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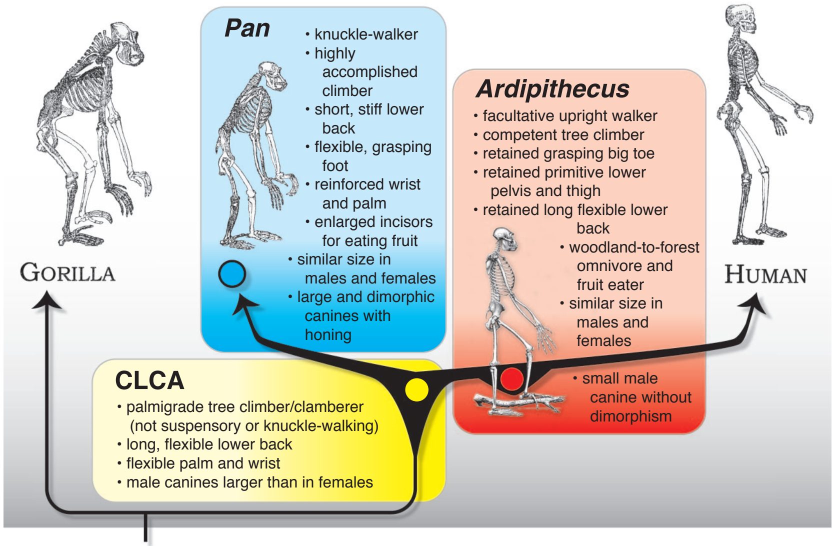
The Great Divides: *Ardipithecus ramidus* Reveals the Postcrania of Our Last Common Ancestors with African Apes

C. Owen Lovejoy, Gen Suwa, Scott W. Simpson, Jay H. Matternes, Tim D. White



Cladogram adding *Ar. ramidus* to images of gorilla, chimpanzee, and human, taken from the frontispiece of *Evidence as to Man's Place in Nature*, by Thomas H. Huxley (London, 1863) (with the positions of *Gorilla* and *Pan* reversed to reflect current genetic data). Numerous details of the *Ar. ramidus* skeleton confirm that extant African apes do not much resemble our last common ancestor(s) with them.

Evolutionary biologists have long recognized that the living primates most similar to humans are the great apes, and comparative genomic sequence analyses confirm that we are most closely related to chimpanzees and bonobos (genus *Pan*). Because of our great genomic similarity (sometimes even cited as ~99%), the presumption that we evolved from a chimpanzee-like ancestor has become increasingly common wisdom. The widely held view that the genomic and phyletic split between *Pan* and humans was as recent as 5 to 6 million years ago also fuels the often uncritical acceptance of a *Pan*-like last common ancestor. *Ardipithecus ramidus* at 4.4 million years ago provides the first substantial body of fossil evidence that temporally and anatomically extends our knowledge of what the last common ancestor we shared with chimpanzees was like, and therefore allows a test of such presumptions.

Until now, *Australopithecus afarensis*, which lived 3 to 4 million years ago, represented the most primitive well-known stage of human evolution. It had a brain only slightly larger than that of chimpanzees, and a snout that projected more than in later hominids. Assuming some variant of a chimpanzee-like ape ancestry, the bipedality of *Au. afarensis* has been widely interpreted as being so primitive that it probably could not have extended either its hip or knee joints and was a clumsy upright walker. Some researchers have even postulated that *Au. afarensis* could walk but not run, or vice versa. Still others have suggested that *Au. afarensis* had a grasping ape-like foot. Similarly, it has been suggested that *Au. afarensis* had forelimbs that were ape-like, including long, curved fingers used to forage daily in the arboreal canopy, and that its immediate ancestors must have knuckle-walked. *Australopithecus* males were noticeably larger than females, and this has often been interpreted as signifying a single-male, polygynous, *Gorilla*-like mating system. Unlike gorillas, it has diminutive canines, but these were argued to be a consequence of its huge postcanine teeth. Early hominids have even been posited to have possibly interbred with chimpanzees until just before the appearance of *Australopithecus* in the fossil record.

The *Ar. ramidus* fossils and information on its habitat now reveal that many of these earlier hypotheses about our last common ancestor with chimpanzees are incorrect. The picture emerging from *Ar. ramidus* is that this last common ancestor had limb proportions more like those of monkeys than apes. Its feet functioned only partly like those of apes and much more like those of living monkeys and early apes such as *Proconsul* (which lived more than 15 million years ago). Its lower back was mobile and probably had six lumbar vertebrae rather than the three to four seen in the stiff backs of African apes. Its hand was unpredictably unique: Not only was its thumb musculature robust, unlike that of an ape, but its midcarpal joint (in the wrist) allowed the wrist to bend backward to a great degree, enhancing its ability to move along tree branches on its palms. None of the changes that apes have evolved to stiffen their hands for suspension and vertical climbing were present, so its locomotion did not resemble that of any living ape.

The hominid descendant of the last common ancestor we shared with chimpanzees (the CLCA), *Ardipithecus*, became a biped by modifying its upper pelvis without abandoning its grasping big toe. It was therefore an unpredicted and odd mosaic. It appears, unlike *Au. afarensis*, to have occupied the basal adaptive plateau of hominid natural history. It is so rife with anatomical surprises that no one could have imagined it without direct fossil evidence.

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C. Owen Lovejoy,[1]* Gen Suwa,[2]* Scott W. Simpson,[3] Jay H. Matternes,[4] Tim D. White[5]

Genomic comparisons have established the chimpanzee and bonobo as our closest living relatives. However, the intricacies of gene regulation and expression caution against the use of these extant apes in deducing the anatomical structure of the last common ancestor that we shared with them. Evidence for this structure must therefore be sought from the fossil record. Until now, that record has provided few relevant data because available fossils were too recent or too incomplete. Evidence from *Ardipithecus ramidus* now suggests that the last common ancestor lacked the hand, foot, pelvic, vertebral, and limb structures and proportions specialized for suspension, vertical climbing, and knuckle-walking among extant African apes. If this hypothesis is correct, each extant African ape genus must have independently acquired these specializations from more generalized ancestors who still practiced careful arboreal climbing and bridging. African apes and hominids acquired advanced orthogrady in parallel. Hominoid spinal invagination is an embryogenetic mechanism that reoriented the shoulder girdle more laterally. It was unaccompanied by substantial lumbar spine abbreviation, an adaptation restricted to vertical climbing and/or suspension. The specialized locomotor anatomies and behaviors of chimpanzees and gorillas therefore constitute poor models for the origin and evolution of human bipedality.

Thomas Huxley published *Evidence as to Man's Place in Nature* (*1*) only 4 years after Darwin's *On the Origin of Species*. Its frontispiece featured a human skeleton and four suspensory adapted apes, each posed upright and each obviously more human-like than any pronograde Old World monkey. By century's end, Keith was enumerating a cornucopia of characters in support of a brachiationist human past (*2*). Even our pericardial-diaphragmatic fusion, hepatic bare area, and colic mesenteries were interpreted as adaptations to orthogrady, evolved to tame a flailing gut in the arboreal canopy. Bipedality was simply habitual suspension brought to Earth (*3*). The "suspensory paradigm" for early hominid evolution was born.

Challenges, however, were mounted. Straus enumerated disconcertingly primitive human features in "The Riddle of Man's Ancestry" (*4*), and Schultz doubted that brachiation "… opened the way automatically for the erect posture of modern man" [(*5*), pp. 356–357]. Although withdrawal of the ulna from its primitive pisotriqetral recess was thought to be the sine qua non of suspension (*6*), a functional equivalent was discovered to have evolved in parallel in the wrists of never-suspensory lorisines (*7*). African ape knuckle-walking (*8*), considered by many too bizarre to have evolved independently in *Gorilla* and *Pan*, came to be viewed in light of emergent molecular phylogenetics (*9*) as a natural successor of suspensory locomotion—and by some as the almost-certain default engine of bipedality (*10*).

A flood of morphometric analyses appeared to confirm arguments for knuckle-walking hominid ancestors [reviewed in (*11*)], even though hints of the behavior were also seen in captive orangutans (*12*). Knuckle-walking was surmised to be a natural consequence of irreversible modifications of the forelimb skeleton to facilitate advanced suspension and vertical climbing (*11*). It was thereby hypothesized to be an adaptive signal of the first two phases of a deterministic succession leading to bipedality: advanced suspension/vertical climbing → terrestriality/knuckle-walking → bipedality.

A compendium of observations of chimpanzees and bonobos performing upright stance and locomotion followed. Accumulating molecular biology propelled this troglodytian paradigm (conceived as a natural succession to its older, suspensory counterpart) to near-consensus. Chimpanzee-human protein homologies and DNA base sequence comparisons (*9*, *13*–*16*) established *Homo* and *Pan* as likely sister clades [today further confirmed by comparative genomics (*17*, *18*)]. The only question remaining seemed to be whether the bonobo or chimpanzee represented the best living proxy for the last common ancestor (*19*–*22*).

The Chimpanzee model and *Australopithecus*. The discovery and recognition of the then-primitive *Australopithecus afarensis* during the 1970s (*23*) pushed the hominid record back to 3.7 million years ago (Ma). Although its postcranium was recognized to harbor unusually sophisticated adaptations to bipedality [reviewed in (*24*)], a feature confirmed by human-like footprints at Laetoli (*25*, *26*), many interpreted these fossils to represent the closing argument for the troglodytian paradigm [see, e.g., (*27*)]. Only the recovery of earlier, chimpanzee-like fossils from the Late Miocene seemed necessary to complete this scenario [even though newer *Australopithecus* fossils have led at least one discoverer to doubt a chimpanzee-like ancestry (*28*)]. Until now, the few available fossils of appropriate antiquity have remained largely uninformative (*29*–*31*).

The *Ardipithecus ramidus* fossils from 4.4 Ma Ethiopia are obviously not old enough to represent the chimpanzee/human last common ancestor (CLCA; the older common ancestor of hominids and both *Gorilla* and *Pan* is hereafter the GLCA). However, their morphology differs substantially from that of *Australopithecus*. The *Ar. ramidus* fossils therefore provide novel insights into the anatomical structure of our elusive common ancestors with the African apes. For that reason, and because of its phylogenetic position as the sister taxon of later hominids (*32*), this species now provides opportunities to examine both the suspensory and troglodytian paradigms with greater clarity than has previously been possible. Here we first provide evidence of limb proportions, long considered to bear directly on such issues, and then review key aspects of the entire *Ar. ramidus* postcranium. Comparing the basic proportions and postcranial anatomy of *Ar. ramidus* (Fig. 1) with those of apes enables us to propose the most probable anatomies of the last common ancestors of *Gorilla*, *Pan*, and the earliest hominids. Much of the relevant information on *Ar. ramidus* is based on the partial skeleton from Aramis (*32*).

Body mass. The geometric means of several metrics of the capitate and talus are strongly related to body mass in extant primates (correlation coefficient $r = 0.97$; fig. S1), and can be used to estimate body mass in *ARA-VP-6/500*, as well as in *A.L. 288-1*. Restricting the sample to large-bodied female hominoids predicts that *ARA-VP-6/500* had a mass of about 51 kg. The metrics for *A.L. 288-1* fall below those of all extant hominoids. We therefore used the female anthropoid regression to estimate the body mass of *A.L. 288-1* (26 kg), which is consistent with previous estimates (*33*) (table S1). Based on several shared metrics, *ARA-VP-7/2*, a partial forelimb skeleton (*32*), was slightly smaller than *ARA-VP-6/500* [supporting online material (SOM) Text S1].

Given the apparent minimum body size dimorphism of *Ar. ramidus* (*32*, *34*), the predicted

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body mass of *ARA-VP-6/500* serves as a reasonable estimate for the general body mass of *Ar. ramidus*. Although *ARA-VP-6/500* was one of the larger individuals of the Aramis sample (*32*), it was probably more representative of its species than was *A.L. 288-1* [the latter clearly lies at the lower end of the *Au. afarensis* species range based on larger samples (*35*)]. Unfortunately, *ARA-VP-6/500* tells us little about the body mass of the CLCA and GLCA because these predate *Ar. ramidus* by wide margins and may have still been primarily arboreal. The limited available (mostly dental and cranio-mandibular) samples indicate that the size of Late Miocene hominids (*29*–*31*) was similar to that of *Ar. ramidus* (*34*), and estimated body weight for the 6 Ma *Orrorin* femoral remains is 30 to 50 kg (*36*). Although body mass in early Miocene forms appears to have varied greatly (*37*, *38*), it is likely that the CLCA and GLCA were either equal to or smaller than *Ar. ramidus*, and possibly even substantially so. Only additional fossils can resolve this issue.

Limb segment proportions. Radial, ulnar, and tibial lengths can be accurately determined for *ARA-VP-6/500* (SOM Text S1). The specimen's radius/tibia ratio (0.95; fig. S2) is similar to those of generalized above-branch quadrupeds such as the Old World monkey *Macaca* (0.90 to 0.94; table S2) and the Miocene ape *Proconsul heseloni* (0.88 in *KNM-RU 2036*) (*38*). The ratio is unlike that of African apes (*P. troglodytes,* 1.11 ± 0.04; *Gorilla*, 1.13 ± 0.02) (*39*) and is, remarkably, 17 standard deviations below that of *Pongo* (1.47 ± 0.03).

The *Ardipithecus* skeleton's nearly intact tibia allows estimation of femoral length because the crural index (CI: tibia length/femur length × 100) is highly conserved in African apes and humans (*5*, *40*) (81 to 84; SOM Text S1). Tibial length in *A.L. 288-1* can likewise be estimated from its effectively complete femur. Although no humerus was recovered for *ARA-VP-6/500*, one belonging to *ARA-VP-7/2* is almost complete and can be used to estimate humerus length in *ARA-VP-6/500* by simple proportion of shared elements (SOM Text S1). The *A.L. 288-1* humerus is intact, and its radius length was previously estimated by regression (*41*). These data allow calculation of the more familiar intermembral index (IMI; forelimb length/hindlimb length × 100). The IMIs of both specimens resemble those of *Proconsul* and Old World monkeys (table S3).

ARA-VP-6/500 also allows interpolation of other key limb proportions. The brachial indices (BI: radius length/humerus length × 100) of *Proconsul*, *Equatorius*, *A.L. 288-1*, and *ARA-VP-6/500* are each within the observed range of *Pan* (fig. S3). It is therefore likely that the BI has remained largely unmodified since the GLCA, especially in light of the relationship of radius length to estimated body mass (fig. S4). In contrast, the BIs of *Homo* and *Gorilla* are both derived, albeit by obviously different routes (fig. S3). Humans have greatly shortened radii in conjunction with their novel antebrachial/manual proportions for grasping and manipulation [(*41*, *42*) and see below]; *Gorilla* appears to have experienced both humeral elongation and possibly slight radial shortening (figs. S4 and S5), most likely to reduce joint stresses at the elbow imposed by the immense mass of adult males. The BIs of *Pan* and *Ar. ramidus* are similar (fig. S3), but *Pan* exhibits a much higher IMI (table S3). Therefore, both *Pan* and *Gorilla* have undergone forelimb elongation and hindlimb reduction since the GLCA (table S2 and figs. S4 to S6). The IMIs of hominids appear to have remained primitive until 2.5 Ma (*41*, *43*). The relatively high BI of *Pongo* reflects its entirely different evolutionary history.

Manual anatomy and proportions. Compared to estimated body size, the manual phalanges of *Ar. ramidus* and *Gorilla* are long relative to those of the Miocene ape *Proconsul* (fig. S7). They are relatively even more elongate in *Pan*, but dramatically abbreviated in *Homo*. These conclusions are supported by similar calculations using the means of observed body mass (table S3). There is no evidence that the manual phalanges of *Au. afarensis* were elongated relative to those of *Ar. ramidus*.

In contrast to their manual phalanges, the posterior (medial) metacarpals 2 to 5 (Mc2-5) of *Proconsul* and *ARA-VP-6/500* are substantially

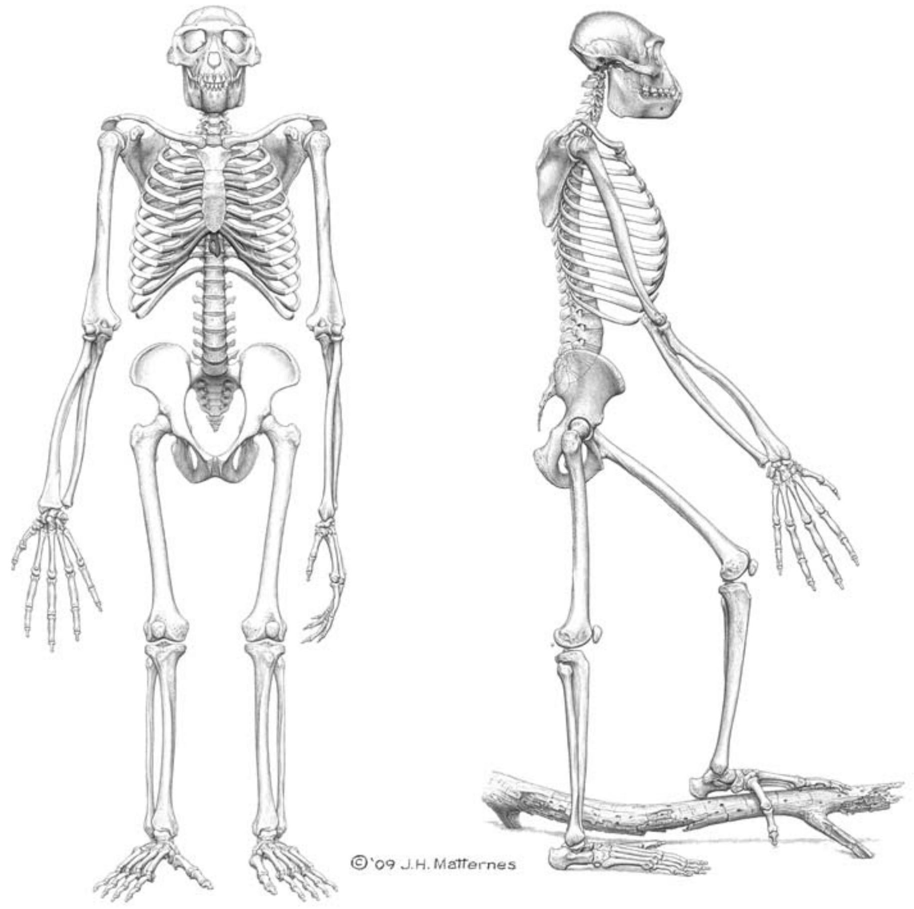

Fig. 1. Reconstructed frontal and lateral views of the skeleton of *ARA-VP-6/500*. Major long-bone lengths were determined directly from preserved skeletal elements (radius, tibia), by crural index (femur), by regression from adjacent elements (ulna), or by ratio and regression (humerus) from a marginally smaller forelimb skeleton (*ARA-VP-7/2*) via ratios of commonly preserved elements (SOM Text S1). All manual and pedal elements were drawn directly from casts. Pelvis was traced from frontal and lateral computer tomography (CT) scans of reconstructed pelvis (*59*). Vertebral column and thorax were based on six lumbars, 12 thoracics, and four sacrals (*58*). No attempt has been made to indicate failure of lateral fusion between the transverse processes of S4 and S5 [i.e., failure of complete closure of either of the fourth sacral foramina (the state preserved in both *A.L. 288-1* and *KNM-WT 15000*)]. Such four-segment sacra may have been modal in *Ar. ramidus*, but the five-segment form shown here was also a likely variant of high frequency [for discussion, see (*59*)]. Pectoral girdle and thorax were based on preserved portions of clavicle, first rib, and common elements known in *Au. afarensis*. Skull and mandible were based on models generated by restoration of cranium using both CT/rapid prototyping and "cast-element-assembly" methods (*79*). Reconstruction by J. H. Matternes was based on full-scale (life-size) architectural drawings circulated among authors for multiple inspections and comments. Stature (bipedal) is estimated at 117 to 124 cm and body weight at 51 kg. [Illustrations: Copyright 2009, J. H. Matternes]

shorter than are those of any extant ape (figs. S8 and S9). Viewed in the context of relative limb length patterns (see above), as well as the anatomical details of the hand (*44*), the short Mcs of *Ar. ramidus* strongly suggest that *Pan* and *Gorilla* independently acquired elongate Mcs as a part of an adaptation to vertical climbing and suspensory locomotion. Elongation of Mc2-5 in African apes demanded heightened resistance to torsion and consequent fixation of the carpometacarpal joints within the central joint complex (CJC) (*44*).

The retention of the primitively short Mcs in *Ar. ramidus* suggests that the GLCA/CLCA also did not have elongate Mcs, and engaged in a form of above-branch quadrupedal locomotion involving deliberate bridging and careful climbing. We hypothesize that this was retained from Middle Miocene precursors of the GLCA. A retained short metacarpus would optimize palmar conformity to substrates, an adaptation later abandoned by extant African apes.

The thumb metacarpal of *ARA-VP-6/500* was more aptly proportioned for manual grasping than are those of extant apes (figs. S10 and S11) (*44*). In extant apes, elongation of the posterior (medial) metacarpus may have been achieved by increased expression of *Hoxd11* or one of its targets, which do not affect the first ray (SOM Text S2) (*42*, *45*). However, the Mc1 of apes does seem moderately less robust than that of *Ar. ramidus*, and its soft tissues have undergone substantial involution (*4*, *42*). This suggests that some degree of down-regulation of *Hoxd13* may have been responsible for elongation of the posterior (medial) metacarpus.

Ar. ramidus greatly illuminates the natural history of the thumb in higher primates. Its robusticity in hominids, while certainly enhanced during the past 3 million years, is nevertheless at least partially primitive. In contrast, in taxa adapted to vertical climbing and suspension, lengthening of the palm has become so dominant as to eclipse some of the thumb's function, a condition that has reached its apogee in *Ateles* and, to a lesser extent, large-bodied extant apes. These findings strongly suggest that the target of recently discovered major cis-regulatory modification of gene expression in the first ray (*46*) was not manual but pedal—it is the human hallux, not our largely primitive pollex, that is highly derived (*47*).

Additional relevant hand anatomy leads to the same conclusions. *Ar. ramidus* is the only hominid fossil thus far recovered with a metacarpal head reminiscent of the metacarpophalangeal (MP) joint structure seen in many Miocene hominoids [such as *Equatorius*, *Proconsul*, *Dryopithecus*, and *Pierolapithecus* (*48*)]. The collateral ligament facets in these taxa colocate with deep symmetric invaginations of the metacarpal head's dorsum. This morphology is typical of Old World monkeys and is thereby associable with substantial dorsiflexion of the MP joint, an obvious manifestation of their palmigrady. The trait is only moderately expressed in *Oreopithecus*. Modern human and orangutan MP joints are substantially less constricted, and neither taxon exhibits appreciable locomotor-related MP dorsiflexion.

Constricted metacarpal head morphology appears to be primitive because it is still partially present in *Ar. ramidus*, albeit substantially reduced compared to early Miocene hominoids and Old World monkeys. Its retention suggests moderately frequent MP dorsiflexion, a finding consistent with the remarkable adaptations to palmigrady seen in the *Ar. ramidus* wrist [see below and (*44*)].

The metacarpal heads of knuckle-walking apes are also somewhat constricted by their collateral facets, but are heavily flattened and broadened to withstand excessive compression during dorsiflexion. Constriction by their collateral ligament facets is therefore only minimal. Moreover, the origins of their collateral ligaments have been substantially expanded volarly, presumably because such positioning improves their capacity to restrict abduction or adduction during MP dorsiflexion imposed by knuckle-walking. Joint flattening enhances cartilage contact and is likely at least partially a cartilage-modeling trait [cartilage modeling; Type 4 (*49*)].

Loss of MP dorsiflexion in *Pongo* is readily explicable by its extreme metacarpal and phalangeal elongation and curvature. These can safely be presumed to have eliminated any appreciable functional MP dorsiflexion. Modern humans lack any dorsiflexion because our hand plays no important role in locomotion. The trait is also absent in *Au. afarensis*, suggesting that either its hand no longer played any role in locomotion, or that such use no longer included an MP dorsiflexive component of palmigrady. The former seems far more likely, given the paramount adaptations to bipedality in the species' lower limb (*24*, *50*, *51*).

The primitive metacarpal head morphology within the overall primitive hand anatomy (*44*) of *Ar. ramidus* carries obvious implications for reconstruction of GLCA/CLCA locomotion. The unique combination of marked midcarpal mobility, ulnar withdrawal, and moderate MP dorsiflexion in *Ar. ramidus*, probably mostly primitive retentions, implies that the GLCA/CLCA locomotor pattern was also characterized by some form of arboreal palmigrade quadrupedality, unlike that in any extant descendant great ape.

Finally, it is clear now that phalangeal length of *Ar. ramidus* is not related to suspensory locomotion, but instead reflects a more general grasping adaptation. This renders phalangeal length moot regarding the hypothesis that manual (or even pedal) phalangeal lengths are an active signal of suspensory locomotion in *Au. afarensis* [contra (*52*, *53*)]. It is more probable that selection had not reduced their length in the younger species, and that such reduction did not occur until selection for tool-making became more intense later in the Pliocene (*43*, *54*).

Pedal proportions. Pedal phalangeal evolution appears to have closely paralleled its manual counterpart in each clade (compare figs. S7 and S12). However, pedal phalanges of African apes and hominids appear to have been substantially abbreviated, rather than elongated. Functional demands of terrestrial locomotion, perhaps similar to those acting on papionins (which also exhibit pedal phalangeal shortening), are a probable explanation. *Pongo* represents a marked contrast, with substantial pedal phalangeal elongation. It is thus reasonable to infer that the GLCA/CLCA's pedal phalanges were longer than those of the partially terrestrial extant African apes and *Ar. ramidus*.

The metatarsus of *Ar. ramidus*, chimpanzees, and gorillas presents a striking contrast to their metacarpus. Like the foot phalanges, the metatarsals also appear to have been universally shortened in all hominoids subsequent to *Proconsul* (figs. S13 and S14) (*47*). The basis of this universal shortening, however, is somewhat unclear, because tarsal evolution contrasts dramatically in hominids and African apes. The modern ape foot has obviously experienced functional reorganization into a more hand-like grasping organ. The *Ar. ramidus* foot did not. This suggests that substantial elements of a more lever-based, propulsive structure seen in taxa such as *Proconsul* and Old World Monkeys [robust plantar aponeurosis; retained quadratus plantae; robust peroneal complex (*47*)] were preserved in the GLCA/CLCA. These structures were sacrificed in both African ape clades to enhance pedal grasping for vertical climbing (*55*, *56*). The moderate shortening of the metatarsus in *Ar. ramidus* and both African apes may therefore simply reflect negative allometry of metatarsal (Mt) lengths with an increase in body size. The human foot has been lengthened primarily by tarsal elongation (*5*, *47*), presumably because of the likely high failure rate of metatarsal shafts during forceful fulcrumation.

In summary, a comparison of the pedal proportions of *Ar. ramidus* and the extant African apes suggests that the GLCA/CLCA hindlimb remained dominant for body mass support during bridging and arboreal clambering, to the extent that it later proved permissive to bipedality in transitionally terrestrial hominids.

Trunk structure. Knowledge of the role of selector genes in early vertebral column formation [especially the role of the *Hox* code on column differentiation (*57*, *58*)] has advanced our ability to interpret the vertebral formulae of extant hominoids. It now appears that the modal number of lumbar vertebrae in *Australopithecus* was six, and that a four-segment sacrum was also probably common (*57*, *58*). This axial formula is unlike that of any extant ape. Comparison of the axial columns of extant species further indicates that postoccipital somite number in the GLCA/CLCA was probably either 33 or 34, and that lumbar column reduction occurred independently in chimpanzees, bonobos, gorillas, and hominids. This probably resulted from either transformation of vertebral identities, or a combination of such transformation and reduction in the number of somites contributing to the lumbosacral region (fig. S15). The most likely vertebral patterns for *Ar. ramidus* are therefore those also inferred for the GLCA/CLCA and *Australopithecus*.

Pelvic structure indicates that *Ar. ramidus* retained a primitive spine. Its iliac and acetabular regions establish not only that it was habitually bipedal when terrestrial, but also that this was achieved by combining situational anterior pelvic tilt to accentuate substantial lordosis during upright walking (*59*). Such rotation placed the still partially primitive anterior gluteal musculature into a position of functional abduction for single support stabilization. In contrast to *Ar. ramidus*, *Au. afarensis* is known to have exhibited highly evolved mechanisms of hip abduction, confirmed by the distinctly stereotypic trabecular profile of its femoral neck (*24*).

The *Ar. ramidus* pelvis retained other elements in common with extant African apes (and presumably the GLCA/CLCA). These include a long, expansive and rugose ischial region and shorter pubic rami (but not a long pubic corpus) (*59*). The species' highly flexible lower lumbar column, coupled with its narrower interacetabular distance, still must have provided a moderately reflexive hindlimb for arboreal climbing. Not until hominids became habitually terrestrial bipeds with broad interacetabular distances, reduced and angulated ischial tuberosities (possibly indicating hamstring deceleration of the hindlimb at heel strike), and extremely shortened, flared, and broadened ilia did they then exchange such flexibility for the much more rigid constraints of lower-limb stabilization that characterize *Australopithecus* (*50*, *51*).

The combined pelvic and vertebral data imply that the morphological elements of extant great apes emerged separately rather than in concert. Vertebral column invagination and its associated gracilization of the retroauricular pelvic space preceded specialized iliac modification and the radical lumbar column shortening seen in the African apes (*58*). The *ARA-VP-6/500* pelvis shows that hominid ilia shortened and broadened to establish permanent lumbar lordosis. African ape ilia were instead modified to increase abdominal stiffness. The posterior pelvic changes and pronounced lordosis in hominids subsequently promoted even more dramatic vertebral column invagination (*60*). This trend is eventually reflected in more dorsally oriented transverse processes of hominid thoracic vertebrae compared to those of apes (*60*). In extant apes, vertebral column invagination and shortening were acquired both independently and noncontemporaneously, the first being a deeply rooted embryogenetic mechanism that posterolateralized the pectoral girdle for a more lateral-facing glenoid; the second, an independent means of increasing abdominal rigidity. We hypothesize that hominids never participated in the second (SOM Text S3), having rather evolved from a careful climber in which deliberate bridging placed no undue stress on the lower spine. Not until the ancestors of African apes embarked (separately) on their adaptations to vertical climbing and suspension did the lumbar spine undergo its dramatic reduction in length.

The last common ancestors. Integration of the data and observations reviewed above allows us to hypothesize about the postcranial adaptations and locomotion of the GLCA and CLCA. The extensive array of highly distinctive specializations seen in modern *Gorilla* and *Pan* (in part shared with *Pongo*) indicates that these are derived features most likely related to vertical climbing and suspension.

Not only does *Ar. ramidus* fail to exhibit these specialized modifications, it exhibits others (e.g., a palmar position of the capitate head that facilitates extreme dorsiflexion of the midcarpal joint rather than its limitation; a robust os peroneum complex limiting plantar conformity to substrates rather than its facilitation) that are effectively their functional opposites. The expression of some of these characters (e.g., capitate head position) is even more extreme than it is in either the Miocene apes preceding *Ardipithecus* or in *Australopithecus* that follows. It is therefore highly unlikely that *Ar. ramidus* descended from a *Pan*/*Gorilla*-like ancestor and then (re)evolved such extreme characters. Conversely, some other detailed differences in *Pan* and *Gorilla* structure [e.g., scapular form (*61*), iliac immobilization of lumbar vertebrae (*58*), appearance of a prepollex (*62*)] suggest that each of these ape clades independently acquired their anatomical adaptations to vertical climbing and/or suspension.

Therefore, we hypothesize that *Ar. ramidus* retains much of the ancestral GLCA and CLCA character states, i.e., those that relate to above-branch quadrupedality. In particular, contra *Gorilla* and *Pan*, the GLCA carpometacarpal, midcarpal, radiocarpal, and ulnotrochlear joints must have lacked notable adaptations to suspension and/or vertical climbing (*44*). The GLCA foot seems to have been only partially modified for manual-like grasping. Its hindlimb remained fully propulsive at its midtarsal and tarsometatarsal joints (*47*). Although its shoulder joint must have been fully lateralized, its lumbar column nevertheless was still long (*58*) (fig. S15). Its limb proportions were still primitive (see earlier). If body size was as large as in *Ar. ramidus*, it may have been too large for habitual, unrestricted above-branch quadrupedality, but this remains uncertain. Assuming considerable reliance on arboreal subsistence, it is likely that body mass did not exceed 35 to 60 kg [i.e., combined probable range of *Ar. ramidus* and 6 Ma *Orrorin* (*36*)].

The GLCA picture that emerges, therefore, is one of generalized, deliberate bridging with quadrupedal palmigrady and preference for large-diameter substrates. This may have involved either suspension or vertical climbing, but without sufficient frequency to elicit morphological adaptations specific to these behaviors. It is likely that these hominoids ranged mostly in the lower canopy, and perhaps were even partially terrestrial. However, their mode of terrestrial locomotion remains unknown.

The GLCA therefore represents a foundation for two adaptive paths. *Gorilla* and *Pan* independently specialized for both suspension and vertical climbing (and eventually knuckle-walking). Gorillas might have acquired larger body size in relation to mixing higher-canopy frugivory with a more terrestrial herbaceous or folivorous dietary component. Lacking definitive fossil evidence, it is currently impossible to determine when the large body mass of *Gorilla* evolved, but it probably occurred in concert with its more herbaceous diet. The 10 Ma *Chororapithecus*, which shows incipient signs of *Gorilla*-like molar morphology (*63*), may be an early representative of the *Gorilla* clade. If so, then this clade's shift toward increased body mass and terrestriality must have occurred early in its phyletic history.

The other adaptive pathway retained palmar flexibility, with a short metacarpus that lacked notable syndesmotic restriction. This was combined with retention of an essentially rigid midtarsal joint that was insufficiently flexible to perform vertical climbing (*55*, *56*), but was fully satisfactory for less specialized careful climbing, clambering, and bridging. This is the hypothesized structure of the CLCA, from which *Pan* would have evolved a greater reliance on vertical climbing and suspension than occurred in the *Gorilla* clade, never reaching as large a body size.

In contrast to *Pan*, the forebears of *Ar. ramidus* early in the hominid clade must have relied increasingly on lower arboreal resources and terrestrial zones, without being dependent on higher-canopy resources (such as ripe fruits). From the comparative evidence now available from *Ar. ramidus* and *Pan* dental anatomy and isotopes, we posit that the chimpanzee clade increasingly developed a preference for (or dependency on) ripe fruit frugivory, whereas hominids retained a more primitive dental complex adequate for the range of transitional arboreal/terrestrial resources (*34*).

The likely K-selected demographic adaptation of all hominoids in a setting of almost certain competition with the surging Old World monkey radiation would have been a major factor (*64*, *65*) driving such very different evolutionary trajectories of early African apes and hominids. The earliest fossil evidence for cercopithecid radiation (an early colobine) is now close to 10 Ma (*66*). A much better record of both fossil hominoids and cercopithecids from the late Middle to early Late Miocene is needed to clarify these suggested patterns of ape-cercopithecid evolution.

Orthogrady, suspension, knuckle-walking, and bipedality. *Ar. ramidus* affords new insights into ape and hominid bauplan evolution

(Fig. 2 and Table 1). The most fundamental is the clear demonstration that the GLCA lacked the suspensory adaptations long recognized to be common to all extant apes.

The chimpanzee and gorilla clades each independently increased their reliance on higher-canopy resources, and modified characters originally associable with advanced bridging to those more useful in vertical climbing and suspension. These include an elongated posterior (medial) metacarpus, broadened radiocarpal joint with reduced midcarpal mobility, syndesmotically and morphologically buttressed carpometacarpal joints, expanded long antebrachial flexor tendons, a redistributed long pollical flexor tendon (to the elongated second ray), a modified enthesis for the deltopectoral complex, a retroflexed trochlear notch, elongate forelimbs (*44*), abbreviated hindlimbs, elimination of the os peroneum complex (*47*), lumbar column reduction (*58*), and iliac fixation of remaining lumbars [acquired by iliac elongation and sacral narrowing (*58*, *59*)]. Viewed from the perspective of *Ar. ramidus*, all of these can now be visualized as having been acquired independently. All represent adaptations related directly to suspension, vertical climbing, and/or knuckle-walking.

In African apes, terrestrial travel may have become the primary means of overcoming expanding canopy gaps. A return to partial terrestrial pronogrady would have necessitated compensatory energy-absorptive mechanisms to ameliorate ground reaction in heavily modified forelimbs (which would have suffered an increased risk of injury). Knuckle-walking filled this role because it promotes eccentric contraction and/or energy dissipation (and storage) in the wrist and digital flexors (especially their connective tissue components) during impact loading in a completely extended forelimb, without compromising the animal's newly acquired adaptations to either suspension or vertical climbing (*44*). More elaborate mechanisms of negotiating gaps in trees (*67*) evolved separately in orangutans, in which both manual and pedal rays radically elongated, possibly to more effectively gather and assemble multiple lianas necessary to negotiate such gaps.

Thus, *Ar. ramidus* allows us to infer that GLCA anatomy was exaptive for suspension and vertical climbing. Early hominids continued to practice palmigrade, above-branch quadrupedal clambering. Ulnar retraction, common to both *Pan* and *Gorilla*, therefore appears to have emerged for forelimb flexibility as part of arboreal clambering and bridging before the GLCA (*7*), and not as an adaptation to suspension [as has been argued (*6*)]. Initialized in forms like *Proconsul*, the combination of enhanced forelimb flexibility and hindlimb propulsive dominance, without anatomical modifications for forelimb suspension, may have reached an apogee in the GLCA.

These observations also conform to evidence available from the steadily increasing Miocene hominoid fossil record. European near-contemporaries of the African CLCA to GLCA exhibited only various degrees of adaptation to suspension, suggesting a separate Miocene trend toward increasing forelimb dominance. At 12 Ma, *Pierolapithecus* had ulnar withdrawal and partial spinal invagination (*68*), but likely retained a long lumbar spine. Its hand lacked the degree of metacarpal or phalangeal elongation seen in extant apes. More recent *Dryopithecus*, which did display both an African ape-like CJC (*44*) and elongate metacarpals relative to body size, nevertheless retained palmigrady (*68*, *69*). Suspensory locomotion was therefore likely independently derived (minimally) in *Dryopithecus*, *Pan*, and *Gorilla* (and certainly so in *Pongo*). Hypotheses that hominid ancestry included suspensory locomotion and vertical climbing (*52*, *53*), as projected from electromyographic and kinematic analyses of living ape behavior, are now highly unlikely.

From their beginning, accounts of human evolution relied on postural similarities between living humans and apes. The inference that habitual orthogrady was central to the origin of bipedality has been taken as largely self-evident (*2*, *70*). Until now, no fossils of sufficient age and anatomical representation have been available for seriously testing these presumptions. *Ar. ramidus* requires comprehensive revision of such entrenched, traditional canons. Its anatomy makes clear that advanced orthogrady evolved in parallel in hominids and apes, just as it has in an array of other primates, both living and extinct [including prosimians such as *Propithecus* and *Megaladapis*, some ceboids, gibbons, and a variety of Miocene hominoids, especially *Nacholapithecus* (*71*), and *Oreopithecus* (*72*)]. The long-held view that dorsal transposition of the lumbar transverse processes onto their pedicles implies orthogrady is now falsified, because *Ar. ramidus* establishes that such relocation is a direct correlate of ventral invagination of the entire spinal column within a context of above-branch quadrupedal palmigrady that established increased shoulder mobility for bridging and clambering (SOM Text S3).

In hominids, from an above-branch quadrupedal ancestry, advanced orthogrady was the independent consequence of terrestrial bipedality made possible by a mobile lumbar spine and largely primitive limbs. It is sobering to consider one profound implication—if emergent hominids had actually become as adapted to suspension or vertical climbing as are living apes, neither bipedality nor its social correlates would likely have evolved. It is therefore ironic that these locomotor modes have played so prominent a role in explanations of bipedality. In retrospect, it seems clear that they would instead have likely prevented it (SOM Text S3).

Conclusions. *Ar. ramidus* implies that African apes are adaptive cul-de-sacs rather than stages in human emergence. It also reveals an unanticipated and distinct locomotor bauplan for our last common ancestors with African apes, one based on careful climbing unpreserved in any extant form. Elaborate morphometric statistical procedures were the culmination of a 20th-century trend toward objectivity, in which metrics came to be regarded as more informative than careful comparative anatomy—a trend accompanied by too many presumptions and too few

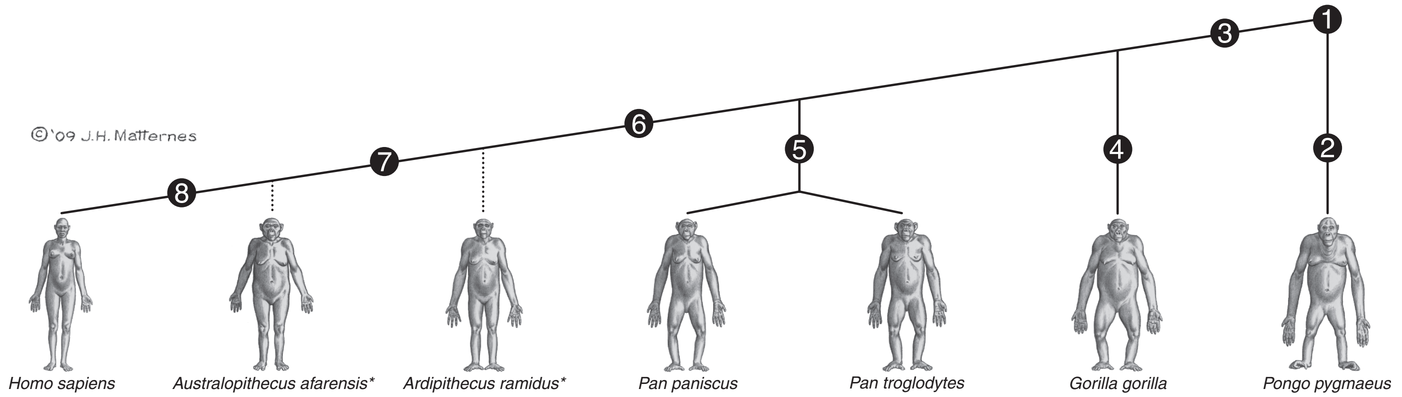

Fig. 2. Branching diagram to illustrate cladistic relationships of extant hominoids. Branching order among the extant forms shown here is well established by molecular evidence. The two fossil forms are possible phyletic ancestors of the human clade, but are shown here in a sister relationship to the extant forms. Circled numbers indicate evolutionary derivations, itemized in Table 1, hypothesized to have occurred on each lineage. [Illustrations: Copyright 2009, J. H. Matternes]

Table 1. Evolutionary derivations of various hominoid clades with fossil and modern representation. Numbers refer to circles on Fig. 2.

1. Basal node. An inferred generalized ancestor of the great ape clade, which lived probably more than 18 Ma. We infer this primate to have been an above-branch palmigrade, plantigrade quadruped, with generalized limb proportions, an anteriorly oriented pectoral girdle, and long lumbar vertebral column with transverse processes located ventrally on their bodies. It would have also been characterized by an extensive postauricular iliac region for a massive erector spinae, a long olecranon process, an anteriorly oriented trochlea, a capitate head located mid-body, and a primitive central joint complex in the wrist. It would have featured a full wrist mortise with pisotriquetral contact and a moderately long midtarsus for fulcrumation on its metatarsal heads. It was presumably tailless (*80*).

2. *Orangutan* clade. Dramatic elongation of entire forelimb, posterior (medial) metacarpus and phalanges, extreme elongation of posterior (lateral) metatarsus and phalanges but abbreviation of thigh and leg, partial involution of first pedal and manual rays. Abbreviation of lumbar vertebral column (average four elements) by means of sacralization of lumbar vertebrae, reduction in axial length by two segments, and craniocaudal shortening of lumbar centra (*58*). Entrapment of caudal-most lumbars by articulation with variable cranial extension of ilia and reduction in breadth of sacral alae. Invagination of spine with posterolateralization of pectoral girdle and reduction of deltopectoral crest. Retroflexion of trochlear notch, extreme abbreviation of olecranon process, and elevation of lateral margin of trochlea. Ulnar withdrawal with elimination of wrist mortise. Modification of central joint complex for torsional resistance during suspension. Frequent postnatal fusion of os centrale and scaphoid.

3. Extant African ape and hominid clade (GLCA). Minor abbreviation of midtarsal length, elongation of manual phalanges, and shortening of posterior (lateral) metatarsus. Invagination of spine with posterolateralization of pectoral girdle, mediolateral proportionality shift of sacroiliac region, craniocaudally shortened vertebral centra, and relocation of lumbar transverse processes to corporopedicular junction or onto pedicle. Abbreviation of olecranon and elevation of lateral margin of trochlea. Ulnar withdrawal with elimination of wrist mortise (i.e., loss of pisotriquetral contact) and deepening of carpal tunnel. Fusion of os centrale to scaphoid.

4. *Gorilla* clade. Elongation of forelimb (by disproportionate elongation of humerus) and abbreviation of hindlimb (global change in limb proportions), moderate elongation of posterior (medial) metacarpus, moderate shortening of manual phalanges. Abbreviation of lumbar vertebral column (average 3.5 elements) by means of sacralization of lumbars and reduction in axial length by one segment (*58*). Entrapment of most caudal lumbars by articulation with cranially extended ilia and reduction in breadth of sacral alae. Moderate increase in cranial orientation of scapular spine and glenoid plane, reduction of deltopectoral crest. Retroflexion of ulnar trochlear notch with attendant abbreviation of olecranon process, expansion of long digital flexor (emergence of "flexion tubercle" on ulna), subduction or gracilization of long flexor tendon of thumb to expanded long digital flexor, increased osseo-ligamentous resistance to torque in CJC via distal prolongation of the volar portion of the capitate with corresponding evacuation of the Mc3 base (creating a mediolateral block-to-joint rotation by novel abutment of Mc2 and Mc3), dorsalization and enlargement of capitate head, frequent formation of prepollex (*62*) on trapezium, anterior relocation of collateral ligament attachments of metacarpophalangeal joints (with simultaneous expansion of attachment facets on metacarpals), expansion of metacarpal heads, reduced capacity for dorsiflexion at midcarpal joint. Introduction of lateral spiral pilaster with loss of third trochanter, elimination of os peroneal complex and substantial shortening of midtarsus, especially proximodistal abbreviation of navicular and cuboid, and abbreviation of dorsoplantar dimensions of metatarsal bases. Gracilization of plantar aponeurosis with loss of plantaris and reduction/elimination of quadratus plantae.

5. Basal chimpanzee/bonobo clade. Elongation of forelimb and abbreviation of hindlimb (global change in limb proportions) but less extreme than in **4**. Substantial elongation of posterior (medial) metacarpus and further elongation of manual phalanges. Chimpanzees exhibit higher intermembral index than bonobos and are probably derived in this regard. Abbreviation of lumbar vertebral column (three or four elements) by transformation of vertebral type and/or reduction in axial length by one segment [chimpanzees and bonobos differ substantially in number of axial elements, and bonobo is clearly primitive in this regard (*58*)]. Entrapment of most caudal lumbars by articulation with cranially extended ilia and reduction in breadth of sacral alae. Further immobilization by novel lumbo-inguinal ligaments (*81*). Elongation of iliac isthmus. Dramatic mediolateral narrowing of scapula, marked increase in cranial orientation of scapular spine and glenoid plane, reduction of deltopectoral crest (intermuscular fusion?). Retroflexion of ulnar trochlear notch with attendant abbreviation of olecranon process, expansion of long digital flexor (emergence of "flexion tubercle" on ulna), subduction or gracilization of long flexor tendon of thumb to expanded long digital flexor, increased osseo-ligamentous resistance to torque in CJC via distal prolongation of the volar portion of the capitate with corresponding evacuation of the Mc3 base (creating a mediolateral block to joint rotation by novel abutment of Mc2 and Mc3), dorsalization and enlargement of capitate head, elimination of mobility in hamate/Mc4/Mc5 joint, possible gracilization of Mc1, reduced capacity for dorsiflexion at midcarpal joint, reduction and anterior relocation of collateral ligament "grooves" of metacarpophalangeal joints (but expansion of attachment facets on metacarpals), expansion of metacarpal heads. Introduction of lateral spiral pilaster with loss of third trochanter, elimination of os peroneal complex and substantial shortening of midtarsus, especially proximodistal abbreviation of navicular and cuboid, abbreviation of dorsoplantar dimensions of metatarsal bases. Gracilization of plantar aponeurosis with loss of plantaris and reduction/elimination of quadratus plantae.

6. Hominid clade, Late Miocene. Substantial superoinferior abbreviation of iliac isthmus and pubic symphyseal body, increased sagittal orientation and mediolateral broadening of ilium with novel growth plate for anterior inferior iliac spine, introduction of slight (obtuse) greater sciatic notch, (inferred) facultative lumbar lordosis, probable broadening of sacral alae to free most caudal lumbar for lordosis. Possible increased size and robusticity of fibularis longus, increased robusticity of second metatarsal base/shaft and doming of dorsal metatarsal heads related to toe-off.

7. Hominid clade, Mid-Pliocene. Shortening of ischial length and angulation of ischial tuberosity, further mediolateral expansion of iliac fossa with introduction of substantial (acute) greater sciatic notch, further invagination of lumbar vertebral column and fixation of lordosis (no longer facultative). Reduction of thoracic column from 13 to 12 elements associated with reduction in axial length by one segment [or this occurred at **6** (*58*)]. Elongation of pubic rami and femoral neck. Posterior relocation of third trochanter and emergence of true hypotrochanteric fossa. Elevation of quadriceps attachments to form "true" linea aspera, signaling fundamental shift in knee extensor/hip extensor proportions conducive to primary propulsion by quadriceps. Probable emergence of tibial dominant knee and transverse tibial plafond (or these occurred at **6**). Expansion of fibularis longus attachment to include markedly remodeled medial cuneiform and permanent adduction of great toe, elevation of sustentaculum tali to create mediolateral and longitudinal plantar arches, likely development of "spring ligament," marked inflation of calcaneal tuber (with secondary introduction of distinct lateral plantar process) for energy absorption at heel strike, gracilization of second metatarsal base, relocation of fibularis longus tendon to more proximo-plantar location (with inferred attendant change in short and long plantar ligaments [see (*47*)] to support novel transverse arch during toe-off and foot-flat, introduction of "dual phase" metatarsofulcrumation (addition of transverse axis to oblique axis of fulcrumation). Dorsalization and expansion of capitate head and broadening of trapezoid for greater palmar span, slight reduction in dorsal mobility of Mc5/hamate joint, anterior relocation and near elimination of collateral ligament "grooves" for metacarpophalangeal joint.

8. Hominid clade, Plio-Pleistocene. Elongation of lower limb, global modification of pelvis to expand birth canal (late) including abbreviation of femoral neck and pubic rami. Reduction of modal lumbar column by one (from six to five typically by sacralization of most caudal lumbar). Slight reduction in glenoid angulation of scapula, increased robusticity of thumb, transfer of styloid body from capitate to third metacarpal, palmar rotation of hamulus, loss of growth plate from pisiform, increased robusticity of terminal phalangeal tufts in carpus. Substantial abbreviation of posterior metacarpus, antebrachium, and carpal phalanges. Substantial anteroposterior thickening of navicular and length and eccentricity of calcaneal process of cuboid. Increased robusticity of Mt1. Reduction in frequency of calcification of os peroneum, abbreviation of tarsal phalanges—especially intermediates.

fossils. Contemporary morphogenetics now show that organisms as diverse as sticklebacks and fruit flies can display remarkable parallel evolution merely because they share fundamentally similar genomic toolkits (*73*, *74*). Knuckle-walking in chimpanzees and gorillas appears now to be yet one more example of this phenomenon.

In retrospect, it is impressive that the straightforward cogency of Schultz and the detailed dissections of Straus more accurately predicted the early course of human evolution than the more objective quantitative and technologically enhanced approaches heralded in the last quarter of the 20th century. Recent work in genetics and developmental biology has identified fundamental mechanisms by which morphological structures emerge during evolution. In the study of fossils, such insights have had their primary value as heuristic guides with which to construct and test hypotheses. Understanding the morphogenesis underlying profound shifts in the hominoid bauplan evidenced by *Ar. ramidus* may take years, perhaps even decades, but is likely to further transform our understanding of human natural history.

Ardipithecus has thus illuminated not only our own ancestry, but also that of our closest living relatives. It therefore serves as further confirmation of Darwin's prescience: that we are only one terminal twig in the tree of life, and that our own fossil record will provide revealing and unexpected insights into the evolutionary emergence not only of ourselves, but also of our closest neighbors in its crown.

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Supporting Online Material

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