VIVAMUS

Morphometrics of the Callitrichid Forelimb: A Case Study in Size and Shape

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Mosimann and colleagues formulated a technique that distinguishes between size and shape, based on the concept of geometric similarity and the distinction between "log size-and-shape" and "log shape" variables. We extend these formulations in an examination of the forelimb of three callitrichid species (adult Saguinus oedipus, Saguinus fuscicollis, *and* Callithrix jacchus*). We employ principal components analysis to explore the relationship between variance explained by size-and-shape versus shape alone. Independence of shape vectors is examined via correlation analysis. Then we use log shape data to construct intersample (species means) and total sample (between all pairs of individuals) matrices of average taxonomic distances. These distance matrices are subjected to cluster analysis and principal coordinate ordinations. Results of principal components analysis suggest that after isometric size is removed, there remains sufficient shape information to discriminate among the three taxa. Careful examination and quantification of the relationships between shape and size suggest that size information (e.g., geometric mean) is fundamental for understanding shape differences within and among callitrichid species; in other words, most aspects of forelimb shape are significantly correlated with size. Contrary to conventional wisdom, we also demonstrate that such correlations are not "spurious." Ordinations and clustering of log*

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shape distance matrices (based on means and individuals) support the notion that, despite differences in size, the two tamarins are more similar in shape than either is to C. jacchus *(despite size similarity between* S. fuscicollis *and* C. jacchus*). Although shape variation in the forelimb of callitrichids may have a functional component, the phylogenetic signal remains strong and serves to group individuals accordingly.*

INTRODUCTION

The analysis of *size* and *shape* and studies of organismal scaling or "allometry" continue to be a major concern of many primate biologists and other quantitative morphologists (McMahon and Bonner, 1983; Calder, 1984; Jungers, 1985; McKinney, 1988; Rohlf and Bookstein, 1990). Opinions differ greatly as to what criteria most properly define these two terms (Gould, 1966, 1975a,b; Mosimann, 1970; Rao, 1971; Corruccini, 1973, 1987; Mosimann and Malley, 1979; Humphries *et al.,* 1981; Bookstein *et al.,* 1985; Cheverud and Richtsmeier, 1986; Bookstein, 1989; Lestrel, 1989; Rohlf, 1990; Rohlf and Bookstein, 1990; Lele, 1991). Mosimann and colleagues formulated a valuable approach to this problem based on an explicit notion of geometric similarity and the distinction between "log size-and-shape" and "log shape" variables (Mosimann and James, 1979; Darroch and Mosimann, 1985; James and McCulloch, 1990). More specifically, for Darroch and Mosimann (1985) the geometric mean of all variables represents *size,* and *shape* variables are generated as logged ratios of each variable and the geometric mean; "size-and-shape" refers to raw data. Shape may or may not be correlated with size in such an analytical framework; i.e., this is an empirical determination. This logarithmic-based method is similar in some ways to "doubling-centering" methods used with raw standardized data (Corruccini, 1973, personal communication; Howells, 1989).

The geometric mean of *n* variables is calculated as

$$GM_Y = \sqrt[n]{\prod_{i=1}^{n} Y_i}$$

Each variable is then divided by the geometric mean for that individual to create a scale-free, or dimensionless, shape variable. This ratio variable is then log-transformed to create a log-shape variable. Therefore, shape is something inherent in the object of study, and not a function of the comparative

sample. In contrast, the shape of an individual, defined as its residual from an empirically determined allometric relationship, will change as a function of the comparative sample (Hartman, 1988). In other words, the residual value can change, but clearly the shape of the individual has not. Residuals are greatly influenced by the largest and smallest members of the study sample and ignore those aspects of shape that are correlated with size differences (Susman and Creel, 1979; Lemen, 1983; Corruccini, 1987; Corruccini *et al.*, 1987). Empirical relationships are simply that, *empirical*, and need not imply "functional" or any other type of equivalence; hence, their use as lines of subtraction is logically suspect. Other approaches to shape, such as finite element scaling (Cheverud and Richtsmeier, 1986) and principal warps (Rohlf and Bookstein, 1990), are pairwise by design and compute shape differences instead of shape itself.

The Darroch and Mosimann shape variables that exhibit a significant positive or negative correlation with size are said to be "allometric"; i.e., shape has not been preserved with size differences (Mosimann and James, 1979). Geometric similarity or "isometry" is indicated by a nonsignificant correlation. Either parametric or nonparametric tests can be employed, depending on the distribution of the shape variables. Multivariate versions of this approach are also available (Darroch and Mosimann, 1985; Jungers *et al.*, 1988). For example, the eigenvalues of principal components of log size-and-shape (i.e., logged raw variables) can be contrasted with those of the principal components of log shape alone to determine the extent to which overall differences among individuals and groups can be attributed to a combination of size-and-shape versus shape only. This distinction has been shown elsewhere to be very valuable in studies of human skeletal growth (Jungers *et al.*, 1988), wherein shape differences among individuals were found to be smaller in comparison to size differences. In other cases, it can be demonstrated that shape variation is almost as great as size-and-shape variation, for example, Darroch and Mosimann's (1985) analysis of size and shape in *Iris*. Log shape variables can also be used directly in other forms of phenetic comparisons, such as methods based on measures of distance (including ordinations and clustering).

We examine the extent to which the forelimbs of three callitrichid species vary in terms of overall size-and-shape versus shape alone. Within-group and among-group allometries are assessed by both parametric and nonparametric correlation analysis. Finally, we explore the utility of these formulations of "log size-and-shape" and "log shape" in multivariate ordination and hierarchic cluster analysis of forelimb morphology in tamarins and marmosets. For this sample, body size is smallest in *Callithrix jacchus* (310 g) and is largest in *Saguinus oedipus* (465 g); *Saguinus fuscicollis* (363 g) is much more similar in body size to the marmoset. Our goal is to determine whether or not the two

congeneric tamarin species are more similar in shape despite significant size differences or if the smaller-bodied *S. fuscicollis* is more similar overall to a marmoset of comparable body size (*C. jacchus*). These results should provide insights as to whether callitrichid forelimb osteology is constrained more by phylogeny or by size-required aspects of locomotor function.

MATERIALS AND METHODS

We measured a total of 160 tamarin and marmoset skeletons: 66 of *Saguinus fuscicollis illigeri*, 62 of *Saguinus oedipus oedipus*, and 32 of *Callithrix jacchus jacchus*. We used adults only, as judged by the fusion of all long bone epiphyses. The sample of *Saguinus* is a mixture of wild-caught and captive-born animals from the Marmoset Research Center of the Oak Ridge Associated Universities and the University of Tennessee—Knoxville. The series of *Callithrix* is drawn partially from these sources and is supplemented with wild-shot individuals from the National Museum of Natural History in Washington, DC. Previous studies report that there is no significant difference between wild- and captive-born specimens with regard to postcranial measures. Accordingly, the wild and captive samples are pooled for all analyses (Glassman, 1983; Falsetti, 1986). We pooled sexes across species after preliminary analyses demonstrated no significant sexual dimorphism in forelimb size and shape.

We designed 24 linear measurements to describe the overall size and shape of the scapula, humerus, radius, and ulna (Table I). Eight variables pertain specifically to the size and form of the scapula. Sixteen additional variables represent the overall lengths and breadths of the forelimb long bones (humerus, ulna, radius). We recorded measurements to the nearest 0.01 mm. The log size of each individual is defined as the logged geometric mean of the 24 measurements. Log shape variables were generated by log-transforming each individual variable and then subtracting the logged geometric mean from each variable in the row. This is mathematically equivalent to the procedure described in the introduction.

We used the log shape and the log size-and-shape (logged raw) variables to construct separate variance-covariance matrices that were subjected to principal components analysis (PCA). Darroch and Mosimann (1985) and others (Jolicoeur, 1963a,b, 1984; Humphries *et al.*, 1981; Cheverud, 1982; Shea, 1985; Jungers *et al.*, 1988; Jungers and Hartman, 1988; Masterson and Leutenegger, 1990) demonstrated PCA to be especially valuable for discerning multivariate relationships between size and shape variables. For example, a comparison of eigenvalues between the PCA of logged raw measurements and that of log shape variables can disclose the extent to which individuals

Table I. Forelimb Measurements[a] and Abbreviations

	Measurement	Abbreviation
(1)	Maximum length of the scapula	SML
(2)	Maximum breadth of the scapula	SMB
(3)	Length of scapular spine	SLS
(4)	Length of supraspinous line	SSL
(5)	Length of infraspinous line	ISL
(6)	Glenoid cavity breadth	GCB
(7)	Glenoid cavity height	GCH
(8)	Length from glenoid cavity to inferior angle	GIL
(9)	Humerus maximum length	HML
(10)	Breadth of upper epiphysis of humerus	BUE
(11)	Maximum diameter of humeral midshaft	MDS
(12)	Minimum diameter of humeral midshaft	MDM
(13)	Maximum diameter of humeral head	MDH
(14)	Biepicondylar breadth of humerus	EBR
(15)	Least circumference of humeral shaft	LCS
(16)	Ulna maximum length	UML
(17)	Maximum breadth of olecranon process	BOP
(18)	Minimum breadth of olecranon process	MBO
(19)	Maximum width (AP) of olecranon process	WOP
(20)	Length from olecranon process to radial notch	ORL
(21)	Length from olecranon process to coronoid process	OCL
(22)	Radius maximum length	RML
(23)	Maximum diameter of radial head	RDH
(24)	Maximum diameter of radial shaft	MCS

[a] See Martin (1928) and Bass (1987) for definitions and illustrations of these measurements.

are distinguished by a combination size and shape versus shape alone. Using Anderson's (1936) data for three species of *Iris*, Darroch ad Mosimann (1985) demonstrated a substantial similarity in the original total variance based on the log measurements of four sepal–petal dimensions and the eigenvalue associated with the corresponding log shape measurements. The total variance from the log size-and-shape analysis is 3229.9, of which 3046.2 is accounted for by log shape (the sepal and petal ratios). Thus, log shape data, in their analysis, contain 94% of the original total variance and provide excellent discriminatory power for these three closely related species. In other situations, it may be found that size information is a more prominent part of the overall variation compared to shape variation, e.g., different samples of blackbirds (Darroch and Mosimann, 1985) and modern human growth (Jungers *et al.*, 1988).

The pairwise correlation between log shape variables and log size (logged geometric mean) was determined for each variable using both Pearson and Spearman correlation coefficients. Only the parametric Pearson correlation coefficients are reported because the two methods yielded virtually identical results. Recall that no significant correlation implies "isometry" or no predictable change in shape with change in size; positive and negative correlations imply significant size-related shape modifications or "allometry." We examine such correlations both intraspecifically and interspecifically.

Log shape data can also be employed directly for other types of analyses, for instance, distance calculations and hierarchic classifications (Sneath and Sokal, 1973). In our case, a matrix of average taxonomic distances,

$$d_{jk} = \sqrt{\Delta^2_{jk}/n} \, ,$$

among taxonal *means* was calculated following standardization $(\bar{y} = 0,$ $s = 1)$ of the shape dimensions and used as the basis for clustering (e.g., unweighted pair-group method with arithmetic averages or UPGMA) and for principal coordinates ordination. Clustering provides a graphical unidimensional representation of the distance matrix; ordination can accomplish the same goal in two or three dimensions and also permits one to assess differential variable contributions to observed patterns of similarity. Because clustering of taxa was the same regardless of algorithm employed, we report only the UPGMA results. Subsequently, we also calculated a matrix of the average taxonomic distances among *individual* specimens and subjected them to the same hierarchical clustering and multidimensional ordinations. We performed ordination of log shape distances via principal coordinates in lieu of traditional discriminatory algorithms, such as those used to calculate canonical variate scores, primarily because our data did not meet the primary assumption of homogeneity of variance–covariance structure. Additionally, if one is interested in deriving canonical variate scores, one must first perform a rather complex and cumbersome algebraic transformation on the pooled-within class covariance matrix, as the last row and column of this matrix are otherwise lost in computation when log shape variables are used (Darroch and Mosimann, 1985). Resemblances and differences in morphometrics among taxa and individuals are always evaluated in terms of overall similarity in shape, and these results are contrasted to findings based on a combination of size and shape.
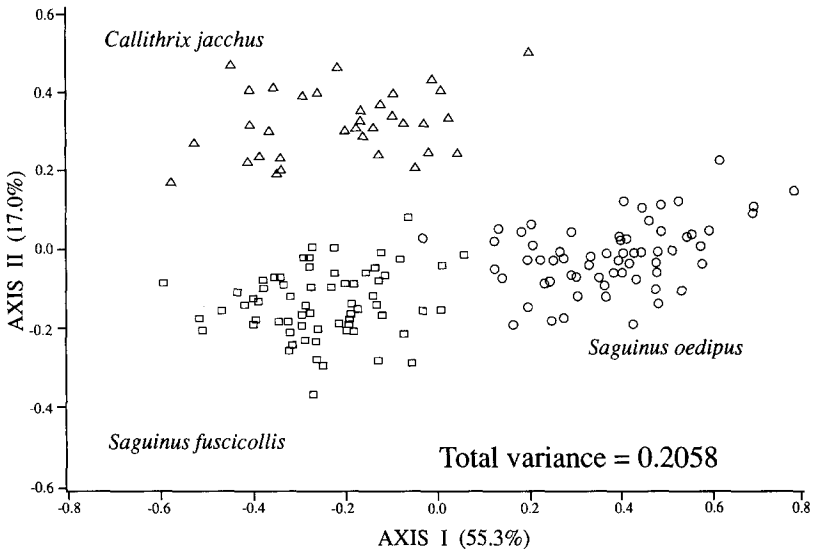
Fig. 1. Principal components of log size-and-shape variables (logged raw data). Note that the largest species, *S. oedipus*, is separated along Axis I from the other two, more similarly sized species. *Callithrix* is removed from both *Saguinus* species along Axis II.

RESULTS AND DISCUSSION

Variance in Size-and-Shape Versus Shape

The PCA of log size-and-shape results in a first principal component that accounts for 55.3% of the original total sample variance. The primary separation of taxa along this axis is between *S. fuscicollis* and *C. jacchus* on the left and *S. oedipus* on the right (Fig. 1). The scores on this axis are highly correlated with log size ($r = 0.996$, $p < 0.0001$), and all of the eigenvector coefficients are positive (Table II). An examination of the correlations between the scores and the original variables reveals that all variable loadings are significant, and contribute in differing degrees to this separation. In ontogenetic and single-species adult samples, this axis usually describes variation in size-related (allometric) shape (Jolicoeur, 1963b; Shea, 1985). If interpreted in this fashion, isometry would be indicated by coefficients equal to

$$\frac{1}{\sqrt{p}},$$

where p equals the number of variables, or 0.204 in this case. Biepicondylar breadth (EBR) exhibits the strongest positive allometry (with a value of
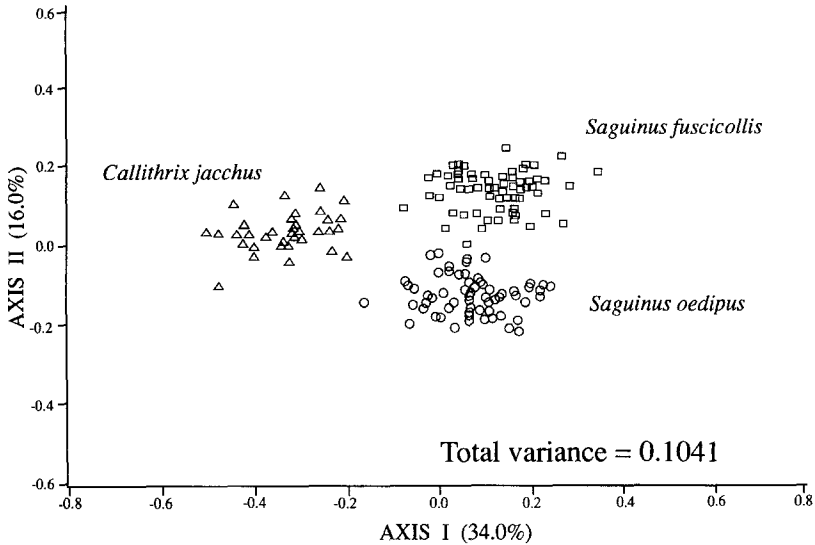
Fig. 2. Principal components of log shape variables. Note that the *Saguinus* species now occupy a similar position along Axis I and are consistently contrasted with *Callithrix* individuals.

0.3115), and maximum radial length (RML) is characterized by the most negative allometry (coefficient equal to 0.075).

The second component of log size-and-shape accounts for 17% of the total variance and represents aspects of morphological shape variation that are unrelated to size ($r = 0.033, p > 0.5$); it serves to separate *Callithrix* from the two species of *Saguinus* (Fig. 1).

The principal components analysis of the log shape matrix demonstrates a major reduction in the total variance when isometric size variation is removed (Fig. 2). The total variance is reduced from 0.2058 to 0.1041; this implies that absolute size accounted for approximately one-half of the original total variance. The remaining variance is presumably in shape, although a portion of this may still be size correlated. The first principal component accounts for 34% of the variance and serves to separate *Callithrix* from both species of *Saguinus*. The variation in shape along this axis is *not* significantly correlated with log size ($r = -0.121, p > 0.1$). The eigenvalue is similar in magnitude and the coefficients of this component (Table II) are similar in rank to those of the second eigenvector of log size-and-shape (Table II); the Pearson correlation calculated between these axes is 0.99 ($p < 0.0001$). This suggests that the first component of the log size-and-shape analysis is extremely similar to the isometric vector that was explicitly removed in the analysis of shape alone. Aspects of olecranon process shape seem to be contrasted along this first shape

Table II. Principal Components of Log Size-and-Shape and Log Shape Variables

| | Eigenvector coefficient | | | |
| | Log size–and–shape | | Log shape | |
	I	II	I	II
SML	0.202	-0.063	-0.074	-0.044
SMB	0.155	-0.074	-0.072	-0.140
SLS	0.170	-0.081	-0.084	-0.097
SSL	0.275	0.034	-0.003	0.242
ISL	0.109	0.048	0.063	-0.274
GCB	0.120	0.054	0.064	-0.198
GCH	0.154	-0.072	-0.070	-0.141
GIL	0.160	-0.129	-0.126	-0.168
HML	0.130	-0.122	-0.112	-0.205
BUE	0.165	-0.136	-0.138	-0.076
MDS	0.182	0.114	0.104	-0.025
MDM	0.252	-0.030	-0.059	0.144
MDH	0.175	-0.067	-0.073	-0.038
EBR	0.315	0.084	0.033	0.369
LCS	0.262	-0.126	-0.156	0.142
UML	0.130	-0.193	-0.181	-0.218
BOP	0.175	0.293	0.281	0.028
MBO	0.116	0.797	0.793	-0.013
WOP	0.316	-0.180	-0.226	0.327
ORL	0.213	0.176	0.153	0.150
OCL	0.299	-0.124	-0.168	0.330
RML	0.075	-0.126	-0.099	-0.361
RDH	0.289	0.052	0.009	0.313
MCS	0.164	0.151	0.145	-0.043
Eigenvalue	0.1140	0.0350	0.0354	0.0166
% of total variance	0.5537	0.1700	0.3401	0.1602

axis (BOP and MBO vs WOP) such that *Saguinus* possess relatively thinner (AP) but broader (ML) olecranons. The second component of log shape accounts for 16% of the original total variance, and the scores along this axis are significantly correlated with size ($r = 0.807, p < 0.0001$). The size-related aspects of shape along this axis (Table II) may be seen in part as a slightly different expression of the weakly "allometric" trends that were described in the first component of log size-and-shape; $r = 0.957$, and $p < 0.0001$ (Fig. 1, Table II). The correlation between the second eigenvector of log shape and the third axis of log size-and-shape (not shown) is a nonsignificant $r = -0.064$.

Correlations Between Shape and Size

Mosimann and James (1979) suggested that the independence of ratio or shape vectors may be tested directly against size in order to evaluate the magnitude and direction of the association between these two components. Table III presents the results of such an analysis. Intraspecific correlations between the log shape variables and log size (logged geometric mean) are significant for all species except for *one* variable pair [log shape (MCS) vs log size in *Callithrix jacchus*], which overwhelmingly suggests that shape variation is size related (nonisometric) in these groups. Interspecific correlations reinforce these results, though variations in the magnitude of *r* may be detected when viewing results across species. For example, a plot (Fig. 3A) of the shape of the humerus at midshaft versus log size demonstrates clear separation of the three groups and overall negative correlation but with considerable scatter. Furthermore, an examination of the plot (Fig. 3B) of the maximum length of the ulna versus size shows very good separation interspecifically with relatively little scatter intraspecifically. Note that "size" as estimated by the GM accurately reflects the natural distribution of body weights (*S.o.* > *S.F.* > *C.j.*).

In order to determine whether or not the patterns of covariation found here are sample-specific or may in any other fashion be considered "spurious" (Prothero, 1986), we calculated additional correlations between log shape variables and log size, again using Anderson's (1936) data for three species of *Iris*. It has been argued that the correlation between a given variable (e.g., mass or GM) and any ratio with that variable in the denominator will be artificially high and simply an artifact of the method (Jungers, 1984). Our recent experience with data taken from a variety of organisms is rather different from Prothero's generalization based on simulations. The results presented in Table IV and in Figs. 4A and B rather conclusively demonstrate that the procedure used here to create shape variables need not result in significant correlations between shape and size. None of the correlations within the sample of *I. virginica* is significant, and only half of them are significant in *I.versicolor*. All four are significant in *I. setosa*, recalling the intraspecific results seen in the callitrichid forelimb. Interspecific correlations are all significant; this result obtains because the smallest species, *I. setosa*, is different in shape from the other two species: *I. versicolor* and *I. virginica*. The direction and magnitude of covariation within species may or may not be the same as the pattern found interspecifically for all variable pairs, but this must also be determined empirically. Also recall that log shape data provide more than adequate separation of these taxa (Darroch and Mosimann, 1985). Accordingly, the use of data generated as ratios does not produce "spurious" results; instead, they provide readily interpretable information regarding the *covariation* of morphological structures with size.

Table III. Correlation Between Log Shape Variables and Log Size (Geometric Mean)

Variable	Pearson Correlation Coefficient							
	Within-S.f.i.		Within-S.o.o.		Within-C.j.j.		Pooled species	
	r	p	r	p	r	p	r	p
SLSML	-0.756	0.0001	-0.835	0.0001	-0.752	0.0001	-0.807	0.0001
SLSMB	-0.865	0.0001	-0.921	0.0001	-0.856	0.0001	-0.915	0.0001
SLSLS	-0.889	0.0001	-0.928	0.0001	-0.838	0.0001	-0.899	0.0001
SLSSL	-0.461	0.0001	-0.524	0.0001	-0.536	0.0011	-0.477	0.0001
SLISL	-0.749	0.0001	-0.667	0.0001	-0.727	0.0001	-0.844	0.0001
SLGCB	-0.831	0.0001	-0.859	0.0001	-0.618	0.0001	-0.874	0.0001
SLGCH	-0.698	0.0001	-0.800	0.0001	-0.700	0.0001	-0.789	0.0001
SLGIL	-0.775	0.0001	-0.923	0.0001	-0.809	0.0001	-0.884	0.0001
SLHML	-0.945	0.0001	-0.943	0.0001	-0.939	0.0001	-0.957	0.0001
SLBUE	-0.873	0.0001	-0.883	0.0001	-0.746	0.0001	-0.852	0.0001
SLMDS	-0.697	0.0001	-0.648	0.0001	-0.708	0.0001	-0.760	0.0001
SLMDM	-0.777	0.0001	-0.711	0.0001	-0.686	0.0001	-0.652	0.0001
SLMDH	-0.897	0.0001	-0.877	0.0001	-0.760	0.0001	-0.846	0.0001
SLEBR	-0.879	0.0001	-0.872	0.0001	-0.813	0.0001	-0.528	0.0001
SLLCS	-0.456	0.0001	-0.524	0.0001	-0.713	0.0001	-0.446	0.0001
SLUML	-0.958	0.0001	-0.971	0.0001	-0.966	0.0001	-0.931	0.0001
SLBOP	-0.740	0.0001	-0.606	0.0001	-0.438	0.0096	-0.705	0.0001
SLMBO	-0.498	0.0001	-0.502	0.0001	-0.753	0.0001	-0.650	0.0001
SLWOP	-0.835	0.0001	-0.840	0.0001	-0.645	0.0001	-0.411	0.0001
SLORL	-0.796	0.0001	-0.775	0.0001	-0.565	0.0005	-0.674	0.0001
SLOCL	-0.834	0.0001	-0.688	0.0001	-0.666	0.0001	-0.455	0.0001
SLRML	-0.985	0.0001	-0.985	0.0001	-0.970	0.0001	-0.971	0.0001
SLRDH	-0.877	0.0001	-0.901	0.0001	-0.847	0.0001	-0.592	0.0001
SLMCS	-0.776	0.0001	-0.701	0.0001	-0.218	0.2152[a]	-0.700	0.0001

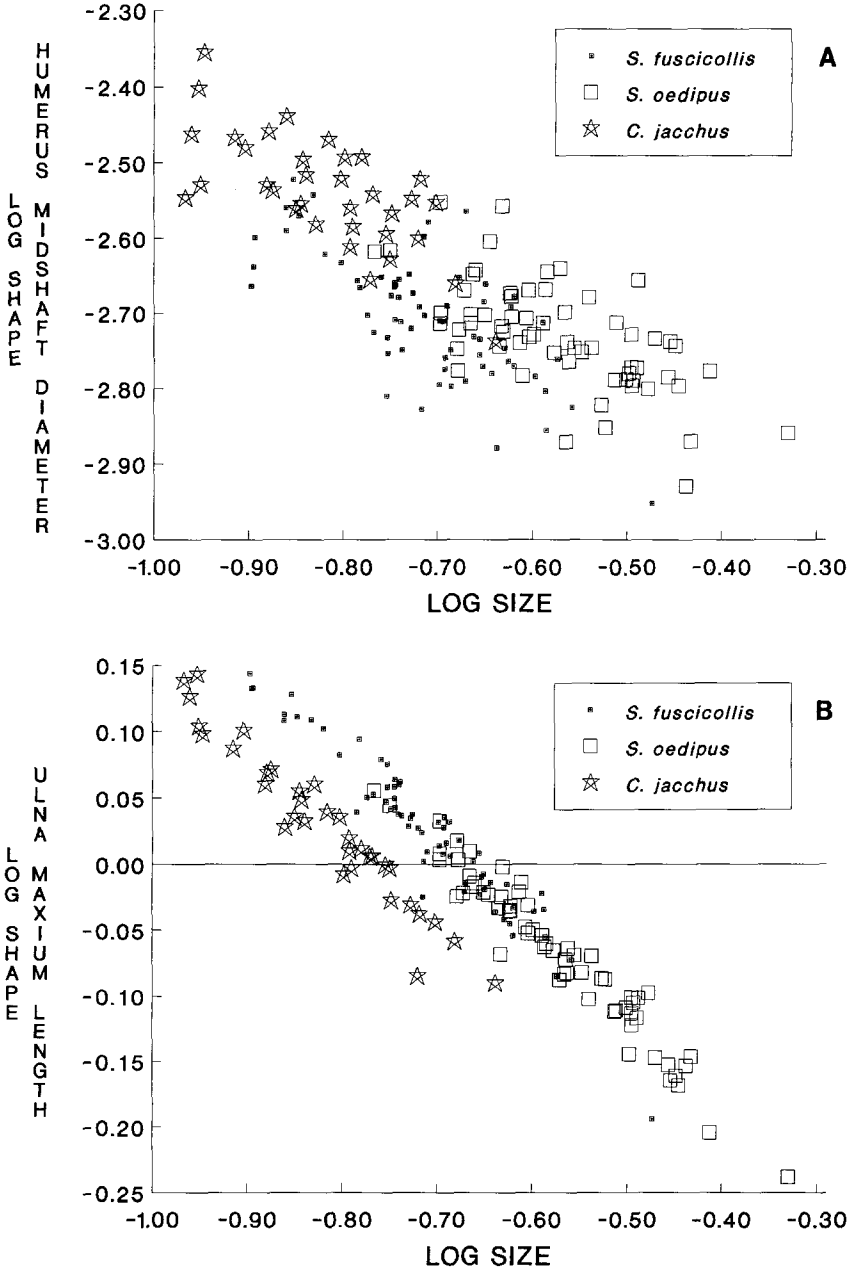[a]Not significantly correlated with log size.

Fig. 3. (A) Intra- and interspecific plots of humerus midshaft diameter (log shape) versus size (logged geometric mean); (B) intra- and interspecific plots of ulna maximum length (log shape) versus size (logged geometric mean). In callitrichids, these two measurements of shape are strongly correlated with size both within and among species.

Table IV. Correlations of Log Shape Variables[a] with Log Size (Geometric Mean)

| Shape variable | Pearson correlation coefficient | | | | | | | |
| | Within-setosa | | Within-versicolor | | Within-virginica | | Pooled species | |
	r	p	r	p	r	p	r	p
SEPALL	-0.851	0.0001	-0.523	0.0001	-0.150	0.2978	-0.970	0.0001
SEPALW	-0.621	0.0001	-0.103	0.4724	-0.019	0.8928	-0.960	0.0001
PETALL	-0.560	0.0001	0.049	0.7309	-0.145	0.3131	0.837	0.0001
PETALW	0.822	0.0001	0.505	0.0002	0.205	0.1520	0.966	0.0001

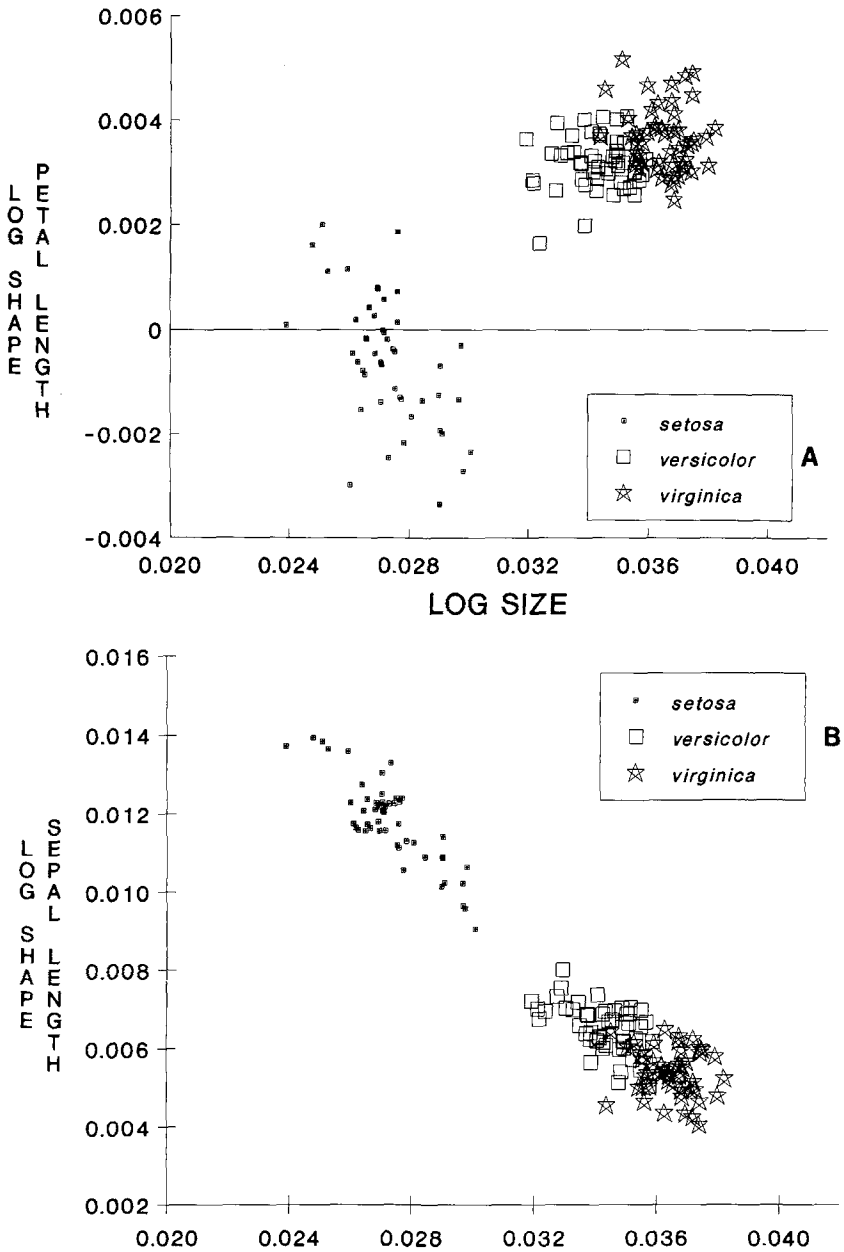[a] Data are from Anderson (1936).

Fig. 4. (A) Intra- and interspecific plots of petal length (log shape) versus size (logged geometric mean); (B) intra- and interspecific plots of sepal length (log shape) versus size (logged geometric mean). In the first instance, shape shows no within species relationship with size, but there is an allometric interspecific trend. For the second variable, significant allometries both within and between species recall those seen in callitrichids.

Table V. Average Taxonomic Distances Among Taxa Means

	Log size-and-shape			Log shape		
	S.f. illigeri	S.o. oedipus	C.j. jacchus	S.f. illigeri	S.o. oedipus	C.j. jacchus
S.f.i.	0.0000			0.0000		
S.o.o	1.5613	0.0000		1.2805	0.0000	
C.j.j.	0.9771	1.6146	0.0000	1.5796	1.3656	0.0000

Overall Similarity

Log shape data were also subjected to other types of phenetic analyses, including clustering methods, such as the unweighted pair-group arithmetic average clustering algorithm (UPGMA) and principal coordinates ordination of average taxonomic distance matrices (Sneath and Sokal, 1973). Table V presents a comparison of matrices of the average taxonomic differences based on species means for the log size-and-shape and log shape variables. UPGMA clustering of the log size-and-shape matrix (Fig. 5A; cophenetic $r = 0.997$) shows that *S. fuscicollis* is more similar to *C. jacchus* than to its larger congener, *S. oedipus*. But once isometric size is removed, the two *Saguinus* species are more similar in shape (Fig. 5B; cophenetic $r = 0.720$). In other words, *S. fuscicollis* and *C. jacchus* are more similar in overall size but not in overall shape, and the three callitrichid taxa are distinguished along familiar phylogenetic lines when isometric size is removed.

These patterns of similarity were also revealed in a separate analysis of individual specimens. We performed these analyses in order to examine whether the distances derived from *species means* could in any fashion disguise underlying taxonomic or functional information. UPGMA clustering of the matrix of average taxonomic distances calculated between all pairs of individual specimens for the standardized log shape variables again showed that, once isometric size is removed, the two species of *Saguinus* are more similar in shape, and the individual specimens of *Callithrix* remain segregated and distinct from the tamarins.

In order to present a better representation of the relationships among the individual specimens in this study, and to discover what variables serve to drive the taxa apart, ordinations were also carried out via principal coordinates analysis. Two eigenvectors were extracted from the *standardized* log shape matrix of average taxonomic distances between all pairs of individuals. The correlation between the distances implied by the two-dimensional ordination and the original distance matrix is 0.93. This
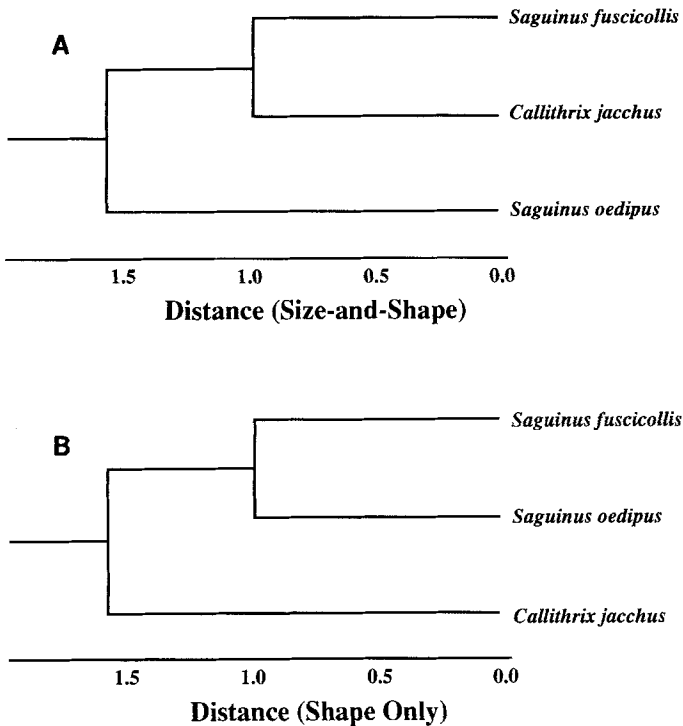
Fig. 5. (A) UPGMA clustering of species based on means of log size-and-shape variables (logged raw data); (B) UPGMA clustering of species based on means of log shape variables. The first cluster is driven primarily by size similarity, whereas shape information unites the species of *Saguinus*, presumably reflecting their close phylogenetic relationship.

suggests that the ordination procedure provides more than adequate representation of these relationships. The first principal coordinate axis accounts for 42.5% of the variance and serves mainly to separate *S. fuscicollis* from the other taxa (Fig. 6A) and is weakly, but significantly, correlated with log size ($r = -0.430, p < 0.0001$). The second axis is also moderately correlated with log size ($r = -0.650, p < 0.0001$) and accounts for 26.6% of the original variance. This axis separates *Callithrix* from *S. oedipus*, with *S. fuscicollis* taking an intermediate position. Together these axes contribute a picture of phenetic resemblances and dissimilarities that more or less reflect the results of the principal components analysis of log shape data (Fig. 2); the apparent difference in angulation between the two procedures is most likely due to the *effects of standardization* before the calculation of distances.

A plot (Fig. 6B, Table VI) of the significant Pearson correlations greater than 0.5 between the log shape variables and the scores on the first two coordinate axes illustrates the variables that are most strongly influencing the differences among taxa/individuals in this ordination space. This is a useful visual technique for discovering those variables that contribute individually or in combination to the separation of the specimens under study. The first axis orders individuals via measure of the scapula (maximum breadth, scapular spine length, length from glenoid cavity to inferior angle), the upper limb (humerus maximum length and breadth of upper epiphysis), and the forearm (ulna and radius maximum lengths) versus the elbow (biepicondylar breadth of the humerus, olecranon process breadth, and head of the radius). The second axis separates individuals via contrasts that include the length of the olecranon process to coronoid process and the maximum width of the olecranon process from glenoid cavity breadth and the length of the infraspinous line. A prevalent segregation is seen between specimens of *Saguinus* and those of *C. jacchus* based primarily on similarity and difference due to our measures of elbow and scapula shape. The species of *Saguinus* are contrasted with each other obliquely on the basis of olecranon versus proximal humeral shape. Although we suspect that there is useful functional information embedded in these contrasts, we hesitate to offer specific functional hypotheses at this time until detailed information on positional behavior is available for all three species.

CONCLUSIONS

Although methodological and philosophical issues will continue to generate discussion and dissenting points of view as to what is the "best" technique to analyze size and shape in comparative anatomy and functional morphology, the work of Mosimann and colleagues provides a useful alternative based on the definition of log size-and-shape versus log shape variables and the explicit assumption that shape should be a scale-free or dimensionless feature intrinsic to the object of study. Empirical examination of the relationship between quantitative shape and overall size provides a reasonable foundation from which to make inferences regarding the relative importance of the association or disassociation of these constructs. Recognition and comprehension of these relationships are fundamental steps that logically precede pronouncements regarding phylogeny or function or both (Corruccini, 1987; Bookstein, 1989).
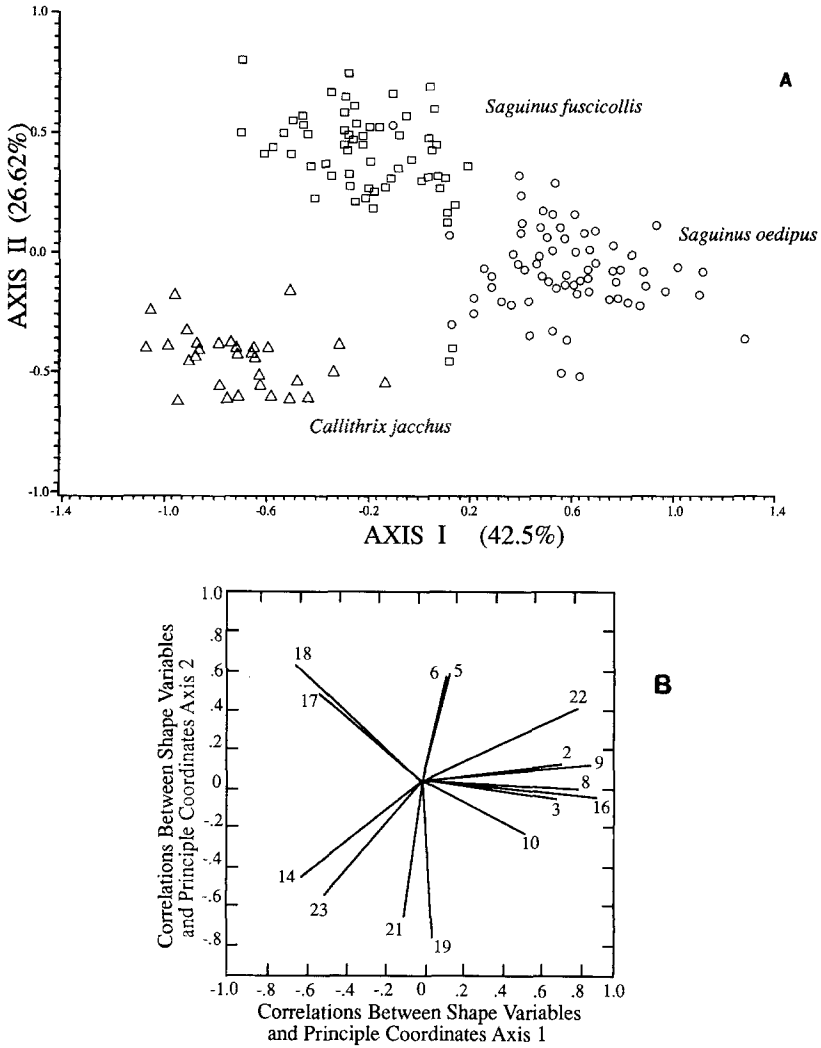
Fig. 6. (A) Principal coordinates of log shape variables; (b) significant Pearson correlation
coefficients greater than −0.5 or 0.5.

In the application of this strategy to the forelimb skeleton of tamarins
and marmosets, it is clear that morphological affinities based on size-and-
shape are different from those derived from a consideration of shape
information alone. Much of what distinguishes these three callitrichid

Table VI. Correlations Among Log Shape Variables and the Scores for the First Two Principal Coordinate Axes (All Individuals; Standardized Data; Average Taxonomic Distances)

	Variable	Correlation between scores and log shape variables	
		I	II
(1)	SML	0.327*	−0.150
(2)	SMB	0.731*	0.089
(3)	SLS	0.697*	−0.083
(4)	SSL	−0.218*	−0.270*
(5)	ISL	0.149	0.572*
(6)	GCB	0.130	0.549*
(7)	GCH	0.313*	0.034
(8)	GIL	0.800*	−0.037
(9)	HML	0.874*	0.092
(10)	BUE	0.545*	−0.269*
(11)	MDS	−0.260*	0.360*
(12)	MDM	−0.119	−0.376*
(13)	MDH	0.345*	−0.226*
(14)	EBR	−0.624*	−0.525*
(15)	LCS	0.042	−0.307*
(16)	UML	0.894*	−0.071
(17)	BOP	−0.539*	0.458*
(18)	MBO	−0.632*	0.624*
(19)	WOP	0.043	−0.820*
(20)	ORL	−0.481*	0.105
(21)	OCL	−0.098	−0.704*
(22)	RML	0.823*	0.378*
(23)	RDH	−0.527*	−0.572*
(24)	MCS	−0.332*	0.495*
	LSIZE	−0.426*	−0.648*

*Significant at the 0.05 level.

species is size, but consistent shape differences, which we believe reflect heritage to a considerable degree, are also evident. In other words, congeneric tamarins are shown to be more similar in shape to each other than either is to the marmoset. More specifically, results from the standard numerical taxonomic methods, based on distance measures and clustering, also emphasize the importance of partitioning shape from raw size-and-shape data. Once isometric size is eliminated, phenetic resemblances among these three taxa make sense in phylogenetic terms. In other words, the two congeneric tamarins are more similar in overall shape than either is to the marmoset (despite size similarity between *S. fuscicollis* and *C. jacchus*).

ACKNOWLEDGMENTS

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