

# Economy and Endurance in Human Evolution

Herman Pontzer

Hunter College, City University of New York, New York Consortium for Evolutionary Primatology, New York, NY 10065, USA

Correspondence: [hpontzer@hunter.cuny.edu](mailto:hpontzer@hunter.cuny.edu)

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The evolutionary pressures shaping humans' unique bipedal locomotion have been a focus of research since Darwin, but the origins of humans' economical walking gait and endurance running capabilities remain unclear. Here, I review the anatomical and physiological determinants of locomotor economy (e.g., limb length and posture) and endurance (e.g., muscle volume and fiber type) and investigate their development in the hominin fossil record. The earliest hominins were bipedal but retained ape-like features in the hind limb that would have limited their walking economy compared to living humans. Moreover, the evolution of bipedalism and the loss of the forelimbs in weight support and propulsion would have reduced locomotor endurance in the earliest hominins and likely restricted ranging. *Australopithecus* evinced longer hind limbs, extended limb posture, and a stiff midfoot, suggesting improved, human-like economy, but were likely still limited in their endurance compared to modern humans. The appearance of skeletal traits related to endurance (e.g., larger limb joints, spring-like plantar arch) in *Homo* was somewhat mosaic, with the full endurance suite apparent only ~1 million years ago. The development of endurance capabilities in *Homo* appears to parallel the evolutionary increase in brain size, cognitive sophistication, and metabolic rate.

## Introduction

Habitual bipedalism — walking and running on two legs — is a defining feature of the human lineage, distinguishing our earliest ancestors from their ape-like forbears. The evolutionary costs and benefits of adopting a two-legged gait have been debated since Darwin [1]. Much of the research in human locomotor evolution over the past four decades has focused on the energetics of human bipedalism. Laboratory studies have shown that modern humans walk much more economically than chimpanzees, covering nearly twice as much distance for the same number of calories [2,3]. Improved walking economy could provide a powerful evolutionary advantage, enabling early hominins to range farther without increasing daily energy costs [4,5] or to channel more energy toward increased reproduction, longer life-spans, larger brains, and other metabolically costly traits that make humans distinct [6,7]. More recently, researchers have recognized that humans are also exceptional runners compared to other primates, leading to the hypothesis that selection for endurance capabilities, particularly long-distance running, played a key role in shaping the human lineage [8–11]. In these models, endurance running made hominins formidable hunters and scavengers, underpinning the dramatic anatomical and ecological changes that mark our lineage.

Evaluating the roles of economy and endurance in shaping hominin evolution is hampered by a lack of clarity and consensus in discussions regarding hominin locomotor performance. *Economy* and *endurance* are often conflated, without differentiation of these two distinct performance criteria or the anatomical features that affect them. Consequently, there is little agreement on the timing and ecological context of the evolutionary changes that improved economy and endurance. Some have argued that improved economy was evident in the earliest hominins and drove the adoption of bipedalism and expansion into the savannah [4,5,12]. Others have argued that economy and

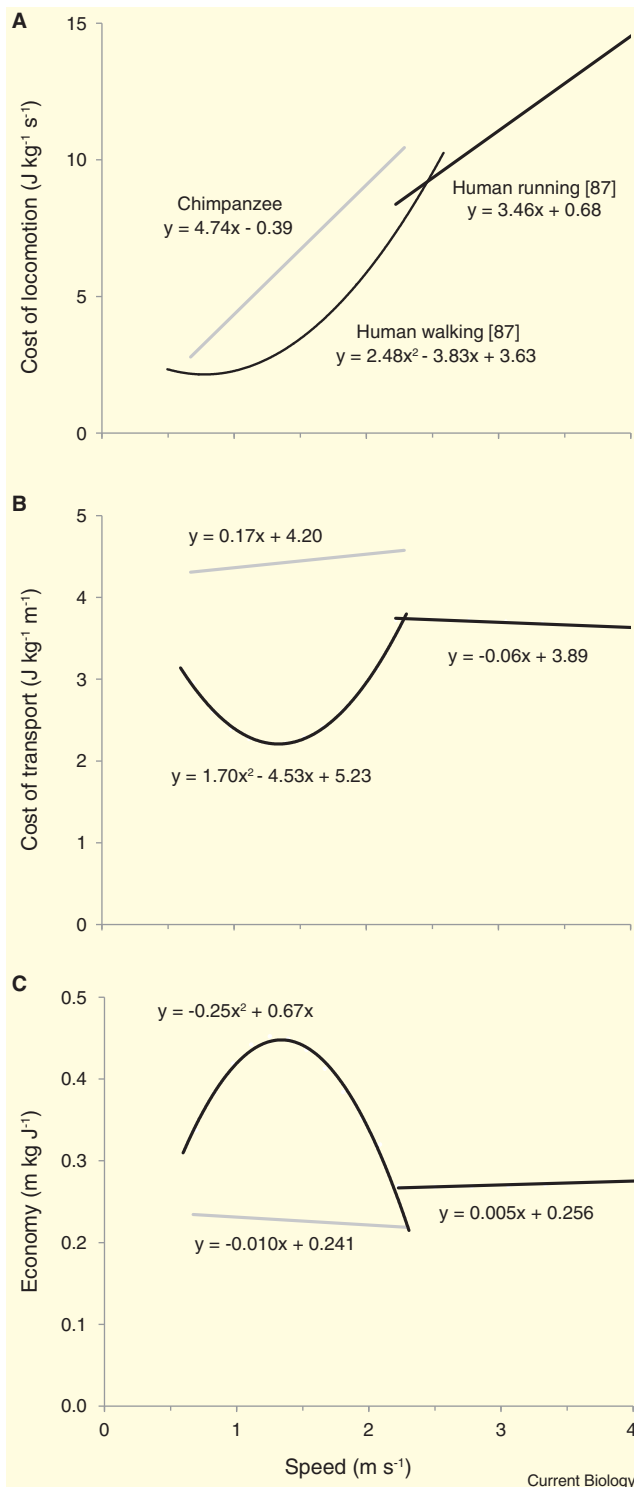
endurance evolved together, quite recently, with the origins of the genus *Homo* roughly 2 million years ago [9,13].

In this review, I integrate recent experimental work in locomotor energetics and endurance with the current evidence from the human fossil record in order to develop a synthetic and coherent reconstruction of hominin locomotor evolution. I begin with a discussion of economy and endurance in humans and apes, defining these performance criteria and discussing the anatomical traits that determine them. I then move chronologically through the ~7 million year fossil record of hominin evolution, focusing on the musculoskeletal traits known to affect economy and endurance, and the ecological contexts in which these traits change.

## Economy versus Endurance in Legged Locomotion

### Economy

Animals expend energy to walk and run, and the rate of expenditure generally increases with speed. Energy expenditure during walking and running also increases with body size: larger animals use more energy to move. The mechanics of locomotion as they relate to energy expenditure apply equally well across legged terrestrial species. Reptiles, mammals, and other vertebrates as well as insects and arthropods all follow the same allometry of locomotor cost increasing with speed and size [14–18]. Therefore, to compare locomotor costs among species of different sizes and ranges of speed, researchers often divide locomotor expenditure by body mass to give the mass-specific cost of locomotion ( $\text{J kg}^{-1} \text{s}^{-1}$ ), and then divide by speed ( $\text{m s}^{-1}$ ) to give the cost of transport ( $\text{J kg}^{-1} \text{m}^{-1}$ ), the energy expended to move one kilogram of body mass one meter. We can define *locomotor economy* ( $\text{m kg J}^{-1}$ ), the mass-specific distance traveled per unit of energy expended, as the inverse of the cost of transport (Figure 1). Note that the term *efficiency* in locomotion should be reserved for comparing the mechanical work done to move



**Figure 1. Locomotor cost and economy.**

(A) The mass-specific cost of locomotion ( $\text{J kg}^{-1} \text{s}^{-1}$ ) increases curvilinearly during walking and linearly during running in humans (black; trend lines from [97]). Chimpanzees' cost of locomotion (gray; trend line for quadrupedal locomotion [3]) increases linearly with speed; walking and running costs are similar, as are quadrupedal and bipedal travel [3]. Values shown are net costs, subtracting basal metabolic rate (estimated from body mass following [6]). Mean body mass for chimpanzees ( $n=5$ ) and humans ( $n=11$ ) in these samples

the center of mass and limbs to the amount of metabolic energy expended (e.g., [19,20]).

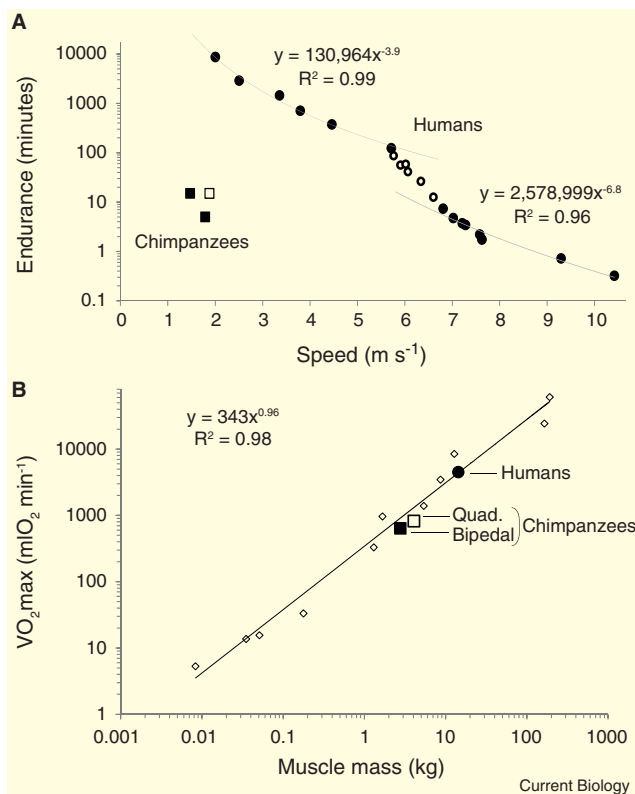
Variation in locomotor anatomy and gait dictates whether a species has a higher or lower cost of transport than expected for its size. Longer legs smooth out the rollercoaster-like trajectory of the body's center of mass as it rises and falls with each step, reducing the volume of muscle activated per step and the number of steps per meter [17,18,21,22]. Crouched postures — walking and running with flexed limb joints — reduce mechanical advantage at the joints and increase the muscular effort needed to support and propel the body, which increases cost [18,23–25]. The skeletal morphology of the joints can also affect the mechanical advantage of the muscles, affecting cost [18,23–25]. Subtle adaptations in gait to smooth the oscillations in the body's center of mass [22,26], exchange potential and kinetic energy throughout the stride cycle when walking [20,21], and store and release elastic strain energy in tendons and ligaments when running [27,28] reduce the work required of the muscles and thereby reduce cost. The mechanics of leg length, posture, and gait apply equally well whether the animal moves on two, four, six or eight legs: the number of legs used in locomotion has no effect on cost [2,3,14,15,29].

Humans have evolved long hind limbs and a straight-legged walking gait that greatly reduces the cost of transport during walking, particularly in comparison to our ape relatives [2,3] (Figure 1). The cost of transport for human walking has a distinctive U-shaped curve when plotted against speed (Figure 1), likely due to our walking mechanics and long legs [18–20]. When walking near the minimum cost of transport speed, humans' locomotor economy is twice that of chimpanzees (Figure 1). Chimpanzees do not exhibit a marked difference in the cost of transport between walking and running, and their locomotor cost and economy are the same whether traveling quadrupedally or bipedally [2,3,29]. The economy of locomotion for human running is only marginally better than that of chimpanzees (Figure 1) because humans use relatively flexed knees and hips when running, which increases muscular effort and metabolic cost [3,18,25].

### Endurance

The physiology underlying locomotor *endurance*, defined here as the maximum amount of time that an individual can sustain a given speed, is not as well understood as that for locomotor energy expenditure. Current models propose that endurance is modulated by central governors in the brain that integrate several peripheral indices of fatigue (e.g., muscle oxygenation, fuel reserves, lactate production) and limit performance, slowing and then stopping the individual before they damage their body [30,31]. Given the difficulty in eliciting maximal performance in laboratory settings, race times at various event distances provide a useful dataset for investigating endurance [32] (Figure 2; Table S1).

was similar (60 kg). (B) Dividing the cost of locomotion by travel speed gives the cost of transport ( $\text{J kg}^{-1} \text{m}^{-1}$ ). (C) The inverse of cost of transport is defined here as locomotor *economy* ( $\text{m kg J}^{-1}$ ), the mass-specific distance traveled per energy consumed. Humans are nearly twice as economical as chimpanzees during walking, moving a kg of mass nearly twice as far for a given amount of energy when traveling at peak economy speed (the zenith of the economy curve). Human running is only marginally more economical than chimpanzee locomotion.



**Figure 2. Endurance and  $\text{VO}_2\text{max}$ .**

(A) World records across a range of race distances (Table S1) show the decline in endurance with speed for elite human runners (circles) which is pronounced near  $\text{VO}_2\text{max}$  speeds,  $\sim 6 \text{ m s}^{-1}$  (open circles) [33]. The decline in endurance with speed is steeper above  $\sim 6 \text{ m s}^{-1}$ , reflecting the dependence on anaerobic respiration [32]. Maximum recorded endurance capabilities for chimpanzees (squares: filled, bipedal; open, quadrupedal [3,29]) are much reduced compared to humans and lower during bipedal running (Figure S1). (B)  $\text{VO}_2\text{max}$  is strongly correlated with muscle volume across mammals [34] including humans (circle) and chimpanzees (squares). In chimpanzees, maximum energy expenditures are lower during bipedal running (Bipedal) than quadrupedal running (Quad.), corresponding to the reduction in muscle volume with loss of use of the forelimbs in locomotion (Figure S1).

Unlike the cost of transport or locomotor economy, endurance is strongly dependent on running speed in humans and other animals: slower speeds can be maintained for longer periods. Energy consumption, and therefore oxygen consumption, rises with running speed (Figure 1), and a distinct break is evident in the speed-related decline in endurance as running speed and the accompanying oxygen demand approach two important and related physiological thresholds, the lactate threshold and  $\text{VO}_2\text{max}$ .  $\text{VO}_2\text{max}$  is an organism's maximum rate of oxygen consumption ( $\text{mlO}_2 \text{ min}^{-1}$ ), and represents the maximum rate of energy expenditure that can be maintained through aerobic respiration; the speed at which oxygen demand equals  $\text{VO}_2\text{max}$  is an individual's  $\text{VO}_2\text{max}$  speed,  $\sim 6 \text{ m s}^{-1}$  for elite human runners [33]. As an individual approaches and then exceeds their  $\text{VO}_2\text{max}$  speed, pyruvate produced by the exercising muscles is converted to lactate (i.e., lactic acid) rather than oxidized as fuel, and lactate levels in the blood begin to rise [33], contributing to fatigue [30,31]. Endurance drops precipitously above the

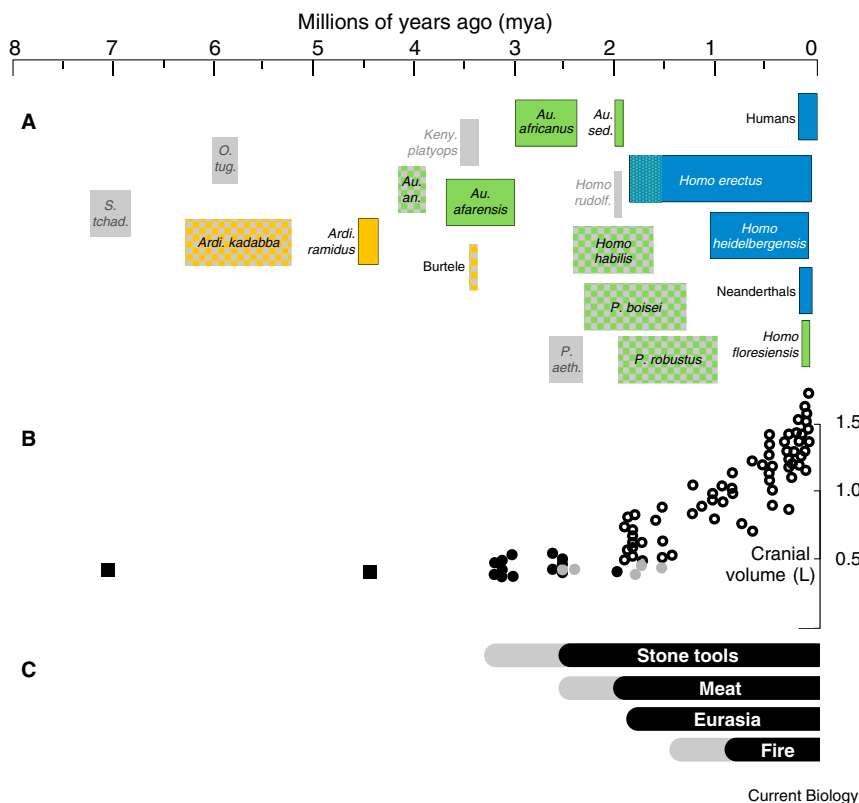
$\text{VO}_2\text{max}$  speed, falling below 15 minutes in humans (Figure 2).  $\text{VO}_2\text{max}$  therefore defines the limit of truly sustainable speed, and is the standard physiological measure used to compare endurance capabilities across species [34].

Among mammals,  $\text{VO}_2\text{max}$  corresponds strongly with the volume of mitochondria in the muscles available to uptake oxygen [34], and is in turn dependent on the volume and type of muscle used in locomotion (Figure 2). Humans and chimpanzees are no exception, with  $\text{VO}_2\text{max}$  values (for chimpanzees, maximum recorded oxygen consumption; Figure S1 in Supplemental Information, published with this article online) falling near the mammalian trendline with muscle volume (Figure 2). Unlike locomotor cost or economy, there is a clear effect of bipedalism on endurance in chimpanzees. Maximum sustained energy expenditures and speeds are both  $\sim 22\%$  lower in bipedalism, consistent with the  $\sim 30\%$  reduction in available muscle mass as the forelimbs are removed from their role in weight support and propulsion (Figure 2; Figure S1). Capuchin monkeys exhibit similar reductions in speed and expenditure in bipedal trials (Figure S1). Humans carry much more hind limb muscle ( $\sim 250 \text{ g}$  per  $\text{kg}$  body mass) than chimpanzees ( $\sim 170 \text{ g/kg}$ ), equivalent to the summed total of fore and hind limb muscle in chimpanzees ( $\sim 240 \text{ g/kg}$ ) [35,36]. While few studies have compared muscle properties across humans and apes, human limb muscle also appears to be derived in terms of muscle physiology and mitochondrial density. Fiber type comparisons between humans and chimpanzees of major muscles in the calf (soleus and gastrocnemius) indicate that humans have 2- to 3-times the proportion of fatigue resistant, mitochondria rich, Type I ('slow twitch') fibers [37]. Comparisons of thigh muscle (vastus) indicate that human muscle has a derived metabolic profile compared to that of chimpanzees and macaques [38].

For a given body mass,  $\text{VO}_2\text{max}$  speed is proportional to the product of  $\text{VO}_2\text{max}$  (the maximum aerobically sustained rate of energy expenditure) and locomotor economy (the distance traveled per unit of energy consumed). Species could evolve broader ranges of sustainable speed through increases in  $\text{VO}_2\text{max}$ , economy, or both. Humans' greater  $\text{VO}_2\text{max}$  speed and broader range of sustainable speeds relative to chimpanzees (Figure 2) is mostly a result of greater  $\text{VO}_2\text{max}$ , as the difference in running economy between species is marginal (Figure 1). While a suite of derived skeletal features has been identified that are likely related to long distance running in *Homo* [9], humans' prowess as endurance runners is due primarily to an evolved increase in hind limb muscle volume and evolutionarily derived muscle physiology, which improve our  $\text{VO}_2\text{max}$  relative to apes and other primates.

### Tracking Locomotor Performance in the Hominin Fossil Record

The mechanics and physiology underlying locomotor cost and endurance (Figures 1, 2) frame and focus our examination of the fossil record. To assess locomotor cost, we must reconstruct hind limb length and posture, which are accessible through analyses of femur and tibia length and joint morphology. Further, we need to assess whether walking and running gaits permitted the efficient transfer of potential and kinetic energy during walking, and of elastic strain energy and kinetic energy during running. Such evaluations are somewhat tenuous due to the difficulties



**Figure 3. Hominin evolution overview.**

(A) Hominin species age ranges [41] and their inferred locomotor capabilities. Yellow: poor economy and low endurance. Green: good economy but limited endurance. Blue: human-like economy and endurance. Hatched: economy and endurance inferred from limited evidence. Gray: insufficient fossil evidence to determine economy or endurance. See text. (B) Brain sizes (cranial volumes) increase beginning ~2 mya. Open circles: *Homo*; closed circles: *Australopithecus*; gray circles: *Paranthropus*; squares: other. Redrawn from [12,44,88]. (C) Earliest proposed appearance (gray) and widespread evidence (black) for stone tool use [98], butchery of game animals (meat) [86,87], expansion into Eurasia [51], and the control and use of fire [99].

### Early Hominins

Fossils from the oldest widely recognized hominin species, *Sahelanthropus tchadensis* and *Orrorin tugenensis* [44,45], indicate that the earliest hominins most likely walked bipedally, but reveal little else about their locomotion (Figure 3). In *Sahelanthropus*, dated to 6–7 mya [44], the base of the skull and orientation of the orbits indicates the spinal column was held vertically [46], the trunk upright (Figure 4). In *Orrorin*, dated to 5.8 mya, markings from the *obturator externus*

muscle on the proximal femur and analysis of cortical bone thickness in the femoral neck are consistent with bipedal walking [47]; but see [48]. Hind limb length and posture cannot be determined for either species. Analyses of their dentition and reconstructions of their habitats suggest the dietary ecology of these early hominins was not radically different from living apes [44,45].

By far the best known early hominin is *Ardipithecus ramidus*, dated to 4.4 mya, for which a nearly complete skeleton has been reconstructed from over 100 fossils representing several individuals [12,49,50] (Figure 4). From its cranial base anatomy and inferred trunk orientation, as well as a pelvis that wrapped transversely around the trunk, it is evident that *Ar. ramidus* was bipedal when on the ground. However, its long forelimb and long, curved manual phalanges indicate that *Ar. ramidus* still regularly climbed and clambered in the forest canopy, and these hominins retained several primitive, climbing-related, ape-like features in the hind limb, including a grasping foot [49] and an ape-like ischium, the posterior portion of the pelvis that serves as the attachment for the hamstring muscles [50]. Its hind limb was also short relative to body mass, similar to chimpanzees and gorillas [51] (although initial analyses likely overestimated body mass [52]). The posture of *Ar. ramidus*, whether it walked with flexed or straight legs, is uncertain.

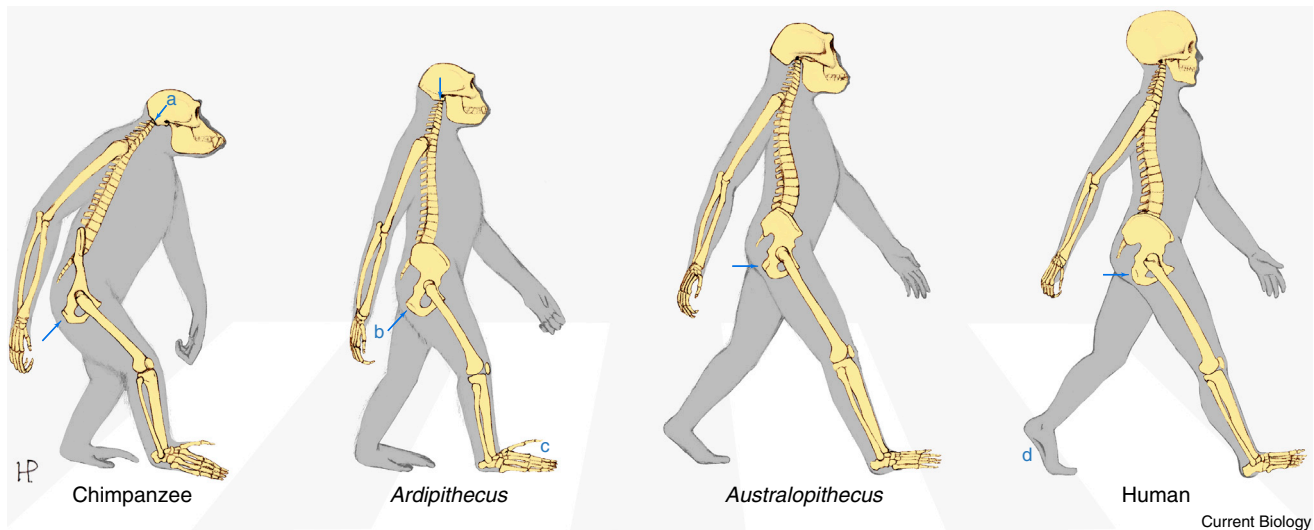
While we lack the anatomical evidence for a detailed analysis of gait in *Sahelanthropus* or *Orrorin*, experimental evidence and theoretical considerations strongly indicate that the evolutionary transition from quadrupedal to bipedal walking would have had no effect on locomotor cost or economy: bipedal and quadrupedal walking are equally costly [2,3,29]. Ape-like hind limb

Assessments of locomotor endurance are inherently more circumstantial, because the primary determinants of  $\text{VO}_2\text{max}$ , muscle mass and mitochondrial density, do not fossilize. However, two lines of evidence can serve as indicators of long distance walking and running. First, walking and (especially) running mechanically stress the hind limb skeleton, which may result in greater robusticity of the bones and selection pressure for larger joints to reduce strain [9]. Second, dietary ecology affects locomotor demands, with carnivores traveling ~4-times farther per day than similarly sized herbivores [39], and there is some evidence, in lizards, that longer daily travel distances are correlated with increased endurance [40]. Thus, skeletal evidence for increased hind limb robusticity and ecological evidence for a dietary shift to include more meat in the diet provide indirect evidence for increased endurance.

The hominin fossil record stretches back ~7 million years to our last common ancestor with chimpanzees and bonobos, and is marked by considerable anatomical diversity both over time and among contemporaneous species [41]. At least 20 distinct species have been recovered [41] (Figure 3). While these species are typically distinguished through craniodental characters, there is notable diversity within the hind limb anatomy as well [41–43]. Nonetheless, it is possible to distinguish patterns in locomotor anatomy and ecology over time and across species, particularly with respect to features related to cost and endurance.

in reconstructing the subtleties of gait from skeletal measures, but analyses of the foot, which in humans acts as a stiff lever during walking and as a spring during running, can provide some insight.





Current Biology

**Figure 4. Locomotor anatomy in chimpanzees, humans, and fossil hominins.**

Individuals are depicted at similar body mass for comparison. In chimpanzees (shown walking bipedally) and other apes, the foramen magnum is positioned posteriorly along the base of the skull (a) and angles somewhat dorsally, reflecting the habitually horizontal orientation of the spine during quadrupedal travel. Hominins have the foramen magnum positioned more anteriorly and angling vertically downward (see arrow on the skull of *Ardipithecus*) reflecting the vertical orientation of the spine in bipedalism [46]. The ilium (upper portion of the pelvis) of *Ardipithecus* wraps transversely about the trunk, as in later hominins, but the ischium (b) is long and projects inferiorly (downward), as in chimpanzees. This ischium morphology increases the power of the hamstring muscles to extend the hip during climbing, but likely limits the range of hip extension during walking relative to the shorter, more dorsally projecting morphology in *Australopithecus* and humans (arrows). *Ardipithecus* also retains an opposable, grasping hallux (c; the first toe), unlike *Australopithecus* and later hominins. *Australopithecus* and humans have longer hind limbs (measured from the hip joint to ankle) than do apes and *Ardipithecus*, yet *Australopithecus* retains the long forelimb and fingers seen in apes and *Ardipithecus*, as well as a long foot [42]. Humans have a spring-like plantar arch (d), but it is unclear whether this is evident in *Australopithecus* or early *Homo* species. Note the much larger brain and reduced jaw size in humans. Illustration by the author.

length in *Ar. ramidus* [51] suggests ape-like locomotor cost, and its flexible, grasping foot further suggests a less efficient transfer of force as the foot pushed off with each step [53]. However, locomotor economy in *Ar. ramidus* would have been somewhat better than that of chimpanzees if it used a more upright, straight-legged gait [3,25]. Thus, locomotor cost in *Ar. ramidus* was likely intermediate between that of chimpanzees and humans, closer to chimpanzees if it walked with flexed hind limbs. Anatomical similarities in the closely related *Ar. kadabba* and the enigmatic Burtale foot, with its abducted, grasping hallux, suggest comparable locomotor economy in these populations (Figure 3).

The adoption of habitual bipedalism in the earliest hominins would have meant a substantial decrease in endurance compared to their ape-like forbears. As discussed above, evidence from chimpanzees suggests a ~22% reduction in  $\text{VO}_2\text{max}$  when transitioning from quadrupedal and bipedal locomotion, due to the lost contribution of the forelimb muscles to locomotor effort (Figure 2). It is unclear how long such a deficit in endurance might have persisted in the hominin lineage: overcoming it would have required a considerable evolutionary increase in hind limb muscle volume, which is difficult to ascertain from fossils. Together with ape-like (or perhaps marginally better) locomotor economy, reduced endurance suggests that early hominin evolution was marked by reduced daily travel and contracted home ranges. This reconstruction stands in sharp contrast to models suggesting that bipedalism in early hominins enabled increased ranging and expansion into savannah habitats [4,5].

### ***Australopithecus***

Nearly a century has passed since the initial discovery of fossils from the genus *Australopithecus* and their publication by Dart [54], who correctly inferred they were bipedal. Hundreds of fossils have since been recovered from sites in east and southern Africa, including several partial skeletons. At least 5 species within the genus are now widely recognized, stretching from 4.2–2.0 mya [40] (Figure 3). However, only three species, *Au. afarensis*, *Au. africanus*, and *Au. sediba*, are represented by sufficient postcranial remains to reconstruct their locomotor cost and endurance (Figure 4). Like earlier hominins, *Australopithecus* species retained long arms and some ape-like elements of forelimb anatomy, and the consensus view (still debated by some) holds that these hominins regularly used the trees to forage and perhaps to sleep [55–57]. Unlike earlier hominins, *Australopithecus* species lacked an abducted, grasping hallux, and had a comparatively reduced, more human-like ischium [42,50,57] (Figure 4). The *Australopithecus* foot varies somewhat across species [42] but in general was longer relative to hind limb length than that of humans. Nonetheless, the midfoot was relatively stiff [42], indicating that the foot was an effective lever to push off against the ground during walking.

Fossil discoveries in the 1970s, particularly the famous AL 288-1 ‘Lucy’ skeleton, sparked decades of debate regarding the nature of *Australopithecus* bipedalism. Some argued that *Australopithecus* gait was essentially human-like [58], while others suggested these hominins had short, ape-like hind limbs [59] and walked with a crouched posture [55–57]. As additional

fossils have been recovered and new analytical techniques developed, this debate has been largely resolved in favor of a more human-like gait (Figure 4). Computer modeling of *Au. afarensis* gait [60,61] and analyses of the Laetoli footprints (ascribed to *Au. afarensis*) [62,63] do not indicate a crouched ape-like gait and instead suggest a more human-like, extended hind limb posture. Anatomical analyses of the knee joint and calcaneus likewise suggest the hind limb was extended at heel strike [57], and analyses of trabecular bone within the *Au. africanus* talus suggest human-like hind limb extension throughout the stance phase of the gait cycle [64]. Hind limb lengths in the small-bodied AL 288-1 *Au. afarensis* and STS-14 *Au. africanus* skeletons are somewhat ambiguous because at body sizes below ~30 kg, the human and ape ranges overlap [51,65]. However, hind limb lengths of larger-bodied *Australopithecus* specimens fall clearly with humans [51].

Overall, analyses of the fossil and footprint evidence suggest that *Australopithecus* walking was kinematically distinct but functionally very similar to modern humans. A long and extended hind limb, paired with a stiff, non-grasping foot, and more human-like pelvis are all consistent with human-like locomotor cost and economy. Variation in hind limb anatomy and inferred walking mechanics within the genus [42,43,66] may reflect minor differences in cost, but do not contradict the view of *Australopithecus* species as effective and economical bipeds. The endurance capabilities of *Australopithecus* are less clear, but were likely quite limited compared to humans. *Australopithecus* has relatively small hind limb joints and lacks other skeletal indices of long distance running [9]; its midfoot was stiff but likely did not have a spring-like plantar arch for storing and returning elastic strain energy [9] (but see [67,68]). Further, while *Australopithecus* appears to have been flexible in what it ate [69,70], including some evidence for termites [71,72] and perhaps even occasional meat [73] (but see [74]), its large, thick-enameled molars and robust chewing anatomy indicate that the *Australopithecus* diet was largely plant-based, suggesting modest daily travel distances [39].

Comparatively little is known about the postcranial anatomy of two contemporaneous genera, *Kenyanthropus* and *Paranthropus*, making it difficult to reconstruct their economy and endurance. *Kenyanthropus* and *P. aethiopicus* are known only from craniodental material [41]. Roughly 40 postcranial fossils, mostly incomplete, are attributed to *P. boisei* and *P. robustus*, including a few partial femora and other hind limb bones [75,76]. Based on broad postcranial affinities with *Australopithecus*, it can be inferred, provisionally, that *P. boisei* and *P. robustus* shared similar locomotor capabilities (Figure 3).

### The Genus *Homo*

Recent discoveries in Ethiopia have pushed the evolutionary origins of the genus *Homo* back to 2.8 mya, but the oldest postcranial material, assigned to *H. habilis* and *H. erectus*, is 1.8 million years old [41,42]. More than half a century has passed since the initial discovery of *H. habilis*, the oldest member of the genus with associated postcrania, yet its locomotor anatomy remains poorly known. The OH 8 foot from Tanzania (1.8 mya) retains primitive features of the talus and metatarsals, but appears to have had a plantar arch [42], which enables the foot to store and return elastic strain energy during running [77]. However,

the only partial skeleton of *H. habilis*, the badly fragmented OH 62 specimen, suggests long forelimbs and an *Australopithecus*-like locomotor ecology [78–80]. The conservative inference is that *H. habilis* retained locomotor capabilities similar to *Australopithecus*, with good walking economy but limited endurance (Figure 3).

The discovery in 1984 of a 1.5 mya nearly complete and remarkably human-like *H. erectus* skeleton from Kenya (KNM-WT 15000) shaped the view that modern human locomotor anatomy and capabilities arose in early *H. erectus* (sometimes called *H. ergaster*) [9,80,81]. More recent finds suggest that the locomotor capabilities of *Australopithecus* and early *H. erectus* were not as distinct as initially thought [51]. A partial skeleton and other hind limb fossils from *H. erectus* from the Republic of Georgia, dated to 1.8 mya, retain some primitive features of the foot and lower leg, including a less robust and *Australopithecus*-like first metatarsal (like OH 8) and a lack of tibial torsion [13]. The earliest evidence of a fully human-like foot dates to ~1 mya [82]. A wide, laterally flaring fossil pelvis from Ethiopia, assigned to *H. erectus* and dated between 1.4 and 0.9 mya, along with material from *H. heidelbergensis* and Neanderthals [83], suggest that the narrow pelvis of modern humans may have only evolved some 200,000 years ago with the origin of our species [84]. Long hind limbs, previously thought to have evolved with *H. erectus* [9,13,81], are evident much earlier, in *Australopithecus* [51].

With (nearly) human-like locomotor economy established in *Australopithecus*, the emergence of *H. erectus* at 1.8 mya likely signals a change in locomotor endurance rather than cost. Initially, not all aspects of the endurance suite [9] were present. Given the retention of primitive features in the foot and trunk, it seems likely that endurance capabilities in early *H. erectus* were at least marginally restricted compared to modern humans' (Figure 3). Nonetheless, their larger joint sizes and the robusticity of the femur and tibia indicate an increase in mechanical stress on the hind limb skeleton, suggesting that the endurance demands on early *H. erectus* were substantially greater than for *Australopithecus* [9–11]. Bramble and Lieberman have taken this view the furthest [9,10], proposing that a suite of traits evident in early *H. erectus* (but not *Australopithecus*) reflect long distance running to pursue and exhaust prey. Certainly by ~1 mya, populations in Africa and Eurasia are postcranially so similar to modern humans [82–85] (pelvic breadth notwithstanding) that economy and endurance were most likely equivalent to living humans.

Other physiological and archeological evidence supports this view of endurance capabilities arising in *Homo*. Stone tool butchery marks on fossil animal bones begin to appear at ~2.5 mya and are well-established in the archeological record by ~2.0 mya [86,87], signaling a dietary shift to meat that would have necessitated an increase in ranging [39,51]. Brain size also begins to increase at ~2.0 mya [88,89] (Figure 3), reflecting increases in both cognitive capacity and metabolic demand, as the brain is energetically costly to grow and maintain [90,91]. Increasing brain size is matched with increasing technological sophistication and ecological flexibility, beginning with the expansion into Eurasia ~1.8 mya and continuing to the present day (Figure 3). Humans' greater reproductive output and longer lifespan likely evolved over this period as well, although the

timing of these life history changes is debated [7,92]. Together, the fossil and archeological evidence point to an evolved physiological shift to a high-energy strategy in *Homo*, with increased energy demands and throughput, consistent with the elevated metabolic rates of modern humans relative to living apes [6]. Endurance prowess would have played a critical role in meeting daily energy demands and physiological workload in Pleistocene *Homo*.

Notably, skeletal traits for improved endurance are not evident in *H. floresiensis*, the enigmatic small-bodied species from the Indonesian island of Flores dated to 100–60 thousand years ago [93]. Economy appears to have been poor relative to living humans, with long feet and short hind limbs [94,65], and a long forelimb and fingers suggest frequent climbing. Brain size is small as well, indicating either that the endurance capabilities and brain size of its *H. erectus* ancestors were both lost, or that it descended from an earlier and more primitive group [94]. Similarly, *H. naledi*, recently discovered in South Africa and dated to ~230,000 years ago, appears to be a relic population of early *H. erectus* that persisted until quite recently in southern Africa [95]. The hind limb anatomy of *H. naledi*, and its inferred locomotor repertoire, is similar to early *H. erectus* [96].

## Conclusion

Over the past three decades, advances in locomotor biomechanics and an expanding fossil record have improved our understanding of hominin locomotor evolution (Figures 3, 4). The evidence reviewed here suggests bipedalism in the earliest hominins conferred little, if any, advantage in economy and likely was not an adaptation for increased ranging. On the contrary, early bipedalism may have limited ranging capabilities by reducing endurance. By ~4 mya, hind limb adaptations in *Australopithecus* suggest an economical walking gait, kinematically distinct but functionally equivalent to modern humans. The large and thick-enameled molars of *Australopithecus* [41] indicate a dependence on lower quality foods, and one may hypothesize that their increased ranging economy was part of an adaptive response to drier, more challenging environments where food energy was more difficult to acquire.

Increased brain size, a dietary shift to eating meat, and increasing technological sophistication and ecological flexibility, begin to emerge ~2 mya in the genus *Homo* (Figure 3). Evidence for improved endurance begins to appear then too, and the growing consensus is that sustained physical activity, including distance running, was important in the development of hunting and gathering ecology [9–11]. It remains unclear exactly when and how changes in muscle volume and physiology, the key adaptations underpinning humans' endurance prowess, evolved. Piecing together these changes and integrating them with evolutionary changes in hominin life history, diet, and metabolic rate remain important tasks for future research.

## SUPPLEMENTAL INFORMATION

Supplemental Information contains one figure and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.05.031>.

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