Dental development and ontogeny of late Miocene large-bodied hominoids from Yunnan, China

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Abstract   Late Miocene large-bodied hominoids from Yunnan, China are critical to the understanding of hominid and hominoid origins and evolution in Asia. The aim of the present study is to examine dental development and ontogeny of *Lufengpithecus* from Yuanmou and Lufeng. Based on scanning electron microscope observations of enamel incremental markings, the mean crown formation time of *Lufengpithecus* incisors was estimated to be 3.7–4.6 years, which is longer than that of *Proconsul*, *Paranthropus*, and early *Homo*, and closer to that of *Australopithecus afarensis*, *Pan*, and *Homo sapiens*. The dental eruption characteristics of *Lufengpithecus lufengensis*, including age at first molar emergence, eruption sequence of dentition, and M_1/I_1 eruption pattern, show an ape-like, not human-like, developmental pattern. High and regular frequency of linear enamel hypoplasia indicates that late Miocene *L. lufengensis* suffered from regular physiological stress associated with seasonal dietary fluctuations.

Key words: *Lufengpithecus,* dental development, crown formation time, dental eruption, linear enamel hypoplasia

Introduction

Since the late 1950s, several thousand specimens of Neogene hominoids (mostly teeth) have been recovered from four late Miocene localities of Yunnan Province in southwestern China: *Lufengpithecus keiyuanensis* from Xiaolongtan in Kaiyuan county; *Lufengpithecus lufengensis* from Shihuiba in Lufeng county; *Lufengpithecus hudienensis* from Zhupeng, Xiaohe, and Leilao in Yuanmou county; and *Lufengpithecus* sp. from Yangyi in Baoshan county (Wu, 1957, 1958, 1987; Zhang, 1987; Xu, 1992; Zheng and Zhang, 1997; Gao, 1998; Harrison et al., 2002). There is no doubt that the *Lufengpithecus* fossils are a key to understanding hominoid evolution in Asia.

During the last two decades it has been recognized that information on growth and development in hominoids can be derived from the study of their teeth. The aims of the present study are to examine the dental development and life history of *Lufengpithecus lufengensis* and *Lufengpithecus hudienensis*, respectively, from Lufeng and Yuanmou. The following aspects are examined: (1) enamel incremental markings—intervals and periodicity of perikymata; (2) crown formation times of incisors; (3) age at first molar eruption in *L. lufengensis*; (4) eruption sequence of dentition and M_1/I_1 eruption pattern in *L. lufengensis*; and (5) linear enamel hypoplasia of *L. lufengensis*.

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Incremental Markings and Perikymata Periodicity in *Lufengpithecus*

During enamel development, an underlying systemic rhythm is expressed as regular incremental markings, such as perikymata on the outer enamel surface, striae of Retzius, and cross striations within the enamel. Tooth crowns form incrementally from cusp toward the cervix with new layers superimposed on earlier layers. The striae of Retzius represent successive surfaces of the forming enamel where the enamel is less calcified, and striae of Retzius reach the crown surface and form perikymata. Considerable evidence from in vivo experiments in extant large hominoids suggests a 6–12 day cycle of striae of Retzius and perikymata, and a daily rhythm of cross striations (FitzGerald, 1998). There is also good evidence to support the hypothesis that perikymata are near-weekly incremental phenomena with a probable periodicity of 7, 8, or 9 days (we estimate two likely mean scores of either 7 or 9 days and will use both values in our analyses) in fossil hominids (Dean, 1987). The periodicity of perikymata can be estimated by counting the number of cross striations along the enamel prism between adjacent striae of Retzius.

A total of seven permanent incisors, three of *L. lufengensis* from Lufeng, and four of *L. hudienensis* from Yuanmou (Table 2), were studied by scanning electron microscopy (SEM) (JSM-1600, 12 kV, 50–200× amplification) in order to examine the perikymata intervals and counts on the buccal surface. These teeth are unworn or only slightly worn at the incisal edge and have complete crowns with well-preserved perikymata. Another two tooth fragments, one lower incisor (YV2013) of *L. hudienensis* and a lower

canine (PA728) of *L. lufengensis*, were also sectioned longitudinally in a buccolingual direction for observation (500–1500× amplification) of cross striations and periodicity of striae of Retzius.

Under SEM, perikymata were easily visible on the whole buccal surfaces of all incisors studied. The number of perikymata/mm increases cervically, is less than 10 perikymata/mm at the incisal third of the tooth crown, and more than 20 perikymata/mm at the cervical third. The pattern of decreasing perikymata spacing indicates a cervically decreasing extension rate of incisor crown formation.

Perikymata provide a good record of the crown formation process. Compactness of perikymata can reflect the extension rate of crown formation. In human permanent incisors, the extension rate decreases from a relatively high value in the occlusal region to a slow rate cervically. The slow extension rate in the later stages of crown formation is manifested at the tooth surface by increased density of perikymata in the cervical region. The incisors of modern great apes appear not to express such a decreasing extension rate at later stages of crown formation as in humans. Similar analyses of hominid specimens have shown different perikymata compactness in lower incisors between *Australopithecus afarensis* and species of *Paranthropus*. *Australopithecus afarensis* shows progressive slowing of crown extension rates similar to the modern human condition, whereas species of *Paranthropus* show a faster crown extension rate which is nearly constant (Beynon and Dean, 1988). In this feature, both *L. lufengensis* and *L. hudienensis* are similar to *A. afarensis* and modern humans, and different from species of *Paranthropus* and extant great apes.

In the buccolingual longitudinal sections of the lower incisor YV2013 and lower canine PA728, the striae of Retzius and cross striations were easily visible in the outer enamel. There are nine cross striations between adjacent striae of Retzius in both specimens, i.e. the periodicity of the striae of Retzius and perikymata was 9 days. The *Lufengpithecus* specimens are within the range of variation of the extant great apes and modern humans (Table 1). In contrast, however, monkeys and gibbons have shorter perikymata

periodicities of about 4–5 days, and African Early Miocene *Proconsul* a shorter periodicity of 5–6 days. Therefore this characteristic in *Lufengpithecus* may reflect a synapomorphy of dental development with later great hominoids. The perikymata periodicity of *Lufengpithecus* is 1–3 days longer compared to *Dryopithecus* and *Afropithecus*, although whether this developmental feature is of significance needs further examination.

Crown Formation Times of Incisors of *Lufengpithecus*

Crown formation extends from the cusp to the cervix. Estimation of crown formation time is founded on the assumption that cross striations, striae of Retzius, and perikymata correspond to incremental lines forming with a regular and systematic periodicity. The crown formation times of incisors can be calculated from perikymata counts by the following formula:

crown formation time = total number of perikymata × periodicity + cuspal formation time.

The incremental lines of the cusp lie beneath the surface and do not reach the outer surface as perikymata; therefore the cusp formation time can only be estimated in nondestructive studies. The cuspal region of the incisor, however, is a smaller proportion of the entire tooth in contrast with postcanine teeth, so that an estimate would not introduce large errors into crown formation time calculations. Moreover, cuspal enamel thickness of hominoid lower incisors is similar and does not show marked variation between taxa as reported for premolars and molars. Therefore we can use the cusp formation time of modern human lower incisors (6 months or so) as an estimate for the incisors of fossil hominoids (Dean, 1987).

Considering the 9-day cycle of periodicity in YV2013 and PA728, the uniformity within the anterior dentition and the variety of estimates of modern hominoids (Dean, 1987; FitzGerald, 1998), we argue that the perikymata periodicity of Yunnan hominoids is likely to be between 7 and 9 days. We also suggest that the cusp formation time of incisors was likely to be around 6 months (Zhao et al., 2000, 2002a).

The mean number of perikymata in four lower incisors (range 163–191) of *L. hudienensis* is 175, which is more than the 128 perikymata of the lower incisor PA895 of *L. lufengensis*. Combining the other two upper incisors, the mean perikymata number in *L. lufengensis* from Lufeng is 150, which is still less than that of *L. hudienensis* from Yuanmou. Given that perikymata periodicity is 7 or 9 days, the mean incisor crown formation time is 3.9 or 4.8 years for *L. hudienensis*, and 3.4 or 4.2 years for *L. lufengensis*. Therefore the mean crown formation time of *L. hudienensis* incisors is approximately half a year longer than that of *L. lufengensis*. Because overlap in range still exists, a significant difference between the two needs to be established by further testing with a larger sample. Combining the whole sample, incisor crown formation times of Yunnan *Lufengpithecus* are between 3.0 and 5.2 years, with means of 3.7 and 4.6 years.

The present study indicates that the crown formation time of *Lufengpithecus* is relatively long (Table 2). For example,

Table 1. Periodicity of perikymata in fossil and extant hominoids

Taxon	*n*	Periodicity	Source
Fossils			
Proconsul heseloni	2	5	Beynon et al. (1998)
Proconsul nyanzae	2	6	Beynon et al. (1998)
Afropithecus turkanensis	2	7, 8	Smith et al. (2003)
Dryopithecus laietanus	3	6, 7	Kelley et al. (2001)
Lufengpithecus lufengensis	1	9	Zhao et al. (2000)
Lufengpithecus hudiensis	1	9	Zhao et al. (2002a)
Paranthropus robustus	1	9	Dean et al. (1993)
Paranthropus boisei	1	7	Dean (1987)
Modern			
Hylobates lar	1	4	Dirks (1998)
Pongo pygmaeus	24	8–11	Schwartz and Dean (2001)
Gorilla gorillas	36	7–10	Schwartz and Dean (2001)
Pan troglodytes	20	6–9	Schwartz and Dean (2001)
Homo sapiens	82	6–12	Reid et al. (2002)

Table 2. Crown formation times of of incisors in fossil and extant hominoids

Taxon	n	Perikymata counts		Crown formation times (yr)		Source
		Range	Mean	Range	Mean[a]	
Proconsul heseloni	2			0.77–0.81	0.79	Beynon et al. (1998)
Lufengpithecus lufengensis	3	128–172	150	3.0–4.7	3.4/4.2	Zhao et al. (2000)
Lufengpithecus hudiensis	4	165–191	175	3.6–5.2	3.9/4.8	Zhao et al. (2002a)
Australopithecus afarensis	4	116–180	149	2.7–4.9	3.4/4.2	Beynon and Dean (1988)
Australopithecus africanus	1	135	135		3.1/3.8	Beynon and Dean (1988)
Paranthropus robustus	5	57–86	69	1.6–2.6	1.8/2.2	Beynon and Dean (1988)
Paranthropus boisei	4	82–101	90	2.1–3.0	2.2/2.7	Beynon and Dean (1988)
Early *Homo*	4	95–123	108	2.3–3.5	2.6/3.2	Beynon and Dean (1988)
Hylobates lar	2			1.43–1.79	1.61	Dirks (1998)
Pan troglodytes	7			4.0–5.4	4.8	Reid et al. (1998)
Homo sapiens	10	165–202	188	3.7–5.5	4.1/5.1	Bromage and Dean (1985)

[a] Crown formation times on either side of / were calculated by 7 and 9 days periodicity of perikymata, respectively.

compared to gibbons and early Miocene *Proconsul*, the crown formation cycle in *Lufengpithecus* is relatively longer. This is also true when compared to early hominids, such as *A. africanus* and *Paranthropus* and early *Homo*. The incisor crown formation times of *Lufengpithecus* are, however, closer to *A. afarensis* and *Pan* and *Homo sapiens*. Dean et al. (2001) thought that the crown formation times in early *Australopithecus* and early *Homo erectus* were shorter than those in modern humans, which supports the suggestion of Smith (1991) that modern dental development emerged relatively late in human evolution. The evolutionary meaning of the longer crown formation times of the 8 Ma *Lufengpithecus* is a very interesting question.

Estimation of the Age at First Molar Emergence in *Lufengpithecus lufengensis*

Two juvenile mandibles of *L. lufengensis*, PA868 and PA822, show a similar stage of dental development with their first molars erupting just out of their alveolar crypts (Figure 1 and Plate 1 of Zhao et al., 2002b). The question is: how can we determine the age of these two individuals at the time of death? Specimen PA868 reveals some important information in its incisor development. An X-ray photograph of PA868 shows that the crowns of its central and lateral incisors have not yet completely formed, though they are close to complete development based on measurements taken by the authors. From the three incisors of *L. lufengensis* examined (Table 2), we suggested that the average incisor crown formation time of *L. lufengensis* is 3.4–4.2 years, and the postnatal delay in the onset of incisor calcification is 4 months. Thus the age at incisor crown completion is about 3.7–4.5 years. Because PA868 is close to the stage of complete incisor crown development, we think it likely that this individual died between the ages of 3.2 and 4.0 years, maybe 6 months before crown completion. In this instance, the age at first molar emergence is also the age at which PA868 died, i.e. approximately 3.2–4.0 years (Table 3). This is similar to the condition of extant great apes and other Miocene hominoids, australopithecines, and early *Homo*, as opposed to modern humans, in which the first molar emerges at around 6 years of age (Dean and Wood, 1981; Smith et al., 1995;

Table 3. Ages at first molar emergence

Taxon	Age at M1 emergence (yr)	Source
Lufengpithecus lufengensis PA868	3.2–4.0	This study
Afropithecus turkanensis KNM-MO 26	2.4–3.6	Kelley and Smith (2003)
Sivapithecus parvada GSP 11536	2.2–4.5	Kelley (1997)
Australopithecines and early *Homo*	3–4	Smith et al. (1995)
Gorilla	3.5	Dean and Wood (1981)
Pan	3.3	Dean and Wood (1981)
Modern human	6.1	Dean and Wood (1981)

Kelley, 1997; Kelley and Smith, 2003).

Age at first molar emergence is correlated with a variety of life history traits, such as brain weight, weaning age, age at first reproduction, and longevity. The present result indicates that the life history of *Lufengpithecus* is great ape-like, not human-like.

Eruption Sequence and M_1/I_1 Eruption Pattern in *Lufengpithecus lufengensis*

Five juvenile mandibles of *L. lufengensis* (from the collections of the Institute of Vertebrate Paleontology and Paleoanthropology), PA663, PA868, PA822, PA673, and PA823, were examined radiographically for eruption sequence analysis (Zhao et al., 2002b).

In this study a tooth was scored as erupted when any part of the crown had erupted above the alveolar margin. One tooth is considered to precede another in the sequence if either: (a) one is erupted and the other is not erupted; (b) both teeth have erupted but there are differences between them in wear pattern or location relative to full occlusion (or alveolar margin); and (b) both teeth are not erupted and there is a difference between them in crown and root development stages and locations relative to alveolar margin. The eruption sequence is established without considering sex.

Our study of the five juvenile mandibles indicates: (1) M_1

is the first tooth to erupt; (2) canine and M_3 are the last two teeth to erupt; (3) M_2 precedes the two premolars; (4) the two incisors precede the two premolars and M_2; (5) I_1 precedes I_2; (6) P_3 precedes P_4; (7) canine precedes M_3. Consequently the whole eruption sequence in *L. lufengensis* is suggested to be M_1, I_1, I_2, M_2, P_3, P_4, C_1, and M_3.

The sequence of eruption of the permanent teeth shows a remarkable shift through the order Primates (Schultz, 1935). The pattern of eruption of permanent teeth in extant apes and humans is distinctive, as is its overall timing. The ape tooth eruption pattern is M_1, I_1, I_2, M_2, P_3, P_4, C_1, and M_3; the corresponding human pattern is M_1, I_1, I_2, P_3, C_1, P_4, M_2, and M_3. The principal difference is that in apes the canine erupts after the second molar, while in humans it precedes the second molar; in apes the second molar precedes the premolars, while in humans it erupts after premolars. Apparently the eruption sequence pattern of permanent teeth in *L. lufengensis* is ape-like, not human-like.

From the juvenile mandible PA868, we gained information concerning M_1/I_1 eruption patterns in *L. lufengensis*. Specimen PA868 is a juvenile right corpus with two erupted (dm_2 and M_1) and five unerupted teeth in the corpus (right P_3, P_4, I_1, I_2, and left I_1). The first molar crown is complete and has begun to erupt out of the alveolar border (crypt), though it is still not in a position of complete occlusion. The radiograph of PA868 shows that its I_1 crown is not yet complete and is still in an early stage of development, with its root not yet formed. Usually in great apes and humans the permanent incisor erupts out of the alveolar bone when its root is around 50% complete in length, which takes around 2 years. Therefore the first permanent I_1 of the PA 868 juvenile was unlikely to erupt for another 2 years, i.e. 2 years after the eruption of the first molar.

Modern humans are unique among primates in that the first permanent incisors and first permanent molars erupt together within a relatively brief time span (usually within 4 months of each other). Thus, at first molar eruption stage in modern humans the permanent central incisor crown and root development are well advanced. Great apes, on the other hand, delay their first permanent incisor eruption for some 2.0–2.5 years after eruption of the first molar (Dean and Wood, 1981; Dean, 1985). Therefore, the M_1/I_1 eruption pattern in *L. lufengensis* PA868 is similar to that of apes and different from that of modern humans.

Linear Enamel Hypoplasia of *Lufengpithecus lufengensis*

Linear enamel hypoplasia (LEH) is a developmental defect of enamel, appearing as one or more horizontal lines or grooves on the surface of a tooth crown. The defect forms when physiological stress, such as disease or poor nutrition, disturbs enamel matrix formation, resulting in a deficiency of enamel thickness. The expression of LEH is a sensitive dental indicator of physiological stress. Our analysis of LEH is focused on the permanent teeth of the late Miocene *L. lufengensis* of Yunnan. In all, 246 permanent teeth from 26 mandibles were examined with a 10× hand lens for the presence of surface disturbances of enamel formation. In percentage terms, 85% of the permanent teeth examined (209 of

246) were affected by LEH (Table 4). Most of the teeth, especially canines and first premolars, have repetitive LEH (rLEH), and the spacing between episodes of rLEH is almost uniform. Based on perikymata counts between episodes of rLEH, i.e. the periodicity of rLEH, *Lufengpithecus* was found to exhibit a semi-annual pattern, the same as that found in modern West African chimpanzees and gorillas as well as orangutans in Borneo and Sumatra. The apparent ubiquity of twice-yearly stress in Asian and African apes is attributed to regular seasonal moisture cycles, which can lead to both disease and nutritional stress.

Although LEH is ubiquitous among the permanent teeth of *L. lufengensis*, the incidence of LEH on the first permanent molars, which are the earliest forming permanent teeth, is very low at just 5.7% of the 35 first permanent molars examined. This indicates that *L. lufengensis* is not overtly affected by LEH during the crown-forming stage of the first molar, which is probably before the age of weaning.

The palaeohabitat of most Miocene fossil primates has been considered to consist of highly stable and relatively non-seasonal tropical forests. This situation began to change by the late Miocene as environments worldwide became generally cooler and drier. Animals such as the great apes that were widespread throughout Africa, Europe, and Asia, and exhibited considerable species diversity, began to disappear as forest environments became more seasonal and less reliable producers of high-energy yielding foods (Jablonski, 1995). Previous analyses and discussions on the palaeoclimate during the period of *L. lufengensis* have indicated a climate that alternated between wet and dry seasons, as observed today in the Sino-India region with its tropical monsoons (Chen et al., 1986). The authors suggest that the LEH of *Lufengpithecus* might have been caused by stress induced by insufficient food supply, in relation to the apparently seasonal habitat of *L. lufengensis*.

Conclusions

This study demonstrates that the pattern of dental development in *Lufengpithecus* is ape-like, not human-like, in the following respects: eruption sequence of the dentition (M_1, I_1, I_2, M_2, P_3, P_4, C_1, and M_3); a relatively longer time span (2 years) between eruption of the first permanent molar and incisor than in modern humans; and an earlier age (about 3.2–4.0 years) of eruption of the mandibular first permanent molar (which is a key parameter of primate life history) than in modern humans.

The mean crown formation time of *Lufengpithecus* incisors is estimated at 3.7–4.6 years, which is longer than that of early Miocene *Proconsul* and Pliocene–Pleistocene *Paranthropus* and early *Homo*, and closer to *A. afarensis*, *Pan*, and *Homo sapiens*. The mean crown formation time of

Table 4. Linear enamel hypoplasia (LEH) in *Lufengpithecus lufengensis*

Specimens	I1	I2	C	P3	P4	M1	M2	M3	Total
n	23	31	31	36	38	35	32	20	246
LEH	20	31	31	36	38	2	30	20	209
LEH%	87.0	100	100	100	100	5.7	93.8	100	85.0

L. hudienensis incisors is approximately half a year longer than that of *L. lufengensis*. Because overlap in range exists, further testing by a larger sample is needed to establish a significant difference between the two species.

High and regular frequency of linear enamel hypoplasia indicates that late Miocene *Lufengpithecus lufengensis* suffered from regular physiological stress associated with seasonal nutritional fluctuations in diet.

Acknowledgments

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