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Reconstructing diet and behaviour of Neanderthals from Central Italy through dental macrowear analysis

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Summary - *Neanderthals have been traditionally considered at the top of the food chain with a diet mostly consisting of animal proteins. New findings challenged this view and suggested that Neanderthals living in areas with more favourable climatic conditions exploited various food sources, including plant materials. In this study, the attention is focused on dental macrowear of Neanderthals from Central Italy, whose diet has been largely unexplored. Three-dimensional digital models of teeth have been examined through occlusal fingerprint analysis (OFA), a method used to understand how wear facets are formed. The results show a close similarity between the specimens of Saccopastore 1 and 2, with a wear pattern that indicates the use of diverse sources of food, but with a predominance of animal proteins. On the other hand, the specimens of Guattari 2 and 3 display a slightly different dental wear from each other, which probably reflects the chronological sequence of the Guattari Cave. It appears that at the end of the marine isotope stage (MIS) 5 the occupants of this cave consumed marginally more plant foods, while during MIS 3 they relied more on animal proteins. Finally, a close look at the Saccopastore maxillary molars reveals the presence of a distinct type of wear that has been previously described in some Neanderthals and early Homo sapiens from Near East, and it provides additional information about the culture and lifestyle of these Pleistocene human populations.*

Keywords – *Occlusal compass, Wear facets, Saccopastore, Guattari.*

Introduction

The Middle and Late Pleistocene were characterised by severe climatic fluctuations with alternating phases of glacial and interglacial periods. Such climatic instability produced dramatic environmental changes that shaped the dispersion and evolution of European hominins (Hublin, 1998, 2009; Stewart & Stringer, 2012). The emergence of glacial events determined local extinctions at higher latitudes, forcing human populations to retreat towards refugial environments in southern Europe (Dennell *et al.*, 2011; Jennings *et al.*, 2011). These areas were characterised by a high biodiversity and elevated habitat heterogeneity, which provided abundant and variable food sources. Although Neanderthals have been traditionally viewed as hunter-gatherers with a diet exclusively composed of meat, recent studies demonstrated that the populations from Mediterranean and Near Eastern regions relied on broader dietary spectrum (Stiner, 1994; Albert *et al.*, 200; Barton, 2000; Hardi, 2001, 204, 2010; Madella *et al.*, 2002; Stringer *et al.*, 2008; Henry *et al.*, 2010, 2014; El Zaatari *et al.*, 2011; Fiorenza *et al.*, 2011a; Hardy & Moncel, 2011; Salazar-Garci *et al.*, 2013).

In this context, the Italian peninsula with its peculiar geography and ecology is of great evolutionary importance and may help us to better understand the role of refugia and climate change during the last 150,000 years. Although Italy is distinguished by an abundant fossil record (with numerous Neanderthal remains), we still know very little about the subsistence strategies adopted by these extinct human populations. This study therefore aims to reconstruct the diet of Neanderthals from Central Italy by looking at their dental wear.

Neanderthals from Central Italy

In a quarry just outside Rome, a locality known as Saccopastore, two Neanderthal skulls were recovered in 1929 and 1935. The geochronology of the site and faunal remains from the same level suggested a date of about 100-130 Ka (Segre, 1983; Caloi *et al.*, 1998; Manzi *et al.*, 2001a,b; Giacobini & Manzi, 2005a; Bruner & Manzi, 2006). The two crania of Saccopastore, assigned to an adult female (Saccopastore 1) and to a young adult male (Saccopastore 2), show a combination of derived and plesiomorphic traits commonly seen in "Classic Neanderthals" and in *Homo heidelbergensis*. In this context, their "intermediate" phenotype is consistent with their chronology and perfectly fits the four steps of the "accretion model" (Hublin, 1998, 2009).

Grotta Guattari is a prehistoric cave site located along the Tyrrhenian side of the promontory of Monte Circeo, just 100 km south of Rome, where the remains of three Neanderthal adult males were recovered (Sergi, 1954; Sergi & Ascenzi, 1955; Giacobini & Manzi, 2005b). A well-preserved cranium (Guattari 1) and an incomplete mandible (Guattari 2) were recovered from the cave surface in 1939, while another incomplete mandible (Guattari 3) was excavated from a breccia near the cave entrance in 1950. U-series and ESR dating of the stratigraphic layer that includes the remains of Guattari 1 and 2 give an age estimate of 50-60 Ka while Guattari 3 is placed at the end of MIS 5, between 60 and 74 ka (Grün & Stringer, 1991; Schwarcz *et al.*, 1991). The fossil humans from Guattari's Cave exhibit all the distinctive traits of the "classic" morphotype and for this reason are considered to represent Würmian Neanderthals (Sergi, 1948, 1962; Howell, 1957).

Occlusal fingerprint analysis

Information about diet of the Neanderthals of Saccopastore and Guattari is scant. The analysis of the faunal remains from the stratigraphic layers of Guattari's Cave suggests episodes of scavenging (Khun, 1991; Stiner, 1991a,b; Stiner & Khun, 1992; Marean & Assefa, 1999) while the study of occlusal microwear texture indicates a flexible diet and consumption of hard items in Saccopastore, and a diet mostly consisting of meat in Guattari 3 (El Zaatari *et al.*, 2011).

Here, the occlusal fingerprint analysis (OFA) method, which describes the major occlusal movements in a three-dimensional (3D) space (Kullmer *et al.*, 2009), is used to analyse the wear patterns in the specimens of Saccopastore and Guattari. The method focuses on the analysis of macroscopic wear facets (flat and shiny areas with well-defined borders) that are produced during occlusion by the contact between upper and lower teeth. The OFA method provides information about development, spatial position and enlargement of wear facets (Kullmer *et al.*, 2009). Because there is a close relationship between jaw movements and occlusal wear, it is possible to understand how wear facets are created and what occlusal movements are responsible for their formation. These occlusal movements are closely related to the masticatory processes occurring during the chewing cycle, which in turn depend on the physical properties of the food eaten (Kay & Hiiemae, 1974). Thus, the information decoded with the OFA method can be used to reconstruct the diet in fossil and extant species (Ulhaas *et al.*, 2007; Kullmer *et al.*, 2009; Fiorenza *et al.*, 2011a; Harvati *et al.*, 2013). In addition, the OFA method is used here to examine an unusual type of wear initially observed in Saccopastore maxillary molars (named para-facets), which may be related to the use of teeth as tools (Fiorenza *et al.*, 2011b; Fiorenza & Kullmer, 2013).

Materials and Methods

For the OFA analysis we used high-quality dental casts that have been digitised through a 3D-scanning system with a resolution of 55 μ (smartSCAN3D C-5, Breuckmann GmbH)

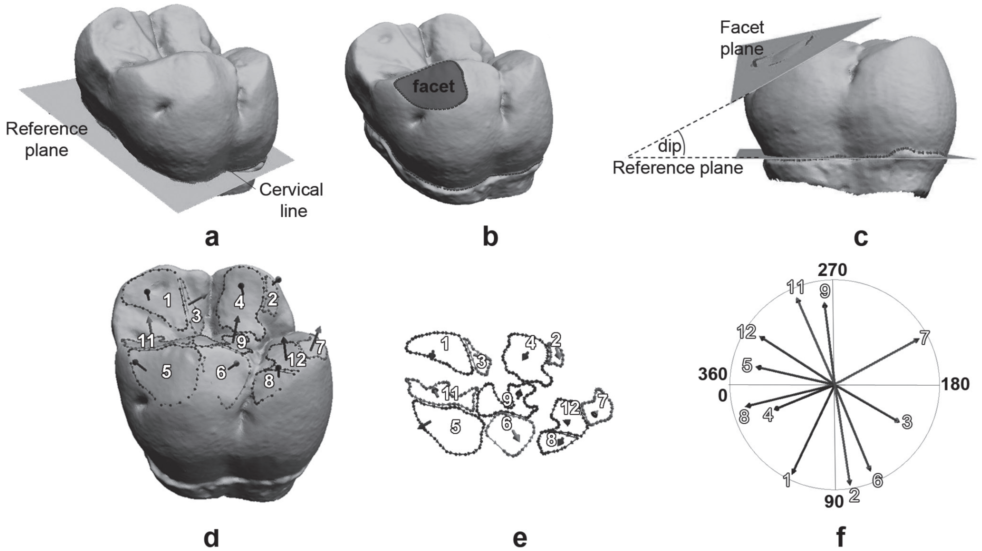

Fig. 1 - Occlusal Fingerprint Analysis method: orientation (a), wear facets identification and area (b), facet plane (c), direction (d and e), and occlusal compass (f) (From Fiorenza & Kullmer, 2013).

(Fiorenza *et al.*, 2009). The examination of polygonal 3D models of teeth is based on four major steps and was performed using PolyWorks® v.12 (InnovMetric Software) (Fig. 1):

1) Orientation: each polygonal model was oriented by created a reference plane along its cervical line (Fig. 1a).
2) Wear facet identification and area: wear facets were manually outlined onto the 3D surface model and labeled following the terminology of Maier & Schneck (1981) (Fig. 1b). For the dietary reconstruction, occlusal wear facets were grouped by chewing cycle phases: buccal phase I facets (facets 1, 2, 3 and 4), lingual phase I facets (facets 5, 6, 7 and 8), and phase II facets (9, 10, 11, 12, 13 and tip crush) (Fig. 2). The wear facets ratio divided into chewing cycle phases closely corresponds to specific masticatory processes that are necessary to reduce the food bolus to small pieces before swallowing (e.g. Kay & Hiiemae, 1974). For instance, if a diet mostly consists of tough and fibrous foodstuffs such as raw meat, we would expect a wear pattern dominated by buccal phase I facets (Van Valkenburgh, 1989; Janis, 1990; Fiorenza *et al.*, 2011a). On the contrary, a diet rich in hard and abrasive food objects will likely result in large lingual phase I facets. The area of each facet (in mm²) was automatically calculated by selecting all the triangles within the facets perimeter. Thus, the proportion of crushing and shearing wear can be used to reconstruct the diet of extant and fossil species.
3) Direction: the facet plane was created through the least square best-fit method by selecting all the digital triangles included within the facet perimeter (Fig. 1c). Thus it was possible to measure the dip direction (the angle between the projected and the reference vectors). The dip directions were calculated by projecting the perpendicular vectors to the facet area (Fig. 1d) to the reference plane (Fig. 1e).

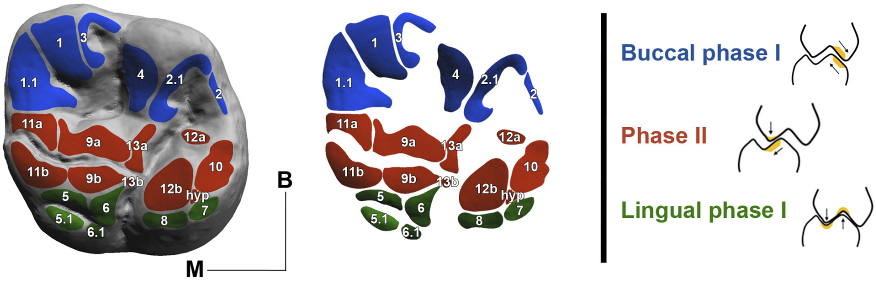

Fig. 2 - Digital 3D model, wear facets, and masticatory processes occuring during the chewing phases (maxillary first molar). Wear facets have been labelled following the numbering system created by Maier & Schneck (1981) and grouped by chewing cycle phases (Kay & Hiiemae, 1974; Janis, 1990): lingual phase I facets (green), phase II facets (red) and buccal phase I facets (blue). Orientation: mesial (M) and buccal (B). The colour version of this figure is available at the JASs website.

4) Occlusal compass: the facet vectors (that were afterwards projected onto the facet planes) were translated to an arbitrary point with a standardized length (10 mm) (Fig. 1f).

Because advanced degree of wear precludes the identification and analysis of occlusal wear facets, the sample analysed in this study was limited to teeth with a slight and moderate wear (wear stages 2-5; Smith, 1984) (Table 1). Both Saccopastore specimens show a moderate to discrete degree of tooth wear, with a more pronounced dentine exposure in the first molars (wear stage 5). The only tooth remaining in the mandible of Guattari 2 is the right M_3, which is moderately worn (Sergi, 1954; Giacobini & Manzi, 2005b). In contrast, the dentition of Guattari 3 mandible is better preserved, showing most of the teeth and both molar series with a significantly lower level of wear (Sergi & Ascenzi, 1955). Finally, the dentition of Guattari 1 was not considered in this study because the dentition is poorly preserved. For each individual, only one molar was chosen (*n* = 4).

The OFA results for Saccopastore and Guattari specimens have been compared with data published in Fiorenza *et al.* (2011a), where Neanderthals and Anatomically Modern Human (AMH) samples were grouped together into three eco-geographical contexts based on paleoenvironmental data: steppe/coniferous forest (SCF, *n* = 9), deciduous woodland (DEW, *n* = 12), and Mediterranean evergreen (MED, *n* = 10). From a broad ecological point of view, both steppe and coniferous forests can be considered equivalent since plant foods are very scarce (Fiorenza *et al.*, 2011a). Yet, dental macrowear studies are unable to distinguish between marine and terrestrial animal foods, or between small and large mammals. Because the human fossil record is extremely fragmentary, we preferred considering these two small Neanderthal sub-sample as a single group. The SCF group includes the Neanderthal specimens of Monsempron 2 and 3 (France), Vindija V259 (Croatia) and Le Moustier 1 (France), and the AMH specimens of Mladeč 2 (Czech Republic), Barma Grande 3 and 4 (Italy), Sungir 2 (Russia) and Pataud 224 (France). The DEW sample consists only of Neanderthal specimens from the Krapina site (Croatia). Finally, the MED group includes the Neanderthal specimens of Tabun 1 and Amud 1 (Israel) and Shanidar 2 (Iraq), and the AMH specimens from Qafzeh (Israel).

For the analysis of the non-masticatory tooth wear, only maxillary molars of Saccopastore specimens characterised by the presence of parafacets (n = 5) were used. In order to understand what occlusal movements are responsible for the creation of this unique type of wear, dental occlusal compasses were generated (Kullmer *et al.*, 2009). Because normal masticatory movements are easily identifiable and depicted by specific angle ranges (Douglass & DeVreugd, 1997),

Tab. 1 - List of Neanderthal specimens and teeth analysed in this study, and type of information provided. Dental wear was assessed by using the amount of dentin exposure and cusp removal (Smith, 1984).

SPECIMENS	N MOLARS	TOOTH TYPE	WEAR	PRESERVATION	PARA-FACETS	TYPE OF INFORMATION
Saccopastore 1	5	upper LM1	5	good	no	
		upper LM2	4	good	yes	Culture
		upper LM3	3	good	yes	Culture
		upper RM2	4	good	no	Diet
		upper RM3	3	good	no	
Saccopastore 2	6	upper LM1	5	good	yes	Culture
		upper LM2	3	good	no	
		upper LM3	3	good	no	
		upper RM1	5	good	yes	Culture
		upper RM2	3	good	yes	Diet and Culture
		upper RM3	3	good	no	
Guattari 2	1	lower RM3	4	good		Diet
Guattari 3	6	lower LM1	3	good		
		lower LM2	3	poor		
		lower LM3	2	poor		
		lower RM1	5	acceptable		
		lower RM2	3	good		Diet
		lower RM3	3	good		

it is possible to distinguish between masticatory and non-masticatory facets. These mandibular movements, and the corresponding occlusal contacts, can be summarised into four distinct groups: lateroretrusion (LRT; facets 1, 1.1, 4, 5, 5.1 and 8), lateroprotrusion (LPT; facets 2, 2.1, 3, 6, 6.1 and 7), mediotrusion and immediate sideshift (MT/ISS; facets 9, 11 and 12), and medioprotrusion (MPT; facets 10 and 13). In addition, flat worn areas can be also recognized on the apex of dental cusps, and they are known as tip crushing (Gordon, 1984; Janis, 1990). On the other hand, para-facets do not show a preferred direction or exhibit opposite directions to LRT and LPT vectors, the sole occlusal masticatory movements responsible for the creation of wear facets on the buccal side of upper teeth (Fiorenza *et al.*, 2011c; Fiorenza & Kullmer, 2013). Information about the OFA method and occlusal compass is explained in detail elsewhere (Kullmer *et al.*, 2009, 2012, 2013; Fiorenza *et al.*, 2010, 2011a,b; Fiorenza & Kullmer, 2013).

Statistical analysis

As Saccopastore and Guattari samples size is rather small, a descriptive statistical analysis

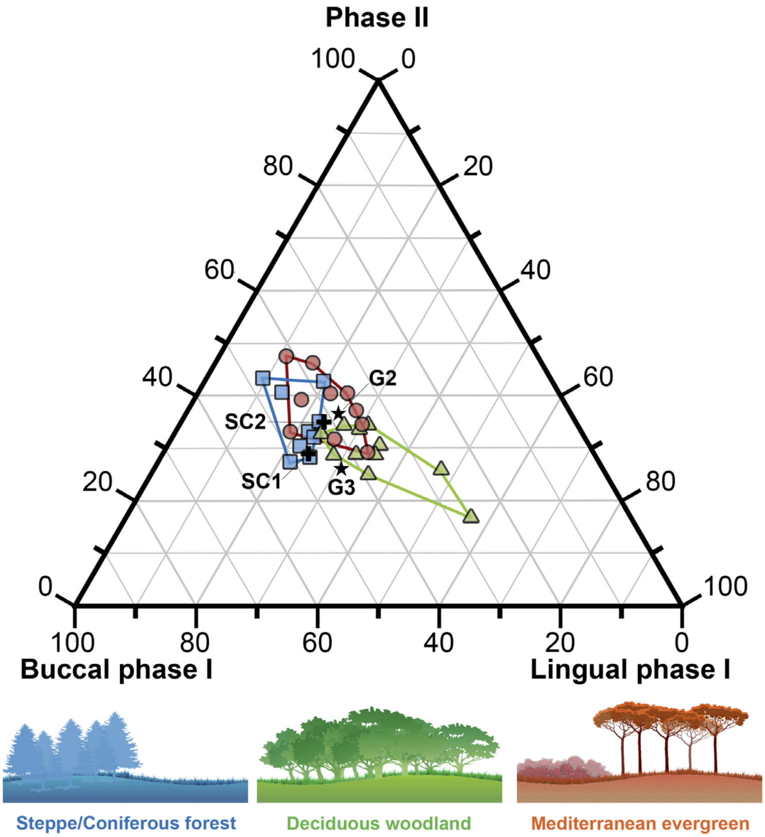

Fig. 3 - Ternary diagram showing the proportions (in %) of relative wear areas of buccal phase I facets, lingual phase I facets, and phase II facets, which are positioned in an equilateral triangle. Each base of the triangle represents a ratio of 0% while the vertices correspond to a percentage of 100%. Saccopastore specimens (here labeled as SCP1 and SCP2) are symbolically represented with "plus", while Guattari (G2 and G3) with a "star". Their wear patterns have been compared with published data (Fiorenza* et al.*, 2011a) where Neanderthals and Anatomically Modern Humans were grouped into three distinct eco-geographical contexts: steppe/coniferous forest (SCF, blue squares), deciduous woodland (DEW, green triangles), and Mediterranean evergreen (MED, red circles). The colour version of this figure is available at the JASs website.

was preferred over inferential statistical methods. The proportions of buccal, lingual, and phase II facets (relative values obtained dividing each facet area by the total occlusal wear area) have been described by using mean relative areas and the ternary diagram, a triangular coordinate system that graphically depicts the ratios of three variables that must sum to 100% (Hammer & Harper, 2006).

Occlusal compass movements are enclosed in a circular space of 360°, and therefore standard statistical methods are not directly applicable to the analysis of directional data (see also Fiorenza *et al.*, 2011c; Fiorenza & Kullmer, 2013). Basic statistic parameters have been calculated using the mean vector concept, such as the mean angle, the 95% confidence interval, and the circular standard deviation. In addition, in order

Tab. 2 - Descriptive statistics of relative wear facet areas (in %) within the fossil biome groups and Saccopastore and Guattari individuals. Data for the three eco-geographical groups (steppe/coniferous forest, deciduous woodland and Mediterranean evergreen) is published in Fiorenza* et al. *(2011a).

		BUCCAL PHASE I		LINGUAL PHASE I		PHASE II	
GROUPS/SPECIMENS*	N	MEAN	SD	MEAN	SD	MEAN	SD
SCF	9	45,1	4,0	19,9	5,3	30,9	5,6
DEW	12	36,5	5,2	34,5	9,1	27,8	5,3
MED	10	39,3	4,2	23,0	7,1	36,7	6,1
Saccopastore 1	1	47,4		24,1		28,5	
Saccopastore 2	1	40,5		24,4		35,0	
Guattari 2	1	38,7		24,9		36,4	
Guattari 3	1	43,3		30,5		26,2	

*Groups: Steppe/Coniferous forest (SCF), Deciduous Woodland (DEW) and Mediterranean Evergreen (MED).

to assess the departure of the distribution from a perfect circle, the maximum likelihood estimate of the concentration parameter (k) was taken into account (Batschelet, 1981; Fisher, 1993; Mardia & Jupp, 2000). Finally, to ascertain if facet's directions exhibit a preferred direction or follow a random distribution, Rayleigh's test and the Rao's Spacing test were used. Parafacet directions and major occlusal movements have been schematically represented with rose diagrams, which are circular histograms divided into sectors to display the frequency and orientation of directional data (Hammer & Harper, 2006). Software PAST v.2.17c (PAlaeontological STatistics) (Hammer *et al.*, 2001) was used for the creation of the ternary diagram while statistical analysis and rose diagrams were generated by using a circular statistic software program (Oriana™ v. 4.00, Kovach Computing Services).

Results

Saccopastore 1 and 2 plot close to each other, roughly in between the three main eco-geographic groups but slightly closer to the SCF sample (Fig. 3). Both individuals are characterised by large buccal phase I facets (more developed in Saccopastore 1), and less pronounced lingual phase I facets (Tab. 2). Phase II facets display intermediate values. On the other hand, the Guattari specimens exhibit slightly different wear patterns between each other, with Guattari 2 characterised by more developed phase II facets but less pronounced buccal and lingual phase I facets than Guattari 3. Thus, while Guattari 2 falls within the MED group, Guattari 3 clusters near the DEW sample.

The statistical analysis of the circular data of Saccopastore maxillary molars confirms that the LRT and LPT directions (large κ values) fall within a von Mises distribution (the equivalent of the normal distribution for linear data) (Tab. 3). The LRT and LPT vectors display preferred directions, as definite by the significant p values obtained through the Rayleigh's test and Rao's spacing test (<0.05). In contrast, MT/ISS and MPT directions are characterised by a high level of anisotropy, as demonstrated by the large circular standard deviation, small concentration parameters, and not significant Rayleigh's and Rao's p values. Finally, the para-facets' vectors show a preferred direction, which is opposite to the LRT and LPT vectors and that can be graphically seen on the rose diagrams (Fig. 4).

Tab. 3 - Basic circular statistic parameters measured for the major occlusal and para-facet directions in Saccopastore maxillary molars. Significant p values (<0.05) are highlighted in bold.

FACETS	MEAN	SD	K	95%	RAYLEIGH (*P*)	RAO (*P*)
LRT	67,0	7,5	28,6	(57.5, 76.4)	**0,001**	**<0.01**
LPT	103,3	16,3	6,3	(83.0, 123.7)	**0,003**	**<0.01**
MT/ISS	321,3	76,2	0,5	***	0,45	>0.10
MPT	129,9	94,5	0,0	***	0,739	>0.95
P	248,5	31,3	1,9	***	**0,015**	**<0.05**

[1]Facets: Lateroretrusion (LRT), Lateroprotrusion (LPT), Mediotrusion and immediate sideshift (MT/ISS), Medioprotrusion (MPT) and Para-facets (P).

Discussion

The information encoded in the occlusal wear, both on the micro- and macroscopical level, has been widely used to understand the relationships between mastication and food physical properties in human and non-human primates, and for the reconstruction of extinct species' diets (e.g. Kay & Hiiemae, 1974; Janis, 1990; Teaford & Ungar, 2000; Scott *et al.*, 2005; Ungar & Sponheimer, 2011). In particular, the OFA method revealed to be a valuable digital tool for explaining the mechanisms behind wear facets formation (e.g. Ulhaas *et al.*, 2007; Kullmer *et al.*, 2009). Unlike microwear, dental macrowear is a cumulative process that occurs throughout the individual's lifetime and thus reflects long-term diet. The interpretation of the OFA results related to diet and cultural habits of Neanderthals from Saccopastore and Guattari's Cave will be discussed separately.

Diet

Overall, the wear patterns analysed in this study show a general tendency towards a mixed diet, which includes both animal and plant materials. The two Saccopastore specimens exhibit comparable wear patterns, indicating most likely the exploitation of similar food sources. This is in agreement with the analysis of occlusal molar microwear, where both Saccopastore 1 and 2 were characterised by a similar microwear texture (El Zaatari *et al.*, 2011). According to the geochronology data, the two Neanderthals from Saccopastore should be both placed in the last interglacial period, MIS 5e (Segre, 1983). However, the analysis of the faunal assemblage from the same stratigraphic level suggests a younger age, probably around 100,000 years ago, which corresponds to MIS 5c (Caloi *et al.*, 1998; Manzi, 2001b; Bruner & Manzi, 2006). The palinological data of the MIS 5 from the Central Italy indicates the presence of landscapes dominated by steppe and grassland during cold phases (MIS 5d and MIS 5b) and forested environments of deciduous and Mediterranean trees during the warmer sub-stages (MIS 5c and MIS 5a) (Follieri *et al.*, 1998). While microwear signatures place the Saccopastore specimens together with Neanderthals from wooded environments (and therefore with climates from warmer sub-stages) (El Zaatari *et al.*, 2011), the macrowear features found here fit better with the existence of colder environments. Although the wear patterns of Saccopastore cluster in the middle of the three main eco-geographic groups (thus suggesting the use of a mixed diet), the presence of large buccal phase I facets may indicate an inclination towards animal proteins (Fiorenza *et al.*, 2011a). An increase in meat consumption to the detriment of plant foods correlates better with deteriorated habitats, typical for colder chronological phases.

The "Behavioural Ecology Theory" applied to Neanderthals suggests that plant foods are

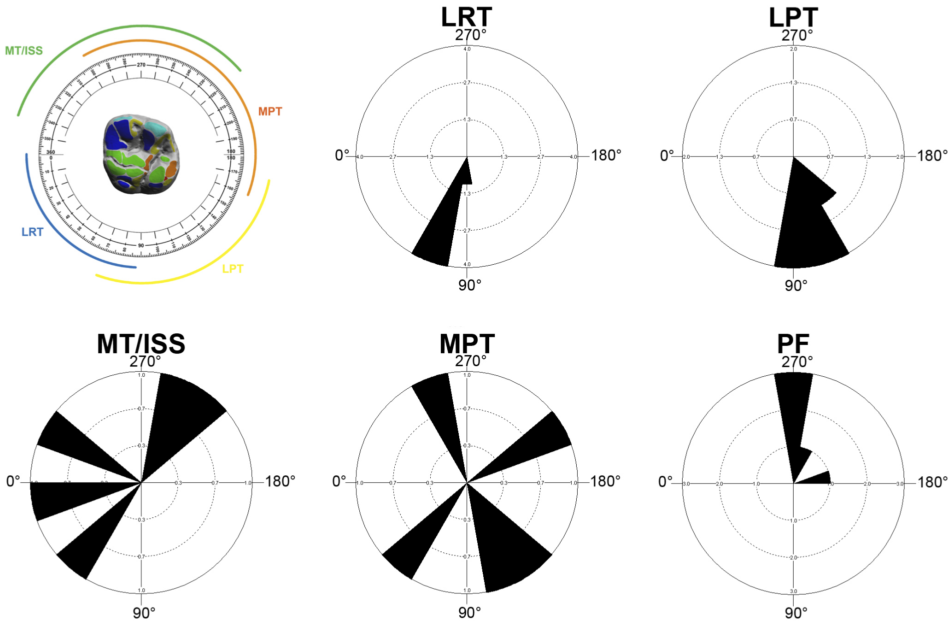

Fig. 4 - Occlusal compass (top left) and rose diagrams describing the major occlusal movements and para-facets' directions in Saccopastore maxillary molars. The major directions of possible movements starting from the maximum intercuspation are described as occlusal compass: LRT (lateroretrusion, in blue), LPT (lateroprotrusion, in yellow), MT/ISS (mediotrusion and immediate sideshift, in green) and MPT (medioprotrusion, in orange) (Douglass & DeVreugd, 1997; Kullmer* et al.*, 2009). The para-facets (P, in pale blue), located on the extreme buccal side of the occlusal crown, are not created by normal chewing movements. The rose diagrams show the frequency (divided into sectors) and orientation of wear and para-facets. The colour version of this figure is available at the JASs website.

low-ranked food sources which were mostly consumed during cold periods when preferred foods, like meat, were scarce (Kuhn & Stiner, 2006; Stiner, 2006). However, the consumption of a low-diversity diet (mainly consisting of animal proteins) in a warm environment (such as the Mediterranean evergreen), paired with the availability of a high-diversity of food source is greatly contradictory. Yet, the "Behavioural Ecology Theory" focuses only on costs and benefits of a specific diet without taking into account the importance of micronutrients. It has been demonstrated that the amount of animal proteins in humans must be limited to 35-40% of energy: exceeding this protein ceiling can be extremely dangerous and can cause "rabbit starvation", a form of food poison that in severe circumstances can bring to death (Speth & Spielmann, 1983; Cordain *et al.*, 2000; Hardy, 2010). A recent study shows that a diet exclusively focused on terrestrial animal proteins would have killed Neanderthal mothers and their babies (Hockett, 2012). Consequently, to prevent protein toxicity, Neanderthals must have implemented plant foods (rich in micronutrients) in their daily diets. The intake of alternative food sources is demonstrated by an overwhelming evidence that suggests that Neanderthals from southern and warmer latitudes had a highly diversified diet, consuming different types of food sources, such as small animals, fish and marine mammals, and a wide range of plants (Stiner, 1994; Albert *et al.*, 200; Barton, 2000; Hardi, 2001, 204, 2010; Madella *et al.*, 2002; Stringer *et al.*, 2008;

Henry *et al.*, 2010, 2014; El Zaatari *et al.*, 2011; Fiorenza *et al.*, 2011a; Hardy & Moncel, 2011; Salazar-Garci *et al.*, 2013).

Both Guattari 2 and 3 indicate the consumption of a diet composed of animal and plant foods. However, the two specimens slightly differ between each other, with Guattari 2 falling within the MED group and Guattari 3 clustering together with the DEW sample. A deciduous wooded environment would have offered a more varied food source, rich in edible vegetable materials, while Mediterranean habitats would have provided a more balanced proportion of animal and plant foods (depending on the aridity level). The analysis of the stratigraphic sequence of the Guattari's Cave places the specimens of Guattari 1 and 2 in an age range between 50 and 60 ka, and Guattari 3 to older chronological levels, bracketing between 60 and 74 ka (Grün & Stringer, 1991; Schwarcz *et al.*, 1991). Regional pollen sequences indicate an increase in open habitats dominated by grassland, tundra, and steppe formations from the beginning of MIS 4, culminating during the last glacial maximum (van Andel & Tzedakis, 1996; Follieri *et al.*, 1998). The macrowear patterns of Guattari specimens reflect this chronological sequence, with a narrowing of the food spectrum at later MIS stages, when the climatic conditions were harsher. In this scenario, one should expect a tooth wear similar to those of Neanderthals from MIS 3 (SCF group), with an extremely carnivorous diet, as seen from microwear analysis of Guattari 3 (El Zaatari *et al.*, 2011). However, when reconstructing the eco-geographical context of fossil sites other parameters, as the presence of a river or the vicinity to shoreline areas, should be taken into account as well (Hardy, 2004). For example, the area of Monte Circeo is characterised by varied habitats, from rocky terrains to coastal plains (Caloi & Palombo, 1989). In addition, the Guattari Cave was very close to the modern shoreline, and never more than 10 km from the sea (Stiner & Khun, 1992). This would have provided favourable microhabitats even in severe climatic conditions, offering various types of food sources. The discovery of faunal assemblages composed of marine and small mammals, tortoise, fish, and molluscs in Mousterian caves from Mediterranean coastlines demonstrates that alternative sources of food contributed regularly to the Neanderthal diet (Stiner, 1994; Barton, 2000; Stringer *et al.*, 2008). This is corroborated by the analysis of faunal and lithic data from Guattari and Moscerini caves, where the adoption of scavenging practices has been suggested: when plant foods were abundant, Neanderthals tended to scavenge rather than hunt while during other times, when plant food was scarce, they hunted regularly (Khun, 1991; Stiner, 1991a,b; Stiner & Khun, 1992; Marean & Assefa, 1998).

Culture

It is generally accepted that information about cultural lifestyles of past human populations can be inferred by looking at their dental wear (e.g. Molnar, 1971, 1972; Smith, 1984; Eshed *et al.*, 2006). In particular, the presence of heavily worn frontal teeth in Neanderthals, with large dentine exposures and rounded labial wear, has been interpreted as evidence for the use of the anterior dentition to process food and other materials (Molnar, 1972; Lumley, 1973; Trinkaus, 1983; Frayer & Russel, 1987; Bermudez de Castro *et al.*, 1988; Lalueza Fox & Frayer, 1997). More recently, the discovery of unusual wear patterns in upper molars of prehistoric and historic hunter-gatherer populations has demonstrated that also posterior teeth can play an important role in daily task activities (Fiorenza *et al.*, 2011c). These areas, called para-facets, develop along the lingual slopes of metacone and paracone cusps, and are characterised by regular and polished surfaces. However, in contrast to standard occlusal wear facets (which are created by the sliding contact between upper and lower dentition occurring during mastication), para-facets do not show any antimeric contact in the mandibular teeth. The analysis of their spatial position, directional angles, and inclination with the occlusal plane suggests a continuous abrasive orthal movement. This observation, together with numerous ethnographic evidences in modern hunter-gatherers, has associated the development of para-facets with non-masticatory activities such as the production of basketry, clothing, and netting (Fiorenza *et al.*, 2011c).

Similar wear patterns have been found in Neanderthals and early *Homo sapiens* from Near Eastern Middle Palaeolithic sites but not in European Neanderthals (Fiorenza & Kullmer, 2013). In this context, the two Saccopastore specimens represent an exception since they both show well-developed para-facets along their maxillary molars. Although it is not possible to verify the presence or absence of antimeric occlusal contacts in the lower teeth, the directional difference between para-facets and LRT/LPT vectors strongly indicates that this unusual type of wear was not created during a normal chewing cycle. In fact, all wear facets that develop along the buccal maxillary cusps should be created by LRT and LPT occlusal movements (Douglass & DeVreugd, 1997). In Saccopastore molars, as in other Neanderthals and AMH, para-facets are oriented in the opposite direction, thus suggesting a non-masticatory origin. As seen in other human populations, the Neanderthals of Saccopastore probably used their posterior teeth as tools, for tearing, holding, and shaping a variety of objects. While in some hunter-gatherer groups a gender differentiation in task activities is reflected also in the dental wear (e.g. Molnar, 1971), the non-masticatory wear pattern of Saccopastore 1 and 2 (one adult female and one adult male respectively) do not show any sexual division of labour. Similarly, the general wear pattern found in early *Homo sapiens* individuals from Skhul and Qafzeh (Israel) has suggested that the task activities related to this type of wear were commonly performed by all members of the population (Fiorenza & Kullmer, 2013).

Conclusions

The OFA method is an important tool to understand how dental wear facets are formed. Because there is a close relationship between masticatory food processes, jaw movements, and attritional wear, it is possible to obtain information about the diets of past human populations through wear facets analysis. Although the Neanderthal sample size of this study is rather small, it was possible to show their flexible dietary habits and the importance of the Mediterranean coastal areas, in terms of natural resources, for the evolutionary dynamics of these Pleistocene humans.

The macrowear patterns of the two Neanderthal specimens from Saccopastore suggest the intake of various food sources but with higher proportions of animal proteins, which is consistent with the presence of cold habitats, such as steppe and grasslands. On the other hand the macrowear patterns of Guattari 2 and 3 reflect their chronological sequence, indicating the use of a broader dietary spectrum during warmer periods and increase of meat consumption at colder MIS stages. Finally, the identification of an unusual type of wear in Saccopastore maxillary molars, which is not related to a normal chewing behavior, permits to extrapolate few information about the cultural habits of these Neanderthals from Central Italy, suggesting the use of posterior teeth as tools for daily task activities.

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