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Evolutionary Implications of Pliocene Hominid Footprints

Abstract. *Hominid footprints discovered at the Pliocene (3.6 to 3.8 million years ago) site of Laetoli in northern Tanzania represent the earliest evidence of bipedalism in human evolution. This new evidence emphasizes the mosaic pattern of human evolution.*

The site of Laetoli in northern Tanzania (3°12′S, 35°11′E) has yielded abundant fossils of Pliocene age. Included among the 5000 vertebrate specimens recovered from Laetoli are remains of 24 hominid individuals (*1*). The Laetolil Beds include a laminated airfall tuff (Tuff 7) that bears the tracks of Pliocene animals ranging in size from millipedes to large elephantids (*2*). Vertebrate fossils and tracks from the Laetolil Beds are radiometrically dated to between 3.6 and 3.8 million years (*1*).

Hominid footprints were discovered at Laetoli site G by Dr. Paul Abell in July of 1978. Illustrations and descriptions of the discoveries are available (*2*). The footprints are undoubtedly in situ and as old as reported.

Excavations at site G in 1978 and 1979 revealed trails of at least two hominid individuals. Portions of the trails are eroded but several intact prints are preserved. The uneroded footprints show a total morphological pattern like that seen in modern humans. Heel strike is pronounced. The great toes appear fully adducted, lying immediately ahead of the ball of the foot. The medial longitudinal arch of the foot is well developed. Spatial relationships of the footprints are strikingly human in pattern. Preliminary observations and experiments suggest that the Laetoli hominid trails at site G do not differ substantially from modern human trails made on a similar substrate.

Discoveries of fossilized hominid remains at Hadar in Ethiopia (2.6 to 3.3 million years ago) (*3*) and Laetoli in Tanzania (3.6 to 3.8 million years ago) (*1*) provide a new perspective on hominid evolution during Pliocene and Pleistocene times. These sites provide the earliest skeletal evidence of the Hominidae. The fossil material is assigned to *Australopithecus afarensis* (*4*), the only hominid species known from rocks of this age.

Numerous investigators have estimated stature in early hominids by using skeletal remains (*5, 6*). The Laetoli footprints can be used in a similar manner, but stature estimates derived from footprint dimensions are based on numerous assumptions. If it is assumed that (i) Laetoli hominids had foot proportions like modern humans, (ii) the individuals represented were adult, (iii) the footprints are good indicators of foot length, and (iv) the reported measurements are accurate; then stature estimates are as given in Table 1 (*7*). These estimates are consistent with those derived from the postcranial skeleton of *A. afarensis*. All available evidence makes it probable that the Laetoli hominid footprints were made by members of this Pliocene species.

Table 1. Stature reconstruction. Stature estimates for the two Laetoli individuals are given here. These estimates are based on average values for modern human populations and are based on several assumptions; M, male; F, female.

Human (*7*)	Foot-length average (%)*	Stature estimates (meters) (*2*) of Laetoli hominids: Larger†	Smaller‡
Bushmen (San)	M 14.6	1.47	1.27
	F 14.4	1.49	1.29
Mawambi Pygmy	M 15.6	1.38	1.19
	F 15.5	1.39	1.18
Japanese	M 13.8	1.56	1.34
	F 14.9	1.44	1.24
American Negro	M 15.9	1.35	1.16
	F 16.1	1.34	1.15
American White	M 15.0	1.43	1.23
	F 14.0	1.54	1.32

*Percentage of body height. †Footprint length, 21.5 cm. ‡Footprint length, 18.5 cm.

The acquisition of erect posture and striding bipedal gait by human ancestors represented a major evolutionary event. Anatomical correlates of this form of stature and locomotion have been the subjects of many comparative studies (*8–11*). Anthropologists and zoologists define the family Hominidae on the basis of anatomical features associated with habitual bipedal locomotion (*9, 10, 12–14*).

Students of human evolution have speculated freely on the origins of bipedal locomotion. They have suggested that the protohominid involved in the transition to habitual striding bipedalism was like the gibbon (*15*), the pygmy chimpanzee (*16*), or even *Gigantopithecus* (*17*). Selective factors posited to account for this transition have included vision over tall grass, carrying food or offspring, eating seeds, intimidating rivals or predators (or both), and using tools (*18*).

In the absence of fossil evidence, scholars were forced to speculate on the evolution of structures like the human foot by relying on comparative anatomy and embryology (*14, 19, 20*). Calling on Darwinian gradualism and a *scala naturae* of modern primates, most comparative anatomists predicted that, when fossil hominids were found, they would show various stages of intermediacy between modern humans and chimpanzees (*21*). Early interpretations of Neanderthals and *Homo erectus* were undoubtedly influenced by such reasoning, and hence many reconstructions were depicted with semidivergent great toes (*22*). There has been a persistent reluctance on the part of human paleontologists to acknowledge fossil hominid postcranial remains as indicative of a fully modern human gait (*23*). When information on the skeletal anatomy of *Australopithecus* was gathered in the Transvaal, it was recognized that these fossils were very old (*24*) and anatomically distinct from modern humans in their crania (*11, 25, 26*), shoulder girdles (*27*), arms (*28*), hands (*29*), pelves (*11, 13, 30–34*), femora (*34–36*), ankles (*20, 26, 37*), and limb proportions (*38*).

The significance of these differences

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was assessed by scientists using anatomical, morphometrical, and biomechanical analyses. Some considered *Australopithecus* to be an inefficient biped (*11, 32-34, 39-41*) only capable of "jog-trotting" (*42*), "shuffling" (*11*), "waddling" (*40*), or a "shambling half-run" (*43*). Such interpretations have been incorporated in textbooks on human evolution (*43, 44*). Other investigators, most notably Lovejoy and his associates, interpreted the anatomy of the same fossils as commensurate with a striding, bipedal form of gait—one which was as mechanically adapted to upright walking and running as that of modern humans (*20, 31, 36, 45, 46*). The recovery of 1.0- to 3.0-million-year-old fossil hominid postcranial remains from eastern Africa did not resolve the controversy. Several investigators hinted at a dichotomy in locomotor types for these fossils (*47*). Some have stated that *Australopithecus robustus* was incapable of an efficient bipedal mode of locomotion, and others even suggested that knuckle-walking was the locomotor mode of at least some Pleistocene hominids (*6, 42, 48*).

The new Hadar and Laetoli fossils combine to show that 3.0 to 4.0 million years ago hominids were widespread, successful, sexually dimorphic, small-brained creatures with primitive teeth, jaws, and crania. The Laetoli footprints show that the unique striding bipedal mode of locomotion employed by modern people had been established much earlier than previous evidence had suggested. This is strong evidence for mosaic evolution (*46, 49*). It convincingly indicates that older scenarios of human evolution that postulated a direct feedback mechanism between technology, brain expansion, canine reduction, and bipedalism should be replaced by alternative models.

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