Geometric morphometric analysis of functional divergence in mangabey facial form

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Summary – *Positive facial scaling is a well known phenomenon in Old World monkeys, but non-homologous displacements of facial allometries in mangabeys (Papionini:* Cercocebus *and* Lophocebus*) result in facial shortening and retraction relative to other cercopithecines. Both* Cercocebus *and* Lophocebus *are known to feed on a variety of resistant foods, and mangabey facial geometries have been viewed as adapted for the forceful incision and powerful mastication associated with hard-object feeding. Observed differences between mangabey genera in the relative frequency of incision and mastication have been linked to significant differences in mandibular shape, but analogous differences in facial form have yet to be identified. The hypothesis of functional divergence in facial form can be tested relative to criteria derived from the constrained lever model of the primate masticatory system. Specifically, if* Lophocebus *is adapted for forceful incision, facial retraction, reduced molar row length, and expansion of the incisal region are expected. Conversely, if* Cercocebus *facial form has been optimized for postcanine crushing, medially positioned tooth rows, increased biarticular breadth and decreased tooth row length are expected. These predictions were tested using geometric morphometric analysis. Three-dimensional craniometric landmarks capturing functional aspects of the masticatory complex were recorded for a large sample of cercopithecines and selected colobines. Procrustes-aligned coordinates were subjected to principal components analysis, and principal axes of shape variation were explored statistically and graphically. The hypothesis that the* Lophocebus *masticatory system is adapted for forceful incisal biting was supported.* Cercocebus *failed to conform to predictions, despite the fact that it is known to engage in forceful postcanine mastication. It is suggested that changes in the relative proportions of the postcanine dentition permit* Cercocebus *to circumvent functional constraints on facial retraction and generate large postcanine bite forces while still maintaining structural safety margins.*

Keywords – Cercocebus, Lophocebus, *mastication, functional allometry, constrained lever model.*

Introduction

Allometric scaling of craniofacial dimensions is a general phenomenon in cercopithecine primates, accounting for a significant proportion of cranial shape variation within and among taxa (Profant & Shea, 1994; Ravosa & Profant, 2000). Among cercopithecines, tribe Papionini - the monophyletic group comprising macaques (genus *Macaca*), mangabeys (*Cercocebus* and *Lophocebus*), mandrills and drills (*Mandrillus*), and baboons (*Papio* and *Theropithecus*) - is remarkable both for the degree to which allo-

metric scaling determines cranial form (Profant & Shea, 1994; Ravosa & Profant, 2000) and for the extensive, nonhomologous similarities between like-sized members of its two African sub-clades (Fleagle & McGraw, 1999; Lockwood & Fleagle, 1999; Collard & O'Higgins, 2001; Fleagle & McGraw, 2001; Singleton, 2002; Leigh *et al.*, 2003; Singleton, 2005). Specifically, the small-bodied, quasi-arboreal mangabeys are characterized by moderate facial prognathism, facial retraction, and deeply excavated suborbital fossae (Kuhn, 1967; Thorington & Groves, 1970; Hill, 1974; Szalay & Delson,

1979; Strasser & Delson, 1987). Recent ontogenetic analyses have demonstrated that *Cercocebus* and *Lophocebus* exhibit similar but non-homologous growth allometries distinct from those of their respective sister taxa, *Mandrillus* and *Papio*, as well as the more distantly related macaques (Collard & O'Higgins, 2001; Leigh *et al.*, 2003).

Whereas ontogenetic scaling in closely related taxa is typically associated with selection for altered body size, dissociations of allometric relationships, as observed among the papionins, are frequently indicative of natural selection for novel size-shape relationships (Gould, 1966, 1971, 1975; Shea, 1983, 1985). Such dissociations may reflect the need to preserve biomechanical equivalence as species evolve into new size ranges (Gould, 1971; Shea, 1983; Ravosa, 1992; Smith, 1993; Shea, 1995; Vinyard & Ravosa, 1998) or selection for new or enhanced functional capacities in response to specific adaptive challenges (Demes *et al.*, 1986; Ravosa, 1990, 1992; Shea, 1995). In the case of the mangabeys, allometric dissociation is responsible for the marked facial shortening and retraction that distinguish *Cercocebus* and *Lophocebus* from most other cercopithecines (Singleton, 2005). Under the classic lever model of the masticatory system, facial retraction is linked to increased mechanical advantage of the masseter and anterior temporalis muscles, thus mangabeys are expected to exhibit increased relative bite forces (Du Brul, 1977; Hylander, 1977, 1979b; Ravosa, 1990; Antón, 1996; Singleton, 2005). This functional interpretation of mangabey facial form accords well with available ecological data: both *Cercocebus* and *Lophocebus* are known to feed on a variety of resistant foods including sclerocarp fruits and hard seeds and nuts routinely shunned by sympatric guenons (Haddow, 1952; Tappen, 1960; Chalmers, 1968; Jones & Sabater Pi, 1968; Cashner, 1972; Happel, 1988; Kingdon, 1997; Fleagle & McGraw, 1999). Thus, mangabey facial geometries have been interpreted as adapted for the forceful incision and powerful mastication associated with hard-object feeding (Chalmers, 1968; Happel, 1988; Kingdon, 1997).

But despite their many similarities, it has been noted that the two mangabey genera differ in the relative frequency of these feeding behaviors. Specifically, *Lophocebus* is thought to engage more frequently in incisal preparation of hard-skinned fruits, whereas *Cercocebus* engages in more postcanine crushing of seeds and nuts (Daegling & McGraw, 2000). Consistent with this hypothesis, Daegling and McGraw (2000) have demonstrated significant differences in mangabey mandibular morphology. The *Lophocebus* mandible, with its greater relative depth, is better suited to resist parasagittal bending moments during powerful incision; conversely, the relatively thicker mandibular corpus of *Cercocebus* is capable of resisting transverse bending moments associated with forceful postcanine biting (Hylander, 1979b; Daegling & McGraw, 2000).

While these findings are persuasive, the hypothesis of functional divergence would be substantially strengthened by identification of analogous differences in facial form. However, the predictions of the simple lever model cannot distinguish between these functional alternatives. By contrast, the constrained lever model put forward by Greaves (Greaves, 1978) and subsequently modified by Spencer (Spencer & Demes, 1993; Spencer, 1998,1999), makes substantially different predictions concerning the morphologies associated with incision versus mastication. Under this model (Fig. 1), masticatory geometries are constrained by the need to avoid potentially injurious distractive forces at the balancing-side temporomandibular joint (TMJ). For bite points within Region I, corresponding roughly to the antemolar dentition, predictions are essentially identical to those of the classic model. Because Region I bite points define triangles of support enclosing midline muscle resultant forces, mechanical advantage, and thus relative bite force, increases as bite points shift posteriorly; thus, facial shortening and retraction are expected to enhance maximum incisal bite forces (Greaves, 1978; Spencer, 1999). At the same time, compensatory shortening of the molar row may be required to avoiding pushing distal molars into Region III, where TMJ distraction is

unavoidable (Hylander, 1977; Spencer & Demes, 1993; Spencer, 1999). Bite points in Region II, by contrast, are associated with support triangles that cannot enclose a midline muscle resultant force (Greaves, 1978; Spencer, 1999). To prevent distraction of the TMJ, balancing side muscle activity is decreased, shifting the muscle resultant towards the working side (Hylander, 1979a, b; Spencer, 1999). As bite points shift posteriorly, any mechanical advantage gained is offset by a compensatory reduction in balancing side muscle activity. Thus, facial retraction confers no masticatory benefit. Instead, the constrained model predicts that selection for increased postcanine bite forces will result in more medially positioned tooth rows relative to biarticular breadth (Hylander, 1977; Spencer, 1999). Because the anteroposterior length of Region II decreases medially, a compensatory decrease in postcanine tooth row length is also expected (Spencer, 1999). These contrasting predictions permit a test of alternate hypotheses of the functional significance of mangabey facial form. If *Lophocebus* facial geometries are principally adapted for forceful incision, facial retraction, reduced molar row length, and expansion of the incisal region are expected. Conversely, if *Cercocebus* facial form has been optimized for postcanine crushing, more medially positioned tooth rows, increased biarticular breadth, and decreased tooth row length should be observed.

Functional hypotheses of primate facial form are typically tested by regression analysis of linear distances interpreted within the context of the bivariate allometric model (Huxley, 1932; Gould, 1966). However, geometric morphometric analysis of cranial allometries offers certain advantages over traditional methods, particularly when functional interpretation of allometric dissociations is desired (Singleton, 2005). In comparison with bivariate analyses, which test the scaling of variables individually and sacrifice information concerning relative position, landmark-based geometric analyses permit simultaneous examination of covariation among all variables (landmarks) while preserving geometric relationships (Rohlf & Marcus, 1993). By
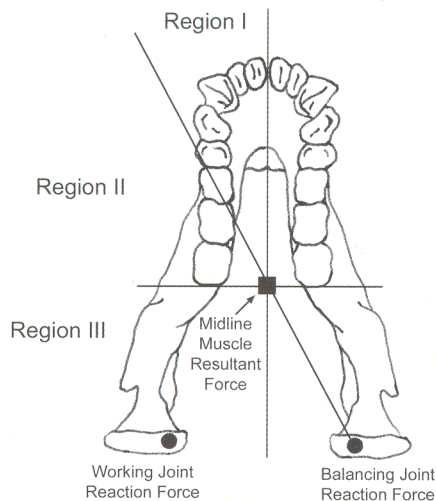
Fig. 1 - *Diagram of dental regions defined by the constrained lever model of the masticatory system (Greaves, 1978; Spencer, 1999). See text for discussion of biomechanical differences among regions. Figure redrawn after Spencer (1999).*

describing how the functional geometry of an entire morphological complex changes with changing size, this approach facilitates functional interpretations of both allometric and residual (size-independent) shape variation (Singleton, 2005). In this study, a comparative geometric analysis of the cercopithecine masticatory system is performed to test the hypothesis of functional divergence in mangabey facial form.

Materials and methods

The study sample comprised crania of 486 adult individuals representing most commonly recognized cercopithecine genera and two colobine outgroups (Tab. 1). The sample was largely limited to wild-collected specimens of known provenience; however, for taxa otherwise poorly represented in museum collections (e.g., *Theropithecus*), zoo specimens lacking obvious pathology and deemed to represent wild-type morphology were included. Adult status was defined by complete eruption of the permanent dentition and closure of the sphenoccipital synchondrosis. Following previously published protocols (Singleton, 2002; Frost *et al.*, 2003), three-dimensional landmark coordinates were recorded using a Microscribe 3-DX digitizer (Immersion Corp., San Jose, CA). Missing data were estimated either by reflection (bilateral landmarks) or substitution of sex-specific taxon mean values (unpaired landmarks). A high proportion of specimens (19%) exhibited at least one missing landmark; however, estimated values account for only 0.01% of data analyzed so are not expected to affect results. From an original set of 45 standard osteometric landmarks (see Frost *et al.*, 2003 for landmark definitions), a subset of eighteen (Fig. 2) was chosen to capture functional aspects of the masticatory complex pertinent to the constrained level model, including: 1) the relative positions of the TMJ, zygomatic root, and palate; 2) palate shape and relative length; and, 3) the positions of maxillary bite points.

Masticatory landmark configurations were subjected to generalized Procrustes analysis - an iterative least-squares procedure that eliminates the effects of translation, rotation and scale (Slice *et al.*, 1996; Dryden & Mardia, 1998) - using *Morpheus et al.* (Slice, 1998). Principal components analysis (PCA) of the covariance matrix of aligned coordinates was performed as a means of data reduction and to compensate for the lack of statistical independence among landmarks due to morphological integration and the constraints of Procrustes superimposition (Dryden & Mardia, 1998; Rohlf, 1999). PCA ordinates specimens relative to mutually orthogonal axes of shape variation, the principal shape components. The resulting shape component (SC) scores are statistically independent shape variables that summarize the majority of sample variation (Dryden & Mardia, 1998; Rohlf, 1999). It should be emphasized that because GPA does not eliminate allometric effects, shape component scores incorporate both size-correlated (allometric) and size-independent (residual) shape variation. Patterns of shape variation for selected shape components were explored graphically using *Morphologika* (O'Higgins & Jones, 1999) to conduct PCA of sex-specific mean forms and generate wireframe representations of shape trends along individual axes. In some cases, the resulting mean scores differed slightly from those of the full sample analysis, but these deviations do not substantively affect interpretations of functional shape variation.

Results of the full sample PCA were used as the basis of all statistical analyses. Bivariate scatterplots of SC scores against log centroid size (Slice *et al.*, 1996) were used to identify potential allometric relationships, the strengths of which were assessed by correlation analysis. Between-species differences in scaling were tested using analysis of covariance (ANCOVA) of SC scores by log centroid size, and differences in regression elevations were assessed by pairwise comparison of least-squares means, i.e., species means adjusted for the effects of centroid size. Where heterogeneity of slopes precluded statistical testing of elevations across the entire sample, ANCOVA analyses were rerun for the mangabeys alone. For non-allometric shape components, differences in shape between mangabey species were tested using analysis of variance (ANOVA) of SC scores.

Table 1. Study sample by sex

|	F	M
Colobus angolensis cottoni	12	22
Colobus guereza kikuyuensis	10	20
Cercopithecus ascanius ngamiensis	19	8
Cercopithecus mona	23	20
Allenopithecus nigroviridis	3	3
Erythrocebus patas	4	9
Miopithecus ougouensis	15	6
Cercocebus galeritis agilis	9	7
Cercocebus torquatus torquatus	11	18
Lophocebus albigena johnstoni	15	24
Macaca fascicularis	17	26
Macaca nemestrina	4	9
Mandrillus leucophaeus	8	19
Mandrillus sphynx	8	13
Papio hamadryas anubis	21	42
Theropithecus gelada	13	25
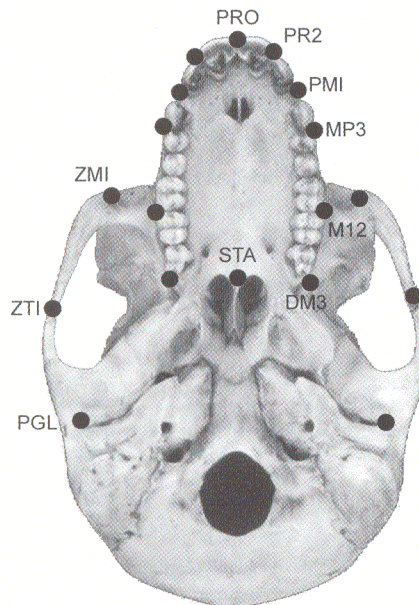
Fig. 2 - *Ventral view of representative cercopithecine skull (female* L. albigena johnstoni*) showing masticatory landmarks employed in this study. See Frost* et al. *(2003) for landmark definitions.*

Results

The first ten principal shape components account for 90% of total shape variance. Of these, only the first four achieve meaningful separation among sample taxa. The 1st Principal Shape Component (SC1) accounts for 61% of total variance and appears to ordinate specimens by size (Figure 3a), with small-bodied taxa (*Miopithecus* and *Cercopithecus*) falling at the negative end of the axis and large-bodied taxa (*Papio* and *Mandrillus*) occupying its positive extreme. Smaller taxa are characterized by relatively short, broad palates and anteriorly positioned zygomatic roots; large taxa exhibit decreased biarticular breadth and narrow, elongate palates, which are located well anterior to the zygomatics. SC1 is significantly correlated with log centroid size both across (r = 0.89, p < 0.0001) and within cercopithecine species (see Tab. 2). ANCOVA confirms that allometric effects account for a large proportion of variation in SC1 (adjusted R^2 = 0.96, F = 374.95, p <

0.001) and finds significant differences among species in the scaling of SC1 relative to log centroid size (Tab. 3). Heterogeneity of slopes among sample species (p < 0.01) precludes statistical comparison of regression elevations. It is nevertheless clear that *Cercocebus* and *Lophocebus* regressions are strongly negatively displaced relative to other cercopithecines and exhibit extensive overlap with colobines (Figure 4a). As a result, both mangabey genera are characterized by decreased palate length, increased palate breadth, and increased biarticular breadth when compared with similarly sized cercopithecines. *Cercocebus torquatus*, by virtue of its greater average size (Delson *et al.*, 2000), shows significantly greater SC1 scores than either *C. galeritis* or *L. albigena* (see Tab. 4). However, when effects of size are controlled, it is *C. galeritis* which differs from other mangabey species. It shows significantly lower least-squares means than either *C. torquatus* or *L. albigena* (Tab. 4); the latter taxa are not statistically distinguishable. Thus, at similar body sizes, *C. torquatus* and *L. albigena* are

Table 2. Correlation of SC scores with log centroid size

	SC1	SC2	SC3	SC4
Across Species	0.89	0.15	0.26	0.00NS
Within Species				
Colobus angolensis cottoni	0.65	0.49**	0.00NS	0.62
Colobus guereza kikuyuensis	0.71	0.52**	0.54**	0.54**
Cercopithecus ascanius ngamiensis	0.83	0.77	0.47*	0.43*
Cercopithecus mona	0.80	0.54	0.36*	0.78
Allenopithecus nigroviridis	0.42NS	0.93**	0.53NS	0.97**
Erythrocebus patas	0.93	0.91	0.64*	0.74**
Miopithecus ougouensis	0.76	0.59**	0.46*	0.13NS
Cercocebus galeritis agilis	0.81	0.67**	0.21NS	0.71**
Cercocebus torquatus torquatus	0.88	0.30NS	0.20NS	0.65
Lophocebus albigena johnstoni	0.90	0.35*	0.09NS	0.45**
Macaca fascicularis	0.81	0.43**	0.02NS	0.73
Macaca nemestrina	0.93	0.06NS	0.24NS	0.62*
Mandrillus leucophaeus	0.90	0.73	0.07NS	0.90
Mandrillus sphynx	0.89	0.68	0.04NS	0.82
Papio hamadryas anubis	0.89	0.38**	0.07NS	0.81
Theropithecus gelada	0.86	0.46**	0.70	0.77

All correlations significant at p < 0.001 except as indicated:
* p < 0.05
** p < 0.01
NS Not Significant

Table 3. ANCOVA of SC scores

	F	p	Partial Eta^2
SC1			
Log Centroid Size	603.59	0.000	0.58
Slope	2.31	0.004	0.07
Total Adjusted R^2	0.96	0.000	
SC2			
Log Centroid Size	164.04	0.000	0.28
Slope	3.83	0.000	0.12
Total Adjusted R^2	0.67	0.000	
SC4			
Log Centroid Size	256.15	0.000	0.37
Slope	1.45	0.118	0.05
Total Adjusted R^2	0.73	0.000	

geometrically similar with respect to SC1, while *C. galeritis* exhibits a somewhat greater biarticular breadth and a wider and shorter palate.

The 2nd Principal Shape Component (6.4% of shape variance) separates cercopithecins from papionins and *Colobus* and describes differences in palate shape and position (Fig. 3a). Cercopithecins (negative scores) exhibit a shorter, more parabolic palate that is relatively anteriorly positioned, while papionins (more positive scores) are characterized by palates that are longer, squarer, and relatively closer to the TMJ. SC2 is uncorrelated with log centroid size across taxa (r = 0.15, p = 0.001), but moderately correlated within the majority of species (Tab. 2). Thus, within species, relative distance between the palate and TMJ tends to decrease with increasing body size. Allometric effects account for a smaller proportion of variance in SC2 (adjusted R^2 = 0.67, p < 0.001). Heterogeneity of slopes (p < 0.001) prevents testing of differences in elevations across cercopithecines; however, the obvious negative displacement of papionin trajectories (Figure 4b) implies greater retraction of the palate relative to TMJ than in like-sized cercopithecins.

Like other papionins, mangabeys fall towards the positive end of SC2 (Figure 3a), but *Lophocebus* shows significantly more positive SC2 scores than either *Cercocebus* species (Tab. 4), indicating a relatively more posteriorly positioned palate. In comparisons restricted to mangabey species, differences in scaling account for a relatively small, albeit significant, proportion of variance in SC2 (adjusted R^2 = 0.23, p < 0.001). Homogeneity of slopes is confirmed, and when size effects are controlled, *Lophocebus* shows a more positive estimated marginal mean (Tab. 4) than either *Cercocebus* species. In summary, both mangabey genera share the papionin tendency towards relatively posterior palate position, but *Lophocebus* exhibits stronger palatal retraction than *Cercocebus*, irrespective of size.
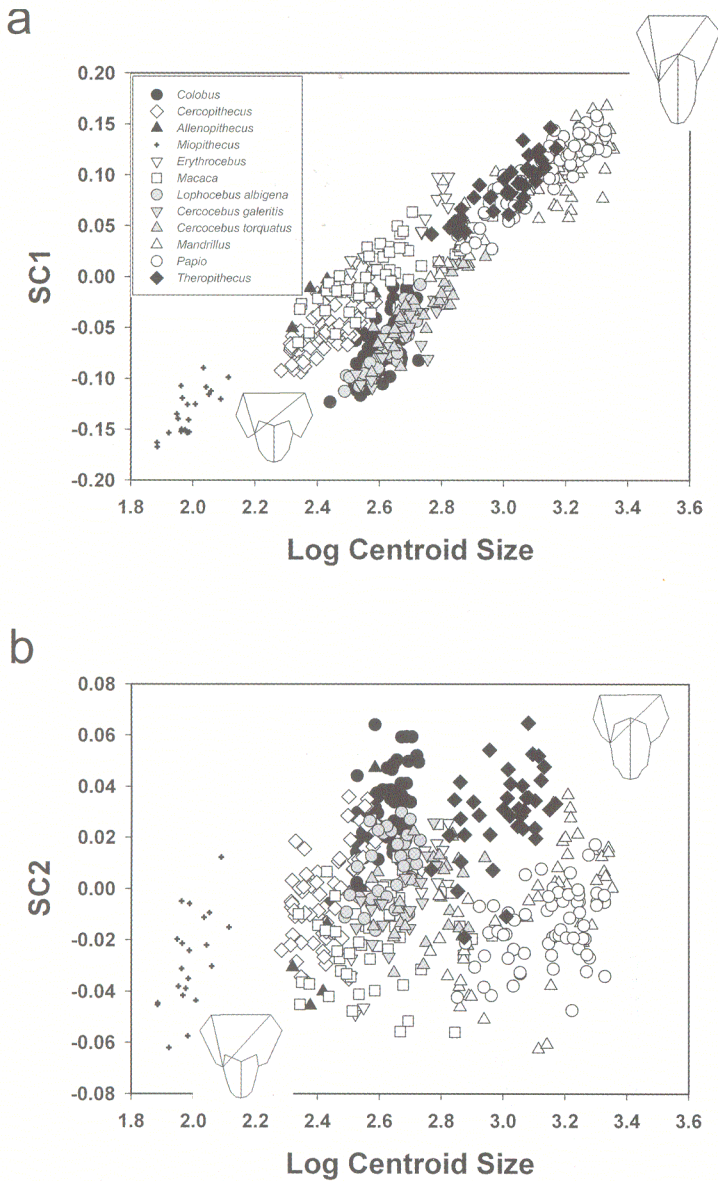
The 3rd Principal Shape Component (5.7 % total shape variance) separates males and females within species (not shown). SC3 is only weakly correlated with log centroid size across species (r = 0.26, p. < 0.0001) and either weakly correlated or uncorrelated within the majority of species, and is therefore inferred to summarize non-allometric sexual shape dimorphism. Within species, males (more positive scores) exhibit more flaring zygomatics and relatively expanded canine regions, while females (more negative scores) show narrower zygomatics and more parabolic palates.

The 4th Principal Shape Component (4.5% total shape variance) appears to summarize dif-
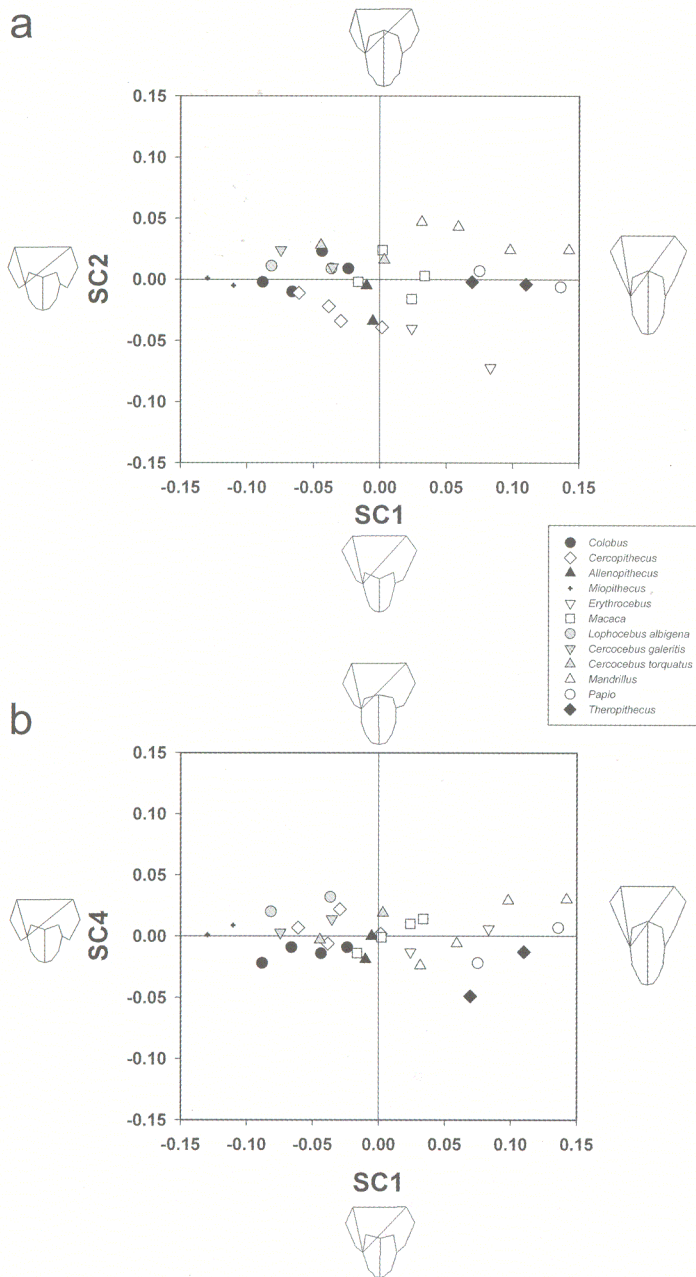
Fig. 3 - *Shape variation summarized by principal shape components: a) Plot of SC1 by SC2; b) Plot of SC1 by SC4. Symbols represent male and female mean values for each species. Wireframes represent extremes of shape variation along shape component axes.*

Fig. 4 - *Allometric scaling of principal shape components: a) SC1 by log centroid size; b) SC2 by log centroid size. Wireframes represent extremes of shape variation for each component*

Table 4. *Mean SC scores and pairwise comparisons*

	SC1		SC2		SC3		SC4	
	Mean	LS Mean	Mean	LS Mean	Mean	LS Mean	Mean	LS Mean
Taxon Means								
L. albigena	-0.064	-0.048	0.007	0.010	-0.020	–	0.020	0.023
C. torquatus	-0.025	-0.046	-0.003	-0.007	-0.025	–	-0.001	-0.007
C. galeritis	-0.068	-0.061	-0.005	-0.002	-0.019	–	0.001	0.002
Comparisons								
albigena-torquatus	***	NS	*	***	NS	–	***	***
albigena-galeritis	NS	*	*	*	NS	–	***	***
torquatus-galeritis	***	*	NS	NS	NS	–	NS	NS

Results for significant ANOVA and ANCOVA analyses only. LS Means adjusted for effects of log centroid size. Bonferroni adjusted significance levels:
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
NS Not Significant

ferences in dental arcade proportions (Fig. 3b). Relatively positive scores signify expansion of the incisal region and reduction of the molar row posterior to M^1; more negative scores indicate narrower incisal regions and relative expansion of the tooth row anterior to M^2. *Lophocebus* occupies the positive extreme of variation on this axis, and is thus characterized by increased relative breadth of the incisor row and reduction of the posterior molar row. *Cercocebus* species exhibit significantly less positive scores (Tab. 4), resulting in decreased incisal breadth and a relative expansion of the premolar region relative to *Lophocebus*. SC4 is uncorrelated with log centroid size across taxa but strongly correlated within most species (Tab. 2). ANCOVA (Tab. 3) confirms homogeneity of slopes among study taxa, and comparison of least-squares means identifies significant differences in regression elevations between the mangabey genera (Tab. 4). At comparable sizes, *Lophocebus* possesses relatively larger incisors and smaller posterior molars while *Cercocebus* species possess relatively enlarged premolars.

Discussion

The results of the present study are substantially similar to those of Singleton (2005), but with the inclusion of additional landmarks, functional distinctions between mangabeys and other cercopithecines are more pronounced and differences among mangabey species are now evident. The first two principal shape components describe intertaxic differences in relative palate shape and position that contribute to variation in facial prognathism. As is common for such studies, the 1st Principal Shape Component is a common allometric vector describing a pattern of increased palate length, decreased palate breadth, and enhanced facial prognathism with increasing size. ANCOVA of SC1 by centroid size confirms this relationship, which is consistent with established patterns of cercopithecine facial scaling (Zuckerman, 1926; Freedman, 1962, 1963; Swindler & Sirianni, 1973; Swindler *et al.*, 1973; McNamara *et al.*, 1976; Cochard, 1985; Ravosa, 1990; Richtsmeier *et al.*, 1993; O'Higgins &

Jones, 1998; Ravosa & Profant, 2000; Collard & O'Higgins, 2001; O'Higgins & Collard, 2002; Leigh *et al.*, 2003). As in the prior study, negative displacement of mangabey regression lines results in masticatory forms distinct from most cercopithecines and similar in many respects to colobines. That the inclusion of additional landmarks results in more extensive overlap between mangabey and *Colobus* allometric trajectories suggests that prior results are not an artifact of landmark selection but reflect pervasive functional differences between mangabeys and other cercopithecines. The 2nd Principal Shape Component also summarizes size-correlated differences in palate shape and position. But scaling of SC2 is considerably more complex, with a pattern of inter- and intra-tribal differences similar to - and perhaps functionally linked with - those previously described for relative gape (Singleton, 2005).

Mechanical Advantage

The first principal shape component describes variation in relative palate proportions and the relative position of the zygomatic root, while the second summarizes variation in dental arcade shape and the position of the palate relative to the TMJ. Considered jointly, these components permit an assessment of relative masticatory advantage. Under the constrained lever model, reduced facial prognathism provides increased mechanical advantage at Region I bite points and is functionally associated with forceful incision, while increases in the ratio of biarticular breadth to arcade breadth increase mechanical advantage at Region II bite points and are linked with powerful molar biting (Greaves, 1978, 1995; Spencer, 1999). Relative to similarly sized cercopithecines, both *Lophocebus* and *Cercocebus* exhibit marked facial shortening and strong facial retraction and are therefore expected to generate greater relative incisal bite forces. All mangabey species sampled are characterized by increased biarticular breadth relative to size, but concomitant increase in relative palate breadth implies no net increase in Region II mechanical advantage. On the contrary, because palatal breadth scales with stronger

negative allometry than biarticular breadth (Spencer, 1999) - meaning relative molar bite forces increase with increasing size - the negative displacement of mangabey trajectories is expected to result in *smaller* relative bite forces than in similarly sized cercopithecines.

Small but statistically significant differences in functional scaling among mangabey species are revealed by comparisons of size-adjusted SC scores. Negative displacement of the *C. galeritis* trajectory results in increased relative interarticular and palatal breadths and more pronounced facial shortening in comparison with *C. torquatus* and *L. albigena*; the latter taxa have similar adjusted mean SC1 values and are not statistically distinguishable. The significantly more positive size-adjusted SC2 mean of *Lophocebus* signifies relatively greater retraction of the palate than in either *Cercocebus* species. Based on these findings, it is expected that *Lophocebus* and *C. galeritis* will exhibit relatively greater incisal bite forces than *C. torquatus*, the latter due to more pronounced facial shortening, the former because of stronger facial retraction. For reasons outlined above, it is also expected that *C. galeritis* will exhibit smaller relative molar bite forces.

Dental Proportions

The 4th Principal Shape Component summarizes allometric variation in relative dental proportions. Within species, increasing size is accompanied by increased relative incisal breadth but relative decrease in the length of the post-M^1 molar row. Under the constrained lever model, facial retraction is expected to be accompanied by a reduction in the length of the posterior molar row, a necessary accommodation to prevent distractive forces at the balancing-side TMJ during posterior molar biting (Greaves, 1978, 1995; Spencer, 1999). Increased molar bite force, by contrast, is expected to be accompanied by a shorter postcanine tooth row, a geometric consequence of more medial tooth row position (Spencer, 1999). *Lophocebus* occupies one pole of variation with respect to SC4, and is characterized by relatively enlarged incisors and a relatively shortened posterior molar row in comparison with most cercopithecids. Comparisons of raw

and size-adjusted mean SC4 scores show *Lophocebus* to have significantly broader incisors and shorter posterior molar rows than either *Cercocebus* species. The relatively more negative mean scores of *Cercocebus* indicate a relative expansion of the tooth row anterior to M^2. Differences in the total relative length of the postcanine tooth row are not apparent on this, or any, principal shape component.

That *Lophocebus* possesses relatively broad incisors is well-known (Hill, 1974; Swindler & Sirianni, 1975; Groves, 1978; Szalay & Delson, 1979; Kingdon, 1997), and relative reduction of the molar row has previously been noted (Hylander, 1979b; Szalay & Delson, 1979). The finding of posterior molar reduction conforms with biomechanical predictions (Greaves, 1978, 1995; Spencer, 1999) and mirrors studies in which facial retraction has been linked to M^3 reduction or loss (Hylander, 1977; Shea, 1992; Spencer & Demes, 1993). Thus, posterior molar row reduction in *Lophocebus* is plausibly interpreted as a secondary adaptation to avoid distraction of the balancing-side TMJ during posterior molar biting. Predictions of tooth row shortening in *Cercocebus* are contingent upon a medial shift in tooth row position. Since relative palatal breadths in *Cercocebus* equal or exceed those of *Lophocebus*, the absence of a significant decrease in relative tooth row length is unsurprising. The apparent expansion of the pre-M^2 tooth row was not predicted, but accords with observations that *Cercocebus* is characterized by expanded first molars and markedly expanded fourth premolars (Fleagle & McGraw, 1999, 2001).

Lophocebus

The functional divergence hypothesis (Daegling & McGraw, 2000) posits that differences between the mangabeys in the relative frequency of specific feeding behaviors are linked to biomechanical differences in facial form. If *Lophocebus* is principally adapted for forceful incision, it is expected to exhibit relative facial shortening and retraction, decreased molar row length, and relative expansion of the incisal region. Consistent with these predictions,

Lophocebus exhibits decreased relative palate length, strong retraction of the palate relative to the TMJ, a reduction in post-M[1] tooth row length, and a markedly expanded incisal region. The selective advantage of enlarged incisors for animals engaging in habitual, forceful incision is well-established; increased incisor breadth both extends functional tooth life and increases working surface area, giving maximum return relative to muscular effort (Hylander, 1975; Eaglen, 1984; Ungar, 1998). By increasing mechanical advantage, facial shortening and retraction also increase masticatory efficiency, maximizing incisal bite forces relative to muscle force. Thus, the hypothesis that *Lophocebus* facial form is optimized for forceful incisal biting is supported.

These results are consistent with previous findings that the *Lophocebus* mandible is engineered to resist large parasagittal bending moments such as are incurred during anterior dental loading (Hylander, 1979b; Daegling & McGraw, 2000). Behavioral data for *Lophocebus* are sparse, but it is known to feed regularly on large, sclerocarp fruits (Haddow, 1952; Tappen, 1960; Chalmers, 1968; Happel, 1988). Use of incisors to crack resistant pericarps has been directly observed (Chalmers, 1968), as has incisal bark stripping (Chalmers, 1968; Cashner, 1972). It is thus reasonable to infer that the *Lophocebus* masticatory complex is adapted for incisal preparation of the hard-skinned fruits that are a major component of its diet (Tappen, 1960; Chalmers, 1968; Jones & Sabater Pi, 1968; Kingdon, 1997). As in the well known case of the Inuits (Hylander, 1977; Spencer & Demes, 1993), this adaptation appears to come at the cost of reduced molar row length and, perhaps, surface area (Spencer & Demes, 1993). Dental metric studies are needed to confirm this finding and to assess its implications for masticatory function in *Lophocebus* mangabeys.

Cercocebus

If *Cercocebus* facial form has been optimized for postcanine crushing, more medially positioned tooth rows, increased biarticular breadth, and decreased tooth row length should be observed. But contrary to predictions, *Cercocebus*

exhibits neither medially positioned tooth rows nor decreased tooth row length. Biarticular breadth is increased relative to size in *C. torquatus*, but no more so than in *Lophocebus*. In the case of *C. galeritis*, allometric displacement actually produces a less favorable ratio of biarticular breadth to palatal breadth with the result that relative molar bite forces are decreased in comparison with *Lophocebus* and other cercopithecines. Thus, by the criteria of the constrained lever model, the hypothesis that *Cercocebus* facial form is specifically adaptive for postcanine mastication is not supported. Yet, the fact remains that *Cercocebus* mangabeys routinely masticate objects of exceptional hardness and without apparent difficulty or ill effects (Happel, 1988; Fleagle & McGraw, 1999, 2001). Biomechanical evidence, too, suggests that *Cercocebus* mandibular form has been selected to resist transverse bending moments generated during forceful postcanine biting (Hylander, 1979b; Daegling & McGraw, 2000).

The answer to this paradox might lie in the relative proportions of the *Cercocebus* tooth row. Fleagle and McGraw hypothesized that premolar expansion in *Cercocebus* is an adaptation to hard-object feeding (Fleagle & McGraw, 1999, 2001), and forceful premolar biting has been reported by Happel (1988) and McGraw (W.S. McGraw, pers. com.). The constrained lever model permits two possible interpretations of these observations. Teeth within Region II are characterized by greater occlusal surface area, and an abrupt decrease in tooth size typically marks its anterior boundary (Greaves, 1995). Thus, premolar expansion in *Cercocebus* may indicate that the region of maximum force (Region II) has been extended to include these teeth. How this extension might have been achieved is not clear. The constrained lever model predicts that lateral movement of the TMJ - as seen in mangabeys generally and *C. galeritis* in particular - will be accompanied by a *reduction* in the effective length of Region II. Alternatively, it is possible that P[4] remains within Region I, and that extreme facial shortening in *Cercocebus* confers sufficient mechanical advantage to permit forceful mastication outside the region of maximum

force (Greaves, 1995). Studies incorporating the position of the jaw adductor resultant force are needed to clarify where the fourth premolar lies relative to the Region I-Region II boundary and to establish which, if either, of these explanations might account for the relatively high bite forces of which *Cercocebus* is capable.

Why either of these strategies might have been adopted in preference to the expected decrease in palate breadth is somewhat puzzling until one recalls that *Cercocebus* also engages in incisal food preparation, albeit with lower frequency and less vigor than *Lophocebus* (Chalmers, 1968; Happel, 1988; Daegling & McGraw, 2000). Increased jaw breadth is the most efficient means to resist cranial torsion associated with large anterior dental loads (Greaves, 1995). Thus, medial positioning of the tooth row is achieved only at the cost of decreased safety margins during forceful incisal biting. It seems likely that *Cercocebus* facial form represents a compromise between the functional demands of incision and mastication. To avoid structural failure during anterior dental loading, relative palatal breadth is maintained. But by transferring forceful mastication to the mesial extent of the postcanine tooth row, *Cercocebus* is able to generate adequate postcanine bite forces while preserving TMJ integrity.

Conclusions and summary

Geometric morphometric analysis offers an efficient and effective means of exploring the functional consequences of allometric and size-independent variation in primate facial form. In this study, geometric methods were employed to test a hypothesis of functional divergence in mangabey facial form against the predictions of the constrained lever model of masticatory function. Consistent with predictions, *Lophocebus* is characterized by marked facial shortening and retraction, increased incisal breadth, and reduction of the posterior molar row. Thus, the hypothesis that *Lophocebus* facial form is adapted for powerful incision is supported. By contrast, the hypothesis that *Cercocebus* facial form is adapted for postcanine mastication was not sup-

ported, and the predicted morphological pattern of increased biarticular breadth, decreased palatal breadth, and reduced tooth row length was not observed. Rather, *Cercocebus* is characterized by increased interarticular breadth, a relatively short, broad palate, and expanded anterior tooth row. This finding is counter to traditional interpretations of mangabey facial form and is directly contradicted by behavioral and biomechanical studies that confirm the ability of *Cercocebus* to generate and safely dissipate large postcanine occlusal loads. To explain this discrepancy, it is hypothesized that *Cercocebus* facial form represents a biomechanical compromise between the functional demands of anterior and posterior dental loading. It is suggested that by transferring forceful mastication to the anterior-most extent of the postcanine tooth row, *Cercocebus* circumvents theoretical constraints on facial retraction while maintaining functional safety margins. Further studies incorporating the location of muscle resultant forces will be required to assess this hypothesis. These, it is hoped, will clarify the significance of mangabey facial form and furnish new insights into functional constraints limiting primate cranial diversity.

Acknowledgements

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