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Comparison of Intercusp Distances of *Pan troglodytes* and *Homo sapiens* Mandibular Molars

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Abstract Intercusp distances of mandibular permanent first and second molars of *Pan troglodytes* and *Homo sapiens* were investigated. Three-dimensional coordinates of the cusp tip at both the enamel dentine junction (EDJ) and outer enamel surface (OES) were obtained for each cusp from high resolution digital reconstructions of these surfaces of the molar crown. These coordinates were then analyzed using Euclidean distance matrix analysis (EDMA). According to the ratio values in the form difference matrices, interspecific difference was more pronounced in the distance between OES and EDJ of each cusp, which corresponds to cuspal enamel thickness, than in the intercusp distances of either surface. Comparison of the intercusp distances on the EDJ revealed that in the first molars of *Pan*, entoconid position was more distant from the other cusps than in the *Homo* counterpart. This was true in the case of second molars, but the distance between the other cusps also tended to be larger in *Pan*. These results are interpreted in relation to function and evolutionary significance of molar crown design.
Key words: Intercusp distance, Enamel thickness, Mandibular molar, *Pan troglodytes*, *Homo sapiens*

Measuring distance between cusps is an alternative way to numerically evaluate molar crown morphology. A few studies did this for the molars of modern humans (Kraus, 1952; Smith *et al.*, 1997), extant hominoid species (Hartman, 1988, 1989; Shimizu, 1998), and fossil hominoids with reference to extant species (Ungar, 1994; Liu *et al.*, 2001a, 2001b). Most of these studies, however, measured distances on the surface of the molar crown, the OES. Only two studies, concerning human molars, attempted to measure intercusp distances on the EDJ surface. An earlier attempt was made by Kraus (1952) by exposing the EDJ through removal of enamel tissue. In his work, the relationship between cusp tip positions on OES and EDJ was not restorable. More recently, Smith *et al.* (1997) non-destructively presented intercusp distances on both OES and EDJ and distances between the two surfaces at each cusp through the use of serial computed tomography (CT) images. They compared the lower deciduous second and permanent first molars of modern humans in order to evaluate differences in ontogeny of the two teeth (Smith *et al.*, 1997).

Studies of fossil and extant hominoids mainly focused on the phylogenetic differences of molar crown design. Ungar *et al.* (1994) were the first to analyze intercusp distances for the purpose of assessing taxonomic affinities, followed by two recent papers of similar perspective (Liu *et al.*, 2001a, 2001b). Neither of these studies attempted to measure intercusp distances on the EDJ surface. In the former study, comparison of intercusp distances was made between lower first molars of *Pan troglodytes* and *Homo sapiens* as part of an effort to reassess the phylogenetic position of the Lukeino molar, KNM-LU 335, and a significant difference was suggested between the two extant species (Unger *et al.*, 1994). Recently, two papers have tried to elucidate the taxonomic affinity of *Lufengpithecus* and the Yuanmou hominoids, with each other and also with extant taxa (Liu *et al.*, 2001a, 2001b).

The EDJ and OES of a tooth represent two distinct stages of its developmental history, with the former appearing earlier (*e.g.*, Butler, 1956; Smith *et al.*, 1997). The apex of dentine horn is the first structure to be formed of a cusp during the bell stage of odontogenesis, while cusp tip of the OES is completed only as the appositional enamel tissue formation ceases (*e.g.*, Butler, 1956; Ten Cate, 1998). Thus EDJ morphology is expected to reflect its phylogenetic status more strictly, while OES is expected to bear more variation. Taxonomically important signals should appear more clearly on the former surface.

Methodological difficulty of defining "cusp tip" on the OES must be considered, on the other hand. While the analytical method adopted in these studies, EDMA, is a coordinate system free method, the actual procedure of defining cusp tip on the OES is highly dependent on the orientation of the molar crown and is inevitably subjective to some extent. This is especially manifested in the case of human molars characterized by more bulbous cusps. On the contrary, cusp tip on the EDJ surface, in other words the dentine horn apex, is easily distinguished as a "point" and therefore able to serve as a consistent "landmark".

This paper presents the results of the first attempt to evaluate taxonomic difference of intercusp distances measured not only on the OES, but also at the EDJ, accompanied by the distance between the two surfaces of each cusp. Mandibular molars of *Homo sapiens* and *Pan troglodytes* were studied. Combined with our knowledge of enamel distribution patterns of the entire molar crown (Kono, 2002; Kono *et al.*, 2002), evolutionary and functional significance of molar crown design of these taxa will be discussed.

Table 1. Number of teeth included in this study

	LM1	LM2
Homo sapiens	13	13 (7)[1)]
Pan troglodytes	6 (4)[2)]	6 (5)[2)]

[1)] The number of five-cusped molars is bracketed.
[2)] The number of teeth on which cusp tips at OES were measured is bracketed.

Materials and Methods

The sample of this study consists of unworn or minimally worn lower first and second molars of *Homo sapiens* and *Pan troglodytes* (Table 1). Specimens of *Homo* are either of modern Asian, Edo, or Jomon population from the skeletal collections housed in The University Museum, The University of Tokyo (Asian and Jomon), and the National Science Museum, Tokyo (Edo). Most of the *Pan* molars are from the collection of the Cleveland Museum of Natural History, while two of them are housed at the University of California, Berkeley. Sex is unknown for most of the molars, since they were taken from juvenile individuals.

Coordinates of each cusp tip were taken from digitally reconstructed molar crown data. These reconstructions have been developed through our research project of enamel thickness (Kono, 2002; Kono *et al.*, 2002) and are highly accurate (Kono *et al.*, 2000; Suwa *et al.*, 2000). Detailed explanations for the reconstruction methods are given elsewhere (Kono, 2002; Kono *et al.*, 2000, 2002). The exact position of the cusp tip was defined in the present study as the highest point on each of the two surfaces, OES and EDJ, with the orientation of molar crown aligned by maximizing projected area of occlusal fovea delineated on the EDJ surface (Kono, 2002; Kono *et al.*, 2002; Suwa and Kono-Takeuchi, 1998). Three-dimensional analytical software, 3D-Rugle and CT-Rugle (Medic Engineering Inc., Kyoto, Japan), was used for the handling of reconstructed data and the extraction of coordinates (Kono *et al.*, 2000, 2002; Suwa *et al.*, 2000). Figure 1 shows examples of defined position of cusp tips on both OES and EDJ surfaces.

The coordinates of ten landmarks (two each for five cusps) were then analyzed by the EDMA method (*e.g.*, Lele and Richtsmeier, 1991). In this method, distances are calculated between all possible pairs of landmarks in each specimen or sample. These distances are put into a matrix

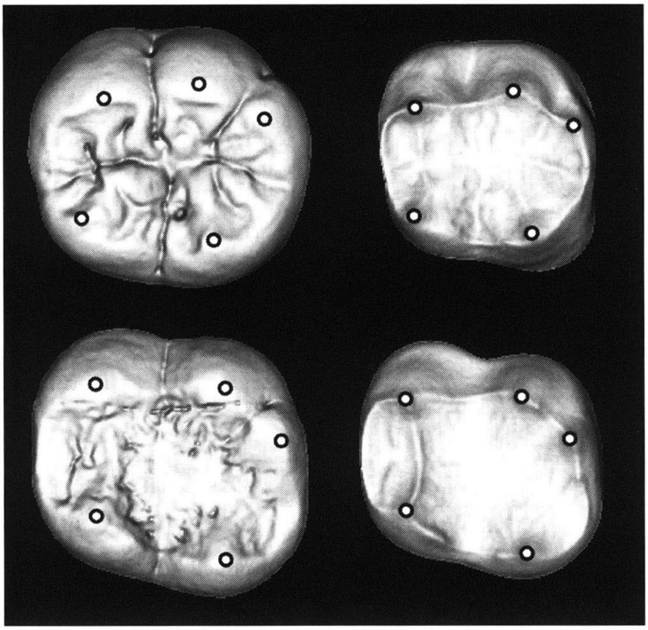

Fig. 1. Cusp tip positions on the OES (left) and EDJ (right), shown for mandibular first molars of *Homo sapiens* (top) and *Pan troglodytes* (bottom).

(form matrix, FM). The difference in form and size between groups is expressed as the matrix of ratios of these distances (form difference matrix, FDM).

In the present study, the FM of each tooth element of each species was calculated by simply averaging the individual FMs of all constituent specimens of a sample, following Smith *et al.* (1997) (contra Lele, 1993). This was partly because some of the second molars of *Homo* were four-cusped and three chimpanzee molars showed wear facets which were very small but might affect the position of the highest point on the OES. Therefore it was not possible to obtain all ten landmarks for these molars, but no effort was made to estimate missing landmarks. They were simply included in the calculation of distance only when the points of both ends were present. Microsoft Excel was used in the calculation of distances and ratios.

Results

Table 2 shows the FMs of each molar of *Homo* and *Pan*, respectively. Variances of intercusp distances tended to be greater on the OES than on the EDJ in all four matrices.

The FDMs were then calculated between species and between molar types (Tables 3 and 4). The distance between OES and EDJ at a cusp, which corresponds to cuspal enamel thickness, was most prominently different between species, judging from the ratio value. Comparison between tooth types of each species also revealed some characteristics seen for cuspal enamel thickness. In *Homo*, enamel thickness at protoconid tip was markedly thin in the first molar than in the second, while in *Pan*, the same tendency was seen for the metaconid.

In all of these four comparisons, the overall pattern of intercusp distances measured on the OES was mostly the same as that seen on the EDJ. Therefore the following investigations are focused on the EDJ results.

Distances between the five cusp tips on the EDJ surface were plotted in a manner proposed by Cole and Richtsmeier (1998) in order to localize the distance which differs substantially be-

Table 2. Form matrices (FMs) of four comparative groups[1)]

Homo LM1		EDJ					OES				
		prd	med	hyd	end	hld	prd	med	hyd	end	hld
EDJ	prd	—	**0.14**	**0.14**	**0.32**	**0.22**	0.02	0.15	0.23	0.49	0.30
	med	**4.54**	—	**0.25**	**0.30**	**0.20**	0.21	0.02	0.24	0.38	0.33
	hyd	**4.58**	**6.73**	—	**0.25**	**0.22**	0.10	0.28	0.03	0.38	0.28
	end	**7.24**	**5.11**	**5.63**	—	**0.15**	0.34	0.28	0.29	0.03	0.24
	hld	**7.02**	**7.71**	**2.87**	**4.49**	—	0.33	0.23	0.20	0.20	0.02
OES	prd	1.11	4.99	4.78	7.60	7.29	—	**0.27**	**0.19**	**0.57**	**0.41**
	med	4.81	1.31	7.18	5.58	8.23	**5.00**	—	**0.28**	**0.38**	**0.39**
	hyd	4.85	6.98	1.63	5.88	3.43	**4.70**	**7.14**	—	**0.47**	**0.39**
	end	7.47	5.32	6.01	1.56	5.02	**7.62**	**5.42**	**5.84**	—	**0.47**
	hld	7.35	8.09	3.34	4.88	1.74	**7.37**	**8.35**	**3.00**	**4.86**	—

Homo LM2		EDJ					OES				
		prd	med	hyd	end	hld	prd	med	hyd	end	hld
EDJ	prd	—	**0.20**	**0.27**	**0.21**	**0.40**	0.06	0.21	0.27	0.29	0.50
	med	**4.16**	—	**0.32**	**0.23**	**0.42**	0.20	0.05	0.33	0.36	0.55
	hyd	**4.59**	**6.64**	—	**0.39**	**0.49**	0.40	0.47	0.02	0.47	0.26
	end	**6.65**	**4.92**	**5.20**	—	**0.37**	0.24	0.32	0.52	0.03	0.48
	hld	**6.33**	**7.53**	**2.38**	**4.50**	—	0.61	0.77	0.56	0.45	0.04
OES	prd	1.63	4.81	4.90	7.16	6.71	—	**0.20**	**0.52**	**0.34**	**0.77**
	med	4.63	1.44	7.18	5.40	7.96	**4.81**	—	**0.51**	**0.48**	**0.88**
	hyd	4.94	6.95	2.08	5.68	3.42	**4.56**	**7.08**	—	**0.71**	**0.63**
	end	7.06	5.26	5.75	1.75	5.12	**7.19**	**5.27**	**5.58**	—	**0.47**
	hld	6.76	7.89	3.19	4.86	1.96	**6.68**	**8.01**	**2.84**	**4.79**	—

Pan LM1		EDJ					OES				
		prd	med	hyd	end	hld	prd	med	hyd	end	hld
EDJ	prd	—	**0.14**	**0.03**	**0.16**	**0.03**	0.00	0.21	0.06	0.12	0.23
	med	**4.78**	—	**0.03**	**0.06**	**0.07**	0.21	0.00	0.04	0.07	0.18
	hyd	**4.58**	**6.88**	—	**0.14**	**0.07**	0.06	0.02	0.00	0.07	0.12
	end	**8.01**	**5.46**	**6.44**	—	**0.09**	0.07	0.13	0.14	0.01	0.04
	hld	**7.02**	**7.76**	**2.86**	**5.04**	—	0.03	0.08	0.04	0.05	0.00
OES	prd	0.78	5.55	4.68	8.73	7.27	—	**0.23**	**0.09**	**0.15**	**0.26**
	med	4.99	0.53	7.05	5.54	7.83	**5.65**	—	**0.07**	**0.16**	**0.24**
	hyd	5.01	7.39	0.79	6.86	2.89	**5.03**	**7.45**	—	**0.09**	**0.10**
	end	8.34	5.59	6.83	0.72	5.32	**8.93**	**5.57**	**7.04**	—	**0.47**
	hld	7.29	8.16	3.04	5.52	0.87	**7.48**	**8.20**	**2.84**	**5.66**	—

Pan LM2		EDJ					OES				
		prd	med	hyd	end	hld	prd	med	hyd	end	hld
EDJ	prd	—	**0.40**	**0.10**	**0.34**	**0.15**	0.03	0.49	0.09	0.33	0.15
	med	**5.56**	—	**0.26**	**0.14**	**0.33**	0.56	0.01	0.34	0.15	0.32
	hyd	**4.43**	**7.42**	—	**0.25**	**0.12**	0.45	0.40	0.02	0.19	0.17
	end	**7.99**	**5.36**	**6.45**	—	**0.24**	0.52	0.19	0.38	0.01	0.29
	hld	**7.14**	**8.25**	**3.12**	**5.02**	—	0.32	0.32	0.13	0.22	0.01
OES	prd	0.82	5.99	4.56	8.37	7.25	—	**0.55**	**0.36**	**0.46**	**0.35**
	med	5.77	0.76	7.58	5.50	8.33	**6.12**	—	**0.44**	**0.18**	**0.37**
	hyd	4.68	7.68	0.96	6.72	3.22	**4.65**	**7.82**	—	**0.32**	**0.18**
	end	8.25	5.43	6.63	0.87	5.18	**8.62**	**5.53**	**6.90**	—	**0.47**
	hld	7.26	8.46	3.13	5.40	0.99	**7.37**	**8.60**	**3.07**	**5.50**	—

[1)] Distances and variances are in the lower left and upper right half of the matrix, respectively. Values appearing in bold type are distances within each of EDJ and OES, while values underlined are cuspal enamel thicknesses. Prd, protoconid; med, metaconid; hyd, hypoconid; end, entoconid; hld, hypoconulid.

Table 3. Form difference matrices (FDMs) calculated between the first and second molars of each species[1)]

Homo		EDJ					OES				
		prd	med	hyd	end	hld	prd	med	hyd	end	hld
EDJ	prd	—									
	med	**0.92**	—								
	hyd	**1.00**	**0.99**	—							
	end	**0.92**	**0.96**	**0.92**	—						
	hld	**0.90**	**0.98**	**0.83**	**1.00**	—					
OES	prd	1.47	0.96	1.02	0.94	0.92	—				
	med	0.96	1.10	1.00	0.97	0.97	**0.96**	—			
	hyd	1.02	0.99	1.28	0.97	1.00	**0.97**	**0.99**	—		
	end	0.95	0.99	0.96	1.12	1.02	**0.94**	**0.97**	**0.96**	—	
	hld	0.92	0.97	0.96	1.00	1.13	**0.91**	**0.96**	**0.95**	**0.99**	—

Pan		EDJ					OES				
		prd	med	hyd	end	hld	prd	med	hyd	end	hld
EDJ	prd	—									
	med	**1.14**	—								
	hyd	**0.97**	**1.06**	—							
	end	**0.98**	**0.96**	**0.96**	—						
	hld	**1.00**	**1.05**	**1.04**	**0.97**	—					
OES	prd	1.05	1.08	0.98	0.96	1.00	—				
	med	1.16	1.43	1.08	0.99	1.06	**1.08**	—			
	hyd	0.93	1.04	1.22	0.98	1.11	**0.92**	**1.05**	—		
	end	0.99	0.97	0.97	1.20	0.97	**0.97**	**0.99**	**0.98**	—	
	hld	1.00	1.04	1.03	0.98	1.14	**0.99**	**1.05**	**1.08**	**0.97**	—

[1)] The second molar distance is the numerator. Values appearing in bold type are distances within each of EDJ and OES, while values underlined are cuspal enamel thicknesses. See Table 1 for abbreviations of cusp names.

Table 4. Form difference matrices (FDMs) calculated between species for each tooth type[1)]

LM1		EDJ					OES				
		prd	med	hyd	end	hld	prd	med	hyd	end	hld
EDJ	prd	—									
	med	**1.07**	—								
	hyd	**1.00**	**1.03**	—							
	end	**1.12**	**1.08**	**1.17**	—						
	hld	**1.00**	**1.00**	**1.01**	**1.13**	—					
OES	prd	0.70	1.11	0.98	1.15	1.00	—				
	med	1.04	0.40	0.98	0.99	0.95	**1.13**	—			
	hyd	1.03	1.06	0.49	1.17	0.84	**1.07**	**1.04**	—		
	end	1.12	1.05	1.13	0.46	1.06	**1.17**	**1.03**	**1.21**	—	
	hld	0.99	1.01	0.91	1.13	0.50	**1.02**	**0.98**	**0.95**	**1.17**	—

LM2		EDJ					OES				
		prd	med	hyd	end	hld	prd	med	hyd	end	hld
EDJ	prd	—									
	med	**1.34**	—								
	hyd	**0.97**	**1.11**	—							
	end	**1.19**	**1.08**	**1.22**	—						
	hld	**1.11**	**1.08**	**1.26**	**1.10**	—					
OES	prd	0.50	1.24	0.93	1.17	1.08	—				
	med	1.25	0.53	1.06	1.02	1.05	**1.27**	—			
	hyd	0.95	1.11	0.46	1.18	0.94	**1.02**	**1.10**	—		
	end	1.17	1.03	1.15	0.50	1.01	**1.20**	**1.05**	**1.24**	—	
	hld	1.07	1.07	0.98	1.11	0.51	**1.10**	**1.07**	**1.08**	**1.15**	—

[1)] The *Pan* distance is the numerator. Values appearing in bold type are distances within each of EDJ and OES, while values underlined are cuspal enamel thicknesses. See Table 1 for abbreviations of cusp names.

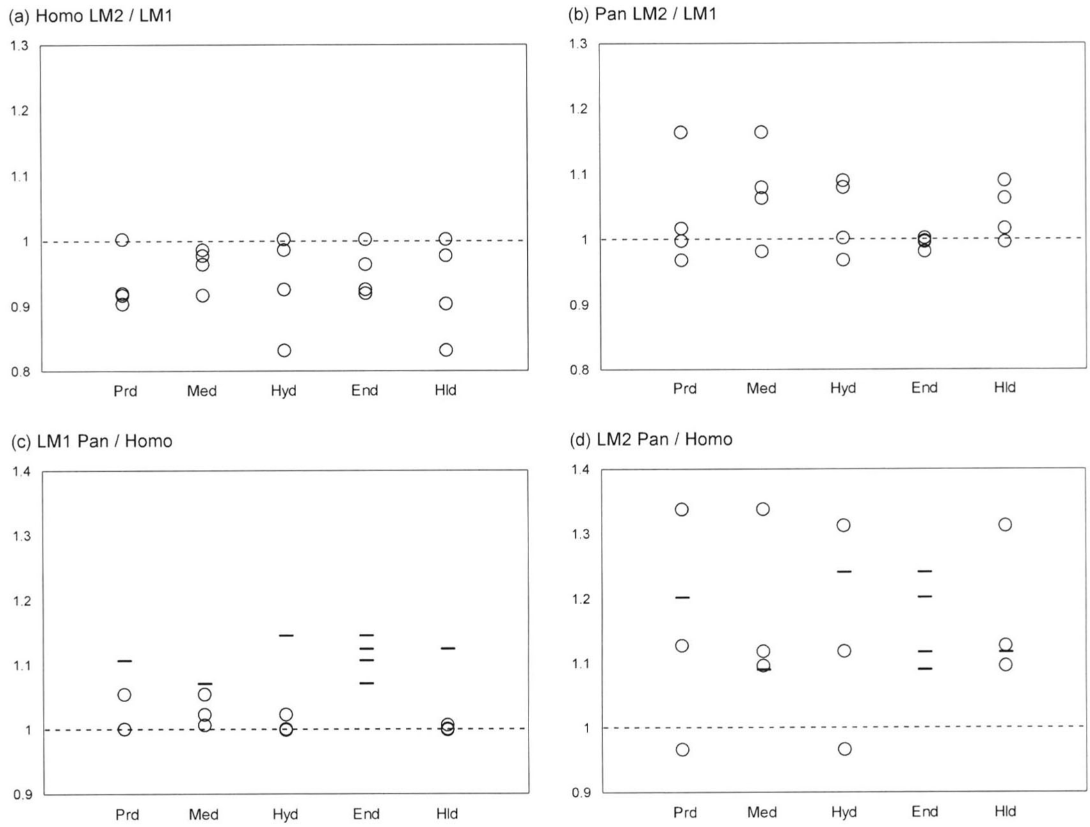

Fig. 2. Graphical display of FDM values. Each of the 10 distances measured on the EDJ are plotted with reference to one of the cusps, so that they are plotted twice. Value of 1.0 indicates that the distance is identical in the compared specimens. Distances from the entoconid are depicted with dashes in c and d. Abbreviations for cusp names are given in Table 1.

tween the two groups under consideration (Fig. 2). The resulting pattern is diagrammatically summarized in Figure 3 following Ungar *et al.* (1994). In the comparison between tooth types, intercusp distances tended to be smaller in the second molars of *Homo* than in the first molars, while the opposite condition was seen in the molars of *Pan*. Interspecific comparisons revealed that intercusp distances of the lower first molar were very similar in these two species, except for the distances from entoconid (highlighted with dashes in Fig. 2) which were greater in *Pan*. The second molar presented a more distinct pattern of difference between species. As in the case of the first molar, most of the distances were longer in *Pan*, but to a greater degree. While entoconid was again confirmed to be more separated from the other cusps in the chimpanzee molar, this pattern was not so striking as in the case of the first molar since the other distances also differed greatly. These observations were further confirmed by student's *t*-test (Table 5).

Discussion

Intercusp distances were usually measured on the OES in previous studies, mostly because of the difficulty of accessing internal structures such as the EDJ. In this study, distances on the OES were shown to vary more than those measured on the EDJ. While it is not clear whether this variation simply reflects individual differences, or if it was caused by methodological instability, it can be said that it is more appropriate to use the less

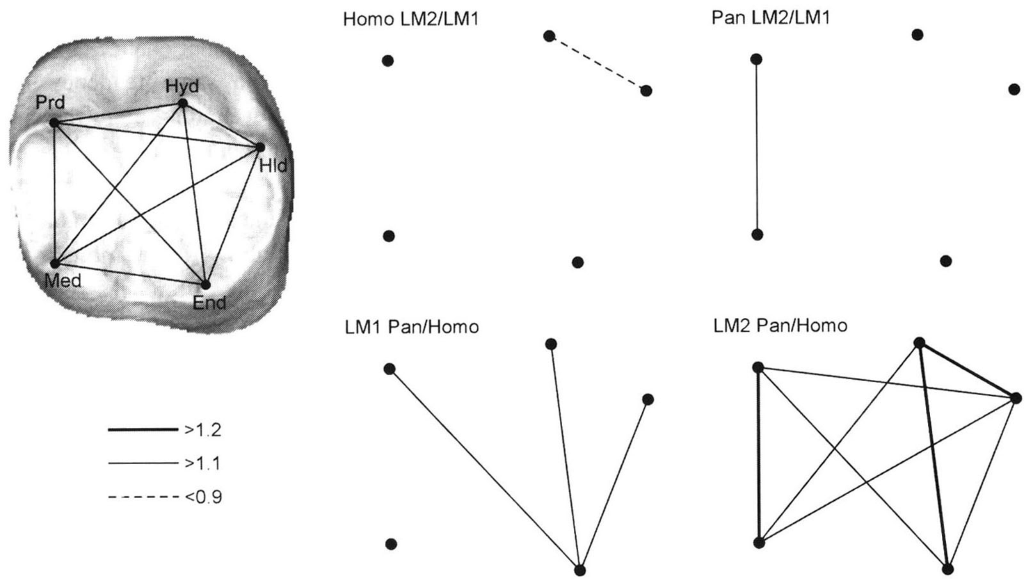

Fig. 3. Diagrammatic presentation of the difference seen between tooth types or species. Three arbitrary values were chosen in schematically depicting the relatively large magnitudes of differences. Abbreviations for cusp names are given in Table 1.

variable distances between cusp tips on the EDJ surface, especially when investigating interspecific differences.

The pattern of interspecific difference of the first molar shown in the present study differs from the single example published so far (Ungar *et al.*, 1994). In their study, significant difference among intercusp distances was detected only in the distance between hypoconid and hypoconulid, with humans having longer distances than chimpanzees (Ungar *et al.*, 1994). This discrepancy may be explained by the inconsistency in defining the position of cusp tip on the OES.

Investigation of FDMs between species revealed that interspecific difference was most prominently present in enamel thickness at the cusp tips. Difference of intercusp distances were relatively small, according to the ratio values. Absolute differences in enamel thickness between species are also large, tending to be as large as the largest intercusp differences. This indicates that the difference of molar crown morphology between *Homo* and *Pan* is not necessarily achieved through differentiating positional relationships between cusps, but that the difference of enamel thickness plays a strong role in determining species differences in OES morphology. Presumably other elements not studied in this paper such as the depth of occlusal fovea, degree of basal flare, and/or inclination of lateral wall are also significant. This seems quite plausible, considering that the cusp tips on the EDJ surface are formed at an earlier stage of odontogenesis (*e.g.*, Butler, 1956; Ten Cate, 1998), and so that they may tend to retain a phylogenetically conservative condition. The other morphological characteristics mentioned above, as with enamel thickness, are formed at a later stage of the odontogenetic sequence. The recent suggestion that molar enamel thickness is likely to be highly sensitive to selective pressures, and thus prone to change over evolutionarily short periods (Hlusko *et al.*, in press), is also in support of the interpretation that species characteristics of OES morphology is greatly influenced by structures formed later in odontogenesis.

With regard to the distribution pattern of enamel thickness, chimpanzee molars are characterized by distinctly thin enamel at the occlusal fovea (Kono, 2002). This unique thinness was in-

Table 5. *T*-test results comparing intercusp distances on the EDJ[1)]

		prd	med	hyd	end	hld
LM1 vs LM2						
Homo		EDJ				
		prd	med	hyd	end	hld
EDJ	prd	—				
	med	*	—			
	hyd			—		
	end	**			—	
	hld	*				—
Pan		EDJ				
		prd	med	hyd	end	hld
EDJ	prd	—				
	med	*	—			
	hyd		*	—		
	end				—	
	hld					—
Pan* vs *Homo						
LM1		EDJ				
		prd	med	hyd	end	hld
EDJ	prd	—				
	med		—			
	hyd			—		
	end	**		**	—	
	hld				**	—
LM2		EDJ				
		prd	med	hyd	end	hld
EDJ	prd	—				
	med	***	—			
	hyd		**	—		
	end	***		***	—	
	hld	*		*		—

[1)] Significant differences are indicated in the lower half of the matrix.
* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

terpreted as adaptationally obtained so that the capacity of space enclosed by the occlusal fovea increases (Kono, 2002). In the present study, the lower first molar was shown to be very similar between *Homo* and *Pan* with regard to intercusp distances, but with the entoconid more separated from the other cusps in chimpanzees. The separation of entoconid can be regarded as a part of the above described adaptational change. In the case of second molars, the same tendency is detectable but not so outstanding as in the case of the first molars. Rather, most of the distances between cusps tend to be larger in chimpanzees. This may be explained by higher interspecific and intraspecific variability in the more posterior molars. In any case, the differences seen in the second molars between the two species can also be interpreted as reflecting the above suggested adaptational direction of *Pan* molars to enlarge its occlusal fovea capacity.

Conclusions

In the present study, investigation of intercusp distances is shown to be an alternative, meaningful tool to evaluate molar crown morphology. Comparisons of intercusp distance variability suggest that the use of cusp tip positions on the EDJ surface is to be recommended when discussing taxonomic differences. Another advantage of using the EDJ is that specimens with some wear can be included. This magnifies potential sample size of fossil hominoids and hominids, on the condition that a non-destructive imaging device is available. The data presented here suggests that the difference of molar crown form between *Pan* and *Homo* has been achieved through evolutionary differentiation of enamel thickness, as well as with the positional change of cusps. Species differences in both enamel thickness and cusp positions conform with a tendency to increase the spatial capacity of the occlusal fovea in *Pan* molars.

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Literature Cited

Butler, P. M., 1956. The ontogeny of molar pattern. *Biol. Rev.*, **31**: 30–70.

Cole, T. M. III., and Richtsmeier, J. T., 1998. A simple method for visualization of influential landmarks when using Euclidean distance matrix analysis. *Am. J. Phys. Anthropol.*, **107**: 273–293.

Hartman, S. E., 1988. A cladistic analysis of hominoid molars. *J. Hum. Evol.*, **17**: 489–502.

Hartman, S. E., 1989. Stereophotogrammetric analysis of occlusal morphology of extant hominoid molars: phenetics and function. *Am. J. Phys. Anthropol.*, **80**: 145–166.

Hlusko, L. J., Suwa, G., Kono, R. T., and Mahaney, M. C., in press. Genetics and the evolution of primate enamel thickness: A baboon model. *Am. J. Phys. Anthropol.*, published on-line: DOI: 10.1002/ajpa.10353.

Kono, R. T., 2002. Comparative analysis of molar enamel thicknesses and distribution patterns among extant great apes and humans. PhD thesis. The University of Tokyo.

Kono, R. T., Suwa, G., and Tanijiri, T., 2000. Three-dimensional reconstruction and analysis of serially scanned CT image data using CT-Rugle software. *Gazolabo,* **11**(7): 48–52 (in Japanese).

Kono, R. T., Suwa, G., and Tanijiri, T., 2002. A 3-dimensional analysis of enamel distribution patterns in human permanent first molars. *Arch. Oral Biol.*, **47**: 867–875.

Kraus, B. S., 1952. Morphologic relationships between enamel and dentin surfaces of lower first molar teeth. *J. Dent. Res.*, **31**: 248–256.

Lele, S., 1993. Euclidean distance matrix analysis (EDMA): estimation of mean form and mean form difference. *Math. Geol.*, **25**: 573–602.

Lele, S., and Richtsmeier, J. T., 1991. Euclidean distance matrix analysis: a coordinate-free approach for comparing biological shapes using landmark data. *Am. J. Phys. Anthropol.*, **86**: 415–427.

Liu, W., Hlusko, L. J., and Zheng, L., 2001a. Morphometric analysis of hominoid lower molars from Yuanmou of Yunnan Province, China. *Primates*, **42**: 123–134.

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

Shimizu, D., 1998. Mechanical analysis of the upper molar tooth of African apes using the finite elements methods. *Primate Res.*, **14**: 153–163 (in Japanese with English abstract).

Smith, P., Gomorri, J. M., Spitz, S., and Becker, J., 1997. Model for the examination of evolutionary trends in tooth development. *Am. J. Phys. Anthropol.*, **102**: 282–294.

Suwa, G., Kono, R. T., and Tanijiri, T., 2000. A three-dimensional measurement system using analytical softwares, 3D-Rugle and CT-Rugle. *Gazolabo*, **11**(8): 35–40 (in Japanese).

Suwa, G., and Kono-Takeuchi, R., 1998. A refined method of measuring basal crown and cusp areas by use of a three-dimensional digitizing system. *Anthropol. Sci.*, **106** (Supplement) : 95–105.

Ten Cate, A. R., 1998. *Oral Histology: development, structure, and function*. Mosby-Year Book Inc., St. Louis.

Ungar, P. S., Walker, A., and Coffing, K., 1994. Reanalysis of the Lukeino molar (KNM-LU 335). *Am. J. Phys. Anthropol.*, 94: 165–173.