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REVIEW

Rethinking the evolution of the human foot: insights from experimental research

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ABSTRACT

Adaptive explanations for modern human foot anatomy have long fascinated evolutionary biologists because of the dramatic differences between our feet and those of our closest living relatives, the great apes. Morphological features, including hallucal opposability, toe length and the longitudinal arch, have traditionally been used to dichotomize human and great ape feet as being adapted for bipedal walking and arboreal locomotion, respectively. However, recent biomechanical models of human foot function and experimental investigations of great ape locomotion have undermined this simple dichotomy. Here, we review this research, focusing on the biomechanics of foot strike, push-off and elastic energy storage in the foot, and show that humans and great apes share some underappreciated, surprising similarities in foot function, such as use of plantigrady and ability to stiffen the midfoot. We also show that several unique features of the human foot, including a spring-like longitudinal arch and short toes, are likely adaptations to long distance running. We use this framework to interpret the fossil record and argue that the human foot passed through three evolutionary stages: first, a great ape-like foot adapted for arboreal locomotion but with some adaptations for bipedal walking; second, a foot adapted for effective bipedal walking but retaining some arboreal grasping adaptations; and third, a human-like foot adapted for enhanced economy during long-distance walking and running that had lost its prehensility. Based on this scenario, we suggest that selection for bipedal running played a major role in the loss of arboreal adaptations.

KEY WORDS: Human evolution, Foot biomechanics, Longitudinal arch, Primate locomotion, Running, Fossil hominin

Introduction

Human feet differ from those of other animals, including our closest living relatives, the great apes [in this article, we use the term ‘great apes’ to refer to the paraphyletic group including all extant members of the Family Hominidae other than humans (i.e. chimpanzees, bonobos, gorillas and orangutans)], in numerous features related to our unique form of bipedal locomotion. These include a large heel bone, short toes, an adducted and non-opposable hallux (see Glossary), and well-developed longitudinal and transverse arches (see Glossary; Fig. 1A). Most adaptive explanations for these features are based on observed differences in human and great ape foot function during locomotion. Humans use their feet as stiff levers during bipedal walking, whereas great ape feet appear to flex in the midfoot (see Glossary) region during push-off (see Glossary), presumably owing to their lack of arches and mobile midfoot joints for enhanced prehensility in arboreal locomotion (see Glossary; Fig. 1B) (DeSilva, 2010; Elftman and Manter, 1935a). Other studies have documented how great apes use their long toes, opposable halluces and mobile ankles for grasping arboreal supports (DeSilva, 2009; Holowka et al., 2017a; Morton, 1924). These observations underlie what has become a consensus model of human foot evolution: that selection for bipedal walking came at the expense of arboreal locomotor capabilities, resulting in a dichotomy between human and great ape foot anatomy and function. According to this way of thinking, anatomical features of the foot characteristic of great apes are assumed to represent adaptations for arboreal behavior, and those unique to humans are assumed to be related to bipedal walking.

This dichotomy has long guided reconstructions of fossil hominin (see Glossary) locomotion and, by extension, theories of the evolution of human bipedalism. All early hominin feet exhibit varying mosaics of human- and great ape-like features; consequently, early hominin locomotor behaviors are typically reconstructed as falling along a continuum between humans and great apes. Because of the assumed trade-off between arboreal and bipedal locomotion, species with great ape-like feet are inferred to be less effective bipeds, and species with more human-like feet are inferred to be less arboreal. This framework often leads to conflicting reconstructions of fossil hominin locomotion. For example, foot bones from the early hominin *Australopithecus afarensis* have been interpreted as indicating this species either retained climbing adaptations that compromised bipedal walking abilities (Harcourt-Smith and Aiello, 2004; Susman et al., 1984), or was a modern human-like biped no longer reliant on arboreal locomotion (Latimer and Lovejoy, 1989; Ward et al., 2011). This contradiction represents an all-too-common impasse in reconstructions of fossil hominin locomotion, in which the dominant interpretive framework is based on a human–great ape dichotomy, hindering interpretations of the evolution of complex and uniquely human features related to bipedalism.

One major problem with this dichotomy is the assumption that all features unique to the human foot are adaptations for bipedal walking, which neglects the possibility that the human foot could be adapted for non-walking behaviors such as running (Bramble and Lieberman, 2004). Further, it assumes that great ape feet are adapted primarily for arboreal locomotion, even though terrestrial quadrupedalism is an important component of locomotor behavior in all African apes (Doran, 1996), and non-locomotor behaviors such as fighting could also have been selected for (Carrier and Cunningham, 2017). A second problem is the argument from design, that anatomical structures in extant species with particular behaviors can be used to infer those same behaviors in fossils, even though many assumed structure–function relationships have little empirical support when tested (Lauder, 1995). Addressing these problems requires developing and testing biomechanical models of specific aspects of foot function. If a model can be empirically

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Glossary

Arboreal locomotion
Locomotor behaviors such as climbing that involve travel on branches, tree trunks and other vegetative structures.

Australopithecines
Fossil hominin species (see below) belonging to the genus *Australopithecus* that existed roughly 2–4 million years ago in Africa and preceded the genus *Homo*.

Cercopithecines
A taxonomic group including most Asian and African monkey species, including macaques and baboons. They are more closely related to humans and great apes than are South American monkey species.

Collisional energy loss
As weight support is transferred from one foot to the other during bipedal walking, the body's center of mass velocity is directed forward and downward, and then must be redirected forward and upward. Collisional energy loss describes the mechanical work that must be performed to redirect the body's center of mass velocity during this step-to-step transition.

Endurance running
Running in humans that is sustained for a long period of time at a moderate pace under aerobic metabolism.

Hallux
The first pedal ray, including the metatarsal and phalanges. In humans this is what is referred to as the 'big toe', and in non-human primates the hallux is opposable with the other pedal digits, like the thumb is with the fingers.

Hominins
Humans, and all fossil species that are more closely related to humans than chimpanzees.

Impact force
A spike in ground reaction force following initial foot contact caused by conservation of momentum as the limb is rapidly decelerated.

Intrinsic foot muscles
Muscles that originate and insert on bones of the foot, including abductor hallucis, flexor digitorum brevis and quadratus plantae.

Last common ancestor
Term used to describe the last common ancestor of chimpanzees and humans, the species from which the lineages leading to chimpanzees and humans emerged that existed roughly 6–9 million years ago. Commonly abbreviated as LCA.

Longitudinal arch
A raised region of the foot that is unique to humans, running longitudinally from the heel to the toes. It is defined by the bony conformation of the tarsal and metatarsal bones and maintained by ligaments and muscles. It is higher on the medial side of the foot than on the lateral side.

Metatarsophalangeal joints
The joints between the heads of the metatarsal bones and the proximal phalanges (toe bones).

Midfoot
The region of the foot distal to the heel and ankle including all the joints proximal to the metatarsophalangeal joints. In humans, the longitudinal arch spans the whole midfoot.

Midtarsal break
A phenomenon observed during terrestrial walking in great apes immediately following heel lift. As the heel is lifted from the ground, the foot flexes in the midfoot region such that part of the midfoot briefly maintains contact with the ground.

Plantar aponeurosis
A broad sheet of ligamentous connective tissue with distinctive lateral and central portions that attaches proximally to the plantar calcaneal tubers and distally to the bases of the proximal phalanges and the soft tissue structures under the metatarsal heads.

Plantigrady
A foot posture used during locomotion where the entire plantar surface of the foot including the heel contacts the ground.

Push-off
The period in the second half of stance phase of a walking or running step in humans beginning when the heel starts to rise off the ground and ending when the toes leave the ground.

Stance
Phase of gait when the foot is on the ground.

Transverse arch
A raised region of the foot in the segment's transverse plane, defined proximally by the conformation of the cuboid and cuneiform bones and distally by the metatarsals. It is present in humans, and argued to be present, but lower, in great apes, although this difference has not been quantified.

Windlass mechanism
In humans, dorsiflexion of the toes creates a moment about the metatarsophalangeal joints that is converted to linear force on the plantar aponeurosis. This increases tension on the plantar aponeurosis, and pulls the calcaneus towards the metatarsal heads, raising the longitudinal arch and stiffening the foot.

determined to behave *in vivo* as predicted, it can be applied more broadly to infer function from anatomy in living and fossil species. This model-based approach is particularly critical for testing hypotheses about the foot, given its fundamental role in locomotion and the differences between the feet of humans, great apes and other mammals. The basic mechanics of moving the center of mass during walking and running are similar across mammals of different body sizes (Cavagna et al., 1977), but whereas most mammals contact the ground with just their digits (digitigrady) or the tips of their toes (unguligrady), humans and great apes are plantigrade, bringing the whole foot down, including the heel (Fig. 1) (Hildebrand and Goslow, 2001; Schmitt and Larson, 1995). As recent experimental studies have shown, plantigrady (see Glossary) in general, and the human foot postures in particular, have important biomechanical implications at both foot strike and push-off during walking and running.

Here, we use a model-based interpretive framework to review the evolution of the human foot, focusing on three major kinematic and

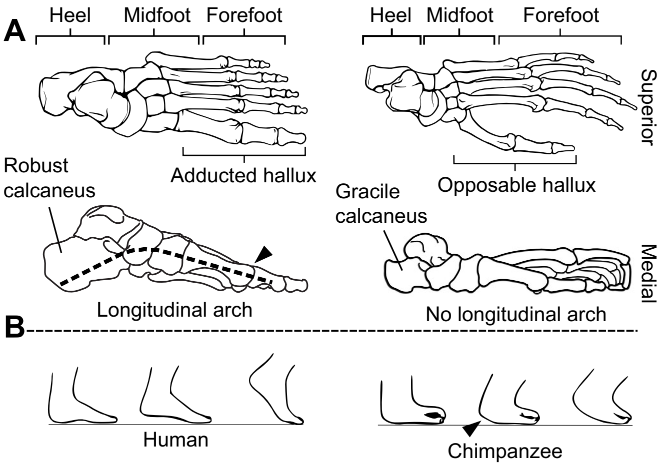


Fig. 1. Human and chimpanzee feet. (A) Human and chimpanzee foot skeletons, superior view (above) and medial view (below). Arrowhead indicates dorsal doming of metatarsal head, present in humans but not chimpanzees. (B) Gross kinematics of human and chimpanzee feet during push-off in bipedal walking. At midstance, the plantar surface of the foot is flat on the ground in both species. This posture is referred to as 'plantigrady'. Subsequently, the longitudinal arch helps convert the human foot into a stiff lever, allowing the heel and midfoot to be lifted off the ground simultaneously during push-off. In chimpanzees, the midfoot briefly maintains contact with the ground after heel lift owing to dorsiflexion at the mobile midfoot joints. This motion is called the 'midtarsal break' and is indicated by the arrowhead. Modified from Elftman and Manter (1935a).

kinetic challenges of walking and running: (1) how the foot copes with impact forces (see Glossary) when the lower extremity initially collides with the ground, (2) how the foot creates a propulsive lever for push-off and (3) how the foot stores and releases elastic energy during running. We use this Review to interpret new data from experimental studies of great ape foot biomechanics, then apply these insights to the hominin fossil record to evaluate the selective forces that shaped human foot anatomy, and more broadly the evolution of bipedalism. Because we focus on the foot, we do not directly cover the ankle (talocrural and subtalar joints), but we refer readers to Pontzer et al. (2014), O'Neill et al. (2015) and Zelik and Adamczyk (2016) for overviews of comparative ankle biomechanics in humans and great apes. Additionally, we restrict our review to studies of terrestrial locomotion, but recommend Cartmill (1985), Richmond (2007), DeSilva (2009), Venkataraman et al. (2013), Holowka et al. (2017a) and Wunderlich and Ischinger (2017) for discussions of primate foot biomechanics and pedal grasping during arboreal locomotion. Finally, we acknowledge the role of the foot in behaviors other than steady-state locomotion that may have major consequences for fitness, such as fighting, maneuvering and accelerating. These behaviors have received less attention in foot biomechanics studies, but are nevertheless important to consider in understanding the evolution of the foot, and we therefore refer readers to discussions in Reeser et al. (1983), Carrier et al. (1994) and Carrier and Cunningham (2017).

Foot strike and collision

One quintessential characteristic of human bipedal walking is foot strike, in which the heel contacts the ground before the rest of the foot. Great apes also frequently heel strike during bipedal and quadrupedal walking (Elftman and Manter, 1935a; Schmitt and Larson, 1995), although they sometimes touch down with the heel and lateral side of the foot simultaneously (Vereecke et al., 2003). Several derived aspects of human calcaneus morphology are proposed adaptations to bipedal heel striking, including a robust calcaneal tuber and a lateral plantar process (Fig. 1A). Because great ape calcanei, which lack a lateral plantar process, are considered too gracile to withstand the loads encountered during bipedalism (Latimer and Lovejoy, 1989), calcaneal morphology has been used to reconstruct fossil hominin locomotion (e.g. DeSilva et al., 2013). However, comparative studies have not clearly articulated or tested whether a gracile calcaneus hampers bipedal performance, nor have they argued why a heel strike is advantageous in human-like walking.

It is well known that walking and running bipedally with a heel strike entails a temporary, rapid increase in vertical ground reaction force at the beginning of stance (see Glossary), called an impact force (Fig. 2A,C). These impact forces have been implicated in tissue damage leading to joint degenerative disease and other musculoskeletal injuries (Whittle, 1999), although the biomechanical factors determining these forces and how they are transmitted through the body is not fully understood. Recently, several studies have developed and tested a biomechanical model of foot strike in humans that demonstrates that impact forces occur when some portion of the lower extremity, the effective mass, decelerates abruptly, requiring rapid dissipation of mechanical energy (Chi and Schmitt, 2005; Lieberman et al., 2010). According to this model, the impact peak is a function of foot velocity at impact, ankle and knee joint compliance, and the duration of deceleration, itself dependent on compression of a thick, fibrous fat pad below the calcaneal tuber (Gefen et al., 2001). This heel pad dissipates 17–45% of the energy returned from the ground at impact in humans (Gefen et al., 2001; Pain and Challis, 2001). Great apes often produce impact forces when walking bipedally (Fig. 2B) (Crompton et al., 2008; Pontzer et al., 2014), but also possess thick heel pads that presumably dissipate some energy at foot strike (Raven, 1936; Vereecke et al., 2003). In addition, based on the above-described model, great apes should be capable of mitigating impact forces during bipedal walking by reducing velocity of the foot prior to touchdown and landing with more compliant joint postures. In particular, by using greater knee flexion angles, great apes could potentially reduce the effective mass of the limb that decelerates at foot strike.

Recently, Webber and Raichlen (2016) demonstrated that humans can reduce or avoid impact forces during walking by first contacting the ground with the forefoot. Additionally, by using digitigrade postures during walking humans could increase the length of the lower limb from hip to point of ground contact, which would theoretically increase the distance traveled per stride. Why

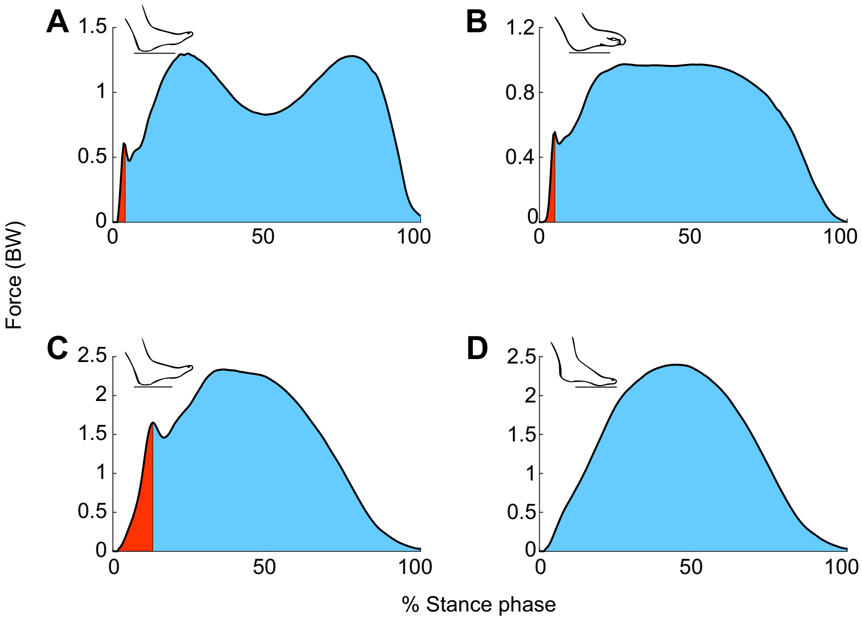


Fig. 2. Vertical ground reaction forces during stance phase in bipedal locomotion. Red indicates impact force. Force is in units of body weight (BW). Both humans (A) and chimpanzees (B) produce an impact peak following foot strike during bipedal walking. Humans produce a high impact peak force when running with a heel strike (C), but typically do not produce an impact peak force when running with a forefoot strike (D). Foot images modified from Elftman and Manter (1935a).

then do humans walk with heel strikes and plantigrade postures? One potential reason is provided by the collisional model of center of mass support: at heel strike, the body's center of mass is moving forward and downward, but must be redirected forward and upward. The amount of negative work the leading limb must perform to effect this change, called 'collisional energy loss' (see Glossary), is proportional to the square of the angle between the limbs at foot strike (Donelan et al., 2002). By landing on the back of the foot (the heel) with the leading limb and pushing-off from the front of the foot (the toes) with the trailing limb, humans dramatically reduce this angle and, therefore, the cost of walking (Adamczyk and Kuo, 2013). Indeed, Cunningham et al. (2010) found that humans must perform more work to overcome collisional losses when walking with digitigrade rather than plantigrade postures. Furthermore, they found that plantigrady reduces the external joint moments the ankle muscles must resist when compared with digitigrady. This strategy distinguishes humans from other terrestrial bipeds (Usherwood et al., 2012), and may partly account for the relatively low metabolic cost of walking in humans (Biewener et al., 2004; Cunningham et al., 2010). Additionally, Webber and Raichlen (2016) demonstrated that use of a heel strike at the beginning of stance during plantigrade walking allows the center of pressure to roll forward under the foot during stance phase, effectively increasing stride length and improving human walking economy.

Because great apes use plantigrade foot postures, we hypothesize that they also benefit from the advantages described above during bipedalism. However, because great apes use a variety of foot strike postures (Schmitt and Larson, 1995; Vereecke et al., 2003), we would predict that they have the longest effective stride lengths and lowest collisional costs when landing with a heel strike. Whether great ape heel strikes generate higher impact forces than other foot strike postures, as in humans (Webber and Raichlen, 2016), remains to be tested.

Although heel striking is energetically favorable for bipedal walking, during human running it causes impact forces and loading rates roughly two to four times greater than those experienced during walking when barefoot (Fig. 2C) (Chi and Schmitt, 2005; Lieberman et al., 2010). To avoid these painful and potentially damaging forces, barefoot humans tend to forefoot or midfoot strike when running (Fig. 2D). Unlike walking, running is a mass-spring gait in which there are no periods of double-limb contact, removing any energetic advantage to using a heel strike (Cunningham et al., 2010; Perl et al., 2012). Forefoot and midfoot strikes involve landing with a more plantarflexed ankle than heel strikes, enabling controlled ankle dorsiflexion that allows individuals to avoid impact peaks in three ways: by reducing the effective mass of the limb that rapidly decelerates, by increasing lower extremity compliance and by converting the translational energy generated at impact into rotational energy at the ankle (Lieberman et al., 2010). Thus, humans appear capable of mitigating the high impact forces associated with bipedal running through kinematic adjustments, rather than by relying on anatomical adaptations.

Push-off and propulsion

As plantigrade bipeds, humans use the foot to generate considerable positive power at the ankle in the second half of stance phase in both walking and running (Farris and Sawicki, 2012). Effective propulsion requires stiffening the midfoot joints, which are the joints between the calcaneus and metatarsals (Fig. 1A), in the face of high external moments. For decades, the consensus has been that midfoot stiffness is enabled by the longitudinal arch (see Glossary), a uniquely human feature (Fig. 1). The longitudinal arch is defined by the bones of the midfoot, which are held in place by ligaments, muscles, and most superficially, the plantar aponeurosis (see Glossary), a broad sheet of ligamentous connective tissue. This complex structure attaches proximally to the calcaneal tuber and distally to the bases of the proximal phalanges, as well as the soft tissue structures under the metatarsal heads. Because of this distal attachment, dorsiflexion moments at the metatarsophalangeal joints (see Glossary) are converted into linear force that tenses the plantar aponeurosis, actuating the 'windlass mechanism' (see Glossary) of the foot (Fig. 3A,B) (Hicks, 1954). This tension pulls the calcaneus towards the metatarsal heads, effectively raising the longitudinal arch and stiffening the midfoot during push-off. In their seminal study of bipedal walking in chimpanzees, Elftman and Manter (1935a) observed that, unlike in humans, the chimpanzee midfoot briefly maintains contact with the ground following heel lift – a 'midtarsal break' (see Glossary) subsequently observed in other great apes (Fig. 1B) (D'Août et al., 2002; DeSilva, 2010). Most researchers assumed the absence of a midtarsal break in humans is due to passive stiffening of the longitudinal arch via the windlass

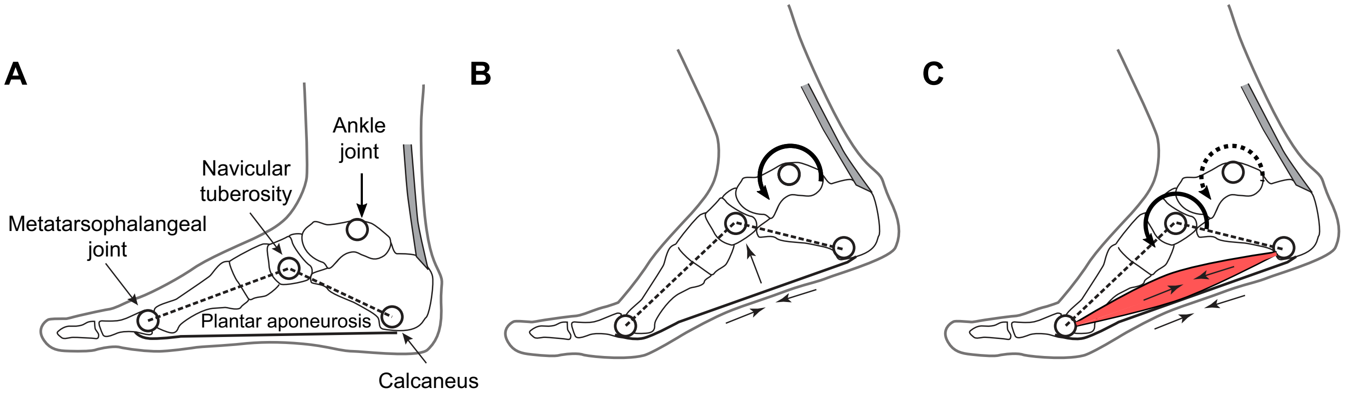


Fig. 3. The windlass mechanism of the human foot. (A) The plantar aponeurosis attaches proximally to the calcaneus, and distally to the proximal phalanges, and the navicular tuberosity indicates the height of the longitudinal arch. (B) During push-off, the metatarsophalangeal joints dorsiflex, and the plantar aponeurosis wraps around the heads of the metatarsals, creating tension that exerts a linear force that pulls the calcaneus forward and effectively raises the longitudinal arch. This makes the foot a stiff lever for effective power transmission from the ankle joint. (C) Recent studies indicate that intrinsic foot muscles (in red in diagram) augment the windlass mechanism by actively stiffening the midfoot. These mechanisms enable the midfoot joints to generate power that contributes to the push-off power produced at the ankle.

mechanism, and that great apes are therefore unable to stiffen the midfoot during walking (Bojsen-Møller, 1979).

The windlass model of human foot function has recently been refined to include the contribution of the intrinsic foot muscles (see Glossary) (Fig. 3C). Many of these muscles attach proximally to the plantar surface of the calcaneus and distally to the toes, and thus should be capable of resisting compression of the longitudinal arch when contracted, similar to the resistance provided by the plantar aponeurosis when the toes are dorsiflexed (McKeon et al., 2014). In line with this expectation, Kelly and colleagues found that several intrinsic foot muscles plantarflex the midfoot joints when electrically stimulated during sitting and contract isometrically following heel lift during walking (Kelly et al., 2014, 2015). These findings suggest that foot stiffness is augmented by activation of intrinsic foot muscles, which help to oppose high dorsiflexion moments at the midfoot joints during push-off.

This insight helps explain two recent, surprising discoveries from experimental studies of great ape locomotion. First, Bates et al. (2013) measured plantar pressure distributions during bipedal walking in humans, bonobos and an orangutan, and found that some of the great ape steps overlapped with some of the human steps in the magnitude of pressure peaks thought to be indicative of midfoot compliance (see also DeSilva et al., 2015). Second, using three-dimensional (3-D) kinematics, Holowka et al. (2017b) found only small (but significant) differences between humans and two chimpanzees in the total amount of midfoot dorsiflexion during the single-limb support period of bipedal walking when the heel is being lifted (Fig. 4). These findings suggest that great apes can stiffen their midfoot joints during bipedal walking even without a longitudinal arch, undermining a major assumption of the dichotomy between human and great ape foot function. Based on the amended windlass model, the most likely mechanism behind this stiffening is activation of the foot muscles, whose attachments and sizes are generally similar in great apes and humans (Oishi et al., 2018). Although *in vivo* electromyography data are currently lacking, we predict that intrinsic foot muscle activity is closely correlated with foot stiffness during walking in great apes. If so, then great apes can transform the foot into a moderately stiff lever during terrestrial locomotion, as well as maintain mobile midfoot joints for arboreal support grasping (Holowka et al., 2017a). Nevertheless, great apes do not appear to be able to stiffen their feet as much as humans during bipedal walking (Bates et al., 2013; Holowka et al., 2017b), potentially limiting the power that their muscles can deliver to the ground during push-off, although this remains to be measured.

A second amendment to the windlass model follows from the recognition of sites of significant positive and negative work within the foot. Following heel lift, the center of pressure moves anteriorly under the foot, creating high dorsiflexion moments at the metatarsophalangeal joints which must be resisted by the digital flexor muscles (Rolian et al., 2009) (Fig. 5A). The magnitude of these moments should be correlated with toe length, which approximates the distance of the center of pressure from these joints at push-off and, by extension, the load arm of the ground reaction force acting upon them. In a study of human subjects, Rolian et al. (2009) found that toe length has no appreciable effect on the estimated muscle force required to resist metatarsophalangeal joint moments during walking, but does have a significant effect on estimated muscle forces during running, as running entails much higher ground reaction forces on a single limb during push-off. Great apes possess longer toes than humans (Schultz, 1963), and therefore we hypothesize that they need to produce even greater digital flexor forces during bipedalism. However, chimpanzees and bonobos walk with lower peak metatarsophalangeal joint dorsiflexion angles at the end of stance than humans (Fernández et al., 2016; Griffin et al., 2010). Accordingly, humans possess dorsally oriented articular surfaces on their metatarsal heads (‘dorsal doming’; Fig. 1A), reflecting the capacities of their metatarsophalangeal joints to withstand high compressive loads in the highly dorsiflexed postures used during bipedal push-off (Susman et al., 1984). Great apes, by contrast, exhibit plantarly oriented metatarsal heads, which are thought to be better suited to the joint postures used when grasping arboreal supports.

New models of human walking acknowledge the metatarsophalangeal joints as potentially important sites of work within the foot (Zelik et al., 2015), but recent findings suggest that the windlass model of human foot function should be amended to accommodate positive work at the midfoot joints (Fig. 3C). Multi-segment kinematic models of the human foot show

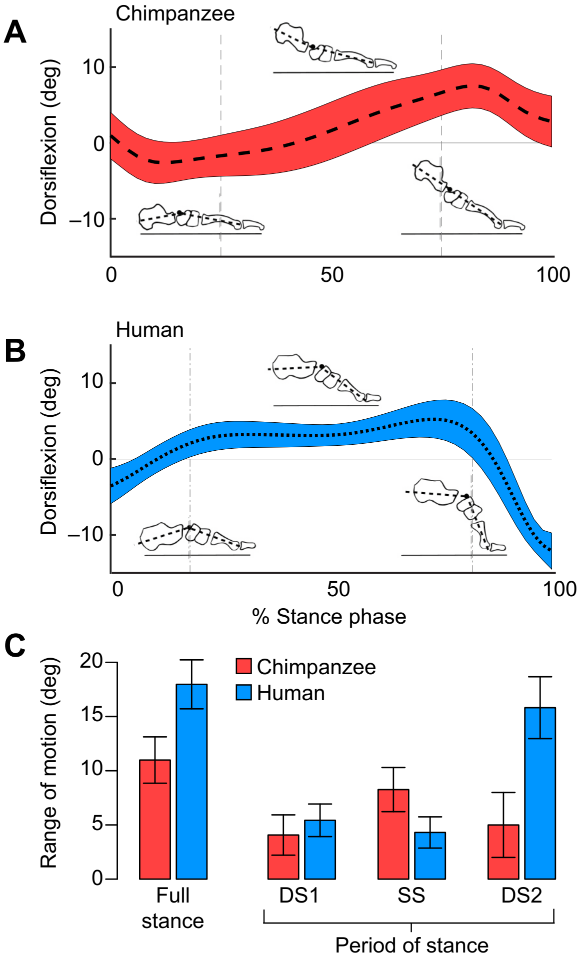


Fig. 4. Midfoot motion in humans and chimpanzees during bipedal walking. Total sagittal plane motion for the midfoot joints between the calcaneus and metatarsals during stance phase in (A) chimpanzees and (B) humans. Dorsiflexion angles are positive and plantarflexion angles are negative. Vertical dashed lines indicate the beginning and end of single-limb support. (C) Average ranges of motion over full stance, first double-limb support (DS1), single-limb support (SS) and second double-limb support (DS2). Note that chimpanzees used slightly but significantly less motion during SS, which is consistent with a slightly less stiff foot during push-off. However, humans used significantly more plantarflexion during DS2 and total motion overall, suggesting a more mobile midfoot during bipedal walking than in chimpanzees. Modified from Holowka et al. (2017b).

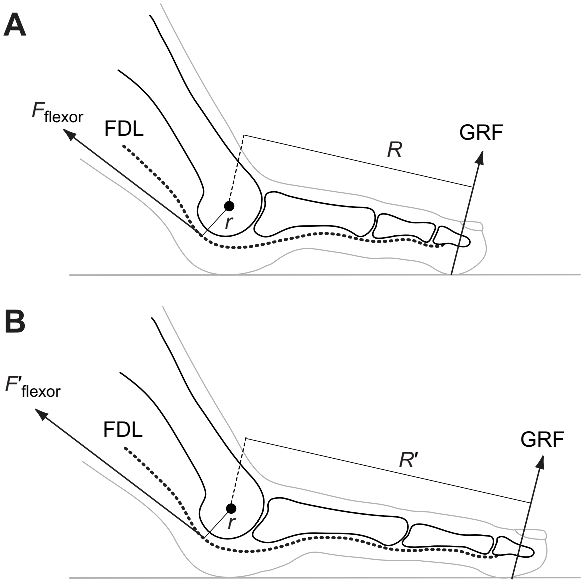


Fig. 5. Effect of toe length on flexor force requirement during bipedal locomotion. During push-off, an external moment is generated around the metatarsophalangeal joints as the product of the ground reaction force (GRF) and its moment arm to the joint (*R*). In a typical human foot (A), this moment is countered by force (F_{flexor}) from the flexor digitorum longus (FDL), whose moment arm (*r*) is very small. In an early hominin foot with longer phalanges (B), but with a similar metatarsal head radius (*r*), this moment is increased (*R*′), requiring more force (F'_{flexor}) from the FDL. Modified from Rolian et al. (2009).

considerable midfoot plantarflexion that coincides with metatarsophalangeal joint dorsiflexion during push-off (e.g. Takahashi et al., 2017). According to inverse dynamics estimates, the power generated at the midfoot joints more than offsets energy loss at the metatarsophalangeal joints and coincides with the spike in ankle power at the end of stance, contributing to the net positive work produced by the foot during push-off (Takahashi et al., 2017; Zelik and Honert, 2018). Holowka et al. (2017b) found that chimpanzees use significantly less midfoot plantarflexion than humans at the end of stance (Fig. 4), suggesting less ability to generate power during push-off. Furthermore, the amount of midfoot motion used by humans during push-off is even greater than that exhibited by chimpanzees during the midtarsal break, which counters the notion that humans walk with more rigid feet than great apes, and highlights the dynamic mobility of the human foot during propulsion. These findings demonstrate that gross observations of midfoot motion during walking do not accurately characterize differences in intrinsic foot kinematics between humans and great apes, and reveal the need for more experimental data on midfoot joint kinetics. However, based on the studies summarized above, we hypothesize that humans produce more intrinsic foot power during push-off in bipedal locomotion than great apes.

All the models reviewed thus far have assumed that the primary structure responsible for stiffening the foot is the longitudinal arch, making this structure the dominant focus of comparative hominoid foot biomechanics for decades. However, Venkadesan and colleagues have recently proposed that the transverse arch also plays a vital role in stiffening the human foot (Venkadesan et al., 2017 preprint; Yawar et al., 2017 preprint). The transverse arch is defined by the conformation of the cuboid and cuneiform bones, the metatarsal bases and torsion of the metatarsal shafts (Fig. 6). In their model, Venkadesan and colleagues analogize these bones to a thin plate loosely curled at one end in the transverse plane, like a folded dollar bill, and geometrically demonstrate that this shape provides significant resistance to sagittal plane bending. They argue that this shape is maintained in humans by the tibialis posterior muscle proximally, and by the transverse metatarsal ligament distally, and assert that the transverse arch provides the majority of the human foot's passive stiffness. In support of this notion, they show that human feet are roughly two times stiffer than those of monkeys, even after accounting for the stiffness provided by the plantar aponeurosis (Bennett et al., 1989). Great apes also display transverse arching of their tarsal bones and metatarsal bases (Drapeau and Harmon, 2013), which may in part account for some of their foot stiffness during bipedal walking (Bates et al., 2013; Holowka et al., 2017b). However, because of the mobile halluces of great apes, their transverse metatarsal ligaments do not tightly bind the first pedal ray to the lateral rays as in humans (Raven, 1936), likely limiting stiffness provided by the transverse arch.

Elastic energy storage and release

Although traditional comparisons of human and great ape foot anatomy advanced the idea that the human foot evolved a stiffening mechanism for bipedal walking (Elftman and Manter, 1935b), Ker et al. (1987) transformed our understanding of foot biomechanics by showing that the longitudinal arch functions like an energy-saving spring during running. The running body can be modeled as a spring-loaded inverted pendulum, with the body's center of mass falling in the first half of stance phase, stretching tendons in the lower extremity that store potential energy as the joints are flexed. In the second half of stance, these tendons recoil as the limb is extended, helping propel the center of mass upwards and forwards while also saving mechanical energy. Because humans walk and run with plantigrade postures, the tendons crossing the foot joints are not situated to store and release energy as in other animals (Alexander, 1991). However, compression of the longitudinal arch under loading provides a unique mechanism for elastic energy savings by stretching elastic structures in the foot, which subsequently recoil during push-off. Ker et al. (1987) first tested this spring model by mounting cadaveric human feet in an apparatus that cyclically loaded the longitudinal arch in three-point bending using forces similar to those experienced when running at 4.5 m s^{-1} (Fig. 7). By quantifying motion of the longitudinal arch during these cycles they estimated that the energy saved by the foot is approximately 17% of the energy necessary to support body weight during stance phase of a running step.

Although this model was highly influential, it was not tested *in vivo* until Stearne et al. (2016) measured elastic energy storage in human feet during walking and running in minimal athletic shoes and athletic shoes with custom-fitted insoles designed to restrict longitudinal arch deformation. Based on a mechanical model derived from Ker et al. (1987), they predicted the amount of energy stored in the longitudinal arch in the 'normal' versus 'insole' shoe conditions and compared their predictions with the measured metabolic cost of transport. They found good agreement between datasets when subjects ran at 2.7 m s^{-1} on level ground, with the 'insole' shoe increasing energy expenditure by an average of 7% and 6% relative to the 'normal' shoe in the model predictions and metabolic cost measurements, respectively. These costs equate to the energy saved owing to deformation and recoil of the longitudinal arch in the 'normal' shoe condition. Although these savings are considerably below those predicted by Ker et al. (1987), that study simulated forces for running speeds that were 67% faster than those used in Stearne et al. (2016), and thus expected to yield greater energy savings. Finally, Stearne et al. (2016) found no difference in

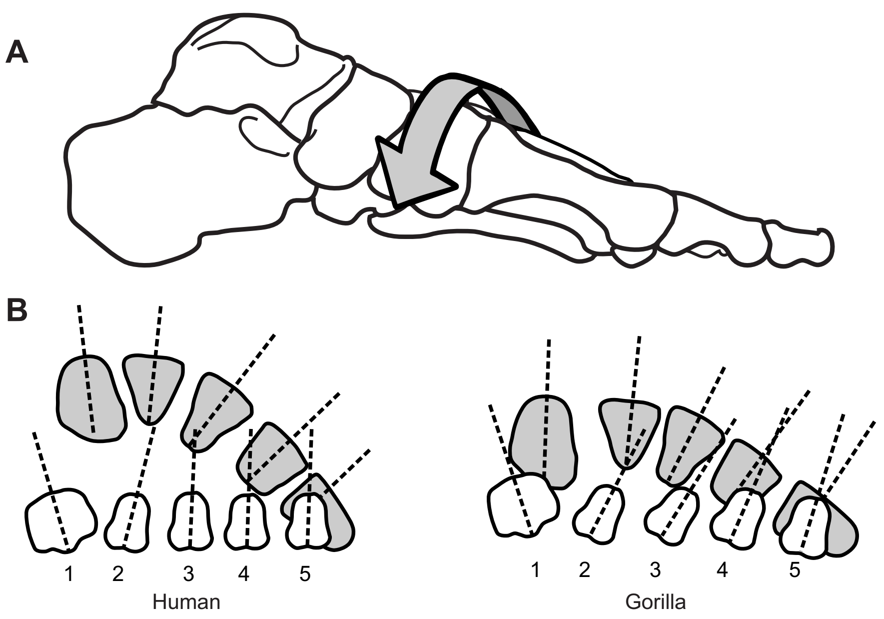


Fig. 6. The transverse arch of the foot. (A) The transverse arch in the human foot (medial view) is defined by the conformation of the cuboid, cuneiform bones and metatarsals, as indicated by the arrow. Foot skeleton modified from Elftman and Manter (1935a). (B) Schematic transverse plane view of metatarsal bases (gray) and heads (white) in humans and gorillas. Dashed lines indicate approximate orientations of heads and bases. Note the greater offsets in orientations of heads and bases in metatarsals 3–5 in humans, creating a more clearly defined transverse arch compared with that of gorillas. Modified from Morton (1922).

the metabolic costs of walking in the ‘normal’ and ‘insole’ conditions, indicating that the longitudinal arch does not function as a spring during walking.

Recently, McDonald et al. (2016) and Wager and Challis (2016) used 3-D musculoskeletal modeling to argue that the plantar aponeurosis is a major site of elastic energy storage during running. Furthermore, Kelly et al. (2015) found evidence that the intrinsic foot muscles also stretch actively to absorb energy in the first half of stance during running, potentially storing energy that could be released when they shorten in the second half of stance. Elastic energy storage potentially occurs in these muscles’ central tendons, the extracellular matrix surrounding their fibers and the titin molecules of their myofilaments (Roberts, 2016). Regardless of which tissues in the foot act as springs, elastic energy storage in the foot is contingent on the presence of a longitudinal arch, and we therefore hypothesize that great ape feet cannot save significant energy during running.

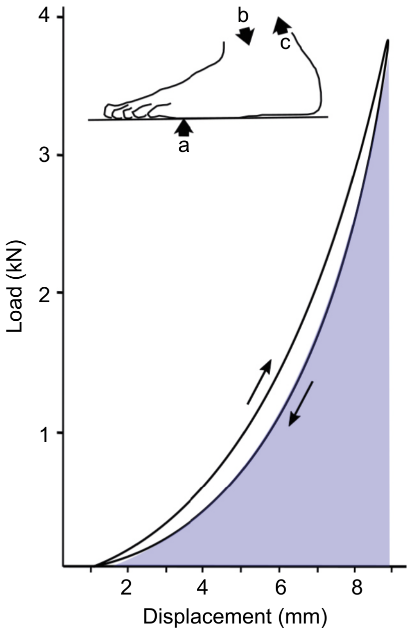


Fig. 7. Elastic energy storage and release in the human foot. Force–displacement curve modified from Ker et al. (1987) for a cadaveric foot under a simulated load at midstance for a 70 kg person running at 4.5 m s^{-1}. A load was applied to the base of the foot using an actuator to simulate ground reaction force (a) and triceps surae force (b), resulting in the total compressive force on the arch (c). Arch displacement was measured as the displacement of the actuator. As force is applied, the arch deforms (upward arrows) and then recoils (downward arrows), losing some energy (area between the curves), but returning most energy (shaded blue region under the curve).

The evolution of the human foot

The studies reviewed thus far undermine the notion that great ape feet are adapted primarily for climbing and human feet are adapted only for bipedal walking. Previous studies have used this dichotomy to reconstruct the locomotion of fossil hominins that display a mosaic of foot features as walking with a form of bipedalism somewhere along a continuum of human-like to great-ape-like, or walking with human-like bipedalism but mostly abandoning arboreal behavior. Based on the models reviewed here, we instead propose a three-stage scenario of human foot evolution following the divergence of hominins from the last common ancestor (LCA; see Glossary) of chimpanzees and humans (Fig. 8). (1) First, a generally great ape-like foot with some adaptations for greater bipedal walking economy but no major trade-offs with pedal grasping abilities, as represented by fossils attributed to *Ardipithecus ramidus*. (2) Second, a foot with adaptations for heel strike plantigrady and enhanced midfoot stiffening during bipedal walking, but that would have retained some pedal grasping adaptations, as represented by fossils and footprints attributed to *Australopithecus afarensis*. (3) Third, a foot that had surrendered most of its prehensility in favor of adaptations for elastic-energy-storing capabilities and other features helpful for long-distance walking and running, as represented by fossils and footprints attributed to early members of the genus *Homo*.

Stage 1: *Ardipithecus ramidus*

The earliest likely fossil hominin for which extensive pedal remains have been recovered is *A. ramidus*, from the Middle Awash region of Ethiopia (Fig. 8A) (Lovejoy et al., 2009). These fossils are dated to 4.4 million years old, some 2–5 million years after the LCA (Moorjani et al., 2016). Unfortunately, no footprints associated with

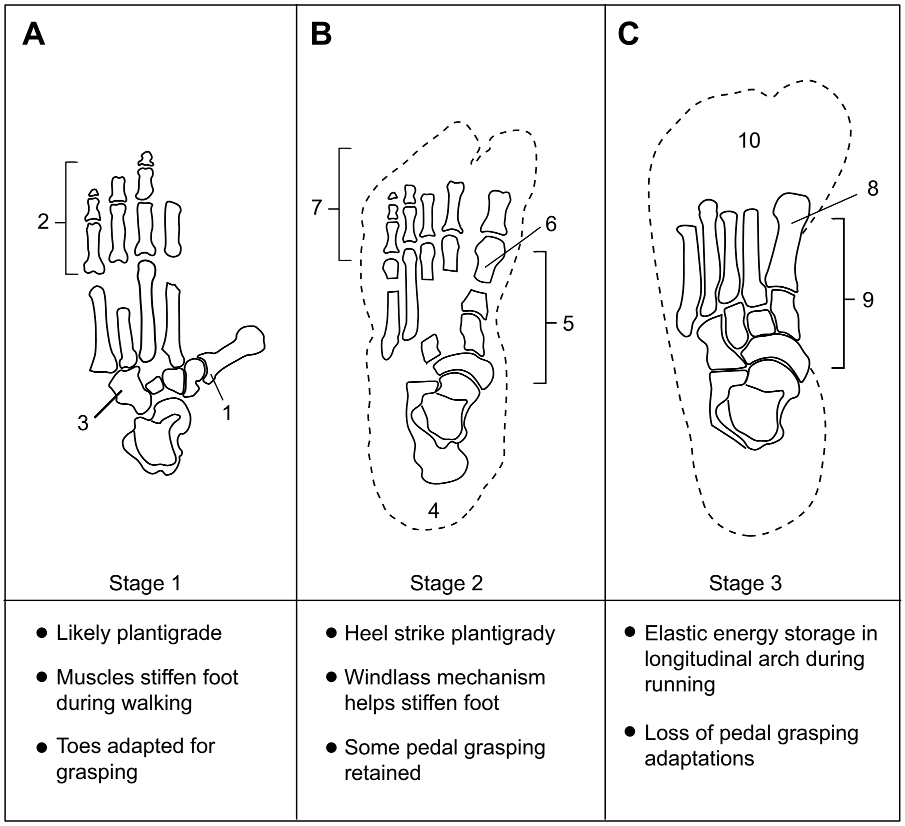


Fig. 8. Three-stage scenario of evolution of the human foot. (A) Stage 1 is represented by *Ardipithecus ramidus* fossils (Lovejoy et al., 2009), and is characterized by retention of a widely abducent and opposable hallux (1) and long toes (2), but elongation of the midfoot (3). (B) Stage 2 is represented by *Australopithecus afarensis* fossils (Latimer et al., 1982; Ward et al., 2011) and the Laetoli footprints (dashed outline; Leakey and Hay, 1979), and is characterized by heel strike plantigrady (4) and a low longitudinal arch (5), but retention of slight hallucal abduction (6) and long toes (7). (C) Stage 3 is represented by *Homo habilis* and *Homo erectus* fossils (Day and Napier, 1964; Pontzer et al., 2010), as well as the Ileret footprints (dashed outline; Bennett et al., 2009), and is characterized by a fully adducted hallux (8), a human-like longitudinal arch (9) and apparently short toes based on footprint evidence (10).

this species have been discovered, and thus there is no direct evidence that it walked with a plantigrade foot posture or used a heel strike, although it is likely given that humans and great apes do both. Nevertheless, sufficient fossil material is preserved to apply other models of foot biomechanics to reconstruct *A. ramidus* gait. First, the presence of a widely divergent and opposable hallux, similar to that in chimpanzees (Lovejoy et al., 2009), likely indicates the absence of a longitudinal arch, as a mobile hallux would undermine the integrity of the arch's medial side, which is its most pronounced region in humans. If so, *A. ramidus* would have been unable to take advantage of elastic energy savings in the foot during running. Additionally, like great apes, *A. ramidus* possessed long, curved digits useful for pedal grasping (Richmond, 2007; Susman et al., 1984), but that would have caused high metatarsophalangeal joint moments during running (Rolian et al., 2009).

Even in the absence of a human-like longitudinal arch, *A. ramidus* was probably still able to stiffen its foot during push-off via other mechanisms such as activation of the intrinsic foot muscles (Bates et al., 2013). Additionally, Lovejoy et al. (2009) argued that *A. ramidus* could have used the peroneus longus muscle to stiffen the foot, based on the presence of a facet on the cuboid for a sesamoid bone, the os peroneum, which is typically embedded in the muscle's tendon in cercopithecines (see Glossary) and gibbons. Lovejoy et al. (2009) argue that this bone increases the lever arm of the peroneus longus tendon and thus improves its ability to stiffen the midfoot. Further, largely based on this mechanism, they argue that the foot of the human–chimpanzee LCA functioned similarly to that in cercopithecines. However, this argument is undermined by evidence that gibbons and cercopithecines have highly compliant feet relative to humans and chimpanzees (DeSilva, 2010; Greiner and Ball, 2014; Vereecke and Aerts, 2008), and the lack of solid evidence that the peroneus longus can stiffen the midfoot in humans. Thus, the functional implications of the os peroneum are unclear. Based on the many chimpanzee-like features in the foot of *A. ramidus* (Pilbeam and Lieberman, 2017), we suggest that the human–chimpanzee LCA likely possessed a great-ape-like foot, in both form and function.

Nevertheless, several features of the foot of *A. ramidus* appear to be derived adaptations for bipedal walking not present in great apes. Most notably, its cuboid proportions indicate a relatively longer midfoot region than chimpanzees, within the range of humans (Lovejoy et al., 2009). Assuming *A. ramidus* used plantigrade walking postures, an elongated midfoot would have increased the overall length of the foot, and therefore the distance traveled by the center of pressure under the foot over stance phase. This would have effectively reduced collisional energy loss (Adamczyk and Kuo, 2013) and increased the effective length of lower limb to improve walking economy (Webber and Raichlen, 2016). Furthermore, dorsal doming of the third metatarsal head suggests that the lateral (non-hallux) metatarsophalangeal joints were loaded in highly dorsiflexed joint postures during bipedal walking (Lovejoy et al., 2009; Fernández et al., 2018). However, the first metatarsal head is not dorsally domed, suggesting that *A. ramidus* utilized push-off mechanics different from those of humans, perhaps owing to its opposable hallux.

Stage 2: the australopithecines

The oldest evidence for more human-like feet appears in the form of 3.66-million-year-old footprint trackways from the Laetoli site in Tanzania, which are most commonly attributed to the australopithecine (see Glossary) *A. afarensis* (Fig. 8B) (Leakey and Hay, 1979; Masao et al., 2016). These footprints are characterized by deep heel impressions, indicating human-like (and chimpanzee-like) use of the heel in weight support (Crompton et al., 2012; Hatala et al., 2016a; Raichlen and Gordon, 2017). They also show evidence of slightly abducted halluces relative to those habitually barefoot modern humans (Bennett et al., 2009), but which had likely lost the opposability of those of great apes (Day and Wickens, 1980). Additionally, the best preserved Laetoli footprint trackway displays a relatively shallow medial midfoot region indicative of a longitudinal arch, albeit lower on average than has been measured in a large sample of modern human footprints (Hatala et al., 2016a). However, because this trackway represents just one individual and shows some overlap with footprints from the modern human sample, these conclusions should be interpreted cautiously.

These inferences from footprints are supported by several aspects of foot bone morphology preserved in 3.2-million-year-old adult *A. afarensis* fossils from the Hadar formation in Ethiopia (Fig. 8B), as well as a recently described 3.3-million-year-old juvenile *A. afarensis* fossil foot from the Dikika formation in Ethiopia (DeSilva et al., 2018). The adult Hadar fossils display a large, human-like calcaneal tuber with a moderately developed lateral plantar process, which some have interpreted as an adaptation for bipedal walking with a heel strike (Latimer and Lovejoy, 1989; Prang, 2015a), although the role of calcaneus morphology in dissipating impact forces remains to be tested. Additionally, the orientations of the joint articular surfaces in the adult and juvenile tarsal and metatarsal fossils resemble those of modern humans and thus have been argued to be indicative of longitudinal and transverse arches (DeSilva et al., 2018; Prang, 2015b; Ward et al., 2011). Based on these features, and those preserved in the Laetoli footprints, we conclude that *A. afarensis* likely walked with heel strike plantigrady and utilized some form of transverse and longitudinal arches to stiffen the foot.

The morphology of the *A. afarensis* hallucal tarsometatarsal joint is intermediate between that of humans and great apes in articular surface concavo-convexity (DeSilva et al., 2018; Gill et al., 2015; Proctor, 2010), suggesting a big toe that could be slightly abducted (but see Latimer and Lovejoy, 1990). This may indicate retention of some ability to use the hallux in pedal grasping during arboreal locomotion. This notion is supported by morphology of the articular surface of the first metatarsal head, which is plantarly oriented similar to that of chimpanzees (Fernández et al., 2016, 2018), indicating stability in grasping postures. Observations of human hunter-gatherers indicate that the hallux can be extremely useful for grasping during climbing, even in the absence of opposability with the other digits (Kraft et al., 2014). The presence of a more mobile hallux may have resulted in *A. afarensis* pushing off from its second and third metatarsal heads during bipedalism rather than the first as in humans (Fernández et al., 2016), corresponding to the relatively shallow impressions under the first metatarsal head in the Laetoli footprints (Crompton et al., 2012; Hatala et al., 2016b). Additionally, *A. afarensis* retained relatively long toes (Susman et al., 1984), which would have improved pedal grasping without compromising bipedal walking economy (Rolian et al., 2009). This species possessed human-like cuboid–metatarsal joint morphology, which has been argued to indicate a relatively rigid midfoot poorly suited for climbing (DeSilva, 2010; Ward et al., 2011). However, both bipedal kinematic data and cadaveric range-of-motion data from humans and chimpanzees show no major difference between species in midfoot mobility (Greiner and Ball, 2014; Holowka et al., 2017b), suggesting this feature is not a good indicator of arboreal locomotor capabilities.

These findings support the notion that *A. afarensis* could walk bipedally with foot mechanics similar to those of humans, while retaining some pedal grasping adaptations for arboreal locomotion. However, features in the foot of *A. afarensis* suggest that bipedal running was not an important component of this species' locomotor behavior. First, if *A. afarensis* did possess a longitudinal arch, it was likely relatively low (DeSilva et al., 2018; Hatala et al., 2016a), and therefore may not have been able to store much elastic energy. Second, the relatively long toes of *A. afarensis* would likely have caused high metatarsophalangeal joint moments during running, and therefore required the production of relatively high forces by the digital flexor muscles (Rolian et al., 2009). Although human running is no more costly than in other mammals of similar mass (Rubenson et al., 2007), features of the *A. afarensis* foot along with other postcranial features may have equated to a relatively higher metabolic cost of running that would have precluded reliance on long-distance running for subsistence (Bramble and Lieberman, 2004).

Research on australopithecine foot evolution has largely focused on *A. afarensis*, but several other fossil hominins existed around the same time with morphologically distinct feet. A 3.4-million-year-old unattributed hominin foot from Burtele, Ethiopia, displays an opposable hallux like that of African apes, and thus may have used bipedal walking mechanics similar to those of *A. ramidus* (Haile-Selassie et al., 2012). In South Africa, a 3.2-million-year-old foot from Sterkfontein, probably *Australopithecus africanus*, has also been described as possessing morphology indicative of an opposable hallux (Clarke and Tobias, 1995), but this assessment has been contested (McHenry and Jones, 2006). Additionally, a 2-million-year-old foot from Malapa, South Africa, attributed to *Australopithecus sediba*, displays several features argued to affect bipedal walking mechanics, most notably a gracile calcaneus lacking a lateral plantar process (Zipfel et al., 2011). This bone has been argued to indicate that *A. sediba* would have used different foot-strike postures than modern humans because its heel could not have withstood high impact forces (DeSilva et al., 2013; Prang, 2015a), but again, the relationship between calcaneal morphology and resistance to fracture remains to be tested. Thus, it remains unclear whether *A. sediba* walked bipedally with foot mechanics different from those of *A. afarensis*.

Stage 3: *Homo* and the evolution of the modern human foot

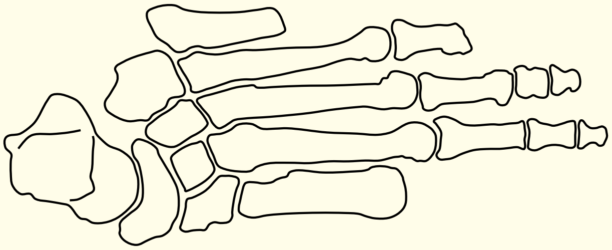
Two geologically contemporaneous but geographically distant sites have yielded the earliest fossil remains attributed to the genus *Homo* (Fig. 8C). A 1.8-million-year-old foot from Olduvai in Tanzania, commonly attributed to *Homo habilis*, includes all tarsal and metatarsal bones and provides strong evidence of a fully adducted hallux and modern human-like midfoot joint morphology (Day and Napier, 1964; Susman and Stern, 1982). Associated fossil metatarsals and a medial cuneiform attributed to *Homo erectus* from the 1.8-million-year-old Dmanisi site in Georgia also provide evidence of a fully adducted hallux, as well as metatarsal torsion patterns indicative of a human-like transverse arch (Pontzer et al., 2010). Two 1.5-million-year-old footprint trackways from the Koobi Fora formation in Kenya provide further evidence of foot morphology in early *Homo* (Fig. 8C). Sizes of the prints suggest hominins with modern human-like body sizes (Behrensmeyer and Laporte, 1981; Dingwall et al., 2013), and have thus been attributed to *H. erectus* (Bennett et al., 2009). Morphology of the footprints indicates that *H. erectus* possessed a more adducted hallux and a longitudinal arch that was higher than that apparent in the Laetoli footprints (Bennett et al., 2009; Hatala et al., 2016b), suggesting that evolution of a human-like arch may have come at the expense of hallucal grasping abilities. These footprints are roughly contemporaneous with the nearly complete but footless skeleton of an adolescent *H. erectus* individual from the nearby site of

Nariokotome that displays many anatomical features argued to represent adaptations for endurance running (see Glossary) (Bramble and Lieberman, 2004). Taken together, these findings suggest that the appearance of a high, human-like longitudinal arch in *H. erectus* may have been in part an adaptation for elastic energy savings during running.

The evolution of shorter toes would represent another clear trade-off between running economy and pedal grasping (Rolian et al., 2009), but we have yet to discover fossil toe bones that can be firmly attributed to *H. erectus* or *H. habilis*. Unsurprisingly, *Homo neanderthalensis* has short toes (Trinkaus and Hilton, 1996), but this species post-dates the first appearance of *H. erectus* by over a million years. Intriguingly, 230,000- to 330,000-year-old foot bones from *Homo naledi* discovered at the Rising Star cave site in South Africa preserve evidence of modern human-like toe proportions, but with phalangeal shaft curvature similar to that of gorillas (Harcourt-Smith et al., 2015). This curvature is argued to indicate strong pedal grasping abilities, but the presence of a fully adducted, non-opposable hallux suggests that *H. naledi* did not retain significant arboreal adaptations in its foot. Otherwise, the foot of *H. naledi* is very modern-human-like, although orientations of the head of the talus and the sustentaculum tali suggest a relatively low longitudinal arch. However, the associations between these features and arch height in modern humans are low and require further testing. Thus, all derived features of the modern human foot related to energetic efficiency during running appear in the genus *Homo* (but for one perplexing exception, see Box 1).

Box 1. The odd foot of *Homo floresiensis*

A 60,000- to 100,000-year-old nearly complete foot specimen (LB1) from the island of Flores is attributed to the enigmatic fossil hominin *Homo floresiensis* (Sutikna et al., 2016). This species is distinguished from all contemporaneous hominins by its remarkably short stature and small endocranial size, as well as an interesting mix of features shared with *Homo* as well as with earlier hominins including australopithecines (Brown et al., 2004; Jungers et al., 2009a; Larson et al., 2009). The foot of *H. floresiensis* is no exception. Overall, the LB1 foot is extremely long relative to leg length, in part because of long toes proportioned similarly to those in chimpanzees (Jungers et al., 2009b). The foot also displays a fully adducted hallux, but its first metatarsal is relatively short, and its cuboid and navicular bones are shaped similarly to those of African apes, suggesting a longitudinal arch that was only weakly developed or absent (Jungers et al., 2009b). These features do not preclude effective bipedal walking, as a long foot should reduce metabolic costs assuming the use of heel-strike plantigrady (Cunningham et al., 2010; Webber and Raichlen, 2016), and alternative mechanisms could have been utilized to stiffen the foot even in the absence of a longitudinal arch (Bates et al., 2013; Venkadesan et al., 2017 preprint). However, lacking a human-like longitudinal arch, *H. floresiensis* would have been unable to take advantage of significant elastic energy savings in its foot (Stearne et al., 2016), and its long toes would have required high muscle force production during running (Rolian et al., 2009). Thus, these features are inconsistent with adaptation to endurance running, which is unsurprising given that *H. floresiensis* was probably endemic to a small forested island. Whether this species retained its foot morphology from a primitive australopithecine-like ancestor or secondarily evolved it upon inhabiting Flores remains to be determined (Jungers et al., 2009b). Foot skeleton image modified after Jungers et al. (2009b).



Concluding remarks

The remarkable differences between the feet of humans and those of the great apes have led to over a century of debate on how and why the human foot evolved to become the way it is. Newly developed and recently refined biomechanical models help us to understand the adaptive functions of features unique to the human foot, as well as recent experimental data from studies of great ape locomotion, and allow us to define a new framework for understanding hominoid foot evolution. We argue that instead of simply dichotomizing human and great ape foot anatomy, we must recognize that these species share some features such as the use of plantigrade foot postures and the ability to stiffen the midfoot joints during push-off that would have been advantageous for bipedalism in their LCA. Early hominins subsequently evolved features such as an incipient longitudinal arch and a relatively adducted hallux that would have enhanced push-off mechanics during bipedal walking while allowing for the retention of some pedal grasping abilities. Finally, with a greater commitment to terrestrial locomotion and a reliance on long-distance walking and running, hominins lost most of their arboreal adaptations in favor of a fully developed longitudinal arch with elastic-energy-storing capabilities.

Recent evidence supporting the spring model of the human foot in running but not walking has important implications for understanding the adaptive value of a longitudinal arch. Considering the alternative mechanisms for stiffening the midfoot during walking (e.g. intrinsic foot muscle activity, the transverse arch), a major selective advantage of the longitudinal arch may be to enable elastic-energy storage during long-distance running. If true, then the primary trade-off of evolving a modern human-like foot may not be for walking versus climbing, but rather climbing versus running, fitting the scenario proposed by Bramble and Lieberman (2004) more generally for the evolution of human postcranial anatomy. Future research should focus on testing this trade-off by exploring how features such as arch height and stiffness in humans influence running versus walking performance and intrinsic foot mobility. Additionally, more research is needed on how the foot functions in behaviors outside of steady-state locomotion, such as aggressive interactions, situations that require rapid acceleration, or maneuvering in complex environments. Such behaviors could also have major effects on fitness, and therefore studying them is critical to determining the selective forces that shaped the modern human foot.

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Competing interests

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