Step Into History: The Creation and Critique of an Anatomical Fidelity Rubric for Assessing Quality in Individual Hominin Footprints

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Dedication

This thesis is dedicated to my grandparents, Gregory “Greg” Bunner and Grandma Linda Bunner, to whom I owe everything for my love of curiosity of the world around me, both in prehistory and in the present.

Grandma, I love and miss you dearly (July 11, 1948 – October 17, 2019).

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Grandpa "**Greg**" **Bunner**

Jose; **Conrad** and the gang

My three beautiful cats: **Paperclip** (F, née July 2017, Calico); **Mouse** (F, née July 2017, sister to Paperclip, Calico); **Cayde** (M, né August 2023, Tabby)

Abstract of Thesis

Step Into History: The Creation and Critique of an Anatomical Fidelity Rubric for Assessing Quality in Individual Hominin Footprints

Fossilized hominin footprints have been discovered on every continent except for Antarctica, from the oldest site at Laetoli, Tanzania (3.66Ma), to sites only a few hundred years old in the western hemisphere. **However, not enough research has been done on how individual hominin footprint fidelity (how much the footprint accurately reflects soft-tissue anatomy) is gauged in the interpretation of footprints**. Few tetrapod footprint fidelity models exist; Belvedere and Farlow (2018)'s revised scheme for ancient tetrapod footprint preservation quality cannot be directly translated for usage as human footprints only score a 2.2 out of 3 on average regardless of how well preserved they are, which per Belvedere and Farlow (2018)'s model, is too low to be considered as samples and for shape analyses**.**

In this thesis, I evaluate whether sedimentological variables correlate with anatomical fidelity. I suggest 'grading' hominin footprints using a modified morphological anatomical fidelity rubric (where S is best, followed by "A", "B", "C" and terminated at an "F"). In this thesis, I test the hypothesis that sedimentological variables predict anatomical fidelity scores by applying this novel rubric to published footprints from 19 different sites across three continents (Africa, North America, and Europe). A Cumulative Link Mixed (CLM) model and a Proportional Odds Logistic Regression (POLR) model were used to test for a relationship between substrate type and fidelity score and visualized using a raster plot. In these results, we expected to find high-fidelity scores clustered in fine-grained sand and tuff substrates, as suggested in the literature.

Results show that there is no straightforward predictable relationship between simple substrate type and anatomical fidelity score.

Hominin track fidelity should be reassessed and used in future interdisciplinary studies of the human tracks as revised anatomical fidelity of individual footprints may reveal a more representative and behaviorally realistic hominin footprint record, even if they depict deformational features such as drag marks or incomplete anatomical features. **The lack of a rigorous system for grading individual hominin footprints prohibits identification of vulnerable sites which may have unique locomotor behavior, such as running, formed by substrate differences, kinematics, and distortion by natural and anthropogenic causes seen throughout footprint quality in research**. Finally, this study encourages the continuation of digital preservation methods (*e.g.* 3D scanning, photogrammetry, LiDAR) of footprints and associated trackways, even if analyses do not occur for each one. As digital storage becomes more reliable and cheaper, a higher number of fossil footprints will be captured digitally.

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Chapter 1: Introduction to Hominin Footprints

Fossilized hominin footprints have been found on every continent except Antarctica and span from the oldest known site at Laetoli, Tanzania (~3.66 Ma) (McNutt *et al.,* 2021), to sites in the western hemisphere that are only a few hundred years old. Footprints have been widely used to study locomotion (gait, speed, body size), infer social behavior (group composition, probable direction), and anatomy (kinematics, lower limb anatomical structure, soft tissue impressions) in paleontological and paleoanthropological studies (Anna K. Behrensmeyer & Leo Laporte, 1981; Ashton *et al.,* 2014; Bennett *et al.,* 2013; Bustos *et al.,* 2018; Díaz-Martínez *et al.,* 2024; Dingwall *et al.,* 2013; Hatala *et al.,* 2023; Lockley *et al.,* 2008; McNutt *et al.,* 2021; Tuttle, 2008; Urban *et al.,* 2019). Footprints can only be created and preserved in a cohesive substrate (Gatesy & Falkingham, 2017) such as some fine-grained sediments. In order for footprints to retain sufficient anatomical detail to be identified as hominin, the substrate that is disrupted by plantar pressure must meet ideal substrate conditions – too soft of a substrate distorts fidelity, and too hard of a substrate will not leave an impression (Farlow, 2018). An ideal substrate for creating footprints, however, does not mean that the human footprints will undergo sedimentary lithification (Gatesy & Falkingham, 2017) as every distortion caused by geological events such as erosion, landscape changes, water level fluctuations, and bioturbation has the potential to erase footprints before they are discovered and digitized for archival, cultural heritage, or research purposes.

Despite technological advancements in digitizing and preserving hominin footprint sites (Hatala *et al.,* 2020), **a formal and objective system has yet to be created**

to grade and evaluate anatomical footprint fidelity in hominins. Anatomical fidelity refers to how much a footprint reflects the anatomical soft tissue expected of the original trackmaker. In this thesis, I highlight that while we can never see the true anatomy of the fossil footprint maker, an objective system for grading anatomical fidelity can aide researchers in eliminating a major source of confounding footprint variation, namely the inconsistencies caused by plantar pressure distribution and sediment displacement. This variation of footprint morphology is supported by both the works of Bennett *et al.,* (2014), Farlow (2018), and Marty *et al.,* (2009). With the exception of extant human footprint studies, there naturally exists an impossibility of knowing who the original trackmaker is at hominin footprint sites. This introduces a level of ambiguity to studies, especially where multiple species of hominins have been recorded (Bennett *et al.,* 2014; Hatala *et al.,* 2024) and therefore, it is important to investigate how different substrate compositions can change the morphological features fossilized footprints regardless of dimensional measurements (even if this information exists), such as length, size, width, etc.

The need for anatomical fidelity metrics for modern human experimental footprints

The creation of a qualitative rubric for objectively quantifying footprint 'quality' is not a new concept (e.g. Falkingham *et al.,* 2014). Substrate plays an undeniable role in the preservation of a footprint, and several authors (Agnew & Demas, 2015.; Marty *et al.,* 2009.; Díaz-Martínez *et al.,* 2024; Falkingham *et al.,* 2014, 2020; Farlow, 2018; Gatesy & Falkingham, 2017; Marchetti *et al.,* 2019; McLarty *et al.,* 2025) have attempted to quantify how much different hydration levels affects sediment cohesion to determine the

extent of morphological variability in a footprint while retaining enough morphological detail to still be identified as a footprint. Marchetti *et al.* (2019) did an experimental study (modified after Marty *et al.,* 2009) to investigate the morphological variability of extant human footprints caused by water over-saturation over a seven-day period after impressing prints into thick microbial mats (Figure 1). Microbial mats are dense, thick, layers of microorganisms living as complex ecosystems, primarily bacteria and archaea that form on surfaces, often near sediment-water interfaces (Marty *et al.,* 2009) such as the surface layer of footprints.

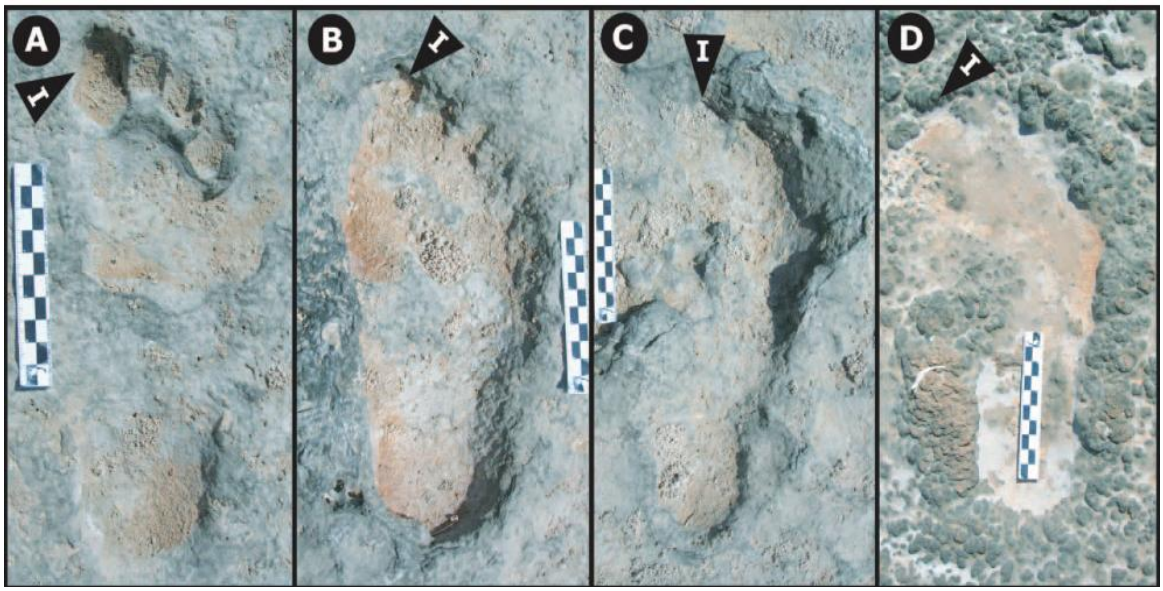


Figure 1 Morphology modification of experimental footprints exposed to and consolidated by the (continued) growth of microbial mats. Adapted from Marty et al., (2009)

The results were highly interesting; each footprint reflected a slightly different morphological modification, notably in the deeper impressions where the microbial mat had overgrowth due to overhydration. However, discussions of these morphological variations are most commonly found in paleontological literature for non-hominin

footprints; Belvedere and Farlow (2016, 2018a) did a series of experiments on extant emu footprints (their footprints are the closest living analog for bipedal therapods) and found that in a hydrated fine-grained substrate there is a considerable variation amongst the emu prints (Belvedere *et al.,* 2016).

Differences between hominin and non-hominin footprints

The inclusion of these morphological variability and substrate hydration studies cannot be accurately translated for usage at hominin footprint sites due to the lack of direct comparison between the pedal anatomy of theropods (Bennett, 2014) and humans. Marked differences in human vs. non-human footprints frequently mentioned in the literature are the existence of a medial-lateral arch (MLA), evidence of 'heel-strike' in the posterior of the track, and lack of a drag mark or distal isolated impressions caused by claws during the terminal swing phase (toe off) (see McNutt *et al.,* 2021; Agnew & Demas, 1998; Ashley, 2003; Lockley & Pemberton, 1992; Morse *et al.,* 2010, 2013; Wiseman & De Groote, 2018).

Additionally, human bipedalism records pronounced heel-first loading patterns ("heel strike") and midfoot mechanics described as the midtarsal-break (DeSilva, 2020). During heel strike the calcaneus (the heel bone, largest and most proximal of all seven tarsals in the foot) contacts the ground first, and the subsequent rapid transfer of body weight displaces sediment around it to leave a pronounced heel impression in many hominin tracks when substrate conditions permit (Buatois, 2011; Hatala *et al.,* 2016). The heel imprint is frequently one of the most recognizable morphological traits of an individual human footprint; its presence and clarity can be treated as a practical indicator

of anatomical fidelity and overall footprint interpretability. By comparison, non-avian theropod trackways often show limited evidence of the equivalent 'heel-strike' loading behavior. For example, footprint pressure reconstructions from late Jurassic (161.5 – 145 Ma) bipedal track sets suggest relatively even pressure distribution across the foot, reducing the likelihood of a discrete, posterior heel impression (Marty *et al.,* 2018).

Midfoot mechanics are also relevant to footprint fidelity. As load (synonymous with weight transfer) progresses through the proximal ("heel") to the distal ("hallux") end of the foot, the forces of shifting bodyweight from the tarsals to the metatarsals concentrate towards push-off (DeSilva, 2020). The amount of morphological and anatomical detail that is visible in the midfoot human footprints varies greatly because of sediment settling, as well as erosion activity (DeSilva, 2020; Hatala *et al.,* 2016). These anatomical details are more easily distorted than their deeper heel impression counterparts or lost entirely to the substrate matrix (DeSilva *et al.,* 2020). These morphological features still exist--as the midfoot break is naturally present during human bipedal locomotion (DeSilva, 2010) --but cannot be reliable landmarks due to highly variable fossilization potential.

Lastly, the hallux, or big toe, is easily recognizable in many hominin footprints due to being the final anatomical feature to imprint into a cohesive substrate. As will be discussed, the hallux is important to human bipedalism and human tracks as it not only provides balance during locomotion but also serves as demarcation for total length of a footprint. The hallux is also often the deepest impression among the digits (DeSilva *et al.,* 2020; McNutt *et al.,* 2021).

Figure 2 Adapted from Farlow (2018). Possible ornithopod footprints

Significance of Studying Human Locomotion Through Footprints

Body fossils attributed to the genus *Homo* have been found in Africa and Europe since the late 1800s (Wood & Harrison, 2011). Footprints are underrepresented in the paleoanthropology fossil record due to the complex sedimentological requirements of fossilization necessary to preserve and protect them, compared to permineralized bone

which protects body (including teeth) fossils for millions of years. Studying footprints provides a novel method of observing a short period of time in an organism's behavior; footprints are a long exposure snapshot in time that can provide insights into possible group behavior, including speed, group size, and activity (Chapter 2). Studying comparative primate (including human) foot (and footprint) anatomy provides insights about the range of behavioral capabilities (*i.e.,* variance) detectable in substrates, and footprints also reflect the interaction between the soft tissue at the point of contact with a responsive substrate (Chapter 4). The study of footprints ultimately reduces our ignorance (Wood, B. pers. comms) about how hominins interacted with their environment through both the body and trace fossil evidence we discover. Within the field of ichnology, the study of trace fossils including footprints and fossilized evidence of general movement of organisms without the presence of the organism itself, there is always uncertainty in the

true identification of tracks, especially if there is no modern analog of the taxon that made the tracks, such as in the case of *Australopithecus* or other extinct taxa.

Footprints also add information about the adaptability of hominins' problem-solving capabilities such as the case of early humans running up the side of a slippery cliff at Roccamonfina, Italy (Figure 3) (Panarello *et al.,* 2017, 2020). The slippery slope traversed at Roccamonfina is an incredible addition to the collection of hominin footprints due to the rarity of its potential to preserve. Furthermore, the evidence of passive linear marks interpreted as possible technology used for transportation of resources, such as hand carts described at White Sands in New Mexico, USA (Bennett *et al.,* 2025), adds to our knowledge about possible hominin locomotor behavior beyond the existence of only footprints. In sum, footprints can even add to our knowledge about what, and how, hominins may have been doing with their upper limbs while traversing

Figure 3. Adapted from (Panarello et al.,2020)): a western view of the trampled tuff-slope at Roccamonfina, Italy.

their environments.

Anatomy of the Human Foot

In order to understand how footprints are identified and evaluated for their "preservation quality" (Gatesy & Falkingham, 2017) in the fossil record, a brief overview of the anatomy and musculoskeletal layout of the human foot is warranted.

The human foot contains 26 bones in total; seven of those are the tarsals in the proximal area of the human foot (Chauhan and Taqi, 2025) (Figure 4).

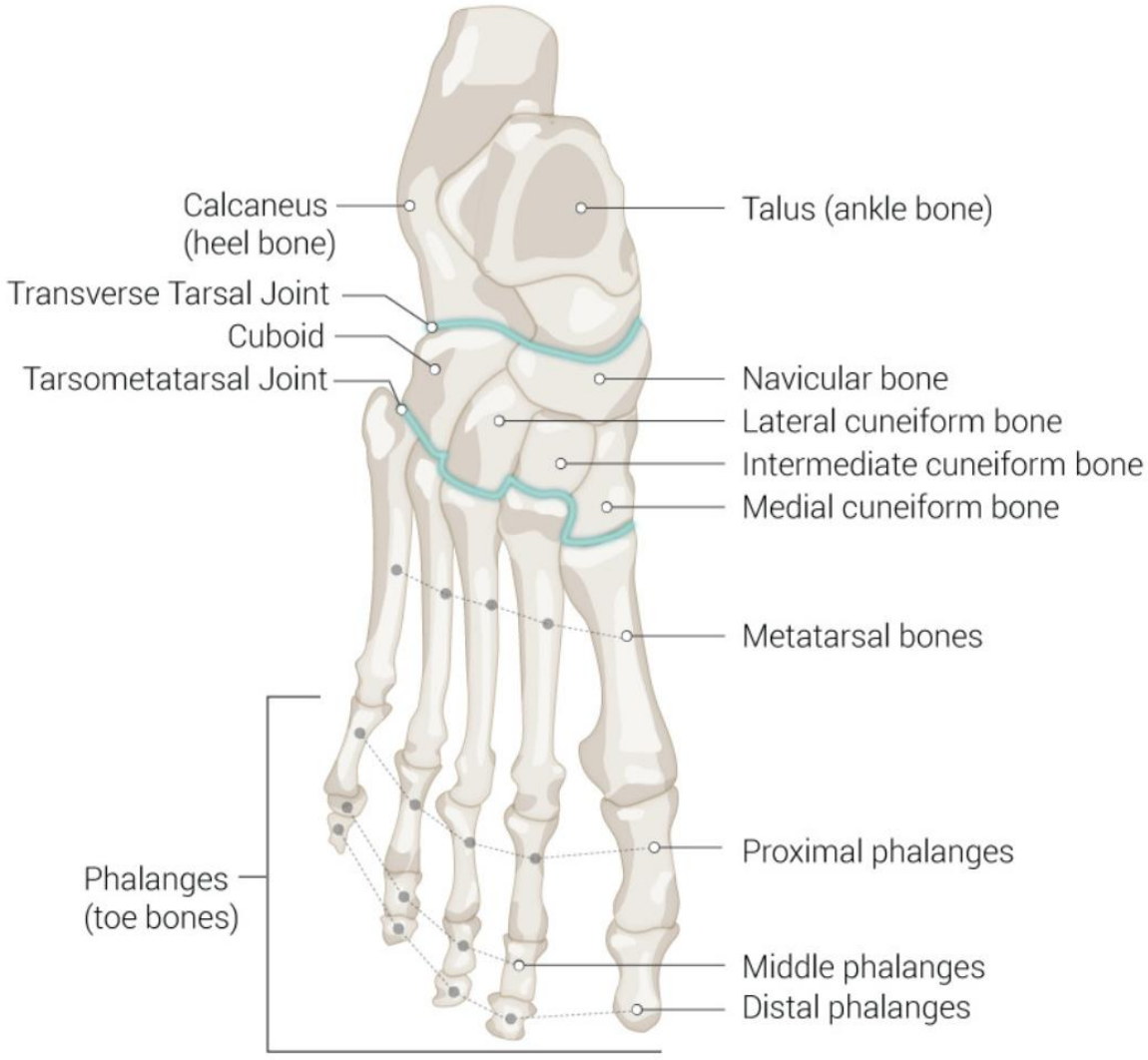


Figure 4. Anatomy of the foot, including bones of the tarsus, metatarsus, and phalanges

The human foot is divided into three parts (White and Folkens, 2005): the hindfoot, midfoot, and the forefoot. The hindfoot is comprised of two of the largest tarsal bones: the calcaneus (heel) and the talus (ankle). The midfoot consists of the navicular, cuboid, as well as the medial, intermediate, and lateral cuneiform. The forefoot consists of fourteen phalanges (the big toe has two phalanges, and the other four toes have three phalanges each), metatarsals, and a few sesamoid bones.

The talus forms the ankle joint superiorly to the calcaneus with the tibia and fibula in articulation, while the calcaneus forms the point of contact during heel-strike. The first point of contact between the foot and the substrate begins with heel strike and ends with toe-off of the hallux (big toe). This unique form of bipedal weight distribution contributes significantly to a fluid gait and low metabolic cost (Thompson *et al.,* 2021) produced during human bipedal locomotion (DeSilva, 2022). The subtalar joint is lined internally by a synovial membrane and three ligaments (White and Folkens, 2005): the posterior talocalcaneal ligament, medial talocalcaneal ligament, and the lateral talocalcaneal ligament (Chauhan and Taqi, 2025). These three ligaments provide support to the human foot as it enters and terminates each stage of bipedalism (stance phase, swing phase, toe-off, see Harcourt-Smith, 2013; Prang, 2019).

There are three arches in the human foot: the Medial Longitudinal Arch (MLA), the Lateral Longitudinal Arch (LLA), and the Anterior Transverse Arch (Chauhan and Taqi, 2025). The MLA forms through the combined structure of the tarsal and metatarsal bones along with several supporting ligaments and tendons. The MLA also acts as a shock absorber to transfer and distribute the body weight from the trunk (above the pelvis) to the each of the legs to retain balance and lower energetic costs (DeSilva, 2009).

Together, these musculoskeletal elements provide energy-saving elastic recoil during human bipedal locomotion (Ker *et al.,* 1987). The development of the arches is a function of human bipedalism that becomes increasingly advantageous as hominins travelled longer distances in more open environments (Bennett *et al.,* 2016; Fan *et al.,* 2025).

Key Terminology for Describing Hominin Tracks and Trackways

By understanding the anatomy and locomotive repertoire of human bipedal gait, footprints become less of a strange impression in the substrate and instead become reflective of how the soft tissue anatomy of the human foot (and therefore people) move around and interact with their environments. In order to interpret footprints as being of hominin origin, key morphological markers are required, including the deep impressions from both the hallux and calcaneus as well as the negative impression caused by the MLA. This allows for footprints and entire trackways, to be viewed as the commonly expressed long exposure "snapshot in time" (Hatala *et al.,* 2024) that provides key information about behavior not always attainable in body fossils.

Definitions of accepted terms used for footprints in this thesis are adapted from Bennett *et al.,* (2014) and Hatala *et al.,* (2021). A *track* is a singular footprint, regardless of presumed species, and includes prints made by both left and right feet. *Track* is synonymous with *footprint* (Hatala *et al.,* 2021), and both sides are not required for track classification; however, evidence of lateral symmetry (*i.e.* a left footprint followed by a right footprint, or vice versa) significantly aids with identification. A *trackway* is a minimum of two individual footprints, not necessarily requiring them to be consecutive, but preferably so. A *track site* is a distinct geographical location at which one or more

tracked surfaces exist. A *track-maker* is an individual organism (a hominin, for example) who made the track (Bennett, 2014). The *tracked surface* is the imprinted surface on which the track-maker locomoted. *Registration* is a term used frequently in ichnological studies (Bennett *et al.,* 2014; Marchetti *et al.,* 2019), especially for footprints, and references the original individual who made the track; a footprint's registration is complete when the foot has terminally lifted from the ground at toe-off.

When describing footprints in-situ (as compared to excavated tracks, Chapter 2) in the substrate, a few terms are useful to reference. *Overprinting* occurs when successive trackmakers traverse the same surface, resulting in the partial or complete superimposition of later impressions upon earlier ones. While overprinting typically degrades morphological fidelity, the stratigraphic sequence of superimposed tracks can preserve temporal information — the order of impression allows researchers to reconstruct the relative timing of passage and, by extension, evaluate potential group behavior or faunal association (Chapter 2). In terms of describing hominin track fidelity, overprint can be a negative attribute due to loss of distinguishable morphological features; the result of organisms/individuals moving across existing footprints causes distortion of anatomical details. A footprint in *concave epirelief* reflects a 'typical' impression, where the digits are pressed into the substrate and the morphology is preserved as a depression. *Convex hyporelief*, by contrast, represents the natural cast of that depression — the morphology protrudes outward, as sediment that once filled the impression is now viewed in positive relief. *Bioturbation* refers to the physical disturbance of sediment by biological activity — including burrowing, tree roots and growth, and trampling by non-track making organisms — which can obscure or alter the

morphological integrity of footprint impressions post-deposition. A *true track* represents the original impression made at the substrate surface, preserving the highest potential morphological detail. *Undertracks* are secondary impressions transmitted through underlying sediment layers by the compressive force of the trackmaker's foot and are characteristically less detailed — digits and fine anatomical features are often absent or smoothed, as the transmitted stress attenuates with depth. *Ichnotaxonomy* involves the classification of tracks into ichnospecies or ichnogenera (Hatala *et al.,* 2021) based on similarities or differences in track morphology. The usage of *ichnotaxa* (and *ichnospecies*, when possible) when describing footprints is a customary practice in paleontology due to a lack of modern taxa comparisons.

Anatomical Drivers of Footprint Morphology

Bipedalism is a type of terrestrial locomotion in which an organism moves on only two feet. Bipedalism is obligatorily practiced by *Homo sapiens* and has been inferred from fossils of extinct hominins and hominids as early *Sahelanthropus tchadensis* (7-8 Ma, Brunet *et al.,* 2002). Not surprisingly, bipedalism is not unique to the human lineage--- several species of animals are obligatorily bipedal, including birds, many insects such as cockroaches (who can run bipedally at faster speeds; Hatala *et al.,* 2016), kangaroos, and even some lizards such as the basilisk lizard (*Basiliscus basiliscus)*. Bipedalism is associated with a variety of distinct postural and locomotor behaviors including standing, walking, skipping, hopping, and running which can be identified through the variation that exists in stride length, speed, and foot anatomy. Humans perform all of these locomotor behaviors at different energetic and metabolic

costs (Hatala *et al.,* 2016), but the most metabolically efficient method of bipedalism for *Homo sapiens* consists of long-distance endurance which means sustaining longer periods of travel at slower speeds (Alexander, 2004). Long distance endurance has been proposed as a driving factor behind the genus *Homo*'s adaptability to different environments, especially as landscape usage increased (Bennett *et al.,* 2009). This is consistent with the appearance of the (geologically) earliest body and trace fossil evidence of *Australopithecus* in the fossil record (Sekhavati *et al.,* 2025).

Chapter 2: Literature Review on Hominin Footprint Sites and Their Respective Substrates

Hominin footprint sites are commonly found near the shoreline of low-energy basins due to the high possibility of rapid burial by sediment and cementing, minerals which hastens the fossilization process. In this thesis I describe 19 hominin footprint sites organized by substrate type and secondly by age. The relationship between substrate type and footprint anatomical fidelity is further explored in Chapter 5. A summary is placed at the end of this chapter (Chapter 2).

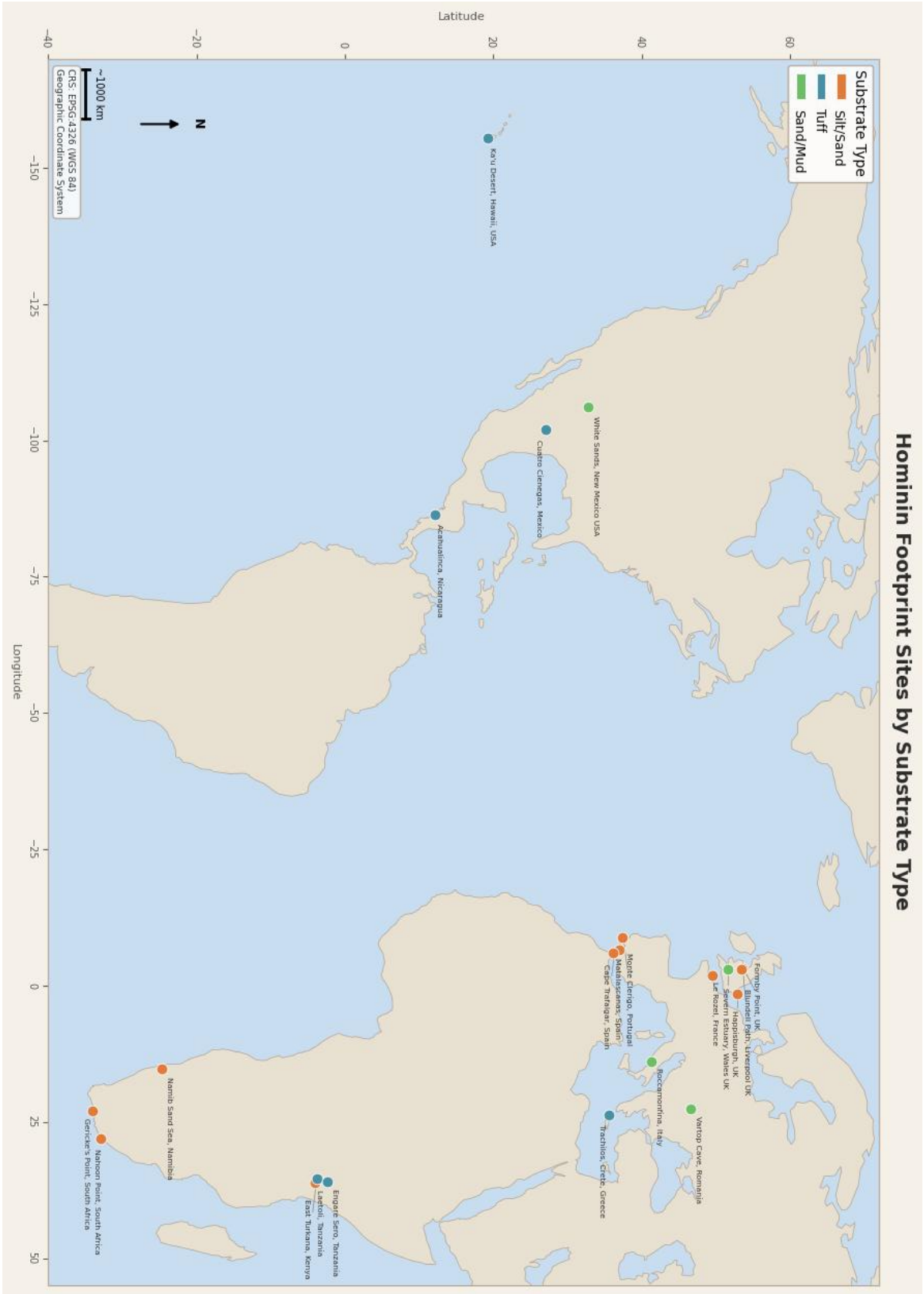


Figure 5. World Map depicting geographical site (n=19) locations

SUBSTRATE TYPE: "Silt, Sand" (11 sites, 72 footprints)

Happisburgh, United Kingdom

The Happisburgh footprint surface, exposed briefly on the Norfolk coast of England before coastal erosion erased it within two weeks of discovery, represents the third oldest hominin trackway known, dating to 1.0–0.78 Ma (Ashton *et al.,* 2014). At this time, only *Homo antecessor* is known to exist in this locality. Hominin footprints depicted at Happisburgh preserve anatomical details consistent with modern human anatomical footprint details including a lateral arch and a large, slightly abducted hallux (Figure 6, top right).

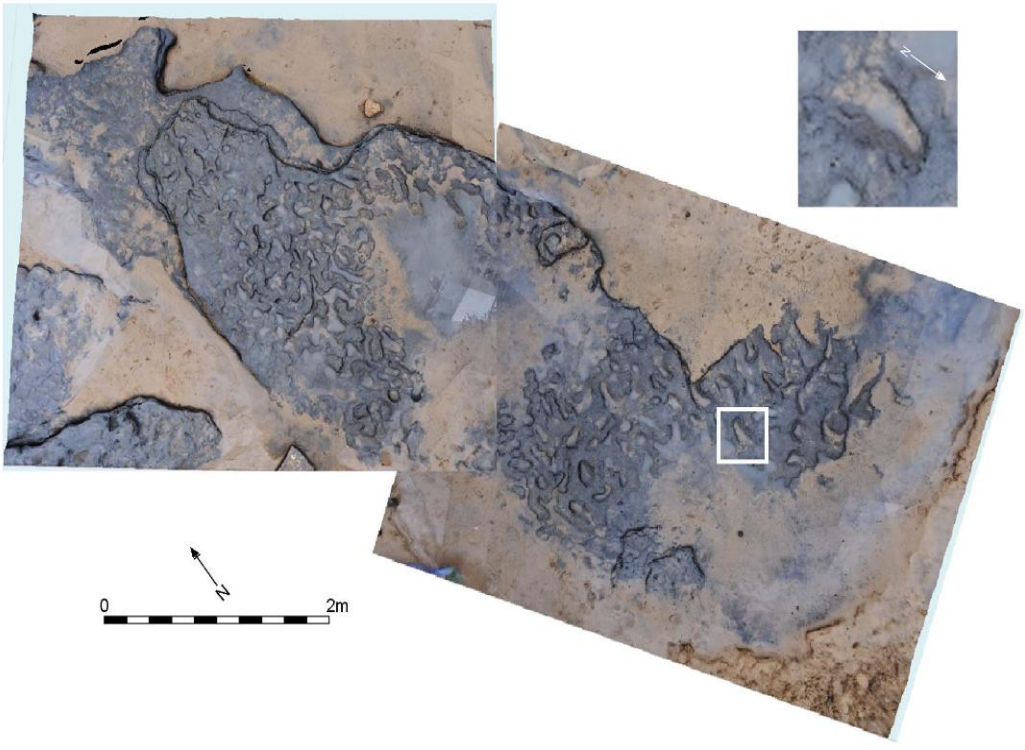


Figure 6 Adapted from Ashton et al., (2014) showing the site of Happisburgh and a footprint.

East Turkana, Kenya

There are a few hominin footprint sites concentrated within the Koobi Fora Formation; each one is preserved in a silty fine-grained sand substrate. The Ileret footprint site dates over 1.5 Ma and has evidence of multiple extinct hominin species existing at the same time and making trackways within hours of each other (Hatala *et al.,* 2024). Nearby to Ileret, another hominin trackway site also in the Okote Member of the Koobi Fora Formation was discovered in 1978 by Kimolo Mulwa and Bernard Kanunga of the National Museum of Kenya (Behrensmeyer & Laporte, 1981). Made up of poorly consolidated tuffaceous sands and silts, the tracks in the Okote Member site were produced in highly erodible substrate that was deemed to be more important to 'record and rescue' (Bennett *et al.,* 2013) than to focus on site preservation.

Site ET-2022-103-FE22 (abbreviated FE22; Hatala *et al.,* 2024) is a prominent hominin footprint site discovered in 2021 within the KBS member of the Koobi Fora Formation which retains at least five likely track surfaces (TS-1 to TS-5). For clarity, the trackway surface is deemed TS-2, which contains "…61 bird, 30 bovid, and 3 equid tracks" (Hatala *et al.,* 2024, p. 1). FE22's track bearing surface 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" (Hatala *et al.,* 2024). The FE22 site is summarized as having evidence of sympatry between two different hominin species (*Paranthropus boisei* and *Homo erectus)* in the same locality contemporaneously; Hatala *et al.,* (2024) suggest this could influence competition interpretations between different groups of hominins in the same landscape.

Matalascanas, Spain

The footprints found at Matalascanas are estimated to be 298ka ± 17ka, during the Middle Pleistocene "…specifically at the transition between MIS 9 and MIS 8" (Mayoral *et al.,* 2022, p. 10). The track site contains at least 87 hominin footprints and associated animal tracks, discovered at the El Asperillo cliff close to Matalascañas in the Doñana National Park, southwestern Spain (Mayoral *et al.,* 2022). Of these, 31 footprints were complete, and 10% are considered "well preserved" (Mayoral *et al.,* 2022, p. 10). The wide range of footprint sizes suggests a social group dominated by non-adult individuals. The footprints are preserved on microbial mats (see Formby Point, p.30) with undetermined tracks also preserving remains of microbial mat trapped beneath them. The preservation of the footprints are linked to this biogenic substrate, which captured and retained the impressions. The footprints were formed in an aeolian (wind-deposited) dune system associated with fluctuating sea levels (Mayoral *et al.,* 2022).

Nahoon Point, East London, South Africa

Mountain *et al.,* (1966) describes the Nahoon Footprints that are embedded in calcareous sandstone. There exist other possible faunal tracks at Nahoon point; Mountain *et al.,* (1966) suggests they may be birds and hyenas. The footprints were first described by Mountain *et al.,* (1966) and were originally proposed to be 28 ka, but resampling of sediment using OSL, Optically Stimulated Luminescence -- which is used to determine the last time mineral grains were heated by the sun (but also by features, like a hearth) --

predated the footprints' registration to ~127 ka. They are attributed to *Homo sapiens* and are shown in Figure 7. Mountain *et al.,* (1966), p. 107) state that the "…rock in which the footprints occur is a typical calcareous sandstone and both above and below the footprint horizon it is fairly uniform in character. It is well bedded splitting into thin slabs generally less than a half an inch thick." The sandstones' grain size assortment is due to the low sea levels of the Pleistocene, which exposed the sands to be transported by wind (Mountain *et al.,* 1966). However, they also note that the entire deposit cannot be of wind-blown origin.

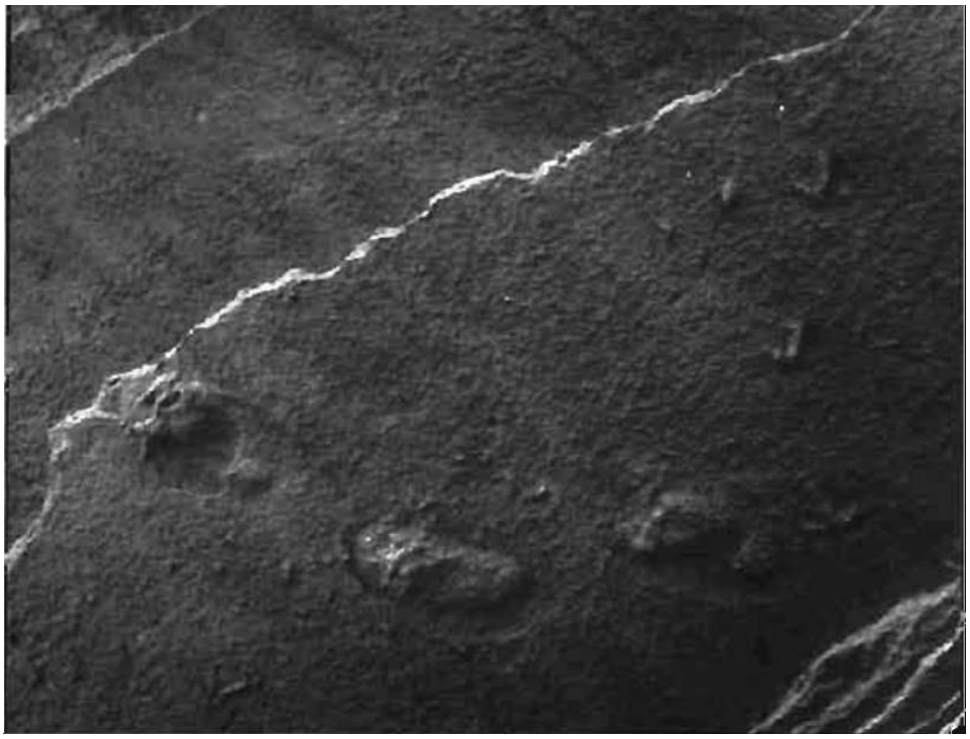


Figure 7. Adapted from Mountain et al., (1966) showing the footprints found at Nahoon Point

Monte Clerigo, Portugal

Monte Clerigo is a cliff-front dune climbing which has a section containing hominin footprints dated to be approximately 78 ka through OSL dating. “It starts by a beachrock conglomerate overlain by the alluvial fan deposits of the Bugalheira formation. A weakly-cemented sandstone of eolian origin shows dispersed pebbles of local (Paleozoic basement) origin” (De Carvalho *et al.,* 2025, p. 9).

Figure 8. Adapted from (De Carvalho et al., 2025)

Le Rozel, Normandy, France

The footprint site of Le Rozel, France, includes 257 footprints dated to 80 ka which belong to both adult and juvenile *Homo neanderthalensis* individuals, and is the “…largest known Neandertal ichnological assemblage to date” (Duveau *et al.,* 2019). The footprints were made in “…a single sub horizontal stratigraphic unit…made up of fine and medium brown to black sand dated to ~80 ka…” (Duveau *et al.,* 2019, p. 1) and are

concentrated in the sandy muds of two lower subunits. Figure 9 shows a few examples of the Le Rozel footprint tracks. Like many footprint sites (Hatala *et al.,* 2016, 2020, 2024; Liutkus-Pierce *et al.,* 2016), the tracks found at Le Rozel were rapidly covered by aeolian sand, allowing for their long-term preservation.

Figure 9. Examples of tracks described at Le Rozel, France Adapted from (Duveau et al., 2019, Figure 1).

Gericke's Point, South Africa

Gericke's Point is a hominin tracksite composed of weathered sandstone (fossilized aeolianite) and located near Sedgefield in the Western Cape province of South Africa, within the coastal section of the Garden Route National Park (Helm *et al.,* 2020, 2023, 2024). The Gericke's Point tracksite was identified as part of the Cape South Coast Ichnology Project, initiated in 2008 by Dr. Charles W. Helm and colleagues (Helm *et al.,*

2020, 2023). Over nearly a decade of systematic survey (2007–2016) of aeolianites across a 350 km stretch of coastline, Helm's team identified more than 250 track sites in the southern Cape, but the Garden Route National Park site — near Gericke's Point — was the first hominin tracksite found in the region (Helm *et al.,* 2023, 2024). Aeolianites extend intermittently along much of South Africa's present-day coastline and are well exposed in bays on or near the shoreline. They are composed of medium- to fine-grained sand with a high carbonate content derived from marine shell fragments (Helm *et al.,* 2020).

Formby Point, United Kingdom

The Holocene Mesolithic footprint site Formby Point in Northwest England were originally established by Gordon Roberts, "...a local resident… who noticed the prints while walking his dog" (Pastoors & Lenssen-Erz, 2021, p. 298). Studies of the footprint site published in 1978 through the early 2000s (Pastoors & Lenssen-Erz, 2021) include several faunal animal tracks, including red deer, aurochs, a crane, unshod horses, and smaller mammals (Pastoors & Lenssen-Erz, 2021). The footprints were dated using OSL through several sediment samples and a "…set of red deer antlers with good stratigraphic context… [near the footprinted site]" averaging between 3,000 ka and 4,500 ka (Pastoors & Lenssen-Erz, 2021, p. 298). Several tracks extending over 4 m by 1.5 m were recorded at Formby Point--which lies in close proximity to the (now eroded) tracks at Blundell Path (Chapter 2) – and are associated with *Homo sapiens* (Pastoors & Lenssen-Erz, 2021). The sediments in which the older prints were made have been shown to be nearshore, intertidal, marine sediments based on the sedimentological and micro- and

macrofossil evidence (Lockley *et al.,* 2008). The younger prints are associated with the lowest sedimentary units in a dune/dune slack succession.

Namib Sand Sea, Namibia

Holocene footprints found south of the Namib Sand Sea, Namibia, have been described as exhibiting an arrangement of 'typical print typologies' (Figure 10; discussed in Chapter 5; Bennett *et al.,* 2014), as well as the largest depiction of potential juvenile footprints. Juvenile footprints, and smaller footprints (in dimension) have a lower potential to fossilize due to their lack of vertical surface area feature (Zimmer *et al.,* 2018); several juvenile footprints found at Engare Sero, in northern Tanzania have eroded away since the site's initial discovery in 2006 (Hatala *et al.,* 2020; Liutkus-Pierce *et al.,* 2016; Zimmer *et al.,* 2018). Morse *et al.,* (2013) which sought to explore intratrail footprint variability at this site associated with differences in the substrate properties, including grain size and sediment disturbance (both human-caused and natural).

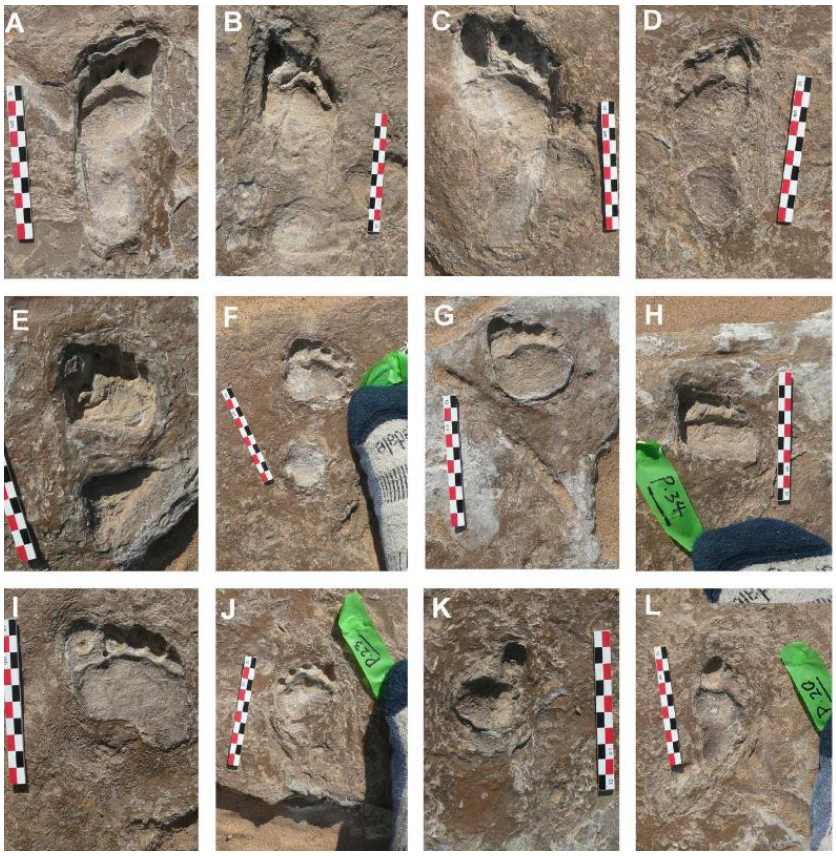


Figure 10 Adapted from Bennett et al., (2014) depicting the 5 print typologies exhibited at Namibia

Morse *et al.* (2013) analyzed the morphological variation depicted within footprints at Namibia to understand the "…role that substrate has on the variation in print typology…" (Morse *et al.,* 2013, page 7). Their results state that any form of trampling or activity in proximity to the hominin footprints resulted in weaker overall consolidation of sediment, leading to footprints that were equally more susceptible to destruction and erosion, as well as infilled by water or other sediments.

Cape Trafalgar, Spain

Cape Trafalgar is a coastal aeolianite site in Spain dated to 100ka and attributed to *Homo neanderthalensis*. (de Carvalho *et al.,* (2025a) describes the overall site, while (de

Carvalho *et al.,* 2025b) describes the substrate characteristics. The few footprints which have been reported from this site are described as being "…surrounded by expulsion rims... [and with] …preservation of the toe prints" (de Carvalho *et al.,* 2025, page 5).

Blundell Path, Liverpool, United Kingdom

(Pastoors & Lenssen-Erz, 2021, p. 298 - 315) describe the footprint site of Blundell Path C which is estimated to be between 3371ka – 7311ka (from two sediment samples, see p. 298). "The mixed stratigraphy of this bed indicates the existence of a dynamic intertidal environment which experienced both periods of flooding, resulting in the deposition of sand, and periods of reduction in relative sea level, which enabled the sediment …to gradually accumulate in three distinct layers of hardened silt...The bed was finally buried beneath the sand where it remained intact until its…exposure…" (Pastoors & Lenssen-Erz, 2021, p. 298). Human footprints dominate the footprinted area, which also includes 6 faunal and avian species. Interestingly, the human prints do not overprint the faunal prints, which may indicate awareness of others. 11 different individuals including adult men and children (n=4) are inferred to have created the footprints.

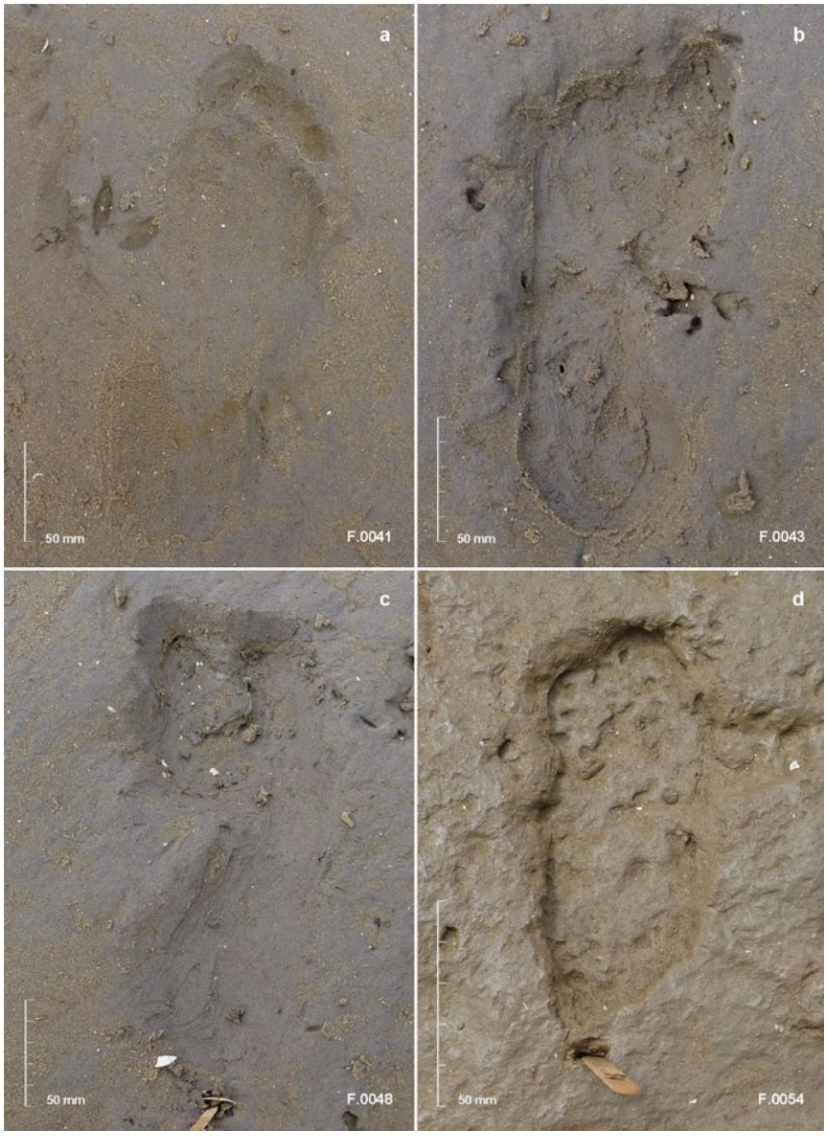


Figure 11. Footprints from Blundell Path including 3 adults (a, b, c) and a juvenile (d). Adapted from (Pastoors & Lenssen-Erz, 2021)

SUBSTRATE TYPE: TUFF (4 sites, 21 footprints)

Trachilos, Crete, Greece

The possible late Miocene (c. 5.7Ma) hominin footprints found in 2017 in Crete, Greece by Gierliński *et al.,* (2017) indicate bipedal, plantigrade, and pentadactyl impressions that were initially viewed as possible 'Messinian-age' tracks. However, the site has been largely discredited due to being under the deep marine sea during the timeframe when track registration would have occurred (Kirscher *et al.,* 2021; Zachariasse & Lourens, 2022). Figure 12 depicts the Trachilos "footprints" and showcases how substrate can mislead interpretations about trace fossil origins—even for experts—and how non-biological impressions may be perceived as footprints when diagnostic expectations do not account for geological and taphonomic events, such as erosion and faunal activity respectively. Figure 12 additionally provides a window into the difficulty of hominin footprint identification; the impressions depicted at Trachilos seem to present a medial-to-lateral angled depression, a foot length exceeding foot breadth and width in the midfoot, (Hatala *et al.,* 2016), indications of a medial lateral arch (arch in the foot, DeSilva, 2020) and the evidence of heel strike (DeSilva, 2020).

The Trachilos "ichnofossils" (Meldrum & Sarmiento, 2018; Zachariasse, 2025; Zachariasse & Lourens, 2022) are interesting due to the overall morphology and dimensions of the possible tracks, even if the site was discredited. Despite its contested ichnotaxonomic status, the site of Trachilos was included in this literature review because its age — dated closer to the predicted *Pan-Homo* divergence at 6-8 Ma (McNutt *et al.,* 2021) — makes it particularly instructive for evaluating what anatomical features

constitute a minimum threshold for inferring bipedality. Its depositional complexity and taphonomic history (Gierliński *et al.,* 2017; Kirscher *et al.,* 2021; Zachariasse, 2025; Zachariasse & Lourens, 2022) further illuminate how preservation conditions mediate morphological interpretation at the margins of the hominin record.

Figure 12 Two possible tracks (circled in red) from Trachilos

Laetoli, Tanzania

The late Pliocene Laetoli footprint beds in northern Tanzania, were discovered by Richard Hay and Mary Leakey in 1979, attributed to *Australopithecus afarensis,* and make up the geologically oldest and most significant hominin footprint site known to date (Harrison *et al.,* 2025; Hatala *et al.,* 2016; Hay & Leakey, 1982; Masao *et al.,* 2016;

McNutt *et al.,* 2021; Raichlen *et al.,* 2010). The significance of the Laetoli footprints is "…clear proof that 3.5 million years ago…" early humans "…walked fully upright with a bipedal human gait" (Hay & Leakey, 1982:56); this is the earliest evidence of habitual (obligate bipedalism used synonymously here) in the fossil record. A previous hypothesis of taxonomically classifying the Laetoli trackmaker as an ursid was ultimately disproved in an experimental study involving 50 hours of ursid footage (McNutt *et al.,* 2021) which showed that *Ursus americanus* (n= 3) walked unsupported bipedally for less than 0.09% of the collected footage, and additionally noted that ursids "…if present at all…were rare on the landscape" (McNutt *et al.,* 2021, p. 469).Laetoli is comprised of 9500 tracks at 9 sites with at least 18 trackways, but the best known and preserved ones are the G-1 trackway, which depicts a small individual about a meter – 1.15 meters tall; and the G2/3 trackway, which is two overlapping trackways of larger individuals who heights are estimated to 1.32 – 1.52m tall (Hay & Leakey, 1982). Site-A preserves clear tracks over an area of 800 square meters (Hay & Leakey, 1982). Laetoli has been extensively studied (see Hatala *et al.,* 2016; Hay & Leakey, 1982; Ichumbaki *et al.,* 2019; Masao *et al.,* 2016; McNutt *et al.,* 2021 Leakey & Hay, 1979; see Bennett *et al.,* 2013; Raichlen *et al.,* 2008, 2010 for kinematics and 3D preservation).

An attempt to protect the footprints from damage by local acacia tree growth was undertaken in 1994 (Feibel *et al.,* 1995) by permanently reburying them; they remain this way except for a few excavations (McNutt *et al.,* 2021) during the past two decades. The preservation methods undertaken to preserve the footprints at Laetoli have allowed digital contributions to the fossil record without disturbing the fragile sediment layers below the prints. The success of the preventative measures at Laetoli showcase that sediment

reburial is currently the best long term natural preventative maintenance (as opposed to excavation or introducing artificial cements, see Agnew & Demas, 1998) method used to protect footprints from additional damage caused by erosion and human population growth (Agnew & Demas, 1998; Feibel *et al.,* 1995).

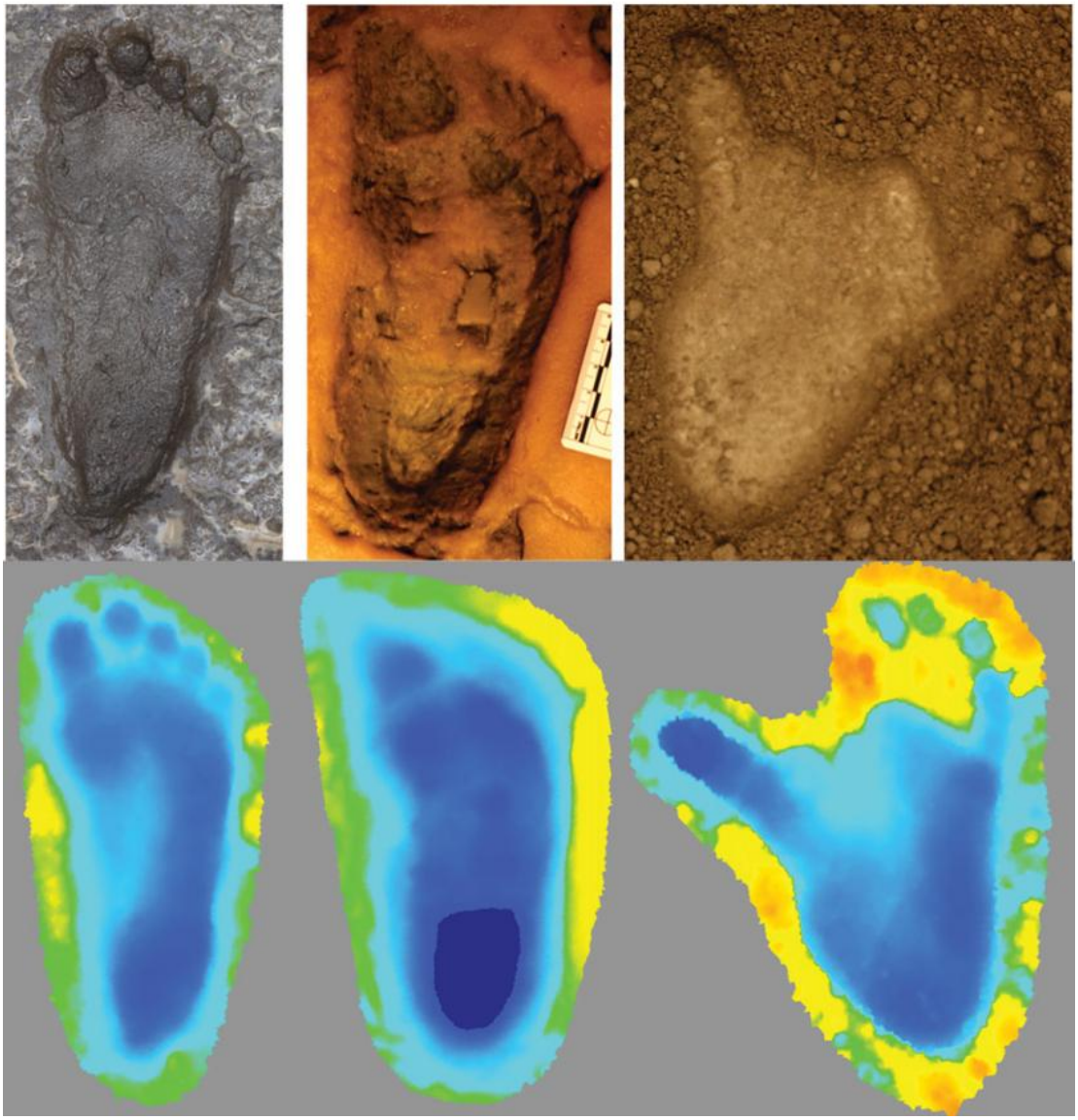


Figure 13 Examples of human (left, experimental), Laetoli hominin (center, G1-25) and chimpanzee footprints (right). Adapted from Hatala et al. (2016) Fig 1.

Engare Sero, Tanzania

The Engare Sero site preserves at least 23 footprint trails consisting of over 400 footprints made by several modern humans *(Homo sapiens)*. Due to the general direction of the footprints, more tracks are assumed to continue under the dunes in the northeast most area; future excavations may continue once long-term preservation methods of the existing exposed tracks can be implemented (Liutkus-Pierce *et al.,* 2016). Engare Sero has the largest assemblage of modern human footprints in all of Africa (Zimmer *et al.,* 2018). The Engare Sero footprints are made of volcanic ash and debris flow from several eruptions over the past 120,000 years of the nearby unique carbonatite volcano, Ol Doinyo Lengai (pictured in the background of Figure 14). Carbonatite is an unusual type of igneous rock primarily composed of carbonate minerals, with less than 10% silicate minerals. The minerals and nutrients in the ashfall enrich the soil for future plant growth, and when combined with rainfall, this ashy soil can form a mud-like surface – perfect for footprint making.

Ultimately, volcanic ash was washed down towards Lake Natron during numerous rainfalls before becoming buried and naturally exposed by the elements. (Liutkus-Pierce *et al.,* 2016) describes the overall preservation and sedimentological composition of the Engare Sero footprint site: “The Engare Sero footprints are preserved in two distinct units: a lower dark gray volcaniclastic sandstone…and an upper dark gray brown volcaniclastic paraconglomerate of varying thickness, containing cobbles of varying sizes and compositions…” (Liutkus-Pierce *et al.,* 2016, p. 5).

Figure 14. Adapted from Zimmer et al., (2018) Figure 2 with a view of the Engare Sero footprint Site

Ka'u Desert, Kɪ ʔlauea, Hawaii National Park, USA

A series of human footprints were discovered by Ruy H. Finch, a geologist, in 1919, on the largest and most southern island in Hawaii. At least two ash layers in which the prints are impressed are separated by a "varying thickness of interbedded eolian sands", suggesting that the original trackmakers -- the army of Keoua (c. 1750s, see Meldrum *et al.,* 2004) or a travelling group (Nakamura, 2003; Moniz, 2009) -- may have been travelling towards the Kilauea Caldera. The footprint site in Hawaii National Park was studied in 1998 and 2000 and is described as having over 1700 footprints

representing a minimum of 441 individuals (Moniz, 2009). Figure 15 depicts one of the prints that are impressed into volcanic ash from an eruption from nearby volcano Kilauea that erupted multiple times during 1500 AD (Moniz, 2009).

Figure 15. Adapted from (Moniz Nakamura, 2009, Figure 2)

Acahualinca, northern Nicaragua

The footprint site of Acahualinca in Nicaragua represents the chronologically earliest confirmed discovery of human footprints. The tracks were initially described in 1884 (Flint, 1884) and are attributed to at least 15 *Homo sapiens* individuals. The footprints have been dated to 2100 years old (Schmincke *et al.,* 2010) "…The footprint layer occurs within a series of rapidly accumulated basaltic andesitic tephra..." (Schmincke *et al.,* 2010, p. 279). (Schmincke *et al.,* 2010, p. 286, 287) describe the intricate hydration requirements for the registration (and preservation) of the footprints (an example provided in Figure 16):

"The excellent preservation of the imprints is due to a combination of favorable circumstances including: (i) a thin layer of fine-grained freshly fallen wet ash covering a

thicker, coarser…firm base for the tracks to retain their shape; (ii) a physical consistency of the wet ash [for track registration retention]; (iii) quick hardening…; (iv) quick [burial]…"

Their consensus is that if the water hydration properties had differed, no clear footprints would have remained. "…on the other hand, had the ash been much coarser grained and mostly dried, no or only vague imprints could have been made." (Schmincke *et al.,* 2010, p. 287).

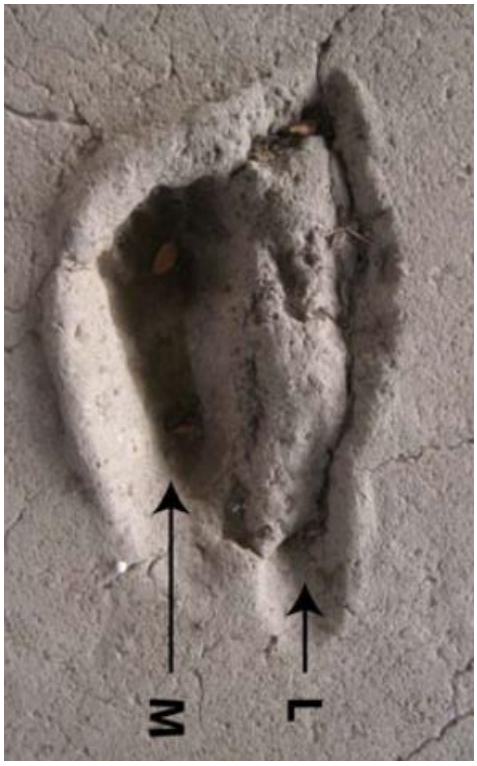


Figure 16 Individual M walked so closely to individual L that it deformed the original print (L). Depth is 15cm. Adapted from (Schmincke et al., 2010)

Cuatro Cienegas, Mexico

Cuatro Cienegas is reported to be a Holocene site attributed to *Homo sapiens* and was originally represented by two tracks that were discovered in 1961, but the rediscovery of the footprinted site in 2006 found "…more than 20 additional well-preserved prints in at least 4 trackways…" (Gonzalez *et al.,* 2009, p. 12). Importantly, the Cuatro Cienegas footprints are embedded in Tufa deposits (Figure 17). which are distinct from tuff deposits (Chapter 4).

Figure 17. Adapted from (Lockley et al., 2008). Left footprint in Tufa deposit

SUBSTRATE TYPE: "Sand, Mud" (3 sites, 10 footprints)

White Sands, New Mexico, USA

There are two human footprint sites within the White Sands National Park in New Mexico (USA) which are "…visible only under specific moisture conditions" (Bustos *et al.,* 2018, p. 4). White Sands National Park is one of the largest concentrations of Cenozoic tracks in North America, with a modern human (*Homo sapiens)* footprint site dating to 15 ka where trackways left by modern humans transected trackways left by a giant ground sloth (Bennett *et al.,* 2020, 2025; Urban *et al.,* 2018) and columbian mammoths (Bennett *et al.,* 2020). The humans who left these footprints may have used transport technology such as a cart (Bennett *et al.,* 2020).

Bennett *et al.,* (2020) described linear traces and Holocene footprints identified in 2019 found to the west of Bustos *et al.,* (2018)'s study site of animal fossil footprints and modern human fossil footprints that are impressed into gypsiferous lake sediments. They are dated between 10 ka - 15.56 ka with at least two human trackways measuring more than 1.5 kilometers in length Bennett *et al.,* (2020), one of the longest fossil human footprint trackways in the world. The site includes both human tracks and inorganic linear traces that were likely made by humans dragging "… either single or multiple poles potentially as improved travois, which broadly includes any form of vehicle fashioned from a single wooden pole with a load, as well …more complex vehicles consisting of two or more crossed poles" (Bennett *et al.,* 2025) or "…the transport of firewood" (Bennett *et al.,* 2025).

The human footprints at White Sands are preserved in three forms of fine-grained sediments: dolomite-cemented pedestals (a, epirelief); cemented hyporelief and epirelief tracks (b); and in negative, consolidated but uncemented impressions (c, hyporelief). Figure 18 describes these three forms visually. All three forms consist of infill of sediment. The human tracks record the "…longest Late Pleistocene-age double human trackway in world…" and are morphologically variable between left and right footprints, indicating possible child carrying (Bennett *et al.,* 2025) due to the consistent depth variation exhibited in one of each trackway's side (*e.g.* the left side of the trackway was consistently deeper compared to the right, and vice versa). The study area of the site is located on the western edge of an alkali flat, which is an arid basin covered with accumulated salts and a high pH soil. Tracks were made by unshod humans and were impressed into "…thinly bedded gypsiferous and siliciclastic muds and sands" (Bennett *et al.,* 2020).

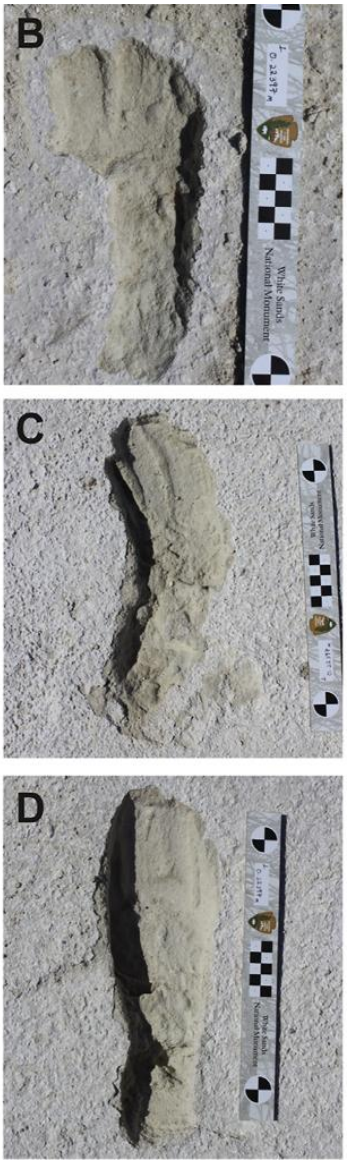


Figure 18 describing the three forms of human footprints found at White Sands National Park. Adapted from Bennett et al., (2020). (B) epirelief; (C) cemented hyporelief and epirelief; (D) hyporelief.

Vârtop Cave, Romania

Onac *et al.,* (2005) describe the "…first clear *Homo neanderthalensis* footprint" (Figure 19) impressed into calcareous mud dated 62 ka (Onac *et al.,* 2005) from Vârtop Cave, Romania. The total area of the site is approximately 1.5m^2 and consists of three total footprints found in 1974. This site is one of the few examples where a footprint was

excavated from the hardened calcareous mud substrate; successful excavation of footprints is highly variable and should only be used as a last resort because of the high potential to damage, destroy, and remove contextual in-situ information relating to that footprint.

Figure 19 Adapted from Onac et al., (2005), depicting the "...best preserved footprint." (Onac et al., 2005, p. 1152).

Severn Estuary, Wales, United Kingdom, Europe

The footprint site of Severn Estuary is in a mudflat silt substrate originally found in 1986 and dated to 8,000 ka (Holocene) using radiocarbon dating of peat and associated organic material (Alhouse-Green *et al.,*1993). Due to their age, the prints belong to *Homo sapiens*, specifically during the Mesolithic period. Primary site documentation is recorded in Aldhouse-Green *et al.,* (1993), Allen (1997), and Kim *et al.,* (2008), although little geological background is provided in the former two studies; Allen (1997) focuses upon the non-hominin tracks present. Kim *et al.,* (2008) state that during their own hominin footprint literature review "…we were surprised to learn that even at accessible and well-known sites … very little information on the tracks was available" (Kim *et al.,* 2008, p.

127). Kim *et al.,* (2008) attempted to remedy this issue by visiting footprint sites to collect missing measurements on available footprint dimensions. However, they published only two footprint images from this site (Kim *et al.,* 2008).

Figure 20. A footprint recorded at Severn Estuary, Wales (Adapted from Kim et al., 2008, Figure 2)

Roccamonfina, Italy

Roccamonfina, Italy (Panarello *et al.,* 2017, 2020) preserves numerous trackways dating to approx. 350 ka with two trackways (see "Devils Trails", Panarello *et al.,* 2017) in particular taking place on the side of a mountain transecting up a slippery slope (Figure 3) (Panarello *et al.,* 2017). The site was dated using ^{40}Argon/^{39}Argon radiometric data (Panarello *et al.,* 2017). A minimum of 81 hominin impressions related to at least 4 trackmakers (likely *Homo heidelbergensis,* see Panarello *et al.,* 2017) were recorded, and the primary tracks (trackways A, B, and C) contain several hominin and mammalian scattered prints (Panarello *et al.,* 2017).

Site	Age	Substrate	Tracks Identified	Dating Method	Hominin Species
Happisburgh, UK	1.0-0.78 Ma	Silt, sand	~minimum of 12, but up to 49 impressions	Biostratigraphy, paleomagnetism, fossil flora and fauna	*H. antecessor*
Ileret, East Turkana, Kenya	>1.5 Ma	Fine-grained sand, silt	97 hominin (of 400+ total across all sites)	Radiometric	*H. erectus and Paranthropus spp.*
East Turkana, Kenya	>1.5 Ma (KBS Mbr)	Silt / fine sand (32 cm unit)	5 track surfaces	Stratigraphic	*Paranthropus boisei*, *H. erectus*
Matalascanas, Spain	298 +/- 17 ka	Microbial mat / aeolian dune	87 initially, up to 300.	OSL	*H. neanderthalensis*
Cape Trafalgar, Spain	~100 ka	Aeolianite	Few (unspecified)	OSL	*H. neanderthalensis*
Le Rozel, France	~80 ka	Fine/medium sand, sandy mud	257	Not specified	*H. neanderthalensis*
Monte Clerigo, Portugal	~78 ka	Weakly cemented aeolian sandstone	Unknown	OSL	*H. sapiens*
Nahoon Point, South Africa	~127 ka	Calcareous sandstone	3 tracks	OSL	*H. sapiens*
Blundell Path, UK	3,371-7,311 ka	Intertidal silt (3 hardened layers)	11 individuals inferred	Sediment sampling	*H. sapiens*
Namib Sand Sea, Namibia	Holocene	Intertidal silt	Not specified	Not specified	*H. sapiens*
Gericke's Point, South Africa	~153 ka	Weathered sandstone (aeolianite)	Few (unspecified)	OSL	*H. sapiens*
Formby Point, UK	~ 8 ka	Intertidal marine sediment / dune silt	Unknown	Radiocarbon Dating	*H. sapiens*
Trachilos, Crete, Greece	~5.7 Ma (contested)	Deep Marine	2 (contested)	Stratigraphic	Contested

Site	Age	Substrate	Tracks Identified	Dating Method	Hominin Species
Laetoli, Tanzania	~3.5 Ma	Tuff	9,500+ (18+ trackways)	Radiometric	*Australopithecus afarensis*
Engare Sero, Tanzania	~5.7 - 20 ka	Volcaniclastic sandstone / paraconglomerate	400+ (23+ trails)	Ar-Arg Radiometric	*H. sapiens*
Ka'u Desert, Hawaii, USA	c. 1500 AD	Volcanic ash	1,700+ (441+ individuals)	Historical record	*H. sapiens*
Acahualinca, Nicaragua	~2,100 years BP	Basaltic andesitic tephra	Unknown	Radiometric	*H. sapiens*
Cuatro Cienegas, Mexico	Holocene	Tufa deposit	20+ tracks (initially)	OSL	*H. sapiens*
Roccamonfina, Italy	~350 ka	Not specified	2 trackways	Argon-Argon (Ar/Ar) radiometric	Early *Homo*
Vartop Cave, Romania	~62 ka	Calcareous mud	3 human tracks	Uranium-Thorium (U-Th) radiometric dating	*Homo neanderthalensis*
Severn Estuary, Wales, UK	~8,000 years BP	Mudflat silt	35 human tracks	Radiocarbon dating of the peat layer	*H. sapiens*
White Sands, New Mexico, USA	10-15.56 ka	Gypsiferous lake sediment (mud/sand)	2 trackways (>1.5 km)	Radiocarbon	*H. sapiens*

Table 1. Summary of Sites and Relevant Information

Chapter 3: Introduction of the Footprint Fidelity Rubric

In this thesis, I use a novel rubric based on the visibility of morphological anatomical features to determine if sediment variables predict anatomical fidelity in hominin footprints. Sedimentological variables such as quartz content, alkalinity (high pH), grain size (fine-grained sand) (Zimmer *et al.,* 2018), and sufficient hydration of sediment are important factors in the preservation of footprints (Gatesy & Falkingham, 2017). To understand how footprints are affected by properties of the sediment in which they were impressed, an overview of sedimentary rocks is warranted. There exists three primary geological rock-types: igneous, metamorphic, and sedimentary rock. Sedimentary rocks can be produced primarily in two ways: accumulation of small particles from other rocks (clastic sedimentary rocks), or the accumulation of the skeletons of microorganisms (organic sedimentary rocks, such as limestone). Here, I focus on the former description to describe sedimentary variables.

Sedimentary rocks are variously organized into groups based upon their composition, angularity, color, and texture (Prothero *et al.,* 2014). Color is "…one of the more striking properties…" as it "…reflects some aspect of the rock's composition" (Prothero *et al.,* 2014, p. 14) and is generally controlled by the rate of infill by other smaller minerals. While not included in this study, the existence of salts in substrates is expected to influence anatomical fidelity scores negatively due to the potential destructive measure of salt, which contributes to the desiccation (cracking) of and overall damage to footprints over time (Bennet *et al.,* 2014; Masao *et al.,* 2016). Salts are also commonly mentioned in the literature and are found near river basins and low-energy

fluvial environments, where footprints are commonly exposed by fluvial and aeolian erosion. pH can play a role in carbonate and sulfate production, which is important for the hardening of footprints through authigenic mineral precipitation — new minerals forming *in place* from pore waters (Masao *et al.,* 2016). Two of the earliest cements to precipitate *(i.e.,* form) are carbonate (calcite, aragonite) and sulfates (gypsum, anhydrite), which precipitate in solution when the pH rises or when ion concentration increases.

Falkingham *et al.,* (2014) state that in order for an impression to be registered by the substrate (Marchetti *et al.,* 2019; Gatesy and Falkingham, 2017; Falkingham and Gatesy, 2014, 2020), there must be a "just right" combination of sediment hydration, pressure, and grain size. They term this relationship the Goldilock's Effect (GE), and apply it to all trace fossils, including footprints. The substrate cannot be too wet, too dry, too coarse, or too fine. If these conditions are not met, a footprint may not be registered, and if so, they may not have the potential for high anatomical fidelity (Falkingham *et al.,* 2014, 2018). The GE is not the only factor which produces a footprint; there are a number of considerable forces which are at play to create a footprint: body weight *(i.e.,* plantar pressure, DeSilva *et al.,* 2021); substrate plasticity which allows for the substrate to deform around the foot as a result of plantar pressure; and substrate cohesion (the inverse of plasticity; the ability to hold shape). Each of these characteristics, and more *(i.e.,* speed of travel, faunal activity, floral growth, high energy environments), play a significant role in how, and if, a footprint preserves in each substrate (Falkingham *et al.,* 2014; Morse *et al.,* 2013; Webb *et al.,* 2025).

Previous Research on Hominin and extinct Tetrapod Tracks and Tracksite Quality

Belvedere and Farlow (2018); Farlow (2018); and Bennett (2013)'s typology models (Chapter 5), described below, have been the primary references from which the anatomical fidelity model proposed in this thesis has been adapted. The assessment of anatomical fidelity is not new to the discipline of ichnology (study of trace fossils), but a direct translation onto hominin footprints cannot be made due to missing key anatomical details between ancient tetrapods and modern ones (humans).

Farlow (2018): a non-hominin taxa fidelity rubric

Research into ancient theropod pedal mechanics (Farlow, 2018; Ashley, 2003; Behrensmeyer, 1978; Bennett *et al.,* 2013, 2014; Marty *et al.,* 2009; Morse *et al.,* 2010) suggest that under the right substrate conditions, a theropod foot might make an ornithopod-like footprint (Figure 2). This gap in the research about what morphological quality ('fidelity') parallels with the needs in human footprint identification: Laetoli's original trackmaker was proposed to be ursids, rather than human; is there the possibility that there is a higher number of species diversity than currently recognized? More research is needed to discover what other factors influence footprint fidelity, such as variable grain size (Gatesy & Falkingham, 2017), fluid dynamics, and speed (Bennett, 2014).

Farlow (2018)'s preservation class scheme (reproduced in Figure 21) for tetrapod footprints attempted to answer the second concern: fluid dynamics. Farlow (2018) used experimental emu footprints in different hydration of sediment to address how much

variation could exist before an emu footprint is no longer recognizable. They gauged the footprints quality using an ordinate scale (Figure 21): 1 (poor preservation) to 4 (excellent preservation), with the inclusion of intermediate scores (1.5, 2.5, and 3.5 denoting intermediate cases where a track does not match either class). This scheme was later critiqued and modified under concerns for ambiguity of language: "The use of such a scale is not intended to replace qualitative descriptions of morphology, but rather to integrate it with a numerical value, resulting in improved understanding of the morphological features present in the specimens" (Belvedere and Farlow, 2014, p. 1).

Building on these prior efforts to formalize the description of footprint fidelity in non-hominins, Chapter 4 will introduce my novel anatomical fidelity scheme, and test whether sediment characteristics predict anatomical fidelity as gauged by this scheme.

Class	Description
1 (Poor)	Toemarks poorly discernible or unrecognizable
2 (Fair)	Toemarks faint, blurred, or distorted, but recognizable
3 (Good)	Toemarks fairly clear and sharp, at least over substantial portions; some digital pads recognizable
4 (Excellent)	All digit impressions nearly or completely sharp and clear; scale impressions may be present

Figure 21 Emu footprint preservation classes (adapted from Farlow, 2018)

Chapter 4: Materials and Methods

In this thesis, I ask the question of whether substrate categories can predict anatomical fidelity of hominin footprints by applying a novel ordinal and categorical rubric designed to assess individual footprint fidelity in footprints created by hominins.

Footprint Fidelity Rubric

This fidelity rubric focuses upon anatomical fidelity—how accurately the footprint reflects the hominin foot's soft tissue which is impressed into the substrate. Using anatomical fidelity as a focus point for choosing which footprints are appropriate for scientific research is not a new concept, as designating tracks as "well-preserved" or 'optimal' (Bennett *et al.,* 2013; Falkingham & Gatesy, 2020; Gatesy & Falkingham, 2017, Hatala *et al.,* 2024) is used consistently throughout the literature. However, strict designations for what defines "well-preserved" in terms of both anatomical fidelity and substrate has not been clearly defined. Therefore, a Likert-scale rubric was chosen to examine hominin footprints more closely (where S is "Beyond Expectations", and F is "Unusable", Table 2), while removing the impact of taphonomy -- which often leads to disqualification in sample sizes -- caused by natural destructive measures (fluvial or aeolian transport), or other trace fossil motions (*e.g.* foot-dragging motions, overprinting by other fauna or individuals, Falkingham *et al.,* 2020).

Anatomical fidelity was measured by identifying and marking key anatomical features in each human track based on existing literature (Bennett *et al.,* 2009, 2020;

Wiseman *et al.,* 2020; Morse *et al.,* 2013; Gatesy & Falkingham, 2017; McNutt *et al.,* 2021; Falkingham, 2018). Footprint images were graded individually using PNG images uploaded to Procreate (version 5.4.9) on an iPad Pro (2022, 6th generation) with an Apple Pencil (2nd generation). To account for sampling bias, anatomical fidelity was not measured until after substrate data had been collected for each site. The key anatomical features used here are reflected in Chapter 1: the existence of a medial-lateral arch (MLA), evidence of 'heel-strike' in the posterior of the track; and a visible toe off impression (preferably caused by the hallux).

S	**Beyond expectations**	All 5 digits distinct, heel is 80% or more diagnostic, minimal "squish ring", minimal or no cracking/desiccation. Outline is 100% measurable.
A	**Ideal**	Some digits preserved (3-4), outline diagnostic, heel more than 50% diagnostic (U-shape), some squish/distortion present (less than a few mm) outline is more than 80% measurable. No/non-significant amount of cracking/desiccation (not enough to deter accurate measurements).
B	**Moderate**	Some digits diagnostic (1-2), outline diagnostic, heel less than 50% diagnostic (U-shape), more than 50% shape outline measurable.
C	**Ideal Worst**	No digits preserved, arch is present, heel less than 50% diagnostic. Squish/distortion ring present. Outline may be less than 50% measurable (due to digit loss).
D	**Minimum**	Heel non-diagnostic, at least one digit diagnostic (preferably the hallux) or faint outline; foot-shaped, significant distortion by post-registration erosion.
F	**Unscorable**	No diagnostic features preserved, amorphous depression only. Arch may be present, but it cannot be distinguished from a natural sedimentological depositional mound.

Table 2 Anatomical Fidelity Rubric

A rigorous rubric (Table 2) was developed using a Likert-scale structure rather than a strictly quantitative, ordinate system. The benefit of using a Likert-scale allows footprints which do not conform neatly to a single fidelity category (*e.g. Laetoli, White Sands,* Chapter 2*)* overall but may have individual footprints with observable

morphological characteristics. While not intended to be exhaustive, this rubric provides clear, objective criteria for each fidelity level, thereby establishing realistic expectations for footprint preservation studies. Even lower-tier scores, such as a D "Minimum" (which is considered a minimal threshold for footprint identification and usage in research) are incorporated into sample sizes, which reflect a more realistic representation of the fossil footprint record and more broadly human bipedality in all its various stages and perspectives.

Footprints that exceed expectations of anatomical detail (digits preserved, hallux and heel present, for example) were given an "S", followed by an "A" for Ideal prints, "B" for Moderate anatomical fidelity, "C" for Ideal Worst fidelity, and finally "D" for the bare Minimum rating to denote the footprint as a trace fossil of hominin origin. Any footprints marked with an "F" score were deemed unusable for research. Supplemental data collected was the age of the footprint site; species (ichnospecies when available); foot length and foot width (when available); and general substrate information. These variables will allow for closer examination of the relationship between footprint fidelity and other factors besides substrate. as well as removing subjectivity from possible distortions caused by erosion (sediment fluvial/aeolian transport), foot-dragging motions, or overprinting by other fauna/individuals that might otherwise provide anatomical fidelity (Falkingham *et al.,* 2020). Accordingly, footprints that preserve a discrete heel impression and any coherent midfoot-to-forefoot loading pattern (such as a midtarsal break; DeSilva *et al.,* 2010) provide critical anatomical landmarks for track fidelity scoring than tracks lacking these features. These marked differences highlight the soft-tissue impressions that researchers treat as diagnostic when assessing whether a track is

genuinely of hominin registration. When expected features are absent, ambiguous, or inconsistent – particularly under challenging substrate conditions – foot-shaped impressions can (and have been, see Gierliński *et al.,* 2017) be misidentified, as illustrated by the disproven Trachilos track site in Greece.

Data collection consisted of 2D image screenshots (n=103) in PNG format (chosen for high resolution reproducibility, Chapter 6) from publications available on or before December 2025 from 19 human footprint sites ranging from the late Pliocene through the Holocene. This sample size reflects the scarcity of high-quality images available for a comprehensive review of individual human tracks' fidelity.

The distribution of tracks identified reflect the following anatomical fidelity levels summarized in Table 3: S "Beyond Expectations" (n = 13 tracks); A "Ideal" (n = 11 tracks); B "Moderate" (n = 15 tracks); C "Ideal Worst" (n = 26 tracks); D "Minimum" (n = 30 tracks); and F "Unusable" (n = 8 tracks). Substrate categories have been compiled into Table 4.

S "Beyond Expectations"	13 tracks
A "Ideal"	11 tracks
B "Moderate"	15 tracks
C "Ideal Worst"	26 tracks
D "Minimum"	30 tracks
F "Unusable"	8 tracks

Table 3 Number of tracks identified in each Fidelity Category

Sand, Mud	5 tracks identified
Tuff	20 tracks identified
Silt, Sand	26 tracks identified

Table 4. Number of Tracks in each Substrate Category

A few sites listed below were either over- or under-represented in the sample for various logistical reasons, explored below.

White Sands National Park, New Mexico, USA

While highly intriguing for its ichnofossils of extinct fauna, the footprints reported in Bustos *et al.,* (2018) were excluded from this study due to not having any hominin footprints described, despite being close in association to the well-known early human footprint site described by Bennett *et al.,* (2020, 2025; Urban *et al.,* 2018).

East Turkana, Kenya

Data from the East Turkana footprint sites is remarkably scarce for this study, despite having a vast and well-documented wealth of information and research out of the Koobi Fora Formation. Unfortunately, digital images were unavailable due to inaccessible data (copyright by National Museum of Kenya). However, four tracks (HT1, HT1-12, HT1-13, HT1-8) were published and available to be used in this study. Kenya represents 6 footprints out of a total collection of 103 footprints (5.8%) of the dataset.

Le Rozel, Normandy, France

The footprint site of Le Rozel, in Normandy, France includes the highest number of (n=36, 34%) footprints used within this study due to the release of supplemental documentation published by Duveau *et al.,* (2019).

Laetolil "Laetoli" Beds, Northern Tanzania

The Laetoli data reflects a common issue of digital preservation and accessibility of fossil footprint images. There are abundant quantitative footprint measurements available, but few 2D photographs (see McNutt *et al.,* 2021) have been published. Laetoli's anatomical fidelity scores may have been negatively skewed due to the low-resolution quality of the original 3D scans (which were built using the 4 original photos taken in 1977, see McNutt *et al.,* 2021) that were not taken with future analyses in mind, see McNutt *et al.,* 2021). While casts of the Site A prints existed at one point, they have not been successfully recovered (McNutt *et al.,* 2021). The impact of (the lack of) prints discovered during the late 1900s overall is briefly discussed in Chapter 6.

Cuatro Ciénegas, Mexico

The footprinted site of Cuatro Ciénegas (Lockley *et al.,* 2008, Gonzalez *et al.,* 2009) represents a singular outlier in the dataset (n=1 track). While additional footprint images (n=6 tracks) were discovered too late to be included in analysis, they can be found in (Gonzalez *et al.,* 2009, Figure 2 and 7). However, the footprint site as a whole is preserved in tufa, a freshwater carbonate precipitate that is petrogenetically distinct from the volcanic tuff deposits that characterize the remaining sites in this substrate category,

as discussed in Chapter 2. Despite this difference in origin, the track was placed within the tuff substrate category because both substrates share sedimentological properties directly relevant to track preservation — namely fine grain size, high mineral activity, moisture retention at time of impression, and rapid lithification. This classification is further supported by the fidelity scores at Cuatro Ciénegas, which are consistent with those recorded at other tuff-bearing sites in the dataset (*e.g.,* Laetoli, Engare Sero, Acahualinca), suggesting comparable preservation outcomes across both substrate types.

Choosing Anatomical Fidelity versus Substrate Fidelity

Substrate properties vary naturally due to geological processes, so understanding how different substrates affect preservation has become important in ichnological studies, including hominin footprint research. The influence and impact that substrate and sedimentological variables have on morphological variation is due in part to different sections of the foot contacting the substrate. When extant humans run at greater speeds, there is less contact with the substrate due to the change in gait (DeSilva *et al.,* 2020). This impacts the amount of sediment displacement resulting in partial or incomplete imprints in a willing substrate. In short, anatomical fidelity was chosen for this study due to its easy replicability and identification in each track image.

Overprinting was also considered when assessing footprint fidelity, though it should be noted that overprinting does not determine the overall fidelity as damage by overprinting is to be expected in the fossil record due to bioturbation.

Justification of POLR and CLM Models to describe Footprint Fidelity

Fine grained substrate type has been widely discussed in the literature as being correlated with high footprint fidelity, and therefore a Cumulative Link Mixed Model (CLM) model and a Proportional Odds Logistic Regression (POLR) model was used to evaluate the statistical significance of substrate categories as predictors for high morphological fidelity. Additionally, The POLR Model respects the ordering without imposing false numerical precision on the intervals.

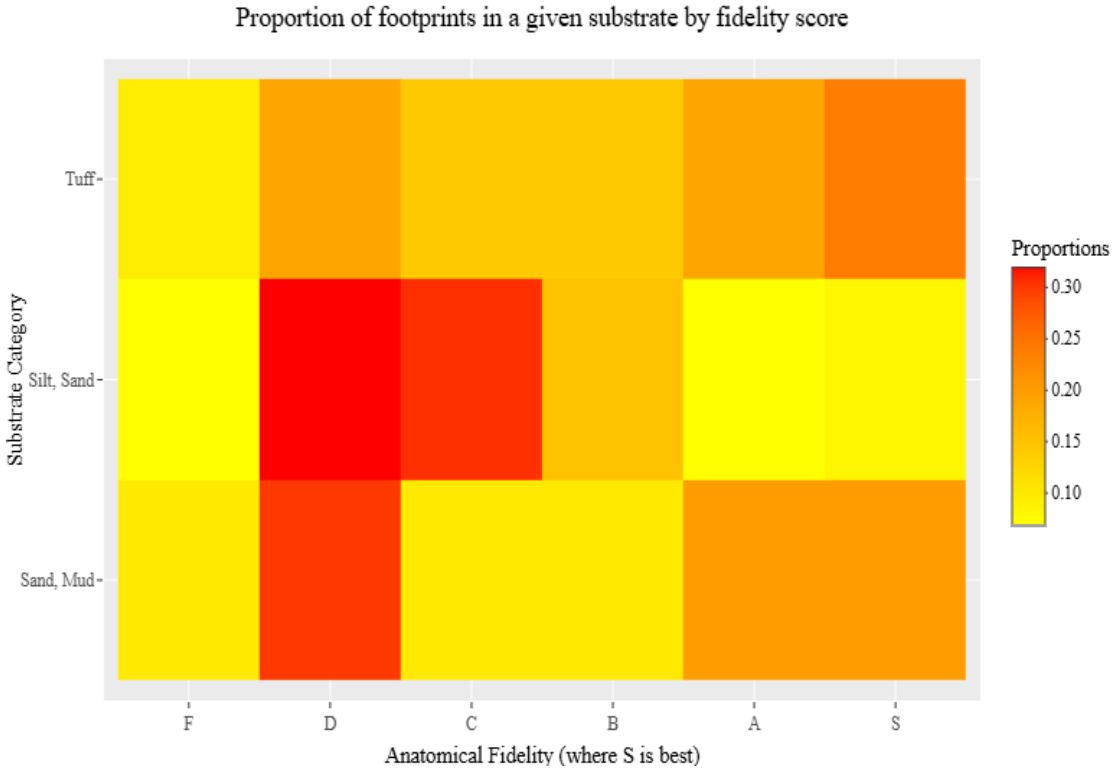
The predictor (independent) variable chosen for both the POLR model and CLM model was substrate, while the outcome (dependent) variable is the given categorical Fidelity (or Farlow *et al.,* 2018) graded track scores. Quantitative footprint dimensions — including length, width, depth — and trackway speed were considered as predictor variables but excluded from both models due to insufficient data coverage across the 19 sites used here. Complete measurements existed for only three sites (Engare Sero, Laetoli, and Le Rozel) and speed data was only available from one site (Engare Sero). This low sample size reflects the scarcity of available high quality digital hominin footprint images available for study. Therefore, the requirement of quantitative measurements would decrease the already small sample size (n=19 sites) of the dataset to only 3 sites with suitable footprint images (n=36 footprints total: n= 4 at Engare Sero; n=4 at Laetoli; and n=28 at Le Rozel,). I chose not to use these quantitative measurements due to how the low sample sizes will misrepresent the reality of the hominin ichnofossils record, regardless of the significance of the site (*e.g.* Laetoli). This is discussed further in Chapter 6.

Additionally, the decision to use the name of the footprint site (*e.g. Laetoli)* as a random effect rather than the unique footprint identifier (*e.g. G1-25*) was chosen to prevent oversampling. Footprints were nested within sites -- which share the same substrate classification – therefore treating each footprint as an independent observation would artificially inflate the sample size and misrepresent the data (Table 4). Site name (*e.g. Laetoli)* was used as the random effect to account for this within-site clustering.

Chapter 5: Results

Raster Plot Results: Proportion of Footprint Fidelity per Substrate Category in the Raster

A raster plot (Figure 22) was created using RStudio (version 4.5.2) to visualize the distribution of the proportional of anatomical fidelity scores based against substrate



category. Substrate categories were based on published descriptions which varied in detail across sources. Broad categories like “Silt, Sand" reflect the heterogeneity of reporting standards in the literature; therefore, the exclusion of substrate types with less than three footprints was necessary to avoid skewed results in the visualization of the raster model.

Figure 22 Proportion of Footprints in a given substrate, organized by fidelity score

The “Silt, Sand” substrate category has a strong concentration at fidelity scores D and C (the dark red blocks), meaning this substrate produces a lot of medium-to-poor quality footprints. The “Tuff” substrate category shows relatively even distribution across most fidelity scores, with slightly higher proportions at the extremes. The “Sand, Mud” substrate category show higher proportions at the lower quality end (“D - Minimum”, “C – Ideal Worst”) and higher end (“A – Ideal”, “S – Beyond Expectations”) with less in the middle. Different substrate types preserve footprints with different quality levels: silt-sand mixtures tend to produce moderate-quality prints, while tuff and sand-mud can produce both very good and very poor impressions depending on conditions (moisture, compaction, etc.). The wide variation seen across the “Tuff” substrate category produces variable preservation quality, making it unpredictable regarding fidelity scores. These results are surprising due to the high number of footprint sites which occur in proximity to and have volcanic-substrate origins despite “Tuff” sites being slightly underrepresented at 25% of sites used here. The largest representation of substrate category is "Silt, Sand" at 55%, and "Sand, Mud" is 20% of sites.

Cumulative Link Mixed (CLM) Model

A **Cumulative Link Mixed (CLM) model** is a type of broad regression analysis where the distances between grade categories (such as "S" is best, and "F" is deemed "Unscorable") cannot be assumed as equals. The model estimates the probability of an observation falling at or below each grade threshold on a continuous scale, with fixed effects shifting the probably as a factor of predictor variables. The variables and their output are described below.

Site names (n=19) were chosen to represent the random (dependent) variable in the CLM model rather than count of individual footprints to account for oversampling and misrepresentation of the data. Substrate type was chosen to represent the fixed (independent) effect in the CLM model due to the abundance of literature supporting how fluid dynamics and adhesion of sediment affects how impressions form and how long they last undisturbed (Bennett *et al.,* 2013; Falkingham *et al.,* 2020; Falkingham & Gatesy, 2020; Marchetti *et al.,* 2019, 2020; Marty *et al.,* 2009, 2018; Scott *et al.,* 2008). The CLM model with a Laplace approximation (which are used to estimate complicated probability distributions) reports substrate type was not a significant predictor of preservation fidelity. Relative to "Silt, Mud" (reference substrate used), neither Silt/Sand ($\beta = 0.46$, $SE = 1.11$, $z = 0.41$, $p = .680$) nor Tuff ($\beta = 1.75$, $SE = 1.29$, $z = 1.36$, $p = .175$) differed significantly in fidelity grade, though Tuff showed a positive trend. Site-level random effects accounted for considerable variance in fidelity scores ($\sigma^2 = 1.76$), indicating that factors beyond substrate type contribute meaningfully to preservation outcomes across sites.

Proportional Odds Logistic Regression (POLR) Model

A **Proportional Odds Logistic Regression (POLR) model** is used to model an ordinal dependent variable, meaning a variable with ordered categories like "poor," "fair," "good," or "excellent". It handles ordered outcomes by assuming that the effect of the predictors (such as geological age of footprint site, denoted substrate, foot length and width measurements, for example) are all consistent across all categories, which simplifies the model and allows for a single odds ratio to be interpreted. The POLR model used to represent fidelity reflects an Akaike Information Criterion (AIC) value of 357.259 (compared to an AIC value of 254.627 for Farlow (2018) scores) while specifying the Hessian parameter as true in order to get standard errors. AICs are mathematical method for estimating how well a model fits the data that it was generated from – much like a linear regression model, while also assuming equality among categories, as mentioned above. In general, a lower AIC value reflects greater parsimony, and the value is penalized (resulting in higher values) when there are multiple parameters present; this indicates that the parameters chosen are not a best fit for the model chosen. Additionally, AIC values are significant only when compared against an equal predictor variable, such as substrate categories. The higher AIC value in the Fidelity POLR model used here is interesting because while both POLR models use substrate as a predictor (independent) variable, Farlow (2018) uses fewer categories (n=4) (broader) categories for footprint fidelity, compared to the six (6) categories used here. Coefficients in both POLR models are negative (Table 5); with the Fidelity POLR model being slightly less so. The values reflected in the Fidelity model report that “Silt, Sand” substrates are negative and non-significant (t = -0.81), a lower fidelity than “Sand, Mud”, while

“Tuff”’s t-values are positive and non-significant (t = 0.51). In contrast, Farlow (2018) scores reflect negative and approaching significance t-values (t = -1.82); this still reflects lower fidelity than “Sand, Mud”. “Tuff” substrates reflect a negative (compared to positive in the former model) and non-significant (t = -0.09) values. POLR models reflect no significant substrate effects.

Predictor / Threshold	Coefficient	Std. Error	t-value
Fidelity Model (S is best; reference category: Sand, Mud)			
Silt, Sand	-0.5252	0.6478	-0.8108
Tuff	0.3754	0.7351	0.5108
Intercepts			
F | D	-2.8284	0.6982	-4.0511
D | C	-0.8822	0.6275	-1.4059
C | B	0.1793	0.6232	0.2878
B | A	0.9124	0.6256	1.4583
A | S	1.6882	0.6462	2.6125
AIC: 357.26 Residual Deviance: 343.26			
Farlow Model (3 is best; reference category: Sand, Mud)			
Silt, Sand	-1.2548	0.6879	-1.8242
Tuff	-0.0682	0.7518	-0.0908
Intercepts			
0 | 1	-2.2315	0.6835	-3.2645
1 | 2	-0.1154	0.6517	-0.1770
2 | 3	0.9749	0.6584	1.4808
AIC: 264.63 Residual Deviance: 254.63			

Table 5. Proportional Odds Logistic Regression (POLR) coefficients for substrate category as a predictor of anatomical fidelity across two rubrics. Sand, Mud serves as the reference category.

An interesting discrepancy here is that Tuff substrates---which are well regarded for preserving large amounts of footprints through rapid burial and having beneficial minerals (such as feldspars and carbonates Liutkus-Pierce *et al.,* 2016) that support fossilization---suggests that the two rubrics (Fidelity and Farlow, 2018) are capturing something different about footprints categorized in Tuff substrates. The Fidelity rubric here rates Tuff favorably compared to Farlow (2018)'s rubric, which may be related to the broader morphological presence scale used within the latter rubric.

Evaluation of Geological Age (Epoch) as a factor of footprint fidelity

In order to explore other variables which may influence the values reflected in Fidelity scores (Figure 23), I explored the relationship between Fidelity scores and geological age (*i.e.* epoch). Geological ages used here, in descending order, Late Plio-Early Pleistocene (5.3 Ma – 2.5 Ma); the Pleistocene (2.5 Ma – 11.7 ka); and the Holocene (12,000 years – Present). Older epochs were expected to have worse fidelity due to diagenetic processes over time, but interestingly here "Plio-Early Pleistocene" category performs well (Figure 23). I believe that this reinforces the argument that substrate makes a difference in footprint quality, or it points towards site-specific preservation conditions. Its highly important to note that while this dataset is dominated by Holocene sites (n= 11, 58% of the 19 total sites), Holocene and the Late Plio-Early Pleistocene sites have the highest proportion of high-fidelity scores ("S" and "A") – which is expected due to the presumption that less damage will occur to geologically younger exposed footprints compared to geologically older footprint sites, which were expected to have worse fidelity due to having experienced more (in terms of quantity, rather than intensity)

erosion and bioturbation activity. Pleistocene hominin footprint sites are dominated by the “C” and “D” categories. In general, Pliocene hominin footprint sites show a spread

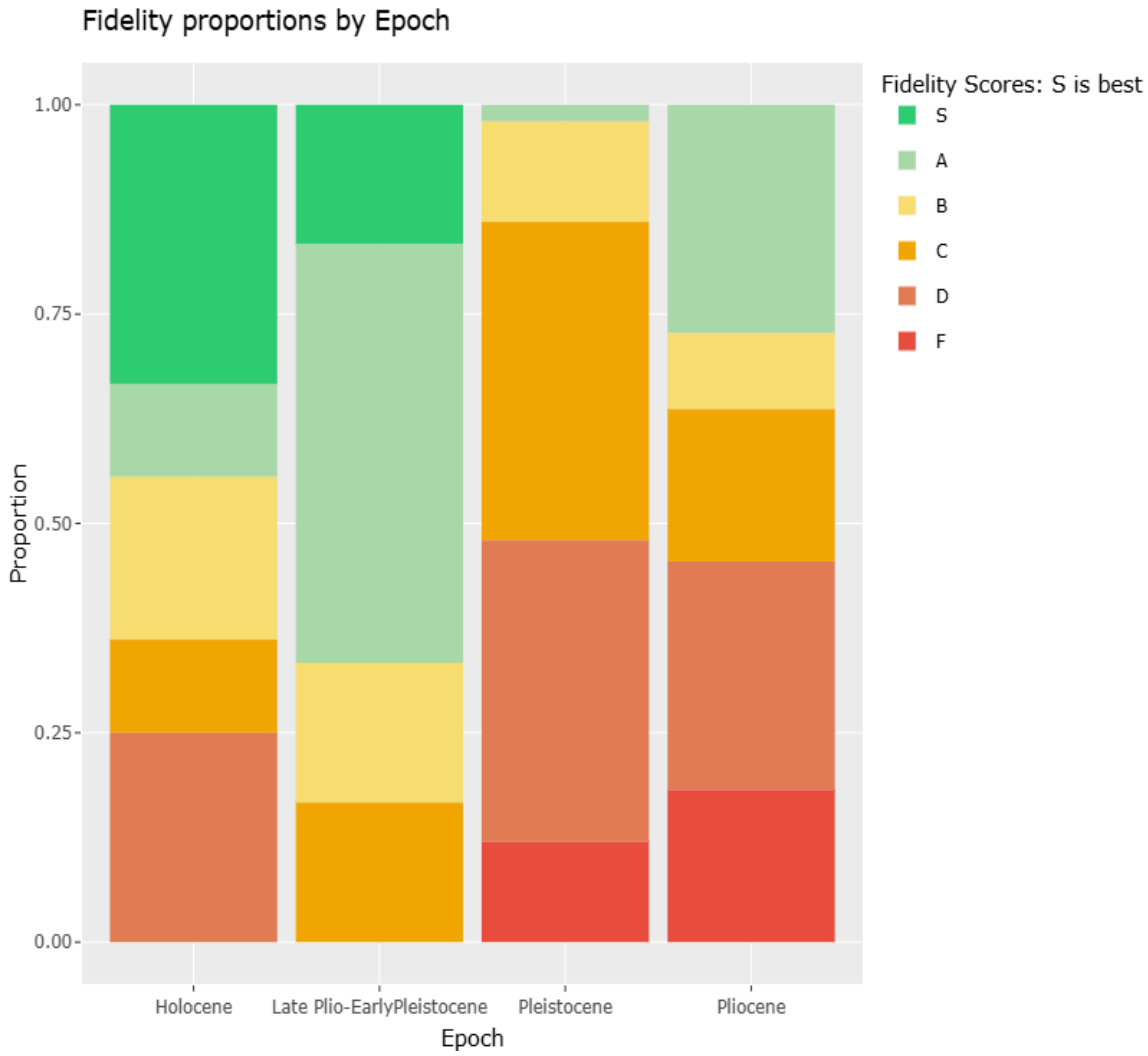


Figure 23. Fidelity score proportions reflected by Epoch, colored by Fidelity Score Type

across all categories but with a significant presence at “D” and “F” scores.

This result reflects that epoch classifications are not contributing significantly to Fidelity scores. The Holocene sites (n= 11 sites) have the largest sample size. The other three epochs have markedly fewer sites in comparison: the Late Plio-Pleistocene (n=1); Early Pleistocene (n=6) and Pliocene (n=1).

Chapter 6: Discussion and Future Directions

The lack of statistical significance in the statistical models reported here reflects the fact that many factors influence footprint registration and subsequent preservation. Thus, it is not possible to predict anatomical fidelity from simple characterizations of sediment type.

Is there a need for a hominin footprint fidelity model?

Footprints are "…neither bones nor feet" (Falkingham & Gatesy, 2017). The study of trace fossils, which includes footprints, explores the interpretation of trackway preservation by attempting to describe the morphological boundaries of what a track should reflect in a trackway. The concept of creating rubrics to define fidelity is not a new concept. Discussions about what *fidelity* meant in the field of ichnology began through early paleontological research (see Thulborn, 1990 for a short review) to describe the locomotive behavior of an organism without the presence of the organism in real time (Falkingham & Gatesy, 2020; Marchetti, Belvedere, *et al.,* 2019; Marchetti *et al.,* 2020; Marchetti *et al.,* 2019, Klein, *et al.,* 2019; Marty *et al.,* 2009). "…[the] ichnological tradition is for preservation quality to denote a specimen's *fidelity to pedal anatomy",* rather than a specimen's *"…accuracy of reproduction."* (Falkingham and Gatesy, 2017, p. 6). Like body fossils, fossilized tracks exhibit post-formational modifications from myriad destructive forces which can prevent taxonomic classifications. Falkingham & Gatesy (2017)'s study attempted to address this concern by utilizing both the presence of morphological characteristics (*i.e.,* deep impressions from hallux and heel strike

compared to digits), and track reproduction to reaffirm that footprint fidelity, aka preservation quality, should be assessed using postmortem modifications as a feature of footprint identification rather than a discriminatory function.

As representations of past behavior, footprints cannot be "alive" in the sense that extant species are alive; they are instead considered to be "dead" because the true trackmaker may not, and sometimes cannot, be known" (Falkingham and Gatesy, 2017). This implies that footprints can experience their own unique form of taphonomy, and therefore most fossil footprints will be imperfect. More importantly, the search for the "perfect" footprint may not be the question we should be asking ourselves as researchers; it is very likely that "perfect footprint(s)" do not exist and that the continued exclusion of "lesser quality" footprints in research will hinder realistic interpretations of human locomotor behavior. Researchers should instead, ideally, determine whether "S" and "A" footprint fidelity-types are the 'bare minimum' for utilization in research, or if "B", "C" and even "D"-level footprints can produce similar results. In this thesis, I follow the recommendations of Gatesy & Falkingham (2017) that the highest-fidelity footprints, "S" and "A" footprints, should be reserved for determining ichnotaxa because determining ichnotaxa is difficult enough without body fossils to supplement the data. Furthermore, the subjectivity of hominin footprint sites as quantitative (rather than purely qualitative) sources of scientific data, especially for 3D geometric analyses, remains an ongoing issue.

A difficult consideration in this model is whether the usage of broad substrate categories are a methodological hindrance or if these categories reflect part of the reality

of depicting fidelity in large clusters of hominin footprint sites. If every substrate is a reflection of the environment, and every environment is slightly different, then creating infinitely unique substrate categories may introduce even further ambiguity and prevent clustering of expected results. Therefore, the choice was made to use broader, simpler, categories to represent the 19 footprint sites used in this thesis. Table 4 depicts an assortment of substrate categories that were used in the research process to describe the relationship between anatomical fidelity and substrate type.

While the sedimentological and geological background was robust in many of the footprint sites (*i.e.* Laetoli, Engare Sero, White Sands National Park), several footprint sites (*i.e.* Severn Estuary, Cuatro Cienegas, Kilauea) reflected fewer qualitative descriptions of the substrate. I believe this is at the discretion of the researcher depending upon the research questions being asked as several of these studies focused upon ichnotaxa identification (*e.g.,* Ileret, White Sands National Park, Roccamonfina), rather than geological background.

For the purpose of choosing sedimentological variables to compare against, I focused on prior paleontological and ichnological work (*e.g.* Bates *et al.,* 2013; Bennett *et al.,* 2013; Falkingham *et al.,* 2014; Gatesy & Falkingham, 2017) which aimed to understand pressure distribution patterns caused by the level of hydration in sediment rather than the environmental and geological background. The results from these studies present the theme that a footprint's anatomical fidelity score may instead be a byproduct of the cohesive ability of the substrate, rather than the amount of plantar pressure or

stature of the original trackmaker (Bennett *et al.,* 2013). This provided additional justification for the qualitative nature of this rubric.

Determining When Physical Preservation of Hominin Trackways Is Warranted in Place of Digital Preservation Methods

The application of 2D digital footprint images for research reflect the challenges of footprint identification in the field. Of the 103 tracks scored in this thesis, only 23.3% (n=24) achieved a high-fidelity rating of S ("Beyond Expectations", Table 2) or A ("Ideal", Table 2), while the remaining 76.6% (n = 79) fell below this threshold. This indicates that many preserved footprints may be unsuitable for detailed shape analyses, despite being used in ichnological studies. Despite this limitation, the lower brackets of anatomical fidelity scores (such as B, "Moderate"; and C, "Ideal Worst") can demonstrate the visual reality of footprint identification (only considering the 'perfect' footprint for usage in research) and provide a potential answer to improving sample sizes of hominin tracks, which may otherwise be documented during field research. However, due to the discretion of each researcher, not every footprint is digitized, or recorded in depth. With respect to extreme erosive situations where coastal erosion can destroy footprints within a matter of weeks, it is also possible that the very few digital captures of footprints discovered (*e.g.* Happisburgh) limited opportunities for track documentation. Similarly, Engare Sero reflects the largest assemblage of over 400 early human footprints but is only represented by five published track images. White Sands in New Mexico, USA, also only accounts for five tracks despite identifying 427 footprints (140 of which were excavated, 90 (64.2%) of that batch were used for research, Bennet *et al.,* 2020).

The lack of published images is not a reflection on the methodology of the researchers but instead highlights the need to collect supplemental 2D (3D when applicable) images and metadata (Bennett *et al.,* 2014; Falkingham & Gatesy, 2017; Hatala *et al.,* 2024) to understand the realistic morphological variation among hominin footprints beyond the "well preserved", or otherwise deemed high-fidelity footprints identified. It is important that the digital accumulation of tracks continue even if analyses do not occur for each one, if not only to increase digital archival collections and future sample sizes in research. Footprints with low anatomical fidelity can still provide valuable insights about site-specific erosion patterns, such as describing footprint sites that may be more vulnerable to human population growth (thus reflecting high rates of damage over time) as well as examples of climbing and running on "…slippery and unstable surfaces" (Bennet *et al., 2020,* Panarello *et al.,* 2020).

The findings here justify prioritizing digital conservation for vulnerable sites, such as Ileret or Laetoli, over others with lower erosion risk and greater long-term stability.

In defense of the use of 2D photographs in this study

Due to the age of discovery and accessibility of most of the footprint sites evaluated in this thesis, the usage of 2D photographs seemed mostly sufficient for this study despite the poor quality of some of the photos (*e.g.* Matalascañas). Low resolution footprint images only made up six photos from a singular site (*e.g.* Matalascañas) of the total 106 footprints (5.66% of the total dataset); or 3.8% of total data collection. It is unlikely that this impacted the study since the analyses chosen statistically treat the

proportion of each fidelity score equally; this prevents the results of the rubrics used here (Farlow (2018)'s and the rubric proposed here) from being skewed negatively by the quality of the images. Additionally, while 3D scans would have brought significant quality for assessing the presence of morphological markers in footprint images due to their ability to reflect depth and the ability of the scans themselves to be manipulated in 3 dimensions, the usage of 3D scans would have further skewed anatomical fidelity results and lowered the sample size of this dataset significantly to 2 sites.

Nonetheless, future work should continue to encourage the collection of, and usage of 3D scans over 2D images when available for discerning anatomical fidelity and suggested in the literature. 3D scans are superior, in most cases, to 2D images due to the multitude of accessible metadata available to them such as texture qualities and geometry which can (and have been) used in physics-based simulations to quantify erosion (Bates *et al.,* 2013; Bennett *et al.,* 2016; Morse *et al.,* 2010; Urban *et al.,* 2018). The absence of 3D scans in earlier footprint studies is largely attributable to technological limitations: early scanning systems were expensive, difficult to transport, and constrained by limited digital storage capacity. Early ichnological studies relied heavily on hand-drawn or digitally outlined footprints, which preserved little to no quantitative information (e.g., depth or volumetric variation). Falkingham *et al.,* (2018) corroborate that an outline of footprints should be considered as "…interpretation, *not* data…" because of the lack of crucial metadata retrievable. Since the 1970s, advances in digital imaging have since made 3D data collection more accessible, with compact, high-resolution scanning devices now widely available, not to mention the currently easily accessible technology *(e.g.* nearly every cellphone and tablet available today). Improvements in digital preservation

methods—including LiDAR, photogrammetry, and quantitative analytical methods like geometric morphometrics have substantially enhanced our ability to quantify erosion (Zimmer *et al.,* 2018), reconstruct paleoenvironmental conditions, and assess morphological variation in both body and trace fossils.

For this study, both JPEG and PNG image formats were acceptable for inclusion in the dataset. PNG files were highly preferred due to their lossless compression and make up 100% of the filetypes used. Lossless compression formats preserve image information during compression and subsequent edits, ensuring that annotations and markups do not degrade image quality. This preservation of detail provides more accurate identification of anatomical features and improves overall analytical reliability.

Bennett et al., (2014) Footprint Typology Rubric

As mentioned, Bennett *et al.,* (2014)'s footprint typology model is a useful and interesting rubric developed to show how footprint typology varies with load-bearing capacity (*i.e.* plantar pressure). Bennett's (2014) Typology Scores (2014) are given based upon the following rubric where Type 1 footprints are more likely to be associated with larger individuals and more detailed full-footed anatomical details, while Type 5 generally represents the smallest individuals, and prints that do not reflect full 'heel-strike-off' footprint patterns (Bennett *et al.,* 2014). Generally, T5's are solely the forefoot and at minimum 1-2 digits for reference. The heel is sometimes not visible or diagnostic. Several morphological themes in Bennett *et al.,* (2014)’s typology model overlap with the Fidelity Rubric used here (Table 2), but it is important to acknowledge that Bennett *et al.,* (2014)’s typology model does not measure anatomical fidelity; it instead measures the

expected variation of a given footprint when accounting for body size, stature, and speed, despite showcasing hominin footprints with high levels of variation of preservation.

While not used in the analyses here, Bennett *et al.,* (2014) is mentioned because it represents one of the only other hominin footprint rubrics depicted in the literature. It ultimately was not used as a comparative model in the analysis because the aims of Bennett *et al.,* (2014) did not meet the criteria of this study. Bennett *et al.,* (2014)'s study analyzed the impact of soft sediment on inferred smaller body size ranges in proposed juvenile fossilized footprints at Namibia. Bennett *et al.,* (2014)'s footprint typology model depicts limited surface impressions on firm substrates associated with areas of peak plantar surface (the midtarsal, distant tarsals, and heel), whereas softer substrates are associated with deeper prints. Substrates of medium bearing capacity give displacement rims that can distort and distract from the true fidelity of a footprint; this in whole obscures the true form of the medial longitudinal arch. Bennett *et al.,* (2014) argues that despite uniform substrate conditions at the Namibia footprint site, trackways still depict massive typological variation due to variation in plantar pressure (body mass, stature, gait); behavioral variation ("playful" movement patterns); and age-related difference (juvenile vs adult gait).

Conclusion

Even though footprint fidelity has long been assumed to depend strongly on substrate, and substrate must in some ways influence fidelity, the data presented here suggests that the relationship is far more complex than previous literature implies. Hominin footprints occupy a behaviorally informative space in the paleoanthropological record as they describe a "snapshot in time" (Hatala *et al.,* 2024). However, hominin footprints and their anatomical fidelity have been underexamined. Substrate type has functioned as an implicit proxy for preservation quality (Falkingham & Gatesy, 2017)– fine-grained tuffs and saturated silts have been treated in the literature as reliable predictors of anatomical fidelity (*e.g*. Liutkus-Pierce, 2002; Marchetti *et al.,* 2019, 2020), while coarser or more chemically complex substrates (Webb *et al.,* 2025) have been regarded with skepticism. Across 106 footprints from 19 sites spanning three continents and over three million years of hominin locomotor history, no statistically significant relationship between substrate category and anatomical fidelity was identified. However, I do not interpret this lack of statistical significance as a failure of the anatomical fidelity rubric, rather, it shows evidence that refining the characteristics which define anatomical fidelity requires a multi-criterion model, such as implementing quantitative measurements, sedimentological values (*e.g.* pH level and chemical properties leading to lithification processes), and a much more robust sample size of footprints in various substrate types to reflect anatomical fidelity more fully.

The implications of this finding extend beyond the concerns for the broad methodology. If anatomical fidelity cannot be reliably inferred from broad substrate categories and the usage of complex substrates would introduce further ambiguity to the

discovery of the relationship between anatomical fidelity and substrate type, then it is possible that the field's existing practice of using substrate as a shorthand for data quality introduces an unexamined source of bias into the hominin footprint record. Chapter 6 discussed the interpretative biases that exist when describing hominin footprints. High-fidelity footprints preserved in unexpected substrates have been undervalued; lower fidelity prints in otherwise favorable substrates may have granted unfair biases in the hominin fossil record. Therefore, the anatomical fidelity rubric developed and applied in this thesis offers a corrective context by insisting that morphological evidence should be evaluated on its own terms without replacing the geological context, before broader inferences are drawn from it. As stated above, the lack of statistical significance in the results reported here reflects the fact that many factors influence footprint registration and subsequent preservation. A footprint can be well-preserved in the geological sense while still failing to reproduce the soft-tissue morphology necessary for confident hominin footprint identification or locomotor inference. The same logic can be applied to geological age, as the results from evaluating epoch did not emerge as a reliable predictor of anatomical fidelity score, despite the expectation that older sites would show greater diagenetic degradation (Liutkus-Pierce *et al.,* 2016; Masao *et al.,* 2016). Instead, the substrate type results in Chapter 5 suggest that site specific preservation conditions, including substrate chemistry, burial history, depositional setting, exposure by erosion, and bioturbation may influence anatomical fidelity more than total elapsed time since the creation of the track.

Thus, it is not possible to predict footprint anatomical fidelity from simple characterizations of sediment type or from geological age. The findings presented here

suggest that much of the hominin footprint record deserves further scrutiny to determine what it truly means for a footprint to be "well-preserved" (Hatala *et al.,* 2024, McNutt *et al.,* 2021). This is not a criticism of the methodology of the researchers. Locomotor reconstructions derived from high-fidelity prints at sites such as Laetoli or Engare Sero may not be representative of the full range of hominin movement preserved in the fossil record if the only footprints being recognized, digitized, and analyzed are the "well-preserved" ones. Prints scoring below the ideal threshold identified in this fidelity rubric (a "D" for "Ideal Worst" fidelity) are still real hominin footprints, and their exclusion from analyses may continue to systematically skew interpretations towards circumstances of optimal preservation, rather than the highly variable, challenging (to classify) substrates across which hominins moved. However, I acknowledge that studies employing 3D geometric morphometric (3D GM) analyses in footprint morphology may continue to face challenges in assembling large sample sizes. The anatomical fidelity rubric proposed here attempts to mitigate this by adopting inclusive criteria: the absence of minor morphological features — such as distal digit impressions or a complete foot outline — does not disqualify a footprint from analysis, provided that more diagnostically significant features, such as the heel depression from heel-strike are identifiable. Nevertheless, if researchers require those minor features to be present, sample size constraints for 3D GM research will persist.

Footprints are one of the only sources of evidence in the paleoanthropological record of hominins behaving – moving, navigating, and interacting with their environments. The varied anatomical fidelity hominin footprint record suggests how researchers should proceed with analyzing hominin footprint sites, especially vulnerable

ones (*e.g.* Laetoli, Happisburgh, Engare Sero). For sites like these, the footprints which received a "D" or "F" score reflect the need for additional measures to conserve and protect them compared to sites which reflect higher anatomical fidelity scores. The hominin footprint record may never be fully representative of the full locomotive repertoire early humans were capable of; therefore, the anatomical fidelity rubric used here can help provide the necessary context for more extensive, variable, and instructive footprint fidelity models.

References

Agnew, N., & Demas, M. (1998). Preserving the Laetoli footprints. *Scientific American, 279*(3), 44–55. https://doi.org/10.1038/scientificamerican0998-44

Alexander, R. McN. (2004). Bipedal animals, and their differences from humans. *Journal of Anatomy, 204*(5), 321–330. https://doi.org/10.1111/j.0021-8782.2004.00289.x

Aldhouse-Green, S. H. R., Whittle, A. W. R., Allen, J. R. L., Caseldine, A. E., Culver, S. J., Day, M. H., Lundquist, J., & Upton, D. (1993). Prehistoric human footprints from the Severn Estuary at Uskmouth and Magor Pill, Gwent, Wales. *Archaeologia Cambrensis, 149*, 14–55.

Allen, J. R. L. (1997). Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S. W. Britain: Mechanics of formation, preservation and distribution. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 352*(1352), 481–518. https://doi.org/10.1098/rstb.1997.0035

Ashley, G. (2003). Tracks, trails and trampling by large vertebrates in a rift valley paleo-wetland, lowermost Bed II, Olduvai Gorge, Tanzania. *Ichnos, 9*(1–2), 23–32. https://doi.org/10.1080/10420940190034058-369

Ashton, N., Lewis, S. G., De Groote, I., Duffy, S. M., Bates, M., Bates, R., Hoare, P., Lewis, M., Parfitt, S. A., Peglar, S., Williams, C., & Stringer, C. (2014). Hominin footprints from early Pleistocene deposits at Happisburgh, UK. *PLoS ONE, 9*(2), e88329. https://doi.org/10.1371/journal.pone.0088329

Balashova, A., Mattsson, H. B., Hirt, A. M., & Almqvist, B. S. G. (2016). The Lake Natron footprint tuff (northern Tanzania): Volcanic source, depositional processes

and age constraints from field relations. *Journal of Quaternary Science, 31*(5), 526–537. https://doi.org/10.1002/jqs.2876

Bates, K. T., Savage, R., Pataky, T. C., Morse, S. A., Webster, E., Falkingham, P. L., Ren, L., Qian, Z., Collins, D., Bennett, M. R., McClymont, J., & Crompton, R. H. (2013). Does footprint depth correlate with foot motion and pressure? *Journal of the Royal Society Interface, 10*(83), 20130009. https://doi.org/10.1098/rsif.2013.0009

Behrensmeyer, K., & Laporte, L. (1981). Footprints of a Pleistocene hominid in northern Kenya. *Nature, 289*, 167–169.

Belvedere, M., & Farlow, J. (2014). A numerical scale for quantifying the quality of preservation of vertebrate tracks. *Ichnos, 22*(3–4), 1–7.

Bennett, M. R., Bustos, D., Odess, D., Urban, T. M., Lallensack, J. N., Budka, M., Santucci, V. L., Martinez, P., Wiseman, A. L. A., & Reynolds, S. C. (2020). Walking in mud: Remarkable Pleistocene human trackways from White Sands National Park (New Mexico). *Quaternary Science Reviews, 249*, 106610. https://doi.org/10.1016/j.quascirev.2020.106610

Bennett, M. R., Falkingham, P., Morse, S. A., Bates, K., & Crompton, R. H. (2013). Preserving the impossible: Conservation of soft-sediment hominin footprint sites and strategies for three-dimensional digital data capture. *PLoS ONE, 8*(4), e60755. https://doi.org/10.1371/journal.pone.0060755

Bennett, M. R., Harris, J. W. K., Richmond, B. G., Braun, D. R., Mbua, E., Kiura, P., Olago, D., Kibunjia, M., Omuombo, C., Behrensmeyer, A. K., Huddart, D., & Gonzalez, S. (2009). Early hominin foot morphology based on 1.5-million-year-

old footprints from Ileret, Kenya. *Science, 323*(5918), 1197–1201. https://doi.org/10.1126/science.1168132

Bennett, M. R., Reynolds, S. C., Morse, S. A., & Budka, M. (2016). Footprints and human evolution: Homeostasis in foot function? *Palaeogeography, Palaeoclimatology, Palaeoecology, 461*, 214–223. https://doi.org/10.1016/j.palaeo.2016.08.026

Bennett, M. R., Urban, T. M., Bustos, D. F., Reynolds, S. C., Jolie, E. A., Strehlau, H. C., Odess, D., Springer, K. B., & Pigati, J. S. (2025). The ichnology of White Sands (New Mexico): Linear traces and human footprints, evidence of transport technology? *Quaternary Science Advances, 17*, 100274. https://doi.org/10.1016/j.qsa.2025.100274

Bennett, M. R. (with Morse, S. A.). (2014). *Human footprints* (1st ed.). Springer International Publishing.

Bennett, M. R., & Budka, M. (2019). *Digital technology for forensic footwear analysis and vertebrate ichnology*. Springer International Publishing. https://doi.org/10.1007/978-3-319-93689-5

Bromley, R. G. (1996). *Trace fossils*. Springer US. https://doi.org/10.1007/978-1-4899-2875-7

Bustos, D., Jakeway, J., Urban, T. M., Holliday, V. T., Fenerty, B., Raichlen, D. A., Budka, M., Reynolds, S. C., Allen, B. D., Love, D. W., Santucci, V. L., Odess, D., Willey, P., McDonald, H. G., & Bennett, M. R. (2018). Footprints preserve terminal Pleistocene hunt? Human-sloth interactions in North America. *Science Advances, 4*(4), eaar7621. https://doi.org/10.1126/sciadv.aar7621

Chauhan HM, Taqi M. Anatomy, Bony Pelvis and Lower Limb: Arches of the Foot. [Updated 2025 Aug 27]. In: StatPearls [Internet]. Treasure Island (FL): StatPearls Publishing; 2026 Jan-. Available from: https://www.ncbi.nlm.nih.gov/books/NBK587361/

DeSilva, J. M. (2009). Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proceedings of the National Academy of Sciences, 106*(16), 6567–6572. https://doi.org/10.1073/pnas.0900270106

DeSilva, J. M. (2010). Revisiting the "midtarsal break." *American Journal of Physical Anthropology, 141*(2), 245–258. https://doi.org/10.1002/ajpa.21140

DeSilva, J. M. (2022). *First steps: How upright walking made us human* (1st paperback ed.). Harper.

Neto De Carvalho, C., Helm, C., Goldstein, D., Camens, A. B., Belaústegui, Z., Baucon, A., & Muñiz, F. (2025a). Walk the world and beyond: Hominin footprints. In *Vertebrate ichnology* (pp. 105–206). Elsevier. https://doi.org/10.1016/B978-0-443-38351-9.00007-4

De Carvalho, C. N., Cunha, P. P., Belo, J., Muñiz, F., Baucon, A., Cachão, M., Figueiredo, S., Buylaert, J.-P., Galán, J. M., Belaústegui, Z., Cáceres, L. M., Zhang, Y., Ferreira, C., Rodríguez-Vidal, J., Finlayson, S., Finlayson, G., & Finlayson, C. (2025b). Neanderthal coasteering and the first Portuguese hominin tracksites. *Scientific Reports, 15*(1). https://doi.org/10.1038/s41598-025-06089-4

Duveau, J., Berillon, G., Verna, C., Laisné, G., & Cliquet, D. (2019). The composition of a Neandertal social group revealed by the hominin footprints at Le Rozel

(Normandy, France). *Proceedings of the National Academy of Sciences, 116*(39), 19409–19414. https://doi.org/10.1073/pnas.1901789116

Falkingham, P. L., Bates, K. T., Avanzini, M., Bennett, M., Bordy, E. M., Breithaupt, B. H., Castanera, D., Citton, P., Díaz-Martínez, I., Farlow, J. O., Fiorillo, A. R., Gatesy, S. M., Getty, P., Hatala, K. G., Hornung, J. J., Hyatt, J. A., Klein, H., Lallensack, J. N., Martin, A. J., … Belvedere, M. (2018). A standard protocol for documenting modern and fossil ichnological data. *Palaeontology, 61*(4), 469–480. https://doi.org/10.1111/pala.12373

Falkingham, P. L., & Gatesy, S. M. (2020). Discussion: Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present by Lorenzo Marchetti et al. *Earth-Science Reviews, 208*, 103320. https://doi.org/10.1016/j.earscirev.2020.103320

Falkingham, P. L., Hage, J., & Bäker, M. (2014). Mitigating the Goldilocks effect: The effects of different substrate models on track formation potential. *Royal Society Open Science, 1*(3), 140225. https://doi.org/10.1098/rsos.140225

Falkingham, P. L., Turner, M. L., & Gatesy, S. M. (2020). Constructing and testing hypotheses of dinosaur foot motions from fossil tracks using digitization and simulation. *Palaeontology, 63*(6), 865–880. https://doi.org/10.1111/pala.12502

Fan, B., Li, Y., Wang, F., Yang, J., Zhang, Z., Xu, Q., Hao, Q., Ge, Y., Li, B., Xu, D., Xie, F., Deng, C., & Lu, H. (2025). Relatively open vegetation landscapes promoted early Pleistocene hominin evolution. *Communications Earth & Environment, 6*(1), 1014. https://doi.org/10.1038/s43247-025-02983-x

Farlow, J. O. (2018). *Noah's ravens: Interpreting the makers of tridactyl dinosaur footprints*. Indiana University Press.

Feibel, C. S., Agnew, N., Latimer, B., Demas, M., Marshall, F., Waane, S. A. C., & Schmid, P. (1995). The Laetoli hominid footprints—A preliminary report on the conservation and scientific restudy. *Evolutionary Anthropology: Issues, News, and Reviews, 4*(5), 149–154. https://doi.org/10.1002/evan.1360040502

Flint, E., (1884). *HUMAN_FOOT_PRINTS_IN_NICARAGUA*. The American Antiquarian and Oriental Journal. https://www.proquest.com/docview/89638416?fromopenview=true&pq-origsite=gscholar&sourcetype=Scholarly%20Journals

Gierliński, G. D., Niedźwiedzki, G., Lockley, M. G., Athanassiou, A., Fassoulas, C., Dubicka, Z., Boczarowski, A., Bennett, M. R., & Ahlberg, P. E. (2017). Possible hominin footprints from the late Miocene (c. 5.7 Ma) of Crete? *Proceedings of the Geologists' Association, 128*(5–6), 697–710. https://doi.org/10.1016/j.pgeola.2017.07.006

Harrison, T., Rein, T. R., & Kwekason, A. (2025). New fossil hominins from the upper Laetolil Beds, Laetoli, Tanzania. *Journal of Human Evolution, 206*, 103733. https://doi.org/10.1016/j.jhevol.2025.103733

Hatala, K. G., Demes, B., & Richmond, B. G. (2016). Laetoli footprints reveal bipedal gait biomechanics different from those of modern humans and chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 283*(1836), 20160235. https://doi.org/10.1098/rspb.2016.0235

Hatala, K. G., Gatesy, S. M., & Falkingham, P. L. (2021). Integration of biplanar X-ray, three-dimensional animation and particle simulation reveals details of human 'track ontogeny.' *Interface Focus, 11*(5), 20200075. https://doi.org/10.1098/rsfs.2020.0075

Hatala, K. G., Harcourt-Smith, W. E. H., Gordon, A. D., Zimmer, B. W., Richmond, B. G., Pobiner, B. L., Green, D. J., Metallo, A., Rossi, V., & Liutkus-Pierce, C. M. (2020). Snapshots of human anatomy, locomotion, and behavior from Late Pleistocene footprints at Engare Sero, Tanzania. *Scientific Reports, 10*(1), 7740. https://doi.org/10.1038/s41598-020-64095-0

Hatala, K. G., Roach, N. T., & Behrensmeyer, A. K. (2023). Fossil footprints and what they mean for hominin paleobiology. *Evolutionary Anthropology: Issues, News, and Reviews, 32*(1), 39–53. https://doi.org/10.1002/evan.21963

Hatala, K. G., Roach, N. T., Behrensmeyer, A. K., Falkingham, P. L., Gatesy, S. M., Williams-Hatala, E. M., Feibel, C. S., Dalacha, I., Kirinya, M., Linga, E., Loki, R., Alkoro, A., Longaye, M., Lonyericho, E., Loyapan, I., Nakudo, N., Nyete, C., & Leakey, L. N. (2024). Footprint evidence for locomotor diversity and shared habitats among early Pleistocene hominins. *Science, 386*(6725), 1004–1010. https://doi.org/10.1126/science.ado5275

Hay, R. L., & Leakey, M. D. (1982). The fossil footprints of Laetoli. *Scientific American, 246*(2), 50–57.

Helm, C. W., Carr, A. S., Cawthra, H. C., De Vynck, J. C., Dixon, M. G., Hattingh, S., Rust, R., Stear, W., Thesen, G. H. H., Van Berkel, F., & Zipfel, B. (2024). A

cluster of Pleistocene hominin ichnosites on South Africa's Cape south coast. *Ichnos*, 1–24. https://doi.org/10.1080/10420940.2024.2415141

Helm, C. W., Carr, A. S., Lockley, M. G., Cawthra, H. C., De Vynck, J. C., Dixon, M. G., Stear, W., & Thesen, G. H. H. (2023). Dating the Pleistocene hominin ichnosites on South Africa's Cape south coast. *Ichnos, 30*(1), 49–68. https://doi.org/10.1080/10420940.2023.2204231

Helm, C. W., Lockley, M. G., Cawthra, H. C., De Vynck, J. C., Dixon, M. G., Helm, C. J. Z., & Thesen, G. H. H. (2020). Newly identified hominin trackways from the Cape south coast of South Africa. *South African Journal of Science, 116*(9/10). https://doi.org/10.17159/sajs.2020/8156

Ichumbaki, E. B., Cherin, M., Masao, F. T., & Moggi-Cecchi, J. (2019). Local people's interpretations of the hominin footprints at Laetoli, Tanzania. *Journal of Community Archaeology & Heritage, 6*(2), 122–138. https://doi.org/10.1080/20518196.2019.1594035

Jones, F. W. (1916). *Arboreal man* (1st ed.). Edward Arnold.

Kenhub, GmbH. K. (with Pascoe, M.). (2023). *Kenhub atlas of human anatomy* (1st ed.). Kenhub.

Ker, R. F., Bennett, M. B., Bibby, S. R., Kester, R. C., & Alexander, R. McN. (1987). The spring in the arch of the human foot. *Nature, 325*(6100), 147–149. https://doi.org/10.1038/325147a0

Kim, J. Y., Kim, K. S., Lockley, M. G., & Matthews, N. (2008). Hominid ichnotaxonomy: An exploration of a neglected discipline. *Ichnos, 15*(3–4), 126–139. https://doi.org/10.1080/10420940802467868

Kirscher, U., El Atfy, H., Gärtner, A., Dallanave, E., Munz, P., Niedźwiedzki, G., Athanassiou, A., Fassoulas, C., Linnemann, U., Hofmann, M., Bennett, M., Ahlberg, P. E., & Böhme, M. (2021). Age constraints for the Trachilos footprints from Crete. *Scientific Reports, 11*(1), 19427. https://doi.org/10.1038/s41598-021-98618-0

Leakey, M. D., & Hay, R. L. (1979). Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania. *Nature, 278*, 317–323. https://doi.org/10.1038/278317a0

Liutkus-Pierce, C. M., Zimmer, B. W., Carmichael, S. K., McIntosh, W., Deino, A., Hewitt, S. M., McGinnis, K. J., Hartney, T., Brett, J., Mana, S., Deocampo, D., Richmond, B. G., Hatala, K., Harcourt-Smith, W., Pobiner, B., Metallo, A., & Rossi, V. (2016). Radioisotopic age, formation, and preservation of Late Pleistocene human footprints at Engare Sero, Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology, 463*, 68–82. https://doi.org/10.1016/j.palaeo.2016.09.019

Lockley, M. G., & Pemberton, S. G. (1992). Dinosaur tracks, a book review. *Ichnos, 2*(1), 79–90. https://doi.org/10.1080/10420949209380078

Lockley, M., Roberts, G., & Kim, J. Y. (2008). In the footprints of our ancestors: An overview of the hominid track record. *Ichnos, 15*(3–4), 106–125. https://doi.org/10.1080/10420940802467835

Mansfield, F. A. M., & Vaneechoutte, M. (2024). Current evidence indicates a Eurasian origin for the last common ancestor of African apes and humans, and supports a new hypothesis suggesting that the Zanclean Megaflood (5.3 Ma) may have

played a role in the ultimate divergence of *Pan* and *Homo*. *Ideas in Ecology and Evolution, 17*. https://doi.org/10.24908/iee.2024.17.1.n

Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, S., & Melchor, R. N. (2020). Reply to discussion of "Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present" by Marchetti et al. (2019). *Earth-Science Reviews, 208*, 103319. https://doi.org/10.1016/j.earscirev.2020.103319

Marty, D., Belvedere, M., Razzolini, N. L., Lockley, M. G., Paratte, G., Cattin, M., Lovis, C., & Meyer, C. A. (2018). The tracks of giant theropods (*Jurabrontes curtedulensis* ichnogen. & ichnosp. nov.) from the Late Jurassic of NW Switzerland: Palaeoecological & palaeogeographical implications. *Historical Biology, 30*(7), 928–956. https://doi.org/10.1080/08912963.2017.1324438

Marty, D., Strasser, A., & Meyer, C. A. (2009). Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: Implications for the study of fossil footprints. *Ichnos, 16*(1–2), 127–142. https://doi.org/10.1080/10420940802471027

Masao, F. T., Ichumbaki, E. B., Cherin, M., Barili, A., Boschian, G., Iurino, D. A., Menconero, S., Moggi-Cecchi, J., & Manzi, G. (2016). New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins. *eLife, 5*, e19568. https://doi.org/10.7554/eLife.19568

Mayoral, E., Duveau, J., Santos, A., Ramírez, A. R., Morales, J. A., Díaz-Delgado, R., Rivera-Silva, J., Gómez-Olivencia, A., & Díaz-Martínez, I. (2022). New dating of

the Matalascañas footprints provides new evidence of the Middle Pleistocene (MIS 9-8) hominin paleoecology in southern Europe. *Scientific Reports, 12*(1), 17505. https://doi.org/10.1038/s41598-022-22524-2

McLarty, J. A., McKenzie, Z., Hayes, W. K., Clawson, R., Baltazar, H. D., Alves, E. F., Nick, K. E., & Esperante, R. (2025). Let that sink in: Track depth as a driving factor in the formation of dinosaur tail traces. *Historical Biology*, 1–11. https://doi.org/10.1080/08912963.2025.2481520

McNutt, E. J., Hatala, K. G., Miller, C., Adams, J., Casana, J., Deane, A. S., Dominy, N. J., Fabian, K., Fannin, L. D., Gaughan, S., Gill, S. V., Gurtu, J., Gustafson, E., Hill, A. C., Johnson, C., Kallindo, S., Kilham, B., Kilham, P., Kim, E., … DeSilva, J. M. (2021). Footprint evidence of early hominin locomotor diversity at Laetoli, Tanzania. *Nature, 600*(7889), 468–471. https://doi.org/10.1038/s41586-021-04187-7

From Biped to Strider: The Emergence of Modern Human Walking, Running, and Resource Transport, edited by D. Jeffrey Meldrum and Charles E. Hilton. Kluwer Academic Plenum Publishers, New York, 2004

Meldrum, J., & Sarmiento, E. (2018). Comments on possible Miocene hominin footprints. *Proceedings of the Geologists' Association, 129*(4), 577–580. https://doi.org/10.1016/j.pgeola.2018.05.006

Moniz Nakamura, J. J. (2009). Hominid footprints in recent volcanic ash: New interpretations from Hawaii Volcanoes National Park. *Ichnos, 16*(1–2), 118–123. https://doi.org/10.1080/10420940802471001

Morse, S. A., Bennett, M. R., Gonzalez, S., & Huddart, D. (2010). Techniques for verifying human footprints: Reappraisal of pre-Clovis footprints in Central Mexico. *Quaternary Science Reviews, 29*(19–20), 2571–2578. https://doi.org/10.1016/j.quascirev.2010.03.012

Morse, S. A., Bennett, M. R., Liutkus-Pierce, C., Thackeray, F., McClymont, J., Savage, R., & Crompton, R. H. (2013). Holocene footprints in Namibia: The influence of substrate on footprint variability. *American Journal of Physical Anthropology, 151*(2), 265–279. https://doi.org/10.1002/ajpa.22276

Mountain, E. (1966). Footprints in calcareous sandstone at Nahoon Point. *The South African Journal of Science, 62*, 103–104.

Nakamura, J. M. (2003). *Keonehelelei: Archaeological inventory survey of the Footprints National Register Site, Ahupua'a of Kapapala, Hawai'i Volcanoes National Park* (p. 249).

Onac, B., Viehmann, I., Lundberg, J., Lauritzen, S., Stringer, C., & Popita, V. (2005). U-Th ages constraining the Neanderthal footprint at Vartop Cave, Romania. *Quaternary Science Reviews, 24*(10–11), 1151–1157. https://doi.org/10.1016/j.quascirev.2004.12.001

Panarello, A., Palombo, M. R., Biddittu, I., Di Vito, M. A., Farinaro, G., & Mietto, P. (2020). On the devil's tracks: Unexpected news from the Foresta ichnosite (Roccamonfina volcano, central Italy). *Journal of Quaternary Science, 35*(3), 444–456. https://doi.org/10.1002/jqs.3186

Panarello, A., Santello, L., Farinaro, G., Bennett, M. R., & Mietto, P. (2017). Walking along the oldest human fossil pathway (Roccamonfina volcano, central Italy).

Journal of Archaeological Science: Reports, 13, 476–490. https://doi.org/10.1016/j.jasrep.2017.04.020

Pastoors, A., & Lenssen-Erz, T. (Eds.). (2021). *Reading prehistoric human tracks: Methods & material*. Springer International Publishing. https://doi.org/10.1007/978-3-030-60406-6

Patane, A. (2024). *Bipedalism is a balancing act: Talus landmarking in facultatively bipedal primates* [Unpublished honors thesis]. University of Northern Colorado. https://digscholarship.unco.edu/honors/99/

Prang, T. C. (2019). The origin and evolution of human bipedalism as revealed by foot morphology. *Evolutionary Biology, 46*(4), 1–20.

Prothero, D. R., & Schwab, F. L. (2014). *Sedimentary geology: An introduction to sedimentary rocks and stratigraphy* (3rd ed.). Freeman.

Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E. H., Foster, A. D., & Haas, Wm. R. (2010). Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics. *PLoS ONE, 5*(3), e9769. https://doi.org/10.1371/journal.pone.0009769

Schmincke, H.-U., Rausch, J., Kutterolf, S., & Freundt, A. (2010). Walking through volcanic mud: The 2,100 year-old Acahualinca footprints (Nicaragua) II: The Acahualinca people, environmental conditions and motivation. *International Journal of Earth Sciences, 99*(S1), 279–292. https://doi.org/10.1007/s00531-009-0438-0

Scott, J. J., Renaut, R. W., & Owen, R. B. (2008). Preservation and paleoenvironmental significance of a footprinted surface on the Sandai Plain, Lake Bogoria, Kenya

Rift Valley. *Ichnos, 15*(3–4), 208–231. https://doi.org/10.1080/10420940802470573

Sekhavati, Y., Prang, T. C., & Strait, D. (2025). A phylogenetic perspective on the evolution of early hominin foot morphology. *Journal of Human Evolution, 203*, 103682. https://doi.org/10.1016/j.jhevol.2025.103682

Thompson, N. E., Rubinstein, D., Parrella-O'Donnell, W., Brett, M. A., Demes, B., Larson, S. G., & O'Neill, M. C. (2021). The loss of the 'pelvic step' in human evolution. *Journal of Experimental Biology, 224*(16), jeb240440. https://doi.org/10.1242/jeb.240440

Thulborn, T. (1990). *Dinosaur tracks* (1st ed.). Chapman and Hall.

Urban, T. M., Bustos, D., Jakeway, J., Manning, S. W., & Bennett, M. R. (2018). Use of magnetometry for detecting and documenting multi-species Pleistocene megafauna tracks at White Sands National Monument, New Mexico, U.S.A. *Quaternary Science Reviews, 199*, 206–213. https://doi.org/10.1016/j.quascirev.2018.07.012

Webb, D., Zacharias, L., & Tripp, K. (2025). Human trackway parameters on hard and soft substrates. *American Journal of Biological Anthropology, 188*(4), e70179. https://doi.org/10.1002/ajpa.70179

White, T. D., & Folkens, P. A. (2005). *The human bone manual*. Elsevier Academic Press.

Wiseman, A. L. A., & De Groote, I. (2018). A three-dimensional geometric morphometric study of the effects of erosion on the morphologies of modern and

prehistoric footprints. *Journal of Archaeological Science: Reports, 17*, 93–102. https://doi.org/10.1016/j.jasrep.2017.10.044

Wiseman, A. L. A., Stringer, C. B., Ashton, N., Bennett, M. R., Hatala, K. G., Duffy, S., O'Brien, T., & De Groote, I. (2020). The morphological affinity of the early Pleistocene footprints from Happisburgh, England, with other footprints of Pliocene, Pleistocene, and Holocene age. *Journal of Human Evolution, 144*, 102776. https://doi.org/10.1016/j.jhevol.2020.102776

Wood, B. (2025). *Personal communication*. Science and Engineering Hall, Washington, D.C.

Wood, B., & Harrison, T. (2011). The evolutionary context of the first hominins. *Nature, 470*(7334), 347–352. https://doi.org/10.1038/nature09709

Wrangham, R., & Pilbeam, D. (2002). African apes as time machines. In B. M. F. Galdikas, N. E. Briggs, L. K. Sheeran, G. L. Shapiro, & J. Goodall (Eds.), *All apes great and small* (pp. 5–17). Kluwer Academic Publishers. https://doi.org/10.1007/0-306-47461-1_2

Zachariasse, W. J., & Lourens, L. J. (2022). About the age and depositional depth of the sediments with reported bipedal footprints at Trachilos (NW Crete, Greece). *Scientific Reports, 12*(1), 18471. https://doi.org/10.1038/s41598-022-23296-5

Zachariasse, W. J., & van Hinsbergen, D. J. J. (2025). Is there a Cretan supradetachment basin? Insights from detailed mapping on northwestern Crete (Greece). *Τεκτονικα, 3*(2), 81–107. https://doi.org/10.55575/tektonika2025.3.2.97

Zimmer, B., Liutkus-Pierce, C., Marshall, S. T., Hatala, K. G., Metallo, A., & Rossi, V. (2018). Using differential structure-from-motion photogrammetry to quantify

erosion at the Engare Sero footprint site, Tanzania. *Quaternary Science Reviews, 198*, 226–241. https://doi.org/10.1016/j.quascirev.2018.07.006