

## Comparative Study of Crown Cusp Areas in the Upper and Lower Molars of African Apes\*

By

**Hirofumi MATSUMURA<sup>1)</sup>, Masato NAKATSUKASA<sup>2)</sup>  
and Hidemi ISHIDA<sup>3)</sup>**

<sup>1)</sup>Department of Anthropology, National Science Museum, Tokyo

<sup>2)</sup>Department of Anatomy, Osaka Medical College, Osaka

<sup>3)</sup>Laboratory of Physical Anthropology, Faculty of Science, Kyoto University, Kyoto

**Abstract** Characteristics of the upper and lower molar series in terms of crown cusp areas were described for *Pan* and *Gorilla*, and then affinities between these African apes and living and fossil hominids were discussed. The conclusions are summarized as follows. 1) intraspecific comparisons indicate that the area variability within the distal cusps tends to be larger than those within the mesial cusps. 2) the relative cusp areas of  $M_1$  display a marked interspecific variation among the apes and hominids compared. 3) the interspecific variation of  $M_1$  can not be explained from allometric or phylogenetic factors, but may be affected by environmental ones such as diet. 4) as for *Pan*'s  $M_1$ , the close resemblance to its  $M_2$  implies that *Pan*'s  $M_1$  has a more primitive pattern of the relative cusp areas than other hominoids'  $M_1$ .

### Introduction

Occlusal surfaces of the hominoid teeth consist of the four principal cusps in the upper molar series and of the five cusps in the lower molar series (Fig. 1). The measurements of the crown cusps for determine the taxonomic and evolutionary relationships of the hominoid species have attracted considerable attentions. ERDBRINK (1965, 1967) first applied the quantitative method to the crown cusp patterns with the aim to reveal the relationships with the fissure patterns in the human lower molars. As for fossil materials, WOOD *et al.* (1983) examined the relative cusp areas of the lower molars in the Plio-Pleistocene hominids, and found the distinctive characteristics of the early hominid taxa. For the upper molars, HANIHARA *et al.* (1970) attempted to measure and compare the relative hypocone areas in the humans including some fossil series. HILLS *et al.* (1983) and KANAZAWA *et al.* (1985) examined the allometry in the cusp areas of the lower molars of several hominoid species.

With regard to the great apes, the previous descriptions and comparisons of the cusp areas were mainly restricted within the lower first molar. The first aim of the

\* Part of this study was preliminarily presented at the XIII th congress of the International Primatological Society, held in Nagoya and Kyoto, 18-24 July 1990, (MATSUMURA, NAKATSUKASA and ISHIDA, 1991)

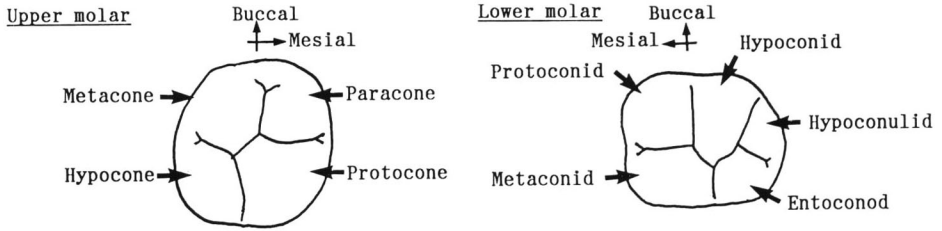


Fig. 1. Principal cusps of the hominoid right molars.

present article is to give comprehensive descriptions of the principal cusp areas in the upper and lower molar series of *Pan troglodytes* and *Gorilla gorilla*. The second one is to reveal the affinities of the patterns in the relative cusp areas between the African apes and hominid species including fossil humans.

### Materials

The materials used in the present study were plaster casts of the right side molars of *Pan troglodytes* and *Gorilla gorilla*, taken from the skeletal samples housed in the Department of Mammalogy of the C. R. S. N. in Zaire and the Department of Mammalogy of the American Museum of Natural History in the U. S. A.. When the right side was inappropriate for examination, then a cast from the left side teeth was used as substitute.

The data of Plio-Pleistocene fossil hominids were quoted from HANIHARA *et al.* (1970), WOOD and ABBOTT (1983) and WOOD *et al.* (1983). The data of the modern *Homo sapiens* were provided by the present study. They were taken from the skeletal series of the Japanese which are kept in the Department of Prehistory and Anthropology of the University Museum of the University of Tokyo in Japan.

### Methods

To take occlusal photographs for measuring cusp areas, the tooth cast was positioned in the standard plane where its cervical line was perpendicular to the optical axis of the lens. The occlusal pictures were taken with a single-lens reflex camera with bellows focusing attachment and lens ( $f=105$  mm). The photograph was enlarged to five times normal size, then the cusp boundaries were traced on the digitizer (0.1 mm of accuracy) and each cusp area was computed. The cusp area included marginal ridge and other accessory formations. When a sixth or seventh cusp was present in the lower molars, the accessory cusp was divided into halves and added to the neighboring cusps after WOOD *et al.* (1983). The absolute and relative cusp areas to the total cusp area were calculated for each molar.

The data obtained from both sex were combined and analyzed in the following

steps with several statistical methods. Firstly, in order to recognize the general trends of variation in the molar cusp areas of the two African apes, the area variability within each cusp was determined and compared between different kinds of cusp for each molar. In addition, the allometric trend of cusp area with crown area was also examined. Secondly, the relative cusp areas were compared within the African apes. Lastly, on the basis of the relative cusp areas, affinities between these African apes and the living and fossil hominids were examined. Then, the similarities between  $M_1$  and  $M_2$  were also compared between the different species.

## Results

### *Variation of cusp areas within each cusp of African apes*

The basic statistics of the absolute cusp areas of the upper and lower molars in *Pan* and *Gorilla* are given in Table 1. Table 2 shows the relative cusp areas of them. In order to recognize the general trend of variability in each cusp area, coefficients of variation ( $CV=100 \times S. D./Mean$ ) were calculated for the absolute and relative cusp areas. They are diagrammed in Fig. 2. In the upper molars, the variability of cusp area tends to be greater in either metacone or hypocone of distal cusps than in the two mesial cusps. In the lower molars, a rather conspicuous uniformity is recognized between the first and second molars, as well as between the two species, namely both of the entoconid and hypoconulid of distal cusps show greater variability than

Table 1. Absolute cusp areas in the upper and lower molars of two African apes.

Tooth	Cusp	<i>Pan troglodytes</i>				<i>Gorilla gorilla</i>			
		N	M (mm <sup>2</sup> )	SD	CV	N	M (mm <sup>2</sup> )	SD	CV
$M^1$	Paracone	22	38.0	5.3	13.9	26	44.6	4.5	10.3
	Protocone	22	47.6	7.1	14.7	26	64.7	8.2	12.7
	Metacone	22	35.7	5.2	14.6	26	45.4	5.5	12.0
	Hypocone	22	37.9	6.0	15.9	26	44.7	6.3	14.1
$M^2$	Paracone	18	39.7	5.1	12.8	26	53.4	7.2	13.5
	Protocone	18	56.4	7.1	12.7	26	76.3	10.1	13.2
	Metacone	18	35.1	6.5	18.7	26	46.7	7.3	15.7
	Hypocone	18	38.1	4.8	12.7	26	52.6	8.5	16.3
$M_1$	Protoconid	20	33.9	3.4	10.2	25	48.1	6.7	13.9
	Metaconid	20	36.1	4.2	11.6	25	43.9	5.7	13.0
	Hypoconid	20	31.0	3.7	11.9	25	42.2	4.9	11.6
	Entoconid	20	29.5	4.9	16.8	25	27.7	5.0	18.1
	Hypoconulid	20	21.2	2.7	12.9	25	27.0	4.3	15.9
$M_2$	Protoconid	14	39.5	5.5	13.9	23	60.3	7.0	11.6
	Metaconid	14	40.3	5.2	12.9	23	56.9	7.7	13.5
	Hypoconid	14	32.1	4.1	12.9	23	49.6	4.7	9.6
	Entoconid	14	31.1	4.8	15.4	23	37.4	6.8	18.2
	Hypoconulid	14	25.1	5.3	21.1	23	39.5	6.5	16.5

Table 2. Relative cusp areas in the upper and lower molars of two African apes.

Tooth	Cusp	<i>Pan troglodytes</i>			<i>Gorilla gorilla</i>		
		Mean	SD	CV	Mean	SD	CV
M <sup>1</sup>	Paracone	0.239	0.027	11.2	0.224	0.017	7.6
	Protocone	0.299	0.031	10.4	0.324	0.025	7.7
	Metacone	0.224	0.022	9.8	0.228	0.018	7.9
	Hypocone	0.238	0.030	12.7	0.224	0.021	9.4
M <sup>2</sup>	Paracone	0.235	0.023	9.8	0.233	0.023	9.9
	Porotocone	0.334	0.033	9.9	0.333	0.023	6.9
	Metacone	0.206	0.028	13.6	0.304	0.019	9.3
	Hypocone	0.225	0.019	8.4	0.230	0.021	9.2
M <sub>1</sub>	Protoconid	0.224	0.014	6.3	0.255	0.022	8.7
	Metaconid	0.238	0.016	6.7	0.232	0.024	10.3
	Hypoconid	0.204	0.017	8.3	0.223	0.021	9.4
	Entoconid	0.194	0.023	11.9	0.147	0.019	12.9
	Hypoconulid	0.140	0.015	10.7	0.143	0.018	12.6
M <sub>2</sub>	Protoconid	0.235	0.021	8.9	0.247	0.016	6.5
	Metaconid	0.240	0.018	7.5	0.234	0.017	7.3
	Hypoconid	0.191	0.018	9.4	0.204	0.010	4.9
	Entoconid	0.185	0.017	9.2	0.153	0.020	13.1
	Hypoconulid	0.149	0.021	14.1	0.162	0.020	12.3

the other three cusps.

For the statistical estimation of allometric trend in each cusp area, the regression slopes of log cusp area to log crown area are presented in Table 3. In the upper molars, no significant allometry is found in either species, while in the lower molars, there are common allometric trends between M<sub>1</sub> and M<sub>2</sub>, as well as between the two species. The hypoconid area shows negative allometry except in *Pan*'s M<sub>1</sub>. In *Pan*, the entoconid area shows positive allometry in both M<sub>1</sub> and M<sub>2</sub>.

#### *Comparison of relative cusp areas within African apes*

For each species, the relative cusp areas were compared between the first and second molars. The results of *t*-test are shown in Table 4. As a common trend in both species, the relative metacone area of M<sup>2</sup> is smaller than that of M<sup>1</sup>, and the relative hypoconid area of M<sub>2</sub> is smaller than that of M<sub>1</sub>. The differences between the first and second molars are apparently marked in *Gorilla* compared with *Pan*.

Next, the relative cusp areas of each molar were compared between the two species. The results are given in Table 5. There are highly significant differences in the upper and lower molars. In both M<sub>1</sub> and M<sub>2</sub>, *Gorilla* carries a smaller entoconid than *Pan*. In M<sub>1</sub>, the protoconid and hypoconid are larger in *Gorilla* than in *Pan*. Among the four kinds of molars, the differences of the relative cusp areas between the two species are most remarkable in M<sub>1</sub>.

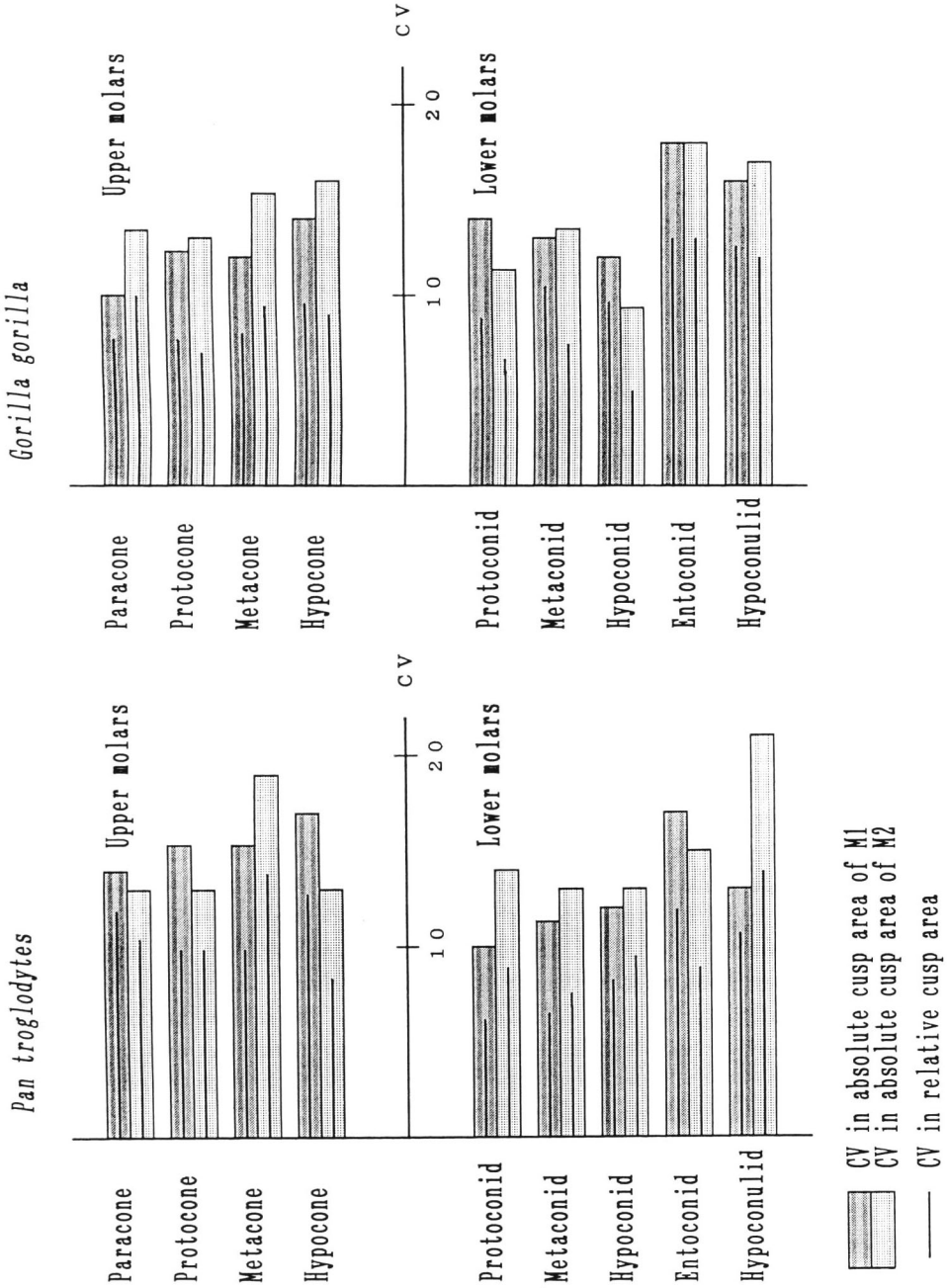


Fig. 2. Coefficients of variation (CV) in the absolute and relative cusp areas of the two African apes.

Table 3. Regression slopes of log cusp area on log crown area.

Tooth	Cusp	<i>Pan</i>				<i>Gorilla</i>				
		C1	C2	Slope	SE	C1	C2	Slope	SE	
M <sup>1</sup>	Paracone	-0.303	0.549	0.665	0.219	-0.249	0.721	0.815	0.188	
	Protocone	0.195	0.739	1.154	0.227	0.094	0.803	1.063	0.190	
	Metacone	0.046	0.749	1.054	0.201	0.005	0.774	1.013	0.199	
	Hypocone	0.040	0.711	1.115	0.238	0.084	0.740	1.055	0.231	
M <sup>2</sup>	Paracone	-0.138	0.630	0.838	0.288	-0.163	0.732	0.900	0.194	
	Protocone	-0.165	0.608	0.812	0.296	-0.079	0.849	0.956	0.137	
	Metacone	0.287	0.707	1.395	0.390	0.060	0.791	1.044	0.187	
	Hypocone	0.035	0.760	1.035	0.247	0.216	0.842	1.182	0.175	
M <sub>1</sub>	Protoconid	-0.176	0.785	0.872	0.077	0.162	0.778	1.145	0.113	
	Metaconid	0.009	0.788	0.996	0.087	-0.149	0.581	0.815	0.140	
	Hypoconid	-0.107	0.677	0.890	0.108	-0.236	0.602	0.758	0.120	
	Entoconid	0.263	0.738	1.347	0.137	+	0.151	0.662	1.154	0.160
	Hypoconulid	-0.127	0.594	0.859	0.130	0.121	0.676	1.215	0.162	
M <sub>2</sub>	Protoconid	-0.115	0.779	0.912	0.096	-0.092	0.830	0.949	0.077	
	Metaconid	-0.195	0.813	0.866	0.078	0.075	0.829	1.034	0.085	
	Hypoconid	-0.333	0.713	0.727	0.090	-	-0.362	0.889	0.835	0.052
	Entoconid	0.257	0.867	1.253	0.091	+	0.158	0.679	1.208	0.159
	Hypoconulid	0.351	0.781	1.411	0.219	0.025	0.638	1.017	0.149	

C1: Correlation of relative cusp area with crown area.

C2: Correlation of log absolute cusp area with log crown area.

Significance level: +, 0.05; positive allometry.

-, 0.05; --, 0.01; negative allometry.

### Comparison with fossil and living hominids

For the upper molars, the relative hypocone areas of *Pan* and *Gorilla* were compared with those of the living and fossil hominids. The other cusp areas were not compared in the present study because the data of fossil hominids were not available. The relative hypocone areas of the five taxa are compared in Fig. 3. As for the difference between M<sup>1</sup> and M<sup>2</sup>, the relative hypocone areas of M<sup>1</sup> and M<sup>2</sup> are almost the same in each species except the modern *Homo sapiens* in which M<sup>2</sup>'s hypocone is considerably reduced. Between the species, the relative hypocone areas of the two apes are slightly smaller than those of *Australopithecus* and larger than those of *Homo sapiens*. The relative hypocone areas are within range from 0.20 to 0.26 throughout the species except for the modern *sapiens*.

For the lower molars, the affinities of *Pan* and *Gorilla* with the living and fossil hominids were estimated by PENROSE's shape distances based on the relative areas of the five cusps. The comparative data are summarized in Table 6. The pooled standard deviations obtained from the African apes were used for the computation of distance. The results are shown in Table 7 as a matrix. Fig. 4 represents the two dimensional expressions of the multidimensional scaling applied to the distance matrix. In the comparison of M<sub>2</sub>, all of the species except for *Homo sapiens* show close affinities

Table 4. The results of *t*-test for the differences of relative cusp areas between the first and second molars.

Upper molars	<i>Pan</i>			<i>Gorilla</i>		
	<i>t</i> -value	M <sup>1</sup>	M <sup>2</sup>	<i>t</i> -value	M <sup>1</sup>	M <sup>2</sup>
Paracone	0.454			1.691		
Protocone	3.097		<<	1.355		
Metacone	2.191		>	4.673		>>>
Hypocone	1.501			0.953		
Lower molars	<i>t</i> -value	M <sub>1</sub>	M <sub>2</sub>	<i>t</i> -value	M <sub>1</sub>	M <sub>2</sub>
Protoconid	1.906			1.229		
Metaconid	0.339			0.109		
Hypoconid	2.067		>	4.130		>>>
Entoconid	1.289			1.181		
Hypoconulid	1.382			3.507		<<

Significance level: >, 0.05; <<, 0.01; >>>, 0.001.

Table 5. The results of *t*-test for the differences of relative cusp areas between *Pan* and *Gorilla*.

Upper molars	M <sup>1</sup>		M <sup>2</sup>	
	<i>t</i> -value	<i>Pan Gorilla</i>	<i>t</i> -value	<i>Pan Gorilla</i>
Paracone	2.089	>	0.199	
Protocone	2.828	>	0.021	
Metacone	0.719		0.362	
Hypocone	1.841		0.677	
Lower molars	M <sub>1</sub>		M <sub>2</sub>	
	<i>t</i> -value	<i>Pan Gorilla</i>	<i>t</i> -value	<i>Pan Gorilla</i>
Protoconid	5.423	<<<	1.960	
Metaconid	0.846		1.132	
Hypoconid	3.289	<<	2.688	<
Entoconid	7.496	>>>	4.770	>>>
Hypoconulid	0.550		1.939	

Significance level: ><, 0.05; <<, 0.01; >>> <<<, 0.001.

for each other. *Pan*'s M<sub>1</sub> and M<sub>2</sub> are located in the center of the scattergram and closely tied with each other. Other species' M<sub>1</sub>s are scattered peripherally without the M<sub>2</sub>'s distribution. In the M<sub>1</sub>'s dispersion, *Gorilla* is the closest to *Australopithecus africanus* and *Homo habilis*. On the other hand, *Homo sapiens*, *Australopithecus robustus* and *boisei* are quite distant from them. As a whole, this scattergram indicates that the variation of pattern in the relative cusp areas is larger in M<sub>1</sub> than in M<sub>2</sub>.

Similarity between M<sub>1</sub> and M<sub>2</sub> was also noticeable for each species. In order to recognize it more evidently, the distance between M<sub>1</sub> and M<sub>2</sub> is diagrammed for

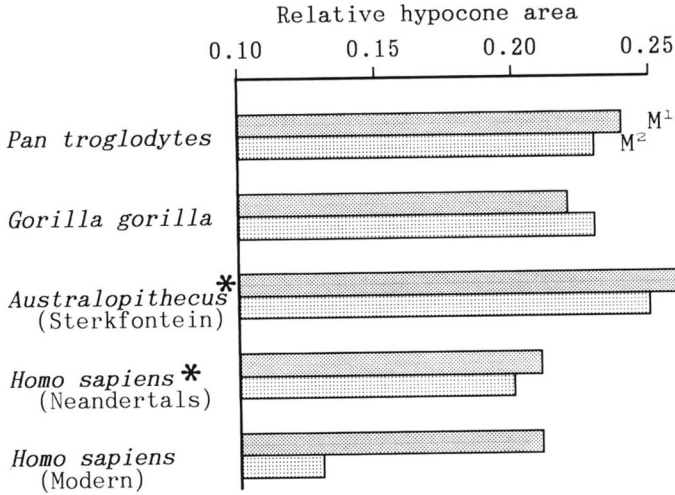


Fig. 3. Relative hypocone areas of the living and fossil hominoids (\*HANIAHARA *et al.* 1970).

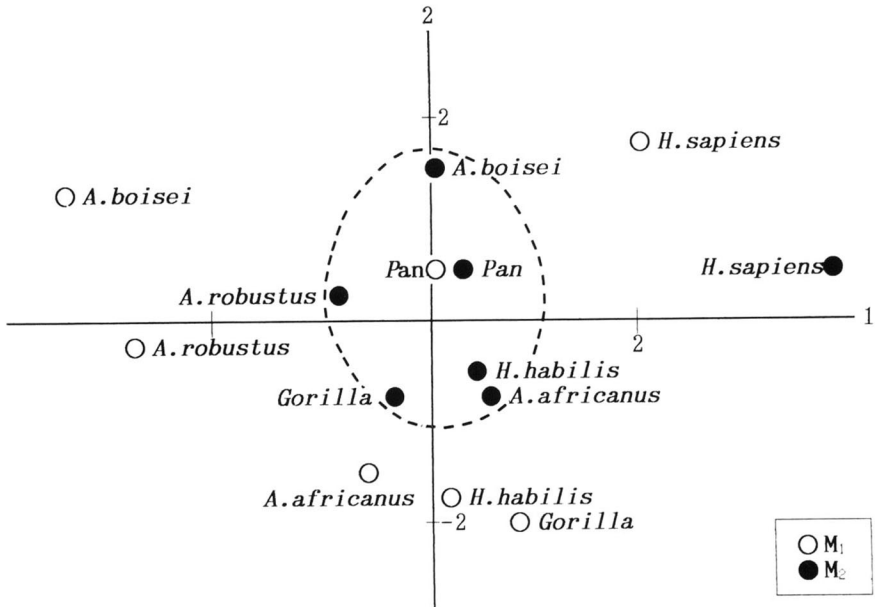


Fig. 4. Two dimensional expression of the MDS applied to the PENROSE'S shape distances of Table 7 (Contribution rate in the 1st axis: 48.7%, and in the 2nd axis: 25.1%).

each species in Fig. 5. *Pan* has the smallest distance, while the distances in *Homo sapiens* and *Australopithecus boisei* are apparently larger than those of the other hominoids.



Table 6. Crown areas and relative cusp areas in the lower molars of living and fossil hominoids.

M <sub>1</sub>	Total area					Hld.
	Prd.	Med.	Hyd.	End.	Present study	
Living apes	<i>Pan Gorilla</i>	0.224	0.238	0.204	0.194	0.140
	<i>A. africanus</i>	0.255	0.232	0.223	0.147	0.143
	<i>A. robustus</i>	0.235	0.243	2.216	0.156	0.154
	<i>A. boisei</i>	0.212	0.222	0.214	0.171	0.180
	<i>H. habilis</i>	0.209	0.220	0.197	0.193	0.188
Living human		0.244	0.238	0.227	0.153	0.145
		0.253	0.205	0.203	0.213	0.125
M <sub>3</sub>	Total area					Hld.
	Prd.	Med.	Hyd.	End.	Present study	
Living apes	<i>Pan Gorilla</i>	0.235	0.240	0.191	0.185	0.149
	<i>A. africanus</i>	0.247	0.234	0.204	0.153	0.162
	<i>A. robustus</i>	0.253	0.229	0.212	0.160	0.145
	<i>A. boisei</i>	0.234	0.221	0.203	0.173	0.167
	<i>H. habilis</i>	0.220	0.233	0.188	0.204	0.146
Living human		0.258	0.228	0.204	0.159	0.153
		0.280	0.227	0.185	0.196	0.112

Table 7. PENROSE's shape distances based on the five relative cusp areas in the lower molars.

	M <sub>1</sub>					M <sub>2</sub>							
	<i>Pan Gor.</i>	<i>A. af.</i>	<i>A. rb.</i>	<i>A. bs.</i>	<i>H. hb.</i>	<i>H. hb.</i>	<i>H. sp.</i>	<i>Pan</i>	<i>Gor.</i>	<i>A. af.</i>	<i>A. rb.</i>	<i>A. bs.</i>	<i>H. hb.</i>
M <sub>1</sub>	<i>Pan Gorilla</i>	1.42											
	<i>A. africanus</i>	0.72	0.39										
	<i>A. robustus</i>	1.47	2.09	1.06									
	<i>A. boisei</i>	1.80	3.55	2.09	0.38								
	<i>H. habilis</i>	1.05	0.18	1.66	3.07								
	<i>H. sapiens</i>	1.43	2.34	2.75	3.74	2.45							
M <sub>2</sub>	<i>Pan Gorilla</i>	0.23	1.33	0.63	1.46	1.12	1.67						
	<i>A. africanus</i>	1.12	0.51	0.27	1.08	0.52	2.51	0.62					
	<i>A. robustus</i>	0.91	0.15	0.35	1.70	2.69	0.23	0.70	0.26				
	<i>A. boisei</i>	0.84	1.14	0.62	0.43	1.01	1.95	0.57	0.32	0.63			
	<i>H. habilis</i>	1.15	0.38	1.36	1.57	1.32	1.99	0.25	1.47	1.51	0.89	1.54	
	<i>H. sapiens</i>	2.41	2.65	3.38	6.00	2.44	3.05	2.07	2.93	1.91	3.37	2.62	1.93

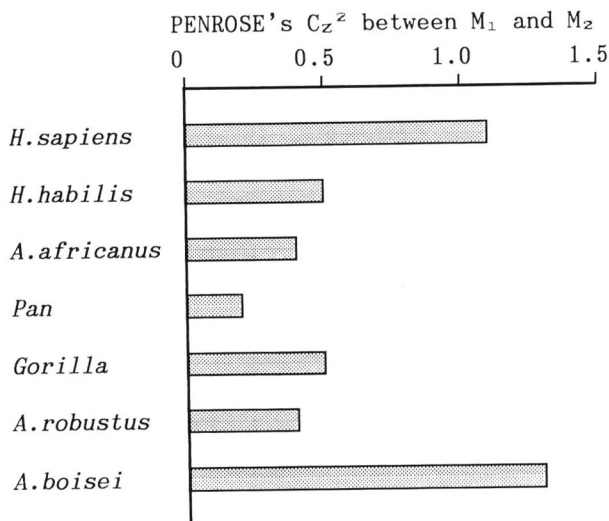
Fig. 5. PENROSE'S shape distances between  $M_1$  and  $M_2$  of Table 7.

Table 8. Principal component analysis based five relative cusp areas in the lower molars.

Cusp	CP 1	CP 2
Protoconid	-0.2349	0.9147
Metaconid	0.5341	0.2731
Hypoconid	0.8106	0.2160
Entoconid	-0.8932	-0.3417
Hypoconulid	0.5168	-0.7957
Eigenvalue	2.062	1.707
Contribution (%)	41.250	34.154

In order to elucidate the actual conditions of the differences of the relative cusp areas between  $M_1$  and  $M_2$ , as well as between the species, the principal component analysis was applied to the relative areas of the five cusps. For this procedure, the mean values of the seven species were used. Table 8 gives the eigenvectors and eigenvalues of the first two principal components. The first principal component has a positive correlation with the relative hypoconid area and a negative one with the relative entoconid area. The second principal component has a positive correlation with the relative protoconid area and a negative one with the relative hypoconulid area. On the basis of these eigenvectors, the principal component scores were calculated for  $M_1$  and  $M_2$  of each species using the standardized relative areas of the five cusps. Fig. 6 is a plot of the first and second principal component scores. The horizontal axis shows the first component score, and vertical axis reflects the second ones. Toward each end of the axis, the named cusp is larger in relative area. The circle

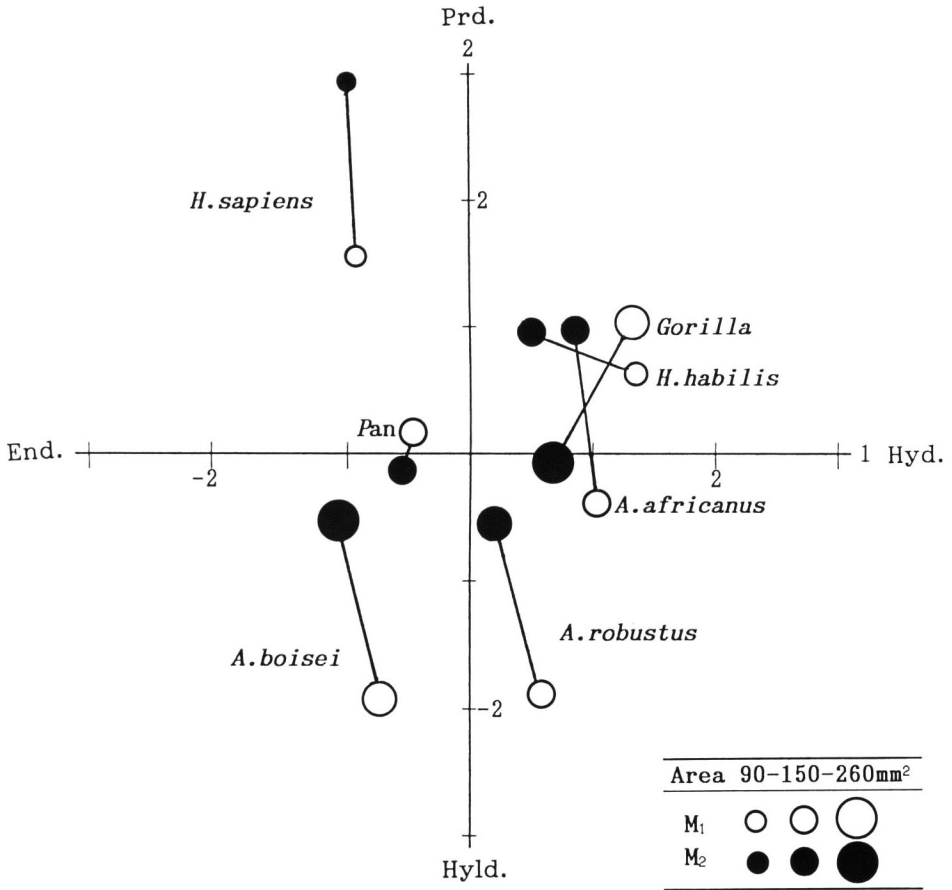


Fig. 6. Plots of the first and second principal component scores for the lower molars of living and fossil hominoids.

size reflects each crown area of the each species. In most of the species, the difference between M<sub>1</sub> and M<sub>2</sub> is ascribed to the relative protoconid and hypoconid areas. *Pan* shows again the smallest distance between M<sub>1</sub> and M<sub>2</sub>. *Gorilla*'s lower molars, as well as those of *Australopithecus africanus* and *Homo habilis*, are characterized by relatively smaller entoconid and larger hypoconid. *Pan* and *Gorilla* are uniquely contrasted in the direction of the line with the other hominids. This contrast is due to the reverse relationship of the relative hypoconid and protoconid areas between M<sub>1</sub> and M<sub>2</sub>.

### Discussion

As to the morphological variability of crown surface in hominoid taxa, it is generally pointed out that the distal cusps have larger variability by tooth reduction than the mesial ones (DAHLBERG, 1953; CORRUCINI, 1979; YAMADA *et al.*, 1988; YAMADA, 1992). In the present study of the two African apes, the area variability within each cusp showed the noticeable uniformity between the first and second molars, and also between the two species. That is, the coefficients of variation for the metacone, hypocone, entoconid and hypoconulid tended to be greater than those for the other cusps, as a whole. These findings mostly correspond to those of the examinations by the previous authors.

In the comparison of the relative cusp areas between the first and second molars, the metacone of the upper molar and the hypoconid of the lower molar were significantly smaller in the second than those in the first molars in both apes. These differences were rather remarkable in *Gorilla* as shown in the significance test. In consideration of the occlusal relationship between the metacone and a part of the hypoconid, the smallness of the metacone and hypoconid in the second molars may be associated with each other, though it is not clear why these cusps are reduced in *Gorilla*'s second molars.

Between *Pan* and *Gorilla*, highly significant differences of the relative cusp areas were found in the lower molars. The smallness of entoconid in both  $M_1$  and  $M_2$  was *Gorilla*'s most remarkable feature as compared between the two apes. In addition to this, highly significant differences were also observed in the  $M_1$ 's protoconid and hypoconid. Their relative cusp areas were larger in *Pan* than in *Gorilla*. As a whole, differences of the relative cusp areas between the two apes were prominent in  $M_1$ . Interestingly, the comparison with the living and fossil hominids also suggested that the interspecific variations of the relative cusp areas were also larger in  $M_1$  than in  $M_2$ . The relative cusp areas of  $M_1$  display significant interspecific variation among the apes and hominids. However, this variation does not coincide with the phylogenetic relationships among them (Fig. 4).

Fig. 6 drawn by the principal component scores provided another informative facts. Regarding on the lines connecting between  $M_1$  and  $M_2$ , *Gorilla* and *Pan* showed unique direction reverse to that of the hominids. It seems that this contrast of the apes with the humans is mainly due to the reverse relationships of the relative hypoconulid area between  $M_1$  and  $M_2$ . In most of the hominids, the relative hypoconulid area in  $M_1$  is larger than in  $M_2$ . On the contrary, those of the African apes are larger in  $M_2$  than in  $M_1$ . This contrast with the hominids is quite evident in *Gorilla*. These relationships between  $M_1$  and  $M_2$  may yield meaning information concerning the divergence of the humans' and apes' lineages.

On the other hand, the smallness of the interspecific variation of  $M_2$  suggests that  $M_2$  has a rather more primitive pattern of the relative cusp areas than  $M_1$ , except for *Homo sapiens*. As for *Pan*'s  $M_1$ , however, the small difference from its  $M_2$ , implies

that *Pan*'s  $M_1$  also has a relatively primitive pattern as compared with the other hominoids'  $M_1$ . For more advanced arguments, more extensive research of the cusp areas will be expected for the primitive and ancestral hominoids such as *Dryopithecus*.

In order to understand the relation of cusp area to crown area, allometry has been examined for several hominoid molars by previous authors. In regard to *Gorilla*'s  $M_1$ , HILLS *et al.* (1983) revealed that there was not any allometry in all kinds of cusps. Present study of the allometry for *Gorilla* agrees with their result except for the hypoconid. The negative allometry of the hypoconid area was found as a general trend in the lower molars of *Pan* and *Gorilla*. This allometric trend means that the hypoconid is smaller in relative area as the crown is larger. When the two apes were compared in the relative hypoconid area, however, *Gorilla* had the larger hypoconid despite its larger crown area. Thus the differences in the relative cusp areas between *Pan* and *Gorilla* are not allometric phenomenon.

It is well known that "robust" type of *Australopithecus* carries relatively small mesial cusps and large hypoconulid (CORRUCCINI and MCHENRY, 1980; MCHENRY and CORRUCCINI, 1980; WOOD *et al.*, 1983). The hypothesis that such pattern of relative cusp areas of the "robust" *Australopithecus* is due to the allometric phenomenon has been proposed and argued by the previous authors. HILLS *et al.* (1983) did not find the evidence of allometric trends supporting the hypothesis in the comparisons between the modern *sapiens*, *Pongo* and *Gorilla*. On the contrary, KANAZAWA *et al.* (1985) considerably validate the hypothesis by their findings of the allometric trends in the modern *sapiens*'s  $M_1$ . In the present study of the African apes, no intraspecific allometry of cusp area supporting the hypothesis is found. Concerning the relation of cusp area between the African apes and fossil hominids, *Gorilla* has relatively smaller distal cusps than the "robust" *Australopithecus* whereas their lower molar sizes are comparable to each other. These findings do not substantiate the proportion that the larger-toothed taxa have reduced mesial cusps and enlarged distal ones in relative areas. If the mention made by KANAZAWA *et al.* is accepted, there is a possibility that such allometric trend is restricted to the hominid taxa.

HARTMAN (1988) made a cladistic analysis using linear measurements for detailed landmarks on the crown surfaces of the several hominoid molars. According to him, the occlusal morphology such as the location, size and height of cusps might be defined by functional diet-related adaptation. In the present study, as mentioned above, the variations of the relative cusp areas between the living and fossil hominoid molars seem to reflect neither allometric phenomenon nor phylogenetic relationships. This conclusion seems to support HARTMAN's suggestion, whereas the direct relationship of relative cusp area to dietary environment is unknown in the present study.

The tooth kinds examined in the present study were restricted in the first and second molars. According to CORRUCCINI's (1977) liner measurements of crown surface, there is informative crown component variation even in the hominoid third molars. The cusp areas of the third molars also should be examined for further

arguments.

### Acknowledgments

The authors present great gratitude to Dr. A. BALEGAMIRE, Director of the Department of Mammalogy, Dr. B. BAJOPE, C. R. S. N., Zaire, Dr. G. MUSSER, Director of the Department of Mammalogy, American Museum of Natural History, U. S. A., and Dr. T. AKAZAWA, Department of Physical Anthropology and Prehistory, University Museum, University of Tokyo, Japan for their permission to investigate skeletal collections of the African apes and Japanese. Thanks are also due to the staff of the C. R. S. N. and the American Museum of Natural History for their excellent assistance into our researches, and to Dr. B. YAMAGUCHI, Director of the Department of Anthropology, National Science Museum, Tokyo for his valuable suggestion. This study was supported by Grant-in-Aid for Scientific Research on Priority Areas from the Ministry of Education, Science and Culture, Japan, in 1989, (No. 63041082) and 1992 (No. 04454034).

### References

- CORRUCCINI, R. S., 1977. Crown component variation in hominid lower third molars. *Z. Morph. Anthropol.*, **68**: 14–25.
- CORRUCCINI, R. S., 1979. Molar cusp-size variability in relation to odontogenesis in hominoid primates. *Arch. Oral Biol.*, **24**: 633–634.
- CORRUCCINI, R. S. and H. M. MCHENRY, 1980. Cladometric analysis of Pliocene hominids. *J. Hum. Evol.*, **9**: 209–221.
- DAHLBERG, A. A., 1953. Concept of occlusion in physical anthropology and comparative anatomy. *J. Am. Dent. Assoc.*, **46**: 530–535.
- ERDRINK, D. P., 1965. A quantification of the *Dryopithecus*- and other lower molar patterns in Man and some of the Apes. *Z. Morph. Anthropol.*, **57**: 70–108.
- ERDRINK, D. P., 1967. A quantification of lower molar patterns in deuterio-Malayans. *Z. Morph. Anthropol.*, **59**: 40–56.
- HANIHARA, K., M. TAMADA and T. TANAKA, 1970. Quantitative analysis of the hypocone in the human upper molars. *J. Anthrop. Soc. Nippon*, **78**: 200–207.
- HARTMAN, S. E., 1988. A cladistic analysis of hominid molars. *J. Human Evolution*, **17**: 489–502.
- HILLS, M., S. H. GRAHAM and B. A. WOOD, 1983. The allometry of relative cusp size in Hominid mandibular molars. *Am. J. Phys. Anthropol.*, **62**: 311–316.
- KANAZAWA, E., M. SEKIKAWA, J. AKAI and T. OZAKI, 1985. Allometric variation on cuspal areas of the lower first molar in three racial populations. *J. Anthrop. Soc. Nippon*, **93**: 425–438.
- MATSUMURA, H., M. NAKATSUKASA and H. ISHIDA, 1991. Comparative study of crown cusp areas in the dentition of African apes. In: *Primate Today*, Proceedings of the XIIIth congress of the International Primatological Society Nagoya and Kyoto, 18–24 July 1990 (A. EHARA, T. KIMURA, O. TAKENAKA and M. IWAMOTO eds.), pp. 539–540. Elsevier Science Publishers B. V., Amsterdam.
- MCHENRY, H. M. and R. S. CORRUCCINI, 1980. On the status of *Australopithecus afarensis*. *SCIENCE*, **207**: 1103–1104.
- WOOD, B. A. and S. A. ABBOTT, 1983. Analysis of the dental morphology of Plio-Pleistocene

- hominids I. Mandibular molars: crown area measurements and morphological traits. *J. Anat.*, **136**: 197-219.
- WOOD, B. A., S. A. ABBOTT and S. H. GRAHAM, 1983. Analysis of the dental morphology of Plio-Pleistocene hominids II. Mandibular molars-study of cusp areas, fissure pattern and cross sectional shape of the crown. *J. Anat.*, **137**: 287-314.
- YAMADA, H., K. KAWAMOTO, S. TAKADA, Y. HOTTA, J. CHEN and T. SAKAI, 1988. Numerical study of distolingual crown portion on the basis of hypocone variability in upper molars. *J. Growth*, **27**: 63-74. (In Japanese, with English summary.)
- YAMADA, H., 1992. On the "Talonid" in Japanese lower molars. *Jpn. J. Oral Biol.*, **34**: 15-24. (In Japanese, with English summary.)

