



Hip extensor mechanics and the evolution of walking and climbing capabilities in humans, apes, and fossil hominins

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The evolutionary emergence of humans’ remarkably economical walking gait remains a focus of research and debate, but experimentally validated approaches linking locomotor capability to postcranial anatomy are limited. In this study, we integrated 3D morphometrics of hominoid pelvic shape with experimental measurements of hip kinematics and kinetics during walking and climbing, hamstring activity, and passive range of hip extension in humans, apes, and other primates to assess arboreal–terrestrial trade-offs in ischium morphology among living taxa. We show that hamstring-powered hip extension during habitual walking and climbing in living apes and humans is strongly predicted, and likely constrained, by the relative length and orientation of the ischium. Ape pelvis permit greater extensor moments at the hip, enhancing climbing capability, but limit their range of hip extension, resulting in a crouched gait. Human pelvis reduce hip extensor moments but permit a greater degree of hip extension, which greatly improves walking economy (i.e., distance traveled/energy consumed). Applying these results to fossil pelvis suggests that early hominins differed from both humans and extant apes in having an economical walking gait without sacrificing climbing capability. *Ardipithecus* was capable of nearly human-like hip extension during bipedal walking, but retained the capacity for powerful, ape-like hip extension during vertical climbing. Hip extension capability was essentially human-like in *Australopithecus afarensis* and *Australopithecus africanus*, suggesting an economical walking gait but reduced mechanical advantage for powered hip extension during climbing.

hominin | locomotion | ischium | evolution | pelvis

Although there is broad consensus that early hominins walked bipedally when on the ground (1–3), it is unclear when, and under what conditions, hominins developed an economical human-like gait, and whether adaptations for improved walking economy resulted in reduced climbing ability (1–6). Resolving this central debate in human evolution is hampered by traditional analytical approaches, which provide rich comparative detail about a fossil taxon’s skeletal morphology but rarely validate functional inferences against experimental tests in living humans and apes. Recent studies have demonstrated the value of integrating anatomical and experimental analyses to reconstruct the walking mechanics and energetics of fossil hominins, but to date they have drawn solely from human experimental data (7) or relied on taxonomically limited comparisons (e.g., with chimpanzees) (8–12); none has examined the effects of these traits on climbing capabilities. More detailed anatomical analyses have identified a suite of features in early hominins associated with climbing (2, 4–6), but have not empirically validated

their effects on climbing performance or tested whether these traits constrain walking and running performance.

Human bipedalism relies on a suite of hind limb adaptations, including a laterally oriented iliac blade and hip abductor complex, adducted hallux, and stiff midfoot (13), but few of these features have been linked empirically and in vivo to locomotor economy (i.e., the distance traveled per unit energy consumed). One derived feature tentatively tied to humans’ remarkable walking economy is a shorter and more dorsally projecting ischium, which permits hip extensor muscle torque production at full extension of the hip (180° hip angle between the trunk and leg) (4, 9, 14–16) (Fig. 1). The resulting straight-legged gait substantially improves walking economy compared with nonhuman apes by reducing the muscle activity needed to support body weight each step (8, 9). Conversely, the shorter human ischium likely reduces the mechanical advantage of hip extensors (hamstring muscles) relative to apes and other nonhuman primates, especially in the flexed-hip postures needed to propel the

Significance

The evolution of humans’ distinct bipedal gait remains a focus of research and debate. Many reconstructions of hominin locomotor evolution assume climbing capability trades off against walking economy, with improvement in one requiring diminishment of the other, but few have tested these functional inferences experimentally. In this study, we integrate experimental locomotor mechanics from humans and other primates with osteological measurements to assess the locomotor capabilities of early hominins. Our analyses show that changes in the ischium and hamstrings would have made walking more economical without reducing the utility of these muscles for climbing in early hominins. A wider set of evolutionary solutions may have been available to early hominins than previously recognized.

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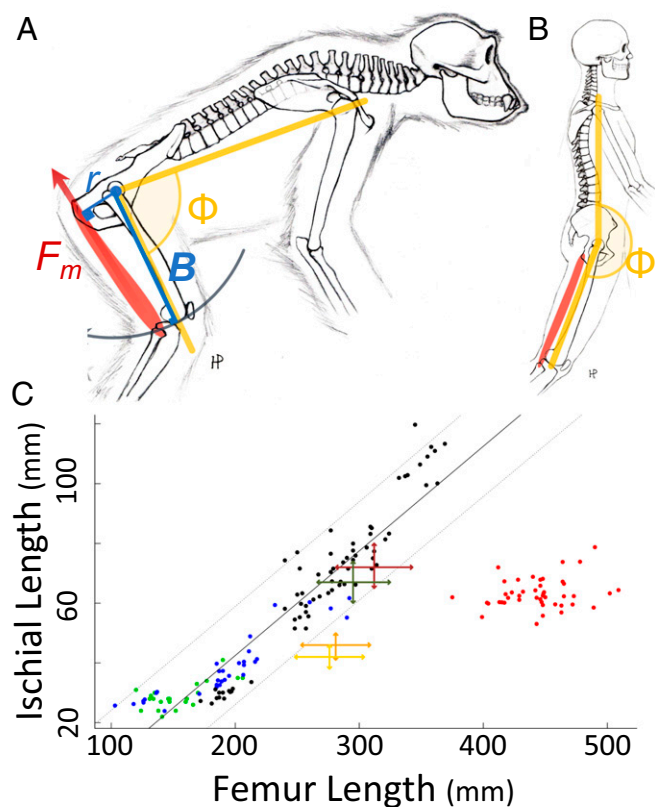


Fig. 1. Ischial morphology and hip mechanics. (A) The hamstrings muscle group exerts a force F_m , which results in a hip extension moment $F_m \times r$, where r is the orthogonal distance from the F_m vector to the center of rotation for the hip. The resulting force at the knee, F_k , is equal to $F_m \times (r/B)$, where B is the orthogonal distance from the F_k vector to the center of rotation for the hip. The hamstrings group inserts on the proximal tibia and fibula, very near the knee, making femur length a useful proxy measure for B . The ratio r/B thus gives the DMA for the hamstrings group (i.e., the force F_k exerted at the knee for a given F_m). DMA is a function of hip flexion angle, Φ . Greater DMA allows the hip extensors to generate greater F_k , but also requires more shortening of the hamstrings group (i.e., muscle strain) per degree of hip extension. This graphic presents a chimpanzee, with its highly flexed hip. (B) Humans' shorter and reoriented ischium results in lower peak DMA but a greater functional range of hip extension, enabling the hamstrings to hyperextend the hip beyond 200° , as shown here. (C) Ischial length (which defines maximum r) relative to femoral length (which defines B) in fossil and extant taxa. Solid line is the nonhuman primate linear regression ($R^2 = 0.89$; $P < 0.001$), with dashed lines showing 95% prediction interval. The linear relationship test between femur and ischial length in humans yields a P value of 0.12. Arrows for fossil taxa represent $\pm 10\%$ range. Red dots, humans; black dots, nonhuman apes; blue dots, catarrhines; green dots, platyrrhines; green arrow, *E. nyanzae*; brown arrow, *Ar. ramidus*; orange, *Au. afarensis*; yellow, *Au. africanus*. (See *SI Appendix, Tables S1 and S2*.)

body upward during climbing (moving up a substrate inclined at 45° or more to the horizontal) (14–18). It remains unclear, however, whether ischial morphology actually limits hip extension in nonhuman apes as proposed, or whether changes in ischial morphology in the hominin lineage reflect arboreal–terrestrial trade-offs in hip extensor mechanics (4, 8, 9, 14–18).

In this study, we investigated early hominin ischial morphology, using an integrated anatomical–experimental approach. We combined *in vivo* biomechanical analyses of hip extension during walking and climbing across a range of living hominoid genera with detailed comparative pelvic anatomy to develop an experimentally validated link between ischial morphology and locomotor mechanics. We then examined pelvic morphology in

Ardipithecus and *Australopithecus* to test the hypothesis that early hominins retained ischial proportions and orientation that favored greater force production during climbing but limited their ability to hyperextend the hip and walk as economically as modern humans.

We characterized pelvic shape using a set of 23 3D landmarks in living hominoids: *Homo*, *Pan*, *Gorilla*, *Pongo*, *Hylobates*, and *Nomascus*; three early hominins: *Ardipithecus ramidus*, *Australopithecus afarensis*, and *Australopithecus africanus*; and a Miocene ape, *Ekembo nyanzae* (*Methods* and *SI Appendix, Fig. S1* and *Tables S1* and *S2*). For greater phylogenetic breadth, we also included smaller samples of five large-bodied Old World monkey genera (*Mandrillus*, *Papio*, *Procolobus*, *Colobus*, and *Macaca*) and four New World monkey genera (*Ateles*, *Lagothrix*, *Cebus*, and *Alouatta*; *Methods* and *SI Appendix, Table S1*). The length and orientation of the ischium were combined with femur lengths for each specimen to determine the dimensionless mechanical advantage (DMA) for the hamstring muscles (in this study, the semimembranosus, semitendinosus, and biceps femoris longus, but not the biceps femoris brevis), which act to extend the hip. DMA for these muscles, calculated as (muscle moment arm)/(femur length), represents the moment, or rotational force, generated at the distal femur for a given unit of hamstring tension, and changes as a function of hip angle (Fig. 1). Plotting DMA against hip angle produces a performance envelope for the hamstring muscles that circumscribes the effective range of hip flexion for these muscles and the hip angle at which they can produce the most torque (Fig. 2). Estimated this way, maximum DMA is determined by the ratio of (ischial length)/(femur length), whereas the range of hamstrings-powered hip extension (i.e., range of hip angles for which $DMA > 0$) is determined by ischial orientation (*Methods* and Fig. 1). These calculations are independent of body mass, and thus do not rely on estimates of body size.

To test whether hamstring performance envelopes are reliable indicators of locomotor capabilities, we compared these envelopes with ranges of hip extension during level quadrupedal walking and vertical climbing in nonhuman apes, as well as bipedal walking in humans; kinetic data for humans, chimpanzees, and bonobos; electromyographic recordings of hamstring activity in humans, chimpanzees, bonobos, and hylobatids; and passive ranges of hip extension in hominoids and other primates. We then examined hamstring DMA envelopes in our fossil sample to reconstruct their walking and climbing mechanics. Sensitivity analyses were performed to ensure that differences in reconstructed DMA envelopes were robust to variation imposed by measurement error and uncertainty in pelvic orientation (i.e., pelvic tilt in the sagittal plane), femur length, hamstrings attachment, or sacral width.

Results

Extant Taxa. Anatomical analyses clearly distinguish the hamstrings DMA envelopes of nonhuman apes from humans. *Pongo*, *Gorilla*, and *Pan* all exhibit high maximum DMA at a relatively low range of hip angles, and are similar in these respects to extant monkeys. The orientation of the ape ischium results in a DMA envelope constrained between 0° and $\sim 160^\circ$ hip extension (Fig. 2 and *SI Appendix, Table S3*), suggesting these taxa cannot use their hamstrings for powered hip extension beyond $\sim 160^\circ$. Their long ischia (Fig. 1) produce large hamstrings moment arms and greater peak DMA (Fig. 2 and *SI Appendix, Table S3*). The hylobatids are similar to other apes in the effective range of hip extension, yet have relatively low peak DMA. Humans are characterized by low DMA amplitudes (a function of a shorter ischium; Fig. 1) and a rightward shift in the DMA envelope, which falls between $43^\circ \pm 6^\circ$ (flexed hip) and $223^\circ \pm 6^\circ$ (hyperextended hip; Fig. 2), with a peak near 140° . Humans' higher range is a function of ischial orientation and allows for

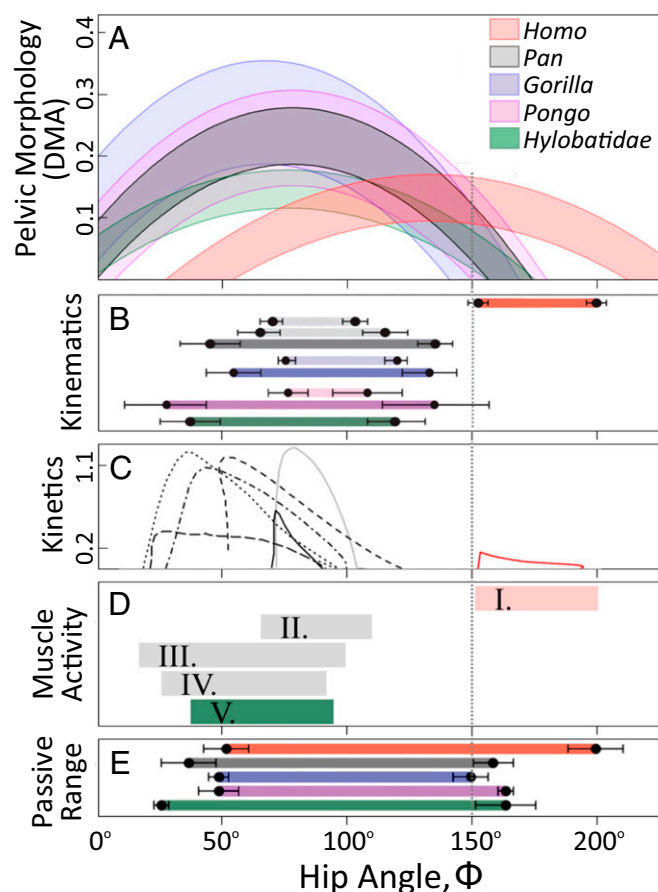


Fig. 2. Hip extensor DMA and locomotor mechanics. Red, *Homo*; gray, *Pan*; blue, *Gorilla*; purple, *Pongo*; green, hylobatidae. (A) Skeletally derived DMA in extant hominoids. Shaded regions represent 95% prediction interval for DMA in each taxon. (B) Bars represent mean range of flexion and extension with SDs while climbing (19) (dark colors), and while walking quadrupedally or bipedally on level ground (light colors). For *Homo*, only bipedal walking is shown. For level walking in *Pan*, both *P. troglodytes* (Upper) and *P. paniscus* (Lower) are shown. For hylobatidae, only vertical climbing is shown. (C) Hip moments (dimensionless, scaled to body mass and tibia length) in humans, chimpanzees, and bonobos. Red line, *Homo* level bipedal walking; gray line, *P. troglodytes* level quadrupedal walking; dashed line, *P. paniscus* level quadrupedal walking; dot-dashed line, *P. paniscus* 45° incline climbing; dotted line, *P. paniscus* vertical climbing. (D) Hamstrings electromyography activity in humans and chimpanzees and gibbons (25–27). (I) Human level bipedal walking; (II) *P. troglodytes* level quadrupedal walking; (III) *P. paniscus* 45° incline climbing; (IV) *P. paniscus* vertical climbing; (V) *Hylobates* vertical climbing. (E) Passive in vivo hip extension ranges for nonhuman primates (pooled sexes) (29) and for humans (30). (Data are in *SI Appendix, Table S3*.)

hamstrings-powered hip extension beyond 180°. Sensitivity analyses show that differences in DMA envelopes between humans and nonhuman apes are robust to measurement error and uncertainty in pelvic orientation, femur length, and hamstrings attachment (*SI Appendix, SI Text, Figs. S2 and S3, and Table S4*).

Experimental analyses show that anatomically determined DMA envelopes correspond closely with hip angles habitually used during locomotion (Fig. 2B and *SI Appendix, Table S3*). During both level quadrupedal walking and vertical climbing (19), hip extension does not exceed 150° in nonhuman apes, and ranges of hip flexion and extension are quite similar across these taxa. The range of motion in the sagittal plane is greater when climbing vertically than when walking quadrupedally, with vertical climbing requiring a more flexed hip than walking

quadrupedally. Orangutans extend their hips more than other apes when climbing (Fig. 2B), yet remain within their hamstrings performance envelopes (Fig. 2A and *SI Appendix, Table S3*). Similarly, although hylobatids engage in bipedalism often, they do not extend their hips to 180° when walking quadrupedally (Fig. 2B), walking bipedally (20), or leaping (21). In contrast, during human walking, hip extension spans between 156° ± 4° and 200° ± 4° (22). Humans can flex their hips as much as apes when climbing trees (23), but nonhuman apes do not habitually extend their hips as much as bipedal humans do.

DMA envelopes also correspond strongly with patterns of hamstrings muscle activity and powered hip extension in humans, chimpanzees, bonobos, and gibbons, the only hominoids for whom these have been measured (Fig. 2C and D and *SI Appendix, Table S3*) (8, 9, 24–27). Chimpanzees and bonobos activate the hamstrings and produce hip extension moments as they extend the hip over a range of 10–100° during vertical climbing (90° substrate), incline climbing (45°), and level walking (0°). Maximum hip extensor moments occur near 25° and 75° hip extension for incline climbing and level quadrupedal walking, respectively (Fig. 2C). In contrast, humans activate the hamstrings group during stance phase (26) and generate extensor hip moments over a range of ~150–200° hip extension, outside the ape DMA envelope (*SI Appendix, Table S3*). These differences between *Homo* and *Pan* suggest that hamstrings DMA predicts when these muscles are active and when the hip joint produces the most torque.

As a final empirical test, we compared DMA envelope with the range of passive hip extension, which is constrained by the bony morphology and ligaments of the hip (28, 29). Although DMA ranges were generally broader than in vivo ranges, mean values of maximum hip extension from DMA envelopes closely corresponded with published ranges of passive hip extension measured in vivo on anesthetized apes and humans (refs. 29 and 30; Fig. 2E and *SI Appendix, Table S3*). Apes, particularly orangutans, can approach 180° hip extension in their passive range of motion (29), and occasionally during bipedal walking (e.g., refs. 31 and 32). However, hyperextension (>180°) of the hip, which is a critical component of straight-legged, economical human walking, falls outside of ape capabilities, consistent with ischium morphology.

Empirically tested differences in ischial mechanics demonstrate a clear trade-off between walking and climbing capabilities in living hominoids. The greater peak of great apes' DMA envelopes indicates greater torque at the hip per unit of hamstrings muscle force, permitting more powerful hip extension that may be critical during vertical climbing and arboreal scrambling. The lower range of apes' DMA envelopes reflects flexed-hip postures during walking and climbing, but prevents hamstrings-powered hyperextension of the hip. In contrast, humans' higher DMA range permits powered hyperextension, an essential component of humans' economical striding bipedalism (8, 9, 13). Humans' short ischium and reduced DMA peak likely reflect the lower power requirements of walking and may also reduce hamstring muscle strain (i.e., shortening). Kinematic and anatomical strategies to reduce muscle strain have been shown to improve locomotor efficiency in other species (33), and reduced hamstring strain might similarly contribute to the efficiency of human walking.

The mechanics of hip extension in humans and apes also provide insight into the evolution of the gluteus maximus in hominins. In chimpanzees, orangutans, and gibbons, gluteus maximus is much smaller than in humans and does not extend the hamstrings' range of powered hip extension (34–36). In humans, the gluteus maximus is greatly enlarged and serves a distinct and complementary role with the hamstrings in powering hip extension. In human walking, hyperextension of the hip is powered in part by the hamstrings (ref. 26; Fig. 2), and the

gluteus maximus is notably quiet throughout stance phase (34, 35). Instead, the gluteus maximus is active when the hip is more flexed; for example, during the early portion of stance phase during running and climbing (34, 35). The enlarged gluteus maximus appears to compensate for humans' derived ischial morphology and the reduced effectiveness of the hamstrings when the hip is flexed, particularly at angles $<40^\circ$, where the hamstrings cannot power extension (Fig. 2).

Fossil Taxa. The overlap in DMA envelopes for monkeys and nonhuman apes is unsurprising, given the broad similarity in their ranges of hip extension during walking and when passively measured in vivo (refs. 29 and 37; Fig. 2E and *SI Appendix, Table S3*), and suggests this aspect of ischial mechanics may be a primitive condition for hominoids. The only Miocene hominoid pelvis that is sufficiently complete for this analysis, that of *E. nyanzae* (38, 39), is consistent with this hypothesis, exhibiting a DMA envelope that is broadly similar to that of monkeys and nonhuman apes (*SI Appendix, Fig. S4*). Material from other Miocene apes is needed to test this hypothesis.

Unlike extant hominoids, *Ardipithecus* ischial morphology does not exhibit a trade-off between climbing and walking capabilities. As noted in its initial description (17), the *Ardipithecus* ischium is long, falling within the range observed for apes of equivalent femur length (Fig. 1C), which results in a peak DMA similar to apes and substantially greater than in humans (*SI Appendix, Table S5*). Nonetheless, DMA envelopes for *Ardipithecus* indicate a nearly human-like range of hip extension. We examined hamstrings DMA envelopes for a wide range of pelvis and trunk orientations to account for uncertainty in the forward tilt of the pelvis relative to the spine (*Methods*; Fig. 3, and *SI Appendix, Fig. S5*). With any mechanically feasible bipedal trunk orientation, powered hip extension would fail between 195° and 205° , depending on the degree of pelvic tilt and lumbar lordosis or trunk inclination (Fig. 3 and *SI Appendix, Table S5*). The *Ardipithecus* range exceeds the chimpanzees' by $\sim 40^\circ$ and approaches that of humans (*SI Appendix, Table S3*).

These results suggest greater hip extension and more economical walking in *Ardipithecus* relative to living and Miocene apes (although marginally less than that of modern humans), without a substantial loss of the hip extension moment essential

for climbing. Notably, this dual capability in the *Ardipithecus* pelvis derives not from changes in the ischium itself, which remains quite primitive (17), but from changes in ilium morphology that reorient the ischium relative to the sacrum and vertebral column. Derived changes in ilium morphology that unite hominins (17) are generally discussed in terms of lateral stabilization of the trunk during single-leg stance. Results here highlight the underappreciated effects of ilium morphology on the mechanics of hip extension.

Hamstrings DMA envelopes for the *Australopithecus* specimens indicate a reduced maximum DMA relative to *Ardipithecus*, but a broadly similar range of powered hip extension (Fig. 3 and *SI Appendix, Table S5*). The reduction in peak DMA brings the hamstrings moment arm down into the human range and reflects the shorter ischia in both *Au. afarensis* and *Au. africanus*, which fall below the range for apes and monkeys (Fig. 1C). Over the range of mechanically feasible pelvic tilt, maximum hip angles for *Au. afarensis* ($200\text{--}215^\circ$; Fig. 3 and *SI Appendix, Table S5*) approach the lower range of humans, suggesting nearly human-like capability for powered hip hyperextension and walking economy (Fig. 3), consistent with previous reconstructions of their gait (40–43). *Au. africanus* maintains greater DMA in more flexed positions and loses its capacity for powered hip extension between 180° and 200° (Fig. 3 and *SI Appendix, Table S5*), possibly indicating a marginally less hyperextended hip during walking compared with *Au. afarensis*.

Enlargement of the gluteus maximus has been linked to the evolution of endurance running capabilities in *Homo* (34). However, the derived ischial morphology evident in *Australopithecus* (Fig. 3) suggests this enlargement of the gluteus maximus and its complementarity with the hamstrings (discussed earlier) might have begun earlier, possibly under selection pressure to enable powerful hip extension when the hip was flexed (e.g., during climbing). This hypothesis is consistent with previous analyses of pelvic morphology and mechanics in *Australopithecus*, suggesting its gluteus maximus size was intermediate between apes and humans (34, 44). Given the rightward shift of the *Ardipithecus* DMA envelope relative to other nonhuman primates (Fig. 2), it is even possible that gluteus maximus enlargement and complementarity with the hamstrings began with earlier hominins.

Discussion

Integrated anatomical and experimental analyses here indicate that *Ardipithecus*, the earliest hominin with a preserved pelvis, avoided the arboreal–terrestrial trade-off in ischial mechanics evident among living hominoids, and was instead capable of both powerful hip extension during climbing and economical hip hyperextension during walking. It remains unclear whether, and to what extent, any other of *Ardipithecus*' retained adaptations for arboreality (e.g., elongated forelimb, curved phalanges, and grasping hallux; refs. 17, 45, and 46) limited its walking economy or endurance. For example, a mobile, grasping foot is generally thought to reduce the efficacy of toe-off at the end of stance phase during walking (10), but experimental work shows negligible effects of foot anatomy on economy: plantigrade, digitigrade, and unguligrade species have similar running costs (47), and mechanical models ignoring tarsal and metatarsal anatomy successfully predict variation in locomotor economy among hominoids and other taxa (9). Initial descriptions of the *Ardipithecus* skeleton (17) suggested it had a relatively short, ape-like hind limb length (48), a feature known to reduce walking economy (9) and that might improve climbing. However, more recent analyses suggest a smaller body mass for *Ardipithecus*, which would bring its hind limb length more in line with later hominins (49). An intriguing possibility suggested by results here is that economical walking

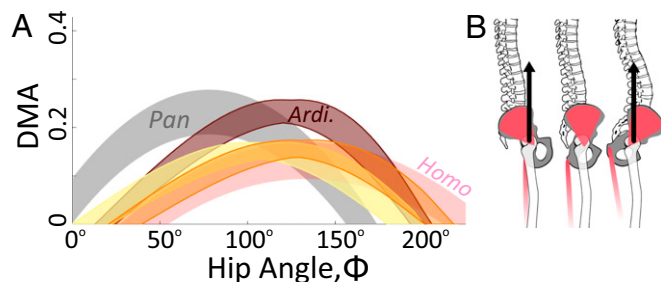


Fig. 3. DMA and pelvic orientation in fossil taxa. (A) *Homo*, pink; *Pan*, gray; *Ar. ramidus*, brown; *Au. afarensis*, orange; *Au. africanus*, yellow. Skeletally derived envelopes for hamstrings DMA. Shaded regions for *Pan* and *Homo* represent 95% prediction intervals. Shaded regions for fossils represent the full range of mechanically feasible pelvic pitch angles plus a range of reconstructed sacral breadths and femur lengths (see *Methods*). (B) The range of pelvic tilt angles for bipedal orientation is based on the requirement that some portion of the medial gluteals (red regions on the ilia) must be aligned vertically to oppose gravity and to stabilize the trunk during single-leg stance. In the most dorsal-superior orientation (Left), the anterior border of the medial gluteals is aligned vertically over the acetabulum; in the most ventral-inferior orientation (Right), the posterior border of the medial gluteals is aligned vertically over the acetabulum. (See *SI Appendix, Table S5*.)

capabilities evolved in early hominins without any hindrance from or detriment to arboreal adaptations.

Ischial morphology in *Australopithecus* suggests reduced power in hip extension and an increased range of hip hyperextension, relative to earlier hominins. A shorter ischium might have further improved walking economy by reducing hamstrings muscle strain, as discussed earlier for humans. Hallux adduction in *Australopithecus* might have contributed to improved walking economy, but further testing is needed. Regardless, although these changes in hind limb morphology suggest selection for improved walking economy, their effect on arboreal capabilities is unclear and warrants further testing. For example, despite the loss of an elongated forelimb, long curved phalanges, and a grasping foot, humans are just as energetically efficient when climbing as arboreal primates (50). Rather than a functional trade-off between walking and climbing capability, hind limb changes in *Australopithecus* could reflect reduced time spent arboreally and weakened selection for traits to maintain safety in the canopy (13). Although locomotor capabilities are inherently multivariate, identifying specific performance variables (e.g., safety, economy, speed) to test empirically will improve our reconstructions of hominin locomotor evolution.

Reconstructions of locomotor capabilities and ecology in extinct taxa have traditionally used a “fossil-first” approach, starting with a detailed description of the preserved morphology and deducing its function from first principles (e.g., ref. 4) or by assigning it to an extant functional group. Although useful, these approaches often prove inconclusive or misleading when traits, or trait combinations, fall outside those of modern taxa, which is a common occurrence in fossil analyses. Results here demonstrate the utility of a complementary “function-first” approach, focusing on empirically validated determinants of locomotor performance (e.g., hip hyperextension) and integrating detailed anatomical measures with experimental data to resolve locomotor capabilities in fossil taxa. Given the breadth of morphological solutions and locomotor capabilities among fossil apes and hominins, not to mention the diversity of extinct taxa throughout the paleontological record, both fossil-first and function-first approaches are needed to reconstruct the ecology of species past and the origins of modern groups.

Methods

Morphological Sample. The fossil sample consists of the pelvis generated from ARA-VP 6/500 (*A. ramidus*) (17), as well as the American Museum of Natural History reconstructions of the pelvis for A.L. 288–1 (*Au. afarensis*), STS 14 (*Au. africanus*), and a cast of KNM-MW 13124 (*E. nyanzae*). All apes ($n = 69$), cercopithecids ($n = 32$), and platyrrhines ($n = 24$) are wild shot adult specimens from the American Museum of Natural History and Smithsonian Museum (SI Appendix, Table S1). The human sample consists of 18 adults from the American Museum of Natural History Medical Collection, including both African-American and Caucasian individuals (SI Appendix, Table S1).

Landmarks and measurements. Using a Microscribe, a set of 23 landmarks (51) (SI Appendix, Fig. S1 and Table S6) was collected on one os coxae of each specimen. Ischial length was defined as the distance between the deepest point of the acetabulum and the midpoint of the most dorsal/superior point and the most dorsal/inferior point of the ischial tuberosity. Femur length was measured as the distance from the most superior point on the femoral head to the most inferior point on the medial condyle. Sacral breadth was measured as the distance between the most lateral aspects of the right and left alae. For the fossil sample, landmarks were collected from model reconstructions, and estimated femur lengths and sacral breadths were obtained from the literature (15, 38, 52) (SI Appendix, Table S2). We estimate the sacral breadth for ARA-VP 6/500 at 105 mm, based on the report that its estimated interacetabular distance is 115% wider than in A.L. 288–1 (17). In addition, we analyzed ranges of $\pm 10\%$ on estimated femur lengths and sacral breadths to account for the possible error in these estimates.

Orientation. Each landmark set underwent a series of translations and rotations to place all specimens in anatomical orientation (SI Appendix, Fig. S6). For humans, the degree of pelvic tilt in the sagittal plane was determined from published dissection data (53), which indicate an angle of 15° relative

to horizontal for the segment connecting the posterior superior iliac spine and anterior superior iliac spine (ASIS) reflected in the sagittal plane (SI Appendix, Fig. S4). There are no comparable nonhuman primate dissection data published. Therefore, we measured the angle between the trunk and the line connecting the superior pubic symphysis and the ASIS (SI Appendix, Fig. S7) on digital photos of mounted skeletons in lateral view in 12 nonhuman primates (five apes, three cercopithecoids, and four platyrrhines; mean = 43.2° , SD = 5.2° , SI Appendix, Fig. S7 and Table S7). We used a 40° quadrupedal orientation for nonhuman primates with an included $\pm 10^\circ$ in sensitivity analyses to account for variation. This approach is consistent with observed trunk orientations in the sagittal plane for bipedal humans and chimpanzees (54).

The human orientation, based on ASIS position, would be inappropriate for early hominins human evolution because the ASIS has moved anteriorly in *Homo* relative to earlier hominins. Instead, for *Ardipithecus*, *Au. afarensis*, and *Au. africanus*, bipedal pelvic orientation was calculated over the full-range positions where the iliac crest is positioned above the acetabulum, under the assumption that some portion of the abductor muscle fibers must run vertically over the acetabulum to oppose gravity in single-leg stance (Fig. 3). At one extreme of this range, the posterior-most aspect of the posterior iliac crest lies directly above the posterior-most aspect of the acetabulum. At the other extreme of the range, the ASIS lies directly above the anterior-most aspect of the acetabulum (Fig. 3 and SI Appendix, Fig. S3). At the midpoint of this range, the midpoint between the ASIS and posterior-most aspect of the posterior iliac crest lies directly above the center of the acetabulum. This functional range of pelvic orientation is supported by the human osteological data set: mean displacement from midpoint position was $1.2^\circ \pm 6.8^\circ$ (range, -9.3° to $+13.3^\circ$) for human specimens in our sample, and none fell outside the maximum range of pelvic tilt applied to fossil hominins.

DMA. Hip angle is defined as the angle between the femur and trunk axis in the sagittal plane (ϕ in Fig. 1). Moment arm and DMA were calculated across a range of angles (0 – 250° at 5° intervals) for each specimen. The hamstring moment arm (r) is the perpendicular distance between the hip center of rotation (approximated as the deepest point of the acetabulum) and the line of action (i.e., the force vector) for the hamstring muscles (the line connecting the origin and insertion points of the hamstrings) in the sagittal plane. The angle between the femur and hamstrings (α) was calculated from the coordinates of the acetabulum, distal femur, and ischial attachment of the hamstrings, using the law of cosines (SI Appendix, Fig. S3). The moment arm r is then given by $r = \sin(\alpha) B$, where B is femur length. DMA is the ratio of the moment arm r/B , and it defines the tangential force exerted at the knee for each newton of hamstring force.

DMA sensitivity analyses. We performed sensitivity analyses to assess how robust results are to input parameter variation (SI Appendix, SI Text, Figs. S2 and S3, and Table S4). DMA values will be affected by sacral breadth, femur length, pelvic pitch, the location of the origin of the hamstrings on the ischium, and the location of hamstrings insertion on the tibia/fibula and knee flexion. To evaluate the effects of variation or uncertainty in sacral breadth and femur length, we varied these parameters by $\pm 10\%$ and examined changes in DMA envelopes (SI Appendix, SI Text 1). Next we varied pelvic pitch by $\pm 10^\circ$ and examined the effects on DMA (SI Appendix, Table S4). Finally, we measured the combined effect of varying pelvic pitch by $\pm 10^\circ$ and varying the point of origin of the hamstrings to the most superior and to the most inferior points of the ischial tuberosity face (SI Appendix, Fig. S1). The effect of hamstrings attachment on the tibia/fibula and knee flexion is modeled in SI Appendix, Fig. S4. In all sensitivity analyses, the pattern of DMA differences among humans, fossil hominins, and nonhuman apes was robust to variation and uncertainty in model parameters.

Kinematics. Hip angles during quadrupedal level locomotion were measured for captive *Pongo* spp., *Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Macaca fuscata* (Fig. 2B and SI Appendix, Table S3). High-speed videos (300 frames/s, taken with Casio Exilim FX 1) of apes moving perpendicular to the camera line of sight were analyzed in the program Kinovea (version 0.8.14; www.kinovea.org/). Videos were recorded from public viewing platforms at 10 Association of Zoos and Aquariums-accredited US zoos (Zoo Atlanta, Columbus Zoo, Dallas Zoo, Franklin Park Zoo, Indianapolis Zoo, Jacksonville Zoo, Lincoln Park Zoo, Milwaukee County Zoo, North Carolina Zoo, and Oklahoma City Zoo). Hunter College and all participating zoos provided Institutional Animal Care and Use Committee approval before data collection. The hip angle is defined, following previous studies (8, 27), as the angle between the shoulder, hip, and knee centers of rotation. To obtain the range of hip flexion and extension, hip angles were measured at touch down (first frame of contact with substrate) and toe-off (last frame of contact with the substrate).

A subset of five videos were measured twice at a 1-wk interval to evaluate interobserver error (mean error, 1.45°). A paired *t* test showed that the two data sets were not significantly different from each other (*P* = 0.39). Hip angles for apes climbing and human walking were taken from the literature (7, 19).

Kinetics. Human and chimpanzee moment data were collected within a locomotor energetics study (8). Bonobo kinetic data were collected as part of a bonobo locomotor study (kinematics reported in refs. 27 and 55). Moments were rendered dimensionless by dividing them by body weight and lower leg length. Hip angles were extracted from high-speed video using the same

approach as for kinematic trials. All animal research was conducted with prior institutional approval (8, 27, 55). Bonobo data have not been previously published.

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- Dart AR (1925) *Australopithecus africanus*: The man-ape of South Africa. *Nature* 2884: 195–199.
- White TD, et al. (2009) *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326:75–86.
- Zollikofer CPE, et al. (2005) Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature* 434:755–759.
- Stern JT, Jr, Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. *Am J Phys Anthropol* 60:279–317.
- Latimer B (1991) Locomotor adaptations in *Australopithecus afarensis*: The issue of arboreality. *Origine(s) de la bipédie chez les Hominidés*, eds Senut B, Coppens Y (CNRS, Paris), pp 169–176.
- Ward CV (2002) Interpreting the posture and locomotion of *Australopithecus afarensis*: Where do we stand? *Am J Phys Anthropol* 119(Suppl 35):185–215.
- DeSilva JM, et al. (2013) The lower limb and mechanics of walking in *Australopithecus sediba*. *Science* 340:1232999.
- Sockol MD, Raichlen DA, Pontzer H (2007) Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc Natl Acad Sci USA* 104:12265–12269.
- Pontzer H, Raichlen DA, Sockol MD (2009) The metabolic cost of walking in humans, chimpanzees, and early hominins. *J Hum Evol* 56:43–54.
- Holowka NB, O'Neill MC, Thompson NE, Demes B (2017) Chimpanzee and human midfoot motion during bipedal walking and the evolution of the longitudinal arch of the foot. *J Hum Evol* 104:23–31.
- Bramble DM, Lieberman DE (2004) Endurance running and the evolution of *Homo*. *Nature* 432:345–352.
- Thompson NE, Demes B, O'Neill MC, Holowka NB, Larson SG (2015) Surprising trunk rotational capabilities in chimpanzees and implications for bipedal walking proficiency in early hominins. *Nat Commun* 6:8416.
- Pontzer H (2017) Locomotor ecology and evolution in chimpanzees and humans. *Chimpanzees and Human Evolution*, eds Muller MN, Wrangham RW, Pilbeam DR (Harvard Univ Press, Cambridge, MA), pp 259–285.
- McHenry HM (1975) The ischium and hip extensor mechanism in human evolution. *Am J Phys Anthropol* 43:39–46.
- Robinson JT (1972) *Early Hominid Posture and Locomotion* (Chicago Univ Press, Chicago).
- Lewton KL, Scott JE (2017) Ischial form as an indicator of bipedal kinematics in early hominins: A test using extant anthropoids. *Anat Rec (Hoboken)* 300:845–858.
- Lovejoy CO, Suwa G, Spurluck L, Asfaw B, White TD (2009) The pelvis and femur of *Ardipithecus ramidus*: The emergence of upright walking. *Science* 326:71e1–71e6.
- Foster AD, Raichlen DA, Pontzer H (2013) Muscle force production during bent-knee, bent-hip walking in humans. *J Hum Evol* 65:294–302.
- Isler K (2005) 3D-kinematics of vertical climbing in hominoids. *Am J Phys Anthropol* 126:66–81.
- Vereecke EE, D'Août K, Aerts P (2006) Locomotor versatility in the white-handed gibbon (*Hyllobates lar*): A spatiotemporal analysis of the bipedal, tripodal, and quadrupedal gaits. *J Hum Evol* 50:552–567.
- Channon AJ, Usherwood JR, Crompton RH, Günther MM, Vereecke EE (2012) The extraordinary athletic performance of leaping gibbons. *Biol Lett* 8:46–49.
- Kerrigan DC, Lee LW, Collins JJ, Riley PO, Lipsitz LA (2001) Reduced hip extension during walking: Healthy elderly and fallers versus young adults. *Arch Phys Med Rehabil* 82:26–30.
- Venkataraman VV, Kraft TS, Dominy NJ (2013) Tree climbing and human evolution. *Proc Natl Acad Sci USA* 110:1237–1242.
- Larson SG, Stern JT, Jr (2009) Hip extensor EMG and forelimb/hind limb weight support asymmetry in primate quadrupeds. *Am J Phys Anthropol* 138:343–355.
- Kumakura H (1989) Functional analysis of the biceps femoris muscle during locomotor behavior in some primates. *Am J Phys Anthropol* 79:379–391.
- Benedetti MG, Agostini V, Knaflitz M, Bonato P (2012) Muscle activation patterns during level walking and stair ambulation. *Applications of EMG in Clinical and Sports Medicine*, ed Steele C (InTech, London), pp 117–130.
- D'Août 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.
- MacLatchy LM (1998) Reconstruction of hip joint function in extant and fossil primates. *Primate Locomotion*, eds Strasser E, Fleagle J, McHenry H, Rosenberger A (Plenum, New York), pp 111–130.
- 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.
- Hallaçeli H, et al. (2014) Normal hip, knee and ankle range of motion in the Turkish population. *Acta Orthop Traumatol Turc* 48:37–42.
- Thorpe SKS, Holder RL, Crompton RH (2007) Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* 316:1328–1331.
- Watson J, Payne R, Chamberlain A, Jones R, Sellers WI (2009) The kinematics of load carrying in humans and great apes: Implications for the evolution of human bipedalism. *Folia Primatol (Basel)* 80:309–328.
- Roberts TJ, Marsh RL, Weyand PG, Taylor CR (1997) Muscular force in running turkeys: The economy of minimizing work. *Science* 275:1113–1115.
- Lieberman DE, Raichlen DA, Pontzer H, Bramble DM, Cutright-Smith E (2006) The human gluteus maximus and its role in running. *J Exp Biol* 209:2143–2155.
- Bartlett JL, Sumner B, Ellis RG, Kram R (2014) Activity and functions of the human gluteal muscles in walking, running, sprinting, and climbing. *Am J Phys Anthropol* 153:124–131.
- Stern JT, Susman RL (1981) Electromyography of the gluteal muscles in *Hyllobates*, *Pongo*, and *Pan*: Implications for the evolution of hominid bipedality. *Am J Phys Anthropol* 55:153–166.
- Demes B (2011) Three-dimensional kinematics of capuchin monkey bipedalism. *Am J Phys Anthropol* 145:147–155.
- Ward CV, Walker A, Teaford MF, Odhiambo I (1993) Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. *Am J Phys Anthropol* 90:77–111.
- McNulty KP, Begun DR, Kelley J, Manthi FK, Mbua EN (2015) A systematic revision of *Proconsul* with the description of a new genus of early Miocene hominoid. *J Hum Evol* 84:42–61.
- Nagano A, Umberger BR, Marzke MW, Gerritsen KG (2005) Neuromusculoskeletal computer modeling and simulation of upright, straight-legged, bipedal locomotion of *Australopithecus afarensis* (A.L. 288-1). *Am J Phys Anthropol* 126:2–13.
- Raichlen DA, Gordon AD, Harcourt-Smith WE, Foster AD, Haas WR (2010) Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics. *PLoS One* 5:e9769.
- Hatala KG, Demes B, Richmond BG (2016) Laetoli footprints reveal bipedal gait biomechanics different from those of modern humans and chimpanzees. *Proc Biol Sci* 283:20160235.
- Crompton RH, Yu L, Weijie W, Günther M, Savage R (1998) The mechanical effectiveness of erect and “bent-hip, bent-knee” bipedal walking in *Australopithecus afarensis*. *J Hum Evol* 35:55–74.
- Haeussler M (2002) New insights into the locomotion of *Australopithecus africanus* based on the pelvis. *Evol Anthropol* 11:53–57.
- Lovejoy CO, Simpson SW, Asfaw B, White TD, Suwa G (2009) Careful climbing in the Miocene: The forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science* 326:70e1–70e8.
- Lovejoy CO, Latimer B, Suwa G, Asfaw B, White TD (2009) Combining prehension and propulsion: The foot of *Ardipithecus ramidus*. *Science* 326:72e1–72e8.
- Taylor CR, Heglund NC, Maloij GMO (1982) Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J Exp Biol* 97:1–21.
- Pontzer H (2012) Ecological energetics in early *Homo*. *Curr Anthropol* 53(S6): S346–S358.
- Grabowski M, Hatala KG, Jungers WL, Richmond BG (2015) Body mass estimates of hominin fossils and the evolution of human body size. *J Hum Evol* 85:75–93.
- Hanna JB, Schmitt D, Griffin TM (2008) The energetic cost of climbing in primates. *Science* 320:898.
- Bookstein FL (1991) *Morphometric Tools for Landmark Data: Geometry and Biology* (Cambridge Univ Press, Cambridge, UK).
- Johanson DC, et al. (1982) Morphology of the Pliocene partial hominid skeleton (AL 288-1) from the Hadar formation, Ethiopia. *Am J Phys Anthropol* 57:403–451.
- Visser JJ, Hoogkamer JE, Bobbert MF, Huijijng PA (1990) Length and moment arm of human leg muscles as a function of knee and hip-joint angles. *Eur J Appl Physiol Occup Physiol* 61:453–460.
- O'Neill MC, et al. (2015) Three-dimensional kinematics of the pelvis and hind limbs in chimpanzee (*Pan troglodytes*) and human bipedal walking. *J Hum Evol* 86:32–42.
- Schoonaert K, et al. (2016) Gait characteristics and spatio-temporal variables of climbing in bonobos (*Pan paniscus*). *Am J Primatol* 78:1165–1177.