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Abstract

Objective: Three‐dimensional relative enamel thickness (3DRET) is important for assessing hypotheses about taxonomy, phylogeny, and dietary reconstruction for primates. However, its weaknesses have not been thoroughly investigated. Here, we analyze its weaknesses and propose an index aiming at better taxonomic discrimination.
Materials and Methods: The dimensionless 3D index, ratio of enamel‐thickness to dentine‐thickness (3DRED), which is defined as the cubic root of the ratio of 3D average enamel thickness (3DAET) to 3D average dentine thickness (3DADT), is proposed here. To compare 3DRET and 3DRED and their sensitivity to voxel size, a fossil orangutan molar was scanned 14 times with different resolutions ranging from 10 to 50 μm. Enamel thickness analysis was carried out for each resultant digital model. In addition, enamel thickness measurements of 179 mandibular permanent molars (eight genera) were analyzed, followed by investigating the relationship between 3DRET and 3DAET and between 3DRED and 3DAET.
Results: Regarding sensitivity, 3DRED is more robust than 3DRET. In addition, 3DRET is correlated with 3DAET by linear curve with regression coefficients approximating or larger than 0.8 in most cases, while 3DRED shows less correlation with 3DAET. Furthermore, there are clear separations between different taxa in the bivariate plot of 3DRED against 3DAET, indicative of the taxonomic value of 3DRED.
Conclusion: Under certain conditions, 3DRED promises to be a robust and reliable alternative to 3DRET in taxonomic study.

KEYWORDS
enamel/dentine thickness ratio, hominid teeth, relative enamel thickness, taxonomic assessment, voxel size sensibility.

Primate 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 & Swanson, 2008; Simmer et al., 2010; Vogel et al., 2008). This mineralized dental tissue appears to respond relatively quickly in evolutionary time to dietary/ecological changes (Grine & Daegling, 2017; Hlusko, Suwa, Kono, & Mahaney, 2004; Le Luyer & Bayle, 2017), thus being prone to homoplasy (Smith, Olejniczak, et al., 2012). 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, Constantino, Wood, & Lawn, 2008; Martin, Olejniczak, & Maas, 2003; Schwartz, 2000; Teaford, 2007; Teaford & Ungar, 2015; Vogel et al., 2008), it is intimately related to dietary abrasiveness and selectively responsive to lifetime dental wear resistance (Pampush et al., 2013; Rabenold & Pearson, 2011). Despite some degree of plasticity of enamel thickness, it is still considered an important indicator of taxonomy, phylogeny, and dietary signals in extant and fossil primates (e.g., Alba et al., 2013; Kono, Zhang, Jin, Takai, & Suwa, 2014; Lockey, Alemseged, Hublin, & Skinner, 2020; Macchiarelli, Bayle, Bondioli, Mazurier, & Zanolli, 2013; Pan et al., 2016; Skinner, Alemseged, Gaunitz, & Hublin, 2015; Smith, Tafforeau, Pouech, & Begun, 2019; Thiery, Guy, & Lazzari, 2019; Thiery, Lazzari, Ramdarshan, & Guy, 2017; Zanolli et al., 2017; Zanolli, Biglari, et al., 2019; Zanolli, Kullmer, et al., 2019).

Since the pioneering studies of Gantt (1977), Kay (1981), and Martin (1983, 1985), enamel thickness has been investigated in various ways. In early works, enamel thickness was measured on physical ground section of tooth (e.g., Andrews & Martin, 1991; Beynon & Wood, 1986; Dean & Schrenk, 2003; Schwartz, 2000; Smith, Martin, & Leakey, 2003) or virtual section of digital tooth model acquired via conventional computed tomography (CT) instruments (e.g., Conroy & Vannier, 1991; Schwartz, Thackeray, Reid, & van Reenan, 1998; Shimizu, 2002). The former approach is destructive, limiting both intrataxon and intertaxon comparisons among sufficiently large samples. Besides, the manually cut ground section is inevitably oblique to the ideal plane (a plane passing through the mesial cusp tips and perpendicular to the cervix plane), potentially leading to biased result (Olejniczak, 2006). For conventional CT, its scanning voxel size is generally at the scale of 100 μm and the voxel size is not small enough to reconstruct a precise digital substitute of tooth sample. Considering these situations, the advent of micro‐CT (subsequently attracted widespread interests owing to its high resolution, thus allowing both nondestructive access to the details of three‐dimensional (3D) tooth internal structural organization and precise quantitative analyses of bidimensional (2D) and 3D enamel thickness (Benazzi et al., 2014; Feeney et al., 2010; Kono, 2004; Macchiarelli et al., 2004; Macchiarelli, Bondioli, & Mazurier, 2008; Macchiarelli, Mazurier, Illerhaus, & Zanolli, 2009; Olejniczak, 2006; Tafforeau, 2004).

During the past two decades, an increasing number of micro‐CT‐based studies were presented to elucidate and compare enamel thickness pattern in taxonomically broad samples, including fossil hominins (e.g., Becam & Chevalier, 2019; Fornai et al., 2014; Olejniczak, Smith, Feeney, et al., 2008; Olejniczak, Smith, Skinner, et al., 2008; Skinner et al., 2015; Smith, Harvati, et al., 2009; Smith, Olejniczak, et al., 2009; Smith, Olejniczak, et al., 2012; Zanolli, Biglari, et al., 2019), fossil hominoids (e.g., Alba, Fortuny, & Moya‐Sola, 2010; Kono et al., 2014; Olejniczak, Smith, Wang, et al., 2008; Smith et al., 2019; Zanolli et al., 2016; Zanolli, Kullmer, et al., 2019), extant hominoids (e.g., Kono & Suwa, 2008; Olejniczak, Tafforeau, Feeney, & Martin, 2008; Smith et al., 2011; Smith, Kupczik, Machanda, Skinner, & Zermeno, 2012), and extant cercopithecoids (e.g., Beaudet et al., 2016; Kato et al., 2014; Olejniczak, Tafforeau, et al., 2008). Moreover, efforts have been extended from 2D to 3D analysis (e.g., Buti et al., 2017; Guy, Lazzari, Gilissen, & Thiery, 2015; Hu & Zhao, 2015; Martín Francés et al., 2018; Pan et al., 2016; Zanolli, Kullmer, et al., 2019; Zhang & Zhao, 2013). Other than the classic enamel thickness indices like the average enamel thickness (AET) and relative enamel thickness (RET) (Kono, 2004; Martin, 1985), attempts were made to develop

derivatives like the lateral RET to study worn teeth (e.g., Benazzi et al., 2011; Kono & Suwa, 2008; Toussaint et al., 2010; Zanolli et al., 2018). Most recently, a novel metric was proposed, the absolute crown strength estimated on 2D sections, to estimate tooth crown resistance to fracture (Schwartz, McGrowsky, & Strait, 2020).

Despite the flexibility associated with micro‐CT technology, it is very important to bear in mind that digital model is an approximation to the studied sample, and its quality is controlled by the voxel size (spatial resolution). Consequently, some elements (e.g., dentine horns) would lose details, if voxel size is too large. Olejniczak (2006) has noted that the model quality is reduced when spatial resolution is low. Nevertheless, a further study to investigate the effect of voxel size on enamel thickness indices is missing in his study or in others. Furthermore, an increasing number of studies have applied multivariable‐based method (e.g., adjusted Z‐score statistics, Maureille, Rougier, Houët, & Vandermeersch, 2001; Scolan, Santos, Tillier, Maureille, & Quintard, 2012) to indicate the taxonomic status for given samples. To ensure the effectiveness and accuracy of multivariable‐based statistics, it is better to avoid linear correlations among variables. 3DAET and 3DRET are two indices widely adopted in multivariable‐based statistics and hence it is significant to ascertain their relationship. Given the above reasons, we test how much 3DRET and 3DAET are sensitive to voxel size of the microtomographic scans in this contribution. We then test the correlation between 3DRET and 3DAET. In parallel to these tests, we introduce an analogue to 3DRET, the ratio of enamel‐thickness to dentine‐thickness (3DRED). For this index, its sensitivity to voxel size and its correlation with 3DAET were also analyzed.

2 MATERIALS AND METHODS

2.1 An analogue to 3DRET

The definitions of 3DAET and 3DRET are shown in Equations (1) and (2), respectively.

$$3DAET = \frac{V_e}{S_{edj}} \quad (1)$$

$$3DRET = 100 \times \frac{3DAET}{\sqrt[3]{V_{cdp}}} = 100 \times \frac{V_e}{S_{edj}\sqrt[3]{V_{cdp}}} \quad (2)$$

where Ve is the enamel volume (mm3) and Vcdp is the coronal dentine volume (including the volume of the pulp cavity) in mm3. Sedj is the enamel–dentine junction (EDJ) surface area (mm2). The analogue to 3DRET that we developed here is 3DRED. This dimensionless index is defined as the cubic root of the ratio of 3DAET to 3DADT, which is expressed as

$$3DRED = 10 \times \left(\frac{3DAET}{3DADT}\right)^{\frac{1}{3}} \quad (3)$$

The ratio is multiplied by 10 for ease interpretation. For the 3D average dentine thickness (3DADT, mm), the equation is as follows:

$$3DADT = \frac{V_{cdp}}{S_{edj}} \quad (4)$$

3DADT describes the average thickness from EDJ surface to cervical plane. Substituting the

expressions of 3DAET (Equation (1)) and 3DADT (Equation (4)) into Equation (3) yields simpler expression of 3DRED, as shown in the following.

$$3DRED = 10 \times \left(\frac{3DAET}{3DADT}\right)^{\frac{1}{3}} = 10 \times \left(\frac{V_e}{S_{edj}} / \frac{V_{cdp}}{S_{edj}}\right)^{\frac{1}{3}} = 10 \times \left(\frac{V_e}{V_{cdp}}\right)^{\frac{1}{3}} \quad (5)$$

From Equation (5), it can be seen that 3DRED only depends on two basic variables cubic root of Ve and cubic root of Vcdp) in essential. One could be curious about why we extracted the cubic root, since the ratio of enamel volume to coronal dentine volume (Ve/Vcdp) has been dimensionless. Indeed, extracting the cubic root will not change the ability of 3DRED to spot differences between taxa. The significance is that extracting the cubic root makes the basic variables involved in 3DRED be linear scale (1D, cubic root of Ve and cubic root of Vcdp), which generally shows less sensitive to spatial resolution compared to higher dimensional parameters like enamel volume (3D) and coronal dentine volume (3D).

2.2 Materials and methods for assessing sensitivity

To assess the effect of voxel size on enamel thickness measurements, a nearly unworn Pleistocene orangutan lower third molar (specimen NX‐C2‐9, Figure 1) from the site of Naxian cave, Guangxi, China, was selected for study due to the following reasons. First, this specimen bears complete sinuous cervical line (Figure 1). Therefore, all routine methods for analyzing enamel thickness can be adopted. Second, no apparent diagenesis signals and fractures are observed in this molar, so that the contrast between enamel and dentine in Micro‐CT images is obvious (Figure 2) and hence manual correction, which may bring in operator‐dependent differences, is minimized.

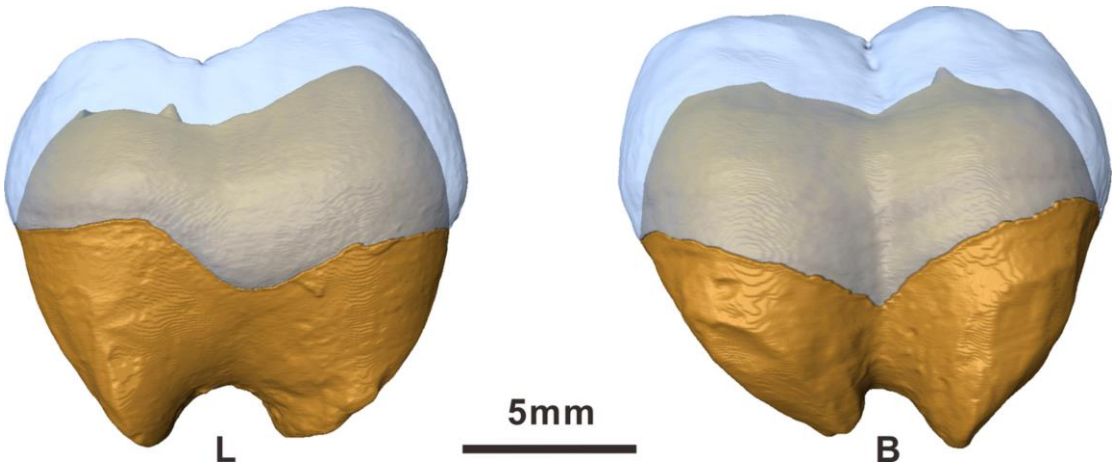

FIGURE 1. Virtual three‐dimensional (3D) reconstruction of the fossil Pongo molar with a voxel size of 20 μm. The enamel is rendered in semitransparency, showing the underlying enamel–dentine junction (EDJ) surface. L: lingual, B: buccal.

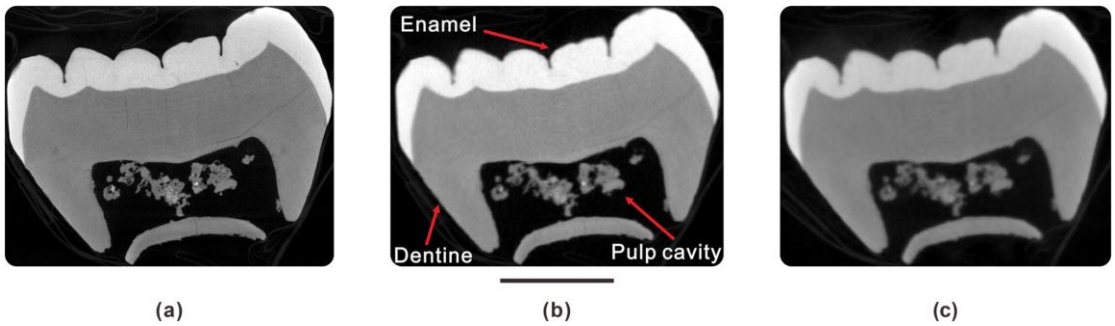

FIGURE 2. Slices from image stacks with voxel size of (a) 10, (b) 29, and (c) 50 μm, respectively. Scale bar is 5 mm

This molar was scanned 14 times with a nanoVoxel4000 Micro‐CT (Sanying Precision Instruments, Tianjin, China). Only the distance between X‐ray source and object and the distance between X‐ray source and detector differed for each acquisition (Supplementary Material Table 1). After scanning, volume dataset was reconstructed with VoxelStudio Recon (Sanying Precision Instruments) and 14 image stacks with isometric voxel size ranging from 10 to 50 μm were obtained accordingly (Supplementary Material Table 1). These image stacks were segmented using watershed algorithm in Avizo 8.0 and surface renderings were generated with constrained smoothing algorithm (kernel size: 3). The resultant digital models were imported in Geomagic Design X.2016 to create dental crown and measure dental metrics (e.g., enamel volume).

Following Benazzi et al. (2014), three different protocols were generally used to separate the crown from the roots (denoted by 3D‐a, 3D‐b, and 3D‐c, respectively). The main difference among these methods lies in the definition of the reference plane or surface that separates the crown from the roots. In 3D‐a, a best fitting plane is produced according to the cervical line path (Tafforeau, 2004). In 3D‐b, the cervical line is used to create a digitized spline curve. After that, the curve is interpolated into a smooth surface (Benazzi et al., 2014). In 3D‐c, the most apical plane (Plane A) containing a continuous ring of enamel at the cervix is first located, and parallel to that plane, another plane that contains the most apical enamel extension is further defined as Plane B. The final cervical plane is the average plane between Planes A and B (Olejniczak, 2006). Once the target plane or surface has been created, the crown is separated from the roots and 3D measurements (enamel volume, EDJ surface area, and dentine volume) are performed. The 3DAET, 3DRET, and 3DRED are then calculated in accordance with Equations (1)–(3-(1)–(3), respectively (Kono, 2004; Olejniczak, 2006; Tafforeau, 2004).

All routine protocols mentioned above were tested here on the fossil Pongo molar. Besides, 3D enamel thickness distribution was analyzed through the “surface distance” module in Avizo 8.0. All postprocessing, including segmentation, digitizing cervical line, and determining cervical plane/surface were done by a single observer to avoid interobserver variation. In addition, the measurements have been repeated three times over a period of 6 months. Intraobserver variation (calculated as the maximum deviation from the mean of three measurements) was less than 2% for 3DAET, 3DRET, and 3DRED.

2.3 Materials and methods for assessing correlation between enamel thickness variables

Additionally, to test the newly introduced 3DRED index, we used a sample consisting of 179 mandibular permanent first, second, and third molars of various fossil and extant hominid taxa as listed in Table 1. Detailed information on these samples are documented in Supplementary Material Table 2. Dental measurements of some molars (n = 146) were directly cited from references and we only calculated 3DRED according to their results. Other molars (n = 33) are from open‐source database, including NESPOS, ESRF, and Morphosource. These original Micro‐CT data were segmented and then converted into surface model following the methods mentioned above. Dental crown was separated in line with the protocol 3D‐c (Olejniczak, 2006). After that, dental measurements were performed in Geomagic Design X.2016.

TABLE 1. Dental material included in this study

Taxon	**M1**	**M2**	**M3**	**Total**	Source[a]
Hylobates. sp. (extant)	6	6	3	15	1, 7
Symphalangus syndactylus	5	9	3	17	1
Pongo. sp. (extant)	6	9	7	22	1, 2
Gorilla gorilla	4	4	0	8	1
Pan troglodytes	10	9	7	26	1, 7
Neanderthals	16	6	9	31	3, 4, 7, 8
Modern humans	15	12	11	38	1, 5, 9
Paranthropus robustus	6	8	8	22	5, 6
Total	68	63	48	179	

[a]Source: 1‐Olejniczak, Tafforeau, et al., 2008; 2‐Zanolli, Kullmer, et al., 2019; 3‐Olejniczak, Smith, Feeney, et al., 2008; 4‐Becam & Chevalier, 2019; 5‐Pan et al., 2016; 6‐Olejniczak, Smith, Skinner, et al., 2008; 7‐ESRF, 2020; 8‐NESPOS Database, 2020; 9‐Morphosource, 2020.

3 RESULTS AND DISCUSSION

3.1 Sensitivity of enamel thickness indices to voxel size

The raw data of 3D dental measurements for the fossil Pongo (mesiodistal and buccolingual diameters are 14.34 and 12.22 mm, respectively) are provided in Supplementary Material Table 3. Detailed analysis is summarized below.

When using Micro‐CT scanning to assess enamel thickness, the final voxel size may vary depending on the size of the sample. However, for the same sample, depending if the voxel size is small or large, differences in enamel thickness measurements may be noted. As we can see in Figure 3a, 3DAET will not change significantly when the voxel size is smaller than 40 μm, while with a voxel size that is larger than 40 μm, the result deviate drastically from the 10 μm value. In other

words, substantive details have been revealed under the condition of voxel size smaller than 40 μm for calculating 3DAET, but the digital model reconstructed at voxel size larger than 40 μm cannot be taken as a reasonable representative of the study molar. In this work, the result measured at 10 μm digital model is taken as the reference. Relative error (calculated as the difference from the result at 10 μm voxel size) for each scan is provided in Figure 3b. The maximum relative error can reach up to ~20% at voxel size of 50 μm, highlighting the significance of selecting an appropriate resolution. If voxel size is smaller than 40 μm, all relative errors are less than 5%, indicating that 3DAET estimates are reliable and comparable under this condition.

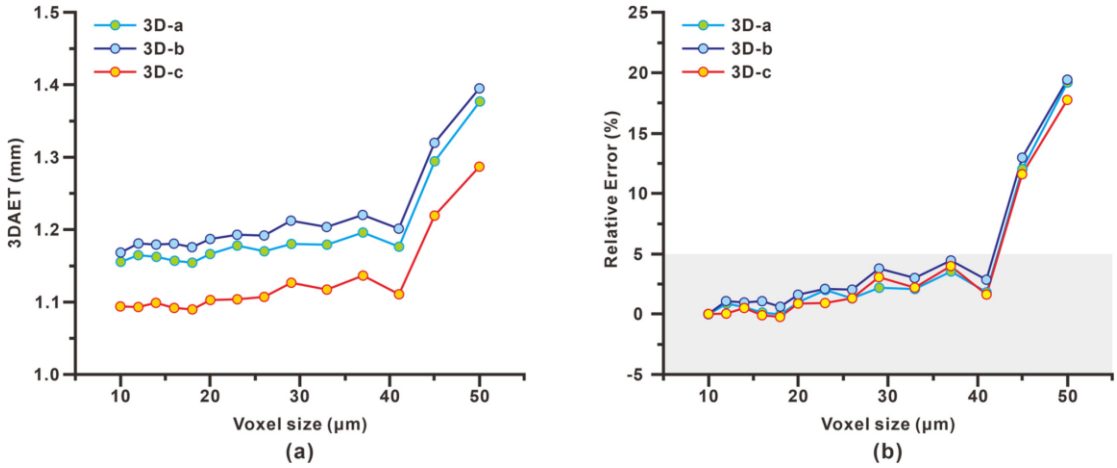

FIGURE 3. (a) Three - dimensional average enamel thickness (3DAET) results at different voxel sizes and (b) their corresponding relative errors. Here and later, light shading zone marks the slight deviation with relative error ranging from −5 to 5%.

Figure 4 shows the enamel thickness map at different voxel size. The first two figures (left and middle) display similar distribution pattern and rich details, since both were reconstructed from image stacks with smaller voxel size (10 and 29 μm, respectively). However, the third one (right) shows evident discrepancy, with much thicker enamel around the cusp tips and occlusal ridges, indicating that enamel thickness is clearly overestimated when the fossil Pongo molar is reconstructed with 50 μm voxel size. This finding is consistent with the result shown in Figure 3.

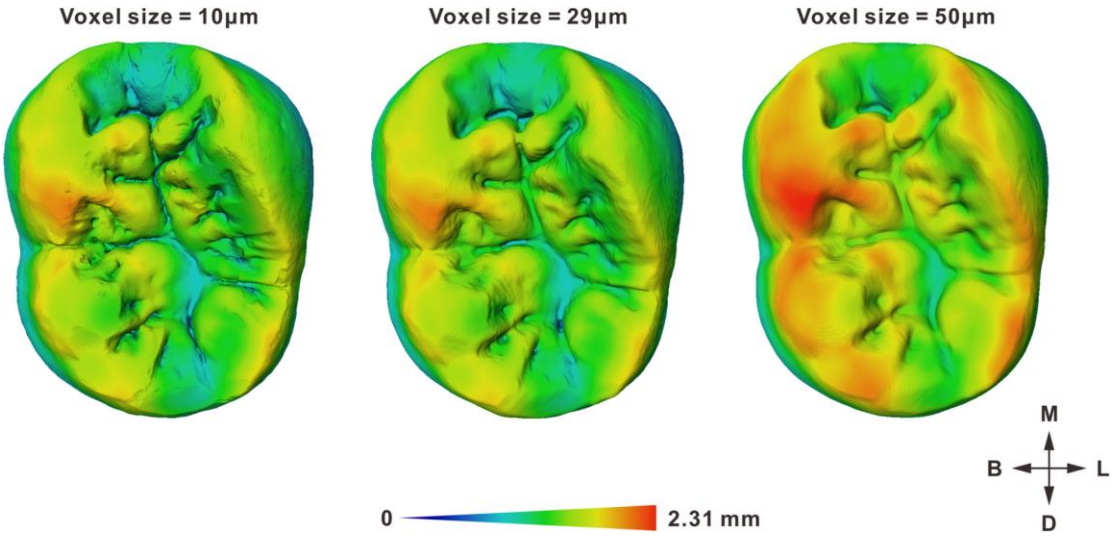

FIGURE 4. Three‐dimensional (3D) enamel thickness distributions at voxel size of 10 μm (left), 29 μm (middle), and 50 μm (right). M: mesial, B: buccal, D: distal, L: lingual.

Figure 5 shows that 3DRET is positively correlated with voxel size. To obtain a reliable 3DRET for this fossil Pongo molar, the critical voxel size is about 30 μm (Figure 5b), which is smaller than that for 3DAET (40 μm) (Figure 3b). Compared to 3DRET, 3DRED is more robust to voxel size (Figure 5a). For the former, the maximum relative error can reach up to ~14% (Figure 5b), while for the latter, relative errors are less than 5% in most cases and the maximum is about 5% (Figure 5c). Among the three enamel thickness indices (3DAET, 3DRET, and 3DRED), 3DRED is the most robust one and 3DAET is more robust than 3DRET. Micro‐CT volume data is an approximation to the studied sample, somewhat like using Legos to build the target. Therefore, the linear relationship between 3DRET and voxel size is mainly due to the voxelization nature of Micro‐CT but not to the tooth morphology. The sensitivity of 3DRET to voxel size thus most likely exists in other taxa and other kind of teeth, meaning that discrepancies could occur between specimens scanned at different resolutions. For instance, Benazzi et al. (2014) scanned a gorilla skull and analyzed the enamel thickness of a lower molar. Their result showed that 3DRET is 14.12. However, Olejniczak, Tafforeau, et al. (2008) systematically analyzed enamel thickness in a relatively larger sample of gorilla mandibular molars (n = 8) and the mean 3DRET is 9.40 (ranging from 7.12 to 11.74). Although the two research groups have scanned different gorilla specimens and there could exist interspecific variations, this discrepancy may well lie with the voxel size difference between them since in the study by Benazzi et al. (2014), the entire skull was scanned at a voxel size of 61 μm, while in Olejniczak, Tafforeau, et al. (2008), the molars were scanned separately at a voxel size of 30.3 μm.

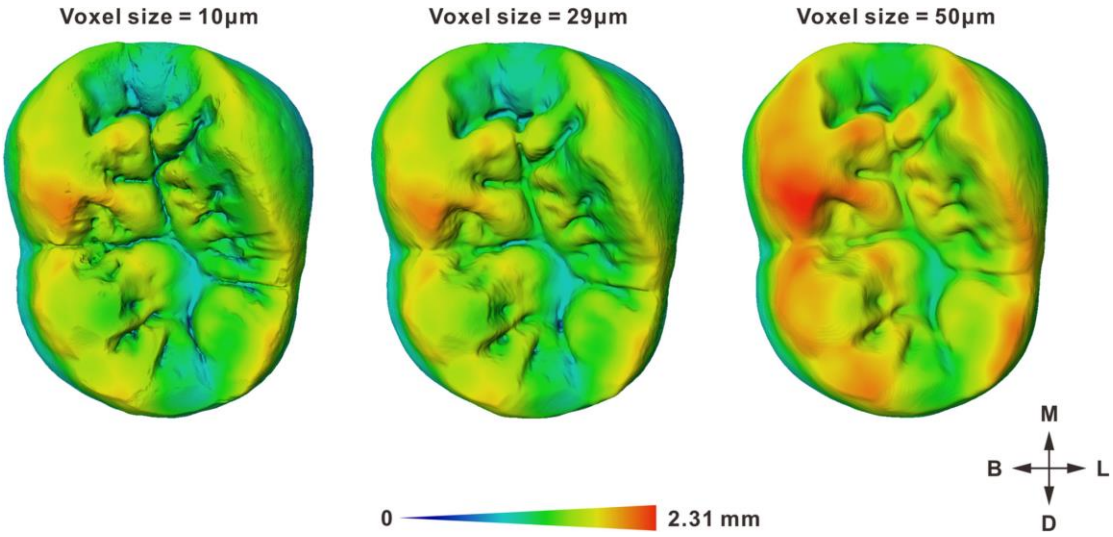

FIGURE 5. (a) Three‐dimensional relative enamel thickness (3DRET) and ratio of enamel‐thickness to dentine‐thickness (3DRED) at different voxel sizes and the relative errors of (b) 3DRET and (c) 3DRED. See caption of Figure 3 for graph description.

Why 3DAET, 3DRET, and 3DRED present diverse sensitivity patterns to voxel size? To interpret this disparity, we shift attention to the effect of voxel size on enamel volume (Figure 6a), EDJ surface area (Figure 6b), cubic root of coronal dentine volume (Figure 6c) and cubic root of enamel volume (Figure 6d), since these basic parameters are involved in the calculation of enamel thickness indices. It can be seen that all parameters will be affected by the voxel size (Figure 6a–d). And there exists threshold voxel size for these parameters. When voxel size is smaller than the threshold, these parameters show slight sensitive to the fluctuation of spatial resolution. Yet if voxel size is larger than the threshold value, relative error is getting larger. Here and later, our analysis is mainly focused on the sensitivity patterns of enamel thickness indices when voxel size is larger than the threshold. A significant finding is that the higher the parameter dimension is, the larger the maximum error is. In specific, the maximum errors of Ve (3D), Sedj (2D), cubic root of Vcdp (1D), and cubic root of Ve (1D) are about 35, 15, 8, and 11%, respectively (Figure 6e–h). 3DAET is the ratio of Ve to Sedj, and the variation of Sedj compensates to the variation of Ve to some extent since these two parameters show similar trend (getting larger) after 40 μm. However, the Sedj variation cannot completely offset the Ve variation, because these two parameters are of different dimensions and thus show varying sensitivity to voxel size (Figure 6e,f). Compared to 3DAET, 3DRET needs additional parameter: cubic root of Vcdp. Consequently, the sensitivity pattern of 3DRET to voxel size is different from that of 3DAET. 3DRET relates to the ratio of 3DAET to cubic root of Vcdp (Equation (2)). When voxel size is smaller than the threshold, 3DAET shows slight positive trend with the increasing voxel size (Figure 3a) while cubic root of Vcdp presents slight negative relationship with voxel size (Figure 6c), both leading to slightly overestimated 3DRET (Figure 5a). When voxel size is larger than the threshold, cubic root of Vcdp is also getting larger. However, the variation of cubic root of Vcdp (1D) cannot completely counterweigh the variations of Ve (3D) and Sedj (2D), so that 3DRET still show moderate relative error at larger voxel size (e.g., 50 μm). Unlike 3DAET and 3DRET where basic parameters (Ve, Sedj, and cubic root of Vcdp) are of different dimensions, 3DRED is essentially affected by two comparable parameters with the same dimension (1D, cubic root of Ve, and cubic root of Vcdp). Low‐dimensional parameters show less sensitivity

to voxel size (see the differences among Figures 6e–h) and the variation of cubic root of Vcdp substantively counterbalance the variation of cubic root of Ve owing to their homogeneity. These two reasons together improve the robustness of 3DRED.

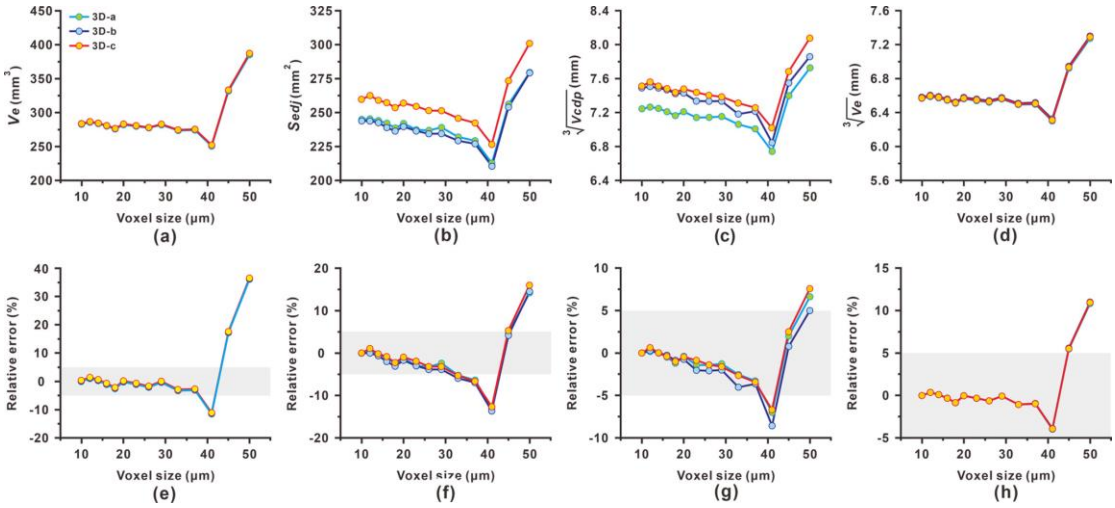

FIGURE 6. The sensitivity of four parameters to voxel size, including (a) enamel volume, (b) enamel–dentine junction (EDJ) surface area, (c) cubic root of coronal dentine volume, and (d) cubic root of enamel volume. The first two parameters (a,b) affect the result of three‐dimensional average enamel thickness (3DAET), the first three (a‐c) for three‐dimensional relative enamel thickness (3DRET), and the last two (c,d) for three‐dimensional ratio of enamel‐thickness to dentine‐thickness (3DRED). For these four parameters, their relative errors varying with voxel size are shown below in figures (e–h), respectively.

Another question is why there exists threshold voxel size. A possible explanation is that when voxel size gets larger, the small parts (e.g., dentine horn tip and small fissures) in the tooth could be over simplified or even melted down, thus causing measurement deviation. It is necessary to mention that the threshold voxel size repeated above (~40 μm) is only relevant for the sample studied here (NX‐C2‐9). It is most likely that the threshold voxel size will be different from 40 μm for other larger (e.g., Gorilla) or smaller (e.g., Hylobates) hominid teeth due to the size and structure differences from sample to sample.

3.2 Correlation between 3DAET and 3DRET, and between 3DAET and 3DRED

To investigate the relationship between 3DRET and 3DAET and the relationship between 3DRED and 3DAET, enamel thickness measurements for a total of 179 M were analyzed and the results are detailed in full in Supplementary Material Table 2. Figure 7 presents the results for eight hominid genera. For all taxon except modern humans, 3DRET is correlated with 3DAET by linear relationship. The regression coefficients are close to 0.8 or above in most cases, indicating that 3DRET is not an independent variable with respect to 3DAET. In contrast, 3DRED shows less degree of correlation with 3DAET, with R2 smaller than 0.5 in most cases. Thus, a question arises: Why there exists a linear relationship between 3DAET and 3DRET? As shown in Equation (2), there are three parameters involved in the calculation of 3DRET: Ve, Sedj, and cubic root of Vcdp.

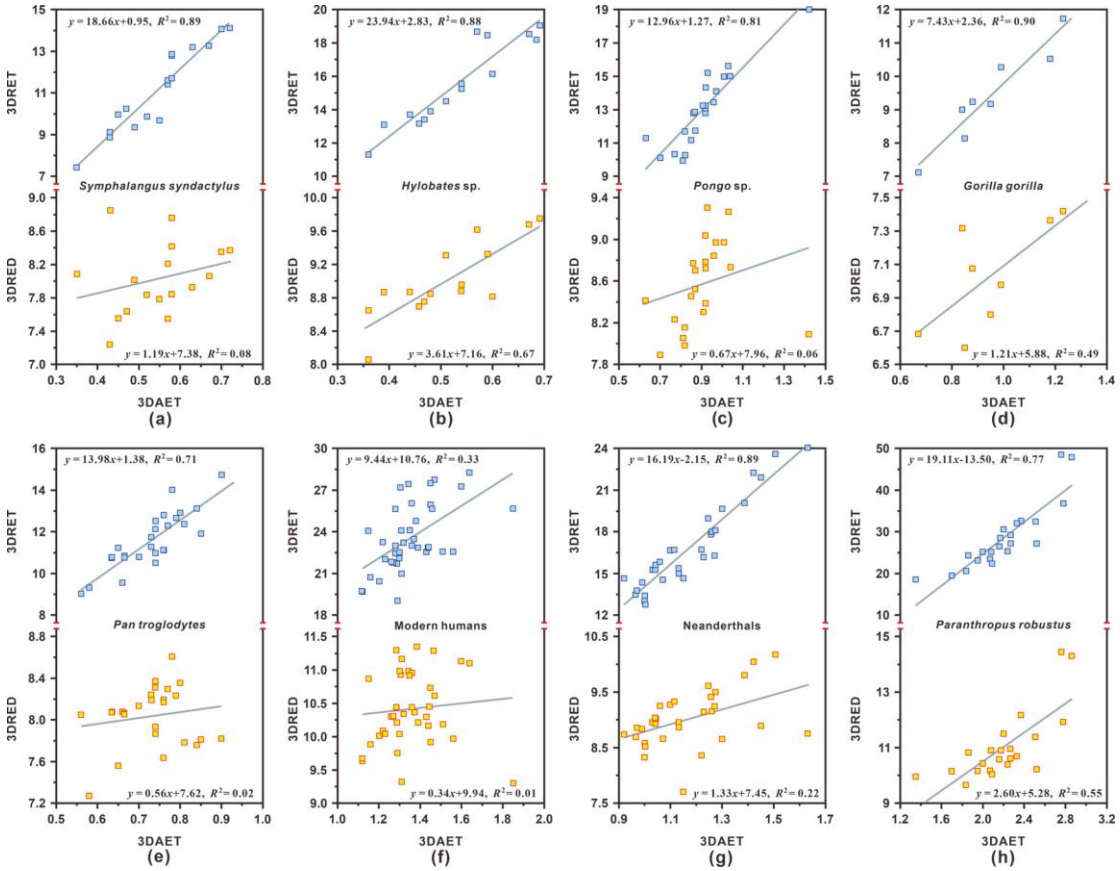

FIGURE 7. The relationship between three‐dimensional relative enamel thickness (3DRET) and three‐dimensional average enamel thickness (3DAET), and between three‐dimensional ratio of enamel‐thickness to dentine‐thickness (3DRED) and 3DAET for (a) Symphalangus syndactylu, (b) extant Hylobates, (c) extant Pongo, (d) Gorilla gorilla, (e) Pan troglodytes, (f) modern humans, (g) Neanderthals, and (h) Paranthropus robustus. All teeth are mandibular molars. In each figure, the upper part shows the relationship between 3DRET and 3DAET, while the lower part shows the relationship between 3DRED and 3DAET

For specific taxa (genus or species), the variation of Ve and Sedj exist between different samples, but the variation of cubic root of Vcdp may be very small, if the coronal dentine volume differences are not large enough. For instance, the ranges of Ve, Sedj, and cubic root of Vcdp for Neanderthals ($n = 31$) can be expressed as 252.78 ± 43.72 (mean and SD), 219.67 ± 40.74, and 7.01 ± 0.45, respectively. Compared to the ranges of Ve and Sedj, the range of cubic root of Vcdp is much smaller. Under this condition, the three parameters bear uneven influences on 3DRET, and cubic root of Vcdp can be approximately regarded as a constant. Therefore, Equation (2) can be reformulated as Equation (6).

$$3DRET \approx 100 \times \frac{V_e / S_{edj}}{a} + b \approx 100 \times \frac{3DAET}{a} + b \quad (6)$$

where a and b are constants that related to the taxonomic affinity of the studied tooth.

As we can see in Figure 7g, 3DRET shows an evident linear relationship with 3DAET (Neanderthals, R2 = .89), which is consistent with Equation (6). Compared to other primates, modern humans have reduced crown size with respect to their body size, in relation with the drastic and accelerated

reduction of the face that occurred in modern humans since the end of the Late Pleistocene (Brace, Rosemberg, & Hunt, 1987; Macchiarelli & Bondioli, 1986). During this recent evolutionary phase, allometric reorganization in enamel and dentine proportions may have occurred in modern humans (Grine, 2005). This could explain why modern humans show such a strange relationship (Figure 7f, not linear) between 3DRET and 3DAET compared with other hominids. It is necessary to mention that no guarantee can be given that Equation (6) is valid for all species. It depends on the relative variations (i.e., the ratio of SD to mean) of Ve, Sedj, and cubic root of Vcdp. However, the phenomenon that the linear correlation between 3DRET and 3DAET is fairly common in our study samples (Figure 7). This phenomenon will lead to two consequences. First, it is not practicable to use bivariate plot of 3DRET and 3DAET (just like traditional bivariate plot of the mesiodistal and buccolingual diameters) to offer diagnostic information for specimen with uncertain taxonomic affinity, because the two variables would probably form a line (Figure 8a–c) but not define a discriminative polygon. Curiously, the usage of bivariate plot of 3DRET and 3DAET are really rare in previous studies. Possibilities for that include the linear relationship between 3DRET and 3DAET. Second, discriminant information could be double counted, if both 3DAET and 3DRET are used to diagnosis the taxonomic status of a given tooth. For example, Zanolli, Kullmer, et al. (2019) utilized adjusted Z‐score statistics to assess the taxonomy of Indonesian fossil hominid and compared both 3DAET and 3DRET to that of other fossil and extant hominid, including Pongo, Gigantopithecus blacki, Homo erectus/ergaster, Homo erectus, Lufengpithecus, Sivapithecus, modern humans, and Neanderthals. In their supplementary figure 20, 3DAET and 3DRET show similar pattern and for some samples (e.g., Arjuna 9 LM2, SMF‐8855, and SMF‐8865), the results are even overlapped. On account of the high similarity between the pattern of 3DAET and 3DRET, it is plausible that one of them is likely redundant in the sense of taxonomic assessment.

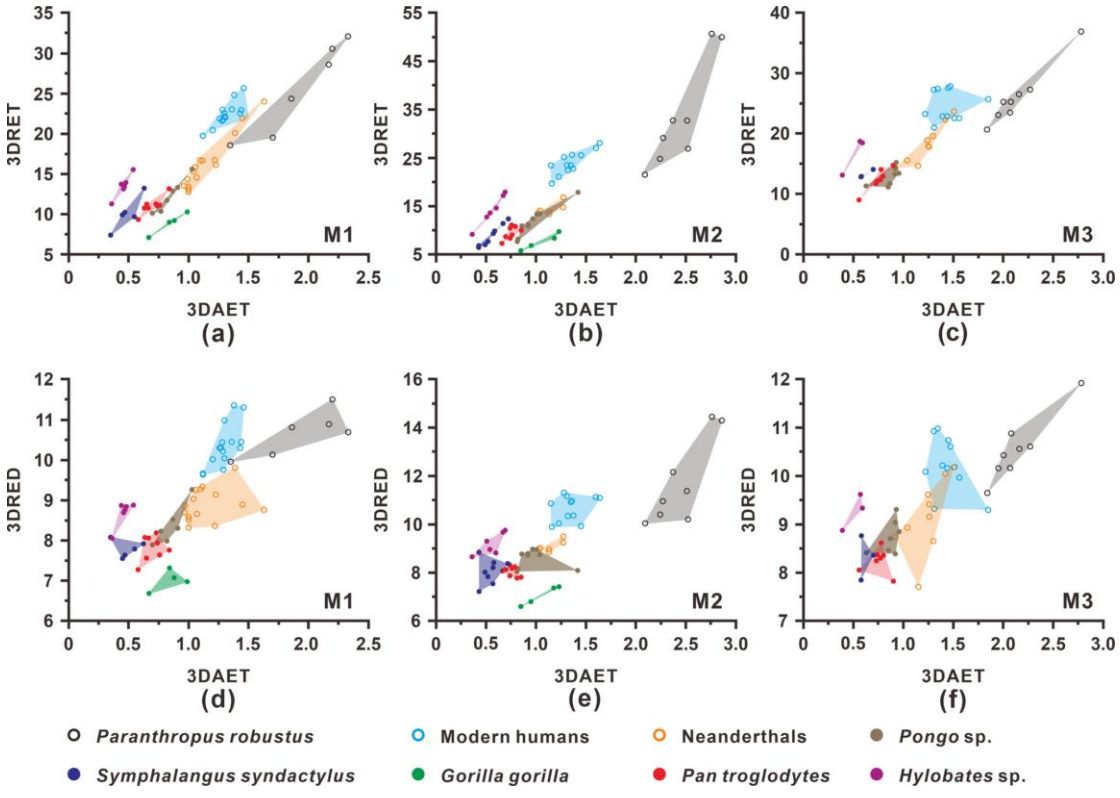

FIGURE 8. The taxonomic bivariate plot of three‐dimensional relative enamel thickness (3DRET)

and three‐dimensional average enamel thickness (3DAET) for (a) first molars, (b) second molars, and (c) third molars. The bivariate plot of three‐dimensional ratio of enamel‐thickness to dentine‐thickness (3DRED) and 3DAET for (d) first molars, (e) second molars, and (f) third molars

Unlike the definition of 3DRET (Equation (2)) where parameters probably have different relative variations, relative variations of components in 3DRED differ moderately. For example, the relative variations of 3DAET and 3DADT are 15.01 and 18.43%, respectively, for Neanderthals. Owing to that, the two components constituting 3DRED have relative even influences and 3DRED show less linear correlation with 3DAET (Figure 7), enabling to better discriminate extant and fossil hominid taxa (Figure 8d–f). This is notably the case for the first and second molars (Figure 8d,e), for which only minimal overlap occurs between taxa. For the third molars, moderate overlap can be observed (Figure 8f). This result is in accordance with previous studies suggesting a larger variance of hominid third molars (Martinón‐Torres, de Castro, Gomez‐Robles, Prado‐Simon, & Arsuaga, 2012; Skinner et al., 2015). Generally, a significant classification has been reached with the bivariate plot of 3DRED and 3DAET. This clear discrimination between taxa may be partly related to the fact that 3DRED is less correlation with 3DAET, but also to its inherent value to better capture the taxonomic signal (compared to 3DRET); see below.

Table 2 lists the results of the Kruskal–Wallis pairwise comparisons for 3DRET (bottom) and 3DRED (top) among the study taxa at each molar position. For the first molars, there are four pairs statistically showing indistinct 3DRED differences, while six for 3DRET. Similarly, less pairs show insignificant 3DRED differences compared to that of 3DRET for the second molars (three for 3DRED and five for 3DRET). For the third molars, eight pairs show insignificant 3DRET differences and the same to 3DRED. Overall, 3DRED bears more discriminative information compared to 3DRET for the study samples. This better discriminating capability could possibly attribute to that the taxa with large coronal dentine size generally show thicker ADT, thus lowering more 3DRED value. For example, due to allometric effect, Gorilla has larger dentine size compared to other extant apes, so that this taxon has smaller 3DRED than that of other apes (Supplementary Material Table 2). For the same reason, Gorilla statistically present distinct 3DRED differences compared to all other apes in the study sample while it is not easy to distinguish some apes (Symphalangus and Pan) from Gorilla by 3DRET (Table 2).

TABLE 2. Comparison between 3DRET (bottom) and 3DRED (top), Kruskal–Wallis test[a]

Taxon	***Gorilla***	***Sympha.***	***Pan***	***Pongo***	***Hylobates***	**Nean.**	**Mo. hu.**	***Pa. rob.***
First molars								
Gorilla								
Sympha.	0.327		0.624					
Pan		0.142						
Pongo		0.068	0.278		0.15			
Hylobates				0.2		0.461		
Nean.								
Mo. hu.								0.269

Pa. rob.							0.269	
Second molars								
Gorilla								
Sympha.	0.44		0.895					
Pan	0.064	0.402						
Pongo								
Hylobates				0.099		0.873		
Nean.					0.873			
Mo. hu.								0.143
Pa. rob.								
Third molars								
Gorilla		-	-	-	-	-	-	-
Sympha.	-		0.569	0.138		0.091		
Pan	-	0.425						
Pongo	-	0.909	0.798		0.053	0.097		
Hylobates	-	0.127	0.053	0.138		0.735	0.052	
Nean.	-				0.612			
Mo. hu.	-							0.621
Pa. rob.	-						0.97	

[a]Note: Sympha. = Symphalangus syndactylus. Nean. = Neanderthals. Mo. hu. = Modern humans. Pa. rob. = Paranthropus robustus.

Abbreviations: 3DRED, three‐dimensional ratio of enamel‐thickness to dentine‐thickness; 3DRET, three‐dimensional relative enamel thickness.

a Blank cell indicates significant differences ($p < .05$). A hyphen indicates no molars of that position of that taxon.

4 CONCLUDING REMARKS

Compared to 3DRET, 3DRED shows some advantages. Specifically, 3DRET is sensitive to voxel size while 3DRED is more robust. Besides, 3DRET shows a linear link to 3DAET in a considerable number of cases, probably causing information redundancy during taxonomic assessments. In contrast, 3DRED shows less correlation with 3DAET, so that they can used in combination in multivariable‐based statistics. Furthermore, 3DRED shows more taxonomic value compared to 3DRET in a large sample size. Despite the significance of 3DRED, it does not mean that this index could replace 3DRET, especially considering the important role of 3DRET in dietary reconstruction. Under certain conditions, 3DRED is promising to be a robust and reliable alternative to 3DRET in taxonomic study. These conditions mainly include: (a) the tooth sample is scanned at relatively low spatial resolution, or (b) 3DRET needs to be coupled with 3DAET (like the 3DRET‐3DAET bivariate plot or adjusted Z‐score statistics with both 3DRET and 3DAET included) to deduce the taxonomic status of a given sample.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Zhixing Yi: Conceptualization; methodology; validation; writing‐original draft; writing‐review and editing. Wei Liao: Investigation; validation; writing‐original draft; writing‐review and editing. Clément Zanolli: Methodology; writing‐original draft; writing‐review and editing. Wei Wang: Conceptualization; funding acquisition; investigation; validation; writing‐original draft; writing‐review and editing.