

Supporting Online Material for

Liang Bua *Homo floresiensis* mandibles and mandibular teeth: A contribution to the comparative morphology of a new hominin species

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Materials and methods

The ability of a limited number of mandibular dimensions to discriminate between closely related species was first examined through multivariate comparisons of variation within a living primate genus. *Pan* was chosen for this purpose as body-size and levels of sexual dimorphism fall closer to the known *Homo* range than do other large hominoid primates. The genus *Pan* is subdivided into two species, *P. paniscus* (Pp) and *P. troglodytes* (Pt), with the latter split into at least three subspecies, *P.t. troglodytes* (Ptt), *P. t. schweinfurthii* (Pts) and *P. t. verus* (Ptv) (Shea et al., 1993; Morin et al., 1994; Braga, 1995; Uchida, 1996; Gagneux et al., 1999; Taylor and Groves, 2003). Cranial, dental, and mandibular morphology, supported by genetic data, indicates that the greatest distinction is between Pp and Pt, with less agreement over subspecific variation within Pt. While the Pt subspecies are geographically separated, genetic data suggest some limited gene flow between them (Gagneux et al., 1999; Gonder, 2000; Won and Hey, 2005). Using an isolation with migration model, Won and Hey (2005) estimated that Pp and Pt may have diverged as recently as 0.86-0.89 m. yr., and the western and central subspecies at around 0.42 m. yr. The adult skeletal sample we use here contains 30 Pp specimens (14 male, 16 female), 33 Pts specimens (16 male, 17 female) and 72 Ptt specimens (30 male, 42 female), all measured by PB and TM together.

Mandibular and dental measurements were restricted to those that could be recorded in the LB1 and LB6 *H. floresiensis* mandibles, and had previously been recorded for our global *H. sapiens* sample. For the multivariate comparisons, nine linear dimensions were recorded on the mandibles (Table S1). As the *Pan* samples only contained adults, it was not possible to explore the influence of ontogeny on group mandibular and dental differentiation. However, ontogenetic scaling of mandibular size and shape in *Pan* has previously been examined by Taylor and Groves (2003). Following Taylor and Groves (2003), basicranial length (basion-nasion) was used to standardize mandibular and dental dimensions in multivariate

comparisons. The extent and pattern of multivariate differentiation between groups, probabilities of group membership, and the influence of individual variables on distributions were explored using discriminant function analysis (DFA) and principal components analysis (PCA), with nine mandibular and dental dimensions (Table S1). For the final multivariate comparisons, the sexes were pooled as the individual male and female samples displayed very similar group-based distributions and multivariate characteristics. We also considered that this would provide the most robust solution given the sex of most Plio-Pleistocene hominin mandibles is unknown. Statistical and graphical procedures were performed using SYSTAT 11 (Systat, 2002), PAST 1.34 (Hammer et al., 2001), and SPSS 14 (SPSS, 1990).

Statistical results and discussion

Descriptive statistics for the three *Pan* samples are provided in Table S1. In the same-sex pairwise comparisons of mean linear dimensions between the three *Pan* groups, all but one of the significant differences in size is between Pp and the two Pt subspecies. For all of the mandibular and dental dimensions, Pp is smaller (Table S2). These results agree with those previously published for the mandible and cranium of this genus (Shea, 1985; Shea et al., 1993; Taylor and Groves, 2003). Shape differences (proportions) also occur with the highest frequency in Pp when compared with same-sex Pt samples (Table S3). Pp males and females have a relatively low and thick symphysis, a relatively low and thin posterior mandibular corpus, and a relatively narrow mandibular ramus. There are no significant differences in proportions between the same-sex Pts and Ptt groups. These results are consistent with Taylor and Groves' (2003) broader comparison of variation in mandibular shape within *Pan*.

Table S1. Descriptive statistics for the *Pan* groups, by taxon and sex.

Variable (mm)	sex	<i>Pan paniscus</i>				<i>P.t. schweinfurthii</i>				<i>P.t. troglodytes</i>			
		n	Mean	sd	CV	n	Mean	sd	CV	n	Mean	sd	CV
Symphyseal height	M	19	31.4	1.76	0.05	19	43.2	3.00	0.07	35	43.4	3.73	0.08
	F	21	32.6	2.56	0.07	23	40.2	3.21	0.08	46	40.6	3.66	0.09
Symphyseal thickness	M	19	12.9	1.12	0.08	19	16.6	1.30	0.07	35	16.5	1.51	0.09
	F	22	13.1	1.37	0.10	23	15.1	1.24	0.08	46	15.8	1.26	0.07
Corpus height M ₂	M	18	21.7	1.49	0.06	19	28.5	1.74	0.06	35	27.5	2.21	0.08
	F	21	22.7	1.88	0.08	23	27.1	1.60	0.05	46	27.2	2.47	0.09
Corpus thickness M ₂	M	19	10.9	0.93	0.08	19	14.1	1.19	0.08	35	14.7	1.20	0.08
	F	21	11.1	0.70	0.06	23	14.0	1.13	0.08	46	14.5	1.53	0.10
Bigonial breadth	M	19	74.4	6.25	0.08	17	90.6	7.68	0.08	33	89.1	8.40	0.09
	F	20	68.8	4.96	0.07	21	90.1	6.25	0.06	44	84.6	7.23	0.08
Ramus minimum breadth	M	20	37.4	2.36	0.06	19	47.0	2.84	0.06	35	46.6	3.08	0.06
	F	22	36.0	2.79	0.07	23	42.2	2.77	0.06	46	42.5	2.72	0.06
External arch breadth M ₂	M	17	50.1	2.11	0.04	19	56.3	3.29	0.05	33	56.7	2.55	0.04
	F	19	49.0	1.80	0.03	22	55.5	2.22	0.04	45	56.2	2.48	0.04
P ₃ buccolingual	M	19	8.6	0.86	0.09	18	7.6	0.63	0.08	34	8.1	0.90	0.11
	F	22	6.0	0.56	0.09	22	7.48	0.72	0.09	46	7.7	0.74	0.09
P ₃ mesiodistal	M	19	6.4	0.86	0.13	18	10.1	1.27	0.12	34	10.6	1.18	0.11
	F	22	8.1	0.82	0.10	23	10.0	1.17	0.11	46	10.3	1.10	0.10
M ₁ buccolingual	M	18	8.7	0.48	0.05	19	10.5	0.53	0.05	34	9.9	0.45	0.04
	F	20	8.7	0.62	0.07	22	9.53	0.74	0.07	44	9.6	0.51	0.05
M ₁ mesiodistal	M	17	9.4	0.79	0.08	18	10.7	0.66	0.06	34	10.7	0.47	0.04
	F	21	9.1	0.78	0.08	23	10.6	0.69	0.06	45	10.6	0.59	0.05
Symphyseal module (H/T)	M	19	2.4	0.22	0.09	19	2.6	0.18	0.07	35	2.6	0.25	0.09
	F	21	2.4	0.32	0.13	23	2.6	0.26	0.10	46	2.5	0.31	0.12
Corpus module (H/T)	M	18	2.0	0.23	0.11	19	2.0	0.18	0.09	35	1.88	0.16	0.08
	F	21	2.0	0.19	0.09	23	1.9	0.17	0.09	46	1.8	0.23	0.12
P ₃ module (MD/BL)*100	M	17	78.2	7.38	0.09	15	74.3	9.00	0.12	32	76.1	7.54	0.09
	F	19	77.0	7.40	0.09	17	73.2	5.55	0.07	42	77.0	6.54	0.08
Maximum femur length	M	7	295.5	9.25	0.03	4	300.2	19.03	0.06	17	301.4	9.49	0.03
	F	10	294.0	8.98	0.03	6	294.0	24.4	0.08	31	291.2	14.96	0.05
Basion-nasion	M	20	89.7	3.29	0.03	19	102.3	4.00	0.03	34	101.9	4.29	0.04
	F	21	88.2	3.81	0.04	21	100.4	3.81	0.03	45	98.7	4.09	0.04

Discriminant function analysis (DFA) was performed for the *Pan* raw data using nine variables as predictors of membership in the three pooled-sex groups (Table S4). The analysis included 144 cases, and none were identified as multivariate outliers with $p < 0.001$. Evaluation of statistical assumptions of linearity, normality, and homogeneity of variance-covariance matrices indicated that the analysis was robust. Two discriminant functions were calculated with $\chi^2 = 343$, $p = 0.000$ (81.3% variance). There was still a strong association between groups and predictors after the removal of the first function, with $\chi^2 = 113.7$, $p = 0.000$ (12.2% variance). The loading matrix of correlations between predictors and discriminant functions indicated that the best predictors for distinguishing between the groups are symphyseal height, ramus minimum breadth, dental arch breadth at M2, corpus thickness, and symphyseal thickness. For the second function, none of the variables were particularly strong predictors. A plot of the function scores illustrates the ability of the variables to discriminate Pp from the other two Pt subspecies, with none of the bonobos being classified as chimpanzees (Figure S1). These results are consistent with those obtained previously when Pp mandibles and crania were compared with Pt (Shea et al., 1993; Taylor and Groves, 2003). Using pooled-sex samples, complete separation of Pp from Pt has been demonstrated simply on the basis of a single dimension, mandibular length (Cramer, 1977). While Pp forms a distinct morphological unit, the intergroup distances between Pts and Ptt are relatively small, with considerable overlap in their distributions (Tables S2 and S3). Using a larger mandible variable set, and including *P.t. verus* (Ptv) in their subspecific sample, Taylor and Groves (2003) found that Pts and Ptt were morphologically more similar than either were to Ptv. Overall, 68% of the original group cases were correctly classified. The separation of Pp mandibles from the other *Pan* groups, is primarily a function of size rather than shape, with all mean linear dimensions being significantly smaller in Pp. DFA of the size-adjusted data based on basicranial length

reduced dispersion between groups, but classification accuracy was still greater for the single sex Pp group, than Pts or Ptt (Figure S1). Two discriminant functions were calculated with $\chi^2 = 120.7$, $p = 0.000$ (67.8% variance). There was still a significant association between groups and predictors after the removal of the first function, with $\chi^2 = 18.7$, $p = 0.016$ (11.6% variance). Correlations between predictors and functions were highest for M1 buccolingual breadth and arch width at M2 for function 1, and minimum ramus width for function 2. In the pooled-sex adjusted DFA, group classification accuracy, based on cross-validation, was reduced for Pp (86.6%) and Pts (50%) compared with the unadjusted data (Pp 100%, Pts 74.3%), while Ptt remained at a similar level. Mahalanobis D^2 distances between group centroids were reduced between all group pairs in the size-adjusted DFA, but for Pts/Ptt the movement was minor compared with Pp/Pts and Pp/Ptt, highlighting the impact of size (allometry) on the morphological distinction of Pp (Tables S5 and S6).

Table S2. Results of same-sex pairwise comparisons for statistical differences in mean linear dimensions between taxa in *Pan*¹

Variable	Pp/Pts		Pp/Ptt		Pts/Ptt	
	m	f	m	f	m	f
Basion-nasion	*	*	*	*	NS	NS
Symphyseal height	*	*	*	*	NS	NS
Symphyseal width	*	*	*	*	NS	NS
M ₂ corpus height	*	*	*	*	NS	NS
M ₂ corpus width	*	*	*	*	NS	NS
M ₂ - M ₂ arch breadth	*	*	*	*	NS	NS
Bigonial breadth	*	*	*	*	NS	NS
Ramus min. breadth	*	*	*	*	NS	NS
P ₃ mesiodistal	*	*	*	*	NS	NS
M ₁ buccolingual	*	*	*	*	NS	NS
Symphyseal module	NS	NS	NS	NS	NS	NS
Corpus module	NS	NS	NS	NS	NS	NS

* p < 0.05; NS, not significant.

¹Bonferroni-adjusted one-way ANOVA

Table S3. Results of same-sex pairwise comparisons for statistical differences in mean shape ratios between taxa in *Pan*¹

Measurement vs. Basicranial length	Pp/Pts		Pp/Ptt		Pts/Ptt	
	m	f	m	f	m	f
Symphyseal height	*	*	*	*	NS	NS
Symphyseal width	*	*	*	*	NS	NS
M ₂ corpus height	*	NS	*	*	NS	NS
M ₂ corpus width	*	*	*	*	NS	NS
M ₂ - M ₂ arch breadth	NS	NS	NS	NS	NS	NS
Bigonial breadth	NS	*	NS	*	NS	NS
Ramus min. breadth	*	NS	*	*	NS	NS
P ₃ mesiodistal	NS	NS	NS	*	NS	NS
M ₁ buccolingual	NS	NS	NS	NS	NS	NS

* p < 0.05; NS, not significant.

¹Bonferroni-adjusted one-way ANOVA

Table S4. Pooled within-group correlations between discriminating variables and standardized canonical discriminant functions, for the unadjusted and size-adjusted *Pan* pooled-sex DFA. Variables ordered by absolute size of correlation within function.

Unadjusted	Function		Size-adjusted	Function	
	1	2		1	2
Symphyseal height	0.657*	0.001	M1 BL	-0.549*	0.095
Arch breadth M2	0.636*	-0.052	Arch breadth M2	-0.494*	0.262
Corpus thickness	0.613*	-0.322	Symphyseal height	0.359*	0.245
Corpus height	0.595*	0.291	Corpus thickness	0.241*	0-.069
Ramus min breadth	0.507*	0.073	Bigonial breadth	0.036	0.748*
Symphyseal thickness	0.483*	-0.171	Corpus height	0.074	0.481*
P3 mesiodistal	0.420*	-0.145	Ramus min breadth	-0.155	0.422*
M1 buccolingual	0.379*	-0.261	P3 MD	0.066	0.085*
Bigonial breadth	0.531	0.658*	Symphyseal thickness	-0.019	0.020*

* Largest absolute correlation between each variable and any discriminant function.

Table S5. Group classification results for discriminant function analysis of the pooled-sex *Pan* samples completed on raw/size-adjusted data^{1,2}.

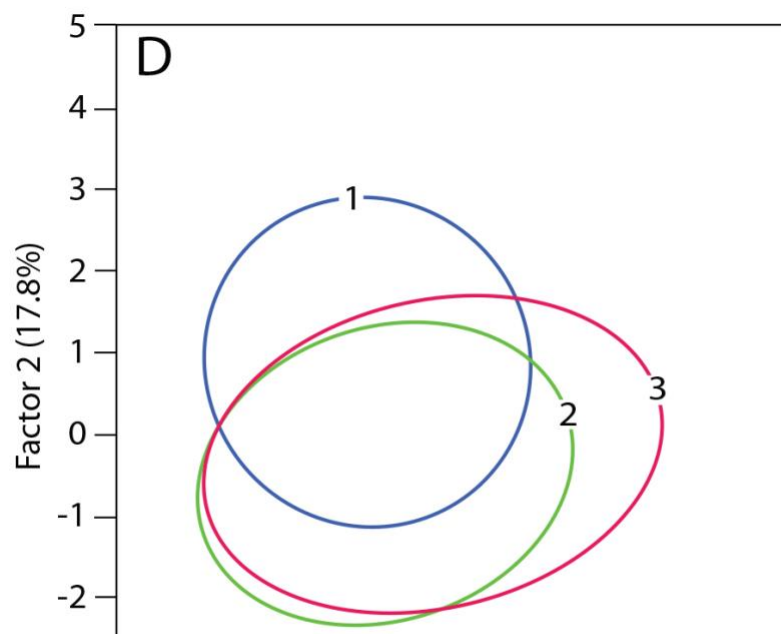
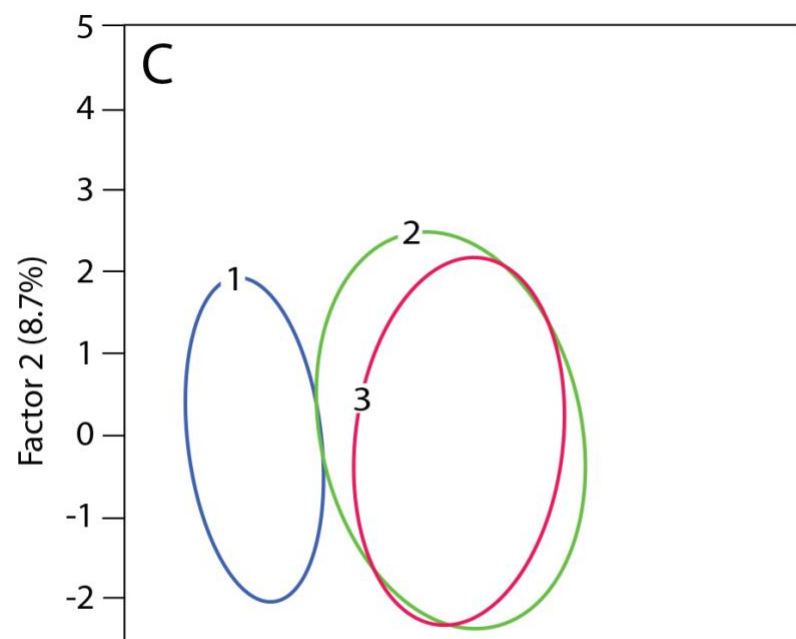
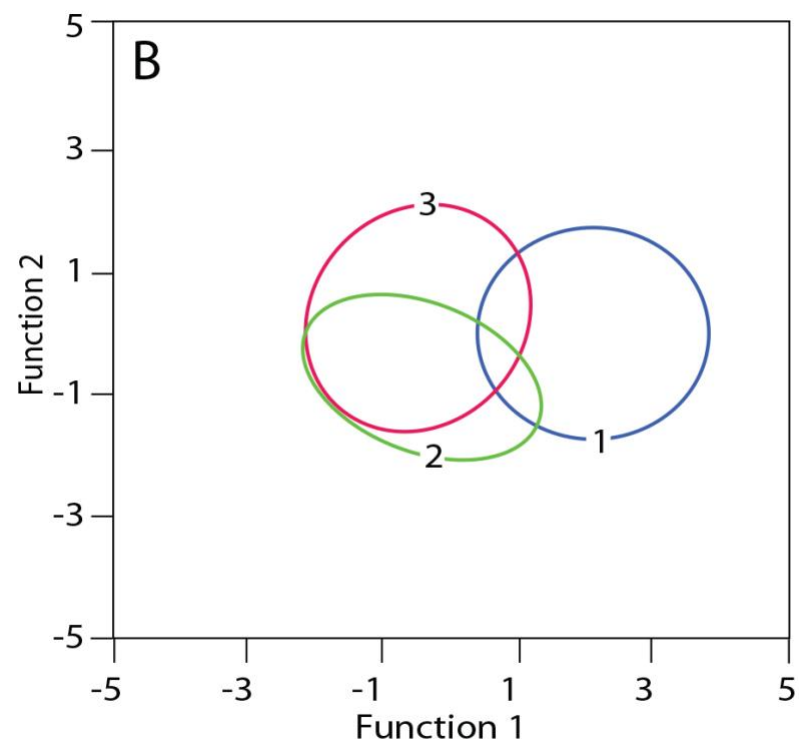
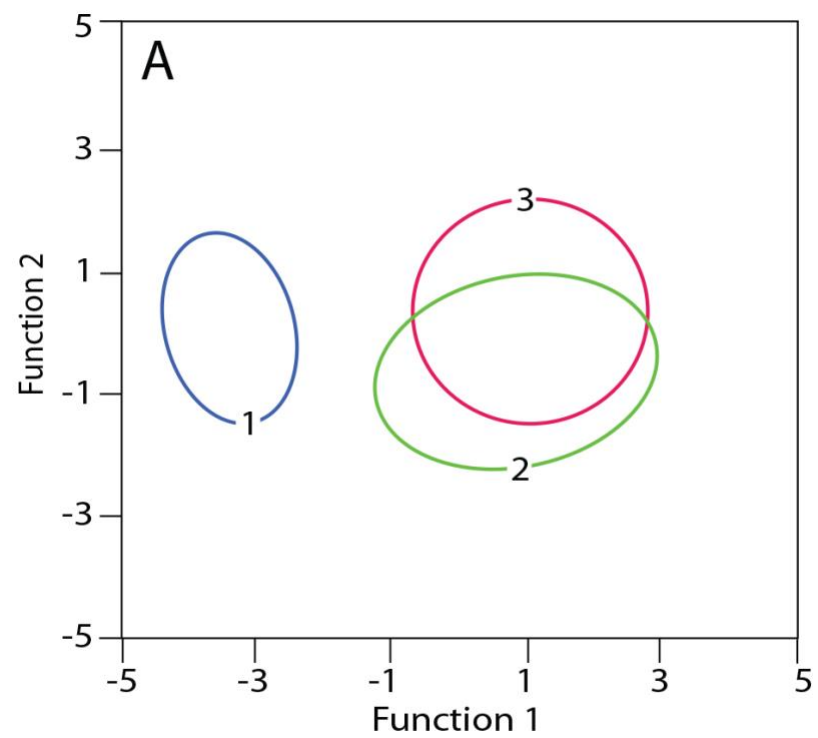
	Pp	Pts	Ptt	Total	% Correct
Pp	32/26	0/1	0/3	32/30	100/86.6
Pts	0/4	22/16	13/12	35/32	74.3/50
Ptt	0/7	30/16	47/44	77/67	68.8/65.60

¹ Group classification based on cross-validation in which each case is classified by the functions derived from all cases excluding that case.

² The probability of group membership is based on unequal sample sizes.

Table S6. Intergroup centroid Mahalanobis distances on raw and size-adjusted data for *Pan* pooled-sex samples.

	Pp	Pts	Ptt
Pp	0.000		
Pts	24.57/15.30	0.000	
Ptt	25.87/15.36	9.99/8.79	0.000



PCA of the *Pan* raw data set extracted two components with eigenvalues >1.0 . Principal component one (64.5% of variance) gives the highest scores to mandibles that are largest overall (Table S7). Principal component two (8.7% of variance) gives the highest positive scores to mandibles with small P_3 and M_1 dimensions and negative values for larger teeth. The component matrix and plot indicated that all of the linear dimensions had a similar level of influence in separating cases with component one, with differences in overall size being the most important contributor to dispersion. With component two, differences in the two dental dimensions are equally important, but their influence on the distribution of cases is more complex than with the other variables. A plot of the confidence ellipses for the PCA scores obtained a similar result to the DFA (Figure S1). While there is a great deal of overlap between the *Pt* subspecies, *Pp* is distinct. PCA of the size-adjusted data extracted three components with eigenvalues >1.0 . The first component (31.9% of variance) gave the highest scores to the largest mandibles. For the second component (17.8% of variance), symphyseal height, followed by corpus height, M_1 buccolingual breadth, and arch breadth were most important. As expected, following the DFA, a plot of the confidence ellipses for the first two factor scores demonstrated that group separation was greatly reduced with the size-adjusted data. Based primarily on their relative symphysis and corpus dimensions, *Pp* formed the most distinctive group, while the *Pt* groups had a similar range of dispersion.

Table S7. Variable loadings for the first two components in the unadjusted and size-adjusted *Pan* PCA.

	Unadjusted data		Size-adjusted data	
	Component 1	Component 2	Component 1	Component 2
Symphyseal height	0.855	0.287	0.090	0.846
Symphyseal thickness	0.806	0.157	0.633	0.197
Corpus height	0.845	0.237	0.425	0.619
Corpus thickness	0.845	0.158	0.441	0.333
Bigonial breadth	0.775	-0.144	0.619	-0.079
M2 arch breadth	0.866	-0.109	0.757	-0.410
M ₁ buccolingual	0.727	-0.421	0.722	-0.409
P ₃ mesiodistal	0.669	-0.576	0.594	-0.035
Ramus min breadth	0.819	0.234	0.510	0.128

The *Pan* univariate, DCA, and PCA results, based on a limited number of mandibular dimensions, support previous statistical comparisons of cranial, mandibular, and dental variation within this genus (Shea et al., 1993; Uchida, 1996; Taylor and Groves, 2003; Taylor, 2006). There are size and shape

differences that distinguish the skeletons of bonobos from chimpanzees, but distinctive patterns of variation are not present for the chimpanzee subspecies. While there are behavioral, morphological, and genetic differences between bonobos and chimpanzees (Zihlman, 1978; Kuroda, 1980; Burrows and Ryder, 1997; Guillen et al., 2005), the time depth of the split in the Pp and Pt lineages (Stone et al., 2002; Yu et al., 2003; Won and Hey, 2005), and the factors behind the observable morphological and behavioral differences, are the subject of continued debate (Johnson, 1981; Wrangham and Peterson, 1996). Currently restricted to closed forest, it has been suggested that Pp consumes a higher quantity of terrestrial herbaceous vegetation (THV) than the Pt subspecies, which would have implications for cranio-facial morphology and masticatory load resistance in Pp. One might predict that the greater mechanical demands of consuming a larger proportion of THV would result in a somewhat more gorilla-like masticatory system in bonobos relative to chimpanzees. However, Taylor's (2002) detailed study found no systematic differences that could be clearly linked to diet. If bonobos favor high quality THV, which is low in cellulose (Malenkey and Stiles, 1991; Wrangham et al., 1996), then the masticatory effort of consuming an increased quantity of foliage may be mechanically insignificant (Taylor, 2002). Rather than the physical properties of diet, the relatively smaller body size, and somewhat paedomorphic development in bonobos could be the result of geographic isolation and behavioral adjustments resulting from the absence of competition with gorillas (Wrangham and Peterson, 1996). Regardless of when or why the two *Pan* species diverged, their separation is reflected in their mandibular dimensions, as clearly as in other aspect of skeletal or dental morphology. On this basis, the same set of mandibular dimensions were applied to the Liang Bua mandibles to see if they could be discriminated from *H. sapiens*.

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Figure caption

Figure S1. Bivariate plots of the unadjusted (A) and size-adjusted (B) pooled-sex *Pan* DFA and the unadjusted (C) and size-adjusted (D) *Pan* PCA analyses, with the sample distributions represented by 90% confidence ellipses. Ellipse labels: *Pan paniscus* (1), *Pan troglodytes schweinfurtii* (2), and *Pan troglodytes troglodytes* (3).