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ARTICLE



# A micro-CT based study of molar enamel thickness and its distribution pattern in Late Miocene *Lufengpithecus lufengensis* from Yunnan in Southwestern China

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## ABSTRACT

Molar enamel thickness and distribution pattern inform on the functional and dietary adaptation of extant and fossil primates. However, no systematic analysis of enamel thickness has been conducted on *Lufengpithecus*, a large-bodied fossil hominoid that lived in Southwest China during the late Miocene. In this study, we quantify two-dimensional (2D) enamel thickness and distribution of 68 lightly worn molars of *Lufengpithecus (L.) lufengensis* using micro-CT scanning data and compare it with modern humans, extant great apes, and fossil hominoids. The results indicate *L. lufengensis* has relatively thick enamel. It is slightly thicker than extant *Pongo* and comparable to some thick-enamel fossil pongines, but thinner than modern humans and most fossil hominins. The enamel distribution of *L. lufengensis* is distinctively unbalanced with relatively more enamel deposited on the cuspal region than the basal region in the molar crown, different from that found in modern humans and extant great apes. Concerning its palaeoecological and functional adaptations, we suggest that the features of thick-enamel and unbalanced distribution pattern in *L. lufengensis* is related to its adaptation to tough food and broader diets in a seasonal subtropical habitat.

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late Miocene hominoid;  
micro-CT; enamel thickness;  
dietary adaptation

## Introduction

*Lufengpithecus*, a large-bodied fossil hominoid from Late Miocene Southwest China that has been unearthed with a large assemblage of isolated teeth (Xu et al. 1978; Zhang et al. 1987; Qi and Dong 2006; Xu and Lu 2008), is critical in investigating the evolution of hominoids in East Asia. It has been considered as three species: *Lufengpithecus (L.) keiyuanensis*, *L. hudienensis*, and *L. lufengensis* (Wu 1987; Qi et al. 2006). At present, the evolutionary history of *Lufengpithecus* is still unclear, although scholars published a series of study since its first discovery (e.g. Wu 1987; Kelley and Etlar 1989; Qi et al. 2006; Xu and Lu 2008; Kelley and Gao 2012; Ji et al. 2013). Molar enamel thickness and distribution pattern are informative for assessing taxonomy, functional adaptation, and dietary ecology of extant and fossil primates (Molnar and Grant 1977; Kay 1981; Martin 1985; Macho and Spears 1999; Schwartz 2000; Kono et al. 2002, 2014; Smith et al. 2005, 2012a; Kono and Suwa 2008; Lucas et al. 2008; Suwa et al. 2009; Zanolli et al. 2019). It is therefore essential to investigate the enamel thickness and the dietary and ecological adaptations of *Lufengpithecus*.

Few previous studies have evaluated the enamel thickness of *Lufengpithecus* (Schwartz et al. 2003; Zanolli et al. 2019). Schwartz et al. (2003) analysed the ontogeny of crown formation and enamel thickness in two physical molar sections of *L. hudienensis* to compare them to *L. lufengensis* and a wide range of other hominoids, concluding that relative enamel thickness of *L. hudienensis* molar was more similar to that of *Pongo* than to any other extant ape, while *L. lufengensis* have considerably thick enamel as modern humans (Schwartz et al. 2003). Using occlusal fingerprint analysis and various morphometric approaches, Zanolli et al. (2019)

analysed hominid molars collected from the Early to Middle Pleistocene deposits of Java, Indonesia, and included *L. lufengensis* and *L. hudienensis* molars for comparison. The three-dimensional (3D) enamel distribution of *Lufengpithecus* shows relatively thick enamel at the periphery of the occlusal basin, similar to that of fossil hominid Trinil 11620 (Zanolli et al. 2019).

Although the enamel thickness and distribution of *Lufengpithecus* were preliminarily investigated, there is still no large-scale systematic analysis. In this study, we quantify the enamel thickness of *Lufengpithecus* by selecting 68 *L. lufengensis* molars from the Shihuiba site in Lufeng County, Yunnan, China (as demonstrated in Table 1), where the most abundant isolated teeth and other fossil remains of *Lufengpithecus* unearthed (Xu and Lu 2008). Micro-CT technique was used to scan the teeth and create virtual models. We aimed to analyse the 2D enamel thickness and distribution pattern of *L. lufengensis*, and compare it with modern humans, extant great apes, and other fossil hominoids. Concerning its palaeoecology and dietary adaptation, we try to provide the new dental information in understanding the ecological and functional adaptation of *Lufengpithecus*.

## Materials and methods

### Samples

A total of 68 isolated molars of *L. lufengensis* from Shihuiba site in Lufeng County, Yunnan, were collected, including 32 upper molars and 36 lower molars (Table 1). Sex was not incorporated into our analysis as a variable. We also collected the comparative samples, 25 molars from modern humans and 41 molars from extant great apes

**Table 1.** *L. lufengensis* and comparative specimens in present study.

Taxon	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	Total	Occlusal wear <sup>a</sup>	Sources <sup>b</sup>
<i>L. lufengensis</i>	9	16	7	5	16	15	68	66(1), 2(2)	IVPP
<i>Homo sapiens</i>	2	4	3	5	7	4	25	24(1), 1(2)	IVPP
<i>Pongo pygmaeus</i>	2	2	2	2	2	2	12	8(1), 4(2)	MCZ (6), IVPP (6)
<i>Pan troglodytes</i>	1	4	2	1	3	3	14	13(1), 1(2)	AMNH (7), IVPP (7)
<i>Gorilla gorilla</i>	2	1	2	4	3	3	15	13(1), 2(2)	AMNH (5), IVPP (10)

<sup>a</sup>The wear stage is estimated according to (Molnar 1971). e.g. 66(1) means 66 teeth are in occlusal wear 1.

<sup>b</sup>IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China  
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA ([www.morphosource.org](http://www.morphosource.org))

AMNH: American Museum of Natural History, New York, New York, USA ([www.morphosource.org](http://www.morphosource.org))

e.g. AMNH (5) means five specimens are provided by AMNH.

(Table 1) from the American Museum of Natural History (AMNH), Museum of Comparative Zoology (MCZ), and Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP) (see details in Table 1).

Table 1. *L. lufengensis* and comparative specimens in present study

### Micro-computed tomography and virtual reconstruction

The teeth provided by IVPP were scanned using the 225 kV micro-computerised tomography (developed by the Institute of High Energy Physics (IHEP), Chinese Academy of Sciences (CAS)) at the Key Laboratory of Vertebrate Evolution and Human Origins, CAS. The scanning was carried out with beam energy of 140kV and a flux of 120  $\mu$ A using a 360° rotation with a step size of 0.5°. A total of 720 projections were reconstructed into a 2048 × 2048 pixels of 1536 slices using a two-dimensional reconstruction software developed by IHEP. Isometric voxel size ranged from 10.04 to 62.70  $\mu$ m.

Enamel and dentine of each specimen were digitally segmented in MIMICS 16.0 ([www.materialise.com](http://www.materialise.com)). For teeth showing occlusal wear of early phase of stage 2 (Table 1), the missing enamel was reconstructed employing unworn occlusal surface as models. Reconstructions were also made for fractures on some teeth (see details in SOM Figure 1).

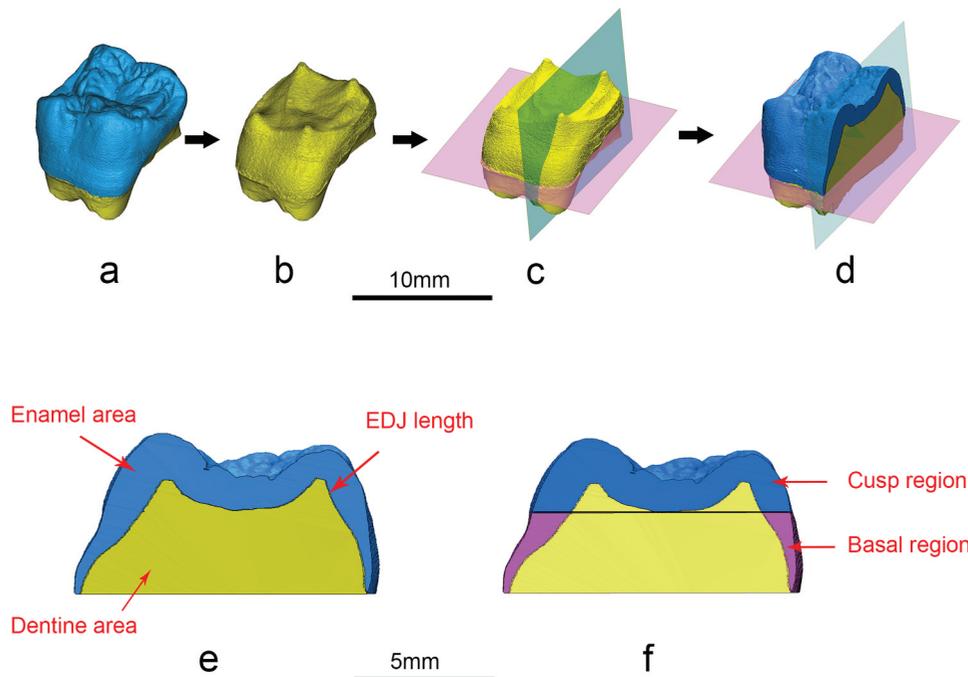
### Two-dimensional measurements of enamel thickness

Martin (1983, 1985) established widely used 2D enamel thickness measurement protocols in the ideal mesial planes. Benazzi et al. (2014) summarised the methods to identify the ideal mesial planes. In this study, we used the ‘2D-a’ method described by Tafforeau (2004) and Benazzi et al. (2014): the mesial cusp sections (MCS) pass through two mesial dentine horn tips and are perpendicular to the best-fit plane of the cervical line (as described in Figure 1). 2D enamel thickness was measured using 3-matic 6.0 ([www.materialise.com](http://www.materialise.com)). First, we applied the ‘Create Datum Plane’ option in the ‘Analyse’ module to create the best-fit plane of the cervical line and the mesial cusps plane (Figure 1c). Second, the enamel and dentine models were cut by the mesial cusp plane through the ‘Cut’ option in the ‘Design’ module (Figure 1d). Third, we computed the 2D enamel thickness data through the ‘Measure’ and ‘Properties’ module.

In the 2D measurements, the variables obtained for each specimen are categorised into two groups.

Group 1: Measurements of the whole MCS (Figure 1e) (Martin 1983, 1985)

1. EA, the enamel area, in  $\text{mm}^2$ .
2. DA, the area of dentine and pulp enclosed by EDJ and straight line between the buccal and lingual cervices, in  $\text{mm}^2$ .
3. EDJL, the enamel-dentine junction (EDJ) length, in mm.
4. 2DAET, the two-dimensional average enamel thickness, in mm. 2DAET is the quotient of EA and EDJL, yielding the average straight-line distance from the EDJ to the outer enamel surface. 2DAET was calculated as:  $2DAET = EA/EDJL$ .



**Figure 1.** 2D enamel thickness measurements on virtual mesial cusp sections of *L. lufengensis* molar (M<sup>1</sup>, PA674.48). a, segmentation of enamel and dentine; b, dentine model; c and d, the mesial cusp section; e, enamel area, dentine area, and enamel-dentine junction (EDJ) length measured on the mesial cusp section; f, the cusp and basal region.

5. 2DRET, the two-dimensional relative enamel thickness, a scale-free measurement. 2DRET is 2DAET divided by the square root of dentine area, then multiplied by 100. 2DRET was calculated as:  $2DRET = 100 \times 2DAET/DA^{1/2}$ .

Group 2: Measures of the enamel distribution.

To compare enamel distribution patterns, the MCS was divided into two parts: cuspal and basal (Figure 1f). The boundary between cuspal and basal parts was set at the line passing through the lowest point of the enamel between the lingual and buccal cusp tips, parallel to the straight line between the buccal and lingual cervices (modified from Kono 2004). Average and relative thickness were calculated for each subdivision.

1. CEA and BEA, enamel area of the cuspal region and enamel area of the basal region, in  $\text{mm}^2$ .

2. CEDJL and BEDJL, EDJ length of the cuspal region, and EDJ length of the basal region, in mm.

3. CAET, the quotient of CEA and CEDJL, yielding the average straight-line distance from the EDJ to the outer enamel surface of the cusp region. CAET was calculated as:  $CAET = CEA/CEDJL$ .

4. BAET, the quotient of BEA and BEDJL, yielding the average straight-line distance from the EDJ to the outer enamel surface of the basal region. BAET was calculated as:  $BAET = BEA/BEDJL$ .

5. CRET, CRET is CAET divided by the square root of the whole dentine area (DA in Group 1), then multiplied by 100. CRET was calculated as:  $CRET = 100 \times CAET/DA^{1/2}$ .

6. BRET, BRET is BAET divided by the square root of the whole dentine area (DA in Group 1), then multiplied by 100. BRET was calculated as:  $BRET = 100 \times BAET/DA^{1/2}$ .

### 3 Results

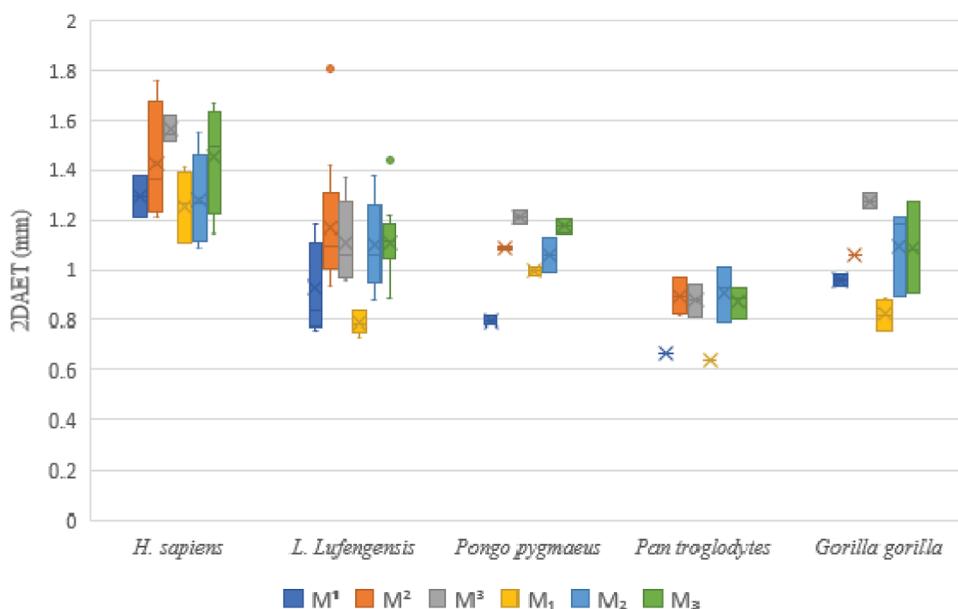
#### Enamel thickness

The results of enamel thickness measurements of *L. lufengensis* are listed in Table 2. The mean value of 2DAET is 1.08 mm with a range of 0.73–1.81 mm. The second and the third molar possess larger mean values of 2DAET than the first molar on both maxilla and the mandible, especially  $M_3$  is significantly larger than  $M_1$  in 2DAET. *L. lufengensis* 2DAET values range widely, similar to *Homo* (*H. sapiens*). Nearly half of their ranges overlap. The *L. lufengensis* data almost completely overlap with the ranges of extant apes (Figure 2).

For 2DRET, values range from 11.36–28.40 (average = 17.95), and it increases from the first molar to the third molar. Here, the overlap of *L. lufengensis* and *H. sapiens* is small in per tooth type

**Table 2.** Measurements of 2D molar enamel thickness of *L. lufengensis*.

Tooth	n	Enamel area	Dentine area	EDJ Length ( $\text{mm}^2$ )	2DAET	2DRET
		( $\text{mm}^2$ )	( $\text{mm}^2$ )		(mm)	
		Mean & range	Mean & range	Mean & range	Mean & range	Mean & range
$M^1$	9	16.21 (11.27–22.60)	33.02 (24.71–39.78)	17.30 (14.56–19.11)	0.93 (0.76–1.18)	16.21 (12.89–20.38)
$M^2$	16	24.28 (17.71–39.90)	46.47 (31.86–64.74)	20.64 (17.28–25.40)	1.17 (0.94–1.81)	17.32 (13.15–23.46)
$M^3$	7	18.95 (13.55–24.25)	34.42 (23.10–56.15)	17.11 (13.96–21.43)	1.11 (0.96–1.37)	19.43 (12.87–24.20)
$M_1$	5	14.01 (11.60–16.73)	35.78 (25.82–48.82)	17.59 (15.24–19.81)	0.79 (0.73–0.84)	13.44 (12.09–15.25)
$M_2$	16	20.87 (16.34–27.16)	40.51 (27.77–60.04)	18.94 (15.84–22.82)	1.10 (0.88–1.38)	17.73 (11.36–24.35)
$M_3$	15	17.98 (13.86–21.68)	29.39 (25.01–37.53)	16.14 (14.78–18.34)	1.11 (0.89–1.44)	20.70 (16.73–28.40)
Mean	68	19.72 (11.27–39.90)	37.49 (23.10–64.74)	18.22 (13.93–25.40)	1.08 (0.73–1.81)	17.95 (11.36–28.40)



**Figure 2.** Comparison of the 2D average enamel thickness (2DAET). Standard box and whisker plots reveal the interquartile range (boxes: 25%–75% percentiles of the data), 1.5 interquartile ranges (whiskers) and the median values (black line in a box). Outliers more than 1.5 interquartile from the box are indicated by circles.

(Figure 3). *Pongo* 2DRET values fall in the middle range of *L. lufengensis* values, while *Pan* and *Gorilla* fall in the lower end of the *L. lufengensis* values (Figure 3).

Table 3 lists the 2D relative enamel thickness (2DRET) of *L. lufengensis*, and extant and fossil hominoids. In general, *L. lufengensis* has thinner enamel than most other hominins, comparable to thick-enamel members of pongines. The 2DRET results indicate that most extant and fossil hominins have ‘thick’ (e.g. *H. sapiens*, *Australopithecus afarensis*, African *H. erectus*) or even ‘hyper thick’ (*Paranthropus robustus*) enamel (Table 3). *L. lufengensis* is similar to Asian *H. erectus* in M<sup>1</sup> and M<sup>2</sup>. The range of extant and fossil pongines in Asia is wide, from intermediate/thin (extant *Pongo abelli*) to thick (*Sivapithecus*, *Khoratpithecus*, and *Gigantopithecus*). The mean value of *L. lufengensis* is slightly thicker than that of extant *Pongo* in per tooth type (Table 3). However, there are significant overlaps between *L. lufengensis* and living and fossil orangutans in 2DRET (Smith et al. 2011, 2012b, 2018).

Previous results for *Lufengpithecus* fall into the 2DRET range determined in this study (Schwartz et al. 2003; Zanolli et al. 2019). The 2DRET of *L. lufengensis* based on physical sections (Schwartz et al. 2003) was 24.2 (M<sub>2</sub>), which is as thick as that found for *H. sapiens* and early hominins. It is nearly equal to the maximum 2DRET for M<sub>2</sub> found in this study (24.35). While *L. hudienensis* show an ‘intermediate/thin’ enamel thickness (2DRET = 14.1, M<sub>1</sub>) (Schwartz et al. 2003). It is close to the mean value of 2DRET for M<sub>1</sub> of *L. lufengensis* in this study (13.44). Another study of *Lufengpithecus* based on CT scanning showed that the mean value of 3D relative enamel thickness (3DRET) in 7 molars of *L. lufengensis* and *L. hudienensis* was 15.66 (all molar positions were uncertain) (Zanolli et al. 2019), which is slightly thinner than the mean value in this study (17.95). The present study indicates the sample size and the tooth type are effective for the results of enamel thickness comparison.

### Enamel distribution pattern

The 2D enamel thickness for the whole enamel area (EA, 2DAET and 2DRET), cuspal region (CEA, CAET, and CRET), and basal region (BEA, BAET, and BRET) are provided in Table 4. The data for each species are separated by upper and low molars, although differences in molar enamel thickness can also exist within the upper and lower rows (see Table 2).

The results of enamel thickness distribution are shown in three ways: 1) comparisons of cuspal enamel area (CEA) and basal enamel area (BEA); 2) comparisons of CAET and BAET; 3) comparisons of 2DRET, CRET, and BRET among taxa.

The proportions of cuspal and basal enamel areas in upper and lower molars are shown in Figures 4 and 5. Cuspal enamel area is larger than basal enamel area, especially in *L. lufengensis* and *H. sapiens* (Table 4, Figures 4 and 5). The CEA/BEA shows the ratio of cuspal enamel area to basal enamel area. We compared CEA/BEA using a Mann Whitney U-test to test for significant differences between *L. lufengensis* and comparative specimens (Table 5). *L. lufengensis* and *H. sapiens* are significantly different in upper molars but similar in lower molars, while *L. lufengensis* and other hominoids are significantly different in both upper and lower molars (Table 5).

Cuspal enamel (CAET) is thicker than basal enamel (BAET) in all species examined (Table 4). For both upper and lower molars, *H. sapiens* shows the thickest CAET and *L. lufengensis* ranks second. In contrast, for BAET, *L. lufengensis* has the thinnest enamel. This suggests that the enamel distribution of *Lufengpithecus* molars shows relatively more enamel deposits in the cuspal than the basal region. Cuspal and basal average enamel thickness differed significantly in *H. sapiens* and *L. lufengensis* while they did not for *Pongo*, *Pan*, and *Gorilla* (Table 6).

For relative basal enamel thickness (BRET), *L. lufengensis* has the thinnest basal enamel for both upper and lower molars. In contrast, for relative cuspal enamel thickness (CRET), *L. lufengensis* ranks second (Table 4). The differences of relative enamel thickness in the whole enamel area, the cuspal region, and the basal region between *L. lufengensis* and comparative species are shown in Table 7. *L. lufengensis* shows significantly thinner enamel than *H. sapiens* for all regions. For 2DRET, *L. lufengensis* is comparable to *Pongo*, but for cuspal enamel, *L. lufengensis* is significantly thicker, and for basal enamel, *L. lufengensis* is significantly thinner. *Pan* molars tend to have a thinner cuspal region, but a thicker basal enamel region than *L. lufengensis*. The enamel of *Gorilla* molars is thinner than that found for *L. lufengensis* in the whole enamel area and the cuspal enamel region, but the basal enamel of *L. lufengensis* and *Gorilla* do not differ significantly from each other.

The present results reveal that *L. lufengensis* shows a distinctly unbalanced distribution pattern, different from that of modern humans and extant great apes. Relatively more enamel is deposited

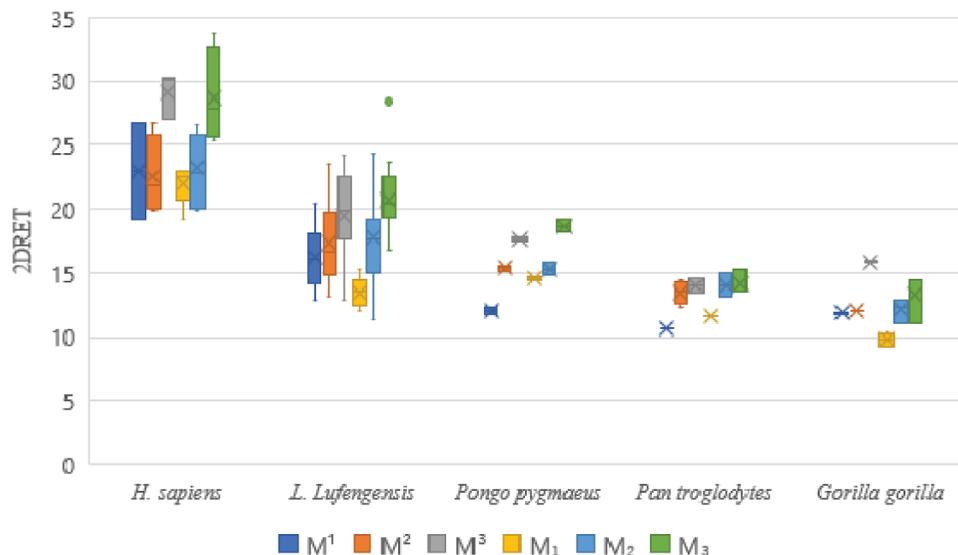


Figure 3. Comparison of the 2D relative enamel thickness (2DRET). See Figure 2 for the explanation of the figure.

Table 3. 2D relative enamel thickness in *L. lufengensis*, extant and fossil hominoids (from greatest to least).

Taxon	M <sup>1</sup> (range)	M <sup>2</sup> (range)	M <sup>3</sup> (range)	M <sub>1</sub> (range)	M <sub>2</sub> (range)	M <sub>3</sub> (range)	N	Mean	References	Category <sup>a</sup>
<i>Australopithecus boisei</i>				28.74	29.42(24.82–36.65)	33.88(30.30–36.81)	3	31.01	Skinner et al. (2015)	Hyper thick
South African early Homo				29.0(28.7–29.3)			8	29.15	Smith et al. (2012a)	Hyper thick
<i>Paranthropus robustus</i>	28.82(28.61–29.03)	29.5	25.81(22.49–30.31)	28.24(24.95–30.47)	35.68		9	28.38	Olejniczak et al. (2008b)	Hyper thick
<i>Oreopithecus turkiae</i>				27.3	26.10(25.28–26.92)	25.80	1	27.3	Gül-Eç et al. (2007)	Hyper thick
<i>Australopithecus aethiopicus</i>					25.5		3	26.00	Skinner et al. (2015)	Thick
<i>Oreanopithecus macedoniensis</i>					23.15(19.88–26.63)	28.69(25.35–33.67)	3	25.5	Smith et al. (2004)	Thick
<i>Homo sapiens</i>	22.92(19.13–26.72)	22.53(19.83–26.71)	29.13(27.05–30.14)	21.95(19.13–22.96)	20.5(14.8–27.7)	21.7(17.2–31.8)	25	24.40	This study	Thick
<i>Homo sapiens</i>	18.7(14.0–23.9)	21.4(16.5–28.0)	21.8(17.0–30.0)	17.0(11.8–22.6)			271	20.04	Smith et al. (2006)	Thick
<i>Australopithecus afarensis</i>				19.49(18.37–20.61)	24.82(21.73–28.44)	24.45(24.08–24.82)	8	23.39	Smith et al. (2012a)	Thick
<i>Afropithecus turkanensis</i>					22.91(19.88–25.96)	24.4	4	23.28	Skinner et al. (2015)	Thick
<i>Africa Homo erectus</i>				19.59	24.26(22.67–25.13)	23.03(20.17–25.89)	6	23.07	Maclatchy et al. (2019)	Thick
<i>Australopithecus africanus</i>	22.54		25.60	21.73(15.69–27.76)	23.93(16.54–31.32)	21.89(17.91–26.81)	9	22.79	Olejniczak et al. (2008b)	Thick
<i>Gigantopithecus blacki</i>	19.88(14.20–23.97)	22.45(16.76–31.02)		21.49(14.76–27.13)	25.63(22.74–30.99)		18	21.31	Zhang and Zhao (2013)	Thick
<i>Australopithecus anamensis</i>				21.40(16.56–25.71)	17.97(16.71–19.16)	21.27(18.87–22.65)	13	20.31	Skinner et al. (2015)	Thick
East African early Homo	15.63	18.67		21.50	26.18		4	20.50	Smith et al. (2012a)	Thick
<i>Griphopithecus sp.</i>		19.0(17.8–20.2)		17.2	18.4(16.5–20.7)	22.0(20.9–23.0)	8	19.3	Smith et al. (2003)	Thick
<i>Sivapithecus sivalensis</i>	17.2(16.3–18.2)				20.8		3	19.2	Martin (1985)	Thick
<i>Sivapithecus parvada</i>				18.9			1	18.9	Smith et al. (2006)	Thick
Fossil Homo sapiens	18.2(15.7–20.9)	19.8		18.0(15.2–23.3)	18.3(16.3–20.2)	20.5(19.2–21.9)	17	18.52	Mahoney et al. (2007)	Thick
Asian Homo erectus	15.8(15.3–16.3)	19.4	20.2(18.7–22.5)				6	18.48	Smith et al. (2012a)	Thick
<i>Equatorius africanus</i>	17.7	20.4		17.1(15.2–19.0)	17.6	17.3	6	17.87	Smith et al. (2019)	Thick
<i>Lufengpithecus lufengensis</i>	16.21 (12.89–20.38)	17.32 (13.15–23.46)	19.43 (12.87–24.20)	13.44 (12.09–15.25)	17.73 (11.36–24.35)	20.70 (16.73–28.40)	68	17.95	This study	Thick
<i>Lufengpithecus lufengensis</i>					24.2(24.1–24.6)		-	24.2	Schwartz et al. (2003)	Thick
<i>Khoratpithecus piriyai</i>					17.6		1	17.6	Chaimanee et al. (2006)	Thick
<i>Khoratpithecus</i>					17.52(17.23–17.80)			17.52 <sup>b</sup>	Chaimanee et al. (2003)	Thick
<i>Ekembo heseloni</i>										
<i>Ekembo cf. nyanzae</i>						17.0	1	17.0	Beynon et al. (1998)	Intermediate/ thick
<i>Sivapithecus indicus</i>	16.5					16.69	1	16.69	Maclatchy et al. (2019)	Intermediate/ thick
<i>Homo neanderthalensis</i>	15.2(13.80–16.93)	18.1(15.65–20.85)	18.0(14.30–18.87)	15.9(13.77–20.46)	15.7(14.21–16.80)	16.6(15.28–18.34)	42	16.44	Olejniczak et al. (2008a)	Intermediate/ thick
<i>Oreopithecus bambolii</i>	13.0			17.4	17.0	15.8(15.1–16.5)	5	15.8	Zanolli et al. (2016)	Intermediate/ thick
<i>Hylobates muelleri</i>				13.3(10.4–15.6)	14.9(13.9–15.8)	18.5(15.0–21.8)	10	15.76	Olejniczak (2006)	Intermediate/ thick
<i>Pongo pygmaeus</i>	12.03(11.82–12.25)	15.33(15.12–15.54)	17.64(17.45–17.84)	14.57(14.46–14.68)	15.29(14.83–15.74)	18.62(18.13–19.10)	12	15.58	This study	Intermediate/ thick
Fossil Pongo (mainland Asia)	15.04	14.26	16.29	11.29	16.07	14.61	15	15.55	Hu and Zhao (2015)	Intermediate/ thick
<i>Rangwapithecus gordonii</i>						14.9	1	14.9	Smith et al. (2003)	Intermediate/ thick
<i>Pierolapithecus catalaunicus</i>	14.31(13.99–14.63)	14.48(14.39–14.56)	16.88				5	14.89	Alba et al. (2013)	Intermediate/ thick
<i>Anoiapithecus brevirostris</i>	14.09(13.94–14.24)	15.16(12.97–17.31)	14.77				7	14.80	Alba et al. (2013)	Intermediate/ thick
<i>Rudapithecus hungaricus</i>	11.3	13.5	17.5	12.8(12.3–13.4)	15.4(15.0–15.9)	16.1	8	14.38	Smith et al. (2019)	Intermediate/thin
<i>Pongo pygmaeus</i>	12.3(9.0–15.1)	15.2(10.8–18.2)	16.2(10.1–22.2)	11.8(9.7–15.8)	14.6(11.0–19.5)	16.3(11.2–22.5)	75	14.28	Smith et al. (2012b)	Intermediate/thin
<i>Lufengpithecus hudienensis</i>				14.1			1	14.1	Schwartz et al. (2003)	Intermediate/thin

(Continued)

Table 3. (Continued).

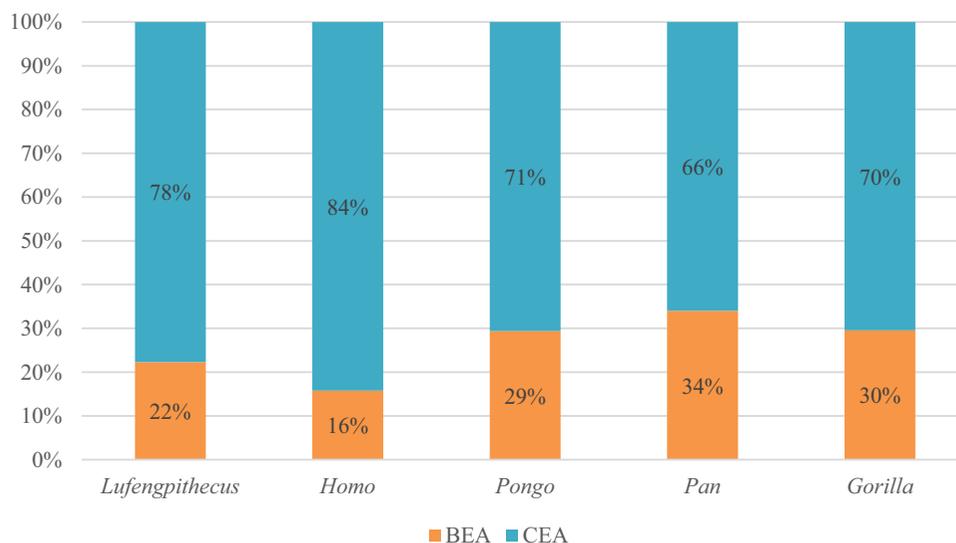
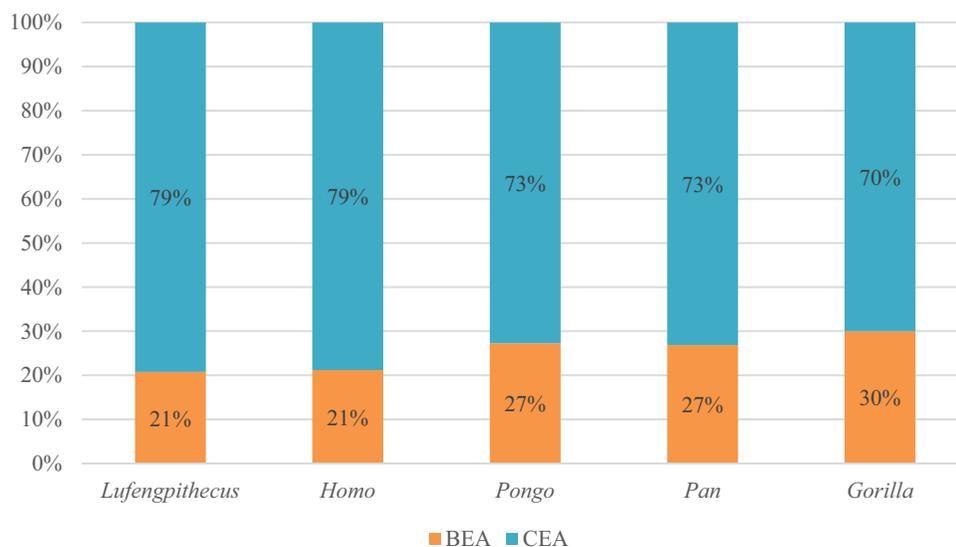
Taxon	M <sup>1</sup> (range)	M <sup>2</sup> (range)	M <sup>3</sup> (range)	M <sub>1</sub> (range)	M <sub>2</sub> (range)	M <sub>3</sub> (range)	N	Mean	References	Category <sup>a</sup>
<i>Pongo abelli</i>	12.0(9.0–16.3)	14.0(11.2–19.2)	16.8(12.2–22.1)	12.1(8.6–14.7)	14.2(11.2–18.5)	14.8(9.8–19.1)	45	13.86	Smith et al. (2012b)	Intermediate/thin
<i>Pan troglodytes</i>	10.58	13.50(12.38–14.36)	13.98(13.38–14.58)	11.68	14.05(13.21–14.91)	14.19(15.31–13.64)	14	13.49	This study	Intermediate/thin
<i>Pan troglodytes</i>	10.7(8.5–13.1)	11.7(10.7–12.5)	12.0(9.0–15.0)	12.5(10.3–14.1)	13.2(10.9–16.6)	14.1(12.4–16.6)	72	-	Smith et al. (2005) MacLatchy et al. (2019)	Intermediate/thin
<i>Pan paniscus</i>							1	13.6	Smith et al. (2003)	Intermediate/thin
<i>Hispanopithecus laietanus</i>	13.1(12.7–13.4)	14.3					3	13.47	Andrews et al. (1991)	Intermediate/thin
<i>Proconsul major</i>				12.0(11.4–12.6)	14.7(12.3–17.2)	13.7	5	13.43	MacLatchy et al. (2019)	Intermediate/thin
cf. <i>Khoratpithecus</i> sp.		13.35(13.11–13.58)					2	13.35	Smith et al. (2003)	Intermediate/thin
<i>Dryopithecus fontani</i>		12.48	12.95				2	12.72	Chaimanee et al. (2019)	Intermediate/thin
<i>Symphalangus syndactylus</i>				10.8(9.02–12.65)	13.6(11.8–15.7)	12.7(10.5–15.6)	17	12.58	Alba et al. (2013)	Intermediate/thin
<i>Nyanzapithecus alesi</i>	12.2						1	12.2	Olejniczak (2006)	Intermediate/thin
<i>Gorilla gorilla</i>	11.82(11.69–11.96)	12.08	15.83(15.75–15.91)	9.77(9.27–10.32)	12.11(11.10–12.93)	13.30(11.07–14.47)	15	12.18	Nengo et al. (2017)	Intermediate/thin
<i>Gorilla gorilla</i>	9.3(7.0–10.2)	10.7(8.9–13.0)	10.8(9.6–12.4)	9.1(7.8–12.6)	11.4(8.6–15.2)	12.7(11.1–15.1)	38	-	This study	Intermediate/thin
<i>Morotopithecus bishopi</i>			12.9				2	11.98	Smith et al. (2005)	Thin
<i>Hylobates lar</i>					11.1		2	11.98	MacLatchy et al. (2019)	Intermediate/thin
<i>Proconsul africanus</i>	8.5					11.0	1	11.0	MacLatchy et al. (2019)	Thin
							1	8.5	Martin (1983)	
									Andrews et al. (1991)	

<sup>a</sup>Enamel thickness categories are named according to 2DRET (Martin 1985): thick (17.49 < RET ≤ 26.20), intermediate/thick (14.64 < RET ≤ 17.49), intermediate/thin (11.30 < RET ≤ 14.64), thin (8.90 < RET ≤ 11.30). The value of 2DRET greater than that of 'thick' belongs to 'hyper thick' (Grine and Martin 1988).

<sup>b</sup>17.52 is the mean value for both sexes combined; male only is 17.23 and female only is 17.80 (Chaimanee et al. 2003).

**Table 4.** Enamel thickness of the whole enamel area, cuspal region, and basal region for upper (UM) and lower molars (LM).

Tooth	Taxon	n	Whole enamel area						Cuspal region						Basal region					
			EA	SD	2DAET	SD	2DRET	SD	CEA	SD	CAET	SD	CRET	SD	BEA	SD	BAET	SD	BRET	SD
UM	<i>Homo</i>	9	26.14	3.57	1.44	0.18	24.82	4.06	22.01	2.91	1.86	0.27	31.95	5.75	4.13	1.23	0.64	0.10	10.91	1.07
	<i>Lufengpithecus</i>	32	20.85	5.92	1.09	0.22	17.47	3.10	16.23	4.86	1.43	0.35	22.94	4.88	4.66	1.54	0.60	0.11	9.59	1.38
	<i>Pongo</i>	6	21.31	4.32	1.03	0.17	15.00	2.31	15.05	4.55	1.17	0.27	16.94	3.64	6.26	0.43	0.80	0.02	11.59	0.53
	<i>Pan</i>	7	17.60	2.84	0.86	0.10	13.22	1.31	11.61	2.62	0.93	0.16	14.32	2.18	5.99	0.74	0.74	0.05	11.45	0.97
	<i>Gorilla</i>	5	28.90	3.95	1.11	0.15	13.48	1.93	20.36	3.82	1.25	0.21	15.24	2.68	8.54	0.61	0.86	0.07	10.55	1.10
LM	<i>Homo</i>	16	22.23	3.64	1.32	0.18	24.16	3.65	17.52	2.53	1.72	0.30	31.39	5.70	4.71	1.78	0.70	0.13	12.76	1.96
	<i>Lufengpithecus</i>	36	18.57	3.71	1.05	0.16	17.98	3.52	14.50	3.84	1.39	0.23	23.83	4.72	3.80	0.88	0.54	0.07	9.31	1.67
	<i>Pongo</i>	6	21.49	1.72	1.08	0.09	16.16	1.81	15.62	1.15	1.27	0.13	19.03	2.46	5.86	0.96	0.77	0.06	11.52	1.00
	<i>Pan</i>	7	16.87	3.22	0.86	0.11	13.77	1.10	12.33	3.27	0.96	0.17	15.31	1.89	4.53	0.55	0.66	0.05	10.72	1.04
	<i>Gorilla</i>	10	27.19	6.50	0.98	0.18	11.53	1.81	19.40	5.78	1.08	0.23	12.59	2.32	8.15	1.14	0.81	0.08	9.55	0.70


**Figure 4.** The proportions of the cuspal and basal enamel area in the upper molars.

**Figure 5.** The proportions of the cuspal and basal enamel area in the lower molars.

on the cuspal region (or upper part) than the basal region (or lower part) of the molar crown. The main reason seems to be that *L. lufengensis* shows a relatively thinner and longer enamel distribution pattern near the cervical line in the basal enamel region, compared with *H. sapiens* and extant great apes (Figure 6, also see BAET and BRET in Table 4).

The mesial cusp sections are derived from microtomography. The left side of each section is lingual, and the right side is buccal. The long red lines pass through the lowest point of the enamel between the lingual and buccal cusp tips. The short red lines are cervical lines, the straight line connecting the buccal and lingual cervices. These two types of red lines are parallel, dividing the

**Table 5.** Results of the Mann-Whitney U-test for differences in CEA/BEA between *L. lufengensis* and comparative specimens.

Group 1	Group 2		UM	LM
<i>Lufengpithecus</i>	<i>Homo</i>	P	<b>0.000</b>	0.685
		Z	3.497	0.405
	<i>Pongo</i>	P	<b>0.016</b>	<b>0.014</b>
		Z	-2.363	-2.413
	<i>Pan</i>	P	<b>0.000</b>	<b>0.020</b>
		Z	-3.807	-2.296
<i>Gorilla</i>	P	<b>0.002</b>	<b>0.000</b>	
	Z	-2.889	-3.579	

The bold number indicates that the group comparison is significant ( $P < 0.05$ ).

**Table 6.** Results of the Mann-Whitney U-test for differences between CAET and BAET.

Tooth		<i>Lufengpithecus</i>	<i>Homo</i>	<i>Pongo</i>	<i>Pan</i>	<i>Gorilla</i>
UM	P	<b>0.000</b>	<b>0.000</b>	0.026	0.026	0.008
	Z	-6.877	-3.578	-2.181	-2.239	-2.611
LM	P	<b>0.000</b>	<b>0.000</b>	0.002	0.007	0.003
	Z	-6.983	-4.824	-2.882	-2.619	-2.873

The bold number indicates that the group comparison is significant ( $P < 0.001$ ).

**Table 7.** Results of the Mann-Whitney U-test for differences in 2DRET, CRET, and BRET between *L. lufengensis* and comparative specimens.

Group 1	Group 2		UM			LM		
			2DRET	CRET	BRET	2DRET	CRET	BRET
<i>Lufengpithecus</i>	<i>Homo</i>	P	<b>0.000</b>	<b>0.000</b>	<b>0.007</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
		Z	3.811	3.402	2.630	4.413	3.987	4.626
	<i>Pongo</i>	P	0.106	<b>0.010</b>	<b>0.001</b>	0.171	<b>0.014</b>	<b>0.008</b>
		Z	-1.641	-2.522	3.003	-1.401	-2.413	2.569
	<i>Pan</i>	P	<b>0.000</b>	<b>0.000</b>	<b>0.001</b>	<b>0.004</b>	<b>0.000</b>	<b>0.030</b>
		Z	-3.294	-3.916	3.111	-2.794	-3.720	2.154
<i>Gorilla</i>	P	<b>0.007</b>	<b>0.001</b>	0.140	<b>0.000</b>	<b>0.000</b>	0.470	
	Z	-2.577	-3.021	1.511	-4.255	-4.628	0.747	

The bold number indicates that the group comparison is significant ( $P < 0.05$ ).

mesial cusp section into two parts: cuspal and basal. The missing enamel over cusp tips was reconstructed (the green area in 'h').

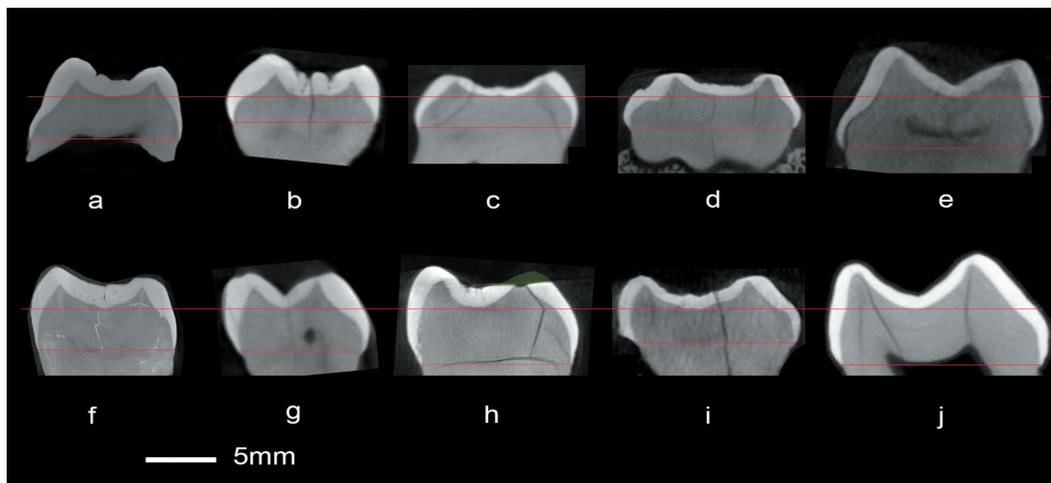
a:  $M^1$ , *L. lufengensis*; b:  $M^2$ , *H. sapiens*; c:  $M^2$ , *Pongo pygmaeus*; d:  $M^2$ , *Pan troglodytes*; e:  $M^3$ , *Gorilla gorilla*

f:  $M_2$ , *L. lufengensis*; g:  $M_1$ , *H. sapiens*; h:  $M_2$ , *Pongo pygmaeus*; i:  $M_2$ , *Pan troglodytes*; j:  $M_2$ , *Gorilla gorilla*

## Discussion

Enamel thickness has been widely used to interpret functional and dietary adaptation of primates (Molnar and Gantt 1977; Kay 1981; Dumont 1995; Shimizu 2002; Vogel et al. 2008; Kono et al. 2014). Molnar and Gantt (1977) first discussed the functional significance of enamel based on linear measurements of enamel thickness of extant great apes and modern human molars. They concluded that human teeth with thick enamel and low cusps were able to adapt to a crushing-grinding function for a long period. Kay (1981) established an association between thick enamel and diets of hard fruit, seeds, and nuts, such that thin enamel would be consistent with a diet of less abrasive and soft food. *Pongo* has relatively thick enamel, which might be an adaptation to eating very hard fruits, while *Gorilla* has relatively thin enamel and well-developed shearing crests, which are likely to be adaptations to leaf-eating (Kay 1981). Moreover, Kono (2004) explored the 3D enamel distribution pattern in 74 extant great apes and modern human molars. The examination supported the view that the functional side of the molars had thicker enamel than the opposite side (e.g. Macho and Berner 1993; Schwartz 2000; Kono et al. 2002). However, it should be noted that there is no specific value of enamel thickness that separates hard- and soft-object feeders. Dietary inferences based on the thickness of enamel should be made within an appropriate context (Dumont 1995). *L. lufengensis* shows a wide range of 2DRET, thinner than most of hominins, but similar to Asian *H. erectus* in  $M^1$  and  $M^2$  (Table 4). When compared with members of pongines, *L. lufengensis* is comparable to thick-enamel fossil pongines, such as *Sivapithecus* and *Khoratpithecus*, and they overlap with a wide range of living and fossil orangutans (Smith et al. 2011, 2012b, 2018). However, the comparison of enamel thickness distribution demonstrates that the cuspal enamel of *L. lufengensis* is significantly thicker than that of *Pongo*. This indicates that *L. lufengensis* is different from *Pongo* in the functional adaptation to its diet.

The unbalanced enamel thickness distribution associated with the abrasive diet may be related to the environment in which *L. lufengensis* lived. Fossils of *L. lufengensis* with a flora and a mammalian fauna were unearthed from beds 2–6 in section D at the Shihuiba site (Qi 1993; Xu and Lu 2008). Judging from the deposits, floral and faunal communities, Qi (1993) proposed that these hominoids lived in a woodland environment with bushes and grass at the edges. The spore-pollen assemblage showed the predominant fruits such as *Myrica* and some nuts including

**Figure 6.** Virtual mesial sections of molars of *L. lufengensis* and comparative specimens.

*Corylus*, *Carya*, and *Juglans* (Sun and Wu 1980), which were edible for *Lufengpithecus* (Xu and Lu 2008). Chang et al. (2015) analysed the pollen data from Shuitangba section, another site bearing fossil remains of *L. lufengensis* (Ji et al. 2013). They concluded that when the hominoid lived, evergreen broad-leaved forests with evergreen *Quercus* were predominant, while grasses including Poaceae began to expand, and simultaneously conifers decreased, indicating a tropical or subtropical climate. But the amounts and the kinds of spores and pollens varied through the different beds, indicating the climate changed from warm-humid to warm-drier then cooler-humid. This produced a shift from the woodland type to an environment with deciduous arboreal and bush vegetation (Sun and Wu 1980; Qi 1993; ). Furthermore, 85% of *Lufengpithecus* permanent teeth display a semi-annual pattern of linear enamel hypoplasia (LEH) that might be caused by the twice-yearly nutritional stress (Zhao 2004; Wang and Zhao 2015). Previous investigation of modern primate dietary ecology concluded that most primates preferred ripe fruit when available but consume ‘fallback’ foods when preferred foods are unavailable (Wrangham 1980; Chapman and Chapman 1990; Marshall and Wrangham 2007). For example, *Lophocebus albigena* have thick enamel and are commonly considered a hard-object consumer, but they consumed hard foods (e.g. seeds and bark) as ‘fallbacks’ when the softer foods (e.g. high-quality rape fruits) were unavailable during critical periods (Lambert et al. 2004). It noted to us that what primates eat during their lifetimes may differ from what they are adapted to eating (Guatelli-Steinberg 2018). Although we demonstrated that *L. lufengensis* molars have more enamel deposited on the cuspal region of the dental crowns than that of extant great apes, the occlusal surface with fine wrinkles are always flat, smooth, or heavily worn (Xu and Lu 2008). This may imply that *L. lufengensis* have taken fallback food – perhaps nuts, seeds, or even bark – when their preferred food was unavailable due to seasonal climate change.

In addition, the postcranium bones of *Lufengpithecus* reveal that it could be well adapted to arboreal and terrestrial substrates simultaneously (Xu and Lu 1986, 2008; Lin et al. 1987). The scapula, the clavicle, and the proximal phalanges display some specialised suspensory features (pear-shaped glenoid cavity, the twisted clavicle shaft, developed fibrous flexor sheaths and moderate phalangeal curvature, etc.) as seen in the tree-dwelling orangutans (Xu and Lu 1986, 2008; Deane and Begun 2008). Compared with the upper limb bones, the lower limb bones possess more terrestrial characteristics. The proximal femur shows the ability to walk bipedally with short steps, while the first metatarsal morphology (the ellipsoid-shaped central articular surface and relatively straight shaft) is similar to that of terrestrial hominoids (Xu and Lu 2008). Thick enamel may be related to increasing degrees of abrasion in the diet related to the use of foods from terrestrial sources, and/or to the incorporation of particularly tough food such as may be present in more strongly seasonal and harsher environments (Andrews et al. 1997). Thus, thick enamel in the cuspal region, different from that of arboreal orangutan, may be helpful for *L. lufengensis* if they forage for diverse food in the open ground environment during the dry season.

Future studies including 3D enamel distributions, enamel-dentine junction (EDJ) morphology, and the growth pattern of the whole dentition would be helpful to better understand the taxonomy, functional, and dietary adaptation of *Lufengpithecus*.

## Conclusions

The present study indicates that *L. lufengensis* has relatively thick enamel. It is comparable to thick-enamel members of pongines, but

thinner than modern human and most fossil hominins. In enamel distribution, *L. lufengensis* shows a distinctly unbalanced distribution pattern, relatively with more enamel deposited on the cuspal region than the basal region in the molar crown, which is different from that found in *Pongo*, and also different from that found in modern humans and extant Africa great apes. Concerning its palaeoecological and functional adaptations, we suggest that the features of thick-enamel and unbalanced distribution pattern in *L. lufengensis* is related to its adaptation to tough food and broader its diets in a seasonal subtropical habitat.

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## Disclosure statement

The authors declare that they have no conflict of interest.

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