

First steps of bipedality in hominids: evidence from the atelid and *Proconsul* pelvis

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Upright walking absent a bent-hip-bent-knee (BHBK) gait requires lumbar lordosis, a ubiquitous feature in all currently known hominids. Its first appearance is therefore a central problem in human evolution. Atelids, which use the tail during suspension, exhibit demonstrable lordosis and can achieve full extension of their hind limbs during terrestrial upright stance. Although obviously homoplastic with hominids, the pelvic mechanisms facilitating lordosis appear largely similar in both taxa with respect to abbreviation of upper iliac height coupled with broad sacral alae. Both provide spatial separation of the most caudal lumbar(s) from the iliac blades. A broad sacrum is therefore a likely facet of earliest hominid bipedality. All tailed monkeys have broad alae. By contrast all extant apes have very narrow sacra, which promote "trapping" of their most caudal lumbar(s) to achieve lower trunk rigidity during suspension. The alae in the tailless Miocene hominoid *Proconsul nyanzae* appear to have been quite broad, a character state that may have been primitive in Miocene hominoids not yet adapted to suspension and, by extension, exaptive for earliest bipedality in the hominid/panid last common ancestor (LCA). This hypothesis receives strong support from other anatomical systems preserved in *Ardipithecus ramidus*.

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**First steps of bipedality in hominids: evidence from the atelid and
Proconsul pelvis**

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35 **Abstract**

36 Upright walking absent a bent-hip-bent-knee (BHBK) gait requires lumbar lordosis, a ubiquitous feature
37 in all currently known hominids. Its first appearance is therefore a central problem in human evolution.
38 Atelids, which use the tail during suspension, exhibit demonstrable lordosis and can achieve full
39 extension of their hind limbs during terrestrial upright stance. Although obviously homoplastic with
40 hominids, the pelvic mechanisms facilitating lordosis appear largely similar in both taxa with respect to
41 abbreviation of upper iliac height coupled with broad sacral alae. Both provide spatial separation of the
42 most caudal lumbar(s) from the iliac blades. A broad sacrum is therefore a likely facet of earliest
43 hominid bipedality. All tailed monkeys have broad alae. By contrast all extant apes have very narrow
44 sacra, which promote "trapping" of their most caudal lumbar to achieve lower trunk rigidity during
45 suspension. The alae in the tailless Miocene hominoid *Proconsul nyanzae* appear to have been quite
46 broad, a character state that may have been primitive in Miocene hominoids not yet adapted to
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48 ancestor (LCA). This hypothesis receives strong support from other anatomical systems preserved in
49 *Ardipithecus ramidus*.

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51 Key Words: lordosis, *Ardipithecus*, *Proconsul*, *Brachyteles*, muriqui, bipedalism

52

53 **Introduction**

54 Bipedal walking is arguably the most distinctive character of all known hominids. While the
55 subject of past debate (Stern 2000), there is general consensus that striding bipedality was maturely
56 developed in all species of *Australopithecus* as evidenced by a short broad pelvis, adducted great toe,
57 strong bicondylar angle, and a lumbar spine containing 6 functional segments based on zygapophyseal
58 orientation (Kimbel & Deleuzene 2009; Lovejoy 2005a; Lovejoy 2005b; Lovejoy 2007; Ward 2003; Ward
59 2013; Williams & Russo 2015). Bipedal adaptations also are advanced in the earlier hominid,
60 *Ardipithecus ramidus* given its short and laterally flared iliac crest, large interauricular distance, and
61 despite its abducent great toe, mid-foot rigidity and habitual toe-off from its lateral digits (White et al.
62 2009b). Similar adaptations for bipedality also may have been present in *Orrorin tugenensis* based on
63 proximal femoral morphology (Richmond & Jungers 2008).

64 Africa is by far the most likely locus of the adoption of bipedality because the three most
65 closely related clades (panids, gorillids, and hominids¹) are all also African (Prado-Martinez et al. 2013;
66 Suwa et al. 2007). Environmental reconstructions for *Ardipithecus* show that it occupied a partially
67 forested and/or closed woodland habitat (Pickford & Senut 2001; Vignaud et al. 2002; White et al.
68 2009a). Given environmental trends of the Mio-Pliocene, it is reasonable to presume that the
69 environmental setting occupied by the last common ancestor (LCA) was at least as forested, and that
70 bipedality was not simply a response to occupation of more open habitats. Instead, the "why" of earliest
71 bipedality is more likely an element of a broad adaptive shift in social structure, as evidenced by the
72 simultaneous loss of the sectorial canine complex (Lovejoy 1981; Lovejoy 2009; Suwa et al. 2009; White
73 et al. 2009b).

74 Characterizations of the initial morphological transition of "how" an ancestral quadruped *first*
75 became adapted to bipedality have gone largely unexplored. While bipedal walking is achievable for
76 short bouts in apes, such efforts involve a bent-hip-bent-knee (BHBK) gait that can be fatiguing and
77 would presumably have discouraged its habitual adoption (Crompton et al. 1998). Instead, in all
78 hominids in which the lumbar spine and/or pelvis are available for examination, separation of the most
79 caudal lumbar from the iliac wings permits lordosis necessary for complete hind limb extension. This
80 reflects two major morphological shifts: 1) reduction of iliac height relative to the lumbosacral junction,
81 and 2) relatively broad sacral alae. Both help eliminate physical contact between the transverse
82 processes (TPs) of the most caudal lumbar vertebrae and the iliac blades, and these two features

¹ We recognize these taxa at the family level: hominidae, panidae, and gorillidae (White et al. 2009b).

83 characterize all known hominids. What is currently unknown is how and when either appeared in
84 hominid phylogeny.

85 *Pelvic Anatomy in Ardipithecus*

86 There is mounting evidence that the LCA of panids and hominids lacked most of the specialized
87 (derived) characters associable with suspension and vertical climbing seen in extant African apes [e.g.,
88 narrowed sacrum, elongated iliac isthmus, modification of femoral insertion characters of the hip
89 musculature, reduction in the number of lumbar vertebrae to an average of 3.5, elongated sacra (by
90 conversion of somite fates from lumbar to sacral) and elongated thorax (by conversion of somite fates
91 to thoracic—especially advanced in the bonobo)] (Almecija et al. 2013; Lovejoy & McCollum 2010;
92 McCollum et al. 2010). It is unlikely that these characters were present in the LCA, since the metacarpus,
93 carpus, limb proportions, foot, femur, humerus and ulna in ARA-VP-6/500 (“Ardi”) exhibit morphologies
94 that lack definitive modifications for suspension (Almecija et al. 2015; Lovejoy et al. 2009a; Lovejoy et al.
95 2009b). They are instead more consistent, based on the considerably likely substantial body mass of
96 *Ardipithecus*, with deliberate quadrumanal climbing and bridging accompanied by ulnar withdrawal
97 and posterolateral shoulder relocation with attendant invagination of the vertebral column (see below)
98 (Lovejoy et al. 2009c; White et al. 2015). These were accompanied by substantial lateral enlargement of
99 the iliac blade and reduction of the retroauricular region of the os coxa in *Ar. ramidus* indicating spinal
100 invagination into the thorax (Lovejoy & McCollum 2010; Lovejoy et al. 2009d).

101 Exceptions to the generalized primitive state in *Ar. ramidus* are its “upper” pelvis and lateral
102 foot, which are consistent with moderately advanced upright walking. Its ilium is similar to those of later
103 hominids and includes an anterior inferior iliac spine (AIIS) likely developed by a separate ossification
104 center, a hominid apomorphy. Unfortunately, the specimen lacks both a lumbar column and a sufficient
105 amount of its sacrum to permit *direct* demonstration of its capability for lordosis (Lovejoy et al. 2009a;
106 Lovejoy et al. 2009b; Lovejoy et al. 2009c; Lovejoy et al. 2009d). This presents an interpretive
107 conundrum. How can we then deduce how lordosis was likely achieved in the earliest phases of upright
108 walking in the hominid clade?

109

110 *The lumbosacral and pelvic anatomy of the LCA*

111 The pelvis of the middle Miocene *Proconsul* was generally similar to those of Old World
112 monkeys (OWMs) (Ward 1991; Ward 1993; Ward et al. 1993). Its ilia were superoinferiorly long with a
113 substantial gap between the sacral promontory and pubic symphysis, and the iliac fossa was quite
114 narrow. The os coxa exhibits a relatively massive retroauricular portion (i.e., the iliac tuberosity) (Ward

115 1991). It is now clear that *Proconsul* and other Miocene hominoids such as *Nacholapithecus* lacked tails
116 (Nakatsukasa et al. 2003a; Nakatsukasa et al. 2003b; Nakatsukasa et al. 2004; Ward et al. 1991), even
117 though most were still largely above branch quadrupeds (Ward 1993; Ward 2015). Tail loss was likely a
118 hominoid synapomorphy by at least 17.9 mya (Nakatsukasa et al. 2004). The lumbar column was long,
119 probably numbering six or seven ribless vertebrae (McCollum et al. 2010; Ward 1991).

120 A dramatic shift in pelvic proportions is present in *Ar. ramidus*. The relative sizes of its pre- and
121 retro-auricular portions are almost fully modern and very unlike those of *Proconsul*, having been
122 transformed by substantial vertebral column invagination and virtually certain migration of the lumbar
123 TPs from mid-centrum to pedicle (Lovejoy et al. 2009c; White et al. 2009b). A pelvic fragment of the
124 Miocene taxon *Pierolapithecus catalaunicus* (Hammond et al. 2013) and the os coxa of the late Miocene
125 *Oreopithecus bambolii* have been described (Harrison 1986; Harrison 1991; Rook et al. 1999; Straus
126 1963; Wood & Harrison 2011), although the latter's poor state of preservation appears not to have been
127 fully appreciated (White et al. 2015). Arguments that its lumbar vertebral bodies show wedging to
128 facilitate lordosis (Kohler & Moya-Sola 1997) have been rigorously rejected (Russo & Shapiro 2013). The
129 specimen's extreme compression during fossilization puts little confidence in claims that it exhibited a
130 "true" AHS [i.e., one developed via a secondary apophysis (White et al. 2015)], as its preserved
131 morphology is wholly unlike those of hominids [*contra* (Harrison 1991; Harrison & Rook 1997; Straus
132 1963)]. Nevertheless, these Miocene fossils do provide a basis for reconstructing the LCA's general pelvic
133 form.

134 The iliac isthmus in late Miocene pelvises must have still been superoinferiorly long with a
135 substantial "promontory-symphysis vertical gap," but likely with some lateral expansion (i.e., "flaring")
136 of the iliac fossa (Hammond et al. 2013). *P. catalaunicus* suggests some modifications of the limbs,
137 thorax and pelvis for more competent arboreal clambering and deliberate climbing (including ulnar
138 withdrawal and a more elliptical thorax), but not to the degree seen in *Ar. ramidus* (Moya-Sola et al.
139 2004). This is especially true of the position of the lumbar TPs, whose origins were not yet fully
140 pedicular. In the present paper we distinguish "deliberate climbing" as a form of relatively cautious
141 arboreal locomotion, based on the relatively large body mass of several Miocene specimens that would
142 render the leaping and acrobatic behavior seen in smaller primates hazardous because of substrate
143 reactive elasticity in the arboreal canopy. We distinguish "vertical climbing" (*sensu stricto*) as that form
144 of large substrate ascension performed specifically by living African apes [see (DeSilva 2009; Fleagle et
145 al. 1981) for illustration].

146 This pelvic form of Miocene apes such as *Proconsul*, when combined with a relatively long
147 lumbar column, provide a basis for two key questions concerning the acquisition of lordosis: 1) how
148 permissive were the vertebral column and pelvis of the LCA for lordosis, and 2) which of the two
149 morphological shifts observed in *Ardipithecus* (reduction of iliac height and/or expansion of sacral
150 breadth) was more likely to have occurred first in the evolution of earliest hominid bipedality?

151

152 *Atelids as a model for the relationships between the pelvis and lumbar column*

153 New World atelids (*Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*) are unique because they
154 frequently engage in caudal suspension (Cant 1986; Iurck et al. 2013; Johnson & Shapiro 1998; Lemelin
155 1995; Mittermeier & Fleagle 1976), which requires their lower spines to enter into substantial sagittal
156 recurvature similar to lordosis in hominids (Figure 1a). Examination of their pelvic and sacral
157 morphology therefore may provide indirect evidence of the potential pathway toward lordosis in
158 earliest hominids.

159 To address this we have reviewed lumbar and pelvic form and function in primates. First, we
160 report observations of terrestrial behavior of northern muriquis (*Brachyteles hypoxanthus*) that
161 demonstrate the importance of lordosis for extended hind limb posture. We also utilize opportunistic
162 observations of bipedal locomotion in *Ateles* which can help place their posture in context. We then
163 report both osteological and anatomical analyses of iliac height, sacral width, and lower lumbar
164 ligamentous support in relevant extant and fossil anthropoids. Finally, we provide a possible scenario for
165 the role of pelvic and sacral form in the evolution of bipedality.

166

167 **Methods**

168 *Brachyteles bipedality*

169 Observations of northern muriquis (*Brachyteles hypoxanthus*) were conducted at the Reserva
170 Particular de Patrimônio Natural-Feliciano Miguel Abdala in Caratinga, Minas Gerais, Brazil. In recent
171 years, as a consequence of substantial local demographic change, we have noted an increase in the
172 frequency and duration of bouts of terrestrial behavior in one population of unprovisioned northern
173 muriquis living at high density (Mourthe et al. 2007; Tabacow et al. 2009). These enable terrestrial
174 behavior to be monitored in a naturalistic setting. We photographed and video recorded bouts of
175 terrestrial behavior to determine the general nature of their bipedal posture (Figure 1 and
176 Supplementary videos 1 & 2). Methods were approved by the University of Wisconsin Animal Care

177 Committee (protocol L00104 through April 2011; then a Wildlife Waiver). The Brazilian government,
178 CNPq, and the administration of the field site provided permission.

179 Given the likely kinematic variability in bipedal locomotion of non-human primates, we also
180 surveyed video resources for further examples of bipedal behavior of atelids (youtube.com and
181 arkive.com). As these involved opportunistic observations the descriptions we have provided are
182 necessarily qualitative.

183

184 *Iliac and Sacral Anatomy*

185 In order to compare the ligamentous anatomy of primates (especially atelids and OWMs) with
186 free (potentially lordotic) versus constrained (restrictive of significant lordosis) last lumbar vertebrae, we
187 conducted detailed dissections of spider (*Ateles sp.*), miquiqui (*Brachyteles*), howler (*Alouatta sp.*), and
188 langur (*Presbytis sp.*) monkeys as well as a single gibbon (*Hylobates sp.*). These specimens are housed in
189 the collections of the Cleveland Museum of Natural History, Kent State University, Northeastern Ohio
190 Medical University, and Case Western Reserve University.

191 We also collected metric and nonmetric data from the pelves of 150 skeletonized specimens in
192 the Cleveland Museum of Natural History and Harvard Museum of Comparative Zoology (Table 1). We
193 paid particular attention to the position of the sacral promontory in relation to the iliac crest and
194 ischiopubic ramus (Figure 2). From these data we calculated the relative iliac height above the sacral
195 promontory within the pelvis (see Figure 3 and its legend). For size normalization we used the
196 mediolateral breadth of the first sacral body and acetabular diameter (Plavcan et al. 2014). To
197 determine the relationship between genus means of log alar breadth and log centrum breadth we
198 performed an analysis of covariance (ANCOVA) with a binary categorical variable (monkey versus ape) as
199 a covariate. To account for potential autocorrelation in related taxa, we used a phylogenetic generalized
200 least squares (pGLS) regression in the 'caper' package in R (Orne et al. 2011; Team 2012). The
201 phylogenetic tree and branch lengths were obtained using from the 10kTrees Project (Supplemental
202 Figure 1) (Arnold et al. 2010).

203

204 *Sacral reconstruction in Proconsul*

205 The partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya, includes a portion of
206 the first sacral body (S-1:KNM-MW 13142-M) (Ward et al. 1993). We used a Kenya National Museum
207 cast as the "core" of our reconstruction of the sacrum. The specimen's inferior portion includes the rim
208 of the first sacral foramen on the left side, thus indicating the craniocaudal height of the S-1 body, and

209 its posterior portion indicates overall thickness of S-1 just lateral to the left articular process (see Figure
210 2 in Ward et al. 1993). The superior surface of the S-1 centrum is essentially intact with only minor
211 abrasion. We used "extra firm" oil-based modeling clay to build the left ala and the (missing) articular
212 facets of S1, incorporating but not obscuring the fossil's S-1 fragment. Elements 2-5 were added as well
213 to create a reasonable facsimile of the likely entire structure of the original specimen, although these
214 details have no bearing on the role of our reconstruction for the current report. Most importantly, for
215 the auricular portion of the sacrum, clay was molded to exactly conform to the well-preserved auricular
216 surface of the nearly complete *os coxa* of KNM-MW-13142-D (also a Kenya National Museum cast). This
217 molded surface was then mated to the S-1 cast absent the addition of any material not needed merely
218 to successfully fuse the clay auricular mold to the left side of the specimen's S-1 plaster body as
219 preserved in the cast. Ward et al. (1993) describe the left ala as being "preserved adjacent to the first
220 sacral body, but [with] its ventral edges...eroded away" (p. 84). Our reconstruction thus minimized the
221 effects of this erosion and produced essentially a 3-D version of Ward et al.'s drawing of the likely pelvic
222 structure of the specimen (their Figure 14), although their version appears to indicate the addition of
223 more material than was actually required for our version. Nevertheless, the latter produced a slightly
224 broader ala than indicated in their scaled drawing (see below). Reconstruction was completed by mirror
225 imaging the (missing) opposite side. The clay model was then molded and cast in plaster.
226 Dimensions of the original specimen are available from Ward et al (1993: p. 85). They report that the
227 "articular surface of the first sacral body is elliptical in outline, 19.6 dorsoventrally and 30.0
228 mediolaterally" .

229

230 **Results**

231 *Lordosis and upright posture in atelids*

232 Atelids have previously been observed during bouts of terrestrial behavior only rarely (Campbell
233 et al. 2005; Dib et al. 1997; Mourthe et al. 2007). Systematic analyses of substrate use in *Brachyteles*
234 showed that by 2005 murequis of all age-sex classes in our study group occasionally engaged in
235 terrestriality, and by 2007 adult males were spending 1.5% of their time on the ground, nearly a 50%
236 increase from the 0.8% of time they spent on the ground in 2006 (Tabacow et al. 2009). Their terrestrial
237 activities had also diversified to include both essential ones (e.g., drinking, traveling across gaps in the
238 forest, and feeding) and nonessential ones (e.g., socializing, including mating, resting, and traveling in
239 areas where arboreal alternatives were available). Increasing terrestriality has continued to be present
240 in this group and in the other three murequi groups in our study population (Strier, Unpublished). In

241 2011, with the use of strategically-deployed motion-sensitive camera traps, we were able to
242 demonstrate for the first time that their terrestriality occurs in the absence of observers. Video images
243 (Supplementary videos 1 & 2) show adult male muriquis descending to the ground to feed on fallen
244 fruits in an open area within the forest, engaging in reassuring social contact as they move through the
245 area with a combination of quadrupedal and bipedal postures. Thus, despite the overall rarity of
246 terrestriality in *Brachyteles*, examination of posture in these naturalistic bouts makes it clear that
247 individuals can readily achieve both a fully erect trunk and a completely extended lower limb. Examples
248 of these postures are shown in Figures 1B-D. These observations indicate that the conformation of
249 muriqui lumbar, pelvic and sacral anatomy are sufficient to produce fully extended hind limb postures,
250 and that such behaviors are not dependent on habituation or training in captive animals.

251 We also searched for other instances of videos depicting bipedal posture and locomotion in
252 atelids to confirm the capacity of bipedal posture and locomotion in other species. As expected these
253 tended to be highly variable given their primary use of quadrupedal locomotion. However, opportunistic
254 observations of spider monkeys (*Ateles* sp.) demonstrate that near or actually fully extended hip and
255 knee postures are utilized during bouts of bipedal locomotion in this species as well (Figure 4,
256 Supplementary video 3).

257 It is important to also note that atelids have undergone a significant degree of spinal
258 invagination which is likely associated with their capacity to lordose. Typical atelid lumbar are shown in
259 Figure 5 (for muriqui see Supplemental Figure 2) and it is quite clear that its TPs are much more dorsally
260 located than are those in specimens of cercopithecoids. Given that a powerful tail is obviously a key
261 adaptation in atelids, it is reasonable to conclude that such invagination is central to their capacity to
262 lumbar lordose—a capacity that is very likely not available to cercopithecoids nor to early hominoids
263 such as *Proconsul*, in which the TPs emanate more ventrally from the vertebral body.

264 This raises a very interesting question with respect to the origins of upright walking, which
265 require at least partial lordosis for reasonable success. Since the LCA obviously lacked a prehensile tail,
266 we may ask whether spinal invagination, which was part of the major shift in bauplan that permitted
267 lateralization of the shoulder, was not also a *critical* exaptation that would eventually facilitate the
268 adoption of upright walking in a descendant of the LCA? Based on TP position in some Miocene
269 hominoids such as *Pierolapithecus* and a similar TP location in atelids (that facilitates their caudal
270 suspension), we suggest that there is a strong probability that it was.

271

272 *Pelvic height reduction*

273 A second and obvious feature (and likely a primary one) that permits lordosis in atelids is the
274 minimal height of its ilium above the sacral promontory, such that the most caudal lumbar is no longer
275 restricted by contact or bilateral ligamentous restriction between the dorsal portions of their shortened
276 iliac blades. This is visually apparent when comparing atelids, such as howler monkey and a miqui, to
277 other anthropoids, such as a langur and a chimpanzee (Figure 2). Metrically this can be demonstrated by
278 an analysis of relative iliac height (Figure 3). Our metric successfully isolates atelids from other monkey
279 and ape groups. Also note the similarly reduced pelvic height compared to humans.

280

281 *Ligamentous support*

282 Either direct articulation of the TPs or bilateral ligamentous attachment would limit mobility in
283 vertebrae located directly between the iliac crests. All the dissected atelids exhibited a free last lumbar
284 vertebra, while the most caudal lumbar in the langur and gibbon were instead located between the
285 more dorsally extended ilia. Dissection revealed significantly less ligamentous restriction in the atelids
286 than in the gibbon and langur, but ligamentous tissue was generally denser and more elaborate in the
287 langur than in the gibbon (Figure 6). Presumably this is related to the retention of a massive erector
288 spinae in the cerpithecoids such as the langur (Figure 5) (Benton 1967), and loss of the tail (with some
289 partial invagination of the spine) in the gibbon. It appears that any lordosis in the langur is accomplished
290 mostly by the superoinferior length and number of its lumbar vertebrae (along with some presumed
291 differential disc compression).

292

293 *Sacral Alar Breadth*

294 Alar breadth and the transverse breadth of the first sacral centrum (as a measure of body size)
295 are plotted in Figure 7. A comparison of the respective regression lines representing monkeys and apes
296 is of interest. The sacra of both NWMs and OWMs are broader than those of suspensory apes. In
297 contrast, *Homo* and *Australopithecus* individuals plot well above the combined monkey regression line.

298 The especially narrow sacrum in apes might be a product of tail loss. However, this is unlikely
299 because sacral breadth is also a critical dimension of the birth canal, which, unlike those of the extant
300 apes, *is much more restrictive in both OWMs and NWMs* (Rosenberg & Trevathan 1995). It is therefore
301 much more likely that the narrowed sacrum in apes is a mechanism that restricts lower lumbar mobility
302 as a response to an increased reliance on suspensory locomotion. Such a change in extant apes is made
303 permissible by their unusually ample birth canal (Lovejoy & McCollum 2010; Schultz 1949).

304

305 *The sacrum of Proconsul*

306 Given the differences in alar breadth between monkeys and apes, it is of great interest to know
307 the sacral dimensions in KNM-MW-13142, assigned to *Proconsul nyanzae*, since it exhibits a primitive
308 pelvis and lumbar column after tail loss. However, the specimen's lateral alar portions are both partially
309 eroded. Ward reported the mediolateral breadth of the first sacral centrum to be 30 mm (see Methods),
310 and that "[t]he farthest lateral point on the *preserved* portion of the wing is 25.7 from the midline"
311 (Ward et al. 1993:85 emphasis added). This would be an unrealistic minimum value of 10.7 mm for alar
312 breadth less centrum breadth ($25.7 - 30/2$), since a substantial portion of each ala is obviously missing—
313 the fundamental question being "how much?" Ward et al. provided a drawing of their reconstruction of
314 the pelvis (see Figure 14 in Ward et al. 1993), and based on its scale they appear to have added
315 approximately 7 mm to each ala to complete its pelvic ring.

316 The left os coxa of KNM-MW-13142 is nearly complete and includes an intact auricular surface
317 and almost the entirety of the lower pelvis, which lacks only a small portion of the pubic symphysis. We
318 physically reconstructed the missing portions and its sacrum to form a realistic true pelvis (see earlier).
319 Essentially this required adding only sufficient material to each ala (presuming bilateral symmetry) to
320 fully articulate the (missing) sacral auricular surface with the three-dimensional surface of the os coxa—
321 the posterior portion of the latter being substantially involuted. The reconstructed sacrum's dimensions
322 are in full agreement with those of Ward et al.'s. These would seem to be a reasonable *minimum*
323 because the strong mediolateral angulation (about 45°) of the specimen's auricular surface requires the
324 anterior surfaces of its sacral alae to be as least as large as the ones both Ward and we reconstructed.
325 Admittedly these are crude estimates (theirs at 17.7mm and ours at 18.7mm), but when plotted in
326 Figure 7, the specimen falls above the regression line defined by monkeys and not with that
327 representing the extant African apes.

328 Such a reconstruction, although seeming quite reasonable, should be considered here mainly as
329 a means of illustrating a hypothesis, which will hopefully be tested by not yet recovered more complete
330 specimens. In any case, these data do indicate that the hominoid sacrum did not undergo substantial
331 reduction in breadth simply due to tail elimination.

332

333 **Discussion**

334 The potential parallelisms between atelids and hominoids with respect to suspensory
335 locomotion have long been observed (Erickson 1963; Larson 1998). However, the lumbar column,
336 thorax, and pelvis of spider, miqui, woolly, and howler monkeys differ substantially from those of

337 hominoids in many ways, especially since monkeys retain external tails. The presence of a tail is also
338 shared with OWMs, although those of atelids are more massive, highly innervated, and prehensile. As in
339 OWMs, their iliac isthmus is superoinferiorly long with a substantial gap between the sacral promontory
340 and pubic symphysis. Other NWM, OWM and early hominoid (e.g., *Proconsul*) spinal columns are
341 essentially uninvginated (Kagaya et al. 2008; Kagaya et al. 2009). Thus, atelids differ from OWMs
342 because they have evolved partial invagination similar in degree to that in gibbons and *Pierolapithecus*
343 (Figure 2) (Moya-Sola et al. 2004).

344 *Brachyteles* individuals achieve bipedal posture with both an extended torso (at the hip) and
345 knee joints that are accompanied by a lordotic curvature of the lower back. *Ateles* can also attain a
346 similar posture and can walk with a more extended gait than typical of African apes and other monkeys
347 (Figure 4, Supplemental video 3) (Okada 1985; Stern & Larson 1993). For example, Okada (1985) reports
348 that a spider monkey attains a maximum hip angle of 160° during bipedal walking and an angle of 140°
349 at toe off. Each of these are approximately 20° greater than observed in a chimpanzee and gibbons
350 (Okada 1985). These approximately match the levels of extension observed in the spider monkey in
351 Figure 4. This is despite the fact that atelids retain only 4 – 5 ribless or approximately 6 functional
352 lumbar vertebrae (Williams 2011). Full extension of the knee is, of course, readily obtainable in other
353 primates, but the unusual attribute available to these atelids is their additional capacity to
354 simultaneously extend the hip, a combination that is lacking in extant African apes (Pontzer et al. 2014).
355 Such lordosis in atelids appears to be facilitated by a shorter iliac crest and reduced ligamentous
356 restriction of the caudal lumbar vertebrae, as well as partial lumbar invagination. These, in combination
357 with their broader sacrum, allow the caudal lumbar vertebrae to contribute to lordosis. It is important to
358 note that spinal invagination and low iliac height occur in *Alouatta* as in other atelids (Figures 3 & 4). In
359 combination with potential parallel evolution of suspensory specializations in *Ateles* and *Brachyteles*
360 (Iurck et al. 2013; Jones 2008), this indicates that these features need not have evolved in the context of
361 forelimb brachiation or suspension. Instead, the ability to lordose in atelids was likely a response to
362 occasional tail-assisted hind limb suspension in an otherwise arboreal quadruped (Cant 1986). These
363 data enable us to hypothesize the process by which lumbar lordosis could have evolved in earliest
364 hominids.

365 African ape sacra have strikingly narrowed alae (Figure 6). This is very likely an adaptation to
366 vertical climbing and/or suspension, and includes a reduction in lumbar number by conversion of lumbar
367 to thoracic and/or sacral vertebrae. Together these render the ape spine virtually rigid (Lovejoy &
368 McCollum 2010; McCollum et al. 2010; Schultz 1969). As a consequence, the African apes cannot easily

369 locate their center of mass (COM) over their pedal support and must rely on the classic BHBK gait during
370 upright walking (Fleagle et al. 1981).

371 Given the importance of lordosis for achieving extended hind limb bipedal posture, it is likely
372 that significant alar breadth was *retained in the LCA* and was a feature in earliest hominids (Figure 7).
373 The alternative hypothesis, that alar breadth and lumbar column length were first reduced in mid-
374 Miocene hominoids only to then be re-broadened in bipedal hominids is decidedly more complex than
375 the more modest alternative that the *Ardipithecus* postcranium presents, i.e., that some late Miocene
376 taxa had undergone modifications for effective clambering and cautious climbing *without* sacral
377 narrowing. The lack of derived suspensory adaptations in early members of the *Pongo* clade such as
378 *Sivapithecus* (Madar et al. 2002; Morgan et al. 2015; Pilbeam et al. 1990) indicate that lumbar
379 shortening and sacral narrowing very likely occurred in parallel in Asian apes (Larson 1998; Ward 2015),
380 as did spinal invagination (Figure 7A). Therefore, within the African ape and human clade, when simply
381 considering character state transitions of lumbar spine length, sacral width and iliac height, homoplasy
382 due to reversal is equivalent to parallel evolution between lineages. If the lumbar column was reduced
383 and the sacrum narrowed prior to the African ape and human LCA, these features would have
384 necessarily been reversed in early hominids while iliac height was reduced (Figure 7B). Alternatively,
385 lumbar reduction and sacral narrowing could have occurred in parallel between the *Gorilla* and *Pan*
386 lineages, and simple iliac height reduction occurred in early hominids (Figure 7A). Each of these
387 scenarios posits five transitions associated with the evolution of bipedality and suspensory/vertical
388 climbing behaviors . However, reversal implies fluctuating selective pressures in a single lineage. And *Ar.*
389 *ramidus* does not exhibit *any* of the numerous additional adaptations to suspension found in all other
390 extant apes (White et al. 2015). It is therefore difficult to explain the pressures underlying a transition
391 from a suspensory/knuckle-walking primate to a palmigrade quadrupedal arboreal climber/clamberer
392 combined with terrestrial bipedality. An "*adaptively simpler*" scenario is that the African ape ancestor
393 shared the primitive morphological state preserved in much of *Ar. ramidus*. While this scenario requires
394 significant parallelism among African apes, such homoplasy must have already very likely occurred in
395 gibbons and orangutans. Moreover, it has been frequently observed during animal evolution, and can be
396 facilitated by shared genetic variation and genomic organization in closely related taxa (Reno 2014).

397 It is difficult to overemphasize the special problem in any analysis of hominid evolution: there
398 are no extant models of non-suspensory tailless anthropoids that can be reliably compared to *Ar.*
399 *ramidus*, i.e., *no living ape is a suitable comparator because all have a long history of substantial vertical*
400 *climbing and/or suspension*. Hominids are unique. ARA-VP-6/500 suggests no history of adaptation to

401 suspension in any of its major anatomical character complexes, including those of the wrist, hand,
402 elbow, humerus, foot, and limb proportions (Lovejoy et al. 2009c; White et al. 2015). Therefore, it very
403 likely retained a sacrum and lumbar column *also* unmodified for suspension.

404 In this light, the evidence from atelids raises the possibility that the earliest special adaptation to
405 upright walking in hominids was a similar reduction in upper iliac height, added to a significant degree of
406 exaptive spinal invagination achieved as part of the generally derived hominoid bauplan of the LCA. This
407 is reasonable to presume because moderately broad sacral alae are likely to have already been present.
408 Based on *Brachyteles*, this would have permitted near or even complete simultaneous extension of the
409 hip and knee during erect stance. However, further expansion of the sacral alae was also certainly a
410 possible mechanism for further lumbar emancipation, although it may not have been fully developed
411 until the *Australopithecus* grade of human evolution (Lovejoy 2005a).

412 This conclusion bears on the morphology of the pelvis of *Ardipithecus*, which likely included both
413 a broad sacrum (implied (Lovejoy et al. 2009d)) and reduced iliac height (observed) but *also* with a
414 substantially shortened iliac isthmus (observed). The latter suggests considerable age for upright walking
415 in *Ardipithecus*, since upper iliac shortening as seen in the atelids (which lack *lower* iliac shortening) may
416 well have preceded any major modifications of the iliac isthmus. Thus the earliest morphological
417 adaptation to upright walking may well have been a shortening of the upper ilium in convergence with
418 atelids (Figure 7).

419 What likely followed was a *secondary* adaptation, *viz*, a superoinferior abbreviation of the iliac
420 isthmus, whose primary role was to improve trunk control by the anterior gluteals during single support.
421 Such shortening would have also reduced the height of the trunk's COM, an especially important factor
422 during and immediately following heel strike (Lovejoy 2005a).

423 Finally, one point requires stringent reiteration as we close our discussion. The possibility and
424 ease with which bipedality could have been adopted are only considerations required in reconstructing
425 the transition from arboreal clambering and cautious (i.e., low velocity) climbing to terrestrial upright
426 walking—they are not of themselves an *adaptive cause for such behavior*—the underlying bases of the
427 adoption of bipedality are still far more likely to be related to social and/or demographic forces that
428 bore directly on fitness, rather than simple "locomotor inertia." Indeed, the 20-fold increase in
429 terrestriality documented over the past 23 years in northern muriquis has been attributed to a
430 coincidental increase in population size and population density (Tabacow et al. 2009); this demography-
431 driven expansion of their vertical niche may, in turn, underlie the unexpected increase in their fertility
432 (Strier & Ives 2012). Similar *types* of forces are likely to have contributed to the shift to upright walking

433 in hominids (White et al. 2015); that is, no matter how facile the transition to bipedality might have
434 been, the adoption of this kinematically unstable means of locomotion almost certainly introduced a
435 period of locomotor disequilibrium that was unlikely to have had, *by itself as a locomotor mechanism*,
436 any directly positive effect on fitness.

437

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Figure 1(on next page)

Bipedal posture in marmosets.

Lumbar lordosis facilitates an erect trunk and fully extended hind limb in northern marmosets.

A) Female in partial caudal suspension; note marked lordosis. **B)** Male; note complete extension of the right lower limb. **C)** Male; note complete extension of both hind limbs and fully erect trunk and that the tail is not being used for support. **D)** Female with infant preparing to climb; note that the left hind limb is in extension in combination with an entirely vertical trunk. **E)** Adult male standing without brachial or caudal support; note the extended back. The bipedal postures shown in B-C & E were adopted during brief resting bouts, while that in D was adopted during a transition from terrestrial to arboreal substrate. See Supplementary videos 1 & 2 for context of typical bipedal behaviors. Photo credits as follows: A: Daniel Ferraz; B, C & E: Fernanda P. Tabacow; D: Schultz de Cristo.

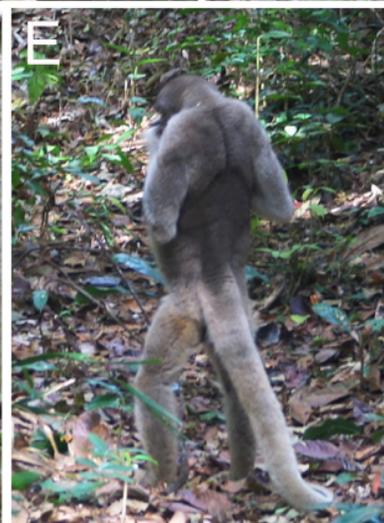


Figure 2 (on next page)

Comparison of iliac height and lumbar entrapment.

A. Comparison of the relationships between the most caudal lumbar in a langur (left) and howler monkey (right). The deep iliac "well" in which the langur's L7 is positioned limits its potential motion through ligamentous attachments (see Figure 6), whereas the howler monkey's L5 is more mobile by virtue of the reduced height of its ilia. Metric definitions are indicated. Dashed lines are for reference; solid lines indicate measured distances. Iliac height = A; Acetabular breadth = B; Centrum breadth = C; Total sacral breadth = D; Alar breadth = $(D - C)/2$. **B.** Pelvis of an adult male miqui demonstrating the low iliac height and free caudal lumbar vertebrae typical of atelids. This individual is from the same study group as those depicted in Figure 1. Specimen housed at the Museu Nacional Rio de Janeiro (National Museum of Brazil). Photo credit: Sérgio L. Mendes. **C.** As shown in this chimpanzee, vertebral motion is restricted by the direction of their transverse processes and ilia. Note the narrow inter-iliac distance as marked. Arrows indicate articulation between lumbar transverse processes and iliac crest. It is important to note that the langur condition (A, left) is not equivalent to that in extant African apes.

Figure 3(on next page)

Box plot illustrating relative iliac height across anthropoids.

Iliac Height Ratio = (Iliac height X 100)/Acetabulum diameter. Analysis of Variance (ANOVA) demonstrates highly significant difference between means whether atelids are grouped as a family or as individual species. Significance values indicated from Bonferroni posthoc pairwise test between combined atelids and other groups (** > P=0.01; *** > p=0.001; ns = non-significant). Atelids that engage in caudal suspension most often have the lowest iliac height except for bipedal humans. The three New World monkey lower outliers are specimens of *Chiropotes santanus*, *Aotus vociferans*, and *Callicebus* sp.

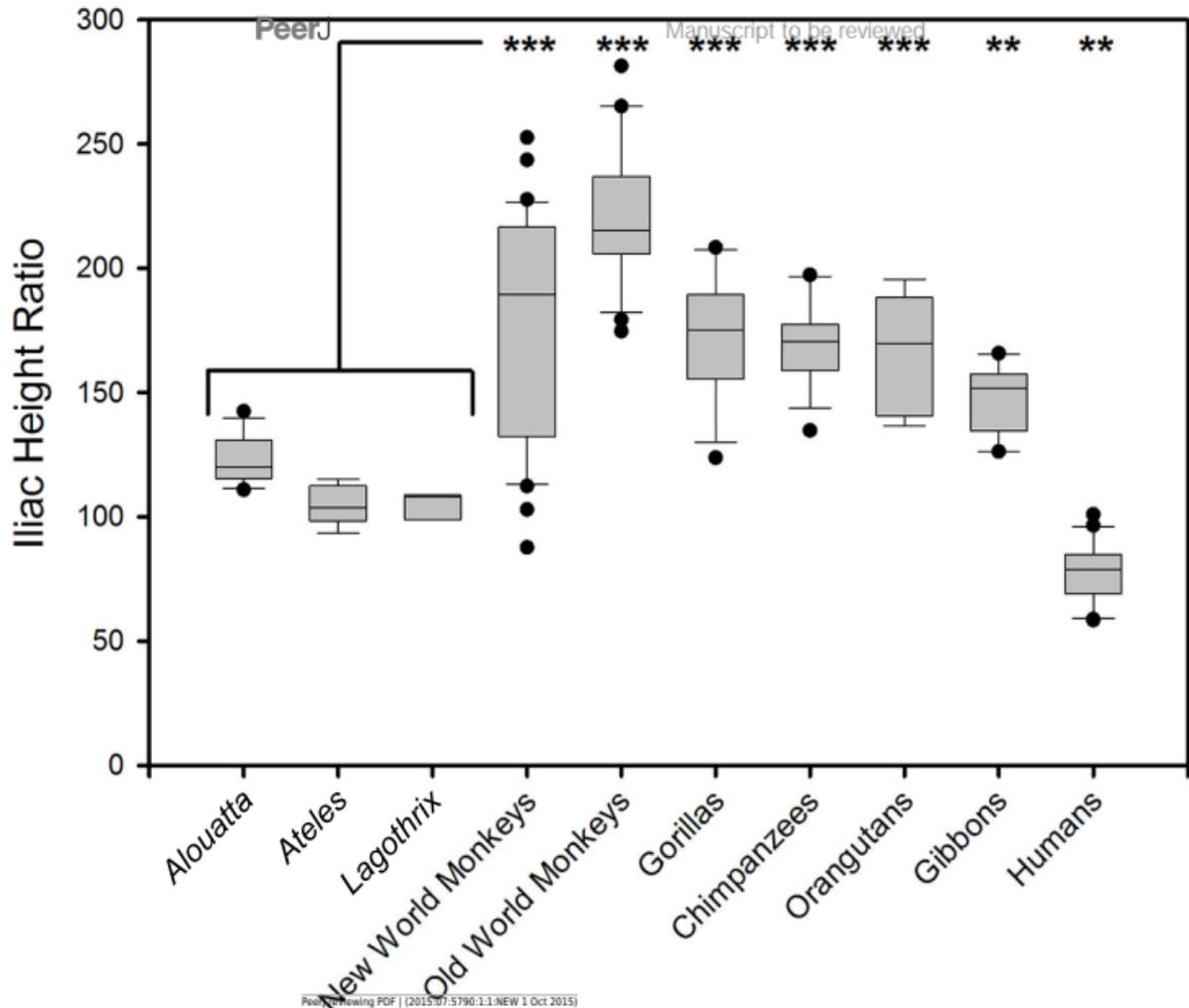


Figure 4(on next page)

Bipedal posture in a spider monkey.

Screen captures of video demonstrating bipedal posture and locomotion. **A)** Posterior lateral view demonstrating that the spider monkey attains erect hip and back during bipedal standing without relying on support. **B)** Lateral view illustrating that hip extension approximates 160°. Images from (BigLividVideos 2012) ; full video can be seen as Supplemental Video 3.

A

Pook

**B**

Manuscript to be reviewed



Figure 5(on next page)

Ultimate lumbar vertebrae in atelids and an Old World monkey.

Note that transverse process position in atelids shows partial invagination. A) Howler monkey (CMNH 1172) L5. B) Spider monkey (CMNH 1237) L5. C) Woolly monkey (CMNH 5699) L4. D) Colobus monkey (CMNH 2144) L7. The transverse processes (TP) location in atelids is similar to that in gibbons and *Pierolapithecus* (Moya-Sola et al. 2004). In the 'semi-brachiating' *Colobus*, the TPs originate from the vertebral body.

A

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**C****D**

Figure 6 (on next page)

Iliolumbar (1), intertransverse (2), and iliosacral (3) ligament anatomy observed during primate dissections.

Superficial ligaments are shown on the left, and deeper tissues shown on the right. Lumbar numbers are based on rib count, as articular facet orientation could not be observed without further destructive dissection. A) Spider monkey [3 lumbar] and B) spider monkey [4 lumbar]: Iliolumbar ligament spans L2 or L3 and the ilium, and a thin intertransverse ligament spans the transverse processes of L3 or L4, ilium and sacrum. These ligaments likely provide lumbar support, while permitting substantial mobility. C) Muriqui [5 lumbar]: An iliolumbar ligament runs from L3, L4, and L5 to the ilium. A thin intertransverse ligament spans the transverse processes of the lumbar vertebrae. As in the spider monkey, these ligaments likely provide lumbar support, while permitting substantial mobility. D) Howler monkey [5 lumbar]: An iliolumbar ligament runs from L4 and L5 to the ilium. This tissue is narrower and covers less surface area on the ilium than the corresponding ligament in the spider monkeys, but serves a similar function. A thin intertransverse ligament spans the transverse processes of the lumbar vertebrae and runs from L5 to the ilium. E) Gibbon [5 lumbar]: A thick iliolumbar ligament runs horizontally and obliquely between L3, L4, and L5 and the ilium. A thick intertransverse ligaments run between each lumbar transverse process. The orientation of the ligamentous fibers is more similar to those of atelids than those of the langur, but the thickness was intermediate between the two. The ligamentous tissue would not have been as restrictive as in the langur. F) Langur [7 lumbar]: Iliolumbar ligaments run from the 3 most caudal lumbar vertebrae to the ilium. A thick intertransverse ligament spans the transverse processes of the lumbar vertebrae and runs from L7 to the ilium to join both structures to the transverse processes of L6. Since the L7 is positioned deeply between the iliac blades, its motion is highly restricted. The ligamentous tissue of the langur is substantially denser than that of all the other specimens and would have restricted motion more substantially. The iliolumbar ligament is hypothesized to have developed in

primates associated with stabilizing the back while upright or lordosing and is possibly formed by collagenation of the fibers of the quadratus lumborum (Luk et al. 1986; Pun et al. 1987). It has not been found in other quadrupedal animals like cats and dogs (Pun et al. 1987).

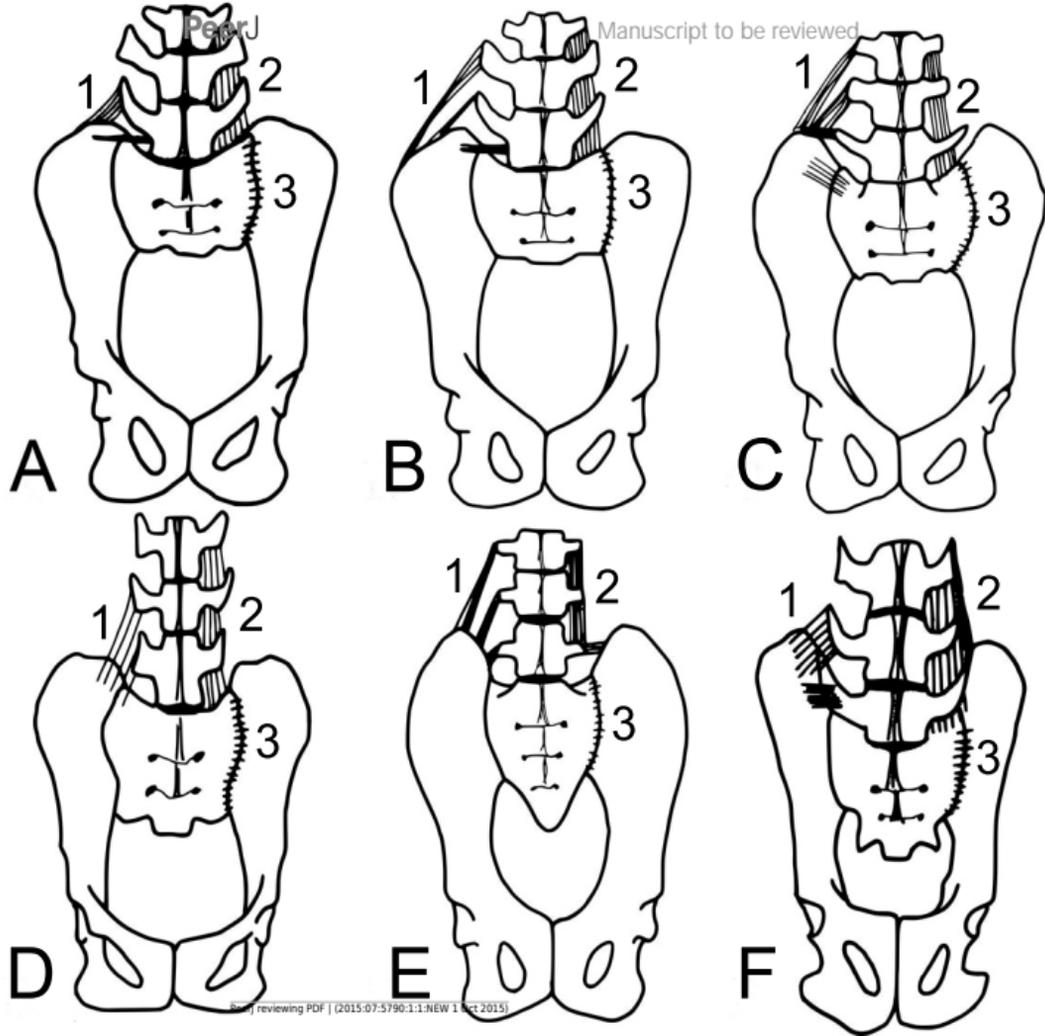
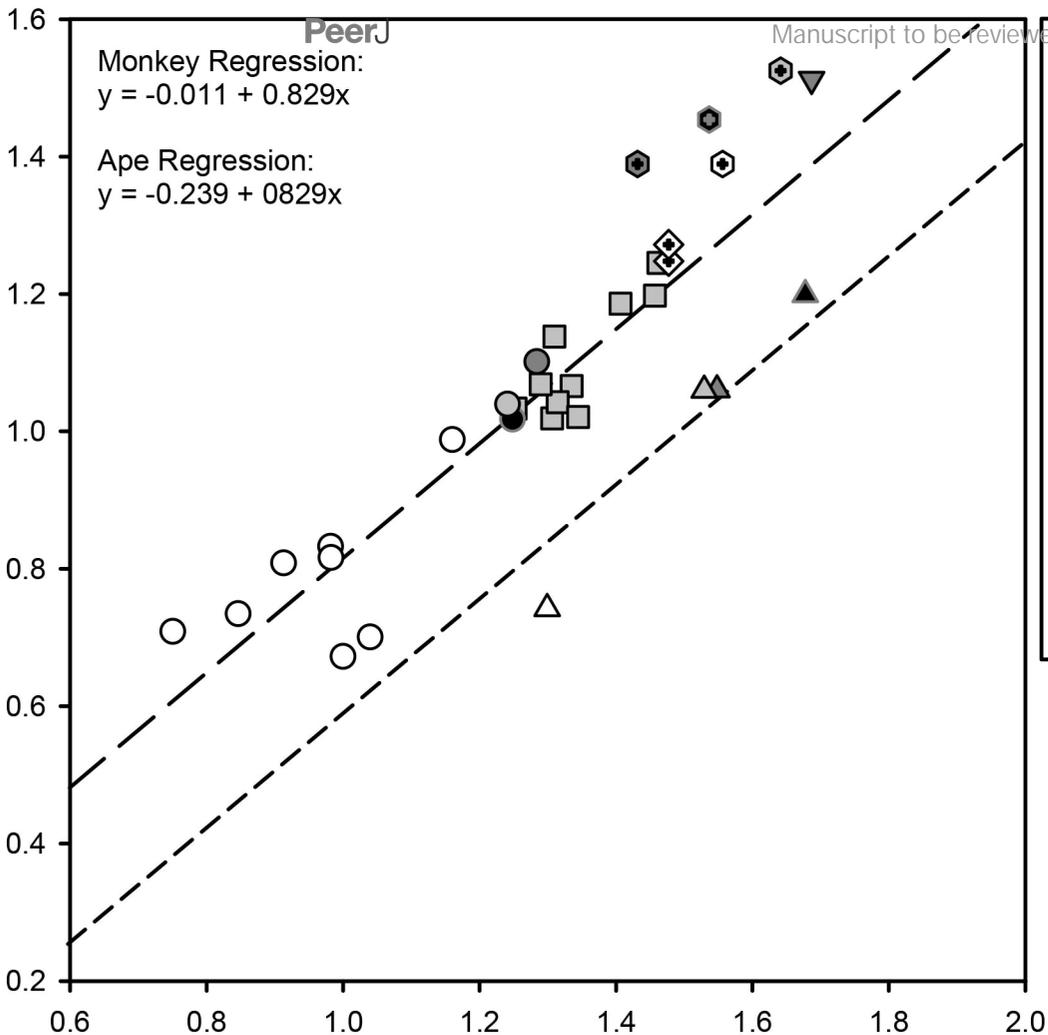


Figure 7 (on next page)

Sacral alar breadth compared to centrum breadth (for definitions see Figure 2).

Data represents genus means for extant taxa. Regression formulas are provided from a phylogenetic Analysis of Covariance (ANCOVA). Slopes do not differ significantly, however there is a significant difference in elevation ($p < 0.0001$) between monkeys (long dashes) and apes (short dashes). Two points are plotted for *Proconsul* (KNM-MW-13142) representing the two alar breadth estimates discussed in the text. Hominids, including *Au. afarensis* (A.L. 288-1 and KSD-VP-1/1), *Au. africanus* (Sts-14), and *H. erectus* [BSN49/P27 (Simpson et al. 2008)], plot above the monkey regression line.

\log_{10} Alar Breadth



\log_{10} Centrum Breadth

Figure 8(on next page)

Models depicting the evolution of the lumbar column, sacrum, and ilium in hominoids.

A) Ancestral apes such as *Proconsul* had an uninvaginated spine, long lumbar columns (≥ 6 vertebrae), wide sacrum, and tall iliac height (sacral promontory/ilic crest distance). The presence of Eurasian Miocene hominoids with ancestral morphologies (indicated by dashed line from *Proconsul*) suggests that gibbons and orangutans invaginated their spines (A) and narrowed their sacra (C) in parallel. The orangutan lumbar column length was further shortened to 4 elements (B). Shared morphologies between African apes, humans and *Ardipithecus* (i.e., reduced retroauricular portion of the pelvis) indicate spinal invasion and broader thorax with dorsally placed scapula were characteristic of the LCA. However, the lack of derived suspensory features in arboreal *Ardipithecus*, suggests that the LCA retained a long lumbar column and wide sacrum. Thus, lumbar reduction (B) and sacral narrowing (C) occurred in parallel among African apes, and iliac height reduction (C) occurred in early hominids (5 transitions) as an initial adaptation for bipedality. In New World monkeys, similar morphologies evolved in parallel with spinal invasion (A) and reduced iliac height (D) occurring in the common ancestor of atelids, with lumbar column reduction occurring in spider monkeys (B) and marmosets (not shown). **B)** An alternative model posits that the African ape and human LCA had already evolved numerous suspensory and vertical climbing specializations including spinal invagination (A), lumbar reduction (B) and sacral narrowing (C). In such a case, lumbar length (B') and sacral width (C') would have reversed in early hominids. Both models provide similar numbers of evolutionary transitions. Note that our depiction of these models does not include the additional transitions to 6 functional lumbar in *Australopithecus* and back to 5 functional lumbar in humans nor the potential parallel lumbar shortening in chimpanzees and bonobos (McCollum et al. 2010).

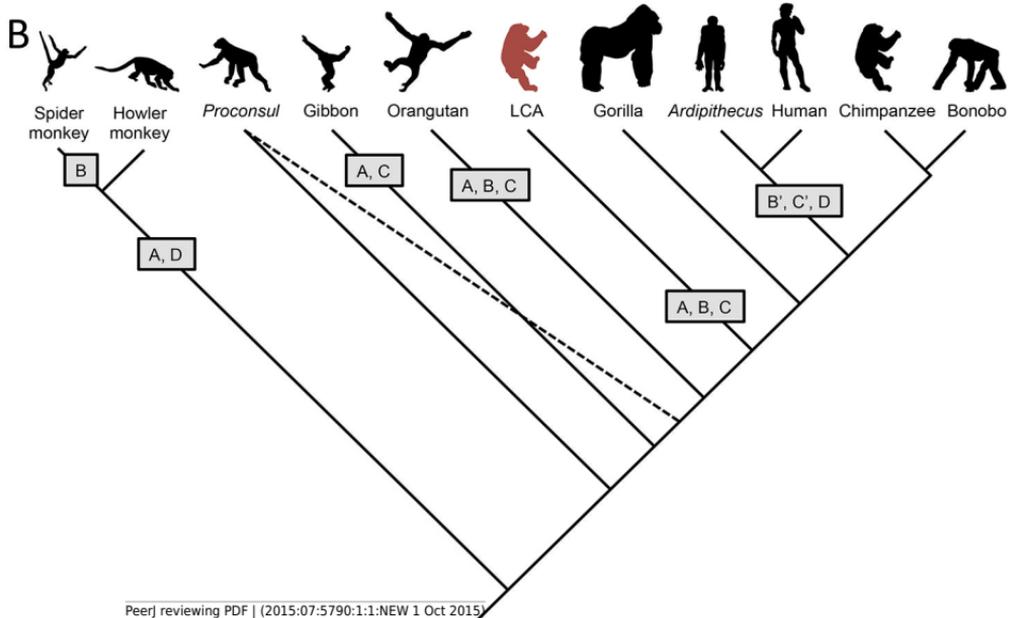
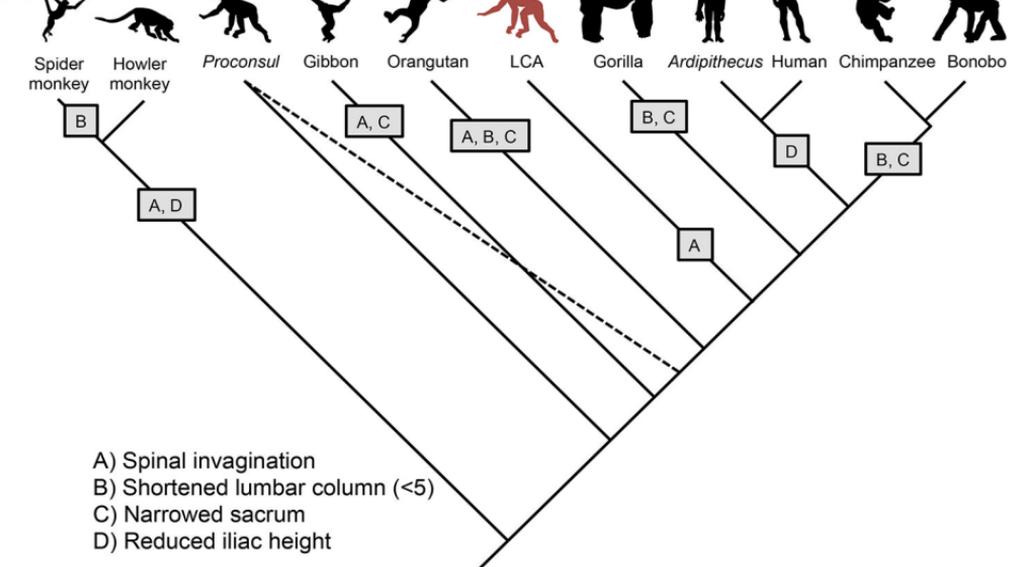


Table 1 (on next page)

Table 1. Comparative sample of pelvic metrics.

1
2 **Table 1.** Comparative sample of pelvic metrics.
3

4	Species	N	Species	N
5	Atelids	24	Old World monkeys	27
6	<i>Alouatta palliata</i>	6	<i>Cercopithecus torquatus</i>	2
7	<i>Alouatta guariba</i>	3	<i>Cercopithecus mona</i>	1
8	<i>Alouatta caraya</i>	1	<i>Chlorocebus aethiops</i>	6
9	<i>Alouatta seniculus</i>	1	<i>Colobus guereza</i>	4
10	<i>Aloutta sp.</i>	1	<i>Macaca fascicularis</i>	1
11	<i>Ateles geoffroyi</i>	8	<i>Macaca mulatta</i>	1
12	<i>Ateles sp.</i>	1	<i>Macaca silenus</i>	1
13	<i>Lagothrix lagotricha</i>	3	<i>Papio hamadryas</i>	3
14			<i>Presbytis cristata</i>	1
15	Other New World monkeys	32	<i>Presbytis rubicunda</i>	2
16	<i>Aotus vociferans</i>	1	<i>Pygathrix sp.</i>	1
17	<i>Calliцеbus sp.</i>	4	<i>Semnopithecus entellus</i>	1
18	<i>Callithrix jacchus</i>	2	<i>Theropithecus gelada</i>	2
19	<i>Cebuella pygmaea</i>	2	<i>Trachypithecus pileatus</i>	1
20	<i>Cebus albifrons</i>	2		
21	<i>Cebus capucinus</i>	4	Hominoids	67
22	<i>Cebus apella</i>	4	<i>Homo sapiens</i>	20
23	<i>Cebus sp.</i>	1	<i>Pan troglodytes</i>	15
24	<i>Chiropotes santanas</i>	1	<i>Gorilla gorilla</i>	15
25	<i>Leontopithecus rosalia</i>	4	<i>Pongo pygmaeus</i>	7
26	<i>Saguinus geoffroyi</i>	1	<i>Hylobates lar</i>	10
27	<i>Saguinus midas</i>	1		
28	<i>Saguinus oedipus</i>	1	Total	150
29	<i>Saimiri sciureus</i>	4		
30				
31				
32				
33				