



Short Communications

Associated *Australopithecus afarensis* second and third metatarsals (A.L. 333-133) from Hadar, EthiopiaJeremy M. DeSilva^{a,*}, Ellison McNutt^b, Bernhard Zipfel^c, Carol V. Ward^d, William H. Kimbel^e^a Department of Anthropology, Dartmouth College, Hanover, NH, 03755, USA^b Keck School of Medicine, University of Southern California, Los Angeles, CA, 90033, USA^c Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa^d Integrative Anatomy Program, Department of Pathology and Anatomical Sciences, School of Medicine, University of Missouri, Columbia, MO, 65212, USA^e Institute of Human Origins and School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, 85287, USA

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1. Introduction

The 3.2-million-year-old A.L. 333 locality of the Hadar site, Afar region, Ethiopia, has yielded nearly 260 fossils representing a minimum of 17 adult and subadult individuals of the species *Australopithecus afarensis* (Johanson et al., 1982; Behrensmeyer, 2008). Included in the sample are nearly 50 pedal specimens (Latimer et al., 1982; Ward et al., 2012). Every element of the adult *A. afarensis* foot is known except the intermediate cuneiform, cuboid, and some distal phalanges. Although the distal end of the second metatarsal is represented by both A.L. 333-72 and A.L. 333-115b (Latimer et al., 1982), the base of the second metatarsal has remained unknown for this taxon. Here, we describe A.L. 333-133, conjoined proximal second and third metatarsals of a single individual.

Although the foot of *A. afarensis* is well documented, its interpretation has remained controversial. Some scholars have

identified derived aspects of the Hadar foot bones (e.g., Latimer, 1991), whereas others have highlighted more primitive morphologies (Stern and Susman, 1983). Proponents of a humanlike bipedal gait for *A. afarensis* emphasize that the Hadar pedal fossils possess a humanlike ankle joint (Latimer et al., 1987; DeSilva, 2009), a robust calcaneus adapted for heel-striking bipedalism (Latimer and Lovejoy, 1989; Prang, 2015a), a humanlike navicular (Prang, 2016), a nongrasping hallux (Latimer and Lovejoy, 1990a), and humanlike dorsiflexion at the metatarsophalangeal joints (Latimer and Lovejoy, 1990b) in a foot that featured both transverse and longitudinal arches (Ward et al., 2011; Prang, 2015b). Others interpret these fossils differently and see evidence in the Hadar pedal remains for some hallux mobility (Berillon, 1999), a less derived toe-off mechanism (Fernández et al., 2016), grasping potential with relatively long, curved pedal phalanges (Susman et al., 1984), and a flat foot devoid of a longitudinal arch (Harcourt-Smith and Aiello, 2004). The Laetoli footprints have featured prominently in this debate as well, although they too have received different interpretations, with some emphasizing their humanlike shape and inferred function (Day and Wickens, 1980; White and Suwa, 1987; Tuttle et al., 1990; Raichlen et al., 2010; Crompton et al., 2012) and others finding evidence for more hallux divergence and less medial weight transfer in a relatively flat foot (Stern and Susman, 1983; Bennett et al., 2009; Hatala et al., 2016). Our intention is not to resolve this debate here, but to contribute to it by formally describing and introducing a previously unknown element from the *A. afarensis* foot.

Regardless of whether the *A. afarensis* foot is interpreted as more or less derived in a humanlike direction, consensus appears to be building that the lateral column of the foot evolved adaptations for a bipedal gait before the medial column of the foot (Kidd, 1999; Lovejoy et al., 2009; Fernández et al., 2018; McNutt et al., 2018; DeSilva et al., 2019). Pliocene foot bones of *Ardipithecus ramidus* and the partial foot from the Burtele locality at Woranso-Mille possess morphology consistent with lateral midfoot rigidity, which is argued to be related to propulsion off the oblique axis of the foot,

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but retain a primitive divergent hallux (Lovejoy et al., 2009; Haile-Selassie et al., 2012). Isolated foot bones attributed to *Australopithecus africanus* from Sterkfontein, South Africa, are derived laterally in having tall, dorsoplantarly flat bases (Zipfel et al., 2009; DeSilva, 2010; DeSilva et al., 2019) but retain some apelike features in the medial forefoot (Clarke and Tobias, 1995; Deloison, 2004; DeSilva et al., 2012, 2019).

Because they can reflect hallucal function and medial foot flexibility, fossils representing the medial forefoot are critical for understanding foot evolution. Yet these elements are exceptionally rare. Only a single dorsally damaged medial cuneiform (A.L. 333-28) and single isolated proximal first metatarsal (A.L. 333-54) are known for *A. afarensis*. The proximal second metatarsal has remained unknown until now and is described in the following section.

2. Materials and methods

The A.L. 333-133 metatarsals were recovered during fieldwork in 1975 or 1976 but were not recognized as hominin until curation and preparation of bone fragment-bearing nodules of CaCO₃ matrix in storage was undertaken in the 1990s. These nodules, with bone fragments at the nucleus, are frequently encountered on the surface and in the in situ horizon at A.L. 333. The dark manganese staining of the bone is also common in the A.L. 333 hominin sample. As prepared from the nodule, the bases of the A.L. 333-133 metatarsals were articulated, in which state they remain. Other examples of such articulation are known in the A.L. 333 hominin assemblage. During the 1970s fieldwork at the locality, conjoined pairs of hand and foot bones were recovered from the in situ horizon: A.L. 333x-13a, b, immature proximal and intermediate hand phalanges and A.L. 333x-21a, b, intermediate foot phalanges. In addition, the metatarsal and phalangeal elements of the A.L. 333-115 foot were recovered in partial articulation from a single nodule (although not in situ).

A.L. 333-133 was compared with fossil second and third metatarsals listed in Table 1. Original fossils were studied and measured in all cases except OH 43, for which a high-resolution cast from the Kenya National Museum was used, and Omo 323-1976-2117, for which measurements were obtained from Daver et al. (2018). All linear measurements were taken to the nearest 0.1 mm using Mitutoyo digital calipers.

Metatarsals of *Pan troglodytes* and *Gorilla gorilla* were measured at the Cleveland Museum of Natural History, the American Museum of Natural History, and the Harvard Museum of Comparative Zoology. Metatarsals of *Homo sapiens* were measured at the Harvard Peabody Museum of Archaeology and Ethnology and consist of individuals from the Mistihalj (Montenegro) and small-bodied Merida (Mexico) populations. Sample sizes are listed in Figure 2.

The maximum mediolateral width and dorsoplantar height of the proximal base of the second metatarsal were measured using calipers. In addition, photographs of second metatarsals were taken in dorsal view using a Nikon D7000. These images were imported into ImageJ, and the angle formed between the proximal base and the long axis of the metatarsal shaft was measured using the angle tool. Statistically significant differences among extant taxa were determined using a Student's t-test in Microsoft Excel.

3. Results

3.1. Preservation and description

A.L. 333-133 (Fig. 1) is a conjoined fossil of the bases and partial shafts of the left second and third metatarsal (Mt). The Mt2 is preserved from the base to approximately the midshaft. There is a clean break between the base and the shaft, and the two pieces, roughly similar in size, have been glued together. A bone fragment, probably a part of the shaft of the Mt3, adheres to the distal part of the preserved Mt2 shaft. A large portion of the plantomedial shaft has been damaged distally, and the medial base is eroded,

Table 1
Measurements of hominin metatarsals.

Element	Catalog number	Species	Age (Ma)	Base ML width (mm)	Base DP height (mm)
Mt2	StW 573	<i>Australopithecus prometheus?</i>	3.67?	13.5	15.1
Mt2	BRT-VP-2/73b	Unknown	3.4	12.8	14.2
Mt2	DIK-1-1f	<i>A. afarensis</i>	3.3	5.7	7.9
Mt2	A.L. 333-133	<i>A. afarensis</i>	3.2	12.1	15.9
Mt2	StW 89	<i>A. africanus?</i>	2.0–2.6	11.0	12.8
Mt2	StW 377	<i>A. africanus?</i>	2.0–2.6	13.2	14.9
Mt2	StW 595	<i>A. africanus?</i>	2.0–2.6	11.7	13.2
Mt2	Omo 323-1976-2117	<i>A. boisei?</i>	2.12	16.7	19.8
Mt2	OH 8	<i>A. boisei? H. habilis?</i>	1.8	11.2	14.4
Mt3	A.L. 333-133	<i>A. afarensis</i>	3.2	11.0 (est.)	15.8
Mt3	A.L. 333-157	<i>A. afarensis</i>	3.2	13.6	18.7
Mt3	StW 238	<i>A. africanus?</i>	2.0–2.6	12.1	16.3
Mt3	StW 387	<i>A. africanus?</i>	2.0–2.6	10.9	16.7
Mt3	StW 388	<i>A. africanus?</i>	2.0–2.6	12.6	18.5
Mt3	StW 435	<i>A. africanus?</i>	2.0–2.6	13.3	20.1
Mt3	StW 477	<i>A. africanus?</i>	2.0–2.6	12.0	16.5
Mt3	StW 496	<i>A. africanus?</i>	2.0–2.6	10.9	16.8
Mt3	KNM-ER 1500	<i>A. boisei</i>	1.89	12.0	17.7
Mt3	KNM-ER 997	<i>A. boisei?</i>	1.85	10.1	16.2
Mt3	SKX 38529	<i>A. robustus?</i>	1.8–2.0	12.1	–
Mt3	OH 8	<i>A. boisei? H. habilis?</i>	1.8	11.9	16
Mt3	OH 43	<i>A. boisei?</i>	1.8	10.0	–
Mt3	Omo F.511-16	<i>Homo?</i>	1.7	14.6	20.7
Mt3	KNM-ER 1823	<i>A. boisei?</i>	1.7	12.8	–
Mt3	KNM-ER 803	<i>Homo erectus</i>	1.53	12.7	20.5
Mt3	SKX 247	<i>A. robustus?</i>	1.1–1.7	12.2	16.3

ML = mediolateral; DP = dorsoplantar; est. = estimate.

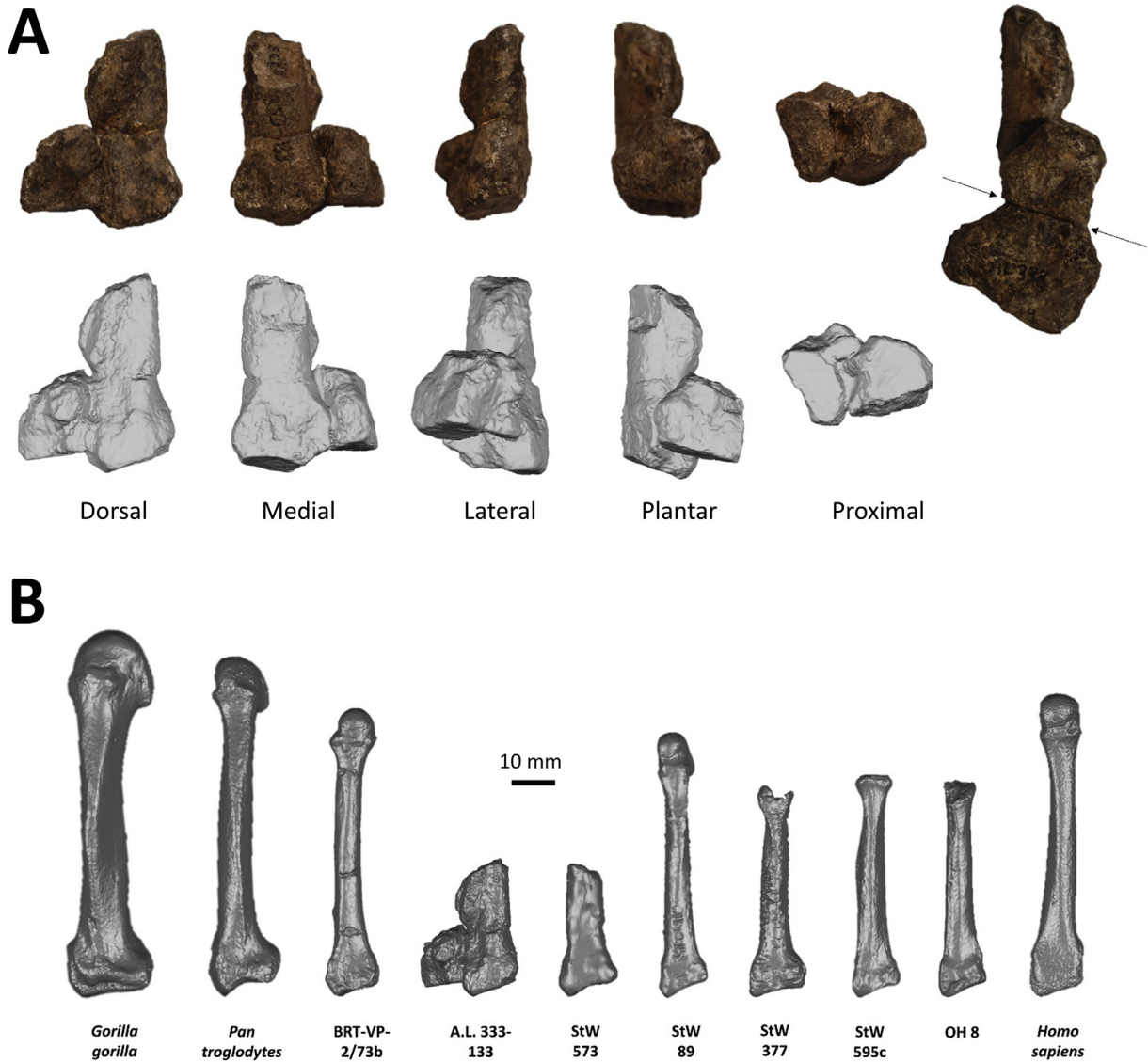


Figure 1. (A) A.L. 333-133. Top row: images of the original fossil. Bottom row: similarly positioned 3D surface scans that are provided to show anatomical detail difficult to see in the photographs of the fossil. From left to right: dorsal view of Mt2; medial view of Mt2; lateral view of Mt2; plantar view of Mt2; proximal view of Mt2 and Mt3. Far right, A.L. 333-79 lateral cuneiform articulated with A.L. 333-133. Arrows indicate the adjoining surfaces of the two bones. (B) Hominid second metatarsals shown in dorsal view. Fossils are arranged chronologically from the 3.4 Ma Burtele locality (BRT-VP-2-73b) to the 1.85 Ma Olduvai foot (OH 8). BRT-VP-2/73b and StW 595c have been reversed so that all appear as the left foot. Notice the sharply angled base of the Mt2 in the modern human and most fossil hominins. Scale bar is 10 mm.

precluding characterization of the facet for the medial cuneiform. The plantolateral side of Mt2 is obscured by the conjoined Mt3 fragment. The proximal facet for the intermediate cuneiform has some erosion around the perimeter, especially plantarly. The Mt3 fragment is considerably smaller and is damaged dorsally such that two fragments have broken off and re-adhered dorsal to their anatomical position. The medial side of the bone is obscured by the conjoined Mt2, which is medially rotated relative to the Mt3.

As preserved, the Mt2 is 30.9 mm long. The base is 12.1 mm wide mediolaterally and 15.9 mm deep dorsoplantarly. Medially, there is a small roughened area that would have contacted the base of the Mt1. The proximal articular surface is moderately concave mediolaterally and flat dorsoplantarly. The preserved facet for the intermediate cuneiform measures 11.4 mm mediolaterally and 12.0 mm dorsoplantarly, although the latter dimension is a minimum owing to some plantar erosion. Because the Mt3 is adhered distal to the base of the Mt2, the lateral facets are difficult to

observe. However, the Mt2 is recessed; the dorsal facet for the lateral cuneiform is visible and is separated from the eroded plantar cuneiform facet by a groove. The Mt3 proximal facet for the lateral cuneiform measures 8.7 mm wide mediolaterally (minimum) and 12.9 mm deep dorsoplantarly. The base of the Mt3 is 15.8 mm deep dorsoplantarly, while the mediolateral dimension is difficult to measure because of erosion; it is approximately 11.0 mm.

3.2. Quantitative comparative anatomy

Humans have a second metatarsal base that is dorsoplantarly deep compared with mediolateral width. The depth-to-width ratio of the Mt2 base is 1.33 ± 0.11 in humans, which is significantly lower ($t = 9.41$; $p < 0.001$) than the Mt2 bases in gorillas (1.14 ± 0.08) and significantly lower ($t = 13.98$; $p < 0.001$) than the Mt2 bases in chimpanzees (1.04 ± 0.08 ; Fig. 2A). A.L. 333-133 is humanlike, with a width-to-depth ratio of 76.1.

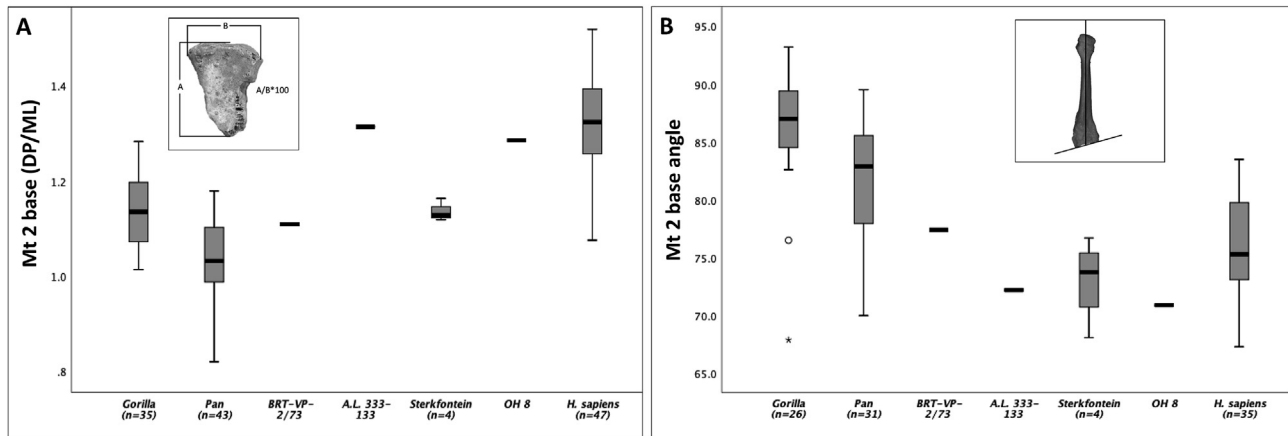


Figure 2. (A) Box plot showing the ratio between the dorsoplantar (DP) depth of the Mt2 base and the mediolateral (ML) width of the base (see measurement in the upper left) in African apes, modern humans, and hominin fossils. Modern humans, OH 8, and the new Hadar Mt2 (A.L. 333-133) have relatively tall Mt2 bases, whereas the BRT-VP-2/73 foot, StW 573, and three Mt2 bases from Sterkfontein Member 4 (*A. africanus*) are relatively dorsoplantarly shallow, as found in African ape feet. (B) Box plot comparing the angle formed between the Mt2 base and the shaft of the bone (see measurement in the upper right) in African apes, modern humans, and hominin fossils. A.L. 333-133 has a strongly angled base within the low end of the range for *Pan* and is barely in the range of *Gorilla* and much more humanlike. Sample sizes are in parentheses after the sample name for both graphs. Box plots illustrate the median value (black bars), 25th to 75th percentiles (gray boxes), range of values (whiskers), outliers (circles), and extreme outliers (stars).

The angle formed between the base of the Mt2 and the shaft in humans ($75.8^\circ \pm 4.40^\circ$) is significantly more acute ($t = 4.77$, $p < 0.001$) than the base angle in chimpanzees ($81.6^\circ \pm 5.44^\circ$) and significantly more acute ($t = 7.67$, $p < 0.001$) than the base angle in gorillas ($86.1^\circ \pm 6.15^\circ$; Fig. 2B). The base angle in A.L. 333-133 is 72° relative to the shaft, again a humanlike value.

4. Discussion and conclusion

The A.L. 333-133 fossil preserves an element — the base of the second metatarsal — that was previously unknown in the foot of *A. afarensis* (Table 1). In modern humans, the base of the Mt2 is dorsoplantarly tall relative to the mediolateral width — an anatomy hypothesized to provide rigidity to the medial side of the midfoot (Lovejoy et al., 2009). For this measure, A.L. 333-133 falls squarely within the modern human range, as does the Mt2 from the Pleistocene foot OH 8. The Mt2 from the contemporaneous Burtele foot (Haile-Selassie et al., 2012), the StW 573 foot (Deloison, 2003), and those from Sterkfontein Member 4 (presumably *A. africanus*) are, however, more apelike in having shallower Mt2 bases (Fig. 2A; DeSilva et al., 2012, 2019). These observations are consistent with the conclusion that *A. afarensis* possessed medial midfoot rigidity, whereas the medial midfoot in the Burtele specimen, StW 573, and *A. africanus* may have been more mobile (Fig. 1B).

The dorsal surface of the A.L. 333-133 Mt2 lacks the paired chondral invaginations found on the *A. ramidus* Mt2 (Lovejoy et al., 2009). A.L. 333-133 also has a gently concave intermediate cuneiform facet on the Mt2, unlike the more V-shaped facet found in apes. The A.L. 333-133 Mt2 possesses a strongly medially angled base relative to the long axis of the shaft. Although A.L. 333-133 falls within the extreme lower distribution of apes for this measure, only a small number of gorillas ($n = 2/26$) and chimpanzees ($n = 2/31$) exhibit this morphology, making the base angle of A.L. 333-133 more typical of humans. Even apes that have a high, more humanlike angle often do so because of a proximally extended lateral facet for the Mt3, quite unlike the anatomy found in modern humans and A.L. 333-133.

Importantly, there is a discernible roughened area on A.L. 333-133 probably for contact with the lateral aspect of the base of the

Mt1 (Singh, 1960). Zipfel (2004) found a similar elevation, often rough to the touch, on nearly 70% ($n = 149/209$) of human Mt2s using Singh's (1960) definition of Mt1 contact facets. Of those, approximately 90% ($n = 112/125$) possessed a smooth facet, both with and without well-defined margins on the Mt1, for contact with the Mt2. A contact facet is never present in nonhuman primates with an abducent hallux (Le Minor and Winter, 2003). The presence of a comparable roughened area on A.L. 333-133 indicates that the Mt1 of this individual was in contact with the Mt2 and, presumably then, adducted, providing additional and independent evidence for the absence of hallucal divergence in *A. afarensis* (Latimer and Lovejoy, 1990a).

The A.L. 333-133 Mt3 is not as well preserved, but is similar anatomically to A.L. 333-157 (Ward et al., 2012), although smaller. The base appears dorsoplantarly tall, although this assessment is based on visual qualitative evidence only because of the poor preservation of the bone.

The A.L. 333-133 Mt3 articulates with the A.L. 333-79 lateral cuneiform (Fig. 1), matching it in both size and shape, making it possible that the two belong to the same foot. Associated hominin foot bones are exceptionally rare. Among Plio-Pleistocene hominin foot fossils, only the left foot from *A. ramidus* (ARA-VP-6/500; Lovejoy et al., 2009), the *A. afarensis* DIK 1-1 foot (DeSilva et al., 2018), OH 8, and possibly A.L. 333-79/133 possess an associated Mt2, Mt3, and lateral cuneiform. A.L. 333-79 is humanlike in being dorsoplantarly deep and possessing an oblique facet for Mt4. The tarsometatarsal joint morphology of A.L. 333-133 mirrors the condition also seen in the A.L. 333-160 Mt4 and likely reflects midfoot stiffness compared with the dorsoplantarly shallower and convex Mt4 base typical of apes (Ward et al., 2011; DeSilva et al., 2019).

A.L. 333-133 provides the first evidence of a proximal second metatarsal for *A. afarensis*, enhancing our understanding of the foot of this species. Together with other material from A.L. 333 at Hadar, this specimen strengthens the conclusion that *A. afarensis* possessed a more humanlike foot (Fig. 3), with an adducted hallux and dorsoplantarly tall metatarsal bases adapted to resist tarso-metatarsal dorsiflexion and contribute to converting the foot into a lever during the push-off phase of terrestrial bipedal locomotion.

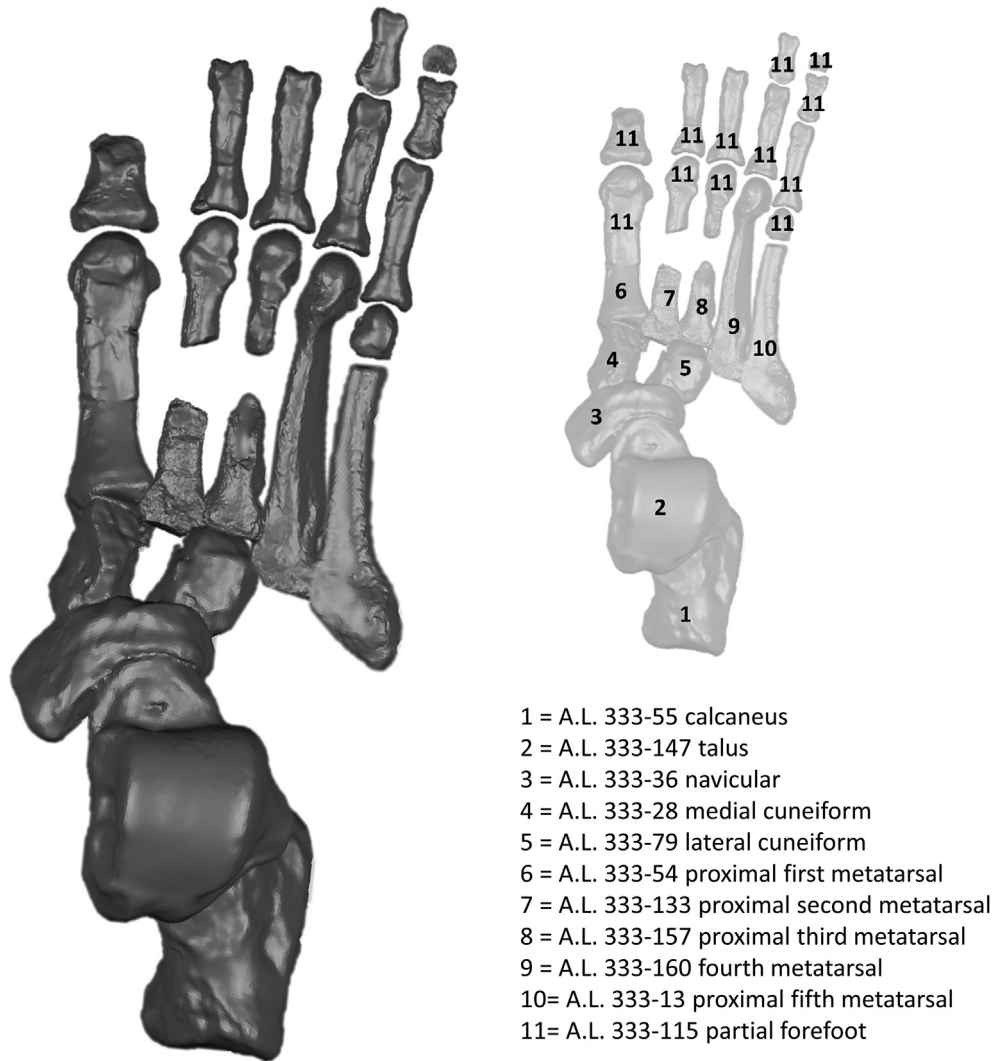


Figure 3. Composite *Australopithecus afarensis* foot skeleton from the Hadar 333 locality. Specimens were mirrored so that they are consistently from the right side (dorsal view). Only the Mt1–3,5 heads and phalanges are clearly from the same foot (A.L. 333-115). It is likely that A.L. 333-133 (Mt2) and A.L. 333-79 (lateral cuneiform) are from the same foot as outlined in this article. In addition, based on similar patina and adjoining articular surfaces, the A.L. 333-36 navicular and A.L. 333-28 medial cuneiform are likely from the same foot. The other bones (calcaneus: A.L. 333-55; talus: A.L. 333-147; Mt1 base: A.L. 333-54; Mt3 base: A.L. 333-157; Mt4: A.L. 333-160; Mt5: A.L. 333-13) do not have clear associations. Because these bones are derived from different feet, caution should be exercised when inferring foot proportions from this composite, although the bones were scaled when overlapping anatomies occurred (e.g., A.L. 333-160 and A.L. 333-115 Mt4 heads). In addition, specific specimens were chosen (e.g., A.L. 333-36 over A.L. 333-47) to better match the size of unassociated specimens (A.L. 333-147 talus in this case). Note that the intermediate cuneiform and cuboid remain the only missing tarsals of an *A. afarensis* adult foot. A rugosity on the medial aspect of A.L. 333-133, along with the proximal orientation of the Mt1 facet on the medial cuneiform, supports the alignment of the hallux with the lateral digits.

Conflict of interest

No conflict of interest.

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