DIET AND CRANIOFACIAL VARIATION IN THREE WEST AFRICAN COLOBINES

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By

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ABSTRACT

Primate craniofacial morphology has been linked to differences in masticatory stresses. The various demands that occlusal forces place on the maxillo-facial complex are often in opposing areas and, as such, maintain a system of balance and counter balance. It has been shown that primates with diets requiring greater masticatory forces tend to exhibit increased facial retraction, vertically deeper faces and a more anteriorly-placed masseter muscle attachment. I compared the crania of three sympatric colobine species to test the effect of dietary differences on craniofacial form. If a phenotype favoring increased facial retraction provides a mechanical advantage for durphagy, then I expect those areas of the cranium influencing mastication to be most important for discrimination of these species.

Procolobus badius, *Colobus polykomos* and *Procolobus verus* are sympatric species that differ significantly in diet. *C. polykomos* exploits tough seeds, *P. badius* feeds on fruits as well as leaves, and *P. verus* feeds primarily on young leaves. A series of measurements were taken on the maxillo-facial complex on the specimens (n=52) from the Tai Forest of Côte d'lvoire.

Discriminant functions were calculated using forward stepwise methodology and assessed by a leave-one-out hit-rate estimate comparison. All functions were significant at $p < 0.05$. Measurements most important for discrimination were malar subtense, malar length bimaxillary subtense, and basion-prostion length (at 92.6 – 99.7%). *C. polykomos* does not show the typical phenotypic pattern for an obdurate feeder. However, the features most clearly separating taxa are those that relate to generally increased bite forces and presumably diet. This is likely due to the complex nature of mastication, and the difficulty of capturing this complexity with 2-D linear modeling.

Dedicated to my parents Bashir and Ghazala Ulvi

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PUBLICATIONS

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2. Kolatorowicz, A., Ulvi, O. (2007) Classificatory Power of Non-Standard Measurements for Sex Determination in Human Crania. *Midwest Bio-archeology association online journal* (abstract)

3. Ulvi O.S., McGraw W.S., Guatelli-Steinberg D. (2008) Anterior alveolar process curvature and diet in two West African colobine species. *Am. J. Phys. Anthropol.* 135:212

4. McKee J.K., Kolatorowicz A., Reitsema L., Ruth A., Schlecht S., Ulvi O., Weston T. (2008) Backpedaling in human evolution – adaptive values of bipedalism in reverse. *Am. J. Phys. Anthropol.* 135: 152-153

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CHAPTER 1

INTRODUCTION

The prevailing opinion among functional morphologists is that skeletal form reflects the mechanical activity and behavior patterns of living primates. This assumption has great implications for reconstructing past behavior from fossil primate taxa, including those that fall in the human lineage. However, this purported connection between feeding behavior and elements of craniofacial morphology is somewhat tenuous. Critics suggest that the multiple functional demands, as well as genetic effects, will confound results and that there cannot be a completely definitive link between dietary behavior and elements of morphology (Smith 1983; Brown 1997). While we may never be able to create a complete link between elements of skeletal form and behavior, an increasing body of evidence points towards a link between diet and cranial morphology (Hylander 1979; Ravosa 1990, 1991; Cole 1992; Daegling 1992; Anton 1996). This study is intended to be another layer of evidence that points to a significant relationship between facial form and dietary differences.

Variation in the maxillofacial complex in primates has been attributed to differences in masticatory stresses which relate to dietary disparity between species (Du Brul 1974, 1977; Ravosa 1990; Spencer 1997, 2000). Differences in food properties exploited by primate species influence variation in occlusal forces. Various demands placed on the maxillo-facial complex by occlusal forces are often in opposing areas and as such, a system of balance and counter-balance is maintained. Torsion and forces caused by mastication must be dissipated across the maxilla for efficient food processing. This idea suggests the hypothesis that selection for the most efficient bite force will lead to structural modifications of the splanchocranium leading to increased mechanical advantage of the masticatory process (Spencer 1997). Changes in the morphology of the maxillo-facial complex have been associated with selection pressures due to differences in occlusal forces (Du Brul 1974, 1977; Carlson and van Gerven 1977; Hylander 1977; Smith 1978; Ward and Molnar 1980; Jablonski 1993; Rak 1983; Bouvier 1986, Daegling 1989, 1992; Spencer 1997, 2000). Because of the modular nature of craniofacial development during ontogeny, an adaptive response to one area may significantly impact additional areas of the complex.

Primates with diets requiring greater occlusal forces to process food items exhibit morphologies adapted for increased mechanical advantage (Kinzey 1974; Hylander 1977; Ravosa 1990, 1991; Daegling 1992, Anton 1996; Daegling and McGraw 2002). For example, macaques with diets requiring greater masticatory forces tend to exhibit increased facial retraction, vertically deeper faces and a more anteriorly-placed masseter muscle attachment (Anton 1996) (see Figure 1). These changes in facial form decrease the length of the masseter load arm and, in doing so, increase bite force. The masticatory apparatus is a 3rd class lever system. The fulcrum is at the end of the lever, and the effort is placed between the fulcrum and the load. By reducing the load arm, the distance from the masseter muscle to the end of the mandible, there is an increased mechanical advantage because less effort is needed to raise the load arm. If effort by the masseter muscle remains constant, there is increased bite force when the load arm is reduced.

The mechanical properties of food also influence the amount of force, torsion and bending that must be dissipated through the facial skeleton (Lucas and Corlett 1991; Anton 1996). In particular, cranial changes producing greater facial retraction have been linked to selection for increased mechanical advantage of the masseter and anterior temporalis muscles (Du Brul 1977, Ravosa 1990, Anton 1996).

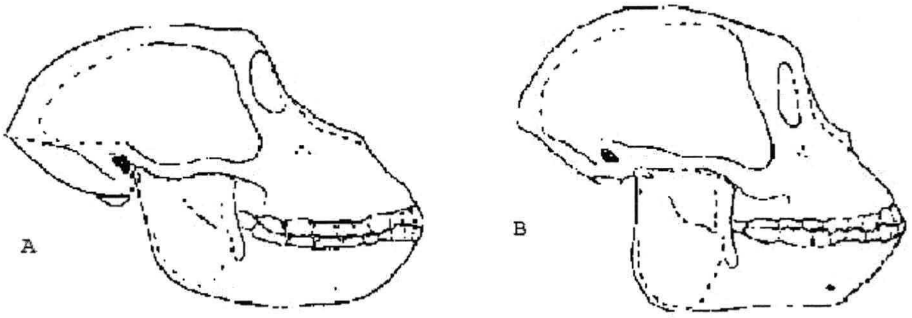


Figure 1: From Anton (1996): lateral views of macaque skulls. **(A)** pigtailed macaque (*Macaca nemestrina*) and **(B)** Japanese macacque (*Macaca fuscata*). These macaques are of comparable size, but differ in diet, with the Japanese macaque showing adaptation for durophagy.

An adaptive modification in the relative amount of facial prognathism has implications for the rest of the system. The change in facial form affects the placement of the teeth and muscles. It also influences the breadth of the maxillary and mandibular corpus for the benefit of hard object mastication.

Increased facial retraction, a more anterior placed masseter muscle, vertically taller faces, and a more robust mandibular corpus all aid in dissipating greater occlusal forces during mastication, or provide a biomechanical advantage for hard object feeding (Anton 1996). A reduction in facial length and a more anteriorly-placed masseter muscle provide a phenotype that is more suited for hard object feeding by bringing the bite point in molar mastication in line with the muscles of mastication (Hylander 1972, 1977; Cartmill 1974). This morphology reduces bending moments in the face while also abating the axial torsion load on the mandibular corpus (Hylander 1972, 1985; Anton 1996). The resultant effects of this morphology may also help to decrease the horizontal force vector in mastication, which contributes heavily to axial torsion and wishboning on the mandibular symphysis (Hylander and Johnson 1994, Anton 1996). The phenotype may also require less masseter muscle force to produce the bite forces necessary for a high-attrition diet, thus offering a more energetically efficient way to process harder and tougher food items (Anton 1996). This particular suite of characteristics seems to represent a biomechanical adaptation for a high-attrition diet, and we would expect to see similar morphologies in primates with diets that require greater masticatory forces in food processing.

A collection of sympatric west African colobine monkeys provides a sample with which to test the implications of dietary differences on the morphology of the maxillo-facial complex. The western black and white colobus (*Colobus polykomos),* the red colobus *(Procolobus badius)*, and the olive colobus (*Procolobus verus)* are closely related species that are sympatric throughout most of their ranges (Wachter et al. 1997).

At the Tai Forest of Côte d'Ivoire the diet of *C. polykomos* consists of a large portion of hard/tough seeds (≤ 33%); the other portion is made up of fruits, and leaves. *P. badius* exploits a large amount of ripe fruit, mature leaves and flowers. *P. verus* feeds primarily on young leaves. These species differ significantly in diet and challenge the assumption that all colobine monkeys are dedicated folivores (Schaff 1995; Watcher et al. 1997; Davies et al. 1999). An interesting feature of the diet of *C. polykomos* is that it is able to process the thick, woody pods and tough seeds of *Pentaclethera macrophylla*. The seed pods are large and extremely tough; monkeys often spend upwards of 15 minutes processing these pods to get at the seeds (Davies et al. 1999; Oates 1994; McGraw and Zuberbuhler 2007). The seasonal processing of *P. macrophylla* seed pods by *C. polykomos* is likely to involve greater masticatory forces than those of the other two species. There is evidence that seed predation is such an important component of their diet that it is predictable from dental and mandible morphology (Lucas and Teaford 1994; Daegling and McGraw 2002). Dietary behavior in these three species should be distinct enough to be reflected in the morphologies of splanchnocrania.

Variability in colobine species is more diverse than is often assumed. One of the first attempts at cataloging the inter-specific cranial variability of the species was done by Schultz (1957). The degree of facial prognathism has been described as one of the most distinctive characteristics of *C. polykomos*. *P. verus* on the other hand is described as orthognath and gracile in comparison to the other two species (Schultz 1957, Groves 2007*)*. *C. polykomos* and *P. badius* do not greatly differ in body size: mean body weights of 9.9 kg (N=5; sd= 1.3; male); 8.2 kg (N=10; sd= 1.1; female) for *C. polykomos;*

and 8.3 kg (N=9; sd=1.0; male); 8.2 kg (N=14; sd=1.1; female) for *P. badius* (Oates et al. 1990). *P. verus* is significantly smaller than the other two species, and as such size was controlled for in this study by using z-score data for comparison.

These taxa represent a natural experiment that involves closely related sympatric species that differ significantly in a single component of behavior and diet. Because the species are closely related, the effects of phylogeny and body size on morphology should be minimized; morphologic differences in craniofacial morphology should be related primarily to biomechanical function. It is important to again note that the connection between the mechanical properties of food and craniofacial form is suggestive. There are multiple conflicting functional demands as well as probable phylogenetic effects that cannot be accounted for (Smith 1983). However, due to the increasing body of evidence for a consistent relationship between food properties and craniofacial form, significant differences between these three species should be related to diet (Hylander 1972,1979; Ravosa 1990, 1991; Cole 1992; Daegling 1992; Anton 1996).

Mastication involves the production of force and torsion as well as reaction forces that act on the maxillary region of the cranium. If feeding or dietary differences do indeed impact the morphology of this region, then a morphologic survey of this area should reveal variation between these three populations of colobines. If cranial variation producing increased facial retraction provides mechanical advantage for durophagy, then I expect those areas of the cranium influencing facial prognathism to be most important for delineation of these species.

Dietary differences between these three taxa should be sufficient to discriminate taxon-specific dietary adaptations related to the morphology of the maxillofacial complex. Based upon this hypothesis, I am testing three specific predictions:

(1) *C. polykomos* will show evidence for the morphology described by Anton (1996) associated with increased biomechanical advantage for a more durphagous diet. Specifically, the three species should show a statistically significant difference in both facial retraction and the anterior placement of the masseter muscle. *C. polykomos* will show the greatest amount of facial retraction, and the most anteriorly-placed masseter muscle due to the seasonal processing of *P. macrophylla*.

(2) Cranial ontogenetic development occurs in structural modules that likely derive from complex interactions among cranial units (Lieberman et al. 2002). As such, selection for facial retraction should have an effect on anterior dental complex morphology. Initial facial retraction will affect the outward curvature of the anterior alveolar process. This is the least invasive way to decrease facial length without influencing large changes in the entire masticatory complex. A decrease in anterior alveolar curvature will also shorten the load arm giving a biomechanical advantage for a durophagous diet. Specifically within this group, anterior alveolar process curvature will decrease with increased facial retraction.

(3) The morphologic differences in the maxillofacial complex in these three colobines should be due primarily to differences in diet. Discrimination will be greatest in those areas associated with a mechanical advantage for obdurate feeding.

CHAPTER 2

MATERIALS AND METHODS

I examined 52 colobine skulls collected from the Tai Forest region of Côte d'Ivoire in western Africa. The sample is housed at the Ohio State University and used courtesy of Dr. W.S. McGraw. Three species were examined, *Colobus polykomos* (n=20), *Procolobus badius* (n=25) and *Procolobus verus* (n=7). Several standard and non-standard measurements were taken on maxillo-facial complex: alveolar curvature, palatal length, palatal breadth, malar length, malar subtense, bimaxillary breadth, bimaxillary subtense, bijugal breadth, cheek height, basion-prosthion length (see appendix A for measurement definitions and visual representations of the measurements). These measurements were chosen because they provide a good representation of craniofacial form. This provides a base with which to examine inter-species variation in this area. All measurements were taken on the cranium to the nearest hundredth of a millimeter. Sided measurements were taken on the left side of the cranium.

Measurements were taken with standard digital calipers, as well as coordinate calipers for the subtense measurements. Alveolar curvature was measured using a bifocal light digital microscope. Alveolar curvature was calculated using the phlangeal curvature method described in Susman et al. (1984) (see figure 2). This method uses included angle as a length-independent measure of curvature derived from a series of linear measurements of length and breadth. This method requires that the radius of curvature for a given specimen represents a portion of an arc on the perimeter of a circle (Susman et al. 1984). The measurements were collected and recorded for statistical analysis.

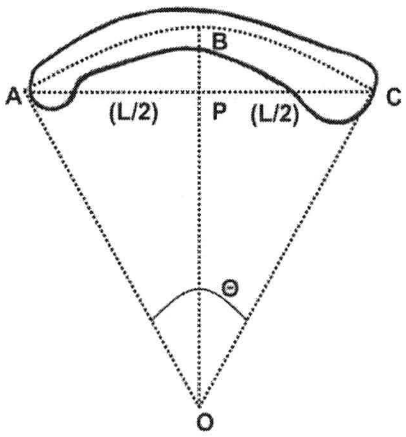


Figure 2: Curvature calculation from Susman et al. (1984). Radius of curvature (R) ¼ OA ¼ OB ¼ OC can be calculated if values are known for PB and PC. Image from Deane et al. (2005)

Anterior position of the masseter muscle was estimated by taking two linear measurements. A measurement of maximum cranial length and a measurement from the most posterior point of the cranium to the anterior insertion point of the masseter muscle were taken using standard digital calipers on all crania (see figure 3). The measure of anterior insertion of the masseter was divided by the total length of the crania to create a proportion that controlled for size difference, while also giving an approximation of the position of the masseter. As the proportion approaches one, the further the masseter attachment is in the anterior direction.

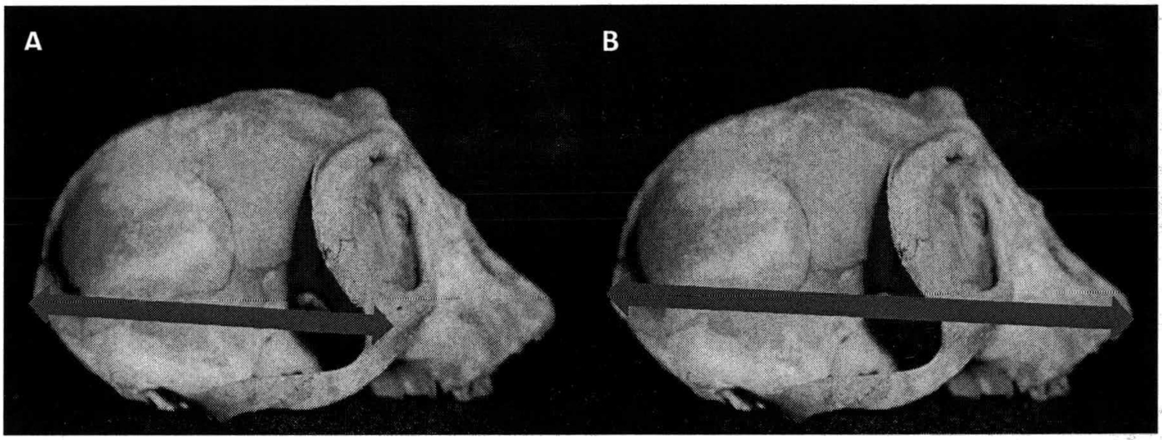


Figure 3: Anterior position of the masseter muscle was estimated by taking **(A)** a measurement from the posterior of the crania to the anterior insertion point of the masseter and subtracting this from **(B)** total cranial length.

All measurements were converted to z-scores to control for possible size differences between species. One way ANOVA was performed on each variable mean in order to determine whether or not the variable differed significantly among species. Linear regression was used between variables to determine if two areas of the cranium were linked. Three variables were chosen to test the relationship between facial retraction and alveolar curvature. Predictive linear discriminant functions (DFs) were calculated using forward stepwise methodology and assessed by a leave-one-out hit-rate estimate comparison (Iscan & Steyn, 1999). Discriminant function analysis is a multivariate procedure which takes into account all variables and creates large matrices to determine the distinguishing power of each variable for each group.

Discriminant functions place unknown objects into known categories based on distance to group centroids. The stepwise method selects particular measurements that have the greatest distinguishing power for delineating the species in question. This methodology is primarily used in human craniometrics as a method of identification based on sex or ancestry (Giles and Elliot 1963; Giles 1963; Cunha and van Vark 1991; Franklin et al. 2005; Walker 2008). All statistical analyses were performed using SPSS 15.0. All functions were significant at $p > 0.05$. The measured areas of the cranium most important for delineating between species, (i.e. where species show the greatest variation) should be related to elements of facial retraction. This kind of result would indicate that dietary differences are important for variation in colobine craniofacial morphology.

CHAPTER 3

RESULTS

Statistical tests were first run as two separate groups: males and females. Results of the one way ANOVA and the discriminant function analysis did not show a statistically significant difference when males and females were run separately (see appendix B for results of males and females separately). Therefore, males and females were pooled for all further tests. The grouping variable for all further statistical analysis was species distinction.

The results of the one-way ANOVA were varied (see table 1). Several variables showed a significant difference in means between the three species. These include: alveolar curvature ($p=0.029$), malar subtense ($p<0.001$), basion-prostion length ($p<0.001$), palatal length ($p=0.043$), malar length ($p=0.009$) and bimaxillary subtense ($p<0.001$). However, a number of variables were not significantly different between the three species including palatal breadth, bimaxillary breadth, cheek height, bizygomatic breadth and bijugal breadth. It is important to note that some of the variables showed significant difference when two species were compared. However, when the third group was added, the delineating power of the variable either decreased or became nonstatistically significant. This is most likely due to the fact that the addition of a third group created overlap in the measurements across the other two species. The one-way ANOVA allowed for a general summary of which variables should be most important in delineating the species, which were confirmed by the stepwise discriminant function analysis.

Measurement	**$F_{2,49}$**	**ANOVA Sig.**	**Measurement**	**$F_{2,49}$**	**ANOVA Sig.**
Alveolar Curvature	3.811	.029	**Palatal Breadth**	3.142	.051
Malar Subtense	433.01	<.001	**Malar Length**	5.122	.009
Bas-Pros Length	76.02	<.001	**Bijugal Breadth**	2.621	.082
Bimaxillary Subtense	355.32	<.001	**Cheek Height**	0.569	.569
Palatal Length	3.351	.043	**Bizygomatic Breadth**	1.105	.339
Bimaxillary Breadth	2.901	.064			

Table 1: Results summary for One-Way ANOVA comparing all three species

I tested the effect of alveolar curvature on elements of facial retraction and compared measurements using a standard linear regression. Alveolar curvature, palatal length, basion-prostion length, and bimaxillary subtense all differed significantly in the one way ANOVA, between species. There were no statistically significant correlations with alveolar curvature (see figures 4a-4c). Linear regression was run comparing curvature with palatal length, basion-prostion length and bimaxillary subtense, which are

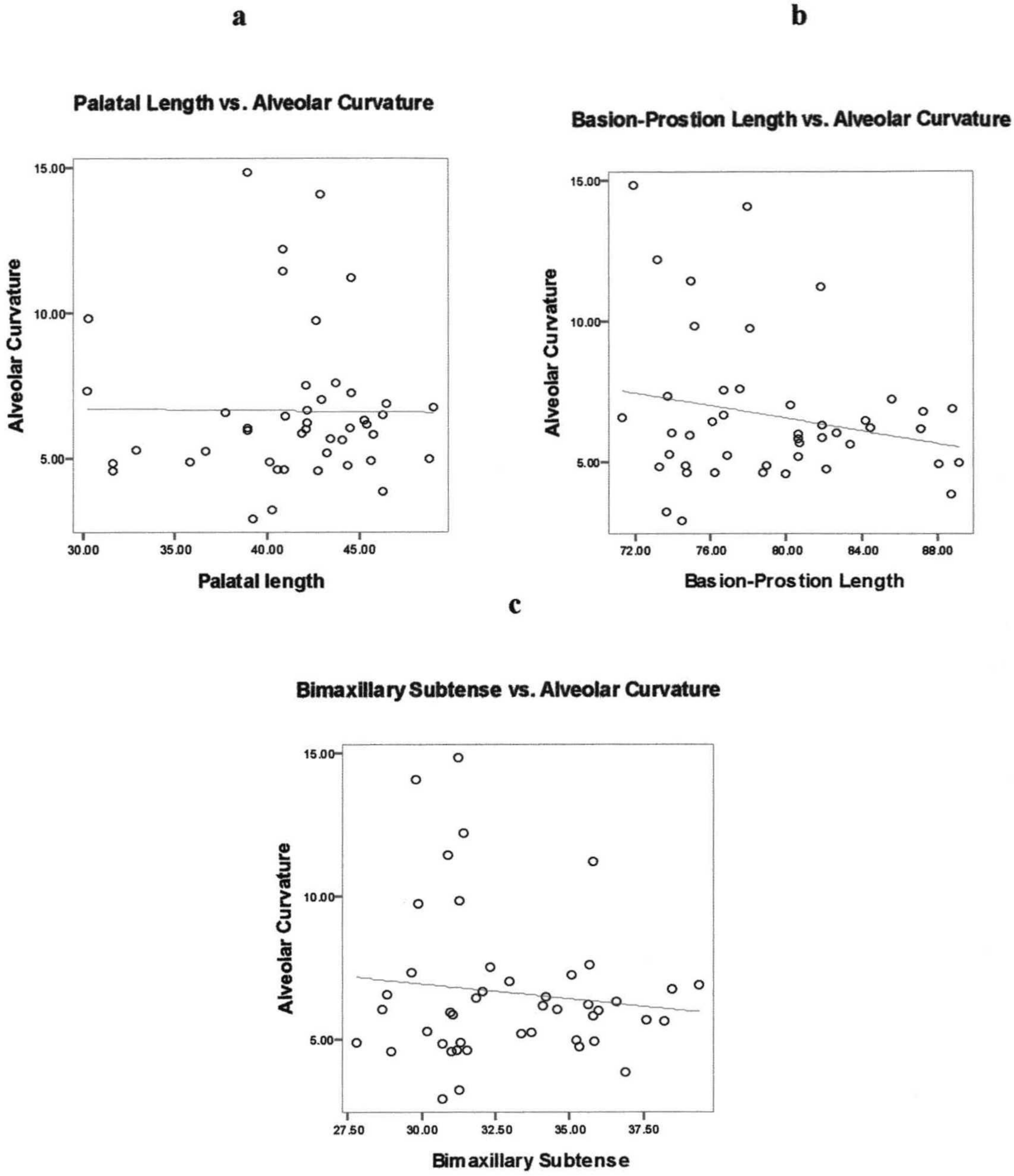


Figure 4 (a): Linear Regression comparing alveolar curvature and palatal length. No correlation, (r^2 value = 0.001). **4 (b)**: Linear Regression comparing alveolar curvature and basion-prostion length. No correlation (r^2 value = 0.11). **4 (c)**: Linear Regression comparing alveolar curvature and bimaxillary subtense. No correlation (r^2 value = 0.05) all measures of relative facial projection. Results indicated that there was no evidence of a relationship, with r^2 values of 0.001, 0.11, and 0.05 respectively. Elements of facial retraction do not seem to be linked with differences in the amount of curvature of the alveolar process.

A one-way ANOVA was run comparing a proportional measurement estimating the position of the anterior insertion of the masseter. The placement of the masseter muscle did not differ significantly between *C. polykomos* and *P. badius* (p=0.174). However, when *P. Verus* was added into the ANOVA, the differences became significant (p=0.009). *P. Verus* shows the most anterior placement of the masseter between the three species, followed by *C. polykomos*, and finally *P. badius* (see figure 5).

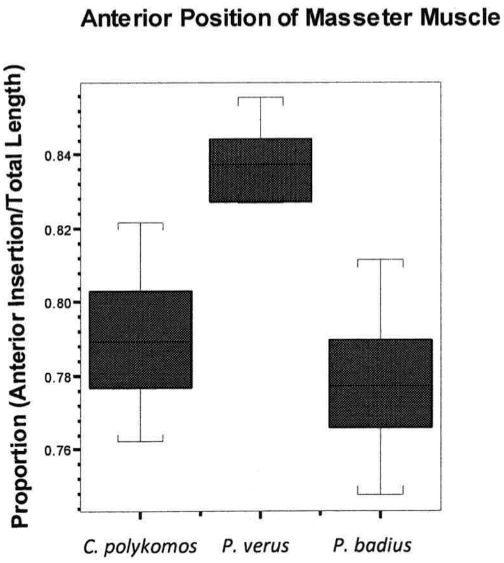


Figure 5: Graphical distribution of the proportion estimate of the anterior placement of the masseter.

Discriminant functions (DFs) were calculated using forward stepwise methodology and assessed by a leave-one-out hit-rate estimate comparison. All functions were significant at $p < 0.05$ using both F-test as well as Wilks λ methods for significance. Measurements that were selected by the stepwise method for greatest delineation of species were: malar subtense, malar length, bimaxillary subtense, and basion-prostion length (discriminating power of 92.6 – 99.7%). These four measurements also showed the largest F-values in the one-way ANOVA, with values at 433.01, 5.122, 355.32, and 76.02 respectively. This indicates that these species show greatest differences in areas associated with mastication as hypothesized. Malar subtense alone had a discriminating power of 99.7%. Measurements not selected by the stepwise method also were not shown to be significant in the one way ANOVA as well. DFs also provide a visual output of separation along group centroids (see figure 6).

Results also indicated that there is increased overlap in measurements between *Procolobus badius* and *Procolobus verus*. Further analysis of the output data revealed that those variables pulled out by the DF analysis also showed little overlap between the three species when ANOVA graphs were created. These graphs plot the mean and show the range of standard error for measurements across the three species. (see figures 7a-7d). However, if the four measurements selected by the DF are removed and the canonical discriminant function analysis is rerun, there is not a clear separation of the groups (see figure 8). There is again evidence for increased overlap between groups, especially between *P. badius* and *P. verus*.

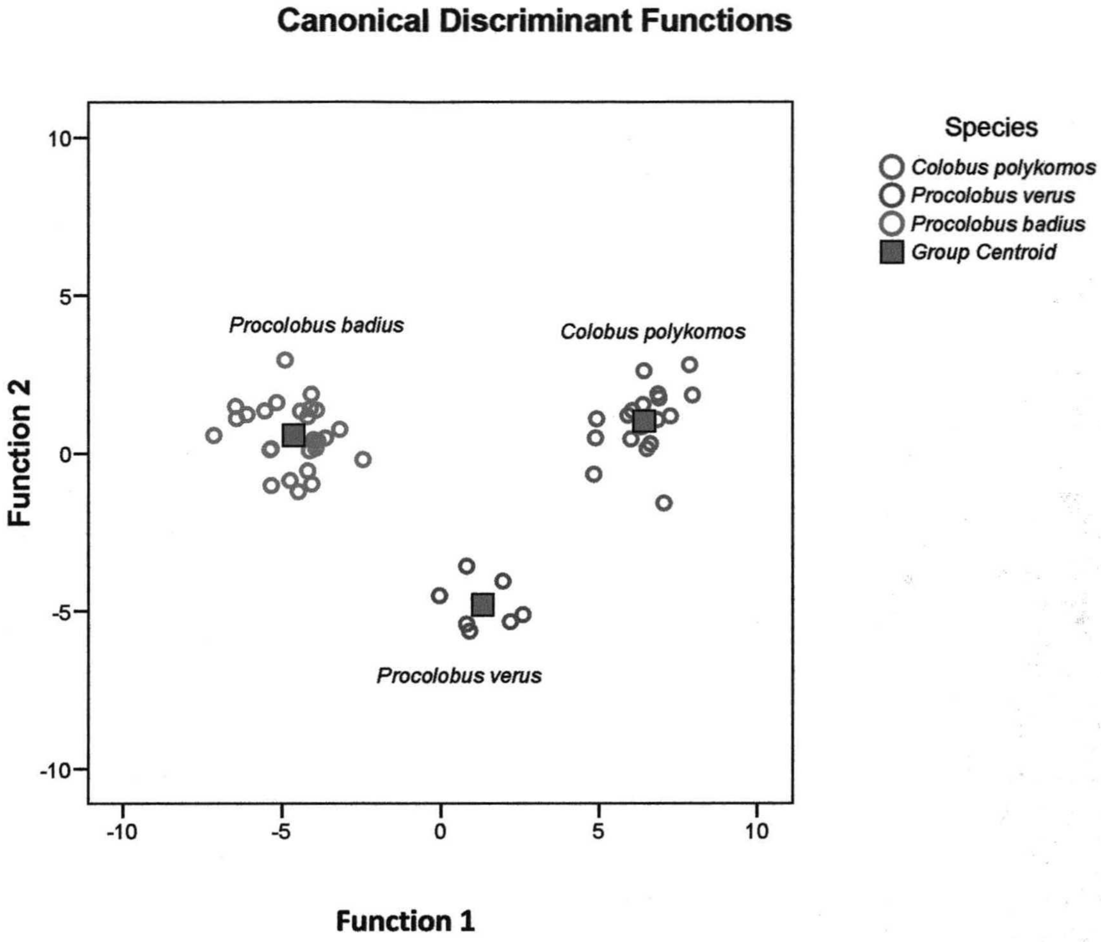


Figure 6: Canonical Discriminant Function analysis output showing separation at each of the group centroids when all variables are considered. The discriminant function analysis created two functions (one less than the number of groups being considered) and compared these two functions. The function plots the mean for each group (the group centroid) and then plots each individual into the display. There is no overlap between the three species when all variables are considered.

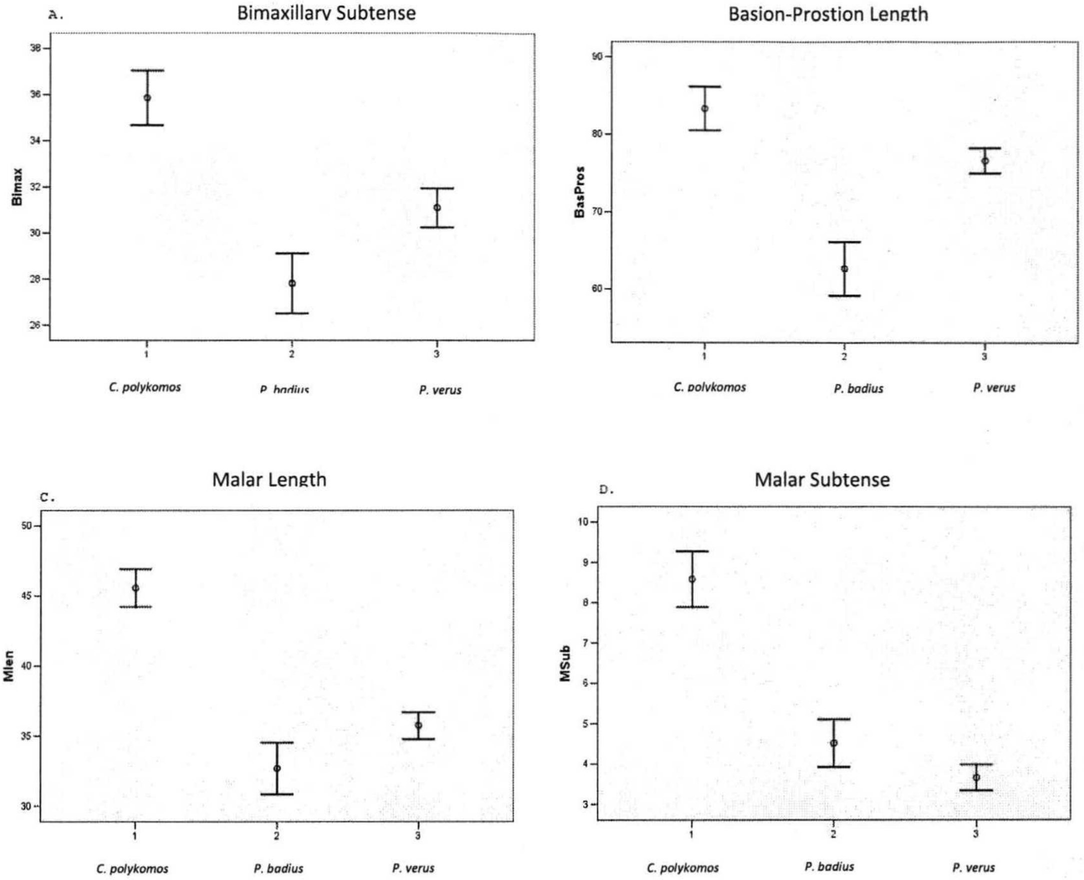


Figure 7: ANOVA analysis data outputs of mean (+/-) standard error, for the four measurements pulled out by the step-wise function of the discriminant function analysis. **(a)** Bimaxillary subtense **(b)** Basion-prostion length **(c)** Malar length, and **(d)** Malar subtense. Interestingly there is some overlap between *P. badius* and *P. verus*, however very little between either of these and *C. polykomos.*

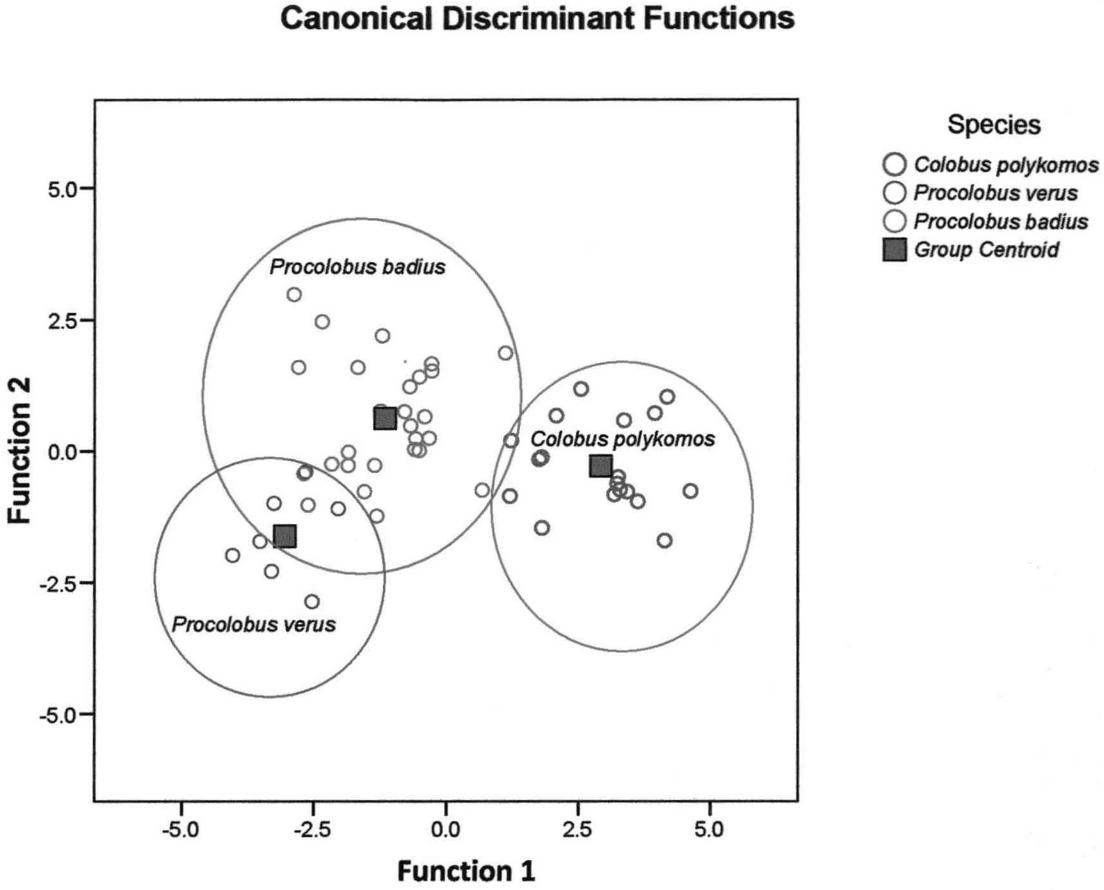


Figure 8: Canonical Discriminant Function run without the four measurements selected as most important for delineation of the species. Results do not show the clear separation seen in figure 6. There is also increased overlap primarily seen between *P. verus* and *P. badius*.

CHAPTER 4

DISCUSSION

This study is another layer of evidence for primate diet influencing primate cranial morphologies. This study and others have added to the increasing body of evidence that primates with diets requiring greater occlusal forces to process food items exhibit morphologies adapted for increased mechanical advantage (Kinzey 1974; Hylander 1977; Ravosa 1990, 1991; Daegling 1992, Anton 1996; Daegling and McGraw 2002). For example, Anton (1996) was able to demonstrate that Japanese macaques (*Macaca fuscata*) exhibited elements of facial retraction vertically deeper faces, and a more anteriorly placed masseter, as a function for increased mechanical advantage for hard object feeding. However, in the examination of craniofacial variability among these three species of colobus, results indicate that *Colobus polykomos* does not show the expected facial retraction associated with durophagy. In fact, *C. polykomos* shows the greatest prognathism between the three species included in this study which corroborates the results of Schultz (1957) and Groves (2007). This is perhaps the result of selection for enlarged canine size. *C. polykomos* displays increased canine size relative to *Procolobus badius*, and *Procolobus verus*, and also exhibits reduced sexual dimorphic differences (Plavcan and van Schaik 1992; Hayes et al. 1996). Because the larger canines in *C. polykomos* show reduced dimorphism between sexes, this may indicate that there is a dietary function for the canines, instead of a competitive or signaling function. *C. polykomos* will process tough the seed pods of *Pentaclethera macrophylla* for extended lengths of time, tearing the pods open with their anterior dentition (Oates 1994, Davies et al. 1999). Enlarged canines require increased space; if selection for increased canine size is stronger than selection for facial retraction, this could explain the results. Other unseen biomechanical and epigenetic factors may also be confounding outcomes.

The anterior position of the masseter in *C. polykomos* does not fall into line with the expected phenotype for a more durophagous primate. The species with the least strenuous diet, *P. verus*, exhibits the most anterior placement of the masseter. This may be due to the more gracile nature of the *P. verus*, along with its smaller body size (Schultz 1957; Groves 2007). The result for *C. polykomos* could be explained if increased reliance on the seed pod of *P. macrophylla* is a relatively novel dietary pattern. If dependency on these seeds is new, selection may still be working, and morphologic features associated with hard object feeding are not yet present.

The results of the one-way ANOVA and the discriminant function analysis indicate that the three species differ most in areas associated with mastication and the processing of food. Malar length and malar subtense are two measurements directly associated with the placement and size of the masseter muscle. Both measurements were pulled out in the stepwise discriminant function as measurements important for delineating these species. The other two measurements essential for separating the species were bimaxillary subtense and basion-prostion length. Interestingly, these measurements are associated with elements of facial prognathism. The results suggest that facial projection is an important feature separating these species; however it is not related to mastication in the way that was hypothesized. Elements associated with increased width, such as palatal breadth, bimaxillary breadth and bijugal breadth did not show a great amount of variation between the species. The pattern found in the results of the statistical tests illustrate that components of craniofacial morphology are influenced by dietary differences, as hypothesized. However, elements of facial retraction are not associated with diet in these three species in the manner postulated.

Alveolar curvature was not associated with elements of facial retraction in these species. There was no relationship between alveolar curvature and the measured areas associated with facial prognathism. Results from the one way ANOVA indicated that alveolar curvature, as well as elements of facial projection are indeed significantly different amongst these three species, yet are not associated with one another. This may be related to the fact that facial retraction is not related to durophagy in the way proposed within these three species. Alveolar curvature may have an unrelated function in food processing linked to the incisors and not associated with molar processing. The curvature of the incisors is likely linked to the curvature of this area in relation to the root system of the incisors, as well as the development of incisors pre-eruption. The curvature of the anterior alveolar process is likely due to a dietary adaptation, but it is apparent that this difference is not associated with elements of facial retraction.

Alveolar curvature may differ among the three species to give a biomechanical advantage to *C. polykomos* during the anterior processing of tough food items. A flattening of the anterior dental arc, in the medio-lateral plane, has been shown to provide a mechanical advantage, by bringing the incisor bite point closer to the muscle resultant of mastication, thus increasing leverage at the incisors (Spencer and Demes 1993; Spencer 1998; Wright 2005). The flattening of the anterior dental arcade also shortens the load arm, providing an advantage for the processing of tough food items (Greaves 1978; Spencer and Demes 1993; Spencer 1998; Wright 2005). *C. polykomos* shows a decrease in alveolar curvature relative to *P. badius* (see figure 9). This decrease may be related to the mechanical advantage provided by a flattening of the anterior dentition. This relatively small shift in the placement of the anterior dentition could be enough to give *C. polykomos* the advantage necessary for the processing of tough food items. However, further research is needed to test the relationship between the 'squaring off' of the anterior dentition and the curvature of the alveolar process before a definitive link can be made.

Results indicated that a variable could be significant when a comparison was made between two species, however when the final species was added, the result would become non-significant. The power of delineation would also often decrease after a third species was added. This is most likely related to increased overlap of two species when the third is added. The result may be linked to the purported phylogenetic relationship between these three primates. The phylogenetic relationship between these species has been debated over the past 50 years. Verheyen (1962) placed the black and white colobus and red colobus in the genus *Colobus* and placed the olive colobus in the genus *Procolobus*. Kuhn (1967) and later Grubb et al. (2003) transferred the red colobus

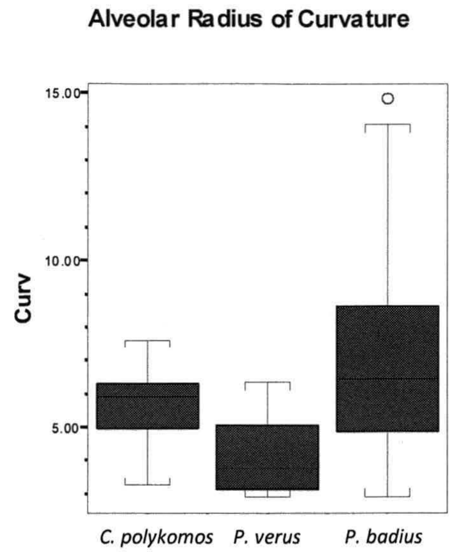


Figure 9: Distribution in z-score data of the radius of curvature of the anterior alveolar process. *P. badius* shows the greatest amount of curvature, followed by *C. polykomos* and finally *P. verus*. A decrease in curvature may provide a mechanical advantage for processing tough food items with the anterior dentition.

into the genus *Procolobus*, but created a separate genus for the olive colobus, *Piliocolobus*. Still others maintain that all three species should be in the separate genera: *Colobus*, *Procolobus* and *Piliocolobus* (Groves 2001 and 2007). Recent genetic evidence however points to a relationship that places the red colobus and the olive colobus into the same genus *Procolobus* and places the black-and-white colobus in *Colobus* (Kingdon 1997, Disotell and Rauum 2002, and Tosi et al. 2004). This purported genetic relationship is the one used for this study.

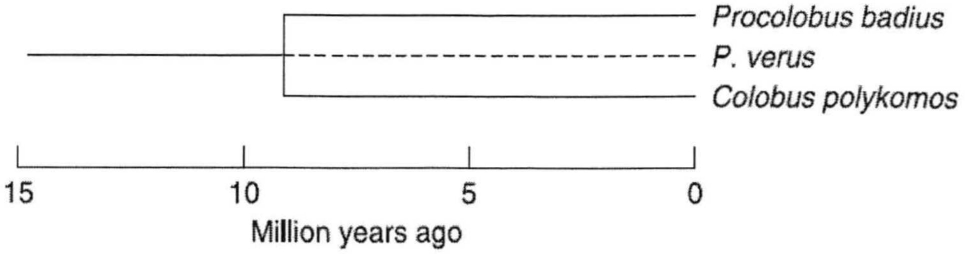


Figure 10: Purported phylogenetic relationships and approximate dates of divergence of the colobine species in the Taï forest. The relationship here is tenuous, but *P. badius* and *P. verus* seem to be more closely related to each other than either is to *C. polykomos.* *(From: McGraw and Zuberbuhler 2007)*

P. badius, and *P. verus* seem to be genetically more closely related then either is with *C. polykomos* (see figure 10). This relationship is also corroborated by the results of the Canonical Discriminant Function analysis. There seems to be greater overlap in the measurements between *P. badius* and *P. verus* then there is with *C. polykomos*. While these data are not a test for phylogenetic relationships, they do support the taxonomy advocated by Kingdon (1997), Disotell and Rauum (2002), and Tosi et al. (2004) and are at odds with those suggested by Groves (2001 and 2007), Kuhn (1967), and Grubb et al. (2003).

CHAPTER 5

IMPLICATIONS

A careful analysis of the morphology of the splanchnocranium in three colobine species reveals that within this particular group of primates, morphology does not follow the typical pattern for an obdurate diet. There are a number of possible causes for this result, however further research is needed to understand the morphologic nature of these primates. An examination of bone density in the maxillary region of these primates is needed to see if differences in masticatory stresses are inducing variability in the layering of cortical bone in developmental pattern. A disparity in the way bone is layered between these three species would indicate that the dietary differences are indeed causing variation in the masticatory forces experienced by these species. In addition, an examination of osteon counts in the maxilla could provide increased support to the argument for variation in diet inducing selection for greater mechanical advantage in these species.

The discrepancy found in this study may be explained by the complex biomechanical nature of mastication and the difficulty of capturing this intricacy with two-dimensional linear modeling. Recent morphologic studies have shown that the cranium is an active three dimensional object with complex material properties contributing to stress, force and torsion dissipation (Hylander et al. 1991; Dechow and Hylander 2000; Daegling et al. 2008). Perhaps the complex nature of this area cannot be captured with linear measurements, which would help explain the inconsistency found in these types of studies. Instead, the material properties of bone need to be considered in how masticatory stresses are dissipated. Selection and adaptations may be occurring at a level that is not captured by variation in linear measurements. Linear measurement studies can only indicate certain trends seen as statistically significant across species. While these types of studies are important in cataloging variation, we must be aware that there are influences beyond the scope of two dimensional modeling that are also at play.

Further research is also needed in order to fully understand the inter-specific variability within the colobine lineage. In order to control for confounding genetic and behavioral effects, *in vivo* studies are needed. These types of studies would allow for outside variables to be controlled, and a more efficient test of dietary differences could be conducted. For example, if diets could be controlled completely, we could test if variation is due to ontogeny and obdurate feeding, or if there are genetic factors influencing facial form that do not differ with increasingly hard food items during development. This would help elucidate hidden genetic factors, while also revealing the phenotypic plasticity of species due to dietary differences. Furthermore, a complete examination of the genetic variability in genes associated with craniofacial and masticatory development is also needed. This would allow for selection factors to be examined gene by gene.

LIST OF REFERENCES

Anton, S.C. (1996). Cranial adaptation to a high attrition diet in Japanese macaques. *Int. J. Primatol,*17. 401-427.

Bouvier, M. (1986). A biomechanical analysis of mandibular scaling in Old World monkeys. *Am. J. phys. Anthrop.* 69, 473–482

Brown B. (1997) Miocene hominoid mandibles: Functional and phylogeneticperspectives. In Begun DR, Ward CV, and Rose MD (eds.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations.* Plenum, New York, pp. 153-171.

Carlson, D. S., van Gerven, D. P. (1977). Masticatory function and post-pleistocene evolution in Nubia. *Am. J. phys. Anthrop.* 46, 495–506.

Cole, T. M. (1992). Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons. J. Hum. Evol.* 23: 253–282.

Cunha E, van Vark G. (1991). The construction of sex discriminant functions from a large collection of skulls of known sex. *Int J Anthropol* 6:53–66.

Daegling,D. J. (1989). Biomechanics of cross-sectional size and shape in the hominoid mandibular corpus. *Am. J. Phys. Anthropol.* 80: 91–106.

Daegling, D. J. (1992) Mandibular morphology and diet in the genus *Cebus. Int. J. Primatol.* 13: 545–570.

Daegling,D. J. (1993). The relationship of *in vivo* bone strain to mandibular corpus morphology in *Macaca fascicularis. J. Hum. Evol.* 25: 247–269.

Daegling, D. J., Hylander, W. L. (1998). Biomechanics of torsion in the human mandible. *Am. J. Phys. Anthropol.* 105: 73–87.

Daegling, D. J., McGraw, W.S. (2002), Feeding, Diet, and Jaw Form in West African Colobus and Procolobus, *Int. J. Primatol.* 22: 1033-1055

Davies,A.G., Oates, J. F., Dasilva,G. L. (1999). Patterns of frugivory in threeWest African colobine monkeys. *Int. J. Primatol.* 20: 327–357.

Deane A.S., Kremer E.P., Begun D.R. (2005) New Approach to Quantifying Anatomical Curvatures using High Resolution Polynomial Curve Fitting (HR-PCR). *Am J Phys Anthropol.* 128: 630-638.

Dechow, P.C., Hylander, W.L. (2000). Elastic properties and masticatory bone stress in the Macaque mandible. *Am. J. Phys. Anthropol.* 112: 553-574

Disotell, T.R. (2003) *Primates: Phylogenetics. Encyclopedia of the Human Genome.* London: Nature Publishing Group.

Disotell, T.R., Raaum, R.L. (2002). Molecular timescale and gene tree congruence in the guenons. In *The Guenons: Diversity and Adaptation in African Monkey*, ed. M. Glenn and M. Cords. New York: Kluwer Academci/Plenum, pp. 27-36

Du Brul, E. L. (1974). Origin and evolution of the oral apparatus. In (Y. Kawamura, Ed.) *Frontiers of Oral Physiology*, pp. 1–30.

Du Brul, E. L. (1977). Early hominid feeding mechanisms. *Am. J. phys. Anthrop.* 47, 305–320.

Fleagle, J. G., McGraw, W. S. (1999). Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. *Proc. Natl. Acad. Sci.* 96: 1157–1161.

Franklin D, Freedman L, Milne N. (2005). Sexual dimorphism and discriminant function sexing in indigenous South African crania. *Homo* 55:213–228

Giles E. (1964). Sex determination by discriminant function analysis of the mandible. *Am J Phys Anthropol* 22:129–135.

Giles E, Elliot O. (1963). Sex determination by discriminant function analysis of crania. *Am J Phys Anthropol* 21:53–68.

Groves, C.P. (2001). *Primate taxonomy.* Washingtion: Smithsonian Institution Press

Groves, C.P. (2007). The taxonomic diversity of the Colobinae of Africa. *J. Anthro. Sci.* 85: 7-34

Grubb, P., Butynski, T.M., Oates, J.F. (2003). Assessment of the diversity of African primates. *Int. J. Primatol.* 24: 1301-1357

Hayes, V.J., Freedman, L., Oxnard, C.E. (1996) Dental Sexual Dimorphism in African Colobus Monkeys as Related to Diet. *Int. J. Primato.* 17: 725-757

Hull, D.B. (1979) A craniometric study of the black and white *Colobus* Illiger 1811(Primates: Cercopithecidea). *Am. J. Phys. Anthrop.* 51: 163-182

Hylander, W. L. (1977). The adaptive significance of Eskimo craniofacial morphology. In Dahlberg, A.A., Graber, T.M. (eds) *Orofacial Growth and Development*, The Hague: Mouton. 129–170.

Hylander, W. L. (1978). Incisal bite force direction in humans and the functional significance of mammalian mandibular translation. *Am. J. phys. Anthrop.* 48, 1–7.

Hylander, W. L. (1979*a*). An experimental analysis of temporomandibular joint reaction force in macaques. *Am. J. phys. Anthrop.* 51, 433–456.

Hylander, W. L. (1979*b*). The functional significance of primate mandibular form. *J. Morphol.* 160, 223–240.

Jablonksi, N. G. (1993). Theropithecus: *The Rise and Fall of a Primate Genus.* Cambridge: Cambridge University Press.

Kingdon, J. (1997). *The Kingdon Field Guide to African Mammals.* New York: Academic Press

Kinzey, W. G. (1974). Ceboid models for the evolution of hominoid dentition. *J. Human Evol.* 3: 191–203.

Kinzey, W. G. (1978). Feeding behaviour and molar features in two species of titi monkeys. In Chivers, D.J., Herbert, J. (eds.), *Recent Advances in Primatology: Vol. I. Behaviour,* Academic Press, London, 373–385.

Kuhn, H.J. (1967). Zur Systematik der Cercopithecidae. In. Starck, D., Schneider, R., Kuhn, H.J (eds.) *Progress in Primatology.* Gustav Fischer, Stuttgart. 25-46

Liberman, D.E., McBratney, B.M., Krovitz, G. (2002). The evolution and development of cranial form in Homo sapiens. *Proc Nat Acad Sci.* 99: 1134-1139

Lucas, P. W., Luke, D. A. (1984). Chewing it over: Basic principles of food breakdown. In Chivers, D. J., Wood, B. A., Bilsborough, A. (eds.), *Food Acquisition and Processing in Primates,* Plenum, New York. 283–301.

Lucas, P. W., Teaford, M. F. (1994). Functional morphology of colobine teeth. In Davies, A. G., Oates, J. F. (eds.), *Colobine Monkeys: Their Ecology, Behavior and Evolution,* Cambridge University Press, Cambridge,. 173–203.

McGraw, W.S., Zuberbuhler, K.(2007). The monkeys of the Tai forest; an introduction. In McGraw, W.S., Zuberbuhler, K., Noe, R. (eds.) *Monkeys of the Tai Forest: An African Primate Community.* Cambridge University Press, Cambridge. 1-48.

Oates, J. F. (1994). The natural history of African colobines. In Davies, A. G., and Oates, J. F. (eds.), *Colobine Monkeys: Their Ecology, Behavior and Evolution,* Cambridge University Press, Cambridge. 75–128.

Plavcan JM, van Schaik CP (1992). Intrasexual competetion and canine dimorphism in anthropoid primates. Am J Phys Anthropol 87: 461-477

Rak, Y. (1983). *The Australopithecine Face*. New York: Academic.

Ravosa, M. J. (1990). Functional assessment of subfamily variation in maxillomandibular morphology among Old World monkeys. *Am. J. Phys. Anthropol.* 82: 199–212.

Ravosa, M. J. (1991). Structural allometry of the prosimian mandibular corpus and symphysis. *J. Human Evol.* 20: 3–20.

Ravosa, M. J. (1996). Jaw morphology and function in living and fossil OldWorld monkeys. *Int. J. Primatol.* 17: 909–932.

Smith, R. J. (1978). Mandibular biomechanics and temporomandibular joint function in primates. *Am. J. phys. Anthrop.* 49, 341–350.

Spencer, M.A., Demes, B. (1993). Biomechanical analysis of masticatory system configuration in Neandertal and Inuits. *Am. J. Phys. Anthropol.* 91: 1-20

Spencer, M.A. (1998). Force production in the primate masticatory system: electromyographic tests of biomechanical hypotheses. *J. Hum. Evol.* 34: 25-54.

Spencer, M.A. (1999) Constraints on masticatory system evolution in anthropoid primates. *J. Morphol.* 235: 157-175.

Stern JT Jr, Susman RL. (1983). Locomotor anatomy of Australopithecus afarensis. *Am J Phys Anthropol* 60:279–317.

SusmanRL, Stern JT Jr, JungersWL (1984) Arborealityand bipedality in the Hadar hominids. *Folia Primatol.* 43: 113-156

Tosi, A.J.; Melnick, D.J.; Disotell, T.R. (2004) Sex chromosome phylogenetics indicate a single transition to terrestriality in the guenons (tribe Cercopithecini). *J. Hum. Evol* 46: 223–237.

Verheyen, W.N. (1962) Contribution a la craniologie compare des Primates: les genres *Colobus* Illiger 1811 et *Cercopithecus* Linne 1758. *Annalen Koninklijeke Museum Belgisch Congo, Zool. Wet.*, 105: 1-255

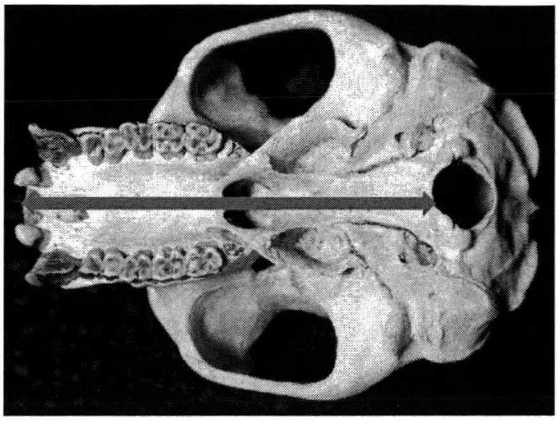
Walker, P.L. (2008) Sexing Skulls using Discriminant Function Analysis of Visually Assessed Traits. Am J Phys Anthropol. 136:39–50

Wachter, B., Schabel, M., Noe, R. (1997). Diet overlap and polyspecific associations of red colobus and diana monkeys in the Tai National Park, Ivory Coast. *Ethology* 103: 514–526

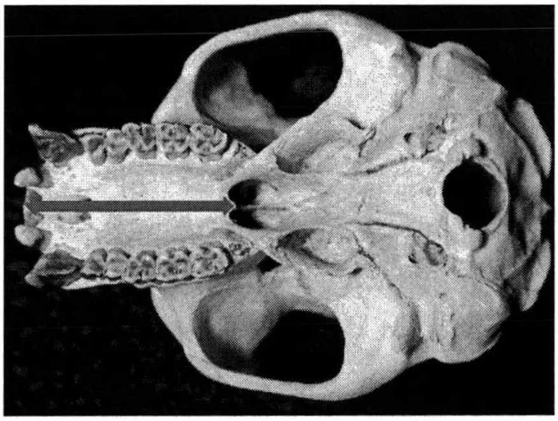
Wright, B.W. (2005). Craniodental biomechanics and dietary toughness in the genus *Cebus. J. Human Evol.* 48: 473-492

APPENDIX A

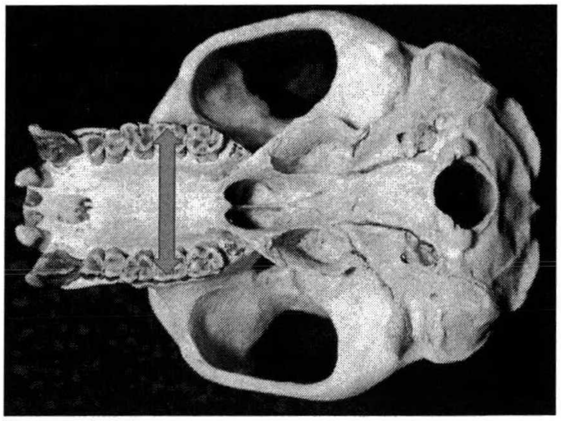
MEASUREMENT DEFINITIONS



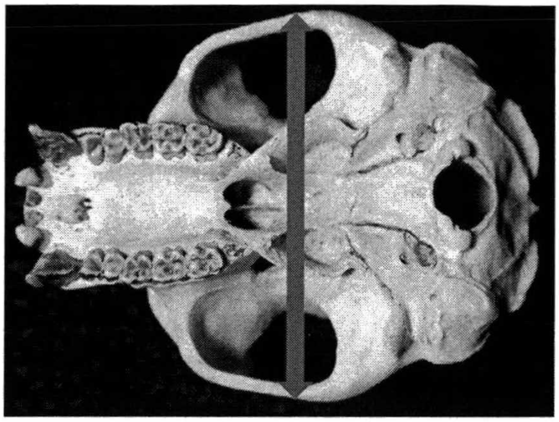
Basion-Prostion Length: The crainal length from prosthion to basion



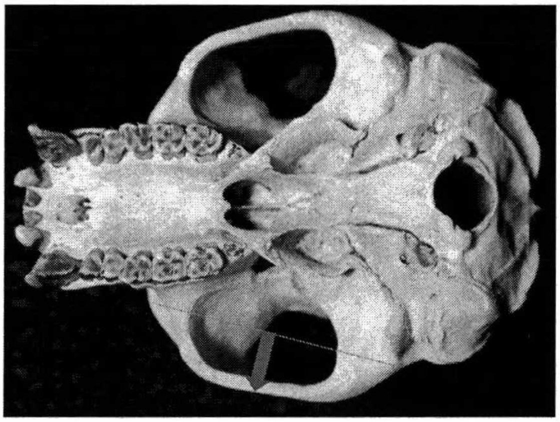
Palatal Length: The maximum length of the palat



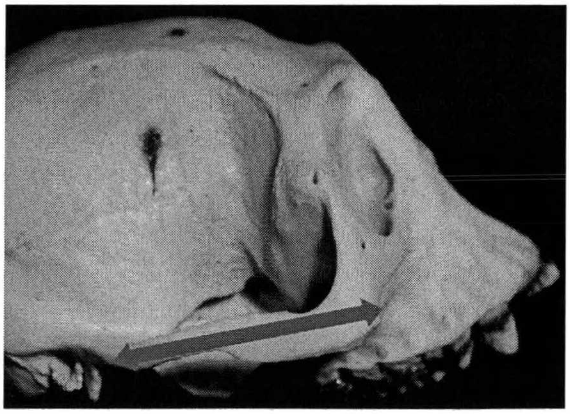
Palatal Breadth: The maximum breadth across the palat



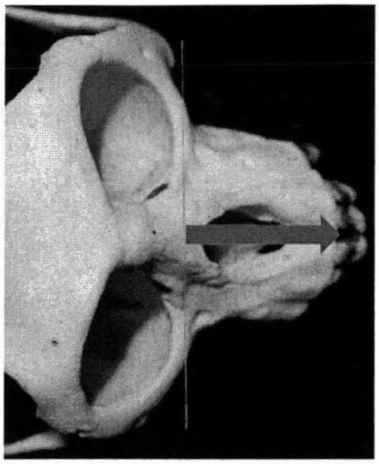
Bizygomatic Breadth: greatest breadth between points overlying the zygomatic arches perpendicular to the midsagittal plane



Malar Subtense: The maximum subtense from the convexity of the malar angle to the maximum length of the bone, at the level of the zygomaticofacial foramen

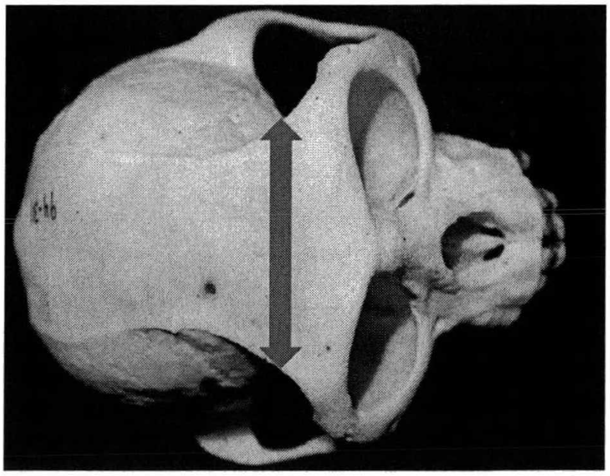


Malar Length: The direct distance from zygomaxillare anterior to the lowest point of the zygo-temporal suture on the external surface

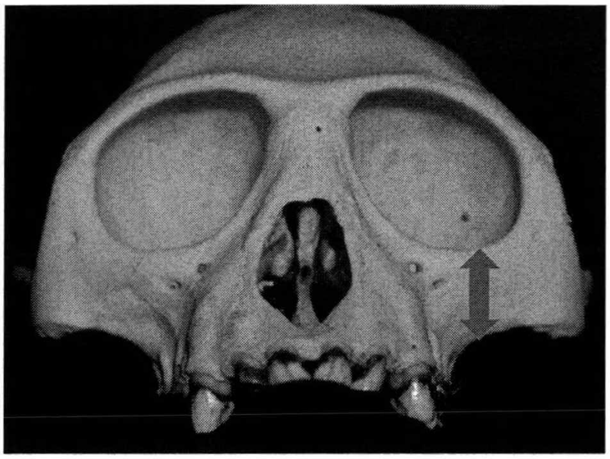


Bimaxillary Subtense: Projection of subtense of the maxilla from the subspinale

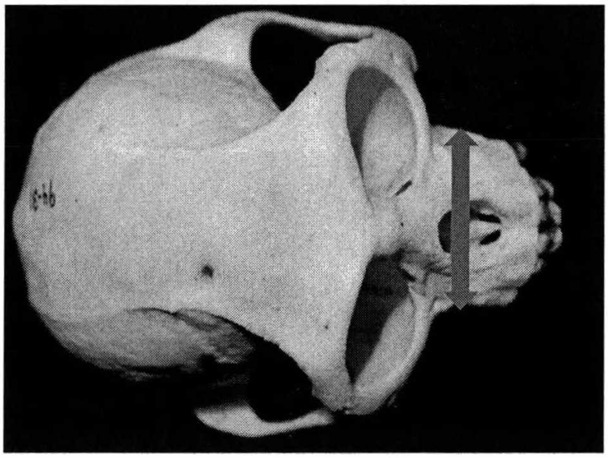
Alveolar Curvature: Radius of curvature of the frontal alveolar process of the maxilla



Bijugal Breadth: The external breadth across the malars at the jugalia, i.e., at the deepest points in the curvature between the frontal and temporal process of the malars



Cheek Height: The minimum distance, in any direction, from the lower border of the orbit to the lower margin of the maxilla, mesial to the masseter attachment



Bimaxillary Breadth: The maximum breadth across the maxilla

APPENDIX B

MALE/FEMALE COMPARISONS WITH ONE-WAY ANOVA

Measurement	ANOVA Sig. (Male)	ANOVA Sig. (Female)
Alveolar Curvature	p=0.024	p=0.029
Bimaxillary Subtense	p<0.001	p<0.001
Bimaxillary Breadth	p=0.058	p=0.062
Palatal Breadth	p=0.051	p=0.051
Palatal Length	p<0.001	p<0.001
Bizygomatic Breadth	p=0.334	p=0.329
Cheek Height	p=0.569	p=0.569
Basion-Prostion Length	p<0.001	p<0.001
Bijugal Breadth	p=0.081	p=0.080
Malar Length	p<0.001	p<0.001
Malar Subtense	p<0.001	p<0.001

Table 2: Comparison of significance values indicates that the two groups are not separate and can be pooled together.