| By |
| :---: |
| Darshana F. Shapiro |
| A dissertation submitted to the |
| Graduate School-New Brunswick |
| Rutgers, The State University of New Jersey |
| In partial fulfillment of the requirements |
| For the degree of |
| Doctor of Philosophy |
| Graduate Program of Anthropology |
| Written under the direction of |
| And approved by Scott |

## New Brunswick, NJ

October, 2016

## ABSTRACT OF THE DISSERTATION

Characterizing density and anisotropy in the trabecular architecture of the primate ilium and ischium
by DARSHANA F. SHAPIRO
Dissertation Director:
Dr. Robert S. Scott

Trabecular bone remodels in response to its mechanical loading environment. Thus, different types of loading and locomotion should produce distinctive trabecular architecture, enabling the reconstruction of locomotor regime from trabecular bone. While this relationship has been investigated in the appendicular skeleton of extant and fossil primates, it has yet to be examined in the pelvis, in spite of its central role in hindlimb-driven locomotion.

This dissertation explores the relationship between loading, locomotion, and trabecular architecture in the ilium and ischium of a sample of extant primates and attempts to reconstruct locomotion in one fossil specimen, Rudapithecus hungaricus. Based on the general principles of bone functional adaptation, that trabecular architecture remodels via changes in density and anisotropy in response to use, the general predictions of this work are that primates subjecting their innominates to greater, more stereotyped loads will have denser and/or more anisotropic trabecular architecture relative to primates that load their pelves less or in less stereotyped ways. I used high-resolution X-ray computed tomography scans of 29 innominates to compare standard measures of density and anisotropy within and between seven species of primates utilizing different locomotor modes.

My results provided mixed support for loading and locomotor hypotheses. In the ilium,
intraspecific analyses and interspecific density results sometimes corresponded to predictions, while interspecific comparisons of anisotropy more clearly indicated support for locomotor hypotheses (as has been seen in previous work). Specifically, these comparisons suggested that semi-terrestrial/terrestrial quadrupeds have more anisotropic trabecular architecture than arboreal suspensors. Additionally, for non-human primates, comparisons within phylogenetic groups produced anisotropy results that conformed to locomotor predictions. In the ischium, bending (dorsal compression/ventral tension) appears to be the dominant loading regime in non-human primates, as the dorsal column of trabecular bone tends to be denser and more anisotropic than the ventral column. In terms of the interspecific locomotor hypotheses, differences appear to exist between the trabecular architecture of terrestrial and arboreal primates, as well as between taxa belonging to different locomotor categories, though these differences did not always conform to predictions. Results of the attempt to reconstruct loading in Rudapithecus (proposed to be an arboreal quadruped with adaptations to below-branch suspension) suggested that it had the greatest similarity in trabecular architecture to Symphalangus syndactylus, which is not inconsistent with its predicted locomotor regime.

## Acknowledgments

Thank you to my advisor, Dr. Rob Scott, for everything, including (but not limited to): support, guidance, endless encouragement, letting me choose a non-diet project, and one small live lobster. I also want to thank Dr. Susan Cachel for loans from her extensive library and many helpful drop-in discussions, particularly when I was working late on grant proposals, and Dr. Erin Vogel for agreeing to be on my committee with nary a live orangutan in sight. Köszönöm to Dr. David Begun for giving me the opportunity to work in the Miocene and on such an excellent fossil.

I am incredibly grateful to the Wenner-Gren Foundation for the funding to carry out this project, and to Dr. Matt Colbert and Dr. Jessie Maisano for making the scanning happen and for all their CT advice over the years. Many thanks also go to the museum personnel behind the specimen loans: Linda Gordon, Darrin Lunde, and Esther Langan (NMNH); Eleanor Hoeger, Neil Duncan, and Eileen Westwig (AMNH); Dr. Janet Monge, Lynn Grant, and Anne Brancati (UPenn); and Stacy Drake and Marybeth Tomka (TARL).

I want to thank my fellow graduate students for keeping things fun. I am especially grateful to Susan Coiner-Collier for all of her contributions to \#TeamTrabeculae - without her, I would still be losing the fight against ImageJ. Thanks also go to Fred Foster for engineering help. Additional assistance with fun was provided by the Princeton crew, including my various roommates over the years and the rotating cast of $12-\mathrm{PL}$; I appreciate all of their hard work in this matter. Special thanks go to Seth Davidovits for all the things.

Finally, thank you to my parents for never even trying to talk me out of the whole paleontology thing. Someday, I will be in charge of dusting the fossils.

## Table of Contents

Abstract ..... ii
Acknowledgments ..... iv
Table of Contents ..... v
List of Tables ..... viii
List of Figures ..... ix
Chapter 1: Introduction. ..... 1
1.1 Background .....  1
1.2 Data and Methodology ..... 5
1.3 Dissertation Organization .....  6
References. ..... 8
Chapter 2: Characterizing trabecular density and anisotropy in the primate lower ilium in the context of loading and locomotion ..... 12
2.1 Abstract ..... 12
2.2 Introduction ..... 13
2.3 Methods ..... 20
2.4 Predictions ..... 25
2.5 Results. ..... 43
2.6 Discussion ..... 54
2.7 Conclusion ..... 67
References. ..... 127
Chapter 3: Characterizing the trabecular architecture of the primate ischium with respect to
loading and locomotion ..... 134
3.1 Abstract ..... 134
3.2 Introduction ..... 135
3.3 Hypotheses and Predictions ..... 139
3.4 Methods ..... 144
3.5 Results. ..... 149
3.6 Discussion ..... 159
3.7 Conclusion ..... 167
References. ..... 193
Chapter 4: Reconstructing locomotion in Rudapithecus hungaricus from the trabecular architecture of the innominate ..... 197
4.1 Abstract ..... 197
4.2 Introduction. ..... 197
4.3 Methods ..... 201
4.4 Results ..... 206
4.5 Discussion ..... 210
4.6 Conclusion ..... 218
References. ..... 237
Chapter 5: Conclusion. ..... 242
5.1 Contributions and Summary of Conclusions ..... 242
5.2 Future Work. ..... 244
References. ..... 247
Appendices. ..... 250
Appendix A. ..... 250
Appendix B ..... 252
Appendix C.i.a. ..... 254
Appendix C.i.b ..... 262
Appendix C.ii.a ..... 270
Appendix C.ii.b ..... 277
Appendix D.i.a. ..... 284
Appendix D.i.b. ..... 289
Appendix D.ii.a ..... 294
Appendix D.ii.b ..... 298
Appendix D.iii.a. ..... 302
Appendix D.iii.b. ..... 303
Appendix D.iii.c. ..... 304
Appendix D.iii.d. ..... 307
Appendix E.i ..... 310
Appendix E.ii. ..... 312

## List of Tables

Table 2.1 ..... 68
Table 2.2 ..... 69
Table 2.3 ..... 70
Table 3.1 ..... 169
Table 3.2 ..... 170
Table 3.3 ..... 171
Table 3.4 ..... 172
Table 3.5 ..... 173
Table 3.6 ..... 174
Table 4.1 ..... 220
Table 4.2 ..... 221
Table 4.3 ..... 222
Table 4.4 ..... 223

## List of Figures

Figure 2.1 ..... 71
Figure 2.2 ..... 72
Figure 2.3 ..... 73
Figure 2.4. ..... 74
Figure 2.5 ..... 75
Figure 2.6 ..... 76
Figure 2.7A ..... 77
Figure 2.7B ..... 78
Figure 2.7C ..... 79
Figure 2.7D. ..... 80
Figure 2.8A. ..... 81
Figure 2.8B ..... 82
Figure 2.9A ..... 83
Figure 2.9B. ..... 84
Figure 2.10 ..... 85
Figure 2.11A ..... 86
Figure 2.11B ..... 87
Figure 2.12A. ..... 88
Figure 2.12B ..... 89
Figure 2.13 ..... 90
Figure 2.14A. ..... 91
Figure 2.14B ..... 92
Figure 2.15A ..... 93
Figure 2.15B ..... 94
Figure 2.15C ..... 95
Figure 2.15D. ..... 96
Figure 2.16A. ..... 97
Figure 2.16B. ..... 98
Figure 2.17A ..... 99
Figure 2.17B ..... 100
Figure 2.18A. ..... 101
Figure 2.18B. ..... 102
Figure 2.19A. ..... 103
Figure 2.19B ..... 104
Figure 2.20A. ..... 105
Figure 2.20B ..... 106
Figure 2.21A. ..... 107
Figure 2.21B ..... 108
Figure 2.22A ..... 109
Figure 2.22B. ..... 110
Figure 2.23A. ..... 111
Figure 2.23B ..... 112
Figure 2.24A. ..... 113
Figure 2.24B ..... 114
Figure 2.25 A . ..... 115
Figure 2.25B ..... 116
Figure 2.26 ..... 117
Figure 2.27 ..... 118
Figure 2.28. ..... 119
Figure 2.29 ..... 120
Figure 2.30 ..... 121
Figure 2.31 ..... 122
Figure 2.32 ..... 123
Figure 2.33 ..... 124
Figure 2.34. ..... 125
Figure 2.35 ..... 126
Figure 3.1A. ..... 175
Figure 3.1B/C ..... 176
Figure 3.1D/E ..... 177
Figure 3.1F ..... 178
Figure 3.2. ..... 179
Figure 3.3. ..... 180
Figure 3.4. ..... 181
Figure 3.5. ..... 182
Figure 3.6. ..... 183
Figure 3.7. ..... 184
Figure 3.8. ..... 185
Figure 3.9. ..... 186
Figure 3.10. ..... 187
Figure 3.11 ..... 188
Figure 3.12 ..... 189
Figure 3.13 ..... 190
Figure 3.14. ..... 191
Figure 3.15 ..... 192
Figure 4.1. ..... 224
Figure 4.2. ..... 225
Figure 4.3 ..... 226
Figure 4.4A/B ..... 227
Figure 4.4C. ..... 228
Figure 4.5A/B ..... 229
Figure 4.5C ..... 230
Figure 4.6A. ..... 231
Figure 4.6B ..... 232
Figure 4.6C ..... 233
Figure 4.7. ..... 234
Figure 4.8. ..... 235
Figure 4.9 ..... 236

## Chapter 1. Introduction

### 1.1 Background

The pelvis is a complicated skeletal element, comprising two innominates (each composed of three bones) and the sacrum. The three bones that make up the innominate (also called the os coxa) are the ilium, ischium, and pubis, which come together and fuse to form the acetabulum during growth and development. The innominates articulate with each other ventrally at the pubic symphysis and with the sacrum dorsally, at the sacroiliac joints. The pelvis is subjected to the forces experienced by and the weight of the upper body via the sacroiliac joints, and to the forces generated by the interaction between hindlimb and substrate via the acetabulum (Slijper 1946, Badoux 1974, Kummer 1975, Pauwels 1980, Dalstra \& Huiskes 1995, Preuschoft 2004). For the purposes of this dissertation, loading often refers to the general forces (e.g., compression, tension, torsion) experienced by the particular regions of the pelvis, while locomotion or locomotor loading refers to the specific conditions or variables (e.g., arboreal versus terrestrial ground reaction forces) that generate those forces.

In addition to its external morphology, the pelvis also has an internal architecture made up of trabeculae. Trabecular bone models and remodels (via changes in density and anisotropy) according to the mechanical stresses that it is subjected to (Wolff 1892, Wolff 1986, Huiskes et al. 2000, Tanck et al. 2001, Pontzer et al. 2006, Ruff et al. 2006, van der Meulen et al. 2006, Volpato et al. 2008, Barak et al. 2011). Thus, it should theoretically be possible to reconstruct loading and locomotion in a given skeletal element (even in a fossil taxon) from the patterning of its trabecular architecture, provided that particular types of loading and locomotion produce distinctive patterns. The purpose of this dissertation is to explore these relationships between loading, locomotion, and trabecular architecture in the primate ilium and ischium, and then
apply this understanding to reconstructing locomotion in the Miocene ape, Rudapithecus hungaricus.

Hypothesized loading regimes for the pelves of bipeds and quadrupeds derive from the biomechanical models of Pauwels (1980) and Slijper (1946), Badoux (1974), and Kummer (1975), respectively. The bones of the human pelvis have been modeled as acting like a series of arcs connected by joints (referred to as "the ring model" by Lewton [2015]) or beams that are cantilevered during single limb support and bent during double limb support in bipedal locomotion (Pauwels 1980). The quadruped pelvis has generally been modeled in the sagittal plane as a series of bony levers (Slijper 1946, Badoux 1974, Kummer 1975). It was initially considered by Slijper (1946) to be part of the "bow-and-string" model, in which the vertebral column is the bow and the abdominal musculature is the string, causing a dorsal rotation of the pelvis at the sacroiliac joint. This model was extended by Badoux (1974) and Kummer (1975), who proposed that the quadruped ilium would likely be subject to two opposite rotational moments around the sacroiliac joint and acetabulum (i.e., subject to bending in the sagittal plane), which would be counteracted by the abdominal musculature, ischiosacral ligaments, and ischiocaudal muscles. These two soft tissue structures (the ischiosacral ligaments and ischiocaudal muscles) would also potentially serve to resist the sagittal bending of the ischium by the hamstrings (Badoux 1974, Kummer 1975). More recently, Lewton (2015) proposed the development of a regional model of pelvic biomechanics in which each of the bones of the innominate is loaded like a long bone would be in the bent beam model. If this is the case, one side of each bone should be loaded in tension and the other in compression (Currey 2002). These biomechanical models are the basis for the general loading hypotheses considered here.

In addition to considering general loading hypotheses, this work also considers a number of the specific factors that affect the different locomotor modes of primates. Observational data
from wild populations (where possible) of living primates form the basis for these considerations (Fleagle 1976, Rawlins 1976, Rose 1976, Bauer 1977, Cant 1987, Hunt 1991, Hunt 1992, Doran 1992, Doran 1993, Hunt et al. 1996, Fleagle 1999, Wells \& Turnquist 2001, Thorpe \& Crompton 2006, Manduell et al. 2011), which also take into account things like differences in forces experienced between arboreal and terrestrial primates (e.g., Schmitt \& Hanna 2004), and those utilizing different categories of locomotion (Waterman 1929, Steudel 1981, Yirga 1987, Fleagle \& Anapol 1992). Additional information about differences in soft tissue anatomy and bony morphology are also considered in the context of observed locomotor behavior (Straus 1929, Waterman 1929, Yirga 1987, Payne et al. 2006, Channon et al. 2009, Hammond 2014). These behavioral and morphological data allow for the generation of hypotheses about differences in loading regimes between primate taxa utilizing different locomotor modes.

Ultimately, the hypotheses proposed here about loading and locomotion allow for the generation of predictions about trabecular architecture. The theoretical framework underlying bone functional adaptation was initially explored in the works of Meyer (1867), Rauber (1876), Roux (1881), and Wolff $(1892,1986)$ (Roesler 1987). Meyer's work (1867) was one of the earliest collaborations in bone biomechanics, showing that the pattern of trabecular bone in the femoral head was determined by the direction of principle stresses placed on it (cited from Roesler 1987), while Rauber (1876) performed the first systematic investigation into the material properties of bone, including anisotropy (cited from Roesler 1987). The contributions of Wolff (1892, 1986) and Roux (1881) were summarized over a century later by Ruff et al. (2006: 484) as, "the general concept that bone adapts to its mechanical environment during life, and therefore that differences in morphology can be used to investigate differences in past mechanical environments." More recently, bone's ability to remodel in response to mechanical loading (both use and disuse) has been experimentally validated (Pontzer et al. 2006, van der Meulen et al.

2006, Volpato et al. 2008, Barak et al. 2011) and the cellular mechanism behind it has been proposed to be the coupled action of osteblasts and osteoclasts, potentially in response to local strain perturbations in the mineralized matrix of bone (Huiskes et al. 2000). In the anthropological literature, the current understanding of bone functional adaptation has been used as the basis for comparative work on primates utilizing different locomotor modes, often in an attempt to find a clear functional signal that can be used for reconstructing locomotion in fossil taxa (Galichon \& Thackeray 1997, Macchiarelli et al. 1999, Rook et al. 1999, Fajardo \& Müller 2001, Macchiarelli et al. 2001, Ryan \& Ketcham 2002, Martinon-Torres 2003, Maga et al. 2006, Mazurier et al. 2010, Saparin et al. 2011, DeSilva \& Devlin 2012, Su et al. 2013). This dissertation extends that work to the trabecular architecture of the primate ilium and ischium, with the general expectation that primates transmitting greater forces through their pelves (due to the specific nature of their locomotor behaviors) will have denser and/or more anisotropic trabecular architecture as a result.

In addition to being the first quantitative investigation of trabecular architecture in the primate pelvis, this dissertation advances the field of evolutionary anthropology through its use of trabecular architecture as a proxy for reconstructing specific patterns of loading in the ilium and ischium. Using trabecular architecture in this way has the potential to generate greater understanding of the way forces are transmitted through the pelves of extant primates. This is important both in terms of validating proposed biomechanical models of the pelvis and because this information is currently impossible to get from in vivo studies, as the methods needed to do so are too invasive to be used on captive primates (whose locomotion may be compromised in comparison to their wild conspecifics anyway). A better understanding of the relationship between force transmission (loading) and pelvic trabecular architecture in extant primates will, in turn, allow for more accurate predictions to be made about loading in the pelves of extinct
primates. Thus, this dissertation also has the potential to inform reconstructions of locomotion in fossil primates (both at the species level and at the level of the individual specimen), which may ultimately lead to being able to contribute to important debates in the field of paleoanthropology. These debates include assessing the relative degrees of arboreality and terrestriality in the australopithecines (Galichon \& Thackeray 1997, Macchiarelli et al. 1999, Macchiarelli et al. 2001, DeSilva \& Devlin 2012, Barak et al. 2013), and the question of how to reconstruct locomotion in fossil taxa with no extant analog (like many of the Miocene apes) (Rook et al. 1999, Scherf 2008, Ward et al. 2008, Morgan et al. 2015).

### 1.2 Data and Methodology

My research explores the variation in the trabecular architecture of the primate lower ilium and ischium within the theoretical framework of bone functional adaption, specifically with respect to hypothesized loading regimes and locomotor categories. While previous work has found correlations between trabecular variables and locomotor mode in other skeletal elements (humerus: Fajardo \& Müller 2001; calcaneus: Maga et al. 2006; femur: Fajardo \& Müller 2001, MacLatchy \& Müller 2002, Ryan \& Ketcham 2002, Fajardo et al. 2007, Scherf 2008; talus: Su et al. 2013; tibia: Barak et al. 2013), no such quantitative analyses have been undertaken for the pelvis.

This dissertation attempts to determine if there are species-specific patterns of trabecular architecture in the primate pelvis that can be linked to hypothesized loading regimes and/or locomotor categories in predictable ways, and whether these patterns can inform locomotor reconstructions of fossil taxa. High-resolution X-ray computed tomography (HRXCT) scans of the innominates of six extant taxa (Macaca mulatta, Papio anubis, Pan troglodytes, Pongo pygmaeus, Symphalangus syndactylus, and Homo sapiens) and one fossil specimen
(Rudapithecus hungaricus) were obtained, and their trabecular architecture was sampled in ImageJ (Rasband 1997-2016) and analyzed in Quant3D (Ryan \& Ketcham 2002, Ketcham \& Ryan 2004) to produce measures of density (bone volume divided by total volume, BVTV) and fabric anisotropy (directionality, DA) that could be compared within and between taxa. In total, 788 volumes of interest (VOIs) were selected from the complete ilium sample ( $\mathrm{n}=27$ ), 771 from the ischium sample ( $\mathrm{n}=28$ ), and 11 from Rudapithecus hungaricus (1570 for the entire dissertation). HRXCT scanning was selected as the method of data collection and analysis for this study as its resolution is sufficiently superior to that of traditional radiographs to make its increased cost worthwhile, and it allows for both the accurate quantification and precise reconstruction of three-dimensional structures (Odgaard 1997, Fajardo et al. 2002, Golder \& Christian 2002). HRXCT also allows for the scanning of larger skeletal elements than $\mu \mathrm{CT}$, such as complete innominates, and has been applied previously to both extant and fossil taxa (Ryan \& Ketcham 2002, Maga et al. 2006, Fajardo et al. 2007, Scherf 2008, Ryan \& Shaw 2012, Su et al. 2013, Ryan \& Shaw 2015). HRXCT is preferred over medical CT for the analysis of fossils, as the process of fossilization can alter the rate of absorption of X-rays by the fossil, such that accurate imaging by medical CT becomes impossible (Scherf 2008, DeSilva \& Devlin 2012).

### 1.3 Dissertation Organization

Chapter 2 presents the first quantitative characterization of the trabecular architecture of the primate lower ilium $(\mathrm{n}=27)$ by HRXCT, and investigates the patterning of trabecular density and anisotropy within and between taxa. These variables are explored in the context of hypothesized loading regimes and traditional locomotor categories, to determine whether trabecular architecture is diagnostic of locomotor mode. The trabecular architecture of the ilium was isolated from HRXCT scans and analyzed using ImageJ and Quant3D. The resulting data were
compared intra- and interspecifically via descriptive statistics and principal component analyses.

Chapter 3 explores the relationship between hypothesized loading regimes, locomotor categories, and trabecular architecture in the primate ischium via HRXCT scans ( $n=28$ ). The data collection and analysis protocol in this chapter was similar to that of Chapter 2, with the trabecular architecture of the ischium being isolated from HRXCT scans and analyzed in ImageJ and Quant3D. As the primate ischium does not vary in morphology as much as the lower ilium does, the sampling coverage of this region of the pelvis was more complete, allowing for additional statistical testing of loading and locomotor hypotheses.

Chapter 4 describes the preserved trabecular architecture of the innominate of the Miocene ape Rudapithecus hungaricus (Ward et al. 2008), placing it in comparative context with extant taxa in order to test the proposed locomotor hypothesis for this species. The trabecular data sets from the previous two chapters were rescaled to sample homologous trabecular regions to those preserved in Rudapithecus, with all trabecular variables again coming from ImageJ and Quant3D. The trabecular variables from the extant sample were compared to those of Rudapithecus to produce a locomotor reconstruction.

## References

Badoux DM. 1974. An introduction to biomechanical principles in primate locomotion and structure, in: Primate Locomotion. Jenkins FA, ed. Academic Press, New York: 1- 43.
Barak MM, Lieberman DE, Hublin JJ. 2011. A Wolff in sheep's clothing: trabecular bone adaptation in response to changes in joint loading orientation. Bone 49:1141-1151.
Barak MM, Lieberman DE, Raichlen D, Pontzer H, Warrener AG, Hublin J.J. 2013. Trabecular evidence for a human-like gait in Australopithecus africanus. PLoS ONE, 8, e77687.
Bauer HR. 1977. Chimpanzee bipedal locomotion in the Gombe National Park, East Africa. Primates 18:913-921.
Cant JGH. 1987. Positional behavior of female Bornean orangutans (Pongo pygmaeus). American Journal of Primatology 12:71-90.
Channon AJ, Günther MM, Crompton RH, Vereecke EE. 2009. Mechanical constraints on the functional morphology of the gibbon hind limb. Journal of Anatomy 215:383-400.
Currey JD. 2002. Bone: Structure and Mechanics. Princeton University Press: Princeton.
Dalstra M, Huiskes R. 1995. Load transfer across the pelvic bone. Journal of Biomechanics 28:715-724.
DeSilva JM, Devlin MJ. 2012. A comparative study of the trabecular bony architecture of the talus in humans, non-human primates, and Australopithecus. Journal of Human Evolution 63:536-51.
Doran DM. 1992. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: A case study of paedomorphism and its behavioral correlates. Journal of Human Evolution 23:139-157.
Doran DM. 1993. Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. American Journal of Physical Anthropology 91:83-98.
Fajardo RJ, Müller R. 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. American Journal of Physical Anthropology 115:327-336.
Fajardo RJ, Muller R, Ketcham RA, Colbert M. 2007. Nonhuman anthropoid primate femoral neck architecture and its relationship to locomotor mode. The Anatomical Record 290:422-436.
Fajardo RJ, Ryan TM, Kappelman J. 2002. Assessing the accuracy of high-resolution X-ray computed tomography of primate trabecular bone by comparisons with histological sections. American Journal of Physical Anthropology 118:1-10.
Fleagle JG. 1976. Locomotion and posture of the Malayan siamang and implications for hominoid evolution. Folia Primatologica 26:245-269.
Fleagle JG. 1999. Primate Adaptation and Evolution. Academic Press: New York.
Fleagle JG, Anapol FC. 1992. The indriid ischium and the hominid hip. Journal of Human Evolution 22:285-305.
Galichon V, Thackeray JF. 1997. CT scans of trabecular bone structures in the ilia of Sts 14 (Australopithecus africanus), Homo sapiens and Pan paniscus. South African Journal of Science 93:179-180.
Golder W, Christian A. 2002. Quantitative CT of dinosaur bones. Journal of Computer Assisted Tomography 26:821-824.
Hammond AS. 2014. In vivo baseline measurements of hip joint range of motion in suspensory and nonsuspensory anthropoids. American Journal of Physical Anthropology. 153:417-34.
Huiskes R, Ruimerman R, van Lenthe GH, Janssen JD. 2000. Effects of mechanical forces on maintenance and adaptation in trabecular bone. Nature 405:704-706.

Hunt KD. 1991. Positional behavior in the Hominoidea. International Journal of Primatology 12:95-118.
Hunt KD. 1992. Positional behavior of Pan troglodytes in the Mahale Mountains and Gombe Stream National Parks, Tanzania. American Journal of Physical Anthropology 87:83-105.
Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardized descriptions of primate locomotor and postural modes. Primates 37:363-387.
Ketcham RA, Ryan TM. 2004. Quantification and visualization of anisotropy in trabecular bone. Journal of Microscopy 213:158-171.
Kummer B. 1975. Functional adaptation to posture in the pelvis of man and other primates, in: Primate Functional Morphology and Evolution. Tuttle RH, ed. Aldine, Chicago: 281-290.
Lewton KL. 2015. In vitro bone strain distributions in a sample of primate pelves. Journal of Anatomy 226:458-77.
Macchiarelli R, Bondioli L, Galichon V, Tobias PV. 1999. Hip bone trabecular architecture shows uniquely distinctive locomotor behavior in South African australopithecines. Journal of Human Evolution 36:211-232.
Macchiarelli R, Rook L, Bondioli L. 2001. Comparative analysis of the iliac trabecular architecture in extant and fossil primates by means of digital image processing techniques: implications for the reconstruction of fossil locomotor behaviors, in: Hominoid Evolution and Climatic Change in Europe 2 - Phylogeny of the Neogene Hominoid Primates of Eurasia. De Bonis L, Koufos GD, and Andrews P, eds. Cambridge University Press, Cambridge: 60-101.
MacLatchy L, Müller R. 2002. A comparison of the femoral head and neck trabecular architecture of Galago and Perodicticus using micro-computed tomography. Journal of Human Evolution 43:89-105.
Maga M, Kappelman J, Ryan TM, Ketcham RA. 2006. Preliminary observations on the calcaneal trabecular microarchitecture of extant large-bodied hominoids. American Journal of Physical Anthropology 129:410-417.
Manduell KL, Morrogh-Bernard HC, Thorpe SK. 2011. Locomotor behavior of wild orangutans (Pongo pygmaeus wurmbii) in disturbed peat swamp forest, Sabangau, Central Kalimantan, Indonesia. American Journal of Physical Anthropology. 145:348-59.
Martinon-Torres M. 2003. Quantifying trabecular orientation in the pelvic cancellous bone of modern humans, chimpanzees, and the Kebara 2 Neanderthal. American Journal of Human Biology 15:647-661.
Mazurier A, Nakatsukasa M, Macchiarelli R. 2010. The inner structural variation of the primate tibial plateau characterized by high-resolution microtomography. Implications for the reconstruction of fossil locomotor behaviors. Comptes Rendus Palevol 9:349-359.
Meyer GH. 1867. Die Architektur der Spongiosa. Archiv fur Anatomie, Physiologie, und Wissenschaftliche Medicin 34:615-628.
Morgan ME, Lewton KL, Kelley J, Otárola-Castillo E, Barry JC, Flynn LJ, Pilbeam D. 2015. A partial hominoid innominate from the Miocene of Pakistan: Description and preliminary analyses. Proceedings of the National Academy of Sciences 112:82-7.
Odgaard A. 1997. Three-dimensional methods for quantification of cancellous bone architecture. Bone 20:315-328.
Pauwels F. 1980. Biomechanics of the Locomotor Apparatus: Contributions on the Functional Anatomy of the Locomotor Apparatus. (Trans. Maquet P, Furlong R). Springer, New York. (Original work published 1965).
Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Gunter MM, Thorpe SKS, D’Aout K. 2006. Morphological analysis of the hindlimb in apes and humans. I. Muscle architecture. Journal
of Anatomy 208:709-724.
Pontzer H, Lieberman DE, Momin E, Devlin MJ, Polk JD, Hallgrimsson N, Cooper DML. 2006. Trabecular bone in the bird knee responds with high sensitivity to changes in load orientation. Journal of Experimental Biology 209:57-65.
Preuschoft H. 2004. Mechanisms for the acquisition of habitually bipedality: Are there biomechanical reasons for the acquisition of upright bipedal posture? Journal of Anatomy 204:363-384.
Rasband WS. 1997-2016. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.
Rauber AA. 1876. Uber Elastizitat und Festigkeit der Knochen. Wilhelm Engelmann, Leipzig.
Rawlins RG. 1976. Locomotor ontogeny in Macaca mulatta: I. Behavioral strategies and tactics. American Journal of Physical Anthropology 44:201.
Roesler H. 1987. The history of some fundamental concepts in bone biomechanics. Journal of Biomechanics 20:1025-1034.
Rook L, Bondioli L, Kohler M, Moya-Sola S, Macchiarelli R. 1999. Oreopithecus was a bipedal ape after all: Evidence from the iliac cancellous architecture. Proceedings of the National Academy of Sciences of the United States of America 96:8795-8799.
Rose MD. 1976. Bipedal behavior of olive baboons (Papio anubis) and its relevance to an understanding of the evolution of human bipedalism. American Journal of Physical Anthropology 44:247-262.
Roux W. 1881. Der zuchtende Kampf der Teile, oder die 'Teilauslese' im Organismus. (Theorie der 'funktionellen Anpassung'). Wilhelm Engelmann, Leipzig.
Ruff C, Holt B, Trinkaus E. 2006. Who's afraid of the big bad Wolff?: "Wolff's Law" and bone functional adaptation. American Journal of Physical Anthropology 129:484-498.
Ryan TM, Ketcham RA. 2002. The three-dimensional structure of trabecular bone in the femoral head of strepsirrhine primates. Journal of Human Evolution 43:1-26.
Ryan TM, Shaw CN. 2012. Unique suites of trabecular bone features characterize locomotor behavior in human and non-human anthropoid primates. PLoS One 7:e41037.
Ryan TM, Shaw CN. 2015. Gracility of the modern Homo sapiens skeleton is the result of decreased biomechanical loading. Proceedings of the National Academy of Sciences. 112:372-7.
Saparin P, Scherf H, Hublin JJ, Fratzl P, Weinkamer R. 2011. Structural adaptation of trabecular bone revealed by position resolved analysis of proximal femora of different primates. Anatomical Record 294:55-67.
Scherf H. 2008. Locomotion-related femoral trabecular architecture in primates - high resolution computed tomographies and their implications for estimations of locomotor preferences of fossil primates, in: Anatomical imaging: Towards a new morphology. Endo H and Frey R, eds. Springer, New York: 39-59.
Slijper EJ. 1946. Comparative Biologic-Anatomical Investigations on the Vertebral Column and Spinal Musculature of Mammals. North-Holland, Amsterdam.
Steudel, K. 1981. Functional aspects of primate pelvic structure: A multivariate approach. American Journal of Physical Anthropology 55:399-410.
Straus WL. 1929. Studies on primate ilia. American Journal of Anatomy 43:403-460.
Su A, Wallace IJ, Nakatsukasa M. 2013. Trabecular bone anisotropy and orientation in an Early Pleistocene hominin talus from East Turkana, Kenya. Journal of Human Evolution 64:667677.

Tanck E, Homminga J, van Lenthe GH, Huiskes R. 2001. Increase in bone volume fraction
precedes architectural adaptation in growing bone. Bone 28:650-654.
Thorpe, SKS and Crompton, RH. 2006. Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. American Journal of Physical Anthropology 131:384-401.
Van der Meulen MCH, Morgan TG, Yang X, Baldini TH, Myers ER, Wright TM, Bostrom MPG. 2006. Cancellous bone adaptation to in vivo loading in a rabbit model. Bone 38:871-877.

Volpato V, Viola TB, Nakatsukasa M, Bondioli L, Macchiarelli R. 2008. Textural characteristics of the iliac-femoral trabecular pattern in a bipedally trained Japanese macaque. Primates 49:16-25.
Ward CV Begun D, Kordos L. 2008. New partial pelvis of Dryopithecus brancoi from Rudabánya, Hungary. American Journal of Physical Anthropology 135:218.
Waterman HC. 1929. Studies on the evolution of the pelvis of man and other primates. American Museum of Natural History Bulletin 58:585-642.
Wells JP, Turnquist JE. 2001. Ontogeny of locomotion in rhesus macaques (Macaca mulatta): II. Postural and locomotor behavior and habitat use in a free-ranging colony. American Journal of Physical Anthropology. 115:80-94.
Wolff J. 1892. Das Gesetz der Transformation der Knochen. A. Hirchwild Berlin.
Wolff J. 1986. The law of bone remodeling. Springer-Verlag Berlin.
Yirga S. 1987. Interrelation between ischium, thigh-extending muscles and locomotion in some primates. Primates 28:79-86.

# Chapter 2. Characterizing trabecular density and anisotropy in the primate lower ilium in the context of loading and locomotion 

### 2.1 Abstract

Recent work in the primate appendicular skeleton has found support for a relationship between locomotor regime and trabecular variables in several skeletal elements, but no such analyses have been undertaken for the pelvis. This is likely due to its large size and complex structure, which complicates attempts to understand how it is loaded. However, the pelvis plays a functionally important role as an anatomical nexus, as it is acted on by both the weight of the upper body and the forces generated by the hindlimbs, making it a potentially informative area for locomotor analyses. This study specifically looked at the trabecular architecture of the lower ilium, which experiences loading from both the sacroiliac joint and the acetabulum. Biomechanical models, limited experimental work, and observations of locomotor behavior formed the basis for intraspecific loading predictions, which (in combination with previous work on the relationship between body size and trabecular variables) then informed interspecific locomotor predictions. Generally, those taxa that experience stronger forces (and thus, greater loading), were predicted to have denser and/or more anisotropic trabecular architecture. The innominates of six species $(\mathrm{n}=27)$ were imaged using high-resolution X-ray computed tomography, 788 volumes of interest were sampled in ImageJ from the complete set of scans, and trabecular density and anisotropy were calculated in Quant3D. Intra- and interspecific predictions were assessed descriptively, and principal component analyses were also performed on a reduced interspecific data set. The intraspecific analyses found some support for previous work on loading patterns in the primate ilium, but were generally mixed overall in their correspondence with predicted patterns. The interspecific results were similarly mixed for
trabecular density; it does not appear to be correlated with locomotor behavior. However, relative degree of anisotropy in the lower ilium does seem to carry a locomotor signal, as has been seen in other skeletal elements.

### 2.2 Introduction

Reconstructions of the locomotor habits of fossil primates have largely relied on analyses of the external morphology of the pelvis, comparing the anatomy of the fossils to living primates with diverse locomotor modes (e.g., Straus 1929, Le Gros Clark 1955, McHenry \& Corruccini 1975, Berge 1994, Ward et al. 2008). Advances in non-destructive imaging have provided an alternative approach to reconstructing loading history, allowing the internal architecture of certain skeletal elements to be used for this purpose (Galichon \& Thackeray 1997, Macchiarelli et al. 1999, Rook et al. 1999, Scherf 2008, Mazurier et al. 2010, Shaw \& Ryan 2012). However, in order to be able to reconstruct locomotion in fossil primates using bone microstructure, it is first necessary to understand the relationship between locomotor behavior and trabecular architecture (Kivell 2016). This study is broadly concerned with clarifying the relationship of bone functional adaptation to mechanical loading using CT scan data, specifically focusing on elucidating this relationship within the ilium (Roesler 1987, Ruff et al. 2006). Bone microstructure is potentially informative for this, as trabeculae form the internal support structure of bone and change throughout life in response to the stresses placed on them (Wolff 1892, Wolff 1986, Ruff et al. 2006). Thus, trabecular architecture may reflect a primate's locomotor behavior and history (Rudolf 1922, Macchiarelli et al. 1999, Fajardo \& Müller 2001, MacLatchy \& Müller 2002, Ryan \& Ketcham 2002, Fajardo et al. 2007, Cunningham \& Black 2009, Mazurier et al. 2010, Abel \& Macho 2011, Shaw \& Ryan 2012). The ilium was chosen because it has been identified as one of the few locations in the pelvis where predictions about external
morphological variation related to locomotor mode have been supported (Lewton 2010) and its trabecular structure has not been quantified previously. Understanding the extent and range of bone functional adaptation in the extant primate pelvis is the essential precursor to interpretations of locomotion in fossil species (Kivell 2016). Reconstructing locomotion in the past has been critical for analyses of the hominid fossil record and for understanding human origins since Dart's $(1925,1949)$ description of Australopithecus africanus as a biped, linking that trait to the human lineage.

In a living primate, working out the relationship between mechanical loading and trabecular architecture would seem to be a relatively straightforward task: their locomotor behavior is observable and their trabecular architecture theoretically reflects these loads (Roux 1881, Wolff 1892, Wolff 1986). Unfortunately, while primates are frequently categorized by their most typical locomotor behavior (e.g., Napier \& Walker 1967, Lewton 2010, Ryan \& Shaw 2012, Fajardo et al. 2013), the actual stresses that these regimes place on the pelvis are still not well understood, as the pelvis is a relatively complex skeletal element and the methods used to study bone strain in vivo (i.e., the placement of strain gauges directly onto bone, underneath any overlying musculature/soft tissue) are quite invasive (Lewton 2015). While some in vitro data on bone strain in the primate pelvis exist (Lewton 2015), there remains an underlying theoretical conflict in the literature about what it means in terms of loading when large strains are observed in a bone (as reviewed in Lewton 2010).

Mechanical loading places stress (force per area) on bone, which may cause deformation (measured as strain: the change in length of an object divided by its original length). Stresses and strains cause bone modeling and remodeling governed at the cellular level by the coupled action of osteoblasts and osteoclasts potentially in response to local strain perturbations in the mineralized matrix of a bone (Huiskes et al. 2000). According to the optimization/trade-off
theory, bone models and remodels to produce a structure with the optimal balance between mass and strength (e.g., Weinans et al. 1992, Huiskes et al. 2000, Currey 2002, Lieberman et al. 2003, Turner 2007), a general principle that has been recognized since the earliest work on bone biomechanics (Bourgery 1832, Bell 1834, cited from Roesler 1987; Roux 1895, cited from Fung 1993). Increased stresses place increased strains on a bone, causing osteocytes to signal the deposition of bone until the strains are normalized, with the opposite happening under conditions of decreased strain (Lanyon et al. 1982, Rubin 1984, Burger \& Klein-Nulend 1999, Huiskes et al. 2000). Thus, a structure experiencing high strain should show additional trabecular reinforcement, via the constant maintenance feedback loop between strain and bone deposition (i.e., if loading were to stop, bone should begin to remodel, and when loading begins again, this should signal continued deposition of bone) (Figure 2.1). This prediction of high strain in regions that resist stress or rather, that optimization does not occur to mitigate high strains (e.g., Rubin et al. 1990, Weinans et al. 1992, Hylander \& Johnson 1997), is countered by proponents of the strain-reduction theory, which suggests that bones are adapted to minimize stresses and strains, such that high strains are only seen in bones that are not well-adapted to that loading regime (Grine et al. 2010). If this is the case, then bones (or regions of bones) that are observed to have low strains under normal loading conditions should show evidence of increased bony deposition (e.g., trabecular reinforcement) in that region, as they should have already adapted to reduce strain. While attempting to determine which of these theories is correct is beyond the scope of this project, combining Lewton's (2015) in vitro bone strain data from the primate pelvis with analyses of iliac trabecular architecture may potentially shed some light on the issue.

The internal architecture of the ilium is defined by the arrangement of spongy trabecular bone between layers of dense, relatively nonporous cortical bone, described in the engineering literature as a 'sandwich construction,' combining high strength with low weight (Jacob et al.,
1976). Thus, the ilium appears to have evolved to optimize strength for weight. The trabeculae form the internal support structure of bone and change throughout life in response to the stresses placed on them (Roux 1881, Wolff 1892, Wolff 1986, Ruff et al. 2006). Traditionally, trabecular density has been a primary variable in the study of internal bone architecture (Mednick 1955, Odgaard 1997). It has been demonstrated repeatedly that trabecular density corresponds to stresses placed on bone (Wolff 1892, 1986), with areas of higher stress showing denser accumulations of trabeculae (Mednick 1955, Carter et al. 1989, Goldstein 1987, Dalstra et al. 1993, Giesen et al. 2003). In one early study, Mednick (1955) compared human and chimpanzee ilia, and found that they exhibit different patterns of thick and thin bone, attributing this ultimately to their differences in locomotor regime and proximally to the different roles of the muscles of the pelvis and lower limb (whose origins and attachments can be used to infer loading). This idea was further investigated in the orthopedic clinical literature by Dalstra et al. (1993:532) in their examination of the mechanical properties of trabecular bone in the human ilium, which found that "the two high-density areas (upper part of the acetabulum to the sacroiliac joint area and the middle part of the pubic bone) coincide with the major areas of load transfer" in the pelvis (see also Macchiarelli et al. 1999, Rook et al. 1999, Cunningham \& Black 2009, Abel \& Macho 2011). Even as methods for quantifying bone microstructural properties have advanced, trabecular density remains one of the main variables used in these types of analyses. It is measured as bone volume divided by total volume and is often referred to as bone volume fraction (BVTV).

Along with trabecular density, the orientation or directionality of the trabeculae within a bone serves as an indicator of loading history (Carter et al. 1989, Goldstein et al. 1993, Biewener et al. 1996, Barak et al. 2011). Trabeculae that are more organized tend to exhibit a higher degree of anisotropy (directionality), indicating a need to withstand greater stresses from those
directions (Dalstra \& Huiskes 1995, Giesen et al. 2001, Abel \& Macho 2011). It has been experimentally demonstrated in both mammals and birds that anisotropy increases in response to habitual loading (e.g., via locomotion) (Carter et al. 1989, Macchiarelli et al. 1999, Pontzer et al. 2006, Volpato et al. 2008, Barak et al. 2011). This response has also been seen in the changes the trabeculae of the human proximal femur undergo during the transition to unassisted bipedal walking in infants (Ryan \& Krovitz 2006). Anisotropic areas of trabecular bone tend to be areas of higher trabecular density as well (in terms of both volume and trabecular morphology), demonstrating a two-fold response in bone to withstanding recurring stresses (Dalstra \& Huiskes 1995, Macchiarelli et al. 2001, Barak et al. 2011). Degree of anisotropy (DA) is typically quantified in CT analyses along with BVTV, as these two variables have been directly correlated with variation in the Young's modulus of trabecular bone (Ryan \& Ketcham 2002). According to Goldstein et al. (1993), BVTV and DA together account for $>80 \%$ of trabecular bone's mechanical properties, while more recent work by Maquer et al. (2015) suggests that these two variables together explain up to $98 \%$ of the variation in trabecular stiffness (Young's elastic modulus).

Additional experimental support exists for considering trabecular density and anisotropy as responses to loading. Using an ontogenetic series of pigs, Tanck et al. (2001) found that the trabecular organization of adult pig proximal tibia and vertebrae was more mechanically efficient than that of juveniles, reflecting habitual loading at full body weight (consistent with predictions about anisotropy). Van der Meulen et al. (2006) demonstrated in vivo the expected increase in bone volume fraction and degree of anisotropy with cyclic compressive loading in a rabbit model. Volpato et al. (2008) examined the relationship between iliac trabecular structure and species-atypical locomotor behavior in bipedally-trained Macaca fuscata, concluding that iliac trabeculae exhibit the expected remodeling response to atypical loading. This is particularly important, as it demonstrates the plasticity of iliac trabecular architecture in non-human
primates and suggests that trabecular patterns are not so genetically or phylogenetically canalized that locomotor loading cannot significantly alter them.

In terms of the trabecular architecture of the pelvis specifically, investigations have largely focused on humans. While Dalstra et al. (1993) initially posited that the bone of the human pelvis is not highly anisotropic, recent studies have found that there are three overlapping regions of trabecular organization in the human ilium, termed the ilioischial, sacropubic, and iliocotyloid bundles (Macchiarelli et al. 1999, Martinon-Torres 2003) (Figure 2.2). These bundles meet in an area superior to the acetabulum called the trabecular chiasma and form in response to the loads transmitted across the pelvis during bipedal locomotion, in which the greatest concentration of force passes superior to the acetabulum along the paths indicated by the bundles (Dalstra \& Huiskes 1995, Macchiarelli et al. 1999). While these bundles correspond to the forces produced by bipedalism, they are present at a gross level in neonates (Cunningham \& Black 2009). This suggests that the stress-strain environment is not the only factor in producing these bundles, but is rather a later modifier of a pre-existing pattern that may be evolutionarily and genetically determined (Cunningham \& Black 2009).

Extant non-human primate studies have often focused on comparing the iliac trabecular structure of Pan to that of humans, drawing contrasts between their close evolutionary history and divergent locomotor regimes. In comparing Pan to Homo sapiens, it is clear that Pan lacks the trabecular organization characteristic of humans. The sacro-pubic bundle is present and may be relatively dense, but its trabeculae are thinner and more isotropic than in human ilia, and a true ilio-ischial bundle is entirely absent (Rook et al. 1999, Macchiarelli et al. 1999, Macchiarelli et al. 2001). Due to its lack of an ilio-ischial bundle, the trabeculae do not form a dense, well defined, organized chiasma, as is found in humans (Galichon \& Thackeray 1997, Rook et al. 1999, Macchiarelli et al. 1999, Macchiarelli et al. 2001). These observations are consistent with Pan as
a facultative biped, as they do not habitually transmit the same forces through their ilia as humans do, and suggest that a quantifiable causal relationship exists between locomotor mode and trabecular architecture.

Given the likely relationship between iliac trabecular architecture and locomotor loading, one might be able to reverse engineer the forces that produced a particular trabecular pattern. This is potentially important both for understanding loading in the pelves of extant primates and for reconstructing locomotion in fossil primates. Understanding loading (and its relationship to trabecular architecture) in the pelves of extant primates is crucial both for validating biomechanical models of force transmission in the pelvis, as testing these models in vivo is not possible at this time due to the invasive nature of the methods needed to do so (Lewton 2015), and for being able to accurately reconstruct locomotion in fossil primates. If this type of reverse engineering of forces can be done via trabecular architecture for extinct taxa, this will provide additional detail (at the species level) to reconstructions based on external morphology alone and may allow for the reconstruction of intraspecific locomotor variability at the individual level. It will also potentially allow for locomotor reconstruction in fossils that lack preserved features characteristic of particular locomotor regimes and/or in taxa for which only a few skeletal elements are known.

While there has been very little work done on the pelvic structural biomechanics of nonhuman primates, the few models that exist (Badoux 1974, Kummer 1975, Pauwels 1980) and the single experimental study to investigate strain in this skeletal element (Lewton 2015) can serve to guide predictions about trabecular patterning in this project in combination with the previous discussion of trabecular architecture and its theoretical response to loading. In an attempt to clarify the relationship between locomotion and the trabecular architecture of the primate ilium, the following overarching questions will be addressed:

1) Are there species-specific patterns of trabecular bone in the lower ilium? What do they look like for each of the species included in this study (Macaca mulatta, Papio anubis, Pan troglodytes, Pongo pygmaeus, Symphalangus syndactylus, and Homo sapiens) and can they be explained by locomotion?
2) Can these patterns be used to distinguish between taxa with different loading regimes and at what resolution?

## Methods 2.3

The methods in this paper are described prior to the Predictions section, as specific details of the volume of interest (VOI) sampling and labeling system need to be defined and discussed before they are referenced in the predictions.

## Sample

Adult, wild-shot non-human primate specimens of both sexes were selected from the collections at the National Museum of Natural History (NMNH), the American Museum of Natural History (AMNH), and the Penn Museum (UPenn) (Appendix A). These included Papio anubis $(n=6)$, Symphalangus syndactylus $(n=4)$, Pan troglodytes $(n=5)$, Pongo pygmaeus ( $n=$ 5), and Macaca mulatta ( $n=4$ ). Human innominates $(n=3)$ came from the Texas Archaeological Research Laboratory (TARL). The sample included a variety of locomotor modes (Papio: terrestrial quadrupedalism; Symphalangus: brachiation; Pan: knuckle-walking; Pongo: quadrumanous clambering; Macaca: arboreal/terrestrial quadrupedalism; Homo: bipedalism), both to test the hypothesis that different loading regimes produce distinct trabecular patterns and to inform future comparative work on fossil specimens. The sample sizes are relatively small due to the cost of scanning large innominates at high resolution, but are comparable to those used in similar previous work (Maga et al. 2006, Kivell et al. 2011, Saparin et al. 2011, Barak et
al. 2013, Fajardo et al. 2013, Kuo et al. 2013).

## CT Scanning

All specimens were scanned on the North Star Imaging (upgraded ACTIS) scanner at the High-Resolution X-ray Computed Tomography Facility at the University of Texas at Austin (UTCT). The specimens were mounted in foam and oriented vertically or sub-vertically (depending on innominate size and specific morphology) in the scanning tube. This allowed for the collection of serial transverse slices through the innominates, covering the entire bone. Specimens were scanned either singly or in pairs, depending on the size of the specimens. The scans were collected using FeinFocus energy source settings of 180 or 190 kV and $0.15,0.17,0.19$, or 0.3 mA, with $3600,12003,12004,15304,17761,18003,18004$, or 18013 projections. Isotropic voxel sizes ranged from $0.0378-0.0793 \mathrm{~mm}$ depending on the size of the specimen and represented the highest possible resolution given specimen size and scanning budget (Appendix B). Between 2044 and 4505 slices were collected for each innominate. The images were reconstructed as 16bit TIFF and 8-bit JPEG grayscale images. The 8-bit JPEG images were used for all analyses in Quant3D (Ryan \& Ketcham 2002, Ketcham \& Ryan 2004).

## Image Processing/Volume of Interest Sampling

The CT scan data for each specimen were obtained from UTCT, and then cropped and sampled in the free software ImageJ (Rasband 1997-2016) according to the following protocols. The cropping protocol first isolated the lower ilium by loading the entire stack of ilium slices in the 3D Viewer plugin, rotating the reconstruction so that its bottom edge was parallel to the 3D Viewer window in lateral view, and cropping out all of the bone above the level of the posterior inferior iliac spine and below the level of a horizontal line drawn tangent to the upper-most edge of the acetabulum (Figure 2.3A). The protocol was slightly modified for the Homo specimens, as they would otherwise have almost no lower ilium for comparison. In postero-lateral view (gluteal
attachment surface of the ilium turned flat to the viewer), the 3D image was rotated such that a horizontal line could be drawn between the anterior inferior iliac spine and the posterior inferior iliac spine, and the bone above that was removed. A parallel line to that one was then used for cropping out the acetabulum.

Volumes of interest (VOIs) were then sampled by loading the lower ilium crop, determining where in the upper part of the image stack at least two cubes of maximum size (defined by voxel measurements) could be placed without including any cortical bone and with sufficient trabeculae for analysis, and then either cropping and saving those two cubes or placing two more cubes (for a total of four), depending on the size and morphology of the specimen (Figure 2.3B). The cubes were placed as close to the medial, lateral, dorsal, and ventral margins of the bone as possible, taking into account superior to inferior changes in lower iliac shape. In some specimens, the decision was made to only place one cube, rather than not sample that level at all, resulting in missing data. Additionally, Homo required the modification of the sampling protocol again. Rather than maximize the size of the individual VOIs, the decision was made to maximize the coverage of the ilium. This resulted in the creation of more sets of slightly smaller VOIs, rather than fewer sets of larger VOIs (i.e., three or four sets, rather than two or three). The cropped cubes for all specimens were then loaded into UTCT's free threedimensional fabric analysis program, Quant3D (Ryan \& Ketcham 2002, Ketcham \& Ryan 2004), and analyzed using these parameters: centered spherical VOIs, iterative thresholding (Ridler \& Calvard 1978, Trussell 1979), and 513 uniform orientations with random rotation and dense vectors (Ketcham \& Ryan 2004). Uniform orientations generates a grid for analysis, and implementing random rotation and dense vectors is required to mitigate potential biases caused by analyzing the grid (Ketcham \& Ryan 2004). The star volume distribution method was used to compute anisotropy (Cruz-Orive et al. 1992, Ketcham \& Ryan 2004). Trabecular density was
measured as bone volume fraction (bone volume divided by total volume, BVTV) and degree of anisotropy (DA) were then taken from the program's output for further analysis, as these two variables have been shown to explain more than $80 \%$ of the variance in bone's mechanical properties (Goldstein et al. 1993).

## CT Data Analysis

A total of 788 VOIs were selected from the complete ilium sample, and the size and specific morphology of each specimen dictated the number and placement of its VOls. These conditions meant that both data reduction and standardization were necessary before data analysis could proceed. The complete data sets of BVTV and DA values were used to generate a reduced, standardized data set consisting of BVTV and DA scaled to the same relative anatomical locations across specimens at intervals of $20 \%$ of total lower iliac height, with VOIs labeled " 0 " corresponding to the level of the posterior inferior iliac spine (the top of the lower ilium crop) and those labeled " 10 " corresponding to the level of a line drawn tangent to the upper-most curve of the acetabulum (the bottom of the lower ilium crop) (see Figure 2.3B).

Each of the VOI cubes referenced in the image processing/VOI sampling section were labeled as "Med," "Lat," "Dors," and "Vent" based on their relative anatomical position (medial, lateral, dorsal, and ventral). The complete set of VOIs from each position (e.g., all Med VOIs) are referred to as columns in the subsequent sections. Within column comparisons are those looking at superior to inferior variation within a single VOI column (e.g., the medial column consists of all medial VOIs from the posterior inferior iliac spine to the acetabulum), while between column comparisons are those looking at the variation within a single horizontal level (e.g., Med0 vs Lat0). In most of the sampled taxa, the morphology of the lower ilium is such that the medial and lateral trabecular bone was more extensively sampled than the dorsal and ventral bone. The exception to this was Macaca, in which the pattern is reversed (more
extensive dorsal/ventral sampling than medial/lateral sampling). It should be noted that this study is based on small sample sizes; these results are preliminary and are intended as an initial description of the trabecular bone of the lower ilium, both within and across taxa.

## Intraspecific and Interspecific Comparisons

Intraspecific
The small sample size for each species does not allow for statistically testing the significance of the proposed species-specific patterns. Instead, these predictions were assessed via dot plots (modified from BoxPlotR, Spitzer et al. 2014) and comparisons of VOI medians, with the goal of providing an initial quantitative characterization and description of the nature of the trabecular architecture in the primate lower ilium and ultimately guiding future work.

## Interspecific

As was the case for the intraspecific predictions, interspecific statistical comparisons (at least at the level of one species to another) were also hampered by small sample sizes. Additionally, because this set of predictions focused on generally comparing overall trabecular measures between taxa (rather than being specific to the level of column or VOI), further data reduction was necessary to facilitate meaningful comparisons. To that end, means were generated for each VOI column for each specimen, such that each ilium could be described by eight numbers: four BVTV values (one per column) and four DA values (one per column). Eight dot plots were then generated with BoxPlotR, one for each column for BVTV and the same for DA, to compare and describe general interspecific trends while still showing intraspecific variation. The median values from these plots were used to order the taxa from lowest to highest and assign each a rank, with one being the lowest and six being the highest. The rankings from each column were then added to create composite scores for BVTV and DA for each taxon that could be directly compared.

Two principal component analyses, one for BVTV and one for DA, were also performed on the standardized medial and lateral VOI data set using prcomp in R. These two VOIs are more completely sampled than the dorsal and ventral VOIs, due to morphological variation in the shape of the lower ilium between taxa. The analyses did not include one of the Symphalangus specimens or any of the Macaca specimens, again due to variation in the shape of the lower ilium preventing complete coverage of all VOIs ( $n=22$ ).

### 2.4 Predictions

Predictions follow from the current general understanding of bone remodeling in the ilium, descriptions of the locomotor behavior of the sampled taxa in the wild (when possible), and relevant experimental work. The predictions that include data from experimental work are based on Lewton's (2015) paper on in vitro bone strain in the primate pelvis. For the sake of clarity, a brief description of her experimental setup is necessary to provide context and explain specific terminology. The specimens used for testing consisted of complete pelvic girdles, both femora, and a short section of the lumbar spine (Lewton 2015). Articulated pelves with their muscular tissue removed were mounted in a materials testing system in such a way as to allow regular movement at the sacroiliac joint and pubic symphysis, and 19 strain gauges were affixed to the innominates: 13 on the loaded side innominate, including one reference gauge, and six on the unloaded side (Figure 2.4A) (Lewton 2015). The "loaded side" was the side that experienced loading via the femur at three different angles of limb excursion $\left(45^{\circ}, 90^{\circ}, 105^{\circ}\right)$ while the "unloaded side" did not (Figure 2.4B) (Lewton 2015). Generally, the strains experienced in the most flexed position $\left(45^{\circ}\right)$ differ more from the two other positions than they do from each other, average shear strain magnitude tends to increase with increasing limb extension, and interspecific differences in mean ilium strain are more pronounced in the most flexed position
(though much of the interspecific difference at $45^{\circ}$ appears to be the result of high mean ilium strain in Ateles geoffroyi, a species that is not included in this study) (Lewton 2015). More relevant for this work is that Hylobates has high mean ilium strain in the two more extended leg positions in comparison to the two quadrupedal monkeys (Macaca and Papio), suggesting that this type of loading is likely atypical for a brachiator and more typical for a quadruped (Lewton 2015). Different deformation regimes were not reported for the different limb angles (Lewton 2015). This experiment obviously does not take into account muscular loading and the effects of soft tissue on dissipating loads in the bones, as it would be impossible to place strain gauges on the innominates in vivo without disrupting the overlying muscle (Lewton 2015). As in vivo work of this type is impossible, Lewton (2015) represents the only data on bone strain in non-human primates, and thus, shapes many of the predictions herein.

## Intraspecific Predictions

In this section, observational data on primate postural and locomotor behavior will be reviewed in conjunction with the few biomechanical models and the little experimental data that exist for the pelvis. These bodies of work will inform predictions about trabecular architecture, based on likely potential loading regimes, allowing for the generation of expected trabecular patterns for each species. For the purpose of generating these predictions, Lewton's (2015) in vitro bone strain data will be interpreted using the optimization/trade-off theory of bone modeling/remodeling as it more closely corresponds to the theoretical framework typically used in studies of trabecular architecture (that loading causes stress, which causes strain, which is reflected in trabecular patterning) (as reviewed in Kivell 2016).

## Macaca mulatta

Locomotor/Postural Behavior
What little locomotor and postural behavioral data there is for Macaca mulatta comes
from the free-ranging colony at Cayo Santiago, which may or may not engage in the same patterns of substrate use as their wild conspecifics. On Cayo Santiago, M. mulatta is both arboreal and terrestrial, with the percentage of time spent utilizing each substrate changing throughout ontogeny (Rawlins 1976, Wells \& Turnquist 2001). Adults spend the majority of their time on the ground (about 64\%), while juveniles split their time approximately equally between arboreal and terrestrial substrates (Rawlins 1976, Wells \& Turnquist 2001). When adults utilize arboreal substrates, they prefer horizontal ones of relatively larger diameter (i.e., the inflexible bases of major branches of trees with trunks four inches to two feet in diameter) (Wells \& Turnquist 2001). Arboreal substrate use approximately $36 \%$ of the time is likely to be enough to preserve an arboreal trabecular signal (if one exists), as the ilia of bipedally-trained M. fuscata preserve a trabecular signal of bipedalism in spite of the monkeys spending most of their time locomoting quadrupedally (Nakatsukasa et al. 1995, Volpato et al. 2008). The primary M. mulatta locomotor mode is quadrupedal walking, while the primary postural mode is overwhelmingly sitting (>70\% for all animals older than six months and $>90 \%$ for adults) (Wells \& Turnquist 2001). More generally, macaques are a geographically widespread, varied group of Old World monkeys whose members occupy arboreal and terrestrial niches throughout Asia and parts of North Africa (Rodman 1979, Fleagle 1999, Chatani 2003). All of the members of this genus are capable of both arboreal and terrestrial locomotion, but each species varies in their patterns of substrate use (Fleagle 1999). For the purposes of this paper, M. mulatta may be characterized as a generalized quadruped with the capacity for above-branch locomotion on large, horizontal branches.

## Biomechanical Models/Experimental Work

Early biomechanical models of the non-human primate pelvis proposed that it acts like a series of levers and attempted to predict the stress regimes experienced by the entire pelvic
girdle as a whole, rather than for each bone individually (Badoux 1974, Kummer 1975, Lewton 2015). Based on these models, the ilium of a quadruped would likely be subject to two opposite rotational moments around the sacroiliac and hip joints (i.e., bending stress in the sagittal plane), which would be counteracted by the abdominal musculature and soft tissues attached to the ischium (the ischiosacral ligaments and ischiocaudal muscles) (Figure 2.5) (Badoux 1974, Kummer 1975). Differentiating between arboreal and terrestrial quadrupedal locomotion is outside of the scope of these models.

Experimental work on in vitro bone strain in the primate pelvis found that the Macaca loaded side ilium experienced axial compression medially and ventrally, and tension dorsally, while the unloaded side experienced torsion (Lewton 2015). Mean shear strain (often used to indicate overall strain) for the gauges experiencing torsion was higher than those experiencing compression (Lewton 2015). The combination of ventral compression and dorsal tension suggests dorso-ventral bending as a likely loading regime (Lewton 2015), in agreement with previously proposed biomechanical models (Badoux 1974, Kummer 1975). No strains were reported from the lateral side of the ilium, as no gauges were placed there (Lewton 2015). Trabecular Hypotheses

Lewton's (2015) finding of dorso-ventral bending suggests that BVTV and DA within the Macaca ilium should be greater in the more centrally placed dorsal and ventral VOIs (Dors4,6 and Vent4,6, which are the greatest distance from the sacroiliac and hip joints) than in the VOIs closer to the posterior inferior iliac spine superiorly and the acetabulum inferiorly, and higher overall in the ventral VOIs than in the dorsal VOIs. Her finding of torsion potentially suggests trabecular reinforcement of both medial and lateral VOIs (Lewton 2015). Another possibility would be that lateral BVTV could also increase toward the acetabulum, as the trabeculae in this region would experience greater mechanical stimulus via hindlimb loading than those farther
away from this joint. The predictions for trabecular bone distribution in M. mulatta are:
(P1) Resistance to dorso-ventral bending is greater in the centrally-placed VOIs. This implies that BVTV and DA will be:
a. BVTV: Dors4,6 > Dors0,2,8,10; Vent4,6 > Vent0,2,8,10
b. DA: Dors4,6 > Dors0,2,8,10; Vent4,6 > Vent0,2,8,10
(P2) Resisting dorso-ventral bending (ventral compression/dorsal tension) results in greater ventral than dorsal reinforcement:
a. BVTV: Vent > Dors
b. DA: Vent > Dors
(P3) Resisting torsion caused by the downward force of the sacroiliac joint and the upward force of the hindlimb at the acetabulum results in balanced medial and lateral trabecular bone:
a. BVTV: Med = Lat
b. DA: Med = Lat
(P4) Mechanical stimulus via hindlimb loading is greater closer to the acetabulum:
a. BVTV: Lat6 < Lat8 < Lat10

## Papio anubis

## Locomotor/Postural Behavior

Papio anubis is a large-bodied, plantigrade terrestrial catarrhine that spends up to $97 \%$ of its total locomotor time walking quadrupedally (Hunt 1991), but also incorporates bipedal postures while feeding (Rose 1976). In one study, Papio spent approximately $28 \%$ of the time in the trees, compared to $72 \%$ on the ground (Hunt 1992). Knuckle walking has been observed in a single individual following a wrist injury that left it incapable of normal plantigrady (Hausfater 1976). While it exhibits the range of behavioral plasticity common to primates, the amount of
time that Papio spends in quadrupedal locomotion far outweighs any other type (Hunt 1991). The main non-locomotor positional behavior of Papio is sitting; it spends approximately $75 \%$ of the time sitting (Hunt 1991). Compared to Macaca (with the caveats that the locomotor data from both taxa come from a very small number of studies and the Macaca data is based on the Cayo Santiago population, which is not a native habitat for this taxon), Papio and Macaca divide their time between arboreal and terrestrial substrates similarly (Papio: 28\% vs. 72\%, Macaca: $36 \%$ vs. $64 \%$, respectively), though Macaca is a bit more arboreal (Rawlins 1976, Hunt 1991, Wells \& Turnquist 2001).

## Biomechanical Models/Experimental Work

The biomechanical model discussed for the Macaca pelvis in the previous section is likely to also apply to the Papio pelvis, as they are relatively closely related, primarily quadrupedal monkeys. Based on this model, dorsal tension and ventral compression (i.e., sagittal bending) of the lower ilium would be expected (Badoux 1974, Kummer 1975).

Interestingly, while the predicted dorso-ventral bending was found by Lewton (2015) in Macaca, this was not the case for Papio. Her experimental work on in vitro bone strain in the non-human primate pelvis found that the Papio loaded side ilium experienced axial compression medially in the one strain gauge that was placed in a location analogous to the Medo/Med2 VOI locations and strong compression in two dorsally-placed strain gauges (but along the mediolateral axis of the bone), as well as medial and ventral torsion more generally (Lewton 2015). The unloaded side ilium experienced torsion (Lewton 2015). No strain gauges were placed on the lateral side of the ilium (Lewton 2015). The difference in strains found between Papio and Macaca could be due to morphology (the Macaca lower ilium tends to be medio-laterally compressed and greater in dorso-ventral dimensions compared to the Papio lower ilium) or due to differences in trabecular architecture.

## Trabecular Hypotheses

Based on the finding of torsion along both axes of the ilium (Lewton 2015), similar BVTV and DA values are predicted for all VOI columns. Combined with the findings of axial compression supero-medially and along the medio-lateral axis dorsally, additional reinforcement against bending (higher BVTV and DA) may be an alternate prediction for the medial and lateral columns. Lateral BVTV should also increase toward the acetabulum, as the trabeculae in this region potentially experience greater mechanical stimulus via hindlimb loading than those farther away from this joint.
(P1) Resistance to torsion along both medio-lateral and dorso-ventral axes necessitates
reinforcement of all sides of the lower ilium:
a. BVTV: Med $=$ Lat $=$ Dors $=$ Vent
b. DA: Med = Lat $=$ Dors $=$ Vent
(P2) Resistance to medio-lateral compression/bending suggests greater reinforcement of those columns, relative to the dorsal and ventral ones:
a. BVTV: Med, Lat > Dors, Vent
b. DA: Med, Lat > Dors, Vent
(P3) Mechanical stimulus via hindlimb loading is greater closer to the acetabulum:
a. BVTV: Lat0,2,4 < Lat6 < Lat8 < Lat10

## Pan troglodytes

## Locomotor/Postural Behavior

Knuckle-walking is a specialized terrestrial mode of locomotion practiced by Pan that makes up a significant percentage ( $\sim 92 \%$ ) of its locomotor behavior, at least in some populations (Hunt 1991, 1992). Knuckle-walking likely places a different set of stresses on the pelvis than pronograde quadrupedalism, as the torso is held in a more orthograde position. While knuckle-
walking is the primary terrestrial mode of locomotion in Pan, it also exhibits a highly plastic locomotor repertoire that includes arboreal climbing, unimanual suspension, brachiation, and limited bipedalism (Bauer 1977, Hunt 1991, Hunt 1992). These different types of locomotion occur at different frequencies between age classes, with infants and juveniles under two years of age having a more forelimb-dominated positional behavior repertoire (including more suspension during arboreal locomotion) as compared to older individuals who spend more time engaging in terrestrial quadrupedalism, but who tend to climb more when in the trees (Hunt 1991, Doran 1992, Doran 1997). There are also sex differences in substrate use in Pan; females spend more time in the trees than males do, at least in P. troglodytes verus (Doran 1993a, 1993b). In addition to age and sex differences in substrate use, there are population-level differences as well, e.g., Gombe chimpanzees spend less time on the ground than Mahale chimpanzees (47.2\% versus 60.7\%) (Hunt 1992).

## Biomechanical Models/Experimental Work

While there are no experimental bone strain data for Pan, a prediction of dorso-ventral bending is potentially supported by biomechanical models that suggest the ilium is subject to two opposite rotational moments around the sacroiliac and hip joints, which are counteracted by musculature (Badoux 1974, Kummer 1975). Similarly, off-axis torsion or medio-lateral bending could be hypothesized to result from the combined upward force of the hindlimb on the acetabulum and the downward force of body weight acting on the sacroiliac joint, given their relative positions on the innominate (Badoux 1974, Kummer 1975). However, Preuschoft (2004) suggests the opposite: that the Pan ilium is unlikely to experience strong bending moments or torsion at the sacroiliac joint, due to the combination of its short lumbar spine and long lower ilium (and that the same is generally true for the other great apes). In terms of in vivo hip joint flexibility, Pan has a large range of motion relative to non-suspensory taxa, though its hip is less
mobile than that of Pongo (Hammond 2014). This suggests that, while knuckle-walking may dominate the Pan locomotor time budget, it still retains pelvic adaptations to arboreality (Hammond 2014).

## Trabecular Hypotheses

If the ilium is bent dorso-ventrally (i.e., in dorsal compression and ventral tension), there should be trabecular reinforcement (increased BVTV and/or DA) of the dorsal margin, concentrated in the central VOIs (Dors 4 and Dors 6). If the ilium is loaded in torsion, all VOI columns should be roughly equal in trabecular measures. If the ilium is bent medio-laterally, either the medial or the lateral VOI column should be reinforced, depending on which is greater: the downward force of the weight of the upper body at the sacroiliac joint or the upward force generated by the hindlimb interacting with the substrate.
(P1) Resistance to dorso-ventral bending (dorsal compression/ventral tension) suggests greater reinforcement of the dorsal margin:
a. BVTV: Dors > Vent
b. DA: Dors > Vent
(P2) Resistance to dorso-ventral bending is greater in the centrally-placed VOIs:
a. BVTV: Dors4,6 > Dors0,2,8,10; Vent4,6 > Vent0,2,8,10
b. DA: Dors4,6 > Dors0,2,8,10; Vent4,6 > Vent0,2,8,10
(P3) Resistance to torsion along both medio-lateral and dorso-ventral axes necessitates reinforcement of all sides of the lower ilium:
a. BVTV: Med $=$ Lat $=$ Dors $=$ Vent
b. DA: Med = Lat $=$ Dors $=$ Vent
(P4) To resist medio-lateral bending, either the medial or the lateral column should be reinforced, depending on which is greater: the downward force of the weight of the
upper body at the sacroiliac joint or the upward force generated by the hindlimb interacting with the substrate:
a. BVTV: Med > Lat or Med < Lat
b. DA: Med > Lat or Med < Lat

## Pongo pygmaeus

## Locomotor/Postural Behavior

Pongo locomotor behavior is mostly a combination of suspension (hanging) and orthograde clambering, defined by Hunt et al. (1996: 380) as "horizontal progression in a forelimb-suspensory torso-orthograde mode, but with the hindlimbs assisting. All four limbs act as propulsors, with most body weight borne by the abducted forelimbs." Pongo combines this slow, quadrumanous climbing/clambering with the potential for fast, acrobatic motion in certain situations (Cant 1987, Thorpe \& Crompton 2006). It is the most arboreal of the great apes, utilizing an incredible variety of quadrumanous postures on complex, dynamic substrates; climbing, clambering, and transferring between branches and trees makes up roughly 60-75\% of its locomotor repertoire, with arm hanging/brachiating accounting for another approximately 12-20\% (Hunt 1991 and references therein, Manduell et al. 2011). In contrast to Pan, age and sex seem to have a limited effect on locomotion in Pongo, at least in one recent study, with orthograde suspension dominating all other locomotor modes for all age-sex categories (Manduell et al. 2011). Also in contrast to the other great apes, Pongo does not knuckle-walk during terrestrial locomotion, but fist-walks instead (Tuttle 1967). These locomotor differences between Pongo and Pan should produce distinct differences in trabecular architecture. Biomechanical Models/Experimental Work

No comprehensive biomechanical models exist for the Pongo pelvis; it is unlikely to be easily described by either a biped- or quadruped-based model, given its unique locomotor
regime. However, some of the possible loadings suggested by Pauwels' (1980) bipedal/human models may still apply, given the variety of positions in which Pongo loads its ilia (Figure 2.6). In these models, the bones of the pelvis either act as a series of arcs connected by joints or as bent beams (Pauwels 1980, Lewton 2015). In the double-support (both hindlimbs loaded) model, loading at the sacroiliac joint rotates the ilium dorsomedially, potentially causing compression in the lower ilium (Pauwels 1980, Lewton 2015). In the single-support model, a bending moment at the unsupported hip with inferior displacement of the innominate is predicted to result from the combined forces of the body weight and the unsupported limb (Pauwels 1980, Lewton 2015). However, Preuschoft (2004) suggests that the Pongo ilium is unlikely to experience strong bending moments or torsion at the sacroiliac joint, due to the combination of its short lumbar spine and long lower ilium (as was also predicted for Pan).

The experimental work that has been carried out on the Pongo pelvis consists of a study on in vivo hip joint range of motion, which largely confirmed previous suggestions of high hip mobility from observational data (Hammond 2014). Pongo possesses a large range of motion in hip abduction and external rotation (compared to other suspensory and nonsuspensory taxa) likely as a result of its unusual ligamentum teres morphology (i.e., that it lacks a subchondral insertion), which acts to prevent hip dislocation in extreme arboreal positions (Crelin 1988, Hammond 2014).

## Trabecular Hypotheses

If Pauwels' (1980) double-support model is correct, there should be trabecular reinforcement (BVTV and/or DA) of the dorsal column in response to dorso-ventral bending/dorsal compression. If single-support stances dominate the loading regime, there should be reinforcement against medio-lateral bending/lateral compression. Given its hip mobility and varied locomotor regime, it is likely that Pongo subjects its ilia to a huge variety of
different stresses. The magnitude of the forces generated by these loadings are likely moderated by both its frequent use of its forelimbs in arboreal locomotion and by the fact that the ground reaction forces affecting the pelvis via the hindlimb are lower on arboreal substrates than on terrestrial ones (Schmitt \& Hanna 2004). If Preuschoft (2004) is correct and the sacroiliac joint/lower ilium do not experience strong bending or torsional moments, then the iliac trabeculae should be generally adapted to loading in all directions, in response to arboreal, multidirectional loading.
(P1) Resistance to dorso-ventral bending (dorsal compression/ventral tension) suggests greater reinforcement of the dorsal margin:
a. BVTV: Dors > Vent
b. DA: Dors > Vent
(P2) Resistance to medio-lateral bending (lateral compression/medial tension) suggests greater reinforcement in the lateral column:
a. BVTV: Lat > Med
b. DA: Lat > Med
(P3) Multidirectional loading in a complex, arboreal environment suggests a need to resist stresses from all directions:
a. BVTV: Med $=$ Lat $=$ Dors $=$ Vent
b. DA: Med = Lat = Dors = Vent

## Symphalangus syndactylus

## Locomotor/Postural Behavior

The Hylobatidae, including Symphalangus, are true brachiators, utilizing this locomotor mode a majority of the time, particularly during travel (Napier 1963, Sigmon 1971, Fleagle 1976, Hunt 1991). They have also been observed climbing, leaping, and engaging in bipedalism,
exhibiting the locomotor plasticity common among hominoids (Sigmon 1971, Fleagle 1976, Hunt 1991). Climbing, for example, is often used during feeding, while bipedalism is used around 6\% of the time during travel and 3\% of the time during feeding (Fleagle 1976). The main postural modes utilized by Symphalangus are sitting and arm-hanging (Hunt 1991). The Symphalangus locomotor regime is forelimb-dominated, making it unlikely that they subject their pelves to high loads.

## Biomechanical Models/Experimental Work

As was the case for Pongo, a specific biomechanical model for loading in the Symphalangus pelvis does not exist. Applying the human models proposed by Pauwels (1980) is potentially interesting, as Symphalangus is orthograde and does engage in some bipedalism, but should be done cautiously. Symphalangus is much smaller in body size and is not a striding biped; the upper body weight will not generate the same amount of downward force that it would in a larger animal and its arboreal environment will not generate the same ground reaction forces that terrestrial substrates would (Schmitt \& Hanna 2004). That being said, Pauwels (1980) suggested loading at the sacroiliac joint during double limb support, causing the ilium to rotate dorsomedially and potentially causing compression in the lower ilium (Pauwels 1980, Lewton 2015). In single limb support, a bending moment at the unsupported hip with inferior displacement of the innominate is predicted to result from the combined forces of the body weight and the unsupported limb (Pauwels 1980, Lewton 2015).

Given the similarities between the pelvis and locomotor regime of Symphalangus and those of the other hylobatids, the Hylobates data from Lewton's (2015) experimental bone strain study seem appropriate to use as the basis for predictions about loading in the Symphalangus ilium, in spite of the slightly greater size of the Symphalangus pelvis (Waterman 1929, Straus 1929, Schultz 1936, Hunt 1991). In her study, the Hylobates loaded side ilium experienced
torsion medially, cranio-caudally-oriented tension ventrally, weak cranio-caudal compression dorsally, and strong medio-lateral compression dorsally (Lewton 2015). No strains were reported from the lateral side of the ilium (Lewton 2015). The unloaded side ilium experienced torsion (Lewton 2015). The combination of dorsal compression and ventral tension suggests dorsoventral bending, while the strong medio-lateral compression dorsally potentially suggests mediolateral bending. These bending regimes, along with the finding of medial torsion, are not incompatible with Pauwels' (1980) models.

## Trabecular Hypotheses

If dorso-ventral bending is the primary load experienced by the Symphalangus ilium, this should result in greater trabecular reinforcement of the compressed dorsal side. Medio-lateral compression dorsally could either result in buttressing of both the medial and lateral sides, or could simply be another load acting on the dorsal margin, adding to its reinforcement. If torsion is the dominant loading regime, then all of the columns should be roughly equal in trabecular values.
(P1) Resistance to dorso-ventral bending (dorsal compression/ventral tension) suggests greater reinforcement of the dorsal margin:
a. BVTV: Dors > Vent
b. DA: Dors > Vent
(P2) Compression on both the medial and lateral sides suggests similar trabecular architecture on both:
a. BVTV: Med = Lat
b. DA: Med = Lat
(P3) Resistance to torsion along both medio-lateral and dorso-ventral axes necessitates reinforcement of all sides of the lower ilium:

> a. BVTV: Med = Lat = Dors = Vent
b. DA: Med = Lat $=$ Dors $=$ Vent

## Homo sapiens

## Locomotor/Postural Behavior

While other primates may be facultatively bipedal, utilizing a flexed or bent-knee, benthip bipedal gait (Hunt et al. 1996), humans are the only extant obligate bipeds. Human bipedalism involves an extended hip and knee, with the center of gravity balanced over the hip joints, in which forward motion is made by alternating between placing each foot in front of the other. The ability to balance the body on one leg during walking is important in classifying true human bipedalism and distinguishes it from the facultative bipedal gaits of apes (Snell \& Donhuysen 1968). The human gait is frequently referred to as striding bipedalism, differentiating it from bipedal hopping, in which both feet leave and return to the ground relatively simultaneously, as well as from flexed bipedalism (Hunt et al. 1996).

## Biomechanical Models/Experimental Work

As has been previously discussed for Pongo and Symphalangus, Pauwels (1980) proposed the main biomechanical models for the human pelvis. In these models, the bones of the pelvis either act as a series of arcs connected by joints or as bent beams (Pauwels 1980, Lewton 2015). In the double-support (both hindlimbs loaded) model, loading at the sacroiliac joint rotates the ilium dorsomedially, potentially causing compression in the lower ilium (Pauwels 1980, Lewton 2015). In the single-support model, a bending moment at the unsupported hip is predicted to result from the combined forces of the body weight and the unsupported limb (Pauwels 1980, Lewton 2015).

Some three-dimensional finite element (FE) models of the pelvis exist that aim to reconstruct complicated stress patterns realistically (e.g., Dalstra \& Huiskes 1995, Anderson et al.
2005), but the majority of these studies come from the clinical literature and include assumptions that cannot be validated in vivo. The main potential issue that comes from a lack of in vivo validation is that muscles and soft tissue likely modulate loading in living animals. For example, in Dalstra and Huiskes (1995) their FE model of the human pelvis produced differing strain magnitudes depending on the application (or lack thereof) of muscle forces. While it is important to be aware of these limitations, FE models can still be used to generate predictions about loading, that can then be "tested" via trabecular bone. Dalstra and Huiskes (1995) found that the highest stresses were located in the posterior ilium (what is being referred to here as the dorsal column) and in the lateral lower ilium just superior to the acetabulum, whereas Anderson et al. (2005) found similar results for the lateral ilium, but the opposite condition for the dorsal ilium (low levels of strain), and, instead, found higher strains in the ventral (anterior) ilium. Dalstra and Huiskes' (1995) results more closely match Pauwels' (1980) model, suggesting dorsal compression and medio-lateral bending as potential loading regimes for the human pelvis.

## Trabecular Hypotheses

Dorsal compression should result in preferential trabecular reinforcement of the dorsal column. If the Anderson et al. (2005) FE model is correct about ventral strain, then preferential reinforcement of the ventral column should take place, contra the first prediction. Medio-lateral bending, particularly with strong compression on the lateral side as in the two FE models (Dalstra and Huiskes 1995, Anderson et al. 2005), should result in buttressing of the lateral column.
(P1) Dorsal compression should result in preferential trabecular reinforcement of the dorsal column:
a. BVTV: Dors > Vent
b. DA: Dors > Vent
(P2) Ventral strain should result in preferential trabecular reinforcement of the ventral column:
a. BVTV: Vent > Dors
b. DA: Vent > Dors
(P3) Medio-lateral bending, particularly with strong compression on the lateral side, should result in buttressing of the lateral column:
a. BVTV: Lat > Med
b. DA: Lat > Med

## Interspecific Predictions

## Bone Volume Fraction

In order to make informed interspecific predictions about bone volume fraction, it is necessary to understand the relationship between BVTV and body size. Unfortunately, the literature disagrees on the nature of this relationship. In some studies, BVTV is independent of body size across mammals ranging in size from 0.002 kg (Suncus etruscus, Etruscan shrew) to 3400 kg (Elephas maximus, Asian elephant); the lowest femoral head BVTV (0.210) was found in Equus caballus (horse) and the highest (0.659) in Sylvilagus brasiliensis (tapeti or Brazilian cottontail) (Doube et al. 2010, Barak et al. 2013). In primates, femoral head BVTV ranges from 0.231 (Galago thomasi) to just over 0.7 (Pan sp.) (Doube et al. 2010, Shaw \& Ryan 2012). Contra Doube et al. (2010), Ryan \& Shaw (2013) found a positive allometric relationship between body size and femoral head BVTV in a sample of primates with a wide range in body size (from Microcebus murinus to Gorilla sp.); as body size increases, so does BVTV. From this, one would expect size to be a good predictor of relative BVTV, but recent modern humans do not fit this pattern, having lower femoral head BVTV than would be expected based on body mass (Chirchir
et al. 2014, Ryan \& Shaw 2015). However, this can be explained by differences in activity levels; recent modern humans only have low femoral head BVTV compared to similarly-sized primates if they were part of a sedentary population (e.g., agriculturalists), but if they were mobile forager/hunter-gatherers, they have the expected BVTV for their body size (Ryan \& Shaw 2015). The conflict in the literature allows for two possible predictions in this study: all of the taxa will have the same BVTV (P1) or BVTV will increase with increasing body size (P2). One additional prediction may also be made based on the patterns of locomotor loading described in the previous section: (P3) that terrestrial taxa loading their ilia more frequently and in more stereotyped regimes will have higher BVTV than arboreal taxa with less frequent loading and more complex, multidirectional loading regimes (i.e., higher bone density results locally from more frequent use potentially via increased mechanical signaling of osteocytes) (Biewener et al. 1996, Huiskes et al. 2000, Jacobs 2000, Carlson \& Patel 2006, Barak et al. 2011).
(P1) Macaca $=$ Symphalangus $=$ Papio $=$ Pan $=$ Pongo $=$ Homo
(P2) Macaca < Symphalangus < Papio < Pan < Pongo = Homo
(P3) Symphalangus < Pongo < Macaca < Papio < Pan < Homo

## Degree of Anisotropy

Similar to the situation described above for BVTV, there is also disagreement about the relationship between degree of anisotropy and body size. In Doube et al. (2010), DA did not scale significantly with body size and in Barak et al. (2013) and Fajardo et al. (2013) DA was independent of body size, while Ryan and Shaw (2013) found that DA was negatively allometric, scaling inversely with body size in a wide sample of primates. However, along with other specific trabecular variables, DA has been found to be useful in grouping primates based on locomotion and thus, potentially contains a locomotor signal as well (MacLatchy \& Müller 2002, Ryan \& Shaw 2012, Fajardo et al. 2013). In Ryan and Shaw's (2012) study of the trabecular bone of the
primate femoral head, they found that the trabecular architecture of: Pan was dense and isotropic; Macaca fascicularis was dense and anisotropic; Papio ursinus was dense and anisotropic; Symphalangus and Pongo were less dense and isotropic. A later study by these same authors found that Homo sapiens are anisotropic relative to hominoids generally, regardless of population mobility level (Ryan \& Shaw 2015). While the Macaca and Papio species included in Ryan and Shaw (2012) are not the same as those in this study (M. mulatta and P. anubis), they are relatively similar enough in their locomotor regimes that they may be used to inform predictions about DA. As was the case for BVTV above, these predictions are partially based on previous work on the trabecular bone of the femoral head, as no quantitative work on iliac trabecular architecture has been undertaken and the proximal femur is the other skeletal element involved in hip joint loading. From the disagreement in the literature about the factors affecting DA, two predictions may be made: (P1) DA in the lower ilium scales inversely with body size or (P2) DA instead corresponds to the locomotor loading acting on it, as has been found in previous studies (Carter et al. 1989, Macchiarelli et al. 1999, MacLatchy \& Müller 2002, Pontzer et al. 2006, Volpato et al. 2008, Barak et al. 2011), with terrestriality and stereotyped loading leading to greater anisotropy compared to arboreality and locomotor flexibility (Scherf 2008, Ryan \& Shaw 2012).
(P1) Homo = Pongo < Pan < Papio < Symphalangus < Macaca
(P2) Symphalangus < Pongo < Pan < Macaca < Papio < Homo

### 2.5 Results

Raw BVTV and DA data are reported in Appendix C.i. The following analyses use the reduced, standardized BVTV and DA data sets reported in Appendix D.i.

## Intraspecific

## Macaca mulatta

The lack of superior medial and lateral VOIs is a consequence of the size and morphology of the Macaca lower ilium, and the limitations of the sampling methodology. Overall, while there is a great deal of overlap and variation in Macaca BVTV and DA, both within and between VOI columns, these comparisons are still potentially informative for the four loading predictions. First, median ventral BVTV increases toward the central and inferior VOIs, as predicted, though the highest median BVTV is found in Vent6 and Vent8, not in Vent4 (Figure 2.7A). Median dorsal BVTV remains relatively constant, but with an increase at Dors8 (Figure 2.7B). Median ventral DA is highest in Vent2 and Vent8, not in Vent4 and Vent6, contra the predicted pattern (Figure 2.7C). Median dorsal DA has a very similar pattern to median dorsal BVTV (Figure 2.7D). Second, median BVTV tends to be greater in the Macaca ventral VOI column than in the dorsal column, as predicted, and greater than the medial and lateral columns as well (Figure 2.8A). There is a similar pattern in median DA, except in the superior- and inferior-most VOIs (Figure 2.8B). Third, in the available medial and lateral VOIs, median BVTV is higher in the lateral column than in the medial column (Figure 2.9A), but no such pattern exists for the DA data (Figure 2.9B). Thus, the predicted similarity in trabecular variables between the two VOIs is not supported. Fourth, given the variation and overlap in the data, it is difficult to determine if BVTV increases inferiorly in any meaningful way, as was predicted (Figure 2.10).

## Papio anubis

The lack of superior dorsal and ventral VOIs is a consequence of the size and morphology of the Papio lower ilium, and the limitations of the sampling methodology. As a result, it is difficult to identify patterns in these columns. With respect to the first prediction, there is variation between all VOI columns in median BVTV (Figure 2.11A) and generally more
consistency in median DA (Figure 2.11B), contra the pattern predicted by torsion. The second prediction (greater reinforcement of the medial and lateral VOIs, relative to the dorsal and ventral VOIs) was not supported, as median lateral and dorsal BVTV tend to be higher than medial and ventral BVTV (Figure 2.12A), though all columns have similar median DA values (Figure 2.12 B ). The third prediction (progressively higher BVTV closer to the acetabulum) was partially supported, as lateral median BVTV values are a bit higher inferiorly (Lat0,2,4< Lat6,8,10), but there is considerable overlap in the data (Figure 2.13).

## Pan troglodytes

The lack of superior dorsal and ventral VOIs is a consequence of the size and morphology of the Pan lower ilium, and the limitations of the sampling methodology. Assessing the first prediction about dorso-ventral bending is difficult, because of the relative lack of data from these two VOI columns; however, from the VOIs for which there is more than a single data point (Dors/Vent6,8,10), median dorsal BVTV tends to be higher than median ventral BVTV (Figure 2.14A). Dorsal and ventral median DA is similar for all VOls except for Dors/Vent6, where both ventral DA data points are higher than the dorsal data points (Figure 2.14 B ). With respect to the second dorso-ventral bending prediction, BVTV is higher in the central VOIs, Dors4/6 (Figure 2.15A) and Vent4/6 (Figure 2.15B), and declines inferiorly, while DA remains relatively similar across all VOIs (with the exception of a high median value at Vent6) (dorsal and ventral comparisons in Figures 2.15C and 2.15D, respectively). Median BVTV (Figure 2.16A) and DA (Figure 2.16B) vary both within and across columns, contra the third prediction (but see Discussion for a possible alternative explanation). Median lateral BVTV tends to be higher than median medial BVTV (except at Med0/Lat0, where the two are very similar) (Figure 2.17 A ), but no such pattern exists for DA (Figure 2.17B), making the outcome of the fourth prediction difficult to determine.

## Pongo pygmaeus

With respect to the first prediction (high BVTV and DA in the dorsal VOIs, relative to the ventral VOIs), median dorsal BVTV is higher than median ventral BVTV, in all VOI locations except DorsO/Vent0 (Figure 2.18A). Contra the prediction, median ventral DA is higher than median dorsal DA for all VOI locations, though there is a great deal of variability in DA within each location and there is typically overlap between the dorsal and ventral columns (Figure 2.18B). As suggested by the second prediction, medial lateral BVTV is higher than median medial BVTV for all VOI locations (Figure 2.19A), while no such pattern exists for DA (Figure 2.19B). Overall (and with respect to the third prediction), Pongo median BVTV varies more between than within VOI columns, with lateral and dorsal BVTV typically being higher than medial and ventral BVTV (Figure 2.20A). Median DA varies widely both within and between columns, and shows the opposite pattern from BVTV; median medial and ventral DA tends to be higher than lateral and dorsal DA for all of the dorsal/ventral pairs and in three of the medial/lateral pairs (Med2,4,6) (Figure 2.20B). The prediction of equal BVTV and DA for all VOI columns is not met.

## Symphalangus syndactylus

Most of the dorsal and ventral VOI columns could not be sampled for Symphalangus as a result of the size and morphology of its lower ilium. This makes it difficult to assess some of the loading predictions made for this taxon. Per the first prediction, median dorsal BVTV is very slightly higher than median ventral BVTV, for the two sampled VOI locations (Figure 2.21A). The opposite pattern is found in median DA (Figure 2.21B). With respect to the second prediction, median lateral BVTV is higher than median medial BVTV for all VOI locations except MedO/Lat0 (Figure 2.22 A ). Median medial and lateral DA are not equivalent either, but do not have the same pattern as the BVTV data (Figure 2.22B). The third prediction, of all columns being equal at each horizontal level, was also not substantiated (Figure $2.23 \mathrm{~A}, \mathrm{~B}$ ). While there are no data for
most of the dorsal and ventral VOIs, for the two inferior-most locations that exist, median dorsal and lateral BVTV are greater than ventral and medial BVTV (Figure 2.23A). In the rest of the VOIs, for which only medial and lateral data exist, median lateral BVTV tends to be greater than median medial BVTV (Figure 2.23A). For the two inferior-most locations (8 and 10), median lateral and ventral DA are higher than median medial and dorsal DA (Figure 2.23B). In the other VOI locations ( $0,2,4$, and 6 ), neither median medial nor median lateral DA is consistently higher than the other (Figure 2.23B).

## Homo sapiens

The Homo results are based on the maximizing coverage VOI sampling protocol, as this necessitated less interpolation during the size scaling process. With respect to the first and second predictions, the BVTV data are unclear. Median dorsal BVTV is greater than median ventral BVTV for the 0,2 , and 8 VOI pairs (though median values for 8 are very nearly equal and the highest BVTV value in this pair is actually ventral), while median ventral BVTV is greater in the 4,6 , and 10 pairs (Figure 2.24 A ). There is a more consistent pattern in the DA data, with median dorsal DA exceeding median ventral DA at all of the VOI locations except for 6 , where the median ventral DA is slightly higher (Figure 2.24B). Additionally, there is a trend in the dorsal DA toward increasing values superiorly and inferiorly, with the lowest DA at Dors6 (Figure 2.24B). Per the third prediction, median lateral BVTV is very similar throughout the lower ilium and is consistently higher than median medial BVTV (Figure 2.25A). The DA data are more complicated; median lateral DA is higher than median medial DA at the $4,6,8$, and 10 VOI locations, though the difference in median DA between medial and lateral VOIs at 4 is very minimal (Figure 2.25B). Median medial DA is higher than median lateral DA at 0 and 2, contra the prediction. Median medial DA decreases superiorly to inferiorly, while median lateral DA increases superiorly to inferiorly (Figure 2.25B).

## Interspecific

## BVTV Comparisons

Median BVTV in the medial column ranged from 0.176 in Macaca to 0.278 in Pongo, with the overall pattern being: Macaca $(0.176)<$ Pan $(0.216)<$ Symphalangus $(0.226)<$ Papio $(0.235)$ < Homo (0.239) < Pongo (0.278) (Figure 2.26). A Macaca specimen had the highest overall BVTV (0.358) and the range for this species included all of the other taxa, as well. There was substantial overlap in medial column BVTV across taxa.

Median BVTV in the lateral column ranged from 0.286 in Macaca to 0.330 in Homo, with the overall pattern being: Macaca (0.286) < Pongo (0.309) < Papio (0.320) < Pan (0.323) < Symphalangus (0.324) < Homo (0.239) (Figure 2.27). Again, a Macaca specimen had the highest BVTV (0.444) and the range for this species included all of the other taxa. The medians and ranges for Papio, Pan, Pongo, and Symphalangus were very similar, and median BVTV in the lateral column varied less between species and was higher overall than in the medial column.

Median BVTV in the dorsal column ranged from 0.228 in Macaca to 0.371 in Papio, with the overall pattern being: Macaca $(0.228)<$ Pongo $(0.286)<$ Pan $(0.291)<$ Homo $(0.333)<$ Symphalangus (0.345) < Papio (0.371) (Figure 2.28). A Papio specimen had the highest BVTV (0.464), and Macaca, Papio, and Pan had similar levels of intraspecific variation. The ranges of BVTV found in Macaca and Pan encompass the variation found in all of the other taxa except for Papio, whose entire range of BVTV is shifted upward relative to the other taxa. Dorsal BVTV is generally similar to lateral BVTV (i.e., higher than medial BVTV), but varies more between species.

Median BVTV in the ventral column ranged from 0.241 in Pongo to 0.308 in Homo, with the overall pattern being: Pongo $(0.241)<$ Symphalangus $(0.283)<$ Pan $(0.286)<$ Papio $(0.302)<$ Macaca (0.306) < Homo (0.308) (Figure 2.29). The BVTV range of Macaca encompassed that of
all of the other taxa except for Pan, which had a single specimen below the Macaca range. Pongo had relatively little intraspecific variation and its range was shifted downward compared to the other taxa. Overall, ventral column BVTV was similar to lateral and dorsal column BVTV in terms of actual density values, and similar to the dorsal column in terms of amount of intraspecific variation.

In order to directly compare overall BVTV across taxa and test predicted relationships, a composite score for each species was generated using its ranking for each column (Table 2.1A). The median values from the plot of each column were used to order the taxa from lowest to highest and assign each a rank (one being the lowest and six being the highest). The rankings from each column were then added to create composite scores for BVTV and DA for each taxon that could be directly compared. A low composite score for BVTV corresponds to relatively less dense trabecular architecture and a low composite score for DA corresponds to more isotropic trabecular architecture. Based on these composite scores, the pattern of relative BVTV within these taxa is: Macaca < Pongo < Pan < Symphalangus < Papio < Homo.

Macaca and Pongo have generally low median BVTV, but in one column each (ventral and medial, respectively) they have the second highest and highest median BVTV (respectively). Pan has a relatively low composite score, with moderate to low median BVTV rankings in all columns. Symphalangus has a higher composite score but more variation between columns, with its medial and ventral columns having low median BVTV and its lateral and dorsal columns having high median BVTV. Papio has moderate median BVTV in all columns, except in its dorsal column, where it has the highest BVTV rank. Homo has generally high median BVTV in all columns. These composite scores are intended to be a useful tool for making general comparisons between taxa but should be interpreted with caution, as they represent a simplification of a large volume of data, a complicated skeletal element, and both inter- and
intraspecific variation.

## DA Comparisons

Median DA in the medial column ranged from 2.589 in Homo to 5.568 in Pan, with the overall pattern being: Homo (2.589) < Pongo (3.491) < Symphalangus (3.600) < Papio (3.646) < Macaca (3.893) < Pan (5.568) (Figure 2.30). Pan and Papio had the greatest ranges of intraspecific variation ( 5.048 and 4.470 , respectively), while Homo was the least variable with a range of 0.346 . In general, the distributions of DA in the medial column make it appear as though Pan is the shifted upward version of Papio, which is the shifted upward version of Macaca. A similar generalization could be made for Symphalangus and Pongo as well, with Symphalangus being the slightly shifted upward version of Pongo.

Median DA in the lateral column ranged from 3.053 in Homo to 5.022 in Papio, with the overall pattern being: Homo (3.053) < Symphalangus (3.155) < Macaca (3.374) < Pongo (4.021) < Pan (4.628) < Papio (5.022) (Figure 2.31). Homo and Pan had the widest ranges of variation (4.741 and 4.044, respectively), while Symphalangus was the least variable (range: 0.706). A Pan specimen had the absolute highest DA (7.364). Compared to the medial column, the lateral column had less intraspecific variation overall, and Macaca, Papio, Pan, and Pongo had generally lower DA.

Median DA in the dorsal column ranged from 2.592 in Pongo to 4.317 in Homo, with the overall pattern being: Pongo (2.592) < Symphalangus (2.666) < Macaca (3.111) < Pan (3.250) < Papio (4.098) < Homo (4.317) (Figure 2.32). Papio had the most intraspecific variation (range: 3.261) as well as the individual with the highest DA overall (5.882). Generally, the distribution of dorsal DA in Macaca, Pan, and Papio looks somewhat similar (e.g., greater variation and higher overall), while being distinct from the distribution in Symphalangus and Pongo (e.g., less variation and lower overall). Homo is more like the Macaca/ Pan/Papio group but has the lowest
sample size, so its relatively high median is difficult to interpret. The dorsal column has less intraspecific variation than the medial column and DA is typically lower than in the lateral column.

Median DA in the ventral column ranged from 2.613 in Homo to 4.747 in Macaca, with the overall pattern being: Homo $(2.613)$ < Symphalangus $(3.417)$ < Pongo $(4.133)$ < Pan $(4.312)$ < Papio (4.406) < Macaca (4.747) (Figure 2.33). Papio had the widest range of intraspecific variation (4.846) and the specimen with the highest DA overall (8.603). Homo had the least intraspecific variation (range: 0.283 ). The order of median DA in the ventral column is most similar to that of the lateral column, except for the position of Macaca. Ventral column DA tends to be higher overall than dorsal column DA, with the exception of Homo, in which the pattern is reversed.

In order to directly compare overall DA across taxa and test predicted relationships, a composite score for each species was generated using its ranking for each column (Table 2.1B). Based on these composite scores, the pattern of relative DA within these taxa is: Homo = Symphalangus < Pongo < Macaca < Pan < Papio.

The composite scores for median DA seem to separate the taxa into two groups, one with relatively high median DA (Macaca, Papio, and Pan) and one with relatively low median DA (Pongo, Symphalangus, and Homo). Within the high group, Papio and Pan are more similar to each other in terms of having generally high median DA values in all columns than they are to Macaca, which has somewhat lower median DA in its lateral and dorsal columns. Within the low group, Pongo ranked differently in all columns, with its highest median DA being in the lateral column, while Symphalangus and Homo were somewhat more consistent in their rankings. Homo broke its pattern of ranking the lowest in the dorsal column, where it had the highest median DA.

## Principal Component Analyses

Two principal component analyses, one on BVTV and one on DA, were conducted on the standardized data set of medial and lateral VOIs (see Appendix E for PC scores). In the BVTV PCA, the first three principal components combined to explain $72.5 \%$ of the variability in the data. PC1 explained $43.9 \%$ of the variability, with the strongest loadings on Lat0 and Med2. The more central medial VOIs (Med2,4,6) are more strongly loaded than the superior- and inferior-most, and the lateral VOIs decrease from superior to inferior in terms of the strength of their loadings. PC1 expresses relative trabecular density in these regions, with low PC values corresponding to high BVTV and vice versa. PC2 explained $15.6 \%$ of the variability, with the strongest loadings on Lat6,8,10. PC2 expresses trabecular density in the inferior lateral VOIs (i.e., those closest to the superior edge of the acetabulum), with low PC values corresponding to low BVTV in these VOIs. PC3 explained $12.9 \%$ of the variability, with the strongest loadings on Lat2 and Med6. PC3 expresses trabecular density in these two VOIs, with high PC values corresponding to high BVTV in Lat2 and low BVTV in Med6, and vice versa.

Plotting PC1 by PC2 (Figure 2.34) showed that the greatest differentiation between any of the taxa along PC1 was between Symphalangus and Homo, with Symphalangus having relatively low BVTV and Homo having relatively high BVTV, though the taxa generally overlapped. Having Symphalangus and Homo at opposite ends of a plot of BVTV fits with both interspecific P2 and P3 (BVTV is positively allometric with body size and BVTV is related to loading type and frequency, respectively), but the overlap of the other three taxa in the center of the plot makes it difficult to support either prediction over the other. Along PC2 (inferior lateral BVTV) there was more separation of the taxa, with the order of taxa from highest BVTV to lowest being: Symphalangus > Pan > Papio > Homo > Pongo. This more closely resembles the order of taxa predicted by P3 (Homo > Pan > Papio > Pongo > Symphalangus), at least for Pan, Papio, and

Pongo. The placement of Homo on PC2 does not align with its lateral column composite score for BVTV above (where it ranked the highest), which suggests that the BVTV in the superior lateral VOIs in Homo is relatively high compared to those of the other taxa. Plotting PC1 by PC3 did not produce any different results.

In the DA PCA, the first three principal components combined to explain 79.1\% of the variability in the data. PC1 explained $52.8 \%$ of the variability, with the strongest loading (by far) on Med6. PC1 mostly expresses outliers in the DA data at this VOI location, with negative values corresponding to very high DA values. PC2 explained $14.6 \%$ of the variability, with the strongest loadings on Med4 and Lat10. PC2 expresses DA at these VOI locations in particular, with negative values corresponding to high DA at Med4 (and the other superior medial VOIs) and low DA at Lat10. It also seems to express DA overall more generally, as many of the other loadings are relatively similar. PC3 explained $11.5 \%$ of the variability, with the strongest loadings on Med2 and Lat10. PC3 expresses the DA at these two VOI locations, with high PC values corresponding to high DA at Lat10.

Plotting PC1 by PC2 (Figure 2.35) suggests that Symphalangus, Pongo, and Homo have relatively low medial central DA based on their positive PC scores along PC1, while Pan and Papio have wide ranges of intraspecific variation and high outliers at this VOI location. This is generally in agreement with the composite rankings above and suggests that ranking the taxa by their medians was likely a better choice than ranking them by their means, as medians are affected less by outliers. The splitting of taxa into two groups along PC1 (higher DA: Pan/Papio versus lower DA: Symphalangus/Homo/Pongo) provides partial support for both of the interspecific predictions about DA (P1: DA is inversely correlated with body size; P2: DA reflects locomotor loading). In P1, Pan and Papio are predicted to have higher DA than Homo and Pongo, while in P2, they are predicted to have higher DA than Symphalangus and Pongo. For P1, Symphalangus
is out of position (based on body size, it should have the highest DA), while for P2, Homo is out of position (it should have the highest DA). Generally, PC1 seems to differentiate between terrestrial quadrupeds and non-terrestrial quadrupeds, mostly on the basis of high DA outliers. Along PC2, Pan encompasses the ranges of all of the other taxa and most of them overlap with each other as well. Symphalangus is the most distinct species grouping along this axis, due to its relatively high DA in the superior medial VOIs. Plotting PC1 by PC3 did not produce any different results.

### 2.6 Discussion

In this study, predictions concerning the correlation of trabecular architecture in the primate lower ilium to patterns of locomotor loading were tested via high-resolution x -ray computed tomography. Predictions for each taxon individually were based on observed locomotor and postural behavior, biomechanical models, and experimental work. Interspecific predictions took those factors into account, along with previous work on the effects of body size and locomotor loading on two trabecular variables: bone volume fraction (a measure of density) and degree of anisotropy (a measure of directionality/organization). Although based on a relatively small sample, this study is the first to quantitatively characterize patterns of trabecular architecture in the primate ilium. In general, values for trabecular density in this study are in line with previously published work on primates; bone volume fraction tends to be less than $50 \%$ in all taxa (with very few outliers), though this can vary by skeletal element (Doube et al. 2011, Shaw \& Ryan 2012). The anisotropy data vary widely, both intraspecifically and interspecifically, and can be difficult to compare across studies, as there are several methods used to calculate anisotropy (e.g., mean intercept length versus star volume distribution).

## Intraspecific

## Macaca mulatta

Predictions about trabecular architecture in the Macaca ilium were made based on hypothesized loading regimes from biomechanical models and in vitro strain data (Badoux 1974, Kummer 1975, Lewton 2015). The hypothesized loading regimes were dorso-ventral bending (dorsal tension/ventral compression), torsion, or both. The first two predictions (reinforcement of central VOIs and the ventral column) concerned dorso-ventral bending and the data tentatively support them. Dorso-ventral bending is likely a real loading regime in the Macaca ilium. Median ventral BVTV increases toward the central and inferior VOIs, as predicted, and is generally higher than median dorsal BVTV, likely due to compression on that side of the bone. These findings are consistent with Badoux's (1974) and Kummer's (1975) biomechanical models of the quadruped ilium, wherein ventral compression results from the downward force of the upper body on the sacroiliac joint and the upward force of the hindlimb contacting the substrate, and with Lewton's (2015) experimental work.

Support for the third prediction (torsion) was more equivocal. Median lateral BVTV was higher than median medial BVTV, contra the prediction of equal trabecular bone distribution, while median DA alternated between being higher medially and laterally (Med6 < Lat6, Med8 > Lat8, Med10 < Lat10). If torsion were occurring, it would either have to be off-center of the main longitudinal axis of the ilium to potentially result in the observed asymmetrical distribution of trabecular bone or, alternatively, torsion could be having no effect on BVTV. It may, instead, be affecting the distribution of relative anisotropy, if the alternating pattern of higher DA is interpreted as reinforcing the bone via spiraling in the opposite direction of the lower ilium's rotation. Determining if this is the case would require a more holistic, fine-grained sampling of the trabecular bone throughout the entirety of the lower ilium and/or experimental or FE
modeling work. Alternatively, the higher lateral BVTV values might suggest medio-lateral bending (lateral compression/medial tension) of the ilium caused by hindlimb loading and the action of the gluteal muscles. The fourth prediction, increasing lateral BVTV toward the acetabulum, is difficult to assess. While median lateral BVTV does increase very slightly from Lat6 to Lat8 to Lat10, there is too much overlap in the data to be confident in stating that hindlimb loading is definitely the cause.

## Papio anubis

The lower ilium of Papio was predicted to have trabecular architecture resulting from loading in torsion and/or medio-lateral compression/bending. Per the first prediction, the variation in BVTV between columns suggests that torsion, if it is occurring, is off-center of the long axis of the bone or that it does not have an effect on BVTV (similar to the situation suggested for Macaca). The relatively consistent values for median DA within and between all of the VOI columns offer greater support for the prediction of torsion, particularly if torsion is the loading regime experienced by the unloaded-side ilium, as was found in Lewton (2015).

The second prediction, that medio-lateral bending is a more important loading regime than dorso-ventral bending (in effect, pitting experimental data [Lewton 2015] against predictions from biomechanical models [Badoux 1974, Kummer 1975]), was not substantiated. Median lateral and dorsal BVTV tend to be higher than median medial and ventral BVTV, suggesting that bending is occurring in both sagittal and coronal planes. Higher median lateral BVTV could potentially result from bending forces generated by the action of the gluteal muscles and the hindlimb, while the higher median dorsal BVTV requires additional explanation. Dorsoventral bending is occurring in the opposite direction (dorsal compression/ventral tension) from what Badoux (1974) and Kummer (1975) predicted. Dorsal compression, however, is what Lewton (2015) found in her experimental work. An alternative explanation for the lack of
concordance between the biomechanical models and the relatively higher BVTV values in the dorsal column is that the models are meant to explain quadrupedal locomotion rather than habitual positional behavior. Papio spends approximately $75 \%$ of its time in an orthograde seated position (Hunt 1991), which places the highest forces on its lumbar spine (and thus, the pelvis via the sacroiliac joint) of any of its postures (Ledet et al. 2005). The Papio iliac blade is angled dorsally (relative to the acetabulum and ischium) if the animal is seated upright, placing the dorsal column of the lower ilium in compression. This may explain its higher BVTV. The third prediction (greater lateral BVTV inferiorly, due to hindlimb loading) also returned equivocal results. While median lateral BVTV is a bit higher inferiorly (Lat $0,2,4$ versus Lat $6,8,10$ ) there is considerable overlap in the data, which makes it difficult to say anything definitive.

## Pan troglodytes

The hypothesized loading regimes responsible for the trabecular architecture of the Pan lower ilium were dorso-ventral bending (two different predictions), torsion, and medio-lateral bending. The two predictions concerned with dorso-ventral bending were that the dorsal column would be reinforced relative to the ventral column (as a result of dorsal compression and ventral tension) and that the central VOIs (" 4 " and " 6 ") would be reinforced relative to the more superior and inferior VOIs. For the VOIs for which there is more than a single data point (Dors/Vent6,8,10), median dorsal BVTV tends to be higher than median ventral BVTV, as predicted. Dorsal and ventral median DA is similar for all VOIs except for Dors/Vent6, where both ventral DA data points are higher than the dorsal data points. In the central VOIs (Dors/Vent4,6), BVTV is higher and then declines inferiorly, while DA remains relatively similar across all VOIs (with the exception of a high median value at Vent6), lending some support to the prediction of reinforcement against bending in the central VOIs.

The third prediction, torsion, suggested that all VOI columns would be reinforced
equally. This was not the case, as median lateral and dorsal BVTV tend to be higher than median medial and ventral BVTV, but no such pattern exists for the DA data. Instead, median dorsal and ventral DA tend to be very similar (except at Dors6/Vent6), while median medial and lateral DA alternate which is higher (Med0 < Lat0, Med2 > Lat2, Med4 > Lat4, Med6 > Lat6, Med8 < Lat8, Med10 < Lat10). As was suggested previously for Macaca, perhaps this alternating DA does indicate that the ilium is loaded in torsion, if the alternating regions of relative anisotropy spiral opposite the direction of the bone's rotation. Again, more experimental work is needed to determine if this is the case.

The final prediction, that of medio-lateral bending, was concerned with determining if that loading regime is a likely one for the Pan ilium, and then, if so, whether the force of that bending was stronger laterally (lateral compression/medial tension) or medially (medial compression/lateral tension). Median lateral BVTV tends to be higher than median medial BVTV (except at Med0/Lat0, where the two are very similar), but this is not the case for DA (as discussed above in the context of torsion). The higher median lateral BVTV may simply be a response to compressive forces generated by hindlimb loading (as was seen in vivo in van der Meulen et al. 2006) or increasing trabecular density may be the preferred response to bending loads (over anisotropy).

## Pongo pygmaeus

The Pongo lower ilium was predicted to have trabecular architecture resulting from dorso-ventral bending, medio-lateral bending, and/or multidirectional loading (such that no single loading regime or combination of the previous two adequately describes it). The prediction of dorso-ventral bending (dorsal compression/ventral tension) was based on Pauwels' (1980) human double-support model and received mixed support from the trabecular data. Median dorsal BVTV was generally higher than median ventral BVTV, but the opposite pattern
was true for DA. This suggests either complementary strategies for optimizing trabecular bone mechanically (Weinans et al. 1992, Tanck et al. 2001) or that different loading regimes are acting on the ventral and dorsal columns, creating different trabecular patterns. There is a great deal of variability within VOI locations and overlap between these columns in the BVTV and DA data, which may be explained by sex; female BVTV and DA tends to be lower than male BVTV and DA (Table 2.2), creating the ranges seen in Figure 2.18A and B. This is likely due to the degree of sexual dimorphism found in Pongo, as the males in the sample average approximately 88.5 kg , while the females average 39 kg (based on their listed weights in the NMNH database). The smaller body mass of the females means that they are not placing as much force on their pelves as the males are and, thus, do not have to maintain the same trabecular density and degree of anisotropy to mitigate and distribute these forces.

The second prediction concerned medio-lateral bending (lateral compression/medial tension) and was based on Pauwels' (1980) single-support model. As was the case for dorsoventral bending, BVTV conforms to the prediction (median lateral BVTV is higher than median medial BVTV), while the DA data do not. Again, there is variability within the data that can be partitioned by sex, more so for DA than for BVTV (though one of the females [USNM 145300] has the highest values for DA at Med2,4,6 of any of the specimens). Incidentally, that same specimen has the lowest medial BVTV and the NMNH/USNM database indicates that she was shot with an infant; in addition to its mechanical functions, trabecular bone also stores calcium (Freemont 1993, Kovacs 2001), which is depleted during pregnancy and lactation (Ilich \& Kerstetter 2000, Kovacs 2001), so the combination of low BVTV and high DA in USNM 145300 is suggestive of the idea that one of the ways that trabecular architectural compensation/optimization occurs is through the selective resorption of previously laid down high-density/isotropic trabecular bone, leaving behind more efficient trabecular architecture with lower density but higher anisotropy
(Tanck et al. 2001, Cunningham \& Black 2009, Acquaah et al. 2015). If she is removed from the medial/lateral comparison, then median lateral DA is higher than median medial DA at all VOI locations except Med0/Lat0, conforming to the predicted pattern.

The third prediction, multidirectional loading, was based on observed Pongo positional/locomotor behavior, which is assumed to dynamically load the ilium in a variety of positions, and posited similar trabecular density and directionality for all four columns. This prediction was not supported. Pongo median BVTV varies more between than within VOI columns, with lateral and dorsal BVTV typically being higher than medial and ventral BVTV. Median DA varies widely both within and between columns, and shows the opposite pattern from BVTV; median medial and ventral DA tend to be higher than lateral and dorsal DA for all of the dorsal/ventral pairs and in three of the medial/lateral pairs (Med2,4,6, though this pattern goes away when 145300 is removed from the plot).

## Symphalangus syndactylus

The Symphalangus lower ilium was hypothesized to have trabecular architecture resulting from dorso-ventral bending/dorsal compression, medio-lateral compression, and torsion. These were mainly based on the in vitro strain distributions found for Hylobates by Lewton (2015) in her experimental work. The first prediction, dorso-ventral bending/dorsal compression, is difficult to assess, as only two VOI locations (Dors/Vent8,10) were able to be sampled; the size and morphology of the Symphalangus lower ilium and the VOI selection protocol precluded sampling within the superior/central portions of the bone. For Dors8,10 and Vent8,10, median dorsal BVTV is very slightly higher than median ventral BVTV, while the opposite condition was found in median DA. However, the data in both sets of comparisons overlap enough that calling the prediction supported or not would be premature.

Medio-lateral compression leading to equal trabecular density and similar directionality
in the medial and lateral VOIs was the second prediction. Median lateral BVTV is higher than median medial BVTV for all VOI locations except Med0/LatO. Median medial and lateral DA are also different. That pattern looks like: Med0 > Lat0; Med2 > Lat2; Med4 > Lat4; Med6 = Lat6; Med8 < Lat8; Med10 < Lat10. This suggests that the superior and inferior halves of the lower ilium are experiencing different forces, potentially as a result of loading at the sacroiliac joint and acetabulum.

The third prediction, that of torsion, posited equal BVTV and DA in all four columns. From evaluating the first two predictions, it appears that this is not the case (though the paucity of dorsal and ventral VOIs remains an issue). In VOI locations 8 and 10 (for which there are data from all four columns), median dorsal and lateral BVTV are greater than ventral and medial BVTV. In the superior and central VOIs, for which only medial and lateral data exist, median lateral BVTV tends to be greater than median medial BVTV. For the two inferior-most locations, median lateral and ventral DA are higher than median medial and dorsal DA, while in the other VOI locations, neither median medial nor median lateral DA is consistently higher than the other. More data from the dorsal and ventral columns are needed to be able to evaluate the prediction of torsion.

## Homo sapiens

The hypothesized loading regimes responsible for the trabecular architecture of the Homo lower ilium were either dorsal compression or ventral strain, and lateral compression. These predictions were based on Pauwels' (1980) biomechanical models of bipedal loading and more recent finite element models from the clinical literature (Dalstra \& Huiskes 1995, Anderson et al. 2005). Dorsal compression was predicted by Pauwels (1980), and Dalstra and Huiskes (1995), and should result in greater BVTV and DA in the dorsal column than in the ventral column. The second prediction, ventral strain, was based on Anderson et al.'s (2005) FE model
and should result in the opposite relationship for BVTV and DA (ventral > dorsal). The BVTV data for these predictions are unclear; they do not support one loading regime over the other, but rather provide support for parts of both. Median dorsal BVTV is greater than median ventral BVTV for the 0,2 , and 8 VOI pairs (though median values for 8 are very nearly equal and the highest BVTV value in this pair is actually ventral), while median ventral BVTV is greater in the 4, 6, and 10 pairs. In terms of human lower iliac morphology, the two VOI locations for which median dorsal BVTV is unequivocally higher than median ventral BVTV are the superior-most ones. Given the angle at which the Homo lower ilium was cropped from the CT stack, this means that those two dorsal VOIs come from very close to/within the sciatic notch and are likely experiencing the full downward force of the weight of the upper body via the sacroiliac joint. A potential reason for the higher median ventral BVTV in the central/inferior VOI locations might be the presence of the anterior inferior iliac spine, which serves as an attachment point for the tendon of rectus femoris (Gray 1918). This muscle (a flexor of the leg at the hip), actually has two heads, the second of which attaches to the ilium just cranial to the acetabulum (thus, also on the ventral surface of the lower ilium), potentially adding to the strain experienced by the ventral trabecular bone (Anemone 1993). The DA data are more consistently in support of the models of Pauwels (1980) and Dalstra and Huiskes (1995), with median dorsal DA exceeding median ventral DA at all of the VOI locations except for 6, where the median ventral DA is slightly higher. Additionally, median dorsal DA decreases from superior to central VOI locations and then increases again inferiorly $(0>2>4>6<8<10)$, perhaps in response to the forces experienced at the sacroiliac and hip joints.

The third prediction, lateral compression, was based on the findings of both FE models and suggested higher lateral than medial BVTV and DA (Dalstra \& Huiskes 1995, Anderson et al. 2005). Median lateral BVTV is very similar throughout the lower ilium and is consistently higher
than median medial BVTV, though there is some overlap in the data for the 0,2 , and 4 pairs. The DA data are less supportive of the prediction; median lateral DA is higher than median medial DA at the $4,6,8$, and 10 VOI locations, though the difference in median DA between medial and lateral VOIs at 4 is very minimal. Median medial DA is higher than median lateral DA at 0 and 2, contra the prediction. These results are actually very similar to the pattern seen in the dorsal and ventral columns, and are potentially explained by the same things: downward force at the sacroiliac joint and upward force at the acetabulum. Median medial DA decreases from superior to inferior, while median lateral DA increases from superior to inferior, which also lends some support to the idea that the pattern of DA in the Homo lower ilium is a response to both body weight and limb loading.

## Interspecific

Three alternative hypotheses about relative BVTV were made based on previous work: all of the taxa would have the same BVTV (P1: Macaca $=$ Symphalangus $=$ Papio $=$ Pan $=$ Pongo $=$ Homo), BVTV would increase with increasing body size (P2: Macaca < Symphalangus < Papio < Pan < Pongo = Homo), or BVTV would correlate with locomotor behavior (P3: Symphalangus < Pongo < Macaca < Papio < Pan < Homo). The actual pattern found for median BVTV (Macaca < Pongo < Pan < Symphalangus < Papio < Homo) did not exactly match any of the predicted patterns (Table 2.3A).

Macaca was predicted to have the lowest BVTV in the body size-based prediction, which did match the actual pattern; it had generally low median BVTV in all of the VOI columns except the ventral one, where it had the second highest median BVTV. This makes sense in light of the biomechanical models of Badoux (1974) and Kummer (1975), and Lewton's (2015) experimental findings: the Macaca ventral lower ilium is likely loaded in compression, which is not the case for any of the other taxa. Pongo was predicted to have relative low BVTV in the locomotor behavior-
based prediction and it was found to have generally low median BVTV, with the exception of one column; it had the highest median BVTV of any of the taxa in the medial column. As the medial ilium seems unlikely to be loaded in compression (at least by locomotor activities) in any species, it is possible that the high median value in this column is the result of the combination of large upper body size and orthogrady. Pan has a relatively low composite score, but moderate median BVTV rankings in all columns; its actual relative ranking is closest to its predicted ranking from body size. Symphalangus has a much higher actual ranking than was predicted based on body size or on locomotion, which is the result of having high median lateral and dorsal column BVTV. It should be noted, however, that all of the lateral BVTV medians are very similar (range: 0.043) and that the Symphalangus dorsal column disproportionately represents the inferior VOIs (though the same sampling issue applies to both Pan and Papio, as well). In considering the composite score ranking of only the apes (Pongo < Pan < Symphalangus), BVTV appears inversely correlated with body size. Papio had moderate median BVTV in all columns, except in the dorsal column where it had the highest median BVTV. As in Symphalangus, the dorsal column is disproportionately represented by inferior VOIs, i.e., those closest to the acetabulum. The locomotor behavior-based predicted ranking for Papio is similar to its actual ranking and, as predicted by both body size and locomotion, it ranks above Macaca. The actual BVTV ranking for Homo matched both the body size-based and locomotor behavior-based predictions; Homo has high BVTV in all columns. As they shed no light on the predictions, the most interesting thing that can be said about these Homo specimens is that they do indeed appear to come from mobile foraging populations (Ryan \& Shaw 2015).

Two alternative hypotheses about relative DA were made: one based on the idea that DA is inversely related to body size (P1: Macaca $>$ Symphalangus $>$ Papio $>$ Pan $>$ Pongo $=$ Homo) and the other based on the hypothesized relationship between locomotor loading and DA (P2:

Symphalangus < Pongo < Pan < Macaca < Papio < Homo). The actual pattern of relative DA was:

Homo $=$ Symphalangus $<$ Pongo $<$ Macaca $<$ Pan $<$ Papio (Table 2.3B).

The actual ranking is fairly similar to the ranking predicted by locomotion, with two exceptions (the overall position of Homo and the order of Macaca/Pan). The correspondence between that prediction and the actual outcome can be discussed in two ways: by the two groupings of taxa created by the composite scores themselves (taxa with relatively low median DA [Pongo, Symphalangus, and Homo] versus those with relatively high median DA [Macaca, Papio, and Pan]) and by the relative position of taxa with respect to phylogeny. In terms of the two groupings, what is striking about the low group is the inclusion of Homo; both Pongo and Symphalangus were predicted to have low DA on the basis of their locomotor behavior. In Ryan and Shaw (2015), Homo was found to be anisotropic relative to all other hominoids, regardless of population mobility level; this is obviously the opposite of what is seen here. It should be noted that, while it ranks the lowest in three of the columns, Homo does have the highest median DA of all taxa in the dorsal column (though Pan and Papio have specimens with absolutely higher values for DA), which is likely the result of experiencing strong compressive loading in that part of the lower ilium, as modeled by Pauwels (1980) and Dalstra and Huiskes (1995). One possible explanation for the generally low median DA is that these Homo specimens have generally high median BVTV, suggesting either that these two variables may be complementary in terms of their contribution to bone strength or that, given that median dorsal BVTV is slightly lower than in the other columns, that there is some critical threshold for BVTV after which anisotropy becomes a more efficient way of optimizing load distribution, as suggested by developmental studies of trabecular architecture (Tanck et al. 2001, Cunningham \& Black 2009, Acquaah et al. 2015). In terms of the high grouping, Papio ranked above Pan and Macaca, as predicted, but the actual order of Pan and Macaca was the opposite of their
predicted order. Given the high levels of intraspecific variation and frequent overlap in DA values in these two taxa, attempting to explain the switching of their order based on a composite score difference of two seems unnecessarily speculative. The specific division of taxa into high and low median DA groups is consistent with locomotor predictions (terrestrial/semi-terrestrial quadrupeds versus arboreal suspensors), with the exception of Homo.

With respect to phylogeny, the ranking can be broken down into non-human hominoids (Symphalangus < Pongo < Pan) and cercopithecines (Macaca < Papio), with each group being internally consistent with the order predicted by locomotor loading. No prediction was made $a$ priori about the contribution of phylogeny to trabecular architecture, as recent work has suggested high levels of evolvability and low levels of integration in the primate pelvis (Grabowski et al. 2011, Lewton 2012), and trabecular architecture has been demonstrated to respond to loading, regardless of species-typical locomotor modes (Huiskes et al. 2000, van der Meulen et al. 2006). Additionally, phylogenetic signals in hominoid trabecular architecture were discussed recently by Scherf et al. (2013) in their paper on the proximal humerus of humans, Pan, and Pongo. If there was a strong phylogenetic component to trabecular architecture, their prediction was that humans and Pan would be more similar than humans and Pongo. They found that this was not the case, suggesting that loading played a greater role in determining trabecular architecture (Scherf et al. 2013). However, the results here suggest that comparisons within phylogenetic groups may more closely correspond to loading predictions than comparisons between groups. It is clear that more work on the relative contributions of genetics/evolutionary history and mechanical loading to trabecular architecture is needed, as has been suggested by previous studies (e.g., Lovejoy et al. 2003, Tsegai et al. 2013, Chirchir et al. 2014, Kivell 2016).

### 2.7 Conclusion

This work represents the first quantitative characterization of trabecular bone density and anisotropy in the primate ilium based on high-resolution computed tomography and is the first data set generated for this skeletal element. While largely descriptive, the intraspecific analyses found some support for previous work on loading patterns in the primate ilium, but were generally mixed overall in their correspondence with predicted patterns. The interspecific results were similarly mixed for trabecular density; it does not appear to be correlated with locomotor behavior (at least, as locomotor behavior was conceived of in this paper). However, relative degree of anisotropy does seem to carry a locomotor signal. Ignoring Homo, semiterrestrial/terrestrial quadrupeds have more anisotropic trabecular structure than arboreal suspensors and, within phylogenetic groups, anisotropy does appear to track locomotor loading. Given the paucity of mechanical modeling of and experimental work on non-human primate pelves, and the fact that in vivo work on loading in this structure will likely continue to be challenging, perhaps using trabecular bone structure, specifically anisotropy, to "back-solve" loading patterns is the best option available at present. It should be stressed that these results are largely descriptive and based on a small number of specimens from relatively few taxa. Future work will include further statistical analyses of these data (including combined BVTV/DA analyses along with other trabecular variables), as well as additional extant and fossil specimens/taxa.

Table 2.1. (A) Composite scores for median bone volume fraction (BVTV) in the four columns of the lower ilium for interspecific comparisons. Each species received a ranking for each column, with one being the lowest and six being the highest. Higher total scores reflect higher median BVTV (i.e., denser trabecular architecture) in the lower ilium. (B) Composite scores for median degree of anisotropy (DA) in the four columns of the lower ilium for interspecific comparisons. Each species received a ranking for each column, with one being the lowest and six being the highest. Higher total scores reflect higher median DA (i.e., more anisotropic trabecular architecture) in the lower ilium.

A - Bone volume fraction

|  | Macaca | Papio | Pan | Pongo | Symphalangus | Homo |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Medial rank | 1 | 4 | 2 | 6 | 3 | 5 |
| Lateral rank | 1 | 3 | 4 | 2 | 5 | 6 |
| Dorsal rank | 1 | 6 | 3 | 2 | 5 | 4 |
| Ventral rank | 5 | 4 | 3 | 1 | 2 | 6 |
| Total score: | $\mathbf{8}$ | $\mathbf{1 7}$ | $\mathbf{1 2}$ | $\mathbf{1 1}$ | $\mathbf{1 5}$ | $\mathbf{2 1}$ |

B - Degree of anisotropy

|  | Macaca | Papio | Pan | Pongo | Symphalangus | Homo |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Medial rank | 5 | 4 | 6 | 2 | 3 | 1 |
| Lateral rank | 3 | 6 | 5 | 4 | 2 | 1 |
| Dorsal rank | 3 | 5 | 4 | 1 | 2 | 6 |
| Ventral rank | 6 | 5 | 4 | 3 | 2 | 1 |
| Total score: | $\mathbf{1 7}$ | $\mathbf{2 0}$ | $\mathbf{1 9}$ | $\mathbf{1 0}$ | $\mathbf{9}$ | $\mathbf{9}$ |

Table 2.2. Comparison of bone volume fraction and degree of anisotropy dorsal and ventral column means by sex in Pongo pygmaeus. Bone volume fraction and degree of anisotropy tend to be lower in females than in males, likely due to sexual dimorphism.

| Sex | Mean dorsal <br> column BVTV | Mean ventral <br> column BVTV | Mean dorsal <br> column DA | Mean ventral <br> column DA |
| :---: | :---: | :---: | :---: | :---: |
| Male | 0.2922 | 0.2537 | 2.9354 | 4.4468 |
| Female | 0.2719 | 0.2344 | 2.5057 | 3.2686 |

Table 2.3. (A) Fit of interspecific predictions about bone volume fraction (BVTV) to the actual order of taxa produced by the composite scores. Three alternative hypotheses about relative BVTV generated the following predictions: (P1) all of the taxa would have the same BVTV; (P2) BVTV would increase with increasing body size; (P3) BVTV would correlate with locomotor behavior. The actual pattern resulting from the composite scores of median BVTV rankings did not exactly match any of the predicted patterns. (B) Fit of interspecific predictions about degree of anisotropy (DA) to the actual order of taxa produced by the composite scores. Two alternative hypotheses about relative DA generated the following predictions: (P1) DA is inversely related to body size; (P2) DA is related to locomotor loading. The actual ranking is fairly similar to the ranking predicted by locomotion, with two exceptions (the overall position of Homo and the order of Macaca/Pan).

A - Bone volume fraction

| P1 | Macaca $=$ | Symphalangus $=$ | Papio $=$ | Pan $=$ | Pongo $=$ | Homo |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| P2 | Macaca $<$ | Symphalangus $<$ | Papio $<$ | Pan $<$ | Pongo $<$ | Homo |
| P3 | Symphalangus $<$ | Pongo $<$ | Macaca $<$ | Papio $<$ | Pan $<$ | Homo |
| Actual | Macaca $<$ | Pongo $<$ | Pan $<$ | Symphalangus $<$ | Papio $<$ | Homo |

B - Degree of anisotropy

| P1 | Homo $=$ | Pongo $<$ | Pan $<$ | Papio $<$ | Symphalangus $<$ | Macaca |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| P2 | Symphalangus $<$ | Pongo $<$ | Pan $<$ | Macaca $<$ | Papio $<$ | Homo |
| Actual | Homo $=$ | Symphalangus $<$ | Pongo $<$ | Macaca $<$ | Pan $<$ | Papio |

Figure 2.1. Proposed relationships between loading influences, stress, strains, and trabecular architecture in the primate pelvis. Arrow sizes are not representative of the relative contribution of each influence or the strength of any relationship. Modified from Huiskes et al. (2000).


Figure 2.2. Schematic model of the trabecular architecture of the human ilium, indicating the bundles along which the greatest concentrations of locomotor forces pass during bipedalism. Modified from Macchiarelli et al. (1999).


Figure 2.3. (A) Schematic view of the scan cropping and VOI sampling protocol. The lower ilium is cropped out of the stack of CT slices from the level of the posterior inferior iliac spine superiorly and the top of the acetabulum inferiorly. (B) One to four VOls are placed within each set of slices in transverse view. During data standardization, the VOls at the $20 \%$ intervals of total lower iliac height are selected and labeled ( $0,2,4,6,8,10$ ), with " 0 " being the most superior VOI and " 10 " being the most inferior.

> A B


Figure 2.4. (A) Locations of strain gauges on the pelvis. The right innominate was loaded in the materials testing system while the left innominate remained unloaded. (B) The three different angles of limb excursion at which the innominate was loaded, representing flexion ( $45^{\circ}$ ), midstance $\left(90^{\circ}\right)$, and extension ( $105^{\circ}$ ). Modified from Lewton (2015).


Figure 2.5. Simplified drawing of the quadruped pelvis with relevant soft tissue structures. Opposite rotational moments occur around the sacroiliac and hip joints causing bending stress in the sagittal plane. These moments are counteracted by the ventral abdominal musculature (especially rectus abdominis), ischiosacral ligaments, and ischiocaudal muscles (Badoux 1974, Kummer 1975).


Figure 2.6. A simplified biomechanical model of the biped pelvis (in coronal plane). Pauwels (1980) proposed that the bones of the human pelvis act like a series of arcs connected by joints. The pelvis experiences a downward force from the weight of the upper body at the sacroiliac joints and upward forces from the legs at the hip joints. The combination of these forces causes the pubic symphysis to be loaded in tension. Modified from Pauwels (1980) and Lewton (2015).


Figure 2.7. (A) Comparison of bone volume fraction (BVTV) between all volumes of interest (VOIs) in the Macaca mulatta ventral ilium. Vent0 represents the most superior/cranial VOI and Vent10 represents the most inferior/caudal. Center lines show the medians.

A


Figure 2.7. (B) Comparison of bone volume fraction (BVTV) between all volumes of interest (VOIs) in the Macaca mulatta dorsal ilium. Dors0 represents the most superior/cranial VOI and Dors10 represents the most inferior/caudal. Center lines show the medians.

B


Figure 2.7. (C) Comparison of degree of anisotropy (DA) between all volumes of interest (VOIs) in the Macaca mulatta ventral ilium. Vent0 represents the most superior/cranial VOI and Vent10 represents the most inferior/caudal. Center lines show the medians.

C


Figure 2.7. (D) Comparison of degree of anisotropy (DA) between all volumes of interest (VOIs) in the Macaca mulatta dorsal ilium. Dors0 represents the most superior/cranial VOI and Dors10 represents the most inferior/caudal. Center lines show the medians.

D


Figure 2.8. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors0 versus Vent0) of the Macaca mulatta lower ilium. Dors0/Vent0 represent the most superior/cranial VOIs and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

A


Figure 2.8. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors0 versus Vent0) of the Macaca mulatta lower ilium. Dors0/Vent0 represent the most superior/cranial VOIs and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.9. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., Med6 versus Lat6) of the Macaca mulatta lower ilium. Med6/Lat6 represent the more superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.

A


Figure 2.9. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., Med6 versus Lat6) of the Macaca mulatta lower ilium. Med6/Lat6 represent the more superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.10. Comparison of bone volume fraction (BVTV) in the inferior volumes of interest (VOIs) from the lateral column of the Macaca mulatta lower ilium. Lat6 represents the more superior/cranial VOI and Lat10 represents the most inferior/caudal. Center lines show the medians.


Figure 2.11. (A) Comparison of bone volume fraction (BVTV) between all volumes of interest (VOIs) from the Papio anubis lower ilium. The medial and lateral columns are represented by VOIs from all possible superior/cranial-inferior/caudal levels (Med0/Lat0 to Med10/Lat10), while the dorsal and ventral columns are only represented by Dors8/Vent8 and Dors10/Vent10, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by level, rather than by column, as the relevant comparison is between VOIs from the same level. Center lines show the medians.


Figure 2.11. (B) Comparison of degree of anisotropy (DA) between all volumes of interest (VOIs) from the Papio anubis lower ilium. The medial and lateral columns are represented by VOIs from all possible superior/cranial-inferior/caudal levels (Med0/Lat0 to Med10/Lat10), while the dorsal and ventral columns are only represented by Dors8/Vent8 and Dors10/Vent10, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by level, rather than by column, as the relevant comparison is between VOIs from the same level. Center lines show the medians.

B


Figure 2.12. (A) Comparison of bone volume fraction (BVTV) by column between all volumes of interest (VOIs) from the Papio anubis lower ilium. The medial and lateral columns are represented by VOIs from all possible superior/cranial-inferior/caudal levels (Med0/Lat0 to Med10/Lat10), while the dorsal and ventral columns are only represented by Dors8/Vent8 and Dors10/Vent10, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOls are grouped by column, rather than by level, as the relevant comparison is between columns. Center lines show the medians.

A
(2)

Figure 2.12. (B) Comparison of degree of anisotropy (DA) by column between all volumes of interest (VOIs) from the Papio anubis lower ilium. The medial and lateral columns are represented by VOIs from all possible superior/cranial-inferior/caudal levels (Med0/Lat0 to Med10/Lat10), while the dorsal and ventral columns are only represented by Dors8/Vent8 and Dors10/Vent10, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. VOls labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by column, rather than by level, as the relevant comparison is between columns. Center lines show the medians.

B

Figure 2.13. Comparison of bone volume fraction (BVTV) in the volumes of interest (VOIs) from the lateral column of the Papio anubis lower ilium. Lat0 represents the most superior/cranial VOI and Lat10 represents the most inferior/caudal. Center lines show the medians.


Figure 2.14. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors4 versus Vent4) of the Pan troglodytes lower ilium. Dors4/Vent4 represent the more superior/cranial VOIs and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

A


Figure 2.14. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors4 versus Vent4) of the Pan troglodytes lower ilium. Dors $4 /$ Vent 4 represent the more superior/cranial VOIs and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.15. (A) Comparison of bone volume fraction (BVTV) between all volumes of interest (VOIs) in the Pan troglodytes dorsal ilium. Dors4 represents the more superior/cranial VOI and Dors10 represents the most inferior/caudal. Center lines show the medians.


Figure 2.15. (B) Comparison of bone volume fraction (BVTV) between all volumes of interest (VOIs) in the Pan troglodytes ventral ilium. Vent4 represents the more superior/cranial VOI and Vent10 represents the most inferior/caudal. Center lines show the medians.

B


Figure 2.15. (C) Comparison of degree of anisotropy (DA) between all volumes of interest (VOIs) in the Pan troglodytes dorsal ilium. Dors4 represents the more superior/cranial VOI and Dors10 represents the most inferior/caudal. Center lines show the medians.


Figure 2.15. (D) Comparison of degree of anisotropy (DA) between all volumes of interest (VOIs) in the Pan troglodytes ventral ilium. Vent4 represents the more superior/cranial VOI and Vent10 represents the most inferior/caudal. Center lines show the medians.


Figure 2.16. (A) Comparison of bone volume fraction (BVTV) between all volumes of interest (VOIs) from the Pan troglodytes lower ilium. The medial and lateral columns are represented by VOIs from all possible superior/cranial-inferior/caudal levels (Med0/Lat0 to Med10/Lat10), while the dorsal and ventral columns are missing Dors0/Vent0 and Dors2/Vent2, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by level, rather than by column, as the relevant comparison is between Vols from the same level. Center lines show the medians.

A


Figure 2.16. (B) Comparison of degree of anisotropy (DA) between all volumes of interest (VOIs) from the Pan troglodytes lower ilium. The medial and lateral columns are represented by VOIs from all possible superior/cranial-inferior/caudal levels (Med0/Lat0 to Med10/Lat10), while the dorsal and ventral columns are missing Dors0/Vent0 and Dors2/Vent2, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by level, rather than by column, as the relevant comparison is between VOIs from the same level. Center lines show the medians.

B


Figure 2.17. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., Med0 versus Lat0) of the Pan troglodytes lower ilium. Med0/Lat0 represent the most superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.

A


Figure 2.17. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., MedO versus Lat0) of the Pan troglodytes lower ilium. Med0/Lat0 represent the most superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.18. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors0 versus Vent0) of the Pongo pygmaeus lower ilium. Dors0/Vent0 represent the most superior/cranial VOIs and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

A


Figure 2.18. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors0 versus Vent0) of the Pongo pygmaeus lower ilium. Dors0/Vent0 represent the most superior/cranial VOIs and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.19. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., MedO versus Lat0) of the Pongo pygmaeus lower ilium. Med0/Lat0 represent the most superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.

A


Figure 2.19. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., MedO versus Lat0) of the Pongo pygmaeus lower ilium. Med0/Lat0 represent the most superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.20. (A) Comparison of bone volume fraction (BVTV) between all volumes of interest (VOIs) from the Pongo pygmaeus lower ilium. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by level, rather than by column, as the relevant comparison is between VOls from the same level. Center lines show the medians.

A


Figure 2.20. (B) Comparison of degree of anisotropy (DA) between all volumes of interest (VOIs) from the Pongo pygmaeus lower ilium. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by level, rather than by column, as the relevant comparison is between VOIs from the same level. Center lines show the medians.

B


Figure 2.21. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors8 versus Vent8) of the Symphalangus syndactylus lower ilium. Dors0/Vent0 to Dors6/Vent6 are missing, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. Dors8/Vent8 represent the more superior/cranial VOI and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

A
(2.0

Figure 2.21. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors8 versus Vent8) of the Symphalangus syndacty/us lower ilium. Dors0/Vent0 to Dors6/Vent6 are missing, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. Dors8/Vent8 represent the more superior/cranial VOI and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.22. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., Med0 versus Lat0) of the Symphalangus syndacty/us lower ilium. Med0/Lat0 represent the most superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.


Figure 2.22. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., Med0 versus Lat0) of the Symphalangus syndactylus lower ilium. Med0/Lat0 represent the most superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.


Figure 2.23. (A) Comparison of bone volume fraction (BVTV) by column between all volumes of interest (VOIs) from the Symphalangus syndactylus lower ilium. The medial and lateral columns are represented by VOls from all possible superior/cranial-inferior/caudal levels (Med0/Lat0 to Med10/Lat10), while the dorsal and ventral columns are only represented by Dors8/Vent8 and Dors10/Vent10, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by level, rather than by column, as the relevant comparison is between VOIs from the same level. Center lines show the medians.


Figure 2.23. (B) Comparison of degree of anisotropy (DA) by column between all volumes of interest (VOIs) from the Symphalangus syndactylus lower ilium. The medial and lateral columns are represented by VOls from all possible superior/cranial-inferior/caudal levels (Med0/Lat0 to Med10/Lat10), while the dorsal and ventral columns are only represented by Dors8/Vent8 and Dors10/Vent10, due to morphological variation impeding sampling these columns in the more superior/cranial portion of the bone. VOIs labeled as " 0 " represent the most superior/cranial portion of the bone, while those labeled as " 10 " represent the most inferior/caudal portion. VOIs are grouped by level, rather than by column, as the relevant comparison is between VOIs from the same level. Center lines show the medians.


Figure 2.24. (A) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors0 versus Vent0) of the Homo sapiens lower ilium. Dors0/Vent0 represent the most superior/cranial VOIs and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

A


Figure 2.24. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the dorsal and ventral columns (e.g., Dors0 versus Vent0) of the Homo sapiens lower ilium. Dors0/Vent0 represent the most superior/cranial VOIs and Dors10/Vent10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.25. (A) ) Comparison of bone volume fraction (BVTV) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., MedO versus Lat0) of the Homo sapiens lower ilium. Meds0/Lat0 represent the most superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.

A


Figure 2.25. (B) Comparison of degree of anisotropy (DA) between paired volumes of interest (VOIs) from the medial and lateral columns (e.g., Med0 versus Lat0) of the Homo sapiens lower ilium. Meds0/Lat0 represent the most superior/cranial VOIs and Med10/Lat10 represent the most inferior/caudal. Center lines show the medians.

B


Figure 2.26. Interspecific comparison of mean bone volume fraction (BVTV) for the medial column of the lower ilium. Data points represent BVTV averaged over all of the medial volumes of interest within a specimen. Center lines show the medians.


Figure 2.27. Interspecific comparison of mean bone volume fraction (BVTV) for the lateral column of the lower ilium. Data points represent BVTV averaged over all of the lateral volumes of interest within a specimen. Center lines show the medians.


Figure 2.28. Interspecific comparison of mean bone volume fraction (BVTV) for the dorsal column of the lower ilium. Data points represent BVTV averaged over all of the dorsal volumes of interest within a specimen. Center lines show the medians.


Figure 2.29. Interspecific comparison of mean bone volume fraction (BVTV) for the ventral column of the lower ilium. Data points represent BVTV averaged over all of the ventral volumes of interest within a specimen. Center lines show the medians.


Figure 2.30. Interspecific comparison of mean degree of anisotropy (DA) for the medial column of the lower ilium. Data points represent DA averaged over all of the medial volumes of interest within a specimen. Center lines show the medians.


Figure 2.31. Interspecific comparison of mean degree of anisotropy (DA) for the lateral column of the lower ilium. Data points represent DA averaged over all of the lateral volumes of interest within a specimen. Center lines show the medians.


Figure 2.32. Interspecific comparison of mean degree of anisotropy (DA) for the dorsal column of the lower ilium. Data points represent DA averaged over all of the dorsal volumes of interest within a specimen. Center lines show the medians.


Figure 2.33. Interspecific comparison of mean degree of anisotropy (DA) for the ventral column of the lower ilium. Data points represent DA averaged over all of the ventral volumes of interest within a specimen. Center lines show the medians.


Figure 2.34. Plot of the first two principal components (PC1 and PC2) from a principal component analysis of bone volume fraction from the standardized data set of medial and lateral volumes of interest. PC1 explained 43.9\% of the variability, with the strongest loadings on Lat0 and Med2. The more central medial VOIs (Med2,4,6) are more strongly loaded than the superiorand inferior-most, and the lateral VOIs decrease from superior to inferior in terms of the strength of their loadings. PC1 expresses relative trabecular density in these regions, with low PC values corresponding to high BVTV and vice versa. PC2 explained $15.6 \%$ of the variability, with the strongest loadings on Lat6,8,10. PC2 expresses trabecular density in the inferior lateral VOIs (i.e., those closest to the superior edge of the acetabulum), with low PC values corresponding to low BVTV in these VOIs.


PC 1

Figure 2.35. Plot of the first two principal components (PC1 and PC2) from a principal component analysis of degree of anisotropy from the standardized data set of medial and lateral volumes of interest. PC1 explained 52.8\% of the variability, with the strongest loading on Med6. PC1 mostly expresses outliers in the DA data at this VOI location, with negative values corresponding to very high DA values. PC2 explained $14.6 \%$ of the variability, with the strongest loadings on Med4 and Lat10. PC2 expresses DA at these VOI locations in particular, with negative values corresponding to high DA at Med4 (and the other superior medial VOIs) and low DA at Lat10. It also seems to express DA overall more generally, as many of the other loadings are relatively similar.


PC 1

## References

Abel R, Macho GA. 2011. Ontogenetic changes in the internal and external morphology of the ilium in modern humans. Journal of Anatomy 218:324-335.
Acquaah F, Brown KA, Ahmed F, Jeffery N, Abel RL. 2015. Early trabecular development in human vertebrae: Overproduction, constructive regression, and refinement. Frontiers in Endocrinology 6:67.
Anderson AE, Peters CL, Tuttle BD, Weiss JA. 2005. Subject-specific finite element model of the pelvis: Development, validation and sensitivity studies. Journal of Biomechanical Engineering 127:364-373.
Anemone RL. 1993. The functional anatomy of the hip and thigh in primates, in: Postcranial Adaptation in Nonhuman Primates. Gebo DL, ed. Northern Illinois University Press, DeKalb: 150-174.
Badoux DM. 1974. An introduction to biomechanical principles in primate locomotion and structure, in: Primate Locomotion. Jenkins FA, ed. Academic Press, New York: 1- 43.
Barak MM, Lieberman DE, Hublin JJ. 2011. A Wolff in sheep's clothing: trabecular bone adaptation in response to changes in joint loading orientation. Bone 49:1141-1151.
Barak MM, Lieberman DE, Raichlen D, Pontzer H, Warrener AG, Hublin J.J. 2013. Trabecular evidence for a human-like gait in Australopithecus africanus. PLoS ONE, 8, e77687.
Bauer HR. 1977. Chimpanzee bipedal locomotion in the Gombe National Park, East Africa. Primates 18:913-921.
Bell C. 1834. Illustration of Paley's Natural Theology. (Cited from Roesler 1987).
Berge C. 1994. How did the australopithecines walk? A biomechanical study of the hip and thigh of Australopithecus afarensis. Journal of Human Evolution 26:259-273.
Biewener AA, Fazzalari NL, Koznieczynski DD, Baudinette RV. 1996. Adaptive changes in trabecular architecture in relation to functional strain patterns and disuse. Bone 19:1-8.
Bourgery JM. 1832. Traité Complet de l'Anatomie de l'Homme. I. Osteologie. Paris. (Cited from Roesler 1987).
Burger EH, Klein-Nulend J. 1999. Mechanotransduction in bone-Role of the lacuno-canalicular network. The FASEB Journal 13:S101-12.
Cant JGH. 1987. Positional behavior of female Bornean orangutans (Pongo pygmaeus). American Journal of Primatology 12:71-90.
Carlson KJ, Patel BA. 2006. Habitual use of the primate forelimb is reflected in the material properties of subchondral bone in the distal radius. Journal of Anatomy 208:659-70.
Carter DR, Orr TE, Fyhrie DP. 1989. Relationships between loading history and femoral cancellous bone architecture. Journal of Biomechanics 22:231-244.
Chatani K. 2003. Positional behavior of free-ranging Japanese macaques (Macaca fuscata). Primates 44:13-23.
Chirchir H, Kivell TL, Ruff CB, Hublin JJ, Carlson KJ, Zipfel B, Richmond BG. 2015. Recent origin of low trabecular bone density in modern humans. Proceedings of the National Academy of Sciences. 112:366-71.
Crelin ES. 1988. Ligament of the head of the femur in the orangutan and Indian elephant. The Yale Journal of Biology and Medicine 61:383-388.
Cruz-Orive LM, Karlsson LM, Larsen SE, Wainschtein F. 1992. Characterizing anisotropy: a new concept. Micron and Microscopic Acta 23:75-76.
Cunningham CA, Black SM. 2009. Anticipating bipedalism: trabecular organization in the newborn ilium. Journal of Anatomy 214:817-829.

Currey JD. 2002. Bone: Structure and Mechanics. Princeton University Press: Princeton. Dalstra M, Huiskes R. 1995. Load transfer across the pelvic bone. Journal of Biomechanics 28:715-724.
Dalstra M, Huiskes R, Odgaard A, van Erning L. 1993. Mechanical and textural properties of pelvic trabecular bone. Journal of Biomechanics 26:523-535.
Dart RA. 1925. Australopithecus africanus: The man-ape of South Africa. Nature 115:195-199.
Dart RA. 1949. Innominate fragments of Australopithecus prometheus. American Journal of Physical Anthropology 7:301-334.
Doran DM. 1992. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: A case study of paedomorphism and its behavioral correlates. Journal of Human Evolution 23:139-157.
Doran DM. 1993a. Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. American Journal of Physical Anthropology 91:83-98.
Doran DM. 199b. Sex differences in adult chimpanzee positional behavior: The effect of body size on locomotion and posture. American Journal of Physical Anthropology 91:99-115.
Doran DM. 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. Journal of Human Evolution 32:323-344.
Doube M, Kłosowski MM, Wiktorowicz-Conroy AM, Hutchinson JR, Shefelbine SJ. 2010. Trabecular bone scales allometrically in mammals and birds. Proceedings of the Royal Society of London B: Biological Sciences 278:3067-3073.
Fajardo RJ, Desilva JM, Manoharan RK, Schmitz JE, Maclatchy LM, Bouxsein ML. 2013. Lumbar vertebral body bone microstructural scaling in Small to Medium-Sized Strepsirhines. The Anatomical Record 296:210-26.
Fajardo RJ, Müller R. 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. American Journal of Physical Anthropology 115:327-336.
Fajardo RJ, Müller R, Ketcham RA, Colbert M. 2007. Nonhuman anthropoid primate femoral neck architecture and its relationship to locomotor mode. The Anatomical Record 290:422-436.
Fleagle JG. 1976. Locomotion and posture of the Malayan siamang and implications for hominoid evolution. Folia Primatologica 26:245-269.
Fleagle JG. 1999. Primate Adaptation and Evolution. Academic Press: New York.
Freemont AJ. 1993. Basic bone cell biology. International Journal of Experimental Pathology 74:411-416.
Fung YC. 1993. Biomechanics: Mechanical Properties of Living Tissues. Springer, New York. Galichon V, Thackeray JF. 1997. CT scans of trabecular bone structures in the ilia of Sts 14 (Australopithecus africanus), Homo sapiens and Pan paniscus. South African Journal of Science 93:179-180.
Giesen EBW, Ding M, Dalstra M, van Eijden TMGJ. 2001. Mechanical properties of cancellous bone in the human mandibular condyle are anisotropic. Journal of Biomechanics 34:799803.

Giesen EBW, Ding M, Dalstra M, van Eijden TMGJ. 2003. Reduced mechanical load decreases the density stiffness and strength of cancellous bone of the mandibular condyle. Clinical Biomechanics 18:358-363.
Goldstein SA. 1987. The mechanical properties of trabecular bone: Dependence on anatomical location and function. Journal of Biomechanics 20:1055-1061.
Goldstein SA, Goulet R, McCubbrey D. 1993. Measurement and significance of three-dimensional architecture to the mechanical integrity of trabecular bone. Calcified Tissue International

53:S127-S133.
Grabowski MW, Polk JD, Roseman CC. 2011. Divergent patterns of integration and reduced constraint in the human hip and the origins of bipedalism. Evolution 65:1336-1356.
Gray H. 1918. Anatomy of the Human Body. Barnes \& Noble Books, New York.
Grine FE, Judex S, Daegling DJ, Ozcivici E, Ungar PS, Teaford MF, Sponheimer M, Scott J, Scott RS, Walker A. 2010. Craniofacial biomechanics and functional and dietary inferences in hominin paleontology. Journal of Human Evolution. 58:293-308.
Hammond AS. 2014. In vivo baseline measurements of hip joint range of motion in suspensory and nonsuspensory anthropoids. American Journal of Physical Anthropology. 153:417-34.
Hausfater G. 1976. Knuckle walking by a baboon (Papio cynocephalus). American Journal of Physical Anthropology 43:303-306.
Huiskes R, Ruimerman R, van Lenthe GH, Janssen JD. 2000. Effects of mechanical forces on maintenance and adaptation in trabecular bone. Nature 405:704-706.
Hunt KD. 1991. Positional behavior in the Hominoidea. International Journal of Primatology 12:95-118.
Hunt KD. 1992. Positional behavior of Pan troglodytes in the Mahale Mountains and Gombe Stream National Parks, Tanzania. American Journal of Physical Anthropology 87:83-105.
Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardized descriptions of primate locomotor and postural modes. Primates 37:363-387.
Hylander WL, Johnson KR.1997. In vivo bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. American Journal of Physical Anthropology 102:203-32.
Ilich JZ, Kerstetter JE. 2000. Nutrition in bone health revisited: A story beyond calcium. Journal of the American College of Nutrition 19:715-737.
Jacob HAC, Huggler AH, Dietschi C, Schreiber A. 1976. Mechanical function of subchondral bone as experimentally determined on the acetabulum of the human pelvis. Journal of Biomechanics 9:625-627.
Jacobs CR. 2000. The mechanobiology of cancellous bone structural adaptation. Journal of Rehabilitation Research and Development 37:209-216.
Ketcham RA, Ryan TM. 2004. Quantification and visualization of anisotropy in trabecular bone. Journal of Microscopy 213:158-171.
Kivell TL. 2016. A review of trabecular bone functional adaptation: What have we learned from trabecular analyses in extant hominoids and what can we apply to fossils? Journal of Anatomy 228:569-94.
Kivell TL, Skinner MM, Lazenby R, Hublin JJ. 2011. Methodological considerations for analyzing trabecular architecture: an example from the primate hand. Journal of Anatomy 218:209225.

Kovacs CS. 2001. Calcium and bone metabolism in pregnancy and lactation. The Journal of Clinical Endocrinology \& Metabolism 86:2344-2348.
Kummer B. 1975. Functional adaptation to posture in the pelvis of man and other primates, in: Primate Functional Morphology and Evolution. Tuttle RH, ed. Aldine, Chicago: 281-290.
Kuo S, Desilva JM, Devlin MJ, Mcdonald G, Morgan EF. 2013. The effect of the Achilles tendon on trabecular structure in the primate calcaneus. The Anatomical Record 296:1509-17.
Lanyon LE, Goodship AE, Pye CJ, MacFie JH. 1982. Mechanically adaptive bone remodelling. Journal of Biomechanics 15:141-54.
Ledet EH, Tymeson MP, DiRisio DJ, Cohen B, Uhl RL. 2005. Direct real-time measurement of in vivo forces in the lumbar spine. The Spine Journal 5:85-94.

Le Gros Clark WE. 1955. The os innominatum of the recent ponginae with special reference to that of the australopithecinae. American Journal of Physical Anthropology 13:19-27.
Lewton KL. 2010. Locomotor function and the evolution of the primate pelvis (Doctoral dissertation, Arizona State University).
Lewton KL. 2012. Evolvability of the primate pelvic girdle. Evolutionary Biology 39:126-139.
Lewton KL. 2015. In vitro bone strain distributions in a sample of primate pelves. Journal of Anatomy 226:458-77.
Lieberman DE, Pearson OM, Polk JD, Demes B, Crompton AW. 2003. Optimization of bone growth and remodeling in response to loading in tapered mammalian limbs. Journal of Experimental Biology 206:3125-38.
Lovejoy CO, McCollum MA, Reno PL, Rosenman BA. 2003. Developmental biology and human evolution. Annual Review of Anthropology 32:85-109.
Macchiarelli R, Bondioli L, Galichon V, Tobias PV. 1999. Hip bone trabecular architecture shows uniquely distinctive locomotor behavior in South African australopithecines. Journal of Human Evolution 36:211-232.
Macchiarelli R, Rook L, Bondioli L. 2001. Comparative analysis of the iliac trabecular architecture in extant and fossil primates by means of digital image processing techniques: Implications for the reconstruction of fossil locomotor behaviors, in: Hominoid Evolution and Climatic Change in Europe 2 - Phylogeny of the Neogene Hominoid Primates of Eurasia. De Bonis L, Koufos GD, and Andrews P, eds. Cambridge University Press, Cambridge: 60-101.
MacLatchy L, Müller R. 2002. A comparison of the femoral head and neck trabecular architecture of Galago and Perodicticus using micro-computed tomography. Journal of Human Evolution 43:89-105.
Maga M, Kappelman J, Ryan TM, Ketcham RA. 2006. Preliminary observations on the calcaneal trabecular microarchitecture of extant large-bodied hominoids. American Journal of Physical Anthropology 129:410-417.
Manduell KL, Morrogh-Bernard HC, Thorpe SK. 2011. Locomotor behavior of wild orangutans (Pongo pygmaeus wurmbii) in disturbed peat swamp forest, Sabangau, Central Kalimantan, Indonesia. American Journal of Physical Anthropology. 145:348-59.
Maquer G, Musy SN, Wandel J, Gross T, Zysset PK. 2015. Bone volume fraction and fabric anisotropy are better determinants of trabecular bone stiffness than other morphological variables. Journal of Bone and Mineral Research 30:1000-8.
Martinon-Torres M. 2003. Quantifying trabecular orientation in the pelvic cancellous bone of modern humans, chimpanzees, and the Kebara 2 Neanderthal. American Journal of Human Biology 15:647-661.
Mazurier A, Nakatsukasa M, Macchiarelli R. 2010. The inner structural variation of the primate tibial plateau characterized by high-resolution microtomography. Implications for the reconstruction of fossil locomotor behaviors. Comptes Rendus Palevol 9:349-359.
McHenry HM, Corruccini RS. 1975. Multivariate analysis of early hominid pelvic bones. American Journal of Physical Anthropology 43:263-270.
Mednick LW. 1955. The evolution of human the ilium. American Journal of Physical Anthropology 13:203-216.
Nakatsukasa M, Hayami S, Preuschoft H. 1995. Postcranial skeleton of a macaque trained for bipedal standing and walking and implications for functional adaptation. Folia Primatologica 64:1-29.
Napier JR. 1963. Brachiation and brachiators. Symposia of the Zoological Society of London 10:183-195.

Napier JR, Walker A. 1967. Vertical clinging and leaping - A newly recognized category of locomotor behavior of primates. Folia Primatologica, vol.6, pp.204-219.
Odgaard A. 1997. Three-dimensional methods for quantification of cancellous bone architecture. Bone 20:315-328.
Pauwels F. 1980. Biomechanics of the Locomotor Apparatus: Contributions on the Functional Anatomy of the Locomotor Apparatus. (Trans. Maquet P, Furlong R). Springer, New York. (Original work published 1965).
Pontzer H, Lieberman DE, Momin E, Devlin MJ, Polk JD, Hallgrimsson N, Cooper DML. 2006. Trabecular bone in the bird knee responds with high sensitivity to changes in load orientation. Journal of Experimental Biology 209:57-65.
Preuschoft H. 2004. Mechanisms for the acquisition of habitually bipedality: Are there biomechanical reasons for the acquisition of upright bipedal posture? Journal of Anatomy 204:363-384.
Rasband WS. 1997-2016. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.
Rawlins RG. 1976. Locomotor ontogeny in Macaca mulatta: I. Behavioral strategies and tactics. American Journal of Physical Anthropology 44:201.
Ridler TW, Calvard S. 1978. Picture thresholding using an iterative selection method. IEEE Transactions on Systems, Man, and Cybernetics. 8:630-2.
Roesler H. 1987. The history of some fundamental concepts in bone biomechanics. Journal of Biomechanics 20:1025-1034.
Rodman PS. 1979. Skeletal Differentiation of Macaca fascicularis and Macaca nemestrina in Relation to Arboreal and Terrestrial Quadrupedalism. American Journal of Physical Anthropology 51:51-62.
Rook L, Bondioli L, Kohler M, Moya-Sola S, Macchiarelli R. 1999. Oreopithecus was a bipedal ape after all: Evidence from the iliac cancellous architecture. Proceedings of the National Academy of Sciences of the United States of America 96:8795-8799.
Rose MD. 1976. Bipedal behavior of olive baboons (Papio anubis) and its relevance to an understanding of the evolution of human bipedalism. American Journal of Physical Anthropology 44:247-262.
Roux W. 1881. Der zuchtende Kampf der Teile, oder die 'Teilauslese' im Organismus. (Theorie der 'funktionellen Anpassung'). Wilhelm Engelmann, Leipzig. (Cited from Roesler 1987).
Roux W. 1895. Gesammelte Abhandlungen über Entwickelungsmechanik der Organismen: Bd. Entwicklungsmechanik des Embryo. Wilhelm Engelmann, Leipzig. (Cited from Fung 1993).
Rubin CT. 1984. Skeletal strain and the functional significance of bone architecture. Calcified Tissue International 36:S11-8.
Rubin CT, McLeod KJ, Bain SD. 1990. Functional strains and cortical bone adaptation: epigenetic assurance of skeletal integrity. Journal of Biomechanics 23:43-54.
Rudolf G de M. 1922. Correlation between habit and the architecture of the mammalian femur. Journal of Anatomy 56:137-146.
Ruff C, Holt B, Trinkaus E. 2006. Who's afraid of the big bad Wolff?: "Wolff's Law" and bone functional adaptation. American Journal of Physical Anthropology 129:484-498.
Ryan TM, Ketcham RA. 2002. The three-dimensional structure of trabecular bone in the femoral head of strepsirrhine primates. Journal of Human Evolution 43:1-26.
Ryan TM, Krovitz GE. 2006. Trabecular bone ontogeny in the human proximal femur. Journal of Human Evolution 51:591-602.
Ryan TM, Shaw CN. 2012. Unique suites of trabecular bone features characterize locomotor
behavior in human and non-human anthropoid primates. PLoS One 7:e41037.
Ryan TM, Shaw CN. 2013. Trabecular bone microstructure scales allometrically in the primate humerus and femur. Proceedings of the Royal Society of London B: Biological Sciences 280:20130172.
Ryan TM, Shaw CN. 2015. Gracility of the modern Homo sapiens skeleton is the result of decreased biomechanical loading. Proceedings of the National Academy of Sciences. 112:372-7.
Saparin P, Scherf H, Hublin JJ, Fratzl P, Weinkamer R. 2011. Structural adaptation of trabecular bone revealed by position resolved analysis of proximal femora of different primates. Anatomical Record 294:55-67.
Scherf H. 2008. Locomotion-related femoral trabecular architecture in primates - high resolution computed tomographies and their implications for estimations of locomotor preferences of fossil primates, in: Anatomical imaging: Towards a new morphology. Endo H and Frey R, eds. Springer, New York: 39-59.
Scherf H, Harvati K, Hublin JJ. 2013. A comparison of proximal humeral cancellous bone of great apes and humans. Journal of Human Evolution 65:29-38.
Schultz AH. 1936. Characters common to higher primates and characters specific to man (Continued). The Quarterly Review of Biology 11:425-455.
Schmitt D, Hanna JB. 2004. Substrate alters forelimb to hindlimb peak force ratios in primates. Journal of Human Evolution 46:237-52.
Shaw CN, Ryan TM. 2012. Does skeletal anatomy reflect adaptation to locomotor patterns? Cortical and trabecular architecture in human and nonhuman anthropoids. American Journal of Physical Anthropology 147:187-200.
Sigmon BA. 1971. Bipedal behavior and the emergence of erect posture in Man. American Journal of Physical Anthropology 34:55-60.
Snell CARD, Donhuysen HWA. 1968. The pelvis in the bipedalism of primates. American Journal of Physical Anthropology 28:239-246.
Spitzer M, Wildenhain J, Rappsilber J, Tyers M. 2014. BoxPlotR: A web tool for generation of box plots. Nature Methods. 11:121-2.
Straus WL. 1929. Studies on primate ilia. American Journal of Anatomy 43:403-460.
Tanck E, Homminga J, van Lenthe GH, Huiskes R. 2001. Increase in bone volume fraction precedes architectural adaptation in growing bone. Bone 28:650-654.
Thorpe, SKS and Crompton, RH. 2006. Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. American Journal of Physical Anthropology 131:384-401.
Trussell HJ. 1979. Comments on "Picture thresholding using an iterative selection method". IEEE Transactions on Systems, Man, and Cybernetics. 9:311.
Tsegai Z, Kivell TL, Gross T, Nguyen NH, Pahr DH, Smaers JB, Skinner MM. 2013. Trabecular bone structure correlates with hand posture and use in hominoids. PloS one 8:e78781.
Turner CH. 2007. Skeletal adaptation to mechanical loading. Clinical Reviews in Bone and Mineral Metabolism 5:181-94.
Tuttle RH. 1967. Knuckle-walking and the evolution of hominoid hands. American Journal of Physical Anthropology 26:171-206.
Van der Meulen MCH, Morgan TG, Yang X, Baldini TH, Myers ER, Wright TM, Bostrom MPG. 2006. Cancellous bone adaptation to in vivo loading in a rabbit model. Bone 38:871-877.

Volpato V, Viola TB, Nakatsukasa M, Bondioli L, Macchiarelli R. 2008. Textural characteristics of the iliac-femoral trabecular pattern in a bipedally trained Japanese macaque. Primates 49:16-25.

Ward CV Begun D, Kordos L. 2008. New partial pelvis of Dryopithecus brancoi from Rudabánya, Hungary. American Journal of Physical Anthropology 135:218.
Waterman HC. 1929. Studies on the evolution of the pelvis of man and other primates. American Museum of Natural History Bulletin 58:585-642.
Weinans H, Huiskes R, Grootenboer HJ. 1992. The behavior of adaptive bone-remodeling simulation models. Journal of Biomechanics 25:1425-41.
Wells JP, Turnquist JE. 2001. Ontogeny of locomotion in rhesus macaques (Macaca mulatta): II. Postural and locomotor behavior and habitat use in a free-ranging colony. American Journal of Physical Anthropology 115:80-94.
Wolff J. 1892. Das Gesetz der Transformation der Knochen. A. Hirchwild Berlin.
Wolff J. 1986. The law of bone remodeling. Springer-Verlag Berlin.

# Chapter 3. Characterizing the trabecular architecture of the primate ischium with respect to loading and locomotion 

### 3.1 Abstract

Trabecular bone responds to mechanical loading by remodeling via changes in density and anisotropy to better resist the stresses placed on it. Thus, skeletal elements that are subject to locomotor loading should contain trabecular architecture that reflects these loads. The primate ischium varies in relative length, which has been found to be correlated with locomotor mode due to the functional role of the ischium as the lever for the hamstring musculature. Biomechanical models of the pelvis have proposed that the ischium is loaded in bending in the sagittal plane, while experimental work has suggested that torsion may also be an important loading regime in this region of the pelvis. This study attempts to use our understanding of bone functional adaptation to determine whether the ischium carries a trabecular signal of either of these types of loading and whether additional locomotion-related variables (degree of arboreality, general locomotor category, and the presence/absence of ischial callosities) explain the variation in trabecular architecture seen in the ischium. High-resolution X-ray computed tomography was used to image the innominates of six species of primates ( $n=28$ ), ImageJ was used to select 771 volumes of interest (VOIs), and Quant3D was used to calculate trabecular density and anisotropy in those VOIs. These trabecular variables were then statistically compared intra- and interspecifically to assess loading and locomotor predictions. In terms of assessing bending versus torsion, dorsal trabecular architecture tends to be preferentially reinforced over ventral trabecular architecture in the ischia of non-human primates, suggesting that dorsal compression/ventral tension (dorso-ventral bending) may be taking place. Interspecific locomotor results were equivocal, though there appear to be some differences in
the trabecular architecture of arboreal and terrestrial primates, and between primates using different locomotor regimes.

### 3.2 Introduction

The pelvis is a complex skeletal element whose primary roles include visceral support, parturition, and locomotion. The pelvis serves as the attachment point for the musculature of the trunk and hindlimb, as well as the functional link through which the forces of locomotor loading are transferred from the appendicular to the axial skeleton. This places the pelvis at the center of anthropological debates about the evolution of bipedalism in the hominin lineage, with pelvic morphology linked to adaptation in locomotor function (e.g., Ward 2002, Lovejoy et al. 2009). These correlations between pelvic form and function are often derived from comparative anatomical studies of extant primates (Straus 1929, Waterman 1929, Schultz 1936, Zuckerman et al. 1973, Steudel 1981), using what is known about their locomotor regimes to support biomechanical inferences based on morphological variation. However, empirical studies of loading in the primate pelvis are few in number, particularly for non-human primates (but see Lewton 2015), and mainly come from the clinical orthopedic literature (e.g., Bergmann et al. 1993, Dalstra \& Huiskes 1995, Anderson et al. 2005). A greater understanding of pelvic biomechanics is essential for formulating and testing hypotheses about loading and its relationship to skeletal morphology in this complex structure, but in vivo studies of this kind are currently impossible, as the methods involved are too invasive to be used on living primates (Lewton 2015). Instead, it may be possible to investigate indirectly the predictions made by biomechanical models of the pelvis using trabecular architecture as a proxy for loading.

In the few biomechanical models of the pelvis that currently exist, the human pelvic bones have been modeled as acting like a series of arcs (what Lewton [2015] refers to as "the
ring model") or beams (bent during double limb support versus cantilevered during single limb support) in bipedal locomotion (Pauwels 1980), while the quadruped pelvis has more often been considered to act like a series of bony levers, in what Slijper (1946) called the "bow-and-string model," and what Badoux (1974) and Kummer (1975) termed a "two-armed lever model" (Figure3.1A, B, C). More recently, Lewton (2015) suggested that the development of a regional model of pelvic biomechanics (as opposed to the previously proposed "global" models) might provide a more realistic picture of the way in which the pelvis is actually loaded, with each pelvic "strut" being loaded like a long bone would be in the bent beam model. If this is the case, one side of each strut should be loaded in tension and the other in compression (Currey 2002). With respect to the ischium, Badoux (1974) and Kummer (1975) actually proposed something similar, positing that the hamstring muscles subject the ischium to these kinds of bending stresses in the sagittal plane (with the anterior ischium in compression and the posterior ischium in tension, resisted by the ischiosacral and ischiocaudal ligaments), resulting in trabecular architecture resembling a trajectorial pattern (arching along presumed stress trajectories) in a bent beam (Figure 3.2). Another possibility suggested by these models in combination with Slijper's (1946) "bow-and-string model" is that the combined upward forces of the ischiocaudal and ischiosacral ligaments and those of the hindlimb via the acetabulum result in posterior compression of the ischium.

As is the case for the biomechanical models above, the literature on empirically derived bone strains in the pelvis is limited (e.g., Dalstra \& Huiskes 1995, Anderson et al. 2005, Lewton 2015). Placing strain gauges on the pelvis in vivo would be invasive, requiring too much interference with the overlying musculature (Lewton 2015), necessitating the use of in vitro modeling approaches. There are three-dimensional finite element models of the pelvis that aim to reconstruct complicated pelvic stress patterns more realistically, but the majority of these
studies come from the clinical literature, include assumptions that cannot be validated in vivo (i.e., those concerning the effects of soft tissue), and/or focus solely on the human pelvis, which makes them difficult to generalize to non-bipeds (e.g., Dalstra \& Huiskes 1995, Anderson et al. 2005). Additionally, most are concerned with the loading of the acetabulum (i.e., for hip implants), rather than with the ischium (Anderson et al. [2005] did not place a strain gauge on the body of the ischium in their experimental set up). The main issue arising from a lack of in vivo validation is that muscles and soft tissue likely modulate loading in living animals. For example, in Dalstra and Huiskes (1995) their finite element model of the human pelvis produced differing strain magnitudes depending on the application (or lack thereof) of muscle forces, and in Fechner et al. (2013) they found that the presence or absence of the ischiopubic membrane in a finite element model of the domestic fowl os coxa was important in modulating bone strain during loading.

Lewton (2015) attempted to model strain in the non-human primate pelvis in vitro, mounting four pelves of different species in a materials testing system, placing eighteen strain gauges on them, and then loading them in three different positions. She found that Macaca, Papio, and Hylobates loaded their ischia in torsion, while the ischium of Ateles was loaded in compression. These results (combined with those from the ilium and pubis) suggest that modeling the individual bones of the pelvis as bent beams during loading may be of use in conceptualizing pelvic biomechanical models, though it is clear that simple bending is not the only loading regime acting on the pelvis. One potential limitation of this study is that there was only one strain gauge placed on the ischium (on the medial side), though her findings of compression and torsion for this bone (Lewton 2015) were not inconsistent with predictions based on other models, particularly those of Badoux (1974) and Kummer (1975).

One potential alternate method of investigating Badoux's (1974) and Kummer's (1975)
predictions of bending, and Lewton's (2015) finding of torsion is through the trabecular architecture of the ischium, which Kummer (1975) observed to be consistent with hypothesized bending (Fig). Trabecular bone remodels itself in response to mechanical loading to resist the stresses to which it is exposed (Meyer 1867, Rauber 1876, Roux 1881, Wolff 1892, Wolff 1986, Roesler 1987, Ruff et al. 2006), and thus can theoretically be used to reconstruct loading history (e.g., Rudolf 1922, Macchiarelli et al. 2001, Abel \& Macho 2011). This process, often referred to as Wolff's Law or more generally as bone functional adaption (Ruff et al. 2006), has been computationally modeled at the cellular level to show that mechanical loading is the feedback mechanism governing the remodeling process (Huiskes et al. 2000) and experimentally validated in vivo in mammals and birds (Tanck et al. 2001, Pontzer et al. 2006, van der Meulen et al.2006, Barak et al. 2011). Two of the major ways that trabecular bone remodels are changes in density (measured as bone volume divided by total volume and referred to as bone volume fraction or BVTV) and degree of anisotropy (measured via star volume distribution and referred to as DA); together, these two variables explain > 80\% of bone's mechanical properties (Cruz-Orive et al. 1992, Goldstein et al. 1993, Huiskes et al. 2000, van der Meulen et al. 2006, Maquer et al. 2015). In the anthropological literature, Wolff's Law (in its general form) is used as the theoretical framework for testing the hypothesis that particular patterns of trabecular architecture distinguish particular locomotor regimes (e.g., Fajardo \& Müller 2001, MacLatchy \& Müller 2002, Volpato et al. 2008, Ryan \& Shaw 2012), thus enabling the reconstruction of the locomotor regimes of fossil primates (e.g., Macchiarelli et al. 1999, Rook et al. 1999, Scherf 2008, Barak et al. 2013, Su et al. 2013).

The aim of this study is to investigate the relationship between Badoux's (1974) and Kummer's (1975) biomechanical model, Lewton's (2015) experimental findings, and the trabecular architecture of the primate ischium, using high-resolution $x$-ray CT scans of the ischia
of extant primates of diverse locomotor modes. If trabecular architecture in the ischium responds to loading as it has been experimentally demonstrated to (by remodeling via changes in density and anisotropy, governed by mechanical stress on osteocytes) (Huiskes et al. 2000, Tanck et al. 2001, Pontzer et al. 2006, van der Meulen et al.2006, Barak et al. 2011), then this process of bone functional adaptation should generate predictable patterns of trabecular architecture based on patterns of loading (generally) and locomotion (specifically). Given that the various biomechanical models under consideration here should result in different types of loading on the ischium, trabecular architecture should allow for the discrimination between different models, potentially adding to our understanding of actual loading patterns in the primate ischium.

### 3.3 Hypotheses and Predictions

In order to investigate the relationship between biomechanical models, experimental findings, and the trabecular architecture of the primate ischium, two different sets of hypotheses (and the bases for them) will be discussed. The first set (H1-3) will deal with loading patterns (i.e., bending versus torsion) and the second set (H4-6) will deal with locomotor categories. In the first set, a series of alternative hypotheses about general loading patterns with corresponding trabecular predictions are proposed for the entire sample of primates. In the second set, a series of hypotheses about various aspects of locomotion and locomotion-related morphology with corresponding predictions about trabecular architecture in particular species/groups are proposed.

## Ischial Loading Patterns

Different proposed loading patterns in the primate ischium should result in different patterns of trabecular architecture. The bases for these different loading patterns are discussed
below, followed by the corresponding trabecular predictions. H1-3 below represent potential loading scenarios, based on different interpretations of biomechanical models and experimental work. H 1 and H 2 are alternative hypotheses about dorso-ventral bending, while H 3 is concerned with torsion as the major loading regime for the ischium. H1-3 should be considered mutually exclusive options.

According to the biomechanical models of Badoux (1974) and Kummer (1975), the ischium is loaded in dorso-ventral bending by the action of the hamstrings, and experiences compression ventrally and tension dorsally (Figure 3.1C, D). Given that compressive loading has been experimentally shown to cause increases in bone volume fraction (BVTV) and degree of anisotropy (DA) (van der Meulen et al. 2006), the ventral ischium is predicted to have higher BVTV and DA than the dorsal ischium. This both results from and serves to resist bending by the hamstrings.
(H1) The ischium is loaded in tension dorsally and compression ventrally.
P1a. Trabecular density (BVTV) should be higher in the ventral ischium than in the dorsal ischium.

P1b. Degree of anisotropy (DA) should be higher in the ventral ischium than in the dorsal ischium.

Alternatively, if one combines the models of Badoux (1974) and Kummer (1975) with that of Slijper (1946) (Figure 3.1B, C, E), and preferences the upward forces of the ischiosacral and ischiocaudal ligaments and the hindlimb over the downward force of the hamstrings, then the ischium is predicted to still be loaded in dorso-ventral bending, but with ventral tension and dorsal compression. If this is the case, then the dorsal ischium will have higher BVTV and DA than the ventral ischium.
(H2) The ischium is loaded in tension ventrally and compression dorsally.

P2a. Trabecular density (BVTV) should be higher in the dorsal ischium than in the ventral ischium.

P2b. Degree of anisotropy (DA) should be higher in the dorsal ischium than in the ventral ischium.

Lewton (2015) found that Macaca, Papio, and Hylobates each loaded their ischium in torsion. If the ischium is loaded in torsion perfectly around its long axis (Figure 3.1F), then both the ventral and dorsal sides will be reinforced to resist torque.
(H3) The ischium is loaded in torsion.
P3a. Trabecular density (BVTV) should be equal on both dorsal and ventral sides of the ischium.

P3b. Degree of anisotropy (DA) should be equal on both dorsal and ventral sides of the ischium.

## Locomotor Variables

Various aspects of locomotion and locomotion-related morphology may be used to generate hypotheses about loading and corresponding predictions about trabecular architecture. The following comparisons will be discussed below: arboreality versus terrestriality; differences between general locomotor categories (quadrupedalism versus bipedalism versus brachiation); and differences between taxa with and without ischial callosities.

Relative ischial length and angular projection varies by locomotor regime in primate taxa, with a longer ischium providing a longer lever arm (and thus, greater mechanical advantage) for the hamstrings (Waterman 1929, Steudel 1981, Yirga 1987, Fleagle \& Anapol 1992). For example, relatively longer ischia are found in terrestrial quadrupeds that climb (e.g., Pan), as they require the additional muscular power gained from a longer lever arm, while relatively shorter, more dorsally projecting ischia are seen in leaping primates, which require
speed rather power in hindlimb extension (Steudel 1981, Yirga 1987, Fleagle \& Anapol 1992). This difference in ischium length between terrestrial and arboreal taxa has also been seen in closely related species with different locomotor regimes. In a comparison between two species of Macaca, Rodman (1979) found a significant difference in the relative ischial lengths of sympatric $M$. nemestrina and $M$. fascicularis, which are terrestrial and arboreal, respectively, with the terrestrial taxon having the longer ischium. $M$. nemestrina ranged over an estimated 10 $\mathrm{km}^{2}$, traveling on the ground between fruit trees (Rodman 1979), while M. fascicularis ranged over $1 \mathrm{~km}^{2}$ and spent only $2 \%$ of its time on the ground (Wheatley 1978, Rodman 1979).

Thus, if differences in degree of arboreality are related to variation in external ischial morphology even in closely-related taxa, then it seems likely that there will be differences in trabecular architecture between less closely-related species using different locomotor regimes as well. However, it is important to note that bone functional adaptation, at least at the level of trabecular development and modeling during ontogeny, is likely under some amount of genetic control (Tanck et al. 2001, Lovejoy et al. 2003, Cunningham \& Black 2009, Acquaah et al. 2015). This suggests that considering phylogeny in making trabecular predictions is reasonable (especially in light of the results from the ilium chapter of this dissertation), even though previous work has not found that it plays a major role in comparisons of trabecular architecture between taxa (Scherf et al. 2013).
(H4) If more terrestrial taxa (with longer ischia) have more powerful hamstring loading than more arboreal taxa (among non-human primates), then this will cause greater trabecular reinforcement of the ischium (a). Additionally, comparisons within cercopithecoids and hominoids may more closely conform to predicted relationships than comparisons across all primate taxa included in this study due to the currently unknown contribution of phylogeny to trabecular architecture (b).
a. Symphalangus, Pongo < Macaca < Pan, Papio
b. Macaca < Papio; Symphalangus < Pongo < Pan

Relative ischial length can also discriminate between major primate groups (prosimians, catarrhines, platyrrhines, and hominoids), though some taxa do not conform to these groupings (i.e., those using specialized locomotion, like Homo and Hylobates) (Waterman 1929). The relatively short ischia of gibbons and humans have been linked to their use of bipedalism/bipedal postures or, in the case of the hylobatids, also to their forelimb-dominated locomotor mode (Waterman 1929, Yirga 1987). In combination with the previously discussed details about ischial length in quadrupeds from the prior hypothesis, a prediction can be made about the relative trabecular patterns of quadrupeds versus bipeds versus brachiators.
(H5) Quadrupeds will experience greater loading than bipeds and brachiators due to differences in relative ischial length, causing greater trabecular reinforcement. Between the taxa with shorter ischia, the bipeds will have denser, more anisotropic trabecular architecture than the brachiators, due to both greater frequency of hindlimb use (Chivers 1972, Fleagle 1976, Hunt 1991) and experiencing higher ground reaction forces on the hindlimb from terrestrial substrate use compared to those experienced during arboreal substrate use (Schmitt \& Hanna 2004). Pongo is excluded from this comparison, as it does not fit neatly into any of the proposed locomotor groups.

- Symphalangus < Homo < Pan, Papio, Macaca

Another ischial feature that may be used to distinguish between primate taxa is the presence or absence of ischial callosities. Rose (1974:375) describes ischial callosities as "specialized areas of skin and sub-dermal tissue overlying the ischial tuberosity," which are present in the Cercopithecidae and Hylobatidae. In these groups, the ischial tuberosity "has a flat surface which flares out from the lower end of the ischial body and is devoid of muscle
attachments" (Rose 1974: 375). In all other primate groups, the ischial tuberosity lacks that flare, has a rounded surface, and is a muscle attachment site (Waterman 1929, Rose 1974). As the presence or absence of ischial callosities plays a role in the attachment location of the ischial musculature, this variation may lead to differences in the way the ischium is loaded.
(H6) There will be differences in the trabecular architecture of the inferior ischium between taxa with ischial callosities and those without.

- Macaca, Papio, Symphalangus $=$ Pan, Pongo, Homo


### 3.4 Methods

Sample

The innominates of wild-shot, adult non-human primate specimens of both sexes ( $\mathrm{n}=$ 28) were chosen from the mammal collections of the National Museum of Natural History (NMNH), the American Museum of Natural History (AMNH), and the Penn Museum (UPenn) (Appendix A). The taxa selected for analysis were: Papio anubis $(\mathrm{n}=6)$, Symphalangus syndactylus $(n=4)$, Pan troglodytes $(n=5)$, Pongo pygmaeus $(n=5)$, and Macaca mulatta $(n=$ 4). Human innominates $(\mathrm{n}=4)$ were provided by the Texas Archaeological Research Laboratory (TARL). Taxa were selected on the basis of locomotor regime, such that the complete sample represents much of the locomotor diversity seen in extant primates.

CT Scanning

All of the specimens in this study were scanned at the High-Resolution X-ray Computed Tomography Facility at the University of Texas at Austin (UTCT) on the North Star Imaging (upgraded ACTIS) scanner. The specimens were mounted in foam vertically or sub-vertically (depending on the size and morphology of the innominate) for scanning. Serial transverse slices were collected through the innominates, covering the entire bone. Specimens were scanned
individually or in pairs, depending on specimen size (as was necessary given budgetary constraints). The scans were collected using FeinFocus high power energy source settings of 180 or 190 kV and $0.15,0.17,0.19$, or 0.3 mA , with $3600,12003,12004,15304,17761,18003$, 18004, or 18013 projections, with isotropic voxels. Voxel sizes ranged from $0.0378-0.0793 \mathrm{~mm}$ depending on the size of the specimen and were of the highest possible resolution given specimen size and scanning budget (Appendix B). For each innominate, between 2044 and 4505 slices were collected. The images were reconstructed as 8-bit JPEG and 16-bit TIFF grayscale images. The 8-bit JPEG images were used in Quant3D for all analyses (Ryan \& Ketcham 2002, Ketcham \& Ryan 2004).

## Image Processing/Volume of Interest Sampling

The CT scans of each specimen were cropped and the volumes of interest (VOIs) were sampled in the free software ImageJ (Rasband 1997-2016) according to the following protocols. The ischium was first isolated by loading a subset of the CT stack containing the acetabulum and ischium in the 3D Viewer plugin, and then (in lateral view) orienting the long axis of the ischium vertically, such that it would be perpendicular to a line drawn tangent to the inferior-most curve of the acetabulum (Figure 3.3A). All CT slices above this line were then cropped out, leaving only the ischium and the ischiopubic ramus. Then, the 3D reconstruction was rotated so the view was "flat" to the obturator foramen, such that the next crop did not include any of the body of the ischium. From that view, a vertical line was drawn perpendicular to where the horizontal crop line intersected with the obturator foramen, cropping out the ischiopubic ramus and leaving only the ischium (Figure 3.3B).

Volumes of interest were selected by placing three cubes of maximum possible size within the first complete CT slice of each ischium stack (in transverse view) (Figure 3.3C). The height of the cubes (in lateral view) dictated how many VOIs could be sampled from an ischium
in the superior-inferior/cranial-caudal dimension, such that the total number of VOIs sampled from a given specimen was three times this number of VOIs. This sampling method accounted for size variation within the sample, as the VOI sizes were limited by the size of the ischium itself. The three VOIs (in transverse view) sampled trabecular bone from the ventral, central, and dorsal ischium, with the ventral and dorsal cubes positioned as close to the transition between trabecular and cortical bone as possible. The placement of the middle VOI was more variable and, in cases where the quantity of trabecular bone sampled would have been unusably tiny if all three VOIs had been placed, the choice was made to prioritize sampling the dorsal and ventral regions. As a result, the central trabecular bone is not as well sampled as the other two and was excluded from further analysis here.

The sampled cubes for all specimens were analyzed in UTCT's free three-dimensional fabric analysis program, Quant3D (Ryan \& Ketcham 2002, Ketcham \& Ryan 2004), using the following options: centered spherical VOIs with iterative thresholding (Ridler \& Calvard 1978, Trussell 1979), and 513 uniform orientations with random rotation and dense vectors (Ketcham \& Ryan 2004). By selecting uniform orientations, a grid is generated for analysis, with random rotation and dense vectors being implemented to control for potential biases that arise from analyzing the grid (Ketcham \& Ryan 2004). Anisotropy was computed with the star volume distribution method (Cruz-Orive et al. 1992, Ketcham \& Ryan 2004). Degree of anisotropy and trabecular density (measured as bone volume divided by total volume, BVTV) were selected from Quant3D's output for further analysis (Goldstein et al. 1993, Maquer et al.2015) (Appendix C.ii.).

## CT data analysis

A total of 771 ischial VOIs were sampled, varying in number from 12 to 51 per specimen, with the size and specific morphology of each specimen dictating the placement and number of its VOIs. The large number of VOIs sampled and these conditions required both data reduction
and standardization before analysis could proceed. After the central VOIs were removed, the complete data sets of BVTV and DA $(\mathrm{n}=510)$ were used to generate a reduced, standardized data set by scaling the data from each ischium to the same relative anatomical locations across specimens at intervals of $25 \%$ of total ischial height, with VOIs labeled " 0 " corresponding to the level of a horizontal line tangent to the inferior-most curve of the acetabulum (the top of the ischium crop) and those labeled " 1 " corresponding to the last complete set of CT slices preserving trabecular bone from the ischial tuberosity (Figure 3.3C) (Appendix D.ii.). Thus, the reduced, standardized data sets represent BVTV and DA from anatomically homologous VOIs taken at $0 \%, 25 \%, 50 \%, 75 \%$, and $100 \%$ of total ischium height. These reduced data sets were mostly used to simplify data visualization/plotting.

## Statistical analysis

To assess the general ischial loading predictions, species mean BVTV and DA for the dorsal and ventral VOIs were plotted at the same relative anatomical locations (0\%, 25\%,50\%, $75 \%$, and $100 \%$ of total ischium height) to see which side of the ischium (if either) had higher BVTV and DA across all taxa. A three-level nested ANOVA was performed on a linear model in R that used the rank-transformed standardized BVTV and DA data sets to determine if the differences between dorsal and ventral regions were statistically significant. The three levels included were species, relative superior-inferior anatomical location, and dorsal versus ventral. Structuring the test this way was necessary due to the hierarchical structure of the data. A posthoc Tukey's HSD test was used to explore whether any of the different relative anatomical locations contributed disproportionately to the differences between dorsal and ventral VOI data.

In order to assess whether the relationship between dorsal and ventral BVTV and DA differed in different taxa, each species was plotted individually and Wilcoxon signed-rank tests (which controlled for relative anatomical location by using paired dorsal and ventral VOI data)
were performed on the complete data set from each species to check for statistical significance. The complete data set from each species (rather than the standardized, reduced data set) was used here to increase the power of the analyses by including the maximum number of VOI pairs from each specimen and to reduce any error resulting from standardizing the data.

The second set of predictions concerning locomotor differences in BVTV and DA between: arboreal and terrestrial taxa; quadrupeds, brachiators, and bipeds; and taxa with ischial callosities versus those without were assessed. Each of these different sets of predictions were plotted using the column means of the anterior and posterior trabecular measures of the complete data set (with the exception of the prediction about ischial callosities - it used the means of the inferior halves of the ischia only) as an initial visualization of the data. Nonparametric ANOVAs were performed on the complete data set to check for statistically significant differences between taxa using the built-in Kruskal-Wallis test in the dunn.test $R$ package (Dinno 2015). If significance was achieved at the $p<0.05$ level, a post-hoc HolmBonferroni adjusted Dunn's test was used for pairwise comparisons between groups (also using the dunn.test R package, Dinno 2015). While the predictions make some assumptions about which taxa form groups, all taxa were considered independently for the Dunn's tests, to ensure that the grouped taxa were not significantly different from each other (i.e., to validate the assumed groups). Wilcoxon-Mann-Whitney (Wilcoxon rank sum) tests (instead of KruskalWallis/Dunn's tests) were used to analyze the prediction about arboreality versus terrestriality in the cercopithecoid subsample and the prediction about ischial callosities, as there were only two groups being compared in these two predictions.

To summarize this section of the methods, for the general ischial loading hypotheses (H1-3), (1) species means plots of BVTV and DA were used to visualize the data and assess possible directionality of the relationship between ventral and dorsal BVTV and DA, a three-level
nested ANOVA was used to determine if the differences visualized on the BVTV and DA plots were significant, and a post-hoc Tukey's HSD was used to explore whether any of the relative anatomical VOI locations were disproportionately affecting the results of the ANOVA. (2) To examine intraspecific variation in general ischial loading, plots of BVTV and DA were created for each species individually and Wilcoxon signed-rank tests were performed on the complete data set of each species.

For the locomotor hypotheses (H4-6), different tests were carried out for each individual hypothesis. (1) To assess arboreality versus terrestriality (H4a), a Kruskal-Wallis test with a posthoc Holm-Bonferroni adjusted Dunn's test was performed on the complete data set from the entire sample (excluding Homo). For the cercopithecoid subset of this hypothesis (H4b) a Wilcoxon-Mann-Whitney test was performed as there were only two taxa being compared. (2) To assess differences in locomotor categories (H5), a Kruskal-Wallis test with a post-hoc HolmBonferroni adjusted Dunn's test was performed on the complete data set from the entire sample (excluding Pongo). (3) To determine whether there are differences in taxa with and without ischial callosities (H6), Wilcoxon-Mann-Whitney tests were performed on the BVTV and DA data from the inferior halves of the ischium of the two groups.

### 3.5 Results

Raw BVTV and DA data are reported in Appendix C.ii. The reduced, standardized BVTV and DA data sets are reported in Appendix D.ii. In this section, tests on the raw data are reported as being on the complete data set, while tests on the reduced, standardized data set (those from $0 \%, 25 \%, 50 \%, 75 \%$, and $100 \%$ of total ischial height) are reported as being on the standardized data set.

Ischial Loading

Across Primates

The plots of species means for BVTV and DA are shown to visualize differences between dorsal and ventral VOIs and determine whether statistical testing of these differences was warranted (Figure 3.4A, B).

Mean dorsal BVTV tends to be higher than mean ventral BVTV across all taxa (i.e., there is greater trabecular density in the dorsal ischium than there is in the ventral ischium) (Figure 3.4A). The relationship between mean dorsal DA and mean ventral DA seems to follow a similar pattern, albeit without as clearly defined a separation (Figure 3.4B). Generally, trabecular bone in the dorsal ischium is more anisotropic than trabecular bone in the ventral ischium.

The result of the nested ANOVA on the linear model of the standardized BVTV data set was significant (multiple $R^{2}=0.4829$; adjusted $R^{2}=0.4111 ; F[34,245]=6.73, p<0.001$ ). Controlling for species and relative anatomical location (superior-inferior position), ventral and dorsal BVTV are significantly different across the complete taxonomic sample. From the post-hoc Tukey's HSD, this difference appears to be driven by the VOIs at $25 \%$ and $75 \%$ of total ischial height, with the $50 \% \mathrm{VOI}$ approaching the level of significant difference as well. Trabecular density tends to be higher in the dorsal ischium than in the ventral ischium (Figure 3.4A).

The result of the nested ANOVA on the linear model of the standardized DA data set was also significant (multiple $R^{2}=0.3945 ;$ adjusted $R^{2}=0.3105 ; F[34,245]=4.695, p<0.001$ ). Controlling for species and relative anatomical location (superior-inferior position), ventral and dorsal DA are significantly different across the complete taxonomic sample. From the post-hoc Tukey's HSD, this difference appears to be driven by the VOIs at 50\% of total ischial height. As was the case for trabecular density, degree of anisotropy tends to be higher in the dorsal ischium than in the ventral ischium (Figure 3.4B).

## Intraspecific Differences

In order to assess intraspecific differences in the relationship between ventral and dorsal trabecular architecture, ventral versus dorsal BVTV and DA were plotted for each individual species, and Wilcoxon signed-rank tests were performed on the data from each species to test for differences. These additional tests controlled for species by considering each individually and controlled for differences in relative superior-inferior position by doing paired comparisons of dorsal and ventral data from the same level. It was not possible to determine which VOIs specifically contributed to the differences between ventral and dorsal columns due to sample size constraints.

In Macaca, dorsal BVTV tends to be higher than ventral BVTV at the level of the individual specimen and across the species as a whole (Figure 3.5A). For example, one specimen (USNM 173813) has ventral BVTV that is higher than the dorsal BVTV of the other specimens, though it is still lower than its own dorsal BVTV (i.e., it has relatively high BVTV throughout the ischium in comparison to other individuals). Ventral and dorsal BVTV in the complete Macaca data set were significantly different (see Table 3.1 for a complete list of $p$-values from all of the intraspecific Wilcoxon signed-rank tests).

In terms of DA, the relationship between ventral and dorsal VOIs is less clear (Figure 3.5B). There are wider ranges of DA in the superior and inferior VOIs, which mostly converge between two and four at the $50 \%$ VOI. DA in the dorsal VOIs seems to vary more than DA in the ventral VOIs, though both are quite variable. Ventral and dorsal DA in the complete Macaca data set were also significantly different (Table 3.1).

Both BVTV and DA are significantly different between ventral and dorsal VOIs in Macaca, with the plotted subset of VOIs showing that the trabecular architecture of the dorsal ischium tends to be denser and more anisotropic than the trabecular architecture of the ventral ischium.

In Papio, dorsal BVTV tends to be higher than ventral BVTV at the individual level, though there is a great deal of overlap in BVTV in the ventral and dorsal VOIs generally (Figure 3.6A). BVTV in the ventral VOIs seems to have a more consistent pattern across specimens than BVTV in the dorsal VOIs, which vary more in terms of which ones are relatively higher and lower. Ventral and dorsal BVTV in the complete Papio data set were significantly different (Table 3.1). The relationship between dorsal and ventral DA is similar to that seen in BVTV; dorsal DA tends to be higher than ventral DA, though there is a fair amount of variation and overlap between the two (Figure 3.6B). Very high values in ventral DA in the superior-most VOI may reflect sampling errors, as the ischium in this region tends to be quite narrow. Specimens with relatively high DA (USNM 354987 and USNM 397476) are also those with relatively lower BVTV. DA appears to be somewhat more consistent (i.e., has a narrower range of variation) in the inferior-most VOIs than in the more superior VOIs. Ventral and dorsal DA in the complete Papio data set were also significantly different (Table 3.1).

Both BVTV and DA are significantly different between ventral and dorsal VOIs in Papio, with the plotted subset of VOIs suggesting that the trabecular architecture of the dorsal ischium tends to be denser and more anisotropic than the trabecular architecture of the ventral ischium.

In Pan, dorsal BVTV is higher than ventral BVTV, both at the level of the individual and across the species, with the only exceptions being in the most superior and most inferior VOIs (and even then the overlap is minimal) (Figure 3.7A). BVTV generally increases from the superior-most VOI (" 0 ") to the central VOI (" 0.5 ") and then decreases slightly and either stays constant throughout the inferior VOIs (in most of the VOIs) or increases again to approximately the same value as at the 0.5 VOI (in the ventral VOIs of two specimens). Ventral and dorsal BVTV in the complete Pan data set were significantly different (Table 3.1).

The relationship between ventral and dorsal DA is less consistent than see in the plot of

BVTV (Figure 3.7B). While dorsal DA tends to be higher than ventral DA in the superior VOIs, the two columns start to overlap around the central ("0.5") VOI and continue to do so throughout the rest of the ischium, though at the specimen level, dorsal DA does still appear to generally be higher than ventral DA. There is more variation in DA in the superior VOIs; the range narrows in the inferior VOIs. Ventral and dorsal DA in the complete Pan data set were also significantly different (Table 3.1).

Both BVTV and DA are significantly different between ventral and dorsal VOIs in Pan, with the plotted subset of VOIs suggesting that the trabecular architecture of the dorsal ischium is definitely denser and tends to be more anisotropic than the trabecular architecture of the ventral ischium.

In Pongo, dorsal BVTV tends to be higher than ventral BVTV, both at the specimen level and across the species (with a single exception at the specimen level in one individual at the " 0.5 " VOI) (Figure 3.8A). Dorsal BVTV tends to increase from the superior-most VOI (" 0 ") to the next VOI (" 0.25 ") and then either decrease only to being to rebound again at the " 0.75 " VOI (three specimens) or continue to gently increase to the " 0.75 " VOI before decreasing again (two specimens). Ventral BVTV tends to increase from the superior ischium to the center of the bone and then decrease again. Ventral and dorsal BVTV in the complete Pongo data set were significantly different (Table 3.1).

Ventral and dorsal DA are not as clearly separated as ventral and dorsal BVTV (Figure 3.8B). Dorsal DA is often higher than ventral DA at the specimen level, at least between the " 0.25 " and " 0.75 " VOIs, though there is a great deal of variation and overlap in DA overall. DA varies more in the superior-most VOI (" 0 ") than in the rest of the VOIs, with the inferior-most ("1") VOI having narrowest range of DA (with one exception). It is difficult to describe any other consistent patterns in either the ventral or dorsal columns. Ventral and dorsal DA in the
complete Pongo data set were also significantly different (Table 3.1).
Both BVTV and DA are significantly different between ventral and dorsal VOIs in Pongo, with the plotted subset of VOIs suggesting that the trabecular architecture of the dorsal ischium is definitely denser and tends to be more anisotropic than the trabecular architecture of the ventral ischium.

In Symphalangus, dorsal and ventral BVTV have a relatively narrow range and one is not consistently higher than the other across all specimens (Figure 3.9A). In some specimens, ventral and dorsal alternate in terms of which has the higher BVTV, while in another, dorsal BVTV is higher than ventral BVTV at all locations. Ventral BVTV generally increases from the superiormost VOI to the central (" 0.5 ") VOI, then decreases to the " 0.75 " VOI, before increasing again to the inferior-most VOI. Dorsal BVTV does not have as consistent a pattern, though it is generally lower in the superior-most VOI than in the inferior-most VOI. At the individual level, the only VOI location at which dorsal BVTV is higher than ventral BVTV across all specimens is the " 0.75 " location. Ventral and dorsal BVTV in the complete Symphalangus data set were significantly different (Table 3.1), in spite of the overlapping data in the reduced plotted set (Figure 3.9A).

Dorsal DA tends to be higher than ventral DA in Symphalangus, though one specimen (USNM 141160) does not follow this pattern (Figure 3.9B). Both ventral and dorsal DA across specimens seem to converge in the central (" 0.5 ") VOI, with ventral DA being around two and dorsal DA being between three and four. There is less variation in this VOI and in the " 0.75 " VOI than in the more superior and inferior VOIs. Ventral and dorsal DA in the complete Symphalangus data set were also significantly different (Table 3.1).

Both BVTV and DA are significantly different between ventral and dorsal VOIs in Symphalangus, though the plotted subset of VOIs suggests that the trabecular architecture of the dorsal ischium is similar in density to, but tends to be more anisotropic than, the trabecular
architecture of the ventral ischium.
In Homo, two of the specimens have dorsal BVTV that is higher than their ventral BVTV counterparts (i.e., at the same relative anatomical location), while two of them have ventral and dorsal BVTV that varies in which is higher from location to location (Figure 3.10A). Overall, BVTV in Homo is relatively high and relatively consistent/narrow in range, similar to the pattern seen in Symphalangus, with a lot of overlap in values. There is more variation in BVTV in the superiormost VOI (" 0 ") than there is in the inferior-most (" 1 "), which has the smallest range of variation of any of the VOI locations. Ventral and dorsal BVTV in the complete Homo data set were not significantly different (Table 3.1).

There is a wide range of variation in DA in the superior VOIs relative to the inferior VOIs, with most specimens converging on similar DA values around the central ("0.5") VOI and staying relatively similar throughout the rest of the ischium (Figure 3.10B). It is difficult to identify any other consistent patterns in the plot of Homo DA. Ventral and dorsal DA in the complete Homo data set were not significantly different (Table 3.1).

Neither BVTV nor DA differ significantly between ventral and dorsal VOIs in Homo. The plotted subset of VOIs shows that the trabecular architecture of the dorsal ischium is similar in density to that of the ventral ischium, both being relatively high, but that there appear to be no consistent trends in anisotropy between the two columns, beyond being relatively similar in the inferior VOls.

To summarize the intraspecific results, all of the non-human primate taxa show statistically significant differences between ventral and dorsal BVTV and DA, with the dorsal VOIs having denser, more anisotropic trabecular bone than the ventral VOIs Homo was the only sampled species that did not have significant differences between ventral and dorsal BVTV and DA.

## Locomotor Variables

In order to both simplify the data for clearer visualization and to preserve the signal of both ventral and dorsal columns, the full data set for each specimen was used to calculate column means for ventral and dorsal BVTV and DA, such that each specimen could be plotted using these four means as coordinates. For the results concerning differences between groups with and without ischial callosities, column means of only the inferior ischial VOIs (i.e., from below $50 \%$ of total ischial height to the final sampled VOI in the ischial tuberosity) were used. In cases where there were odd number of sets of CT slices the central set was excluded, as specimens with an even number of sets did not contribute the entirety of this same region to the analysis. Ventral data is always plotted on the horizontal axis and dorsal data is always plotted on the vertical axis. Column means were preferred over another method of data reduction as they did not preference the contribution of any single VOI location over another. All of the following statistical tests utilize the complete data set and were carried out on both ventral and dorsal trabecular measures, as the previous section demonstrated significance differences between the two within taxa (Appendix C.ii.).

## Terrestrial vs. Arboreal Taxa (Degree of Arboreality)

Plots of the column means of ventral and dorsal ischial BVTV and DA for the complete non-human primate sample showed both considerable overlap in both measures between taxa, as well as some potential differences (Figure 3.11A, B). In terms of BVTV (Figure 3.11A), Papio and Macaca had relatively high levels of intraspecific variation relative to the hominoids, while in the plot of DA, Pan joined them in being a highly variable species (Figure 3.11B). In the plot of BVTV, Symphalangus had relatively dense ventral trabecular bone compared to the other taxa (Figure 3.11A), while being relatively isotropic (along with Pongo) in the plot of DA (Figure 3.11B). These data were analyzed, and the differences in ventral BVTV (Kruskal-Wallis: $\chi^{2}=$
62.8314, $\mathrm{p}<0.001$ ), dorsal BVTV (Kruskal-Wallis: $\mathrm{\chi}^{2}=27.9323, \mathrm{p}<0.001$ ), and dorsal DA (KruskalWallis: $\chi^{2}=22.3144, \mathrm{p}<0.001$ ) were found to be significant (Table 3.2A, B, C). For ventral BVTV, Papio is significantly different from Macaca, Pan, and Pongo, and Symphalangus is significantly different from Macaca, Pan, and Pongo (Holm-Bonferroni adjusted Dunn's test: p < 0.001), Table 3.2A). These differences appear to be caused by both Papio and Symphalangus having relatively high ventral BVTV. For dorsal BVTV, Macaca is significantly different from Pan, Symphalangus, and Papio, and Papio is different from Pongo (Holm-Bonferroni adjusted Dunn's test: p < 0.05), Table 3.2B). The differences between Macaca and the other taxa appear to result from its relatively low dorsal BVTV, combined with its high level of intraspecific variation. The difference between Papio and Pongo is likely due to the low BVTV of Pongo. For dorsal DA, Pongo is significantly different from Macaca, Pan, and Papio (Holm-Bonferroni adjusted Dunn's test: p < 0.001 ), Table 3.2C). This is likely due to its relatively low DA.

The complete set of taxa was split into two subsets (cercopithecoids and hominoids) for additional plotting and analyses. The plots of the cercopithecoids (Papio and Macaca) showed that Macaca has relatively lower BVTV than Papio (Figure 3.12A), but generally higher dorsal DA (Figure 3.12B). These data were analyzed, and ventral BVTV and dorsal BVTV were found to be significantly different between the two taxa (Wilcoxon-Mann Whitney, $\mathrm{p}<0.001$ ) (Table 3.3).

The plots of the hominoid subset of species (Pan, Pongo, and Symphalangus) showed differences in ventral BVTV between Pan/Pongo and Symphalangus (Symphalangus > Pan, Pongo), and differences in dorsal BVTV between Pan/Symphalangus and Pongo (Pan, Symphalangus > Pongo) (Figure 3.13A), as well as differences in dorsal DA between the three (Pan > Symphalangus > Pongo) (Figure 3.13B). These data were analyzed, and the differences between taxa in ventral BVTV (Kruskal-Wallis: $\chi^{2}=37.1822, p<0.001$ ), dorsal BVTV (KruskalWallis: $\chi^{2}=9.4936, p=0.01$ ), and dorsal DA (Kruskal-Wallis: $\chi^{2}=12.615, p<0.001$ ) were found to
be significant (Table 3.4A, B, C). For ventral BVTV, Pan and Pongo were significantly different from Symphalangus (Holm-Bonferroni adjusted Dunn's test: $\mathrm{p}<0.001$ ), Table 3.4A). For dorsal BVTV, Pongo was significantly different from Pan and Symphalangus (Holm-Bonferroni adjusted Dunn's test: $\mathrm{p}<0.05$ ), Table 3.4B). For dorsal DA, Pongo was significantly different from Pan (Holm-Bonferroni adjusted Dunn's test: $\mathrm{p}<0.001$ ), Table 3.4 C ). The significant differences in the complete data sets from these taxa correspond to the differences seen in the plots of column means (Figure 3.13A, B).

## General Locomotor Categories

Ventral and dorsal column means of BVTV and DA for each specimen of Symphalangus, Homo, Pan, Papio, and Macaca were plotted to compare differences in trabecular variables between general locomotor categories (Figure 3.14A, B). As is typical in these plots, there were areas of overlap between most taxa. In the BVTV plot, ventral column BVTV in Pan, Papio, and Macaca tended to be lower than in Symphalangus and Homo, while dorsal column BVTV was relatively lower in Macaca than in the other taxa (Figure 3.14A). In the plot of DA, the space delimited by the Homo specimens did not overlap with the spaces of any of the other taxa as a result of its relative low dorsal DA, while the spaces bounded by the Macaca, Papio, and Pan specimens both overlapped with each other and were much larger due to their greater intraspecific variability and higher DA (Figure 3.14B). Symphalangus occupied an intermediate dorsal DA space on this plot (Figure 3.14B).

Four Kruskal-Wallis tests were performed to test for significant differences between the species. Three of the tests were statistically significant: ventral BVTV, dorsal BVTV, and dorsal DA. Post-hoc Dunn's tests identified which pairs were driving the differences (Table 3.5A, B, C). For ventral BVTV: Homo was significantly different from Macaca, Pan, and Papio; Papio was significantly different from Homo, Macaca, and Pan; and Symphalangus was significantly
different from Macaca and Pan (Table 3.5A). Homo has relatively high ventral BVTV overall, Papio has a relatively high degree of intraspecific variation, Macaca has relatively low ventral BVTV (with a single exception), and Symphalangus has relatively high BVTV compared to Macaca and Pan. For dorsal BVTV, Macaca was significantly different from Homo and Papio (Table 3.5B). This is likely due to Macaca specimens having generally low dorsal BVTV. For dorsal DA, Homo was significantly different from Macaca, Pan, and Papio (Table 3.5C). Homo has relatively low DA compared to the other taxa.

## Presence/Absence of Ischial Callosities

Ventral and dorsal column means of inferior BVTV and DA from the complete sample were plotted to visualize differences in trabecular architecture between groups (Figure 3.15A, B). In terms of BVTV, many of the taxa overlapped, with Homo being the most different species (Figure 3.15A). In terms of DA, Pan, Pongo, and Homo had relatively low mean DA in both the ventral and dorsal columns (though several specimens of Pan were more anisotropic), while Symphalangus, Macaca, and Papio had relatively higher mean DA, particularly in the dorsal column (Figure 3.15B). These data were analyzed and significant differences were found between the two groups (Pan, Pongo, and Homo vs. Symphalangus, Macaca, and Papio) in ventral DA (Wilcoxon-Mann-Whitney: $\mathrm{p}:<0.05$ ) and dorsal DA (Wilcoxon-Mann-Whitney: $\mathrm{p}:<$ 0.001 ). Neither of the tests of BVTV were significant (Table 3.6).

### 3.6 Discussion

In this study, loading patterns predicted by previous work and general locomotor categories were tested via analyses of trabecular architecture from high-resolution x -ray CT scans of primate ischia. Hypotheses based on previous work come from the biomechanical models of Slijper (1946), Badoux (1974), and Kummer (1975) and from Lewton's (2015) experimental study
on in vitro bone strains in the primate pelvis. Hypotheses based on general locomotor categories come from observed variation in ischial morphology between primate taxa thought to be related to locomotor mode (mainly via the role of the ischium as the lever arm of the hamstring musculature) (e.g., Waterman 1929, Steudel 1981, Yirga 1987, Fleagle \& Anapol 1992). Two trabecular variables that together account for $>80 \%$ of bone's mechanical properties (Goldstein et al. 1993), BVTV and DA, were quantified throughout one entire ischium of each specimen comprising the sample and analyzed for differences in accordance with the two sets of hypotheses. This study is the first to quantitatively characterize the trabecular architecture of the primate ischium and, as such, will hopefully serve as a starting point for trabecular analyses of this skeletal element. In addition to being novel, the results from the trabecular architecture of the ischium are important because its morphology has been shown to vary with locomotor mode (Waterman 1929, Steudel 1981, Yirga 1987, Fleagle \& Anapol 1992) and the loading regime that it is subjected to has not been thoroughly characterized (Badoux 1974, Kummer 1975, Lewton 2015). Being able to use trabecular architecture as a way to indirectly investigate loading will both shed light on how forces are transmitted through the ischium and will potentially be useful for reconstructing locomotion in fossil taxa from this skeletal element.

## Ischial Loading

Three predictions were made about different possible configurations of the trabecular architecture of the ischium and its relationship to hypothesized loading regimes. The first hypothesis (H1) was that the ischium is loaded in compression ventrally and tension dorsally, such that ventral BVTV and DA were predicted to be higher than dorsal BVTV and DA (Badoux 1974, Kummer 1975). The second (H2) was that the ischium is loaded in compression dorsally and tension ventrally, such that dorsal BVTV and DA would be higher than ventral BVTV and DA (Slijper 1946, Badoux 1974, Kummer 1975). These two predictions attempt to explain the
trabecular effects of dorso-ventral bending in the sagittal plane. The third hypothesis (H3) was that the ischium is loaded in torsion, resulting in a prediction of equal distribution of trabecular reinforcement on both dorsal and ventral sides (Lewton 2015).

The second hypothesis (H2), dorso-ventral bending (dorsal compression/ventral tension), appears to be generally supported; in all of the non-human primates, dorsal and ventral BVTV and DA are significantly different, with plots of the data suggesting that dorsal BVTV and DA are higher than ventral BVTV and DA. However, in Homo there are no significant differences between dorsal and ventral trabecular variables. The difference in results between the nonhuman primates and Homo makes sense in light of the differences in their ischial morphology and hamstring anatomy and function. Homo has a relatively short ischium, providing a short lever arm for the hamstring muscles; as terrestrial bipeds, humans do not require the capabilities for producing the kind of powerful hip flexion/leg extension needed by arboreal primates (Sigmon 1975, Steudel 1981, Yirga 1987). It is interesting to note that the plot of BVTV in Symphalangus (Figure 3.9A) is relatively more similar to that of Homo (Figure 3.10A) than it is to those of the other non-human primates. Both taxa have relatively high BVTV in both ventral and dorsal columns, as well as relatively less variation between the two (though the difference between them in Symphalangus was statistically significant). This similarity may simply be the consequence of having relatively short, stout ischia, but, if that is the case, then the fact that Symphalangus does have that significant difference between ventral and dorsal trabecular density requires explanation. Differences in the arrangement of the hip and thigh musculature may be the reason: Sigmon $(1974,1975)$ suggested that Symphalangus has musculature similar to that of the African apes, while Homo is quite different, due to our bipedally-adapted pelvis. Additionally, if strain on the dorsal ischium due to hamstring use is the reason for reinforcement of that trabecular architecture, then it should be noted that Symphalangus does still climb,
though it often involves more hip flexion than leg extension (i.e., it is not powerful climbing) (Fleagle 1976).

There are two potential caveats to simply accepting that having denser, more anisotropic trabecular architecture in the dorsal ischium can only be explained by a loading regime of dorsoventral bending in the sagittal plane during locomotion. The first is that torsion could also cause this pattern if the bone were being twisted in such a way that the forces did not perfectly align with the long axis of the bone (i.e., off-axis torsion). Given that the ischium is not a cylindrical beam, this seems like a possibility, particularly given that primates often use their hindlimbs in abducted postures. Additionally, it is currently unknown how trabecular architecture responds to torsion. Either in vivo work in a model animal or CT scanning of a skeletal element known to be subject to this loading regime (e.g., bat wings, Swartz et al. 1992) could potentially address this issue. The second potential caveat is in assuming that dorsal compression results from locomotor loading, rather than from sitting. Most of the taxa included in this sample spend a nontrivial proportion of their day (33-90\%) sitting (Chivers 1972, Rose 1977, Sugardjito \& van Hooff 1986, Hunt 1991, Hunt 1992, Wells \& Turnquist 2001), though the lack of differences between the ventral and dorsal trabecular architecture in Homo suggest that this may not be a better explanation than one based on locomotion.

## Locomotor Variables

Three hypotheses were made about various aspects of locomotion that have been suggested to be related to ischial morphology, which were then assessed on the basis of trabecular architecture. These three hypotheses dealt with the degree of arboreality of a species (i.e., arboreal vs semi-arboreal/semi-terrestrial versus terrestrial taxa) (H4), its general locomotor classification (i.e., quadrupedal versus bipedal versus forelimb-dominated brachiation) (H5), and whether it has ischial callosities or not (H6). The first two hypotheses are related to observed
differences in relative ischial length between taxa, while the third is related to the potential effect that the presence or absence of ischial callosities has on the location of muscle attachments.

The first hypothesis (H4a), that more terrestrial taxa (which tend to have relatively long ischia) will have greater trabecular reinforcement against dorso-ventral bending (following from the previous set of predictions about ischial loading patterns) than more arboreal taxa, proposed this order for the sampled species: Symphalangus, Pongo < Macaca < Pan, Papio. It also included the secondary prediction (H4b) that proposed differences in trabecular architecture should be more consistent within phylogenetic groups (i.e., Macaca < Papio and Symphalangus < Pongo < Pan). Homo was not included in this hypothesis, as they do not have the relatively long ischia common to terrestrial non-human primates. While there were statistically significant differences between taxa in ventral BVTV, dorsal BVTV, and dorsal DA, the plots of the complete sample did not necessarily conform to the predicted order of taxa. For example, in ventral BVTV, Symphalangus was significantly different from Pongo, but not from Papio. Taking the BVTV plot as a whole, Macaca was the species with the least dense trabecular architecture, contra the prediction. In terms of dorsal DA, the plot matches the predicted order of taxa somewhat better (at least in terms of the most committed arboreal and terrestrial taxa), but Macaca again is not in its expected intermediate position. This could potentially be explained as an issue of comparing taxa with differing body masses, as BVTV has been shown to be slightly positively allometric with body size (Ryan \& Shaw 2013), but Symphalangus is also a relatively small-bodied species (at least in comparison to the other hominoids) and it has higher ischial BVTV than Pongo, so it is unlikely that body size is the only confounding issue here. Without Macaca, both plots correspond more closely to the predicted order of taxa. The problematic position of Macaca may be due to variation in locomotor behavior at the level of the individual animal; the
relative proportion of arboreal to terrestrial locomotion in these particular individuals is unknown (and has not been documented for the wild populations from which they were drawn), which may be responsible for the disagreement between prediction and results.

The secondary prediction (H4b) proposing better correspondence between the predicted order within phylogenetic groups (cercopithecoids and hominoids) is only really supported by the plot of BVTV in the two cercopithecoids (Figure 3.12A). Macaca has less dense trabecular bone in the ischium than Papio. The single specimen (USNM 173813) that groups more closely with Papio may be an outlier due to it being from a different subspecies of Macaca mulatta than the other specimens; it is listed as M. mulatta villosa in the USNM database. This specimen also has the lowest mean DA of any of the Macaca individuals. In terms of DA generally, Macaca appears to have more anisotropic trabecular architecture than Papio, contra the predicted relationship (Figure 3.12B). This may be the result of the potentially complementary nature of density and anisotropy in optimizing trabecular architecture, i.e., that there is a critical density threshold past which resorption of specific trabeculae in favor of greater directionality of the remaining struts is the preferred strategy, as has been seen in some developmental studies (Weinans et al. 1992, Tanck et al. 2001, Cunningham \& Black 2009, Acquaah et al. 2015). It is possible that Macaca reaches this threshold in the ischium by having relatively large hamstring muscles for its size, thus subjecting its ischium to higher loads, resulting in highly anisotropic, low density trabecular architecture (Yirga 1987, Payne et al. 2006).

The hominoid-only prediction (H4b) also was not entirely supported by the trabecular data. It was predicted on the basis of their relative degrees of arboreality (and inferred hindlimb use resulting from this) that Symphalangus would have the lowest BVTV and DA, and that Pan would have the highest, with Pongo being intermediate between the two. In terms of trabecular
density, Pan and Pongo have similar ventral BVTV, while Pan and Symphalangus have similar dorsal BVTV (Figure 3.13A). Symphalangus has denser trabecular architecture throughout the ischium than expected, such that the actual order of taxa for ventral BVTV is Symphalangus > Pan = Pongo and the actual order for dorsal BVTV is Symphalangus $=$ Pan > Pongo. The results for DA are similarly problematic: ventral DA does not differ significantly between the taxa, while dorsal DA only differs significantly between Pan and Pongo (p $<0.001$ ). Symphalangus occupies an intermediate position between the other two taxa in dorsal DA (Figure 3.13B), contra the prediction. Perhaps, as was suggested above, the higher than expected BVTV and DA in Symphalangus is just a consequence of its short and stout ischial morphology.

The second hypothesis (H5) attempted to differentiate between taxa based on their typical locomotor mode, grouping the sample into quadrupeds, bipeds, and brachiators. Theoretically, quadrupeds should experience greater loading of their ischia than bipeds and brachiators, as a result of having more powerful hamstrings attached to longer ischia. Between bipeds and brachiators, the bipeds should have denser, more anisotropic trabecular architecture due to frequency of hindlimb use and ground reaction forces. The predicted order of taxa was Symphalangus < Homo < Pan, Papio, Macaca. Pongo was not included in the prediction, due to its unique locomotor mode. While there were statistically significant differences between taxa in both ventral and dorsal BVTV ( $\mathrm{p}<0.001$ ), plotting the species did not place them in the order predicted by locomotor mode (Figure 3.14A). In terms of ventral BVTV, Homo was significantly different from all of the quadrupeds, Symphalangus was significantly different from Macaca and Pan, and the quadrupedal specimens clustered together (though with some outliers) on the plot. However, the quadrupeds actually had lower ventral BVTV than Symphalangus and Homo, though Homo did have higher BVTV than Symphalangus, as predicted. Essentially, there was some differentiation of taxa by locomotor mode, but not in the direction predicted, with the
actual order of taxa by locomotor mode being: quadrupeds < brachiator < biped. Dorsal BVTV only showed significant differences between Macaca (with the lowest BVTV) and Homo and Papio (with higher BVTV); generally all of the specimens were between 0.25 and just over 0.40.

Dorsal DA also differed significantly between taxa ( $p<0.001$ ), with the differences being driven by Homo separating from the quadrupeds, but again, the taxa did not plot in the expected order (Figure 3.14B). Homo had the lowest DA and the quadrupeds had the highest, with Symphalangus intermediate between the two (biped < brachiator < quadrupeds). One possible explanation for the combination of one low and one high trabecular variable (e.g., high BVTV/low DA or low BVTV/high DA) was discussed above for Macaca, but applies here to Homo and the quadrupeds; density and anisotropy are likely complementary pathways to trabecular optimization (Weinans et al. 1992, Tanck et al. 2001, Cunningham \& Black 2009, Acquaah et al. 2015). This could suggest that Homo has not yet reached the hypothetical threshold needed to cause resorption of dense, disorganized trabecular architecture, but that the quadrupeds have. This may be explained by powerful hamstring use in the quadrupeds, as previous studies have found a correlation between locomotor mode and degree of anisotropy (e.g., MacLatchy \& Müller 2002, Ryan \& Shaw 2012, Fajardo et al. 2013). If this is the case, the intermediate DA position of Symphalangus could be the result of either the climbing behavior or the forces experienced upon landing during brachiation (Channon et al. 2009). Future comparisons with Hylobates and/or Ateles would likely provide better resolution on this issue.

The third hypothesis (H6) proposed that there would be differences in inferior ischial trabecular architecture between primates with and without ischial callosities, possibly due to the differences in muscle attachments caused by the presence or absence of those structures (Macaca, Papio, Symphalangus $\neq$ Pan, Pongo, Homo). This was a potentially interesting comparison, as it places Symphalangus with the cercopithecoids, not the hominoids, and groups
together taxa with very different locomotor regimes. There were no significant differences in BVTV between the groups, but there were in both ventral and dorsal DA (p $<0.05$ and $p<0.001$, respectively). The group without callosities (Pan, Pongo, and Homo) tended to have more isotropic trabecular architecture than the group with callosities (Symphalangus, Macaca, and Papio) in support of the prediction, though there was some overlap between the groups (mostly in ventral DA, which was not significantly different between taxa in any of the previous comparisons of the complete ischium). It is possible that the difference in DA may be related to the differences in muscle attachment locations between the two groups. In primates with callosities, the hamstring musculature originates from around the periphery of the flattened ischial tuberosity, while in primates without callosities, these muscles originate from the curved surface of the tuberosity itself (Rose 1974). Perhaps this results in variation in the size of the attachments themselves, with the smaller peripheral attachments resulting in more concentrated forces, causing the trabeculae to become more anisotropic. This is currently purely speculative, but could potentially be tested by a combination of dissection and CT scanning of the same specimens.

### 3.7 Conclusion

This study is the first to quantify trabecular architecture in the primate ischium and provide an initial description and characterization of intra- and interspecific variation in this skeletal element. While many of the results contained here are equivocal or difficult to interpret, it seems reasonable to say that dorsal trabecular architecture tends to be preferentially reinforced over ventral trabecular architecture in the ischia of non-human primates. To better understand what causes this, more work needs to be done on in vivo loading of the primate pelvis, though this is unlikely to occur due to the highly invasive nature of attempting to place
strain gauges onto the pelvic bone of living primates. There also appear to be some real differences in the trabecular architecture of arboreal and terrestrial primates, and between primates using different locomotor regimes, but it is difficult to confidently say this with the small sample (both in number and in taxonomic breadth) used in this study. Future work should consider targeted scanning of only the ischium, to increase the sample size at a relatively lower cost. Additionally, finite element analysis (both of the pelvis itself and specifically of the trabecular architecture) should be explored as a way to resolve the issues of lack of good data on pelvic loading and to clarify the relationship between loading and trabecular architecture.

Table 3.1. Results of a series of Wilcoxon signed-rank tests comparing bone volume fraction and degree of anisotropy between paired ventral and dorsal volumes of interest within each species. Significant results are indicated in bold.

| Species | N | Bone volume <br> fraction <br> medians <br> (ventral, dorsal) | Bone volume <br> fraction p-value | Degree of <br> anisotropy <br> medians <br> (ventral, dorsal) | Degree of <br> anisotropy p- <br> value |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Macaca mulatta | $48 / 47$ | $0.2035,0.2864$ | $<0.001$ | $3.2195,4.5668$ | $<\mathbf{0 . 0 0 1}$ |
| Papio anubis | 78 | $0.2902,0.3618$ | $<0.001$ | $2.7580,4.1609$ | $<0.001$ |
| Pan troglodytes | 55 | $0.2420,0.3430$ | $<0.001$ | $2.8717,4.4033$ | $<\mathbf{0 . 0 0 1}$ |
| Pongo pygmaeus | 39 | $0.2431,0.3076$ | $<0.001$ | $2.4132,2.9185$ | $\mathbf{0 . 0 3 3 1 3}$ |
| Symphalangus <br> syndactylus | 26 | $0.3183,0.3361$ | $\mathbf{0 . 0 1 2 9 5}$ | $2.4440,3.2111$ | $\mathbf{0 . 0 4 0 7 5}$ |
| Homo sapiens | 28 | $0.3455,0.3661$ | 0.1042 | $2.3711,2.2035$ | 0.9375 |

Table 3.2. (A) Pairwise differences between arboreal and terrestrial species of non-human primates by bone volume fraction (BVTV) in all ventral volumes of interest resulting from a HolmBonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the Kruskal-Wallis test: $\chi^{2}=62.8314, p<0.001$. (B) Pairwise differences between arboreal and terrestrial species of non-human primates by BVTV in all dorsal volumes of interest resulting from a Holm-Bonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the Kruskal-Wallis test: $\chi^{2}=$ 27.9323, $\mathrm{p}<0.001$. (C) Pairwise differences between arboreal and terrestrial species of nonhuman primates by degree of anisotropy (DA) in all dorsal volumes of interest resulting from a Holm-Bonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the KruskalWallis test: $\chi^{2}=22.3144, p<0.001$. As the decision to reject the null hypothesis in a sequential test depends on the ordering of the comparisons as well as on the p-values, significant adjusted $p$-values are in bold.

A - Ventral BVTV

|  | Macaca | Pan | Papio | Pongo |
| :---: | :---: | :---: | :---: | :---: |
| Pan | 0.2674 | - | - | - |
| Papio | $<0.001$ | $<0.001$ | - | - |
| Pongo | 0.3059 | 0.3938 | $<\mathbf{0 . 0 0 1}$ | - |
| Symphalangus | $<\mathbf{0 . 0 0 1}$ | $<\mathbf{0 . 0 0 1}$ | 0.1167 | $<\mathbf{0 . 0 0 1}$ |

B - Dorsal BVTV

|  | Macaca | Pan | Papio | Pongo |
| :---: | :---: | :---: | :---: | :---: |
| Pan | $\mathbf{0 . 0 1 1 6}$ | - | - | - |
| Papio | $<\mathbf{0 . 0 0 1}$ | 0.3611 | - | - |
| Pongo | 0.7189 | 0.0449 | $<\mathbf{0 . 0 0 1}$ | - |
| Symphalangus | $\mathbf{0 . 0 2 3 3}$ | 0.3817 | 0.7029 | 0.0539 |

C-Dorsal DA

|  | Macaca | Pan | Papio | Pongo |
| :---: | :---: | :---: | :---: | :---: |
| Pan | 0.8141 | - | - | - |
| Papio | 0.9867 | 0.4211 | - | - |
| Pongo | $<\mathbf{0 . 0 0 1}$ | $<\mathbf{0 . 0 0 1}$ | $<\mathbf{0 . 0 0 1}$ | - |
| Symphalangus | 0.1331 | 0.1593 | 0.1510 | 0.3731 |

Table 3.3. Results of four Wilcoxon-Mann-Whitney tests comparing bone volume fraction and degree of anisotropy in paired ventral and dorsal volumes of interest between Macaca and Papio (the cercopithecoids). Macaca has an $N$ of 48 for bone volume fraction, but an $N$ of 47 for degree of anisotropy. Comparisons are across rows, not columns. Significant results are indicated in bold.

|  | Macaca mulatta | Papio anubis | p-values |
| :---: | :---: | :---: | :---: |
| N | $48 / 47$ | 78 | -- |
| Ventral bone volume <br> fraction medians | 0.2035 | 0.2902 | Ventral BVTV: $<0.001$ |
| Dorsal bone volume <br> fraction medians | 0.2864 | 0.3618 | Dorsal BVTV: $<\mathbf{0 . 0 0 1}$ |
| Ventral degree of <br> anisotropy medians | 3.2195 | 2.7580 | Ventral DA: 0.1843 |
| Dorsal degree of <br> anisotropy medians | 4.5668 | 4.1609 | Dorsal DA: 0.5873 |

Table 3.4. (A) Pairwise differences between hominoids with differing degrees of arboreal behavior by bone volume fraction (BVTV) in all ventral volumes of interest resulting from a HolmBonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the Kruskal-Wallis test: $\chi^{2}=37.1822, p<0.001$. (B) Pairwise differences between hominoids with differing degrees of arboreal behavior by BVTV in all dorsal volumes of interest resulting from a Holm-Bonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the Kruskal-Wallis test: $\chi^{2}=$ $9.4936, p=0.01$. (C) Pairwise differences between hominoids with differing degrees of arboreal behavior by degree of anisotropy (DA) in all dorsal volumes of interest resulting from a HolmBonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the Kruskal-Wallis test: $\chi^{2}=12.615, p<0.001$. As the decision to reject the null hypothesis in a sequential test depends on the ordering of the comparisons as well as on the $p$-values, significant adjusted $p$ values are in bold.

A - Ventral BVTV

|  | Pan | Pongo |
| :---: | :---: | :---: |
| Pongo | 0.3800 | - |
| Symphalangus | $<\mathbf{0 . 0 0 1}$ | $<\mathbf{0 . 0 0 1}$ |

B - Dorsal BVTV

|  | Pan | Pongo |
| :---: | :---: | :---: |
| Pongo | $\mathbf{0 . 0 0 8 2}$ | - |
| Symphalangus | 0.4073 | $\mathbf{0 . 0 1 1 7}$ |

C- Dorsal DA

|  | Pan | Pongo |
| :---: | :---: | :---: |
| Pongo | $<0.001$ | - |
| Symphalangus | 0.0889 | 0.0920 |

Table 3.5. (A) Pairwise differences between primates belonging to different locomotor categories by bone volume fraction (BVTV) in all ventral volumes of interest resulting from a HolmBonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the Kruskal-Wallis test: $\chi^{2}=87.1397, p<0.001$. (B) Pairwise differences between primates belonging to different locomotor categories by BVTV in all dorsal volumes of interest resulting from a Holm-Bonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the Kruskal-Wallis test: $\chi^{2}=$ 24.6215, $p<0.001$. (C) Pairwise differences between primates belonging to different locomotor categories by degree of anisotropy (DA) in all dorsal volumes of interest resulting from a HolmBonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. Results of the Kruskal-Wallis test: $\chi^{2}=30.7158, p<0.001$. As the decision to reject the null hypothesis in a sequential test depends on the ordering of the comparisons as well as on the $p$-values, significant adjusted $p$ values are in bold.

A - Ventral BVTV

|  | Homo | Macaca | Pan | Papio |
| :---: | :---: | :---: | :---: | :---: |
| Macaca | $<0.001$ | - | - | - |
| Pan | $<0.001$ | 0.2398 | - | - |
| Papio | $<0.001$ | $<0.001$ | $<0.001$ | - |
| Symphalangus | 0.0988 | $<0.001$ | $<0.001$ | 0.1308 |

B - Dorsal BVTV

|  | Homo | Macaca | Pan | Papio |
| :---: | :---: | :---: | :---: | :---: |
| Macaca | $<0.001$ | - | - | - |
| Pan | 0.1943 | 0.0251 | - | - |
| Papio | 0.4824 | $<0.001$ | 0.2991 | - |
| Symphalangus | 0.4277 | 0.0336 | 0.3523 | 0.6255 |

C - Dorsal DA

|  | Homo | Macaca | Pan | Papio |
| :---: | :---: | :---: | :---: | :---: |
| Macaca | $<\mathbf{0 . 0 0 1}$ | - | - | - |
| Pan | $<\mathbf{0 . 0 0 1}$ | 0.8168 | - | - |
| Papio | $<0.001$ | 0.9729 | 0.4143 | - |
| Symphalangus | 0.0668 | 0.1279 | 0.1474 | 0.1386 |

Table 3.6. Results of four Wilcoxon-Mann-Whitney tests comparing bone volume fraction and degree of anisotropy between primates with and without ischial callosities. Comparisons are across columns (i.e., comparing ventral BVTV between primates with and without callosities). Significant results are indicated in bold.

|  | Callosities (Papio, <br> Macaca, <br> Symphalangus) | No Callosities (Pan, <br> Pongo, Homo) | p-values |
| :---: | :---: | :---: | :---: |
| N | 68 | 56 | -- |
| Ventral bone volume <br> fraction medians | 0.2612 | 0.2530 | Ventral BVTV: 0.5722 |
| Dorsal bone volume <br> fraction medians | 0.3428 | 0.3298 | Dorsal BVTV: 0.7882 |
| Ventral degree of <br> anisotropy medians | 2.6128 | 2.1262 | Ventral DA: $\mathbf{0 . 0 1 2 6}$ |
| Dorsal degree of <br> anisotropy medians | 3.3620 | 2.2605 | Dorsal DA: $<\mathbf{0 . 0 0 1}$ |

Figure 3.1. (A) A simplified biomechanical model of the biped pelvis (in coronal plane). Pauwels (1980) proposed that the bones of the human pelvis act like a series of arcs connected by joints. The pelvis experiences a downward force from the weight of the upper body at the sacroiliac joints and upward forces from the legs at the hip joints. The combination of these forces causes the pubic symphysis to be loaded in tension. Modified from Pauwels (1980) and Lewton (2015).

A


Figure 3.1. (B) A modified version of Slijper's (1946) biomechanical model of the quadruped pelvis in lateral view. In the "bow-and-string" model, the vertebral column is the bow and the abdominal musculature is the string, causing a dorsal rotation of the pelvis at the sacroiliac joint. (C) An extended version of the "bow-and-string" model, proposed by Badoux (1974) and Kummer (1975). The quadruped ilium would likely be subject to two opposite rotational moments around the sacroiliac joint and acetabulum (i.e., subject to bending in the sagittal plane), which would be counteracted by the abdominal musculature, ischiosacral ligaments, and ischiocaudal muscles. These two soft tissue structures (the ischiosacral ligaments and ischiocaudal muscles) would also potentially serve to resist the sagittal bending of the ischium by the hamstrings (Badoux 1974, Kummer 1975). Lateral view, left is cranial, right is caudal.


C


Figure 3.1. (D) According to the biomechanical models of Badoux (1974) and Kummer (1975), the ischium is loaded in dorso-ventral bending by the action of the hamstrings, and experiences compression ventrally and tension dorsally (H1). Given that compressive loading has been experimentally shown to cause increases in bone volume fraction (BVTV) and degree of anisotropy (DA) (van der Meulen et al. 2006), the ventral ischium is predicted to have higher BVTV and DA than the dorsal ischium. (E) Alternatively, if one combines the models of Slijper (1946), Badoux (1974), and Kummer (1975), and preferences the upward forces of the ischiosacral/ischiocaudal musculature and the hindlimb over the downward force of the hamstrings, then the ischium is predicted to be loaded in dorso-ventral bending, but with ventral tension and dorsal compression. If this is the case, then the dorsal ischium should have higher BVTV and DA than the ventral ischium (H2). Lateral view, left is cranial, right is caudal.


E


Figure 3.1. (F) Lewton (2015) found that Macaca, Papio, and Hylobates loaded their ischium in torsion. If the ischium is loaded in torsion perfectly around its long axis, then both the ventral and dorsal sides should be reinforced in order to resist torque (H3). Lateral view, left is cranial, right is caudal.


Figure 3.2. On the left, the patterns of stress (trajectories) proposed by Kummer (1975) to exist in a bent beam. On the right, a radiograph of the human ischium showing this trajectorial patterning in its trabecular architecture (Kummer 1975).


Figure 3.3. (A) The ischium was first isolated by loading a subset of the CT stack containing the acetabulum and ischium in the ImageJ 3D Viewer, and then (in lateral view) orienting the long axis of the ischium vertically, such that it would be perpendicular to a line drawn tangent to the inferior-most curve of the acetabulum. All CT slices above this line were then cropped out, leaving only the ischium and the ischiopubic ramus. (B) Then, the 3D reconstruction was rotated so the view was "flat" to the obturator foramen, such that the next crop did not include any of the body of the ischium. From that view, a vertical line was drawn perpendicular to where the horizontal crop line intersected with the obturator foramen, cropping out the ischiopubic ramus and leaving only the ischium. (C) Schematic of volume of interest (VOI) placement protocol. VOIs were selected by placing three cubes of maximum possible size within the first complete CT slice of each ischium stack (in transverse view). For scaling, the uppermost set was labeled " 0 " and lowest was labeled "1."


Figure 3.4. (A) Species mean bone volume fraction (BVTV) in the ventral and dorsal columns of the ischium. (B) Species mean degree of anisotropy (DA) in the ventral and dorsal columns of the ischium. Ventral volumes of interest (VOIs) are in blue and dorsal VOIs are in maize. Legends are organized by VOI position, as this is the intended comparison


B


Figure 3.5. (A) Plot of the scaled bone volume fraction (BVTV) data by specimen for the Macaca mulatta ischium, for the visualization of differences between ventral and dorsal BVTV. (B) Plot of the scaled degree of anisotropy (DA) data by specimen for the $M$. mulatta ischium, for the visualization of differences between ventral and dorsal DA. Each specimen is represented by a ventral and a dorsal line. Ventral volumes of interest (VOIs) are in blue and dorsal VOIs are in maize. Legends are organized by specimen, not VOI position, to facilitate comparisons within and between specimens.

A


B


Relative anatomical location of volume of interest ( $0=$ superior, $1=$ inferior)

Figure 3.6. (A) Plot of the scaled bone volume fraction (BVTV) data by specimen for the Papio anubis ischium, for the visualization of differences between ventral and dorsal BVTV. (B) Plot of the scaled degree of anisotropy (DA) data by specimen for the $P$. anubis ischium, for the visualization of differences between ventral and dorsal DA. Each specimen is represented by a ventral and a dorsal line. Ventral volumes of interest (VOIs) are in blue and dorsal VOIs are in maize. Legends are organized by specimen, not VOI position, to facilitate comparisons within and between specimens.

A


B


Figure 3.7. (A) Plot of the scaled bone volume fraction (BVTV) data by specimen for the Pan troglodytes ischium, for the visualization of differences between ventral and dorsal BVTV. (B) Plot of the scaled degree of anisotropy (DA) data by specimen for the P. troglodytes ischium, for the visualization of differences between ventral and dorsal DA. Each specimen is represented by a ventral and a dorsal line. Ventral volumes of interest (VOIs) are in blue and dorsal VOIs are in maize. Legends are organized by specimen, not VOI position, to facilitate comparisons within and between specimens.

A


B


Figure 3.8. (A) Plot of the scaled bone volume fraction (BVTV) data by specimen for the Pongo pygmaeus ischium, for the visualization of differences between ventral and dorsal BVTV. (B) Plot of the scaled degree of anisotropy (DA) data by specimen for the $P$. pygmaeus ischium, for the visualization of differences between ventral and dorsal DA. Each specimen is represented by a ventral and a dorsal line. Ventral volumes of interest (VOIs) are in blue and dorsal VOIs are in maize. Legends are organized by specimen, not VOI position, to facilitate comparisons within and between specimens.

A


B


Figure 3.9. (A) Plot of the scaled bone volume fraction (BVTV) data by specimen for the Symphalangus syndactylus ischium, for the visualization of differences between ventral and dorsal BVTV. (B) Plot of the scaled degree of anisotropy (DA) data by specimen for the $S$. syndactylus ischium, for the visualization of differences between ventral and dorsal DA. Each specimen is represented by a ventral and a dorsal line. Ventral volumes of interest (VOIs) are in blue and dorsal VOIs are in maize. Legends are organized by specimen, not VOI position, to facilitate comparisons within and between specimens.

A


B


Figure 3.10. (A) Plot of the scaled bone volume fraction (BVTV) data by specimen for the Homo sapiens ischium, for the visualization of differences between ventral and dorsal BVTV. (B) Plot of the scaled degree of anisotropy (DA) data by specimen for the $H$. sapiens ischium, for the visualization of differences between ventral and dorsal DA. Each specimen is represented by a ventral and a dorsal line. Ventral volumes of interest (VOIs) are in blue and dorsal VOIs are in maize. Legends are organized by specimen, not VOI position, to facilitate comparisons within and between specimens.

A


B


Figure 3.11. (A) Plot of the column means of ventral and dorsal ischial bone volume fraction for the complete non-human primate sample, comparing trabecular density in terrestrial, semi-arboreal/semi-terrestrial, and arboreal primates. (B) Plot of the column means of ventral and dorsal ischial degree of anisotropy for the complete non-human primate sample, comparing levels of trabecular directionality in terrestrial, semi-arboreal/semi-terrestrial, and arboreal primates. Terrestrial taxa are in blue, the semi-arboreal/semi-terrestrial taxon is in red, and arboreal taxa are in green.

A


B


Figure 3.12. (A) Plot of the column means of ventral and dorsal ischial bone volume fraction for the subset of cercopithecoids, comparing trabecular density in a terrestrial taxon and a semi-arboreal/semi-terrestrial one. (B) Plot of the column means of ventral and dorsal ischial degree of anisotropy for the subset of cercopithecoids, comparing levels of trabecular directionality in a terrestrial taxon and a semi-arboreal/semi-terrestrial one. The terrestrial taxon is in blue and the semi-arboreal/semi-terrestrial taxon is in red.

A


B


Figure 3.13. (A) Plot of the column means of ventral and dorsal ischial bone volume fraction for the subset of hominoids, comparing trabecular density between primates with differing degrees of arboreality. (B) Plot of the column means of ventral and dorsal ischial degree of anisotropy for the subset of hominoids, comparing levels of trabecular directionality between primates with differing degrees of arboreality. The most terrestrial taxon is in blue and the most arboreal taxon is in green, with the intermediate one in orange.
A

B


Figure 3.14. (A) Plot of the column means of ventral and dorsal ischial bone volume fraction in quadrupedal, bipedal, and brachiating primates, comparing variation in trabecular density between taxa belonging to different general locomotor categories. (B) Plot of the column means of ventral and dorsal ischial degree of anisotropy in quadrupedal, bipedal, and brachiating primates, comparing variation in levels of trabecular directionality between taxa belonging to different general locomotor categories. The quadrupeds are in blue, the biped is in yellow, and the brachiator is in green.

A


B


Figure 3.15. (A) Plot of the column means of ventral and dorsal ischial bone volume fraction in primates with and without ischial callosities, comparing variation in trabecular density between these two groups. (B) Plot of the column means of ventral and dorsal ischial degree of anisotropy in primates with and without ischial callosities, comparing variation in levels of trabecular directionality between these two groups. The taxa with ischial callosities are shown in blue, while the taxa without callosities are shown in red.

A


B


## References

Abel R, Macho GA. 2011. Ontogenetic changes in the internal and external morphology of the ilium in modern humans. Journal of Anatomy 218:324-335.
Acquaah F, Brown KA, Ahmed F, Jeffery N, Abel RL. 2015. Early trabecular development in human vertebrae: Overproduction, constructive regression, and refinement. Frontiers in Endocrinology 6:67.
Anderson AE, Peters CL, Tuttle BD, Weiss JA. 2005. Subject-specific finite element model of the pelvis: Development, validation and sensitivity studies. Journal of Biomechanical Engineering 127:364-373.
Badoux DM. 1974. An introduction to biomechanical principles in primate locomotion and structure, in: Primate Locomotion. Jenkins FA, ed. Academic Press, New York: 1- 43.
Barak MM, Lieberman DE, Hublin JJ. 2011. A Wolff in sheep's clothing: trabecular bone adaptation in response to changes in joint loading orientation. Bone 49:1141-1151.
Barak MM, Lieberman DE, Raichlen D, Pontzer H, Warrener AG, Hublin J.J. 2013. Trabecular evidence for a human-like gait in Australopithecus africanus. PLoS ONE, 8, e77687.
Bergmann G, Graichen F, Rohlmann A. 1993. Hip joint loading during walking and running, measured in two patients. Journal of Biomechanics 26:969-990.
Channon AJ, Günther MM, Crompton RH, Vereecke EE. 2009. Mechanical constraints on the functional morphology of the gibbon hind limb. Journal of Anatomy 215:383-400.
Chivers JD. 1972. The siamang and the gibbon in the Malay peninsula, in: The Gibbon and the Siamang, Vol.1. Rumbaugh DM, ed. Karger, Basel: 103-135. (Cited from Hunt 1991).
Cruz-Orive LM, Karlsson LM, Larsen SE, Wainschtein F. 1992. Characterizing anisotropy: a new concept. Micron and Microscopic Acta 23:75-76.
Cunningham CA, Black SM. 2009. Anticipating bipedalism: trabecular organization in the newborn ilium. Journal of Anatomy 214:817-829.
Currey JD. 2002. Bone: Structure and Mechanics. Princeton University Press: Princeton.
Dalstra M, Huiskes R. 1995. Load transfer across the pelvic bone. Journal of Biomechanics 28:715-724.
Dinno A. 2015. Nonparametric pairwise multiple comparisons in independent groups using Dunn's test.
Fajardo RJ, Desilva JM, Manoharan RK, Schmitz JE, Maclatchy LM, Bouxsein ML. 2013. Lumbar vertebral body bone microstructural scaling in Small to Medium-Sized Strepsirhines. The Anatomical Record 296:210-226.
Fajardo RJ, Müller R. 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. American Journal of Physical Anthropology 115:327-336.
Fechner R, Stratmann M, Gößling R, Sverdlova N. 2013. The functional role of the ischiopubic membrane for the mechanical loading of the pubis in the domestic fowl (Gallus gallus). Journal of Anatomy 222:305-312.
Fleagle JG. 1976. Locomotion and posture of the Malayan siamang and implications for hominoid evolution. Folia Primatologica 26:245-269.
Fleagle JG, Anapol FC. 1992. The indriid ischium and the hominid hip. Journal of Human Evolution 22:285-305.
Goldstein SA, Goulet R, McCubbrey D. 1993. Measurement and significance of three-dimensional architecture to the mechanical integrity of trabecular bone. Calcified Tissue International 53:S127-S133.

Huiskes R, Ruimerman R, van Lenthe GH, Janssen JD. 2000. Effects of mechanical forces on maintenance and adaptation in trabecular bone. Nature 405:704-706.
Hunt KD. 1991. Positional behavior in the Hominoidea. International Journal of Primatology 12:95-118.
Hunt KD. 1992. Positional behavior of Pan troglodytes in the Mahale Mountains and Gombe Stream National Parks, Tanzania. American Journal of Physical Anthropology 87:83-105.
Ketcham RA, Ryan TM. 2004. Quantification and visualization of anisotropy in trabecular bone. Journal of Microscopy 213:158-171.
Kummer B. 1975. Functional adaptation to posture in the pelvis of man and other primates, in: Primate Functional Morphology and Evolution. Tuttle RH, ed. Aldine, Chicago: 281-290.
Lewton KL. 2015. In vitro bone strain distributions in a sample of primate pelves. Journal of Anatomy 226:458-77.
Lovejoy CO, McCollum MA, Reno PL, Rosenman BA. 2003. Developmental biology and human evolution. Annual Review of Anthropology 32:85-109.
Lovejoy CO, Suwa G, Spurlock L, Asfaw B, White TD. 2009. The pelvis and femur of Ardipithecus ramidus: The emergence of upright walking. Science 326:71-71e6.
Macchiarelli R, Bondioli L, Galichon V, Tobias PV. 1999. Hip bone trabecular architecture shows uniquely distinctive locomotor behavior in South African australopithecines. Journal of Human Evolution 36:211-232.
Macchiarelli R, Rook L, Bondioli L. 2001. Comparative analysis of the iliac trabecular architecture in extant and fossil primates by means of digital image processing techniques: Implications for the reconstruction of fossil locomotor behaviors, in: Hominoid Evolution and Climatic Change in Europe 2 - Phylogeny of the Neogene Hominoid Primates of Eurasia. De Bonis L, Koufos GD, and Andrews P, eds. Cambridge University Press, Cambridge: 60-101.
MacLatchy L, Müller R. 2002. A comparison of the femoral head and neck trabecular architecture of Galago and Perodicticus using micro-computed tomography. Journal of Human Evolution 43:89-105.
Maquer G, Musy SN, Wandel J, Gross T, Zysset PK. 2015. Bone volume fraction and fabric anisotropy are better determinants of trabecular bone stiffness than other morphological variables. Journal of Bone and Mineral Research 30:1000-8.
Meyer GH. 1867. Die Architektur der Spongiosa. Archiv fur Anatomie, Physiologie, und Wissenschaftliche Medicin 34:615-628.
Pauwels F. 1980. Biomechanics of the Locomotor Apparatus: Contributions on the Functional Anatomy of the Locomotor Apparatus. (Trans. Maquet P, Furlong R). Springer, New York. (Original work published 1965).
Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Gunter MM, Thorpe SKS, D’Aout K. 2006. Morphological analysis of the hindlimb in apes and humans. I. Muscle architecture. Journal of Anatomy 208:709-724.
Pontzer H, Lieberman DE, Momin E, Devlin MJ, Polk JD, Hallgrimsson N, Cooper DML. 2006. Trabecular bone in the bird knee responds with high sensitivity to changes in load orientation. Journal of Experimental Biology 209:57-65.
Rasband WS. 1997-2016. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.
Rauber AA. 1876. Uber Elastizitat und Festigkeit der Knochen. Wilhelm Engelmann, Leipzig.
Ridler TW, Calvard S. 1978. Picture thresholding using an iterative selection method. IEEE Transactions on Systems, Man, and Cybernetics. 8:630-2.
Roesler H. 1987. The history of some fundamental concepts in bone biomechanics. Journal of

Biomechanics 20:1025-1034.
Rodman PS. 1979. Skeletal Differentiation of Macaca fascicularis and Macaca nemestrina in Relation to Arboreal and Terrestrial Quadrupedalism. American Journal of Physical Anthropology 51:51-62.
Rook L, Bondioli L, Kohler M, Moya-Sola S, Macchiarelli R. 1999. Oreopithecus was a bipedal ape after all: Evidence from the iliac cancellous architecture. Proceedings of the National Academy of Sciences of the United States of America 96:8795-8799.
Rose MD. 1974. Ischial tuberosities and ischial callosities. American Journal of Physical Anthropology 40:375-383.
Rose MD. 1977. Positional behaviour of olive baboons (Papio anubis) and its relationship to maintenance and social activities. Primates 18:59-116.
Roux W. 1881. Der zuchtende Kampf der Teile, oder die 'Teilauslese' im Organismus. (Theorie der 'funktionellen Anpassung'). Wilhelm Engelmann, Leipzig. (Cited from Roesler 1987).
Rudolf G de M. 1922. Correlation between habit and the architecture of the mammalian femur. Journal of Anatomy 56:137-146.
Ruff C, Holt B, Trinkaus E. 2006. Who's afraid of the big bad Wolff?: "Wolff's Law" and bone functional adaptation. American Journal of Physical Anthropology 129:484-498.
Ryan TM, Ketcham RA. 2002. The three-dimensional structure of trabecular bone in the femoral head of strepsirrhine primates. Journal of Human Evolution 43:1-26.
Ryan TM, Shaw CN. 2012. Unique suites of trabecular bone features characterize locomotor behavior in human and non-human anthropoid primates. PLoS One 7:e41037.
Ryan TM, Shaw CN. 2013. Trabecular bone microstructure scales allometrically in the primate humerus and femur. Proceedings of the Royal Society of London B: Biological Sciences 280:20130172.
Scherf H. 2008. Locomotion-related femoral trabecular architecture in primates - high resolution computed tomographies and their implications for estimations of locomotor preferences of fossil primates, in: Anatomical imaging: Towards a new morphology. Endo H and Frey R, eds. Springer, New York: 39-59.
Scherf H, Harvati K, Hublin JJ. 2013. A comparison of proximal humeral cancellous bone of great apes and humans. Journal of Human Evolution 65:29-38.
Schultz AH. 1936. Characters common to higher primates and characters specific to Man (Continued). The Quarterly Review of Biology 11:425-455.
Schmitt D, Hanna JB. 2004. Substrate alters forelimb to hindlimb peak force ratios in primates. Journal of Human Evolution 46:237-52.
Sigmon BA. 1974. A functional analysis of pongid hip and thigh musculature. Journal of Human Evolution 3:161-185.
Sigmon BA. 1975. Functions and evolution of hominid hip and thigh musculature, in: Primate functional morphology and evolution. Tuttle RH, ed. Aldine, Chicago:235-252.
Slijper EJ. 1946. Comparative Biologic-Anatomical Investigations on the Vertebral Column and Spinal Musculature of Mammals. North-Holland, Amsterdam.
Steudel K. 1981. Functional aspects of primate pelvic structure: A multivariate approach. American Journal of Physical Anthropology 55:399-410.
Straus WL. 1929. Studies on primate ilia. American Journal of Anatomy 43:403-460.
Su A, Wallace IJ, Nakatsukasa M. 2013. Trabecular bone anisotropy and orientation in an Early Pleistocene hominin talus from East Turkana, Kenya. Journal of Human Evolution 64:667677.

Sugardjito J, van Hooff JA. 1986. Age-sex class differences in the positional behaviour of the

Sumatran orang-utan (Pongo pygmaeus abelii) in the Gunung Leuser National Park, Indonesia. Folia Primatologica 47:14-25.
Swartz SM, Bennett MB, Carrier DR. 1992. Wing bone stresses in free flying bats and the evolution of skeletal design for flight. Nature 359:726-729.
Tanck E, Homminga J, van Lenthe GH, Huiskes R. 2001. Increase in bone volume fraction precedes architectural adaptation in growing bone. Bone 28:650-654.
Trussell HJ. 1979. Comments on "Picture thresholding using an iterative selection method". IEEE Transactions on Systems, Man, and Cybernetics. 9:311.
Van der Meulen MCH, Morgan TG, Yang X, Baldini TH, Myers ER, Wright TM, Bostrom MPG. 2006. Cancellous bone adaptation to in vivo loading in a rabbit model. Bone 38:871-877.

Volpato V, Viola TB, Nakatsukasa M, Bondioli L, Macchiarelli R. 2008. Textural characteristics of the iliac-femoral trabecular pattern in a bipedally trained Japanese macaque. Primates 49:16-25.
Ward CV. 2002. Interpreting the posture and locomotion of Australopithecus afarensis: Where do we stand? Yearbook of Physical Anthropology 45:185-215.
Waterman HC. 1929. Studies on the evolution of the pelvis of man and other primates. American Museum of Natural History Bulletin 58:585-642.
Weinans H, Huiskes R, Grootenboer HJ. 1992. The behavior of adaptive bone-remodeling simulation models. Journal of Biomechanics 25:1425-41.
Wells JP, Turnquist JE. 2001. Ontogeny of locomotion in rhesus macaques (Macaca mulatta): II. Postural and locomotor behavior and habitat use in a free-ranging colony. American Journal of Physical Anthropology 115:80-94.
Wheatley BP. 1978. The behavior and ecology of the crab-eating macaque (Macaca fascicularis) in the Kutai Nature Reserve, East Kalimantan, Indonesia (Doctoral dissertation, University of California, Davis). (Cited from Rodman 1979).
Wolff J. 1892. Das Gesetz der Transformation der Knochen. A. Hirchwild Berlin.
Wolff J. 1986. The law of bone remodeling. Springer-Verlag Berlin.
Yirga S. 1987. Interrelation between ischium, thigh-extending muscles and locomotion in some primates. Primates 28:79-86.
Zuckerman S, Ashton EH, Flinn RM, Oxnard CE, Spence TF. 1973. Some locomotor features of the pelvic girdle in primates. Symposia of the Zoological Society of London 33:71-165.

# Chapter 4. Reconstructing locomotion in Rudapithecus hungaricus from the trabecular architecture of the innominate 

### 4.1 Abstract

Rudapithecus hungaricus, a 10 million year old Miocene hominoid, has been proposed to be an arboreal quadruped with adaptations to below-branch suspension on the basis of its postcranial anatomy. One of these preserved postcranial elements is a partial innominate (RU 210), preserving much of the ilium and ischium. Previous work on trabecular architecture in the primate postcranial skeleton has suggested it may be possible to reconstruct locomotor loading on the basis of trabecular variables (notably anisotropy), though this type of analysis has not yet been extended to the innominate. Here we compare high-resolution X-ray computed tomography scans of the innominates of six extant primate taxa $(\mathrm{n}=28)$ to those of Rudapithecus to determine its closest locomotor analog. There were 11 volumes of interest that preserved sufficient trabecular bone for analysis in ImageJ and Quant3D, which were compared descriptively and statistically to homologous trabecular regions from the extant sample. From the external morphology of the innominate, Rudapithecus was predicted to have locomotor similarities to Pongo and Symphalangus. This prediction was tentatively supported by the trabecular architecture of the ilium and ischium.

### 4.2 Introduction

Rudapithecus hungaricus is a 10 million year old Miocene hominoid from the site of Rudabánya, Hungary (Begun 2010), which has been reconstructed as a generalized suspensory arboreal quadruped on the basis of its postcranial anatomy (a partial distal humerus and proximal ulna, phalanges, carpals, a nearly complete femur, and a partial pelvis), as well as the
morphology of its bony labyrinth. The distal humerus and proximal ulna tend to group quantitatively and qualitatively with those of extant hominoids, comprising an elbow joint that was both highly stable and mobile (Morbeck 1983, Begun 1992). The phalanges are long and strongly curved (Begun 1993) and of the published carpals, the scaphoid is most similar to that of Pongo (indicating greater mobility), while the capitate resembles the plesiomorphic hominoid condition, all of which suggest generalized arboreal capabilities with indications of enhanced mid-carpal mobility and suspensory behavior (Kivell \& Begun 2006, 2009). The other carpals also have features in common with the African apes and Pongo (Begun \& Kordos 2011). The femur has been described as having "many characters typical of great apes, including a large head, low neck-shaft angle, and a robust, curved and platymeric shaft" (Begun \& Kordos 2011: 86). In addition to analyses of postcrania, the morphology of the semicircular canal of Rudapithecus is also consistent with slower, less agile locomotor behavior, as it had a relatively small canal for its body mass (Ryan et al. 2012). This is not inconsistent with its reconstruction as a generalized arboreal quadruped with adaptations for suspension, as many of the other Miocene hominoids and the extant great apes are also characterized as being relatively less agile by Ryan et al. (2012).

The partial pelvis (RU210) is particularly important, as it is relatively complete (Figure 4.1). The largest preserved portion of pelvis is a partial left innominate (described as small, but morphologically similar to those of the great apes), including the acetabulum, most of the ischium (sans tuberosity), approximately half of the superior pubic ramus, and a widely flaring iliac blade broken at or near the level of the auricular surface (Begun \& Kordos 2007, Ward et al. 2008). The size of the acetabulum is similar to that of Ateles or Symphalangus and the length of the sacroiliac to hip joint measurement is similar to that of the hylobatids, as well, though the shape of the lower ilium itself has been described as being more primitive (Ward et al. 2008).

Rudapithecus is also suggested to have had a capacity for greater hip abduction than Ekembo nyanzae, further supporting the interpretation of suspensory arboreal locomotion (Hammond et al. 2013a).

While these reconstructions have largely relied on external bony morphology, another way to test this locomotor hypothesis is by examining the trabecular architecture of the innominate via high-resolution x-ray computed tomography (HRXCT). Trabeculae form the internal support structure of bone and change throughout life in response to the stresses placed on them (often referred to as Wolff's Law or more generally as bone functional adaptation) (Wolff 1892, Wolff 1986, Ruff et al. 2006). Thus, trabecular architecture may reflect a primate's locomotor behavior and history (Fajardo \& Müller 2001, MacLatchy \& Müller 2002, Fajardo et al. 2007, Abel \& Macho 2011, Barak et al. 2011, Barak et al. 2013). This general principle has been experimentally demonstrated in mammals and birds (Pontzer et al. 2006, van der Meulen et al. 2006, Barak et al. 2011), and in primates utilizing species-atypical locomotor behaviors. Volpato et al. (2008) examined the relationship between species-atypical locomotor behavior and iliac trabecular architecture in bipedally-trained Macaca fuscata, and found that the iliac trabeculae exhibit the expected remodeling response to atypical loading (i.e., the greater compressive loading of the ilium caused by adopting habitual orthograde postures results in denser, more anisotropic trabecular architecture along the paths that these forces take through the bone). This work demonstrates the plasticity of iliac trabecular architecture in non-human primates and suggests that the mechanical loading environment plays an important role in shaping it.

There has been relatively little work done on the pelvic trabecular architecture of fossil primates, except for Australopithecus africanus, Oreopithecus bambolii, and the Kebara 2 Neandertal, none of which has used HRXCT, but these studies have yielded interesting results nonetheless (Galichon \& Thackeray 1997, Rook et al. 1999, Martinon-Torres 2003). All three
studies focused on the ilium, and included both comparisons to modern human ilia and discussions of the implications of the fossil morphologies for bipedalism. The structural pattern described by Macchiarelli et al. $(1999,2001)$ for modern humans also occurs to a lesser degree in Au. africanus; they tend to show both an ilioischial and sacropubic bundle, as well as a trabecular chiasma (superior to the acetabulum, formed by the intersection of the ilioischial and sacropubic bundles), though the ilioischial bundle is not organized or defined to the degree that it is in modern human ilia and the trabecular chiasma is differently shaped (Galichon \& Thackeray 1997, Macchiarelli et al. 1999). They suggested that Au. africanus was likely bipedal, but potentially with a different mode than modern humans. This reconstruction was supported by more recent microCT work on the Au. africanus tibia (Barak et al. 2013). The trabecular architecture of Oreopithecus has also been analyzed and bipedal postures have been proposed based on its morphology and trabecular structure (Kohler \& Moya-Sola 1997, Rook et al. 1999). Its sacropubic and ilioischial bundles are described as being well defined and not fading into the marginal bundles, as occurs in monkeys and apes (Rook et al. 1999). Additionally, the densest area of the Oreopithecus ilium is the trabecular chiasma region, which is more developed than in any extant ape (aside from gorillas, whose large size likely accounts for this), though less developed than in humans or australopithecines (Rook et al. 1999). Given recent work on this species suggesting that it was not adapted to habitual bipedal locomotion (Russo \& Shapiro 2013), greater understanding of the relationship between locomotion and trabecular architecture is needed to clarify this issue. Martinon-Torres (2003) compared trabecular orientation above the acetabulum in humans, chimpanzees, and the Kebara 2 Neandertal. She found that humans and chimpanzees possessed subtle differences in the trabecular architecture of this region that could be explained by observed locomotor differences, and that the Neandertal pattern was quite similar to the human one, likely reflected their shared bipedal
locomotion (Martinon-Torres 2003). At the present time, no one has examined the trabecular architecture of the primate ischium, extant or otherwise.

This study is the first to assess the trabecular architecture of the Rudapithecus innominate (specifically the ilium and ischium, as the pubis is not preserved). The innominate of Rudapithecus is very important for evaluating the diversity of Miocene hominoid locomotor adaptations, as well as providing the evolutionary context for the rise of the locomotor regimes of the African ape and human lineages, particularly if one accepts the possibility that the African hominines evolved from a European ancestor (Begun et al. 2012). As Almécija et al. (2013) proposed in their paper on Orrorin tugenensis, why assume extant apes are the best model for early hominins when there are actual fossil apes that may more closely approximate the primitive pelvic morphology of early hominids/hominins? The aim of the project is to characterize the trabecular architecture of the innominate of Rudapithecus in comparative context via HRXCT and test the prevailing locomotor hypothesis for this taxon. Rudapithecus is predicted to exhibit trabecular patterns generally similar to those of Pongo and Symphalangus based on its proposed postcranial adaptations to deliberate climbing and suspension.

### 4.3 Methods

## Sample

Adult, wild-shot non-human primate specimens of both sexes were selected from collections at the National Museum of Natural History (NMNH), the American Museum of Natural History (AMNH), and the Penn Museum (UPenn). The extant sample comprised: Papio anubis $(\mathrm{n}=6)$, Symphalangus syndactylus $(\mathrm{n}=4)$, Pan troglodytes $(\mathrm{n}=5)$, Pongo pygmaeus $(\mathrm{n}=$ $5)$, and Macaca mulatta $(n=4)$. Human innominates $(n=3 / 4)$ came from the Texas Archaeological Research Laboratory (TARL) and were associated with mobile forager/hunter-
gatherer populations. As these specimens came from archaeological contexts, they varied in their degree of preservation; breaks in the cortical bone allowed sediment to get into several of the specimens, impacting their usefulness for CT analysis. This resulted in only three ilia and four ischia being suitable for analysis. The sample was chosen to represent a range of the diverse locomotor modes seen in extant primates, such that a good analog for Rudapithecus might be found. For full sample details, see Appendix A.

## CT Scanning

All specimens from extant taxa were scanned on the North Star Imaging (upgraded ACTIS) scanner at the High-Resolution X-ray Computed Tomography Facility at the University of Texas at Austin (UTCT). The innominates were mounted in foam and oriented vertically or subvertically (depending on specimen size and morphology) in the scanner. Serial transverse slices were collected covering the entire innominate. Specimens were scanned either in pairs or alone, depending on the sizes of the innominates. The scans were collected using FeinFocus energy source settings of 180 or 190 kV and $0.15,0.17,0.19$, or 0.3 mA , with $3600,12003,12004$, 15304, 17761, 18003, 18004, or 18013 projections (Appendix B). Rudapithecus was scanned on the ACTIS5 scanner at the Max Planck Institute for Evolutionary Anthropology. The entire innominate was scanned in serial transervse slices. The scans were collected using energy source settings of 130 kV and 0.1 mA with a 0.25 mm brass filter, in 2500 projections, and were reconstructed in Amira. Isotropic voxel sizes in the extant sample ranged from 0.0378-0.0793 mm , depending on the size of the specimen and represented the highest possible resolution given specimen size and scanning budget. Rudapithecus was scanned at an isotropic voxel size of 0.0324802 and reconstructed as 8 -bit TIFF grayscale images with a $2048 \times 2048$ pixel matrix. The 8-bit images of both the extant and fossils scans were used for all analyses in Quant3D (Ryan \& Ketcham 2002, Ketcham \& Ryan 2004).

## Volume of Interest Sampling and Analysis

Extant comparative CT data come from previously collected datasets on the ilium and ischium (see chapters 2 and 3, respectively, for sampling protocols). The Rudapithecus innominate was cropped and sampled according to these protocols, with the few slight modifications discussed below.

The Rudapithecus innominate was first visually assessed for trabecular preservation by opening the entire CT dataset and examining each of the slices in ImageJ (Rasband 1997-2016). While the majority of the trabecular architecture was too highly mineralized or too broken for analysis, two potential regions of intact trabecular architecture were identified: a smaller one in the lower ilium (approximately 6.12 mm in height) (Figure 4.2A) and a slightly larger one in the ischium (approximately 7.79 mm in height) (Figure 4.3A).

In order to obtain trabecular data comparable to the extant ilium dataset, the most superior slice of the well-preserved iliac region was found and the largest possible cubic volume of interest (VOI) was placed on it, such that only trabecular bone was included. The dimensions of the sides of the square then dictated the height of the sampling cube ( 3.05312 mm ). It was only possible to place a single (ventral) VOI within the superior-most set of CT slices due to both the size and preservation of the specimen. Within the next set of slices (inferior to the first VOI), three VOIs were sampled (medial, lateral, and ventral); no dorsal trabecular bone was suitable for sampling (Figure 4.2B). These four VOIs represent the only trabecular data from the Rudapithecus ilium. Then, to be able to align the sampled Rudapithecus VOI sets with the extant dataset and compare homologous anatomical regions, the total number of slices between the posterior inferior iliac spine (PIIS) and the top of the acetabulum was divided by the number of slices included in each set of Rudapithecus VOIs. If it had been possible to sample the entire ilium, there would likely have been approximately 14 sets of VOIs (the specimen is broken
around the level of the PIIS); as it stands, the four VOIs that exist represent sets 10 and 11 (i.e., closer to the top of the acetabulum than to the PIIS).

The protocol for cropping and sampling the ischium was similar to that of the ilium, in terms of locating the top of the region of well-preserved ischial trabeculae and choosing where to place the VOIs within it. For the ischium, three VOIs of 2.5984 mm were placed within each set of CT slices, sampling trabeculae from the ventral/anterior, central, and dorsal/posterior regions. Seven VOIs total were sampled, representing three sets of CT slices; three VOIs each came from the ventral and dorsal regions, while only a single central VOI could be sampled (Figure 4.3B). To align the Rudapithecus ischium with the extant data to compare homologous regions, a conservative estimate of the total possible number of CT sets was made based on where the ischium is broken. Given that it is likely only lacking its tuberosity, an estimate of nine sets was made; this means that the sampled sets would be numbers five to seven and represent more inferior ischial trabecular architecture (i.e., closer to the ischial tuberosity than to the acetabulum).

The cropped cubes for all specimens were analyzed using UTCT's free three-dimensional fabric analysis program, Quant3D (Ryan \& Ketcham 2002, Ketcham \& Ryan 2004), using the following parameters: centered spherical VOIs, iterative thresholding (Ridler \& Calvard 1978, Trussell 1979), and 513 uniform orientations with random rotation and dense vectors (Ketcham \& Ryan 2004). The star volume distribution method was used to compute anisotropy (Cruz-Orive et al. 1992). Bone volume fraction (BVTV) and degree of anisotropy (DA) were extracted from the program's output for comparison, as these two variables have been shown to explain more than 80\% of the variance in bone's mechanical properties (Goldstein et al. 1993, Maquer et al. 2015). Data Standardization and Analysis

The Rudapithecus sets were used as the reference for aligning the extant data. The BVTV
and DA values from the extant sample were scaled to the same relative anatomical locations as the Rudapithecus VOIs. The scaling was done by estimating the relative anatomical location (by percentage of total height) from which the CT sets from the Rudapithecus ilium and ischium containing usable trabecular bone came. For the ilium, those relative locations were $69.2 \%$ and $76.9 \%$ of total iliac height. For the ischium, those locations were $50 \%, 62.5 \%$, and $75 \%$ of total ischial length. The extant BVTV and DA data were then scaled via interpolation (where necessary) to match those anatomical locations, in order to compare homologous regions of trabecular bone. All raw data can be found in Appendix C and the data set used here for analysis can be found in Appendix D.iii.

The small size of the dataset from the Rudapithecus ilium precluded signficant statistical analyses, though the four VOIs were plotted against each other to check for correlations. As plotting the BVTV data for the ventral $76.9 \% \mathrm{VOI}$ onto the ventral $69.2 \% \mathrm{VOI}$ produced an $\mathrm{R}^{2}$ of 0.9229, the $69.2 \%$ VOI was discarded in favor of analyzing only the three VOIs from the $76.9 \%$ level. The high degree of correlation between the two VOIs is not surprising, as trabecular bone is an interconnected network and these two samples were taken very close together. Descriptive comparisons of the BVTV and DA between the three remaining VOls were made between the fossil and the extant taxa using dot plots created in BoxPlotR (Spitzer et al. 2014), and the BVTV and DA data for the VOIs were also plotted together, to examine the relationships between trabecular variables and the Cartesian space each taxon occupies. Additionally, a nonparametric one-way analysis of variance (Kruskal-Wallis test) was performed for both the BVTV and DA data to check for significant differences between species. All of the VOIs plotted (medial, lateral, and ventral) were pooled together for the analysis to improve sample size, as running individual ANOVAs by VOI would have only included a single VOI from Rudapithecus in each.

The ischium data were also analyzed in a series of Kruskal-Wallis tests (all VOIs together,
all ventral VOIs, and all dorsal VOIs, for both BVTV and DA), with post-hoc Dunn's tests using the Holm-Bonferroni adjustment used for pairwise comparisons between taxa. These tests were performed using the dunn.test R package (Dinno 2015). The decision to split the data into ventral and dorsal VOIs and analyze them separately was made after plotting the data, noting a consistent separation between ventral and dorsal VOIs in both BVTV and DA (dorsal > ventral), and then performing a Wilcoxon signed-rank test to determine if the ventral and dorsal VOIs differed significantly in BVTV and DA. Central VOIs were not tested separately, as there is only a single central VOI from Rudapithecus. The significant results were then plotted to visualize differences.

### 4.4 Results

llium
Dot plots were used to compare BVTV and DA between Rudapithecus and the extant sample, and scatterplots were used to visualize these two variables together for each VOI, with the expectation that primates using similar locomotor regimes would have similar trabecular architecture. While the Kruskal-Wallis ANOVA did not find significant differences between taxa for either BVTV or DA, given that only a single small region of preserved trabecular bone exists in the Rudapithecus ilium, it seemed worthwhile to show the data that exist regardless.

The position of Rudapithecus on the BVTV dot plots varied greatly, though generally there was a lot of interspecific overlap in BVTV. BVTV in the Rudapithecus medial VOI was relatively high (0.3396) compared to the extant sample, with only single specimens from Papio (0.3397), Macaca (0.3973), Symphalangus (0.3638), and Pongo (0.3737) having higher values (Figure 4.4A). Rudapithecus did not overlap with the ranges of Homo and Pan. Lateral BVTV was shifted upward in the extant sample relative to medial BVTV but with less intraspecific variation,
though it decreased in Rudapithecus (0.2804) (Figure 4.4B). Rudapithecus falls into the lower end of the Pongo range (0.2432-0.3538) and just below the lowest Papio data point (0.2844), but does not overlap with any of the other extant taxa. Rudapithecus ventral BVTV (0.2609) was within the lower range of Macaca (0.2466-0.5015) and the upper range of Pongo (0.17000.2681 ), and was close to the median values for Pan (0.2761) and Symphalangus (0.2710) (Figure 4.4C). The plot of ventral BVTV included the fewest extant specimens, as variation in lower iliac morphology affected trabecular sampling in a number of taxa (most notably Papio). Pongo is the only taxon that Rudapithecus overlaps at all three VOI locations, while it never overlaps with Homo. It overlaps with Macaca and Symphalangus at the medial and ventral VOI locations, while the other taxa (Papio and Pan) it only overlaps at one VOI location.

Generally, the dot plots of DA had very large ranges of intraspecific variation, which should be considered in the interpretation of these results. Rudapithecus medial DA (2.474) is relatively low (isotropic) in comparison to extant taxa, overlapping with the lower ranges of Papio (2.117-4.659), Macaca (2.027-4.458), Symphalangus (1.595-3.807), and Pongo (2.3477.068), and falling close to the median for Homo (2.261) (Figure 4.5A). Lateral DA had even greater intraspecific variation than medial DA and was generally higher, though the DA of Rudapithecus remained relatively low (2.199) (Figure 4.5B). Lateral DA in Rudapithecus overlapped with the low end of the Homo range (1.893-7.194) and was similar to the Macaca median (2.210); it did not overlap with any of the other taxa. Ventral DA had less intraspecific variation than medial and lateral DA, likely due to the sampling issue mentioned above. Rudapithecus ventral DA (3.611) was similar to that of the single Papio specimen (3.649), and overlapped with the upper ranges of Pan (2.287-4.253) and Symphalangus (2.782-4.323), and with the lower range of Pongo (3.009-4.706) (Figure 4.5C). Rudapithecus did not overlap with any of the extant taxa at all three VOI locations, but did with five of them at two: Homo (medial,
lateral); Papio (medial, ventral); Macaca (medial, lateral); Symphalangus (medial, ventral); and Pongo (medial, ventral). The only taxon that Rudapithecus did not overlap with at two VOI locations was Pan.

Three scatterplots of BVTV and DA were generated to visualize the space occupied by the trabecular architecture of each of the VOIs, allowing Rudapithecus to be placed in comparative context. The medial VOI plot produced a similar outcome to the dot plots; there is a great deal of overlap between taxa in BVTV and DA at this VOI location, particularly in the region bounded by 0.2-0.35 on the x-axis (BVTV) and 2-4 on the y-axis (DA) (Figure 4.6A). Every polygon representing extant taxa intersects with all of the other polygons. Rudapithecus falls on the edge of the region defined by the Symphalangus data points, though the closest actual specimen to it is Papio. The lateral scatterplot showed a bit more separation between taxa; not all of the polygons intersect with each other (Figure 4.6B). The extant taxon that overlaps with the fewest other taxa is Pongo; it only overlaps the Homo and Papio regions. Rudapithecus is closest to Pongo and Macaca (two specimens of each). It also occupies the lowest combined BVTV and DA position. The scatterplot of the ventral VOI data produced the greatest separation between taxa, with the hominoids (including Rudapithecus) forming a cluster distinct from Macaca and the single Papio specimen (Figure 4.6C). Some of separation is likely due to the smaller sample size for this VOI; however, the results are still potentially informative. Pan is the only taxon that truly intersects with other species (Pongo, Symphalangus, and Homo), though one of the Homo specimens does graze one of the edges of the Symphalangus region. The Macaca region occupies the highest combined BVTV and DA location, and is completely distinct from all of the other taxa. Rudapithecus falls within the Symphalangus region and just touches one of the lines bounding the Pan region.

In considering the three plots together, Rudapithecus is within the boundaries of (or is
on the boundary of) the Symphalangus region in the medial and ventral VOI plots, barely touches the Pan line on the ventral VOI plot, and is closest to Pongo and Macaca on the lateral VOI plot.

Ischium

For all of the VOIs combined (ventral, central, and dorsal from the $0.5,0.625$, and 0.75 height levels), Rudapithecus BVTV is significantly different from Macaca, Pan, Papio, and Pongo, but not from Homo or Symphalangus (Kruskal-Wallis: $\chi^{2}=53.9653, p<0.001$; post-hoc HolmBonferroni adjusted Dunn's test: $\mathrm{p}<0.05$, Table 4.1). This is shown in Figure 4.7 as a plot of the minimum and maximum BVTV values (regardless of VOI location) from each taxon at each of the three height levels, enabling the visual comparison of the BVTV ranges for each species. While there were also significant differences in DA between taxa, none of the pairwise comparisons between Rudapithecus and the other taxa were significant. This is potentially due to sample size.

A pair of analyses comparing ventral to dorsal BVTV and DA were both significant (Wilcoxon signed rank tests: $\mathrm{p}<0.001$, Table 4.2), suggesting that each region should be analyzed separately to more specifically determine where the differences and similarities between Rudapithecus and the other taxa lie.

In analyzing only the ventral VOIs, it was found that Rudapithecus has significantly different BVTV from Macaca and Pan, but not from Homo, Papio, Pongo, or Symphalangus (Kruskal-Wallis: $\chi^{2}=39.0282, \mathrm{p}<0.001$; Holm-Bonferroni adjusted Dunn's test: $\mathrm{p}<0.05$, Table 4.3). This is shown in Figure 4.8 as a plot of the minimum and maximum ventral BVTV values from each taxon at each of the three height levels, enabling the visual comparison of the ventral BVTV ranges for each species. While there were also significant differences in DA between taxa, none of the pairwise comparisons between Rudapithecus and the other taxa were significant. This is potentially due to sample size.

In analyzing only the dorsal VOIs, it was found that Rudapithecus has significantly different BVTV from Macaca and Pongo, but not from Homo, Papio, Pan, or Symphalangus (Kruskal-Wallis: $\chi^{2}=21.6606, \mathrm{p}<0.001$; Holm-Bonferroni adjusted Dunn's test: $\mathrm{p}<0.05$, Table 4.4, Figure 4.9). While there were also significant differences in DA between taxa, none of the pairwise comparisons between Rudapithecus and the other taxa were significant. This is potentially due to sample size.

To summarize the results: Rudapithecus is significantly different from some extant taxa in BVTV, but not in DA. Which taxa are significantly different differ when considering all of the VOIs together versus only the ventral VOIs versus only the dorsal VOIs, though Rudapithecus never significantly differs from Homo or Symphalangus. Rudapithecus is always significantly different from Macaca, but is only significantly different from Pan in the ventral VOIs and from Pongo in the dorsal VOIs; the difference with Papio must be driven by the central VOIs.

### 4.5 Discussion

In this study, trabecular bone microstructural properties were used to test a locomotor hypothesis for the Miocene ape Rudapithecus hungaricus by comparing these properties to those of the trabecular architecture of extant primate taxa of known locomotor mode. The Rudapithecus innominate was predicted to have trabecular architecture similar to that of Pongo and Symphalangus on the basis of its proposed locomotor regime (generalized arboreal quadrupedalism with adaptations for suspension) and external pelvic morphology. As is often the case both in studies investigating the correlation between trabecular architecture and locomotion (e.g., DeSilva \& Devlin 2012, Fajardo et al. 2013, Kuo et al. 2013, Su et al. 2013), and in studies of the morphological affinities of Miocene apes (e.g., Rook et al. 1999, Hammond et al. 2013, Russo \& Shapiro 2013, Morgan et al. 2015), the results of this study are equivocal.

## Trabecular Architecture in the Ilium

In the ilium, there were no statistically significant differences in BVTV or DA between taxa. This could be a result of the small sample of Rudapithecus trabecular bone used in the analyses and/or an artifact of preservation issues affecting this sample, or it could reflect a real lack of difference in trabecular architecture at this location in the ilium. Given the limitations that exist when conducting these kinds of analyses on fossils and that lower iliac cross-sectional area has been shown to be an adaptation to locomotor loading (Lewton 2010), the results of these trabecular analyses are worth describing, in spite of the lack of significant differences.

The only taxon that Rudapithecus falls within the BVTV range of at all three VOI locations (medial, lateral, and ventral) is Pongo, which is consistent with locomotor predictions. In order of decreasing similarity, Rudapithecus falls within the BVTV range of the other taxa at the following number of VOI locations: Symphalangus and Macaca (2), Pan and Papio (1), and Homo (0). This order is also fairly consistent with locomotor predictions (Symphalangus is a relatively smallbodied suspensory ape and Macaca is a competent above-branch arboreal/generalized quadruped), though BVTV has not typically been found to be highly correlated with locomotor mode (e.g., MacLatchy \& Müller 2002, Griffin et al. 2010, Fajardo et al. 2013). In terms of general BVTV patterns in the ilium, it is interesting to note that Rudapithecus has higher medial than lateral BVTV; this is the opposite of the pattern seen in all of the extant taxa, which again suggests that a preservation issue exists, given how consistent the pattern is across all locomotor regimes.

In terms of DA, there was a great deal of variation within each taxon and overlap between taxa, particularly in the medial and lateral VOIs, as they had larger samples than the ventral VOI. In comparative context, the Rudapithecus medial VOI was relatively isotropic, as were the lateral and ventral VOIs, though the ventral VOI had a higher DA than the other two.

Unlike the case for BVTV, Rudapithecus did not fall into the ranges of any of the extant taxa at all three VOI locations, but it did with five of the taxa at two: Homo and Macaca in the medial and lateral VOIs; and Papio, Symphalangus, and Pongo in the medial and ventral VOIs. The only taxon that Rudapithecus did not overlap with the range of at two VOI locations was Pan (ventral only). This high degree of overlap in DA makes these results difficult to interpret, which is unfortunate because anisotropy has been found to correlate with locomotor categories in previous studies (e.g., Fajardo \& Müller 2001, Maga et al. 2006, Saparin et al. 2011, Ryan \& Shaw 2012, Su et al. 2013). What may be suggested by these results is that the general similarity in median medial DA might indicate that the forces acting on the medial ilium may be less differentiated by locomotor mode than those acting on the ventral and lateral ilium. In the ventral VOI, Rudapithecus has slightly higher DA than Homo, but lower DA than Macaca. Previous work on loading in the ilium (Lewton 2015, and chapter 2) suggests that this might indicate that the Rudapithecus ventral ilium was not subject to strong compressive loading (as is seen in Macaca). Rudapithecus falling within the ranges of ventral DA of Papio, Pan, Symphalangus, and Pongo is somewhat consistent with locomotor predictions, but does not suggest a specific similarity to one taxon over another. In the lateral VOI, Rudapithecus DA is not like that of Papio, Pan, Symphalangus, or Pongo, but it is similar to that of Macaca and overlaps with the very bottom of the Homo range. The similarity to Macaca is consistent with locomotor predictions, but given the relationship of medial to lateral BVTV mentioned above and what it likely means in terms of trabecular preservation, interpreting this similarity further seems unfounded.

Plotting BVTV and DA together to visualize the space occupied by each taxon for each VOI location yielded somewhat more easily interpretable results. To summarize the three plots: Rudapithecus is within the boundaries of (or is on the boundary of) the Symphalangus region in the medial and ventral VOI plots, barely touches the Pan line on the ventral VOI plot, and is
closest to Pongo and Macaca on the lateral VOI plot. Considering BVTV and DA together is important, as the two properties are part of a single system working to optimize a bone's trabecular network, in terms of both mechanical strength and metabolic efficiency (Weinans et al. 1992, Huiskes et al. 2000, Tanck et al. 2001). This means that BVTV and DA are potentially complementary; trabecular density does not have to be high if trabeculae are strongly anisotropic and vice versa (Weinans et al. 1992, Tanck et al. 2001). Developmentally, this optimization seems to occur through the selective resorption of previously laid down dense, isotropic trabecular bone, which leaves behind more efficient (anisotropic) trabecular architecture along the axes of loading, but it also occurs in response to patterns of use/disuse via the signaling of osteocytes by mechanical loading (Huiskes et al. 2000, Tanck et al. 2001, Cunningham \& Black 2009, Acquaah et al. 2015). Preservation issues aside, when BVTV and DA are considered together for Rudapithecus, its iliac trabecular architecture most closely resembles that of Symphalangus, with additional similarities to Pongo, Macaca, and Pan. This is not inconsistent with its predicted locomotor regime.

## Trabecular Architecture in the Ischium

While significant differences in BVTV between Rudapithecus and the extant taxa were found in the more well-sampled, well-preserved ischium, no significant differences were found in DA (between Rudapithecus and the extant taxa) in any of the analyses (which may be a result of sample size). Again, this is complicates the interpretation of the results, as DA has been correlated with locomotion and BVTV has not (Fajardo \& Müller 2001, MacLatchy \& Müller 2002, Maga et al. 2006, Griffin et al. 2010, Saparin et al. 2011, Ryan \& Shaw 2012, Fajardo et al. 2013, Su et al. 2013). In the "all VOIs" analysis (including ventral, central, and dorsal VOIs grouped together), Rudapithecus was significantly different from Macaca, Pan, Papio, and Pongo, but not from Homo or Symphalangus. In the analysis of only the ventral VOIs, Rudapithecus differed
from Macaca and Pan, but not from Homo, Papio, Pongo, or Symphalangus. In the analysis of the dorsal VOIs, Rudapithecus differed from Macaca and Pongo, but not from Homo, Papio, Pan, or Symphalangus. Generally, Rudapithecus never differs significantly from Homo or Symphalangus, but is always different from Macaca. The difference with Papio in the "all VOIs" analysis is driven by the central VOIs (of which there are fewer sampled), while the differences between Rudapithecus and Pan, and Rudapithecus and Pongo are driven by the ventral and dorsal VOIs, respectively. The lack of significant differences with Symphalangus is consistent with locomotor predictions.

Perhaps the best way to consider these results is in terms of the consistent similarities and differences between Rudapithecus and the extant taxa. Rudapithecus' lack of significant differences from Homo and Symphalangus is likely due to its relatively high BVTV and the small range of variation seen in this trabecular measure (Figures 4.7, 4.8, 4.9). Both Homo and Symphalangus also have relatively high BVTV and narrow ranges of variation in comparison to the other taxa as well. This may be partially influenced by sample size (both $n=4$ ), though Macaca has the same sample size and a much wider range of variation in BVTV (which is likely what is driving the finding of consistent significant differences between this taxon and Rudapithecus, along with Macaca's lower minimum BVTV values).

There is one possible functional explanation for the similarities (or, the lack of significant differences) between Rudapithecus, Homo, and Symphalangus. Assuming that the preserved Rudapithecus trabecular bone accurately represents the trabecular architecture as it was in life, none of these taxa seem to load their ischia in ways that require substantial resorption of trabeculae (in favor of maximizing efficiency via anisotropy - though this would be atypical for Homo, as they tend to be anisotropic relative to other hominoids [Ryan \& Shaw 2015]), leaving them with the combination of high BVTV and low DA (Weinans et al. 1992, Huiskes et al. 2000,

Tanck et al. 2001, Acquaah et al. 2015). High BVTV in these taxa could be explained by a decrease in hamstring loading; this muscle group originates on the ischial tuberosity (Anemone 1993), is involved in hip flexion and leg extension (as in powerful climbing), and similarities in gross musculature and muscle moment arms have been identified between gibbons and humans (Payne et al. 2006a, 2006b). It has been suggested that the relatively short ischia of hylobatids and humans is related to their affinities for bipedality and/or the lack of need for a longer lever arm to provide mechanical advantage for the hamstrings (Waterman 1929, Yirga 1987). However, Rudapithecus does not appear to have a similarly proportionally short ischium, though it is impossible to be certain, as both the ischium and ilium are broken, preventing total length measurements from being taken. If Rudapithecus does not have external ischial morphology like that of Homo and Symphalangus, and given that its BVTV appears to be relatively high, then perhaps the most plausible explanation for the lack of significant differences between the fossil and extant taxa is that Rudapithecus has artificially high BVTV due to preservation issues.

## Locomotion in Rudapithecus and Broader Implications

Considering the results of the analyses of the ilium and ischium together suggest that Rudapithecus loaded its innominate in ways that produced trabecular architecture with the greatest similarity to that of Symphalangus, with some additional resemblance to that of Pongo, though it does not consistently plot with any single taxon to the exclusion of all others. While some of this resemblance is based on BVTV (which has not been shown to correlate with locomotor regime), the DA data from the ilium do contribute to the similarity (and proposed locomotion), as well (Fajardo \& Müller 2001, MacLatchy \& Müller 2002, Maga et al. 2006, Griffin et al. 2010, Saparin et al. 2011, Ryan \& Shaw 2012, Fajardo et al. 2013, Su et al. 2013). It is also possible that iliac trabecular architecture (specifically DA) carries a stronger signal of specific locomotion than ischial trabecular architecture does (which is consistent with the findings of
chapters 2 and 3 of this dissertation).

The resemblance to Symphalangus and Pongo is consistent with the locomotor regime of generalized suspensory arboreal quadrupedalism predicted for Rudapithecus. The similarities between Rudapithecus and Symphalangus do not necessarily suggest that Rudapithecus was brachiating in the way that a modern siamang would, but rather than it may have had similar levels of hindlimb loading and/or utilized orthograde postures. However, it would not be inconceivable for a Miocene hominoid to be somewhat more gibbon-like in locomotion (at least in terms of below-branch suspension), as the recent discovery of Pliobates cataloniae (which, at 11.6 million years old is older than Rudapithecus) indicates that suspensory adaptations in the wrist may be homologous among stem hominoids (Alba et al. 2015).

The reconstruction of Rudapithecus as a generalized arboreal quadruped with suspensory adaptations can also be discussed in the context of the evolution of the primate pelvis, and in terms of the evolution of hominoid locomotion. Generally, the primate pelvis is characterized by high levels of evolvability and low levels of integration (Grabowski et al. 2011, Lewton 2012). This suggests that major morphological changes (like the transition from a quadrupedal hominoid pelvis to that of a biped) could happen relatively quickly (Lewton 2012) and it creates a situation that potentially favors homoplasy. This is particularly important, as Miocene hominoid taxa with preserved postcranial and pelvic remains (like Pierolapithecus catalaunicus and Sivapithecus indicus) are often described as having mosaic morphologies (combining both primitive and derived traits in their postcranial skeleton) suggesting locomotor regimes that lack extant analogs, and making it difficult to resolve hominoid phylogeny (Hammond et al. 2013b, Alba et al. 2015, Morgan et al. 2015). What is clear from the Miocene fossil record is that the hominoids of that time (including Rudapithecus) did not have particularly chimpanzee-like postcrania (and pelves, specifically), suggesting that the morphology of Pan
does not represent ancestral hominoid pelvic anatomy or locomotor regime (White et al. 2009, Almécija et al. 2013).

The locomotor interpretation of Rudapithecus is also supported by paleoecological reconstructions of the Rudabánya 2 site as a forested lake margin/swamp environment with a subtropical climate (Kordos \& Begun 2002, Bernor et al. 2003, Bernor et al. 2004, Daxner-Hock 2005, Merceron et al. 2007, Andrews \& Cameron 2010). These reconstructions are based on multiple lines of evidence, all of which indicate that the Rudabánya 2 site was likely the type of forested environment that could support arboreal primates. The preserved stratigraphy of the site and the various site formation processes that produced the layers of mud, marl, lignite, and clay found there suggest the presence of swamp-like conditions and vegetation during the periods in which Rudapithecus was present (Andrews \& Cameron 2010). This vegetation included hackberry (Celtis) and swamp cypress (Taxodium), as well as other warm-temperate/subtropical taxa, and several of the site's layers contain substantial amounts of wood (Kordos \& Begun 2002, Andrews \& Cameron 2010). The composition of the faunal assemblage collected at the site also suggests that it was a humid forested environment, as it contains (in addition to primates) sciurids, glirids, beavers, and bunodont suids (Kordos \& Begun 2002, Bernor et al. 2004, DaxnerHock 2005, Andrews \& Cameron 2010). The dental meso- and microwear patterns of the herbivores from the site are consistent with those of traditional browsers and mixed feeders (browsers/grazers), leading to paleoenvironmental interpretations of dense forest with restricted clearings proximal to the site itself (Merceron et al. 2007), potentially with more open habitats distal to the site (Bernor et al. 2003). Given the high degree of arboreality of both Symphalangus and Pongo, and the similarities found between Rudapithecus and these taxa, the presence of Rudapithecus in a densely forested environment is consistent with its proposed locomotor regime.

## Potential Issues

It is important to note that the results here are based on a small amount of preserved trabecular bone and to be cognizant of the preservation issues that may have affected these results. Trabecular analyses of fossilized bone are complicated by a number of factors, both at the level of the fossil itself and at the methodological level. At the level of the fossil itself, breakage and deformation resulting in the loss of trabecular connections can affect the accurate quantification of both BVTV and DA. Breaks in a fossil may also allow matrix to fill in the intertrabecular spaces, which, if the matrix is a similar radiodensity to bone, may mean that it is impossible to differentiate bone from matrix in the scans. At the methodological level, even studies of trabecular bone in non-fossil specimens often produce equivocal results because these types of analyses are sensitive to differences in VOI location and size, as well as scan resolution (Kivell et al. 2011). For fossils, these methodological issues are compounded by those unique to CT scanning, e.g., trabeculae can vary in their degree of mineralization, affecting their radiodensity, which, in turn, affects their ability to be measured accurately by the scanner (Scherf 2008, Scherf \& Tilgner 2009). Various fossilization processes can influence this, such as the coating of trabeculae by dissolved minerals in groundwater, leading to their thickening and producing artificially high BVTV values (Scherf 2013). This is a possible issue in the Rudapithecus innominate, given its relatively high BVTV.

### 4.6 Conclusion

This study is the first to analyze the trabecular bone of the Rudapithecus innominate in an attempt to reconstruct locomotion in this Miocene ape. While it should be stressed that these conclusions are based on a small sample (both in terms of taxonomic breadth, number of specimens, and quantity of trabecular bone), these analyses do provide some support for

Rudapithecus being a generalized arboreal quadruped with suspensory adaptations. This study also suggests that even small amounts of preserved trabecular bone may be useful for investigating locomotion in fossil taxa, which may be very important for fragmentary fossils that do not preserve much distinctive morphology and/or for fossil taxa whose morphology lacks an extant analog. Two potentially interesting Miocene hominoid taxa (with preserved partial innominates) to target for scanning are Pierolapithecus catalaunicus (Hammond et al. 2013b) and Sivapithecus indicus (Morgan et al.2015), as both have been reconstructed as having locomotor repertoires including arboreal quadrupedalism and some amount of orthogrady/suspension. They would also provide interesting locomotor context for Rudapithecus. Future work in the area of reconstructing locomotion in fossil primates should include more CT scanning of extant and fossil taxa, as well as continued work on the relationship between loading patterns, external morphology, and trabecular architecture.

Table 4.1. Pairwise differences between species by bone volume fraction (BVTV) in all volumes of interest (VOIs) from the ischium (all levels, all VOI locations combined sample) resulting from a Holm-Bonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. As the decision to reject the null hypothesis in a sequential test depends on the ordering of the comparisons as well as on the $p$-values, significant adjusted $p$-values are in bold. Comparisons between Rudapithecus and extant taxa are highlighted. Results of the Kruskal-Wallis test: $\chi^{2}=53.9653, p<0.001$. BVTV in Rudapithecus is significantly different at the adjusted p < 0.05 level from Macaca, Pan, Papio, and Pongo, but not from Homo or Symphalangus.

|  | Homo | Macaca | Pan | Papio | Pongo | Rudapithecus |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Macaca | $<\mathbf{0 . 0 0 1}$ | - | - | - | - | - |
| Pan | $\mathbf{0 . 0 0 2 1}$ | 0.2366 | - | - | - | - |
| Papio | $\mathbf{0 . 0 1 0 1}$ | 0.0632 | 0.5030 | - | - | - |
| Pongo | $<\mathbf{0 . 0 0 1}$ | 0.2820 | 0.2770 | 0.1594 | - | - |
| Rudapithecus | 0.3526 | $<\mathbf{0 . 0 0 1}$ | $\mathbf{0 . 0 0 1 1}$ | $\mathbf{0 . 0 0 3 3}$ | $<\mathbf{0 . 0 0 1}$ | - |
| Symphalangus | 0.2998 | $\mathbf{0 . 0 0 1 5}$ | 0.1570 | 0.2945 | $\mathbf{0 . 0 0 5 1}$ | 0.0664 |

Table 4.2. Results of two Wilcoxon signed-rank tests comparing bone volume fraction and degree of anisotropy between paired ventral and dorsal volumes of interest across all species. Significant results are indicated in bold.

| Trabecular <br> variable | N | Ventral medians | Dorsal medians | p -value |
| :---: | :---: | :---: | :---: | :---: |
| Bone volume <br> fraction | 87 | 0.2806 | 0.3552 | $<0.001$ |
| Degree of <br> anisotropy | 87 | 2.2048 | 3.0737 | $<0.001$ |

Table 4.3. Pairwise differences between species by bone volume fraction (BVTV) in all ventral volumes of interest (VOIs) from the ischium (all levels combined) resulting from a HolmBonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. As the decision to reject the null hypothesis in a sequential test depends on the ordering of the comparisons as well as on the p-values, significant adjusted p-values are in bold. Comparisons between Rudapithecus and extant taxa are highlighted. Results of the Kruskal-Wallis test: $\chi^{2}=39.0282, p<0.001$. Rudapithecus has significantly different ventral BVTV at the adjusted $\mathrm{p}<0.05$ level from Macaca and Pan, but not from Homo, Papio, Pongo, or Symphalangus.

|  | Homo | Macaca | Pan | Papio | Pongo | Rudapithecus |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Macaca | $<\mathbf{0 . 0 0 1}$ | - | - | - | - | - |
| Pan | $<\mathbf{0 . 0 0 1}$ | 0.8947 | - | - | - | - |
| Papio | $\mathbf{0 . 0 1 4 0}$ | 0.2538 | 0.6442 | - | - | - |
| Pongo | $\mathbf{0 . 0 0 2 9}$ | 0.7302 | 0.2989 | 0.7357 | - | - |
| Rudapithecus | 0.5196 | $\mathbf{0 . 0 0 3 2}$ | $\mathbf{0 . 0 1 2 0}$ | 0.0694 | 0.0266 | - |
| Symphalangus | 0.7061 | $\mathbf{0 . 0 0 3 3}$ | $\mathbf{0 . 0 2 0 2}$ | 0.2397 | 0.0718 | $\mathbf{0 . 7 4 2 3}$ |

Table 4.4. Pairwise differences between species by bone volume fraction (BVTV) in all dorsal volumes of interest (VOIs) in the ischium (all levels combined) resulting from a Holm-Bonferroni adjusted Dunn's test post-hoc to a Kruskal-Wallis test. As the decision to reject the null hypothesis in a sequential test depends on the ordering of the comparisons as well as on the pvalues, significant adjusted p-values are in bold. Comparisons between Rudapithecus and extant taxa are highlighted. Results of the Kruskal-Wallis test: $\chi^{2}=21.6606, p<0.001$. Rudapithecus has significantly different dorsal BVTV at the adjusted p < 0.05 level from Macaca and Pongo, but not from Homo, Papio, Pan, or Symphalangus.

|  | Homo | Macaca | Pan | Papio | Pongo | Rudapithecus |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Macaca | 0.1173 | - | - | - | - | - |
| Pan | 1.0000 | 0.4038 | - | - | - | - |
| Papio | 1.0000 | 0.4188 | 0.4824 | - | - | - |
| Pongo | $\mathbf{0 . 0 1 5 9}$ | 1.0000 | 0.1142 | 0.1004 | - | - |
| Rudapithecus | 0.5466 | $\mathbf{0 . 0 1 8 9}$ | 0.2215 | 0.2098 | $\mathbf{0 . 0 0 4 6}$ | - |
| Symphalangus | 1.0000 | 0.5396 | 1.0000 | 0.8920 | 0.2306 | 0.2227 |

Figure 4.1. (A) Ventromedial, (B) lateral, (C) dorsal, and (D) dorsomedial views of RU 210, a partial left innominate of Rudapithecus hungaricus.


Figure 4.2. (A) Three-dimensional CT reconstruction of the RU 210 lower ilium, rotated to show the orientation in which the upper limit was cropped. The red box represents the approximate location from which the volumes of interest were sampled (not to scale). (B) Volume of interest locations in transverse view from the set of slices that preserve the greatest quantity of trabecular bone.


Figure 4.3. (A) Three-dimensional CT reconstruction of the RU 210 ischium, rotated to show the orientation in which the upper limit was cropped. The red box represents the approximate location from which the volumes of interest were sampled (not to scale). (B) Volume of interest locations in transverse view from the inferior-most set of slices.


Figure 4.4. (A) Interspecific comparison of bone volume fraction in the medial volume of interest from the lower ilium. (B) Interspecific comparison of bone volume fraction in the lateral volume of interest from the lower ilium. Center lines show the medians.


B


Figure 4.4. (C) Interspecific comparison of bone volume fraction in the ventral volume of interest from the lower ilium. Center lines show the medians.


Figure 4.5. (A) Interspecific comparison of degree of anisotropy in the medial volume of interest from the lower ilium. (B) Interspecific comparison of degree of anisotropy in the lateral volume of interest from the lower ilium. Center lines show the medians.

A


B


Figure 4.5. (C) Interspecific comparison of degree of anisotropy in the ventral volume of interest from the lower ilium. Center lines show the medians.


Figure 4.6. (A) Interspecific comparison of bone volume fraction by degree of anisotropy in the medial volume of interest from the lower ilium.

A


- Rudapithecus
- Papio
- Symphalangus
- Pan
+ Pongo
* Macaca
- Homo

Figure 4.6. (B) Interspecific comparison of bone volume fraction by degree of anisotropy in the lateral volume of interest from the lower ilium.


Figure 4.6. (C) Interspecific comparison of bone volume fraction by degree of anisotropy in the ventral volume of interest from the lower ilium.

C


Figure 4.7. Minimum and maximum ischial bone volume fraction (BVTV) values (regardless of volume of interest location [ventral, central, dorsal]) from each taxon at each of the three height levels ( $0.5,0.625,0.75$ ), enabling the visual comparison of the BVTV ranges for each species. The upper line for each species represents the maximum BVTV values, while the lower line represents the minimum values. Rudapithecus has relatively high BVTV compared to the extant taxa.


Figure 4.8. Minimum and maximum ventral bone volume fraction (BVTV) values from each taxon at each of the three height levels $(0.5,0.625,0.75)$, enabling the visual comparison of the ventral BVTV ranges for each species. The upper line for each species represents the maximum BVTV values, while the lower line represents the minimum values. Rudapithecus is represented by a single line, as there are only three ventral volumes of interest preserved in the ischium. Rudapithecus has relatively high BVTV compared to the extant taxa.


Figure 4.9. Minimum and maximum dorsal bone volume fraction (BVTV) values from each taxon at each of the three height levels $(0.5,0.625,0.75)$, enabling the visual comparison of the dorsal BVTV ranges for each species. The upper line for each species represents the maximum BVTV values, while the lower line represents the minimum values. Rudapithecus is represented by a single line, as there are only three dorsal volumes of interest preserved in the ischium. Rudapithecus has relatively high BVTV compared to the extant taxa.


## References

Abel R, Macho GA. 2011. Ontogenetic changes in the internal and external morphology of the ilium in modern humans. Journal of Anatomy 218:324-335.
Acquaah F, Brown KA, Ahmed F, Jeffery N, Abel RL. 2015. Early trabecular development in human vertebrae: Overproduction, constructive regression, and refinement. Frontiers in Endocrinology 6:67.
Alba DM, Almécija S, DeMiguel D, Fortuny J, de los Ríos MP, Pina M, Robles JM, Moyà-Solà S. 2015. Miocene small-bodied ape from Eurasia sheds light on hominoid evolution. Science 350:aab2625.
Almécija S, Tallman M, Alba DM, Pina M, Moyà-Solà S, Jungers WL. 2013. The femur of Orrorin tugenensis exhibits morphometric affinities with both Miocene apes and later hominins. Nature Communications 4:2888.
Andrews P, Cameron D. 2010. Rudabànya: Taphonomic analysis of a fossil hominid site from Hungary. Palaeogeography, Palaeoclimatology, Palaeoecology. 297:311-329.
Anemone RL. 1993. The functional anatomy of the hip and thigh in primates, in: Postcranial Adaptation in Nonhuman Primates. Gebo DL, ed. Northern Illinois University Press, DeKalb: 150-174.
Barak MM, Lieberman DE, Hublin JJ. 2011. A Wolff in sheep's clothing: trabecular bone adaptation in response to changes in joint loading orientation. Bone 49:1141-1151.
Barak MM, Lieberman DE, Raichlen D, Pontzer H, Warrener AG, Hublin J.J. 2013. Trabecular evidence for a human-like gait in Australopithecus africanus. PLoS ONE, 8, e77687.
Begun DR. 1992. Phyletic diversity and locomotion in primitive European hominids. American Journal of Physical Anthropology 87:311-340.
Begun DR. 1993. New catarrhine phalanges from Rudabánya (Northeastern Hungary) and the problem of parallelism and convergence in hominoid postcranial morphology. Journal of Human Evolution 24:373-402.
Begun DR. 2010. Miocene hominids and the origins of the African apes and humans. Annual Review of Anthropology 39:67-84.
Begun DR, Kordos L. 2007. New skeletal elements of Dryopithecus brancoi from Rudabánya, Hungary. American Journal of Physical Anthropology 132:71.
Begun DR, Kordos L. 2011. New postcrania of Rudapithecus hungaricus from Rudabánya (Hungary). American Journal of Physical Anthropology 144:86.
Begun DR, Nargolwalla MC, Kordos L. 2012. European Miocene hominids and the origin of the African ape and human clade. Evolutionary Anthropology: Issues, News, and Reviews. 21:10-23.
Bernor RL, Armour-Chelu M, Kaiser TM, Scott RS. 2003. An evaluation of the late MN 9 (Late Miocene, Vallesian age) Hipparion assemblage from Rudabánya (Hungary): Systematic background, functional anatomy and paleoecology. Coloquios de Paleontología. 1(2003):35-45.
Bernor RL, Kordos L, Rook L, Agusti J, Andrews P, Armour-Chelu M, Begun DR, Cameron DW, Damuth J, Daxner-Höck G, De Bonis L. 2004. Recent advances on multidisciplinary research at Rudabánya, Late Miocene (MN9), Hungary: A compendium. Palaeontographia Italica 89:3-36.
Cruz-Orive LM, Karlsson LM, Larsen SE, Wainschtein F. 1992. Characterizing anisotropy: a new concept. Micron and Microscopic Acta 23:75-76.
Cunningham CA, Black SM. 2009. Anticipating bipedalism: trabecular organization in the newborn ilium. Journal of Anatomy 214:817-829.

Daxner-Höck GU. Eomyidae and Gliridae from Rudabánya. 2005. Palaeontographia Italica 90:14355.

DeSilva JM, Devlin MJ. 2012. A comparative study of the trabecular bony architecture of the talus in humans, non-human primates, and Australopithecus. Journal of Human Evolution 63:536-51.
Dinno A. 2015. Nonparametric pairwise multiple comparisons in independent groups using Dunn's test.
Fajardo RJ, Desilva JM, Manoharan RK, Schmitz JE, Maclatchy LM, Bouxsein ML. 2013. Lumbar vertebral body bone microstructural scaling in Small to Medium-Sized Strepsirhines. The Anatomical Record 296:210-26.
Fajardo RJ, Müller R. 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. American Journal of Physical Anthropology 115:327-336.
Fajardo RJ, Müller R, Ketcham RA, Colbert M. 2007. Nonhuman anthropoid primate femoral neck architecture and its relationship to locomotor mode. The Anatomical Record 290:422-436.
Galichon V, Thackeray JF. 1997. CT scans of trabecular bone structures in the ilia of Sts 14 (Australopithecus africanus), Homo sapiens and Pan paniscus. South African Journal of Science 93:179-180.
Goldstein SA, Goulet R, McCubbrey D. 1993. Measurement and significance of three-dimensional architecture to the mechanical integrity of trabecular bone. Calcified Tissue International 53:S127-S133.
Griffin NL, D’Août K, Ryan TM, Richmond BG, Ketcham RA, Postnov A. 2010. Comparative forefoot trabecular bone architecture in extant hominids. Journal of Human Evolution 59:202-13.
Hammond AS, Plavcan JM, Kordos L, Begun DR, Ward CV. 2013a. In vivo-validated digital models of hip joint range of motion applied to fossil hominoids. American Journal of Physical Anthropology 150:142.
Hammond AS, Alba DM, Almécija S, Moyà-Solà S. 2013b. Middle Miocene Pierolapithecus provides a first glimpse into early hominid pelvic morphology. Journal of Human Evolution. 64:658-66.
Huiskes R, Ruimerman R, van Lenthe GH, Janssen JD. 2000. Effects of mechanical forces on maintenance and adaptation in trabecular bone. Nature 405:704-706.
Ketcham RA, Ryan TM. 2004. Quantification and visualization of anisotropy in trabecular bone. Journal of Microscopy 213:158-171.
Kivell TL, Begun DR. 2006. Functional morphology of new Dryopithecus carpals from Rudabánya, Hungary. American Journal of Physical Anthropology 129:114.
Kivell TL, Begun DR. 2009. New primate carpal bones from Rudabánya (late Miocene, Hungary): Taxonomic and functional implications. Journal of Human Evolution 57:697-709.
Kivell TL, Skinner MM, Lazenby R, Hublin JJ. 2011. Methodological considerations for analyzing trabecular architecture: an example from the primate hand. Journal of Anatomy 218:209225.

Kohler M, Moya-Sola S. 1997. Ape-like or hominid-like? The positional behavior of Oreopithecus bambolii reconsidered. PNAS:USA 94:11747-11750.
Kordos L, Begun DR. 2002. Rudabánya: A Late Miocene subtropical swamp deposit with evidence of the origin of the African apes and humans. Evolutionary Anthropology: Issues, News, and Reviews 11:45-57.
Kuo S, Desilva JM, Devlin MJ, Mcdonald G, Morgan EF. 2013. The effect of the Achilles tendon on trabecular structure in the primate calcaneus. The Anatomical Record 296:1509-17.

Lewton KL. 2010. Locomotor function and the evolution of the primate pelvis (Doctoral dissertation, Arizona State University).
Lewton KL. 2012. Evolvability of the primate pelvic girdle. Evolutionary Biology 39:126-139.
Lewton KL. 2015. In vitro bone strain distributions in a sample of primate pelves. Journal of Anatomy 226:458-77.
Macchiarelli R, Bondioli L, Galichon V, Tobias PV. 1999. Hip bone trabecular architecture shows uniquely distinctive locomotor behavior in South African australopithecines. Journal of Human Evolution 36:211-232.
Macchiarelli R, Rook L, Bondioli L. 2001. Comparative analysis of the iliac trabecular architecture in extant and fossil primates by means of digital image processing techniques: Implications for the reconstruction of fossil locomotor behaviors, in: Hominoid Evolution and Climatic Change in Europe 2 - Phylogeny of the Neogene Hominoid Primates of Eurasia. De Bonis L, Koufos GD, and Andrews P, eds. Cambridge University Press, Cambridge: 60-101.
MacLatchy L, Müller R. 2002. A comparison of the femoral head and neck trabecular architecture of Galago and Perodicticus using micro-computed tomography. Journal of Human Evolution 43:89-105.
Maga M, Kappelman J, Ryan TM, Ketcham RA. 2006. Preliminary observations on the calcaneal trabecular microarchitecture of extant large-bodied hominoids. American Journal of Physical Anthropology 129:410-417.
Maquer G, Musy SN, Wandel J, Gross T, Zysset PK. 2015. Bone volume fraction and fabric anisotropy are better determinants of trabecular bone stiffness than other morphological variables. Journal of Bone and Mineral Research 30:1000-8.
Martinon-Torres M. 2003. Quantifying trabecular orientation in the pelvic cancellous bone of modern humans, chimpanzees, and the Kebara 2 Neanderthal. American Journal of Human Biology 15:647-661.
Merceron G, Schulz E, Kordos L, Kaiser TM. 2007. Paleoenvironment of Dryopithecus brancoi at Rudabánya, Hungary: Evidence from dental meso-and micro-wear analyses of large vegetarian mammals. Journal of Human Evolution 53:331-49.
Morbeck ME. 1983. Miocene hominoid discoveries from Rudabánya, in: New interpretations of ape and human ancestry. Ciochon RL, Corruccini RS, eds. Springer, USA: 369-404.
Morgan ME, Lewton KL, Kelley J, Otárola-Castillo E, Barry JC, Flynn LJ, Pilbeam D. 2015. A partial hominoid innominate from the Miocene of Pakistan: Description and preliminary analyses. Proceedings of the National Academy of Sciences 112:82-7.
Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Gunter MM, Thorpe SKS, D’Aout K. 2006a. Morphological analysis of the hindlimb in apes and humans. I. Muscle architecture. Journal of Anatomy 208:709-724.
Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Gunter MM, Thorpe SKS, D’Aout K. 2006b. Morphological analysis of the hindlimb in apes and humans. I. Moment arms. Journal of Anatomy 208:725-742.
Pontzer H, Lieberman DE, Momin E, Devlin MJ, Polk JD, Hallgrimsson N, Cooper DML. 2006. Trabecular bone in the bird knee responds with high sensitivity to changes in load orientation. Journal of Experimental Biology 209:57-65.
Rasband WS. 1997-2016. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.
Ridler TW, Calvard S. 1978. Picture thresholding using an iterative selection method. IEEE Transactions on Systems, Man, and Cybernetics. 8:630-2.
Rook L, Bondioli L, Kohler M, Moya-Sola S, Macchiarelli R. 1999. Oreopithecus was a bipedal ape after all: Evidence from the iliac cancellous architecture. Proceedings of the National

Academy of Sciences of the United States of America 96:8795-8799.
Ruff C, Holt B, Trinkaus E. 2006. Who's afraid of the big bad Wolff?: "Wolff's Law" and bone functional adaptation. American Journal of Physical Anthropology 129:484-498.
Russo GA, Shapiro LJ. 2013. Reevaluation of the lumbosacral region of Oreopithecus bambolii. Journal of Human Evolution 65:253-65.
Ryan TM, Ketcham RA. 2002. The three-dimensional structure of trabecular bone in the femoral head of strepsirrhine primates. Journal of Human Evolution 43:1-26.
Ryan TM, Shaw CN. 2012. Unique suites of trabecular bone features characterize locomotor behavior in human and non-human anthropoid primates. PLoS One 7:e41037.
Ryan TM, Shaw CN. 2015. Gracility of the modern Homo sapiens skeleton is the result of decreased biomechanical loading. Proceedings of the National Academy of Sciences. 112:372-7.
Ryan TM, Silcox MT, Walker A, Mao X, Begun DR, Benefit BR, Gingerich PD, Köhler M, Kordos L, McCrossin ML, Moyà-Solà S. 2012. Evolution of locomotion in Anthropoidea: The semicircular canal evidence. Proceedings of the Royal Society of London B: Biological Sciences. 279:3467-75.
Saparin P, Scherf H, Hublin JJ, Fratzl P, Weinkamer R. 2011. Structural adaptation of trabecular bone revealed by position resolved analysis of proximal femora of different primates. Anatomical Record 294:55-67.
Scherf H. 2008. Locomotion-related femoral trabecular architecture in primates - high resolution computed tomographies and their implications for estimations of locomotor preferences of fossil primates, in: Anatomical imaging: Towards a new morphology. Endo H and Frey R, eds. Springer, New York: 39-59.
Scherf H, Harvati K, Hublin JJ. 2013. A comparison of proximal humeral cancellous bone of great apes and humans. Journal of Human Evolution 65:29-38.
Scherf H, Tilgner R. 2009. A new high-resolution computed tomography (CT) segmentation method for trabecular bone architectural analysis. American Journal of Physical Anthropology. 140:39-51.
Spitzer M, Wildenhain J, Rappsilber J, Tyers M. 2014. BoxPlotR: A web tool for generation of box plots. Nature Methods. 11:121-2.
Su A, Wallace IJ, Nakatsukasa M. 2013. Trabecular bone anisotropy and orientation in an Early Pleistocene hominin talus from East Turkana. Journal of Human Evolution 64:667-677.
Tanck E, Homminga J, van Lenthe GH, Huiskes R. 2001. Increase in bone volume fraction precedes architectural adaptation in growing bone. Bone 28:650-654.
Trussell HJ. 1979. Comments on "Picture thresholding using an iterative selection method". IEEE Transactions on Systems, Man, and Cybernetics. 9:311.
Van der Meulen MCH, Morgan TG, Yang X, Baldini TH, Myers ER, Wright TM, Bostrom MPG. 2006. Cancellous bone adaptation to in vivo loading in a rabbit model. Bone 38:871-877.

Volpato V, Viola TB, Nakatsukasa M, Bondioli L, Macchiarelli R. 2008. Textural characteristics of the iliac-femoral trabecular pattern in a bipedally trained Japanese macaque. Primates 49:16-25.
Ward CV Begun D, Kordos L. 2008. New partial pelvis of Dryopithecus brancoi from Rudabánya, Hungary. American Journal of Physical Anthropology 135:218.
Waterman HC. 1929. Studies on the evolution of the pelvis of man and other primates. American Museum of Natural History Bulletin 58:585-642.
Weinans H, Huiskes R, Grootenboer HJ. 1992. The behavior of adaptive bone-remodeling simulation models. Journal of Biomechanics 25:1425-41.
White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, WoldeGabriel G. 2009.

Ardipithecus ramidus and the paleobiology of early hominids. Science 326:64-86.
Wolff J. 1892. Das Gesetz der Transformation der Knochen. A. Hirchwild Berlin.
Wolff J. 1986. The law of bone remodeling. Springer-Verlag Berlin.
Yirga S. 1987. Interrelation between ischium, thigh-extending muscles and locomotion in some primates. Primates 28:79-86.

## Chapter 5. Conclusion

### 5.1 Contributions and Summary of Conclusions

The aim of this dissertation was to explore the relationships between loading, locomotion, and trabecular architecture in the primate pelvis in the context of bone functional adaptation. In doing so, this work contributes to the field of evolutionary anthropology in several ways.

The results of this dissertation are perhaps its most direct contribution to the field. The results from the analysis of the trabecular architecture of the ilium suggest that, as in previous work, trabecular density does not appear to be correlated with locomotor behavior (MacLatchy \& Müller 2002, Griffin et al. 2010, Fajardo et al. 2013), but degree of anisotropy does (Fajardo \& Müller 2001, Maga et al. 2006, Saparin et al. 2011, Ryan \& Shaw 2012, Su et al. 2013). Specifically, the ilium results indicated that quadrupeds (both semi-terrestrial and terrestrial) have more anisotropic trabecular architecture than arboreal suspensors, and that variation in anisotropy conforms to locomotor predictions in comparisons of non-human primates grouped by phylogeny (i.e., within-group comparisons of cercopithecoids and hominoids).

The results from the ischium indicate that the trabecular architecture of the dorsal region is denser and more anisotropic than that of the ventral region in non-human primates. This implies that bending in the sagittal plane is likely occurring, with the ischium loaded in dorsal compression and ventral tension (Slijper 1945, Badoux 1974, Kummer 1975). Interspecific variation in how different the dorsal and ventral regions are can potentially be explained by differences in locomotor mode; for example, the range between dorsal and ventral trabecular measures in Pan is much greater than it is in Symphalangus, likely due to its greater reliance on hindlimb loading generating stronger bending loads. It is, however, impossible to rule out torsion
as a potential loading regime at this time (Lewton 2015), as there appear to be no good data on trabecular architecture in bones that are habitually twisted. In terms of the interspecific comparisons, there are differences in density and anisotropy between quadrupeds and arboreal suspensors/bipeds, but these differences typically do not match predictions based on locomotion. For example, Homo (in both the ischium and ilium analyses) tends to have much higher bone volume fraction (BVTV) and a lower degree of anisotropy (DA) than expected (Ryan \& Shaw 2015). One taxon that does tend to conform to predictions about relative BVTV and DA is Pongo. Additional work on the relationship between BVTV and DA seems necessary, in order to try to account for the disagreement between predictions and results.

One set of analyses that did produce the expected results were those on the trabecular architecture of the innominate of Rudapithecus hungaricus. Rudapithecus has been proposed to be an arboreal quadruped with below-branch adaptations and the external morphology of its innominate has some similarities to those of Ateles and Symphalangus (Begun \& Kordos 2007, Ward et al. 2008). The results of chapter 4 support these morphological affiinities; the extant taxon to which Rudapithecus bears the greatest resemblence in trabecular architecture is Symphalangus. However, this conclusion is based on two small regions of preserved trabecular bone that may have been altered during the fossilization process. An additional important contribution of this work is that it appears as though even small amounts of trabecular bone can yield useful information for locomotor reconstructions in fossil taxa.

Before being able to generate results, this project necessitated the production of a novel data set of HRXCT scans of innominates of primates of different locomotor modes and represents the first quantitative characterization of the trabecular architecture of this skeletal element. While previous qualitative and/or radiographic studies on the trabecular architecture of the primate ilium exist (Galichon \& Thackeray 1997, Macchiarelli et al. 1999, Macchiarelli et al. 2001,

Abel \& Macho 2011), no such work had been undertaken for the ischium. This makes the creation of this data set an important contribution to the field in its own right, particularly given how costly HRXCT scanning can be. I intend to share this data set with other researchers after completing and publishing future work.

Methodologically, this research is an initial attempt at analyzing the complete trabecular architecture of a large, complex skeletal element and describing its variation within and between specimens, and within and between species. Previous work has generally focused on smaller, less complex skeletal elements, like the humeral head (Fajardo \& Müller 2001), vertebral body (Smit 2002), metacarpals (Tsegai et al. 2013, Skinner et al. 2015), and femoral head/neck (Ryan \& Ketcham 2002, Fajardo et al. 2007, Scherf 2008), and has typically sampled fewer volumes of interest (VOIs) from within those regions (e.g., two per specimen in Fajardo et al. 2007). As the first attempt at analyzing pelvic trabecular bone, this project brings to light important methodological issues for future work, such as how to deal with a huge number of VOIs and how to compensate for sampling difficulties arising from working on a morphologically variable skeletal element. Essentially, I see two ways to address the issue of multiple VOIs in future work: either use a more targeted sampling approach, focusing only on the trabecular architecture underlying homologous anatomical structures, or devise a way to treat the entirety of the trabecular architecture as a single unit. While this latter option has been explored recently by Tsegai (2013), Skinner et al. (2015), and Kivell (2016) with the creation of "medtool," it is still prohibitively expensive and lacks the same quantitative capabilities as traditional VOI-based methods of analysis, though it creates excellent visualizations of trabecular data.

### 5.2 Future Work

Given that this dissertation is the first quantitative characterization of the trabecular
architecture of the primate pelvis, there is great deal of room for further research. Future work on the pelvis is necessary to better understand the actual loading regimes that it experiences during locomotion. While in vivo work of this type is still likely to be considered too invasive to be undertaken in primates (Lewton 2015), it may be possible to attempt it using other model organisms (Pontzer et al. 2006, van der Meulen et al. 2006, Barak et al. 2011), borrowing methods from the orthopedic clinical literature on prosthetics (e.g., Bergmann et al. 1993). Finite element analysis (FEA) represents another possible way to address questions about pelvic loading (Dalstra \& Huiskes 1995, Anderson et al.2005), though validating these models still relies on having in vivo or in vitro data, which currently do not exist for the non-human primate pelvis (with the exception of Lewton 2015). Comparisons of the pelvic trabecular architecture between wild primates and captive conspecifics might also prove informative about loading (at least in terms of frequency and general type) (Volpato et al. 2008), if good observational data on locomotor and postural behavior could be kept for both sets of animals. In the short term, general comparisons of this type could be made, based on factors that clearly differentiate between zoos and the wild (e.g., enclosure size versus home range size) (Hosey 2005, Cooke \& Schillaci 2007).

Considering trabecular architecture more holistically (Kivell 2016), in combination with analyses of cortical bone (Schaffler \& Burr 1984, Lewton et al. 2016), soft tissue anatomy, and the three-dimensional geometry of the pelvis (Sylvester et al. 2016) is also an important potential avenue for future research. Cortical and trabecular bone are complementary parts of the same skeletal element and thus, are subject to the same locomotor loading. Being able to both account for variation in soft tissue anatomy (Payne et al. 2006, Channon et al. 2009, Channon et al. 2010) by first dissecting and then scanning then same specimens might prove informative, as muscles and soft tissue likely modulate loading in living animals (Dalstra \&

Huiskes 1995, Fechner et al 2013), and then one would be able to associate the underlying trabecular structure with particular muscle attachment points. The incorporation of methods from three-dimensional geometric morphometrics might provide a way to sample more VOIs more systematically, allowing for greater understanding of variation in microstructure within a bone (Sylvester et al. 2016).

Finally, the creation of larger data sets of scans will ultimately provide a broader context for the study of pelvic trabecular architecture, allowing us to better address questions about intra- and interspecific variation within primates and other mammals, the ontogeny of trabecular architecture, and (potentially) locomotion in fossils with no extant analog. Comparisons between primates and other mammalian orders with both arboreal and terrestrial representatives have proven informative for considering external morphological features related to locomotion and positional behavior (Russo \& Kirk 2013, Russo \& Shapiro 2015), and may also be so for trabecular architecture. Trabecular architecture has been shown to change during ontogeny in humans with changes in locomotion (Ryan \& Krovitz 2006, Gosman \& Ketcham 2009, Abel \& Macho 2011, Raichlen et al. 2015), but this has not been investigated in non-human primates, whose locomotion also changes during growth and development (Hunt 1991, Doran 1992, Doran 1997). The results of chapter 4 of this dissertation suggest that even small amounts of preserved trabecular bone may be useful for investigating locomotion in fossil taxa, which makes several other Miocene apes (Ekembo nyanzae, Oreopithecus bambolii, Pierolapithecus catalaunicus, and Sivapithecus indicus) good potential candidates for scanning (Ward et al. 1993, Rook et al. 1999, Hammond et al.2013, Morgan et al. 2014, McNulty et al. 2015).

## References

Abel R, Macho GA. 2011. Ontogenetic changes in the internal and external morphology of the ilium in modern humans. Journal of Anatomy 218:324-335.
Anderson AE, Peters CL, Tuttle BD, Weiss JA. 2005. Subject-specific finite element model of the pelvis: Development, validation and sensitivity studies. Journal of Biomechanical Engineering 127:364-373.
Badoux DM. 1974. An introduction to biomechanical principles in primate locomotion and structure, in: Primate Locomotion. Jenkins FA, ed. Academic Press, New York: 1- 43.
Barak MM, Lieberman DE, Hublin JJ. 2011. A Wolff in sheep's clothing: trabecular bone adaptation in response to changes in joint loading orientation. Bone 49:1141-1151.
Begun DR, Kordos L. 2007. New skeletal elements of Dryopithecus brancoi from Rudabánya, Hungary. American Journal of Physical Anthropology 132:71.
Bergmann G, Graichen F, Rohlmann A. 1993. Hip joint loading during walking and running, measured in two patients. Journal of Biomechanics 26:969-990.
Channon AJ, Günther MM, Crompton RH, Vereecke EE. 2009. Mechanical constraints on the functional morphology of the gibbon hind limb. Journal of Anatomy 215:383-400.
Channon AJ, Crompton RH, Günther MM, Vereecke EE. 2010. Muscle moment arms of the gibbon hind limb: implications for hylobatid locomotion. Journal of Anatomy 216:446-462.
Cooke CM, Schillaci MA. 2007. Behavioral responses to the zoo environment by white handed gibbons. Applied Animal Behaviour Science 106:125-133.
Dalstra M, Huiskes R. 1995. Load transfer across the pelvic bone. Journal of Biomechanics 28:715-724.
Doran DM. 1992. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: A case study of paedomorphism and its behavioral correlates. Journal of Human Evolution 23:139-157.
Doran DM. 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. Journal of Human Evolution 32:323-344.
Fajardo RJ, Desilva JM, Manoharan RK, Schmitz JE, Maclatchy LM, Bouxsein ML. 2013. Lumbar vertebral body bone microstructural scaling in Small to Medium-Sized Strepsirhines. The Anatomical Record 296:210-226.
Fajardo RJ, Müller R. 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. American Journal of Physical Anthropology 115:327-336.
Fajardo RJ, Müller R, Ketcham RA, Colbert M. 2007. Nonhuman anthropoid primate femoral neck architecture and its relationship to locomotor mode. The Anatomical Record 290:422-436.
Fechner R, Stratmann M, Gößling R, Sverdlova N. 2013. The functional role of the ischiopubic membrane for the mechanical loading of the pubis in the domestic fowl (Gallus gallus). Journal of anatomy 222:305-312.
Galichon V, Thackeray JF. 1997. CT scans of trabecular bone structures in the ilia of Sts 14 (Australopithecus africanus), Homo sapiens and Pan paniscus. South African Journal of Science 93:179-180.
Gosman JH, Ketcham RA. 2009. Patterns in ontogeny of human trabecular bone from SunWatch Village in the prehistoric Ohio Valley: General features of microarchitectural change. American Journal of Physical Anthropology 138:318-332.
Grabowski MW, Polk JD, Roseman CC. 2011. Divergent patterns of integration and reduced constraint in the human hip and the origins of bipedalism. Evolution 65:1336-1356.

Griffin NL, D’Août K, Ryan TM, Richmond BG, Ketcham RA, Postnov A. 2010. Comparative forefoot trabecular bone architecture in extant hominids. Journal of Human Evolution 59:202-213.
Hammond AS, Alba DM, Almécija S, Moyà-Solà S. 2013. Middle Miocene Pierolapithecus provides a first glimpse into early hominid pelvic morphology. Journal of Human Evolution. 64:658-66.
Hosey GR. 2005. How does the zoo environment affect the behaviour of captive primates?. Applied Animal Behaviour Science 90:107-129.
Hunt KD. 1991. Positional behavior in the Hominoidea. International Journal of Primatology 12:95-118.
Kivell TL. 2016. A review of trabecular bone functional adaptation: What have we learned from trabecular analyses in extant hominoids and what can we apply to fossils? Journal of Anatomy 228:569-594.
Kummer B. 1975. Functional adaptation to posture in the pelvis of man and other primates, in: Primate Functional Morphology and Evolution. Tuttle RH, ed. Aldine, Chicago: 281-290.
Lewton KL. 2015. In vitro bone strain distributions in a sample of primate pelves. Journal of Anatomy 226:458-477.
Lewton KL, Ritzman T, Copes LE, Garland Jr T, Capellini TD. 2016. Effects of exercise-induced loading on internal bone morphology of the mouse ilium: implications for lower ilium robusticity in primates. American Journal of Physical Anthropology 159:208.
Macchiarelli R, Bondioli L, Galichon V, Tobias PV. 1999. Hip bone trabecular architecture shows uniquely distinctive locomotor behavior in South African australopithecines. Journal of Human Evolution 36:211-232.
Macchiarelli R, Rook L, Bondioli L. 2001. Comparative analysis of the iliac trabecular architecture in extant and fossil primates by means of digital image processing techniques: Implications for the reconstruction of fossil locomotor behaviors, in: Hominoid Evolution and Climatic Change in Europe 2 - Phylogeny of the Neogene Hominoid Primates of Eurasia. De Bonis L, Koufos GD, and Andrews P, eds. Cambridge University Press, Cambridge: 60-101.
MacLatchy L, Müller R. 2002. A comparison of the femoral head and neck trabecular architecture of Galago and Perodicticus using micro-computed tomography. Journal of Human Evolution 43:89-105.
Maga M, Kappelman J, Ryan TM, Ketcham RA. 2006. Preliminary observations on the calcaneal trabecular microarchitecture of extant large-bodied hominoids. American Journal of Physical Anthropology 129:410-417.
McNulty KP, Begun DR, Kelley J, Manthi FK, Mbua EN. 2015. A systematic revision of Proconsul with the description of a new genus of early Miocene hominoid. Journal of Human Evolution 84:42-61.
Morgan ME, Lewton KL, Kelley J, Otárola-Castillo E, Barry JC, Flynn LJ, Pilbeam D. 2015. A partial hominoid innominate from the Miocene of Pakistan: Description and preliminary analyses. Proceedings of the National Academy of Sciences 112:82-87.
Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Gunter MM, Thorpe SKS, D’Aout K. 2006. Morphological analysis of the hindlimb in apes and humans. I. Muscle architecture. Journal of Anatomy 208:709-724.
Pontzer H, Lieberman DE, Momin E, Devlin MJ, Polk JD, Hallgrimsson N, Cooper DML. 2006. Trabecular bone in the bird knee responds with high sensitivity to changes in load orientation. Journal of Experimental Biology 209:57-65.
Raichlen DA, Gordon AD, Foster AD, Webber JT, Sukhdeo SM, Scott RS, Gosman JH, Ryan TM. 2015. An ontogenetic framework linking locomotion and trabecular bone architecture with
applications for reconstructing hominin life history. Journal of Human Evolution 81:1-12.
Rook L, Bondioli L, Kohler M, Moya-Sola S, Macchiarelli R. 1999. Oreopithecus was a bipedal ape after all: Evidence from the iliac cancellous architecture. Proceedings of the National Academy of Sciences of the United States of America 96:8795-8799.
Russo GA, Kirk EC. 2013. Foramen magnum position in bipedal mammals. Journal of human evolution 65:656-670.
Russo GA, Shapiro LJ. 2013. Reevaluation of the lumbosacral region of Oreopithecus bambolii. Journal of Human Evolution 65:253-265.
Ryan TM, Ketcham RA. 2002. The three-dimensional structure of trabecular bone in the femoral head of strepsirrhine primates. Journal of Human Evolution 43:1-26.
Ryan TM, Krovitz GE. 2006. Trabecular bone ontogeny in the human proximal femur. Journal of Human Evolution 51:591-602.
Ryan TM, Shaw CN. 2012. Unique suites of trabecular bone features characterize locomotor behavior in human and non-human anthropoid primates. PLoS One 7:e41037.
Ryan TM, Shaw CN. 2015. Gracility of the modern Homo sapiens skeleton is the result of decreased biomechanical loading. Proceedings of the National Academy of Sciences. 112:372-377.
Saparin P, Scherf H, Hublin JJ, Fratzl P, Weinkamer R. 2011. Structural adaptation of trabecular bone revealed by position resolved analysis of proximal femora of different primates. Anatomical Record 294:55-67.
Schaffler MB, Burr DB. 1984. Primate cortical bone microstructure: relationship to locomotion. American Journal of Physical Anthropology 65:191-197.
Scherf H. 2008. Locomotion-related femoral trabecular architecture in primates - high resolution computed tomographies and their implications for estimations of locomotor preferences of fossil primates, in: Anatomical imaging: Towards a new morphology. Endo H and Frey R, eds. Springer, New York: 39-59.
Skinner MM, Stephens NB, Tsegai ZJ, Foote AC, Nguyen NH, Gross T, Pahr DH, Hublin JJ, Kivell TL. 2015. Human-like hand use in Australopithecus africanus. Science 347:395-399.

Slijper EJ. 1946. Comparative Biologic-Anatomical Investigations on the Vertebral Column and Spinal Musculature of Mammals. North-Holland, Amsterdam.
Smit TH. 2002. The use of a quadruped as an in vivo model for the study of the spinebiomechanical considerations. European Spine Journal 11:137-144.
Su A, Wallace IJ, Nakatsukasa M. 2013. Trabecular bone anisotropy and orientation in an Early Pleistocene hominin talus from East Turkana, Kenya. Journal of Human Evolution 64:667677.

Sylvester AD, Terhune CE, Taylor AB. 2016. Trabecular mapping: Leveraging sliding landmarks for analyses of bone microstructure. American Journal of Physical Anthropology 159:309.
Tsegai ZJ, Kivell TL, Gross T, Nguyen NH, Pahr DH, Smaers JB, Skinner MM. 2013. Trabecular bone structure correlates with hand posture and use in hominoids. PloS one 8:e78781.
Van der Meulen MCH, Morgan TG, Yang X, Baldini TH, Myers ER, Wright TM, Bostrom MPG. 2006. Cancellous bone adaptation to in vivo loading in a rabbit model. Bone 38:871-877.

Volpato V, Viola TB, Nakatsukasa M, Bondioli L, Macchiarelli R. 2008. Textural characteristics of the iliac-femoral trabecular pattern in a bipedally trained Japanese macaque. Primates 49:16-25.
Ward CV Begun D, Kordos L. 2008. New partial pelvis of Dryopithecus brancoi from Rudabánya, Hungary. American Journal of Physical Anthropology 135:218.
Ward CV, Walker A, Teaford MF, Odhiambo I. 1993. Partial skeleton of Proconsul nyanzae from Mfangano Island, Kenya. American Journal of Physical Anthropology 90:77-111.

Appendix A. Complete sample of specimens/taxa.

| Taxon | Specimen | Sex | Locomotor Modes | Used in chapter(s) |
| :---: | :---: | :---: | :---: | :---: |
| Papio anubis neumanni | USNM-384228 | F | Terrestrial quadrupedalism (TQ) | 2, 3, 4 |
| Papio anubis neumanni | USNM-354987 | M | TQ | 2, 3, 4 |
| Papio anubis neumanni | USNM-397476 | F | TQ | 2, 3, 4 |
| Papio anubis neumanni | USNM-384234 | M | TQ | 2, 3, 4 |
| Papio anubis neumanni | USNM-395440 | M | TQ | 2, 3, 4 |
| Papio anubis neumanni | USNM-384227 | F | TQ | 2, 3, 4 |
| Symphalangus syndactylus | USNM-141161 | F | Brachiation (BR) | 2, 3, 4 |
| Symphalangus syndactylus | USNM-141162 | F | BR | 2, 3, 4 |
| Symphalangus syndactylus | USNM-141160 | M | BR | 2, 3, 4 |
| Symphalangus syndactylus | AMNH-M-106581 | M | BR | 2, 3, 4 |
| Pan troglodytes troglodytes | USNM-220327 | M | Knuckle-walking (KW), Arboreal/terrestrial quadrupedalism (AQ/TQ) | 2, 3, 4 |
| Pan troglodytes troglodytes | USNM-220065 | M | KW, AQ/TQ | 2, 3, 4 |
| Pan troglodytes troglodytes | USNM-176227 | F | KW, AQ/TQ | 2, 3, 4 |
| Pan troglodytes troglodytes | USNM-220064 | F | KW, AQ/TQ | 2, 3, 4 |
| Pan troglodytes verus | USNM-481804 | M | KW, AQ/TQ | 2, 3, 4 |
| Pongo pygmaeus | USNM-153823 | M | Quadrumanous clambering (QC) | 2, 3, 4 |
| Pongo pygmaeus | USNM-145300 | F | QC | 2, 3, 4 |
| Pongo pygmaeus | USNM-145302 | F | QC | 2, 3, 4 |
| Pongo pygmaeus | USNM-145301 | M | QC | 2, 3, 4 |
| Pongo pygmaeus | USNM-145304 | M | QC | 2, 3, 4 |
| Macaca mulatta | USNM-253780 | F | AQ/TQ | 2, 3, 4 |
| Macaca mulatta villosa | USNM-173813 | M | AQ/TQ | 2, 3, 4 |
| Macaca mulatta | AMNH-M-43086 | M | AQ/TQ | 2, 3, 4 |


| Macaca mulatta | UPENN- 86-12-44 | F | AQ/TQ | $2,3,4$ |
| :--- | :--- | :--- | :--- | :--- |
| Homo sapiens | TARL-B22 | M | Bipedalism (BP) | $2,3,4$ |
| Homo sapiens | TARL-TMM2165 | F | BP | $2,3,4$ |
| Homo sapiens | TARL-B-3 | M | BP | 3,4 |
| Homo sapiens | TARL-TARLAC-60 | M | BP | $2,3,4$ |
| Rudapithecus <br> hungaricus | RU 210 | - | AQ/BR (?) | 4 |

Appendix B. High-resolution X-ray computed tomography scanner settings and scan details for each specimen.

| Taxon | Specimen | Scanner and energy source settings | No. of projections | Voxel size (mm) | Total no. of slices |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Papio anubis neumanni | USNM-384228 | NSI; FeinFocus high power, $180 \mathrm{kV}, 0.15 \mathrm{~mA}$, aluminum filter | 3600 | 0.0608 | 3267 |
| P. a. neumanni | USNM-354987 | NSI; FeinFocus high power, $180 \mathrm{kV}, 0.15 \mathrm{~mA}$, aluminum filter | 3600 | 0.0608 | 3267 |
| P. a. neumanni | USNM-397476 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 17761 | 0.0509 | 3482 |
| P. a. neumanni | USNM-384234 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18004 | 0.0534 | 3970 |
| P. a. neumanni | USNM-395440 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18004 | 0.0534 | 3970 |
| P. a. neumanni | USNM-384227 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 17761 | 0.0509 | 3482 |
| Symphalangus syndactylus | USNM-141161 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 15304 | 0.0475 | 3264 |
| S. syndactylus | USNM-141162 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 15304 | 0.0475 | 3264 |
| S. syndactylus | USNM-141160 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18004 | 0.0378 | 4505 |
| S. syndactylus | $\begin{aligned} & \text { AMNH-M- } \\ & 106581 \end{aligned}$ | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18003 | 0.0769 | 2044 |
| Pan <br> troglodytes troglodytes | USNM-220327 | NSI; FeinFocus high power, $180 \mathrm{kV}, 0.19 \mathrm{~mA}$, aluminum filter | 3600 | 0.0744 | 3795 |
| P. t. troglodytes | USNM-220065 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18013 | 0.0753 | 3785 |
| P.t. <br> troglodytes | USNM-176227 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18004 | 0.0635 | 4161 |
| P. t. troglodytes | USNM-220064 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18004 | 0.0793 | 3354 |
| P. t. verus | USNM-481804 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18004 | 0.0635 | 4161 |
| Pongo pygmaeus | USNM-153823 | NSI; FeinFocus high power, 180kV, 0.19 mA , aluminum | 3600 | 0.0744 | 3795 |


|  |  | filter |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| P. pygmaeus | USNM-145300 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 3771 | 0.063 | 3771 |
| P. pygmaeus | USNM-145302 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 3771 | 0.063 | 3771 |
| P. pygmaeus | USNM-145301 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 3785 | 0.0753 | 3785 |
| P. pygmaeus | USNM-145304 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 3354 | 0.0793 | 3354 |
| Macaca mulatta | USNM-253780 | NSI; FeinFocus high power, $180 \mathrm{kV}, 0.19 \mathrm{~mA}$, aluminum filter | 3600 | 0.044 | 3078 |
| M. m. villosa | USNM-173813 | NSI; FeinFocus high power, $180 \mathrm{kV}, 0.15 \mathrm{~mA}$, aluminum filter | 3600 | 0.0563 | 2983 |
| M. mulatta | $\begin{aligned} & \text { AMNH-M- } \\ & 43086 \end{aligned}$ | NSI; FeinFocus microfocal, 190kV, 0.3 mA , no filter | 12003 | 0.0399 | 2737 |
| M. mulatta | $\begin{aligned} & \text { UPENN- 86- } \\ & 12-44 \end{aligned}$ | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 18004 | 0.0413 | 3401 |
| Homo sapiens | TARL-B22 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 12004 | 0.0786 | 2421 |
| H. sapiens | TARL- <br> TMM2165 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 12003 | 0.0786 | 2618 |
| H. sapiens | TARL-B-3 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 12004 | 0.0813 | 2641 |
| H. sapiens | TARL-TARLAC60 | NSI; FeinFocus high power, 190kV, 0.3 mA , no filter | 12003 | 0.0786 | 2756 |
| Rudapithecus hungaricus | RU 210 | ACTIS5; 130 kV, 0.1 mA , 0.25 mm brass filter | 2500 | 0.03248 | 3580 |

Appendix C.i.a. Raw bone volume fraction (BVTV) data from the lower ilium of the complete

| Specimen | Taxon |  | BVTV | BVTV | BVTV | BVTV |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Stack |  |  |  |  |
|  |  | No. M | Med | Lat D | Dors | Vent |
| RU 210 | Rudapithecus | 1 - |  | - - | - |  |
|  |  | 2 - |  | - - | - | - |
|  |  | 3 - |  | - - | - | - |
|  |  | 4 - |  | - - | - | - |
|  |  | 5 - |  | - - | - | - |
|  |  | 6 - |  | - - | - | - |
|  |  | 7 - |  | - - | - | - |
|  |  | 8 - |  | - - | - | - |
|  |  | 9 - |  | - - | - | - |
|  |  | $10-$ |  | - - | - | 0.314887 |
|  |  | 11 | 0.339672 | 0.2804 - |  | 0.26098 |
|  |  | 12 - |  | - - | - | - |
|  |  | 13 - |  | - - | - | - |
|  |  | 14 - |  | - - | - | - |
| USNM 384228 | Papio | 1 | 0.341312 | 0.352455 - |  | - |
|  |  | 2 | 0.279117 | 0.381013 - |  | - |
|  |  | 3 | 0.308804 | 0.311793 - |  | - |
|  |  | 4 | 0.207932 | 0.328372 - |  | - |
|  |  | 5 | 0.313027 | 0.374198 - |  | - |
|  |  | 6 | 0.290532 | 0.400748 - |  | - |
|  |  | 7 | 0.317333 | 0.433508 - |  | - |
|  |  | 8 | 0.263793 | 0.439592 - |  | - |
|  |  | 9 | 0.315096 | 0.397592 - |  | - |
|  |  | 10 | 0.275375 | 0.345368 - |  | - |
|  |  | 11 | 0.252232 | 0.351598 | 0.285702 | 0.472812 |
|  |  | 12 | 0.340811 | 0.423599 | 0.424372 | 0.391362 |
|  |  | 13 | 0.312755 | 0.417557 | 0.407543 | 0.277382 |
| USNM 354987 | Papio | 1 | 0.270471 | 0.230898 - |  | - |
|  |  | 2 | 0.200861 | 0.16836 - |  | - |
|  |  | 3 | 0.168223 | 0.19718 - |  | - |
|  |  | 4 | 0.160619 | 0.215948 - |  | - |
|  |  | 5 | 0.177804 | 0.248753 - |  | - |
|  |  | 6 | 0.202245 | 0.200891 - |  | - |
|  |  | 7 | 0.258791 | 0.208739 - |  | - |
|  |  | 8 | 0.264479 | 0.125183 - |  | - |
|  |  | 9 | 0.151874 | 0.232175 - |  | - |
|  |  | 10 | 0.166748 | 0.233194 - |  | - |
|  |  | 11 | 0.163356 | 0.230472 - |  | - |
|  |  | 12 | 0.178747 | 0.33967 | 0.22124 | 0.251217 |


|  | 13 | 0.233164 | 0.306956 | 0.29774 | 0.234852 |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
|  | 14 | 0.18115 | 0.34364 | 0.386194 | 0.312599 |  |  |
| USNM 397476 Papio | 15 | 0.126566 | 0.351761 | 0.383258 | 0.251475 |  |  |
|  |  | 1 | 0.205454 | $0.251977-$ |  |  |  |
|  |  | 2 | 0.179858 | $0.273345-$ | - | - | - |


|  |  | 7 - | - | - |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 8 | 0.307135 - | - |  |  |
|  |  | 9 | 0.29531 | 0.376757 - |  |  |
|  |  | 10 | 0.248823 | 0.352087 - |  |  |
|  |  | 11 | 0.139325 | 0.357438 - |  |  |
|  |  | 12 | 0.186912 | 0.261897 | 0.349555 | 0.308396 |
|  |  | 13 | 0.338921 | 0.354436 | 0.367682 | 0.365963 |
|  |  | 14 | 0.321115 | 0.320141 | 0.380997 | 0.281777 |
|  |  | 15 | 0.206483 | 0.271201 | 0.32359 | 0.315924 |
| USNM 141161 | Symphalangus | 1 | 0.148558 - | - |  |  |
|  |  | 2 - |  | - |  |  |
|  |  | 3 | 0.266288 - | - |  |  |
|  |  | 4 | 0.146627 | 0.468168 - |  |  |
|  |  | 5 | 0.29193 | 0.416885 - |  |  |
|  |  | 6 | 0.345176 | 0.356658 - |  |  |
|  |  | 7 | 0.318135 | 0.392307 - |  |  |
|  |  | 8 | 0.3717 | 0.440123 | 0.402239 | 0.396307 |
|  |  | 9 | 0.360263 | 0.400322 | 0.330089 | 0.331488 |
|  |  | 10 | 0.450009 | 0.351305 | 0.366438 | 0.342758 |
|  |  | 11 | 0.437538 | 0.406269 | 0.316812 | 0.340446 |
| USNM 141162 | Symphalangus | 1 | 0.250937 | 0.221593 - |  |  |
|  |  | 2 | 0.182222 - | - |  |  |
|  |  | 3 | 0.192929 | 0.198746 - |  |  |
|  |  | 4 | 0.168296 | 0.22291 - |  |  |
|  |  | 5 | 0.201266 | 0.2284 - |  |  |
|  |  | 6 | 0.280326 | 0.475704 - |  |  |
|  |  | 7 | 0.265472 | 0.305568 - |  |  |
|  |  | 8 | 0.219002 | 0.406254 | 0.401595 | 0.274738 |
|  |  | 9 | 0.235756 | 0.454308 | 0.353869 | 0.195422 |
|  |  | 10 | 0.242564 | 0.39629 | 0.343604 | 0.208516 |
| USNM 141160 | Symphalangus | 1 | 0.276753 | 0.0924788 - |  |  |
|  |  | 2 | 0.084354 - | - |  |  |
|  |  | 3 - |  | 0.0644923 - |  |  |
|  |  | 4 |  | 0.14913 - |  |  |
|  |  | 5 - |  | 0.166457 - |  |  |
|  |  | 6 - |  | 0.30869 - |  |  |
|  |  | 7 | 0.179461 | 0.367614 - |  |  |
|  |  | 8 | 0.0969302 | 0.392383 - |  |  |
|  |  | 9 | 0.198706 | 0.371671 - |  |  |
|  |  | 10 | 0.215539 | 0.359101 | 0.442993 | 0.254001 |
|  |  | 11 | 0.201207 | 0.397907 | 0.473369 | 0.328391 |
|  |  | 12 | 0.210671 | 0.363508 | 0.232828 | 0.299215 |
|  |  | 13 | 0.25723 | 0.385009 | 0.294158 | 0.280298 |
| AMNH 106581 | Symphalangus | 1 | 0.267263 | 0.244768 - |  |  |


|  |  | 2 | 0.207576 | 0.312358 - |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 3 | 0.0843351 | 0.243514 - |  |  |
|  |  | 4 | 0.0831225 | 0.281479 - |  |  |
|  |  | 5 | 0.13683 | 0.309473 - |  |  |
|  |  | 6 | 0.163987 | 0.402233 - |  |  |
|  |  | 7 | 0.2801 | 0.420254 | 0.331967 | 0.284824 |
|  |  | 8 | 0.286016 | 0.412853 | 0.345975 | 0.235925 |
|  |  | 9 | 0.366525 | 0.415487 | 0.305417 | 0.276713 |
|  |  | 10 | 0.336065 | 0.406017 | 0.309723 | 0.310392 |
| USNM 220327 | Pan | 1 | 0.228524 | 0.175016 - |  |  |
|  |  | 2 | 0.203662 | 0.168394 - |  |  |
|  |  | 3 | 0.188022 | 0.201275 - |  |  |
|  |  | 4 | 0.12874 | 0.32135 - |  |  |
|  |  | 5 | 0.194715 | 0.283827 - |  |  |
|  |  | 6 | 0.0768761 | 0.270981 - |  |  |
|  |  | 7 | 0.183362 | 0.246879 - |  |  |
|  |  | 8 | 0.203459 | 0.277125 - |  |  |
|  |  | 9 | 0.178278 | 0.258346 - |  |  |
|  |  | 10 | 0.183389 | 0.378209 | 0.24657 | 0.231663 |
|  |  | 11 | 0.234757 | 0.325736 | 0.1788 | 0.185475 |
|  |  | 12 | 0.195289 | 0.314896 | 0.318486 | 0.206642 |
|  |  | 13 | 0.286082 | 0.286939 | 0.277099 | 0.202133 |
| USNM 220065 | Pan | 1 | 0.182616 | 0.165963 - |  |  |
|  |  | 2 | 0.172084 | 0.177614 - |  |  |
|  |  | 3 | 0.163619 | 0.38251 - |  |  |
|  |  | 4 | 0.161671 | 0.275555 - |  |  |
|  |  | 5 | 0.144413 | 0.27351 - |  |  |
|  |  | 6 | 0.265489 | 0.383025 - |  |  |
|  |  | 7 | 0.154319 | 0.520572 - |  |  |
|  |  | 8 | 0.273913 | 0.398683 | 0.295831 | 0.305751 |
|  |  | 9 | 0.264988 | 0.358999 | 0.271875 | 0.306641 |
|  |  | 10 | 0.307907 | 0.332211 | 0.291212 | 0.267221 |
| USNM 176227 | Pan | 1 | 0.309869 | 0.332868 |  |  |
|  |  | 2 | 0.247809 | 0.288452 |  |  |
|  |  | 3 | 0.254187 | 0.381168 |  |  |
|  |  | 4 | 0.221652 | 0.38188 |  |  |
|  |  | 5 | 0.229909 | 0.409618 | 0.361758 | 0.433395 |
|  |  | 6 | 0.361957 | 0.414071 | 0.373582 | 0.425681 |
|  |  | 7 | 0.276618 | 0.464793 | 0.466134 | 0.362178 |
|  |  | 8 | 0.281332 | 0.41077 | 0.267291 | 0.211512 |
|  |  | 9 | 0.220086 | 0.339205 | 0.279755 | 0.219072 |
| USNM 220064 | Pan | 1 | 0.214224 | 0.209382 - |  |  |
|  |  | 2 | 0.18352 | 0.242138 - |  |  |
|  |  | 3 | 0.194357 | - |  |  |


|  |  | 4 | 0.203184 - | - |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 5 | 0.159181 - | - |  |  |
|  |  | 6 | 0.171201 | 0.287449 - |  |  |
|  |  | 7 | 0.165817 | 0.323704 - |  |  |
|  |  | 8 | 0.143419 | 0.349566 - |  |  |
|  |  | 9 | 0.203581 | 0.378169 | 0.248691 | 0.224546 |
|  |  | 10 | 0.267924 | 0.259055 | 0.198566 | 0.143217 |
| USNM 481804 | Pan | 1 | 0.217006 | 0.303059 - |  |  |
|  |  | 2 | 0.234139 | 0.347973 - |  |  |
|  |  | 3 | 0.225339 | 0.406772 - |  |  |
|  |  | 4 | 0.239056 | 0.389939 - |  |  |
|  |  | 5 | 0.104395 | 0.363137 | 0.361106 | 0.430944 |
|  |  | 6 | 0.195561 | 0.312971 | 0.438533 | 0.342332 |
|  |  | 7 | 0.0913321 | 0.366038 | 0.418438 | 0.314452 |
|  |  | 8 | 0.190525 | 0.428684 | 0.2744 | 0.316101 |
|  |  | 9 | 0.380924 | 0.370942 | 0.398543 | 0.258241 |
|  |  | 10 | 0.387289 | 0.246506 | 0.341094 | 0.201758 |
|  |  | 11 | 0.3882 | 0.385953 | 0.287581 | 0.205751 |
| USNM 153823 | Pongo | 1 | 0.31825 | 0.437527 | 0.252801 | 0.289765 |
|  |  | 2 | 0.332271 | 0.429168 | 0.301313 | 0.300974 |
|  |  | 3 | 0.329779 | 0.360027 | 0.460732 | 0.29299 |
|  |  | 4 | 0.283473 | 0.389112 | 0.393998 | 0.262002 |
|  |  | 5 | 0.174391 | 0.389821 | 0.28063 | 0.263445 |
|  |  | 6 | 0.27509 | 0.331313 | 0.285546 | 0.234251 |
|  |  | 7 | 0.252631 | 0.308181 | 0.207167 | 0.229523 |
| USNM 145300 | Pongo | 1 | 0.143115 | 0.163139 - |  | 0.33779 |
|  |  | 2 | 0.145939 | 0.234999 | 0.375694 | 0.302691 |
|  |  | 3 | 0.170206 | 0.312506 | 0.389055 | 0.20485 |
|  |  | 4 | 0.211337 | 0.286642 | 0.339949 | 0.301473 |
|  |  | 5 | 0.187078 | 0.347091 | 0.317245 | 0.250897 |
|  |  | 6 | 0.117033 | 0.267644 | 0.235133 | 0.279702 |
|  |  | 7 | 0.0981522 | 0.330034 | 0.32995 | 0.212135 |
|  |  | 8 | 0.118142 | 0.286651 | 0.145997 | 0.243536 |
|  |  | 9 | 0.195279 | 0.27787 | 0.225311 | 0.13699 |
|  |  | 10 | 0.290373 | 0.317707 | 0.254124 | 0.188028 |
|  |  | 11 | 0.232764 | 0.271122 | 0.25004 | 0.222034 |
| USNM 145302 | Pongo | 1 | 0.275965 | 0.333568 | 0.223399 | 0.271701 |
|  |  | 2 | 0.274149 | 0.345142 | 0.251146 | 0.258074 |
|  |  | 3 | 0.276702 | 0.34894 | 0.246492 | 0.303705 |
|  |  | 4 | 0.222418 | 0.324093 | 0.207873 | 0.29595 |
|  |  | 5 | 0.246152 | 0.367144 | 0.34124 | 0.276361 |
|  |  | 6 | 0.268028 | 0.398536 | 0.339362 | 0.252349 |
|  |  | 7 | 0.269176 | 0.330695 | 0.301055 | 0.23016 |
|  |  | 8 | 0.306683 | 0.279819 | 0.165942 | 0.22904 |


|  |  | 9 | 0.247619 | 0.322848 | 0.124074 | 0.219225 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 10 | 0.277328 | 0.302119 | 0.189878 | 0.173016 |
|  |  | 11 | 0.272181 | 0.239954 | 0.270122 | 0.17239 |
|  |  | 12 | 0.310307 | 0.239133 | 0.280472 | 0.196653 |
| USNM 145301 | Pongo | 1 | 0.186431 | 0.215303 | 0.30296 | 0.198187 |
|  |  | 2 | 0.138527 | 0.241671 | 0.331966 | 0.186507 |
|  |  | 3 | 0.191784 | 0.247355 | 0.269336 | 0.271186 |
|  |  | 4 | 0.195067 | 0.324539 | 0.312964 | 0.266519 |
|  |  | 5 | 0.158151 | 0.257956 | 0.274664 | 0.206683 |
|  |  | 6 | 0.171521 | 0.249539 | 0.271673 | 0.232233 |
|  |  | 7 | 0.217562 | 0.233109 | 0.272466 | 0.19106 |
|  |  | 8 | 0.254589 | 0.300819 | 0.260321 | 0.163347 |
| USNM 145304 | Pongo | 1 | 0.259368 | 0.302196 | 0.234514 | 0.297633 |
|  |  | 2 | 0.340558 | 0.32586 | 0.323927 | 0.301563 |
|  |  | 3 | 0.308282 | 0.317012 | 0.333366 | 0.274831 |
|  |  | 4 | 0.337025 | 0.294663 | 0.241769 | 0.300853 |
|  |  | 5 | 0.380451 | 0.320219 | 0.2914 | 0.258206 |
|  |  | 6 | 0.368626 | 0.297737 | 0.276264 | 0.263312 |
| USNM 253780 | Macaca | 1 - |  |  | 0.123739 | 0.095861 |
|  |  | 2 - |  |  | 0.142822 | 0.156885 |
|  |  | 3 - |  |  | 0.170009 | 0.185127 |
|  |  | 4 - |  |  | 0.169821 | 0.167032 |
|  |  | 5 - |  |  | 0.19351 | 0.20995 |
|  |  | 6 - |  |  | 0.196056 | 0.269695 |
|  |  | 7 - |  |  | 0.238095 | 0.28928 |
|  |  | 8 | 0.108191 | 0.261202 | 0.294718 | 0.242841 |
|  |  | 9 | 0.206834 | 0.277466 | 0.298446 | 0.216387 |
|  |  | 10 | 0.228632 | 0.25528 | 0.180447 | 0.212472 |
| USNM 173813 | Macaca | 1 - |  |  | 0.342668 | 0.338869 |
|  |  | 2 - |  |  | 0.324915 | 0.346539 |
|  |  | 3 - |  |  | 0.346826 | 0.475568 |
|  |  | 4 - |  |  | 0.35765 | 0.473967 |
|  |  | 5 - |  |  | 0.340804 | 0.430695 |
|  |  | 6 - |  |  | 0.33636 | 0.379585 |
|  |  | 7 - |  |  | 0.318272 | 0.404721 |
|  |  | 8 - |  |  | 0.37017 | 0.387135 |
|  |  | 9 | 0.349382 | 0.415785 | 0.398676 | 0.591169 |
|  |  | 10 | 0.394566 | 0.455521 | 0.380278 | 0.521589 |
|  |  | 11 | 0.398676 | 0.416931 | 0.458914 | 0.497885 |
|  |  | 12 | 0.396884 | 0.477742 | 0.38379 | 0.502712 |
|  |  | 13 | 0.339251 | 0.51798 | 0.350673 | 0.493847 |
|  |  | 14 | 0.298583 | 0.456309 | 0.387135 | 0.523046 |
|  |  | 15 | 0.321976 | 0.415546 | 0.370863 | 0.505101 |


| AMNH 43086 | Macaca | 1 - | - |  | 0.267129 - |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 2 - | - |  | - |  |
|  |  | 3 - | - |  | - |  |
|  |  | 4 - | - |  | 0.236363 - |  |
|  |  | 5 - | - |  | 0.267924 - |  |
|  |  | 6 - | - |  | 0.17108 | 0.172428 |
|  |  | 7 - | - |  | 0.240978 | 0.255375 |
|  |  | 8 | 0.141679 | 0.160969 | 0.197577 | 0.241289 |
|  |  | 9 | 0.102842 | 0.123341 | 0.219614 | 0.29169 |
|  |  | 10 | 0.119867 | 0.181036 | 0.240131 | 0.304912 |
|  |  | 11 | 0.189384 | 0.303028 | 0.321332 | 0.325221 |
|  |  | 12 | 0.153346 | 0.249654 | 0.288388 | 0.272884 |
|  |  | 13 | 0.247718 | 0.327036 | 0.314263 | 0.283134 |
|  |  | 14 | 0.225958 - |  | 0.283307 | 0.325221 |
| UPENN-86-12- |  |  |  |  |  |  |
| 44 | Macaca | 1 - | - |  | 0.197366 | 0.272783 |
|  |  | 2 - | - |  | 0.20257 | 0.287002 |
|  |  | 3 - | - |  | 0.188875 | 0.188134 |
|  |  | 4 - | - |  | 0.19119 | 0.207084 |
|  |  | 5 - | - |  | 0.20156 | 0.393722 |
|  |  | 6 - | - |  | 0.235253 | 0.482539 |
|  |  | 7 - | - |  | 0.269637 | 0.408439 |
|  |  | 8 | 0.26327 | 0.309724 | 0.227326 | 0.395218 |
|  |  | 9 | 0.215357 | 0.342868 | 0.194834 | 0.453628 |
|  |  | 10 | 0.138111 | 0.262566 | 0.173557 | 0.421341 |
|  |  | 11 | 0.172943 | 0.273179 | 0.20881 | 0.375564 |
|  |  | 12 | 0.19812 | 0.348277 | 0.222441 | 0.309443 |
| B22-A | Homo | 1 | 0.228993 | 0.277762 | 0.388651 | 0.282766 |
|  |  | 2 | 0.210673 | 0.340572 | 0.220549 | 0.352746 |
|  |  | 3 | 0.2545 | 0.337786 | 0.427827 | 0.41545 |
| B22-B | Homo | 1 | 0.216127 | 0.251148 | 0.343933 | 0.262717 |
|  |  | 2 | 0.22525 | 0.323106 | 0.411627 | 0.232968 |
| TMM2165-A | Homo | 1 | 0.161039 | 0.326818 | 0.261793 | 0.269556 |
|  |  | 2 | 0.280676 | 0.33915 | 0.238357 | 0.318438 |
|  |  | 3 | 0.26346 | 0.322706 | 0.219085 | 0.305867 |
| TMM2165-B | Homo | 1 | 0.192483 | 0.284583 | 0.293503 | 0.269615 |
|  |  | 2 | 0.296036 | 0.365273 | 0.230288 | 0.342196 |
| TARLAC-60-A | Homo | 1 | 0.388869 | 0.33535 | 0.419657 | 0.274999 |
|  |  | 2 | 0.350947 | 0.38676 | 0.388475 | 0.321274 |
|  |  | 3 | 0.278066 | 0.36635 | 0.358942 | 0.314934 |
|  |  | 4 | 0.270034 | 0.392779 | 0.261869 | 0.319517 |


| TARLAC-60-B | Homo | 1 | 0.326252 | 0.325899 | 0.400663 | 0.276641 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: |
|  | 2 | 0.273545 | 0.335365 | 0.353848 | 0.300652 |  |
|  | 3 | 0.26437 | 0.371231 | 0.266365 | 0.322332 |  |

Appendix C.i.b. Raw degree of anisotropy (DA) data from the lower ilium of the complete

| Specimen | Taxon |  | DA | DA |  | DA |  | DA |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Stack |  |  |  |  |  |  |
|  |  | No. M | Med | Lat |  | Dors |  | Vent |
| RU 210 | Rudapithecus | 1 - |  | - |  | - |  | - |
|  |  | 2 - |  | - |  | - |  | - |
|  |  | 3 - |  | - |  | - |  | - |
|  |  | 4 - |  | - |  | - |  | - |
|  |  | 5 - |  | - |  | - |  | - |
|  |  | 6 - |  | - |  | - |  | - |
|  |  | 7 - |  | - |  | - |  | - |
|  |  | 8 - |  | - |  | - |  | - |
|  |  | 9 - |  | - |  | - |  | - |
|  |  | 10 - |  | - |  | - |  | 3.6556 |
|  |  | 11 | 2.47411 |  | 2.19947 - |  |  | 3.61158 |
|  |  | 12 - |  | - |  | - |  | - |
|  |  | 13 - |  | - |  | - |  | - |
|  |  | 14 - |  | - |  | - |  | - |
| USNM 384228 | Papio | 1 | 3.4537 |  | 2.63108 - |  |  | - |
|  |  | 2 | 6.33706 |  | 2.74475 |  |  | - |
|  |  | 3 | 2.5891 |  | 2.90728 - |  |  | - |
|  |  | 4 | 2.44227 |  | 4.09197 - |  |  | - |
|  |  | 5 | 2.45375 |  | 2.80516 - |  |  | - |
|  |  | 6 | 4.03172 |  | 2.80955 |  |  | - |
|  |  | 7 | 1.65714 |  | 7.11134 |  |  | - |
|  |  | 8 | 2.37663 |  | 4.50531 - |  |  | - |
|  |  | 9 | 1.57329 |  | 3.83803 - |  |  | - |
|  |  | 10 | 3.04736 |  | 4.55907 - |  |  | - |
|  |  | 11 | 2.15255 |  | 3.88868 |  | 3.16199 | 2.67575 |
|  |  | 12 | 3.03341 |  | 2.3213 |  | 1.969 | 3.45472 |
|  |  | 13 | 4.47354 |  | 3.19599 |  | 4.92583 | 8.60382 |
| USNM 354987 | Papio | 1 | 4.46286 |  | 7.90235 |  |  | - |
|  |  | 2 | 4.85011 |  | 14.5385 |  |  | - |
|  |  | 3 | 3.86976 |  | 4.50869 - |  |  | - |
|  |  | 4 | 2.83015 |  | 2.91377 - |  |  | - |
|  |  | 5 | 7.95188 |  | 4.05102 - |  |  | - |
|  |  | 6 | 3.3728 |  | 2.24216 - |  |  | - |
|  |  | 7 | 1.98818 |  | 3.44776 |  |  | - |
|  |  | 8 | 2.46442 |  | 2.34627 - |  |  | - |
|  |  | 9 | 2.27346 |  | 5.09707 - |  |  | - |
|  |  | 10 | 8.04072 |  | 5.50168 - |  |  | - |
|  |  | 11 | 6.01011 |  | 3.54248 - |  |  | - |
|  |  | 12 | 4.14975 |  | 2.76268 |  | 6.63457 | 4.17538 |


|  | 13 | 6.57077 | 11.0915 | 2.37752 | 5.22678 |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: |
|  |  | 14 | 3.04169 | 7.8713 | 2.89385 | 2.49121 |
| USNM 397476 | Papio | 15 | 4.1713 | 4.04462 | 5.97028 | 9.13181 |
|  |  |  |  |  |  |  |
|  |  | 1 | 1.98836 | $3.19046-$ | - |  |
|  |  | 2.27543 | $4.69439-$ | - | - |  |
|  |  | $4-$ |  | $2.625-$ | - | - |


|  |  | 7 - | - | - |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 8 | 2.05786 - | - |  |  |
|  |  | 9 | 2.38956 | 5.31847 - |  |  |
|  |  | 10 | 2.47151 | 4.89626 - |  |  |
|  |  | 11 | 3.69963 | 2.80246 - |  |  |
|  |  | 12 | 4.95636 | 3.76057 | 2.02908 | 3.75867 |
|  |  | 13 | 1.52213 | 3.73999 | 2.02502 | 2.54061 |
|  |  | 14 | 3.8188 | 5.10618 | 3.25844 | 2.85589 |
|  |  | 15 | 2.19299 | 3.89953 | 7.06753 | 4.55879 |
| USNM 141161 | Symphalangus | 1 | 4.11144 - | - |  |  |
|  |  | 2 - | - | - |  |  |
|  |  | 3 | 3.10879 - | - |  |  |
|  |  | 4 | 6.1443 | 2.62765 - |  |  |
|  |  | 5 | 3.5125 | 1.80243 - |  |  |
|  |  | 6 | 2.33873 | 2.06766 - |  |  |
|  |  | 7 | 1.6166 | 2.31746 - |  |  |
|  |  | 8 | 2.41871 | 3.37673 | 1.79317 | 2.41694 |
|  |  | 9 | 3.12432 | 4.45889 | 3.19569 | 3.72561 |
|  |  | 10 | 1.96419 | 2.39662 | 4.77331 | 2.87657 |
|  |  | 11 | 1.90598 | 3.14473 | 2.55238 | 2.81328 |
| USNM 141162 | Symphalangus | 1 | 2.15707 | 3.19995 - |  |  |
|  |  | 2 | 2.4172 - | - |  |  |
|  |  | 3 | 2.32792 | 3.58778 - |  |  |
|  |  | 4 | 2.25029 | 2.88328 - |  |  |
|  |  | 5 | 3.02394 | 1.62846 - |  |  |
|  |  | 6 | 2.04174 | 1.4558 - |  |  |
|  |  | 7 | 3.01216 | 5.80263 - |  |  |
|  |  | 8 | 2.58544 | 3.0252 | 2.79021 | 2.88614 |
|  |  | 9 | 2.69478 | 2.40205 | 3.52107 | 2.69804 |
|  |  | 10 | 3.09262 | 4.96912 | 3.56238 | 2.05409 |
| USNM 141160 | Symphalangus | 1 | 1.99285 | 2.85372 - |  |  |
|  |  | 2 | 10.0122 - | - |  |  |
|  |  | 3 - |  | 7.3933 - |  |  |
|  |  | 4 - |  | 5.28503 - |  |  |
|  |  | 5 - |  | 5.53938 - |  |  |
|  |  | 6 - |  | 2.479 - |  |  |
|  |  | 7 | 4.44208 | 2.53717 - |  |  |
|  |  | 8 | 4.76787 | 1.88384 - |  |  |
|  |  | 9 | 4.53196 | 3.19039 - |  |  |
|  |  | 10 | 4.32603 | 5.55889 | 1.82662 | 4.6023 |
|  |  | 11 | 2.05965 | 3.12294 | 2.07321 | 3.3859 |
|  |  | 12 | 2.60316 | 2.94608 | 2.95801 | 4.88299 |
|  |  | 13 | 1.91649 | 3.07994 | 2.61664 | 3.26226 |
| AMNH 106581 | Symphalangus | 1 | 4.10038 | 2.55158 - |  |  |


|  |  | 2 | 2.04336 | 2.03113 - |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 3 | 6.79494 | 2.30782 - |  |  |
|  |  | 4 | 25.3339 | 2.02482 - |  |  |
|  |  | 5 | 3.25382 | 3.99 - |  |  |
|  |  | 6 | 2.39628 | 1.96948 - |  |  |
|  |  | 7 | 1.70661 | 2.69389 | 2.40464 | 3.21233 |
|  |  | 8 | 1.58587 | 2.80305 | 1.7922 | 2.74408 |
|  |  | 9 | 4.69191 | 2.99032 | 3.04356 | 3.05241 |
|  |  | 10 | 2.9206 | 4.83354 | 2.87639 | 4.36655 |
| USNM 220327 | Pan | 1 | 8.17771 | 5.43146 - |  |  |
|  |  | 2 | 10.6556 | 3.52162 - |  |  |
|  |  | 3 | 18.4437 | 2.38451 - |  |  |
|  |  | 4 | 2.42731 | 3.22492 - |  |  |
|  |  | 5 | 2.38334 | 4.7579 - |  |  |
|  |  | 6 | 7.00786 | 9.51126 - |  |  |
|  |  | 7 | 33.0089 | 3.54529 - |  |  |
|  |  | 8 | 10.8228 | 7.53112 - |  |  |
|  |  | 9 | 16.7623 | 28.2924 - |  |  |
|  |  | 10 | 9.72367 | 8.37955 | 4.0847 | 3.63212 |
|  |  | 11 | 6.2136 | 10.0397 | 2.31986 | 6.34768 |
|  |  | 12 | 8.84284 | 7.06756 | 4.50298 | 5.63734 |
|  |  | 13 | 6.01634 | 6.37845 | 4.39532 | 6.92851 |
| USNM 220065 | Pan | 1 | 2.24451 | 2.35937 - |  |  |
|  |  | 2 | 2.1121 | 2.74878 - |  |  |
|  |  | 3 | 3.02489 | 2.96392 - |  |  |
|  |  | 4 | 1.76296 | 2.37572 - |  |  |
|  |  | 5 | 7.42077 | 6.22391 - |  |  |
|  |  | 6 | 3.31282 | 2.57637 - |  |  |
|  |  | 7 | 3.11217 | 4.44162 - |  |  |
|  |  | 8 | 2.77375 | 3.12659 | 3.99568 | 4.17297 |
|  |  | 9 | 2.19727 | 2.09368 | 1.72974 | 2.703 |
|  |  | 10 | 5.49311 | 3.71045 | 2.95505 | 3.96107 |
| USNM 176227 | Pan | 1 | 6.06062 | 5.63181 |  |  |
|  |  | 2 | 9.49764 | 3.50354 |  |  |
|  |  | 3 | 6.91715 | 1.78726 |  |  |
|  |  | 4 | 4.25517 | 4.67772 |  |  |
|  |  | 5 | 3.60996 | 3.4933 | 5.69371 | 3.09203 |
|  |  | 6 | 2.50899 | 5.518 | 2.0217 | 4.19189 |
|  |  | 7 | 2.86089 | 3.25328 | 2.42252 | 2.00467 |
|  |  | 8 | 2.48937 | 4.32354 | 2.15228 | 3.8626 |
|  |  | 9 | 8.29117 | 6.43036 | 3.96646 | 6.21799 |
| USNM 220064 | Pan | 1 | 1.71685 | 1.62081 - |  |  |
|  |  | 2 | 1.82888 | 3.03814 - |  |  |
|  |  | 3 | 2.20262 - | - |  |  |


|  |  | 4 | 3.80286 - | - |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 5 | 19.464 - | - |  |  |
|  |  | 6 | 24.419 | 6.56938 - |  |  |
|  |  | 7 | 19.9081 | 8.17784 - |  |  |
|  |  | 8 | 6.46213 | 5.36711 - |  |  |
|  |  | 9 | 2.51627 | 4.85283 | 1.41511 | 1.58984 |
|  |  | 10 | 2.11218 | 6.92366 | 2.53997 | 2.89589 |
| USNM 481804 | Pan | 1 | 1.25952 | 3.25788 - |  |  |
|  |  | 2 | 2.36209 | 2.28867 - |  |  |
|  |  | 3 | 5.37531 | 2.39301 - |  |  |
|  |  | 4 | 10.0636 | 5.77208 - |  |  |
|  |  | 5 | 11.738 | 3.30212 | 3.17114 | 3.32093 |
|  |  | 6 | 4.19864 | 4.29794 | 6.03386 | 5.9143 |
|  |  | 7 | 9.35678 | 4.22538 | 2.01102 | 7.45594 |
|  |  | 8 | 3.87038 | 3.32817 | 7.37765 | 4.09128 |
|  |  | 9 | 2.86365 | 4.22111 | 4.72144 | 2.54997 |
|  |  | 10 | 9.57446 | 12.0102 | 2.15711 | 6.16365 |
|  |  | 11 | 2.81607 | 3.43509 | 11.1113 | 4.26027 |
| USNM 153823 | Pongo | 1 | 2.96159 | 2.6375 | 1.94336 | 3.45635 |
|  |  | 2 | 4.03013 | 3.86623 | 2.98125 | 4.03013 |
|  |  | 3 | 4.53068 | 4.37486 | 1.71027 | 5.50001 |
|  |  | 4 | 3.03899 | 3.5762 | 4.17844 | 5.50107 |
|  |  | 5 | 3.91908 | 3.05009 | 2.35092 | 2.76076 |
|  |  | 6 | 2.70816 | 3.73062 | 2.11635 | 5.373 |
|  |  | 7 | 5.24405 | 6.61035 | 2.78541 | 6.14105 |
| USNM 145300 | Pongo | 1 | 2.31354 | 4.87697 - |  | 2.53398 |
|  |  | 2 | 4.60713 | 2.45066 | 1.59743 | 1.83056 |
|  |  | 3 | 5.13889 | 1.79849 | 1.34187 | 3.86722 |
|  |  | 4 | 3.94952 | 2.25372 | 1.35906 | 1.98938 |
|  |  | 5 | 5.43684 | 2.7672 | 1.39808 | 3.07404 |
|  |  | 6 | 4.23908 | 4.62853 | 2.82083 | 2.8841 |
|  |  | 7 | 7.33177 | 3.11963 | 1.28688 | 3.91484 |
|  |  | 8 | 17.1303 | 4.16427 | 12.8979 | 4.19416 |
|  |  | 9 | 2.54724 | 2.70883 | 4.92902 | 2.47666 |
|  |  | 10 | 3.80972 | 2.371 | 2.08714 | 1.9318 |
|  |  | 11 | 2.58518 | 6.13396 | 4.00695 | 2.27145 |
| USNM 145302 | Pongo | 1 | 2.15692 | 2.05135 | 2.35776 | 3.97545 |
|  |  | 2 | 4.71914 | 1.58192 | 2.191 | 3.21421 |
|  |  | 3 | 1.64443 | 1.25606 | 3.8033 | 3.08861 |
|  |  | 4 | 4.78445 | 1.87519 | 3.86071 | 3.79003 |
|  |  | 5 | 2.39561 | 2.22988 | 2.11057 | 3.16726 |
|  |  | 6 | 2.876 | 1.87571 | 1.91963 | 5.97697 |
|  |  | 7 | 1.49103 | 3.12358 | 3.17722 | 3.85602 |
|  |  | 8 | 2.27772 | 2.35193 | 1.73579 | 2.33053 |

$\left.\begin{array}{crrrrr} & 9 & 3.1047 & 2.74157 & 3.19535 & 4.05702 \\ & 10 & 1.46484 & 2.88377 & 1.54711 & 5.04683 \\ \text { USNM 145301 } & \text { Pongo } & 11 & 1.73078 & 6.33581 & 2.58825\end{array}\right) 3.07846$

| AMNH 43086 | Macaca | 1 - | - |  | 3.34304 - |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 2 - | - |  | - |  |
|  |  | 3 - | - |  | - |  |
|  |  | 4 - | - |  | 2.23257 - |  |
|  |  | 5 - | - |  | 8.26796 - |  |
|  |  | 6 - | - |  | 3.77773 | 6.99914 |
|  |  | 7 - | - |  | 3.04135 | 8.71569 |
|  |  | 8 | 2.47847 | 3.00596 | 2.22328 | 7.39299 |
|  |  | 9 | 2.37627 | 5.56001 | 3.97344 | 2.55878 |
|  |  | 10 | 10.514 | 8.05789 | 3.61363 | 3.24165 |
|  |  | 11 | 3.10496 | 1.61947 | 8.5153 | 6.58455 |
|  |  | 12 | 3.67936 | 2.48754 | 4.07187 | 7.47079 |
|  |  | 13 | 3.1149 | 2.8089 | 2.87547 | 16.1408 |
|  |  | 14 | 5.98639 - |  | 5.37659 | 2.2544 |
| UPENN-86-12- |  |  |  |  |  |  |
| 44 | Macaca | 1 - | - |  | 3.10733 | 1.46666 |
|  |  | 2 - | - |  | 3.44731 | 4.37709 |
|  |  | 3 - | - |  | 3.05987 | 7.77952 |
|  |  | 4 - | - |  | 4.14079 | 7.34601 |
|  |  | 5 - | - |  | 4.26514 | 3.95118 |
|  |  | 6 - | - |  | 1.43938 | 3.37918 |
|  |  | 7 - | - |  | 1.52193 | 4.4878 |
|  |  | 8 | 3.13358 | 2.8136 | 2.70301 | 5.74505 |
|  |  | 9 | 2.21134 | 1.91421 | 2.17631 | 4.17229 |
|  |  | 10 | 1.81397 | 2.55644 | 3.31443 | 5.91048 |
|  |  | 11 | 2.29093 | 3.23072 | 9.40596 | 7.38607 |
|  |  | 12 | 2.90801 | 3.42782 | 2.41475 | 3.23287 |
| B22-A | Homo | 1 | 4.81814 | 1.80811 | 3.13597 | 1.67946 |
|  |  | 2 | 1.98985 | 1.66496 | 2.2306 | 2.68229 |
|  |  | 3 | 2.13046 | 2.08974 | 3.41743 | 3.45541 |
| B22-B | Homo | 1 | 1.75141 | 2.05523 | 3.63799 | 2.484 |
|  |  | 2 | 1.99533 | 1.7594 | 1.4308 | 1.66257 |
| TMM2165-A | Homo | 1 | 3.43344 | 2.18882 | 6.38349 | 2.0491 |
|  |  | 2 | 2.09787 | 2.71684 | 3.44529 | 4.07908 |
|  |  | 3 | 2.40172 | 4.36714 | 4.79856 | 2.14627 |
| TMM2165-B | Homo | 1 | 3.80689 | 2.2851 | 4.36676 | 1.57126 |
|  |  | 2 | 1.85988 | 4.05086 | 5.18565 | 2.11887 |
| TARLAC-60-A | Homo | 1 | 1.51599 | 5.59707 | 6.8656 | 3.57602 |
|  |  | 2 | 2.55257 | 3.6374 | 3.58402 | 2.16639 |
|  |  | 3 | 4.08997 | 4.50315 | 2.52874 | 3.21525 |
|  |  | 4 | 1.75309 | 13.2899 | 4.65043 | 1.44405 |


| TARLAC-60-B | Homo | 1 | 4.93981 | 3.05175 | 3.87594 | 3.606 |
| ---: | :--- | :--- | :--- | ---: | ---: | ---: |
|  |  | 2 | 4.26374 | 4.85626 | 3.4892 | 3.67727 |
|  | 3 | 2.67113 | 7.74234 | 4.72779 | 1.58403 |  |

Appendix C.ii.a. Raw bone volume fraction (BVTV) data from the ischium of the complete

| Specimen | Taxon | Stack No. | BVTV <br> Ventral | BVTV <br> Central | BVTV <br> Dorsal |
| :---: | :---: | :---: | :---: | :---: | :---: |
| RU 210 | Rudapithecus | 1 - |  | - - | - |
|  |  | 2 - |  | - | - |
|  |  | 3 - |  | - | - |
|  |  | 4 - |  | - | - |
|  |  | 5 | 0.400454 - |  | 0.433431 |
|  |  | 6 | 0.41706 - |  | 0.450249 |
|  |  | 7 | 0.392311 | 0.422949 | 0.47618 |
|  |  | 8 - |  | - | - 0.476 |
|  |  | 9 - |  | - | - |
| USNM 384228 | Papio | 1 | 0.347959 - |  | 0.539679 |
|  |  | 2 | 0.339883 - |  | 0.625152 |
|  |  | 3 | 0.40747 - |  | 0.657182 |
|  |  | 4 | 0.47737 - |  | 0.59983 |
|  |  | 5 | 0.462511 - |  | 0.46353 |
|  |  | 6 | 0.447804 | 0.365008 | 0.52733 |
|  |  | 7 | 0.410816 | 0.443348 | 0.476944 |
|  |  | 8 | 0.415212 | 0.45842 | 0.397509 |
|  |  | 9 | 0.347777 | 0.439302 | 0.415288 |
|  |  | 10 | 0.336568 | 0.449964 | 0.403836 |
|  |  | 11 | 0.322773 | 0.402634 | 0.559329 |
|  |  | 12 | 0.362651 | 0.379578 | 0.427379 |
| USNM 354987 | Papio | 1 | 0.0444134 | 0.266944 | 0.557578 |
|  |  | 2 | 0.12971 | 0.198452 | 0.50508 |
|  |  | 3 | 0.241111 | 0.260294 | 0.32556 |
|  |  | 4 | 0.244679 | 0.253644 | 0.237335 |
|  |  | 5 | 0.214121 | 0.223267 | 0.245266 |
|  |  | 6 | 0.21827 | 0.211497 | 0.258246 |
|  |  | 7 | 0.152071 | 0.198842 | 0.27048 |
|  |  | 8 | 0.175472 | 0.217257 | 0.30507 |
|  |  | 9 | 0.194949 | 0.227085 | 0.271941 |
| USNM 397476 | Papio | 1 | 0.264159 | 0.261391 | 0.326925 |
|  |  | 2 | 0.317891 | 0.262897 | 0.309892 |
|  |  | 3 | 0.313633 | 0.186337 | 0.342408 |
|  |  | 4 | 0.293573 | 0.19426 | 0.26422 |
|  |  | 5 | 0.281345 | 0.297132 | 0.26784 |
|  |  | 6 | 0.387912 | 0.336066 | 0.374741 |
|  |  | 7 | 0.40601 | 0.269574 | 0.406877 |
|  |  | 8 | 0.198412 | 0.432975 | 0.362225 |


|  |  | 9 | 0.255521 | 0.378909 | 0.344324 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 10 | 0.221727 | 0.331716 | 0.423668 |
|  |  | 11 | 0.182747 | 0.269361 | 0.426055 |
|  |  | 12 | 0.145714 | 0.222761 | 0.321009 |
|  |  | 13 | 0.217408 | 0.248205 | 0.375624 |
|  |  | 14 | 0.278577 | 0.316507 | 0.31158 |
| USNM 384234 | Papio | 1 | 0.362606 | 0.277675 | 0.361495 |
|  |  | 2 | 0.287289 - |  | 0.315053 |
|  |  | 3 | 0.292594 - |  | 0.285937 |
|  |  | 4 | 0.204833 - |  | 0.341442 |
|  |  | 5 | 0.311512 | 0.30497 | 0.361231 |
|  |  | 6 | 0.33247 | 0.265667 | 0.272886 |
|  |  | 7 | 0.35085 | 0.282557 | 0.370902 |
|  |  | 8 | 0.302105 | 0.348203 | 0.459225 |
|  |  | 9 | 0.300157 | 0.354803 | 0.419567 |
|  |  | 10 | 0.298496 | 0.4859 | 0.421136 |
|  |  | 11 | 0.323498 | 0.2686 | 0.389041 |
|  |  | 12 | 0.27952 | 0.315809 | 0.341396 |
|  |  | 13 | 0.284596 | 0.29484 | 0.393739 |
|  |  | 14 | 0.29767 | 0.374913 | 0.412714 |
|  |  | 15 | 0.304236 | 0.325091 | 0.456005 |
|  |  | 16 | 0.312498 | 0.401829 | 0.427679 |
|  |  | 17 | 0.395412 | 0.386325 | 0.390233 |
| USNM 395440 | Papio | 1 | 0.298345 | 0.186274 | 0.281221 |
|  |  | 2 | 0.32057 | 0.185472 | 0.282322 |
|  |  | 3 | 0.175949 | 0.23203 | 0.235013 |
|  |  | 4 | 0.246429 | 0.170138 | 0.273909 |
|  |  | 5 | 0.32453 | 0.269291 | 0.342384 |
|  |  | 6 | 0.278609 | 0.307776 | 0.430142 |
|  |  | 7 | 0.270669 | 0.35057 | 0.373176 |
|  |  | 8 | 0.287855 | 0.323326 | 0.317248 |
|  |  | 9 | 0.247725 | 0.333796 | 0.176833 |
|  |  | 10 | 0.261784 | 0.256322 | 0.321444 |
|  |  | 11 | 0.268335 | 0.217519 | 0.331564 |
|  |  | 12 | 0.26707 | 0.280131 | 0.275956 |
|  |  | 13 | 0.273446 | 0.254152 | 0.202822 |
|  |  | 14 | 0.227382 | 0.181934 | 0.215164 |
|  |  | 15 | 0.243374 | 0.251725 | 0.233552 |
|  |  | 16 | 0.261804 | 0.258852 | 0.255068 |
|  |  | 17 | 0.307396 | 0.232308 | 0.282733 |
| USNM 384227 | Papio | 1 | 0.278434 | 0.187412 | 0.262343 |
|  |  | 2 | 0.237215 | 0.263589 | 0.314816 |
|  |  | 3 | 0.359466 | 0.286409 | 0.367998 |


|  |  | 4 | 0.374257 | 0.332349 | 0.50267 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 5 | 0.376229 | 0.370623 | 0.43979 |
|  |  | 6 | 0.300087 | 0.286577 | 0.375628 |
|  |  | 7 | 0.207765 | 0.287824 | 0.43117 |
|  |  | 8 | 0.23077 | 0.29449 | 0.452637 |
|  |  | 9 | 0.326805 | 0.343162 | 0.442761 |
| USNM 141161 | Symphalangus | 1 | 0.263809 - |  | 0.270988 |
|  |  | 2 | 0.32104 | 0.360339 | 0.453507 |
|  |  | 3 | 0.425584 | 0.367396 | 0.423835 |
|  |  | 4 | 0.419972 | 0.428291 | 0.39725 |
|  |  | 5 | 0.363639 | 0.395988 | 0.382391 |
|  |  | 6 | 0.342271 | 0.29409 | 0.404642 |
|  |  | 7 | 0.367943 | 0.284174 | 0.34913 |
| USNM 141162 | Symphalangus | 1 | 0.266564 | 0.204964 | 0.315269 |
|  |  | 2 | 0.329857 | 0.282659 | 0.268501 |
|  |  | 3 | 0.3143 | 0.270771 | 0.313293 |
|  |  | 4 | 0.349386 | 0.335473 | 0.323106 |
|  |  | 5 | 0.346294 | 0.387034 | 0.37001 |
|  |  | 6 | 0.283706 | 0.425974 | 0.427119 |
|  |  | 7 | 0.315602 | 0.356469 | 0.42393 |
|  |  | 8 | 0.326922 | 0.407395 | 0.421043 |
| USNM 141160 | Symphalangus | 1 | 0.246707 | 0.192949 | 0.265522 |
|  |  | 2 | 0.339111 | 0.306715 | 0.390948 |
|  |  | 3 | 0.30146 | 0.316097 | 0.283936 |
|  |  | 4 | 0.327865 | 0.32096 | 0.277348 |
|  |  | 5 | 0.260718 | 0.308073 | 0.280853 |
|  |  | 6 | 0.251687 | 0.288418 | 0.28759 |
|  |  | 7 | 0.273396 | 0.272277 | 0.292545 |
| AMNH 106581 | Symphalangus | 1 | 0.227189 | 0.133683 | 0.242441 |
|  |  | 2 | 0.290664 | 0.239014 | 0.296394 |
|  |  | 3 | 0.321819 | 0.326967 | 0.391499 |
|  |  | 4 | 0.31082 | 0.269628 | 0.409569 |
| USNM 220327 | Pan | 1 | 0.0933572 | 0.111195 | 0.356179 |
|  |  | 2 | 0.10952 | 0.0627709 | 0.317205 |
|  |  | 3 | 0.134863 | 0.0757752 | 0.323816 |
|  |  | 4 | 0.159286 | 0.171319 | 0.31062 |
|  |  | 5 | 0.192775 | 0.223617 | 0.344351 |
|  |  | 6 | 0.254766 | 0.270264 | 0.39408 |
|  |  | 7 | 0.216137 | 0.263155 | 0.363391 |
|  |  | 8 | 0.189106 | 0.274164 | 0.423477 |
|  |  | 9 | 0.204514 | 0.290851 | 0.375769 |


|  | 10 | 0.188236 | 0.305466 | 0.341283 |  |
| :---: | :---: | ---: | ---: | ---: | ---: |
| USNM 220065 | Pan | 11 | 0.226673 | 0.339147 | 0.358941 |
|  |  | 12 | 0.293421 | 0.338111 | 0.381843 |
|  |  | 1 | 0.146472 | 0.147234 | 0.190831 |
|  |  | 2 | 0.196828 | 0.197166 | 0.291312 |
|  |  | 3 | 0.223063 | 0.226618 | 0.268147 |
|  |  | 4 | 0.245103 | 0.318043 | 0.388178 |
|  |  | 5 | 0.281833 | 0.305542 | 0.427616 |
|  |  | 6 | 0.324584 | 0.336674 | 0.460767 |
|  |  | 7 | 0.281894 | 0.343106 | 0.405298 |
|  |  | 8 | 0.259322 | 0.276417 | 0.346903 |
|  |  | 10 | 0.248573 | 0.285436 | 0.323145 |
|  |  | 11 | 0.249855 | 0.234754 | 0.350832 |
|  |  |  |  |  | 0.2463 |


|  |  | 7 | 0.253568 | 0.340892 | 0.364896 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 8 | 0.212365 | 0.284078 | 0.32762 |
|  |  | 9 | 0.234844 | 0.237649 | 0.292668 |
|  |  | 10 | 0.277964 | 0.275528 | 0.246856 |
| USNM 153823 | Pongo | 1 | 0.178488 | 0.118683 | 0.197776 |
|  |  | 2 | 0.147265 | 0.194162 | 0.314433 |
|  |  | 3 | 0.239939 | 0.266549 | 0.390749 |
|  |  | 4 | 0.28879 | 0.426996 | 0.423537 |
|  |  | 5 | 0.31384 | 0.404673 | 0.343241 |
|  |  | 6 | 0.310127 | 0.31119 | 0.294972 |
|  |  | 7 | 0.275209 | 0.306667 | 0.28392 |
|  |  | 8 | 0.267367 | 0.311222 | 0.330537 |
|  |  | 9 | 0.244249 | 0.285077 | 0.353638 |
| USNM 145300 | Pongo | 1 | 0.178992 | 0.160364 | 0.204748 |
|  |  | 2 | 0.158962 | 0.174583 | 0.30313 |
|  |  | 3 | 0.200249 | 0.25179 | 0.317323 |
|  |  | 4 | 0.203845 | 0.232973 | 0.252909 |
|  |  | 5 | 0.193587 | 0.237098 | 0.244849 |
|  |  | 6 | 0.189533 | 0.254025 | 0.292567 |
| USNM 145302 | Pongo | 1 | 0.15816 | 0.164236 | 0.209149 |
|  |  | 2 | 0.179152 | 0.225076 | 0.299732 |
|  |  | 3 | 0.248784 | 0.268053 | 0.329531 |
|  |  | 4 | 0.269385 | 0.296025 | 0.358528 |
|  |  | 5 | 0.292004 | 0.313339 | 0.314902 |
|  |  | 6 | 0.236527 | 0.25395 | 0.346178 |
|  |  | 7 | 0.209514 | 0.264085 | 0.306789 |
|  |  | 8 | 0.182599 | 0.232309 | 0.299699 |
| USNM 145301 | Pongo | 1 | 0.182121 | 0.127898 | 0.165743 |
|  |  | 2 | 0.169283 | 0.165538 | 0.238914 |
|  |  | 3 | 0.258672 | 0.2479 | 0.354254 |
|  |  | 4 | 0.252738 | 0.285129 | 0.260802 |
|  |  | 5 | 0.275289 | 0.324906 | 0.225859 |
|  |  | 6 | 0.25326 | 0.283357 | 0.248176 |
|  |  | 7 | 0.245737 | 0.277337 | 0.268333 |
|  |  | 8 | 0.286177 | 0.2952 | 0.316722 |
|  |  | 9 | 0.290247 | 0.302101 | 0.315678 |
| USNM 145304 | Pongo | 1 | 0.206052 | 0.122558 | 0.239152 |
|  |  | 2 | 0.200842 | 0.254379 | 0.323468 |
|  |  | 3 | 0.295805 | 0.301996 | 0.330026 |
|  |  | 4 | 0.312782 | 0.320493 | 0.366373 |
|  |  | 5 | 0.272708 | 0.314179 | 0.351553 |


|  |  | 6 | 0.241996 | 0.298428 | 0.308418 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| USNM 253780 | Macaca | 1 | 0.134151 | 0.156856 | 0.365584 |
|  |  | 2 | 0.240186 - |  | 0.333339 |
|  |  | 3 | 0.172585 - |  | 0.262962 |
|  |  | 4 | 0.150958 - |  | 0.197959 |
|  |  | 5 | 0.236138 - |  | 0.248347 |
|  |  | 6 | 0.206164 | 0.202433 | 0.213812 |
|  |  | 7 | 0.216429 | 0.284473 | 0.267515 |
|  |  | 8 | 0.183627 | 0.252529 | 0.196094 |
|  |  | 9 | 0.0644274 | 0.210815 | 0.191426 |
|  |  | 10 | 0.0842676 | 0.0960974 | 0.220116 |
|  |  | 11 | 0.224325 - |  | 0.238073 |
| USNM 173813 | Macaca | 1 | 0.37033 | 0.27688 | 0.385612 |
|  |  | 2 | 0.244078 - |  | 0.313696 |
|  |  | 3 | 0.275207 - |  | 0.305375 |
|  |  | 4 | 0.296114 | 0.30479 | 0.378128 |
|  |  | 5 | 0.293772 | 0.307758 | 0.358581 |
|  |  | 6 | 0.330441 | 0.331487 | 0.407815 |
|  |  | 7 | 0.374971 | 0.292643 | 0.467982 |
|  |  | 8 | 0.399557 | 0.330588 | 0.430142 |
|  |  | 9 | 0.418519 | 0.301716 | 0.38902 |
|  |  | 10 | 0.366065 | 0.324755 | 0.426505 |
|  |  | 11 | 0.237744 | 0.312985 | 0.388581 |
|  |  | 12 | 0.226434 | 0.295256 | 0.362365 |
|  |  | 13 | 0.174837 | 0.249389 | 0.444003 |
|  |  | 14 | 0.255305 | 0.226935 | 0.317898 |
| AMNH 43086 | Macaca | 1 | 0.255794 | 0.093349 | 0.291024 |
|  |  | 2 | 0.235865 - |  | 0.120907 |
|  |  | 3 | 0.196842 - |  | 0.18029 |
|  |  | 4 | 0.235722 - |  | 0.292921 |
|  |  | 5 | 0.218552 | 0.292763 | 0.405207 |
|  |  | 6 | 0.222245 | 0.154384 | 0.282978 |
|  |  | 7 | 0.183796 | 0.208767 | 0.211526 |
|  |  | 8 | 0.200994 | 0.201037 | 0.230434 |
|  |  | 9 | 0.168293 | 0.186985 | 0.243552 |
| UPENN-86-12-44 | Macaca | 1 | 0.131195 - |  | 0.154974 |
|  |  | 2 | 0.15936 - |  | 0.202209 |
|  |  | 3 | 0.140453 | 0.135613 | 0.249996 |
|  |  | 4 | 0.153691 | 0.198083 | 0.289905 |
|  |  | 5 | 0.21535 | 0.184342 | 0.229449 |
|  |  | 6 | 0.178056 | 0.159929 | 0.279769 |
|  |  | 7 | 0.188208 | 0.285536 | 0.331081 |


|  | 8 | 0.187883 | 0.261463 | 0.309868 |
| :--- | ---: | ---: | ---: | ---: |
|  | 9 | 0.179794 | 0.189604 | 0.3067 |
|  |  | 10 | 0.132884 | 0.146804 |
| B22 | 11 | 0.0871274 | 0.261935 | 0.233537 |
|  |  | 12 | 0.124243 | 0.201218 |

Appendix C.ii.b. Raw degree of anisotropy (DA) data from the ischium of the complete sample.

| Specimen | Taxon |  | DA | DA | DA |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Stack No. | Ventral | Central | Dorsal |
| RU 210 | Rudapithecus | 1 - | - | - . | - |
|  |  | 2 - | - | - - | - |
|  |  | 3 - |  | - - | - |
|  |  | 4 - | - | - - | - |
|  |  | 5 | 2.64093 |  | 1.94756 |
|  |  | 6 | 1.84777 |  | 3.47559 |
|  |  | 7 | 1.9416 | 1.91909 | 2.30637 |
|  |  | 8 - |  | - - | - |
|  |  | 9 - | - | - - | - |
| USNM 384228 | Papio | 1 | 2.1351 |  | 3.42859 |
|  |  | 2 | 4.8789 |  | 4.00835 |
|  |  | 3 | 4.00621 |  | 5.61725 |
|  |  | 4 | 1.89675 |  | 3.27499 |
|  |  | 5 | 2.21793 |  | 4.40803 |
|  |  | 6 | 2.63303 | 7.10144 | 2.53121 |
|  |  | 7 | 2.59576 | 3.14279 | 3.5556 |
|  |  | 8 | 2.11933 | 3.33827 | 2.76677 |
|  |  | 9 | 1.93737 | 2.95836 | 2.41319 |
|  |  | 10 | 1.9915 | 6.38751 | 1.47573 |
|  |  | 11 | 4.90673 | 9.61666 | 2.08351 |
|  |  | 12 | 4.23545 | 6.09985 | 8.59536 |
| USNM 354987 | Papio | 1 | 14.9366 | 4.66201 | 5.00852 |
|  |  | 2 | 9.74073 | 6.71103 | 4.02793 |
|  |  | 3 | 2.26357 | 4.19353 | 3.23803 |
|  |  | 4 | 2.32381 | 3.44014 | 5.68615 |
|  |  | 5 | 5.73478 | 8.43407 | 8.45496 |
|  |  | 6 | 2.3199 | 5.58683 | 10.0005 |
|  |  | 7 | 1.76348 | 3.72734 | 3.65903 |
|  |  | 8 | 2.21926 | 7.60136 | 2.8712 |
|  |  | 9 | 2.22897 | 2.83563 | 2.33502 |
| USNM 397476 | Papio | 1 | 11.5497 | 4.0439 | 5.36436 |
|  |  | 2 | 4.14827 | 4.54558 | 4.5318 |
|  |  | 3 | 4.02836 | 7.85801 | 2.21273 |
|  |  | 4 | 10.4824 | 9.37483 | 5.69739 |
|  |  | 5 | 4.43538 | 2.04596 | 5.62163 |
|  |  | 6 | 4.23751 | 2.26073 | 7.79104 |
|  |  | 7 | 2.46002 | 3.23185 | 4.04653 |
|  |  | 8 | 3.07246 | 3.14996 | 6.03728 |
|  |  | 9 | 2.84313 | 2.84313 | 5.93793 |
|  |  | 10 | 2.11816 | 3.44753 | 3.3574 |


|  |  | 11 | 1.97115 | 5.67064 | 1.9038 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 12 | 2.71444 | 11.4182 | 4.48312 |
|  |  | 13 | 1.90748 | 2.22827 | 7.43574 |
|  |  | 14 | 4.38679 | 3.19952 | 3.31529 |
| USNM 384234 | Papio | 1 | 2.58496 | 10.8581 | 4.93162 |
|  |  | 2 | 3.3733 - |  | 10.6046 |
|  |  | 3 | 2.89217 - |  | 12.4071 |
|  |  | 4 | 4.12981 - |  | 36.4968 |
|  |  | 5 | 2.04511 | 4.73936 | 12.8526 |
|  |  | 6 | 4.89455 | 4.56318 | 15.0149 |
|  |  | 7 | 2.98835 | 2.57753 | 3.87604 |
|  |  | 8 | 4.13719 | 3.62107 | 2.48705 |
|  |  | 9 | 1.68472 | 6.91982 | 5.14698 |
|  |  | 10 | 4.50235 | 2.43988 | 3.50973 |
|  |  | 11 | 1.64274 | 3.35632 | 4.27527 |
|  |  | 12 | 3.14575 | 1.81813 | 4.58224 |
|  |  | 13 | 1.65771 | 2.2328 | 5.56815 |
|  |  | 14 | 1.74483 | 3.81065 | 4.57716 |
|  |  | 15 | 2.21072 | 4.41444 | 4.66956 |
|  |  | 16 | 3.11107 | 4.74528 | 7.22098 |
|  |  | 17 | 4.06292 | 5.66033 | 6.90013 |
| USNM 395440 | Papio | 1 | 5.88019 | 1.97201 | 6.06874 |
|  |  | 2 | 3.34736 | 7.25969 | 6.89874 |
|  |  | 3 | 7.05734 | 4.43763 | 9.32704 |
|  |  | 4 | 6.21296 | 23.523 | 6.11288 |
|  |  | 5 | 3.15694 | 5.45874 | 3.79954 |
|  |  | 6 | 2.80159 | 3.38646 | 2.48004 |
|  |  | 7 | 1.77096 | 1.72654 | 5.07518 |
|  |  | 8 | 2.60716 | 2.99114 | 2.58173 |
|  |  | 9 | 1.94774 | 2.3066 | 3.67464 |
|  |  | 10 | 5.04 | 3.23677 | 4.62289 |
|  |  | 11 | 1.78834 | 1.33166 | 2.51851 |
|  |  | 12 | 3.12113 | 2.24207 | 2.38568 |
|  |  | 13 | 2.55218 | 2.62619 | 2.01716 |
|  |  | 14 | 1.84176 | 1.42243 | 4.87811 |
|  |  | 15 | 3.15971 | 2.18808 | 3.14525 |
|  |  | 16 | 2.53818 | 1.53795 | 3.17097 |
|  |  | 17 | 3.16106 | 3.22167 | 1.67186 |
| USNM 384227 | Papio | 1 | 2.38762 | 6.94397 | 4.5775 |
|  |  | 2 | 2.08893 | 3.79142 | 3.10364 |
|  |  | 3 | 1.58844 | 6.94985 | 3.72229 |
|  |  | 4 | 2.61388 | 3.88762 | 3.77359 |
|  |  | 5 | 1.56574 | 2.72233 | 4.50835 |


|  |  | 6 | 1.63701 | 3.43309 | 3.43511 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 7 | 5.06862 | 2.11622 | 3.37607 |
|  |  | 8 | 2.88312 | 6.87349 | 2.72923 |
|  |  | 9 | 3.43278 | 8.19957 | 3.87162 |
| USNM 141161 | Symphalangus | 1 | 2.79516 - |  | 4.10629 |
|  |  | 2 | 3.41358 | 2.2127 | 2.78314 |
|  |  | 3 | 1.50025 | 1.62752 | 2.53444 |
|  |  | 4 | 2.09753 | 1.85637 | 3.0737 |
|  |  | 5 | 1.8205 | 5.50217 | 1.62012 |
|  |  | 6 | 2.05137 | 3.55888 | 2.47472 |
|  |  | 7 | 10.8357 | 5.33682 | 2.97608 |
| USNM 141162 | Symphalangus | 1 | 6.2486 | 5.12161 | 5.63608 |
|  |  | 2 | 2.41229 | 3.74634 | 5.96121 |
|  |  | 3 | 2.19562 | 3.54614 | 5.69591 |
|  |  | 4 | 2.72822 | 4.48512 | 3.47032 |
|  |  | 5 | 1.74942 | 3.30773 | 3.16761 |
|  |  | 6 | 1.79604 | 4.62024 | 2.88996 |
|  |  | 7 | 2.32134 | 5.3301 | 2.45185 |
|  |  | 8 | 2.71421 | 2.67993 | 1.85527 |
| USNM 141160 | Symphalangus | 1 | 1.56287 | 1.825 | 2.72042 |
|  |  | 2 | 2.47577 | 1.97078 | 3.71889 |
|  |  | 3 | 2.56669 | 3.49468 | 6.16595 |
|  |  | 4 | 5.3211 | 3.00163 | 3.25462 |
|  |  | 5 | 3.92026 | 2.72022 | 2.74179 |
|  |  | 6 | 5.16031 | 1.53106 | 2.00373 |
|  |  | 7 | 3.46811 | 1.70806 | 4.91107 |
| AMNH 106581 | Symphalangus | 1 | 2.04181 | 2.46249 | 4.81444 |
|  |  | 2 | 1.66723 | 1.98962 | 4.14805 |
|  |  | 3 | 1.99255 | 1.86456 | 3.5947 |
|  |  | 4 | 3.21898 | 1.69892 | 6.79673 |
| USNM 220327 | Pan | 1 | 4.22467 | 57.3074 | 7.03529 |
|  |  | 2 | 2.91495 | 16.4487 | 5.67404 |
|  |  | 3 | 3.99149 | 3.51175 | 8.05608 |
|  |  | 4 | 2.74244 | 9.98251 | 9.0872 |
|  |  | 5 | 2.8717 | 7.82063 | 10.575 |
|  |  | 6 | 2.82132 | 10.5857 | 9.82027 |
|  |  | 7 | 4.60424 | 8.19908 | 17.7162 |
|  |  | 8 | 3.08659 | 5.51937 | 6.67758 |
|  |  | 9 | 4.97859 | 5.69179 | 4.17941 |
|  |  | 10 | 2.33523 | 4.32125 | 4.12266 |
|  |  | 11 | 3.55092 | 2.31123 | 1.9858 |


|  |  | 12 | 3.06693 | 3.28614 | 3.12915 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| USNM 220065 | Pan | 1 | 1.96443 | 2.29188 | 5.94319 |
|  |  | 2 | 2.3645 | 3.62384 | 2.75175 |
|  |  | 3 | 2.44543 | 1.99803 | 4.34501 |
|  |  | 4 | 2.56296 | 2.97096 | 1.96134 |
|  |  | 5 | 2.03822 | 2.23031 | 2.61422 |
|  |  | 6 | 2.06985 | 2.1883 | 3.30853 |
|  |  | 7 | 1.9215 | 2.16366 | 1.98874 |
|  |  | 8 | 1.74999 | 2.56682 | 1.47227 |
|  |  | 9 | 1.4892 | 2.00399 | 2.03541 |
|  |  | 10 | 2.46515 | 1.72646 | 1.66772 |
|  |  | 11 | 1.86936 | 1.88658 | 1.96925 |
| USNM 176227 | Pan | 1 | 3.99938 | 8.73455 | 12.6867 |
|  |  | 2 | 2.99709 | 8.3622 | 27.1931 |
|  |  | 3 | 4.22656 | 7.68863 | 13.4046 |
|  |  | 4 | 4.83235 | 6.6772 | 4.52559 |
|  |  | 5 | 4.82609 | 3.39974 | 5.83066 |
|  |  | 6 | 3.80329 | 10.9892 | 8.56793 |
|  |  | 7 | 4.36505 | 6.69141 | 5.50844 |
|  |  | 8 | 1.73169 | 9.6888 | 6.02502 |
|  |  | 9 | 1.93809 | 7.58983 | 3.44385 |
|  |  | 10 | 3.1404 | 3.42076 | 3.76809 |
|  |  | 11 | 2.31151 | 3.85757 | 5.37832 |
|  |  | 12 | 2.32655 | 3.26587 | 5.32902 |
|  |  | 13 | 7.35093 | 2.97514 | 4.7093 |
| USNM 220064 | Pan | 1 | 14.249 | 7.21418 | 15.1789 |
|  |  | 2 | 6.42256 | 9.55413 | 6.37918 |
|  |  | 3 | 2.98002 | 2.15461 | 3.93669 |
|  |  | 4 | 2.72318 | 3.37389 | 4.78203 |
|  |  | 5 | 2.20977 | 3.89959 | 2.99263 |
|  |  | 6 | 1.46987 | 2.80202 | 4.09382 |
|  |  | 7 | 1.87919 | 3.43827 | 2.18476 |
|  |  | 8 | 2.0292 | 2.41003 | 1.92248 |
|  |  | 9 | 1.83733 | 1.46164 | 1.71447 |
| USNM 481804 | Pan | 1 | 3.41538 | 27.373 | 7.68096 |
|  |  | 2 | 4.19418 | 4.78011 | 9.15746 |
|  |  | 3 | 2.86858 | 3.95228 | 6.84116 |
|  |  | 4 | 4.47703 | 5.87883 | 4.26488 |
|  |  | 5 | 5.50216 | 5.23491 | 4.6222 |
|  |  | 6 | 5.64323 | 5.06152 | 4.40333 |
|  |  | 7 | 3.86177 | 4.08066 | 3.81817 |
|  |  | 8 | 1.92358 | 3.11544 | 2.66794 |


|  | Pongo | 9 | 2.94621 | 2.23262 | 1.97624 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 10 | 2.06431 | 3.44379 | 2.52711 |
| USNM 153823 |  | 1 | 2.18804 | 6.40937 | 8.05133 |
|  |  | 2 | 3.9101 | 5.95323 | 5.62479 |
|  |  | 3 | 2.58619 | 4.46565 | 3.56003 |
|  |  | 4 | 2.06869 | 2.06181 | 2.22782 |
|  |  | 5 | 2.88184 | 1.78178 | 3.41732 |
|  |  | 6 | 2.14466 | 2.81774 | 2.57392 |
|  |  | 7 | 2.20488 | 2.50544 | 2.97022 |
|  |  | 8 | 1.78579 | 1.60179 | 2.07116 |
|  |  | 9 | 2.10774 | 2.2684 | 2.34283 |
| USNM 145300 | Pongo | 1 | 8.09731 | 15.7124 | 2.67381 |
|  |  | 2 | 2.84865 | 3.1096 | 2.81407 |
|  |  | 3 | 1.89512 | 2.21113 | 4.6922 |
|  |  | 4 | 3.8554 | 2.97372 | 3.29751 |
|  |  | 5 | 3.28531 | 2.34916 | 1.44783 |
|  |  | 6 | 1.69184 | 1.42856 | 2.3364 |
| USNM 145302 | Pongo | 1 | 3.1572 | 4.03082 | 3.93714 |
|  |  | 2 | 4.10879 | 2.71114 | 2.70193 |
|  |  | 3 | 1.92192 | 1.87554 | 2.51892 |
|  |  | 4 | 2.43594 | 1.75768 | 4.04535 |
|  |  | 5 | 1.87462 | 1.75557 | 3.31885 |
|  |  | 6 | 2.58613 | 2.11729 | 3.45443 |
|  |  | 7 | 1.42769 | 2.2169 | 3.1461 |
|  |  | 8 | 2.56383 | 1.77067 | 2.14811 |
| USNM 145301 | Pongo | 1 | 3.49492 | 9.3998 | 3.54459 |
|  |  | 2 | 4.99375 | 3.91455 | 5.659 |
|  |  | 3 | 2.28559 | 4.23817 | 2.45778 |
|  |  | 4 | 2.14997 | 2.21142 | 2.86682 |
|  |  | 5 | 2.61634 | 2.99729 | 2.47648 |
|  |  | 6 | 2.58139 | 2.57651 | 1.79771 |
|  |  | 7 | 1.53455 | 1.78478 | 3.07182 |
|  |  | 8 | 1.45305 | 3.18386 | 1.93638 |
|  |  | 9 | 3.99904 | 3.43614 | 1.7444 |
| USNM 145304 | Pongo | 1 | 5.22786 | 7.09534 | 4.30951 |
|  |  | 2 | 3.74479 | 4.98137 | 4.65689 |
|  |  | 3 | 1.86507 | 3.40706 | 3.22823 |
|  |  | 4 | 1.71771 | 3.89593 | 3.03655 |
|  |  | 5 | 2.39065 | 3.05725 | 2.03948 |
|  |  | 6 | 2.3157 | 2.94044 | 1.94517 |


| USNM 253780 | Macaca | 1 | 42.4438 | 16.8129 | 8.98497 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 2 | 2.0179 - |  | 3.66257 |
|  |  | 3 | 3.91818 - |  | 4.62426 |
|  |  | 4 | 11.4073 - |  | 13.2764 |
|  |  | 5 | 3.21956 - |  | 4.56683 |
|  |  | 6 | 7.00279 | 4.75737 | 3.86202 |
|  |  | 7 | 6.76146 | 3.29638 | 3.84689 |
|  |  | 8 | 3.42739 | 4.38499 | 3.36676 |
|  |  | 9 | 4.37195 | 3.0592 | 4.09827 |
|  |  | 10 | 2.01746 | 3.52549 | 2.46378 |
|  |  | 11 | 3.77274 - |  | 2.1827 |
| USNM 173813 | Macaca | 1 | 3.26488 | 3.37739 | 6.59966 |
|  |  | 2 | 4.41497 - |  | 4.69327 |
|  |  | 3 | 2.48821 - |  | 2.36506 |
|  |  | 4 | 2.49304 | 6.59954 | 3.42886 |
|  |  | 5 | 3.17014 | 2.8095 | 2.81522 |
|  |  | 6 | 1.777 | 3.06239 | 4.68045 |
|  |  | 7 | 2.31848 | 5.93965 | 3.14325 |
|  |  | 8 | 1.91902 | 3.22104 | 2.98582 |
|  |  | 9 | 1.64699 | 10.9725 | 2.98509 |
|  |  | 10 | 1.67298 | 2.17434 | 1.87623 |
|  |  | 11 | 3.83919 | 3.05647 | 2.62244 |
|  |  | 12 | 2.98552 | 2.35905 | 5.81037 |
|  |  | 13 | 2.08697 | 1.89873 | 1.78204 |
|  |  | 14 | 1.33164 | 2.02759 | 1.57052 |
| AMNH 43086 | Macaca | 1 | 3.44259 | 11.408 | 7.04558 |
|  |  | 2 | 2.90303 - |  | 12.3212 |
|  |  | 3 | 4.96363 - |  | 3.88009 |
|  |  | 4 | 4.6426 - |  | 5.14372 |
|  |  | 5 | 3.00729 | 2.58465 | 3.562 |
|  |  | 6 | 2.23448 | 4.30926 | 6.78987 |
|  |  | 7 | 5.31577 | 1.71081 | 9.9199 |
|  |  | 8 | 3.62912 | 3.90598 | 4.86416 |
|  |  | 9 | 2.92162 | 3.8719 | 7.29801 |
| UPENN-86-12-44 | Macaca | 1 | 8.57558 - |  | 22.9028 |
|  |  | 2 | 7.23525 - |  | 19.6942 |
|  |  | 3 | 2.42612 | 3.64915 | 9.55464 |
|  |  | 4 | 12.3797 | 6.24752 | 4.6628 |
|  |  | 5 | 8.91257 | 15.7883 | 10.422 |
|  |  | 6 | 2.97801 | 2.61519 | 6.99563 |
|  |  | 7 | 4.01828 | 5.04131 | 2.70382 |
|  |  | 8 | 1.5254 | 5.87648 | 3.49583 |
|  |  | 9 | 4.61678 | 3.02952 | 3.29332 |


|  |  | 10 | 7.4267 | 4.14236 | 11.3007 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 11 | 2.80447 | 2.68251 | 10.1638 |
|  |  | 12 | 3.61171 | 7.76292 | 5.60413 |
|  |  | 13 | 2.6299 | 3.23881 | 1.98757 |
|  |  | 14 | 1.56515 | 7.29024 | 6.08877 |
| B22 | Homo | 1 | 4.37266 | 2.30484 | 2.09489 |
|  |  | 2 | 11.3096 | 5.69791 | 1.84077 |
|  |  | 3 | 2.40984 | 2.40369 | 2.90146 |
|  |  | 4 | 2.86517 | 2.9851 | 1.85714 |
|  |  | 5 | 1.78849 | 1.81298 | 1.53014 |
|  |  | 6 | 1.9524 | 1.45605 | 1.981 |
|  |  | 7 | 2.02668 | 2.18983 | 2.0831 |
| TMM2165 | Homo | 1 | 5.292 | 4.16969 | 2.67281 |
|  |  | 2 | 2.38924 | 2.94442 | 2.6462 |
|  |  | 3 | 2.56413 | 3.00376 | 3.72571 |
|  |  | 4 | 1.95929 | 2.65925 | 5.95185 |
|  |  | 5 | 1.45851 | 3.00399 | 2.05392 |
|  |  | 6 | 1.24606 | 1.53274 | 2.14504 |
|  |  | 7 | 2.99827 | 2.4491 | 2.59027 |
| TARL B-3 | Homo | 1 | 4.23158 | 2.92965 | 3.64517 |
|  |  | 2 | 6.19305 | 2.65461 | 6.45642 |
|  |  | 3 | 3.02183 | 1.43012 | 3.75137 |
|  |  | 4 | 2.3531 | 3.40055 | 2.2578 |
|  |  | 5 | 1.43678 | 2.85418 | 1.89882 |
|  |  | 6 | 1.56773 | 3.83768 | 1.83251 |
|  |  | 7 | 2.17949 | 5.76755 | 2.44256 |
| TARLAC-60 | Homo | 1 | 4.2531 | 6.81346 | 4.11167 |
|  |  | 2 | 2.26382 | 3.68508 | 3.0004 |
|  |  | 3 | 2.7725 | 2.03216 | 2.55683 |
|  |  | 4 | 2.33077 | 1.92458 | 1.50802 |
|  |  | 5 | 1.59257 | 2.12224 | 1.86099 |
|  |  | 6 | 2.20942 | 1.61374 | 2.14936 |
|  |  | 7 | 2.47755 | 1.51217 | 1.55996 |

Appendix D.i.a. Standardized bone volume fraction (BVTV) data from the lower ilium of the extant sample.

| Specimen Taxon | Level | BVTV <br> Med | BVTV <br> Lat | BVTV <br> Dors | BVTV <br> Vent |
| :---: | :---: | :---: | :---: | :---: | :---: |
| USNM 384228 Papio | 0 | 0.341312 | 0.352455 |  | - |
|  | 2 | 0.268479419 | 0.3184206194 |  | - |
|  |  | 0.2951008769 | 0.3953555269 |  | - |
|  | 6 | 0.27417575 | 0.431092 |  | - |
|  | 8 | 0.2614334337 | 0.349121012 |  | - |
|  | 10 | 0.312755 | 0.417557 | 0.407543 | 0.277382 |
| USNM 354987 Papio | 0 | 0.270471 | 0.230898 |  | - |
|  | 2 | 0.16214193 | 0.2121891429 |  | - |
|  |  | 0.2359838512 | 0.2055736036 |  | - |
|  | 6 | 0.1578649167 | 0.2325854306 |  | - |
|  | 8 | 0.1894771127 | 0.3332193521 | 0.236324507 | 0.2479900986 |
|  | 10 | 0.126566 | 0.351761 | 0.383258 | 0.251475 |
| USNM 397476 Papio | 0 | 0.205454 | 0.251977 | - | - |
|  | 2 | 0.222919467 | 0.2896139279 |  | - |
|  |  | 0.2597816824 | 0.3164297403 |  | - |
|  | 6 | 0.3763524675 | 0.3896352597 |  | - |
|  | 8 | 0.3158458961 | 0.357755961 | 0.3594664805 | 0.4222961169 |
|  | 10 | 0.285482 | 0.339412 | 0.412352 | 0.367989 |
| USNM 384234 Papio | 0 | 0.300165 | 0.302078 |  | - |
|  | 2 | 0.2254408 | 0.282413 - |  | - |
|  | 4 | 0.1889452 | 0.4158948 |  | - |
|  | 6 | 0.2462124 | 0.3896508 |  | - |
|  | 8 | 0.223058 | 0.344509 |  | - |
|  | 10 | 0.243112 | 0.345525 | 0.356105 | 0.353476 |
| USNM 395440 Papio | 0 | 0.245393 | 0.330236 |  | - |
|  |  | 0.2100869362 | 0.2403599615 |  | - |
|  |  | 0.1384624595 | 0.2171905033 |  | - |
|  |  | 0.1877119341 | 0.3529615934 |  | - |
|  | 8 | 0.2543834615 | 0.4001592088 |  | - |
|  | 10 | 0.36473 | 0.359826 | 0.46482 | 0.28722 |
| USNM 384227 Papio | 0 | 0.177241 | 0.200697 - |  | - |
|  | 2 | 0.1251822605 | 0.2623642504 |  | - |
|  |  | 0.2422820074 | 0.3240315009 |  | - |
|  |  | 0.2765860694 | 0.3668204722 |  | - |
|  | 8 | 0.2168856056 | 0.2801441268 | 0.353129338 | 0.3197472394 |
|  | 10 | 0.206483 | 0.271201 | 0.32359 | 0.315924 |


| USNM 141161 Symphalangus | 0 | 0.148558 - |  | - | - |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | 2 | 0.266288 - |  | - | - |
|  | 4 | 0.29193 | 0.416885 - |  | - |
|  | 6 | 0.318135 | 0.392307 - |  | - |
|  | 8 | 0.360263 | 0.400322 | 0.330089 | 0.331488 |
|  | 10 | 0.437538 | 0.406269 | 0.316812 | 0.340446 |
| USNM 141162 Symphalangus | 0 | 0.250937 | 0.221593 - |  | - |
|  | 20.19078933490 .2010286436 - |  |  |  | - |
|  | 40.1881613930 .2262178862 - |  |  |  |  |
|  | 60.27443792790 .4082627027 - |  |  |  | - |
|  | 80.22232261260 .4 |  | 0.4157782162 | 0.3921357928 | 0.2590177117 |
|  | 10 | 0.242564 | 0.39629 | 0.343604 | 0.208516 |
| USNM 141160 Symphalangus | 0 | 0.276753 | 0.0924788 - |  | - |
|  | 20.11098450780 .0983270588 - |  |  |  | - |
|  | 40.15663550260 .2798015771 - |  |  |  | - |
|  | 60.11752768330 .3881912857 - |  |  |  | - |
|  |  | 0.20690526510. | 0.3824781084 | 0.4612917952 | 0.298814253 |
|  | 10 | 0.25723 | 0.385009 | 0.294158 | 0.280298 |
| AMNH |  |  |  |  |  |
| 106581 Symphalangus | 0 | 0.267263 | 0.244768 - |  | - |
|  | 20.10896331120 .2572716452 - |  |  |  | - |
|  | 40.11548284550 .2983462069 - |  |  |  | - |
|  | $60.21001377480 .4093764595-$ |  |  |  | - |
|  |  | 0.30197273870 | 0.41337505410 | 0.3379364775 | 0.2440091081 |
|  | 10 | 0.336065 | 0.406017 | 0.309723 | 0.310392 |
| USNM 220327 Pan | 0 | 0.228524 | 0.175016 - |  | - |
|  | 20.16432343340 .2492761705 - |  |  |  | - |
|  | 40.10080992680 .2735901039 - |  |  |  | - |
|  | 60.19836284520 .2733244881 - |  |  |  | - |
|  | 80.2143335783 |  | 0.3465987590 | 0.2057446988 | 0.2038389036 |
|  | 10 | 0.286082 | 0.286939 | 0.277099 | 0.202133 |
| USNM 220065 Pan | 0 | 0.182616 | 0.165963 - |  | - |
|  | 20.16531062840 .3415639995 - |  |  |  | - |
|  | 40.15127254830 .2743228275 - |  |  |  | - |
|  | 60.22142161260 .4375481351 - |  |  |  | - |
|  | 80.27214408110 .3908177027 |  |  | 0.291082964 | 0.3059273964 |
|  | 10 | 0.307907 | 0.332211 | 0.291212 | 0.267221 |
| USNM 176227 Pan | 0 | 0.309869 | 0.332868 - |  | - |
|  | 2 | 0.2516358 | 0.3440816 - |  | - |
|  | 4 | 0.2233034 | 0.3874276 - |  | - 0.4272238 |
|  | 6 | 0.3355474 | 0.4131804 | 0.3712172 | 0.4272238 |
|  | 8 | 0.2785036 | 0.4431838 | 0.3865968 | 0.3019116 |


|  | 10 | 0.220086 | 0.339205 | 0.279755 | 0.219072 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| USNM 220064 Pan | 0 | 0.214224 | 0.209382 - |  | - |
|  | 20.19219135590 .2511912374 - |  |  |  | - |
|  | 40.17667090060 .271560767 - |  |  |  | - |
|  | 60.16906680180 .3018203514 - |  |  |  | - |
|  | 8 | 0.1553430 .3552350631 - |  |  | - |
|  | 10 | 0.267924 | 0.259055 | 0.198566 | 0.143217 |
| USNM 481804 Pan | 0 | 0.217006 | 0.303059 - |  | - |
|  | 2 | 0.225339 | 0.406772 - |  | - |
|  | 4 | 0.104395 | 0.363137 | 0.361106 | 0.430944 |
|  | 6 | 0.0913321 | 0.366038 | 0.418438 | 0.314452 |
|  | 8 | 0.380924 | 0.370942 | 0.398543 | 0.258241 |
|  | 10 | 0.3882 | 0.385953 | 0.287581 | 0.205751 |
| USNM 153823 Pongo | 0 | 0.31825 | 0.437527 | 0.252801 | 0.289765 |
|  | 20.3317728992 |  | 0.41534810020 | 0.3331776621 | 0.2993781585 |
|  | $\begin{aligned} & 40.3112510444 \\ & 60.2181544371 \end{aligned}$ |  | 0.37166448950 .43 | 0.4340303935 | 0.2805910822 |
|  |  |  | 0.38953655090 .3 | 0.3261129701 | 0.2628660719 |
|  |  | 80.2550715241 | 0.34294410840 | 0.2845687229 | 0.2400546265 |
|  | 10 | 0.252631 | 0.308181 | 0.207167 | 0.229523 |
| USNM 145300 Pongo | 0 | 0.143115 | 0.163139 - |  | 0.33779 |
|  | 2 | 0.170206 | 0.312506 | 0.389055 | 0.20485 |
|  | 4 | 0.187078 | 0.347091 | 0.317245 | 0.250897 |
|  | 6 | 0.0981522 | 0.330034 | 0.32995 | 0.212135 |
|  | 8 | 0.195279 | 0.27787 | 0.225311 | 0.13699 |
|  | 10 | 0.232764 | 0.271122 | 0.25004 | 0.222034 |
| USNM 145302 Pongo | 0 | 0.275965 | 0.333568 | 0.223399 | 0.271701 |
|  | 20.26583325630 .3439651331 |  |  | 0.238759703 | 0.3021522937 |
|  | $\begin{array}{lr} 4 & 0.254864105 \\ 6 & 0.2918450659 \end{array}$ |  | 0.37964584680 | 0.3404920875 | 0.2667982341 |
|  |  |  | 0.29994576920 | 0.2193932967 | 0.2294830769 |
|  | 80.2714514945 |  | 0.30621924180 | 0.1768618242 | 0.1821562418 |
|  | 10 | 0.310307 | 0.239133 | 0.280472 | 0.196653 |
| USNM 145301 Pongo | $\begin{array}{lr}0 & 0.186431 \\ 2 & 0.159822341\end{array}$ |  | 0.215303 | 0.30296 | 0.198187 |
|  |  |  | 0.24394380390 | 0.3069227717 | 0.2203667402 |
|  | $\begin{aligned} & 40.1944026106 \\ & 60.1608623986 \end{aligned}$ |  | 0.30891906980 .30 | 0.3041348863 | 0.2674634731 |
|  |  |  | 0.25624905590. | 0.2740574336 | 0.2118644685 |
|  | 8 | 0.199209993 | 0.2396580210 | 0.2721499091 | 0.2074716154 |
|  | 10 | 0.254589 | 0.300819 | 0.260321 | 0.163347 |
| USNM 145304 Pongo | 0 | 0.259368 | 0.302196 | 0.234514 | 0.297633 |
|  | 2 | 0.340558 | 0.32586 | 0.323927 | 0.301563 |
|  | 4 | 0.308282 | 0.317012 | 0.333366 | 0.274831 |
|  | 6 | 0.337025 | 0.294663 | 0.241769 | 0.300853 |


|  |  | 8 | 0.380451 | 0.320219 | 0.2914 | 0.258206 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 10 | 0.368626 | 0.297737 | 0.276264 | 0.263312 |
| USNM 253780 Macaca |  | 0 |  | - | 0.123739 | 0.095861 |
|  |  | 2 |  | - | 0.1645760051 | 0.1794831761 |
|  |  | 4 |  | - | 0.184094318 | 0.192891355 |
|  |  | 6 |  | - | 0.2127201081 | 0.2774584234 |
|  |  | 8 | . 1277418649 | 0.2644254955 | 0.2954568829 | 0.2375978649 |
|  |  | 10 | 0.228632 | 0.25528 | 0.180447 | 0.212472 |
| USNM 173813 Macaca |  | 0 |  | - | 0.342668 | 0.338869 |
|  |  | 2 |  |  | 0.3554821681 | 0.4742876485 |
|  |  | 4 |  | - | 0.3255675772 | 0.3945826968 |
|  |  |  | . 3675811111 | 0.4317897778 | 0.3912656944 | 0.5631437222 |
|  |  | 8 | . 3855197465 | 0.4856762535 | 0.3772598873 | 0.5009639718 |
|  |  | 10 | 0.321976 | 0.415546 | 0.370863 | 0.505101 |
| AMNH 43086 | Macaca | 0 |  | - | 0.267129 |  |
|  |  | 2 |  |  | 0.240468688 - |  |
|  |  | 4 |  | - | 0.1846964935 | 0.1885865065 |
|  |  | 6 | . 1104076494 | 0.1306711299 | 0.2153210779 | 0.2818716234 |
|  |  | 8 | . 1748751948 | 0.2815397662 | 0.3080688312 | 0.3041502597 |
|  |  | 10 | 0.225958 |  | 0.283307 | 0.325221 |
| UPENN 86-12- |  |  |  |  |  |  |
| 44 | Macaca | 0 |  | - | 0.197366 | 0.272783 |
|  |  | 2 |  |  | 0.1893385094 | 0.1919281694 |
|  |  | 4 |  | - | 0.2149782188 | 0.4290933217 |
|  |  | 6 |  | - | 0.2440644176 | 0.4004482857 |
|  |  |  | . 1533904286 | 0.2784499121 | 0.1777656374 | 0.4277274396 |
|  |  | 10 | 0.19812 | 0.348277 | 0.222441 | 0.309443 |
| B22-A | Homo | 0 | 0.228993 | 0.277762 | 0.388651 | 0.282766 |
|  |  | 2 | 0.221665 | 0.302886 | 0.3214102 | 0.310758 |
|  |  | 4 | 0.214337 | 0.32801 | 0.2541694 | 0.33875 |
|  |  | 6 | 0.2194384 | 0.3400148 | 0.2620046 | 0.3652868 |
|  |  | 8 | 0.2369692 | 0.3389004 | 0.3449158 | 0.3903684 |
|  |  | 10 | 0.2545 | 0.337786 | 0.427827 | 0.41545 |
| B22-B | Homo | 0 | 0.216127 | 0.251148 | 0.343933 | 0.262717 |
|  |  | 2 | 0.2179516 | 0.2655396 | 0.3574718 | 0.2567672 |
|  |  | 4 | 0.2197762 | 0.2799312 | 0.3710106 | 0.2508174 |
|  |  | 6 | 0.2216008 | 0.2943228 | 0.3845494 | 0.2448676 |
|  |  | 8 | 0.2234254 | 0.3087144 | 0.3980882 | 0.2389178 |
|  |  | 10 | 0.22525 | 0.323106 | 0.411627 | 0.232968 |
| TMM2165-A | Homo | 0 | 0.161039 | 0.326818 | 0.261793 | 0.269556 |
|  |  | 2 | 0.2088938 | 0.3317508 | 0.2524186 | 0.2891088 |


|  |  | 4 | 0.2567486 | 0.3366836 | 0.2430442 | 0.3086616 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 6 | 0.2772328 | 0.3358612 | 0.2345026 | 0.3159238 |
|  |  | 8 | 0.2703464 | 0.3292836 | 0.2267938 | 0.3108954 |
|  |  | 10 | 0.26346 | 0.322706 | 0.219085 | 0.305867 |
| TMM2165-B | Homo | 0 | 0.192483 | 0.284583 | 0.293503 | 0.269615 |
|  |  | 2 | 0.2131936 | 0.300721 | 0.28086 | 0.2841312 |
|  |  | 4 | 0.2339042 | 0.316859 | 0.268217 | 0.2986474 |
|  |  | 6 | 0.2546148 | 0.332997 | 0.255574 | 0.3131636 |
|  |  | 8 | 0.2753254 | 0.349135 | 0.242931 | 0.3276798 |
|  |  | 10 | 0.296036 | 0.365273 | 0.230288 | 0.342196 |
| TARLAC-60-A | Homo | 0 | 0.388869 | 0.33535 | 0.419657 | 0.274999 |
|  |  | 2 | 0.3661135245 | 0.3661990849 | 0.4009459289 | 0.3027667768 |
|  |  | 4 | 0.3363795361 | 0.3826804465 | 0.3825719401 | 0.32000676 |
|  |  | 6 | 0.2926989847 | 0.3704479023 | 0.3648716104 | 0.3162069398 |
|  |  | 8 | 0.274858024 | 0.3769057267 | 0.3201711021 | 0.3167644474 |
|  |  | 10 | 0.270034 | 0.392779 | 0.261869 | 0.319517 |
| TARLAC-60-B | Homo | 0 | 0.326252 | 0.325899 | 0.400663 | 0.276641 |
|  |  | 2 | 0.3051692 | 0.3296854 | 0.381937 | 0.2862454 |
|  |  | 4 | 0.2840864 | 0.3334718 | 0.363211 | 0.2958498 |
|  |  | 6 | 0.27171 | 0.3425382 | 0.3363514 | 0.304988 |
|  |  | 8 | 0.26804 | 0.3568846 | 0.3013582 | 0.31366 |
|  |  | 10 | 0.26437 | 0.371231 | 0.266365 | 0.322332 |

Appendix D.i.b. Standardized degree of anisotropy (DA) data from the lower ilium of the extant

| Specimen | Taxon | DA |  | DA DA | DA | DA |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Level |  | Lat D | Dors | Vent |
| USNM |  |  |  |  |  |  |
| 384228 | Papio | 0 | 3.4537 | 2.63108 - |  | - |
|  |  | 2 | 2.5304032533 | 3.3808715606 - |  | - |
|  |  | 4 | 3.7112243011 | $2.8086583632-$ |  | - |
|  |  | 6 | 2.2140492857 | 4.3702652381 - |  | - |
|  |  | 8 | 2.5083178313 | 4.1552206024 - |  | - |
|  |  | 10 | 4.47354 | 3.19599 | 4.92583 | 8.60382 |
| USNM |  |  |  |  |  |  |
| 354987 | Papio | 0 | 4.46286 | 7.90235 - |  | - |
|  |  | 2 | 3.0383632073 | $3.2332007563-$ |  | - |
|  |  | 4 | 2.5466498192 | 2.9614957441 - |  | - |
|  |  | 6 | 4.5963841667 | 5.2600379167 - |  | - |
|  |  | 8 | 4.6271342254 | 4.40498253525 | 5.7951516901 | 4.3826983099 |
|  |  | 10 | 4.1713 | 4.04462 | 5.97028 | 9.13181 |
| USNM |  |  |  |  |  |  |
| $397476$ | Papio | 0 | 1.98836 | 3.19046 - |  | - |
|  |  | 2 | 2.5717649129 | 3.2271880312 - |  | - |
|  |  | 4 | 2.1931531756 | 4.0040579221 - |  | - |
|  |  | 6 | 4.0097637662 | 4.809714026 - |  |  |
|  |  | 8 | 2.8412571429 | 5.4106301299 | 3.6504709091 | 5.1276042857 |
|  |  | 10 | 4.15239 | 11.8171 | 2.95695 | 2.38722 |
| USNM |  |  |  |  |  |  |
| $384234$ | Papio | 0 | 3.09703 | 4.72649 - |  | - |
|  |  | 2 | 3.18133 | 3.647848 - |  | - |
|  |  | 4 | 11.71704 | 3.303048 - |  | - |
|  |  | 6 | 11.42056 | 6.346576 - |  | - |
|  |  | 8 | 2.4039 | 9.968224 - |  | - |
|  |  | 10 | 4.33136 | 4.747 | 2.62146 | 4.0613 |
| USNM |  |  |  |  |  |  |
| 395440 | Papio | 0 | 6.53124 | 3.76769 - |  | - |
|  |  | 2 | 3.9662705941 | 4.2676846865 - |  | - |
|  |  | 4 | 3.5021211597 | 9.4464360394 - |  | - |
|  |  | 6 | 22.5802615385 | 5.671619011 - |  | - |
|  |  | 8 | 4.2231564835 | 3.9797987912 - |  | - |
|  |  | 10 | 3.77623 | 5.42179 | 3.64965 | 4.75182 |
| USNM |  |  |  |  |  |  |
| 384227 | Papio | 0 | 2.32953 | 2.68466 - |  | - |


|  |  | 2 | 5.6663861625 | 3.607185394 |  | - |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 4 | 3.4219727056 | 4.5297107881 |  | - |
|  |  | 6 | 2.42256763895 | 5.1484131944 |  | - |
|  |  | 8 | 4.2791878873 | 3.7565119718 | 2.0282794366 | 3.5184891549 |
|  |  | 10 | 2.19299 | 3.89953 | 7.06753 | 4.55879 |
| USNM | Symphalangu |  |  |  |  |  |
| 141161 | $s$ | 0 | 4.11144 - |  | - | - |
|  |  | 2 | 3.10879 - |  | - | - |
|  |  | 4 | 3.5125 | 1.80243 |  | - |
|  |  | 6 | 1.6166 | 2.31746 |  | - |
|  |  | 8 | 3.12432 | 4.45889 | 3.19569 | 3.72561 |
|  |  | 10 | 1.90598 | 3.14473 | 2.55238 | 2.81328 |
| $\begin{aligned} & \text { USNM } \\ & 141162 \end{aligned}$ | Symphalangu |  |  |  |  |  |
|  | $s$ | 0 | 2.15707 | 3.19995 |  | - |
|  |  | 2 | 2.34576153393 | 3.5490319082 |  | - |
|  |  | 4 | 2.7164368383 | 2.1272141102 |  | - |
|  |  | 6 | 2.426410991 | 3.1788677477 |  | - |
|  |  | 8 | 2.6071109912 | 2.9016927928 | 2.9350651351 | 2.8488589189 |
|  |  | 10 | 3.09262 | 4.96912 | 3.56238 | 2.05409 |
| $\begin{aligned} & \text { USNM } \\ & 141160 \end{aligned}$ | Symphalangu |  |  |  |  |  |
|  | s | 0 | 1.99285 | 2.85372 |  | - |
|  |  | 2 | 8.45253431646 | 6.5504981873 |  | - |
|  |  | 4 | 5.7788981055 | 3.1005825568 |  | - |
|  |  | 6 | 4.7201263095 | 2.1482608333 |  | - |
|  |  | 8 | 2.9607408434 | 4.091450241 | 1.9751681928 | 3.8695289157 |
|  |  | 10 | 1.91649 | 3.07994 | 2.61664 | 3.26226 |
| AMNH$106581$ | Symphalangu |  |  |  |  |  |
|  | $s$ | 0 | 4.10038 | 2.55158 |  | - |
|  |  | 2 | 5.8453939022 | 2.2525268323 |  | - |
|  |  | 4 | 12.0300035592 | 3.208898645 |  | - |
|  |  | 6 | 2.12289729732 | 2.2566335135 |  | - |
|  |  | 8 | 2.20148153152 | 2.8401665766 | 2.0402172973 | 2.8051904505 |
|  |  | 10 | 2.9206 | 4.83354 | 2.87639 | 4.36655 |
| USNM |  |  |  |  |  |  |
| 220327 | Pan | 0 | 8.17771 | 5.43146 |  | - |
|  |  | 2 | 12.0409894718 | 2.7204722209 |  | - |
|  |  | 4 | 6.06859070498 | 8.5458224851 |  | - |
|  |  | 6 | 12.024841666711 | 11.732807619 |  | - |
|  |  | 8 | 7.60917 | 9.3796403614 | 3.0215433735 | 5.2679995181 |
|  |  | 10 | 6.01634 | 6.37845 | 4.39532 | 6.92851 |
| USNM |  |  |  |  |  |  |
| 220065 | Pan | 0 | 2.24451 | 2.35937 |  | - |


|  |  | 2 | 2.8424799001 | 2.9209268593 - |  | - |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 4 | 5.1719566305 | 4.6943674526 - |  | - |
|  |  | 6 | 3.2332830631 | 3.3157483784 - |  | - |
|  |  | 8 | 2.6594927027 | 2.92186909913 | 3.5465747748 | 3.8816245946 |
|  |  | 10 | 5.49311 | 3.71045 | 2.95505 | 3.96107 |
| USNM |  |  |  |  |  |  |
| 176227 | Pan | 0 | 6.06062 | 5.63181 - |  | - |
|  |  | 2 | 7.949346 | 2.473772 - |  | - |
|  |  | 4 | 4.126128 | 4.440836 - |  | - |
|  |  | 6 | 2.729184 | 5.11306 | 2.756102 | 3.971918 |
|  |  | 8 | 2.712282 | 3.681384 | 2.314424 | 2.747842 |
|  |  | 10 | 8.29117 | 6.43036 | 3.96646 | 6.21799 |
| USNM |  |  |  |  |  |  |
| 220064 | Pan | 0 | 1.71685 | 1.62081 - |  | - |
|  |  | 2 | 2.1279325574 | 3.7436895147 - |  | - |
|  |  | 4 | 13.2391566396 | 5.3311560795 - |  | - |
|  |  | 6 | 22.6308954955 | 7.2069677477 - |  | - |
|  |  | 8 | 5.6800676577 | 5.2651806306 - |  | - |
|  |  | 10 | 2.11218 | 6.92366 | 2.53997 | 2.89589 |
| USNM |  |  |  |  |  |  |
| 481804 | Pan | 0 | 1.25952 | 3.25788 - |  | - |
|  |  | 2 | 5.37531 | 2.39301 - |  | - |
|  |  | 4 | 11.738 | 3.30212 | 3.17114 | 3.32093 |
|  |  | 6 | 9.35678 | 4.22538 | 2.01102 | 7.45594 |
|  |  | 8 | 2.86365 | 4.22111 | 4.72144 | 2.54997 |
|  |  | 10 | 2.81607 | 3.43509 | 11.1113 | 4.26027 |
| USNM |  |  |  |  |  |  |
| 153823 | Pongo | 0 | 2.96159 | 2.6375 | 1.94336 | 3.45635 |
|  |  | 2 | 4.13017991 | 3.96789494 | 2.7272065786 | 4.3239295438 |
|  |  | 4 | 3.933825033 | 4.05530018 | 2.6978341212 | 5.5004341272 |
|  |  | 6 | 3.56599 | 3.26116407193. | 3.0841166467 | 3.8601658084 |
|  |  | 8 | 2.9488850602 | 3.5953339157 | 2.1629813855 | 4.8536992771 |
|  |  | 10 | 5.24405 | 6.61035 | 2.78541 | 6.14105 |
| USNM |  |  |  |  |  |  |
| 145300 | Pongo | 0 | 2.31354 | 4.87697 - |  | 2.53398 |
|  |  | 2 | 5.13889 | 1.79849 | 1.34187 | 3.86722 |
|  |  | 4 | 5.43684 | 2.7672 | 1.39808 | 3.07404 |
|  |  | 6 | 7.33177 | 3.11963 | 1.28688 | 3.91484 |
|  |  | 8 | 2.54724 | 2.70883 | 4.92902 | 2.47666 |
|  |  | 10 | 2.58518 | 6.13396 | 4.00695 | 2.27145 |
| USNM |  |  |  |  |  |  |
| 145302 | Pongo | 0 | 2.15692 | 2.05135 | 2.35776 | 3.97545 |


|  |  | 2 | 2.2731248735 | 1.3800222222 | 3.8147946315 | 3.2290483278 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 4 | 2.5869250547 | 2.0888319912 | 2.0345282495 | 4.2862254705 |
|  |  | 6 | 1.966501978 | 2.6571981319 | 2.306026044 | 2.9340205495 |
|  |  | 8 | 1.7892079121 | 2.8556425275 | 1.8731354945 | 4.8510434066 |
|  |  | 10 | 2.13823 | 5.15509 | 2.21457 | 1.81034 |
| USNM |  |  |  |  |  |  |
| 145301 | Pongo | 0 | 3.28515 | 1.63998 | 2.26839 | 3.121 |
|  |  | 2 | 4.3862672129 | 3.9354140476 | 1.6469293697 | 5.2663944748 |
|  |  | 4 | 3.7064420237 | 3.958233545 | 2.1694208304 | 6.3028177251 |
|  |  | 6 | 3.6540287413 | 5.4818426573 | 4.538563007 | 2.3504425175 |
|  |  | 8 | 3.3034174126 | 7.5526471329 | 3.1682158741 | 4.6975690909 |
|  |  | 10 | 2.61335 | 6.90259 | 5.04668 | 3.06509 |
| USNM |  |  |  |  |  |  |
| 145304 | Pongo | 0 | 2.19963 | 3.13056 | 2.85578 | 3.83261 |
|  |  | 2 | 1.81402 | 2.95392 | 2.47147 | 4.33438 |
|  |  | 4 | 2.60616 | 3.60595 | 3.36528 | 4.94863 |
|  |  | 6 | 2.52946 | 4.64074 | 5.10382 | 3.56775 |
|  |  | 8 | 4.82154 | 4.44634 | 2.3674 | 4.91558 |
|  |  | 10 | 3.21101 | 6.68979 | 2.43509 | 5.50527 |
| USNM |  |  |  |  |  |  |
| 253780 | Macaca | 0 - |  | - | 2.97669 | 2.73989 |
|  |  | 2 - |  | - | 3.3767405293 | 5.933488296 |
|  |  | 4 - |  | - | 2.0232363505 | 5.3095414182 |
|  |  | 6 - |  | - | 3.1422654054 | 7.1077821622 |
|  |  | 8 | 8.6161288288 | 2.8602704505 | 4.9906559459 | 7.1210118018 |
|  |  | 10 | 3.30315 | 3.60734 | 3.56719 | 4.04962 |
| USNM |  |  |  |  |  |  |
| 173813 | Macaca | 0 - |  | - | 2.00191 | 2.09676 |
|  |  | 2 - |  | - | 3.1081254902 | 3.3302023249 |
|  |  | 4 - |  | - | 1.8992576634 | 4.9173172601 |
|  |  | 6 | 4.6766823611 | 4.3796069444 | 2.19572875 | 3.5019393056 |
|  |  | 8 | 4.1495721127 | 2.9413335211 | 2.7710214085 | 8.2525423944 |
|  |  | 10 | 2.81789 | 5.70441 | 2.23701 | 2.71037 |
| AMNH 43086 Macaca |  | 0 - |  | - | 3.34304 - |  |
|  |  | 2 - |  | - | 2.3807609705 - |  |
|  |  | 4 - |  | - | 3.6342793506 | 7.3335328571 |
|  |  | 6 | 2.3961790909 | 5.0624677922 | 3.6324997403 | 3.5005092208 |
|  |  | 8 | 3.3362119481 | 1.9689527273 | 6.7263866234 | 6.9413479221 |
|  |  | 10 | 5.98639 | - | 5.37659 | 2.2544 |
| UPENN 86- |  |  |  |  |  |  |
| 12-44 | Macaca | 0 - |  | - | 3.10733 | 1.46666 |
|  |  | 2 - |  | - | 3.2762918262 | 7.6927226183 |


|  |  | 4 - |  | - | 3.1397826258 | 3.7233813129 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 6 - |  | - | 2.2357695604 | 5.2476763736 |
|  |  | 8 | 1.8925706593 | 2.4294054945 | 3.0893073626 | 5.5666621978 |
|  |  | 10 | 2.90801 | 3.42782 | 2.41475 | 3.23287 |
| B22-A | Homo | 0 | 4.81814 | 1.80811 | 3.13597 | 1.67946 |
|  |  | 2 | 3.686824 | 1.75085 | 2.773822 | 2.080592 |
|  |  | 4 | 2.555508 | 1.69359 | 2.411674 | 2.481724 |
|  |  | 6 | 2.017972 | 1.749916 | 2.467966 | 2.836914 |
|  |  | 8 | 2.074216 | 1.919828 | 2.942698 | 3.146162 |
|  |  | 10 | 2.13046 | 2.08974 | 3.41743 | 3.45541 |
| B22-B | Homo | 0 | 1.75141 | 2.05523 | 3.63799 | 2.484 |
|  |  | 2 | 1.800194 | 1.996064 | 3.196552 | 2.319714 |
|  |  | 4 | 1.848978 | 1.936898 | 2.755114 | 2.155428 |
|  |  | 6 | 1.897762 | 1.877732 | 2.313676 | 1.991142 |
|  |  | 8 | 1.946546 | 1.818566 | 1.872238 | 1.826856 |
|  |  | 10 | 1.99533 | 1.7594 | 1.4308 | 1.66257 |
| TMM2165-A Homo |  | 0 | 3.43344 | 2.18882 | 6.38349 | 2.0491 |
|  |  | 2 | 2.899212 | 2.400028 | 5.20821 | 2.861092 |
|  |  | 4 | 2.364984 | 2.611236 | 4.03293 | 3.673084 |
|  |  | 6 | 2.15864 | 3.0469 | 3.715944 | 3.692518 |
|  |  | 8 | 2.28018 | 3.70702 | 4.257252 | 2.919394 |
|  |  | 10 | 2.40172 | 4.36714 | 4.79856 | 2.14627 |
| TMM2165-B | Homo | 0 | 3.80689 | 2.2851 | 4.36676 | 1.57126 |
|  |  | 2 | 3.417488 | 2.638252 | 4.530538 | 1.680782 |
|  |  | 4 | 3.028086 | 2.991404 | 4.694316 | 1.790304 |
|  |  | 6 | 2.638684 | 3.344556 | 4.858094 | 1.899826 |
|  |  | 8 | 2.249282 | 3.697708 | 5.021872 | 2.009348 |
|  |  | 10 | 1.85988 | 4.05086 | 5.18565 | 2.11887 |
| TARLAC-60-A Homo |  | 0 | 1.51599 | 5.59707 | 6.8656 | 3.57602 |
|  |  | 2 | 2.138000201 | 4.421150408 | 4.8964550855 | 2.7301574137 |
|  |  | 4 | 2.8598657147 | 3.8104462242 | 3.3730904945 | 2.3760362751 |
|  |  | 6 | 3.7812921456 | 4.329325457 | 2.740618214 | 3.0046607881 |
|  |  | 8 | 3.1566215315 | 8.0125726727 | 3.3761417117 | 2.5078337838 |
|  |  | 10 | 1.75309 | 13.2899 | 4.65043 | 1.44405 |
| TARLAC-60-B Homo |  | 0 | 4.93981 | 3.05175 | 3.87594 | 3.606 |
|  |  | 2 | 4.669382 | 3.773554 | 3.721244 | 3.634508 |
|  |  | 4 | 4.398954 | 4.495358 | 3.566548 | 3.663016 |
|  |  | 6 | 3.945218 | 5.433476 | 3.736918 | 3.258622 |
|  |  | 8 | 3.308174 | 6.587908 | 4.232354 | 2.421326 |
|  |  | 10 | 2.67113 | 7.74234 | 4.72779 | 1.58403 |

Appendix D.ii.a. Standardized bone volume fraction (BVTV) data from the ischium of the extant

| Specimen | Taxon | Level | BVTV <br> Ventral | BVTV Central | BVTV <br> Dorsal |
| :---: | :---: | :---: | :---: | :---: | :---: |
| USNM 384228 | Papio | 0 | 0.348719 | 0.553139 | 0.706321 |
|  |  | 0.25 | 0.4599142244 |  | 0.6141522266 |
|  |  | 0.5 | 0.42931 | 0.404178 | 0.502137 |
|  |  | 0.75 | 0.344943956 | 0.4419967912 | 0.4123935385 |
|  |  | 1 | 0.371761 |  | 0.411729 |
| USNM 354987 | Papio | 0 | 0.0444134 | 0.266944 | 0.557578 |
|  |  | 0.25 | 0.241111 | 0.260294 | 0.32556 |
|  |  | 0.5 | 0.214121 | 0.223267 | 0.245266 |
|  |  | 0.75 | 0.152071 | 0.198842 | 0.27048 |
|  |  | 1 | 0.194949 | 0.227085 | 0.271941 |
| USNM 397476 | Papio | 0 | 0.264159 | 0.261391 | 0.326925 |
|  |  | 0.25 | 0.2905199753 | 0.2199445566 | 0.2651238231 |
|  |  | 0.5 | 0.302211 | 0.3512745 | 0.384551 |
|  |  | 0.75 | 0.1923654416 | 0.2847472987 | 0.425466 |
|  |  | 1 | 0.278577 | 0.316507 | 0.31158 |
| USNM 384234 | Papio | 0 | 0.362606 | 0.277675 | 0.361495 |
|  |  | 0.25 | 0.311512 | 0.30497 | 0.361231 |
|  |  | 0.5 | 0.300157 | 0.354803 | 0.419567 |
|  |  | 0.75 | 0.284596 | 0.29484 | 0.393739 |
|  |  | 1 | 0.395412 | 0.386325 | 0.390233 |
| USNM 395440 | Papio | 0 | 0.298345 | 0.186274 | 0.281221 |
|  |  | 0.25 | 0.32453 | 0.269291 | 0.342384 |
|  |  | 0.5 | 0.247725 | 0.333796 | 0.176833 |
|  |  | 0.75 | 0.273446 | 0.254152 | 0.202822 |
|  |  | 1 | 0.307396 | 0.232308 | 0.282733 |
| USNM 384227 | Papio | 0 | 0.278434 | 0.187412 | 0.262343 |
|  |  | 0.25 | 0.359466 | 0.286409 | 0.367998 |
|  |  | 0.5 | 0.376229 | 0.370623 | 0.43979 |
|  |  | 0.75 | 0.207765 | 0.287824 | 0.43117 |
|  |  | 1 | 0.326805 | 0.343162 | 0.442761 |
| USNM 141161 | Symphalangus | 0 | 0.263809 |  | 0.270988 |
|  |  | 0.25 | 0.373312 | 0.3638675 | 0.438671 |
|  |  | 0.5 | 0.419972 | 0.428291 | 0.39725 |
|  |  | 0.75 | 0.352955 | 0.345039 | 0.3935165 |
|  |  | 1 | 0.367943 | 0.284174 | 0.34913 |


| USNM 141162 | Symphalangus | 0 | 0.266564 | 0.204964 | 0.315269 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 0.25 | 0.31818925 | 0.273743 | 0.302095 |
|  |  | 0.5 | 0.34784 | 0.3612535 | 0.346558 |
|  |  | 0.75 | 0.2917357622 | 0.4084762378 | 0.4263161748 |
|  |  | 1 | 0.326922 | 0.407395 | 0.421043 |
| USNM 141160 | Symphalangus | 0 | 0.246707 | 0.192949 | 0.265522 |
|  |  | 0.25 | 0.3202855 | 0.311406 | 0.337442 |
|  |  | 0.5 | 0.327865 | 0.32096 | 0.277348 |
|  |  | 0.75 | 0.2562025 | 0.2982455 | 0.2842215 |
|  |  | 1 | 0.273396 | 0.272277 | 0.292545 |
| AMNH 106581 | Symphalangus | 0 | 0.227189 | 0.133683 | 0.242441 |
|  |  | 0.25 | 0.2748000111 | 0.2126891506 | 0.2829097969 |
|  |  | 0.5 | 0.3062274957 | 0.2829509646 | 0.3439037498 |
|  |  | 0.75 | 0.3190775075 | 0.3126752973 | 0.3960029339 |
|  |  | 1 | 0.31082 | 0.269628 | 0.409569 |
| USNM 220327 | Pan | 0 | 0.0933572 | 0.111195 | 0.356179 |
|  |  | 0.25 | 0.153186967 | 0.1474593272 | 0.3139153707 |
|  |  | 0.5 | 0.2354515 | 0.2667095 | 0.3787355 |
|  |  | 0.75 | 0.2003997802 | 0.2945449011 | 0.3670527582 |
|  |  | 1 | 0.293421 | 0.338111 | 0.381843 |
| USNM 220065 | Pan | 0 | 0.146472 | 0.147234 | 0.190831 |
|  |  | 0.25 | 0.234083 | 0.2723305 | 0.3281625 |
|  |  | 0.5 | 0.324584 | 0.336674 | 0.460767 |
|  |  | 0.75 | 0.2539475 | 0.2809265 | 0.335024 |
|  |  | 1 | 0.249855 | 0.234754 | 0.350832 |
| USNM 176227 | Pan | 0 | 0.204918 | 0.180153 | 0.218162 |
|  |  | 0.25 | 0.284543 | 0.28846 | 0.314295 |
|  |  | 0.5 | 0.301378 | 0.354276 | 0.356504 |
|  |  | 0.75 | 0.252369 | 0.260627 | 0.283253 |
|  |  | 1 | 0.24901 | 0.270866 | 0.285366 |
| USNM 220064 | Pan | 0 | 0.188459 | 0.203733 | 0.231325 |
|  |  | 0.25 | 0.250347 | 0.265965 | 0.339437 |
|  |  | 0.5 | 0.242051 | 0.324231 | 0.395859 |
|  |  | 0.75 | 0.253922 | 0.264624 | 0.325331 |
|  |  | 1 | 0.251515 | 0.306436 | 0.315626 |
| USNM 481804 | Pan | 0 | 0.186003 | 0.171505 | 0.348447 |
|  |  | 0.25 | 0.2192524896 | 0.2849466166 | 0.4052305707 |
|  |  | 0.5 | 0.2761895 | 0.362442 | 0.412088 |


|  |  | 0.75 | 0.2227585495 | 0.2984094595 | 0.337022955 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1 | 0.277964 | 0.275528 | 0.246856 |
| USNM 153823 | Pongo | 0 | 0.178488 | 0.118683 | 0.197776 |
|  |  | 0.25 | 0.239939 | 0.266549 | 0.390749 |
|  |  | 0.5 | 0.31384 | 0.404673 | 0.343241 |
|  |  | 0.75 | 0.275209 | 0.306667 | 0.28392 |
|  |  | 1 | 0.244249 | 0.285077 | 0.353638 |
| USNM 145300 | Pongo | 0 | 0.178992 | 0.160364 | 0.204748 |
|  |  | 0.25 | 0.16928375 | 0.19388475 | 0.30667825 |
|  |  | 0.5 | 0.202047 | 0.2423815 | 0.285116 |
|  |  | 0.75 | 0.1961515 | 0.23606675 | 0.246864 |
|  |  | 1 | 0.189533 | 0.254025 | 0.292567 |
| USNM 145302 | Pongo | 0 | 0.15816 | 0.164236 | 0.209149 |
|  |  | 0.25 | 0.231376 | 0.25730875 | 0.32208125 |
|  |  | 0.5 | 0.2806945 | 0.304682 | 0.336715 |
|  |  | 0.75 | 0.2297265245 | 0.2565014685 | 0.3362618881 |
|  |  | 1 | 0.182599 | 0.232309 | 0.299699 |
| USNM 145301 | Pongo | 0 | 0.182121 | 0.127898 | 0.165743 |
|  |  | 0.25 | 0.258672 | 0.2479 | 0.354254 |
|  |  | 0.5 | 0.275289 | 0.324906 | 0.225859 |
|  |  | 0.75 | 0.245737 | 0.277337 | 0.268333 |
|  |  | 1 | 0.290247 | 0.302101 | 0.315678 |
| USNM 145304 | Pongo | 0 | 0.206052 | 0.122558 | 0.239152 |
|  |  | 0.25 | 0.22458275 | 0.26628325 | 0.3251075 |
|  |  | 0.5 | 0.3042935 | 0.3112445 | 0.3481995 |
|  |  | 0.75 | 0.2827265 | 0.3157575 | 0.355258 |
|  |  | 1 | 0.241996 | 0.298428 | 0.308418 |
| USNM 253780 | Macaca | 0 | 0.134151 | 0.156856 | 0.365584 |
|  |  | 0.25 | 0.1617715 - |  | 0.2304605 |
|  |  | 0.5 | 0.206164 | 0.202433 | 0.213812 |
|  |  | 0.75 | 0.1240272 | 0.231672 | 0.19376 |
|  |  | 1 | 0.224325 - |  | 0.238073 |
| USNM 173813 | Macaca | 0 | 0.37033 | 0.27688 | 0.385612 |
|  |  | 0.25 | 0.2955292614 | 0.3055310351 | 0.3732476047 |
|  |  | 0.5 | 0.387264 | 0.3116155 | 0.449062 |
|  |  | 0.75 | 0.2694076234 | 0.3158892857 | 0.3979388701 |
|  |  | 1 | 0.255305 | 0.226935 | 0.317898 |
| AMNH 43086 | Macaca | 0 | 0.255794 | 0.093349 | 0.291024 |


|  |  | 0.25 | 0.196842 - |  | 0.18029 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 0.5 | 0.218552 | 0.292763 | 0.405207 |
|  |  | 0.75 | 0.183796 | 0.208767 | 0.211526 |
|  |  | 1 | 0.168293 | 0.186985 | 0.243552 |
| UPENN 86-12-44 | Macaca | 0 | 0.131195 - |  | 0.154974 |
|  |  | 0.25 | 0.1690857048 | 0.1946522172 | 0.2748106541 |
|  |  | 0.5 | 0.1880455 | 0.2734995 | 0.3204745 |
|  |  | 0.75 | 0.0984179896 | 0.2335260519 | 0.2609812857 |
|  |  | 1 | 0.161066 | 0.173621 | 0.222123 |
| B22 | Homo | 0 | 0.289357 | 0.219591 | 0.41698 |
|  |  | 0.25 | 0.319894 | 0.307821 | 0.39669 |
|  |  | 0.5 | 0.385692 | 0.380496 | 0.424449 |
|  |  | 0.75 | 0.4000775 | 0.403809 | 0.4080325 |
|  |  | 1 | 0.370682 | 0.397707 | 0.391127 |
| TMM2165 | Homo | 0 | 0.270634 | 0.268458 | 0.272958 |
|  |  | 0.25 | 0.34569 | 0.2791255 | 0.301075 |
|  |  | 0.5 | 0.33515 | 0.293653 | 0.327554 |
|  |  | 0.75 | 0.3090525 | 0.302237 | 0.369684 |
|  |  | 1 | 0.334797 | 0.289082 | 0.376367 |
| TARL B-3 | Homo | 0 | 0.431063 | 0.432238 | 0.427195 |
|  |  | 0.25 | 0.396467 | 0.3742875 | 0.3762495 |
|  |  | 0.5 | 0.395114 | 0.364369 | 0.443472 |
|  |  | 0.75 | 0.3794565 | 0.341292 | 0.455238 |
|  |  | 1 | 0.346158 | 0.376194 | 0.308338 |
| TARLAC-60 | Homo | 0 | 0.344955 | 0.302371 | 0.326119 |
|  |  | 0.25 | 0.3418025 | 0.3331915 | 0.3311585 |
|  |  | 0.5 | 0.360403 | 0.369159 | 0.32751 |
|  |  | 0.75 | 0.3347605 | 0.343876 | 0.323561 |
|  |  | 1 | 0.306649 | 0.291653 | 0.343259 |

Appendix D.ii.b. Standardized degree of anisotropy (DA) data from the ischium of the extant sample.

| Specimen | Taxon | Level | DA | DA | DA |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | Ventral | Central | Dorsal |
| USNM 384228 | Papio | 0 | 1.87141 | 3.73525 | 2.66075 |
|  |  | 0.25 | $2.4235348405-$ |  | 3.8599108141 |
|  |  | 0.5 | 2.614395 | 5.122115 | 3.043405 |
|  |  | 0.75 | 1.9510512088 | 3.8250682418 | 2.1762495604 |
|  |  | 1 | 3.54656 - |  | 5.58397 |
| USNM 354987 | Papio | 0 | 14.9366 | 4.66201 | 5.00852 |
|  |  | 0.25 | 2.26357 | 4.19353 | 3.23803 |
|  |  | 0.5 | 5.73478 | 8.43407 | 8.45496 |
|  |  | 0.75 | 1.76348 | 3.72734 | 3.65903 |
|  |  | 1 | 2.22897 | 2.83563 | 2.33502 |
| USNM 397476 | Papio | 0 | 11.5497 | 4.0439 | 5.36436 |
|  |  | 0.25 | 8.9726108713 | 7.5449950975 | 5.6784746294 |
|  |  | 0.5 | 2.76624 | 3.190905 | 5.041905 |
|  |  | 0.75 | 2.0074251948 | 5.1220803896 | 2.2624805195 |
|  |  | 1 | 4.38679 | 3.19952 | 3.31529 |
| USNM 384234 | Papio | 0 | 2.58496 | 10.8581 | 4.93162 |
|  |  | 0.25 | 2.04511 | 4.73936 | 12.8526 |
|  |  | 0.5 | 1.68472 | 6.91982 | 5.14698 |
|  |  | 0.75 | 1.65771 | 2.2328 | 5.56815 |
|  |  | 1 | 4.06292 | 5.66033 | 6.90013 |
| USNM 395440 | Papio | 0 | 5.88019 | 1.97201 | 6.06874 |
|  |  | 0.25 | 3.15694 | 5.45874 | 3.79954 |
|  |  | 0.5 | 1.94774 | 2.3066 | 3.67464 |
|  |  | 0.75 | 2.55218 | 2.62619 | 2.01716 |
|  |  | 1 | 3.16106 | 3.22167 | 1.67186 |
| USNM 384227 | Papio | 0 | 2.38762 | 6.94397 | 4.5775 |
|  |  | 0.25 | 1.58844 | 6.94985 | 3.72229 |
|  |  | 0.5 | 1.56574 | 2.72233 | 4.50835 |
|  |  | 0.75 | 5.06862 | 2.11622 | 3.37607 |
|  |  | 1 | 3.43278 | 8.19957 | 3.87162 |
| USNM 141161 | Symphalangus | 0 | 2.79516 - |  | 4.10629 |
|  |  | 0.25 | 2.456915 | 1.92011 | 2.65879 |
|  |  | 0.5 | 2.09753 | 1.85637 | 3.0737 |
|  |  | 0.75 | 1.935935 | 4.530525 | 2.04742 |
|  |  | 1 | 10.8357 | 5.33682 | 2.97608 |


| USNM 141162 | Symphalangus | 0 | 6.2486 | 5.12161 | 5.63608 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 0.25 | 2.2497875 | 3.59619 | 5.762235 |
|  |  | 0.5 | 2.23882 | 3.896425 | 3.318965 |
|  |  | 0.75 | 1.9282833566 | 4.798946014 | 2.7796665734 |
|  |  | 1 | 2.71421 | 2.67993 | 1.85527 |
| USNM 141160 | Symphalangus | 0 | 1.56287 | 1.825 | 2.72042 |
|  |  | 0.25 | 2.52123 | 2.73273 | 4.94242 |
|  |  | 0.5 | 5.3211 | 3.00163 | 3.25462 |
|  |  | 0.75 | 4.540285 | 5.7074472289 | 2.37276 |
|  |  | 1 | 3.46811 | 1.70806 | 4.91107 |
| AMNH 106581 | Symphalangus | 0 | 2.04181 | 2.46249 | 4.81444 |
|  |  | 0.25 | 1.7608469037 | 2.1078020312 | 4.3145975158 |
|  |  | 0.5 | 1.8297437669 | 1.9271462152 | 3.8716237339 |
|  |  | 0.75 | 2.2982367568 | 1.8232743544 | 4.3928035736 |
|  |  | 1 | 3.21898 | 1.69892 | 6.79673 |
| USNM 220327 | Pan | 0 | 4.22467 |  | 7.03529 |
|  |  | 0.25 | 3.0543589769 | 8.366599637 | 8.8297035864 |
|  |  | 0.5 | 3.71278 | 9.39239 | 13.768235 |
|  |  | 0.75 | 4.310488022 | 5.3453897802 | 4.1650665934 |
|  |  | 1 | 3.06693 | 3.28614 | 3.12915 |
| USNM 220065 | Pan | 0 | 1.96443 | 2.29188 | 5.94319 |
|  |  | 0.25 | 2.504195 | 2.484495 | 3.153175 |
|  |  | 0.5 | 2.06985 | 2.1883 | 3.30853 |
|  |  | 0.75 | 1.619595 | 2.285405 | 1.75384 |
|  |  | 1 | 1.86936 | 1.88658 | 1.96925 |
| USNM 176227 | Pan | 0 | 3.99938 | 8.73455 | 12.6867 |
|  |  | 0.25 | 4.83235 | 6.6772 | 4.52559 |
|  |  | 0.5 | 4.36505 | 6.69141 | 5.50844 |
|  |  | 0.75 | 3.1404 | 3.42076 | 3.76809 |
|  |  | 1 | 7.35093 | 2.97514 | 4.7093 |
| USNM 220064 | Pan | 0 | 14.249 | 7.21418 | 15.1789 |
|  |  | 0.25 | 2.98002 | 2.15461 | 3.93669 |
|  |  | 0.5 | 2.20977 | 3.89959 | 2.99263 |
|  |  | 0.75 | 1.87919 | 3.43827 | 2.18476 |
|  |  | 1 | 1.83733 | 1.46164 | 1.71447 |
| USNM 481804 | Pan | 0 | 3.41538 | 27.373 | 7.68096 |
|  |  | 0.25 | 3.2710544374 | 4.4343510171 | 6.196510279 |
|  |  | 0.5 | 5.572695 | 5.148215 | 4.512765 |


|  |  | 0.75 | 2.4124927928 | 3.3589189189 | 2.9580881081 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1 | 2.06431 | 3.44379 | 2.52711 |
| USNM 153823 | Pongo | 0 | 2.18804 | 6.40937 | 8.05133 |
|  |  | 0.25 | 2.58619 | 4.46565 | 3.56003 |
|  |  | 0.5 | 2.88184 | 1.78178 | 3.41732 |
|  |  | 0.75 | 2.20488 | 2.50544 | 2.97022 |
|  |  | 1 | 2.10774 | 2.2684 | 2.34283 |
| USNM 145300 | Pongo | 0 | 8.09731 | 15.7124 | 2.67381 |
|  |  | 0.25 | 2.6102675 | 2.8849825 | 3.2836025 |
|  |  | 0.5 | 2.87526 | 2.592425 | 3.994855 |
|  |  | 0.75 | 3.4278325 | 2.5053 | 1.91025 |
|  |  | 1 | 1.69184 | 1.42856 | 2.3364 |
| USNM 145302 | Pongo | 0 | 3.1572 | 4.03082 | 3.93714 |
|  |  | 0.25 | 2.4686375 | 2.08444 | 2.5646725 |
|  |  | 0.5 | 2.15528 | 1.756625 | 3.6821 |
|  |  | 0.75 | 2.2944947552 | 2.1423666434 | 3.3768084615 |
|  |  | 1 | 2.56383 | 1.77067 | 2.14811 |
| USNM 145301 | Pongo | 0 | 3.49492 | 9.3998 | 3.54459 |
|  |  | 0.25 | 2.28559 | 4.23817 | 2.45778 |
|  |  | 0.5 | 2.61634 | 2.99729 | 2.47648 |
|  |  | 0.75 | 1.53455 | 1.78478 | 3.07182 |
|  |  | 1 | 3.99904 | 3.43614 | 1.7444 |
| USNM 145304 | Pongo | 0 | 5.22786 | 7.09534 | 4.30951 |
|  |  | 0.25 | 3.27486 | 4.5877925 | 4.299725 |
|  |  | 0.5 | 1.79139 | 3.651495 | 3.13239 |
|  |  | 0.75 | 2.222415 | 3.26692 | 2.2887475 |
|  |  | 1 | 2.3157 | 2.94044 | 1.94517 |
| USNM 253780 | Macaca | 0 |  | 16.8129 | 8.98497 |
|  |  | 0.25 | 7.66274 - |  | 8.95033 |
|  |  | 0.5 | 7.00279 | 4.75737 | 3.86202 |
|  |  | 0.75 | 3.89967 | 3.722095 | 3.732515 |
|  |  | 1 | 3.77274 - |  | 2.1827 |
| USNM 173813 | Macaca | 0 | 3.26488 | 3.37739 | 6.59966 |
|  |  | 0.25 | 2.6620948765 | 5.6532621326 | 3.2756494928 |
|  |  | 0.5 | 2.11875 | 4.580345 | 3.064535 |
|  |  | 0.75 | 3.3046706494 | 2.8388015584 | 2.4383102597 |
|  |  | 1 | 1.33164 | 2.02759 | 1.57052 |
| AMNH 43086 | Macaca | 0 | 3.44259 | 11.408 | 7.04558 |


|  |  | 0.25 | 4.96363 - |  | 3.88009 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 0.5 | 3.00729 | 2.58465 | 3.562 |
|  |  | 0.75 | 5.31577 | 1.71081 | 9.9199 |
|  |  | 1 | 2.92162 | 3.8719 | 7.29801 |
| UPENN 86-12-44 | Macaca | 0 | 8.57558 - |  | 22.9028 |
|  |  |  | 11.514044655 |  |  |
|  |  | 0.25 | 4 | 8.629613316 | 6.1007276983 |
|  |  | 0.5 | 2.77184 | 5.458895 | 3.099825 |
|  |  |  |  |  | 10.444333766 |
|  |  | 0.75 | 3.9450202597 | 3.0427327273 | 2 |
|  |  | 1 | 1.56515 | 7.29024 | 6.08877 |
| B22 | Homo | 0 | 4.37266 | 2.30484 | 2.09489 |
|  |  | 0.25 | 6.85972 | 4.0508 | 2.371115 |
|  |  | 0.5 | 2.86517 | 2.9851 | 1.85714 |
|  |  | 0.75 | 1.870445 | 1.634515 | 1.75557 |
|  |  | 1 | 2.02668 | 2.18983 | 2.0831 |
| TMM2165 | Homo | 0 | 5.292 | 4.16969 | 2.67281 |
|  |  | 0.25 | 2.476685 | 2.97409 | 3.185955 |
|  |  | 0.5 | 1.95929 | 2.65925 | 5.95185 |
|  |  | 0.75 | 1.352285 | 2.268365 | 2.09948 |
|  |  | 1 | 2.99827 | 2.4491 | 2.59027 |
| TARL B-3 | Homo | 0 | 4.23158 | 2.92965 | 3.64517 |
|  |  | 0.25 | 4.60744 | 2.042365 | 5.103895 |
|  |  | 0.5 | 2.3531 | 3.40055 | 2.2578 |
|  |  | 0.75 | 1.502255 | 3.34593 | 1.865665 |
|  |  | 1 | 2.17949 | 5.76755 | 2.44256 |
| TARLAC-60 | Homo | 0 | 4.2531 | 6.81346 | 4.11167 |
|  |  | 0.25 | 2.51816 | 2.85862 | 2.778615 |
|  |  | 0.5 | 2.33077 | 1.92458 | 1.50802 |
|  |  | 0.75 | 1.900995 | 1.86799 | 2.005175 |
|  |  | 1 | 2.47755 | 1.51217 | 1.5599 |

Appendix D.iii.a. Bone volume fraction (BVTV) data standardized for comparison with the
volumes of interest from the Rudapithecus lower ilium.

| Specimen | Taxon | BVTV <br> Med769 | BVTV <br> Lat769 | BVTV <br> Vent692 | BVTV <br> Vent769 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| RU 210 | Rudapithecus | 0.339672 | 0.2804 | 0.314887 | 0.26098 |
| USNM 384228 | Papio | 0.2700772048 | 0.3467941446 | - |  |
| USNM 354987 | Papio | 0.1751130139 | 0.3138871389 |  |  |
| USNM 397476 | Papio | 0.339701 | 0.368612 |  | 0.433097 |
| USNM 384234 | Papio | 0.22756044 | 0.34979636 |  |  |
| USNM 395440 | Papio | 0.2472129231 | 0.4048698462 |  |  |
| USNM 384227 | Papio | 0.1756761806 | 0.2844552917 |  |  |
| USNM 141161 | Symphalangus | 0.36380847 | 0.41266031 |  | 0.35158189 |
| USNM 141162 | Symphalangus | 0.2227698378 | 0.3980902703 |  |  |
| USNM 141160 | Symphalangus | 0.2122581807 | 0.3679843012 |  | 0.2710300361 |
| AMNH 106581 | Symphalangus | 0.2855363243 | 0.4134530811 | 0.2738107117 | 0.2398897838 |
| USNM 220327 | Pan | 0.1951479398 | 0.3661971084 |  | 0.2210898434 |
| USNM 220065 | Pan | 0.2642161892 | 0.4085658919 |  | - |
| USNM 176227 | Pan | 0.277334528 | 0.456581504 | 0.391643392 | 0.339276768 |
| USNM 220064 | Pan | 0.1452350541 | 0.3474690811 |  | - |
| USNM 481804 | Pan | 0.32190031 | 0.38884202 | 0.31596908 | 0.2761776 |
| USNM 153823 | Pongo | 0.2362662892 | 0.3538703012 | 0.2590483133 | 0.2455065181 |
| USNM 145300 | Pongo | 0.17136653 | 0.28059211 | 0.24102392 | 0.17001926 |
| USNM 145302 | Pongo | 0.2613308462 | 0.3132807692 | 0.223 | 0.1978977692 |
| USNM 145301 | Pongo | 0.1892290769 | 0.2432197692 | 0.2283022308 | 0.2163972308 |
| USNM 145304 | Pongo | 0.37371997 | 0.31625782 | 0.28123538 | 0.264816285 |
| USNM 253780 | Macaca | - | - | 0.2788207658 | 0.2466063243 |
| USNM 173813 | Macaca | 0.3973071111 | 0.4633838472 | 0.5052299014 | 0.5015722917 |
| AMNH 43086 | Macaca | 0.189384 | 0.303028 | 0.304912 | 0.325221 |
| UPENN 86-12- |  |  |  |  |  |
| 44 | Macaca | 0.179705 | 0.3058055385 | 0.4311626154 | 0.4387263077 |
| B22-A | Homo | 0.234251926 | 0.339073132 | 0.376824336 | 0.386480752 |
| B22-B | Homo | 0.223142587 | 0.306483702 | 0.242130692 | 0.239840019 |
| TMM2165-A | Homo | 0.271413792 | 0.330303128 | 0.313610736 | 0.311674802 |
| TMM2165-B | Homo | 0.272115257 | 0.34663361 | 0.319841052 | 0.325429789 |
| TARLAC-60-A | Homo | 0.2756057477 | 0.3744453694 | 0.3152780691 | 0.3163378018 |
| TARLAC-60-B | Homo | 0.26860885 | 0.354660908 | 0.30897712 | 0.31231584 |

Appendix D.iii.b. Degree of anisotropy (DA) data standardized for comparison with the volumes of interest from the Rudapithecus lower ilium.

| Specimen | Taxon | DA | DA | DA | DA |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Med769 | Lat769 | Vent692 | Vent769 |
| RU 210 | Rudapithecus | 2.47411 | 2.19947 | 3.6556 | 3.61158 |
| USNM 384228 | Papio | 2.8425239759 | 4.4056072289 - | - | - |
| USNM 354987 | Papio | 4.5890016667 | 2.9467994444 |  | - |
| USNM 397476 | Papio | 2.11785 | 5.25747 - |  | 3.64979 |
| USNM 384234 | Papio | 2.6308324 | 10.85053112 |  | - |
| USNM 395440 | Papio | 3.6647715385 | 4.9022361538 - |  | - |
| USNM 384227 | Papio | 4.6596320833 | $3.5343495833-$ |  | - |
| USNM 141161 | Symphalangus | 2.9055809 | 4.1234204 |  | 3.3199223 |
| USNM 141162 | Symphalangus | 2.6200389189 | 3.250397027 - |  | - |
| USNM 141160 | Symphalangus | 3.8072201205 | 5.0012628916 |  | 4.323846988 |
| AMNH 106581 | Symphalangus | 1.5956597297 | 2.7941991892 | 3.1068682883 | 2.7820462162 |
| USNM 220327 | Pan | 8.92016 | 8.7595843373 - |  | 4.2537542169 |
| USNM 220065 | Pan | 2.8011894595 | 3.2332140541 |  | - |
| USNM 176227 | Pan | 2.80441896 | 3.41595952 | 3.01954008 | 2.28707536 |
| USNM 220064 | Pan | 7.5523437838 | 5.595007027 - |  | - |
| USNM 481804 | Pan | 3.1757363 | 3.9442986 | 4.3604528 | 3.0277761 |
| USNM 153823 | Pongo | 3.1750207229 | 3.468246988 | 3.1541696386 | 4.3658713253 |
| USNM 145300 | Pongo | 7.0679886 | 3.1600164 | 4.1718144 | 3.009085 |
| USNM 145302 | Pongo | 2.3478415385 | 2.8072007692 | 3.3929853846 | 4.5138553846 |
| USNM 145301 | Pongo | 3.5167884615 | 7.0115215385 | 2.2516615385 | 3.80739 |
| USNM 145304 | Pongo | 4.4662676 | 4.476472 | 4.1877518 | 4.70666635 |
| USNM 253780 | Macaca | - | - | 5.2866018919 | 7.1342689189 |
| USNM 173813 | Macaca | 4.4580083333 | 4.7181611111 | 5.8016126761 | 8.2960193056 |
| AMNH 43086 | Macaca | 3.10496 | 1.61947 | 3.24165 | 6.58455 |
| UPENN 86-12- |  |  |  |  |  |
| 44 | Macaca | 2.0279384615 | 2.2106238462 | 4.7771976923 | 4.9745315385 |
| B22-A | Homo | 2.06549818 | 1.89349164 | 2.97916808 | 3.09822856 |
| B22-B | Homo | 1.93898448 | 1.82773673 | 1.91557044 | 1.85232033 |
| TMM2165-A | Homo | 2.2613413 | 3.6047014 | 3.33688096 | 3.03922822 |
| TMM2165-B | Homo | 2.30963931 | 3.64296944 | 1.95020612 | 1.99237209 |
| TARLAC-60-A | Homo | 3.3741689189 | 7.1945869369 | 3.082277027 | 2.6727202703 |
| TARLAC-60-B | Homo | 3.40691582 | 6.40897104 | 2.87346584 | 2.55110688 |

Appendix D.iii.c. Bone volume fraction (BVTV) data standardized for comparison with the volumes of interest from the Rudapithecus ischium.

| Specimen | Taxon | Level | BVTV <br> Ventral | BVTV <br> Central | BVTV <br> Dorsal |
| :---: | :---: | :---: | :---: | :---: | :---: |
| RU 210 | Rudapithecus | 0.5 | 0.400454 |  | 0.433431 |
|  |  | 0.625 | 0.41706 |  | 0.450249 |
|  |  | 0.75 | 0.392311 | 0.422949 | 0.47618 |
| USNM 384228 | Papio | 0.5 | 0.42931 |  | 0.502137 |
|  |  | 0.625 | 0.4146806154 |  | 0.407111033 |
|  |  | 0.75 | 0.344943956 | 0.4419967912 | 0.4123935385 |
| USNM 354987 | Papio | 0.5 | 0.214121 |  | 0.245266 |
|  |  | 0.625 | 0.21827 |  | 0.258246 |
|  |  | 0.75 | 0.152071 | 0.198842 | 0.27048 |
| USNM 397476 | Papio | 0.5 | 0.302211 |  | 0.384551 |
|  |  | 0.625 | 0.2511321688 |  | 0.3546284156 |
|  |  | 0.75 | 0.1923654416 | 0.2847472987 | 0.425466 |
| USNM 384234 | Papio | 0.5 | 0.300157 |  | 0.419567 |
|  |  | 0.625 | 0.323498 |  | 0.389041 |
|  |  | 0.75 | 0.284596 | 0.29484 | 0.393739 |
| USNM 395440 | Papio | 0.5 | 0.247725 |  | 0.176833 |
|  |  | 0.625 | 0.268335 |  | 0.331564 |
|  |  | 0.75 | 0.273446 | 0.254152 | 0.202822 |
| USNM 384227 | Papio | 0.5 | 0.376229 |  | 0.43979 |
|  |  | 0.625 | 0.300087 |  | 0.375628 |
|  |  | 0.75 | 0.207765 | 0.287824 | 0.43117 |
| USNM 141161 | Symphalangus | 0.5 | 0.419972 |  | 0.39725 |
|  |  | 0.625 | 0.3778065808 |  | 0.386127994 |
|  |  | 0.75 | 0.352955 | 0.345039 | 0.3935165 |
| USNM 141162 | Symphalangus | 0.5 | 0.34784 |  | 0.346558 |
|  |  | 0.625 | 0.3226593706 |  | 0.3915756364 |
|  |  | 0.75 | 0.2917357622 | 0.4084762378 | 4263161748 |


|  | USNM 141160 | Symphalangus | 0.5 | $0.327865-$ |  |
| :--- | ---: | ---: | ---: | ---: | ---: |
|  |  | 0.625 | $0.2776052695-$ | 0.277348 |  |
|  | 0.75 | 0.2562025 | 0.2982455 | 0.2841503 |  |
|  |  |  |  |  |  |

$\begin{array}{llrr}\text { AMNH } 106581 \text { Symphalangus } \quad 0.5 & 0.3062274957-3439037498\end{array}$

|  |  | 0.75 | 0.3190775075 | 0.3126752973 | 0.3960029339 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| USNM 220327 | Pan | 0.5 | 0.2354515 - |  | 0.3787355 |
|  |  | 0.625 | 0.1923734835 - |  | 0.4162138571 |
|  |  | 0.75 | 0.2003997802 | 0.2945449011 | 0.3670527582 |
| USNM 220065 | Pan | 0.5 | 0.324584 - |  | 0.460767 |
|  |  | 0.625 | 0.276251 - |  | 0.39069925 |
|  |  | 0.75 | 0.2539475 | 0.2809265 | 0.335024 |
| USNM 176227 | Pan | 0.5 | 0.301378 - |  | 0.356504 |
|  |  | 0.625 | 0.251136 - |  | 0.324038 |
|  |  | 0.75 | 0.252369 | 0.260627 | 0.283253 |
| USNM 220064 | Pan | 0.5 | 0.242051 - |  | 0.395859 |
|  |  | 0.625 | 0.245041 - |  | 0.354413 |
|  |  | 0.75 | 0.253922 | 0.264624 | 0.325331 |
| USNM 481804 | Pan | 0.5 | 0.2761895 - |  | 0.412088 |
|  |  | 0.625 | 0.2696407568 - |  | 0.3688492973 |
|  |  | 0.75 | 0.2227585495 | 0.2984094595 | 0.337022955 |
| USNM 153823 | Pongo | 0.5 | 0.31384 - |  | 0.343241 |
|  |  | 0.625 | 0.310127 - |  | 0.294972 |
|  |  | 0.75 | 0.275209 | 0.306667 | 0.28392 |
| USNM 145300 | Pongo | 0.5 | 0.202047 - |  | 0.285116 |
|  |  | 0.625 | 0.20256275 - |  | 0.2519015 |
|  |  | 0.75 | 0.1961515 | 0.23606675 | 0.246864 |
| USNM 145302 | Pongo | 0.5 | 0.2806945 - |  | 0.336715 |
|  |  | 0.625 | $0.2710546434-$ |  | 0.3267125175 |
|  |  | 0.75 | 0.2297265245 | 0.2565014685 | 0.3362618881 |
| USNM 145301 | Pongo | 0.5 | 0.275289 - |  | 0.225859 |
|  |  | 0.625 | 0.25326 - |  | 0.248176 |
|  |  | 0.75 | 0.245737 | 0.277337 | 0.268333 |
| USNM 145304 | Pongo | 0.5 | 0.3042935 - |  | 0.3481995 |
|  |  | 0.625 | 0.30777275 - |  | 0.3645205 |
|  |  | 0.75 | 0.2827265 | 0.3157575 | 0.355258 |
| USNM 253780 | Macaca | 0.5 | 0.206164 - |  | 0.213812 |
|  |  | 0.625 | 0.2082285 - |  | 0.24965975 |
|  |  | 0.75 | 0.1240272 | 0.231672 | 0.19376 |
| USNM 173813 | Macaca | 0.5 | 0.387264 - |  | 0.449062 |
|  |  | 0.625 | 0.4117067922 - |  | 0.3938881818 |


|  |  | 0.75 | 0.2694076234 | 0.3158892857 | 0.3979388701 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| AMNH 43086 | Macaca | 0.5 | 0.218552 - |  | 0.405207 |
|  |  | 0.625 | 0.222245 - |  | 0.282978 |
|  |  | 0.75 | 0.183796 | 0.208767 | 0.211526 |
| UPENN 86-12-44 | Macaca | 0.5 | 0.1880455 - |  | 0.3204745 |
|  |  | 0.625 | 0.1737017922 - |  | 0.3117437662 |
|  |  | 0.75 | 0.0984179896 | 0.2335260519 | 0.2609812857 |
| B22 | Homo | 0.5 | 0.385692 - |  | 0.424449 |
|  |  | 0.625 | 0.4011246347 - |  | 0.4119826826 |
|  |  | 0.75 | 0.4000775 | 0.403809 | 0.4080325 |
| TMM2165 | Homo | 0.5 | 0.33515 - |  | 0.327554 |
|  |  | 0.625 | 0.319027994 - |  | 0.3840405269 |
|  |  | 0.75 | 0.3090525 | 0.302237 | 0.369684 |
| TARL B-3 | Homo | 0.5 | 0.395114 - |  | 0.443472 |
|  |  | 0.625 | $0.3868722335-$ |  | 0.4875663114 |
|  |  | 0.75 | 0.3794565 | 0.341292 | 0.455238 |
| TARLAC-60 | Homo | 0.5 | 0.360403 - |  | 0.32751 |
|  |  | 0.625 | 0.347394018 - |  | 0.320395479 |
|  |  | 0.75 | 0.3347605 | 0.343876 | 0.323561 |

Appendix D.iii.d. Degree of anisotropy (DA) data standardized for comparison with the volumes of interest from the Rudapithecus ischium.

| Specimen | Taxon |  | DA DA | DA | DA |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Level | Ventral C | Central | Dorsal |
| RU 210 | Rudapithecus | 0.5 | 2.64093 - |  | 1.94756 |
|  |  | 0.625 | 1.84777 - |  | 3.47559 |
|  |  | 0.75 | 1.9416 | 1.91909 | 2.30637 |
| USNM 384228 | Papio | 0.5 | 2.614395 - |  | 3.043405 |
|  |  | 0.625 | 2.1769204396 - |  | 2.8621230769 |
|  |  | 0.75 | 1.9510512088 | 3.8250682418 | 2.1762495604 |
| USNM 354987 | Papio | 0.5 | 5.73478 - |  | 8.45496 |
|  |  | 0.625 | 2.3199 - |  | 10.0005 |
|  |  | 0.75 | 1.76348 | 3.72734 | 3.65903 |
| USNM 397476 | Papio | 0.5 | 2.76624 - |  | 5.041905 |
|  |  | 0.625 | 2.7489780519 - |  | 5.6027962338 |
|  |  | 0.75 | 2.0074251948 | 5.1220803896 | 2.2624805195 |
| USNM 384234 | Papio | 0.5 | 1.68472 - |  | 5.14698 |
|  |  | 0.625 | 1.64274 - |  | 4.27527 |
|  |  | 0.75 | 1.65771 | 2.2328 | 5.56815 |
| USNM 395440 | Papio | 0.5 | 1.94774 - |  | 3.67464 |
|  |  | 0.625 | 1.78834 - |  | 2.51851 |
|  |  | 0.75 | 2.55218 | 2.62619 | 2.01716 |
| USNM 384227 | Papio | 0.5 | 1.56574 - |  | 4.50835 |
|  |  | 0.625 | 1.63701 - |  | 3.43511 |
|  |  | 0.75 | 5.06862 | 2.11622 | 3.37607 |
| USNM 141161 | Symphalangus | 0.5 | 2.09753 - |  | 3.0737 |
|  |  | 0.625 | 1.8901722156 - |  | 1.985691018 |
|  |  | 0.75 | 1.935935 | 4.530525 | 2.04742 |
| USNM 141162 | Symphalangus | 0.5 | 2.23882 - |  | 3.318965 |
|  |  | 0.625 | 1.7670247552 - |  | 3.0627631469 |
|  |  | 0.75 | 1.9282833566 | 4.798946014 | 2.7796665734 |
| USNM 141160 | Symphalangus | 0.5 | 5.3211 - |  | 3.25462 |
|  |  | 0.625 | 4.2725670659 - |  | 2.8707652096 |
|  |  | 0.75 | 4.540285 | 2.12564 | 2.37276 |
| AMNH 106581 | Symphalangus | 0.5 | 1.8297437669 - |  | 3.8716237339 |
|  |  | 0.625 | 1.9516047198 - |  | 3.66434549 |


|  |  | 0.75 | 2.2982367568 | 1.8232743544 | 4.3928035736 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| USNM 220327 | Pan | 0.5 | 3.71278 |  | 13.768235 |
|  |  | 0.625 | 3.2700421978 |  | 8.0119186813 |
|  |  | 0.75 | 4.310488022 | 5.3453897802 | 4.1650665934 |
| USNM 220065 | Pan | 0.5 | 2.06985 |  | 3.30853 |
|  |  | 0.625 | 1.8786225 |  | 1.8596225 |
|  |  | 0.75 | 1.619595 | 2.285405 | 1.75384 |
| USNM 176227 | Pan | 0.5 | 4.36505 |  | 5.50844 |
|  |  | 0.625 | 1.83489 |  | 4.734435 |
|  |  | 0.75 | 3.1404 | 3.42076 | 3.76809 |
| USNM 220064 | Pan | 0.5 | 2.20977 |  | 2.99263 |
|  |  | 0.625 | 1.46987 |  | 4.09382 |
|  |  | 0.75 | 1.87919 | 3.43827 | 2.18476 |
| USNM 481804 | Pan | 0.5 | 5.572695 |  | 4.512765 |
|  |  | 0.625 | 4.5358359459 |  | 4.0395818919 |
|  |  | 0.75 | 2.4124927928 | 3.3589189189 | 2.9580881081 |
| USNM 153823 | Pongo | 0.5 | 2.88184 |  | 3.41732 |
|  |  | 0.625 | 2.14466 |  | 2.57392 |
|  |  | 0.75 | 2.20488 | 2.50544 | 2.97022 |
| USNM 145300 | Pongo | 0.5 | 2.87526 |  | 3.994855 |
|  |  | 0.625 | 3.78413875 |  | 3.0663 |
|  |  | 0.75 | 3.4278325 | 2.5053 | 1.91025 |
| USNM 145302 | Pongo | 0.5 | 2.15528 |  | 3.6821 |
|  |  | 0.625 | 2.1433020979 |  | 3.370048042 |
|  |  | 0.75 | 2.2944947552 | 2.1423666434 | 3.3768084615 |
| USNM 145301 | Pongo | 0.5 | 2.61634 |  | 2.47648 |
|  |  | 0.625 | 2.58139 |  | 1.79771 |
|  |  | 0.75 | 1.53455 | 1.78478 | 3.07182 |
| USNM 145304 | Pongo | 0.5 | 1.79139 |  | 3.13239 |
|  |  | 0.625 | 1.8018275 |  | 2.91191625 |
|  |  | 0.75 | 2.222415 | 3.26692 | 2.2887475 |
| USNM 253780 | Macaca | 0.5 | 7.00279 |  | 3.86202 |
|  |  | 0.625 | 5.9279425 |  | 3.7268575 |
|  |  | 0.75 | 2.71897 | 5.3793325 | 2.8181275 |
| USNM 173813 | Macaca | 0.5 | 2.11875 |  | 3.064535 |
|  |  | 0.625 | 1.6503653247 - |  | 2.8410822078 |

$\begin{array}{llll}0.75 & 3.3046706494 & 2.8388015584 & 2.4383102597\end{array}$

| AMNH 43086 | Macaca | 0.5 | 3.00729 - |  | 3.562 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 0.625 | 2.23448 - |  | 6.78987 |
|  |  | 0.75 | 5.31577 | 1.71081 | 9.9199 |
| UPENN 86-12-44 | Macaca | 0.5 | 2.77184 |  | 3.099825 |
|  |  | 0.625 | 4.9817046753 - |  | 4.3332394805 |
|  |  |  |  |  | 10.444333766 |
|  |  | 0.75 | 3.9450202597 | 3.0427327273 | 2 |
| B22 | Homo | 0.5 | 2.86517 - |  | 1.85714 |
|  |  | 0.625 | 2.0592717964 - |  | 1.612379521 |
|  |  | 0.75 | 1.870445 | 1.634515 | 1.75557 |
| TMM2165 | Homo | 0.5 | 1.95929 - |  | 5.95185 |
|  |  | 0.625 | 1.5844546707 - |  | 3.0342377246 |
|  |  | 0.75 | 1.352285 | 2.268365 | 2.09948 |
| TARL B-3 | Homo | 0.5 | 2.3531 - |  | 2.2578 |
|  |  | 0.625 | 1.6672317365 - |  | 1.9891023952 |
|  |  | 0.75 | 1.502255 | 3.34593 | 1.865665 |
| TARLAC-60 | Homo | 0.5 | 2.33077 - |  | 1.50802 |
|  |  | 0.625 | 1.7782250898 - |  | 1.7722191018 |
|  |  | 0.75 | 1.900995 | 1.86799 | 2.005175 |

Appendix E.i. Principal component analysis centroid scores for bone volume fraction from the
medial and lateral volumes of interest from the lower ilium.

| Specimen | Species | PC1 | PC2 | PC3 | PC4 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| USNM 384228 | Papio | -0.181825009 | 0.050534655 | -0.063275461 | 0.04881532 |
| USNM 354987 | Papio | 0.153428658 | -0.116858063 | -0.093505152 | 0.09307409 |
| USNM 397476 | Papio | -0.074032054 | 0.005075788 | -0.051216073 | -0.15039162 |
| USNM 384234 | Papio | -0.051923337 | 0.003548185 | -0.035333972 | 0.04838296 |
| USNM 395440 | Papio | 0.041440711 | 0.107606284 | 0.021580859 | 0.0255974 |
| USNM 384227 | Papio | 0.087788057 | -0.10687759 | -0.027681213 | -0.08978263 |
| USNM 141162 | Symphalangus | 0.079194951 | 0.071631362 | -0.135058447 | -0.03280225 |
| USNM 141160 | Symphalangus | 0.263881108 | 0.082619154 | -0.108944693 | 0.04756295 |
| AMNH 106581 | Symphalangus | 0.076209372 | 0.175468497 | -0.005367387 | -0.01464534 |
| USNM 220327 | Pan | 0.162516102 | -0.011124205 | 0.037473463 | -0.01307644 |
| USNM 220065 | Pan | 0.079851916 | 0.092758626 | 0.04374389 | -0.08125693 |
| USNM 176227 | Pan | -0.154647627 | 0.038990072 | -0.078504477 | -0.01457353 |
| USNM 220064 | Pan | 0.134888516 | -0.064336156 | 0.017452537 | 0.02472739 |
| USNM 481804 | Pan | -0.035609835 | 0.1618968 | 0.216194756 | 0.05631801 |
| USNM 153823 | Pongo | -0.243394522 | -0.054646801 | 0.027937392 | 0.10500935 |
| USNM 145300 | Pongo | 0.155448894 | -0.094947797 | 0.111984063 | 0.02764424 |
| USNM 145302 | Pongo | -0.131950674 | -0.091999256 | 0.054335129 | -0.02523827 |
| USNM 145301 | Pongo | 0.142135148 | -0.11774563 | 0.058541136 | 0.01834402 |
| USNM 145304 | Pongo | -0.188386111 | -0.037837901 | 0.040455516 | -0.10132299 |
| B22-A | Homo | -0.002807487 | -0.027590211 | 0.011067469 | 0.01512437 |
| TMM2165-A | Homo | -0.058757764 | -0.057998244 | 0.038543005 | -0.05941714 |
| TARLAC-60-A | Homo | -0.25344901 | -0.00816757 | -0.08042234 | 0.07190705 |
| Specimen | Species | C5 | C6 | PC7 | C8 |
| USNM 384228 | Papio | 0.035557785 | 0.047351777 | 0.0130778298 | -0.04554847 |
| USNM 354987 | Papio | -0.076025768 | -0.044741059 | 0.0614758827 | -0.001278694 |
| USNM 397476 | Papio | 0.001838791 | 0.005355744 | 0.0237674259 | -0.008092598 |
| USNM 384234 | Papio | 0.074432687 | 0.013857093 | -0.0619195156 | -0.032336741 |
| USNM 395440 | Papio | -0.113924212 | -0.060383281 | -0.0185180106 | -0.02864523 |
| USNM 384227 | Papio | 0.077172332 | -0.002207115 | 0.0093969809 | -0.029872388 |
| USNM 141162 | Symphalangus | -0.024547159 | -0.038694418 | 0.0221665142 | 0.01468804 |
| USNM 141160 | Symphalangus | 0.011749102 | 0.097105623 | 0.0005474772 | 0.00410475 |
| AMNH 106581 | Symphalangus | 0.007079468 | -0.006761996 | -0.0115979589 | -0.044308209 |
| USNM 220327 | Pan | -0.045128397 | -0.002238085 | -0.0707578413 | 0.029378746 |
| USNM 220065 | Pan | 0.057474368 | -0.022348027 | 0.0310247466 | 0.070344274 |
| USNM 176227 | Pan | 0.063862703 | -0.057301994 | -0.0431345777 | 0.026338 |
| USNM 220064 | Pan | -0.024441769 | -0.025384447 | -0.0476697977 | 0.045229904 |
| USNM 481804 | Pan | 0.002931787 | 0.011640038 | 0.0341499108 | -0.003148451 |
| USNM 153823 | Pongo | 0.022088211 | -0.051021501 | 0.0173212773 | 0.011890168 |
| USNM 145300 | Pongo | 0.085521868 | 0.024112547 | 0.0290014686 | 0.031927988 |
| USNM 145302 | Pongo | -0.023824447 | 0.014752048 | -0.0719658784 | -0.008826909 |
| USNM 145301 | Pongo | -0.01777241 | 0.033131909 | 0.0027348215 | -0.050157847 |
| USNM 145304 | Pongo | -0.124850927 | 0.073721912 | 0.0146315918 | 0.01936471 |


| B22-A | Homo | 0.009749648 | -0.014424376 | 0.0099279419 | -0.006034211 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| TMM2165-A | Homo | 0.01357312 | -0.049204928 | 0.0374978825 | -0.047080849 |
| TARLAC-60-A | Homo | -0.012516782 | 0.053682536 | 0.0188418284 | 0.052064017 |
| Specimen | Species | PC9 | PC10 | PC11 | PC12 |
| USNM 384228 | Papio | 0.0365226565 | -0.008216473 | -0.025640147 | -0.0093196836 |
| USNM 354987 | Papio | -0.0622876018 | 0.01522624 | -0.007409134 | 0.000212511 |
| USNM 397476 | Papio | -0.0066985835 | -0.009135632 | 0.006515177 | 0.0027040043 |
| USNM 384234 | Papio | -0.013601641 | -0.021106532 | 0.01072159 | 0.0190799086 |
| USNM 395440 | Papio | 0.0562603515 | -0.001462307 | 0.006302987 | 0.0051430864 |
| USNM 384227 | Papio | 0.007572313 | 0.027797705 | -0.010751592 | 0.0092755552 |
| USNM 141162 | Symphalangus | 0.0215754381 | -0.02256152 | 0.004043366 | 0.015119045 |
| USNM 141160 | Symphalangus | 0.0142552038 | 0.02103786 | 0.032014892 | 0.0045160265 |
| AMNH 106581 | Symphalangus | -0.0260016307 | 0.025174223 | -0.020918724 | -0.0120715126 |
| USNM 220327 | Pan | -0.0327573818 | -0.015751135 | -0.020792113 | 0.0048552741 |
| USNM 220065 | Pan | 0.0191086091 | 0.007956385 | -0.027377091 | 0.00390926 |
| USNM 176227 | Pan | -0.0514857024 | 0.003208964 | 0.023322718 | -0.0063349457 |
| USNM 220064 | Pan | 0.0423349705 | -0.003232697 | 0.00396024 | -0.021140146 |
| USNM 481804 | Pan | -0.0412037047 | -0.003416256 | 0.010484457 | 0.0042160778 |
| USNM 153823 | Pongo | 0.0383725067 | 0.03054142 | 0.005467999 | 0.013774168 |
| USNM 145300 | Pongo | 0.0173363739 | -0.00828846 | 0.013004955 | -0.001048951 |
| USNM 145302 | Pongo | -0.0027222788 | 0.026022 | -0.005266152 | -0.0039475557 |
| USNM 145301 | Pongo | -0.0007364909 | -0.018017627 | -0.015836914 | 0.0063997799 |
| USNM 145304 | Pongo | -0.0054505463 | 0.009186678 | 0.0160009 | 0.0064681713 |
| B22-A | Homo | -0.0021063331 | -0.019866204 | 0.003848943 | -0.0007698938 |
| TMM2165-A | Homo | 0.0021850024 | -0.017637674 | 0.017946554 | -0.0233168135 |
| TARLAC-60-A | Homo | -0.0104715306 | -0.017458958 | -0.019642911 | -0.008691313 |

Appendix E.ii. Principal component analysis centroid scores for degree of anisotropy from the
medial and lateral volumes of interest from the lower ilium.

| Specimen | Species | PC1 | PC2 |  | PC3 |  |
| :--- | :--- | ---: | ---: | ---: | ---: | :---: |
| USNM 384228 | Papio | 4.4618642 | -0.7041128 | -0.4608376 | 1.2731881 |  |
| USNM 354987 | Papio | 1.9240505 | 2.4504076 | -0.1213601 | 1.6688804 |  |
| USNM 397476 | Papio | 2.6177219 | 3.5577505 | 4.8228252 | -2.9917809 |  |
| USNM 384234 | Papio | -7.5335168 | -2.591599 | -1.4822791 | -4.687295 |  |
| USNM 395440 | Papio | -15.6440153 | 2.2834501 | 3.8337089 | 7.1114328 |  |
| USNM 384227 | Papio | 3.5485408 | 0.6568001 | -1.4332484 | 1.083996 |  |
| USNM 141162 | Symphalangus | 5.1806139 | -1.0180062 | 1.7498753 | 1.201079 |  |
| USNM 141160 | Symphalangus | 1.5657836 | -2.0138232 | -3.1339917 | 0.8073385 |  |
| AMNH 106581 | Symphalangus | 2.2855863 | -5.2247473 | -4.8673048 | -2.9202272 |  |
| USNM 220327 | Pan | -10.1989496 | 9.4148676 | -6.8759743 | -0.8486718 |  |
| USNM 220065 | Pan | 3.1690252 | -1.7210369 | -0.5809256 | 1.2573813 |  |
| USNM 176227 | Pan | 2.5954496 | 4.4031762 | -4.3802187 | 0.3570639 |  |
| USNM 220064 | Pan | -17.9492481 | -5.3617113 | 3.2680393 | -1.3772181 |  |
| USNM 481804 | Pan | -4.4145618 | -5.7513491 | -2.8034195 | -1.7549693 |  |
| USNM 153823 | Pongo | 2.9765042 | 0.6062062 | 0.4348047 | 0.1759576 |  |
| USNM 145300 | Pongo | -0.2931412 | -1.502191 | 0.5101845 | 0.6115421 |  |
| USNM 145302 | Pongo | 5.974383 | -1.7765578 | 2.1002436 | 1.2976232 |  |
| USNM 145301 | Pongo | 1.9564204 | 2.043231 | 0.6657049 | -1.9994806 |  |
| USNM 145304 | Pongo | 4.0416556 | 1.2332916 | 2.473116 | -0.3805353 |  |
| B22-A | Homo | 6.0884334 | -2.3884828 | -0.6995818 | 4.1965525 |  |
| TMM2165-A | Homo | 5.3461689 | -0.7013927 | 1.0164403 | 1.7675475 |  |
| TARLAC-60-A | Homo | 2.3012313 | 4.1058291 | 5.9641989 | -5.8494048 |  |


| Specimen | Species | PC5 | PC6 |  | PC7 |  |
| :--- | :--- | ---: | ---: | ---: | ---: | ---: |
| USNM 384228 | Papio | -2.0460568 | -1.0619129 | -0.95066293 | 0.97743702 |  |
| USNM 354987 | Papio | -3.529585 | -0.2827165 | 3.09244824 | -1.22587883 |  |
| USNM 397476 | Papio | 0.9785959 | 1.7105001 | -1.06748836 | 0.1527573 |  |
| USNM 384234 | Papio | -3.5840234 | -1.4240047 | 0.95642971 | 2.00970799 |  |
| USNM 395440 | Papio | 0.6627848 | 1.0557813 | 0.31714793 | 1.32473012 |  |
| USNM 384227 | Papio | 1.4709328 | -2.2153684 | -0.45341528 | -0.97543 |  |
| USNM 141162 | Symphalangus | -0.4474978 | -0.3156516 | 0.40750734 | -0.01019411 |  |
| USNM 141160 | Symphalangus | 4.0466074 | -1.8763991 | 2.63323645 | 1.89813459 |  |
| AMNH 106581 | Symphalangus | 1.1209394 | 2.3934132 | -0.80672506 | -0.61335262 |  |
| USNM 220327 | Pan | 0.4472952 | -1.3488788 | -0.98359259 | -1.38053191 |  |
| USNM 220065 | Pan | -1.0541172 | 0.8991875 | -1.76328985 | 1.22263803 |  |
| USNM 176227 | Pan | -0.7535945 | 4.0219809 | 0.05207036 | 0.85236915 |  |
| USNM 220064 | Pan | 0.2528303 | -0.1364304 | -1.21758819 | -1.20079666 |  |
| USNM 481804 | Pan | 0.169209 | 0.3061228 | 0.53357444 | -0.6937036 |  |
| USNM 153823 | Pongo | 0.6575408 | 1.4167865 | -0.88208624 | 1.39438356 |  |
| USNM 145300 | Pongo | 0.9036374 | 1.8856087 | 2.0613734 | -1.63936285 |  |
| USNM 145302 | Pongo | -0.0777194 | -0.1514591 | -0.65316712 | -1.02239268 |  |
| USNM 145301 | Pongo | 0.8087005 | -2.6141736 | -1.35879882 | 0.88259698 |  |
| USNM 145304 | Pongo | -0.7447817 | -0.9589642 | -1.01441125 | -1.10050682 |  |


| B22-A | Homo | -0.1678424 | -0.6031922 | -0.18590825 | -0.68537824 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| TMM2165-A | Homo | -0.2451035 | -1.0084522 | -0.50501738 | -0.20386121 |
| TARLAC-60-A | Homo | 1.1312481 | 0.3082228 | 1.78836345 | 0.03663477 |
| Specimen | Species | PC9 | PC10 | PC11 | PC12 |
| USNM 384228 | Papio | 0.33349188 | -0.054975712 | -0.34159809 | -0.451448805 |
| USNM 354987 | Papio | 1.07204141 | 0.893112835 | -0.33111087 | -0.030127461 |
| USNM 397476 | Papio | 0.08129616 | -0.689490303 | -0.18752173 | -0.205740947 |
| USNM 384234 | Papio | -1.15809346 | -0.40934976 | 0.28441002 | 0.07774642 |
| USNM 395440 | Papio | -0.87862083 | 0.837707698 | 0.6389879 | -0.098055857 |
| USNM 384227 | Papio | 1.35372319 | 0.237116189 | 0.79100388 | -0.474396817 |
| USNM 141162 | Symphalangus | 0.6604134 | -0.245748169 | -0.49190978 | -0.34207201 |
| USNM 141160 | Symphalangus | 0.88690103 | -0.144244142 | -0.52614963 | 0.141104177 |
| AMNH 106581 | Symphalangus | -1.1192862 | 2.061013735 | -0.05162991 | -0.17751519 |
| USNM 220327 | Pan | -0.34793395 | -0.195145435 | 0.02271963 | 0.124534109 |
| USNM 220065 | Pan | 1.63993069 | 0.202303097 | 1.05260812 | 0.287619053 |
| USNM 176227 | Pan | 0.19364779 | -0.753004744 | -0.51640858 | -0.136231202 |
| USNM 220064 | Pan | 1.05399553 | -0.190194655 | -1.11890849 | -0.058864601 |
| USNM 481804 | Pan | 0.53143955 | -0.760520365 | 0.86369698 | 0.034972048 |
| USNM 153823 | Pongo | 0.93158292 | 0.006219874 | -0.43335303 | 0.345789597 |
| USNM 145300 | Pongo | -0.42587734 | -1.18259004 | 0.42099549 | 0.107051066 |
| USNM 145302 | Pongo | -1.0757001 | -0.905437068 | 0.47436109 | -0.004707027 |
| USNM 145301 | Pongo | -1.08307249 | -0.108087741 | -0.13241065 | -0.033781094 |
| USNM 145304 | Pongo | 1.28831246 | 0.643448942 | -0.11215321 | 0.564702923 |
| B22-A | Homo | -2.12769668 | 0.031619444 | -0.69461746 | 0.292089847 |
| TMM2165-A | Homo | -1.21863507 | -0.117200319 | 0.02152502 | 0.020584573 |
| TARLAC-60-A | Homo | -0.59185987 | 0.843446641 | 0.36746328 | 0.016747199 |

