# Bipedalism

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*Homo sapiens* is the only extant mammal that habitually strides only on its extended hindlimbs—a type of locomotion referred to as bipedalism. Certainly there have been (e.g., theropod dinosaurs) and there continue to be (e.g., ratite birds) other striding bipeds. Additionally, many mammals are habitually upright and use saltatory locomotion (e.g., kangaroos, jerboas, springhares). Some even are facultative bipeds: they stride, albeit infrequently, on two feet during short bouts of locomotion. This has been observed in pangolins, some bears, and in modern apes. Humans are unique among mammals in being obligate bipeds.

While it remains unclear why bipedalism evolved, this form of locomotion has two obvious advantages. First, it releases the upper limb from any locomotor responsibilities and thus provides a form of transport consistent with the development of and eventual reliance on tools. Darwin (1871) (see DARWIN, CHARLES R.) himself hypothesized that the freeing of the hands for stone tool construction was a critical selective pressure that drove bipedal locomotion. As the discovery and accurate dating of fossils and artifacts necessary to test this hypothesis occurred first in the 1960s and 1970s (e.g., 1.85 Ma Oldowan tools; 3.66 Ma Laetoli footprints), the antiquity of bipedalism in relation to stone tool construction appeared to refute Darwin's hypothesis about the origins of upright walking. However, since the evidence for stone tool production and use was pushed back to ~3.4 Ma and the oldest secure evidence for habitual bipedalism somewhere between 3.66 Ma and 4.2 Ma, the temporal gap is closing and this hypothesis may deserve a second look. A second advantage of upright walking is that it is a remarkably economic form of locomotion. Although humans are slow by comparison with other mammals, we use considerably less energy to move than do quadrupedal animals. While many have investigated the mechanics of walking in humans, the extraordinary work of Verne Inman (Saunders, Inman, and Eberhart 1953) was the first to detail the major determinants of bipedal gait efficiency in humans. Skeletal correlates of bipedal gait are listed below.

## Musculoskeletal adaptations for bipedalism

By comparison with the musculoskeletal system of our closest ape relatives, the human one has evolved (or, for some anatomies, ontogenetically developed) characters functionally correlated with our unique form of locomotion. Many will be described below, but this should not be regarded as a complete list. The human foramen magnum is in an anterior position, which balances the head atop a nearly vertical spine. The spine itself is curved, with lordotic lumbar and cervical regions and a kyphotic thoracic region. The pelvis is greatly modified by comparison with the ape pelvis. The ilia are short and stout, which lowers the center of mass by reducing the distance between the sacroiliac joint and the acetabulum. Furthermore, the iliac blades are sagittally oriented, which repositions the lesser gluteals (gluteus medius and gluteus minimus) and converts them into abductors. This reorientation prevents pelvic tilt during single-legged stance phase. Humans possess long legs, which are functionally important for increasing stride length. The weight-bearing joints of the lower limb are enlarged and have a large volume of trabecular bone, which is able to dissipate the high forces incurred on an upright skeleton and to spare nonrenewable cartilage. The distal femur possesses a bicondylar, or carrying angle, which positions the knees and the feet directly under the center of mass and reduces inefficient mediolateral weight transfer during walking. This anatomy is not present at birth; it develops in toddlers as they begin walking. Humans have a thick

patella, which increases the moment arm (i.e., length) for the quadriceps—a muscle important for preventing buckling of the knee during the single-legged stance phase and for leg extension during the swing phase. The tibia is orthogonal in relation to the foot, which aligns the lower limbs and positions the foot in an everted set.

Unsurprisingly, many adaptations to bipedalism can be found in the foot, which is the only part of our body that is in contact with the substrate during locomotion. The Achilles tendon is long and the arch of the foot is well developed. These soft-tissue adaptations are thought to increase the elastic energy return so as to aid in propulsion, particularly while running. The relative expansion of the proximal calcaneus and the plantar position of the lateral plantar process have been proposed as adaptations that dissipate the large forces directed through the calcaneus during heel strike. The great toe is adducted—fully aligned with the other digits. This orientation, together with the attachment of the plantar aponeurosis (a thick band of tissue running from the calcaneus to the proximal phalanges), renders the foot stiff during heel lift and helps convert the foot into a rigid propulsive lever. The tarsals are relatively elongated, while the phalanges are quite short. Finally, the metatarsal heads are domed and the proximal phalanges canted—anatomies that indicate dorsiflexion of the metatarsophalangeal joints during the push-off phase of bipedal walking. Thus the human skeleton (see SKELETAL BIOLOGY IN ANTHROPOLOGY) exhibits anatomies that are likely to be under genetic control and are true adaptations for bipedalism (e.g., reorientation of the ilia) and anatomies that only develop in the context of bipedalism (e.g., bicondylar angle).

## When did bipedalism evolve?

While the evidence for a striding bipedal gait in hominins around 3.66 Ma is unequivocal, determining how far back in time this locomotion extends has been more difficult. In our opinion, the oldest convincing skeletal evidence for habitual bipedal gait in hominins can be found in the 4.2-million-year-old KNM-KP 29285 tibia assigned to *Australopithecus anamensis* (see AUSTRALOPITHECINE/AUSTRALOPITH).

The proximal tibia possesses an expanded tibial plateau, adaptive for dissipating high forces at the knee during bipedal gait. Furthermore, the distal tibial shaft is orthogonal to the plane of the ankle joint, which would have positioned the knee directly above the foot—an orientation found in humans that functionally minimizes the costly displacement of the center of mass in the coronal plane and is correlated with a bicondylar angle. This latter point is particularly important, given evidence that the bicondylar angle is developmentally plastic and appears to occur only in the context of extended knee bipedalism.

Material assigned to *Ardipithecus ramidus* from the 4.4-million-year-old Aramis site in the Middle Awash, Ethiopia has been proposed to come from a bipedal hominin. These claims are based primarily on the morphology of the pelvis, femur, and partial foot (White et al. 2009). The reconstructed pelvis possesses a human-like ilium and a more ape-like ischium. Most salient are the somewhat flaring, sagittally oriented ilia, which would allow the lesser gluteals to act as abductors during bipedal gait in *Ardipithecus*. Furthermore, the ilia appear to be well spaced in the coronal plane, freeing the lumbar vertebrae to be lordotic during bipedal gait. However, the pelvis is crushed and this interpretation relies on a digital reconstruction of the fragmented remains. Recovery of additional material or an independent assessment of this pelvic reconstruction will help test the hypothesis proposed. While the medial column of the foot is ape-like in possessing a grasping, abducted hallux, the lateral column is rigid and may have facilitated a primitive form of bipedal locomotion. *Ardipithecus* (see ARDIPITHECUS) possesses robust metatarsal bases, domed heads of the lateral metatarsals, and dorsally canted proximal phalanges. However, the talus is ape-like in possessing a high trochlea laterally, an anatomy that suggests that the foot of *Ardipithecus* was in an inverted set and not in an everted position, as in the later *Australopithecus*. Given the functional link between a valgus knee and a varus ankle, this ankle anatomy in *Ardipithecus* would be consistent only with a weakly developed bicondylar angle, and thus with infrequent bipedalism.

Bipedal locomotion has also been proposed for *Ardipithecus kadabba* on the basis of the

dorsal tilt of a pedal phalanx (AME-VP-1/71) from 5.2-million-year-old sediments in the Middle Awash, Ethiopia (Haile-Selassie 2001). This anatomy, canted to the proximal facet, suggests dorsiflexion at the metatarsophalangeal joint and a more human-like toe off mechanism. While the anatomy of this fossil is tantalizing, it is difficult to assess bipedalism in a species on the basis of a single toe bone; further finds will be needed to test this hypothesis.

Three proximal femora, including a well-preserved one (BAR 1002'00), have been recovered from the 5.8–6.2-million-year-old Kenyan fossil *Orrorin tugenensis* (see ORRORIN) and hypothesized to come from a bipedal hominin. In fact, early observations suggested that the *Orrorin* femur was more human-like than specimens assigned to *Australopithecus* (Senut et al. 2001). Continued work on this specimen finds either little difference between *Orrorin* and australopiths or similarities between *Orrorin* and Miocene hominoid femora. The *Orrorin* femur has a moderately elongated neck, a hominin feature that would increase the mechanical advantage of the lesser gluteals during the single-legged stance phase of walking. However, the distribution of cortical bone around the femoral neck is not as asymmetrical as anticipated in a biped and may be evidence of a different form of gait. Again, only additional fossils will help assess claims for bipedalism in *Orrorin*.

*Sahelanthropus tchadensis* (see SAHELANTHRO-PUS) is a ~7-million-year-old hominid from Chad, Central Africa. There are no published postcranial bones from this Miocene taxon; bipedalism has been inferred instead from the position of the foramen magnum on both the original skull (Brunet et al. 2002) and its digital reconstruction. The foramen magnum is anteriorly positioned and forms an angle with the plane of the orbits that is closer to the range of this angle in humans and australopiths than to the range in African great apes. However, this interpretation has been contested on the basis of (1) the morphology of the nuchal plane and (2) uncertainty in the relationship between the position of the foramen magnum and bipedal locomotion. The foramen magnum's position may indicate an upright, orthograde posture in *Sahelanthropus*, but

confirmation of bipedal locomotion will necessitate the recovery or publication of postcranial elements.

Some have proposed that the late Miocene (~8 Ma) Italian ape *Oreopithecus* may have been bipedal on the basis of anatomies of the pelvis and the foot (Köhler and Moyà-Solà 1997). Of course, bipedal locomotion in *Oreopithecus* would be fascinating and scientifically quite important precisely because this hominoid is unlikely to be an ancestor to hominins and would therefore provide an example of parallelism. However, most of the scientific community remains unconvinced that *Oreopithecus* was bipedal.

In sum, habitual bipedalism undoubtedly evolved about 4 Ma, but evaluating claims that this form of locomotion was an important part of the locomotor repertoire of hominins earlier in the Pliocene, or even in the late Miocene, will require additional fossil evidence. Furthermore, although bipedalism is often presented as a defining feature of the hominin lineage, current evidence suggests that this form of locomotion may have evolved well after the hominin split with the *Pan* lineage, given the paucity of fossils from the late Miocene and estimates that place the divergence data as far back as at least 7–8 Ma.

## From what did bipedalism evolve?

Just as uncertain as *when* bipedalism evolved is the question of the body form *from which* bipedalism evolved. A handful of different models have been proposed to explain how this locomotion could evolve from our ape ancestry. Most researchers have recognized that the modern hominoids are all orthograde animals, capable of holding their bodies in an upright posture—potentially preadapting our ancestors to bipedalism. Early scholars embraced a hylobatid model for the origins of bipedalism (e.g., Keith 1923). Gibbons will occasionally locomote on two legs and are highly upright in an arboreal context. Keith (see KEITH, ARTHUR) (1923), and later on Morton (see MORTON, DUDLEY J.) (1926), hypothesized that an upright form of locomotion in an orthograde ape may have predisposed our lineage to bipedalism. As it became clear that

humans are most closely related to the African great apes and to chimpanzees in particular, Washburn (see WASHBURN, SHERWOOD L.) (1967) hypothesized that humans developed bipedalism from a chimpanzee-like ancestor and that we had passed through a knuckle-walking stage. This "ground-up" approach to bipedal origins, in which a knuckle walker evolves into a biped, contrasts with a "top-down" approach, in which upright walking evolves from an already upright, vertically climbing, arboreal ape. Tuttle (1981) challenged the idea that bipedalism evolved from a knuckle-walking ancestor and instead proposed that an arboreal climber was a more likely predecessor. Most recently, Thorpe, Holder, and Crompton (2007) found evidence for frequent bouts of hand-assisted bipedality in orangutans and proposed that upright walking may have emerged from a highly arboreal, orthograde animal that was bipedal in the trees. These models for the origins of bipedalism are ape-based (either generally, Morton 1926, or specifically, Washburn 1967) and stem from the fact that humans are orthograde hominoids. However, Straus (see STRAUS, WILLIAM L.) (1949) recognized decades ago that humans share many features with cercopithecoid monkeys. He interpreted these data to mean that humans represent a deep evolutionary lineage, separate from that of the apes. Yet the same data could also mean that the human form is more primitive and that the modern apes have become highly derived in the time since the Miocene radiation of hominoids. Most recently Lovejoy et al. (2009) have supported this interpretation in their analysis of *Ardipithecus*. While there is growing evidence that modern apes have evolved considerably since the last common ancestor, it still remains unclear what the body form of the last common ancestor may have been, and therefore from what locomotion bipedalism evolved. The paucity of fossils from the very period in which bipedalism was probably emerging (4–8 Ma) hampers efforts to test the hypotheses presented above. Furthermore, efforts to use modern primates as models for the origins of bipedalism are problematic if the body form from which bipedalism evolved turned out to be a generalized ape with no extant representation.

## Why did bipedalism evolve?

Just as it is still unclear precisely when bipedalism evolved and from what, *why* bipedal locomotion was selectively advantageous in the hominin lineage remains a mystery. Given the complete absence of another habitually bipedal mammal to serve as an analogue, testing origin stories is difficult, if not impossible (Cartmill 1990). Nevertheless, hypotheses as to why hominins evolved bipedal locomotion abound (see Rose 1991 for a full treatment, with bibliography). As we have seen, Darwin (1871) and scholars after him suggested that bipedal locomotion freed the hands for tool use. Others distanced the carrying hypothesis from tools and instead invoked the carrying of infants or of valuable food items—as is occasionally observed in chimpanzees. Food gathering, specifically by females, was proposed as a possible selective advantage for bipedalism (Tanner and Zihlman 1976), as was the freeing of the hands for picking seeds, as witnessed in modern baboons (Jolly 1970). Food carrying is also the foundation for Lovejoy's (1981) provisioning model, which posits that a bipedal male could carry more food to attract and provision a mate and that this would eventually lead to the evolution of an adaptive complex consisting of bipedalism, canine reduction, concealed ovulation, and pair-bonding. Food gathering is also the centerpiece of Kevin Hunt's "low-hanging fruit" hypothesis, which uses modern chimpanzee behavior to argue that bipedalism evolved initially as a postural adaptation for acquiring food.

While the use of modern chimpanzees as a model for understanding the origins of bipedalism has been criticized, it remains commonplace (see GREAT APES AS MODELS FOR HUMAN EVOLUTION). Bipedal locomotion occurs in chimpanzees during aggressive display bouts and may have been advantageous in hominins by freeing up their fists for fighting. There is a less aggressive variant of the vigilance hypothesis (nicknamed the "peek-a-boo" hypothesis), in which bipedalism evolved as a way for hominins to safely scan the grassy savannah for predators. An alternative but essentially untestable idea (the "trenchcoat" hypothesis) proposes that bipedalism evolved as a strategy for displaying one's

genitalia. Assuming that the first bipeds occupied an open grassland (savannah hypothesis), some have argued that bipedalism reduces the surface area of the body exposed to sunlight and therefore may have evolved as a thermoregulatory adaptation (Wheeler, 1991). This view has been challenged by proponents of the thesis that bipedalism first appeared in a wooded habitat (White et al. 2009). Data showing that a bipedal gait is energetically efficient (Sockol, Raichlen, and Pontzer 2007) lend support to the notion that this form of locomotion may have evolved in the context of patchy resources and widely spaced woodland environments. Moving from one grove of fruit trees to the next may have been energetically efficient on two legs rather than on four. One final hypothesis ("the aquatic ape") suggests that bipedalism evolved in hominins wading through shallow water. While this idea has been effectively dismantled, Richard Wrangham and a team of colleagues have repurposed the hypothesis into one of the "swamp ape," in order to position early bipedal hominins in a watery, sedge-rich habitat similar to today's Okavango Delta in Botswana.

It seems at times that there are as many hypotheses for why bipedalism evolved as there are researchers in our field. Why? Some of these hypotheses are untestable and cannot be properly refuted and relegated to the dustbin of science. Additionally, the absence of another habitually bipedal mammal hampers our ability to use comparative methods to test these hypotheses. It still remains unclear exactly *when* we took our first steps and *from what* body form this unusual form of locomotion arose. The current absence of these data makes it difficult to place origin hypotheses into sharper focus. Assuming that the last common ancestor of humans and chimpanzees included some bipedal posture and gait in its locomotor repertoire, it remains possible that bipedalism evolved more than once, and for different reasons. Furthermore, whether bipedalism evolved once or multiple times, it is unlikely that there was only *one* reason for it; hence many of the above hypotheses—and likely some yet to be conceived—may explain how and why bipedalism evolved, persisted, and flourished into the Pliocene.

## Bipedalism in *Australopithecus*

Regardless of the selective reasons for bipedalism, this became the dominant (though probably not the only) form of locomotion in Pliocene australopiths. As discussed earlier, convincing evidence for habitual bipedalism can be found in the 4.2-million-year-old *Australopithecus anamensis* tibia collected by a team led by Meave Leakey at Kanapoi, Kenya. Fossil footprints from Laetoli, Tanzania demonstrate that around 3.66 Ma a hominin was fully bipedal (Day and Wickens 1980). The great toe is in line with the other digits, there is an incipient arch, and there is also evidence for a prominent human-like heel strike in a hominin who likely walked with an extended hip and knee. However, others have suggested that the great toe is more divergent than originally proposed (Bennett et al. 2009). Furthermore, the G trackway was made by a hominin with an arch flatter than in most humans today and with less medial weight transfer to the great toe. Further experimental work on footprint formation, for example by Hatala, suggests that the individual who produced the G trackway walked with a more flexed posture than humans do today. Therefore, although the Laetoli footprints are superficially quite human-like, they record subtle differences in walking kinematics between the makers of the prints (presumably *Australopithecus afarensis*) and modern humans.

Considerable disagreement also surrounded the functional analysis of the *A. afarensis* fossil material from 3.0–3.4 Ma deposits at Hadar, Ethiopia, including the all-important Lucy skeleton (Johanson et al. 1982). Work done primarily by C. Owen Lovejoy and Bruce Latimer (e.g., Latimer and Lovejoy 1989) interpreted the Hadar lower limb and foot fossils as deriving from a hominin with a bipedal gait not unlike that found in humans today. The hip joint, while morphologically different from that found in modern humans, would have been functionally equivalent in preventing pelvic tilt during the single-legged stance phase (Lovejoy, 1988). The internal morphology of the femoral neck was consistent with this human-like role of the lesser gluteals during bipedal walking. The morphology of the knee and ankle demonstrate a human-like

geometry of the lower limb and evidence for a fully extended leg during walking. The large robust heel, the human-like great toe, and the dorsally domed metatarsal heads combined with dorsally canted phalanges were presented as evidence for a foot with a human-like push-off mechanism. These human-like, derived interpretations of the Hadar fossils were systematically published in response to initial interpretations of the Hadar material as more ape-like in form and in inferred function. Stern and Susman (1983) identified more primitive anatomies in the Hadar collection and interpreted them as evidence for a primitive bipedal gait, in which the hominins walked with a bent hip and bent knee. Stern and Susman (1983) noted that the *A. afarensis* pelvis may have been more ventrally positioned, as in modern apes; the femoral head was small; the legs were short; the knee, ankle, and great toe may have been more mobile; and the toes were longer and more curved. While many of these anatomies were consistent with arboreality, the researchers further argued that the Hadar material was inconsistent with a human-like bipedal gait in *A. afarensis*. The Stony Brook University interpretation of the Hadar material used the anatomy of the fossils to reconstruct the daily life of *Australopithecus* and provided strong evidence for an arboreal component to the locomotor repertoire of *A. afarensis*, which was practiced minimally to prevent predation at night. However, Latimer (1991) and others have argued that climbing would have been adaptively insignificant, since the vector of evolutionary change was in a direction that led away from arboreality. Ward (2002) summarized this argument clearly and explained how the seeming differences in the interpretation of the Hadar material are in part a result of researchers asking different questions of the fossils (e.g., daily life of *Australopithecus* versus anatomical targets of selection over time). Even granting this, the two research groups proposed conflicting interpretations of how *A. afarensis* walked. More recent work on the postcranial skeleton (e.g., Haile-Selassie et al. 2010) would support the interpretation that *A. afarensis* possessed a broadly human-like gait; however, there were likely subtle differences in hip and knee kinematics, weight transfer across the foot, and the push-off mechanism in *A. afarensis* (Fernández

et al. 2016). These data point to a bipedal gait in *A. afarensis* that would have been recognizably more human-like than ape-like, but likely outside the range of modern human walking mechanics.

However, new fossil discoveries from Ethiopia have shown that *Australopithecus afarensis* was not the only biped at this time. Haile-Selassie et al. (2012) described a 3.4 million-year-old foot from Burtele that was morphologically more like that of *Ardipithecus* than like that of *A. afarensis*. The Burtele foot has not found a taxonomic home, though there is craniodental evidence for another hominin—*A. deyerimeda*—in the area, and for yet another—*Kenyanthropus platyops*—in Kenya at this time. While the Burtele foot possessed domed lateral metatarsal heads and canted phalanges (consistent with a form of bipedalism), the great toe was divergent and the metatarsal bases were weakly developed, as found in apes (specifically in modern gorillas). Thus this important fossil convincingly demonstrates diversity in bipedal walking during the Pliocene. The South African hominin "Little Foot" (StW 573), which may represent *Australopithecus prometheus*, was originally proposed to also possess an abducent hallux (Clarke and Tobias 1995), but subsequent analysis has revealed that the great toe is in line with the other digits. The ankle, however, appears more primitive that that found in *A. afarensis* (Harcourt-Smith and Aiello, 2004) and "Little Foot" may very well provide additional evidence for bipedal variation in the Pliocene. However, this hypothesis remains on hold until a full description of the StW 573 skeleton is published.

Bipedal diversity likely continued into the early Pleistocene as well. Primarily on the basis of pelvic and femoral remains from Sterkfontein and Swartkrans, South Africa, Robinson (see ROBINSON, JOHN TALBOT) (1972) hypothesized that *Australopithecus africanus* and *Paranthropus robustus* locomoted in a different manner, the former being more human-like. Harcourt-Smith and Aiello (2004) made a similar argument on the basis of differences in foot morphology in *A. afarensis*, *A. africanus*, and *Homo habilis*. These authors proposed that *A. afarensis* possessed a human-like ankle in combination with a more ape-like forefoot, while *A. africanus* had a more human-like forefoot but a primitive tarsus. The

late South African australopith *A. sediba* also possesses a mosaic of foot morphology unlike that found in other Plio-Pleistocene hominins (Zipfel et al. 2011), which suggests a distinct, perhaps autapomorphic, hyperpronatory form of bipedal locomotion (DeSilva et al. 2013). These variations on an australopith *Bauplan* are likely due to differences in local ecologies, substrates, and degrees of reliance on other forms of locomotion, such as climbing.

While most regard the foot of the 1.85-million-year-old OH 8 (Olduvai Hominid 8, accepted by many as *H. habilis*) as evidence for a human-like form of bipedal locomotion (Day and Napier 1964), there is some evidence that early *Homo* was not fully modern in its locomotor mechanics (Ruff 2009; Pontzer et al. 2010), and there is growing evidence for locomotor diversity in our genus as well. These data derive from an early Pleistocene *Homo* femur and pelvis from Kenya (Ward et al. 2015); unique anatomy in the South African hominin *Homo naledi* (Harcourt-Smith et al. 2015); and anatomies of the late Pleistocene island species *Homo floresiensis* (Jungers et al. 2009) that would be consistent with a distinct form of bipedal locomotion (see HOMO).

General consensus has emerged that bipedal locomotion kinematically indistinct from that found in modern humans first evolved in *Homo erectus* (or African *Homo ergaster*). This evidence derives from footprint data (e.g., Bennett et al. 2009) and from skeletal morphology primarily discerned from a single, nearly complete juvenile skeleton from Nariokotome, Kenya (KNM-WT 15000). However, it must be noted that the postcranial anatomy of *Homo erectus* still differs from that of modern humans in subtle ways (e.g., more flared ilia; platymeric femora; dorsoplantarly squat talus). How these differences impacted gait mechanics or energetic efficiency remains unknown. Furthermore, while the postcranial anatomy of Middle Pleistocene hominins is predominantly human-like, subtle anatomical differences have also been noted, for instance, in the Sima de los Huesos hominins from Atapuerca, in the 250,000-year-old Jinnuishan skeleton from China, and even in Neanderthals. These differences are not generally attributed to unique gait mechanics but to more strenuous activity patterns, which often require more mediolateral motion on more varied substrates. Footprints and skeletal morphology of late Pleistocene humans are consistent with modern human gait mechanics. However, changes in activity patterns related to a more sedentary lifestyle at the boundary between Pleistocene and Holocene has resulted in a more delicate skeleton, which consists of less dense trabecular networks in our joints (Chirchir et al. 2015).

## Costs of bipedalism

Bipedalism was obviously a selectively beneficial form of locomotion for our ancestors and extinct relatives—otherwise it would not have evolved. However, there is no such thing as an evolutionary "free lunch", and there are significant costs to bipedalism. Changes to the pelvis associated with the evolution of bipedalism reduces the size of the birth canal and renders childbirth in humans more difficult than in apes (e.g., Krogman 1951). While this "obstetrical dilemma" (Washburn 1960) predicts locomotor costs to women who have not been supported by recent evidence (Warrener et al. 2015), high cephalopelvic ratios and therefore long, difficult labors may have existed since the Pliocene and are likely a consequence of bipedalism.

There are also other costs to bipedalism. Humans cannot gallop, and therefore our maximum speed is quite slow by comparison with that of quadrupeds. Even the fastest human on earth (Usain Bolt: 44.7 km/h) is considerably slower than the African mammals our hominin ancestors may have wanted to catch—the wildebeest—or to avoid—the lion (both clocked at ~80.5 km/h, almost twice the speed of the fastest human). By evolving bipedalism, humans therefore sacrificed speed. Additionally, we sacrificed stability, given that with each stride we are positioned on a single support.

Bipedalism also causes musculoskeletal problems. Our vertical spine is subject to high compressive forces that can exacerbate already uneven mediolateral loads during development and may lead to scoliosis—a condition not uncommon in humans but exceptionally rare in other mammals (Latimer 2005). Furthermore, the vertebral column has several curves in the sagittal plane. In humans, compressive forces at the apex

of these curves result in a high frequency of compression fractures and, in the lumbar region, in a high frequency of spondylolysis. Bipedal locomotion also takes its toll on the human foot, through injuries ranging from collapsed arches to ankle sprains (e.g., the anterior talofibular ligament is the most frequently sprained ligament in the body). These injuries in humans are not solely the result of a modern lifestyle. Both KSD-VP-1/1, a large male *Australopithecus*, and KNM-ER 2596, a small hominin from Koobi Fora, possess skeletal evidence for healed ankle fractures. OH 35 has a healed high-ankle sprain. OH 8 has osteoarthritis along the lateral forefoot and the cotylar fossa. Furthermore, Lucy preserves evidence for a spinal pathology. Thus it appears that the musculoskeletal costs of bipedal locomotion have been with us for some time. Despite these costs, bipedalism was selectively advantageous and became the dominant form of locomotion for the hominin clade sometime after its divergence from the panin lineage.

SEE ALSO: Biomechanics/mechanobiology; East African fossil record; Functional morphology, postcranial, human; Hadar; *Homo*, early; Leakey, Mary; Malapa; Postcranial morphology, nontraditional analysis; Schultz, Adolph H.; South African fossil record; Terrestrial locomotion; Turkana Basin

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