

Title: Footprint evidence for locomotor diversity and shared habitats among early Pleistocene hominins

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Abstract: For much of the Pliocene and Pleistocene, multiple hominin species coexisted in the same regions of eastern and southern Africa. Due to limitations of the skeletal fossil record, questions about their interspecific interactions remain unanswered. Here, we report the discovery of ~1.5 Ma footprints from Koobi Fora, Kenya that provide the first evidence of two different patterns of Pleistocene hominin bipedalism appearing on the same footprint surface. New analyses show that this is observed repeatedly across multiple contemporaneous sites in the eastern Turkana Basin. These data indicate a sympatric relationship between *Homo erectus* and *Paranthropus boisei*, suggest the importance of lake margin habitats to both species, and highlight the possible influence of varying levels of coexistence, competition, and niche partitioning in human evolution.

Main Text:

Introduction

5 The fossil record provides evidence that two or more hominin species coexisted at the same time in the same regions of eastern and southern Africa (1). Co-occurrence of closely related taxa in the same ecosystems is often explained by adaptive niche partitioning, in which disparate morphological and behavioral adaptations limit direct competition by allowing different species to access different resources on their shared landscape (2, 3). However, the hypothesized sympatry of hominin taxa is typically based on co-occurrence of their skeletal fossils within deposits that span tens to hundreds of square kilometers, and that accumulated over thousands to tens of thousands of years (4, 5). The current spatiotemporal resolution of hominin fossil data is not sufficient to determine whether different species actually inhabited the same landscapes at the same time, in terms of ecological time (years to decades), nor to address what role interspecific competition may have played in human evolution, including in the emergence of our own genus (6).

15 Beyond the spatiotemporal limitations of the skeletal fossil record, which constrain what we know about sympatry, we also have limited knowledge about potential adaptive divergences between contemporaneous taxa such as *Homo erectus* and *Paranthropus boisei* (7, 8). A substantial amount of work has focused on hypothesized dietary differences (9–12) because most fossils confidently attributed to these taxa are cranial and dental remains (7). Apart from diet, another hypothesis posits that *H. erectus* was the earliest hominin to practice fully modern human-like bipedal walking and endurance running, and that this key adaptation set them on a different evolutionary trajectory from their contemporaries (13). With a sparse record of postcranial fossils that are mostly isolated, fragmentary, and/or difficult to attribute taxonomically, there is little direct skeletal evidence allowing comparisons of bipedal locomotion in *H. erectus* and *P. boisei* (14, 15).

20 The early Pleistocene deposits of the Turkana Basin, northern Kenya, provide new evidence bearing on sympatric relationships between *H. erectus* and *P. boisei* (7, 8). Here, we present the discovery of an early Pleistocene footprint site in the upper KBS Member of the Koobi Fora Formation (16). We analyze the hominin footprints and re-examine an extensive suite of sites and track assemblages of similar age in the same geographic region (East Turkana) (17–19). Fossil footprints record information on foot anatomy, gait, and environmental context within extremely narrow spatial and temporal scales (e.g., tens of square meters over periods of hours to days), allowing us to test hypotheses about hominin locomotion and behavior that are inaccessible with skeletal fossil data (20). By applying new analytical techniques (21) to the growing sample of footprint sites at East Turkana, we consistently find evidence for two different patterns of hominin foot kinematics. These two patterns occur adjacent to each other on the same footprint surfaces and are recorded across multiple sites. Our results offer: 1) the first direct evidence of differing locomotor kinematics among early Pleistocene hominins, and 2) a spatially- and temporally-limited snapshot of data appropriate for demonstrating ecological sympatry (on a scale of hours to days), showing that two different hominin taxa repeatedly crossed paths ~1.5 million years ago in lake margin environments.

Site description

Site ET-2022-103-FE22 (abbreviated FE22) was discovered in 2021 in East Turkana Area 103, within the uppermost KBS Member of the Koobi Fora Formation (Fig. 1A). The footprint surface was recognized when R.L. discovered a hominin track while excavating hominin skeletal fossils from overlying sediments (see *Materials and Methods*). The track surface is stratigraphically about 10 m below the Elomaling'a Tuff (Fig. 1B and C), recently dated to ~1.52 Ma (22). Tephrostratigraphic correlations (16) indicate that this site is slightly older than any of the hominin footprint sites previously known from the Turkana Basin (17–19).

The track-bearing surface at FE22 was formed on a 32 cm thick, homogeneous silt unit, which is stratified in a 3.5 m thick sequence of alternating fine sand and silt units (Fig. 1D; Fig. S1). Throughout the upper 2.5 m, bedding irregularities indicate cross-sections of vertebrate tracks (Fig. 1D; Fig. S1) – at least five likely track surfaces are preserved, including two impressed into 30–35 cm thick homogeneous silt units (numbered Track Surfaces (TS) 1–5 on Fig. 1D). Both surfaces were covered by laminated sandy silt and sand, which infilled and preserved the tracks. The sandy, laminated units immediately above the track surface excavated here (TS-2) contain vertebrate body fossils and are the source of hominin skeletal fossils also found at this site. The lower 1.3 m includes two bivalve-dominated shell beds with preserved root and plant stem structures interpreted as evidence of reed beds. The upper of these two shell beds has dish-shaped sedimentary structures identified as fish nests (23). Overlying sediments are ripple- or horizontally laminated sands and silty sands, interbedded with several massive silt and silty clay units, with only one 25 cm deep cut and fill structure indicating local channeling (Fig. 1D). There are few root traces and no evidence of mud-cracking that would indicate prolonged sub-aerial exposure.

On the TS-2 surface, we uncovered one continuous trackway made by a single hominin individual and three isolated hominin tracks that, based on sizes and orientations, appear to represent three additional, different individuals (Fig. 2; *Supplementary Text*). The excavated TS-2 surface also includes 61 bird tracks, 30 bovid tracks, and 3 tracks attributed to equids. Many of the bird tracks are unusually large, the largest being 27 cm wide and several others over 20 cm (Fig. 2E). The size and morphology of these tracks are consistent with those of marabou storks, such as the 'giant' *Leptoptilos cf. falconeri* (24). Skeletal fossils from that taxon are currently known only from the Pliocene (24), but large bird tracks in Okote Member footprint sites are tentatively attributed to this taxon as well (25).

Results and discussion

The lithofacies at FE22 represent an aggrading lake margin sequence in the uppermost part of the KBS Member of the Koobi Fora Formation, ~10 m below the Elomaling'a Tuff, which is dated at ~1.52 Ma (22). The sequence of depositional units (Fig. 1D) records a transition from sedimentation in a stable shoreline with reedbeds to rapid accumulation with minimal sediment reworking, possibly resulting from deposition by a distributary channel on a shallow delta margin. At least 5 depositional horizons show evidence of vertebrate tracks in cross-section (TS-1 to TS-5, Fig. 1D; Fig. S1). Short hiatuses in sedimentation allowed stabilization of two relatively thick silt beds, one of which formed the TS-2 surface that recorded the vertebrate tracks presented here. Based on the track cross-section in Fig. 1D (also Fig. S1) and track features evident in Figs. S3 to S17, the TS-2 surface was slightly more cohesive in the

top few cm and softer below. The track surfaces were gently covered with fine sand and silty sand and preserved under the accumulating strata. Although some tracks may have experienced minor water damage as they were buried, there is no evidence for erosion into these surfaces (e.g., rip-up clasts, coarser basal lag), supporting continuous, rapid sediment accumulation over the track surfaces. Animals were walking and standing in shallow water or very close to the shoreline on a wet substrate that was supportive but deformable. The lack of mud-cracking and rooting indicates that the TS-2 surface was sub-aqueous or minimally sub-aerially exposed, and the limited number of overprints also suggests a very short time interval (hours to a few days at most) before renewed sedimentation buried the track surface.

The morphology of the tracks and the information that they retain regarding foot morphology and gait is partly dependent on the nature of the substrate (21, 26). The TS-2 substrate was soft enough to allow hominins to sink deeply (~ 4 to 8.5 cm), but cohesive enough to record fine details of their track morphology (Figs. S3-S17). The substrate appears to have been sufficiently stable for hominins to walk at a steady pace. The HT1 trackway is characterized by relatively consistent step lengths (mean = 87.28 cm, standard deviation = 4.05 cm) and narrow step widths (mean = 2.63 cm, standard deviation = 3.66 cm). The hominin that made the trackway was not slipping or otherwise experiencing any obvious gait perturbations. Based on stride lengths (mean = 171.85 cm), we estimate that this individual was moving at about 1.81 m/s, which corresponds to a modestly fast walking rate (27). Given the speed, consistency and lack of out-of-plane motion, we assume the HT1 tracks likely represent this individual's normal gait when moving over a soft substrate.

The depths of tracks vary laterally across the TS-2 surface, and the isolated tracks all fall within the range of depths observed in the HT1 trackway. With one exception (track HT1-9; Fig. S10), the isolated tracks and those within the HT1 trackway all display a similar degree of fine morphological detail (e.g., ridges between toe impressions; Figs. S3-S17). Their similar depths and level of morphological detail, combined with their immediate proximity (Fig. 2), make it likely that the isolated tracks and HT1 trackway were made under similar substrate conditions. Importantly, our analyses also account for the ways in which track morphology varies with track depth, allowing tracks of varying depth across the TS-2 surface to be compared.

The patterns of foot kinematics recorded by the TS-2 tracks were evaluated using new methods developed from biplanar X-ray studies of how track morphology is shaped by foot motion (28). Previous work has shown that the longitudinal arching of human tracks, quantified as relative arch volume (RAV), is the product of modern human heel-sole-toe rollover kinematics (21). Human tracks follow a distinctive pattern wherein RAV increases logarithmically with a track's relative depth (depth scaled to track size). Changes to foot motion and substrate resistance cause humans to make more highly arched tracks as they sink more deeply. Quantitative comparisons of RAV, in the context of relative depth, allow for the detection of different kinematic patterns expressed in fossil hominin tracks (21). Two of the isolated TS-2 tracks (H2 and H3) have human-like RAV values for their depth, and therefore show evidence of human-like foot kinematics (Fig. 3). However, the tracks in the HT1 trackway, which provide a large sample from a single individual walking on the same substrate, all show evidence of a different kinematic pattern. The bottom of these tracks is much flatter for their depth, making them similar in this way to ~3.66 Ma tracks known from Laetoli Sites G and S (Fig. 3). At the same time, many of the HT1 tracks are pitched in the opposite direction from the Laetoli G1 and S1 tracks (deeper forefoot compared with heel impressions), perhaps indicating

heel strike and/or push-off patterns that differed not only from those observed in modern humans but also from those evidenced at those Laetoli sites (21). Within our comparative sample of 340 modern human tracks (which includes multiple populations making footprints across multiple types of substrates), the probability of sampling a set of at least five footprints from the same person, which falls this far from the human RAV-relative depth logarithmic regression line, is zero (see *Materials and Methods*). Further, the pattern of consistent step lengths and widths along the HT1 trackway makes it unlikely that quantitative differences from modern human-like track morphology are due to walking in an unstable manner.

When looking more broadly at the entire sample of hominin footprints currently known from East Turkana at ~1.5 Ma, we now recognize further evidence for two different patterns of bipedal kinematics. One subset of tracks recovered near Ileret, Kenya (18, 19, 29), has RAV values that fall within the limits of the 95% prediction interval of the modern human RAV-relative depth regression. A second subset has RAV values well outside of the 95% prediction interval of the modern human regression that are very similar to those from the TS-2 HT1 trackway (Fig. 3). Recognition of two different patterns of foot kinematics in the Ileret samples, one human-like and one not, requires some revision to prior interpretations of those sites (see *Supplementary Text*). One track from GaJi10 (17), which is close to FE22 but at a higher stratigraphic level than the TS-2 surface, could be quantified in this way. It too shows a low RAV value similar to those observed within the HT1 trackway (also within the Laetoli G1 and S1 trackways; Fig. 3). Our prior work demonstrated that the pattern of longitudinal track arching captured by RAV is generated primarily through heel-sole-toe rollover patterns, and deviations from the RAV-relative depth trend observed in modern humans indicate different foot kinematics (which may, in turn, be coupled with differences in foot anatomy; 21). Evaluation of all available evidence from multiple ~1.5 Ma East Turkana sites strongly suggests that two different patterns of locomotor kinematics are recorded on the same footprint surfaces, with some trackways indicating modern human-like motion patterns and others something different.

In addition to the kinematic differences implied by RAV, hallux impressions within the HT1 trackway also imply differences in foot anatomy and/or function when compared with footprints of modern humans. In absolute terms, hallucial abduction angles measured from the HT1 tracks tend to exceed those observed among modern human footprints (Fig. 4A; see *Materials and Methods*). The same is true for the Laetoli G1 trackway, although neither approaches the highly abducted hallux impressions of chimpanzee tracks. In addition to being more abducted, the orientations of the hallucial impressions within the HT1 trackway are more variable than those of modern human tracks. When comparing mean-centered hallucial abduction across groups, the HT1 and Laetoli G1 samples span broader ranges than modern human samples, showing greater variability in step-to-step positioning of the hallux (Fig. 4B). The differences between maximum and minimum abduction angles measured from both right and left footprints within the HT1 trackway (15.9 degrees for the left foot, 19.1 degrees for the right foot) fall well outside 95% confidence limits derived from iterative resampling of experimental footprints made by modern humans (1.4 degrees to 10.6 degrees; see *Materials and Methods*). Comparable levels of variation in hallucial abduction angles are observed in Laetoli G1 and chimpanzee footprints (Fig. 4B). We note, however, that hallucial abduction in the HT1 and Laetoli G1 tracks is different from that observed in chimpanzees. In the former, the hallux abducts from the long axis of the foot at the first metatarsophalangeal joint, whereas in the latter abduction initiates at the tarsometatarsal joint. Based on observed differences in track morphology, we hypothesize that the makers of the HT1 and Laetoli G1 tracks differed from modern humans

(and from chimpanzees) in morphology and/or kinematics at the first metatarsophalangeal joint. Again, patterns similar to those observed in the HT1 and Laetoli G1 tracks are evident at other ~1.5 Ma hominin footprint sites near Ileret, Kenya (*Supplementary Text*; Fig. S2).

5 Assuming that our analyses appropriately account for potential variation due to substrate (see *Materials and Methods*), the observed patterns of track morphology at FE22 might be explained by early Pleistocene hominins having much greater intraspecific variation in foot anatomy and walking kinematics than observed in modern humans (including modern humans from 400-500 years ago, 26). However, the evidence presented above and the skeletal fossil data described below leads us to propose that the TS-2 footprints record the co-occurrence of two
10 different taxa, exhibiting different patterns of foot morphology and kinematics, represented within the growing number of early Pleistocene track assemblages at East Turkana.

15 Despite a sparse record of confidently attributed skeletal fossils, the known evidence of early Pleistocene hominin postcranial morphology has been linked to locomotor variation among different taxa. Robinson (30) analyzed hominin lower limb (including foot) fossils from southern Africa attributed to *Paranthropus* and inferred a locomotor pattern for that taxon that was distinct from contemporaneous hominins (31). Subsequent comparative analyses of early Pleistocene talar fossils from East Turkana, Kenya and Olduvai Gorge, Tanzania identified morphological differences that were hypothesized to reflect different patterns of bipedalism in
20 *Paranthropus* and *Homo* (32, 33). More recent studies of pedal fossil morphology have applied new 3D methods, used novel analytical approaches, and incorporated more recently discovered fossils. These studies have continued to highlight an emerging picture of locomotor diversity among early Pleistocene hominins. For example, variable heel strike patterns have been hypothesized based on differences in calcaneal morphology (34), and variation in rearfoot and midfoot kinematics and longitudinal arch morphology have been inferred from diverse talar
25 morphologies (34–36). Differences in push-off kinematics have also been hypothesized based on metatarsal robusticity patterns (37). Taken together, the morphologies observed in currently known skeletal fossils suggest considerable variation in how early Pleistocene hominin feet functioned (15, 38). The morphological differences observed among early Pleistocene skeletal fossils are consistent with our finding of two kinematically distinct gaits recorded by the
30 differently arched morphologies of their tracks.

35 Directly relevant to our analyses, the morphology of the first metatarsal base in *Paranthropus* has been linked to the capacity for greater hallucial abduction than is observed in modern humans (39). Prior studies have also identified dorsal narrowing of the first metatarsal head as a characteristic that differentiates *Paranthropus* first metatarsals from those of fossil and modern *Homo* (40–42). Dorsal narrowing has likewise been observed in first metatarsals of
40 *Australopithecus afarensis* (42), the commonly presumed maker of the Laetoli G1 tracks. These studies have inferred that dorsal narrowing would result in a different pattern of toe-off than observed in modern humans. We hypothesize that the morphologies of *Paranthropus* and *Au. afarensis* first metatarsals are linked to a more abducted and more variable position of the hallux during ground contact, and that this kinematic pattern is evident in the morphologies of the TS-2 HT1 and Laetoli G1 tracks. Based on this premise, we hypothesize that the HT1 trackway on the FE22 TS-2 surface was created by *P. boisei* and the isolated tracks by *H. erectus* (43).

The co-occurrence of different hominin track morphologies, and their association with other mammal and bird tracks on the TS-2 surface, was geologically instantaneous. The

characteristics of the FE22 lithofacies are similar to those of previously reported track-bearing deposits in Area 103 (17) and Ileret Area 1A (18, 19), which occur at different stratigraphic levels between ~1.4 and 1.6 Ma. Based on this evidence, it is clear that that hominins were repeatedly visiting lake margin habitats, walking on wet substrates, wading into shallow water, and potentially interacting with other animals frequenting these environments (e.g., hippo, birds).

Skeletal fossils of *H. erectus* and *P. boisei* have long been known to co-occur within the same geological members of the Koobi Fora Formation (8). Multiple lines of evidence point to adaptive niche divergence between these taxa (9–13), suggesting that they may have occupied different parts of their landscapes at different times. Prior analyses have shown that one taxon or the other is more common as fossils in certain paleoenvironments (5). Lake margin sediments preserve *Homo* and *Paranthropus* fossils at roughly even frequencies, suggesting that these environments may have supported ecological sympatry. However, skeletal fossil assemblages represent a time- and space-averaged data source and are subject to post-mortem displacement, thus are not ideal for directly evaluating this hypothesis (6). Fossil footprints, on the other hand, provide *in situ* snapshots that are uniquely focused, in terms of both space and time, allowing interspecific interactions to be inferred more directly (6, 20, 45).

At FE22 and at site FwJj14E near Ileret (18, 19, 29), we have documented two distinct patterns of hominin track morphology on the same footprint surfaces. We propose that these patterns represent two different taxa, characterized by disparate foot anatomies and locomotor kinematics. This interspecific co-occurrence on such a fine spatiotemporal scale, within meters and hours to days of each other, implies that *H. erectus* and *P. boisei* coexisted and potentially interacted with each other in lake margin environments during the early Pleistocene. Furthermore, given different locations (~40 km apart), and depositional and temporal differences between sites recording these two hominin track morphologies within the same ~200 kyr time interval, this points to a sustained pattern of hominin sympatry in the eastern Turkana Basin. Presumably the lake margin and deltaic environments where the co-occurring tracks are recorded, as well as the larger surrounding ecosystems, offered resources that were accessible and desirable to both taxa, despite the apparent adaptive differences in their skeletal and dental morphologies. If such levels of sympatry between *Homo* and *Paranthropus* persisted since earlier in time, perhaps since the origins of the genus *Homo* at ~2.8 Ma (46), we hypothesize low to neutral levels of competition between these two hominin genera. This scenario seems plausible given their apparent adaptations for consuming different resources available on their shared landscapes (9–13). Later, climate-caused environmental shifts could have changed the balance of resource availability (3), leading to increased competition among hominin taxa and potentially driving adaptive shifts towards the riskier, higher-reward food acquisition strategies that later defined our genus (13, 47, 48). Testing such hypotheses will require detailed analyses of multiple sources of environmental and behavioral data and will benefit from integrating fossil footprints with other types of fossil and archaeological evidence.

References and Notes

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44. While it is plausible that either set of footprints may have been produced by *H. habilis* or *H. rudolfensis*, the last appearance dates of confidently attributed specimens of these taxa currently known from the Koobi Fora Formation are 1.75 Ma and 1.78 Ma, respectively (1). Given that stromatolite marker bed A6 appears below the TS-2 track surface, the footprints analyzed here are most likely younger than 1.6 Ma (16, 45). The last appearance dates of confidently attributed specimens of *H. erectus* (*sensu lato*) and *P. boisei* in the Koobi Fora Formation are 1.44 Ma and 1.41 Ma, respectively (1). Based on this premise, it is most parsimonious to hypothesize attribution of the tracks to these two taxa.
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Data and materials availability: All data relevant to the analyses presented here are available in the main text or in the supplementary materials. 3D models of individual tracks, and of the entire TS-2 track surface, are available on MorphoSource ([Temporary link for peer reviewers](#)).

Supplementary Materials

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Materials and Methods

Supplementary Text

Figs. S1 to S17

Tables S1 to S3

References (43–53)

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Data S1 to S3

Code S1 to S2

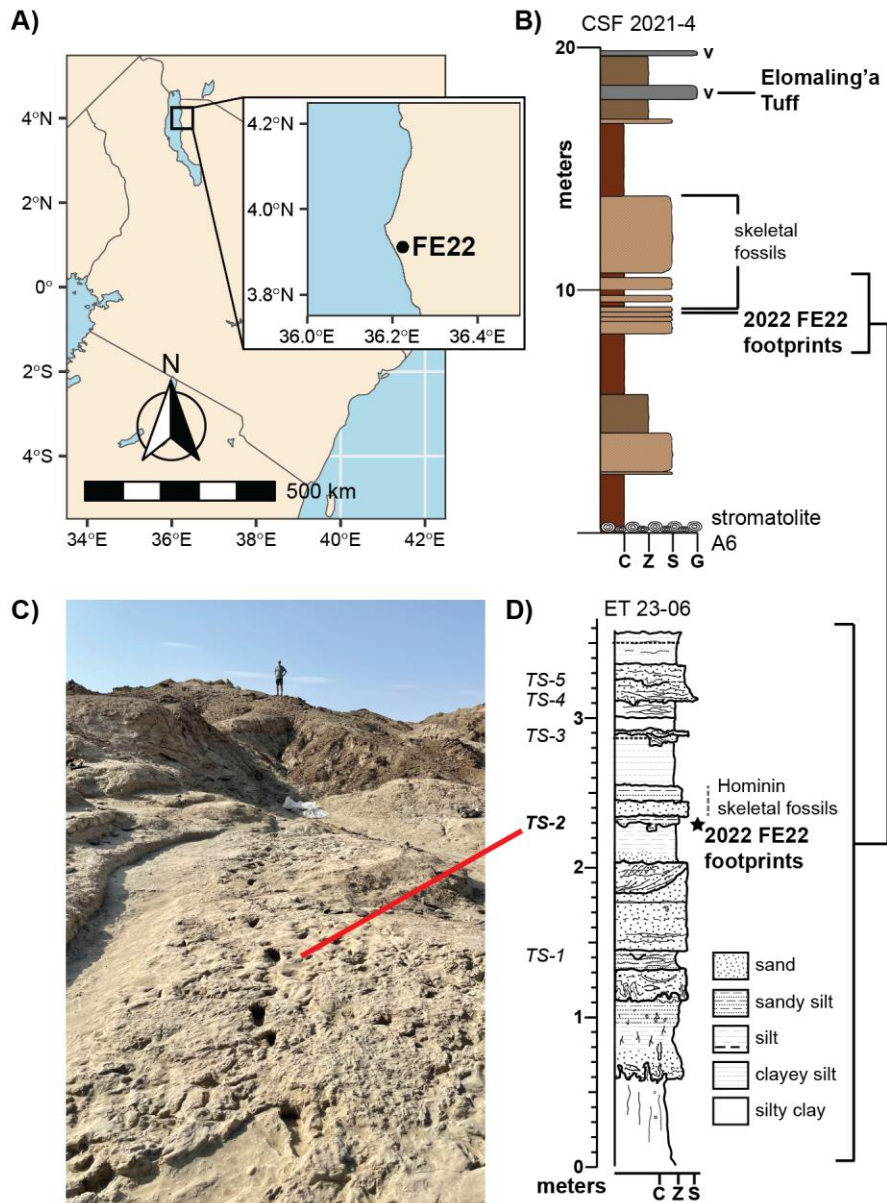


Fig. 1. Context of site ET-2022-103-FE22. (A) Map indicating location of ET-2022-103-FE22 in northern Kenya, near the eastern shore of Lake Turkana. (B) Geological section showing the general stratigraphic context of the footprint surface and relationship to the Elomaling'a Tuff, dated at 1.52 Ma (22). The "v" annotations indicate volcanic tuff layers, while horizontal axis labels "C", "Z", "S", and "G" indicate clay, silt, sand, and gravel, respectively. (C) Photograph of TS-2 track surface at site ET-2022-103-FE22, looking approximately north (photo credit N.T.R.). (D) Detailed stratigraphic section of the site showing the location of TS-2 (see also Fig. S1). Horizontal axis labels "C", "Z", and "S" indicate clay, silt, and sand, respectively. Labels "TS-" indicate levels of track surfaces. TS-2 is <25 cm below sediments from which hominin skeletal fossils were recovered, 10.2 meters below the Elomaling'a Tuff. The track surface occurs on a 32 cm thick silt layer in a sequence of sands and silts. The absence of mud cracking and the presence of mollusc and stromatolite layers in this sequence indicate a shallow sub-aquatic environment with a stable water table associated with a lake margin (25).

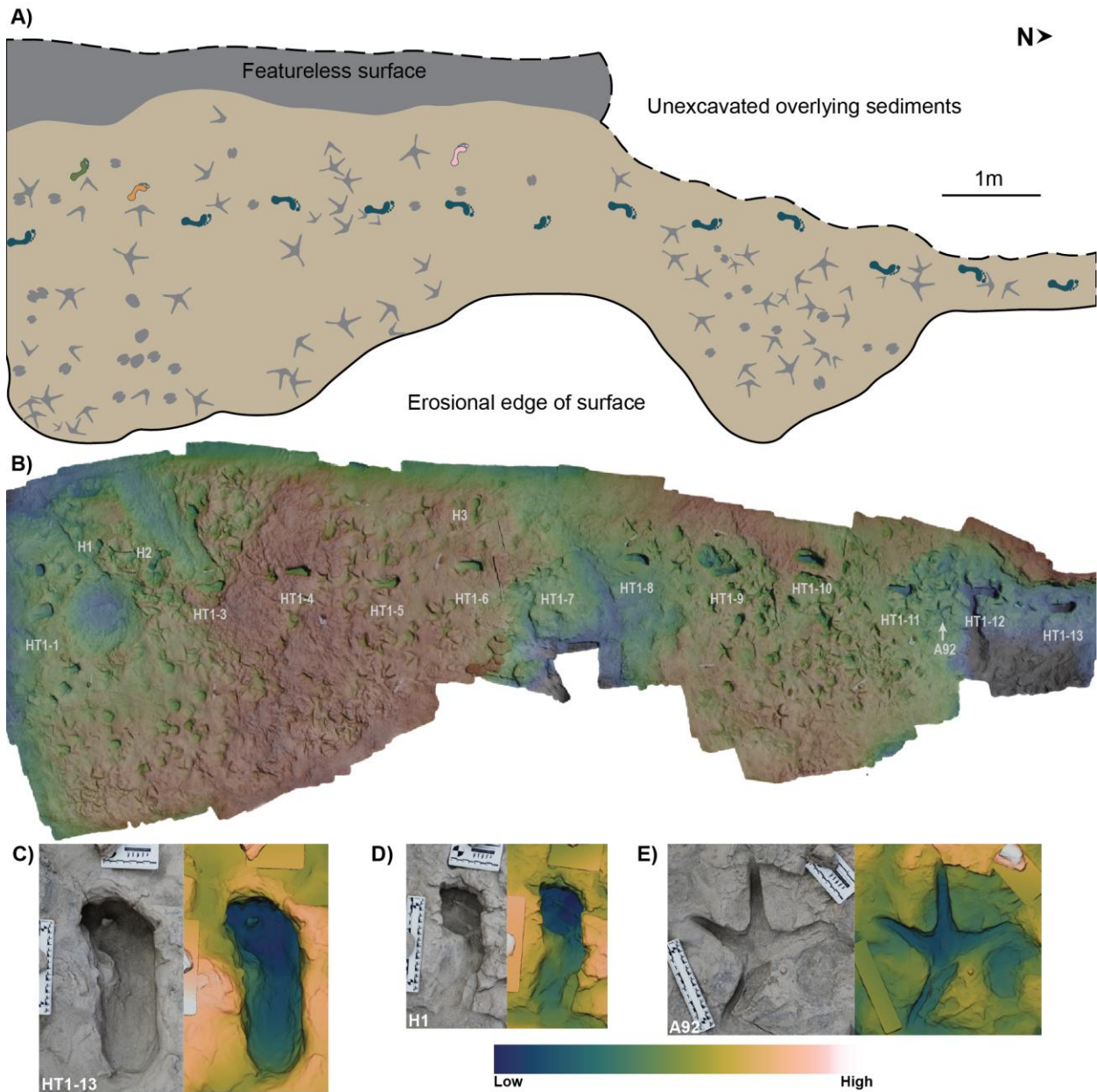


Fig. 2. The TS-2 track surface and selected individual tracks. (A) Schematic map of the TS-2 surface. The continuous HT1 trackway appears in dark blue. Isolated tracks, H1 (green), H2 (orange), and H3 (pink), are oriented nearly perpendicular to the HT1 trackway. (B) Complete 3D model of the TS-2 surface. The isolated tracks (H1-H3) and the HT1 trackway (HT1-1 to HT1-13) are labeled, as is the bird track (A92) from panel E. The original color of the photogrammetric model is blended with a height map (height map spans 30 cm from blue to red). (C) Standard image (left) and height map (right) of track HT1-13. (D) Standard image (left) and height map (right) of H1, a track smaller than those within the HT1 trackway, oriented in a different direction. (E) Standard image (left) and height map (right) of A92, a large bird track. Images C-E include the same 15 cm and 8 cm scale bars and are resized to similar scale to facilitate comparisons. Height maps span 13, 9, and 8 cm, respectively, from blue to white.

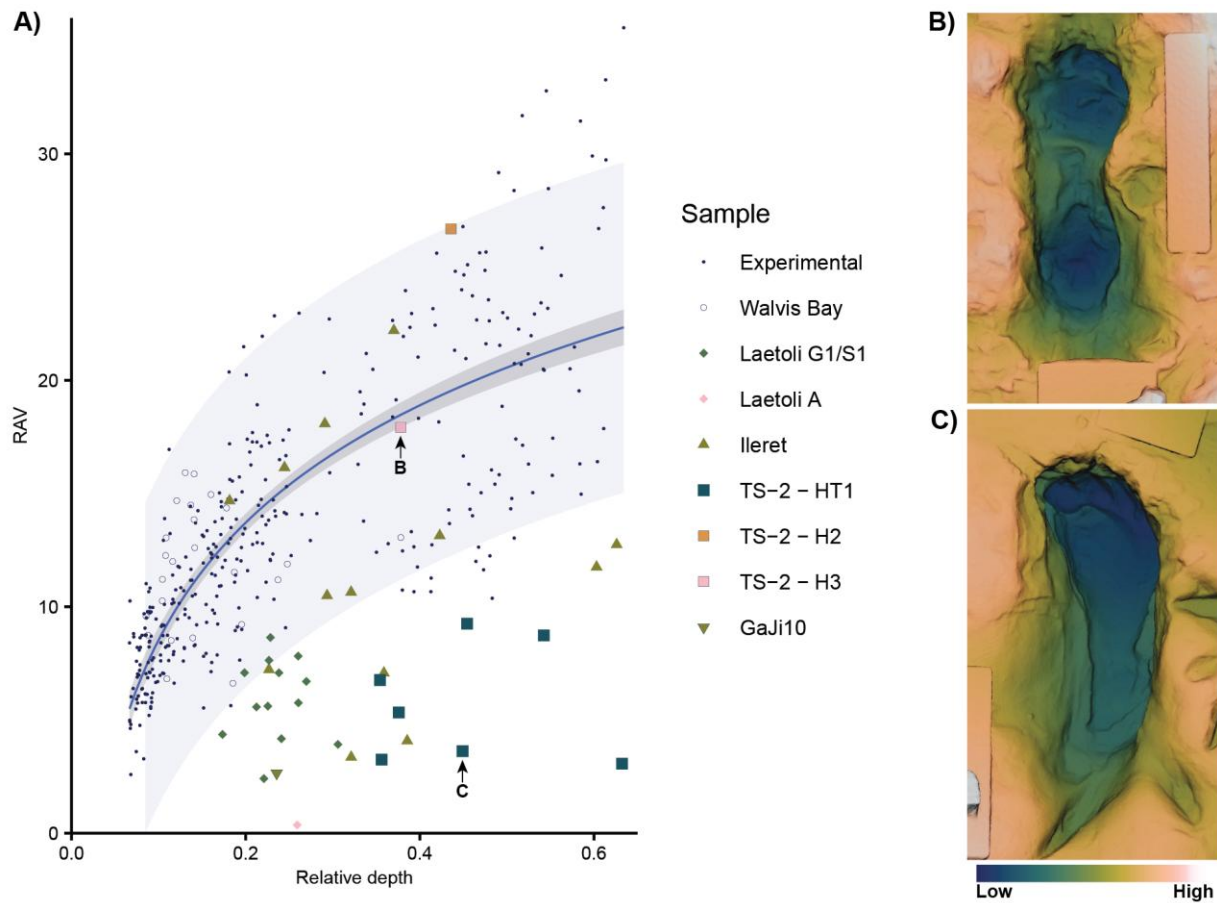


Fig. 3. Patterns of arching among modern experimental and fossil tracks. (A) Scatterplot of human and fossil tracks showing relative depth values versus relative arch volume (RAV). The 95% prediction interval (PI) from the modern human RAV-relative depth logarithmic regression is shaded in light blue (regression line in dark blue with 95% confidence interval in gray). Tracks from the TS-2 HT1 trackway fall well below the modern human 95% PI, as do some tracks from Ileret, an isolated track from site GaJi10, and most tracks from Laetoli. In contrast, two isolated tracks from TS-2 (H2 and H3) fall within the modern human 95% PI, as do some tracks from Ileret and all ~400-500-year-old human tracks from Walvis Bay, Namibia (26; see *Materials and Methods*). Tracks from panels B and C are labeled. (B) Track H3, which has a RAV of 17.93 at a relative depth of 0.38. (C) Track HT1-5, which has a RAV of 3.62 at a relative depth of 0.45. Height maps in B and C span 8 and 15 cm, respectively, from blue to white.

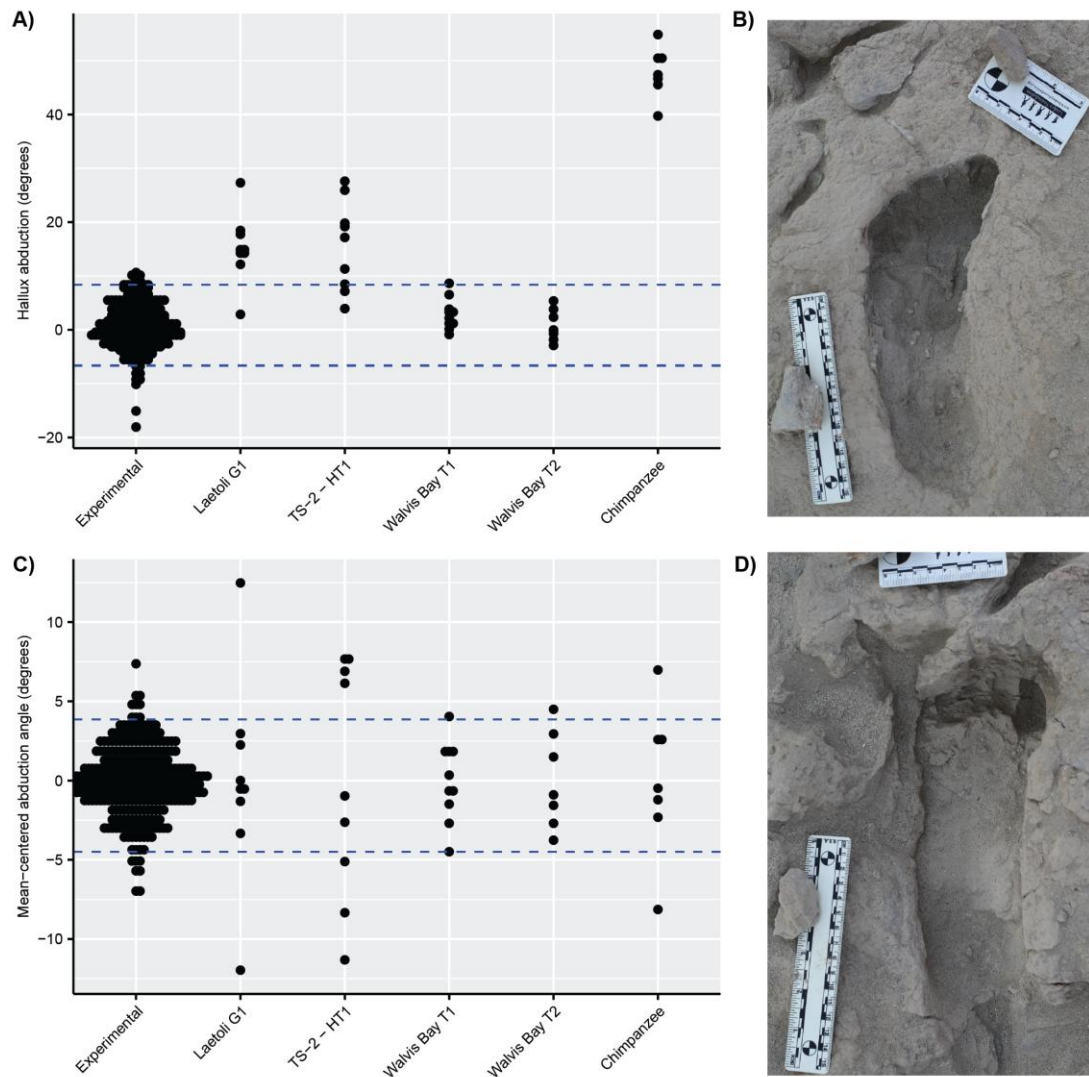


Fig. 4.

Hallucial abduction angles among modern experimental and fossil tracks. (A) Dotplot showing raw hallucial abduction angles among several track samples. Dashed blue lines indicate the 95% confidence interval (CI) of abduction angles from modern human tracks. TS-2 HT1 tracks, and those from Laetoli G1, span well above the upper bound of the modern human 95% CI, but their hallux impressions are not nearly as abducted as those of chimpanzee tracks. Abduction angles measured from ~400-500-year-old human tracks at Walvis Bay fall almost exclusively within the modern human 95% CI. (B) Track HT1-8, with a relatively high hallucial abduction angle (19.18 degrees). Scale bars are 15 cm and 8 cm (photo credit: K.G.H.). (C) Dotplot showing mean-centered hallucial abduction angles, to compare variation within samples. Again, dashed blue lines represent the modern human 95% CI. The TS-2 HT1, Laetoli G1, and chimpanzee tracks all span ranges broader than the modern human 95% CI. The Walvis Bay tracks fall almost exclusively within the human 95% CI. This highlights greater step-to-step variation in hallux orientation within the TS-2 HT1 trackway (and Laetoli G1). (D) Track HT1-12, with a relatively low hallucial abduction angle (3.94 degrees). Scale bars are 15 cm and 8 cm. HT1-8 and HT1-12 are similarly deep (relative depths of 0.43 and 0.45, respectively; photo credit: K.G.H.).