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Dental macrowear and cortical bone distribution of the Neanderthal mandible from Regourdou
(Dordogne, Southwestern France)

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ABSTRACT

Tooth wear is an important feature for reconstructing diet, food processing and cultural habits of past human populations. In particular, occlusal wear facets can be extremely useful for detecting information about diet and non-masticatory behaviors. The aim of this study is to reconstruct the diet and cultural behavior of the Neanderthal specimen Regourdou 1 (Dordogne, Southern France) from the analysis of the macrowear pattern, using the occlusal fingerprint analysis method. In addition, we have also examined whether there is any association between the observed dental macrowear and mandibular bone distribution and root dentine thickness. The posterior dentition of Regourdou 1 is characterized by an asymmetric wear pattern, with the right side significantly more worn than the left. In contrast, the left lower P₃ shows a more advanced wear than the right premolar, with unusual semicircular enamel wear facets. The results from occlusal fingerprint analysis of this unique pattern suggest tooth-tool uses for daily task activities. Moreover, the left buccal aspect of the mandibular cortical bone is thicker than its right counterpart, and the left P₃ has a thicker radicular dentine layer its antimer. These results show a certain degree of asymmetry in cortical bone topography and dentine tissue that could be associated with the observed dental macrowear pattern. The molar macrowear pattern also suggests that Regourdou 1 had a mixed diet typical of those populations living in temperate deciduous woodlands and Mediterranean habitats, including animal and plant foods. Although this study is limited to one Neanderthal individual, future analyses based on a larger sample may further assist us to better understand the existing relationship between mandibular architecture, occlusal wear and the masticatory apparatus in humans.

Keywords: Pleistocene humans; Wear facets; Asymmetry; Tooth-tool uses; Strain distribution

1. Introduction

Tooth wear analyses are important for reconstructing diet, food processing and cultural habits of recent and extinct hominins (e.g., Molnar, 1972; Hinton, 1982; Smith, 1984; Hillson, 2002; Kaifu et al., 2003; Fiorenza et al., 2015a; Ungar, 2017). Dental wear is considered a natural physiological process that results in a gradual loss of the enamel layer and reduction in the height of the entire crown. It results from the combination of multiple mechanisms (attrition, abrasion and erosion), some more prominent than others, depending on biological and behavioral variation (Addy and Shellis, 2006; Kaidonis, 2008; Burnett, 2016). In particular, wear facets (visible to the naked eye, and characterized by polished surfaces with well-delineated borders) are created by the contact of opposing teeth during mastication. They can be extremely useful for detecting information about diet and non-masticatory behaviors (Fiorenza et al., 2015a). Each of these facets are generated by specific occlusal movements that are closely related to diet and to the masticatory processes occurring during the chewing cycle (Kay and Hiiemae, 1974). Thus, the information obtained from the analysis of the macrowear patterns can be used to reconstruct the chewing behavior and to infer diet in fossil and extant species (Butler, 1952, 1973; Kay, 1977; Janis, 1990; Ulhaas et al., 2007; Kullmer et al., 2009, 2012; Fiorenza, 2015; Fiorenza et al., 2011a; Harvati et al., 2013). The occlusal fingerprint analysis (OFA) is a well-established virtual method that uses three-dimensional (3D) digital models of tooth crowns to quantify structural parameters of wear facets, such as facet area, perimeter, occlusal relief, inclination and spatial orientation (Kullmer et al., 2009). It has been successfully and extensively used to record information about diet in non-human primates, modern human hunter-gatherers, and Paleolithic human populations (Ulhaas et al., 2004, 2007; Benazzi et al., 2011; Fiorenza et al., 2011a, b, 2015a, b; Fiorenza, 2015; Harvati et al., 2013; Knight-Sadler and Fiorenza, 2017; Oxilia et al., 2018; Zanolli et al., 2019). It has also been used to associate unique wear patterns with specific cultural habits in ancient and prehistoric populations (Fiorenza et al., 2011c, 2018; Fiorenza and Kullmer, 2013, 2015; Fiorenza, 2015), and to recognize oral pathological conditions (Fiorenza and Kullmer, 2016) and early dental treatments (Oxilia et al., 2015).

Regourdou 1 is a partial skeleton from a young adult, probably between 23–30 years old (Volpato et al., 2012) but of indeterminate sex (Vandermeersch and Trinkaus, 1995; Plavcan et al., 2014), dated to Marine Isotope Stage (MIS) 4 (Plavcan et al., 2014). It was discovered in 1957 in a burial-like context associated with La Quina-type Mousterian lithics within the homonym karst cavity at Montignac-sur-Vézère, on top of the hill near Lascaux Cave, in Dordogne, France (for an historical review of the excavations and the context, see Maureille et al., 2015a; Pelletier et al., 2017). Regourdou 1 is missing its cranium but preserves a nearly intact mandible with a complete set of moderately worn permanent teeth (Maureille et al. 2001; Macchiarelli et al., 2008, 2013; Bayle et al., 2011; Volpato et al., 2012; Fig. 1). During the last decade, a systematic revision of the faunal remains and associated sediments from the early excavations has allowed the identification of 59 additional postcranial remains attributed to the same individual, mostly from the axial skeleton (Couture, 2008; Madelaine et al. 2008; Meyer et al., 2011a; Maureille et al., 2015b). However, no additional cranial elements were recovered.

In this study we apply the OFA method to measure and quantify the occlusal tooth wear pattern of Regourdou 1, with the aim of obtaining information about its masticatory behavior, subsistence strategy and cultural habits. Compared to the variation in Neanderthals, the lower dentition of Regourdou 1 is characterized by a modest crown size, especially for the mesiodistal diameter, and by a reduced left P₃ (Maureille et al., 2001). However, according to Volpato et al. (2012), despite the relatively small size of its posterior crowns, canine breadth in this individual is large (10.0 mm), greater than European MIS 4–3 Neanderthal females (mean = 8.2 mm, range = 7.5–9.7 mm, $n = 10$) and at the high-end of the range reported for Neanderthal males (mean = 9.5 mm, range = 8.8–10.1 mm, $n = 12$; Volpato et al., 2012). In the original description of the specimen, Piveteau (1964) argued that the unusual morphology of the occlusal surface in the left P₃ is probably the result of "a deterioration occurred during fossilization" (Piveteau, 1964:184, our translation from the original in French). In addition, Maureille et al. (2001) observed that the right teeth of Regourdou 1 were more worn than their antimeres. The asymmetric pattern of Regourdou 1 was further examined by Volpato

et al. (2012), who analyzed the orientation of the microwear striations over the labial surfaces of incisors and canines. The predominance of right oblique scratches, typical of right-handed manipulations, was probably caused by the use of the anterior teeth as a vice or a third hand. Asymmetric variation in enamel thickness was also found on the posterior dentition, more evident in the third premolars (Macchiarelli et al., 2013:Fig. 11.2).

In the present study, our goal is to investigate the nature and possible causes of the unusual wear found on the left P₃. In the process, we also provide the first quantitative macrowear analysis of the Regourdou 1 dentition, which sheds light on the masticatory processes, diet and cultural habits of this individual. In addition, because asymmetric masticatory loads in the mandible could generate local variation in cortical bone thickness (Demes et al., 1984; Daegling and Grine, 1991; Masumoto et al., 2001; Daegling and Hotzman, 2003; Ichim et al., 2007), we analyze if there is any asymmetric mandibular bone distribution in the premolar area. Variation in the mandible seems to be functionally related to mechanical loadings generated during masticatory and paramasticatory regimes (Bouvier and Hylander, 1981; Lieberman et al., 2004; Holmes and Ruff, 2011). Accordingly, we investigate if cortical bone asymmetry in Regourdou 1 is biomechanically related to non-masticatory stresses (Maureille et al., 2001; Volpato et al., 2011a, 2012; Macchiarelli et al., 2013). Furthermore, we also investigate possible asymmetry of the radicular dentine thickness distribution and variation between the left and right third premolars, using 'virtual cartography' methods (Bayle et al., 2011; Macchiarelli et al., 2013; Zanolli et al., 2014, 2018). As a whole, this information should help us to better understand the relationships between mandibular architecture, occlusal wear and how the masticatory system functions in some Neanderthals.

2. Materials and methods

2.1. Image acquisition

Three-dimensional data of the Regourdou 1 mandible and dentition, housed at the Périgord Museum of Art and Archaeology (Périgueux, France), were acquired through microtomographic

scanning (SR- μ CT) at the beamline ID 17 of the European Synchrotron Radiation Facility (ESRF) in Grenoble, France (experiment SC1587c; Macchiarelli et al., 2006; Mazurier et al., 2006; Bayle et al., 2011). The mandible was imaged according to the following parameters: energy, 70 keV; projections, 1500 in half acquisition mode; integration time, 29.91 ms. The final sections were reconstructed from sinograms and saved in a 32-bit floating-point raw format at an isotropic voxel size of 45.5 μ m. The SR- μ CT record of the Regourdou 1 mandible is available at the NESPOS website (<https://www.nespos.org/display/openspace/Home>; Fig. 1).

Following segmentation (see *infra*), intra- and inter-observer tests for accuracy of the (SR) μ CT-based measures and estimates run by two to four observers (depending on the variables) provided differences less than 4%, which agrees with previous tests on similar μ CT-based quantitative analyses performed on fossil teeth (e.g., Bayle et al., 2010; Skinner et al., 2015; Martín-Francés et al., 2018; Zanolli et al., 2018).

2.2. Occlusal fingerprint analysis

We used high-resolution replicas of teeth made in epoxy resin obtained by combining the resin LARIT L-160 with the hardener LARIT 502 (Lange und Ritter, GmbH). Since the epoxy is transparent, we combined this mix with an opaque black pigment compatible with epoxy material (Fiorenza et al., 2009).

The wear facets labeling system follows the terminology proposed by Maier and Schneck (1981) and Kullmer et al. (2009), who described 13 complementary pairs of facets in hominoid molars. For this study, we have divided the wear facets into three different groups based on the masticatory processes acting during the normal chewing cycle (Kay and Hiiemae, 1974; Janis, 1990), following the color coding used in Fiorenza et al. (2011a): buccal phase I facets (colored in blue; facets 1, 1.1, 2, 2.1, 3 and 4); lingual phase I facets (colored in green; facets 5, 5.1, 6, 6.1, 7 and 8); and phase II facets (colored in red; facets 9, 10, 11, 12 and 13).

To recognize non-masticatory wear patterns, we utilize the dental occlusal concept (Douglass

and DeVreugd, 1997; Schultz 2003; Schulz and Winzen, 2004; Kullmer et al., 2009, 2012; Fiorenza et al., 2011a; Fiorenza and Kullmer, 2013, 2015, 2016; Fiorenza, 2015), which takes into account the possible three-dimensional occlusal movements responsible for wear facets formation starting from a position of maximum intercuspation (or centric occlusion). Facets 1, 1.1, 4, 5 and 8 are in contact during lateroretrusive movements (LRT; colored in blue). Facets 2, 2.1, 3, 6 and 7 are produced by lateroprotrusion (LRT, colored in yellow) while facets 9, 11 and 12 are in contact during mediotrusion (MT, colored in green) and immediate side shift (ISS, colored in red). Lastly, facets 10 and 13 correspond to medioprotrusive movements (MPT, colored in orange; Kullmer et al., 2009, 2012; Fiorenza et al., 2011c).

The OFA analysis consists of five consecutive steps (Fiorenza, 2009). The first one is the creation of a reference plane. This is achieved by translating and aligning the occlusal plane (defined by three landmarks selected on the lowest surface point of the second molars and central incisor) to the xy coordinate system (Ulhaas et al., 2004, 2007; Kullmer et al., 2009, 2012). The second step consists of the manual identification of each facet and dentine area directly onto the polygonal model using the polyline tool in the IMEdit™ of Polyworks® V12 (InnovMetric software, Québec, Canada), a 3D metrology software. Once all facets and dentine exposures are identified, we measure the area by selecting all triangles within their perimeter (step 3). Successively we generate the average plane of each facet using the best-fit plane function in Polyworks® V12. The facet inclination angle is measured between the facet and reference plane (step 4). Finally, we import the digital data into the IMInspect™ module for calculating the directions of each facet using facet normal vectors projected to the reference plane and afterward onto the individual facet planes (step 5). The final result of this last step is the creation of a three-dimensional occlusal compass of the facet pattern of each tooth that contains visual information on the direction of all facets and on their inclinations (Kullmer et al., 2009; Fiorenza et al., 2010, 2011c; Fiorenza and Kullmer, 2013, 2015, 2016; Fiorenza, 2015). It is important to note that in this study we compared the relative wear facet areas of a lower molar of Regourdou 1 with published results obtained from a Neanderthal and AMH sample mostly consisting

of upper molars (Fiorenza et al., 2011a; Harvati et al., 2013; Fiorenza, 2015) because we do not have lower molar macrowear data for these two Pleistocene human species.

2.2. Cortical bone distribution

To test cortical bone distribution on a portion of the mandible, between approximately the mesial aspect of the canine and the mesial aspect of the first molar, we virtually separated the endosteal surface of the cortical shell from the trabecular bone and investigated its right and left sides for asymmetry in cortical bone topographic thickness of buccal and lingual components. Based on a semiautomatic segmentation, a preliminary map of cortical bone thickness distribution of the Regourdou 1 mandible was firstly performed by Volpato et al. (2011a) (Supplementary Online Material [SOM] Fig. S1).

The different steps of the procedure, developed through the software packages Avizo v.9.5 (Terma Fisher™-FEI, Hillsboro, Oregon, USA) and ImageJ (Schneider et al., 2012), are detailed in SOM S1 and illustrated in SOM Fig. S2. Although the process described above is time-consuming, the segmentation of the selected portion of the Regourdou 1 mandible was facilitated by the extremely limited presence of sedimentary matrix infill and by its poor degree of mineralization. However, because of the local presence of some thicker plate-like trabecular structures (Gibson, 1985; Stauber and Müller, 2006), at some sites, the otherwise distinct endosteal contour has been defined by local manual corrections and interpolation every ten virtual slices (step 7 of the segmentation procedure; SOM Fig. S2). The minor discontinuities along the buccal and lingual cortical shells related to the oblique fracture running in the original specimen from the apex of the right canine towards the base of the corpus, just at the level of the left I₂, have been virtually integrated; conversely, as they do not affect the analysis, the lack on both sides of two alveolar bone splinters at I₂-C₁ level has been ignored.

Cortical bone thickness topographic variation in the selected left and right portions of the Regourdou 1 mandible was measured by computing the distance between the triangulated periosteal

and endosteal surfaces of the cortical shell; for each vertex of one surface, the closest point on the other surface was computed. Cortical thickness distribution was virtually rendered for the buccal and the lingual aspects of each side using a chromatic scale increasing from dark blue (thin) to red (thick). This synthetic visual descriptor allows the quick identification of similarities and differences in bone topographic distribution and the qualitative assessment of structural asymmetries (Bondioli et al., 2010; Mazurier et al., 2010; Bayle et al., 2011; Volpato et al., 2011b; Puymeraill et al., 2012; Macchiarelli et al., 2013; Cazenave et al., 2017). Besides morphometric maps, cortical bone thickness was measured at three buccal and three lingual 2×2 mm sites geometrically defined at homologous spots on both sides of the mandible. The first measure (U, upper) was taken below the P₃ apex; the second measure (L, lower) was taken between the P₃ apex and the lower mandibular margin; the last measure (I, intermediate) was taken between the upper and the lower sites (Fig. 2).

2.3. Radicular dentine thickness

In order to identify any possible difference in the pattern of root dentine thickness distribution between the left and right third premolars, we digitally segmented the 60–85% portion (i.e., the subcervical portion) of the total P₃ root length along a predefined vertical line at the middle of the lingual aspect and then unrolled and projected it onto a morphometric map (Bondioli et al., 2010; Bayle et al., 2011; Macchiarelli et al., 2013; Zanolli et al., 2014, 2018) generated by a custom routine developed in R v.3.5.0 (R Development Core Team, 2018) with the packages Momocs (Bonhomme et al., 2014), spatstat (Baddeley et al., 2015) and gstat (Pebesma, 2004). We applied the same ‘unrolling’ protocol to investigate the dentine topography in P₃ belonging to modern human male individuals ($n = 3$) from the Pretoria Bone Collection, Johannesburg, South Africa (L'Abbé et al., 2005). These three individuals, aged 26 (A), 32 (B), and 56 years (C), show a low (stages 1–2 following Smith, 1984) to moderate (stage 3) degree of occlusal wear. In this assemblage, slight right vs. left wear differences are only found in the oldest individual, where the right P₃ crown (stage 3) shows a small dentine exposure on the protoconid, which is absent on its antimere (stage 2). The

modern human sample was scanned using an X-Tek (Metris) XT H225L industrial microtomographic system at the South African Nuclear Energy Corporation (NECSA), Pelindaba, at a resolution ranging from 47 to 90 μm . In all cases, dentine thickness values have been standardized between 0 and 1 and each morphometric map has been set within a grid of 80 columns and 100 rows.

2.4. Statistical analyses

To visually compare the Regourdou 1 molar wear pattern with that of other human samples, we have used the data currently available for Neanderthal and anatomically modern human (AMH) specimens (Fiorenza et al., 2011a; Fiorenza, 2015). In order to create a robust and more homogenous sample, from each specimen we selected only one maxillary molar in wear stages 2 and 3 (Fiorenza et al., 2011a). For Regourdou 1, we selected the right M_2 (the relative wear areas of its antimere are similar).

We have used the ternary plot, which is a diagram depicting the proportions of three variables (in this specific case, represented by the relative areas of buccal, lingual and phase II facets), which have to sum to 1 or 100%. Moreover, we have employed circular statistical methods to analyze facet directions to establish whether or not the unique pattern found on the left P_3 is due to non-masticatory processes (Fiorenza et al., 2011c; Fiorenza and Kullmer, 2013, 2015, 2016; Fiorenza, 2015). Because the occlusal compass movements are enclosed in a circular space of 360° , standard statistical investigations are not directly applicable to the analysis of directional data (Hammer and Harper, 2006). For example, the difference between a value of 350° and 10° is not 340° but only 20° . We have described the facet's directions using basic descriptive parameters, such as the mean angle, the 95% confidence interval, and the circular standard deviation. One of the first steps in circular statistics is to investigate if the data is taken from a von Mises distribution (the equivalent of the normal distribution for linear data). To measure the departure of the circular distribution from a perfect circle, the maximum likelihood estimate of the concentration parameter (k) was calculated (Batschelet,

1981; Fisher, 1993; Mardia and Jupp, 2000). As k gets large, the von Mises distribution approaches the normal distribution.

In order to evaluate whether the facet directions follow a random distribution or specific directions of occlusal movements (described by the dental occlusal concept; Douglass and DeVreugd, 1997), we used the Rayleigh's test and the Rao's spacing test (Batschelet, 1981; Fisher, 1993; Mardia and Jupp, 2000). The Rao's spacing test is based on the idea that if the underlying distribution is uniform, successive observations should be evenly spaced. Large deviations from this distribution suggests directionality (Levitin and Russell, 1999). Similarly, the Rayleigh's test is used to assess whether the distribution of mean angles of direction departs randomly from circular uniformity. For example, if vectors of similar wear facets point toward the same direction, the Rayleigh's test will be characterized by small p values, indicating thus a significant departure from uniformity.

To visually display a facet's major directions, we used the rose diagrams, which are circular histograms divided into sectors to display the data frequency and orientation (Hammer and Harper, 2006). The ternary plot was created using the software PAST v.3.13 (Hammer et al., 2001). Directional statistic results and rose diagrams were obtained using a circular statistic software program (OrianaTM v. 4.00, Kovach Computing Services, Pentraeth, UK).

3. Results

3.1. Occlusal fingerprint analysis

The anterior teeth of the Regourdou 1 mandible show a more advanced degree of wear than the postcanine dentition, with large dentine exposures and rounded labial wear (Fig. 3). The incisors display a pronounced dentine exposure on the incisal edge, wherein each incisor possesses a complete enamel rim enclosing a dentine area. The canines show a very similar wear pattern. They differ from the incisors in also possessing steep triangular wear facets (on this distolabial face) which were

probably generated by contact with the mesiolingual wall of the upper canine due to a slight horizontal overlap between maxillary and mandibular opposing teeth (Kaifu et al. 2003).

A close look at the occlusal wear in the postcanine teeth highlights the presence of several dentine areas, flatter lingual facets and a lower metaconid in the right molars, especially observable in the first molar (Table 1). In particular, we notice a marked asymmetric pattern in absolute area exposed by dentine, with the right side (61.87 mm^2) significantly more worn than the left (46.45 mm^2). In contrast, the left lower P₃ shows a more advanced degree of wear than its antimere, and a mesiodistally elongated dentine exposure is visible on the buccal aspect of the occlusal surface.

The presence of a well-developed, polished and semicircular enamel wear (Fig. 4) between the protoconid tip and the mesial marginal ridge excludes the possibility that taphonomic and/or diagenetic processes. On the other hand, the oblique surfaces of the occlusal enamel wear facets are slightly inclined mesially.

If we look more in detail at the left P₃ wear facets and the exposed dentine area, we can see in mesiodistal direction that the wear surface is shaped like a saddle. The wear area represents a groove with changing inclination from mesial to distal. It is mesiodistally elongated and ends with a steeply inclined distal margin running parallel to the crown wall. In contrast, the right P₃ is characterized by a normal wear pattern enclosing a smaller dentine exposure around the protoconid. Both P₄ display similar wear patterns, with facets forming buccally, along the protoconid, metaconid and entoconid. Finally, the left P₄ is the only tooth in the postcanine dentition on which no dentine exposure is detectable.

The first molars show the most advanced wear of all postcanine dentition, with the exception of the left P₃ discussed above. Large dentine areas are visible in all five main cusps of the lower M₁. The dentine exposure on the entoconid coalesces with the dentine of the lingual slope of the hypoconulid, creating one dentine basin with a convex distal margin.

The wear pattern in the M₂ is characterized by large facets that do not coalesce (Fig. 5). Relatively small dentine basins are pronounced on the mesiobuccal side of the entoconid, also visible

in the slightly less worn third molars, although the dentine exposure in the right side decreases from M₂ to M₃. The wear pattern on the third molars is characterized by marked differences in hypoconid and hypoconulid areas, where the facets tend to fuse, forming a flat concave area especially evident on the left M₃. Distobuccally, a concave basin likely occludes with the hypocone of the upper M³, and seems to function structurally as a mortar-and-pestle system, particularly suitable for grinding and crushing food items.

Among other features, the Neanderthal lower molars are characterized by the presence of the mid-trigonid crest (Vanderbroek, 1967; Zubov, 1992; Wu and Turner, 1993), a well-developed mesial fovea (Bailey, 2002) and a well-developed metaconid. In all molars of Regourdou 1, we observe that around the mid-trigonid region, wear facets develop along its mesial slopes and are characterized by steep planes, particularly on the buccal side of the metaconid. In contrast, in the distal part of the occlusal molar surface, the amount of dentine exposure increases, the height of the entoconid and protoconid decrease, and the resulting wear facets tend to be flatter. In terms of relative facet areas, the percentages of the various chewing phases are similar among the postcanine tooth elements (Table 2).

In particular, phase II areas are more developed in M₁ when compared with those of M₂ and M₃, probably because of the advanced degree of wear. Similarly, the wear planes of phase II areas are flatter than buccal and lingual phase I facets in M₁ and M₂; the opposite situation is found in M₃ (Table 3). It is also interesting to note that the inclination of buccal and lingual phase I facets in M₁ is generally steeper than that of adjacent teeth. The opposite situation is found for phase II areas. Generally, first molars are characterized by flatter wear facets than second and third molars, simply because they erupt earlier and therefore are exposed to wear for a longer period of time. Teeth with a higher degree of wear are also characterized by a flatter occlusal wear pattern (Fiorenza, 2009; Fiorenza et al., 2018).

3.2. Ecogeographic analysis

For the comparative analysis of relative wear facet areas, we used the right M₂ of Regourdou 1, which is characterized by 30% of buccal phase I facets, 38% of lingual phase I facets and 32% of phase II areas (Table 4). In the ternary diagram (the schematic graphic representation of these proportions), Regourdou 1 plots near the Neanderthals from temperate regions dominated by deciduous woodland forest (DEW group; Fig. 6, in green), and thus differs from the individuals from cold steppe and coniferous forests (SCF; Fig. 6, in blue) and warmer Mediterranean evergreen forests (MED; Fig. 6, in red; see also Fiorenza et al, 2011a). The two latter groups are characterized by large buccal phase I facets and small lingual phase I areas (SCF), and by equally large buccal phase I facets and phase II areas (MED).

3.3. Cultural habits

Circular statistical analysis of Regourdou 1 lower molars and premolars confirm that all the major movements (large κ values) described by the dental occlusal concept (Douglass and DeVreugd, 1997) fall within a von Mises distribution, displaying preferred directions, with statistically significant values for both the Rayleigh's test and Rao's spacing tests ($p < 0.05$; Table 5). Based on their special position, the two semicircular facets (here labeled as P1 and P2) should be equivalent to facets 1 and 10 (Kullmer et al., 2009), and they should correspond to LRT and MPT movements, respectively. However, when we visually inspect the major occlusal directions using the rose diagram (Fig. 7), the vectors of P1 and P2, which are characterized by non-significant Rayleigh values, fall outside these major orientations pointing to different areas of the compass (LPT and MT respectively). This indicates a high level of anisotropy and a circular random distribution.

3.4. Cortical bone distribution

The morphometric maps of the Regourdou 1 mandible reveal cortical bone thickness topographic variation between the right and left side (Fig. 8.) While the thickness-related signal around the perialveolar and periradicular areas (in blue) on the buccal aspect should be considered as

indicative only (due to the combined effects of real bony thinness and local damages, especially at the level of the canines), the left cortex is noticeably thicker than its right counterpart across the entire intermediate level of the mandibular body, especially below the premolars. Within the set of 12 measurements considered in this study, the differences among the thickness values specifically assessed at the upper (U), lower (L) and intermediate (I) levels of the mandibular body (Fig. 2) confirm this pattern (Table 6). Compared to the buccal aspect, the differences in bone thickness distribution between the two lingual cortical shells appear less distinct and randomly spread, but in this case it is the right side that shows a slightly thicker average cortex (Fig. 8; see also the mandible in basal view in SOM Fig. S1).

3.5. Radicular dentine thickness

The standardized morphometric maps rendering radicular dentine thickness topographic variation across the 60-85% root length portion of the right and left Regourdou 1 P₃ are shown in Figure 9, where they are compared to the maps generated for the same region of interest for the lower P₃ pairs of three recent adult humans (Fig. 9A–C; see Materials and methods) showing a low to moderate degree of occlusal wear (stages 1–2 to 3; Smith, 1984).

In Regourdou 1, the virtually extracted and unrolled chromatic-related root projections reveal some distinct topographic differences. Specifically, the thickened dentine of the left P₃ uniquely displays a proportionally wide and vertically extended buccal reinforcement exactly where the antimere tends to show relatively thinner tissue. Conversely, the two premolars share a thick, pillar-like vertical lingual strip, an absolutely and relatively thinner distal strip and, to a lesser extent, a thinner mesial strip.

Even if associated with absolutely thinner dentine, approximately the same structural signature displayed by the Regourdou 1 right P₃ (thicker lingual vs. thinner distobuccal dentine) is homogeneously found in both maps of the two younger modern human individuals used in this study for comparison (A and B, 26 and 32 years old, respectively), both displaying low occlusal wear

(stages 1–2) with no macroscopic evidence of side differences. However, similar to Regourdou 1, a slightly more contrasted pattern is shown by the 56 year old individual (C). Perhaps associated with a slightly more advanced degree of occlusal wear affecting the crown of its right P₃ (stage 3; Smith, 1984), where a dentine spot is present on the buccal cusp, its morphometric map reveals a small vertical buccal reinforcement absent on the root of its occlusally slightly less worn (stage 2) antimere (Fig. 9).

4. Discussion

4.1. Dental macrowear

Regourdou 1 shows a typical Neanderthal wear pattern, with incisors and canines exhibiting heavier wear than molars. Heavy anterior tooth wear is a morphological feature almost ubiquitous among adult Neanderthals and other Middle Pleistocene hominins (such as Kabwe), which has been interpreted as a habitual use of teeth as tools for cutting, holding, and shaping a variety of objects (e.g., Brace, 1967; Molnar, 1972; Bermudez de Castro et al., 1988; Trinkaus, 1992; Lalueza Fox and Frayer, 1997).

The study of Volpato et al. (2012) confirmed the para-masticatory interpretation associating the predominance of oblique scratches found on the right mandibular incisors of Regourdou 1 with right-handed manipulations performed at the front of the mouth. This asymmetric pattern in dental wear was first observed by Maureille et al. (2001), and it is supported by our results (see also Macchiarelli et al., 2013). Differences in the macrowear pattern are found between the right and left sides of this mandible, with the right teeth showing a flatter occlusal surface and prominently larger dentine areas. However, the opposite situation is observed in third premolars, where the left P₃ shows more wear than its right antimere.

Asymmetry in tooth wear in human populations can be considerable (Smith, 1984). The wear asymmetry observed in Regourdou 1 could be simply due to preferential chewing on one side (Molnar

et al., 1983; Martinez-Gomis et al., 2009). Alternatively, asymmetry in macrowear patterns could be related to asymmetry in the masticatory apparatus, typical of X-occlusion (or alternate intercuspation), where upper and lower teeth can meet in maximum contact on either left or right sides, but not on both sides together (Barrett, 1953; Brown et al., 2011; Oxilia et al., 2018). However, it is difficult to reconstruct the intercuspation with only the mandible preserved. Nonetheless, it is noteworthy that besides a certain degree of outer tooth crown size asymmetry (Maureille et al., 2001), fluctuating endostructural antimeric variation in Regourdou 1 has been detected also in tooth tissue proportions of its postcanine dentition, notably for the variables total volume of pulp (V_p), volume of crown pulp (V_{cp}), volume of crown dentine (V_{cd}), and volume of crown dentine + pulp (V_{cdp} ; Macchiarelli et al., 2013:Table 11.1). However, the relationship between function and development of this antimeric variation needs to be further explored (Macchiarelli et al., 2013).

4.2. Non-masticatory behavior

The use of teeth as tools is not exclusively found in the anterior dentition, but it also involves the postcanine teeth. For instance, dental enamel chipping in molars and premolars has been found in various human populations and different fossil hominins, and it has been associated with masticatory and non-masticatory activities (Turner and Cadien, 1969; Lukacs and Hemphill, 1990; Milner and Larsen, 1991; Bonfiglioli et al., 2004; Belcastro et al., 2007; Constantino et al., 2010; Scott and Winn, 2010). More recently, we have described a unique wear pattern found on the posterior maxillary dentition in various recent hunter-gatherer populations, in some Neanderthals and in anatomically modern humans from the Mediterranean region, which was not created during normal mastication but more likely result from the attritional and abrasive contacts generated through daily task activities for foods processing and/or object manufacturing (Fiorenza et al., 2011c; Fiorenza and Kullmer, 2013, 2015; Fiorenza, 2015). We named these wear areas, forming along the buccal side of maxillary molars, parafacets, to reflect their non-masticatory etiology (Fiorenza et al., 2011c).

In order to test whether the unique wear found of the left P₃ of the Regourdou 1 mandible is associated with non-masticatory activities, we examined the dip directions (the angle between the projected and the reference vectors) of these wear areas to see whether they correspond to the directions of major occlusal movements, which could be responsible for their formation. In normal occlusion, the vectors (encoded in a circular space ranging from 0° to 360°) of these specific wear facets should fall within the major directions described by the dental occlusal compass concept (Douglass and DeVreugd, 1997; Kullmer et al., 2009). Our analysis shows, however, that the two facets found on the left P₃ do not fall within the space range of the occlusal directions, the lateroretrusive and lateroprotrusive movements, and therefore differ from a normal masticatory behavior.

We have also examined if the semicircular shape (Fig. 10A) of this wear could be the product of a repetitive abrasive movement with a cord-like object, similar to those described for modern human populations, such as the Natufians, where teeth were used as tools while making baskets or fishing nets (Larsen, 1985; Minozzi et al., 2003; Bonfiglioli et al., 2004; Eshed et al., 2006; Molleson, 2007; Erdal, 2008). This pattern of dental wear has been described as an enamel rim surrounding depressed dentine area, usually circular in shape ('cup-shaped' topography), probably produced by a pulling action across the first molar and second premolar (Eshed et al., 2006).

Through a CAD (computer-aided design) model, we have virtually simulated how a cord-like object would fit around the semicircular wear found on the left P₃ (Fig 10B). Based on the shape and inclination of this unique wear, it is possible that the object was pulled toward the lingual side. Elongated grooves on the occlusal surfaces are generally reported in the anterior dentition, but they have also been found on premolars and molars (Larsen, 1985; Eshed et al., 2006). However, it is important to note that the wear found in Natufians dentition was symmetrical (Eshed et al., 2006) and that it ran in a different direction from those seen in Regourdou 1; therefore, this interpretation cannot be confirmed here.

Another possible cause of this wear could be the presence of a supernumerary tooth, rotated premolar, or transposed canine in the maxillary dentition. Supernumerary teeth are extremely rare. In modern humans, for instance, the presence of supernumerary teeth is between 0.1% and 3.4% (Ceperuelo et al., 2015). In the literature review of the human fossil record we did not find any specimen with supernumerary teeth. However, we suspect that a supernumerary (or rotated) premolar would not generate similar wear as observed in Regourdou 1. For example, we recently described the occlusion of an adult male gorilla with a fully erupted, 180° rotated extra maxillary premolar (Fiorenza and Kullmer, 2016). This individual did not show the same wear as the Regourdou 1 left third premolar. The occlusal simulation and kinematic analysis of the adult gorilla specimen revealed a high level of overlap in facet directions, combined with the absence of common occlusal contacts and lack of semicircular facets. In addition, Rougier et al. (2006) described a number of rotated Neanderthal lower third premolars from the Croatian site of Krapina and none of these cases show a wear pattern similar to that found in Regourdou 1.

Build-up bone and root dentine suggest asymmetrical forces placed on the left P₃ that could result from idiosyncratic use (masticatory or non-masticatory). However, at this stage, we are unable to tease apart the cause of wear on the left P₃ (non-masticatory versus masticatory activities), and we can only observe its unique shape and unusual occlusal directions depicted in the dental occlusal compass. Further investigations of the original through scanning electron microscopy, will be necessary to identify the striations within P₃ facets and their orientations. In addition, virtual occlusal simulation and experimental replication of striations (Oxilia et al., 2015, 2017) could help us to precisely determine the nature of this wear pattern.

4.3. Dietary signals

To date, no studies have investigated and reconstructed the ecology and diet of the Neanderthal from Regourdou. A previous study based on the analysis of upper molars in Neanderthals and AMH found a wear pattern dominated by buccal phase I facets in meat eater populations, and a

pattern with large lingual phase I facets in populations that relied on mixed food resources including a large percentage of plant material (Fiorenza et al., 2011a). However, in a recent macrowear study of an Australian aboriginal population from Yuendumu (Northern Territory, Australia), an asymmetric distribution (not statistically significant) was found between upper and lower molars, especially for lingual and buccal phase I facets (Oxilia et al., 2018). However, the other two Neanderthal lower molars included in our comparative sample (Guattari 2 and 3) fall well within the upper molar sample (Fiorenza, 2015).

In the light of this new information, we can interpret the predominance of lingual phase I facets, and equally distributed phase II and buccal phase I facets of Regourdou 1, with the intake of mixed food resources, including meat and plant materials. Similar patterns have been described in the Neanderthals from Krapina that lived in deciduous forests and Mediterranean evergreen woodland of northern Croatia during a warm phase of the Eemian Interglacial period (MIS 5e; Rink et al., 1995; Van Andel and Tzedakis, 1996), and in Neanderthals and AMH from Mediterranean environments in the Near East during MIS 5e. This conclusion is in agreement with the analysis of the stratigraphy and faunal remains from Level 4 at Regourdou, which suggests a moderately warm phase within MIS 4 (Bonifay et al., 2007; Plavcan et al., 2014). The macrofauna consists of *Ursus arctos*, Cervidae, Bovidae, *Castor*, *Sus* and *Lepus*, typical of temperate climates (Vandermeersch and Trinkaus, 1995). In addition, a recent paleoclimate study places Regourdou 1 in a warm temperate and mesic ecogeographic zone (Nicholson, 2017). Evidence suggests that Neanderthals living during interglacial warmer phases, or at the southern latitudes near the Mediterranean area, had a broader dietary niche compared to those populations from colder phases. These niches included the intake of marine shellfish, small mammals and birds, and a large range of plants such as legumes, fruit, acorn, wild grasses and underground storage organs (Stiner, 1994; Albert et al., 2000; Madella et al., 2002; Lev et al., 2005; Stringer et al., 2008; Brown et al., 2011; El Zaatari, 2011; Fiorenza et al., 2011a, 2015a, 2018; Blasco et al., 2013; Fiorenza and Kullmer, 2013; Fiorenza, 2015; Henry et al., 2011, 2014; Harvati et al., 2013; Estalrich et al., 2017; Weyrich et al., 2017; Power et al., 2018).

However, for a more accurate assessment of the diet of Regourdou 1, it will be important to extend the macrowear analysis also to Neanderthal and AMH lower molars.

4.4. Cortical bone distribution and root dentine thickness variation

Variation in cortical bone distribution in the mandible is a common feature found in all anthropoids, with the lingual side thinner than the buccal side under the molars (Demes et al., 1984; Daegling, 1989; Daegling and Grine, 1991). This asymmetric cortical pattern has been interpreted as an adaptation to reduce strains on the lingual sides under the combining action of twisting and occlusal loads (Demes et al., 1984; Dechow and Hylander, 2000). According to Daegling and Hotzman (2003), a thickened cortex along the buccal side of the mandibular corpus may indicate a structural response to magnified local loads.

In the mandibular area located between the canine and the first molar, we found that cortical bone distribution of the lingual side of the Regourdou 1 is generally thicker than the buccal side (Volpato et al., 2011a; Thibeault, 2017). As indicated by Ichim et al. (2007), who found asymmetric strain distribution on the working and balancing side of the human mandible, the thicker lingual mandibular side found in Regourdou 1 could be interpreted as a response to higher mechanical forces at the lingual aspect (Martinez-Maza et al., 2011).

Our analysis has revealed a slight asymmetry in cortical bone thickness distribution at the level of the P₃, with the left buccal cortex being systematically thicker at all three spots measured along a vertical strip below the root apex (Fig. 2). Conversely, no consistent directional differences have been recorded across the homologous sites measured on the lingual side.

Bone is a dynamic tissue that responds to alterations of its mechanical environment (e.g., Huiskes, 1995; Pearson and Lieberman, 2004; Ruff et al., 2006). The mandibular corpus exhibits strong developmental plasticity, where variation in masticatory loadings and paramasticatory regimes seems responsible for localized differences in bone mass, and morphology (Daegling and Hotzman, 2003; Fukase, 2007; Fukase and Suwa, 2008; Holmes and Ruff, 2011; Gröning et al., 2012).

Accordingly, we associate the local variation in cortical bone thickness of the Regourdou 1 mandible to possible asymmetric mechanical loads caused by the use of his/her teeth as tools, as highlighted by the analysis of the macrowear pattern. In this respect, our results indicate an association between tooth macrowear and cortical bone distribution, suggesting that cortical bone asymmetry is probably biomechanically related to masticatory and/or non-masticatory differential loadings. However, given the current lack of immediately comparable evidence from other extant and/or fossil adult human mandibles, the interpretation of a direct functional link between occlusal crown wear and jaw bone asymmetry deserves further investigation. In addition, it is important to highlight that we have found an asymmetric distribution also in the P₃ radicular dentine, expressed by an absolutely thicker buccal dentine on the left tooth.

To the best of our knowledge, functionally-related asymmetry in tooth radicular dentine thickness distribution has not been investigated and quantitatively assessed. However, thanks to the current availability of 'virtual unrolling' techniques (Bondioli et al., 2010), with the aim of tentatively detecting some taxon-related signal, morphometric maps imaging the pattern of root dentine thickness repartition have been generated for modern and fossil humans, including Neanderthals, AMH, *Homo erectus* and *Homo heidelbergensis* (Bayle et al., 2011; Macchiarelli et al., 2013; Zanolli et al., 2014, 2018). In this still limited comparative context, it is interesting to note that, differently from the present analysis of its P₃, the standardized morphometric maps previously generated for the root portions 15–85% of the lower lateral incisors (I₂) from Regourdou 1 did not evidence any noticeable difference in tissue repartition, including along the labial aspect (SOM Fig. S3).

While harder than bone, dentine is softer than enamel but, by combining rigidity and elasticity, it has greater compressive and tensile strength and better resists crack propagation (Berkovitz et al., 2002). Also, after the primary dentine deposition is complete (following root completion and apical closure), dentine formation continues to respond physiologically to a variety of stressors (e.g., abrasion, attrition, erosion, crown fracture, caries). This deposition, responsible for the so-called regular secondary dentine formation, lasts as long as the pulp remains vital and supplied by blood

(reviewed in Dean, 2017). While no information is available for the premolar and molar teeth, there is evidence that the pulp of extant human incisors contains high-threshold sensory mechanoreceptors not involved in the sensation of pain, which act as a protective mechanism limiting the maximum bite force by monitoring the stress on compressed dentine (Paphangkorakit and Osborn, 1998). Accordingly, the pattern of structural asymmetry in radicular dentine thickness topography revealed by the morphometric maps of the Regourdou 1's P₃ is compatible with the action of mechanoreceptors playing a long-term role in slightly adapting pulp morphology to resist repetitive strains and stresses through life by locally adapting dentine thickness (M.C. Dean, pers. comm.). The thickened vertical buccal reinforcement uniquely displayed by the left P₃ root could, thus represent a site-specific compensatory secondary dentine formation to slow continuous occlusal/axial forces.

A direct functional link in Regourdou 1 between the asymmetric variation in radicular dentine, macrowear patterns and mandibular cortical bone distribution cannot be unequivocally established. However, we predict that high-resolution analyses of tooth root organization across diverse hominin dentitions, adapted to a variety of dietary and culturally-related functional patterns, should help us to better understand this functional relationship (Kupczik and Dean, 2008; Kupczik and Hublin, 2010; Bayle et al., 2011; Le Cabec et al., 2012, 2013; Macchiarelli et al., 2013).

5. Conclusions

In this study we have combined occlusal fingerprint analysis of the tooth crowns with endostructural virtual imaging to investigate the masticatory behavior, subsistence strategy and cultural habits of the Neanderthal adult individual Regourdou 1. The results indicate that Regourdou 1 preferably chewed on its right side and likely exploited various food sources, including plant and animal food typical of temperate forest habitats. The disproportionately heavy anterior tooth wear suggests the habitual use of teeth as tools. Similarly, the unique wear pattern identified on its left P₃, may have been produced by non-masticatory activities. However, further analyses are necessary to precisely identify the nature of this wear.

Left vs. right assessment of cortical bone distribution across the canine-first molar portion of the mandibular body also reveals a slightly thicker cortex in correspondence of the left buccal side, which we interpret as a structural response to locally magnified loads likely related to paramasticatory activities. A fully compatible asymmetrical signature is also provided by the root dentine topography of the left P₃, further supporting the interpretation of functionally driven morphostructural changes.

Future studies using the present and other analytical approaches could further investigate whether the overall asymmetric wear pattern and the cortical distribution covary across the entire mandible of this Neanderthal individual. Specifically, finite element analysis can help to predict the biomechanical responses in mandibular models and to clarify the relationships between dental wear, mandibular architecture and occlusal loadings. In addition, with the application of the occlusal fingerprint analysis software, which permits the detection and quantification of collision areas between 3D models of upper and lower teeth during occlusal movements (Benazzi et al., 2011), it is possible to accurately generate realistic simulations that allow an investigation of how dental and bone tissues deform under different biting scenarios (Benazzi et al., 2012, 2013, 2016; Fiorenza et al., 2015b).

The masticatory apparatus is a rather complex structure and variation in cortical bone distribution can affect different areas of this functional unit; in turn, it can be influenced by various morphological and biocultural features that relate to masticatory function and facial types (Masumoto et al., 2001; Daegling and Hotzaman, 2003; Ichim et al., 2007; Grine and Daegling, 2017). However, only future analyses based on the extended record from bioculturally and chronologically diverse samples may allow the understanding of the evolutionary dynamic relationships among occlusal wear patterns, inner tooth structural organization, mandibular architecture and the masticatory system as a whole.

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FIGURES

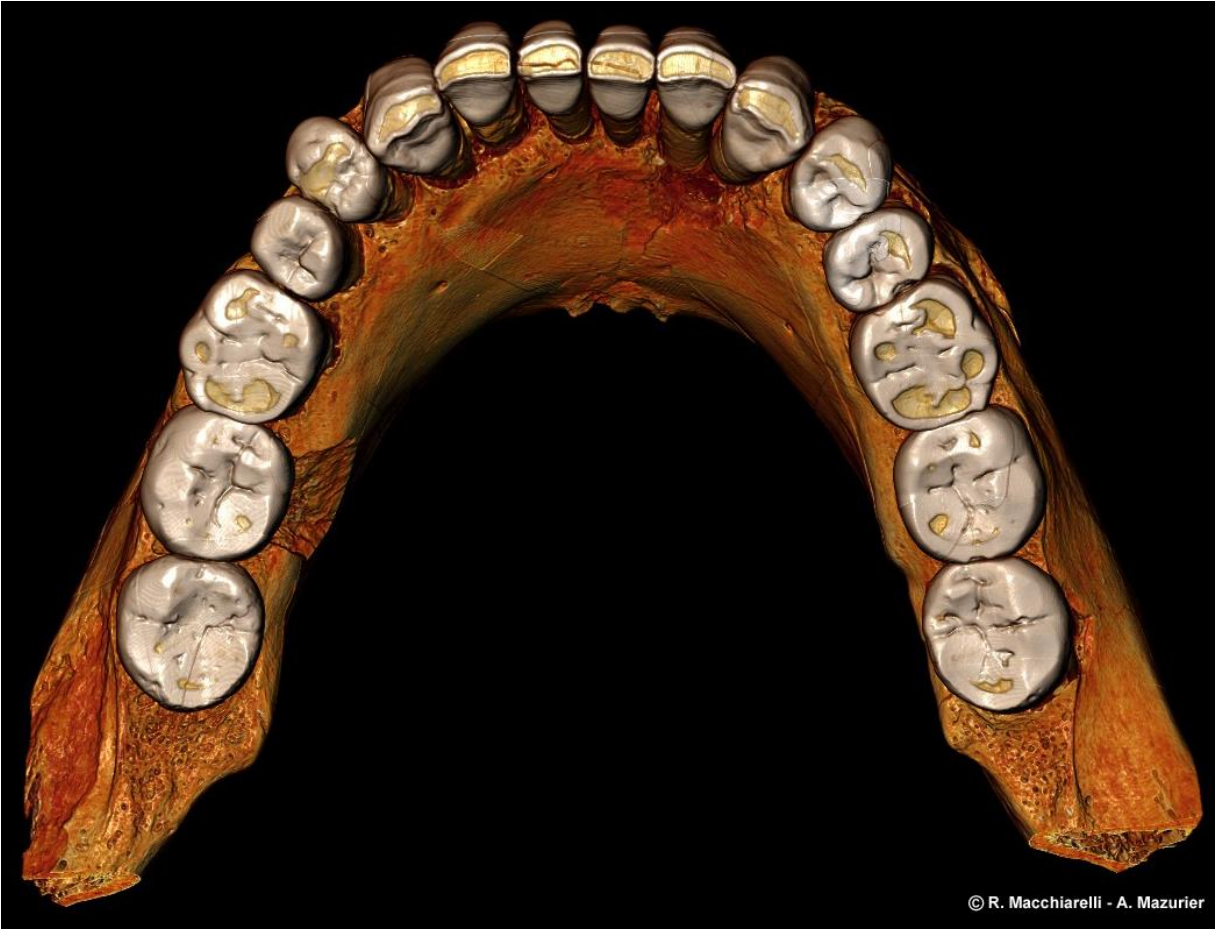


Figure 1. Two-dimensional rendering of the 3D virtual model of the Regourdou 1 mandible in occlusal view. Scale bar = 10 mm.

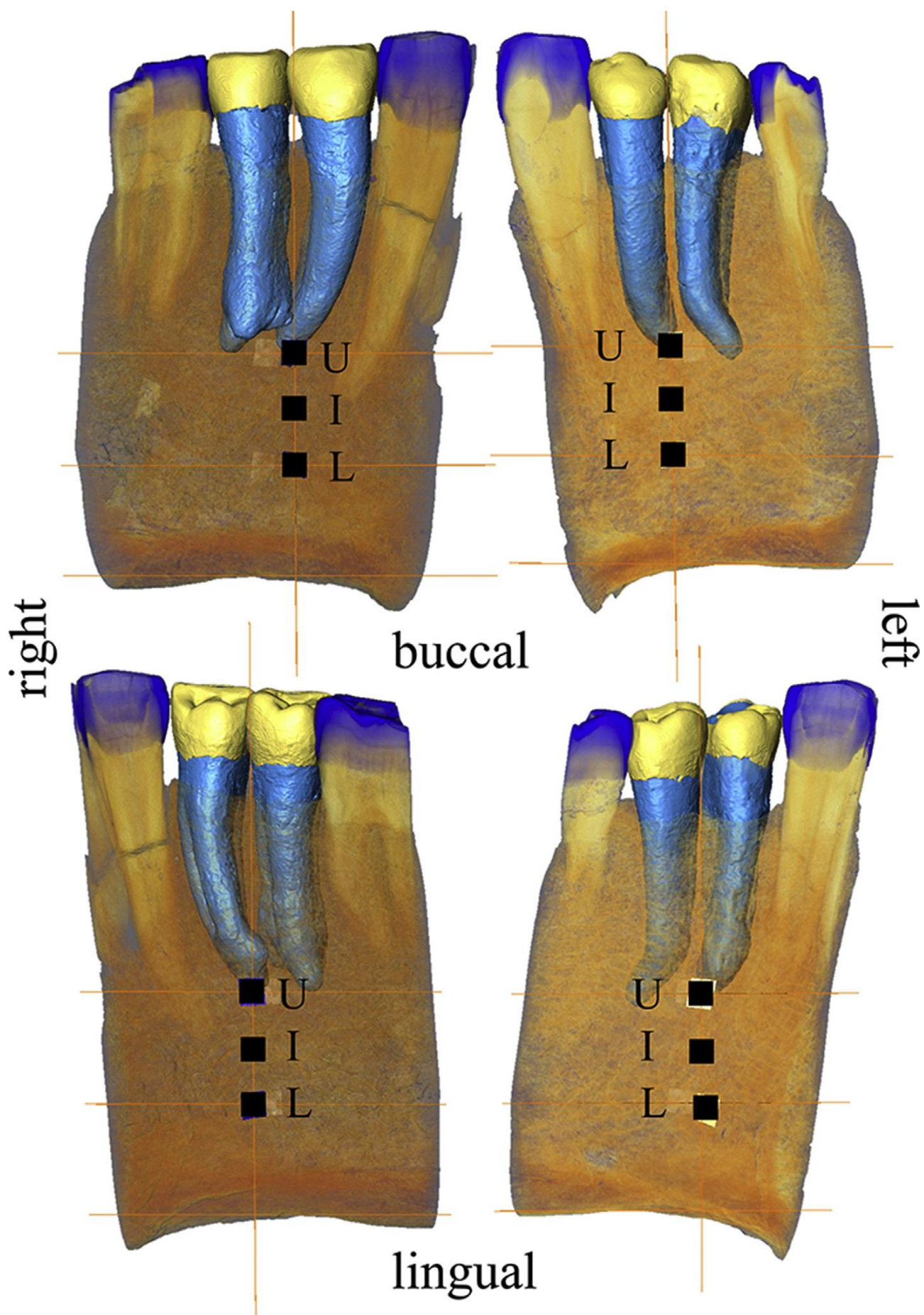


Figure 2. Location on each selected right (R) and left (L) portions of the Regourdou 1 mandible between the canine and the first molar of the three 2×2 mm homologous sites below the P₃ radicular apex on the buccal (upper) and lingual (lower) aspects where the periosteal-endosteal thickness of the cortex (here in semitransparency) has been assessed. Abbreviations: I = intermediate spot; L = lower spot; U = upper spot. Scale bar = 5 mm.



Figure 3. Anterior and posterior teeth (in occlusal view) of Regourdou 1 mandible showing dentine exposure (highlighted in red).

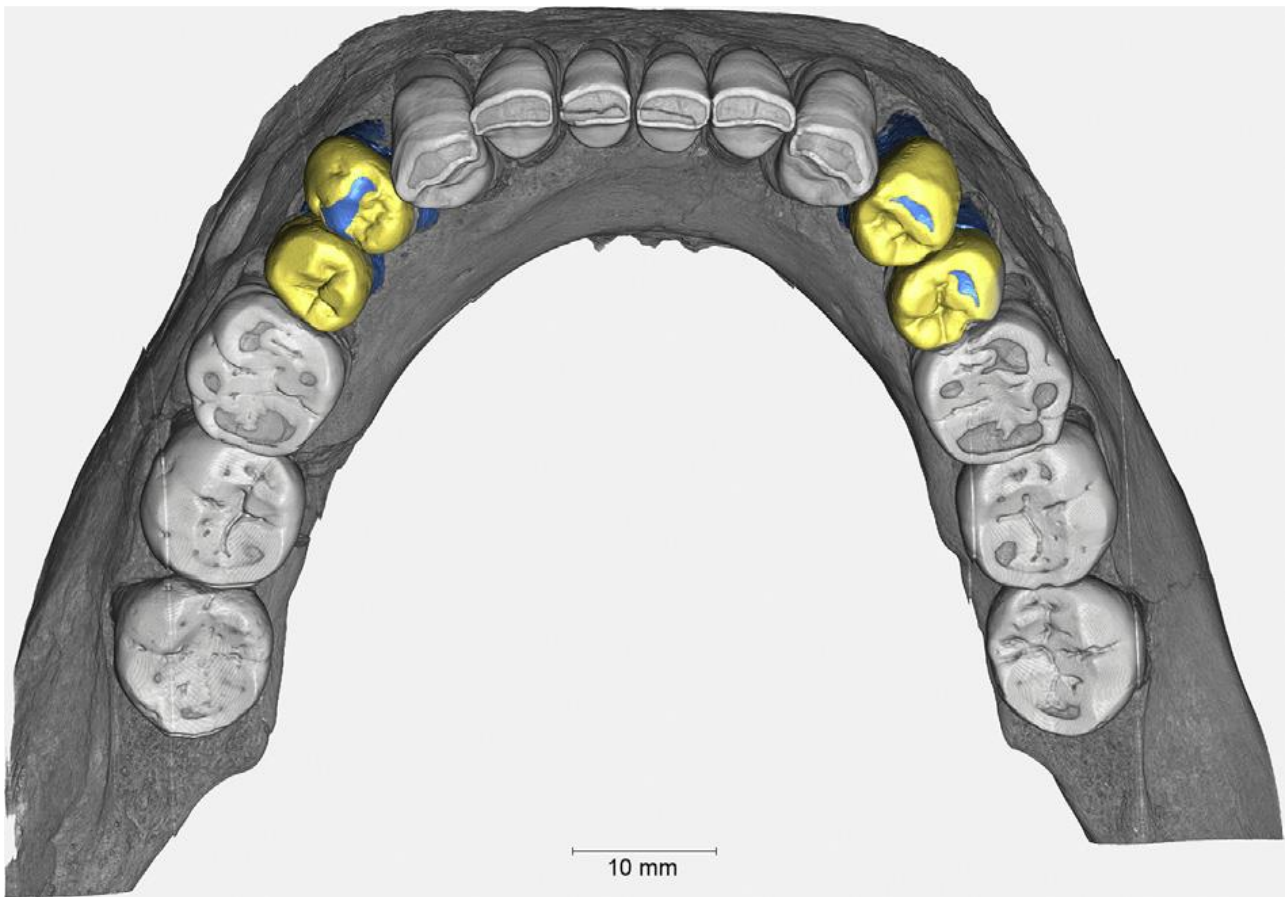


Figure 4. Three-dimensional model of the Regourdou 1 mandible in occlusal view showing the left and right premolars (in yellow) and their dentine exposure areas (in blue).

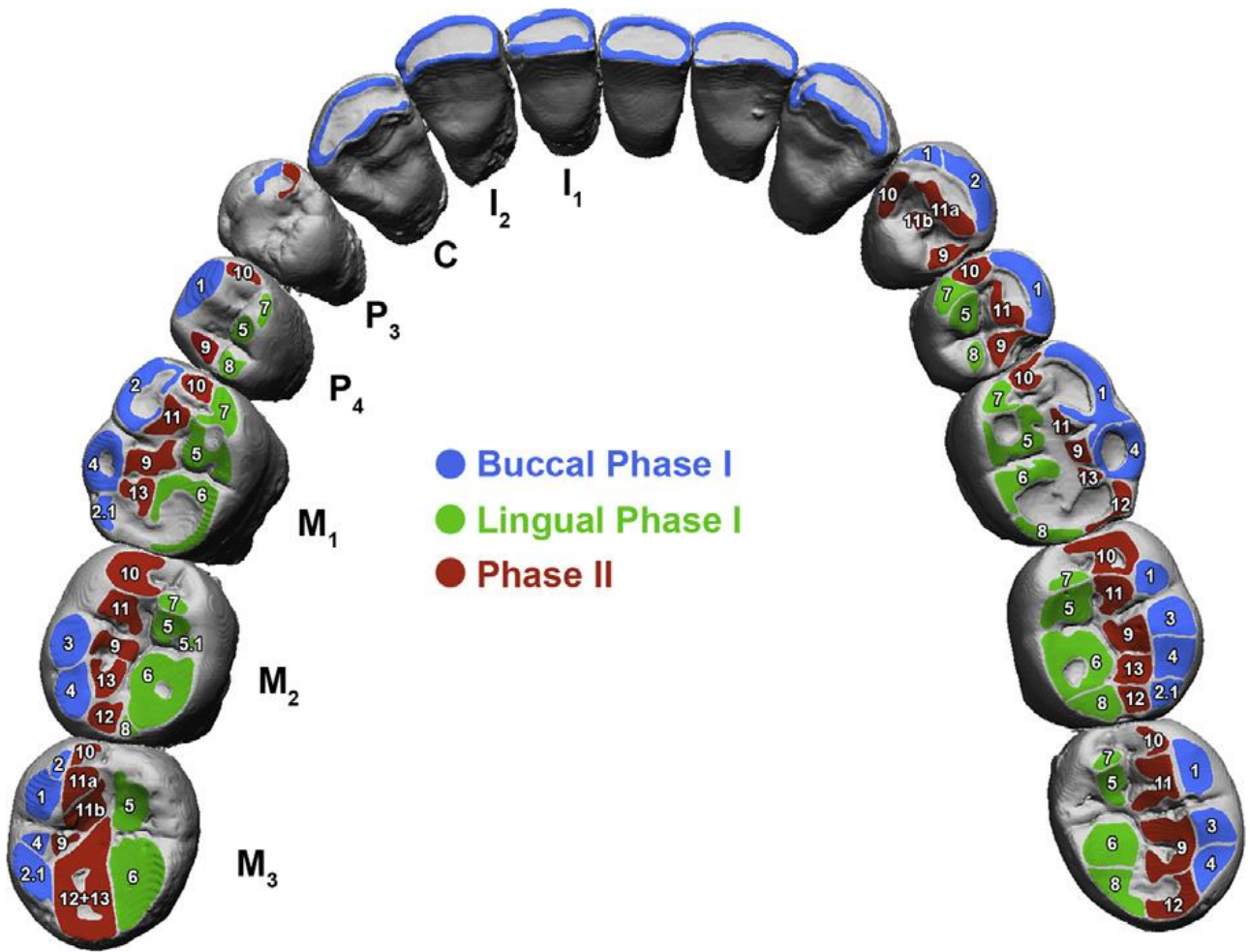


Figure 5. Dental macrowear analysis showing the different wear facets grouped by chewing cycle phases (Kay and Hiiemae, 1974): buccal phase I wear facets (Facets 1–4; blue), phase II wear facets (Facets 9–13; green), and lingual phase I wear facets (Facets 5–8; red).

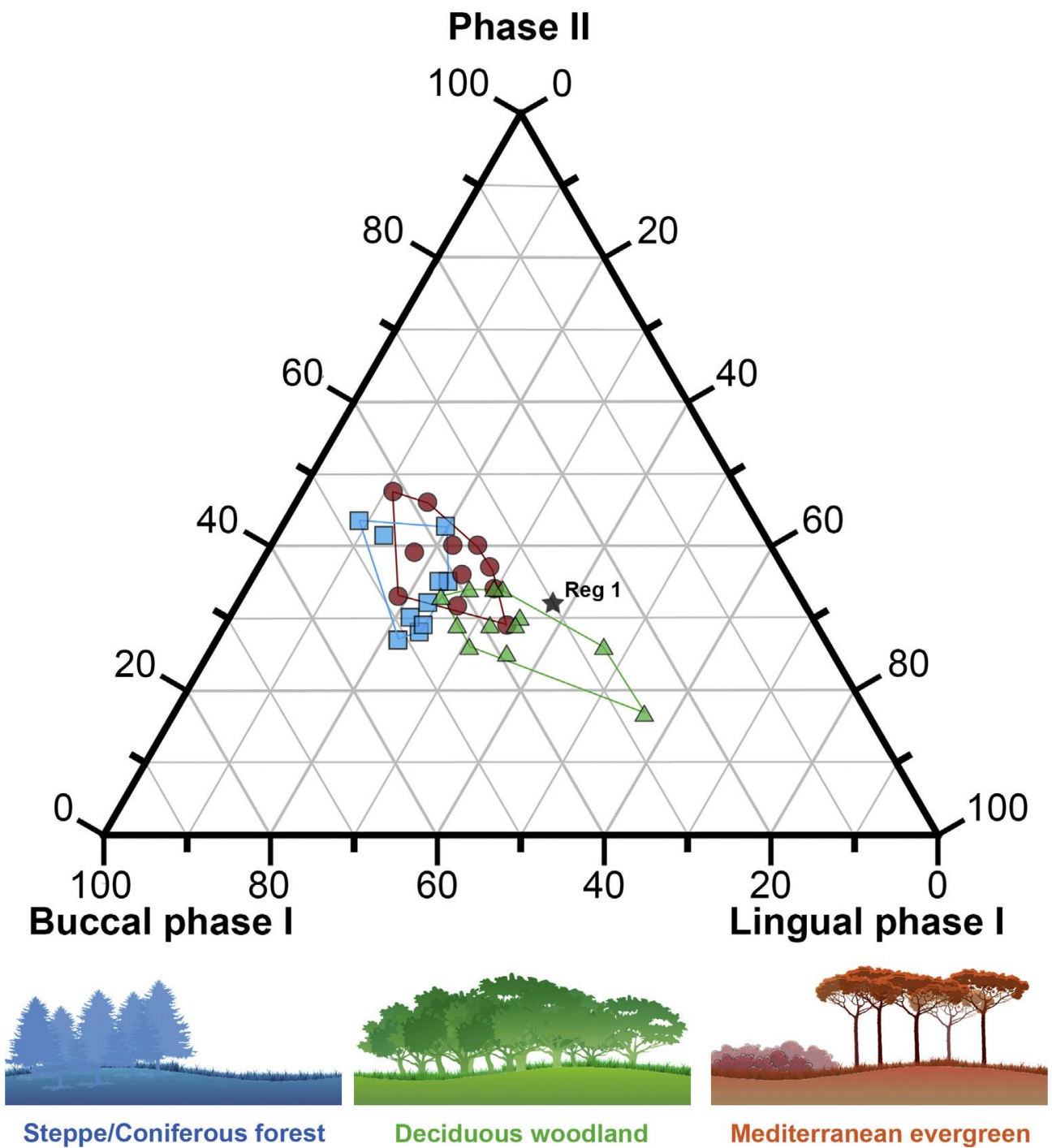


Figure 6. Ternary diagram showing the proportions (in %) of relative wear areas of buccal phase I facets, lingual phase I facets, and phase II facets of the M₂, which are positioned in an equilateral triangle. Each base of the triangle represents a ratio of 0% while the vertices correspond to a percentage of 100%. Regourdou 1 is represented by a star. Its wear pattern is compared to published data (Fiorenza et al., 2011a; Fiorenza, 2015), where Neanderthals and anatomically modern humans were grouped into three distinct ecogeographical contexts: steppe/coniferous forest (SCF, blue

squares), deciduous woodland (DEW, green triangles), and Mediterranean evergreen (MED, red circles).

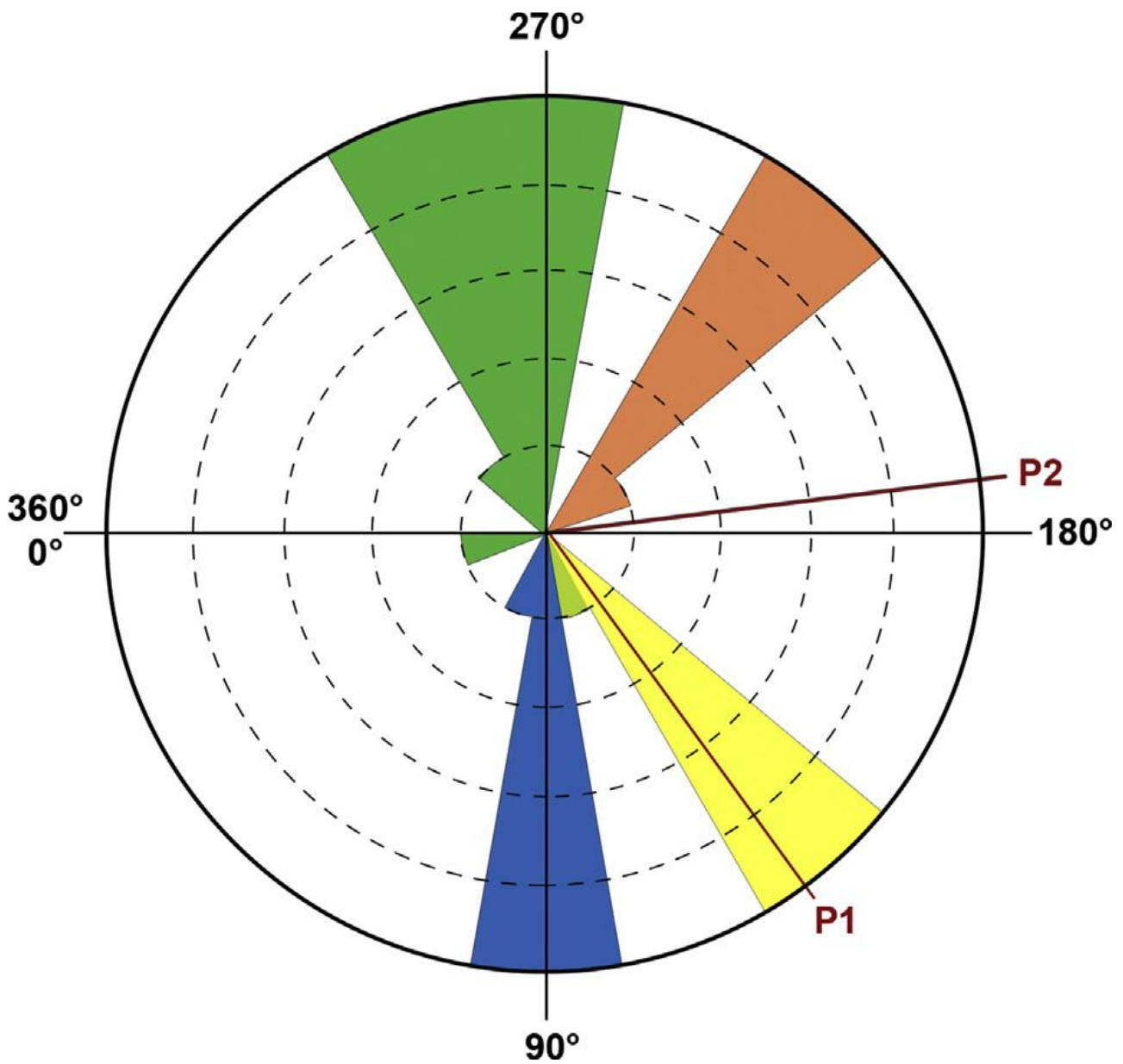


Figure 7. Rose diagram describing the major occlusal movements and para-facets' directions in the posterior dentition of the Regourdou 1 mandible. The major directions of possible movements starting from the maximum intercuspation are described as LRT (lateroretrusion, in blue), LPT (lateroprotrusion, in yellow), MT/ISS (mediotrusion and immediate sideshift, in green), and MPT (medioprotrusion, in orange; Douglass and DeVreugd, 1997; Kullmer et al., 2009). The vector of the two para-facets found on the left P₃ are highlighted in dark red and are labeled as P1 and P2. The rose diagrams show the frequency (divided into sectors) and orientation of wear and para-facets.

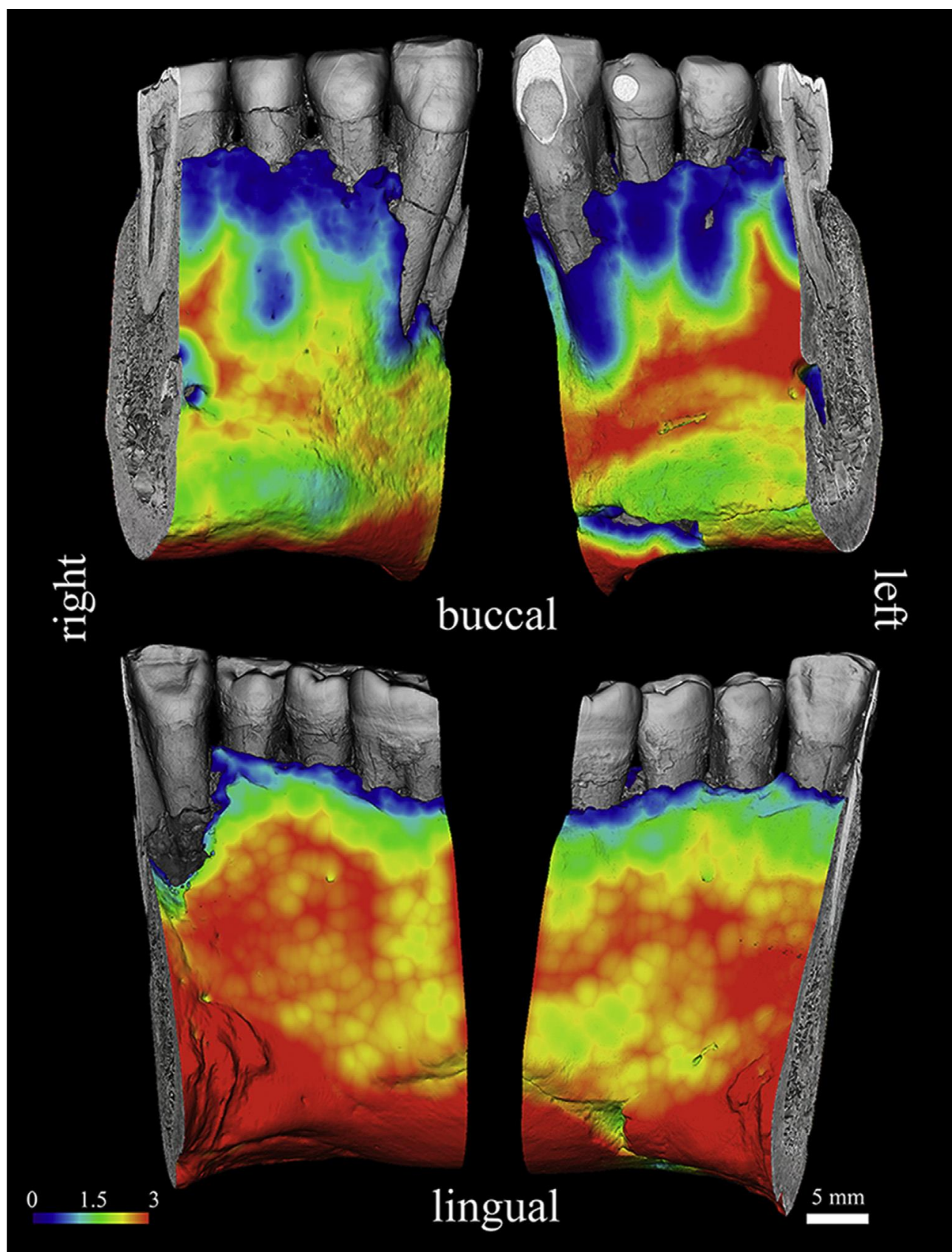
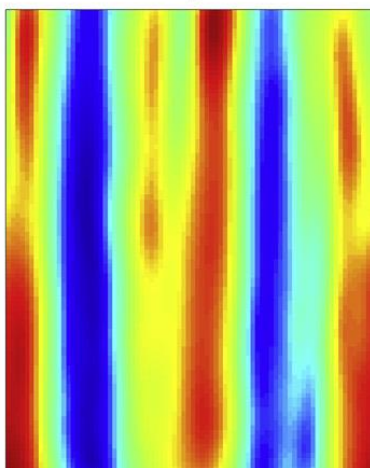
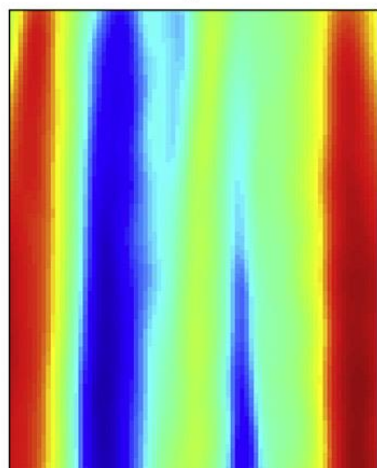


Figure 8. SR- μ CT-based map of cortical bone thickness topographic distribution across each selected right and left portions of the Regourdou 1 mandible between the canine and the first molar on the buccal (upper) and lingual (lower) aspects. Periosteal-endosteal thickness variation rendered by a chromatic scale increasing from thinner dark blue (0 mm) to thicker red (3 mm). Scale bar = 5 mm.

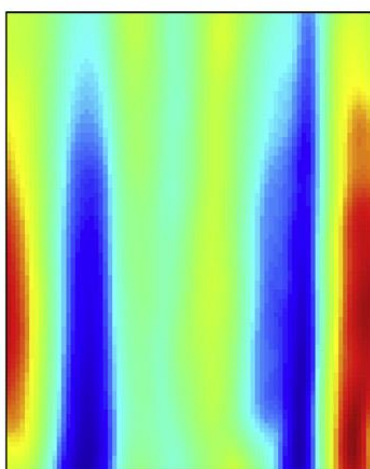
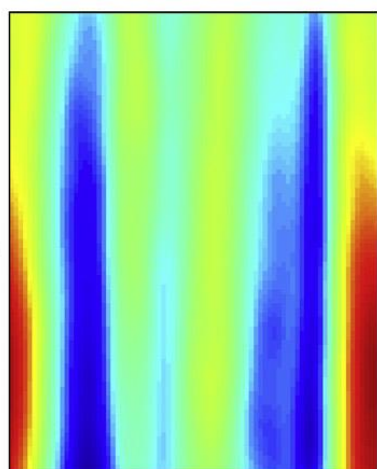
Regourdou 1

r

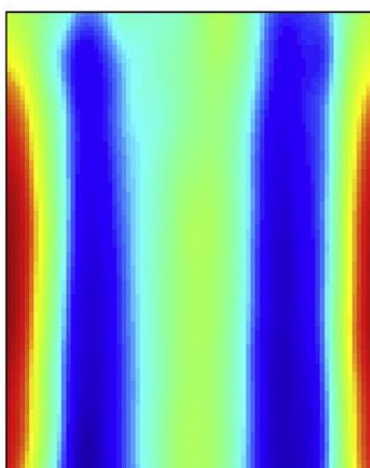
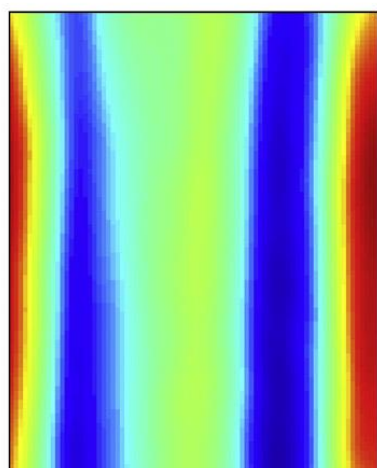
l



A



B



C

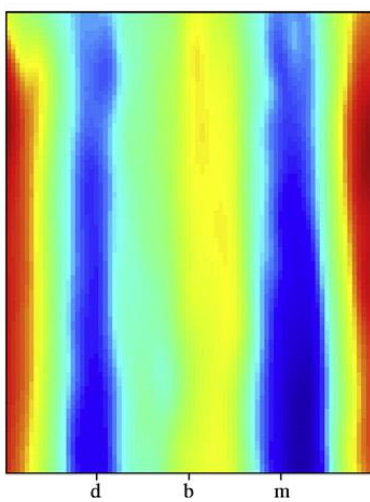
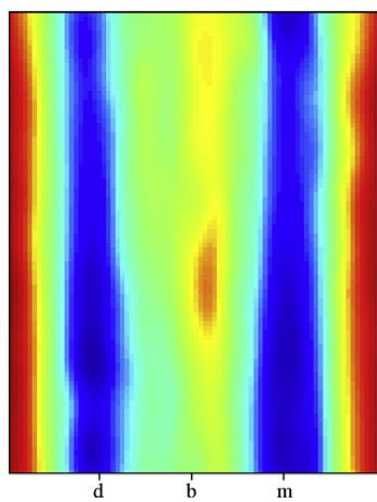
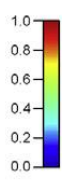
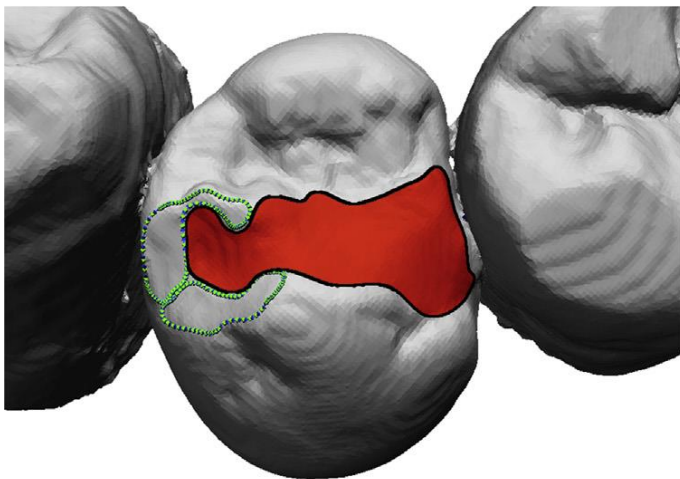
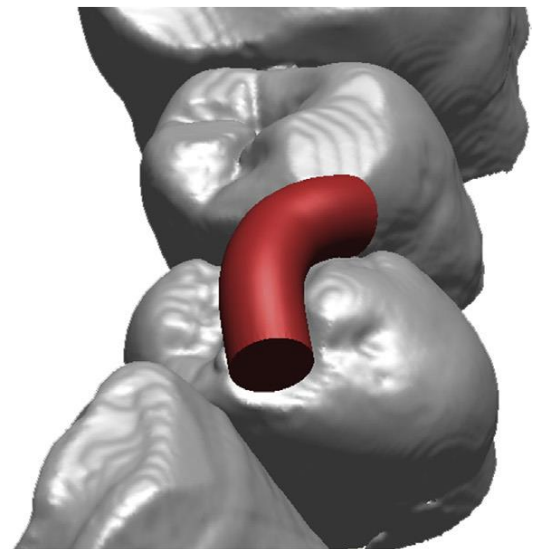


Figure 9. Standardized morphometric maps of radicular dentine thickness variation for the 60-85% root length portion (cervical) of the right (top left) and left (top right) P₃ of the Regourdou 1 mandible. The maps are compared to those generated for the right and left P₃ pairs from three individuals aged 26 (A), 32 (B), and 56 years (C), showing a low to moderate degree of occlusal wear (stages 1–2 to 3; Smith, 1984). In this comparative assemblage, slight right vs. left crown wear differences are only found in C (right P₃: stage 3; left P₃: stage 2). Each map is set within a grid made of 90 columns (X) running along the distal (d), buccal (b), and mesial (m) aspects of the root and of 100 rows (Y). Topographic thickness variation rendered by a chromatic scale increasing from thinner dark blue (0) to thicker red (1).



A



B

Figure 10. Digital models of the left P₃ of the Regourdou 1 mandible showing the semicircular facets (in green) and dentine exposure (in red; (A), and a cord-like CAD object fitting into the semicircular wear pattern (B).

TABLES

Table 1

Dentine exposure areas (mm²) and wear scores (after Smith, 1984) of the Neanderthal mandible of Regourdou 1.

Tooth	Side	Dentin area	Wear score
I ₁	L	3.53	5
I ₁	R	6.52	5
I ₂	L	7.89	5
I ₂	R	7.15	5
C ₁	L	7.34	5
C ₁	R	7.52	5
P ₃	L	9.59	7
P ₃	R	4.05	4
P ₄	L	—	3
P ₄	R	2.33	4
M ₁	L	15.31	4
M ₁	R	28.7	4
M ₂	L	0.95	3
M ₂	R	3.36	3
M ₃	L	1.84	3
M ₃	R	2.24	3

Abbreviations: L = left; R = right.

Table 2

Relative wear facet areas (in %) of left and right molars of the Neanderthal Regourdou 1 mandible.

Tooth	Buccal	Lingual	Phase II
L M ₁	0.34	0.40	0.57
L M ₂	0.24	0.39	0.37
L M ₃	0.23	0.34	0.43
R M ₁	0.38	0.42	0.58
R M ₂	0.30	0.38	0.32
R M ₃	0.30	0.34	0.36

Abbreviations: L = left; R = right.

Table 3

Wear facet inclinations of left and right molars of the Neanderthal Regourdou 1 mandible.

Tooth	Buccal	Lingual	Phase II
L M ₁	23.50	30.91	10.02
L M ₂	23.34	22.52	19.83
L M ₃	20.90	24.52	27.64
R M ₁	21.64	24.48	14.77
R M ₂	23.60	22.07	19.63
R M ₃	20.87	22.84	28.33

Abbreviations: L = left; R = right.

Table 4

Descriptive statistics of relative wear facet areas (in %) within the fossil biome groups and Regourdou 1 individual. Data for the three ecogeographic groups (steppe/coniferous forest, deciduous woodland and Mediterranean evergreen) are from [Fiorenza et al. \(2011a\)](#) and [Fiorenza \(2015\)](#).

Groups/specimens ^a	n	Buccal Phase I		Lingual Phase I		Phase II	
		Mean	SD	Mean	SD	Mean	SD
DEW	13	37	5.3	34.2	8.8	28.8	4.7
MED	11	39.3	4	23.2	6.7	37.5	5.6
SCF	11	45	3.8	20.6	5	34.4	5.8
Regourdou 1	1	30	–	38	–	32	–

^a Groups: DEW = Deciduous woodland (DEW); MED = Mediterranean evergreen; SCF = Steppe/coniferous forest (SCF).

Table 5

Basic circular statistic parameters measured for the major occlusal and parafacet directions in Regourdou 1 posterior dentition. Significant values ($p < 0.05$) are highlighted in bold.

Facets ^a	Mean	SD	K	95%	Rayleigh (P)	Rao (P)
LPT	123.1	3.6	150.3	(81.3, 164.8)	<1E-12	0.004
LRT	87.9	9.4	21.7	(56.3, 119.5)	1.04E-04	0.004
MPT	233.9	17.8	6.3	(189.3, 278.5)	6.99E-04	0.004
MT/ISS	298.7	32.8	2.1	(269.8, 327.6)	0.007	0.0178
P1	126.4	–	–	–	0.512	–
P2	187.1	–	–	–	0.512	–

^a Directions: LRT (lateroretrusion), LPT (lateroprotrusion), MT/ISS (mediotrusion and immediate sideshift), MPT (medioprotrusion) and P1 and P2 (parafacets).

Table 6

Cortical bone thickness (in mm) measured on homologous upper (u), intermediate (i) and lower (l) locations on the buccal and lingual aspects of the right (R) and left (L) sides of the Regourdou 1 mandible. See [Figure 2](#) for the three measurement locations.

Level	Buccal R	Buccal L	Lingual R	Lingual L
Upper (u)	2.15	2.60	2.71	2.72
Intermediate (i)	2.53	2.71	2.64	2.60
Lower (l)	2.19	2.39	3.23	2.37