

Allometric Scaling and Locomotor Function in the Primate Pelvis

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ABSTRACT Identification of positional behavior adaptation in the pelvis of primates is complicated by possible confounding effects of body size and phylogeny. Previous work on primate pelvic allometry has focused primarily on sexual dimorphism and its relationship to obstetric constraints in species with large fetal size relative to maternal size. This study investigates patterns of pelvic scaling with a specific aim to understand how pelvic scaling relates to locomotor function. Patterns of scaling of nine pelvic dimensions were examined in a broad comparative sample of 40 species of primates, covering both haplorhines and strepsirrhines, while accounting for phylogenetic nonindependence. Phylogenetic reduced major axis regressions on pelvic scaling patterns suggest that primate-wide patterns are reflected in haplorhine- and strepsirrhine-specific analyses. Many measures scale isometrically with pelvis size,

but notably, features of the ilium tend to scale allometrically. As predicted, ilium width and lower ilium cross-sectional area scale with positive allometry, while lower iliac height scales with negative allometry. Further regression analyses by locomotor group suggest that these ilium measures, as well as pubic symphysis and ischium lengths, differ in their scaling patterns according to locomotor mode. These results suggest that scaling differences within primates, when present, are related to functional differences in locomotor behavior and mechanics. This study supports recent work that identifies adaptations to locomotor loading in the ilium and highlights the need for a better understanding of the relationship between pelvic structural mechanics and the mechanical requirements of primate locomotion. *Am J Phys Anthropol* 156:511–530, 2015. © 2015 Wiley Periodicals, Inc.

Scaling patterns can yield important insights into skeletal mechanical function because the skeletal system must maintain functional equivalence throughout a range of body sizes (Rollinson and Martin, 1981; Jungers, 1984; Schmidt-Nielsen, 1984). Animals of differing body size experience differences in loading patterns; large animals encounter absolutely larger loads than small animals due to the effects of gravity and increasing mass on anatomical structure (Hildebrand, 1985; Biewener, 2003). Previous work on primate postcranial scaling has shown that features related to limb strength (e.g., diaphyseal cross-sectional cortical area) scale with slight positive allometry to maintain bone safety factor, but do not achieve functional (dynamic) similarity (e.g., Schaffler et al., 1985; Demes and Jungers, 1993; Jungers and Burr, 1994). Instead of increasing bone strength alone, quadrupedal mammals mostly compensate for increased forces by altering other correlates of positional behavior (i.e., posture and locomotion), such as joint posture and limb angular excursion (Schmidt-Nielsen, 1984; Biewener, 1990; Polk, 2004). However, postural accommodations become less effective at large body sizes (i.e., greater than 100 kg), requiring very large mammals to rely on bone shape changes to maintain functional equivalence (Galilei, 1638; Biewener, 1983).

While studies of primate limb bone scaling are relatively common (Jungers, 1978, 1982, 1988; Jungers and Fleagle, 1980; Schaffler et al., 1985; Ruff, 1988; Godfrey et al., 1991; Demes and Jungers, 1993; Jungers and Burr, 1994), less attention has been paid to scaling patterns in pelvic dimensions. The pelvis as a whole—and ilium in particular—distributes the forces that occur during locomotion from the hindlimb to the torso (Dal-

stra and Huiskes, 1995). The ilium is, therefore, a critical pathway of force transmission both in humans and in non-human primates, and is a region that encounters moderate levels of strain during loading (Dalstra and Huiskes, 1995; Lewton, 2010). Given the role of the pelvis in force transmission, it is likely that aspects of pelvic shape that function to resist forces will scale with body size in such a way as to maintain functional equivalence (i.e., mechanical similarity *sensu* Jungers, 1984). Indeed, a small number of studies have related allometric scaling patterns of the pelvis to positional behavior (Stuedel, 1981a; Ward 1991, 1993) and found that size-related differences in loading seem to be reflected in some aspects of pelvic bony morphology (Ward, 1991; MacLatchy, 1995; Lewton, 2015). For example, dimensions of the acetabulum—a region of the pelvis that must resist locomotor forces transmitted from the hindlimb—appear to scale with slight positive allometry (Ward, 1991; MacLatchy, 1995), which is in accord with

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studies on other hindlimb joint surfaces (e.g., Jungers, 1988).

Other research on primate pelvic scaling has focused on the influences of obstetrical requirements and neonatal brain size on pelvic shape (Leutenegger, 1974, 1982; Tague, 2005) especially in relation to the evolution of bipedality and relatively large brain size in early hominin species (Reynolds, 1931; Dart, 1949; Le Gros Clark, 1955; Day, 1973; Lovejoy et al., 1973; Brain et al., 1974; McHenry, 1975; Ashton et al., 1981; Berge, 1984; Berge and Kazmierczak, 1986; Rak and Arensburg, 1987; Berge, 1991; Rak, 1991; Fleagle and Anapol, 1992; Rosenberg, 1992; Berge, 1994; Ruff, 1995; MacLatchy, 1996; Macchiarelli et al., 1999; Marchal, 2000; Haeusler, 2002; Lovejoy, 2005; Lovejoy et al., 2009; Weaver and Hublin, 2009; Ruff, 2010). Research on the obstetrical functions of the pelvis has demonstrated that aspects of the bony birth canal—dimensions of the pelvic inlet, midplane, and outlet—differ intra- and interspecifically, with selection favoring females with larger pelvic diameters in species that have large neonates relative to maternal size (Schultz, 1949; Black, 1970; Leutenegger, 1974). Other research on primate pelvic allometry has focused on identifying sexual dimorphism in taxonomically narrow samples (Schultz, 1949; Black, 1970; Gingerich, 1972; Leutenegger, 1973; Mobb and Wood, 1977; Leutenegger and Larson, 1985; Tague, 1991, 1992, 1993, 1995; Hager, 1996; St. Clair, 2007; Kurki, 2011). This previous research has identified patterns of maternal-fetal size relationships and intraspecific size relationships relating to obstetrics. However, there remains a gap in our understanding regarding how pelvic scaling may relate to positional behavior, and whether broad patterns of scaling of pelvic anatomy can be used to interpret general relationships among pelvic size, shape, and locomotor function within primates.

Given the focus of recent work to interpret primate pelvic functional morphology and evolution within the context of reconstructing evolutionary history and locomotion in the fossil record (Hammond et al., 2013; Lewton, 2012; Lewton, 2015), it is necessary to understand patterns of pelvic scaling and how they relate to locomotor behavior and adaptation across primate species. The aims of this article are two-fold: first to test hypotheses of scaling in the primate pelvis, and second, to relate those patterns to locomotor function. This project examines patterns of pelvic scaling in a broad comparative sample of primates. Scaling patterns are analyzed for primates as a whole, and for Haplorhini and Strepsirhini separately, with a specific focus on scaling patterns within and among locomotor groups. The results of this study augment recent work that tests hypotheses of locomotor adaptation in strepsirrhines (Lewton, 2015) and that aims to construct a mechanical model of how the pelvis responds to simulated locomotor loading (Lewton, 2010, in review).

HYPOTHESIZED EFFECTS OF BODY SIZE, LOCOMOTOR FORCES, AND POSTURE ON SCALING

To contextualize pelvic allometry within primate biology as a whole, the relationships between body size and positional behavior mechanics must be understood, especially the average substrate reaction forces encountered during locomotion and the typical postures in which loading is applied. The following section relates the rela-

tionships among body size, locomotor loading, and postural mechanics in locomotor groups to scaling hypotheses proposed here. This work uses broad positional behavior categories derived from Napier and Napier (1967) to classify primate species by the positional behavior in which a species spends the majority of its travel time. Although primates exhibit remarkably diverse positional behaviors, this study groups non-human primates into four major categories: arboreal quadrupeds (AQ), terrestrial quadrupeds (TQ), suspensors, and vertical clingers and leapers (VCL). The strength of using this simplified classification system is that it facilitates hypothesis generation from mechanical models of locomotion.

Body size and positional behavior are loosely correlated (Fleagle and Mittermeier, 1980; Garber, 2011). Within primates as a whole, there is so much variation in substrate support use and positional behaviors that general 'rules' governing these relationships have many exceptions (Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995; McGraw, 1998, 2000). However, it is still useful to consider some broad associations between body size and positional behavior. For arboreal species, small primates tend to be above-branch quadrupeds while large species tend to be below-branch suspensors. There are both small (tarsiers and galagos) and large (indriids) vertical clingers and leapers that differ in locomotor mechanics, specifically in force generation, which is either from the leg and foot (small-bodied) or thigh (large-bodied) (Demes et al., 1996). Terrestrial species are mostly medium-to-large in size, and are either quadrupedal or bipedal. Because this study is interested in broad patterns that are generalizable across primates, these basic associations between body size and positional behavior are useful for forming hypotheses about how pelvic size and scaling may relate to body size and locomotion.

All forms of locomotion result in substrate reaction forces on the limbs of a primate, and these forces must be resisted by the musculoskeletal locomotor system. Typical substrate reaction forces encountered during locomotion have been experimentally determined using *in vivo* approaches in both natural and laboratory settings, and these forces vary among locomotor groups (Kimura, 1985; Demes et al., 1995, 1999; Schmitt and Hanna, 2004; Franz et al., 2005; Hanna et al., 2006).

Likely due to the compliant substrates on which they move, arboreal quadrupeds encounter low substrate reaction forces during walking and running compared with other primates, with average loads between 0.5 and 0.8 times body weight (Schmitt, 1998, 2003; Schmitt and Hanna, 2004; Franz et al., 2005). Terrestrial quadrupeds move on harder and less compliant substrates and, accordingly, encounter slightly higher forces, between 0.6 and 1.0 times body weight, on average (Kimura, 1985; Schmitt and Hanna, 2004; Hanna et al., 2006). Remarkably, vertical clingers and leapers encounter between 5.0 and 14.0 times their body weight during takeoff and landing of a leap (Demes et al., 1995, 1999). It is worth noting that all of this force in vertical clingers and leapers is imposed on the hindlimbs, as the forelimbs primarily steer and maneuver the animal (Demes et al., 1994), which makes the large forces vertical clinging and leaping primates encounter all the more incredible for being distributed among only two limbs as opposed to all four. In addition, there are body size effects in the mechanics of vertical clinging and leaping.

Small-bodied vertical clinging and leaping taxa experience relatively larger substrate reaction forces than large-bodied vertical clinging and leaping taxa (Demes et al., 1995, 1999) as a result of absolutely shorter hindlimbs, which decrease the time period for acceleration (Alexander, 1995; Preuschoft et al., 1996), and relatively larger muscle masses, which increase force production (Preuschoft et al., 1996). Finally, although there are experimental data on walking and running of suspensory taxa (Kimura, 1985; Schmitt and Hanna, 2004; Verbeeke et al., 2005), these data are not naturalistic because they do not capture the loads that occur during suspensory behaviors and because they were collected on terrestrial substrates. The variation in substrate reaction forces that primates experience during their preferred forms of locomotion should have an effect on limb morphology. In addition, these forces likely combine with those resulting from body size (i.e., forces due to gravity acting on the body), and the locomotor limb system must be capable of withstanding these resulting forces, either through morphological adaptation or postural modification.

The differences outlined above in body size, substrate reaction forces, and postural loading across locomotor groups are the foundation for understanding how these factors might result in different scaling relationships between pelvic traits and size, and ultimately to demonstrating how locomotor adaptation and pelvic allometry are related. This article tests hypotheses of scaling in nine dimensions of the primate pelvis and contextualizes these results within a broader adaptive framework.

Scaling predictions

Across primates, pelvic traits related to resisting large forces (e.g., joint surface areas and cross-sectional areas) should scale with positive allometry. Aspects of pelvic anatomy that are likely subjected to bending (i.e., bony levers such as ilium length) should exhibit negative allometry to decrease bending moments. Pelvic traits that do not distribute large forces or are not subjected to bending should exhibit isometric scaling with size. Specific predictions for each pelvic measure examined here are listed below.

Pubic rami and symphysis lengths. The functional role of the pubis in locomotion is not well known, and pubic rami lengths have been associated more closely with sexual dimorphism (Gingerich, 1972; Leutenegger, 1973; Mobb and Wood, 1977; Schultz, 1949; Steudel, 1981a) and obstetric requirements (in terms of increasing pubic ramus length to increase birth canal dimensions, Rosenberg, 1988, 1992) than with locomotor function. Similarly, the relationship between pubic symphysis form and function is not well understood. Based on Ward's (1991) finding of isometric scaling in pubic rami lengths in catarrhines, and a lack of previous research that suggests otherwise, this study predicts isometry of pubic rami and symphysis lengths in both haplorhines and strepsirrhines.

Ilium length. Total ilium length includes the lower ilium and the upper ilium (formed by the variably shaped iliac blade and crest), which forms the site of attachment for various muscles of the hip and back. Ward (1991) demonstrated negative allometry of ilium

length in catarrhine monkeys, but isometry in hominoids. Given that there is no reason to suggest negative allometry of ilium length characterizes all primates except hominoids, this study predicts isometric scaling of ilium length across primates.

Ilium width. The extensor muscles of the spine and the gluteal muscles attach along the width of the iliac blade. Both Ward (1991, 1993) and Steudel (1981a) demonstrated slight positive allometry of ilium width in catarrhines, which has been hypothesized to be related to increasing muscle mass given the negatively allometric scaling of muscle mass with body size in mammals (Biewener, 1989). Accordingly, this study predicts positive allometry of ilium width across primates.

Lower iliac height and cross-sectional area. The lower ilium is a critical region of the pelvis because it distributes forces from the hindlimb to the trunk via the coxal and sacroiliac joints (Dalstra and Huiskes, 1995). As a result, lower ilium morphology has been found to be related to the forces that occur during locomotion. As proposed by paleoanthropologists over the past several decades (Le Gros Clark, 1955; Robinson, 1972; Leutenegger, 1974; Lovejoy et al., 2009), lower iliac height decreases to resist bending as forces increase (Lewton, 2015), while the cross-sectional area of the lower ilium increases to provide a larger area for force distribution (Lewton, 2015). Larger primates should have relatively shorter lower ilia to counteract the increased gravitational forces associated with larger mass, as well as relatively larger lower ilium cross-sectional areas to provide a larger area for force distribution. This study predicts that lower iliac height will scale with negative allometry while lower ilium cross-sectional area will scale with positive allometry.

Ischium length. The length of the ischium is related to the effective mechanical advantage of the hamstring musculature that attaches to its distal surface and that extends the thigh. There is no immediately apparent relationship between ischium length and either distribution of locomotor forces or resisting bending. Ward (1991) found isometric scaling of ischium length in catarrhine monkeys and apes, and in accordance, this study predicts isometric scaling of ischium length across all primates.

Acetabulum diameter. The acetabulum articulates with the femoral head and distributes forces associated with locomotion. Previous work has found slight positive allometry of acetabulum diameter (Steudel, 1981a; Ward, 1991), and this supports other studies of hindlimb joint areas which also demonstrate slight positive allometry (Jungers, 1984; Jungers and Burr, 1994). Therefore, this study predicts positive allometry of acetabulum diameter across primates.

MATERIALS AND METHODS

Morphometric data were collected on a sample of 787 os coxae from 40 species deriving from the major taxonomic divisions of primates: Catarrhini, Lemuriformes, and Lorisiformes. This sample is phylogenetically

TABLE 1. Sampled taxa ($N = 40$ species)

Taxon	N^a	Locomotion ^b	Size ^c	
			♂	♀
Haplorhini	28 Species			
Catarrhini	406			
<i>Cercopithecus mitis</i>	24	AQ	5.9	3.9
<i>Erythrocebus patas</i>	6	TQ	12.4	6.5
<i>Chlorocebus aethiops</i>	20	AQ/TQ	4.3	3.0
<i>Miopithecus talapoin</i>	15	AQ	1.4	1.1
<i>Cercocebus torquatus</i>	11	AQ/TQ	9.5	5.5
<i>Mandrillus sphinx</i>	8	TQ	31.6	12.9
<i>Theropithecus gelada</i>	6	TQ	19.0	11.7
<i>Papio hamadryas</i>	45	TQ	12.3–29.8	
<i>Macaca nemestrina</i>	13	TQ	11.2	6.5
<i>Macaca fascicularis</i>	37	AQ	5.4	3.6
<i>Colobus guereza</i>	23	AQ	9.9	7.9
<i>Procolobus badius</i>	10	AQ	8.4	8.2
<i>Nasalis larvatus</i>	20	AQ	20.4	9.8
<i>Hylobates hoolock</i>	13	Susp	6.9	6.9
<i>Hylobates lar</i>	24	Susp	5.9	5.3
<i>Symphalangus syndactylus</i>	10	Susp	11.9	10.7
<i>Gorilla gorilla</i>	21	TQ	169.3	75.7
<i>Homo sapiens</i>	40	Bipedal	60.2	53.6
<i>Pan troglodytes</i>	41	TQ	42.7	33.7
<i>Pongo pygmaeus</i>	19	Susp	78.3	35.8
Platyrrhini	139			
<i>Alouatta caraya</i>	20	AQ	6.4	4.3
<i>Ateles</i> spp.	21	Susp	7.29–9.16	
<i>Lagothrix lagotricha</i>	10	AQ	7.3	7.0
<i>Cebuella pygmaea</i>	12	AQ	0.1	0.1
<i>Leontopithecus</i> spp.	19	AQ	0.6	0.6
<i>Cebus albifrons</i>	15	AQ	3.2	2.3
<i>Cebus apella</i>	22	AQ	3.7	2.5
<i>Saimiri</i> spp.	20	AQ	0.662–0.911	
Strepsirrhini	12 Species			
Lemuriformes	144			
<i>Lepilemur</i> spp.	20	VCL	0.8	0.8
<i>Indri indri</i>	7	VCL	5.8	6.8
<i>Propithecus</i> spp.	34	VCL	3.3	3.0
<i>Eulemur fulvus</i>	22	AQ	2.2	2.3
<i>Hapalemur</i> spp.	16	VCL	1.0	0.9
<i>Lemur catta</i>	23	AQ/TQ	2.2	2.2
<i>Varecia variegata</i>	14	AQ	3.5	3.5
<i>Daubentonia madagascariensis</i>	8	AQ	2.6	2.5
Lorisiformes	98			
<i>Perodicticus potto</i>	24	AQ	0.8	0.8
<i>Nycticebus coucang</i>	15	AQ	0.7	0.6
<i>Galago senegalensis</i>	30	VCL	0.2	0.2
<i>Otolemur crassicaudatus</i>	29	AQ	1.2	1.1
Total:	787			

^a Number of individuals unless otherwise noted.

^b AQ: arboreal quadruped, TQ: terrestrial quadruped, AQ/TQ: semi-terrestrial, Susp: suspensory, VCL: vertical clinger and leaper.

^c Sex-specific species means derived from Smith and Jungers (1997) and Smith and Cheverud (2002).

broader than previous studies of pelvic allometry and captures nearly all of the variation in both body size and positional behavior present in extant primates (Table 1). Species in this sample range from 0.1 kg (*Cebuella pygmaea*) to 170 kg (*Gorilla gorilla*).

Data collection methods have been described in detail elsewhere (Lewton, 2012). Briefly, nine measures designed to capture functionally relevant aspects of pelvic shape were calculated from a series of 17 three-dimensional landmarks (Fig. 1, Table 2, also see Lewton,

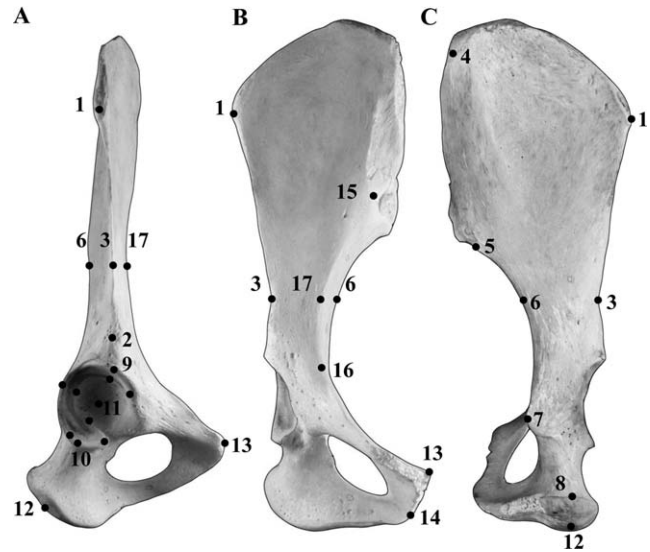


Fig. 1. Locations of 3D landmarks in (A) lateral, (B) ventral, and (C) dorsal views. Some landmarks are shown in multiple views. See Table 2 for landmark definitions.

2012, 2015). Landmarks were collected using a Microscribe G2X digitizer on the right os coxa of articulated specimens (when the right side was broken or otherwise unsuitable for data collection, the left side of the pelvis was used and antimeres were calculated). The measurement protocol was repeated twice for the majority of specimens and sample-wide mean landmark error was 0.32 mm (range: 0.21–0.48 mm); mean percent error was 1.62% (for more details on measurement error calculations, see Lewton, 2012). Both males and females were sampled, with the goal of obtaining equal sample sizes between the sexes if possible. Only adult specimens were measured. Because pelvic epiphyses fuse after individuals reach dental maturity, adulthood was instead determined based on epiphyseal fusion of the iliac crest and ischial tuberosity.

Interlandmark distances were used to calculate the nine functional measures ultimately used in all analyses here (Table 3). These measures have previously been suggested to vary according to positional behavior across primates (Straus, 1929; Waterman, 1929; Ward, 1991; Fleagle and Anapol, 1992; Anemone, 1993; MacLatchy 1998, Lewton, 2015). Eight measures are linear (e.g., ilium length, ischium length), and the remaining measure estimates the cross-sectional area of the lower ilium, which is often qualitatively referred to in the literature as being functionally important for resisting bending during bipedality (Le Gros Clark, 1955; Robinson, 1972; Leutenegger, 1974; Kummer, 1975; Steudel, 1981b; Lovejoy et al., 2009), but has only recently been quantified (Lewton, 2010, 2012, 2015). All measures were ln-transformed before analysis, and analyses were performed on species means (see Table 4 for summary statistics of raw species values for sex-specific samples).

Regression model choice for analyses of allometry is a subject about which common consensus has changed over time. In allometric analyses, the goal is to understand how a biological variable scales with a measure of size, and the regression coefficient of most interest is usually the slope of the linear fit, although elevation may also be of interest. In other types of regression

TABLE 2. Three-dimensional landmarks and their definitions

No.	Landmark	Definition	Type
1	ASIS	The anterior-most point on the lateral extent of the iliac crest (anterior superior iliac spine); site of attachment for <i>m. sartorius</i> .	II
2	AIIS	The anterior-most point on the anterior inferior iliac spine. If only a bony roughening, the point in the center of the AIIS rugosity; site of attachment for <i>m. rectus femoris</i> .	II
3	Lateral ilium	The lateral-most point on the lateral aspect of the iliac margin, above the AIIS, where the cross-section of the lower ilium is smallest.	III
4	PSIS	The superomedial-most point on the posterior iliac crest.	II
5	Inferior auricular surface	The inferior-most extent of the auricular surface, on the dorsal aspect of the pelvis.	II
6	Dorsal ilium	The dorsal-most point on the dorsal aspect of the lower ilium, where the cross-section of the lower ilium is smallest. Taken directly across from Landmark 3.	III
7	Ischial spine	The dorsal-most projection of the spine located on the posterior ischium, medial to the acetabulum.	II
8	Ischial tuberosity	The dorsal-most point on the posterior ischium, medial to the acetabulum.	II
9	Superior acetabulum	The point on the superior rim of the acetabulum that marks the intersection of the iliac margin and acetabulum, which is defined as the extension of the line connecting ASIS and AIIS.	III
10	Inferior acetabulum	The point on the inferior rim of the acetabulum directly across from Landmark 9, along the long axis of the ischium.	III
11	Mid-acetabulum	The center of the acetabulum; defined as the midpoint of the line between Landmarks 9 and 10.	III
12	Ischium	The distal-most point on the ischium that forms a line with the center of the acetabulum that is parallel to the long axis of the ischium.	III
13	Superior pubic symphysis	The superior-most point on the pubic symphysis, taken on the most medial point of the pubis.	II
14	Inferior pubic symphysis	The inferior-most point on the pubic symphysis, taken on the most medial point of the pubis.	II
15	Lateral sacrum ^a	The point that marks the intersection of the arcuate line of the ilium and the sacrum.	I
16	Transverse pelvis ^a	The point on the arcuate line that constitutes the maximum distance between the arcuate line of the opposing os coxa.	II
17	Medial ilium	The medial-most point on the medial aspect of the lower ilium, where the cross-section of the ilium is the smallest. Taken directly across from Landmarks 3 and 6.	III

^a From Tague (2005).

TABLE 3. Definition of linear measures

Pelvic measure	Interlandmark definition
Superior pubic ramus length	11–13
Inferior pubic ramus length	12–14
Pubic symphysis length	13–14
Ilium length	1–9
Lower iliac height	5–11
Ilium width	1–4
Ischium length	11–12
Acetabulum diameter	9–10
Lower ilium cross-sectional area	Area formed by L3, 6, 17

analyses the goal may be to predict the value of the dependent variable given the independent variable. Several researchers have demonstrated that when the analytical aim is to examine patterns of scaling, and not to predict one variable from another, reduced major axis regression (RMA) is preferred over the more traditional ordinary least squares method (OLS) (Harvey and Pagel, 1991; Warton et al., 2006; Smith, 2009). However, a recent article suggests that studies of allometry across species should not use RMA regressions when biological variation is present in the sample (Hansen and Bartoszek, 2012). Importantly, when the correlation coefficient between the two model variables is high, RMA and OLS give nearly identical slope estimates (Smith, 2009), although the OLS method will always underestimate the

true model slope when error is present in the X-variable (Warton et al., 2006; Smith, 2009), and an OLS slope will always be smaller than the RMA slope when the correlation coefficient is less than 1.0. Given the lack of consensus regarding regression model choice, and to conform to recent work that reports RMA results, this study reports the results of both RMA and OLS regressions, but interpretation of allometric results is based on the RMA slope estimates. Correlations are high for all variables (R^2 average 0.89) except for the regression of inferior pubic ramus length on pelvic size (inferior pubic ramus R^2 ranges from 0.57 to 0.72). Therefore, with these high correlations, the RMA and OLS models used here will yield similar slope estimates for most variables.

To account for dependence of species values due to phylogenetic relatedness, phylogenetic reduced major axis (pRMA) and phylogenetic generalized least squares (PGLS) regressions were conducted to investigate scaling relationships between each pelvic measure and overall pelvic size. Body mass estimates were not available for the majority of the specimens examined here; as a result, the geometric mean of pelvic size was used as a proxy for body size (following Mosimann, 1970; Jungers et al., 1995; Gordon et al., 2008). The pelvic geometric mean was calculated as the cubic root of the product of pelvic length (the sum of ilium and ischium length), width (bi-iliac breadth), and depth (anteroposterior

TABLE 4. Summary statistics for nine measures of the pelvis (all measures in mm except as noted)

Species	Sex	N	Superior pubic ramus length			Inferior pubic ramus length			Pubic symphysis length			Ilium length			Lower iliac height			Ischium length			Acetabulum diameter			Ilium width			Lower ilium cross-sectional area (mm ²)			Geometric mean		
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
<i>Alouatta caraya</i>	F	10	40.4	1.4	41.8	2.6	20.8	1.7	51.8	3.5	41.8	3.9	30.7	0.9	18.0	0.8	30.9	3.4	71.8	9.7	77.9	3.1										
<i>Alouatta caraya</i>	M	10	42.1	2.8	43.4	3.9	22.8	1.0	59.1	8.7	44.5	4.5	33.7	2.8	19.1	1.4	29.8	2.3	81.8	12.5	81.8	6.2										
<i>Ateles spp.</i>	F	9	43.3	3.7	44.7	4.7	27.2	5.1	73.4	4.7	57.1	3.6	40.6	2.4	22.9	1.2	40.1	2.9	102.8	16.7	107.1	4.0										
<i>Ateles spp.</i>	M	11	40.5	2.1	43.0	3.3	27.2	3.9	72.9	7.9	52.4	3.7	41.6	2.2	23.2	1.6	41.4	3.5	98.2	18.2	103.8	4.6										
<i>Ateles spp.</i>	U	1	43.1		45.0		26.1		73.2		54.9		39.0		23.0		39.1		112.1		100.9											
<i>Cebuella pygmaea</i>	F	5	9.6	1.4	9.3	0.8	7.3	1.0	14.9	0.9	10.6	1.4	8.9	0.2	4.1	0.1	5.4	0.5	2.2	0.7	17.7	1.3										
<i>Cebuella pygmaea</i>	M	7	9.0	0.4	9.7	0.7	5.9	1.0	14.2	0.6	9.8	0.8	8.7	0.6	4.2	0.3	5.3	0.5	2.5	0.7	17.2	1.0										
<i>Cebus albifrons</i>	F	8	26.3	2.1	32.4	8.0	22.9	15.9	51.2	4.4	33.0	3.0	27.5	1.6	12.7	0.8	19.3	2.0	28.4	7.7	58.1	3.9										
<i>Cebus albifrons</i>	M	7	24.1	1.2	28.3	3.8	20.9	3.4	56.4	3.5	32.8	1.5	30.1	2.1	13.2	1.4	22.2	2.3	37.7	10.2	59.0	4.7										
<i>Cebus apella</i>	F	8	26.0	1.9	28.5	2.9	18.2	3.1	54.5	4.5	34.7	2.3	28.3	2.4	13.3	0.7	18.8	1.1	25.8	4.1	61.1	4.6										
<i>Cebus apella</i>	M	14	24.1	1.4	27.6	2.6	21.3	2.8	55.5	3.3	32.8	2.7	31.4	1.2	13.7	0.5	20.9	1.7	34.1	4.8	60.9	3.7										
<i>Cercocebus torquatus</i>	F	5	36.5	4.1	36.2	6.7	30.5	11.5	70.2	11.1	41.7	3.7	34.6	3.7	16.4	2.0	28.9	5.3	42.8	11.7	77.0	6.2										
<i>Cercocebus torquatus</i>	M	5	40.6	6.2	43.1	8.3	46.3	6.2	87.6	13.2	49.6	7.1	45.1	4.5	22.2	1.1	41.2	2.9	111.8	33.8	96.2	9.7										
<i>Cercocebus torquatus</i>	U	1	37.1		36.7		40.3		78.6		51.9		40.2		20.3		35.5		59.7													
<i>Cercopithecus mitis</i>	F	13	37.4	2.1	38.1	8.1	22.3	9.1	68.9	4.5	41.2	2.6	32.8	1.7	15.8	0.8	29.1	3.0	34.3	7.6	75.3	2.9										
<i>Cercopithecus mitis</i>	M	10	35.8	2.7	35.2	6.9	37.8	8.0	78.4	7.5	43.2	3.1	42.0	2.5	18.2	1.1	35.1	3.7	59.9	14.7	85.0	4.0										
<i>Cercopithecus mitis</i>	U	1	36.5		43.6		14.5		73.6		46.5		33.0		14.6		28.4		30.5		75.1											
<i>Chlorocebus aethiops</i>	F	9	34.9	2.3	36.5	8.1	23.3	9.6	60.5	3.3	38.4	1.7	31.8	1.7	14.2	1.0	26.7	3.1	32.0	5.9	68.3	4.0										
<i>Chlorocebus aethiops</i>	M	10	31.9	2.5	32.0	5.0	33.5	8.6	68.4	5.6	38.4	3.5	37.9	4.2	16.1	1.6	30.6	4.0	47.8	12.8	73.1	5.5										
<i>Chlorocebus aethiops</i>	U	1	30.2		21.9		31.7		56.2		37.9		30.5		15.5		27.9		35.7		62.0											
<i>Colobus guereza</i>	F	12	39.6	2.5	38.1	7.8	38.2	8.6	76.0	4.8	43.9	4.0	37.1	2.1	20.7	1.0	36.5	2.6	56.8	10.0	87.1	3.5										
<i>Colobus guereza</i>	M	7	35.8	2.4	40.2	5.8	43.6	4.0	79.3	4.2	47.1	3.6	40.9	2.8	21.7	1.3	38.5	2.6	68.3	8.6	90.3	4.0										
<i>Colobus guereza</i>	U	4	36.5	1.5	34.0	3.7	41.9	2.3	77.5	7.6	44.9	4.5	37.3	5.1	20.8	0.8	35.9	3.7	67.1	4.5	86.6	4.1										
<i>Daubentonia madagascariensis</i>	F	2	25.7	0.2	27.1	0.5	17.7	0.6	46.2	0.3	25.8	0.4	26.9	0.6	14.0	0.5	13.2	0.6	14.1	2.8	50.2	1.1										
<i>Daubentonia madagascariensis</i>	M	4	21.7	1.2	26.6	2.2	16.3	1.9	40.8	6.3	26.1	1.6	26.2	1.4	14.3	0.6	15.9	2.4	12.8	1.9	46.6	2.4										
<i>Daubentonia madagascariensis</i>	U	2	20.2	1.5	24.8	4.3	17.1	1.0	43.4	2.5	26.7	1.2	24.9	1.9	14.1	0.7	14.0	2.0	14.2	4.2	46.4	1.9										
<i>Erythrocebus patas</i>	F	1	37.0		35.2		42.2		70.2		49.2		36.6		18.0		29.7		37.1		85.2											
<i>Erythrocebus patas</i>	M	3	40.5	0.5	45.3	2.8	51.4	6.5	85.3	1.8	48.8	2.5	45.0	5.9	22.3	0.6	41.0	5.5	82.8	15.1	96.2	3.0										
<i>Erythrocebus patas</i>	U	2	39.4	1.2	32.4	7.9	53.7	13.0	69.7	14.6	43.7	6.9	42.0	11.3	19.6	2.5	43.6	15.9	69.5	36.1	82.8	18.9										
<i>Eulemur fulvus</i>	F	12	23.2	0.9	24.5	1.9	15.6	1.5	48.2	2.1	32.7	2.1	23.4	1.3	13.4	0.7	19.0	1.3	16.1	1.8	56.4	1.8										
<i>Eulemur fulvus</i>	M	4	22.9	0.9	25.2	1.5	12.5	1.6	48.3	2.6	31.9	1.0	23.3	0.8	12.8	0.8	18.8	2.0	19.0	2.8	55.1	0.4										
<i>Eulemur fulvus</i>	U	6	22.6	0.9	25.7	2.5	13.5	1.5	48.5	1.1	29.7	1.4	23.3	0.8	12.7	0.4	18.2	1.2	15.1	2.1	55.2	1.0										
<i>Galago senegalensis</i>	F	10	10.8	0.7	11.0	0.8	5.1	0.7	22.2	2.1	15.8	1.5	7.4	0.7	6.7	0.6	6.9	0.7	2.0	0.4	22.1	2.2										
<i>Galago senegalensis</i>	M	15	10.6	1.0	11.9	1.0	4.8	1.0	21.7	2.4	15.7	1.5	7.3	0.7	6.9	0.5	7.0	0.9	2.1	0.7	21.4	2.6										
<i>Galago senegalensis</i>	U	5	10.2	0.7	10.9	0.3	5.0	0.9	21.2	1.4	17.0	1.0	6.6	0.5	6.3	0.5	6.5	0.6	1.6	0.5	20.4	1.3										
<i>Gorilla gorilla</i>	F	10	92.5	5.7	93.0	11.0	40.7	4.1	121.1	17.9	94.5	9.0	92.0	6.1	48.4	1.7	175.6	10.8	488.6	67.8	230.9	21.8										
<i>Gorilla gorilla</i>	M	11	104.0	11.6	106.8	11.2	67.1	9.6	144.4	12.4	102.9	10.0	110.5	7.8	58.1	4.3	209.9	15.2	624.5	62.3	272.1	15.5										
<i>Hapalemur spp.</i>	F	6	18.6	1.4	20.6	1.8	8.3	0.8	36.0	3.2	24.4	1.3	16.7	0.5	9.2	0.6	15.8	1.8	9.4	2.2	43.3	2.2										
<i>Hapalemur spp.</i>	M	3	17.3	2.4	17.8	2.0	8.0	1.0	34.9	2.0	23.5	1.1	16.6	0.6	9.2	1.8	16.0	3.3	8.1	2.6	44.7	4.0										
<i>Hapalemur spp.</i>	U	7	19.2	2.0	20.8	2.3	9.3	1.4	38.2	2.4	23.8	1.7	17.7	0.9	9.3	0.5	15.5	1.5	11.5	5.8	43.7	2.8										
<i>Homo sapiens</i>	F	20	77.6	6.3	86.4	5.4	33.1	3.9	60.7	6.1	77.2	5.8	69.1	4.8	49.2	3.4	145.4	9.8	502.2	101.9	147.6	9.0										
<i>Homo sapiens</i>	M	20	73.5	5.5	83.4	5.0	36.0	3.2	63.8	6.3	77.2	6.9	76.3	5.5	53.3	3.1	147.7	7.2	666.5	133.3	145.8	6.0										
<i>Hylobates hoolock</i>	F	6	37.4	2.5	32.9	2.9	34.8	2.5	67.7	7.1	49.5	4.1	33.1	0.8	21.0	0.9	40.6	4.9	72.6	13.8	94.8	6.8										
<i>Hylobates hoolock</i>	M	7	34.7	2.3	31.8	1.8	34.8	3.0	66.8	4.3	46.0	6.7	32.4	1.4	20.9	0.7	42.4	2.3	79.4	8.8	92.5	3.1										
<i>Hylobates lar</i>	F	11	33.6	0.9	25.1	2.8	27.2	4.5	61.0	4.0	53.9	3.9	29.6	1.8	20.5	0.8	39.1	2.9	73.4	18.1	88.4	3.5										

TABLE 4. Continued

Species	Sex	N	Superior pubic ramus length		Inferior pubic ramus length		Pubic symphysis length		Ilium length		Lower iliac height		Ischium length		Acetabulum diameter		Ilium width		Lower ilium cross-sectional area (mm ²)		Geometric mean	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Hylobates lar</i>	M	13	32.6	2.1	24.9	2.1	27.1	4.4	63.1	3.1	50.1	2.8	31.1	1.5	20.5	1.3	37.5	3.3	80.4	11.6	88.0	3.9
<i>Indri indri</i>	F	2	31.9	0.1	22.7	2.9	29.6	0.5	62.6	0.0	33.8	4.3	30.7	0.6	25.6	1.3	34.6	2.0	66.9	11.9	76.0	1.7
<i>Indri indri</i>	M	2	27.9	0.9	24.9	0.5	25.2	2.1	64.4	0.5	35.6	1.2	29.5	1.6	23.6	0.6	34.6	1.4	70.2	2.5	76.6	1.7
<i>Indri indri</i>	U	3	27.0	2.2	23.9	3.0	26.4	3.5	56.7	5.3	33.0	2.4	28.2	2.2	22.4	1.6	34.9	3.3	76.0	17.3	73.5	6.2
<i>Lagothrix lagothricha</i>	F	3	45.2	1.0	42.6	1.4	24.2	3.6	68.2	3.7	42.9	5.4	34.3	0.6	19.4	1.0	28.7	1.1	74.3	12.2	87.7	4.7
<i>Lagothrix lagothricha</i>	M	6	40.8	1.8	39.8	2.8	25.2	3.0	63.8	4.4	43.0	3.1	35.3	1.8	19.8	1.1	30.8	1.7	83.3	9.2	86.1	3.8
<i>Lagothrix lagothricha</i>	U	1	37.8		39.5		19.8		58.1		37.7		28.4		16.7		22.9		53.2		72.8	
<i>Lemur catta</i>	F	3	23.4	1.0	24.9	0.5	12.9	1.5	46.9	2.8	28.8	2.1	24.4	1.6	13.3	0.4	22.1	1.5	23.5	2.5	55.5	2.8
<i>Lemur catta</i>	M	6	22.2	1.0	26.2	1.4	12.6	1.7	45.6	2.8	30.1	2.5	23.8	1.2	13.3	0.8	21.7	2.4	23.3	3.0	55.1	1.4
<i>Lemur catta</i>	U	14	22.9	1.8	26.2	2.1	12.1	0.9	48.0	2.8	31.5	1.7	23.2	1.5	13.3	0.8	22.0	1.9	21.7	3.2	56.3	3.1
<i>Leontopithecus spp.</i>	F	10	16.9	0.9	18.8	2.0	9.5	1.6	26.9	1.1	17.4	1.1	18.2	1.1	8.2	0.4	11.1	0.9	9.4	1.9	32.0	1.0
<i>Leontopithecus spp.</i>	M	9	15.8	1.0	18.1	1.0	10.4	0.9	26.1	1.0	17.2	0.9	18.5	0.8	8.1	0.3	11.2	1.1	11.1	2.0	30.5	1.8
<i>Lepilemur spp.</i>	F	12	13.4	1.6	15.6	1.5	7.8	1.7	35.2	3.5	22.7	2.7	15.0	2.1	8.8	1.1	11.1	2.5	5.6	2.6	38.6	4.8
<i>Lepilemur spp.</i>	M	8	13.6	2.6	16.1	2.6	7.1	1.4	32.9	3.4	21.8	2.0	15.1	1.9	9.4	1.3	11.1	3.0	5.6	2.9	36.7	4.4
<i>Lepilemur spp.</i>	U	13	33.1	3.6	31.0	7.8	21.9	6.5	60.3	5.0	40.2	2.8	28.7	1.8	14.1	0.7	25.1	2.2	30.9	6.0	70.2	3.7
<i>Macaca fascicularis</i>	M	21	32.0	2.5	31.7	3.9	32.3	2.5	67.4	5.2	41.6	2.8	34.7	2.9	16.7	1.2	29.7	3.4	46.7	11.7	77.0	4.5
<i>Macaca fascicularis</i>	F	3	30.1	2.7	31.3	2.3	33.0	6.7	70.3	8.0	40.0	4.9	36.3	4.6	17.2	1.6	28.9	2.3	48.0	8.1	77.4	5.9
<i>Macaca fascicularis</i>	U	3	39.7	2.0	34.0	8.1	35.5	10.5	74.0	3.2	42.1	3.4	33.3	2.3	18.3	2.3	34.1	2.1	65.9	15.9	80.0	1.2
<i>Macaca nemestrina</i>	M	9	40.7	6.1	42.1	8.0	43.2	7.8	86.1	9.6	48.4	5.6	43.1	5.4	21.2	2.8	39.0	6.4	99.4	33.7	94.6	10.7
<i>Macaca nemestrina</i>	U	1	37.8		43.7		40.8		87.8		53.9		45.8		21.0		36.8		107.7		98.6	
<i>Mandrillus sphinx</i>	F	3	41.4	3.9	41.0	13.0	39.4	15.0	86.8	8.4	51.4	1.6	42.5	2.8	21.6	2.4	46.0	1.7	83.1	24.9	96.8	3.4
<i>Mandrillus sphinx</i>	M	4	52.7	2.4	48.9	6.1	65.6	6.4	103.5	15.0	63.8	5.8	60.9	4.2	30.3	3.0	69.4	5.5	225.5	55.8	128.2	11.1
<i>Mandrillus sphinx</i>	U	1	56.9		58.1		62.0		99.8		58.0		58.4		28.0		60.8		171.4		125.6	
<i>Miopithecus talapoin</i>	F	11	25.9	2.4	24.9	5.6	15.0	6.0	42.6	1.9	28.3	1.5	20.9	1.8	9.3	0.7	17.1	1.5	8.9	3.3	49.2	2.2
<i>Miopithecus talapoin</i>	M	4	22.2	2.3	19.4	2.9	23.2	1.2	45.1	2.2	26.4	2.1	23.8	2.0	10.3	0.6	17.3	1.2	16.1	6.2	47.6	2.3
<i>Miopithecus talapoin</i>	F	7	42.0	2.2	36.2	5.6	38.9	5.9	74.8	3.2	47.1	2.7	40.1	2.3	22.5	1.1	42.5	3.1	91.2	14.9	95.3	4.8
<i>Nasalis larvatus</i>	M	11	44.5	4.0	40.8	4.0	52.5	4.3	83.4	7.7	47.5	3.8	49.4	2.2	27.2	1.4	51.5	2.6	150.7	44.4	108.1	5.0
<i>Nasalis larvatus</i>	U	2	43.6	0.9	44.6	1.6	44.3	8.3	77.8	10.4	49.0	2.4	45.1	7.5	25.2	5.0	50.6	5.6	135.3	87.3	106.6	10.3
<i>Nasalis larvatus</i>	F	4	26.4	4.2	27.2	3.4	6.4	1.3	34.9	4.7	27.2	2.6	12.3	1.3	10.0	0.7	10.1	2.6	8.0	6.7	33.4	3.8
<i>Nycticebus coucang</i>	M	4	25.3	3.2	26.5	3.0	6.1	0.2	35.9	2.2	26.4	0.9	12.8	0.6	10.0	0.8	10.1	1.1	8.1	2.4	35.4	3.2
<i>Nycticebus coucang</i>	U	7	23.4	1.9	24.1	2.5	5.9	2.4	33.3	2.7	25.6	1.3	12.9	1.5	9.7	0.9	9.0	0.6	5.7	1.2	32.0	2.0
<i>Nycticebus coucang</i>	F	6	18.6	1.5	19.5	2.3	10.0	2.3	35.5	1.3	25.4	1.9	14.0	0.8	11.6	0.9	11.9	0.6	8.4	3.4	36.4	2.3
<i>Otolemur crassicaudatus</i>	M	23	19.4	1.3	21.8	1.9	10.6	1.8	37.8	2.9	25.6	2.8	14.4	0.9	11.8	0.7	12.6	1.2	8.7	1.7	38.2	2.7
<i>Otolemur crassicaudatus</i>	F	21	66.1	3.8	75.8	6.1	42.3	3.3	115.6	7.4	92.6	5.6	76.8	5.4	38.6	2.8	115.4	9.6	275.3	64.0	188.9	9.0
<i>Pan troglodytes</i>	M	20	65.7	3.7	81.9	6.1	44.5	7.0	122.3	6.3	91.6	5.3	78.0	5.7	40.8	3.6	120.0	7.5	265.2	45.3	193.8	7.4
<i>Pan troglodytes</i>	F	14	46.6	3.7	48.8	8.0	40.0	11.4	88.3	8.2	59.1	6.1	46.8	4.9	24.5	2.2	51.4	6.5	115.1	29.9	111.4	9.2
<i>Papio hamadryas</i>	M	23	50.6	4.0	48.1	5.6	55.4	8.2	95.4	6.0	61.4	6.2	53.8	5.0	27.9	2.4	61.8	7.9	164.3	32.6	119.5	7.5
<i>Papio hamadryas</i>	U	8	49.7	5.6	48.4	7.8	53.4	11.0	95.3	14.5	63.3	9.3	54.6	8.7	27.2	2.6	58.9	8.3	167.9	47.0	119.6	15.2
<i>Perodicticus potto</i>	F	3	30.6	1.7	32.2	3.1	4.4	2.1	42.3	3.9	28.9	3.0	14.7	1.6	10.8	3.1	9.5	0.7	8.7	1.2	42.2	3.9
<i>Perodicticus potto</i>	M	11	28.7	2.5	29.9	3.8	5.6	2.0	40.7	2.3	26.3	2.4	14.2	1.1	11.2	1.3	9.6	1.0	10.0	2.1	40.6	3.5
<i>Perodicticus potto</i>	U	10	27.7	3.1	28.1	3.5	5.5	1.1	40.3	2.4	25.6	2.7	13.4	1.0	10.5	0.9	9.6	0.6	7.9	2.2	39.0	3.1
<i>Pongo pygmaeus</i>	F	2	68.0	1.9	59.6	11.4	34.7	1.1	90.4	1.0	74.1	0.1	66.1	3.9	36.5	0.6	105.7	2.3	181.6	0.3	166.5	5.3
<i>Pongo pygmaeus</i>	M	15	77.5	4.0	72.1	8.8	47.8	9.3	110.1	8.9	81.9	8.3	75.9	6.1	44.1	3.9	124.5	11.7	314.8	66.4	194.6	14.6
<i>Pongo pygmaeus</i>	U	2	67.0	2.5	67.8	0.6	31.2	3.0	99.1	0.6	80.5	2.2	63.0	7.1	36.7	2.9	104.6	1.3	196.4	19.2	174.5	0.2
<i>Procolobus badius</i>	F	5	36.7	2.0	33.0	5.1	33.3	2.5	70.1	3.5	42.8	5.3	37.3	2.9	18.9	0.8	40.8	4.0	69.8	15.4	88.4	5.6

TABLE 4. Continued

Species	Sex	N	Superior pubic ramus length			Inferior pubic ramus length			Pubic symphysis length			Ilium length			Lower iliac height			Ischium length			Acetabulum diameter			Ilium width			Lower ilium cross-sectional area (mm ²)			Geometric mean		
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
<i>Procolobus badius</i>	M	5	33.9	2.4	31.1	2.9	35.2	1.8	67.1	4.0	37.8	2.0	39.1	1.9	20.6	0.8	41.2	2.8	88.8	15.7	80.8	4.0										
<i>Propithecus spp.</i>	F	6	23.8	2.0	19.0	2.7	18.3	3.5	44.7	1.1	27.9	1.9	20.9	0.8	15.6	1.3	26.1	2.8	36.7	12.1	58.1	2.5										
<i>Propithecus spp.</i>	M	9	22.1	1.4	19.4	3.7	15.9	2.5	45.8	3.6	27.4	2.4	21.4	1.4	15.5	1.1	25.0	1.7	39.4	12.2	57.3	4.2										
<i>Propithecus spp.</i>	U	19	24.4	1.7	20.7	3.3	16.8	2.5	46.7	3.1	28.0	2.0	22.1	1.3	16.2	1.0	26.9	2.4	42.3	6.9	60.2	3.8										
<i>Saimiri spp.</i>	F	10	18.0	0.8	20.1	1.5	10.7	1.9	31.0	2.1	19.1	1.4	18.8	0.8	8.3	0.4	12.9	1.4	7.5	1.4	36.0	2.3										
<i>Saimiri spp.</i>	M	10	15.1	1.3	19.2	1.8	12.7	2.2	31.1	1.6	19.4	1.3	19.9	1.1	8.7	0.4	13.3	1.2	9.0	2.0	34.6	1.9										
<i>Symphalangus syndactylus</i>	F	8	44.9	4.0	31.5	6.0	36.2	3.5	66.2	3.4	58.1	2.9	34.1	2.7	25.1	1.7	61.7	4.1	95.1	12.7	109.8	3.8										
<i>Symphalangus syndactylus</i>	M	2	48.2	3.5	38.7	10.9	45.9	0.4	76.5	9.1	60.1	5.4	39.2	0.1	30.0	1.1	65.4	4.1	137.7	27.2	119.3	4.8										
<i>Theropithecus gelada</i>	F	5	44.6	1.7	49.1	4.8	39.5	5.9	80.5	9.1	55.2	4.9	49.0	1.7	22.7	1.6	47.2	3.9	101.1	9.9	104.6	4.8										
<i>Theropithecus gelada</i>	M	1	47.6		57.0		43.8		98.5		64.4		54.3		26.2		50.7		119.9		123.6											
<i>Varecia variegata</i>	F	2	25.6	0.3	30.5	0.7	14.5	1.1	58.9	0.7	38.0	2.3	26.7	0.4	18.2	0.1	18.3	1.5	19.6	1.3	60.3	0.9										
<i>Varecia variegata</i>	M	5	25.6	1.2	30.1	2.1	14.9	1.8	56.5	1.6	36.9	1.2	26.6	1.7	17.4	1.1	19.2	1.7	22.7	3.9	61.1	3.2										
<i>Varecia variegata</i>	U	7	24.9	1.9	29.6	2.1	13.6	2.3	55.5	5.9	36.0	4.8	25.9	2.2	15.7	2.0	18.7	0.9	19.5	1.8	61.3	5.8										

^aF, female; M, male; U, unknown.

diameter). The pRMA analyses were performed in the “phytools” package (Revell, 2012) in R v 3.1.1 (R Development Core Team, 2014); PGLS analyses were performed in the “caper” R package (Orme et al., 2013). Regressions were performed for each ln-transformed pelvic variable on the ln-transformed geometric mean at several taxonomic levels, and a null hypothesis of isometric scaling (slope = 1 for linear measures, slope = 2 for areal measures) was tested. Two major sets of analyses were performed: 1) by taxonomic group, to assess overall scaling patterns, 2) by locomotor group, to assess the influence of locomotion on pelvic scaling patterns. In the second set of analyses, each species was assigned a broad locomotor category based on the locomotor mode in which it spends the majority of its time during travel, as described earlier (Napier and Napier, 1967; Fleagle, 1999; Garber 2011; Table 1). Four semiterrestrial and bipedal species were excluded from these analyses due to uncertain mechanical implications of semiterrestrial locomotion and small sample sizes, respectively.

In both sets of analyses, tests were performed for all primates, and for haplorhines and strepsirrhines separately. For each level of analysis, three sets of tests were performed: 1) combined sexes, 2) males, and 3) females. All phylogenetic analyses conducted here relied on a consensus primate phylogeny from the 10kTrees project (version 3, Arnold et al., 2010) estimated from GenBank data and sampled using Bayesian inference. Slopes, intercepts, correlations, and 95% confidence intervals for the slope estimates are reported for each test. An interpretation of allometry occurs when the 95% confidence intervals for the slope do not contain the slope of isometry.

RESULTS

Results of pRMA and PGLS scaling analyses were generally consistent across combined-sex and separate-sex samples, and within the all-primate and separate haplorhine and strepsirrhine samples. Therefore, the combined-sex results will primarily be presented below. A summary of all pRMA allometric results are given in Table 5. First, the results of the primate-wide analyses are described, and slight deviations from these patterns are discussed as they pertain to haplorhines and strepsirrhines separately. Second, the results of the locomotor group analyses are discussed. Tables 6–9 show the results of both pRMA and PGLS regressions for each level of analysis.

Primate-wide analyses

Phylogenetic RMA scaling analyses demonstrated isometry for six of the nine pelvic traits tested (Table 6). Pelvic measures that are characterized by isometry in the primate-wide sample are pubic ramus lengths, pubic symphysis length, ilium length, ischium length, and acetabulum diameter. All of these were hypothesized to scale with isometry except for acetabulum dimensions, which was predicted to scale with positive allometry.

Lower iliac height, ilium width, and lower ilium cross-sectional area were all significantly allometric, as predicted. Only lower iliac height demonstrates significant negative allometry (combined-sex $\beta = 0.86$, 95% confidence interval: 0.80–0.92, Fig. 2A), whereas positive allometry characterizes ilium width (combined-sex $\beta = 1.32$, 95% confidence interval: 1.20–1.44, Fig. 2B) and lower ilium cross-sectional area (combined-sex $\beta = 2.45$, 95% confidence interval: 2.27–2.63, Fig. 2C). Even given

TABLE 5. Summary of pRMA allometric results

	Superior pubic ramus length	Inferior pubic ramus length	Pubic symphysis length	Ilium length	Ilium width	Lower iliac height	Ischium length	Acetabulum diameter	Lower ilium cross-sectional area
Primate-wide (<i>n</i> = 40)									
Combined sex	Isometry	Isometry	Isometry	Isometry	+	-	Isometry	Isometry	+
Males	Isometry	Isometry	Isometry	Isometry	+	-	Isometry	Isometry	+
Females	Isometry	Isometry	Isometry	Isometry	+	-	Isometry	Isometry	+
Haplorhini (<i>n</i> = 28)									
Combined sex	-	Isometry	Isometry	Isometry	+	-	Isometry	Isometry	+
Males	-	Isometry	Isometry	-	+	-	Isometry	Isometry	+
Females	-	Isometry	Isometry	Isometry	+	-	Isometry	Isometry	+
Strepsirrhini (<i>n</i> = 12)									
Combined sex	Isometry	Isometry	+	Isometry	+	-	Isometry	Isometry	+
Males	Isometry	Isometry	+	Isometry	+	-	Isometry	Isometry	+
Females	Isometry	Isometry	+	Isometry	Isometry	Isometry	+	Isometry	+
Arboreal quadruped (<i>n</i> = 19)									
Suspension (<i>n</i> = 5)	Isometry	Isometry	Isometry	-	+	-	Isometry	Isometry	-
Terrestrial quadruped (<i>n</i> = 7)	Isometry	Isometry	-	-	+	-	-	Isometry	Isometry
Vertical clinging and leaping (<i>n</i> = 5)									
	Isometry	-	+	-	+	-	Isometry	Isometry	+

+ : positive allometry, - : negative allometry.

the positive allometry in ilium width in primates, hominoids and indriids have relatively wider ilia than expected given their size (Fig. 2B). Similarly, the lower ilium is more robust than expected in callitrichids, indriids, and humans (Fig. 2C), which may be related to increased loading forces due to leaping and/or bipedal behaviors.

Haplorhines

The haplorhine sample demonstrates similar results as the primate-wide analysis, in which ilium width (combined-sex $\beta = 1.31$, 95% confidence interval: 0.90–1.17, Fig. 2B) and lower ilium cross-sectional area (combined-sex $\beta = 2.34$, 95% confidence interval: 2.14–2.54, Fig. 2C) are positively allometric, and lower iliac height is negatively allometric (combined-sex $\beta = 0.87$, 95% confidence interval: 0.83–0.91, Fig. 2A). In addition, while ilium length is isometric in the combined-sex haplorhine sample, negative allometry is evident within males (male ilium length $\beta = 0.86$, 95% confidence interval: 0.75–0.97, Table 6). Finally, in contrast to the primate-wide regression, superior pubic ramus length is negatively allometric in haplorhines (combined-sex $\beta = 0.89$, 95% confidence interval: 0.83–0.95, Table 6).

Strepsirrhines

As in the all-primate sample, ilium width and lower ilium cross-sectional area are also positively allometric in the combined-sex sample of strepsirrhines. Within females alone, however, the slope between ilium width and pelvic size has large confidence limits that contain the slope of isometry (females $\beta = 1.34$, 95% confidence interval, 0.98–1.70, Table 8). In addition, although lower iliac height is negatively allometric in the combined-sex and male strepsirrhine samples, it is isometric in females (females $\beta = 0.82$, 95% confidence interval: 0.59–1.05, Table 8), although again, the slope is quite small but has a large confidence interval. Lorises have relatively longer lower ilia than expected based on all regression fits, while indriids have relatively shorter lower ilia than expected (Fig. 2A), which suggests that lower ilium shortening is related to the large forces incurred during leaping.

Unlike haplorhines, the strepsirrhine sample demonstrates positive allometry of pubic symphysis length in both sexes (combined-sex $\beta = 1.60$, 95% confidence interval: 1.15–2.05, Fig. 2D). A further analysis separating lemuriformes and loriformes demonstrates that it is only the lemurs (and not loriformes) that exhibit positive allometry of pubic symphysis length (combined-sex lemurs $\beta = 1.79$, $P = 0.006$ for test of isometry, lorises $\beta = 1.22$, $P = 0.77$ for test of isometry). Indeed loriformes have short pubic symphyses that often do not articulate with each other (personal observation).

Phylogenetic regression by locomotor group

Within the combined-sex sample, the four locomotor groups—arboreal quadruped (AQ), terrestrial quadruped (TQ), suspensory, vertical clinger and leaper (VCL)—all demonstrate positive allometry of ilium width, and all but AQ demonstrate negative allometry of lower iliac height (Table 9, Fig. 3A–B). This primate-wide positive allometry in ilium width, regardless of locomotor mode, suggests that scaling of this trait is not primarily related to the mechanics of locomotion, but is instead related primarily to body size. Species with shorter lower ilia than expected given their size are the scrambling and/or leaping callitrichids, indriids, and *Saimiri*, again linking high locomotor forces with short lower ilia.

Isometry characterized superior pubic ramus length, inferior pubic ramus length, ischium length, and acetabulum diameter across groups (except for negative allometry in inferior pubic ramus length in VCL taxa, and negative allometry in ischium length in TQ taxa) (Table 9). Similarly, negative allometry of ilium length is found in all locomotor groups except for AQ, in which it is isometric (Table 9). Vertical clingers and leapers, slow lorises, and suspensors all have shorter ischia than expected for their size, while *Daubentonia*, *Saimiri*, and callitrichids have longer ischia than expected given their size (Fig. 3C).

Locomotor differences in pelvic allometry

Pelvic traits that differ in their allometric scaling across locomotor groups include pubic symphysis length

TABLE 6. Phylogenetic reduced major axis and phylogenetic generalized least squares slopes and confidence intervals for tests of isometry for the combined sex sample

	Combined sex: pRMA					Combined sex: PGLS				
	Scaling Prediction	Allometric Result ^a	Intercept	Slope	R ²	Intercept	Slope	R ²	SE	Slope 95% Confidence Interval
All primates										
Superior pubic ramus length	isometry	isometry	-0.41	0.92	0.89	-0.23	0.87	0.90	0.05	0.78-0.96
Inferior pubic ramus length	isometry	isometry	-0.44	0.93	0.82	-0.12	0.85	0.83	0.06	0.73-0.98
Pubic symphysis length	isometry	isometry	-1.87	1.14	0.77	-1.32	1.00	0.77	0.09	0.83-1.17
Ilium length	isometry	isometry	0.21	0.91	0.89	0.51	0.83	0.89	0.05	0.74-0.92
Ilium width	+	+	-2.29	1.32	0.90	-2.13	1.28	0.92	0.06	1.16-1.40
Lower iliac height	+	-	0.01	0.86	0.95	0.09	0.84	0.95	0.03	0.78-0.90
Ischium length	isometry	isometry	-0.73	0.97	0.92	-0.57	0.93	0.92	0.04	0.84-1.01
Acetabulum diameter	+	isometry	-1.40	1.01	0.92	-1.22	0.97	0.93	0.04	0.88-1.05
Lower ilium cross-sectional area	+	+	-6.74	2.45	0.89	-6.26	2.34	0.94	0.09	2.15-2.52
Haplorhini										
Superior pubic ramus length	isometry	-	-0.36	0.89	0.93	-0.26	0.87	0.97	0.03	0.81-0.93
Inferior pubic ramus length	isometry	isometry	-0.47	0.92	0.84	-0.22	0.86	0.85	0.07	0.73-1.00
Pubic symphysis length	isometry	isometry	-1.30	1.04	0.79	-0.66	0.90	0.78	0.09	0.72-1.07
Ilium length	isometry	isometry	-0.004	0.94	0.87	0.39	0.85	0.88	0.06	0.73-0.96
Ilium width	+	+	-2.19	1.31	0.90	-2.01	1.27	0.92	0.07	1.13-1.41
Lower iliac height	-	-	-0.09	0.87	0.96	-0.13	0.88	0.98	0.02	0.84-0.93
Ischium length	isometry	isometry	-0.48	0.92	0.93	-0.33	0.89	0.92	0.05	0.79-0.99
Acetabulum diameter	+	isometry	-1.48	1.00	0.93	-1.43	0.99	0.97	0.04	0.92-1.06
Lower ilium cross-sectional area	+	+	-6.16	2.34	0.88	-5.45	2.17	0.94	0.10	1.97-2.37
Strepsirrhini										
Superior pubic ramus length	isometry	isometry	-0.98	1.08	0.82	-0.59	0.97	0.80	0.15	0.69-1.26
Inferior pubic ramus length	isometry	isometry	-0.79	1.04	0.72	-0.21	0.89	0.70	0.17	0.55-1.23
Pubic symphysis length	isometry	+	-3.70	1.60	0.77	-2.95	1.40	0.77	0.23	0.95-1.85
Ilium length	isometry	isometry	0.29	0.91	0.95	0.24	0.92	0.96	0.06	0.81-1.03
Ilium width	+	+	-2.45	1.35	0.84	-2.26	1.31	0.88	0.14	1.03-1.59
Lower iliac height	+	-	0.39	0.84	0.77	0.39	0.77	0.87	0.09	0.59-0.94
Ischium length	isometry	isometry	-1.58	1.18	0.93	-1.44	1.15	0.93	0.09	0.96-1.33
Acetabulum diameter	+	isometry	-1.89	1.17	0.89	-1.74	1.13	0.90	0.11	0.91-1.35
Lower ilium cross-sectional area	+	+	-9.12	3.07	0.92	-8.58	2.93	0.92	0.26	2.41-3.44

^a Interpretation of allometry is based on the 95% confidence interval for the pRMA slope.
 + : positive allometry, - : negative allometry.

TABLE 7. Phylogenetic reduced major axis and phylogenetic generalized least squares slopes and confidence intervals for tests of isometry for the male sample

	Males: pRMA				Males: PGLS						
	Scaling Prediction	Allometric Result ^a	Intercept	Slope	R ²	Slope 95% Confidence Interval	Intercept	Slope	R ²	SE	Slope 95% Confidence Interval
All primates											
Superior pubic ramus length	isometry	isometry	-0.50	0.93	0.91	0.84-1.02	-0.33	0.89	0.91	0.04	0.80-0.98
Inferior pubic ramus length	isometry	isometry	-0.59	0.97	0.84	0.85-1.09	-0.27	0.89	0.84	0.06	0.77-1.01
Pubic symphysis length	isometry	isometry	-1.67	1.09	0.80	0.94-1.24	-1.22	0.98	0.80	0.08	0.82-1.13
Ilium length	isometry	isometry	0.21	0.91	0.90	0.82-1.00	0.46	0.85	0.90	0.04	0.76-0.93
Ilium width	+	+	-2.16	1.29	0.90	1.17-1.41	-2.03	1.26	0.92	0.06	1.14-1.38
Lower iliac height	+	-	-0.01	0.86	0.95	0.80-0.92	0.04	0.85	0.95	0.03	0.79-0.91
Ischium length	isometry	isometry	-0.63	0.95	0.91	0.86-1.04	-0.47	0.90	0.91	0.05	0.82-0.99
Acetabulum diameter	+	isometry	-1.30	0.99	0.91	0.91-1.07	-1.13	0.95	0.93	0.04	0.86-1.03
Lower ilium cross-sectional area	+	+	-6.28	2.35	0.89	2.15-2.55	-5.92	2.27	0.93	0.10	2.07-2.47
Haplorhini											
Superior pubic ramus length	isometry	-	-0.56	0.93	0.95	0.87-0.99	-0.36	0.89	0.97	0.03	0.83-0.95
Inferior pubic ramus length	isometry	isometry	-0.77	0.99	0.91	0.86-1.12	-0.38	0.90	0.88	0.06	0.77-1.03
Pubic symphysis length	isometry	isometry	-0.93	0.97	0.83	0.82-1.12	-0.54	0.88	0.84	0.08	0.73-1.03
Ilium length	isometry	-	0.37	0.86	0.95	0.75-0.97	0.39	0.85	0.89	0.06	0.74-0.96
Ilium width	+	+	-2.12	1.30	0.95	1.16-1.44	-1.88	1.24	0.92	0.07	1.10-1.39
Lower iliac height	-	-	-0.15	0.88	0.96	0.84-0.92	-0.12	0.88	0.98	0.02	0.83-0.92
Ischium length	isometry	isometry	-0.44	0.92	0.95	0.82-1.02	-0.18	0.86	0.92	0.05	0.76-0.96
Acetabulum diameter	+	isometry	-1.39	0.99	0.98	0.92-1.06	-1.34	0.98	0.96	0.04	0.91-1.05
Lower ilium cross-sectional area	+	+	-5.59	2.22	0.94	2.02-2.42	-4.98	2.08	0.94	0.10	1.89-2.28
Strepsirrhini											
Superior pubic ramus length	isometry	isometry	-1.08	1.10	0.82	0.82-1.38	-0.73	1.01	0.82	0.14	0.73-1.28
Inferior pubic ramus length	isometry	isometry	-0.82	1.05	0.65	0.69-1.41	-0.43	0.95	0.70	0.19	0.59-1.31
Pubic symphysis length	isometry	+	-3.82	1.63	0.75	1.19-2.07	-3.15	1.45	0.78	0.23	1.01-1.89
Ilium length	isometry	isometry	0.16	0.94	0.94	0.80-1.08	0.16	0.94	0.94	0.07	0.79-1.08
Ilium width	+	+	-2.28	1.31	0.86	1.05-1.57	-1.52	1.07	0.85	0.13	0.81-1.33
Lower iliac height	+	-	0.35	0.78	0.84	0.59-0.97	0.46	0.75	0.84	0.10	0.56-0.94
Ischium length	isometry	isometry	-1.55	1.17	0.90	0.95-1.39	-1.44	1.15	0.91	0.11	0.93-1.36
Acetabulum diameter	+	isometry	-1.73	1.12	0.85	0.86-1.38	-1.52	1.07	0.85	0.13	0.81-1.33
Lower ilium cross-sectional area	+	+	-9.01	3.05	0.92	2.56-3.54	-7.91	2.75	0.92	0.25	2.25-3.24

^a Interpretation of allometry is based on the 95% confidence interval for the pRMA slope.
 + : positive allometry, - : negative allometry

TABLE 8. Phylogenetic reduced major axis and phylogenetic generalized least squares slopes and confidence intervals for tests of isometry for the female sample

	Females: pRMA				Females: PGLS						
	Scaling Prediction	Allometric Result ^a	Intercept	Slope	R ²	Slope 95% Confidence Interval	Intercept	Slope	R ²	SE	Slope 95% Confidence Interval
All primates											
Superior pubic ramus length	isometry	isometry	-0.38	0.92	0.85	0.83-1.01	-0.23	0.87	0.90	0.05	0.78-0.96
Inferior pubic ramus length	isometry	isometry	-0.53	0.96	0.75	0.81-1.11	-0.08	0.84	0.76	0.08	0.70-0.99
Pubic symphysis length	isometry	isometry	-2.03	1.17	0.66	0.95-1.39	-1.10	0.94	0.65	0.11	0.72-1.15
Ilium length	isometry	isometry	0.19	0.92	0.87	0.82-1.02	0.56	0.82	0.87	0.05	0.72-0.92
Ilium width	+	+	-2.36	1.33	0.87	1.19-1.47	-2.11	1.27	0.89	0.07	1.13-1.41
Lower iliac height	+	-	-0.08	0.88	0.93	0.81-0.95	0.03	0.85	0.93	0.04	0.78-0.93
Ischium length	isometry	isometry	-0.77	0.97	0.92	0.88-1.06	-0.61	0.93	0.91	0.05	0.84-1.02
Acetabulum diameter	+	isometry	-1.54	1.05	0.9	0.96-1.14	-1.31	0.98	0.92	0.05	0.89-1.08
Lower ilium cross-sectional area	+	+	-7.00	2.50	0.88	2.33-2.67	-6.36	2.34	0.95	0.09	2.17-2.52
Haplorhini											
Superior pubic ramus length	isometry	-	-0.31	0.89	0.93	0.82-0.96	-0.15	0.86	0.96	0.03	0.79-0.92
Inferior pubic ramus length	isometry	isometry	-0.62	0.95	0.88	0.79-1.11	-0.20	0.86	0.82	0.08	0.71-1.02
Pubic symphysis length	isometry	isometry	-1.34	1.04	0.66	0.85-1.23	-0.31	0.80	0.72	0.10	0.61-0.99
Ilium length	isometry	isometry	0.29	0.87	0.92	0.74-1.00	0.45	0.83	0.86	0.06	0.70-0.95
Ilium width	+	+	-2.24	1.32	0.93	1.16-1.48	-2.02	1.27	0.90	0.08	1.11-1.43
Lower iliac height	-	-	-0.2	0.90	0.95	0.85-0.95	-0.16	0.89	0.98	0.02	0.85-0.94
Ischium length	isometry	isometry	-0.56	0.93	0.94	0.83-1.03	-0.33	0.88	0.92	0.05	0.79-0.98
Acetabulum diameter	+	isometry	-1.55	1.01	0.97	0.94-1.08	-1.50	1.00	0.97	0.04	0.93-1.07
Lower ilium cross-sectional area	+	+	-6.61	2.41	0.92	2.19-2.63	-5.81	2.22	0.94	0.11	2.01-2.44
Strepsirrhini											
Superior pubic ramus length	isometry	isometry	-1.36	1.19	0.79	0.86-1.52	-0.86	1.06	0.78	0.17	0.73-1.38
Inferior pubic ramus length	isometry	isometry	-1.05	1.11	0.57	0.69-1.53	-0.13	0.87	0.59	0.21	0.45-1.28
Pubic symphysis length	isometry	+	-4.51	1.81	0.62	1.20-2.42	-3.11	1.44	0.65	0.31	0.83-2.05
Ilium length	isometry	isometry	0.24	0.92	0.92	0.76-1.08	0.14	0.95	0.93	0.08	0.79-1.11
Ilium width	+	isometry	-2.45	1.34	0.79	0.98-1.70	-1.84	1.18	0.79	0.18	0.82-1.54
Lower iliac height	-	isometry	0.21	0.82	0.76	0.59-1.05	0.35	0.78	0.80	0.12	0.55-1.01
Ischium length	isometry	+	-1.80	1.24	0.93	1.04-1.44	-1.76	1.23	0.93	0.10	1.03-1.43
Acetabulum diameter	+	isometry	-2.30	1.27	0.85	0.99-1.55	-2.18	1.24	0.87	0.14	0.96-1.52
Lower ilium cross-sectional area	+	+	-8.91	3.00	0.91	2.49-3.51	-7.74	2.69	0.91	0.26	2.18-3.19

^a Interpretation of allometry is based on the 95% confidence interval for the pRMA slope.

+ : positive allometry, - : negative allometry

TABLE 9. Phylogenetic reduced major axis and phylogenetic generalized least squares slopes and confidence intervals for each locomotor group for the combined-sex sample

	Combined sex: pRMA					Combined sex: PGLS						
	Scaling Prediction	Allometric Result ^a	Intercept	Slope	R ²	pRMA Slope 95% Confidence Interval		Intercept	Slope	R ²	PGLS Slope 95% Confidence Interval	
						SE	SE					
Arboreal quadruped												
Superior pubic ramus length	isometry	isometry	-0.32	0.90	0.92	0.76-1.05	0.11	0.79	0.86	0.86	0.64-0.94	
Inferior pubic ramus length	isometry	isometry	-0.18	0.89	0.91	0.75-1.03	0.47	0.71	0.84	0.84	0.57-0.85	
Pubic symphysis length	isometry	isometry	-1.58	1.08	0.83	0.78-1.37	-2.07	1.22	0.78	0.78	0.92-1.52	
Ilium length	isometry	isometry	0.10	0.95	0.96	0.86-1.04	0.24	0.91	0.96	0.96	0.82-1.00	
Ilium width	+	+	-1.70	1.15	0.96	1.03-1.28	-1.84	1.20	0.95	0.95	1.08-1.33	
Lower iliac height	-	isometry	-0.15	0.90	0.97	0.80-1.00	0.11	0.83	0.94	0.94	0.73-0.93	
Ischium length	isometry	isometry	-0.51	0.92	0.93	0.78-1.06	-0.49	0.92	0.91	0.91	0.79-1.06	
Acetabulum diameter	+	isometry	-1.34	1.00	0.96	0.88-1.12	-0.95	0.88	0.92	0.92	0.76-1.01	
Lower ilium cross-sectional area	+	+	-6.57	2.40	0.95	2.20-2.60	-5.94	2.25	0.96	0.96	2.05-2.45	
Suspension												
Superior pubic ramus length	isometry	isometry	-1.28	1.07	0.99	0.96-1.19	-1.26	1.07	0.99	0.99	0.96-1.18	
Inferior pubic ramus length	isometry	isometry	-2.58	1.32	0.85	0.75-1.89	-2.11	1.22	0.81	0.81	0.65-1.79	
Pubic symphysis length	isometry	isometry	0.15	0.71	0.57	0.18-1.24	0.98	0.54	0.42	0.27	0.01-1.07	
Ilium length	isometry	-	0.93	0.71	0.95	0.53-0.90	1.02	0.70	0.93	0.93	0.51-0.88	
Ilium width	+	+	-3.58	1.60	0.94	1.14-2.07	-3.33	1.55	0.91	0.24	1.09-2.01	
Lower iliac height	-	-	0.84	0.68	0.95	0.53-0.84	1.03	0.64	0.94	0.08	0.48-0.79	
Ischium length	isometry	isometry	-1.88	1.18	0.95	0.89-1.48	-1.75	1.15	0.93	0.15	0.86-1.45	
Acetabulum diameter	+	isometry	-1.43	0.99	0.99	0.89-1.09	-1.41	0.99	0.99	0.05	0.88-1.09	
Lower ilium cross-sectional area	+	-	-3.77	1.79	0.99	1.61-1.97	-3.73	1.79	0.99	0.09	1.61-1.97	
Terrestrial quadruped												
Superior pubic ramus length	isometry	isometry	-0.74	0.97	0.92	0.85-1.09	-0.01	0.82	0.97	0.97	0.70-0.94	
Inferior pubic ramus length	isometry	isometry	-0.43	0.91	0.96	0.81-1.01	-0.41	0.91	0.98	0.05	0.81-1.01	
Pubic symphysis length	isometry	-	0.93	0.59	0.16	0.33-0.85	3.40	0.09	0.08	0.13	-0.17-0.35	
Ilium length	isometry	-	1.95	0.54	0.90	0.45-0.63	2.13	0.50	0.95	0.04	0.41-0.59	
Ilium width	+	+	-3.73	1.63	0.98	1.53-1.73	-3.34	1.55	0.99	0.05	1.45-1.65	
Lower iliac height	-	-	0.55	0.74	0.90	0.64-0.84	0.48	0.76	0.97	0.05	0.65-0.86	
Ischium length	isometry	-	-0.26	0.88	0.98	0.83-0.94	-0.12	0.86	0.99	0.03	0.80-0.91	
Acetabulum diameter	+	isometry	-1.26	0.95	0.98	0.89-1.01	-1.09	0.92	0.99	0.03	0.85-0.98	
Lower ilium cross-sectional area	+	isometry	-5.67	2.19	0.92	1.89-2.50	-3.77	1.82	0.96	0.16	1.51-2.12	
Vertical clinger and leaper												
Superior pubic ramus length	isometry	isometry	-0.56	0.92	0.93	0.70-1.15	-0.21	0.82	0.93	0.11	0.60-1.05	
Inferior pubic ramus length	isometry	-	0.64	0.59	0.94	0.42-0.76	0.71	0.57	0.91	0.09	0.40-0.74	
Pubic symphysis length	isometry	+	-3.57	1.60	0.92	1.14-2.06	-2.73	1.35	0.89	0.23	0.90-1.81	
Ilium length	isometry	-	0.65	0.79	0.99	0.71-0.87	0.66	0.79	0.99	0.04	0.71-0.87	
Ilium width	+	+	-2.69	1.46	0.96	1.17-1.76	-2.27	1.34	0.95	0.15	1.05-1.63	
Lower iliac height	-	-	0.98	0.58	0.99	0.53-0.63	0.98	0.58	0.99	0.03	0.53-0.63	
Ischium length	isometry	isometry	-1.23	1.07	0.99	0.95-1.18	-1.30	1.09	0.99	0.06	0.97-1.21	
Acetabulum diameter	+	isometry	-2.07	1.22	0.88	0.80-1.63	-1.28	0.99	0.84	0.21	0.57-1.40	
Lower ilium cross-sectional area	+	+	-10.07	3.36	0.94	2.58-4.15	-8.93	3.03	0.93	0.40	2.25-3.82	

^a Interpretation of allometry is based on the 95% confidence interval for the pRMA slope.
 + : positive allometry, - : negative allometry

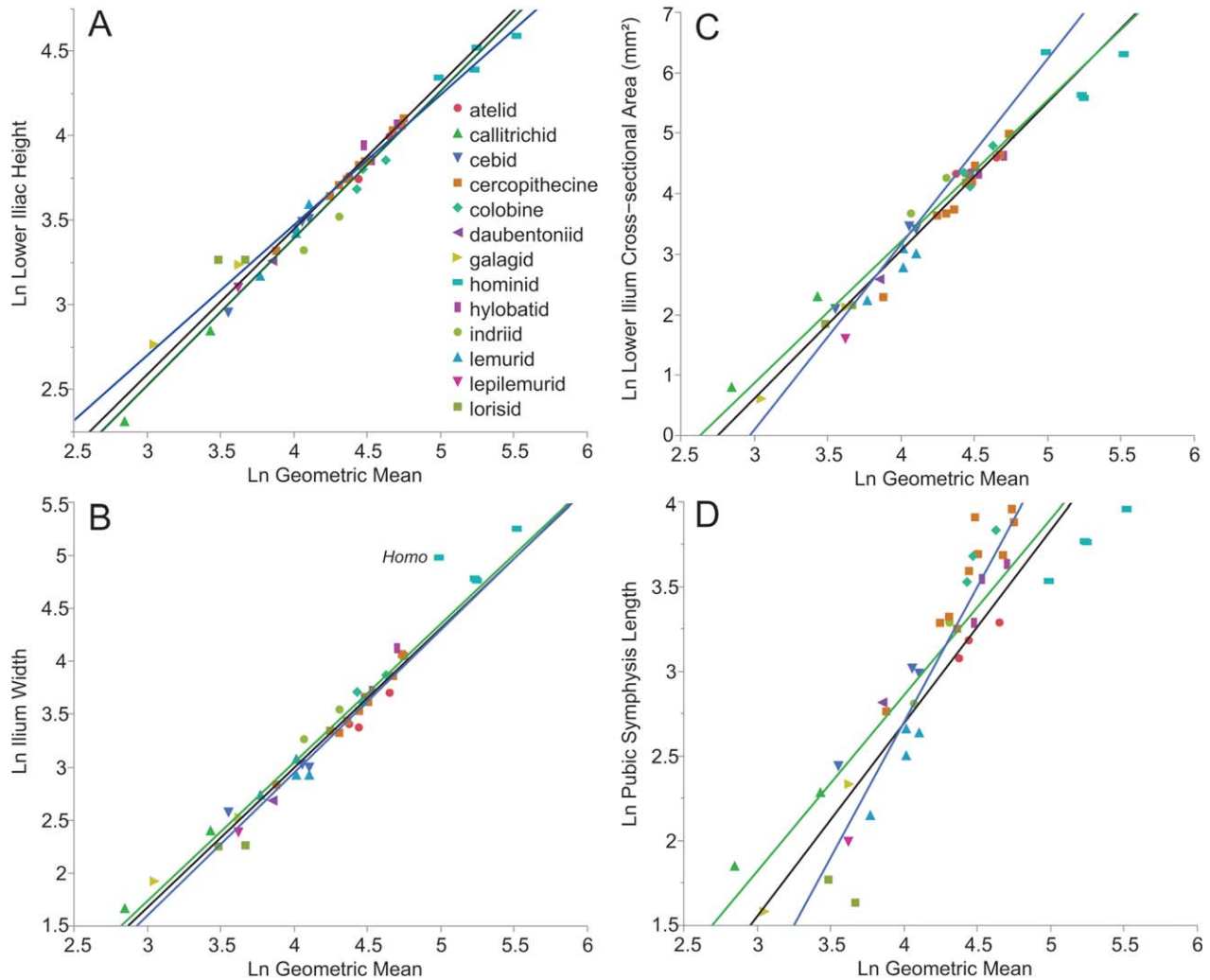


Fig. 2. pRMA regression fits for all-primates (black lines), haplorhines (green lines), and strepsirrhines (blue lines). **(A)** All regressions of ln-lower iliac height on ln-geometric mean demonstrate significant negative allometry (all-primates $\beta = 0.86$, 95% confidence interval: 0.80-0.92; haplorhine $\beta = 0.87$, 95% confidence interval: 0.83-0.91; and strepsirrhine $\beta = 0.77$, 95% confidence interval: 0.59-0.95). **(B)** All regressions of ln-ilium width on ln-geometric mean demonstrate positive allometry (all-primates $\beta = 1.32$, 95% confidence interval: 1.20-1.44; haplorhine $\beta = 1.31$, 95% confidence interval: 1.17-1.45; and strepsirrhine $\beta = 1.35$, 95% confidence interval: 1.07-1.63). **(C)** All regressions of ln-lower ilium cross-sectional area on ln-geometric mean demonstrate positive allometry (all-primates $\beta = 2.45$, 95% confidence interval: 2.27-2.63; haplorhine $\beta = 2.34$, 95% confidence interval: 2.14-2.54; and strepsirrhine $\beta = 3.07$, 95% confidence interval: 2.56-3.58). **(D)** Regressions of ln-pubic symphysis length on ln-geometric mean exhibit isometry, except for in strepsirrhines, which exhibit positive allometry (all-primates $\beta = 1.14$, 95% confidence interval: 0.97-1.31; haplorhine $\beta = 1.04$, 95% confidence interval: 0.86-1.22; and strepsirrhine $\beta = 1.6$, 95% confidence interval: 1.15-2.05). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

and lower iliac cross-sectional area (Table 9). Pubic symphysis length is isometric in AQ and suspensory taxa, but positively allometric in VCL and negatively allometric in terrestrial quadrupedal species (Fig. 3D). Lower ilium cross-sectional area is isometric in terrestrial quadrupeds, but positively allometric in arboreal quadrupeds and VCL primates, and negatively allometric in suspensory species (Fig. 3E). The scrambling and leaping callitrichids and indriids have more robust lower ilia than expected for primates of their size.

DISCUSSION

This study aimed to characterize scaling patterns in pelvic traits and to relate these patterns to differences in locomotor behavior across primates. Predictions of

pelvic scaling were based on a biomechanical assessment of body size, locomotor forces, and postural loading. The results demonstrate that most bony pelvic dimensions scale with isometry relative to pelvic size, while measures of the ilium tend to scale allometrically. It is clear that lower iliac height, lower ilium cross-sectional area, and ilium width scale allometrically with overall pelvis size in this study. This supports previous work on pelvic scaling by Ward (1991, 1993) which showed allometric scaling in ilium length, lower iliac height, and ilium width in catarrhines. Furthermore, there are some differences across locomotor groups in the specifics of how these aspects of ilium morphology scale with size. These locomotor group differences in pelvic allometry suggest that there may be functional differences in scaling that are related to the structural and mechanical

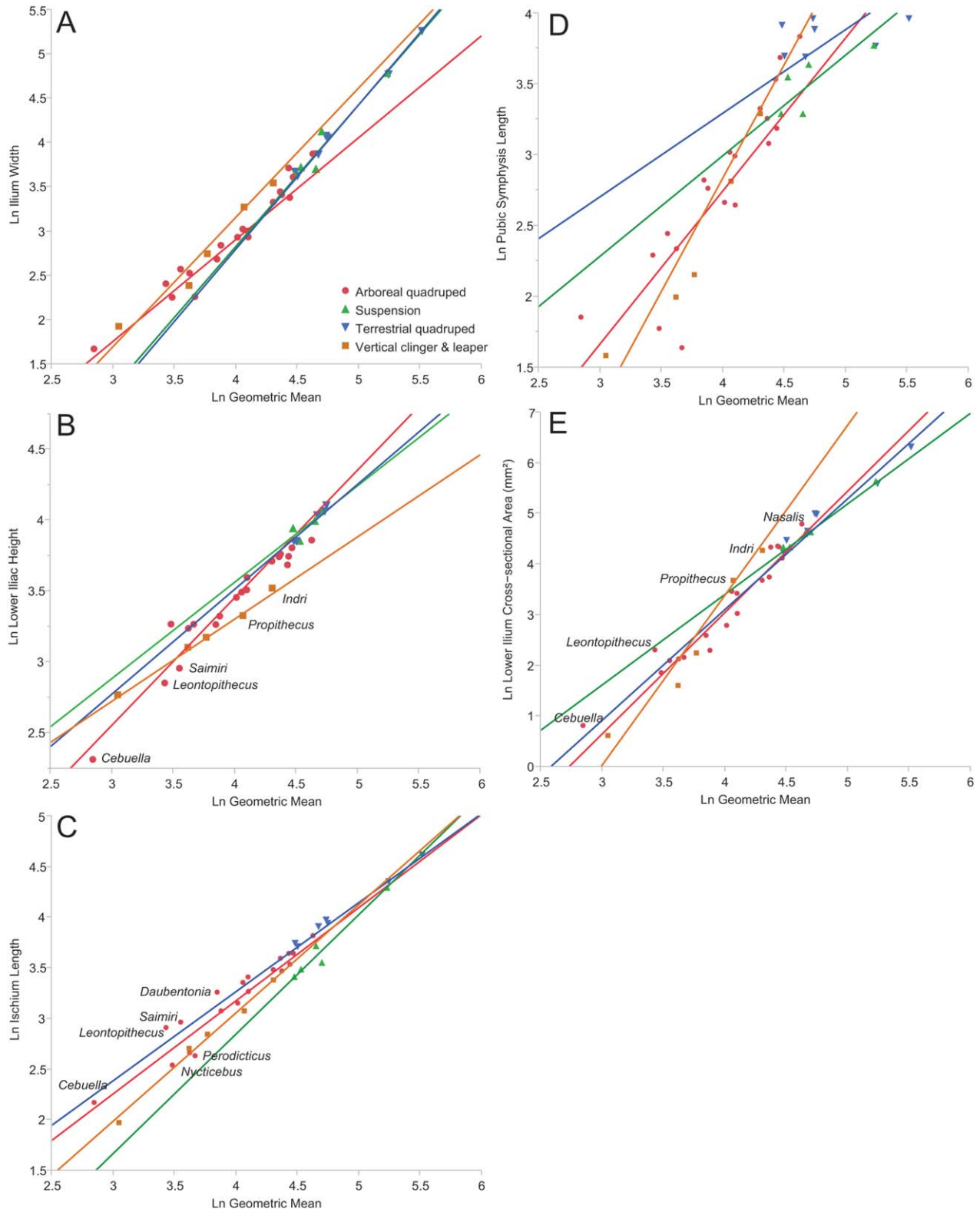


Fig. 3.

requirements of locomotion. There are both kinematic and kinetic differences in stereotypical locomotor modes, and recent work on pelvic locomotor adaptation has demonstrated that pelvic anatomy differs across locomo-

tor groups with differences in locomotor loading (Lewton, 2015). This recent study on locomotor adaptation within strepsirrhines found that lower ilium cross-sectional area differed across locomotor groups (arboreal

quadrupeds, terrestrial quadrupeds, and vertical clingers and leapers) as predicted based on posture and substrate reaction forces (Lewton, 2015). Lower ilium cross-sectional area was supported as an adaptation to the forces that occur during locomotion; species that encounter larger ground reaction forces during locomotion exhibited relatively more robust lower ilia (Lewton, 2015). Therefore, differences in pelvic scaling across locomotor groups is expected in features that are adapted to resist the combined loads of body size and ground reaction forces that are encountered during locomotion. The following discussion focuses on functional explanations for scaling patterns of allometric pelvic traits, and in particular the roles of body size, locomotor forces, and posture in pelvic scaling.

Ilium width

These results demonstrate that ilium width scales with positive allometry across primates. Ward also demonstrated positive allometry in ilium width in separate regressions of catarrhine monkeys and apes (1991, 1993). In addition, Lewton (2015) showed that there are morphological differences in ilium width by locomotor group in strepsirrhines, but the cause of these differences was not entirely clear. There appeared to be an interaction between body size and locomotion (Lewton, 2015), but a larger sample of primates was necessary to investigate more fully the effect of size on ilium width. The current study provides that larger sample and suggests that positive allometry of ilium width across primates may allow maintenance of functional similarity in muscle power (given the negatively allometric relationship between muscle mass and body mass) (Ward, 1991, 1993). The muscles that attach to the ilium are the abdominal wall musculature; *m. latissimus dorsi* via the thoracolumbar fascia, which is functionally important during orthograde climbing, and to a minor extent in quadrupedal walking (Larson and Stern, 2007); *m. iliacus*, a hip flexor; and *m. gluteus medius*, which is primarily a hip extensor in non-human primates. In this sample, the large orthograde species (hominoids and indriids) exhibit even wider ilia than expected given their size, suggesting that wide ilia may be related to maintaining an erect back or, in the case of hominoids, to forelimb suspension and climbing (Jungers, 1976; Ward, 1991). However, increased broadening of the iliac blades with body size may be related to other, nonmuscular functions. Future work will need to test specific hypotheses of the relationship among muscle function,

orthograde, and ilium width to determine the functional cause of wide ilia.

Lower iliac height and robusticity

Lower iliac height is negatively allometric across primates, except for arboreal quadrupeds, in which the 95% confidence interval for the slope includes the slope of isometry at its upper bound (slope = 0.90, 95% confidence interval: 0.80–1.00). An examination of the plot of lower iliac height on the pelvic geometric mean shows that species with a significant leaping component in their positional behavior (callitrichids, indriids, and *Saimiri*) have even shorter lower ilia than expected for a primate of their size (Fig. 3B). In addition, lower iliac height is shorter in taxa that experience larger forces either as a result of relatively larger body size or larger locomotor loads (Lewton, 2015). Thus, as body size or locomotor forces increase, lower iliac height decreases. This finding supports the idea that the ilium responds to increased forces by decreasing its length, which is thought to decrease the bending moment around the ilium (Robinson, 1972; Leutenegger, 1974; Steudel, 1981b). The negative allometry of lower iliac height across primates observed here provides additional support for the hypothesis posited in the mid-20th century that the lower ilium is functionally linked to forces related to body size and locomotor loading. Ward's examination of lower iliac height, however, revealed isometry within hominoids, but negative allometry within catarrhine monkeys (1991). This previous finding of isometry within hominoids may be related to the relatively small number of species that comprise the hominoid sample.

Lower ilium cross-sectional area (LICSA) is positively allometric across all primates in this sample, including within haplorhines and strepsirrhines. Although demonstrating isometry within the small sample of terrestrial quadrupeds (species $N = 7$, slope = 2.19, 95% confidence interval: 1.89–2.50), LICSA in this sample is positively allometric in all other locomotor groups. Furthermore, callitrichids, indriids, and colobines, in particular, have even more robust lower ilia than expected given their size, which suggests that forces related to leaping behaviors influence lower ilium robusticity (Figs. 2C and 3E). Lewton (2015) has recently shown that LICSA is larger in strepsirrhine species that experience large locomotor forces, demonstrating that LICSA is larger in vertical clinging and leaping and terrestrial quadrupedal lemurs than in arboreal quadrupedal lemurs, and that LICSA scales with positive allometry in strepsirrhines. This increase in lower ilium robusticity and the presence of positive allometry in LICSA in

Fig. 3. pRMA regression fits for arboreal quadrupeds (red lines), suspensors (green lines), terrestrial quadrupeds (blue lines), and vertical clingers and leapers (orange lines). (A) ln-ilium width on ln-geometric mean (arboreal quadrupeds $\beta = 1.15$, 95% confidence interval: 1.03–1.28; suspensors $\beta = 1.6$, 95% confidence interval: 1.14–2.07; terrestrial quadrupeds $\beta = 1.63$, 95% confidence interval: 1.53–1.73; and vertical clingers and leapers $\beta = 1.46$, 95% confidence interval: 1.17–1.76). (B) ln-lower iliac height on ln-geometric mean (arboreal quadrupeds $\beta = 0.90$, 95% confidence interval: 0.80–1.00; suspensors $\beta = 0.68$, 95% confidence interval: 0.53–0.84; terrestrial quadrupeds $\beta = 0.74$, 95% confidence interval: 0.64–0.84; and vertical clingers and leapers $\beta = 0.58$, 95% confidence interval: 0.53–0.63). (C) ln-ischium length on ln-geometric mean (arboreal quadrupeds $\beta = 0.92$, 95% confidence interval: 0.78–1.06; suspensors $\beta = 1.18$, 95% confidence interval: 0.89–1.48; terrestrial quadrupeds $\beta = 0.88$, 95% confidence interval: 0.83–0.94; and vertical clingers and leapers $\beta = 1.07$, 95% confidence interval: 0.95–1.18). (D) ln-pubic symphysis length on ln-geometric mean (arboreal quadrupeds $\beta = 1.08$, 95% confidence interval: 0.78–1.37; suspensors $\beta = 0.71$, 95% confidence interval: 0.18–1.24; terrestrial quadrupeds $\beta = 0.59$, 95% confidence interval: 0.33–0.85; and vertical clingers and leapers $\beta = 1.60$, 95% confidence interval: 1.14–2.06). (E) ln-lower ilium cross-sectional area on ln-geometric mean (arboreal quadrupeds $\beta = 2.40$, 95% confidence interval: 2.20–2.60; suspensors $\beta = 1.79$, 95% confidence interval: 1.61–1.97; terrestrial quadrupeds $\beta = 2.19$, 95% confidence interval: 1.89–2.50; and vertical clingers and leapers $\beta = 3.36$, 95% confidence interval: 2.58–4.15). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

strepsirrhines has been related to strengthening the ilium by increasing the cross-sectional area of the bone to withstand large locomotor forces. The present study additionally demonstrates positive allometry of LICSA in haplorhines, thus identifying a primate-wide pattern of LICSA positive allometry.

Some groups consistently differ from expectations based on the regressions; the small, scrambling and leaping callitrichids (i.e., *Cebuella*, *Leontopithecus*) and the vertical clinging and leaping indriids have shorter and more robust lower ilia than expected for primates of their size. Both of these features appear to reduce bending in the ilium by decreasing the distance between the centers of rotation of the hip and sacroiliac joints, and by increasing the area available to withstand large forces as they are transmitted through the ilium. Thus, these species illustrate the relationship between large locomotor forces and ilium dimensions.

A short, robust lower ilium has, however, frequently been suggested to be an adaptation to bipedality, and is present in australopiths and the genus *Homo* (e.g., Le Gros Clark, 1955; Robinson, 1972; Leutenegger, 1974; Kummer, 1975; Steudel, 1981b; Lovejoy et al., 2009). Kibii et al. (2011) even suggest that reduced lower iliac height is a derived feature of genus *Homo* and that the presence of this trait in *Australopithecus sediba* is evidence either of homoplasy or of synapomorphy with *Homo*. However, the presence of short lower ilia in other catarrhine and strepsirrhine species, and the scaling patterns highlighted here suggest that a short, robust lower ilium is an adaptive response to large loads generally, and that those loads can result from various locomotor behaviors including leaping and orthograde, and are not limited to bipedal hominins.

Departures from predicted scaling patterns

Some other aspects of pelvic shape demonstrate variation in locomotor differences in allometry, or were found to depart from scaling predictions. Ilium length exhibits negative allometry in three of four locomotor groups, but isometry in all primate-wide analyses; pubic symphysis length is also variable in its scaling across locomotor groups in particular; ischium length scales differently in terrestrial quadrupeds than in the rest of primates; and acetabulum diameter clearly scales isometrically, and not with positive allometry as predicted. Although interpretation of regression analyses of locomotor groups must take into account the small sample sizes of behavioral categories other than arboreal quadrupedalism, this study can still offer some general conclusions.

Ilium length. Ilium length scales isometrically across primates, but with negative allometry in all locomotor groups except arboreal quadrupeds. However, this may be related to sampling; the arboreal quadruped group has a much larger sample ($N = 19$ species) than the other locomotor groups (suspension $N = 5$, terrestrial quadruped $N = 7$, vertical clinging and leaping $N = 5$). As estimates of regression parameters have less power at small sample sizes, it may be that negative allometry in suspensors, TQ, and VCL is a spurious consequence of small sample sizes.

Pubic symphysis length. The functional relevance of variation in pubic symphysis length scaling among loco-

motor groups is not immediately apparent (isometric in haplorhines, positively allometric in strepsirrhines; isometric in AQ and suspensors, negatively allometric in TQ, and positively allometric in VCL). This study found that lemurs drive positive allometry of pubic symphysis length in strepsirrhines. Given that VCL strepsirrhine species are divided into two groups (large lemuriform species and small lorisiform species), positive allometry in lemuriform strepsirrhines is likely a result of the consequences of very large locomotor forces during vertical clinging and leaping in these large species.

Hypotheses regarding functional causes of variation in pubic morphology have generally been lacking in the literature. In his section on pelvic adaptation to locomotion in mammals, Howell noted "it is probable that the extent of the symphysis pubis is without much interest here . . . all mammals of any weight need a good symphysis" (1944, p. 168). However, Howell did acknowledge that there is great variation among mammals in symphysis length and in whether the opposing sides of the pubic bones meet at a symphyseal joint at all. Clearly, additional research is needed to determine the functional relationships between pubic morphology and locomotion in primates.

Ischium length. Given the primate-wide pattern of ischium length isometry, and Ward's (1991) finding of isometry in ischium length, it is likely that ischium length scales isometrically in primates and that the negative allometry in ischium length in terrestrial quadrupeds found here may be a spurious consequence of small sample sizes. Alternatively, negative allometry in ischium length in TQ taxa may be related to other aspects of ischial morphology, such as its angular projection. Fleagle and Anapol (1992) demonstrated that many species differ in the angular projection of the ischium rather than in its length alone (both measures being ways of increasing the moment arm of the hamstring musculature), and it is possible that the variation in the results here is related more to variation in ischial projection, which was not measured for this analysis.

Acetabulum diameter. It was predicted that acetabulum diameter would scale with slight positive allometry, as other studies have found (Steudel, 1981a; Ward, 1991); however, this study clearly demonstrated isometry in acetabulum diameter in all analyses. Given that this study more than doubles the sample size of previous work, it may be that previous studies did not have sufficient power to detect isometry.

The slight differences in scaling patterns observed between the primate-wide sample and the locomotor subsamples may be a result of differences in locomotor function among taxa. It was predicted that measures related to resisting bending or distributing forces would scale allometrically with body size while the remaining measures would scale isometrically. Across primates and within locomotor groups, these predictions are variably upheld. Instead of a clear and consistent pattern across locomotor groups, there is some variation in the scaling relationships of a small number of pelvic traits; for a given trait, scaling relationships may differ across locomotor groups. This difference in scaling of pelvic traits among locomotor groups is interesting because it reveals a potential interaction between scaling and locomotor function; the effects of increasing body size are not the

same for each type of locomotion, likely as a consequence of other mechanically relevant factors on skeletal biology including the ground reaction forces that are incurred during locomotion.

CONCLUSION

Patterns of pelvic scaling are generally uniform across primates, with haplorhines and strepsirrhines exhibiting almost identical scaling patterns. Furthermore, there are few sex differences in scaling across primates, with males and females generally exhibiting the same patterns as the combined-sex sample. The majority of pelvic traits scale isometrically with pelvic size. These isometric traits—including certain measures of the pubis and ischium—have not been found to differ across functional locomotor groups, suggesting that their morphology may be more strongly related to functions other than resisting locomotor forces, such as obstetrical requirements or muscle leverage. However, ilium measures, especially ilium width, lower iliac height, and lower ilium cross-sectional area scale allometrically with body size and appear to be related to different loading regimes experienced by the various locomotor behavioral groups. These allometric patterns suggest that the lower ilium becomes shorter and more robust in species that encounter large locomotor forces. Future work is necessary to determine how bony microarchitecture of the lower ilium may also adapt to the forces that it transmits.

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