



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 pelves permit greater extensor moments at the hip, enhancing climbing capability, but limit their range of hip extension, resulting in a crouched gait. Human pelves 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 pelves 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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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 unguigrade 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

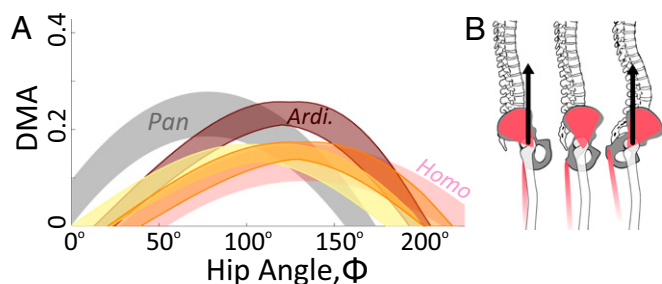


Fig. 3. DMA and pelvic orientation in fossil taxa. (A) *Homo*, pink; *Pan*, gray; *Ar. ramidus*, brown; *Au. afarensis*, orange; *Au. africanus*, yellow. Skeletally derived envelopes for hamstrings DMA. Shaded regions for *Pan* and *Homo* represent 95% prediction intervals. Shaded regions for fossils 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 model 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 (S1) (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 (θ 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 (ω) 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 $r = \sin(\omega) B$, 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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