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Large mammal tracks in 1.8-million-year-old volcanic ash (Tuff I^F, Bed I) at Olduvai Gorge, Tanzania

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ABSTRACT

Large animal tracks, unequivocally attributable to terrestrial mammals, are reported for the first time in sediment from uppermost Bed I (Tuff I^F; ~1.803 million years ago) at Olduvai Gorge, Tanzania. One track in particular (attributed to the ichnogenus *Pecoripeda*) retains an exceptional level of detail, demonstrating the excellent trackway-preserving potential of the volcanic ash fall (tuff) layers at this important hominin archaeological locality. Olduvai Gorge is renowned for its abundant Plio-Pleistocene (zoo)archaeological discoveries and fossiliferous deposits vis-à-vis studies of human evolution. Fossil trackways, and trace fossils more widely, provide an important additional tool for characterizing ancient ecosystems, which remain underexplored at Olduvai. Considered together with fossil hominin remains, information derived from coeval fossil animal tracks provides additional insight into our ancestors' behaviour and their interactions with the surrounding palaeoenvironment. A range of large herbivore tracks indicates the availability of nearby resources (i.e., freshwater, vegetation preferred by grazers/browsers). These newly-discovered tracks are of archaeological and palaeontological significance because they highlight the potential for future discovery of animal or hominin tracks and trackways preserved in tuff at Olduvai and in other archaeological localities.

KEYWORDS
Tracks; Olduvai Gorge; mammal; palaeoecology; volcanic tuff; hominin evolution

Introduction

Fossil assemblages of bones and teeth provide an excellent basis for interpreting ancient ecosystems. However, the processes involved in the burial and fossilization of animal material often results in biased assemblages. Over time, taphonomic processes (i.e., mode of deposition, scavenging, chemical and physical weathering at surface, and post-burial diagenesis) alter the fossil assemblage from that of the original animal community. True species abundances are commonly distorted and species richness is underrepresented (Behrensmeyer, 1978). For example, disarticulated skeletal remains can be transported long distances (i.e., by water or predators) or a specific species may be over-represented in one location (i.e., predator bias). These processes can obscure the original ecological provenience of an ancient animal. Fossil tracks and trackways associated with fossil bone assemblages can provide additional information about faunal communities and help alleviate some of the taphonomic biases.

Tracks and other trace fossils provide direct evidence that the track maker was present in a specific environment or location. Tracks can also convey aspects of behaviour, such as mode and speed of locomotion, and even inter/intra-species interactions if multiple individuals are represented on a single tracking surface (Cohen et al., 1993; Lockley, 1998). Despite the preservation bias towards larger, heavier animals, tracks and trackway assemblages provide complementary palaeoecological information that helps to eliminate some preservation biases associated with fossil assemblages.

Fossil trackways in Africa

Despite their overall rarity, animal and hominin trackways are well described from Plio-Pleistocene sediments from East and South Africa (Figure 1). Some track sites are critical to our understanding of hominin evolution. The 3.6-million-year-old Pliocene hominin trackways preserved in volcanic ash at the Laetoli

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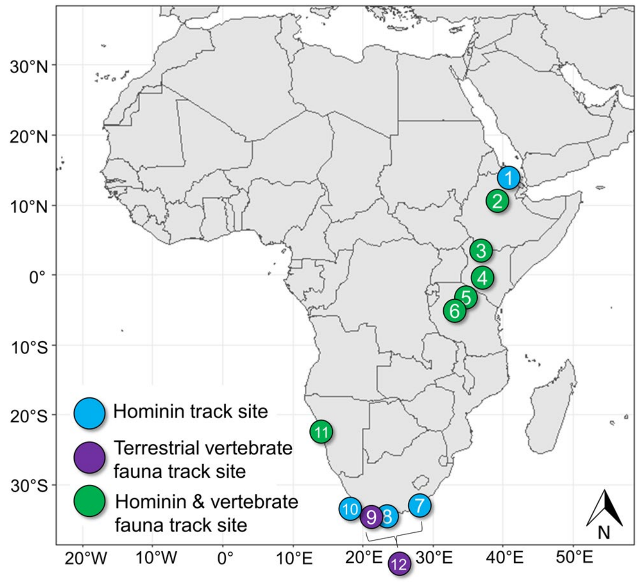

Figure 1. African Plio-Pleistocene and Holocene records of hominin and large animal fossil track sites. 1 – Danakil Desert, Eritrea (~800 ka) (Archaeology News Network, 2016); 2 – Melka Kunture (Upper Awash Valley), Ethiopia (~700 ka) (Altamura et al., 2018); 3 – Koobi Fora (~1.5 Ma), Ileret (~1.52 Ma), and GaJi10 sites (~1.43 Ma) (Okote Member, Koobi Fora Formation), Lake Turkana, Kenya (Behrensmeyer & Laporte, 1981; Bennett et al., 2009; 2014; Brown et al., 2006; Hatala et al., 2017; Roach et al., 2016); 4 – Sandai Plain (Loboi Silts), Lake Bogoria, Kenya (Late Pleistocene) (Scott et al., 2008); 5 – Engare Sero, Lake Natron, Tanzania (5760 ± 30 to 19.1 ± 3.1 ka) (Balashova et al., 2016; Hatala et al., 2020; Liutkus-Pierce et al., 2016; Zimmer et al., 2018); 6 – Laetoli, Tanzania (~3.6 Ma) (Day & Wickens, 1980; Leakey, 1978b; Raichlen et al., 2010); 7 – Nahoon Site, Eastern Cape Province, South Africa (~124 ka) (Jacobs & Roberts, 2009; Roberts, 2008); 8 – Brenton-on-Sea, Western Cape Province, South Africa (~90 ka) (Helm, McCrea, et al., 2018); 9 – Still Bay, Western Cape Province, South Africa (~90 ka) (Helm, Cawthra, de Vynck, et al., 2019; Roberts et al., 2008); 10 – Langbaan Lagoon, Western Cape Province, South Africa (~117 ka) (Berger & Hilton-Barber, 2000; Roberts & Berger, 1997); 11 – Namib Sand Sea, Walvis Bay, Namibia (late Holocene) (Morse et al., 2013); 12 – Cape south coast sites, South Africa (Late Pleistocene) (Helm, Cawthra, Combrink, et al., 2020; Helm, Cawthra, Cowling, et al., 2020; Helm, Cawthra, de Vynck, et al., 2019; Helm, Cawthra, et al., 2018; Helm et al., 2017; Helm et al., Cawthra, Hattingh, 2019; Roberts, 2008; Roberts et al., 2008).

site (40 km south of Olduvai Gorge) remain the earliest unequivocal evidence of bipedalism in early human ancestors (Day & Wickens, 1980; Leakey, 1978a; 1978b; Raichlen et al., 2010). Hundreds of posited *Homo erectus/ergaster* tracks preserved in ancient lakeshore sediments from the Ileret site (Koobi Fora Formation) near Lake Turkana, Kenya demonstrate that these early human ancestors utilized lakeshore habitats and evolved an essentially modern style of locomotion and foot function by 1.5 million years ago (Bennett et al., 2009; Roach et al., 2016; 2018). Fossil footprints attributed to *Homo erectus* are reported from the Danakil Desert, Eritrea from an ancient lake shore deposit dated to ~800 ka (Archaeology News Network, 2016). Additional sites within the Koobi Fora Formation record Pleistocene bipedal hominin and large vertebrate tracks and trackways - including rare examples of trackways produced by swimming hippopotami (Behrensmeyer & Laporte, 1981; Bennett et al., 2009; 2014; Brown et al., 2006; Hatala et al., 2017; Roach et al., 2016).

Additional records of Pleistocene hominin/early *Homo sapiens* and vertebrate fauna track sites from East Africa are rare. Tracks are typically preserved in palaeolake margin settings or ancient volcanic ash. Known sites include a single hominin track at the Sandai Plain site at Lake Bogoria, Kenya and the Engare Sero site at Lake Natron, Tanzania (Balashova et al., 2016; Hatala et al., 2020; Liutkus-Pierce et al., 2016; Scott et al., 2008; Zimmer et al., 2018). The Engare Sero site yielded over 400 human footprints attributed to a (predominantly female) group of 16 individuals, providing insight into early human group composition and dynamics (Hatala et al., 2020). An extensive record of hominin and animal (bovid, hippopotamus, equid and bird) tracks are reported from the ~700 ka Melka Kunture site (Upper Awash Valley) in Ethiopia (Altamura et al., 2018). The surface may indicate the presence very young children and is preserved alongside coeval archaeological evidence of flint knapping and a butchered hippopotamus carcass (Altamura et al., 2018).

Abundant Quaternary fossil track sites are reported from South Africa from the coastal aeolianites of the Cape south coast. These include a single record of forty hominin tracks (90 ka), making it the best preserved late Pleistocene archive of its kind for the region (Helm, McCrea, et al., 2018; Roberts, 2008). Additional late Pleistocene human track sites from the region include Nahoon (~124 ka) in Eastern Cape Province, and Brenton-on-Sea (~90 ka) and Langbaan Lagoon (~117 ka), both in Western Cape Province (Berger & Hilton-Barber, 2000; Helm, McCrea, et al., 2018; Jacobs & Roberts, 2009; Roberts, 2008; Roberts & Berger, 1997). Numerous fossil animal tracks and trackway sites preserved in aeolianites (i.e., from Witsand to Robberg Nature Reserve) that represent contemporary animal genera were also discovered along the Cape south coast (Helm, Cawthra, Combrink, et al., 2020; Helm, Cawthra, Cowling, et al., 2020; Helm, Cawthra, de Vynck, et al., 2019; Helm, Cawthra, Hattingh, et al., 2019; Helm, Cawthra, et al., 2018; Helm et al., 2017; Roberts, 2008; Roberts et al., 2008). Megafauna are well-represented at these sites (e.g., artiodactyls, giraffe, elephant, rhinoceros, long-horned buffalo, giant Cape horse), as well as reptiles and birds (Helm, Cawthra, Combrink, et al., 2020; Helm, Cawthra, de Vynck, et al., 2019; Helm et al., Cawthra, Hattingh, 2019). Records are currently sparse for the west coast of Africa, although a late Holocene human and animal (bovid, giraffe, elephant, carnivore, and bird) track site is reported from the Namib Sand Sea, near Walvis bay, Namibia (Morse et al., 2013).

Palaeogeography and Ecology of Olduvai Gorge

Olduvai Gorge is on the western margin of the East African Rift Valley system (Figure 2). The contemporary gorge is situated between the Serengeti Plains to the west and the Ngorongoro volcanic highlands to the east. Prior to incision of the modern gorge by fluvial processes ~50 ka, the palaeoenvironment included a saline-alkaline lake and less saline wetland lake-margin habitats.

Saline-alkaline lake and lakeshore habitats dominated the Olduvai Gorge landscape during Bed I time (~2.1 to 1.75 Ma). Throughout this interval, the Bed I sedimentary record indicates that a mosaic of habitats existed, including lake, lake-margin, wetland, woodland (>80% tree [canopy] cover), and grassland (<10% tree cover) (Ashley et al., 2009; Hay, 1976; Magill et al., 2013; 2016). Groundwater springs were also present close to the lake. Palaeo-lake Olduvai expanded and contracted with seasonal and global changes in rainfall patterns (Ashley & Hay, 2002; Hay, 1976; Hay & Kyser, 2001; McHenry, 2012). The surrounding palaeoenvironment transitioned through time from closed woodland habitat during middle Bed I time, to more open woodland and grassland during lower Bed II time (Bibi et al., 2018; Fernández-Jalvo et al., 1998). However, this transition was not gradual or unidirectional (Magill et al., 2013). The overall trend towards aridity in East Africa coincided with high latitude glacial cycles (DeMenocal, 1995; 2004; Shackleton, 1995).

At Olduvai Gorge, the lacustrine and near-shore sedimentary record from the late Pliocene to the Holocene is rich in faunal remains, early hominin fossils (*Paranthropus boisei*, *Homo habilis*, *Homo erectus*), and stone tools from the Oldowan and Acheulian industries (Bibi et al., 2018; Clarke, 2012; Diez-Martín et al., 2015; Domínguez-Rodrigo et al., 2013; Egeland, 2007; Kimura, 2002; Kovarovic et al., 2013; Leakey, 1971). The stratigraphic succession (Figure 3) comprises alternating weathered clays and well-dated volcanic ash deposits (marker tuffs). A diverse Pleistocene faunal community occupied the landscape at Olduvai Gorge during Bed I and II times. The large herbivore fossil assemblage is composed of Bovidae (Alcelaphini, Antilopini, Tragelaphini, and Bovini tribes), Suidae, Proboscidea, Hippopotamidae, Giraffidae, and Rhinocerotidae. Large-bodied carnivores – Canidae, Felidae, and Hyaenidae – preyed upon the diverse range of herbivores (Egeland, 2007). This well-dated

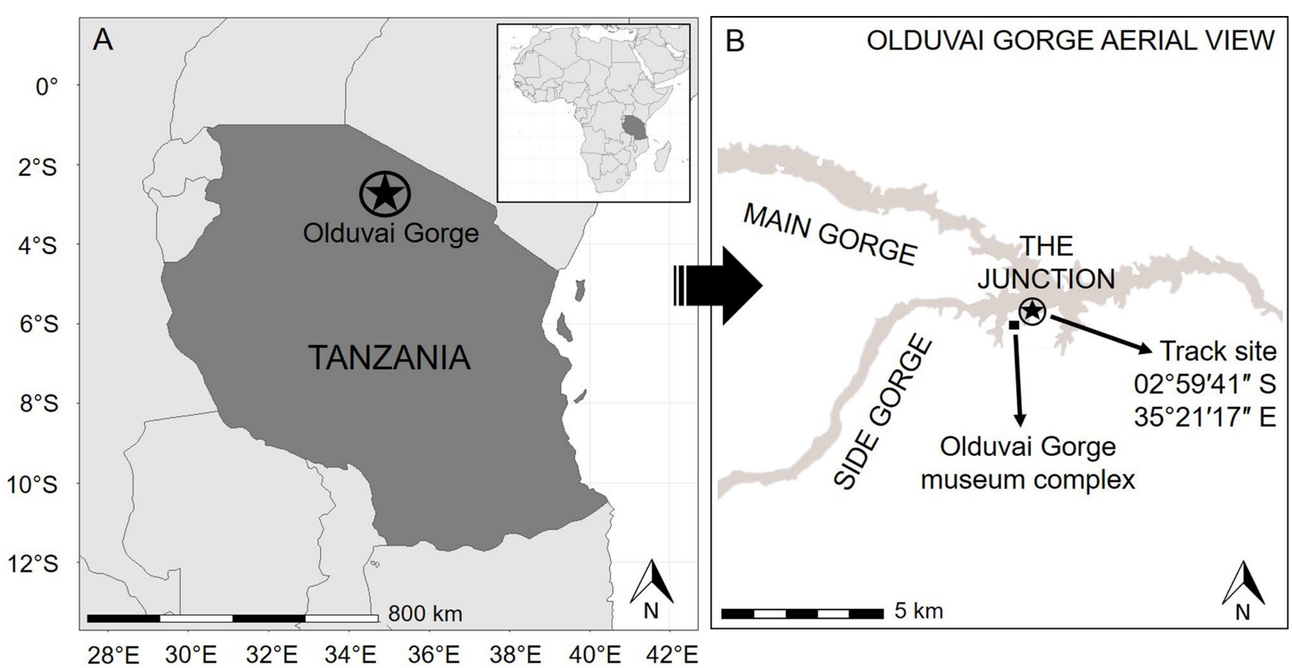

Figure 2. A. Olduvai Gorge, northern Tanzania. B. Olduvai Gorge, with the location of the fossil track site indicated by a star.

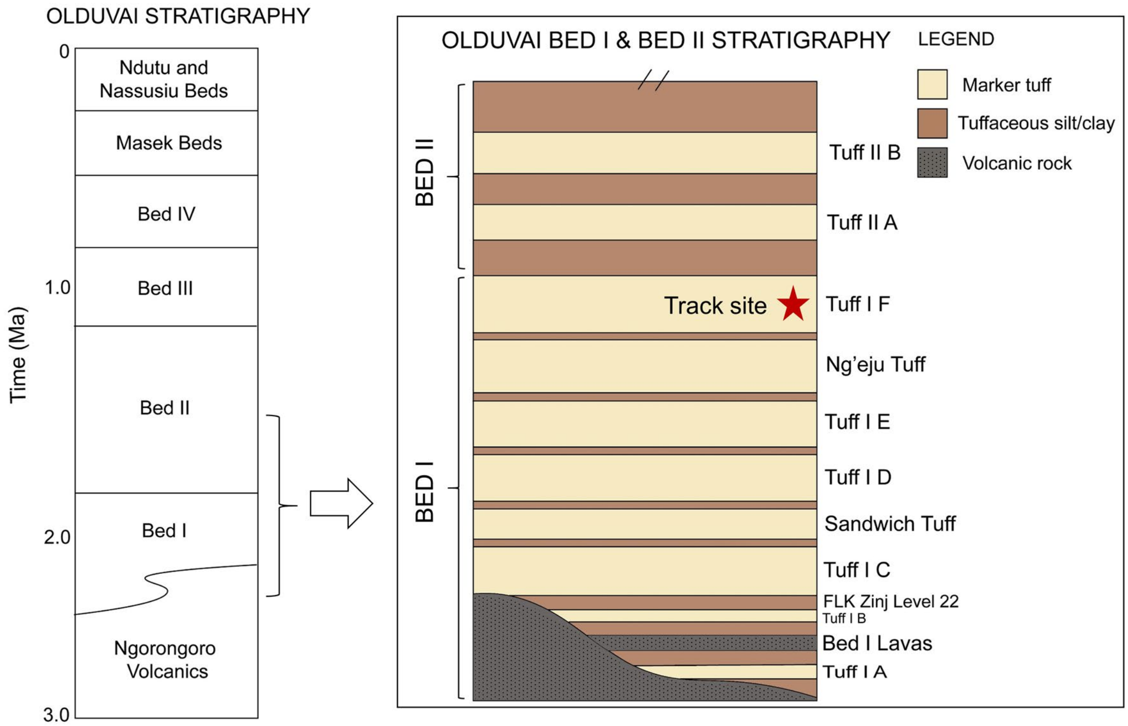

Figure 3. A simplified stratigraphic column for Bed I and Lower Bed II at Olduvai Gorge (based on geological information from Reck, 1914, Hay, 1963, 1976, Leakey, 1978a, McHenry, 2012, Bibi et al., 2018, and Uno et al., 2018).

stratigraphic succession provides an important window into early human evolution and the palaeoecology of the East African landscape over the past 4 million years.

Methods

A single locality that exposed track-bearing surface(s) within Tuff I^F was identified and surveyed in June 2019. The tracks and track casts were photographed and measured, while stratigraphic context was identified on site.

Results

Locality: Olduvai Gorge, Ngorongoro Conservation Area, Northern Tanzania

Stratigraphic context: Tuff I^F, upper Bed I

Outcrop coordinates: 02°59′41″ S and 35°21′17″ E

Site elevation: 1430 m

Multiple, large-bodied terrestrial animal tracks were discovered in an exposure of Tuff I^F, upper Bed I at Olduvai Gorge, Tanzania (Figures 2 and 3). Tracks and track dimensions are presented in Figures 4–7. Tuff I^F is an ~1.80 Ma deposit that contains reworked, high-energy pyroclastic material (Bibi et al., 2018; Deino, 2012). Tuff I^F caps the stratigraphic sequence of Bed I and is sandwiched between the Ng'eju tuff and the base of Bed II (Figure 3).

The exposure is approximately 345 m northeast of the Olduvai Gorge museum building complex. Three individual blocks of laminated tuff containing fossil animal tracks were discovered eroding out of the same exposure (Figure 8). The three separate tracks were found within 10 m of one another. Animal tracks preserved in fine-grained sediment produce morphologically distinct patterns (Figure 9). This can include true tracks that formed in contact with the foot of the animal, undertracks, and various styles of sediment deformation peripheral to the track. None of the discovered tracks appeared to be over-printed.

The degree of preservation and the level of detail varies among the three separate tracks. This could indicate *i*) the presence of multiple track surfaces within the same ash layer or *ii*) that the same continuous track-bearing surface had spatially-variable consistency (i.e., more or less cohesive) at the time the tracks were made.

Discussion

Ichnotaxonomy

Ichnogenus *Pecoripeda* (Vyalov, 1965; 1966)

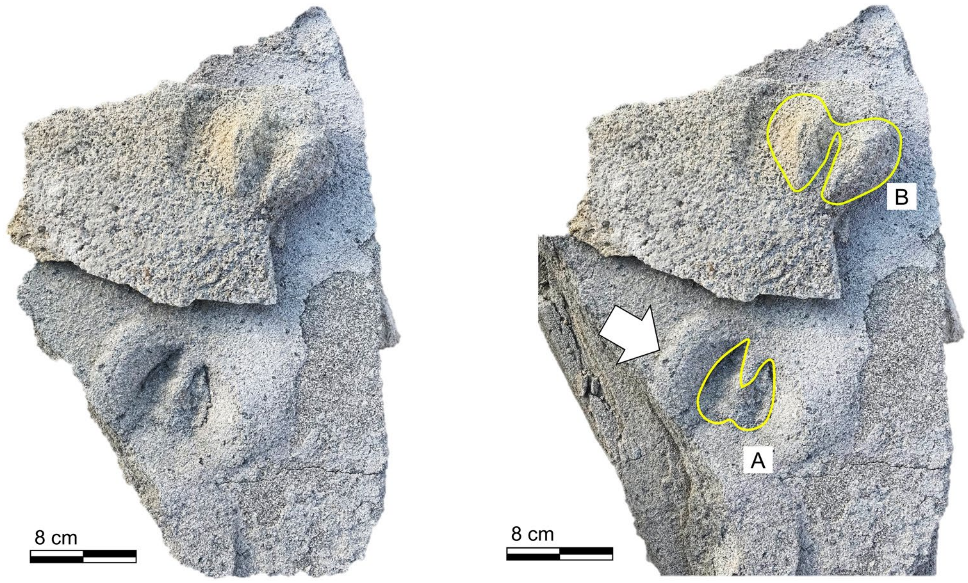

Figure 4. Block of pyroclastic tuff containing Track 1. The fossil track (A) and corresponding track cast (B) are preserved with a high degree of detail. The marginal ridge is indicated by a white arrow.

Ichnospecies *Pecoripeda isp.*

Descriptions:

Track 1: Single print produced by an artiodactyl (cloven-hoofed animal) (Figure 4). The lateral digit impression is larger than the medial digit impression, which is indicative of a left-side track. Track and corresponding track cast (Figure 4) were discovered near one another. This substrate was cohesive at the time of print formation, as demonstrated by the crisp detail and the presence of a marginal ridge surrounding the print (Figure 4). In addition, the sharp edge of the underside of the keratinous hoof-wall has left a clear indentation in the tuff.

Track 2: Single track cast produced by an artiodactyl . The indentations created by the anterior tips of the hooves are clearly visible (Figure 5). The track surface substrate was cohesive at the time of print formation, and a concave reverse impression of a marginal ridge is visible (Figure 5). The keratinous ridge on the underside of the tips of the hooves is also visible (Figure 5). A stratigraphically lower surface preserving silicified roots was present in the same block of tuff.

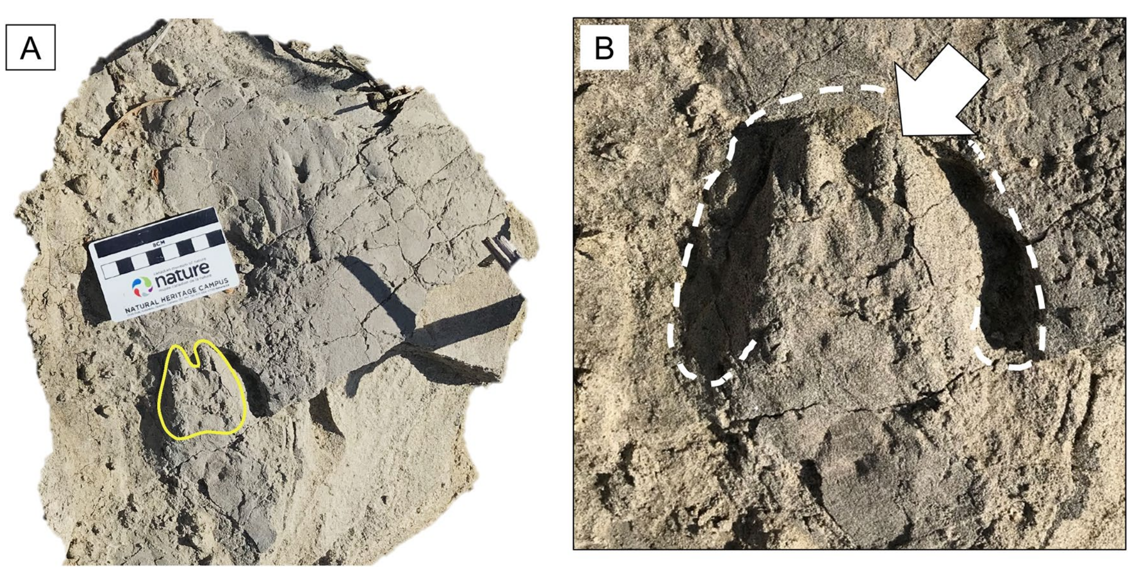

Figure 5. A. Block of pyroclastic tuff containing Track 2. Only the fossil track cast was located. B. The concave reverse impression created by the marginal ridge surrounding Track 2 (indicated with dashed white line). The impression left by the keratinous ridge on the underside of the hoof is also visible (indicated by a white arrow).

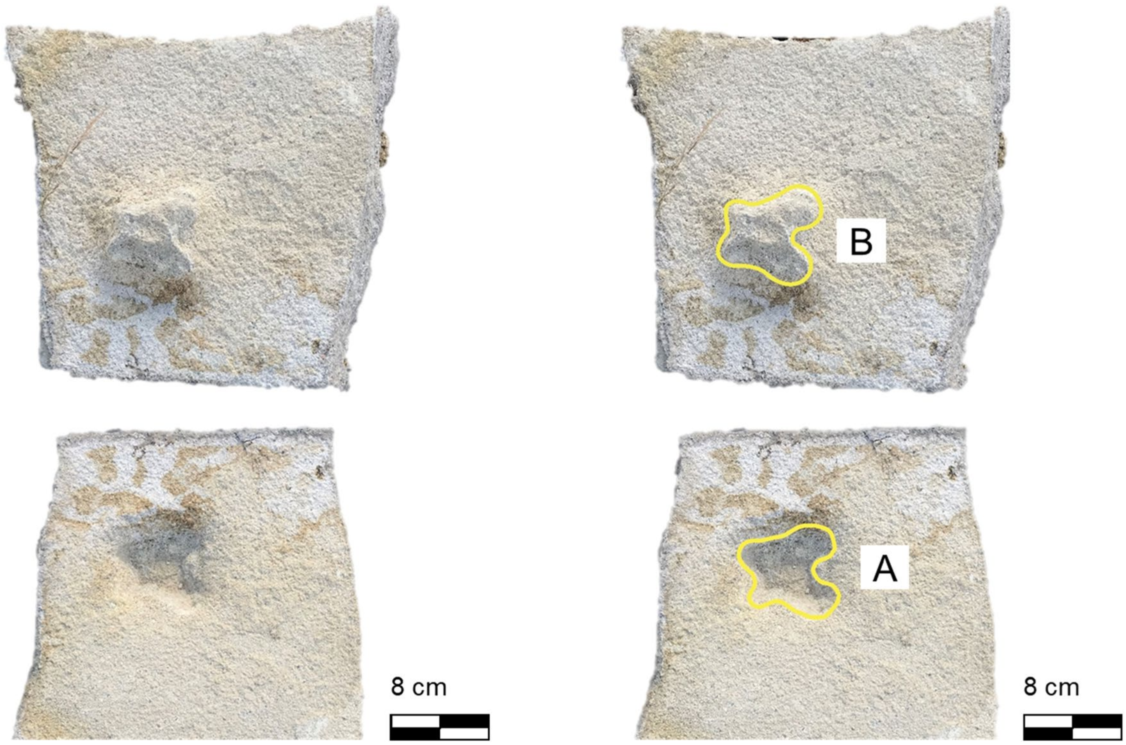

Figure 6. Block of pyroclastic tuff containing Track 3. The fossil track (A) and corresponding track cast (B) are preserved with minimal detail.

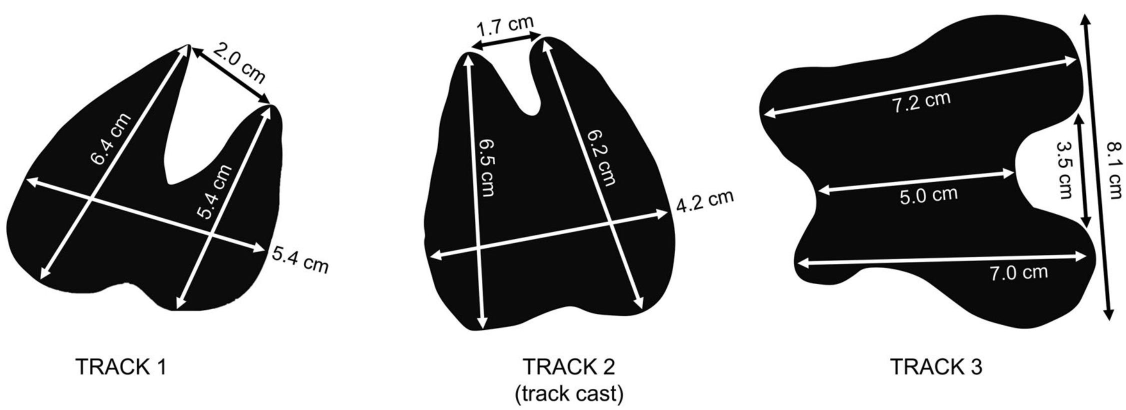

Figure 7. Track measurements.

The Cenozoic vertebrate ichnotaxonomic group *Pecoripeda* incorporates all footprints of ruminant artiodactyls that possess horns and antlers (except for Tylopoda, or camels and camelids) (Lucas & Hunt, 2007; Vyalov, 1965; 1966). This ichnogenus includes giraffes, bovids, and antelopes. Tracks from this ichnogenus are characterized by elongated, wedge-shaped tracks with two mirror-image hooves separated by an interdigit space (Bromley et al., 2009; Morgan & Williamson, 2000; Sarjeant & Langston, 1994; Vyalov, 1965).

Ichnogenus *Megapecoripeda* (Kordos, 1985)

Ichnospecies *Megapecoripeda isp.*

Description:

Track 3: Single print produced by a large even-toed ungulate. Track and corresponding track cast were discovered together (Figure 6). The track was infilled with coarse-grained sediment. The track is poorly preserved with minimal detail, and the marginal ridge is very weakly developed.

The asymmetrical track shape and dimensions suggest a large track maker belonging to the ichnogenus *Megapecoripeda* (Hágen et al., 2014; Kordos, 1985). The Cenozoic vertebrate ichnotaxonomic grouping *Megapecoripeda* incorporates the larger even-toed ungulates. Tracks from this ichnogenus are larger than

Figure 8. The exposure of Tuff I^{F}, Bed I, where the tracks were discovered. A block of tuff containing a footprint is indicated by arrow 'A', and scale is indicated by geological hammer (32 cm long) at arrow 'B'. Photograph taken facing East.

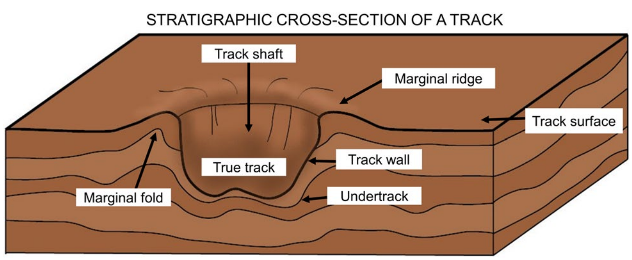

Figure 9. A simplified block diagram illustrating the morphological features of a track in cross-section. Modified from Allen (1997) and Melchor (2015).

Pecoripeda and are characterized by a medial digit shifted distally and slightly diverging toes (Kordos, 1985, Hágen et al., 2014).

Vertebrate palaeoecology

Tracks unequivocally attributable to large terrestrial mammals have not been previously reported from Pleistocene deposits at Olduvai Gorge. Undulating palaeo-wetland sediments at Olduvai have been attributed to widespread trampling (bioturbation) by large vertebrates, and large trough-shaped structures in lowermost Bed II claystones are hypothesized to be ancient hippo trails (Ashley, 2003). However, the only confirmed fossil animal tracks at Olduvai occur in the Bird Print Tuff (BPT) in lower Bed II. The BPT is a yellow laminated vitric tuff that contains abundant footprints of shore birds (Hay, 1976).

All three tracks appear morphologically consistent with those made by members of Artiodactyla (even-toed ungulates). This is unsurprising, given that members of Bovidae dominate the fossil assemblages of Bed I and II (Bibi et al., 2018; Egeland, 2007; Gentry & Gentry, 1978). Tracks 1 and 2 are morphologically consistent with those made by medium-bodied members of Artiodactyla, possibly Bovidae. Comparison with modern African Bovidae tracks (Figure 10), both in the field and in reference guides, suggest that Track 1 was made by an animal similar in size and hoof-morphology to a modern Waterbuck

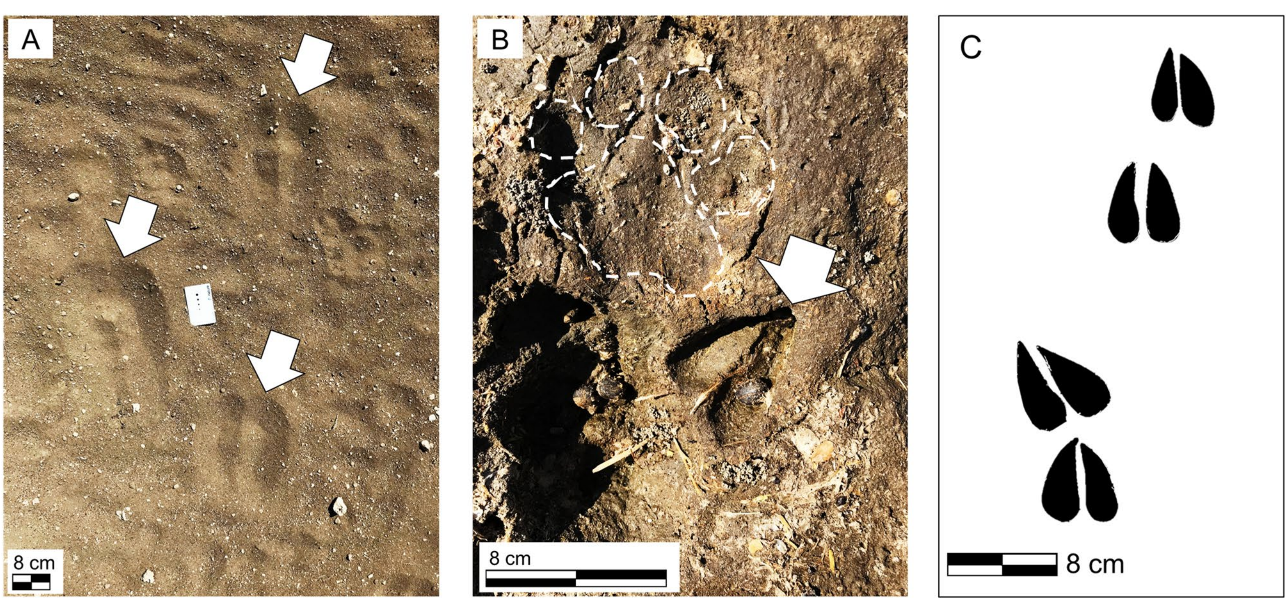

Figure 10. Modern artiodactyl tracks from Olduvai Gorge region. A. Fresh giraffe (*Giraffa camelopardalis*) footprints in loose sandy sediment from the plains surrounding Olduvai Gorge. The tracks were produced by a small herd of individuals of different ages/sizes. B. Arrow indicating medium-sized bovid footprint (probably wildebeest, gazelle, or antelope) in the soft muddy lakeshore sediments of the present-day saline/alkaline Lake Ndutu, Tanzania (situated approximately 35 km west of Olduvai Gorge). Dashed white outline indicates a carnivore track in the same image. Photographs from June 2019. C. Outline of a modern Waterbuck trackway from Tanzania. Silhouette modified from photograph (2019).

(weighing 130 kg or more) (Liebenberg, 1990). A smaller member of Bovidae, perhaps belonging to Antilopini, may have made Track 2.

Track 3 is the largest and preserved in the least degree of detail. The track is larger and asymmetrical, suggesting a large artiodactyl with a complex foot structure.

Although more specific track maker associations cannot be constructed based on current evidence, the fossil record at Olduvai Gorge supports our initial ichnotaxonomic interpretations. Artiodactyla is one of the most abundant mammal groups found in fossil deposits from Olduvai Gorge (Gentry & Gentry, 1978). Bovidae fossils are abundant in Bed I and II at Olduvai Gorge (Gentry & Gentry, 1978), where Bovinae, Hippotraginae, Alcelaphinae, Antilopinae, and Caprinae are well represented.

Palaeoecological implications

Tracks of large herbivores provide direct evidence that essential resources occurred at Olduvai Gorge during the mid-Pleistocene. Today, the nearby Serengeti Plains are a well-established migratory pathway for wildebeest, zebra, antelope, and gazelle. These animals follow the rains in order to access nutritious grazing and better quality water sources. Many African species of Bovidae require open grasslands or shrub grasslands to survive. The presence of tracks attributed to these taxa imply that grassland and an adequate supply of freshwater occurred (at least seasonally) at Olduvai Gorge during the early to mid-Pleistocene. This agrees with what is known about early hominin site choice. Hominin archaeological sites and freshwater springs and lakes are closely associated with the rift valley axis and fault zone, where groundwater springs remain available even when there is a seasonal scarcity of surface water (Cuthbert et al., 2017).

Future research directions

Further investigation of the Olduvai Gorge track site is required to identify the precise trackway surface within Tuff I^F and determine if it is continuous or if multiple tracked surfaces exist. Such surfaces record a snapshot in time and allow rare, direct observation of ancient inter- and intra-species interaction and behaviour. The discovery of trackways (instead of isolated tracks) would allow additional research into the locomotion style and speed of track makers at Olduvai (Falkingham, 2014; Lockley, 1998). Tracks and skeletal fossils are rarely found in the same strata, and the discovery of additional tracks and trackways would further our palaeoecological understanding of Olduvai Gorge during the early- to mid-Pleistocene.

The discovery of well-preserved fossil tracks has important implications for palaeoanthropological research at Olduvai Gorge. Habitat diversity and crucial resources (i.e., raw materials and freshwater) attracted a variety of hominin species to Olduvai Gorge during the late Pliocene and throughout the Pleistocene. This new discovery highlights the potential to discover faunal and hominin tracks or trackways from well-dated tuff deposits that have direct stratigraphic association with well-described fossil and tool assemblages from Olduvai Gorge.

Conclusions

Tracks belonging to the ichnogenera *Pecoripeda* and *Megapecoripeda* were discovered in volcanic ash Tuff I^F, upper Bed I at Olduvai Gorge. Track morphology suggests track-makers were medium to large-bodied members of Artiodactyla (c.f., Bovidae). One track retains an exceptional level of detail and demonstrates the optimal trackway preservation potential of Tuff I^F. The individual tracks show variable levels of detail, indicating that substrate consistency varied in time and space, or perhaps that tracks were made on multiple surfaces. Further investigation is required to identify the precise trackway surface(s) within Tuff I^F. The preservation of these three tracks indicates there is the potential for future discovery of *in situ* fauna and hominin tracks or trackways in tuff deposits at Olduvai Gorge.

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Disclosure statement

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