A Large *Homo erectus* Talus from Koobi Fora, Kenya (KNM-ER 5428), and Pleistocene Hominin Talar Evolution

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ABSTRACT

KNM-ER 5428 is a very large probable *Homo erectus* talus from ~1.6 Ma deposits at Koobi Fora, Kenya. Though preliminarily described in 1985, here we provide a more detailed anatomical description and comparison of KNM-ER 5428 with fossil hominin, modern human, and extant ape tali. KNM-ER 5428 is exceptionally large, with body mass estimates >90kg—over 4 standard deviations larger than average *H. erectus* from the Early Pleistocene of Eastern Africa. Though human-like in most respects, KNM-ER 5428 and other Plio-Pleistocene hominins maintained a mediolaterally wide but dorsoplantarly short talar body that contrasts with the relatively tall modern human talus. *H. sapiens* tali therefore have increased in volume through vertical expansion during the last 100 ka. Reasons for this dorsoplantar expansion of the talar body remain unclear.

INTRODUCTION

KNM-ER 5428 (Figure 1) is a large right talus discovered in 1978, in the upper part of the KBS member of Area 119 at Koobi Fora, Kenya (Leakey and Walker 1985; Wood and Leakey 2011). Original dating of this site yielded an age of 1.6 Ma for KNM-ER 5428 (Feibel et al. 1989). A fossil recovered from Area 119 (KNM-ER 5429) has recently been redated to 1.54 Ma (McDougall et al. 2012), though KNM-ER 5428 was not singled out for date correction and thus we proceed as though the original 1.6 Ma remains accurate. Although this fossil was found in isolation, most attribute it to *Homo erectus* (Antón 2003; Walker 1994; Wood and Leakey 2011). Some are more cautious, assigning it to Hominidae gen. et sp. Indet. (McHenry 1994). Wood and Constantino (2007) note, though, that craniodental fossils also found at Area 119 (KNM-ER 1509 and KNM-ER 5429) are attributable to *Paranthropus boisei*. They therefore suggest that the classification of KNM-ER 5428 into *H. erectus* requires a comparison with KNM-ER 1464, a presumed *P. boisei* talus (but see Gebo and Schwartz 2006). We tentatively accept KNM-ER 5428 as *H. erectus* due to its exceptionally large size and shared anatomies with the fragmentary talus KNM-ER 803, associated with a partial skeleton of *H. erectus* (Day and Leakey 1974). Additional support for KNM-ER 5428's inclusion in *H. erectus* based in part on comparisons with KNM-ER 1464 is discussed in more detail below.

Hominin tali are relatively well represented in the fossil record compared to other tarsal bones. Surprisingly little is known, though, about early *H. erectus* foot or talar anatomy. The most studied *Homo erectus* skeleton—KNM-WT 15000—does not preserve a talus and even the attribution of a first metatarsal to this skeleton remains uncertain (Walker and Leakey 1993). The partial skeleton KNM-ER 1808 does not preserve any foot bones, and another partial skeleton KNM-ER 803 preserves a fragmentary talus, two broken metatarsals, and five phalanges (Day and Leakey 1974). Given the paucity of *H. erectus* pedal remains, the recent description of foot bones from the early *Homo* site of Dmanisi, Georgia, takes on added importance (Pontzer et al. 2010).

In the absence of a substantial collection of *H. erectus* tarsals, the 1.5 Ma footprints from Ileret, Kenya, have been useful in drawing conclusions about bipedal walking in this species (Bennett et al. 2009; Dingwall et al. 2013). Bennett et al. (2009) propose that *H. erectus/ergaster* made these footprints, and that this hominin had a relatively human-like foot, already in possession of a modern medial longitudinal arch and adducted hallux, a conclusion supported by the fossil evidence (Pontzer et al. 2010). However, any subtle differences between early *H. erectus* and modern *H. sapiens* foot morphology are indeterminable without additional fossils and continued comparative anatomical analyses. KNM-ER 5428 is thus an important and underappreciated specimen in this context.

KNM-ER 5428 was preliminarily described by Leakey and Walker (1985). The entirety of the description is replicated below:

> "This is a right talus from the Koobi Fora Tuff Complex in Area 119. It is a large talus with the head slightly damaged and the posteromedial corner missing. The long

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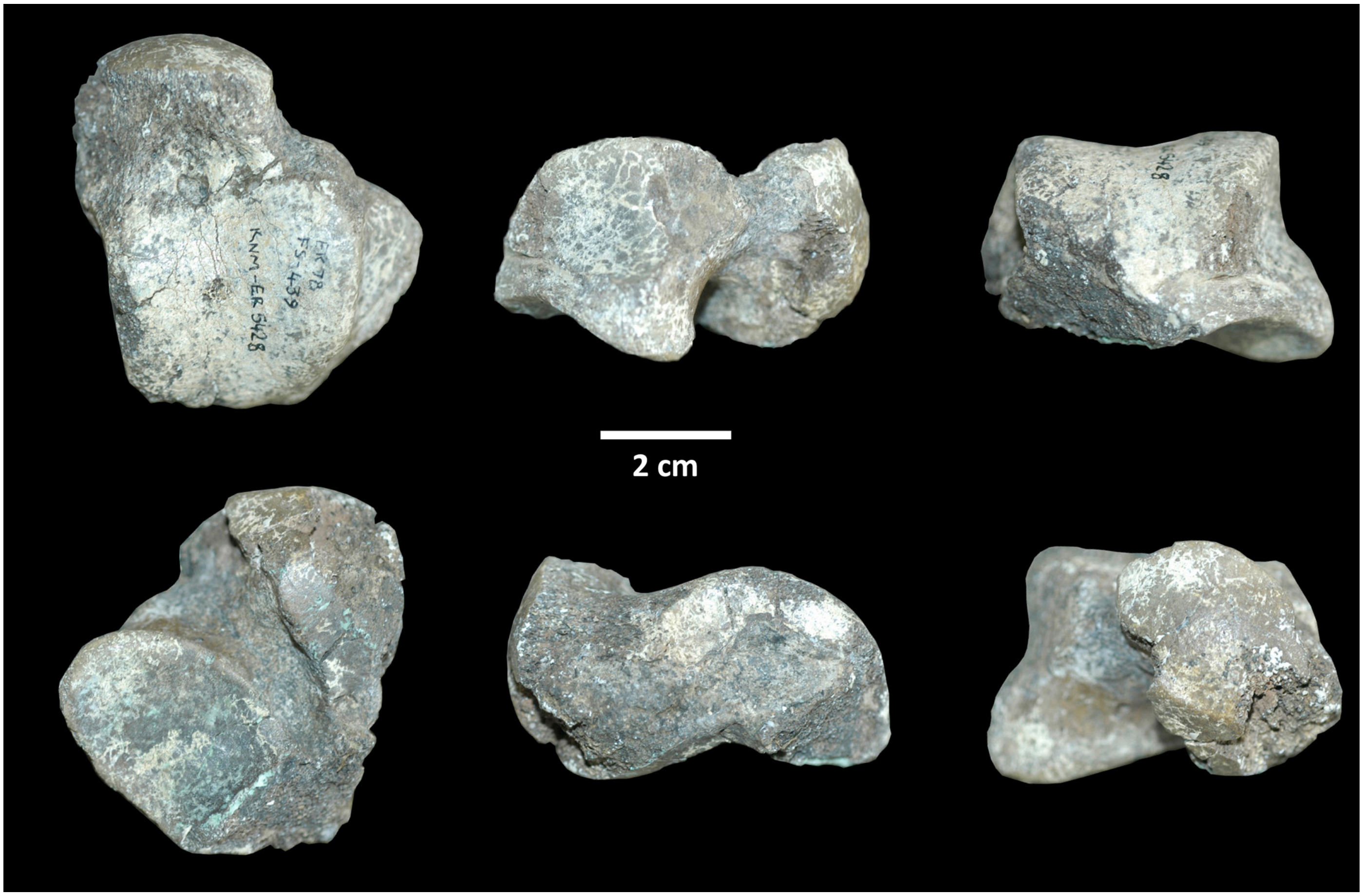


Figure 1. KNM-ER 5428 right talus in (left to right) dorsal, lateral, and posterior views above, and plantar, medial, and anterior views below.

> axis of the head is set obliquely to the trochlear axis and the head itself has a clear division between the navicular and the anterior and middle calcaneal facets. The trochlea is markedly wedged, being 38.0 wide anteriorly and 30 (estimated) at the posterior break. The neck is broad and short. The sinus tarsi is deep (up to 7.0) and wide (up to 10.0). Both malleolar facets are extensive and extend well posteriorly. The posterior calcaneal facet is of elliptical outline and is part of an internal cylinder with a 50 radius whose long axis runs 90 degrees to the axis of the ellipse."

Although this fossil has not been thoroughly described, it is perhaps more surprising that this bone has been generally ignored in comparative analyses of hominin tali (though see Susman et al. 2001; Zipfel et al. 2011). Here we provide a more detailed anatomical description and comparison of KNM-ER 5428 with fossil hominin, modern human, and extant ape tali. With so few definitive *Homo erectus* tarsals on record, a systematic analysis of this fossil enriches our understanding of bipedalism in *H. erectus*, and reveals how talar anatomy has evolved in the human lineage since the early Pleistocene. Furthermore, the striking size of KNM-ER 5428 permits a reanalysis of body mass variation in *H. erectus*.

MATERIALS AND METHODS

Extant tali measured in this study are listed in Table 1. Original fossils (Table 2) were studied at the National Museums of Kenya (Nairobi), Ditsong Museum (Pretoria), University of the Witwatersrand School of Anatomical Sciences and Institute for Human Evolution (now Evolutionary Studies Institute), Johannesburg, South Africa, and National Museum and House of Culture (Dar es Salaam). High quality research casts of Ethiopian fossils were studied at the Boston University Biological Anthropology laboratory, Peabody Museum (Harvard), and the Cleveland Museum of Natural History. Data from late Pleistocene tali and some *H. erectus* body mass estimates were obtained from the literature. Body mass estimates from isolated tali were calculated using the average of the three human-based regression equations in McHenry (1992).

Measurements taken on the talus followed DeSilva (2008) and are illustrated in Figure 2. Angular measurements followed Day and Wood (1968). Seven functionally relevant measures of the talar head and body were entered into a discriminant function analysis (DFA) in SPSS 19.0. These included the mediolateral width of the anterior and posterior trochlear body, a measure of relative talar wedging (DeSilva 2009), the maximum dorsoplantar height and

TABLE 1. EXTANT TALI MEASURED IN THIS STUDY.

Species	Male	Female	Sex Unknown	Total
Homo sapiens	13	21	11	45
Pan troglodytes	19	22	10	51
Pan paniscus	2	1	0	3
Gorilla gorilla gorilla	23	19	3	45
Gorilla gorilla beringei	10	3	0	13
Pongo pygmaeus	12	18	7	37
Hylobates lar	17	17	2	36
Symphalangus syndactylus	4	3	1	8

mediolateral width of the talar head, the anteroposterior length and dorsoplantar height of the lateral fibular facet, and the dorsoplantar depth of the trochlear keel. These latter three measurements are meant to capture (linearly) talar morphologies recently identified by Dunn et al. (2013) to differentiate mountain and lowland gorillas. A geometric mean of these seven measurements was calculated and each measurement was divided by the geometric mean to produce a size-standardized metric. These seven size-standardized metrics were entered into the discriminant function analysis, along with fossil tali >1 Ma for which all seven of these measures could be taken—KNM-ER 5428, KNM-ER 1464, StW 88, A.L. 288-1, Omo 323-76-898, and specimens from the Sima de los Huesos locality for which these same measurements were published (Pablos et al. 2013).

RESULTS

PRESERVATION

KNM-ER 5428 is relatively complete, except for the loss of several features in the plantar and medial dimensions. It does not preserve the dorsal corner of the head on the anterolateral side, the plantar most half of the head and neck, inferiorly and medially, and most of the anterior and middle calcaneal facets. Additionally, the medial tubercle of the posterior process is missing, as well as the posteromedial corner of the posterior calcaneal facet. The groove for the flexor hallucis longis tendon, therefore, is not preserved.

There is significant abrasion on the dorsal surface of the neck on the medial side, as well as along the medial trochlear rim, and at the anterior and posterior corners of the trochlea on the lateral side. There is also abrasion along

TABLE 2. FOSSIL TALI.

Ardipithecus	ARA-VP-6/500[1]
Australopiths	A.L. 288-1; A.L. 333-147[2]; StW 88; StW 102; StW 347; StW 363; StW 486; U.W. 88-98; TM 1517; KNM-ER 1476; KNM-ER 1464
Early Pleistocene *Homo*	Omo 323-76-898[3]; SKX 42695[3]; OH 8[3]; KNM-ER 813[3]; KNM-ER 5428; KNM-ER 803; ATD6-95[4]
Middle to Late Pleistocene *Homo*	AT-575[5]; AT-860[5]; AT-965[5]; AT-966[5]; AT-980[5]; AT-1322[5]; AT-1477[5]; AT-1716[5]; AT-1822[5]; AT-1930[5]; AT-1931[5]; AT-2495[5]; AT-2803[5]; AT-3132[5]; AT-4425[5]; Jinniushan[6]; Omo-Kibish[7]; Skhul 6[8]; Amud 1[8]; La Chapelle 1[8]; La Ferrassie 1[8]; La Ferrassie 2[8]; Kiik-Koba 1[8]; Krapina 236[8]; Krapina 237[8]; La Quina 1[8]; Regourdou 1[8]; Spy 2[8]; Tabun C1[8]

[1] Lovejoy et al. (2009)

[2] Ward et al. (2012)

[3] *Homo* status uncertain (may be australopith)

[4] Pablos et al. (2012)

[5] Pablos et al. (2013)

[6] Lu et al. (2011)

[7] Pearson et al. (2008)

[8] Rhoads and Trinkaus (1977)

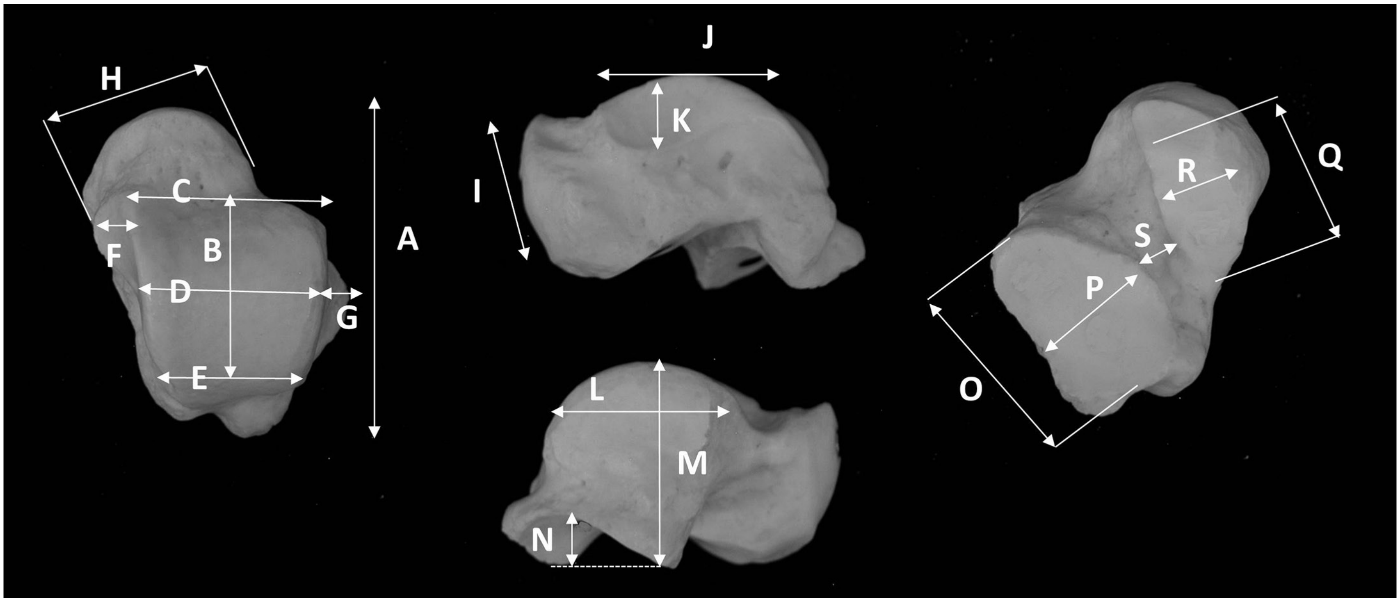


Figure 2. Talar measurements taken in this study. The letters correspond to values reported in Table 3.

the lateral margin of the posterior calcaneal facet, with some small cracks that extend from its medial margin to the middle calcaneal facet. Cracks are also found on the medial and lateral malleolar surfaces, the anterior surface of the head, and on the dorsal articular surface of the trochlea.

MORPHOLOGY

The specimen measures 57.3mm long anteroposteriorly, and 26.4mm tall dorsoplantarly, resulting in a bone that is rather long but strikingly squat (Table 3). It appears to be from an adult, due to its very large size and well-defined articular surfaces. The superior surface of the neck is roughened by two large depressions and vascular foramina. There are smooth facets for ligaments on the anterolateral corner of the trochlea. There is also a tubercle for the anterior talofibular ligament on its inferolateral edge.

The trochlea is considerably flat, with only a subtle midline groove. The talar axis angle is 8.7°, similar to that found in modern humans and indicative of an orthogonal ankle joint (DeSilva 2009). There is marked proximodistal trochlear asymmetry; the lateral ridge is 32.7mm long and the medial ridge is estimated to be 26.1mm long. The trochlea is also moderately wedged, broader mediolaterally along the anterior margin (estimated to be 36.6mm) than the posterior one (30.9mm). The anterior edge of the trochlea is slightly concave in superior view, due to the depressions caused by two vascular foramina, which help to create a modest sulcus that separates the trochlea from the neck. A slight lip extends from the medial edge of the left vascular foramen laterally across the anterior trochlear margin. Where it is preserved, the posterior end of the trochlea is slightly convex.

The tibial malleolar facet is 29.4mm anteroposteriorly and 14.3mm dorsoplantarly. It is flat along the dorsal portion and mildly cupped plantarly and anteriorly, where the cotylar fossa projects out 3.6mm. In contrast, the fibular facet is quite concave laterally, flaring 9.5mm. It measures 33.2mm anteroposteriorly by 22.6mm dorsoplantarly.

At a minimum, the middle calcaneal facet is 27.1mm long by 7.7mm wide, and 4.2mm deep. Where is it preserved, its anterior half is convex mediolaterally, while its posterior half is slightly concave. The part of the posterior calcaneal facet that is preserved is broader anterolaterally than posteromedially. It measures, at a minimum, 29.6mm long by 23.6mm wide, and 5.6mm deep. The tarsal sinus has minimum dimensions of 7mm deep, 8.7mm wide, and 21.8mm long.

The head and neck form a horizontal angle of 20° relative to the long axis of the trochlear body. The angle of inclination of the talar head and neck is 41°, while the head exhibits torsion of 39° relative to the horizontal plane of the trochlear body. All of these angular measures fall within the range of variation in modern humans (Day and Wood 1968).

Internal anatomy of KNM-ER 5428 is unknown. Su et al. (2013) employed computed tomography (CT) scanning in attempts to view the internal bone structure of this specimen, but report that trabecular bone was not discernable enough to characterize.

Perhaps most notable is the strikingly large size of this fossil. McHenry (1992) calculated a body mass of 86.7kg from KNM-ER 5428, assuming this talus is human-like in proportion. Our own measurements yield a body mass estimate of 93.4±3.3kg. Using the SEE reported for the LSQ equation in McHenry (1992), the KNM-ER 5428 talus is from an individual 89.9kg (range: 78.3–103.2kg). Any of these estimates yields a body size significantly greater than other Early Pleistocene hominin tali from Eastern Africa (Figure 3), including KNM-ER 1464, which yields a mass of 48.7kg based on the same equation (McHenry 1992).

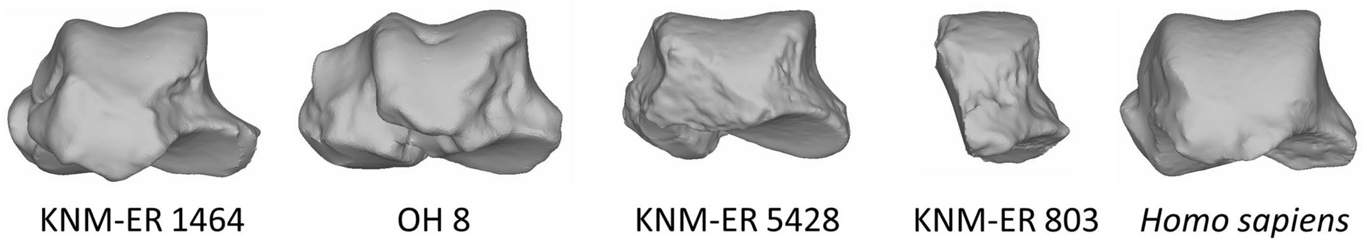
It is clear from comparisons in posterior view (Figure 4) that while KNM-ER 5428 has a mediolaterally flat talar

TABLE 3. KNM-ER 5428 MEASUREMENTS (mm).

Anteroposterior length (A)	57.3 (est.)
Anteroposterior length of trochlear along center (B)	28.7
Mediolateral breadth of trochlear anterior margin (C)	36.1
Mediolateral breadth of trochlear at midpoint (D)	33.7
Mediolateral breadth of trochlear posterior margin (E)	30.9 (est.)
Cotylar fossa medial projection (F)	3.7
Fibular facet lateral projection (G)	9.5
Width of talar head (H)	36.7
Height of talar head (I)	24.1
Length of tibial facet (J)	29.2
Height of tibial facet (K)	14.3
Length of fibular facet (L)	33.2
Height of fibular facet (M)	22.6
Depth of posterior calcaneal facet (N)	5.1
Min. length posterior calcaneal facet (O)	29.6
Max. transverse breadth posterior calcaneal facet (P)	23.6
Min. length of middle calcaneal facet (Q)	27.1
Transverse breadth of middle calcaneal facet (R)	7.7
Min. breadth of tarsal sinus (S)	8.7
Depth of tarsal sinus (Not pictured)	9.3
Angle of torsion of the head and neck	39°
Angle of inclination of the neck	41°
Horizontal angle of the neck	20°

body, as is found in modern humans and KNM-ER 803, KNM-ER 1464 is quite curved, similar to that found in OH 8 and KNM-ER 1476. Furthermore, while the trochlea body and head of KNM-ER 1464 deflect medially, KNM-ER 5428 has a more human-like anteroposteriorly straight orientation of the trochlear body (see Figure 3). While the horizontal angle of the head and neck (20°) of KNM-ER 1464 is identical to that of KNM-ER 5428, the angle of inclination (22°) and angle of head and neck torsion (24°) in KNM-ER 1464 are both outside the range of modern human variation (Zipfel et al. 2011), and are distinct from the more human-like 41° and 39° angles measured respectively in KNM-ER 5428. Based on these considerable morphological differences, we suggest that KNM-ER 5428 and KNM-ER 1464 were from species with subtly different talocrural, subtalar, and talonavicular joint function and should not be classified as the same species. Given the taxa currently known, we therefore regard them as *H. erectus* and *P. boisei* (or even

Figure 3. Casts of (from left to right) OH 8, KNM-ER 1476, KNM-ER 813, KNM-ER 1464, and KNM-ER 5428 tali in dorsal view. Tali have been mirrored so that all appear from the right side. Notice the strikingly large size of KNM-ER 5428 compared to the other tali. Additionally, note the medial "twisting" of the trochlear body of OH 8, KNM-ER 1464, and minimally in KNM-ER 1476. In contrast, KNM-ER 5428 has a relatively straight, anteriorly oriented trochlear body. Bar=1cm.



KNM-ER 1464 OH 8 KNM-ER 5428 KNM-ER 803 *Homo sapiens*

Figure **4.** *Tali in posterior view. These bones have been scaled so that the mediolateral width of the trochlear body is roughly the same in each specimen. Note the deep trochlear groove in OH 8 and KNM-ER 1464. In contrast, note the flat trochlear surface that KNM-ER 5428 shares with KNM-ER 803 and modern* H. sapiens. *Despite these similarities, note the squatness of the KNM-ER 5428 trochlear body compared to the vertically tall trochlea of the modern* H. sapiens *talus.*

H. habilis), respectively. However, these taxonomic assignments should be considered extremely tentative until a partial skeleton with an associated talus is discovered from *P. boisei*.

As illustrated in Figure 5, human tali are easily discriminated from non-human hominoid tali along the first function, which explains 68.8% of the variation. This function is not size-related as the variables were all size-standardized before being entered into the DFA. All of the hominin fossils cluster within the human range of distribution and there is some overlap between human and mountain gorilla tali. Function 1 is being driven primarily by the size of the talar head and the width of the posterior aspect of the trochlear body (to the left) and the depth of the trochlear keel and anterior width of the talar body (to the right) (Table 4).

DISCUSSION

Like other hominin tali, KNM-ER 5428 is quite similar to modern human tali (see Figure 5), reflecting adaptations of both the talocrural and subtalar joints to the rigors of habitual bipedality. Even the angular measures of KNM-ER 5428, such as the torsion of the talar head, horizontal angle of the head and neck, and talar inclination angle (Day and Wood 1968) all fall within the range of modern humans. This latter point is important given that these angular measures often differ between modern humans and Plio-Pleistocene tali and differ most notably between KNM-ER 5428 and KNM-ER 1464 (Day and Wood 1968; Kidd et al. 1996; Zipfel et al. 2011). These human-like anatomies of KNM-ER 5428, in conjunction with its extremely large size, make it at least reasonable to hypothesize—as others have done (Antón 2003; Walker 1994; Wood and Leakey 2011)—that this talus belonged to an adult male *H. erectus*.

Early Pleistocene *H. erectus* tali are rare in the assemblage of fossil hominin foot bones. The only early African *H. erectus* talus associated with a skeleton, KNM-ER 803, is fragmentary and barely preserves anatomies that are useful for comparative analysis (Day and Leakey 1974). What is preserved suggests that the talus of KNM-ER 803 was mediolaterally flat, as is KNM-ER 5428 (see Figure 4). The Dmanisi talus (Pontzer et al. 2010) also exhibits a flat trochlea. Therefore, the mediolaterally flat talar trochlea found in specimens such as KNM-ER 5428, KNM-ER 803, and the Dmanisi talus may be useful in distinguishing *Homo erectus* tali from *Paranthropus* tali which may possess a more deeply keeled midtrochlear groove, as is found in KNM-ER 1464 and OH 8 (Gebo and Schwartz 2006).

KNM-ER 5428 is one of the largest bones (based on body mass calculations) attributed to *Homo erectus* (Table 5). At ~90kg, this individual would be over four standard deviations larger than the average *H. erectus* in the sample (average 56.2±9.0kg). As a comparison, Ruff (2010) suggested that the purported *H. erectus* pelvis from Gona (BSN49/P27) was too small to be considered *H. erectus*. In our

TABLE 4. STRUCTURE MATRIX FOR DISCRIMINANT FUNCTION ANALYSIS[1].

Variable	Function 1	Function 2	Function 3
Mediolateral breadth of trochlear anterior margin (C)	.021	-.277	.052
Mediolateral breadth of trochlea posterior margin (E)	-.371	.331	-.172
Width of talar head (H)	-.484	-.276	.196
Height of talar height (I)	-.399	-.307	-.323
Height of fibular facet (M)	-.079	-.088	-.205
Length of fibular facet (L)	-.083	-.269	-.251
Depth of trochlear keel (not pictured)	.426	.427	.153

[1] Pooled within-group correlations between variables and first three discriminant functions.

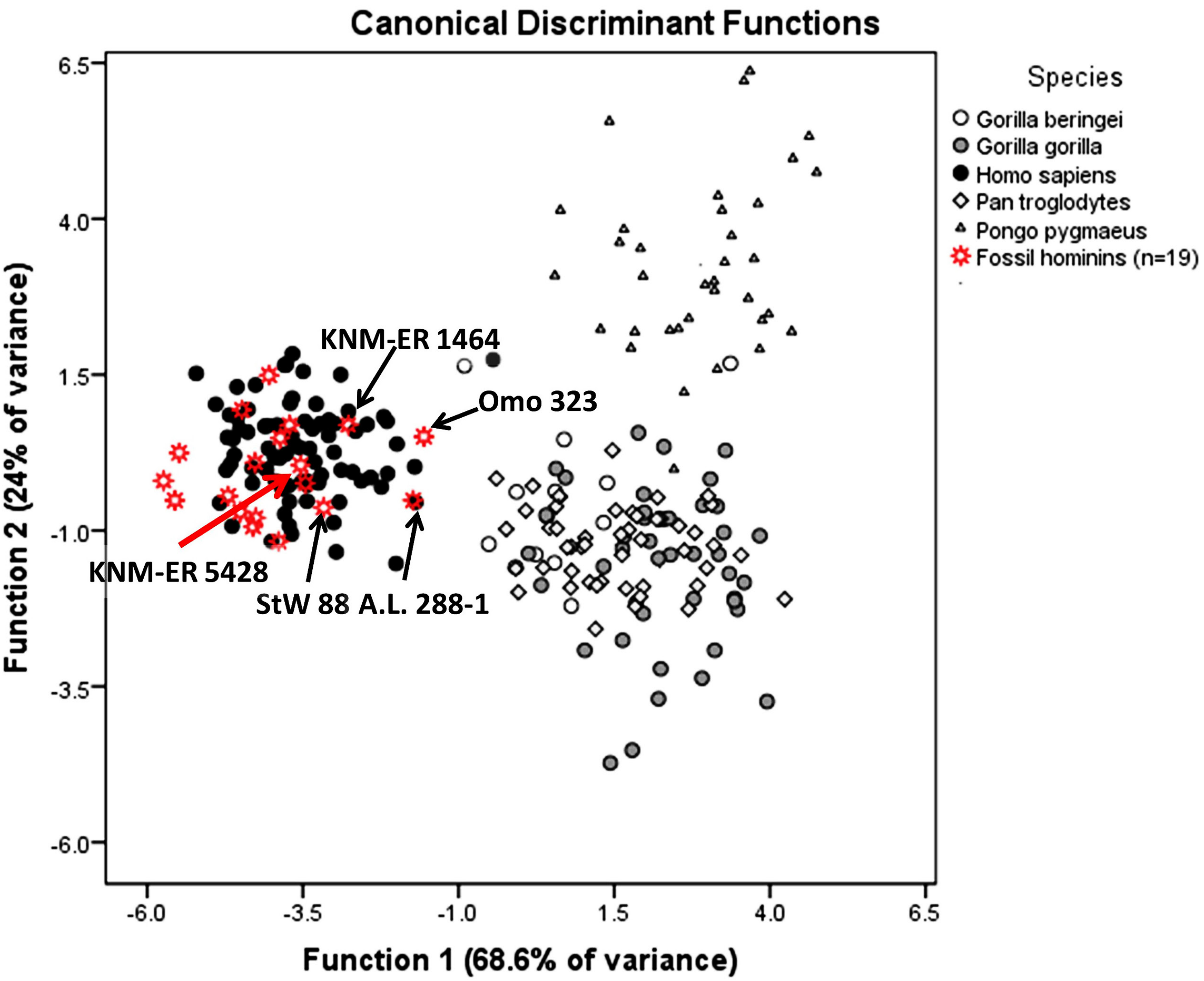


Figure 5. Discriminant function analysis showing position of KNM-ER 5428 relative to modern humans, apes, and fossil hominins. Unlabeled fossil hominins are the Late Pleistocene specimens described in Pablos et al. (2013). Human tali can be differentiated from ape tali along Function 1, but not Function 2. All of the hominin fossils, including KNM-ER 5428, generally fit within the range of distribution found in modern human tali.

sample, we find that the Gona pelvis, though small, is still within three standard deviations of the average *H. erectus* and is thus less unusual in its size than the KNM-ER 5428 talus (Figure 6A). Moreover, KNM-ER 5428 yields the largest body mass estimate based on an isolated hominin talus before 300 ka, nearly double the size of other contemporaneous specimens (Figure 6B).

The increased body size of *Homo erectus* has been an often noted, and critically important, aspect of the paleobiology of this species (Aiello and Kay 2002; Aiello and Wells 2002; Antón 2003; Antón et al. 2014; Foley and Lee 1991; Leonard and Robertson 1994; McHenry 1994; McHenry and Coffing 2000; Pontzer 2012; Ruff and Walker 1993; van Arsdale 2013). Recently, however, newly recovered fossils have complicated interpretations of *H. erectus* body size. Fossil crania from Ileret (Spoor et al. 2007) and Olorgesailie (Potts et al. 2004) suggest that some female erectines may have been rather small. Additionally, the pelvis from Gona, Ethiopia (Simpson et al. 2008), is strikingly small, estimated to only be from a 33.2kg female (Ruff 2010). Although this small size suggests to Ruff (2010) that the Gona pelvis has been misattributed to *H. erectus*, there is reason to suspect based on obstetrics alone (Wells et al. 2012) that Simpson et al. (2008) were correct and that *H. erectus* females were smaller than originally supposed. Further complicating matters is the recent discovery that male *P. boisei* may have been quite large (~50kg), overlapping in size with *H. erectus* (Domínguez-Rodrigo et al. 2013). Attribution of isolated specimens in regions where *P. boisei* and *H. erectus* coexisted based solely on size is therefore a questionable practice. Though we find it unlikely that any *P. boisei* individuals exceeded 90kg, we can no longer assume based on size alone

TABLE 5. ESTIMATED BODY MASSES FOR PRESUMED *HOMO ERECTUS* FOSSILS.

Specimen	Age (Ma)	Estimated Body Mass (kg)
KNM-ER 164	1.78[1]	51.7[2]
KNM-ER 736	1.58[3]	62.0†[4] 79.6†[2]
KNM-ER 737	1.60[1]	52.0†[4]
KNM-ER 741	1.57[1]	47.6[2]
KNM-ER 803	1.53[1]	67.4†[2]
KNM-ER 1808	1.60[3]	59.0†[4]
KNM-ER 1472	2.01[3]	47.0[4] 52.1[5]
KNM-ER 1481	1.95-1.98[6]	46.0[4] 61.2[5]
KNM-ER 3228	1.95[1]	62.0[2] 67.1[5]
KNM-ER 3728	1.89[1]	45.0[4]
KNM-ER 3733	1.65[3]	59.6[7]
KNM-ER 3883	1.57[1]	47.0[7]
KNM-ER 5428	1.6[1]	93.4[2]
KNM-WT 15000	1.47[3]	52.0†[4] 57.5[7] 77.8[5]
Dmanisi	1.77[8]	48.8[8] 52.6[5]
Gona (BSN49/P27)	0.9-1.4[5]	33.2[5]
OH 28	<.78[4]	54.0†[4] 72.3[5]
OH 34	1.0[4]	51.0[4]

†based on femur

[1] Feibel et al. (1989)

[2] based on average of three human-regression equations from McHenry (1992)

[3] McDougall et al. (2012)

[4] Antón (2003)

[5] Ruff (2010)

[6] Joordens et al. (2013)

[7] Kappelman (1996)

[8] Pontzer et al. (2010)

that isolated specimens, such as KNM-ER 5428, belong to *H. erectus*. However, as discussed above, the large size only in combination with human-like anatomies consistent with those found in KNM-ER 803 and the Dmanisi talus lead us to conclude that KNM-ER 5428 is best attributed to *H. erectus*. A comparison with the ~1.0 Ma Daka talus BOU-VP-2/95 (Gilbert and Asfaw 2009)—presumably also from *H. erectus*—will undoubtedly assist with the proper taxonomic identification of KNM-ER 5428.

The anatomical modernity of KNM-ER 5428 is undermined by its height (Figure 7). For its breadth, this talus is substantially shorter than modern human or most Neanderthal tali. When compared with other fossil hominins, however, KNM-ER 5428 is less peculiar. It follows a pattern of having a vertically short talar body height that persists through Pleistocene *Homo* up through the Sima de los Huesos tali (Pablos et al. 2013), and even continuing into specimens attributed to early *Homo sapiens* from Omo-Kibish (Pearson et al. 2008). The origin of the dorsoplantarly squat talus most likely can be traced to the origins of obligate bipedalism and the establishment of an orthogonal ankle joint, made possible in part by the reduction of the height of the lateral rim of the talus (DeSilva 2009; Latimer et al. 1987; see Figure 7). While modern human tali are very similar to earlier *H. sapiens*, *H. neanderthalensis*, and *H. erectus* in breadth and morphology, they are noticeably taller. Why the talus—the proportions of which remain generally similar throughout the Plio-Pleistocene—evolved a dorso-

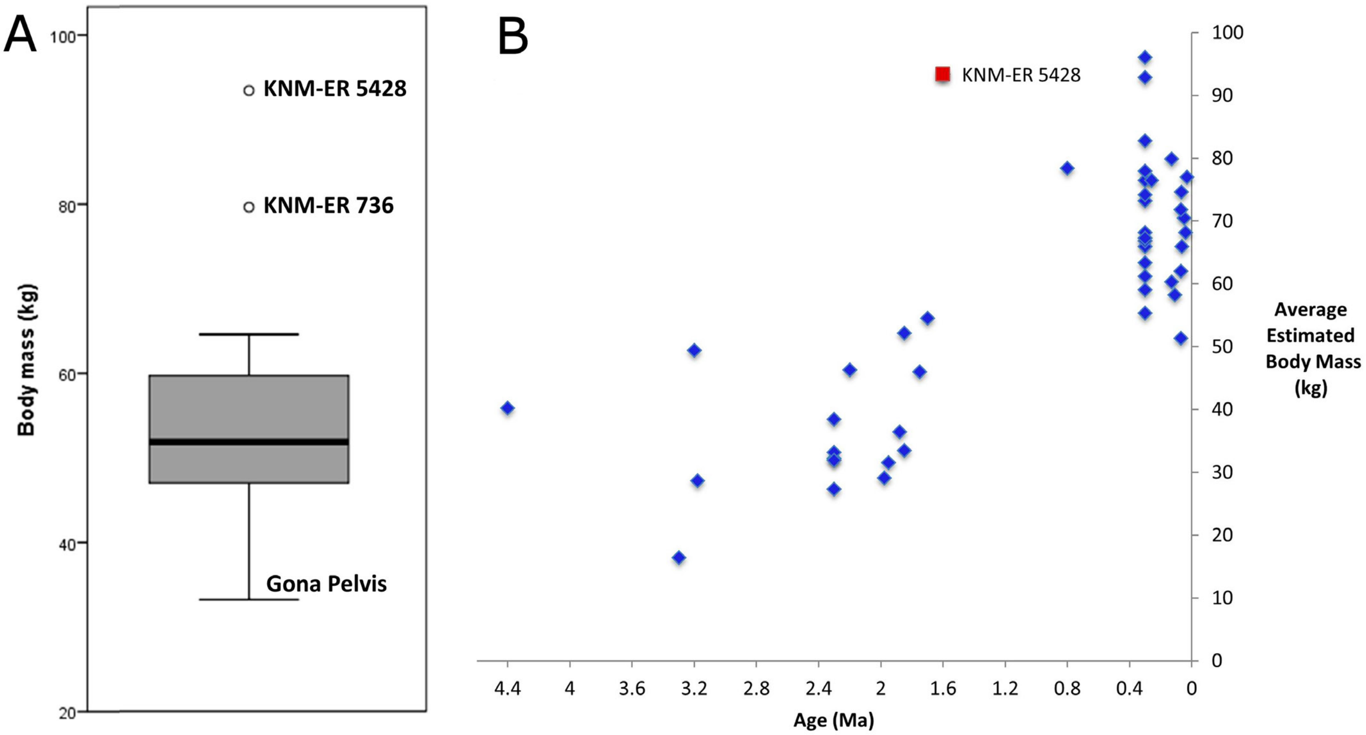


Figure 6. *(A): Boxplot of body mass estimates in fossils attributed to* Homo erectus *(see Table 5 for individual specimens). The boxplot shows the median (black bar), interquartile ranges (gray box) and overall range of the data (whiskers). Outliers defined as >1.5 times the interquartile range are shown as open circles. KNM-ER 5428 is an obvious outlier, demonstrably larger than other* H. erectus *postcrania. Notice that the unusually small pelvis from Gona, Ethiopia, is not considered an outlier in this boxplot. (B): Scatter plot comparing body mass estimates based only on talar width for fossil hominins over time. Body mass estimates from the tali were calculated using the average of the three human-based regression equations in McHenry (1992). KNM-ER 5428 is a clear outlier for its time period, larger than other hominin tali in the Early Pleistocene.*

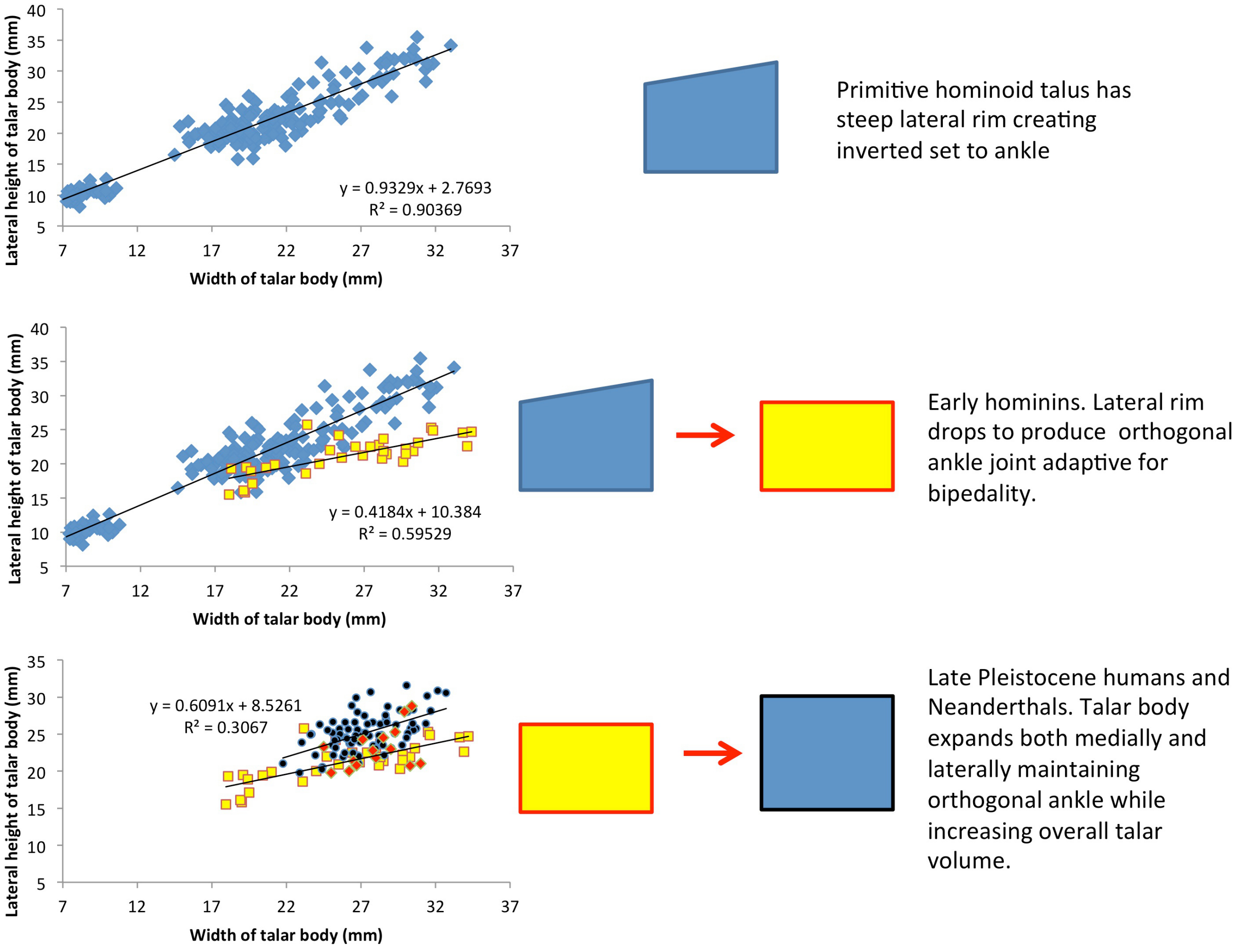
plantarly taller body recently in human evolution remains unclear.

This general increase in size of the talus—and in particular the trochlear surface—in Late Pleistocene *Homo* has been described as a response to greater biomechanical stress and a function of increased robustness of the skeleton (Pablos et al. 2012; Rhoads and Trinkaus 1977). We address this and other potential explanations for the increase in the height of the talar body below, treating these as hypotheses worthy of future exploration.

The vertically tall talus may be related to maintaining a high longitudinal arch in the foot, as a vertically expanded talar body and therefore a vertically translated talar head, would place the navicular in an elevated position. Anderson et al. (1997) found that flat-footed adult humans possessed tali that were statistically shorter (in vertical height) than individuals with “normally” arched feet. While skeletal correlates of the modern human arch are not entirely clear, the talar declination angle of KNM-ER 5428 would suggest at least a minimally arched rearfoot in this individual. While some have proposed that a modern longitudinal arch evolved by 1.9 Ma in *H. erectus* as a long distance running adaptation (Bramble and Lieberman 2004), others have maintained that the modern arched foot is more recent (Lu et al. 2011). The relationship between relative talar body height and longitudinal arch height could help determine whether this vertical increase in talar body height has anything to do with the evolution of the arched foot.

Another possibility is that a taller talus could have been a response to the innovation of shoes in *H. sapiens*. Trinkaus (2005) describes changes in pedal phalanges between the Middle and Upper Paleolithic as shoe-wearing becomes more frequent, but the impact of shoes on talar morphology has not been studied. However, we are skeptical of this as a driving mechanism given that the presumably minimally shod Libben population possesses a relatively taller talar body ($p<0.001$) than the tali from the Hamann-Todd collection.

One final hypothesis is that the increase in talar height is an adaptation to dissipating high loads in the ankle, which has been proposed by others (Pablos et al. 2012; Rhoads and Trinkaus 1977). Weight-bearing bones such as the talus become highly susceptible to microdamage and weakening with age (Pearson and Lieberman 2004). An increase in talar height and therefore trabecular bone volume (Cotter et al. 2009), would increase compliance and may help spare articular cartilage from degeneration. This also would provide some insurance against cartilage damage particularly associated with aging (Bailey et al. 1999). Caspari and Lee (2004) hypothesize that an increase in longevity began as



Primitive hominoid talus has steep lateral rim creating inverted set to ankle

Early hominins. Lateral rim drops to produce orthogonal ankle joint adaptive for bipedality.

Late Pleistocene humans and Neanderthals. Talar body expands both medially and laterally maintaining orthogonal ankle while increasing overall talar volume.

Figure 7. (A): There is a conserved scaling relationship between the width of the talar body and the height of the lateral rim of the talar trochlea in apes. Here and throughout, least-squares regression equation is presented on the graph. (B): Trochlear anatomy in the modern apes is interpreted as primitive, resulting in a lateral side of the talar body that is dorsoplantarly taller than the medial side and an inverted set to a mobile, arboreally-adapted foot. (C): In yellow are Plio-Pleistocene hominin tali (listed in Table 2). (D): In early hominins, the lateral rim drops and produces an orthogonal ankle joint adaptive for bipedal locomotion by everting the feet and positioning the ankle directly under the knees. (E): Addition of Late Pleistocene (from Pablos et al. 2013) and Neanderthal (from Rhoads and Trinkaus 1977) tali (red diamonds) and modern human tali (black circles). (F): In Late Pleistocene humans and in some Neanderthals, the talar body expands dorsoplantarly on both the medial and lateral sides, increasing talar volume while maintaining an orthogonal ankle joint. The adaptive significance of such a change in the talus is unclear, but hypotheses are presented in the text.

recently as the Late Pleistocene, which could temporally coincide with the talar height increase. However, if long life expectancy evolved earlier in the Pleistocene as some researchers argue (see O'Connell et al. 1999), or during the Holocene (see Trinkaus 2011), then there may be no correlation between this vertical height increase and the durability the talus must exhibit over a long lifetime. Additionally, it is unclear why population level differences (as we detected between the Libben and Hamann-Todd collections) would exist if the talar body increased in volume as a longevity adaptation in all humans.

The observed talar height increase in early *H. sapiens* thus accompanies a suite of currently unexplained changes in the modern human body plan that have arisen only within the last hundred thousand years of our evolution. These include a slight decrease in brain size (Hawks in press) and modification of the pelvic girdle (Rosenberg 1992). Further experimental and comparative research is obviously needed to elucidate the functional and adaptive relevance of these changes.

CONCLUSION

Based on both size and morphology, we suggest that the 1.6 Ma talus KNM-ER 5428 belonged to a large male *H. erectus*. While the differences between this talus and modern human tali are subtle, differences in dorsoplantar height of the trochlear body undermine arguments that fully human foot anatomies had evolved in *Homo erectus*.

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