Received: 13 January 2016 | Revised: 11 August 2016 | Accepted: 1 September 2016

DOI 10.1002/ajpa.23102

BRIEF COMMUNICATION

WILEY American Journal of PHYSICAL ANTHROPOLOGY

Perikymata distribution on anterior teeth of Miocene *Lufengpithecus lufengensis* from Yunnan, southern China

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Funding Information
Grant sponsor: National Natural Science Foundation of China; Grant sponsor: 41672022, 41072016.

Abstract

Objectives: The present study investigated the distribution of perikymata on anterior teeth of Miocene *Lufengpithecus lufengensis* so as to broaden the comparative data of developmental variation within and among hominoids. We also compared perikymata-spacing pattern of *Lufengpithecus lufengensis* with hominins and extant African great apes to understand the implication of dental development.

Materials and methods: A total of 30 anterior teeth (including 6 I1, 10 I2, and 14 C) of *Lufengpithecus lufengensis* were examined using a scanning electron microscope and Keyence VHX-600EOS digital microscope to document the number and distribution of perikymata on their labial surfaces. The labial crown height of each tooth was divided into 10 equal deciles and the total perikymata number in each decile was recorded. The mean number of perikymata per millimeter was then calculated for each decile. SPSS statistical software was used to perform analyses of these data, including *t*-tests for sexual dimorphism and plots showing the perikymata distribution in *Lufengpithecus lufengensis*.

Results: Perikymata counts of *Lufengpithecus lufengensis* in the first three deciles are fewer than the remaining deciles, and with perikymata becoming increasingly more closely packed as growth progresses from cusp to cervix, but decrease in density in the cervical decile. Besides, total labial perikymata counts of canines tend to display very significant sexual dimorphism.

Discussion: *Lufengpithecus lufengensis* anterior teeth are more similar in their distribution of labial perikymata to those of *Australopithecus* than those of other hominins and extant African great apes from previous studies.

KEYWORDS
enamel, *Lufengpithecus lufengensis*, perikymata

1 | INTRODUCTION

Perikymata are typical enamel growth markings seen on anterior teeth, and their spacing patterns have often been utilized in ontogenetic and taxonomic studies of fossil apes and humans. Previous studies suggested that perikymata spacing on anterior teeth was helpful in distinguishing *Paranthropus* from *Australopithecus*, early *Homo*, and modern humans (Bromage & Dean, 1985; Dean, 1987; Beynon & Dean, 1988; Ramirez-Rozzi, 1993, 1998; Dean & Reid, 2001; Dean et al., 2001; Lacruz, Ramirez-Rozzi, & Bromage, 2006). Similar studies of perikymata on anterior teeth have also revealed varying patterns of perikymata distribution among fossil hominins (Ramirez-Rozzi & Bermúdez de Castro, 2004; Guatelli-Steinberg, Reid, & Bishop, 2007; Guatelli-Steinberg, Reid, Bishop, & Larsen, 2005; Modesto-Mata et al., in press; Ramirez-Rozzi & Bermudez de Castro, 2004; Xing et al., 2015).

Less attention has been paid to the distribution of perikymata in fossil and extant great apes than to perikymata spacing in hominid anterior teeth. However, total labial perikymata counts with taking the method of counting perikymata per millimeter of crown height have often been used to estimate lateral enamel formation time in fossil and extant great apes (Beynon, Dean, Leakey, Reid, & Walker, 1998; Bey- non, Dean, & Reid, 1991; Hu & Zhao, 2012; Reid, Schwartz, Dean, & Chandrasekera, 1998; Zhao, Lu, & Xu, 2000; Zhao, Ouyang, & Lu,1999), and these studies have typically

included brief accounts of perikymata spacing. Zhao et al. (1999, 2000) documented the distribution of perikymata in four permanent anterior teeth of the late Miocene hominoid *Lufengpithecus lufengensis*. These authors demonstrated that the density of perikymata showed a gradual increase towards the cervix, and that the pattern of compactness of the perikymata was similar to that seen in modern humans. Hu & Zhao (2012) studied perikymata spacing in the anterior teeth of fossil orangutans from south China. They noted that the density of the perikymata in the cuspal third of an average tooth was lower than 10/mm, and that both the middle and cervical thirds had 10–15 perikymata/mm. Dean & Reid (2001) pioneered a comparative database of perikymata spacing in the anterior teeth of extant African great apes, and also pointed out that a particularly clear difference in perikymata distribution existed between these apes on one hand and fossil hominins on the other. Collecting more information on perikymata distribution patterns in fossil great apes will broaden the available comparative dataset and facilitate better understanding of developmental variation within and among hominoids.

The late Miocene hominoid *Lufengpithecus lufengensis* from the Shihuiba site in Yunnan, southern China is known from many specimens, including hundreds of isolated teeth. These fossils are potentially invaluable for understanding dental development in Miocene hominoids. Zhao et al. (1999, 2000) described the pattern of perikymata distribution in four permanent anterior teeth from Shihuiba (only including RI^1, RI^2, RI_1, and LC). In the present study, we use an enlarged sample of *Lufengpithecus lufengensis* anterior teeth to further investigate the perikymata distribution pattern seen in this taxon. We assess the number and spacing of the perikymata in 30 well-preserved anterior teeth, and investigate whether significant differences in perikymata counts exist between the upper and lower anterior teeth or among the different tooth types in the sample. Based on these results, we compare the perikymata spacing pattern seen in *Lufengpithecus lufengensis* with corresponding data provided by Dean & Reid (2001) for *Australopithecus*, *Paranthropus*, *Homo sapiens*, and extant African great apes, and with other published data.

2 | MATERIALS AND METHODS

2.1 | Samples

A total of 30 anterior teeth, including 23 isolated permanent teeth and 7 in situ permanent teeth from two mandibles (male PA548 and female PA580) of *Lufengpithecus lufengensis* (see Table 1), were examined in this study. The latter ones were chosen to expand the samples to better understand the differences of perikymata distribution in each tooth type. All these teeth are housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, and are almost unworn, allowing reliable microscopic observations to be made on their labial surfaces. They include 6 central incisors, 10 lateral incisors, and 14 canines. Of the 30 teeth, 15 can be assigned to males and 15 to females based on dental morphology and size (Wu, Xu, & Lu, 1985, 1986; Xu & Lu, 2008).

2.2 | Perikymata observation and counting

A Keyence VHX-600EOS digital microscope and a Hitachi S-3700 scanning electron microscope (SEM) were used to observe the Miocene *Lufengpithecus lufengensis* anterior teeth considered in this study and count their perikymata. Surface residues were cleaned from the enamel of each tooth with dilute acetone. On the labial surface of each tooth, the number of perikymata was counted and the crown height was measured using the Keyence VHX-600 EOS digital microscope at successively higher magnifications (20X-50X), with the tooth oriented orthogonally to the microscope's optical axis. The SEM was used only on the isolated teeth, as opposed to the in situ ones, and the X-ray source voltage was set to 3 kV. A perikymata count was obtained for each isolated tooth from the SEM images. When some part of the tooth surface was not clearly visible, the two types of microscopy were able to complement each other. Moreover, the total perikymata counts for each tooth arising from the two types of microscopy could be matched to each other. Where discrepancies between the Keyence and SEM results occurred, the perikymata counts were retaken using both methods until the problem was resolved.

Studies mapping the distribution of perikymata have typically counted the number of perikymata in each decile of crown height (e.g., Dean & Reid, 2001; Guatelli-Steinberg & Reid, 2010; Xing et al., 2015). This method has been more commonly applied in the past few years, because it allows for comparisons of the distribution of perikymata across teeth of differing sizes (Smith, 2008). In the present study, the labial crown height of each tooth was divided into 10 deciles, the perikymata were counted within each decile, and the mean number of perikymata per millimeter was calculated for each division (see Table 1). For teeth in which a single decile contained indistinct perikymata, counts were estimated from adjacent deciles (Dean & Reid, 2001). As a check, all counts were carried out repeatedly at different times by the first author. For isolated teeth, only when an apparently matching perikymata counts could be found in both two methods, was it accepted and finally numbered. Intraobserver error in counting the number of perikymata is estimated to be 5% or less (Dean et al., 2001; Guatelli-Steinberg & Reid, 2010).

2.3 | Statistical methods

Firstly, *t*-tests were used to determine whether there were significant differences in total perikymata counts within the sample. Because significant differences were indeed detected by the *t*-tests, we followed Dean & Reid (2001) and excluded the male canines in our sample from the rest of the analysis, on the grounds that the male canines were probably enlarged due to sexual dimorphism and were inflating the mean perikymata values (Schwartz & Dean, 2001). We then produced box-plots of the perikymata distribution in the central incisors, lateral incisors and canines of *Lufengpithecus lufengensis*. SPSS 17.0 statistical software was also used to produce plots showing raw and normalized (perikymata/mm) perikymata counts in individual deciles, averaged for the anterior teeth (incisors and female canines) of *Lufengpithecus lufengensis*. Other taxa were added to these plots based on data from Dean

TABLE 1 Perikymata counts of anterior teeth of *Lufengpithecus lufengensis*

Tooth type	Sex	Specimens	Crown height (mm)	Perikymata counts per decile										Pk	Pk/mm	
				1	2	3	4	5	6	7	8	9	10			
I^1	M	PA675.2	15.48	13	14	14	15	19	22	24	23	23	22	189	12	13
	M	PA550	13.38	15	16	18	18	19	22	22	19	19	18	186	14	
	M	PA649.1	14.78	10	11	12	18	20	22	22	21	23	22	181	12	
	F	PA674.55	12.29	10	11	10	13	16	18	20	22	20	20	160	13	
I^2	M	PA716	10.14	10	11	14	16	17	18	19	19	17	16	157	15	16
	M	PA675.13	10.78	11	11	12	14	17	18	18	21	20	19	161	15	
	F	PA620	7.70	7	8	8	14	12	15	13	15	13	11	116	15	
	F	PA713	8.87	11	11	10	12	16	15	20	22	20	18	155	17	
	F	PA714	7.67	8	10	10	12	13	13	18	16	14	13	127	17	
	F	PA715	8.23	8	13	13	15	17	17	18	19	17	16	153	19	
C^0	M	PA732	19.74	18	24	25	27	31	32	34	35	32	30	288	15	15
	M	PA552	19.75	18	25	26	29	30	34	38	37	30	28	295	15	
	M	PA559	18.17	19	19	20	23	23	24	24	25	23	22	222	12	
	M	PA1196	15.50	15	18	18	20	22	25	29	30	23	19	219	14	
	F	PA725	13.21	13	14	16	16	20	22	26	27	28	26	208	16	
	F	PA723	12.36	11	13	15	16	19	21	22	23	23	21	184	15	
	F	PA674.11	13.05	12	13	15	17	18	24	24	26	24	24	197	15	
I_1	M	PA548-R	14.22	11	11	12	21	19	20	21	21	18	18	172	12	12
	M	PA548-L	15.37	11	12	14	18	18	23	22	20	20	19	177	12	
I_2	M	PA548-R	13.72	10	10	16	18	20	22	21	19	17	16	169	12	13
	M	PA548-L	13.65	9	11	15	21	21	22	19	16	16	14	164	12	
	F	PA580-R	11.56	9	10	13	16	18	18	21	17	18	17	157	14	
	F	PA580-L	10.86	9	10	13	15	15	18	19	21	19	15	154	14	
C_0	M	PA646.6	22.70	21	21	29	37	40	37	36	39	34	34	328	14	15
	M	PA649.8	19.71	14	18	25	28	42	43	36	40	34	28	308	16	
	F	PA630	12.91	11	11	12	15	21	22	24	28	30	24	198	15	
	F	PA655.12	13.52	17	18	17	18	19	20	20	23	22	20	194	14	
	F	PA573	12.64	11	12	14	18	21	22	23	25	26	21	193	15	
	F	PA674.17	11.80	11	12	13	19	20	23	24	25	23	20	190	16	
	F	PA580-R	11.83	9	10	11	16	20	20	25	27	24	22	184	16	

& Reid (2001), resulting in two comparative graphs that were produced using Adobe Photoshop CS4v11.0.

3 | RESULTS

Table 1 lists the perikymata counts and perikymata counts per decile for teeth of *Lufengpithecus lufengensis*, arranged by tooth type. Deciles were numbered 1 (incisal)−10 (cervical). All the teeth show a similar distribution of perikymata from cusp to cervix. Relatively few perikymata are present in the first three deciles, and the perikymata generally become increasingly closely packed from cusp to cervix. However, the perikymata count decreases in the cervical decile. An example of the labial perikymata distribution on an upper lateral incisor (PA713), as viewed under SEM, can be seen in Figure 1. All the anterior teeth show an apparent gradual growth from the cuspal region to the middle region, with a slight decrease in the cervical region. This pattern is consistent with the general trend in the sample. Table 1 also shows that total perikymata counts for upper canines, lower canines and upper lateral incisors, averaged across all teeth in each category, are 15–16/mm. The corresponding values for upper and lower central incisors, and lower lateral incisors, are 12–13/mm.

The results of the *t*-tests (with a 95% confidence interval) on the perikymata counts for the incisors and canines (Table 2) indicate that: (1) there is no significant difference in perikymata counts between upper and lower teeth of corresponding types ($p > .05$); and (2) very significant sexual dimorphism in perikymata counts exists for canines ($p = .006$) but not for central or lateral incisors ($p > .05$). Figure 2 shows perikymata distributions for central incisors, lateral incisors, and male and female canines, respectively. Similar trends occur for each tooth type, although both central and lateral incisors exhibit their greatest density of

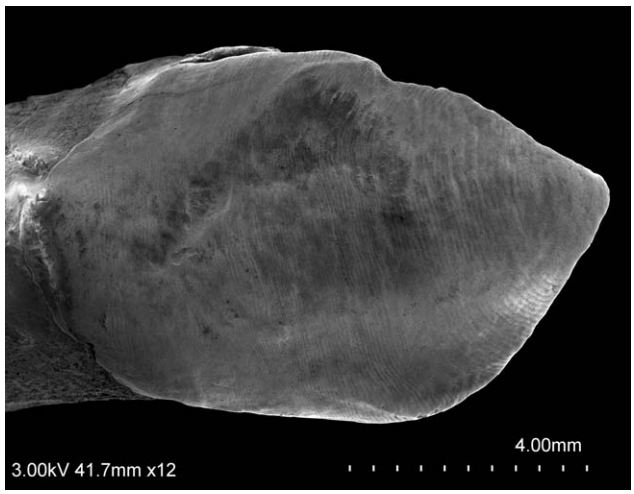

FIGURE 1 Perikymata of an upper lateral incisor (PA713)of *Lufengpithecus lufengensis*

perikymata in the 7th decile whereas male and female canines exhibit theirs in the 8th decile. In addition, male canines tend to have a higher number of perikymata than do incisors and female canines from decile 1 to decile 10, which may be related to their crown height.

4 | DISCUSSION AND CONCLUSIONS

The *t*-test results reveal that the total perikymata count for the labial surface is sexually dimorphic, at a very significant level, in the case of the canine teeth. Accordingly, we excluded the six male canines from the sample when comparing the perikymata distributions seen in *Lufengpithecus lufengensis* to those for other taxa (Dean & Reid, 2001), leaving only incisors and female canines. Figure 3 shows plots of mean values for the total and distance-normalized perikymata counts for each decile of the labial surface, based on new data for *Lufengpithecus lufengensis* and comparative data from Dean & Reid (2001).

TABLE 2 Results of statistics tests of perikymata counts of anterior teeth in *Lufengpithecus lufengensis*

Comparison	Statistic	*p* value	Sig. level
I^1 vs I_1		.674	N.S
I^2 vs I_2		.094	N.S
C^0 vs C_0	Small sample *t*-test	.930	N.S
Male vs female I1	($a = 0.95$)	.48	N.S
Male vsfemale I2		.45	N.S
Male vs female C		.006	**

Note. N.S represts nonsignificant difference ($p > .05$); ** represts very significant difference ($p < .01$).

As mentioned by Dean & Reid (2001), the distinction between modern African great apes and fossil hominins is particularly clear. In *Pan* and *Gorilla*, the numbers of perikymata per division and per millimeter are both higher than in hominin taxa even in the first decile, and rise to a peak at around 70% of tooth height. After this they fall to values below those for the first decile. *Homo sapiens* shows a different

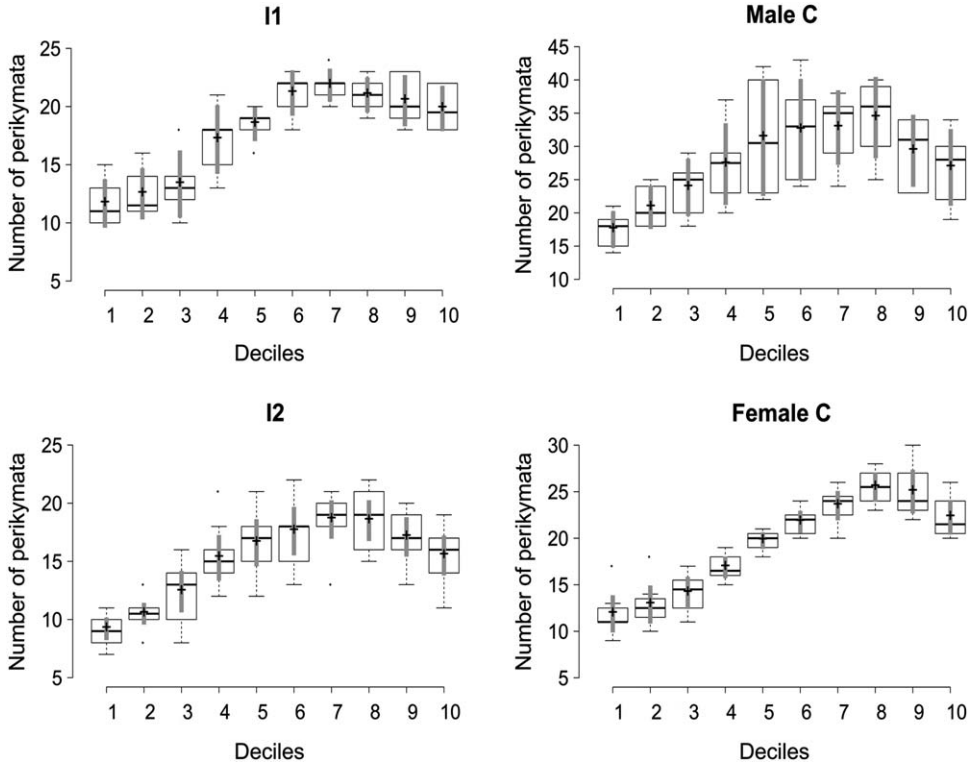

FIGURE 2 Box-Plots of perikymata packing pattern in central incisors, lateral incisors, male and female canines for *Lufengpithecus lufengensis*. Average values ("+") with 95% confidence limits (grey bars) are given for each decile

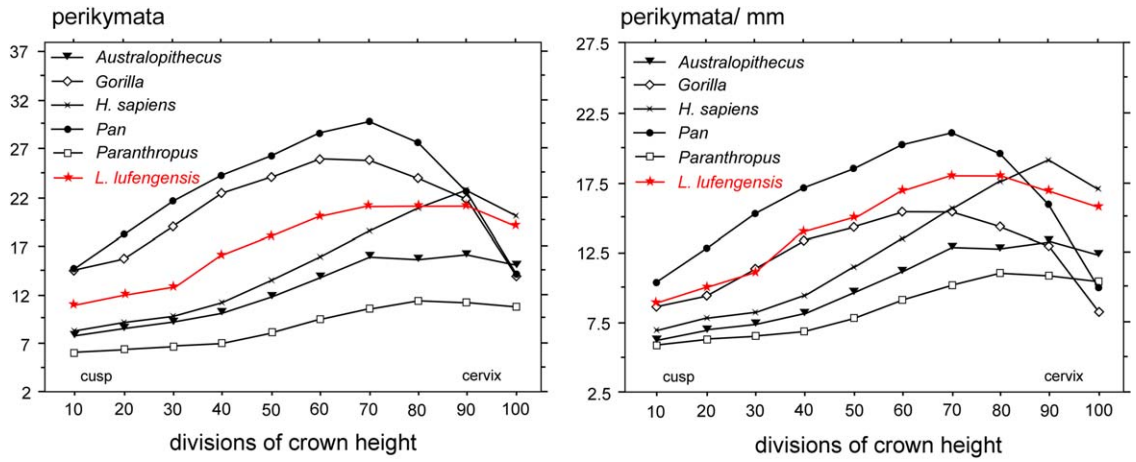

FIGURE 3 Plots of the mean values for total and distance-normalized perikymata counts per millimeter on the labial surfaces of anterior teeth for several taxa, showing variation in perikymata distribution. Figures are modified from Dean & Reid (2001), and the *x*-axis is divided into 10 equal divisions of crown height. The first decile is the cuspal 10% and the last decile is the cervical 100%

distribution of perikymata from cusp to cervix, in that the number of perikymata rises throughout the first 90% of tooth height and decreases slightly at the cervix. *Australopithecus* and *Paranthropus* essentially follow the same pattern as *Homo sapiens*, but with consistently lower total perikymata and perikymata/mm counts for each decile. In *Lufengpithecus lufengensis*, fewer perikymata are present in the first three deciles than in the last seven deciles. The perikymata then become increasingly more closely packed, peaking in deciles 7–9 with respect to the raw count and deciles 7–8 with respect to the normalized count as growth progresses from cusp to cervix. The raw and normalized counts decrease in the last decile and the last two deciles, respectively. The general trend seen in *Lufengpithecus lufengensis* is more similar to that in *Australopithecus*, *Paranthropus* and *Homo sapiens* than that in extant African great apes. Among these hominin taxa, *Lufengpithecus lufengensis*is more similar to *Australopithecus* than to *Paranthropus* and *Homo sapiens* over the whole crown, but consistently has more perikymata (in total and per millimeter) than *Australopithecus* within each division of tooth height. The counts per millimeter for *Lufengpithecus lufengensis* exceed those for *Homo sapiens* from 10% to 70% of crown height, are about equal to those for *Homo sapiens* around 80% of crown height, and drop below those for *Homo sapiens* in last two deciles. Distance-normalized counts for *Lufengpithecus lufengensis* are similar to those for *Gorilla* over the cuspal halves of the crowns, but higher than those for *Gorilla* over the cervical halves.

Recent studies have suggested that hominin species differ in the distribution of perikymata in the lateral enamel of the anterior teeth, but have overlapping ranges (Dean & Reid, 2001; Guatelli-Steinberg et al., 2007; Guatelli-Steinberg & Reid, 2010; Modesto-Mata et al., 2015; Xing et al., 2015). Anterior teeth of *Lufengpithecus lufengensis* differ from Qafzeh teeth (data from Guatelli-Steinberg & Reid, 2010), in that perikymata counts decrease in the last decile only in the former. Neandertal teeth show a more gradual increase in the number of perikymata from cusp to cervix (Ramirez-Rozzi & Bermúdez de Castro, 2004; Guatelli-Steinberg et al., 2007), differing from anterior teeth of *Lufengpithecus lufengensis* in the cervical region.

Furthermore, Hu & Zhao (2012) pointed out that in fossil *Pongo* from south China the perikymata density is lower than 10/mm in the cuspal third of the crown and about 10–15/mm in the middle and cervical thirds. The perikymata of the cervical region are thus clearly less densely packed in *Pongo* than in *Lufengpithecus lufengensis*.

Therefore, *Lufengpithecus lufengensis* anterior teeth are more similar in their distribution of labial perikymata to those of *Australopithecus* than those of other hominins and extant African great apes. With regard to the interpretation of the perikymata distribution patterns seen in various hominid taxa, studies have suggested that differences in enamel extension rates, enamel secretion rates, enamel thickness, and/or the paths of the striae of Retzius may be responsible for the observed variations (Guatelli-Steinberg & Reid, 2010; Guatelli-Steinberg & Reid, 2012). The issue is complicated by the fact that different combinations of these variables could produce similar perikymata distribution patterns. Any interpretations must await histological information from *Lufengpithecus lufengensis* and other taxa.

ACKNOWLEDGMENTS

We are grateful for assistance with microscopy from Dr. Zhang Wending and Zhang Zhaoxia in the Key Laboratory of Vertebrate Evolution and Human Origins at the IVPP. We also thank Dr. Xing Song for discussion and Liu Wenhui for help with images. We would like to thank Dr. Corwin Sullivan and Dr. Li Tao for improving the English text of this paper. We also thank the editors and reviewers for their thoughtful suggestions, which helped us to improve this manuscript.

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