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Evidence for an elongated Achilles tendon in *Australopithecus*

Ellison J. McNutt[1] 🔶 | **Jeremy M. DeSilva[2]** 🔶

[1]Department of Integrative Anatomical Sciences, Keck School of Medicine, University of Southern California, Los Angeles, California

[2]Department of Anthropology, Dartmouth College, Hanover, New Hampshire

Correspondence
Ellison J. McNutt, 1333 San Pablo Street BMT 321, Keck School of Medicine, University of Southern California, Los Angeles, CA 90033.
Email: emcnutt@usc.edu

Abstract

Modern humans have the longest Achilles tendon (AT) of all the living primates. It has been proposed that this anatomy increases locomotor efficiency and that its elongation may have played a crucial role in the origin and early evolution of the genus *Homo*. Unfortunately, determining the length of the AT in extinct hominins has been difficult as tendons do not fossilize. Several methods have been proposed for estimating the length of the AT from calcaneal morphology, but the results have been inconclusive. This study tested the relationship between the area of the superior calcaneal facet and AT length in extant primates. The superior facet is instructive because it anchors the retro-calcaneal bursa, a soft tissue structure which helps to reduce friction between the AT and the calcaneus. Calcanei from 145 extant anthropoid primates from 12 genera were photographed in posterior view and the relative superior facet size quantified. AT lengths were obtained from published sources. The relative area of the superior facet is predictive of AT length in primates ($R^2 = 0.83$; $p < .001$) and differs significantly between the great apes and humans ($p < 0.001$). When applied to fossil *Australopithecus* calcanei, our results suggest that australopiths possessed a longer, more human-like, AT than previously thought. These findings have important implications for the locomotor capabilities of *Australopithecus*, including their capacity for endurance running and climbing.

KEYWORDS

Achilles tendon, *Australopithecus*, calcanei, endurance running, hominin

1 | INTRODUCTION

The Achilles tendon (AT), also called tendocalcaneus or calcaneal tendon, is the longest, strongest tendon in the human body. It serves as the common tendon of the triceps surae muscle (i.e., the gastrocnemius, soleus, and plantaris muscles), which originates from areas on the distal femur, as well as the proximal tibia and fibula. These muscles collectively insert on the posterior surface of the calcaneus (Figure 1) (Grey & Lewis, 1918). In mammals, a long AT serves as a cursorial adaptation that increases the efficiency of rapid locomotion by stretching and releasing stored

energy in elastic recoil (Biewener & Blickhan, 1988; Janis, Buttrill, & Figueirido, 2014; Preuschoft & Günther, 1994). Although the AT provides some energy savings during walking (Sawicki, Lewis, & Ferris, 2009), the most significant impact is during running (Bramble & Lieberman, 2004; Sellers, Pataky, Caravaggi, & Crompton, 2010). In humans, the AT can save as much as 35% of the metabolic cost of running (Ker, Bennett, Bibby, Kester, & Alexander, 1987). It has been proposed that the elongation of the AT may have enhanced the endurance running (i.e., running many kilometers over several hours) abilities of early members of the genus *Homo* (Bramble & Lieberman, 2004).
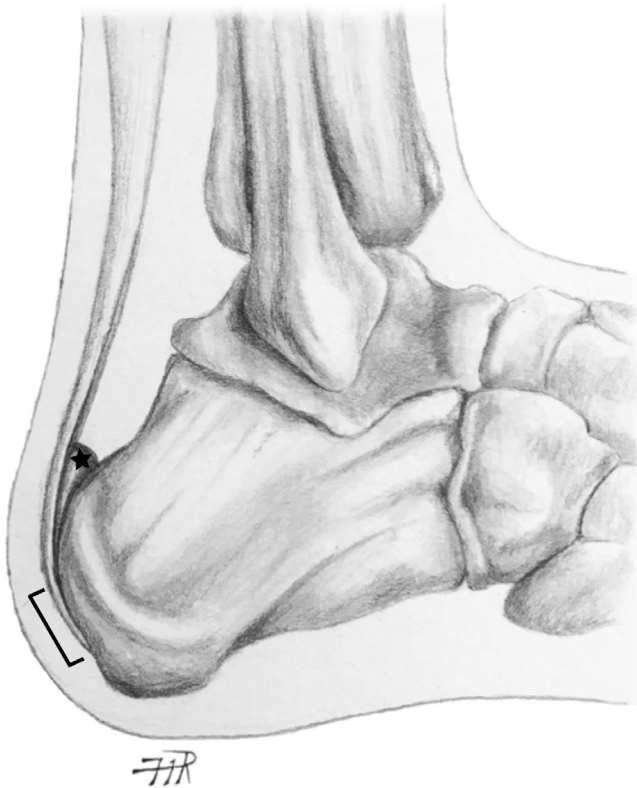
FIGURE 1 Image showing the relationship between the Achilles tendon, the retrocalcaneal bursa, and the calcaneus. The black star demarcates the retrocalcaneal bursa, which rests on the superior facet of the posterior calcaneal tuberosity. The black bracket surrounds middle facet of the posterior calcaneus, where the Achilles tendon inserts

The length of the AT is an informative indicator of locomotor capabilities across species of closely related mammals. For instance, the pattern in rodents (i.e., length of AT in swimmers < climbers < leapers) (Grassé, 1971) suggests that AT length is closely related to function, rather than exclusively a consequence of phylogeny. In general, primates follow the same pattern, as the longest ATs are found in the cursorial/leaping primates (tarsiers, galagos, and humans) and the shortest in the slower climbing primates (lorises, ateline platyrrhines, and great apes) with gibbons and cercopithecoids intermediate in length (Burmeister, 1846; Hanna & Schmitt, 2011; Kuo, DeSilva, Devlin, Mcdonald, & Morgan, 2013; Rauwerdink, 1991).

There is an inverse relationship between the AT length and muscle fiber length within primates. It has been shown in modern humans that decreasing muscle fiber length in the gastrocnemius results in increased stiffness of the AT (Csapo, Maganaris, Seynnes, & Narici, 2010), and this relationship suggests that individuals with increased fiber length are capable of a greater range of motion at the talocrural joint (Venkataraman, Kraft, & Dominy, 2013). It is hypothesized that the long muscle fibers found in the nonhuman great apes and ateline

FIGURE 2 Graphic showing the difference in relative Achilles tendon length to total muscle in modern humans (left) and chimpanzees (right)

platyrrhines improves their climbing ability by increasing the joint excursion of their ankles to facilitate flexed-ankle vertical climbing bouts (see Figure 2 for a comparison of human and chimpanzee AT lengths) (DeSilva, 2009; Myatt, Schilling, & Thorpe, 2011; Thorpe, Crompton, Guenther, Ker, & McNeill, 1999). This is advantageous because higher degrees of dorsiflexion at the ankle allow these primates, like chimpanzees (DeSilva, 2009), to bring their centers of mass closer to the vertical substrate.

Unfortunately, reconstructing the evolutionary history of the AT from the hominin fossil record has been difficult because tendons, like all soft tissues, do not easily mineralize. A number of different methods have been employed to attempt to estimate AT length from various

aspects of the morphology of the calcaneus. These have included the microstructure of the trabecular bone of the calcaneus (Kuo et al., 2013; Maga, Kappelman, Ryan, & Ketcham, 2006), and the orientation of the calcaneal tuber and the presence of Sharpey's fibers (Zipfel et al., 2011). So far, the results of these methods have been inconclusive, making the determination of AT length based on fossils difficult (Bramble & Lieberman, 2004). Nevertheless, early hominins have generally been assumed to possess a shorter (Latimer & Lovejoy, 1989), even ape-like AT length (Bramble & Lieberman, 2004), with tendon elongation occurring later in the genus *Homo* (Lieberman, Bramble, Raichlen, & Shea, 2009).

This study proposes a new method for estimating the length of the AT from the posterior surface of the calcaneal tubercle. The posterior surface of the primate calcaneus is divided into three facets: the inferior facet which is rough and covered by the fat and fibrous tissue of the heel; the middle facet which is also rough and serves as the insertion site for much of the AT; and the superior facet which is smooth and contacts the retrocalcaneal bursa—a soft tissue structure which helps to reduce friction between the AT and the calcaneus (Grey & Lewis, 1918; Kachlik et al., 2008). The distinct separation between these facets is variable, but always expressed (Kachlik et al., 2008). Given that the retrocalcaneal bursa functions to reduce friction between the AT and the calcaneus, it is hypothesized that species with a longer AT will possess a relatively larger superior facet. Here, we test the relationship between relative superior facet size and AT length in anthropoid primates. Furthermore, we test the hypothesis that the *Australopithecus* AT length is best characterized as modern great ape-like.

2 | MATERIALS AND METHODS

Adult calcanei from modern humans were measured on two groups: unprovenanced anatomical specimens ($n = 15$) from the biological anthropology laboratories at Boston University and Dartmouth College, as well as a sample from a prepastoral, habitually unshod hunter-gatherer population ($n = 18$), approximately 5–7 Kyr old from the Florisbad Quaternary Research Station, National Museum, Bloemfontein, South Africa. Adult wild-shot primates ($n = 137$) were measured at the Harvard Museum of Comparative Zoology (Cambridge, MA) and the American Museum of Natural History (New York, NY). Comparative species were chosen based on availability of published AT length data, which was typically reported as a percentage of the total tendon-muscle unit. Published AT length data were collected in similar, although not identical, methods. For example,

some estimates were based on the ratio between the tendon length of *M. gastrocnemius* and tibial length (e.g., Kuo et al., 2013; Rauwerdink, 1991) compared to others calculated as the inverse of the ratio between muscle belly length of the *M. triceps surae* and the total muscle-tendon unit (i.e., from origin to insertion of the muscle) (e.g., Payne et al., 2006). A complete list of extant specimens and their sample sizes is shown in Table 1. While not ideal, the AT lengths present in this study represent the best basis currently available for comparison of this anatomy across primate species until a more systematic review of AT lengths can be performed.

Each specimen was photographed to provide a detailed image of the posterior tubercle of the calcaneus (as shown in Figure 3a). Calcanei were aligned so that, when viewed from above, the middle facet was centered in the camera view (as shown by the dotted lines in Figure 3b) and the sustentaculum tali was perpendicular to the dorsoplantar axis through the posterior tubercle. Specimens were photographed using a camera stand after adjusting light sources to improve contrast between the facets.

The area of the superior facet (i.e., black area on Figure 3b)—a proxy for the area of the retrocalcaneal bursa—and the total area of the superior plus the middle facets (i.e., total shaded area on Figure 3b) were calculated from the photographs using the open source imaging software, ImageJ (Schneider, Rasband, & Eliceiri, 2012). A ratio was used to assess the size of the superior facet to limit the effect of body size as a confounding factor in the analysis (i.e., large primates should naturally have the bigger superior facets due to the increased size of their calcanei). For each photograph, the areas of interest were defined in two steps using the freehand shape tool. First, the total area for the two facets was isolated by tracing around the visible edge of the posterior tubercle and along the inferior edge of the line separating the middle facet from the inferior facet which demarcates the inferior edge of the insertion for the AT. The "Measure" function was used to calculate the area (in pixels). Second, the area of the superior facet was isolated using the outline from the previous measurement and the inferior edge of the line separating the superior and middle facets (see Figure 3c for an example of the areas of interest drawn in ImageJ).

For each specimen, a ratio was computed between the area of the superior facet and the total area of the upper two facets. The facet ratios for each species were averaged and plotted against the length of the AT (as the percent of the total tendon-muscle unit) in that species (values listed in Table 1). For species with AT length measurements from multiple sources the estimates were averaged. Additionally, the AT length in *Ateles* spp.

TABLE 1   List of all extant primate species and their samples sizes included in the analysis[a]

Species	Sample size (n)	Average facet ratio[b] $\pm$ SD	Facet ratio range	Tendon length (as percent of tendon-muscle unit)[c]	Original source
Ateles spp.	8	0.36 $\pm$ 0.06	0.26–0.44	"Ratio similar to chimpanzees"	Hanna & Schmitt, 2011
Cebus capucinus	11	0.45 $\pm$ 0.15	0.25–0.67	~30%	Rauwerdink, 1991
Chlorocebus aethiops	4	0.37 $\pm$ 0.04	0.34–0.43	~25%	Rauwerdink, 1991
Gorilla gorilla gorilla	24	0.36 $\pm$ 0.08	0.22–0.52	4% 21.8%	Payne et al., 2006; Gregory, 1950
Homo sapiens	33	0.51 $\pm$ 0.09	0.35–0.72	~53% ~65%	Rosso et al., 2012; Prejzner-Morawska & Urbanowicz, 1981
Hylobates lar	20	0.51 $\pm$ 0.13	0.26–0.74	36% ~45%	Payne et al., 2006; Vereecke, D'Aout, Payne, & Aerts, 2005
Lagothrix lagotricha	2	0.35 $\pm$ 0.03	0.32–0.37	~5%	Rauwerdink, 1991
Macaca mulatta	4	0.39 $\pm$ 0.09	0.26–0.45	~25%	Rauwerdink, 1991
Pan paniscus	4	0.37 $\pm$ 0.05	0.30–0.43	7% 10%	Payne et al., 2006; Vereecke et al., 2005
Pan troglodytes	20	0.38 $\pm$ 0.07	0.26–0.54	7.5%	Rauwerdink, 1991
Papio hamadrayas	5	0.44 $\pm$ 0.11	0.25–0.52	~40%	Rauwerdink, 1991
Pongo pygmaeus	10	0.38 $\pm$ 0.09	0.22–0.49	18% 18.3%	Payne et al., 2006; Myatt et al., 2011

[a]Table adapted from Kuo et al. (2013).
[b]Facet ratio calculated based on the area of the superior facet/total area of the superior and middle facets of the posterior calcaneal tuberosity.
[c]For species with multiple values represented, associated references are inline with values.
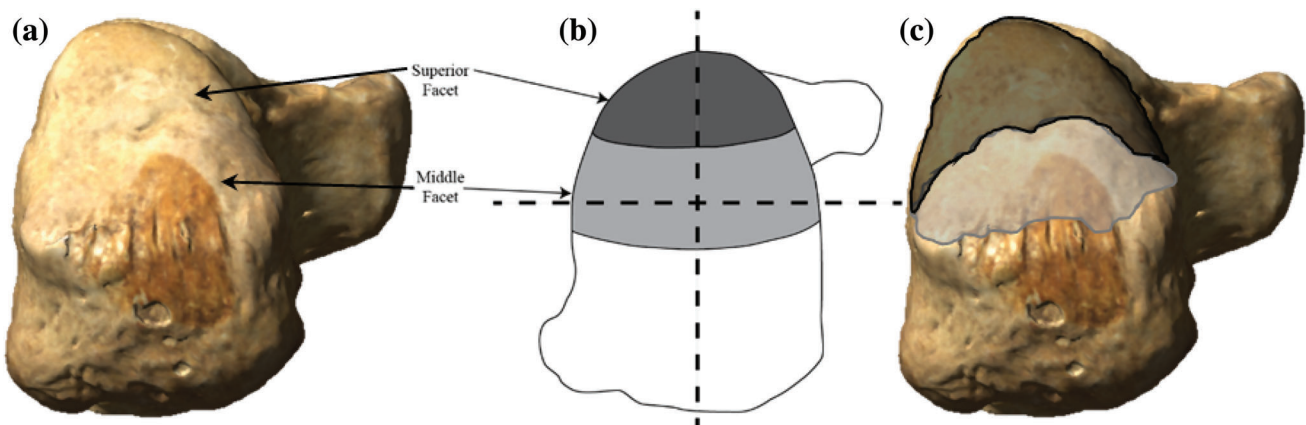

FIGURE 3   (a) Example of a human posterior calcaneal tubercle showing the location of the superior and middle facets. (b) Diagram of the specimen orientation during photographic data collection. Camera was centered on the middle facet as shown by dotted lines. (c) Areas of interest as isolated in ImageJ. Black area represents the superior facet. Total shaded area represents the combined superior and middle facets

was approximated as 7.5% based on the observation (Hanna & Schmitt, 2011) that *Ateles* AT length was chimpanzee-like. A Pearson's rho correlation coefficient and its associated p value were calculated to test the strength of the association between the two variables. The data were modeled using an ordinary least squares regression (OLS).

The potential for errors introduced by variation in calcaneal orientation during data collection was assessed. A modern human calcaneus was anchored in fixed position, oriented based on the methods described above, and attached to one arm of a mounted goniometer. A photograph was taken of this "neutral" study position. The bone was then moved through a $\pm10°$ arc around this

neutral position with photographs taken every 2° to simulate extreme variations in the superior–inferior orientation of the calcaneus. The facet ratio was then calculated for each of the 11 photographs and the percent error relative to neutral was calculated.

Intraobserver error was assessed by remeasuring the ratio for 30 of the 145 specimens and using a matched-pairs t test to determine whether or not the difference between the mean of two sets of ratios calculated by the same observer (E.J.M.) was statistically different from zero at the 95% confidence level. Interobserver error was assessed by J.M.D., who independently remeasured the ratios of 10 randomly selected calcanei.

The majority of known Miocene hominoid and Plio-Pleistocene hominin calcanei have had their posterior tubercle either badly damaged or completely sheared off. For instance, while the tubercle is still present in *Oreopithecus*, it has been crushed making it unreliable for use in this study. Currently, there are only five published calcanei in the Miocene hominoid and Plio-Pleistocene fossil record which sufficiently preserve the posterior calcaneal tubercle (Table 2). Original Hadar calcanei (A.L. 333-8, -37, -55) were studied at the National Museums of Ethiopia (Addis Ababa). There is extensive dorsal damage to the calcaneal tuber in A.L. 333-37 preventing its use in this study. There is slight damage to the dorso-medial edge of the posterior tubercle for both A.L. 333-8 and A.L. 333-55. This damaged area was excluded from all measurements, making the resulting ratio reported a minimum for the two Hadar specimens. The Malapa calcaneus (U.W. 88-99) was studied at the Evolutionary Studies Institute at the University of the Witwatersrand (Johannesburg, South Africa).

There is only one Miocene hominoid calcaneus that sufficiently preserves the posterior tubercle: KPS VIII T-19, an *Ekembo heseloni* calcaneus from the Kasawanga Primate Site, Rusinga Island, Kenya. We studied the original fossil at the National Museum of Kenya (Nairobi). Three dimensional scans were taken using a Creaform

Go! Scan 20 and used to capture images of the posterior tubercle for analysis.

Positioning of the Hadar calcanei was complicated by the absence of the distal portion of both bones, including the majority of the sustentaculum tali. The orientation of these specimens was estimated by centering the camera field on the middle facet, as was done with the comparative material and using the bases of the sustentaculum tali which are still preserved. The superior facet ratio for each fossil was entered into the equation from the OLS regression (based on Smith, 2009) to estimate AT lengths in those specimens.

A Kruskal–Wallis analysis was run in JMP to test for differences between the facet ratios across the nonhuman great apes. The relative size of the superior calcaneal facet was compared between humans and great apes using a Welch's t test. *Australopithecus* calcanei were compared to modern ape and human calcanei using the single observation with the mean test (Sokal & Rohlf, 1995). Additionally, we used resampling statistics to test the likelihood of sampling the variation in facet morphology found in the Hadar hominins compared with the Malapa hominin. This was done by randomly sampling two human calcanei and averaging the calcaneal facet ratio (modeling the Hadar calcanei) and randomly sampling an additional human calcaneus (to represent Malapa) and taking the difference using the Microsoft Excel resampling macro. This approach was repeated 5,000 times and used to assess the likelihood of sampling calcanei with the facet differences found in the australopiths from a modern human population. All bivariate analyses were run in the statistical program R using a preset $\alpha = .05$.

3 | RESULTS

The range of variation in facet ratio for each of the study species are shown in Figure 4. There was a strong, positive association between the relative area of the superior facet and the relative AT length ($r = 0.91$, $p < 0.001$). The resulting OLS regression equation was $y = 2.71x − 0.87$, where $x =$ the superior calcaneal facet ratio and $y =$ the relative AT length ($R^2 = 0.83$; $p < 0.001$). The standard error for the estimate was 7%. OLS model is shown in Figure 5. The model separated species based on their locomotor behaviors, with those species that engage in more frequent vertical climbing displaying low facet ratios while those that are more generalized quadrupeds, leapers, or bipeds displayed higher facets ratios.

An error assessment was done to examine potential effects of calcaneal orientation on facet ratio calculations. The range of facet ratio was 0.37–0.42, with an average facet ratio of 0.40. The largest percent error observed was 6%.

TABLE 2 List of all available fossil calcanei with sufficiently preserved posterior tubercles

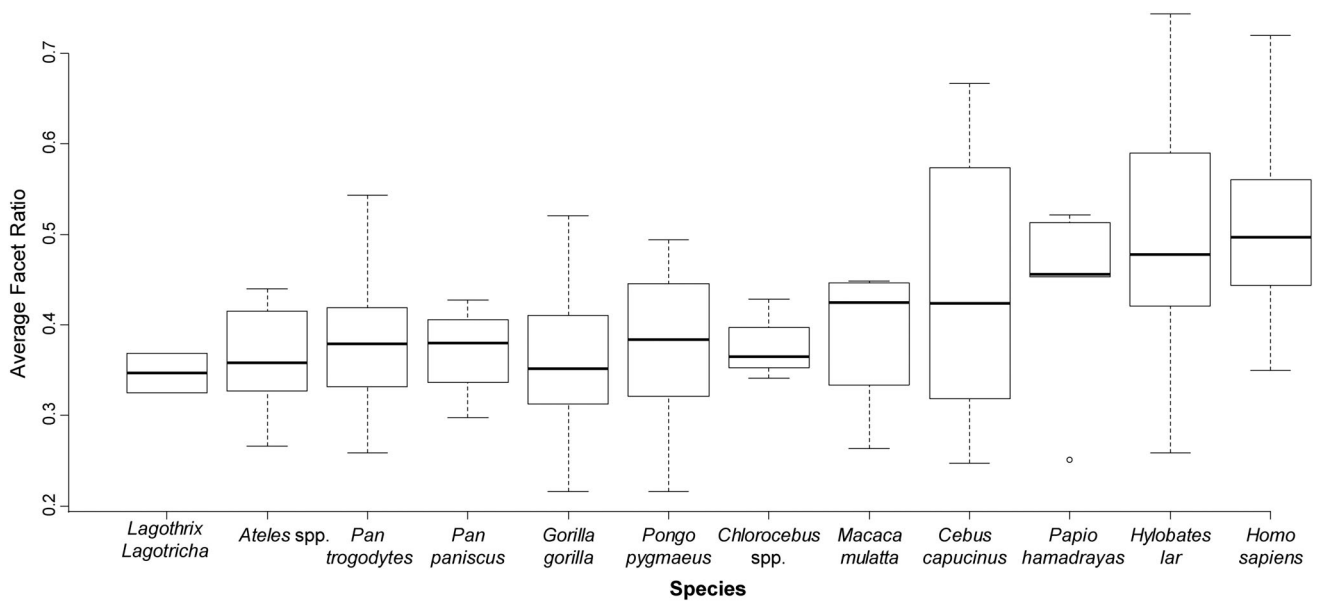| Specimen ID	Taxon	Date (Ma)	Average facet ratio
U.W. 88-99	*Australopithecus sediba*	1.977	0.4680
A.L. 333-8	*Australopithecus afarensis*	3.2	0.5747
A.L. 333-55	*Australopithecus afarensis*	3.2	0.5304
KPS VIII T19	*Ekembo heseloni*	17.8	0.4622

FIGURE 4 Boxplot showing the distribution of facet ratios for all extant primates included in the study
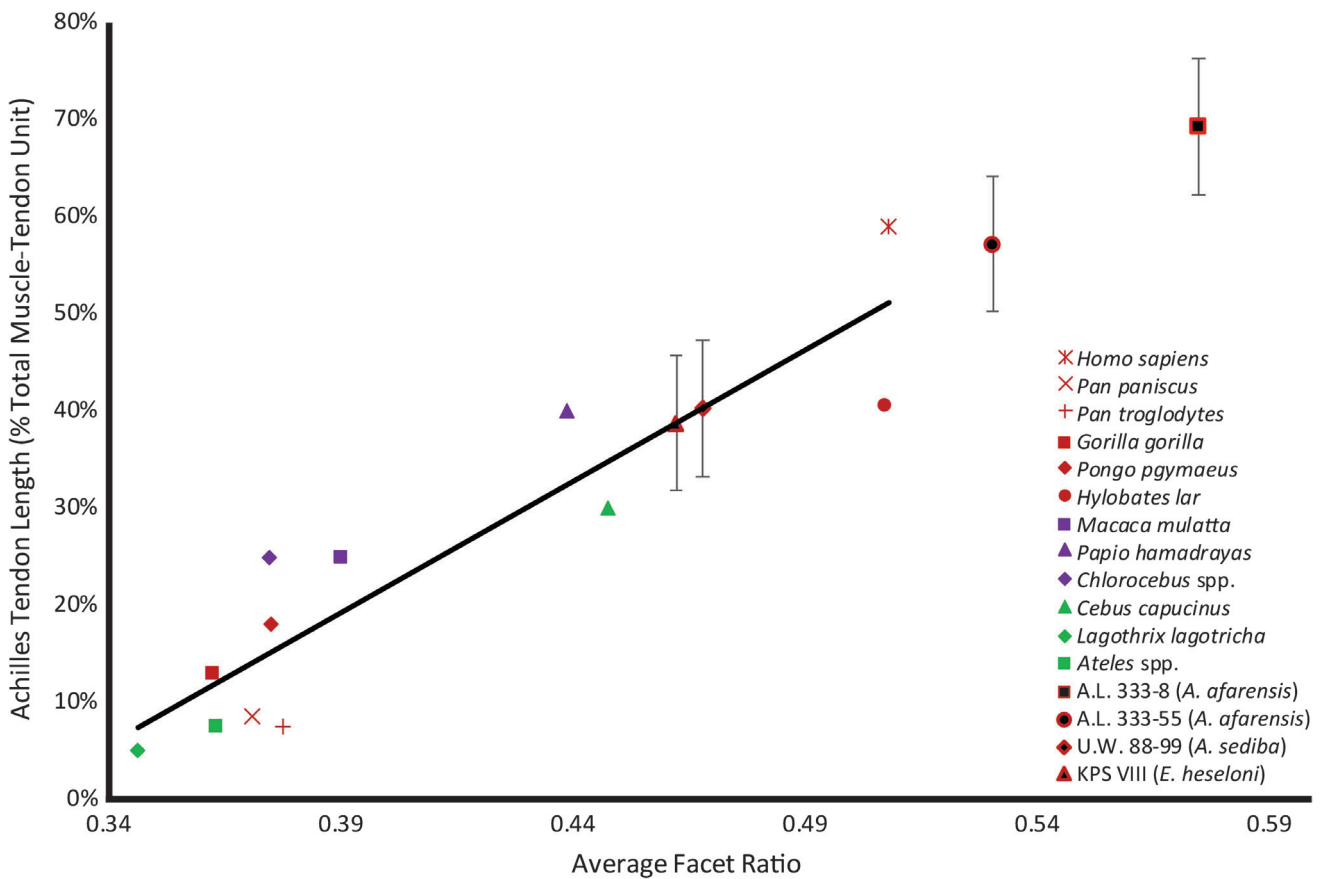

FIGURE 5 Graph of the calculated average ratio between the relative superior facet size and relative Achilles tendon length (see Table 1): cercopithecoids (green), platyrrhines (purple), hominoids (red), and *Homo sapiens* (red star). Black line shows the least square regression ($R^2 = 0.87$). AT values for fossils (black with red outlines) are estimates derived for the OLS equation. Vertical lines represent standard error around the fossil estimates. OLS, ordinary least squares
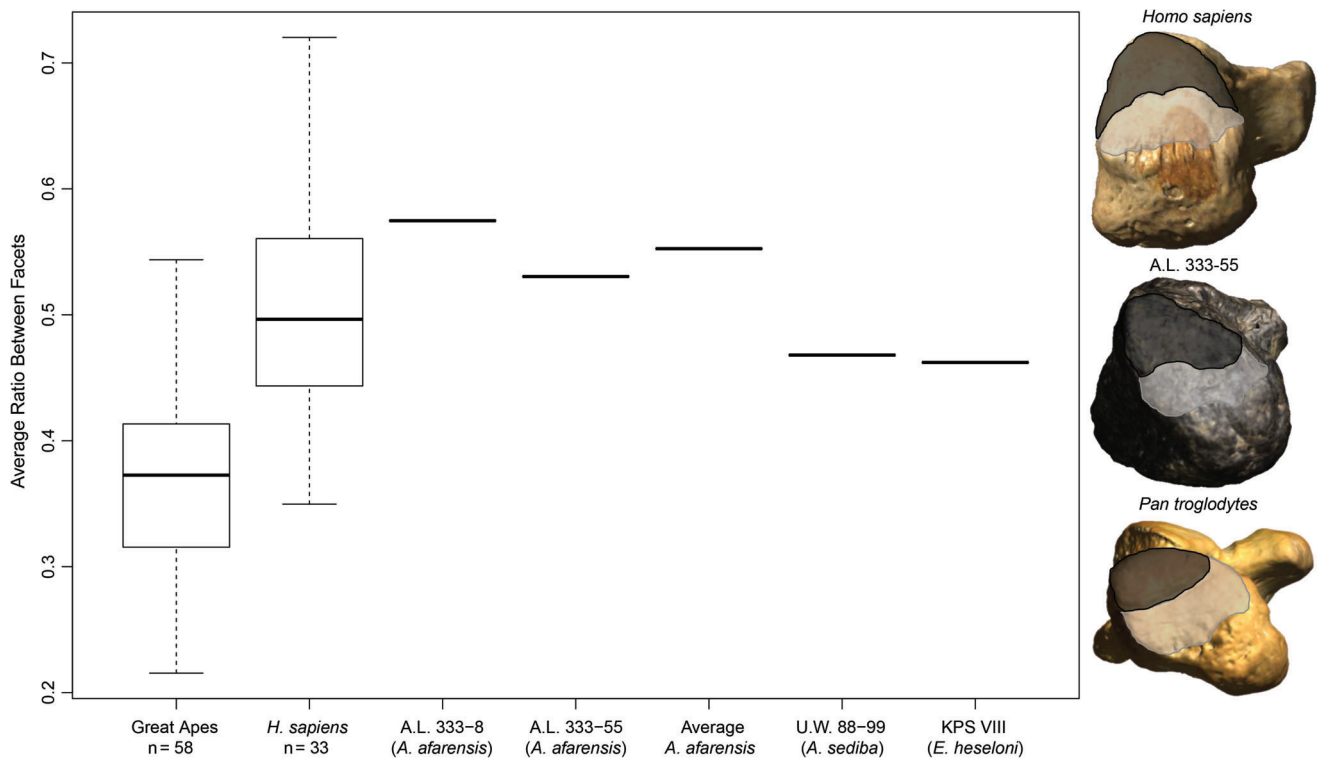
FIGURE 6 Boxplot showing the distribution of facet ratios for nonhuman great apes, *H. sapiens*, and fossil primates. On right, posterior images of representative calcanei from a modern human, chimpanzee, and *A. afarensis*

Intraobserver error was calculated for 30 of the calcanei. The mean ratios of the two trials were $\bar{x} = 0.379$ and $\bar{x} = 0.372$. There were no statistical differences between the two trials using a matched-pairs t test ($p = 0.497$). Intraobserver error was calculated for 10 of the calcanei. There was no statistical difference between the two trials using a matched-pairs t test ($t = 0.363$; $p = 0.73$).

A Kruskal–Wallis test was run comparing the four nonhuman great ape facet ratios. There were no significant differences between them ($p = 0.86$). Differences between the mean average ratio in the great apes ($\bar{x} = 0.37$) and in modern humans ($\bar{x} = 0.55$) were significant ($p < 0.001$); the null hypothesis that there is no difference between humans and nonhuman great apes must be rejected.

From the OLS equation of the superior calcaneal facet ratio to AT length in primates, we estimated the relative Achilles length in *Australopithecus afarensis* to average 63% (with a range of 54–70% based on the standard error of the OLS equation) [A.L. 333-8 = 69% (62–76%) and A.L. 333-55 = 57% (50–64%)] of the muscle-tendon length whereas *Australopithecus sediba* was a shorter 40% (33–47%). *Ekembo heseloni* was predicted to be 39% (32–46%) of the muscle-tendon unit. A single observation with the mean test (Sokal & Rohlf, 1995) finds that the facet ratio from the Hadar calcanei are statistically distinct from the great apes (A.L. 333-8: $p = 0.008$, $df = 57$; A.L. 333-55: $p = 0.036$, $df = 57$), but fit well within the

modern human range of variation, while resting on the edge of the great ape distribution (see Figure 6 for comparison of ratios between fossil calcanei, humans, and other great apes). However, using the same test, the Malapa calcaneus fits within the distribution of both nonhuman great apes ($p = 0.195$, $df = 57$) and modern humans ($p = 0.650$, $df = 32$). We used a resampling approach to test whether the differences we found between the *A. afarensis* Hadar calcanei and the *A. sediba* Malapa calcaneus were statistically significant and perhaps functionally meaningful, using a modern human population as a model (Figure S1). We could not refute the null hypothesis that the difference between the facet ratios of *A. afarensis* and *A. sediba* were within of the range of intraspecific variations that could be observed within a single species ($p = 0.39$), suggesting that these two species are functionally equivalent in terms of facet ratio, though this result could change as samples sizes increase.

4 | DISCUSSION

Finding an effective method for determining AT length from fossil hominin specimens has proved to be challenging (Kuo et al., 2013; Maga et al., 2006; Zipfel et al., 2011). This study examined the hypothesis that the relative area of the retrocalcaneal bursa (approximated by

the area of the superior facet of the calcaneus on which it rests) was predictive of the relative AT length in primates. The high correlation coefficient ($r = 0.91$) and the fact that species with similar locomotor patterns (e.g., the ateline platyrrhines and the nonhuman great apes) have similar relative superior facet areas, regardless of their body size, validate this new method as a way to predict the relative length of the AT in hominin fossil calcanei. We utilized this relationship between superior calcaneal facet area and AT length to test the null hypothesis that australopiths had ape-like AT lengths. While calcanei from Hadar indicate a modern-human like AT, the calcaneus from Malapa presents a more mixed signal and all fossil hominins, save for A.L. 333-8, fall within range of variation of nonhuman great apes, as well as modern humans.

Possessing a longer AT could have important implications for locomotion in *Australopithecus*. The AT stores elastic energy during walking (e.g., Sawicki et al., 2009) and would have improved bipedal energetic economy in *Australopithecus*. However, an elongated tendon might also reduce ankle joint excursion (Myatt et al., 2011; Thorpe et al., 1999), which is important during vertical climbing bouts in modern great apes (DeSilva, 2009). However, Venkataraman et al. (2013) have documented remarkable plasticity in the human gastrocnemius, indicating that even in species with a long AT (e.g., *Homo sapiens*), habitual climbing is still possible. Others (Stern & Susman, 1983; Susman, Stern, & Jungers, 1984) have identified skeletal correlates of large peroneal musculature, including a large peroneal trochlea and wide peroneal groove of the fibula, in *A. afarensis* as evidence for frequent climbing in this taxon. Latimer and Lovejoy (1989) countered that in the absence of a human-like AT, *A. afarensis* may have used the peroneals as plantarflexors during bipedal heel lift. However, our findings that the AT may have already been human-like in *A. afarensis* challenges that interpretation and may provide some support for the hypothesis that the enlarged peroneal musculature may indeed be evidence for foot eversion during occasional climbing (e.g., Stern & Susman, 1983), especially in the juveniles (DeSilva, Gill, Prang, Bredella, & Alemseged, 2018).

Our results suggesting that the AT in *Australopithecus* had reached modern human-like length is especially interesting given the growing body of literature examining the evolution of the capacity for endurance running in humans (e.g., Lieberman et al., 2009). Endurance running is unique to humans among all extant primates (Bramble & Lieberman, 2004). Researchers have hypothesized that specific anatomical changes, including the elongations of the AT, enhanced the endurance running abilities of early members of the genus *Homo*.

However, Bramble and Lieberman (2004) never argue that all of the anatomical adaptations for distance running would necessarily occur in concert in *Homo erectus*, only that the suite of features adaptive to endurance running would be present by that time in our evolutionary history. In this light, our finding of increased AT length in *Australopithecus* is perhaps not all that surprising. It is reasonable to expect that some of the adaptations thought to be related to endurance running were already present in earlier hominins. Indeed, there is evidence from the ischial tuberosity of KSD-VP-1/1 (a 3.6 Ma skeleton attributed to *A. afarensis*) for a modern human-like origin for the hamstring muscles, which has been hypothesized to help prevent avulsion injuries of the ischial apophysis in children and adolescence during high energy running bouts (Lovejoy, Latimer, Spurlock, & Haile-Selassie, 2016). The mosaic nature of the postcranial skeleton in *Australopithecus* and even *Homo* (e.g., Harcourt-Smith et al., 2015; Jungers et al., 2009; Marchi et al., 2017) suggests that some of the anatomies that are hypothesized to improve endurance running performance actually began in *Australopithecus* and that different Pleistocene hominins evolved different combinations of features functionally correlated with running.

The above scenario assumes that a long AT is a derived feature in modern humans. Unfortunately, the polarity of this trait is still poorly understood. Given the dearth of well-preserved proximal calcanei in the hominin fossil record, this remains difficult to test. However, this study provides a viable method for assessing the polarity of a long AT within primates, so that when sufficient fossil evidence has been recovered researchers will be able to make inferences about the potential locomotor patterns of the last common ancestor of all hominoids and hominids. We find it intriguing that the one Miocene ape (*Ekembo*) for which this measure can be taken reveals a relatively long AT; however, this ape is over 10 million years removed from the human–chimpanzee last common ancestor. Perhaps of more importance is the foot morphology of *Ardipithecus ramidus*, which does not preserve a posterior calcaneus, but does have talar trochlear morphology that is consistent with habitual dorsiflexion and perhaps therefore a short, great ape-like, AT (DeSilva, McNutt, Benoit, & Zipfel, 2019; McNutt, Zipfel, & DeSilva, 2018).

There were several limitations to this study. Relative AT lengths reported in Table 1 were based on previous research from several different sources, collected in slightly variable ways. The availability of primates for dissection is generally limited by their long-life spans, ease of disease transmission to humans, and the endangered status of many primates, especially great apes. Due to these issues it is possible that the sample sizes used in these studies may not be sufficiently large to cover the

range of variation found in AT length in those species. Further dissections of both modern humans and extant primates, completed in a systematic way, will be needed to verify the reported relative AT length measurements in Table 1, and to assess whether any potential methodological differences in dissection techniques may have occurred between these studies that would prevent pooling of their data. It is also possible that there are relevant variations in muscle fiber properties across primate species that may complicate cross-species comparisons, although it has been suggested that primates do not display large-scale differences in fiber types with the *M. triceps surae* (Hanna & Schmitt, 2011). Furthermore, it is unclear how retrotrochlear bursa anatomy and AT length are related to one another within a species. There is some evidence supporting the presence of intraspecific variation in AT length among different modern human populations (Butler & Dominy, 2016), but further work is needed to assess whether this variation has osteological correlates. Finally, our assessments of AT length in *Austalopithecus* were based on only three fossils. As the human fossil record improves, and more calcanei are discovered, the hypotheses presented in this article should be reassessed.

Despite these potential limitations, this new model for predicting AT length from fossil calcanei has the potential to provide important insights into the paleobiology of *Australopithecus*, as well as other early hominins. The ability to accurately predict AT length allows for a better understanding of foot function in early hominins and provides context for pedal evolution in our own genus (McNutt et al., 2018). The potential for a modern human-like AT tendon in *Australopithecus* is an important finding, suggesting that, while the majority of anatomical adaptations for endurance running occur with the genus *Homo* (Bramble & Lieberman, 2004), these behaviors may trace—to a smaller degree—their origins earlier in our own lineage and suggest that early hominins, like *A. afarensis*, may have occasionally utilized high energy running in order to survive (Lovejoy et al., 2016).

ORCID
Ellison J. McNutt https://orcid.org/0000-0002-7723-9103
Jeremy M. DeSilva https://orcid.org/0000-0001-7010-1155

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.