These bones were made for jogging: an analysis of the lower limb skeletal evidence for the endurance running hypothesis

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THESE BONES WERE MADE FOR JOGGING

AN ANALYSIS OF THE LOWER LIMB SKELETAL EVIDENCE FOR THE ENDURANCE RUNNING HYPOTHESIS

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Abstract

The endurance running hypothesis proposes that the anatomical features observed in the genus Homo evolved to increase long distance running capabilities. Proponents of this theory argue that the need for nutrient-dense high quality food packages to sustain a larger brain and body size would require Homo to hunt and track game over large distances. In order to hunt proficiently, Pleistocene hominins would need a suite of anatomical features that would allow running over sustained periods of time. This paper investigates the skeletal indicators associated with endurance running within the fossil hominin archaeological record. Data on the character of these skeletal indicators in Plio-Pleistocene hominins was analysed from the literature. A complete suite of anatomical features related to endurance running is not seen until Homo ergaster at 1.8 million years ago. However, a mosaic of these features is present in earlier Australopiths. This, combined with the lack of evidence for long range projectile weapons in the Pleistocene, indicates these features may have been positively selected for to increase walking efficiency and increased endurance running capabilities were just a fortunate by-product. Currently, there is insufficient evidence to support the notion that anatomical changes observed in early Homo evolved to increase running capabilities.

Keywords
Hominin Fossil Record, Evolutionary Morphology, Plio-Pleistocene, Locomotion, Hunting Strategies

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Introduction

The endurance running hypothesis poses that early members of the genus *Homo* developed the ability to run over long distances and periods of time. Although poor sprinters compared to other mammalian species (Cavanagh and Kram 1989, 469), humans are more adept at long distance or endurance running. This type of running can only be sustained at speeds ranging from 2.5 – 6 m/s^{-1} (Cavanagh and Kram 1989, 469), but can be maintained over a significant amount of time. Sprinting animals lack the ability to sustain their speed over longer periods of time, making it necessary for them to stop intermittently to cool down before the next sprint (Bramble and Carrier 1983, 253; Garland 1983, 166). The endurance running hypothesis proposes that early hominins developed the ability for long distance running to take advantage of this fact, which would have made it possible to hunt wild game into overheating (Bramble and Lieberman 2004, 351; Carrier 1984, 486; Lieberman et al. 2006, 77). This in turn would allow hominins to acquire the prime portions of meat before other animals would encroach to scavenge the remaining meat (Lieberman et al. 2006, 78).

During the early Pleistocene several hominin species inhabited the African landscape. During this time period, early *Homo* species, such as *Homo habilis* and *Homo ergaster*, show a significant increase in brain and body size compared to the earlier *Australopithecines* (Antón et al. 2014, 3). Larger brain sizes require more energy to maintain and thus more nutrient-dense food packages (Antón et al. 2014, 8; Pontzer, 2012, 347), which were probably attained by an increase in meat-eating (Kaplan et al. 2000, 156). The endurance running hypothesis proposes that long distance running and persistence hunting strategies were adopted by hominins to allow them to compete for meat with other African carnivores. Persistence hunting requires knowledge of animal behaviour, the ability to track, and the necessity of sharing with peers (Pickering and Bunn, 2007, 436) in order to hunt successfully. If the endurance-hunting hypothesis can be proven to be true, this will further our understanding of when increased cognitive and social skills evolved in the hominin lineage.

In 2004, the seminal paper by Bramble and Lieberman summarising the anatomical traits necessary for endurance running concluded that the capability to run over long distances and the associated hunting strategies did not evolve until the appearance of *Homo erectus* at 1.8 million years ago. The authors hypothesised that the ability to persistence hunt would have played a significant role in the dispersal of these creatures into Eurasia (Bramble and Lieberman 2004, 350). However, the validity of the endurance running hypothesis has been questioned by scholars that were unconvinced that the skeletal markers described by Lieberman and Bramble were indicative of increased running efficiency and not increased walking efficiency (Steudel-Numbers 2006, 451; Steudel-Numbers and Wall-Scheffler 2009, 359). The lack of post-cranial remains for many early *Homo* fossils also made it difficult to test whether these anatomical features were present. It has been over 10 years since the Bramble and Lieberman paper was published. Since then, new fossil finds of *Australopithecus afarensis* (Haile-Selassie et al. 2010, 12121; Ward et al. 2012, 2), *Australopithecus sediba* (Zipfel et al. 2011, 1417), *Homo georgicus/erectus* (Lordkipanidze et al. 2007, 305), *Homo floresiensis* (Jungers et al. 2009, 539) and *Homo naledi* (Berger et al. 2015, 5) have been discovered. These new finds may provide further evidence in support or against the endurance running hypothesis. This paper aims to re-assess the validity of the endurance running hypothesis in light of these new discoveries.

Feature	First seen
Narrow pelvis*	*Homo*
Enlarged illiac pillar	*Homo erectus*
Stabilised sacroiliac joint*	*Homo erectus*
Expanded surface area for mm. erector spinae origin*	*Homo erectus*
Expanded surface area for m. gluteus maximus origin*	*Homo erectus*
Long legs	*Homo erectus*
Expanded hindlimb joint surface area/robusticity	*Homo erectus*
Shorter femoral neck	*Homo sapiens*
Plantar/Longitudinal arch*	*Homo*
Close-packed calcaneocuboid joint/cuboid flange*	*Homo habilis*
Enlarged tuber calcaneus*	*Homo*
Permanently adducted hallux	*Homo habilis*
Short toes	*Homo habilis*

* argued to be beneficial for running efficiency alone

Table 1. Lower limb anatomical features related to endurance running (After Bramble and Lieberman 2004, 348).

Methodology

Bramble and Lieberman (2004, 348) identified 26 anatomical traits related to running efficiency. Of these, 13 were features that can be identified on the lower limb (tab. 1). This study focuses on several features in the lower limb. The reason for this limitation was threefold: 1) the lower limb is the only part of the body that makes contact with the substrate during locomotion. This makes the lower limb the most likely location where endurance running capabilities would be reflected in the morphology of skeletal elements; 2) many of the species under study have associated lower limb skeletal elements; 3) detailed descriptions of lower limb bone morphology and measurable data have been reported in the literature for these skeletal elements. While the pelvis is also involved in locomotion, this bone was excluded from this analysis due to the fact that its morphology is also heavily influenced by changes in ontogeny and growth and development within early *Homo* species (Rosenberg and Trevathan 2005, 164). A subset of the lower limb features described by Bramble and Lieberman (2004, 348) was analysed in this study (tab. 2), as these features were most commonly reported in the literature.

Feature	**Function**	**Comments**
Shorter Achilles tendon (shorter calcaneal tuber)	Energy storage	Running requires more energy storage and release in muscles and tendons than walking. A shorter calcaneal tuber, which is indicative of a short Achilles tendon, has been correlated with running efficiency (Raichlen et al. 2011, 304)
Longitudinal arch	Shock absorption and energy storage	Stores 17 percent of strain energy, which is needed during push-off in running (Kerr et al. 1987, 148).
Cuboid flange	Shock absorption and energy storage	A secondary indicator of the presence of a longitudinal arch (Bojsen-Møller 1979, 166).
Increased lower limb length	Increased stride length and energy efficiency	Longer stride length requires less oxygen consumption during locomotion in many terrestrial mammals, making it more energy efficient (Cavanagh and Williams 1982, Pontzer 2007, 1760)
Increased lower limb/joint robusticity	Stress reduction	Running causes an increase in mechanical loading.
Shortened toes	Stability and efficiency	Shorter toes are beneficial for running economy (Rolian et al 2009, 718)

Table 2. Anatomical features used in this study.

Feature	**Improves Walking Efficiency?**	**Improves Running Efficiency**	**First Seen**
Achilles tendon length	No1	Yes,2,3	*Homo sapiens*3
Longitudinal arch	Yes4	Yes5	*Australopithecus afarensis*?6, *Homo habilis*7
Cuboid medial flange	Yes4	Yes5	*Australopithecus afarensis*6
Increased lower limb length	Yes8	Yes9	*Homo habilis*10
Increased lower limb/joint robusticity	Probably11	Yes12	*Homo erectus*13
Shortened toes	Yes4	Yes14	*Homo habilis*7, *Homo sapiens/Homo neanderthalensis*14

Table 3. Appearance of anatomical features in the fossil record.

Gaining access to original fossil hominin specimens is incredibly difficult, and thus this paper is limited to assembling the necessary data exclusively from literary sources. Any and all literature on skeletal elements of fossils ranging from 3.2 million years old to modern humans were examined for the presence or absence of a set of skeletal traits (tab. 2). Where possible, measurements from the femur were collected to infer if changes in morphology between hominin species. Due to differences in measuring techniques between articles, not enough data could be collected to run statistical tests.

Results

The results of this analysis (fig 1. And tab. 3) contradict the earlier findings that indicated that these anatomical traits were first observed in *Homo erectus*, and that they are more likely related to running efficiency as opposed to walking efficiency (Bramble and Lieberman 2004, 346). All lower limb skeletal features under study in this paper, with the exception of the calcaneal tuber and increased robusticity of the lower limb can be identified in hominin species older than *Homo erectus* (tab. 3). Femoral length, which was used as a proxy for limb length, increased over evolutionary time. An increase can already be observed between *Australopithecus afarensis* and *Homo habilis* (fig. 1).

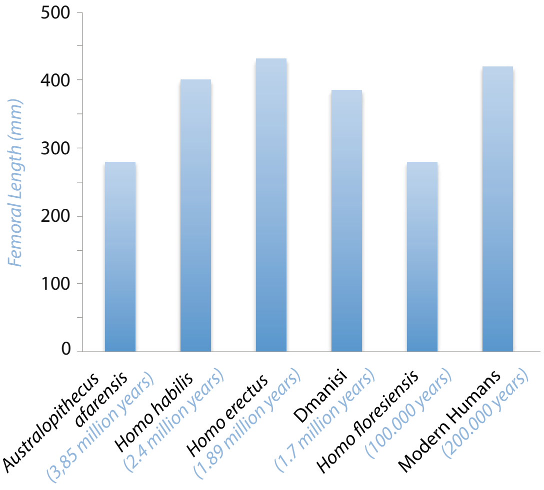

Figure 1. Femoral Lengths Across Fossil Hominins (Data taken from Jungers et al. 2009, 543; Lordkipanidze et al. 2007, 307; Trinkhaus and Ruff 2012, 35)

Discussion

Proponents of the endurance running hypothesis argue that the anatomical traits described by Bramble and Lieberman (2004, 348) are more related to increasing running efficiency than walking efficiency. The results of this study suggest that some of these features are already present in hominins that are just starting to become bipedal (tab. 3). This would suggest that these features may have evolved to increase walking efficiency rather than running efficiency. However, it should be kept in mind that an early presence of these features does not exclude the possibility that their morphology did not become further adapted for efficient bipedal locomotion or running over evolutionary time. When a feature is solely related to running, as is the case with the calcaneal tuber, this still cannot provide conclusive evidence that endurance running evolved at around 1.8 million years ago with *Homo erectus*. Calcaneal tuber length is related to Achilles tendon length and solely correlated with running efficiency (Raichlen et al. 2011, 303). The comparison of calcaneal tuber length between modern humans and Neanderthals has shown that the latter does not exhibit a shortened tuber, which is correlated with efficient running, while the former does exhibit this feature (Raichlen et al. 2011, 304). Whether this represents an evolutionary reversal, or that shorter calcaneal tubers did not evolve until *Homo sapiens* cannot be answered until a *Homo erectus* calcaneus is found. Until such as fossil is found, it is only safe to say that modern humans exhibit the elongated Achilles tendon necessary for endurance running. An increase in robusticity of the calcaneal tuber is observed in modern humans. This feature, combined with a shortened tuber, may be indicative of endurance running. Although too damaged to assess tuber length, a calcaneus from *Homo naledi* exhibits a gracile calcaneal tuber whose robusticity falls outside the range of modern human variation (Harcour-Smith et al. 2015, 2). This would indicate that this species may have been capable of running, but most likely did not engage in endurance running behaviours similar to that of modern humans. However, it has not been possible at this time to date these fossil remains to an accurate age range, which makes it impossible to assess where these creatures fall within the hominin sequence (Berger *et al*. 2015, 24; Dembo *et al*. 2016, 24; Stringer 2015, e10627; Thakerey 2015, 1).

Not only do most features described (tab. 3) appear before the appearance of *Homo erectus*,it is questionable whether these features are indicative of running at all. The increase in lower limb length (with the exception of *Homo floresiensis*) would be indicative of endurance running capabilities according to Bramble and Lieberman (2004, 348) and does occur in *Homo habilis* and *Homo erectus*. However, analysis of differences in cost of transport in walking and running in modern humans indicated that increased limb length was beneficial for both types of locomotion (Steudel-Numbers et al. 2007, 195) and that endurance walking during persistence hunting is more energy efficient than endurance running (Steudel-Numbers et al. 2007, 195; Steudel-Numbers and Wall-Scheffler 2009, 359). Although it cannot be denied that *Homo erectus* shows a significant increase in lower limb length that may have been beneficial for endurance running, it should be noted that this trend of increased limb length can be observed in earlier *Homo* species as well. It could be argued that this increase in limb length may be an artefact of increased bipedal walking, not running. New fossil finds of *Australopithecus afarensis* (Ward et al. 2012, 39) further indicate that features such as the longitudinal arch were present much sooner in evolutionary history and are more likely related to increased bipedal walking capabilities, not running ability. The fact that shorter toes can already be observed in *Homo habilis* (Kidd et al. 1996, 285) further corroborates this notion.

A limitation of this study to testing the endurance running hypothesis is that it focused on the lower limb. Only one lower limb feature solely related to running efficiency was assessed; the calcaneal tuber length. The results of this study do indicate that anatomical markers in the lower limb that were identified as indicators of running in previous studies could instead be markers of increased walking ability instead of running behaviours. Including other skeletal elements in the analysis may be beneficial. Bramble and Lieberman (2004, 348) describe several other skeletal features in the upper segment of the skeleton, such as the restructuring of the shoulders and thorax, and the shortening of the forearms, that according to the authors are solely related to running efficiency. The majority of these skeletal features are related to trunk stabilisation and redistribution of the centre of gravity during running (Bramble and Lieberman 2004, 349). Running involves a 'flight phase' where neither limb touches the ground, which would require greater control of balance than bipedal walking (Levine et al 2012, 57). However, these features may also be beneficial in walking. Future research should try to not only identify the presence of these features in the fossil hominin record, but also test their validity as markers of running efficiency over. Aside from skeletal markers, Bramble and Lieberman (2004, 348) list a number of soft tissue features, such as the increased size of the gluteus maximus, the erector spinae, and the presence of the nuchal ligament. Ascertaining the effect of differences in size of muscle insertions related to habitual running may provide additional skeletal markers to examine in the future.

Apart from the skeletal features described above as indicators of endurance running, several other lines of evidence also contradict that endurance running and persistence hunting had a significant role in the evolution of later *Homo* species. Before 400,000 years ago (Shea 2006, 823), there is no evidence of projectile weaponry, which would be necessary to initially injure the animal before running it into overheating (Pickering and Bunn 2007, 436). If *Homo erectus* did not have the technological means to persistence hunt, it is questionable that specific anatomical traits evolved to support this behaviour. This behaviour is also rarely seen in hunter-gatherers today (Pickering and Bunn 2007, 436) and less efficient than endurance walking (Steudel-Numbers and Wall-Scheffler 2009, 359). Persistence hunting would also require the ability to track prey across large distances. Pickering and Bunn (2007, 435) note that the savannah-woodland environment in which these hominins lived, which was characterised by dense soil and vegetation covered ground, was ill-suited for tracking prey across large distances as these environmental conditions are not optimal for leaving tracks.

Finally, new finds in Georgia have indicated that as early as 1.7 million years ago, hominins migrated out of Africa (Dennell and Roebroeks 2005, 1099; Lordkipanidze et al. 2007, 307). These hominins do not yet have all the features necessary for endurance running. For example, the morphology of the longitudinal arch of the Dmansi hominins does not yet resemble that of modern humans and may have impeded efficient walking and running to a degree (Lordkipanidze et al. 2007, 307; Pontzer et al. 2010, 501). The Indonesian find of *Homo floresiensis* has elongated toes, but a bipedally adapted lower limb. This elongation of the toe is puzzling, as this species is thought to be younger than *Homo erectus*. This elongation may represent an evolutionary reversal. However, it is unlikely that a feature so vital to efficient walking would reverse itself in a habitual biped (Jungers et al. 2009, 549). These new finds suggests that hominins inefficient in endurance running were able to disperse across Eurasia, contrary to Bramble and Lieberman's (2004, 351; Lieberman et al. 2006, 78) belief that running and persistence hunting would be necessary to achieve this.

Conclusion

The aim of this study was to assess whether new fossil evidence discovered over the past decade could shed new light on the appearance of the anatomical features related to endurance running. Although limited to the lower-limb, this study cannot corroborate Bramble and Lieberman's conclusion that these features evolved for endurance running around 1.8 million years ago with the appearance of *Homo erectus*. The skeletal features discussed in this paper are beneficial to running efficiency. However, with exception of the calcaneal tuber, these features also increase walking efficiency. The results of this study suggest that endurance running may have been practiced from 1.8 million years onwards, but the earlier presence of many of these features in the fossil record suggest that endurance running most likely was not a driving force behind the evolution of these anatomical features. Furthermore, the lack of lithic evidence for persistence hunting associated with early *Homo* and the primitive morphology of the Dmanisi and *Homo floresiensis* lower-limb indicate that early *Homo* travelled long distances before the evolution of all features related to endurance running occurred. The most likely scenario at this time seems to be that the lower limb features discussed here evolved to improve walking efficiency in fossil hominins, and that increased running efficiency proved to be a beneficial by-product. Further analyses should focus on testing the validity of anatomical features identified to be solely related to running, such as the decoupling of the thorax (Bramble and Lieberman 2004, 349), which may help identify these behaviours in the fossil record. Another avenue of study should be the effect of running behaviour on the internal structure of bone. Trabecular bone responds more sensitively to changes in mechanical loading than cortical bone (Ortner 2003, 22) and running behaviours may be reflected sooner in trabecular bone than in outer bone morphology. Combining analyses of outer bone and inner bone morphology in relation to running may give more insight or evidence in support of the endurance running hypothesis in the future.

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