Ischial Form as an Indicator of Bipedal Kinematics in Early Hominins: A Test Using Extant Anthropoids

KRISTI L. LEWTON [1,2]* AND JEREMIAH E. SCOTT[3]

[1]Department of Cell and Neurobiology, Keck School of Medicine, University of Southern California, Los Angeles, California
[2]Department of Biological Sciences, University of Southern California, Los Angeles, California
[3]Department of Anthropology, Southern Illinois University, Carbondale, Illinois

ABSTRACT

Human ischia contrast with those of great apes in being craniocaudally short and dorsally projecting. This configuration is thought to facilitate greater hip extension in humans during bipedal locomotion. This link has been used to infer kinematics in early hominins, but the consequences of variation in ischial configuration for gait remain uncertain. Kinematic data for a limited sample of extant nonhuman primates demonstrate that there is variation in hip extension in these taxa during bipedal behaviors—specifically, *Hylobates* and *Ateles* are capable of greater extension than *Pan* and *Macaca*. In this study, we tested the hypothesis that ischial length and orientation are functionally linked with hip extension during bipedalism among these taxa. As expected, humans have the shortest ischia, followed by gibbons, spider monkeys, chimpanzees, and macaques. Our predictions for ischial orientation are not supported, however: macaques, gibbons, and spider monkeys do not vary in this trait, and they have ischia that are less dorsally angled than that of the chimpanzee. The results for ischium length provide limited support for the idea that the early hominin *Ardipithecus ramidus*, with its long, caudally oriented ischium was not capable of humanlike extended-hip bipedalism, and that the ischial shortening observed in post-*Ardipithecus* hominins reflects a shift toward a more humanlike gait. In contrast, while our results do not necessarily refute a link between ischial orientation and hip extension in hominins, they do not provide comparative support, making changes in ischial orientation in this part of the fossil record more difficult to interpret. Anat Rec, 300:845–858, 2017. © 2017 Wiley Periodicals, Inc.

Key words: pelvis; primates; ischium; hip; bipedalism

Explaining the origin of habitual upright bipedality in the hominin lineage remains one of the most challenging problems in paleoanthropology. None of the several hypotheses that have been proposed has gained widespread support (Darwin, 1871; Hewes, 1961; Rodman and McHenry, 1980; Lovejoy, 1981; Wheeler, 1984; Day, 1986; Jablonski and Chaplin, 1993; Hunt, 1994; Videan and McGrew, 2002; Sockol et al., 2007; Thorpe et al., 2007). One factor contributing to this lack of consensus is that our ability to test adaptationist hypotheses using the comparative method is severely limited because no other extant organism is characterized by our form of

TABLE 1. Estimates of peak or peak average hip extension angle (relative to trunk) during bipedalism for species in the primary sample (angles in degrees)

	Ateles	*Macaca*	*Hylobates*	*Pan*	*Homo sapiens*
Yamazaki and Ishida, 1984			~160		~192
Yamazaki, 1985	~130	~110	~160	~100	~200[b]
Okada, 1985	~150	~125	~130	~135	~190
D'Aout et al., 2002				137	
Schmitt, 2003					~190
Vereecke et al., 2006			151		
Winter, 2009					~190
Pontzer et al., 2014				~110–120[a]	

~: Designates values that are estimates from figures in original papers when tables of values were not provided.
[a]Range of values given are estimated from trials of varying speed.
[b]This is an estimated average of three individuals.

locomotion (Cartmill, 2002). This constraint also complicates functional interpretations of the postcranial anatomy of earlier hominins. As our window on hominin evolutionary history expands further back in time, the morphological differences between known bipeds and inferred bipeds become more marked, lowering confidence in reconstructions of locomotor and postural behaviors (Stern and Susman, 1983; Latimer and Lovejoy, 1990; Latimer, 1991; Ward, 2002; Lovejoy et al., 2009b; Wood and Harrison, 2011; White et al., 2015).

A related problem concerns the form of locomotion that preceded bipedalism and the extent to which the last common ancestor (LCA) of *Homo* and *Pan* resembled African apes in its morphology and behavior (Washburn, 1967; Tuttle, 1974; Stern, 1975; Prost, 1980; Gebo, 1996; Richmond et al., 2001; Orr, 2005; Kivell and Schmitt, 2009). Recent studies of postcranial remains of Miocene apes and the early hominin *Ardipithecus ramidus* suggest that the LCA lacked derived features associated with knuckle-walking, vertical climbing, and suspensory locomotion, indicating that the LCA was unlike *Pan* and *Gorilla* in how it moved through its environment (Lovejoy et al., 2009a,b; Almécija et al., 2015; White et al., 2015; but see Young et al., 2015). This inference requires corroboration from additional fossil discoveries, but if it is accepted as the working hypothesis, then reconstructing the locomotor and postural repertoire of the LCA represents an additional complication to understanding the origin of bipedalism. Such reconstructions add another layer of uncertainty to functional interpretations of the morphocline between the LCA and the first undoubted bipeds.

Given that many important aspects of human anatomy and locomotion are unique among primates, these problems are likely to remain intractable for many of the traits associated with hominin bipedality. However, previously documented variation in hip extension during bipedalism in nonhuman primates provides an opportunity to strengthen the comparative framework used to infer locomotor behavior in early hominins. Studies of bipedal kinematics in nonhuman primates have focused primarily on only a few anthropoid genera: *Ateles*, *Macaca*, *Hylobates*, and *Pan*.[1] Kinematic data show that when these primates walk bipedally, they do so with a hip

that is more flexed than the posture typically adopted by humans (e.g., O'Neill et al., 2015), but, importantly, there is variation among these taxa. Measured relative to the trunk, human peak hip extension averages approximately 190–200 degrees (Yamazaki and Ishida, 1984; Okada, 1985; Yamazaki, 1985; Schmitt, 2003; Winter, 2009). The data for the other primates that have been examined are imprecise, but they suggest two groupings: gibbons and spider monkeys overlap each other and exhibit the most hip extension (~130–160 degrees and ~130–150 degrees, respectively; Yamazaki and Ishida, 1984; Okada, 1985; Yamazaki, 1985), whereas chimpanzees and macaques also overlap each other and demonstrate the least amount of hip extension (for *Pan*, ~100–135 degrees; Okada, 1985; D'Aout et al, 2002; Pontzer et al., 2014; for macaques, 110–125 degrees; Okada, 1985; Yamazaki, 1985) (Table 1).

Variation in the configuration of the ischium has been linked to differences in hip extension and hip extensor moment capabilities between apes and hominins (Robinson, 1972; Fleagle and Anapol, 1992; Sockol et al., 2007; Foster et al., 2013; Pontzer et al., 2014). Humans, fossil *Homo*, and australopiths have shorter and more dorsally projecting ischia than apes (Robinson, 1972; Lovejoy et al., 1973, 2009a; McHenry, 1975; Stern and Susman, 1983). It has been argued that this distinction reflects kinematic and kinetic differences: greater hip extension, increased hamstrings extensor moment arms during extended hip postures, and striding bipedality in hominins versus restricted hip extension, decreased hamstrings extensor moment arms during extended hip postures, and bent-hip, bent-knee bipedality in apes (Sockol et al., 2007; Foster et al., 2013; Pontzer et al., 2014). If ischial morphology can be interpreted in this way, then it has implications for reconstructing locomotion in earlier parts of the hominin fossil record. For example, *Ardipithecus ramidus* has a long, African-ape-like ischium (Lovejoy et al., 2009a), which may indicate a bent-hip, bent-knee gait (Foster et al., 2013; Pontzer et al., 2014; but see Lovejoy and McCollum, 2010).

In this study, we test this functional relationship by examining variation in ischial morphology in *Ateles*, *Macaca*, *Hylobates*, *Pan*, and *Homo*. We predict that because gibbons and spider monkeys tend to extend their hips to a greater degree than chimpanzees and macaques when adopting bipedal postures and locomotion, they will have relatively shorter and more dorsally oriented ischia. In other words, we expect that the

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[1]Studies on primate kinematics vary in how study species are referenced; many studies refer only to the generic designation or common name of a species. Therefore, here we use the genus as the operational unit.

ischial morphology of gibbons and spider monkeys will diverge from chimpanzees and macaques in the direction of humans. We acknowledge the possibility that there are finer-grained kinematic distinctions among these genera than our groupings recognize, but we do not think that the currently available data allow us to make such distinctions with confidence. We emphasize that we are not arguing that natural selection has shaped these nonhuman primates for bipedal locomotion. Rather, it is likely that the observed differences in hip-extension capability in these taxa are related to other aspects of their locomotor and postural repertoires, and that the differences in their bipedal kinematics are incidental. Nevertheless, such differences allow us to test for a functional (i.e., not necessarily adaptive) association.

MATERIALS AND METHODS

Sample

The dataset comprised 554 anthropoid individuals representing 29 taxa (Table 2). In addition to the primary analysis involving *Homo*, *Pan*, *Hylobates*, *Ateles*, and *Macaca*, we conducted a secondary analysis that investigated patterns of variation in ischial form across anthropoids by examining taxa whose bipedal kinematics have not been characterized. Depending on the outcome of our primary analysis, this more inclusive comparative perspective may identify species that can provide further tests of the link between ischial morphology and hip extension when bipedal kinematic data for these taxa become available. The platyrrhine sample included three atelid genera, five cebids, and one pitheciid. The catarrhine sample included 10 species of cercopithecines, 3 species of colobines, each genus of great apes, 3 hylobatids, and humans. The majority of specimens were wild-shot, but some of the individuals were from captive or unknown rearing situations. Adulthood was assessed by fusion of the pelvic epiphyses, which fuse later than the emergence of the third molars. Some congeneric species were pooled to increase sample sizes (i.e., *Ateles*, *Leontopithecus*, *Pithecia*, *Saimiri*, and *Papio*), but only when such species did not exhibit significant differences in the measurements used for this study (see Lewton, 2012).

Data Collection

Ischium measures were calculated from three-dimensional landmarks using Euclidean distances (Fig. 1; see also Lewton, 2012, 2015). Ischial length is the distance from the center of the acetabulum to the caudal-most projection of the ischium, taken parallel to the ischial long axis. Ilioischial angle is the angle in degrees between the iliac plane and the long axis of the ischium. The iliac plane was defined by three landmarks: (1) anterior superior iliac spine, (2) the intersection of the arcuate line and the sacrum, and (3) the center of the acetabulum. Our approximation of ilioischial angle is similar to that of Berge et al. (1984) but differs in construction of the iliac axis. Using a two-dimensional planar projection in sagittal view, Berge et al. (1984) defined a line between the center of the acetabulum and the ventralmost point of the auricular surface at the iliosacral junction (following Rickenmann, 1957) and calculated the angle between this axis and the ischial axis. Instead of projecting anatomy into a sagittal plane, our method defined a reference plane through the ilium. Because we use the iliac plane as a reference plane for defining ilioischial angle, ilium orientation can potentially influence ilioischial angle. However, in most of the taxa included in this study, the iliac plane—as defined here—is oriented approximately coronally, which limits the effects of differences in ilium orientation. *Homo*, with laterally oriented ilia, is the obvious exception to this description (e.g., Lovejoy et al., 1999); as a result, *Homo* was excluded from ilioischial angle analyses. Thus, the angulation of the ischium relative to the coronal iliac plane represents degree of dorsal orientation; a larger ilioischial angle indicates a more dorsally oriented ischium (Fig. 1).

Because ilioischial angle is a dimensionless variable, it can be compared across taxa of different body sizes, but ischial length requires size adjustment. As body mass data were not available for the majority of museum specimens, ischial length was converted to a shape ratio (*sensu* Jungers et al., 1995) by dividing it by the superoinferior diameter of the acetabulum. The latter measurement has been used as an independent size variable in previous studies of ischial morphology (e.g., Robinson, 1972; Stern and Susman, 1983; Fleagle and Anapol, 1992). Acetabular diameter was taken as the distance from (1) the point on the superior acetabular rim that marks the intersection of the iliac margin and acetabulum to (2) the point on the inferior rim directly across from the first point and parallel to the long axis of the ischium. All analyses except for intraspecific regressions were performed on ln(ischial length/acetabulum diameter).

Data Analysis

Two sets of analyses were performed. First, a narrowly focused taxonomic sample was used to test for a link between ischial morphology and known ranges of hip extension. This primary sample included species for which there are ample kinematic data on bipedal behaviors: *Ateles* spp., *Macaca* spp., *Hylobates* spp., *Pan troglodytes*, and *Homo sapiens*. Second, an exploratory analysis was performed on a broader comparative sample that included other platyrrhines, cercopithecoids, and hominoids (Table 2). To examine variation in ischial morphology across the primary sample, an analysis of variance (ANOVA) was performed on each ischial variable with taxon as the factor. Pairwise comparisons among genera were made using Tukey's HSD procedure. Our predictions were as follows: for relative ischium length, $Homo < Ateles/Hylobates < Macaca/Pan$; for ilioischial angle, $Ateles/Hylobates > Macaca/Pan$ (humans were excluded for the reason noted above, but they do have a dorsally oriented ischium, Robinson, 1972). Because the ANOVA was performed on a limited number of genera using data for individuals (i.e., not species means), phylogenetic comparative methods were not feasible. For the broader comparative portion of the analysis, we simply present box plots for various taxa to contextualize the patterns documented in the primary analysis.

We also investigated the relationship between relative ischium length and ilioischial angle using (1) interspecific phylogenetic generalized least squares regression (PGLS) on species means of ilioischial angle on ln-ischium length scaled by acetabulum diameter, and (2)

TABLE 2. Sample composition and summary statistics for ischium length, acetabulum diameter, and ilioischial angle

Taxon	Locomotion	N	Ischium length (mm)		Acetabulum diameter (mm)		Ilioischial angle (degrees)	
			Mean	SD	Mean	SD	Mean	SD
ATELIDAE								
Alouatta caraya	AQ/Suspension	20	32.2	2.5	18.5	1.3	36.5	4.4
Female		10	30.7	0.9	18.0	0.8	37.9	4.0
Male		10	33.7	2.8	19.1	1.4	35.1	4.6
Ateles spp.	Suspension	21	41.0	2.3	23.1	1.4	40.9	4.1
Female		9	40.6	2.4	22.9	1.2	40.1	2.9
Male		11	41.6	2.2	23.2	1.6	41.7	5.0
Unknown		1	39.0		23.0		39.2	
Lagothrix lagotricha	AQ/Suspension	10	34.3	2.6	19.4	1.3	35.0	3.9
Female		3	34.3	0.6	19.4	1.0	35.6	0.8
Male		6	35.3	1.8	19.8	1.1	33.8	4.5
Unknown		1	28.4		16.7		40.1	
CEBINAE								
Cebus albifrons	AQ	15	28.7	2.3	12.9	1.1	30.9	5.2
Female		8	27.5	1.6	12.7	0.8	29.7	5.2
Male		7	30.1	2.1	13.2	1.4	32.4	5.2
Cebus apella	AQ	22	30.3	2.3	13.5	0.6	28.1	3.5
Female		8	28.3	2.4	13.3	0.7	29.5	3.8
Male		14	31.4	1.2	13.7	0.5	27.3	3.2
Saimiri spp.	AQ	20	19.4	1.1	8.5	0.4	25.7	3.0
Female		10	18.8	0.8	8.3	0.4	25.1	2.8
Male		10	19.9	1.1	8.7	0.4	26.3	3.3
CALLITRICHINAE								
Cebuella pygmaea	AQ	12	8.8	0.5	4.2	0.3	14.5	5.6
Female		5	8.9	0.2	4.1	0.1	12.8	6.3
Male		7	8.7	0.6	4.2	0.3	15.7	5.2
Leontopithecus spp.	AQ	19	18.3	0.9	8.2	0.3	15.9	3.4
Female		10	18.2	1.0	8.2	0.4	16.5	3.5
Male		9	18.5	0.8	8.1	0.3	15.2	3.3
PITHECIINAE								
Pithecia spp.	AQ/Leaping	9	25.3	1.6	12.6	0.9	24.4	5.3
Male		8	25.6	1.4	12.7	0.8	24.2	5.7
Unknown		1	23.1		11.5		26.3	
CERCOPITHECINAE								
Cercocebus torquatus	AQ/TQ	11	39.9	6.4	19.4	3.2	44.0	8.0
Female		5	34.6	3.7	16.4	2.0	40.9	9.3
Male		5	45.1	4.5	22.2	1.1	48.4	5.3
Unknown		1	40.2		20.3		37.5	
Cercopithecus mitis	AQ	24	36.6	5.0	16.8	1.6	36.8	6.5
Female		13	32.8	1.7	15.8	0.8	36.7	6.5
Male		10	42.0	2.5	18.2	1.1	38.3	5.4
Unknown		1	33.0		14.6		23.9	
Chlorocebus aethiops	AQ/TQ	20	34.8	4.5	15.2	1.6	35.8	7.8
Female		9	31.8	1.7	14.2	1.0	36.1	9.9
Male		10	37.9	4.2	16.1	1.6	35.9	6.3
Unknown		1	30.5		15.5		32.1	
Erythrocebus patas	TQ	6	42.6	7.1	20.7	2.2	41.4	6.8
Female		1	36.6		18.0		37.9	
Male		3	45.0	5.9	22.3	0.6	46.0	7.1
Unknown		2	42.0	11.3	19.6	2.5	36.2	1.0
Macaca fascicularis	AQ	37	32.7	4.0	15.8	1.7	43.7	6.3
Female		13	28.7	1.8	14.1	0.7	39.7	6.1
Male		21	34.7	2.9	16.7	1.2	45.6	5.7
Unknown		3	36.3	4.6	17.2	1.6	47.9	1.5
Macaca nemestrina	TQ	13	41.1	6.4	20.5	2.8	40.0	9.2
Female		3	33.3	2.3	18.3	2.3	42.0	4.9
Male		9	43.1	5.4	21.2	2.8	38.2	10.2
Unknown		1	45.8		21.0		50.4	
Mandrillus sphinx	TQ	8	53.7	9.8	26.8	4.9	38.3	7.6
Female		3	42.5	2.8	21.6	2.4	37.6	9.7
Male		4	60.9	4.2	30.3	3.0	41.3	5.5
Unknown		1	58.4		28.0		28.7	

TABLE 2. *Continued*

Taxon	Locomotion	N	Ischium length (mm)		Acetabulum diameter (mm)		Ilioischial angle (degrees)	
			Mean	SD	Mean	SD	Mean	SD
Miopithecus talapoin	AQ	15	21.7	2.2	9.6	0.8	36.5	5.0
Female		11	20.9	1.8	9.3	0.7	36.1	5.7
Male		4	23.8	2.0	10.3	0.6	37.8	2.5
Papio spp.	TQ	45	51.8	6.5	26.7	2.8	50.1	7.0
Female		14	46.8	4.9	24.5	2.2	54.1	4.5
Male		23	53.8	5.0	27.9	2.4	48.3	7.0
Unknown		8	54.6	8.7	27.2	2.6	48.6	8.5
Theropithecus gelada	TQ	6	49.9	2.7	23.3	2.0	49.8	6.5
Female		5	49.0	1.7	22.7	1.6	49.8	7.3
Male		1	54.3		26.2		49.7	
COLOBINAE								
Colobus guereza	AQ/Leaping	23	38.3	3.3	21.0	1.1	44.5	7.4
Female		12	37.1	2.1	20.7	1.0	46.3	6.2
Male		7	40.9	2.8	21.7	1.3	43.2	5.6
Unknown		4	37.3	5.1	20.8	0.8	41.5	12.8
Nasalis larvatus	AQ/Leaping	20	45.7	5.2	25.3	2.8	41.3	4.6
Female		7	40.1	2.3	22.5	1.1	43.3	2.8
Male		11	49.4	2.2	27.2	1.4	40.0	5.4
Unknown		2	45.1	7.5	25.2	5.0	41.5	4.5
Procolobus badius	AQ/Leaping	10	38.2	2.5	19.8	1.2	41.7	9.8
Female		5	37.3	2.9	18.9	0.8	46.0	9.3
Male		5	39.1	1.9	20.6	0.8	36.3	8.3
HOMINOIDEA								
Gorilla gorilla	TQ	21	101.7	11.7	53.5	5.9	34.9	6.1
Female		10	92.0	6.1	48.4	1.7	34.1	5.4
Male		11	110.5	7.8	58.1	4.3	35.6	6.8
Homo sapiens	Bipedal	40	72.7	6.3	51.2	3.8	56.6	6.6
Female		20	69.1	4.8	49.2	3.4	56.9	7.1
Male		20	76.3	5.5	53.3	3.1	56.2	6.2
Hylobates hoolock	Suspension	13	32.7	1.2	21.0	0.7	38.0	3.9
Female		6	33.1	0.8	21.0	0.9	38.2	3.5
Male		7	32.4	1.4	20.9	0.7	37.9	4.5
Hylobates lar	Suspension	24	30.4	1.8	20.5	1.1	44.8	4.8
Female		11	29.6	1.8	20.5	0.8	45.1	5.8
Male		13	31.1	1.5	20.5	1.3	44.5	3.9
Pan troglodytes	TQ	41	77.4	5.5	39.7	3.4	46.5	4.6
Female		21	76.8	5.4	38.6	2.8	46.4	4.5
Male		20	78.0	5.7	40.8	3.6	46.7	4.9
Pongo pygmaeus	Suspension	19	73.5	7.5	42.5	4.7	44.1	7.8
Female		2	66.1	3.9	36.5	0.6	38.5	11.1
Male		15	75.9	6.1	44.1	3.9	44.3	7.8
Unknown		2	63.0	7.1	36.7	2.9	48.6	4.4
Symphalangus syndactylus	Suspension	10	35.1	3.2	26.1	2.6	42.5	8.6
Female		8	34.1	2.7	25.1	1.7	42.0	9.1
Male		2	39.2	0.1	30.0	1.1	46.3	

AQ: arboreal quadruped, TQ: terrestrial quadruped.

intraspecific ordinary least squares (OLS) regressions of ilioischial angle on ln-ischium length on individuals within taxa. The PGLS was carried out using a consensus phylogeny obtained from the 10kTrees Project (Arnold et al., 2010). Tree branch lengths were transformed using a maximum likelihood lambda transformation. This portion of the analysis tested Fleagle and Anapol's (1992) suggestion that a short ischium is correlated with a high degree of dorsal projection in taxa that typically use extended hip postures. Analyses were run separately for males, females, and the combined-sex sample. The results of these separate analyses were similar, and thus only the combined-sex results are presented.

All analyses were conducted using JMP Pro (Version 12.1.0, SAS Institute Inc.), except for PGLS, which was performed using the "caper" package (Orme et al., 2013) in R (R Core Team, 2016).

RESULTS
Analysis of Genera with Kinematic Data

Relative ischium length differs across genera in the primary sample ($F = 225.3$, $P < 0.0001$). Humans have relatively shorter ischia than spider monkeys and gibbons, and the latter two have shorter ischia than macaques and chimpanzees, as predicted. Our predictions did not differentiate spider monkeys from gibbons, or
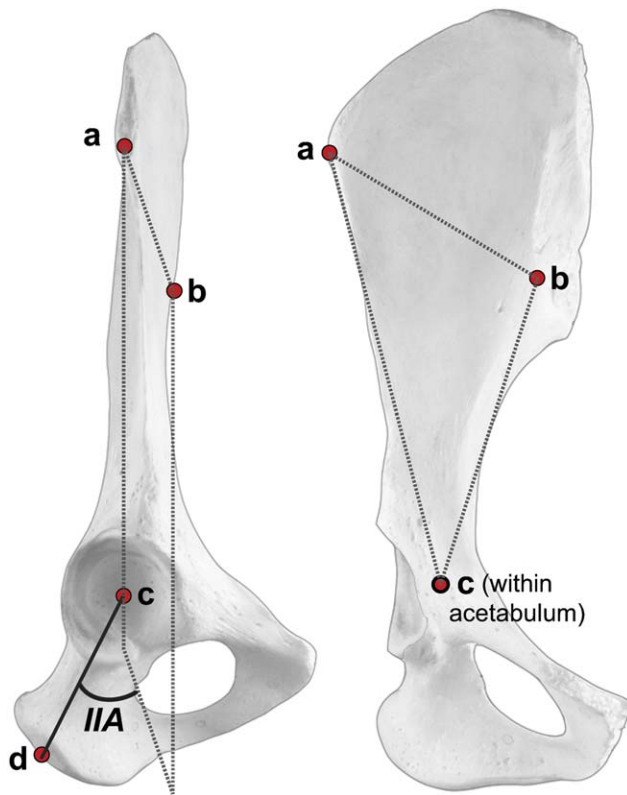
Fig. 1. Measurements used in this study. Ischial length is the distance from the center of acetabulum (c) to the most distal point on the ischium that forms a line with the center of the acetabulum that is parallel to the long axis of the ischium (d). Ilioischial angle (IIA) is the angle between the line defined by points c and d and the common plane of points a, b, and c: respectively, the anterior superior iliac spine, the intersection of the arcuate line and the sacrum, and the center of the acetabulum. Not shown is the superoinferior diameter of the acetabulum (see description in Materials and Methods section).
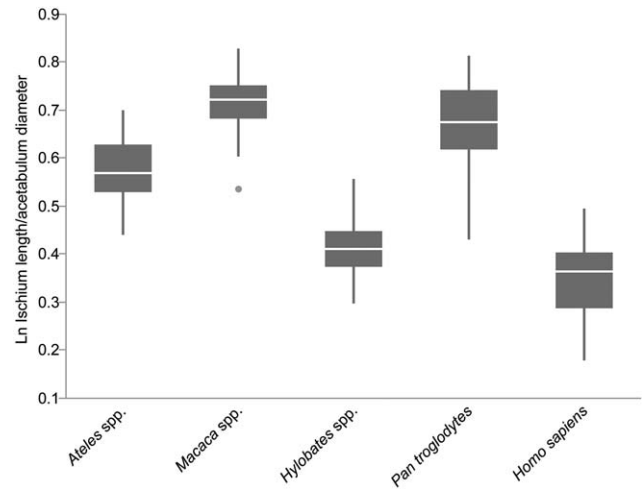

Fig. 2. Boxplots of relative ischial length in the primary sample. Chimpanzees and macaques have the longest ischia relative to acetabulum diameter, spider monkeys and gibbons are intermediate, and humans have the shortest ischia. All pairwise comparisons are statistically significant.
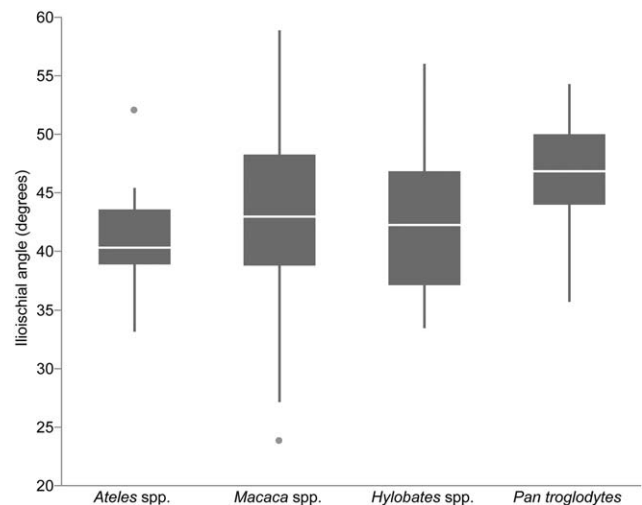

Fig. 3. Boxplots of ilioischial angle in the primary sample (humans are excluded from analysis). Although chimpanzees are significantly different from the other taxa, note the broad overlap in ranges among all four taxa.

macaques from chimpanzees, because, in our view, the existing kinematic data on ranges of hip extension did not permit it. However, post hoc comparisons demonstrate that each genus is significantly different from all others ($P < 0.03$): listed from shortest to longest relative ischium length: humans, gibbons, spider monkeys, chimpanzees, and macaques (Fig. 2).

The ANOVA on ilioischial angle is statistically significant ($F = 5.78$, $P = 0.0009$). However, post hoc comparisons demonstrate that, contrary to predictions, chimpanzees have a larger ilioischial angle than the other three taxa, and spider monkeys, gibbons, and macaques are not statistically distinguishable from each other (Fig. 3). The prediction that nonhuman taxa that are capable of greater hip extension when moving bipedally would have more dorsally angled ischia is therefore not supported.

Variation across Anthropoidea

Placed in the broader context of anthropoid variation, hylobatids and humans have shorter ischia than all of the other taxa in our sample (Fig. 4). Cercopithecines, cebines, and callitrichines have the longest ischia. Between these two extremes are *Pithecia*, African apes,

colobines, atelids, and *Pongo* in roughly that order, although there is much overlap in their ranges. A few notable patterns are evident. First, within the Platyrrhini, atelids have the shortest ischia, with *Lagothrix* and *Alouatta* being very similar to *Ateles*. Second, *Pongo* has a shorter ischium than the African apes and is intermediate between the latter group and hylobatids and humans. Moreover, *Pongo* is similar to atelids.

With regard to ilioischial angle, there is little variation in catarrhines, and hylobatids do not have larger angles than other catarrhines (Fig. 5). In fact, *Hylobates hoolock* has one of the lowest angles, on average, in the catarrhine sample. There is more variation among platyrrhines, with atelids having the largest angles,
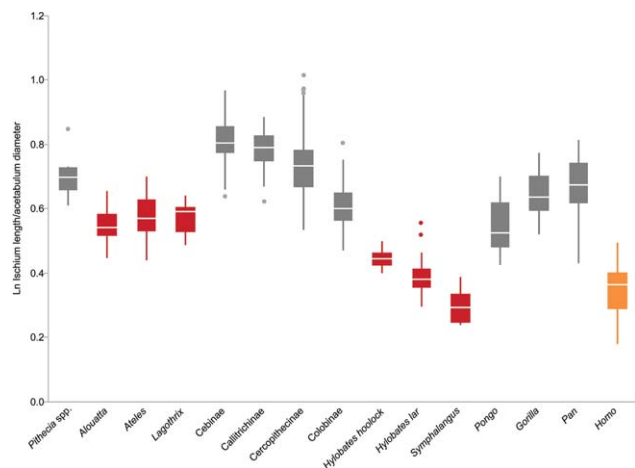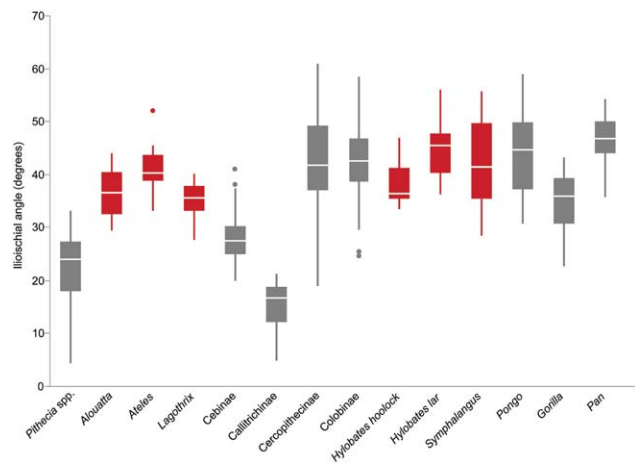
Fig. 4. Boxplots of relative ischial length in the anthropoid sample. Hominoids and atelids are listed by species, while the other taxa are summarized by subfamily. Suspensory hylobatids and atelids are colored red, while humans are orange. Among platyrrhines, atelids have the shortest ischia, cebids have the longest ischia, and *Pithecia* is intermediate. Among hominoids, hylobatids and humans have the shortest ischia, African great apes have the longest ischia, and *Pongo* is intermediate.

Fig. 5. Boxplots of ilioischial angle in the anthropoid sample. Hominoids and atelids are listed by species, while the other taxa are summarized by subfamily. Suspensory hylobatids and atelids are colored red. Note the large ranges of ilioischial variation within groups, and the broad overlap in ilioischial angle among groups and between platyrrhines and catarrhines. Among platyrrhines, callitrichines have the least dorsally projecting ischia, atelids have the most dorsally projecting ischia, and cebines and *Pithecia* are intermediate.

callitrichines having the smallest angles, and *Pithecia* and Cebinae being intermediate. Atelids are similar to catarrhines, whereas the other platyrrhines tend to have smaller angles.

Relationship between Ilioischial Angle and Ischium Length

The PGLS regression computed using species means demonstrates that the relationship between ilioischial angle and relative ischium length is not significant

(combined-sex $r = -0.36$, $P = 0.06$, Fig. 6 and Table 3). However, this relationship is statistically significant within the male primate sample ($P = 0.03$), indicating a possible trend. The majority of the intraspecific OLS regressions of ilioischial angle on ln-ischium length (i.e., not size-adjusted) are not statistically significant. Overall, these results offer little support for the idea that ischium length and angle are functionally correlated.

DISCUSSION

Differences in ischial length and orientation between apes and hominins have previously been linked to differences in hip extension capabilities and hip extensor moment arms in these species (e.g., Robinson, 1972). An apelike ischium (i.e., long and caudally oriented) has been associated with limited hip extension, while a humanlike ischium (i.e., short and dorsally oriented) has been associated with greater hip extension, facilitating striding bipedalism. In this study, we tested this functional association by examining patterns of variation in ischial length and orientation in a small sample of primates that are characterized by differences in hip extension during bipedal postures and locomotion. Our predictions were supported for ischial length, but not for ilioischial angle. Nonhuman primates that exhibit greater hip extension during bipedal behaviors (*Hylobates*, *Ateles*) have relatively shorter ischia than genera with less hip extension (*Pan*, *Macaca*), as predicted. Furthermore, our analysis indicated that the nonhuman genera can be ordered based on ischium length in the following sequence: *Hylobates* < *Ateles* < *Pan* < *Macaca*. Therefore, if there is a functional link between ischium length and hip extension, as our results suggest, then this ordering predicts finer-grained distinctions in hip-extension capabilities during bipedal locomotion among these genera. This prediction can be tested by future kinematic studies that acquire data that are higher in resolution than what is currently available in the literature (Table 1). In contrast to our results for ischium length, *Ateles*, *Macaca*, and *Hylobates* are not distinguishable from each other in ilioischial angle, but all three have significantly smaller angles than *Pan*. Thus, in opposition to our predictions, *Pan* has a more dorsally oriented ischium than *Hylobates* and *Ateles*.

A broader exploration of patterns of ischial variation in anthropoid primates confirmed and extended the morphological characterizations made using the more restricted primary sample. Hylobatids and humans have the shortest ischia among anthropoids, with *Symphalangus* having an ischium that is slightly shorter than that of humans, on average. *Ateles* falls in the middle of the anthropoid range of variation in ischium length and it overlaps the other atelids, colobines, and *Pongo*. The latter genus is intermediate between African apes ($P < 0.002$) and hylobatids and humans ($P < 0.02$). This observation is notable because there is anecdotal evidence that orangutans extend their hips more than African apes when moving bipedally (Crompton et al., 2003; Thorpe et al., 2007). The fact that *Pongo* has a shorter ischium than other great apes is consistent with this claim, but quantitative data on orangutan bipedal kinematics are necessary to establish the existence of differences in hip extension that mirror differences in ischium length. Viewed from the perspective of the evolution of
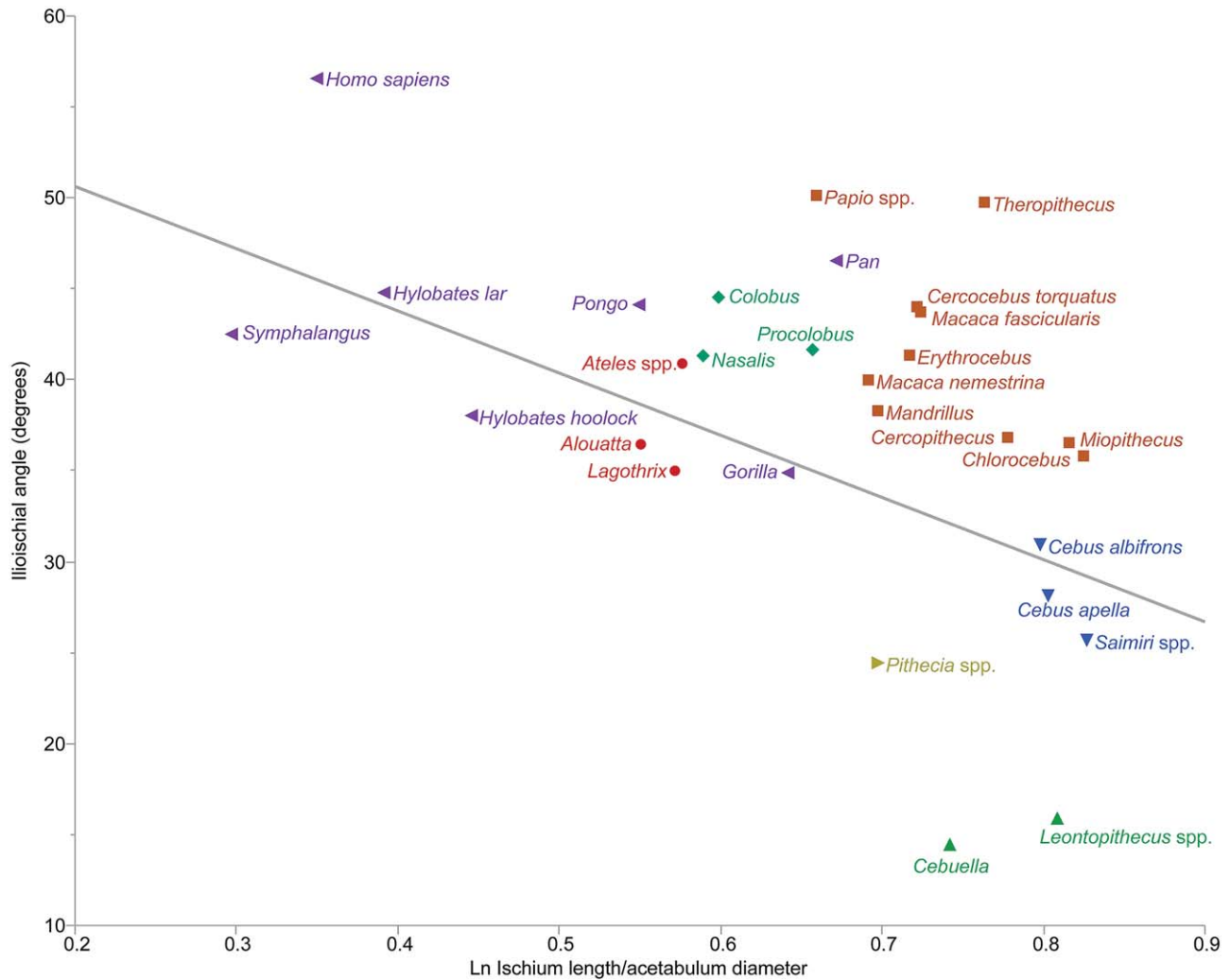
Fig. 6. Bivariate relationship between ilioischial angle and relative ischial length in the combined-sex sample of anthropoids. Data points are taxon means. *Homo sapiens* is included for visual comparison but was not part of the statistical analysis. The two variables are uncorrelated among anthropoids (r = −0.36). The phylogenetic generalized least squares regression equation is: $y = 50.8 - 24.1$(ln-ischium length/ acetabulum diameter). Labels as follows: hominoids purple, cercopithecines brown, colobines teal, atelids red, cebines blue, *Pithecia* yellow, and callitrichines green. See Table 3 for all regression results.

bipedal kinematics in early hominins, such data are critical.

The broader comparative analysis also reinforces the lack of a clear functional signal in ischial orientation. Hylobatids and *Ateles* are not consistently differentiated from other atelids or catarrhines. The taxa that stand out in this portion of the analysis are *Pithecia*, cebines, and callitrichines, all of which have, for the most part, more caudally oriented ischia than the remaining anthropoids. Unexpectedly, Old World monkeys have large ilioischial angles, indicative of a dorsally projecting ischium. This result may be influenced by the presence of ischial callosities in these species, which result in dorsoventral and mediolateral expansion and flaring of the distal surface of the ischium (Rose, 1974). The presence of ischial callosities in hylobatids (Miller, 1945; Rose, 1974) may also confound comparisons of ischial dorsal projection in this group. However, *Pan* lacks ischial callosities and has a large ilioischial angle as well, indicating that our conclusion regarding the absence of a functional signal in this feature is not compromised by the presence or absence of ischial callosities.

We did not detect a relationship between ilioischial angle and ischium length. These results run contrary to expectations derived from previous work by Fleagle and Anapol (1992), who concluded that species that use extended hip postures have shorter and more dorsally projecting ischia, while quadrupeds exhibit longer and more distally projecting ischia. There are methodological differences between our study and Fleagle and Anapol's that could account for the contrasting results. First, Fleagle and Anapol (1992) used different measurements. Instead of ischium length as computed here, they used distal projection, the distance from the center of the acetabulum to the most caudal point on the ischium, parallel to the long axis of the ilium in lateral view. Similarly,

TABLE 3. Interspecific and intraspecific regression results

	Intercept	Slope	*r*	SE	Slope 95% confidence interval	*P*
Interspecific PGLS regression of ilioischial angle on ln-ischium length/acetabulum diameter, primate-wide sample						
Combined sex	50.8	−24.1	−0.36	12.4	−48.35–0.20	0.06
Female	51.8	−25.4	−0.38	12.2	−49.39–−1.40	0.05
Male	53.1	−27.3	−0.41	11.8	−50.36–−4.18	**0.03**
Intraspecific OLS regression of ilioischial angle on ln-ischium length, combined sex sample						
ATELIDAE						
Alouatta caraya	56.4	−36.3	−0.43	17.9	−71.41–−1.21	0.06
Ateles spp.	30.1	18.8	0.30	13.5	−7.67–45.18	0.18
Lagothrix lagotricha	28.4	11.5	0.14	28.9	−45.11–68.06	0.70
CEBINAE						
Cebus albifrons	26.6	5.4	0.06	23.4	−40.47–51.24	0.82
Cebus apella	49.1	−26.2	−0.49	10.3	−46.38–−5.97	**0.02**
Saimiri spp.	39.6	−16.9	−0.33	11.3	−38.98–5.26	0.15
CALLITRICHINAE						
Cebuella pygmaea	39.9	−34.3	−0.40	24.7	−82.64–14.11	0.20
Leontopithecus spp.	12.3	4.4	0.05	23.1	−40.84–49.66	0.85
PITHECIINAE						
Pithecia spp.	67.7	−62.0	−0.84	16.1	−93.60–−30.46	**0.01**
CERCOPITHECINAE						
Cercocebus torquatus	54.6	−14.7	−0.18	26.1	−65.92–36.47	0.59
Cercopithecus mitis	59.5	−29.1	−0.38	15.1	−58.77–0.57	0.07
Chlorocebus aethiops	54.3	−22.4	−0.26	19.3	−60.34–15.46	0.26
Erythrocebus patas	59.3	−25.1	−0.37	31.1	−86.00–35.86	0.47
Macaca fascicularis	48.4	−6.5	−0.05	20.0	−45.81–32.78	0.75
Macaca nemestrina	48.5	−12.3	−0.09	43.1	−96.92–72.22	0.78
Mandrillus sphinx	20.5	25.5	0.21	48.6	−69.79–120.72	0.62
Miopithecus talapoin	37.9	−1.6	−0.02	18.7	−38.29–35.06	0.93
Papio spp.	41.3	13.4	0.16	12.8	−11.76–38.50	0.30
Theropithecus gelada	118.2	−89.7	−0.67	49.1	−185.94–6.55	0.14
COLOBINAE						
Colobus guereza	41.1	5.7	0.05	22.9	−39.13–50.59	0.80
Nasalis larvatus	41.3	−0.02	−0.0003	21.0	−41.19–41.15	1.00
Procolobus badius	39.9	2.7	0.02	55.3	−105.69–111.16	0.96
HOMINOIDEA						
Gorilla gorilla	26.9	12.5	0.15	19.1	−24.87–49.88	0.52
Homo sapiens	58.3	−5.0	−0.05	16.1	−36.55–26.52	0.76
Hylobates hoolock	32.7	12.0	0.09	42.5	−71.37–95.31	0.78
Hylobates lar	54.5	−24.7	−0.32	15.6	−55.23–5.74	0.13
Pan troglodytes	53.0	−9.8	−0.19	8.5	−26.42–6.76	0.25
Pongo pygmaeus	64.3	−36.5	−0.37	23.2	−81.91–8.88	0.13
Symphalangus syndactylus	44.4	−6.4	−0.04	63.5	−130.81–118.01	0.92

Bold denotes statistical significance at $P < 0.05$.

instead of ilioischial angle, they used dorsal projection, the distance from the center of the acetabulum to the most dorsal point on the ischium, perpendicular to the long axis of the ilium in lateral view. Second, Fleagle and Anapol focused mainly on strepsirrhines and tarsiers, specifically specialized vertical clingers and leapers. While our sample contains some species that can be classified as leapers (e.g., *Pithecia*, *Cebuella*, perhaps some of the colobines), none of them is as specialized as strepsirrhine and tarsier leapers (Fleagle and Anapol, 1992). Moreover, our sample included cercopithecoids, whereas theirs did not. Given these considerations, we interpret our results as not necessarily contradicting the arguments presented by Fleagle and Anapol (1992); rather, we conclude that the relationship between ischial length and orientation is not straightforward, with multiple factors influencing these variables together and independently, making it difficult to identify a general relationship between them across primates.

Because the pattern of support for our predictions is mixed, it is important to emphasize that there are other aspects of anatomy, not accounted for in our analysis, that influence hip extension. Such factors include the architecture of the hip muscles (fiber length and orientation), the arrangement of ligaments (more versus less restrictive), and the ability to position various components of the trunk and forelimbs in a way that facilitates balance on two legs (e.g., mobility of the lumbar vertebral column; Machnicki et al., 2016). The number of alternative pathways by which two species can achieve similar degrees of hip extension may weaken the interspecific relationship between aspects of ischial form (i.e., ischial orientation) and hip extension to the point where broader phylogenetic and functional sampling is required to detect it.

Relevant in this context is Fleagle and Anapol's (1992) use of the hypothesized link between ischial form and hip extension in hominins as a framework for evaluating the functional morphology of the pelvis in vertical clingers and leapers (VCLs; e.g., tarsiers, indriids). They argued that VCLs and hominin bipeds are similar in at least one key respect: they both rely on extended hip

postures and emphasize speed of limb excursion over hip extensor power, requiring a short, dorsally oriented ischium, which increases the moment arm of the hip extensors when the hip is fully extended. Although Fleagle and Anapol were interested in explaining the distinctive ischial morphology of VCLs, the analogy can be interpreted as providing reciprocal support for the proposed link between ischial form and hip extension in hominins. However, as we outline below, the strength of this analogy is uncertain due to the lack of a well-corroborated functional model for interpreting variation in the ischium and its associated musculature. The significance of the similarity between hominins and VCLs is therefore unclear.

Ischial Functional Morphology and the Role of the Hamstrings during Locomotion

The ischial tuberosity and distal aspect of the ischiopubic ramus serve as the origin for the hamstrings muscles, which insert on the thigh and leg: *mm. semitendinosus*, *semimembranosus*, long head of *biceps femoris*, and the posterior portion of *adductor magnus*. Three of the hamstrings muscles are biarticular and cross both the hip and knee joints, resulting in the capacity to extend the hip and flex the knee. The remaining muscle—*m. adductor magnus*—only crosses the hip. Robinson's (1972) connection between ischial morphology and locomotor efficiency, and his placement of *Australopithecus* and *Paranthropus* within this functional context, was influential for modern studies of early hominin locomotion, particularly with regard to the role of the hamstrings (see also Lovejoy et al., 1973). He described great ape ischia as being approximately perpendicular to the long axis of the femur in quadrupedal stance, but nearly parallel to the femur during bipedal postures (i.e., perpendicular to the substrate). Robinson hypothesized that this configuration in large-bodied apes increases the moment arm of the hamstrings during quadrupedalism but decreases the moment arm and restricts the ability to extend the thigh beyond vertical during bipedalism. Robinson contrasted this functional scenario with that proposed for humans, where the dorsally projecting ischium facilitates thigh extension beyond vertical and ultimately allows humans "to stride and to complete a stride with power" (Robinson, 1972, p. 73). Recent experimental biomechanics studies on locomotor kinematics and kinetics in both chimpanzees and humans have also suggested that dorsal ischial orientation in humans is an adaptation for striding bipedalism because it increases the hamstrings' ability to generate large hip moments during extended limb postures by increasing the hamstrings moment arm (Sockol et al., 2007; Foster et al., 2013; Pontzer et al., 2014).

At the core of Robinson's (1972) functional hypothesis linking ischial anatomy to locomotor efficiency are assumptions of hamstrings function during bipedality. Testing his hypothesis requires data on how the hamstrings function during bipedal behaviors in humans. The implicit assumption of the hypothesis correlating ischial orientation with hip extensor mechanics is that the hamstrings muscle group actively extends the thigh at the end of single and/or full stance phase. Both clinical and musculoskeletal modeling research in humans demonstrates that the hamstrings muscle group is a secondary extensor of the hip, the primary extensor being *m. gluteus maximus* (Waters et al., 1974; Arnold et al., 2005). Furthermore, clinical research on human gait indicates that the hamstrings muscles are capable of producing a large hip-extension moment, especially when the hip is flexed and the hamstrings moment arm is relatively long (Pohtilla, 1969; Waters et al., 1974; Németh and Ohlsén, 1985; Dostal et al., 1986; Arnold et al., 2005; Hicks et al., 2008). However, the primary function of the hamstrings during gait is not to extend the hip, but to decelerate the limb at the end of swing phase, thereby controlling the limb's contact with the substrate at heel-strike (Battye and Joseph, 1966; Winter and Robertson, 1978; Neptune et al., 2004).

Electromyographic (EMG) studies on lower extremity muscle activations during stance and swing phases of human walking gait support this idea (Battye and Joseph, 1966; Waters et al., 1974; Mann et al., 1986). Hamstrings activation is variably biphasic in humans, with the first contraction occurring in all subjects at the end of swing phase to decelerate the limb, and the second contraction (which is low in magnitude) occurring in only 50% of subjects at the end of stance phase to prevent forward pitching of the trunk (Battye and Joseph, 1966). These EMG studies also demonstrate that the hamstrings, as a group, contribute 31%–48% of the total hip extensor moment during a variety of thigh postures from full extension (i.e., standing) to 90 degrees of hip flexion (Waters et al., 1974). Importantly, the capacity of the hamstrings to exert a hip extensor moment is greatest when the hip is flexed (Waters et al., 1974), as the hamstrings moment arm is greatest at approximately 35 degrees of hip flexion (Németh and Ohlsén, 1985). The flexed hip position in which the hamstrings are capable of greatest torque is in postures where large force production is required, such as in climbing (Waters et al., 1974). Thus, human hamstrings leverage and torque capacity are functionally linked to extending the hip from relatively flexed postures. In other words, the hamstrings play a multifunctional role in gait and physical activities, and do not appear to be exclusively adapted for the mechanical demands that occur during walking.

If a dorsally oriented ischium in humans is an adaptation for increasing the mechanical advantage of the hamstrings during extended limb postures, then there should be a decrease in hip-muscle moments when walking with a bent-hip, bent-knee (BHBK) gait (Stern and Susman, 1983). However, in living humans, there are no differences between extended and BHBK postures in either active hip-muscle volume or hip moments during bipedal walking (Foster et al., 2013). Instead, differences in cost between striding bipedalism and BHBK gait are driven by an increase in active knee-muscle volume and knee moments (Foster et al., 2013). These observations suggest that knee anatomy contributes more toward total energetic cost than hip anatomy and do not provide support for the hypothesis that a dorsally oriented ischium in humans is an adaptation for increasing the mechanical advantage of the hamstrings during extended limb postures.

In sum, there is no evidence that the activity of the hamstrings is critical for extending the hindlimb at the end of stance phase in human bipedalism. Returning to Fleagle and Anapol's (1992) analogy between bipedal hominins and VCLs, we note that, although these two

forms of locomotion are both characterized by extended-hip postures, they differ kinematically and kinetically in important ways (leapers: Demes et al., 1996, 1999, humans: Winter, 2009), and the short, dorsally oriented ischia observed in both groups may not serve the same biological roles (*sensu* Bock and von Wahlert, 1965). Fleagle and Anapol (1992) emphasized the increase in the hamstrings mechanical advantage at extreme ranges of extension provided by the ischia of vertical clingers and leapers: "we propose that the dorsally extended ischium of vertical clingers, like that of bipedal hominids, is an adaptation to increase the lever arm of the hip extensors when the hip is near full extension, i.e., in line with the trunk" (p. 298). However, our review of the relevant literature on human bipedalism presented above suggests that mechanical advantage at high degrees of extension is unlikely to explain the configuration found in humans because the hamstrings do not extend the hip at this point during the bipedal gait cycle. Thus, an analogy between bipedal hominins and VCLs that relies on the mechanical advantage of the hamstrings may not be appropriate.

An alternative hypothesis is that ischial shortening and dorsal reorientation in hominins and VCLs permits greater hip extension by removing a physical barrier. A long, caudally oriented ischium and its associated muscles, tendons, and ligaments may obstruct extension of the femur when a primate that is typically quadrupedal adopts a bipedal posture. According to this scenario, the modifications observed in hominins and VCLs clear the way for greater hip extension. However, this idea is challenged by Hammond's (2014) analysis of passive ranges of joint motion in anesthetized primates. Although her data suggest that *Hylobates* is capable of greater hip extension than some other nonhuman anthropoids, consistent with our results for ischial length, other aspects of her analysis are not congruent with ours. Most significantly, her data for *Ateles* suggest that this genus has an unexceptional range of passive hip extension in comparison to the other species in her sample, including those that have longer and more caudally oriented ischia, such as *Cebus* (cf. Figs. 5 and 6). This observation contradicts the hypothesis that a long, caudally oriented ischium acts as a physical constraint on hip extension, regardless of how well passive ranges of motion reflect the movements that primates use under their own power. Thus, we conclude that the functional significance of ischial length and orientation remains an open question, and that the relevance of vertical clingers and leapers to this issue remains to be demonstrated. We note, however, that trait-behavior correlations do not necessarily need to be thoroughly understood if the goal is simply to use the trait to infer behavior (Ross et al., 2002).

Reconstructing Early Hominin Posture and Locomotion

As noted in the introduction, the pelvic remains of *Ardipithecus ramidus* indicate that this species had a relatively long and caudally oriented ischium, similar to African apes and different from those of geologically younger hominins (Lovejoy et al., 2009a). This morphological distinction has led to suggestions that hip extension in *Ar. ramidus* was limited, whereas later hominins

were capable of adopting a more humanlike striding gait (Foster et al., 2013; Pontzer et al., 2014). Our data provide comparative support for a link between ischium length and hip-extension capability in primates and are therefore consistent with the idea that the ischial shortening observed in post-*Ardipithecus* hominins reflects a greater ability to extend the hip during bipedal locomotion, implying that *Ar. ramidus* relied on a BHBK posture when moving bipedally (e.g., Foster et al., 2013; Pontzer et al., 2014; but see Lovejoy and McCollum, 2010). Such a conclusion comports with other aspects of the anatomy of *Ar. ramidus* that also suggest that this early hominin did not use a humanlike striding gait when walking bipedally (e.g., its prehensile foot; Lovejoy et al., 2009c). A number of caveats apply to this inference, however.

First, the association between ischium length and hip extension is based on a contrast among three groups: humans versus *Hylobates/Ateles* versus *Pan/Macaca*. Such an association is suggestive, and it provides critical evidence for reconstructing locomotor behaviors, but the correlation cannot be considered particularly strong, because it is based on a limited sample of phylogenetically distant species. Second, as noted above, there are differences within this sample that we did not predict owing to the imprecision of the kinematic data. For example, based on the broadly overlapping ranges of extension values documented for *Ateles* and *Hylobates* in different studies (Table 1), we did not predict a difference between them, but our results show that *Hylobates* has a shorter ischium. This distinction might indicate a subtle difference in extension capability between these genera, as already discussed, or it might indicate that these two genera achieve similar degrees of hip extension in different ways. The same can be said for *Pan* and *Macaca*. This possibility, in combination with the small sample of taxa used to support the association, limits our confidence with regard to inferring lower degrees of hip extension in *Ar. ramidus* during bipedal movement in comparison to the more derived hominins. Third, using the association between ischium length and hip extension is further complicated by the fact that the other aspect of ischial morphology examined here—orientation—did not vary in the predicted way in our analysis. With regard to hominins, ischial length and orientation are typically discussed as part of an integrated functional complex. The fact that they varied independently among the taxa in our primary sample (i.e., taxa with kinematic data) presents a challenge to the functional hypothesis proposed for them.

To be clear, we do not view our results as necessarily refuting the existence of a link between ischial orientation and hip extension during bipedal locomotion in hominins. Interpreted strictly, our results simply mean that we are unable to corroborate this hypothesized functional relationship. The marked differences between apes and humans, as well as the changes observed in the hominin fossil record, suggest that there is a connection. Moreover, it is not difficult to develop a hypothesis to resolve the conflict between our results and the other observations. For example, note that hylobatids are similar to humans in ischial length (Figs. 2 and 4) even though hylobatids do not extend their hips to the degree that humans do during bipedal locomotion. Thus, one might hypothesize that the difference between humans

and gibbons in hip extension is related, at least in part, to ischial orientation. Perhaps there is some factor that constrains how short the ischium can be, and that once this limit is reached, additional modifications to the ischium that allow greater hip extension take the form of a change in orientation. In other words, perhaps the relationships among hip extension, ischium length, and ischial orientation are not linear. However, because humans are so unusual, the original problem posed in the introduction returns: we cannot test this hypothesis using currently available data because none of the primates in our sample extend their hips to the degree that humans do when moving bipedally.

This discussion of ischial orientation highlights deficiencies in the framework used to infer locomotor and postural behaviors in fossil hominins that are not always explicitly acknowledged. Importantly, this point applies to other aspects of pelvic morphology. The reconstructed ilium of *Ar. ramidus* provides an example. The ilium of this species is characterized by a number of features that align it with later hominins and distinguish it from the ilia of extant apes: a short and more sagittally oriented iliac blade, distinct anterior inferior iliac spine, and less vertical separation between the acetabulum and auricular surface (Lovejoy et al., 2009a; White et al., 2015). It is reasonable to hypothesize that these features indicate bipedal locomotion in *Ardipithecus*, but it is also important to recognize the limits of our current functional framework and view these reconstructions with appropriate skepticism (Wood and Harrison, 2011). Two observations are relevant here. First, as noted above, mounting evidence indicates that the LCA of *Pan* and *Homo* was not particularly similar to extant apes (Lovejoy et al., 2009a; Almécija et al., 2013, 2015). Second, the postcranial skeleton of *Ar. ramidus* has been described as differing "dramatically from that of any living primate" and having "unique adaptations for both arboreal and terrestrial locomotion" (White et al., 2015, p. 4879). These characterizations of the LCA and earliest hominins inject considerable uncertainty into our understanding of the ancestral hominin locomotor and postural adaptations, complicating attempts to link pelvic form specifically to bipedal locomotion. A *Pan*-like LCA would provide a strong anchor for interpreting the more plesiomorphic end of the hominin iliac morphocline (e.g., *Ar. ramidus*). In contrast, recognizing that the LCA was functionally unique with respect to extant primates, and specifically that it was very different from living apes, removes that anchor and raises the possibility that some of the humanlike morphologies documented in the *Ardipithecus* ilium represent adaptations for something other than bipedalism, and that these traits were exapted or modified for bipedalism in subsequent hominins.

Given that the functional implications of the deviations from human pelvic morphology observed in various fossil hominins are unclear, we argue that features traditionally used to diagnose bipedality need to be subjected to greater scrutiny, especially when they are used to make inferences about the earliest part of the hominin fossil record. Applying greater skepticism to existing form-function links has the potential to stimulate creative approaches to looking at the hominin fossil record that may advance our understanding of the critical earliest period of our evolutionary history in unexpected ways.

CONCLUSION

In this study, we tested the hypothesis that ischial length and orientation are linked with hip-extension capability in a sample of primates that are known to differ in this variable when adopting bipedal postures and locomotion. Our predictions received mixed support. Variation in ischial length in nonhuman primates conformed to our expectations, with taxa that use greater extension during bipedalism (*Hylobates*, *Ateles*) having shorter ischia than taxa that rely on flexed-hip postures (*Pan*, *Macaca*). On the other hand, we did not find the predicted relationship between ischial orientation and hip extension. These results provide limited support for previous attempts to use ischial morphology to infer bipedal kinematics in early hominins. It has been suggested, for example, that the long, caudally oriented ischium of *Ardipithecus ramidus* indicates that this species used a bent-hip, bent-knee posture when it moved bipedally. Our results for ischial length are consistent with this idea, and with the related argument that ischial shortening in subsequent hominins (e.g., *Australopithecus afarensis*) signals greater hip extension and a shift to a more humanlike mode of striding bipedalism. On the other hand, the lack of association between ischial orientation and hip extension in our comparative sample complicates attempts to link it with changes in bipedal kinematics during this important period of hominin evolution.

LITERATURE CITED

Almécija S, Tallman M, Alba DM, Pina M, Moyá-Solá S, Jungers WL. 2013. The femur of *Orrorin tugenensis* exhibits morphometric affinities with both Miocene apes and later hominins. Nat Commun 4:2888. doi: 10.1038/ncomms3888.

Almécija S, Smaers JB, Jungers WL. 2015. The evolution of human and ape hand proportions. Nat Commun 6:717. doi: 10.1038/ncomms8717.

Arnold AS, Anderson FC, Pandy MG, Delp SL. 2005. Muscular contributions to hip and knee extension during the single limb stance phase of normal gait: a framework for investigating the causes of crouch gait. J Biomech 38:2181–2189.

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

Battye CK, Joseph J. 1966. An investigation by telemetering of the activity of some muscles in walking. Med Biol Eng 4:125–135.

Berge C, Orban-Segebarth R, Schmid P. 1984. Obstetrical interpretation of the australopithecine pelvic cavity. J Hum Evol 13: 573–587.

Bock WJ, von Wahlert G. 1965. Adaptation and the form-function complex. Evolution 19:269–299.

Cartmill M. 2002. Paleoanthropology: science of mythological charter? J Anthropol Res 58:83–201.

Crompton RH, Thorpe S, Weijie W, Yu L, Payne R, Savage R, Carey T, Aerts P, Van Elsacker L, Hofstetter A, et al. 2003. The biomechanical evolution of erect bipedality. Cour Forsch-Inst Senckenberg 243:135–146.

D'Aout K, Aerts P, De Clercq D, De Meester K, Van Elsacker L. 2002. Segment and joint angles of hind limb during bipedal and quadrupedal walking of the bonobo (*Pan paniscus*). Am J Phys Anthropol 119:37–51.

Darwin C. 1871. The descent of man, and selection in relation to sex. London: John Murray.

Day MH. 1986. Bipedalism: pressures, origins, and modes. In: Wood B, Martin L, Andrews P, editors. Major topics in primate and human evolution. New York: Cambridge University Press. p. 188–201.

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

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

Dostal WF, Soderberg GL, Andrews JG. 1986. Actions of hip muscles. Phys Ther 66:351–359.

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

Foster AD, Raichlen DA, Pontzer H. 2013. Muscle force production during bent-knee, bent-hip walking in humans. J Hum Evol 65: 294–302.

Gebo DL. 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. Am J Phys Anthropol 101:55–92.

Hammond AS. 2014. In vivo baseline measurements of hip joint range of motion in suspensory and nonsuspensory anthropoids. Am J Phys Anthropol 153:417–434.

Hewes GW. 1961. Food transport and the origin of hominid bipedalism. Am Anthropol 63:687–710.

Hicks JL, Schwartz MH, Arnold AS, Delp SL. 2008. Crouched postures reduce the capacity of muscles to extend the hip and knee during the single-limb stance phase of gait. J Biomech 41:960–967.

Hunt KD. 1994. The evolution of human bipedality: ecology and functional morphology. J Hum Evol 26:183–202.

Jablonski NG, Chaplin G. 1993. Origin of habitual terrestrial bipedalism in the ancestor of the Hominidae. J Hum Evol 24:259–280.

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

Kivell TL, Schmitt D. 2009. Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. Proc Natl Acad Sci USA 106:14241–14246.

Latimer B. 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Senut B, Coppens Y, editors. Origine(s) de la bipédie chez les Hominidés. Paris: CNRS. p. 169–176.

Latimer B, Lovejoy CO. 1990. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. Am J Phys Anthropol 82:125–133.

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

Lewton KL. 2015. Pelvic form and locomotor adaptation in strepsirrhine primates. Anat Rec 298:230–248.

Lovejoy CO. 1981. The origin of man. Science 211:341–350.

Lovejoy CO, Cohn MJ, White TD. 1999. Morphological analysis of the mammalian postcranium: a developmental perspective. Proc Natl Acad Sci USA 96:13247–13252.

Lovejoy CO, Heiple KG, Burstein AH. 1973. The gait of *Australopithecus*. Am J Phys Anthropol 38:757–780.

Lovejoy CO, McCollum MA. 2010. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait. Phil Trans R Soc B 365:3289–3299.

Lovejoy CO, Suwa G, Spurlock L, Asfaw B, White TD. 2009a. The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. Science 326:71e1–71e6. doi: 10.1126/science.1175831.

Lovejoy CO, Suwa G, Simpson SW, Matternes JH, White TD. 2009b. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestor with African apes. Science 326:100–106.

Lovejoy CO, Latimer B, Suwa G, Asfaw B, White TD. 2009c. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. Science 326:72e1–72e8. doi: 10.1126/science.1175832.

Machnicki AL, Spurlock LB, Strier KB, Reno PL, Lovejoy CO. 2016. First steps of bipedality in hominids: evidence from the atelid and proconsulid pelvis. PeerJ 4:e1521. doi: 10.7717/peerj.1521.

Mann RA, Moran GT, Dougherty SE. 1986. Comparative electromyography of the lower extremity in jogging, running, and sprinting. Am J Sports Med 14:501–510.

McHenry HM. 1975. The ischium and hip extensor mechanism in human evolution. Am J Phys Anthropol 43:39–46.

Miller RA. 1945. The ischial callosities of primates. Am J Anat 76: 67–91.

Németh G, Ohlsén H. 1985. In vivo moment arm lengths for hip extensor muscles at different angles of hip flexion. J Biomech 18: 129–140.

Neptune RR, Zajac FE, Kautz SA. 2004. Muscle force redistributes segmental power for body progression during walking. Gait Posture 19:194–205.

Okada M. 1985. Primate bipedal walking: comparative kinematics. In: Kondo S, editor. Primate morphophysiology, locomotor analyses and human bipedalism. Tokyo: University of Tokyo Press. p. 47–58.

O'Neill MC, Lee LF, Demes B, Thompson NE, Larson SG, Stern JT, Jr, Umberger BR. 2015. Three-dimensional kinematics of the pelvis and hind limbs in chimpanzee (*Pan troglodytes*) and human bipedal walking. J Hum Evol 86:32–42.

Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2013. caper: Comparative Analyses of Phylogenetics and Evolution in R. R Package version 0.5.2. http://CRAN.R-project.org/package=caper.

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.

Pohtilla JF, 1969. Kinesiology of hip extension at selected angles of pelvifemoral extension. Arch Phys Med Rehabil 50:241–250.

Pontzer H, Raichlen DA, Rodman PS. 2014. Bipedal and quadrupedal locomotion in chimpanzees. J Hum Evol 66:64–82.

Prost JH. 1980. Origin of bipedalism. Am J Phys Anthropol 52: 175–189.

R Core Team. 2016. R: A language and environment for statistical computing. Available from: http://www.r-project.org/

Richmond BG, Begun DR, Strait DS. 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. Yrbk Phys Anthropol 44:70–105.

Rickenmann E. 1957. Beiträge zur vergleichenden Anatomie, insbesondere des Beckens bei Catarrhinen. Acta Anatomica 1–118.

Robinson JT. 1972. Early hominid posture and locomotion. Chicago: University of Chicago Press.

Rodman PS, McHenry HM. 1980. Bioenergetics and the origin of hominid bipedalism. Am J Phys Anthropol 52:103–106.

Rose MD. 1974. Ischial tuberosities and ischial callosities. Am J Phys Anthropol 40:375–384.

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

Schmitt D. 2003. Insights into the evolution of human bipedalism from experimental studies of humans and other primates. J Exp Biol 206:1437–1448.

Sockol MD, Raichlen DA, Pontzer H. 2007. Chimpanzee locomotor energetics and the origin of human bipedalism. Proc Natl Acad Sci USA 104:12265–12269.

Stern JT. 1975. Before bipedality. Yrbk Phys Anthropol 19:59–68.

Stern JT, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. Am J Phys Anthropol 60:279–317.

Thorpe SKS, Holder RL, Crompton RH. 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science 316:1328–1331.

Tuttle R. 1974. Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. Curr Anthropol 15: 389–398.

Videan EN, McGrew WC. 2002. Bipedality in chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*): testing hypotheses on the evolution of bipedalism. Am J Phys Anthropol 118:184–190.

Ward CV. 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? Yrbk Phys Anthropol 45: 185–215.

Washburn SL. 1967. Behaviour and the origin of man. Proc R Anthropol Inst 1967:21–27.

Waters RL, Perry J, McDaniels JM, House K. 1974. The relative strength of the hamstrings during hip extension. J Bone Joint Surg Am 56:1592–1597.

Wheeler PE. 1984. The evolution of bipedality and loss of functional body hair in hominids. J Hum Evol 13:91–98.

White TD, Lovejoy CO, Asfaw B, Carlson JP, Suwa G. 2015. Neither chimpanzee nor human, *Ardipithecus* reveals the surprising ancestry of both. Proc Natl Acad Sci USA 112:4877–4884.

Winter DA. 2009. Biomechanics and motor control of human movement. Hoboken: John Wiley & Sons, Inc.

Winter DA, Robertson DGE. 1978. Joint torque and energy patterns in normal gait. Biol Cybernetics 29:137–142.

Wood B, Harrison T. 2011. The evolutionary context of the first hominins. Nature 470:347–352.

Yamazaki N. 1985. Primate bipedal walking: computer simulation. In Kondo S, editor. Primate morphophysiology, locomotor analyses and human bipedalism. Tokyo: University of Tokyo Press. p. 105–130.

Yamazaki N, Ishida H. 1984. A biomechanical study of vertical climbing and bipedal walking in gibbons. J Hum Evol 13:563–571.

Young NM, Capellini TD, Roach NT, Alemseged Z. 2015. Fossil hominin shoulders support an African ape-like last common ancestor of humans and chimpanzees. Proc Natl Acad Sci USA 112:11829–11834.