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**HAL Id: hal-03002826**

**<https://hal.science/hal-03002826v1>**

Submitted on 12 Nov 2020

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The Neanderthal mandible BD 1 from La Chaise-de-Vouthon Abri Bourgeois-Delaunay (Charente, Southwestern France, OIS 5e). Dental tissue proportions, cortical bone distribution and endostructural asymmetry.

*La mandibule néandertalienne BD 1 de la Chaise-de-Vouthon Abri Bourgeois-Delaunay (Charente, Sud-Ouest de la France, OIS 5e). Proportions des tissus dentaires, distribution de l'os cortical et asymétrie endostructurale.*

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## ABSTRACTS

The 23 fossil human remains found at La Chaise-de-Vouthon Abri Bourgeois-Delaunay (Charente, Southwestern France) are all attributed to Neanderthals. The BD 1 mandible represents one of the best preserved specimens recovered in this assemblage, still bearing the entire set of 16 teeth, and attributed to an adult - likely 20-35 years old –individual. The geochronological and paleontological data indicate that the Neanderthals from Abri Bourgeois-Delaunay lived in a temperate environment between 127 and 116 ka (*i.e.*, during the OIS 5e). In this study, we integrate and expand the morphometric record of BD 1 by quantifying the tissue proportions of its entire permanent dentition, including radicular thickness repartition of four front teeth, and comparing its degree of endostructural asymmetry in tooth tissue organization and postcanine cortical bone topography with the patterns shown by Regourdou 1. Our results show that crown and radicular dental internal signature is typically Neanderthal, comparable with the available data for Regourdou 1, and is unambiguously distinct from the fossil and extant modern human patterns. Asymmetry in tooth tissue proportions in BD 1 and Regourdou 1 is clearly non-directional, as side dominance is nearly equally distributed between the left and the right antimeres. Similarly, both Neanderthal mandibles show no marked cortical bone asymmetry at the molar level, even if a slight right dominance is found in BD 1. Even if these results are globally consistent for the two Neanderthal mandible, extensive methodological research on the patterns of age- and sex-related endostructural variation displayed by human population samples from diverse chrono-geographic, socio-economic and biocultural contexts is still needed to more confidently evaluate the evolutionary and adaptive significance of the signals from the fossil record.

Les 23 restes humains fossiles découverts à La Chaise-de-Vouthon Abri Bourgeois-Delaunay (Charente, Sud-Ouest de la France) sont tous attribués à des Néandertaliens. La mandibule BD 1 représente un des spécimens les mieux préservés de l'assemblage, conservant encore ses 16 dents, et a été attribuée à un individu adulte – vraisemblablement âgé d'environ 20-35 ans. Les données géochronologiques et paléontologiques indiquent que les Néandertaliens de l'Abri Bourgeois-Delaunay vivaient dans un environnement tempéré il y a environ 127 à 116 ka (*i.e.*, pendant l'OIS 5e). Dans cette étude, nous apportons des informations morphométriques complémentaires sur la structure de BD 1 en quantifiant les proportions des tissus de l'ensemble de ses dents permanentes, incluant la distribution d'épaisseur de dentine radiculaire de quatre

dents antérieures, et en comparant le degré d'asymétrie endostructurale de l'organisation des tissus dentaires et de la topographie de l'os cortical au niveau des dents post-canines avec les patrons structuraux de Regourdou 1. Nos résultats montrent que la signature interne de la couronne et de la racine des dents est typiquement néandertalienne, comparable à celle de Regourdou 1, et clairement distincte des patrons humains modernes fossile et actuel. L'asymétrie des proportions des tissus dentaires de BD 1 et Regourdou 1 est non-directionnelle, sans dominance marquée entre les antimères gauches et droites. De la même manière, les deux mandibules néandertaliennes ne montrent pas de d'asymétrie marquée d'épaisseur de l'os cortical au niveau des molaires, même si une faible dominance droite est observée chez BD 1. Même si ces résultats sont globalement concordants pour les deux mandibules néandertaliennes, l'étude méthodologique étendue des patrons de variation de l'endostructure liés à l'âge et au sexe montrée par des populations humaines issues de divers contextes chrono-géographiques, socio-économiques et bioculturels reste nécessaire afin de mieux évaluer la valeur évolutive et adaptative des signaux observés dans le registre fossile.

## INDEX

Key-words: La Chaise-de-Vouthon, Eemian, Neanderthal mandible, tooth endostructure, cortical bone thickness, asymmetry.

Mots-clés: La Chaise-de-Vouthon, Eémien, mandibule néandertalienne, endostructure dentaire, épaisseur corticale, asymétrie.

## **Introduction**

The Middle to Late Pleistocene site complex of La Chaise-de-Vouthon, in the department of Charente, western France, is located on the left bank of an affluent of the Charente River, the Tardoire. It is located within a Middle Jurassic (Bajocian/Bathonian) limestone platform which underwent intense erosion across the Cenozoic (Tournepiche 1998) resulting in the formation of a network of mainly NW-oriented rock shelters and karstic cavities. The galleries extend over several tens of meters and open out c. 10 m above the Tardoire River through three main cave shelters ("porches"): Duport, Bourgeois-Delaunay and Suard (Debénath 1974a, 1977, 2006). This prehistoric locality was discovered in 1850 by J. Fermond and, following some preliminary field work conducted since 1865 by the abbots Bourgeois and Delaunay, it was excavated starting in the '30s by P. David, especially between 1945 and 1963, and then by A. Debénath, between 1967 and 1983 (Debénath 1974a, 1992, 2006; Debénath and Tournepiche 1996).

Human fossil remains at La Chaise-de-Vouthon, all attributed to Neanderthals, have been so far discovered at the Abri Suard, the Abri Bourgeois-Delaunay and, more recently, at the Tour of La Chaise cave ("grotte de la Tour"). The deposits of the Abri Suard and Abri Bourgeois-Delaunay, mostly of lacustrine origin and covered by a colluvial sequence intercalated with slump deposits and speleothems (Bertran 1999), were originally referred to a period ranging from Riss II to Riss-Würm, and from Riss III to Würm III, respectively (Debénath 1974a, 1977, 2006; Schvoerer *et al.* 1977; Schwarcz and Debénath 1979; Blackwell *et al.* 1983, 1990, 1992). According to a set of  $^{230}\text{Th}/^{234}\text{U}$  speleothem dates (Couchoud 2006; Vieilleveigne *et al.* 2008), the human remains from the Abri Suard, associated to a typically cold mammal fauna (Griggo 1996; see also Bouchud and Bouchud 1953; David and Prat 1965), belong to the Oxygen Isotope Stage (OIS) 6 and are likely younger than 163 thousand years (ka), while the age of the human fossil assemblage from Bourgeois-Delaunay, associated to a temperate fauna (Armand 1998; see also David and Prat 1965), is estimated between 127 and 116 ka, *i.e.*, to the OIS 5e (Debénath 2006). The Tour of La Chaise cave, located about 130 m W of the Suard rock shelter, was discovered in 2006 during speleological exploration. So far, it has provided a fossil human femoral shaft from a typically hyena den context whose mammal assemblage suggests a chronological attribution to the OIS 3 (Puymerail *et al.* 2012; *cf.* Tournepiche 1996, 2010).

The human fossil record from La Chaise-de-Vouthon consists of a whole of at least 76 dental (including isolated teeth), cranial and postcranial remains representing subadult and adult

individuals. Specifically, 52 specimens come from Suard, 23 from Bourgeois-Delaunay and one from the Tour of La Chaise (David and Bordes 1950; David and Piveteau 1953a, b; Piveteau 1955, 1970; Debénath 1967, 1974b, 1977; Debénath and Piveteau 1969; Genet-Varcin 1974, 1975a, b, 1976; Thoma 1975; Legoux 1976; Lacombe 1977; Saban 1978; Krukoff 1979; Hublin 1980; Tillier and Genet-Varcin 1980; Piveteau and Condemi 1988; Coqueugniot *et al.* 1996; Condemi 2001; Teilhol 2001, 2003; Macchiarelli *et al.* 2006, 2007; Puymeraill *et al.* 2012, 2013; an exhaustive list of the anthropological studies before the '90s can be found in Debénath 1992).

One remarkable specimen among those forming the Abri Bourgeois-Delaunay's human fossil assemblage is represented by the adult mandible BD 1, bearing the entire set of 16 teeth. Recovered on September 12<sup>th</sup> 1967 (Debénath 1967, 1974b), the specimen was described in detail by Condemi (2001). In agreement with the associated geochronological and technocultural context, the morphological and dimensional affinities (Condemi 2001: tables VII-1 and VII-2) of BD 1 indicate that it belongs to a Neanderthal individual likely 20-35 years old (Condemi 2001).

### *Research goals*

Intra-individual antimeric variation in tooth size is considered a measure of developmental instability, and fluctuating *vs.* directional odontometric asymmetry is used to assess the amount of relative stress a population experienced (*e.g.*, Corruccini *et al.* 2005; Hoover *et al.* 2005; Guatelli-Steinberg *et al.* 2006; Rizk *et al.* 2013; Scott *et al.* 2018). However, because of the usually advanced degree of occlusal crown wear, such external measures are barely useful in the study of fossil specimens, where an alternative approach consists in assessing antimeric variation in tooth tissue proportions and root size (*e.g.*, Braga *et al.* 2010; Kupczik and Hublin 2010; Prado-Simón *et al.* 2012; Macchiarelli *et al.* 2013). With this respect, a previous study on three-dimensional (3D) endostructural asymmetry assessed on the complete dentition of the adult Neanderthal mandible Regourdou 1 (Maureille *et al.* 2001), likely of comparable age at death of BD 1 (Volpato *et al.* 2012), has revealed some discrepancies in antimeric variation between the signals provided by the outer tooth crowns and the proportions displayed by their inner tissue components (Macchiarelli *et al.* 2013). Specifically, mostly based on a quantitative parameter often used to characterize endostructural tooth organization, *i.e.*, the percent of crown volume that is dentine and pulp, the study has shown that antimeric variation in Regourdou 1 is fluctuating (*i.e.*, non-directional) and globally modest (Macchiarelli *et al.* 2013). Additionally, a recent structural analysis of the same specimen has revealed a likely functional

link among degree of occlusal wear, root dentine thickness variation and site-specific variation in cortical bone distribution (Fiorenza *et al.* 2019). However, no comparative endostructural evidence from the complete permanent dentition of other Neanderthals is currently available.

In the present study, we integrate and expand the morphometric record of BD 1 (Condemi 2001) by quantifying the tissue proportions of its entire permanent dentition, including radicular thickness repartition of four front teeth, and comparing its degree of endostructural asymmetry in tooth tissue organization and postcanine cortical bone topography with the patterns shown by Regourdou 1 (Macchiarelli *et al.* 2008, 2013; Fiorenza *et al.* 2019).

## **Materials**

*BD 1* - Because of its *in situ* anatomical orientation, the slightly obliquely oriented dental arcade facing downwards, BD 1 suffered some breakage and bone loss, notably at the level of the nearly completely missing left ramus and of large portions of the body and of the perialveolar bone anterior to both first molars. Parts of the missing symphyseal region and the lower margin of the mental protuberance have been reconstructed by plaster to provide support to the incisor, canine and premolar teeth of both sides, whose roots are completely exposed (Condemi 2001: photos VII-1 to VII-8 and photo VIII-6; figs VII-1 to VII-5 and fig. VIII-9). As seen in anterior and posterior views, relatively large bony flakes are also missing at different points of the body, especially on the posterior aspect of the specimen. Nonetheless, following careful consolidation and restoration, BD 1 preserves a large portion of the right ramus, including most of the coronoid process, the mandibular notch and the condyle, as well as the postcanine body portion of both sides. The dentition, including the third molars, is complete and all crowns are rather well preserved with modest postdepositional damages. However, on the right side, the lower half of the root of the central incisor and the entire root of the canine are missing. Despite some locally exposed dentine patches, especially on the first molars, postcanine occlusal wear in this individual is moderate and relatively homogeneously spread between the antimeres, while occlusal enamel has been almost entirely removed on the incisors and, to a lesser extent, on the canines.

*Regourdou 1 (R1)* - For the purposes of the present study, we compared the BD 1's dental and bony endostructural features to those virtually extracted from the OIS 4 (71-57 ka) mandible Regourdou 1, from the eponym site at Montignac-sur-Vézère, in Dordogne (France) (Piveteau, 1959; for details and an historical review, see Maureille *et al.* 2015a, b). The R1 nearly intact

mandible, just slightly more robust compared to BD 1 (Condemi 2001: tables VII-1 and VII-2), presents a complete set of teeth showing a degree of occlusal wear macroscopically comparable to that of the specimen from the abri Bourgeois-Delaunay (Maureille *et al.* 2001; Macchiarelli *et al.* 2008, 2013; Volpato *et al.* 2012; Fiorenza *et al.* 2019;). However, Maureille *et al.* (2001) observed that in R1 the teeth of the right arcade were slightly more worn than their antimeres, a characteristic recently supported for the posterior dentition by the quantitative analysis performed by Fiorenza *et al.* (2019). This asymmetric pattern was also investigated by Volpato *et al.* (2012). By assessing the orientation of the microwear striations over the labial surfaces of incisors and canines, they concluded that the predominance in R1 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. In this specimen, enamel thickness asymmetry was also found on the postcanine teeth, especially between the third premolars (Macchiarelli *et al.* 2013; Fiorenza *et al.* 2019).

### **Methods of analysis**

Both mandibles BD 1 and Regourdou 1 were scanned in 2005 at the beamline ID 17 of the European Synchrotron Radiation Facility, Grenoble, France (experiment SC1587c), according to the following parameters: energy, 70 keV; projections, 1500 in half acquisition mode; integration time, 22.9 ms. The final sections were reconstructed from sinograms and saved in a 32-bit floating-point raw format at a voxel size of 45.5\*45.5\*45.7  $\mu\text{m}$  for the scans of the teeth and with an isotropic voxel size of 350  $\mu\text{m}$  for the whole mandible.

We used routinely applied standard procedures of semiautomatic threshold-based segmentation to virtually reconstruct tooth volume (for technical details, see Kono 2004; Macchiarelli *et al.* 2006; Olejniczak *et al.* 2008; Zanolli *et al.* 2014, 2018).

A 3D virtual rendering of BD 1 in various perspectives is provided in fig. 1.

[figure 1 here]

### *Enamel thickness distribution maps*

For all teeth of both arcades, enamel occlusal distribution and thickness variation (occlusal-labial for the front teeth) were comparatively rendered in BD 1 and Regourdou 1 through 3D topographic mapping (cartographies) generated using a tooth-specific chromatic scale, where thickness increases from dark blue (thinner enamel) to red (thicker enamel) and white indicates



emerging underlying dentine patches (*cf.* Macchiarelli *et al.* 2008, 2013; Bayle *et al.* 2011; Zanolli 2015).

#### *Dental tissue proportions*

Twelve linear, surface, and volumetric variables describing tooth structural organization and proportions were measured or calculated for each virtually extracted tooth: volume of enamel cap ( $V_e$ ,  $\text{mm}^3$ ); total volume of dentine ( $V_d$ ,  $\text{mm}^3$ ); total volume of pulp ( $V_p$ ,  $\text{mm}^3$ ); total volume of cementum ( $V_{cem}$ ,  $\text{mm}^3$ ; not available for Regourdou 1); total tooth volume ( $V_t$ ,  $\text{mm}^3$ ); volume of crown dentine + pulp ( $V_{cdp}$ ,  $\text{mm}^3$ ); volume of the root dentine + pulp ( $V_{rdp}$ ,  $\text{mm}^3$ ; not available for Regourdou 1); surface area of enamel-dentine junction (SEDJ,  $\text{mm}^2$ ); percent of crown volume that is dentine and pulp ( $V_{cdp}/V_c$ , %); percent of the root volume that is cementum ( $V_{cem}/V_{rdp}$ , %; not available for Regourdou 1); 3D average enamel thickness (3D AET, mm); the scale-free 3D relative enamel thickness (3D RET).

#### *Radicular dentine thickness distribution*

To assess root dentine thickness repartition in the BD 1's front teeth (except for the roots of the right central incisor and canine, respectively incomplete and absent) and to compare this topographic pattern with that displayed by Regourdou 1, in each available specimen we virtually unzipped the 15-85% portion (15% being closer to the dental cervix) of the total root length along a predefined vertical line established at the middle of the labial aspect. By using a custom routine developed in R v.3.6 (R Development Core Team 2019) with the packages Momocs (Bonhomme *et al.* 2014), spatstat (Baddeley *et al.* 2015) and gstat (Pebesma 2004), we then virtually unrolled it and projected its local properties into a morphometric map (Bondioli *et al.* 2010; Bayle *et al.* 2011; Macchiarelli *et al.* 2013; Zanolli *et al.* 2014, 2018). In the analysis, dentine thickness values have been standardized between 0 and 1 and each morphometric map has been set within a grid of 90 rows and 100 columns.

#### *Cortical bone distribution*

As previously noted, the BD 1's corpus presents on both sides some taphonomic breaks and local bone loss that complicate the task of reliably assessing structural variation of the cortical shell at volumetric scale. However, following the segmentation procedure recently applied to

the Regourdou 1 mandible (for technical details, see Fiorenza *et al.* 2019), it was possible to confidently separate its endosteal surface from the immediately underlying cancellous bone. We then measured left *vs.* right cortical bone topographic thickness distribution on two bucco-lingual slices taken perpendicular to the occlusal plane and virtually extracted between the first and second molars (M1/M2) and between the second and third molars (M2/M3), respectively. The upper limit of each section was arbitrarily established immediately below the perialveolar area, where cortical bone wears thin (Zanolli *et al.* 2017). For comparison, the homologous slices were extracted on Regourdou 1. In processing the record of the two fossil specimens, minor local discontinuities along the periosteal and endosteal contours were virtually integrated by manual corrections. In the four extracted individual slices (two for each side on each mandible), cortical bone thickness topographic variation was measured by computing the distance between the periosteal and endosteal surfaces of the cortical shell where, for each point of one surface, the closest point on the other surface was computed (Fiorenza *et al.* 2019). Visualization of bone thickness variation has been rendered using the R v.3.6 package ggplot2 3.2 (Wickman 2016). To allow direct comparisons between BD 1, proportionally smaller, and Regourdou 1, proportionally larger, we calculated the scale-free bi-dimensional (2D) Relative Cortical Thickness (2D RCT) index (see Cazenave *et al.* 2017). It is given as the average cortical thickness (2D ACT) multiplied by 100 and divided by the square root of the trabecular area (TBA, in mm<sup>2</sup>) ( $2D\ RCT = 2D\ ACT \times 100/TBA^{1/2}$ ), where 2D ACT is the ratio between cortical area (CA, in mm<sup>2</sup>) and the endosteal contour length (in mm).

### *Asymmetry*

For each variable measurable on both dental antimeres (84/96 of cases) and on two cortical bone virtual sections (2D RCT), percent asymmetry was calculated as:  $(L-R)/([L+R]*0.5)$ , where L and R correspond to the left and right side, respectively (Corruccini *et al.* 2005).

## **Results**

### *Enamel thickness distribution maps*

In terms of amount and patterns of macroscopic occlusal crown wear (*cf.* Smith 1984) and of left *vs.* right side distribution, BD 1 and Regourdou 1 are globally comparable (fig. 2), the only

exception being represented by the peculiar wear pattern displayed by the left P3 in Regourdou 1 (Maureille *et al.* 2001; Volpato *et al.* 2012; for a recent quantitative assessment and functional interpretation, see Fiorenza *et al.* 2019). Otherwise, together with a relatively homogeneous distribution between the antimeres of both front and postcanine teeth, the two specimens share a more marked wear on the incisors and canines, which is a typical likely functionally-related Neanderthal feature (Volpato *et al.* 2012). However, also occlusal molar topography is partially obliterated, including on the M3s. In these two Neanderthal representatives, the thickest enamel is nearly invariably found on the labial (front teeth) and buccal (postcanine dentition) aspects. Their lateral incisors display thicker enamel than the I1s. Interestingly, BD 1's front teeth show slightly thicker enamel compared to Regourdou 1, while no difference is appreciable for the post-canine crowns, showing relatively thicker enamel at the base of the buccal cusps and thinner enamel in the occlusal basin, including in the unworn areas.

[figure 2 here]

#### *Dental tissue proportions*

Tooth tissue proportions in BD 1 are shown in tab. 1. For the tooth size-independent percent of crown that is dentine and pulp ( $V_{cdp}/V_c$ ), its values overlap the estimates available for Regourdou 1 (*cf.* Macchiarelli *et al.* 2013: tab. 1), some very minor differences uniquely concerning the P3s, the M1s and the M3s, whose proportions are slightly lower in BD 1. In terms of enamel thickness, the P4s and M3s, *i.e.*, the proportionally least worn postcanine crowns in BD 1 (stage 2 to 3 following Smith 1984), have an average 3D RET of 15.3 and 14.6, respectively. Here again, the estimates for this scale-free parameter are comparable to those assessed in Regourdou 1, where BD 1 displays an only slightly higher value for the M3, but not the P4. As previously noted, in BD 1 the roots of the right I1 and C are respectively incomplete and missing, thus limiting tissue proportion estimates to the crown. As shown by the percent of root volume that is cementum, in BD 1 a rather thick layer of cementum covers most roots. Indeed,  $V_{cem}/V_{rdp}$  ranges from 11.6%, on the left M3, to 43.5%, on the left I1, but no direct comparison can be performed with the pattern displayed by Regourdou 1, as its cementum distribution has not been reported yet.

[table 1 here]

In BD 1, antimeric differences in tooth tissue proportions (84 cases calculated on 96) are extremely variable, as they range from nearly zero to 92% (M3  $V_{cem}/V_{rdp}$ ), the highest values systematically concerning the parameters also or uniquely integrating the radicular components.

With this respect, the impact of cementum thickness variation is evident. However, when uniquely the crown is considered, absolute values of asymmetry range from 1% (M2 Vcdp) to 18.6% (M1 SEDJ), 37 out of 48 cases showing an asymmetry below 10%. The Vcdp/Vc is in absolute the least asymmetric parameter (range 0.6-4.9%). Importantly in this study, asymmetry is globally fluctuating, side dominance being nearly equally distributed between the left and the right antimeres (51% vs. 49%, respectively). This is also shown by the three variables Vcdp/Vc, 3D AET and 3D RET (fig. 3).

[figure 3 here]

#### *Radicular dentine thickness distribution*

The standardized cartographies of radicular dentine thickness distribution in four anterior teeth of BD 1 (three left and one right roots) and Regourdou 1 (one left and three right roots) are illustrated in fig. 4. The two Neanderthals exhibit a nearly identical repartition pattern, with relatively and absolutely thicker dentine found across the lingual and labial aspects, while the mesial and distal sides systematically display the thinnest dentine, notably towards the root apices. However, in all front teeth suitable for such kind of analysis, BD 1 shows more contrasted maps with relatively thicker radicular dentine spread across a larger surface than measured in Regourdou 1, even if absolutely thickest dentine is found on the right I2 of the latter specimen (c. 3.7 mm vs. c. 3.2 in BD 1). Unfortunately, intra-individual asymmetry in both specimens can be only assessed for the I2s. With this respect, the dentine of the right lateral incisor is distinctly thicker and more spread in BD 1 at all investigated sites, while only a modest site-specific left prevalence is found in Regourdou 1.

[figure 4 here]

#### *Cortical bone distribution*

Cortical bone thickness topographic variation (absolute distance values between the periosteal and the endosteal contours) assessed in BD 1 and Regourdou 1 across two homologous bucco-lingual slices virtually extracted at the M1/M2 and M2/M3 positions of both left and right mandibular sides is shown in fig. 5. Even if some site-specific differences are notable on both slices, especially across the inferior and buccal portions of the corpus, the two specimens show a globally similar distribution pattern, where bone thickness progressively increases from the perialveolar lingual aspect towards the inferior margin, and then progressively thins towards the perialveolar buccal margin. At nearly all sites captured by the two slices, and especially across their inferior portion, BD 1 shows absolutely thinner cortical bone compared to

Regourdou 1, except at the buccal aspect of the M1/M2 right slice, where BD 1 exhibits slightly thicker cortical bone than measured in Regourdou 1.

[figure 5 here]

This is also shown by the scale-free Relative Cortical Thickness index (2D RCT). For this parameter, percent asymmetry in BD 1 indicates slight right dominance at both sites (absolute values range: 9.3-12.9%), while Regourdou 1 shows no asymmetry at M1/M2 level and slight right dominance (-7.5%) at M2/M3 level (tab. 2)

[table 2 here]

## **Discussion and conclusions**

Despite the modest preservation conditions and incompleteness of the supporting mandibular bone, the dentition of the adult Neanderthal specimen BD 1, from the Bourgeois-Delaunay shelter of the La Chaise-de-Vouthon site complex, Charente (France), is among the best preserved complete lower dentitions from the western European Eemian (OIS 5e) human fossil record (Conдеми 2001). The microtomographic-based analysis of its inner structural organization performed in this study allowed a detailed comparison with the homologous features of another exceptionally-preserved Neanderthal permanent dentition: that of the c. 90 km apart OIS 4 specimen Regourdou 1 (Maureille *et al.* 2001), likely of similar age at death (Volpato *et al.* 2012) and of comparable external morphometric characteristics, including the degree of occlusal crown wear (Fiorenza *et al.* 2019).

By relying upon some previous analyses of the Regourdou 1 mandible and dentition (Maureille *et al.* 2001; Macchiarelli *et al.* 2008, 2013; Volpato *et al.* 2011, 2012; Fiorenza *et al.* 2019), here we comparatively assessed the degree of asymmetry in BD 1 of tooth tissue proportions (entire dentition), radicular dentine thickness repartition (anterior teeth), and cortical bone topography of the molar region. Besides their acknowledged taxonomic and phylogenetic significance, such genetically-controlled features are also sensible individual indicators of environmental (including nutritional) and/or systemic physiological perturbations (growth disruption) experienced during development (*e.g.*, Rizk *et al.* 2013), and also tend to record the variable impact of the biomechanical environment (loading regimes related to masticatory/paramasticatory activities) on the structural organization of dental and bony tissues (rev. in Fiorenza *et al.* 2019).

Preliminarily, it is anyhow relevant to note that the BD 1's crown and radicular dental endostructural signature is typically Neanderthal (*cf.* Macchiarelli *et al.* 2006, 2008, 2013; Olejniczak *et al.* 2008; Kupczik and Hublin 2010; Bayle *et al.* 2011, 2017; Prado-Simón *et al.* 2012; Le Cabec *et al.* 2013; Martin *et al.* 2017; Zanolli *et al.* 2018) and is unambiguously distinct from the fossil and extant modern human patterns (*cf.* Le Luyer 2016).

In BD 1, asymmetry in tooth tissue proportions is clearly non-directional, as side dominance is nearly equally distributed between the left and the right antimeres. This pattern is even more accentuated than that observed in Regourdou 1, where a right dominance is found in 64% of cases (Macchiarelli *et al.* 2013). However, this percentage decreases and approaches the BD 1's condition if the P3s are excluded from the analysis. In fact, compared to its antimeres, Regourdou 1's left third premolar bears unusual semi-circular enamel wear facets likely resulting from some tooth-tool uses for daily task activities (Fiorenza *et al.* 2019). Also, compared to BD 1, the posterior dentition of Regourdou 1 is characterized by a more asymmetric wear pattern, the right side being more worn than its counterpart (Maureille *et al.* 2001; Fiorenza *et al.* 2019), a condition that likely affected the quantitative assessment of at least some among the parameters considered in our analyses.

Similarly to Regourdou 1, fluctuating endostructural asymmetry in BD 1 is globally moderate, notably for the parameters not directly affected by the variably thick coat of radicular cementum present in this specimen and, of course, for those generally poorly affected by moderate occlusal wear. With this respect, it is noteworthy that when BD 1 and Regourdou 1 are compared for the total volume of dentine (Vd) or the surface area of enamel-dentine junction (SEDJ), for example, their degree of asymmetry is comparable (*cf.* tab. 1 with tab. 1 in Macchiarelli *et al.* 2013). In some cases, asymmetry does not even exceed the measurement error reported for such kind of variables in tests run for intra- and inter-observer accuracy (*e.g.*, Macchiarelli *et al.* 2008). Even if currently based on the record from two individuals only, this evidence tends to support previous suggestions that, among Neanderthals, at least nutritional stresses during growth were not especially elevated compared with those affecting several present-day populations (Hutchinson *et al.* 1997). However, in both BD 1 and Regourdou 1 dental wear has also to be taken into account as additional parameter to any possible developmental noise (Benazzi *et al.* 2013; Macchiarelli *et al.* 2013). Finally, it should be pointed out that, at the best of our knowledge, no comparative quantitative data from representative extant/recent human samples is available on tooth tissue proportion antimeric variation, which currently limits our interpretations.

The significance of radicular dentine intra- and inter-individual variation is also difficult to interpret because of similar lack of comparative information from controlled reference series, as well as of the paucity of evidence from the human fossil record, limited to a handful of specimens (Bayle *et al.*, 2011; Macchiarelli *et al.*, 2013; Zanolli *et al.*, 2014, 2018). A recent study of the Regourdou 1 mandible has suggested a likely cause-effect functional relationship among uneven masticatory and/or non-masticatory loadings, occlusal crown macrowear, asymmetric variation in radicular dentine and postcanine cortical bone distribution (Fiorenza *et al.* 2019). However, the relative role of genetic *vs.* functional factors in the distribution of root dentine is not yet elucidated. Nonetheless, while few studies have investigated the long-term impact on the radicular dentine mechanoreceptors of variably frequent and intense strains and stresses (Dean 2017), the capacity of bone as dynamic tissue to respond to alterations of its mechanical environment is very-well reported, notably for the mandible, where thicker cortical bone is commonly found in areas facing higher strains (*e.g.*, Masumoto *et al.* 2001; Daegling and Hotzman 2003; Lieberman *et al.* 2004; Fukase 2007; Fukase and Suwa 2008; Martínez-Gomis *et al.* 2009; Holmes and Ruff 2011; Gröning *et al.* 2012; but see Ichim *et al.* 2007). Unfortunately, the evidence from the hominin/human fossil record is extremely limited (*e.g.*, Daegling and Grine 1991; Grine and Daegling, 2017; Zanolli *et al.* 2017; Fiorenza *et al.* 2019), the reason of the interest here of a direct comparison between BD 1 and Regourdou 1 for evaluating if markedly uneven biomechanical demands and preferences over the molar region may have resulted into distinct cortical bone asymmetry. Limitedly to the evidence captured from two virtual sections extracted across the M1/M2 and M2/M3 boundaries, this does not seem to be the case in the two Neanderthal individuals, even if a slight right dominance is found in BD 1.

In conclusion, the results scattered from the present endostructural analysis of the OIS 5e BD 1 specimen from Bourgeois-Delaunay, which integrate and expand similar research performed on the mandible and dentition of the OIS 4 individual Regourdou 1 (Macchiarelli *et al.* 2008, 2013; Volpato *et al.* 2011, 2012; Fiorenza *et al.* 2019), provide new original evidence on antimeric variation in Neanderthal osteodental organization. Nonetheless, extensive methodological research to be developed on the patterns of age- and sex-related endostructural variation displayed by human population samples from diverse chrono-geographic, socio-economic and biocultural contexts is needed to more confidently evaluate the evolutionary and adaptive significance of the signals from the fossil record.

## ACKNOWLEDGMENTS

*The fossil specimen BD 1 is curated at the Musée d'Angoulême, while Regourdou 1 is at the Musée d'Art et d'Archéologie du Périgord, Périgueux. For access to Regourdou 1, we are indebted to F. Couturas, G. Marchesseau and V. Merlin-Anglade. Scanning of both mandibles BD 1 and Regourdou 1 was performed within the framework of the European "TNT Project" at the ESRF beamline ID 17 (Grenoble) thanks to the local collaboration provided by A. Bravin, C. Nemoz and P. Tafforeau. For contribution to the documentation and analysis of both fossils, we thank P. Bayle, S. Benazzi, A. Bergeret, L. Bondioli, L. Fiorenza, F. Gröning, O. Kullmer, and especially V. Volpato. For discussion, we also thank C. Dean, L.C. Fitton, B. Maureille, P. O'Higgins, P. Sémal and B. Vandermeersch.*

*Among the authors, J.-F.T., A.M. and R.M. acknowledge the stimulating role and unique contribution provided by A. Debénath during the European "TNT Project".*

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**Table 1** - Antimeric variation (% asymm.; Corruccini *et al.* 2005) in tooth tissue proportions (variables from Ve to Vcem/Vrdp) and 3D enamel thickness (AET and RET) assessed in the Neanderthal mandible BD 1. See the text for the meaning of the variables. Negative values indicate right dominance; for each variable, italics and bold indicate the lowest and the highest values, respectively (*cf.* Macchiarelli *et al.* 2013: table 1). Note that, because of incomplete/missing root, some variables were not measured/calculated for the right central incisor (I1) and canine (C).

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| Tooth     |          | Ve<br>(mm <sup>3</sup> ) | Vd<br>(mm <sup>3</sup> ) | Vp<br>(mm <sup>3</sup> ) | Vcem<br>(mm <sup>3</sup> ) | Vt<br>(mm <sup>3</sup> ) | Vcdp<br>(mm <sup>3</sup> ) | Vrdp<br>(mm <sup>3</sup> ) | SEDJ<br>(mm <sup>2</sup> ) | Vcdp/Vc<br>(%) | Vcem/Vrdp<br>(%) | 3D AET<br>(mm) | 3D RET     |
|-----------|----------|--------------------------|--------------------------|--------------------------|----------------------------|--------------------------|----------------------------|----------------------------|----------------------------|----------------|------------------|----------------|------------|
| <b>I1</b> | left     | 41.98                    | 365.23                   | 15.89                    | 115.29                     | 423.10                   | 116.21                     | 264.91                     | 104.13                     | 73.46          | 43.52            | 0.40           | 8.26       |
|           | right    | 38.83                    | -                        | -                        | -                          | -                        | 101.57                     | -                          | 92.80                      | 72.34          | -                | 0.42           | 8.97       |
|           | % asymm. | 7.8                      | -                        | -                        | -                          | -                        | 13.4                       | -                          | 11.5                       | 1.5            | -                | -3.7           | -8.2       |
| <b>I2</b> | left     | 56.80                    | 483.34                   | 21.93                    | 108.59                     | 562.07                   | 130.63                     | 374.38                     | 115.40                     | 69.69          | 29.01            | 0.49           | 9.70       |
|           | right    | 52.92                    | 479.63                   | 21.91                    | 95.95                      | 554.47                   | 126.05                     | 375.43                     | 109.05                     | 70.43          | 25.56            | 0.49           | 9.68       |
|           | % asymm. | 7.1                      | <i>0.8</i>               | <i>0.1</i>               | 12.4                       | <i>1.4</i>               | 3.6                        | <i>-0.3</i>                | 5.7                        | -1.1           | 12.6             | 1.4            | <i>0.2</i> |
| <b>C</b>  | left     | 76.46                    | 565.91                   | 25.65                    | 155.41                     | 668.02                   | 163.02                     | 433.38                     | 128.82                     | 68.07          | 35.86            | 0.59           | 10.87      |
|           | right    | 71.44                    | -                        | -                        | -                          | -                        | 142.93                     | -                          | 116.30                     | 66.67          | -                | 0.61           | 11.75      |
|           | % asymm. | 6.8                      | -                        | -                        | -                          | -                        | 13.1                       | -                          | 10.2                       | 2.1            | -                | -3.4           | -7.8       |
| <b>P3</b> | left     | 77.64                    | 382.53                   | 17.54                    | 75.17                      | 477.72                   | 113.62                     | 286.55                     | 106.66                     | 59.40          | 26.23            | 0.73           | 15.03      |
|           | right    | 77.34                    | 351.71                   | 19.43                    | 91.91                      | 448.48                   | 114.91                     | 256.45                     | 109.42                     | 59.77          | 35.84            | 0.71           | 14.54      |
|           | % asymm. | <i>0.4</i>               | 8.4                      | -10.2                    | -20.0                      | 6.3                      | -1.1                       | 11.1                       | -2.6                       | <i>-0.6</i>    | -31.0            | 2.9            | 3.3        |
| <b>P4</b> | left     | 91.13                    | 357.56                   | 20.34                    | 94.87                      | 469.03                   | 119.60                     | 258.49                     | 119.54                     | 56.76          | 36.70            | 0.76           | 15.47      |
|           | right    | 100.15                   | 421.62                   | 24.32                    | 104.87                     | 546.10                   | 134.75                     | 311.30                     | 129.18                     | 57.36          | 33.69            | 0.78           | 15.12      |
|           | % asymm. | -9.4                     | <b>-16.4</b>             | <b>-17.8</b>             | -10.0                      | <b>-15.2</b>             | -11.9                      | -18.5                      | -7.8                       | -1.1           | 8.6              | -1.7           | 2.3        |
| <b>M1</b> | left     | 123.14                   | 812.81                   | 48.27                    | 130.09                     | 984.22                   | 271.38                     | 589.96                     | 179.84                     | 68.79          | 22.05            | 0.68           | 10.58      |
|           | right    | 147.34                   | 742.25                   | 50.58                    | 177.93                     | 940.17                   | 318.27                     | 475.00                     | 216.80                     | 68.36          | 37.46            | 0.68           | 9.95       |
|           | % asymm. | <b>-17.9</b>             | 9.1                      | -4.7                     | -31.1                      | 4.6                      | <b>-15.9</b>               | <b>21.6</b>                | <b>-18.6</b>               | 0.6            | -51.8            | <i>0.8</i>     | 6.1        |
| <b>M2</b> | left     | 160.10                   | 925.70                   | 64.64                    | 124.21                     | 1150.44                  | 313.15                     | 612.55                     | 220.46                     | 66.17          | 20.28            | 0.73           | 10.69      |
|           | right    | 184.01                   | 981.75                   | 65.94                    | 130.05                     | 1231.69                  | 313.44                     | 668.43                     | 217.32                     | 63.01          | 19.46            | 0.85           | 12.46      |

|           |          |        |        |       |              |        |        |        |        |            |              |              |              |
|-----------|----------|--------|--------|-------|--------------|--------|--------|--------|--------|------------|--------------|--------------|--------------|
|           | % asymm. | -13.9  | -5.9   | -2.0  | -4.6         | -6.8   | -1.0   | -8.7   | 1.4    | <b>4.9</b> | 4.1          | <b>-15.3</b> | <b>-15.3</b> |
| <b>M3</b> | left     | 146.84 | 661.94 | 50.64 | 56.62        | 859.41 | 222.97 | 489.96 | 169.27 | 60.29      | 11.56        | 0.87         | 14.31        |
|           | right    | 158.25 | 616.89 | 48.76 | 139.74       | 823.90 | 221.19 | 444.94 | 174.79 | 58.29      | 31.41        | 0.91         | 14.97        |
|           | % asymm. | -7.5   | 7.0    | 3.8   | <b>-84.7</b> | 4.2    | 0.8    | 9.6    | -3.2   | 3.4        | <b>-92.4</b> | -4.3         | -4.6         |

**Table 2** - Antimeric variation (% asymm.; Corruccini *et al.* 2005) of the scale-free bi-dimensional (2D) Relative Cortical Thickness (2D RCT) index (Cazenave *et al.* 2017) comparatively assessed in bucco-lingual slices virtually extracted between the first and second molars (M1/M2) and the second and third molars (M2/M3) in the Neanderthal mandibles BD 1 and Regourdou 1. Negative values indicate right dominance.

**Tableau 2** - Variations entre antimères (% asymm.; Corruccini *et al.* 2005) de l'indice bidimensionnel (2D) et sans échelle d'épaisseur relative de l'os cortical (2D RCT) (Cazenave *et al.* 2017) estimées pour les sections bucco-linguales extraites virtuellement entre les premières et secondes molaires (M1/M2) et deuxième et troisièmes molaires (M2/M3) des mandibules néandertaliennes BD 1 et Regourdou 1. Les valeurs négatives indiquent une dominance du côté droit.

| <b>Virtual slice position</b> | <b>BD 1</b> | <b>Regourdou 1</b> |
|-------------------------------|-------------|--------------------|
| M1/M2 left                    | 10.9        | 15.5               |
| M1/M2 right                   | 12.4        | 15.5               |
| % asymm.                      | -12.9       | 0.0                |
| M2/M3 left                    | 11.3        | 14.2               |
| M2/M3 right                   | 12.4        | 15.3               |
| % asymm.                      | -9.3        | -7.5               |

## Captions to the tables

**Table 1** - Antimeric variation (% asymm.; Corruccini *et al.* 2005) in tooth tissue proportions (variables from Ve to Vcem/Vrdp) and 3D enamel thickness (AET and RET) assessed in the BD 1 Neanderthal mandible. See the text for the meaning of the variables. Negative values indicate right dominance; for each variable, italics and bold indicate the lowest and the highest values, respectively (*cf.* Macchiarelli *et al.* 2013: table 1). Note that, because of incomplete/missing root, some variables were not measured/calculated for the right central incisor (I1) and canine (C).

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## Captions to the figures

**Figure 1** – Photographs in superior view from the left side (A) and in lateral view showing the reconstructed portion of the inferoanterior aspect of the Neanderthal mandible BD 1 (B),



and microtomographic-based 3D rendering in semi-transparency of the specimen in anterior (C), superior (D), slightly obliquely-oriented lateral left (E), and slightly obliquely-oriented lateral right (F) views. Note that the reconstructed part of the symphyses made with plaster (A) was reinforced using a bended transverse metallic bar visible on the virtual renderings (C-F). Scale bar: 1 cm.

**Figure 1** – Photographies en vues supérieure depuis le côté gauche (A) et en vue latérale montrant la portion reconstruite de l’aspect inféro-antérieur de la mandibule néandertalienne BD 1 (B), et rendus 3D en semi-transparence basés sur le registre microtomographique du spécimen en vues antérieure (A), supérieure (B), latérales gauche (C) et droite (D) légèrement obliques. Echelle: 1 cm.

**Figure 2** - Enamel thickness cartographies of the entire set of virtually reconstructed teeth (I1-M3) of the Neanderthal mandibles BD 1 and Regourdou 1. Topographic variation is rendered by a tooth-specific thickness-related chromatic scale ranging from dark blue (thinner enamel) to red (thicker enamel); white areas correspond to complete enamel removal (emerging underlying dentine patches) following occlusal wear. Scale bar: 1 cm.

**Figure 2** - Cartographies d’épaisseur de l’émail de l’ensemble des dents virtuellement reconstruites (I1-M3) des mandibules néandertaliennes BD 1 et Regourdou 1. Les variations topographiques sont représentées par une échelle de couleur propre à chaque dent allant du bleu foncé (émail plus fin) au rouge (émail plus épais); les zones blanches correspondent à l’usure de l’émail (flots de dentine visibles à la surface occlusale). Echelle: 1 cm.

**Figure 3** - Barplot of the antimeric variation (% asymm.; Corruccini *et al.* 2005) of three parameters representing crown enamel and dentine proportions ( $V_{cdp}/V_c$ , 3D AET, 3D RET) in the entire set of teeth of the Neanderthal mandible BD 1. See the text for the meaning of the variables. Negative values indicate right dominance.

**Figure 3** - Diagramme en bâtons des variations d’asymétrie entre antimères (% asymm.; Corruccini *et al.* 2005) pour les trois paramètres représentant les proportions des tissus de l’émail et de la dentine de la couronne ( $V_{cdp}/V_c$ , 3D AET, 3D RET) de l’ensemble des dents de la mandibule néandertalienne BD 1. Voir le texte pour la signification des variables. Les valeurs négatives indiquent une dominance du côté droit.

**Figure 4** - Standardized morphometric maps of the virtually unrolled root dentine (15-85% of the total root length, where 15% is closer to the dental cervix) of four anterior teeth (incisors

and canine) of the Neanderthal mandibles BD 1 and Regourdou 1. Dentine topographic variation is rendered by a thickness-related chromatic scale ranging from dark blue (0) to red (1). LC: left canine; LI1: left central incisor; LI2: left lateral incisor; RI1: right central incisor; RI2: right lateral incisor. d: distal; lab: labial; ling: lingual; m: mesial.

**Figure 4** - Cartographies morphométriques standardisées de la dentine radiculaire déroulée (15-85% de la longueur totale de la racine, où 15% est plus proche du cervix) de quatre dents antérieures (incisives et canines) des mandibules néandertaliennes BD 1 et Regourdou 1. Les variations topographiques de la dentine sont représentées par une échelle de couleur propre à chaque dent allant du bleu foncé (0) au rouge (1). LC: canine gauche; LI1: incisive centrale gauche; LI2: incisive latérale gauche; RI1: incisive centrale droite; RI2: incisive latérale droite; d: distal; lab: labial; ling: lingual; m: mésial.

**Figure 5** - Bucco-lingual slices virtually extracted between the first and second molars (M1/M2) and the second and third molars (M2/M3) from the Neanderthal mandibles BD 1 (A) and Regourdou 1 (B) and cortical bone thickness variation (in  $\mu\text{m}$ ) measured across these sections: C, left M1/M2 section; D, right M1/M2 section; E, left M2/M3 section; F, right M2/M3 section. b: buccal side; i: inferior portion; l: lingual side.

**Figure 5** - Sections bucco-linguales extraites virtuellement entre les premières et secondes molaires (M1/M2) et deuxième et troisièmes molaires (M2/M3) des mandibules néandertaliennes BD 1 (A) et Regourdou 1 (B) et mesures des variations d'épaisseur de l'os cortical (en  $\mu\text{m}$ ) au niveau de ces sections : C, section M1/M2 gauche; D, section M1/M2 droite; E, section M2/M3 gauche; F, section M2/M3 droite. b: aspect buccal; i: portion inférieure; l: aspect lingual.

A



B



C



D



E



1 cm

F









