Pelvic Form and Locomotor Adaptation in Strepsirrhine Primates

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ABSTRACT

The pelvic girdle is a complex structure with a critical role in locomotion, but efforts to model the mechanical effects of locomotion on its shape remain difficult. Traditional approaches to understanding form and function include univariate adaptive hypothesis-testing derived from mechanical models. Geometric morphometric (GM) methods can yield novel insight into overall three-dimensional shape similarities and differences across groups, although the utility of GM in assessing functional differences has been questioned. This study evaluates the contributions of both univariate and GM approaches to unraveling the trait-function associations between pelvic form and locomotion. Three-dimensional landmarks were collected on a phylogenetically-broad sample of 180 pelves from nine primate taxa. Euclidean interlandmark distances were calculated to facilitate testing of biomechanical hypotheses, and a principal components (PC) analysis was performed on Procrustes coordinates to examine overall shape differences. Both linear dimensions and PC scores were subjected to phylogenetic ANOVA. Many of the null hypotheses relating linear dimensions to locomotor loading were not rejected. Although both analytical approaches suggest that ilium width and robusticity differ among locomotor groups, the GM analysis also suggests that ischiopubic shape differentiates groups. Although GM provides additional quantitative results beyond the univariate analyses, this study highlights the need for new GM methods to more specifically address functional shape differences among species. Until these methods are developed, it would be prudent to accompany tests of directional biomechanical hypotheses with current GM methods for a more nuanced understanding of shape and function. Anat Rec, 298:230–248, 2015.   © 2014 Wiley Periodicals, Inc.

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The identification of adaptation to biological function has been a goal of evolutionary biology since the time of Darwin. Within the field of biological anthropology, adaptations to diet and/or locomotion have been examined via hypothesis-testing of craniodental anatomy (Lieberman and Crompton, 2000; Ravosa et al., 2000; Daegling and McGraw, 2001; Spencer, 2003; Vinyard et al., 2003; Terhune, 2013), shoulder anatomy (Taylor, 1997), long bone morphology (Fleagle, 1976; Polk, 2002), and hand and foot anatomy (Orr, 2005; Patel, 2010; Tocheri et al., 2011). However, systematic hypothesis-testing of pelvic adaptations has been relatively limited

because the mechanical rules that govern pelvic shape are not well understood.

Among other requirements, identifying morphological adaptations necessitates a clear association between a morphological trait and its presumed function, as well as evidence that the trait performs the function (e.g., Kay and Cartmill, 1977; Anthony and Kay, 1993). The comparative method is used to distinguish form-function correlations in broad samples of extant taxa (Felsenstein, 1985; Harvey and Pagel, 1991; Ross et al., 2002). Although accurately inferring function from morphology is difficult because one cannot directly observe a particular trait performing a biological function, the strength of trait-function associations increases when they can be demonstrated to occur convergently and repeatedly in a comparative sample (Szalay, 2007). A rigorous comparative approach also incorporates the formation and testing of *a priori* functional hypotheses to demonstrate that the trait "has" the function (Kay and Cartmill, 1977).

Early studies of primate pelvic adaptation to locomotion focused on describing shape differences across primate species and correlating these observed differences to differences in locomotor behavior. Although some aspects of primate pelvic shape were described qualitatively in the late 1800s (Mivart, 1867; Flower, 1870), the earliest work to systematically assess pelvic shape in a range of primate species was performed by Harriet Waterman in 1929. In the same year, William Straus qualitatively compared aspects of ilium length and width across many primate species (Straus, 1929). Much of the subsequent work in the late 20th century focused on more quantitative comparative research on primate pelvic shape and proposed hypotheses of pelvic adaptation to locomotion (Schultz, 1969; Jungers, 1976; Jenkins and Camazine, 1977; Sigmon and Farslow, 1986; Ward, 1991; Fleagle and Anapol, 1992; Anemone, 1993; MacLatchy, 1998). Many current hypotheses relating pelvic form to function have not been systematically tested or are not derived from clearly defined mechanical models of the requirements of different locomotor behaviors (i.e., traits hypothesized to be "adaptations" to locomotion have not been shown to perform the specified function). However, the development of functional and adaptive hypotheses relies on an understanding of the biomechanical foundation of the system, from which predictions of pelvic levers and other aspects of morphology can be derived using optimality criteria [similar to Rudwick's (1964) paradigm method]. Although a general mechanical model of the forces acting on the pelvis has been proposed, it has not been used to derive clear expectations of shape for various locomotor modes.

A further obstacle to understanding pelvic form–function relationships is its complex three-dimensional (3D) shape, which is difficult to accurately quantify using linear measures of its various dimensions. The pelvic girdle comprises four bones that are oriented in different anatomical planes relative to each other, that have complex curvatures, and that contribute to three different types of joints. [The hip joint is synovial, while the pubic symphysis and sacroiliac joints are mostly nonsynovial joints; the pubic symphysis is a cartilaginous synarthrosis and the sacroiliac joint is likely an *amphiarthrosis* (exhibiting features of both a nonsynovial cartilaginous synarthrosis and a synovial diarthrosis (Puhakka et al., 2004; Vleeming et al., 2012))]. This structural complexity makes understanding the association between shape and function of the pelvic girdle difficult. A related problem is that of atomization: it can be difficult to determine how to deconstruct a complex structure into discrete components that are amenable to hypothesis-testing (Lauder, 1996).

However, complex structures can be quantified, visualized, and analyzed using geometric morphometrics (GM), a powerful method that permits multivariate analysis of 3D coordinates. Geometric morphometrics differs from traditional multivariate analyses in that it retains all of the geometry of a study specimen, preserving the spatial relationships among landmarks. Furthermore, it incorporates both size and shape, thus permitting an examination of *form* (Richtsmeier et al., 2002). In GM methods, differences in size across specimens are accounted for by superimposing landmark configurations and scaling, rotating, and translating them to remove the effects of non-shape parameters (i.e., size, Dryden and Mardia, 1998; Zelditch et al., 2004). Once the effects of size and orientation are removed from the analysis, GM methods allow ordination of transformed coordinates (often Procrustes coordinates) in conventional ways, including principal component analysis (PCA). An advantage of PCA of transformed landmark coordinates is the ability to project the coordinates back into shape space (Kendall, 1984) in order to visualize the shape differences along principal component axes, effectively examining principal component score loadings (O'Higgins and Jones, 1998). Further details on specifics of GM methods can be found in Bookstein (1991), Dryden and Mardia (1998), Zelditch et al. (2004), and a review by Slice (2007).

Within biological anthropology, GM studies of shape differences across species include work on the forelimb (Taylor and Slice, 2005; Young, 2006, 2008; Tallman, 2012; Rein and Harvati, 2013), hindlimb (Harmon, 2007; Harcourt-Smith et al., 2008; Jungers et al., 2009; Turley et al., 2011; Cooke and Tallman, 2012), skull (O'Higgins and Jones, 1998; Lockwood et al., 2002; Singleton, 2002; Harvati, 2003; Baab and McNulty, 2009; Bastir et al., 2010; Harvati et al., 2010; Terhune, 2013), and spine (Russo, 2010). However, very little GM work has encompassed interspecific comparisons of pelvic shape (but see Berge, 1996; Bouhallier et al., 2004; Bouhallier and Berge, 2006; Lewton, 2012; Lycett and von Cramon-Taubadel, 2013). There have been few intraspecific GM analyses in humans, and these have focused only on clinical (Brown et al., 2013) and forensic (Gonzales et al., 2009; Bytheway and Ross, 2010) aspects of pelvic anatomy.

Most studies of function and adaptation test directional hypotheses (those that suggest not only a difference between groups, but also predict the direction of difference) using conventional linear-based methods, but are unable to assess the functional morphology of multiple aspects of structure simultaneously. Similarly, most studies of shape and form rely solely on GM methods; although GM approaches do allow a comprehensive multivariate analysis of three-dimensional shape, they cannot currently test directional hypotheses (new approaches that use GM as an additional tool to interpret adaptive tests are needed). For complex structures such as the pelvic girdle, therefore, an integration of
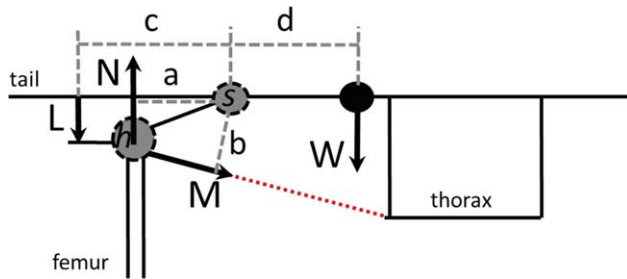
Fig. 1. Model of forces acting on the pelvis in the sagittal plane. Joints: h: hip, s: sacroiliac. Forces: N: vertical force at the hip joint, W: force of body weight at the center of mass, M: force of the abdominal musculature, L: force of ischiosacral ligaments. Moment arms: a: distance from N to sacroiliac joint, b: normal distance from sacroiliac to M, c: distance from L to sacroiliac, d: distance from sacroiliac to W. Equilibrium occurs when sacroiliac moments $N*a = M*b$ and $L*c = W*d$. Adapted from Badoux (1974).

these two approaches may yield more insight into pelvic functional morphology than either one alone.

This study has two major aims: 1) to test adaptive hypotheses relating pelvic shape to locomotion in lemuriform strepsirrhine primates, and 2) to assess the utility of GM methods in addressing these functional hypotheses. Lemuriformes is an appropriate group for this study because they exhibit a variety of positional behaviors (various forms of arboreal quadrupedalism, two styles of vertical clinging and leaping) and body sizes. Furthermore, these primates are closely related, permitting a narrow phylogeny approach (Ross et al., 2002) to studying adaptation.

PELVIC AND LOCOMOTOR MECHANICS

Hypotheses regarding how pelvic form is related to locomotor function are best derived from an understanding of the underlying mechanics of both the pelvic structure and the form of locomotion. Thus, a brief review of pelvic structural mechanics and the biomechanics of primate locomotion is given below, followed by the study hypotheses.

Mechanical Model of the Pelvic Girdle

Although biomechanical modeling of the pelvis in nonhuman primates has not been a major subject of study, two basic interrelated models have been proposed (Badoux, 1974; Kummer, 1975; Pauwels, 1980), and are used here as a basis for deriving adaptive hypotheses of form–function relationships between pelvic shape and locomotion.

Badoux (1974) modeled the pelvis based on the mammalian bow-and-string model of quadrupedalism (Slijper, 1946) in which the vertebral column is the "bow," the dorsal muscles extend the spine, while the ventral muscles flex the spine, thus acting as "bow strings." In this configuration, a moment at the sacroiliac joint is caused by the force of body weight inducing dorsal rotation of the sacrum, which is resisted by the ischiosacral ligaments and ischiocaudal muscles. In addition, the vertical force through the hip joint induces a ventral rotation torque at the sacroiliac joint, which is resisted by the ventral muscles attaching to the pubis (i.e., rectus
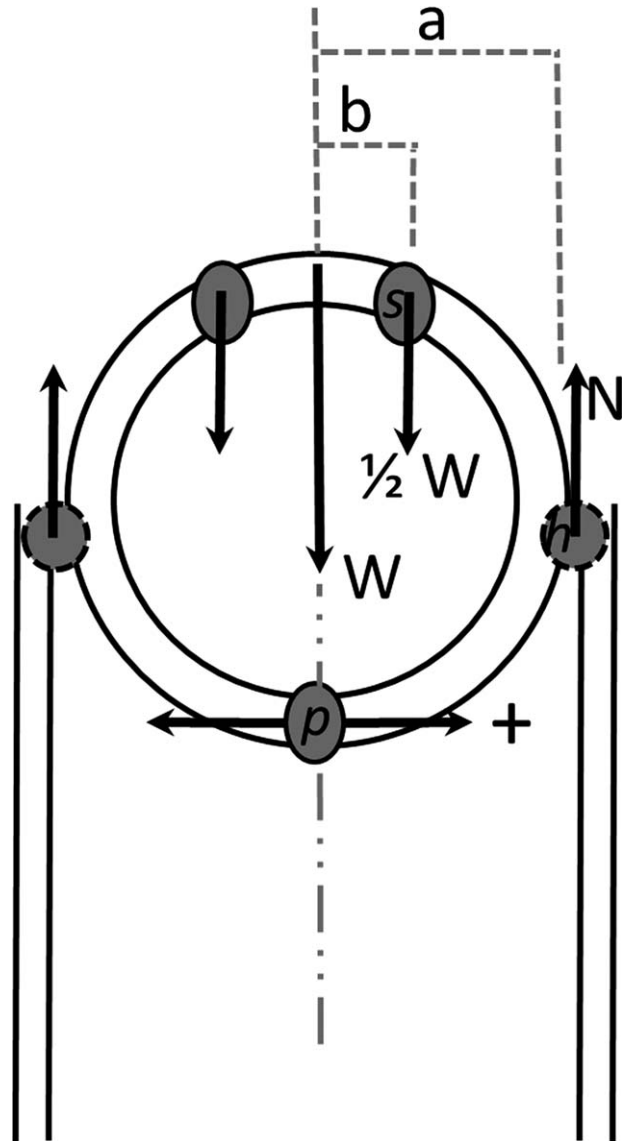

Fig. 2. Model of forces acting on the pelvis in the transverse plane. Joints: h: hip, s: sacroiliac, p: pubic symphysis. Forces: N: vertical force at the hip joint, W: force of body weight. Force at each sacroiliac joint is one-half body weight. +: Tensile force at the pubic symphysis. Moment arms: a: distance from sagittal plane to hip joint force, N, b: distance from sagittal plane to sacroiliac joint force, $\frac{1}{2}$ W. Adapted from Badoux (1974).

abdominis, Fig. 1). This model is essentially the same as Kummer's (1975) model of the pelvis as a two-armed lever, with the ilium and ischium constituting the two arms of the lever (Fig. 1). Pelvic mechanics has also been modeled in the transverse plane during stance phase (Badoux, 1974; Pauwels, 1980) in which the pelvis is a ring of bones comprising two arcs that attach to each other at dorsal (sacroiliac) and ventral (pubic symphysis) joints. In this model, the lower ilium tends to rotate dorsomedially (i.e., counterclockwise), loading the pubic symphysis in tension (Fig. 2; Badoux, 1974 p. 22).

These mechanical models—one modeling forces in the sagittal plane and the other modeling forces in the transverse plane—can be used to predict bone and joint

loading during primate locomotion, and importantly, how these structures should be optimized to resist these loads. Optimization predictions will differ across species based on body posture used during locomotion (i.e., orthograde vs. pronograde) and on the particularities of biomechanics for different locomotor categories. It is important to note that this study considers bone strength and its relationship to locomotor loading, but there are many other bone mechanical properties that likely vary as a result of loading differences (e.g., bone volume fraction and density; trabecular number, thickness, and anisotropy; bone strain), and investigation of these parameters is beyond the scope of this study.

Primate Locomotor Biomechanics

Because the forces on the pelvis result from the overall mechanics of the behaviors an organism engages in, it is necessary to take locomotor biomechanics into account when generating and testing hypotheses of pelvic adaptation to locomotion. Kinetic and kinematic differences among broad locomotor groups are outlined here and form the basis for the adaptive hypotheses to follow. This discussion focuses on arboreal quadrupedalism and vertical clinging and leaping because those are the dominant forms of locomotion exhibited by lemuriform primates.

As a group, primates are unique among mammals in experiencing greater vertical forces on their hindlimbs than their forelimbs (e.g., Kimura, 1985; Reynolds, 1985; Demes et al., 1994; Schmitt and Hanna, 2004; Schmidt, 2005; Hanna et al., 2006; Kivell et al., 2010), because hindlimbs provide propulsive force, while forelimbs perform steering and braking functions (Demes et al., 1994). However, there are a few strepsirrhine exceptions to this observation: experimental studies have shown lorises and *Eulemur fulvus* to have higher forelimb than hindlimb forces (Schmitt and Lemelin, 2004; Demes et al., 2005; Franz et al., 2005). In general, though, because the hindlimb encounters a relatively higher force than the forelimb, the pelvic girdle should also encounter relatively high forces and should adapt to counter these loads.

Quadrupedalism is a relatively simple system to model: with the trunk approximately horizontal, the four limbs move parasagittally. The motion of limbs is often modeled as an inverted pendulum, with body mass vaulted over stiff limbs in an exchange of potential and kinetic energy (Biewener, 2006). Predictions of the inverted pendulum model have been tested and they do match the behavior of quadrupeds (Cavagna et al., 1977; Griffin et al., 2004). During primate quadrupedalism, compression is the dominant form of load applied to the limbs (Tuttle, 1969; Whitehead, 1993).

Primate arboreal quadrupeds (AQ) are generally small-bodied, which allows them to maneuver in an irregular environment comprising small, compliant branches in the forest canopy (Preuschoft et al., 1996; Biewener, 2003). As a result of the need to maintain arboreal stability, AQ have a low body center of mass and large center of support (Jenkins, 1974; Hildebrand, 1985; Schmitt, 1998, 1999), which is achieved by using more flexed and abducted limb joint postures (Jenkins, 1974; Schmitt, 1998, 1999; Polk, 2002, 2004).

Locomotor kinetics relate to substrate compliance, body size, and the distance over which forces are applied. Experimental studies indicate that substrate reaction forces (SRF), measured in multiples of body weight, are lowest among primates in arboreal quadrupeds ($0.5-0.8 \times$ body weight, Schmitt, 1998, 2003; Schmitt and Hanna, 2004; Franz et al., 2005). Compared to quadrupeds, vertical clingers and leapers (VCL) require more power to produce the forces necessary for a leap and thus encounter much higher SRF, for both small- and large-bodied VCL ($5-14 \times$ body weight, Demes et al., 1995, 1999). Vertical clinging and leaping involves clinging to arboreal vertical supports during resting postures and moving between vertical supports by leaping with the trunk in an orthograde position; the hindlimbs provide the propulsive force in takeoff and land first (Napier and Walker, 1967; Preuschoft et al., 1996; Biewener, 2003). The leap comprises three phases of motion: takeoff, airborne, and landing. Because leaping is mechanically more complex than quadrupedal walking, and because leaping is a critical component of many strepsirrhine species locomotor repertoires, it is requisite to outline the mechanics of each phase of a leap.

The takeoff phase is critical to a successful leap because it is there that the power required for the leap is generated (Biewener, 2003). To attain maximal jump height and/or distance, kinetic energy (and subsequently, velocity) must be maximized. Kinetic energy is usually supplied by muscle force or elastic energy stored in tendons (Aerts, 1998; Biewener, 2003) via rapid extension of the hindlimbs (Preuschoft et al., 1996). The horizontal distance of a leap is determined by the velocity takeoff, leap height, limb length, and muscle force (Biewener, 2003); as any of these quantities increase, so, too, will leap distance. As mentioned above, limb length is the distance over which acceleration occurs; longer limbs allow more time and distance over which to accelerate for takeoff (Peters and Preuschoft, 1984; Preuschoft et al., 1995; Demes et al., 1996; Biewener, 2003). Accordingly, VCL taxa do have relatively long limbs that increase the distance over which acceleration occurs (Demes et al., 1996), and large hindlimb angular excursions that they achieve through maintaining a range of hindlimb postures in preparation for the leap, from deeply flexed (during clinging) to fully extended (midleap). The mathematically derived optimum takeoff angle is 45° (Marsh, 1994; Sellers and Crompton, 1994), but this may vary depending on body size and leap distance (Crompton et al., 1993; Marsh, 1994; Sellers and Crompton, 1994); larger-bodied animals will use a smaller-than-optimum takeoff angle because they have relatively less muscle force available than smaller-bodied animals (Biewener, 2003).

The airborne phase of leaping is governed by the law of conservation of angular momentum, which dictates that in the absence of external forces, angular momentum of a projectile will not change, and will continue along a prescribed parabolic trajectory (Freedman and Young, 2003). After takeoff, however, the animal must accomplish mid-air rotations to correctly position the body for landing, and these rotations must occur via movement of the body about three principal axes: mediolateral, anteroposterior, and craniocaudal (Peters and Preuschoft, 1984; Dunbar, 1988; Preuschoft et al., 1996; Demes et al., 1996). Because angular momentum is the product of moment of inertia and angular velocity, an

TABLE 1. Univariate measures and predictions

Pelvic measure	Interlandmark definition	Prediction[a]
Superior pubic ramus length	11–13	AQ < VCL (small-VCL = large-VCL)
Inferior pubic ramus length	12–14	AQ < VCL (small-VCL = large-VCL)
Pubic symphysis length	13–14	AQ < VCL (small-VCL = large-VCL)
Ilium length	1–9	VCL < AQ (small-VCL = large-VCL)
Lower iliac height	5–11	large-VCL < small-VCL < AQ
Lower ilium cross-sectional area	area formed by L3, 7, 17	AQ < small-VCL < large-VCL
Ilium width	1–4	AQ < small-VCL < large-VCL
Ischium length	11–12	VCL < AQ (small-VCL = large-VCL)
Acetabulum diameter	9–10	AQ < large-VCL < small-VCL
Geometric mean of pelvic size		
Pelvic length	ilium length + ischium length	
Pelvic breadth	twice the distance between L1 and sagittal plane formed by L13, 14, 18	
Pelvic depth	13–18	

[a]Predictions for each locomotor mode are based on known differences in substrate reaction forces during experimental studies of locomotion. Average peak vertical forces encountered during locomotion: AQ, 0.5-0.8 times body weight (Schmitt and Hanna, 2004; Franz et al., 2005; Hanna et al. 2006); VCL, 5.0–14.0 times body weight (Demes et al., 1999). Predictions are for each shape variable (linear measure/geometric mean).

animal may change its momentum by altering its moment of inertia (Dunbar, 1988), which is accomplished by moving the limbs and/or tail.

During the landing phase of leaping, the lower limb causes deceleration of the body. Hindlimb length is directly proportional to the time required for landing; longer limbs provide more time for deceleration and consequently act to prevent injury from landing with high velocity (Peters and Preuschoft, 1984). The hindlimbs land first, followed by the forelimbs (Demes et al., 1996).

Body size has considerable effects on velocity and takeoff forces; small-bodied vertical clingers and leapers have absolutely short hindlimbs that reduce the distance and time over which acceleration is attained (Alexander, 1995; Preuschoft et al., 1996) and experience relatively larger substrate reaction forces as a result (Demes et al., 1995, 1999), while large-bodied vertical clingers and leapers have less muscle force available for acceleration due to the negative allometry of skeletal muscle (Preuschoft et al., 1996) and have longer hindlimbs that increase the time and distance available for acceleration. As a result of these morphological and physiological factors, large vertical clingers and leapers experience relatively lower substrate reaction forces than small VCL taxa (Demes et al., 1995, 1999). Although landing forces are somewhat smaller than takeoff forces in vertical clingers and leapers (Demes et al., 1995, 1999), both are an order of magnitude larger than reaction forces in quadrupedal taxa.

ADAPTIVE HYPOTHESES

The differences in locomotor loading regimes outlined above should be reflected by differences in strepsirrhine pelvic morphology. Because the pelvis must resist stresses associated with locomotion, it should exhibit adaptations to resist stresses in taxa that encounter larger forces (either due to body size or substrate) and should provide muscle leverage to resist joint moments. Hypotheses regarding nine pelvic dimensions were tested here, and each hypothesis will be reviewed below subsequent to a brief discussion of the different categories under which each hypothesis falls. The typical sub-

strate reaction forces, requirements of muscular force generation, and typical postural features (e.g., pronograde vs. orthogrady) of each locomotor group are considered simultaneously to derive predictions of pelvic shape. The rationale for specific predictions for arboreal quadrupeds, small-bodied vertical clinger and leapers, and large-bodied vertical clinger and leapers is given in the text and summarized in Table 1. Vertical clinger and leapers were divided into small- and large-bodied subgroups because they have been shown to differ in both muscle morphology (Demes et al., 1998) and locomotor kinetics and kinematics (Dunbar, 1988; Demes et al., 1995, 1996) as explained above.

Joint Moment Resistance

Bony levers act as sites of muscle attachment and are directly related to muscle moment arms. As a result, the lengths of these levers should vary according to the mechanical requirements of each locomotor mode; lever lengths should increase to facilitate behaviors that must generate or sustain large forces. Pelvic traits likely to vary according to muscle requirements are: superior pubic ramus length, inferior pubic ramus length, ilium length, ilium width, and ischium length.

Stress Resistance

Elements of the pelvis that are likely load-bearing should differ in their size or cross-sectional area among locomotor groups according to differences in loading. Pelvic struts that are exposed to large loads during locomotion should have relatively larger cross-sectional areas than those that are not. This expectation is related to the necessity of bones to resist stresses incurred during locomotion; large forces require a larger area to provide resistance to stress. This hypothesis is supported by studies of long bone cross-sectional geometry that have shown that bone strength is related to typical load (i.e., bone shaft diameter and/or cortical thickness increases in relation to applied load) (e.g., Schaffler et al., 1985; Demes and Jungers, 1993; Jungers et al., 1998; Ruff, 2002, 2003; Carlson, 2005; Shaw and Stock, 2009). An additional way of resisting stress is to shorten the

distance over which stresses can be applied (i.e., shorten the bony lever). Pelvic traits likely to reflect stress resistance are pubic symphysis length, lower iliac height, acetabulum diameter, and lower ilium cross-sectional area.

3D Pelvic Shape

Overall three-dimensional pelvic shape should vary in a consistent way among locomotor categories. This broad hypothesis assumes that variation in pelvic shape due to locomotion will reflect pelvic morphotypes for each locomotor category. While phylogenetic and developmental constraints make identification of clearly defined morphotypes unlikely, the mechanical requirements of locomotion do vary among locomotor categories, and general pelvic shape should also vary. Similarities in 3D pelvic shape will be explored using GM, and are not subjected to *a priori* hypothesis-testing because there is not currently a mechanical rationale for how total shape should differ across animals that experience different loading regimes.

Specific Predictions for Each Univariate Pelvic Measure

Superior pubic ramus length and inferior pubic ramus length. The length of the pubic rami in mammals has been related to obstetric requirements [wherein the pubic rami increase pelvic breadth to allow the passage of a fetus (Rosenberg, 1988, 1992)] and only tangentially associated with locomotor function. However, Howell (1944) suggested that cursorial quadrupeds, who limit hindlimb movement to the parasagittal plane, have short pubic rami because these animals do not rely on hindlimb adduction during locomotion. In a study on prosimian pelves, Anemone (1993) also stated this hypothesis, but suggested that there may be other (currently unexplored) factors affecting pubic rami length in vertical clingers and leapers such as body size and the mechanics of clinging postures, but there is no clear working hypothesis relating these parameters to pubic rami length. On the basis of the Howell's (1944) hypothesis, the current study predicts that because arboreal quadrupeds are the most cursorial taxa studied here, they will have shorter rami than both vertical clingers and leapers, but there will be no difference between the non-cursorial small and large bodied VCL taxa.

Pubic symphysis length. Badoux (1974), Kummer (1975), and Pauwels' (1980) models of pelvic mechanics predict that the pubic symphysis is loaded in tension during stance phase. The magnitude of tension at the pubic symphysis is related to the magnitude of the substrate reaction force; as SRF increases, so too will the tensile load on the symphysis. Experimental studies have demonstrated that average SRF encountered during species-typical locomotion differs across locomotor groups as described above. The SRF in arboreal quadrupeds is less than one body weight unit (∼0.5–0.8 times body weight, Schmitt, 1998, 2003; Schmitt and Hanna, 2004; Franz et al., 2005), while SRF in vertical clingers and leapers ranges from 5 to 14 times body weight (Demes et al., 1995, 1999). This study predicts that the

pubic symphysis will be longest in VCL taxa and shortest in AQ species.

Ilium length. Various muscles find their origins along the length of the Ilium (measured here as the distance between the anterior superior iliac spine and the cranial aspect of the acetabulum). Ventrally, the iliopsoas attaches to the iliac fossa, while dorsally the lesser gluteal muscles attach to the iliac blade. The iliopsoas is a hip flexor, the lesser gluteals are hip extensors, and both of these muscle groups are quite active during quadrupedalism. Although *in vivo* data on muscle activation patterns are not available for vertical clingers and leapers, it is likely that these muscles are not involved in force generation of the hindlimb (in the hip, muscle forces are instead generated by the ischiocrural muscles and the quadriceps, Demes et al., 1998). Increasing ilium length increases the moment arm of the hip extensors and flexors (which is advantageous during quadrupedalism). Therefore, this study predicts that arboreal quadrupeds will have longer ilia than vertical clingers and leapers.

Lower iliac height and lower ilium cross-sectional area. The region of the lower ilium between the sacroiliac joint and the center of the hip joint transmits forces from the hindlimb to the trunk that occur during loading (Dalstra and Huiskes, 1995). Although this region is subjected to compressive loading in the coronal plane (Badoux, 1974; Kummer, 1975; Pauwels, 1980), it experiences dorsoventral bending in the sagittal plane (Badoux, 1974). Shortening this region helps resist bending stresses. Thus, species that experience large substrate reaction forces should have the shortest lower ilium, and the cross-sectional area of the lower ilium should increase in size when under greater loading. Independent of substrate reaction forces, large-bodied taxa should have relatively shorter lower ilia due to the increased gravitational forces due to body weight. This study predicts that vertical clingers and leapers will have shorter lower ilia with larger cross-sectional areas than arboreal quadrupeds. Large VCL taxa should have shorter lower ilia and larger cross-sectional areas than small VCL taxa because of the increased forces resulting from larger body size.

Ilium width. The width of the cranial aspect of the ilium (here the distance between the superior iliac spines) accommodates the attachment of the erector spinae muscles and the gluteal muscles, which extend the spine and hindlimb, respectively. The erector spinae attach to the cranial aspect of the ilium, sometimes restricted to the region of the iliac tuberosity, and in other species continuing laterally along the iliac crest. In quadrupeds, these muscles give flexibility to the spine, especially in the lumbar region. In the vertical clingers and leapers, who are primarily orthograde, the muscles likely act to maintain verticality of the spine. Increasing the width of the ilium thus increases the area of attachment for these extrinsic muscles of the spine. The gluteal muscles function to extend the thigh in both forms of locomotion. Thigh extension is an important component of leaping in large-bodied vertical clingers and leapers. This study predicts that vertical

TABLE 2. Sampled strepsirrhine taxa (N = 180)

Taxon	♀	♂	Unknown	Total N	Wild	Captive[a]	Locomotion[b]	Collection[c]
Lepilemur mustelinus[d]	12	8		20	18	2	Small-VCL	AMNH, NHM
Indri indri	2	2	3	7	6	1	Large-VCL	AMNH, MNHN, NHM
Propithecus verreauxi[e]	6	9	19	34	31	3	Large-VCL	AMNH, BMOC, FMNH, MNHN
Eulemur fulvus	12	4	6	22	19	3	AQ	AMNH, MNHN, NHM
Hapalemur spp.[f]	6	3	7	16	12	4	Small-VCL	AMNH, FMNH, MNHN, NHM, NMNH
Varecia variegata	2	5	7	14	6	8	AQ	AMNH, FMNH, MNHN
Daubentonia madagascariensis	2	4	2	8	8		AQ	MNHN, NHM
Galago senegalensis	10	15	5	30	16	14	Small-VCL	AMNH, FMNH, MNHN, NHM, NMNH
Otolemur crassicaudatus	6	23		29	14	15	AQ	AMNH, FMNH, NHM, NMNH

[a]Includes wild-shot/captive-raised, captive, and specimens of unknown rearing.
[b]AQ: arboreal quadruped, VCL: vertical clinger and leaper.
[c]AMNH: American Museum of Natural History, NY, BMOC: Beza Mahafaly Osteological Collection, Madagascar, FMNH: Field Museum of Natural History, Chicago, MNHN: Muséum national d'Histoire naturelle, Paris, NHM: Natural History Museum, London, NMNH: National Museum of Natural History, Washington, DC.
[d]One specimen was recorded as *Lepilemur* spp.
[e]One specimen was recorded as *Propithecus* spp.
[f]All *Hapalemur griseus* except one *H. simus* and one *H.* spp.

clingers and leapers will have wider ilia than arboreal quadrupeds due to the requirement of the torso extensors to maintain orthograde postures. Large-bodied vertical clingers and leapers should have wider ilia than small VCL taxa to compensate for the negative allometry of muscle mass with body mass.

Ischium length. The ischium provides attachment for the ischiocrural muscles (i.e., hamstrings) that extend the hip and flex the knee. Increasing the length of the ischial lever increases the moment arm of the ischiocrural muscles. Quadrupeds should have longer ischia than vertical clingers and leapers because the former rely on strong hip extension during walking and running while VCL taxa rely more on the quadriceps for knee extension. Although hip extension is an important component of vertical clinging and leaping (Demes et al., 1996), the vertical takeoff posture in combination with large femoral angular excursion requires the ischium to project dorsally from the hip joint and does not necessitate an increase in ischium length (Fleagle and Anapol, 1992). This study predicts that arboreal quadrupeds will have longer ischia than vertical clingers and leapers.

Acetabulum diameter. The femoroacetabular joint distributes forces due to loading across the lunate articular surface. Species that encounter large hindlimb substrate reaction forces should have relatively larger acetabulum dimensions. This study predicts that vertical clingers and leapers will have a larger acetabulum diameter than arboreal quadrupeds; small VCL species will have larger acetabulae than large VCL species.

For each pelvic variable, rejection of the null-hypothesis will occur if the predicted directional difference between arboreal quadrupeds and vertical clingers and leapers is upheld. Null hypotheses will not be rejected if small and large bodied vertical clingers and leapers differ from each other in unpredicted ways because there are limited experimental data available regarding the magnitude of difference in locomotor kinetics between small and large VCL species upon which these predictions are based.

MATERIALS AND METHODS
Taxonomic and Landmark Samples

Eighteen three-dimensional landmarks were collected on 180 adult os coxae from nine lemuriform strepsirrhine taxa using a Microscribe G2X digitizer (Tables 2, 3, Fig. 3). The majority of specimens were wild-shot, but where necessary samples were supplemented with specimens of unknown or captive rearing (Table 2). Taxa were chosen to represent the diversity of locomotor modes and body sizes that exist within strepsirrhines. The sample includes small- and large-bodied vertical clingers and leapers (hereafter referred to as small-VCL and large-VCL) and arboreal quadrupeds (AQ). The species measured here are relatively small among primates; the smallest species is *Galago senegalensis* (species average 0.21 kg, Smith and Cheverud, 2002) and the largest included here is *Indri indri* (species average 6.34 kg, Smith and Jungers, 1997). Locomotor category was determined as the form of locomotion in which the species is reported to spend the highest proportion of time.

Although Type I landmarks (defined as the meeting of separate structures, *sensu* Bookstein 1991) are preferable in GM studies, the pelvis consists mostly of Type II (based on maxima and minima) and Type III landmarks (those dependent on the position of another landmark). The landmarks used here are a mix of the three types, with a majority of Types II and III (Table 3). Landmarks were usually collected on the right os coxa, but when it was unavailable, antimeres of the landmarks on the left side of the pelvis were used.

Landmark Measurement Error

The procedure for calculating measurement error associated with these methods is explained in detail in Lewton (2012) and follows McNulty (2005). Briefly, Lewton (2012) sampled five individuals from five species (from an expanded sample of primates) to calculate

TABLE 3. 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 *m. sartorius*.	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 *m. rectus femoris*.	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
18	Superior promontory	The ventral-most point on the midline of the sacral promontory.	II

[a]From Tague, 2005

measurement error both across species and across landmarks. A complete landmark configuration was collected twice for each specimen. The mean value of the two replicates for each landmark was calculated, and the deviations from individual landmark replicates to the mean (i.e., Euclidean distances from replicates to the landmark mean) were calculated. The mean deviation of each replicate was scaled by the distance between the landmark mean and specimen centroid to derive percent error. Mean landmark error across species is 0.32 mm and mean percent error is 1.62% (Lewton, 2012).

Univariate Methods

Linear pelvic dimensions were derived from Euclidean interlandmark distances (Table 1). Mosimann shape variables (i.e., ratio of morphometric variable to size measure, Mosimann, 1970; Darroch and Mosimann, 1985; Jungers et al., 1995) were created to account for differences in body size across species. While some have argued against the use of ratios as data because of their supposed tendency toward non-normality (Albrecht, 1978; Atchley, 1978; Atchley and Anderson, 1978; Albrecht et al., 1993, 1995), ratios are a favorable form of data because they retain important information about allometry and are readily interpretable (Jungers et al., 1995). Although body mass is the most intuitive measure

of overall body size, these data are not available for the majority of museum specimens. Instead, the most commonly used proxy for overall body size is the geometric mean of several measures that reflect overall size (e.g., Mosimann, 1970; Jungers et al., 1995; Gordon et al., 2008). In this case, the geometric mean was chosen to represent overall pelvic size and is the third root of the product of pelvis length (the sum of ilium length and ischium length), width (bi-iliac breadth), and depth (anteroposterior diameter). The resulting shape variables (measure/geometric mean) were used in subsequent statistical analysis of species means.

The scaling relationships between pelvic measures and size were examined using phylogenetic reduced major axis regression (pRMA) in the "phytools" package (Revell, 2012) in R (R Development Core Team, 2013), which accounts for phylogenetic non-independence of observations. The phylogeny used here is derived from GenBank data and obtained from the 10kTrees project (version 3, Arnold et al., 2010). The regression was performed on species means of each ln-variable on ln-geometric mean, and an hypothesis of isometry was tested.

To assess adaptive hypotheses of each pelvic dimension, shape variables were analyzed using simulation-based phylogenetic analyses of variance (pANOVA) in the "phytools" R package (Revell, 2012). Individual pANOVAs were performed for each shape variable, with
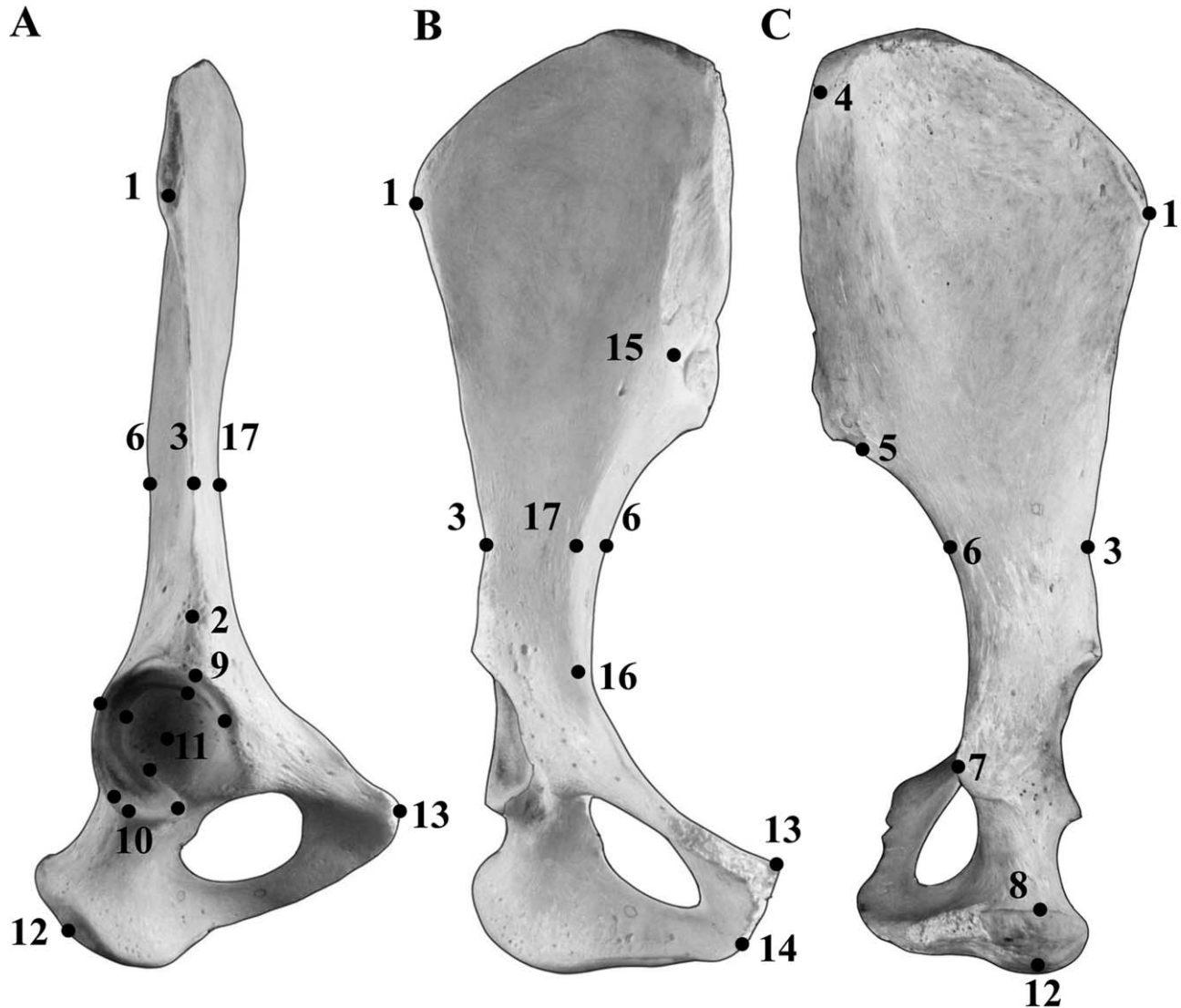
Fig. 3. Locations of 3D landmarks in (**A**) lateral, (**B**) ventral, and (**C**) dorsal views. Some landmarks are shown in multiple views, landmark 18 (sacral promontory) is not shown here. See Table 3 for landmark definitions.

locomotor category as the factor with three levels (AQ, small-VCL, large-VCL). Distributions of the F-statistic were generated using 1,000 simulations of character evolution along the phylogeny (Garland et al., 1993; Revell, 2012). When the F test was statistically significant, *post hoc* multiple comparisons among groups were performed and P values were corrected for multiple tests using the Holm method (1979). Group differences were visualized using boxplots.

Multivariate Geometric Morphometric Methods

To assess the hypothesis that overall 3D pelvic shape differs according to locomotion, all specimens with complete landmark configurations were included in GM analyses ($N = 170$). Landmarks were rotated, translated, and scaled using generalized procrustes analysis to remove the effects of size and other non-shape parame-

ters (Rohlf and Slice, 1990; Goodall, 1991; Dryden and Mardia, 1998) using *morphologika2* (O'Higgins and Jones, 2006). A standard principal component analysis (PCA) of Procrustes coordinates was conducted to identify individual measures that influence differences in overall pelvic shape across locomotor groups. Although the taxa in the PCA are not statistically independent observations due to phylogenetic relatedness (Felsenstein, 1985; Harvey and Pagel, 1991), a PCA that accounts for phylogeny (pPCA) was not used here due to a recent critique of its efficacy in studies of adaptation (Polly et al., 2013). Instead, the phylogeny was mapped onto the standard PCA plot using MorphoJ to visualize the effects of phylogeny on pelvic morphology in morphospace (Klingenberg, 2011). Eigenvalues were then examined to investigate the proportion of shape variance described by each principal component, and variation in shape was assessed by bivariate plots of taxon-mean

TABLE 4. Summary statistics for standardized pelvic measures (mean and standard deviation)

Pelvic measure	Lepilemur mustelinus		Indri indri		Propithecus verreauxi		Eulemur fulvus		Hapalemur spp.		Varecia variegata		Daubentonia madagascariensis		Galago senegalensis		Otolemur crassicaudatus	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Superior pubic ramus length/GM	0.356	0.030	0.382	0.039	0.399	0.023	0.412	0.016	0.426	0.033	0.414	0.016	0.470	0.044	0.497	0.043	0.511	0.029
Inferior pubic ramus length/GM	0.418	0.033	0.319	0.041	0.341	0.054	0.447	0.040	0.462	0.053	0.492	0.035	0.555	0.058	0.538	0.059	0.569	0.055
Pubic symphysis length/GM	0.197	0.029	0.361	0.054	0.285	0.048	0.259	0.032	0.200	0.031	0.232	0.025	0.354	0.019	0.231	0.035	0.277	0.038
Ilium length/GM	0.909	0.043	0.806	0.037	0.783	0.030	0.864	0.033	0.842	0.057	0.923	0.037	0.900	0.074	1.018	0.058	0.988	0.038
Lower iliac height/GM	0.593	0.038	0.453	0.039	0.474	0.032	0.568	0.032	0.548	0.032	0.600	0.054	0.552	0.037	0.748	0.066	0.672	0.045
Lower ilium cross-sectional area/GM[a]	0.060	0.011	0.112	0.007	0.107	0.013	0.072	0.006	0.072	0.017	0.075	0.006	0.077	0.008	0.065	0.013	0.078	0.009
Ilium width/GM	0.291	0.040	0.463	0.029	0.444	0.032	0.336	0.025	0.359	0.038	0.309	0.026	0.312	0.058	0.322	0.032	0.332	0.036
Ischium length/GM	0.397	0.023	0.390	0.014	0.368	0.017	0.419	0.019	0.393	0.024	0.430	0.015	0.549	0.037	0.338	0.031	0.379	0.019
Acetabulum diameter/GM	0.239	0.021	0.315	0.025	0.270	0.020	0.235	0.013	0.211	0.016	0.273	0.029	0.300	0.021	0.315	0.037	0.309	0.016

[a]Square root of LICSA/GM.

principal component scores. The consensus shapes described by the principal component axes were visually examined to understand the shape changes of groups in morphospace. The association between pelvic shape and size was examined using a phylogenetic generalized least squares regression (PGLS) of each PC score on ln-centroid size (i.e., square root of the sum of squared distances of each landmark to the specimen centroid). Locomotor group differences in principal component scores were investigated using pANOVA, and *post hoc* comparisons among locomotor groups were performed as with the univariate data.

RESULTS

Univariate

Summary statistics for each shape variable (linear measure/geometric mean) are given for each species in Table 4. Scaling relationships for each ln-variable on ln-geometric mean are given in Table 5. All but two variables scale isometrically; pubic symphysis length and LICSA scale with positive allometry.

The pANOVA on each shape variable indicates that there are statistically significant differences according to locomotion in inferior pubic ramus length, ilium width, and lower ilium cross-sectional area (Table 6). There were no differences due to locomotor category for the remaining six variables and will not be discussed further. The F tests for pubic symphysis length and lower iliac height were near statistical significance at $P = 0.06$ and 0.08, respectively.

Inferior pubic ramus length. Arboreal quadrupeds have significantly longer inferior pubic rami than large-bodied vertical clingers and leapers $(P = 0.01$, Table 7, Fig. 4), but are not significantly different from small vertical clingers and leapers. This result is in the opposite direction than predicted (prediction: AQ < VCL).

Ilium width. Large vertical clingers and leapers have significantly wider ilia than both arboreal quadrupeds $(P = 0.003)$ and small leapers $(P = 0.004$, Table 7, Fig. 4). This result partially supports the prediction that AQ < small-VCL < large-VCL. Large vertical clingers and leapers do have the widest ilia, but the null hypothesis of no difference between arboreal quadrupeds and small vertical clingers and leapers was not rejected.

Lower ilium cross-sectional area. All three locomotor groups are statistically different from each other in lower ilium cross-sectional area, but this appears to be due to size and not locomotor behavior. Small leapers have the smallest LICSA, arboreal quadrupeds are intermediate in size, and large leapers have much larger ilium cross-sections than the other two groups (*post hoc P* values in Table 7, Fig. 4). Like the ilium width result, the LICSA null hypothesis was rejected and the predictions (AQ < small-VCL < large-VCL) are partially supported, but only in the relationships between large-VCL and the other two groups.

The results of univariate hypothesis-testing of pelvic adaptations to locomotion are mixed. In general, the data failed to reject the null adaptive hypotheses, rendering specific predictions unsupported. There is partial support for hypotheses of adaptation for ilium width and

TABLE 5. Phylogenetic reduced major axis regression results for the test of isometry[a]

Variable	r	Slope	P	Isometry rejected?
Superior pubic ramus length	0.97	1.00	0.96	No
Inferior pubic ramus length	0.90	0.97	0.84	No
Pubic symphysis length	0.95	1.54	0.006	Yes: positive allom.
Ilium length	0.98	0.93	0.34	No
Ilium width	0.95	1.25	0.11	No
Lower iliac height	0.95	0.81	0.10	No
Ischium length	0.97	1.19	0.10	No
Acetabulum diameter	0.95	1.19	0.17	No
Lower ilium cross-sectional area	0.96	3.00	0.005	Yes: positive allom.

[a]Regressions of each ln-variable on ln-geometric mean. For all linear measures, slope of isometry is 1. Because LICSA is an areal measure, its slope of isometry is 2. r is phylogenetic correlation.

TABLE 6. Phylogenetic ANOVA results

Variable	F	P value
Superior pubic ramus length	0.89	0.436
Inferior pubic ramus length	8.15	**0.020**
Pubic symphysis length	4.26	0.056
Ilium length	3.07	0.111
Ilium width	25.78	**0.002**
Lower iliac height	3.54	0.075
Ischium length	1.61	0.262
Acetabulum diameter	0.56	0.582
Lower ilium cross-sectional area	70.20	**0.001**

Bold indicates statistical significance at $P < 0.05$.

TABLE 7. Post hoc comparisons of inferior pubic ramus length, ilium width, and lower ilium cross-sectional area among locomotor groups

Inferior pubic ramus length			
	AQ	Small-VCL	Large-VCL
AQ		1.06	4.01
Small-VCL	0.32		−2.92
Large-VCL	**0.012**	0.064	
Ilium width			
	AQ	Small-VCL	Large-VCL
AQ		−0.11	−6.69
Small-VCL	0.93		6.26
Large-VCL	**0.003**	**0.004**	
Lower ilium cross-sectional area			
	AQ	Small-VCL	Large-VCL
AQ		3.05	−9.45
Small-VCL	**0.02**		11.52
Large-VCL	**0.003**	**0.003**	

P values under the diagonal, t statistics above the diagonal. Bold denotes significance at $P < 0.05$.

lower ilium cross-sectional area, but the results do not fully support the predictions that are derived from our current understanding of pelvic and locomotor biomechanics.

Multivariate Geometric Morphometrics

Principal component analysis. The PCA results illustrate the phylogenetic and functional influences on pelvic shape. The lemur phylogeny is mapped onto a bivariate plot of species means for PCs 1 and 2, which shows little overlap among locomotor modes (Fig. 5). Arboreal quadrupeds, small vertical clingers and leapers, and large vertical clingers and leapers plot in distinct areas of morphospace, with slight overlap of the AQ taxon *Otolemur* with the small-VCL group. Taxon locations in morphospace are related to both their phylogenetic relationships and their similarities in locomotor pattern. For example, *Otolemur* groups closest to its vertical clinging and leaping sister taxon (*Galago senegalensis*) and not with the other arboreal quadrupeds. On the other hand, while *Lepilemur* spp. is the sister group to the indriids, they plot far apart, perhaps because *Lepilemur* is a small-bodied vertical clinger and leaper, while indriids are large-bodied. This difference is likely related to the known differences in leaping biomechanics between small-bodied leapers (i.e., foot-powered leapers) and large-bodied leapers (i.e., thigh-powered leapers, Demes et al., 1996, 1998).

The results of the phylogenetic generalized least squares analysis are listed in Table 8. Of the first five principal components, PC1 is the only one that is significantly correlated with ln-centroid size ($r = 0.73$,

$P = 0.03$). Size increases on PC1 correspond to shorter ischiopubic rami, longer pubic symphysis, larger acetabulum, a longer ischium, and a shorter lower ilium. Together, these features contribute to a more robust pelvis with a wide ilium and square-shaped ischiopubis in large bodied strepsirrhines, while smaller taxa have a more rectangular ischiopubis and slender, longer ilium.

While the pelvic shapes associated with changes in PC1 are largely related to body size (see above), differences along PC2 appear to be more related to differences in locomotor mode. Arboreal quadrupeds plot largely on the negative end of PC2 while both groups of vertical clingers and leapers plot on the positive end of PC2 (note that the sign of principal component scores is arbitrary and are only described here for ease of reference). Mean pelvic shapes on the negative end of PC2 have long ischia, long pubic symphyses, small acetabulae, and are more robust overall (the AQ lemurids). Mean pelvic shapes on the positive end of PC2 have short ischia, short pubic symphyses, large acetabulae, and are more slender overall (the galagids).

Phylogenetic ANOVA. The phylogenetic ANOVA results are listed in Table 8. Pelvic shape differs according to locomotor category for the first PC only ($F = 11.8$, $P = 0.002$). *Post hoc* tests reveal that large vertical
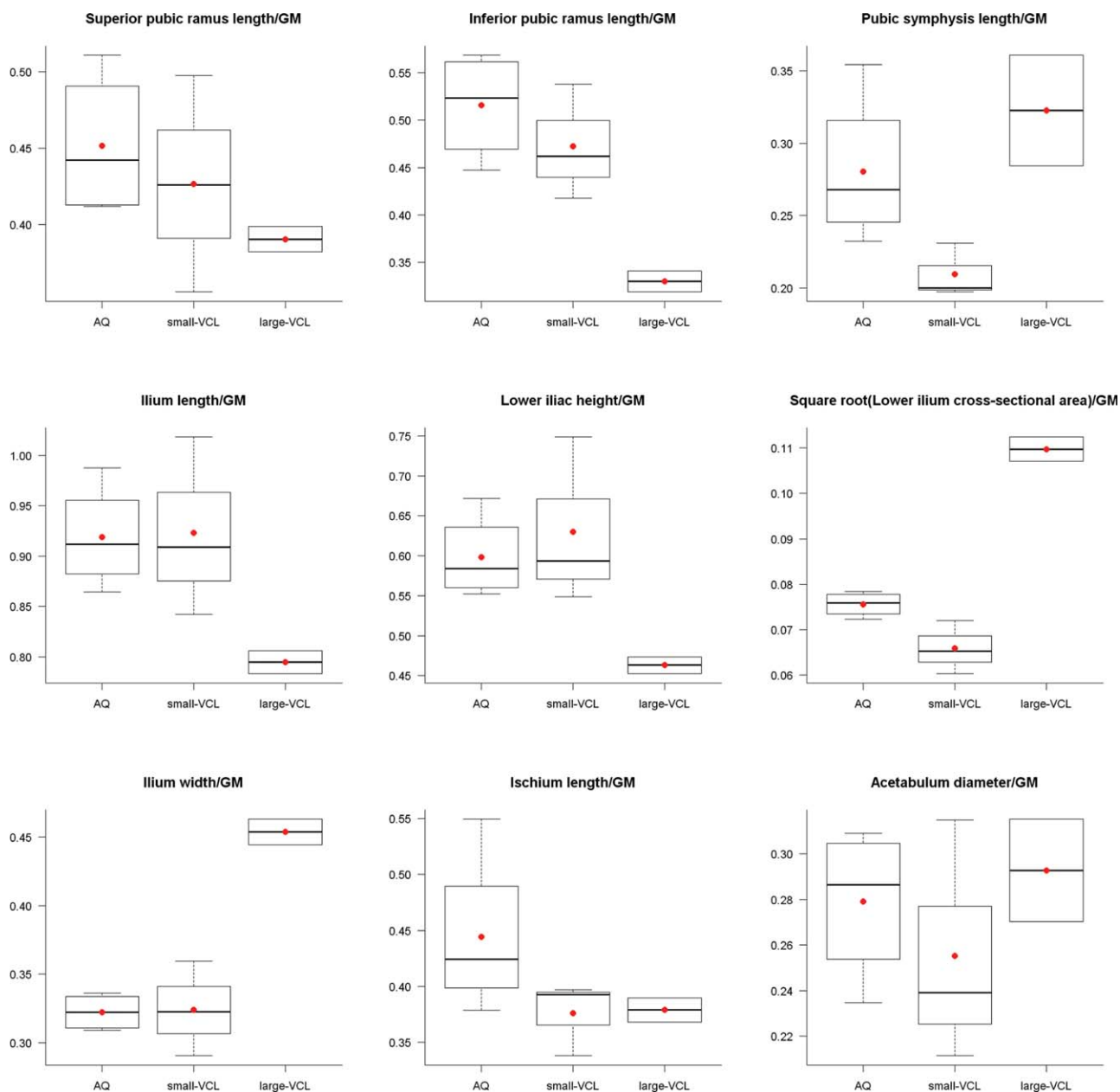
Fig. 4. Boxplots of the nine shape variables by locomotor category. Horizontal lines in boxes are medians, red dots are means. AQ: arboreal quadruped, small-VCL: small vertical clinger and leaper, large-VCL: large vertical clinger and leaper.

clingers and leapers are significantly different from small-VCL and arboreal quadrupeds in overall pelvic shape. Taken together with the PGLS results, this difference in pelvic shape along the first principal component is driven by body size differences in these taxa.

DISCUSSION

The pelvic girdle is a complex three-dimensional structure and its shape has historically been difficult to capture using univariate methods. Quantitative studies of its overall form have been few, and those have not focused on the aspects of shape that are thought to be related to the mechanical requirements of locomotion. The goals of this study were two-fold: to test adaptive hypotheses relating aspects of pelvic shape to a model of pelvic mechanics derived from the work of Badoux (1974), Kummer (1975), and Pauwels (1980), and to relate pelvic form as a whole to locomotor function using GM methods.

Although many of the adaptive hypotheses were unsupported, the combination of univariate and multivariate GM analyses used here is critical to differentiating features that appear to be related to pelvic and
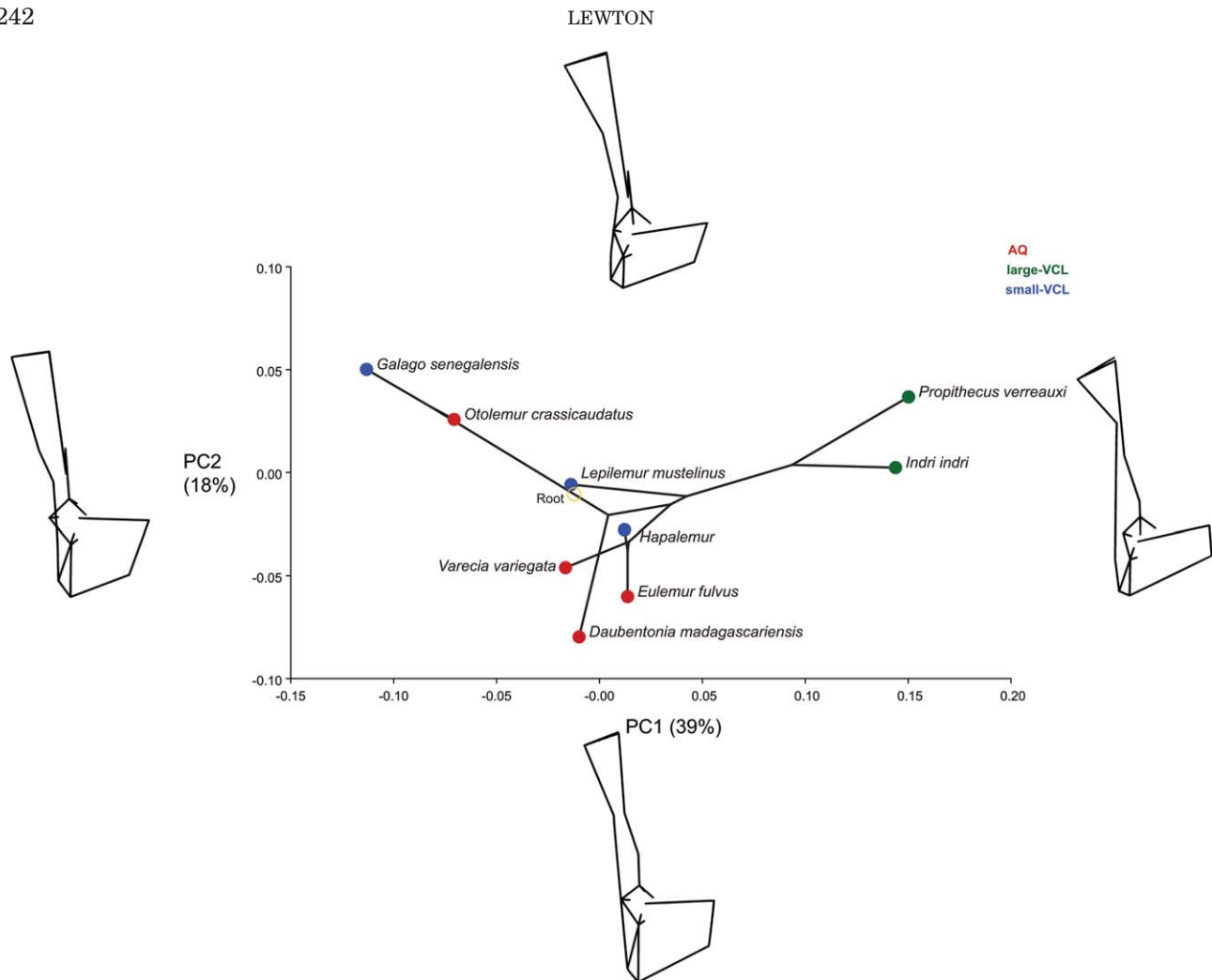
Fig. 5. Bivariate plot of species means of principal components 1 and 2. The phylogeny is mapped onto the plot to demonstrate the effect of phylogeny on species' location. Red: arboreal quadrupeds, blue: small vertical clingers and leapers, green: large vertical clingers and leapers. Wireframe models (generated from morphologika2, O'Higgins and Jones, 2006) demonstrate mean shapes at the ends of each principal component axis.

TABLE 8. Phylogenetic ANOVA and GLS results

Principal component (% variance summarized)	Phylogenetic ANOVA		Phylogenetic GLS regression	
	F	P value	r	P value
1 (39%)	11.81	**0.002**	−0.73	**0.025**
2 (18%)	1.76	0.253	−0.4	0.28
3 (6.9%)	2.60	0.127	−0.49	0.18
4 (5.7%)	0.26	0.801	−0.24	0.53

locomotor mechanics as we currently understand them, and traits that do not vary as predicted by current mechanical models. Furthermore, this study highlights the need for continued inquiry into the basic mechanics of the pelvic girdle and how pelvic structure responds to loads that occur *in vivo* during positional behaviors. Aspects of pelvic shape that do not vary as predicted are likely influenced by the effects of body size and scaling,

phylogeny, and other aspects of pelvic function including obstetrics and the coupling of the pelvis and torso. Until these varied facets of pelvic form are examined in an integrative manner, our understanding of the effects of locomotor requirements on pelvic shape will remain limited.

Nine measures of pelvic shape were examined here and predictions were made based on the typical substrate reaction forces that are incurred during locomotion, the scaling principles that act on the musculoskeletal system, and optimization criteria of pelvic levers and cross-sections. Most of these adaptive predictions were not supported. Only three of these measures exhibited significant differences according to locomotor category: inferior pubic ramus length, lower ilium cross-sectional area, and ilium width. Pubic symphysis length and lower iliac height exhibit trends toward differences across groups. The remaining four measures (superior pubic ramus length, ilium length, ischium length, and acetabulum diameter) did not

exhibit significant differences across locomotor categories.

Geometric morphometric analyses augmented the univariate analyses by corroborating the univariate results and also by adding novel information about aspects of pelvic shape that did not have *a priori* mechanical predictions. The results of GM analyses support the univariate results by identifying the same traits as driving differences across groups, but they also suggest some differences in ischiopubic shape across locomotor groups that were not detected by the testing of linear measures alone.

Locomotor-based Variation in Pelvic Dimensions

This study is the first to rigorously test adaptive hypotheses relating pelvic anatomy to locomotion using predictions derived from a model of pelvic mechanics, and builds on an existing foundation of pelvic functional morphology (e.g., Jenkins and Camazine, 1977; Ward, 1991; Fleagle and Anapol, 1992; Anemone, 1993; Ward, 1993; Ruff, 1995; MacLatchy, 1998). Of the three measures for which the null adaptive hypothesis was rejected, two of these [lower ilium cross-sectional area (LICSA) and ilium width] partially support the predictions.

Lower ilium cross-sectional area. It was predicted that LICSA would be smallest in arboreal quadrupeds and largest in large vertical clingers and leapers. While there were significant differences among all three locomotor categories, the direction of differences differed slightly from predicted. Large vertical clingers and leapers do indeed have the largest LICSA relative to pelvis size, but the smallest LICSA is actually observed in small vertical clingers and leapers, and not in arboreal quadrupeds (Fig. 4). In general, the pattern observed here indicates that the smallest species have small LICSA and the largest species have large LICSA.

This pattern of difference in LICSA dimensions has multiple implications. It may suggest that locomotor forces interact with body size in currently unknown ways. An additional possibility is that pelvic and hindlimb musculature modulates the forces that are placed upon the bony pelvis, thereby "protecting" the bony girdle from experiencing the full impact of large loads. The latter explanation has some support in finite element studies of the human pelvic girdle. Dalstra and Huiskes (1995) found that a finite element model of the human pelvis that includes the contribution of muscle forces results in lower bone strains than a model that excludes muscular information. This simulation study suggests that muscles may act as a buffer to modulate forces that act on the pelvic girdle, but further study using *in vivo* experimental data are needed to confirm this hypothesis. Unfortunately, the collection of *in vivo* data is not feasible due to the invasive nature of disrupting the hip, thigh, and pelvic musculature in order to place the necessary strain gauges directly on the pelvic bones.

The cross-sectional area of the lower ilium appears to be an adaptation to locomotor mechanics, but our current understanding of pelvic mechanics is not sufficient to determine the precise relationship between locomotor forces, body size, and LICSA. However, the results of this study are significant because it is the first quantita-tive evidence to provide preliminary support for the hypothesis that LICSA is a pelvic character that differs according to locomotor loading.

Ilium width. The prediction for ilium width incorporated two components: a prediction based on the requirement for orthogrady in vertical clinging and leaping taxa, and a second prediction based on the requirement in large VCL taxa for powerful hindlimb extension during leaping. There is partial support for the first prediction, and full support for the second. First, large vertical clingers and leapers have the widest ilium, which is significantly wider than both small vertical clingers and leapers and arboreal quadrupeds, as predicted. However, there is no statistical difference between arboreal quadrupeds and small VCL taxa. Thus, there is partial support for the prediction that ilium width in these groups is related to the maintenance of orthogrady. Like LICSA, there appears to be an effect of body size on ilium width that is not fully accounted for by the geometric mean size correction.

There is full support, however, for the second component of the ilium width prediction that large VCL taxa should have wider ilia to facilitate their thigh-powered style of leaping. The relatively narrow ilium in both arboreal quadrupeds and small VCL species decreases the space available for the lesser gluteals, thus indicating less reliance on powerful thigh extension than large vertical clingers and leapers.

Inferior pubic ramus length. Inferior pubic ramus length differs according to locomotion, but the directions of the differences do not support the model predictions. Arboreal quadrupeds have longer inferior pubic rami than large vertical clingers and leapers, which is in the opposite direction than predicted. Howell's (1944) observation that cursorial quadrupeds have (and should have) short pubic rami because hindlimb movements are primarily parasagittal is not supported in this sample of lemuriform primates. There are two general explanations for the observation that arboreal quadrupeds have longer pubic rami than VCL taxa. First, perhaps Howell's hypothesis is more pertinent to primate terrestrial quadrupeds (some, but not all, of whom meet the definition of cursorial) than arboreal quadrupeds. Second, the original hypothesis was presumably not conceived with specialized vertical clinging and leaping behaviors in mind. This hypothesis may well prove to be upheld in other groups of primate quadrupeds and even suspensrhine taxa, but the form of the pubic rami in strepsirrhine VCL taxa may be related to the specialization of this locomotor mode and may have an entirely different functional underpinning. Indeed, Anemone (1993) suggested that clinging to vertical substrates may require short pubic rami, and this hypothesis remains to be investigated.

Non-locomotor Influences on Pelvic Adaptation and Shape

The majority of the pelvic traits tested here (superior pubic ramus length, pubic symphysis length, ilium length, lower iliac height, ischium length, and acetabulum diameter) do not differentiate taxa based on the differing loading regimes of alternate locomotor behaviors,

and the results of this study contradict the hypothesis that they constitute locomotor adaptation to stress resistance or muscle leverage as predicted by the mechanical models used here.

In the multivariate analysis of pelvic form, many of these traits that were not significant in univariate tests of adaptation, in fact do drive differences among locomotor groups and are also strongly correlated with differences in body size. Overall pelvic form is statistically different along principal component 1, with the large vertical clingers and leapers being significantly different from the smaller VCL species and the arboreal quadrupeds. Furthermore, there were obvious ischiopubic shape changes along the size-correlated first principal component that were not evident in the univariate analyses. Specifically, ischiopubic form varies in taxa from a mediolaterally long and rectangular shape in arboreal quadrupeds and small vertical clingers and leapers, to a mediolaterally short and craniocaudally deep square shape in large vertical clingers and leapers. Ilium morphology varies from wide and short in large-bodied lemurs to long and slender in the smaller-bodied species. Shape variation in principal component 1 is statistically correlated with size, suggesting that ischiopubic morphology varies in a systematic manner with body size. Because body size and locomotor behavior are strongly linked within primates (e.g., Fleagle and Mittermeier, 1980), determining whether shape is primarily related to one or the other is difficult. It is likely that there is an interaction effect between body size and locomotion that ultimately shapes pelvic form. Furthermore, some aspects of the pelvis may be more related to forces due to locomotor loading (i.e., lower ilium cross-sectional area), while others may be more related to muscle leverage and allometric scaling (i.e., the ischiopubis).

There are a range of factors that might explain the lack of support found for the univariate hypotheses tested here. First, the fact that the univariate analyses relating ischiopubic shape to locomotor loading were generally unsupported, but the GM analyses uncovered clear differences among locomotor groups, suggests that the mechanical models upon which these predictions are based may be invalid, or that locomotion is not the primary influence on pelvic shape. Second, the locomotor classifications used here may not accurately reflect the mechanics of the behaviors in which these animals engage in life. Third, we have seen that body size and phylogeny clearly have a strong effect on pelvic form. Lastly, in terms of the functional aspects of pelvic shape, locomotion is not the only function that the pelvis must accommodate. The bony pelvis is also a critical component of gestation and birth, and it is linked to torso shape in ways that are unexplored here. These various factors affecting pelvic shape are discussed in more detail below.

Mechanical models. Modeling of pelvic mechanics has not been a major area of study, and the few models that have been proposed—the two-armed lever model and the pelvic ring model—have not received much attention in the literature. Consequently, there has been little work done to evaluate the validity of these models; if current models do not accurately describe the structural mechanics of the pelvic girdle, then the predictions

that have been derived from them will be unsound. A first step in validating these models would be to use experimental studies of *in vitro* strain patterns during loading (although *in vivo* studies would be preferable, these are not feasible with current methods, see above; Lewton, in prep). Coupled with *in vitro* strain data for model validation, finite element analysis is a promising approach to generate hypotheses about patterns of pelvic stress and strain that has shown success in other complex structures such as the skull (e.g., Dumont et al., 2005; Rayfield, 2007; Strait et al., 2009; Ross et al., 2011).

Locomotor classification. Just as there is a need to use simplified models to characterize the mechanics of the pelvis, we must also categorize primate species into coarse locomotor groups. The locomotor classifications used here are based on the locomotor mode in which each species spends the highest proportion of time. It is possible that broad locomotor categorizations such as those used in this study do not accurately reflect the varied behaviors that primates exhibit in their natural environments. Species with more variability in their locomotor repertoires will not be as well described by singular locomotor assignments. This problem of "fuzzy" boundaries between some locomotor categories may result in "noise" in the data that can obscure real functional signals in pelvic variation. This is likely not a problem for the vertical clinging and leaping taxa because they are generally stereotyped in their locomotor behaviors, but it could be problematic for arboreal quadrupeds, a group that could conceivably be broken into smaller groups (e.g., arboreal scramblers, arboreal leapers, springers, etc., Napier and Napier, 1967). However, using more fine-grained categories runs the risk of parsing data to such an extent that it results in a lack of clear functional patterns. Furthermore, the current dataset on locomotor mechanics (kinetics and kinematics of locomotor types) does not encompass a large enough sample of primates to include these narrower categories.

Body size, allometric shape differences, and phylogeny. Body size, locomotor behavior, and phylogeny are all strongly correlated with each other. For example, within primates as a whole, terrestrial quadrupeds tend to be large-bodied catarrhines. Only tarsiers and strepsirrhines are vertical clingers and leapers, and VCL taxa weigh <10 kg. This tight link between size, behavior, and phylogeny makes it difficult to determine the effects of each on shape.

Both the univariate and multivariate GM analyses presented here suggest that pelvic shape is strongly related to body size and scaling, which may in turn be correlated with the forces encountered during locomotion. Aspects of shape that appear to be linked to size are ilium width and length, lower ilium cross-sectional area, and the shape of the ischiopubis. However, scaling analyses presented here suggest that, with two exceptions, the pelvic traits tested herein scale with isometry relative to body size. Thus, the effects of scaling are unlikely to solely account for this study's unsupported predictions.

The univariate analyses used shape variables to account for the effects of body size on pelvic shape. However, another approach that may be more useful would

be to use body size as a covariate in the statistical analysis. An advantage of this method would be its ability to also investigate the interaction effect between body size and locomotor behavior; future work on pelvic shape may benefit from this approach.

The pelvic girdle is a multifunctional system. Adaptive inference in structures that perform multiple functions can prove difficult. The pelvic girdle is a complex and multifaceted structure that facilitates locomotion, gestation, and parturition, anchors tail musculature, supports the abdominopelvic viscera, and constitutes a portion of the torso. These other functions of the pelvic girdle may very well affect our ability to differentiate its locomotor adaptations. Because the other functional roles of the pelvis likely constrain its overall shape, incomplete accordance of pelvic form to the expectations of locomotor function should be expected. One approach to this issue is to test bony function experimentally—for example, to gather *in vivo* data of bone strain during loading—but such studies are difficult to perform on the pelvic girdle because it is enveloped in musculature and viscera. Using *in vitro* experimental methods on cadaver specimens is the next best approach, but has a number of limitations, including the lack of muscular contribution to stress resistance (Lewton, 2010).

Because the pelvis is also part of the torso, its shape will be constrained by the shape of the thorax. That is, the pelvis and the thorax will have approximately similar breadth dimensions (Ward, 1993). There is, then, likely morphological integration between the abdominal and thoracic portions of the trunk, and this is an area of research that is ripe for investigation.

In addition to incorporating the suggestions given above, future work on the association between pelvic shape and locomotion should integrate more experimental research to determine how pelvic bony architecture—both microarchitecture and macroarchitecture—responds to loads, and how muscles act to modulate the forces that act on the pelvic girdle. Furthermore, while form-function patterns have now been examined in strepsirrhines, a study on primate-wide patterns of pelvic shape is needed (and forthcoming, Lewton, in prep).

Toward an Integrative Approach to Studies of Adaptation and Function

Understanding form-function relationships in primate biology is required to identify functional causes of variation across species, and it is a critical step in reconstructing behaviors in the fossil record. There are various approaches to functional morphology, and many include testing *a priori* hypotheses that relate discrete measures of form to function. Although current GM methods can test whether groups under study statistically differ in overall shape, they cannot test directional hypotheses of adaptation. It is for this reason that many current studies of adaptation do not include geometric morphometrics, or that the GM toolkit is only used in preliminary, exploratory examinations of shape change across species. However, GM approaches can provide valuable, novel information to research on adaptation that is not available in conventional studies of individual aspects of shape. The GM results in the current study

provide a more nuanced understanding of the interaction between body size and locomotion in strepsirrhines. Furthermore, GM results indicate new avenues of research, and are instrumental in generating new hypotheses about the functional causes of 3D morphology. There is a salient need for development of new GM methods that can more directly evaluate adaptive tests. Future studies of function should integrate directional tests of adaptive hypotheses with geometric morphometrics to yield results that are more informative than either method alone can provide.

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LITERATURE CITED

Aerts P. 1998. Vertical jumping in *Galago senegalensis*: the quest for an obligate mechanical power amplifier. Phil Trans R Soc 353: 1607–1620.

Albrecht GH. 1978. Some comments on the use of ratios. Syst Zool 27:67–71.

Albrecht GH, Gelvin BR, Hartman SE. 1993. Ratios as a size adjustment in morphometrics. Am J Phys Anthropol 91:441–468.

Albrecht GH, Gelvin BR, Hartman SE. 1995. Ratio adjustments in morphometrics: a reply to Dr. Corruccini. Am J Phys Anthropol 96:193–197.

Alexander RM. 1995. Leg design and jumping technique for humans, other vertebrates and insects. Phil Trans R Soc 347:235–248.

Anemone RL. 1993. The functional anatomy of the hip and thigh in primates. In: Gebo DL, editor. Postcranial adaptation in nonhuman primates. DeKalb: Northern Illinois University Press. p 150–174.

Anthony MRL, Kay RF. 1993. Tooth form and diet in Ateline and Alouattine primates: reflections on the comparative method. Am J Sci 293A:356–382.

Arnold C, Matthews LJ, Nunn CL. 2010. The 10kTrees website: a new online resource for primate phylogeny. Evol Anthropol 19: 114–118.

Atchley WR. 1978. Ratios, regression intercepts, and the scaling of data. Syst Zool 27:78–83.

Atchley WR, Anderson D. 1978. Ratios and the statistical analysis of biological data. Syst Zool 27:71–78.

Baab KL, McNulty KP. 2009. Size, shape, and asymmetry in fossil hominins: the status of the LB1 cranium based on 3D morphometric analyses. J Hum Evol 57:608–622.

Badoux DM. 1974. An introduction to biomechanical principles in primate locomotion and structure. In: Jenkins, FA, editor. Primate locomotion. New York: Academic Press. p 1–43.

Bastir M, Rosas A, Stringer C, Cuétara JM, Kruszynski R, Weber GW, Ross CF, Ravosa MJ. 2010. Effects of brain and facial size on basicranial form in human and primate evolution. J Hum Evol 58:424–431.

Berge C. 1996. The evolution and growth of the hominid pelvis: a preliminary thin-plate spline study of ilium shape. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE, editors. Advances in morphometrics. New York: Plenum Press. p 441–448.

Biewener AA. 2003. Animal locomotion. Oxford: Oxford University Press.

Biewener AA. 2006. Patterns of mechanical energy change in tetrapod gait: pendula, springs and work. J Exp Zool 305A:899–911.

Bookstein FL. 1991. Morphometric tools for landmark data: geometry and biology. New York: Cambridge University Press.

Bouhallier J, Berge C. 2006. Analyse morphologique et fonctionnelle du pelvis des primates Catarrhiniens: consequences pour l'obstétrique. C R Palevol 5:551–560.

Bouhallier J, Berge C, Penin X. 2004. Procrustes analysis of the pelvic cavity in australopithecines (AL 288, Sts 14), humans and chimpanzees: obstetrical consequences. C R Palevol 3:295–304.

Brown KM, Handa VL, Macura KJ, DeLeon VB. 2013. Three-dimensional shape differences in the bony pelvis of women with pelvic floor disorders. Int Urogynecol J 24:431–439.

Bytheway JA, Ross AH. 2010. A geometric morphometric approach to sex determination of the human adult os coxa. J Forensic Sci 55:859–864.

Carlson KJ. 2005. Investigating the form-function interface in African apes: relationships between principal moments of area and positional behaviors in femoral and humeral diaphyses. Am J Phys Anthropol 127:312–334.

Cavagna GA, Heglund NC, Taylor CR. 1977. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am J Physiol Regul Integr Comp Physiol 2:R243–R261.

Cooke SB, Tallman M. 2012. New endemic platyrrhine femur from Haiti: descriptioin and locomotor analysis. J Hum Evol 63:560–567.

Crompton RH, Sellers WI, Gunther MM. 1993. Energetic efficiency and ecology as selective factors in the saltatory adaptation of prosimian primates. Proc R Soc Lond B 254:41–45.

Daegling DJ, McGraw WS. 2001. Feeding, diet, and jaw form in West African *Colobus* and *Procolobus*. Int J Primatol 22:1033–1055.

Dalstra M, Huiskes R. 1995. Load transfer across the pelvic bone. J Biomech 28:715–724.

Darroch JN, Mosimann JE. 1985. Canonical and principal components of shape. Biometrika 72:241–252.

Demes B, Fleagle JG, Jungers WL. 1999. Takeoff and landing forces of leaping strepsirhine primates. J Hum Evol 37:279–292.

Demes B, Fleagle JG, Lemelin P. 1998. Myological correlates of prosimian leaping. J Hum Evol 34:385–399.

Demes B, Franz TM, Carlson KJ. 2005. External forces on the limbs of jumping lemurs at takeoff and landing. Am J Phys Anthropol 128:348–358.

Demes B, Jungers WL. 1993. Long bone cross-sectional dimensions, locomotor adaptations and body size in prosimian primates. J Hum Evol 25:57–74.

Demes B, Jungers WL, Fleagle JG, Wunderlich RE, Richmond BG, Lemelin P. 1996. Body size and leaping kinematics in Malagasy vertical clingers and leapers. J Hum Evol 31:367–388.

Demes B, Jungers WL, Gross TS, Fleagle JG. 1995. Kinetics of leaping primates: influence of substrate orientation and compliance. Am J Phys Anthropol 96:419–429.

Demes B, Larson SG, Stern JT, Jungers WL, Biknevicius AR, Schmitt D. 1994. The kinetics of primate quadrupedalism: "hindlimb drive" reconsidered. J Hum Evol 26:353–374.

Demes B, Qin Y-X, Stern JT, Larson SG, Rubin CT. 2001. Patterns of strain in the macaque tibia during functional activity. Am J Phys Anthropol 116:257–265.

Dryden IL, Mardia KV. 1998. Statistical shape analysis. New York: Wiley.

Dumont ER, Piccirillo J, Grosse IR. 2005. Finite-element analysis of biting behavior and bones stress in the facial skeletons of bats. Anat Rec 283A:319–330.

Dunbar DC. 1988. Aerial maneuvers of leaping lemurs: the physics of whole-body rotations while airborne. Am J Primatol 16:291–303.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Fleagle JG. 1976. Locomotor behavior and skeletal anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Yearb Phys Anthropol 20:440–453.

Fleagle JG, Anapol FC. 1992. The indriid ischium and the hominid hip. J Hum Evol 22:285–305.

Fleagle JG, Mittermeier RA. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. Am J Phys Anthropol 52:301–314.

Flower WH. 1870. On the correspondence between the parts composing the shoulder and pelvic girdles of the Mammalia. J Anat Physiol 4:239–245.

Franz TM, Demes B, Carlson KJ. 2005. Gait mechanics of lemurid primates on terrestrial and arboreal substrates. J Hum Evol 48:199–217.

Freedman RA, Young HD. 2003. University physics. Pearson: Addison-Wesley.

Garland TG, Jr, Dickerman AW, Janis CM, Jones JA. 1993. Phylogenetic analysis of covariance by computer simulation. Syst Biol 42:265–292.

Gonzales PN, Bernal V, Perez SI. 2009. Geometric morphometric approach to sex estimation of human pelvis. Forensic Sci Int 189:68–74.

Goodall C. 1991. Procrustes methods in the statistical analysis of shape. J R Stat Soc Ser B (Method) 53:285–339.

Gordon AD, Green DJ, Richmond BG. 2008. Strong postcranial size dimorphism in *Australopithecus afarensis*: results from two new resampling methods for multivariate data sets with missing data. Am J Phys Anthropol 135:311–328.

Griffin TM, Main RP, Farley CT. 2004. Biomechanics of quadrupedal walking: how do four-legged animals achieve inverted pendulum-like movements? J Exp Biol 207:3545–3558.

Hanna JB, Polk JD, Schmitt D. 2006. Forelimb and hindlimb forces in walking and galloping primates. Am J Phys Anthropol 130:529–535.

Harcourt-Smith WEH, Tallman M, Frost SR, Wiley DF, Rohlf FJ, Delson E. 2008. Analysis of selected hominoid joint surfaces using laser scanning and geometric morphometrics: a preliminary report. In: Sargis EJ, Dagosto M, editors. Mammalian evolutionary morphology: a tribute to Frederick S. Szalay. New York: Springer Science. p 373–383.

Harmon EH. 2007. The shape of the hominoid proximal femur: a geometric morphometric analysis. J Anat 210:170–185.

Harvati K. 2003. Quantitative analysis of Neanderthal temporal bone morphology using three-dimensional geometric morphometrics. Am J Phys Anthropol 120:323–338.

Harvati K, Hublin JJ, Gunz P. 2010. Evolution of middle-late Pleistocene human cranio-facial form: a 3D approach. J Hum Evol 59:445–464.

Harvey PH, Pagel MD. 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press.

Hildebrand M. 1985. Walking and running. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. Functional vertebrate morphology. Cambridge: Harvard University Press. p 38–57.

Holm S. 1979. A simple sequentially rejective multiple test procedure. Scand J Statist 6:65–70.

Howell AB. 1944. Speed in animals: their specialization for running and leaping. New York: Hafner Publishing Company.

Jenkins FA. 1974. Tree shrew locomotion and the origins of primate arborealism. In: Jenkins FA, editor. Primate locomotion. New York: Academic Press. p 85–115.

Jenkins FA, Camazine SM. 1977. Hip structure and locomotion in ambulatory and cursorial carnivores. J Zool 181:351–370.

Jungers WL. 1976. Hindlimb and pelvic adaptations to vertical climbing and clinging in *Megaladapis*, a giant subfossil prosimian from Madagascar. Yearb Phys Anthropol 20:508–524.

Jungers WL, Burr DB, Cole MS. 1998. Body size and scaling of long bone geometry, bone strength, and positional behavior in cercopithecoid primates. In: Strasser E, Fleagle JG, Rosenberger A, McHenry HM, editors. Primate locomotion: recent advances. New York: Plenum Press. p 309–330.

Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. Yearb Phys Anthropol 38:137–161.

Jungers WL, Harcourt-Smith WEH, Wunderlich RE, Tocheri MW, Larson SG, Sutikna T, Due RA, Morwood MJ. 2009. The foot of *Homo floresiensis*. Nature 459:81–84.

Kay RF, Cartmill M. 1977. Cranial morphology and adaptations of *Palaechthon naeimienti* and other Paromomyidae (Plesiadapoidea,?Primates), with a description of a new genus and species. J Hum Evol 6:19–53.

Kendall DG. 1984. Shape manifolds, procrustean metrics, and complex projective spaces. Bull Lond Math Soc 16:81–121.

Kimura T. 1985. Bipedal and quadrupedal walking of primates: comparative dynamics. In: Kondo S, editor. Primate morphophysiology, locomotor analyses and human bipedalism. Tokyo: University of Tokyo Press. p 81–104.

Kivell TL, Schmitt D, Wunderlich RE. 2010. Hand and foot pressures in the aye-aye (*Daubentonia madagascariensis*) reveal novel biomechanical trade-offs required for walking on gracile digits. J Exp Biol 213:1549–1557.

Klingenberg CP. 2011. MorphoJ: an integrated software package for geometric morphometrics. Mol Ecol Res 11:353–357.

Kummer B. 1975. Functional adaptation to posture in the pelvis of man and other primates. In: Tuttle RH, editor. Primate functional morphology and evolution. Chicago: Aldine. p 281–290.

Lauder GV. 1996. The argument from design. In: Rose MR, Lauder GV, editors. Adaptation. New York: Academic Press. p 55–91.

Lewton KL. 2010. Locomotor function and the evolution of the primate pelvis. PhD dissertation, Arizona State University.

Lewton KL. 2012. Evolvability of the primate pelvic girdle. Evol Biol 39:126–139.

Lieberman DE, Crompton AW. 2000. Why fuse the mandibular symphysis? A comparative analysis. Am J Phys Anthropol 112:517–540.

Lieberman DE, Polk JD, Demes B. 2004. Predicting long bone loading from cross-sectional geometry. Am J Phys Anthropol 123:156–171.

Lockwood CA, Lynch JM, Kimbel WH. 2002. Quantifying temporal bone morphology of great apes and humans: an approach using geometric morphometrics. J Anat 201:447–464.

Lycett SJ, von Cramon-Taubadel N. 2013. Understanding the comparative catarrhine context of human pelvic form: a 3D geometric morphometric analysis. J Hum Evol 64:300–310.

MacLatchy L. 1998. Reconstruction of hip joint function in extant and extinct fossil primates. In: Strasser E, Fleagle JG, Rosenberger A, McHenry HM, editors. Primate locomotion: recent advances. New York: Plenum Press. p 111–130.

Marsh RL. 1994. Jumping ability of anuran amphibians. Adv Vet Sci Comp Med 38B:51–111.

McNulty KP. 2005. A geometric morphometric assessment of the hominoid supraorbital region: affinities of the Eurasian Miocene hominoids *Dryopithecus*, *Graecopithecus*, and *Sivapithecus*. In: Slice DE, editor. Modern morphometrics in physical anthropology. New York: Kluwer Academic Publishers. p 349–373.

Mivart SG. 1867. On the appendicular skeleton of the primates. Philos Trans R Soc Lond 157:299–429.

Mosimann JE. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. J Am Stat Assoc 65:930–945.

Napier JR, Napier PH. 1967. A handbook of living primates. London: Academic Press.

Napier JR, Walker AC, 1967. Vertical clinging and leaping—a newly recognized category of locomotor behaviour of primates. Folia Primatol 6:204–219.

O'Higgins P, Jones N. 2006. Tools for statistical shape analysis. Hull York Medical School. Available at: http://sites.google.com/site/hymsfme/resources.

Orr CM. 2005. Knuckle-walking anteater: a convergence test of adaptation for purported knuckle-walking features of African Hominidae. Am J Phys Anthropol 128:639–658.

Patel BA. 2010. Functional morphology of cercopithecoid primate metacarprals. J Hum Evol 58:320–337.

Pauwels F. 1980. Biomechanics of the locomotor apparatus: contributions on the functional anatomy of the locomotor apparatus. Maquet P, Furlong R, translators. New York: Springer-Verlag.

Peters A, Preuschoft H. 1984. External biomechanics of leaping in *Tarsius* and its morphological and kinematic consequences. In: Niemitz C, editor. Biology of tarsiers. New York: Gustav Fischer Verlag. p 227–255.

Polk JD. 2002. Adaptive and phylogenetic influences on musculoskeletal design in cercopithecine primates. J Exp Biol 205:3399–3412.

Polk JD. 2004. Influences of limb proportions and body size on locomotor kinematics in terrestrial primates and fossil hominins. J Hum Evol 47:237–252.

Polly PD, Lawing AM, Fabre A-C, Goswami A. 2013. Phylogenetic principal components analysis and geometric morphometrics. Hystrix 24:1–9.

Preuschoft H, Witte H, Christian A, Fischer M. 1996. Size influences on primate locomotion and body shape, with special emphasis on the locomotion of "small mammals." Folia Primatol 66:93–112.

Preuschoft H, Witte H, Fischer M. 1995. Locomotion in nocturnal prosimians. In: Alterman L, Doyle GA, Izard MK, editors. Creatures of the dark: the nocturnal prosimians. New York: Plenum Press. p 453–472.

Puhakka KB, Melsen F, Jurik AG, Boel LW, Vesterby A, Egund N. 2004. MR imaging of the normal sacroiliac joint with correlation to histology. Skeletal Radiol 33:15–28.

R Development Core Team. 2013. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Ravosa MJ, Noble VE, Hylander WL, Johnson KR, Kowalski EM. 2000. Masticatory stress, orbital orientation and the evolution of the primate postorbital bar. J Hum Evol 38:667–693.

Rayfield EJ. 2007. Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. Annu Rev Earth Planet Sci 35:541–576.

Rein TR, Harvati K. 2013. Exploring third metacarpal capitate facet shape in early hominins. Anat Rec 296:240–249.

Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3:217–223.

Reynolds TR. 1985. Stresses on the limbs of quadrupedal primates. Am J Phys Anthropol 67:351–362.

Richtsmeier JT, DeLeon VB, Lele SR. 2002. The promise of geometric morphometrics. Yearb Phys Anthropol 45:63–91.

Rohlf FJ, Slice D. 1990. Extensions of the procrustes method for the optimal superimposition of landmarks. Syst Zool 39:40–59.

Rosenberg KR. 1988. The functional significance of Neandertal pubic length. Curr Anthropol 29:595–617.

Rosenberg KR. 1992. The evolution of modern human childbirth. Yearb Phys Anthropol 35:89–124.

Ross CF, Berthaume MA, Dechow PC, Iriarte-Diaz J, Porro LB, Richmond BG, Spencer M, Strait D. 2011. *In vivo* bone strain and finite-element modeling of the craniofacial haft in catarrhine primates. J Anat 218:112–141.

Ross CF, Lockwood CA, Fleagle JG, Jungers WL. 2002. Adaptation and behavior in the primate fossil record. In: Plavcan JM, editor. Reconstructing behavior in the primate fossil record. New York: Kluwer Academic/Plenum Publishers. p 1–41.

Rudwick MJS. 1964. The inference of function from structure in fossils. Br J Philos Sci 15:27–40.

Ruff CB. 1995. Biomechanics of the hip and birth in early *Homo*. Am J Phys Anthropol 98:527–574.

Ruff CB. 2002. Long bone articular and diaphyseal structure in Old World monkeys and apes, I: locomotor effects. Am J Phys Anthropol 119:305–342.

Ruff CB. 2003. Ontogenetic adaptation to bipedalism: age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. J Hum Evol 45:317–349.

Russo GA. 2010. Prezygapophyseal articular facet shape in the catarrhine thoracolumbar vertebral column. Am J Phys Anthropol 142:600–612.

Schaffler MB, Burr DB, Jungers WL, Ruff CB. 1985. Structural and mechanical indicators of limb specialization in primates. Folia Primatol 45:61–75.

Schmidt M. 2005. Quadrupedal locomotion in squirrel monkeys (Cebidar: *Saimiri sciureus*): a cineradiographic study of limb kinematics and related substrate reaction forces. Am J Phys Anthropol 128:359–370.

Schmitt D. 1998. Forelimb mechanics during arboreal and terrestrial quadrupedalism in old world monkeys. In: Strasser E, Fleagle JG, Rosenberger A, McHenry HM, editors. Primate locomotion: recent advances. New York: Plenum Press. p 175–200.

Schmitt D. 1999. Compliant walking in primates. J Zool 248:149–160.

Schmitt D. 2003. Mediolateral reaction forces and forelimb anatomy in quadrupedal primates: implications for interpreting locomotor behavior in fossil primates. J Hum Evol 44:47–58.

Schmitt D, Hanna JB. 2004. Substrate alters forelimb to hindlimb peak force ratios in primates. J Hum Evol 46:239–254.

Schmitt D, Lemelin P. 2004. Locomotor mechanics of the slender loris (*Loris tardigradus*). J Hum Evol 47:85–94.

Schultz AH. 1969. Observations on the acetabulum of primates. Folia Primatol 11:181–199.

Sellers WI, Crompton RH. 1994. A system for 2- and 3D kinematic and kinetic analysis of locomotion, and its application to analysis of the energetic efficiency of jumping locomotion. Zeitschrift Morphol Anthropol 80:99–108.

Shaw CN, Stock JT. 2009. Intensity, repetitiveness, and directionality of habitual adolescent mobility patterns influence the tibial diaphysis morphology of athletes. Am J Phys Anthropol 140:149–159.

Sigmon BA, Farslow DL. 1986. The primate hindlimb. In: Swindler DR, Erwin J, editors. Comparative primate biology: systematics, evolution, and anatomy. Vol. I. New York: Alan R. Liss. p 671–718.

Singleton M. 2002. Patterns of cranial shape variation in the Papionini (Primates: Cercopithecinae). J Hum Evol 42:547–578.

Slice DE. 2007. Geometric morphometrics. Annu Rev Anthropol 36:261–281.

Slijper EJ. 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Amsterdam: North-Holland Publishing Company.

Smith RJ, Cheverud JM. 2002. Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch's rule in primates. Int J Primatol 23:1095–1135.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523–559.

Spencer MA. 2003. Tooth-root form and function in platyrrhine seed-eaters. Am J Phys Anthropol 122:325–335.

Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Dechow PC, Ross CF, Grosse IR, Wright BW, Constantino P, Wood BA, Lawn B, Hylander WL, Wang Q, Byron C, Slice DE, Smith AL. 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. Proc Natl Acad Sci USA 106:2124–2129.

Straus WL, Jr. 1929. Studies on primate ilia. Am J Anat 43:403–460.

Szalay FS. 2007. Ancestral locomotor modes, placental mammals, and the origin of euprimates: lessons from history. In: Ravosa MJ, Dagosto M, editors. Primate origins: adaptation and evolution. New York: Springer. p 457–487.

Tague RG. 2005. Big-bodied males help us recognize that females have big pelves. Am J Phys Anthropol 127:392–405.

Tallman M. 2012. Morphology of the distal radius in extant hominoids and fossil hominins: implications for the evolution of bipedalism. Anat Rec 295:454–464.

Taylor AB. 1997. Relative growth, ontogeny, and sexual dimorphism in *Gorilla* (*Gorilla gorilla gorilla* and *G. g. beringei*): evolutionary and ecological considerations. Am J Primatol 43:1–31.

Taylor AB, Slice DE. 2005. A geometric morphometric assessment of the relationship between scapular variation and locomotion in African apes. In: Slice DE, editor. Modern morphometrics in physical anthropology. New York: Kluwer Academic/Plenum. p 299–318.

Terhune CE. 2013. How effective are geometric morphometric techniques for assessing functional shape variation? An example from the great ape temporomandibular joint. Anat Rec 296:1264–1282.

Tocheri MW, Solhan CR, Orr CM, Femiani J, Frohlich B, Groves CP, Harcourt-Smith WEH, Richmond BG, Shoelson B, Jungers WL. 2011. Ecological divergence and medial cuneiform morphology in gorillas. J Hum Evol 60:171–184.

Turley K, Guthrie EH, Frost SR. 2011. Geometric morphometric analysis of tibial shape and presentation among catarrhine taxa. Anat Rec 294:217–230.

Tuttle RH. 1969. Terrestrial trends in the hands of the Anthropoidea: a preliminary report. In: Proceedings of the Second International Congress of Primatology. Basel: Karger. p 192–200.

Vinyard CJ, Wall CE, Williams SH, Hylander WL. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. Am J Phys Anthropol 120:153–170.

Vleeming A, Schuenke MD, Masi AT, Carreiro JE, Danneels L, Willard FH. 2012. The sacroiliac joint: an overview of its anatomy, function and potential clinical implications. J Anat 221:537–567.

Ward CV. 1991. Functional anatomy of the lower back and pelvis of the Miocene hominoid *Proconsul nyanzae* from Mfangano Island, Kenya. PhD dissertation, The Johns Hopkins University.

Ward CV. 1993. Torso morphology and locomotion in *Proconsul nyanzae*. Am J Phys Anthropol 92:291–328.

Waterman HC. 1929. Studies on the evolution of the pelvis of man and other primates. Bull Brit Mus Nat Hist 58:585–642.

Whitehead PF. 1993. Aspects of the anthropoid wrist and hand. In: Gebo DL, editor. Postcranial adaptation in nonhuman primates. DeKalb: Northern Illinois University Press. p 96–120.

Young NM. 2006. Function, ontogeny and canalization of shape variance in the primate scapula. J Anat 209:623–636.

Young NM. 2008. A comparison of the ontogeny of shape variation in the anthropoid scapula: functional and phylogenetic signal. Am J Phys Anthropol 136:247–264.

Zelditch ML, Swiderski DL, Sheets HD, Fink WL. 2004. Geometric morphometrics for biologists: a primer. San Diego: Elsevier Academic Press.