

Cranial Evolution in Sakis (*Pithecia*, Platyrrhini) I: Interspecific Differentiation and Allometric Patterns

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ABSTRACT Patterns of interspecific differentiation in saki monkey (*Pithecia*) skulls are quantitatively described. The taxonomic arrangement previously proposed by Hershkovitz ([1987] *Am. J. Primatol.* 12:387–468) is consistent with quantitative differences in saki morphology. Discriminant analyses on 39 skull traits show that *Pithecia* species and subspecies are well-differentiated. Morphological distances (D^2) among sakis clearly show the morphological unity of the *pithecia-chrysocephala* (*Pithecia*) and *irrorata-vanzolinii-monacha* (*Monacha*) species groups. The *Pithecia* species group is distributed north of the Amazon and has a smaller cranium than the

Monacha group, distributed south of that river. Despite the size difference, multivariate static allometric patterns among sakis are quite similar. After removing size and allometric changes in shape from the data, species and subspecies are still differentiated, although to a lesser extent. D^2 distances obtained from these scale-corrected data are similar in magnitude and pattern to the original D^2 , but show a closer similarity of *P. monacha* with the *Pithecia* group. *P. monacha* is a scaled-up version of the smaller sakis. *Am J Phys Anthropol* 125:266–278, 2004.

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Size and shape are important biological properties of organisms, arising from their genetic basis in complex association and sometimes interaction with the external and internal environment. Usually, a large fraction of the variability in morphometric data is due to size variation among individuals. Scaling effects might result in shape changes associated with changing size due to allometric relationships among traits, unless all morphological components grow or scale at the same rates (isometry). A long tradition in morphometrics has been to regard size as a nuisance factor in comparisons of organisms, with several methods being used to adjust size before comparisons (Bookstein et al., 1985; Somers, 1986; Rohlf and Bookstein, 1987; Lleonart et al., 2000). The rationale behind this approach is to regard size as a plastic feature of organisms and shape changes, unassociated with size (nonallometric), as adaptive (Sundberg, 1989). But size is as much a property of organisms as is shape, with important functional and ecological implications. For example, a simple increase in skull size (and concomitant allometric shape changes) might result in larger animals being able to handle larger and harder food items and therefore explore new resources or niches.

Saki monkeys (*Pithecia*) are medium-sized (weighing 1.7–2.4 kg) arboreal primates and one of the poorest known New World monkey groups, with sparse information available about their ecology, natural history, systematics, and evolution (Kinsey, 1997; Vié et al., 2001). *Pithecia* are highly frugivo-

rous, being seed-predators feeding on relatively hard fruit. They often live in relatively small family groups (Vié et al., 2001), occurring in a variety of habitats north and south of the Amazon, from highland to lowland forests, including seasonally flooded forests (*igapó*), secondary forests, and disturbed habitats. Their taxonomy was confused, until recently, by a failure to recognize external sexual dimorphism in diagnosing species. The review by Hershkovitz (1987) was a major advance, establishing a much clearer picture of *Pithecia* taxonomy. Two species groups were recognized by Hershkovitz (1987): the *Pithecia* group distributed north of the Amazon, with *P. pithecia pithecia* and *P. pithecia chrysocephala*; and the *Monacha* group distributed south

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of the Amazon, with *P. monacha monacha*, *P. m. milleri*, *P. irrorata irrorata*, *P. i. vanzolinii*, *P. aequatorialis*, and *P. albicans*. However, to date, no quantitative analyses of interspecific differentiation patterns have been undertaken. The present paper is a quantitative investigation of the taxonomic consistency of the arrangement by Hershkovitz (1987), as well as an investigation of size and shape variation in saki crania.

Before considering the evolutionary and taxonomic significance of our results, it is necessary to define what we mean by "species" throughout this paper. We refer the reader to de Queiroz (1998) for a particularly instructive discussion about the general agreement among current concepts and criteria used to recognize species (see also O'Hara, 1993). While there is no consensus about the meaning of species, de Queiroz (1998) showed that current species concepts, from the "biological" or isolation concept to the many versions of the phylogenetic concept, all share a fundamental idea: that species are segments of population-level evolutionary lineages (a lineage being a single line of direct ancestry and descent). We should also be aware that the recognition of species is a process of systematic generalization, analogous to the process of cartographic generalization applied to produce maps that are simplifications of the real world (O'Hara, 1993). When implementing that generalization, systematists pull together all the relevant information (e.g., ecology, range, and phenotypic and genetic character distribution) about the organisms, and based on any of the modern species definitions (ecological, cohesion, phylogenetic, evolutionary, isolation, recognitions, and others), judge whether or not discontinuities among groups are definitive and deserving of specific status (O'Hara, 1993). Our rationale here is that morphological discontinuities among sakis are relevant clues to be considered together along with the geographical position of populations in determining discontinuities in ancestor-descent relationships, and translating these into an informative taxonomic arrangement.

MATERIALS AND METHODS

Sample and measurements

Specimens of *Pithecia* were examined and measurements were obtained from 243 crania deposited at the following institutions: the American Museum of Natural History (AMNH), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Nacional do Rio de Janeiro (MNRJ), Museu Paranaense Emílio Goeldi (MPEG), and National Museum of Natural History (USNM). A complete list of measured specimens sorted by taxon and museum collection can be obtained from the authors upon request. The taxonomic arrangement used here generally follows Hershkovitz (1987). Except for *P. monacha milleri*, all taxa recognized by Hershkovitz (1987) were sampled. Only adult crania were used in the subsequent analyses. Specimens were consid-

ered adult when they had fully erupted and functional dentition, as well as closed or fused sphenoccipital and/or sphenothmoid sutures. The resulting sample sizes for each taxon are: *P. p. chrysocephala*, N = 50; *P. p. pithecia*, N = 40; *P. irrorata*, N = 51; *P. vanzolinii*, N = 24; *P. monacha*, N = 68; *P. aequatorialis*, N = 2; and *P. albicans*, N = 4.

Three-dimensional coordinates were recorded for 36 landmarks (Fig. 1), using a Polhemus 3D digitizer. The general procedure for measuring specimens followed Cheverud (1995). A set of 70 linear measurements describing cranial morphology was calculated from the coordinate values. This was reduced to a set of 39 measurements, after averaging measurements present on both sides of the skull (Tables 1 and 2). Whenever one of the skull sides was damaged, preventing us from taking any particular measurement, the other side was used. All results are presented in millimeters.

In total, 239 skulls with all 39 measurements (without missing values) were used in the analyses below. The geographic distribution of samples with their taxonomic designations is provided in Figure 2. In this study, we tested for differences between taxa and sexes, and for an interaction between sexes and taxa using a multivariate analysis of variance (MANOVA). Given that *Pithecia* species present sexual dimorphism, with males usually larger than females, data from the two sexes were pooled within each species or subspecies after adding the mean differences between males and females to each individual female measurement (no interaction between species and sex was detected). These data, corrected for sexual dimorphism, were used in all subsequent analyses.

Analyses

Interspecific differentiation. Differences among saki skulls were examined through a linear discriminant function (DF) analysis. We report both original and jackknifed percentages of cases correctly classified by DF analyses. This is useful, because the comparison of both percentages quantifies the uncertainty in assigning individuals to groups according to the estimated DFs based on our sample (Manly, 1997). If the DF analysis is reliable, the original and jackknifed percentages should be quite similar. Conversely, if the functions are unreliable in assigning individuals skulls to their correct groups, jackknifed percentages should be substantially lower in relation to the original ones. For estimating the degree of differentiation among sakis, Mahalanobis D^2 distances between group centroids were calculated. Morphological D^2 distances were also employed in a cluster analysis using the average linkage method (UPGMA), as recommended by Sneath and Sokal (1973), to inspect the pattern of morphological similarity among saki skulls. Additionally, the cophenetic correlation between the tree distance and the D^2 values used to produce it was

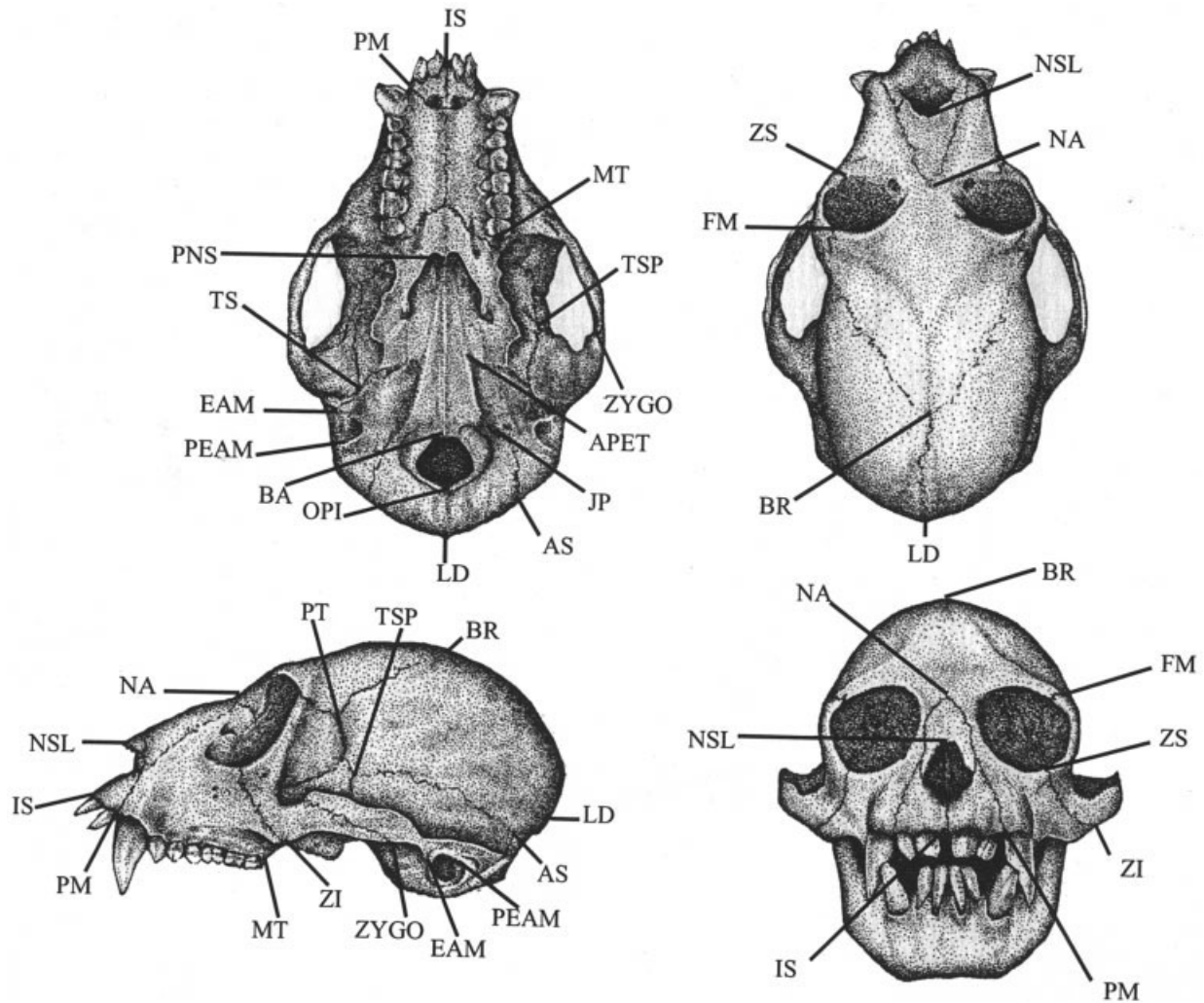


Fig. 1. Craniofacial landmarks recorded from saki skulls, using three-dimensional digitizer. Refer to Table 1 for description of landmarks.

calculated in order to evaluate how reliably the cluster diagrams represent the morphological distances. The cluster diagram is presented here as a useful graphic representation of the overall skull similarity in sakis, and is not intended to represent phylogenetic relationships among these taxa.

Allometry and scaling correction. The first principal component extracted from the variance/covariance matrix of each *Pithecia* species was computed. The 39 standardized PC1 coefficient values of each species were divided by $(1/\sqrt{39})$ to assess divergence from isometry (Jolicœur, 1963). In order to compare allometric coefficients among sakis, it is important to determine the associated error of those values. There are no analytical formulae for standard errors of multivariate allometric coefficients (ACs). A jackknife procedure was used to set 95% confidence limits to the allometric coefficients (see Box 18.6 in Sokal and Rohlf, 1995). The jackknife procedure consist of splitting the observed data into groups (with one specimen per group) and comput-

ing principal components coefficients n times (where n is the total number of specimens for each species), each time ignoring a different one of the i groups of observation. The resulting samples of n estimates of the PC1 coefficient were then normalized to a length of one and divided by $(1/\sqrt{39})$ to obtain a sample of allometric coefficients. Each recalculation produces a jackknife estimate St_{-i} of the ACs, which is converted to a pseudo-value ϕ , using the following equation:

$$\phi_i = nSt - (n - 1)St_{-i}$$

where St stands for the original sample statistic or, in our case, the original ACs. The jackknifed estimates (S_{St}) of the allometry coefficients are obtained from the average of those pseudo-values. The approximate standard error of the jackknife estimate was obtained as the square root of the sum of squared deviations, $\sqrt{\sum(\phi_i - \bar{\phi})^2/n(n - 1)}$ and was used to construct 95% confidence limits for the ACs of each species.

TABLE 1. Landmarks recorded in pithecia skulls, using three-dimensional digitizer¹

Landmark	Description	Position(s)
IS	Intradentale superior, A	Midline
PM	Premaxillary suture at alveolus, A	Right, left
NSL	Nasale, A	Midline
NA	Nasion, A	Midline
BR	Bregma, AP	Midline
PT	Pterion, AP	Right, left
FM	Fronto-malare, A	Right, left
ZS	Zygomaxillare superior, A	Right, left
ZI	Zygomaxillare inferior, A	Right, left
MT	Maxillary tuberosity, A	Right, left
PNS	Posterior nasal spine, A	Midline
APET	Anterior petrous temporal, A	Midline
BA	Basion, AP	Midline
OPI	Opisthion, AP	Midline
EAM	Anterior external auditory meatus, A	Right, left
PEAM	Posterior external auditory meatus, A	Right, left
ZYGO	Inferior zygo-temporal suture, A	Right, left
TSP	Temporo-spheno-parietal junction, A	Right, left
TS	Temporo-sphenoidal junction at petrous, AP	Right, left
JP	Jugular process, AP	Right, left
LD	Lambda, P	Midline
AS	Asterion, P	Right, left

¹ Designation A (anterior) or P (posterior) after landmark name indicates which position(s) of skull the landmark was recorded in. Landmarks are also identified in Figure 1.

The overall similarity of allometric patterns was quantified with vector correlations, which measure similarity of vector orientation in a p-dimensional space (p being the number of traits). Vector correlations are equal to the cosine of the angle between vectors. The expected range of vector correlations commonly occurring among 39-element vectors by chance alone is $-0.4 < r < 0.4$ (Ackermann and Cheverud, 2000). Additionally, because there is a sampling error associated with each estimated allometric vector, we used a self-correlation procedure to calculate allometric vector repeatability (Cheverud, 1995; Marroig and Cheverud, 2001). Allometric vector repeatability was estimated by correlating the observed PC1 and each of 1,000 PC1 bootstrap replicates obtained from a random resampling procedure. The bootstrap was done by sampling with replacement, using the n specimens from the observed sample of each species as a parent population. These correlations provided a distribution of self-correlation (Cheverud et al., 1989). We then used the mean of this distribution to measure allometry vector repeatability. To help judge how high allometric vector correlations were among species and subspecies, we adjusted the observed between-species vector correlations for estimation error by dividing the observed correlation by the square root of the product of the two vector repeatabilities (Cheverud, 1995; Marroig and Cheverud, 2001).

Given variation in size of saki species and consequently in shape variation associated with those size differences, we applied a normalization technique to scale data and remove allometric effects (Lleonart et al., 2000). This method was derived from theoretical equations of allometric growth removing all the in-

TABLE 2. Thirty-nine linear skull measurements (distances between landmarks) and membership in two major cranial regions¹

Measurement	Region
IS-PM	Face
IS-NSL	Face
IS-PNS	Face
PM-ZS	Face
PM-ZI	Face
PM-MT	Face
NSL-NA	Face
NSL-ZS	Face
NSL-ZI	Face
NA-BR	Neurocranium
NA-FM	Face
NA-PNS	Face
BR-PT	Neurocranium
BR-APET	Neurocranium
PT-FM	Face
PT-APET	Neurocranium
PT-BA	Neurocranium
PT-EAM	Neurocranium
PT-ZYGO	Face
PT-TSP	Neurocranium, face
FM-ZS	Face
FM-MT	Face
ZS-ZI	Face
ZI-MT	Face
ZI-ZYGO	Face
ZI-TSP	Face
MT-PNS	Face
PNS-APET	Neurocranium
APET-BA	Neurocranium
APET-TS	Neurocranium
BA-EAM	Neurocranium
EAM-ZYGO	Face
ZYGO-TSP	Face
LD-AS	Neurocranium
BR-LD	Neurocranium
OPI-LD	Neurocranium
PT-AS	Neurocranium
JP-AS	Neurocranium
BA-OPI	Neurocranium

¹ Table 1 defines each landmark, and Figure 1 shown their locations in a saki skull.

formation related to size, not only scaling all individuals to the same size, but also adjusting their shape to account for allometry (Lleonart et al., 2000). We adapted the method of Lleonart et al. (2000) by using the first principal component (PC1) score of the natural log data as the overall size measure, and regressing all 39 traits onto PC1. The correction according to Lleonart et al. (2000) is

$$Y^*_i = Y_i[X_0/X_i]^b$$

where Y_i and X_i are the values of a specific trait and overall size (antilog_e of the PC1 score) in individual "i," respectively, Y^*_i is the theoretical value for the trait at the average size, X_0 is the average antilog_e of the PC1 scores, and "b" is the PC1 coefficient for each of the 39 traits. For example, specimen AMNH 73535 had a original value (Y_i) of 9.947 for trait IS-PM, and a PC1 score of 0.918 (2.505 after taking its antilog_e). The average size X_0 is 1.575, and the PC1 coefficient of IS-PM is 0.0584. Therefore the, corrected value (Y^*_i) for this specimen is 9.681. After this correction, the original data of all saki species

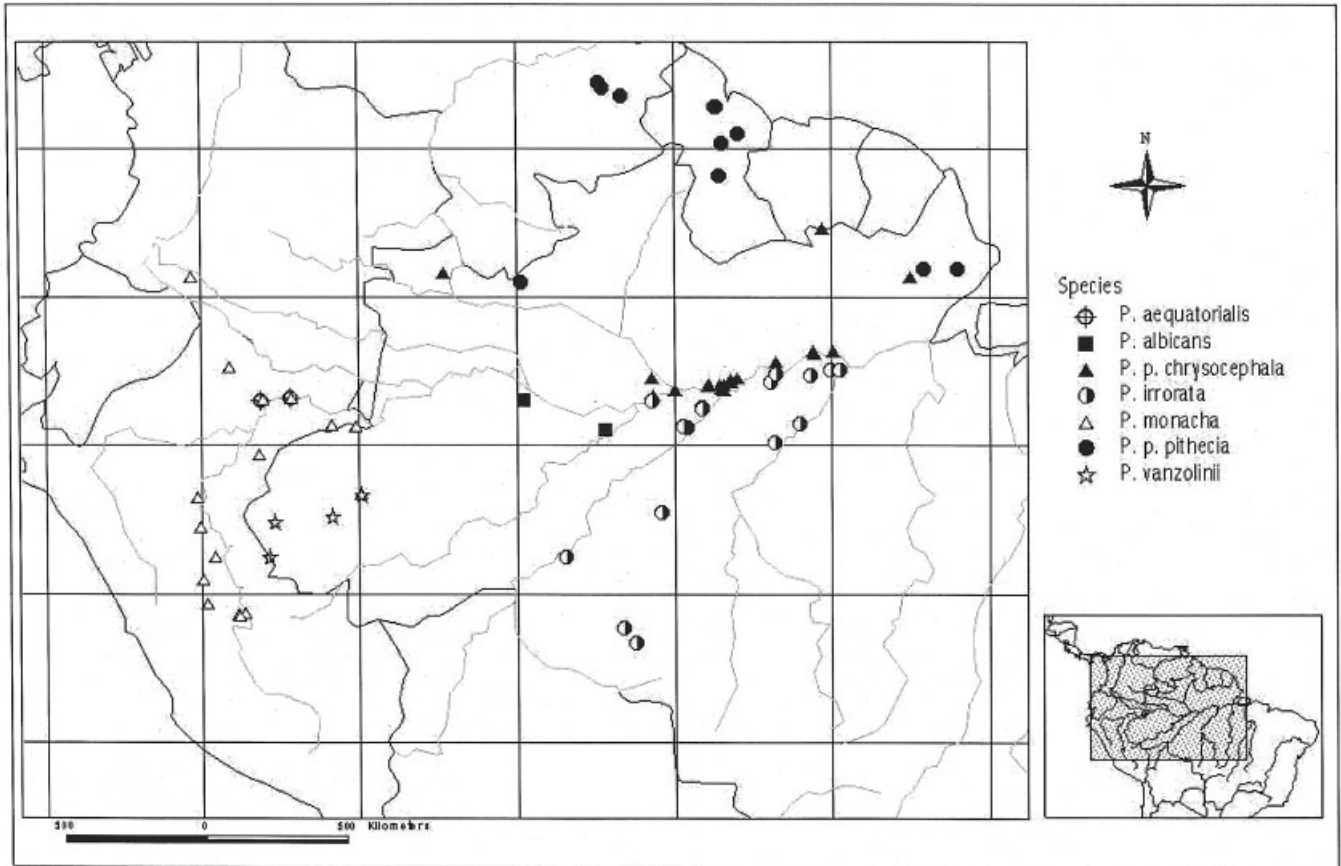


Fig. 2. Distribution of our skull samples of sakis species and subspecies in South America.

and subspecies were scaled to the same size, also adjusting their shape for allometric scaling effects. These scale-corrected data were used to explore whether differences among sakis were size-dependent. This was done by comparing the results of discriminant analyses, using the original and scale-corrected data.

RESULTS

A MANOVA was performed on the 39 measurements using sex, taxon, and sex by taxon interaction as independent variables in order to determine whether sexual dimorphism needs to be accounted for in the analyses. Two hundred thirty-three individuals were analyzed, and significant multivariate (Wilk's $\Lambda = 0.594$, $df = 39, 185$, $P < 0.001$) sexual dimorphism was detected. Twenty-seven of the 39 traits had significant univariate ($P > 0.01$) differences between the sexes. Conversely, there was no significant multivariate sex by taxon interaction (Wilk's $\Lambda = 0.430$, $df = 156, 739$, $P = 0.176$), and only two traits (NAPNS and BRAPET) had significant univariate sex by taxon interactions ($P > 0.01$). These two significant results most likely represent a type I error, given the lack of multivariate significance and their failure to reach Bonferroni levels of significance ($P < 0.05/39$). The lack of significant interaction indicates that sexual dimorphism does

not differ among the taxa. There were highly significant multivariate differences among the taxa (Wilk's $\Lambda = 0.010$, $df = 156, 739$, $P < 1.0 \times 10^{-6}$). Statistically significant univariate differences among taxa were observed in 32 of the 39 measurements, using the conservative sequential Bonferroni levels of significance (Rice, 1989). Given that significant sexual dimorphism was found, but no significant sex by taxon interaction was detected, all subsequent analyses were performed using sex-corrected data. While this simplifies the presentation of results, it is worth noting that using non-sex-corrected data does not affect the degree and pattern of differentiation observed in sakis.

The sample sizes and basic statistics for males and females of the seven saki taxa may be found in the Appendix. The linear discriminant analysis shows that all six functions are significant at least at $P < 0.0005$, the first function accounting for 57.1% of the total variance, and corresponding figures for the second, third, fourth, and fifth functions were 19.2%, 10.4%, 5.8%, and 5.1%, respectively. The canonical correlations of the first five functions were, from the first to the fifth, 0.95, 0.87, 0.79, 0.69, and 0.67. Figure 3 presents the canonical scores plot of the first two discriminant functions (DF1 and DF2), which together account for 76.3% of the total between-taxon variation. The first function separates

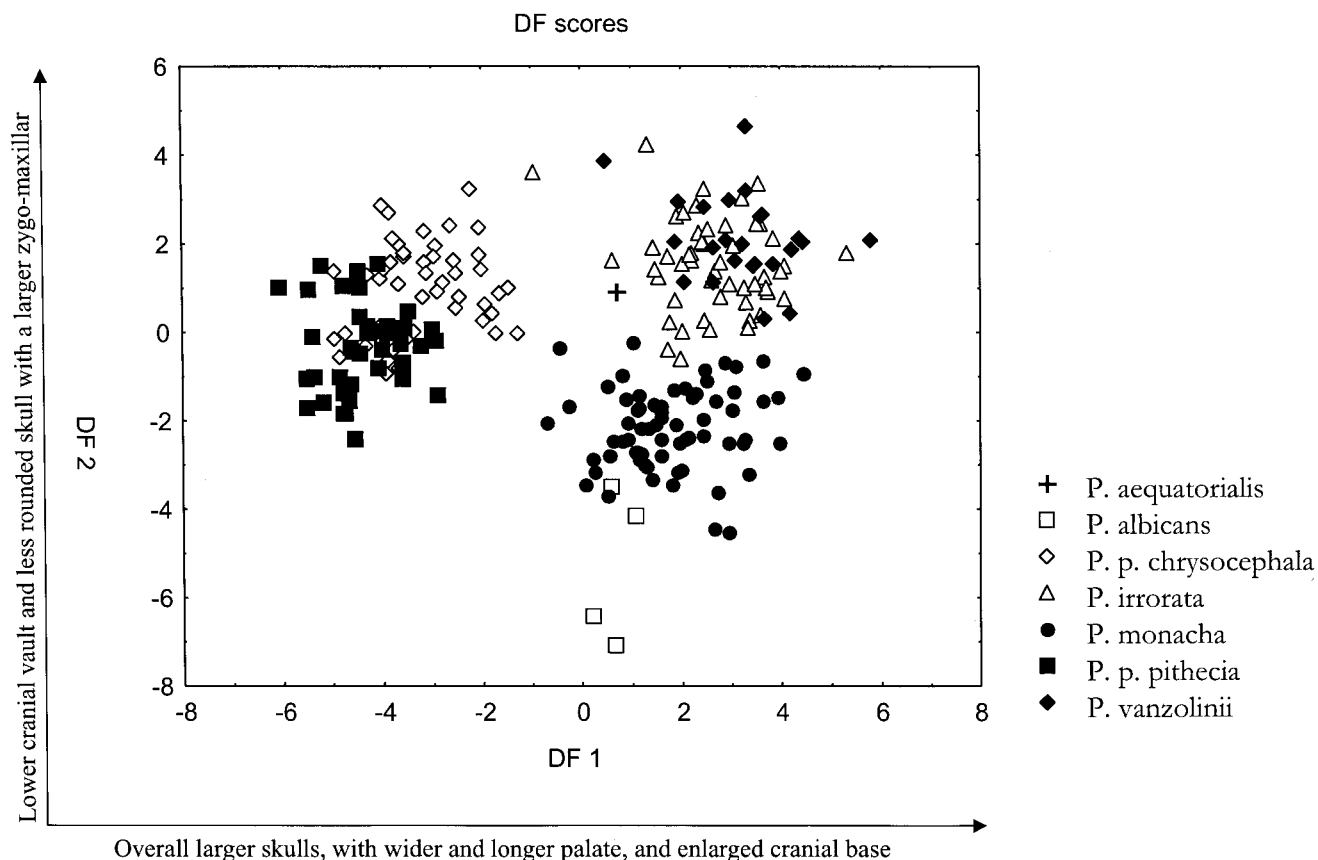


Fig. 3. Plot of saki species scores against first two discriminant functions (DF1 and DF2) obtained from original data (size and shape variation).

saki species into two groups, the Pithecia group and the Monacha group. This DF1 can be interpreted as a size function, which distinguishes a small-bodied group of species, the Pithecia group, from a large-bodied group, the Monacha group. Larger scores are associated with an overall larger palate, both in length and width, indicating a wider gape in the Monacha group. Characters PMMT, JPAS, PNSAPET, ISPM, NAFM, PMZI, PTAS, ISPNS, PTBA, BAEAM, MTPNS, APETBA, and LDAS make the largest contribution to DF1, with correlations with the function ranging from 0.78 (PMMT) to 0.47 (LDAS). DF2 further separates species within each of these two groups, *P. albicans* from *P. m. monacha* from *P. i. irrorata*, *P. aequatorialis*, and *P. i. vanzolinii* in the Monacha group, and *P. p. pithecia* from *P. p. chrysocephala* in the Pithecia group. Characters BRAPET, BRLD, PTEAM, EAMZYGO, ZSZI, MTPNS, and PTZYGO make the largest contribution to DF2, with correlations ranging from -0.58 (BRAPET) to -0.30 (PTZYGO) with the function. Larger scores on DF2 are associated with a lower cranial vault and a less rounded skull with a larger zygo-maxillary complex. Ninety-six percent of the total cases were classified correctly according to the discriminant functions, while 88% were classified correctly for the jackknifed classification matrix. The following percentages were found for the classifica-

tion of individuals per species: *P. aequatorialis*, 100% (100%); *P. albicans*, 100% (100%); *P. p. chrysocephala*, 94% (86%); *P. i. irrorata*, 96% (86%); *P. m. monacha*, 96% (91%); *P. p. pithecia*, 98% (85%); and *P. i. vanzolinii*, 100% (92%), the first and second values being the original and the jackknifed values, respectively. Table 3 shows the Mahalanobis squared distances (D^2) among saki species. The smallest distance is between *P. p. chrysocephala* and *P. p. pithecia* (12.7), and the largest is between *P. albicans* and *P. i. vanzolinii* (122.7). *P. albicans* is by far the most divergent of the saki species, showing the largest distances in relation to the other species. This is reflected in their more basal position in the cluster topology (Fig. 4). Distances between species within groups are smaller than distances between species of distinct groups, which is reflected in the close clustering of *P. p. pithecia* with *P. p. chrysocephala*, and of *P. i. irrorata* with *P. m. monacha* and *P. i. vanzolinii*. The cophenetic correlation between cluster diagram distances and the morphological distances used to produce it is 0.92, a statistically significant result ($P < 0.0005$), indicating that 85% of the information in the D^2 distances is represented in the phenogram.

Table 4 shows the multivariate allometric coefficients (ACs), corresponding standard deviations obtained from the jackknife, and the lower and upper

TABLE 3. Mahalanobis D^2 morphological distances among saki species based on raw data are shown below diagonal, with scale-free morphological distances above diagonal

	1	2	3	4	5	6	7
<i>P. aequatorialis</i>	0.0	114.3	58.0	58.6	66.3	53.9	66.7
<i>P. albicans</i>	119.7	0.0	78.0	87.7	65.7	66.2	117.9
<i>P. p. chrysocephala</i>	76.4	104.1	0.0	13.2	10.8	13.1	20.4
<i>P. i. irrorata</i>	61.5	92.3	43.5	0.0	19.9	20.5	20.8
<i>P. m. monacha</i>	67.9	67.8	38.0	20.6	0.0	11.3	26.7
<i>P. p. pithecia</i>	80.0	100.5	12.7	58.8	46.5	0.0	33.7
<i>P. i. vanzolinii</i>	67.4	122.7	54.3	21.1	28.2	75.9	0.0

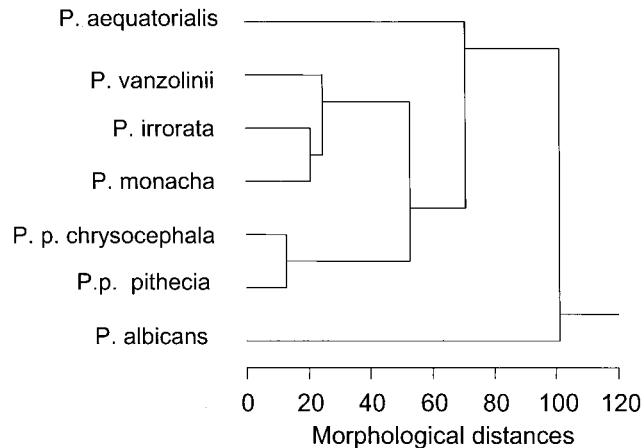


Fig. 4. Morphological relationships among saki species derived from UPGMA analysis of original data Mahalanobis D^2 values.

95% confidence limits for each species. Those ACs with confidence limits not encompassing one (isometry) were considered either negatively (below 1) or positively (above 1) allometric. Significant negative allometric coefficients range from 21% (*P. p. chrysocephala*) to 38% (*P. i. irrorata*) of all coefficients of each species, while positive ACs account for only 3% (*P. p. chrysocephala*) to 23% (*P. i. irrorata*). Other traits display isometry. In *P. i. vanzolinii*, about half of the positive ACs are for facial traits, and half are for neurocranial traits. In *P. m. monacha*, only 17% of the positive ACs are for the face, while most positive ACs are for facial traits in *P. i. irrorata* (100%) and *P. p. pithecia* (80%). Table 5 presents the original (uncorrected) allometry vector correlation, vector repeatability, and corrected vector correlation between species. All observed correlations are outside the range of vector correlations expected by chance alone. Allometric vector repeatabilities range from 0.60 in *P. i. vanzolinii* to 0.85 in *P. i. irrorata* and *P. m. monacha*. Although species are not identical in a qualitative inspection of the static allometric patterns, sakis are so similar in those patterns as were inferred from our sample because all observed vector correlations are indeed higher than expected, given their repeatabilities.

The discriminant analysis with the scale-corrected data generally agrees with the DF analysis done on the original data. The scale-free linear discriminant analysis shows that all six functions are

significant at least at $P < 0.0008$, the first function accounting for 39.8% of the total variance, and corresponding figures for the second, third, fourth, and fifth functions were 20.9%, 13.7%, 11.6%, and 9.5%, respectively. The canonical correlations of the first five functions were, from the first to the fifth, 0.88, 0.80, 0.73, 0.70, and 0.66. Correct classifications of specimens according to functions were to some extent reduced, with the following figures found: *P. aequatorialis*, 100% (100%); *P. albicans*, 100% (100%); *P. p. chrysocephala*, 90% (72%); *P. i. irrorata*, 94% (78%); *P. m. monacha*, 91% (81%); *P. p. pithecia*, 85% (78%); and *P. i. vanzolinii*, 96% (88%), with the first and second values being the original and the jackknifed values, respectively. Curiously, the DF1 of this second analysis had a vector correlation of 0.83, with the DF2 of the original analysis supporting the interpretation that the DF1 of the original analysis was a size function. Morphological distances among sakis in this second DF analysis (Table 3) were similar in magnitude and pattern to those found for the original data, with a matrix correlation of 0.89 ($P = 0.0007$ in the Mantel test) between both sets of D^2 distances. Cluster analysis of D^2 values derived from rescaled data showed that *P. m. monacha* now groups with *P. p. chrysocephala*, and both are linked tightly with *P. p. pithecia*, with this group then clustering with *P. i. irrorata*, *P. i. vanzolinii*, *P. aequatorialis*, and *P. albicans*, respectively (Fig. 5). This is also reflected in the canonical scores plot of the first two discriminant functions (DF1 and DF2), which together account for 60.7% of the total between-taxon variation (Fig. 6). The cophenetic correlation between the scale-free D^2 distances and the cluster distances was 0.88 ($P < 0.0008$), indicating that a substantial portion of the information (77%) in the morphological distances is represented in the cluster diagram. Yet the cluster diagram derived from rescaled data (Fig. 5) seems less resolved than the original (Fig. 4), partly because the magnitude of D^2 distances was somewhat reduced in relation to the original D^2 .

DISCUSSION

There is substantial phenotypic differentiation among sakis, as indicated by the results of our discriminant analyses. Besides the discriminant functions being highly significant, the general agreement between original and jackknifed classification results indicates that this analysis is reliable, de-

TABLE 4. Multivariate allometry coefficients (ac), theirs standard errors (se ac), and 95% confidence limits (l1 and l2) for each of five species based on first principal component extracted from each species' v/cv matrix¹

Allometric coefficients	<i>P. i. vanzolinii</i>				<i>P. p. pithecia</i>				<i>P. p. chrysocephala</i>				<i>P. i. irrorata</i>				<i>P. m. monacha</i>			
	AC	SEAC	L1	L2	AC	SEAC	L1	L2	AC	SEAC	L1	L2	AC	SEAC	L1	L2	AC	SEAC	L1	L2
ISPM	0.28	0.10	0.09	0.49	0.50	0.11	0.31	0.73	0.33	0.13	0.09	0.60	0.40	0.07	0.27	0.54	0.42	0.08	0.27	0.60
ISNSL	0.43	0.24	-0.03	0.92	0.56	0.28	0.05	1.13	0.27	0.21	-0.13	0.71	1.22	0.12	1.01	1.48	0.66	0.19	0.31	1.06
ISPNS	0.86	0.20	0.51	1.28	1.12	0.43	0.33	2.01	0.96	0.27	0.48	1.55	1.64	0.13	1.41	1.93	1.23	0.22	0.85	1.70
PMZS	1.21	0.31	0.64	1.87	1.00	0.35	0.37	1.72	0.69	0.28	0.19	1.28	1.15	0.11	0.96	1.38	0.46	0.20	0.08	0.87
PMZI	1.34	0.23	0.93	1.85	1.38	0.36	0.74	2.15	1.20	0.39	0.51	2.04	1.87	0.17	1.56	2.23	0.71	0.24	0.27	1.20
PMMT	0.48	0.17	0.16	0.84	0.58	0.14	0.33	0.88	0.86	0.25	0.42	1.41	0.75	0.14	0.49	1.03	0.54	0.17	0.23	0.89
NSLNA	0.56	0.31	-0.03	1.19	0.58	0.39	-0.16	1.37	1.05	0.44	0.25	1.97	0.45	0.16	0.14	0.77	0.69	0.31	0.11	1.32
NSLZS	1.42	0.22	1.05	1.90	1.03	0.46	0.17	1.99	0.81	0.25	0.37	1.35	0.99	0.13	0.76	1.25	0.78	0.27	0.27	1.34
NSLZI	1.89	0.24	1.50	2.42	1.92	0.45	1.13	2.90	1.51	0.37	0.87	2.33	2.15	0.20	1.79	2.57	1.30	0.28	0.80	1.89
NABR	0.71	0.61	-0.46	1.93	0.98	0.42	0.20	1.85	2.36	0.40	1.71	3.29	1.04	0.23	0.60	1.52	1.33	0.41	0.58	2.18
NAFM	0.94	0.13	0.72	1.24	0.24	0.13	0.01	0.50	0.56	0.25	0.10	1.09	0.81	0.16	0.52	1.13	0.51	0.19	0.17	0.89
NAPNS	0.67	0.15	0.40	0.98	1.00	0.29	0.48	1.62	1.20	0.27	0.74	1.80	1.23	0.10	1.04	1.45	1.18	0.17	0.89	1.54
BRPT	0.01	0.44	-0.84	0.87	0.40	0.34	-0.25	1.08	1.63	0.45	0.84	2.62	0.22	0.18	-0.12	0.57	0.56	0.46	-0.31	1.48
BRAPET	0.52	0.33	-0.10	1.18	0.40	0.21	-0.01	0.83	0.92	0.30	0.38	1.57	0.40	0.19	0.02	0.79	1.41	0.21	1.06	1.87
PTFM	0.13	0.20	-0.26	0.54	0.63	0.30	0.07	1.26	0.66	0.52	-0.31	1.71	0.57	0.24	0.11	1.05	-0.06	0.34	-0.72	0.61
PTAPET	1.18	0.20	0.83	1.62	0.74	0.30	0.19	1.36	0.27	0.44	-0.58	1.15	0.77	0.17	0.45	1.11	1.56	0.30	1.03	2.21
PTBA	2.01	0.23	1.65	2.54	1.59	0.23	1.21	2.13	0.92	0.47	0.07	1.90	1.55	0.15	1.28	1.85	2.23	0.22	1.87	2.75
PTBAM	1.66	0.19	1.36	2.09	1.24	0.37	0.59	2.02	1.08	0.52	0.12	2.18	1.24	0.18	0.90	1.62	1.75	0.26	1.30	2.32
PTZYG0	1.85	0.17	1.59	2.25	1.74	0.44	0.97	2.68	1.48	0.61	0.38	2.77	1.44	0.19	1.08	1.83	1.92	0.38	1.23	2.73
PTTSP	1.18	0.28	0.67	1.78	0.39	0.30	-0.18	1.01	0.03	0.55	-1.04	1.11	0.41	0.21	0.01	0.83	1.32	0.35	0.68	2.06
FMZS	-0.06	0.18	-0.41	0.29	0.02	0.17	-0.32	0.35	0.77	0.24	0.35	1.28	0.35	0.14	0.07	0.63	0.69	0.20	0.32	1.11
FMMT	1.03	0.11	0.86	1.28	1.46	0.17	1.21	1.86	1.40	0.19	1.11	1.87	1.46	0.14	1.20	1.76	1.20	0.20	0.86	1.64
ZSZI	0.79	0.24	0.35	1.29	1.20	0.20	0.86	1.66	0.77	0.23	0.35	1.27	1.06	0.17	0.73	1.42	0.41	0.27	-0.10	0.96
ZIMT	0.80	0.14	0.56	1.11	1.00	0.34	0.38	1.73	0.56	0.28	0.06	1.14	0.93	0.12	0.70	1.18	0.59	0.14	0.33	0.89
ZIZYG0	1.25	0.43	0.46	2.13	2.04	0.41	1.34	2.94	1.77	0.46	0.97	2.79	1.04	0.21	0.64	1.47	1.07	0.35	0.43	1.79
ZITSP	1.19	0.23	0.79	1.67	1.31	0.31	0.78	1.98	1.13	0.32	0.57	1.82	1.35	0.14	1.09	1.66	1.27	0.31	0.70	1.93
MTPNS	0.50	0.16	0.20	0.84	0.32	0.14	0.06	0.61	0.56	0.13	0.34	0.84	0.39	0.11	0.18	0.60	0.33	0.11	0.12	0.56
PNSAPET	1.25	0.36	0.60	2.00	1.10	0.19	0.78	1.54	1.34	0.44	0.56	2.30	1.09	0.17	0.78	1.44	0.65	0.22	0.23	1.11
APETBA	0.92	0.22	0.52	1.39	0.83	0.12	0.63	1.10	0.46	0.28	-0.05	1.03	0.77	0.13	0.53	1.04	0.64	0.15	0.36	0.96
APETTS	0.18	0.10	-0.02	0.39	0.51	0.24	0.08	1.00	0.30	0.32	-0.31	0.95	0.26	0.09	0.08	0.45	0.08	0.17	-0.25	0.41
BAEAM	0.48	0.19	0.13	0.87	0.65	0.17	0.35	1.01	0.51	0.17	0.21	0.88	0.65	0.10	0.46	0.85	0.72	0.19	0.37	1.13
EAMZYGO	0.72	0.39	-0.01	1.51	-0.47	0.44	-1.35	0.37	-0.01	0.23	-0.46	0.43	0.58	0.19	0.21	0.97	0.37	0.41	-0.42	1.19
ZYGOTSP	0.90	0.16	0.63	1.25	1.36	0.15	1.13	1.72	1.10	0.17	0.83	1.51	1.03	0.12	0.81	1.27	0.36	0.15	0.07	0.68
LDAS	0.10	0.20	-0.29	0.49	0.61	0.19	0.27	1.01	0.86	0.24	0.43	1.39	0.17	0.16	-0.14	0.48	-0.03	0.18	-0.39	0.32
BRLD	0.20	0.52	-0.81	1.22	0.40	0.51	-0.57	1.42	-0.72	0.60	-1.94	0.42	0.46	0.38	-0.27	1.21	0.43	0.47	-0.46	1.36
OPILD	0.53	0.55	-0.53	1.64	1.12	0.44	0.31	2.04	1.11	0.27	0.66	1.70	0.07	0.23	-0.38	0.52	0.53	0.28	-0.01	1.11
PTAS	1.81	0.27	1.34	2.41	1.05	0.34	0.43	1.78	0.98	0.38	0.29	1.79	1.22	0.18	0.88	1.60	1.69	0.22	1.31	2.18
JPAS	0.52	0.20	0.14	0.93	0.47	0.24	0.02	0.97	0.55	0.29	0.01	1.16	0.42	0.11	0.22	0.64	1.06	0.19	0.72	1.48
BAOPI	-0.21	0.18	-0.57	0.13	-0.06	0.14	-0.35	0.21	0.39	0.23	-0.03	0.87	0.18	0.10	-0.02	0.38	0.16	0.15	-0.13	0.45

¹ PC1 vectors were normalized and each coefficient was divided by (1/39)^{1/2} to obtain AC. Standard deviation estimates were obtained from jackknife analysis. Allometric coefficients with L1 higher than one (isometry) were considered positively allometric with general size (shown in bold), and conversely, AC with L2 lower than one were considered negatively allometric (normal font) with size. ACs with confidence limits encompassing 1.0 were considered to be isometric with size (italic).

TABLE 5. Correlations between saki allometric vectors (below diagonal), vector repeatability (bold diagonal), and adjusted correlations between allometric vectors (above diagonal)

	1	2	3	4	5
<i>P. i. vanzolinii</i>	0.60	1.41	1.23	1.30	1.29
<i>P. p. pithecia</i>	0.91	0.69	1.27	1.21	1.12
<i>P. p. chrysocephala</i>	0.80	0.89	0.71	1.08	1.04
<i>P. i. irrorata</i>	0.93	0.93	0.84	0.85	1.04
<i>P. m. monacha</i>	0.92	0.86	0.81	0.88	0.85

spite the low sample size of *P. aequatorialis* and *P. albicans*. Further support came from a discriminant analysis excluding these two latter species (results not shown), which is fully consistent with the discriminant analysis including all seven saki taxa. Discriminant analysis indicates that there are significant size differences between the small-bodied Pithecia group, distributed north of the Amazon River, and the large-bodied Monacha group, distributed south of the Amazon (Figs. 2, 3). In a complementary study, Marroig et al. (2004b) described the pairwise morphological differences among sakis, structuring the comparison within species groups. *P. p. chrysocephala* has a smaller, less prognathic, and

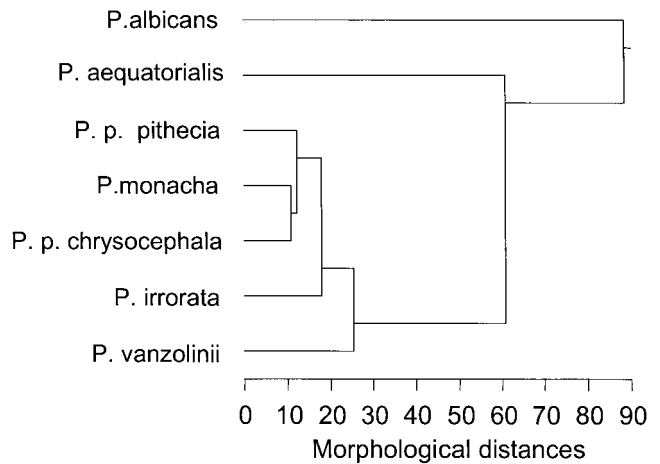


Fig. 5. Morphological relationships among saki species derived from UPGMA analysis of scale-free Mahalanobis D² values.

less spherical cranial vault than *P. p. pithecia*. *P. irrorata* has a longer prognathic face, short cranial base, lower cranial vault, and landmark zygomaxillary inferior (ZI) dislocated posteriorly relative to the face when compared to both *P. monacha* and *P.*

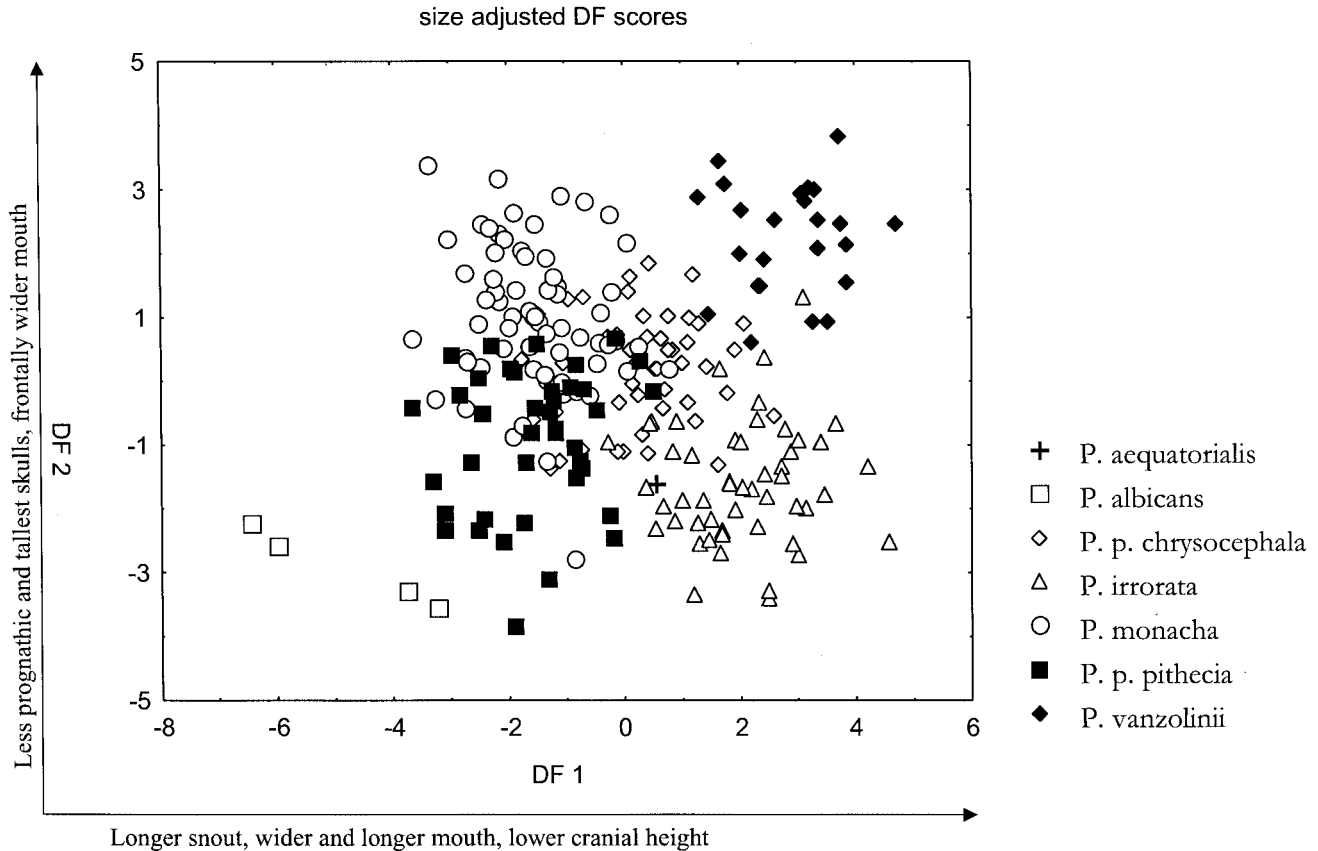


Fig. 6. Plot of saki species scores against first two discriminant functions (DF1 and DF2) obtained from scale-free data (shape variation).

vanzolinii. *P. vanzolinii* has a lower cranial vault and smaller oral and cranial base regions compared to *P. monacha*, but both share a deeper mandible in relation to others sakis (Fig. 7). This deeper mandible might be associated with an inflation of the hyoid apparatus. Given our present knowledge, or lack of it, about saki species ecology, it is difficult to associate morphological differences with adaptations to diet or other environmental factors. Perhaps the larger gape of the Monacha group allows the southern Amazon sakis to exploit larger and perhaps harder fruits that the smaller Pithecia group.

Our results suggest that the taxa recognized by Hershkovitz (1987) are morphologically distinct. Although species within groups are generally less differentiated than are species between groups, morphological distances among saki taxa are similar to the range of distances usually found for full rank species (Marroig et al., 2004a), even being in the range of distances found among Platyrrhini genera using the same 39 measurements used here (Marroig and Cheverud, 2001). This is not saying that species are recognized by some threshold level of morphological (or genetic) differentiation, but instead should be interpreted as a comparative statement: different genera present morphological differentiation similar to that observed in sakis while using the same methods and 39 traits used here.

This suggests that the taxonomic arrangement of Hershkovitz (1987) might be too conservative in terms of the number of specific taxa. For example, Hershkovitz (1987) considered *P. i. irrorata* and *P. i. vanzolinii* as subspecies of *P. irrorata*, and included them together with *P. m. monacha* and *P. aequatorialis* within the Monacha group. However, *P. vanzolinii* is more differentiated from both *P. irrorata* and *P. monacha* than either is from each other. Moreover, *P. vanzolinii* is clearly different, both in the original and size-adjusted DFs, from its nearest saki neighbor, *P. monacha*. Indeed, the skull sample distributions suggest that *P. monacha* and *P. vanzolinii* might be partially sympatric in the region between the upper Juruá and Javari rivers (Fig. 2). *P. monacha* is also clearly distinct from the sympatric *P. aequatorialis*. There is a gap of more than 700 km between the closest sample locations of *P. irrorata* and *P. vanzolinii*. These two taxa are geographically quite separate, making it impossible to test whether or not their morphology intergrades at their geographical boundaries. Thus, we suggest that both should be treated as “good species.” This is a logical consequence drawn from the meaning of species as evolutionary independent sequences of ancestral-descent populations (lineages), as described above. *P. irrorata* and *P. vanzolinii* are probably allopatric and well-differentiated in skull mor-

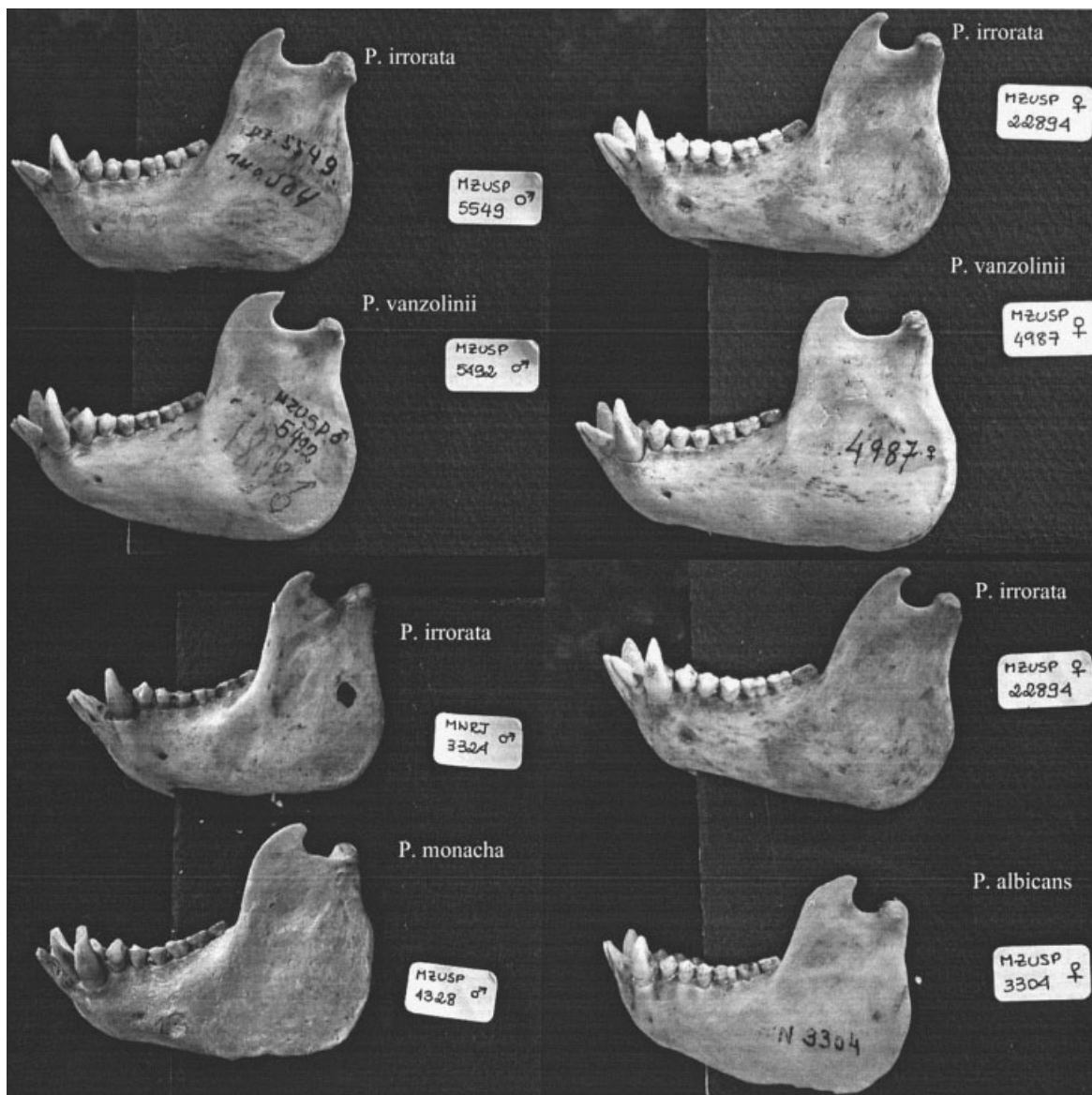


Fig. 7. Mandible depth in sakis. Note extreme depth in *P. monacha* and *P. vanzolinii*, possibly associated with inflation of hyoid apparatus in these two species.

phology as well as in pelage patterns, and we see no reason to retain them at a subspecific level.

Quantitative analyses presented here also suggest that *P. p. pithecia* and *P. p. chrysocephala* form another cluster of closely related taxa that may be considered as separate species. However, the differentiation observed among these northern sakis is smaller than that observed in the southern group, and their pelage patterns also seem more consistent with grade than clade variation (Hershkovitz, 1987). Our data do not allow for a detailed examination of the contact zone between these two northern forms, but suggest that they might be less differentiated in those localities close to each other's range borders. Therefore, we prefer to keep *P. p. pithecia* and *P. p. chrysocephala* at a subspecific level, pending a detailed investigation of their geographic variation

patterns. Given the quantitative differentiation among saki crania as well as pelage color pattern diversity (Hershkovitz, 1987), allo-parapatric distribution, and lack of evidence for hybridization in nature, the remaining saki lineages of the southern group deserve full rank species status. We suggest that all subspecies in the Monacha group considered here be elevated to a full species taxonomic level, and therefore that the following names should be applied from now on: *P. irrorata*, *P. vanzolinii*, and *P. monacha*.

Scale-corrected allometry-free discriminant function analysis uncovered an interesting pattern of scaling in the saki diversification. After removing size and associated allometric scaling effects, *P. monacha* is morphologically more similar to the small clade group (*P. pithecia*) of sakis than to the

APPENDIX

Trait	<i>P. aequatorialis</i>				<i>P. albicans</i>				<i>P. vanzolinii</i>				<i>P. irrorata</i>									
	F		M		F		M		F		M		F		M							
	N	Mean	N	Mean	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD						
ISPM	1	9.06	1	9.95	2	8.26	0.08	2	9.25	0.73	12	9.60	0.58	12	9.79	0.46	25	9.17	0.71	27	9.56	0.58
ISNSL	1	13.58	1	14.75	2	11.79	0.49	2	13.69	0.69	12	14.58	0.95	12	14.73	1.10	25	14.13	1.53	27	15.46	1.40
ISPNS	1	27.96	1	31.53	2	27.13	0.02	2	30.29	0.31	12	29.69	1.56	12	29.29	1.17	25	28.31	1.73	27	29.95	1.98
PMZS	1	18.35	1	18.32	2	17.68	1.59	2	19.32	0.58	12	18.76	1.58	12	19.75	1.67	26	17.76	1.35	27	19.11	1.38
PMZI	1	25.31	1	28.17	2	23.25	0.48	2	25.04	1.52	12	27.09	1.73	12	27.69	1.85	26	27.14	2.02	27	28.19	2.32
PMMT	1	23.98	1	24.07	2	22.77	0.09	2	25.97	0.77	12	25.26	0.89	12	25.57	1.49	26	24.15	1.09	27	25.00	1.04
NSLNA	1	15.57	1	16.26	2	14.94	1.33	2	14.66	0.86	12	16.70	1.54	12	17.10	1.35	26	16.33	1.02	27	16.70	1.27
NSLZS	1	19.60	1	20.94	2	19.61	0.79	2	21.88	0.28	12	20.46	1.84	12	21.65	1.54	26	19.24	1.26	27	20.48	1.44
NSLZI	1	32.31	1	36.57	2	30.43	0.19	2	32.91	1.18	12	34.50	2.14	12	35.46	2.53	26	34.56	2.06	27	35.74	2.57
NABR	1	40.50	1	45.00	2	40.96	3.43	2	44.89	1.69	12	42.97	2.84	12	43.13	1.66	26	40.69	1.74	27	42.29	1.90
NAFM	1	18.67	1	20.09	2	19.08	0.26	2	20.04	0.04	12	19.72	1.43	12	19.66	1.07	26	19.20	1.16	27	19.79	1.23
NAPNS	1	24.30	1	23.91	2	24.61	0.19	2	25.22	1.44	12	25.12	1.08	12	24.27	1.01	26	24.31	1.38	27	25.42	1.58
BRPT	1	33.47	1	35.79	2	34.02	1.12	2	34.86	0.11	12	37.06	1.51	12	35.69	1.67	26	34.09	1.10	27	35.20	1.60
BRAPET	1	33.95	1	34.40	2	34.65	1.46	2	36.03	2.40	12	35.74	1.31	12	34.43	1.45	26	33.83	1.09	27	34.15	1.19
PTFM	1	10.11	1	10.46	2	10.52	0.21	2	11.46	1.09	12	9.75	1.06	12	10.02	1.20	26	10.00	0.85	27	10.75	1.34
PTAPET	1	23.42	1	24.63	2	24.27	1.63	2	24.67	0.63	12	25.12	1.65	12	24.46	1.82	26	24.21	1.34	27	24.15	1.27
PTBA	1	37.75	1	38.28	2	36.77	0.95	2	39.69	1.50	12	39.19	2.63	12	39.06	1.89	26	37.45	1.59	27	38.48	1.99
PTEAM	1	25.25	1	25.98	2	24.58	1.47	2	26.46	1.63	12	25.57	2.22	12	25.67	1.42	26	24.50	1.63	27	25.27	1.69
PTZYGO	1	19.44	1	21.49	2	19.17	1.45	2	21.98	0.74	12	20.16	2.27	12	20.19	1.80	26	19.55	1.90	27	20.09	2.04
PTTSP	1	10.79	1	13.62	2	12.44	1.30	2	13.24	0.57	12	10.65	1.80	12	10.90	1.38	26	10.24	1.38	27	10.47	1.77
FMZS	1	11.51	1	13.61	2	10.70	0.06	2	12.11	0.16	12	11.82	0.77	12	12.32	1.06	26	12.99	0.78	27	12.87	0.99
FMMT	1	26.16	1	28.36	2	26.49	1.43	2	29.09	1.68	12	26.81	1.49	12	27.01	1.03	26	26.71	1.42	27	27.75	1.82
ZSZI	1	15.99	1	17.66	2	15.14	0.44	2	14.84	1.11	12	16.65	0.88	12	16.59	1.71	26	17.78	1.30	27	17.66	1.55
ZIMT	1	12.45	1	15.93	2	12.43	0.38	2	12.77	0.93	12	14.06	1.31	12	14.31	1.18	26	13.54	1.19	27	14.29	1.46
ZIZYGO	1	16.06	1	15.74	2	13.90	0.17	2	16.48	3.18	12	15.44	1.62	12	16.94	2.51	26	14.54	1.83	27	15.89	2.05
ZITSP	1	14.42	1	17.34	2	14.80	0.42	2	15.60	1.43	12	15.31	1.52	12	16.05	1.73	26	15.30	1.63	27	16.85	1.83
MTPNS	1	7.85	1	9.57	2	8.27	0.35	2	10.14	1.58	12	8.86	0.89	12	8.86	0.63	26	8.95	0.59	27	9.36	0.80
PNSAPET	1	18.65	1	17.79	2	15.41	0.34	2	17.82	1.60	12	18.83	1.88	12	20.24	1.76	26	19.07	1.40	27	20.12	1.60
APETBA	1	16.12	1	15.41	2	14.41	0.26	2	16.76	1.26	12	15.71	1.41	12	16.31	1.03	26	15.00	0.89	27	16.07	1.36
APETTS	1	10.26	1	10.69	2	10.13	0.03	2	11.51	0.58	12	9.11	0.71	12	9.06	0.68	26	9.70	0.70	27	10.07	0.88
BAEAM	1	21.52	1	22.46	2	20.97	0.57	2	22.23	1.34	12	22.34	0.96	12	22.68	0.68	26	21.45	0.97	27	22.01	0.97
EAMZYGO	1	12.73	1	15.53	2	14.89	0.38	2	15.81	0.19	12	13.71	1.85	12	12.85	1.22	26	13.16	1.27	27	14.35	1.83
ZYGOTSP	1	11.01	1	13.60	2	11.39	0.94	2	13.74	0.62	12	12.53	1.34	12	12.39	0.92	26	11.90	1.38	27	12.55	1.35
LDAS	1	20.20	1	20.06	2	18.92	0.19	2	19.77	1.22	12	19.94	0.93	12	19.35	1.44	26	19.04	0.86	27	19.26	1.27
BRLD	1	30.34	1	26.74	2	27.07	0.54	2	29.68	1.76	12	26.20	2.28	12	25.95	2.09	26	27.22	1.88	27	26.80	2.35
OPILD	1	22.66	1	20.45	2	20.14	0.35	2	20.34	0.47	12	21.26	2.40	12	21.22	1.18	26	20.41	1.59	26	20.43	1.50
PTAS	1	39.67	1	40.82	2	37.76	1.10	2	40.76	1.29	12	40.89	2.46	12	41.00	1.53	26	39.44	1.76	27	40.46	1.48
JPAS	1	18.46	1	20.78	2	17.74	0.25	2	18.23	0.52	12	19.49	1.21	12	20.01	1.44	26	19.09	0.90	27	19.47	0.99
BAOPI	1	9.40	1	10.78	2	10.18	0.08	2	10.02	1.29	12	9.75	0.81	12	9.03	0.84	26	9.74	0.73	26	9.89	0.58

other taxa in their own large clade. This suggests that *P. monacha* is a southern Amazonian, scaled-up version of the smaller sakis inhabiting northern Amazonia. It will be interesting in the future to compare these morphological evolutionary patterns to a phylogenetic hypothesis of sakis species and infer whether or not the shared form of *P. monacha* and the Pithecia group is a convergent or shared ancestral feature. Another interesting result of this discriminant analysis is that morphological differences among sakis were not entirely dependent on size and allometry. Saki species are also well-differentiated in a scale-free morphological space after variation relating to size and allometric scaling is removed, giving further support to considering these taxa as full species.

Allometric coefficients among saki species are quite similar (Table 5), although some significant differences are also apparent (Table 4). Because the saki sample studied here includes only adult animals, it is important to remember that the allometric coefficients reported here are static allometry coefficients. In mammals, including primates, various cranial organs grow at different rates during different life stages and under the influence of different physiological systems (Moore, 1981; Cheverud, 1995). In particular, early (neural) and late (somatic) growth factors could be distinguished dur-

ing mammalian ontogeny, at least for Eutheria (for a discussion about differences between “marsupials” and “placental” mammalian skull development, see Smith, 1997). The brain and eye complete their growth early, before the influence of the growth hormone axis is manifest. Facial features, especially those influenced by the size of attaching muscles and the oral cavity, continue to grow after birth under the influence of the growth hormone. If static allometric coefficients reflect the general growth processes in *Pithecia* species, facial traits are expected to be more positively allometric than neurocranial traits, which is apparent in our results for 3 of the 5 species (Table 4). Cheverud (1983) found that while some similarity in ontogenetic and static allometric patterns was present in macaques, these two types of allometry were not the same. Therefore, while the static allometric patterns described for sakis are influenced by ontogeny, they should not be interpreted as shape changes associated with changes in size deriving directly and only from the growth processes, but as shape variation associated with size differences in adult forms. The overall similarity in scaling patterns among sakis points to a shared evolutionary allometry, indicating that, to some extent, diversification of skull morphology was a result of scaling up or down the general size of the skulls. Actually, we might quantify the extent of

APPENDIX (Continued)

<i>P. monacha</i>						<i>P. pithecia</i>						<i>P. chrysocephala</i>					
F			M			F			M			F			M		
N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
29	9.29	0.55	39	9.61	0.56	16	8.14	0.59	24	8.53	0.56	19	8.42	0.63	32	8.84	0.55
29	14.29	1.04	39	15.09	1.10	16	12.88	1.26	24	14.06	0.90	19	13.33	0.87	31	14.21	0.83
29	28.97	1.39	39	30.11	1.42	16	26.67	1.51	24	28.13	1.47	19	26.24	1.28	32	27.44	1.14
29	18.78	0.90	39	19.75	1.16	16	17.38	1.31	24	18.87	1.23	19	17.46	1.38	32	18.26	1.00
29	25.75	1.14	39	26.67	1.24	16	23.69	1.27	24	25.33	1.65	19	24.18	1.52	32	24.85	1.22
29	23.98	1.13	39	24.56	0.90	16	22.04	0.75	24	22.38	0.73	19	22.54	1.20	32	22.80	1.02
29	16.79	1.43	39	17.09	1.23	16	16.23	1.27	24	17.34	1.28	19	14.72	1.55	31	15.96	1.32
29	20.38	1.29	39	21.42	0.95	16	19.47	1.28	24	20.71	1.59	19	18.89	1.20	31	19.82	0.96
29	33.23	1.37	39	34.52	1.65	16	31.64	1.64	24	33.47	2.21	19	31.56	1.49	31	32.83	1.39
29	40.48	1.54	39	41.49	2.13	16	40.28	1.81	24	41.64	1.71	19	39.53	1.88	32	40.62	1.92
29	18.78	0.88	39	19.43	1.21	16	17.51	0.56	24	17.84	0.81	19	17.66	0.76	32	18.25	0.98
29	24.17	1.15	39	25.07	1.25	16	23.42	0.99	24	24.70	1.35	19	22.75	0.90	32	24.11	1.42
29	34.32	1.78	39	34.62	1.70	16	33.61	1.71	24	34.30	1.09	19	32.31	1.77	32	33.04	1.50
29	35.12	1.18	39	35.91	1.69	16	33.48	0.94	24	34.17	0.95	19	32.11	0.94	32	33.27	1.36
29	9.17	1.32	39	9.76	1.05	16	9.53	1.30	24	10.12	1.16	19	9.72	1.55	32	9.80	1.13
29	24.89	1.29	39	25.12	1.64	16	22.84	1.22	24	23.31	1.06	19	22.61	1.14	32	23.49	1.18
29	38.92	1.52	39	39.68	2.07	16	35.50	1.76	24	36.77	1.31	19	34.90	1.29	32	37.24	1.35
29	25.86	1.23	39	26.74	1.81	16	23.42	1.66	24	24.57	1.34	19	22.84	1.24	32	24.67	1.38
29	20.50	1.56	39	21.32	2.11	16	17.87	2.11	24	19.05	1.76	19	18.25	1.09	32	19.88	1.78
29	11.54	1.61	39	11.94	1.68	16	9.85	1.51	24	10.38	1.06	19	9.50	1.29	32	10.22	1.26
29	12.31	0.93	39	12.55	1.35	16	12.72	0.76	24	12.59	0.97	19	12.66	1.31	32	12.63	1.14
29	26.62	1.13	39	27.80	1.26	16	26.71	1.63	24	28.23	1.11	19	26.30	1.06	32	27.46	1.11
29	15.96	0.95	39	16.13	1.43	16	15.23	1.36	24	15.86	1.30	19	15.91	0.93	32	16.05	1.12
29	12.82	0.82	39	13.68	0.92	16	13.75	1.18	24	15.18	1.37	19	13.44	0.78	32	14.71	0.96
29	15.03	1.51	39	15.78	2.13	16	12.84	2.61	24	14.24	2.08	19	13.85	1.25	32	15.29	2.05
29	15.44	1.58	39	16.25	1.45	16	14.27	1.86	24	16.04	1.11	19	14.80	1.05	32	16.05	1.31
29	9.04	0.56	39	9.32	0.71	16	8.00	0.69	24	8.67	0.53	19	7.73	0.70	32	8.09	0.66
29	18.38	1.17	39	18.87	1.30	16	15.93	1.14	24	16.98	1.40	19	16.96	1.73	32	17.65	1.45
29	15.75	0.92	39	16.40	1.11	16	14.02	1.03	24	15.05	0.83	19	13.75	1.12	32	15.19	1.06
29	9.29	0.77	39	9.58	0.93	16	9.44	0.99	24	9.49	0.86	19	9.14	0.81	32	9.16	0.96
29	22.14	0.94	39	22.58	0.96	16	20.78	0.87	24	21.46	0.74	19	20.35	0.66	32	21.22	0.77
29	14.15	1.56	39	14.92	1.98	16	14.12	1.74	24	15.06	2.06	19	12.86	1.16	32	14.06	1.23
29	11.77	0.73	39	12.85	0.87	16	11.0	1.48	24	12.11	1.37	19	11.38	1.04	32	12.77	1.03
29	19.40	1.00	39	19.28	1.01	16	17.65	0.89	24	18.10	1.15	19	18.00	1.08	32	18.27	1.30
29	28.36	1.81	39	29.15	2.06	16	26.43	1.95	24	25.85	1.74	19	25.02	1.40	32	25.72	1.99
29	20.88	1.60	39	20.85	1.68	16	19.69	1.56	24	20.17	1.89	19	19.51	1.24	32	20.13	1.46
29	40.11	1.64	39	40.94	1.53	16	37.88	1.48	24	38.49	1.55	19	36.27	1.37	32	38.29	1.25
29	18.83	1.39	39	19.39	1.18	16	17.13	1.29	24	17.51	1.15	19	16.44	0.82	32	17.48	1.25
29	9.93	0.87	39	9.99	0.83	16	9.67	0.46	24	9.49	0.97	19	9.28	0.93	32	9.50	0.86

that scaling as 38% of the total variation, considering the eigenvalue of the first principal component calculated from the total sample covariance matrix.

CONCLUSIONS

Mean values of saki cranial features are significantly diverse among species, but share major aspects of their intertrait correlation structure. Morphological distances among sakis are similar to those usually found between taxa of specific and even generic rank, and therefore we suggest that the following taxa should be considered separate species: *P. monacha*, *P. vanzolinii*, and *P. irrorata* within the Monacha group of species. Also, *P. albicans* and *P. aequatorialis* are provisionally allocated within the Monacha group, awaiting further evidence to decide their status. Size differences between the smaller-bodied Pithecia group distributed north of the Amazon and the larger-bodied Monacha group distributed south of the Amazon are strongly significant. Despite this, allometric patterns are quite similar among species, again indicating a similarity of covariance structure. Allometric patterns indicate that facial traits are influenced by size to a larger extent than are neurocranial traits, as expected from the general growth process in eutherian mammals. Differences among saki species are not merely a result of changes in size and allometric

scaling. Instead, there are consistent differences among species, even when size and allometric scaling are controlled for in the analysis.

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