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Science **326**, 71 (2009);
DOI: 10.1126/science.1175831

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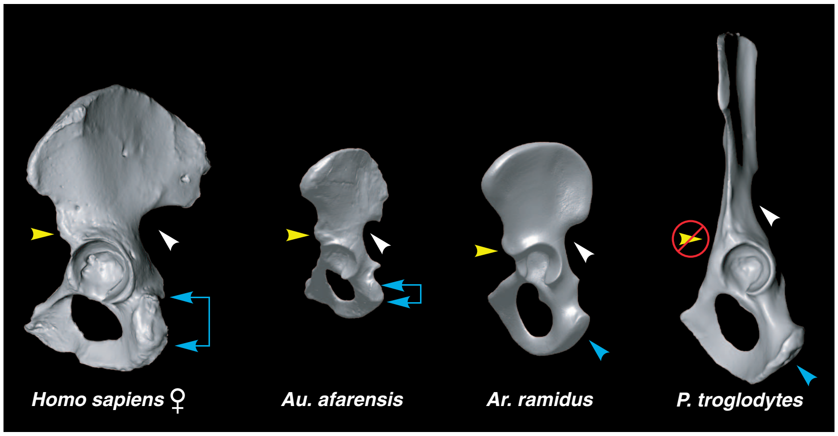
The Pelvis and Femur of *Ardipithecus ramidus*: The Emergence of Upright Walking

C. Owen Lovejoy, Gen Suwa, Linda Spurlock, Berhane Asfaw, Tim D. White



The *Ar. ramidus* pelvis has a mosaic of characters for both bipedality and climbing. Left to right: Human, *Au. afarensis* ("Lucy"), *Ar. ramidus*, *Pan* (chimpanzee). The ischial surface is angled near its midpoint to face upward in Lucy and the human (blue double arrows), showing that their hamstrings have undergone transformation for advanced bipedality, whereas they are primitive in the chimpanzee and *Ar. ramidus* (blue arrows). All three hominid ilia are vertically short and horizontally broad, forming a greater sciatic notch (white arrows) that is absent in *Pan*. A novel growth site [the anterior inferior iliac spine (yellow arrows)] is also lacking in *Pan*.

Virtually no other primate has a human-like pelvic girdle—not even our closest living relatives, the chimpanzee and bonobo. Such uniqueness evolved via substantial modifications of a pelvis more originally suited for life in trees. This arboreal primate heritage has left us rather ungainly. Our legs are massive because they continue to house almost all of the muscles originally required for climbing. Our hamstrings, the large muscles in our posterior thighs, must decelerate the swinging limb with each step, and when we run, the limb's inertia is sometimes too great and these muscles fail (not something one would want to happen on a savanna).

Furthermore, when each limb leaves the ground to be swung forward, it and the pelvis are unsupported and would slump toward the ground were it not for muscles acting on the opposite side of the body (the anterior gluteals). One early anthropologist described human locomotion as a process by which we alternately almost fall on our faces. Chimpanzees and other primates cannot prevent such slumping when walking upright because they cannot reposition these muscles effectively. Their spine is too inflexible and their ilia—the large pelvic bones to which the gluteals attach—are positioned and shaped differently than ours. Modifying a typical chimp or gorilla pelvis to facilitate upright walking would require extensive structural changes.

Until now, the fossil record has told us little about when and how the early hominid pelvis evolved. Even 3 to 4 million years ago (when our brains were still only slightly larger than those of chimpanzees), it had already undergone radical transformation. One of the oldest hominid pelves, that of *Australopithecus afarensis* (*A.L. 288-1*; "Lucy"), shows that her species had already evolved virtually all of the fundamental adaptations to bipedality. Even the kinetics of her hip joint were similar to ours. Although the human pelvis was later further reshaped, this was largely the result of our much enlarged birth canal.

Ardipithecus ramidus now unveils how our skeleton became progressively modified for bipedality. Although the foot anatomy of *Ar. ramidus* shows that it was still climbing trees, on the ground it walked upright. Its pelvis is a mosaic that, although far from being chimpanzee-like, is still much more primitive than that of *Australopithecus*.

The gluteal muscles had been repositioned so that *Ar. ramidus* could walk without shifting its center of mass from side to side. This is made clear not only by the shape of its ilium, but by the appearance of a special growth site unique to hominids among all primates (the anterior inferior iliac spine). However, its lower pelvis was still almost entirely ape-like, presumably because it still had massive hindlimb muscles for active climbing.

Changes made in the upper pelvis rendered *Ar. ramidus* an effective upright walker. It could also run, but probably with less speed and efficiency than humans. Running would also have exposed it to injury because it lacked advanced mechanisms such as those that would allow it to decelerate its limbs or modulate collision forces at its heel. *Australopithecus*, which had given up its grasping foot and abandoned active climbing, had evolved a lower pelvis that allowed it to run and walk for considerable distances.

Ar. ramidus thus illuminates two critical adaptive transitions in human evolution. In the first, from the human-chimp last common ancestor to *Ardipithecus*, modifications produced a mosaic pelvis that was useful for both climbing and upright walking. In the second, from *Ardipithecus* to *Australopithecus*, modifications produced a pelvis and lower limb that facilitated more effective upright walking and running but that were no longer useful for climbing. Because climbing to feed, nest, and escape predators is vital to all nonhuman primates, both of these transitions would likely have been a response to intense natural selection.

When citing, please refer to the full paper, available at DOI 10.1126/science.1175831.

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C. Owen Lovejoy,[1]* Gen Suwa,[2] Linda Spurlock,[3] Berhane Asfaw,[4] Tim D. White[5]

The femur and pelvis of *Ardipithecus ramidus* have characters indicative of both upright bipedal walking and movement in trees. Consequently, bipedality in *Ar. ramidus* was more primitive than in later *Australopithecus*. Compared with monkeys and Early Miocene apes such as *Proconsul*, the ilium in *Ar. ramidus* is mediolaterally expanded, and its sacroiliac joint is located more posteriorly. These changes are shared with some Middle and Late Miocene apes as well as with African apes and later hominids. However, in contrast to extant apes, bipedality in *Ar. ramidus* was facilitated by craniocaudal shortening of the ilium and enhanced lordotic recurvature of the lower spine. Given the predominant absence of derived traits in other skeletal regions of *Ar. ramidus*, including the forelimb, these adaptations were probably acquired shortly after divergence from our last common ancestor with chimpanzees. They therefore bear little or no functional relationship to the highly derived suspension, vertical climbing, knuckle-walking, and facultative bipedality of extant African apes.

The hominid pelvis is among the most distinct osteological complexes of primates. Its distinctiveness derives from the configuration of its superior portion that maintains balance on a single limb during upright walking. These changes are not shared with apes. Therefore, comparison of the pelvis and hip among fossil and extant hominids and apes is critical for reconstructing the evolutionary steps leading to upright walking in humans versus the knuckle-walking and vertical climbing practiced by our nearest ape relatives.

An almost complete but damaged left hip (os coxa), a portion of the right ilium, and a distal sacral fragment were recovered from the Aramis *Ardipithecus ramidus* partial skeleton (*ARA-VP-6/500*) (*1*). The os coxa's overall form is preserved despite postmortem distortions of varying magnitude, most notably the fragmentation, separation, and translation of cranial and caudal portions of the acetabulum (Fig. 1).

The recovered os coxa is fragmented, distorted, friable, and inseparable from internal matrix, preventing restoration by standard methods (*2*–*4*). To aid our analysis, we made a reconstruction by using anatomical and high-resolution tomographic rapid prototyping models. We iteratively adjusted various surface metrics to verify them against the original fossil. Multiple permutations of this process produced a model that conformed to all major undistorted linear measurements of the original fossil (Figs. 1 and 2 and figs. S1 to S3).

The superior portion of the iliac blade was bent anteromedially postmortem, eliminating its original lateral flare. This has been adjusted in the model. The natural curvature of the superior pubic ramus is preserved despite its fragmentation into three sections. These sections were reassembled to form the upper portion of the ischiopubic region. The position of the ischiopubic ramus was restored on this basis. All of our descriptions of the features and linear measurements of the hip and femur are independent of this reconstruction, which was used as a three-dimensional heuristic aid (*5*). Acetabular size and some angles are, by necessity, approximations. We provide probable ranges of likely original values where appropriate.

The majority of the sacrum was not preserved. In reconstructions of the entire pelvis, however, the distance separating the two auricular surfaces is also indicated by the length and angulation of the arcuate line and plane of the pubic surface. The former can be well approximated from the fossil, and the latter is intact. Nevertheless, the exact biacetabular breadth remains unknown as do, therefore, the exact dimensions of the three primary pelvic planes.

The ilium, ischium, and pubis. The *Ar. ramidus* ilium is dramatically mediolaterally broad as in all post-Miocene hominoids, especially *Symphalangus*, *Gorilla*, *Australopithecus*, and *Homo* (*6*). Its iliac fossa is largely intact, from the anterior margin of its auricular surface to the well-preserved anterior iliac margin. Here, a prominent anterior inferior iliac spine (AIIS) maintains an intact relationship to the superior acetabular wall (Fig. 1). As in later hominids, the ilium is laterally flared for relocation of the anterior gluteals and has a forward sweeping anterior superior iliac spine (ASIS). The anterosuperior edge of the ilium is fractured and lacks an intact crest. On the basis of the form of the bone in both apes and humans, we estimated that it would have extended only about 1 cm superior to its broken edge. A further extension would improve the role of the abductor lever arm during upright gait. We based the anterosuperior projection of the ASIS on the well-preserved AIIS and their typical relationship in hominoids. We therefore regard its position in Figs. 1 and 2 and figs. S1 to S3 to be close to that of the original, although it may have terminated less superiorly than reconstructed here.

The protuberant and anteriorly positioned AIIS is associated with a broad, short, and sagittally disposed iliac isthmus. We define the isthmus as the constricted inferior portion of the iliac blade immediately superior to the acetabulum (Figs. 1 and 2 and fig. S3). These features are shared with later hominids, but in both modern and Early Miocene apes and monkeys the isthmus is markedly elongate, and the greater sciatic notch (GSN) angle is more obtuse (Fig. 3B). The *Ar. ramidus* GSN is intermediate between its counterpart in modern apes and those of later fossil hominids (Fig. 3C and fig. S4).

In stark contrast to its distinctly hominid ilium, the preserved *Ar. ramidus* ischium is like that of African apes. Although the ischial tuberosity is not preserved, the ischium is intact from its typical concave surface flare just superior to the tuberosity to the inferior border of the acetabulum (Fig. 1). Even this minimum preserved length of the superior ischial ramus is substantially longer than any known *Australopithecus* example (Fig. 3D) (*7*).

The pubis preserves an intact, superoinferiorly elongate body. However, the outline of the pubic symphyseal face is similar to that of *Homo* and *A.L. 288.-1* and unlike its extreme dorsoventral elongation in African apes (Fig. 3A). This more ovoid shape may be a collateral pleiotropic manifestation [Type 2A effect (*8*)] of the shortened iliac isthmus and elongated superior pubic ramus, especially in *A.L. 288-1* (which exhibits both an unusually broad pubic face and greatly elongated pubic rami) (Fig. 3A) (*7*).

Pelvic form and function. Anthropoid pelvic form is highly conserved, and major proportions are therefore similar from Old World monkeys (cercopithecoids) to *Proconsul* (*9*, *10*). However, features shared by all demonstrate that the last common ancestor of *Gorilla*, *Pan*, and *Homo* (hereafter the GLCA) must have exhibited two substantial modifications of the anthropoid pattern, both largely occurring in the coronal plane (*10*): (i) a lateral expansion of the iliac fossa and crest (fig. S5) and (ii) a corresponding reduction in the retroauricular region or pars sacralis of the ilium (fig. S6) (*10*). Both of these changes appear to be present in some other hominoid ilia, those of *Dryopithecus brancoi* (*11*) and *Oreopithecus bambolii* (*12*), but apparently are absent in *Proconsul* and *Nacholapithecus* (*13*). The breadth of the ilium appears to scale with body mass and

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[1] Department of Anthropology, School of Biomedical Sciences, Kent State University, Kent, OH 44242–0001, USA. [2] The University Museum, The University of Tokyo, Hongo, Bunkyo-ku, Tokyo 113-0033, Japan. [3] Cleveland Museum of Natural History, Cleveland, OH 44106–4930, USA. [4] Rift Valley Research Service, Post Office Box 5717, Addis Ababa, Ethiopia. [5] Human Evolution Research Center and Department of Integrative Biology, 3101 Valley Life Sciences Building, University of California at Berkeley, Berkeley, CA 94720, USA.

*To whom correspondence should be addressed. E-mail: olovejoy@aol.com

may reflect a relatively greater gut volume in larger anthropoids involved in frugivory and/or mid-gut folivory (*14*). The reduction of the pars sacralis (the portion posterior to the iliac fossa/auricular surface boundary), however, was clearly not a simple product of body size but rather a collateral manifestation (pleiotropic but of selective importance; type 2A) (*8*) of thoracic vertebral column invagination associated with posterolateral reorientation of the scapular glenoid (*15*, *16*).

The African ape pelvis has also undergone dramatic craniocaudal differentiation. However, unlike the changes in the iliac fossa and crest breadth, the morphology of the *Ar. ramidus* pelvis implies that these changes in craniocaudal dimensions evolved after the last common ancestor of the African apes and hominids. *Pan* and *Gorilla* show slight positive allometry of maximum iliac height (*17*) as compared with *Proconsul* (fig. S7). *Gorilla* appears to have isometrically increased the height of the lower ilium versus its dimensions in *Proconsul* (fig. S8, lower iliac height). In *Pan*, the lower ilium is extended cranially, principally by elongation of the iliac isthmus. This elongation, at least in *Pan*, is but one element of global change in ape pelvic morphology, in which reduction of the lumbar column and narrowing of the sacral alae (fig. S9) have constricted and dorsally extended lumbar-iliac contact in the sagittal plane (fig. S10, the trans-iliac space). This entraps the caudal lumbar (or lumbars). In combination with reduced vertebral height and fewer lumbar vertebrae (*18*), this effectively eliminates any thoracopelvic mobility in African apes (table S1) (*7*) and appears to be an adaptation to vertical climbing and/or suspension.

There is no evidence of any difference in the relative height of the lower ilium between *Proconsul* and *ARA-VP-6/500* (fig. S8). However, the pelvis of *ARA-VP-6/500* shows that the lower lumbars were not entrapped as in great apes but were clearly free for anteroposterior curvature (lordosis) (figs. S9 to S11). This is because the posterior ilium and pars sacralis did not extend sufficiently superior to have restricted the most caudal lumbar. Given that early hominids most likely had six lumbars, and other manifestly primitive characters (*7*, *15*, *16*, *18*), it seems probable that hominids either quickly reversed or never experienced any tendency for the sacral narrowing seen in extant great apes. A capacity for posturally dependent lower lumbar orientation was a key adaptation to bipedality, an inference made almost a century ago (*19*).

The inferred freedom of the lowermost lumbar (or lumbars) in *Ar. ramidus*, coupled with broadening and more sagittal orientation of the iliac isthmus (fig. S4), would have permitted both lordosis and anterior extension of the lesser gluteals for pelvic stabilization during upright walking (*15*, *16*). These changes, in conjunction with retention of a long lumbar column and a lowered iliac crest [that is, a reduced maximum iliac height (fig. S7)], enhanced lordosis. Lordosis can be situationally achieved by cercopithecoids

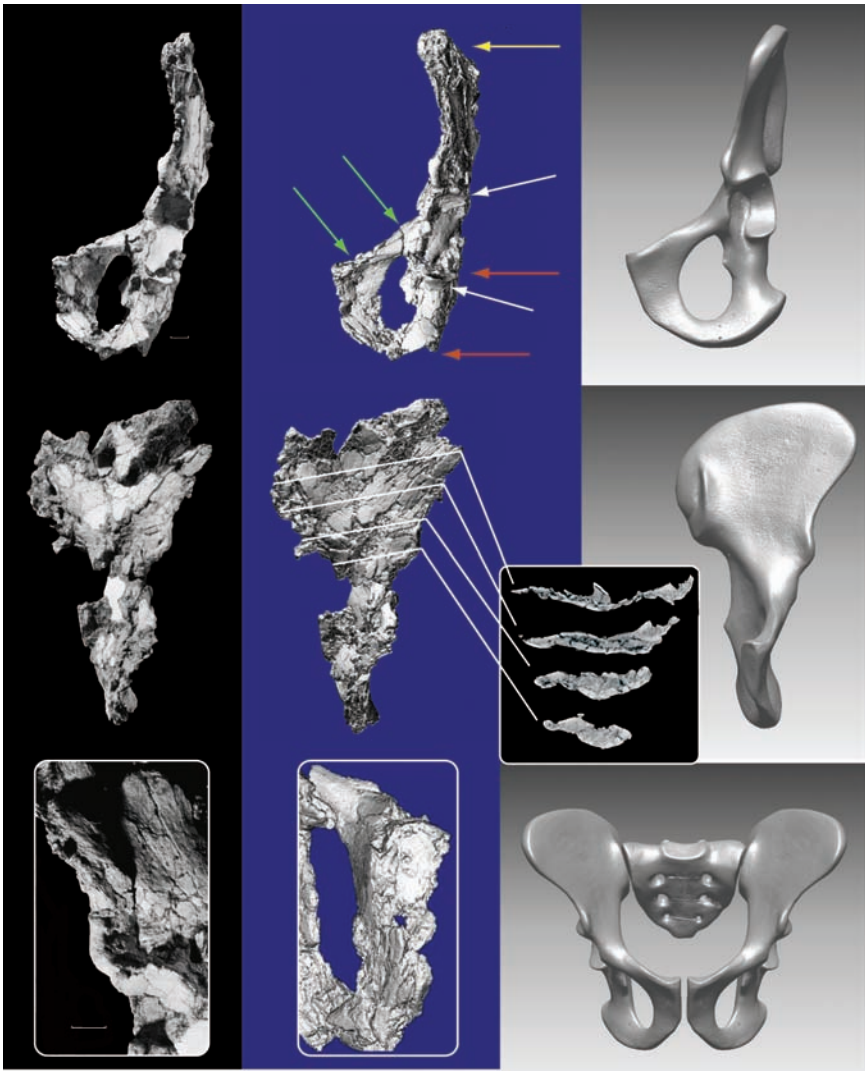

Fig. 1. Original and reconstructed os coxa of *ARA-VP-6/500*. (**Left**) Anterolateral and anteromedial views of the original, with a close-up of the AIIS. (**Middle**) CT scans of same views, except the bottom view is a close-up of the pubic symphyseal face, preserved in its entirety but damaged at its inferior extremity. It is like later hominids in its dorsoventral height and ovoid outline. (**Right**) Anterolateral and anteromedial views of the reconstructed os coxa (11th permutation) and of the entire pelvis using mirror reconstruction and a conjectural sacrum. Various permutations were attempted with respect to sacral breadth; the solution shown provides presumed functional minimal inlet and outlet dimensions for a hominoid of this individual's body size (Fig. 2 and figs. S1 to S3). (Middle) Arrows in the CT images indicate major areas of distortion corrected by reconstruction. The entire iliac blade was bent anteromedially (single yellow arrow) (additional and corrective data were provided by right iliac fragment). Two green arrows indicate primary foci of subduction of three largely intact segments of the superior pubic ramus; obvious overlapping allowed accurate restoration of original length (compare with reconstruction). The acetabulum was separated into two halves (total height of the exploded acetabulum is indicated by white arrows), with substantial intervening matrix infill. This separation greatly elongates its unrestored appearance. The two halves were recompressed on the basis of a calculated rim circumference obtained through the summation of individual segments (a range of probable values is presented in discussions of metric parameters). Two red arrows mark the inferior edge of the intact acetabular rim and the superior edge of the (missing) surface of the ischial tuberosity. These provide a minimum ischial length. Various additional dimensions were corrected by means of surface metrics. The breadth of the iliac fossa was intact from the AIIS to the lateral edge of the auricular surface; the degree of individual fragment separation was assessable from surface observation and CT scan data as indicated. Areas of particular anatomical importance include the protuberant sigmoid AIIS and sagittally oriented iliac isthmus, typical of later hominids, and the notably short, ovoid, pubic symphyseal face. Major metrics and angles are provided in Fig. 3. CT scans were taken at 300-µm voxel resolution on the University Museum, the University of Tokyo, micro-CT system [TX-225 Actis (Tesco, Tokyo)] and processed with the software Analyze 6.0 (Mayo Clinic, Rochester, MN) and Rapidform 2004/2006 (Inus Technology, Seoul).

(*20*) (and presumably in *Proconsul*), even though Old World monkey ilia typically entrap the most caudal lumbar vertebra. Lordosis has been entirely eliminated in the African apes.

The form and size of the AIIS in *ARA-VP-6/500*, as well as its projection anterior to the acetabular margin, indicate that this structure had already begun to appear and mature via a novel physis. Isolation of the AIIS as a separate growth center, which is unique to hominids (*21*), was probably a consequence of its increased separation from the original iliac portion of the acetabular chondroepiphysis. This is because much of iliac broadening must occur at the triradial epiphysis (as well as the posterior iliac crest). An analogous phenomenon occurs in mammals with elongate femoral necks, in which accelerated growth in the region separating the presumptive greater trochanter and femoral head isolates these structures before separate ossification of each epiphysis (*22*).

The emergence of a novel AIIS center of ossification, as seen in *ARA-VP-6/500*, attests to global modification of the entire pelvis. This is also demonstrated by the abbreviated craniocaudal length of the pubic symphyseal face (Figs. 1, 2, and 3A). The anteroventral pubic surface is surmounted by a rugose pectineal line that is continuous with the nonperiosteal attachments of abductor brevis and gracilis muscles. This is a derived character in human females [the ventral arc (*23*)]. It is only rarely present in great apes. There is no lateral displacement of this feature in *Ar. ramidus* as there is in human females (and partially in *A.L. 288-1*).

The systematic reduction of overall craniocaudal pelvic height would have lowered the trunk's center of mass and shortened its moment arm during single support. This would at least partially compensate for retention of the long lumbar column required for anterior lordotic shift of the center of mass during bipedality. Any deletion of thoracic vertebra would also lower the center of mass. Flexibility in its positioning probably maintained ample hind-limb mobility during arboreal climbing and clambering, albeit with considerable attendant risk of lower-back injury.

Given retention by *Ar. ramidus* of multiple primitive skeletal characters (*15*, *16*, *24*, *25*), its exceptionally derived ilium is striking. It implies an early adaptation to habitual terrestrial bipedality before any increase in the lumbar entrapment seen in the African apes, but after the lateral iliac expansion shared with them. This is consistent with the hypothesis that vertebral column invagination (its anterior transpositioning into the thorax and abdomen) was a primary morphogenetic mechanism underlying scapulohumeral reorganization for greater forelimb flexibility during arboreal clambering and bridging. If this is correct, then the extensive reorganization of the column in hominoids was not originally an adaptation to suspensory locomotion or vertical climbing (*15*, *16*, *24*–*27*).

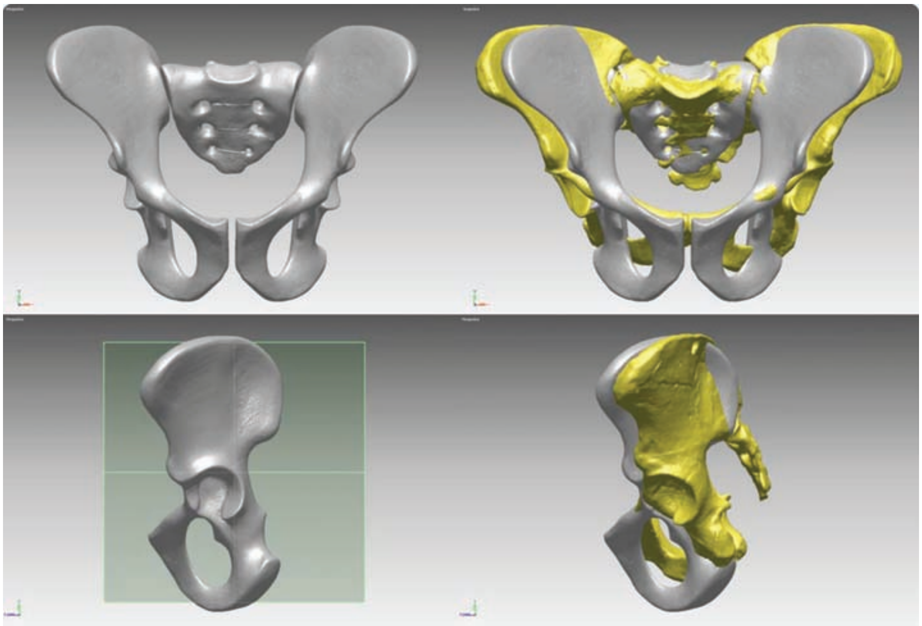

Fig. 2. CT comparison of *ARA-VP-6/500* (left) os coxa reconstruction (11th permutation) and *A.L. 288-1* (right) restoration. Reconstruction of *ARA-VP-6/500* was achieved by means of sculptural modeling on the basis of numerous dimensions and contours preserved on the original fossil (Fig. 1). The sacrum is largely conjectural because only its lower portion was recovered, but four segments are likely (*18*). The enlarged *A.L. 288-1* (115% of actual size) and *ARA-VP-6/500* images have been aligned on their acetabulae. The green scale square (lower left) is 180 mm on a side. The broad sacral alae of *ARA-VP-6/500* are probably because African ape sacra have almost certainly been narrowed since the GLCA (figs. S10 and S11). A novel ossification center for the AIIS and a substantial reduction in the height of the iliac isthmus are derived characters present in both hominids. Length of the ischia was reconstructed on the basis of the position of the ischial spine, shape of the obturator foramen, and (most importantly) the length of an intact surface transect from the lower edge of the acetabulum to the dorsal edge of the (missing) ischial tuber (Fig. 1). The acetabulum was preserved in two separated portions (Fig. 1). Together, they suggest a diameter of 36 to 42 mm. Spatial orientation was made on an assumption of vertical alignment of the pubic tubercle and ASIS, although the primitive form of this pelvis suggests that lumbar lordosis during terrestrial bipedality was partially situational and that the superior pelvis may have been angled less anteriorly during arboreal clambering. There is a dramatic reduction of lower pelvic length and robusticity in *A.L. 288-1*.

Comparisons of the ossa coxae of *Ar. ramidus* and *Au. afarensis* demonstrate the latter's modifications for habitual bipedality following abandonment of arboreal locomotion (Figs. 2 and 3C and figs. S1 to S3). In general, *Au. afarensis* demonstrates even greater global craniocaudal abbreviation of its entire pelvis, and an accompanying increase in platypelloidy via elongation of the pubic rami anteriorly, and deepening of the greater sciatic notch and probable expansion of alar breadth posteriorly (*7*). Such changes appear morphogenetically coordinated and therefore were also likely expressed partially in *Ar. ramidus*, although the actual dimensions of its sacrum remain unknown. This view receives independent support from the remarkable pelvic stasis seen between *A.L. 288-1* and the much more recent [0.9 to 1.4 million years ago (Ma); post-*Au. afarensis*] Busidima pelvis (*BSN49/P27*) (*28*).

The functional importance of platypelloidy in *Au. afarensis* has been widely debated. Viewed now from the perspective of its ancestral state, however, it appears likely to have been a consequence of establishing mobility of the L6/S1 joint as a permanent character. The ancestral morphology presumably involved situationally dependent lordosis (during terrestrial upright walking) for gluteal stabilization during the stance phase. Platypelloidy may also have enhanced gut volume, although a trunk length with six lumbars may have been sufficient. The reduction of lateral iliac flare and more posterior placement of the iliac cristal tubercle in *Homo* therefore probably reflect an ontogenetic predisposition for lumbar lordosis with (i) reduction in lower lumbar positional lability (permitting a reduction from six to five lumbars) after complete abandonment of arboreal activity and (ii) optimization of birth-canal geometry (*4*).

The femur. Two partial proximal femora were recovered at Aramis (Fig. 4). That of the partial skeleton (*ARA-VP-6/500-5*) preserves most of the shaft but is damaged by extensive expanding matrix distortion (*29*). A second (*ARA-VP-1/701*) is in good condition. Although neither preserves a head, neck, or greater trochanter, in conjunction with the os coxa they are informative with respect to the evolution of the gluteus maximus muscle (hereafter simply the maximus).

The African ape posterolateral femoral shaft regularly exhibits a distomedially displaced insertion for the maximus. This is separated from a more superior attachment of the vastus lateralis [to whose tendon, however, the maximus is normally fused (*30*)] by an elevated boss on the shaft [defined as the lateral spiral pilaster (*31*)]. The femora of *Au. afarensis* and subsequent hominids exhibit a strikingly different morphotype that includes a trochanter tertius that surmounts a rugose hypotrochanteric fossa (*31*, *32*). Both structures are clearly associated with hypertrophy of the maximus' ascending tendon, which inserts directly into the lateral aspect of the femur (*30*).

It had been thought that the lateral spiral pilaster of apes was primitive (*31*) and that the hominid morphotype was derived. The femur of *Ar. ramidus* shows that this inference was incorrect. African ape femora never exhibit a third trochanter or hypotrochanteric fossa, whereas *ARA-VP-1/701* exhibits obvious homologs to both. Moreover, the femur of *Proconsul*, millions of years older than *Ar. ramidus*, exhibits a strong gluteal tuberosity immediately inferior to its greater trochanter, as do those of *Nacholapithecus* (*13*) and *Dryopithecus* (*33*).

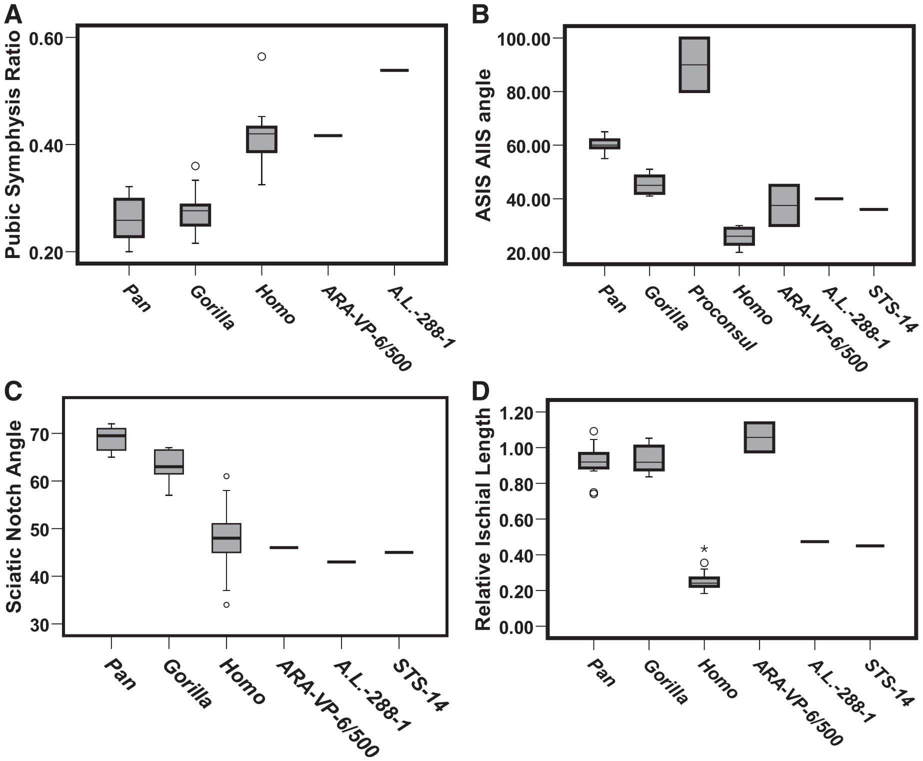

Fig. 3. Some geometric and anatomical traits of the ossa coxae of hominids and African apes. (**A**) Maximum breadth of the pubic symphyseal face normalized by its length. The shortened condition in *ARA-VP-6/500* may reflect an abbreviation of overall pelvic height. The extreme value for *A.L. 288-1* is largely due to the great breadth of its pubic symphyseal face; this might also be a type 2 (*8*) effect of this specimen's greatly elongate superior pubic ramus. Metrics are from originals. *Pan-Homo* differences are highly significant ($n = 15$ specimens each taxon; $P < 0.0001$; two-tailed t test). Boxes represent 25th and 75th percentiles, vertical lines represent 5th and 95th percentiles, and the transverse lines are medians. Values between 1.5 and 3 box lengths from the upper or lower boundaries of a box are shown as open circles (asterisks indicate more than three box lengths). (**B**) Angle made by two chords connecting three landmarks on the ilium: from the superomost point on the auricular surface to the ASIS and from the auricular surface to the AIIS. The angle between these chords was directly measured with a modified goniometer. Maximum value shown for *ARA-VP-6/500* represents the most superior location of the ASIS as described in the text and used in the model (Fig. 2); the lower value would obtain if the ASIS were less protuberant. There is a more elongate ilium (more obtuse angle) in *Pan* as compared with *Gorilla* ($P < 0.001$; two-tailed t test). The overlap of higher possible values in *ARA-VP-6/500* with those of *Gorilla*, and the intermediate values in *A.L. 288-1* and *STS-14*, at least partially reflect ASIS elongation and lateral iliac flare for increased lordosis. The exceptionally high values for *Proconsul* reflect both its extremely tall ilium and the precipitous anterior tilt of its auricular surface. *Pan-Homo* differences are highly significant ($n = 15$ specimens each taxon; $P < 0.0001$; two-tailed t test). (**C**) Angle made by two chords connecting three landmarks on the ilium: from the acetabular center to the caudalmost point on the auricular surface and from the acetabular center to the ischial spine (fig. S4). A third chord was measured (auricular surface to the ischial spine), and the angle was determined trigonometrically. All early hominids lie within the human range because all have a greatly shortened iliac isthmus. The isthmus in *Pan* is significantly longer than that of *Gorilla* ($P < 0.0001$; two-tailed t test). The angle for *ARA-VP-6/500* was estimated from reconstruction. *Pan-Homo* differences are highly significant ($n = 15$ specimens each taxon; $P < 0.0001$; two-tailed t test). (**D**) Minimum ischial length (from inferior acetabular border to juncture of the ischial body and tuberosity surface) normalized by acetabular diameter. Two values for *ARA-VP-6/500* bracket possible extremes for the acetabular diameter. *Pan-Homo* differences are highly significant ($n = 15$ specimens each taxon; $P < 0.0001$; two-tailed t test).

In *ARA-VP-1/701*, the medial border of an obvious hypotrochanteric fossa homolog converges with the spiral line to form a markedly rugose, elevated plane on the posterior femoral surface, but their further course is lost to fracture. A similar morphology is visible on the *ARA-VP-6/500* specimen. A broad linea of low relief is also clearly present in *ASI-VP-5/154*, assigned to *Au. anamensis* (*34*). Its morphology is reminiscent of that of *A.L. 288-1*, in which the linea is still notably broad, but contrasts with that of *MAK-VP-1/1*, which is more modern in form at 3.4 Ma (*31*). Because most of the length of the *ASI-VP-5/154* shaft is preserved, its moderately elevated linea (~11.5 mm in breadth) is distinct and imparts a prismatic cross section at midshaft. Specimen *BAR-1002'00* (*Orrorin tugenensis*) (*35*) presents obvious homologs to these structures. Moreover, both *BAR-1002'00* and *ASI-VP-5/154* exhibit an obvious homolog to the third trochanter, and neither shows any evidence of a lateral spiral pilaster.

African ape morphology can therefore now be interpreted as derived and probably a consequence of global alterations of their hip and lower back for suspensory locomotion. Further narrowing of their iliac cleft from its state in *Proconsul* must have also relocated their maximus insertion more distomedially as well and caused increased separation from its previous position adjacent to that of the vastus lateralis, a hiatus now filled in African ape femora by the lateral spiral pilaster. This has eliminated any evidence of the otherwise ubiquitous Miocene morphotype. The disappearance of any homolog of the hypotrochanteric fossa and third trochanter in extant apes suggests a possible change in muscle and/or enthesis architecture, although fascicle length does not appear to differ substantially in the gluteals of humans and apes (*36*).

In contrast, the gluteal complex in *Ar. ramidus* remains anterolaterally displaced as in *Proconsul* and *Orrorin* and still unlike its more posteromedial position in most *Australopithecus* (Fig. 4) (*31*). Such medial translation of the maximus insertion is probably a consequence of hypertrophy of the quadriceps at the expense of the hamstrings (*31*). Indeed, the combination of a broad, ape-like, expansive ischial tuberosity and broad proto-linea aspera in *Ar. ramidus* suggests that the hamstring/quadriceps exchange had not yet achieved its modern proportions, although some expansion of the maximus was probably present given the substantial restructuring of the ilium and trans-iliac space. In contrast, most *Australopithecus* specimens [such as *MAK-VP-1/1*, *A.L. 333w-40*, and *A.L. 333-110*) (*31*)] had marked elevation and narrowing of a true linea aspera that is typical of later hominids (*37*, *38*).

The thorax. The thorax of *ARA-VP-6/500* is represented by a partial first rib, several associated crushed ribs, and a thoracic vertebral arch. A thoracic arch from a second individual was also recovered (*ARA-VP-6/1001*). Both vertebrae lack centra, so the angulations of their rib facets and their implications for vertebral column invagination (*39*) cannot be determined. It has recently become common wisdom that early hominids had a funnel-shaped thorax. However, this supposition stems from a reconstruction of *A.L. 288-1* (*40*) that relied on (i) an ilium left uncorrected for extensive postmortem fracture of its retroauricular portion (a defect that exaggerates lower thoracic breadth) (*41*), (ii) a highly fragmentary thorax, and (iii) the presumption of a short-backed, great ape–like, ancestral morphology. Because dramatic forelimb elongation, hindlimb abbreviation, and lower thoracic rigidity are seen together in all three great apes, relative constriction of their upper thorax is probably a modification accompanying these advanced adaptations to suspension and/or vertical climbing. *Ardipithecus* reveals, however, that earliest hominids did not regularly engage in these behaviors (*15*, *16*) and that an elongated iliac isthmus and narrowed trans-iliac space are African ape specializations that negate the lordosis required for effective transitional upright walking.

Nearly 30 years have now passed since the observation that the human serratus anterior "lacks the specializations associated with suspensory behavior in large bodied, broad-chested nonhuman primates [suggesting] descent from a small ape with a thoracic shape similar to atelines." (*42*). This seems particularly prescient given a recent examination of thoracic form in primates (*43*), which demonstrates that *Ateles* (also highly skilled at suspension) nevertheless lacks many other great ape-like adaptations, including a funnel-shaped thorax. It follows that this unique thoracic form is likely to emerge only as an element accompanying these other extensive great ape specializations for suspension and vertical climbing. It is therefore unlikely to have ever been present in early hominids. Confirmation of this inference, however, will require additional fossil evidence.

The pelvis, femur, and preserved thoracic elements of *Ar. ramidus* establish that adaptations to upright walking in these regions were well established by 4.4 Ma, despite retention of a capacity for substantial arboreal locomotion. *Ar. ramidus* thus now provides evidence on the long-sought locomotor transition from arboreal life to habitual terrestrial bipedality. This evidence suggests that the transition took place in the absence of any of the characters that today substantially restrict upright walking in extant apes (particularly lumbar column abbreviation, trans-iliac space narrowing, and approximation of iliac crest and thorax, and the muscles that traverse this gap). As a consequence, explications of the emergence of bipedality based on observations made of African ape locomotion no longer constitute a useful paradigm.

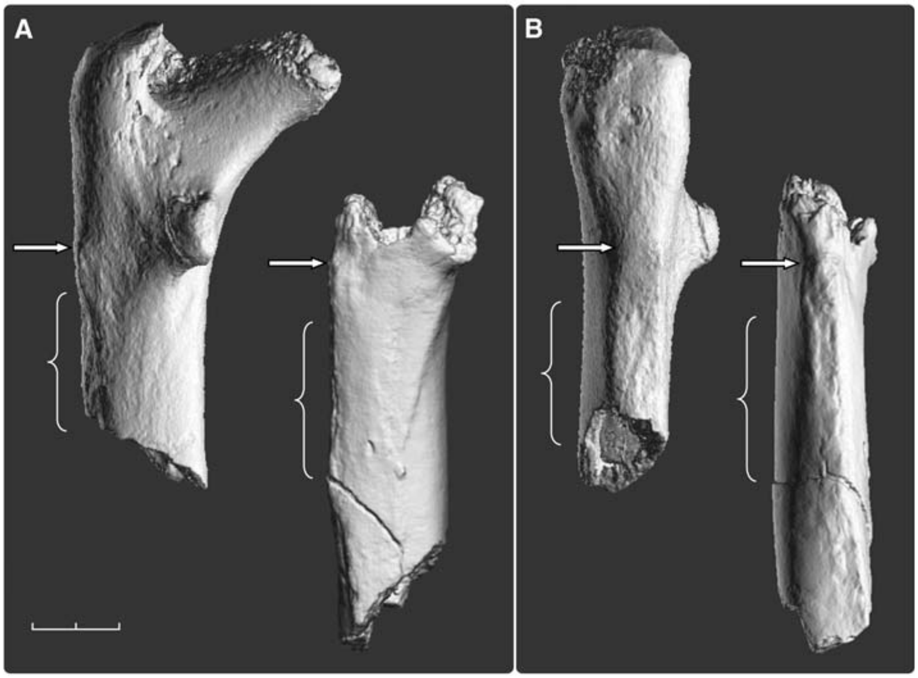

Fig. 4. Lateral and posterior CT scan surface renders of (**A**) *MAK-VP-1/1* (*Au. afarensis*, cast) and (**B**) *ARA-VP-1/701* (*Ar. ramidus*, original). Specimens have been aligned by their lesser trochanters. The preserved portion of the *ARA-VP-1/701* shaft is sufficient to demonstrate the absence of a lateral spiral pilaster and the presence of a distinct rugose insertion area for the gluteus maximus that is homologous to the true hypotrochanteric fossa present in *MAK-VP-1/1* (arrows indicate the third trochanter; brackets indicate hypotrochanteric fossae). In *ARA-VP-1/701*, this area is more laterally placed, as in other early hominid femora, including *BAR-1002'00*. The more posterior position of this insertion in *MAK-VP-1/1* is almost certainly associated with decreased sagittal iliac orientation in *Au. afarensis*, a consequence of further posterior pelvic broadening and increased lateral iliac flare (fig. S1). None of these early hominid specimens shows evidence of a lateral spiral pilaster, which is restricted to African ape femora.

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5. In order to facilitate our examination, we also reconstructed the innominate of *KNM-RU 13142 D* (fig. S4). Our reconstruction does not differ substantially from that drawn by its original descriptor (*17*) but facilitated some three-dimensional comparisons.
6. "The marked difference between the pelvis of *Hylobates* and that of *Symphalangus syndactylus* is ...apparent... [demonstrating] that the siamang has already a pelvis of typical anthropoid ape character, particularly in regard to the broad ilium with its prominent ASIS, whereas the pelves of the gibbons have not yet departed so far from the more primitive condition of catarrhine monkeys" [(*44*) p. 350].
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27. This is also consistent with substantial differences in the soft tissue configuration of the pelvic floor of extant humans and African apes. In African apes, the sphincter ani externus is hypertrophied. It serves as the primary urogenital floor, thus greatly exceeding its distribution in Old World monkeys. In humans, this muscle is instead reduced, and its function alternatively subsumed by hypertrophy of the transversus perinei profundus. "The simplest interpretation of this difference […is] that in the…[GLCA] the sphincter ani and the bulbocavernosus resembled those muscles in the…[Old World monkeys]" (*45*). Elftman was, of course, unaware of *Proconsul* pelvic structure at the time of his observation, but his conclusion was essentially that the GLCA's pelvic floor had remained primitive, such as it presumably was in Early Miocene apes practicing above-branch quadrupedality and remaining underived for suspensory locomotion.
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38. It has been suggested (via canonical variates analysis) that the *Orrorin* proximal femur "exhibits an *Australopithecus*-like bipedal morphology [that] evolved early in the hominin clade and persisted successfully for most of human evolutionary history" [(*46*) p. 1664]. However, *BAR-1002'00* lacks a complete greater trochanter, making such a conclusion dependent on reconstruction. Our examination of both casts and originals leads us to agree that the specimen belongs to a bipedal hominid, but the femoral and pelvic evidence presented here demonstrate that (i) bipedality was not morphologically static from 6 to 2 Ma as claimed nor (ii) is there now any evidence for an "appreciable scansorial component" in the locomotor repertoire of *Australopithecus*. To the contrary, substantial arboreal behavior is now contraindicated by much of the postcranial anatomy that differentiates *Ardipithecus* and *Australopithecus*.
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41. The retroauricular portion of the innominate of *A.L. 288-1* was crushed postmortem, introducing a 90° angulation defect at its juncture with the iliac fossa. Failure to correct this defect results in extreme lateral extension of the ilium, making it *Pan*-like in three-dimensional disposition. Moreover, if uncorrected, the pubic symphyseal face fails to reach midline by several centimeters, once the broken but otherwise undistorted ischiopubic rami are restored. Compare figure 4 in (*40*) and figure 6 in (*47*) with figure 8 in (*37*).
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48. For funding, we thank NSF [this material is based on work supported by grants 8210897, 9318698, 9512534, 9632389, 9729060, 9910344, and 0321893 HOMINID–Revealing Hominid Origins Initiative (RHOI)] and the Japan Society for the Promotion of Science. We thank the Ministry of Tourism and Culture, the Authority for Research and Conservation of the Cultural Heritage, and the National Museum of Ethiopia for permissions and facilitation. We thank the Afar Regional Government, the Afar people of the Middle Awash, and many other field and laboratory workers for contributing directly to the data. We thank the following institutions and staff for access to comparative materials: National Museum of Ethiopia; National Museum of Natural History; Royal Museum of Central Africa Tervuren, and the Cleveland Museum of Natural History. We thank B. Senut and R. Eckhardt for access to the original specimen and casts of *BAR-1002'00* and S. Moya-Sola and M. Kohler for access to multiple specimens in their care. We thank M. Brunet for comparative data and C.V. Ward for access to her large pelvic database which was used extensively in this analysis. We thank D. Kubo and H. Fukase for assistance in computed tomography (CT) scanning; R. Meindl for statistical advice and assistance; and M. A. McCollum, P. L. Reno, M. A. Serrat, M. Selby, D. DeGusta, A. Ruth, L. Jellema, S. W. Simpson, and B.A. Rosenman for aid in data collection and exceptionally helpful discussions. We thank H. Gilbert and J. Carlson for help with figures. We thank A. Sanford and A. Ademassu for the many generations of casts required to complete this study, R. T. Kono for the rapid prototyping models, and L. Gudz and E. Bailey for assistance with illustrations.

Supporting Online Material

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Figs. S1 to S11

Table S1

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4 May 2009; accepted 17 August 2009

10.1126/science.1175831