

New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins

Abstract Laetoli is a well-known palaeontological locality in northern Tanzania whose outstanding record includes the earliest hominin footprints in the world (3.66 million years old), discovered in 1978 at Site G and attributed to *Australopithecus afarensis*. Here, we report hominin tracks unearthed in the new Site S at Laetoli and referred to two bipedal individuals moving on the same surface and in the same direction as the three hominins documented at Site G. The stature estimates for S1 greatly exceed those previously reconstructed for *Au. afarensis* from both skeletal material and footprint data. In combination with a comparative reappraisal of the Site G footprints, the evidence collected here embodies very important additions to the Pliocene record of hominin behaviour and morphology. Our results are consistent with considerable body size variation and, probably, degree of sexual dimorphism within a single species of bipedal hominins.

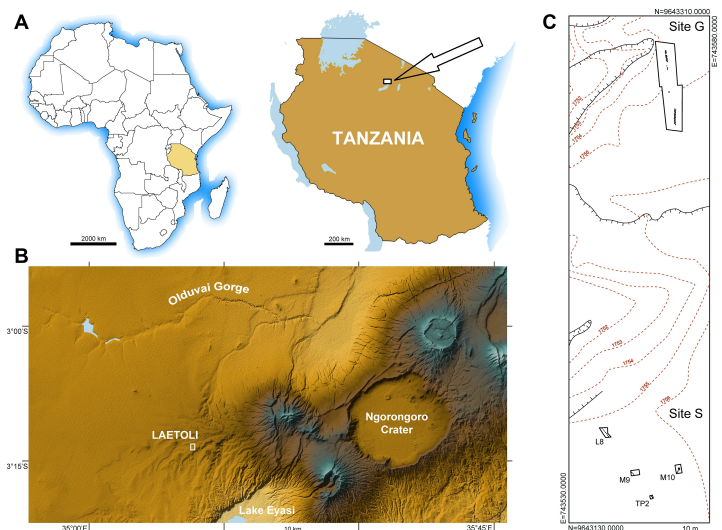
Introduction

Estimates of body size and proportions are crucial in the evolutionary interpretation of Plio-Pleistocene hominin palaeobiology and have been the subject of debates). Within-species variability in body size often relates to sexual dimorphism and/or to adaptation to different ecologies. This is particularly true among extant Hominoidea, which show diverse patterns of variation; for instance, gorillas are polygynous species with strong sexual dimorphism due to intense male-male competition, whereas chimpanzees are promiscuous with definitively smaller sexual dimorphism. In fact, claims that size variation in *Australopithecus* was larger than that in recent human populations include inferences on sexual dimorphism, whereas arguments referring to early *Homo* are usually associated with eco-physiological variants. An analysis of the sexual dimorphism of femoral head diameter in *Au. afarensis* concluded that these early hominins showed human-like sexual dimorphism and were therefore characterised by a monogamous mating system. It is clear that our ability to investigate this important and controversial issue depends on the possibility of evaluating the body size and proportions of extinct creatures.

The new tracks can be referred to two different individuals moving in the same direction and on the same palaeosurface as those documented at Site G.

The site: a brief overview

Laetoli (Figure 1A,B) is one of the most important palaeontological localities in Africa. The region includes sites such as Olduvai Gorge, Lake Ndutu and Laetoli itself and provides a long sequence of volcano-sedimentary deposits that are rich in archaeological and paleontological remains, overlying metamorphic rocks. The paleoanthropological significance of the whole area has been known since the mid 1930s. Mammal, bird and insect prints and trails have been identified in 18 sites out of 33 total palaeontological localities in the Laetoli area. These hominin trackways were found in 1978 at



Site G and were referred to three individuals (G1, G2, G3) of different body size: the smallest individual, G1, walked side by side on the left of the largest individual, G2, while the intermediate-sized individual, G3, superimposed its feet over those of G2.

Discovery and notes on preservation

The new Site S is located about 150 m to the south of Site G, on the surface of the same morphological terrace. It was discovered during systematic survey and excavation activities. In 2015, fourteen hominin tracks always associated with tracks of other vertebrates were unearthed in three test-pits. All these prints are clearly referable to a single individual trackway, with an estimated total length of 32 m. The preservation state of the tracks varies considerably along the trackway, depending on the depth of the Footprint Tuff from the surface. Somewhere, the Tuff is very shallow, not deeper than 20 cm to the south, whereas it even crops out on the scarp of the terrace on the opposite side. Consequently, the Tuff is overlain here only by reworked loose soil, and the tracks are not filled up with compact sediment. Three large rounded holes (green circles in Figure 2) originated from roots of acacia trees that grew on the surface. The situation is different in M9, where about 72 cm of grey soil and unaltered sediments overlie the Footprint Tuff. Small amounts of water were used during the excavation. The infill was finally removed by small dental tools. Unfortunately, some vertical crisscross fractures filled by hard calcite veins preclude a detailed morphological study of the two footprints.

Geological setting

The assessment of the Laetoli Site S sequence within the wider framework of the Eyasi Plateau formations is crucial to understand the stratigraphic relationships between the footprint-bearing units of the newly discovered Site S and those of the historical Site G. These relationships can be discussed at two levels of increasing detail.

The first – and most relevant – level regards verifying whether the unit bearing the new tracks corresponds to the Footprint Tuff, part of Tuff 7 together with the overlying Augite Biotite Tuff, where the Site G tracks were printed. This would imply that the trackways are contemporaneous from a geological/geochronometric point of view. It can be concluded that all the tracks belong to the same general population of hominins. Secondly, stratigraphic relationships can be explored at higher detail, in order to assess whether the tracks of Site S were printed on exactly the same sublevel of the Footprint Tuff as those in Site G. This aspect would mostly concern the behavioural aspects of a hypothetical single group of hominins.

Results

Non-hominin tracks

Tracks and trackways of mammals, birds and insects, as well as raindrop impressions, are recorded from 18 sites at Laetoli, named alphabetically from A to R. More than 11,300 single footprints are recorded from Sites A–R. These tracks testify to a very rich ichnofauna, although a very high percentage of them (more than 88%) can be ascribed to small mammals such as lagomorphs and/or Madoqua-like bovids. Finally, we report some very small tracks of unidentified animals, probably micromammals. The above-mentioned assemblage of terrestrial mammal and bird footprints suggests that the local palaeoenvironment was characterised by a mosaic of dry tropical bushland, woodland, open grassland and riverine forest similar to the extant one.

These bipedal tracks open a window on the behaviour of a group of remote human ancestors: five individuals were walking at the same time, in the same direction and at similar speed. It suggests that reproductive strategies and social structure were closer to a gorilla-like model than to chimpanzees or modern humans.

Morphology of hominin tracks



The only preserved track of S2 shows an abnormal widening of the anterior part. This enlarged morphology is possibly due to a lateral slipping of the foot before the toe-off; the heel has an oval shape and is pressed deeply into the ground.

Speed estimates were computed starting from stride length: the obtained values show that these hominins were all walking at similar low speed (about 0.44 to 0.9 m/s, depending on the analysis method). The average lengths are 180 mm, 225 mm and 209 mm.

The stature and mass of the Laetoli print-makers were

estimated following the relationships between foot/footprint size and body dimensions. Stature and mass estimated are about 165 cm and 44.7 kg, and 146 cm and 39.5 kg.

Materials and methods

Excavation and footprint imaging:

The survey of the new tracks at Site S was focused on obtaining 3D models for documentation and morphometric analysis. The survey method is the Structure from Motion technique, an image-based process supported by in situ topographic measurements. This technique was chosen because of its technical advantages (relatively short time of data acquisition and processing; light and handy equipment; reduced costs) and excellent results in terms of resolution. The equipment used in the fieldwork is a DSLR camera with 15.3 megapixels and two different lenses. When necessary, the camera was mounted on a 4 m-long telescopic rod. A measuring tape and a water level were used for the measurement of the control points. Considering the small size of the surfaces to be detected, this measuring technique provided very high accuracy results.

Data processing

Data processing started by checking measurements in plan and height. The following morphometric measures were taken on the contour maps: footprint length, footprint max width, angle of gait, step length.