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MULTIVARIATE ANALYSIS OF THREE-DIMENSIONAL TRABECULAR BONE  
ARCHITECTURE IN LIVING AND FOSSIL PRIMATES

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## ABSTRACT

Trabecular bone architecture changes in response to mechanical loading from repetitive locomotor behaviors. This has been demonstrated in mammals and birds, and trabecular characteristics have been used in past studies to comment on behaviors of extinct species. This study analyzed the trabecular architecture of the femoral heads of individuals from a sample of small bodied extant primates (n=125) from 14 genera (*Avahi*, *Callithrix*, *Cebus*, *Cheirogaleus*, *Galago*, *Hapalemur*, *Lemur*, *Loris*, *Microcebus*, *Otolemur*, *Perodicticus*, *Propithecus*, *Saimiri*, and *Tarsius*) that engage in three distinct types of locomotor behavior: vertical clinging and leaping, slow climbing, and arboreal quadrupedalism. Using the known locomotor behaviors of these primates, a discriminant function analysis was used to determine whether there were significant differences in the femoral head trabecular structure among the extant locomotor groups. In addition, this multivariate analysis was used to predict the locomotor behaviors of several fossil Eocene primates (*Adapis*, *Apidium*, *Karanisia*, *Parapithecus*, *Omomys*, and *Shoshonius*) based on their femoral head trabecular bone architecture. The results of this study suggest that there are significant structural differences in the trabecular architecture of primates engaging in vertical clinging and leaping, slow climbing, and arboreal quadrupedalism. Three of the fossils, *Karanisia*, *Omomys*, and *Shoshonius*, had well preserved trabecular structure. *Karanisia* was consistently grouped with extant arboreal quadrupeds, and *Shoshonius* with slow climbers, while the group affiliation of *Omomys* depended on the type of DFA analysis. This taxon was predicted as both a slow climber and a vertical clinger and leaper.

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## **Chapter 1**

### **Introduction**

Together fossil and molecular evidence provide context to the timing and patterns of primate evolution. The field of functional, or evolutionary, morphology seeks to complement this understanding by investigating behavioral adaptations and changes over time as a way to understand the adaptations of past species. Locomotor behavior has been of particular interest in primate evolution and different approaches have been taken in an attempt to identify the locomotor adaptations of our earliest ancestors. Classically this has been done by using the external morphology of living primates as referential models (Dagosto et al., 1999; Anemone and Covert, 2000; MacLatchy et al., 2000).

With the advent of virtual paleontology, the application of computational and digital techniques to paleoanthropological questions, there has been a significant increase in studies looking at internal aspects of bony morphology. For example, there have been numerous reconstructions of fossil behavior based on semicircular canal morphology (Walker et al., 2008; Silcox et al., 2009; Ni et al., 2010; Ryan et al., 2012), cortical bone thickness (Lovejoy, 1988; Pina et al., 2012; Trinkaus and Ruff, 2012; Ruff and Higgins, 2013; Shaw and Stock, 2013), and trabecular bone structure (Thomason, 1985 a,b; Fajardo and Müller, 2001; MacLatchy and Müller, 2002; Ryan and Ketcham 2002b; Ryan and Walker, 2010; Desilva and Devlin, 2012; Ryan and Shaw, 2012). This paper seeks to reconstruct the locomotor behaviors of several Eocene primate species based on

the fossilized trabecular bone architecture of their femoral heads using extant primates for comparison.

### **Primate Evolution and Locomotion**

The earliest known primate fossil evidence from the late Paleocene and early Eocene and molecular divergence dates place the origin of primates at approximately 70 million years ago (Steiper and Seiffert, 2012). Molecular analysis by Springer et al. (2007) groups primates into the Euarchontoglires clade of mammals, supporting earlier genetic and morphological studies that came to the same conclusions. Their analysis grouped primates closest to the sister-taxa Dermoptera and Scandentia, made up of flying lemurs and tree shrews, respectively (Springer et al., 2007).

Identifying the earliest adaptations of primates along with the ecological context of these early species is important in understanding the selective pressures that drove early primate evolution. Modern arboreal tree shrews exhibit climbing, leaping, and grasping behaviors, and such behaviors could represent a model for primitive primates (Sargis, 2001). Evidence supports the hypothesis that primates originated in Asia in tropical forest environments (Jablonski, 2005). Unlike their modern counterparts, fossil primate species are distributed across Asia, Europe, and North America in the early Eocene, and found in Africa in the later Eocene when climates were warmer than they are today (Jablonski, 2005; Gingerich, 2012).

Modern non-human primates exhibit a wide range of locomotor behaviors, such as arboreal and terrestrial quadrupedalism, leaping, climbing, brachiation, and knuckle walking (Fleagle, 1999). Locomotor behavioral differences are important in studying adaptive radiation in primates (Ripley, 1967). Locomotion influences posturing behaviors, and has a complex relationship with size and feeding behaviors (Fleagle, 1999). The three types of locomotor



behaviors addressed in this study are vertical clinging and leaping, slow climbing, and arboreal quadrupedalism.

Vertical clinging and leaping was first described by Napier and Walker (1967), who hypothesized that this was the ancestral form of primate locomotion based upon morphological comparisons of modern vertical clinging and leaping primates to Eocene fossil primates (Gebo, 2011). Vertical clinging and leaping is differentiated from other leaping behaviors in that the leaping is done from a vertical posture rather than a horizontal one, there is also an emphasis on the hindlimbs where as other leapers use all four limbs in leaping (Napier and Walker, 1967; Connour et al., 2000; Gebo, 2011). This locomotor behavior may be an adaptation for predator avoidance (Petter, 1962; Crompton and Sellers, 2007). While this behavior is observed in several distantly related species such as tarsiers, galagos, and indriids, it is more likely to be a case of convergent evolution than an ancestral condition (Gebo, 2011).

The extent of homoplasy, or similar traits or behaviors that arise independent of common ancestry, in primate locomotion is not completely clear. While homoplasy can lead to challenges for phylogenetic reconstruction, it is an invaluable tool for assessing morphological adaptations (Lockwood and Fleagle, 1999). Homoplastic features of the internal and external femoral bony anatomy have been used in the past to make inferences of adaptive locomotor behaviors in primates (Ryan and Ketcham, 2002b; Ryan and Ketcham, 2005). Gebo (2011) investigated homoplasy in vertical clinging and leaping behaviors shared by strepsirrhines and haplorrhines, believing that such behavior has evolved independently several times in primate evolution.

Slow climbing, specific to lorisiformes such as *Loris* and *Perodicticus*, is typified by a slow and stealthy climbing behavior with very rare jumping (Walker, 1969; Runestad, 1997). This behavior appears to be highly specialized (Runestad, 1997). In the visual predation hypothesis, Carmill (1972) used lorises as an illustrative example because their specialized locomotor behavior allows for quiet movements, and an increased use of grasping hands for

predation. Slow climbing behaviors therefore may have been an adaptation to allow for arboreal hunting on small branches (Nekaris, 2005).

Arboreal quadrupedalism is the most generalized category of locomotion addressed in this study, and is exhibited by the greatest number of species in the sample. This behavior allows for movement through branches, though the range of possible motions may be constrained by body size with observed leaping behaviors decreasing as body size increases (Fleagle, 1999). A generalized form of this behavior that involves some climbing and leaping has been hypothesized as being the ancestral form of locomotion in primates (Martin, 1972; Gebo, 2011). Arboreal quadrupedalism has been suggested by Cachel (1979) to have been important in early anthropoid evolution by allowing for a dietary shift towards frugivorous feeding and increased body size.

The earliest primates were likely small in size and featured a suite of traits that have been interpreted as indicating arboreality, insectivory, and frugivory (Cartmill, 1974; Fleagle, 1999; Jablonski, 2005). It has been suggested that ancestral primates were similar to modern cheirogaleids from Madagascar (Gebo, 2011). Cheirogaleids, which includes dwarf (*Cheirogaleus*) and mouse (*Microcebus*) lemurs, are a primitive group of nocturnal, omnivorous, arboreal quadrupeds that engage in climbing and leaping behaviors (Fleagle, 1999).

Leaping would have been an important locomotor behavior in the ecological context of early primate habitats (Jablonski, 2005; Gebo, 2011). A possible adaptive explanation is that leaping allows for small animals to quickly bridge gaps between branches (Fleagle, 1999). External morphological analyses of fossil primate postcrania have suggesting leaping behaviors in a variety of early species. Omomyoids have long been studied since their discovery in the 1800's, and they have been widely interpreted as leapers due to their similarities to strepsirrhines and tarsiers (Gingerich, 1981). Two fossil omomyoids in this study, *Omomys carteri* and *Shoshonius cooperi*, have been formally described by Anemone and Covert (2000) and Dagosto et al (1999) respectively as having features associated with leaping.

A grasping leaping hypothesis of early primate locomotion was proposed by Szalay and Dagosto (1988) based on early primate fossils and comparisons to plesiadapids. Grasping hands are an important primate feature both for locomotion and feeding (Fleagle, 1999). This locomotor style could have eventually diverged into the fast vertical clinging and leaping (Szalay and Dagosto, 1988). Grasping is also an important feature of Cartmill's (1972, 1974) visual predation hypothesis and Sussman and Raven's (1978) terminal branch feeding hypothesis.

In summary, leaping and grasping have long been recognized as important primate adaptations. In an arboreal context, locomotor features such as grasping hands and leaping behaviors would have been important in food acquisition and quick branch to branch movement (Cartmill 1974; Szalay and Dagosto, 1988; Fleagle, 1999; Jablonski, 2005). External morphological features have been used to infer leaping behaviors in early fossil primates, and the purpose of this study is to see if trabecular structure can be used to evaluate such reconstructions.

### **The Biomechanics of Trabecular Bone**

The field of functional morphology has seen a huge growth in the use of high resolution computed tomography (microCT) for studying bone and other tissue. Specifically, microCT can offer unique insight into the three dimensional structure of trabecular, or cancellous, bone. Trabecular bone is named for the trabeculae (small rod like structures) which compose it, and it is often described as having a spongy appearance (White, 2005). As depicted in Figure 1, it is difficult to appreciate the complexity of trabecular bone structure from a two dimensional representation.

As described by White (2005), trabecular bone forms throughout the skeleton, but is limited to areas of tendon attachments and the proximal and distal ends of long bones. Trabecular bone is highly porous, and while it makes up a high volume of the skeleton, it only contributes a

very small amount to overall skeletal mass (Swartz, 1993). The bony pores house red marrow and are a site of blood production in the bone (Keaveny et al., 2001; White, 2005). Biologically speaking, the materials that compose trabecular bone are the same as cortical, or compact, bone that comprises most of the skeleton; however, these two types of bone behave very differently mechanically (Swartz, 1993; Keaveny et al., 2001). Trabecular bone is heterogeneous throughout the body; the focus of this paper is only on the architecture of the trabecular bone located within the femoral head. Trabecular bone is also highly anisotropic, meaning its mechanical behavior is affected by orientation (Swartz, 1993; Odgaard et al., 1997; Keaveny et al., 2001).

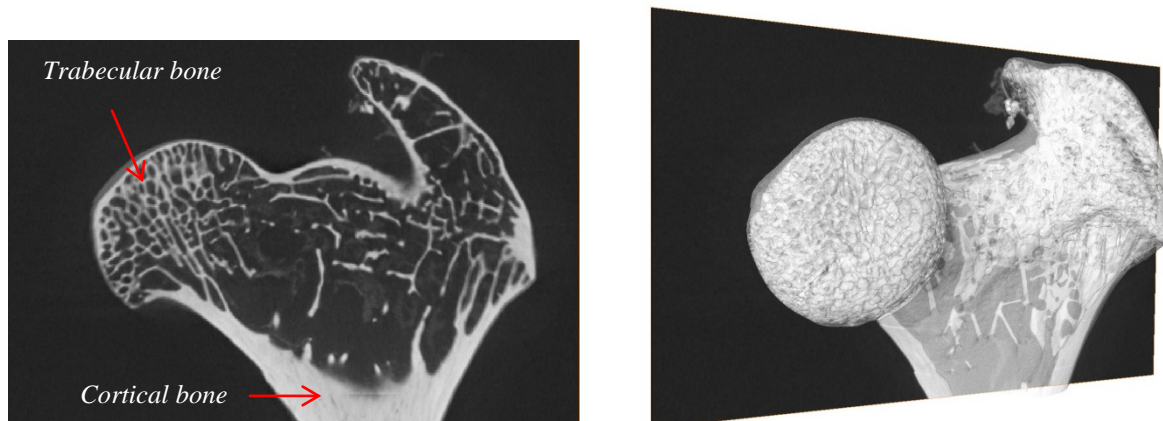


Figure 1: A comparison of a 2D microCT slice (left) and a 3D rendering of stacked microCT slices (right) of a *Lemur fulvus rufus* (MCZ 16355) proximal femur. The 3D image is a semi-transparent to show the complex bony matrix of trabeculae within the head. Both images were created using Avizo 7.0.

The response of bone structure to mechanical loading has been recognized for over a century, and was popularized by Julius Wolff in the late 1800's (Pearson and Leiberman, 2004; Ruff et al., 2006; Barak et al., 2011). Experiments have sought to quantify the three-dimensional structure of trabecular bone to relate it to mechanical and elastic properties of the bone (Odgaard et al., 1997; van Rietbergen et al., 1998). It was shown by van Rietbergen et al. (1998) that bone volume fraction (the measure of bone in a given volume of analyzed trabecular bone) and four different fabric measures are highly correlated with elastic properties of bone.

As recently demonstrated by controlled experiments by Pontzer et al. (2006) in birds and Barak et al. (2011) in sheep, the concept of Wolff's Law, that bone remodels in response to mechanical force, holds true at the trabecular level. Therefore, homoplastic trabecular structures oriented in response to specific locomotor patterns can be quantified and used to infer similar behaviors in fossil mammals. The full extent of the relationship between mechanical loading and bone remodeling is not understood. While Barak et al. (2011) demonstrated trabecular response to controlled mechanical loading, Pearson and Lieberman (2004) bring up the role of ontogeny and bone response and how age may affect the process. Bone remodeling is a complex interplay of development and function, and by using a large, diverse sample of primates this study seeks to see how strong the influence of function is upon the trabecular architecture of the femoral head.

Previous work on trabecular bone variation in extant strepsirrhine primates has produced important insights into the functional morphology of the hip joint. MacLatchy and Müller (2002) applied this idea of trabecular architectural adaptation to locomotor behavior to two species of strepsirrhine, *Galago senegalensis* and *Perodicticus potto*. These closely related primates each exhibit different and highly specialized locomotor behaviors, with *G. senegalensis* being typified by vertical clinging and leaping (VCL) while *P. potto* exhibits a slow climbing behavior (MacLatchy and Müller, 2002). MacLatchy and Müller (2002) came to the conclusion that the overall bone volume and density of the trabecular bone was not different between the species, but that *G. senegalensis* exhibited a much higher degree of anisotropy.

A similar study by Ryan and Ketcham (2002a) compared a greater number of strepsirrhine species (*Cheirogaleus major*, *Avahi laniger*, *Galago senegalensis*, *Galago alleni*, *Loris tardigradus*, *Otolemur crassicaudatus*, and *Perodicticus potto*) at the trabecular level by looking at anisotropy and bone volume fraction. Like MacLatchy and Müller (2002), Ryan and Ketcham (2002a) found high anisotropy in the galagos and other leapers, and lower anisotropy in the slow quadrupedal climbers and the quadrupedal generalist *Cheirogaleus*. Further work by

Ryan and Ketcham (2002b) used trabecular bone structure to reconstruct locomotor behavior in the extinct omomyoids *Shoshonius cooperi* and *Omomys carteri*. They found that *Omomys* showed structural similarities to *Galago* and *Otolemur*, and *Shoshonius* was similar to *Cheirogaleus*, *Loris*, and *Perodicticus* (Ryan and Ketcham, 2002b). The current study expands on this previous work by using multivariate analyses of a large number of trabecular bone structural features in a large sample of small-bodied primates to reconstruct locomotor behavior in several fossil primates from the Eocene. The sample was restricted to small-bodied taxa under 2.5 kg because work suggests a relationship of body size with trabecular variables (Swartz et al., 1998; Doube et al., 2011; Ryan and Shaw, 2013).

## Chapter 2

### Materials and Methods

#### Skeletal Sample

The skeletal sample used in this study consisted of one femur per individual from a sample of extant primates (n=125) from 14 genera, and fossil primates from 6 genera (n=7) (Table 1). The taxa represent a diverse sample of strepsirrhines, as well as several species of small platyrrhines. The extant primates used were wild shot adults that showed no external signs of pathology. Two species used *Cheirogaleus major* and *Tarsius syrichta*, were obtained from the Duke Lemur Center osteological collection and thus represent captive individuals (n=5). The fossil primates included in this study are from the Eocene and represent several genera, *Adapis*, *Apidium*, *Karanisia*, *Omomys*, *Shoshonius*, and *Parapithecus*. *Karanisia* is a probable stem lorisiform, and a candidate common ancestor for modern lorises and galagos (Seiffert, 2007). *Omomys carteri* (UC-68703) and *Shoshonius cooperi* (CM-69764) are both North American Eocene omomyids (Dagosto et al. 1999; Anemone and Covert, 2000). *Adapis parisiensis* (ACQ-263) is a late Eocene adapine (Fleagle, 1999). *Apidium phiomense* (DCP-1030, DCP-18641) and *Parapithecus grangeri* (DCP-6139) are both late Eocene early Oligocene parapithecids, a group of early anthropoids from Egypt (Simmons, 1986; Fleagle and Simmons, 1995).

Body mass values for both living and fossil species were estimated using the methods described by Payseur et al. (1999) using femoral head height (FHH). This measure was chosen because it was consistently the least distorted aspect of the femoral head in the fossil specimens. Measurements of the extant species were collected using digital calipers. Femoral head measurements for the fossils were taken digitally using Avizo 7.0 image visualization software

(Visualization Sciences Group, Inc., Burlington MA). For the fossils, the regression model developed by Payseur et al. (1999) for all primates rather than for specifically strepsirrhines or haplorhines was chosen given the range of fossil species represented in the sample and because of the phylogenetic uncertainty of where some of these fossils fall in the greater picture of primate evolution. The most appropriate regression equation for each extant primate clade was used to estimate body masses for living primates. The body masses, and the equation used from Payseur et al. (1999) can be found in Table 1.

Primate species typically engage in a wide range of locomotor behaviors; however, due to sample and statistical limitations, creating a grouping scheme that encompassed the full range of behaviors for each species was impractical. Locomotor behavior of the extant primates was based on previous literature found in Anemone (1993) and Fleagle (1999), and was defined into three distinct groups: vertical clinging and leaping (VCL), slow climbing (SC), and arboreal quadrupedalism (AQ). The assigned locomotor behavior for each genus can be found in Table 1.



Table 1: Taxonomic sample used in the analysis. Fossil genera are designated with a \*

Genus	Species	Museum	Sample size	Locomotor Category	Estimated Average Body Mass (kg)
<i>Avahi</i>	<i>laniger</i>	MCZ, USNM	4	VCL	1.5456
<i>Callithrix</i>	<i>argentata, geoffroyi, jacchus, melaneura</i>	NMNH	5	AQ	0.3285
<i>Cebus</i>	<i>apella paraguayanus</i>	AMNH	16	AQ	2.3205
<i>Cheirogaleus</i>	<i>major, medius</i>	AMNH, MCZ, DPC	6	AQ	0.2354
<i>Galago</i>	<i>alleni, senegalensis, senegalensis moholi</i>	AMNH, USNM, YPM	19	VCL	0.1811
<i>Hapalemur</i>	<i>griseus griseus</i>	AMNH	2	VCL	0.7775
<i>Eulemur</i>	<i>fulvus rufus</i>	MCZ	2	AQ	1.7310
<i>Loris</i>	<i>tardigradus</i>	AMNH, USNM, YPM	9	SC	0.3113
<i>Microcebus</i>	<i>murinus</i>	AMNH	8	AQ	0.49877
<i>Otolemur</i>	<i>crassicaudatus</i>	USNM	7	AQ	0.9093
<i>Perodicticus</i>	<i>potto, potto ibeanus</i>	AMNH, USNM, YPM	22	SC	1.2319
<i>Propithecus</i>	<i>diadema diadema, diadema edwardisi, verreauxi majori, verreauxi verreauxi</i>	AMNH, MCZ	8	VCL	3.9832
<i>Saimiri</i>	<i>boliviensis boliviensis</i>	AMNH,	15	AQ	0.6948
<i>Tarsius</i>	<i>syrichta</i>	DPC	2	VCL	0.1100
<i>Karanisia*</i>	<i>clarki</i>	DPC	1	unknown	0.4538
<i>Parapithecus*</i>	<i>grangeri</i>	DPC	1	unknown	0.6697
<i>Adapis*</i>	<i>parisiensis</i>	ACQ	1	unknown	2.4503
<i>Apidium*</i>	<i>phiomense</i>	DPC	2	unknown	0.6973
<i>Omomy*s*</i>	<i>carteri</i>	UC	1	unknown	0.2048
<i>Shoshonius*</i>	<i>cooperi</i>	CM	1	unknown	0.1047

Museums:

AMNH – American Museum of Natural History, New York, USA; MCZ – Museum of Comparative Zoology, Harvard University; NMNH, USNM – National Museum of Natural History (Smithsonian Museum), Washington D.C., USA; YPM – Yale Peabody Museum; DPC – Duke Primate Center; CM – Carnegie Museum of Natural History; UC – University of Colorado.

Fossil body mass estimation equation from Payseur et al., (1999):  $\ln(\text{BM})=2.676(\ln(\text{FHH}))+1.50$

### **Trabecular Bone Structure Analysis**

Each bone was scanned using the OMNI-X HD-600 High-Resolution X-ray computed tomography scanner (Varian Inspection Systems, Lincolnshire, IL) at the Center for Quantitative Imaging (CQI) at The Pennsylvania State University (PSU). Bones were mounted in florist foam and the entire femoral head was scanned. Voxel sizes ranged between 0.008 and 0.045 mm, depending on the different sizes of the femoral heads across the represented genera. In all cases the highest-resolution images were obtained for the given size of each specimen. The image slices were reconstructed as 16-bit TIFF grayscale images with a 1024 x 1024 pixel matrix.

For each individual, a centered volume of interest (VOI) was obtained from the femoral head using Avizo 7.0 following published methodology (Ryan and Walker, 2010). The location of the VOI was determined by finding the center of the smallest possible bounding box containing the entire articular surface of the femoral head. The VOI size was based on the size of the joint in each individual and was equal to one-sixth of the proximodistal height of the articular surface. This methodology provides homologous sampling across individuals of different size and femoral head shape. Similar methodology has been used previously in analyses of anthropoid primates in Ryan and Walker (2010) and Ryan and Shaw (2012) as well as a large diverse sample of primates by Ryan and Shaw (2013). The VOIs were then processed using the Scanco Image Processing Language (IPL; Scanco Medical AG, Brüttisellen, Switzerland).

The morphological analysis performed in Scanco IPL was done using thresholding based on the iterative segmentation algorithm of Ridler and Calvard (1978). This resulted in seven standard quantified variables of interest for each individual: bone volume fraction (BV/TV), connectivity density (Conn.D), degree of anisotropy (DA), trabecular thickness (Tb.Th), trabecular spacing (Tb.Sp), trabecular number (Tb.N), and structure model index (SMI). The methodology used to calculate each structural variable follows those previously published in

Ryan and Shaw (2012). Trabecular thickness values were corrected for resolution dependency following the method described in Ryan and Shaw (2012).

## **Statistical Analyses**

### **Phylogenetic Signal**

The possible relationship of phylogeny and trabecular structure has been analyzed in several studies (Doubé et al., 2011; Ryan and Shaw 2012, 2013). The findings of Ryan and Shaw (2013) suggest that there is a weak phylogenetic signal in the femoral head of primates. Therefore the variables used in the current analysis were tested for phylogenetic signal using the K statistic method described by Blomberg et al. (2003). Each variable was tested for phylogenetic signal using both the species mean raw values and species mean body mass-corrected values following least squares regression. Analyses were performed using the specialized Matlab code PHYSIG (Blomberg et al., 2003). There was no statistically significant phylogenetic signal present in either the raw or body size corrected trabecular bone variables. The lack of statistically significant results does not rule out the possibility of phylogenetic influence, but it does allow for the use of the variables in a multivariate analysis (Ryan and Shaw, 2012).

### **Discriminant Functions Analysis**

Multivariate discriminant function analyses (DFA) were used to test whether femoral head trabecular bone variables were capable of discriminating between extant locomotor groups and also to predict group membership for fossil species. Recent analyses have shown an effect of body size on the scaling of trabecular bone structure (Doubé et al., 2011; Fajardo et al., 2013;

Ryan and Shaw, 2013). To remove the potential influence of body mass on the analyses conducted in this study, each variable was  $\log_{10}$  transformed and individually regressed on body mass using ordinary least squares regression. The resulting unstandardized residuals represent size-corrected trabecular bone variables and were used in all subsequent statistical analyses. The mass-corrected variables were analyzed in a multilinear regression to test for collinearity. Variables found to have a high degree of multilinear collinearity on the basis of the variance inflation factor were excluded from the discriminant function analyses. The only predictor that displayed a significant level of collinearity was Tb.Sp.

The unstandardized residuals for all trabecular bone variables for each individual were entered into a DFA using locomotor category as the grouping variable. The predictor variables used in the analyses were Tb.N, Conn.D., SMI, Tb.Th, DA, and BV/TV. A DFA of only the extant sample was run first to determine how well the variables discriminated between the known locomotor groups. The seven fossil specimens were included into a separate DFA as ungrouped individuals to generate predicted locomotor classifications for each. A separate stepwise DFA was also run for all the extant individuals and three of the fossil cases (*Karanisia*, *Omomys*, and *Shoshonius*), which were held as unknowns. The uncorrelated predictor variables (Tb.N, Conn.D, SMI, Tb.Th, DA, and BV/TV) were automatically removed by the stepwise analysis to produce the best model. This test was used in order to generate an f-statistic for between group differences. All statistical analyses were run using SPSS 21.0 (IBM). For all tests, significance levels were set at 0.05.

## Chapter 3

### Results

#### DFA of Extant Primates

The DFA of the sample of extant primates (n=125) correctly classified the primates into their known locomotor behavioral groups 72.0% of the time (90 individuals of 125). The DFA generated two significant discriminant functions, representing 85.0% and 15.0% of the variation, respectively (Figure 2). The arboreal quadruped primates were the most well predicted group and the vertical clinging and leaping were the poorest (Table 2). The breakdown of each variable's influence on the two discriminant functions is found in Table 3. Most of the variation is explained by Conn.D for Function 1 and BV/TV and SMI on Function 2.

Figure 3 is a visualization of the generic variation from the DFA presented in Figure 2. Certain species showed a much higher degree of intraspecific variation along both functions than others. Taxa such as *Galago*, *Propithecus*, and *Saimiri* showed the greatest spread, while taxa including *Cebus* and *Loris* were more tightly grouped. Variation in *Otolemur* was poorly described by Function 1 in all but one individual (Figure 8).

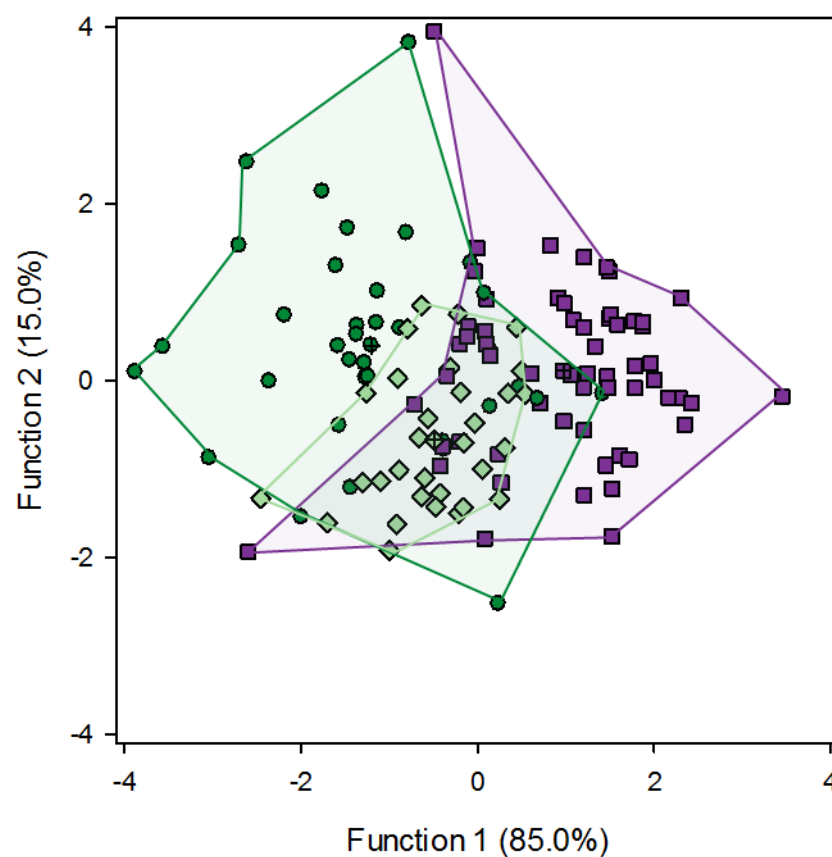


Figure 2: The DFA analysis of just the extant primates. Symbols: green circles, vertical clingers and leapers; purple squares, arboreal quadrupeds; light green diamonds, slow climbers. Group centroids are identified by a crossed symbol.

Table 2 : Classification results for DFA

Locomotion	Predicted Group Membership Count			Total		
	VCL	AQ	SC			
VCL	24	5	6	35		
AQ	6	44	9	59		
SC	5	4	22	31		
Locomotion	Predicted Group Membership Percentages			Total		
	VCL	68.6	14.3		17.1	100.0
	AQ	10.2	74.6		15.3	100.0
SC	16.1	12.9	71.0	100.0		

72.0% of original grouped cases correctly classified

Table 3 : Pooled within-group correlations between discriminating variables and standardized canonical discriminant functions.

Predictor Variable	Function	
	1	2
Conn.D	0.742*	0.010
DA	-0.369*	0.163
BV/TV	0.197	0.591*
SMI	0.027	-0.553*
Tb.N	0.328	0.441*
Tb.Th	-0.399	0.414*

\* Largest absolute correlation between each variable and any discriminant function.

Variables are ordered by absolute size of correlation within function.

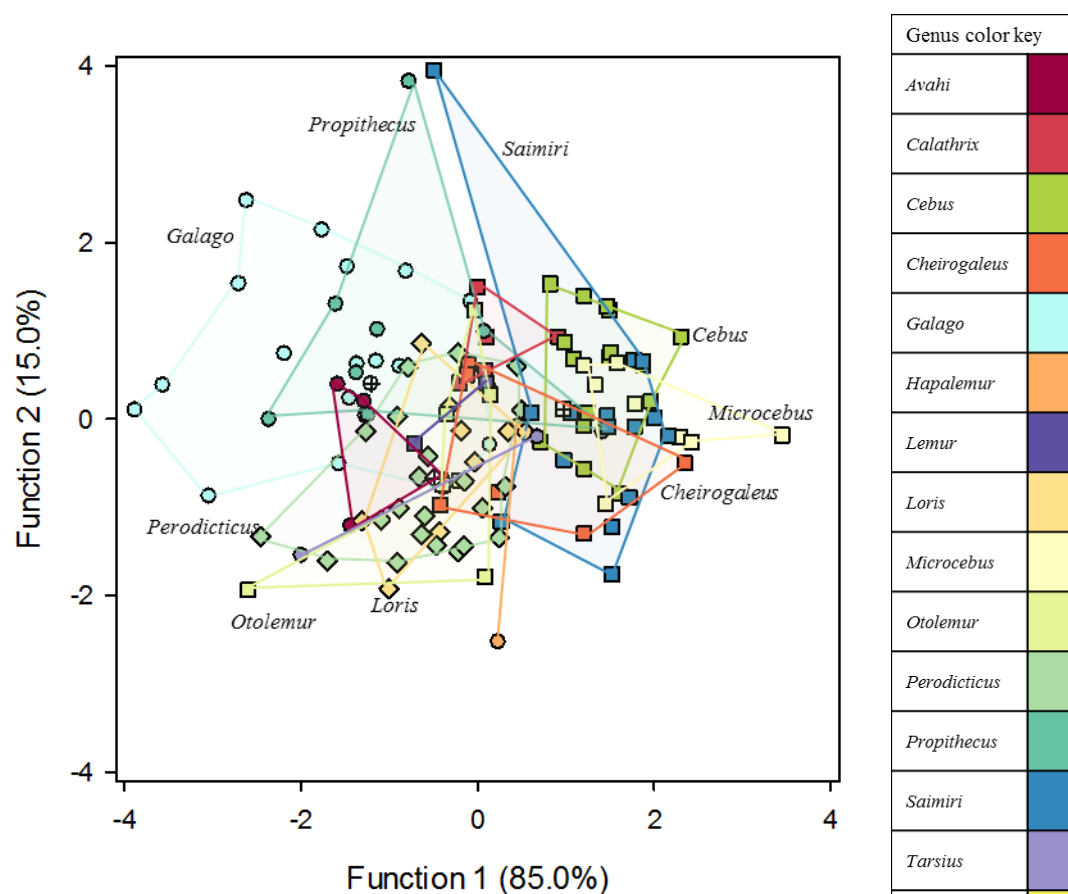


Figure 3: DFA of extant primates categorized into locomotor behavior, with genus visualized and groups with sample size  $n > 4$  labeled.

### **Stepwise DFA for Extant Primates**

The stepwise DFA correctly classified 70.4% of the extant individuals using only Conn.D., BV/TV, Tb.Th, and Tb.N (Figure 4, Table 4). Conn.D accounts for most of the variation along Function 1, while BV/TV and Tb.Th explain most of the variation along Function 2 (Table 5). Table 6 contains the pairwise group comparisons resulting from this stepwise DFA. The locomotor groups were significantly different from each other in spite of the significant overlap on each function.



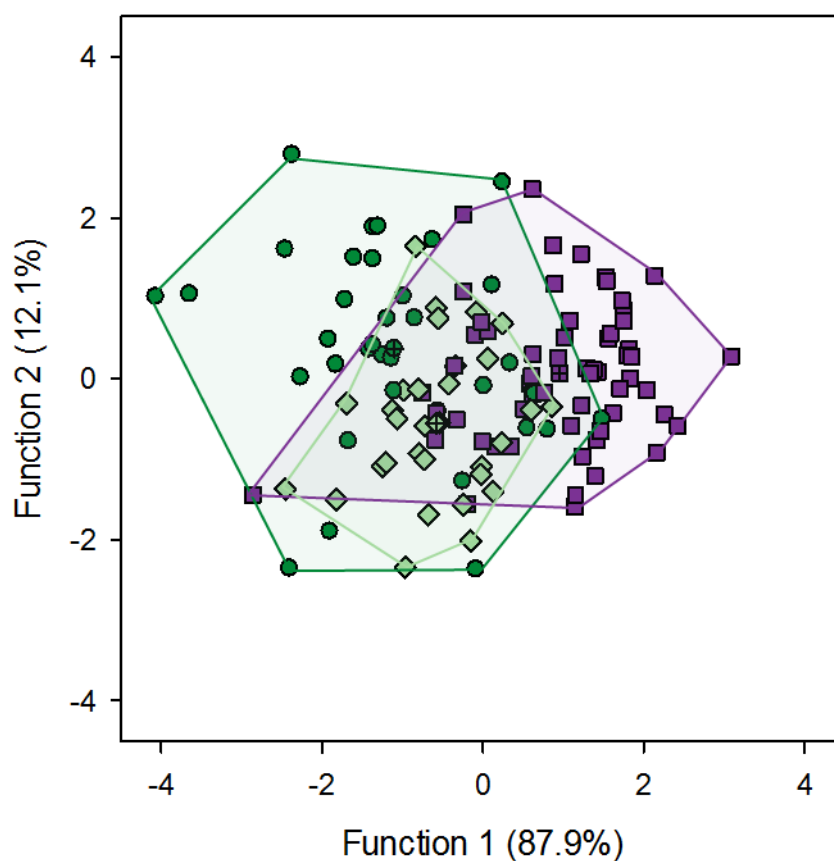


Figure 4: The stepwise DFA of the Extant primates. 70.4% of the individuals were correctly classified. The stepwise DFA kept Conn.D, BV/TV, Tb.Th, and Tb.N as predictors and threw out DA and SMI. Symbols: green circles, vertical clingers and leapers; purple squares, arboreal quadrupeds; light green diamonds, slow climbers.

Table 4:: Classification results for Stepwise DFA

Locomotion	Predicted Group Membership Count			Total
	VCL	AQ	SC	
VCL	22	6	7	35
AQ	4	45	10	59
SC	6	4	21	31
Predicted Group Membership Percentages				
VCL	62.9	17.1	20.0	100.0
AQ	6.8	76.3	16.9	100.0
SC	19.4	12.9	67.7	100.0

70.4% of original grouped cases correctly classified

Table 5: Pooled within-group correlations between discriminating variables and standardized canonical discriminant functions.

Predictor Variable	Function	
	1	2
Conn.D	0.766*	-0.133
BV/TV	0.222	0.653*
Tb.Th	-0.399	0.563*
Tb.N	0.352	0.451*
SMI <sup>b</sup>	-0.078	-0.446*
DA <sup>b</sup>	-0.179	-0.231*

\* Largest absolute correlation between each variable and any discriminant function.

Variables are ordered by absolute size of correlation within function.

b. This variable was not used in the analysis

Table 6: Pairwise group comparisons (DF = 4, 119)

Locomotion	VCL	AQ	SC
VCL	X	<0.001	0.002
AQ	23.007	X	<0.001
SC	4.493	13.639	X

Upper half of plot: p-values; lower half of plot: F-scores

Stepwise analysis included Conn.D, BV/TV, Tb.Th, and Tb.N in the final 'best fit' solution, the results for which are presented here.

### DFA with Fossil Individuals as Unknowns

The results of the DFA illustrated in Figure 6 represent the entire sample of extant and extinct primates. The *Apidium*, *Adapis*, and *Parapithecus* fossils can be seen to be very removed from the rest of the sample, indicating unusually high degrees of connectivity density and structure model index (the full discriminant function structure matrix can be found in Table 8). The femoral heads of the *Apidium* individuals appeared to have high density material between the trabeculae. The *Adapis* and *Parapithecus* fossils displayed better trabecular preservation than the

*Apidium*, but not on par with the other remaining fossils. After attempts to further process these individuals failed to address the issue, these four fossils were removed from the analysis. See the discussion section for further explanation of difficulties with preservation and analyzing fossil individuals.

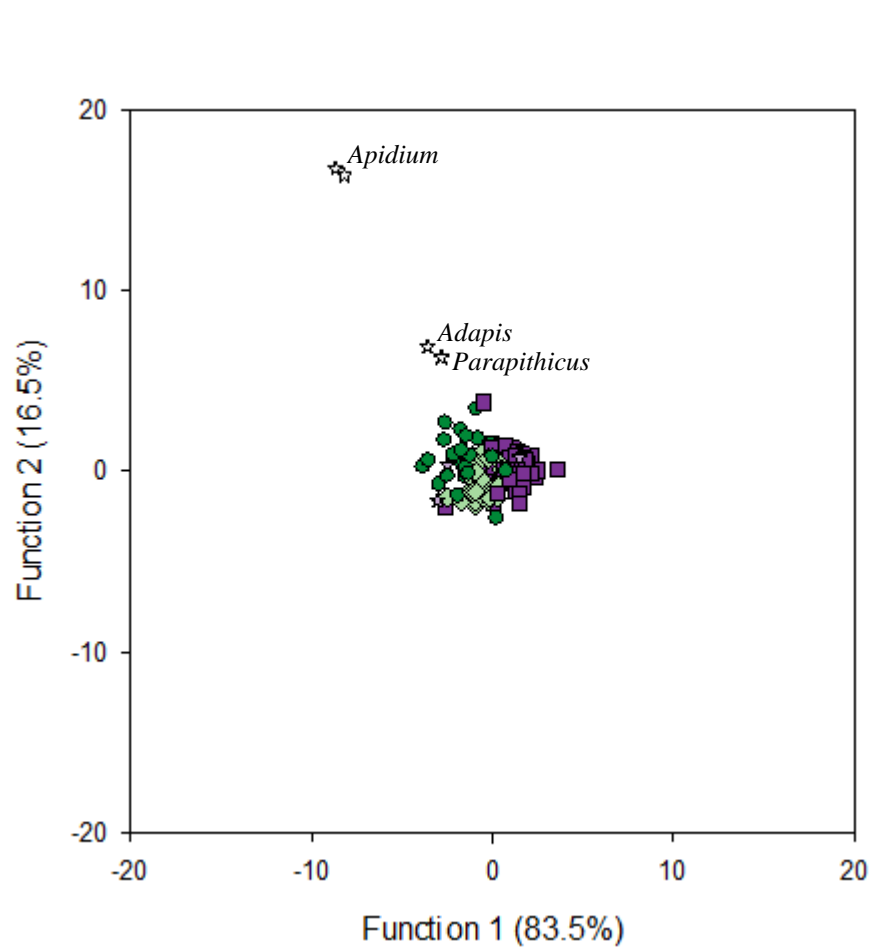


Figure 5: The initial DFA output with the entire sample illustrates some of the problems with the fossil record. The white stars represent *Parapithecus*, *Adapis*, and *Apidium* (n=2).

Table 7: Pooled within-group correlations between discriminating variables and standardized canonical discriminant functions.

Predictor Variable	Function	
	1	2
Conn.D	0.743*	0.018
DA	-0.370*	0.150
BV/TV	0.196	0.592*
SMI	0.026	-0.533*
Tb.N	0.327	0.447*
Tb.Th	-0.402	0.416*

\* Largest absolute correlation between each variable and any discriminant function.

Variables are ordered by absolute size of correlation within function.

The DFA of the extant primates and the three remaining fossils correctly classified primates into their known groups 72.8% of the time (Figure 6, Table 8). The small difference in correct classification between the extant only DFA and this DFA can be attributed to including the fossil individuals in the regression run to correct for body mass in the trabecular variables. Function 1 was responsible for 84.2% of the variation, and Function 2 represented the remaining 15.8%. A comparison of the structure matrices for the DFA of the extant sample (Tables 4 and 9) shows the same trabecular variables contributing similar levels of significance in each DFA. The fossils, held as unknowns in the analysis, were grouped as follows: *Karanisia* in arboreal quadrupedalism, *Omomy*s in vertical clinging and leaping, and *Shoshonius* in slow climbing.

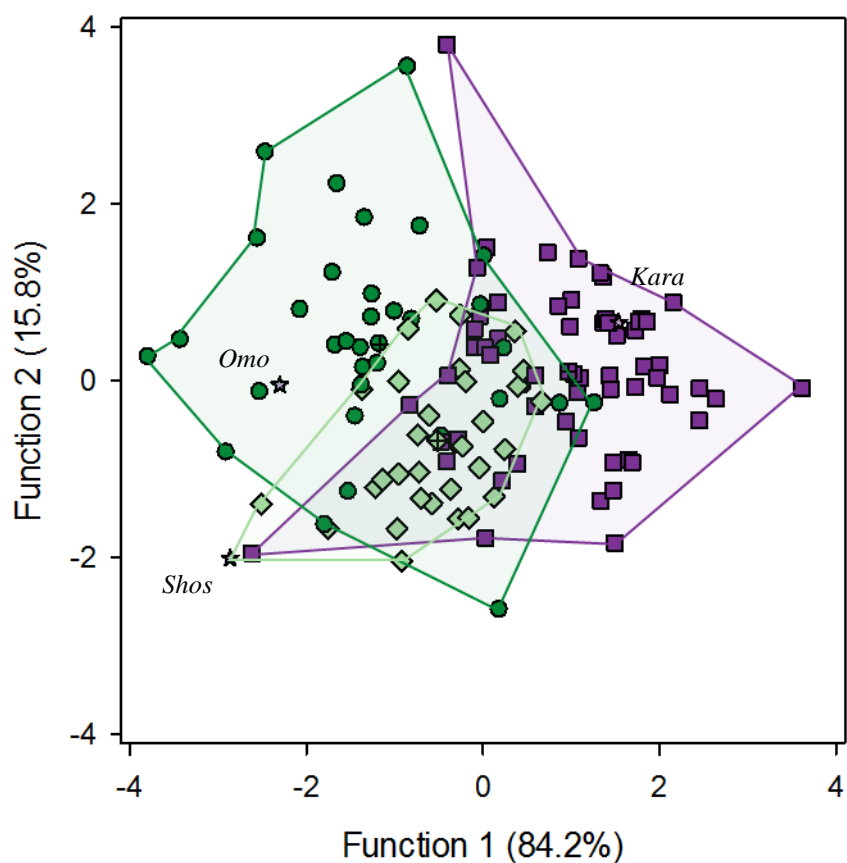


Figure 6: The DFA analysis of the extant primates, and three fossil primates (stars) *Karanisia*, *Shoshonius*, and *Omomys*. Symbols: green circles, vertical clingers and leapers; purple squares, arboreal quadrupeds; light green diamonds, slow climbers. Group centroids are marked by a crossed symbol. 83.5% of the variance is attributed to Function 1, and 16.5% is attributed to function 2.

Table 8: Classification results for DFA

Locomotion	Predicted Group Membership Count			Total
	VCL	AQ	SC	
VCL	25	5	5	35
AQ	6	44	9	59
SC	5	4	22	31
Unknown	1 ( <i>Omomys</i> )	1 ( <i>Karanisia</i> )	1 ( <i>Shoshonius</i> )	3
Predicted Group Membership Percentages				
VCL	71.4	14.3	14.3	100.0
AQ	10.2	74.6	15.3	100.0
SC	16.1	12.9	71.0	100.0
Unknown	33.3	33.3	33.3	100.0

72.8% of original grouped cases correctly classified

Table 9: Pooled within-group correlations between discriminating variables and standardized canonical discriminant functions.

Predictor Variable	Function	
	1	2
Conn.D	0.750*	-0.023
DA	-0.371*	0.164
BV/TV	0.200	0.620*
SMI	0.023	-0.559*
Tb.Th	-0.402	0.442*
Tb.N	0.333	0.441*

\* Largest absolute correlation between each variable and any discriminant function.

Variables are ordered by absolute size of correlation within function.

### Stepwise DFA of Fossil Primates

The stepwise DFA for the fossil taxa used Conn.D., Tb.N., and BV/TV and correctly sorted 64.8% of the extant grouped individuals correctly (Figure 7, Table 10). This analysis replicated the *Karanisia* placement in with arboreal quadrupeds, and the *Shoshonius* placement in

slow climbing. *Omomys* was classified as a slow climber and showed closer affinity with *Shoshonius* when only these three trabecular bone variables were considered. Most of the variation was driven by Conn.D on Function 1 and BV/TV on Function 2 (Table 11). Table 12 contains the pairwise group comparisons, showing significant differences between the locomotor groups when the fossils are considered in the analysis.

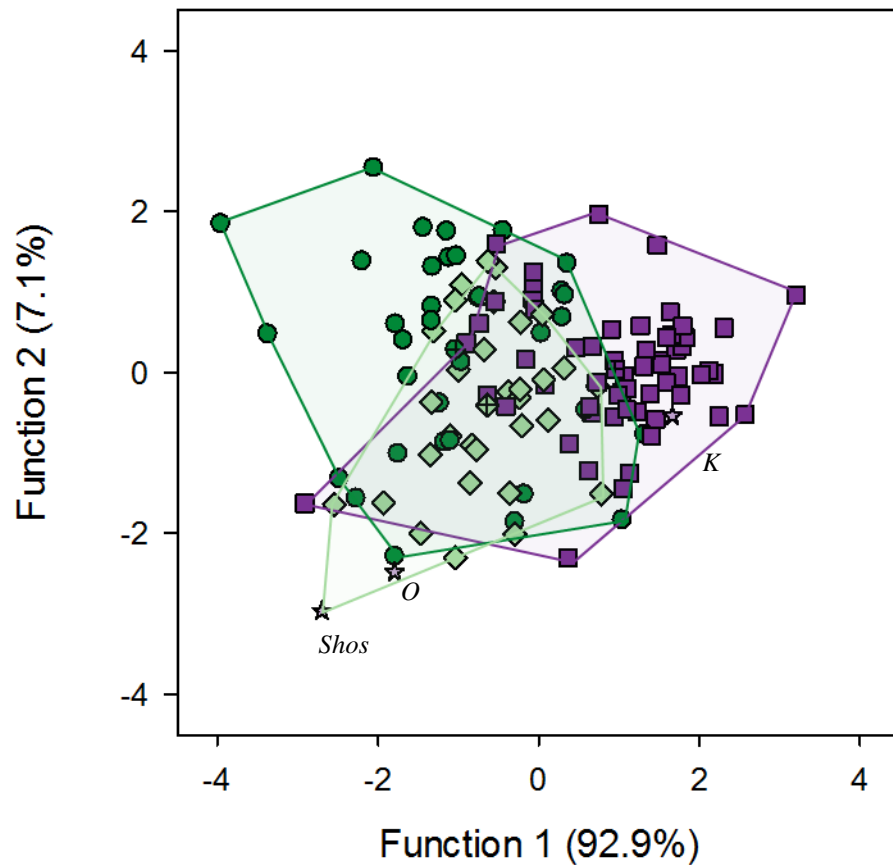


Figure 7: The stepwise DFA of extant primates, *Karanisia*, *Shoshonius*, and *Omomys*. 64.8% of the cases were correctly categorized by the model. Conn.D, BV/TV, and Tb.N were used as predictors. 92.9% of the variation was attributed to function 1, and 7.1% to function 2.

Table 10: Stepwise DFA for locomotor group using 3 trabecular bone variables.

Locomotion	Predicted Group Membership Count			Total
	VCL	AQ	SC	
VCL	18	8	9	35
AQ	8	45	6	59
SC	9	4	18	31
Unknown	0	1 ( <i>Karanisia</i> )	2 ( <i>Shoshonius</i> , <i>Omomys</i> )	3
Predicted Group Membership Percentages				
VCL	51.4	22.9	25.7	100.0
AQ	13.6	76.3	10.2	100.0
SC	29.0	12.9	58.1	100.0
Unknown	0.0	33.3	66.7	100.0

64.8% of original grouped cases correctly classified

Table 11: Pooled within-group correlations between discriminating variables and standardized canonical discriminant functions.

Predictor Variable	Function	
	1	2
Conn.D	0.772*	-0.306
DA <sup>b</sup>	-0.210*	-0.085
BV/TV	0.233	0.931*
SMI <sup>b</sup>	-0.071	-0.772*
Tb.N	0.363	0.594*
Tb.Th <sup>b</sup>	-0.354	0.430*

\* Largest absolute correlation between each variable and any discriminant function.

Variables are ordered by absolute size of correlation within function.

b. This variable was not used in the analysis



Table 12: Pairwise group comparisons (DF = 3, 120)

Locomotion	VCL	AQ	SC
VCL	X	<0.001	<0.001
AQ	28.856	X	<0.001
SC	3.369	18.190	X

Upper half of plot: p-values; lower half of plot: F-scores

Stepwise analysis included Conn.D, Tb.N., and BV/TV in the final 'best fit' solution, the results for which are presented here.

## Chapter 4

### Discussion

#### Extant Primates

This study tested the extent to which trabecular bone structural variation can be used to discriminate differences in locomotor behavior in small primates. A DFA using six measured trabecular bone variables was able to correctly predict known locomotor behavior in 72% of cases (90 out of 125 individuals). It was found that approximately 85% of the variance was driven by connectivity density and degree of anisotropy on the first function. In a stepwise analysis that removed DA, 92.9% of the variation was explained by Conn.D alone. A summary of the 6 predictor DFA results can be found in Table 13.

Table 13: Summary interpretation of group centroids from Figure 3, DFA of extant primates

Group	Function 1 (85.0%)	Function 2 (15.0%)
VCL	<ul style="list-style-type: none"><li>• High DA</li><li>• Low Conn.D</li></ul>	<ul style="list-style-type: none"><li>• High BV/TV, Tb.Th, Tb.N</li><li>• Low SMI (more plate like structures)</li></ul>
AQ	<ul style="list-style-type: none"><li>• High Conn.D</li><li>• Low DA</li></ul>	<ul style="list-style-type: none"><li>• High to low BV/TV, Tb.Th, Tb.N, and SMI</li></ul>
SC	<ul style="list-style-type: none"><li>• High DA</li><li>• Low Conn.D</li></ul>	<ul style="list-style-type: none"><li>• High SMI (more rod like structures)</li><li>• Low BV/TV, Tb.Th, Tb.N</li></ul>

The vertical clinging and leaping and arboreal quadruped groups were well separated by the first function, but there was a high degree of overlap between these two and the slow climbing group. *Otolemur* was categorized as an arboreal quadruped, however as previously mentioned, this label does not encompass the whole range of the genus' locomotor behaviors which includes climbing and leaping behaviors. In Figure 8, *Otolemur* individuals have been highlighted to show

where they fall relative to other arboreal quadruped primates. In an exploratory measure, removing the 6 *Otolemur* individuals from the sample resulted in better overall prediction for arboreal quadrupedalism membership with the total number of incorrectly classified AQ individuals falling from 15 to 7 in a DFA of extant primates only. Overall prediction rose from 72.0% correct classification to 77.1%. The removal of *Otolemur* did not affect the predicted memberships of the fossil specimens.

When *Otolemur* was retained in the DFA of extant primates but categorized as an unknown, all 6 individuals were predicted to belong to the slow climbing group. The reasons that the trabecular architecture of *Otolemur* align most similarly to that of *Loris* and *Perodicticus* (two genera with very different locomotor behaviors from *Otolemur*) might not be biomechanical at all, or at least not related to the biomechanical factors addressed by this analysis. *Otolemur* has a closer evolutionary relationship with vertical clingers and leapers like *Galago*, and slow climbers *Loris* and *Perodicticus*, than it does with any of the included arboreal quadrupeds. As depicted in Figure 4 *Otolemur* is much closer to these genera than any of the more distantly related but more similar, in terms of locomotion, arboreal quadruped primates. Even though no statistically significant locomotor signal was found in these data, there could still be a weak signal of relatedness affecting the results. Most of the variation within *Otolemur* was not well described by Function 1, which was very successful in explaining differences between the vertical clinging and leaping and arboreal quadruped primates and may also account for its predicted slow climbing membership. Further analysis of intraspecific variation should be explored to see the extent to which bone structure is related to phylogeny in different primate genera. The vertical clinging and leaping primates tended to show a much greater amount of within-species variation than the arboreal quadruped primates, but the source of this variation is not clear. One possible explanation is that vertical clinging and leaping primates vary in the proportion of time that they

engage in the behavior, so while *Propithecus* and *Tarsius* are both typically categorized as vertical clinging and leaping, they differ in their activity levels (Gebo, 2011).

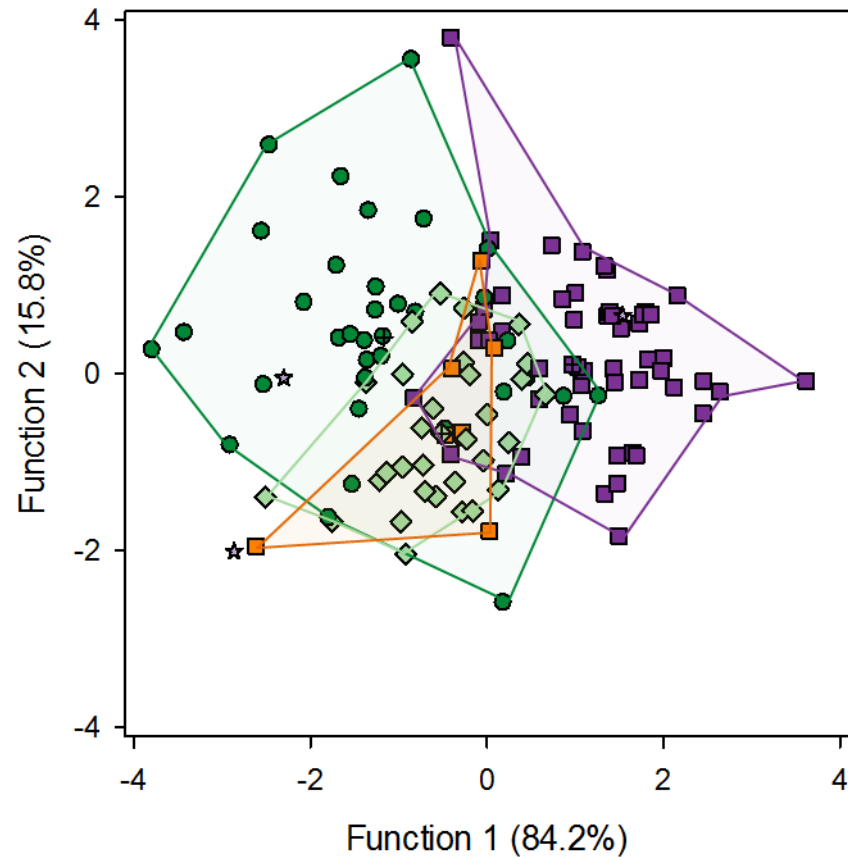


Figure 8: DFA of extant sample and fossil specimens *Karanisia*, *Omomys*, and *Shoshonius*, with *Otolemur* in orange for illustration.

### Fossil Primates

This analysis confirms earlier findings by Ryan and Ketcham (2002b) that despite similar external morphology, the internal trabecular structure of *Omomys* and *Shoshonius* are quantitatively different. While both behave similarly on Function 1, they are separated on

Function 2 by the SMI predictor (Figure 3, Table 5) which describes the relative proportion of rod to plate like trabecular structures. The analysis shows that *Shoshonius* had more rod-like trabecular architecture than *Omomys* which had a more plate-like architecture.

However, unlike the findings of Ryan and Ketcham (2002b), this analysis predicts that *Shoshonius cooperi* is most similar to slow climbers, and that *Omomys carteri* is most similar to vertical clinger and leapers at the trabecular level. *Karanisia* was found to be very different in trabecular structure than *Omomys* and *Shoshonius* and shared architectural similarities with extant arboreal quadruped primates.

Previously published morphological analyses describe *Omomys* as having a unique mosaic suite of features suggestive of quadrupedal and leaping behaviors (Anemone and Covert, 2000). This analysis found that *Omomys* was most similar to modern primates that engage in vertical clinging and leaping behavior. The position of *Omomys* in the DFA was driven by high DA and low Conn.D, which was more typical of vertical clinging and leaping than arboreal quadruped primates. However in the stepwise comparison, *Omomys* was predicted as a slow climbing with *Shoshonius*. These conflicting predictions may indicate that the modern sample does not contain a proper behavioral analog for the omomyoids.

While grouped with slow climbers, *Shoshonius* is far away from all of the group centroids and is near individuals classified into all three locomotor behaviors, including *Otolemur*. Dagosto et al. (1999) hypothesized that based on its external anatomy *Shoshonius* was engaging in mainly quadrupedal and climbing behaviors and may have exhibited some limited leaping ability. This analysis found that *Shoshonius* had low Conn.D, Tb.Th, Tb.N, and BV/TV, and high DA and SMI, sharing structural similarities to slow climbing primates. However, as with *Omomys*, there may be no proper modern behavioral analog for *Shoshonius*. These findings may indicate that phylogenetic relationships are a constraint on using trabecular bone to reconstruct fossil primate behavior.

*Karanisia* was predicted to be an arboreal quadruped with high Conn.D and low DA on Function 1. *Karanisia* was not very much affected by Function 2, but tended towards high BV/TV, Tb.N, and Tb.Th and low SMI. These findings were more consistent with arboreal quadruped primates and fell beyond the range of any of the slow climbing and vertical clinging and leaping primates included in this study. Little has been published on the post cranial elements of *Karanisia*. The genus is hypothesized to represent a stem lorisiforme close to the common ancestor of galagos and lorises (Seiffert, 2007). Galagos and lorises have very different locomotor adaptations, representing vertical clinging and leaping and slow climbing, respectively. Through both analyses it was included in, *Karanisia*'s predicted membership within the arboreal quadruped category was consistent and did not overlap with the slow climbing and vertical clinging groups. Based on this trabecular reconstruction, it could be that the common ancestor of these two groups practiced a generalized arboreal quadrupedalism similar to the extant cheirogaleids, and different from the locomotion in either of the extant lorisiforme clades. This would imply that slow climbing and vertical clinging and leaping are derived behaviors within lorisiformes.

### **Issues with quantifying trabecular structure in fossil species**

As illustrated in Figure 6, several of the fossil individuals (*Adapis*, *Apidium*, and *Parapithecus*) displayed trabecular bone structural characteristics that fell far outside the range of variation seen in modern primates. This is more likely to be a preservation issue than a true reflection of trabecular architecture in these fossils. While the external morphology of these fossil specimens were preserved and clearly visible in the microCT scan data, the trabecular architecture was difficult to examine due to fossilization conditions. Efforts to digitally separate mineralized bone from surrounding matrix were unsuccessful in fully isolating the bone.

Thomason (1995) describes the challenges faced by paleontologists attempting to study bone materials; one of the main difficulties is fossil preservation. This challenge may be in the quality of the preserved trabecular structures or the degree of mineralization over time (Thomason, 1995). As demonstrated by this small sample of 7 fossil femurs, only 3 were able to be used for trabecular analysis despite fairly decent external preservation of all the femoral heads.

One fossil that was analyzed but unexpectedly grouped was the *Shoshonius* specimen. While it was categorized as a slow climber by the discriminant function analyses, it was driven by a very low Conn.D. high DA and high SMI. These variables may have been artificially inflated by the fossilization process. Ryan and Ketcham (2002b) found that the *Omomys* and *Shoshonius* specimens had a high number of mineral inclusions which could have altered interpretations of the measured bone variables. The *Omomys* specimen was not consistently predicted into a specific locomotor group, varying between the vertical clinging and leaping and slow climbing categories. These two forms of locomotion are very different and it is not clear from this analysis whether the placement of *Omomys* is reflective of biomechanical loading or some other factor. Given the hypothesized relationship between the omomyoids and extant primates, it could be that no modern primates are moving in the exact same fashion as the extinct ones. This compliments the analysis of Anemone and Covert (2000) that found a unique suite of external morphological features in that *Omomys* may have had a unique form of generalized arboreal behaviors based on its trabecular structure.

Another potential limitation of the current analysis stems from the body mass estimates. The body mass estimates used in this study derived from the femoral head height were in some cases larger or smaller than published estimates based on tooth size. This could have influenced the results during the body mass correction. The decision to use the FHH measure to estimate body mass instead of the dentition was kept because the results of this study may be applied to future fossil findings that may be only represented by postcranial elements.

## Chapter 5

### Conclusion

The model created by these discriminant function analyses for extant primates was fairly robust in its ability to classify living primates into known locomotor behavioral groups based on trabecular architecture. However, the significant overlap between the primate groups and somewhat suspect classification of primates such as *Otolemur* illustrate the limitations of this model in addressing complex locomotor behaviors. Initially, a scheme of five locomotor classes was proposed that sought to address the diversity but due to limitations with the available sample, this was not usable. This could be addressed by increasing the sample so that statically meaningful group sizes could be obtained to represent different behavioral activity levels.

Future analyses should attempt to increase the specificity of the locomotor categories and should also include a non-primate arboreal quadruped into the sample, such as tree shrews, for comparison. While the femoral morphology of tree shrews is different from that of primates, the loadings have the potential to be similar to the common ancestor between these groups.

This study shows that multiple quantified trabecular bone architectural measures can be used to discriminate between different locomotor behaviors in extant primates. Applying predictive models such as DFA to fossils has potential if the preservation conditions of the fossil favor the internal trabecular microstructure of the femoral head. However, such models may be more appropriate for fossils with living descendants such as *Karanisia*, but not as appropriate for primates that belong to extinct lineages such as the omomyoids



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### **Education**

- M.A. Anthropology (Integrated Undergraduate Graduate Program). The Pennsylvania State University. 2013.
- B.S. Biological Anthropology (with Honors). The Pennsylvania State University. 2013.

### **Honors and Awards**

- Graduate Travel Award – The Department of Anthropology, Pennsylvania State University. 2013.
- External Funding Incentive Award – The College of Liberal Arts, Pennsylvania State University. 2012.
- Graduate Teaching Assistantship – Department of Anthropology, Pennsylvania State University. 2012.
- Integrated Undergraduate/Graduate (IUG) Scholar through the Schreyer Honors College, Pennsylvania State University. 2011—2013
- Schreyer Honors Scholar, Pennsylvania State University. 2008 – 2013.
- Academic Excellence Undergraduate Scholarship – The College of Liberal Arts, Pennsylvania State University 2008 – 2012
- Schreyer Honors College Undergraduate Scholarship. 2008 – 2012

### **Association Memberships/Activities**

- American Association of Physical Anthropologists (AAPA)

### **Research Experience**

- Paleoanthropology Lab, P.I. Timothy Ryan. The Pennsylvania State University. Graduate research assistant, 2011-2013.
- Genomics Lab, P.I. Mark Shriver. The Pennsylvania State University. Undergraduate research assistant, 2010.

### **Research Interests**

- I am interested in applications of 3D digital visualization of postcranial anatomical structures, and using such methods to study questions in paleontology surrounding Paleocene-Eocene boundary primate divergence and Pliocene-Pleistocene hominin evolution.

### **Professional Presentations**

- Perchalski, Bernadette A., Seiffert, Erik R., and Ryan, Timothy M. *Multivariate analyses of trabecular bone structure in the proximal femur of living and extinct strepsirrhine primates*. Presented at the 82nd annual meeting of the American Association of Physical Anthropologists (AAPA), in Knoxville, Tennessee, 2013.