Statistical analyses of metric data of hominoid teeth found in Yuanmou of China

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Abstract Mesial-distal and buccal-lingual dimensions of 1 266 hominoid teeth found in Yuanmou of Yunnan Province during the period of 1986 and 1988 have been measured. The statistical analyses of the metric data show that the tooth sizes of Yuanmou hominoid can be divided into big and small two types, and most tooth dimensions display obvious bimodalities in both histograms and 2 dimensional plots. The coefficients of variance (CV) reveal that the CVs of Yuanmou hominoid tooth sizes are within or close to the CV ranges of *Lufengpithecus* and extant great apes. The comparisons of tooth sizes and their proportions indicate that Yuanmou hominoids have close affinities with Lefeng and Kaiyuan hominoids, and have obvious differences with Gorilla, Chimpanzee and Orangutan. The authors believe that the hominoid fossils found in Yuanmou in the past 10 years represent a single species with highly sexual dimorphism in morphology and this species may have a close evolutionary relationship with the hominoids found in Kaiyuan and Lufeng.

Keywords: human origin, Yuanmou hominoid, dental metrics, statistical analyses.

Since the 1950s, Miocene hominoid fossils have been found at 4 sites of Kaiyuan, Lufeng, Yuanmou and Baoshan in Yunnan Province respectively[1−5]. Among them, the hominoid fossils found in Lufeng and Yuanmou are especially rich. In Yuanmou, since the first discovery of hominoid fossils in 1986, through several excavations and fossil collections in the past years, 1 skull, 8 maxillas, 9 mandibles and about 1400 isolated teeth have been found. According to the description and comparisons of skull, maxillas, mandibles and teeth of Yuanmou homionid, some researchers proposed the opinions about the morphological features and phylogenetic position of Yuanmou hominoid fossils. Zheng and Zhang[6] believe that the size differences of Yuanmou hominoid fossils are obvious and the fossils may represent two types or individual differences between male and female. In classification, the hominoid found in Yuanmou may represent a new species within the genus of *Lufengpithecus*[6]. These studies enrich the research field of Tertiary Hominoid in both China and East Asia, and point out some problems, which concern with the fossil features, phylogenetic position and relationship with other Miocene hominoids for the Yuanmou hominoids. All these problems need further studies. However, we have to admit that current studies of Yuanmou fossils are not enough in both depth and extensiveness, and the research methods are also limited. Many key questions concerning the fossil features, degrees of variations, relationship with other Miocene hominoids, phylogenetic position and role in the research of human origin are not clear. It should be especially pointed out that most of the fossils found in Yuanmou are teeth. Till now, the studies of the teeth mainly focus on the description and comparisons of tooth morphology. The statistical analyses of the metric characteristics, distribution patterns, tooth size differences with Lufeng, Kaiyuan and other extant great apes have not been done. For this reason, present study will use statistical methods to deal with the metric data of Yuanmou hominoid teeth and discuss some problems of classification of Yuanmou hominoid.

1 Materials and methods

(i) Tooth specimens and measurement method. The teeth used in present study's measurement include all the tooth fossils found in the sites of Xiaohe, Zhupeng and Leilao since 1986. Only the teeth with nearly no wear and in good preservation were chosen for study. Altogether 1 266 teeth were measured. Because there are debates on the geological dates for the 3 sites and further research has not been done, plus the reason that present study is just a preliminary study to the hominoid teeth found in Yuanmou, the teeth found in the 3 sites were pooled. Table 1 lists some detailed information of the teeth

used in present study. Because of the damages of tooth roots in most specimens, only crown length (mesio-distal diameter-MD) and breadth (buccal-lingual diameter-BL) were measured. The measuring method described by Wolpoff[7] was used and all the data were read to 0.1 mm.

Table 1 The specimens used in present study

	I1	I2	C	P3	P4	M1	M2	M3	Total
Upper	82	44	75	73	94	118	137	83	706
Lower	32	44	62	53	84	92	115	78	560
Total	114	88	137	126	178	210	252	161	1 266

(ii) Data analysis methods. First, the basic statistics like means, standard deviations, ranges are calculated. Then, further analyses and discussions about the tooth size expression patterns of Yuanmou hominoids and their classification are made.

(1) Test of tooth size distribution patten

Histogram and normal curve: Use all the metric data of each teeth to draw a histogram with normal curve. From this histogram, we can figure out whether the Yuanmou hominoid tooth sizes have the distribution pattern of bimodalities or have two peaks distributed.

Bivariate plots: Put MD and BL data of each teeth on a two-dimensional plan to draw a bivariate plot, which will show if the Yuanmou hominoids can be divided into two groups according to their tooth sizes.

Factor analysis: Principal component analysis (PCA) is used to extract first principal component, which contains most of the variations for each variant. Then the factor scores of first principal component of each tooth is used to draw histograms and further test whether the bimodalities exist or not.

(2) Relationship of Yuanmou with extant great apes and the hominoids from Kaiyuan and Lufeng

Coefficients of variation-CV: By comparing the CVs of Yuanmou with those of Kaiyuan, Lufeng and extant great apes, we figure out whether the variations within the Yuanmou tooth sizes exceed the degree between two biological species.

Proportions of canine crown area with other teeth: From the crown area data of Yuanmou teeth, 6 canine proportions (C/I^{1+2}, C/P^{3+4}, C/M^{1+2+3}, C/I_{1+2}, C/P_{3+4}, C/M_{1+2+3}) are calculated and these proportions are used to compare with those of Kaiyuan, Lufeng and other extant great apes. From these comparisons, we can have some information about the degrees of similarities and differences of canine proportions of Yuanmou with Kaiyuan, Lufeng and other extant great apes.

Comparisons of tooth sizes: Simple line distributions of all upper or lower tooth sizes of Yuanmou, Kaiyuan and Lufeng are drawn, which will give us a general view of the tooth size differences among the three groups.

2 Results and analyses

(i) The basic statistics. Table 2 displays the basic statistics of the Yuanmou hominoid tooth metric data. Most of the fossil teeth used in present study have clear site and stratum information. Also, all the teeth have big amount (over 40) except for lower central incisor which have 29—30 teeth. So, we can get basically accurate information from the metric data of Yuanmou hominoid teeth. Viewed from the statistic distributions of table 2 for Yuanmou hominoid teeth, the varying ranges of both MD and BL of most Yuanmou tooth sizes are quite big, and in most cases BL>MD. In both upper and lower teeth, second molars have the biggest metric values, following with thir molars and first molars, that is M2>M3>M1. However, the size differences between M1 and M3 are not obvious. According to the distributions of standard deviation and ranges, the variations for individual tooth are great in upper and lower canines, third premolars, second molars and third molars. Among them, canines have the greatest variations.

(ii) The characteristics of Yuanmou hominoid tooth size distribution. Three statistic methods were used to display tooth size pattern for each tooth directly by figures.

Histograms: Histograms for each dimension for the 16 teeth in both upper and lower jaws were drawn. Among the 32 histograms, 17 out of which show obvious distributions of two peaks or

Table 2 The basic statistics of Yuanmou hominoid tooth sizes (in mm)

Teeth	MD				BL			
	means	SD	ranges	N	means	SD	ranges	N
				Upper teeth				
I1	9.2	0.88	7.1—11.6	79	8.2	0.94	5.3—10.8	81
I2	5.7	0.64	4.5—7.2	43	6.6	0.88	5.1—9.1	43
C	9.1	2.13	5.0—13.1	74	11.6	2.95	5.7—16.4	72
P3	7.5	0.77	6.0—8.9	71	10.4	1.08	7.5—12.8	70
P4	7.3	0.69	5.6—9.1	93	10.9	1.12	8.3—13.3	92
M1	9.8	0.71	7.6—11.4	110	11.1	0.90	8.5—14.1	118
M2	10.9	1.08	8.7—14.1	132	12.4	1.22	9.3—15.7	136
M3	9.8	1.04	7.7—12.3	82	11.4	1.26	7.0—14.3	83
				Lower teeth				
I1	5.4	0.86	4.3—7.9	29	6.4	1.09	4.6—9.9	30
I2	5.5	0.44	4.6—6.5	41	7.3	1.13	5.2—10.0	43
C	7.5	1.56	5.3—11.6	62	9.9	2.15	6.0—14.8	62
P3	7.3	0.86	5.5—8.9	50	11.1	1.52	6.4—13.8	52
P4	7.6	0.75	5.8—10.1	80	10.1	0.98	7.8—12.9	83
M1	10.5	0.94	8.4—12.6	88	9.3	0.95	7.0—11.6	90
M2	11.9	1.34	7.0—16.2	110	11.0	1.23	8.4—14.8	111
M3	12.0	1.45	8.7—15.3	75	10.9	1.28	8.3—13.8	78

bimodalities. Fig. 1 shows the histograms for MD and BL of upper canines. From fig. 1, both MD and BL in Yuanmou canines can be divided into two groups showing marked bimodalities and deviating normal curves. Compared with MD, BL has more obvious bimodalities with nearly no overlapping between two peaks. Except the 17 dimensions, the other 15 histograms do not show recognizable bimodalities and seem to have no distribution regularities.

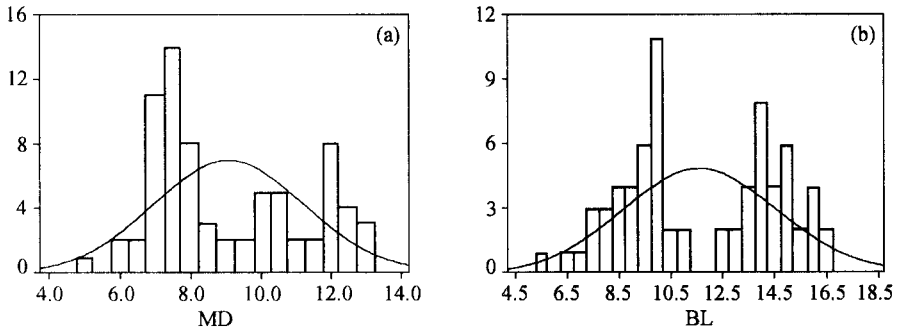

Fig. 1. Histograms of MD and BL of Yuanmou hominoid canines ((a) MD, (b) BL).

Scatter grams: 16 scatter grams were drawn based on MD and BL dimensions of each teeth. Among the 16 figures, 5 out of which show marked bimodalities with two groups separated and no obvious overlapping. There other 7 scatter grams display less obvious bimodalities. Fig. 2 still uses upper canines as an example to show the two-dimensional distribution of MD and BL of Yuanmou hominoid.

Factor analyses: To further study the extent of bimodalities of tooth sizes occurring on the Yuanmou hominoid and the role of different metric items, factor analysis was used to the Yuanmou dental metric data. Factor analysis is a multivariate statistic method, which studies the relationship among different variants and from the numerous variants choose a few variants as common factors. These new factors will keep most of the variation contained in the original variants. Also the methods will transfer the numerous original correlated variants to less numerous independent variants (factors). In the new common factors, the first factor will contain most of the variation information. In present study, we use factor analysis to put the variation information contained in MD and BL into a new variant (factor) and then draw histograms to see the tooth metric distributions. The results from the factor analyses of 16 teeth of Yuanmou hominoid show that the contribution rates of the first factors in

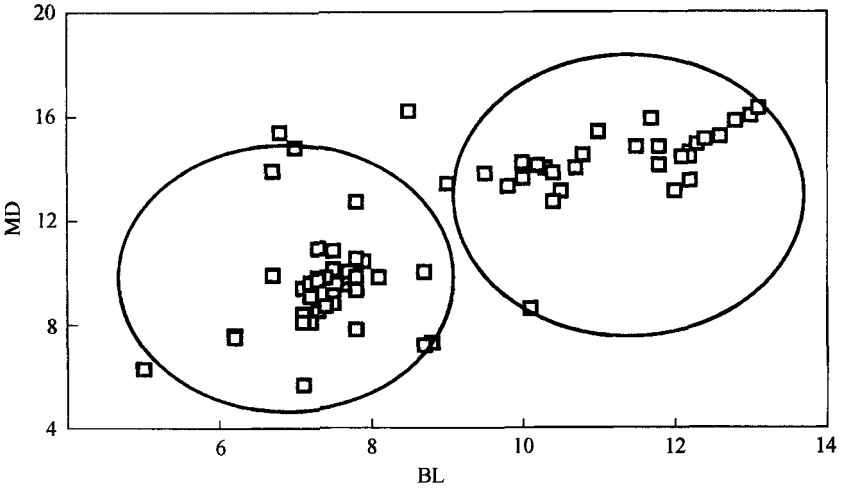

Fig. 2. The two-dimensional distribution of MD and BL of Yuanmou hominoid canines.

most factor analyses are over 80% (see table 3), indicating the results are reliable. Based on the factor analyses, 16 histogram were drawn by using the first factor scores, 10 of which show two obvious peaks or bimodalities patterns. This further supports that the tooth sizes of Yuanmou hominoid have marked differences and can be divided into two groups. Figs. 3 and 4 display the histograms of MD dimension and the first factor scores of MD and BL for lower central incisors respectively.

Table 3 The contribution rates of first factors in Yuanmou hominoid teeth

	I1	I2	C	P3	P4	M1	M2	M3
Upper	79.8	83.9	65.9	81.7	82.3	88.9	93.4	86.2
Lower	51.3	69.3	98.7	73.0	74.3	91.4	91.7	94.6

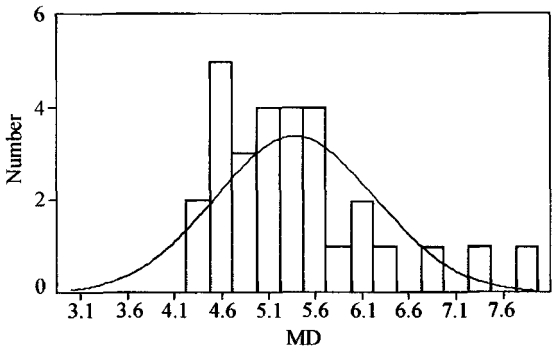

Fig. 3. Histograms of MD Yuanmou hominoid lower central incisors.

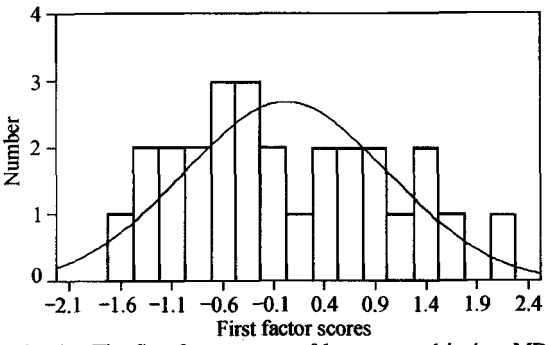

Fig. 4. The first factor scores of lower central incisor MD and BL of Yuanmou hominoid.

Because the first factors represent most part of variant information, analyzing the factor loads relative to the variants will offer the roles of different variants in the analyses. In present study, all 16 tooth crown BL dimensions have bigger factor loads, indicating that in the tooth size variations of Yuanmou hominoid, tooth crown BL dimensions play greater roles.

The results of factor analyes of present are given in table 4. From these results,we can find that the tooth size bimodalities are more obvious in upper and lower canines, upper and lower forth premolars, upper and lower second molars, and lower third molars. Among these teeth, upper and lower canines have the most marked bimodalities.

(iii) Coefficients of variations (CV). In the above analyes, by using direct comparisons of metric data, histograms, bivariate plots and factor analysis, we found that the tooth sizes of Yuanmou

Table 4 The occurrence of bimodalities in Yuanmou hominoid teeth

	Upper				Lower			
	histograms		scatter grams	factor analysis	histograms		scatter grams	factor analysis
	MD	BL	MD+BL	BD+BL	MD	BL	MD+BL	MB+BL
I1	–	–	–	–	–	–	–	+
I2	++	–	+	++	–	++	+	++
C	++	++	++	++	++	++	++	++
P3	++	++	++	++	++	+	+	++
P4	+	+	+	+	++	++	+	++
M1	–	+	–	+	+	–	+	+
M2	++	++	++	++	++	++	+	++
M3	–	–	–	+	++	++	++	++

++, Marked; +, occurring; –, no.

hominoid have great variation ranges. Most of the teeth have big and small two size types. However, whether these tooth size variations exceed the single species variation ranges like Kaiyuan, Lufeng and extant great apes is a question that should be clarified further. For this reason, we use coefficients of variations to compare the differences of the tooth size variation extent between Yuanmou hominoid and other fossil and extant great apes. Coefficients of variations are the percentages of standard deviation divided by sample means (CV=(s/X)×%), which can eliminate the effects caused by different scaling units or different means of two comparing samples. The CVs for each dimension of Yuanmou teeth were calculated and compared with those of other fossil and extant great apes(table 5). In the 32 CVs calculated from Yuanmou teeth, except for the high values of upper and lower canines, all CVs of Yuanmou teeth are within or close to the tooth size variation ranges of Lufeng and extant great apes. Because currently more and more colleagues believe that the Lufeng hominoid fossils found till now belong to single species[8, 9], the CV analyses from present study strongly suggest that the tooth size variations of Yuanmou hominoid may not reach the species variation ranges.

Table 5 Comparison of the coefficients of variations of Yuanmou hominoid teeth with those of other hominoids

	Yuanmou		Lufeng		Gorilla		Pan		Orangutan	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
					Upper					
I1	9.6	11.5	7.6	9.1	12.5	8.8	9.1	6.4	11.2	11.2
I2	11.2	13.3	10.4	11.0	12.9	11.5	11.5	7.6	11.3	12.9
C	23.4	25.4	17.3	18.4	20.9	21.3	14.4	13.8	16.0	17.3
P3	10.3	10.4	11.3	11.1	11.0	8.3	10.6	7.8	9.2	8.9
P4	9.5	10.3	8.8	9.5	8.4	7.6	8.6	6.5	10.7	9.0
M1	7.2	8.1	9.0	8.9	7.1	7.2	5.9	5.0	7.1	6.5
M2	9.9	9.8	9.9	9.8	8.3	7.6	6.7	5.7	10.2	8.3
M3	10.6	11.1	12.0	11.2	10.2	9.8	8.5	6.4	12.2	9.7
					Lower					
I1	15.9	17.0	8.0	11.6	15.9	12.8	10.8	5.9	11.7	9.7
I2	8.0	15.5	8.5	14.1	11.6	13.3	9.6	6.5	12.9	10.1
C	20.8	21.7	17.5	15.7	18.9	17.9	13.0	11.2	20.2	14.1
P3	11.8	13.7	15.0	15.1	12.1	15.3	10.3	13.2	10.5	13.8
P4	9.9	9.7	11.7	9.6	8.7	8.8	7.3	8.9	9.3	9.0
M1	9.0	10.2	9.2	10.4	7.2	7.8	6.0	5.4	6.9	7.1
M2	11.3	11.2	10.2	10.5	7.1	8.6	6.2	5.5	7.9	8.4
M3	12.1	11.7	9.7	10.3	8.3	10.5	7.4	6.4	9.7	10.0

Except Yuanmou hominoid, all CVs are cited from ref. [10].

(iv) Proportions of canine crown area with other teeth. In the studies of the relationship between Miocene hominoids with extant great apes and hominids, canines and their size proportions have been paid great attention, because both in fossil and extant hominoids, the size differences between canines and other teeth are much greater than those of human. So, the comparison of size proportions of canine with other teeth between different fossil and extant great apes will offer valuable information about sample classification. In present study, the crown areas of each teeth for Yuanmou tooth fossils were calculated and then the area size proportions of canines with incisors, premolars, and moalrs were

calcuated and compared with those of Lufeng, Kaiyuan and extant great apes. From the result of table 6, the canine crown area proporitons of Yuanmou are quite close to those of Kaiyuan and Lufeng, and much different from gorilla, chimpanzee, orangutan and extant great apes.

Table 6 The canine crown ares proportions of Yuanmou and other hominoids

Proportions	Yuanmou	Lufeng	Kaiyuan	Gorilla	Pan	Orangutan	*Homo*
C/I^{1+2}	0.95	0.93		1.29	0.84	0.79	0.72
C/P^{3+4}	0.68	0.65	0.58	0.67	0.88	0.54	0.38
C/M^{1+2+3}	0.30	0.26	0.25	0.31	0.40	0.30	0.13
C/I_{1+2}	1.04	0.84		0.98	0.74	0.69	0.70
C/P_{3+4}	0.49	0.42		0.74	0.90	0.71	0.40
C/M_{1+2+3}	0.21	0.18		0.35	0.42	0.36	0.14

(v) Tooth size comparisons of Yuanmou with Kaiyuan and Lufeng. Since the discovery of *Dryopithecus* teeth in Kaiyuan in 1956, the hominoid fossils have been found in Lufeng, Yuanmou and Baoshan of Yunnan Province. The phylogenetic positions and relationship between each other of these fossils have been the focus of researches and in dispute. In present study, simple line distributions of each tooth dimension for the three samples of Yuanmou, Kaiyuan and Lufeng were drawn (fig. 5). Fig. 5 indicates that the tooth sizes from the three sites are very close to each other. Among the three samples, Yuanmou and Kaiyuan are closer than each of them to Lufeng is. The tooth sizes of Lufeng are bigger than those of both Yuanmou and Kaiyuan.

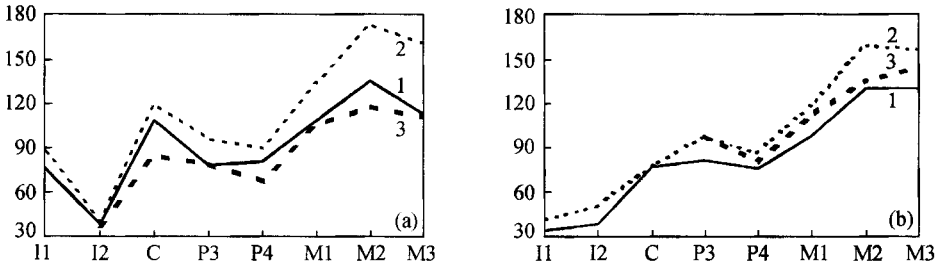

Fig. 5. Tooth crown areas of hominoids found in Yannan ((a) upper; (b) lower). 1, Yuanmou; 2, Lufeng; 3, Kaiyuan.

3 Discussion

(i) The tooth size pattern of Yuanmou hominoid. In the studies of early hominoid and fossil hominoids, especially the Miocene hominoids, one of the key problems, which is often in dispute, is: what reasons cause the morphological and metric differences of fossils from the same site, from the classification or just from the sexual dimorphism?[11]. In the early studies of Lufeng materials, the possibility of two species in the Lufeng fossils was proposed[12]. In later studies, most researchers gradually support the opinion that Lufeng hominoid fauna is composed of single biological species, with highly sexual dimorphism in morphology[13–17]. Wu[11] classified the Lufeng hominoid into the genus *Lufengpithecus*. During this study course of Lufeng fossils, the analyses of dental metric data played important roles. The studies of Lufeng tooth metric data show that Lufeng hominoids can be easily divided into two groups according to tooth sizes. Most of the tooth data display obvious bimodalities in histograms and scatter grams[9, 11]. However, this tooth size differences do not exceed the variation ranges of single species of extant great apes in CV analysis[10, 16]. So, the tooth size studies support the single species opinion for the Lufeng hominoid and further confirm that the teeth of Lufeng hominoid have highly sexual dimorphism.

In the studies of Yuanmou homionid fossils, some researchers noticed that the Yuanmou hominoid fossils can be divided into two types according to their size and morphology and proposed that the two types are similar to the male and female of Lufeng hominoids respectively. But seome differences still exist between the two types, which cannot be explained by sexual dimorphism and my represent two types of hominoids[6]. Based on the reliable provenance and enough sample size of Yuanmou hominoid teeth, present study of Yuanmou tooth metric data reveal that most of the tooth sizes have bimodalities

of two big and small size types and have great variation ranges. The further analyses of CVs indicate that the CVs of Yuanmou tooth sizes are all within or near the variation ranges of single species like Lufeng and extant great apes. So, present authors believe that metric data analyses of Yuanmou hominoid teeth support the single species opinion for Yuanmou hominoids.

Recently, Kelley and Plavcan used a new sexing method[18, 19] to do sex determination for the Lufeng hominoid canines attached in the mandibles. based on this sex determination, the lower molars on the same mandibles were divided into male and female groups, and histograms and bivaraiate plots were drawn. Their results again confirmed the teeth of *Lufengpithecus* have highly sexual dimorphism[9]. Although because of the sample limit, present study did not do sex determination to the Yuanmou teeth, the results of tooth metric analyses are quite similar to those of Kelley and other colleagues. Present authors believe that the two type's varaitions revealed from the tooth metric data analyses of Yuanmou hominoids are the reflection of sexual dimorphism indicating the hominoid fauna of Yuanmou is composed of morphologically highly sexual dimorphism individuals.

(ii) The relationship of Yuanmou hominoid with those of Kaiyuan and Lufeng. According to the results of canine crown area proportion comparisons of Yuanmou with Kaiyuan, Lufeng and extant great apes in table 6, the proportions of Yuanmou are close to Kaiyuan and Lufeng, and quite different with all extant great apes. This results indicate the Yuanmou hominoids are close to those of Lufeng and Kaiyuan in classification, and far from chimpanzee, gorilla and organgutan. Regarding the relationship of Yuanmou with Kaiyuan and Lufeng, the analyses of present study confirm the earlier results that Yuanmou hominoid fossils have shared more features with Kaiyuan than with Lufeng[6]. Putting all analyses results of present study into consideration, authors believe that the Miocene hominoid fauna living different sites of Yunnan Province may be close to each other in classification.

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References

1. Woo Jukang, Dryopithecus teeth from Keiyuan, Yunnan Province, Vertebr PalAsiatica (in Chinese), 1957, 1(1): 25.
2. Woo Jukang, New materials of *Dryopithecus* from Keiyuan, Yunnan, Vertebr PalAsiatica (in Chinese), 1958, 2(1): 38.
3. Wu Rukang, Han Defen, Xu Qinghua et al., *Ramapithecus skull* found first time in the world, Chinese Science Bulletin (in Chinese) 1981, 26(11): 1018.
4. Zhang Xingyong, New materials of *Ramapithecus* from Keiyuan, Yunnnn, Acta Anthropologica Sinica (in Chinese), 1987, 6(2): 81.
5. He Zhiqiang, Yuanmou Hominoid Fauna (in Chinese), Kunming: Yunnan Science Press, 1997, 1—270.
6. Zheng Liang, Zhang Xinyong, Hominoid fossils, Yuanmou Hominoid Fauna (in Chinese), Kunming: Yunnan Science Press, 1997, 21—58.
7. Wolpoff, M. H., Metric Trends in Hominid Dental Evolution, Cleveland: The Press of Case. Western Reserve University, 1971, 1—244.
8. Wu Rukang, A revision of the classification of the Lufeng great apes, Acta Anthropologica Sinica (in Chinese), 1987a, 6(4): 265.
9. Kelley, J., Plavcan, J. M., A simulation test of hominoid species number at Lufeng, China: implications for the use of the coefficient of variation in paleotaxonomy, J. Hum. Evol., 1998, 35: 577.
10. Wood, B. A., Xu, Q., Variation in the Lufeng dental remains, J. Hum. Evol., 1991. 20: 291.
11. Wu Rukang, The sexual dimorphosm of primates, Acta Anthropologica Sinica (in Chinese), 1987b, 6(3): 255.
12. Wu, R., Oxnard, C. E., Ramapithecines from China: evidence from tooth dimensions, Nature, 1983a. 306: 258.
13. Wu, R., Oxnard, C. E., *Ramapithecus* and *Sivapithecus* from China: some implications for higher primate evolution, Am. J. Primatol., 1983b. 5: 303.
14. Wu Rukang, Xu Qinghua, Lu Qingwu, Relationship between Lufeng *Sivapithecus* and *Ramapithecus* and their phylogenetic position, Acta Anthropologica Sinica (in Chinese), 1986, 5(1): 1.
15. Wu Rukang, Wang Linghong, Sexual dimorphism of fossil apes in Lufeng, Acta Anthropologica Sinica (in Chinese), 1987, 6(3): 169.
16. Kelley, J., Etler, D., Hominoid dental variability and species number at the late Miocene site of Lufeng, China, Am. J. Primatol., 1989, 18: 15.
17. Kelley, J., Xu, Q., Extreme sexual dimorphism in a Miocene Hominoid, Nature, 1991, 352: 151.
18. Kelley, J., Sexual dimorphism in canine shape among extant great apes, Am. J. Phys. Anthropol, 1995a, 96: 364.
19. Kelley, J. Sex determination in Miocene catarrhine primates, Am. J. Phys. Anthropol., 1995b, 96: 390.

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