

Morphological convergence in the pubis of slow-moving primates and xenarthrans

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Abstract

Objectives: Determining the functional significance of pubic rami is important for reconstructing locomotor behavior of fossil species. The slow loris pelvis, characterized by long pubic rami, is unusual among primates. Long pubic rami may be related to increasing the moment arm of the abdominal musculature during ventroflexion after the termination of hindlimb suspension, which is a common component of slow arboreal quadrupedalism (AQ). Some extant xenarthran species are also slow AQ taxa, and provide an ideal group to test hypotheses of morphologically convergent adaptations to slow AQ.

Materials and Methods: A model relating abdominal moment arms to pubic morphology is tested in three genera of slow-moving xenarthrans (*Bradypus*, *Choloepus*, and *Cyclopes*) and two species of slow loris (*Nycticebus coucang* and *Perodicticus potto*), using a comparative sample of 37 species of primates and xenarthrans. Phylogenetic analyses of variance and regression were performed on pubic dimensions (superior and inferior pubic ramus length, pubic symphysis length).

Results: As a locomotor group, slow-moving xenarthrans and lorises share superior pubic rami that are longer than all other locomotor groups; at the species level, there is some overlap among slow AQ and non-slow-AQ taxa. Inferior pubic ramus and pubic symphysis lengths also differ according to locomotor category, but multiple comparisons among locomotor groups are non-significant.

Discussion: These results support the hypothesis that superior pubic ramus length is functionally related to slow, suspensory locomotion by increasing the leverage of the ventral abdominal musculature, and demonstrates morphological convergence among two phylogenetically distant groups of mammals that have evolved adaptations for slow, suspensory locomotion.

KEYWORDS

functional morphology, locomotion, pelvis, sloth, slow loris

1 | INTRODUCTION

The pelvis of lorises (i.e., Loridae Gray, 1821: slow and slender lorises, pottos, and angwantibos) is distinctive among primates and is characterized by long, slender, rod-like ilia (Hill, 1953; Waterman, 1929) and ventrally-projecting pubic rami that are relatively longer than any other primate species (Lewton, 2010; Mivart, 1867). The functional morphology of the pubic bones, however, is not well understood in primates nor in mammals more broadly. Pubic rami length has been functionally related to two major biological roles: obstetrics and locomotion. Obstetric dimensions of the pelvis can be increased by lengthening the pubic rami. Primate species that birth relatively large neonates exhibit sexual dimorphism in pubic rami length (e.g., *Homo*, *Saimiri*, *Cebus*), in

which females have longer pubic rami than males to increase the obstetric dimensions of the birth canal (Arsuaga & Carretero, 1994; Leutenegger & Larson, 1985; Mobb & Wood, 1977; Pissinatti et al., 1992; Steudel, 1981; Tague, 1993). Lorises, however, are not sexually dimorphic in pubic morphology (Leutenegger, 1973) and loris neonatal mass is not large relative to maternal mass (Ernest, 2003). This leaves locomotor specialization as a possible functional correlate of long pubic rami in lorises. Determining the functional significance of pubic rami is important for reconstructing both obstetrics and locomotion in the fossil record.

All lorises use slow, stealthy, quadrupedalism (Charles-Dominique, 1977; Dykyj, 1980; Ishida, Hirasaki, & Matano, 1992; Napier & Napier, 1967; Walker, 1969, 1974). Slow lorises and pottos (hereafter, slow

lorises), in particular among Loridae, rely additionally on slow bridging, climbing, cantilever behaviors, and hindlimb suspension (Hill, 1953; Hunt et al., 1996; Ishida et al., 1992; Walker, 1969, 1974). Given their unique form of locomotion among primates, it is reasonable to hypothesize that slow loris pubic morphology may be functionally related to the mechanical demands of slow locomotion.

Extant slow-moving, arboreal xenarthrans (the tree sloths *Bradypus* and *Choloepus*, and the silky anteater *Cyclopes*) provide a comparative group to examine the functional morphology of the pubis in relation to slow locomotion. These species engage in slow, cautious, arboreal locomotor behaviors (see detailed description below under "Locomotor classification"). Although two-toed (*Choloepus*) and three-toed sloths (*Bradypus*) are remarkably similar behaviorally and morphologically, they belong to two distantly related families (Megalonychidae and Bradypodidae, respectively, Delsuc, Catzeflis, Stanhope, & Douzery, 2001). The common ancestor of these diphyletic taxa was not suspensory, but instead likely fossorial (McDonald, 2003); both molecular (Delsuc et al., 2001) and morphological (Gaudin, 1995, 2004; Nyakatura, 2012; Nyakatura & Fischer, 2011) studies have demonstrated that the locomotor behavior and morphology of tree sloths is, therefore, convergent (although there are some morphological differences in the forelimb between the two genera, e.g., Nyakatura & Fischer, 2011). In addition to sharing similar forms of locomotion, slow lorises and tree sloths also share convergent morphological features of the postcranium, including: long vertebral columns (i.e., increased number of pre-sacral vertebrae, Hill, 1953; Straus & Wislocki, 1932); retroverted, short, vertebral spinous processes (Carleton, 1936; Grand, 1978; Granatosky, Miller, Boyer, & Schmitt, 2014; Lamberton, 1947; Shapiro et al., 2005; Straus & Wislocki, 1932); a relatively wide thorax (Straus & Wislocki, 1932); long limbs (Carleton, 1936; Miller, 1935; Straus & Wislocki, 1932); and webs of vascular bundles surrounding the major arteries of the fore- and hindlimbs ("retia mirabilia," which are also shared by the slow-moving silky anteater, *Cyclopes didactylus*, Grand, 1977, 1978; Goffart, 1971; Hill, 1953; Wislocki, 1928; Wislocki & Straus, 1932). Tree sloths and slow lorises have also been described as having long pubic rami (e.g., Godfrey & Jungers, 2002; Simons, Godfrey, Jungers, Chatrath, & Rakotosamimanana, 1992). However, this qualitative observation neither has been quantified nor compared across these taxa, as there has not been a formal comparison of the pelvic girdle of xenarthrans and slow lorises, and pubic bone functional morphology in mammals has not been a focus of research.

All of the features listed above have been functionally related to suspension and slow locomotion (references as above). The vertebral similarities between slow-moving xenarthrans and slow lorises reflect an increased emphasis on abdominal flexion rather than spinal extension during inverted suspensory behaviors (Shapiro et al., 2005). Increased incidence of abdominal flexion is also supported by the increased muscle mass of the trunk flexors relative to trunk extensors in slow-moving xenarthrans and slow lorises (Britton, 1941; Grand, 1977, 1978). The aim of the current study is to test the hypothesis that pubic bone morphology is also related to abdominal flexion in slow-moving lorises and xenarthrans, using a model that relates pubic

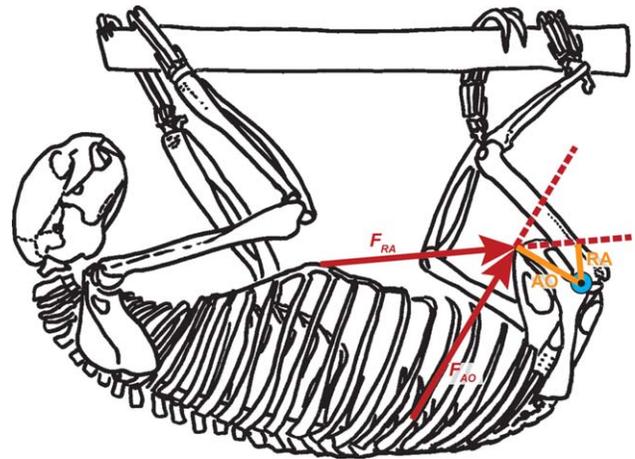


FIGURE 1 Model depicting the effect of ventral abdominal muscle insertions on the moment arms of the rectus abdominis (RA) and abdominal obliques (AO) in a two-toed sloth. The RA and AO insert only on the pubic symphysis in lorises (Curtis, 1995) and additionally along the superior pubic ramus in sloths (Mackintosh, 1870). The line of action of each muscle group is shown here as a red vector denoting the muscle force (F) and its direction of pull. Dotted lines are extensions of muscle force vectors for illustrative purposes. The blue circle is the hip joint center; gold lines are the muscle moment arms. As pubic ramus length increases, the insertion of both groups of ventral abdominal muscles moves ventrally, thereby increasing the moment arm of each muscle group. Model adapted from "Functional Anatomy of the Trunk Musculature in the Slow Loris (*Nycticebus coucang*)," by D. Curtis, 1995, *American Journal of Physical Anthropology*, 97, p. 367. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

ramus length to the moment arm of the abdominal muscles during inverted suspensory activities.

2 | MODEL AND HYPOTHESES

Curtis (1995, modified from Kapandji, 1985) presented a model relating abdominal muscular function and bending of the vertebral spine in lorises that can be tested here. This model relates pubic rami length to the mechanical advantage of the ventral abdominal wall musculature (Figure 1, and described as follows). As a group, the abdominal flexors and trunk rotators (*mm. rectus abdominis* [RA], *external abdominal oblique* [AO], *internal abdominal oblique* [AO]) attach cranially to the xiphoid process of the sternum, the lower ribs, and the costal cartilages, and caudally along the superior pubic ramus, its pubic tubercles, and the iliac crest. As pubic ramus length increases (relative to biacetabular breadth), the caudal insertion of these muscles moves ventrally, thereby increasing their moment arms. This ventral projection of the pubic bones increases the mechanical advantage of these muscles during abdominal flexion, which is a movement that is required during vertical climbing and bimanual pull-up activities (Curtis, 1995) and would be especially critical in resuming a quadrupedal position after hindlimb suspension (a common behavior of both slow-moving xenarthrans and slow lorises, Curtis, 1995; Ishida et al., 1992). This study tests the hypothesis that pubic ramus length is related to the mechanical

advantage of the ventral abdominal muscles using a broad, comparative primate and xenarthran sample. Slow-movers are predicted to have longer pubic rami than other locomotor groups as an adaptation to their specialized form of slow arboreal quadrupedal (AQ) locomotion.

3 | MATERIALS AND METHODS

3.1 | Sample

The sample comprises pelvic girdles of 43 species of primates and xenarthrans (728 total individuals, Table 1). The primate sample includes both strepsirrhines and haplorhines. The xenarthran sample includes species from Orders Pilosa (including suborders Folivora, sloths, and Vermilingua, anteaters) and Cingulata (the nine-banded armadillo, *Dasyus novemcinctus*). Specimens were obtained from collections housed at the American Museum of Natural History, NY; Beza Mahafaly Osteological Collection, Madagascar; Cleveland Museum of Natural History; Field Museum of Natural History, Chicago; Museum of Comparative Zoology (MCZ), Cambridge; Muséum national d'Histoire naturelle, Paris; Natural History Museum, London; and National Museum of Natural History, Washington, DC. Only adult, non-pathological individuals were included in the analyses; adulthood was determined by fusion of the pelvic epiphyses. Species within some genera were pooled (when there were no interspecific differences) to increase sample sizes following Lewton (2012) (these are *Ateles*, *Leontopithecus*, *Saimiri*, *Papio*, *Hapalemur*, *Lepilemur*, *Propithecus*, and *Bradypus*).

3.2 | Locomotor classification

Species classified here as “slow-moving” are the tree sloths *Bradypus* and *Choloepus*, the silky anteater, *Cyclopes didactylus*, and the primates *Nycticebus coucang* and *Perodicticus potto*. Arboreal sloths use hindlimb suspensory feeding behaviors, bridging between branches, and simultaneous forelimb and hindlimb suspension beneath branches (Nyakatura, Petrovitch, & Fischer, 2010 and references therein). The silky anteater is a small-bodied, nocturnal, arboreal anteater that is slow-moving and uses climbing, above branch quadrupedalism, and suspended behaviors (Beebe, 1918; Van Tyne, 1929). The locomotor behavior of silky anteaters has been characterized as antipronograde, defined as “a behavior in which either the upper or lower limbs, or both, are employed in tension during activities of climbing, feeding, or suspended locomotion” (Granatosky et al., 2014, p.42). More specifically, Fujiwara, Endo, and Hutchison (2011) classified silky anteaters as inverted quadrupedal suspensors.

It is difficult to obtain precise locomotor behavioral data on lorises because they are nocturnal and cryptic (Charles-Dominique, 1977). The postural and locomotor behaviors of lorises have been qualitatively described (e.g., Ashton & Oxnard, 1964; Charles-Dominique, 1977; Dykyj, 1980; Roonwal & Mohnot, 1977; Walker, 1969, 1974), but these data do not include percentage of time observed using positional behaviors. Both *Perodicticus potto* and *Nycticebus coucang* use slow, cryptic quadrupedalism characterized by suspension of the body below

fore- and/or hindlimbs (e.g., inverted quadrupedalism, bimanual suspension, bipedal suspension, cantilevers and bridging) and the absence of leaping (Ashton & Oxnard, 1964; Charles-Dominique, 1977; Dykyj, 1980; Napier & Napier, 1967; Roonwal & Mohnot, 1977; Walker, 1974). The use of suspensory behaviors by slow lorises is well established (Ashton & Oxnard, 1964; Charles-Dominique, 1977; Dykyj, 1980; Roonwal & Mohnot, 1977; Walker, 1969, 1974), and even led Ashton & Oxnard (1964) to categorize lorises as “hangers” instead of quadrupeds (p.23). Roonwal & Mohnot (1977) describe *Nycticebus coucang* as “often hang[ing] by its feet” (p.59), which is a common feeding posture (Walker, 1969, 1974). Charles-Dominique (1977) describes *Perodicticus* as moving “equally easily above or below a branch, passing smoothly from one position to the other without any break in rhythm” (p. 69). Inverted quadrupedalism [i.e., quadrupedal suspension, or what Walker (1969) refers to as the “inverted ‘hanging’ posture” (p.2)] has been described as frequently occurring for several strides followed by a spiraling movement as the loris rights itself and continues walking with above branch quadrupedalism (Dykyj, 1980; Walker, 1969).

The locomotor classification of the comparative sample of non-slow-moving primates was based on the positional behavior in which a species spends the majority of its time (Napier & Napier, 1967). Locomotor groups in this study are broad and designed to capture fundamental differences in the ways that species move: arboreal quadrupeds, terrestrial quadrupeds, suspensory, and vertical clinging and leaping. Locomotor classifications were derived from several sources and compilations of behavioral data (Fleagle, 2013; Hunt et al., 1996; Napier & Napier, 1967; Schmitt, 2010).

3.3 | Data collection and analytical methods

Linear measures—superior pubic ramus length, inferior pubic ramus length, pubic symphysis length, and acetabulum diameter (as a proxy for body size)—were collected from each specimen. Acetabulum diameter was chosen as a proxy for body size because it scales isometrically with pelvis size across primates (Lewton, 2015a). Equivalent scaling data for xenarthrans are not available, but previous work has shown that limb joints generally scale isometrically with body mass across mammals (including xenarthrans, Godfrey, Sutherland, Boy, & Gomberg, 1991). Definitions for each measure are shown in Table 2. Measures were usually recorded on the right os coxa; however, when the right side of the pelvic girdle was damaged or missing, data were collected on the left os coxa. The majority of the data were collected by one of the authors (KLL), but some of the MCZ specimens ($N = 17$, including all 10 of the *Tamandua*, *Myrmecophaga*, and *Dasyus* specimens) were collected by HLD. Using a subset of the MCZ sample ($N = 7$ specimens), interobserver measurement error was assessed by calculating the absolute difference between each observer’s measures, dividing by the average interobserver measure, and multiplying by 100 for each variable. Average percent differences between observers were calculated for each measure. Average percent difference between HLD and KLL was 1%, 1.2%, 2.9%, and 1.9% and Pearson product-moment correlations between measures taken by each observer are 0.99, 0.99,

TABLE 1 Sampled taxa (43 species comprising 728 individuals) and summary statistics for linear measures (mm)

Species	Behavior ^a	Sex ^b	N	Superior pubic ramus length		Inferior pubic ramus length		Pubic symphysis length		Acetabulum diameter	
				Mean	SD	Mean	SD	Mean	SD	Mean	SD
PLATYRRHINI											
ATELIDAE											
<i>Alouatta caraya</i>	AQ	F	10	40.4	1.4	41.8	2.6	20.8	1.7	18.0	0.8
<i>Alouatta caraya</i>	AQ	M	10	42.1	2.8	43.4	3.9	22.8	1.0	19.1	1.4
<i>Ateles</i> spp.	Susp	F	9	43.3	3.7	44.7	4.7	27.2	5.1	22.9	1.2
<i>Ateles</i> spp.	Susp	M	11	40.5	2.1	43.0	3.3	27.2	3.9	23.2	1.6
<i>Ateles</i> spp.	Susp	U	1	43.1		45.0		26.1		23.0	
<i>Lagothrix lagotricha</i>	AQ	F	3	45.2	1.0	42.6	1.4	24.2	3.6	19.4	1.0
<i>Lagothrix lagotricha</i>	AQ	M	6	40.8	1.8	39.8	2.8	25.2	3.0	19.8	1.1
<i>Lagothrix lagotricha</i>	AQ	U	1	37.8		39.5		19.8		16.7	
CEBIDAE											
<i>Cebuella pygmaea</i>	AQ	F	5	9.6	1.4	9.3	0.8	7.3	1.0	4.1	0.1
<i>Cebuella pygmaea</i>	AQ	M	7	9.0	0.4	9.7	0.7	5.9	1.0	4.2	0.3
<i>Cebus albifrons</i>	AQ	F	7	26.0	1.9	29.8	2.9	17.2	3.1	12.9	0.7
<i>Cebus albifrons</i>	AQ	M	7	24.1	1.2	28.3	3.8	20.9	3.4	13.2	1.4
<i>Cebus apella</i>	AQ	F	8	26.0	1.9	28.5	2.9	18.2	3.1	13.3	0.7
<i>Cebus apella</i>	AQ	M	14	24.1	1.4	27.6	2.6	21.3	2.8	13.7	0.5
<i>Leontopithecus</i> spp.	AQ	F	10	16.9	0.9	18.8	2.0	9.5	1.6	8.2	0.4
<i>Leontopithecus</i> spp.	AQ	M	9	15.8	1.0	18.1	1.0	10.4	0.9	8.1	0.3
<i>Saimiri</i> spp.	AQ	F	10	18.0	0.8	20.1	1.5	10.7	1.9	8.3	0.4
<i>Saimiri</i> spp.	AQ	M	10	15.1	1.3	19.2	1.8	12.7	2.2	8.7	0.4
CATARRHINI											
CERCOPITHECINAE											
<i>Cercopithecus mitis</i>	AQ	F	13	37.4	2.1	38.1	8.1	22.3	9.1	15.8	0.8
<i>Cercopithecus mitis</i>	AQ	M	10	35.8	2.7	35.2	6.9	37.8	8.0	18.2	1.1
<i>Cercopithecus mitis</i>	AQ	U	1	36.5		43.6		14.5		14.6	
<i>Erythrocebus patas</i>	TQ	F	1	37.0		35.2		42.2		18.0	
<i>Erythrocebus patas</i>	TQ	M	3	40.5	0.5	45.3	2.8	51.4	6.5	22.3	0.6
<i>Erythrocebus patas</i>	TQ	U	2	39.4	1.2	32.4	7.9	53.7	13.0	19.6	2.5
<i>Macaca fascicularis</i>	AQ	F	13	33.1	3.6	31.0	7.8	21.9	6.5	14.1	0.7
<i>Macaca fascicularis</i>	AQ	M	21	32.0	2.5	31.7	3.9	32.3	2.5	16.7	1.2
<i>Macaca fascicularis</i>	AQ	U	3	30.1	2.7	31.3	2.3	33.0	6.7	17.2	1.6
<i>Macaca nemestrina</i>	TQ	F	3	39.7	2.0	34.0	8.1	35.5	10.5	18.3	2.3
<i>Macaca nemestrina</i>	TQ	M	9	40.7	6.1	42.1	8.0	43.2	7.8	21.2	2.8
<i>Macaca nemestrina</i>	TQ	U	1	37.8		43.7		40.8		21.0	
<i>Mandrillus sphinx</i>	TQ	F	3	41.4	3.9	41.0	13.0	39.4	15.0	21.6	2.4
<i>Mandrillus sphinx</i>	TQ	M	4	52.7	2.4	48.9	6.1	65.6	6.4	30.3	3.0
<i>Mandrillus sphinx</i>	TQ	U	1	56.9		58.1		62.0		28.0	
<i>Miopithecus talapoin</i>	AQ	F	11	25.9	2.4	24.9	5.6	15.0	6.0	9.3	0.7
<i>Miopithecus talapoin</i>	AQ	M	4	22.2	2.3	19.4	2.9	23.2	1.2	10.3	0.6
<i>Papio</i> spp.	TQ	F	14	46.6	3.7	48.8	8.0	40.0	11.4	24.5	2.2
<i>Papio</i> spp.	TQ	M	23	50.6	4.0	48.1	5.6	55.4	8.2	27.9	2.4
<i>Papio</i> spp.	TQ	U	8	49.7	5.6	48.4	7.8	53.4	11.0	27.2	2.6
<i>Theropithecus gelada</i>	TQ	F	5	44.6	1.7	49.1	4.8	39.5	5.9	22.7	1.6
<i>Theropithecus gelada</i>	TQ	M	1	47.6		57.0		43.8		26.2	

TABLE 1 (Continued)

Species	Behavior ^a	Sex ^b	N	Superior pubic ramus length		Inferior pubic ramus length		Pubic symphysis length		Acetabulum diameter	
				Mean	SD	Mean	SD	Mean	SD	Mean	SD
COLOBINAE											
<i>Colobus guereza</i>	AQ	F	12	39.6	2.5	38.1	7.8	38.2	8.6	20.7	1.0
<i>Colobus guereza</i>	AQ	M	7	35.8	2.4	40.2	5.8	43.6	4.0	21.7	1.3
<i>Colobus guereza</i>	AQ	U	4	36.5	1.5	34.0	3.7	41.9	2.3	20.8	0.8
<i>Nasalis larvatus</i>	AQ	F	7	42.0	2.2	36.2	5.6	38.9	5.9	22.5	1.1
<i>Nasalis larvatus</i>	AQ	M	11	44.5	4.0	40.8	4.0	52.5	4.3	27.2	1.4
<i>Nasalis larvatus</i>	AQ	U	2	43.6	0.9	44.6	1.6	44.3	8.3	25.2	5.0
<i>Procolobus badius</i>	AQ	F	5	36.7	2.0	33.0	5.1	33.3	2.5	18.9	0.8
<i>Procolobus badius</i>	AQ	M	5	33.9	2.4	31.1	2.9	35.2	1.8	20.6	0.8
HOMINOIDEA											
<i>Gorilla gorilla</i>	TQ	F	10	92.5	5.7	93.0	11.0	40.7	4.1	48.4	1.7
<i>Gorilla gorilla</i>	TQ	M	11	104.0	11.6	106.8	11.2	67.1	9.6	58.1	4.3
<i>Hylobates hoolock</i>	Susp	F	6	37.4	2.5	32.9	2.9	34.8	2.5	21.0	0.9
<i>Hylobates hoolock</i>	Susp	M	7	34.7	2.3	31.8	1.8	34.8	3.0	20.9	0.7
<i>Hylobates lar</i>	Susp	F	11	33.6	0.9	25.1	2.8	27.2	4.5	20.5	0.8
<i>Hylobates lar</i>	Susp	M	13	32.6	2.1	24.9	2.1	27.1	4.4	20.5	1.3
<i>Pan troglodytes</i>	TQ	F	21	66.1	3.8	75.8	6.1	42.3	3.3	38.6	2.8
<i>Pan troglodytes</i>	TQ	M	20	65.7	3.7	81.9	6.1	44.5	7.0	40.8	3.6
<i>Pongo pygmaeus</i>	Susp	F	2	68.0	1.9	59.6	11.4	34.7	1.1	36.5	0.6
<i>Pongo pygmaeus</i>	Susp	M	15	77.5	4.0	72.1	8.8	47.8	9.3	44.1	3.9
<i>Pongo pygmaeus</i>	Susp	U	2	67.0	2.5	67.8	0.6	31.2	3.0	36.7	2.9
<i>Symphalangus syndactylus</i>	Susp	F	8	44.9	4.0	31.5	6.0	36.2	3.5	25.1	1.7
<i>Symphalangus syndactylus</i>	Susp	M	2	48.2	3.5	38.7	10.9	45.9	0.4	30.0	1.1
STREPSIRRHINI											
DAUBENTONIIDAE											
<i>Daubentonia madagascariensis</i>	AQ	F	2	25.7	0.2	27.1	0.5	17.7	0.6	14.0	0.5
<i>Daubentonia madagascariensis</i>	AQ	M	4	21.7	1.2	26.6	2.2	16.3	1.9	14.3	0.6
<i>Daubentonia madagascariensis</i>	AQ	U	2	20.2	1.5	24.8	4.3	17.1	1.0	14.1	0.7
LEMURIDAE											
<i>Eulemur fulvus</i>	AQ	F	12	23.2	0.9	24.5	1.9	15.6	1.5	13.4	0.7
<i>Eulemur fulvus</i>	AQ	M	4	22.9	0.9	25.2	1.5	12.5	1.6	12.8	0.8
<i>Eulemur fulvus</i>	AQ	U	6	22.6	0.9	25.7	2.5	13.5	1.5	12.7	0.4
<i>Haplemur spp.</i>	VCL	F	6	18.6	1.4	20.6	1.8	8.3	0.8	9.2	0.6
<i>Haplemur spp.</i>	VCL	M	3	17.3	2.4	17.8	2.0	8.0	1.0	9.2	1.8
<i>Haplemur spp.</i>	VCL	U	7	19.2	2.0	20.8	2.3	9.3	1.4	9.3	0.5
<i>Lepilemur spp.</i>	VCL	F	12	13.4	1.6	15.6	1.5	7.8	1.7	8.8	1.1
<i>Lepilemur spp.</i>	VCL	M	8	13.6	2.6	16.1	2.6	7.1	1.4	9.4	1.3
<i>Varecia variegata</i>	AQ	F	2	25.6	0.3	30.5	0.7	14.5	1.1	18.2	0.1
<i>Varecia variegata</i>	AQ	M	5	25.6	1.2	30.1	2.1	14.9	1.8	17.4	1.1
<i>Varecia variegata</i>	AQ	U	7	24.9	1.9	29.6	2.1	13.6	2.3	15.7	2.0
INDRIIDAE											
<i>Indri indri</i>	VCL	F	2	31.9	0.1	22.7	2.9	29.6	0.5	25.6	1.3
<i>Indri indri</i>	VCL	M	2	27.9	0.9	24.9	0.5	25.2	2.1	23.6	0.6
<i>Indri indri</i>	VCL	U	3	27.0	2.2	23.9	3.0	26.4	3.5	22.4	1.6
<i>Propithecus spp.</i>	VCL	F	6	23.8	2.0	19.0	2.7	18.3	3.5	15.6	1.3
<i>Propithecus spp.</i>	VCL	M	9	22.1	1.4	19.4	3.7	15.9	2.5	15.5	1.1
<i>Propithecus spp.</i>	VCL	U	19	24.4	1.7	20.7	3.3	16.8	2.5	16.2	1.0

TABLE 1 (Continued)

Species	Behavior ^a	Sex ^b	N	Superior pubic ramus length		Inferior pubic ramus length		Pubic symphysis length		Acetabulum diameter		
				Mean	SD	Mean	SD	Mean	SD	Mean	SD	
LORIDAE												
<i>Galago senegalensis</i>	VCL	F	10	10.8	0.7	11.0	0.8	5.1	0.7	6.7	0.6	
<i>Galago senegalensis</i>	VCL	M	15	10.6	1.0	11.9	1.0	4.8	1.0	6.9	0.5	
<i>Galago senegalensis</i>	VCL	U	5	10.2	0.7	10.9	0.3	5.0	0.9	6.3	0.5	
<i>Nycticebus coucang</i>	Slow	F	5	25.4	4.2	26.8	3.1	6.1	1.3	9.8	0.7	
<i>Nycticebus coucang</i>	Slow	M	4	25.3	3.2	26.5	3.0	6.1	0.2	10.0	0.8	
<i>Nycticebus coucang</i>	Slow	U	8	23.5	1.8	24.3	2.3	5.9	2.2	9.8	0.9	
<i>Otolemur crassicaudatus</i>	AQ	F	6	18.6	1.5	19.5	2.3	10.0	2.3	11.6	0.9	
<i>Otolemur crassicaudatus</i>	AQ	M	23	19.4	1.3	21.8	1.9	10.6	1.8	11.8	0.7	
<i>Perodicticus potto</i>	Slow	F	3	30.6	1.7	32.2	3.1	4.4	2.1	10.8	3.1	
<i>Perodicticus potto</i>	Slow	M	14	28.2	2.5	29.0	3.9	5.8	1.9	11.3	1.2	
<i>Perodicticus potto</i>	Slow	U	11	27.1	3.5	27.3	4.4	5.8	1.5	10.5	0.8	
XENARTHRA												
FOLIVORA												
<i>Bradypus</i> spp.	Slow	F	1	63.6		57.7		5.7		15.0		
<i>Bradypus</i> spp.	Slow	M	1	47.7		39.9		7.8		16.7		
<i>Bradypus</i> spp.	Slow	U	2	50.0	3.8	48.0	1.2	5.7	1.4	17.1	1.5	
<i>Choloepus didactylus</i>	Slow	F	2	63.7	5.9	60.2	1.7	7.8	0.6	19.3	4.1	
<i>Choloepus didactylus</i>	Slow	M	1	55.9		53.9		8.4		17.3		
<i>Choloepus hoffmanni</i>	Slow	F	2	61.6	6.9	59.9	3.1	8.2	0.5	20.0	0.6	
<i>Choloepus hoffmanni</i>	Slow	U	4	57.6	4.5	55.8	5.3	7.2	0.8	21.0	1.1	
VERMILINGUA												
<i>Cyclopes didactylus</i>	Slow	F	5	18.4	1.2	11.7	2.0	3.7	2.1	6.2	0.4	
<i>Cyclopes didactylus</i>	Slow	M	1	22.2		15.3		3.8		7.1		
<i>Cyclopes didactylus</i>	Slow	U	1	16.7		9.0		3.5		6.6		
<i>Myrmecophaga tridactyla</i>	TQ	M	1	70.6		75.0		46.8		32.0		
<i>Myrmecophaga tridactyla</i>	TQ	U	2	108.3	8.5	81.8	1.7	25.4	7.3	37.7	4	
<i>Tamandua tetradactyla</i>	AQ	M	1	40.5		44.4		14.2		18.1		
<i>Tamandua tetradactyla</i>	AQ	U	2	38.4	0.95	39.9	2.7	12.2	0.1	17.3	2	
CINGULATA												
<i>Dasybus novemcinctus</i>	Fossorial	F	1	45.9		39.2		10.2		13.9		
<i>Dasybus novemcinctus</i>	Fossorial	M	1	42.5		50.5		9.1		13.0		
<i>Dasybus novemcinctus</i>	Fossorial	U	2	44.9	4.1	48.5	7.8	8.4	0.01	13.3	0.5	

^aLocomotor behavior, AQ = arboreal quadruped, Susp = Suspensory, TQ = terrestrial quadruped, VCL = vertical clinger and leaper.

^bF = female; M = male; U = unknown.

0.98, and 0.99 for superior pubic ramus length, inferior pubic ramus length, pubic symphysis length, and acetabulum diameter, respectively.

Phylogenetic comparative methods were used to account for the effects of phylogenetic relatedness. The phylogeny used here was derived from a primate phylogeny from the *10kTrees Project* (Arnold, Matthews, & Nunn, 2010). Xenarthrans were added to the phylogeny in Mesquite v. 3.04 (Maddison & Maddison, 2015) using sloth-primate divergence estimates and branch lengths from Bininda-Emonds et al. (2007). To test whether slow-moving species exhibit longer pubic rami as predicted by the model, phylogenetic ANOVA (pANOVA) and phylogenetic generalized least squares (PGLS) regression were performed in

R (R Core Team, 2016) on species means. The pANOVA was performed using the "phytools" R package (Revell, 2012), which simulates a distribution of F-values based on the topology of the phylogeny (Garland, Dickerman, Janis, & Jones, 1993). Using 1,000 simulations of F-values, the pANOVA tested for differences among locomotor groups (arboreal quadrupeds, slow-movers, suspensors, terrestrial quadrupeds, and vertical clingers and leapers) for each pubic variable scaled by acetabulum diameter (i.e., a shape variable *sensu* Jungers, Falsetti, & Wall, 1995). Because the armadillo is the only taxon within the fossorial locomotor category, this species was excluded from the pANOVA. When the pANOVA revealed a significant effect of locomotor group, multiple

TABLE 2 Definition of linear measures

Pelvic measure	Definition
Superior pubic ramus length	distance from (1) middle of acetabulum to (2) superomedial-most point on pubic symphysis
Inferior pubic ramus length	distance from (1) distal-most point on ischium that forms a line with the center of the acetabulum that is parallel to the long axis of the ischium to (2) inferomedial-most point on the pubic symphysis
Pubic symphysis length	distance from superomedial-most to inferomedial-most point of pubic symphysis
Acetabulum diameter	distance from superior rim to inferior rim of acetabulum, parallel to long axis of ischium

post hoc comparisons were performed and Type I errors were corrected using the Holm-Bonferroni method (Holm, 1979). To examine scaling between pubic measures and pelvic size, PGLS was performed on ln-transformed pubic measures on ln-acetabulum diameter [using the “caper” (Orme et al., 2013) R package]. The PGLS model used a maximum likelihood lambda method to transform the branch lengths from which the covariance matrix was derived. Because body mass estimates were not available for most of the museum specimens examined here, acetabulum diameter is used as a proxy for overall body size. There is recent debate among statisticians regarding the most appropriate regression model to address questions of allometry, especially concerning the use of reduced major axis (RMA) regressions (phylogenetic or not) instead of generalized least squares models. For example, in regard to the use of phylogenetic RMA regressions, Hansen and Bartoszek (2012) suggest that “reduced major axis regressions should never be used...when the goal is to estimate the allometric exponent” because RMA overestimates the model slope and uses incorrect assumptions about the distribution of biological error (p. 422). This is in contrast to the recommendations of Warton, Wright, Falster, and Westoby (2006) and Smith (2009) regarding non-phylogenetic regression analysis, who suggest that RMA regression is preferable to ordinary least squares regression when the goal is to examine scaling patterns (as opposed to predicting Y from X). Reporting RMA regression results, however, has become more common in biological anthropology based on the recommendations of Warton et al. (2006) and Smith (2009), among others. Because phylogenetic RMA regression models can overestimate the model slope, our interpretations of allometry in this study are based on PGLS results. However, to facilitate comparison to previously published results on the scaling of primate pelvic dimensions (Lewton, 2015a), we also report phylogenetic RMA results, which are nearly identical to PGLS results when the correlation between the dependent and independent variables is high (as is usually the case when the independent variable is an approximation of body size). Phylogenetic RMA analyses were conducted using the `phyl.RMA` function in the “phytools” R package (Revell, 2012). As in the PGLS regression method used here, branch lengths were transformed using a lambda maximum likelihood optimization. The phylogenetic RMA slope

is equivalent to the PGLS slope divided by the PGLS correlation coefficient (Garland, Harvey, & Ives, 1992).

Because pubic dimensions are sexually dimorphic in some species (i.e., species that birth relatively large neonates), all analyses were performed on sex-specific species means as well as on the combined-sex sample.

4 | RESULTS

The combined-sex and sex-specific samples yielded similar results. Thus, results are reported in the text for the combined-sex samples, except where sex-specific results differed from the entire sample (all results are reported in Tables 3–5).

4.1 | Phylogenetic ANOVA

The pANOVA demonstrated significant effects of locomotor group on all three scaled pubic measures (Table 3). As predicted, slow-movers have statistically significantly longer superior pubic rami than all other locomotor groups (Figure 2). Within their respective clades, slow-moving xenarthrans and lorises have longer superior pubic rami than their non-slow sister taxa. Specifically, sloths and the silky anteater have longer superior pubic rami than non-slow anteaters while slow lorises and pottos have longer superior pubic rami than galagos (Figure 3). Two non-slow-moving species also have relatively long superior pubic rami: the small, arboreal quadrupedal catarrhine *Miopithecus talapoin* and the fossorial armadillo, *Dasypus novemcinctus* (Figure 3). There is an intraspecific difference within *Miopithecus*, with the females of this taxon exhibiting longer superior pubic rami than males (the small *Dasypus* sample does not allow a similar comparison among the sexes). All non-lorise strepsirrhines have short superior pubic rami.

The pANOVA for inferior pubic ramus length shows a similar, albeit weaker pattern; there is a significant effect of locomotor group (Table 3). The boxplot of scaled inferior pubic ramus length shows that as predicted, slow species have longer inferior pubic rami than quadrupeds, suspensors, and vertical clingers and leapers (Figure 4). Post hoc comparisons among locomotor groups, however, are non-significant. The boxplot of scaled inferior pubic ramus length by taxon demonstrates that within xenarthran slow movers, the silky anteater has shorter inferior pubic rami than the tree sloths, and does not overlap the sloth range (Figure 5). The armadillo has longer inferior rami than the rest of the taxonomic sample. Suspensory hylobatids and vertical clinging and leaping indriids have the shortest inferior pubic rami.

Locomotor group also has a significant effect on pubic symphysis length (Table 3); slow movers have shorter pubic symphyses than other locomotor groups, followed by fossorial and vertical clinging and leaping taxa (Figure 6). However, post hoc comparisons among locomotor groups are not statistically significant (Table 3). Within their respective clades, slow-movers have shorter pubic symphyses than their non-slow-moving sister taxa (Figure 7).

4.2 | Phylogenetic regressions

The regression analyses demonstrate that pubic dimensions scale nearly isometrically across the entire sample (Table 4). The 95%

TABLE 3 Phylogenetic ANOVA results and post hoc comparisons among locomotor groups

Combined sex	Females							Males							
	AQ	Slow	Susp	TQ	VCL	AQ	Slow	Susp	TQ	VCL	AQ	Slow	Susp	TQ	VCL
Superior pubic ramus length	F = 19.7, p = .001							F = 26, p = .001							
AQ	0.01	0.01	1	1	1	1	1	0.01	0.01	1	1	1	1	1	1
Slow	0.01	0.01	1	1	1	1	0.01	0.01	1	1	1	1	1	1	1
Susp	1	0.01	1	1	1	1	0.01	0.01	1	1	1	1	1	1	1
TQ	1	0.01	1	1	1	1	0.01	0.01	1	1	1	1	1	1	1
VCL	0.88	0.01	1	1	1	1	0.01	0.01	1	1	0.83	0.01	1	1	1
Inferior pubic ramus length	F = 12.1, p = .02							F = 11.6, p = .01							
AQ	0.41	0.19	1	1	1	1	0.46	0.28	0.28	0.28	0.15	0.04	0.15	0.04	0.15
Slow	0.41	0.19	1	1	1	1	0.46	0.28	0.28	0.28	0.15	0.04	0.15	0.04	0.15
Susp	1	0.41	1	1	1	1	0.46	0.28	0.28	0.28	0.15	0.04	0.15	0.04	0.15
TQ	1	0.41	1	1	1	1	0.46	0.28	0.28	0.28	0.15	0.04	0.15	0.04	0.15
VCL	0.52	0.05	1	1	1	1	0.01	0.01	0.01	0.01	0.46	0.04	0.04	0.04	0.79
Pubic symphysis length	F = 10.8, p = .03							F = 9.9, p = .01							
AQ	0.19	1.00	1.00	1.00	1.00	1.00	0.24	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
Slow	0.19	1.00	1.00	1.00	1.00	1.00	0.24	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
Susp	1.00	0.60	1.00	1.00	1.00	1.00	0.24	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
TQ	1.00	0.10	1.00	1.00	1.00	1.00	0.24	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
VCL	1.00	1.00	1.00	0.87	1.00	1.00	0.24	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08

All measures scaled by acetabulum diameter. Bold indicates statistical significance at $p < .05$. P values under the diagonal, t-statistics above the diagonal.

TABLE 4 Phylogenetic generalized least squares and reduced major axis slopes and confidence intervals

	PGLS						pRMA						
	Intercept	Slope	R ²	SE	Slope	95% Confidence Interval	Intercept	Slope	R ²	SE	Slope	95% Confidence Interval	
Combined sex sample													
Superior pubic ramus length	1.12	0.88	0.89	0.05	0.79	– 0.98	0.98	0.93	0.89	0.05	0.84	– 1.03	
Inferior pubic ramus length	1.10	0.88	0.84	0.06	0.76	– 1.00	0.89	0.96	0.84	0.06	0.85	– 1.08	
Pubic symphysis length	–0.30	1.03	0.82	0.08	0.88	– 1.18	–0.60	1.14	0.82	0.07	0.99	– 1.29	
Female sample													
Superior pubic ramus length	1.30	0.83	0.85	0.06	0.72	– 0.94	1.13	0.90	0.85	0.05	0.80	– 1.01	
Inferior pubic ramus length	1.22	0.83	0.77	0.07	0.69	– 0.98	0.92	0.95	0.77	0.07	0.81	– 1.09	
Pubic symphysis length	–0.10	0.94	0.71	0.10	0.75	– 1.13	–0.55	1.12	0.71	0.09	0.93	– 1.30	
Male sample													
Superior pubic ramus length	1.04	0.90	0.91	0.04	0.82	– 0.99	0.93	0.95	0.91	0.04	0.86	– 1.03	
Inferior pubic ramus length	0.99	0.93	0.86	0.06	0.81	– 1.05	0.79	1.01	0.86	0.06	0.89	– 1.12	
Pubic symphysis length	–0.36	1.07	0.83	0.08	0.92	– 1.22	–0.64	1.18	0.83	0.08	1.03	– 1.33	

confidence interval for ln-superior pubic ramus length in the combined-sex sample is 0.79–0.98, just below the isometric slope of 1.0. Both ln-inferior pubic ramus length and ln-pubic symphysis length are isometric. Bivariate plots of each ln-variable on ln-acetabulum diameter demonstrate that slow-movers have longer pubic rami than expected given their body size and the PGLS regression fit to the comparative sample (Figure 8A and 8B, non-phylogenetic residuals listed in Table 5). The largest positive regression residuals for ln-superior pubic ramus length are exhibited by all slow xenarthrans and lorises, as well as *Miopithecus*, *Dasybus*, and *Myrmecophaga* (but not *Tamandua*, Table 5). Large positive residuals for the regression of ln-inferior pubic ramus length on ln-acetabulum diameter are exhibited only by the armadillo, sloths, and lorises (Figure 8B). Finally, slow-movers have unusually short pubic symphyses relative to body size (Figure 8C, Table 5).

5 | DISCUSSION

Slow AQ xenarthrans and lorises share positional behaviors such as inverted quadrupedalism, hindlimb suspension, bridging, and slow, deliberate arboreal climbing. Additionally, these taxa share morphological features of the thorax, spine, limbs, and vasculature, all of which have been functionally associated with slow, suspensory locomotion and inverted quadrupedalism. Although previous research has anecdotally noted that both slow lorises and tree sloths share long pubic rami (e.g., Godfrey & Jungers, 2002; Simons et al., 1992), this suggested morphological convergence in the pelvis has not previously been quantified. Postcranial morphological convergence has, however, been documented between another group of strepsirrhine primates and tree sloths: species of an extinct clade of sloth lemurs (Palaeopropithecidae) share many postcranial convergences for suspensory behavior with sloths (e.g., Godfrey, 1988; Godfrey & Jungers, 2003; Granatosky et al., 2014; Jungers, Godfrey, Simons, & Chatrath, 1997; Marchi, Ruff, Capobianco, Rafferty, Habib, & Patel, in press; Shapiro et al., 2005; Simons

et al., 1992; Simons, Godfrey, Jungers, Chatrath, & Ravaoarisoa, 1995). These convergences include long forelimbs, short olecranon processes of the ulna (Nyakatura, 2012; Walker, 1974), highly mobile and cranially-oriented humeral and femoral heads (Carleton, 1936), reduced malleoli and a subsequently mobile ankle joint (Carleton, 1936; Simons et al., 1992), hinged metacarpophalangeal joints allowing only flexion and extension (Carleton, 1936), and short vertebral spinous processes (Jungers, Godfrey, Simons, Chatrath, & Rakotosamimanana, 1991). Although pelvic dimensions of palaeopropithecids have not been published, the pubic rami have been qualitatively described as long (e.g., Simons et al., 1992).

This study tested a model that relates pubic rami length to the mechanical efficiency of the ventral abdominal wall musculature, which has important functional roles during abdominal flexion, a movement that occurs to right the body after hindlimb suspensory postures (Curtis, 1995; Ishida et al., 1992; Kapandji, 1985). In this model, long superior pubic rami increase the moment arm of the RA and AO musculature, thereby increasing the mechanical efficiency of these muscles.

Phylogenetic regression and analyses of variance both provide some support for the model hypothesis tested here, showing that slow-movers have longer pubic rami than taxa in other locomotor groups when accounting for body size and phylogeny. However, the regressions of ln-pubic dimensions on ln-acetabulum diameter also demonstrate that xenarthrans as a whole have long pubic rami relative to other animals of their size. Comparisons of mean values of scaled superior pubic ramus length among xenarthran species demonstrates that slow movers and the fossorial armadillo have long superior pubic rami, while the giant anteater and tamandua do not. The significance of long superior pubic rami in the armadillo is uncertain but could be related to fossoriality and is discussed below. This dataset suggests that there are differences among xenarthran species in which slow, suspensory species have longer superior pubic rami than their non-slow sister taxa; larger samples of xenarthran taxa would be useful to more fully support this conclusion.

TABLE 5 Non-phylogenetic residuals from PGLS on combined-sex samples, ordered from largest to smallest

Ln Superior pubic ramus length		Ln Inferior pubic ramus length		Ln Pubic symphysis length	
<i>Choloepus didactylus</i>	0.418	<i>Dasybus novemcinctus</i>	0.450	<i>Erythrocebus patas</i>	1.105
<i>Dasybus novemcinctus</i>	0.391	<i>Choloepus didactylus</i>	0.389	<i>Macaca nemestrina</i>	0.900
<i>Bradypus</i> spp.	0.373	<i>Bradypus</i> spp.	0.302	<i>Mandrillus sphinx</i>	0.898
<i>Choloepus hoffmanni</i>	0.283	<i>Choloepus hoffmanni</i>	0.271	<i>Colobus guereza</i>	0.856
<i>Myrmecophaga tridactyla</i>	0.272	<i>Perodicticus potto</i>	0.139	<i>Nasalis larvatus</i>	0.815
<i>Cyclopes didactylus</i>	0.170	<i>Myrmecophaga tridactyla</i>	0.125	<i>Papio</i> spp.	0.811
<i>Perodicticus potto</i>	0.104	<i>Nycticebus coucang</i>	0.120	<i>Macaca fascicularis</i>	0.790
<i>Miopithecus talapoin</i>	0.098	<i>Tamandua tetradactyla</i>	0.096	<i>Procolobus badius</i>	0.763
<i>Nycticebus coucang</i>	0.055	<i>Alouatta caraya</i>	0.075	<i>Theropithecus gelada</i>	0.752
<i>Alouatta caraya</i>	0.026	<i>Theropithecus gelada</i>	0.042	<i>Miopithecus talapoin</i>	0.741
<i>Tamandua tetradactyla</i>	0.022	<i>Miopithecus talapoin</i>	0.038	<i>Hylobates hoolock</i>	0.719
<i>Cercopithecus mitis</i>	0.000	<i>Pan troglodytes</i>	0.020	<i>Cebuella pygmaea</i>	0.687
<i>Lagothrix lagotricha</i>	0.000	<i>Cercopithecus mitis</i>	0.011	<i>Cercopithecus mitis</i>	0.661
<i>Gorilla gorilla</i>	-0.039	<i>Cebus albifrons</i>	0.003	<i>Cebus apella</i>	0.612
<i>Macaca fascicularis</i>	-0.081	<i>Gorilla gorilla</i>	-0.005	<i>Cebus albifrons</i>	0.604
<i>Theropithecus gelada</i>	-0.086	<i>Lagothrix lagotricha</i>	-0.010	<i>Symphalangus syndactylus</i>	0.585
<i>Macaca nemestrina</i>	-0.089	<i>Saimiri</i> spp.	-0.011	<i>Saimiri</i> spp.	0.548
<i>Pongo pygmaeus</i>	-0.102	<i>Leontopithecus</i> spp.	-0.038	<i>Hylobates lar</i>	0.483
<i>Erythrocebus patas</i>	-0.108	<i>Hapalemur</i> spp.	-0.062	<i>Lagothrix lagotricha</i>	0.440
<i>Papio</i> spp.	-0.119	<i>Cebus apella</i>	-0.074	<i>Leontopithecus</i> spp.	0.433
<i>Mandrillus sphinx</i>	-0.122	<i>Macaca nemestrina</i>	-0.077	<i>Daubentonia madagascariensis</i>	0.392
<i>Ateles</i> spp.	-0.154	<i>Ateles</i> spp.	-0.090	<i>Alouatta caraya</i>	0.379
<i>Hapalemur</i> spp.	-0.157	<i>Macaca fascicularis</i>	-0.101	<i>Ateles</i> spp.	0.365
<i>Cebuella pygmaea</i>	-0.158	<i>Cebuella pygmaea</i>	-0.111	<i>Indri indri</i>	0.340
<i>Cebus albifrons</i>	-0.160	<i>Erythrocebus patas</i>	-0.113	<i>Eulemur fulvus</i>	0.319
<i>Colobus guereza</i>	-0.170	<i>Papio</i> spp.	-0.123	<i>Pan troglodytes</i>	0.282
<i>Pan troglodytes</i>	-0.175	<i>Eulemur fulvus</i>	-0.154	<i>Propithecus</i> spp.	0.268
<i>Symphalangus syndactylus</i>	-0.175	<i>Mandrillus sphinx</i>	-0.154	<i>Pongo pygmaeus</i>	0.220
<i>Leontopithecus</i> spp.	-0.177	<i>Pongo pygmaeus</i>	-0.156	<i>Gorilla gorilla</i>	0.175
<i>Procolobus badius</i>	-0.189	<i>Colobus guereza</i>	-0.161	<i>Hapalemur</i> spp.	0.174
<i>Nasalis larvatus</i>	-0.194	<i>Daubentonia madagascariensis</i>	-0.176	<i>Otolemur crassicaudatus</i>	0.108
<i>Saimiri</i> spp.	-0.203	<i>Varecia variegata</i>	-0.177	<i>Varecia variegata</i>	0.060
<i>Cebus apella</i>	-0.210	<i>Otolemur crassicaudatus</i>	-0.215	<i>Myrmecophaga tridactyla</i>	0.051
<i>Hylobates hoolock</i>	-0.223	<i>Procolobus badius</i>	-0.272	<i>Lepilemur</i> spp.	0.040
<i>Eulemur fulvus</i>	-0.253	<i>Nasalis larvatus</i>	-0.276	<i>Galago senegalensis</i>	-0.067
<i>Hylobates lar</i>	-0.286	<i>Lepilemur</i> spp.	-0.283	<i>Tamandua tetradactyla</i>	-0.093
<i>Otolemur crassicaudatus</i>	-0.333	<i>Cyclopes didactylus</i>	-0.286	<i>Dasybus novemcinctus</i>	-0.167
<i>Daubentonia madagascariensis</i>	-0.359	<i>Hylobates hoolock</i>	-0.311	<i>Nycticebus coucang</i>	-0.291
<i>Varecia variegata</i>	-0.366	<i>Galago senegalensis</i>	-0.342	<i>Cyclopes didactylus</i>	-0.394
<i>Propithecus</i> spp.	-0.397	<i>Symphalangus syndactylus</i>	-0.498	<i>Perodicticus potto</i>	-0.472
<i>Galago senegalensis</i>	-0.436	<i>Hylobates lar</i>	-0.550	<i>Choloepus didactylus</i>	-0.622
<i>Lepilemur</i> spp.	-0.461	<i>Propithecus</i> spp.	-0.553	<i>Bradypus</i> spp.	-0.761
<i>Indri indri</i>	-0.555	<i>Indri indri</i>	-0.720	<i>Choloepus hoffmanni</i>	-0.798

Superior pubic ramus length differs across locomotor groups as expected, but inferior pubic ramus length does not. This may be related to how inferior pubic ramus length is measured here: the distance from

the inferior aspect of the pubic symphysis to the distal-most point on the ischium. Because this measure of inferior pubic ramus length is anchored on one end by the inferior aspect of the pubic symphysis, it

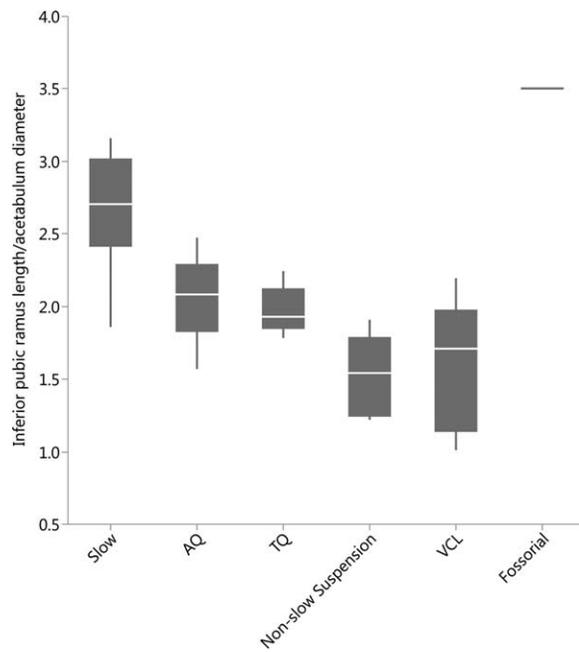


FIGURE 4 Locomotor group boxplot of species means of inferior pubic ramus length scaled by acetabulum diameter. The horizontal line within each boxplot is the median, and the ends of the box are the first and third quartiles. The fossorial group was excluded from statistical tests because there is only a single taxon within the locomotor category, but is plotted here. AQ: arboreal quadruped, TQ: terrestrial quadruped, VCL: vertical clinger and leaper.

lorises; relative to maternal mass, the neonatal mass of both slow xenarthrans and lorises is as expected for mammals of their size (see Figure 9, data from Ernest, 2003; Smith & Jungers, 1997; Smith & Leigh, 1998). Furthermore, sexual dimorphism in pubic anatomy is quite low in lorises (Leutenegger, 1973), suggesting that pubic morphology in these species is more influenced by factors other than obstetrical requirements.

This study also demonstrated that *Dasybus novemcinctus* and *Miopithecus talapoin* have longer pubic rami than expected given their size and locomotion, which may be related to obstetric requirements. There are few data available on armadillo locomotion and pelvic morphology, as the majority of studies have focused on diet and home-range activity of *D. novemcinctus* (reviewed in McDonough & Loughry, 2008). *D. novemcinctus* is monomorphic in body size, but sexually dimorphic in pubic length and pelvic inlet circumference, with females having significantly larger pelvic dimensions than males (Tague, 2015). Females of this species of armadillo give birth to identical quadruplets, but individual neonate mass is smaller than expected given maternal size (Figure 9), suggesting that relatively long pubic bones in this species is not a requirement based on fetal size. *Dasybus* is the only species investigated here that is fossorial; perhaps the unexpectedly long pubic rami in this species is somehow related to the mechanical demands of digging behaviors. Additional research on the bony pelvic girdle requirements of obstetrics and locomotion in this species is warranted.

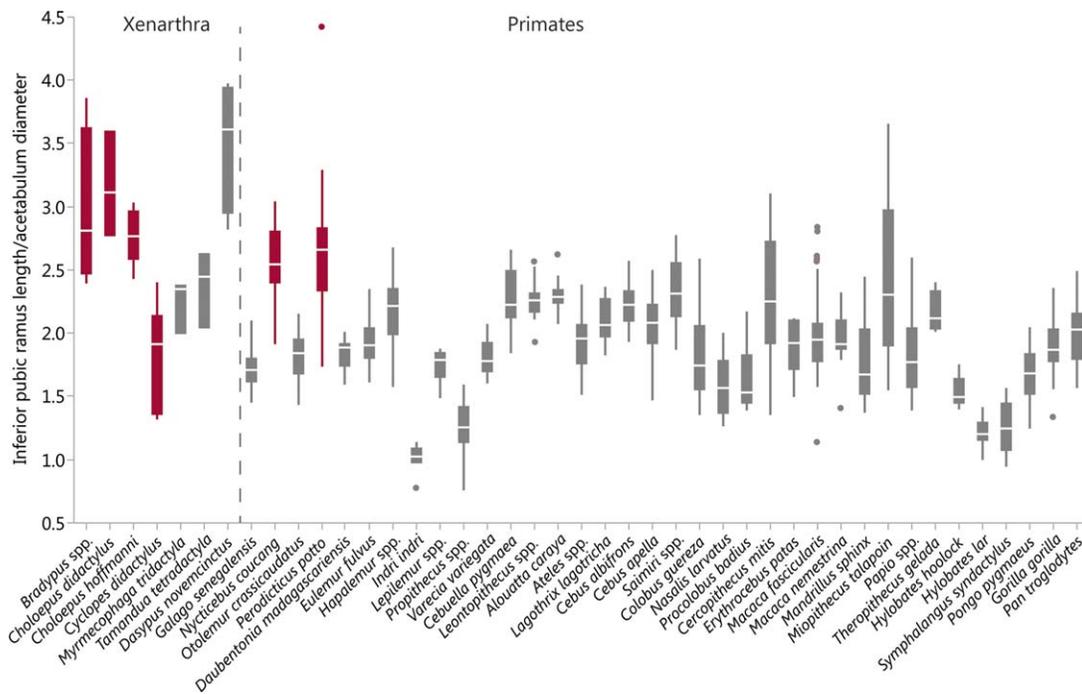


FIGURE 5 Taxon boxplot of inferior pubic ramus length scaled by acetabulum diameter. The horizontal line within each boxplot is the median, the ends of the box are the first and third quartiles, and dots are outliers. Red boxes denote taxa within the slow-moving locomotor category. Taxa are arranged according to phylogenetic groups. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

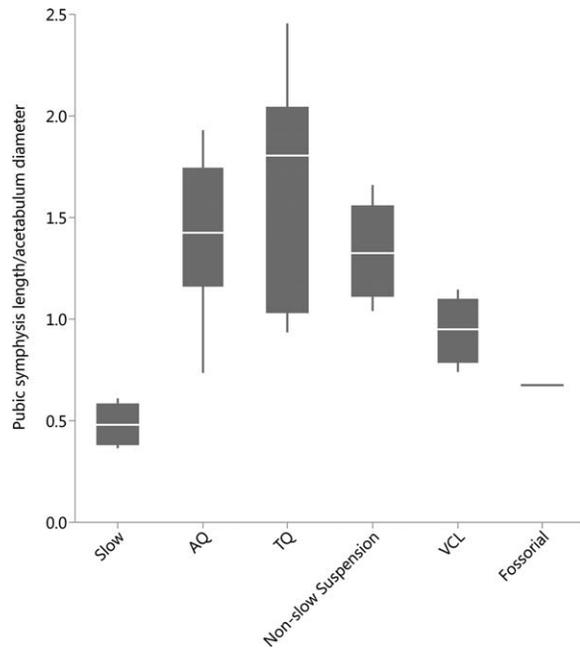


FIGURE 6 Locomotor group boxplot of species means of pubic symphysis length scaled by acetabulum diameter. The horizontal line within each boxplot is the median, and the ends of the box are the first and third quartiles. The fossorial group was excluded from statistical tests because there is only a single taxon within the locomotor category, but is plotted here. AQ: arboreal quadruped, TQ: terrestrial quadruped, VCL: vertical climber and leaper.

Miopithecus talapoin females have long pubic rami compared to other primates. *Miopithecus talapoin* is the smallest catarrhine (Fleagle, 2013) and spends 95% of its time arboreally (Gautier-Hion & Gautier, 1974). Detailed quantitative data describing the percent of time *M. talapoin* spends using various forms of locomotion do not exist (McGraw, 2002). Extrapolating from data on other guenons to *M. talapoin* could be problematic, but nevertheless may be informative. Guenons as a whole are arboreal quadrupeds, with 54–80% of their locomotor activities being walking and running; leaping is not common (McGraw, 2002). *M. talapoin* locomotor activity seems to be similar to other highly arboreal guenon species, and is likely not an explanation for its unusually long pubic bones. Instead, given that only the females of this species have long pubic rami, that these females birth relatively large neonates (approximately 16% of maternal mass, data from Smith & Jungers, 1997; Smith & Leigh, 1998, and see Figure 9), and that they likely use stereotypical cercopithecine locomotor behaviors, long pubic rami in *M. talapoin* seems most likely related to obstetrical requirements.

Previous workers have related pubic ramus morphology to hip adduction functions, suggesting that long pubic rami increase the moment arm of the hip adductor musculature [Howell (1944) cited by Anemone (1988, 1993) and Sargis (2002)]. Howell (1944) hypothesized that cursorial quadrupeds have short pubic rami because the limbs in these species move in a parasagittal plane and do not require substantial abduction and adduction. In non-cursorial mammals, he

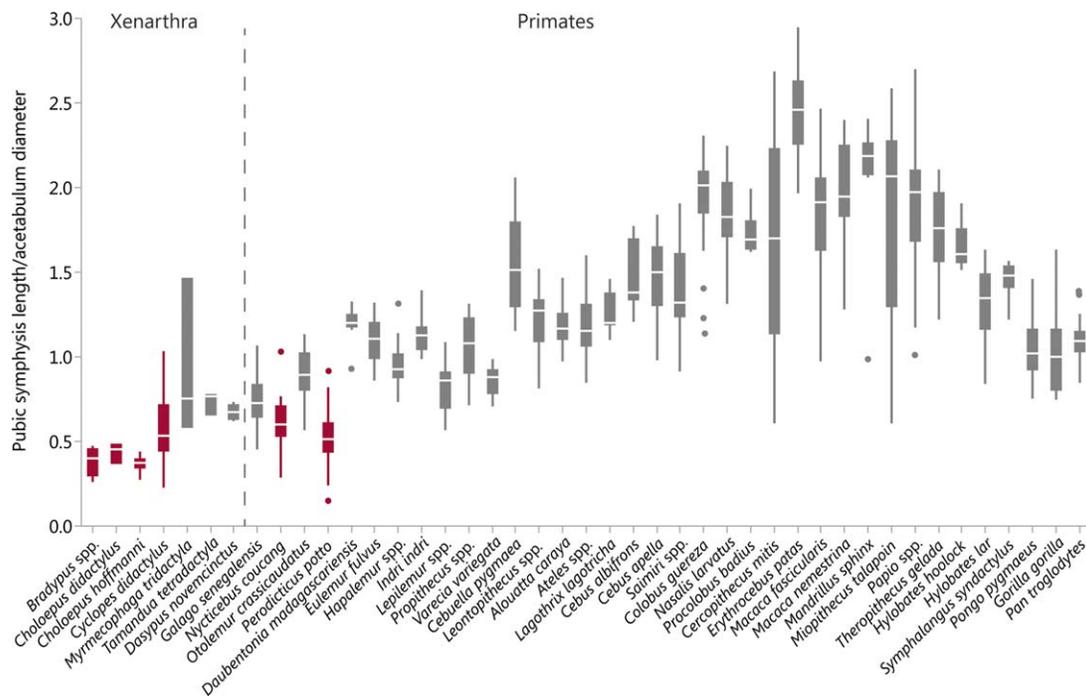


FIGURE 7 Taxon boxplot of pubic symphysis length scaled by acetabulum diameter. The horizontal line within each boxplot is the median, the ends of the box are the first and third quartiles, and dots are outliers. Red boxes denote taxa within the slow-moving locomotor category. Taxa are arranged according to phylogenetic groups. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

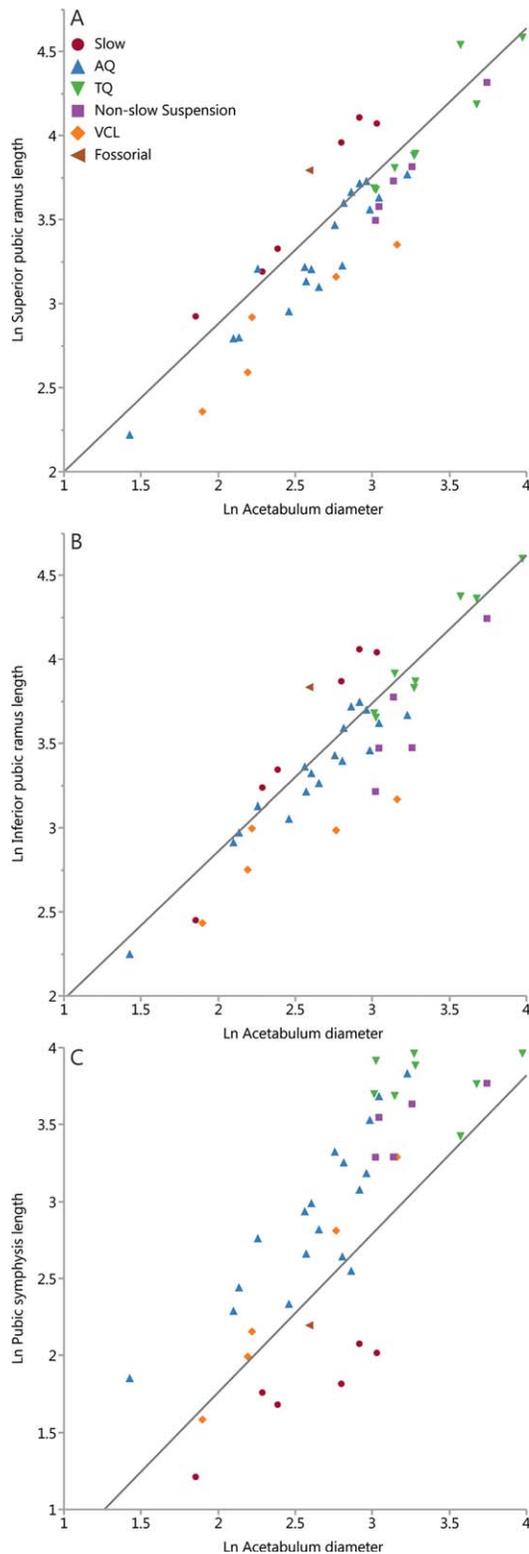


FIGURE 8 Bivariate plots of species means of each In-pubic measure on In-acetabulum diameter. Regression line denotes PGLS fit through combined-sex species means for the entire sample. Symbols are for locomotor groups, legend in (A). (A) Superior pubic ramus length, (B) Inferior pubic ramus length, (C) Pubic symphysis length. AQ: arboreal quadruped, TQ: terrestrial quadruped, VCL: vertical climber and leaper. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

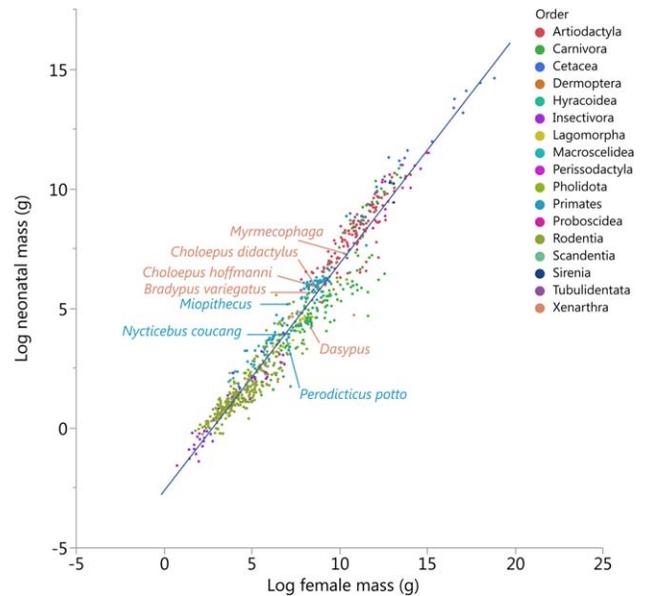


FIGURE 9 Bivariate plot of species means of log neonatal mass on log female body mass across a large sample of mammals (all data from Ernest, 2003, except data for *Miopithecus talapoin* from Smith and Jungers, 1997 and Smith and Leigh, 1998). Xenarthrans and lorises studied here are labeled (there are missing data for *Cyclopes* and *Tamandua*). Slow-moving xenarthrans and lorises do not have particularly large neonates, but are found in this study to have long pubic rami. *Miopithecus talapoin* has a relatively large neonate and subsequently relatively long pubic bones. Mammal-wide ordinary least squares regression: $\log(\text{neonatal body mass}) = 0.95 \times \log(\text{female body mass}) - 2.62$, $R^2 = 0.95$. Artiodactyla: $\log(\text{neonatal body mass}) = 0.82 \times \log(\text{female body mass}) - 0.79$, $R^2 = 0.77$; Carnivora: $\log(\text{neonatal body mass}) = 1.05 \times \log(\text{female body mass}) - 4.15$, $R^2 = 0.84$; Cetacea: $\log(\text{neonatal body mass}) = 0.77 \times \log(\text{female body mass}) + 0.51$, $R^2 = 0.97$; Insectivora: $\log(\text{neonatal body mass}) = 0.79 \times \log(\text{female body mass}) - 2.09$, $R^2 = 0.92$; Lagomorpha: $\log(\text{neonatal body mass}) = 0.79 \times \log(\text{female body mass}) - 1.75$, $R^2 = 0.94$; Macroscelidea: $\log(\text{neonatal body mass}) = 0.91 \times \log(\text{female body mass}) - 1.39$, $R^2 = 0.99$; Perissodactyla: $\log(\text{neonatal body mass}) = 0.69 \times \log(\text{female body mass}) + 0.88$, $R^2 = 0.47$; Pholidota: $\log(\text{neonatal body mass}) = 0.52 \times \log(\text{female body mass}) + 1.04$, $R^2 = 0.72$; Primates: $\log(\text{neonatal body mass}) = 0.84 \times \log(\text{female body mass}) - 1.46$, $R^2 = 0.91$; Rodentia: $\log(\text{neonatal body mass}) = 0.83 \times \log(\text{female body mass}) - 2.11$, $R^2 = 0.87$; Scandentia: $\log(\text{neonatal body mass}) = 0.22 \times \log(\text{female body mass}) + 1.45$, $R^2 = 0.46$; Xenarthra: $\log(\text{neonatal body mass}) = 0.37 \times \log(\text{female body mass}) + 2.11$, $R^2 = 0.21$. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

hypothesized, pubic rami are longer to increase the mechanical advantage of the hip adductors. However, Lewton (2015b) did not find support for this hypothesis in a sample of strepsirrhine species that differ in locomotor mode, and Anemone (1993) suggested that differences in pubic length among strepsirrhine species may be correlated with the effects of body size on locomotor mechanics. Future work would be necessary to examine how pubic rami morphology may relate to hip musculature functions.

6 | CONCLUSIONS

Slow AQ xenarthrans and lorises share long pubic rami that act to increase the mechanical efficiency of the abdominal muscles during slow, deliberate, suspensory movements (hindlimb suspension, slow climbing, inverted quadrupedalism, etc.). In particular, slowly righting the body from a bipedal suspended posture presumably requires large amounts of abdominal muscle effort that is alleviated by increasing the moment arms of the RA and AO muscles. These pelvic girdle results contribute to a large body of data demonstrating behavioral and morphological convergence between slow AQ xenarthrans and lorises. This study also highlights the role of the pubis in locomotor behaviors and suggests a need for future work on pubis functional morphology.

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