

## Midfoot Flexibility, Fossil Footprints, and Sasquatch Steps: New Perspectives on the Evolution of Bipedalism

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**Abstract**—The chimpanzee foot is flexible near its middle, it can bend about the axis of the transverse tarsal joint, whereas the human foot is a comparatively rigid arched platform. Flexion at the transverse tarsal joint—the “midtarsal break”—uncouples the functions of a grasping, or prehensile, forefoot and a propulsive hindfoot during grasp-climbing on vertical or inclined supports. At some point after the transition to habitual bipedalism, these grasp-climbing adaptations were compromised by the evolution of the longitudinal arch, which permits increased mechanical advantage of the flexors of the ankle and improved endurance for long-distance walking and running.

Ape, human, and Plio-Pleistocene hominid footprints were examined for the effects of a midtarsal break. The human footprint reflects arched-foot architecture, combined with a stiff-legged striding gait. Pressure releases occur at particular locations behind the ball and the great toe, or hallux. Early (ca. 3.5 million years ago) hominid footprints from the Laetoli excavation confirm midfoot flexibility, including repeated suggestion of an associated pressure ridge. The Terra Amata footprint (ca. 400,000 years ago), yet to be fully published, exhibits evidence of midfoot flexibility.

Several footprints attributed to an alleged North American ape, commonly known as sasquatch, exhibit a distinctive midtarsal pressure ridge and other indications of midfoot flexibility. In the Patterson-Gimlin film, the feet of the film subject correlate with the kinematics inferred from the footprints, in that a midtarsal break is present. Additional independent examples corroborate the consistent presence of this feature, including examples of half-tracks that record contact beneath the foot only anterior to the midtarsus. These data provide a fresh perspective from which to consider the pattern and timing of the emergence of the distinctive features of modern human bipedalism and bear on the credibility of the possible existence of sasquatch. The observed and inferred sasquatch locomotor anatomy parallels the stable adaptations that marked the greater span of early hominid bipedalism.

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One of the hallmarks of the hominoid, or ape, locomotor system is the grasping foot. A great toe, the hallux, functions in opposition to the relatively long lateral digits in a pincer-like grip. This foot posture is especially evident when the ape is climbing on vertical or inclined supports. The forefoot functions as a grasping, or prehensile organ, maintaining a secure grasp during the contact phase of a

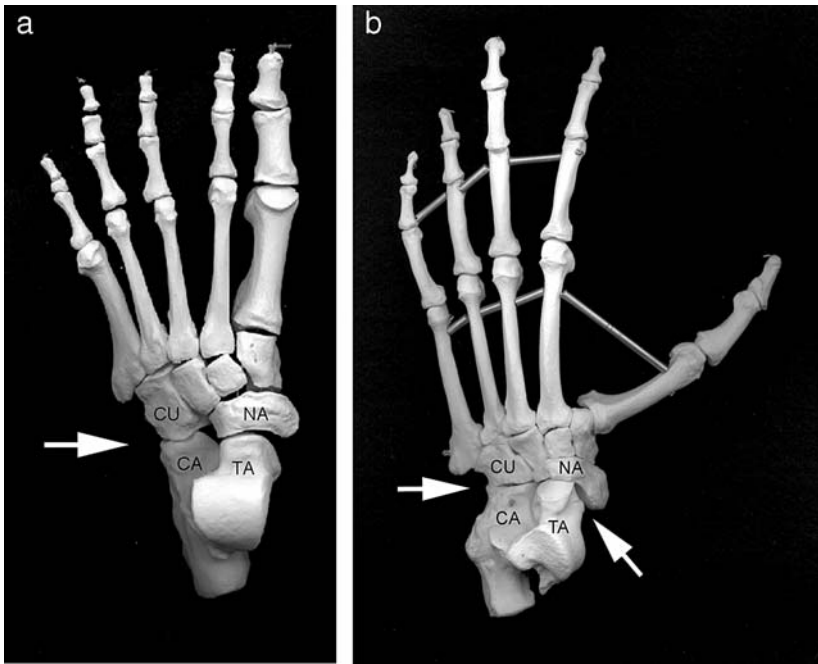


Fig. 1. Foot skeletons of human (a) and chimpanzee (b). Arrows indicate the position of the midtarsal joint complex. CA = calcaneus, TA = talus, NA = navicular, CU = cuboid.

step, while the hindfoot serves as a propulsive organ providing leverage. The plantarflexors of the ankle elevate the heel as the power arm of a lever with its fulcrum at the midtarsal, or transverse tarsal, joint complex. This joint is actually a compound of the articulations between the talus and navicular on the medial aspect of the foot and the calcaneus and cuboid on the lateral aspect (Figure 1).

Elftman and Manter (1935) first drew attention to the flexibility at the midfoot in chimpanzees. They referred to the coordinated flexion/rotation of the talonavicular and calcaneocuboid joints as the “midtarsal break.” The midtarsal break permits the corresponding, but regionally specialized, functions of the forefoot and hindfoot, i.e., prehension and propulsion, respectively.

During terrestrial locomotion, the midtarsal break is also evident in the chimpanzee foot. In studies of the pressures beneath the foot, the elevation of the heel coincides with a shift of the center of pressure to the tarsus distal to the midtarsal joint, especially beneath the cuboid (Meldrum & Wunderlich, 1998). In contrast, the human foot is a comparatively rigid platform, built upon a relatively fixed longitudinal arch. This adaptation incorporates the shank of the foot into a lengthened power arm of the lever. Elevation of the heel in the latter part of the stance phase during human walking shifts the center of pressure beneath the metatarsal heads, especially that of the hallux metatarsal,

which now serves as the primary fulcrum of the foot lever. At some point in human evolutionary history, the hominoid legacy of midfoot flexibility was relinquished in favor of a striding gait on much stiffer arched feet. Selection increased the mechanical advantage of plantarflexors of the ankle, combined with extended legs for increased stride length, thereby improving economy of long-distance walking and running.

Lacking the opportunity to examine directly the kinematics and plantar pressures in early hominid feet, could any signature of this pattern of flat, flexible foot function be identified in the footprints of fossil hominids or extant hominoids? To investigate this question, human footprints in fine damp beach sand were examined for a variety of locomotor speeds and directional changes. Two subjects were particularly studied at length, an adult male and a juvenile male. In addition, an extensive sample of spontaneous trackways made by a variety of human subjects was examined at a public beach. Next, bipedal footprints made in a sand track box by a captive chimpanzee were documented and correlated with simultaneous video recordings of the kinematics of his bipedal walking. These footprints were contrasted with stereophotos and casts of the Laetoli hominid trackway in Tanzania, Africa (ca. 3.5 million years ago). Finally, fossilized footprints of habitually unshod humans were examined in Hawaii (Meldrum, 2004). These are footprints left by native Hawaiians in historic volcanic ash deposits on Kilauea (ca. 200–400 years ago). These provide a natural experiment to contrast early hominid footprints with modern unshod human footprints, both laid down in a substrate of very similar consistency.

It was hypothesized that midfoot flexion associated with a midtarsal break would, under the appropriate substrate conditions, produce a distinct pressure release as weight was transferred distal to the midtarsus (Brown, 1999; Meldrum, 1999). A human foot typically produces such a release proximal to the ball of the foot, behind the hallucial metatarsophalangeal joint. The situation in the chimpanzee footprint is somewhat confounded by the divergent hallux, elongated lateral toes, and high angle of gait (toe-out) associated with chimpanzee facultative bipedalism. It was found that chimpanzee footprints in sand do occasionally demonstrate a pressure release associated with the midtarsal break, as indicated by a primary pressure disc (Figure 2).

After the initial transition to habitual bipedalism, the hominoid grasp-climb adaptation was compromised by shortening of the lateral toes and reduction in the range of divergence of the hallux. The Laetoli hominid footprints, the first direct evidence of hominid bipedalism, exhibit these modifications to the prehensile portion of the foot to a relatively intermediate degree. There has been continuing debate over the extent to which the Laetoli hominids display modern human foot morphology. Some have argued that the footprints imply a foot essentially modern in all aspects (e.g., Lovejoy, 1988; Tuttle, 1996). Others have pointed out features that indicate the retention of more ape-like characteristics of the foot (Deloison, 1992; Meldrum, 2000, 2002, 2004; Susman et al., 1984). I first drew attention to a feature evident in a number of footprints (e.g., G1-25,



Fig. 2. Chimpanzee footprint left in a sand track box, demonstrating a pressure release associated with the “midtarsal break.” Arrows indicate proximal edge of the primary disc.

G1-26) that suggested the retention of the capability for midtarsal flexion (Meldrum, 2000). In a depiction of a reconstruction of the *Australopithecus afarensis* foot skeleton superimposed upon a Laetoli footprint, this feature can be seen to lie immediately proximal to the position of the reconstructed midtarsal joint (White & Suwa, 1987). Some have suggested this is possibly the result of termite burrowing or excavation artifact; however, the repeated and consistent position of the feature, combined with other indications within the footprints of a transverse axis of foot flexion (Deloison, 1992), indicates its interpretation as a pressure ridge is justified. An exceptional example of a midtarsal pressure release is clearly evident in the G1-26 footprint, indicated by plastic flow of the wet ash proximal to the midtarsus (Figure 3). The possibility of this feature resulting from exfoliation of the layers of ash beneath the contact surface of the footprint, or other excavation artifact, is excluded upon

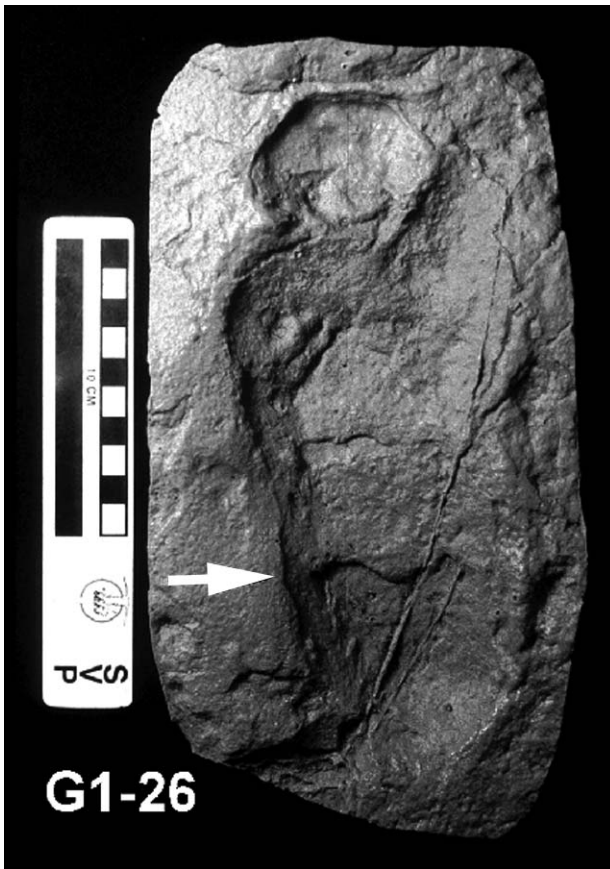


Fig. 3. Cast of a Laetoli hominid footprint (G1-26) exhibiting a midtarsal pressure release indicated by plastic flow of wet ash (arrow).

close examination. The leading edge of the flow is continuously rounded and has the same appearance as the ash extrusion between the first and second toes of the very clear print G1-26. In contrast, the human foot, with a fixed arch and well-developed ball, leaves a very different pressure disk located proximal to the hallucial metatarsal-phalangeal joint. No such midtarsal pressure features were found in the sampled fossil Hawaiian footprints.

Recent analyses of early hominid foot skeletons also indicate midfoot flexibility in australopithecine, and perhaps early *Homo*, feet, such as that represented by the OH8 foot skeleton (Berillon, 2004; Harcourt-Smith et al., 2002; Kidd et al., 1996). At some point thereafter, in the evolution of modern human foot morphology, changes occurred to stabilize the foot platform, increase mechanical advantage of ankle plantarflexors, and improve efficiency and economy in long-distance, endurance walking and running (Hilton and



Fig. 4. Footprint from the Terra Amata site (ca. 400,000 years ago) displaying a midtarsal pressure ridge and relatively long heel, but lacking an arch and well-differentiated ball.

Meldrum, 2004). Determining the timing and pattern of the evolution of these characteristics has remained a challenge due to the paucity of fossilized footprints or foot skeletons from the period spanning 2.0–0.5 million years ago. Two potentially critical specimens have remained largely unpublished. The first of these are the hominid footprints at the Terra Amata site, in southern France (Figure 4). The site dates to approximately 400,000 years ago. The single published photo of one of these footprints suggests a midtarsal pressure ridge and a lack of both a well-developed longitudinal arch and a differentiated ball (White, 1973). The footprint also appears relatively long for its breadth, possibly indicating an elongation of the heel segment. The relative position of the apparent pressure ridge also suggests lengthening of the heel. This would increase mechanical advantage of the plantarflexors of the ankle, in response to increased body mass.

The second specimen is the nearly complete foot skeleton of the Jinniushan hominid from a site in China dating to just less than 200,000 years ago. A photograph of the skeleton appeared in a popular Chinese magazine (Lu, 1987), but detailed descriptions or analysis of the foot skeleton have yet to be published. Features of the foot skeleton visible in the magazine photo suggest that stabilization of the transverse tarsal joint had occurred by that time. Specifically, the projecting calcaneal process of the cuboid indicates that this joint could lock in a stable position supporting a longitudinal arch. Furthermore, the width and proportions of the navicular are similar to those in a modern human foot, and the hallucial metatarsal and phalanges are quite robust. Interestingly, it appears that the heel remains relatively elongated. Therefore, based on this admittedly limited assessment, it appears that the transition to the modern foot form, characterized foremost by the longitudinal arch and well-developed ball and hallux, occurred as recently as less than 200,000 years ago. In that case, it should be recognized that the majority of the history of hominid bipedalism transpired on flat flexible feet, and modern human foot morphology was a relatively recent evolutionary innovation. This observation prompts important questions about the nature of behavioral shifts that accompanied this transition in locomotor adaptation.

Furthermore, one could ask whether there are any extant analogs of this sustained, and apparently successful, strategy of locomoting bipedally on flat, flexible feet. In October 1967, Roger Patterson and Bob Gimlin purported to have captured on film, in a remote region of northern California, a bipedal hominoid, commonly referred to as sasquatch (Kirkpatrick, 1968). The brief film portrays an upright hair-covered figure, exhibiting a compliant gait (walking on flexed knees and hips) on flat, flexible feet. A trackway of clear footprints was left in the loamy sandbar at the site along Bluff Creek. Two exceptionally distinct footprints were cast by Patterson, representing a right and a left foot. These were markedly flat and exhibited little or no dynamic features that might imply the points of flexible articulation, although the exceptionally clear outline does preserve details of contour that appear to indicate such landmark features as the Hallucial metatarsophalangeal joint, the navicular tuberosity, and the tuberosity of the fifth metatarsal. Subsequent events shed additional light on the film subject's foot morphology.

Lyle Laverty, a U.S. Forest Service timber cruiser, came upon the site a short time after the filming and took several color slides of the subject's deeply impressed footprints (Perez, 2003; Laverty, personal communication). The footprints Laverty photographed revealed clear evidence of foot dynamics. Of particular note is the repeated appearance of a midtarsal pressure ridge (Figure 5).

Less than two weeks later, Bob Titmus, a professional taxidermist, visited the site and cast a series of 10 sequential footprints, a number of which had been covered to protect them from the elements.<sup>1</sup> Included was the print with the prominent pressure ridge photographed earlier by Laverty (Figure 6). This



Fig. 5. Footprint photographed by Lyle Laverty at the Patterson-Gimlin film site.

sequence of casts is very informative and exhibits the qualities of variation in apparent length, toe position, and flexibility typical of a “living” trackway.

From enlarged frames of the Patterson-Gimlin film, portions of three step cycles in which the feet are visible have been examined (Figure 7). Several features are noteworthy. First is the indication of the midtarsal break late in the stance phase of gait. This clearly correlates with the presence of the pressure ridge in a number of the footprints photographed and cast. Second, slight plantarflexion recoil at the midtarsal joint can be seen in the early swing phase. This results from the rebounding of the deep plantar ligaments after being stretched during bending of the midfoot during the midtarsal break. The foot flexes about an approximate transverse axis corresponding to the inferred position of the transverse tarsal joint. Third, an elongation of the heel is evident, especially when the calcaneal (Achilles) tendon is slack, during the swing phase. The need for a lengthening of the calcaneus to increase leverage in a biped of this size has been discussed at length by Krantz (1999). Its significance is further emphasized in the context of a foot exhibiting midfoot flexibility. The protruding heel of the film subject was taken by some skeptics as indication of an artificial foot protruding posteriorly beyond the hoaxer’s own heel. Alternatively, it can be seen as a sound and reasonable anatomical adaptation to the animal’s size and foot architecture, and accords with evolutionary trends in hominid locomotion already discussed.

In a reconstruction of the inferred skeletal configuration of the sasquatch foot, this combination of midtarsal flexibility and heel elongation is depicted



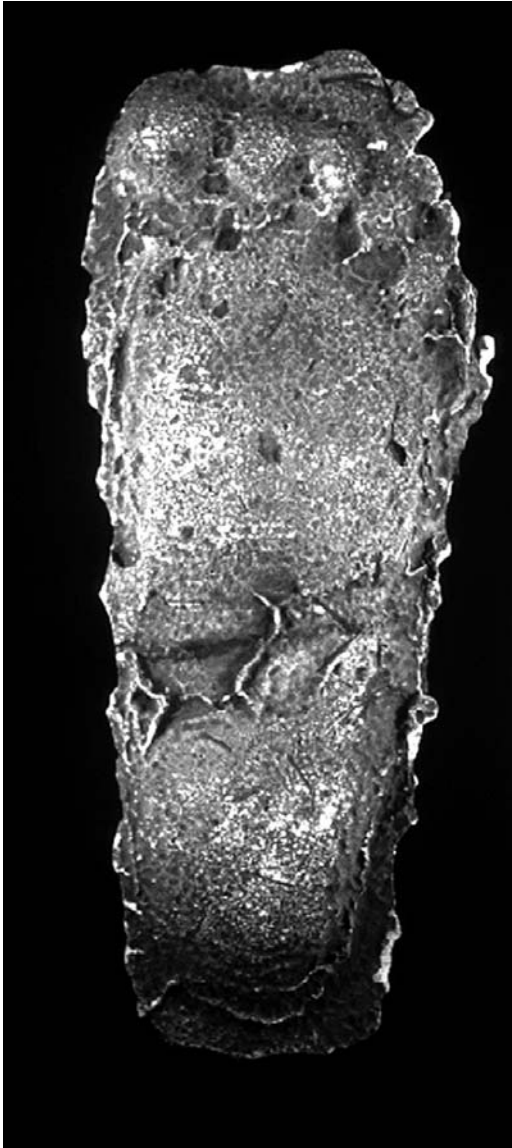


Fig. 6. One of a series of 10 consecutive footprints cast by Bob Titmus at the Patterson-Gimlin film site.

(Figure 8) based on the footprint of the Patterson-Gimlin film subject exhibiting a distinct pressure ridge. The pressure ridge in the proximal portion of the footprint implies the retention of the midtarsal break. Indeed, a number of footprints attributed to sasquatch exhibit what has been interpreted as a midtarsal pressure ridge.



Fig. 7. Three consecutive frames of the Patterson-Gimlin film, in which the subject exhibits midfoot flexibility.

Another manifestation of this midfoot flexibility is evidenced in instances where the sasquatch has run with the heel elevated off the ground. A modern human adopts a *digitigrade* posture when sprinting, balancing support of body mass over the heads of the metatarsals and the toes. This is especially concentrated at the medial ball of the foot, under the hallucial metatarsophalangeal joint, and is accomplished due to the stability of the longitudinal arch of the foot. A hominoid would merely be able to elevate the heel, but not the midfoot, because the foot would flex at the midtarsal joint, without the support of the arch. An example of this running foot posture was first recognized in a set of tracks I was shown near the Blue Mountains in southeastern Washington. One very clear track, deeply impressed in mud, showed no indication of a heel imprint. The inferred position of the midtarsal joint implied by the “half-track,” as I came to refer to them, agreed very well with the position of the pressure ridge in other footprints in the series (Figure 9).

A further example of the half-track was identified in a trackway found in northern California on the Blue Creek Mountain Road. In 1967, shortly before the Patterson-Gimlin filming incident, a long line of tracks was found along a logging road and investigated extensively (Green, 1978). Don Abott, an archeologist from the Royal British Columbia Museum, Victoria, B.C., took a series of color photographs of examples of the footprints (Green, personal communication). One photograph shows a distinct half-track, which, when superimposed on a complete track, can be seen to terminate at the inferred position of the midtarsal joint.

Yet another example comes from the west coast of Washington State. Officer Dennis Heryford, a Deputy Sheriff for Greys Harbor County, responded to a reported disturbance at a construction site in 1982. He discovered a line of

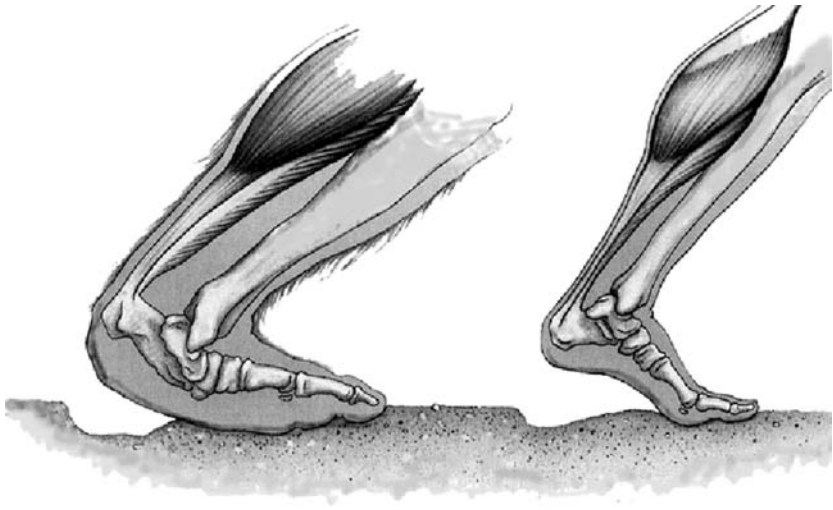


Fig. 8. Hypothetical reconstruction of the sasquatch foot skeleton (left) inferred from footprints exhibiting midfoot flexibility and pressure release. In contrast, the human foot skeleton (right) exhibits a longitudinal arch.

footprints emerging from the timber and crossing a cleared muddy landing. The track returned in the direction of the forest with twice the step length and left a series of half-tracks. In this case the contour of the calcaneocuboid joint is evident on the full-length footprint, and the proximal edge of the half-track terminates at that point. These, and other repeated examples of midtarsal pressure ridges and half-tracks, evidence the presence of a flexible midfoot in sasquatch foot functional anatomy.

Recently Haeusler and McHenry (2003) reevaluated the hindlimb morphology of the 1.8 million year old fragmentary fossil skeleton (OH 62), attributed to *Homo habilis*, and concluded that this early hominid may have had human-like hindlimb proportions and suggested that distance travel might have evolved early in human evolution. This, in spite of the conclusions about the primitive morphology of the OH 8-foot skeleton, which was also attributed to *H. habilis*. By 1.6 million years ago, *Homo ergaster* (or early African *H. erectus*) unquestionably exhibited modern limb proportions, as exemplified by the relatively complete skeleton of the Nariokotome hominid (KNM-WT 15000). This skeleton was of a youthful hominid who was already more than 5 feet in height when he died and would have certainly attained a 6-foot height at maturity. *Homo ergaster* represents the first grade of hominid for which there is clear evidence of expansion of its range beyond the bounds of Africa to extend throughout much of the Old World. It has been assumed that the lengthening of the lower extremities in early hominids was associated with the emergence of a modern type of human walking and running, but the lengthening of the limbs

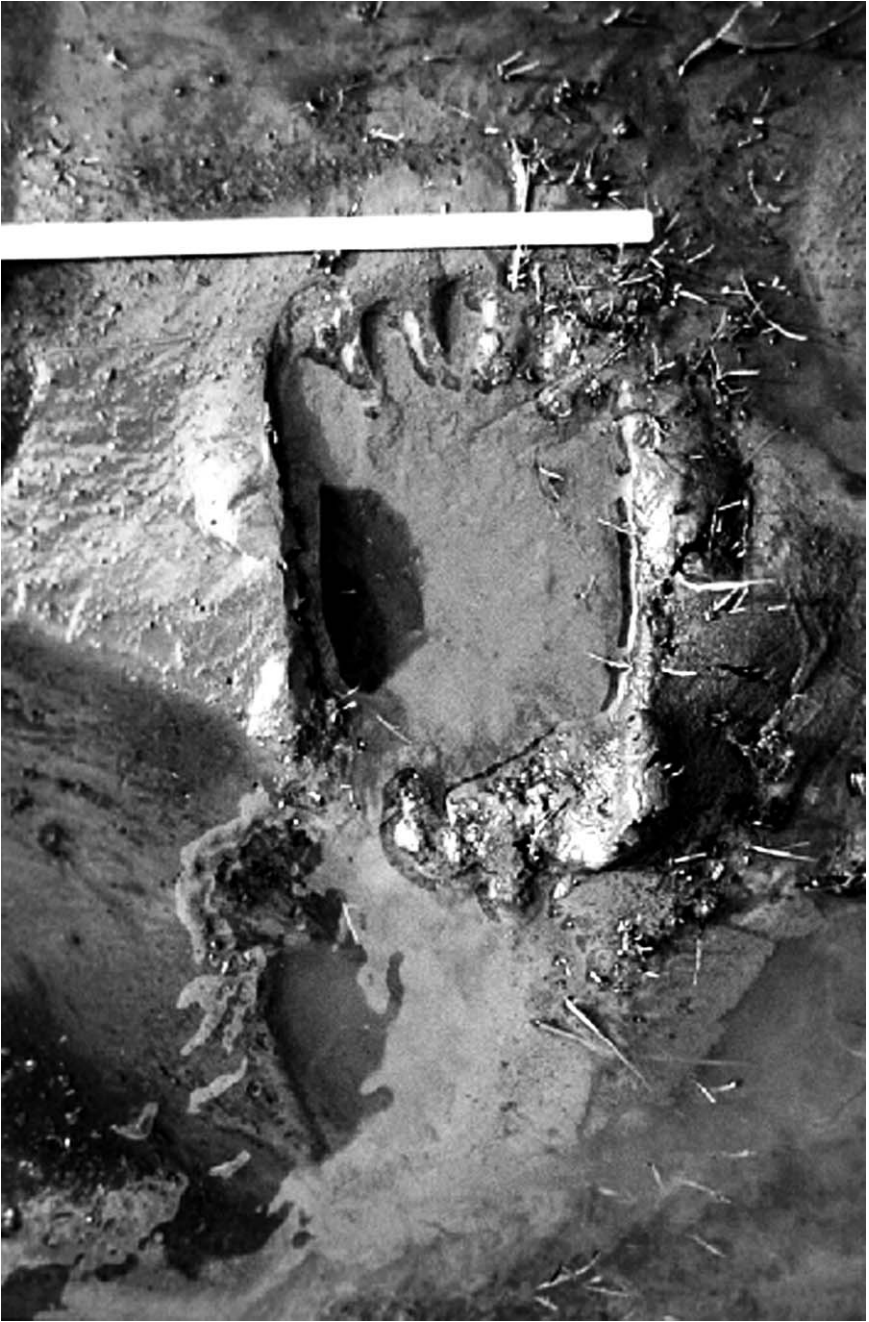


Fig. 9. Single footprint from a trackway photographed by the author in southeastern Washington, demonstrating midtarsal pressure ridge.

in *H. ergaster* is in the extreme upper range for modern equatorial Africans. Such limb proportions in modern African populations also reflect an adaptation for thermal regulation in hot tropical climates (Coon, 1982). The lengthening of the extremities increases the ratio of skin surface area to body mass and increases heat dissipation. This is the reciprocal of a general ecological principle known as Allen's Rule. Thus, the increase in proportionate limb length might reflect a response to heat stress, rather than simply an approximation to modern human locomotor behavior.

Unfortunately, the otherwise extraordinarily complete Nariokotome skeleton does not preserve elements of the foot skeleton, which would lend critical insight into the specific nature of the locomotor strategy of these hominids. Frankly, the fossil record of any *H. ergaster* foot skeleton is nearly nonexistent. One exception is a single hallucial metatarsal, KNM-BK 63, of a hominid from Baringo 500,000 years ago, which is noteworthy for its distinctly gracile proportions as compared with modern humans (Fisher & McBrearty, 2002). The Terra Amata footprint suggests that the older *H. ergaster* foot skeleton had not yet acquired the distinctive features of the modern human foot. Instead, this footprint appears to exhibit features of a flexible midfoot, lacking a fixed longitudinal arch and well-developed ball. Not until Jinniushan (*H. heidlebergensis* or *H. sapiens*) is there any skeletal evidence implying a fixed arch and demonstrating a robust hallux. Subsequent evidence from more recent and more plentiful Neanderthal foot skeletons further demonstrates aspects of the modern human foot, although retaining a greater degree of overall robusticity and relatively elongated heel segment and toes (Trinkaus, 1983).

Should this interpretation of the pattern and timing of hominid foot evolution be borne out by further fossil remains, then it appears that hominids were effective bipeds for well over 3 million years, while yet lacking what has traditionally been considered the hallmark of human bipedalism—the longitudinal arch. The stabilization of the midfoot and associated modifications, especially to the distal foot, i.e., shortening of the toes, increased robusticity of the hallux, development of the ball, shortening of the heel, were relatively recent innovations that marked a shift in hominid locomotor adaptation to skeletal gracilization combined with endurance walking and running.

The evidence of midfoot flexibility in the foot and footprints of sasquatch, and retention of other primitive characteristics of foot proportion, is significant, not only for the assessment of the purported existence of this hominoid, but in that this combination of foot morphology and locomotor behavior provides a novel perspective on the evolution of bipedalism. The sasquatch foot and footprints exhibit intriguing parallelism to the morphology of the hominid foot as here presented. This bipedal hominoid may provide an enlightening analog to hominid locomotor evolution, yielding insights and refinements to our understanding of the pattern and timing of modern human locomotor innovations. The inferred architecture of the sasquatch foot seems well suited to the physical

aspects of the terrain of its purported range. Together with observations of its gait, its locomotor anatomy and behavior present a functionally coordinated complex that parallels the highly stable adaptations that marked the greater span of hominid bipedalism, modified in response to dramatically increased body size. The combination of broad flat flexible feet, elongated heels, prehensile toes, and compliant gait constitute an elegant adaptation for a giant terrestrial biped evolved in a mountainous forested habitat. These observations would seem to lend considerable affirmative evidence for the existence of an unrecognized North American ape.

### Note

<sup>1</sup> The original casts are now housed in the Willow Creek—China Flats Museum, Willow Creek, California. Silastic rubber molds of eight of the 10 original casts are held by the Smithsonian. Copies of a number of these casts are held in the author's laboratory.

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