Is the deciduous/permanent molar enamel thickness ratio a taxon-specific indicator in extant and extinct hominids?

Est-ce que le rapport d'épaisseur de l'émail des molaires déciduales/permanentes est un indicateur taxinomique chez les hominidés actuels et éteints?

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ABSTRACT

Enamel thickness variation stems from an evolutionary interplay between functional/adaptive constraints (ecology) and strict control mechanisms of the morphogenetic program. Most studies on primate enamel thickness primarily considered the permanent teeth, while the extent of covariation in tooth enamel thickness distribution between deciduous and permanent counterparts is unreported. In this preliminary test study on some extant and fossil hominids we investigate the degree of parallelism in enamel proportions between the dm2 and the M1 by a so-called "lateral enamel thickness diphyodontic index". The results did not provide an unambiguous picture, but rather suggest complex patterns likely resulting from the influence of variably interactive factors. Future research should test the congruence of the "diphyodontic signal" between the anterior and the postcanine dentition, as well as between enamel and the enamel-dentine junction topography.

RÈSUMÈ

Le patron de variation d'épaisseur de l'émail est issu d'un compromis évolutif entre contraintes fonctionnelles/adaptatives (écologiques) et mécanismes de contrôle morphogénétique. La majorité des études portant sur l’épaisseur de l’émail des primates s’est concentrée sur les dents permanentes, tandis que le degré de covariation de distribution d’épaisseur de l’émail entre les équivalents déciduaux et permanents reste encore inconnu. Nous explorons ici le degré de parallélisme des proportions d’émail entre dm2 et M1 chez quelques hominidés actuels et fossiles, en élaborant notamment un "indice diphyodonte d’épaisseur de l’émail latéral" comme estimation des proportions de l’émail non-occlusal. Les résultats de cette étude exploratoire ne montrent pas un signal inéquivoque, mais suggèrent plutôt des modèles complexes résultant probablement de l’influence d’interactions entre des facteurs variés. De futures recherches sur le sujet devraient tester le degré de congruence du "signal diphyodonte" entre les dentures antérieures et post-canines, ainsi qu’entre l’émail et la topographie de la jonction émail-dentine.

1. Introduction

Following the pioneering methodological work developed by L.B. Martin for measure procedure standardization (Martin, 1985), the bi-three-dimensional assessment of tooth enamel thickness has become routinely in taxonomic and adaptive/evolutionary studies of fossil and extant primates (e.g., Alba et al., 2013; Kono, 2004; Kono et al., 2014; Macchiarelli et al., 2004, 2009, 2013; Olejniczak et al., 2008a, b, c, d; Pan et al., 2016; Skinner et al., 2015; Smith et al., 2003, 2005, 2011, 2012; Suwa et al., 2009; Zanolli et al., 2015, 2016a). Commonly used to infer durophagy and considered as a proxy of the dietary niches exploited by extinct species (e.g., Constantino et al., 2011, 2012; Lucas et al., 2008; Martin et al., 2003; Schwartz, 2000a; Teaford, 2007; Teaford and Ungar, 2015; Vogel et al., 2008), occlusal enamel thickness is seen as intimately related to dietary abrasiveness and selectively responsive to lifetime dental wear resistance (Pampush et al., 2013).

Enamel thickness variation stems from an evolutionary interplay between functional/adaptive constraints (ecology) and strict control mechanisms of the morphogenetic program (Horvath et al., 2014; Kelley and Swanson, 2008; Kono, 2004; Simmer et al., 2010; Smith et al., 2012; Vogel et al., 2008). It appears to respond relatively quickly in evolutionary time to dietary/ecological changes (Grine and Daegling, 2017; Hlusko et al., 2004), thus being prone to homoplasy (Smith et al., 2012; rev. in Macho, 2015).

Most studies on enamel thickness have primarily considered the permanent teeth, especially the molar series, while the extent of covariation in tooth enamel thickness between deciduous and permanent counterparts has been the object of limited quantitative analyses, including in hominids (for a recent synthetic review of studies on deciduous enamel thickness in humans, see table 1 in Mahoney, 2013; additionally, among other contributions see Benazzi et al., 2011; Fornai et al., 2014, 2016; Macchiarelli et al., 2006, 2013; Zanolli, 2015a; Zanolli et al., 2010a, 2012, 2014). Accordingly, a quantitatively supported answer to a number of questions remains so far elusive. More specifically: whenever, in a comparative intertaxic assessment, we score as relatively "thinly-" or "thickly-enamelled" a permanent hominid tooth and order it accordingly within a series of investigated specimens, does its precursor behave similarly and does it (tend to) occupy a comparable position within the same deciduous series? In another perspective: can we confidently predict an enamel thickness "category" for a hominid deciduous crown based on the measure of its successor (or vice versa)? Does a

precursor-successor predictable pattern exist for tooth enamel thickness in hominids? If so, is it taxon-specific?

The dm2 and M1 are part of the same developmental molar series (rev. in Bailey et al., 2014, 2016; see also Evans et al., 2016), i.e., are meristic elements with a similar and serially repeated structure within the same organism (Butler, 1956, 1967; Kraus and Jordan, 1965). In this preliminary test study on some extant and fossil hominids we thus investigate the degree of parallelism in enamel proportions between the dm2 and the M1. In order to perform intertaxic comparisons, we established a so-called "lateral enamel thickness diphyodontic index" (LETDI; see Materials and methods) as a measure of the proportions in the amount of non-occlusal enamel (Macchiarelli et al., 2016; Zanolli, 2015b). Given the exploratory nature of this study, whose main goal is to capture a tendency, if any, not to assess intraspecific variation, or evolutionary trends, or phylogenetic relationships, the number of cases examined for each taxon (ranging from 1 to 5 tooth pairs) is just minimal. By definition, at this stage of the research the underlying assumption is that the signal revealed by each dm2-M1 crown pair used here, all from mandibular dentitions, represents the average condition of its own taxon, i.e., is taxon-representative.

Apart for some intertaxic differences in developmental timing and patterning between the dm2 and the M1 (Dean, 2000, 2006, 2010; Dean and Cole, 2013), given that the dm2 is in functional occlusion for a much shorter time and commonly experiences lower functional constraints, at least until the weaning process begins (Fleagle, 2013; Swindler, 2002), essentially based on the extant human model (e.g., Gantt et al., 2001; Grine, 2005; Huszár, 1972; Mahoney, 2010; Rossi et al., 1999), we expect that, independently from their relative qualitative "category" ("thinner" vs. "thicker"), all dm2/M1 enamel volume ratios are below the unit.

2. Materials and methods

The hominid taxa considered in this study include the four extant genera *Homo* (HOM), *Pan* (PAN), *Gorilla* (GOR) and *Pongo* (PON), and representatives of four fossil genera: the Plio-Pleistocene hominins *Paranthropus* (*robustus*) (PAR) and *Australopithecus* (*africanus*) (AUS), from the South African sites of Swartkrans and Sterkfontein, respectively, and the Late Miocene European apes *Ouranopithecus* (*macedoniensis*) (OUR), from Macedonia, and *Oreopithecus* (*bambolii*) (ORE), from Sardinia. Besides *H. sapiens*, humans are also represented by two extinct taxa: Neanderthals (Nea) and *H. erectus* from Java (Hej). The

existence of interspecific differences in molar enamel thickness has been ascertained within the australopith clade (e.g., Grine and Daegling, 2017; Grine and Martin, 1988; Olejniczak et al., 2008b; Pan et al., 2016; Skinner et al., 2015), but their consideration here is far beyond the specific purposes of our present work.

Details about the composition and origin of the mandibular dm2 and M1 specimens/samples are provided in Table 1. The extant human teeth, all from individuals of European origins, represent both sexes; conversely, no detailed information, including on their geographic provenance (and if from captive or wild individuals), is available to us on the extant great ape representatives. Except for *H. erectus* and *Oreopithecus*, whose dm2 and M1 are from different individuals, all remaining pairs are from single individuals.

We have used the X-ray microtomographic record available to us of specimens which have been previously scanned at: the University of Poitiers, France, by a Viscom X8050-16 system (all extant taxa and Javanese *H. erectus*; Zanolli, 2013; Zanolli et al., 2012, and original data); the ID 17 beam line of the European Synchrotron Radiation Facility of Grenoble, France (Neanderthals and *Oreopithecus*; Bayle, 2008; Bayle et al., 2009; Macchiarelli et al., 2006; NESPOS Database, 2017; Zanolli et al., 2010b, 2016a); the South African Nuclear Energy Corporation (Necsa), Pelindaba, by a Nikon XTH 225 ST equipment (*Paranthropus* and *Australopithecus*; original data); and the analytical platform set at the Bundesanstalt fur Materialforschung und -prufung (BAM) of Berlin, Germany (*Ouranopithecus*; Macchiarelli et al., 2008, 2009).

The data were reconstructed at a voxel size ranging from 21.0 to 83.2 μm, for the extant teeth, and from 21.6 to 50.0 μm, for the fossil specimens. Using Amira v.5.3 (Visualization Sciences Group Inc.) and ImageJ v.1.46 (Schneider et al., 2012), a semiautomatic threshold-based segmentation was carried out following the half-maximum height method (HMH; Spoor et al., 1993) and the region of interest thresholding protocol (ROI-Tb; Fajardo et al., 2002), taking repeated measurements on different slices of the virtual stack (Coleman and Colbert, 2007).

In order to avoid the problem of occlusal wear nearly invariably affecting at least the dm2 in most molar pairs, we uniquely considered lateral enamel. As lateral enamel thickness topography deeply relates to crown morphology, it is expected to bring a taxon-specific signature, even if likely diluted compared to that provided by occlusal enamel (e.g., Kono and Suwa, 2008; Macchiarelli et al., 2013; Suwa et al., 2009). To quantify lateral enamel, the best-fit plane across the cervicoenamel line was firstly set on each crown and the tooth material below this basal plane eliminated (Olejniczak et al., 2008a). Then, a parallel plane to the

former, tangent to the lowest enamel point of the occlusal basin, was defined and all material above it was also removed (Benazzi et al., 2011; Macchiarelli et al., 2013; Toussaint et al., 2010). Only the crown portion between these two planes was preserved to estimate tissue proportions.

On the new set of virtually simplified crowns, five surface and volumetric variables were digitally measured (or calculated): LVe, the lateral volume of enamel (mm^3); LVcdp, the lateral volume of coronal dentine, including the lateral coronal aspect of the pulp chamber (mm^3); LSEDJ, the enamel-dentine junction (EDJ) lateral surface (mm^2); 3D LAET (=LVe/LSEDJ), the three-dimensional lateral average enamel thickness (mm); 3D LRET (=100*3D LAET/($LVcdp^{1/3}$)), the scale-free three-dimensional lateral relative enamel thickness. Intra- and interobserver tests for measurement accuracy run at different times by four observers revealed differences <4%.

Pearson correlation tests among the variables listed above show that, in each molar pair, the 3D lateral relative enamel thickness (3D LRET) exhibits the highest correlation ($p<0.01$ vs. $p<0.02$ for 3D LAET and $p<0.05$ for LVE). A "lateral enamel thickness diphyodontic index" (LETDI) has been thus calculated as follows: 3D $LRET_{dm2}$/3D $LRET_{M1}$. Statistical analyses were performed with R v.3.2.1 (R Development Core Team, 2017).

To visualize similarities vs. differences in enamel thickness topography within an assemblage of so variably sized and shaped teeth, *ad hoc* imaging techniques were used to virtually unroll lateral enamel and to project it into standardized morphometric maps (Bayle et al., 2011; Bondioli et al., 2010; Macchiarelli et al., 2013; see also Morita et al., 2016, 2017; Puymerail, 2011; Puymerail et al. 2012a, b). By using a custom routine developed in R v.3.2.1 (R Development Core Team, 2017) with the packages spatstat (Baddeley et al., 2015) and gstat (Pebesma, 2004), enamel thickness values were standardized between 0 and 1 and each morphometric map was set within a grid of 40 columns and 180 rows. We then performed a generalized Procrustes analysis (GPA) and a between-group principal component analysis (bgPCA; Mitteroeker and Bookstein, 2011) based on the standardized morphometric map outputs with the package Morpho v.2.4.1.1 (Schlager, 2017) for R v.3.3.3 (R Development Core Team, 2017).

3. Results

The values of the lateral relative enamel thickness (3D LRET) of the dm2 and of the M1 and those of the LETDI "diphyodontic index" assessed for the ten hominid taxa represented in this study are shown in Table 2.

For the 3D LRET of the deciduous second molar, *Ouranopithecus* (12.0), *Paranthropus* and the *Australopithecus* from Sterkfontein (both 10.9) show absolutely thick enamel, while *Pongo* and *Gorilla* (global range: 4.7-6.3) and *Oreopithecus* (6.0) are relatively thin-enamelled. A difference is noticeable between the two African apes, *Pan* having thicker enamel (6.3-8.9), but on average still thinner than measured in extant humans (8.0-9.2). Enamel in Neanderthal is thinner compared to the extant values (6.4-7.1), while the *H. erectus* estimate (9.2) coincides with the upper end of the human range revealed by our sample of five individuals. As a whole, the decreasing order for the lateral relative enamel thickness of the lower dm2 is as follows: *Ouranopithecus* > *Paranthropus* = *Australopithecus* > *H. erectus* ≥ extant humans ≥ *Pan* ≈ Neanderthals > *Oreopithecus* > *Gorilla* ≈ *Pongo*, the variation interval covered by 3D LRET being comprised between 12.0 and 4.7.

Three sets are identifiable for the 3D LRET of the lower M1: the first distinguishes the absolutely thickly-enamelled *Paranthropus* (15.6) and *Ouranopithecus* (13.4), the second assembles the variably intermediate *Homo* (all taxa), *Pan*, *Australopithecus* and *Oreopithecus* (range: 8.3-11.8), while the third includes the thinly-enamelled *Gorilla* and *Pongo* (range: 5.9-8.1)". In this context, *Pan* (8.8-11.8) is indistinguishable from the extant human condition (9.3-11.2). Interestingly, the estimate for the Indonesian composite *H. erectus* representative (9.1) fits the Neanderthal range (8.3-9.1), as well as the value obtained for *Oreopithecus* (9.2). Here, the decreasing pattern is as follows: *Paranthropus* > *Ouranopithecus* > *Australopithecus* ≥ extant humans ≈ *Pan* ≥ *Oreopithecus* ≈ *H. erectus* ≈ Neanderthals > *Gorilla* ≈ *Pongo*, the values globally ranging from 15.6 to 5.9.

The last column of Table 2 presents the values of the LETDI ratio. They widely range from 0.63, in a *Pongo* individual and in *Oreopithecus* (0.65), to 1.01, in *H. erectus* (Fig. 1). Except for the latter taxon, the totality of the ratios are <1.0, even if values near the unit are displayed by an extant human individual (0.99) and by *Australopithecus* (0.98). According to this parameter, even if distinct for its greater amount of enamel, *Paranthropus* (0.70) is closer to *Oreopithecus* (0.65) than to *Ouranopithecus* (0.89), with which it otherwise shares thickly-enamelled dm2 and M1. Within our limited set of investigated cases, *Pongo* and extant humans display larger variation than Neanderthals and the African apes (Fig. 1).

Distinctly for each taxon and for each molar type, the standardized morphometric maps (MM) imaging the virtually unrolled and projected lateral enamel are shown in Fig. 2. For the

extant taxa and Neanderthals, they represent consensus maps generated by interpolating the available individual records into a single dataset (Puymerail, 2011; Puymerail et al., 2012a, b). Because each MM is scaled according to the maximal value of the analysed tooth, the patterns expressed by the dm2s and the M1s are independent from the absolute and relative enamel thickness values.

In all taxa and both molars, enamel is absolutely and relatively thicker towards the occlusal aspect than cervically. For the dm2, thickening is commonly found buccally; however, thickening in *Ouranopithecus* is more evenly distributed around most of the subocclusal contour. The extant human pattern is somehow closer to that displayed by *H. erectus* than by the Neanderthal deciduous molar. The African apes share similar enamel distribution, also displayed, to a lesser extent by *Pongo*. In this context, the least contrasted map is that of *Paranthropus*, which is distinct from *Australopithecus* and, mostly, from *Ouranopithecus*, but which in turn recalls that of *Oreopithecus*. In the MMs of the M1s, thickening is not mainly concentrated buccally, as seen for the dm2s, but more commonly spread buccally/mesiobuccally and also lingually/distolingually. However, this is not exactly the case in *Ouranopithecus* and, to a lesser extent, in *Oreopithecus*, where thickening is essentially concentrated mesiolingually, in the former, and distolingually, in the latter. All human representatives, notably extant humans and Neanderthals, show a similar pattern, even if slightly accentuated distolingual thickening is found in *H. erectus*. With this respect, the extant human and Neanderthal topography resembles that of *Australopithecus*. Here again, the signatures displayed by the African apes are similar to the pattern revealed by *Pongo*, which in turn recalls that of *Paranthropus*. Finally, in terms of intertooth polarity of the signal, the most similar MMs are those of the extant apes (notably *Gorilla* and *Pongo*), while distinct topographic differences are appreciable in *Paranthropus* and *Oreopithecus*.

The bgPCA based on the MM scores only provides modest discrimination among the taxa along both bgPC axes (PC1: 56.37%, PC2: 31.11%). However, the representatives of all extant and fossil hominins (HOM, Nea, Hej, PAR, AUS) tend to regroup on the negative aspect of bgPC1, whereas the extant apes (PAN, GOR and PON) mostly fall in the positive values along this axis (Fig. 3). The two Miocene hominids (OUR and ORE) show distinct signals, *Ouranopithecus* being closer to *Homo,* while *Oreopithecus* more closely resembling *Pan* and *Gorilla*. The specimens in the negative space of bgPC1 display evenly spread relatively thicker enamel deposited towards the more occlusal quarter of the entire surface, while the specimens in the positive space of bgPC1 have two vertically projected thickened "pillars" on the buccal and lingual aspects, respectively, separated by two large strips of

thinner enamel nearly covering the entire mesial and distal crown sides. Along bgPC2, only *Pongo* is slightly discriminated from the other taxa and nears the extreme values of the negative space because of its proportionally thicker intercuspal lingual enamel (Fig. 3).

4. Discussion

A limiting/complicating factor in our analytical approach is represented by the use of non-occlusal enamel compared to the information imprinted occlusally, or even at specific cuspal level (e.g., Grine, 2005; Kono et al., 2002; Macho and Berner, 1993; Mahoney, 2010; Schwartz, 2000b). As expected, a test of "lateral" (LETDI) vs. "occlusal enamel thickness diphyodontic index" (OETDI) preliminarily performed on five specifically selected unworn dm2-M1 crown pairs representing two extant humans and one individual for each extant great ape, systematically provided OETDI < LETDI values (on average, 20% lower), thus indicating a higher degree of volumetric discrepancy in dm2-M1 enamel proportions at occlusal level. However, while occlusal enamel topography is more directly informative in terms of functional activity and adaptive responses (e.g., Guy et al., 2015; Kono, 2004; Kono and Suwa, 2008; Olejniczak et al., 2008b), lateral enamel thickness is also involved in dissipating occlusally-related stresses (Benazzi et al., 2013a, b). Nonetheless, it is also possible that the use of the entirely unrolled and projected lateral crown band introduced inessential, or even somehow noisy information. In fact, while individual morphometric maps clearly reveal site-specific differences among the compartments which relate to occlusal cusp shape and topography (Fig. 2), at this stage we did not yet decompose the band in quarters, and did not examine and compare their sometime distinctly heterogeneous signatures, a task which should also limit the effects of differences in tooth crown architecture, notably outer surface convexity and intercuspal groove depth and extension. This, will require anyhow additional research and the development of an *ad hoc* analytical protocol.

The expectation, formulated in a purely functional perspective, of LETDI ratios all <1.0 is not fully satisfied by present results (for enamel proportions in extant human lower dm1s-dm2s-M1s, see Mahoney, 2010), or is even falsified in three representatives from as much taxa: *H. erectus* (1.01), an extant human individual (0.99), and the *Australopithecus* representative (0.98), even if the large majority of the ratios are around or below 0.8. However, it should be noted again that the *H. erectus* value has been obtained using two individuals (Table 1), which is methodologically inappropriate and may have introduced a bias (see comments below about variation). The two minima for the LETDI correspond to

Oreopithecus (0.65, also obtained from two individuals) and *Paranthropus* (0.70). This is interesting, and may be relevant, as it indicates that a large difference between the dm2 and the M1 in the proportional amount of enamel volume deposited along the crown walls may occur in both absolutely thickly-enamelled and relatively thinly-enamelled hominids. Anyhow, the results (Table 2, Fig. 1) show that also the opposite can occur, i.e., that the deciduous and permanent molars of both thickly-enamelled hominids (e.g., *Ouranopithecus*) and representatives of relatively thinly-enamelled taxa (e.g., *Gorilla*, *Pongo*) may present comparable values of lateral relative enamel thickness (3D LRET). In sum, even if present results tend to support the evidence that primate "deciduous teeth have thinner enamel than permanent teeth" (Swindler, 2002: 14), including in humans (Mahoney, 2010), the extent of their proportions for nonocclusal enamel appears rather variable.

By definition, the study assumed that the signal revealed by each dm2-M1 crown pair represents the average condition of their own taxon (including for the composite *H. erectus* and *Oreopithecus* representatives). However, even if molar enamel thickness does not seem to behave as sexually dimorphic (e.g., Hlusko, 2016; Hlusko et al., 2004; Rossi et al., 1999), a growing body of evidence indicates a considerable amount of interspecific temporal and geographic variation (e.g., Kato et al., 2014; Smith et al., 2011, 2012). Conversely, the extent of intraspecific variation is in most cases from poorly reported to simply unknown, and even in extant humans enamel thickness chrono-geographic variation is far from being appropriately documented and, with very few exceptions (e.g., Feeney et al., 2010; Grine, 2005), most currently available information is limited to European or European-derived population samples (rev. in Le Luyer, 2016; see Zanolli et al., 2017). At any rate, while just representing a signal because of the extremely limited number of investigated cases, present evidence from the African apes (Table 2) suggests variation in lateral enamel thickness may be similarly large in both deciduous and permanent molars.

For more comprehensively interpreting the signal provided by the "lateral enamel thickness diphyodontic index" - or by any kind of "enamel thickness diphyodontic index" (ETDI) suitable for appropriately assessing the precursor-successor tooth enamel volume proportions (and its distribution pattern as well) - a number of biological, behavioural and ecological factors should be taken into account.

The four extant and four extinct hominid genera represented in our analysis are known for exploiting, or are reported to have exploited, respectively, a wide range of food resources in a variety of diverse environments (Fleagle, 2013; Guatelli-Steinberg, 2016; Hartwig, 2002; Merceron et al., 2005; Nelson and Rook, 2016; Scott et al., 2005; Sponheimer and Lee-Thorp,

2015; Ungar, 2007; Ungar and Sponheimer, 2013). Depending on the taxon-specific feeding habits, the mastication timing may be considered as another variable which, together with food abrasiveness, likely plays a role in the selection of enamel thickness because of dental wear resistance, i.e., adaptation is not only resistance to fracture, but also to prolonged wear to which enamel thickness can be related (Grine and Daegling, 2017; Pampush et al., 2013). While the investigative tool used here - the LETDI - did not reveal any immediately obvious link with dietary and/or ecological diversity (for example, relative medium-low [<0.80] values are shared by Neanderthals, *Pan*, *Gorilla*, *Pongo*, *Paranthropus* and *Oreopithecus*, while extant humans *H. erectus*, *Australopithecus* and *Ouranopithecus* provided medium-high values [>0.80]), we note anyhow that in the bgPCA of the morphometric maps (Fig. 3): the more folivorous taxa (*Pan*, *Gorilla*, and perhaps *Oreopithecus*) are found in the positive space of bgPC1; *Pongo*, a slightly more diversified folivorous feeder, is found in the negative space of bgPC2; the omnivorous humans are scattered across the negative space of bgPC1 and the positive space of bgPC2; *Paranthropus*, *Australopithecus* and *Ouranopithecus*, relying on diverse diets but likely sharing the inclusion of hard/gritty food items, occupy a more central position along bgPC2 (Fig. 3). In sum, even if we agree the reliability of enamel thickness as a dietary indicator breaks down in some cases where phylogenetically closely-related species that consume different amounts of hard items are considered (Grine and Daegling, 2017), at a first glance, differences in "dental ecology" (*sensu* Cuozzo et al., 2012) seem to play a role in affecting the polarity of the dm2/M1 ratio used in the present study. If so, additional research - using any kind of *ad hoc* ETDI - should be performed on the front teeth.

The investigated taxa are also diverse in body mass (Fleagle, 2013; Hemmer, 2015), a variable which in extant primates is highly correlated to a number of life history attributes (e.g., weaning age, age at maturity, age at first breeding in females), as well as to tooth size (e.g., molar crown area) (rev. in Hemmer, 2015). However, as shown in Fig. 4, no obvious correlation exists between LETDI and body mass. Even if three among the four relatively smaller body-sized representatives - i.e., *Pan*, *Paranthropus* and *Oreopithecus* - are more closely plotted, the *Australopithecus* is well separate due to its high LETDI. Also, the similarly-sized three representatives of our own taxon (extant humans, Neanderthals, *H. erectus*) differ in terms of LETDI (but see above the point on the composite *H. erectus*), while extant humans and *Gorilla*, which display comparable LETDIs, differ in average body mass. Finally, the two largest-sized taxa considered in our analysis, *Gorilla* and *Ouranopithecus*, provided quite distinct LETDI ratios (Fig. 4).

Our "diphyodontic index" seems also poorly or no related to the age at eruption of the first lower permanent molar, another key life history trait which in hominins marks the end of infancy (Kelley and Bolter, 2013). In fact, while also a strong genetic contribution to variation in timing of primary tooth emergence is well ascertained in humans (Chan et al., 2012), and likely also in hominids (Swindler, 2002), the LETDIs of *Pan* and of the *Australopithecus* representative used here, for example, i.e. of two taxa showing comparable ages at LM1 eruption (Hemmer, 2015: table 15), markedly differ.

5. Concluding remarks

In a previous study, we noted that "some evidence suggests deciduous versus permanent molar enamel thickness distribution and relative proportions vary among extant and fossil hominid taxa… Inner signatures extracted from the primary and secondary dentition, respectively, may or may not provide similar/comparable pictures of time-related intrataxic evolutionary changes in tooth tissue proportions" (Macchiarelli et al., 2013: 259). The results scattered from the present exploratory test using a newly developed analytical tool - the "lateral enamel thickness diphyodontic index" (LETDI) - did not anyhow provide an unambiguous and immediately readable picture, as otherwise predictable on the basis of some ontogenetic and morphological studies using sequential teeth (e.g., Bailey et al., 2014, 2016; Evans et al., 2016), but rather suggest complex patterns likely resulting from the influence of a number of variably interactive factors. However, while increasing evidence exists for lifetime-related enamel thickness and dietary wear association in extant primates (e.g., Pampush et al., 2013) and positive selection for adaptation in human evolution has been shown for the genes coding for the enamel matrix proteins (e.g., Daubert et al., 2016; Horvath et al., 2014), given the high phenotypic plasticity of enamel thickness (e.g., Hlusko, 2016; Kato et al., 2014; Smith et al., 2012), it is also possible that a fraction of the signal provided by any kind of tooth enamel "diphyodontic index" is non-adaptive, or that the degree of adaptability and functional significance of this trait varies topographically across the dentition. With this respect, together with some methodological advancement in the identification of the most reliable parameters and tooth crown areas to be considered for intertaxic investigations, future research should also test the congruence of the "diphyodontic signal" between the anterior and the postcanine dentition, as well as between enamel and the enamel-dentine junction topography.

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