# Functional Analysis of Craniomandibular Morphology in Durophagous, Folivorous, and Sclerocarpic Harvesting Anthropoids

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by:

**Justin Andrew Ledogar**

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Abstract of the Thesis

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Several studies have noted that it is unclear whether enlarged jaw proportions are adaptations for high magnitude biting or if they are more related to fatigue resistance in the context of repeated low-force chewing cycles. Chapter 1 of this thesis examined the relationship between enlarged jaw proportions and proxies of load magnitude and loading frequency by employing stepwise discriminant function analysis on a sample of “heavy loading” and “repetitive loading” primates. The variables determined to characterize each loading regime by the discriminant analysis were also evaluated regarding their relative importance in classifying each dietary group. Results show that medial pterygoid insertion angle, dental arcade width and jaw adductor leverage were all greater in heavy loaders, whereas length of the temporal articular surface, zygomatic arch size, ramus height above the occlusal plane, mandible length and masseter insertion angle were all greater in repetitive loaders. In addition, corpus width, corpus depth and symphysis width were all positively correlated with “heavy loading,” while corpus depth was not significantly correlated with either loading regime. None of the jaw proportions were correlated with “repetitive loading.” Furthermore, infratemporal fossa area, condyle width and condyle length, which were predicted to be greater in the “heavy loading” sample, as well as facial projection, which was expected to be greater in the "repetitive loading" sample, all failed to discriminate between these dietary groups.

Chapter 2 approached the question of incision versus mastication in a group of primates with known variation in dietary behavior and food consistency, the pitheciines. *Chiropotes satanas*, a "heavy loader" that emphasizes incisal and canine biting of hard fruits, and *Pithecia pithecia*, a "heavy loader" that emphasizes postcanine mastication of hard seeds, were compared using the non-parametric Mann-Whitney *U*-test. *Chiropotes* was expected to exhibit features advantageous to forceful anterior, while *Pithecia* was expected to exhibit features favorable to posterior loading. *Cacajao* spp. were also examined and were expected to exhibit features consistent with a morphocline of increasing dental specialization for feeding on hard fruits. Results from this study suggest that taxa adapted to forceful anterior tooth loading should exhibit a deeper mandibular corpus and symphysis, greater condylar articular surface area, a shorter mandible, greater mechanical advantage of the jaw adductors and less $M_3$ occlusal surface area compared to taxa adapted to high magnitude postcanine crushing. Postcanine loaders should exhibit a relative decrease in the width of the dental arcade. The results from this study also suggest that *Cacajao* does not represent the most specialized sclerocarpic harvesting pitheciine.

The results from both of these studies suggest that differences in mandibular condyle dimensions may not be indicative of either heavy or repetitive loading, but that an increase in the proportion of leaves, as well as an increase in food hardness should engender similar adaptations in condyle shape. Together, these studies also suggest that symhysis depth may not be systematically associated with increased load magnitude, but that taxa adapted to the forceful incision of hard foods may be experiencing increased coronal bending of the anterior corpus and may therefore require increases in symphysis depth. Lastly, these studies support the conclusion that increases in load magnitude influence the width of the mandibular symphysis, but that other factors, such as canine size, may play a crucial role.

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# INTRODUCTION TO THE THESIS

Anapol and Lee (1994:252) noted that "The size and shape of the mandible is determined by both (1) the texture or hardness of the foods eaten, and (2) where such foods are processed along the tooth row." Experimental analyses on living primates have shown that the mandible is subjected to a number of bending and twisting moments during incision and unilateral mastication (Hylander, 1979a,b, 1981; Hylander et al., 1987; Hylander and Johnson, 1994).

During the power stroke of mastication the balancing side mandibular corpus is bent in a parasagittal plane as a result of bilateral jaw adductor muscle force (Hylander, 1979a,b, 1981). Parasagittal bending also occurs and is increased when biting at the anterior dentition (Hylander, 1979a,b, 1981). Increasing the depth of the corpus is the most efficient way to counter this load (Hylander, 1979a,b, 1988; Bouvier, 1986a,b; Ravosa, 1991, 1996; Daegling, 1992; Ravosa and Hylander, 1994). Both mandibular corpora are also twisted about their long axes during mastication. Axial torsion is the result of the lateral location of the masseter's origin on the zygomatic arch and the medial location of its insertion along the angle of the mandible. The oblique line of action of the masseter's muscle force inverts the alveolar corpus and everts the basal corpus (Hylander, 1979a). Increasing the mediolateral width of the corpus increases the circularity of the corpus' cross-section and thus increases its resistance to axial torsion (Hylander, 1979a,b, 1981, 1988; Ravosa, 1991, 1996; Daegling, 1992; Ravosa and Hylander, 1994).

Axial torsion of the mandibular corpora also produces bending of the mandibular symphysis in the coronal plane. This results in compression along the alveolar border of the symphysis and increased tension along its basal aspect (Hylander, 1984, 1985, 1988). In anthropoid primates (i.e., those with fused symphyses) this is effectively countered by increasing the dorsoventral depth of the symphysis (Hylander, 1984, 1985, 1988; Daegling, 1992; Ravosa and Hylander, 1994).

The laterally directed jaw adductor muscle force plus the late activity of the balancing side deep masseter during the end of the masticatory power stroke also imposes lateral transverse bending, or "wishboning," stress on the mandibular symphysis. This causes tension along the lingual aspect of the symphysis and compression along its labial aspect (Hylander et al., 1987; Hylander and Johnson, 1994; Ravosa, 1996). Increasing the labiolingual thickness of the symphysis increases resistance to lateral transverse bending (Hylander, 1984, 1985).

These studies, coupled with comparative studies of primates with documented differences in the material properties of their foods, have led researchers to interpret increases in corpus and symphysis dimensions as structural adaptations to resist bending and twisting moments while feeding on resistant foods (e.g., Hylander, 1988; Daegling, 1992). However, it is unclear whether enlarged jaw proportions are adaptations for high magnitude biting or if they are more related to fatigue resistance in the context of repeated low-force chewing cycles (e.g., Hylander, 1979, 1988; Daegling and McGraw, 2001; Daegling and Grine, 2007). For example, Daegling and Grine (2007) recently noted that it is unclear if load magnitude or load frequency is more responsible for producing larger and stronger jaws.

Some highly-resistant foods eaten by primates likely fail only under heavy loads. Foods which fall into this category, such as seeds and nuts, are stress-limiting (Ashby, 1999). These foods resist deformation as they are loaded before reaching catastrophic failure (Lucas et al., 2000; Lucas, 2004). Primates that feed on these foods can be described as "heavy loaders." Other primate foods fail only under repeated loading. These displacement limiting (Ashby, 1999) foods resist crack growth and are only efficiently processed by repetitive masticatory loading cycles (Lucas et al., 2000; Lucas, 2004). Primates that feed on these foods can be termed "repetitive loaders."

Many heavy loaders also emphasize processing of the food with the anterior dentition (e.g., *Chiropotes*) and many repetitive loaders emphasize mastication by the posterior dentition (e.g., most folivores). However, morphological adaptation to incision versus mastication is not a clear dichotomy. Differences in craniomandibular morphology are expected between primates that engage in forceful incision and those that engage in forceful or repeated mastication. For example, mastication produces lateral transverse bending of the symphysis, whereas coronal bending of the anterior corpus is more pronounced during incision (Hylander, 1981, 1984). Additionally, primates that emphasize incision are typically expected to exhibit deeper mandibular corpora compared to those that engage in this behavior less frequently (Taylor, 2006). However, not all of these morphological expectations are supported by empirical data (e.g., Daegling and McGraw, 2007).

This thesis consists of two main chapters. These chapters are written as separate studies, with their own introduction, methods, discussion and conclusions. The first chapter approaches the question of enlarged jaw proportions and their relationship to increased load magnitude and increased loading frequency by examining a group of "heavy loading" and a group of "repetitive loading" anthropoids. It asks: Are large jaws a function of the force applied per chew, the frequency of chewing cycles, or both? The relative importance of several additional variables in classifying "heavy loaders" and "repetitive loaders" is also evaluated. If heavy and repetitive mastication engender similar adaptations in the masticatory apparatus, then drawing dietary inferences for fossil taxa may be problematic. Similarly, this finding would complicate interpretations made from comparative studies of primates with divergent diets. If there are clear differences between these dietary groups then our confidence in functional inferences drawn from both extinct and extant primate taxa would be strengthened.

The "heavy loading" sample in the first chapter includes taxa that exhibit differences in the forces applied to the anterior and postcanine dentition. For example, *Chiropotes satanas* and *Pithecia pithecia* are known to exploit fruits and seeds at different stages of ripeness. Kinzey and Norconk (1990, 1993) have demonstrated that *C. satanas* incises much harder fruits than *P. pithecia*, but *P. pithecia* masticates much harder seeds than *C. satanas* with its postcanine dentition. In addition, Shah (2003) noted that *Lophocebus albigena* engages in more frequent and forceful incision of hard fruits than *Cercocebus albigena*, whereas *C. albigena* engages in more frequent and forceful postcanine crushing of hard seeds and nuts.

Differences between primates that emphasize incision and primates that emphasize mastication are examined in Chapter 2 of the thesis. This second chapter approaches the question of incision versus mastication in a group of primates with documented differences in dietary habitats and the physical properties of their foods: the pitheciines. A third and final chapter presents a synthesis of the results from both studies.

# CHAPTER 1

Enlarged jaw proportions have traditionally been interpreted as a dietary adaptation that structurally reinforces the corpus and symphysis against large bending and twisting moments during feeding on stress-limited foods (e.g., Hylander, 1988; Daegling, 1992). However, several recent studies (e.g., Daegling and Grine, 2007) have noted the uncertainty of the relationship between enlarged corpus proportions, increased load magnitude, and an increase in the number of loading cycles.

Hylander (1979a) suggested that the colobine mandibular corpus should not experience large bending moments as a result of powerful incision and that their deep jaws are most likely an adaptation against fatigue failure. He suggested that the highly fibrous and energy deficient nature of the colobine diet requires an enormous number of loading cycles per day and that the depth of the colobine corpus is a structural adaptation to resist fatigue microdamage resulting from an increase in masticatory loading cycles. Hylander (1979a) cautioned that intermittent high magnitude loading may therefore not be morphologically distinguishable from low-level cyclical loading.

Since then, several researchers seeking to link jaw morphology and diet have interpreted enlarged corpus proportions as a result of an increase in the amount of force *and/or* an increase in the number of chewing cycles. For example, Bouvier and Hylander (1981:9) stated that “differences in mandibular morphology result from higher bone strain levels and/or increased number of strain cycles of hard foods.” Ravosa (2000:320) stated that enlarged corpus proportions in larger bodied primates appear related to “repetitive loading and/or elevated masticatory forces during unilateral mastication related to ingesting a tougher and/or harder diet.” Wall (1999) characterized “resistant foods” as those that require high occlusal loads *or* a large number of chewing cycles. She suggested that these types of foods produce similar morphology in the temporomandibular joint. Similarly, Taylor (2006a) compared masticatory morphology in three populations of orangutan – *Pongo pygmaeus morio*, *P. p. wurmbii* and *P. abelli* – in the context of divergent feeding behaviors. She concluded that populations that feed on more resistant vegetation “are better able to resist repetitive and/or large loads sustained during incision and mastication” (Taylor, 2006a:385). A similar statement was made regarding the masticatory morphology of gorillas which differ in the proportions of herbaceous vegetation in their diets (Taylor, 2006b). More recently, Taylor et al. (2008:614) stated that “we still do not know whether average or peak masticatory forces are the more important determinant of mandibular form.”

Daegling and McGraw (2001:1051) noted that an important issue in primate masticatory studies involves “not how hard a primate chews, but how often.” Likewise, Daegling and Grine (2007:97) recently noted that it is unclear if “increased load magnitudes are themselves instrumental in producing stronger jaws or whether a greater number of loading cycles is responsible.” In addition, several studies have interpreted specializations in the masticatory apparatus, such as a more robust mandibular corpus, as the result of more “resistant” foods without acknowledging that these foods include both hard and tough items. For example, Antón (1996) interpreted enlarged corpus proportions in Japanese macaques as an adaptation to eating hard seeds and nuts as well as tough bark and roots. Despite the fact that researchers stress the importance of considering food material properties, virtually none have investigated possible differences between cyclical and high magnitude loading.

To complicate matters further, Wright (2005a:490) suggested that “the derived craniodental complex of *C. apella*, while seemingly adapted for intermittently biting mechanically challenging foods, is also used in the wild during periods of resource scarcity for cyclically grinding a resource that may not be used during more fruit-abundant periods of the year.” The craniomandibular morphology of this taxon traditionally has been viewed as an adaptation to the production and dissipation of heavy occlusal loads (Bouvier, 1986b; Cole, 1992; Daegling, 1992).

These uncertainties have implications for the fossil record. The enlarged jaws of “robust” australopithecines traditionally have been interpreted as a structural adaptation to reduce bending and torsional loads during the mastication of unusually hard objects (e.g., Grine, 1981; Chamberlain and Wood, 1985; Wood and Aiello, 1998; Hylander, 1988; Daegling, 1989). However, Hylander (1988:76) noted that “if the diet of ‘robust’ australopithecines consisted of primarily of large amounts of low-quality foods that required extensive and prolonged chewing, then perhaps their jaws were primarily adapted to prevent fatigue failure due to an unusually large number of chewing cycles.” Likewise, others have noted that the morphology of “robust” australopithecine molars may actually be adapted to processing large quantities of food rather than small mouthfuls of hard and brittle objects (Walker, 1981; Demes and Creel, 1988).

Similar discrepancies between dental microwear patterns and dentognathic morphology thought to represent trophic adaptations for powerful mastication have been identified for *Australopithecus anamensis* (Grine et al., 2006a), *Praeanthropus afarensis*

(Grine et al., 2006b) and *Parathropus boisei* (Ungar et al., 2008). The enlarged jaws and thickly enameled teeth of these hominins have been suggested to reflect a dietary shift toward harder, more brittle food items (e.g., Grine, 1981; Lucas et al., 1985; Ward et al., 1999, 2001; Teaford and Ungar, 2000; White et al., 2006; Ungar, 2004; Macho et al., 2005). Microwear features, such as striation breadth and the percent of enamel pitting have been shown to reliably discriminate between extant hard-object feeding primates and those that feed chiefly on leaves and other tough vegetation (Grine et al., 2006a). However, the microwear fabrics of these taxa have been shown to be almost identical to those of *Gorilla gorilla beringei*, not to those of hard-object feeding primates such as *Cebus apella* and *Lophocebus albigena* (Grine et al., 2006a,b; Ungar et al., 2008). These results suggest that morphologies traditionally thought to reflect powerful mastication actually may be more related to prolonged chewing of low quality foods.

This study employs a combination of stepwise discriminant function analysis and non-parametric rank correlation on a sample of “heavy loading” and “repetitive loading” primates to investigate whether enlarged corpus proportions are a function of an increase in relative load magnitude or an increase in the number of daily chewing cycles. Stepwise discriminant analysis has been employed by researchers seeking to draw morphological distinctions between groups of mammalian taxa which diverge in their dietary habits, such as grazing and browsing ungulates (Mendoza et al., 2004), as well as fruit, nectar and exudate-feeding mammals (Dumont, 1997). An additional goal is to identify morphologically “meaningful” features that reliably discriminate “heavy loading” primates from “repetitive loading” primates.

This study makes two assumptions: (1) “heavy loaders” produce greater bite force per loading event than “repetitive loaders”, and (2) “repetitive loaders” engage in a larger number of chewing cycles per day than “heavy loaders.” These two masticatory categories can be identified by the physical and nutritional properties of the foods included in their diets. Support for these assumptions comes from a recent study by Norconk et al. (2008:288) who stated that “while breaking down pliant, tough leaves may require significant mechanical work at the molars, manifested as repetitive crack propagation, it may not necessarily involve generating extremely high bite forces during chewing.”

“Heavy loading” primates are defined here as those traditionally viewed as hard-object feeders. Hardness is the food physical property that permits identification of the members of this category. Traditionally, hardness is assessed using indentation or some other sort of puncture resistance test. It is defined as “the force that produces unit area of indentation” (Agrawal et al., 1998:1935) and can be characterized using Young’s modulus (Lucas, 2004). Young’s modulus describes the resistance of a material to elastic deformation. Foods which fall into the “heavy loading” category, such as seeds and nuts, are stress-limiting (Ashby, 1999). Efficiently processing these types of foods requires elevated masticatory forces (Hylander, 1979a; Lucas et al., 2002; Lucas, 2004). For example, foods such as prune pit and popcorn kernel have been shown to influence the rate of unloading of the jaw adductor muscles (Hylander and Johnson, 1994), as well as cause increases in the amount of total muscular force applied during chewing (Hylander et al., 1998).

"Repetitive loading" or "repeat loading" primates are defined here as those that include a relatively high proportion of lower quality foods in their diet. Foods which fall into this category include leaves and other nutrient-deficient vegetation. Leaves can be processed with relatively little masticatory force but require more chews per day (Hylander, 1979a; Lucas, 2004; Williams et al., 2005). The physical property that characterizes leaves is fracture toughness, the energy required to produce a crack of a given area (Lucas, 2004). It describes a material's ability to resist crack growth (Lucas et al., 2000). This property has been hypothesized to play an important role in modulating jaw movements during mastication (Agrawal et al., 1997, 1998; Lucas et al., 2002). These crack displacement-limiting (Ashby, 1999) foods are usually lower in nutrients and therefore their consumers require them in larger quantities per day. This results in longer processing times and an increase in the number of daily chewing cycles. Poor crack growth and propagation in tough foods also requires increased chewing strokes per volume of food to be efficiently broken down. Ross et al. (2009) concluded that size-related increases in daily feeding time due to a decrease in food quality could be explained by an increase in the amount of food consumed per day. This can presumably be extended to primates of comparable body sizes that differ in the nutritional properties of their foods.

Are larger jaws a function of the force produced per chew or the number of chewing cycles per day? Which morphological features are indicative of these loading regimes? These questions are addressed following a two-step process. First, differences between each loading regime are established through stepwise discriminant function analysis. Variables included in the analysis were assumed to vary with diet and are presumably advantageous to either “heavy” or “repetitive” loading. These differences are established with no initial consideration of jaw proportions. Linear corpus and symphysis dimensions are intentionally left out of this analysis, as they may contribute to the overall separation of the groups in multivariate space. This removes some circularity. Therefore, the role of the stepwise discriminant function analysis is to establish differences between “heavy loading” and “repetitive loading” based on other measures and to identify variables that are the most reliable indicators of each loading regime. Second, a non-parametric Spearman’s rank correlation matrix is generated using the discriminant scores from each individual, the variables included in the stepwise discriminant function analysis, as well as the corpus and symphysis dimensions in question. The correlations between the discriminant function and each variable included in the analysis are often presented in the form of a structure matrix. However, a more intuitive approach is to run a correlation analysis between the discriminant scores and values for each variable. This produces *P*-values for each correlation and provides the opportunity to investigate the relationship of additional variables (e.g., corpus and symphysis dimensions) with each loading regime. In the absence of food material properties and chewing frequency data, discriminant scores can serve as a proxy for “heavy loading” and “repetitive loading” by providing a value which measures the strength of each individual’s relationship with the group to which it is classified.

Several hypotheses and biomechanical predictions are tested here. The primary hypothesis concerns corpus and symphysis size. The null hypothesis is that enlarged jaws are related to increased load magnitude and that these dimensions will scale positively with “heavy loading” (positive and negative values for each loading regime are determined after performing the first step in the analysis). Alternatively, some of these dimensions, particularly corpus depth, may scale positively with “repetitive loading.” A final possibility is that some or all of the jaw dimensions will yield insignificant correlations with the discriminant function. This would suggest that such dimensions are not indicative of either loading regime.

The variables included in the discriminant analysis are presumed to vary with diet. Several *a priori* predictions were made regarding each of these variables. For example, jaw adductor leverage, and infratemporal fossa area were expected to be greater in “heavy loaders,” whereas jaw length and dental arcade width were expected to be greater in “repetitive loaders.” A more extensive discussion concerning these predictions is presented below.

## MATERIALS AND METHODS

Five “heavy loading” and five “repetitive loading” specialists were selected from among both catarrhines and platyrrhines (Table 1.1). Phylogenetically diverse taxa were included in order to highlight morphological differences that reflect dietary adaptation rather than similarities which reflect shared ancestry. Taxa in each group were included based on observational studies documenting the diets of each species, as well as dental microwear studies. Microwear features, such as striation breadth and pitting incidence have been shown to reliably discriminate between hard-object feeders and primates that feed chiefly on leaves and other tough vegetation (Grine et al., 2006a). With the exception of *Trachypithecus cristatus* (see below), the proportion of leaves included in the diets of each taxon in the repetitive loading group is summarized in Table 1.2.

*TABLE 1.1*. Taxa included in the dietary groups examined in this study.

| Group | Taxon | n |
|---|---|---|
| Heavy Loader | *Pithecia pithecia* | 22 |
| | *Chiropotes satanas* | 19 |
| | *Cebus apella* | 16 |
| | *Lophocebus albigena* | 13 |
| | *Cercocebus agilis* | 9 |
| Repetitive Loader | *Alouatta palliata* | 13 |
| | *Alouatta belzebul* | 13 |
| | *Trachypithecus cristatus* | 13 |
| | *Procolobus badius* | 13 |
| | *Colobus guereza* | 11 |

### “Heavy loading” sample

***Cebus apella.*** Tufted capuchins are known for their ability to exploit foods that are difficult to process and are not accessible to sympatric species. *Cebus apella* regularly feeds on hard, brittle foods, such as the palm fruit *Astrocaryum* (Izawa, 1975, 1979; Moynihan, 1976; Izawa and Mizuno, 1977; Fleagle et al., 1981; Terborgh, 1983; Janson and Boinski, 1992; Spironelo, 1991; Galetti and Pedroni, 1994). Terborgh (1983) and Spironelo (1991) have suggested that palm fruits are a critical fall-back resource for tufted capuchins during periods of fruit scarcity. Other hard fruits such as *Cariniana legalis* (*Lecythidaceae*), *Hymenae courbaril* (*Caeslpiniaceae*) and *Metrodoria stipularis* (*Euphorbiaceae*) are regular components of the *C. apella* diet (Galetti and Pedroni, 1994). Galetti and Pedroni (1994:30) have gone so far as to suggest that “no seed is protected morphologically from capuchins.”

*Cebus apella* is regularly included as a “hard-object” specialist in studies of dental microwear. These studies have demonstrated that *C. apella* has a strikingly high proportion of molar and premolar enamel pitting which is consistent with a diet requiring elevated bite forces (Teaford and Walker, 1984; Teaford, 1985, 1988; Grine et al., 2006a,b; Scott et al., 2006; Ungar et al., 2006, 2008; McKusick and Teaford, 2007).

***Chiropotes satanas.*** All three pitheciine genera show a preference for unripe fruits over ripe ones (Ayres, 1989; van Roosmalen et al., 1988; Kinzey and Norconk, 1990, 1993; Norconk, 1996). Kinzey and Norconk (1990) found that the puncture resistance of fruit pericarp breached by *Chiropotes satanas* was strikingly higher than the pericarp of fruits eaten by sympatric *Ateles*. This type of frugivory, known as "sclerocarpic harvesting" (Kinzey and Norconk, 1990), is uncommon among primates and may reduce dietary stress during times of fruit scarcity by allowing pitheciines to gain earlier access to fruits (Norconk, 1996; Norconk et al., in press).

Young seeds are also an extremely important part of the pitheciine diet (e.g., Mittermeier and van Roosmalen, 1981; van Roosmalen et al., 1981, 1988; Ayres, 1986, 1989; Kinzey and Norconk, 1990, 1993). Kinzey and Norconk (1993) reported that exclusive seed eating was up to 91% of total feeding time for *Chiropotes satanas*. They also report that 99% of the time spent feeding on fruits also included the mastication of seeds. Van Roosmalen et al. (1988) reported that the hard-shelled seeds of Brazil nuts (*Lecythidaceae*) were particularly important food items in the diet of bearded sakis. Ferrari et al. (2004) observed that, like *Cebus apella*, palm fruits were also important dietary items for *C. satanas*.

Dental microwear studies have shown that the microwear patterns of *Chiropotes satanas* are consistent with a diet that includes hard objects. Compared to taxa that prefer soft fruit, bearded sakis exhibit a high incidence of molar enamel pitting (Kay, 1987; Teaford and Runestad, 1992).

***Pithecia pithecia.*** As previously mentioned, all three pitheciine genera exhibit a preference for unripe fruits and seeds (van Roosmalen et al., 1988; Ayres, 1989; Kinzey and Norconk, 1990, 1993; Norconk, 1996). However, Kinzey and Norconk (1993) have demonstrated that *Chiropotes satanas* and *Pithecia pithecia* are able to remain sympatric and reduce competition by exploiting fruits at different stages of ripeness. Although fruit pericarp incised by *Chiropotes* has a higher puncture resistance than fruit incised by *Pithecia*, the seeds masticated by *P. pithecia* have a significantly higher crushing resistance than seeds masticated by *C. satanas* (Kinzey and Norconk, 1990, 1993).

These findings are also consistent with studies of dental microwear. Teaford and Runestad (1992) have demonstrated that *Pithecia pithecia* microwear fabrics exhibit a higher number of large pits compared to *Chiropotes satanas*. They also note that *P. pithecia* represents the extreme end of the range of enamel pitting in their sample of Venezuelan primates. McKusick and Teaford's (2007) study of mandibular second premolar microwear concluded that *P. pithecia* occupies an intermediate position between *Cebus apella* and *Ateles belzebuth*.

***Lophocebus albigena.*** Although figs and other fruits dominate the diet of *Lophocebus* (Waser, 1977; Freeland, 1979; Tutin et al., 1997; Olupot et al., 1997, 1998; Poulsen et al., 2001), hard-shelled fruits, such as palm fruits, which are not accessible to other sympatric taxa, are an extremely important fallback resource (Chalmers, 1968; Waser, 1977;

Poulsen et al., 2001; Lambert et al., 2004). A particularly important component of their diet is the hard seeds of *Diospyros abyssinica* (Lambert et al., 2004). Shah (2003) observed that *Lophocebus albigena* also engages in more frequent and powerful incision of hard fruits compared to sympatric *Cercocebus agilis*.

Dental microwear studies are consistent with a diet including hard, brittle objects for *Lophocebus albigena*. These studies have shown that *Lophocebus albigena* can be considered alongside *Cebus apella* as the most specialized hard object consumers among primates (Grine et al., 2006a,b). The microwear fabrics of *Lophocebus albigena* exhibit a high proportion of molar enamel pitting when compared to more folivorous and frugivorous taxa (Teaford and Walker, 1984; El-Zaatari et al., 2005; Grine et al., 2006a,b; Ungar et al., 2006, 2008).

***Cercocebus agilis.*** As in *Lophocebus albigena*, the diet of *Cercocebus agilis* consists of hard fruits, nuts and seeds (Waser, 1977, 1984; Fleagle, 1999). Shah (2003) noted that *Cercocebus agilis* engages in more frequent and powerful postcanine crushing of seeds than did *Lophocebus albigena*. No studies of dental microwear have included this taxon.

### “Repetitive loading” sample

***Alouatta palliata.*** Although howlers have been known to include up to 50% fruit in their diet (Estrada and Coates-Estrada, 1986), they are considered the most folivorous of all New World monkeys (Glander, 1975, 1978, 1981; Milton, 1980, 1984; Mittermeier and van Roosmalen, 1981; Pinto, 2002; Di Fiore and Campbell, 2007). Leaves and fruit from *Ficus* spp. may be a particularly important component of the *Alouatta palliata* diet

*TABLE 1.2*. Proportion of leaves in the diets of "repetitive loading" taxa used in this study.

| **Species** | **Percent Leaves** | **Reference** |
|---|---|---|
| *Alouatta palliata* | 54.4% (17–87) | Estrada et al., 1999 |
| | 49.3% (20–100) | Estrada, 1984 |
| | 48.2% (26–84) | Milton, 1980 |
| | 69.3% (64–72) | Glander, 1978 |
| | 68.5% | Stoner, 1996 |
| | 49% (0–95) | Chapman, 1987, 1988 |
| | 55.8% (32–82) | Williams-Guillen, 2003 |
| | 15.3–76.6% | Travers, 1999 |
| | 55.3% (27–87) | Cristobal-Azkarate and Arroyo-Rodriguez, 2007 |
| | 18.3–79.3% | Estrada et al., 1999 |
| | 22–80% | Juan et al., 2000 |
| | 48–85% | Milton, 1977 |
| | >90% | Glander, 1975 |
| | 51% (23–67) | Munoz et al., 2006 |
| | 63.6% | Glander, 1981 |
| | 29.4% | Serio-Silva et al., 2002 |
| | 53.8% | Milton, 1980 |
| | 48.2% | Milton, 1979 |
| *Alouatta belzebul* | 24.8% (11–54) | Pinto and Setz, 2004 |
| | 13.3% (8–15) | Bonvicino, 1989 |
| | 54% | Pinto and Setz, 2001 |
| | 40.8–77.9% | De Souza et al., 2002 |
| *Colobus guereza* | 81% | Oates, 1977, 1994 |
| | 80% | Wasserman and Chapman, 2003 |
| | 86% | Wasserman and Chapman, 2003 |
| | 87% | Wasserman and Chapman, 2003 |
| | 58% | Bocian, 1997 |
| | 54% | Fashing, 2001 |
| | 63% | Plumptre, unpublished |
| | 51% | Plumptre, unpublished |
| | 48% | Fashing, 2001 |
| | 57% | Fashing, 2001 |
| | 78.5–94% | Harris and Chapman, 2007 |
| | 65% | Oates, 1978 |
| | 87.8% | Harris, 2006 |
| *Procolobus badius* | 64% | Marsh, 1981 |
| | 47% | Gatinot, 1978 |
| | 47% | Oates, 1994 |
| | 47% | Starin, 1991 |
| | 31% | Wachter et al., 1997 |
| | 50% | Korstjens et al., 2007 |
| | 52% | Davies et al., 1999 |
| | 61% | Maisels et al., 1994 |
| | ~75% | Chapman and Chapman, 2002 |
| | 83.6% | Struhsaker, 1975 |
| | 78.9% | Clutton-Brock, 1975 |

(Serio-Silva et al., 2002; Munoz et al., 2006; Cristobal-Azkarate and Arroyo-Rodriguez, 2007). Wright (2005b) demonstrated that the toughness of foods in the diet of howlers in a primate community in central Guyana is significantly greater than the five other sympatric platyrrhine taxa. *Alouatta palliata* usually selects immature leaves with a high protein to fiber ratio, but mature leaves make up a larger proportion of their diet during the rainy season (Milton, 1979, 1980; Rockwood and Glander, 1979; Glander, 1981; Estrada et al., 1999; Munoz et al., 2006; Teaford et al., 2006; Cristobal-Azkarate and Arroyo-Rodriguez, 2007). Teaford et al. (2006) found that one population of *Alouatta palliata* fed more on tough leaves during the dry season. They concluded that this may represent seasonal differences in food availability.

The microwear pattern of *Alouatta palliata* is characterized by the predominance of wide striations (Teaford and Walker, 1984; Teaford, 1985, 1988; Teaford and Glander, 1991, 1996; Scott et al., 2006). This pattern is consistent with a diet of tough leaves and differentiates folivorous taxa from durophagous and soft-fruit feeding-primates.

***Alouatta belzebul.*** Like *Alouatta palliata*, *A. belzebul* is one of the most folivorous New World primates. However, among howlers, *Alouatta belzebul* may be one of the most frugivorous taxa (Fleagle, 1999; De Souza et al., 2002; Pinto and Setz, 2004). In general, *Alouatta belzebul* prefer immature leaves over mature ones, but mature leaves can often make up almost 25% of their diet (Pinto and Setz, 2001). De Souza et al. (2002) observed a marked shift in folivory (from 40.8% to 77.9% leaves) during the transition from wet to dry season. This shift was also accompanied by an increase in mature leaves, unlike what occurs in other members of this genus (e.g., Milton, 1980). Two important tree families for *Alouatta belzebul* are *Leguminosae* and *Moraceae* (Pinto and Setz, 2004).

Dental microwear studies have yet to be conducted for *Alouatta belzebul*. However, this species, like other howlers, exhibits well-developed molar shearing crests compared to more frugivorous platyrrhines, such as *Ateles* and *Lagothrix* (Anthony and Kay, 1993).

***Colobus guereza.*** The diet of *Colobus guereza* consists predominately of mature leaves (Clutton-Brock, 1975; Struhsaker and Oates, 1975; Oates, 1977, 1994; Rose, 1978; Harris and Chapman, 2007). However, they have also been known to eat modest amounts of fruits and unripe seeds (Fashing, 2001; Poulsen et al., 2002). *Colobus guereza* focuses mainly on immature leaves with a high protein to fiber ratio (Bocian, 1997; Chapman et al., 2003, 2004; Wasserman and Chapman, 2003) but usually shift to a diet dominated by lower-quality mature leaves during periods when preferred foods are scarce (Clutton-Brock, 1975; Struhsaker, 1975; Oates, 1977; Marsh, 1981; McKey et al., 1981; Dasilva, 1994; Fashing, 2007). Additionally, Clutton-Brock (1975) found that guerezas ate a higher proportion of mature leaves than did sympatric red colobus (*Procolobus badius*). Fashing (2001) reported that the leaves of *Prunus africana* were the most preferred food item for guerezas.

Teaford (1986) identified significant differences in the microwear patterns of *Colobus guereza* and *Procolobus badius*. He found that the more restricted folivorous nature of the guereza diet compared to red colobus (see below) was reflected in a higher proportion of scratches. Similarly, more recent studies (El-Zaatari et al., 2005; Grine et al., 2006a,b) have demonstrated that the microwear signature exhibited by *Colobus guereza* is characterized by deep parallel striations.

***Procolobus badius.*** Although field studies have reported a lower proportion of leaves compared to guerezas, the diet of red colobus monkeys is largely folivorous and consists primarily of young leaves (Clutton-Brock, 1973, 1975; Struhsaker, 1975, 1978; Struhsaker and Oates, 1975; Marsh, 1981; Werre, 2000; Usongo and Amubode, 2001; Chapman and Chapman, 2002; Wasserman and Chapman, 2003).

Teaford (1986) reported that the more varied diet of *Procolobus badius* is reflected in their microwear patterns. He found that red colobus monkeys exhibited more pits and fewer scratches compared to *Colobus guereza*. However, Teaford (1986) did note that the *Procolobus badius* sample was highly variable and that any differences between this species and *Colobus guereza* are best viewed as suggestive. El-Zaatari et al. (2005) found that a predominance of striations characterized the *Procolobus badius* microwear pattern.

***Trachypithecus cristatus.*** The early taxonomy of Asian colobines complicates the identification of reliable ecological data. *Trachypithecus cristatus* was formerly known as *Presbytis cristatus*. *Trachypithecus cristata*, *T. auratus*, *T. germaini* and *T. barbei* have all been used to identify various populations of this genus (Groves, 2001; Brandon-Jones et al., 2004). Denise et al. (2008) recently noted that nearly every population of silvered langurs has achieved separate species designation. For these reasons, the percent of leaves included in the diet of this genus were viewed as unreliable and were excluded from Table 1.2.

However, it is safe to consider *Trachypithecus cristatus* a highly folivorous colobine (Fleagle, 1999). Bernstein (1968) reported that the main component of their diet was young leaves. He also remarked that this species was "reminiscent of howler monkeys" in dietary behavior (Bernstein, 1968:15). *Trachypithecus obscurus*, once considered a subspecies of *T. cristatus* and perhaps a "morphological equivalent" to this taxon (Caton, 1999), is known to include up to 80% leaves in its diet (Brotoisworo and Dirgayuas, 1991; Bennett and Davies, 1994).

Several studies have suggested that *Trachypithecus* spp. are more folivorous and eat a higher proportion of mature leaves than other Asian colobines, such as *Presbytis* spp. (Curtin, 1980; Bennet and Davies, 1994; Yeager and Kool, 2000). This conclusion is supported by the presence of more well-developed shearing crests (Kay, 1975; Kay and Hylander, 1978; Teaford, 1983; Lucas and Teaford, 1994) and a larger foregut (Chivers and Hladik, 1980; Davies, 1991; Chivers, 1994) in the former taxon.

As with other highly folivorous primates, the pattern of dental microwear for *Trachypithecus cristatus* is characterized by the predominance of scratches (Scott et al., 2006; Ungar et al., 2006).

## Measurements

Thirty-three linear variables characterizing the skull and mandible of each taxon were taken from 142 specimens housed at the American Museum of Natural History (AMNH) and the National Museum of Natural History (NMNH). All specimens were wild-shot adult males with third molar in occlusion (*sensu* Cheverud, 1981). Individuals with high levels of dental attrition, pathology or alveolar resorption were excluded. All individuals used in the study are listed in Table 1.3. With the exception of facial projection (FacProj) and jaw adductor muscle leverages (MPm1, MPinc, MPcan, MASSm1, MASSinc, MASScan, TEMPm1, TEMPinc, TEMPcan), which were estimated from lateral and basicranial photographs in ImageJ (United States National Institutes of Health, public domain; Abramoff et al., 2004), all measurements were taken to the nearest 0.01 mm using digital calipers.

### Shape variables

The 33 measurements taken on each individual were used to generate 20 shape variables for the stepwise discriminant analysis. Several variables were expressed as ratios of two measurements, while others were scaled to a biomechanically relevant denominator or the geometric mean of skull size. A complete list of all measurements and shape variables used in the analysis can be found in Table 1.4.

Several variables were scaled against mandible length. They are: temporal articular surface area, zygomatic arch cross sectional area, infratemporal fossa area, ascending ramus height, condyle length, condyle width, dental arcade width, corpus width, corpus depth, symphysis width and symphysis depth. Mandible length approximates the bite moment arm for incision and is frequently used as a scaling variable in studies of jaw biomechanics (e.g., Hylander, 1979a, 1985, 1988; Bouvier, 1986a,b; Daegling, 1989, 1992; Ravosa, 1990, 1991, 1996; Antón, 1996; Vinyard and Ravosa, 1998; Vinyard et al., 2003).

*TABLE 1.3*. Specimens examined in this study (A = AMNH; N = NMNH; HL = Heavy Loading; RL = Repetitive Loading).

| **Species** | **Catalog #** | **Group** | **Locality** |
|---|---|---|---|
| *Pithecia pithecia* | N374763 | HL | Venezuela |
| *Pithecia pithecia* | N374765 | HL | Venezuela |
| *Pithecia pithecia* | N374760 | HL | Venezuela |
| *Pithecia pithecia* | N374762 | HL | Venezuela |
| *Pithecia pithecia* | N374767 | HL | Venezuela |
| *Pithecia pithecia* | N374759 | HL | Venezuela |
| *Pithecia pithecia* | N374754 | HL | Venezuela |
| *Pithecia pithecia* | N374749 | HL | Venezuela |
| *Pithecia pithecia* | A48122 | HL | Guyana |
| *Pithecia pithecia* | A48124 | HL | Guyana |
| *Pithecia pithecia* | A34863 | HL | Guyana |
| *Pithecia pithecia* | A42878 | HL | Guyana |
| *Pithecia pithecia* | A40044 | HL | Guyana |
| *Pithecia pithecia* | A42853 | HL | Guyana |
| *Pithecia pithecia* | A94149 | HL | Brazil |
| *Pithecia pithecia* | A94150 | HL | Brazil |
| *Pithecia pithecia* | A94147 | HL | Brazil |
| *Pithecia pithecia* | A79386 | HL | Brazil |
| *Pithecia pithecia* | A79388 | HL | Brazil |
| *Pithecia pithecia* | A79389 | HL | Brazil |
| *Pithecia pithecia* | A48144 | HL | Guyana |
| *Pithecia pithecia* | A149149 | HL | Guyana |
| *Chiropotes satanas* | N518225 | HL | Brazil |
| *Chiropotes satanas* | N338963 | HL | Guyana |
| *Chiropotes satanas* | N338964 | HL | Guyana |
| *Chiropotes satanas* | N406591 | HL | Venezuela |
| *Chiropotes satanas* | N406588 | HL | Venezuela |
| *Chiropotes satanas* | N388165 | HL | Venezuela |
| *Chiropotes satanas* | N406583 | HL | Venezuela |
| *Chiropotes satanas* | N406582 | HL | Venezuela |
| *Chiropotes satanas* | A94119 | HL | Brazil |
| *Chiropotes satanas* | A95871 | HL | Brazil |
| *Chiropotes satanas* | A94127 | HL | Brazil |
| *Chiropotes satanas* | A94160 | HL | Brazil |
| *Chiropotes satanas* | A96343 | HL | Brazil |
| *Chiropotes satanas* | A77568 | HL | Venezuela |
| *Chiropotes satanas* | A95870 | HL | Brazil |
| *Chiropotes satanas* | A94123 | HL | Brazil |
| *Chiropotes satanas* | A94126 | HL | Brazil |
| *Chiropotes satanas* | A94128 | HL | Brazil |
| *Chiropotes satanas* | A94124 | HL | Brazil |
| *Cebus apella* | N406626 | HL | Venezuela |
| *Cebus apella* | N388196 | HL | Venezuela |
| *Cebus apella* | N518474 | HL | Brazil |
| *Cebus apella* | N461384 | HL | Brazil |
| *Cebus apella* | N518409 | HL | Brazil |

*TABLE 1.3* cont'd

| | | | |
|---|---|---|---|
| *Cebus apella* | N518279 | HL | Brazil |
| *Cebus apella* | N518282 | HL | Brazil |
| *Cebus apella* | N518352 | HL | Brazil |
| *Cebus apella* | N270361 | HL | Brazil |
| *Cebus apella* | N518365 | HL | Brazil |
| *Cebus apella* | A136188 | HL | Columbia |
| *Cebus apella* | A136189 | HL | Columbia |
| *Cebus apella* | A136190 | HL | Columbia |
| *Cebus apella* | A76494 | HL | Peru |
| *Cebus apella* | A75972 | HL | Peru |
| *Cebus apella* | A78499 | HL | Venezuela |
| *Lophocebus albigena* | N164579 | HL | Uganda |
| *Lophocebus albigena* | N452500 | HL | Uganda |
| *Lophocebus albigena* | N578579 | HL | Unknown |
| *Lophocebus albigena* | N452503 | HL | Uganda |
| *Lophocebus albigena* | N452502 | HL | Uganda |
| *Lophocebus albigena* | N220086 | HL | Congo |
| *Lophocebus albigena* | N220094 | HL | Congo |
| *Lophocebus albigena* | A52603 | HL | Zaire |
| *Lophocebus albigena* | A52615 | HL | Zaire |
| *Lophocebus albigena* | A52599 | HL | Zaire |
| *Lophocebus albigena* | A52618 | HL | Zaire |
| *Lophocebus albigena* | A52579 | HL | Zaire |
| *Lophocebus albigena* | A52619 | HL | Zaire |
| *Cercocebus agilis* | A52637 | HL | Zaire |
| *Cercocebus agilis* | A81250 | HL | Zaire |
| *Cercocebus agilis* | A52645 | HL | Zaire |
| *Cercocebus agilis* | A52641 | HL | Zaire |
| *Cercocebus agilis* | A52634 | HL | Zaire |
| *Cercocebus agilis* | A52666 | HL | Zaire |
| *Cercocebus agilis* | A52663 | HL | Zaire |
| *Cercocebus agilis* | A52648 | HL | Zaire |
| *Cercocebus agilis* | A52658 | HL | Zaire |
| *Alouatta palliata* | N361217 | RL | Nicaragua |
| *Alouatta palliata* | N337853 | RL | Nicaragua |
| *Alouatta palliata* | N282850 | RL | El Salvador |
| *Alouatta palliata* | N361219 | RL | Nicaragua |
| *Alouatta palliata* | N339932 | RL | Nicaragua |
| *Alouatta palliata* | N282799 | RL | El Salvador |
| *Alouatta palliata* | N339921 | RL | Nicaragua |
| *Alouatta palliata* | N339919 | RL | Nicaragua |
| *Alouatta palliata* | N339930 | RL | Nicaragua |
| *Alouatta palliata* | N337850 | RL | Nicaragua |
| *Alouatta palliata* | A66712 | RL | Ecuador |
| *Alouatta palliata* | A66713 | RL | Ecuador |
| *Alouatta palliata* | A66709 | RL | Ecuador |
| *Alouatta belzebul* | N549520 | RL | Brazil |
| *Alouatta belzebul* | N461714 | RL | Brazil |

*TABLE 1.3* cont'd

| | | | |
|---|---|---|---|
| *Alouatta belzebul* | N461712 | RL | Brazil |
| *Alouatta belzebul* | N461711 | RL | Brazil |
| *Alouatta belzebul* | A133879 | RL | Brazil |
| *Alouatta belzebul* | A94961 | RL | Brazil |
| *Alouatta belzebul* | A133532 | RL | Brazil |
| *Alouatta belzebul* | A94957 | RL | Brazil |
| *Alouatta belzebul* | A133539 | RL | Brazil |
| *Alouatta belzebul* | A133544 | RL | Brazil |
| *Alouatta belzebul* | A133537 | RL | Brazil |
| *Alouatta belzebul* | A77690 | RL | Unknown |
| *Alouatta belzebul* | A95886 | RL | Brazil |
| *Trachypithecus cristatus* | N114516 | RL | Sumatra |
| *Trachypithecus cristatus* | N142212 | RL | Borneo |
| *Trachypithecus cristatus* | N124725 | RL | Banka |
| *Trachypithecus cristatus* | N114514 | RL | Sumatra |
| *Trachypithecus cristatus* | N144371 | RL | Rhio Arch |
| *Trachypithecus cristatus* | N300018 | RL | Thailand |
| *Trachypithecus cristatus* | N307717 | RL | Thailand |
| *Trachypithecus cristatus* | N115671 | RL | Rhio Arch |
| *Trachypithecus cristatus* | N197645 | RL | Borneo |
| *Trachypithecus cristatus* | N115670 | RL | Rhio Arch |
| *Trachypithecus cristatus* | A102903 | RL | Sumatra |
| *Trachypithecus cristatus* | A106595 | RL | Sumatra |
| *Trachypithecus cristatus* | A106597 | RL | Sumatra |
| *Procolobus badius* | N378673 | RL | Senegal |
| *Procolobus badius* | N378643 | RL | Gambia |
| *Procolobus badius* | N378633 | RL | Gambia |
| *Procolobus badius* | N481795 | RL | Liberia |
| *Procolobus badius* | N481797 | RL | Liberia |
| *Procolobus badius* | N477325 | RL | Ivory Coast |
| *Procolobus badius* | A52306 | RL | Zaire |
| *Procolobus badius* | A52307 | RL | Zaire |
| *Procolobus badius* | A52326 | RL | Zaire |
| *Procolobus badius* | A52311 | RL | Zaire |
| *Procolobus badius* | A52304 | RL | Zaire |
| *Procolobus badius* | A52321 | RL | Zaire |
| *Procolobus badius* | A52302 | RL | Zaire |
| *Colobus guerza* | A27711 | RL | Kenya |
| *Colobus guerza* | A27710 | RL | Kenya |
| *Colobus guerza* | A52206 | RL | Zaire |
| *Colobus guerza* | A52211 | RL | Zaire |
| *Colobus guerza* | A52210 | RL | Zaire |
| *Colobus guerza* | A82429 | RL | Zaire |
| *Colobus guerza* | A52251 | RL | Zaire |
| *Colobus guerza* | A52212 | RL | Zaire |
| *Colobus guerza* | A52216 | RL | Zaire |
| *Colobus guerza* | A52217 | RL | Zaire |
| *Colobus guerza* | A33304 | RL | Kenya |

Mandible length itself was scaled against the geometric mean (GM) of 10 additional cranial measurements (see Table 1.4). An attempt was made to choose variables which are functionally distant from the masticatory system (Coleman, 2008). Using the geometric mean as a surrogate for size may not be appropriate when interpreting the functional significance of shapes (Vinyard, 2008). However, the GM was chosen as the scaling denominator for this variable because of its unclear biological relationship with other variables examined in this study (Mosimann, 1970; Darroch and Mosimann, 1985). The GM of skull size has been previously employed by workers investigating the functional significance of jaw length (e.g., Vinyard et al., 2003).

Facial projection was scaled against cranial length (i.e., prosthion – opisthocranion). Cranial length was chosen in order to capture the degree of prognathism relative to the overall length of the cranium.

Jaw adductor leverages were calculated as the ratio of lever arm length to load arm length measured from basicranial photographs in ImageJ software (Abramoff et al., 2004) following Spencer and Demes (1993). All measurements were taken perpendicular to a line that passes through the tips of both postglenoid processes (Fig. 1.1). Load arms were measured to the center of $M^1$, canine tip and incision. The medial pterygoid lever arm was measured to the most anterior point of the scaphoid fossa. The masseter lever arm was measured to the zygomaticomaxillary suture. The temporalis lever arm was measured to the point where the anterior root of the zygoma intersects the posterior point of the lateral orbital margin, as seen in basicranial view, near the zygomaticofacial suture. It should be noted that this method of calculating jaw adductor leverage only considers the extreme anterior fibers for each muscle. Furthermore, it neglects all non-vertical

*TABLE 1.4.* Measurements and shape variables used in this study.

| Meaurement/Variable | Abbreviation | Description |
|---|---|---|
| Anterior cranial length | AntCL | Nasion - Bregma |
| Ascending ramus height | AramH | Most superior point of condyle to most inferior point on the angle of mandible |
| Bigonial breadth | BigoB | Gonion - Gonion |
| Bipostglenoid breadth | BiPG | Distance between most inferior point of postglenoid processes |
| Bizygomatic breadth | BiZy | Zygion - Zygion |
| Breadth of zygomatich arch | ZygB | Breadth of zygomatic arch taken at zygotemporale suture |
| Canine load arm | CanLO | See text |
| Condyle length[1] | CondL | Maximum anteroposterior length of mandibular condyle |
| Condyle width[1] | CondW | Maximum mediolateral width of mandibular condyle |
| Corpus depth | CorpD | Superoinferior distance of mandibular corpus at $M_1$ |
| Corpus width | CorpW | Mediolateral distance of mandibular corpus at $M_1$ |
| Cranial height | CranH | Basion - Apex |
| Cranial length | CranL | Prosthion - Opisthocranion |
| Cranium geometric mean[2] | GM | $(CranH*CranL*AntCL*PostCL*MaxCW*BiZy*FacH*FacW*BiPG*MinCW)^{1/10}$ |
| Dental arcade width[1] | ArchW | Distance between buccal grooves of left and right mandibular $M_1$ |
| Facial height | FacH | Nasion - Prosthion |
| Facial projection[1] | FacProj | Prosthion perpendicular to a line extending inferiorly from orbitale superius |
| Facial width | FacW | Ectoconchion - Ectoconchion |
| Height of PC occlusal plane | OccPH | Occlusal plane of postcanine dentition to most inferior point on mandibular angle |
| Height of zygomatic arch | ZygH | Height of zygomatic arch taken at zygotemporale suture |
| Incisor load arm | IncLO | See text |
| Infratemporal fossa area[1] | TempFA | $1/2(TempFW) * 1/2(TempFL) * \pi$ |
| Infratemporal fossa length | TempFL | Maximum length of temporal fossa - measured in inferior view |
| Infratemporal fossa width | TempFW | Maximum mediolateral distance from zygomatic arch to medial wall of temporal fossa |

*TABLE 1.4* cont’d

| | | |
|---|---|---|
| $M^1$ load arm | M1LO | See text |
| Mandible length[1] | MandL | Infradentale to most posterior point of mandibular condyle |
| Masseter insertion angle[1] | MassIA | BigoB/BiZy |
| Masseter lever arm | MassLE | See text |
| Masseter leverage at canine | MASScan | MassLE/CanLO |
| Masseter leverage at incisor[1] | MASSinc | MassLE/IncLO |
| Masseter leverage at M1[1] | MASSm1 | MassLE/M1LO |
| Maximum cranial width | MaxCW | Euryon - Euryon |
| Medial pterygoid insertion angle[1] | MedPIA | MedPB/BigoB |
| Medial pterygoid lever arm | MedPLE | See text |
| Medial pterygoid leverage at canine | MPcan | MedPLE/CanLO |
| Medial pterygoid leverage at incisor | MPinc | MedPLE/IncLO |
| Medial pterygoid leverage at M1[1] | MPm1 | MedPLE/M1LO |
| Medial pterygoid origin breadth | MedPB | Distance between anterior junction of left and right medial and lateral pterygoid plates |
| Minimum cranial width | MinCW | BiZy - (2 * TempFW) |
| Posterior cranial length | PostCL | Bregma - Inion |
| Ramus height above occlussal plane[1] | RamH | AramH - OccPH |
| Symphyseal depth | SymD | Superoinferior distance from infradentale to inferoposterior border of symphysis |
| Symphyseal width | SymW | Anteroposterior width of symphysis at its maximum thickness taken perpendicular to SymD |
| Temporal articular surface length[1] | GlenPG | Anteroposterior length of temporal articular surface |
| Temporalis lever arm | TempLE | See text |
| Temporalis leverage at canine | TEMPcan | TempLE/CanLO |
| Temporalis leverage at incisor[1] | TEMPinc | TempLE/IncLO |
| Temporalis leverage at M1[1] | TEMPm1 | TempLE/M1LO |
| Zygomatic arch cross sectional area[1] | ZygA | 1/2(ZygB) * 1/2(ZygH) * π |

[1] Shape variable included in DFA

[2] Geometric mean used to scale MandL (see text)

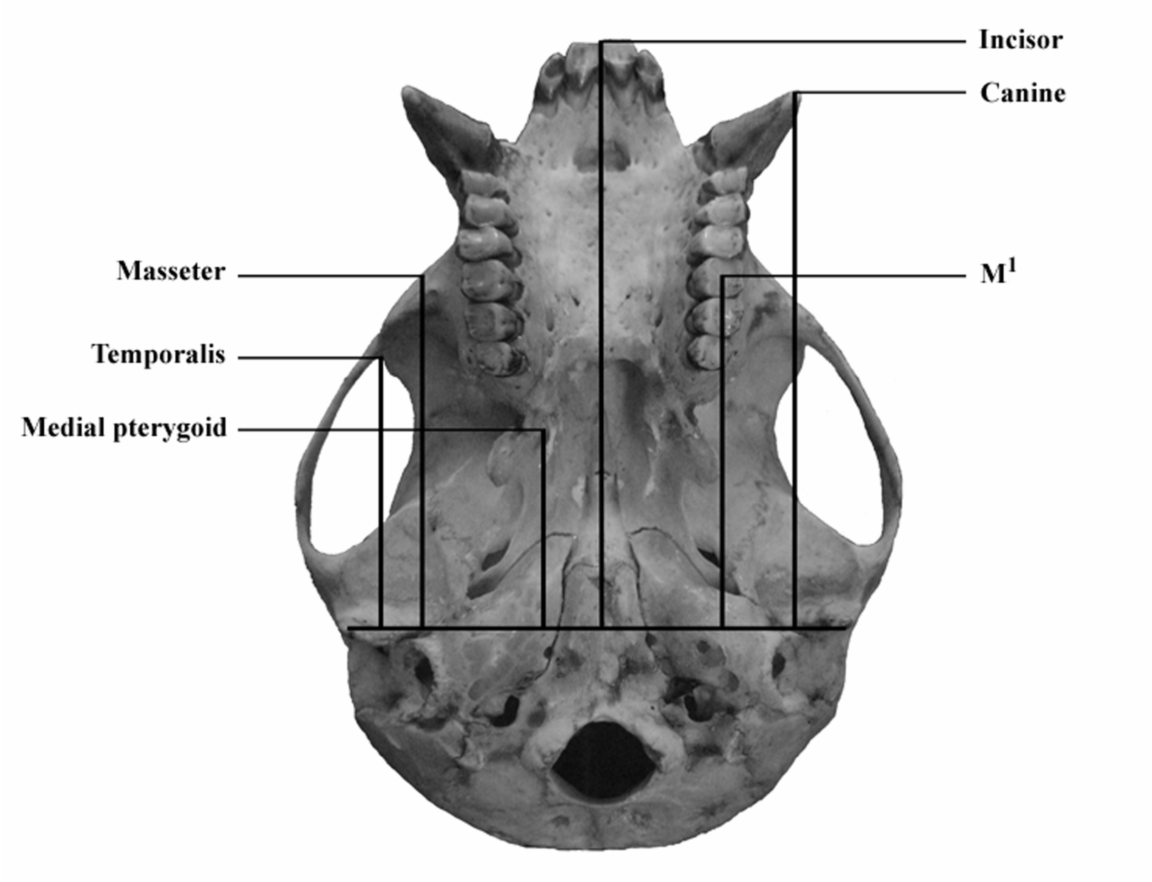

**Fig. 1.1**. Basicranial view of *Chiropotes satanas* (AMNH 94128) illustrating lever and load arm measurements used to calculate anterior jaw adductor leverage (Spencer and Demes, 1993).

components of muscle force. This is an assumption that is both mechanically unrealistic (Davis, 1955; Tattersall, 1974) and empirically simplistic (Hylander, 1978). Therefore, muscle leverage values calculated in this study may be more appropriately termed "anterior leverage" due to underrepresentation of the rest of the muscle. Moreover, this method ignores additional features of the masticatory system which likely play a role in jaw adductor force production, such as height of the ascending ramus. However, this method permits estimation of jaw adductor leverages on a large number of individuals and has been employed in several previous analyses (Spencer and Demes, 1993; Spencer, 2003; Wright, 2005a; Norconk et al., 2008).

## Statistical analyses

This study employs stepwise discriminant function analysis of 20 size-free craniomandibular variables (see Table 1.4) in a sample of "heavy loading" (i.e., durophagous) and "repetitive loading" (i.e., folivorous) primates. The stepwise discriminant function analysis will identify the minimum number of variables which, when combined, explain the maximum amount of between-group variability.

Discriminant analysis is very sensitive to outliers but less so to skewness. Even with modest violations against assuming homogeneity of variances and multivariate normality, discriminant analysis is still relatively robust and likely to produce similar results to when these assumptions are met (Lachenbruch, 1975; Klecka, 1980). Quantile-quantile plots were examined for outliers. This resulted in the omission of two individuals from the analysis (*Cebus apella* A76494 and *Alouatta belzebul* N461714). This method was chosen because traditional tests, such as Kolmogorov-Smirnov and Shapiro-Wilk, may be too conservative for this type of analysis (McGarial et al., 2000). A Box's M test, which tests the null hypothesis of equal population covariance matrices, was significant which indicates that the covariance matrices differ between groups formed by the dependent (Table 1.5). However, sample sizes are large and group log determinants are similar which suggests that no substantial violation of this assumption exists (Table 1.6).

Another assumption of discriminant function analysis is low multicollinearity of the independents (i.e., there are no highly correlated variables). Before the analysis was

*TABLE 1.5*. Results of Box’s M test of equal population covariance matrices.

| **Box's M** | | 80.576 |
|---|---|---|
| **F** | Approx. | 3.656 |
| | df1 | 21.000 |
| | df2 | 62828.450 |
| | Sig. | <0.001 |

*TABLE 1.6*. Group log determinants. The ranks and natural logarithms of determinants printed are those of the group covariance matrices.

| **Group** | **Rank** | **Log Determinant** |
|---|---|---|
| Heavy Loader | 6 | -39.971 |
| Repeat Loader | 6 | -42.320 |
| Pooled within-groups | 6 | -40.426 |

undertaken a Spearman’s rank correlation matrix was generated to assess the level of mulicollinearity. This revealed several highly correlated variables, all of which were jaw adductor leverage ratios. As per McGarial et al. (2000), highly correlated variables were removed from the data set such that there were no correlation coefficients greater or equal to 0.90 and no more than one pair of correlated variables with a correlation coefficient greater than 0.80. Correlated variables removed from the analysis were medial pterygoid leverage at the canine and incisor, masseter leverage at the canine and temporalis leverage at the canine. This reduced the number of variables included in the stepwise discriminant analysis from 20 to 16 (see Table 1.4).

The discriminant function was generated in SPSS 16.0. Taxa in each group were characterized by unequal sample sizes. Therefore, classification probabilities were computed from group sizes. The criterion for selection of those variables included in the discriminant function was based on the minimization of the overall Wilk’s lambda at each step. Because the stepwise method may result is spurious significance levels due to chance associations, classification results for cross-validated cases are also presented (see below).

Determining whether corpus and symphysis dimensions are indicative of either heavy loading or repetitive loading is the main objective of this investigation. As previously mentioned, these dimensions were purposely left out of the discriminant function analysis. Including these variables in the analysis may add to the overall difference between the two dietary groups. Instead, the discriminant scores were correlated against linear corpus and symphysis dimensions, as well as the 16 other variables examined in this study after the discriminant function was generated to asses their relative importance in classifying each group. The relationship between the discriminant scores for each individual, which serve as an indicator of that individual's ability to discriminate between classes, and each variable was examined using Spearman's rank correlation. A positive correlation coefficient indicates a positive relationship between "heavy loading" while a negative correlation coefficient indicates a positive correlation between "repetitive loading."

## RESULTS

The stepwise discriminant function analysis of the final 16 craniomandibular variables identified six features which together significantly differentiate heavy loading from repetitive loading primates (Table 1.7). Combined, these variables contribute 100% of the between-group variability (Table 1.8). Ordered by absolute size of the correlation within the function these are: medial pterygoid leverage at $M^1$, medial pterygoid insertion

*TABLE 1.7*. Standardized canonical discriminant function coefficients.

| Variable | Function |
|---|---|
| | 1 |
| GlenPG | -.510 |
| MedPIA | .369 |
| MassIA | .323 |
| MPm1 | .711 |
| TEMPm1 | 1.025 |
| TEMPinc | -.927 |

*TABLE 1.8*. Eigenvalues and percent of variance explained by the stepwise discriminant function.

| Function | Eigenvalue | % of Variance | Cumulative % | Canonical Correlation |
|---|---|---|---|---|
| 1 | 3.616 | 100.0 | 100.0 | .885 |

*TABLE 1.9*. Classification results of discriminant function analysis. 99.3% of the originally grouped and cross-validated cases are correctly classified by the function.

| | | Group | Predicted Group Membership | | |
|---|---|---|---|---|---|
| | | | Heavy Loader | Repeat Loader | Total |
| Original | Count | Heavy Loader | 77 | 1 | 78 |
| | | Repeat Loader | | 62 | 62 |
| | % | Heavy Loader | 98.7 | 1.3 | 100.0 |
| | | Repeat Loader | .0 | 100.0 | 100.0 |
| Cross-validated[1] | Count | Heavy Loader | 77 | 1 | 78 |
| | | Repeat Loader | | 62 | 62 |
| | % | Heavy Loader | 98.7 | 1.3 | 100.0 |
| | | Repeat Loader | .0 | 100.0 | 100.0 |

[1] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.

angle, temporalis leverage at $M^1$, anteroposterior length of the temporal articular surface, masseter insertion angle and temporalis leverage at incisor. The analysis correctly classified 99.3% of originally grouped and cross-validated cases (77 of 78 heavy loaders and 62 of 62 repetitive loaders; Table 1.9). Group graphs can be found in Figure 1.2. The values for the heavy loading group were almost entirely positive, whereas repetitive loaders have negative values. The variables input at each of the 6 steps of the analysis and the results of the selection criterion can be found in Table 1.10. The values for the functions at group centroids can be found in Table 1.11.

Although the discriminant function explained 100% of the variation between the dietary groups it would be unfortunate to ignore the relationship of the other variables to these loading regimes. These results are often presented in the form of a structure matrix which displays the strength of the correlation within the function. As mentioned above, a more intuitive approach is to run a correlation analysis between the discriminant scores and values for each variable. Table 1.12 shows that the following variables are significantly positively correlated with heavy loading: medial pterygoid insertion angle, dental arcade width, medial pterygoid leverage at $M^1$, masseter leverage at $M^1$, temporalis leverage at $M^1$, temporalis leverage at incisor, corpus width, corpus depth and symphysis width. Variables significantly positively correlated with repeat loading (i.e., negatively correlated with the discriminant function) are: anteroposterior length of the temporal articular surface, zygomatic arch size, ascending ramus height above the occlusal plane, mandible length and masseter insertion angle. Four variables were not correlated significantly with either loading regime. These are: temporal fossa area, condyle width, condyle length and facial projection.

Low, yet significant, positive correlations with the discriminant scores were found for corpus width, corpus depth and symphysis width which indicates a positive relationship between “heavy loading” and corpus robusticity. Symphysis depth did not correlate significantly with the function. None of the jaw proportions correlated significantly with repetitive loading. Because the first step in this study was to establish a function which discriminates between heavy loading and repetitive loading without consideration of the jaw variables in question, the variables found to significantly differentiate the two loading regimes are dealt with first in the following discussion.

*TABLE 1.10*. Variables input into the analysis at each step.

| | Step | Tolerance | F to Remove | Wilks' Lambda |
|---|---|---|---|---|
| 1 | MPm1 | 1.000 | 174.342 | |
| 2 | MPm1 | .963 | 156.830 | .709 |
| | GlenPG | .963 | 46.124 | .442 |
| 3 | MPm1 | .859 | 62.353 | .439 |
| | GlenPG | .949 | 48.267 | .408 |
| | TEMPm1 | .863 | 13.226 | .331 |
| 4 | MPm1 | .840 | 61.416 | .343 |
| | GlenPG | .948 | 37.165 | .301 |
| | TEMPm1 | .301 | 53.231 | .329 |
| | TEMPinc | .299 | 37.487 | .301 |
| 5 | MPm1 | .801 | 43.407 | .301 |
| | GlenPG | .948 | 35.438 | .287 |
| | TEMPm1 | .293 | 41.048 | .297 |
| | TEMPinc | .299 | 35.241 | .287 |
| | MedPIA | .840 | 5.093 | .236 |
| 6 | MPm1 | .703 | 51.341 | .300 |
| | GlenPG | .947 | 31.778 | .268 |
| | TEMPm1 | .291 | 41.819 | .285 |
| | TEMPinc | .299 | 33.513 | .271 |
| | MedPIA | .659 | 10.065 | .233 |
| | MassIA | .566 | 6.443 | .227 |

*TABLE 1.11*. Functions at group centroids. Unstandardized canonical discriminant functions evaluated at group means

| Group | Function |
|---|---|
| | 1 |
| Heavy Loader | 1.683 |
| Repeat Loader | -2.118 |

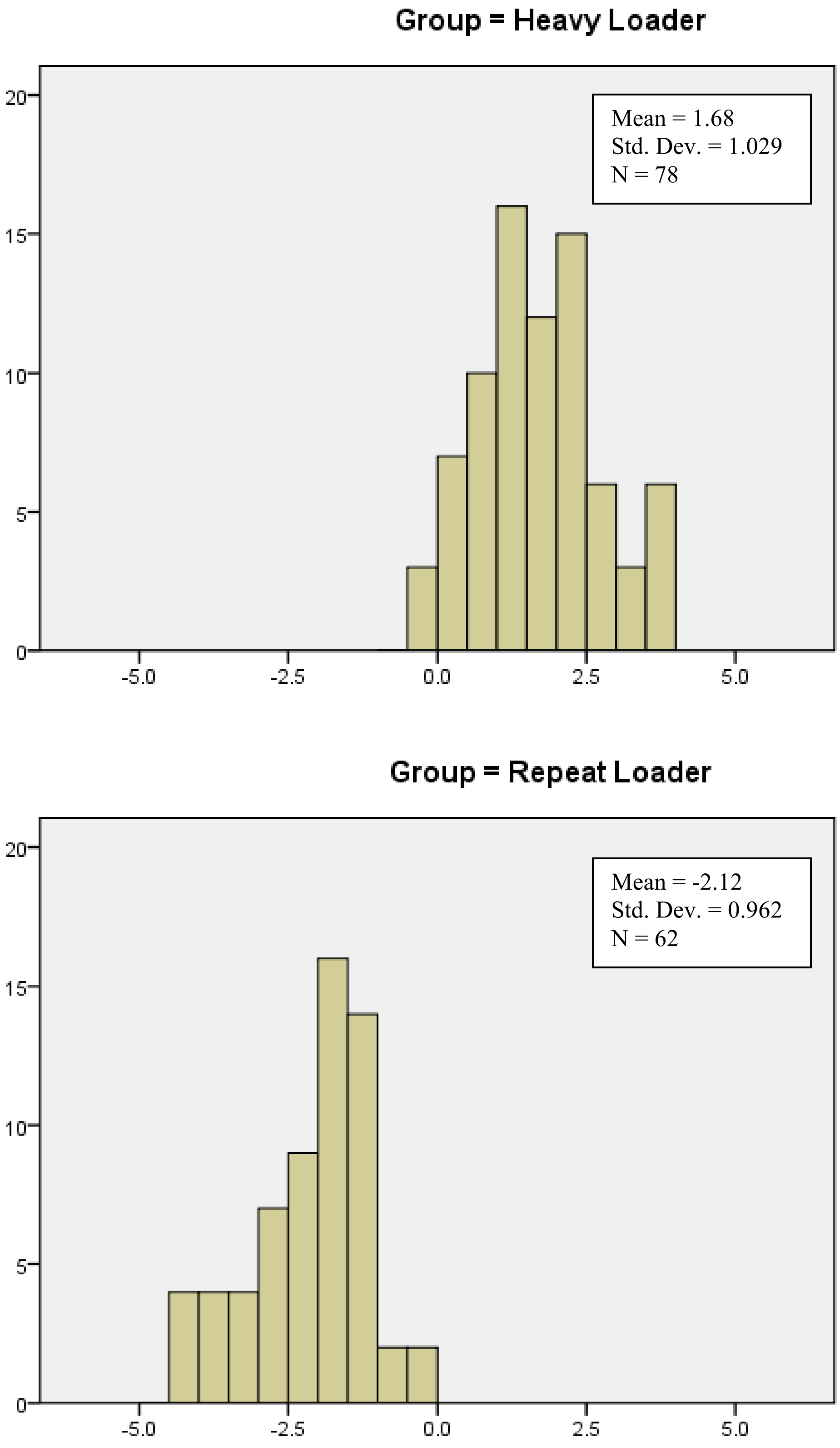

**Fig. 1.2**. Separate group graphs for canonical discriminant function 1.

*TABLE 1.12*. Spearman's rank correlations between the discriminant scores and each variable used in the analysis.

| | | Dscore | | | Dscore |
|---|---|---|---|---|---|
| **CorpW** | Correlation Coefficient | .307** | **ArchW** | Correlation Coefficient | .561** |
| | Sig. (2-tailed) | .000 | | Sig. (2-tailed) | .000 |
| | N | 140 | | N | 140 |
| **CorpD** | Correlation Coefficient | .380** | **CondW** | Correlation Coefficient | -.005 |
| | Sig. (2-tailed) | .000 | | Sig. (2-tailed) | .952 |
| | N | 140 | | N | 140 |
| **SymW** | Correlation Coefficient | .441** | **CondL** | Correlation Coefficient | -.155 |
| | Sig. (2-tailed) | .000 | | Sig. (2-tailed) | .068 |
| | N | 140 | | N | 140 |
| **SymD** | Correlation Coefficient | .062 | **MassIA** | Correlation Coefficient | -.427** |
| | Sig. (2-tailed) | .469 | | Sig. (2-tailed) | .000 |
| | N | 140 | | N | 140 |
| **GlenPG** | Correlation Coefficient | -.639** | **FacProj** | Correlation Coefficient | -.046 |
| | Sig. (2-tailed) | .000 | | Sig. (2-tailed) | .591 |
| | N | 140 | | N | 140 |
| **MedPIA** | Correlation Coefficient | .724** | **MPm1** | Correlation Coefficient | .851** |
| | Sig. (2-tailed) | .000 | | Sig. (2-tailed) | .000 |
| | N | 140 | | N | 140 |
| **TempFA** | Correlation Coefficient | .053 | **MASSm1** | Correlation Coefficient | .660** |
| | Sig. (2-tailed) | .533 | | Sig. (2-tailed) | .000 |
| | N | 140 | | N | 140 |
| **ZygA** | Correlation Coefficient | -.529** | **TEMPm1** | Correlation Coefficient | .718** |
| | Sig. (2-tailed) | .000 | | Sig. (2-tailed) | .000 |
| | N | 140 | | N | 140 |
| **RamH** | Correlation Coefficient | -.298** | **MASSinc** | Correlation Coefficient | .151 |
| | Sig. (2-tailed) | .000 | | Sig. (2-tailed) | .075 |
| | N | 140 | | N | 140 |
| **MandL** | Correlation Coefficient | -.640** | **TEMPinc** | Correlation Coefficient | .179* |
| | Sig. (2-tailed) | .000 | | Sig. (2-tailed) | .034 |
| | N | 140 | | N | 140 |

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

# DISCUSSION

Although the main goal of this study was to investigate the relationship of jaw dimensions with heavy and repetitive loading, the discriminant function also provides the opportunity to asses the relative importance of the independent variables in classifying each group. The discriminant function analysis demonstrated that the following variables combined contribute 100% of between-group variability: medial pterygoid leverage at $M^1$, medial pterygoid insertion angle, temporalis leverage at $M^1$, anteroposterior length of the temporal articular surface, masseter insertion angle and temporalis leverage at incisor. A Spearman's rank correlation matrix showed that the following are significantly positively correlated with the discriminant function (i.e., correlated with "heavy loading"): medial pterygoid insertion angle, dental arcade width, medial pterygoid leverage at $M^1$, masseter leverage at $M^1$, temporalis leverage at $M^1$, temporalis leverage at incisor. The following variables are significantly negatively correlated with the discriminant function (i.e., correlated with "repetitive loading"): anteroposterior length of the temporal articular surface, zygomatic arch size (i.e., the product of zygomatic arch width and depth modeled as an ellipse), ascending ramus height above the occlusal plane, mandible length and masseter insertion angle.

## Variables related to heavy loading

***Medial pterygoid insertion angle.*** This variable represents the degree to which the line of action of the medial pterygoid muscle is oblique or vertical. The line of action is drawn between the origin on the medial aspect of the lateral pterygoid plate and the insertion on the inner surface of the mandibular angle. Antón (1996) predicted that *Macaca fuscata*, a taxon known to feed regularly on hard and tough foods, would have a larger masseter insertion angle when compared to other macaque taxa in her sample. Larger insertion angles for both masseter and medial pterygoid result in a more oblique force vector which increases the degree of side-to-side movement during mastication (Hylander, 1979a; Antón, 1996). Lateral excursion of the mandible is known to increase when chewing stiff or hard tissues (Agrawal et al., 2000). Therefore, a larger medial pterygoid insertion angle is likely advantageous for "heavy loading" taxa in that it increases grinding efficiency of hard foods.

***Dental arcade width.*** The constrained lever model (Greaves, 1978) assumes that the mammalian temporomandibular joint is poorly-suited to resist tensile forces. Forceful biting in the molar region increases the chance of temporomandibular joint distraction by shifting the muscle resultant vector outside of the "triangle of support" formed by the bite point and both mandibular condyles (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1998, 1999). Incisor, canine and premolar bites form triangles that contain the muscle resultant vector and do not put the temporomandibular joint at risk. Narrowing the dental arcade facilitates increased balancing side muscle force while reducing the risk of temporomandibular joint distraction during forceful molar biting (Hylander, 1975; Smith, 1978; Spencer, 1998, 1999). Therefore, it is no surprise that a narrow dental arcade is one characteristic of the "heavy loading" sample.

***Jaw adductor leverage.*** Great medial pterygoid leverage at $M^1$, masseter leverage at $M^1$, temporalis leverage at $M^1$ and temporalis leverage at incisor characterize heavy loaders.

Likewise, the four additional leverage ratios which were removed from the discriminant function analysis (i.e., medial pterygoid leverage at the canine and incisor, masseter leverage at the canine and temporalis leverage at the canine) due to the strong correlation with the other leverage variables included in the analysis are also characteristic of heavy loading primates. These all represent the mechanical advantage of the jaw adductors and can therefore be treated as a group. Increasing the leverage of the jaw adductors increases the amount of muscle force that can be converted into bite force (Hylander, 1979a; Ravosa, 1990; Spencer and Demes, 1993; Spencer, 1998, 1999; Wright, 2005a). The fact that these variables are all positively correlated with the discriminant function adds further support to the conclusion that the mechanical advantage of the jaw adductors is beneficial for primates that engage in forceful biting. Norconk et al. (2008) demonstrated that their “hard-object feeders” have the highest mechanical advantage for the jaw adductors among their sample of platyrrhine taxa. More folivorous taxa in their sample, such as *Alouatta palliata* and *A. seniculus*, showed the lowest mechanical advantage for these muscles which led these authors to conclude that leverage in not an important adaptation among platyrrhine folivores.

### Variables related to repetitive loading

***Anteroposterior length of the temporal articular surface.*** An increase in the anteroposterior length of the temporal articular surface may be more related to increased rotational excursion of the mandible during wide gape than to bite force magnitude (Vinyard et al., 2003). Nonetheless, this variable was expected to be related to the dissipation of large joint reaction forces during heavy loading. It is unlikely that the repetitive loaders examined in this study require large gape during feeding so this is not a likely explanation for this result. However, Wall (1999) found a relationship between height of the ascending ramus and the degree of sagittal sliding of the mandibular condyles over the preglenoid plane. The elongated temporal articular surface area in these taxa is therefore interpreted as being related to an increase in the fore-aft movement of the condyles resulting from a tall mandibular ramus (see below).

***Zygomatic arch size.*** Large zygomatic arches were expected to occur in the heavy loading sample due to their increased reliance on bite force production. There is very little discussion about the size or robusticity of the zygomatic arches in the primate masticatory morphology literature. Scapino (1972) and Anapol and Lee (1994) postulated that deep zygomatic arches indicate a preference for the masseter muscle during mastication. The fact that this variable is related to repetitive loading is interesting in light of the fact that the height of the ascending ramus above the occlusal plane, which increases the attachment area for masseter (Freeman, 1988), and masseter insertion angle are two additional variables significantly correlated with repetitive loading, *not* with heavy loading (see below).

***Ascending ramus height above the occlusal plane.*** An increase in height of the ascending ramus above the occlusal plane was expected for heavy loading primates. Increases in this dimension expands the attachment area for masseter, as well as medial pterygoid (Freeman, 1988). However, a high ramus is also associated with a more even distribution of occlusal forces along the postcanine tooth row (De Wolff-Exalto, 1951;

Maynard Smith and Savage, 1959; Davis, 1964; Turnbull, 1970; Greaves, 1974; Ward and Molnar, 1980), whereas low condyles are associated with scissor-like occlusion of the tooth rows (De Wolff-Exalto, 1951; Greaves, 1974). By uniformly distributing occlusal forces along the tooth row, repetitive loaders might reduce the pressure experienced in the mandibular corpora and may explain, in part, why they do not exhibit enlarged jaw proportions relative to hard-object feeding primates.

Hylander (1979a) and Bouvier (1986a,b) suggested that reducing the strain differential in the postcanine corpus by increasing the height of the ramus may decrease the risk of fatigue failure associated with repetitive loading of low quality vegetation. High rami may not be necessary for heavy loading primates due to an increase in the leverage for the jaw adductors as well as a relative narrowing of the dental arcade. Lower condyles in heavy loaders may even be advantageous since the resulting "scissor-like" occlusion concentrates bite force on food objects situated on the postcanine tooth row.

***Mandible length.*** Assuming that the locations of the jaw adductors remain the same, decreasing the anteroposterior length of the mandible increases the mechanical advantage of the jaw adductor muscles and decreases parasagittal bending loads experienced in the mandibular corpora (Hylander, 1979a; Bouvier, 1986a,b; Antón, 1996). The negative correlation between mandible length and the discriminant function indicates that repetitive loaders are characterized by longer mandibles compared to taxa which require greater bite force. This result adds support to previous findings that primates feeding on harder foods typically exhibit anteroposteriorly short jaws (e.g., Bouvier, 1986a,b; Antón, 1996).

***Masseter insertion angle.*** One result of a great bizygomatic breadth compared to bigonial breadth is a larger insertion angle for the masseter muscle in repetitive loaders. As mentioned above, this results in a more oblique force vector which, in turn, increases the horizontal component of the bite force (Hylander, 1979a; Antón, 1996). An increase in the insertion angle for masseter was expected to occur among the heavy loading sample because transverse jaw movements are expected among taxa which feed on stiff or hard tissues (Agrawal et al., 2000). Furthermore, Walker and Murray (1975) suggested that leaves are more effectively broken down through vertical shear as opposed to transverse grinding. Moreover, the steep cusps of folivorous primates may interlock and limit the degree of side-to-side movement possible (Hylander, 1979a, 1988). This result may be related to the more flaring zygomatic arches in repetitive loaders. Although infratemporal fossa area does not discriminate between the two dietary groups, indicating that they have roughly the same amount of jaw adductor muscle mass contained within this space, a comparison between just the infratemporal fossa depths reveals that repetitive loaders have significantly deeper fossae than heavy loaders ($U = 1773$; $P = 0.003$; Mann-Whitney *U*-test). This result also suggests that a more oblique masseter insertion angle may not increase the degree to which the basal aspect of the corpus is everted by the contraction of this muscle and may not influence the buccolingual width of the corpus as previously suggested (Hylander, 1979a).

## Jaw proportions and diet

The primary objective of this study was to assess the relationship between jaw proportions and heavy versus repetitive loading. Results suggest that corpus width, corpus depth and symphysis width are structural adaptations for resisting heavy loads. The presence of such adaptations are likely related to powerful bending and twisting moments that occur during the mastication of hard foods. Symphysis depth is not necessarily indicative of either loading regime. None of the corpus or symphysis proportions were related to increased load frequency.

***Corpus width.*** During mastication and anterior tooth biting both mandibular corpora are twisted about their long axes. Axial torsion is the result of the lateral location of the masseter's origin on the zygomatic arch and the medial location of its insertion along the angle of the mandible. The oblique line of action of the masseter's muscle force inverts the alveolar corpus and everts the basal corpus (Hylander, 1979a). Increasing the mediolateral width of the corpus has traditionally been viewed as the most effective way to resist torsional loads (Hylander, 1979a,b, 1981, 1988; Ravosa, 1991, 1996; Daegling, 1992; Ravosa and Hylander, 1994).

***Corpus depth.*** Both mandibular corpora are bent in a parasagittal plane during mastication and anterior tooth biting as a result of the bilateral jaw adductor muscle force (Hylander, 1979a,b, 1988). Parasagittal bending is increased relative to axial torsion when biting at the anterior teeth. Most studies have concluded that a relative increase in the depth of the corpus is the most efficient way to resist this load (Hylander, 1979a,b, 1988; Bouvier, 1986a,b; Ravosa, 1991, 1996; Daegling, 1992; Ravosa and Hylander, 1994; Taylor, 2006a; Daegling and McGraw, 2007). Taylor (2002) hypothesized that the most folivorous of the African apes would exhibit the deepest corpora in her sample.

However, this expectation was not met, which led her to conclude that "there is not a consistent link between deep corpora and folivory" (Taylor, 2002:152). The results from the present study indicate that a deep corpus is *not* related to increased load frequency which may explain Taylor's (2002) results.

***Symphysis width.*** One interesting result of this study concerns symphysis width. This variable is usually associated with resistance to lateral transverse bending, or "wishboning" stress resulting from the laterally directed jaw adductor muscle force plus the late activity of the balancing side deep masseter during the terminus of the masticatory power stroke. This produces tensile forces along the lingual aspect of the symphysis and compression along its labial aspect (Hylander et al., 1987; Hylander and Johnson, 1994; Ravosa, 1996). Increasing the labiolingual thickness of the symphysis has been linked with strengthening resistance to this load (Hylander, 1984, 1985).

Although several studies, particularly those on New World monkeys, have identified a clear-cut relationship between symphysis width and increased load magnitude (e.g., Daegling, 1992; Anapol and Lee, 1994), a considerable number of other studies have not (Daegling and McGraw, 2001, 2007, 2009; Taylor et al., 2008; Koyabu and Endo, 2009; see also Chapter 2, this study). Daegling and McGraw (2007) tested the hypothesis that *Cercocebus agilis* would exhibit structurally stiffer symphyses relative to *Lophocebus albigena* based on the observation by Shah (2003) that the former taxon engages in more frequent and powerful postcanine crushing of hard seeds and nuts. They found that the biomechanical properties of the symphysis failed to distinguish the two despite an apparent divergence in feeding behavior. Similarly, Daegling and McGraw

(2001) found that symphysis proportions did not distinguish seed-eating colobines from those which do not regularly consume seeds. Identical results were met when using an asymmetric bending model of the symphysis (Daegling and McGraw, 2009). Additionally, Koyabu and Endo (2009) found that symphysis width was actually shorter in seed-eating colobines compared consumers of young leaves.

Several explanations for the inconsistent relationship between symphysis width and diet have been advanced. One possibility is that allometric increases in symphyseal curvature, which results in elevated wishboning stresses at the symphysis, may have more to do with symphysis thickness than adaptations to a particular diet (Ravosa, 1996). Enlarged symphyses have also been argued to be a function of enlarged canines (Wood, 1978; Smith et al., 1983; Dean and Beyon, 1991; Daegling and McGraw, 2001; Wood and Strait, 2004; Plavcan and Daegling, 2006; see also Chapter 2, this study).

The discriminant function found symphysis width to be the most highly correlated single jaw dimension that differentiates heavy loaders from repetitive loaders. One explanation for the frequent inconsistent relationship between diet and symphysis width might be related to the lack of food material property data (but see Chapter 2, this study). These data are crucial when attempting to link form to function in the masticatory system and are unfortunately vastly underrepresented in the primate ecology literature (Lucas, 2004).

Although neither Daegling and McGraw (2001) nor Koyabu and Endo (2009) found seed-eating colobines to exhibit the expected symphyseal width, both of these studies had the underlying assumption that the seed-eating taxa require increased bite force relative to those taxa which do not eat seeds. This may not always be the case. As

Lucas has pointed out (Lucas and Teaford, 1994; Lucas, 2004), there is no uniform material property among the broad range of seeds consumed by primates. Seeds may vary from very hard to very soft and pliable. Lucas and Teaford (1994) noted specifically that the seeds eaten by some colobines consist of a thin and flexible outer coating that contains tougher tissues. These "tough seeds" differ from those eaten by hard-object consumers, such as *Cebus apella*, and may not require elevated masticatory loads.

Similarly, the hypotheses proposed by Daegling and McGraw (2007) rely on the assumption that *Cercocebus agilis* engages in more frequent and forceful mastication of hard seeds and nuts, while *Lophocebus albigena* engages in more frequent and forceful incision of hard fruits. These assumptions were based on field observations discussed in Shah (2003) rather than food material properties or chewing frequency data for different food objects. Basing biomechanical hypotheses such as the ones proposed by Daegling and McGraw (2007) on field observations alone may be problematic.

Another potential drawback of the Daegling and McGraw (2007) study was the inclusion of multiple species of *Lophocebus* and *Cercocebus*. The authors acknowledged the importance of species-level differences but chose to focus on the generic level due to small sample sizes and the purported importance of genus-level distinctions. However, for some genera, there are significant differences between included species with observed divergences in dietary habits in their feeding biomechanics. This is true for *Cebus* (Bouvier, 1986b; Cole, 1992; Daegling, 1992; Wright, 2005a), *Macaca* (Takahashi and Pan, 1994; Antón, 1996) and *Gorilla* (Taylor, 2002, 2003, 2005). Therefore, it may not be surprising that some of the predictions made by Daegling and McGraw (2007) were not supported.

***Symphysis depth.*** The lack of a strong relationship between symphysis depth and either loading regime was a somewhat surprising result. Hylander (1979a) argued that the deep corpora of colobine monkeys is related to the relatively large number of chewing cycles per day, whereas increased symphysis depth has been associated with coronal bending of the symphysis. Axial torsion of the mandibular corpora produces compression along the alveolar border of the symphysis and increased tension along its basal aspect (Hylander, 1984, 1985, 1988). This bending is thought to be effectively countered by increasing the dorsoventral depth of the symphysis (Hylander, 1984, 1985, 1988; Daegling, 1992; Ravosa and Hylander, 1994). Coronal bending of the symphysis is also expected to be exacerbated during incisor and canine biting. Thus, one might expect to find a relationship between increased load magnitude and depth of the symphysis.

Several studies have observed an inconsistent relationship between symphysis depth and diet. For example, Hylander (1988) concluded that the jaws of "robust" australopithecines were adapted to resist powerful bending and torsion associated with forceful mastication of exceedingly hard or tough foods. However, he found that they possess relatively shallow symphyses. Likewise, Taylor (2002) rejected the hypothesis that African apes with a more obdurate diet exhibit relatively deeper symphyses. This led her to conclude that "deeper symphyses are not systematically associated with species hypothesized to experience higher torsion based on diet" (2002:147). In fact, symphysis depth is not significantly different for heavy loaders and repeat loaders in this study and the data ranges for the two groups overlap extensively (Mann-Whitney *U*-test; $U = 2316$; $P = 0.67$).

Although the results of this study suggest that corpus width, corpus depth and symphysis width are greater in heavy loaders than in repeat loaders, the correlation coefficients supporting these conclusions are rather low. This may be due in part to the somewhat simplistic view that jaw form is governed by load magnitude, which is approximated by food hardness, or load frequency, which is approximated by food toughness and nutritional value. Indeed, this issue may be more complex than a simple dichotomous relationship. The square root of the product of the elastic modulus and fracture toughness may be the best index for describing the stress-limited pattern of food breakdown, whereas the square root of the elastic modulus divided by fracture toughness may be the most appropriate index for describing a food's displacement-limited properties (Agrawal et al., 1997, 1998; Lucas, 2004). A combination of both the fracture toughness and the elastic modulus of foods may therefore be the most appropriate variable influencing the shape of the corpus and symphysis. Further studies investigating the fracture properties of primate foods should incorporate these values.

None of the corpus and symphysis proportions examined in this study scaled positively with increased chewing frequency. This implies that larger jaws do not necessarily provide greater resistance to fatigue stress during cyclical jaw loading. Hert et al. (1969, 1972) concluded that cyclical loading induces bone remodeling to resist fatigue fractures which may coalesce during repetitive chewing. He suggested that this process maintains the structural integrity of jaw form while minimizing bone weight. Bouvier and Hylander (1981) tested this hypothesis by comparing the degree of bone remodeling in the mandibular cortex of two groups of monkeys which were fed diets that differ in the amount of processing time and number of chews required. They found that the cyclical loading group exhibited more extensive Haversian remodeling of cortical bone and concluded that cyclic stress was an important factor in bone remodeling and fatigue resistance. These studies suggest that primates that load their mandibles more frequently may protect against fatigue damage via Haversian remodeling of mandibular cortical bone. This might explain the poor relationship between jaw enlargement and repetitive loading in primates. The buildup of small microcracks in the mandible may be easily safeguarded via bone remodeling, while large bending and twisting loads might only be effectively countered through enlargement of the jaw itself.

One potential limitation of the present study is the use of external linear measurements where cross-sectional data might be more appropriate. External linear dimensions provide only first-order approximations of cross-sectional geometry and may not faithfully track bending and torsional moments imposed on the mandible (Daegling, 1989, 2007; Daegling and Hylander, 1998). Daegling (2007) has recently argued that corpus breadth in particular is an unreliable approximation for torsional stiffness and strength and that overall corpus size (i.e., the product of corpus width and depth modeled as an ellipse) might be a more reliable proxy for describing the resistance to masticatory forces than are single dimensions. He does, however, note that corpus width is not completely uninformative; it simply might not be the most reliable indicator of torsional resistance. The relationship between the discriminant function and corpus "size" observed here attests to these conclusions: although all three corpus dimensions are positively correlated with the function, the relationship with corpus size is by far the strongest ($r_s = 0.471$; $P<0.0001$).

## Uninformative variables

Infratemporal fossa area, mandibular condyle width, mandibular condyle length and facial projection do not discriminate between heavy and repetitive loaders. The first three were expected to be relatively greater among the heavy loading sample, whereas facial projection was expected to be greater among the repetitive loading sample. These variables, when examined alone, may not be informative regarding functional differences between taxa or when attempting to draw dietary inferences from fossil taxa.

***Infratemporal fossa area.*** In life, the infratemporal fossa is filled largely by the temporalis muscle. The area of the fossa is correlated with the temporalis physiological cross-sectional area (Corrucini and Ciochon, 1979; Corrucini, 1980; Weijs and Hillen, 1984; Demes et al., 1986; Perry, 2008). The physiological cross-sectional area of skeletal muscle, which is proportional to force exerted (Weijs and Hillen, 1984, 1986; Maughan et al., 1986; Weijs, 1989; Weijs and van Ruijen, 1990), is also suggested to increase in mammals which require higher occlusal bite force (e.g., Langenbach et al., 2003; Taylor et al., 2008). Therefore, primates which feed on hard foods, such as seeds or nuts, were expected to have more spacious infratemporal fossae to accommodate the temporalis muscle.

One reason for the lack of a difference between the dietary groups examined here may relate to the histology of the jaw adductor muscle fibers. Skeletal muscle contains a mixture of fibers that differ in their force capability, contraction velocity and resistance to fatigue (e.g., Langenbach et al., 2007). Muscles which contain predominately slow twitch, or Type I, fibers contract more slowly, produce less force and are more resistant to fatigue than muscle containing predominately fast twitch, or Type II, fibers (Bottinelli et al., 1996). Fast twitch muscle fibers are less resistant to fatigue but are characterized by rapid contraction and high force production (Herring et al., 1979; Gibbs et al., 1984; Nielsen and Miller, 1988). A fiber-type analysis by Wall et al. (2008) demonstrated that the superficial anterior temporalis of *Papio anubis* was particularly active when chewing hard foods and that this portion of the temporalis muscle has a strikingly high proportion of Type II fibers. They concluded that a high proportion of Type II muscle fibers is associated with rapid and powerful force production during the mastication of hard foods. Muscles also differ in their amount of daily activity based on fiber type composition (Monster et al., 1978; Kernell and Hensbergen, 1998; van Wessel et al., 2005, 2006; Langenbach et al., 2007). Muscles with predominately slow twitch fibers show a greater duration of daily activity (Monster et al., 1978; Kernell and Hensbergen, 1998). These fatigue-resistant fibers are advantageous for mammals that chew for a greater proportion of the day.

Although the size of the infratemporal fossae in heavy and repetitive loaders is comparable, it is likely that primates requiring intermittent high magnitude bites exhibit a higher proportion of fast twitch fibers, whereas primates that engage in a larger number of chewing cycles per day should exhibit a higher proportion of slow twitch fibers. Studies on muscle physiological cross-sectional area, fiber length and pinnation should make an attempt to include fiber typing as well. Unfortunately, fiber-type studies typically require specimens that are frozen immediately after death due to rapid degeneration of the myosin enzymes. These specimens are extremely difficult to obtain when dealing with protected species. However, recent advances in the relatively new technique known as immunocytochemistry allow the study of cadavers preserved in formaldehyde. This technique involves staining of the myosin antibodies that persist after death and are resistant to the degenerative effects of chemical preservatives (Jouffroy and Medina, 2004).

***Condyle length and width.*** Condylar length and width also failed to discriminate between the two dietary groups. The mandibular condyles are loaded in compression during incision and mastication (Hylander, 1979c; Hylander and Bays, 1979). Increasing the condylar surface area dissipates condylar reaction force (Hylander, 1979b; Smith et al., 1983; Herring, 1985; Bouvier, 1986a,b; Wall, 1999). Hylander and Bays (1979) found that peak compressive forces were applied to the lateral aspect of the condyles. Therefore, a relative increase in the mediolateral width of the condyles may be of more interest when examining differences in dietary adaptation related to high magnitude biting. The anteroposterior length of the condyle might be related to increased condylar reaction forces along the posterior aspect of the condyles during forceful anterior tooth biting (Smith et al., 1983; Bouvier, 1986a). Conversely, an increase in the anteroposterior length of the condyles might be more related to increased rotational excursion of the mandible during wide gape (Vinyard et al., 2003). Regardless, both variables were examined and were expected to be relatively greater in the heavy loading sample.

The lack of a significant relationship for these variables is difficult to explain. However, these results are not completely unexpected. Bouvier (1986b) found that the hard-object feeding taxa in her primate sample did not systematically exhibit the expanded condylar dimensions as expected and rejected Smith et al.'s (1983) conjecture that the condyles of *Cercocebus* are adapted to nut-cracking. Morever, Bouvier (1986a) found that *Cebus apella*, a known hard-object consumer (e.g., Izawa, 1975), possesses the widest condyle in her sample but has the smallest condylar area. Similarly, Taylor (2002) found no consistent relationship between condyle shape and diet among African apes.

The results presented here indicate that high magnitude and repetitive compressive loads at the temporomandibular joint engender similar adaptations in mandibular condyle size (see also Vinyard, 1999). This result has implications for the fossil record. Without additional aspects of the masticatory apparatus, condylar surface area alone cannot be considered a reliable indicator of diet. However, when examining finer dietary differences between closely related taxa (e.g., *Pithecia pithecia* and *Chiropotes satanas*; see Chapter 2, this study), comparisons of condylar surface area are likely to lead to robust inferences regarding dietary behavior. This includes differences in load magnitude as well as load frequency. It is also possible that species with disparate diets vary in the orientation of condylar trabeculae (van Ruijven et al., 2002). However, this has yet to be adequately explored.

***Facial projection.*** Lastly, facial projection was expected to be less in heavy loading primates. If there is no change in locations of the jaw adductors, decreasing the anteroposterior length of the face increases the mechanical advantage of the jaw adductors and reduces bending stresses experienced in the face during forceful incision and mastication (Maynard Smith and Savage, 1959; DuBrul, 1977; Hylander, 1977, 1979a; Ward and Molnar, 1980; Proffit et al., 1983; Rak, 1983; Demes et al., 1986; Preuschoft et al., 1986; Weijs, 1989; Ravosa, 1990; Spencer and Demes, 1993; Antón, 1996; Greaves, 2000). The orthognathic face of "robust" australopithecines has long been considered an adaptation for the production and dissipation of heavy occlusal loads (e.g., DuBrul, 1977; Rak, 1983). The results from this study show no consistent differences in facial projection between the two groups. Moreover, the two taxa with the longest faces, *Lophocebus albigena* and *Cercocebus agilis*, are both hard-object feeders. These results suggest that short faces alone do not necessarily confer greater bite force and that the actual position of the jaw adductors themselves must be considered.

## CONCLUSIONS

Several recent studies have noted the unclear biological relationship between enlarged jaw proportions, load magnitude and load frequency (e.g., Daegling and Grine, 2007; Taylor et al., 2008). The primary objective of this study was to discern whether increased mandibular corpus and symphysis dimensions are related to the force produced per bite or the number of loading events per day using a broad sample of durophagous and folivorous primate taxa.

Results show that corpus width, corpus depth and symphysis width are all positively correlated with the discriminant function. This indicates a positive relationship between these dimensions and increased load magnitude. This is consistent with previous studies demonstrating that primates that feed on hard objects have large jaws (e.g., Bouvier, 1986a,b; Hylander, 1988; Cole, 1992; Daegling, 1992). Symphysis depth was not significantly correlated with the discriminant function which indicates that this variable may not be indicative of either loading regime.

Several recent studies have identified apparent discrepancies between symphysis width and diet (e.g., Daegling and McGraw, 2001, 2007; Koyabu and Endo, 2009). However, these studies may be suspect due to the lack of known variation in the physical properties of foods eaten by their sample taxa. Food physical properties are crucial when attempting to interpret the influence of diet on jaw form. Further studies that incorporate these data will likely shed some light on these issues. Differences in canine size may also account for differences in symphysis width that are not clearly the result of divergent dietary habits (Wood, 1978; Smith et al., 1983; Dean and Beyon, 1991; Daegling and McGraw, 2001; Wood and Strait, 2004; Plavcan and Daegling, 2006; see also Chapter 2, this study).

None of the corpus and symphysis proportions are negatively correlated with the discriminant function which indicates that large corpora and symphyses are not the result of increased load frequency and fatigue resistance. Instead, primates that engage in a larger number of daily chewing cycles may protect their jaws against fatigue through more extensive Haversian remodeling of mandibular cortical bone (Hert et al., 1969, 1971; Bouvier and Hylander, 1981). A tall mandibular ramus may also decrease the severity of chewing stresses experienced in the jaw by evenly distributing occlusal forces along the tooth row (De Wolff-Exalto, 1951; Maynard Smith and Savage, 1959; Davis, 1964; Turnbull, 1970; Greaves, 1974; Ward and Molnar, 1980). This may lessen the need for large and strong jaws (Hylander, 1979a; Bouvier, 1986a,b). Primates that differ in the forces produced per bite and the frequency of daily chewing cycles are also likely to exhibit differences in the proportions of slow and fast twitch jaw adductor muscle fibers.

This study also provided the opportunity to explore the relationship between each loading regime and several additional craniomandibular variables suggested to vary with diet. The stepwise discriminant function analysis identified the minimum number of variables which combined explain 100% of between-group variability. These were: medial pterygoid leverage at $M^1$, medial pterygoid insertion angle, temporalis leverage at $M^1$, anteroposterior length of the temporal articular surface, masseter insertion angle and temporalis leverage at incisor. A closer examination of each variable used in the analysis revealed that medial pterygoid insertion angle, dental arcade width, medial pterygoid leverage at $M^1$, masseter leverage at $M^1$, temporalis leverage at $M^1$, temporalis leverage at incisor were all greater in heavy loaders, whereas anteroposterior length of the temporal articular surface, zygomatic arch size, ascending ramus height above the occlusal plane, mandible length and masseter insertion angle were all greater in repeat loaders.

Interestingly, infratemporal fossa area, facial projection and the dimensions of the mandibular condyle did not distinguish heavy loading from repetitive loading primates. These variables, when examined alone, may not be informative regarding functional differences between taxa or when attempting to draw dietary inferences from fossil taxa.

The goal of this study was to shed light on the issue of load magnitude and load frequency. Future studies should make an attempt to record the number chews during the mastication of various foods. It may be unrealistic to gather the number of chewing cycles in wild primates; laboratory studies would be ideal in this regard. Foods with known material properties could be fed to primates in a laboratory setting and the number of chews could be realistically recorded using video analysis. The material properties of foods eaten by primates in the wild could then be measured and an estimate of the number of chews can be made. Future studies should also begin recording the square root of the product of the elastic modulus and fracture toughness, as this may be the best index for describing the stress-limited pattern of food breakdown, and the square root of the elastic modulus divided by fracture toughness, which may be the most appropriate index for describing a food's displacement-limited properties (Agrawal et al., 1997, 1998; Lucas, 2004). Lastly, studies of jaw muscle architecture should begin incorporating muscle fiber-typing (e.g., Wall et al., 2008). The proportion of Type I to Type II muscle fibers in primates which diverge in their dietary habits would be beneficial to the question of high magnitude versus repetitive loading.

# CHAPTER 2

Extant pitheciines (*Pithecia* spp., *Chiropotes* spp., *Cacajao* spp.) are among the most frugivorous of all New World monkeys, with fruit composing up to 90% of the diet (Mittermeier and van Roosmalen, 1981; van Roosmalen et al., 1981, 1988; Ayres, 1989; Kinzey and Norconk, 1990, 1993). All pitheciines show a preference for unripe fruits over ripe ones (Ayres, 1986, 1989; van Roosmalen et al., 1988; Kinzey and Norconk, 1990, 1993). This type of frugivory, known as "sclerocarpic harvesting" (Kinzey and Norconk, 1990), is uncommon among primates and may reduce dietary stress during periods of fruit scarcity by allowing pitheciines to gain earlier access to fruits (Norconk, 1996; Norconk et al., 2008, in press).

Young seeds are also an extremely important part of the pitheciine diet (e.g., Mittermeier and van Roosmalen, 1981; van Roosmalen et al., 1981, 1988; Ayres, 1986, 1989; Kinzey and Norconk, 1990, 1993; Boubli, 1999). Norconk et al. (in press) note that pitheciines appear to be the only primate group adapted primarily for seed eating. Kinzey and Norconk (1993) found that *Pithecia pithecia*, the white-faced saki, spent 33-88% of feeding time exclusively on seeds. They reported that exclusive seed eating was higher, up to 91% of total feeding time, for *Chiropotes satanas*, the bearded saki. They also note that 99% of time spent feeding on fruits also included the mastication of seeds for both sakis. Ayres (1986) reported that the *Cacajao calvus*, the bald uakari, spent up to 97% of feeding time eating seeds. Boubli (1999) reported that 81% of feeding time for the black-headed uakari, *Cacajao melanocephalus*, was spent eating seeds. Kinzey and Norconk

(1993) have suggested that feeding on unripe fruits and seeds may represent a trade-off between the nutrients and toxins in each type of food. As the fruit ripens and becomes softer, the seeds harden, lose water content and develop higher levels of toxic secondary compounds (Ayres, 1986; van Roosmalen et al., 1988; Kinzey and Norconk, 1990).

Pitheciines exhibit a suite of morphological specializations related to their unique diet. These include large and laterally divergent wedge-shaped canines, laterally compressed and procumbent incisors, molarized fourth premolars, quadritubercular molars with expanded occlusal basins, crenulated enamel, low occlusal relief, strong molar enamel prism decussation, deep and wide mandibles, and large chewing muscles which are shifted anteriorly to increase muscle leverage (Cachel, 1979; Hershkovitz, 1985; Bouvier, 1986a; Kay, 1990; Kinzey, 1992; Anapol and Lee, 1994; Spencer, 1995; Martin et al., 2003; Wright, 2005a; Norconk et al., 2008). However, with the possible exception of tooth morphology (Kinzey, 1992), how these reported dietary adaptations differ among the pitheciines has yet to be adequately explored.

Sclerocarpic harvesting in pitheciines first involves a forceful gouge through the hard pericarp of an unripe fruit using large, robust, wedge-shaped canines and procumbent incisors (Kinzey, 1992). The wedge-like morphology of the canines reduces wear and conserves muscle force by facilitating crack propagation in the opposing food (Lucas and Teaford, 1994). In addition, pitheciine canines splay laterally from the incisal and postcanine tooth rows, which reduces interference with the incisors during fruit puncture (Anapol and Lee, 1994). The procumbent incisors are then used to scoop fruit mesocarp from the inside of fruit husks (Kay, 1990; Kinzey, 1992). The exaggerated degree of incisor procumbency may also enhance gape and increase the force produced by the jaw adductor muscles by reducing the degree of mandibular excursion, thereby reducing masticatory muscle fiber stretch (Rosenberger, 1992). A smaller gape angle may also reduce tensile stresses experienced in the temporomandibular joint during forceful incisal and canine biting (Greaves, 1978). Incision is followed by mastication of the seeds by the postcanine dentition (Kinzey, 1992). Molars with expanded crushing surfaces and low occlusal relief aid in the breakdown of resistant seeds (Kinzey, 1992). The highly crenulated enamel of pitheciines facilitates secondary breakdown of seed particles (Lucas and Luke, 1984) and may also help position the seeds during mastication (Lucas and Teaford, 1994). Although pitheciines have relatively thin enamel, they do exhibit strong molar enamel prism decussation and Hunter-Schreger bands which structurally defend the enamel against crack propagation (Martin et al., 2003).

*Chiropotes* and *Pithecia* are broadly sympatric and are most commonly found in non-flooded forests, whereas *Cacajao* are mainly found in seasonally flooded forests (Cruz Lima, 1944; Fontaine, 1981; Ayres, 1989; Barnett and Brandon-Jones, 1997; Barnett et al., 2005). Fleagle (1984) noted that dietary differentiation is expected to be most apparent between sympatric congeners. Several authors have discussed the importance of differential habitat preference and dietary niche separation in sympatric *Chiropotes* and *Pithecia* (e.g., Mittermeier and van Roosmalen, 1981; Kinzey and Norconk, 1993). For example, *Chiropotes satanas* and *Pithecia pithecia* are able to remain sympatric and reduce competition by exploiting fruits at different stages of ripeness. Physical properties for fruits and seeds eaten by pitheciines (Kinzey and Norconk, 1990, 1993) have demonstrated that seeds masticated by *P. pithecia* have a significantly higher crushing resistance than seeds masticated by *C. satanas*, but fruit

*TABLE 2.1*. Material properties of fruits and seeds eaten by *Pithecia pithecia* and *Chiropotes satanas*. Data from Kinzey and Norconk (1990, 1993).

| | ***Pithecia pithecia*** | ***Chiropotes satanas*** |
|---|---|---|
| **Average fruit puncture resistance** | 1.20 ± 0.29 kg/mm$^2$ | 2.15 ± 0.37 kg/mm$^2$ |
| **Maximum fruit puncture resistance** | 6.77 kg/mm$^2$ | 37.8 kg/mm$^2$ |
| **Average seed crushing resistance** | 8.76 ± 2.13 kg/mm$^2$ | 4.63 ± 0.55 kg/mm$^2$ |
| **Maximum seed crushing resistance** | 37 kg/mm$^2$ | 9.1 kg/mm$^2$ |

pericarp incised by *Chiropotes* has a higher puncture resistance than fruit incised by *Pithecia* (Table 2.1). In addition, although *P. pithecia* masticates seeds that are approximately the same hardness as the fruits incised by *C. satanas*, Kinzey and Norconk (1993) reported that during times of fruit scarcity *P. pithecia* consumes a larger amount of flowers, whereas *C. satanas* falls back on even harder fruits.

Although food physical properties are not currently available for *Cacajao*, Ayres (1986, 1989) reported that *Cacajao calvus* prefers fruits with extremely hard husks. Similarly, Lehman and Robertson (1994) and Boubli (1999) reported that the top three fruits eaten by *Cacajao melanocephalus* are covered by very hard shells. Furthermore, several studies have noted that *Cacajao melanocephalus ouakary* feeds predominantly on hard fruits (Barnett and da Cunha, 1991; Barnett et al., 2000, 2002). However, Barnett et al. (2005) found that the majority of fruits eaten by golden-backed uakaris were of either soft or medium hardness and that only 37% of fruits were hard-husked. This finding led them to conclude that *Cacajao* may not rely on hard-shelled fruits as much as previously thought.

*Cacajao* is not sympatric with either *Pithecia* or *Chiropotes* and is thought to occupy a near competition-free hard-fruit-feeding niche (Kinzey, 1992; Barnett and Brandon-Jones, 1997). Additionally, Ayres (1989) noted that the diets of *Chiropotes* *satanas* and *Cacajao calvus* were strikingly similar and suggested that this may explain their mutual avoidance of each other. Conversely, Kinzey (1992) suggested that *Pithecia*-*Chiropotes*-*Cacajao* represents a morphocline of increasing dental specialization for harvesting unripe fruits. Likewise, previous studies have demonstrated that, compared to *Chiropotes*, *Pithecia* possesses relatively small canines (Kay, 1990; Kinzey, 1992; Anapol and Lee, 1994) and a gracile mandible (Anapol and Lee, 1994; Norconk et al., 2008).

## Morphological predictions

Pitheciine monkeys provide an ideal test case for morphological predictions related to dietary adaptation. Their well-established monophyly (Ford, 1986; Schneider and Rosenberger, 1996) largely eliminates the confounding effect of separate phylogenetic history (Felsenstein, 1985; Harvey and Pagel, 1991; Miles and Dunham, 1993; Garland and Adolph, 1994). Comparing closely-related species largely eliminates phylogenetic "noise" and helps highlight differences which reflect the mechanical demands of a presumed behavioral deviation (Coddington, 1988). In addition, size-related differences are most likely trivial due to the fact that living pitheciines occupy a narrow body mass range (1.94 - 3.45 kg; Smith and Jungers, 1997).

Here, I hypothesize that *Chiropotes satanas* exhibits a number of morphological specializations associated with forceful and more frequent incision and anterior tooth biting of hard fruits. I also hypothesize that *Pithecia pithecia* exhibits features associated with powerful postcanine crushing of hard seeds. Heavy loads during mastication likely favor many of the same adaptations expected for heavy loads during incision. For example, the mechanical advantage of the jaw adductors should be favorable in both. This leads to the expectation that the face and mandible will be shorter in both. Therefore it is difficult to generate mutually exclusive predictions for *Chiropotes* and *Pithecia*.

Nevertheless, one might expect some morphological differences between skulls adapted to masticatory loading versus those adapted to incisal loading. For example, *in vivo* studies have demonstrated that mastication produces lateral transverse bending of the symphysis, whereas coronal bending of the anterior corpus is more pronounced during incision (Hylander, 1981, 1984). Additionally, primates that emphasize incision are typically expected to exhibit deeper mandibular corpora compared to those that engage in this behavior less (Taylor, 2006).

Differences related to incision versus mastication have been discussed using extant mangabeys as a model. Mangabeys have long been considered hard-object consumers (Chalmers, 1968). However, Shah (2003) observed that *Lophocebus albigena* engages in more frequent and powerful incision of hard fruits compared to sympatric *Cercocebus agilis*, whereas *C. agilis* engages in more frequent and powerful postcanine crushing of hard nuts and seeds. Singleton (2004, 2005) found that *Lophocebus* exhibited features related primarily to increasing the mechanical advantage of the jaw adductors, thereby implying a greater necessity for increased jaw adductor leverage during incisal loading. Daegling and McGraw (2007) demonstrated that, as expected, *Lophocebus* exhibited a deeper postcanine corpus than *Cercocebus*. However, their predictions of a thicker symphysis in *Cercocebus* and deeper symphysis in *Lophocebus* were not supported.

If masticatory loads are equal to incisal loads, then adaptations to resist those loads are likely more pronounced in species that emphasize incision. Incision is at a mechanical disadvantage compared to mastication because whereas the moment arms of the muscles are unchanged, the bite moment arm is greatly increased. Primates that emphasize powerful incision are expected to have especially mechanically advantageous jaw adductors compared to primates that emphasize equally powerful mastication. This may be achieved in tandem with very forceful jaw adductors (more active and/or possessing greater cross-sectional areas). Furthermore, jaw length beyond the anterior attachments of the jaw adductor muscles is expected to be less relative to jaw depth in incisal loaders in order to resist a greater expected degree of bending stress.

For many morphological traits that are favorable to both anterior and posterior loading, it is unclear which of *Chiropotes* or *Pithecia* should outperform the other. Data on the forces experienced during incision and mastication in these primates would be beneficial in this regard. However, the only relevant data available for pitheciines are the material properties of the foods they eat (Kinzey and Norconk, 1990, 1993). These data do not allow us to compare the forces during incision to those during mastication because puncture resistance data cannot be compared to crushing data. Furthermore, it is difficult to compare the degree of gape at ingestion and mastication in these taxa.

With these limitations in mind, I offer the following predictions:

***Prediction 1:*** **Chiropotes satanas** ***has a relatively deeper mandibular corpus than*** **Pithecia pithecia.** Both mandibular corpora are bent in the parasagittal plane during mastication and anterior tooth biting as a result of the bilateral jaw adductor muscle force

(Hylander, 1979a,b, 1988). Parasagittal bending is increased relative to axial torsion when biting at the anterior teeth. Increasing the depth of the corpus is the most efficient way to resist this load (Hylander, 1979a,b, 1988; Bouvier, 1986a,b; Ravosa, 1991, 1996; Daegling, 1992; Ravosa and Hylander, 1994).

***Prediction 2:* C. satanas *has a relatively deeper mandibular symphysis than* P. pithecia.** Axial torsion during incision and anterior tooth biting also results in vertical bending of the mandibular symphysis in the coronal plane. This produces compression along the alveolar border of the symphysis and increased tension along its basal aspect (Hylander, 1984, 1985, 1988). This is effectively countered by increasing the dorsoventral depth of the symphysis (Hylander, 1981, 1984, 1985, 1988; Daegling, 1992; Ravosa and Hylander, 1994).

***Prediction 3*: P. pithecia *has a relatively thicker mandibular symphysis than* C. satanas.** The laterally directed jaw adductor muscle force plus the late activity of the balancing side deep masseter during the terminus of the masticatory power stroke imposes lateral transverse bending, or “wishboning,” stress on the mandibular symphysis. This produces tensile forces along the lingual aspect of the symphysis and compression along its labial aspect (Hylander et al., 1987; Hylander and Johnson, 1994; Ravosa, 1996). Increasing the labiolingual thickness of the symphysis strengthens resistance against lateral transverse bending associated with the forceful mastication of seeds (Hylander, 1984, 1985). The increased proportion of leaves in the diet of *Pithecia*

(Kinzey and Norconk, 1993) might exacerbate lateral transverse bending loads and further necessitate a thicker symphysis.

***Prediction 4: The articular surface area of the mandibular condyle is larger in* C. satanas *than in* P. pithecia.** The mandibular condyles are loaded in compression during incision and anterior tooth biting (Hylander, 1979c; Hylander and Bays, 1979). Compressive joint loads are expected to be highest during anterior bites because these require greater amounts of muscle force to achieve the same measure of bite force produced during postcanine biting (cf. Spencer, 1998, 1999). Larger articular surface area provides an expanded surface for the dissipation of this compressive stress (Hylander, 1979b; Smith et al., 1983; Herring, 1985; Bouvier, 1986a,b; Wall, 1999).

***Prediction 5:* C. satanas *has a relatively shorter mandible than* P. pithecia.** If there is no change in the locations of the jaw adductors, then a shorter jaw increases bending rigidity and increases the mechanical advantage of the jaw adductors at all bite points (Hylander, 1979a; Bouvier, 1986a,b; Antón, 1996). However, bite force production declines at wider gapes (i.e., during incision) when the jaw muscle fibers are stretched beyond their resting length (Dechow and Carlson 1982, 1986, 1990). This becomes more of a problem for taxa which require forceful incisor and canine bites. Spencer (1998, 1999) demonstrated that incisal loads fell below those at the postcanines. Therefore, a shorter jaw is expected to be more advantageous for *Chiropotes* than *Pithecia*.

***Prediction 6:* C. satanas *has greater anterior leverage for masseter, temporalis and medial pterygoid than* P. pithecia.** Increasing the leverage of the jaw adductors increases the amount of muscle force that can be converted into bite force (Hylander, 1979a; Ravosa, 1990; Spencer and Demes, 1993; Spencer, 1998, 1999; Wright, 2005a). Although *P. pithecia* is expected to produce higher levels of postcanine bite force, this is not expected to result in changes in the relative anteroposterior positions of the jaw adductors. This is consistent with Greaves' (1978) constrained lever model that states that the mammalian temporomandibular joint is poorly suited to resist tensile forces. Forceful biting in the molar region increases the chance of temporomandibular joint distraction by shifting the muscle resultant vector outside of the triangle of support formed by the bite point and both mandibular condyles (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1998, 1999). Instead, *Pithecia* is expected to exhibit a relative narrowing of the dental arcade (see Prediction 7).

***Prediction 7:* P. pithecia *has a relatively narrower mandibular dental arcade than* C. satanas.** The constrained lever model (Greaves, 1978) assumes that the mammalian temporomandibular joint is poorly suited to resist tensile forces. Narrowing the dental arcade facilitates increased balancing side muscle force while reducing the risk of temporomandibular joint distraction during forceful molar biting (Hylander, 1975; Smith, 1978; Spencer, 1998, 1999).

***Prediction 8:* C. satanas *has a relatively smaller* $M_3$ *occlusal surface area than* P. pithecia.** Shifting the attachment of the jaw adductor muscles anteriorly increases leverage at the anterior teeth but puts the temporomandibular joint more at risk of distracting during forceful molar biting. This reduces the functional area of the molar tooth row and is expected to result in a decrease in third molar occlusal surface area in taxa that produce forceful anterior bites (Spencer and Demes, 1993; Wright, 2005a).

In addition to these predictions I compare *Cacajao calvus* and *Cacajao melanocephalus* to *Chiropotes satanas* to investigate if *Cacajao* exhibits craniomandibular adaptations consistent with Kinzey's (1992) morphocline of increasing dental specialization. If *Cacajao* does, in fact, incise fruits harder than those consumed by *C. satanas,* then it should exhibit the most exaggerated specialization for sclerocarpic harvesting among pitheciines. It should also exhibit less exaggerated features related to high magnitude postcanine loading. This is because the fruits eaten by *Cacajao* are presumably at an earlier stage of ripeness and should contain relatively softer seeds than those eaten by *Chiropotes* (Ayres, 1986; van Roosmalen et al., 1988; Kinzey and Norconk, 1990). Alternatively, relaxed food competition may allow *Cacajao* to procure a wider range of fruits at varying stages of ripeness, including those preferred by *Chiropotes* (Ayres, 1989). Access to these food sources may result in adaptations to foods with mechanical properties comparable to those eaten by *Chiropotes*.

## MATERIALS AND METHODS

### Sample

The sample includes crania and mandibles of *Pithecia pithecia* (n = 22) and *Chiropotes satanas* (n = 19). In addition, a comparative sample of *Cacajao calvus* (n =

10) and *Cacajao melanocephalus* (n = 5) was measured. All specimens were wild-shot adult males with third molar in occlusion (*sensu* Cheverud, 1981). Individuals with high levels of dental attrition, pathology or alveolar resorption were excluded. All measurements were taken using Mitutoyo digital calipers (500 series) accurate to 0.01 mm, except for facial projection and anterior jaw adductor leverage. The latter were measured from lateral and basicranial photographs in ImageJ (United States National Institutes of Health, public domain; Abramoff et al., 2004). All measurements are listed in Table 2.2.

## Shape variables

Corpus height, symphysis width, symphysis depth, the square root of condylar surface area and dental arcade width were scaled against mandible length. Mandible length approximates the bite moment arm during anterior tooth biting and is frequently used as a scaling variable in studies of jaw biomechanics (e.g., Hylander, 1979a, 1985, 1988; Bouvier, 1986a,b; Daegling, 1989, 1992; Ravosa, 1990, 1991, 1996; Antón, 1996; Vinyard and Ravosa, 1998; Vinyard et al., 2003).

Mandible length and the square root of $M_3$ occlusal area were scaled against the geometric mean (GM) of 10 additional cranial measurements (see Table 2.2). The GM was chosen as the scaling denominator for these variables because of their unclear biological relationship with other variables examined in this study (Mosimann, 1970; Darroch and Mosimann, 1985; Vinyard, 2008). Using a skull size GM as the scaling denominator has been previously employed by workers investigating the functional

*TABLE 2.2*. Measurements and shape variables used in this study.

| **Variable** | **Abbreviation** | **Description** |
|---|---|---|
| Cranial height | CranH | Basion - Apex |
| Cranial length | CranL | Prosthion - Opisthocranion |
| Anterior cranial length | AntCL | Nasion - Bregma |
| Posterior cranial length | PostCL | Bregma - Inion |
| Maximum cranial width | MaxCW | Euryon - Euryon |
| Bizygomatic breadth | BiZy | Zygion - Zygion |
| Facial height | FacH | Nasion - Prosthion |
| Facial width | FacW | Ectoconchion - Ectoconchion |
| Bipostglenoid breadth | BiPG | Distance between tips of postglenoid processes |
| Minimum cranial width | MinCW | BiZy - (2 * TempFW) |
| Cranium geometric mean | GM | $(\text{CranH} * \text{CranL} * \text{AntCL} * \text{PostCL} * \text{MaxCW} * \text{BiZy} * \text{FacH} * \text{FacW} * \text{BiPG} * \text{MinCW})^{1/10}$ |
| Corpus depth | CorpD | Superoinferior distance of mandibular corpus at $M_1$ |
| Symphyseal depth | SymD | Superoinferior distance from infradentale to most inferoposterior point of symphysis |
| Symphyseal width | SymW | Labiolingual width of symphysis at its maximum thickness taken perpendicular to SymD |
| Condyle length | CondL | Maximum anteroposterior length of mandibular condyle |
| Condyle width | CondW | Maximum mediolateral width of mandibular condyle |
| Condyle area | CondA | $1/2(\text{CondW}) * 1/2(\text{CondL}) * \pi$ |
| Mandible length | MandL | Infradentale to most posterior point of mandibular condyle |
| Masseter lever arm | MassLE | Anteroposterior distance from a line passing through both postglenoid processes to the zygomaticomaxillary suture |
| Medial pterygoid lever arm | MedPLE | Anteroposterior distance from a line passing through both postglenoid processes to the most anterior point of the scaphoid fossa |
| Temporalis lever arm | TempLE | Anteroposterior distance from a line passing through both postglenoid processes to the posterior point of the lateral orbital margin |
| Canine load arm | CanLO | Anteroposterior distance from a line passing through both postglenoid processes to the canine tip |
| Incisor load arm | IncLO | Anteroposterior distance from a line passing through both postglenoid processes to incision |
| $M_1$ load arm | M1LO | Anteroposterior distance from a line passing through both postglenoid processes to the center of $M_1$ |
| Dental arcade width | ArchW | Mediolateral distance between buccal grooves of left and right mandibular $M_1$ |
| $M_3$ mesiodistal length | MoMD | Maximum mesiodistal length of the mandibular $M_3$ crown |
| $M_3$ buccolingual width | MoBL | Maximum buccolingual width of mandibular $M_3$ crown |
| $M_3$ occlusal area | MoTA | MoMD * MoBL |

significance of both jaw length (e.g., Vinyard et al., 2003) and molar occlusal surface area (e.g., Spencer, 2003). To generate the GM, I chose variables that are presumably functionally distant from the masticatory system (Coleman, 2008).

Jaw adductor leverages were calculated as the ratio of muscle moment arm length to bite moment arm length measured from basicranial photographs in ImageJ software (Abramoff et al., 2004) following the method outlined in Spencer and Demes (1993) and Wright (2005a). Because this is a simplified estimate of muscle leverage, it is referred to it as “anterior leverage” to highlight that is over-represents the anterior parts of the muscles. All measurements were taken perpendicular to a line which passes through the tips of right and left postglenoid processes (see Fig. 1.1). Bite moment arms were measured to the center of $M^1$, the tip of the canine and incision. The medial pterygoid moment arm was measured to the most anterior point of the scaphoid fossa. The masseter moment arm was measured to the zygomaticomaxillary suture. The temporalis moment arm was measured to the point where the anterior root of the zygoma intersects the posterior point of the lateral orbital margin, near the zygomaticofacial suture (as seen in basicranial view).

## Statistical analyses

I conducted multiple pairwise morphometric comparisons using two-tailed Mann-Whitney *U*-tests. First, *Pithecia pithecia* was compared to *Chiropotes satanas* to see if there was a significant difference in the predicted direction. Second, *Cacajao calvus* and *C. melanocephalus* were each compared to *C. satanas* with the prediction that the *Cacajao* species in each case will exhibit the more specialized morphology for sclerocarpic harvesting (Kinzey, 1992). Thus all differences between *Cacajao* and *Chiropotes* were predicted to be in the same direction as the predicted differences between *Chiropotes* and *Pithecia*, respectively. All analyses were conducted using SPSS 16.0.

Comparisons between multiple, possibly non-independent, variables increase the risk of committing Type I errors. The Bonferroni correction is a simple method for protecting against spurious positives and does not require statistical independence. This correction adjusts the critical *P*-value by the number of comparisons such that $\alpha/n$. However, this technique reduces power, increases the risk of committing Type II errors and requires very large sample sizes to detect significant differences (Nakagawa, 2004). I adopt a less conservative approach, known as the sequential Bonferroni method (Rice, 1989), to protect against the chance of accepting a null hypothesis when it is false. For each set of pairwise comparisons, this method ranks the *P*-values from smallest ($P_1$) to largest ($P_k$) and adjusts each alpha value by dividing *P* by its position in the rank. First, the smallest *P*-value ($P_1$) is considered. If $P_1 \leq \alpha/k$, the next smallest *P*-value is considered by computing $\alpha/k$-1. This process is repeated until the inequality is no longer met (Rice, 1989). This results in a distinct “protected *P*-value” for each comparison.

Because two of the scaling variables used in this study are also presumed to vary with diet (i.e., mandible length and dental arcade width), the difference between taxa in these two variables might account for most of the variation in all shape variables. This may result in a spurious signal. To address this, I repeated each comparison between *P. pithecia* and *C. satanas* using the geometric mean of 10 additional skull variables as the scaling denominator. These results comparisons yielded nearly the same interpretation of the results and are not reported here.

## RESULTS

### *Pithecia pithecia* vs. *Chiropotes satanas*

With one exception, all biomechanical predictions are supported by the data. Fifteen of the 16 pairwise comparisons are statistically significant in the predicted direction (Table 2.3). Symphysis width was predicted to be larger in *Pithecia*. However, this comparison yielded a significant result in the opposite direction of the predicted difference. Possible explanations for this result are discussed below.

### *Chiropotes satanas* vs. *Cacajao* spp.

Of the 16 pairwise comparisons between *Chiropotes satanas* and *Cacajao calvus* only two conform to prediction, 11 were not significant and three yielded significant differences in the opposite direction (Table 2.4). None of the comparisons between *C. satanas* and *C. melanocephalus* yielded significant differences (Table 2.5).

## DISCUSSION

*Pithecia pithecia* and *Chiropotes satanas* exhibit the predicted morphology in all but one of the 16 comparisons. These results are consistent with Kinzey and Norconk (1993) who found that *C. satanas* incises much harder fruits than *P. pithecia*, whereas *P. pithecia* masticates harder seeds with its postcanine dentition. Similar results were reported by Anapol and Lee (1994) who concluded that *Chiropotes* possesses more

*TABLE 2.3*. Results of pairwise morphometric comparisons between *Pithecia pithecia* and *Chiropotes satanas*. *Cs>Pp* and *Pp>Cs* indicate direction of predicted difference. The taxon indicated in the third column has the larger value for that particular measure.

| **Shape variable** | **Protected *P*-value** | ***P. pithecia* vs. *C. satanas*** |
|---|---|---|
| Symphyseal depth (*Cs>Pp)* | 0.05/16 = 0.0003125 | *Cs* ($U$=0; $P$<0.0001) |
| Condyle area (*Cs>Pp)* | 0.05/15 = 0.0033333 | *Cs* ($U$=5; $P$<0.0001) |
| Symphyseal width (*Pp>Cs*) | 0.05/14 = 0.0035714 | *Cs* ($U$=22; $P$<0.0001) |
| Dental arcade width (*Cs>Pp)* | 0.05/13 = 0.0038461 | *Cs* ($U$=31; $P$<0.0001) |
| Temporalis : $M^1$ (*Cs>Pp)* | 0.05/12 = 0.0041666 | *Cs* ($U$=32; $P$<0.0001) |
| Medial pterygoid : $M^1$ (*Cs>Pp)* | 0.05/11 = 0.0045454 | *Cs* ($U$=34; $P$<0.0001) |
| $M_3$ occlusal area (*Pp>Cs)* | 0.05/10 = 0.005 | *Pp* ($U$=0; $P$<0.0001) |
| Mandible length (*Pp>Cs)* | 0.05/9 = 0.0055555 | *Pp* ($U$=49; $P$<0.0001) |
| Corpus depth at $M_1$ (*Cs>Pp*) | 0.05/8 = 0.00625 | *Cs* ($U$=56; $P$<0.0001) |
| Temporalis : Incisor (*Cs>Pp)* | 0.05/7 = 0.0071428 | *Cs* ($U$=60; $P$=0.0001) |
| Medial pterygoid : Canine (*Cs>Pp)* | 0.05/6 = 0.0083333 | *Cs* ($U$=61; $P$=0.0001) |
| Masseter : Canine (*Cs>Pp)* | 0.05/5 = 0.01 | *Cs* ($U$=66; $P$<0.001) |
| Masseter : $M^1$ (*Cs>Pp)* | 0.05/4 = 0.0125 | *Cs* ($U$=46; $P$<0.001) |
| Masseter : Incisor (*Cs>Pp)* | 0.05/3 = 0.0166666 | *Cs* ($U$=68; $P$<0.001) |
| Temporalis : Canine (*Cs>Pp)* | 0.05/2 = 0.025 | *Cs* ($U$=68; $P$<0.001) |
| Medial pterygoid : Incisor (*Cs>Pp)* | 0.05/1 = 0.05 | *Cs* ($U$=71; $P$<0.001) |

robust canines, greater jaw adductor leverage and a more robust mandible compared to *Pithecia*.

With greater relative corpus depth, *Chiropotes* jaws are better suited to resist increased parasagittal bending moments imposed on the corpus (Hylander, 1979a,b, 1988; Bouvier,1986a; Ravosa, 1991, 1996a; Daegling, 1992; Ravosa and Hylander, 1994). An increase in the relative depth of the symphysis also equips *Chiropotes* with a jaw that is more efficient at countering coronal bending and dorsoventral shear when wedging apart unripe fruits.

*TABLE 2.4*. Results of pairwise morphometric comparisons between *Chiropotes satanas* and *Cacajao calvus*. *Cc*>*Cs* and *Cs*>*Cc* indicate direction of predicted difference. The taxon indicated in the third column has the larger value for that particular measure.

| **Shape variable** | **Protected *P*-value** | ***C. satanas* vs. *C. calvus*** |
|---|---|---|
| Temporalis : $M^1$ (*Cc*>*Cs*) | 0.05/16 = 0.0003125 | *Cc* ($U$=5; $P$<0.0001) |
| Temporalis : Canine (*Cc*>*Cs*) | 0.05/15 = 0.0033333 | *Cc* ($U$=15; $P$<0.001) |
| Mandible length (*Cs*> *Cc*) | 0.05/14 = 0.0035714 | *Cc* ($U$=18; $P$<0.001) |
| Symphyseal depth (*Cc*>*Cs*) | 0.05/13 = 0.0038461 | *Cs* ($U$=19; $P$<0.001) |
| $M_3$ occlusal area (*Cs*>*Cc*) | 0.05/12 = 0.0041666 | *Cc* ($U$=13; $P$=0.003) |
| Symphyseal width (*Cs*>*Cc*) | 0.05/11 = 0.0045454 | ns ($U$=35; $P$<0.01) |
| Temporalis : Incisor (*Cc*>*Cs*) | 0.05/10 = 0.005 | ns ($U$=39; $P$=0.011) |
| Masseter : Incisor (*Cc*>*Cs*) | 0.05/9 = 0.0055555 | ns ($U$=40; $P$=0.012) |
| Dental arcade width (*Cc*>*Cs*) | 0.05/8 = 0.00625 | ns ($U$=42; $P$=0.016) |
| Medial pterygoid : Incisor (*Cc*>*Cs*) | 0.05/7 = 0.0071428 | ns ($U$=49; $P$=0.037) |
| Medial pterygoid : Canine (*Cc*>*Cs*) | 0.05/6 = 0.0083333 | ns ($U$=51; $P$=0.046) |
| Masseter : Canine (*Cc*>*Cs*) | 0.05/5 = 0.01 | ns ($U$=58; $P$=0.094) |
| Condyle area (*Cc*>*Cs*) | 0.05/4 = 0.0125 | ns ($U$=71; $P$=0.281) |
| Medial pterygoid : $M^1$ (*Cc*>*Cs*) | 0.05/3 = 0.0166666 | ns ($U$=71; $P$=0.281) |
| Corpus depth at $M_1$ (*Cc*>*Cs*) | 0.05/2 = 0.025 | ns ($U$=72; $P$=0.302) |
| Masseter : $M^1$ (*Cc*>*Cs*) | 0.05/1 = 0.05 | ns ($U$=89; $P$=0.801) |

The expanded articular surface area of the mandibular condyles in *Chiropotes* can presumably withstand high levels of condylar reaction force. Hylander and Bays (1979) found that peak compressive forces were applied to the lateral aspect of the condyles. Therefore, a relative increase in the mediolateral width of the condyles may be of more interest when examining differences in dietary adaptation related to forceful biting. Several additional studies have suggested that an increase in the anteroposterior length of the condyles may be more related to increased rotational excursion of the mandible during wide gape (Vinyard et al., 2003). Conversely, some have suggested that anteroposteriorly long condyles may be related to increased condylar reaction forces

*TABLE 2.5*. Results of pairwise morphometric comparisons between *Chiropotes satanas* and *Cacajao melanocephalus*. *Cm*>*Cs* and *Cs*>*Cm* indicate direction of predicted difference. The taxon indicated in the third column has the larger value for that particular measure.

| **Shape variable** | **Protected *P*-value** | ***C. satanas* vs. *C. melanocephalus*** |
|---|---|---|
| Symphyseal depth (*Cm*>*Cs*) | 0.05/16 = 0.0003125 | ns ($U$=2; $P$=0.001) |
| Temporalis : Canine (*Cm*>*Cs*) | 0.05/15 = 0.0033333 | ns ($U$=6; $P$<0.01) |
| $M_3$ occlusal area (*Cs*>*Cm*) | 0.05/14 = 0.0035714 | ns ($U$=2; $P$<0.01) |
| Masseter : Incisor (*Cm*>*Cs*) | 0.05/13 = 0.0038461 | ns ($U$=9; $P$<0.01) |
| Dental arcade width (*Cm*>*Cs*) | 0.05/12 = 0.0041666 | ns ($U$=10; $P$<0.01) |
| Temporalis : $M_1$ (*Cm*>*Cs*) | 0.05/11 = 0.0045454 | ns ($U$=17; $P$=0.03) |
| Corpus depth at $M^1$ (*Cm*>*Cs*) | 0.05/10 = 0.005 | ns ($U$=25; $P$=0.118) |
| Masseter : Canine (*Cm*>*Cs*) | 0.05/9 = 0.0055555 | ns ($U$=28; $P$=0.177) |
| Masseter : $M_1$ (*Cm*>*Cs*) | 0.05/8 = 0.00625 | ns ($U$=28; $P$=0.177) |
| Temporalis : Incisor (*Cm*>*Cs*) | 0.05/7 = 0.0071428 | ns ($U$=28; $P$=0.177) |
| Medial pterygoid : Canine (*Cm*>*Cs*) | 0.05/6 = 0.0083333 | ns ($U$=34; $P$=0.356) |
| Medial pterygoid : $M_1$ (*Cm*>*Cs*) | 0.05/5 = 0.01 | ns ($U$=35; $P$=0.394) |
| Condyle area (*Cm*>*Cs*) | 0.05/4 = 0.0125 | ns ($U$=36; $P$=0.434) |
| Mandible length (*Cs*>*Cm*) | 0.05/3 = 0.0166666 | ns ($U$=41; $P$=0.67) |
| Symphyseal width (*Cs*>*Cm*) | 0.05/2 = 0.025 | ns ($U$=42; $P$=0.722) |
| Medial pterygoid : Incisor (*Cm*>*Cs*) | 0.05/1 = 0.05 | ns ($U$=44; $P$=0.831) |

along the posterior aspect of the condyles during anterior tooth biting (Smith et al., 1983; Bouvier, 1986a). Several other researchers have opted to use total articular surface area (e.g., Wall, 1999; Taylor, 2005). It should be noted, however, that a comparison of just mediolateral condylar width in *Pithecia* and *Chiropotes* reveals that *Chiropotes* possesses significantly wider condyles than *Pithecia* (Mann-Whitney *U*-test; $U = 77$; $P<0.001$). Even if anteroposterior length of the condyle is not related to the degree of compressive joint force, one might still expect this dimension to be greater in *Chiropotes satanas*. This is because average fruit breadth is greater for *C. satanas* than for *P. pithecia* (Norconk et al., 2008). These fruits would presumably require increased gape and would thus necessitate relatively longer condyles (Vinyard et al., 2003). However, both *Chiropotes* and *Pithecia* avoid biting the fruit at its greatest dimension; instead, they align the cutting edge of the incisors perpendicular to the fruit's long axis (Norconk et al., 2008). Therefore, whether or not maximum ingestive gape is greater in *C. satanas* is unclear.

The mandible is shorter in *Chiropotes satanas* than in *Pithecia pithecia*. Along with an increase in the superoinferior depth of the corpus, a relative decrease in the length of the mandible decreases the intensity of parasagittal bending experienced in the corpus (Hylander, 1979; Bouvier, 1986a,b; Greaves, 1991; Antón, 1996). *Chiropotes satanas* has significantly greater anterior leverage for all three jaw adductor muscles at canine, incisor and $M^1$ bite points. Because of this and because of the short jaws in *Chiropotes*, a higher proportion of jaw adductor force is converted into bite force than in *Pithecia.*

In primates with fused symphyses such as *Cebus* spp. (Wright, 2005a), Neanderthals and Inuits (Spencer and Demes, 1993), anterior migration of the masticatory muscles reflects adaptations for high magnitude incisal and canine loading rather than postcanine loading. By contrast, selection for increased molar loading should favor a relative decrease in the mediolateral width of the dental arcade (Spencer, 1998, 1999). Narrowing the width of the dental arcade decreases the risk of temporomandibular joint distraction and increases the effective contribution of the balancing side jaw adductors (Hylander, 1975; Smith, 1978; Spencer, 1998, 1999). Therefore, although *Pithecia pithecia* is expected to produce greater bite forces at $M^1$, I did not expect it to have a short bite moment arm. As discussed previously, this is because forceful biting on the molars increases the risk of temporomandibular joint distraction.

Anapol and Lee (1994) found the postcanine occlusal area to be relatively larger in *Pithecia pithecia* than in *Chiropotes satanas*. They attributed this difference to greater leaf consumption in the former taxon. Although *Pithecia* does consume leaves in greater proportion than *Chiropotes* (Kinzey and Norconk, 1993) it may be premature to attribute an increase in total postcanine occlusal area to this behavior. Several studies have linked increased jaw adductor leverage with third molar reduction and agenesis (Spencer and Demes, 1993; Spencer, 2003; Wright, 2005a). With an anterior shift of the muscles, the third molar may fall within Region III of the tooth row (Spencer and Demes, 1993). Forceful biting in this region increases the chances of temporomandibular joint distraction by shifting the muscle resultant vector outside of the triangle of support formed by both mandibular condyles and the bite point (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1998, 1999). Thus the functional area of the postcanine tooth row is reduced and the expected result is a reduction of third molar occlusal surface area or even agenesis of the tooth. Therefore, small postcanine occlusal area in *Chiropotes* may be more related to the relatively anterior position of its jaw adductors and less related to its lesser emphasis on leaves. In fact, a comparison between *P. pithecia* and *C. satanas* $M_1$ occlusal surface area (Mann-Whitney *U*-test; $U = 77$; $P<0.001$) using the same individuals from the current sample reveals substantial overlap in their distributions compared to $M_3$ occlusal area (Fig. 2.1). This indicates a more rapid drop-off in $M_3$ occlusal surface area and suggests selection for third molar reduction in *Chiropotes*. Spencer (2003) arrived at a similar conclusion in his study of platyrrhine tooth root area. He observed a decrease in the number of molar tooth roots and molar tooth root surface area in a gradient from M1-M3 in *Chiropotes*, but not *Pithecia* (Spencer, 2003).

The only comparison which did not conform to prediction concerned width of the symphysis (Prediction 3). Wishboning stress on the symphysis is the result of the late activity of the balancing side deep masseter during the end of the power stroke of mastication (Hylander et al., 1987; Hylander and Johnson, 1994; Ravosa, 1996). *Pithecia pithecia* was expected to exhibit a wider mandibular symphysis (in the labiolingual dimension) compared to *Chiropotes satanas* due to its tendency to crush very hard seeds with its postcanine dentition. Several recent studies have noted the apparent mismatch between symphysis width and diet (e.g., Daegling and McGraw, 2001, 2007; Koyabu and Endo, 2009). Daegling and McGraw (2007) tested the hypothesis that *Cercocebus agilis* would exhibit structurally stiffer symphyses relative to *Lophocebus albigena* based on the observation by Shah (2003) that the former engages in more frequent and powerful postcanine crushing of hard seeds and nuts. They found that the biomechanical properties of the symphysis failed to distinguish the two despite a reported difference in feeding behavior. Similarly, Daegling and McGraw (2001) found that symphysis proportions did not distinguish seed-eating colobines from colobines that do not regularly consume seeds. Moreover, Koyabu and Endo (2009) found that symphysis width was actually less in seed-eating colobines compared to colobines that specialize on immature leaves.

Several explanations for the inconsistent relationship between symphysis thickness and diet have been advanced. One possibility is that allometric increases in symphyseal curvature, resulting in elevated wishboning stress at the symphysis, might have more to do with symphysis thickness than adaptation to a particular diet (Ravosa, 1996). Others have suggested that symphysis thickness may be more related to size of the canines (e.g., Wood, 1978; Smith et al., 1983; Daegling and McGraw, 2001; Plavcan and

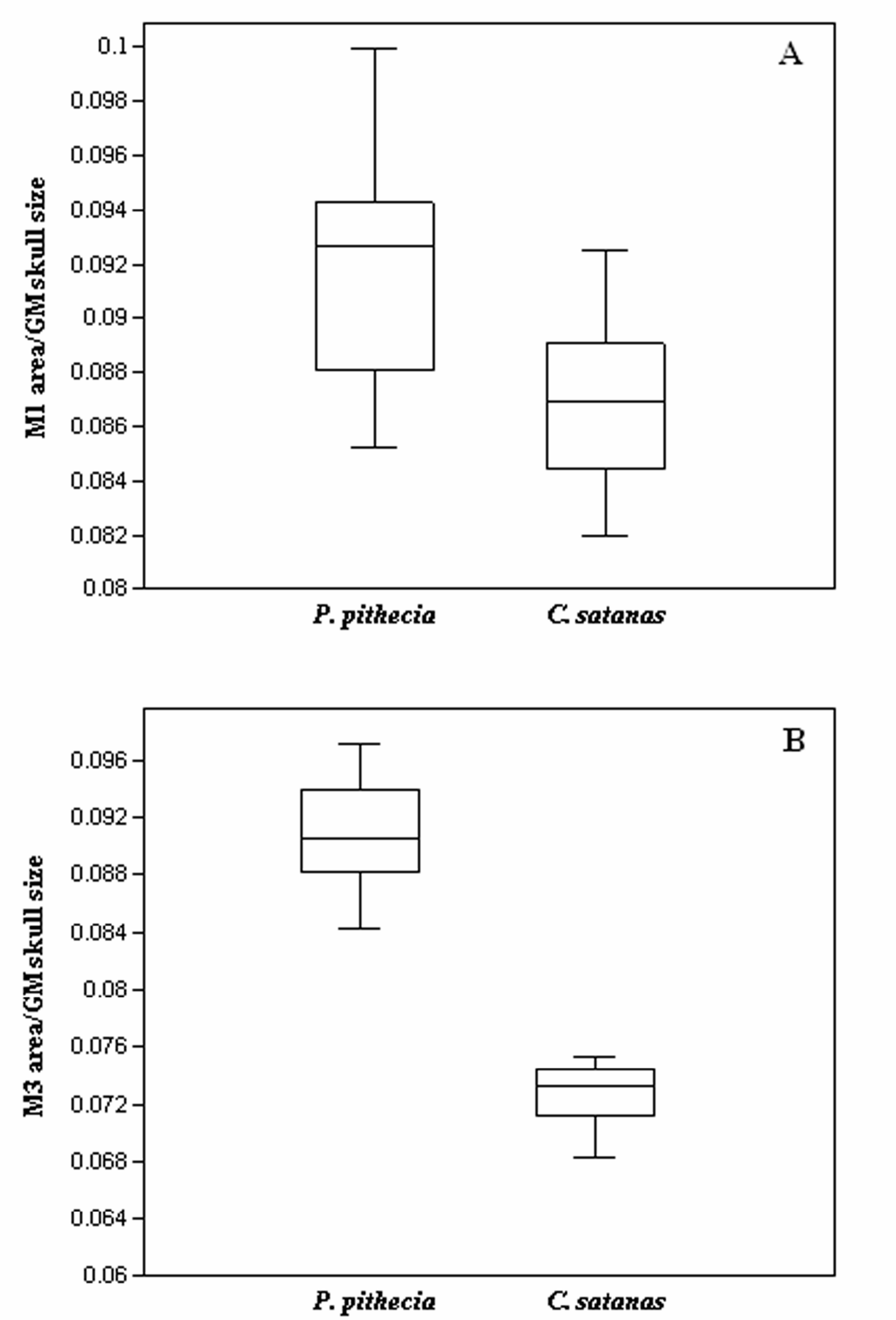

**Fig. 2.1**. Box plots showing species ranges in *Pithecia pithecia* and *Chiropotes satanas* for **(A)** $M_1$ occlusal surface area and **(B)** $M_3$ occlusal surface area.

Daegling, 2006). The results of the present study are consistent with the second possibility. *Chiropotes satanas* has larger and more robust canines than *Pithecia pithecia* (Kinzey, 1992; Anapol and Lee, 1994). The thickness of the *C. satanas* symphysis may therefore be related to the accommodation of these canines rather than to its particular loading environment. Furthermore, an allometric increase in symphysis size is less likely to explain these results (see below).

No prediction regarding the width of the postcanine corpus was offered in this study. Likewise, Daegling and McGraw (2007) made no prediction regarding corpus width when comparing incision versus mastication in *Lophocebus* and *Cercocebus*. These authors did, however, predict equivalent postcanine corpus size between these two taxa. In the absence of true cross-sectional geometry data for the pitheciine sample, this comparison was not made here. Increasing the torisional resistance of the corpus by increasing its buccolingual breadth is presumably of equal importance to taxa which engage in forceful incision and to those which engage in forceful mastication. Forces imposed on the corpus effectively balance out. Moreover, Daegling (2007) has recently argued that corpus breadth may be an unreliable approximation for torsional resistance.

The results from the *Cacajao* comparison reveal that uakaris deviate far less from the condition in *Chiropotes* than does *Pithecia*. This is interesting in light of the proposed morphocline placing *Cacajao* as the most dentally specialized sclerocarpic forager (Kinzey, 1992). *Cacajao calvus* only exhibits the predicted morphology for temporalis leverage at $M^1$ and the canine. None of the comparisons between *Chiropotes satanas* and *C. melanocephalus* yielded significant differences after sequential Bonferroni adjustment.

Two caveats should be kept in mind regarding (1) the use of the adjusted *P*-values and (2) the smaller *n* for the *Cacajao* samples.

The use of correction methods to protect against spurious positives is often employed in comparative studies. However, these corrections may do more harm than good by reducing power and increasing the chance of committing Type II errors (Nakagawa, 2004). Indeed, there is a large debate, particularly among behavioral ecologists, on whether these corrections should even be made (Nakagawa, 2004). When a less conservative *P* of 0.05 is applied there are six additional significant results for the comparisons between *Chiropotes satanas* and *Cacajao calvus*. However, only one of these six conform to prediction (i.e., Temporalis : Incisor). The remaining five were significant in the opposite direction of the predicted difference. Six additional comparisons between *C. satanas* and *C. melanocephalus* are also significant when applying a *P* of 0.05. Only three of these (i.e., Temporalis : Canine, $M_3$ occlusal area and Temporalis : $M^1$) conform to prediction, while the other three are in the opposite direction of prediction.

I also acknowledge that the lack of significant results for the *Cacajao* species comparisons may be partly related to the small *n* for each species. Larger sample sizes may increase the likelihood of obtaining significant results. However, because of the very high significance levels and the considerable number of results in the opposite direction of the predicted difference, increases in sample size should not affect the overall conclusions made in this study.

In many ways, the morphology of both *Cacajao* species closely resembles that of *Chiropotes*. However, the fact that *Cacajao calvus* possesses a shallower symphysis, a longer mandible, and larger $M_3$ surface area compared to *Chiropotes* suggests that *Cacajao* might be *less* specialized for feeding on hard fruits. Likewise, Norconk et al. (2008) used several measurements of the masticatory apparatus to form a biomechanical robusticity index for a large sample of platyrrhine taxa. They found *Chiropotes satanas* to be the most "robust" followed closely by *Cacajao melanocephalus*. The robusticity index for *Pithecia pithecia* fell well below the other two pitheciines. In sum, the features exhibited by uakaris suggest that they may not occupy the most specialized position on a morphocline of increasing sclerocarpic specialization (*contra* Kinzey, 1992). The striking morphological similarity between both uakari species and *Chiropotes satanas* adds support to the suggestion by Ayres (1989) that their dietary similarities explain the lack of overlap between their ranges.

Food competition is most likely much higher between the sympatric *Chiropotes* and *Pithecia* than between *Cacajao* and either genus of saki. This is consistent with the assumption that dietary competition is highest between sympatric congeners (e.g., Fleagle, 1984). The lack of competition may allow uakaris to exploit a wider variety of fruits at various stages of ripeness. The results from this study are also consistent with those of Barnett et al. (2005) who found that a large proportion of fruits eaten by *C. melanocephalus ouakary* were of either soft or medium hardness and who suggested that uakaris might not rely on hard-shelled fruits as much as previously thought. The best test of this hypothesis is to collect mechanical properties for foods eaten by uakaris.

One limitation of this study is the use of external linear measurements as proxies for cross-sectional area. These dimensions provide only first-order approximations of the load-bearing capabilities of the mandible and may not faithfully track bending and

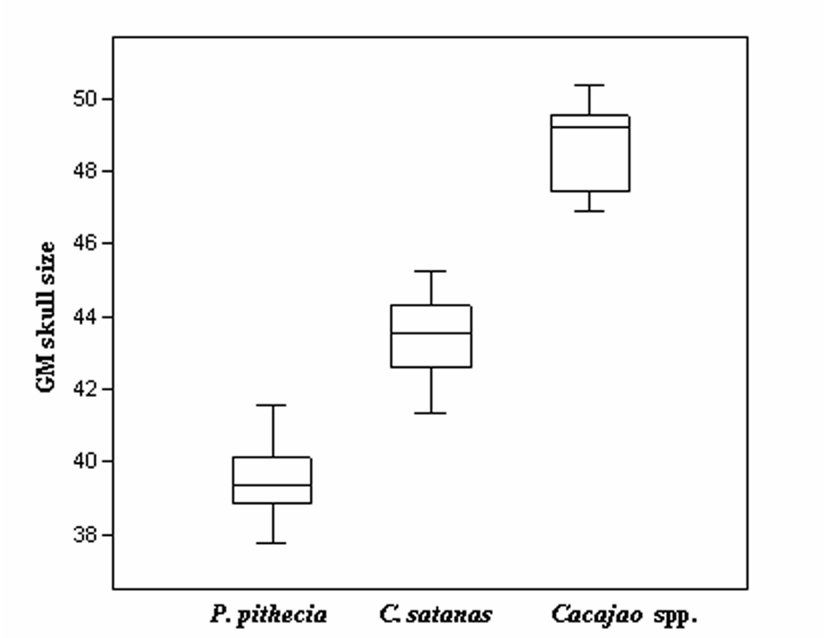

**Fig. 2.2**. Box plots showing species ranges in *Pithecia pithecia*, *Chiropotes satanas* and the combined *Cacajao* species sample for the geometric mean (GM) of skull size. Note the overlap between the ranges for the first two taxa and the complete separation of *Cacajao* spp.

torsional moments imposed on the mandible (Daegling, 1989, 2007; Daegling and Hylander, 1998). Also, the interspecific differences detected might be results of size-related changes and may not reflect differences in diet. Indeed, the jaws of *Chiropotes satanas* appear to be more robust overall than those of *Pithecia pithecia*. Additionally, although no prediction regarding corpus width was made here, previous studies have found this dimension to be greater in *C. satanas* (Anapol and Lee, 1994; Norconk et al., 2008). Together these findings suggest that size-related increases in jaw size might play an important role in shaping jaw morphology. However, the range of the skull geometric mean of *P. pithecia* overlaps with that of *C. satanas* in the current sample, whereas there is no overlap between *C. satanas* and either uakari (Fig. 2.2). This result weakens the case for a strong allometric effect.

Another limitation of this study is the method used to estimate jaw adductor leverage (Spencer and Demes, 1993; Spencer, 2003; Wright, 2005a). This method of calculating jaw adductor leverage considers only the extreme anterior fibers for each muscle, neglects all non-vertical components of muscle force, and considers only the origins of each muscle. This reduces the realism of the model (Davis, 1955; Tattersall, 1974; Hylander, 1978), but this caveat applies equally to all prior studies that employ this method (e.g., Spencer and Demes, 1993; Wright, 2005a). Furthermore, this method ignores other features of the masticatory system which likely play a role in muscle force production, such as height of the ascending ramus. One advantage of this method over more realistic approximations of muscle leverage (e.g., Perry, 2008) is that data can be collected efficiently on many specimens, even ones lacking key areas of muscle attachment. Nevertheless, because this method only considers part of the muscle, the conclusions regarding increased jaw adductor leverage in *Chiropotes* and attendant third molar reduction remain tentative.

## CONCLUSIONS

Relative to *Pithecia pithecia*, *Chiropotes satanas* exhibits craniomandibular specialization for forceful and frequent incision of hard-shelled fruits. Conversely, *P. pithecia* exhibits morphological features related to forceful postcanine crushing of hard seeds. Compared to *Pithecia*, *Chiropotes* possesses a deeper mandibular corpus and symphysis, expanded condylar surface area, a shorter mandible and increased leverage for the jaw adductors. Furthermore, *Chiropotes* exhibits decreased $M_3$ occlusal area as a result of anteriorly shifted jaw adductors and a reduction in the functional area of the postcanine tooth row. *Pithecia* exhibits a relatively narrower dental arcade which facilitates increased balancing side muscle force while reducing the risk of TMJ distraction during postcanine biting. Contrary to expectation, symphysis width is not greater in *Pithecia*; this might be related to canine size. These results are consistent with physical properties of food and ecological data (Kinzey and Norconk, 1990, 1993), as well as dental morphology (Kinzey, 1992).

Most morphological features examined in *Cacajao* suggest that they are not adapted to competition with other members of the Pitheciinae. Most comparisons between *Chiropotes* and *Cacajao* produced insignificant results or results opposite to prediction. This suggests that uakaris do not occupy the most specialized position on a morphocline of increasing sclerocarpic specialization (Kinzey, 1992). *Cacajao* may not be limited to eating very hard fruits and might exploit a wide variety of fruits at different stages of ripeness.

Lastly, this study underlines the importance of food material properties. These are crucial when attempting to link form and function in the masticatory system and are unfortunately vastly underrepresented in the primate ecology literature.

# CHAPTER 3

Chapter 1 of this thesis examined the relationship between enlarged jaw proportions and proxies of load magnitude and loading frequency. The variables determined to characterize “heavy loading” and “repetitive loading” by the stepwise discriminant function analysis were also evaluated regarding their relative importance in classifying each dietary group. The discriminant analysis found that, when combined, six features explain 100% of the difference between these two loading regimes. Ordered by absolute size of the correlation within the function these are: medial pterygoid leverage at $M^1$, medial pterygoid insertion angle, temporalis leverage at $M^1$, anteroposterior length of the temporal articular surface, masseter insertion angle and temporalis leverage at incisor. A non-parametric Spearman’s rank correlation matrix was generated to quantify the relationship between the discriminant scores and each variable used in the stepwise discriminant analysis. This revealed that medial pterygoid insertion angle, dental arcade width, medial pterygoid leverage at $M^1$, masseter leverage at $M^1$, temporalis leverage at $M^1$, temporalis leverage at incisor were all greater in heavy loaders, whereas anteroposterior length of the temporal articular surface, zygomatic arch size, ascending ramus height above the occlusal plane, mandible length and masseter insertion angle were all greater in repetitive loaders. Also, the relationship between the discriminant function and each of the following jaw dimensions was evaluated: corpus width, corpus depth, symphysis width and symphysis depth. Results show that corpus width, corpus depth and symphysis width are all positively correlated with “heavy loading” while corpus depth is not significantly correlated with either loading regime. None of the jaw proportions are correlated with "repetitive loading." Furthermore, several variables failed to discriminate between these dietary groups. These are infratemporal fossa area, condyle width and condyle length, which were predicted to be greater in the "heavy loading" sample, as well as facial projection, which was expected to be greater in the "repetitive loading" sample.

Several of the taxa included in the "heavy loading" sample differ in the force applied to the anterior and postcanine dentition. For example, *Chiropotes satanas* is known to incise fruits with higher puncture resistance than *Pithecia pithecia*, whereas *P. pithecia* crushes harder seeds with its postcanine dentition than *C. satanas* (Kinzey and Norconk, 1990, 1993). A similar pattern has been reported for mangabeys. Shah (2003) observed that *Lophocebebus albigena* incises fruits with much harder pericarp than *Cercocebus albigena*, while the latter masticates seeds with higher crushing resistance.

Chapter 2 approached the question of incision versus mastication in a group of primates with known variation in dietary behavior and food consistency, the pitheciines. *Chiropotes satanas*, a "heavy loader" that emphasizes incisal and canine biting of hard fruits, and *Pithecia pithecia*, a "heavy loader" that emphasizes postcanine mastication of hard seeds, were expected to exhibit features advantageous to forceful anterior and posterior loading, respectively. *Cacajao* spp. were also examined and were expected to exhibit features consistent with a morphocline of increasing dental specialization for feeding on hard fruits. Kinzey (1992) concluded that *Cacajao* represents the most dentally specialized sclerocarpic harvester. Results from this study suggest that taxa adapted to forceful anterior tooth loading should exhibit relatively deep mandibular corpora and symphyses, relatively great condylar articular surface areas, relatively short mandibles, greater mechanical advantage of the jaw adductors and relatively less $M_3$ occlusal surface area compared to taxa adapted to high magnitude postcanine crushing. Postcanine loaders should exhibit a relative decrease in the width of the dental arcade. The results from this study also suggest that *Cacajao* does not represent the most specialized sclerocarpic harvesting pitheciine. Most comparisons with *Cacajao* yielded either insignificant or unpredicted results.

Some of the results from these two studies appear to conflict with each other. For example, mandibular condyle dimensions were not among the variables that reliably discriminate between heavy and repetitive loading (see Chapter 1). Regardless, one of the predictions in Chapter 2 was that *Chiropotes satanas* (a "heavy loader" that emphasizes incision) would have a larger articular surface area of the condyle than *Pithecia pithecia* (a "heavy loader" that emphasizes mastication) based on the assumption that compressive joint loads are highest during anterior bites. This is because, compared to postcanine bites, anterior bites require greater amounts of muscle force to achieve the same degree of bite force (cf. Spencer, 1998, 1999). Together, these results suggest that increases in condylar surface area may not be indicative of broad dietary categories such as durophagy and folivory but that condylar dimensions can be used to infer finer details about dietary adaptation. For example, an increase in the proportion of leaves, as well as an increase in food hardness should engender similar adaptations in the mandibular condyle. Furthermore, taxa adapted to forceful *incisal and canine* biting should exhibit greater condylar dimesions due to increased compressive joint reaction force.

A similar result concerning symphysis depth was also identified. Chapter 1 demonstrated that the depth of the mandibular symphysis does not reliably discriminate between "heavy loading" and "repetitive loading" anthropoids. Nonetheless, *Chiropotes satanas* was predicted to exhibit a relatively deeper symphysis than *Pithecia pithecia* as an adaptation to resist coronal bending of the anterior corpus during the incision of hard fruits (see Chapter 2). Together, these results suggest that symphysis depth may not be indicative of one or the other type of loading (i.e., heavy vs. repetitive) but that symphysis depth may be advantageous for both. Alternatively, taxa adapted for forceful anterior biting may require increased resistance to coronal bending while those adapted for forceful postcanine crushing may not. Hylander (1988) demonstrated that "robust" australopithecines exhibit deep and wide corpora coupled with thickly constructed symphyses. He concluded that these features reflect powerful bending and twisting moments during postcanine mastication of unusually hard objects. However, Hylander (1988) found that these extinct hominins do not possess relatively deep symphyses. Similarly, Taylor (2002) found that African apes with a more obdurate diet do not exhibit relatively deeper symphyses. These studies, combined with the results from this thesis, suggest that deep symphyses are not consistently associated with increased occlusal bite force and the resulting increases in torsion and coronal bending imposed on the mandible. The results from this thesis do, however, indicate that taxa adapted to generating high forces *at the anterior teeth* might be experiencing increased coronal bending of the anterior corpus and may therefore require increases in symphysis depth.

The results regarding symphysis width are also intriguing. Chapter 1 demonstrated that wide mandibular symphyses characterize taxa that produce high occlusal bite force per chew. I predicted in Chapter 2 that *Pithecia pithecia* would exhibit thicker symphyses than *Chiropotes satanas* due to its tendency to crush hard seeds using its postcanine dentition. However, this comparison revealed that *C. satanas* possesses the thicker symphysis. Several other studies have noted an inconsistent relationship between symphysis width and diet (e.g., Daegling and McGraw, 2001, 2007, 2009; Taylor et al., 2008; Koyabu and Endo, 2009). *Chiropotes satanas* has larger and more robust canines than *P. pithecia* (Kinzey, 1992; Anapol and Lee, 1994). Therefore, the thickness of the *C. satanas* symphysis may be related to the accommodation of these canines rather than to its particular loading environment. Combined, these results suggest that although thicker symphyses characterize taxa that require heavy occlusal loads, other factors, such as canine size, may play a critical role. It would be interesting to perform this comparison taking into consideration differences in canine size.

Comparative morphological studies rely heavily on ecological data. However, ecological studies often fail to include the data critical for evaluating biomechanical hypotheses. Furthermore, even if the critical data are presented, they are insufficiently precise to sort out form-function relationships. For example, leaves differ in toughness and seeds differ in hardness (Lucas et al., 2000; Lucas, 2004). Other factors, such as chewing frequency (Ross et al., 2009) and ingested food size (Perry, 2008) likely play a crucial role in shaping primate masticatory morphology. Future studies should focus on collecting a broader range of food physical properties for additional primate species. These data should incorporate the sizes and shapes of primate foods and should record the frequency and duration of chewing bouts in the wild. Such studies would greatly improve our understanding of form and function in the primate masticatory system.

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