



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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ABSTRACT

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 meneghini*) 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

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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 stenoetid 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 strozzi*, *Hippopotamus* sp., *?Pliocrocuta perrieri*, *Ursus* cf. *etruscus*, *Canis* sp., *Vulpes* cf. *alopeoides*, *Homotherium* sp., *Macaca sylvanus*, *Miomys 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 meneghini* (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. meneghini*

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” (HI_{m3} < 1.5), “mesodont” (1.5 < HI_{m3} < 2.5) and “hypsodont” (HI_{m3} > 2.5). We calculated an average HI (Average HI) for each taxon. Due to the lack of unworn lower third molars of *G. meneghini*, 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-Odenaal 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

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