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Tooth Wear Difference Between the Yuanmou Hominoid and *Lufengpithecus*

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*The Late Miocene hominoids recovered from Lufeng (*Lufengpithecus*) and Yuanmou of Yunnan Province, China, are among the most numerous hominoid fossils in Eurasia. They have yielded critical evidence for the evolutionary history, biogeography and paleobiology of Miocene hominoids. We examined and compared the wear pattern and differences of 804 molars of the Yuanmou hominoid and* Lufengpithecus*. Our results indicate that both the upper and lower molars of the Yuanmou hominoids were more heavily worn than those of* Lufengpithecus*. The wear patterns of the individual molars between the Yuanmou hominoid and* Lufengpithecus *also are different. The heaviest wear of lower molars of the Yuanmou hominoid occur in M_2, followed by M_1 and M_3. In* Lufengpithecus*, M_1 and M_3 were more heavily worn than M_2. There are differences in wear between the upper and lower molars for the two hominoids. Among the various factors related to tooth wear, we suggest that the main reason for the tooth wear differences between the Yuanmou hominoid and* Lufengpithecus *may be that they had different diets. More soft dietary items like leaves and berries were probably consumed by* Lufengpithecus*, and the Yuanmou hominoid may mainly have feed on harder or frugivorous diets. This result complements findings from previous studies of tooth size proportion, and the development of lower molar*

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shearing crests in the 2 samples. Enamel thickness, living environment, behavior patterns, and population structure also might account for dental wear differences between the Yuanmou hominoid and Lufengpithecus.

KEY WORDS: Yuanmou hominoid; *Lufengpithecus*; tooth wear.

INTRODUCTION

The late Miocene hominoids found in Lufeng and Yuanmou of Yunnan Province, China, which were initially unearthed in 1970's and 1980's respectively, are among the most prolific fossil hominoids ever found in Eurasia (Wu *et al.*, 1986; Zheng and Zhang, 1997). These two hominoid faunas have offered important evidence recording the evolutionary history and paleobiology of late Miocene hominoids. Even though the taxonomy and phylogeney for the fossils from Lufeng site have been in debate, most colleagues now agree that the Lufeng fossils represent a single, sexually dimorphic species, *Lufengpithecus lufengensis*, which are possibly related to the *Sivapithecus-Pongo* clade (Kelley, 1993; Kelley and Xu, 1991; Wu, 1987). On the contrary, most aspects of the Yuanmou hominoids are still under studies. For the past decade, several excavations have accumulated a large assemblage of fossils (Zheng and Zhang, 1997). Some preliminary studies indicate that the Yuanmou hominoids resemble the *Lufengpithecus lufengensis* in some cranial and dental features (Zheng and Zhang, 1997; Liu *et al.*, 2000, 2001a,b). However the tooth size and some dental morphology differences between the two hominoids led to the proposal of new species, *Lufengpithecus hudienensis* (Harrison *et al.*, 2002). In the past ten years, the fossil feature comparisons between the Yuanmou hominoid and *Lufengpithecus*, and the studies of phylogenetic relationship between the two taxa has been drawing the attentions of colleagues (Liu *et al.*, 2000; Liu *et al.*, 2001a,b; Liu *et al.*, 2002).

In recent years, the behavior pattern, living environment, diets and healthy conditions have received increasing attentions in the research field of Miocene hominoid and early hominid evolution. These studies can, from different channels, provide additional important information related to the behavior and ecology of Miocene hominoids, transition from the Miocene hominoids to the early hominids, and early hominid evolution (Kay and Ungar, 1997; Sponheimer and Lee-Thorp, 1999; Ragir, 2000; Teaford and Ungar, 2000; Backwell and d'Errico, 2001). For the past a few years, we have been doing the field excavation and laboratory analysis of the Yuanmou hominoid and *Lufengpithecus* fossils. We have noticed that very obvious differences of tooth wears exist between the two hominoid faunas. The teeth of Yuanmou hominoid teeth are usually more heavily worn than

those of *Lufengpithecus*. Given the possible close relationships among tooth wear, diets, behavior pattern, living environment and population structure, we compared the tooth wears of the Yuanmou hominoid and *Lufengpithecus* in order to explain the tooth wear patterns of the two faunas.

MATERIALS AND METHOD

The specimens are in collections at the Yunnan Provincial Institute of Archaeology and the Yuanmou County Museum, and include the teeth of the Yuanmou hominoids from Yuanmou and *Lufengpithecus* from Lufeng (Table I). Because molars have bigger occlucal surface and are easily observed, we studied only upper and lower molars. All specimens are isolated molars except 6 teeth that are attached in a mandible of *Lufengpithecus*. We determined first, second and third molars on the basis of the interstitial wear facets (Hooijer, 1948). Because the mesial side of first molars is in contact with the second decidous molars and later, the permanent forth premolars, the mesial side of first molars usually has 2 proximal facets. Second molars only have 1 proximal wear facet. Third molars also have only 1 proximal wear facet and lack a distal facet. Even with this method, some isolated teeth are difficult to identify. Among them, most are either M1 or M2 because M3 is relatively easy to diagnose. Accordingly we put the unidentified teeth into a separate group as M1 or M2.

Because there is no widely accepted standard by which to grade tooth wear in Miocene hominoids, we set our own standard to score upper and lower molars in Yuanmou hominoids and *Lufengpithecus* (Figure 1).

Grade 1: No wear or slight wear on cusps without dentine exposure.

Grade 2: Moderate tooth wear on cusps with point dentine exposure.

Grade 3: Tooth cusps are worn off and dentine exposure occupies a large area on the occlucal surface.

Accordingly, we scored each molar and calculated the frequencies of grades 1, 2 and 3 in the various molars of the Yuanmou hominoid and *Lufengpithecus*(Tables II and III). We used Fisher's exact Chi-square tests to assess the significant level of tooth wear differences between the Yuanmou hominoid and *Lufengpithecus*.

Table I. Specimens

	Upper				Lower				Pooled		
	M^1	M^2	M^3	M^1 or M^2	M_1	M_2	M_3	M_1 or M_2	Upper	Lower	Total
Yuanmou	119	112	79	71	74	97	76	77	381	324	705
Lufeng	16	15	13		19	18	13	5	44	55	99

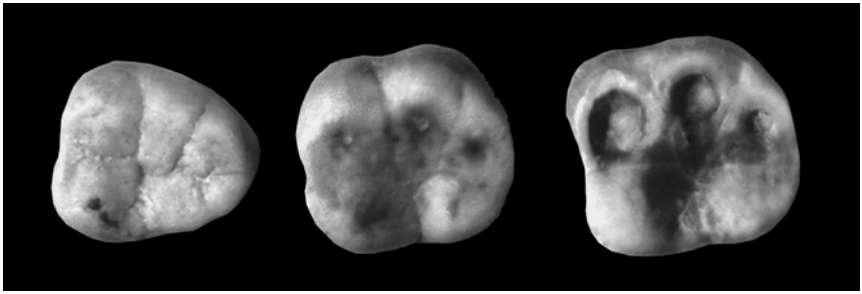

Fig. 1. Tooth wear grades (1–3 from left to right).

From the distribution of scored tooth wear data in Table II and Table III, the characteristics of upper and lower molar wear patterns of the Yuanmou hominoid and *Lufengpithecus* can be summarized as follow.

RESULTS

The Teeth of the Yuanmou Hominoids Are Much More Worn than Those of *Lufengpithecus*

There are notable molar wear differences of the upper and lower molars between the Yuanmou hominoid and *Lufengpithecus* (Tables II and III). The general trend is that much more heavy molar wears occur in the Yuanmou hominoid than in the *Lufengpithecus*. In the pooled data of M1–M3, the percentages of grade 3 tooth wear in Yuanmou hominoid upper and lower molars are 26.2% and 30.9%, respectively. The corresponding percentages for *Lufengpithecus* are only 4.6% and 9.1%, respectively. For grade 2, the same trend is apparent for both upper and lower molars between the Yuanmou hominoids and *Lufengpithecus* with higher frequency in the Yuanmou hominoids (34.4% and 28.7%) than in the *Lufengpithecus*(27.3% and 20%). Contrarily, the occurrences of wear grade 1 in the upper and lower molars of *Lufengpithecus* reach 68.1% and 70.9%, respectively while counterparts for the Yuanmou hominoids are only 39.4% and 40.4%, respectively. Statistical tests (Table IV) show that the tooth wear differences of upper and lower molars between the Yuanmou hominoids and *Lufengpithecus* from the pooled samples are significant at $P < 0.001$.

More grade 2 and 3 wears occur in both the upper and lower molars of the Yuanmou hominoid than in the *Lufengpithecus* (Fig. 2). Grade 1 percentages are much higher in *Lufengpithecus* than in the Yuanmou

Table II. The upper molar wears of the Yuanmou hominoid and *Lufengpithecus*

	Tooth types, N (%)														
	M1			M2			M3			M1 or M2			Pooled		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Yuanmou	43 (36.1)	44 (37.0)	32 (26.9)	43 (38.4)	37 (33.0)	32 (28.6)	38 (48.1)	23 (29.1)	18 (32.9)	26 (36.6)	27 (38.0)	18 (25.3)	150 (39.4)	131 (34.4)	100 (26.2)
Lufeng	11 (68.7)	4 (25.0)	1 (6.3)	10 (66.7)	5 (33.3)	0 (0.0)	9 (69.2)	3 (23.1)	1 (7.7)				30 (68.1)	12 (27.3)	2 (4.6)

Table III. The lower molar wears of the Yuanmou hominoid and *Lufengpithecus*

	Tooth types, N (%)														
	M1			M2			M3			M1 or M2			Pooled		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Yuanmou	26 (35.1)	26 (35.1)	22 (29.7)	34 (35.1)	23 (23.7)	40 (41.2)	38 (50.0)	22 (29.0)	16 (21.0)	33 (42.9)	22 (28.6)	22 (28.6)	131 (40.4)	93 (28.7)	100 (30.9)
Lufeng	10 (52.6)	6 (31.6)	3 (15.8)	16 (88.9)	2 (11.1)	0 (0.0)	8 (61.5)	3 (23.1)	2 (15.4)	5 (100.0)	0 (0.0)	0 (0.0)	39 (70.9)	11 (20.0)	5 (9.1)

Table IV. Chi-square tests for the tooth wear differences between the Yuanmou hominoid and *Lufengpithecus*

	Upper teeth				Lower teeth				
	M^1	M^2	M^3	pooled	M_1	M_2	M_3	M_1 or M_2	pooled
χ^2	6.246	7.630	2.015	17.269	2.210	19.661	0.495	4.623	19.519
P	0.043	0.017	0.351	0.000	0.320	0.000	0.787	0.085	0.000

hominoids. Moreover the wear pattern difference between pooled samples of upper and lower molars follow a similar trend (Fig. 2).

The Wearing Differences Between Tooth Types

M_2 is more heavily worn than M_1 and M_3 in the Yuanmou hominoids, whereas in *Lufengpithecus*, M_2 is least worn, and both M_1 and M_3 are more heavily worn than M_2 (Fig. 3). In the upper molars, there is a similar trend for both the Yuanmou hominoid and *Lufengpithecus*. But wear differences are not so obvious as in the lower molars (Fig. 4). Fisher's exact tests (Table IV) indicate that most of the tooth wear differences between each type of the molars for the Yuanmou hominoid and *Lufengpithecus* are significant at $P < 0.01$.

The occurrences of wear grade 3 in M1, M2 and M3 for both the upper and lower molars of the Yuanmou hominoids are higher than those of the *Lufengpithecus* (Fig. 5; Tables II and III). The most obvious difference of in wear patterns between the 2 samples is in M2. The occurrences of wear grades 3 in the upper and lower M2 of the Yuanmou hominoids are 28.6% and 41.2%, respectively. In *Lufengpithecus*, there is no grade 3 wear in the upper and lower M2.

Wear Differences Between the Upper and Lower Molars

Wear patterns in the upper and lower molars differ to various extents within and between the 2 samples. For lower molars, M_2 is most heavily worn in the Yuanmou hominoids, with grade 3 occurrence of 41.2%, and least worn lower molars in the *Lufengpithecus* are M_2 with grade 3 occurrences of 0%. But this trend does not exactly follow in the upper molars. For the upper molars, in *Lufengpithecus* the wear sequence is like that of its lower molars with heavily worn M^2. But for the upper molars of Yuanmou hominoids, the wear patterns are different from of its lower molars. The difference of grade 3 among M1, M2 and M3 in the upper molars of the

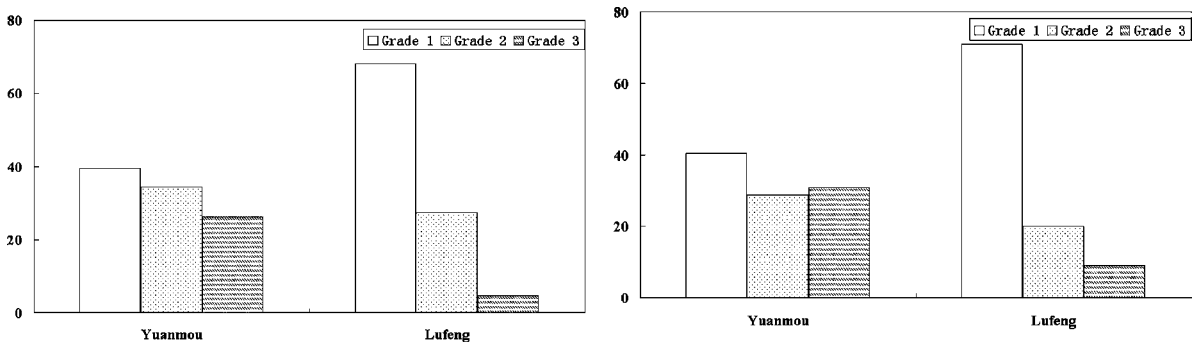

Fig. 2. The frequencies of wearing grades for the pooled upper and lower molars of the Yuanmou hominoid and *Lufengpithecus* (Left: upper molars; Right: lower molars).

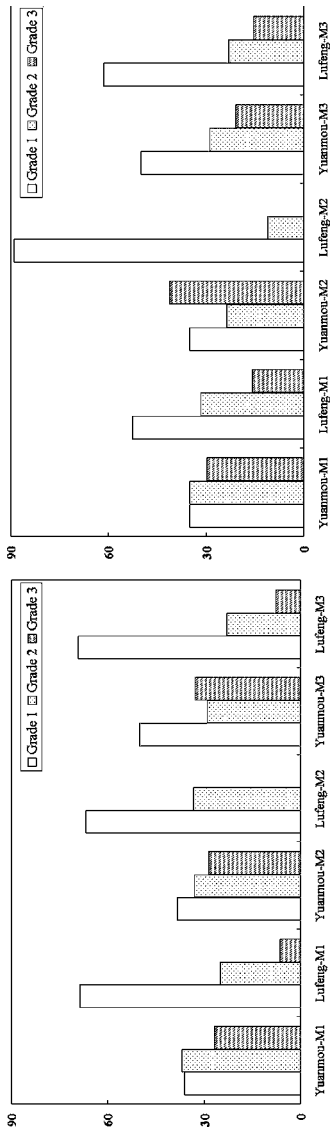

Fig. 3. The tooth wear comparisons for different types of upper and lower molars (Left: upper molars; Right: lower molars).

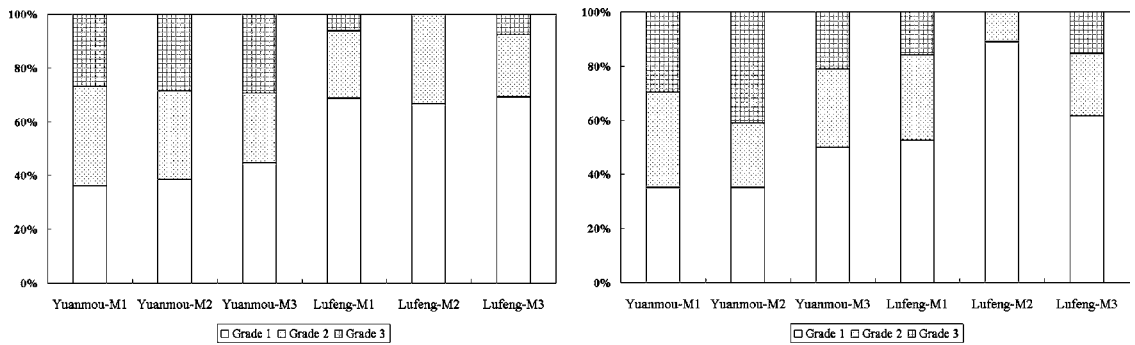

Fig. 4. The percentages of different wear grades for all types of molars in the Yuanmou hominoid and *Lufengpithecus* (Left: upper molars; Right: lower molars).

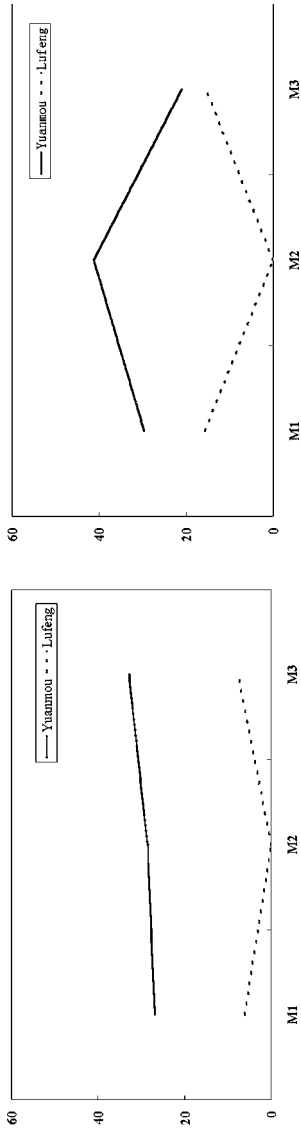

Fig. 5. Wear grade 3 in the upper and lower molars of the Yuanmou hominoid and *Lufengpithecus* (Left: upper molars; Right: lower molars).

Yuanmou hominoids are not as obvious as that in the lower molars (Fig. 5). The frequencies of grade 3 wear for the upper molars of the Yuanmou hominoids are 26.9%, 28.6% and 32.9% respectively. The corresponding frequencies for the lower molars are 29.7% 41.2% and 21.0% respectively. Accordingly, the 3 upper molars in the Yuanmou hominoids have relatively closer wear whereas in the lower molars, M2 is worn more heavily than M1 and M3 are. The main difference is in M^2, which is not as heavily worn as M_2, which causes 2 kinds of different wear patterns between the Yuanmou hominoids and *Lufengpithecus* for the upper and lower molars, respectively.

DISCUSSION

The main function of teeth in modern humans is chewing, smashing and grinding food. For the early hominids and the Miocene hominoids, the teeth may have also been involved with making or using tools and may have served as defending weapons. The wear status of teeth directly records contact by different items on the occlucial surface. Moreover, tooth wear is related to other factors: behavior patterns, living habit, locomotion, and population structure (healthy condition, age composition and ages at death). Because the Miocene hominoids were basically at the evolutionary stage, of almost completely passively adjusting to the environments, to some extent, their tooth wear reflects their environments. The marked tooth wear differences between the Yuanmou hominoid and *Lufengpithecus* suggest more heavy molar wear in the Yuanmou hominoids than in *Lufengpithecus*.

Diets

The wear status of molars is closely related to textures of food. Therefore, the primary reason for the wear differences of the molars between the Yuanmou hominoid and *Lufengpithecus* is most likely the different textures of food consumed by them. We presume that the diets of the Yuanmou hominoids are relatively hard, and that softer diets were eaten by the *Lufengpithecus*. In a previous study of tooth size proportions and M_2 shearing crest developments of the Yuanmou hominoid and *Lufengpithecus* (Liu *et al.*, 2002), we found that the Yuanmou hominoids have relatively bigger front teeth and weakly developed molar shearing crests, indicating they mainly fed on a harder or frugivorous diet, and more soft food like leaves and berries were consumed by *Lufengpithecus*. Different environments for the two hominoid faunas may be further indicated.

Living Environments

Because the diets of the Yuanmou hominoid and *Lufengpithecus* were obviously different the faunas and floras associated with them may be different. Actually, a recent analysis of micromammalian fauna for the 2 hominoid sites indicate different faunal compositions (Ni and Qiu, 2002).

Behavioral Differences

There are other possible causes for the tooth wear differences between the Yuanmou hominoid and *Lufengpithecus*. Although the exact phylogenetic relationship between the Yuanmou hominoid and *Lufengpithecus* is uncertain, morphological differences suggest that they are different species (Liu *et al.*, 2000; Liu *et al.*, 2001a,b; Harrison *et al.*, 2002). If the Yuanmou hominoid and *Lufengpithecus* belong to 2 species, it is very possible that they had different behaviors, including food choices. Even if the Yuanmou hominoid and *Lufengpithecus* lived in similar environments they could have diets with very different textures.

Enamel Thickness

Schwartz *et al.* (2003) found that the relative molar enamel thickness in the one Yuanmou hominoid is 14.1, which is thinner than the average relative enamel thickness (24.2) for *Lufengpithecus*. A obvious difference in enamel thickness of this magnitude between the Yuanmou hominoid and *Lufengpithecus* could notably affect tooth wear differences between them. Kay (1985) demonstrated that extant leaf-eating species generally have thinner enamel than that of fruit-eating species. Kay (1985) and Martin (1985) inferred from thick enamel that australopithecines probably ate very hard, brittle foods. Dean *et al.* (1992) attributed the tooth wear differences between African great apes (chimpanzee and gorilla) and orangutans to enamel thickness. But this view has been challenged by evidence for thin enamel in *Otavipithecus* and *Ardipithecus* (White *et al.*, 1994; Teaford and Ungar, 2000). Also, there are many potential complicating factors related with the functional significance of enamel thickness. For example, thick enamel by itself does not necessarily provide protection against hard objects, which may cause fractures (Pilbeam, 1997; Schwartz, 2000). Accordingly, the correlation between enamel thickness and diet may not be a perfect indicator of diet. Further, the enamel thickness value for the Yuanmou hominoid is from one molar, which may not represent the average for the population.

Wear Pattern Difference Between the Yuanmou Hominoid and *Lufengpithecus*

Like the Yuanmou hominoids and *Lufengpithecus*, African and Asian great apes evidence different wear patterns (Dean *et al.*, 1992; Welsch, 1967). In chimpanzee and gorillas, the first molars are usually most intensively worn, and they also sometimes exhibit more worn than M2 and M1, patterns that are absent in orangutans. The differences of tooth morphology and tooth row orientation between the African and Asian apes may be responsible for the different wear patterns. The Yuanmou hominoid and *Lufengpithecus* are also morphometrically different (Liu *et al.*, 2001a,b). Therefore, we tentatively infer that the differences in tooth wear patterns between the Yuanmou hominoid and *Lufengpithecus* may be due to the differences of tooth morphology and chewing habits between them.

Other Factors

Tooth wear is directly related to age at death, which further reflects the population structure and health conditions for hominoids. If the molar type composition in our samples represent normal populations for the Yuanmou hominoid and *Lufengpithecus*, the much heavier tooth wear of the former suggest that the average age at death of Yuanmou hominoids is older that those of the *Lufengpithecus*. Perhaps *Lufengpithecus* had poorer health, which produced the younger average ages at death and the tooth wear difference between them and the Yuanmou hominoid.

The distance between the sites of the Yuanmou hominoid and *Lufengpithecus* is <100 km and their geological ages might be also close (Ni and Qiu, 2002). The Yuanmou hominoid and *Lufengpithecus* share many similarities, but there are also differences between them (Zheng and Zhang, 1997; Liu *et al.*, 2001a,b; Schwartz *et al.*, 2003). We found notable differences in tooth wear between them, which suggest that their diets, environments, behavior patterns and population structures were probably very different. Although all these factors may be related the tooth wear differences to some extent, we think that dietary differences between the Yuanmou hominoid and *Lufengpithecus* seem to be the main reason for the tooth wear differences. Liu *et al.* (2002) proposed that different diets were consumed by the Yuanmou hominoid and *Lufengpithecus* based on the tooth size and morphology analysis. Tooth wear further supports our diet hypothesis. However, we cannot determine whether the dietary difference was caused by the environment or behaviors related to their phylogenetic status.

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REFERENCES

Backwell, L. R., and F. d'Errico, F. (2001). Evidence of termite foraging by Swartkrans early hominids. *PNAS*. 98: 1358–1363.

Dean, M. C., and Pilley, J. R. (1992). The natural history of tooth year, continuous eruption and Periodontal disease in wild shot great apes. *J. Hum. Evol.* 22: 23–39.

Harrison, T., Ji, X., and Su, D. (2002). On the systematic status of the late Neogene hominoids from Yunnan Province, China. *J. Hum. Evol.* 42: 207–227.

Hooijer, D. A. (1948). Prehistoric teeth of man and the orang-utan from Central Sumatra, with notes on the fossil orang-utan from Java and Southern China. *Zoölogische Mededelingen.* 29: 175–301.

Kay, R. F. (1985). Dental evidence for the diet of *Australopithecus*. *Ann. Rev. Anthropol.* 14: 315–341.

Kay, R. F., and Ungar, P. (1997). Dental evidence for diet in some Miocene catarrhines on the effects of phylogeny on the interpretation of adaptation. In Begun, D. R. *et al.* (eds.), *Function, Phylogeny, and Fossils*, Plenum Press, New York, pp. 131–152.

Kelley, J. (1993). Taxonomic implications of sexual dimorphism in *Lufengpithecus*. In Kimbel, W. H., and Martin, L. B. (eds.), *Species, Species Concepts, and Primate Evolution*, Plenum Press, New York, pp. 429–458.

Kelley, J., and Xu, Q. (1991). Extreme sexual dimorphism in a Miocene hominoid. *Nature* 352: 151–153.

Liu, W., Zheng, L., and Jiang, C. (2000). The statistical analyses of the metric data of hominoid teeth found in Yuanmou of China. *Chin. Sci. Bulletin* 45: 936–942.

Liu, W., Zheng, L., and Walker, A. (2001a). Three-dimensional morphometric analyses of hominoid lower molars from Yuanmou of Yunnan Province, China. *Acta. Anthropol. Sinica*. 20: 163–177.

Liu, W., Hlusko, L., and Zheng, L. (2001b). Morphometric analysis of hominoid lower molars found in Yuanmou of Yunnan Province, China. *Primates* 42: 123–134.

Liu, W., Zheng, L., and Gao, F. (2002). The advances in Miocene hominoid studies and problems. *Chin. Sci. Bulletin* 47: 492–500.

Liu, W., Gao, F., and Zheng, L. (2002). The diet analysis from tooth size and morphology for Yuanmou hominoids, Yunnan Province, China. *Anthropol. Sci.* 110: 149–163.

Martin, L. B. (1985). Significance of enamel thickness in hominoid evolution. *Nature* 314: 260–263.

Ni, X., and Qiu, Z. (2002). The micromammalian fauna from the Leilao, Yuanmou hominoid locality: Implications for biochronology and paleoecology. *J. Hum. Evol.* 42: 535–546.

Pilbeam, D. (1997). Research on Miocene hominoids and hominid origins. The last three decades. In Begun, D. R., Ward, C. V., and Rose, M. D. (eds.), *"Function, Phylogeny, and Fossils,"* Plenum Press, New York, pp. 13–28.

Ragir, S. (2000). Diet and food preparation: rethinking early hominid behavior. *Evol. Anthropol.* 9: 153–155.

Schwartz, G. (2000). Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. *Am. J. Phy. Anthropol.* 111: 221–244.

Schwartz, G., Liu, W., and Zheng, L. (2003). Preliminary investigation of dental microstructure in the Yuanmou hominoid (*Lufengpithecus hudieenensis*), Yunnan Province, *China. J. Hum. Evol.* 44: 189–202.
Sponheimer, M., and Lee-Thorp, J. A. (1999). Isotopic evidence of the diet of an early hominid, *Australopithecus africanus*. *Science* 283: 368–370.
Teaford, M. F., and Ungar, P. (2000). Diet and the evolution of the earliest human ancestors. *PNAS.* 97: 13506–13511.
Welsch, U. (1967). Tooth wear in living pongids. *J. Den. Res.* 46: 989–992.
White, T. D., Suwa, G., and Asfaw, B. (1994). *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371: 306–312.
Wu, R. (1987). A revision of the classification of the Lufeng great apes. *Acta Anthropol. Sinica.* 6: 265–271.
Wu, R., Xu, Q., and Lu, Q. (1986). Relationship between Lufeng Sivapithecus and Ramapithecus and their phylogenetic position. *Acta Anthropol. Sinica.* 5: 1–30.
Zheng, L., and Zhang, X. (1997). Hominoid fossils. In He (ed.), *Yuanmou Hominoid Fauna*, Yunnan Science Press, Kunming, pp. 21–59.