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Fossil footprints and what they mean for hominin paleobiology

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Abstract

Hominin footprints have not traditionally played prominent roles in paleoanthropological studies, aside from the famous 3.66 Ma footprints discovered at Laetoli, Tanzania in the late 1970s. This contrasts with the importance of trace fossils (ichnology) in the broader field of paleontology. Lack of attention to hominin footprints can probably be explained by perceptions that these are exceptionally rare and "curiosities" rather than sources of data that yield insights on par with skeletal fossils or artifacts. In recent years, however, discoveries of hominin footprints have surged in frequency, shining important new light on anatomy, locomotion, behaviors, and environments from a wide variety of times and places. Here, we discuss why these data are often overlooked and consider whether they are as "rare" as previously assumed. We review new ways footprint data are being used to address questions about hominin paleobiology, and we outline key opportunities for future research in hominin ichnology.

KEYWORDS
footprints, ichnology, paleoanthropology, trace fossils, tracks

1 | INTRODUCTION

In vertebrate paleontology, trace fossils have a rich history dating back to the 19th century,[1] and tracks have played invaluable roles in understanding lower limb anatomies,[2] articulated foot anatomies,[3] locomotor patterns,[4] social behaviors,[5] ecological contexts,[6] and evolutionary patterns[7] of extinct organisms. In paleoanthropology, hominin tracks (i.e., footprints; Box 1) have received comparatively less attention, with one famous exception. In 1978, a series of 3.66 Ma hominin tracks was discovered at Laetoli, Tanzania,[12] described at the time as "...amongst the most important discoveries ever made concerning the evolution of man" (p. 149).[13] Such acclaim was warranted, as this discovery directly demonstrated that hominins walked bipedally before they acquired large brains, contradicting one of Darwin's central hypotheses concerning human evolution.[14]

In the decades that followed that discovery, paleoanthropologists debated the proper interpretation of the Laetoli tracks. Some argued that they represent a foot anatomy and gait essentially indistinguishable from those of modern humans,[15–22] and others suggested that they lack some features of a modern human-like foot anatomy and/or gait.[10,23–26] These debates in many ways parallel those concerning the functional anatomy of the postcranial skeleton of *Australopithecus afarensis*,[27] the presumed creator of the Laetoli tracks (but see[28]). Outside of these long-standing debates centered on Laetoli, hominin tracks have not been routinely considered in the development or testing of major hypotheses concerning human evolution.

One might think that hominin tracks receive comparatively less attention because they are "rare" components of the human fossil record.[29–32] Historically speaking, this indeed has been the case. In the same year as the discovery at Laetoli, a hominin trackway dating to about 1.4 Ma was discovered at Koobi Fora, Kenya.[33] These footprints garnered less attention than those from Laetoli, likely because they were not as old. In the two decades that followed, no hominin tracks were discovered that might represent pre-*Homo sapiens* taxa, aside from the somewhat equivocal tracks found at Langebaan, South Africa in 1995.[34] Meanwhile, discoveries of hominin skeletal fossils boomed. Between 1981 and 2004, 10 new Plio-Pleistocene hominin taxa were found and announced, and two

BOX 1 Common ichnological terminology applicable to paleoanthropology. Since trace fossils are not consistently described in the paleoanthropological literature, we define here a general set of ichnological terms common in other areas of vertebrate paleontology.[8,9] We apply these terms throughout this review and encourage greater consistency in paleoanthropology

Term	Definition
Track	A single footprint. "Track" and "footprint" are synonymous.
Trackway	A discernible sequence of tracks produced by the same individual.
Track (or tracked) surface	A bedding plane bounding a layer or layers of sediment that preserves tracks.
Track site	A distinct geographic location at which exist one or more track surfaces.
Track assemblage	Tracks that are associated through close geographic proximity, spatial proximity, or both. The assemblage may include tracks from multiple surfaces and/or sites and should be specifically defined for proper interpretation.
Track morphology	The morphology of a track, which may or may not resemble the morphology of the foot that created it. Tracks are dynamic records and not simple molds of foot anatomy.
Ichnology	The general term for the study of tracks and traces in the fossil record, including the sedimentary processes leading to their formation and preservation.
Ichnotaxonomy	Ichnotaxonomy involves the classification of tracks into ichnospecies or ichnogenera, based on similarities or differences in track morphology. This practice is rare in paleoanthropology (for example see[10,11]), but common in other areas of paleontology.
Bioturbation	The process by which organisms, including humans, interact with sediment to leave tracks, burrows, root channels, or other indications of their activity, often resulting in disrupted sedimentary bedding and even completely homogenized deposits (e.g., paleosols).

more were defined from previously discovered fossils. The publications, theses, and dissertations from this time interval focusing on hominin skeletal fossils exceeded those involving hominin trace fossils by several orders of magnitude.

However, in recent years Pliocene and Pleistocene hominin track sites are being discovered around the world and at much greater

frequency (Figure 1). In some cases hominin track sites occur where skeletal fossils and stone artifacts are largely absent[35]; in other cases, hominin track surfaces are directly associated with excavations that have been ongoing for decades.[36,37] With these discoveries, hominin tracks now represent a substantial proportion of the human fossil record. As more sites are discovered, researchers are also recognizing that these data can be used to address a wide variety of questions about human evolution. For example, track sites reported within the past 5 years capture snapshots of *Homo erectus* walking with modern human-like gaits[30,38] and spending considerable time in lake margin environments,[39,40] of *Homo heidelbergensis* groups making stone tools and butchering animals,[36,37] of Neanderthal social groups comprised of many children,[41] and of Pleistocene *Homo sapiens* hunting sloths in North America,[42] migrating through a green Arabia,[35] and potentially engaging in collaborative foraging in Tanzania.[43]

In the field of paleoanthropology, we are accustomed to exceptionally small data sets, and we make the most of novel opportunities to expand our basis for inference and hypothesis testing. The influx of new data from hominin track sites calls for a re-evaluation of (1) where we might find more footprint sites and (2) how we can leverage this evidence to complement skeletal fossils, stone artifacts, and other "traditional" forms of data to help develop and test major evolutionary hypotheses. Here, we review several recently discovered hominin track sites, focusing on those dated to the Pliocene and Pleistocene. We discuss why these data generally have been overlooked in the past and whether they are as "rare" as often assumed. Finally, we review some new questions that are being addressed, and highlight key challenges and opportunities that exist going forward.

2 | HIGHLIGHTS OF RECENT DISCOVERIES

This review highlights discoveries of hominin track sites that were reported between 2016 and 2021 (for detailed summaries see Supporting Information: SI Text). Other sources provide comprehensive reviews of sites that were announced in earlier years.[44,45] At the older end of the geological time span of hominin ichnofossils, Miocene tracks from Crete were proposed as candidates for the earliest hominin footprints[46] but a great deal of uncertainty surrounds that attribution.[47] From the Pliocene, additional hominin trackways were uncovered at Laetoli, Tanzania, Site S.[31] Tracks from Laetoli Site A were re-excavated and reanalyzed, and ultimately attributed to hominins with different foot anatomies and/or gaits than those at Sites G or S[48] (Figure 2). Many discoveries of Pleistocene hominin tracks have been made in the past 5 years. Ongoing work near Ileret, Kenya revealed five new hominin track surfaces, and a total of 77 additional hominin tracks, all dated to 1.51–1.53 Ma.[30,38] More than 20 additional sites from the same time frame that record nonhominin tracks were also found near Ileret[39,40] (Figure 3). Multiple hominin track surfaces that date to between 1.2
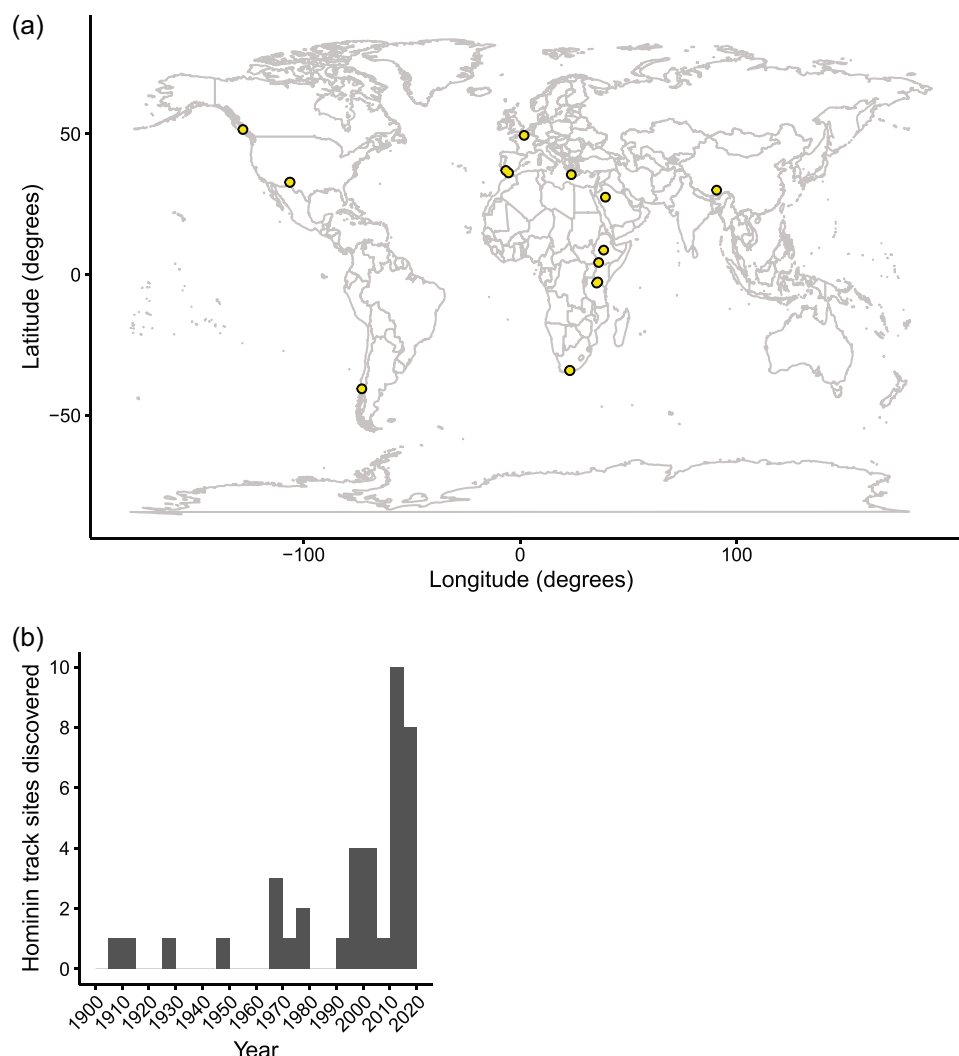
FIGURE 1 (a) Map showing the geographic distribution of Pliocene and Pleistocene hominin track sites published within the past 5 years. Note that the map includes overlapping points that cannot be differentiated at this resolution (Ileret, Kenya; Melka Kunture, Ethiopia; Cape South Coast, South Africa; White Sands, New Mexico). (b) Histogram showing the number of Pliocene and Pleistocene hominin track sites discovered through time.

and 0.7 Ma were discovered at Melka Kunture, Ethiopia.[36,37] Hominin tracks have been announced from unexpected times and places, such as an assemblage of hand and foot traces dating to 226–129 ka near Quesang, Tibet[49] and 120–110 ka human tracks from the Nefud Desert of Saudi Arabia[50] Neanderthal tracks are described from France,[41] Spain,[51] and Gibraltar.[52] Large assemblages of human tracks were discovered along the Cape south coast of South Africa,[53,54] at Engare Sero, Tanzania,[43] and at White Sands, New Mexico, USA.[42,55,56] Smaller assemblages of human tracks were found in Pilauco, Chile[57] and Calvert Island, British Columbia.[58] These discoveries not only sample a wide range of times and places in human evolution but data from these sites have been used to address a wide variety of questions about hominin paleobiology (Supporting Information: SI Text; Supporting Information: Table S1). The rate of site discovery, and the breadth of questions addressed, have increased substantially in recent years.

3 | WHERE ARE HOMININ FOOTPRINTS FOUND AND WHY HAVE THEY BEEN OVERLOOKED?

The recent surge in discoveries of hominin track sites is notable and raises the following questions: Why has this source of data on human prehistory been overlooked in the past? Are paleoanthropologists applying new field methods that are leading to the increased rate of track discovery? Does the number of recent publications reflect growing appreciation for the scientific value of human or hominin trackways?

It is worth taking a moment to consider how vertebrate (including hominin) track surfaces are preserved in the geological record. Whatever the sedimentary environment, track preservation requires: (1) a substrate that is the right consistency to record the impression of a vertebrate foot and (2) burial by sediment, usually

FIGURE 2 Track A3, originally discovered at Laetoli Site A in 1976 and re-excavated in 2019. Earlier analyses were inconclusive, but a recent study by McNutt et al.[48] suggests that this trackway most likely was produced by a hominin. This footprint measures 16.5 cm from the proximal edge of the heel impression to the distal extent of the hallux impression. Photo credit: Jeremy M. DeSilva.

soon after the track is made, that permanently covers but does not otherwise disturb the impression. The buried track surface also must not be subject to later disruption, reworking, or bioturbation, such as desiccation cracking, invertebrate burrowing, or soil formation, which would modify or destroy track morphology.[59] In some cases, the right combination of substrate and burial processes can recur in a single location over an extended period of time, leading to successive sediment layers with footprints. In other cases, such conditions are met only at one time and place. Despite the rather specific requirements for track preservation, most terrestrial animals will make thousands of tracks (or more) throughout their lifetimes, thereby increasing the odds that some will make their way into the fossil record.

Hominin tracks currently are known from lake and other water margin sediments (e.g., Ileret, Kenya; Alathar, Saudi Arabia; White Sands, New Mexico, USA), volcanic ashes (e.g., Laetoli and Engare Sero, Tanzania), sand dunes or coastal aeolianites (e.g., Cape south coast, South Africa; Matalascañas, Spain; Le Rozel, France), and cave sediments. In each of these settings, natural opportunities existed for (1) sediments to be hydrated to the appropriate consistency for

receiving foot impressions, (2) coherent tracks to form, and (3) the tracks to be rapidly buried before they were degraded. Tracks produced in any one of these settings were potentially ephemeral,[40,59–62] but under the circumstances described above, some fortunately were preserved and now have come to light as part of the geological and paleoanthropological record.

Paleoenvironmental contexts in which tracks are likely to occur are relatively common in the sedimentary sequences at some of the most well-studied Plio-Pleistocene hominin fossil localities. For example, Ashley and Liutkus[63] documented 1.75 Ma wetland sediments at Olduvai Gorge, Tanzania with fossil hippo tracks, and they described the potential for more. Unattributed faunal tracks are noted to be present at the bottom layer of the KNM-WT 15000 excavation at Nariokotome, Kenya.[64] Hippopotamus footprints are mentioned in descriptions of lake margin sediments of the lower part of the Olorgesailie Formation in southern Kenya.[65] At Koobi Fora, Kenya, Laporte, and Behrensmeyer documented 20 different track surfaces within a single geological section at one fossil locality.[59]

In our view, it is likely that there are many more vertebrate footprint surfaces in the geological record than currently recognized. So, why have these track sites not been found? We believe that despite their prevalence, trackways have escaped notice in part because the tell-tale indicators (i.e., irregularities visible in cross-sections of bedded sediments; Figure 4) are familiar to sedimentologists, but generally not to paleoanthropologists.

Taking an example from our own research, we can consider approaches applied to extensively studied Pleistocene sediments near Ileret, Kenya. In 1972, KNM-ER 1463, a femur attributed to the genus *Homo*, was the first hominin fossil discovered in the Okote Member sediments of Area 1A.[66] Over the following years, several other hominin skeletal fossils were discovered in Area 1A and other adjacent areas, along with large assemblages of faunal skeletal remains. These projects applied "traditional" paleontological field methods of surveying for fossils and artifacts eroding out of sediments, occasionally excavating sites where fossils and/or artifacts were found in situ. In the late 1970s, Behrensmeyer and colleagues[67] conducted standardized surface sampling in Area 1A and adjacent areas, with targeted paleontological excavations in Areas 8 and 8A of *in situ* mammal remains. Despite recognizing the sedimentary signatures of possible vertebrate tracks and noting the high potential for trace fossil preservation in Koobi Fora Formation sediments in Area 1A and farther south in Area 103,[33,59] several decades passed before this potential was further investigated.

In 2005, the initial discovery of track surfaces in the Ileret region occurred largely by chance. A hominin metacarpal, later attributed to *Paranthropus boisei*,[68] was discovered by Hillary Sale at site FwJj14E in Area 1A, and geologists dug a trench nearby to understand the context of this and subsequent fossil discoveries. Once the trench was dug, Dr. Gail Ashley noticed a sedimentary layer in which she believed cross-sections of animal tracks were evident. This layer was first exposed in 2006 and preserved many clear bovid tracks. In 2007, the continued exposure of this surface, and an additional track-bearing surface higher in the geological sequence, revealed hominin

FIGURE 3 Overhead images of 3-D models of two hominin track surfaces discovered in areas near Ileret, Kenya in 2014 (a) and 2013 (b). These surfaces differ in size—a meter scale is to the left of each panel. Both surfaces include tracks of hominins and several other animals, and they occur at different stratigraphic levels between the Ileret (1.52 ± 0.01 Ma) and lower Ileret (1.53 ± 0.01 Ma) Tuffs.[38] Hominin tracks identified on these surfaces are circled in black. Photo credit: Kevin G. Hatala.
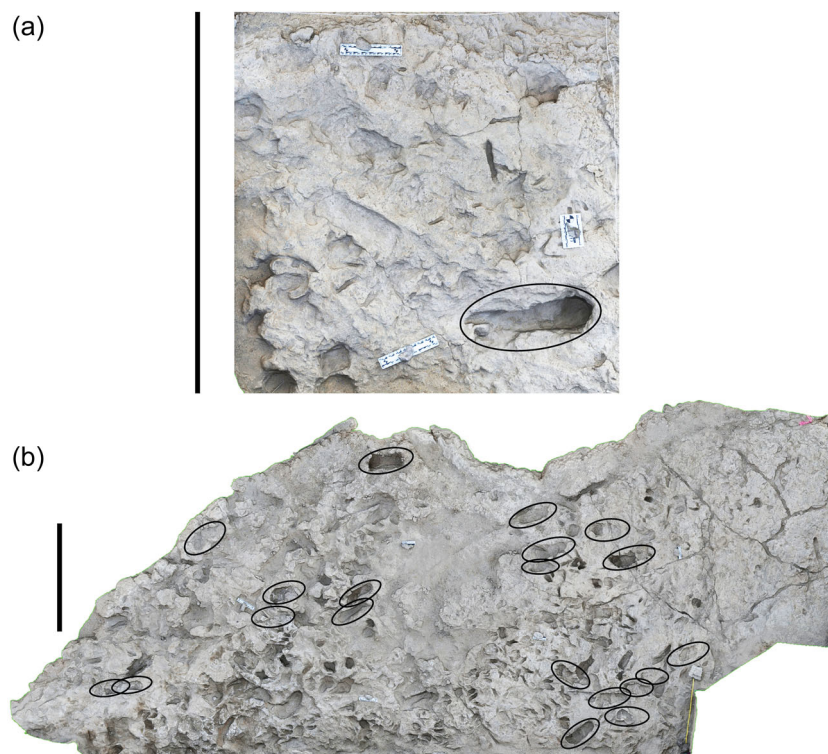
tracks. These footprint discoveries thus were a byproduct of surveys and excavations focused on skeletal fossils and did not begin with the goal of finding fossil tracks. From 2013 to 14, however, our team's field strategies were specifically aimed at locating and excavating potential track surfaces within the Area 1A Okote Member sediments. Through just two field seasons, we uncovered more than 25 track surfaces, including five additional surfaces that preserved hominin tracks[38] (Figures 3 and 5).

Research at other sites has followed similar trajectories. At Melka Kunture, Ethiopia, multiple track sites were discovered directly within the context of paleontological and archaeological excavations active since the 1960s. For several decades, researchers were not looking for track surfaces or expecting to find them, thus sedimentary layers were not exposed in a manner that would allow such occurrences to be recognized.[36,37] At the South African Cape south coast and White Sands, New Mexico (USA) initial discoveries of track surfaces rapidly led to recognition of additional surfaces in the immediate vicinity.[56,69]

Considering the evidence described above, fossil hominin footprints are not "rare" relative to other forms of fossil data. The rarity of these fossils instead depends on location and depositional context, and on the specific approaches employed during paleoanthropological field research and excavation. Several recent discoveries speak to this, showing that these trace fossils can be very abundant in the right depositional environments. They are also accessible for study once paleoanthropologists and archaeologists recognize the sedimentary features of track-bearing strata and develop excavation strategies to test for track preservation.

4 | WHAT HAS THIS GROWING SOURCE OF DATA TAUGHT US ABOUT HUMAN EVOLUTION?

With the recent surge in discoveries of hominin footprint sites has come a variety of analyses that use these data in new ways to increase our understanding of hominin paleobiology. In the past, inferences of body size, or of gait mechanics, were the only types of information routinely drawn from hominin footprints. More recently, a much broader range of questions has been asked with these data. New sites have been evaluated in new ways, and known sites revisited with new analytical techniques (summarized in Supporting Information: Table S1). In general, such analyses can be grouped by their relevance to anatomy and/or locomotion, behavior, and ecology.

4.1 | Hominin anatomy and locomotion

Given their resemblance to foot size, linear dimensions of footprints (e.g., their lengths and widths) can be used to generate estimates of stature or body mass.[70,71] Additionally, many hominin track surfaces preserve footprints created by multiple individuals. In these cases, the tracks are likely to represent individuals who were part of the same population, or who could have interacted with one another on a regular basis. Such group-level data are rare in the hominin fossil record and represent a particular strength of ichnological studies. By drawing body size estimates from the tracks on a single track surface,
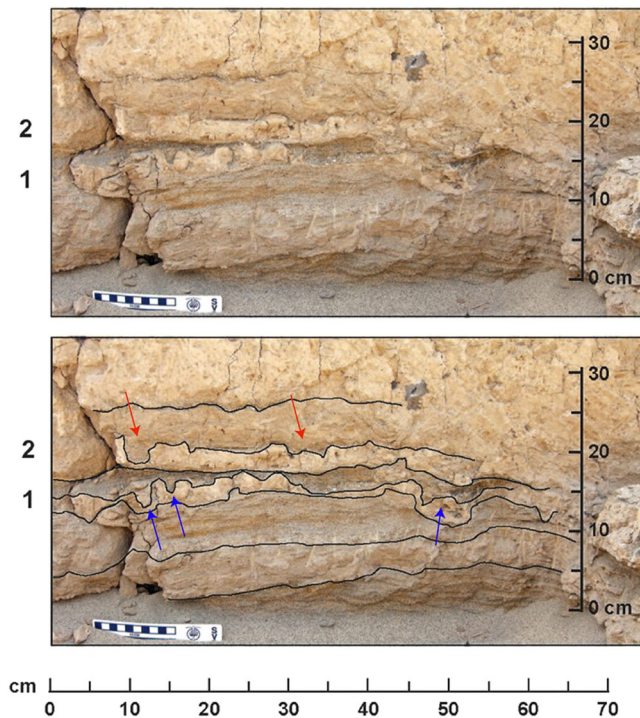
FIGURE 4 Cross-sectional view of footprint-bearing sedimentary layers in an excavated trench wall of East Turkana FwJj14E.[38] Bottom image replicates the top image but includes sketched annotations to aid visualization. This view shows typical irregularities in the bedding planes of two successive layers of fine-grained silt (light buff) that indicate tracks (Trackway Surfaces 1 and 2). Likely tracks are indicated by blue arrows for Surface 1 and red arrows for Surface 2. Black lines in bottom image show distinct sedimentary contacts and are discontinuous where these are not well defined on the trench wall. This ~30 cm sequence represents a vertical transition from active deposition of bedded and cross-bedded sands (0–10 cm, 10–15 cm on the vertical scale) to massive silts that were subjected to soil-forming processes on an exposed land surface (25–30 cm). Two distinct silt beds (1 and 2) within this transition show trampling on a wet but coherent substrate, followed by gentle infilling by sand (gray) that preserved the tracks. Such processes would be expected at a paleo-lake margin, where cycles of quiet water allowed the silt to accumulate (e.g., in a lagoon), alternating with higher energy sand deposition (e.g., gentle wave action). Daily wind cycles today result in similar fine-coarse sediment alternations along the shore of Lake Turkana. The absence of desiccation cracks in the silts shows that they were not dried out before final burial, which also is the case for most known track sites in East Turkana. These beds lack burrows or root traces, indicating rapid aggradation without plant colonization, in contrast to the overlying, pedogenically modified bed (25–30+ cm on the vertical scale), which is bioturbated and has root traces. Photo credit: Anna K. Behrensmeyer.

one can estimate population-level variables such as degree of sexual dimorphism.[72] While a single track surface may not provide a representative sample of a population, or sample that population randomly, it nevertheless affords a degree of association seldom achieved in the skeletal fossil record. This is critical for estimating dimorphism and inferring the population-level social dynamics for which such measures of body size are often considered a proxy.
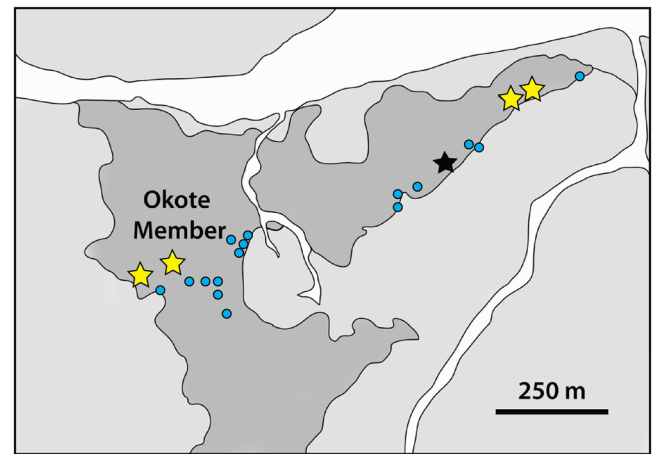

FIGURE 5 Schematic map of Okote Member deposits in Area 1A, near Ileret, Kenya. The black star represents site FwJj14E, the location of the initial hominin track discoveries. Gold stars represent hominin track sites discovered in 2013 and 2014, and blue circles represent track sites discovered in the same years, where only tracks of other animals have been excavated so far. For some locations, a dot or star represents multiple track surfaces,[38] as the space between them cannot be resolved at the scale of this map.

In one recent example, Masao et al.[31] used published regression equations that relate footprint area to body mass in a modern human sample[70] to estimate body mass from the Laetoli Sites S and G tracks. Based on these body mass estimates, the authors suggest that one of the Site S individuals was an adult male, that the four other known Laetoli trackmakers were adult females (S2 and G2) and/or juveniles (G1 and G3), and that the size variation observed among trackmakers implies a high level of sexual dimorphism in *Au. afarensis*.[31] A later analysis by Ruff et al.[71] used a different approach for body mass estimation, which takes into account estimated body shape (i.e., body mass index [BMI]) when predicting body mass from linear footprint dimensions. Because body shape influences volumetric proportions, accounting for this may allow for more accurate body mass estimates at least in those cases where BMI can be confidently estimated from skeletal fossils. With these methods, Ruff et al.[71] estimated that both individuals sampled at Site S (S1 and S2) and one from Site G (G2) are adult males, while the smaller tracks from Site G (G1 and G3) sample adult females. Their estimates of sexual dimorphism are still relatively high, and similar to skeleton-based estimates for *Au. afarensis*.[71] Sexual dimorphism in *H. erectus* has been estimated from the Ileret footprints by Villmoare et al.,[72] who compared the foot/footprint size dimorphism evident at Ileret and Laetoli to patterns observed in extant humans and nonhuman great apes. By directly comparing foot/footprint size dimorphism, these authors bypassed the complicated intermediate step of body mass estimation. Villmoare et al. found slightly higher dimorphism among the Ileret tracks than observed in modern humans but less than in the Laetoli tracks.[72] In this case, the Ileret tracks may offer a better population-level estimate than the combined *H. erectus* skeletal fossil record, which spans an extremely wide range of both time and space.[73]

In addition to foot dimensions (and body size by proxy), footprints record unique and invaluable data on hominin locomotion. Ever since the 1978 discovery of the Laetoli footprints, researchers have applied experimental methods to infer the manner of locomotion that they represent[15,20–22,24,26,74–76] (Supporting Information: Table S1). The most straightforward information that can be gleaned from trackways relates to the speed of movement when tracks were created. Experiments aimed at predicting traveling speeds from stride lengths were among the earliest analyses of the Laetoli trackways,[74,75,77] and similar experiments were used to estimate speed from trackways at Ileret.[70]

Beyond estimating traveling speed, experimentally-based studies demonstrate a variety of ways in which footprints provide more detailed information on locomotor kinematics.[21,22,76,78–83] However, for the sites discovered in the past 5 years, only a few have been analyzed in this way (Supporting Information: Table S1). McNutt and colleagues[48] used data from multiple experiments to compare the spatial arrangements and the 2-D and 3-D morphologies of the Laetoli Site A footprints to tracks made by modern humans, chimpanzees, and bears (once considered potentially responsible for these tracks[18]), all walking bipedally. Although only a small sample of Site A tracks is known and available for comparison (one to three), their analyses all supported a hominin attribution. Linear proportions of the Site A tracks are most similar to those of modern human and other hominin footprints, hallucial divergence (or lack thereof) is distinct from the patterns observed in chimpanzees, and stride width is extremely narrow and more human-like than chimpanzee- or bear-like.[48] At the same time, the narrow stride and the 3-D topography of the tracks suggests a type of bipedal locomotion not represented by the Laetoli Site G and S trackways. The Site A track morphology is quite different from that of modern humans and in some ways is more similar to chimpanzees.[48] The authors suggest that these footprints preserve evidence of bipedal locomotor diversity among Laetoli hominins, with one form more human-like and the second form more nonhuman ape-like, a pattern that has similarly been inferred from foot skeletal fossils of Pliocene hominins.[84]

Experimental approaches have likewise been applied to investigate locomotor patterns evidenced by two other track assemblages. Soon after the announcement of the discovery of Laetoli Site S, Raichlen, and Gordon[85] used experimentally collected data to show that these hominin tracks imply a similar manner of locomotion to the relatively human-like pattern they and other co-authors had previously inferred from Site G.[21] Hatala and colleagues[30] designed experiments to investigate the locomotor patterns preserved by multiple 1.5 Ma trackways from Ileret, Kenya, and showed that they represent a generally modern human-like form of bipedalism in *H. erectus*. The other sites reviewed here have not yet been investigated in this way, perhaps due to their more recent ages—based on postcranial skeletal fossils from similar time periods, it is likely that the locomotor patterns represented at these sites would match those of modern humans. However, tracks record unique information on complete foot anatomy and movements, and even at more recent sites they can offer important insights that complement and extend those from skeletal fossils.

4.2 | Hominin behavior

Track surfaces record living individuals who were moving through the same space, at or around the same time. Given their spatiotemporal association, track sites offer exceptional opportunities to infer hominin behavior and social structure from the fossil record, in ways that are difficult or impossible using any other form of paleontological data. The Laetoli Site G footprints immediately spurred hypotheses regarding the age and sex composition of the group of hominins that created them.[86] The same has been true at more recently discovered sites, where researchers have applied a wide variety of methods to make such inferences (Supporting Information: Table S1). These methods are all based on relationships between footprint size and body size, and how body size relates to age and/or sex in the species assumed to have made the footprints.

In one attempt at estimating the distribution of ages represented on a track surface, Duveau and colleagues first predicted stature from the lengths of tracks within the Le Rozel assemblage and then used a relationship between stature and age derived from Neanderthal skeletal remains to estimate the age of each trackmaker.[41] This led them to conclude that the site recorded a social group consisting primarily of children and adolescents. Recent work by Ruff et al.,[71] which revised body mass estimates by taking into account BMI (as described in Section 4.1), suggested that this group included more adults than initially proposed and highlighted the difficulties in differentiating small adult from adolescent body sizes. Revised estimates from Ruff et al.[71] may be more accurate, assuming that they are based on an accurate estimate of BMI derived from Neanderthal skeletal remains. However, Ruff et al.[71] still agreed with Duveau et al.[41] that the Le Rozel sample was likely derived from a mixed-age Neanderthal group. Elsewhere, Mayoral and colleagues used an approach mirroring that applied at Le Rozel to infer a mixed-age Neanderthal group represented on the track surface at Matalascañas, Spain.[51] Growth curves derived from modern humans have likewise been used to estimate the ages of the Pleistocene humans who created tracks at White Sands.[55,56] At these sites as well, it may be extremely difficult to definitively attribute intermediate-sized tracks because they could represent either smaller adults or larger adolescents. There is also the issue of choosing an appropriate and well-defined growth curve upon which to base age estimates. A growth curve derived from modern human populations living in industrialized contexts and wearing shoes throughout their lives may not offer an appropriate direct comparison for human tracks that are tens to hundreds of thousands of years old. Analyses of the White Sands tracks include discussion of this issue,[55] an important limitation to keep in mind when interpreting the evidence at this and other human track sites.

Estimating sex from fossil tracks is even more difficult than estimating age because it is unclear whether or how track morphology may differ across sexes. At Ileret, Kenya, Hatala and colleagues[30] estimated the body sizes of the individuals who created the tracks, and then applied the mean method[87] to estimate the sex of the various trackmakers from their estimated body sizes. Through this analysis they inferred that a multi-male, mixed-sex group was represented by tracks on the most extensive of the 1.5 Ma track surfaces. Hatala and colleagues

took a different approach to their analysis of the Engare Sero, Tanzania footprints, using a resampling-based analysis of modern human foot size distributions to estimate the probabilities that each trackway was produced by an adult or juvenile male or female (also accounting for differences between foot and footprint size).[43] They inferred that the Engare Sero tracks most likely represented a majority adult female group, but their probabilistic estimates also reflect the uncertainty associated with assigning tracks to a particular age/sex group based on size. We view the approach used in this study as most appropriate among currently available methods, as it acknowledges the uncertainty associated with age/sex attribution and avoids the potential for compounding errors through the additional step of estimating body size from track length. However, there is certainly still room for continued improvement upon this approach.

While estimates of age and sex can inform inferences about group structure, certain track surfaces also offer evidence of collective group behavior (Supporting Information: Table S1). The 0.7 Ma tracks from Melka Kunture, Ethiopia, have been attributed to a mixed-age group, and the co-occurrence of lithics and cut-marked faunal remains motivated Altamura and colleagues to infer that the hominins made stone tools and butchered animals on this same land surface.[36] The co-occurrence of faunal remains and behavioral traces (tracks and lithics) is rare and exciting, but this interpretation is not certain. The authors caution that the only definitive hominin track is one they estimate was generated by an adult.[36] The inferred children's tracks are relatively amorphous, and none retain the complete set of track features observed in the more definitive example (e.g., toe or heel impressions are absent, or the outline shape is unusually distorted).

Hatala and colleagues observed at Engare Sero that a large portion of trackways were organized in a nonoverlapping and subparallel fashion, and appeared to have been created at similar walking speeds, suggesting that they represent a group that traveled together.[43] The most probable age/sex distribution estimated for this group (see above) consisted of mostly adult females. The authors noted that this is consistent with a compositional pattern observed in modern foraging groups when predominantly adult female groups travel to acquire food, and they offered this as one hypothesis for the behavior recorded on the track surface.[43] Other forms of individual or paired behaviors are inferred based on the spatial arrangements of tracks. On one of the White Sands, New Mexico, track surfaces, human and sloth trackways are overlapping in a way that the authors interpret as direct evidence of stalking and hunting of giant ground sloths by Pleistocene humans.[42] At another, they infer that an "out-and-back" trackway was produced by an adult who was carrying the child in at least one of the two directions.[55]

While hypotheses of collective behaviors are fascinating and almost impossible to address using skeletal fossils or archaeological evidence on their own, they are among the most uncertain of inferences gleaned from track sites. An enormous number of questions remain unanswered about how behaviors such as food acquisition, hunting, or carrying can be inferred from fossil footprints. Whether the Melka Kunture tracks provide evidence of collaborative butchery hinges upon the contemporaneity of tracks, lithics, and

butchered faunal remains, as well as the age/sex attributions of the tracks.[36] While contemporaneity is plausible, it is impossible to determine conclusively. The food acquisition hypothesis at Engare Sero is based on group structure and collective motion,[43] but human groups are motivated to walk together in a wide variety of situations. In reference to the White Sands tracks, hunting behavior is extremely difficult to parse from other types of interspecific encounters (e.g., an unexpected run-in), or from noncontemporaneous passage across the same track surface. Evidence for carrying behaviors can be clear in specific contexts, such as where children's tracks exist partway along the length of an adult trackway (as if a child was set down temporarily).[55] However, this behavior would be difficult to conclude if the child were never put down, or if the carried item were different. Gait asymmetries and other evidence might manifest in fossil footprints, but attributing the resulting perturbations to a specific behavior would require much better experimental data on such scenarios, as well as on the normal range of variation in footprint morphologies during steady-state walking. The interpretations cited above all present plausible hypotheses, but are less straightforward than the inferences related to anatomy and locomotion.

Zhang and colleagues recently published an even more contentious hypothesis that traces preserved near ancient hot springs at Quesang in Tibet represent the world's oldest known evidence of parietal art.[49] The interpretation of artistic behavior is based on an arrangement of hand impressions in travertine mud, which clearly represent nonlocomotor behavior. At present, it is difficult to confidently distinguish artistic expression from other circumstances in which one might place their hand on the ground surface (e.g., lowering or raising oneself to or from the ground, or placing a hand down while entering or exiting a hot spring). The hypothesis of artistic behavior is intriguing but, in our view, this remains an open question worthy of continued investigation.

One of the most fascinating aspects of hominin footprints is that they stimulate our imaginations in ways that other fossils might not. The clarity and relatability of a track recording a hominin moving through a specific place at a specific time naturally causes us to wonder who might have created the tracks and what they might have been doing. While tracks do contain unique and exciting behavioral information not found in fossil data, it is important to moderate our tendency to identify with the ancient track-makers or assume we have all the information needed to infer complex behaviors. Analytical methods for discerning various types of behaviors are still in their infancy. It is critical that behavioral interpretations be presented as testable hypotheses, which can then be revisited as analytical methods are developed for evaluating the kinds of behavioral data that might be recorded on track surfaces.

4.3 | Hominin ecology

Track assemblages can contribute in unique and important ways to understanding hominin ecology because they offer a degree of spatiotemporal resolution that is unmatched by skeletal fossils or

other data from the same geological contexts. Laporte and Behrensmeyer[59] and Cohen and colleagues[60,61] conducted experimental work to study track taphonomy in lake margin environments of eastern Africa and found that rapid burial, perhaps on the scale of hours to days, is necessary for high-resolution track surfaces to become a part of the geological record. This result has been supported more recently by experiments that accompanied analyses of track assemblages from Ileret and Engare Sero[40,62] (Figure 6). These confirmed that a single track surface is likely to record animals who lived at the same time and in immediate proximity to each other. When track surfaces include hominins and other animals, they thus offer direct, short-term data on the composition of the animal community to which those hominins belonged (Supporting Information: Table S1).

In many cases, the snapshots of animal communities provided by track surfaces can be surprising. For example, they may reveal the presence of taxa whose skeletal fossils are nonexistent or rare within the same deposits. Among the 1.5 Ma track sites at Ileret, Kenya, the tracks of birds are extremely well-documented, yet their bones are rarely recorded in the fossil record of the same time and place[40] due to susceptibility to destruction by taphonomic processes. The 0.12 Ma track surfaces from Alathar, Saudia Arabia are remarkable for preserving evidence of hominin presence in the absence of their skeletal fossils. These sites also included the tracks of elephants, which extended the last appearance date of elephants in this region by 300 thousand years.[35] Many of the other sites reviewed here preserve remarkable records of the mammalian biodiversity surrounding hominins—for example, sites along the Cape south coast document extensive track assemblages of giraffes, crocodiles, and
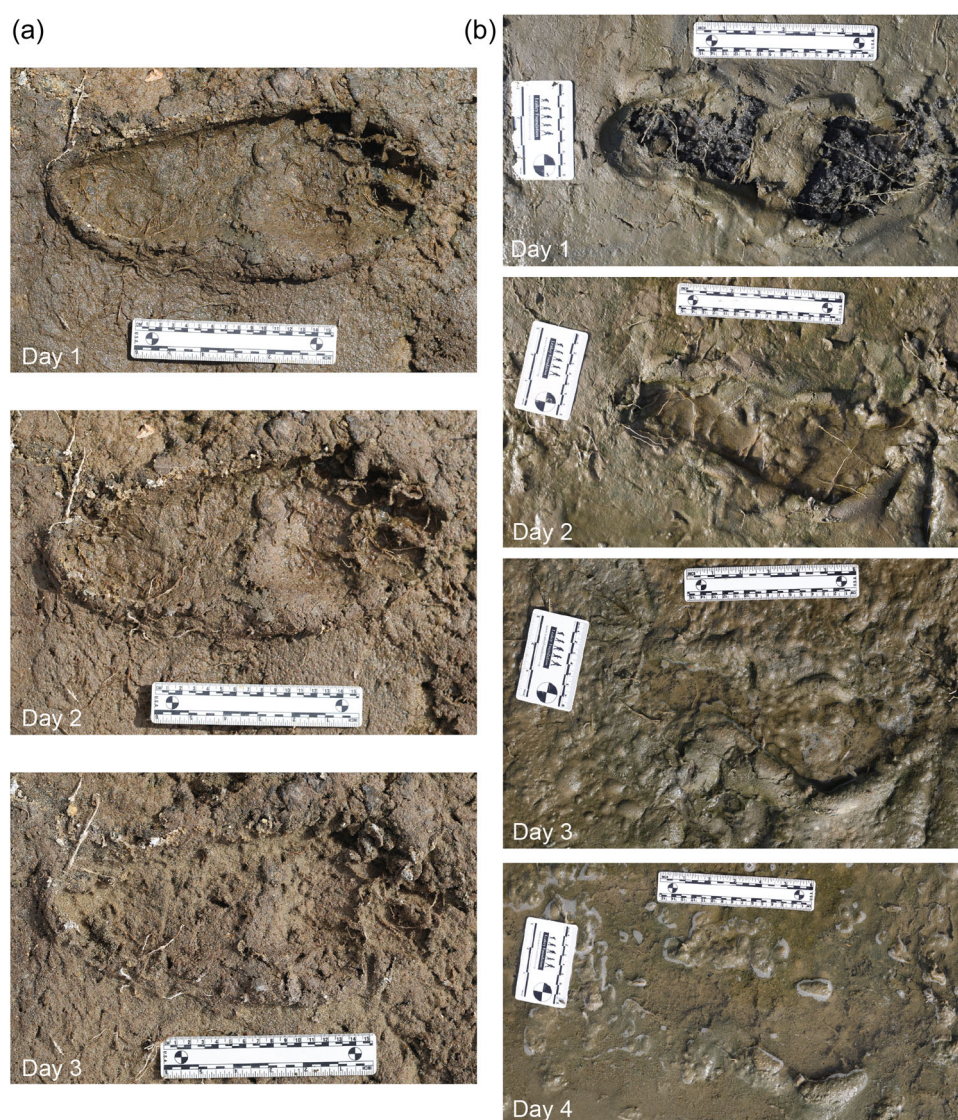

FIGURE 6 Examples from recent footprint taphonomy experiments conducted by the authors on the shore of Lake Turkana. Agents such as over-printing and wind scouring (a) or movement of transient shorelines (b) lead to the degradation of human tracks in lake margin environments within a few days. Large assemblages of high-resolution tracks from hominins and other animals that were formed along similar water margins are most likely to have been created and buried within very short time intervals, that is, days or even hours. Scale bars are 15 cm in (a), and 15 and 8 cm in (b). Photo credit: Kevin G. Hatala.

birds,[69] and the track surface at Matalascañas records a wide variety of differently sized and aged elephant tracks.[88]

In the right depositional contexts, both skeletal fossils and track assemblages can be well-documented within the same geological sequence. Such cases provide opportunities to directly compare the faunal records associated with both types of fossil data and build a more comprehensive picture of local paleoenvironments. Roach and colleagues conducted such work in their analyses of 1.5 Ma track assemblages from Ileret.[39,40] They found that while hominin fossils are uncommon in the skeletal record from around 1.5 Ma, they are surprisingly abundant among the ichnological records from the same time and place. There are several possible explanations for this pattern. Taphonomic processes operate differently on skeletal remains versus trackways, contributing to observed disparities in taxa represented (as in the example of bird tracks vs. bird skeletal fossils). It is also plausible, however, that hominins (presumably *H. erectus*), spent considerable amounts of time in the lake margin environments where their tracks were recorded. Roach et al.[39,40] proposed that these may have been important locations for accessing aquatic foods, or for hunting water-dependent mammals, since archaeological and stable isotope evidence point to *H. erectus* engaging in these behaviors.[89,90] A related hypothesis is that the shoreline environment simply provided a relatively unobstructed corridor for walking and foraging in proximity to water.

While the sites described above offer fascinating insights into the environments and animal communities directly associated with fossil hominins, the potential for trace fossils to inform paleoenvironmental reconstructions remains underexplored. In addition to the studies reviewed here, Musiba and colleagues[91] have recently focused on the analysis and conservation of nonhominin tracks at Laetoli, Tanzania, realizing their untapped potential for providing paleoenvironmental data that are much less susceptible to the space- and time-averaging that characterize other paleoecological proxies. Track assemblages may be the only form of fossil evidence that can reliably indicate true sympatry, yet very few sites have been analyzed with this in mind.

5 | WHAT MORE CAN FOSSIL FOOTPRINTS TELL US ABOUT HUMAN EVOLUTION?

In each of the areas reviewed above, recent work has expanded the breadth and depth of insights that can be gained from the rapidly expanding sample of tracks from the human fossil record. Teams of researchers are raising new questions and developing new methods as they work to glean more information from these data. Most of these techniques are not widely used in paleoanthropology, however, and many are ripe for future research. Here, we identify areas of investigation with strong potential for advances in the coming years.

5.1 | Hominin anatomy and locomotion

Understanding how track morphology is generated from complex interactions between foot anatomy, foot motion, and the deformable substrate is key to resolving the longstanding debates over trackmakers' anatomies and gaits. These interactions are notoriously challenging to unravel because interactions between feet and substrates are very difficult to observe. However, some recent approaches have overcome this obstacle. Falkingham and Gatesy[92] used biplanar X-ray to observe track formation in birds, and they derived particle simulations that accurately represented the 3-D dynamics of footprint creation. These techniques are the first to permit direct study of the mechanical process of track formation, and they opened doors for new analyses aimed at interpreting dinosaur tracks.[93] Hatala and these colleagues[82,83] recently extended biplanar X-ray, 3-D animation, and particle simulation methods for the study of track formation by humans. By using these methods to observe and model the mechanical interactions between foot and substrate, one can then "reverse-engineer" the patterns of foot anatomy and foot motion recorded in fossil hominin tracks. Methods for interpreting functional patterns from skeletal fossils are for the most part rooted in inter-specific comparative morphology of articular surfaces or trabecular bone structure. This means that although they may be more useful for decoding evolutionary patterns in skeletal morphology, the locomotor signals that can be gleaned from them are usually coarser and more generalized. Fossil tracks are instantaneous motion capture events, so with the right tools for interpreting anatomical and kinematic signals within them, these data offer exciting opportunities for directly testing hypotheses about hominin locomotion. Recent studies have been able to isolate specific kinematic signals and reconstruct foot motion patterns from hominin track morphologies.[94] There exists strong potential to decode additional anatomical and kinematic records that are preserved in hominin tracks and that complement inferences based on skeletal fossils.

While these techniques can reconstruct the pattern of locomotion that produced a set of tracks, we also lack critical knowledge about how locomotion varies across different substrates. Studies have shown that humans use different lower limb movement patterns, which incur greater energetic costs, to walk through sand.[78,95] Yet compared with our rich knowledge of how humans walk and run on solid surfaces, very little is known about the biomechanics of humans traversing deformable substrates. Few published biomechanical studies have examined human locomotion in lake-margin muds, or in other substrates in which fossil tracks are frequently preserved.[81] It is important to understand how humans walk on such surfaces but also how patterns observed on soft mud relate to locomotion on hard surfaces and rigid instruments, given that most of our knowledge of human biomechanics is rooted in the latter. Such an understanding is important when considering whether the motion patterns inferred from trackways are likely to represent "typical" or "atypical" motions of the individuals who created them, and for relating locomotor patterns observed in the hominin fossil record to the gait patterns used by humans living today.

5.2 | Hominin behavior

Methods for deriving behavioral inferences from track assemblages are continually emerging. At sites reviewed in this paper, researchers

have inferred patterns of group movement,[43] collaboration,[36] predator-prey interactions,[42] and even artistic behavior[49] (Supporting Information: Table S1). Although the interpretations derived from these sites all serve as reasonable hypotheses, they are based on comparatively indirect methods of inference and are subject to numerous alternate explanations.

The first three of these behavioral interpretations—group movement, collaboration, and predator–prey interactions—imply a level of synchronicity that track surfaces cannot necessarily resolve, despite their exceptional temporal resolution. Track-making events (and tool-making or -using events) recorded on the same surface may have occurred within hours or days of each other,[40,60–62] as opposed to at the same instant. This subtle difference in timing is miniscule on a geological scale, but still critical to certain behavioral interpretations.

In cases of inferring hominin group movement, or collaborative group behaviors, some additional pieces of evidence—such as trackway orientations[43] or artifacts embedded in tracks[36]—may make it more likely that such events occurred at the same time, but uncertainty remains. Rather than relying purely on depositional association, one could seek better understanding of how behavioral patterns manifest on track surfaces. Very few experimental data exist on how human group behavior may be recorded in trackways alone. Wagnild and Wall-Scheffler[96] showed that mixed-sex pairs match their walking speeds in a way that leads to an energetically suboptimal gait for individuals who differ from their partners in body size. These experimental results played a critical role in the analyses of Hatala et al.[43] at Engare Sero, where trackways produced by large (presumed male) individuals displayed shorter relative stride lengths, with estimated speeds matching those of the smaller (presumed female) individuals that made up the majority of the group. Much more experimental work is necessary to provide additional tests for hypotheses about how group behaviors may be recorded by assemblages of fossil human tracks. For example, experiments could be designed to document tracks formed while engaging in tool-making and butchery activities in soft mud, and to contrast these with tracks formed by randomized human movement through an area where tools and butchered fauna are already lying upon the ground. Alternatively, observational studies could be conducted to document tracks from modern human groups performing a variety of activities in track-forming substrates. This would allow the growth of data sets that could provide stronger associations between patterns in track assemblages and specific activities. While these experiments and observational methods would require navigating an extremely broad parameter space, they could improve our ability to test for specific behavioral patterns that may be recorded in the fossil record.

At the same time, it would be valuable to acquire data on how various interspecific encounters are likely to be represented on track surfaces. Bustos et al.[42] quantified the tortuosity, or curvature, of sloth trackways and used these data (along with the observed proximity of human tracks) to hypothesize that a track site at White Sands records a prehistoric hunt. The hypothesis is well-reasoned, but again would be strengthened with direct experimental or observational evidence for how interspecific interactions are reflected on track surfaces. In multiple examples, predator-prey interactions have proven difficult to infer from trackways alone.[97] And while there is a growing body of experimental research on track formation,[98] few if any experimental studies have focused on tracks produced during interspecific encounters.

5.3 | Hominin ecology

While hominin tracks have clear potential to expand our understanding of their maker's anatomy, locomotion, and behavior, such tracks are but one part of a broad and diverse ichnological record. Systematic survey of track assemblages near Ileret, Kenya, in Area 1A, found hominin footprints represented only 4% of the identifiable tracks discovered during random landscape survey.[40] We believe that the remaining 96% of tracks offers a remarkable opportunity to expand understandings of the paleoenvironments that hominins occupied. Using track assemblages to reconstruct past animal communities has its own challenges, however, which we have just begun to appreciate.

The limited depositional contexts required for the formation and preservation of track surfaces mean that the recorded track assemblages represent members of the animal community moving through a fixed location during a time window of hours to perhaps a couple of weeks. Compared with skeletal fossil assemblages, stable isotopes, or other paleoenvironmental proxies that sample geological units representing thousands of years (or more) and broad swaths of land surface, this is remarkable precision (Figure 7). Track attribution beyond broad taxonomic categories such as order/family is often difficult to achieve, however, particularly in speciose groups such as artiodactyls. Attribution to size class categories can refine faunal analyses, but not to the genus or species level that a well-preserved dentition or horn core can provide. Further methodological developments such as the use of machine learning algorithms for non-hominin track identification likely could improve attribution. Otherwise, it will be necessary to develop appropriate analyses to accommodate coarse taxonomic resolution.[99]

Track assemblages preserve ample evidence of birds and other small creatures, suggesting that size-biased preservation is a less serious issue in the ichnological record than in the skeletal record. Certain substrates may be more likely to capture tracks of larger or smaller animals,[100] but tracks of widely different sizes are often preserved on single track surfaces. Other unique modes of preservation bias also exist in track assemblages, however. In the Ileret Area 1A track assemblage, the presence of bovids on a track surface is associated with reduced community diversity and evenness.[39] This has been interpreted as an artifact of situations where bovid trampling wiped out other faunal traces. More analogue studies in modern environments are needed to identify such biases and tease apart how animal communities are represented, or not, by track assemblages. Such studies would also provide valuable insight into current unknowns about track assemblages, such as the weather
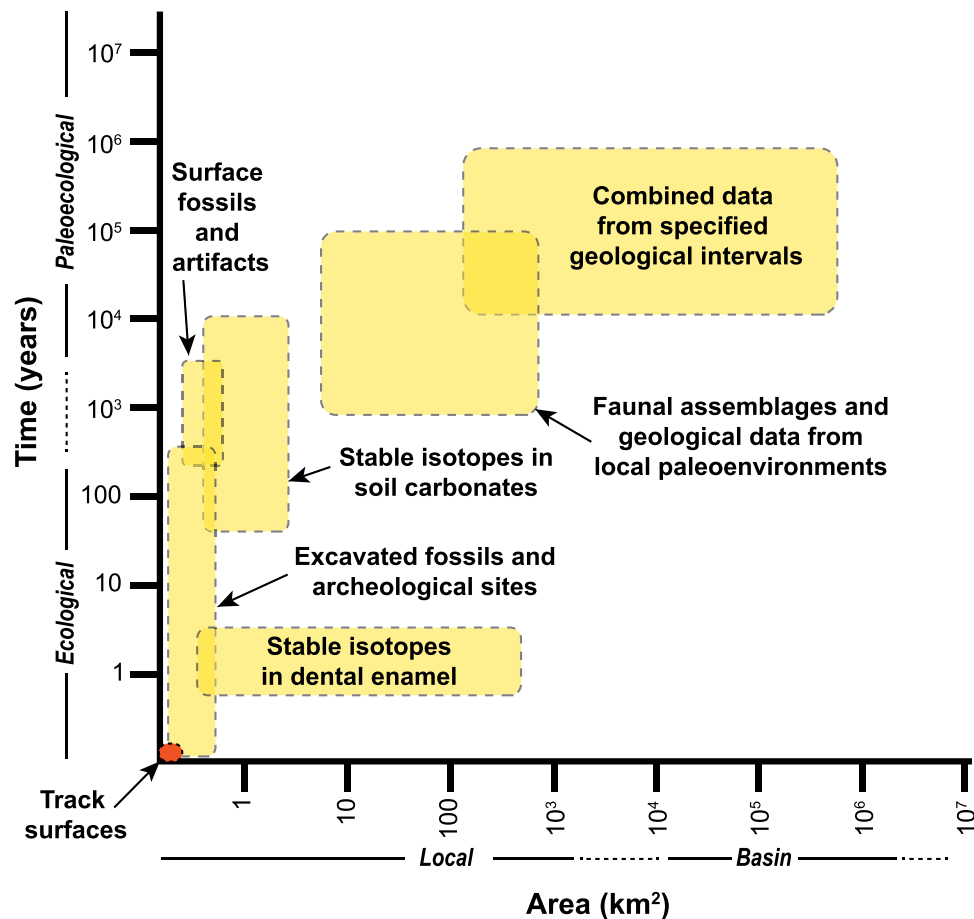
FIGURE 7   Track surfaces record data at finer spatial and temporal resolution than nearly all other forms of fossil evidence. Here, their resolution is compared with the estimated resolutions of other common proxies relevant to paleoenvironmental reconstructions. Track surfaces fall at the intersection of the *X*- and *Y*-axes (log scales), representing the smallest sampling window in both space and time.

conditions required for track preservation, how land use patterns relate to the geography of freshwater sources (e.g., ponds, springs, lakes) or forage locations, and how seasonal land use and resource availability are represented in track assemblages. With such data in hand, future studies could examine hominin land use patterns and ecology in greater detail, moving beyond the broad associations that typify current approaches.

While some limitations of the ichnological record—such as the need for water and unconsolidated, fine-grained sediments lacking vegetation cover—will always affect where preservable tracks are formed, the diversity of contexts reported in the studies reviewed here gives us confidence that the challenges of studying track assemblages pale in comparison to their promise. In our view, significant progress towards understanding what hominins were doing in their environments will occur when we begin to integrate currently disparate lines of evidence. This involves objective evaluation of the strengths and weaknesses of each data set, be it tracks, skeletal fossils, isotopes or archaeology. Each data type has its own spatial, temporal and taxonomic scale, which can be leveraged to create prior expectations and hypotheses for statistical interrogation of the other data types. For example, continent-wide hypotheses regarding hominin avoidance of large carnivores based on the skeletal

fossil record[101] can be examined locally using track assemblages. If such patterns hold across scales, then behavioral inferences will be strengthened and refined. If not, then issues of sampling or bias must be further examined. At a regional scale, hominin paleoecology often represents temporal and spatial averaging that results in reconstructions of "mixed" or "mosaic" environments that explain patterns in the data but are not particularly informative. The effects of averaging over time and space make it impossible to distinguish (1) whether past environments changed at rates beyond the resolving power of the paleontological or geological record or (2) whether these environments were actually heterogenous mosaics at any given point in time. Integrative studies of paleoenvironment that account for the strengths and weaknesses of all proxies,[99] accompanied by increased research in modern analogues, represent a promising way forward.

6 | CONCLUSIONS

Hominin footprints are quickly becoming an important source of data in the human fossil record. In a field that squeezes as much as it can from small samples of fossils, these new data offer tremendous potential for resolving long-standing questions and for addressing

entirely novel ones. Studies highlighted here have underscored the potential for fossil footprints to record snapshots of anatomy, locomotion, behavior, and ecology throughout human evolution. Yet in each of these areas, methods for analyzing fossil footprints are still emerging, and there are many exciting opportunities for expanding knowledge of how fossil tracks can address evolutionary, ecological, and behavioral questions. With increasing realization among the paleoanthropological community that such data are not exceptionally "rare" in the geological record, we look forward to discoveries that will be made in the coming years, and we are optimistic about the insights new footprint data will provide for a fuller picture of human evolutionary history.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.