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Sacral Morphology of Prehensile-Tailed Primates in Relation to Biomechanical Loading

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Sacral Morphology of Prehensile-Tailed Primates in Relation to Biomechanical Loading

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by

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ABSTRACT

The few available comparative studies of prehensile tail anatomy in primates have established that several features of the caudal vertebrae are associated with adaptation to the increased loading of the tail during prehension. Given that the caudal vertebrae are anchored to the sacrum, it stands to reason that sacral morphology should also covary with tail prehensility. Convergent evolution of prehension in ateline and cebine primates and clear variation in the use of tails among taxa raises questions not only of how sacral morphology differs between prehensile and non-prehensile taxa, but whether different prehensile-tailed taxa evolved the same solutions to the biomechanical demands of prehension. The first step in addressing these problems is to document and measure the anatomical correlates of prehension in the sacrum.

A comparative study of primate sacra was completed among the following genera: *Alouatta, Ateles, Cacajao, Cebus, Chiropotes, Lagothrix, Macaca, Pithecia,* and *Saimiri* (total n = 103). The genera were split into fully-, semi-, and non-prehensile groups; *Alouatta, Ateles,* and *Lagothrix* were categorized as fully-prehensile, *Cebus* as semi-prehensile, and the remainder as non-prehensile. Linear measurements for 16 anatomical variables were analyzed. Univariate and multivariate analyses returned some degree of significant results. While some measurements were more meaningful than others, morphological differences in relative size and transverse expansion of spinous processes, relative size of features associated with postulated muscle attachment, and relative size of articular surfaces of sacral vertebrae exist among individuals of varying prehensility. Thus, basic anatomical correlates of prehension were identified, and questions of morphological adaptation to prehension can be asked.

DEDICATION

This thesis is dedicated to my late father, James Showalter, who instilled within me his profound appreciation and love for the natural world. If it weren’t for him, standing in the pouring rain while (possibly) being peed on by a monkey probably would have turned me off to the field of Biological Anthropology. Through this thesis I wish to demonstrate my strength, resilience, and hard-headedness in accomplishing whatever it is that I intend to get done. Thanks for teaching me those things, too, Dad.

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CHAPTER 1: INTRODUCTION

1. PREHENSILE TAILS: INTERSPECIFIC VARIATION

A prehensile tail is one that is capable of fully supporting the weight of an organism. A semi-prehensile tail is still capable of providing assistance in locomotion but is not capable of independently supporting the entire body weight (Emmons and Gentry, 1983). Prehension and semi-prehension have evolved independently numerous times among mammals. Some degree of prehensility is found in 40 mammalian genera in 14 mammalian higher taxa (Organ, 2008). Of the 14 taxa which demonstrate prehension, eight are found in the New World: Atelidae, Cebidae, Didelphidae, Cyclopedidae, Myrmecophagidae, Procyonidae, Erethizontidae, and Microbiotheria. The other six are distributed throughout the Old World, but primarily in southeastern Asia (Emmons and Gentry, 1983). Many authors assert that the frequency of homoplastic evolution of this trait amongst New World arboreal mammalian taxa indicates that such an adaptation is critical for navigation of and feeding within Neotropical forest habitats (Emmons and Gentry, 1983; Jones, 2008; Organ, 2008). However, though this assertion has been made and repeated throughout discussions of prehensility, there is significant variation in both tail use and tail morphology across these taxa.

The relatively few available comparative studies of prehensile tail anatomy in primates have established that features of caudal osteology and myology are associated with properties that allow for improved resistance to high magnitudes of loading (Organ, 2008; Organ and Lemelin, 2011; Russo, 2013). However, tails are directly connected to the pelvis through the sacrum. While there has been some work regarding the primate sacrum, it has been largely focused on morphological correlates of tail length rather than of tail use (Russo and Shapiro, 2011; Russo, 2016; Nishimura and Russo, 2017). Given the degree of variation seen in the caudal vertebrae, there are reasons to expect that sacral morphology should also covary with tail prehensility, as the sacrum anchors the tail musculature and articulates directly with the proximal-most caudal vertebra, and thus must transmit all forces between the tail and the rest of the body (Badoux, 1974; Dalstra and Huiskes, 1995). With evidence that prehensile tails have evolved independently at least twice in New World Monkeys, and that there is clear variation in the use of tails, this raises the question of how sacral morphology differs between prehensile and non-prehensile taxa. Additional questions include whether sacral morphology varies with the type of prehension and whether different taxa evolve the same solutions to the biomechanical demands of prehension (Emmons and Gentry, 1983; Rosenberger, 1983; Lemelin, 1995; Lockwood, 1999). The first step in addressing these problems, and the goal of this thesis, is to carefully document and measure the anatomical correlates of prehension in the sacrum. Once such anatomical correlates, if they exist, are established, then questions of morphological adaptation to prehension can be asked.

Figure 1: Fully-prehensile (*Lagothrix lagotricha*) sacrum on the left, non-prehensile (*Colobus*) on the right.

a. Behavioral context

As with any investigation of form-function relationships, it is necessary to analyze the system in question with regards to both behavior and anatomy. Overall, data support the idea that the prehensile tail serves primarily as an assisting appendage during feeding and foraging; the difference between prehensile and semi-prehensile tails is the amount of weight which the tail is responsible for bearing, which often influences the context in which prehension occurs.

Cebus has been the focus of many of the studies concerning prehensile tails. Capuchins are known to use their prehensile tails as assisting appendages during foraging and feeding

(Garber and Rehg, 1999; Youlatos, 1999; Bezanson, 2012). In *Cebus apella* and *Cebus olivaceus* specifically, Youlatos (1999) observed conservative tail use, most frequently associated with what he describes as “critical situations in the canopy”; these critical situations comprise aberrant behaviors on treacherous substrates, such as climbing down a tree or bridging gaps in the canopy. It is important to note that *Cebus*, the only cebid exhibiting any degree of prehension, primarily utilize their tails for mass-distribution rather than mass-bearing, as they are semi-prehensile. In capuchins, it was observed that the tail bore equal or greater weight compared to any other limb during approximately 19% of feeding/foraging behaviors; the authors suggest that active flexion of the caudal musculature was extensively employed during such rare mass-bearing behaviors (Garber and Rehg, 1999). With regards to the current topic, if muscles are employed at higher frequencies, it follows that the attachment sites, some on the sacrum, must be proportionally robust. The patterns of tail use during various positional and behavioral contexts lead Garber and Rehg (1999, p 11) to postulate that, with respect to *Cebus capucinus*, the prehensile tail serves a “broad adaptive role” in providing access to food resources on small and medium substrates (i.e., tree branches in small and medium diameter, often terminal branches).

It has been suggested that prehension serves a different ecological role for ateline genera. In *Ateles* and *Lagothrix*, tails are fully-prehensile, elongated, and heavier than the forelimbs (Bezanson, 2012). Atelines are thought to represent the most derived condition in the order Primates, but there is still noticeable variation among the genera (Lemelin, 1995). *Ateles* are known as the predominant users of tail-only suspension, most frequently employing their tail for mass-bearing (Lockwood, 1999). Such behaviors are rarely observed in howler monkeys (Garber and Rehg, 1999). Prehension in *Ateles* is speculated to be linked to forelimb suspensory locomotion due to increased tail use during below branch travel and tail assisted arm swinging, while tail use in *Alouatta* is more similar to that of *Cebus capucinus*. Very rarely does *Alouatta* employ its tail as a mass-bearing fifth limb; more often prehension is used to increase access to food and to ensure safety during locomotion (Lockwood, 1999; Wheeler and Ungar, 2002). It has also been speculated that the active use of prehensility in locomotion of *Ateles* and *Lagothrix* functions to reduce lateral sway (Turnquist et al., 1999; Schmitt et al., 2005). Though speculation of varied ecological pressures was previously mentioned, some authors do convey the idea that the purpose of the prehensile tail is to increase ateline access to food and aid in resting behaviors by providing a fifth appendage for support (Lockwood, 1999).

It has also been suggested that allometric effects are noticeable in patterns of prehensile tail use, with larger taxa using their tail more often, but Garber and Rehg (1999) state that most primates extend their foraging radius via suspension (Wheeler and Ungar, 2002; Bezanson, 2012). The ontogeny, in this case the behavioral development, of prehensile tail use was examined in *Cebus capucinus* and *Alouatta palliata* by Bezanson (2012). The author suggests that changes in prehensile tail use should occur throughout life-history in association with body size, based on the hypothesis that if prehensile tail use is associated with the distribution of mass for resource attainment then larger individuals should employ the prehensile tail more frequently in said contexts (Bezanson, 2012). Ultimately there were no predictable patterns of usage, but it was found that infants and juveniles of both species utilized their prehensile tail more often than adult individuals (Bezanson, 2012). Wheeler and Ungar (2002) explored the suggestion of variation in tail use based upon body weight, specifically sexual dimorphism, in *Alouatta palliata*. However, no significant results were produced to support the hypothesis. Multiple studies have attempted to correlate body mass and tail use, but the results have been inconclusive (Grand, 1972; Bergeson, 1998; Wheeler and Ungar, 2002; Bezanson, 2012).

b. Caudal morphology

Very little of the literature directly applies to the sacrum, instead of discussing the sacrum as part of the sacro-caudal complex. Because of this, this review will by necessity focus on studies of caudal morphology that can be related to expected variation in sacral morphology.

i. Osteology

Tails, prehensile or not, can be divided into two morphologically distinct regions: proximal and distal (Ankel, 1972; German, 1982; Organ, 2008). The relatively few available comparative studies of prehensile tail anatomy in primates have established that features of the caudal vertebrae are associated with proximal tail flexibility and increased innervation to well-developed tail musculature. Proximal caudal vertebrae possess ventral and neural arches and a pair of transverse processes and articulate similarly to the manner of lumbar vertebrae; such articulations are suggestive of sagittal flexibility, which is correlated with the number of vertebrae in the proximal sequence (Organ, 2008). In prehensile tails, the proximal region is thought to be elongated, though the absolute length of the proximal caudal vertebrae makes no difference in prehension; the distal region is far more robust in prehensile animals (German, 1982; Organ, 2008). These properties allow for an increased muscular mechanical advantage of the tail abductor and ventrodorsal flexor musculature and improved resistance to high magnitudes of loading in tension (Organ, 2008; Organ and Lemelin, 2011; Russo, 2013). Between proximal and distal regions of the tail is a transitional vertebra, which possesses cranial zygapophyseal articulations and caudal intervertebral disc articulation. Distal caudal vertebrae, in comparison to proximal vertebrae, are longer and rounded with reduced transverse processes, allowing greater motion in all directions (Organ, 2008). Additionally, Organ found that all prehensile-tailed platyrrhines possessed more expanded muscle attachment sites in the distal tail region, which indicates that biomechanical loading in the distal caudal vertebrae of the tail from forces associated with suspension is much greater in prehensile than non-prehensile tails (Organ, 2008).

Rosenberger (1983) made several key observations with respect to atelines and cebids; he proposed that the osteological differences indicated that *Cebus* and *Ateles* are functionally and morphologically divergent, indicating that selection did not act upon them in the same way (Rosenberger, 1983). The tail of *Cebus* more closely resembles that of atelines than other cebids, in that reduced lumbar regions, increased size of ventral muscle bundles, smaller number of caudal vertebrae crossed by tendons of flexor muscles, wide neural arches on caudal vertebrae, and wide transverse processes in the dorsal region of the tail are observed (Garber and Rehg, 1999).

In *Ateles, Alouatta*, and *Lagothrix*, tails are fully-prehensile, elongated and heavier than the forelimbs (Bezanson, 2012). Cebids differ from atelines in that they lack a friction pad on the distal end of the tail, and there are only six proximal elements to the tail; atelines possess said friction pad and have eight proximal elements, with exception of *Alouatta* which has seven (Rosenberger, 1983). Atelines are thought to represent the most derived condition in the order *Primates*, given that non-prehensile primates possess fewer, only four to five, proximal caudal vertebrae (Lemelin, 1995). Conversely, the tails of cebines are only semi-prehensile, shorter relative to body length, comprised of six proximal caudal vertebrae, and weigh less than the forelimbs (Bezanson, 2012). *Ateles* have also demonstrated an increased number of smaller caudal elements in association with a function of decreasing lateral sway during locomotion (Turnquist et al., 1999; Schmitt et al., 2005). While *Ateles* appears to be the most prehensile of the studied species, it is worth noting that cebids and *Lagothrix* share similar uses and structures of tails. Cebids and *Lagothrix* have reduced caudal robusticity (Schmitt et al., 2005; Organ, 2008). As suggested by Rosenberger (1983), such morphological variation may be indicative of variable selective forces. Concerning convergence of prehension in New World Monkeys, Jones (2008) suggests that caudal robusticity and caudal transverse process width are ideal for studying the evolution of tail-assisted behaviors, given the observed variation between prehensile and non-prehensile taxa (Ankel, 1972; German, 1982; Organ, 2008).

However, tails are directly connected to the pelvis through the sacrum. While there has been some work regarding the primate sacrum, it has been largely focused on morphological correlates of tail length rather than of tail use (Russo and Shapiro, 2011; Russo, 2016; Nishimura and Russo, 2017). Additionally, there have been attempts to correlate variation in cortical bone of the sacrum between tailed and tailless primates. Sustained or differential loading over time changes cortical bone concentrations in post-crania, including the sacrum (Nishimura and Russo, 2017). Though trabecular bone contributes the most to bone strength, the contribution of cortical bone may increase when bending is a primary loading force (Nishimura and Russo, 2017). It was found that tailed and tailless primates could be differentiated based on cortical bone thickness, but no such difference exists between prehensile and non-prehensile tailed primates (Nishimura and Russo, 2017). Aside from bone composition, the degree of variation seen in the caudal vertebrae, there are reasons to expect that sacral morphology should also covary with tail prehensility.

ii. Myology

Myology of the prehensile tail largely reflects the patterns of variation seen in both behavior and osteology. Like previously discussed vertebral morphology, muscle morphology varies among prehensile and non-prehensile taxa (Ankel, 1972; German, 1982; Lemelin, 1995; Organ, 2008). Flexor and lateral muscles of prehensile-tailed primates are highly developed, primarily in the distal region of the tail; the masses of the m. extensor caudae lateralis and m. flexor caudae longus are uniformly distributed along the tail, with tendons that cross fewer joint segments than non-prehensile primates (Lemelin, 1995). However, there are few data regarding the true actions of primate tail muscles. Mm. intertransversarii caudae (ITC) have been stimulated, and they appear to produce ventral and lateral flexion toward the site of stimulation, helping the primate maintain contact with the substrate and leaving the body free to move in any direction (Lemelin, 1995; Organ, 2008). All other information regarding tail musculature is only known from descriptions of muscle origins and insertions (Organ, 2008). If fiber architecture in homologous muscles across prehensile and non-prehensile primate taxa is constant, then tendons of insertion crossing fewer joint segments would allow greater flexion and extension of the tail in prehensile taxa (Lemelin, 1995; Organ, 2008). However, though the robusticity of caudal vertebrae in relation to changing musculature has been investigated, there have been limited studies of changing origins and insertions relative to the sacrum (Lemelin 1995).

In atelines and *Cebus*, distribution of extensor and flexor muscles is uniform throughout the tail; additionally, in prehensile-tailed platyrrhines, long tendons cross an increased number of vertebrae before insertion (Lemelin, 1995). Well-developed flexor and intertransversarii caudae muscles further characterize prehensile-tailed primates (Lemelin, 1995). Lemelin suggests that differences in caudal muscle mass distribution are likely related to the grasping role of the prehensile tail; however, the underlying organization of the caudal musculature in prehensile-tailed platyrrhines does not differ significantly from that of non-prehensile-tailed primates (Lemelin, 1995). *Ateles*, arguably the most prehensile platyrrhine, has distinguishing myological features that set it apart: larger ventral muscle mass, expanded abductor caudae medialis, wide transverse processes of caudal vertebrae. This may be due to use of the tail to control lateral movements of the center of gravity during locomotion (Lemelin, 1995; Schmitt et al., 2005). The myology of the *Cebus* tail is most like that of non-prehensile tailed primates, perhaps a reflection of its limited usage (Lemelin, 1995; Garber and Rehg, 1999; Youlatos, 1999; Bezanson, 2012). Further, it has been demonstrated that prehensile-tailed taxa have increased physiologic cross-sectional areas (PCSAs) in all tail regions, which indicates that said taxa have a greater capacity to generate greater maximum forces (Organ et al., 2009; Hazimihalis et al., 2013; Rupert et al., 2014). However, there were no variations in pinnation angles, fiber lengths, or mass to tetanic tension ratios (Organ et al., 2009). Thus, the increased prehensile PSCAs must be driven by the increase in caudal muscle mass demonstrated by prehensile-tailed taxa; the authors speculate that such increases (greater ITC PCSAs) can be functionally linked to mass support during suspensory behaviors (Organ et al., 2009).

Among atelines, *Alouatta* consistently displays lower ITC PCSAs throughout the length of the tail. It is postulated that such morphological variation is due largely in part to phylogeny (Organ et al., 2009). The ratio of PCSAs in the tail of *Cebus* implies a behavioral change from that of atelines. *Cebus* tails have greater PCSAs in the proximal portion of the tail than all other taxa in the study, indicating that *Cebus* may grasp substrates using a more proximal portion of its tail (Organ et al., 2009). Such variation, both morphologically and behaviorally, provides further evidence of convergence on prehension by cebids and atelines.

Understanding the changing bony morphology of the caudal vertebrae in correlation with changing fiber type and composition is seemingly easily extrapolated to the relationship between sacral morphology and prehension. Ultimately, though the robusticity of caudal vertebrae in relation to changing muscular has been investigated, there have been no studies of changing sacral robusticity in congruence with caudal or pelvic musculature (Lemelin 1995).

2: BIOMECHANICAL LOADING AND SACRAL MORPHOLOGY

The sacrum has been repeatedly overlooked as a structure responsible for load bearing in many studies of the non-human primate pelvis. The lengthiest sources of information regarding the sacrum are clinical literature concerning sacroiliac displacement in humans. Studies of the morphology of the non-human primate sacrum do exist, but they concern sacral morphology in terms of bipedalism of extinct hominids. Fragments of information are buried within studies of pelvic loading which focus on the role of the ilium, ischium, and pubis in load transfer from the torso to the lower limb. These patterns are not unlike those seen in previous studies of caudal morphology. Below are overviews of bone response to biomechanical loading as well as current literature regarding pelvic (ilium, ischium, pubis) morphology. The purpose of this thesis is to determine whether sacral morphology varies with the type of prehension; more precisely, does the morphology of the sacrum change when it must have greater material strength?

A study of hominin bipedal adaptation completed by Machnicki et al. (2016) used the atelid lumbar region as a comparative sample to investigate pelvic functional morphology. Atelids exhibit a lordotic curve which is likely associated with their mediolaterally broad thorax and enlarged prehensile tail (Machnicki et al., 2016). While Machnicki et al. stated that lordosis in atelids is facilitated by a shorter iliac crest and reduced ligamentous restriction of the caudal lumbar vertebrae, which is a morphological response to occasional tail-assisted hindlimb suspension, other studies have shown that the ability of the pelvis to respond to selection is generally high among primates, with generally low levels of integration (Lewton, 2012; Machnicki et al., 2016). Many studies have correlated pelvic anatomy with locomotor behavior, but a lack of understanding of pelvic biomechanics has limited hypothesis testing (Lewton, 2015). The previous study correlates atelid lordosis to positional behaviors which are impacted by the action and morphology of the prehensile tail, though the weight-bearing function of the caudal anatomy is not discussed. Thus, interpretations of morphology, particularly of the pelvis, must be done with caution as they require an understanding of functional relevance and information on patterns of morphological integration, constraint, and evolvability (Lewton, 2012).

There have been studies of osteological correlates of tail length in the sacrum, but the results provide no insight regarding prehension. Nishimura and Russo (2017) found that tail-bearing primates have caudal articular surfaces that are mediolaterally broader than those of tailless primates. In addition, longer-tailed primates have well-developed spinous processes that are inferred to enhance leverage of tail abductor and extensor musculature (Nishimura and Russo, 2017). Though outside of the realm of this study, the authors also found that cross-sectional cortical bone thickness may provide insight as to tail presence or absence and length, but not prehension (Nishimura and Russo, 2017).

Prehensile or not, all tails are biomechanically relevant during both posturing and locomotion. The sacrum is directly inferior to the last lumbar vertebra, located between the iliac crests of the os coxae. With all of the focus on the ilium, ischium, and pubis, it seems appropriate that the sacrum should be investigated in the same capacity. Given that the last sacral vertebrae functions as the cranial articulation of the first caudal vertebrae, this bone is responsible for effectively “bridging” the torso and the tail, and thus should reflect changes in loading associated with tail use in prehension. However, though the primary function of the skeleton is one of mechanics, mass and morphology are the consequence of a mosaic of physiological demands (Ruff et al., 2006). Interactions of the mechanical capacity of the skeleton, the environment, and even the development process should be considered in all studies of functional anatomy and adaptation (Bock and Wahlert, 1965; Ruff et al., 2006). This is not to say that variation in consistent loading patterns plays no role in the formation of any structure; many of these other factors are beyond the scope of this study but will remain as point of discussion for this investigation of changing biomechanical demands due to degree of prehension and those consequences for quantitative differences in the non-human primate sacrum. Additionally, it is important to note that the primary use of the prehensile tail, suspension, places the system under tension rather than compression (Youlatos, 1999; Organ, 2008; Bezanson, 2012). Thus, weight-bearing will involve ligaments and muscle as much or more than articular surface area. As seen in studies of caudal vertebrae and musculature, placement of tissue has a varying degree of effect on morphology (Lemelin, 1995; Organ, 2008, 2010). Such differences in ratios and placements of musculature and ligaments could make a huge difference in the biomechanics of a prehensile tail.

CHAPTER 2: METHODS

1. HYPOTHESES

It is reasonable to expect that as rates of loading increase, the robusticity of the sacral morphology will increase. As previously stated, the goal of this study is to identify differences in primate sacra; the following hypotheses will be tested (Table 1). See Figure 1 for images of fully-prehensile and non-prehensile primate sacra.

Table 1: Hypotheses tested concerning quantitative differences in sacral morphology among prehensile groups.

H_0	Adjusting for size, quantitative sacral morphology is uniformly expressed across primates.
H_1	Quantitative variation in sacral morphology is correlated with degree of prehensility, being fully-, semi-, or non-prehensile.
H_{2a}	Prehensile-tailed taxa will show greater quantitative differences in articular surfaces in association with greater load bearing.
H_{2b}	Prehensile-tailed taxa will show greater quantitative differences larger lever arms and areas for attachment of tail muscles.

2. DATA SET COMPOSITION

Data were gathered on the sacra of *Alouatta*, *Ateles*, *Cacajao, Cebus*, *Chiropotes*, *Lagothrix*, *Macaca*, *Pithecia*, and *Saimiri* (total n = 103). All are New World monkeys, with the exception of *Macaca*, which serves here as an Old World, phylogenetic outlier.

With regards to phylogeny, some platyrrhine relationships remain unresolved. Newer molecular studies have generated some consensus though. Following Kiesling et al. (2015), three families are recognized: Cebidae, Atelidae, and Pitheciidae. The genera within each family are shown in Table 2. The issue of convergent prehension within New World monkeys has been discussed since at least 1983 (Emmons and Gentry, 1983). Most importantly, the divergent morphology and behavior of prehensile-tailed species in Cebidae and Atelidae suggest that the trait is not primitive, and therefore independently derived in both groups (Emmons and Gentry, 1983; Rosenberger, 1983; Jones, 2008).

Table 2: Depiction of genera within each family of the order Platyrrhini (Schneider and Sampaio, 2015).

Family	Genera
Cebidae	*Saguinus, Callithrix, Cebuella, Mico, Callimico, Leontopithecus, Saimiri, Cebus, Aotus*
Atelidae	*Alouatta, Lagothrix, Brachyteles, Ateles*
Pitheciidae	*Callicebus, Chiropotes, Cacajao, Pithecia*

All data were collected at the Field Museum of Natural History and the Smithsonian Museum of Natural History. All individuals were adults as determined by museum records and degree of ossification of the primary center and corresponding arches of each sacral body (White and Folkens, 2005, p 244). No individuals with obvious pathologies were included.

The taxa were classified as fully-, semi-, and non-prehensile; *Ateles, Alouatta,* and *Lagothrix* were categorized as fully-prehensile, *Cebus* as semi-prehensile, and the remainder as non-prehensile (Table 3). All individuals within each genus, regardless of sex or species, were pooled together for analysis; differences in means for cranial transverse process expansion are demonstrated in Figures 2 and 3, illustrating the discrepancy. Specimens were lumped by genus to avoid over-partition of variance; though this is a pilot study, the before mentioned methods for analyses indicate that the results must be interpreted with caution. *Ateles, Cebus,* and *Saimiri* were chosen to represent each category of prehension. As seen, while the means do differ, the variation is usually confined to three decimal places. Though small, these discrepancies suggest that the results should be interpreted with appropriate caution. The decision to split the data into the three behavioral categories helps somewhat to mitigate discrepancies in sample size. However, this study is comparative; rather than using species means, these analyses were completed using data from individuals within each group to examine the size of features relative to overall sacral size in an attempt to identify morphological correlates of prehension.

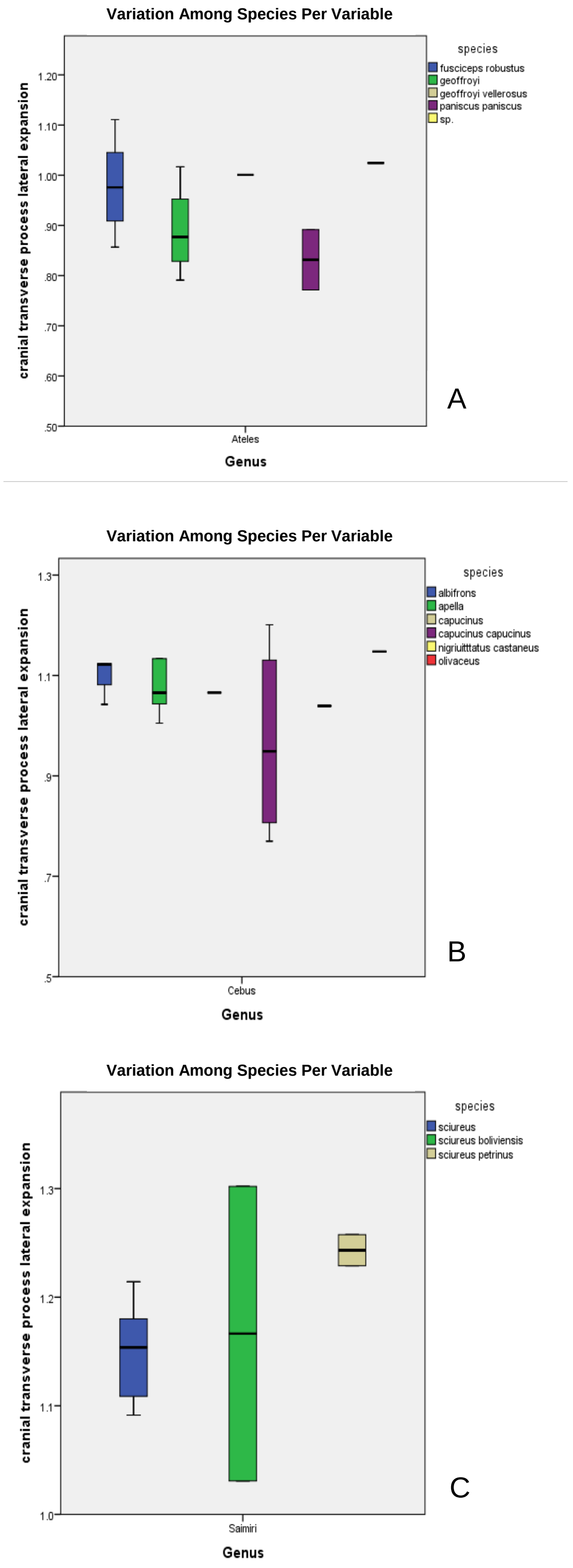

Figure 2: Boxplots A, B, and C showing means of cranial transverse process lateral expansion by species.

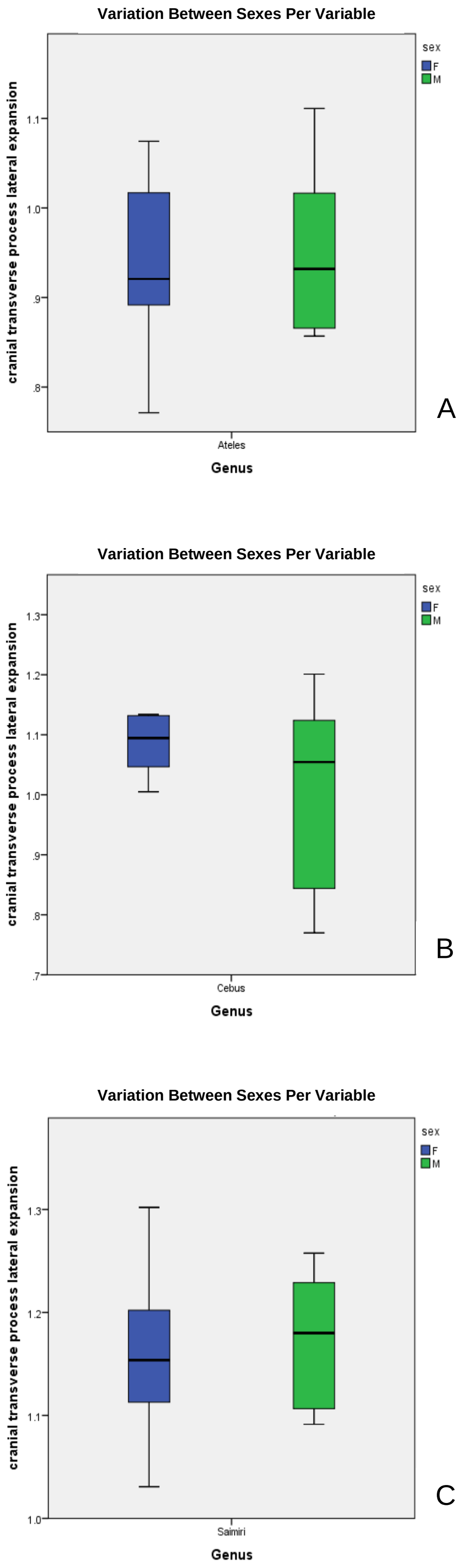

Figure 3: Boxplots A, B, and C showing means of cranial transverse process lateral expansion by sex.

Table 3: Composition of data set; overall number, as well as male and female samples.

Category	Genus	Species	n =	
			M	F
Fully-prehensile	*Alouatta*	*coibensis*	0	1
		fusca	0	2
		palliata	5	3
		seniculus	5	1
	Ateles	*fusciceps*	4	3
		geoffroyi	2	3
		paniscus	0	2
		sp.	0	1
	Lagothrix	*cana*	0	4
		lagotricha	2	5
		lugens	2	1
		poeppigii	0	2
		sp.	0	1
Semi-prehensile	*Cebus*	*albifrons*	3	1
		apella	2	3
		capucinus	4	3
		nigritus	0	1
Non-prehensile	*Cacajao*	*rubicundus*	1	0
	Chiropotes	*satanas*	3	3
	Macaca	*arctoides*	0	1
		cyclopis	1	0
		fascicularis	1	0
		mulatta	4	4
		nemestrina	1	1
		sylvanus	0	1
	Pithecia	*milleri*	*1*	*0*
		pithecia	*7*	*0*
	Saimiri	*sciureus*	*7*	*6*

As mentioned above, there has been some debate as to whether body size influences the type of prehension and frequency of prehensile behaviors employed. Means for body mass of genera included in this study range from .796 kg (*Saimiri)* to 8.56 kg (*Ateles)* (Smith and Jungers, 1997). Results of studies of the effect of body mass on prehensile function have been inconclusive (Lawler and Stamps, 2002; Wheeler and Ungar, 2002; Bezanson, 2012). Moffett et al. (2013) have demonstrated sexual dimorphism in the sacrum of the following catarrhine species: *Homo sapiens, Hylobates lar, Pan troglodytes, Nasalis larvatus, Pongo pygmaeus,* and *Pan paniscus*. Relevant to this study, Moffett et al. (2013) found that relative sacral breadth was highly dimorphic, which the authors attributed to obstetric constraints. In this study, sex was disregarded due to small sample size; however, a Mann-Whitney U was completed prior to lumping species and produced nonsignificant results, suggesting there were no significant differences between sexes within this sample.

Linear measurements for sixteen variables were collected using digital calipers. Measurements were recorded to the nearest one-hundredth of a millimeter (Table 4, Figure 4). Measurements that are not novel to this study were taken from two sources, Russo (2016) and Sachdeva et al., 2011. Each study concerns change in size and shape of the sacrum. Russo (2016) identified morphological correlates of tail length in the sacrum. Sachdeva et al. (2011) is a study of sexual dimorphism in the human sacrum.

It has already been demonstrated that *Ateles* has distinguishing osteological features (wide transverse processes of caudal vertebrae) to accommodate novel myological features associated with prehension (Schmitt et al., 2005; Organ and Lemelin, 2011). Prehensile-tailed taxa have increased PCSAs in all tail regions, which indicates that said taxa have a greater capacity to generate greater maximum forces. This should arguably require larger articular surfaces on the processes and vertebral bodies (Organ et al., 2009). The measurements taken here are not meant to represent the overall sacral size but, rather, features of muscular attachment relative to overall size. For example, transverse expansion of processes could maximize area between the processes could account for greater muscle mass. Essentially, the measurements were chosen to reflect patterns of osteological accommodations seen in caudal vertebrae.

Table 4: Linear measurements and their definitions.

Number	Name	Definition	Citation
1	cranial transverse process lateral expansion	Maximum lateral expansion of the transverse processes of the first sacral vertebra, measured as the transverse distance from the apex of the left transverse process to the apex of the right transverse process	This study
2	caudal transverse process lateral expansion	Maximum lateral expansion of the transverse processes of the last sacral vertebra, measured as the transverse distance from the apex of the left transverse process to the apex of the right transverse process	(Russo, 2016)
3	midventral craniocaudal length of sacrum	Maximum length from the midpoint of the sacral promontory to the middle of the anteroinferior border of the fifth sacral vertebra	(Sachdeva et al., 2011)
4	ventral mediolateral breadth of sacrum	Maximum mediolateral breadth of the ventral surface at the midpoint of the first sacral vertebra	(Sachdeva et al., 2011)
5	mediolateral breadth of cranial articular body (S1)	Maximum transverse distance of the cranial articular surface of the body of the first sacral vertebra	(Sachdeva et al., 2011)
6	mediolateral breadth of ala (left ventral)	Maximum transverse breadth from the maximum lateral expansion of the ala to the lateral edge of the body of the first sacral vertebra. Left side when viewed from the ventral surface of the sacrum.	(Sachdeva et al., 2011)
7	mediolateral breath of ala (right ventral)	Maximum transverse breadth from the maximum lateral expansion of the ala to the lateral edge of the body of the first sacral vertebra. Right side when viewed from the ventral surface of the sacrum.	(Sachdeva et al., 2011)
8	midventral length of S5 body	Maximum craniocaudal length of the last sacral vertebra at the midline of the ventral surface	(Russo, 2016)
9	mediolateral breadth of S5 cranial articular surface	Maximum mediolateral breadth of the cranial articular surface of the last sacral vertebra, taken on the ventral surface	(Russo, 2016)
10	craniocaudal length of sacroiliac articular surface	Maximum craniocaudal length of the sacroiliac articular surface as measured from the apex of the right alae (dorsal) to the apex of the caudal transverse process expansion	This study
11	craniocaudal length of median crest	Maximum craniocaudal length of the median crest as measured from the cranial, dorsal apex to the dorsal, caudal	This study

Table 4 cont.

Number	Name	Definition	Citation
12	dorsoventral height of median crest	Maximum dorsoventral height of the median crest as measured from the highest dorsal to the lowest ventral point at the cranial end of the sacrum	This study
13	dorsoventral height of cranial articular surface	Maximum dorsoventral height from the midpoint of the sacral promontory to the midpoint of the ventral border of the body of the first sacral vertebra	(Sachdeva et al., 2011)
14	dorsoventral spinous process height (caudal)	Maximum spinous process height of the last sacral vertebra	(Russo, 2016)
15	dorsoventral height of caudal articular surface	Maximum dorsoventral breadth f the caudal articular surface of the last sacral vertebra, taken from the midline of the vertebral body	(Russo, 2016)
16	mediolateral breadth of caudal articular surface	Maximum mediolateral breadth of the caudal articular surface of the last sacral vertebra, taken from the midline of the vertebral body	(Russo, 2016)

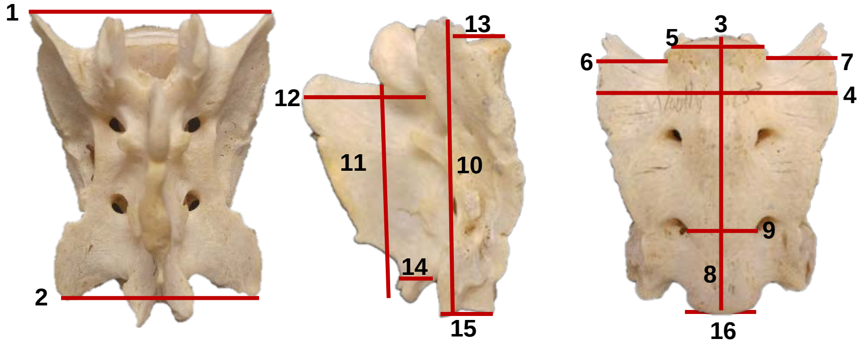

Figure 4: Depiction of measurements described in Table 4.

The goal of this study is to measure overall size as well as the size of biomechanically relevant features relative to the size of the sacral body. The data were transformed using a geometric mean to create Mosimann shape ratios to adjust for size (Jungers et al., 1995; Vinyard, 2008). The geometric mean used here was calculated as GEOM = sqrt(ventral mediolateral breadth * midventral craniocaudal length of the sacrum). Though simple, these two variables best account for the overall size of the sacral body, allowing for quantitative comparisons among taxa of various body mass, an issue that has been previously discussed at great length.

2. ANALYSES

Tests of normality demonstrated quantitative differences which violate many assumptions of parametric statistics. Linearity was not tested here, as the completed statistical analyses do not rely on linear relationships between variables. Due to the nature of the data, the assumption of independence is violated. Phylogenetic relationships influence independence and it is unknown whether specimens from any given taxon were taken from a single population (Nunn and Barton, 2001). Thus, it cannot be assumed that all observations in this sample have an equal probability of being observed. F-tests for two-sample variances were completed between fully- and semi-prehensile, fully- and non-prehensile, and semi- and non-prehensile groups for all variables. To control for multiple comparisons, a Bonferroni correction was applied ($\alpha = 0.05/3 = 0.017$). The homogeneity of variance was frequently violated. Of 64 F-tests, over 60% of them were significant; a few of these results are depicted in Table 5. Because of the violation of homogeneity of variance, non-parametric tests were employed.

Table 5: A representative sample of significant results of F-tests for unequal variances. Measurement numbers correspond to Table 4 ($\alpha = 0.017$).

Pairwise comparison	Measurement	F	*p*-value
Fully- vs. non-prehensile	caudal transverse process lateral expansion	0.27	< 0.001
Fully- vs. semi-prehensile	midventral craniocaudal length of sacrum	4.76	< 0.001
Semi- vs. non-prehensile	ventral mediolateral breadth of sacrum	0.31	0.006

Initial analyses were completed with Mann-Whitney U tests. Pairwise comparisons were completed for fully- vs. non-prehensile, fully- vs. semi-prehensile, and semi-prehensile vs. non-prehensile groups. A Bonferroni method was employed to control for Type I error caused by multiple comparisons; given that three comparisons per variable were being completed simultaneously, the critical alpha was adjusted as such: $\alpha = 0.05/3= 0.0167$.

A principal component analysis (PCA) was performed using all size-adjusted variables. A multivariate analysis of variance (MANOVA) was completed on the original Mosimann shape data in order to investigate the degree to which group means differ in morphospace. A MANOVA relies on the assumption of normality and homogeneity of variances. Because of the heteroscedasticity of the variance of the data used here, results of the MANOVA should be approached with caution. However, congruence between results of the parametric and non-parametric data suggest some robusticity of the MANOVA. Given that the hypotheses tested here are those of differences in shape in regards to the categorical variable of prehension, a multivariate analysis of variance is most appropriate to increase confidence in results from ordination tests, as it compares variation within groups to variation between groups in Euclidean shape space (Jolliffe, 1986, chap 9).

Discriminant function analysis (DFA), including jackknife resampling procedure, was carried out on the Mosimann shape transformed data. DFA can be used to determine whether a set of variables can effectively predict group membership. Though useful, small sample size limits the power of the DFAs, and so the results of this analysis should be approached with caution.

CHAPTER 3: RESULTS

1. PAIRWISE COMPARISONS

The Mann-Whitney U test returned significant results among all pairwise comparisons. Between fully and semi-prehensile groups, only five of 16 variables returned non-significant results (Table 6). The non-significant variables are mostly related to the overall size of the sacral body rather than the relative size of features, with the exception of the mediolateral breadth of the caudal articular surface. Generally speaking, differences between fully and semi-prehensile groups were associated with the width of process expansion, breadth of the sacral body and articular surfaces, and length/height of spinous processes and crests. Between fully and non-prehensile groups, six of 16 variables returned non-significant results. The trends are like those of the previously discussed comparison, though the height and length of the median crest were not significantly different. Lastly, between semi- and non-prehensile groups, seven of 16 variables returned non-significant results. This comparison differed from the previous two in that the non-significance was spread across measurements of overall size and relative feature size. Trends observed in this comparison included differences in spinous process expansion and size of vertebral articular surfaces.

Overall, the Mann-Whitney U demonstrated that transverse process lateral expansion, length/height of articular surfaces, and height of spinous processes differed among categories of prehension. All of these features can be presumed to be related to the size of the sacrocaudal musculature, as the increased bearing of force is associated with increased muscle mass, thus requiring more robust or larger attachment sites (Organ et al., 2009; Organ and Lemelin, 2011). As a whole, the measurements that differed significantly between groups were not unlike those previously observed in caudal vertebrae (Organ, 2008; Organ et al., 2009; Organ, 2010; Organ and Lemelin, 2011; Russo, 2013).

Both the results for the overall and multiple comparisons in the multivariate analysis of variance are significant ($p < 0.001$). The reported Wilks' Lambda for the overall MANOVA indicates that only 6.2% of the observed variance in sacral measurements is not explained by prehensile grouping. Wilks' Lambda is a measure of the percent variance in dependent variables unexplained by differences in levels of independent variables; reporting this value is most appropriate, as it best suits questions of morphological variance explained or unexplained by the degree of prehension. All pairwise comparisons indicate that fully-prehensile, semi-prehensile, and non-prehensile taxa are significantly quantitatively different in sacral morphology, thus supporting the stated alternative hypotheses.

Table 6: Mann-Whitney U results for all comparisons (α = 0.0167).

	Fully vs. semi-prehensile		**Fully vs. non-prehensile**		**Semi- vs. non-prehensile**	
Measurement	*U*	*p-value*	*U*	*p-value*	*U*	*p-value*
cranial transverse process lateral expansion	124.00	**< 0.0001**	183.00	**< 0.0001**	263.00	0.166
caudal transverse process lateral expansion	375.00	0.482	473.00	**< 0.0001**	162.00	**<0.002**
midventral craniocaudal length of sacrum	357.00	0.333	727.00	0.142	277.00	0.254
ventral mediolateral breadth of sacrum	357.00	0.333	727.00	0.142	277.00	0.254
mediolateral breadth of cranial articular body (S1)	222.00	**0.003**	276.00	**< 0.0001**	224.00	0.038
mediolateral breadth of ala (left ventral)	185.00	**< 0.0001**	575.00	**0.005**	274.00	0.233
mediolateral breath of ala (right ventral)	154.00	**< 0.0001**	572.00	**0.005**	278.00	0.262
midventral length of S5 body	357.00	0.333	782.00	0.327	248.00	0.099
mediolateral breadth of S5 cranial articular surface	103.00	**< 0.0001**	710.00	0.106	49.00	**< 0.0001**
craniocaudal length of sacroiliac articular surface	19.00	**< 0.0001**	240.00	**< 0.0001**	256.00	0.131
craniocaudal length of median crest	186.00	**0.001**	761.00	0.243	177.00	**0.004**
dorsoventral height of median crest	270.00	0.025	893.00	1.00	225.00	0.040
dorsoventral height of cranial articular surface	100.00	**< 0.0001**	622.00	**0.017**	275.00	0.240
dorsoventral spinous process height (caudal)	190.00	**0.001**	269.00	**< 0.0001**	248.00	0.099
dorsoventral height of caudal articular surface	281.00	0.037	216.00	**< 0.0001**	127.00	**< 0.0001**
mediolateral breadth of caudal articular surface	331.00	0.177	465.00	**< 0.0001**	116.00	**< 0.0001**

2. PRINCIPAL COMPONENTS ANALYSIS

Principal component (PC) axes 1 through 3 accounted for 80.7% of the overall variation, with axes 1 through 6 accounting for 93.4%. These axes are representative of changes in shape rather than isometric size because the variables were already size-adjusted; all reports of changes in length or breadth are relative to overall sacral size. Axis 1 shows strong positive loadings for cranial transverse process lateral expansion, craniocaudal length of sacroiliac articular surface and craniocaudal length of the median crest, and so reflects the overall expansion of sacral breadth, the articular surface, and the medial sacral spine (Table 7). Axis 2 shows strong positive loadings for cranial transverse process lateral expansion and ventral mediolateral breadth, and strong negative loadings for the midventral craniocaudal length of the sacrum and craniocaudal length of the median crest, reflecting a correlation of expanding sacral breadth with a reduction in length (Table 7). Axis 3 shows a strong positive loading for the caudal transverse process expansion and mediolateral breadth of the caudal articular surface, showing a correlation of expanding breadth and articular surface area. Axis 4 shows a strong positive loading for the craniocaudal length of the sacroiliac articular surface, and strong negative loadings for cranial transverse process lateral expansion and midventral craniocaudal length of the sacrum, reflecting the same correlations seen in Axes 1, 2, and 3. Axes 5 and 6 show no real differences between groups.

Cranial transverse process lateral expansion loads heavily on PCs 1, 2, (positively) and 4 (negatively). Figure 2 shows that fully and semi-prehensile individuals are clearly differentiated by this character, but non-prehensile individuals fall both outside and within the ranges of prehensile individuals. This suggests that the character has functional significance in terms of prehension. Midventral craniocaudal length of sacrum loads heavily on PCs 2, 4, and 6, with all being negative loadings. As seen in Figures 2, 3, and 4, fully-prehensile individuals tend to correlate with negative loadings on axes 2, 3, and 4 in contradistinction to heavily loaded features of cranial transverse process lateral expansion, ventral mediolateral breadth, mediolateral breadth of the caudal articular surface, and caudal transverse process lateral expansion. Therefore, these features may be related to the surface area required to account for an increased cross-sectional area of the musculature of prehensile individuals (Organ et al., 2009). Craniocaudal length of sacroiliac articular surface loads heavily on PCs 1, 4, and 6, further indicating the importance of articular surface size as a biomechanically important feature. This is interesting, however, as it suggests that the structure of the sacroiliac joint is correlated with prehensility. Craniocaudal length of median crest loads heavily on PCs 1, 2, and 6. As previously stated, such a correlation reflects established patterns of the importance of articular and anchoring surfaces seen in caudal vertebrae. This is interesting because the dorsoventral height of median crest loads heavily only on PC5; though, the effect of these two features is expected to be correlated, as each is associated with the surface area of articular surface for sacrocaudal musculature. Overall, the PCA demonstrated patterns that are congruent with those of caudal vertebrae. As discussed above, the sacrum shows similar morphological correlates of prehension and this analysis supports the alternative hypotheses (Table 1).

Table 7: Information from PCA, showing percent variance explained and factor loadings per axis. Bolded numbers are variables that are most highly loaded.

	PC1	**PC2**	**PC3**	**PC4**
% VARIANCE	37.842	26.061	16.803	6.425
LOADINGS				
cranial transverse process lateral expansion	**0.488**	**0.685**	-0.035	**-0.519**
caudal transverse process lateral expansion	0.149	-0.159	**0.860**	-0.154
midventral craniocaudal length of sacrum	0.114	**-0.326**	-0.107	**-0.337**
ventral mediolateral breadth	-0.122	**0.325**	0.099	0.324
mediolateral breadth of cranial articular body (S1)	0.027	0.116	-0.163	0.014
mediolateral breadth of ala LV	0.098	0.140	0.170	0.138
mediolateral breath of ala RV	0.086	0.158	0.161	0.175
midventral length of S5 body	0.055	-0.074	0.061	-0.111
mediolateral breadth of S5 cranial articular surface	0.029	0.011	0.123	0.062
craniocaudal length of sacroiliac articular surface	**0.660**	-0.049	-0.067	**0.608**
craniocaudal length of median crest	**0.493**	**-0.470**	-0.165	-0.170

Table 8 contd.

dorsoventral height of median crest	0.035	0.046	0.090	0.115
dorsoventral breadth of cranial articular surface	-0.084	-0.018	-0.058	-0.068
dorsoventral spinous process height (caudal)	-0.046	-0.018	0.137	-0.008
dorsoventral breadth of caudal articular surface	-0.019	-0.035	0.139	-0.071
mediolateral breadth of caudal articular surface	0.028	-0.049	**0.238**	0.022

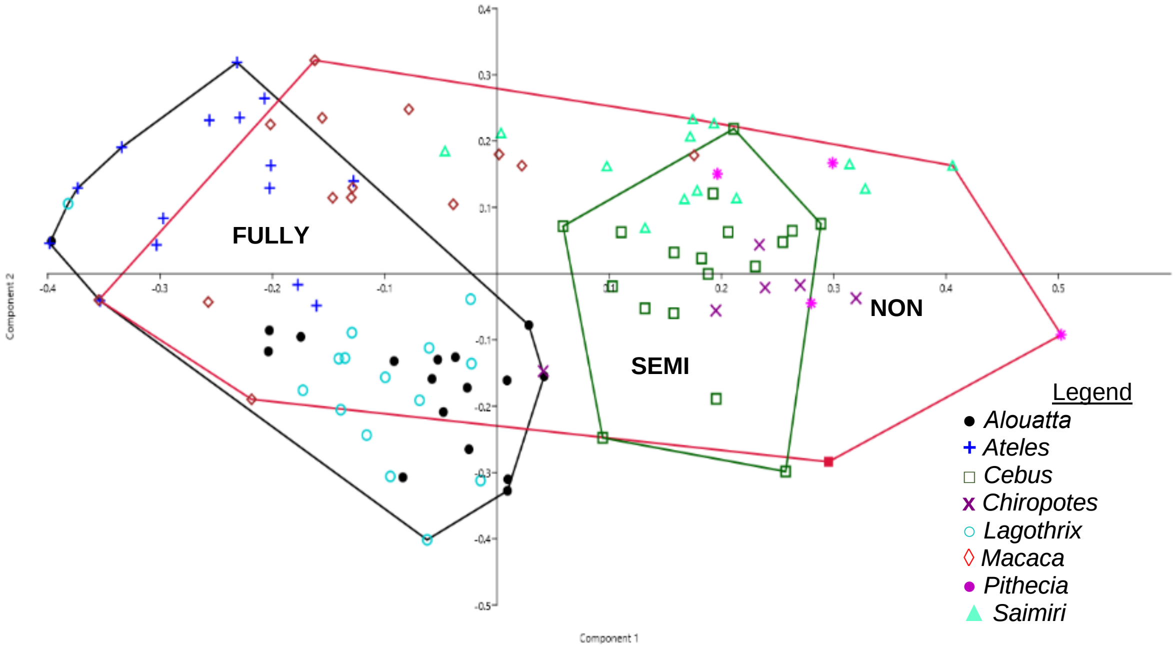

Figure 5: Scatterplot with convex hulls showing PCs 1 and 2.

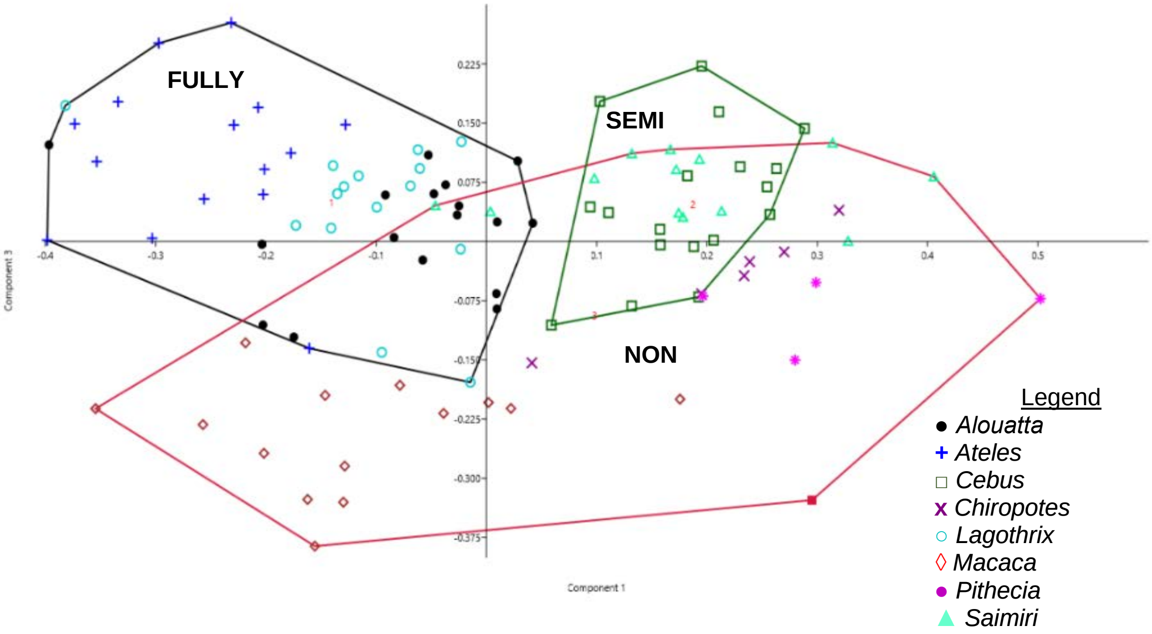

Figure 6: Scatterplot with convex hulls showing PCs 1 and 3.

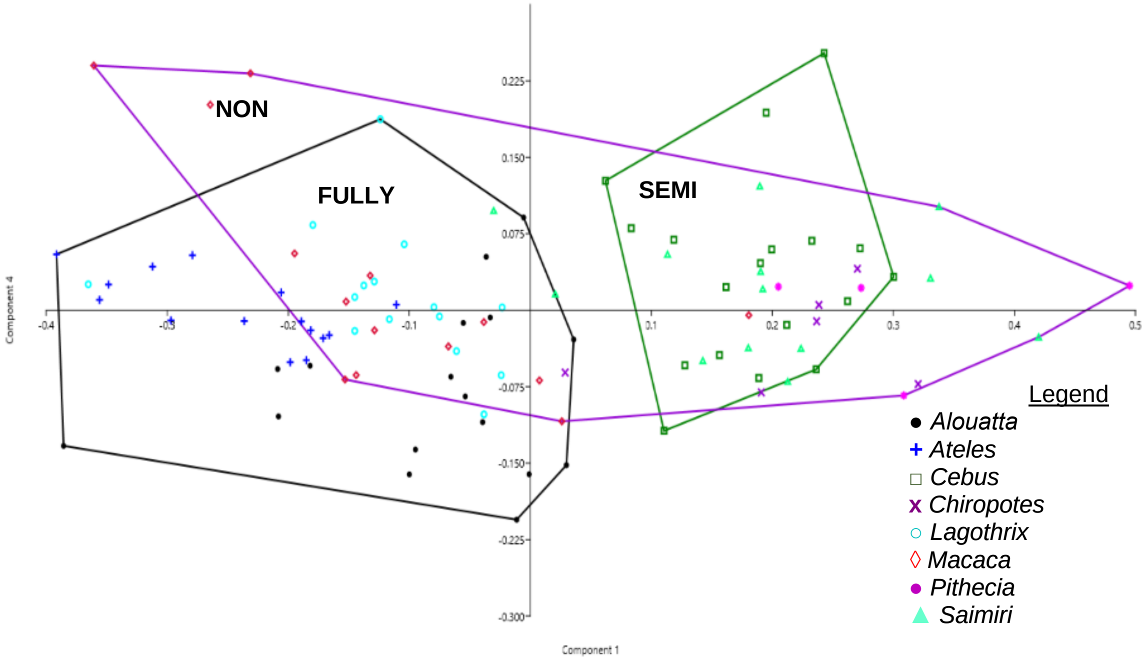

Figure 7: Scatterplot with convex hulls showing PCs 1 and 4.

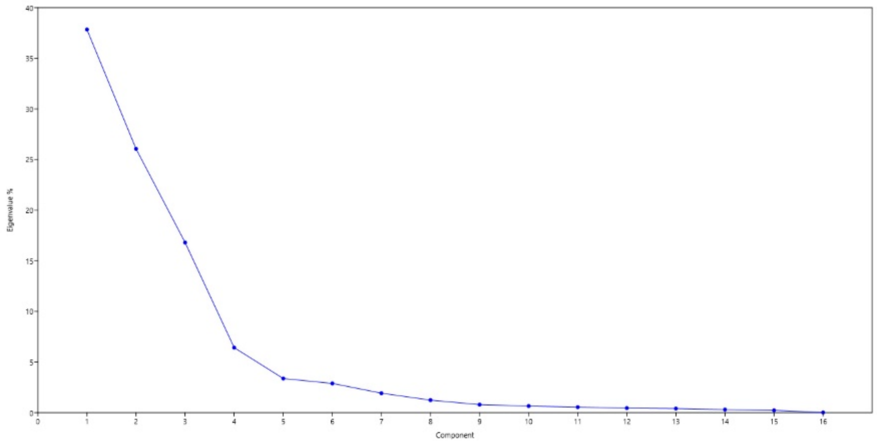

Figure 8: PCA scree plot.

3. DISCRIMINANT FUNCTION ANALYSIS

The DFA results are presented in Figure 9 and Table 8. Axis 1 discriminates most between groups, clearly separating fully-prehensile taxa from semi- and non-prehensile taxa. Measurements of transverse process expansion, mediolateral breadth of the cranial articular body (S1), craniocaudal length of sacroiliac articular surface, and height of median crest are the strongest drivers of axis 1. Axis 2 segregates the semi-prehensile taxa from the non-prehensile

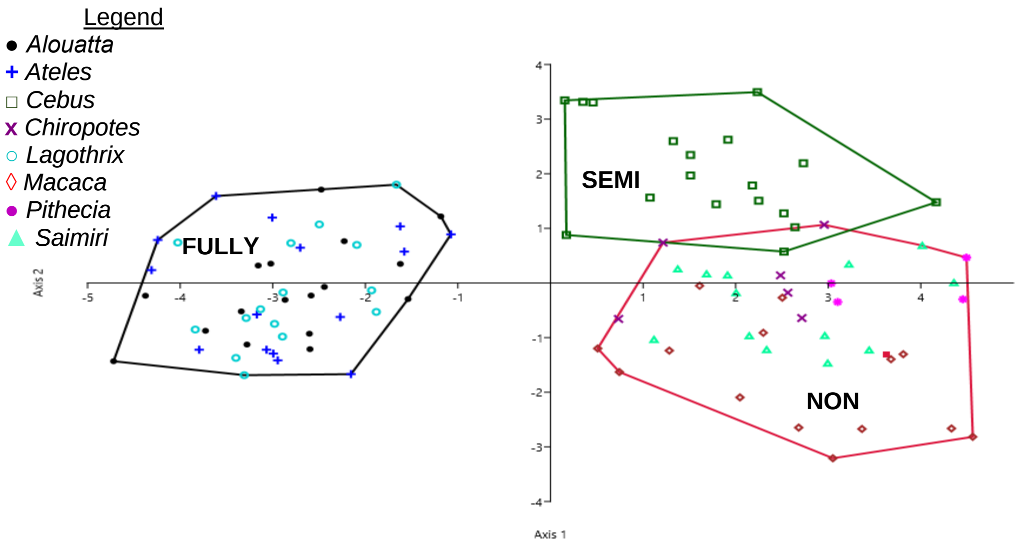

Figure 9: Discriminant function scatterplot showing separation of prehensile groups

taxa, with the fully-prehensile group overlapping both of these to a great extent. Measurements of the mediolateral breadth of the S5 cranial articular surface, the dorsoventral height of median crest, and mediolateral breadth of caudal articular surface load most heavily on axis 2.

Without jackknifing, the classification matrix demonstrates a 97.09% rate in successfully discriminating among prehensile groups based on all measurements. With jackknife resampling procedure, the classification matrix demonstrates a 90.29% success rate.

Table 8: DFA classification matrix. Jackknife resampling procedure results italicized.

	Fully	**Non**	**Semi**	**Total** (Given)	**% Correctly Classified**
Fully	47	0	0	47	100%
	46	*0*	*1*		*97.9%*
Non	0	36	2	38	94.7%
	1	*33*	*4*		*86.8%*
Semi	0	1	17	18	94.4%
	1	*3*	*14*		*77.8%*
Total (Predicted)	47	37	19	103	97.09%
	48	*36*	*19*		*90.29%*

As previously discussed, the results of the DFA must be interpreted with caution due to the relatively small sample size of the data set. However, it can be stated that the results at least suggest marginal discrimination in quantitative differences in sacral morphology among prehensile groups. These results are congruent with those of the PCA, only adding further support to the alternative hypotheses (Table 1).

CHAPTER 4: DISCUSSION

Results demonstrate that the fully-prehensile and semi-prehensile tailed monkeys differ in sacral feature size and shape from each other and non-prehensile tailed monkeys. The Mann-Whitney U tests demonstrated differences in central tendencies among fully, semi-, and non-prehensile groups. The pairwise comparison with the most significant differences was that of fully and semi-prehensile groups, with a total of nine significantly different variables. This is somewhat surprising, as it would seem intuitive that the sacra of those animals that are not prehensile would be most different from those that are prehensile. Of all the comparisons, semi- and non-prehensile sacra are most similar with regards to features hypothesized not to be related to prehension, in that their similarities were seen in relative size rather than shape. The PCA exhibited clear separation between fully and semi-prehensile groups in shape space. Though measurements that were not highly loaded are not to be disregarded as contributors to variation, the repeated appearance of the same variables on PCs 1 and 2, as well as similar anatomical measurements on PC 3, suggests that respect to points of anchorage for musculature strongly influence variation among groups. The MANOVA was most interesting in that Wilk's Lambda demonstrated only 6.2% of the variance in the sample is unexplained by the difference in the degree of prehension. This is especially important as the data were transformed using Mosimann shape variables, meaning that the contribution of isometric size in terms of variation in the sample was drastically reduced. This is corroborated by all significant pairwise comparisons. The MANOVA also functions to provide support and a significance level to the differences seen in the PCA; in this case, these two tests together provide support for all alternative hypotheses. Lastly, the DFA was a useful tool for determination of successful discrimination among groups based on the linear measurements taken.

First, through all analyses, quantitative sacral morphology was not uniformly expressed across primates. Secondly, there appears to be some degree of correlation of sacral morphology and degree of prehensility, as demonstrated by the Mann-Whitney U and PCA.

However, as discussed, the overlap of non-prehensile taxa with the other groups as seen in the PCA figures is somewhat puzzling (Figs. 5, 6, and 7). However, upon closer inspection, it seems that the size of the hulls is driven by outliers within the non- and semi-prehensile groups. The specimens of the non-prehensile group that overlap with the fully-prehensile group are those of the genus *Macaca*. None of the New World non-prehensile species overlap with the fully-prehensile group. Therefore, while it can be said that quantitative variation in sacral morphology is correlated to the degree of prehensility, the degree to which it correlates is variable. Cranial transverse process expansion loads heavily on PC 1; I hypothesize that the cranial breadth of the sacrum may be similar in *Macaca* and *Ateles* due to sitting behavior exhibited by both taxa, which may be responsible for increasing force of body mass transferred through the pelvis, thus requiring a more robust cranial sacroiliac articulation (Hinde and Rowell 1962; Mittermeier 1978). Further investigation with a larger data set that includes additional non-prehensile taxa would likely clarify the differences and similarities seen in the PCA.

Lastly, with regards to prehensile-tailed individuals having larger articular surfaces and larger areas for attachment of muscles, such patterns were seen in every analysis. Even though the PCA did show counterintuitive overlap between groups, the variables that likely caused the overlap were related to overall size rather than the relative size of mass-bearing features. It is important to keep in mind that the DFA was highly successful in classifying groups based on the degree of prehension. When considering the results of the PCA in conjunction with the DFA, it becomes increasingly apparent that the overlap seen in the PCA may have been strongly driven by the outliers. This is not to say that there are not places where the prehensile groups overlap morphologically, but these preliminary results should be considered promising rather than deterring. The linear analysis illustrated clear differences among groups, further supporting the previous statement. In summary, there is strong evidence to support all alternative hypotheses seen in Table 1.

1. SACRAL MORPHOLOGY, PREHENSION, AND ADAPTATION

There are clear differences in the sacral morphology of fully-prehensile, semi-prehensile, and non-prehensile groups. However, contrary to predictions, semi- and non-prehensile sacra are most similar. One would postulate that the sacra of those animals that are not prehensile would be most different from those that are prehensile, suggesting some other factor may be at play. I speculate that it may be due to a similarity in overall size of the cranial end of the sacrum, due to the fact that both the semi- and non-prehensile individuals would not have to morphologically compensate in the way a fully-prehensile animal would. This speculation should be investigated once knowledge of sacrocaudal and sacrolumbar musculature of prehensile-tailed animals has been obtained. Analyses of fully and non/semi-prehensile sacra produced the same number of significant pairwise comparisons, which indicates that perhaps better characters could have been chosen. Every trait cannot be discussed as an adaptation, so there is no reason to assume that all measurements taken can provide information on the structure/function relationship of the sacrum.

It cannot be said that the osteological variation seen here is caused solely by changing myology, due to the limitations of the literature. Organ and Lemelin have described caudal myology at great length, but with little emphasis on the relationship of the first caudal vertebrae to the last sacral vertebrae; further, no comparative dissections of prehensile and non-prehensile pelvic (including sacral) myology have been completed (Lemelin, 1995; Organ et al., 2009; Organ, 2010; Organ and Lemelin, 2011). Thus, any statements on the influence of myology made here are purely speculations based on patterns of functional morphology seen in other parts of the primate body. The breadth of sacral alae has been previously identified as being correlated to the degree of bipedality, demonstrating a relationship between structure and function of the sacrum in behavioral contexts (Machnicki et al., 2016). It has been discussed at great length that functional correlates of prehension exist in caudal bony morphology (see Chapter 1, part *b* of this text). The current knowledge of caudal and sacral correlates of behavior suggests there is no reason to doubt that quantitative differences in morphology demonstrated here may have functional significance.

Biomechanics in and of itself is not sufficient to explain the wide array of morphological adaptations seen throughout primate taxa (Badoux, 1974). For example, brachiation is made possible through a specialized morphological and locomotor repertoire, but that specialized morphology is not enough to ensure survival (Badoux, 1974). When considering the morphological integration of the entire skeleton, one must accept the idea that all features are used and valuable, though there are different approaches to interpreting anatomy (Ward, 2002). Biomechanical adaptations are only one influencing factor on a variety of structural characteristics acquired during evolution (Badoux, 1974; Ross et al., 2002; Ward, 2002; Ruff et al., 2006). Furthermore, the knowledge of the musculature associated with prehension is nearly nonexistent, found only in the works of Lemelin and Organ (Lemelin, 1995; Organ, 2008; Organ et al., 2009; Organ, 2010; Organ and Lemelin, 2011). Even then, this literature is confined only to the musculature of the tail itself, not its attachment to the torso. This study is promising in that it indicates that more extensive research of the osteology of the sacrum and soft tissue surrounding the pelvis could provide insight as to adaptive responses to changing biomechanical loads as a result of behavior.

2. FUTURE DIRECTIONS

Using what is known of the current platyrrhine lineage and postulated selective pressures responsible for the evolution of the prehensile tail, environmental paleo-reconstruction and functional correlates of prehension could provide insight as to the relationship between selective pressures and tail use (Organ, 2010). There has already been research suggesting that sacral morphology is useful in reconstructing tail length of extinct primates, so the idea that sacral correlates of prehension could be identified in the fossil record is not unfounded (Russo and Shapiro, 2011; Russo, 2016; Nishimura and Russo, 2017). While the quantitative changes of the sacrum seen here may provide glimpses into differing responses to the biomechanical demands of prehension, further study including dissection and geometric morphometric comparison is necessary to make stronger statements on the functional role of the sacrum during prehension. It is only known that in linear space, fully, semi-, and non-prehensile individuals have statistically different sacral morphology with regards to features that are associated with muscle attachment, such as the size of spinous processes and length/height of articular surfaces. Ultimately, identification of clear morphological correlates of prehension may lead to the ability to identify its origin in the fossil record, thus aiding in the understanding of the evolution of forest niches themselves.

5. CONCLUSION

Functional correlates of prehension seen in the caudal vertebrae provide reason to hypothesize patterns of covariation in morphology of the sacrum. The ability to ask further questions concerning the effect of morphological response to changing biomechanical loading in association with prehension requires preliminary investigation of sacral morphology. The comparative analyses completed here support hypothesized covariation of sacral morphology and prehension. Throughout all analyses, relative size and transverse expansion of spinous processes, relative size of features associated with postulated muscle attachment, and relative size of articular surfaces of sacral vertebrae differed among individuals of varying prehensility. However, similarity of prehensile and non-prehensile individuals indicates the need for further investigation including an expanded data set and information regarding the myology of the sacro-caudal and sacro-lumbar complex. Future studies should also include prehensile-tailed non-primate mammals, as seen in previous analyses of caudal vertebrae and prehensility.

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