



Preliminary investigation of dental microstructure in the Yuanmou hominoid (*Lufengpithecus hudianensis*), Yunnan Province, China

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Abstract

Fieldwork in the Yuanmou Basin of southern China has uncovered a large assemblage of late Miocene hominoid fossils assigned to *Lufengpithecus hudianensis*. Two mandibular first molars from this species were made available for histological analysis as part of a larger ongoing study on the ontogeny of dental development in Miocene to Recent hominoids. Results are compared with published and unpublished data on tooth growth in a wide range of extant and extinct hominoids. The Yuanmou molars are smaller than those of *Lufengpithecus lufengensis* and have markedly shorter crown formation times, overlapping slightly with *Pan*, but most similar to *Proconsul* and *Dryopithecus*. In other aspects of molar development (including enamel extension rates and enamel thickness), *L. hudianensis* shows similarities with all extant hominoids, in particular, *Pongo*. Ultimately, charting the ontogeny of molar crown formation may help shed light on the relationship of *Lufengpithecus hudianensis* to orang utans, and other Miocene to Recent hominoids. © 2003 Elsevier Science Ltd. All rights reserved.

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Introduction

Since the initial discovery of *Lufengpithecus* in the late 1970s (Xu and Lu, 1979, 1980; Xu et al., 1978), its taxonomy and phylogeny have been

the source of continued debate. Most workers now agree that fossils from the late Miocene site of Shihuiba, Lufeng represent a single, sexually dimorphic species possibly related to the *Sivapithecus-Pongo* clade (e.g., Kelley, 1993; Kelley and Etlar, 1989; Kelley and Plavcan, 1998; Kelley and Xu, 1991; Schwartz, 1990, 1997; Wood and Xu, 1991; Wu, 1987). Since the late 1980s, several campaigns of fieldwork in the Yuanmou Basin, Yunnan Province, southern China, have

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unearthed a large assemblage of *Lufengpithecus* fossils (He, 1997; Ho, 1990; Zheng and Zhang, 1997). The majority of these new remains are isolated teeth. Our goal here is to report on a preliminary investigation into the comparative dental microstructure of the new Yuanmou material, *Lufengpithecus* (from Shihuiba), *Pongo* and other extant and extinct hominoids.

The Yuanmou Basin is situated in the northern part of Yunnan Province, about 110 km northwest of Kunming. In 1986, excavations conducted by the Yunnan Provincial Museum at the site of Zhupeng in the Xiaohé Formation, uncovered many hominoid craniodental remains. From 1987 to 1999, six excavations in the Yuanmou Basin were undertaken by the provincial museum and Institute of Vertebrate Paleontology and Paleoanthropology yielding, to date, a juvenile face, several maxillary and mandibular fragments and over 1,400 isolated teeth.

Based on biostratigraphic, electron spin resonance and paleomagnetic comparisons, the Yuanmou hominoid material dates to the latest Miocene, c. ~7–9 mya (Huang et al., 2000; Ni and Qiu, 2002; Qian, 1997; Yin and Liang, 1998; Yu and Jiang, 1997; Zong, 1996, 1997, 1998; Zong et al., 1991). The Yuanmou hominoid fossils are thought to be closely related to *Lufengpithecus lufengensis* from the nearby locality of Shihuiba, Lufeng County (He, 1997; Jiang, 1996; Liu et al., 2000; Pan, 1996; Pan and Zheng, 1998; Wu, 1987; Zheng and Zhang, 1997). However, their smaller average size and slightly different occlusal morphology led to the proposal of a new species, *Lufengpithecus hudienensis* Zhang et al., 1987 (e.g., Liu et al., 2000; Zhang et al., 1987; Zheng and Zhang, 1997). Other researchers maintain that the Yuanmou material differs from *L. lufengensis* only at the subspecific level (e.g., Zhou et al., 1998), despite the fact that dental size variation within the Yuanmou assemblage fits within that for a single species with a high degree of sexual dimorphism (Liu et al., 2000; Zheng and Zhang, 1997).

Comparisons of tooth size and shape indicate that *Lufengpithecus hudienensis* is more similar to *Lufengpithecus* specimens from the sites of Shihuiba and Xiaolongtan (near Keiyuan city) than to any of the extant large-bodied hominoids

(Liu et al., 2000, 2001). The relationship of these late Miocene hominoids to extinct and extant great apes is still controversial, with various authors suggesting affinities of *L. lufengensis* with the *Sivapithecus*-orangutan clade, African apes or representing the last common ancestor of all extant great apes (e.g., Andrews, 1992; Harrison et al., 2002; Ho, 1990; Kelley and Etler, 1989; Liu et al., 2000; Schwartz, 1990, 1997; Wu et al., 1986; Zhao et al., 1999, 2000; Zheng and Zhang, 1997).

In this light, it is interesting to chart and compare aspects of tooth crown development and morphology in the *Lufengpithecus* assemblages from Shihuiba and Yuanmou, extant and extinct great apes. Here we present preliminary data on the ontogeny of crown formation and on enamel thickness in two of the Yuanmou molars and compare them to *Lufengpithecus lufengensis* from Shihuiba, as well as to a wide range of Miocene to Recent hominoids. Ultimately, our goal is to examine the ontogeny of dental development in larger samples of *L. hudienensis* within a broad comparative context of all extant and extinct hominoids.

Material and methods

Two isolated M_1 s of *L. hudienensis* from the Yuanmou sample (YV 094 and PDYV 30) were chosen for this preliminary analysis. The molars were cleaned, and molds prepared using Coltene™ silicon medium body putty. Prior to sectioning, each specimen was embedded in polyester resin or coated with cyanoacrylate to reduce the risk of splintering. Using a Buehler™ Isomet diamond wafering blade saw, 180–200 μ m thick ground sections were prepared from the plane of the mesial cusps such that each section traversed both cusp tips and dentine horns (Fig. 1). The sections were mounted to microscope slides, lapped to a final thickness of 100–120 μ m, polished with a 3 μ m aluminum powder, placed in an ultrasonic bath to remove surface debris, dehydrated through a graded series of alcohol baths, cleared in HistoClear™, mounted with cover slips in xylene-based DPX™ mounting medium and analyzed using polarized light microscopy. Sections clearly

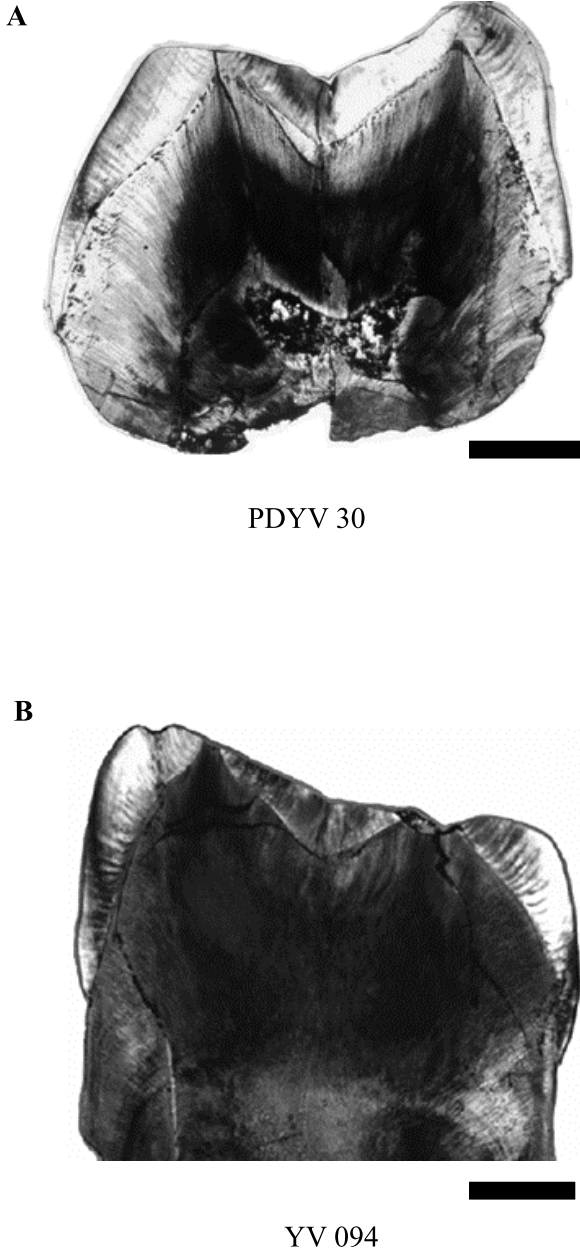


Fig. 1. Yuanmou *L. hudiensis* M₁ sections: (A) PDYV 30, buccal is to the left; and (B) YV 094, buccal is to the right. Scale bar = 2 mm.

showed enamel prism paths, Retzius lines and cross striations (Fig. 2a). Measures of daily secretion rates, striae of Retzius morphology, Retzius line periodicity, crown formation time, and relative

enamel thickness were recorded. All measures were recorded to the nearest micron except for enamel thickness which was in mm².

Enamel thickness was calculated according to the method of Martin (1985). Enamel thickness data included the area of the enamel cap (**c**), the length of the enamel-dentine junction (**e**) and the area of dentine enclosed by the enamel cap and a line drawn between the buccal and lingual cervices (**b**). A dimensionless index of relative enamel thickness was created using the following formula, $[(c/e)/\sqrt{b}]$, which provides a measure of the thickness of enamel relative to overall tooth size. Enamel thickness was measured in only one specimen, PDYV 30, as YV 094 is too heavily worn. Slight wear is present on PDYV 30, especially on the buccal cusp tip and occlusal slope, so that the original occlusal outline of the buccal cuspal region had to be estimated (as in Grine and Martin, 1988; Shellis et al., 1998). Reconstructions were performed three times and intra-observer error was less than 3%. Despite the heavy wear, microstructural detail was preserved very well in YV 094 so that measurements of daily rates of secretion (in enamel and dentine) and the Retzius line periodicity could be determined for both teeth.

Retzius line periodicity was determined in each tooth by directly counting the number of short-period lines in enamel (daily cross striations) between adjacent long-period lines (striae of Retzius) (Figs. 2b and c). Measures of daily secretion rate (DSR) in enamel and dentine were recorded directly through the microscope using a graded eyepiece scale and from digital images for both molar specimens. To obtain enamel DSRs, linear measures were taken along the length of enamel prisms across six daily cross striations, thus representing five days. When divided by five, this yields the enamel DSR. Dentine DSRs were calculated in a similar manner for both teeth; linear measures along dentine tubules were taken across 11 short-period lines in dentine (von Ebner lines), thus bounding 10 days, and then divided by 10.

Total crown formation times (CFTs) are determined by summing the time taken to form the cuspal (appositional) and lateral (imbricational) components of each tooth. The transition between cuspal and lateral enamel is defined by the region

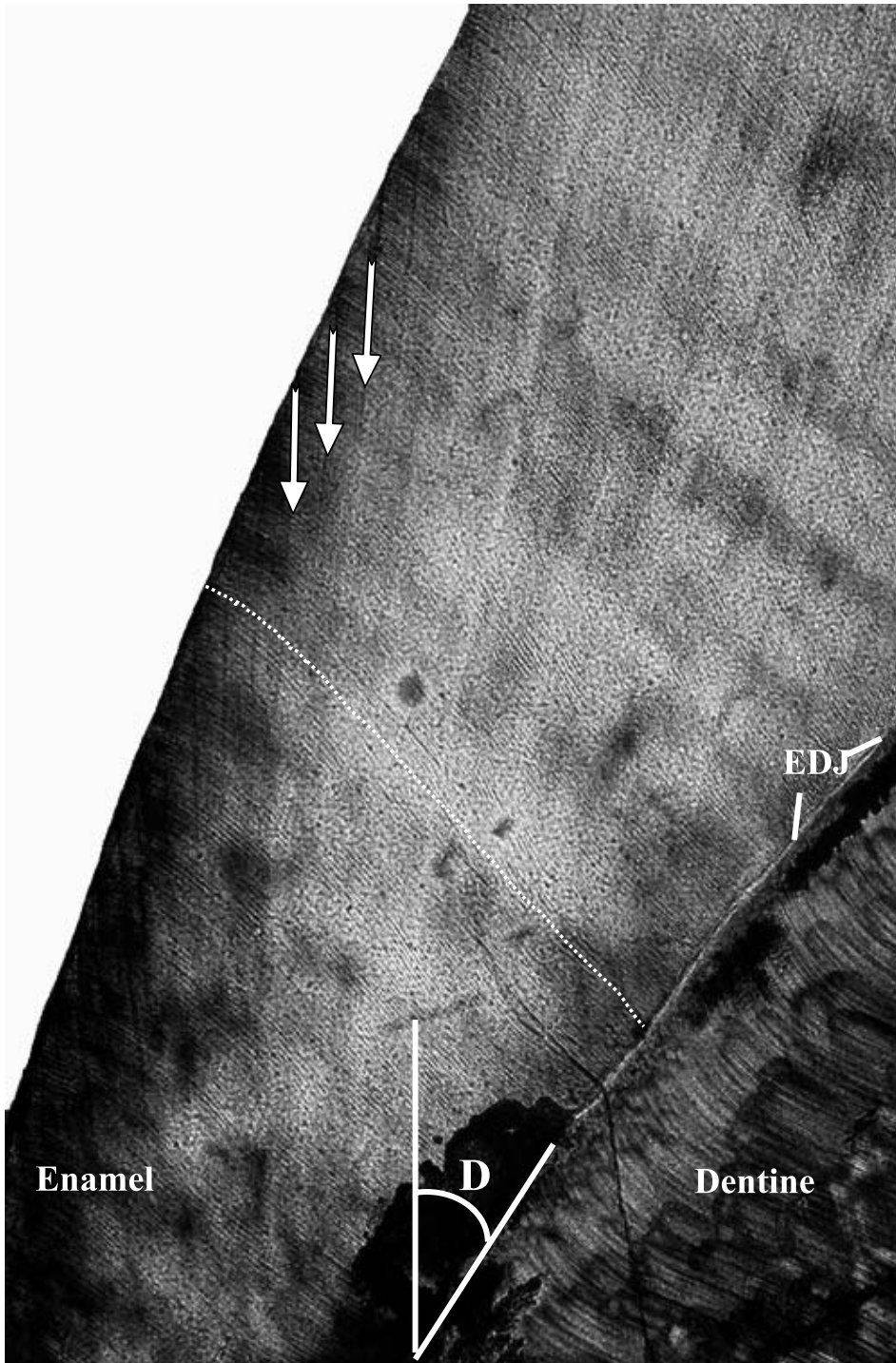


Fig. 2. (A).

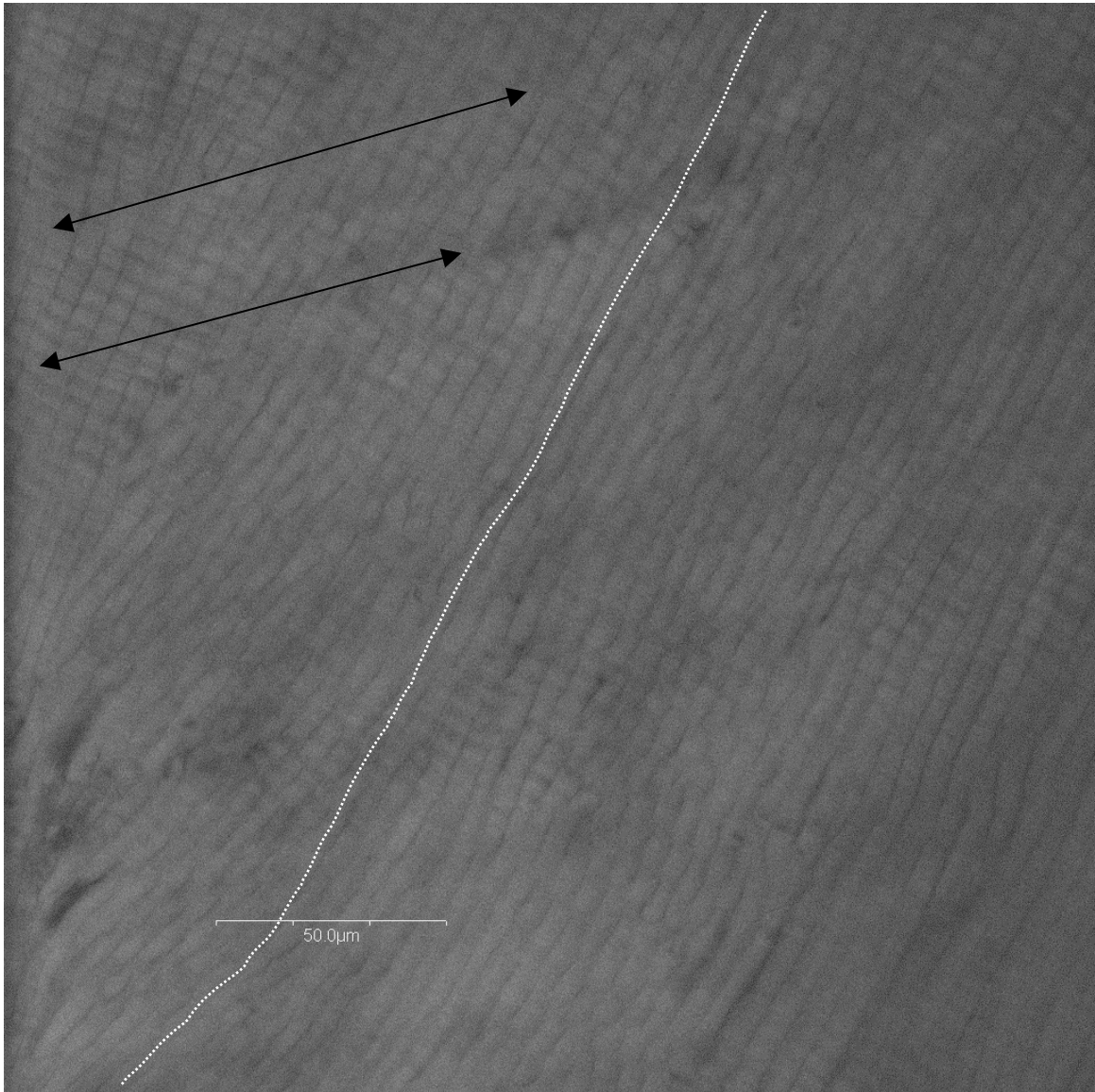


Fig. 2. (B).

where striae of Retzius are no longer completely buried within the cusp region by subsequently formed enamel, but rather reach the surface of the tooth as perikymata. Lateral enamel formation time in days is simply the total number of imbricational striae (perikymata) multiplied by the periodicity. Cuspal formation times can be determined in several ways, most of which require

complete, or virtually complete cusp tips (Dean, 1998; Schwartz et al., 2000). One method uses the following formula: [(cuspal enamel thickness \times correction factor)/mean daily rate of secretion], where the correction factor (usually 1.15) accounts for changes in prism length resulting from prism decussation (Risnes, 1986), and the mean daily rate of secretion is determined by averaging secretion

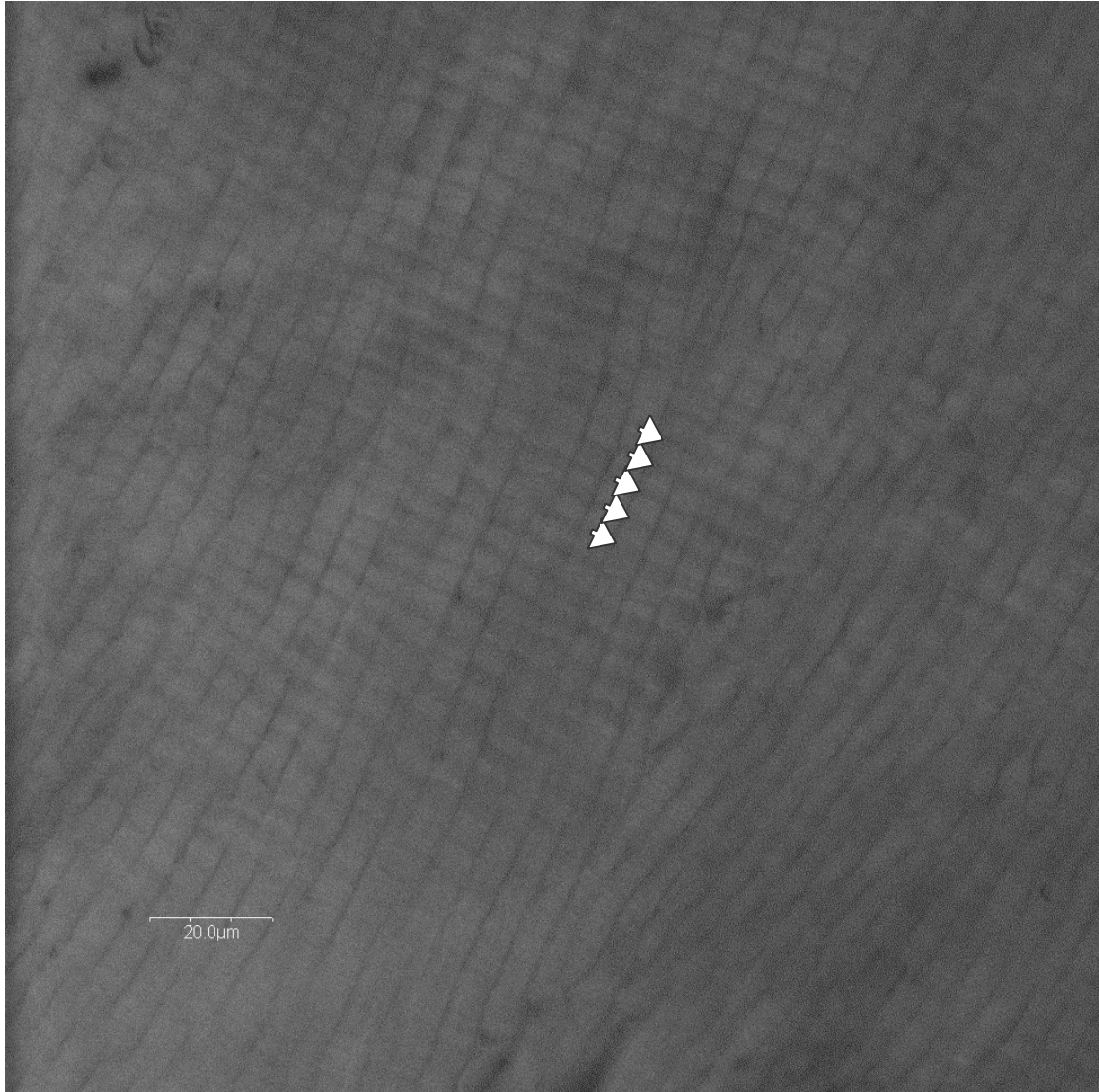


Fig. 2. (C).

Fig. 2 (C) Lateral enamel of PDYV 30 illustrating the striae of Retzius (white arrows) running obliquely from the outer enamel surface (left) to the EDJ. Enamel prisms (dashed line) can be seen coursing perpendicular to the EDJ towards the outer enamel surface. The angulation of the stria of Retzius to the EDJ (Angle D) is also indicated. (B) Laser confocal micrograph of enamel prisms in *L. hudiensis*, specimen PDYV 30. Enamel prisms (dashed line) run diagonally from bottom left to top right of field of view. Short-period lines (i.e., daily cross striations) run transversely across prisms. Two adjacent Retzius lines illustrated by black arrows and show 7 cross striations between them (Scale bar = 50 μm). (C) Higher magnification laser confocal image of Fig. 2B showing daily cross striations (arrowheads) running perpendicular to the long axes of enamel prisms (Scale bar = 20 μm).

rates throughout the cusp tip using $\times 25$ photomontages. Prism decussation is not pronounced in the Yuanmou molar so we used a more conserva-

tive estimate of 1.05 in addition to the 1.15 value (see Dean, 1998; Smith et al., 2001). A second method utilizes rates of cuspal dentine formation.

Table 1
Daily secretion rates in mid- to outer cuspal enamel in various hominoid taxa

Species	Mean (μm)	Range	Reference ^a
<i>Hylobates lar</i>	4.0	3.1–4.9	a
<i>Pan troglodytes</i>	5.3	4.1–6.7	b, c, d
<i>Gorilla gorilla</i>	6.5	5.7–7.4	b, e
<i>Pongo pygmaeus</i>	5.6	4.8–6.6	c
<i>Homo sapiens</i>	5.7	4.0–7.5	b, c
<i>Lufengpithecus huidienensis</i> - (Yuanmou)	5.6	5.1–6.2	This study
<i>Lufengpithecus lufengensis</i>	6.7	5.6–6.9	e
<i>Dryopithecus laietanus</i> ^b	5.3	4.6–5.9	f

^aReferences: a, Dirks (1998); b, Beynon et al. (1998); c, Dean et al. (1998); d, Reid et al. (1998); e, Schwartz et al. (in preparation); f, Kelley et al. (2001).

^bBased on data from an M₂.

Multiplying the linear distance along dentine tubules from the beginning of cuspal formation (i.e., dentine horn) to an Andresen line¹ corresponding to the end of cuspal dentine by the daily dentine secretion rate yields a cuspal formation time. This method does not require unworn cuspal enamel and is therefore ideal in cases where there is slight to moderate occlusal wear or obscured incremental markings in cuspal enamel. Cuspal formation times derived from dentine increments should equal those generated from enamel increments. A range of cuspal, and therefore, crown formation times is presented using both methods.

Another important aspect of tooth development is the enamel extension rate, or the rate at which new ameloblasts are activated (or recruited) cervically (Shellis, 1984). This can be approximated as the angle at which striae of Retzius intercept the enamel-dentine junction (EDJ), and is referred to as Angle D (see Fig. 2a). Measures of Angle D are recorded from the lateral and cervical regions of the Yuanmou molars.

The Yuanmou sections were then compared to a sample of extant and extinct primates, using only M₁s whenever possible. Comparative data for European, African and Asian fossil hominoids

and hominins are preliminary (Schwartz et al., in preparation).

Results

The periodicity of both *L. huidienensis* molars is 7 (Fig. 2b). This is within the known range of periodicities for all great apes and humans with the exception of *Pongo pygmaeus*, which has a periodicity range of 8 to 11 (Schwartz et al., 2001). Periodicity for the *L. huidienensis* molars is also similar to that in the early Miocene proconsulid, *Proconsul nyanzae* (6) (Beynon et al., 1998) and *Dryopithecus laietanus* (6–7) from the late Miocene of Spain (Kelley et al., 2001). Unfortunately, periodicities are largely unknown for the majority of fossil hominoids.

Daily secretion rates in the inner cuspal enamel range from 2.1 to 3.3 μm , with an average of 3.0 μm . Daily secretion rates in the mid- to outer cuspal enamel of *L. huidienensis* average 5.6 μm (range=5.1–6.2 μm) and are closest to mean values of *Pongo* and *Homo* among extant hominoids (Table 1). These data yield a grand mean DSR in the cuspal region of 4.3 μm in PDYV 30. Preliminary data on *L. lufengensis* suggest that enamel daily secretion rates in the mid- to outer region of the cusp are on average slightly higher, reaching close to 7 μm (mean=6.7 μm , range=5.6–6.9 μm) (Schwartz et al., in preparation). Daily rates of

¹ Andresen lines are long-period lines in dentine that correspond in periodicity to the long-period striae of Retzius in enamel.

Table 2
Crown formation in the Yuanmou hominoid molar

	PDYV 30 (M ₁)	
Retzius line periodicity	7	7
Cusp	Protoconid	Metaconid
Cuspal enamel formation time (days)	266–292	–
Number of striae in lateral enamel	72	–
Lateral enamel formation time (days)	504	–
Total enamel formation time (yrs.)	2.11–2.18	–
Thickness of cuspal dentine (μm)	788	804
Axial dentine rate (μm)	3.4	3.4
Cusp formation time (dentine) (days)	232	236
Total CFT (enamel + dentine)	2.02–2.18 yrs.	

enamel secretion in the cervical region of *L. hudiensis* average 3.6 μm (range=3.5–4.0 μm). Secretion rates near the cervix of *L. lufengensis* are similar, with a mean of 3.4 μm (ranging from 2.4–3.9 μm) per day. Using the two correction factors of 1.05 and 1.15, a mean enamel DSR of 4.3 μm, and a mean cuspal enamel thickness of 1,090 μm, yields cuspal enamel formation times ranging from 266 to 292 days (0.73–0.80 years).

Daily dentine secretion rates in the lateral region of the PDYV 30 crown average 1.7 μm (range=1.5–1.8 μm). In cuspal dentine, the distance between Andresen lines ranges from 22.0 to 29.6 μm. Dividing this value by the periodicity (7) yields a range of daily rates of 3.1–4.2 μm with a mean of 3.4 μm. The linear distance along dentine tubules corresponding to the entire period of cuspal formation is 788 μm for the protoconid and 804 μm for the metaconid yielding cuspal formation times of 232 days (0.64 years) and 236 days (0.65 years), respectively.

PDYV 30 has 72 imbricational striae on the protoconid, which multiplied by the 7-day periodicity yields a lateral crown formation time of 504 days (1.38 years). Thus, the range of total CFTs for PDYV 30 using combined data from enamel and dentine is estimated to be 2.02–2.18 years, 1.38 years of lateral enamel formation and 0.64–0.80 years of cuspal formation (Table 2).

The angulation of the striae to the EDJ (“Angle D”) averages 27.6 in the lateral and 40.5 in the cervical regions of the crown (Table 4). “S-shaped” striae are not present, in particular in the lateral

enamel. Striae are instead fairly straight from the EDJ to the outer enamel surface (see Fig. 2a).

Relative enamel thickness for Yuanmou molar PDYV 30 is 14.1 and is more similar to certain proconsulids (*Proconsul major* and *Rangwapithecus gordonii*), *Dryopithecus*, *Oreopithecus* and *Pongo* than it is to *L. lufengensis*, modern *Homo*, early hominins, *Sivapithecus* and *P. nyanzae*, all of which possess much thicker molar enamel (Table 5). For a primate of this size, *L. hudiensis* appears to possess only average molar enamel thickness, compared to *L. lufengensis* from Shihuiba which is among the most thickly-enamelled primates (Fig. 3).

Discussion

While this initial study is based on only two *L. hudiensis* molars from the Yuanmou assemblage, it provides important background comparative data for studies aimed at determining the taxonomy and phylogenetic position of these new fossils and the evolutionary relationships of the Chinese hominoids. Dental developmental data are lacking for the majority of middle to late Miocene European and Asian hominoids, and even for certain extant hominoids, making determinations of the polarity and homology for some of these traits difficult, if not presently impossible. Our goal here is simply to describe tooth formation in *L. hudiensis* within the larger comparative context of available data for other

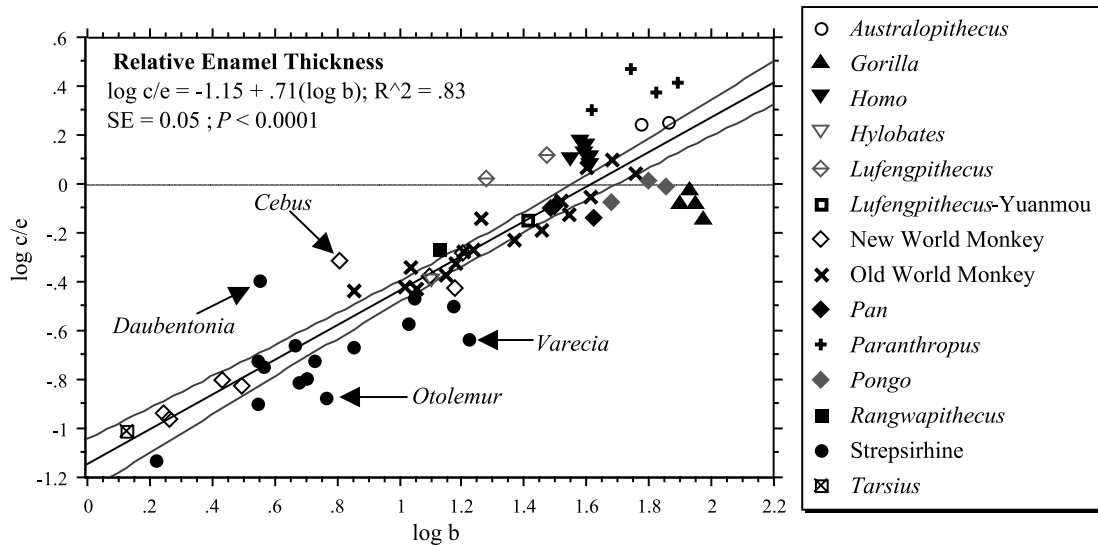


Fig. 3. Log-log least squares regression line of average enamel thickness (c/e) on dentine area (b) for a range of extant and fossil primates. “*Lufengpithecus*” refers to *L. lufengensis* from Shihuiiba. Strepsirhine, New and Old World Monkey data points refer to the following species and are mostly from Shellis et al., (1998): *Lemur catta*, *Eulemur* sp., *Varecia variegatus*, *Nycticebus coucang*, *Otolemur garnetti*, *Otolemur crassicaudatus*, *Perodicticus potto*, *Galago senegalensis*, *Propithecus diadema*, *Propithecus verreauxi*, *Daubentonia madagascarensis*, *Callithrix jacchus*, *Alouatta* sp., *Cebus apella*, *Saimiri sciureus*, *Ateles* sp., *Cercopithecus* sp., *Cercopithecus mona*, *Erythrocebus patas*, *Macaca nemestrina*, *Macaca mulatta*, *Macaca arctoides*, *Papio cynocephalus*, *Theropithecus gelada*, *Presbytis cristatus*. The 95% confidence intervals, standard error (SE) and p -value for the regression line are indicated.

hominoids. Phylogenetic interpretations must await forthcoming data on many other fossil hominoids, including *Griphopithecus*, *Gigantopithecus* and *Dryopithecus* (e.g., Kelley et al., 2001).

Periodicities, daily secretion rates and crown formation times

Among extant hominoids, *L. hudiensis* molars are similar to African apes in certain aspects of molar crown formation (Retzius line periodicity and enamel secretion rates), and to *Pongo* in other aspects (relative enamel thickness). Retzius line periodicity for the two *L. hudiensis* molars (7) resembles *Pan*, *Gorilla*, *Homo* (range of 6 to 11), *D. laietanus* (6–7) and *L. lufengensis* (7–9) and lies outside the known range for *Pongo* (8–11). Rates of cuspal enamel secretion are within the ranges for all hominoids, except *Hylobates*, including the early Miocene *Proconsul nyanzae* (Beynon et al., 1998; Dean, 1998; Dirks, 1998) (Table 1). On average, DSRs in the inner enamel of *L. hudiensis* M_1 s are within the ranges of all hominoids for

which there are data (Beynon et al., 1998; Dean, 1998). Daily rates of enamel secretion in the mid- to outer cuspal region fall closest to *Pongo* and *Homo* and are less than that in *L. lufengensis*. Among all the hominoids in the comparative sample, *L. lufengensis* is most similar to *Gorilla* in possessing the highest average mid- to outer cuspal secretion rates.

Daily rates of dentine secretion and root formation in extant hominoids are critical for providing more complete dental chronologies. These data are only recently making their way into the literature, and little data are available for most fossil apes. Dean (1998, p 456, Fig. 4) reported cuspal dentine lengths (i.e., the linear distance measured along dentine tubules running from the dentine horn to the end of cuspal dentine formation) of 960, 1130, and 1340 μ m in *Pan*, *Pongo* and *Homo*, respectively (on M_2 s, not M_1 s).² With average daily rates of dentine formation of 3.3, 3.0, and

² Sufficient data on metameric variation in aspects of molar crown formation are not yet available for hominoid taxa.

Table 3
Crown formation times (M₁s) in various extinct and extant primates

Species	N	Mean (yrs.)	Range (yrs.)
<i>Lufengpithecus lufengensis</i> ^a	2	3.4	2.8–3.9
<i>Homo sapiens</i>	6	3.4	3.0–3.6
<i>Pan troglodytes</i>	7	3.0	2.1–3.1
<i>Pongo pygmaeus</i>	2	3.0	2.7–3.3
<i>Gorilla gorilla</i>	4	2.9	2.6–3.2
<i>Australopithecus africanus</i>	2	2.8	2.7–3.0
<i>Paranthropus boisei</i>	2	2.4	2.1–2.6
<i>Dryopithecus laietanus</i> ^b	1	2.1	2.0–2.3
<i>L. hudiensis</i> - PDYV 30	–	2.1	2.0–2.2
<i>Proconsul nyanzae</i>	4	2.0	1.8–2.1
<i>Hylobates lar</i>	1	1.3	–
<i>Proconsul heseloni</i>	1	1.2	–

^aFrom work in progress. Based on two molar specimens, PA787 (RM₂) and PA791 (LM₂).

^bBased on data from an M₂ (see Kelley et al., 2001).

2.8 μ m, these yielded cuspal dentine formation times of 290, 376, and 479 days, respectively, in these taxa. Cuspal dentine lengths in the Yuanmou molar are 788 μ m and 804 μ m, with a mean daily rate of 3.4 μ m, yielding cuspal dentine formation times of 232–236 days. Molars of *L. hudiensis* are thus most similar to *Pan* among living great apes despite slightly faster average daily rates.

Cuspal formation times from enamel in the *L. hudiensis* M₁ range from 266 to 292 days (0.73–0.80 yrs.) (see Table 2). This is similar to cuspal formation times in M₁s of *Pan* (mean=0.72 yrs.; range=0.64–0.84 yrs.) and an M₂ of *Dryopithecus laietanus* (mean=0.75; range=0.67–0.83 yrs.) but longer than in *P. heseloni* M₁s (mean=0.44 yrs.; range=0.43–0.45 yrs.) (Beynon et al., 1998; Dean, 1998; Reid et al., 1998; Kelley et al., 2001). Cuspal formation times are markedly longer in *L. lufengensis*, *Pongo* and *Homo* (1.12, 1.04, and 1.26 yrs., respectively), which is associated with much thicker cuspal enamel and larger ratios of cuspal to lateral enamel volume (Dean, 1998; Grine and Martin, 1988; Schwartz, 2000).

Lateral enamel formation time in the *L. hudiensis* M₁ (1.38 yrs.) is less than in M₁s of *Pan* (mean=2.20 yrs.; range=1.53–2.59 yrs.), *Gorilla* (2.21 yrs.), *Pongo* (2.33 yrs.), and modern humans (mean=2.35 yrs.; range=1.92–2.72 yrs.) and greater than in the gibbon, *Hylobates lar* (0.65 yrs.) and *P. heseloni* (mean=0.88 yrs.; range=0.69–

1.18 yrs.) (Beynon et al., 1991b, 1998; Dirks, 1998; Reid et al., 1998a, b). A preliminary lateral enamel formation time for an M₂ of *L. lufengensis* (2.9 yrs.) is much longer than in the *L. hudiensis* molar and similar to M₂ lateral enamel formation time in *Gorilla* (2.7 yrs.) (Schwartz et al., in preparation). Total CFT in the *L. hudiensis* molar, at 2.02–2.18 yrs., is similar to *P. nyanzae* (Beynon et al., 1998). It lies between those of *P. heseloni* and *Hylobates*, on one hand, and extant hominoids, *L. lufengensis* and australopithecines on the other (Table 3). CFTs for *L. lufengensis*, although M₂s, are much longer than in the *L. hudiensis* molar, averaging 3.4 years, the same as modern human M₁s (Schwartz et al., in preparation).

Striae morphology

Dean and Shellis (1998) raised the possibility that certain aspects of striae of Retzius morphology may be of some phylogenetic significance for hominoids. Striae of Retzius represent periodic disturbances in enamel formation over the entire developing enamel front. In cross-section, they are usually more or less straight from the EDJ to the outer enamel surface (see Fig. 2a). “S-shaped” striae differ from ‘normal’ striae in having a shape that is markedly sinuous as it passes from the EDJ towards the outer tooth surface. This is achieved by prism widths remaining constant (or even

Table 4
Comparative data for striae angles (Angle D) in M1s of various hominoid taxa^a

Species	Lateral striae angles at EDJ Mean \pm 1 S.D.	Range	Cervical striae angles at EDJ Mean \pm 1 S.D.	Range
<i>Pan troglodytes</i>	26.0 \pm 2.6	–	31.0 \pm 4.3	–
<i>Gorilla gorilla</i>	23.0 \pm 6.8	–	31.0 \pm 10.7	–
<i>Pongo pygmaeus</i>	30.0 \pm 7.1	–	41.0 \pm 5.6	–
<i>Homo sapiens</i>	27.0 \pm 2.6	–	32.0 \pm 1.8	–
<i>L. hudiensis</i>	27.6 \pm 3.8	20.4–31.8	40.5 \pm 2.6	38.8–43.5
<i>Proconsul heseloni</i>	19.7 \pm 1.5	18.0–21.0	39.3 \pm 9.8	28.0–45.0
<i>Proconsul nyanzae</i>	25.5 \pm 6.3	21.0–30.0	67.5 \pm 3.5	65.0–70.0

^aData for extant hominoids and *Proconsul* from Beynon et al. (1998).

decreasing somewhat) as daily secretion rates increase in the middle enamel and then slow down again towards the tooth surface. “S-shaped” striae were noted in molars of siamangs, *Pongo* and *Proconsul* (Dean and Shellis, 1998). The shared lack of “S-shaped” striae in both *L. hudiensis* and *L. lufengensis* molars is interesting but its possible phylogenetic significance must await a more complete review of this feature in multiple outgroups to establish its polarity and homology during hominoid evolution.

Another important aspect of crown morphology is the angle at which long-period lines (striae in enamel and Andresen lines in dentine) intercept the EDJ, and is commonly referred to as Angle D. In the enamel, this angle is a critical gauge of the enamel extension rate, i.e., the rate at which, during crown formation, additional ameloblasts are activated (or recruited) cervically (Shellis, 1984). Angle D is determined by the combination of extension rate and initial secretion rate of newly recruited ameloblasts, so that it is smaller in teeth, or in regions of teeth, with faster extension rates and vice versa. Measures of Angle D in lateral enamel of *L. hudiensis* molars are well within the ranges of nearly all hominoid taxa (except *P. heseloni*) for which there are data (Table 4). In the cervical region, *L. hudiensis* molars have, on average, slower enamel extension rates compared to African apes and humans and are most similar to *P. heseloni* and *Pongo*.

Angle D can also be measured in dentine, using a combination of information on dentine extension and secretion rates. Values of Angle D in enamel

and dentine will be similar in teeth that share similar daily rates of enamel and dentine secretion, especially close to the EDJ. This results in a similar ratio of enamel to dentine formed over a given time interval, and, therefore, indicating a similar angle of the mineralizing front of both tissues with respect to the EDJ. In the *L. hudiensis* molars, Andresen lines were only visible in pulpal, not lateral, dentine so that measures of Angle D close to the EDJ were not possible. Using daily secretion rates as a rough guide, however, implies a *Proconsul*-like ratio of enamel to dentine formed (see Beynon et al., 1998).

Enamel thickness

Relative enamel thickness in the one *L. hudiensis* molar is more similar to that of *Pongo* than to any other extant ape, and is unlike those of *Paranthropus*, *L. lufengensis* and modern *Homo*, which have considerably thicker enamel (Table 5) (see Schwartz, 2000). The ontogenetic trajectory of crown growth (i.e., a month by month growth profile for the enamel or dentine components of the tooth crown) is also important to consider in comparative analyses of tooth growth (Dean, 1998; Dean et al., 2001). It is unknown at this point whether *L. hudiensis* shares a more similar trajectory of crown growth with *Pongo*, to which it is similar in enamel thickness, or with *L. lufengensis*, to which it is more closely related. The possibility exists that, despite similarities in morphology, *L. hudiensis* and *Pongo* follow different developmental trajectories to achieve a similar

Table 5
Relative enamel thickness in fossil and extant hominoid molars

Taxon	(c/e)/√b	Range
<i>Proconsul africanus</i> ^a	8.5	–
<i>Gorilla gorilla</i> ^a	10.0	6.8–13.4
<i>Pan troglodytes</i> ^a	10.1	7.0–13.3
<i>Hylobates lar</i> ^a	11.0	–
<i>Dryopithecus fontani</i> ^a	12.7	–
<i>Proconsul major</i> ^a	12.8	–
<i>Lufengpithecus hudiensis</i> ^b	14.1	–
<i>Rangwapithecus gordoni</i> ^b	14.9	–
<i>Oreopithecus bambolii</i> ^a	15.5	–
<i>Pongo pygmaeus</i> ^a	15.9	11.3–20.5
<i>Heliopithecus leakeyi</i> ^a	17.4	–
<i>Proconsul heseloni</i> ^c	18.8	14.4–24.4
<i>Griphopithecus</i> sp. ^a	19.7	16.1–22.7
<i>Australopithecus africanus</i> ^a	22.2	21.3–23.1
<i>Homo sapiens</i> ^a	22.4	13.8–32.3
<i>Proconsul nyanzae</i> ^c	24.1	22.3–27.6
<i>Lufengpithecus lufengensis</i> ^d	24.2	24.1–24.6
<i>Graecopithecus freybergi</i> ^a	28.3	–
<i>Paranthropus crassidens</i> ^a	29.6	–
<i>Paranthropus robustus</i> ^a	31.3	–
<i>Paranthropus boisei</i> ^a	34.9	31.0–38.6

Index of relative enamel thickness, [(c/e)/√b]: “c” is the area of the enclosed enamel cap, “e” is the length of the EDJ and “b” is the area of dentine bounded by a line drawn between lingual and buccal cervices.

^aTaken from Martin (1985), Grine and Martin (1988) and Andrews and Martin (1991).

^bNew data.

^cData from Beynon et al. (1998).

^dWork in progress.

degree of enamel thickness. For instance, despite similar measures of relative enamel thickness, species of African apes possess different monthly growth profiles for developing their similar phenotype (Dean, 1998; Schwartz and Dean, 2000, 2001). Modern gorilla molar cusps begin forming at just over 3–4 μm per day, rise quickly within the first few months to 6–7 μm per day, and then level off for the remaining two to three months, whereas those for chimpanzees begin at 2–3 μm per day and increase much more slowly, reaching 5–6 μm in the outer enamel only during the last month of cuspal growth. A pattern similar to chimpanzees occurs in orangutan molar cusps, though enamel secretion rates in the latter rise more quickly, reaching their peak of 5–6 μm at only a half year into cusp

formation (Schwartz and Dean, 2000). Daily rates of enamel formation in the *L. hudiensis* molars start off at 2–3 μm and rise to 5–6 μm towards the outer enamel (see Results and Table 1). Rates for each monthly interval are not available for the *L. hudiensis* teeth used in this study, but the overall pattern of cuspal growth is most similar to chimpanzees and orangutans. The apparent lack of developmental homology in this one aspect of crown formation within extant hominoids underscores the importance of including developmental information in any phylogenetic (Beynon et al., 1991a,b, 1998; Schwartz and Dean, 2000).

Summary

Our preliminary histological study of molar crown ontogeny suggests that *L. hudiensis* molars share more features in common with most extant hominoids and *Proconsul* than they do with *L. lufengensis*. For instance, one of the two *L. hudiensis* molars from Yuanmou (PDYV 30) possesses only average enamel thickness, unlike *L. lufengensis*, and is most similar to *Pongo* among living apes. The Retzius line periodicity in *L. hudiensis* is within the known range of periodicities for extant great apes and humans, with the exception of *Pongo*, and similar to Miocene *Dryopithecus* and *Proconsul*. Daily rates of enamel secretion in *L. hudiensis* molars are most similar to *Pongo* and *Homo*, while daily rates in dentine are equivalent to those in all extant apes. Formation times for the cuspal portion of the molar crown are most similar to *Pan* and *D. laietanus*. Total molar crown formation time is shorter in *L. hudiensis* than in any large-bodied hominoid, in particular *L. lufengensis*, and is most similar to *P. nyanzae* and *D. laietanus*.

Any phylogenetic interpretations from our dental microstructural data must await information on these characters in many of the comparative taxa. More dental developmental data need to be collected in larger samples of anterior and posterior teeth from the Yuanmou locality as well as in all other Miocene to Recent hominoids.

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