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## HOMINOID DENTAL SYSTEMATICS: MULTIVARIATE ANALYSES OF ALLOMETRICALLY CORRECT ODONTOMETRICS

**ABSTRACT.** — *This paper reports on continuing research into the dental evidence for biological affinities among hominoid species and populations. Previous analyses of odontometric data for hominids and pongids have yielded results which are easily reconciled to classifications based upon molecular, biochemical, and cytogenetic data, especially when deciduous data are considered.*

*In these analyses mean buccolingual diameters for both adult and juvenile members of species traditionally assigned to the Hominidae and Pongidae were corrected for allometry using a differential exponentiation method suggested by Corruccini (1978). The corrected data were then subjected to cluster analysis and principal coordinates analysis, and the patterns of affinities elucidated from these analyses were compared to those implied by various classification schemes. The results of these multivariate analyses of allometrically correct odontometrics tend to support the conclusions of previous work with non-corrected data by suggesting that traditional family level distinctions between apes and humans are less tenable than subfamilial ones.*

**KEY WORDS:** *Hominoids — Dental systematics allometry — Multivariate analysis.*

### INTRODUCTION

Although a virtual consensus exists concerning which primate species are subsumed into the superfamily Hominoidea there is a noticeable lack of agreement regarding the patterns of affinities exhibited by those species. Traditional interpretations from comparative anatomy and paleontology favor a classificatory scheme in which the chimpanzee, gorilla, and orangutan are more closely related to one another than to humans and, consequently, are assigned to the family Pongidae while the humans are considered the lone extant representatives of the family Hominidae (see e. g., Napier and Napier 1967; Simons 1972; Simpson 1945, 1963). More recent interpretations of relationships within the Hominoidea have tended to disagree with such an

arrangement. Based upon the analyses of newly exploitable data in biochemistry, cytogenetics, and molecular biology, as well as the development and utilization of cladistic analysis, there is suggested a much closer relationships among humans and the great apes than traditionally accepted. In such schemes chimpanzees, gorillas, and humans are subsumed into a single hominoid family, the Hominidae (subfamily Homininae) with the orangutan assigned variously to the family Hominidae, subfamily Ponginae, or the family Pongidae (Goodman 1975; Goodman et al. 1982; Schwartz, Tattersaal and Eldredge 1978; Szalay and Delson 1979; Yunis and Prakash 1982).

This paper reports the results of continuing research into the relationships between odontometric variation and the patterns of affinities suggested by



the analysis of this variation for the superfamily Hominoidea. As in a previous study of hominoid affinities (Mahaney and Sciulli 1983), the present one applies multivariate statistical techniques to the analysis of both deciduous and succedaneous dentitions. The intent of this investigation is to examine the patterns of relationships elucidated once the effects of variation in size on variability in shape (allometry) have been eliminated. Although size and shape are both important in the consideration of taxonomic and phylogenetic affinities, relationships arrived at on the basis of shape are generally agreed to be of much greater value than those based upon size alone (Corruccini 1978). Interpopulational differences in shape which are related to size are suggested to be the result of selection for overall size (Corruccini 1978; Gould 1975), while differences in shape which are unrelated to size differences are attributable to "independent adaptive processes" (Cheverud 1982: 140). The analyses of allometrically corrected data for closely related hominoid species are expected to yield patterns of relationship a bit more congruent with the degree of phylogenetic and taxonomic distance separating them than the analyses of uncorrected data (Cheverud 1982; Gould 1975).

## MATERIALS AND METHODS

### SAMPLES

This study utilizes the mean buccolingual diameter metrics obtained from the literature for the dentitions of both extant and extinct populations

for six hominoid species. Mesiodistal diameters were not collected because of their reported high degree of variability resulting from interproximal wear in fossil and prehistoric samples (Wolpoff 1971). Measures for both maxillary and mandibular central and lateral incisors ( $i1$ ,  $i2$ ), canines ( $c$ ), and anterior and posterior premolars ( $P^A$ ,  $P^P$ ) were analysed for the deciduous dentitions. The analysis of the succedaneous dentitions included metrics for maxillary and mandibular central and lateral incisors ( $I1$ ,  $I2$ ), canines ( $C$ ), anterior and posterior premolars ( $PA$ ,  $PP$ ), and first, second, and third molars ( $M1$ ,  $M2$ ,  $M3$ ). The juvenile and adult hominoid samples from which the data were collected consist of 16 and 19 groups, respectively, representing *Australopithecus afarensis*, *Homo sapiens* (*sapiens* and *neanderthalensis*), *Pan* (*Pan paniscus*, *Pan* (*Pan*) *troglodytes*, *Pan* (*Gorilla*) *gorilla*, and *Pongo pygmaeus*. Adult and juvenile odontometrics from the same geographical populations were analyzed whenever possible.

### DATA MANAGEMENT AND ALLOMETRY CORRECTION

Prior to correcting the mean buccolingual diameters for allometry it was necessary to estimate the value of the missing maxillary  $i1$  for the *Australopithecus afarensis* juvenile sample. This was accomplished employing a regression procedure for the estimation of missing data ("BMDPAM" in Dixon and Brown 1979; see also Mahaney and Sciulli 1983: 383).

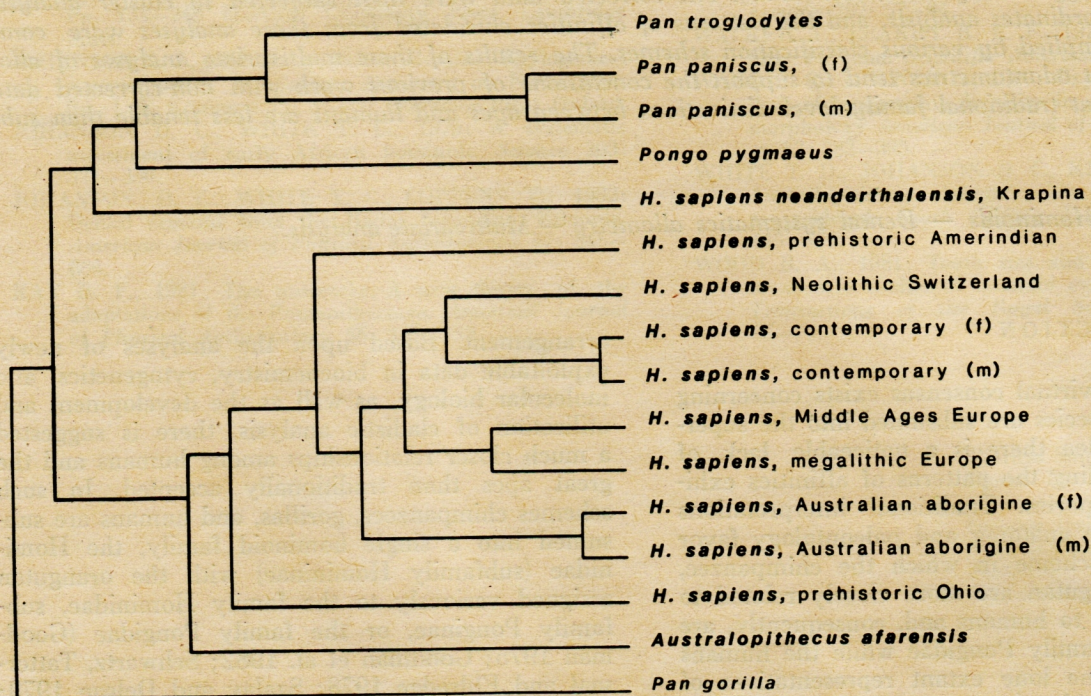


FIGURE 1. Dendrogram resulting from cluster analysis of allometrically correct mean buccolingual diameters for the deciduous dentitions of 16 hominoid groups.



The allometric adjustment of variates from the deciduous and succedaneous data sets was conducted according to the methods described by Corruccini (1978: 223–224). Procedurally the correction is accomplished in the following steps. (1) The raw variates are transformed to their common logarithms. (2) A standard size variable,  $G(x) = \prod x_i^{1/p}$  (i.e., geometric mean), is calculated for each  $\log_{10}$  population vector (over  $p$  traits). (3) Transformed measures for each trait (tooth) are regressed on

Following allometry correction, the data are converted to Euclidean distances,  $D = \sum [(x_{ij} - x_{jk})^2]^{1/2}$ , and cluster analysis is performed on both data sets using the "Cluster Analysis of Cases" package (BMDP 2M) of the BMPD series (Dixon 1981). The algorithm employs a single linkage criterion for the amalgamation of clusters in the production of a dendrogram (Dixon 1981: 456).

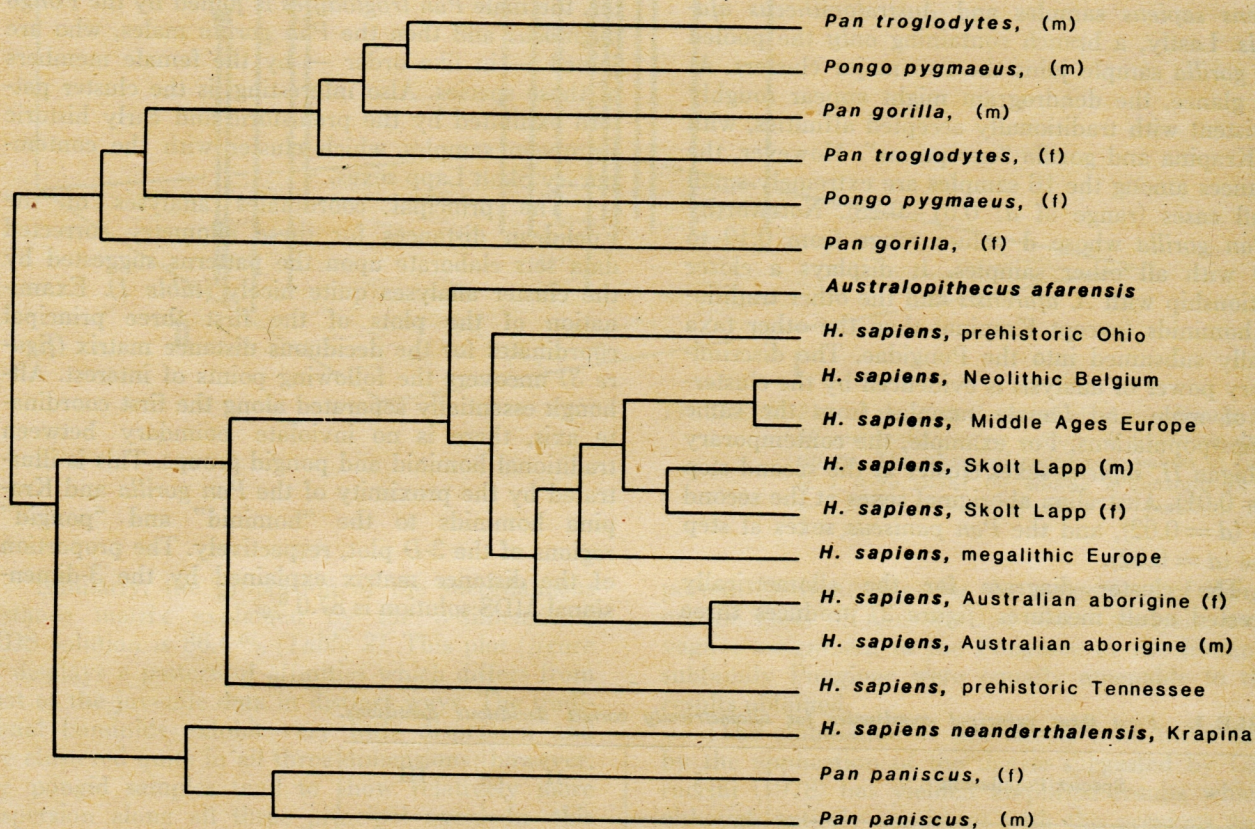


FIGURE 2. Dendrogram resulting from cluster analysis of allometrically correct mean buccolingual diameters for the succedaneous dentitions of 19 hominoid groups.

$G(x)$ . (4) The transformed variates are then exponentiated using  $k$  (regression slope)/ $r$  (regression correlation) to approximate the reduced major axis slope. (5) Subtraction of  $d$  (the y-intercept) from the exponentiated vector is followed by its division by  $G(x)$  to yield  $Z$ , the allometry corrected shape vector or,

$$Z = \frac{x_j^{k/r} - d}{G(x)} \quad (\text{Corruccini 1978: 223–224}).$$

"This correction is automatically applicable without regard for statistical significance of allometry" (Corruccini 1978: 224).

To supplement the cluster analysis, a multi-dimensional scaling (MDS) procedure, principal coordinates analysis, was conducted on the squared elements of the Euclidean distance matrices following their transformations to centered inner product matrices,  $B$ , by the methods described in Mardia, Kent, and Bibby (1979: 394–423) and Mardia (1978). Using the computational algorithms available in the Speakeasy-III software (Cohen and Pieper, 1979), the eigenvalues ( $\lambda_i$ ) and the eigenvectors were obtained. The scaled principal coordinates were then calculated in the following manner  $P.C. j = (\lambda_i)^{1/2} (e_{ij})$ . One of two agreement measures suggested by Mardia (1978: 1237) for determining the proportion of the Euclidean distance matrix explained by the  $k$ -dimensional MDS solution employed in this analysis is:

$$\alpha_k = \left( \sum_{i=1}^k [\lambda_i] / \sum_{i=1}^n [\lambda_i] \right) \cdot 100\%$$

where  $\lambda_k > 0$ .



## RESULTS AND OBSERVATIONS

An examination of the cluster diagrams produced from the Euclidean distance matrices yields the following observations. For the allometry corrected juvenile metrics (figure 1), two major clusters are evident. The smaller of the two contains the three chimpanzee samples, *Pan troglodytes* and the *P. paniscus* sexes, the pooled *Pongo pygmaeus* and *Homo sapiens neanderthalensis*, from Krapina. The larger of the two major clusters consists of groups traditionally recognized as hominids: all the *Homo sapiens sapiens* samples and *Australopithecus afarensis*. Lastly, a branch containing only the pooled *Pan gorilla* sample joins the two major clusters. At first glance, the dendrogram might appear roughly consistent with traditionally accepted affinities, with the Krapina and gorilla "exceptions". However, the distances among the 16 samples are extremely small in all cases (range of  $d$ : 0.01–0.28). Noteworthy is *Pan gorilla* whose  $d$  values range from 0.12 to 0.19 with all other samples. It displays a closer relationship with *A. afarensis* and the other traditional hominids (except Krapina) than the other taxa usually subsumed into the Pongidae. The discriminatory power of analysis is evidenced by the clustering of male and female samples from the same species/populations. For example, the contemporary Michigan *H. sapiens* sexes cluster at the second step ( $d = 0.01$ ), Australian aboriginal sexes at the second step ( $d = 0.02$ ), and the *Pan paniscus* sexes at step three ( $d = 0.02$ ).

The cluster diagram for the allometrically corrected adult measures (figure 2) produces three

relatively distinct but closely related (i.e., very small  $d$  values) clusters. The smallest cluster contains the *Pan paniscus* sexes and the Krapina neandertal samples; the remaining two are composed of traditional hominids, including *A. afarensis*, or traditional pongids only. The range of  $d$  values exhibited by the adults is slightly greater than that for the juvenile analysis ( $d = 0.04$  to 0.37). *Homo sapiens* sexes from the Australian samples and the Skolt Lapp samples, as well as the *Pan paniscus* sexes, each cluster as expected ( $d = 0.04$ , 0.04, and 0.01, respectively). However, in the great ape cluster, the male *Pan troglodytes* is joined by the *Pongo pygmaeus* and then the *Pan gorilla* males, who are joined — in like order — by the female members of those species. Also interesting, is the cluster pattern exhibited by the prehistoric and early historic European samples which cluster with the contemporary Skolt Lapp sexes.

The principal coordinates analyses of the Euclidean distances for these allometry corrected data sets elaborate upon the patterns suggested by the cluster analyses quite nicely (table 1). Examination of the plots of the first three principal coordinates for the deciduous distance matrix (figure 3) uncovers the following points of interest. Although essentially separated along the first coordinate axis, there is no inviolate boundary between traditional hominid and pongid groups. This is illustrated by the proximity of the *Pan gorilla* and Krapina hominids to the "hominid" and "pongid" regions of the 3-D plot, respectively. The proportion of the distance matrix explained by the 3-dimensional MDS solution is 87.0 %.

TABLE 1. First three principal coordinates for allometrically correct deciduous dentitions.

Species/Population	I	II	III
<i>Pan troglodytes</i>	—0.1521	—0.0353	0.0003
<i>Pongo pygmaeus</i>	—0.1388	—0.0364	0.0411
<i>Pan gorilla</i>	—0.0198	—0.0809	0.0536
<i>Pan paniscus</i> , males	—0.1183	—0.0303	—0.0413
<i>Pan paniscus</i> , females	—0.1346	—0.0139	—0.0469
<i>Australopithecus afarensis</i>	0.0843	—0.0271	0.0289
<i>Homo sapiens neanderthalensis</i>	—0.0568	0.0969	0.0091
<i>Homo sapiens</i> , prehistoric Amerindian	0.0640	0.0269	0.0004
<i>Homo sapiens</i> , male Australian aborigine	0.0118	0.0200	0.0073
<i>Homo sapiens</i> , female Australian aborigine	0.0252	0.0080	0.0008
<i>Homo sapiens</i> , Swiss Neolithic	0.0465	—0.0040	0.0075
<i>Homo sapiens</i> , megalithic European	0.0539	0.0288	—0.0062
<i>Homo sapiens</i> , Middle Ages European	0.0812	0.0065	—0.0126
<i>Homo sapiens</i> , prehistoric Ohio Amerindian	0.1318	—0.0239	—0.0406
<i>Homo sapiens</i> , contemporary Michigan males	0.0611	—0.0041	—0.0034
<i>Homo sapiens</i> , contemporary Michigan females	0.0605	—0.0041	0.0022
Cumulative proportion of distance matrix explained:	68.4 %	80.9 %	87.0 %

Data sources: *Pan troglodytes*, Ashton and Zuckerman (1950); *P. paniscus*, Johanson (1974); *Australopithecus afarensis*, Johanson and White (1979); Australian aborigines, Margetts and Brown (1978); prehistoric Ohio Amerindian, Sciuilli (1977); Swiss Neolithic, Brabant (1971); contemporary Michigan, Black (1978); medieval Europe, Lunt (1969); megalithic European, Brabant (1971); prehistoric Amerindian, Black (1979); *P. gorilla*, Ashton and Zuckerman (1950); *H. sapiens neanderthalensis*, Wolpoff (1979); *Pongo pygmaeus*, Ashton and Zuckerman (1950).



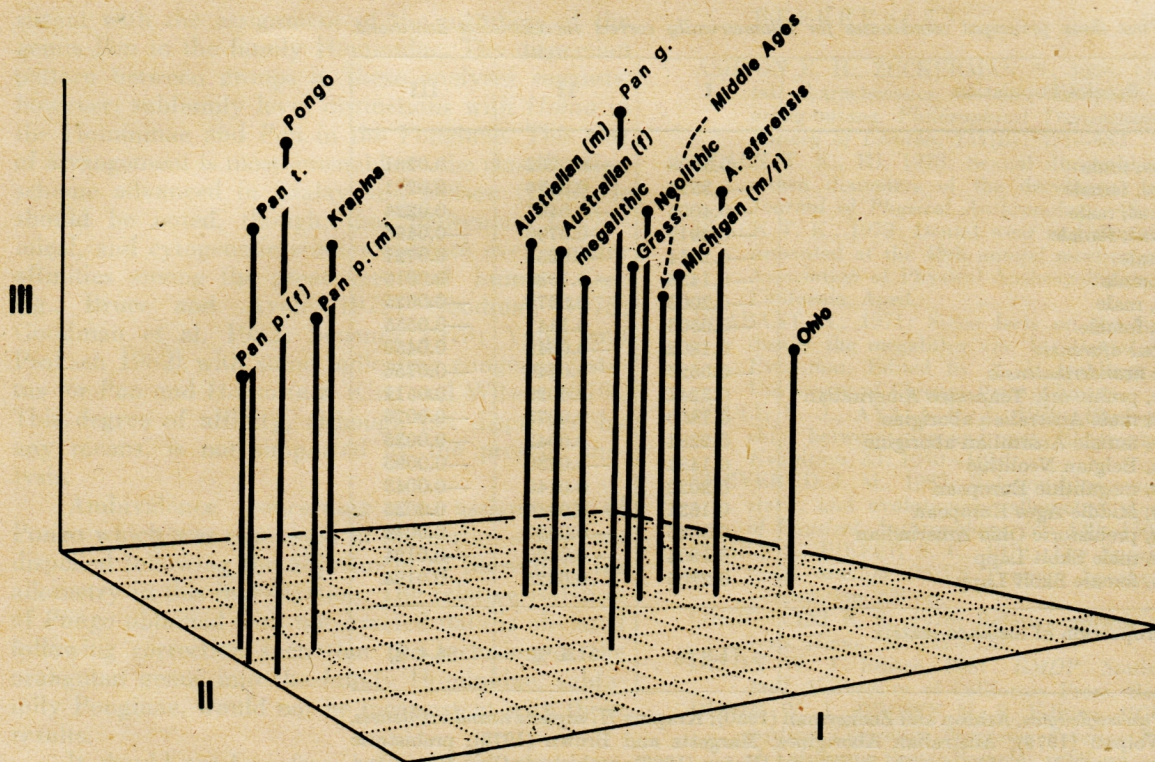


FIGURE 3. Plot of the first three principal coordinates for allometrically correct hominoid deciduous dentitions. The principal coordinate values in Table 1 were coded by adding a constant ( $k = 0.1521$ ) to each of them to facilitate the 3-D plot.

Similarly, the proportion of the succedaneous distance matrix explained by the 3-dimensional MDS solution is 86.4 % (Table 2). This plot (figure 4) displays a pattern of affinities which differs from that of the juvenile data in distinct ways. The traditional hominids exhibit very little dispersion and are clustered quite in all three dimensions; however, the pongid samples tend to show relatively more dispersion along all three principal axes. In this analysis, as in the previous one, the Krapina neandertal sample shows a noticeable proximity to the traditional pongid samples, especially those of female *Pan paniscus* and *Pan gorilla*.

#### DISCUSSION

In a previous study (Mahaney and Sciulli 1983), both cluster and principal coordinates analysis were applied to these same data without first correcting for allometry. The following briefly summarizes the conclusions of that study. (1) Multivariate analyses of the deciduous dentitions yielded patterns appreciably more conservative than those produced for the succedaneous dentitions. This was consistent with the generally agreed upon primitive nature of the deciduous dentitions of "higher" primates. (2) The traditional family level distinctions between the "pongids" and "hominids" were not supported by the analyses of the buccolingual diameter measures. Subsumption of the genus *Pan* into the hominidae, with distinctions made at the subfamily level (Homininae and Ponginae) was sup-

ported. (3) Indications for the assignment of *Pongo* on the basis of noncorrected data analysis were vague; assignment to the Pongidae or the hominid subfamily Ponginae were equally amenable to the results obtained.

The elimination of size effects from these data by the application of the metric suggested by Corruccini (1978) has yielded amplified results which, although entirely consistent with the previous analysis, contain some interesting differences in subtle aspects of the patterns of affinities obtained earlier. The observation of a conservative nature for hominoid deciduous dentitions is supported in these analyses. Both cluster and principal coordinates analyses produce somewhat more compact patterns of relationships for the deciduous teeth than for the succedaneous samples. On the whole, the pattern exhibited by the allometry corrected principal coordinates for the deciduous teeth is not substantially different than that obtained for uncorrected data.

As in the previous study of uncorrected metrics, family level distinction between these traditional pongid and hominid samples cannot be unequivocally supported on the basis of the analysis of allometry corrected buccolingual diameters. Although somewhat separated by both multivariate techniques, the between group dispersion is not interpreted as being indicative of familial distinction, especially when recognized samples of both groups exhibit within group differences as great, or greater than those elucidated between these groups. The results of this analysis are most con-



TABLE 2. First three principal coordinates for allometrically correct succedaneous dentitions.

Species/Population	I	II	III
<i>Pan troglodytes</i> , male	-0.3808	-0.0202	0.0261
<i>Pan troglodytes</i> , female	-0.3524	0.0426	0.0201
<i>Pongo pygmaeus</i> , male	-0.4004	-0.0407	0.0224
<i>Pongo pygmaeus</i> , female	-0.2917	-0.0706	-0.0496
<i>Pan gorilla</i> , male	-0.2714	-0.0254	0.0721
<i>Pan gorilla</i> , female	-0.1438	-0.1580	0.0016
<i>Pan paniscus</i> , male	-0.2003	0.0679	-0.0625
<i>Pan paniscus</i> , female	-0.0503	0.1447	-0.0555
<i>Australopithecus afarensis</i>	0.1802	-0.0049	0.0459
<i>Homo sapiens neanderthalensis</i>	-0.0522	0.0449	-0.0156
<i>Homo sapiens</i> , prehistoric Tennessee Amerindian	0.3241	0.0025	0.0511
<i>Homo sapiens</i> , male Australian aborigine	0.1800	0.0073	-0.0076
<i>Homo sapiens</i> , female Australian aborigine	0.2284	0.0042	-0.0035
<i>Homo sapiens</i> , Belgian Neolithic	0.1484	-0.0230	-0.0095
<i>Homo sapiens</i> , megalithic European	0.2022	0.0140	-0.0043
<i>Homo sapiens</i> , Middle Ages European	0.1631	-0.0144	0.0025
<i>Homo sapiens</i> , prehistoric Ohio Amerindian	0.3066	-0.0227	0.0044
<i>Homo sapiens</i> , male Skolt Lapp	0.1904	-0.0160	-0.0194
<i>Homo sapiens</i> , female Skolt Lapp	0.2205	-0.0325	-0.0194
Cumulative proportion of distance matrix explained:	71.9 %	81.4 %	86.4 %

Data sources: *Pan troglodytes*, Ashton and Zuckerman (1950); Krapina *H. sapiens neanderthalensis*, Wolpoff (1979); Australian Aborigines, Margetts and Brown (1978); prehistoric Tennessee *H. sapiens*, Smith, Smith and Hinton (1980); prehistoric Ohio *H. sapiens*, Sciulli (1979); Skolt Lapps, Kirveskari et al. (1978); megalithic *H. sapiens*, Brabant (1971); medieval European *H. sapiens*, Lunt (1969); Neolithic Belgian *H. sapiens*, Brabant (1971); *P. paniscus*, Johanson (1974); *P. gorilla*, Ashton and Zuckerman (1950); *Australopithecus afarensis*, Johanson and White (1979); *Pongo pygmaeus*, Ashton and Zuckerman (1950).

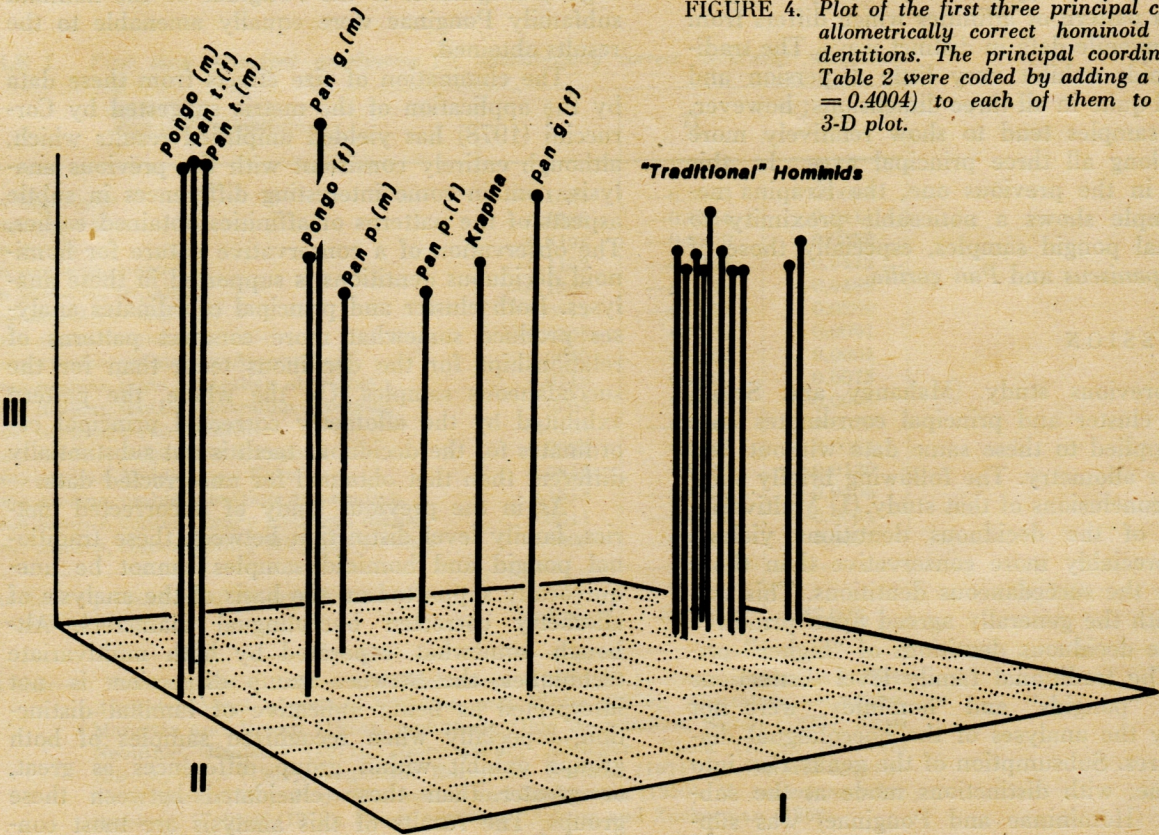


FIGURE 4. Plot of the first three principal coordinates for allometrically correct hominoid succedaneous dentitions. The principal coordinate values in Table 2 were coded by adding a constant ( $k = 0.4004$ ) to each of them to facilitate the 3-D plot.



sistant with the assignment of the members of the genus *Pan* to the family Hominidae. The dispersion pattern between groups in these analyses suggests, however, subfamily level distinctions with *Homo* in the Homininae and *Pan* in the Ponginae. This sort of arrangement is most amenable to the classification scheme advanced in Szalay and Delson (1979). It should be noted, though, that molecular, biochemical, and cytogenetic studies indicate even greater affinities among the great apes and humans (see e.g., Bruce and Ayala 1979; Goodman 1975; Goodman et al. 1982; Seuanez 1979; Yunis and Prakash 1982) with some indicating congeneric status for *Pan* and *Homo* (e.g. King and Wilson 1976). This degree of affinity, although not disproven by any means, is not supported by the present analysis.

Ambivalence concerning the assignment of *Pongo* which was expressed in the earlier study was dispelled following the adjustment of those data for allometry in this investigation. The relative isolation of *Pongo* obtained with uncorrected data is obviated following correction such that the inclusion of the orangutan genus into the family Hominidae, subfamily Ponginae, would not be inconsistent with these results.

It should not be inferred that allometry correction has had no appreciable effect on these analyses when compared to those for non-corrected data. The most discernible effects are found in the analysis of the succedaneous data, especially in the hominid and pongid samples in which the sexes are not pooled. The *Pan paniscus* sexes, for example, as well as the adult *Homo sapiens* from both extant and extinct European populations display a noticeable tendency toward reduction in interpopulational distances and much more than displayed by the deciduous samples. The greater contribution of size to differences in shape in fully grown adult members of closely related hominoid taxa may be responsible in part for the low dispersion in these size-independent vectors. However, Corruccini (1978: 224) notes that the "method (of allometry correction utilized in this study) characteristically has a more marked effect on reduction of within-sample distance in multivariate . . . analyses". That is, the differential correction provided by the  $k/r$  exponentiation in this metric tends to sort closely related groups (such as populations of the single species, *Homo sapiens*) into more discrete clusters without actually altering the distances between less closely related groups (such as different species of hominoids).

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