more arid, open environmental ecosystems that favoured the dispersal of hominin groups into South Western Europe, as testified by the discoveries in Spain (Carbonell et al., 2008; Toro-Moyano et al., 2009), Southern France (Crochet et al., 2009) and Italy (Arzarello et al., 2007). This environmental heterogeneity and broad spectrum of resources probably fostered the settlement of early species of *Homo*, thereby reducing and/or avoiding the competition with more specialized species (Palombo, 2014). Moreover, the recent finding of an isolated tooth of *Hippopotamus* sp. in CSG (Bellucci et al., 2012, 2014) represents the First Occurrence of this taxon in Europe, and provides therefore additional evidence that the dispersal of this African newcomer occurred earlier than previously expected, so pre-dating the dispersal of other African taxa during the Early Pleistocene. Accordingly, early *Homo* could be also part of this dispersal. Here we therefore shed new light on the palaeoclimatic and palaeoenvironmental conditions that characterized the hominin disperal around 2 Ma in the Italian Peninsula.

5. Conclusions

The hypsodonty and mesowear analyses performed on the ungulate community recovered in the site of Coste San Giacomo, allow us to provide for the first time information about their feeding behaviours, and significantly expand our knowledge on how they partitioned the different habitats of the palaeoecological setting of Coste San Giacomo. The abundance of strict browser taxa (*A.* cf. *lyra*, *C.* cf. *ramosus*, *Eucladoceros* sp. and *G. torticornis*), the presence of mixed feeder species (*G. borbonica*, *G. meneghinii* and *Leptobos* sp.), and the finding of a pure grazer equid (*E. stenonis*) strongly reflect an heterogeneous landscape. This environmental context (i.e., a mosaic environment with steppe and woodland/wetland areas) is different from that reported for other similarly-aged Eastern Mediterranean localities (as Sésklo in Greece), and seems to be more similar to that of the French fossil record (as Saint-Vallier) in this time period. Importantly, our data provide new evidence that such an environmental heterogeneity and a wide spectrum of available food resources were the main factors favouring the settlement of early species of *Homo* in Italia.

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