Morphometric Analysis of Hominoid Lower Molars from Yuanmou of Yunnan Province, China

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ABSTRACT. Shape analyses of cross-sectional mandibular molar morphology, using Euclidean Distance Matrix Analysis, were performed on 79 late Miocene hominoid lower molars from Yuanmou of Yunnan Province, China. These molars were compared to samples of chimpanzee, gorilla, orangutan, *Lufengpithecus lufengensis, Sivapithecus, Australopithecus afarensis*, and human mandibular molars. Our results indicate that the cross-sectional shape of Yuanmou hominoid lower molars is more similar to the great apes than to humans. There are few differences between the Yuanmou, *L. lufengensis*, and *Sivapithecus* molars in cross-sectional morphology, demonstrating strong affinities between these three late Miocene hominoids. All three of the fossil samples show strong similarities to orangutans. From this, we conclude that these late Miocene hominoids are more closely related to orangutans than to either the African great apes or humans.

Key Words: Euclidean Distance Matrix Analysis; Hominoids; Miocene; *Lufengpithecus lufengensis*.

INTRODUCTION

Since 1986, excavations at several sites in Yuanmou County, Yunnan Province, China, have unearthed numerous fossil remains of a late Miocene hominoid, including a cranium, maxillae, mandibles, and over 1,000 isolated teeth (HE, 1997). Even though the geological age of Yuanmou hominoids is still in debate (QIAN, 1997; ZHENG & ZHANG, 1997), preliminary studies indicate that these fossils are similar to the hominoid fossils found in Lufeng County, Yunnan Province, currently classified as *Lufengpithecus lufengensis* (WU, 1987). Though the Yuanmou fossils resemble *L. lufengensis*, there are some differences between the two samples. Because of these differences, some researchers proposed that the Yuanmou hominoid represents a new species within the genus *Lufengpithecus* (ZHENG & ZHANG, 1997).

The few published studies of the Yuanmou hominoid are mostly morphological and metric descriptions of the fossils (ZHENG & ZHANG, 1997). The coefficients of variation (CV) of Yuanmou hominoid tooth sizes are within or close to the CV ranges of those of *L. lufengensis* and extant great apes. LIU et al. (2000) show that the Yuanmou hominoid dental metrics are bimodal, indicative of sexual dimorphism. Therefore, it can be safely surmised that the hominoid fossils found in Yuanmou over the past ten years represent a single species with high sexual dimorphism. The comparisons of tooth sizes and their proportions indicate that Yuanmou hominoids have closer affinities with the Chinese hominoid fossils from Lufeng and Kaiyuan, and are different from gorilla, chimpanzee, and orangutan. However, the degree of relatedness between the Yuanmou fossils and *Lufengpithecus* is unclear. Are they separate species, separate genera, or conspecific?

The relationship of both of these late Miocene hominoids to extant great apes is also a subject of controversy (HO, 1990; ZHENG & ZHANG, 1997; KELLEY & PLAVCAN, 1998; LIU et al., 2000). These fossils may be a common ancestor for both Afircan great apes and hominids (WU, 1987), related to orangutans (SCHWARTZ, 1990, 1997), or have close affinities to hominids (ZHENG & ZHANG, 1997). A recent microstructure study of *Lufengpithecus* teeth shows that the crown formation time of *L. lufengensis* is similar to that of *Australopithecus afarensis*, as the pattern of compactness of perikymata is similar to that of modern humans (ZHAO, 1998). Clearly, despite the considerable amount of research dedicated to answering this question, the phylogenetic position of *Lufengpithecus*, and consequently the Yuanmou fossil material, is still obscure.

Recently, Euclidean Distance Matrix Analysis (LELE, 1991, 1993; LELE & COLE, 1996; LELE & RICHTSMEIER, 1991, 1992, 1995) has been used to analyze cross-sectional mandibular molar morphology (HLUSKO, 1999, unpubl.). This research demonstrates the utility of molar cross-sectional analyses to our understanding of extant and fossil hominoid relationships. Unfortunately, the method is not ideal, since unworn molars must be used. However, the large number of teeth from Yuanmou makes them an appropriate sample for this type of analysis, as there are numerous unworn mandibular molars from this site.

In order to increase our understanding of the variation within and between late Miocene Asian hominoids, we used a new method of shape analysis to study the differences between the Yuanmou hominoid fossils and *L. lufengensis*. In light of the debate over the evolutionary relationships of these fossil hominoids to extant great apes, we then compared the Yuanmou hominoids to modern great apes, humans, and the extinct species *Sivapithecus* and *A. afarensis*.

MATERIALS AND METHODS

The sample of Yuanmou hominoids consists of unworn or hardly worn (such that the position of the cusp tips is clear) lower first, second, and third molars ($N = 79$, see Table 1). All these teeth are housed at the Yunnan Provincial Institute of Archaeology, Kunming. The comparative samples are listed in Table 2. Table 3 shows the composition of the samples used in the following analyses.

The determinations of first, second, and third molars were made on the basis of the interstitial wear facets. Because the mesial side of first molars is in contact with the second deciduous molar and later, the permanent fourth premolar, the mesial side of first molar typically has two wear facets. Second molars only have one proximal wear facet. Third molars also have only one proximal wear facet and are lacking a distal facet. This method for determining first, second, and third molars is not new, as it was first introduced by HOOIJER (1948) and more recently used by GROESBEEK (1996).

Molds of the mesial side of casts of all mandibular molars were made with Coltène President© putty. Using a scalpel and microscope, these molds were sliced directly through the tips of the two cusps (protoconid and metaconid) and prepared so as to clearly outline the shape of the tooth crown at this position. This coronal slice was always made through the tips of the protoconid and metaconid, though this section is not always directly perpendicular to the mesiodistal axis of the tooth. A digital camera and Optimas© software were used to capture the outlines of the tooth crowns. Cross-sections were imaged so that the buccal surface is always to the right. Following LELE and RICHTSMEIER (1991, 1992), X and Y coordinates were recorded for seven landmarks (Fig. 1), with the origin consistently placed at the lingual cervix and the X-axis running horizontally through the buccal cervix. The seven landmarks are lingual cervix,

Table 1. The Yuanmou hominoid lower molars used in the present study.

M1(*N*=15)	M2(*N*=40)		M3(*N*=24)
F 4.40	B 3.12	YV 1634	B 3.9
PDYA 0009	F .24	YV 1691	F 4.32
PDYA 0011	F 4.35	YV 1693	F 4.60
PDYA 0030	F 4.61	YV 1697	PDYA 0003
YV 1422	F .5	YV 1783	PDYA 0013
YV 1593	F .8	YV 1832	PDYA 0035
YV 1690	F .83	YV 1865	YV 1354
YV 1845	PDYA 0006	YV 1913	YV 1417
YV 1883	PDYA 0008	YV 2130	YV 1520
YV 1945	PDYA 0010	YV 2143	YV 1535
YV 2010	PDYA 0012	YV 2151	YV 1550
YV 2129	PDYA 0015	YV 2331	YV 1571
YV 2169	PDYA 0020	YV 2505	YV 1657
YV 2511	YV 1316	YV 2507	YV 1678
No number	YV 1317	YV 2514	YV 1696
	YV 1341	YV 2588	YV 1794
	YV 1368		YV 1926
	YV 1371		YV 1929
	YV 1381		YV 1975
	YV 1388		YV 1981
	YV 1393		YV 2056
	YV 1395		YV 2077
	YV 1403		YV 2144
	YV 1616		YV 2512

Table 2. The comparative samples used in the present study.

Comparative sample	*N*	Source
Yuanmou	79	Yunnan Provincial Institute of Archaeology, Kunming
Lufengpithecus lufengensis	6	Yunnan Provincial Institute of Archaeology, Kunming
Sivapithecus	29	Department of Anthropology, The Pennsylvania State University
Gorilla gorilla	30	National Museum of Natural History Smithsonian Institution and The Cleveland Museum of Natural History
Pan troglodytes	34	National Museum of Natural History Smithsonian Institution and The Cleveland Museum of Natural History
Pongo pygmaeus	52	National Museum of Natural History Smithsonian Institution and Field Museum of Natural History
Homo sapiens	26	Terry Collection, National Museum of Natural History Smithsonian Institution
Australopithecus afarensis	7	Casts of AL128-23, AL333-145-35, AL333w-1, AL333-48,L26-1g, Omo212-1950, and W7-508

Table 3. The sample compositions for the present study.

	Yuanmou	Lufeng	Gorilla	Chimpanzee	*Sivapithecus*	Orangutan	*A. afarensis*	Human
M_1	15	2	8	20	8	20	3	7
M_2	40	3	22	14	11	19	4	19
M_3	24	1	0	0	10	13	0	0
Total	79	6	30	34	29	52	7	26

midpoint of lingual side, tip of metaconid, central groove, tip of protoconid, midpoint of buccal side, and buccal cervix. All coordinates were taken three times for each specimen and averaged. See Figure 2 for plots of the coordinates.

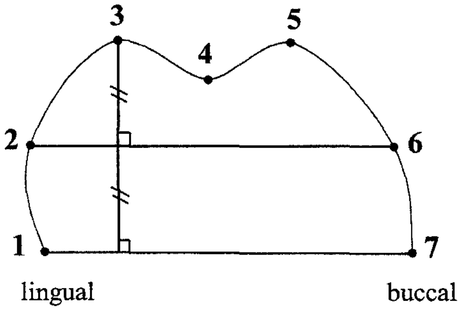

Fig. 1. This figure shows the seven landmarks used in this analysis. 1: Lingual cervix; 2: midpoint of lingual side; 3: metaconid cusp tip; 4: deepest point of occlusal basin; 5: protoconid cusp tip; 6: midpoint of buccal side; 7: buccal cervix.

Analyses were done using samples of first, second, or third molars, and also using pooled samples of all molars for each taxa. When species were compared to each other, we found that inter-taxonomical comparisons outweighed any differences that are identifiable as metameric variation. Therefore, we weigh our conclusions most heavily on those comparisons between taxa in which first, second, and third molars are pooled.

The program SHAPE Version 1.0 for EDMA written by COLE (COLE & RICHTSMEIER, 1998) was used to analyze the data. This method creates matrices of distances between all possible pairs of landmarks for each specimen and then for each sample. These matrices are called form matrices. The mean form matrix of each sample is scaled using its geometric mean, removing the effects of size from the analysis of shape. A mean shape difference matrix is produced by comparing two mean form matrices. The differences between the two matrices are iterated 100 times and confidence intervals calculated. A significance level of 0.1 was used in the following analyses (as per LELE & COLE, 1996).

Results from this type of analysis are difficult to display visually. COLE and RICHTSMEIER (1998) have suggested some methods. Our results here are shown on a hypothetical tooth outline. We chose to use the mean shape form for chimpanzee molars as our hypothetical tooth for all taxa, as this allowed all interlandmark distances to be seen most easily when drawn on the figure. This is for illustrative purposes only, and does not imply that all molars look the same, or that they look like chimpanzee molars, rather it is to convey to the reader, in a visual manner, the nature of the significant differences we found using EDMA.

RESULTS

Yuanmou vs *L. lufengensis*: The Yuanmou sample was compared with six molars of *Lufengpithecus lufengensis*. Both samples included first, second, and third molars. Only four significant differences were found (Fig. 3). In this figure, the solid lines represent those distances that are greater in the first sample than in the second sample, whereas the dotted lines represent those distances that are greater in the second sample than in the first. These differences indicate that the metaconids of *L. lufengensis* molars are taller than are those of the Yuanmou molars. Also, the buccal side of the Yuanmou molars is more flared than is seen in the *L. lufengensis* sample. These differences are relatively few, compared with the results found in

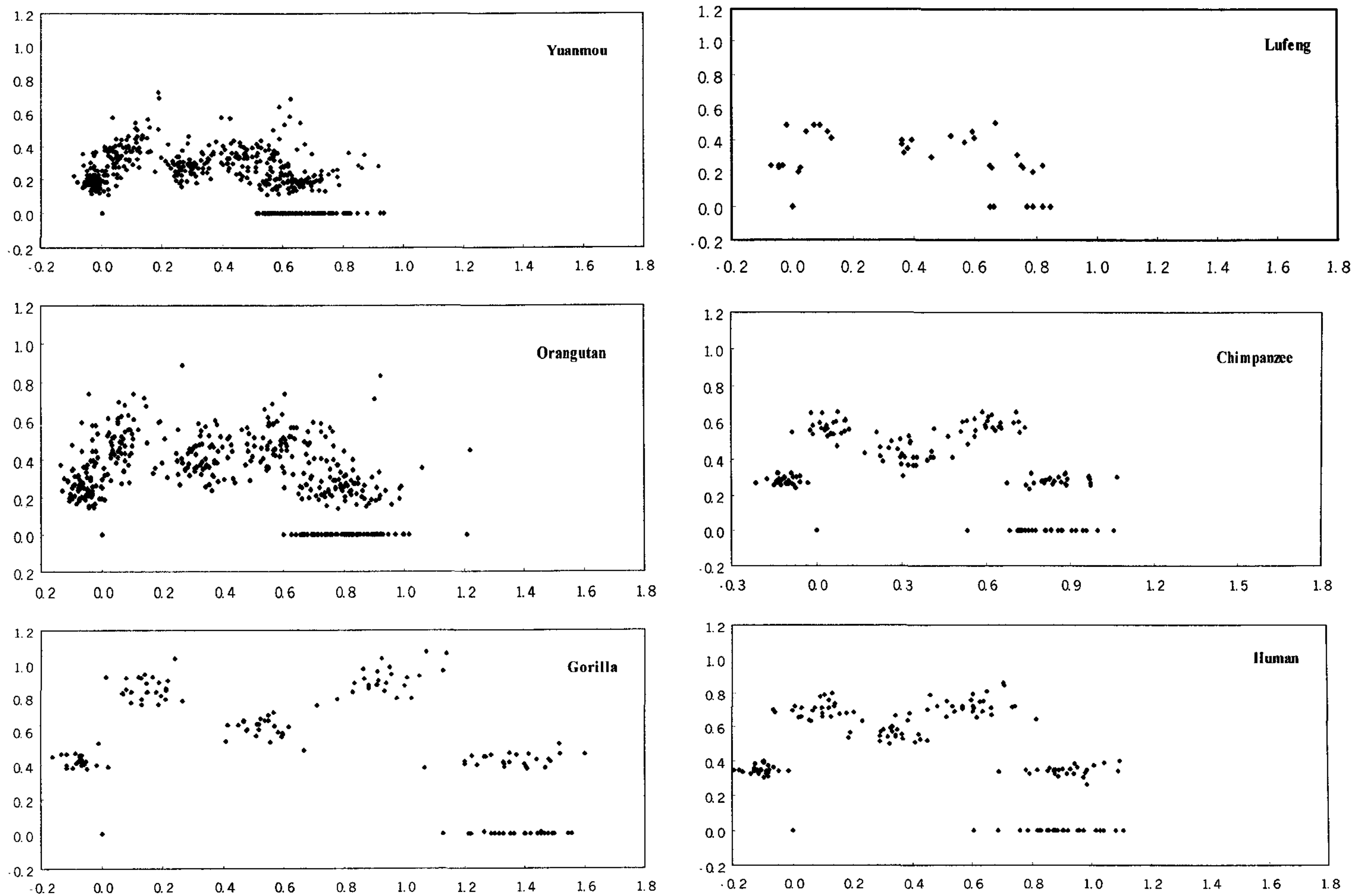

Fig. 2. X,Y coordinates for all molar samples used in these analyses are displayed here. First, second, and third molar data are pooled on each graph. Scale is in centimeters.

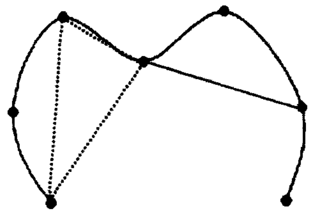

Fig. 3. This figure shows those distances found to be significantly different between the Yuanmou hominoids and *L. lufengpithecus*. Solid lines represent those distances that are farther in the Yuanmou sample. Dotted lines represent distances that are farther in the *L. lufengpithecus* sample. Significance level = 0.10.

other analyses, and may represent geographical or temporal distance between the two samples rather than species-level differences. Since the *L. lufengensis* sample size is quite small, we are hesitant to designate these four differences as species-level variation, and interpret them to be a consequence of either small sample size (for *L. lufengensis*) or geographical/temporal variation within a single species.

Our results suggest that there are significant differences in shape between the large and small teeth within the Yuanmou sample. Smaller molars have greater distances between the lingual and buccal cervices and distances between landmarks on the buccal cusp are relatively farther apart. However, the criterion for designating a tooth big or small was done using buccolingual distance. Therefore, we may have artificially introduced bias into our samples. At present, given the results from previous studies noting a large amount of sexual dimorphism in the population (LIU et al., 2000), we interpret these shape differences to be intraspecific variation, either between the sexes, allometric, or temporal, and not indicative of species or sub-species level variation.

Yuanmou vs Orangutans: In Figure 4, the pair-wise cross-sectional comparisons of molars of the Yuanmou hominoid with chimpanzee, gorilla, orangutan, and human are shown. Compared with the differences between the teeth of Yuanmou and those of the African living great apes, fewer morphological differences are found between Yuanmou hominoid lower molars and orangutan lower molars. There are only two differences between lower first molars of the Yuanmou hominoid and orangutans. Yuanmou lower first molars have wider buccolingual cervical distances than do orangutan first molars. The buccal sides of orangutans are more flared than those of Yuanmou first molars.

There are five differences between the Yuanmou hominoid and orangutan lower second molars. These differences indicate that Yuanmou second molars have wider mesial foveae and buccolingual cervical distances while the buccal sides of orangutan lower second molars are more flared with taller buccal cusps than those of Yuanmou hominoid. The comparisons of the third molars also show the pattern in differences that is like that seen when first and second molars are compared. The two differences between lower third molars of the two samples demonstrate a wider cervical distance in Yuanmou than in orangutan, and orangutans have a more flaring buccal side.

Yuanmou vs Gorillas: Referring to Figure 4, there are four significant differences between Yuanmou first molars and gorilla first molars. The cusp tips are farther apart in Yuanmou than

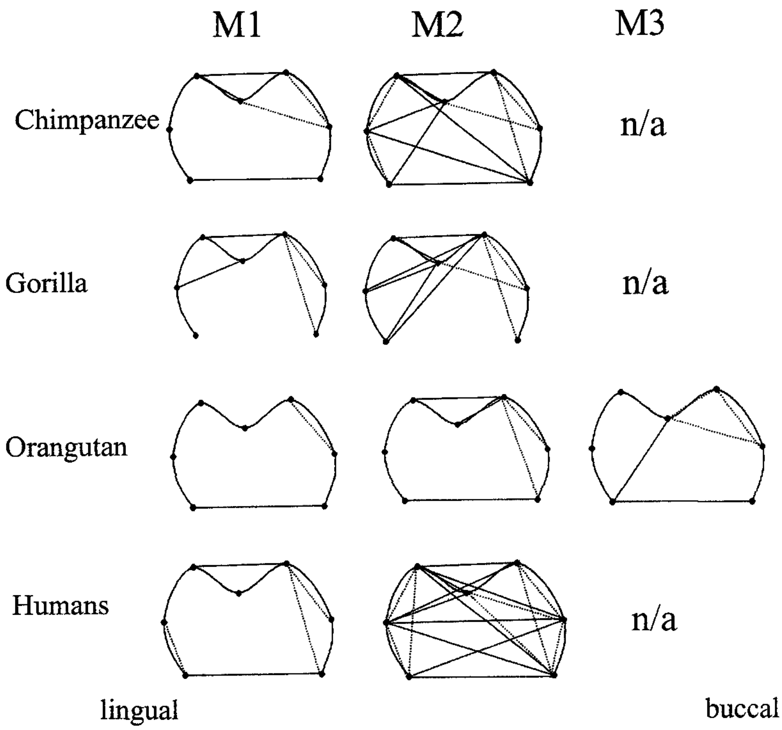

Fig. 4. In this figure, the Yuanmou hominoid molars are compared to the extant taxa, showing differences as they vary between first, second, and third mandibular molar cross-sectional morphology. Solid lines represent distances that are greater in the Yuanmou sample. Dotted lines represent those distances greater in the comparative samples. Third molar comparisons were not available for chimpanzee, gorilla, and human samples. Significance level = 0.10.

in gorillas. Also, the Yuanmou lingual sides are more flared than are those of gorilla. However, gorilla first molar buccal sides are more flared and their buccal cusps are taller than Yuanmou first molars.

There are nine differences between the second molars of these two samples that can be summarized into four main points: (1) the intercusp tip distances are farther apart in Yuanmou than in gorilla; (2) the lingual sides of Yuanmou second molars are more expanded than those of gorilla; (3) the buccal sides of gorilla second molars are more flared; and (4) the buccal cusps of gorilla are taller than Yuanmou second molars.

Yuanmou vs Chimpanzees: Again referring to Figure 4, five significant differences are found between the Yuanmou hominoid and chimpanzee first molars. These differences indicate that the first molars of the Yuanmou hominoid have a greater distance between the metaconid and protoconid tips, or rather, their cusp tips are farther apart than are those of chimpanzees. We also find that Yuanmou hominoid first molars have larger cervical distances than do chimpanzees. The buccal sides of chimpanzees first molars are more flared.

There are 12 differences in cross-sectional shape between Yuanmou hominoid second molars and chimpanzee second molars. The main differences indicate that: (1) the Yuanmou second molars have greater inter cusp tip distance and buccolingual cervical distance than do chimpanzee second molars, indicating that the mesial cusp tips and cervical landmarks of Yuanmou second molars are farther apart than those of chimpanzees; (2) both lingual and buccal sides of chimpanzee second molars are more expanded than are those of the Yuanmou hominoid second molars, though Yuanmou second molars are shifted lingually; and (3) chimpanzee second molars have taller cusps on the buccal side than do Yuanmou second molars. In summary, Yuanmou molars appear more "squat" compared to chimpanzees.

Yuanmou vs Humans: As seen in Figure 4, five significant differences are found between Yuanmou hominoid and human first molars. These differences indicate that both intercusp tip distances and the distance between the two cervical landmarks are greater in Yuanmou hominoid first molars than in humans. Both lingual and buccal sides of human first molars are more flared than those of the Yuanmou hominoid first molars. The buccal cusps of human first molars are also taller than those of the Yuanmou hominoid.

When Yuanmou and human second molars are compared, significant differences are found between almost all possible pair-wise distances. Even at the alpha level of 0.01, 19 of the 21 distances are found to be significantly different. The general pattern within these differences are summarized as follows: (1) all distances lying in a horizontal plane are found to be greater in Yuanmou when compared to humans, giving Yuanmou second molars a flatter look; (2) both the lingual and buccal sides of human second molars are more expanded than those of Yuanmou hominoid second molars; and (3) the two cusp tips are taller in humans than in Yuanmou hominoid second molars.

Yuanmou vs *Sivapithecus*: We also compared the Yuanmou molar sample to 29 molars of the Siwaliks fossil *Sivapithecus*. There are remarkably few differences in mandibular molar cross-sectional shape between these two taxa (see Fig. 5). Only two significant differences were found. The first difference is that the Yuanmou molars have more open occlusal foveae than do *Sivapithecus*. Second, the Yuanmou molars have a greater relative distance between the lingual cusp and the deepest point of the occlusal surface. This suggests that the metaconid is larger in the Yuanmou sample than in the *Sivapithecus* sample. These two differences are similar to those found when Yuanmou is compared to the African great apes, humans, and *A. afarensis*, though the greater inter-cusp tip distance is the same as is found when Yuanmou is compared to orangutans.

Yuanmou vs *A. afarensis*: Given the arguments of ZHENG and ZHANG (1997), we decided to compare the shapes of these two taxa. There are 11 differences found between samples consisting of both first and second molars of Yuanmou hominoid and *A. afarensis* (Fig. 5). The main differences are as follows: (1) the mesial cusp tips of Yuanmou lower molars are farther apart than those of *A. afarensis* indicating the wider mesial fovea of Yuanmou lower molars; (2) compared to the Yuanmou lower molars, the buccal sides of *A. afarensis* lower molars are more expanded and their lingual sides are more flared; and (3) both mesial cusps of *A. afarensis* lower molars are taller than those of Yuanmou lower molars. All of these are similar to the differences found between Yuanmou and the other samples, with the number of significant differences (11) being most similar to the number of differences found between Yuanmou and gorilla (12).

DISCUSSION

Given the few differences found between the Yuanmou and *L. lufengensis* samples, we inter-

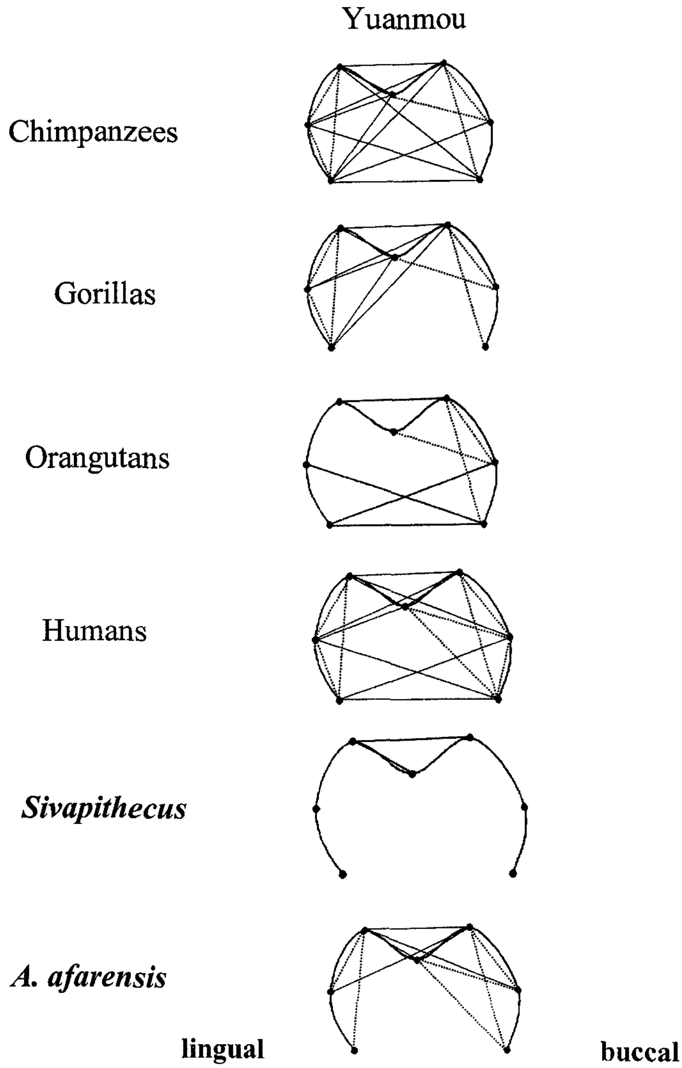

Fig. 5. This figure displays the comparisons between Yuanmou and the comparative samples. Solid lines represent those distances that are greater in the Yuanmou sample. Dotted lines represent those distances greater in the comparative samples. Significance level = 0.10.

pret them to support the close relationship, as suggested by Liu et al. (2000) and Zheng and Zhang (1997). Further analyses will be needed to demonstrate whether they are conspecific, and the differences found here represent merely geographical or temporal variation at a subspecific level, or if they represent closely related but separate taxa.

Within the great apes, the Yuanmou hominoids are found to be most similar to orangutans. The *L. lufengensis* sample, though small, demonstrates similar differences to the orangutan sample as do the Yuanmou hominoids. However, the number of differences is not as low for the *L. lufengensis* sample. In light of the strong similarities between Yuanmou and *L. lufengensis*, we interpret the larger number of differences between *L. lufengensis* and orangutans to result from the small sample size for *L. lufengensis* and not indicative of a more distant phylogenetic relationship between *L. lufengensis* and orangutans compared to that of the Yuanmou hominoids and orangutans.

Much research has been undertaken to investigate the numerous Miocene hominoid fossils found in Asia. However the geographical origins, dispersal patterns, and evolutionary histories of Asian Miocene hominoids is still unclear. The commonly held scenario of great ape evolution proposes that the Asian apes migrated out of Africa 15 myr ago and evolved separately from the African great apes (ANDREWS, 1992). Recently, an analysis of molecular, fossil, and biogeographical data by STEWART and DISOTELL (1998) provides a new scenario for the evolution of hominoids. They proposed that the lineage leading to the living hominoids dispersed out of Africa about 20 million years ago and the common ancestor of living African apes, including humans, migrated back into Africa from Eurasia within the past 10 million years. According to either scenario, late Miocene hominoids of Yuanmou and Lufeng could be ancestral to orangutans. Our lower molar morphological comparisons reveal the strong similarities of both Yuanmou hominoid and *Lufengpithecus* with orangutan, supporting the idea that they may belong to the same clade as orangutans.

Previous studies of *Sivapithecus* reveal strong morphological similarities between these Siwalik fossils and orangutans (ANDREWS & CRONIN, 1982; WARD & KIMBEL, 1983; WARD & BROWN, 1986). Based on these findings, some colleagues believe that *Sivapithecus* represents a sister taxon to modern orangutans and propose a *Sivapithecus-Pongo* clade. *Sivapithecus* may represent the South Asian hominoid radiation from which *Pongo* evolved (WARD, 1997). However, other researchers hold a different opinion (PILBEAM, 1996; ANDREWS & PILBEAM, 1996). They find *Sivapithecus* to have many features that are not shared with modern orangutans at all.

We compared 29 *Sivapithecus* lower molars to those of orangutans. Figure 6 shows the results of this comparison. There are ten significant differences between *Sivapithecus* and modern orangutans when pooled samples of first, second, and third molars are compared. The lingual cusps are taller in *Sivapithecus* than in orangutans, while the buccal cusps are taller in orangutans than in *Sivapithecus*. In contrast, the buccolingual width and expansion of the buccal cusp from the lingual cervical landmark is greater in the fossil sample compared to orangutans.

Referring to the comparisons between the Yuanmou hominoid and orangutans in Figures 4 and 5, fewer significant differences were found between Yuanmou hominoid and orangutans than between *S. sivalensis* and orangutans. Also, it should be noted that by comparing Figures 4 and 5 with Figure 6, nearly all the differences between Yuanmou and orangutan lower molars are also found in the differences between *Sivapithecus* and orangutans. This suggests that *S.*

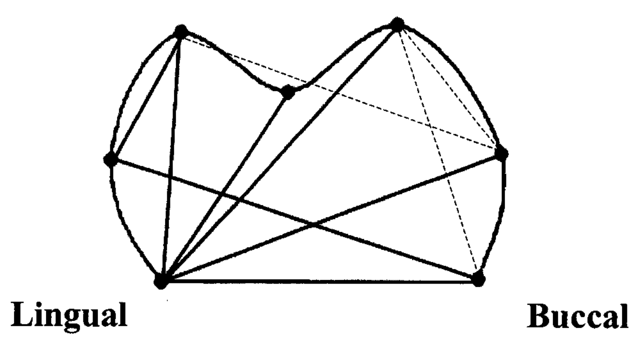

Fig. 6. This figure shows the significant differences between *S. sivalensis* and orangutans for samples consisting of first, second, and third molars. Solid lines represent those distances that are farther in the orangutan sample. Dotted lines represent distances that are farther in the *S. sivalensis* sample. Significance level = 0.10.

sivalensis, the Yuanmou hominoid, and orangutans share many dental morphological features, further demonstrated by the few significant differences found when the Yuanmou sample is compared to *S. sivalensis* (Fig. 5). More research is needed to determine if these shared features are primitive or derived. However, the results presented here suggest that the Yuanmou hominoids more closely resemble orangutans in lower molar morphology than does *S. sivalensis*. The authors believe that these results suggest a closer phenetic, and possibly evolutionary relationship between the Yuanmou hominoid and orangutans than between *S. sivalensis* and orangutans.

CONCLUSION

Results from our Euclidean Distance Matrix Analysis of mandibular molar cross-sectional shape show that there are strong similarities between the Yuanmou hominoids and *Lufengpithecus*. This supports previous findings based on dental metric data (LIU et al., 2000) and cranial morphological studies (ZHENG & ZHANG, 1997). However, some differences are noted between the two samples. Whether or not these differences are caused merely by small sample size is not clear, as only a few *L. lufengensis* molars were available for this analysis. If further analyses demonstrate that the differences are significant, the question then remains as to whether they represent subspecific or a higher taxonomic level of variation. Because of the geographical and temporal proximity of the Yuanmou hominoid and *Lufengpithecus*, it would not be surprising if these two Miocene hominoids have very close evolutionary affinities.

The Yuanmou hominoids are found to be quite similar to modern orangutans in their cross-sectional molar morphology. This result indicates the close relationship between the Asian Miocene hominoid and orangutan, when compared to the African great apes. Our analyses show that these new Asian late Miocene hominoids show strong similarities to modern orangutans, even more than does *Sivapithecus*, and consequently may belong to the same clade as later Asian great apes.

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