

REVIEW ARTICLE

The evolution of the human foot

Ellison J. McNutt^{1,2}  | Bernhard Zipfel³  | Jeremy M. DeSilva^{1,3} ¹Department of Anthropology, Dartmouth College, Hanover, New Hampshire²Ecology, Evolution, Ecosystems, and Society, Dartmouth College, Hanover, New Hampshire³Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa**Correspondence**

Department of Anthropology, Dartmouth College, Hanover, NH 03755.

Email: ellison.j.mcnutt.gr@dartmouth.edu

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Abstract

There are 26 bones in each foot (52 in total), meaning that roughly a quarter of the human skeleton consists of foot bones. Yet, early hominin foot fossils are frustratingly rare, making it quite difficult to reconstruct the evolutionary history of the human foot. Despite the continued paucity of hominid or hominin foot fossils from the late Miocene and early Pliocene, the last decade has witnessed the discovery of an extraordinary number of early hominin foot bones, inviting a reassessment of how the human foot evolved, and providing fresh new evidence for locomotor diversity throughout hominin evolution. Here, we provide a review of our current understanding of the evolutionary history of the hominin foot.

KEYWORDS*Ardipithecus*, *Australopithecus*, bipedalism, hominin, *Homo*

1 | INTRODUCTION

*Man's foot is all his own. It is unlike any other foot. It is the most distinctly human part of his whole anatomical makeup. It is a human specialization and, whether he is proud of it or not, it is his hallmark...*Jones.¹

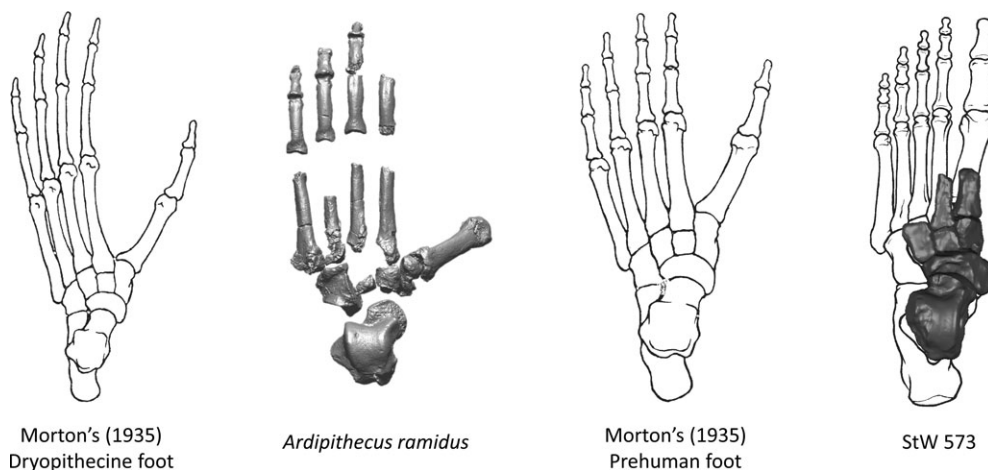
The human foot has long amazed and puzzled scholars. Tyson² in his 1699 anatomical atlas of the chimpanzee remarked on the hand-like properties of the ape foot, and coined the term “quadrumanous.” Years later, Huxley³ also drew attention to the hand-like anatomies of the *Gorilla* foot, with its inverted set, grasping hallux and long, curved toes. But, Huxley also presented detailed musculoskeletal evidence to his readers that apes had a foot at the end of their leg and not another hand. He wrote, “...the resemblances between the foot of Man and the foot of the *Gorilla* are far more striking and important than the differences.”³

In the first half of the 20th century, comparative anatomists and physical anthropologist hypothesized about both the foot from which our own evolved, and the anatomical changes underlying that conversion. Morton^{4–6} provided the most detailed look at foot evolution. He proposed a two-step process by which a “Dryopithecine” foot, which possessed an elongated tarsal region but was otherwise ape-like, evolved into a “prehuman” foot, which retained a grasping hallux (see Box 1). Central to Morton's view of foot evolution were frontal plane changes in metatarsal torsion that would have converted an inverted ape foot into an everted human-like one. Weidenreich⁷ regarded the chimpanzee foot to be the ancestral form, and proposed that expansion of the calcaneal tuber, and an orthogonal ankle joint (positioning

the human foot in a more everted set) were key adaptations for bipedalism. Keith⁸ remarked that the *Gorilla* foot is most like that found in humans and hypothesized that the lateral forefoot must have realigned into an adducted position with a stable first metatarsal. This idea would reemerge later with Lewis,⁹ who imagined this realignment of the forefoot occurring as a medial shift in the orientation of the subtalar axis. Elftman and Manter¹⁰ found it equally likely that the human foot evolved from a chimpanzee or gorilla-like foot, and suggested that plantarflexion and adduction of the transverse tarsal joint was central to foot evolution, and particularly the evolution of the longitudinal arch. All of these early evolutionary scenarios were hypothesized solely based on comparisons with extant primate models and without the benefit of any early hominin foot fossils.

Following the discovery of OH 8 in 1960, and the subsequent decades of fossil discoveries in Eastern Africa, in 1983 Susman¹¹ published a landmark paper on the evolution of the human foot. At the time, the early hominin foot fossil record consisted of a number of isolated elements,¹² the partial foot from Olduvai (OH 8) assigned by most to *Homo habilis*, and the geologically older *Australopithecus afarensis* from Hadar, Ethiopia, in addition to the similarly aged Laetoli footprints (Figure 1).¹³ It was logical and reasonable to use these remains to paint a picture of hominin foot evolution in which the primitive, arboreally adapted chimpanzee foot evolved into the bipedally adapted modern human foot via these fossil intermediates.

In 1995, Clarke and Tobias¹⁴ proposed that bipedal adaptations in the hindfoot (ankle joint and heel) preceded the derived anatomies of



Box 1. WITHOUT THE BENEFIT OF A SINGLE PLIO-PLEISTOCENE HOMININ FOOT FOSSIL, IN 1935 COLUMBIA UNIVERSITY ANATOMY PROFESSOR DUDLEY MORTON OUTLINED THE EVOLUTION OF THE HUMAN FOOT THROUGH TWO INTERMEDIATE STAGES: A DRYOPITHECINE FOOT THAT COULD BE INTERPRETED TO REPRESENT THE HUMAN-APPE LAST COMMON ANCESTOR AND A GORILLA-LIKE “PREHUMAN” FOOT. THE DRYOPITHECINE FOOT MORTON HYPOTHESIZED WAS CHIMPANZEE-LIKE IN MANY RESPECTS, BUT UNLIKE IN MODERN *PAN*, IT POSSESSED A PROXIMODISTALLY MORE ELONGATED MIDTARSUS. MORTON WROTE: “HENCE WE MAY INFER THAT THE PROANTHROPOID (DRYOPITHECINE) STAGE PRESENTED AN INTERMEDIATE CONDITION WHICH CORRESPONDED VERY CLOSELY WITH THE PROPORTIONATE LENGTH OF THESE BONES AS NOW FOUND IN THE HUMAN FOOT.” OUR HYPOTHESIZED HOMININ-PANIN LCA FOOT IS QUITE SIMILAR TO THAT PROPOSED BY MORTON MORE THAN 80 YEARS AGO, AND WE REGARD MANY ASPECTS OF THE *ARDIPITHECUS RAMIDUS* FOOT TO BE INTERMEDIATE BETWEEN THIS HYPOTHETICAL DRYOPITHECINE FOOT AND HIS PREHUMAN FOOT. OTHERS^{14,18} HAVE NOTED SIMILARITIES BETWEEN MORTON’S HYPOTHETICAL FOOT RECONSTRUCTIONS AND HOMININ FOSSILS, PARTICULARLY StW 573 “LITTLE FOOT.” WITH AN ADDUCTED HALLUX, WE REGARD StW 573 AS TOO DERIVED TO REPRESENT THIS PREHUMAN FOOT STAGE. A FOOT INTERMEDIATE IN MORPHOLOGY BETWEEN *ARDIPITHECUS* AND *AUSTRALOPITHECUS* IS CURRENTLY UNKNOWN, AND MAY NOT EVEN EXIST IF FUTURE DISCOVERIES REVEAL *ARDIPITHECUS* TO BE A DEAD-END EVOLUTIONARY EXPERIMENT IN EARLY BIPEDAL EVOLUTION.

the human forefoot. This model was based on their interpretation of the then newly discovered StW 573 foot from Sterkfontein, South Africa, dubbed “Little Foot,” which we address later in this review. Kidd¹⁵ disagreed, and proposed that the foot had evolved from laterally to medially, with the outside of the foot evolving bipedal adaptations prior to the medial side. More recently, based on the *Ardipithecus ramidus* foot, Lovejoy et al.¹⁶ rekindled the interpretations of Straus¹⁷ in proposing that the apparent rigidity of the human foot is not derived, but instead is a retention of the monkey-like primitive form. According to this model, ape feet are more derived than previously thought, though here too the evolution of the human foot unfolds in a lateral to medial manner. Applying new geometric morphometric approaches to StW 573, OH 8, and isolated foot fossils from Sterkfontein, South Africa, Harcourt-Smith and Aiello¹⁸ hypothesized a less linear and more mosaic evolutionary history of the hominin foot. Their predictions have largely been borne out by the discoveries of the past decade.

The last 10 years alone have witnessed the publication of early hominin foot fossils from *Ardipithecus ramidus*¹⁶ and an unclassified hominin from Burtele, Ethiopia.¹⁹ Foot fossils have been recovered and published from known species of *Australopithecus*,²⁰ and from a new species *Au. sediba*.²¹ Foot fossils from early *Homo*²² were accompanied by the pedal remains of the Middle to Late Pleistocene species *Homo naledi*²³ and *Homo floresiensis*.²⁴ Additional Middle Pleistocene *Homo* foot fossils were described from the Spanish localities of Gran Dolina²⁵ and Sima de los Huesos²⁶ in addition to the Jinniushan site in China.²⁷

The last 10 years of exploration have also yielded new fossil footprints from *Australopithecus*,²⁸ early *Homo*,²⁹ later *Homo*³⁰ and Late Pleistocene *Homo sapiens* (see Table 1).³¹ This pace of discovery is likely to continue, given the functional descriptions of a nearly complete juvenile *Australopithecus* foot,³² and a foot of early *Homo*.³³ It is truly an extraordinary time to be studying the evolution of the human foot.

2 | WHAT IS UNIQUE ABOUT THE HUMAN FOOT?

An obvious starting point for reconstructing the evolution of the human foot is to make direct comparisons with the foot anatomy of our closest living ape relatives. Genetic studies have shown that the lineage leading to modern chimpanzees and the hominin lineage diverged sometime in the late Miocene.³⁴ While this comparison between humans and chimpanzees can be very informative, it is important to note that the human foot did not evolve from a chimpanzee one. Since our divergence from a more generalized common ancestor, hominins, and panins are likely to have evolved two different kinds of feet. The former's foot has become well adapted for a stiff push-off mechanism during bipedal locomotion, while the latter's foot has become better adapted for climbing in trees and for terrestrial quadrupedalism (Figure 2). Before attempting to use the chimpanzee foot to understand hominin foot evolution, it is necessary to outline the anatomical differences between our foot and theirs. Some of these differences are soft-tissue in nature and are difficult to infer from skeletal

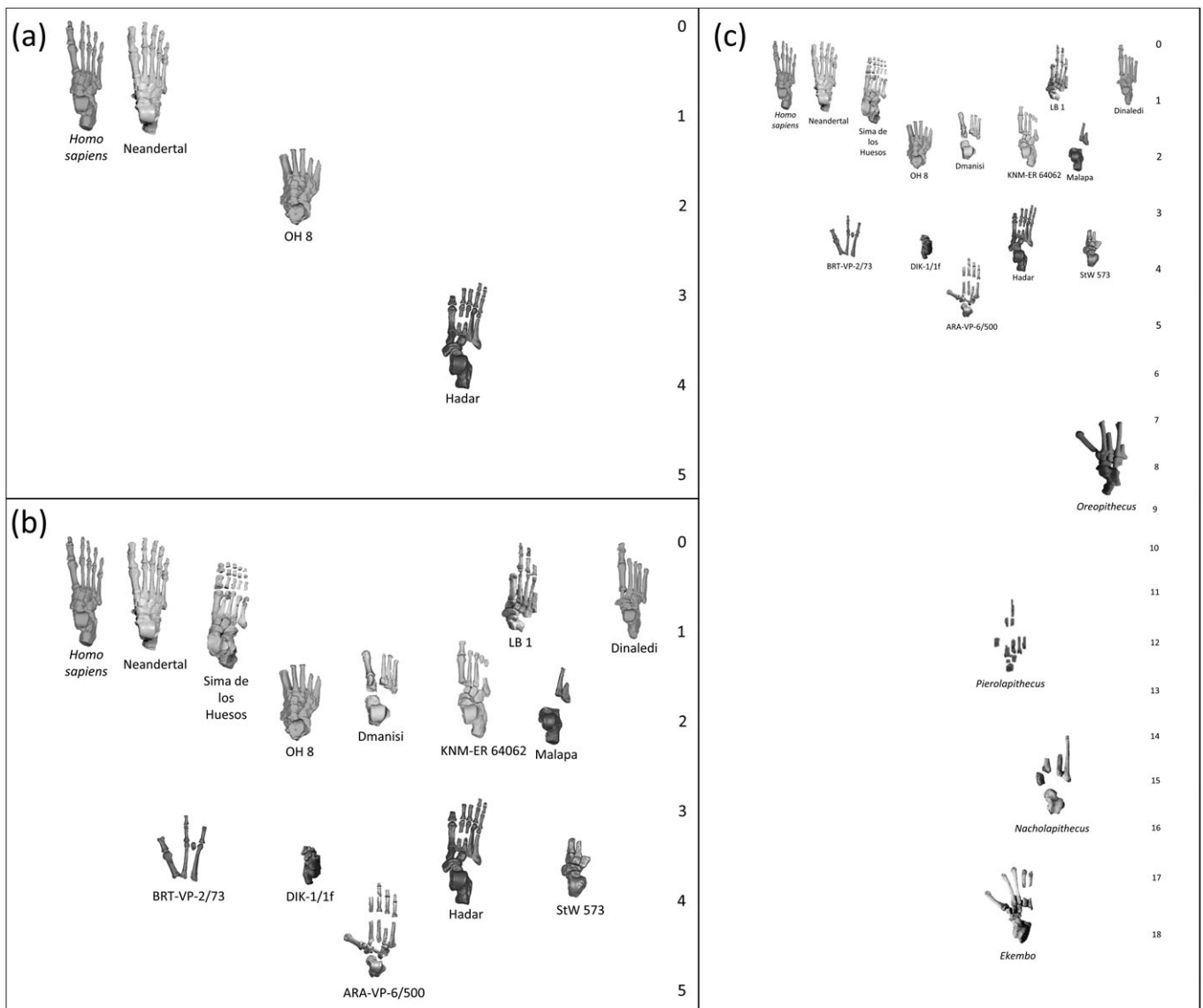


FIGURE 1 The number of hominin foot fossils has grown considerably in the last decade. The numbers arranged vertically in each of these figures represents millions of years before present. (a) The status of the hominin foot fossil record in 1983 when Susman¹¹ wrote his review on the foot fossil record. The only early hominin foot fossil was OH 8. A composite Hadar foot is shown here as well to represent the large collection of material from *Australopithecus afarensis*. (b) Since that time, the number of hominin foot fossils has increased dramatically. Associated foot remains are known from *Ardipithecus*, additional populations of *Australopithecus*, early *Homo*, and later Pleistocene *Homo*. (c) Despite this increase in our knowledge of Plio-Pleistocene hominin foot evolution, there remains a considerable gap in our understanding of the foot from which the earliest hominin foot evolved. Between 4.4 Ma and 11.9 Ma, there is an almost complete absence of hominoid foot fossils. Only *Oreopithecus* is known from this time, and this foot is likely not relevant to our understanding of hominin bipedal origins. *Ekembo nyanzae*⁶¹ redrawn. Foot images not to scale

remains alone. Humans have a robust anterior talofibular ligament, for instance, which helps stabilize a bipedal ankle. This ligament is typically absent in the chimpanzee ankle.³⁵ Additionally, the human foot possesses a thick plantar aponeurosis and long plantar ligament (LPL), which together help stiffen the foot during push-off. These tissues are absent, or weakly developed, in the foot of chimpanzees.³⁶ pers. obs.

2.1 | Tarsals

In chimpanzees, the tibial shaft is obliquely oriented relative to the plane of the ankle joint (Figure 2).³⁷ Additionally, the elevated lateral rim of the talus and resulting high talar axis angle produces an inverted set to the chimpanzee foot.³⁸ In contrast, humans possess an

orthogonal orientation of the tibia and low axis angle of the talus, which results in an everted foot, and a foot positioned directly under the knees. The chimpanzee talus has a mediolaterally expanded distal trochlea, which is hypothesized to dissipate high forces during habitual dorsiflexion, perhaps during bouts of vertical climbing.³⁸ In contrast, the human talar trochlea is less wedged, reflecting the more equal load distribution experienced across the ankle joint during bipedal locomotion. Compared with the chimpanzee talus, human tali have both high head and neck torsion in the coronal plane and plantar inclination (sometimes called declination) of the head and neck in the sagittal plane.³⁹ The latter anatomy is thought to contribute to the longitudinal arch of the foot. In the transverse plane, the chimpanzee talus has a high horizontal angle, while humans have a fairly low

TABLE 1 Hominin foot^a fossils

Accession number	Taxon	Age (Ma)	Elements preserved
ARA-VP-6/500	<i>Ardipithecus ramidus</i>	4.4	Left: cuboid, all cuneiforms, all Mts, PP2-5, IP5 Right: partial calcaneus, talus, int. cun., cuboid, Mt 1-2, PP2-5, IP 4-5, DP Unsidel: PP1, IP 3, DP (x3), hallucal sesamoid, os peroneum
StW 573	<i>Australopithecus prometheus?</i>	3.67?	Talus, navicular, all three cuneiforms, Mt1, Mt2
BRT-VP-2/73	Hominin sp.	3.4	Mt 1,2,4; Mt 3 head; PP 1,2,4; IP 2
DIK-1-1f	<i>Australopithecus afarensis</i>	3.3	All tarsals and bases of all Mts
A.L. 333-115	<i>Australopithecus afarensis</i>	3.2	Forefoot: all Mt heads, all PPs, IP4, IP5, DP5
A.L. 288-1	<i>Australopithecus afarensis</i>	3.18	Talus, PP, IP
StW 595	<i>Australopithecus africanus</i>	2.0-2.6	Mt 1-3; PP1 assumed to be associated based on shared accession number
MH 1 (U.W. 88-16,22,113)	<i>Australopithecus sediba</i>	1.98	Mt 4 and 5, calcaneal apophysis
MH 2 (U.W. 88-98,99; 33)	<i>Australopithecus sediba</i>	1.98	Talus, calcaneus, Mt 5 base
OH 8	<i>Paranthropus? Homo?</i>	1.85	All tarsals and bases & shafts of all Mts
Dmanisi	<i>Homo erectus</i>	1.77	Talus; Mt3-5
KNM-ER 64062	<i>Homo</i> sp.	1.84	All tarsals but medial cuneiform; Mt1-Mt3; Mt4 head; Mt5 head and base; PP1
KNM-ER 803	<i>Homo erectus</i>	1.53	Partial talus; Mt3,5, IP (x2), DP
Atapuerca	<i>Homo heidelbergensis</i>	0.45	Associations not yet published; many partial (or complete) feet likely present.
Dinaledi foot 1	<i>Homo naledi</i>	0.24-0.34	All tarsals but medial cuneiform; all Mts; PP1. Four additional partial feet from Dinaledi.
Jinniushan	<i>Homo heidelbergensis</i>	0.25	Left: all tarsals except navicular and int. cun. Mt1-2; PP(x4); IP(x3); DP(x2) Right: all tarsals except med. & int. cun., PP(x2); IP; DP1
LB1	<i>Homo floresiensis</i>	0.06	Left: all tarsals except calcaneus. Mt 1-5 (some fragmentary); PPs, IPs, DPs Right: talus, navicular, cuboid, lat. cun., Mt1-5 (some fragmentary)
Omo-Kibish	<i>Homo sapiens</i>	0.195	Talus, navicular, med. cun., cuboid, Mt1, fragmentary Mt2-5; PP1, DP1
Assortment	Neandertal	0.2-0.03	Amud, La Chapelle, La Ferrassie, Kiik-Koba, Krapina, Regourdou, Shanidar, Tabun partial feet

Mt = metatarsal; PP = proximal phalanx; IP = intermediate phalanx; DP = distal phalanx.

^a Foot defined as having three or more associated pedal elements.

horizontal angle. Finally, the posterior calcaneal facet is highly convex in chimpanzees, consistent with mobility (inversion and eversion) at the subtalar joint. The human subtalar joint is relatively flat, permitting less mobility and instead increased stability during bipedal gait.⁴⁰

The chimpanzee calcaneus has a gracile posterior tuberosity with a weakly developed, dorsally positioned lateral plantar process. This is in contrast to the human calcaneus, which possesses a robust posterior tuberosity with a large plantarly positioned lateral plantar process, hypothesized to increase calcaneal volume to dissipate peak loads during heel-striking bipedalism.⁴⁰ While the orientation of the sustentaculum tali differs little in the sagittal plane between humans and chimpanzees,^{10,40} it is more strongly angled in the frontal plane in chimpanzees.²³ Chimpanzees have a large, proximally positioned peroneal trochlea, a skeletal correlate of well-developed peroneal musculature (*Mm. peroneus longus* and *peroneus brevis*) recruited during arboreal climbing bouts.⁴¹ The human peroneal trochlea, while quite variable in size, tends to be smaller and more distally positioned. In humans, the cuboid facet of the calcaneus spills onto the medial side of the bone, which together with the beak (a proximally oriented projection of bone)

of the cuboid, contributes to the locking mechanism of the calcaneocuboid joint during push-off. The calcaneocuboid joint in chimpanzees is more mobile allowing the cuboid to pivot around its beak.⁴²

The bones of the midfoot (i.e., the cuboid, medial cuneiform, intermediate cuneiform, lateral cuneiform, and navicular) are all relatively short proximodistally in chimpanzees compared with humans.⁴³ This elongation of the midfoot in humans is hypothesized to convert the foot into a more effective lever during the second half of stance phase. The chimpanzee cuboid has a centrally positioned beak, and a well-developed groove for the tendon of *M. peroneus longus*. In humans, the beak is positioned medially and posteriorly, which allows it to lock against the corresponding extension of the calcaneus creating a stable, close-packed position.⁴² The chimpanzee navicular has a relatively large tuberosity compared to the human navicular and narrows proximodistally along the lateral body of the bone. Human naviculars, in contrast, possess a more proximodistally elongated body.⁴⁴ The chimpanzee medial cuneiform possesses a strongly convex, medially oriented, articular facet for the base of the first metatarsal (Mt1), which orients the big toe in an abducted position. The same facet in

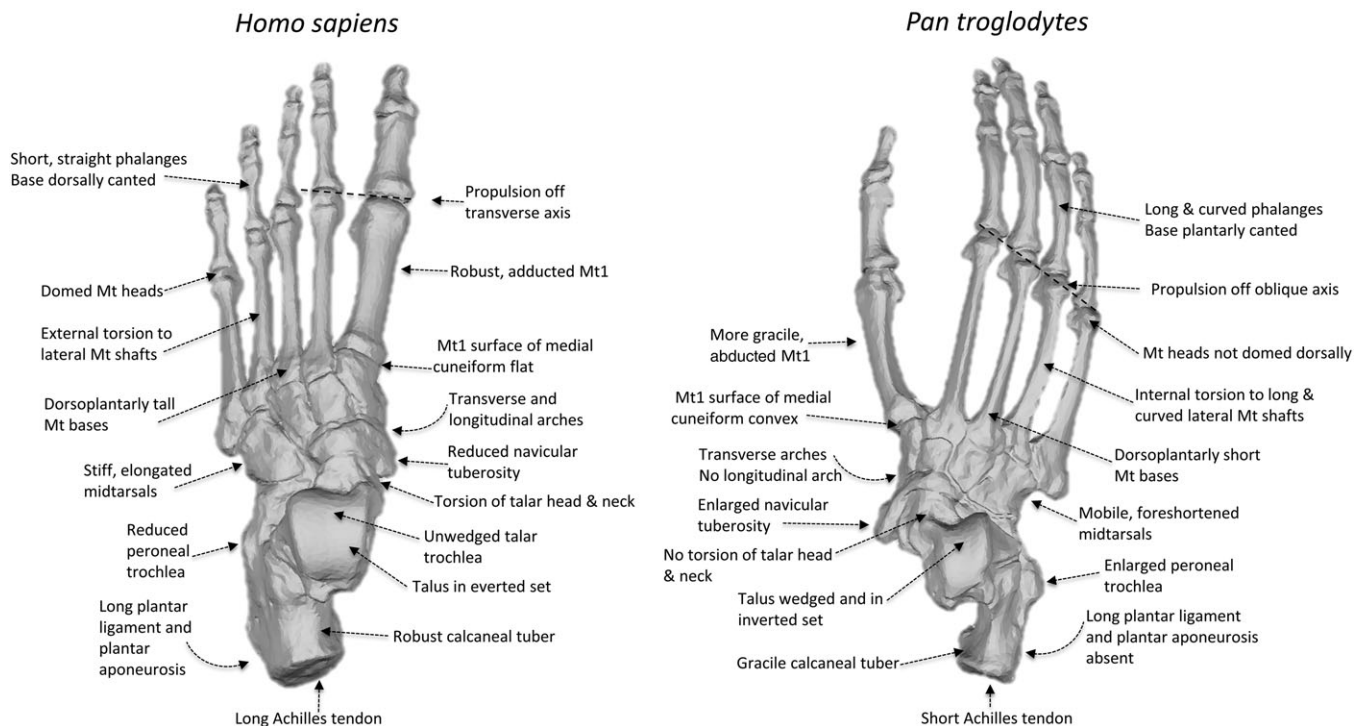


FIGURE 2 Chimpanzees possess the same 26 bones found in the modern human foot skeleton. However, there are subtle differences in foot proportions and in the morphology of these bones, resulting in a human foot well adapted for the rigors of heel-striking bipedalism, and a chimpanzee foot adapted for arboreality. Many (but not all) anatomies that differ between the human foot and the chimpanzee one are shown surrounding these two feet

the human medial cuneiform is flattened and oriented distally, consistent with an adducted, nongrasping hallux.⁴⁵ Additionally, the human medial cuneiform possesses a tubercle for the insertion of *M. peroneus longus*; in chimpanzees, this tendon only inserts on the Mt1 and helps adduct the hallux over a fixed medial cuneiform during pedal grasping.⁴⁵

2.2 | Metatarsals

The chimpanzee Mt1 possesses a concave, sigmoidally shaped proximal articular facet—a skeletal correlate of a divergent, grasping hallux (Figure 2). The Mt1 is also gracile in chimpanzees relative to that in humans and the shaft is torqued, positioning the hallux head toward the lateral digits for grasping. In contrast, human Mt1s are more robust and are aligned with the other digits to facilitate push-off on the transverse axis (Figure 2). Compared with a chimpanzee Mt1, the head of a human Mt1 is mediolaterally expanded dorsally, reflecting high loads at the hallux metatarsophalangeal joint during toe-off.⁴⁶

Human lateral metatarsal heads are dorsally domed (i.e., the articular facet is spherical and rises above the shaft) and often have a gutter behind the head to receive the proximal phalanges during dorsiflexion and bipedal toe-off. In contrast, the Mt shafts of chimpanzees are curved in the sagittal plane and the Mt heads are prolonged plantarly, reflecting their increased reliance on grasping.⁴⁷ Mt5 is typically the most gracile metatarsal in the chimpanzee foot and tends to be straight in the transverse plane. In humans, the Mt5 is frequently the next most robust metatarsal after Mt1 and curves in the transverse plane.⁴⁸

Mts2-5 possess internal torsion in the chimpanzee foot, which positions them in opposition to the hallux and facilitates pedal grasping. In humans, Mts2-5 possess external torsion, which rotates the head of the metatarsal to be flush with the ground while the bases are positioned within the transverse arch of the foot.⁴⁹ The bases of human metatarsals are dorsoplantarily tall relative to those found in chimpanzees, an anatomy thought by many to increase midfoot rigidity during bipedal gait. The bases of Mts4-5 (especially Mt4) are dorsoplantarily convex in chimpanzees, consistent with a midtarsal break.^{10,50} These joints tend to be more dorsoplantarily flat in humans, which typically possess a more rigid lateral midfoot. The dichotomization of the foot as either stiff (human-like) or mobile (ape-like, capable of a midtarsal break) has been challenged by recent findings of considerable foot mobility at times in the human gait cycle,⁵¹ and even a midtarsal break in some humans.^{52,53} Midfoot mechanics are therefore more complicated than originally thought and may require some rethinking.

2.3 | Phalanges

Chimpanzees' phalanges (proximal and intermediate) are longer, more curved, and have more developed flexor ridges than those found in modern humans (Figure 2). While the bases of human proximal phalanges are dorsally canted (i.e., the metatarsal facet is angled dorsodistally to plantoproximally) to allow for a large degree of dorsiflexion of the toes during bipedal push-off, chimpanzee proximal phalanges are plantarly canted, reflecting habitual plantarflexion of the grasping toes.⁴⁷ Human distal phalanges are more robust than chimpanzee phalanges. Additionally, the hallux distal phalanx is both laterally

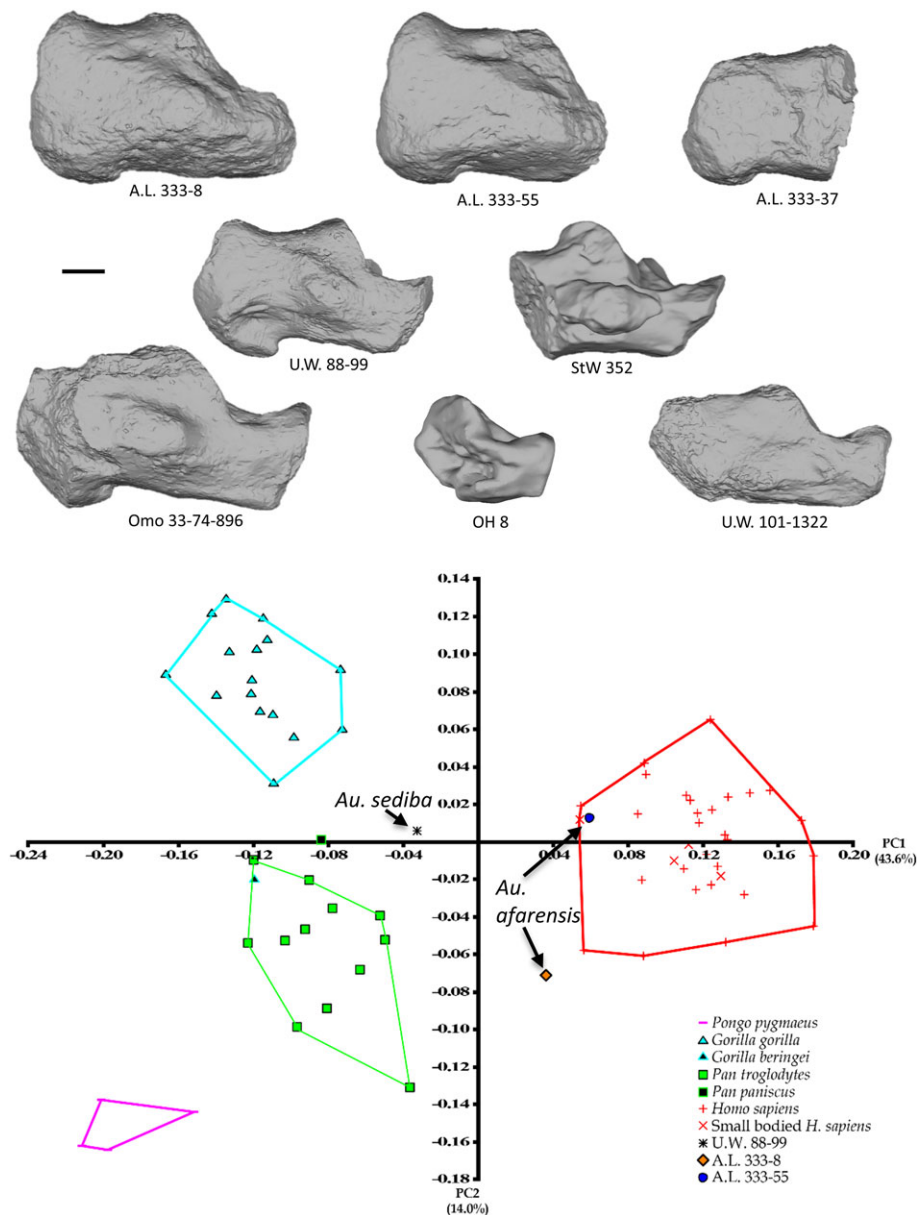


FIGURE 3 The calcaneus is a poorly represented bone in the hominid fossil record and even those known (top) are often incomplete and damaged. Yet, what is preserved reveals considerable morphological variation. Fossils are shown in lateral view, to scale (bar = 1 cm), and reflected if necessary to illustrate the right side (A.L. 333-55, OH 8). Bottom: a Principle Components Analysis (PCA) plot generated from a geometric morphometrics analysis of calcaneal shape in humans, modern apes, Hadar calcanei (A.L. 333-8, -55) and *Australopithecus sediba* (U.W. 88-99). The two fossils from *Australopithecus afarensis* are quite human-like and plot either within (A.L. 333-55) or just outside (A.L. 333-8) the modern human distribution. However, the *Australopithecus sediba* calcaneus is unlike those found in modern humans, or the *Au. afarensis* sample and instead plots near the African ape distribution along PC1. Details of the sample and methods are presented in DeSilva et al., accepted 2018

angled in the transverse plane and medially torqued along the long axis of the bone—anatomies correlated with bipedal propulsion.⁵⁴

Given the close relationship between humans and chimpanzees, it is tempting to use the chimpanzee foot as a substitute for the foot of the *Homo-Pan* last common ancestor (LCA). However, this perspective has been challenged by recent discoveries of foot fossils from Miocene hominoids and Pliocene hominins.¹⁶ There is evidence that aspects of the chimpanzee foot are in fact derived and have evolved since the hominid-panin split to facilitate vertical climbing in a large-bodied ape. Humans, according to this view, may retain some more primitive characteristics in their feet. The evidence for this interpretation will be discussed in the next two sections.

3 | THE FOOT OF THE HUMAN-CHIMPANZEE LAST COMMON ANCESTOR

While there are numerous (largely isolated) hominoid foot fossils from the early Miocene,⁵⁵ the paucity of fossil material from the Late Miocene makes it difficult to reconstruct the ancestral foot from which the hominid foot evolved. *Pierolapithecus catalaunicus* at 11.9 Ma is the latest Miocene hominid to preserve any pedal remains that could inform the foot anatomy of the LCA.⁵⁶ *Ardipithecus ramidus*, at 4.4 Ma, represents the oldest purported hominid for which we have a relatively complete foot.^{16,57} We recognize that the Miocene ape, *Oreopithecus*, was present in Europe at ~7 to 9 Ma; however, its

relationship to crown apes remains uncertain and the most recent phylogenetic analysis suggests it is a Nyanzapithecine,⁵⁸ only distantly related to modern hominoids. Reports that *Oreopithecus* was bipedal⁵⁹ have been contested,⁶⁰ and are not considered here. The current dearth of Late Miocene and Early Pliocene ape fossils means that there is a 7.5 million year gap for which we have no fossil hominid feet. This gap encompasses the critical time period during which the hominin and panin lineages likely diverged. Thus, any reconstructions of the LCA foot are necessarily speculative and testing LCA foot hypotheses will require the recovery of pedal fossils from the nearly barren time period between 4.4 and 11.9 Ma. Nevertheless, foot fossils from Miocene apes and from *Ardipithecus* provide important insights into the foot from which our own evolved.

There are no complete calcanei from either *Pierolapithecus* or *Ardipithecus*, which makes predicting the shape of the LCA calcaneus difficult. However, there are some commonalities found in the calcaneus of both modern and Miocene hominoids that allow us to make broad predictions. Based on the anatomical similarities present across ape calcanei, it is reasonable to infer that the LCA had a narrow posterior tuberosity, a dorsally positioned lateral plantar process, and large proximally positioned peroneal trochlea. These anatomies have even been found, to a lesser degree, in *Au. sediba*.²¹ The LCA is predicted to have both a calcaneocuboid joint and subtalar joint that were more mobile than those found in humans today, consistent with published descriptions of the cuboid and talus of *Ardipithecus ramidus*.¹⁶ The *Ardipithecus* cuboid has a centrally positioned beak, suggesting the lack of a human-like locking mechanism on the calcaneus.¹⁶ Together, these observations suggest a calcaneus in the LCA that was broadly similar to those found in modern apes. However, modern great ape calcanei are morphologically quite distinct from one another (Figure 3) and it currently remains unclear if any one species of modern ape has a calcaneus most similar to that of the LCA. For example, whether the LCA had an elongated proximal tuberosity as found in *Gorilla* or a shortened one, as found in *Pan* and *Pongo*, remains unknown.

Based on functionally relevant commonalities found in the tali of chimpanzees and the early hominin, *Ardipithecus ramidus*, we hypothesize that the talus of the LCA was *Pan*-like. It likely had a high talar axis angle, which would position the foot in an inverted set. Additionally, the talar trochlea is hypothesized to have been strongly wedged (i.e., a mediolaterally wide distal trochlear surface compared with the proximal), which would suggest the LCA was habitually loading its ankle in a dorsiflexed position, perhaps during bouts of vertical climbing.³⁸ There was likely an obliquely angled groove on the posterior surface for the tendon of *M. flexor hallucis longus*. These interpretations are supported by the well-preserved talus from *Ardipithecus ramidus*, which displays a talar axis angle that is within the range of the African apes, and a strongly wedged trochlear body.¹⁶

The tarsal bones of the hominin-panin LCA midfoot (cuboid, navicular, intermediate, and lateral cuneiforms) may have been relatively longer proximodistally than those currently found in the African apes, making tarsal foreshortening a derived, rather than primitive feature of the *Pan* foot.¹⁶ While tarsal lengthening could also be secondarily derived in humans, the alternative interpretation in which the *Pan* foreshortened midtarsus is the derived condition, is supported by the relative length of the currently known midtarsal bones from

Miocene apes as well as those found in *Ardipithecus*, which exceed the relative lengths found in extant apes. However, all of these taxa have tarsals that remain relatively shorter proximodistally than those found in australopiths and modern humans, supporting the hypothesis of an LCA midfoot intermediate in length between that found in modern apes and humans. These observations led Lovejoy et al.¹⁶ to suggest that at least some degree of midtarsal elongation is a primitive hominoid condition and that hominins have further elongated the midfoot, while the extant great apes have reduced their midtarsal length. Based on the currently available fossils from the early Miocene, we agree with this interpretation.

It is reasonable, perhaps even obvious, to state that the hominin-panin LCA had a divergent hallux and a medial cuneiform similar to those found in the nonhuman hominoids today. This hypothesis is based on the anatomical similarities present in the first ray of all extant apes, as well as on preserved anatomy from *Ardipithecus ramidus*.¹⁶ The medial cuneiform of *Ardipithecus* is heavily damaged, but preserves enough of the articular facet with Mt1 to convincingly demonstrate that it was convex and medially oriented, consistent with an opposable, grasping hallux. The first metatarsal in *Ardipithecus* possesses a sigmoidal, concave articular facet to match the corresponding convex facet on the medial cuneiform.

It appears, however, that the hominin-panin LCA may have possessed lateral metatarsal morphology unlike that found in any modern ape. Based on comparisons with Miocene and extant hominoids, it is reasonable to hypothesize that the LCA had dorsoplantarly short Mt2-3 bases. However, the base of Mt4 in the LCA may have been dorsoplantarly taller with a convex articular facet for the cuboid. Figure 4 illustrates the ratio of dorsoplantar height to mediolateral width of the metatarsal base across the preserved hominoid fossil record for Mt2, Mt3, and Mt4, respectively and presents models for their changes over hominoid evolution. The preserved Mt2 from both *Pierolapithecus* and *Ardipithecus* suggests that dorsoplantarly short Mt2s are the primitive condition for hominoids, which has been retained in the extant apes (though *Pan* may have undergone even more Mt2 base shortening). While the base of the Mt2 has elongated dorsoplantarly over the course of hominin evolution, early hominins like *Ardipithecus*, the Burtele foot, and even the *Australopithecus* material from Sterkfontein still retain the shortened Mt2 bases, further supporting the contention that the Mt2 base of the LCA was short.

There are preserved Mt3 bases from the Miocene hominoids *Ekembo* (formerly *Proconsul*),⁶¹ *Afropithecus*,⁶² and *Nacholapithecus*.⁶³ These bones have the same proportions as those found in modern apes, suggesting that a dorsoplantarly short Mt3 base is primitive and that dorsoplantarly tall Mt3 bases are derived indicators of midfoot rigidity critical for efficient bipedal propulsion. Unfortunately, there is only one undistorted Mt4 base from the Miocene (*Ekembo* specimen KNM-RU 5872) for which proportions of the base can be measured. This bone is dorsoplantarly tall, tentatively suggesting that this is the primitive condition. Additional fragmentary Mt4 bases are known from *Afropithecus* and *Nacholapithecus* and, like all other catarrhine primates, the bases are dorsoplantarly convex, consistent with a midtarsal break in Miocene apes. If this hypothesis is correct, then extant apes have shortened their Mt4 bases, but retained the convex

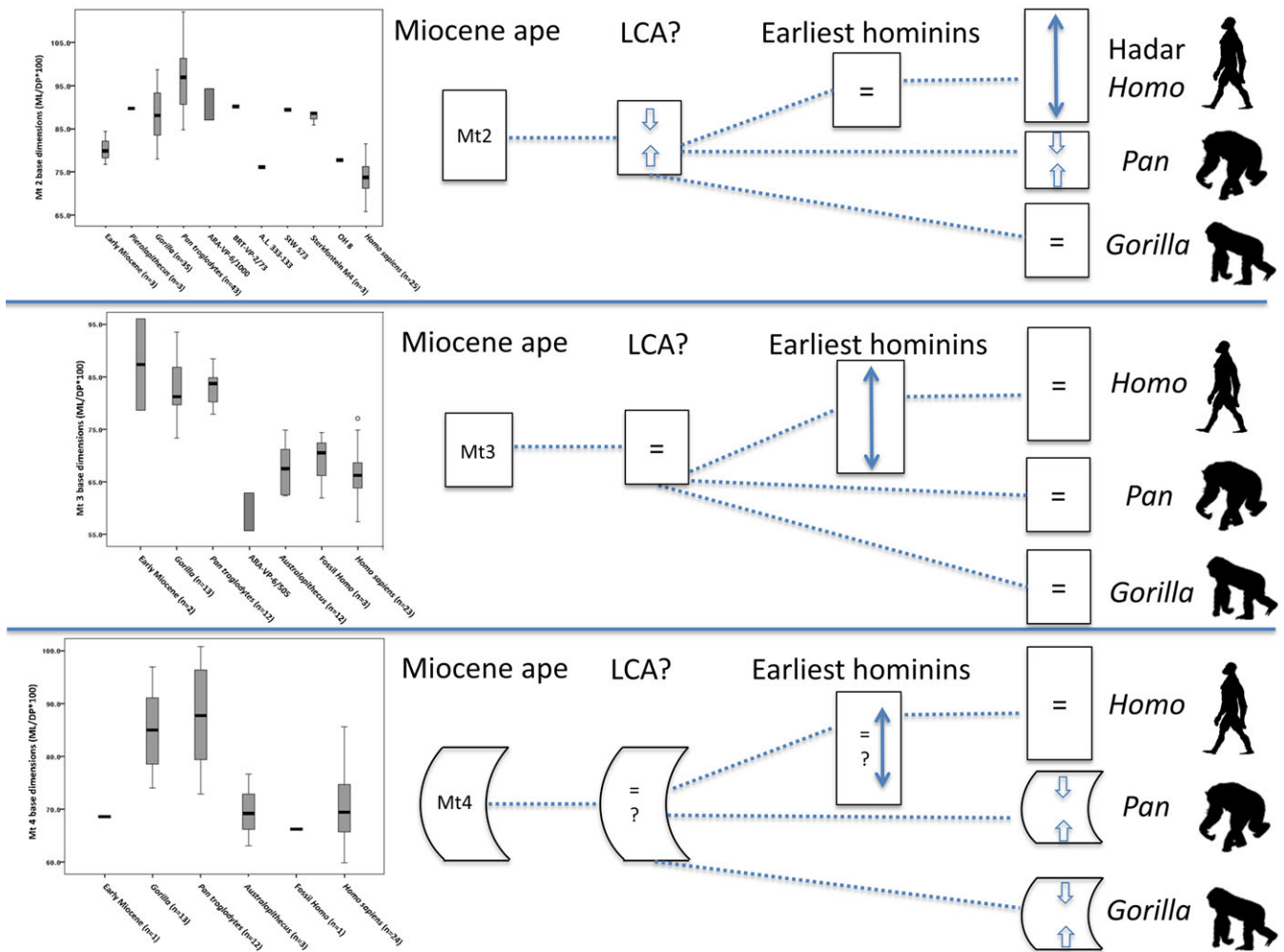


FIGURE 4 Metatarsal (Mt) base evolution. Data from Mt2 are across the top; Mt3 in the middle; and Mt4 at the bottom. The graphs plot the ratio of Mt base mediolateral width divided by dorsoplantar height. **TOP:** The short Mt2 base shared between *Pierolapithecus*, *Ardipithecus*, early hominins, and the African apes indicates that a short Mt2 base is likely primitive in the hominin-panin LCA. This would suggest that the relatively tall Miocene ape Mt2s are not particularly informative for reconstructing the ancestral condition of this particular anatomy. Note that while the Mt2 base remains dorsoplantarly shallow in some hominins (e.g., Sterkfontein), it elongates in *Au. afarensis*, OH 8, and modern humans. **MIDDLE:** The base of Mt3 is dorsoplantarly short in early Miocene hominoids and in modern African apes, suggesting that a short Mt3 base is likely the primitive condition. A tall Mt3 may have evolved to anchor the slips of long plantar ligament, important for stabilizing the midfoot during bipedal propulsion. The presence of a tall Mt3 base in all known hominins, including *Ardipithecus ramidus*, suggests that this is an important and previously overlooked derived hominin pedal anatomy. **BOTTOM:** There are little data on Mt4 morphology in Miocene hominoids. The one specimen preserved (*Ekembo*) suggests that possibly the hominin-panin LCA had a dorsoplantarly tall base, though perhaps not as tall as in humans today. It is perhaps just as likely that during the Miocene, hominoids evolved a dorsoplantarly short Mt4 (as happened with the Mt2 shown above). Nevertheless, the dorsoplantar convexity of the base is found in both Miocene hominoids and in modern African ape Mt4s. The flattening of this base, an anatomy found in *Ardipithecus*, the Burtele (BRT) foot, and all other hominins (except *Au. sediba*) indicates that lateral midfoot stiffness is a key, derived adaptation for facultative, and eventually, obligate bipedal walking. Measurements from *Ardipithecus ramidus* were provided by T. White and G. Suwa

articular surface for the cuboid, thus retaining lateral foot mobility and a midtarsal break.⁵⁰ Again, if correct, early hominins would have inherited a dorsoplantarly tall Mt4 base, but lost the curvature of the proximal facet likely as product of stiffening the midfoot and converting the foot into a more effective lever during bipedal push-off.

The phalanges of the hominin-panin LCA foot are inferred to be relatively long and curved, like the phalanges of modern apes. However, it is possible that the bases of the LCA proximal phalanges were dorsally canted and that this anatomy alone is not necessarily an indicator of bipedal locomotion. While the proximal phalanges of the great apes are plantarly canted, PP5 is occasionally dorsally canted in

Hylobates, and we have observed either neutral or dorsal canting in PP4-5 in *Papio*, *Nasalis*, and *Cebus*. Furthermore, the Kaswanga Primate Site (KPS) individuals of *Ekembo heseloni* preserve proximal phalanges that display dorsal canting,⁶⁴ pers. obs. The phalanges in extant great apes are relatively longer than those found in *Ekembo* and display plantar canting at the bases. Both of these changes represent adaptations to an arboreal life for a large animal and likely evolved to improve grasping and arboreal acrobatics in modern apes.

Although it has been suggested that the chimpanzee foot is too derived, particularly in the midfoot, to serve as a model for the hominin-panin LCA foot,¹⁶ certain elements of the *Pan* foot do appear

TABLE 2 Hominin lateral metatarsals

Metatarsal	Accession number	Taxon	Age (Ma)	Maximum ML base width	Maximum DP base height	Total length (if complete)
2	ARA-VP-6/1000	<i>Ardipithecus ramidus</i>	4.4	18.4–18.8	19.5–21.6	–
2	BRT-VP-2/73b	Hominin sp.	3.4	12.8	14.2	66.9
2	A.L. 333-133	<i>Australopithecus afarensis</i>	3.2	12.1	15.9	–
2	StW 573	<i>Australopithecus prometheus?</i>	3.67?	13.5	15.1	–
2	StW 89	<i>Australopithecus africanus</i>	2.0–2.6	11.0	12.8	61.6
2	StW 377	<i>Australopithecus africanus</i>	2.0–2.6	13.2	14.9	–
2	StW 595c	<i>Australopithecus africanus</i>	2.0–2.6	11.7	13.2	–
2	OH 8	<i>Paranthropus? Homo?</i>	1.85	11.2	14.4	–
3	ARA-VP-6/505	<i>Ardipithecus ramidus</i>	4.4	11.5–13.0	20.5–20.7	–
3	A.L. 333-157	<i>Australopithecus afarensis</i>	3.2	13.5	18.9	–
3	StW 238	<i>Australopithecus africanus</i>	2.0–2.6	12.1	16.3	–
3	StW 387	<i>Australopithecus africanus</i>	2.0–2.6	10.9	16.7	–
3	StW 388	<i>Australopithecus africanus</i>	2.0–2.6	12.6	18.5	–
3	StW 435	<i>Australopithecus africanus</i>	2.0–2.6	13.3	20.1	–
3	StW 477	<i>Australopithecus africanus</i>	2.0–2.6	12.0	16.5	–
3	StW 496	<i>Australopithecus africanus</i>	2.0–2.6	10.9	16.8	–
3	KNM-ER 1500	<i>Paranthropus boisei?</i>	1.89	12	17.7	–
3	OH 8	<i>Paranthropus? Homo?</i>	1.85	11.9	16.0	–
3	KNM-ER 997	<i>Paranthropus boisei?</i>	1.85	10.1	16.2	–
3	F.511-16	<i>Paranthropus? Homo?</i>	1.7	14.6	20.7	–
3	KNM-ER 803	<i>Homo erectus</i>	1.53	12.7	20.5	–
3	SKX 247	<i>Paranthropus robustus?</i>	1.1–1.7	12.2	16.3	–
4	BRT-VP-2/73a	Hominin sp.	3.4	12.7	–	68.7
4	A.L. 333-160	<i>Australopithecus afarensis</i>	3.2	13.1	17.1	59.9
4	StW 485	<i>Australopithecus africanus</i>	2.0–2.6	9.5	14.3	–
4	U.W. 88-22	<i>Australopithecus sediba</i>	1.98	9.2	13.4	56.0 (est.)
4	OH 8	<i>Paranthropus? Homo?</i>	1.85	10.2	15.4	–

ML = mediolateral; DP = dorsoplantar.

Measurements (in mm) from original fossils and published sources.^{19,20} *Ardipithecus* ranges courtesy of T. White and G. Suwa.

consistent with our hypothesized LCA, particularly along the medial column. Generally, the foot of the LCA is hypothesized to have possessed a gracile, ape-like calcaneus; a *Pan*-like talus consistent with an inverted set to the ankle joint; an ape-like medial cuneiform shaped to accommodate a divergent, grasping hallux; and long, curved phalanges. Thus, in the broadest sense, the *Pan* foot is quite similar to the hypothesized LCA foot. However, there were likely important differences as well. There is growing evidence that the LCA midfoot was perhaps stiffer,¹⁶ and more elongated than that found any modern ape (see Box 1). Additionally, it is possible that dorsally canted phalanges may be primitive. These anatomies collectively position the hominin-panin LCA comfortably in an arboreal environment, as reconstructed by the taxa that currently serve as the chronological and phylogenetic bookends to the hominin-panin LCA: *Pierolapithecus catalaunicus* and *Ardipithecus ramidus*.

4 | THE FEET OF THE EARLIEST HOMININS

There are four early hominin taxa currently recognized from the Late Miocene and Early Pliocene: *Sahelanthropus tchadensis*,⁶⁵ *Orrorin tugenensis*,⁶⁶ *Ardipithecus kadabba*,⁶⁷ and *Ar. ramidus*.⁶⁸ There are no

pedal remains recovered from either *Sahelanthropus* or *Orrorin*. Only a single pedal phalanx is known from *Ardipithecus kadabba*. The most complete foot skeleton from these early hominins belongs to *Ardipithecus ramidus* from the Aramis locality in Ethiopia. This foot, discussed below, provides the current basis for our understanding of early hominin foot evolution. However, recently discovered pedal material from Gona, Ethiopia features a more derived talus and first metatarsal than the Aramis *Ardipithecus* revealing variation in bipedal proficiency during the Early Pliocene.⁶⁹

Despite the limitations of the fossil record, some patterns are emerging in our attempt to understand the initial pedal adaptations to bipedalism that evolved soon after the hominin-panin divergence. The very first adaptive modifications for bipedalism appear to happen along the lateral column of the foot.^{15,16,70–72} It is likely that these early changes to the hominin foot rendered the lateral column stiffer for bipedal propulsion, while the medial foot retained mobility critical for climbing. These generalizations are based on quite limited evidence and are subject to change as new fossils are unearthed.

It remains unclear precisely how the lateral foot became more rigid, though two nonmutually exclusive possibilities have emerged. Lovejoy et al.¹⁶ proposed that a moderately stiff lateral midfoot may

actually be the primitive condition, and that one prerequisite for a stiff lateral foot is the os peroneum, a small sesamoid embedded in the tendon of the *M. peroneus longus* as it arcs under the plantolateral surface of the cuboid. In humans, the proximolateral repositioning of the os peroneum is posited to elevate the *M. peroneus longus* tendon out of the groove on the plantar surface of the cuboid and alter its path such that the tendon passes obliquely across the tarsometatarsal joints.¹⁶ Further, this repositioning of the os peroneum at some point in the hominin lineage was associated with a subdivision of the plantar fascial sheet into a short plantar ligament (primitive) and derived long plantar ligament (LPL).¹⁶ *Ardipithecus ramidus* exhibits the primitive form of this anatomy, in which the os peroneum is found within the cuboidal groove as is found in gibbons and cercopithecoid monkeys, but not in great apes.¹⁶ Associated with this primitive anatomy would be the absence of a human-like LPL in *Ardipithecus*. Lovejoy et al.¹⁶ regards the absence of this sesamoid in the great apes to have occurred in parallel as these lineages evolved increasingly arboreally adapted feet. However, we contend that the presence of an os peroneum in both gibbons and modern cercopithecoids suggest that this anatomy is insufficient to stiffen the midfoot alone since these animals also have quite mobile tarsometatarsal joints.⁵⁰ We hypothesize that the evolution of the LPL preceded any changes in the position of the os peroneum and was a key, early hominin innovation that stiffened the lateral midfoot and helped convert a grasping foot into a propulsive lever during facultative bipedal walking. The LPL originates on the plantar surface of the calcaneal body and typically inserts onto the base of Mts 2-5, though insertion patterns vary in humans today.⁷³ This ligament, absent in nonhuman primates,³⁶ spans the lateral tarsometatarsal joint, and would limit dorsiflexion, thus stiffening the lateral midfoot.

The LPL leaves a distinct scar on the plantar surface of the calcaneus just distal to the tuberosity. Its presence, or absence, in an early hominin calcaneus would help test our hypothesis that this ligament played a large role in stiffening the midfoot in the earliest hominins (unfortunately, the calcaneus from *Ardipithecus ramidus* is extensively damaged and does not preserve the plantar aspect of the bone). Ultimately, however, we regard propulsive adaptations along the lateral midfoot in the Aramis skeleton as derived, and evidence for facultative bipedal locomotion in *Ardipithecus ramidus*.

The lateral tarsometatarsal joint of *Ar. ramidus*, in particular Mt4 (ARA-VP-6/500-103), is dorsoplantarily flattened relative to the Mt4 base in cercopithecoids, extant apes, and extinct Miocene apes. This anatomy is consistent with reduced midfoot mobility. Additionally, in *Ardipithecus* the base of Mt3 (ARA-VP-6/505) is dorsoplantarily tall relative to those found in Miocene and extant apes, helping increase foot rigidity while pushing off of the outside of the foot (often called the oblique axis) (Figure 4). A tall Mt3 base appears in all hominin Mt3s for which the anatomy is preserved, suggesting that this is one of the earliest pedal adaptations for bipedal locomotion and may represent a useful diagnostic for examining new fossil finds (Table 2). However, *Ar. ramidus* retains a primitive Mt2 base, and a divergent Mt1 demonstrating the derived lateral, but primitive medial aspects of this foot.

The head of the Mt3 (ARA-VP-6/505) is dorsally domed and functionally corresponds to the dorsally canted bases of the proximal phalanges in *Ar. ramidus*.¹⁶ Together these two anatomies suggest that

this animal was capable of the high degree of dorsiflexion at the metatarsophalangeal joints necessary to effectively push-off the lateral toes. This combination of anatomies is present in all hominin species which preserve these elements, including modern humans. A proximal phalanx (AME-VP-1/71) from *Ar. kadabba* also displays dorsal canting.⁶⁷ This bone provides tantalizing evidence that this species may have also utilized bipedal locomotion. However, the presence of this anatomy in the KPS individuals from *Ekembo heseloni*,⁶⁴ a quadrupedal Miocene ape, calls its validity as a standalone diagnostic for bipedalism into question. The discovery of additional fossil material is necessary to test the bipedal capabilities of *Ar. kadabba*.

We interpret the Aramis *Ardipithecus* foot as one that is ape-like and primitive along the medial column, but fairly derived laterally. The stiffening of the lateral midfoot allowed early hominins to push off the outside of the foot while striding bipedally without sacrificing the grasping ability of the medial forefoot. We therefore support previous suggestions about the mosaic nature of hominin foot evolution proposing a "lateral first" timing on the evolution of the foot.^{15,16,70,71} The medial foot in these Pliocene hominins bears a striking resemblance to that found in modern apes, still retaining an inverted set to the ankle joint (based on the *Ardipithecus* talus), and a divergent, grasping hallux. This combination of anatomies indicates that the earliest facultative bipedal hominins still relied heavily on climbing for their survival.

5 | AUSTRALOPITHECUS FEET

The genus *Australopithecus* (including *Paranthropus*) evolved by 4 Ma and persisted until about 1 Ma. *Australopithecus* represent the largest radiation of hominin species diversity currently known, and recent evidence suggests that different australopiths exhibited not only locomotor diversity, but distinct kinematic differences during bipedal gait. The oldest species attributed to this genus is *Australopithecus anamensis*, which is currently known from 3.7 to 4.2 Ma sites in Eastern Africa. There are only two, heavily damaged and uninformative pedal remains attributed to this species: a segment of Mt2 shaft and partial proximal phalanx.⁷⁴ However, a 4.2 Ma distal tibia from Kanapoi, Kenya^{75,76} has a thin medial malleolus and square-shaped articular facet with the talus suggesting that the forces at the ankle joint were evenly distributed, as occurs in bipedal humans.³⁸

The pedal skeleton of *Australopithecus afarensis* is the best represented from any australopith species, with nearly all elements known. It is likely that this species also made the "G" and "S" footprint trails at Laetoli, Tanzania. The vast majority of *Au. afarensis* pedal fossils come from the 333 Hadar locality in Ethiopia and date to 3.2 Ma.²⁰ The foot of *Au. afarensis* is human-like in a number of ways. The calcaneal tuberosity (A.L. 333-8, -37, -55) is robust and the lateral plantar process is plantarly positioned and expanded, as in the modern human heel. Together these anatomies indicate that *Au. afarensis* was well-adapted for dissipating the high forces caused by heel-striking bipedality.⁴⁰ The trochlea of the talus is only moderately wedged and has a human-like talar axis angle, consistent with a human-like, orthogonally oriented tibia.^{37,38}

The navicular of *Au. afarensis* is mosaic. The body is generally human-like⁷⁷ and possess a strong attachment for the spring ligament,

TABLE 3 Medial cuneiform facet angulation and curvature

Accession number	Taxon	Age	Radius of curvature (cm)	Navicular angle (°)	Dorsoplantar height (mm)
StW 573	<i>Australopithecus prometheus?</i>	3.67?	1.51	103.7	25.0
A.L. 333-28	<i>Australopithecus afarensis</i>	3.2	1.01	94.0	29.5 (est.)
OH 8	<i>Paranthropus? Homo?</i>	1.85	1.50	104.8	24.4

Data from Gill et al.⁸⁰ and original fossils.

which would help support the midfoot.⁷⁸ However, the navicular has both an ape-like projecting tuberosity¹⁸ and angulation between the cuneiform facets.⁷⁹ The lateral cuneiform (A.L. 333-79) is proximodistally elongated, indicative of a human-like elongated midtarsus. While the bones just discussed are unmistakably from a biped, the medial cuneiform (A.L. 333-28) is more controversial. The distal facet for the Mt1 has a human-like distally directed orientation, indicating that the Mt1 was in an adducted position as in humans today.^{45,80} However, the Mt1 facet is also quite convex, indicating more hallucal mobility than is typical of modern humans (Table 3 and Figure 5),⁸⁰ especially in the juveniles.³² Additionally, the base of Mt1 (A.L. 333-54) is intermediate in shape between humans and apes.⁸¹ Some have interpreted

these findings as evidence for retained hallucal grasping and arboreality in *Au. afarensis*,^{41,44} while others contend this anatomy is indicative of a push-off mechanism that is not fully human.⁴⁵ Either way, the *Au. afarensis* foot contains additional evidence that the lateral forefoot evolved human-like anatomies prior to the medial forefoot.

The lateral Mt bases are human-like and dorsoplantarly tall, indicating a stiff lateral midfoot adapted for bipedal push-off.⁸² A complete Mt4 (A.L. 333-160) displays strong external torsion, which is consistent with the presence of a human-like transverse arch. Whether a longitudinal arch was present in the foot of *Au. afarensis* remains controversial with some suggesting its presence,^{82,83} and others its absence.^{18,79} We suggest that dichotomizing this feature

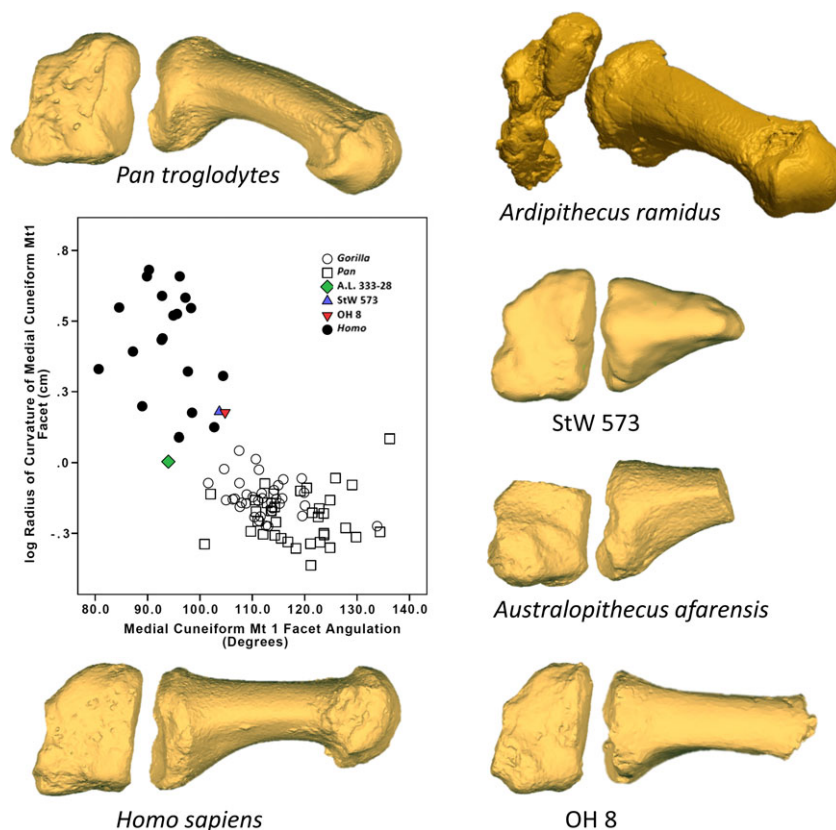


FIGURE 5 Arguably, the most substantial difference between a modern human and ape foot is the orientation of the hallux. In humans (bottom left), the hallux—shown here in medial view—is nongrasping and distally oriented. The chimpanzee (top left), in stark contrast, has a hallux that is divergent and capable of grasping. Notice how the hallucal facet on the medial cuneiform is flat and barely visible on the human bone whereas the facet is convex and spills onto the medial surface of the bone in the chimpanzee. Each fossil has been oriented in the same manner for visual comparison and mirrored to reflect the left foot if necessary. Although it is damaged, the Mt1 facet on the *Ardipithecus ramidus* medial cuneiform is *Pan*-like in being both convex and spilling onto the medial aspect of the bone. In contrast, the medial cuneiform in early hominins (StW 573, Hadar, and OH 8) is more human-like, resulting in a more adducted hallux. We graphed the radius of curvature of the Mt1 facet against the orientation of the facet from data in Gill et al.⁸⁰ and plot them here. Notice that African apes (open circles and squares) plot in a distinct space from humans (black circles). Interestingly, the Hadar medial cuneiform possesses more ape-like convexity, but human-like angulation. StW 573 and OH 8 possess more human-like convexity, but slightly more ape-like angulation. Image of *Ardipithecus ramidus* provided by G. Suwa

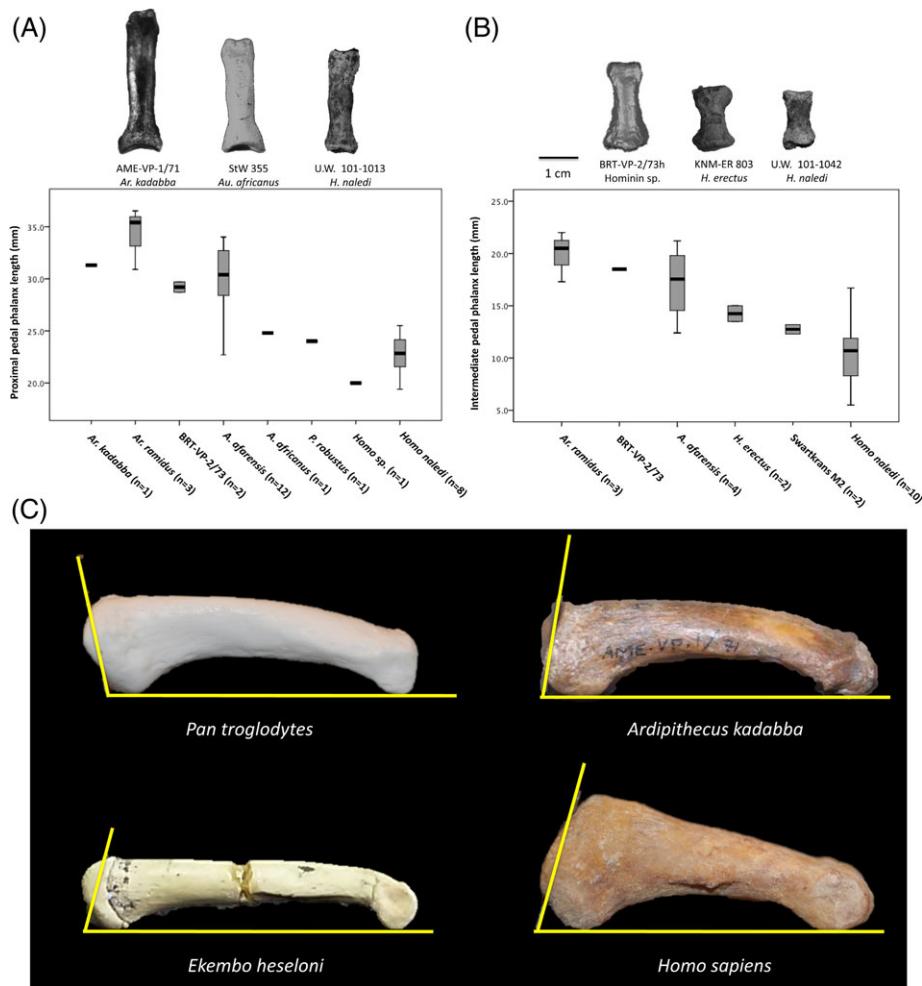


FIGURE 6 Absolute phalangeal lengths are plotted for the proximal (a) and intermediate (b) pedal toe bones. Notice that over time, phalangeal length decreases quite systematically for both bones. These measurements are not standardized by body size, which would likely reveal a more dramatic decrease in relative phalangeal length given elevated body size estimates in *Homo* relative to earlier hominins. (c) Lateral (fourth or fifth) proximal phalanges were photographed from the side. A pin was held against the proximal facet to visualize the orientation of the facet relative to a horizontal; this angle has been redrawn in yellow for clarity, and because the proximal facet is obscured in lateral view by the rim of bone along the edge of the metatarsal facet. Notice that (top left) the chimpanzee proximal facet has a plantar cant. As reported elsewhere,⁶⁷ the *Ar. kadabba* proximal phalanx has a human-like dorsal cant. However, this orientation can also be found on the lateral proximal phalanges of the early Miocene hominoid *Ekembo*.⁶⁴ Shown here are original fossils all scaled to the same proximodistal length

has not been a productive exercise. Instead, the *Au. afarensis* arch was likely variable (as in humans today), and in general more developed than that of modern apes, but less developed than the typical human.³²

A.L. 333-115 is an associated forefoot consisting of all of the Mt heads and parts of eight pedal phalanges.⁷⁸ The heads of the lateral metatarsals all display dorsal doming, which together with the dorsal canting of the lateral phalanges indicate bipedal push-off.⁴⁷ However, while the head of Mt1 is dorsally domed, its dorsally narrow mediolateral width indicates that relative to modern humans, *Au. afarensis* possessed a more primitive push-off mechanism.⁴⁶ Fernández et al.⁸⁵ have found that the morphology of the A.L. 333-115 forefoot is indicative of a biped, but one with less medial weight transfer and a greater reliance on the oblique axis of the foot than most modern humans. The lateral phalanges of *Au. afarensis* are relatively and absolutely long and curved (Figure 6), consistent with *Au. afarensis* utilizing an arboreal environment to forage and survive at night.

The 3.6 Ma Laetoli footprints (trackways “G” and “S”) from Tanzania have generally been attributed to *Au. afarensis*. These footprints were made by bipedal hominins moving with an extended hip and extended knee,⁸⁶ though perhaps with a gait different from that practiced by modern humans.⁸⁷ The prints bear a strong resemblance to those made by modern humans today^{13,88}; however, there are several key differences. One hominin (G1) experienced less medial weight transfer than is typically seen in humans^{52,87} and analyses suggest that while the medial arch was present, it was likely reduced relative to most humans today.^{29,52,83} Additionally, consistent with *Au. afarensis* skeletal material, there seems to be a moderate increase in hallucal mobility compared to the modern human foot.²⁹ Together, these attributes of the prints suggest that *Au. afarensis* was engaging the transverse axis of the foot during the push-off phase of bipedal gait more than is found in the earliest hominins, although medial weight transfer was in general less than in humans today. Some humans today walk in this manner, but this finding in both the Laetoli footprints and the

TABLE 4 Complete hominin lateral phalanges

Accession number	Element	Taxon	Age (Ma)	Length (mm)
AME-VP-1/71	PP4	<i>Ardipithecus kadabba</i>	5.2	31.3
ARA-VP-6/500-094	PP4	<i>Ardipithecus ramidus</i>	4.4	35.4
ARA-VP-6/500-008	PP3	<i>Ardipithecus ramidus</i>	4.4	36.5 (est.)
ARA-VP-6/500-044	PP5	<i>Ardipithecus ramidus</i>	4.4	30.9
BRT-VP-2/73e	PP2	Hominin sp.	3.4	29.7
BRT-VP-2/73d	PP4	Hominin sp.	3.4	28.7
A.L. 288-1	PP	<i>Australopithecus afarensis</i>	3.2	22.7
A.L. 333-26	PP	<i>Australopithecus afarensis</i>	3.2	30.9
A.L. 333-60	PP	<i>Australopithecus afarensis</i>	3.2	27.9
A.L. 333-71	PP	<i>Australopithecus afarensis</i>	3.2	32.5
A.L. 333-168	PP	<i>Australopithecus afarensis</i>	3.2	32.9
A.L. 333-145	PP2	<i>Australopithecus afarensis</i>	3.2	29.6
A.L. 333-154	PP4	<i>Australopithecus afarensis</i>	3.2	27.4
A.L. 333-167	PP2	<i>Australopithecus afarensis</i>	3.2	29.6
A.L. 333-115g	PP2	<i>Australopithecus afarensis</i>	3.2	32.2
A.L. 333-115h	PP3	<i>Australopithecus afarensis</i>	3.2	34.5
A.L. 333-115i	PP4	<i>Australopithecus afarensis</i>	3.2	32.8
A.L. 333-115j	PP5	<i>Australopithecus afarensis</i>	3.2	28.6
StW 355	PP	<i>Australopithecus africanus</i>	2.0–2.6	24.8
DNH 117	PP	<i>Paranthropus robustus</i>	1.4–2.0	24.0
SKX 16699	PP	<i>Homo?</i>	~1.8	20.0
U.W. 101-504	PP	<i>Homo naledi</i>	0.24–0.34	25.5
U.W. 101-976	PP	<i>Homo naledi</i>	0.24–0.34	23.6 (est.)
U.W. 101-1013	PP	<i>Homo naledi</i>	0.24–0.34	22.4
U.W. 101-1034	PP	<i>Homo naledi</i>	0.24–0.34	19.4
U.W. 101-1148	PP	<i>Homo naledi</i>	0.24–0.34	21.5
U.W. 101-1395	PP	<i>Homo naledi</i>	0.24–0.34	21.6
U.W. 101-1441	PP	<i>Homo naledi</i>	0.24–0.34	23.3
U.W. 101-1452	PP	<i>Homo naledi</i>	0.24–0.34	24.7
ARA-VP-6/500-021	IP4	<i>Ardipithecus ramidus</i>	4.4	20.5
ARA-VP-6/500-004	IP5	<i>Ardipithecus ramidus</i>	4.4	17.3
ARA-VP-6/500-128	IP3	<i>Ardipithecus ramidus</i>	4.4	21.5–22.5
BRT-VP-2/73h	IP	Hominin sp.	3.4	18.5
A.L. 333-21a	IP	<i>Australopithecus afarensis</i>	3.2	21.2
A.L. 333-115	IP	<i>Australopithecus afarensis</i>	3.2	18.4
A.L. 333-115l	IP	<i>Australopithecus afarensis</i>	3.2	16.7
A.L. 288-1	IP	<i>Australopithecus afarensis</i>	3.2	12.4
SKX 344	IP	<i>Paranthropus? Homo?</i>	1.1–1.7	12.3
SKX 1261	IP	<i>Paranthropus? Homo?</i>	1.1–1.7	12.3
KNM-ER 803k	IP	<i>Homo erectus</i>	1.53	13.5
KNM-ER 803l	IP	<i>Homo erectus</i>	1.53	15.0
U.W. 101-550	IP	<i>Homo naledi</i>	0.24–0.34	12.7
U.W. 101-661	IP	<i>Homo naledi</i>	0.24–0.34	10.6
U.W. 101-988	IP	<i>Homo naledi</i>	0.24–0.34	11.5
U.W. 101-1042	IP	<i>Homo naledi</i>	0.24–0.34	11.9
U.W. 101-1399	IP	<i>Homo naledi</i>	0.24–0.34	16.7
U.W. 101-1438	IP	<i>Homo naledi</i>	0.24–0.34	10.8
U.W. 101-1484	IP	<i>Homo naledi</i>	0.24–0.34	8.6
U.W. 101-1549	IP	<i>Homo naledi</i>	0.24–0.34	8.3
U.W. 101-1587	IP	<i>Homo naledi</i>	0.24–0.34	5.5
U.W. 101-1594	IP	<i>Homo naledi</i>	0.24–0.34	6.3

PP = proximal phalanx; IP = intermediate phalanx.

Data from published sources^{16,20,23} and measurements taken on original fossils.

Hadar forefoot remains suggest that the push-off mechanism in *Au. afarensis* was less refined than in humans today.

If the foot from *Au. afarensis* is surprisingly human-like, the ~3.4 Ma foot (BRT-VP-2/73) from Burtele, Ethiopia¹⁹ is distinctly not. The Burtele foot is not currently assigned to a taxonomic group. It was discovered close to the location of the recently described taxon *Au. deyiremeda*,⁸⁹ however its primitive nature would also be consistent with a late occurring *Ardipithecus*. Additional discoveries are necessary to resolve the taxonomic identity of the Burtele foot. The medial angulation and sigmoid shaped facet on the base of Mt1 is consistent with moderate hallucal divergence. There is no dorsal doming of the head of Mt1, suggesting that the hallux played a limited role during bipedal propulsion. The Mt2 possesses ape-like internal torsion and a dorsoplantarily foreshortened base, consistent with a mobile, grasping medial midfoot. The Mt2 also displays longitudinal curvature in the transverse plane, which would allow the second digit to oppose the hallux during arboreal grasping behaviors. The Mt4 is unusually long relative to those found in extant hominoids and suggests that the Burtele hominin pushed off the oblique axis during bipedal bouts. Though damaged, the articular facet for Mt4 with the cuboid appears to be relatively flat suggesting that there was decreased lateral midfoot mobility, as in *Ardipithecus* and most *Australopithecus*. The lateral metatarsal heads are dorsally domed, and together with dorsally canted proximal phalanges, are consistent with bipedal propulsion along the oblique axis of the foot. The phalanges are relatively long and curved. The Burtele foot, therefore, provides evidence for a hominin that was still highly dependent on arboreal locomotion, but was also capable of a primitive form of bipedalism. This foot, while contemporaneous with *Au. afarensis*, is morphologically distinct, providing strong evidence for locomotor diversity and different forms of bipedal gait in the Pliocene of Eastern Africa.¹⁹

Meanwhile, recent re-dating of "Little Foot" StW 573 to 3.6 Ma suggests that this South African fossil, perhaps belonging to *Au. prometheus*, may have been contemporaneous with *Au. afarensis* and the Burtele hominin.⁹⁰ The foot of StW 573 is fairly complete, containing the talus, navicular, all three cuneiforms, and the bases of Mt1 and Mt2. The Mt1 was originally described as being divergent,¹⁴ but see.^{16,18,80,91} However, the recovery of the intermediate and lateral cuneiforms and base of Mt2,⁹² change the orientation of the elements of the medial foot such that a divergent hallux no longer seems possible (Figures 1 and 5; Box 1). The anatomy of the Mt1 facet on the medial cuneiform is strikingly similar to that found in the geologically more recent OH 8 foot.⁸⁰ If the 3.6 Ma date is accepted, but see⁹³ then StW 573 would represent some of the oldest evidence for an adducted hallux in the human fossil record.

Pedal remains from the South African australopith *Au. africanus* have only been discovered at Sterkfontein Member 4, dated to ~2.0 to 2.6 Ma.⁹⁴ There is one calcaneus (StW 352) attributed to this species.^{92,95} The posterior tuberosity is missing, but what is preserved is relatively gracile,⁹⁶ and the subtalar joint has an ape-like degree of convexity, suggesting that this joint was fairly mobile.⁹⁷ The tali from Member 4 all display even trochlear rims with unwedged trochlear surfaces, indicating that the tibia was orthogonally positioned relative to the talus, as in humans today.³⁸ Trabecular microarchitecture of the distal tibiae is also consistent with human-like axial loading of the

ankle joint during bipedalism.⁹⁸ However, the talar heads, and necks lack plantar declination, suggesting perhaps that the medial longitudinal arch was not as developed in *Au. africanus*. Two sets of Mt1s (StW 562 and StW 595) and Mt2s (StW 89 and StW 377) in the Member 4 assemblage present a challenge for interpreting locomotion in *Au. africanus*. StW 562 is a large, robust Mt1 with a dorsoplantarily tall base and human-like dorsally domed head. StW 595, in stark contrast, is a relatively long, more ape-like Mt1 that lacks the dorsal doming present on StW 562, and is instead reminiscent of the Burtele Mt1. While possible, we find it unlikely that these two Mts both belong to *Au. africanus*. Similarly, StW 89 resembles the Burtele Mt2 in possessing internal torsion, longitudinal curvature, and a dorsoplantarily short base; while StW 377 is more human-like.⁹⁹ It is possible that these bones are evidence for a mixed taxonomic assemblage at Sterkfontein and yet more locomotor diversity in the australopiths.

The 1.98 Ma foot from *Au. sediba* provides evidence for yet another distinct locomotor strategy compared to that found in other *Australopithecus* species. The calcaneus (U.W. 88-99) is gracile compared to other hominin calcanei,^{21,96} with an ape-like dorsally positioned lateral plantar process. The medial plantar process is also ape-like in being beaked, an anatomy thought to reflect an important role for *M. flexor digitorum brevis* during pedal grasping. The subtalar joint is highly convex,^{21,97} suggesting that a large degree of mobility is possible at this joint. A geometric morphometrics analysis of the *Au. sediba* calcaneus relative to the Hadar calcanei positions U.W. 88-99 outside the human range of variation, near modern gorillas and chimpanzees (Figure 3). Furthermore, unlike every other Mt4 in the hominin fossil record, the base of the Mt4 of *Au. sediba* is dorsoplantarily convex implying lateral midfoot mobility and a "midtarsal break."⁵³ The unusual anatomies present in the *Au. sediba* foot, as well as elsewhere in its postcrania, have led researchers to hypothesize that this australopith frequently climbed, and walked bipedally with a non-pathological hyperpronating gait.¹⁰⁰

Unfortunately, little is known about the foot of the robust australopiths. In South Africa, remains attributed to *Paranthropus robustus* are often co-mingled with early *Homo*, preventing definitive attribution. However, it is generally accepted that TM 1517 D from Kromdraai is a *Paranthropus* talus, Swartkrans fossils SK 1813 and SKX 5017 are *Paranthropus* Mt1s, and Drimolen fossils DNH 115 (proximal Mt1) and DNH 117 (proximal phalanx) are tentatively described as *Paranthropus*.¹⁰¹ While generally human-like, the talus has a deeply keeled trochlea and an unusually large talar head and the Mt1s possess a mediolaterally narrow head dorsally,¹⁰² and the proximal articular surface is ape-like.⁸¹ Lateral foot bones (cuboid, Mt5, and proximal phalanx)⁷² are human-like, consistent with a derived lateral foot in australopiths. However, it is difficult to interpret the functional importance of these isolated fossils (or even taxonomically attribute them to *Paranthropus*) until a more complete *P. robustus* foot is discovered.

As with the South African *Paranthropus* foot, the foot of the Eastern African robust forms is poorly known, again, in part because *P. boisei* remains are found in the same localities as early *Homo*. A calcaneus from Omo (Omo 33-74-896), which possesses a quite gracile tuberosity⁹⁶ could be from *Paranthropus*, or alternatively could be from *Homo*.¹⁰³ There are also fragmentary metatarsals, including a newly described 2.1 Ma Mt2 (OMO 323-1976-2117) from Omo, that

TABLE 5 Talus measurements

Accession number	Taxon	Age (Ma)	Mediolateral width of trochlear body	Dorsoplantar height of lateral body (after ¹¹⁷)
A.L. 333-147	<i>Australopithecus afarensis</i>	3.2	24.1	21.2
A.L. 288-1	<i>Australopithecus afarensis</i>	3.2	18.0	15.5
StW 88	<i>Australopithecus africanus</i>	2.0–2.6	19.1	19.5
StW 102	<i>Australopithecus africanus</i>	2.0–2.6	19.4	18.9
StW 363	<i>Australopithecus africanus</i>	2.0–2.6	19.0	15.8
StW 486	<i>Australopithecus africanus</i>	2.0–2.6	21.0	19.9
Omo 323-76-898	<i>Homo?</i>	2.2	23.2	25.8
U.W. 88-98	<i>Australopithecus sediba</i>	1.98	18.1	19.3 (est.)
KNM-ER 1476	<i>Paranthropus?</i>	1.88	20.4	19.4
KNM-ER 813	<i>Homo?</i>	1.85	24.7	22.0
OH 8	<i>Paranthropus? Homo?</i>	1.85	19.5	17.1
KNM-ER 1464	<i>Paranthropus?</i>	1.7	25.3	24.2
TM 1517	<i>Paranthropus robustus</i>	1.6–1.8	18.9	16.1
SKX 42695	<i>Paranthropus? Homo?</i>	1.5–2.0	23.1	18.6
KNM-ER 5428	<i>Homo erectus</i>	1.60	33.9	22.6
U.W. 101-148/149	<i>Homo naledi</i>	0.24–0.34	20.6	20.5
U.W. 101-520	<i>Homo naledi</i>	0.24–0.34	18.3	20.3
U.W. 101-1417	<i>Homo naledi</i>	0.24–0.34	18.4	18.5
Omo-Kibish	<i>Homo sapiens</i>	0.195	29.2	22.8

Data from original fossils.

may be from *Paranthropus*.¹⁰⁴ Tali are well-represented from Koobi Fora, Kenya and they appear to exist in two morphs, likely attributable to *Paranthropus* and early *Homo*. The likely *Paranthropus* tali (KNM-ER 1464 and ER 1476) possess deeply keeled trochlear surfaces, and a medial deflection of the head and neck in the transverse plane, similar to that found in TM 1517 (*P. robustus*). These anatomies suggest a potentially different mechanism for stabilizing the ankle joint in *Paranthropus*, but functional assessments of the *Paranthropus* foot must remain tentative until more pedal remains definitively associated with *P. boisei* are recovered. Some (including us) believe this has already happened and that the OH 8 foot represents *P. boisei*.¹⁰⁵ We are convinced by the similarities between the OH 8 talus and KNM-ER 1464¹⁰³ that the Olduvai foot is from a robust australopith and not from *H. habilis*. However, the evidence to test this hypothesis remains scarce and we will adopt the traditional views of our field and discuss the OH 8 foot in the next section, the evolution of the *Homo* foot.

Recent discoveries of australopith pedal fossils have revealed extensive variation in bipedal kinematics and variation in locomotor repertoires present throughout the hominin fossil record from ~2 to 4 million years ago. Despite these differences, there are a suite of changes which broadly characterize foot evolution in the transition from an *Ardipithecus*-grade animal to *Australopithecus*. The phalanges decrease in relative size, likely to help improve efficiency during bipedal gait (Table 4). This reduction in phalangeal length would further imply a reduced reliance on pedal grasping (Figure 6). The talocrural joint becomes decidedly human-like, positioning a vertical tibia directly over an everted foot—a geometry of the lower limb consistent with the development of a bicondylar angle. Furthermore, there is the loss of a divergent hallux (but see Burtele foot). Unlike in *Ardipithecus*,

an adducted hallux contributes to push-off along the transverse axis of the foot. However, the transition from the oblique to transverse axis may not be fully complete in australopiths, as both data from the Laetoli footprints and australopith fossils in both Eastern and South Africa are consistent with a hallux that retains slightly more mobility than is found in modern humans. These morphologies are consistent with a weakened push-off mechanism and perhaps a continued reliance on some arboreal behavior.

6 | HOMO FEET

The origin of *Homo* remains contentious, though there is fragmentary craniodental evidence that our genus was evolving between 2 and 3 Ma.¹⁰⁶ There are two foot fossils from the Shungura Formation in the Omo Valley, Ethiopia that have been hypothesized to be early *Homo*: Omo-323-76-898, a ~2.2 Ma talus and Omo-33-74-896 a ~2.36 Ma calcaneus.¹⁰³ The Omo talus is human-like with an unwedged and dorsoplantarly tall trochlear body, a high head/neck torsion angle, and low talar neck angle.¹⁰³ We agree that the Omo talus is quite derived and could represent *Homo*. However, there are some unusual anatomies present in Omo-33-74-896 that make the attribution of that calcaneus to *Homo* suspect.¹⁰⁷ The posterior tuberosity is gracile,⁹⁶ the medial plantar process is beaked, and the peroneal trochlea is large and laterally projecting. These characteristics are primitive and more similar to those found in earlier hominins, making it possible that the Omo calcaneus is from *Paranthropus*.

Among the oldest pedal fossils attributed to *Homo* is the 1.85 Ma foot, OH 8.¹⁰⁸ In general, the OH 8 foot is derived and likely from a human-like striding biped.^{108,109} This partially complete foot includes a

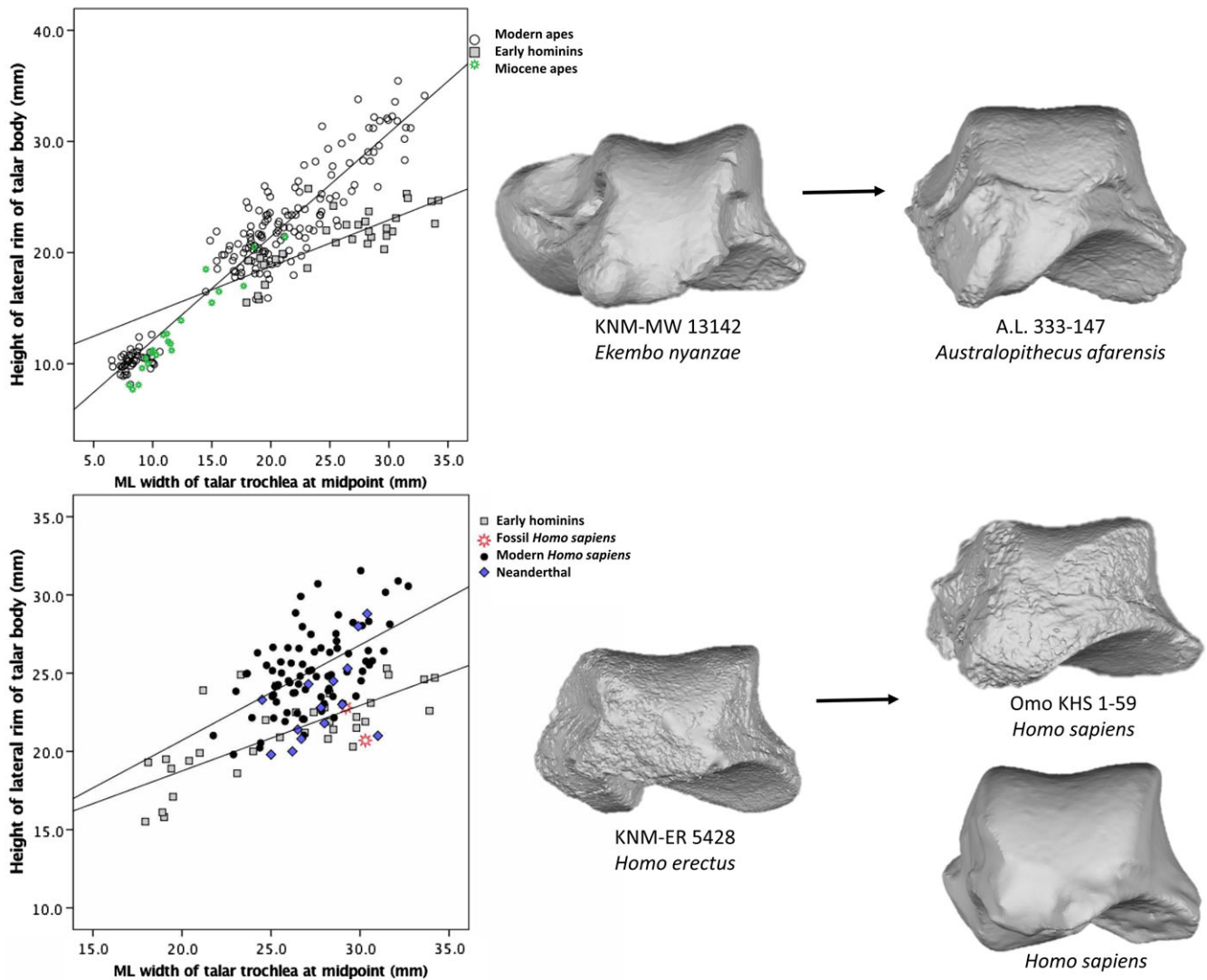


FIGURE 7 Talar evolution (modeled after Boyle and DeSilva).¹¹⁷ Top left: The height of the lateral trochlear rim and the mediolateral width of the talar trochlea are plotted for modern and Miocene ape tali. Lines drawn to represent reduced major axis regressions through modern ape tali (excluding humans) and early hominin fossils. Notice that early hominins (gray squares), have considerably lower lateral talar rims relative to the width of the trochlea. We hypothesize that a crucial, early, evolutionary change in the ankle joint was the relative reduction of the lateral trochlear rim which would lower the talar axis angle and result in an orthogonal tibia over an everted foot and mediolateral talar expansion which would help dissipate high axial loads on the ankle joint during bipedalism. This change is illustrated to the right with a comparison between the high lateral rim in *Ekembo* compared with the parallel trochlear rims found in *Australopithecus* tali. All images of tali scaled to same mediolateral width of trochlear body. Bottom: The same measurements (lateral trochlear rim height and mediolateral width of the talar trochlea) are plotted for early hominins (as in the top graph), but also modern humans, and late Pleistocene *Homo* fossils. Lines represent reduced major axis regressions through modern human tali (top line) and early hominin tali (bottom line). Notice that compared with earlier hominins, modern humans have a taller trochlear body. A dorsoplantarily short talar body characterizes otherwise quite human-like tali found in *H. erectus* and even the earliest *H. sapiens* talus from Omo-Kibish. Why the modern human talus is dorsoplantarily taller than previous hominin tali, including early members of our own species, is unclear

medial cuneiform with a relatively flat facet for the Mt1, and evidence for a fully adducted hallux. The cuboid beak is eccentrically oriented, which indicates the presence of a human-like locking mechanism at the calcaneocuboid joint.¹⁰⁹ The pattern of robusticity within the metatarsals is similar to humans, though unlike the most common human pattern.¹¹⁰ More recent microcomputed tomography (μ CT) analysis of the internal cortical structure of OH 8 reveals metatarsal robusticity patterns unlike humans or apes.¹¹¹ However, the talus of OH 8 is not *Homo*-like at all. The trochlea is deeply keeled, as found in tali from Koobi Fora often assigned to *Paranthropus*. The OH 8 talus also shares similarities in both neck length and head/neck torsion angles with TM

1517, a talus from Kromdraai, South Africa typically thought to belong to *Paranthropus robustus*. These similarities and others have led some researchers to hypothesize that OH 8 may not belong to *H. habilis*.^{103,105} Anticipated publication of the recently discovered, remarkably complete, foot of early *Homo* from Ileret³³ may provide some clarity on the taxonomic status of the OH 8 foot. Jungers (pers. comm.) says of this new fossil: "The Mt1 is gracile but fully adducted and its head is like other fossil Mt1 in being domed but lacking the dorsal broadening and flattening seen in modern humans, whereas the other MT heads are more modern in aspect; the tuber of the calcaneus is inflated and a derived lateral plantar process is present; oddly, the

navicular is very pinched laterally, more so than in LB1 or Little Foot." It is likely that when fully published this fossil will provide much needed clarity regarding the morphology of the early *Homo* foot in Africa.

Early *Homo* foot fossils are also known from the 1.77 Ma locality of Dmanisi, Georgia. These include a talus, medial cuneiform, and several metatarsals. The talus is quite human-like, with an unwedged, unkeeled trochlea, and high head/neck torsion and declination angles.²² The metatarsal shaft torsion is consistent with human-like transverse and longitudinal arches in the Dmanisi hominins. However, Pontzer et al.²² also report some primitive features in this early *Homo* foot. The Mt1 lacks the mediolaterally expanded head and the metatarsal robusticity differs from that typically found in modern humans. These observations tentatively suggest that the Dmanisi hominins had not yet evolved a fully human toe-off during bipedal gait.²² However, footprints from Ileret, Kenya demonstrate that human-like arches and a modern toe-off mechanism were present in *Homo* by 1.5 Ma.^{29,112}

Between approximately 1.7 Ma and 500 ka, there is a relative dearth of hominin foot fossils that make it difficult to characterize Early and early Middle Pleistocene foot evolution, but see.²⁵ However, the number of pedal remains increases dramatically after this period. The 430 ka Sima de los Huesos locality (Atapuerca, Spain) has yielded over 500 foot fossils from a pre-Neandertal taxon.^{26,113} The feet of this late *Homo* population possess most of the same morphologies as modern human feet do today. However, there are some subtle, albeit notable, differences. The tali have a short neck, narrow head, and a more rectangular trochlea (Table 5).^{26,113} The calcaneus is fairly human-like with a long, robust posterior tuberosity.^{26,113} However, the sustentaculum tali is more projecting than that found in modern humans or Neandertals.^{26,113} The naviculars from Sima are relatively broad and the intermediate cuneiform short compared to humans and Neandertals.^{26,113} Similarly, scholars have found subtle differences, particularly along the medial column, between the modern human foot and a late *Homo* foot from the 250 ka site of Jinniushan, China.²⁷ It remains unclear how (or whether) these subtle differences between modern human foot anatomy and those Middle Pleistocene *Homo* fossils have any functional significance.

The Neandertal foot is well-known and well-studied, with every bone of the foot represented.^{113,114} Early work on the Neandertal foot (particularly La Chapelle aux-saints) interpreted the anatomy as being more primitive, including even the possession of a mobile hallux.¹¹⁵ However, the discovery and interpretation of additional remains from La Ferrassie, Kiik-Koba, Shanidar, Tabun, and many other localities demonstrate that Neandertal feet were quite similar to those possessed by modern humans.¹¹⁴ However, differences have been identified. Neandertals tend to have broader talar trochlea and a larger lateral malleolar facet on the talus.¹¹³ The Neandertal calcaneus is mediolaterally wide and the sustentaculum tali is especially broad.¹¹³ The navicular is wide and robust, as are, in general, the metatarsals and phalanges.¹¹³ The proximal hallucal phalanges are short relative to the distal phalanges. Unlike in modern humans, the Neandertal proximal pedal phalanges are wider relative to their height, possibly an adaptation to handle higher mediolateral stress across the phalanges.¹¹⁴ Neandertals also have larger attachment sites for plantar musculature, in particular on the medial tuberosity of the calcaneus, and tend to have more developed flexor ridges than found in

modern humans.¹¹⁴ The Neandertal foot is generally explained as a product of overall postcranial robusticity and perhaps a subtly different activity pattern in this population.¹¹⁴

The Omo I skeleton from Member 1 of the Kibish formation at the KHS locality in the Omo Valley, Ethiopia, at ~195 ka, represents the earliest known partial skeleton from an anatomically modern human.¹¹⁶ A partial right foot is preserved, including the talus, navicular, medial cuneiform, cuboid, Mt1–4, and the hallucal phalanges. Our observations of the Omo I foot find few substantive differences between these pedal remains and the human foot skeleton today. However, we do note that the dorsoplantally narrow trochlear body of the talus found in early hominins and early Pleistocene *H. erectus* persists in the Omo I foot. Why the talar body expanded dorsoplantally in late Pleistocene *H. sapiens* (Figure 7) remains unclear.¹¹⁷

Across the transition from *Australopithecus* to *Homo*, there was a general suite of evolutionary changes that occurred in the hominin foot. Toes decreased in both length and relative curvature to reduce bending forces across the phalanges during bipedal pushoff, particularly during bouts of running.¹¹⁸ The peroneal trochlea reduced in size, suggesting a decreased role of peroneal musculature. *Homo* evolved fully developed foot arches. Last, there is evidence that *Homo* possessed modern human-like weight transfer to the transverse axis of the foot and pushed off a fully adducted hallux, reflecting a nearly complete transition to terrestriality. This suite of changes helped to further improve the efficiency of bipedal locomotion in these species compared to that found in *Australopithecus* and is perhaps related to increased ranges and more economical distance travel in *Homo*. However, just as in *Australopithecus*, there was locomotor variation in fossil *Homo*.

There are two known species of late occurring *Homo* which do not completely fall in line with the trends described above. The first is *Homo naledi*, a ~300 ka species from South Africa.¹¹⁹ The *Homo naledi* foot, known from over 100 pedal remains, shares a number of characteristics with the modern human foot, including an adducted hallux, elongated midtarsal region, Mt dorsal doming, a human-like talus, a stiff lateral mid-foot, and metatarsal torsion consistent with the presence of a human-like transverse arch.²³ However, the pedal phalanges remain relatively curved compared with modern human toes. There is evidence in the talus (low declination angle) and calcaneus (low sustentaculum angle) for a relatively flat foot in *H. naledi*. The calcaneus is fairly gracile, although it does appear to have a modern human-like position for the lateral plantar process.²³ Additionally, the Mt5 diaphysis has unique cortical structure, combining human-like gracility and ape-like bending properties.¹²⁰

The second unusual foot fossil belongs to *Homo floresiensis*, a small-bodied hominin currently known only from Flores, Indonesia and dated to ~60 kya. The foot of *H. floresiensis* has a fully adducted hallux, domed metatarsal heads, and a human-like metatarsal robusticity pattern.²⁴ However, these island hominins are estimated to have had a relative foot length far exceeding that of humans today and instead closer to the relative foot length of bonobos.²⁴ These proportional differences are primarily concentrated in the forefoot, where both the lateral metatarsals and proximal phalanges are relatively longer than expected for a Pleistocene *Homo* foot.²⁴ The navicular is also primitive, with a large tuberosity and a wedge shape, caused by the pinching of the lateral side—anatomies common in australopithecids and great apes, but not in modern humans.²⁴ As of now, the functional

implications for the retention of primitive features in the foot of later Pleistocene *H. naledi* and *H. floresiensis* remain unclear.

The specialized anatomy of the human foot is a product of bare-foot bipedalism, however as a biocultural animal, we must finally consider the role that culture has played, and continues to play, in shaping the *H. sapiens* foot. Skeletal evidence for habitual shoe-wearing becomes apparent in populations by ~40,000 years ago.¹²¹ More recent evidence suggests that footwear may alter intrinsic foot musculature and shape,^{122–125} function (especially when running),^{126,127} and skeletal form.^{53,121,128,129} An unshod lifestyle as suggested in the recent hunter-gatherer archeological record, was associated with a lower frequency of osteological modification.¹²⁸ The influence of modern lifestyle including the use of footwear appears to have some significant negative effect on foot function, potentially resulting in an increase in pathological changes.^{121,128,129}

7 | CONCLUSION

The recent welcome barrage of fossil discoveries has provided a fresh opportunity to reassess how the foot evolved. Despite the glaring absence of foot fossils from 4.4 to 11.9 Ma, it is hypothesized that the lateral column of the foot was the target of selection in the earliest facultative bipeds, providing them a stiffer platform for efficient push-off during the second half of stance phase. The medial column remained ape-like to facilitate arboreal climbing. Changes to the medial column likely happened later in hominin foot evolution, probably in some Pliocene australopiths. It is telling, perhaps, that scholars working on isolated bones of the lateral column of the foot,^{50,71,82} often remarked on how derived early hominin feet are whereas those working along the medial column^{14,18,79,81,99} commonly found more primitive characteristics. Nevertheless, while species level variation exists, Plio-Pleistocene australopiths in general possessed a derived, human-like foot and began utilizing the medial column for bipedal propulsion. However, this general trend in early hominin foot evolution must be couched in recent findings that different australopiths likely possessed both locomotor diversity¹⁸ and perhaps even distinct kinematic gaits.¹⁰⁰ Most of the salient changes to the human foot had evolved by *Homo erectus*, though subtle differences still existed between the foot anatomy of Pleistocene *Homo* and modern *Homo sapiens*. Additionally, the surprising discoveries of *H. naledi* and *H. floresiensis* demonstrate that bipedal diversity continued well into the Late Pleistocene. If the last 10 years are any indicator, the next decade should help answer some lingering questions about hominin foot evolution, and raise new ones we have not yet thought to ask.

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ORCID

Ellison J. McNutt  <http://orcid.org/0000-0002-7723-9103>

Bernhard Zipfel  <http://orcid.org/0000-0002-4251-884X>

Jeremy M. DeSilva  <http://orcid.org/0000-0001-7010-1155>

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AUTHOR BIOGRAPHIES

ELLISON “ELLIE” MCNUTT is a PhD candidate in the Ecology, Evolution, Ecosystems and Society graduate program at Dartmouth College. Her research focuses on reconstructing and understanding the evolution of plantigrady in primates and bipedal locomotion in early hominins, in particular *Australopithecus*. ellison.j.mcnutt.gr@dartmouth.edu

BERNHARD ZIPFEL is the University Curator of Fossil and Rock Collections at the Evolutionary Studies Institute, University of the Witwatersrand in Johannesburg, South Africa. A former podiatrist, Dr. Zipfel now specializes in the anatomy and functional morphology of the early hominin foot. bernhard.zipfel@wits.ac.za

JEREMY DESILVA is an Associate Professor in the Department of Anthropology at Dartmouth College. He studies the paleobiology of early hominins and is particularly interested in the origins and evolution of upright walking. jeremy.m.desilva@dartmouth.edu

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