

A geometric morphometric assessment of hominoid crania: conservative African apes and their liberal implications

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Summary. This study examined the cranial affinities of all extant hominoids using 3D geometric morphometric analysis. A least squares Procrustean superimposition was used to eliminate differences due to location, orientation, and size. Because of a persistent correlation between centroid size and shape variation, an allometric size adjustment was also applied to these data. Phenetic affinities were then examined through a battery of multivariate statistical analyses.

Results of this study indicate a strong affinity between *Hylobates* and *Gorilla*; *Pan* is also similar to these genera, while *Pongo* and *Homo* are each very different. The autapomorphic morphologies of orangutan and modern human crania have been well established from previous studies. The similarity between *Hylobates* and *Gorilla*, however, has important implications for studies of hominoid morphology. First, these results suggest that African ape crania – and particularly those of *Gorilla* – retain an overall morphology that is conservative among hominoids. Secondly, this similarity suggests that character coding of cranial features may tend to overestimate the degree of polymorphism among extant apes. This study concludes that allometry may play a greater role in the morphogenesis of hominoid cranial variation than has been previously thought. While this problem likely has negligible impact on systematic studies of extant hominoids, it seriously affects our ability to place fossil taxa within a phylogenetic framework.

Key words: Morphometrics – Hominoids – Cranial morphology – Allometry

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Introduction

Phylogenetic relationships among the extant hominoids have been largely resolved by advances in molecular techniques (Pilbeam 2002). According to this consensus view, *Hylobates* is the sister taxon to all hominids (great apes and humans), followed by successive branching of *Pongo* and *Gorilla*; *Homo* and *Pan*, then, are thought to be most closely related among extant apes. While this last relationship cannot be strongly supported by morphological evidence, the phylogeny of non-human apes is rooted in a long history of scientific discourse. In particular, the position of hylobatids as the “sister taxon” to the great apes and humans was generally accepted long before such a term became vogue (e.g., Pilgrim 1927; Simpson 1953; Weidenreich 1946).

More recent studies of extant apes have corroborated the distinction between hylobatids and hominids based on descriptive (e.g., Begun et al. 1997), traditional morphometric (e.g., Rae 1993), and geometric morphometric analyses (Guy et al. 2003; McNulty 2003). Yet such results, while conforming to the phylogenetic consensus, are troubling on epistemological grounds. It is an unfortunate fact that the vagaries of evolutionary sampling have left the modern world with a meager five genera of apes. Making matters worse, the greatest phylogenetic distinction among them is superimposed on a dichotomy in body size: the outgroup of great apes and humans is a substantially smaller taxon. Thus, if allometry plays a significant role in the morphogenesis of hominoids – if the differing requirements of a 6 kg gibbon and a 150 kg gorilla have significant structural consequences – analyses of shape will tend to yield the “correct” phylogenetic result for reasons that may be largely allometric.

This is not to imply that allometry and phylogeny are mutually exclusive factors. Indeed, the evolution of a lineage is intimately tied to size differences within that lineage (Simpson 1953). A single evolutionary change in body size, however, can result in a cascade of accompanying morphological changes. Thus, failure to properly distinguish between allometric and phylogenetic effects will inflate the degree of polymorphism ascribed to these taxa, obscuring the evolutionary transformations of affected morphology. The phylogenetic position of a single, small-bodied ape as the sister-taxon to much larger taxa makes this type of error more likely in studies of hominoids.

This project examined the association between size and cranial morphology using 3D coordinate data. Three goals were sought after: (1) analysis of hominoid cranial affinities based on uncorrected data; (2) assessment of the contribution of size to variance in hominoid crania; and (3) examination of phenetic affinities among hominoid crania after applying a size adjustment.

Materials and morphometric methods

The study included a comparative sample of specimens from each of the five extant hominoid genera (see Tab. 1). Specimens from all commonly recognized hominid (i. e., great ape and human) subspecies were included so as to incorporate the morphological diversity within each of these genera. *Hylobates* was represented by specimens of *H. (Hylobates)* and *H. (Symphalangus)*, with the former represented by three subspecies each of *H. agilis* and *H. muelleri*. This allowed for a broad sampling of variability among hylobatids without excessively biasing the study towards this genus.

Data collection was accomplished using a Microscribe 3DX digitizer (Immersion Corp.). All landmarks were measured using the fine tip and recorded in centimeters to four decimal places. Definitions and illustrations of these landmarks are given by McNulty (2003). Intra-observer error was assessed by ten replicate measurements from a single female *Gorilla* specimen. The root mean squared distance across all landmarks, obtained from the square root of the trace of the covariance matrix, was 0.2 mm.

Specimen configurations were superimposed using a generalized Procrustes analysis (e. g., Slice et al. 1996; Dryden and Mardia 1998) performed in *tpsSmall* (Rohlf 1999). This procedure isometrically scales each specimen to a unit centroid size, translates them to a common origin, and rotates them to minimize the sum of squared distances across landmarks and specimens. As Procrustes superimposition maps data to a non-Euclidean space

Table 1. Sample sizes used in analyses. All specimens were measured by the author at the American Museum of Natural History, National Museum of Natural History, Museum of Comparative Zoology, Peabody Museum, Powell-Cotton Museum, Humboldt University Museum für Naturkunde, and Musée Royal de l'Afrique Centrale. Only adult, wild-shot specimens were included.

	<i>Gorilla</i>	<i>Homo</i>	<i>Hylobates</i>	<i>Pan</i>	<i>Pongo</i>
Female	40	18	59	90	30
Male	52	20	69	65	33

(Slice 2001), fitted configurations were projected into a Euclidean space tangent to this one at the sample mean. The correspondence between these two spaces was tested in *tpsSmall* and found to be highly significant ($r = 0.9999$, slope = 0.9957, root mean squared error = 0.0006). These aligned coordinates projected into tangent space (hereafter, fitted coordinates) were used in all subsequent analyses.

Research design and statistical methods

This study comprised three related analyses. First, multivariate statistical techniques were applied to the fitted coordinates to demonstrate the expected phenetic relationships among extant hominoid crania. Next, a series of regressions were used to determine the degree to which size – independent of variance attributable to sex and family membership – is correlated with cranial shape. Finally, the same multivariate methods were applied to size-adjusted coordinates, generating a new set of phenetic relationships. Several variations on this final analysis were conducted in order to test for possible confounding factors. All statistics were computed in *SAS* (SAS Institute, Inc. 1999).

Principal components analysis (PCA) was performed on the covariance matrix of the fitted coordinates to reduce dimensionality in the overall dataset. Because extant hominoid specimens can be reliably assigned to genera, the non-zero principal components were used to compute canonical variates and generate Mahalanobis D^2 values. As this metric is a biased estimator of the true squared Mahalanobis distance, unbiased D^2 values were computed (e. g., Marcus 1969). Hotelling's T^2 was used to test for significant differences, and hierarchical relationships were examined through UPGMA clusters of the corrected D^2 values.

In addition to these multivariate techniques, linear regression was used to assess relationships between landmark data and specific variance factors (e. g., size, sex, taxon membership). Variability due to categorical factors (e. g., sex, family) was removed from the data by regressing coordinates against binary variables corresponding to either membership (1) or non-membership (0) in these categories (e. g., Bookstein 1996; Frost et al. in press). Variance correlated with size was sequestered by regressing fitted coordinates against the logarithm of centroid size; residuals from this regression (hereafter, size-adjusted coordinates) were used in later analyses in order to examine the effect of applying an allometric correction. The influence of all such factors was determined by comparing the sample variance before regression to variance in the residuals.

Phenetic analyses of the size-adjusted coordinates proceeded as those of the fitted coordinates. Additional analyses were conducted on subsets of the data to address three potential confounding factors: differential covariance patterns among genera; sexual dimorphism; and excessive influence of neurocranial landmarks. First, covar-

iance patterns were assessed with a permutation test (see, e.g., O'Higgins 2000), resulting in a cluster analysis that excluded humans. Second, analyses were repeated separately on males and females to assess the effect of sexual dimorphism. Finally, neurocranial landmarks were excluded from one analysis to eliminate differences in brain size or cresting patterns.

Results

Table 2 lists the unbiased D^2 values computed from both fitted coordinates (lower triangle) and size-adjusted coordinates (upper triangle). Clusters based on these values are illustrated in Figure 1, with cluster distances listed in Table 3. Analyses of the fitted coordinates yielded the expected phenetic relationships (see Fig. 1 a): *Homo* was most distinct, followed by *Hylobates*; great apes clustered together with the shortest distance between *Gorilla* and *Pan*. Hotelling's T^2 indicated significant ($p < 0.001$) differences between all pairs. Excepting the autapomorphic human crania, this conforms nicely to the consensus phylogeny.

Further analyses, however, demonstrated that these results might be driven, in large part, by allometry. The first eigenvector, comprising 46.8% of the sample variance, was strongly correlated ($r^2 = 0.8839$; $p < 0.0001$) with centroid size; several additional axes demonstrated significant correlations, but with low r^2 values. Of the total sample variance 36.8% was explained by centroid size; excluding *Homo*, this value jumps to 48.6%. Additionally,

Table 2. Unbiased Mahalanobis D^2 values computed from fitted coordinates (lower triangle) and size-adjusted coordinates (upper triangle).

	<i>Gorilla</i>	<i>Homo</i>	<i>Hylobates</i>	<i>Pan</i>	<i>Pongo</i>
<i>Gorilla</i>	–	887.13	28.23	199.29	591.87
<i>Homo</i>	910.98	–	758.14	814.83	198.73
<i>Hylobates</i>	864.97	1164.58	–	134.74	379.79
<i>Pan</i>	221.43	743.00	680.56	–	455.87
<i>Pongo</i>	596.01	1173.61	1082.16	462.99	–

Table 3. Distances between clusters in phenograms computed from (a) fitted coordinates, (b) size-adjusted coordinates, (c) size-adjusted non-human apes, (d) size-adjusted female specimens, (e) size-adjusted male specimens, and (f) size-adjusted coordinates excluding neurocranial landmarks. Cluster numbers are labeled in Figure 1. Note that (a) has a different cluster topology (Fig. 1 a).

	Cluster 1	Cluster 2	Cluster 3	Cluster 4
a	0.28028	0.67023	1.10869	1.26330
b	0.05181	0.30653	0.87333	1.67879
c	0.09044	0.58754	1.57816	–
d	0.06543	0.22872	0.63416	1.89366
e	0.04593	0.39009	0.80651	1.68859
f	0.04846	0.32773	0.81371	1.71374

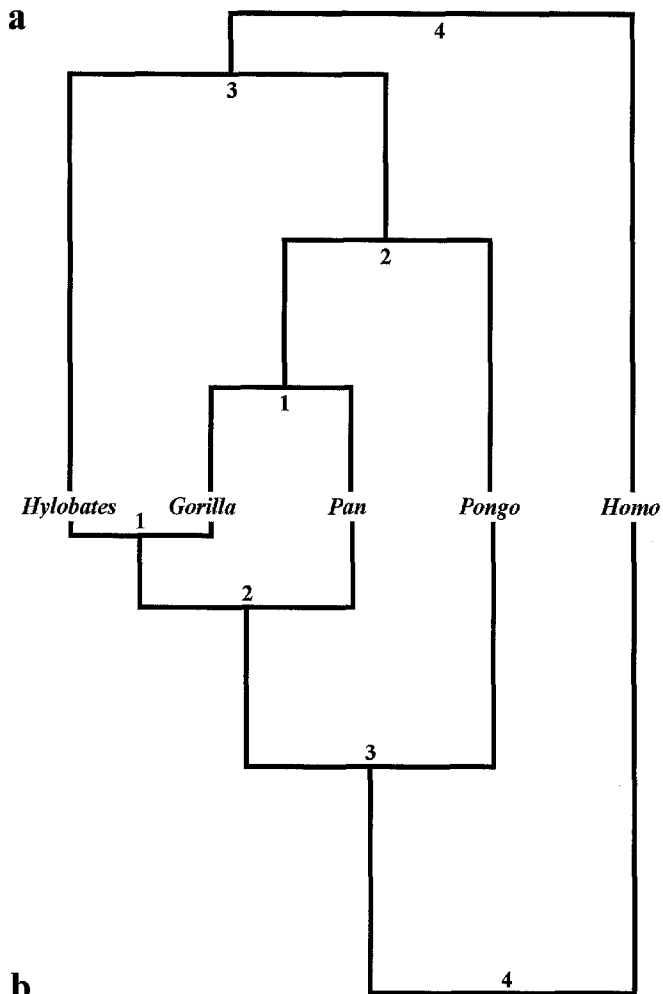


Fig. 1. UPGMA cluster diagrams based on (a) fitted coordinates, and (b) size-adjusted coordinates. Distances between clusters are given in Table 3, referencing the cluster numbers shown here.

size still accounted for 30.8% of the variability after removing the pooled variance due to sex, and 11.2% of the variance after removing family-level (hylobatid vs. hominid) differences. McNulty (2003) obtained similar results after adjusting for variance due to genus membership. Thus, size was shown to strongly correlate with shape, even apart from variability associated with differences in sex and family membership.

Therefore, statistical analyses were performed on size-adjusted coordinates yielding substantially different results (see Tab. 2: upper triangle, Fig. 1 b). All pairwise differences were again significant (Hotelling's T^2 : $p < 0.001$). In this trial, however, *Gorilla* and *Hylobates* were closest among extant apes. *Pan* was also most similar to *Hylobates*, and only slightly more distant from *Gorilla*. *Pongo* was further removed from these, with *Homo* again very distinct. A permutation test (Tab. 4) indicated that the pattern of covariation between centroid size and shape in *Homo* is significantly different from those in the other genera. Therefore, phenetic analyses were repeated using only the samples of non-human apes; the resulting cluster topology, however, was the same. Applying these meth-

Table 4. Permutation test results showing the probability that size vectors between genus pairs have equivalent angles.

	<i>Gorilla</i>	<i>Homo</i>	<i>Hylobates</i>	<i>Pan</i>
<i>Homo</i>	0.9997			
<i>Hylobates</i>	1.0000	0.0001		
<i>Pan</i>	1.0000	0.0001	0.7813	
<i>Pongo</i>	1.0000	0.0001	1.0000	0.2227

ods further to subsets of only males, only females, or only facial landmarks yielded exactly the same sequence of clusters (see Fig. 1 b), albeit with variations in cluster distances (Tab. 3). All of these analyses, therefore, indicate that the African apes, and *Gorilla* in particular, are quite similar cranially to *Hylobates* when size is taken into consideration.

Discussion

Results of the initial phenetic analyses illustrate a potential problem inherent to studies of hominoids. With the exception of *Homo*, affinities among these genera will tend to mimic their phylogenetic relationships: *Gorilla* and *Pan* cluster together, followed by *Pongo*, then *Hylobates* (see Fig. 1 b). Such results are intuitively pleasing, with phenetic evidence conforming to what most regard as the true evolutionary relationships. Yet, if allometry contributes substantially to hominoid cranial morphogenesis, then such conformation may have little to do with the evolutionary transformation of specific characters. If gibbons were to grow to the size of both chimpanzees and gorillas, might we not expect these to look more similar to each other than to the traditional lesser apes?

The influence of allometry on hominoid cranial morphogenesis is difficult to assess, precisely because this dichotomy in body size is superimposed over a major phylogenetic bifurcation. A simple regression found several eigenvectors associated with centroid size. Moreover, size was shown to account for nearly half of the total variability among non-human apes. Yet, the distribution of body sizes across ape phylogeny virtually guarantees that such correlations will exist. Therefore, some attempt was made to examine the influence of size apart from other morphogenetic factors. Even after removing variance due to sex and family-level differences, however, size was shown to correlate substantially with the residual shape variables. Thus, body size is an important factor in hominoid cranial morphogenesis. Such evidence argues that a strong allometric component underlies the pattern of phenetic relationships among apes.

The application of a size adjustment yielded substantially different results. After removing variance associated with centroid size, *Hylobates* and *Gorilla* were shown to be most similar – their D^2 value an order of magnitude smaller than any other pair. *Pan* was also closest to *Hylobates*, and only slightly further from *Gorilla*. Thus, when allometric differences are accounted for, African ape cra-

nia – and those of *Gorilla* in particular – are quite similar to those of hylobatids. This same relationship was also found when examining only non-human apes, only females, only males, and from analyzing only facial landmarks.

Three alternatives can explain the similarity between *Gorilla* and *Hylobates* morphology: it is convergently acquired, shared derived, or shared primitive. Functional convergence seems unlikely given the differences in both diet and postural behavior; indeed, siamangs, whose diet most closely approximates that of *Gorilla*, were least similar of all hylobatids to *Gorilla* (see McNulty 2003). A close phylogenetic relationship can also be discounted based on overwhelming morphological (e.g. Pilgrim 1927; Simpson 1953; Weidenreich 1946; Delson and Andrews 1975; Andrews 1985; Harrison 1987; Rae 1993; Begun 1994; Andrews et al. 1996; Begun et al. 1997) and molecular (Goodman 1963; Sarich and Wilson 1967; Caccone and Powell 1989; Ruvolo 1994; Goodman et al. 1998) evidence. Thus, the hypothesis favored here is that *Hylobates* and *Gorilla* (and *Pan* to a lesser extent) retain a conservative hominoid cranial morphology. In fact, a number of authors (Vogel 1968; Delson and Andrews 1975; Andrews 1985; Harrison 1987) have suggested that the hylobatid skull closely resembles the ancestral hominoid morphotype. Results from this project indicate that *Gorilla* crania may be similarly conservative.

Rae (this volume) has recently presented cladistic evidence that some hylobatid features may be secondarily reverted to a primitive condition. In itself, this does not contradict results shown here, leaving open the question of whether the *Gorilla-Hylobates* affinity is convergent or homologous. It does, however, add a layer of complexity to the interpretation of hominoid cranial evolution.

This work has important implications for analyses of hominoids. The probability of confusing allometric with multiple phylogenetic effects is greatly increased due to the depauperate sample of extant hominoids: the sister taxon to the large-bodied apes is comprised entirely of small-bodied apes. Given the affinities shown here, however, many of the features thought to be derived for hominines may, in fact, be allometric variants of conservative ape morphology. Errors of this sort would inflate the degree of polymorphism recognized among these genera. Worse, such mistakes would go largely unnoticed, because *the final results would appear to be correct*. One can obtain the “right” answer from data that are either miscoded or misunderstood. Committing such errors might only minimally impact phylogenetic analyses of extant hominoids; of much greater significance, however, are the consequences to analyses of fossil taxa. Phylogenetic hypotheses concerning such specimens are, by necessity, based on a limited character set. Miscoding even a few characters, therefore, can drastically alter phylogeny reconstruction among fossil taxa.

There is a vast body of literature associated with allometry and size adjustments. And, while most authors recognize the import of allometry in phylogenetic analyses, there has been no discussion of additional problems

posed by the superimposition of body size and phylogenetic dichotomies among apes. As shown here, this combination makes it difficult to assess allometric effects in hominoids. Moreover, failure to properly account for these effects will likely go unnoticed, as the resulting phylogeny will appear to be correct. Such errors will significantly impact hypotheses of character polarity and evolution, as well as phylogenetic analyses of fossil taxa. It is hoped that future exploration of this issue, incorporating multiple avenues of inquiry, can further our understanding of the relationships among size, phylogeny, and cranial morphology.

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